

Chapter 15

Phylogeny and Taxonomy of the Traversodontidae

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Abstract We review the taxonomic history of traversodontid cynodont genera and species and the previous classifications and phylogenetic analyses of the group. 17 genera and 22 species are accepted as valid taxa within Traversodontidae. The phylogenetic relationships of traversodontids and other gomphodonts (including 6 trirachodontid species and *Diademodon tetragonus*) are analyzed based on 77 characters. *Scalenodon angustifrons* and (*Andescynodon*+*Pascualgnathus*) are found to be the most basal traversodontids. The three species of *Scalenodon* included in the analysis (*Scalenodon angustifrons*, *S. attridgei*, and *S. hirschsoni*) do not form a clade, supporting recognition of a separate genus for the latter two. A monophyletic Gomphodontosuchinae is recovered, as suggested by previous analyses. The distribution of traversodontids is discussed, with Gondwana and especially Africa suggested as the ancestral area for Gomphodontia and Traversodontidae.

Keywords Cynodontia • Gomphodontia • Gondwana • Laurasia • Triassic

Introduction

The Family Traversodontidae was established by von Huene (1936) to include Brazilian Triassic cynodonts with labiolingually expanded postcanines (von Huene 1928,

1936). Representatives of this group were recognized in the Triassic of Argentina shortly thereafter; these taxa were represented by partial skulls, some of them erroneously allied with *Belesodon magnificus*, a Brazilian taxon with sectorial dentition (Cabrera 1943). Crompton (1955) recognized the first representative of this group in Africa, *Scalenodon angustifrons* from the Manda beds of Tanzania. He also recognized the presence of additional traversodontids in this fauna with postcanines resembling those of the Brazilian taxon *Gomphodontosuchus brasiliensis* (Crompton 1955, p. 659). Another African traversodontid, *Scalenodontoides macrodentes*, was described based on a large partial lower jaw including dentition found in Lesotho (Crompton and Ellenberger 1957).

Several important new traversodontid discoveries occurred during the 1960s, most of them in Argentina. Bonaparte (1962, 1963a, 1966a) provided extensive descriptions of the skull, postcranium, and endocranial cavities of *Exaeretodon frenguelli*, based on rich, new material found in successive expeditions to the Upper Triassic Ischigualasto Formation. Bonaparte (1963b, c) also proposed two new traversodontid taxa, *Proexaeretodon vincei* and *Ischignathus sudamericanus*, found in the same deposits as *E. frenguelli*. Several new traversodontid taxa were discovered in earlier rocks in western Argentina: *Massetognathus* (represented by three species, *M. pascuali*, *M. teruggii*, and *M. major*) and the closely related *Megagomphodon oligodens* from the Middle Triassic Chañares Formation (Romer 1967, 1972); *Andescynodon mendozensis* and *Rusconiiodon mignonei* from the Cerro de las Cabras Formation (Bonaparte 1969, 1970); and *Pascualgnathus polanskii* from the Rio Seco de la Quebrada Formation, originally considered a trirachodontid but later reinterpreted as a basal traversodontid (Bonaparte 1966b, 1970; see also Martinelli 2010a). During this period, new discoveries also occurred in Africa, with the description of *Luangwa drysdalli* from the upper Ntawere Formation of Zambia (Brink 1963).

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Crompton (1972, see also Hopson 2013) described three new species from the Manda beds of Tanzania (*Scalenodon attridgei*, *S. charigi*, and *S. hirschsoni*) and also developed a detailed study of postcanine occlusion in traversodontid cynodonts, based mainly on evidence from *Scalenodon* species. Barberena (1974, 1981a, b) produced an extensive review of South American traversodontid cynodonts, including the description of additional material of the poorly known *Traversodon stahleckeri* and the new species *Massetognathus ochagaviae* (see also Teixeira 1987; Liu et al. 2008) from southern Brazil. Chatterjee (1982) described the first Indian traversodontid, the Late Triassic *Exaeretodon statisticae*. Hopson (1984) redescribed the holotype of *Scalenodontoides macrodentes*, adding new information about the snout of this taxon. Hopson (1985) provided a redescription of the type and only specimen of *Gomphodontosuchus brasiliensis* from the Middle Triassic of Brazil and proposed a close relationship with the Late Triassic traversodontids *Exaeretodon* and *Scalenodontoides*.

Goñi (1986; see also Goñi and Goin 1988) presented a detailed description of the dentition and an analysis of dental replacement in the Argentinean traversodontid *Andescynodon mendozensis* and subsequently postulated a hypothesis about the origin of gomphodont morphology in the postcanines of this taxon (Goñi and Goin 1987). Goñi and Abdala (1989) restudied the Argentinean traversodontid *Rusconiiodon mignonei*, including the holotype and additional unpublished material. Goñi and Goin (1990) described unpublished postcanine material of *Exaeretodon frenguelli*, mainly to produce a biomechanical analysis of mastication in this taxon.

Two new traversodontids, *Menadon besairiei* and *Dadadon isaloi*, were recovered from the 'Isalo II' beds of southwestern Madagascar (Flynn et al. 1999, 2000; Kammerer et al. 2008). Recently, new species of Brazilian traversodontids have been described, including *Exaeretodon riograndensis* (Abdala et al. 2002; Oliveira 2006; Oliveira et al. 2007), *Santacruzodon hopsoni* (Abdala and Ribeiro 2003), and *Luangwa sudamericana* (Abdala and Teixeira 2004). The latter taxon represents the first commonality of a traversodontid genus between South America and Africa. The latest addition to the Brazilian traversodontid record is *Protuberum cabralense* (Reichel et al. 2009), represented by a fairly complete skeleton exhibiting bizarre rib morphology with a series of protuberances along their shafts.

Traversodontid records from Laurasia are much rarer than on the southern continents. The first record of traversodontids from the northern hemisphere was reported by Tatarinov (1973, 1988): *Antecosuchus ochevi*, represented by a partial maxilla and postcanines, and *Scalenodon boreus*, represented by isolated teeth, both from the Middle Triassic of Russia.

Hopson (1984) described the first traversodontid from North America: *?Scalenodontoides plemmyridon*, represented by a couple of mandibles without postcanines, an isolated large canine and postcanine. Important additions to the North American traversodontid record occurred during the 1990s, with the discovery of the small traversodontid *Boreogomphodon jeffersoni* from the Upper Triassic of Virginia and North Carolina (Sues and Olsen 1990; Sues et al. 1994; Liu and Sues 2010; Sues and Hopson 2010). In addition, a new upper postcanine tooth of *?Scalenodontoides plemmyridon* was described by Sues et al. (1992), who reassessed the taxonomic identity of this species, placing it in the new genus *Arctotraversodon*. Sues et al. (1999) described another small traversodontid cynodont, *Plinthogomphodon herpetairus*, represented by a fragment of the snout with dentition and postcranial bones from the Upper Triassic of North Carolina.

Hahn et al. (1988) reported the first record of traversodontids in western Europe (see also Sigogneau-Russell and Hahn 1994): two isolated postcanines of *Microscalenodon nanus* from southern Belgium. Although subsequent discoveries have increased the number of nominal traversodontid species from Europe, the more recent finds are also limited to dental records. Godefroit and Battail (1997) described several new cynodonts represented by isolated teeth from the Upper Triassic of Saint-Nicolas-de-Port, France. They reported two new species of traversodontids, *Maubeugia lotharingica* and *Rosieria delsatei*, and also described unnamed traversodontid taxa as genus aff. *Rosieria*, genus aff. *Microscalenodon*, and gen. et sp. indet., each of them represented by one isolated postcanine. Godefroit (1999) described an isolated tooth interpreted as a traversodontid upper postcanine of the new species *Habayia halbardieri* from Upper Triassic levels of southern Belgium. More recently, Hopson and Sues (2006) described an isolated lower postcanine of the new species *Nanogomphodon wildi* from the Middle Triassic of Germany.

Recent revisions of traversodontids have proposed synonymy of several of the nominal species. Abdala and Giannini (2000) studied all the traversodontid material from the Argentinean Chañares Formation (originally assigned to three species of *Massetognathus* and *Megagomphodon oligodens*) and supported previous conclusions (e.g., Hopson and Kitching 1972; Battail 1991) that there was only one species represented (*Massetognathus pascuali*), and that most of the diagnostic characters proposed to differentiate these taxa can be explained as ontogenetic variation. Liu and Powell (2009) considered *Rusconiiodon mignonei* to be a junior synonym of *Andescynodon mendozensis*, and Liu (2007) regarded *Ischignathus sudamericanus* as a junior synonym of *Exaeretodon argentinus*. More recently, Liu and Sues (2010) proposed *Plinthogomphodon* as a junior synonym of *Boreogomphodon*, but a specific differentiation

was tentatively proposed mainly because of their occurrences in different ages (i.e., Carnian and Norian).

In the current study, 22 traversodontid species are recognized as valid: *Andescynodon mendozensis*, *Arctotraversodon plemmyridon*, *Boreogomphodon herpetairus*, *Boreogomphodon jeffersoni*, *Dadadon isaloi*, *Exaeretodon argentinus*, *Exaeretodon riograndensis*, *Gomphodontosuchus brasiliensis*, *Luangwa drysdalli*, *Luangwa sudamericana*, *Mandagomphodon attridgei*, *Mandagomphodon hirschsoni*, *Massetognathus pascuali*, *Massetognathus ochagaviae*, *Menadon besairiei*, *Nanogomphodon wildi*, *Pascualgnathus polanskii*, *Protuberum cabralense*, *Santacruzodon hopsoni*, *Scalenodon angustifrons*, *Scalenodontoides macrodentes*, and *Traversodon stahleckeri* (see discussion below and Table 15.1).

Systematic and Phylogenetic History of Traversodontidae

The Family Traversodontidae originally included three cynodont species from the Brazilian Triassic: *Traversodon stahleckeri*, *?Traversodon major*, and *Gomphodontosuchus brasiliensis* (von Huene 1936). This group was characterized by von Huene (1936) as possessing expanded molars, a skull with proportions similar to that of galesaurids and chiniquodontids, and the anterior root of the zygoma located high on the maxilla, above the level of the teeth. Later, von Huene (1948) included taxa from the Argentinean Triassic described by Cabrera (1943) in this family. Romer (1956) and Watson and Romer (1956) included *T. stahleckeri* in

Table 15.1 List of worldwide traversodontid cynodonts

Taxon	Stratum	Age	Size
South America (9 genera)			
<i>Andescynodon mendozensis</i>	Cerro de las Cabras Formation	Late Anisian/Early Ladinian	Medium
<i>Pascualgnathus polanskii</i>	Río Seco de la Quebrada Formation	Late Anisian/Early Ladinian	Medium
<i>Luangwa sudamericana</i>	Santa Maria Formation	?Early Carnian	Medium
<i>Massetognathus pascuali</i>	Chañares Formation	Early Carnian	Medium
<i>Massetognathus ochagaviae</i>	<i>Dinodontosaurus</i> Assemblage Zone, Santa Maria Formation	Early Carnian	Medium
<i>Traversodon stahleckeri</i>	<i>Dinodontosaurus</i> Assemblage Zone, Santa Maria Formation	Early Carnian	Large
<i>Santacruzodon hopsoni</i>	<i>Santacruzodon</i> Assemblage Zone, Santa Maria Formation	Late Carnian	Medium
<i>Protuberum cabralense</i>	<i>Dinodontosaurus</i> Assemblage Zone, Santa Maria Formation	Early Carnian	Large
<i>Gomphodontosuchus brasiliensis</i>	<i>Hyperodapedon</i> Assemblage Zone, Santa Maria Formation	Early Norian	Medium
<i>Exaeretodon riograndensis</i>	<i>Hyperodapedon</i> Assemblage Zone, Santa Maria Formation	Early Norian	Large
<i>Exaeretodon argentinus</i>	Ischigualasto Formation	Early Norian	Large
Africa (6 genera)			
<i>Luangwa drysdalli</i>	Upper Ntawere Formation	Late Anisian/Early Ladinian	Medium
<i>Luangwa</i> sp.	Upper Omingonde Formation	Middle Triassic	Large
<i>Scalenodon angustifrons</i>	Manda Beds	Late Anisian/Early Ladinian	Medium
<i>Mandagomphodon attridgei</i>	Manda Beds	Late Anisian/Early Ladinian	–
<i>Mandagomphodon hirschsoni</i>	Manda Beds	Late Anisian/Early Ladinian	Medium
<i>Dadadon isaloi</i>	'Isalo II' (=Makay Formation)	Late Carnian	Medium
<i>Menadon besairiei</i>	'Isalo II' (=Makay Formation)	Late Carnian	Large
<i>Scalenodontoides macrodentes</i>	Lower Elliot Formation	Late Norian	Large
India (1 genus)			
<i>Exaeretodon</i> sp.	Lower Maleri Formation	Early Norian	–
North America (2 genera)			
<i>Arctotraversodon plemmyridon</i>	Wolfville Formation, Fundy Group	Carnian	Large
<i>Boreogomphodon jeffersoni</i>	Tomahawk Creek Member, Turkey Branch Formation; Pekin Formation	Carnian	Small
<i>Boreogomphodon herpetairus</i>	Muddy sandstone of Lithofacies Association II, Newark Supergroup	? Early Norian	Small
Europe (1 genus)			
<i>Nanogomphodon wildi</i>	Lower Keuper or Erfurt Formation	Ladinian	Small

Diademodontidae, and erected the new family Gomphodontosuchidae for *G. brasiliensis*. After the discovery of numerous additional South African specimens, Romer (1966) modified his proposal, including all of these forms in Traversodontidae in his third edition of *Vertebrate Paleontology*.

