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Heterochrony, dental ontogenetic diversity, and the circumvention of constraints in marsupial mammals and extinct relatives

Analía M. Forasiepi and Marcelo R. Sánchez-Villagra

Abstract.— In marsupial mammals and their extinct relatives—collectively, metatherians—only the last premolar is replaced, but the timing of dental eruption is variable within the group. Our knowledge of fossils metatherians is limited, but is critical to understanding several aspects of the evolution and morphological diversification of this clade. We analyzed the sequence of eruption of 76 specimens of metatherians, including Sparassodonta, an extinct clade of specialized carnivores from South America. In Sparassodonta (1) the P3/p3 erupt simultaneously, in common with some didelphids (in other didelphids, p3 erupts before P3, whereas in the remaining didelphids, some peramelids, one caenolestid, and *Pucadelphys* this order is reversed); (2) the upper and lower molars at the same locus erupt more in synchrony than in other carnivorous metatherians in which the lower molars clearly precede the upper equivalents; (3) the upper canine in thylacosmilids and proborhyaenids is hypselodont; (4) species with similar molar morphologies have different morphologies of the deciduous premolars, suggesting diverse diets among the juveniles of different taxa; (5) deciduous teeth are functional for a long period of time, with thylacosmilids even retaining a functional DP3 in the permanent dentition. The retention of the DP3 and the hypertrophied and hypselodont upper canine of thylacosmilids represent clear heterochronic shifts. Specializations in the timing of dental eruption and in the deciduous tooth shape of sparassodonts are evolutionary mechanisms that circumvent constraints imposed by the metatherian replacement pattern and increase morphological disparity during ontogeny.

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Introduction

Mammalian teeth are a major subject in studies of macroevolution and development, given their diversity and rich fossil record (Evans et al. 2007). Tooth morphology and the sequence of tooth eruption provide information on life-history evolution (Smith 2002), taxonomy, and phylogeny (Martin 1997; Luo et al. 2004; Asher and Lehmann 2008). In paleontology, the study of dental eruption has become feasible with the development of non-invasive imaging (Cifelli et al. 1996).

Because tooth homologization is required for valid comparisons of dental series across species, studies have analyzed topographical position, morphology, and replacement patterns (Lockett 1993; O'Leary et al. 2013). In mammals, the replacement pattern segregates tooth categories, with two series of teeth in the premolars—deciduous and successional den-

tion—and only one series in the molars (e.g., Owen 1845; Clemens and Lillegraven 1986). In marsupials only the last premolar—DP3—dp3/P3—p3—is replaced by successional dentition (Flower 1867, 1869; Turnbull 1971; Clemens 1979; Cifelli et al. 1996; Cifelli and Muizon 1998; Lockett 1993; Lockett and Woolley 1996; Rougier et al. 1998; Kobayashi et al. 2002; Kielan-Jaworowska et al. 2004; Luo et al. 2004; Ungar 2010; see van Nievelt and Smith 2005a for a discussion about the anterior teeth), possibly linked to prolonged lactation (Tyn-dale-Biscoe and Renfree 1987; Lockett 1993; Luo et al. 2004; but see van Nievelt and Smith 2005a for an alternative view). This feature has been shown to be present in stem marsupials and indeed may characterize Metatheria, the clade that includes all mammals more closely related to extant marsupials than to placentals. Marsupialia is the crown group and is formed

by all the descendants of the last common ancestor of extant marsupials (Rougier et al. 1998).

Determination of the timing of dental eruption in fossils requires a large sample and an understanding of the phylogenetic context. Sparassodonta (Figs. 1, 2), a clade of stem marsupials from the South American Cenozoic (Forasiepi 2009), provides a very suitable case of study given their rich fossil record. Sparassodonta includes about 60 species of continental predators, with a temporal range of approximately 55 Myr, from the Paleocene to the middle Pliocene (Marshall 1978, 1979, 1981; Forasiepi 2009). The group displays tooth morphologies consistent with carnivory. Nearly 90% of the taxa were recognized as hypercarnivores, whereas the remainder have been identified as either mesocarnivores or hypocarnivores (Prevosti et al. 2013). Among Sparassodonta, Thylacosmilidae includes the species with the most specialized dental morphology. This group ranges from the early Miocene to late Pliocene (Goin et al. 2007; Forasiepi and Carlini 2010) (Fig. 2E,F). Thylacosmilids were convergent with placental sabertooth felids (e.g., Marshall 1976, 1978; Prevosti et al. 2010) and this is of great interest in studies of metatherian modularity and evolutionary constraints (Werdelin 1987, 1988; Goswami et al. 2011; Bennett and Goswami 2013). These factors together make sparassodonts an ideal subject for examining character evolution, evolutionary convergences, developmental patterns, and constraint as they relate to dental morphology and eruption, the main objective of this contribution. Specific objectives are (1) to determine the sequence of eruption of the last upper and lower premolars and molars in the Sparassodonta and (2) to interpret the morphology of the deciduous dentition in the context of metatherian phylogeny; and (3) to recognize heterochronies and constraints in the ontogeny in this extinct group of stem marsupials.

Dental Eruption Sequence in Metatherians.—The timing of the postcanine eruption varies within Metatheria. In the stem taxon *Deltaitheridium*, the last definitive premolar erupts at the time of, or even before, the third molar, and the fourth molar is the last element to

erupt (Rougier et al. 1998). In other stem taxa (e.g., *Alphadon*, *Incadelphys*, *Pucadelphys*, *Mayulestes*) and most living marsupials, the eruption of the P3/p3 is delayed, with the last premolar erupting about the same time as the last molar (Cifelli et al. 1996; Cifelli and Muizon 1998; Rougier et al. 1998). Didelphids, the opossums from the Americas, exhibit differences in the precise timing of eruption, including minor variations within individuals of the same species (e.g., Tribe 1990; Martin 2005; van Nievelt and Smith 2005b; Astúa and Leiner 2008). Some didelphids (e.g., *Didelphis*, *Chironectes*, *Lutreolina*, and *Philander*) and microbiotherians (monito del monte) show the M4 erupting slightly after the P3, whereas in *Metachirus* and some species of *Monodelphis* the M4 and the P3 erupt in synchrony. For many other studied didelphids (*Caluromys*, *Lestodelphys*, *Thylamys*, *Marmosa*, and some species of *Monodelphis*), the M4 erupts before the P3 (Tribe 1990; Voss and Jansa 2003; Martin 2005; van Nievelt and Smith 2005b; Astúa and Leiner 2008) (Table 1). One peculiar case in the South American fauna is the Caenolestidae, in which the P3 erupts relatively late in the ontogeny, considerably after the eruption of M4 (Luckett and Hong 2000).

The Australian marsupials exhibit contrasting patterns. The P3 erupts concomitant with M3 in Myrmecobiidae and Phalangeridae, or even with M2 in Phascolarctidae, Burramyidae, Vombatidae, and Petauridae, or is variable as in Macropodidae (Springer et al. 1997; Wroe and Archer 1995). An early P3 eruption is also found in some dasyuromorphians (Flower 1867).

