

## Chapter 11

# The Late Triassic Record of Cynodonts: Time of Innovations in the Mammalian Lineage

Fernando Abdala and Leandro C. Gaetano

**Abstract** The Triassic period witnessed a great diversification of lineages, recovering from one of the worst extinction events known in Earth's history. Therapsids, the lineage that includes mammals as the only living members, enjoyed remarkable success during the Triassic. This clade includes the Late Permian to Early Cretaceous non-mammaliaform cynodonts, represented by a paraphyletic array of taxa successively more closely related to mammaliaforms (considered as basal mammals by several palaeontologists). In the Middle Triassic, cynodonts are represented by numerous taxa that thrived mostly in Gondwana, whereas only one taxon, *Nanogomphodon*, has been registered in Laurasia. Cynodont diversity during this time interval is mainly composed of gomphodonts, featuring bucco-lingually expanded postcanines, whereas the members of their sister-group, the mostly sectorial-toothed probainognathians, are very scarce. On the contrary, Early Jurassic non-mammaliaform cynodonts are most abundant in Laurasia (although also present in Gondwana) and only represented by probainognathians, particularly the sectorial-toothed tritheledontids and the ubiquitous herbivorous tritylodontids. The Late Triassic thus constitutes a pivotal time lapse, marked by an expansion of the geographical distribution and diversification of cynodonts. During this time, cynodont assemblages include representatives of old and new lineages and the first mammaliaforms are documented. This contribution presents a review of the diversity and geographic distribution of Late Triassic to Early Jurassic cynodonts, and summarizes the main morphologies represented in the lineage, including Mammaliaformes, a key group in our understanding of the early evolution of mammals.

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## 11.1 Introduction

Several changes took place in the ancient world of the early Mesozoic, transforming the climate and, with that, the faunal composition of the ecosystems. The Triassic for a start was a time of key changes in faunas (Sues and Fraser 2010) after the colossal extinction event at the end of the Permian that wiped out a massive proportion of the life forms from the Earth (Erwin 1994; Joachimski et al. 2012). For the tetrapod communities, the end of the Permian represented the demise of two main therapsid lineages, biarmosuchians and gorgonopsians, and the extreme decline of therocephalians and dicynodonts, the latter being indeed one of the most diverse and abundant Permian lineages (Rubidge and Sidor 2001; Kemp 2005; Fröbisch 2008). The extinction process also affected the large herbivorous pareiasaurian parareptiles that were key components of Middle and Late Permian faunas. The Triassic witnessed the diversification of cynodonts, a second pulse of diversification of dicynodonts, the continuity and last days of therocephalians, and the diversification of the small procolophonian parareptiles (Kemp 2005; Fröbisch 2008; Abdala and Ribeiro 2010; Huttenlocker and Sidor 2016; Cisneros 2008). Indeed, the Triassic was an important time for amniote evolution, as exemplified by the origin of dinosaurs and of turtles (Rougier et al. 1995; Li et al. 2008; Barrett et al. 2009; Langer et al. 2010; Schoch and Sues 2015; Marsicano et al. 2016).

The Triassic is also the major period during which the evolutionary development of essential mammalian features in the non-mammalian cynodonts, extinct predecessors of living mammals, took place. These characters include differentiation of postcanine morphology, two occipital condyles for articulation with the vertebral column, development of an osseous secondary palate, mandibular masseteric fossa, and basicranial promontorium, among others (Kielan-Jaworowska et al. 2004; Kemp 2005). Here we present an account of cynodont diversification at the end of the Triassic and the last pulse of the non-mammaliaform cynodonts, which produced important morphological novelties. This diversification is represented by the radiation of the herbivorous traversodontid cynodonts, the origin of small-sized insectivorous-carnivorous forms with sectorial postcanines, and the evolution of one of the first rodent-like experiments in the synapsid lineage.

Institutional abbreviations: BP, Evolutionary Studies Institute (formerly Bernard Price Institute for Palaeontological Research), University of the Witwatersrand, Johannesburg, South Africa; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, United States; NHMUK, The Natural History Museum, London, United Kingdom; PVL, Colección Paleontología de Vertebrados Lillo, Universidad Nacional de Tucumán, Argentina; USNM, National Museum of Natural History, Smithsonian Institution, Washington DC, United States.

## 11.2 Cynodont Diversity

Cynodontia is the last therapsid lineage to appear in the fossil record. Two species are known from the early Late Permian *Tropidostoma* Assemblage Zone (AZ) and at least five species are represented in faunal associations closer to the end of the Permian in South Africa (Botha et al. 2007; Botha-Brink and Abdala 2008; Kammerer 2016). By the beginning of the Triassic the number of species remained nearly the same, however, there are no common species between the Permian and Triassic (Abdala and Ribeiro 2010). The Middle Triassic records perhaps the highest peak in diversity in the history of Triassic cynodonts. This epoch, represented in South Africa by the *Cynognathus* AZ (here we consider this AZ as Middle Triassic, but see Ottone et al. 2014 who supports a Carnian age for *Cynognathus* AZ correlated faunas from Argentina), is when Triassic cynodonts reached their largest body sizes and experimented with profound transformations in their dentition, with forms bearing occluding bucco-lingually expanded (gomphodont) postcanines (Abdala and Ribeiro 2010). These two novelties among basal cynodonts (large size and expanded occluding postcanines) are suggestive of a change in the food resources represented in the Middle Triassic terrestrial ecosystems.

Presently, there are ~150 cynodont genera recognized in the fossil record from the Late Permian to the Early Jurassic, 75 of which (50% of the total) are represented in the 36 million year (Ma) extent of the Late Triassic and 42 (28%) in the 27.2 Ma span of the Early Jurassic (Table 11.1). In the Late Triassic-Early Jurassic transition, eucynodonts are represented by traversodontids, members of the monophyletic Cynognathia, and by several taxa of the clade Probainognathia, including prozostroodontids, tritheledontids, tritylodontids, and mammaliaforms (Fig. 11.1).

### 11.2.1 Traversodontid Supremacy

It is mainly among gomphodonts that non-mammaliaform cynodonts explored the development of bucco-lingually expanded postcanine crowns, which allowed for an elementary dental occlusion. The first record of gomphodonts is from the end of the Olenekian. Basal gomphodonts, represented by diademodontids and trirachodontids, had expanded postcanines lacking an occlusal basin. Diademodontids, in particular, presented an extremely heterogeneous postcanine series with simple anteriormost teeth, expanded mid-row elements, and sectorial posterior teeth (Hopson 1971; Grine 1977). These two families are mostly represented at the end of the Early Triassic and in the Middle Triassic, although there is an unusually late record of a form tentatively identified as a diademodontid and originally attributed to levels of the Late Triassic Lower Elliot Formation (Abdala et al. 2007). The horizon of this record was recently reassigned to the Lower Jurassic Upper Elliot Formation (Bordy et al. 2017). Besides diademodontids and trirachodontids, a derived gomphodont clade named Traversodontidae (*sensu* Liu and Abdala 2014) was well represented in

**Table 11.1** Late Triassic-Early Jurassic cynodont taxa

	Genus	Lineage	Country
Carnian (9 Ma) 237–228 My			
1	<i>Titanogomphodon</i>	Diademodontidae	Namibia
2	<i>Aleodon cromptoni</i>	Probainognathia	Namibia, Brazil
3	<i>Massetognathus pascuali</i>	Traversodontidae	Argentina
4	<i>Chiniquodon thetonicus</i>	Probainognathia	Argentina, Brazil
5	<i>Chiniquodon kalanoro</i>	Probainognathia	Madagascar
6	<i>Chiniquodon sp.</i>	Probainognathia	Namibia
7	<i>Probainognathus</i>	Probainognathia	Argentina
8	<i>Exaeretodon argentinus</i>	Traversodontidae	Argentina
9	<i>Ischignathus</i>	Traversodontidae	Argentina
10	<i>Ecteninion</i>	Probainognathia	Argentina
11	<i>Diegocanis</i>	Probainognathia	Argentina
12	<i>Exaeretodon riograndensis</i>	Traversodontidae	Brazil
13	<i>Luangwa sudamericana</i>	Traversodontidae	Brazil
14	<i>Luangwa sp.</i>	Traversodontidae	Namibia
15	<i>Traversodon</i>	Traversodontidae	Brazil
16	<i>Protuberum</i>	Traversodontidae	Brazil
17	<i>Scalenodon ribeiroae</i>	Traversodontidae	Brazil
18	<i>Bonacynodon</i>	Probainognathia	Brazil
19	<i>Protheriodon</i>	Probainognathia	Brazil
20	<i>Charruodon</i>	Probainognathia	Brazil
21	<i>Prozostrodon</i>	Probainognathia	Brazil
22	<i>Therioherpeton</i>	Probainognathia	Brazil
23	<i>Gomphodontosuchus</i>	Traversodontidae	Brazil
24	<i>Santacruzodon</i>	Traversodontidae	Brazil
25	<i>Candelariodon</i>	Probainognathia	Brazil
26	<i>Santacruzognathus</i>	Probainognathia	Brazil
27	<i>Alemoatherium</i>	Probainognathia	Brazil
28	<i>Massetognathus ochagaviae</i>	Traversodontidae	Brazil
29	<i>Deccanodon</i>	?	India
30	<i>Ruberodon</i>	Traversodontidae	India
31	<i>Rewaconodon</i>	Dromatheridae	India, United States
32	<i>Dadadon</i>	Traversodontidae	Madagascar
33	<i>Menadon</i>	Traversodontidae	Madagascar, Brazil
34	<i>Boreogomphodon</i>	Traversodontidae	United States
35	<i>Gondwanadon</i>	Morganucodontidae	India
36	<i>Tikitherium</i>	Docodonta	India
37	<i>Adelobasileus</i>	Stem Mammaliaformes	United States
Norian (14 Ma) 227–213			
38	<i>Chalimnia</i>	Tritheledontidae	Argentina
39	<i>Riograndia</i>	Tritheledontidae	Brazil
40	<i>Brasilodon</i>	Prozostrodontia	Brazil
41	<i>Irajatherium</i>	Tritheledontidae	Brazil

(continued)

**Table 11.1** (continued)

	Genus	Lineage	Country
42	<i>Minicynodon</i>	Prozostrodonia	Brazil
43	<i>Botucaraitherium</i>	Prozostrodonia	Brazil
44	<i>Arctotraversodon</i>	Traversodontidae	Canada
45	<i>Scalenodontoides</i>	Traversodontidae	South Africa, Lesotho
46	<i>Elliotherium</i>	Tritheledontidae	South Africa
47	<i>Microconodon</i>	Dromatheridae	United States
48	<i>Dromatherium</i>	Dromatheridae	United States
49	<i>Thomasia hahni</i>	Haramiyidae	Germany
Late Norian-Rhaetian (19 Ma) 201–220			
50	<i>Microscalenodon</i>	?Traversodontidae	Belgium
51	<i>Meurhodon</i>	Dromatheridae	France
52	<i>Hahnia</i>	Probainognathia	Belgium
53	<i>Gaumia</i>	Probainognathia	Belgium, Luxemburg
54	<i>Lepagia</i>	Probainognathia	Belgium
55	<i>Maubeugia</i>	?Traversodontidae	France
56	<i>Rosieria</i>	?Traversodontidae	France
57	<i>Oligokyphus triserialis</i>	Tritylodontidae	Germany
58	<i>Oligokyphus</i> sp.	Tritylodontidae	Canada
59	<i>Tricuspes</i>	Dromatheridae	Germany, Luxemburg, France and Belgium
60	<i>Mitredon</i>	?	Greenland
61	<i>Pseudotriconodon</i>	Dromatheridae	Luxemburg, Belgium, France, United States
62	<i>Mojo</i>	Multituberculata	Belgium
63	<i>Theroteinus</i>	Haramiyidae	France
64	<i>Brachyostrodon</i>	Morganucodontidae	France
65	<i>Woutersia</i>	Docodonta	France
66	<i>Delsatia</i>	Docodonta	France
67	<i>Megazostrodon chenali</i>	Morganucodontidae	France
68	<i>Paceyodon</i>	Morganucodontidae	France
69	<i>Paikasigudodon</i> cf. <i>yadagirii</i>	Morganucodontidae	France
70	<i>Rosierodon</i>	Morganucodontidae	France
71	<i>Kuehneotherium</i>	Symmetrodonta	France; Luxemburg; United Kingdom; Greenland
72	<i>Fluctuodon</i>	Symmetrodonta	France
73	<i>Thomasia</i>	Haramiyidae	Germany; France; Belgium; Luxemburg; Switzerland; United Kingdom
74	<i>Haramiyavia</i>	Haramiyidae	Greenland
75	<i>Helvetiodon</i>	Morganucodontidae	Switzerland