Bonaparte (1963d) presented an extensive review of traversodontids, with a large list of characters typical for the family that included *Gomphodontosuchus* and *Traversodon* from Brazil; *Exaeretodon*, *Proexaeretodon*, and *Ischignathus* from Argentina; and *Scalenodon* and *Scalenodontoides* from Africa. He proposed that Traversodontidae originated from procynosuchids, independent of the lineage that give rise to thrinaxodontids, cynognathids, and diademodontids. Bonaparte (1963d), based mainly on evidence presented by Crompton and Ellenberger (1957), also considered the possibility that tritylodontids originated from basal traversodontids.

Hopson and Kitching (1972) introduced modifications to traversodontid classification, including all the taxa under the Subfamily Traversodontinae, which along with Diademodontinae and Trirachodontinae were members of the Family Diademodontidae. This group and the Family Tritylodontidae were included under the Superfamily Tritylodontoidea.

Tatarinov (1974) presented a classification of therapsids in which he included the Family Traversodontidae in the Gomphognathoidea. He recognized two subfamilies of traversodontids, Scalenodontinae (including *Scalenodon boreus*) and Traversodontinae (including *Antecosuchus ochevi*).

Hopson (1984, 1985) suggested that *Scalenodon angustifrons* derived from *Andescynodon* and proposed that *Luangwa*, *Traversodon*, and possibly *Scalenodon atridgei* formed a group more derived than *S. angustifrons*. He interpreted *Massetognathus*, *Scalenodon hirschsoni*, *Gomphodontosuchus*, *Exaeretodon*, *Scalenodontoides*, and probably *Scalenodon charigi* as representing a group of the most derived traversodontids. Hopson (1985) presented a cladogram in which *Exaeretodon* and *Scalenodontoides* were sister taxa, whereas *Gomphodontosuchus* and, tentatively, *S. charigi* were basal to the (*Exaeretodon*+*Scalenodontoides*) clade.

Brink (labeled 1982, but published in 1986) listed 15 genera and 17 species in Traversodontidae: nine from South America (*Andescynodon mendozensis*, *Rusconiodon mignonei*, *Pascualgnathus polanskii*, *Massetognathus pascuali*, *Massetognathus teruggii*, *Traversodon stahleckeri*, *Gomphodontosuchus brasiliensis*, *Exaeretodon argentinus*, and *Ischignathus sudamericanus*); three from Africa (*Luangwa drysdalli*, *Scalenodon angustifrons*, and *Scalenodontoides macrodentes*); two from Russia (*Antecosuchus ochevi* and *Scalenodon boreus*); and one from China

(*Traversodontoides wangwuensis*). He also considered two taxa (*Colbertosaurus muralis* from Argentina and *Theropsodon njalilus* from Tanzania) as Traversodontidae *incertae sedis*. Brink's (1986) catalogue was not exhaustive in its coverage of traversodontids and several taxa were not included in his work.

Battail (1991, Fig. 8) considered traversodontids to be a monophyletic group closely related to tritylodontids. He recognized the following valid species: *Andescynodon mendozensis*, *Exaeretodon frenguelli*, *Exaeretodon vincei*, *Gomphodontosuchus brasiliensis*, *Ischignathus sudamericanus*, *Scalenodontoides macrodentes*, *?Scalenodontoides plemmyridon*, *Massetognathus pascuali*, *Pascualgnathus polanskii*, *Rusconiodon mignonei*, *Scalenodon angustifrons*, *Scalenodon hirschsoni*, *Scalenodon atridgei*, *?Scalenodon charigi*, *Scalenodon drysdalli*, *?Scalenodon boreus*, *Theropsodon njalilus*, *Traversodon stahleckeri* and perhaps *Microscalenodon nanus*. The species *E. vincei* presented as a new combination was based on a single specimen originally described as *Proexaeretodon vincei* by Bonaparte (1963). Another new combination was *Scalenodon drysdalli* (originally *Luangwa drysdalli*), based on the similarity of dentition of a second specimen of *L. drysdalli* described by Kemp (1980) with species of *Scalenodon*. Finally, Battail (1991) also proposed the synonymy of the three Argentinian species of *Massetognathus* and *Megagomphodon oligodens*.

The monophyly of Traversodontidae is the subject of current debate, with some scholars (Sues 1985; Hopson and Barghusen 1986; Hopson and Kitching 2001; Sues and Hopson 2010) arguing that tritylodontids are derived from traversodonts, a hypothesis put forward by Crompton and Ellenberger (1957; see also Crompton 1972). Other researchers support the hypothesis of a monophyletic Traversodontidae within Cynognathia (Luo 1994; Abdala 1998, 2007; Liu and Olsen 2010), where tritylodontids are members of Probainognathia, closely related to mammaliaforms.

Flynn et al. (1999, p. 765) proposed a stem-based definition of Traversodontidae as "the clade consisting of all cynodont species sharing a more recent common ancestor with *Exaeretodon* than with *Probainognathus* or Mammalia". This definition is problematic because it would include *Cynognathus*, *Diademodon*, and trirachodontids within this group based on recent phylogenetic hypotheses and is therefore much more inclusive than the traditional meaning of the taxon. More recently, Kammerer et al. (2008, p. 446) considered Traversodontidae to represent the most inclusive clade containing *Traversodon stahleckeri* von Huene 1936, p. 132 but not *Trirachodon kannemeyeri* Seeley 1895, p. 48 or *Diademodon tetragonus* Seeley 1894, p. 1030. We follow the definition of Kammerer et al. (2008) here.

Godefroit and Battail (1997) presented a phylogeny of Traversodontidae based on a reduced set of dental

characters mapped on a tree including 14 genera. Abdala (1998) analyzed the interrelationships of nine traversodontid genera, using a parsimony-based program to generate shortest trees from a data matrix of 11 dental characters. All the following contributions explored the relationships of traversodontids using data sets analyzed by parsimony programs. Flynn et al. (2000) studied the interrelationships of six traversodontid genera using 16 characters. While presenting the phylogeny of non-mammalian cynodonts, Hopson and Kitching (2001) included seven genera and species of traversodontids. Abdala and Ribeiro (2003) presented a phylogeny of 13 traversodontids with 21 dental and seven craniomandibular characters. Abdala et al. (2006) expanded the data set to 42 characters in an analysis designed to recover gomphodont cynodont relationships. Kammerer et al. (2008) presented a phylogeny with a revised version of the data set of Abdala et al. (2006), whereas Reichel et al. (2009) added a new taxon (*Protuberum*) to the analysis of Abdala and Ribeiro (2003). Recently, Sues and Hopson (2010) presented the phylogeny of 17 traversodontid taxa, including for the first time taxa from Laurasia, and recovered a clade composed of *Boreogomphodon*, *Arctotraversodon* and *Nanogomphodon* from the Northern Hemisphere as the sister group to most other known Middle and Late Triassic traversodontids from Gondwana.

In previous phylogenetic analyses, researchers have obtained consensus on the relationships of some Middle and Late Triassic Gondwanan taxa (e.g., *Exaeretodon*, *Gomphodontosuchus*, *Menadon*, *Protuberum*, and *Scalenodontoides* have been consistently found to be more closely related to each other than to other traversodontid taxa). However, important differences exist between these previous analyses regarding the interrelationships of basal traversodontids. To help resolve this issue, we assembled an enhanced dataset including postcranial characters to reexamine the phylogeny of traversodontids, and, based on this result, revise the taxonomy of the group.

Institutional Abbreviations: AMNH FARB, Fossil Amphibians, Reptiles, and Birds Collection, American Museum of Natural History, New York City, NY, USA; BP, Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, South Africa; BSP, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany; CAMZM, University Museum of Zoology, Cambridge, UK; CGP, Council for Geosciences, Pretoria, South Africa; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; FMNH, Field Museum of Natural History, Chicago, IL, USA; GPIT, Institut und Museum für Geologie und Paläontologie der Universität Tübingen, Tübingen, Germany; GSN, Geological Survey of Namibia, Windhoek, Namibia; IRSNB, Institut Royal des Sciences Naturelles de

Belgique, Brussels, Belgium; MACN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; MCN, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; MCP, Laboratório de Paleontologia, Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA; MGB, Museu Guido Borgomanero, Mata, Brazil; MLP, Museo de La Plata, La Plata, Argentina; MNHN, Muséum National d’Histoire Naturelle, Paris, France; NCSM, North Carolina State Museum, Raleigh, NC, USA; NHMUK, Natural History Museum, London, UK; NMQR, National Museum, Bloemfontein, South Africa; NSM, Nova Scotia Museum, Halifax, Canada; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; PULR, Museo de Antropología, Universidad Nacional de La Rioja, La Rioja, Argentina; PVL, Colección de Paleontología de Vertebrados, Instituto Miguel Lillo, Universidad Nacional de Tucumán, Argentina; PVSJ, Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina; SAM, Iziko, the South African Museum, Cape Town, South Africa; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; UA, Université d’Antananarivo, Antananarivo, Madagascar; TSK, collection of Prof. Thomas Kemp, Oxford University, Oxford, UK; UFRGS-PV, Setor de Paleovertebrados, Instituto de Geociências, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; UNC, Collections of the Department of Geology, University of North Carolina, Chapel Hill, USA; USNM, National Museum of Natural History, Washington D.C., USA; VMNH, Virginia Museum of Natural History, Martinsville, VA, USA; YPM-PU, former Princeton University collection, now housed in the Peabody Museum of Natural History, Yale University, New Haven, CT, USA.

Phylogenetic Analysis

All currently accepted valid traversodontid species were included in this analysis except for *Boreogomphodon* (originally *Plinthogomphodon*) *herpetairus*, whose postcranial morphology cannot be differentiated from that of *Boreogomphodon jeffersoni*. The sectorial-toothed cynodonts *Thrinaxodon liorhinus* and *Cynognathus crateronotus* and the gomphodonts *Beishanodon youngi*, *Cricodon metabolus*, *Diademodon tetragonus*, an unnamed South African taxon (CGP JSM100), *Langbergia modisei*, *Sinognathus gracilis*, and *Trirachodon berryi* were also included in this analysis; *Thrinaxodon liorhinus* was used to root the most parsimonious trees (MPTs). The character list includes

18 craniomandibular characters, 16 tooth position characters, 32 dental morphology characters, and 10 postcranial characters (Appendix 15.1).

The homology between sectorial and gomphodont teeth remains an unsolved problem in phylogenetic analyses of cynodont relationships. Abdala and Ribeiro (2003; see also Hopson 2005) accepted the homology of the sectorial border of gomphodont tooth with the sectorial teeth, and considered the lingual border of the former a new structure. However Abdala and Ribeiro (2003; see also Martinelli 2010b) also proposed an explanation of homology based on the rotation of sectorial teeth to constitute the gomphodont postcanines in *Trirachodon*. In this case the aligned main cusps of the sectorial tooth would be homologous with the transverse crest of gomphodont postcanines. In this study, the gomphodont tooth is interpreted as a neomorphic dental structure and the cusps of the gomphodont tooth are not considered homologous with the cusps of the sectorial tooth.

The data matrix (Appendix 15.2) was run in TNT (Goloboff et al. 2008). All characters were equally weighted and multistate characters were treated as unordered. Ten random addition sequences with 10 trees retained per replication in TNT produced seven most parsimonious trees (MPTs) with tree length of 212 steps. The number of MPTs increased to 13 with increase to 50 addition sequences and 50 trees retained per replication. The number of MPTs did not vary with continued increase of these settings.

Traversodontidae and the clade (*Exaeretodon*+*Scalenodontoides*) are the best supported monophyletic groups in our analysis, with a Bremer support of three. Advanced traversodontids (including node Y on Fig. 15.1 and Gomphodontosuchinae, see below) have a Bremer support of two and remaining groups have a support of one.

The base of Traversodontidae in the strict consensus is represented by a large polytomy including seven terminals and five monophyletic groups. In the majority consensus tree (Fig. 15.1), *Nanogomphodon* is placed as the most basal traversodontid. This placement is mainly based on the presence of one or more cuspules located anterolabially in the lower postcanines and the lack of score of most characters. The fact that *Nanogomphodon* is only known by an isolated lower postcanine is therefore the main reason of this basal placement of the taxon. Because of its incompleteness, we produced another analysis removing *Nanogomphodon* from the dataset. This resulted in 26 MPTs retained of 211 steps, whose majority rule consensus is almost identical to Fig. 15.1, other than recovering a monophyletic Trirachodontidae (Fig. 15.2).

In the results of this analysis, traversodontids exhibit a basal polytomy formed by *Scalenodon angustifrons* from Tanzania, a clade formed by the Argentinean taxa *Pascualgnathus* and *Andescynodon*, and another clade including

the remaining traversodontids. The latter clade includes a monophyletic group formed by *Luangwa drysdalli* and *L. sudamericana*, from Zambia and Brazil respectively. A second polytomy follows formed by *Traversodon* from Brazil, a clade formed by *Mandagomphodon hirschsoni* and *M. attridgei* and a clade including the remaining traversodontids. The latter clade is composed of the South American *Santacruzodon*, which is the sister taxon of a monophyletic *Massetognathus*. The next-diverging clade (N in Fig. 15.1) is composed of the Laurasian taxa *Arctotraversodon* and *Boreogomphodon*. The Malagasy traversodontid *Dadadon* represents the sister taxon to Gomphodontosuchinae (sensu Kammerer et al. 2008), a group composed of (*Gomphodontosuchus* (*Menadon* (*Protuberum* (*Scalenodontoides*+*Exaeretodon*))))). The two species of *Exaeretodon* and *Scalenodontoides* form a polytomy.