In the generalized tribosphenic pattern, found in several marsupial clades, the lower molar crests—paracristid—shear against the distal border of the preceding upper molar crests—postmetacrista—(facet 2 sensu Crompton 1971) and the elements act as parts of a functional complex (Ungar 2010). Correspondingly, the eruption of the lower molars precedes that of the equivalent upper element (Petrides 1949; Tribe 1990; Giannini et al. 2004; van Nievelt and Smith 2005a,b; Astúa and Leiner 2008).

Deciduous Premolar in Metatherians.—The generalized mammalian deciduous teeth

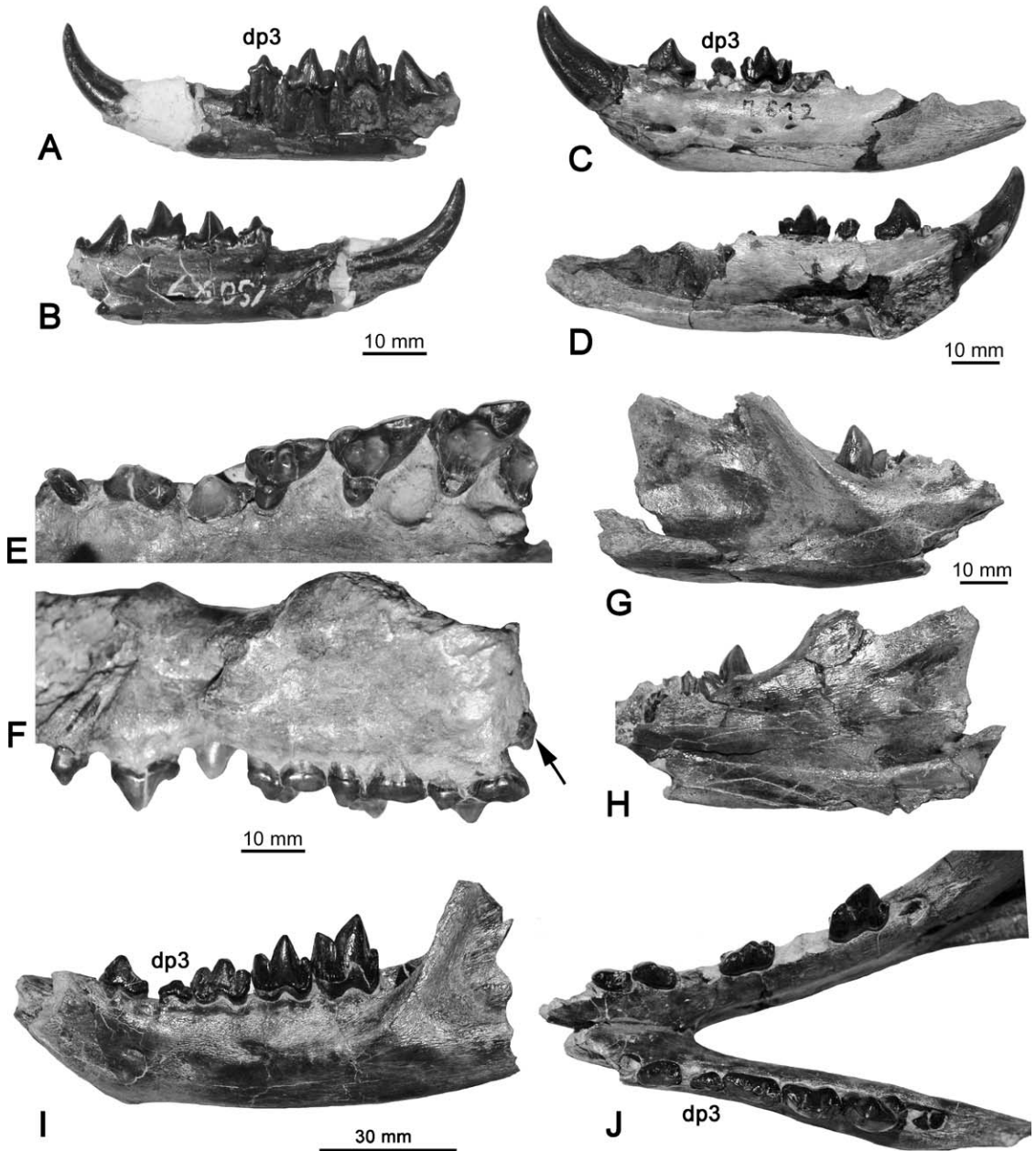


FIGURE 1. A, B, *Cladosictis patagonica* YPM PU 15097, left dentary in labial (A) and lingual (B) views. C–H, *Prothylacynus patagonicus* MACN-A 642, left dentary in labial (C) and lingual (D) views; MACN-A 5931–32, detail of left maxilla with the dentition in occlusal (E) and labial (F) views; MACN-A 5931–32, fragment of right dentary in labial (G) and lingual (H) views (the arrow indicates the position of the M4 whose crown is completely out of its crypt). I, J, *Borhyaena tuberata* MPM-PV 3554, left dentary in labial view (I), both dentaries in occlusal view (J).

(Fig. 3) are usually smaller, narrower and lower, with thinner enamel, slender roots, and crown morphologies different from the permanent teeth (Ungar 2010; Zack 2012). In most living and fossil metatherians, the DP3/dp3

have a complex molariform occlusal shape (Flower 1867; Thomas 1887; Bensley 1903; Petrides 1949; Archer 1976; Cifelli et al. 1996; Rothecker and Storer 1996; Cifelli and Muizon 1998; Voss et al. 2001; Voss and Jansa 2003).