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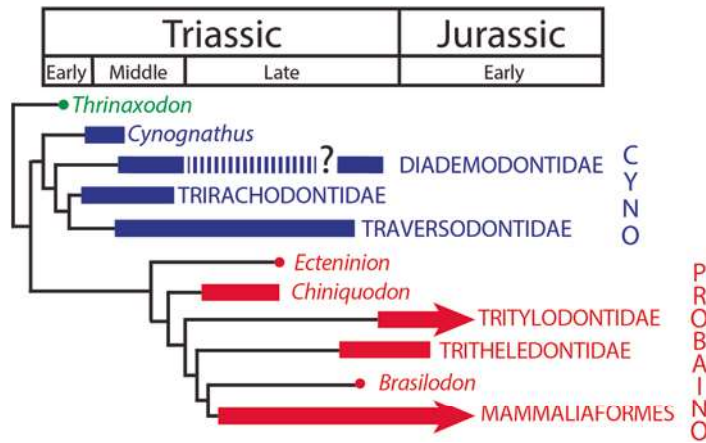
**Table 11.1** (continued)

	Genus	Lineage	Country
76	<i>Morganucodon peyeri</i>	Morganucodontidae	Switzerland, France
77	<i>Hallautherium schalchi</i>	Morganucodontidae	Switzerland; Poland
78	<i>Eozostrodon</i>	Morganucodontidae	United Kingdom
Hettangian-Toarcian (27 Ma) 201–174			
79	<i>Bienotherium magnum</i>	Tritylodontidae	China
80	<i>Bienotherium yunnanense</i>	Tritylodontidae	China
81	<i>Lufengia</i>	Tritylodontidae	China
82	<i>Dianzhongia</i>	Tritylodontidae	China
83	<i>Yunnanodon</i>	Tritylodontidae	China
84	<i>Oligokyphus lufengensis</i>	Tritylodontidae	China
85	<i>Kunminia</i>	?	China
86	<i>Bocatherium</i>	Tritylodontidae	Mexico
87	<i>Tritheledon</i>	Tritheledontidae	South Africa
88	<i>Diarthrognathus</i>	Tritheledontidae	South Africa
89	<i>Tritylodontoideus</i>	Tritylodontidae	South Africa
90	<i>Pachygenelus</i>	Tritheledontidae	South Africa, Canada
91	<i>Tritylodon</i>	Tritylodontidae	South Africa, Lesotho
92	<i>Oligokyphus major</i>	Tritylodontidae	United Kingdom; United States
93	<i>Dinnebitodon</i>	Tritylodontidae	United States
94	<i>Kayentatherium</i>	Tritylodontidae	United States
95	<i>Argentoconodon</i>	Triconodontidae	Argentina
96	<i>Condorodon</i>	Triconodontidae	Argentina
97	<i>Asfaltomylos</i>	Australosphenida	Argentina
98	<i>Henosferus</i>	Australosphenida	Argentina
99	<i>Sinoconodon</i>	Stem Mammaliaformes	China
100	<i>Hadrocodium</i>	basal mammaliaform (more derived than Docodonta but less than Triconodontidae)	China
101	<i>Erythrotherium</i>	Morganucodontidae	Lesotho
102	<i>Bocaconodon</i>	Morganucodontidae	Mexico
103	<i>Victoriaconodon</i>	Triconodontidae	Mexico
104	<i>Huastecconodon</i>	Triconodontidae	Mexico
105	<i>Megazostrodon</i>	Morganucodontidae	South Africa; Lesotho
106	<i>Kuehneotherium</i>	Symmetrodonta	United Kingdom
107	Pantotherid indet	Symmetrodonta	United Kingdom
108	<i>Bridetherium</i>	Morganucodontidae	United Kingdom
109	<i>Paceyodon</i>	Morganucodontidae	United Kingdom
110	<i>Thomasia</i> cf. <i>moorei</i>	Haramiyidae	United Kingdom
111	<i>Dinnetherium</i>	Morganucodontidae	United States
112	<i>Morganucodon</i>	Morganucodontidae	United States, United Kingdom, China

(continued)

**Table 11.1** (continued)

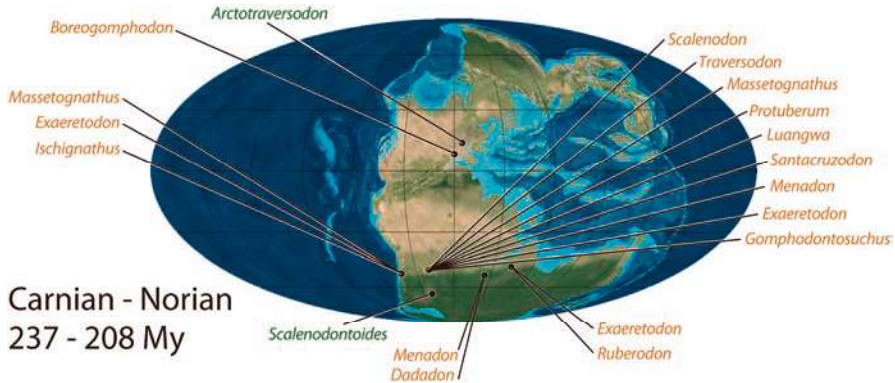
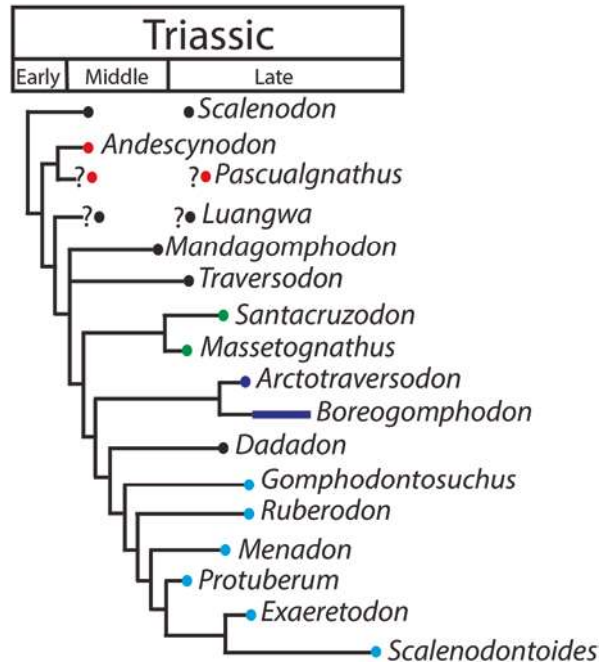
	Genus	Lineage	Country
113	<i>Indozostrodon</i> (Kota Fm.)	Morganucodontidae	India
114	<i>Indotherium</i> (Kota Fm.)	Morganucodontidae	India
115	<i>Dyskritodon</i>	?Triconodontidae	India
116	<i>Paikasigudodon</i> (Kota Fm.)	Morganucodontidae	India
117	<i>Trishulotherium</i> (Kota Fm.)	Symmetrodonta	India
118	<i>Nakunodon</i> (Kota Fm.)	Symmetrodonta	India
119	<i>Kotatherium</i> (Kota Fm.)	Symmetrodonta	India
120	<i>Indobaatar</i> (Kota Fm.)	Multituberculata	India



**Fig. 11.1** Phylogenetic relationships of eucynodonts, plotted against the time scale. Abbreviations: *CYNO* Cynognathia, *PROBAINO* Probainognathia. Phylogeny after Liu and Olsen (2010)

the Middle and Upper Triassic (Fig. 11.2). Twenty-three of the 96 cynodont genera (24%) from the Middle–Late Triassic are traversodontids. This group was already widely distributed through East Africa, South America, and Europe by the Anisian–Ladinian (Kemp 1980; Hopson and Sues 2006; Abdala et al. 2009). Traversodontids are predominantly from Gondwana and a major component of the Late Triassic cynodont faunas from South America (Fig. 11.3). They are dominant in the Carnian fauna of the Chañares Formation in Argentina, represented by *Massetognathus* (Abdala and Giannini 2000; Mancuso et al. 2014). The *Dinodontosaurus* AZ (Santa Maria Formation) in southern Brazil shows a strong faunal correlation with the Chañares Formation. Traversodontids in this Brazilian association are represented by *Massetognathus*, *Traversodon*, *Protuberum*, and the recently discovered *Scalenodon* (Melo et al. 2017), but none of them dominate the faunal assemblage. The Santa Cruz do Sul AZ of the Santa Maria Formation is the only Brazilian fauna in which traversodontids are diverse (including *Santacruzodon*, *Menadon*, and a third as-yet unnamed taxon) and also dominant (Abdala et al. 2001; Melo et al. 2015). The Santa Cruz do Sul fauna correlates biostratigraphically with the fossil

**Fig. 11.2** Phylogenetic relationships of traversodontids plotted against the time scale. Phylogeny after Liu and Abdala (2014) and Ray (2015). Colours indicate monophyletic groups: *light blue*, Gomphodontosuchinae

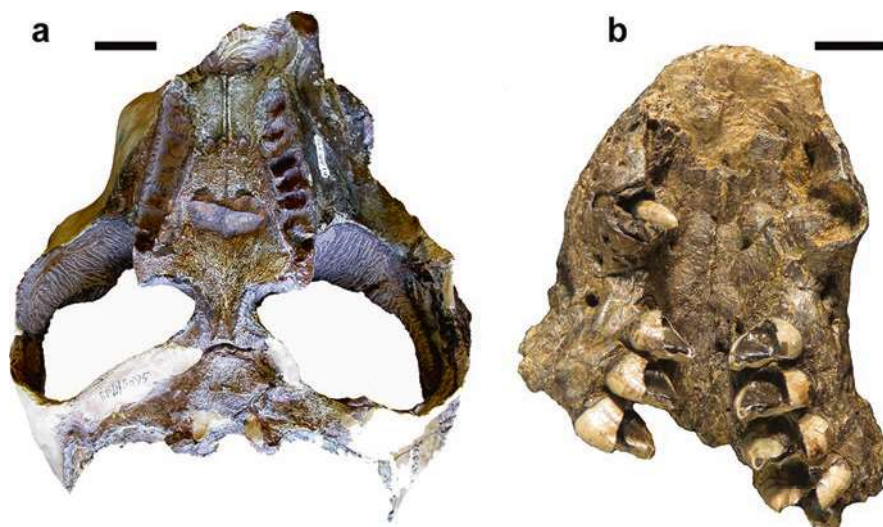


**Fig. 11.3** Paleogeographic reconstruction depicting traversodontid distribution during the Carnian (taxa in red) and Norian (taxa in green). Map modified from Ron Blakey

assemblage of the Makay Formation of Madagascar through the shared occurrence of the traversodontid *Menadon* (Melo et al. 2015). In this latter formation, traversodontids are represented by *Menadon*, only known by a couple of specimens, and *Dadadon*, documented by several specimens representing different ontogenetic stages (Flynn et al. 2000; Kammerer et al. 2012). At the end of the Carnian and the beginning of the Norian, traversodontids are known from the Ischigualasto