A monophyletic Trirachodontidae is only recovered in the majority consensus tree of Fig. 15.2, and consequently there is no unambiguous synapomorphy for this group. The specimen CGP JSM100 [interpreted by Hopson (2005) as a probable juvenile *Trirachodon* of uncertain species] is the most basal trirachodontid followed by a polytomy including *Trirachodon*, *Cricodon*, and a monophyletic group formed by *Langbergia* and the Laurasian *Beishanodon* and *Sinognathus*. This result is slightly different from that of Gao et al. (2010), in which they recognized two monophyletic groups for Laurasian and African forms.

Major interrelationships revealed here are mostly consistent with the previous phylogenetic hypotheses of Abdala and Ribeiro (2003), Abdala et al. (2006), and Kammerer et al. (2008), but differ from those of Sues and Hopson (2010). The primary similarity with previous cladistic analyses of traversodontids is the recovery of a monophyletic Gomphodontosuchinae, but, differing from the recent phylogeny by Reichel et al. (2009), we did not recover a monophyletic group composed of *Menadon* and *Protuberum*. The recovery of a monophyletic group composed of *Santacruzodon* and *Massetognathus* is similar to results by Kammerer et al. (2008) and Sues and Hopson (2010).

As mentioned by Abdala et al. (2006), the placement of basal forms continues to be the most variable area of traversodontid phylogeny. Unlike in Abdala et al. (2006), *Luangwa* never appears as the most basal traversodontid in this study. The most basal traversodontids in the analysis of Sues and Hopson (2010) form a monophyletic group of the Argentinean taxa *Andescynodon* and *Pascualgnathus*, but our result indicates that the African *Scalenodon angustifrons* alone is the most basal traversodontid on 6 of 13 MPTs and together with *Andescynodon* and *Pascualgnathus* on 4 of 13 MPTs that do not consider *Nanogomphodon*. *Andescynodon* plus *Pascualgnathus* occupies the most basal position on 3 of 13 MPTs, is slightly more advanced than S.

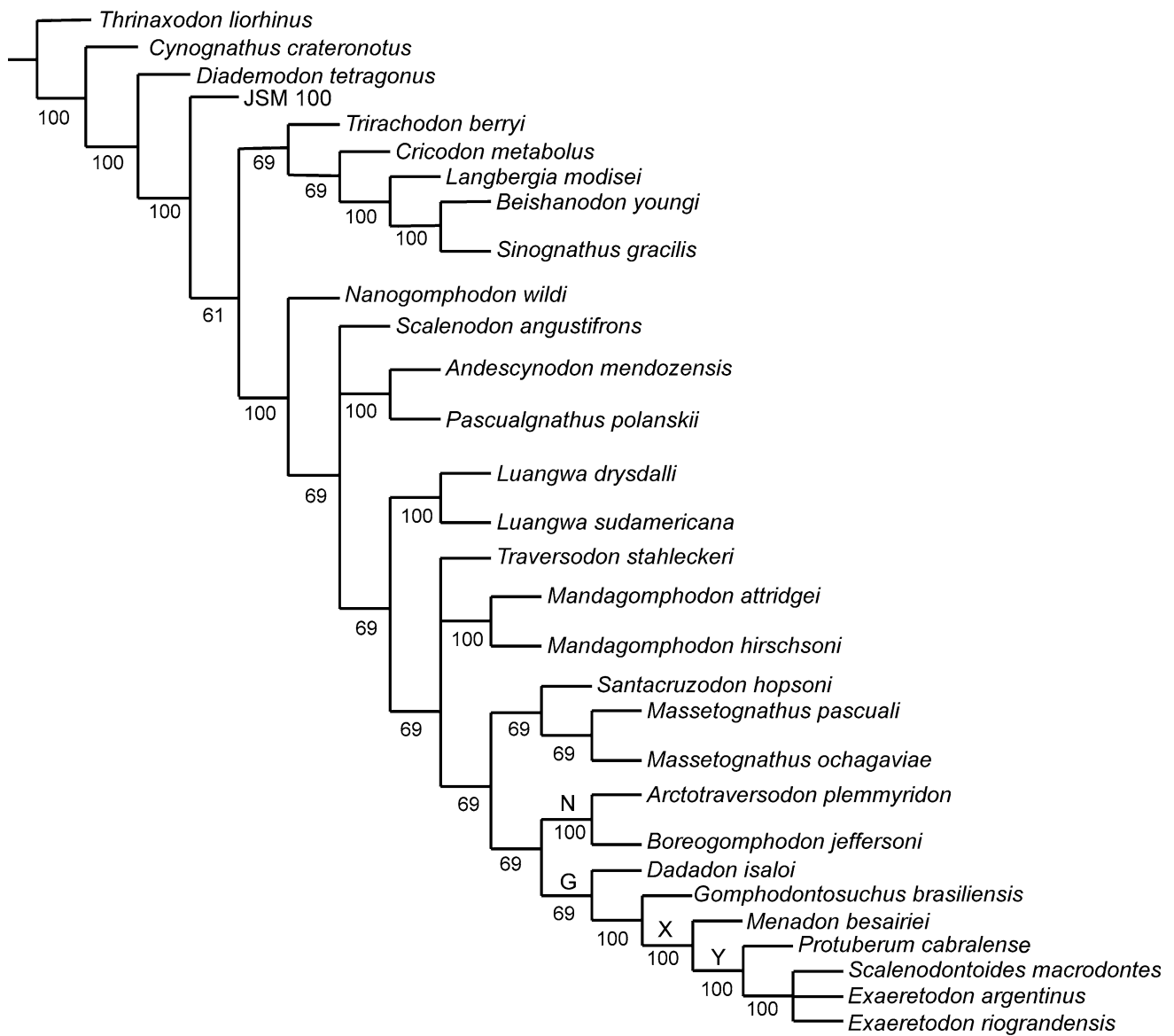


Fig. 15.1 Majority rule consensus tree of 13 most parsimonious trees (tree length = 212) for the data set provided in Appendix 15.2. The numbers indicate the frequency of clades in the fundamental trees. Letters are used to refer to unnamed clades discussed in the text

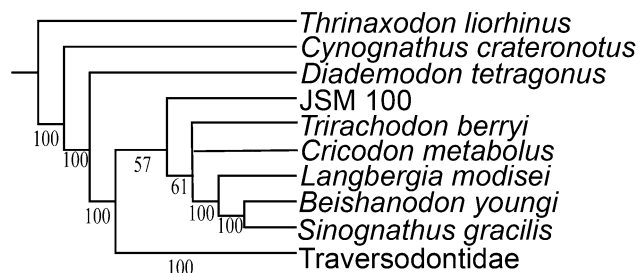


Fig. 15.2 Majority rule consensus tree from the parsimony analysis for the date set provided in Appendix 15.2, after removal of the 'wildcard' taxon *Nanogomphodon*. The interrelationships among traversodontids are the same as those in Fig 15.1 (other than exclusion of *Nanogomphodon wildi*). The numbers indicate the frequency of clades in the fundamental trees

angustifrons on 2 of 13 MPTs, and groups with the Laurasian clade (*Arctotraversodon*+*Boreogomphodon*) on 4 of 13 MPTs. *Scalenodon angustifrons* formed a monophyletic group with *Luangwa* in Sues and Hopson's (2010) hypothesis, and the clade has a derived placement relative to (*Andescynodon*+*Pascualgnathus*) and *Scalenodon hirschsoni* in their majority-rule consensus (Sues and Hopson 2010, Fig. 12B). North American traversodontids occupy a basal position in the cladogram of Sues and Hopson (2010), contra the results of our analysis.

Most multispecific genera other than *Scalenodon* are recovered as monophyletic in our analysis. *Scalenodon hirschsoni* and *S. attridgei* should be placed in a different

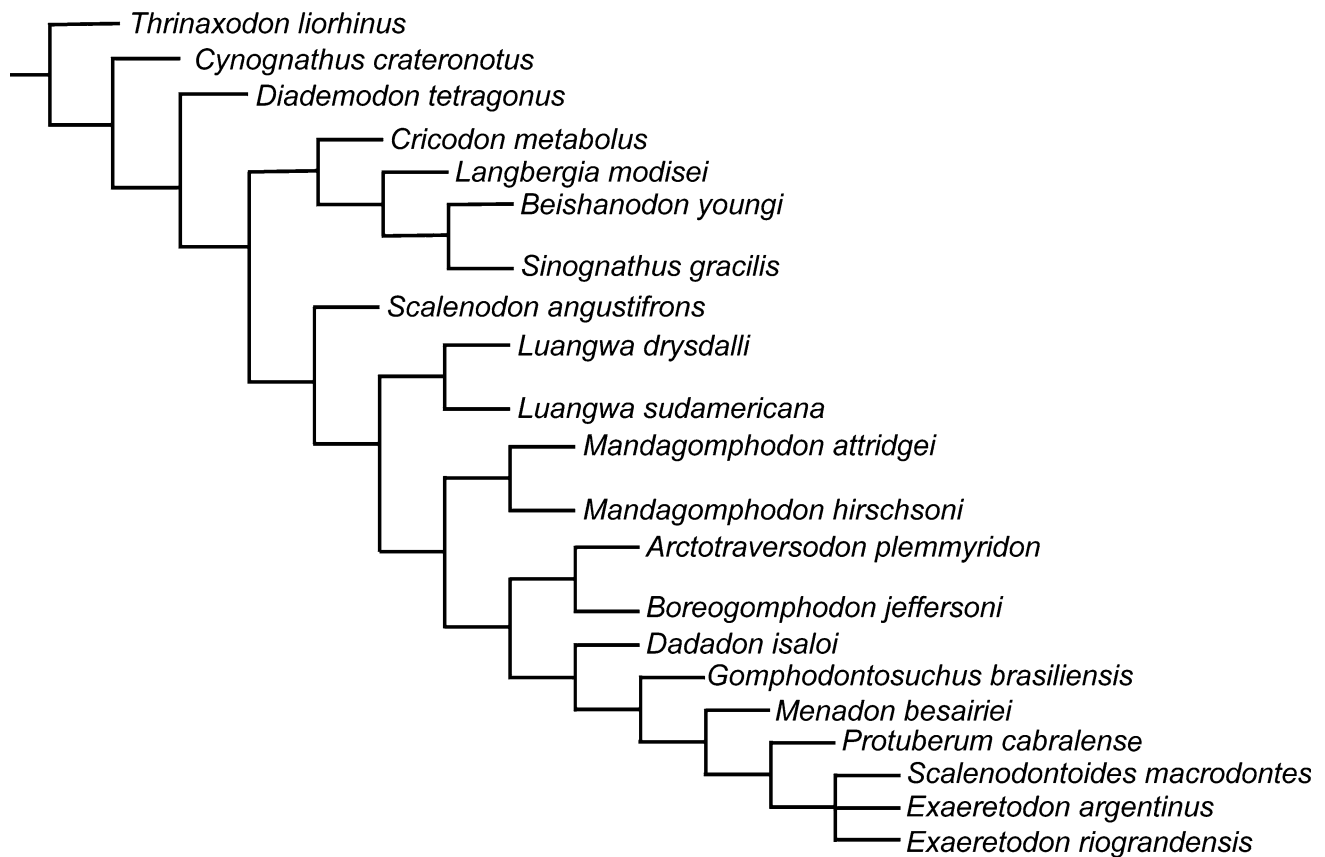


Fig. 15.3 Agreement subtree of 13 most parsimonious trees for the data set provided in Appendix 15.2 without wildcard taxa

genus than *Scalenodon angustifrons*, as proposed by Hopson and Kitching (2001) and Hopson (2013). Following the latter contribution, they are placed in the genus *Mandagomphodon*. The position of *M. hirschsoni* has varied in different phylogenetic hypotheses (Hopson and Kitching 2001; Abdala and Ribeiro 2003; Abdala et al. 2006), and is recovered in yet a different placement here (Figs. 15.1, 15.2). The relationships of *M. atridgei* within traversodontids have not been analyzed in previous phylogenies; here, it forms a clade with *M. hirschsoni*. Battail (1991) synonymized *Luangwa* with *Scalenodon*, but this analysis does not support his hypothesis.

From the agreement subtrees (Fig. 15.3), the wildcard taxa in Traversodontidae include *Traversodon*, *Massetognathus*, and *Santacruzodon* in addition to the previously mentioned (*Andescynodon*+*Pascualgnathus*) and *Nanogomphodon*.

Arctotraversodon plemmyridon was at first tentatively referred to *Scalenodontoides* (Hopson 1984), but Sues et al. (1992) suggested it could possibly be linked to *Boreogomphodon jeffersoni* by the presence of three anterior cusps on the lower postcanines. They indicated the existence of a distinct lineage of traversodontid cynodonts in Europe and eastern North America, which includes *Arctotraversodon*,

Boreogomphodon, *Plinthogomphodon*, and *Nanogomphodon* (Hopson and Sues 2006; Sues and Hopson 2010). *Plinthogomphodon* was recently proposed as a synonym of *Boreogomphodon* (Liu and Sues 2010); in our analysis *Arctotraversodon* forms a clade with *Boreogomphodon*.