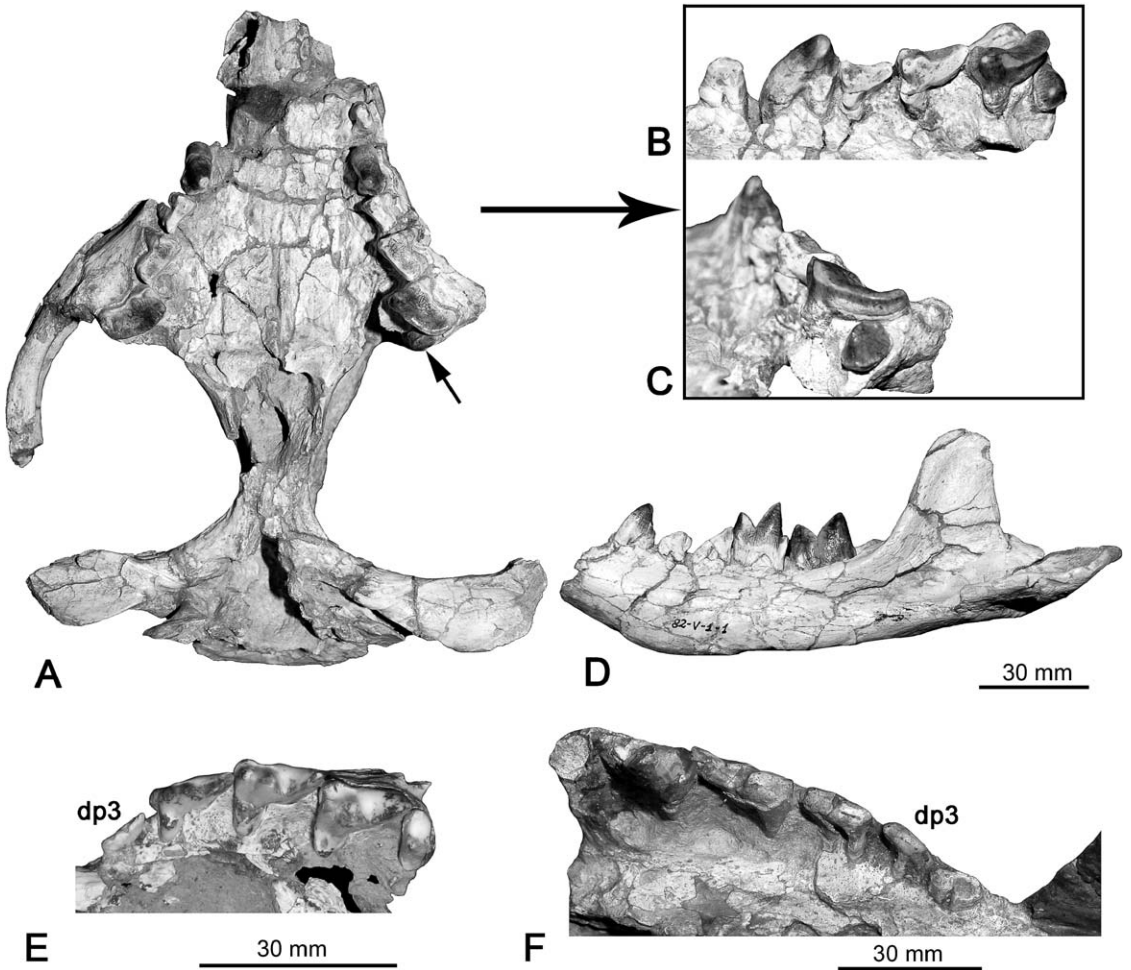


FIGURE 2. A–D, *Arminiheringia* sp. MLP 82-V-1-1, skull in ventral view (A), detail of the left maxilla in occlusal (B) and postero-occlusal (C) views, not in scale; fragment of left dentary in labial (D) view. E, *Patagosmilus goini* MLP 07-VII-1-1, left maxilla in occlusal view. F, *Thylacosmilus atrox* MLP 35-X-41-1, right maxilla in occlusal view.

This is a plesiomorphic trait, as stem mammals (e.g., *Morganucodon*) and diverse Mesozoic mammals (*Dryolestes*, *Zhangotherium*, *Slaughteria*) (Turnbull 1971; Lockett 1993; Martin 1997; Kobayashi et al. 2002; Luo et al. 2004) show a more complex morphology in the deciduous than in the successor tooth at the same locus.

The deciduous premolar is functional in most metatherians, including living marsupials. In natural populations of the didelphids *Didelphis* and *Philander*, the deciduous premolars were found attached to the dentary and maxilla even in sexually mature specimens (Díaz and Flores 2008). The dasyuromorphian *Myrmecobius* exhibits an extreme condition,

retaining the deciduous teeth in adulthood (Winge 1882; Dependoff 1898; Tate 1951; Archer 1975). Alternatively, in other marsupials including some dasyuromorphians (e.g., some species of *Dasyurus*, *Sarcophilus*, and *Thylacinus*; Flower 1869; Thomas 1887; van Nievelt and Smith 2005a) and caenolestids (e.g., *Caenolestes* [Lockett and Hong 2000]), the deciduous premolar is lost early in the development or is vestigial and does not achieve functionality.

Materials and Methods

We observed the tooth eruption in 117 metatherian specimens and restored the sequence of eruption of the last upper and lower

TABLE 1. Inferred sequence of tooth eruption of last premolars and last molars (from data in Supplementary Appendix 1).

Taxon	Sequence of tooth eruption		
	Premolar/ molar	Last premolars	Last molars
<i>Chironectes</i>	P3 → M4 m4 → p3	P3 = p3	m4 → M4
<i>Didelphis</i>	P3 → M4 m4 → p3	P3 → p3	m4 → M4
<i>Lutreolina</i>	P3 → M4 m4 → p3	P3 → p3	m4 → M4
<i>Monodelphis</i>	M4 → P3 m4 → p3	P3 → p3	m4 → M4
<i>Philander</i>	P3 → M4 m4 → p3	P3 → p3	m4 → M4
<i>Caluromys</i>	M4 → P3 m4 → p3	p3 → P3	m4 → M4
<i>Thylacinus</i>	P3 → M4 p3 → m4		m4 → M4
<i>Dasyurus</i>	P3 → M4 p3 → m4		m4 → M4
<i>Echymipera</i>	P3 → M4 m4 → p3	P3 → p3	m4 → M4
<i>Dromiciops</i>	m4 → p3		m4 → M4
<i>Pucadelphys</i>	P3 → M4 p3 → m4	P3 → p3	m4 → M4
cf. <i>Arminiheringia</i>	P3 → M4 p3 → m4		M4 → m4
<i>Lycopsis</i>	p3 → m4	P3 = p3	M4 → m4

molars and premolars in 14 metatherians: *Chironectes minimus*, *Didelphis* spp., *Lutreolina crassicaudata*, *Monodelphis* spp., *Philander opossum*, and *Caluromys* spp. (Didelphidae), *Thylacinus cynocephalus* (Thylacinidae), *Dasyurus* spp. (Dasyuridae), *Echymipera* spp. (Peramelidae), *Dromiciops gliroides* (Microbiotheriidae), *Pucadelphys andinus*, *Aminiheringia* sp., *Lycopsis* sp., and *Thylacosmilus atrox* (stem marsupials), based on the information provided by 76 specimens. Two taxa—*Dasyurus* (four specimens) and *Dromiciops* (two specimens)—and the fossil taxa (mostly only one specimen) were analyzed together with those taxa with six specimens or more. The metatherian specimens analyzed are housed in American Museum of Natural History, New York, USA (AMNH); Instituto Miguel Lillo, Miguel Lillo Collection, Tucumán, Argentina (CML); Field Museum of Natural History, Chicago, USA (FMNH); Hessisches Landesmuseum, Darmstadt, Germany (HLMD); Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Buenos Aires, Argentina (MACN-A, Ameghi-

