Chapter 5
Phylogeny and Diversity of South American Metatherians

Abstract The Metatheria include not only marsupials but all therians more related to Marsupialia than to the Eutheria. Marsupialia is considered as a metatherian crown group including all extant marsupials, their common ancestor and all of their descendants. "Ameridelphia" is not a natural group. Australidelphia includes the Microbiotheria and all Australasian marsupials. Several authors also argue that the Polydolopimorphia are Australidelphians as well. Relationships of Sparassodonta with other Metatheria are a matter of discussion. To several authors, they are more closely related to South American and Australian groups than to basal North American and/or Asian metatherians. Our concept of Didelphimorphia includes the Peradectoidea (Peradectidae and Caroloameghiniidae) and the Didelphoidea (Didelphidae and Sparassocynidae). In several analyses, the Paucituberculata appear as more closely related to the Australidelphia than to the Didelphimorphia. The relationships of the Microbiotheria within the Australidelphia have been subject of much discussion. They have been considered either as sister-taxa of all other Australidelphia, at the base of Diprotodontia, as a sister-taxon of Dasyuromorpha, as a sister-taxon of Phalangeriformes + Diprotodontia, or even related with part of the former.

Keywords Metatheria · Marsupialia · Ameridelphia · Australidelphia · Sparassodonta · Didelphimorphia · Paucituberculata · Microbiotheria · Polydolopimorphia

5.1 Metatherian Phylogenetic Analyses

After its first recognition as a group (Illiger 1811), relationships among living marsupials and their extinct relatives have been largely discussed based on different structures, such as bones (e.g., Szalay 1982), bones and teeth (e.g., Marshall et al. 1990), blood serum (e.g., Kirsch 1977), and genes (e.g., Nilsson et al. 2004, 2010), among other sources. Since Rowe (1988), Marsupialia is conventionally considered

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a crown group including all extant marsupials, their common ancestor and all of their descendants. Following Rowe, Rougier et al. (1998) defined Metatheria as the group including not only Marsupialia but therians more related to Marsupialia than to Eutheria (Rougier et al. 1998), having Metatheria and Eutheria a sister-group relationship (Kielan-Jaworowska et al. 2004). In the last decades, phylogenetic cladistic analyses have progressively become dominant in elucidating metatherian affiliations and classification, being the earlier studies those carried out by the late seventies and early eighties of the last century (e.g., Marshall 1977a; Archer 1982; Sharman 1982).

Among phylogenetic analyses, a broad division can be made between morphological and molecular analyses. Morphological studies have been carried out using craneodentary (e.g., Rougier et al. 1998), dentary (e.g., Goin et al. 2009; Oliveira and Goin 2011; Vullo et al. 2009; Williamson et al. 2012), basicranial (e.g., Ladevèze 2004, 2007), postcranial (Flores 2009), or complete osteological characters (e.g., Sánchez-Villagra 2001; Luo et al. 2003; Horovitz and Sánchez-Villagra 2003; Horovitz et al. 2009; Beck 2008, 2012; Forasiepi 2009). Some specific sets of morphological characters (e.g., the internal nasal skeleton; Macrini 2012) have been used in the testing of previous phylogenetic hypotheses. Molecular phylogenetic analyses use either nuclear (e.g., IRBP, BRCA1, APOb, RAG1, Vwf genes; Amrine-Madsen et al. 2003; Protamine P1, Retief et al. 1995) or mitochondrial DNA (e.g., 12S rRNA, 16S rRNA, tRNA valine; Burk et al. 1999; complete mitochondrial DNA, Nilsson et al. 2003), although some combine the two types of DNA (e.g., Phillips et al. 2006). Some analyses include both morphological and molecular data (e.g., Voss and Jansa 2003, 2009; Jansa and Voss 2005; Flores 2009). Cardillo et al. (2004) state that 158 phylogenetic studies have been published since 1980, which include all or some metatherian lineages.

5.1.1 Relationships Among South American Metatherians

Even though the eutherian-metatherian divergence can be traced back to the Late Jurassic (Luo et al. 2011), the oldest record of a metatherian corresponds to early Cretaceous times: *Sinodelphys szalayi*, from the Barremian of China (Luo et al. 2003). Additional, Cretaceous metatherians have been only recovered from northern continents, mainly from Asia and North America (e.g., Rougier et al. 1998; Luo et al. 2003; Williamson et al. 2012; but see Vullo et al. 2009). Metatherians from the Cretaceous of Asia usually appear either as a distinct group (e.g., Rougier et al. 1998; Beck 2008) or as part of the stem Metatheria (Luo et al. 2003; Horovitz et al. 2009; Beck 2012) along with most North American taxa (e.g., *Holoclemensia, Atokatheridium, Turgidodon, Didelphodon* ; Luo et al. 2003). However, some Cretaceous metatherians from North America, like *Pediomys*, *Glasbius*, and *Ectocentrocristus* have been related to a number of South American groups (e.g., Reig et al. 1985, 1987; Goin et al. 2009; Ladevèze and Muizon 2010; see a more recent review in Williamson et al. 2012, 2014).

When he first recognized the group Australidelphia, Szalay (1982) also acknowledged the "**Ameridelphia**". This group included North and South American metatherians (excluding *Dromiciops*). Subsequent analyses have demonstrated that this is not a natural group (e.g., Rougier et al. 1998; Forasiepi 2009; Ladevèze and Muizon 2010). Other conflictive ordinal group is the Didelphimorphia , which has variously included a number of different lineages of American metatherians, such as didelphids and sparassodonts (e.g., Kirsch 1977) or "… generalized metatherians with a didelphid-like dentition , which form a paraphyletic assemblage stem to the Australidelphia lineage (i.e., pucadelphyids, protodidelphids, didelphids, Types I, III, IV, VI, VII, *Derorhynchus* , *Carolopaulacoutoia*, and *Gaylordia*)." (Ladevèze and Muizon 2010: 759). Horovitz et al. (2009) defined the Didelphimorphia as the natural group comprising the Peradectidae and the Didelphidae . However, more recently the monophyly of the Peradectidae has been put into question (Williamson et al. 2012).

The most ancient South American "ameridelphians" are recorded from the Tiupampa locality (early Paleocene, Bolivia). Even though several species were recognized from this locality, only three are well represented by craniodental remains: *Pucadelphys andinus, Andinodelphys cochabambensis,* and *Mayulestes ferox* (Fig. 5.1). These species have been included in several analyses and they are usually stem to the marsupial radiation (e.g., Luo et al. 2003). In most analyses, *Andinodelphys* and *Pucadelphys* appear as sister-taxa (the Pucadelphyidae; Ladevèze and Muizon 2010; but see Rougier et al. 1998). *Mayulestes* is often recovered at the base of the cladogram. Even though *Mayulestes* was originally interpreted as related to the Sparassodonta (e.g., Muizon 1998) in more recent analyses it has been related to the pucadelphyids (e.g., Horovitz and Sánchez-Villagra 2003; Horovitz et al. 2009; Forasiepi 2009; Ladevèze and Muizon 2007).