Hopson (1984, 1985) proposed close relationships between *Gomphodontosuchus*, *Exaeretodon*, and *Scalenodontoides*. Flynn et al. (2000) added *Menadon* to this clade and Kammerer et al. (2008) applied the name *Gomphodontosuchinae* to this group. Later, *Protuberum* was also included in the clade (Reichel et al. 2009). In the current analysis, the sister taxon of *Exaeretodon* is not *Menadon* as hypothesized by Abdala et al. (2006), but *Scalenodontoides* as suggested by Flynn et al. (2000), Battail (2005), and Kammerer et al. (2008). *Dadadon*, *Massetognathus*, and *Santacruzodon* are always more closely related to *Gomphodontosuchinae* than other Gondwanan traversodontids, although the exact interrelationships among these terminals differ in previous studies (Abdala and Ribeiro 2003; Abdala et al. 2006; Reichel et al. 2009; Gao et al. 2010; Sues and Hopson 2010).

Based on the current phylogenetic hypothesis presented in Figs. 15.1 and 15.2, the pattern of dental evolution in traversodontids is more irregular than proposed by Abdala and Ribeiro (2003), although patterns are partially obscured

by unresolved relationships at the base of the tree. The presence of three upper incisors is a synapomorphy of clade Y, but also convergent with *Pascualgnathus*, *Mandagomphodon hirschsoni*, and *M. attridgei*. The presence of two lower incisors is convergent in *M. hirschsoni* and *Sinognathus*. Enlarged incisors evolved independently in four groups: clade X, *Arctotraversodon*, *M. hirschsoni*, and *Cricodon*. The diastema between the last upper incisor and the upper canine disappears in *Massetognathus* and clade G (Gomphodontosuchinae+*Dadadon*), suggesting parallel evolution in these two groups. The diastema between the upper canine and postcanines is remarkably lengthened in Gomphodontosuchinae. The paracanine fossa is anteromedial with respect to the upper canine in basal traversodontids and changed to a posteromedial position in clade Y, passing through a medial position in *Massetognathus*, *Dadadon*, *Gomphodontosuchus*, and *Menadon*. Because clade N and *Santacruzodon* have the primitive state, parallel evolution may have occurred in *Massetognathus* compared to *Menadon* and *Gomphodontosuchus*. Sectorial teeth present until adulthood is a derived character of *Boreogomphodon*, possibly indicating paedomorphosis in this taxon. A transverse cusp row positioned centrally on the crown in both upper and lower postcanines is the primitive state for gomphodonts. Derived states, transverse cusp row on posterior part of the crown of upper postcanines and on anterior margin of the lower postcanines, are both acquired in Traversodontidae, while a convergent evolution appeared in *Trirachodon* for a posterior position of the transverse cusp row on the crown of some upper postcanines, e.g., BSP 1934 VIII 21 (Broili and Schröder 1935, Fig. 3). Another derived state, transverse cusp row on anterior part of the crown of upper postcanines, is present in *Andescynodon* and *Pascualgnathus*. A slightly developed shouldering [shouldering is defined as the extension of the anterolabial margin of the upper postcanine forward, producing a ‘shoulder-like’ process over the preceding tooth, following Romer (1967) and Abdala et al. (2006)] of the upper gomphodont dentition is a synapomorphy of clade G. The posteriormost postcanines are inclined posteromedially in relation to the longitudinal axis of the skull in many species, e.g., *Exeretodon*, *Traversodon*, and *Mandagomphodon attridgei*, and Abdala and Ribeiro (2003) suggested that this feature is possibly related to the shouldering; however, the correlation of these two features is low for known traversodontids.

Systematic Paleontology

The classification of Traversodontidae summarized here is based on the phylogenetic analysis resulting from this contribution. Diagnosis, stratigraphy and geographic

distribution, and specimen representation for each taxon is presented. Most diagnoses are represented by a distinctive combination of characters and, in several cases, autapomorphies. Ages follow the Triassic Time Scale recently advanced by Walker et al. (2009).

Family Traversodontidae von Huene, 1936

Definition: (revised from Kammerer et al. 2008) The most inclusive clade containing *Traversodon stahleckeri* von Huene, 1936 but not *Trirachodon kannemeyeri* Seeley, 1895.

Diagnosis: Cynognathian cynodonts characterized by the absence of the ectopterygoid; presence of an epipterygoid-quadrate contact; maxillary platform lateral to the postcanine series (convergent in *Trirachodon* and bauriid theroccephalians); labiolingually expanded upper postcanines with a deep occlusal basin; upper gomphodont teeth wider than lowers with outline varying from ellipsoid to rectangular; lower gomphodont teeth quadrangular in shape, with anteriorly positioned transverse crest.

Genus *Andescynodon* Bonaparte, 1969

Synonym: *Rusconiiodon* Bonaparte, 1970.

Type species: *Andescynodon mendozensis* Bonaparte, 1969.

Species *Andescynodon mendozensis* Bonaparte, 1969

Synonym: *Rusconiiodon mignonei* Bonaparte, 1970.

Holotype: PVL 3833, incomplete skull with poorly preserved teeth.

Stratum typicum: Cerro de las Cabras Formation.

Locus typicus: 5 km west of Villa de Potrerillos, Mendoza Province, Argentina.

Referred material: PVL 3834–3836, 3840 (holotype of *Rusconiiodon mignonei*), 3890, 3891, 3892(a, b, c, d), 3894–3900, 3894-1, 3895–3900, 3903, 3907, 4069–4072, 4390, 4423–4432; PVL unnumbered, incomplete pelvis (Abdala 2000; Liu and Powell 2009).

Age: Late Anisian/Early Ladinian, Middle Triassic.

Diagnosis: Small to medium-sized traversodontid, characterized by 9–11 upper postcanines in adults (fewer in larger individuals); transverse crest of upper postcanines located anteriorly; paracanine fossa perforating the snout dorsolaterally in adults; lower postcanines with a cingulum formed by one small cusp anterior to the transverse crest; differentiated from *Pascualgnathus* by the relatively flat skull, having a shorter and narrower temporal region, fewer upper postcanines, and shorter upper tooth row in adults (modified from Liu and Powell 2009).

Comments: All the known specimens of *Andescynodon mendozensis* and *Rusconiiodon mignonei* come from the same locality, and their only significant difference is the dorsolabial perforation of the paracanine fossa in *Rusconiiodon mignonei* (Goñi and Abdala 1989; Abdala 2000). This

feature was recently explained as ontogenetic variation and forms showing the dorsolabially open paracanine fossa are interpreted as adult specimens of *A. mendozensis* (Liu and Powell 2009). FA, however, entertains the possibility that they represent different taxa.

Genus *Pascualgnathus* Bonaparte, 1966

Type species: *Pascualgnathus polanskii* Bonaparte, 1966.

Species *Pascualgnathus polanskii* Bonaparte, 1966

Holotype: MLP 65-VI-18-1, skull and mandibles, and partial postcranial skeleton.

Stratum typicum: Río Seco de la Quebrada Formation, Puesto Viejo Group.

Locus typicus: “Puesto Viejo” locality, west of Colonia Las Malvinas Mendoza, Departamento de San Rafael, Mendoza, Argentina.

Referred material: MLP 65-VI-18-2, skull, mandibles and partial postcranial skeleton; PVL 3466, poorly preserved, dorsoventrally crushed skull and mandible (Bonaparte 1966b); PVL 4416, skull and mandibles articulated but remarkably crushed, connected to the first three cervical vertebrae (Abdala 2000).

Age: Late Anisian/Early Ladinian, Middle Triassic.

Diagnosis: Medium-sized traversodontid with the following combination of characters: three upper incisors; hypertrophied canines; lingual cusp of upper postcanines connected to the transverse ridge located in the anterior part of the crown; one main labial cusp followed by a posterior cusp forming the labial margin; posterior labial cusp distinct and persistent in the last upper postcanines; constricted and large (about 30 % of the skull length) snout with a dorsal perforation of the paracanine fossa; high, long, and sharp parietal crest (modified from Martinelli 2010a).

Genus *Scalenodon* Crompton, 1955

Type species: *Trirachodon angustifrons* Parrington, 1946.

Comments: Five species have been referred to this genus, four from Tanzania (Crompton 1972) and one more recently proposed from Russia (Tatarinov 1973). The Russian species, represented by isolated teeth, is not a traversodontid but a bauriid therocephalian (Sues and Hopson 2010). Two of the Tanzanian species (*S. attridgei*, including *S. charigi* as a junior synonym, and *S. hirschsoni*) do not form a clade with the type species and are here placed in a separate genus.

Species *Scalenodon angustifrons* (Parrington, 1946)

Synonym: *Trirachodon angustifrons* Parrington, 1946.

Holotype: CAMZM T907 (Field Catalogue no. 120B).

Stratum typicum: Lifua Member of the Manda Beds.

Locus typicus: Ruhuhu Valley, Tanzania; Stockley’s bone locality B29 between Gingama and Tschikonge.

Referred material: Many specimens from the same locality as the holotype, including CAMZM T908–918, T925, T946 (Field catalogue nos. 120A, 111B, 110A, 134B, 112B, 111C, 131, 129A, 113D, 112C, 119B) (Crompton 1955, 1972).

Age: Late Anisian/Early Ladinian, Middle Triassic.

Diagnosis: Medium-sized traversodontid with transverse crest formed by three cusps, close to the middle of the crown on most upper postcanines; absence of anterior cingulum or anterolabial accessory cusp on upper postcanines; absence of zygomatic process on the jugal.

Comments: Specimens from the Upper Omingonde Formation of Namibia were referred to this species by Brink (1986), some of these specimens were recently redescribed as *Luangwa* sp. (Abdala and Smith 2009). There is no current evidence for the presence of *Scalenodon angustifrons* in the Middle Triassic of Namibia.

Genus *Luangwa* Brink, 1963

Type species: *Luangwa drysdalli* Brink, 1963.

Age: Middle to ?Late Triassic.

Distribution: Upper Ntawere Formation, Zambia; Upper Omingonde Formation, Namibia; Santa Maria Formation, Brazil.

Diagnosis: Small to medium-sized traversodontid with a rounded margin of the zygomatic process of jugal; short snout; quadrangular temporal opening of the same size or slightly larger than orbits; 7–10 gomphodont postcanines with the last upper teeth inclined obliquely; posterior projection of the angular process of the dentary; posterior cingulum behind the transverse crest in upper postcanines, labial cingulum on anterior portion of upper postcanines.

Comments: Specimens recognized as *Luangwa* sp. were recently described from the Upper Omingonde Formation of Namibia (Abdala and Smith 2009). One particular specimen, CGP R572, is remarkably larger than remaining representatives of this genus.

Species *Luangwa drysdalli* Brink, 1963

Holotype: BP/1/3731 (Karoo Field Catalogue 3727), complete skull and lower jaw.

Stratum typicum: Upper Ntawere Formation.

Locus typicus: Northern part of the Luangwa Valley, Zambia.

Referred material: BP/1/3733, poorly preserved anterior portion of the skull with dentition (Abdala and Teixeira 2004); TSK 121, partial skull with lower jaws and some postcranial bones (Kemp 1980).

Age: Late Anisian/Early Ladinian, Middle Triassic.

Distribution: Upper Ntawere Formation; northern part of the Luangwa Valley, Zambia.

Diagnosis: Larger species of *Luangwa* with a posterior cingulum extending along the entire posterior border of the upper postcanines; absence of a posterior accessory cusp

behind the main cusp on the labial crest of the upper postcanines; four cusps in the transverse crest of the upper postcanines, with a small additional cusp between the central and external cusps, cingulum composed of several tiny cusps in front of the transverse crest of the lower postcanines; tiny cusps forming a labial cingulum on the lower postcanines.

Comments: This species was referred to the genus *Scalenodon* by Batail (1991, p. 59), however, these taxa are clearly distinct (Abdala and Teixeira 2004).

Species *Luangwa sudamericana* Abdala and Teixeira, 2004

Holotype: MCP 3167PV, a well-preserved partial skull and mandible.

Stratum typicum: Santa Maria Formation.

Locus typicus: Exact locality unknown, Rio Grande do Sul, Brazil.

Referred material: UFRGS-PV 0267T, a partial skull and a left lower jaw with three postcanines.

Age: ?Early Carnian, Late Triassic.

Diagnosis: Smaller species of *Luangwa* differing from *L. drysdalli* by the presence of a posterior cingulum extending along part of the posterior border of the upper postcanines; well defined posterior accessory cusp behind the main cusp on the labial crest of the upper postcanines; three cusps in the transverse crest of the upper postcanines; cingulum composed of two tiny cuspules in front of the transverse crest of the lower postcanines; absence of a labial cingulum on the lower postcanines.

Genus *Traversodon* von Huene, 1936

Type species: *Traversodon stahleckeri* von Huene, 1936.

Species *Traversodon stahleckeri* von Huene, 1936

Holotype: GPIT/RE/7170, an incomplete skull, jaw, and some postcranial bones.

Stratum typicum: *Dinodontosaurus* Assemblage Zone, Santa Maria Formation.

Locus typicus: Cynodont Sanga, west of Chiniquá, Paraná Basin, Rio Grande do Sul, Brazil (von Huene 1936).

Referred material: GPIT 1045, 1063, 1069; UFRGS-PV 0224T (specimen described by Barberena 1981a).

Age: Early Carnian, Late Triassic.

Diagnosis: Large traversodontid with short snout; sharp, powerful angular process of the dentary; nine to ten ovoid upper postcanines with a well-developed posterior cingulum; eight lower postcanines lacking cingulum anterior to the transverse crest; with the labial cusp lower than lingual cusp.

Comments: A partial skull lacking lower jaw was described and referred to this species by Barberena (1974, 1981a). Unfortunately, preservation of the dentition and other important traits are poor in this specimen and we are not totally confident that this material is representative of the species *Traversodon stahleckeri*. We consider that

material representing this taxon in the Tübingen collection (particularly a maxilla with a well preserved last postcanine in eruption) may prove to be more closely related (i.e., in the same monophyletic group) to *Luangwa* than is portrayed by the phylogeny presented here.