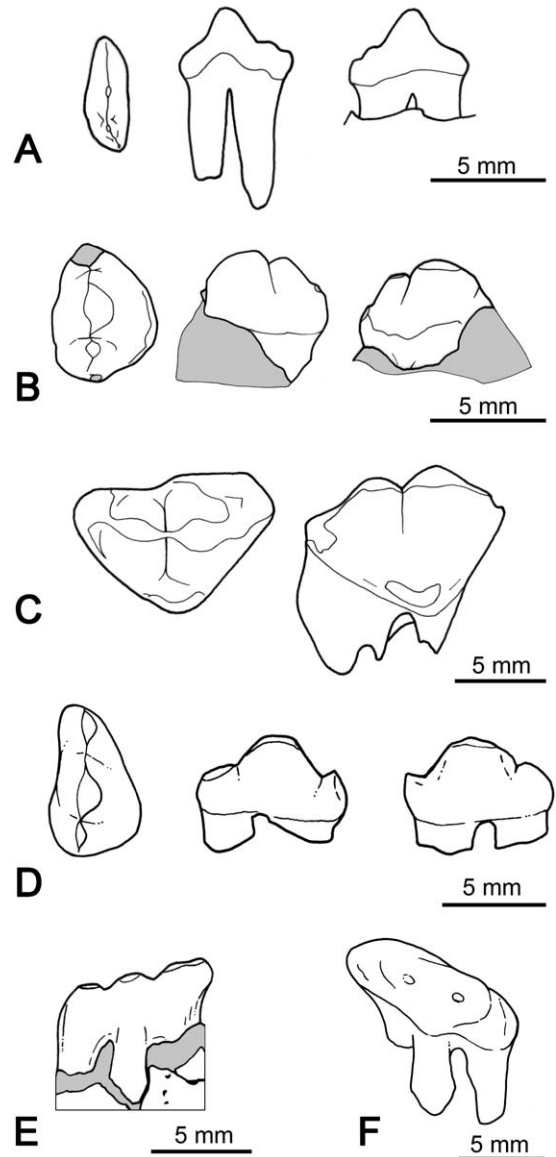


FIGURE 3. Schematic drawings of the deciduous dentition of Sparassodonta. A, Left dp3 of *Cladosictis patagonica* YPM PU 15097, in occlusal, labial, and lingual views. B, Left dp3 of *Prothylacynus patagonicus* MACN-A 642, in occlusal, labial, and lingual views. C, Left DP3 of cf. *Pharsophorus* sp. AMNH 29591, in occlusal and lingual views. D, Left dp3 of *Borhyaena tuberculata* in occlusal, labial, and lingual views. E, Last left permanent upper premolar (DP3) of *Patagosmilus goini* MLP 07-VII-1-1 in lingual view. F, Last right permanent upper premolar (DP3) of *Thylacosmilus atrox* MLP 35-X-41-1 in occlusal view.

no Collection; MACN-Ma, Mastozoology Collection; Museo de La Plata, La Plata, Argentina (MLP); Museo Municipal de Ciencias Naturales de Mar del Plata “Lorenzo

Scaglia," Argentina (MMP); Museum national d'Histoire naturelle, Paris, France (MNHN); Museo Regional Provincial "Padre M. Jesús Molina," Río Gallegos, Argentina (MPM-PV); Natural History Museum, London, England (NHM); Naturhistorisches Museum Basel, Switzerland (NMB); Naturhistorisches Museum Bern, Switzerland (NMBE); Paläontologisches Institut und Museum, Universität Zürich, Switzerland (PIN UZ); Zoologische Sammlung, Tübingen, Germany (SZ); Zoologische Staatssammlung München, Munich, Germany (SZM); University of California, Museum of Paleontology, Berkeley, USA (UCMP); University Museum of Zoology, Cambridge University, Cambridge (UMZC); Yacimientos Petrolíferos Fiscales de Bolivia, Paleontology Collection, Centro de Tecnología Petrolera, Santa Cruz, Bolivia (YPFB Pal), Collection of Princeton University, Yale Peabody Museum, New Haven, USA (YPM PU).

Information about the specimens studied, the stage of eruption of the individuals, and the sequence of eruption restored are provided in the Supplementary Appendix 1, Tables 1 to 4. The timing of tooth eruption and the morphology of the deciduous teeth of the Sparassodonta are described in Supplementary Appendix 2. The identification and taxonomic comments on the fossil specimen MACN-A 642, here assigned to *Prothylacynus patagonicus*, are justified in Supplementary Appendix 2.

The term crypt refers to the bony compartment surrounding a developing tooth. The locus is the specific site of a single tooth. The alveolus is the bone socket formed around each root (Hillson 2005).

We used the condition of the dentition to divide the animals into four age group categories (Anders et al. 2011): (1) juvenile, up to the time that the entire adult dentition is fully erupted; (2) adult, the teeth have moderate wear to the point of the loss of the inner profile of the first molar; (3) late adult show heavy occlusal wear, and (4) senile dentition shows loss of functional structures.

To investigate sequence heterochrony, we analyzed tooth eruption in Sparassodonta with the Event Pairing approach (Smith 2001). We first categorized the individual

tooth eruption state into five states: State 0, non-erupted; State 1, less than half of the crown erupted; State 2, more than half of the crown erupted; State r3, crown of tooth out of crypt but tooth not in the same horizontal plane as the other teeth, or crypt still opened; and State 3, completely erupted (tooth in the same horizontal plane as the other teeth; Fig. 4). Teeth that had been secondarily lost were coded as State 3. If the same locus differed between the left and right sides, the higher state was scored. States were treated as additive.

Pairs of events were plotted in a consensus phylogeny (based on Voss and Jansa 2003; Beck et al. 2008; Forasiepi 2009). If the first element in the event pair occurs first, it is given a score of 0; if the two elements appear simultaneously, the score is 1; if the second element in the event pair occurs first, it is given a score of 2. Some simultaneous events reflect to a great extent lack of resolution (e.g., in *Thylacosmilus* the timing of eruption of m4 and p3 [Fig. 5B], timing of eruption of m4 and p3 [Fig. 5D], and timing of eruption m4 and M4 [Fig. 5F] are unknown but these appear as simultaneous in the trees), something common in studies of ontogenetic sequences (Sánchez-Villagra 2002).

Results

In Sparassodonta, the P3/p3 erupts at a similar time as the M4/m4 (e.g., *Lycopsis longirostris*, UCMP 38061; *Prothylacynus patagonicus*, MACN-A 5931–32; Fig. 1E–H) and the P3/p3 completes its eruption slightly before the M4/m4 (e.g., *Arminiheringia* sp., MLP 82-V-1-1; Fig. 2A–D). Additionally, one specimen of *Borhyaena* (MPM-PV 3554; Fig. 1I,J) demonstrates that the eruption of the last molar starts when the deciduous premolar is still functional and firmly attached. In contrast, the studied dasyuromorphians (*Thylacinus* and *Dasyurus*) show that the complete eruption of P3/p3 is an early event and precedes even the eruption of the M3/m3 (Fig. 5C,D). In our study, the premolar loci homologies of *Dasyurus* follow Luckett (1989, 1993; see Thomas 1887; Archer 1975, 1976 for an alternative interpretation).