Formation through *Exaeretodon* and *Ischignathus* (Bonaparte 1962, 1963). The first is represented by several skeletons whereas only one specimen of the latter has been found. *Exaeretodon* is also well represented in the *Hyperodapedon* AZ from southern Brazil (Abdala et al. 2002; Liparini et al. 2013), along with *Gomphodontosuchus*, which is known only from one specimen (von Huene 1928; Hopson 1985). Detailed prospection in the Ischigualasto Formation makes clear that *Exaeretodon* is outnumbered by rhynchosaurs at the base of this unit and becomes a dominant taxon towards the upper levels (Martinez et al. 2011). A similar condition has been suggested for the distribution and abundance of *Exaeretodon* in different levels of the *Hyperodapedon* AZ in the Santa Maria Formation (Liparini et al. 2013). Traversodontids have also been recorded in Carnian formations in India. Fragments of two *Exaeretodon* specimens of estimated skull length of 200 mm were found in the Maleri Formation (Chatterjee 1982) and, more recently, at least seven lower jaws of the traversodontid *Ruberodon* were described from the Tiki Formation (Ray 2015). The youngest record of traversodontid from Gondwana is represented by the large and bizarre *Scalenodontoides* (Fig. 11.4a) from the Norian Lower Elliot Formation of South Africa (Crompton and Ellenberger 1957; Gow and Hancox 1993; Battail 2005) and by a small fragmentary specimen only preliminary reported (Ribeiro et al. 2011; Martinelli and Soares 2016) from the ?late Norian- ?Early Jurassic *Riograndia* AZ of Brazil (Abdala and Ribeiro 2010; Barboni and Dutra 2013; Rohn et al. 2014).



**Fig. 11.4** Traversodontidae. (a) *Scalenodontoides macrodontes* (BP/1/5395), Lower Elliot Formation, Karoo Basin, South Africa, palatal view of the skull. Scale bar = 40 mm. (b) *Boreogomphodon jeffersoni* (USNM 437636), Vinita Formation, Virginia, United States, palatal view of the snout. Scale bar = 5 mm. These species nearly represent the total range of size in traversodontid cynodonts. Photography of *Boreogomphodon* by Christophe Hendrickx, copyright Smithsonian Institution

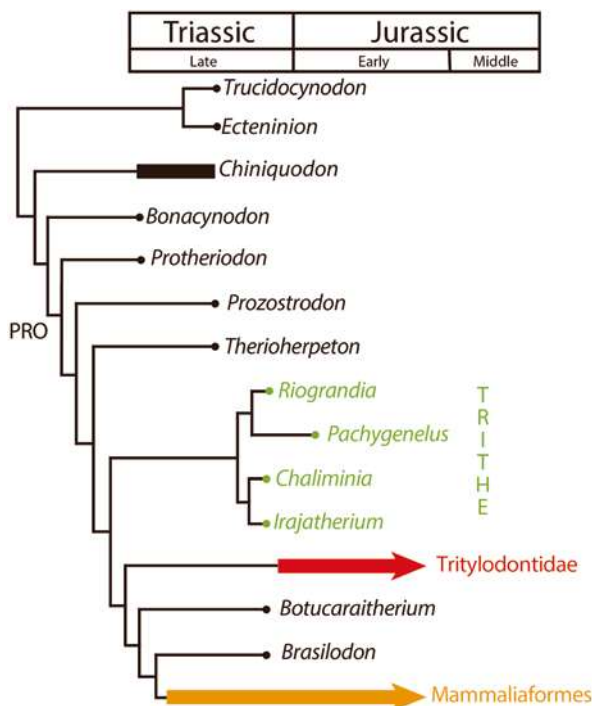
The known history of traversodontids is less extensive in Laurasia. They are restricted to the east side of North America and to only one undisputed record in Europe. Of the four species registered in Laurasia, only the small-sized *Boreogomphodon* from the Carnian Vinita Formation in Virginia, United States, is represented by numerous specimens (Sues and Hopson 2010; Fig. 11.4b). Specimens recovered from the Carnian Pekin Formation and the type and only specimen of *Plinthogomphodon* from the Norian (Sues et al. 1999), both from North Carolina, United States, were also tentatively assigned to *Boreogomphodon* by Liu and Sues (2010). In Europe there is one confirmed record of *Nanogomphodon* represented by an isolated lower tooth from the Ladinian of Germany (Hopson and Sues 2006). Four species from the Norian and Rhaetian of France and Belgium represented by tiny expanded isolated crowns have been assigned to traversodontids (Hahn et al. 1988; Godefroit and Battail 1997; Godefroit 1999); however, their attribution to this group has been questioned and needs stronger validating evidence (Hopson and Sues 2006; Liu and Abdala 2014).

In summary, the traversodontid history is mostly a Gondwanan one (17 taxa versus three from Laurasia) and covers approximately 30 Ma, with the peak of representation clearly in the Late Triassic. There is a trend toward increased morphological complexity of the postcanines (Martinelli and Soares 2016) in the younger representatives of the family as well as to increase the body size. The larger traversodontids are represented in the Carnian-Norian of Argentina (i.e., *Exaeretodon*, *Ischignathus*; Bonaparte 1962, 1963; Abdala et al. 2002), South Africa (i.e., *Scalenodontoides*; Crompton and Ellenberger 1957; Hopson 1984; Gow and Hancox 1993; Battail 2005), and Canada (i.e., *Arctotraversodon*; Hopson 1984; Sues et al. 1992; Sues and Olsen 2015).

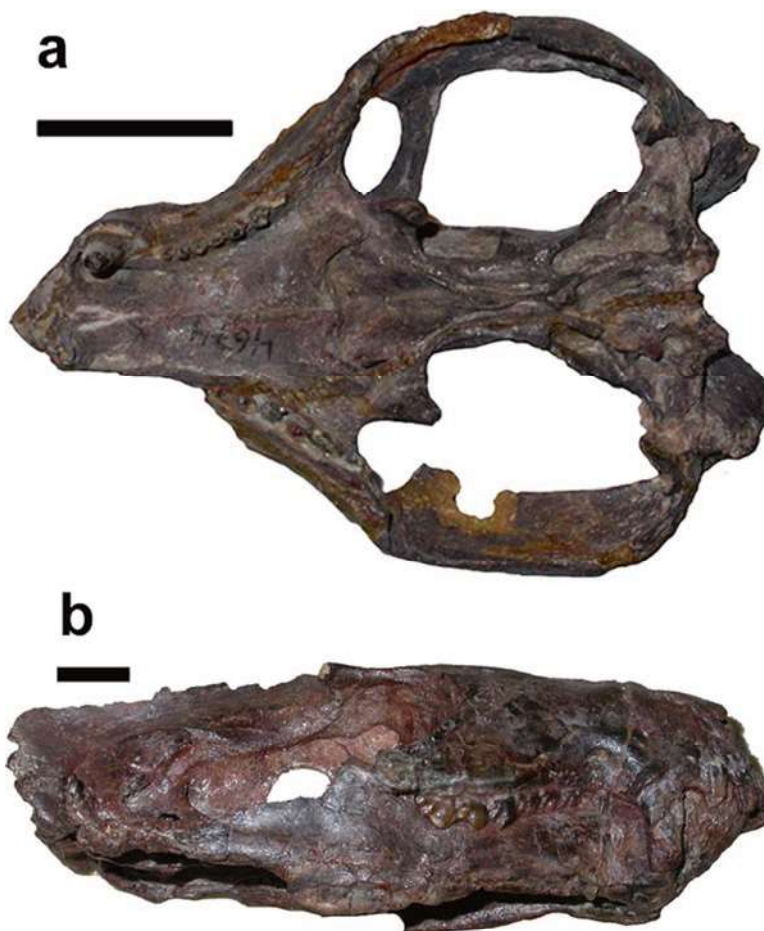
### 11.2.2 Proliferation of the Small Probainognathians

Probainognathians are well represented in the Upper Triassic (Fig. 11.5), although less diverse and clearly not as abundant as traversodontids. The oldest representatives of this group are *Aleodon* and *Cromptodon* from the Middle Triassic of Africa and South America, respectively (Crompton 1955; Bonaparte 1972a), which also have expanded postcanine crowns, although to a lesser degree than gomphodont cynodonts. *Aleodon* was also recently reported from the Carnian *Dinodontosaurus* AZ of southern Brazil (Martinelli et al. 2017b). Other basal probainognathians presented typical sectorial postcanines with different degrees of complexity. *Chiniquodon*, a medium-to-large-sized probainognathian is characterized by the presence of a long osseous secondary palate and posterior sectorial postcanines featuring the main cusp strongly curved backwards (Fig. 11.6a). This genus is represented in faunas ranging from the Carnian to the Norian in South America and Africa (Martinez and Forster 1996; Abdala and Giannini 2002; Abdala and Smith 2009; Kammerer et al. 2010). The uppermost faunal assemblage from the upper Omingonde Formation in Namibia has been considered of possible Ladinian age

**Fig. 11.5** Phylogenetic relationships of probainognathians plotted against the time scale. Abbreviations: *PRO* Prozostrondontia, *TRITHE* Tritheledontidae. Phylogeny after Martinelli et al. (2016)