Even though they have been matter of discussion for decades, other (non-Tiupampian) Paleogene marsupials from southern South America do not usually form part of phylogenetic analyses, mainly because they are represented by scarce materials. Only a few analyses included several Itaboraian taxa from Brazil (Ladevèze and Muizon 2010; Oliveira and Goin 2011) and a few taxa from Argentina (Goin et al. 2009). Due to differences in taxa selection, these analyses are difficult to compare and offer quite dissimilar results. Ladevèze and Muizon (2010) included some Asian, Australian, and American taxa (the latter particularly from Bolivia and Brazil). They found that metatherians from Itaboraí are represented by different monophyletic clades: (1) *Epidolops*, *Gaylordia*, *Carolopaulacoutoia*, and *Derorhynchus* are part of the stem Australidelphia; (2) Protodidelphidae is the sister-taxon of Didelphidae; (3) *Guggenheimia* + *Mirandatherium* is the sister-clade of Marsupialia; (4) Pucadelphidae is the sister-taxon of all the clade represented in (3); (5) Boreometatheria is represented by *Bobbschaefferia*, *Pediomys*, *Didelphodon* , and *Eobrasilia* and they are related to the former. On the other hand, Oliveira and Goin (2011), in an analysis were they include almost exclusively Itaboraian taxa, found different relationships: (1) *Mirandatherium* + *Microbiotherium* + *Khasia* form a monophyletic group; (2) the group in (1) is the sister of Polydolopimorphia

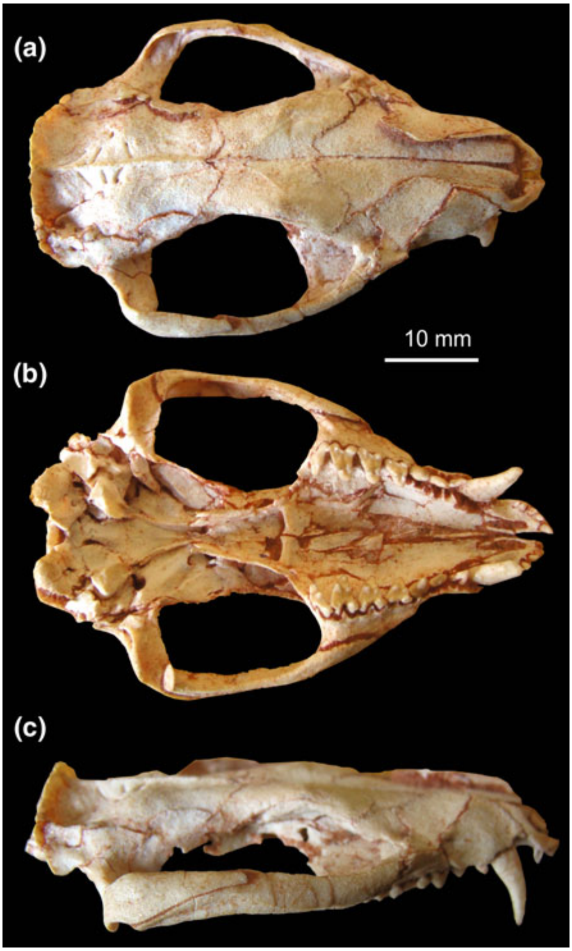

Fig. 5.1 *Mayulestes ferox* ("Ameridelphia," Mayulestidae); specimen MHNC (Museo de Historia Natural de Cochabamba, Bolivia) n° 1249 (type), almost complete skull in dorsal **a**, palatal **b** and lateral (**c** right side) views. (Specimen MHNC 1249 also includes both dentaries and a fairly complete postcranial skeleton). Scale: 10 mm. Total skull length is around 53 mm (see Muizon 1998). Early Paleocene (Tiupampian SALMA). Photographs by Laura Chornogubsky

(in this case *Epidolops* + *Gashternia* + *Roberthoffstetteria* + *Bobbschaefferia*); (3) Protodidelphidae is the sister-taxon from Didelphidae + remaining marsupials of Itaboraí. Finally, Goin et al. (2009) analyzed the relationship among several South American "pseudodiprotodont" taxa and they found two major groups: (1) Polydolopimorphia + *Glasbius* + *Microbiotherium*; and (2) Paucituberculata + *Derorhynchus* + *Pucadelphys*. Among polydolopimorphians, the Bonapartheriiformes includes the Argyrolagidae (*Proargyrolagus* + *Klohnia* in that analysis) *contra* Sánchez-Villagra (2001) who had previously regarded *Argyrolagus* as belonging to the Paucituberculata. Goin et al. (2009) suggested that Polydolopimorphia could be regarded as part of the Australidelphia.

Sparassodonta has been recovered as a natural group in many phylogenetic analyses (e.g., Forasiepi 2009; Forasiepi et al. 2014, among the most recent ones). Their relationships with other Metatheria are, however, a matter of discussion. To several authors, they are more closely related to South American and Australian groups than to basal North American and Asian metatherians (Rougier et al. 1998). In several analyses, Sparassodonta is either placed basally as part of the stem Metatheria, being *Pucadelphys* and *Andinodelphys* most closely related to Marsupialia (represented by *Patene* in Ladevèze and Muizon 2010), or as a sister-taxon of Herpethoteriids + Marsupialia (Forasiepi 2009). Muizon (1999) considered *Mayulestes* as basal to the Borhyaenoidea radiation, a hypothesis not followed subsequently.

Our concept of **Didelphimorphia** includes the Peradectoidea (Peradectidae and Caroloameghiniidae; see Horovitz et al. 2009; Goin 2006) and the Didelphoidea (Didelphidae and Sparassocynidae; Forasiepi et al. 2009 and literature cited). In the last years, a series of broad analyses have been carried out including living didelphids, some of them including molecular plus osteological structures (e.g., Flores 2009) or molecular, osteological and soft tissue structures (Jansa and Voss 2000, 2005; Voss and Jansa 2003, 2009; Jansa et al. 2006). All these works agree on the relationships among the four didelphid subfamilies (Didelphinae, Hyladelphinae, Caluromyinae, and Glironiinae): Didelphinae is the sister-taxon of Hyladelphinae; this clade is more related to the Caluromyinae, while Glironiinae is related to the latter (Voss and Jansa 2009; Flores 2009). Differences in the inferred relationships exist however among the tribes of Didelphinae. Voss and Jansa (2009) included the Didelphini , Marmosini, Metachirini, and Thylamini, an arrangement followed here (Table 5.1).

One South American group that has been variously related with the Australasian radiation is the **Paucituberculata**. The relationships of Paucituberculata, represented in most phylogenetic analyses by the living South American marsupial *Caenolestes* (but see Goin et al. 2009; Abello 2013, for a more complete representation of the group), is also variable, although in several analyses the group appear as more closely related to the Australidelphia (including *Dromiciops*; e.g., Nilsson et al. 2004, 2010; Ladevèze 2004; Ladevèze and Muizon 2007) than to the Didelphimorphia (Burk et al. 1999). Recent phylogenetic analyses support the existence of two main groups within the Paucituberculata: Caenolestoidea (including Caenolestidae) and Palaeothentoidea (including Pichipilidae, Palaeothentidae, and Abderitidae; Abello 2007, 2013; Goin et al. 2009).

Microbiotheria. Szalay's (1982) initial hypothesis of *Dromiciops* (and, consequently, all the Microbiotheria) being more closely related to Australian marsupials than to South American lineages has been repeatedly confirmed by a variety of phylogenetic analyses (see Reig et al. 1987 for a different point of view). Many studies have considered and/or tested the position of Microbiotheria either as sister-group of all other australidelphians or as a group nested within them (see, e.g., Aplin and Archer 1987; Reig et al. 1987; Marshall 1987; Marshall et al. 1990;

Kirsch et al. 1991, 1997; Luckett 1994; Szalay 1994; Springer et al. 1998; Burk et al. 1999; Colgan 1999; Palma and Spotorno 1999; Szalay and Sargis 2001; Phillips et al. 2001, 2006; Amrine-Madsen et al. 2003; Luo et al. 2003; Horovitz and Sánchez-Villagra 2003; Nilsson et al. 2003, 2004, 2010; Asher et al. 2004; Munemasa et al. 2006; Ladevèze 2007; Ladevèze and Muizon 2007, 2010; Meredith et al. 2008; Beck 2008, 2012; Beck et al. 2008; Horovitz