In sparassodonts (*Prothylacynus* MACN-A 5931–32; *Lycopsis longirostris*, UCMP 38061;

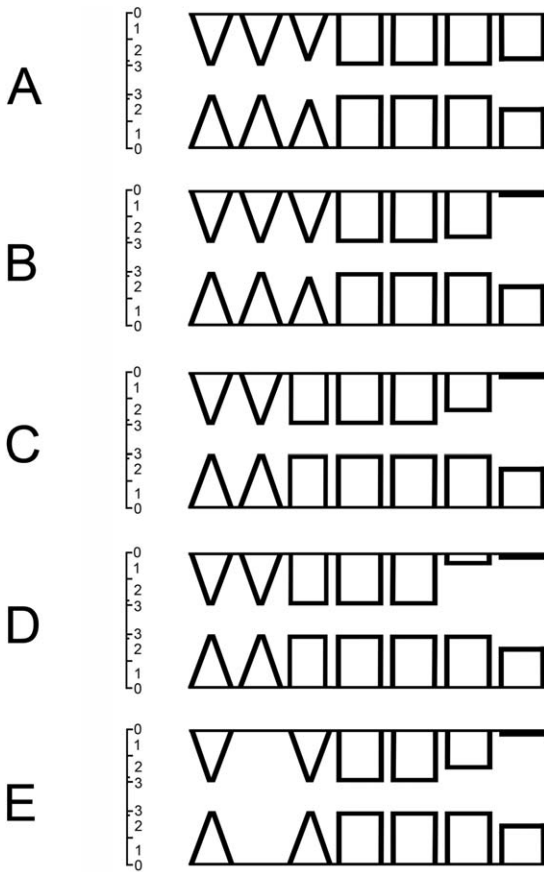


FIGURE 4. Schematic representation of the timing of tooth eruption in sparassodonts (A) and marsupials (B–E), with more than half of the m4 out of its crypt. A, Sparassodonts *Prothylacynus patagonicus* MACN-A 5931–32 and *Lycopsis longirostrus* UCMP 38061. B, C, Didelphimorphians *Didelphis marsupialis* NHM 1949.1.18.2 (B) and *Monodelphis domestica* MACN 14756 (C). D, Microbiotherian *Dromiciops gliroides*, ZSM 1954/215. E, Dasyuromorphian *Sarcophilus harrisi* UMZC A6 9/4. The horizontal line represents the alveolar border. In sparassodonts, when the m4 is more than half out of its crypt, the M4 is completely out of its crypt, but the maxillary bone is retracted.

Arminiheringia sp. MLP 82-V-1-1; Fig. 5E), the equivalent upper and lower molar loci erupt in closer synchrony than in other stem metatherian or faunivorous and carnivorous crown marsupials. The crown of M4 is completely exposed while the base of the crown of its lower counterpart remains inside its crypt (Figs. 1E–H, 2A–D). However, the maxilla around the M4 is retracted, indicating that this tooth is still not functional and the eruption is not completed. In other faunivorous or carnivorous metatherians, as exemplified

by didelphids, *Dromiciops*, and dasyuromorphians (Fig. 4), when the m4 has more than half of the crown exposed, the M4 is less exposed than in sparassodonts or completely inside its crypt. In all the studied marsupials, the M4 precedes the m4 (Table 1). Furthermore, in some specimens, the eruption of the M3 matches that of the m4, and when the M4 is erupting, the lower counterpart has already finished. This condition is evident in *Thylacinus* (Fig. 6E–I), which is a metatherian ecologically comparable to sparassodonts (Figueirido and Janis 2011). In Diprotodontia (e.g., *Phalanger*, *Spilocuscus*, and *Dorcopsis*; Supplementary Appendix 1, Table 1), the eruption of equivalent upper and lower molar loci is simultaneous.

The eruption of upper and lower premolars is variable among the taxa and within the studied specimens. The P3 and p3 erupt in synchrony in sparassodonts, and this pairing is seen in some didelphid specimens (e.g., some specimens of *Chironectes* and *Didelphis*). In other didelphids, the p3 can precede the P3 (e.g., *Caluromys*, *Marmosa*, *Micoureus*), or the order can be reversed (e.g., some specimens of *Chironectes*, some specimens of *Didelphis*, *Lutreolina*, *Philander*, *Monodelphis*), some peramelids (e.g., some specimens of *Echymipera*, *Perameles*), one caenolestid (*Caenolestes*), and *Pucadelphys* (Fig. 5F, Table 1, Supplementary Appendix 1).

The canine of the large-sized sparassodonts (*Lycopsis longirostrus* UCMP 38061, *Prothylacynus patagonicus* MACN-A 5931–32) apparently completes its eruption after the complete eruption of the postcanine dentition. The roots of the upper canines of Thylacosmilidae and Proborhyaenidae were open throughout life (Simpson 1948; Marshall 1978; Marshall et al. 1990; Babot et al. 2002). In adult specimens of Proborhyaenidae (e.g., *Callistoe vincei*, PVL 4187; *A. auceta*, MACN 10972 and 10970; and *P. gigantea*, MACN-A 52–382) open roots were reported in the lower canines, whereas in a senile specimen of *Proborhyaena gigantea* (MLP 79-XII-18-1) the roots were closed (Bond and Pascual 1983). This demonstrates that proborhyaenids have a semihypselodont lower canine in which the roots close in the late adult to senile stage (Babot et al. 2002).