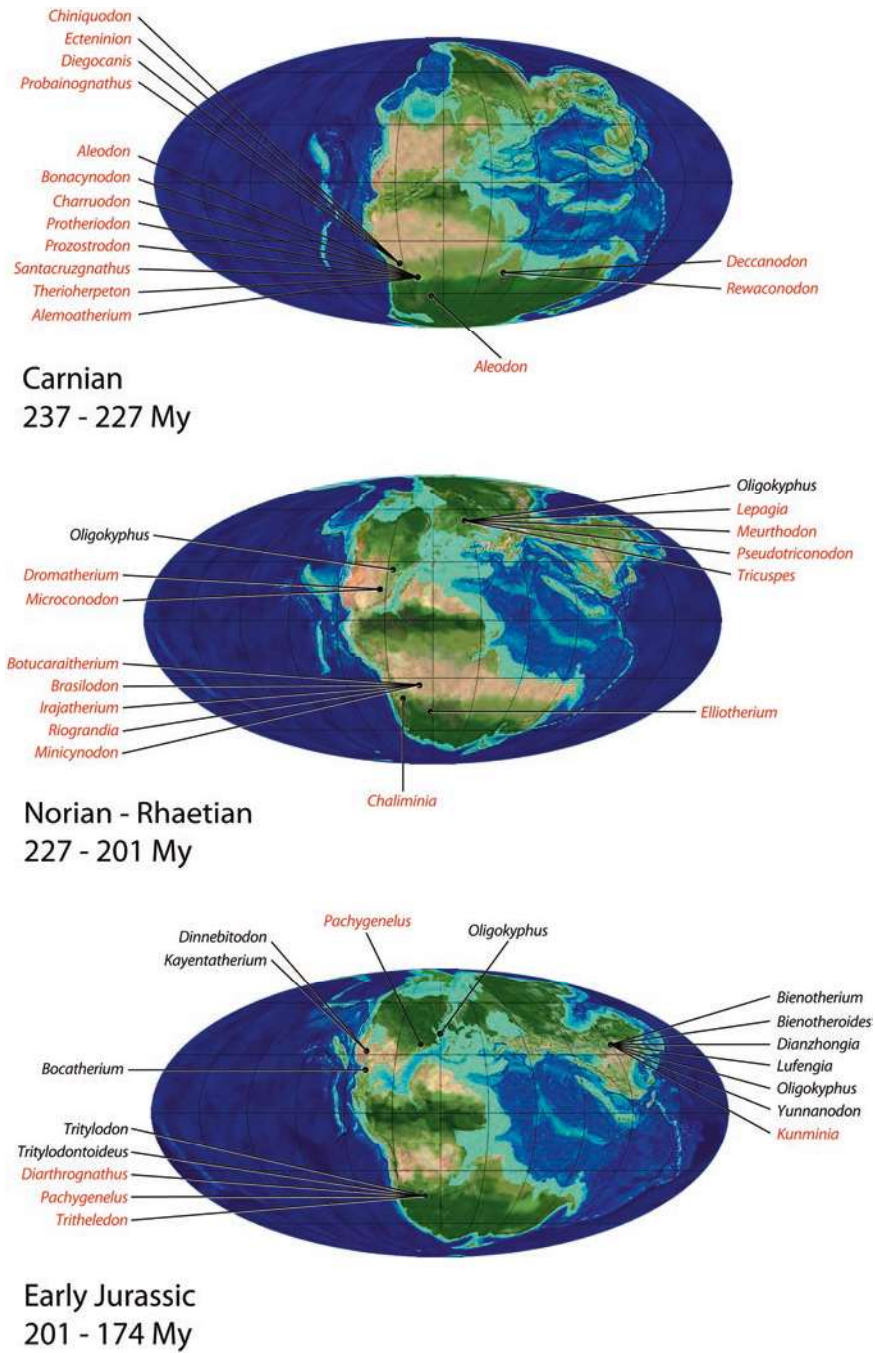


(Abdala and Smith 2009; Abdala et al. 2013), however, the early Carnian geochronologic age recently presented for the Chañares Formation from Argentina (Marsicano et al. 2016) points to the possibility that this Namibian association, correlated with the Chañares and *Dinodontosaurus* AZ faunas from South America, could be of the same age. Other basal probainognathians are represented by the medium-sized *Trucidocynodon* and the tiny *Alemoatherium* from the Carnian *Hyperodapedon* AZ of Brazil (Oliveira et al. 2010; Martinelli et al. 2017a) and the closely related small sized *Ecteninion* (Fig. 11.6b) and *Diegocanis* from the coeval Ischigualastian fauna (Martinez et al. 1996, 2013). Younger records of probainognathians are globally represented by tiny to small animals that are particularly diverse (Bonaparte and Barberena 2001; Bonaparte et al. 2006; Martinelli et al. 2016), and abundant (for example *Riograndia*) in the ?late Norian - ?early Jurassic *Riograndia* AZ (Bonaparte et al. 2003, 2005; Soares et al. 2011). Probainognathians are represented in this Brazilian assemblage zone by five named taxa (following Liu and Olsen 2010 in that *Brasilodon* and *Brasilitherium* likely represent the same taxon), representing the most diverse putative Late Triassic faunal assemblage with prozostrondontians (Fig. 11.7) (Bonaparte et al. 2001, 2003, 2005; Martinelli et al. 2016, 2017a; Pacheco et al. 2017). The record of small probainognathians is also diverse in South Africa where *Elliotherium* is represented in the Norian Lower Elliot Formation (Sidor and Hancox 2006), and three species, the rare *Tritheledon*



**Fig. 11.6** Basal probainognathian (a) *Chiniquodon thetonicus* (PVL 4674), Chañares Formation, Ischigualasto-Villa Union Basin, Argentina, palatal view of the skull. Scale bar = 30 mm; (b) *Ecteninion lunensis* (PVSJ 422) lateral view of the skull. Scale bar = 10 mm

and *Diarthrognathus* from the Lower Jurassic Upper Elliot and the more common *Pachygenelus* from the same unit and also from the Clarens Formation (Gow 1980; Bordy et al. 2017). Dromatheriids also encompass small cynodonts with sectorial postcanines represented by fragmentary specimens (Sues 2001). They are documented mostly in Laurasia, although they were recently described in the Late Triassic of India (Datta et al. 2004). Their phylogenetic placement among non-mammaliaform cynodonts has never been properly tested. Some scholars consider that the morphological evidence only indicates that dromatheriids are eucynodonts (Sues 2001). Other researchers suggest they are the sister taxon to the Brazilian *Therioherpeton*, forming a group that is closely related to tritheledontids (Battail 1991) and finally Hahn et al. (1994) considered dromatheriids to be the sister group



**Fig. 11.7** Paleogeographic reconstructions depicting probainognathian distribution, including tritylodontids (in black) during the Carnian, Norian-Rhaetian and Early Jurassic. Maps modified from Blakey

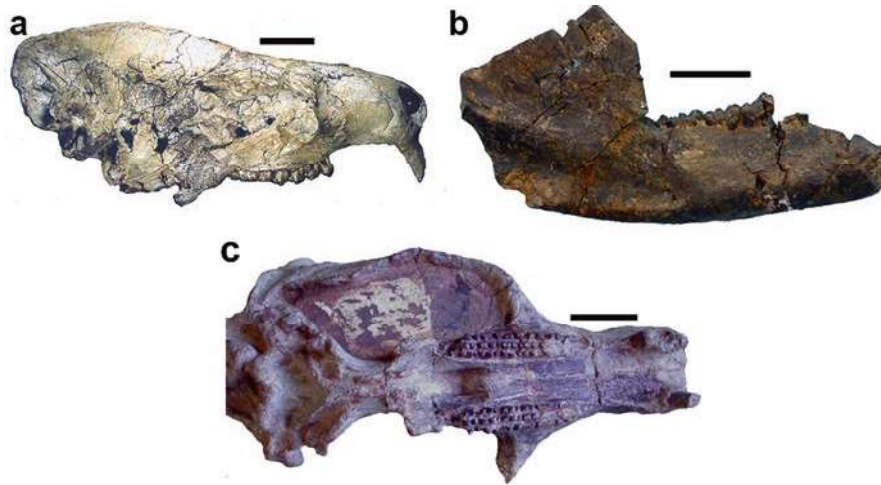
of mammaliaforms. By the Late Triassic and Early Jurassic, mammaliaform and tritylodontid probainognathians develop complex expanded postcanines capable of dental occlusion (Kielan-Jaworowska et al. 2004).

### 11.2.3 *Twilight of the Non-mammaliaform Cynodonts: The Tritylodontids*

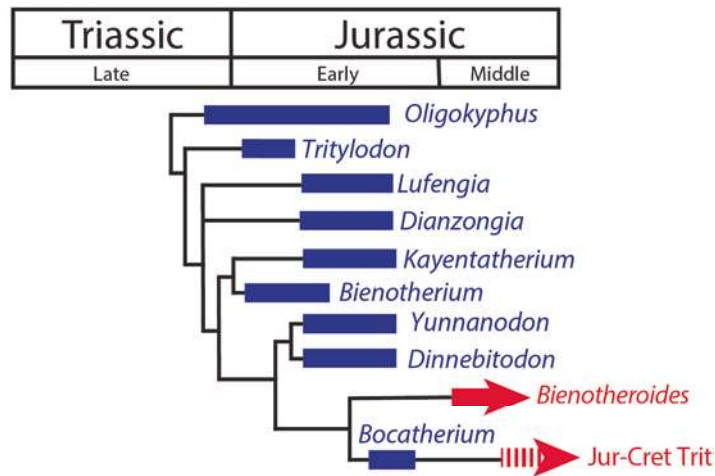
The last vestige of non-mammaliaform cynodonts is characterized by the appearance, diversification, and extinction of tritylodontids, a lineage that features prominently in discussions on mammaliaform ancestry. Most of the scholars consider this group in the probainognathian lineage, representing the sister-taxon of Mammaliaformes or of Tritheledontidae + Mammaliaformes (Kemp 1983; Rowe 1988, 1993; Wible 1991; Luo 1994; Abdala 2007; Liu and Olsen 2010; Ruta et al. 2013; Martinelli et al. 2016) (Fig. 11.1), whereas others interpret tritylodontids as member of the cynognathian lineage (Sues 1985a, b; Sues and Jenkins 2006), closely related to a paraphyletic Traversodontidae (Hopson and Kitching 2001; Sidor and Hopson *in press*), removing them from the ancestry of mammals.

Tritylodontids have a marked size variation with larger forms such as *Kayentatherium* reaching skull total length of 260 mm and *Oligokyphus* being ~90 mm (Gaetano et al. 2017; Fig. 11.8a, b). They have a feeding system with strong propalinal jaw movements, mimicked by that of rodents (Crompton 1972). The dental pattern is quite conservative in the group: at least one large incisor, no canines, and labiolingually expanded molariforms with longitudinal cusp rows separated by furrows into which opposing cusps occlude (Clark and Hopson 1985; Sues 1985b) (Fig. 11.8a, c). The dental conservatism (Hu et al. 2009) contrasts with a disparate variation in skull morphology (see, for example, variation of the snout and palate in Clark and Hopson 1985: figure 3). At the end of the Triassic and beginning of the Jurassic, tritylodontids and haramiyid mammaliaforms shared the presence of expanded postcanines with occluding longitudinal cusp rows for the second time in the cynodont lineage. This pattern was achieved before in non-mammaliaform cynodonts from the Lower Triassic of South Africa, currently only known by isolated teeth (Gaetano et al. 2012).

Tritylodontids are basically a Jurassic group with isolated older records in the Rhaetian of Germany and Canada (Fedak et al. 2015; Fig. 11.9), and the last representatives known from the Early Cretaceous of Russia and Japan (Tatarinov and Matchenko 1999; Matsuoka et al. 2016). The group is almost exclusively Laurasian, with the only Gondwanan record restricted to the Lower Jurassic of South Africa (Fig. 11.7). A putative record from the Norian of Argentina (Bonaparte 1972b) was recently dismissed by Gaetano et al. (2017). Tritylodontids are represented by approximately 23 taxa, including several species from the Lower Jurassic of the United States and China. This group can be envisaged as an Early Jurassic ecological replacement of the traversodontids, a lineage that was particularly prolific in the



**Fig. 11.8** Tritylodontidae (a) *Kayentatherium wellesi* (MCZ 8812), Kayenta Formation, Glen Canyon Group, United States, lateral view of the skull. Scale bar = 40 mm. (b) *Oligokyphus major* (NHMUK R7119), fissure fill limestone “Mendip 14”, Windsor Hill Quarry, United Kingdom, lateral view of the partial right lower jaw. Scale bar = 10 mm. (c) *Tritylodon longaevus* (BP1/4778), upper Elliot Formation, Karoo Basin, South Africa, upper palatal view of the skull. Scale bar = 20 mm



**Fig. 11.9** Phylogenetic relationships of tritylodontids plotted against the time scale. Abbreviations: *JUR-CRET Trit* tritylodontids from the Middle Jurassic of the United Kingdom and from the Early Cretaceous of Russia and Japan

Middle and Late Triassic. During the Late Triassic, 18 taxa of traversodontids thrived during an interval of 35.7 million years, whereas 14 species of tritylodontids are known from the Lower Jurassic, spanning a period of 27.2 Ma. In both groups there are several species that are abundant and sometimes even dominant in their respective faunal assemblages (Luo and Wu 1994; Smith and Kitching 1997; Sues and Hopson 2010; Mancuso et al. 2014). Tritylodontids are in need of an extensive phylogenetic analysis. The most recent and one of the few cladistic analyses published is that by Watabe et al. (2007), who considered only five cranial and six dental features. Following the hypotheses presented by Watabe et al. (2007), the basal-most tritylodontids are represented by the Rhaetian to Sinemurian *Oligokyphus* from Laurasia (Fig. 11.9), and the Hettangian-Sinemurian *Tritylodon* from southern Africa, two taxa with a prominent long snout (Clark and Hopson 1985). These basal forms are followed in a pectinate fashion by Hettangian to Sinemurian species from China and North America (Fig. 11.9). The final diversification of this group comprises several species of *Bienotheroides* from the Middle and Late Jurassic of China and the Early Cretaceous of Mongolia, *Bocatherium* from the Pliensbachian of Mexico, *Stereognathus* from the Middle Jurassic of the United Kingdom, and the geologically youngest representatives from the Early Cretaceous of Russia and Japan. The most profuse record of this group is indeed in China, where it is represented by 10 named taxa (nearly half of the named tritylodontid species) in a temporal sequence that starts in the Hettangian with *Bienotherium* and ends in the Late Jurassic with *Bienotheroides*.