Table 5.1 Classification of Cenozoic South American metatherians

- Class MAMMALIA Linnaeus (1758)
  - Infraclass METATHERIA Huxley (1880)
    - Cohort "AMERIDELPHIA" Szalay (1982)
      - "AMERIDELPHIA" *incertae sedis*
        - Family PEDIOMYIDAE Simpson (1927)
          - *Khasia*
        - Family PUCADELPHYIDAE Muizon (1998)
          - *Andinodelphys*
          - *Mizquedelphys*
          - *Pucadelphys*
        - Family JASKHADELPHYIDAE Muizon (1991)
          - *Jaskhadelphys*
          - *Minusculodelphis*
        - Family MAYULESTIDAE Muizon (1994)
          - *Mayulestes*
        - Family PROTODIDELPHIDAE Marshall (1987)
          - *Carolocoutoia*
          - *Guggenheimia*
          - *Periprotodidelphis*
          - *Protodidelphis*
          - *Zeusdelphys*
        - Family DERORHYNCHIDAE Marshall (1987)
          - *Derorhynchus*
          - *Pauladelphys*
        - Family STERNBERGIIDAE Szalay (1994)
          - *Carolopaulaoutoia*
          - *Didelphopsis*
          - *Itaboraidelphys*
        - Family HERPETOTHERIIDAE Trouessart (1879)
        - Family indet.
          - *Eobrasilia*
          - *Incadelphys*
          - *Gaylordia*
          - *Marmosopsis*
          - *Monodelphopsis*

(continued)

Table 5.1 (continued)

- *Szalinia*
- *Tiulordia*
- Supercohort (continued)
  - Order SPARASSODONTA Ameghino (1884)
    - *Allqokirus*
    - *Nemolestes*
    - *Patene*
    - Family HONDADELPHIDAE Marshall et al. (1990)
    - Family HATHLIACYNIDAE Ameghino (1894)
    - Superfamily BORHYAENOIDEA Ameghino (1894)
      - *Lycopsis*
      - *Pharsophorus*
      - *Plesiofelis*
      - *Prothylacynus*
      - Family BORHYAENIDAE Ameghino (1894)
        - *Arctodictis*
        - *Australohyaena*
        - *Borhyaena*
      - Family PROBORHYAENIDAE Ameghino (1897)
        - *Arminiheringia*
        - *Callistoe*
        - *Paraborhyaena*
        - *Proborhyaena*
      - Family THYLACOSMILIDAE Riggs (1933)
        - *Anachlysictis*
        - *Patagosmilus*
        - *Thylacosmilus*
- Supercohort MARSUPIALIA Gill (1872)
  - Order DIDELPHIMORPHIA Gill (1872)
    - Superfamily PERADECTOIDEA Marshall et al. (1990)
      - Family PERADECTIDAE Crochet (1979)
        - *Peradectes*
      - Family CAROLOAMEGHINIIDAE Ameghino (1901)
        - *Caroloameghinia*
        - *Procaroloameghinia*
    - Superfamily DIDELPHOIDEA Gray (1821)
      - Family **DIDELPHIDAE** Gray (1821)
        - Subfamily GLIRONIINAE Voss and Jansa (2009)
          - *Glironia*
        - Subfamily CALUROMYINAE Kirsch (1977)
          - *Caluromys*
          - *Caluromysiops*
        - Subfamily HYLADELPHINAE Voss and Jansa (2009)
          - *Hyladelphys*
        - Subfamily DIDELPHINAE Gray (1821)
          - Tribe MARMOSINI Hershkovitz (1992)
            - *Marmosa*

(continued)

Table 5.1 (continued)

- *Micoureus*
- *Monodelphis*
- Tribe METACHIRINI Hershkovitz (1992)
- *Metachirus*
- Tribe DIDELPHINI Gray (1821)
- *Chironectes*
- *Didelphis*
- *Hyperdidelphys*
- *Lutreolina*
- *Philander*
- Tribe THYLAMYINI Hershkovitz (1992)
- *Chacodelphys*
- *Cryptonanus*
- *Gracilinanus*
- *Lestodelphys*
- *Marmosops*
- *Thylamys*
- Family SPARASSOCYNIDAE Reig (1958)
- Order PAUCITUBERCULATA Ameghino (1894)
- *Bardalestes*
- *Evolestes*
- *Riolestes*
- Superfamily CAENOLESTOIDEA Trouessart (1898)
- Family **CAENOLESTIDAE** Trouessart (1898)
- *Caenolestes*
- *Lestoros*
- *Rhyncholestes*
- Superfamily PALAEOTHENTOIDEA Sinclair (1906)
- *Perulestes*
- *Pilchenia*
- *Sasawatsu*
- Family PICHIPILIDAE Marshall (1980)
- Family PALAEOTHENTIDAE Sinclair (1906)
- *Carlothentes*
- *Palaeothentes*
- Family ABDERITIDAE Ameghino (1889)
- *Abderites*
- *Parabderites*
- Cohort AUSTRALIDELPHIA Szalay (1982)
- Order MICROBIOTHERIA Ameghino (1887)
- Family WOODBURNODONTIDAE Goin et al. (2007a, b)
- *Woodburnodon*
- Family **MICROBIOTHERIIDAE** Ameghino (1887)
- *Kirutherium*
- *Marambiotherium*

(continued)

Table 5.1 (continued)

Subfamily MICROBIOTHERIINAE Simpson (1929)
Dromiciops
Microbiotherium
Subfamily PACHYBIOTHERIINAE Goin et al. (in press)
Clenia
Eomicrobiotherium
Pachybiotherium
MICROBIOTHERIA or POLYDOLOPIMORPHIA
Family indet.
Mirandatherium
Order POLYDOLOPIMORPHIA Archer (1984)
Family GLASBIIDAE Clemens (1966)
Bobbschaefferia
Chulpasia
Palangania
Suborder BONAPARTHERIIFORMES Pascual (1980)
Superfamily BONAPARTHERIOIDEA Pascual (1980)
Family PREPIDOLOPIDAE Pascual (1980)
Incadolops
Prepidolops
Punadolops
Family BONAPARTHERIIDAE Pascual (1980)
Subfamily BONAPARTHERIINAE Pascual (1980)
Bonapartherium
Subfamily EPIDOLOPINAE Pascual and Bond (1981)
Epidolops
Family GASHTERNIIDAE Marshall (1987)
Gashternia
Family ROSENDOLOPIDAE Goin et al. (2010)
Rosendolops
Hondonadia
Superfamily ARGYROLAGOIDEA Ameghino (1904)
Praedens
Family GROEBERIIDAE Patterson (1952)
Groeberia
Family PATAGONIIDAE Pascual and Carlini (1987)
Patagonia
Family ARGYROLAGIDAE Ameghino (1904)
Argyrolagus
Suborder POLYDOLOPIFORMES Kinman (1994)
Cocatherium
Family SILLUSTANIIDAE Crochet and Sigé (1996)

(continued)

Table 5.1 (continued)

- *Roberthoffstetteria*
- *Sillustania*
- Family POLYDOLOPIDAE Ameghino (1897)
  - *Amphidolops*
  - *Archaeodolpos*
  - *Kramadolops*
  - *Pliodolops*
  - *Polydolops*
  - *Pseudolops*

We include all South American metatherian genera, living or extinct, mentioned in this volume. Families with living representatives are marked in bold. "Ameridelphia" is regarded as paraphyletic (see text). Pediomyidae is included among the South American "ameridelphians" because of *Khasia tiupampina*, here allocated within this family (see text). Classification of Sparassodonta follows Forasiepi (2009; see also Forasiepi et al. 2014), with the addition of *Allqokirus* as a basal member of the order (Muizon 1991). Classification of Didelphimorphia partially follows Horovitz et al. (2009; but see Williamson et al. 2012), with the inclusion of Caroloameghiniidae in Peradectoidea (Goin 2006). Classification within the Didelphidae follows Voss and Jansa (2009). Classification of Paucituberculata follows Abello (2007, 2013; see also Goin et al. 2009). Classification of Microbiotheria follows Goin and Abello (2013) and Goin et al. (in press). Classification of Polydolopimorphia follows Goin et al. (2009 and in press). After Chornogubsky and Goin (2015) we include the basal polydolopiformes *Sillustania* and *Roberthoffstetteria* in the family Sillustaniidae Crochet and Sigé (1996). Classification within the Polydolopidae follows Chornogubsky (2010)

et al. 2008, 2009; May-Collado et al. 2015). In several of these analyses, *Dromiciops* appears as the sister-group of all the extant Australian marsupial radiation (Australidelphia sensu Szalay 1982), being some examples those studies carried out by Amrine-Madsen et al. (2003), and Palma and Spotorno (1999) for molecular phylogenies, and Beck (2012) for an analysis based on morphological data (but using molecular constraints). The relationship between *Dromiciops* and other Australidelphia vary from the one described before (i.e., sister-taxa of all other Australidelphia), at the base of Diprotodontia (e.g., Horovitz and Sánchez-Villagra 2003; Beck 2008; Nilsson et al. 2010), as a sister-taxon of Dasyuromorpha (e.g., Wible et al. 2001; Ladevèze and Muizon 2007), as a sister-taxon of Phalangeriformes + Diprotodontia (Luo et al. 2003), or even related with part of the former (see e.g., Nilsson et al. 2004; Ladevèze and Muizon 2010). Asher et al. (2004) performed both morphological and molecular phylogenetic analyses proving different results (*Dromiciops* as sister-group of Diprotodontia in the former and as sister-taxon of Peramelemorphia in the latter).