Genus *Mandagomphodon* Hopson, 2013

Type species: *Scalenodon hirschsoni* Crompton, 1972.

Age: Late Anisian/Early Ladinian, Middle Triassic.

Distribution: Lifua Member of Manda Beds, Tanzania.

Diagnosis: Traversodontid with three enlarged upper incisors; well-developed anterior and posterior cingulum in upper postcanines.

Species *Mandagomphodon hirschsoni* (Crompton, 1972)

Holotype: NHMUK R8577, partial skull and mandible with well-preserved postcanine teeth.

Stratum typicum: Lifua Member of Manda Beds.

Locus typicus: Ruhuhu Valley, southwest Tanzania locality U12 of the BM(NH)-University of London Joint Palaeontological Expedition, 1963. Between the Hiasi and Njalila streams, just south of the Rutukira River; the most northerly of the expedition's localities west of the Njalila.

Age: Late Anisian/Early Ladinian, Middle Triassic.

Diagnosis: Medium-sized *Mandagomphodon* traversodontid characterized by two lower procumbent incisors; an anterior wall in the posterior postcanines; cingulum in front of the transverse crest of the lower postcanines formed by an enormous isolated cusp.

Species *Mandagomphodon attridgei* (Crompton, 1972) comb. nov.

Synonym: *Scalenodon charigi* Crompton, 1972.

Holotype: NHMUK R8578, a well preserved snout with complete upper dentition of a young individual.

Stratum typicum: Lifua Member of Manda Beds.

Locus typicus: Ruhuhu Valley, S.W. Tanzania; locality U2 of the BM(NH)-University of London Joint Palaeontological Expedition, 1963. Next to the Peramiho-Litumba dirt road, on its southwestern side.

Referred material: CAMZM 922 (Ruhuhu Field catalogue no. 136), partial left maxilla with two postcanines (holotype of *Scalenodon charigi*).

Locality: Ruhuhu Valley, locality B26 of Stockley (1932, p. 620). Gingama south of the Ruhuhu River.

Age: Late Anisian/Early Ladinian, Middle Triassic.

Diagnosis: *Mandagomphodon* traversodontid characterized by upper postcanines with ovoid outline; high anterior transverse ridge on upper postcanines.

Comments: Specimen CAMZM 922 ("*Scalenodon charigi*") is from an individual double the size of the holotype and the two preserved postcanines are worn out. Crompton (1972) provided several diagnostic characters for *Scalenodon charigi*. However, the differences between

NHMUK R8578 and CAMZM 922 may possibly be related to the poor preservation of CAMZM 922 or represent cases of individual variation. For example, the central cusp of the posterior transverse ridge and tiny cuspules of the cingulum are hardly preserved in worn postcanines. The overall similar crown shape of postcanines, the oblique orientation of the last postcanines, and the size of the external anterior accessory cusp in relation to the external cusp support the synonymy between *M. attridgei* and *S. charigi*.

Genus *Massetognathus* Romer, 1967

Synonym: *Megagomphodon* Romer, 1972.

Type species: *Massetognathus pascuali* Romer, 1967.

Age: Early Carnian, Late Triassic.

Distribution: Chañares Formation, La Rioja Province, Argentina; Santa Maria Formation, Rio Grande do Sul, Brazil.

Diagnosis: Medium-sized traversodontid with the posterior extension of the secondary palate beyond the anterior border of orbit; extreme development of the maxillary platform lateral to the postcanine series; absence of the zygomatic process of jugal; mesiodistally enlarged incisors with denticulated cutting margins; upper incisors close to the canine; small canines, the upper ones lateral to the paracanine fossa; incipient shouldering between upper postcanines; two anterolabial accessory cusps on the nearly rectangular upper postcanines; high and sharp transverse crest of lower postcanines; the anterolabial cusp wider than the anterolingual in lower postcanines.

Species *Massetognathus pascuali* Romer, 1967

Synonyms: *Massetognathus teruggii* Romer, 1967; *Massetognathus major* Romer, 1972; *Megagomphodon oligodens* Romer, 1972.

Holotype: PULR 10 (former MLP No. 65-XI-14-1), a complete well preserved skull with lower jaw.

Stratum typicum: Chañares Formation; Ischigualasto-Villa Union Basin.

Locus typicus: About two miles north of the point where the Chañares River debouches into the Campo de Talamaya, in western La Rioja Province, Argentina.

Referred materials: PULR 13 (former MLP No. 65-XI-14-2), skull and jaws (holotype of *M. teruggii*) (Romer 1966); PULR 11 (former MLP No. 65-XI-14-15), skull (holotype of *M. major*), PULR unnumbered (former MLP No. 65-XI-14-16), skull and lower jaws (holotype of *Megagomphodon oligodens*) (Romer 1972); PVL 3901–3906, 4014, 4016, 4168, 4439–4443, 4613, 4614, 4676, 4726–4729, 5441, 5443–5445 (Abdala 2000), PVL 5683; MCZ 3691, 3786, 3798, 3801, 3804, 3806, 3807, 4021, 4138, 4208, 4215, 4216, 4258, 4265; NHMUK R8430 (Abdala and Giannini 2000); BP/1/4245; MCP 3284 (Teixeira 1995).

Age: Early Carnian, Late Triassic.

Distribution: Chañares Formation, Ischigualasto-Villa Union Basin, Argentina and tentatively in the Santa Maria Formation, Rio Grande do Sul, Brazil (Liu et al. 2008).

Diagnosis: Snout is subequal to temporal region; small canines; absence of anterior cingulum on upper postcanines; presence of posterior cingulum on lower postcanine; dorsal margin of the coracoid equal to that of procoracoid in medial view; ‘T’-shaped lumbar ribs with restricted contact between successive ribs.

Comments: The synonymy of *Massetognathus pascuali* and *M. teruggii* was proposed by Hopson and Kitching (1972). Battail (1991) recognized *Massetognathus pascuali* as the only valid traversodontid species from the Chañares Formation, a hypothesis confirmed by the analysis of Abdala and Giannini (2000).

Species *Massetognathus ochagaviae* Barberena, 1981

Holotype: UFRGS-PV 0255T (G), a skull without mandible.

Stratum typicum: *Dinodontosaurus* Assemblage Zone, Santa Maria Formation, Paraná Basin.

Locus typicus: 3.5 km from Prof. Parreira train station, southeast of Melos, General Câmara District, Rio Grande do Sul, Brazil.

Neotype: MCP 3871 PV, a skull without mandible.

Locus neotypicus: Rincão do Pinhal, Agudo Municipality, Rio Grande do Sul, Brazil.

Referred material: UFRGS-PV 0070T, 0071T, 0125T, 0239T, 0241T, 0242T, 0243T, 0245T, 0265T, 0273T, 0397T, 1064T; AMNH FARB 7802, 7803, 21400–21410 (Liu et al. 2008).

Age: Early Carnian, Late Triassic.

Diagnosis: Snout shorter than temporal region; skull and mandible taller than *Massetognathus pascuali*; postcanine number less variable than in *M. pascuali*; isosceles triangular shape of the maxillary platform lateral to the postcanines in ventral view; short lingual ridge forming a nearly triangular basin on upper postcanines; robust lower canines; subrectangularly shaped lower postcanines (modified from Liu et al. 2008).

Comments: The holotype described by Barberena (1981b) could not be located in the UFRGS collection. MCP 3871 PV was recommended as neotype in case of definitive loss of the holotype (Liu et al. 2008).

Genus *Santacruzodon* Abdala and Ribeiro, 2003

Type species: *Santacruzodon hopsoni* Abdala and Ribeiro, 2003.

Species *Santacruzodon hopsoni* Abdala and Ribeiro, 2003

Holotype: MCN PV 2768, fragmentary skull with lower jaws.

Stratum typicum: *Santacruzodon* Assemblage Zone (Soares et al. 2011), Santa Maria Formation.

Locus typicus: Suburbs of the city of Santa Cruz do Sul (S 29° 44' 25", W 52° 27' 01"), Rio Grande do Sul, Brazil (Abdala et al. 2001).

Referred material: MCN PV 2751, MCN PV 2752, MCP 4044 PV three lower jaws; MCN PV 2770 incomplete maxilla with postcanines; MCP 4034 PV fragmentary skull and lower jaw with postcanines (Abdala and Ribeiro 2003).

Age: Late Carnian, Late Triassic.

Diagnosis: Traversodontid characterized by a ball-shaped ventrally projecting suborbital process; incisors flattened labiolingually with a series of 7–9 marginal cuspules; upper postcanines present an anterior small crest formed by a series of cingular cuspules; three labial cusps in the upper postcanines with the posterior cusp very large, representing more than half the length of the labial crest; anterolingual cusp strongly inclined posteriorly on lower gomphodont teeth (modified from Abdala and Ribeiro 2003).

Genus *Arctotraversodon* Sues, Hopson, and Shubin, 1992

Type species: *?Scalenodontoides plemmyridon* Hopson, 1984.

Species *Arctotraversodon plemmyridon* (Hopson, 1984)

Synonym: *?Scalenodontoides plemmyridon* Hopson, 1984.

Holotype: YPM-PU 19190, the horizontal ramus of a right dentary with a small portion of the left dentary.

Stratum typicum: Wolfville Formation, Fundy Group.

Locus typicus: Northeast corner of Burntcoat headland, 1.5 miles northwest of Noel, Hants County, Nova Scotia, Canada.

Age: Carnian, Late Triassic.

Diagnosis: Very large traversodontid with greatly enlarged posterior mental foramen on dentary; broad, chin-like symphyseal region of lower jaw; lower incisors with large mesial and distal marginal cuspules; crowns of postcanine teeth distinctly compressed anteroposteriorly; upper gomphodont teeth with prominent central cusp; three cusps on anterior crest of lower gomphodont teeth; posterior heel of lower gomphodont teeth without raised rim and labial accessory cusp placed high on labial ridge, rather than on margin of heel (after Sues et al. 1992).

Referred material: From Burntcoat shore: YPM-PU 19190-A, a partial canine tooth; YPM-PU 21693, a small partial dentary lacking teeth; NSM 983GF2.1, isolated right lower postcanine tooth from type locality; NSM 990GF89.1, left upper postcanine tooth. From Evangeline Beach (west outcrop), Kings County, Nova Scotia: YPM-PU 22343, fragmentary small dentary without teeth (Hopson 1984; Sues et al. 1992).

Genus *Boreogomphodon* Sues and Olsen, 1990

Synonym: *Plinthogomphodon* Sues, Olsen, and Carter, 1999.

Type species: *Boreogomphodon jeffersoni* Sues and Olsen, 1990.

Age: Late Triassic.

Distribution: North Carolina and Virginia, United States.

Species *Boreogomphodon jeffersoni* Sues and Olsen, 1990

Holotype: USNM 437632, a left maxilla with three teeth.

Stratum typicum: Tomahawk Creek Member of the Turkey Branch Formation, Newark Supergroup.

Locus typicus: Tomahawk locality, near Midlothian, Chesterfield County, Virginia, United States.

Referred material: From Virginia, cranial remains: CM 20050, 76800, 76801, 76803; USNM 437635, 437636, 448562, 448570, 448593, 448599, 448632, 448633; VMNH 3575, 3578. Isolated teeth: CM 76805, 76807, 76808, 76810, 76812, 76815, 76818; USNM 448563–448569, 448571–448573, 448575, 448576, 448578, 448597, 448601, 448625, 448629. Postcranial bones: USNM 448598, 448602; VMNH 3577 (Sues and Hopson 2010). From North Carolina, cranial remains: NCSM 11466, 15295, 16292, 16297, 16358, 16364, 18300, 19587, 20660, 20662, 20692, 20698, 20700, 20704, 20712, 21370, 21371 (Liu and Sues 2010).

Age: Carnian, Late Triassic.

Distribution: Turkey Branch Formation, Virginia and Pekin Formation, North Carolina, United States.

Diagnosis: Small traversodontid with the dorsal surface of the snout presenting pronounced, irregular sculpturing composed of ridges and grooves; jugal without distinct suborbital process; zygomatic arches bowed laterally at about mid-length rather than reaching greatest width posteriorly; presence of sectorial postcanines in adults; upper gomphodont teeth nearly triangular in crown view and posterior cingulum absent; three cusps in the transverse crest of the upper gomphodont teeth, the central and lingual confluent, and separated from the labial cusp by a valley; the transverse crest of lower gomphodont teeth is formed by three cusps in all but the smallest individuals; anterolabial cingular cuspules in front of the transverse crest (modified from Sues and Hopson 2010).

Comments: The North Carolina materials differ from those from Virginia because their lower gomphodont teeth are mostly represented by specimens having two cusps on the anterior ridge. Assessment of a taxonomic distinction must await completion of the study of the cranial material.

Species *Boreogomphodon herpetairus* (Sues, Olsen, and Carter, 1999)

Holotype: UNC 15576, partial snout preserved in two pieces.

Stratum typicum: Muddy sandstone of Lithofacies Association II, Durham sub-basin of Deep River Basin, Newark Supergroup.

Locus typicus: Genlee, Durham County, North Carolina, United States.

Referred material: UNC 15656, a few ingested postcranial elements including a complete humerus.

Age: ?Early Norian, Late Triassic.

Comments: The specimens were found associated with a large “rauisuchian”, and by the fossilization features, interpreted as ingested by this archosaur (Peyer et al. 2008). There is no clear diagnostic feature for this taxon. The species is tentatively accepted because of its different stratigraphic occurrence in relation to *Boreogomphodon jeffersoni* (Liu and Sues 2010).