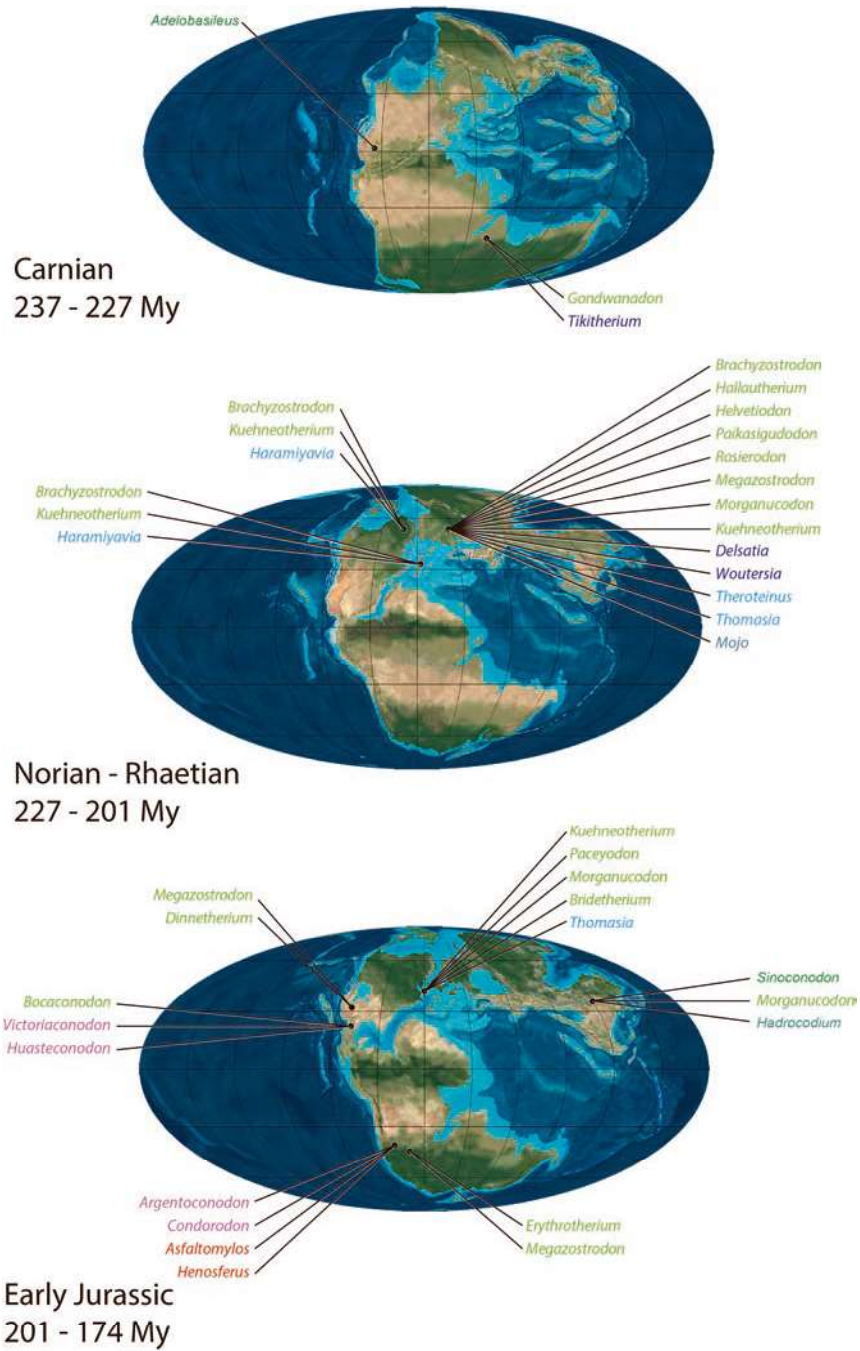
#### 11.2.4 Enter Mammaliaforms

It is among basal mammaliaforms that cynodonts progressively become morphologically closer to what we imagine as the first representatives of living mammals. The evolution of this clade during the Mesozoic has been envisaged as successive diversification events of relatively short-lived clades (Luo 2007).

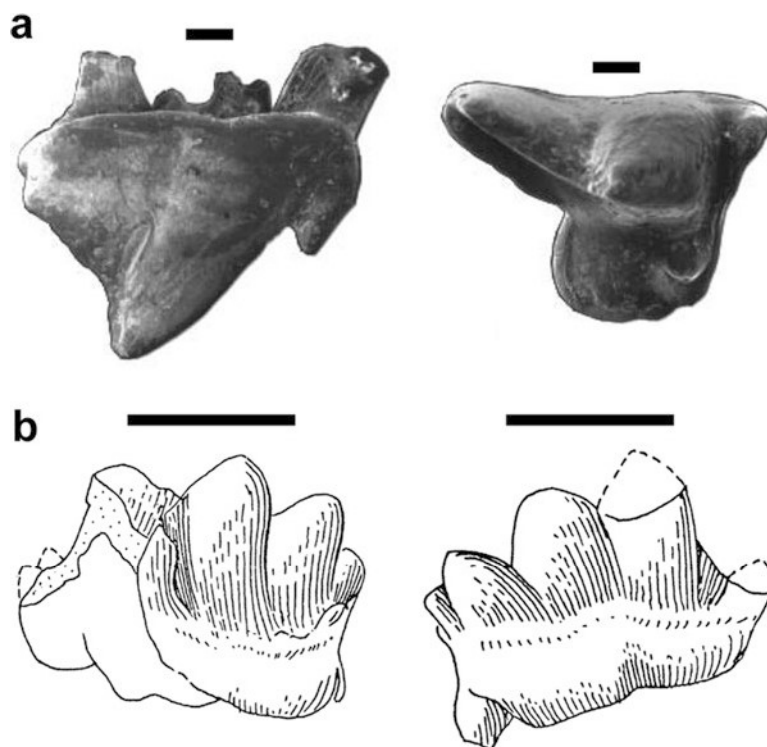
Known from the Carnian Tecovas Formation of Texas (Lucas and Hunt 1990), *Adelobasileus* is only represented by the posterior portion of a skull that shares several features with mammaliaforms, but also retains a set of primitive characters. Phylogenetic studies argued that *Adelobasileus* is a basal mammaliaform (see Kielan-Jaworowska et al. 2004), but it has been suggested that it may well be a dromatheriid (Lucas and Luo 1993; Kielan-Jaworowska et al. 2004).

Mammaliaforms (in the sense of Kielan-Jaworowska et al. 2004) make their appearance in the fossil record with only two records from a single Late Triassic (Carnian) formation (Fig. 11.10). *Gondwanadon* and *Tikitherium*, each of them represented by a single isolated tooth (Fig. 11.11), are known from the Tiki Formation, Madhya Pradesh, India (Datta and Das 1996; Datta 2005). These early representatives already conspicuously differ in their dental anatomy (Kielan-Jaworowska et al. 2004; Kermack et al. 1973; Gill et al. 2014; Luo et al. 2015). *Gondwanadon* (Fig. 11.11a) has been tentatively included in Morganucodonta (Kielan-Jaworowska et al. 2004; Debuyschere





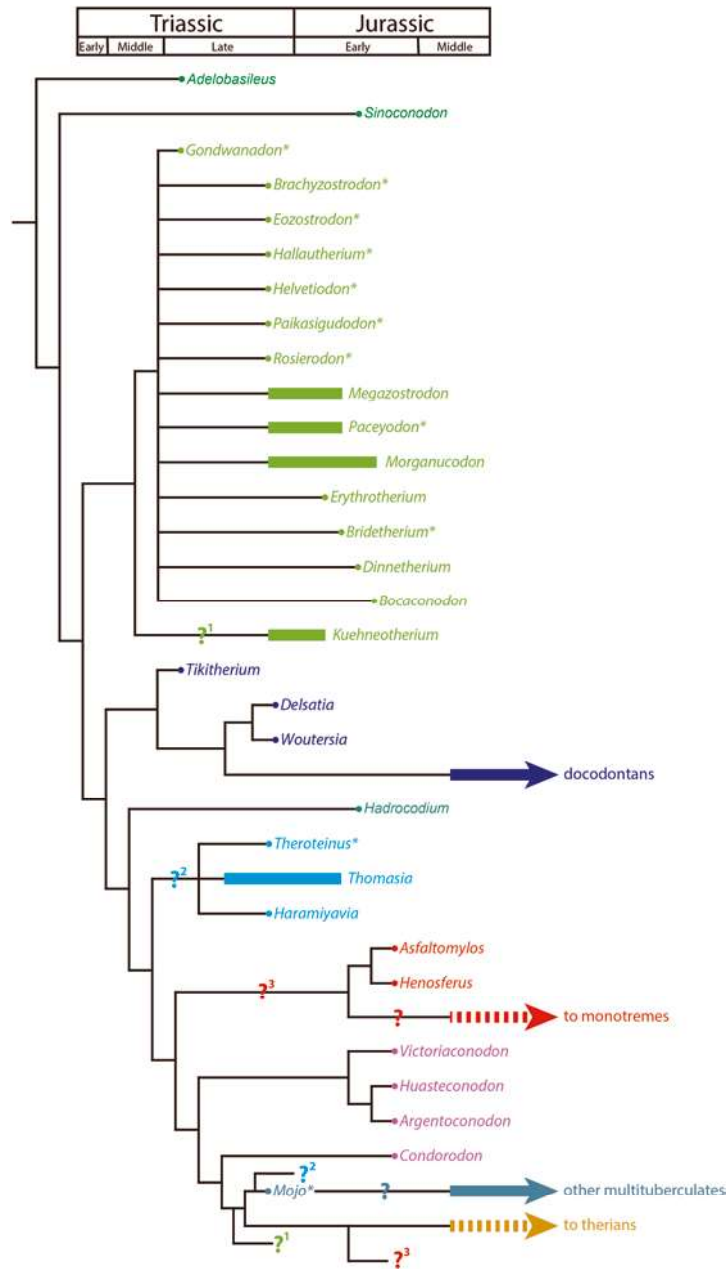
**Fig. 11.10** Paleogeographic reconstructions depicting mammaliaform distribution during the Carnian, Norian–Rhaetian, and Early Jurassic. Maps modified from Ron Blakey. Taxon colors represent the purported phylogenetic placement after the hypothesis presented in Fig. 11.12



**Fig. 11.11** Mammaliaformes (a) *Tikitherium copei*; SEM photographs of upper left molariform in labial and occlusal views. Scale bars = 200  $\mu$ m. (b) *Gondwanadon tapani* line drawing of lower right molariform in lingual and labial views. Scale bars = 1 mm. (a) from Datta (2005) and (b) from Datta and Dass (1996)

et al. 2015). The relationships of most morganucodontans have not been tested phylogenetically. Additionally, there are different opinions regarding the interrelationships of the few morganucodontans that have been cladistically analysed (e.g., Kielan-Jaworowska et al. 2004; Gaetano and Rougier 2012). Morganucodontans are the most abundant and diverse mammaliaforms during the Triassic, particularly the Rhaetian, and they continue to be well represented during the Early and Middle Jurassic.