Polydolopimorphia. The dental pattern of all polydolopimorphians can be easily derived from a microbiotherian one; this argues in favor of regarding the latter as part of the Australidelphian radiation (see also Goin et al. 2009). Examples of basal polydolopimorphians are the Glasbiidae, represented since the Late Cretaceous of North America (the Lancian *Glasbius*) to mid-Paleogene times in South America (e.g., the Riochican *Palangania*; see Table 5.1).

Bonapartheriiformes are one of two major lineages of polydolopimorphians. They were abundant in Paleogene times, though one of its most derived lineages (the Argyrolagidae) evolved since the early Oligocene up to the late Pliocene. Polydolopimorphians successfully occupied frugivorous and omnivorous niches (Bonapartherioidea), as well as more stictly herbivorous ones (Argyrolagoidea).

Even though it was originally considered as a caroloameghinid "opossum-like" marsupial (Marshall et al. 1983), more recent analyses suggest that *Roberthoffstetteria nationalgeographica* belongs with the Polydolopimorphia (Goin et al. 2003), as a basal clade of the Polydolopiformes (sensu Goin et al. 2009; see Table 5.1). More recently Chornogubsky and Goin (2015) have argued in favor of the affinities between *Roberthoffstetteria* and *Sillustania*, the latter from the early Paleogene of Laguna Umayo, Perú. In consequence, they included both genera in the Sillustanidae, a family of Polydolopiformes previously recognized by Crochet and Sigé (1996). In turn, the most derived group of Polydolopiformes (and of all Metatheria, probably) are grouped in the Polydolopidae. They constitute a strictly southern group, restricted to Patagonia and the Antarctic Peninsula (see Woodburne and Zinsmeister 1982, 1984; Chornogubsky 2010; Chornogubsky et al. 2009).

The phylogenetic relationships of all metatherians, and especially of North and South American metatherians, will continue to be the subject of intense scrutiny in the next years. New findings, character sources, and methodological approaches will probably shed additional light; much research is still to be done on the basal "Ameridelphia," for instance. In the following section we offer a brief description of the salient morphological features of South American's major lineages of metatherians (see also Table 5.1). As mentioned previously, the "Ameridelphia" is not regarded here as a natural group.

5.2 Diversity of South American, Cenozoic Metatherians

5.2.1 "Ameridelphia" Incertae Sedis

We provisionally regard as "Ameridelphia" *incertae sedis* a series of (probably, non-marsupial) metatherian lineages whose affinities are still far from clear (cf, e.g., Forasiepi 2009; Ladevèze and Muizon 2010; Oliveira and Goin 2011). Part of the problem lies in the fragmentary nature of many of their representatives (but not all;

among mayulestids and pucadelphyids there are fairly complete specimens; Muizon 1991, 1998). Another problem is the lack of comprehensive phylogenetic analyses that include both North and South American taxa from the late Cretaceous-Cenozoic. A preliminary, welcome study in this regard is the analysis recently performed by Williamson et al. (2012, 2014), including representatives of most North American extinct genera of Metatheria, as well as a few Paleocene South American ones: *Roberthoffstetteria*, *Szalinia*, and *Pucadelphys*. A relevant result of this study is the inclusion of these South American taxa within a group (their Node 19; see Williamson et al. 2014: Fig. 6) that also includes Herpetotheriids, Pediomyids, and "Peradectidae"

Representatives of these "ameridelphian" lineages show, already in the early Paleogene of South America (early Paleocene to early Eocene) many distinctive features that account for their taxonomic and adaptive diversities. A series of phylogenetic analyses are currently being performed on these groups by some of us, so we will refrain from advancing further hypotheses on their relationships until these analyses are made. A few considerations on the morphological diversity and inferred paleobiological aspects of these forms are mentioned in Chap. 6 of this volume.

5.2.2 Sparassodonta

All sparassodonts share some features in the overall morphology of the skull: with very few exceptions (e.g., *Lycopsis longirostrus*) the snout is short to very short; the nasals extend posteriorly overpassing the anterior line of the orbits; a naso-lacrimal contact is common; the orbital process is generally subtle and the orbits are open (except in thylacosmilids); the zygomatic arch is strong; the occipital region is backwardly expanded and the nuchal crest is strong in all taxa. Almost invariably, the palate is posteriorly divergent and incisive and maxillary foramina are present. Several modifications to this overall pattern occur mostly as an adaptive response to diet ; for instance, in most hathliacynids the snout is longer than in the remaining sparassodonts. The sagittal crest is strong; the postorbital constriction is pronounced; the postorbital processes are developed but does not close the orbit; the lateral outline of the skull is flattened; the zygomatic arch is lower; the dentary is dorsoventrally and consistently shallow and the symphysis is ligamentous.

In many borhyaenoids (e.g., *Borhyaena*, *Prothylacynus*, *Lycopsis*), the snout is short; the postorbital constriction is weaker than in hathliacyniids; there is no postorbital bar and the postorbital processes are weak or absent; the sagittal and frontal crests are variably developed; the zygomatic arch is high and strong; the dentary is dorsoventrally deeper and massive; the symphysis may be ankylosed and variably fussed in the adults.

In some borhyaenids (*Arctodictis* (Fig. 5.2), *Australohyaena*) and the majority of proborhyaenids (*Arminiheringia*, *Callistoe*, *Paraborhyaena*), the snout is short; the

Fig. 5.2 *Arctodicts sinclairi* (Sparassodonta, Borhyaenidae); specimen MLP (División Paleontología Vertebrados, Museo de La Plata, Argentina) n° 85-VII-3-1, an almost complete skull in lateral right) view. Many other parts of the postcranial skeleton have also been preserved. Total skull length is 240 mm (see Forasiepi 2009). Early Miocene (Colhuehuapian SALMA). Drawing by Martín Barrios

sagittal crest is weak; the lateral outline of the skull is dome-shaped; the postorbital constriction is weak; there is no postorbital bar; the dentary is dorsoventrally deep and massive; and the fussed symphysis generally extends to the posterior root of p3 or the anterior root of m1.

In the sabre-toothed Thylacosmilidae (Fig. 5.3), the snout is extremely short; the hypertrophied upper canines are implanted dorsally at the posterior border of the orbit; the lateral outline of the skull is dome-shaped; the postorbital bar is complete (*Thylacosmilus*) or nearly complete (*Patagosmilus*); the sagittal crest is strong; the zygomatic arch is high and robust; the back of the skull is high and the nuchal crest is very strong; the dentary is massive, with a conspicuous flange that allocates the hypertrophied upper canines (see Riggs 1934; Marshall 1976, 1977b, 1978, 1979, 1981; Goin and Pascual 1987; Babot et al. 2002; Forasiepi 2009; Forasiepi and Carlini 2010; Forasiepi et al. 2014).

