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Chapter 6

A Polydolopine Marsupial Skull from the Cachapoal Valley, Andean Main Range, Chile

JOHN J. FLYNN AND ANDRÉ R. WYSS

ABSTRACT

The Abanico (= Coya-Machalí) Formation of the Chilean Andes Cordillera continues to yield beautifully preserved fossil mammals of a variety of Cenozoic ages, with previously documented faunas spanning at least the Eocene to early Miocene. We describe here a new species of polydolopine marsupial, *Polydolops mckennai*, based on a skull preserving most of the upper dentition or alveoli. This, only the second polydolopid cranium known, provides important information on dental homologies and phylogeny for the group. The specimen on which this taxon is based is the first reported from new localities in the Río Cachapoal drainage. These localities appear to be early Oligocene or older in age (at least in part), expanding the geographic and temporal distribution of mammalian faunas from the Abanico Formation and bearing on models of the tectonic evolution of the central Chilean Andes.

INTRODUCTION

Marsupials, although depauperate in South America today (represented by only a small number of didelphid, caenolestid, and microbiotheriid species) were vastly more diverse during most, if not all, of the Cenozoic. South America's highly endemic marsupial faunas during this time reflect the continent's long-term geographic isolation, as do its contemporaneous and equally peculiar placental mammal radiations. Marsupials have long been recorded from the classic deposits of Patagonia and surrounding Argentina, augmented by newer discoveries of important assemblages in lower latitudes and the Andean Cordillera. These include some of the earliest (Tiupampan South American Land Mammal "Age" [SALMA], early Paleocene) and best-preserved marsupicarnivorans, a tropical-latitude Deseadan SALMA assemblage (Salla) from Bolivia, the Colombian middle Miocene tropical fauna of La Venta (Laventan SALMA), and the unusual suite of didelphimorphians from the Paleocene (Itaboraian SALMA, early Paleocene) of Brazil (see Flynn and Wyss, 1998 for summary). Since 1986, we and our col-

leagues have uncovered early-middle Cenozoic mammal faunas in several regions of the Chilean southern Andes (Wyss et al., 1987, 1990, 1992, 1993a, 1993b, 1994, 1996; Flynn et al., 1988, 1991, 1995, 2002a, 2002b, 2003; Charrier et al., 1990, 1996, 1997, 2002; Dodson, 1994; Flynn and Swisher, 1995; Hitz, 1997; Flynn and Wyss, 1998, 1999; Hitz et al., 2000; Reguero et al., 2003; Croft, 2000, 2001; Croft et al., 2003a, 2003b). These faunas expand the geographical, temporal, paleoenvironmental, and taxonomic sampling of South American marsupials and other mammals, while providing important information on the geologic history of the Andes.

Recent efforts include extensive paleontological reconnaissance within the south-central Andean Main Range, roughly between 33.5° and 38°S latitude. This work has led to the recovery of several Cenozoic mammal faunas from the Abanico (= Coya-Machalí) Formation, the first known for the region, including the original discovery of the Tinguiririca Fauna. Better illuminating the Eocene-Oligocene transition than perhaps any other land mammal fauna in South

America, the Tinguiririca Fauna includes polydolopid, groeberiid, and didelphimorph marsupials (Flynn and Wyss, 1999). Since that initial find, the Abanico Formation (and its lateral equivalents) of the central Chile Andean Main Range has yielded seven or more Cenozoic faunas, ranging in age at least from the Eocene (Casamayoran) through the early Miocene. Preparation of the hard and brittle volcanoclastic matrix, in which these fossils are typically found, is extremely difficult and labor intensive, with description of key material proceeding as it becomes available. We provide here the first report of a polydolopine skull. Polydolopids were among the earliest-described South American fossil marsupials; although they have a long temporal range and are moderately common elements of most early Cenozoic faunas, this specimen represents only the second polydolopid cranium known. This skull is the first fossil to be described from a locality just north of the Río Cachapoal, discovered in 1996 (Charrier et al., 1997). Analysis of this new specimen from another new fossil-bearing locality within the Abanico Formation in the Chilean Andes seems especially fitting for this festschrift volume, as it provides new systematic and geologic data from strata and a region in which we collaborated early on with our Ph.D. advisor and friend, Malcolm C. McKenna.