Originally listed as a morganucodontan, *Tikitherium* (Fig. 11.11b) is now considered closely related to the docodontan clade (Datta 2005; Luo and Martin 2007). Unlike the labiolingually compressed cheek teeth of morganucodontans with mesiodistally aligned main cusps, *Tikitherium* and docodontans present more complex postcanines with labiolingually expanded crowns and a triangular placement of the cusps (Datta 2005; Luo and Martin 2007). *Delsatia* and *Woutersia* from the Rhaetian of France have been interpreted to be basal to *Tikitherium*, but still closely related to docodontans (Luo and Martin 2007). However, it has been proposed that *Woutersia* (including two species) and *Delsatia* (monospecific) might, in fact, represent different teeth of the same taxon due to morphological



**Fig. 11.12** Phylogenetic relationships of mammaliaforms, plotted against the time scale. The topology is the result of manually assembling different cladistics analysis as well as including several taxa that were never analysed phylogenetically. Taxa from the Kota Formation (India) have not been included due to their probably Early Cretaceous age (see text). *Question marks* followed by superscript numbers are employed to represent the alternative positions of certain taxa. Taxa not included in cladistics analysis are marked with an *asterisk*

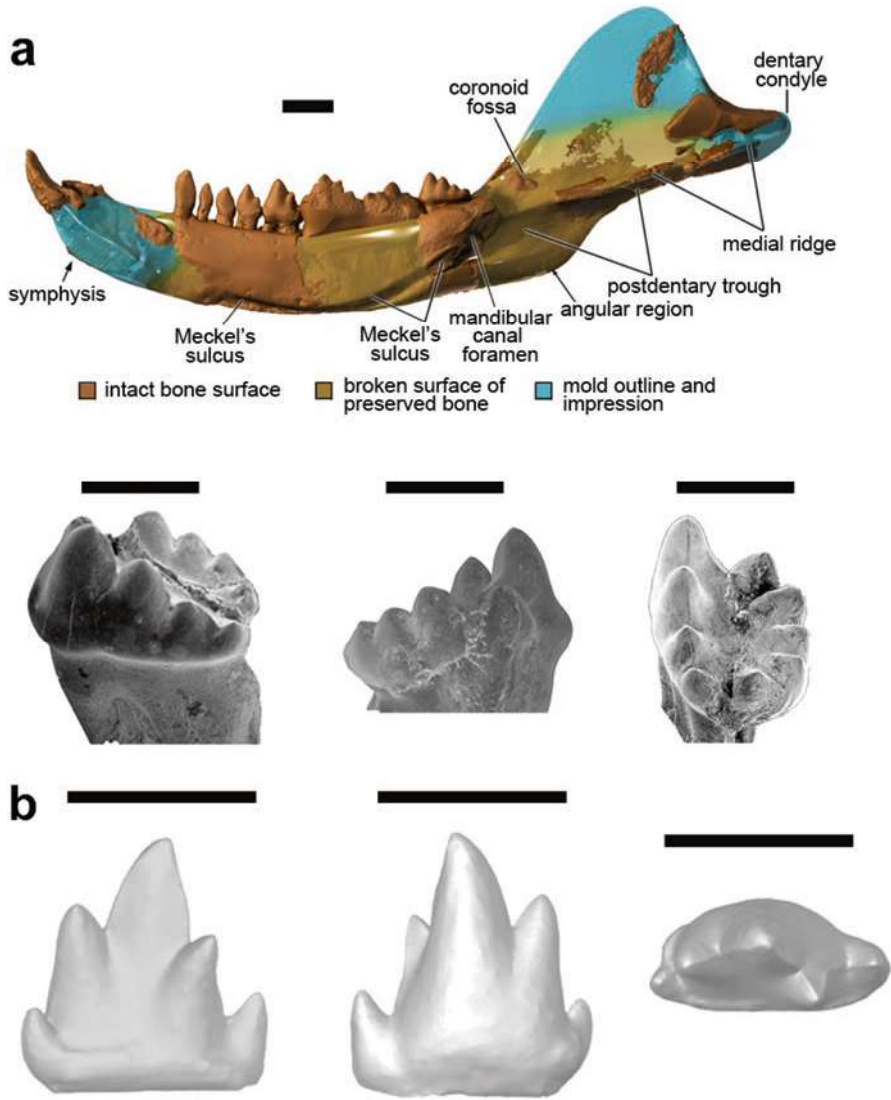
similarities and co-occurrence (Kielan-Jaworowska et al. 2004). This Triassic radiation of stem-docodontans would precede the radiation and initial diversification of the docodont clade in the Middle Jurassic, when some representatives of this group developed morphological adaptations for swimming (Martin and Nowotny 2000; Martin 2005, 2006; Ji et al. 2006).

The single record of *Thomasia hahni* from the Rhaetian of Halberstadt, Germany (Hahn 1973; Butler and Macintyre 1994) is the oldest member of the contested Haramiyida. Four additional taxa including morganucodontans, haramiyidans, and the oldest “symmetrodon” (identified as *Kuehneotherium* sp.; see below) come from Norian to Rhaetian Laurasian units (Jenkins et al. 1997; Swilo et al. 2014; Clemmensen et al. 2015) (Fig. 11.10).

By the Rhaetian, the number of mammaliaform taxa increased greatly, with 15 genera and at least 20 species identified. This time is clearly dominated by the abundant and diverse morganucodontans (9 genera) whereas haramiyidans, docodontans and related taxa, “symmetrodon”s, and tentatively multituberculates, are minor components of the fossil assemblages (Figs. 11.10 and 11.12). Haramiyidans are represented in the Rhaetian by two genera and at least five species. These taxa are the earliest known mammaliaforms with complex quadrangular postcanines with multiple rows of aligned cusps (Fig. 11.13a), a morphology independently acquired in some non-mammaliaform cynodonts. This condition is interpreted as an adaptation to omnivory or herbivory, and contrasts with that of other basal mammaliaforms which have labiolingually compressed molariforms and mesiodistally aligned cusps, or a triangular cusp pattern, suggestive of a more insectivorous or carnivorous diet (Luo et al. 2015). The phylogenetic placement of haramiyidans is currently under debate. Some authors proposed that haramiyidans represent the basal stock of taxa that gave rise to multituberculates, as part of the clade Allotheria and nested within the mammalian crown-group (Zheng et al. 2013; Bi et al. 2014). Other researchers hypothesized instead that haramiyidans are basal mammaliaforms, outside crown-Mammalia, whereas multituberculates are members of the mammalian clade (Zhou et al. 2013; Luo et al. 2015) (Fig. 11.12).

Multituberculates are rodent-like forms that constitute an important component of mammaliaform assemblages from the Middle Jurassic and the remainder of the Mesozoic (Kielan-Jaworowska et al. 2004). It has been proposed that the Rhaetian witnessed the first appearance of this successful clade (Hahn et al. 1987) that survived the K-T extinction, becoming extinct only in the Eocene (Kielan-Jaworowska et al. 2004). This early record consists of a partial isolated tooth of *Mojo usuratus* (Hahn et al. 1987). The fragmentary nature of the specimen, together with the large temporal gap between this record and that of the first undisputed multituberculate in the Middle Jurassic, make the presence of this lineage in the Rhaetian uncertain (Kielan-Jaworowska et al. 2004). Another putative early record of a multituberculate, *Indobaatar zofiae*, was described from the problematic Kota Formation of India (Parmar et al. 2013).

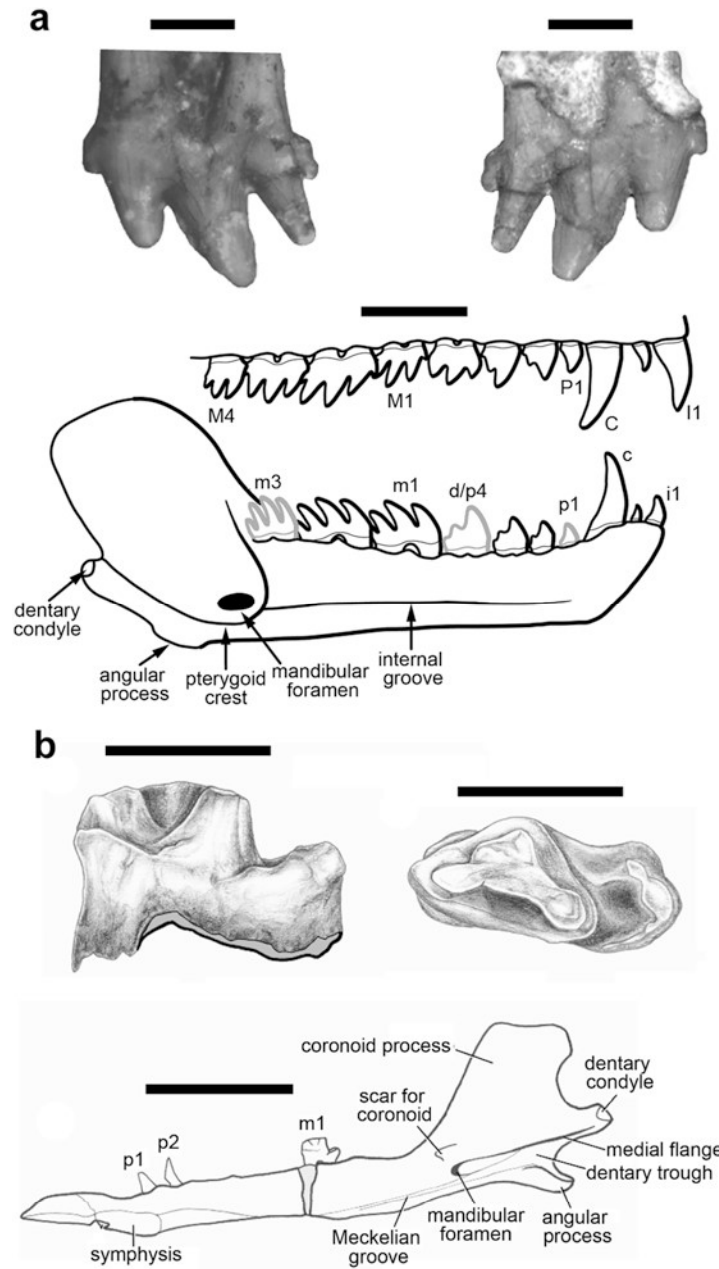
A wide array of poorly known taxa with a reversed-triangle molar pattern is informally known as “symmetrodon”s (Fig. 11.13b). Their molariforms have been interpreted as precursors that led to the evolution of the tribosphenic pattern; however, both the “symmetrodon” and the tribosphenic molariform structure have proven to be



**Fig. 11.13** Mammaliaformes. **(a)** Haramiyidan *Haramiyavia*. Composite reconstruction of the right lower jaw in medial view (*dark red*: original bone with intact periosteal surface; *brown*: broken surface of preserved bone or remnant of bone; *light blue*: morphologies preserved in mold outlines or clear impression). Scale bar = 5 mm. Scanning electron microscopy photographs of left lower molariform (m3) in lingual, labial, and occlusal views. Scale bar = 1 mm. **(b)** “Symmetrodontan” *Kuehneotherium*. Computed tomography scans of a right lower molariform in lingual, labial, and occlusal views. Scale bar = 1 mm. **(a)** From Luo et al. (2015), **(b)** from Conith et al. (2016)

homoplastic throughout mammaliaform phylogeny (Kielan-Jaworowska et al. 2004; Luo 2007; Davis 2011). *Kuehneotherium* is the oldest “symmetrodontan”, known from the late Norian—early Rhaetian of Greenland (Jenkins et al. 1994; Clemmensen et al. 2015). This taxon is also represented by at least two species recorded in Rhaetian formations from France, Luxemburg, and the United Kingdom (Fraser et al. 1985; Sigogneau-Russell and Hahn 1994; Godefroit and Sigogneau-Russell 1995, 1999; Whiteside et al. 2016). Additionally, *Kuehneotherium* has been discovered in different quarries of Early Jurassic (Hettangian) fissure-filling deposits in the United Kingdom (Kermack et al. 1968, 1973; Säilä 2005; Gill et al. 2014; Whiteside et al. 2016). *Kuehneotherium* is regarded as a basal mammaliaform, phylogenetically nested among morganucodontans by some authors (Kielan-Jaworowska et al. 2004) but considered closely related to cladotherians by others (Rougier et al. 2007).