The basic adaptations of the sparassodont molar pattern are related to their faunivorous (e.g., small Hathliacynidae) to hypercarnivorous (e.g., Borhyaenidae) diets. Upper molars have reduced protocones; small paracones which are basally fused to the (much larger) metacones; the postmetacrista is large to very large; the stylar shelf is reduced to absent, and stylar cusps are absent in almost all members

Fig. 5.3 *Thylacosmilus atrox* (Sparassodonta, Thylacosmilidae); specimen MMP (Museo Municipal de Mar del Plata, Argentina) n° 1443; an almost complete skull and jaws in lateral (left) view. Total skull length is 210 mm (Goin and Pascual 1987). Late Pliocene (Chapadmalalan SALMA). Drawing by Martín Barrio. Reproduced from Goin and Pascual (1987: plate1) with permission of the Academia Argentina de Ciencias Exactas, Físicas y Naturales (Buenos Aires)

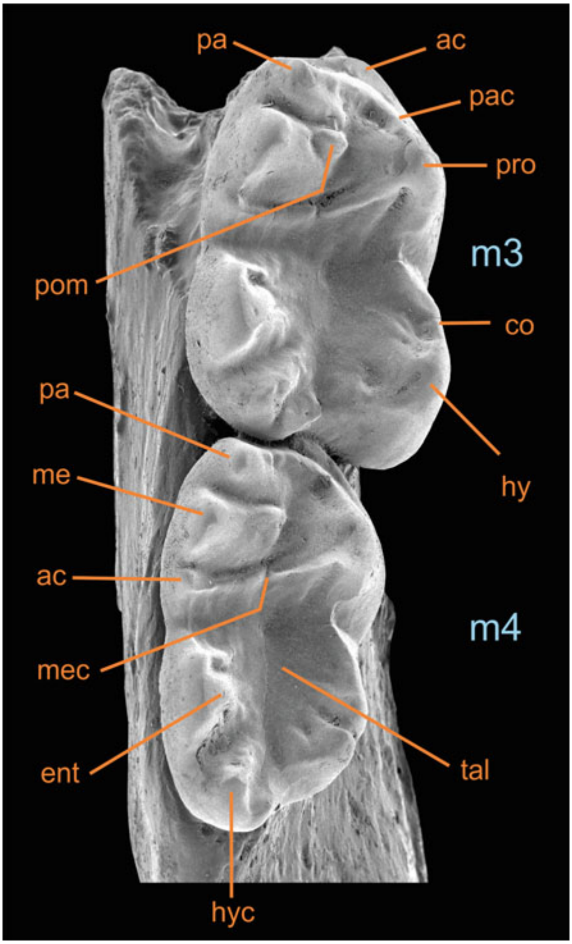

Fig. 5.4 *Caroloameghinia mater* (Didelphimorphia, Peradectoidea; Caroloameghiniidae; see Goin 2006); specimen MLP n° 83-III-1-170b, a fragment of right dentary with m3-4 in occlusal view. Length of m3: 4.13 mm. Late Eocene (Barrancan subage of Casamayoran SALMA). *Abbreviations* ac, anterior cingulum (in m3) and accessory cuspule (in m4); co, cristidobliqua; ent, entoconid; hy, hypoconid; hyc, hypoconulid; me, metaconid; mec, metacristid; pa, paraconid; pac, paracristid; pom, postmetacristid; pro, protoconid

of the order. In turn, lower molars have large to very large paracristids and reduced to absent metaconids in the trigonids, while the talonids are reduced to absent. Summarizing, the crushing structures are reduced to absent, while the cutting ones are well developed. Masticatoy movements were predominantly orthal (vertical; Zimicz 2012) (Fig. 5.4).

5.2.3 *Didelphimorphia*

The skull of living didelphids is anteroposteriorly elongated; the braincase and the rostrum are equally developed, with the nasals extending posteriorly between the

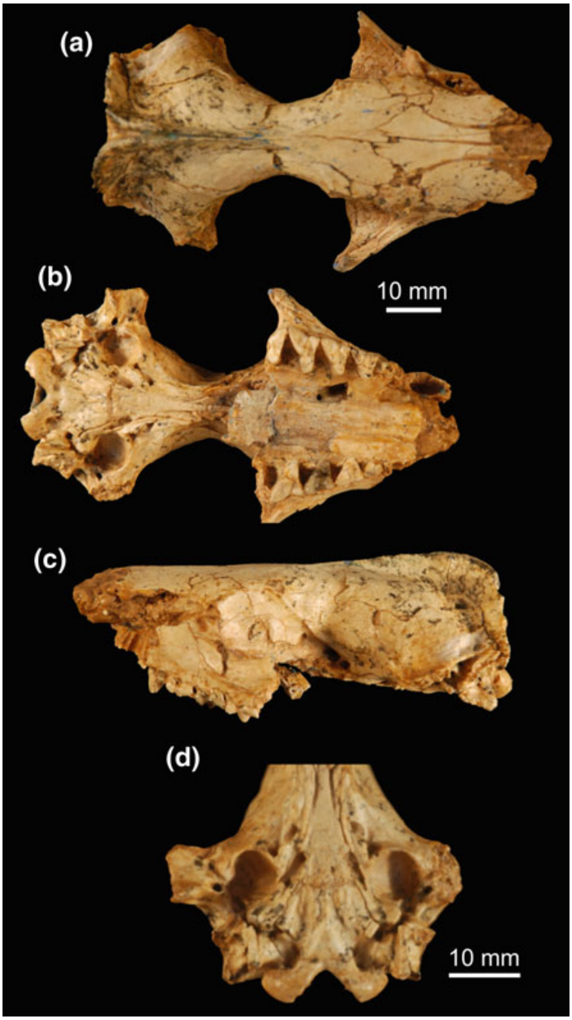

Fig. 5.5 *Hyperdidelphys dimartinoi* (Didelphimorphia, Didelphidae); specimen MBB (Museo Municipal de Bahía Blanca, Argentina) n° 11.248 (type); almost complete skull lacking both jaws, the tip of the snout and the zygomatic archs, in dorsal **a**, palatal **b** and lateral (left, **c**) views. **d** Detail of basicranial region. Skull length is 79 mm (Goin and Pardiñas 1996). Scale: 10 mm. Late Pliocene (Chapadmalalan SALMA). Photograph by Bruno Pianzola

lacrimals—they are wider posteriorly than anteriorly. The only vacuity present in the rostrum is the prominent infraorbitary foramen; the zygomatic arch is variably robust and invariably includes a jugal process. The lacrimals have a facial process and two or more foramina; the orbital margin formed by the lacrimal is smoothly rounded. The interparietal bone is fused to the supraoccipital one; the occiput is not projected backwardly and the nuchal crest is moderated; the sagittal and frontal crests reach different degrees of development, from absent to strong (a strong sagittal crest is well developed in the carnivorous *Hyperdidelphys*; see Fig. 5.5). The palate is perforated by several openings; the incisive foramina are surrounded by the premaxillary–maxillary suture; the maxillopalatine fenestrae are present (except in *Caluromys* and *Caluromysiops*) and never extend posteriorly to the molar row; palatal foramina are absent; the palatine fenestrae are sometimes present; the dentary consists of an anteroposteriorly elongate horizontal ramus, an ascending ramus with well-developed coronoid and condylar processes, and a posteroventral angular process; the mandibular symphysis is never fused; the retromolar space is either imperforate or pierced by tiny nutrient foramina; the masseteric fossa is always imperforate, and its posteroventral border is bounded by a distinct shelf; the articular condyle is transversely elongate and more or less semicylindrical (see Voss and Jansa 2009).