Genus *Nanogomphodon* Hopson and Sues, 2006

Type species: *Nanogomphodon wildi* Hopson and Sues, 2006.

Species *Nanogomphodon wildi* Hopson and Sues, 2006

Holotype: SMNS 51962, left lower postcanine tooth lacking apical portion of the root.

Stratum typicum: Lower Keuper or Erfurt Formation.

Locus typicus: Housing development “Leitenäcker II” in Michelbach an der Bilz, Baden-Württemberg, Germany.

Age: Ladinian, Middle Triassic.

Diagnosis: Traversodontid having lower postcanine with anterior transverse ridge composed of three principal cusps and long basined “heel” bordered posteriorly by a ridge bearing three small cusps; distinct ridge bounding lingual side of basin; anterior cingulum with five cuspules (from Hopson and Sues 2006).

Genus *Dadadon* Flynn et al., 2000

Type species: *Dadadon isaloi* Flynn, Parrish, Rakotosamimanana, Ranivoharimanana, Simpson, and Wyss, 2000.

Species *Dadadon isaloi* Flynn et al., 2000

Holotype: UA 10606, partial skull with complete right upper dentition, excepting the first left incisor and right incisors.

Stratum typicum: Basal ‘Isalo II’ beds (Makay Formation sensu Razafimbelo 1987)

Locus typicus: East of Sakaraha, northern Morondava Basin, Madagascar.

Referred material: UA 10605, edentulous rostrum including the right orbit and nasal chamber, with four incisors, one canine, and nine postcanine alveoli.

Age: Late Carnian, Late Triassic.

Diagnosis: Medium-sized traversodontid with a large, rounded, ventrally projecting suborbital process; the upper tooth row extends posteriorly beyond the anterior margin of the subtemporal fossa; posterior upper postcanines obliquely oriented and with incipient shouldering; a posterolabial projection of the ectoloph forms a metastyle-like structure; strong labial cingulum on the upper postcanines (modified from Flynn et al. 2000).

Subfamily *Gomphodontosuchinae* Watson and Romer, 1956

Type genus: *Gomphodontosuchus* von Huene, 1928.

Composition: *Exaeretodon*, *Gomphodontosuchus*, *Menadon*, *Protuberum*, and *Scalenodontooides*.

Age: Late Triassic.

Distribution: South Africa, Lesotho, Madagascar, India, Argentina, and Brazil.

Diagnosis: A group of traversodontids characterized by high position of anterior root of zygomatic arch; posterior extension of the jugal well-developed dorsally above the squamosal in the zygomatic arch; well-developed angular process of dentary; enlarged incisors, the lowers being procumbent; three upper incisors; last upper incisor close to upper canine and the latter far from the first upper postcanine; reduced lower canine; very oblique orientation of upper gomphodont teeth; anterior wall in upper postcanines; lack of central cusp on posterior transverse crest; presence of distinct anterolingual accessory cusp of upper gomphodont teeth; absence of posterior cingulum on the lower postcanines.

Genus *Gomphodontosuchus* von Huene, 1928

Type species: *Gomphodontosuchus brasiliensis* von Huene, 1928.

Species *Gomphodontosuchus brasiliensis* von Huene, 1928

Holotype: GPIT unnumbered, anterior half of a skull and associated lower jaws.

Stratum typicum: *Hyperodapedon* Assemblage Zone, Santa Maria Formation.

Locus typicus: Santa Maria city, Rio Grande do Sul, Brazil.

Age: Early Norian, Late Triassic.

Diagnosis: Small traversodontid with a short and high rostrum; short and broad secondary palate with its posterior margin located anterior to the orbit; five or six upper and lower postcanines; paracanine fossa placed medially to the upper canine; massive chin-like dentary symphysis; forward position of the anterior border of the coronoid process (at the level of the fourth postcanine); upper postcanine outline varying from triangular anteriorly to quadrangular in the posterior teeth.

Comments: The only known specimen was interpreted as a juvenile, particularly resembling juvenile specimens of *Exaeretodon* (Hopson 1985). FA considers it possible that *Gomphodontosuchus* may be the sister taxon of *Menadon*, or even a juvenile of the latter taxon, although they do not form a monophyletic group in the current analysis.

Genus *Menadon* Flynn et al., 2000

Type species: *Menadon besairiei* Flynn, Parrish, Rakotosamimanana, Ranivoharimanana, Simpson, and Wyss, 2000.

Species *Menadon besairiei* Flynn et al., 2000

Holotype: UA 10601, skull and mandibles with eroded left side.

Stratum typicum: Basal 'Isalo II' beds (Makay Formation); Madagascar.

Locus typicus: East of Sakaraha, northern Morondava Basin, Madagascar.

Referred material: FMNH PR 2104, an isolated mandible; FMNH PR 2444, a partial skull and postcranium; field number 8-31-98-387, an isolated right pelvis (Kammerer et al. 2008).

Locality: Drainage of the Malio River, Morondava Basin, Madagascar.

Age: Late Carnian, Late Triassic.

Diagnosis: Large traversodontid characterized by four large upper incisors; lower incisors procumbent; third and fourth upper incisors caniniform, with fourth upper incisor strongly recurved, presenting serrated margins; upper canines small, of equal height to incisors, distinctly canted forwards; canine alveolus proportionally narrower than incisor alveoli, with a much greater anteroposterior than labiolingual length; low number of postcanines (8 uppers and 6–7 lowers); upper and lower postcanines quadrangular, roughly trapezoidal in outline; axial spine with concave dorsal profile and elongate posterior process overhanging shortened neural spine of subsequent cervical vertebra; expanded ribs present; caudal neural spines very tall; anterior edge of the iliac blade sloping upwards at a $\sim 45^\circ$ angle; acetabular buttresses of the three pelvic bones largely confluent; posterior process of the iliac blade short and directed away from the dorsal edge of the ischium; ischium and pubis extremely constricted, resulting in a large obturator foramen (modified from Kammerer et al. 2008).

Genus *Protuberum* Reichel, Schultz, and Soares, 2009

Type species: *Protuberum cabralensis* Reichel, Schultz, and Soares, 2009.

Species *Protuberum cabralense* Reichel, Schultz, and Soares, 2009

Holotype: MGB 368-100, skull without lower jaw, and several elements of the postcranium.

Stratum typicum: *Dinodontosaurus* Assemblage Zone, Santa Maria Formation.

Locus typicus: Outcrop in the Municipality of Novo Cabrais, Rio Grande do Sul, Brazil.

Referred material: UFRGS-PV 0981T, a proximal fragment of a right cervical rib; UFRGS-PV 0983T, an isolated vertebra; UFRGS-PV 0985T, an isolated vertebra; UFRGS-PV 0986T, an isolated vertebra; UFRGS-PV 1009T, a left cervical rib; UFRGS-PV 1010T, a left thoracic rib; UFRGS-PV 1011T, a fragment of a thoracic rib (Reichel et al. 2009).

Locality: Some vertebrae and ribs of the referred material were found in Rincão do Pinhal, Municipality of Agudo, Rio Grande do Sul, Brazil.

Age: Early Carnian, Late Triassic.

Diagnosis: Large traversodontid with upper postcanines having two main cusps (one labial and one lingual) connected by a sharp transverse crest and lacking shouldering; anteroposteriorly elongated paracanine fossa posteriorly placed in relation to the upper canine; short parietal crest; well-developed descending process of the jugal; bifurcated paroccipital process; incise foramina totally enclosed by the maxillae; a bony thickening that forms wide crests on the dorsal surface of the skull; small upper canine contiguous with the last incisor; ribs with very pronounced processes on their dorsal border, the most proximal of these is generally the largest and the others become smaller distally; the iliac blade has a series of rugosities along its dorsal border (modified from Reichel et al. 2009).

Genus *Exaeretodon* Cabrera, 1943

Synonyms: *Theropis* Cabrera, 1943; *Ischignathus* Bonaparte, 1963; *Proxaeretodon* Bonaparte, 1963.

Type species: *Exaeretodon frenguelli* Cabrera, 1943, a junior synonym of *E. argentinus* (Cabrera, 1943).

Age: Early Norian, Late Triassic.

Distribution: Ischigualasto Formation, San Juan and La Rioja Provinces, Argentina; Santa Maria Formation, Brazil; lower Maleri Formation, India.

Diagnosis: Very large traversodontids lacking internarial bar; upper postcanines with a well-developed posterolabial accessory cusp and extensive shouldering resulting in a separation between a labial lobe and a lingual one (including the occlusal basin); anterolingual cusp of the lower postcanines strongly inclined posteriorly; divergent zygomatic arches; well-developed descending process of the jugal; three lower incisors; large upper canines but reduced lowers; ribs lacking costal plates.

Species *Exaeretodon argentinus* (Cabrera, 1943)

Synonyms: *Belesodon argentinus* Cabrera, 1943; *Exaeretodon frenguelli* Cabrera, 1943; *Theropis robusta* Cabrera, 1943; *Ischignathus sudamericanus* Bonaparte, 1963b; *Proxaeretodon vincei* Bonaparte, 1963c.

Holotype: MLP 43-VII-14-2, incomplete left mandibular ramus.

Stratum typicum: Ischigualasto Formation.

Locus typicus: Hoyada de Ischigualasto, San Juan, Argentina.

Referred material: MLP 43-VII-14-1, 43-VII-14-3, 43-VII-14-4, and some specimens beginning with 61-VIII-2; MACN 18063, skull with lower jaws and some postcranial bones; MACN 18114, skull and articulated lower jaw and some postcranial bones (Bonaparte 1966a); several specimens in PVL (see Abdala 2000), including PVL 2564, skull, mandible, an atlantal arch, and a dorsal vertebra, holotype of *Ischignathus sudamericanus*; MCZ 7047, a complete skull with lower jaws (Chatterjee 1982); MCZ 3779, 4493, 111-64A, 377-58 M; MACN 18114, 18125; MCP 1522PV, PVSJ 157.

Age: Early Norian, Upper Triassic.

Distribution: Ischigualasto Formation, San Juan and La Rioja Provinces, Argentina.

Diagnosis: Variable number of postcanines (from 6 to 10); anterolabial cusp wider than the anterolingual on lower postcanines; absence of crest in the lateral flange of the prootic.

Species *Exaeretodon riograndensis* Abdala, Barberena, and Dornelles, 2002

Holotype: MCP 1522PV, complete skull plus proatlas and atlas arches on the occiput, dislocated from their anatomical position.

Stratum typicum: *Hyperodapedon* Assemblage Zone, Santa Maria Formation.

Locus typicus: Kilometer 136 of the railroad Br 287, 6 km west of the Botucarai hill, in the Candelaria district, Rio Grande do Sul State, Brazil.

Referred material: MCP 2361 PV, skull lacking the anterior portion of the rostrum, same locality as holotype; MCP 3843 PV, skull and lower jaw in occlusion, lacking the right temporal region, right dentary also incomplete, same locality as holotype; UFRGS PV 0715T, skull, lower jaws and some postcranial bones, Sitio Janner (53°17'30''W, 29°39'09.68''S), near Agudo city, Rio Grande do Sul, Brazil (Oliveira et al. 2007).

Age: Early Norian, Late Triassic.

Diagnosis: Presence of a series of crests in the lateral flange of the prootic anterior to the fenestra ovalis, the number of postcanines less variable in ontogeny than in *Exaeretodon argentinus* (from Abdala et al. 2002).

Comments: Several additional, mostly unpublished, specimens of *Exaeretodon riograndensis* have been collected in recent years, making it the most abundant cynodont known from the *Hyperodapedon* Assemblage Zone.

Exaeretodon sp. indet.

Composition: *Exaeretodon statisticae* Chatterjee, 1982.

Material: ISIR 303, a few mandibular fragments; ISIR 304, a partial skull (holotype of *E. statisticae*).

Stratum typicum: Lower Maleri Formation.

Locus typicus: Venkatapur village, District of Adilabad, Andhra Pradesh, south India (Chatterjee 1982).

Age: Early Norian, Late Triassic.

Comments: Although clearly a specimen of *Exaeretodon*, this Indian taxon does not have clear diagnostic characters, therefore it is not possible to place it in any of the recognized species. We entertain the hypothesis that this may represent a different species because of geographical distribution.

Genus *Scalenodontoides* Crompton and Ellenberger, 1957

Type species: *Scalenodontoides macrodontes* Crompton and Ellenberger, 1957.

Species *Scalenodontoides macrodontes* Crompton and Ellenberger, 1957

Holotype: MNHN 1957-23, paired dentaries lacking the region behind the postcanines.

Stratum typicum: Base of the Lower Elliot Formation.

Locus typicus: "Site A" of Crompton and Ellenberger (1957), Morobong Hill, Mohale's Hoek district, Lesotho.

Referred material and distribution: SAM-PK-K336, right half of a large snout, collect at "Site B, approximately 100 yards west of Site A", Morobong Hill, Mohale's Hoek district, Lesotho (Hopson 1984); BP/1/5395, a skull with lower jaw, farm Norwood, Sterkstroom, Eastern Cape Province (Gow and Hancox 1993); MNHN 1955-25, a skull lacking lower jaw, Leribe district, Lesotho (Battail 2005); NMQR 3053, paired premaxillae and maxillae with associated skull fragments, farm Patriotsklip, Jamestown, Eastern Cape Province (Kammerer et al. 2008).

Age: Late Norian, Late Triassic.