The passage from the Triassic to the Early Jurassic is accompanied by a relative decline in haramiyidan diversity, whereas there is an increase in the diversity of “symmetrodontans” and the first occurrence of derived “triconodonts” (“amphilestids” and eutriconodontans, *sensu* Gaetano and Rougier 2011), and australosphenidans (Fig. 11.14). *Sinoconodon*, regarded as the basalmost mammaliaform, has also been found in Early Jurassic rocks (Crompton and Sun 1985; Crompton and Luo 1993). *Thomasia* is the only recognized haramiyidan in Early Jurassic outcrops. Haramiyidans are known from the Norian to the Middle-Late Jurassic (Zheng et al. 2013; Zhou et al. 2013; Bi et al. 2014). Morganucodontans, mainly represented in Europe during the Triassic (except for the Indian *Gondwanadon*), are also well represented in Gondwana during the Early Jurassic. With 10 identified genera, morganucodontans are still major components in Early Jurassic assemblages from China, the United Kingdom, the United States, South Africa, Lesotho, and India. During the Early Jurassic, “symmetrodontans” are for the first time recognized in Gondwana, represented by six different genera; a remarkable difference when compared to the single known genus from the Triassic. However, it is important to bear in mind that *Delsatia* and *Woutersia* from the Rhaetian of France, interpreted as stem-docodontans, could also be considered as “symmetrodontans” on a morphological basis (Butler 1997; Sigogneau-Russell and Godefroit 1997; Kielan-Jaworowska et al. 2004; Luo and Martin 2007). Derived “triconodonts” were recorded in Early Jurassic outcrops from South and North America and India. This distribution suggests that the diversification of these forms was already ongoing by the end of the Early Jurassic, and should have started before the Pliensbachian. The simple plesiomorphic morphology of derived “triconodont” molariforms (labiolingually compressed tooth and mesiodistally aligned main cusps), hampers comparisons with other taxa bearing more specialized dentition. Despite a comparable basic structure of molariforms, derived “triconodonts” (Fig. 11.14a) are not nested among the morganucodontans, but in a more derived clade than docodontans, with some authors including them in the crown-group Mammalia (Luo et al. 2002, 2007; Meng et al. 2006; Luo 2007; Gaetano and Rougier 2011, 2012). Two closely related taxa that come from a single locality in Argentina are the oldest representatives of Australosphenida (Fig. 11.14b). There has been some controversy on the phylogenetic relationships of Mesozoic austra-



**Fig. 11.14** Mammaliaformes. (a) “Triconodont” *Argentoconodon fariasorum*, upper left molariform (M2) of the holotype in labial and lingual views. Scale bar = 1 mm. Reconstruction of the lower jaw and upper and lower dentition in medial view (teeth in grey are not presently known). Scale bar = 5 mm. (b) Australosphenidan *Henosferus molus*, right lower molariform (m1) of the holotype in lingual and occlusal views. Scale bar = 1 mm; right lower jaw of the holotype in medial view. Scale bar = 5 mm. (a) from Gaetano and Rougier (2011) and (b) from Rougier et al. (2007)

losphenidans, which have been alternatively allied with monotremes or therians (Rougier et al. 2007). Although considered not functionally tribosphenic (Davis 2011), australosphenidans represent a Gondwanan radiation of tribosphenic-like forms (Rougier et al. 2007; Luo 2007). Their temporal and geographic distribution contradicts the traditional view that tribosphenic mammals had a single origin on the northern continents, and then moving to southern landmasses (Luo et al. 2001; Luo 2007). Moreover, the age of the oldest australosphenidans places the origin of the crown-group Mammalia (if related to monotremes) and the therian clade as early as the Early Jurassic, just a few million years after the occurrence of the first mammaliaforms.

Considering that mammaliaform ancestry has been inferred to be among South American brasilodontids (Liu and Olsen 2010; Ruta et al. 2013; Martinelli et al. 2016, 2017a) and that one of the places where the oldest known mammaliaforms (Carnian) were found is in India, it is possible that the history of the lineage that ultimately led to mammals began in Gondwana. In this scenario, *Adelobasileus* could represent a radiation into Laurasia of forms very closely related to mammaliaforms. On the other hand, what we know about the Triassic history of this clade is almost entirely a Laurasian tale. During the Norian and Rhaetian, the diversification of mammaliaforms occurred in Europe, where 16 genera and a number of additional putative different taxa have been identified in 18 localities (Table 11.1). This record is mostly represented by isolated teeth, except for a few more complete but still fragmentary discoveries (Kielan-Jaworowska et al. 2004). The fact that cynodonts are mostly found in Gondwana from Lopingian to Norian times, contrasts with their exclusive Laurasian (particularly European) record during the latest Norian and Rhaetian. In the Early Jurassic, cynodonts have a more widespread distribution. In Laurasia, they are represented in China, Europe, and North America. Additionally, the Gondwanan faunal assemblages from Africa, India, and South America have also provided cynodont remains. It is interesting to note that non-mammaliaform cynodonts and mammaliaforms have been discovered in Early Jurassic localities from Africa (South Africa and Lesotho) (Crompton 1964; Gow 1981; 1986), whereas in the remaining Gondwanan landmasses only mammaliaforms are represented.

The Early Jurassic mammaliaform faunas discussed above include a relatively rich assemblage that has been found in the Kota Formation from the Paikasigudem locality in India (Datta 1981; Yadagiri 1984, 1985; Prasad and Manhas 1997, 2002; Vijaya and Prasad 2001; Parmar et al. 2013). However, the age of this unit has been a matter of controversy. Some authors have proposed an Early Jurassic age on the basis of its fossil fish (King 1881; Robinson 1967; Jain 1973, 1980) and a pterosaur (Jain 1974). Others suggested an early Middle Jurassic age on the basis of the presence of the ostracod *Darwinula* (Govindan 1975; Misra and Satsangi 1979). More recently, comparisons of the Kota Formation faunal assemblage with that of coeval horizons and of the underlying Dharmaram Formation led to the conclusion that its age ranged from the Early Jurassic (Sinemurian) to the Middle Jurassic (?Aalenian) (Bandyopadhyay and Roychowdhury 1996; Bandyopadhyay and Sengupta 2006). On the other hand, the palynological analysis of the Upper Member of the Kota Formation showed that this was a transgressive lithological unit, deposited during the late Middle Jurassic to Early Cretaceous (Vijaya and Prasad 2001). The mammaliaform-bearing levels



(Paikasigudem locality) are interpreted as Early Cretaceous (late Hauterivian—early Barremian). According to Vijaya and Prasad (2001), this is the only locality of the Kota Formation from which a diverse microvertebrate assemblage has been recovered, including semionotid and elasmobranch fishes, sphenodontids, lizards, ornithischian and theropod dinosaurs, and mammaliaforms. This vertebrate diversity includes forms closely associated with taxa recorded in Late Jurassic or Cretaceous units (Vijaya and Prasad 2001). In this scenario, Vijaya and Prasad (2001) suggest that an Early Cretaceous age for the Paikasigudem locality levels of the Kota Formation would be more in line with the present knowledge than an Early Jurassic age.