The molar pattern in didelphimorphians does not differ strikingly from that of basal "ameridelphians," one clear difference among the upper molars being the reduced stylar shelf (though usually not the stylar cusps). In the Caroloameghiniidae (Peradectoidea) molars are bunodont and a series of wrinkles on the enamel surface. Other difference is the reduction and/or absence of conules (paraconule and metaconule) at the distal end of the pre- and posprotocristae. In the lower molars, it is noticeable the reduction of the hypoconulid among the Didelphoidea (Didelphidae and Sparassocynidae) . As recently reviewed by Goin (2006), the dental pattern of the Caroloameghiniidae include quite derived features, as the presence of accessory neocusps in the lower molars (see Fig. 5.4). As inferred from paleobiological analyses, the masticatory movements in the Didelphimorphia were predominantly orthal (Zimicz 2012).

5.2.4 Paucituberculata

The cranial anatomy of paucituberculatans is mostly known from representatives of the living genera *Caenolestes*, *Ryncholestes,* and *Lestoros*). The skull is elongated and laterally compressed; the orbits are small; the zygomatic arch is somewhat reduced and laterally expanded; the interorbital zone is wide; the braincase is bulbous, being the largest component of the skull; finally, there are two large vacuities above the infraorbital foramen, anterior to the orbits; the dentary is slender with the ventral border straight; the symphysis is long and weak; the coronoid process is large and broad with the anterior border curved; the masseteric fossa is broad with a tiny foramen in the lower edge; the angular process is moderately inflected.

The most noticeable features of the Paucituberculatan dentition are the proportionally enormous, procumbent lower incisors (see Osgood 1921). The molar pattern is characterized by the gradual acquisition of a quadrangular profile in occlusal view, by means of the expansion of the metaconule. The paracone and metacone basally coalesce, and merge, at the bases of the very large stylar cusps B (at the anterolabial edge of the molar), and C + D (at the posterolabial edge), respectively (Figs. 5.6 and 5.7). Lower molars, except the first one (m1) progressively show a tendence to fuse the paraconid and metaconid, and frequently have

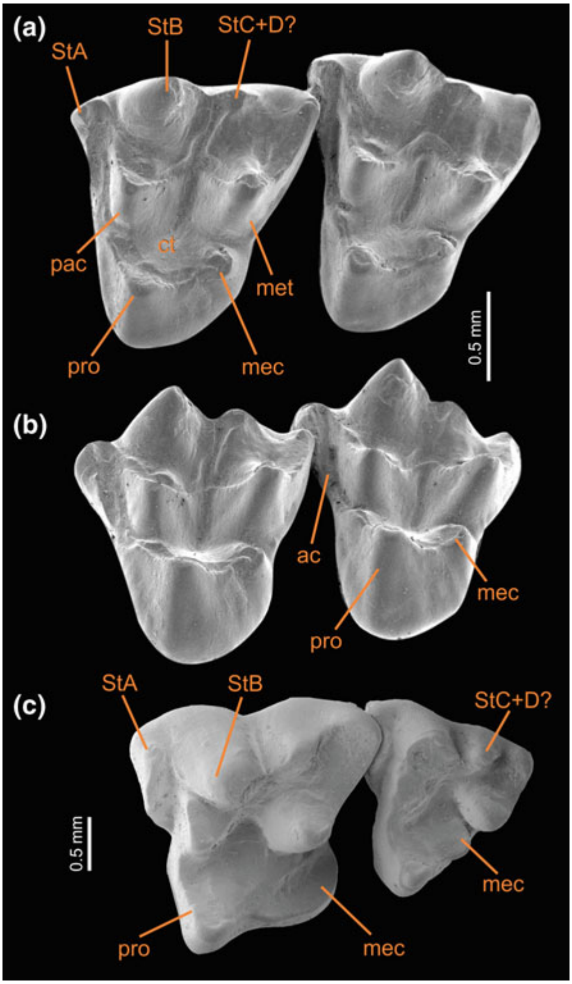

Fig. 5.6 **a**, **b** *Bardalestes hunco* (Paucituberculata, family indet.); specimen LIEB-PV (Laboratorio de Investigaciones en Evolución y Biodiversidad, Esquel, Argentina) n° 1135 (type), left upper molars M2-3, in occlusal (**a**) and occlusal–lingual (**b**) views (Goin et al. 2009). Paso del Sapo Fauna, Early Eocene. **c** *Evolestes hadrommatos* (Paucituberculata, family indet.); specimen MNHN-Bol (Museo Nacional de Historia Natural, La Paz, Bolivia) n° 96-400 (type); detail of left M2-3 in occlusal view (the specimen is a fragmentary skull preserving part of the rostrum, palate, skull roof and a few upper teeth; see Goin et al. 2007a). Salla Beds, Late Oligocene. Scale: 0.5 mm. *Abbreviations* ac, anterior cingulum; ct, trigon basin; mec, metaconule; met, metacone; pac, paracone; pro, protocone; St, stylar cusp

sharp, well-developed crests anterior (and sometimes posterior) to the entoconid. The last upper and lower molars are usually reduced to very reduced. Masticatory movements were inferred as predominantly orthal (Zimicz 2012; Fig. 5.7).

5.2.5 Microbiotheria

The cranial morphology of Microbiotheria is mostly known from the living microbiotheriid *Dromiciops gliroides*. The skull is oval in dorsal view; the snout is relatively short; the nasals do not overpass the orbital line; there is not postorbital

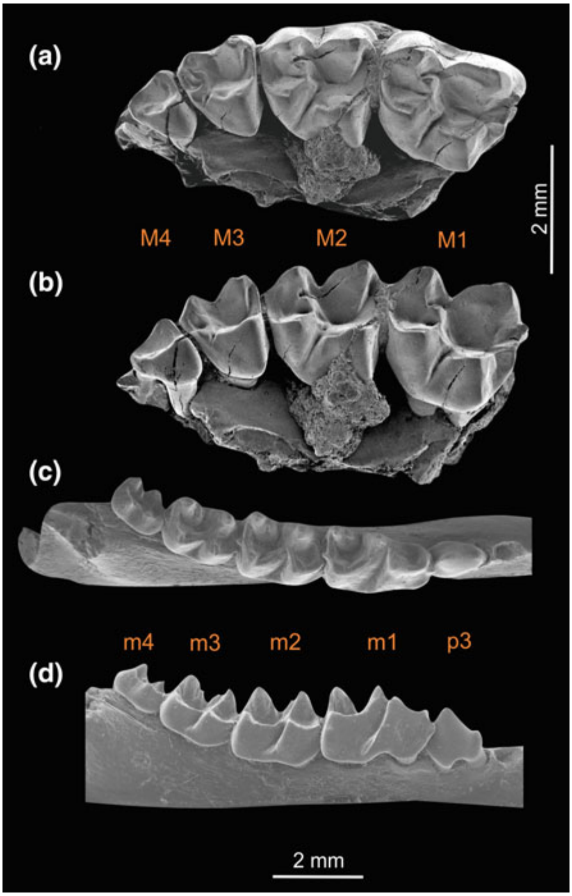

Fig. 5.7 *Palaeothentes minutus* (Paucituberculata, Palaeothentidae). **a**, **b** Specimen MACN (Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina) n° 3286, a right maxillary with M1-4 in occlusal (**a**) and lingual (**b**) views. **c**, **d** Specimen MACN n° 8464 (type), a right dentary with incisors (not shown here) and p3-m4, in occlusal (**c**) and labial (**d**) views. Early middle Miocene (Santacrucian SALMA) (Abello 2007, 2013). Scale: 2 mm. *Abbreviations* M1, M2, M3, M4: upper molars; m1, m2, m3, m4, lower molars; p3, posteriormost lower premolar. We thank Alejandra Abello for facilitating the scanning micrographs of the specimens

process; the orbits are large and open; the zygomatic arch is gracile and strongly inflected at the maxillary–jugal suture; the tympanic bullae are very large, inflated, as well as the brain case; the sphenoid crest is present; the palate is backwardly divergent, the incisive foramens are large; the maxillary foramens are large and occupy the half part of the posterior palate; the dentary is slender, with the ventral inflection weakly defined (see Giannini et al. 2004; Marshall 1982).