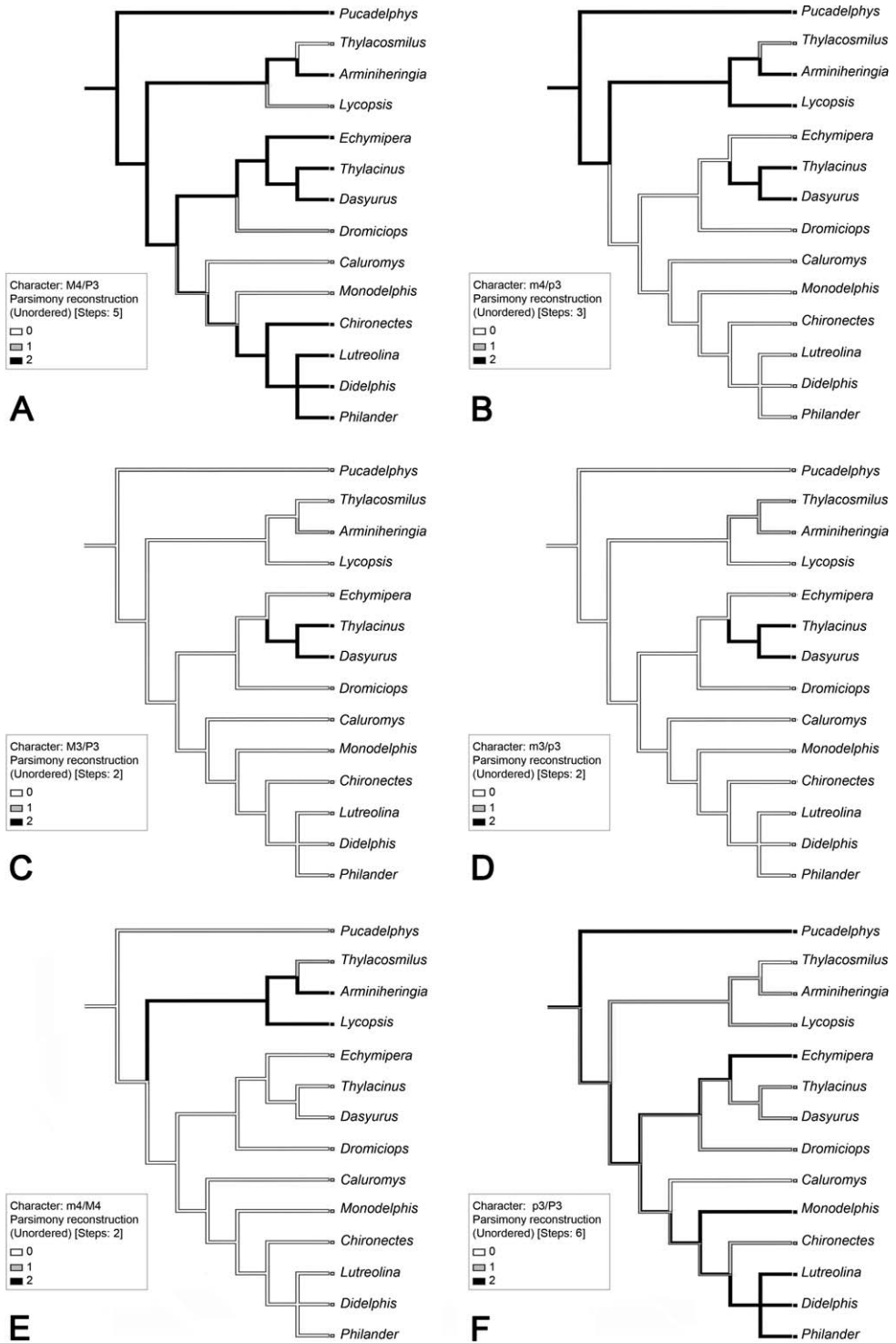


FIGURE 5. Consensus phylogeny of the studied metatherian taxa with plotted event pairs: M4/P3 (A), m4/p3 (B), M3/P3 (C), m3/p3 (D), m4/M4 (E), and p3/P3 (F). White (0), first element in the event pair occurs before the second; gray (1), elements occurs simultaneously; black (2), first element in the event pair occurs after the second.

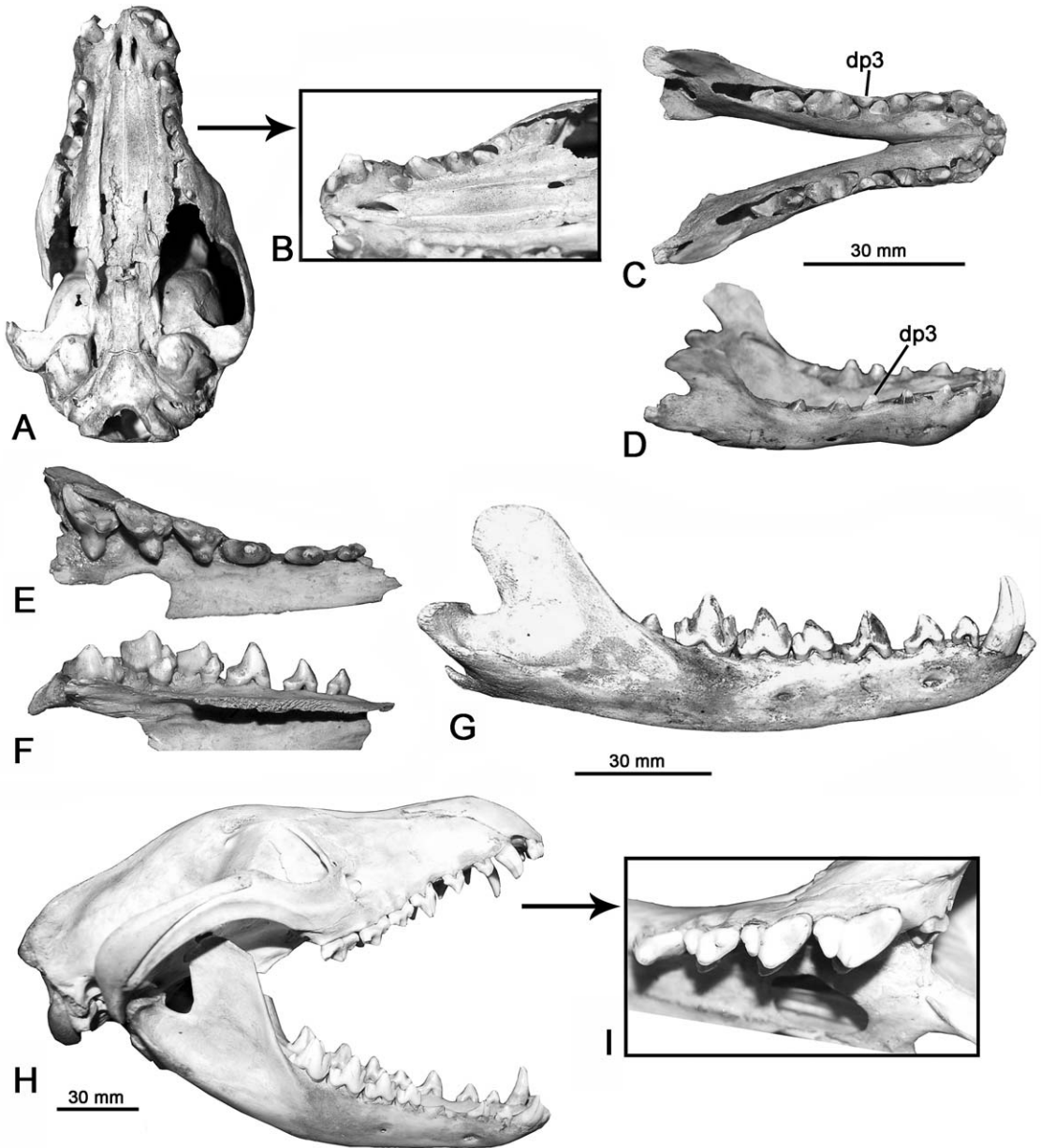


FIGURE 6. *Thylacinus cynocephalus*. A–D, UMZC A6 7/10, skull in occlusal view (A), detail of the right maxilla in medial view (B) not in scale; dentaries in occlusal (C) and labial views (D). E–G, MNHN 1883-352 A 12.413, right maxilla in occlusal (E) and lingual (F) views; right dentary in labial view (G). H, I, UMZC A6 7/7, skull and dentary in lateral view (H) and detail of the left maxilla in latero-occlusal view (I).

The DP3/dp3 in sparassodonts is molariform but simpler than in other stem marsupials and didelphids, with a greater shearing function (Fig. 3). We recorded different morphologies in the deciduous teeth of sparassodonts. In *Prothylacynus* (Figs. 1C,D, 3B) the dp3 is blunt and more robust than in

Borhyaena (Figs. 1I,J, 3D). The dp3 of *Cladosictis* (Figs. 1A,B, 3A) is narrower, with sharp cutting blades and pointed cusps.

Sparassodonts show facets on cusps and crests of the DP3/dp3, suggesting that these were functional teeth in juveniles. In addition, the specimen MLP 82-V-1-1 of *Arminiheringia*

sp. has heavily worn P2 and M1–2/m1–2. The P3/p3 is completely erupted and has only a small facet on the tip of the main cusp (Fig. 2B,D). The worn state of the posterior postcanines suggests that the deciduous premolars would have been extensively used. In contrast, some ecologically equivalent dasyuromorphians (e.g., *Thylacinus*, *Sarcophilus*, and *Dasyurus*) show a vestigial and non-functional deciduous premolar, non-erupted or replaced very early in ontogeny (Flower 1867; Lockett and Woolley 1996). In the youngest studied specimen of *Thylacinus* (UMZC A6 7/10; Fig. 6A–D), the dp3 is represented by a small single cusped tooth, unrooted and very loosely attached to the dentary (see also Flower 1867). The m1 is incompletely erupted and the DP3 is missing, representing a very precocious loss. The P3/p3 are seen inside their crypts, suggesting an early replacement.