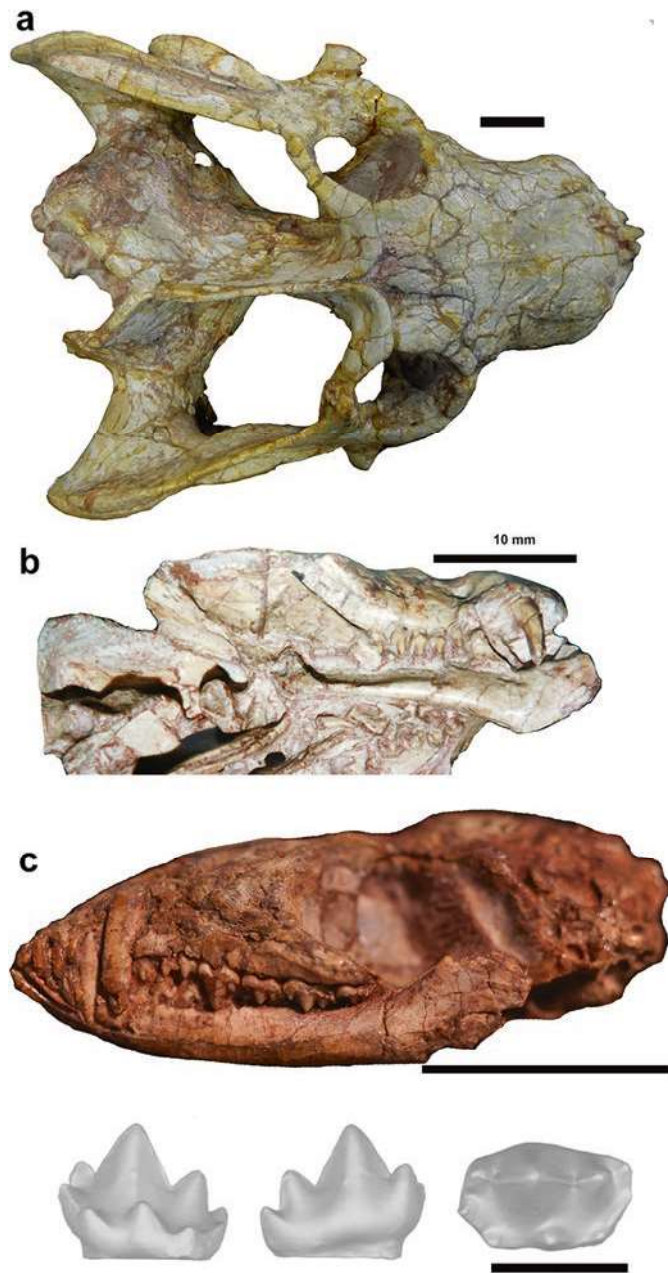
### 11.3 Cynodonts and Biostratigraphy

Cynodonts have an important value as biostratigraphic markers, as similar taxa are represented in different faunas from the same or different landmasses (Abdala and Ribeiro 2010). Concerning the Late Triassic of Gondwana, forms such as the herbivorous *Massetognathus* (Fig. 11.15) and the carnivorous *Chiniquodon* are represented in the early Carnian Chañares fauna from Argentina and *Dinodontosaurus* AZ of the Santa Maria Formation in Brazil (Langer et al. 2007). *Chiniquodon* was more recently documented in faunas from Madagascar and Namibia (Abdala and Smith 2009; Kammerer et al. 2010), and an undescribed chiniquodontid with a similar dentition is also known in the *Santacruzodon* AZ of southern Brazil (Abdala et al. 2001). *Chiniquodon* is even known from the late Carnian-early Norian Ischigualasto fauna from Argentina (Bonaparte 1966; Martinez and Forster 1996; Abdala and Giannini 2002) and is thus one of the longest-lived cynodonts (Abdala and Ribeiro 2010). Recent publications reported the presence of *Aleodon* and *Scalenodon* in the *Dinodontosaurus* AZ fauna from Brazil (Martinelli et al. 2017b; Melo et al. 2017). The probainognathian *Aleodon* was previously documented in Tanzania and Namibia (Crompton 1955; Abdala and Smith 2009), whereas the traversodontid *Scalenodon* was known from Tanzania (Crompton 1955). The traversodontid *Menadon*, first reported from the Makay Formation of Madagascar, was also described for the *Santacruzodon* AZ (Flynn et al. 2000; Melo et al. 2015). This AZ was recently dated to 236.1 Ma (Philipp et al. 2013), whereas the lower levels of the Chañares Formation, with concentrations of fossils in concretions (Mancuso et al. 2014), were dated to 236.3 Ma. The non-fossiliferous top levels of this unit date to 233.7 Ma (Marsicano et al. 2016). These absolute dates point to a temporal correlation of the Santa Cruz do Sul and Chañares faunas. The traversodontid *Exaeretodon* (Fig. 11.16a) is known from the late Carnian-early Norian Ischigualasto Formation from Argentina, the Brazilian *Hyperodapedon* AZ, and the lower Maleri fauna of India (Bonaparte 1962; Chatterjee 1982; Abdala et al. 2002). Norian and Rhaetian taxa are also shared by geographically close faunas from Europe. Thus, teeth of the haramiyid *Thomasia* have been recovered from formations in Germany, France, Belgium, Luxemburg, Switzerland, and the United Kingdom (Kielan-Jaworowska et al. 2004). Sectorial toothed non-mammaliaform cynodonts are also represented in



**Fig. 11.15** Chañares landscape in the Carnian. The traversodontid cynodont *Massetognathus* at the front and the proterochampsid *Chanaresuchus* behind. Art by Jorge Herrmann

different European countries. *Gaumia* is known from Luxemburg and Belgium; *Tricuspes* is documented in those countries as well as in Germany and France, and *Pseudotriciconodon* from Luxemburg, Belgium, France, and perhaps the United States (Sigogneau-Russell and Hahn 1994; Godefroit and Battail 1997; Sues 2001). Taxa only represented by postcanines with a simple pattern (i.e., a single large cusp aligned with anterior and posterior accessory cusps and without a cingulum) such as *Tricuspes* and *Pseudotriciconodon*, should be considered with caution until better specimens come to light. The tritylodontid *Oligokyphus* has been reported in the uppermost Triassic of Germany and eastern Canada, and the Lower Jurassic of the United Kingdom, China, and western United States (Kühne 1956; Sues 1985b; Luo and Sun 1994; Fedak et al. 2015). In the Norian, the same mammaliaform genera appear in different faunas. The iconic fossil *Morganucodon* (Fig. 11.16c) is represented by isolated teeth from the Upper Triassic of France as well as the Lower Jurassic of the United Kingdom, the United States, and China (Debuyschere et al. 2015). The best representation of this form is indeed in the United Kingdom, where hundreds of fragmentary specimens allowed for a detailed description of the taxon (Kermack et al. 1973, 1981; Jenkins and Parrington 1976). From China, a couple of nearly-complete skulls of *Morganucodon* are known (Kermack et al. 1981; Luo et al. 1995). Another Laurasian shared form is *Paceyodon* known from the Rhaetian



**Fig. 11.16** Cynodonts and biostratigraphy. (a) Dorsal view of *Exaeretodon* skull (MCP 1522 PV). Scale = 30 mm. (b) Lateral view of *Pachygenelus* skull (BP/1/5691). Scale bar = 10 mm. (c) Lateral view of *Morganucodon* skull (CUP 2320) (scale bar = 10 mm) and computed tomography scans of a right lower molariform (m4) of *Morganucodon* in lingual, labial, and occlusal views (scale bar = 1 mm). Photography of skull of *Morganucodon* by Zhe-Xi Luo; *Morganucodon* tooth from Conith et al. (2016)

of France and the Early Jurassic of the United Kingdom (Debuyschere et al. 2015). The Laurasia-Gondwana connections are provided by the tritheledontid *Pachygenelus* (Fig. 11.16b), which is known from Early Jurassic localities in South Africa and Canada (Shubin et al. 1991, Sues and Olsen 2015). The mammaliaform *Paikasigudodon* is represented in the Rhaetian of France and in the questionably Lower Jurassic Kota Formation from India, and *Megazostrodon* has been reported in the Rhaetian of France and the Lower Jurassic of southern Africa (Debuyschere et al. 2015).

#### 11.4 Late Triassic Pulses of Cynodont Diversity

In contrast with the approximately 20 taxa represented in the Anisian, mostly from southern and eastern Africa, and the one isolated record from the Ladinian of Germany, there are 68 cynodonts represented in ~35 localities in the Late Triassic, highlighting the notable gap in the Ladinian record of this group. The fauna from the Chañares Formation in Argentina and the *Dinodontosaurus* AZ from Brazil were traditionally considered Ladinian in age, but recent dating of the beds from the Chañares Formation shows they are early Carnian (Marsicano et al. 2016). In the early Carnian there are nine cynodonts recorded in faunas from Argentina and Brazil. Also in the early Carnian *Santacruzodon* AZ from Brazil and the Makay Formation from Madagascar, there are five taxa. In the late Carnian to early Norian the number of taxa increases to 17, and the diversity decreases to 12 in the late Norian. The cynodont record in the Carnian is mostly represented in Gondwana with a few exceptions such as the traversodontid *Boreogomphodon* and the mammaliaform *Adelobasileus* (Figs. 11.3, 11.7, and 11.10). A great diversification of cynodonts occurs in the Norian and Rhaetian, with 25 genera documented. The geography of cynodont Norian record shows some interesting changes, with a poor representation of traversodontids (with only two records in Gondwana and one in Laurasia; Fig. 11.3), whereas probainognathians are well represented in both subcontinents (Fig. 11.7) but mammaliaforms are only known from Laurasia at this age (Fig. 11.10). In the Early Jurassic there are 35 taxa represented (not including the record of the Kota Formation of India). The taxonomic diversity of Laurasia duplicates that of Gondwana, with non-mammaliaform cynodonts (tritylodontids and tritheledontids) only represented in southern Africa in the latter paleocontinent, and tritheledontid in the ?late Norian-?Early Jurassic *Riograndia* AZ from Brazil. The Late Triassic-Early Jurassic transition is thus represented by a temporal and geographic trend in cynodont distribution: in the Carnian, they are mostly represented in Gondwana (although the terrestrial Carnian record of Laurasia is scarce), in the Norian-Rhaetian cynodonts are distributed almost equally in Laurasia and Gondwana and by the Early Jurassic the record is clearly best represented in Laurasia (Figs. 11.3, 11.7, and 11.10).

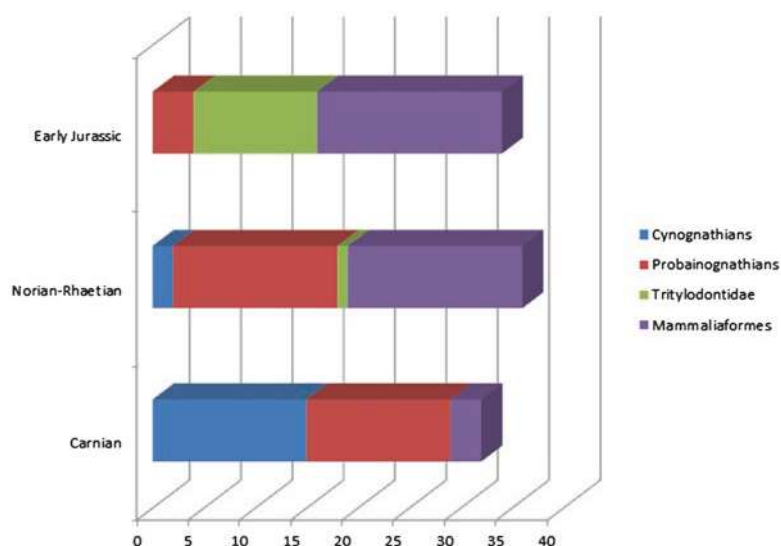


Fig. 11.17 Compared abundance of different cynodont clades during the Carnian, Norian-Rhaetian, and Early Jurassic

### 11.5 Taxonomic Diversity of Cynodonts and Dinosauriforms in the Late Triassic/Early Jurassic Transition

Two lineages can be highlighted as key at the end of the Triassic for different reasons. On one hand, cynodonts represent the climax of the non-mammaliaform history of the synapsid lineage, with several groups represented and, in addition, the first members of the Mammaliaformes, whose basal representatives features some characteristic that are main landmarks in mammalian descendants (Kielan-Jaworowska et al. 2004). On the other hand, a major revolution develops in the archosaur branch of the Tree of Life, with the first records followed by a reasonably rapid diversification of the major lineages of dinosaurs (Barrett et al. 2009; Langer et al. 2010). During the Late Triassic derived cynodonts (Eucynodontia) are exemplified by the diverse and successful traversodontids, basal probainognathians, a good diversity of small tritheledontids, including the closely related brasilodontids, the first record of tritylodontids, and a moderate initial diversity of mammaliaforms. By the Early Jurassic, tritylodontid diversification is a major novelty, accompanied by the last tritheledontids and the increasing diversity of mammaliaform groups (Fig. 11.17). On the archosaur line, the Late Triassic saw the diversification and extinction of basal dinosauriforms, and the first records of the three major lineages of dinosaurs: Sauropodomorpha, Theropoda, and Ornithischia (Langer et al. 2010; Brusatte et al. 2010), with considerable diversity of the first group especially in the Norian and Early Jurassic. A comparison of taxonomic diversity of cynodonts and

dinosauromorphs during the Late Triassic-Early Jurassic transition show very close values for these groups. Cynodonts were represented by 74 taxa and dinosauromorphs by 60 in the Late Triassic, whereas the values come closer in the Early Jurassic where cynodonts are known by 41 taxa and dinosaurs by 45. Even when this quite similar taxonomic diversity, the ecological representation for each group was quite different as the major diversity at the Norian and Early Jurassic was represented by medium to large Sauropodomorpha (Barrett et al. 2009; Langer et al. 2010), whereas cynodont diversity was mostly characterized by tiny probainognathians (including mammaliaforms) and only a few medium-sized tritylodontids having a maximum skull length of ~26 cm, with a body size definitively smaller than most sauropodomorphs documented at that time.

## 11.6 Conclusions

The Upper Triassic was a pivotal time in the evolution of the mammalian lineage. Eucynodonts underwent a remarkable diversification, first with a good representation of herbivorous traversodontids that were particularly prosperous in Gondwana, and towards the end of the Triassic with small carnivorous members of the probainognathians. In the Early Jurassic the only non-mammaliaform cynodonts that remained diverse and abundant in some faunas were the rodent-like tritylodontids, a nearly Laurasian group that replaced the Triassic traversodontids. Mammaliaforms, first documented in the Carnian, had an unprecedented heterogeneity of morphologies at the beginning of the Jurassic, with at least nine groups showing disparate variability in dental morphology. This was indeed the time in which “mammalness” started to manifest strongly in therapsids. In the Late Triassic-Early Jurassic, the therapsid-to-archosaur transition took place, in which non-mammaliaform cynodonts started to fade away and dinosaurs started the road to their dominion for the rest of the Mesozoic.

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