A remarkable aspect of the microbiotherian dentition is, among the lower incisors, the lack of a buttressed ("staggered") i3 (Hershkovitz 1995). The molar pattern is characterized, in the upper molars, by the strong and wide protocones and a reduced stylar shelf, with almost absent stylar cusps; the paracone and the metacone are subequal in size and height, while the centrocrista is straight. Among the most generalized microbiotherians, the Woodburnodontidae, stylar cusps can still be distinguished (Fig. 5.8). In the lower molars the paraconid is reduced, the talonid is wide, and, in the first two molars, the hypoconulid tends to locate quite centrally on the posthypocristid. Masticatory movements were predominantly orthal.

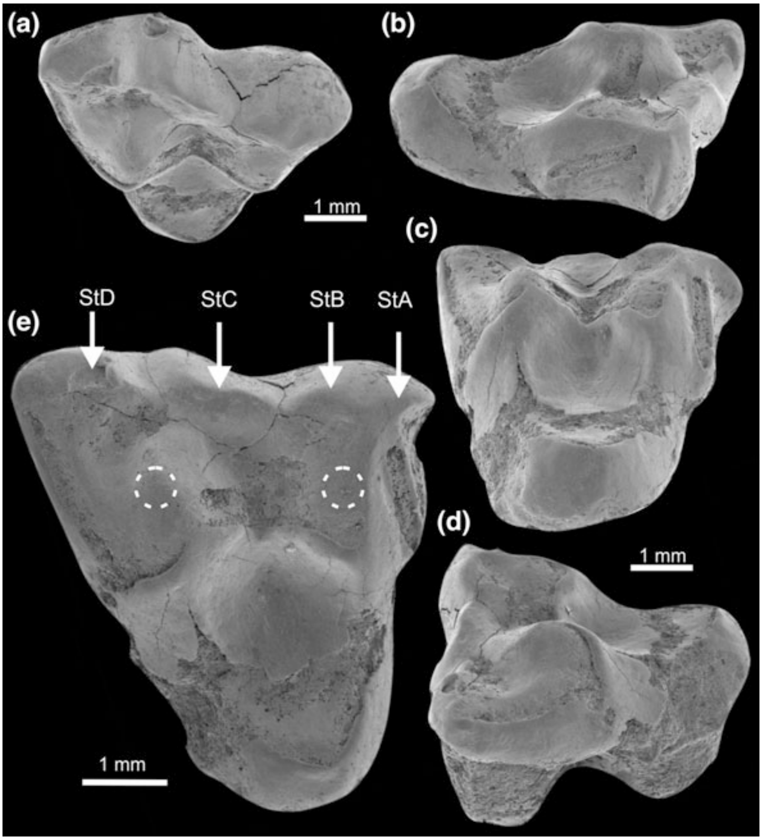

Fig. 5.8 *Woodburnodon casei* (Microbiotheria, Woodburnodontidae); specimen MLP n° 04-III-1-2 (type); upper-right molar (M2 or M3) in labial **a**, anterior **b**, lingual **c**, posterior **d** and occlusal (**e**) views (see Goin et al. 2007b). In (**e**), circles drawn in white dashed lines indicate the inferred location of the (very worn) paracone and metacone cusps (Goin et al. 2007b). Early Eocene (La Meseta Fm). Scale: 1 mm. *Abbreviations* St, stylar cusp. Reproduced from Goin et al. (2007b: Fig. 1) with permission of the Asociación Geológica Argentina (Buenos Aires)

5.2.6 Polydolopimorphia

All known polydolopimorphians share some characteristics in the skull morphology: the braincase is globular, a character most evident in those types with narrows snouts; the nasals are posteriorly expanded to the level of the orbits; the zygomatic arch is strong; the palate widens at the molar row level; the incisive foramina are always present in different sizes and maxillary and palatal foramina are also present. Deviations from this pattern can be observed among representatives of various lineages.

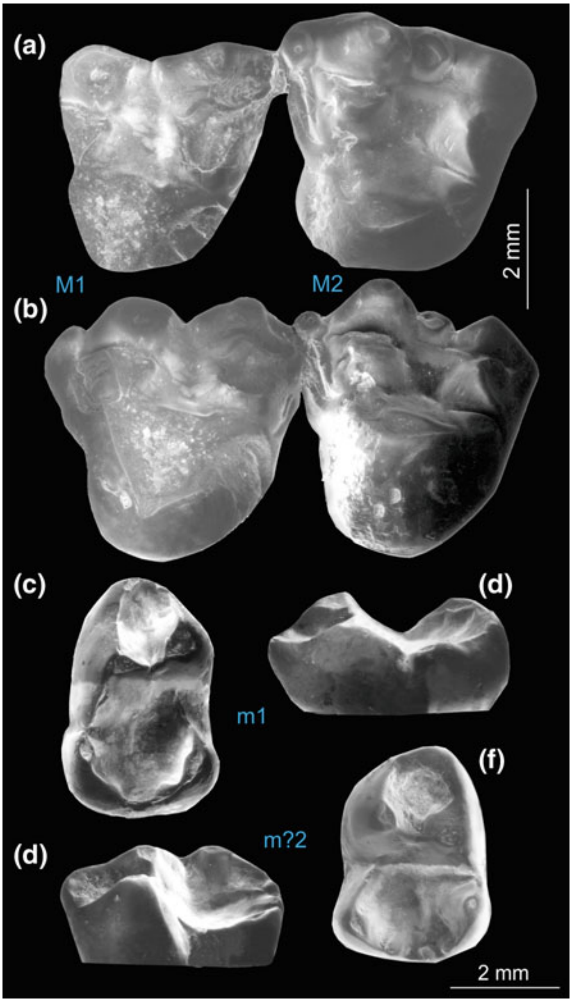

Fig. 5.9 *Palangania brandmayri* (Polydolopimorphia, Glasbiidae; see Goin et al. 1998). **a**, **b** Specimen UNSJB-PV (Vertebrate paleontology Collection, Universidad Nacional de la Patagonia, C. Rivadavia, Argentina) n° 114 (type), left M1-2 in occlusal (**a**) and lingual (**b**) views. **c**, **d** Specimen MLP n° 40-VI-20-19, right m1 in occlusal (**c**) and lingual (**d**) views. **e**, **f** Specimen MLP n° 79-I-17-6, left m?2 in labial (**e**) and occlusal (**f**) views. Early Eocene (Riochican SALMA). Scale: 2 mm

Basal Polydolopimorphians are represented by glasbiids (e.g., *Chulpasia*, *Palangania*) which have a relatively generalized molar pattern (Fig. 5.9). In the Bonapartheriiformes Bonapartheroidea (i.e., *Bonapartherium* and *Epidolops*), the snout is short and wide; the zygomatic arch is lower; the postorbital processes are subtle or absent; the orbit is completely open; the postorbital constriction is moderate; the palate is suboval or diamond-shaped; the incisive foramina are minute and the maxillary fenestrae are apparently large; the dentary is strong and short; the deep masseteric fossa is anteriorly bordered by a strong crest on the anterior border of the high and wide coronoid process; the masseteric crest is well developed and posteriorly wider; the condyle is strong and slightly elevated above the dental level; the angular process is strong and inwardly inflected, with its posterior tip pointing