Discussion

Timing of Dental Eruption.—The eruption of P3/p3 in closer synchrony with the M4/m4 is a symplesiomorphy for Metatheria (excluding *Deltatheridium*; Rougier et al. 1998). This condition is evident in sparassodonts, recorded in stem marsupials and many living species (e.g., Cifelli and Muizon 1998). Australian marsupials show a broader pattern for the P3/p3 eruption (Thomas 1887; Springer et al. 1997). Our study recorded the heterochronic shift of the dasyuromorphians (e.g., *Thylacinus* and *Dasyurus*; Fig. 5C,D) in which the eruption of P3/p3 is accelerated compared with the ancestral condition.

In Sparassodonta, the P3 completes its eruption before the M4. The same sequence was observed in *Mayulestes* and *Pucadelphys* (Cifelli and Muizon 1998) and several didelphid species (van Nievelt and Smith 2005b; Astúa and Leiner 2008) (Table 1). The optimization of this pair of events in our tree (Fig. 5A) supports the hypothesis of van Nievelt and Smith (2005b; Astúa and Leiner 2008) that this is the ancestral marsupial pattern. In some taxa of our sample in which the P3 completes the eruption before the M4, the order in the lower molars is reversed (e.g., some didelphids in Table 1, and for the upper postcanines in *Dromiciops* described in Tribe 1990), sug-

gesting that upper and lower dentitions need to be examined separately.

The pattern of eruption of upper and lower premolars is widely variable among taxa and within the studied specimens. The optimization of this pair of events in our tree (Fig. 5F) is ambiguous for Marsupialia. Among stem marsupials, the sparassodont pattern of P3 and p3 erupting in synchrony is derived considering that in *Pucadelphys* the complete eruption of P3 precedes p3.

The timing of eruption of upper and lower molars seems to be primarily correlated with the type of occlusion. In most marsupials with a generalized tribosphenic molar, the grinding function occurs between the protocone and talonid of the equivalent upper and lower molars, respectively, but the major shearing complex is formed by the paracristid of the lower molars and the postmetacrista of the preceding upper molars (Simpson 1936). Marsupial carnivores have emphasized the paracristid-postmetacrista shearing complex (between a particular molar and the preceding upper molar). This is correlated with the simultaneous eruption of M3 and m4, as in, for example, dasyuromorphians. Marsupial herbivores have emphasized the protoconetalonid grinding complex (between equivalent upper and lower molars) and the M4/m4 eruption is simultaneous. In Sparassodonta we might expect the timing to be the same as their ecological vicars (hypercarnivorous dasyurids and *Thylacinus*), but this is not the case. Our analysis shows that in sparassodonts there has been a heterochronic shift that accelerated the eruption of the upper molars (exemplified here by the M4; Fig. 5E). The crown of M4 is out of its crypt before the m4. However, the border of the maxilla is retracted and the M4 is not functional. If instead the distances between M4/m4 crown bases and the alveolar line defined by M1–M3/m1–m3 are considered, both distances are similar (*Arminiheringia* sp. MLP 82-V-1-1; Fig. 2A–D) or the M4 distance is longer (*Prothylacynus* MACN-A 5931–32; Fig. 1E–H), suggesting that m4 would reach the m1–m3 alveolar line in synchrony or the M4 slightly before. In addition, the m4 is the largest carnassial in metatherians and the sparassodonts for which

we could trace the eruption sequence of the last molars (*Arminiheringia*, *Lycopsis*, *Prothylacynus*) all of which were large sized hypercarnivores (Prevosti et al. 2013). The m4 is the tallest molar whereas the M4 is reduced. Assuming equal eruption rates, the time involved in the m4 eruption should be longer than the upper counterpart because of the different linear sizes. However, different eruption rates between the M4 and m4 cannot be ruled out because different eruptive periods are seen in living marsupials (van Nievelt and Smith 2005b; Astúa and Leiner 2008). It is also worth mentioning that after analyzing a large sample of a single didelphid species, Astúa and Leiner (2008) recorded exceptional specimens in which the upper molars complete the full eruption before the equivalent lower molars. The authors emphasized the importance of examining a large number of specimens to construct a pattern because the variation among individuals is great. Our fossil sample is limited. The observed data suggest that in these large hypercarnivorous sparassodonts studied the M4/m4 erupt in closer synchrony than the M3/m4 parallel eruption of hypercarnivore dasyuromorphians (e.g., *Thylacinus*).

Deciduous Premolars.—Generally in mammals and stem relatives, the deciduous premolars function as molars and are consequently more complex in morphology than the successive elements (Zack 2012; exceptions have already been mentioned and include the vestigial and non-functional deciduous premolar of some marsupials). In sparassodonts, the morphology of the DP3/dp3 favors shearing over grinding, which is consistent with the carnivorous specializations of the permanent dentition (e.g., Butler 1946; Muizon and Langre-Badré 1997). The lower molars of *Prothylacynus* have broader and basined talonids compared with that of *Borhyaena*, which is vestigial and has no grinding area (Marshall 1978, 1981). The blunt and robust dp3 of *Prothylacynus* (Fig. 3B) and the slightly narrower dp3 of *Borhyaena* (Fig. 3D) are consistent with the molar morphology that distinguish these two taxa.

For mammals with complex deciduous premolars, however, the morphology of the

premolars is quite different from that of the molars (Zack 2012). In the sparassodonts in which these teeth are known, the deciduous premolars are smaller (34%–40% antero-posteriorly shorter than the M1/m1), narrower, lower, and with slenderer roots than the molars. The dp3 lacks the talonid and the tooth is basically formed by three aligned cusps. Morphological differences also exist between the deciduous premolars of sparassodont taxa whose molars are structurally very similar. The relative grinding areas (RGA) of the molars of *Prothylacynus* and the smaller hathiacynid *Cladosictis* are similar (RGA = 0.17 for both taxa [Prevosti et al. 2013]) but the narrow and sharp dp3 of *Cladosictis* (Fig. 3A) contrasts with the robust and blunt dp3 of *Prothylacynus*. This suggests a change in the diet between the juvenile and the adult stage, with juveniles of *Cladosictis* more strictly carnivorous than the juveniles of *Prothylacynus*. In the placental Carnivora and stem relatives, the deciduous teeth can differ from their permanent counterparts in structure and function (Zack 2012; Soibelzon 2010), and we interpret the same for sparassodonts.