Diagnosis: Very large traversodontid with a very robust skull, approximately as broad as long; snout short and broad; temporal region remarkably short with the temporal opening being wider than long; overhanging nuchal table in the dorsal portion of the cranium composed mostly of the parietal; lower portion of the symphysis extends ventrally as a chin-like projection; occipital condyles widely separated; labial and lingual lobes of the last upper postcanines clearly distinct and demarcated by a constriction; anterolabial cusp of lower postcanines much larger than the anterolingual

cuspid in crown view; the ridge which passes back from the apex of the lingual cusp to the heel describes a distinct, lingually concave curve (revised from Battail 2005).

Comments: This is the latest traversodontid from Gondwana and quite likely the world. The absence of the nuchal table from a specimen recently described by Battail (2005) represents a remarkable difference in relation to the only previously known cranium of this taxon (Gow and Hancox 1993). This has been interpreted as being related to sexual dimorphism (Battail 2005).

Family Traversodontidae *incertae sedis*

?*Traversodon major* von Huene 1936

Material: GPIT unnumbered.

Stratum: *Dinodontosaurus* Assemblage Zone, Santa Maria Formation.

Locality: Sanga north of house of Theotônio Béles Xavier and Sanga ‘of the tree on the road’, Chiniquá, Rio Grande do Sul, Brazil.

Comments: Six specimens coming from two different “sangas” in the locality of Chiniquá were included in this taxon, including a fragmentary mandibular symphysis, a partial maxilla with empty alveoli and postcranial remains. Von Huene (1936) distinguished this taxon from *Traversodon stahleckeri* primarily based on the larger size of the remains. The maxillary fragment was later transferred to *Exaeretodon major* (Barberena 1974), a conclusion cautiously supported by Abdala et al. (2002, pp. 320–321). We believe that there is no clear diagnostic character that allows a definitive inclusion of this maxilla in *Exaeretodon* and prefer to consider these remains, as well as the other five specimens described by von Huene (1936), as *incertae sedis* and *Exaeretodon major* as a *nomen dubium*.

Theropsodon njalilus von Huene 1950

Holotype: GPIT/RE/7162, a complete but poorly preserved skull with lower jaws in occlusion.

Stratum typicum: Lifua Member of the Manda Beds.

Locus typicus: Ruhuhu Valley, Tanzania.

Age: Late Anisian/Early Ladinian, Middle Triassic.

Distribution: Known only from the holotype.

Comments: This specimen cannot be allocated to a particular traversodontid taxon because the postcanines are not readily available, and it is considered a *nomen dubium* (Hopson and Kitching 1972).

Colbertosaurus muralis (Minoprio, 1954)

Synonym: *Colbertia muralis* Minoprio, 1954

Holotype: Cast of partial pair of lower jaws, AMNH FARB 7610.

Stratum typicum: Potrerillos Formation.

Locus typicus: Obligación Quarry, Cubhilla de las Vacas, 20 km to the west of the city of Mendoza, Argentina.

Age: Middle Triassic.

Distribution: Known only from the holotype.

Comments: The holotype and only specimen of *Colbertosaurus muralis* includes only incomplete lower jaws with a few broken teeth (Minoprio 1954, 1957). Not enough diagnostic information can be found at the genus level, and the name should be considered as a *nomen dubium* (Hopson and Kitching 1972).

Unnamed traversodontid

Material: GSN OM-5.

Stratum: Upper Omingonde Formation.

Locus: Farm Omingonde 96, Etjo Mountain, Namibia.

Age: Ladinian, Middle Triassic.

Comments: This taxon is based on a medium-sized specimen recently described by Abdala and Smith (2009), presenting as the most remarkable feature a long and thin basicranial girder and long sagittal crest. The specimen shows occluding jaws, but the internal view of the postcanines allows the specimen to be recognized as a traversodontid.

Taxa of Uncertain Taxonomic Position

Genus *Microscalenodon* Hahn, Lepage, and Wouters, 1988

Species *Microscalenodon nanus* Hahn, Lepage, and Wouters, 1988

Holotype: IRSNB R405, an upper postcanine.

Stratum typicum: Bonebed Habay-le-Vieille-2, Sables de Mortinsart Formation.

Locus typicus: Habay-le-Vieille, Gaume, Belgium.

Referred material: IRSNB R406, a lower postcanine.

Age: Rhaetian, Late Triassic.

Genus *Maubeugia* Godefroit and Battail, 1997

Species *Maubeugia lotharingica* Godefroit and Battail, 1997

Holotype: IRSNB R172, a left upper postcanine, with its root nearly completely preserved.

Stratum typicum: “Rhaetian” sandstone.

Locus typicus: Quarry at Rosières-aux-Salines, Saint-Nicolas-de-Port (Meurthe-et-Moselle), France.

Age: Late Norian-Early Rhaetian, Late Triassic.

Genus *Rosieria* Godefroit and Battail, 1997

Species *Rosieria delsatei* Godefroit and Battail, 1997

Holotype: IRSNB R173, an upper left postcanine.

Stratum typicum: “Rhaetian” sandstone

Locus typicus: Quarry at Rosières-aux-Salines, Saint-Nicolas-de-Port (Meurthe-et-Moselle), France.

Age: Late Norian-Early Rhaetian, Late Triassic

Comments: A further possible specimen has also been identified, IRSNB R174.

Genus *Habayia* Godefroit, 1999

Species *Habayia halbardieri* Godefroit, 1999

Holotype: IRSNB R203, a right upper postcanine teeth.

Stratum typicum: Bonebed Habay-le-Vieille-3, Grès de Mortinsart.

Locus typicus: Habay-la-Vieille, southern Belgium, side of the speedway E25–E411.

Age: Rhaetian, Late Triassic.

Comments: The four taxa mentioned above are represented by tiny isolated teeth (1 mm or less). Although they resemble traversodontid postcanines in being labiolingually expanded, they also show a morphology that departs quite considerably from indisputable traversodontid teeth. Godefroit and Battail (1997, p. 604), who described two of these species, recognized the possibility that the taxonomy of these forms might be reevaluated with more complete material. In addition, Hopson and Sues (2006, p. 125) were not convinced that these Upper Triassic European teeth represent traversodontids. We are uncertain whether these forms belong in Traversodontidae, as they represent the only Rhaetian evidence of labiolingually expanded tooth forms (not considering the clearly different morphology of tritylodontids and haramyids). Therefore, we leave these four species in limbo until more material can help in reassessing their taxonomy.

Non-traversodontid Taxa

Species *Scalenodon boreus* Tatarinov, 1973

Holotype: PIN 2973/1, left upper postcanine tooth.

Stratum typicum: Donguz Formation.

Locus typicus: Southern Cisuralia, Orenburg Province, Karagachka, Russia.

Referred material: PIN 2973/2, isolated upper postcanine from the same site.

Age: Anisian-Ladinian, Middle Triassic.

Distribution: Only known from the type locality.

Comments: This taxon is based on two ovoid postcanines with morphology reminiscent of the circular teeth of *Neotrirachodon expectatus*, also from the Donguz Formation. The latter was considered a trirachodontid by Tatarinov (2002), but it is in fact a bauriid therocephalian (Abdala and Smith 2009). Therefore we believe that the tooth of *Scalenodon boreus* is also more likely a bauriid, as concluded by Sues and Hopson (2010).

Distribution

Currently, 22 species and 17 genera of traversodontids are considered valid. The distribution of these animals is uneven in space and time (Table 15.1; Fig. 15.4): 11 species in

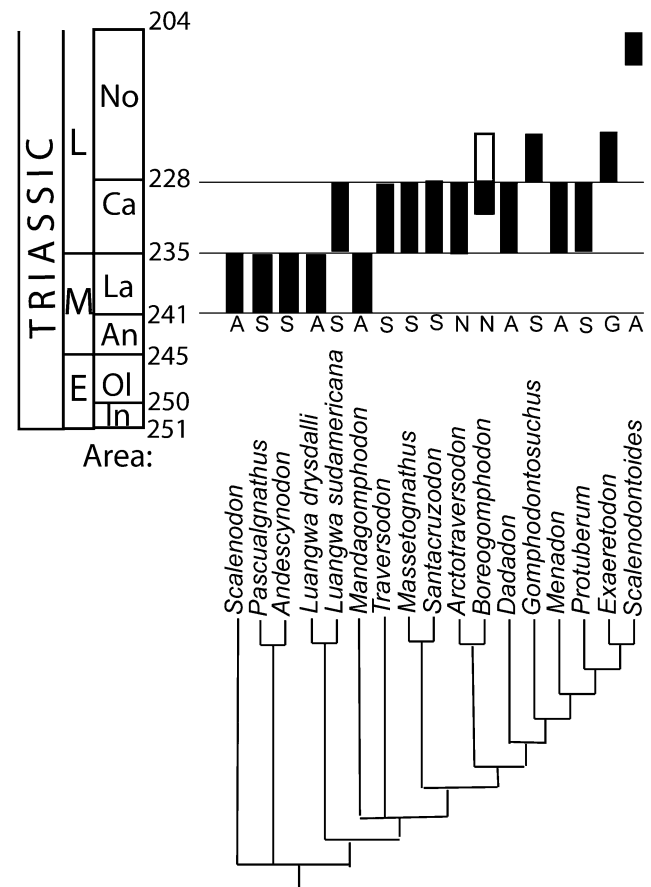


Fig. 15.4 A simplified cladogram from Fig. 15.1 (excluding *Nanogomphodon wildi*) to indicate temporal and spatial distribution of the traversodontid taxa included in the analysis. Time-scale based on Walker and Geissman (2009). The blank box means uncertain time range. An Anisian, La Ladinian, Ca Carnian, In Induan, No Norian, Ol Olenekian. A Africa, E Eurasia, G Gondwana, M Madagascar, N North America, S South America

South America, seven in Africa (including Madagascar), three in North America, and one each in Eurasia and India. Therefore, this diverse group of non-mammaliaform cynodonts is clearly predominantly Gondwanic (with 19 species), with only four species found in Laurasia.

The older traversodontids are known from Anisian/Ladinian localities in Africa and South America and their sudden emergence produced a diversity peak around the end of the Anisian (Abdala and Ribeiro 2010). This group remains well-represented in the Carnian of Gondwana. The oldest record in Laurasia is Ladinian and is restricted to an isolated tooth, reflecting a poor record of this group in comparison with contemporaneous deposits from Gondwana. Small isolated teeth from Norian-Rhaetian deposits of Europe described as traversodontids are not considered here, as we believe that additional material is necessary before these taxa can be included unquestionably in the group (see taxonomic section above). The only, rather small, radiation of Laurasian

traversodontids occurred in the Late Triassic of North America, with one ?Late Ladinian-Early Carnian or Early-Middle Carnian species (Sues and Olsen 1990), one from the Late Carnian (Rayfield et al. 2005), and one from the Late Carnian or Early Norian (Peyer et al. 2008).

A general pattern of size increase in traversodontids from the Middle to the Upper Triassic is recognized (e.g., Battail 2001), with the largest forms being known from the Norian. This trend is clearer in South America, with a variation of skull length from 10 cm in Anisian/Ladinian forms to 45 cm in the Norian (these being the largest traversodontids known). In Africa, some Anisian/Ladinian traversodontids have a skull length of at least 20 cm (Abdala and Smith 2009), larger than that of the Carnian *Menadon* (skull length approximately 16 cm; Flynn et al. 2000), but smaller than the Norian *Scalenodontoides* (skull length 28 cm; Battail 2005) (and some partial remains clearly indicate even larger size in *Scalenodontoides*). It is more difficult to follow this trend in Laurasia because of the restricted record, but it is clear that traversodontids also attained large size at the end of the Carnian, at least in North America (e.g., *Arctotraversodon*).

Every monophyletic group must have a center of origin, or ancestral area (Bremer 1992). The hypothesis in vicariance biogeography that ancestral distribution was identical to the present distribution loses value for a cosmopolitan group. For example, the distribution of the common ancestor of all modern humans is considered to have been restricted to Africa rather than cosmopolitan. For a widespread species, dispersal out of the ancestral area must have occurred after speciation. Some methods have been proposed to find the ancestral area, such as the Progression Rule (Hennig 1966) and Ancestral Area Analysis (Bremer 1992). The Progression Rule assumes that basal members of a monophyletic group will be found near that center of the ancestral area. This method has been criticized, especially because of the bias caused by missing basal taxa in the fossil record (Humphries 1992; Ebach 1999). However, this is not a flaw but rather shows the importance of basal taxa; we can only build our hypothesis on current data, regardless of whether it will be falsified by future discoveries. The distribution of early, basal taxa on a phylogenetic tree is a good indicator of ancestral area. The basal placement of *Scalenodon angustifrons* from Africa suggests that traversodontids originated in Africa. However, considering the weak support of the basal nodes in our phylogeny, this hypothesis requires of additional corroboration. In any case, the origin of traversodontids is indeed circumscribed to Gondwana based on current phylogenetic results. This analysis includes almost all known species of Gomphodontia and the current phylogenetic results strongly indicate that gomphodont cynodonts originated in Africa.

In our results, *Nanogomphodon* does not group with the other two Laurasian taxa *Boreogomphodon* and *Arctotraversodon*, suggesting that traversodontids migrated at least twice from Gondwana to Laurasia. This, however should be considered with extreme caution, as *Nanogomphodon* represents a wildcard in our phylogeny. During the Triassic, major continents were connected as the Pangaeian supercontinent. Based on the faunal assemblages of the Early Triassic, early Middle Triassic, and Early Jurassic, dispersal across the Pangaeian land mass must have been possible for tetrapods during the Triassic. However, only three Early to Middle Triassic genera of Gomphodontia (*Sinognathus*, *Beishanodon*, and *Nanogomphodon*) are known in Eurasia. The poor representation of gomphodonts and traversodontids in particular in the Late Triassic of Eurasia could be the result of bias in preservation and study, e.g., up to now only one possible Late Triassic terrestrial tetrapod has been reported from China (Liu et al. 2001). We hope that further discoveries in this region will improve our understanding of gomphodont evolution in the northern hemisphere.