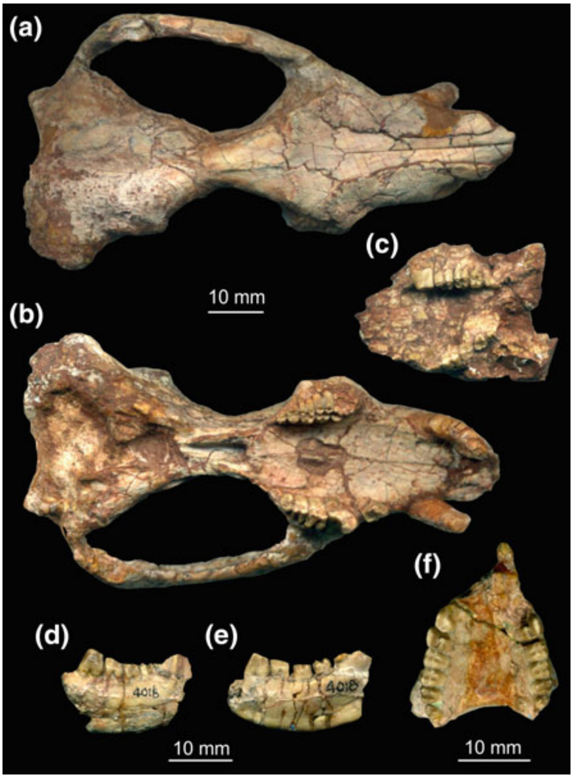

Fig. 5.10 *Bonapartherium hinakusijum* (Polydolopimorphia, Bonapartheriiformes, Bonapartheriidae). **a**, **b** Specimen MMP n° 1408, a partial skull in dorsal (**a**) and palatal (**b**) views. **c** PZVL (Colección Paleozoología Vertebrados, Fundación Miguel Lillo, Tucumán, Argentina) n° 4191, a fragmentary skull in palatal view; **d**–**f** PVL 4018 (type), a partial skull and both jaws; **d** left jaw in labial view; **e** right jaw in lingual view; **f** skull in palatal view (Pascual 1980, 1981). Middle to late Eocene (Lumbrera Fm). Scale: 10 mm. Photographs by Bruno Pianzola

upwards; the symphyseal region is thin and narrow before p2; the maximum height of the bone is below the sectorial complex p3-m1 (see Pascual 1980, 1981; Paula Couto 1952 (Fig. 5.10).

In the Bonapartheriiformes Argyrolagoidea (i.e., *Argyrolagus scagliai*), the snout is narrow with the nasal cavity protruding upon the incisive line; the zygomatic arch is lower and has a prominent jugal process; the infraorbital foramen is large; the orbits are anteriorly closed and backwardly opened with a noticeable orbital border; the temporal region is reduced; the palate is oval with large incisive foramens; the auditive bulla is proportionally enormous and inflated; the dentary is relatively gracile, with very large lower incisors implanted at the level of m3 (Simpson 1970 (Fig. 5.11).

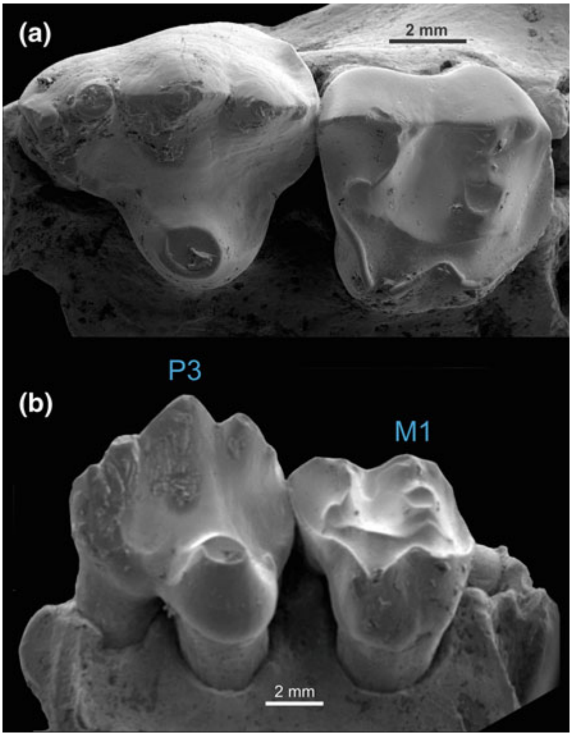

Fig. 5.11 *Gashternia carioca* (Polydolopimorphia, Bonapartheriiformes, Gashterniidae; see Goin and Oliveira 2007); specimen MCN-PV (Museu de CiénciasNaturais, FundacaoZoobotánica do Rio Grande do Sul, Porto Alegre, Brazil) n° 1801 (type); left maxillary with P3-M1 in occlusal (**a**) and lingual (**b**) views. Early Eocene (Itaboraian SALMA). Scale: 1 mm

In the Polydolopiformes (i.e., *Kramadolops mckennai*: the only known skull partially preserved), the snout is elongate and narrow; the palate widens across the molar row reaching the maximum width near the anterior base of the zygomatic arches and the braincase is fairly expanded and globular as in other polydolopimorphians (Flynn and Wyss 2004).

The generalized molar pattern of polydolopimorphians is quadrangular, as in the Paucituberculata; however, its evolution followed a different pathway. In the upper molars, the paracone and metacone ere twinned with the similarly sized StB and StD respectively (see, e.g., Fig. 5.11)—in paucituberculatans, the stylar cusps are proportionally enormous (Fig. 5.7 a-b). At the lingual edge, the expanded metaconule forms the posterolingual corner of the tooth; different from Paucituberculatans, it is leveled with the protocone and the trigon basin. In the lower molars, the paraconid and metaconid are somewhat reduced and close to each other; the hypocone is large though not salient as in most paucituberculatans. Several variants can be observed from this basic pattern; for instance, that of Argyrolagoids (Goin et al. 2010; Goin and Abello 2013) or of the Polydolopiformes (Goin et al. 2003; Chornogubsky et al. 2009; see Fig. 5.12). Ectental, oblique, and propalinal movements have been inferred for several lineages of this order (Zimicz 2011, 2012, 2014).

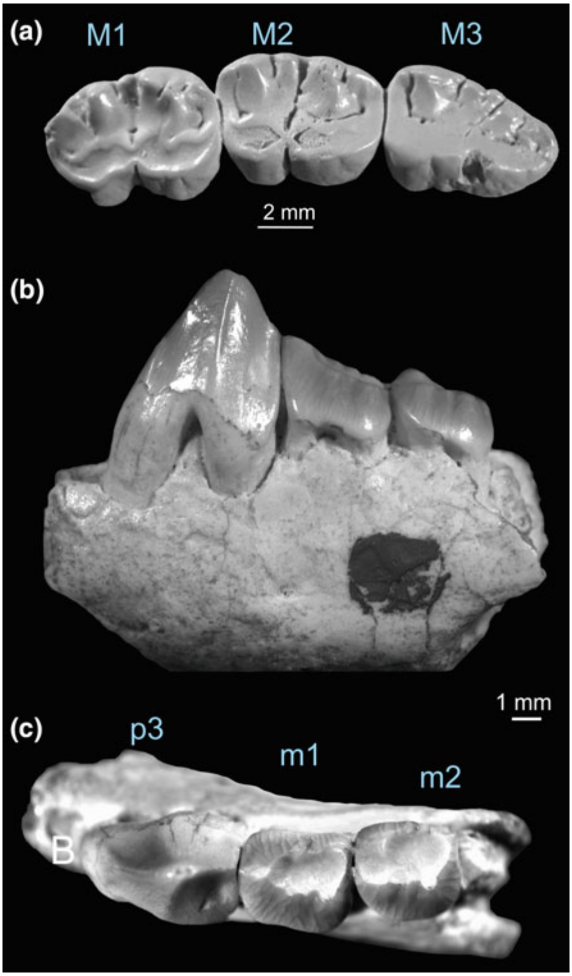

Fig. 5.12 **a** *Kramadolops hernandezi* (Polydolopimorphia, Polydolopiformes, Polydolopidae); cast of specimen AMNH (American Museum of Natural History, New York, USA) n° 28,932 (type); a left maxillary with M1-3. Late Eocene (BarrancanSubage of the Casamayoran SALMA). Scale: 2 mm. **b**, **c** *Pliodolops rothi* (Polydolopimorphia, Polydolopidae); specimen MLP 11-122 (type), a fragment of left dentary with p3-m2 in labial (**b**) and occlusal (**c**) views. Early to middle Eocene. Scales: **a** 2 mm; **b**, **c** 1 mm. For recent reviews on the taxonomy of the Polydolopidae, see Chornogubsky (2010). *Abbreviations* M1, M2, M3, upper molars; m1, m2, lower molars; p3, posteriormost lower premolar

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