Heterochronic Shifts in Thylacosmilids.—Sparassodonts show some patterns of dental eruption that differ from those of other metatherians. In the adult stage of the thylacosmilids *Patagosmilus goini* and *Thylacosmilus atrox*, the last upper premolar is small (41% and 33% smaller than the M1, respectively), molariform, and with three slender roots (Figs. 2E,F, 3E,F). Its morphology suggests that the last upper premolar in thylacosmilids is the deciduous element retained in adulthood (Goin and Pascual 1987; Forasiepi and Carlini 2010). With the probable exception of *Myrmecobius*, no other metatherian known retains the DP3/dp3. The numbat has supernumerary teeth (Charles et al. 2013), which could be explained in part by the retention of the deciduous elements (Winge 1882; Dependoff 1898; Tate 1951; Archer 1975; a different interpretation is presented in Thomas 1887 and Bensley 1903). Ontogenetic studies and fossil evidence have supported the view that the first molar of Metatheria is homologous with the last deciduous premolar of Eutheria (Lockett 1993; O'Leary et al. 2013), which is

never replaced in metatherians. In this phylogenetic context, the condition of thylacosmilids represents the retention of another deciduous element.

The retention of the DP3 in the adult dentition of thylacosmilids represents a clear example of a paedomorphic heterochronic shift, in which the descendant adult has morphological features that occur in the juvenile of the ancestral form (McNamara 1986). The functionality of DP3 already recorded in the juveniles of other sparassodonts was lifelong in thylacosmilids.

A different example is given by the ever-growing sabertooth upper canines. Van Nievelt and Smith (2005b) demonstrated that in *Monodelphis*, the average eruption period for the canines is five days and the upper canine completes its eruption before the M2. Although our sampled marsupials show that the upper canine completes its eruption before the last molar, it has been demonstrated that in some didelphids (Voss and Jansa 2009) and dasyurids (R. M. D. Beck 2013 personal communication) the canine continues growing in adulthood. Similarly, in large sparassodonts (e.g., *Lycopsis*, *Prothylacynus*), canine eruption is not complete until all molar crowns are fully erupted out of their alveoli, and sometimes later. In thylacosmilids, too, upper canine development continues throughout life, unlike in the ancestral condition. In addition, the holotype of *Patagosmilus* is a young adult complete with a sabertooth canine. When compared with another large-sized sparassodont (*Borhyaena*, MACN-A 6203–6265) with similar wear in the molars, *Patagosmilus* appears to have an accelerated growth rate of the upper canine. The morphological consequence is thus a larger tooth than in its ancestor—an example of a peramorphic heterochronic shift (McNamara 1986).

Circumvention of Constraints in Metatherian Evolution.—The morphospace occupied by marsupials is more restricted than that occupied by placentals (Sears 2004; Sánchez-Villagra 2013). The disparity in skull and tooth shape morphology is smaller in marsupials than in placentals (Werdelin 1986, 1987; Wroe and Milne 2007; Prevosti et al. 2011; Smits and Evans 2012; Bennett and Goswami

2013; but find a different view in Goswami et al. 2011). Several authors have linked the reduced disparity in marsupials to their peculiar reproductive biology, suggesting that the early birth and extra uterine development negatively bias the morphological diversification of the group (although see Sánchez-Villagra 2013 for an alternative interpretation and a historical review of this subject).

Some studies have demonstrated that the pattern of tooth eruption in metatherian carnivores gives them narrower morphological disparity than placental carnivores (Werdelin 1987). In the Carnivora, the permanent upper carnassial is preceded by a deciduous tooth, and the carnassial pair (P4/m1) erupts in a position that allows molars to evolve for other specialized functions (Werdelin 1987). In metatherians, each molar erupts at the most advantageous position, halfway between the condyle and the canine (Greaves 1983; Werdelin 1987). There is a relative molar progression with each molar functioning as a carnassial until the eruption of the M3/m4 pair, which occupies the most optimal position in the jaws for a carnassial. This leads to all molars having a carnassial structure, reducing the possibility of evolving different shapes (Werdelin 1987). This pattern of tooth progression of Dasyuridae could have occurred in sparassodonts. Although this pattern likely favors the conservation of molar morphology, metatherians circumvented this constraint, as also exemplified by the carnivorous thylacoleonids (Werdelin 1988; Nedin 1991; Wroe et al. 1999). Through a derived pattern of tooth eruption and different morphologies in the deciduous dentition, the sparassodonts similarly circumvented some constraints, the most peculiar case being thylacosmilids, in which the deciduous upper premolar is not replaced. The morphology of thylacosmilid dentition is also extremely specialized, including ever-growing sabertooth upper canines and an unusual skull and mandible (e.g., massive facial region with the maxilla extending backward between the orbits and meeting at the midline, orbits closed posteriorly by a postorbital bar, well-developed bony tympanic bullae, and a deep mandibular symphysis with a ventral flange [Riggs 1934; Goin and Pascual 1987]), making

them one of the most bizarre forms of the native South American mammalian predators (Riggs 1934; Marshall 1976; Turnbull 1978; Churcher 1985; Goin and Pascual 1987; Forasiepi and Carlini 2010).

Metatherians developed over deep time a plethora of morphological specializations, with some seen in the fossil record that might not have been predicted from consideration of extant forms only (Arena et al. 2011). Their restricted morphospace in comparison to placentals may reflect differential extinction and a lack of ecological opportunity more than a morphological limit imposed by ontogenetic development (Wroe et al. 2004; Sánchez-Villagra 2013). The carnivorous adaptive zone of the terrestrial ecosystems of South America during most of the Cenozoic was shared between Sparassodonta and non-mammalian taxa, such as Sebecidae (crocodiles) and Phorusrhacidae ("terror birds"), and for about 3 Myr, from the late Miocene to the Pliocene, with placental carnivores (Degrange et al. 2010; Prevosti et al. 2013; Scheyer et al. 2013). This would have favored a partitioning of the carnivore adaptive zone (Ercoli et al. 2013) in which each taxonomic group occupied a particular role in the terrestrial ecosystems.

Conclusions

Sparassodonta is a metatherian clade of specialized carnivores. Almost 90% of the taxa were hypercarnivores with limited disparity in molar morphology. This study demonstrates that Sparassodonta have a peculiar combination of patterns of dental eruption and replacement that seems to be derived in the context of metatherian phylogeny: (1) The P3/p3 erupt together (in common with some didelphids); (2) the equivalent upper and lower molar loci erupt in closer synchrony than in other carnivorous metatherians, in which the lower molars clearly precede the equivalent upper elements; (3) the upper canines in thylacosmilids and proborhyaenids are hypselodont; and (4) DP3 in thylacosmilids is retained in adulthood.

Sparassodonts also have some ancestral patterns recorded in stem and some crown-marsupials: (1) The P3/p3 erupt at the same

time as the M4/m4; (2) P3 completes eruption before M4; and (3) deciduous teeth have a complex molariform morphology and are functional in the juvenile for an extended period of time.

In addition, different sparassodont taxa have different morphologies for the DP3/dp3, suggesting different diets in the juveniles.

The specializations in the timing of dental eruption and in the deciduous morphology are evolutionary mechanisms that increase morphological disparity. This is clearly evident from the heterochronic shifts of thylacosmilids (i.e., retention of the DP3 and hypselodont upper canine), in contrast to the otherwise narrow morphospace occupation of Sparassodonta.

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