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Appendix 15.1: List of Morphological Characters

The following abbreviations are used to identify authors that previously used a particular character in data matrices: R, (Rowe 1988); M, (Martínez et al. 1996); F, (Flynn et al. 2000); H, (Hopson and Kitching 2001); A, (Abdala and Ribeiro 2003); Ab, (Abdala et al. 2006); SH, (Sidor and Hancox 2006); K, (Kammerer et al. 2008); S, (Sues and Hopson 2010); L, (Liu and Olsen 2010).

1. Adult maximum skull size: large (greater than 25 cm) (0), medium to small (1).
2. Snout (preorbit) in adults in relation to temporal region: longer (0), subequal (1), shorter (2) [Ab28].
3. Two side of temporal fenestra: divergent posteriorly (0), nearly parallel (1), bulge in the middle (2) [H39, Ab33].
4. Premaxilla forms posterior border incisive foramen: absent (0), present (1) [H1, Ab29].
5. Vomer exposure in incisive foramen (at anterior ends of maxillae on palate): present (0), absent (1) [M21].
6. Vomer: with (0) or without (1) vertical septum extending posteriorly beyond level of secondary palate [SH65].
7. Internarial bar: present (0), absent (1) [F5, A22, Ab21].
8. Parietal foramen in adults: present (0), absent (1) [H7, F6, A24, Ab23].
9. Ectopterygoid: present (0), absent (1) [H9, Ab30].
10. The posterior extension of secondary palate relative to anterior border of orbit: shorter (0), subequal (1), longer (2) [H15, S2].
11. Posterior extension of the jugal dorsally above the squamosal in the zygomatic arch: absent or with a small extension (0), well-developed (1) [F15, A26, Ab25].
12. The position of anterior root of the zygomatic arch relative to the ventral margin of the maxilla: nearly at same level or slightly higher (0), remarkable higher (1).
13. Zygomatic process of the jugal: little projected (0), conspicuously projected (1), absent (2), a ball-like process (3) [F16, H21, A25, Ab24].
14. Diameter of suborbital bar below center of orbit (anterior to suborbital process, where present): greater than 1/2 diameter of bar below posterior part of orbit (posterior to suborbital process) (0), less than 1/2 diameter of bar below posterior part of orbit (1) [S35].
15. Maxilla in the margin of the subtemporal fenestra: excluded (0), included (1) [Ab31].
16. Epipterygoid-quadrate contact: present (0), absent (1) [Ab32].
17. Frontal-epipterygoid contact: present (0), absent (1) [R39, H35].
18. Palatine: does not meet frontal (0), meets frontal but neither element contributes significantly to medial orbit wall (1) [H23].
19. Notch separating lambdoidal crest from zygomatic arch: shallow (0); deep, V-shaped (1) [H43].
20. Lower jaw symphysis as a chin-like process in adult: absent or little developed (0), well developed (1).
21. Dentary with sigmoid ventral curvature: absent (0), present (1) [S34].
22. Dentary angular process: not or very weakly projected posteriorly (0), projected posteriorly as distinct process (1) [A28, Ab27, S32].
23. Elongated mental foramen below postcanine tooth row and above coronoid ridge: absent (0), present (1) [S29].
24. Coronoid ridge anterior to masseteric fossa: absent to low (0), very strong, outturned (1) [S30].
25. Position of the upper canine in relation to paracanine fossa: posterolateral (0), lateral (1), anterolateral (2) [A6, Ab5, S1].
26. Diastema between upper incisors and canine: present (0), absent (1) [A3, Ab2].
27. Diastema between canine and maxillary postcanines in adult: short (0), long (1) [F1].
28. Diastema between canine and dentary postcanines: long (0), absent or very short (less than one tooth length) (1).
29. Maxillary labial platform lateral to the postcanine series: absent (0), present (1) [H77, A23, Ab22].
30. Posteromedial inclination of the last few upper gomphodont postcanines: absent or small (0), oblique (1) [F9, H72, A9, Ab8].
31. Axis of posterior part of maxillary tooth row: directed lateral to subtemporal fossa (0), directed towards center of fossa (1), directed toward medial rim of fossa (2) [H78, Ab36].
32. Maxillary tooth row extent relative to anterior margin of the subtemporal fossa in adult: anterior (0), at the same level (1), posterior (2).
33. Coronoid process of the mandible: covers the last postcanine (0), does not cover (1) [A27, Ab26].
34. Postcanine occlusion: absent (0), present (1) [Ab41].
35. Shearing planes between the outer surface of the main cusp of the lower and the inner surfaces of the main cusps of the uppers postcanines: present (0), absent (1) [Ab42].
36. Upper incisor number: four (0), three (1) [H53, F4, A1, Ab0].
37. Lower incisor number: three (0), two (1) [H54].
38. Incisor procumbency: (0) absent; (1) present [K43].
39. Incisor cutting margins: serrated (0), smoothly ridged (1), denticulated (2) [H55, Ab34].
40. Incisor size: small (0), enlarged (1) [F3, H56, A2, Ab1].
41. Upper canine size: large (0), reduced in size (1) [H57, A4, Ab3].
42. Lower canine size: large (0), reduced in size (1) [H58, A5, Ab4].
43. Canine serrations: present (0), absent (1) [H59, Ab35].
44. Postcanine tooth row in adults: formed by sectorial (0), conical, gomphodont and sectorial (1), gomphodont and sectorial (2), gomphodont (3) [H80, Ab37].
45. Overall morphology of the upper gomphodont postcanines in occlusive view: ovoid-ellipsoid (0), nearly rectangular (1), nearly triangular (2) [A7, Ab6].
46. Labial cingulum on anterior portion of the upper postcanines (external to the sectorial ridge): absent (0), present (1) [H61, A14, Ab13].
47. Posterior cingulum on upper postcanines: present (0), absent (1) [F7, A13, Ab12].

48. Shouldering in the posterior margin of upper postcanines: absent (0), slightly developed (1), well developed (2). [F2, A8, Ab7]
49. Anterior profile of principal labial cusp: convex (0), concave (1) [S31].
50. Number of cusps in the transverse crest of the upper postcanines: two (0), three or more (1) [F8, H63, A11, Ab10].
51. Central cusp of upper transverse row: midway between labial and lingual cusps (0), closer to lingual cusp (1) [H65, A12, Ab11].
52. Anterolabial accessory cusp on upper postcanines: one (0), absent (1), two or more (2) [H67].
53. Posterolabial accessory cusp on upper postcanines: present (0), absent (1) [H68].
54. Position of upper transverse cusp row on crown: central (0), anterior half of crown (1), at posterior part (2) [H64, A10, Ab9].
55. Distinct anterolingual accessory cusp on upper postcanines: absent (0), present (1) [H69, A15, Ab14].
56. Anterior cingulum in the upper postcanines: present (0), absent (1) [Ab39].
57. Anterior transverse crest on upper postcanines: absent or low (0), high (1) [F14, H70].
58. Lingual ridge on upper postcanines: absent (0), present (1) [F10, H71].
59. Overall morphology of the lower gomphodont postcanines in occlusal view: circular (0), ovoid-ellipsoid (1), quadrangular (2) [H62, A17, Ab16].
60. Transverse crest in lower postcanines: central (0), anterior (1) [A18, Ab17].
61. Number of cusps in the transverse crest of the lower postcanines: two (0), three or more (1) [H73, A19, Ab18].
62. Anterior cingulum in the lower postcanines: cuspules disposed on the entire margin (0), one or more cuspules located anterolabially (1), absent (2) [H74, A21, Ab20].
63. Posterior cingulum on the lower gomphodont postcanines: present (0), absent (1) [Ab38].
64. Size of the anterior cusps in the lower postcanines: labial lower than lingual (0), labial higher than lingual (1) [A20, Ab19].
65. Widest lower cusp in transverse row of lower postcanines: lingual (0), labial (1), middle (2) [F11, H76].
66. Anterolingual cusp of lower postcanines: nearly vertical (0); strongly inclined posteriorly (1).
67. Deep occlusal basins in the postcanines: absent (0), present (1) [H75, Ab40].
68. Anapophysis: absent (0), present (1) [L124].
69. Expanded costal plates on ribs: present (0), absent (1) [H82].
70. Lumbar costal plates with ridge overlapping preceding rib: present (0), absent (1) [H83].
71. Procoracoid in glenoid: present (0), barely present or absent (1) [H88].
72. The dorsal margin of the coracoid in medial view in relation to that of the procoracoid: shorter (0), equal or longer than (1).
73. Cranial margin of the procoracoid: convex (0), nearly straight (1), obviously concave (2).
74. Angle between ventral margin on anterior and posterior process of iliac blade: small (e.g., less than 140°) (0), large (1).
75. Length of anterior process of ilium anterior to acetabulum (relative to diameter of acetabulum): less than 1.5 (0), greater than 1.5 (1) [H94].
76. Dorsal profile of ilium: strongly convex (0), flat to concave (1) [H96].
77. The trochanter major position relative to the femoral head: distal (0), close, major part in same height (1).

Appendix 15.2: Character Matrix

<i>Thrinaxodon</i>	1020000000	0020010000	000000000?	0000?00010	0010??00?	-??-??????	??????101	0000000
<i>Cynognathus</i>	0000000000	0000001000	000000010?	0000?00000	0000??00?	-??-??????	??????000	0000000
<i>Diademodon</i>	0000000000	00100001010	0000000000	00(01)1000000	0001000000	-000?00000	000??0100	0001000
<i>Beishanodon</i>	0210?00101	002000??1?	????000?10	10??0?0??	0??00000?	?00?0000??	?????0???	???????
<i>Cricodon</i>	1?0?0?0???	0?0?0?0???	000000?010	1011100001	0002000001	1000?00010	100??0100	?????0?
<i>Langbergia</i>	1110100001	001000?010	0000000000	1011100010	0002000001	0000?00010	100??0???	???????
<i>Sinognathus</i>	121?1?101	00200?0?10	0000000010	1011101010	00?2000001	0110?00010	100??0???	???????
<i>Trirachodon</i>	1110100(01)01	00100001010	0000000010	10(01)1100000	0002000001	(01)11(02)?00010	100??0100	000000?
JSM100	1?0?00??1	?0?0?0???	0000?0000	?0?1??0?	0012100001	1110?00020	100??0???	???????
<i>Andescynodon</i>	11001101?	00000?0?10	0000000010	2101000010	0003101000	-101?11021	011101110?	?111111
<i>Arctotraversodon</i>	0?0?0?0???	????0?0?1	0?11?0?0?	????10?021	????01011	0?120?0?21	1212001???	???????
<i>B. jeffersoni</i>	112?101?2	002001?0?10	0111000010	2111000010	001220(01)111	1(02)12010121	(01)111(01)0101?	112???
<i>Dadodon</i>	11101?01?	?0300?0?1?	????110?11	21?100?010	0?131111111	10120101??	??????1???	???????
<i>E. argentinus</i>	000111111	11111?110	1100211011	2201010111	011310121?	-00-111121	021111101?	?111111
<i>E. riograndensis</i>	000111111	11111?110	1100211?11	22?1010111	011310121?	-00-111121	021111101?	????11?
<i>Gomphodontosuchus</i>	??0?1?0?0?	?1?0?0?0?	1?00110011	2001000?10	111310111?	-?-011121	02111?1???	???????
<i>L. drysdalli</i>	101??00??	00110?0?10	1100000111	2101000000	0003010011	1(02)12000121	0101001101	0001110
<i>L. sudamericana</i>	1?0?0?0?1	?001?0?0?1	1100000111	2101000000	0003010011	1002000121	01010?1???	???????
<i>M. ochagaviae</i>	1211110112	002001?01?	?000110011	2(12)010000?0	0013101111	12120?0121	02?1101?1	???????
<i>M. pascuali</i>	1111110111	0020010010	000011001(01)	2(12)01000020	1113101111	1212000121	020010100?	1111111
<i>Menadon</i>	10111?0?0?	11210?0?10	1100111011	2001000011	110310111?	-01-011121	021??0101?	?0111?
<i>Pascualgnathus</i>	110011?1?	00000?0?10	0000000010	2101010010	0013000000	-101?11021	0?0??01101	00?0011
<i>Protuberum</i>	101?111011	111111?0?1?	????211?11	22?101?111	1?131?1110	-0121111??	??????110?	???????
<i>Santacruzodon</i>	1?0?0?0?0?	?03?0?0?0?	1100000011	2101000020	?113201111	1212000121	0201011???	???????
<i>S. angustifrons</i>	110?0?00??	?0200?0?10	?000000010	2001000000	0003011011	111(02)010021	0100001???	?000?0?
<i>S. attridgei</i>	?00110?1?	????0?0?0?	????000?11	21?101?010	0?13100011	10121011??	??????1???	???????
<i>S. hirschoni</i>	1?0110?11	?0?001?1?0	0?00000011	2101011011	1013100011	1012100121	0100001???	???????
<i>Scalenodontoides</i>	012??0?11?	11?11?0?11	?10021101?	2201010111	?1?310121?	-00-?11121	0211111???	???????
<i>Traversodon</i>	1?0?1?00?1	?1110?0?0?1	1100000011	2101000010	0013110011	1?02000121	02?0?01?01	11??0?1
<i>Nanogomphodon</i>	????0?0?0?	????0?0?0?	????0?0?0?	?1?10?0?0?	????0?0?0?	????0?0?0?	1101101???	???????

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