Simpson (1928, 1948) and Paula Couto (1952) presented important early analyses of the Polydolopidae. Marshall (1982) provided the most recent comprehensive review of the group, and Marshall et al. (1990) proposed a higher-level phylogeny for fossil and modern marsupials. A selection of more recent studies of polydolopids and potential close relatives includes Pascual (1980, 1981), Pascual and Bond (1981), Woodburne and Zinsmeister (1984), Case et al. (1988), and Goin and Candela (1995, 1996). McKenna and Bell (1997) summarized the taxonomy and temporal occurrences for polydolopid taxa then known. Flynn and Wyss (1999) described the youngest known polydolopid, *Polydolops abanicoi*, discussed its systematic and temporal implications, and provided the first phylogenetic definitions for various taxonomic names previously applied to components of this clade (e.g., Marsupialia, Poly-

dolopimorphia, Polydolopoidea, Polydolopiformes, Polydolopidae, and Polydolopinae).

Polydolopids, like most marsupials, are rare in comparison to placentals within most Cenozoic South American assemblages and had been reported only from Paleocene and Casamayoran assemblages until the 1970s (see Marshall, 1982: 9). They do, however, occur with some frequency in many pre-De-seadan assemblages, with well-documented occurrences now ranging from the Paleocene (Itaboraian and Riochican SALMAs; Paula Couto, 1952; Marshall, 1982; Goin and Candela, 1995; and possibly the older Tiupampam SALMA, "*Epidolops* sp.", Gayet et al., 1991) to the earliest Oligocene Tinguiririca Fauna (representing a new pre-Deseadan, post-Mustersan SALMA, the Tinguirirican, see Flynn and Swisher, 1995, Flynn and Wyss, 1999, Flynn et al., 2003), a span of some 30 million years. *Polydolops* itself is quite long-ranging, with species known from that entire span, excepting the earliest (Tiupampam and Itaboraian SALMAs) part during which only *Epidolops*, the polydolopine nearest outgroup, and *Amphidolops* (= *Seumadia*) *yapa*, an advanced polydolopine, are known from Patagonian Argentina and Brazil (Paula Couto, 1952; Marshall, 1982; Goin and Candela, 1995; Bond et al., 1995; see Gayet et al., 1991, for possible older, Tiupampam SALMA occurrence of *Epidolops* in Bolivia). In addition, the polydolopids reported from Antarctica (*Antarctodolops*, *Eurydolops*) have been considered to be closely related to particular *Polydolops* species (Woodburne and Zinsmeister, 1984; Case et al., 1988), either rendering *Polydolops* paraphyletic or the Antarctic taxa assignable to *Polydolops* (see discussion in Flynn and Wyss, 1999).

SYSTEMATICS

MAMMALIA LINNAEUS, 1758 (SENSU ROWE, 1988)

METATHERIA HUXLEY, 1880 (SENSU FLYNN AND WYSS, 1999)

MARSUPIALIA ILLIGER, 1811 (SENSU FLYNN AND WYSS, 1999)

POLYDOLOPIMORPHIA MARSHALL ET AL., 1990 (SENSU FLYNN AND WYSS, 1999)

POLYDOLOPOIDEA AMEGHINO, 1897 (SENSU FLYNN AND WYSS, 1999)



Fig. 6.1. Palatal view of skull and upper dentition of *Polydolops mckennai*.

POLYDOLOPIDAE AMEGHINO, 1897 (SENSU FLYNN AND WYSS, 1999)

POLYDOLOPINAЕ AMEGHINO, 1897 (SENSU FLYNN AND WYSS, 1999)

Polydolops mckennai new species
Figures 6.1–6.2; tables 6.1–6.2

HOLOTYPE (AND SOLE ELEMENT OF HYPODGM): SGOPV 3476 (field number, 3-3-96-676; Loc. C-96-5). SGOPV designates spec-

imens housed in the vertebrate paleontology collections of the Museo Nacional de Historia Natural in Santiago, Chile.

TYPE LOCALITY: “Cachapoal Locality” (new locality, discovered in 1996 by the authors, Reynaldo Charrier and team; see Charrier et al., 1997), Río Cachapoal, Chile. This locality is ~5 km NW of the Río Las Leñas fossiliferous sites (Flynn et al., 1995) and ~100 km N of Termas del Flaco, site of the original discovery of fossil mammals in the Abanico Formation. More detailed locality information is on file at the Field Museum, Chicago.

STRATIGRAPHIC OCCURRENCE: Abanico (= Coya-Machalí) Formation, Chile. The precise stratigraphic provenance of the holotype is uncertain, as it was recovered from an automobile-sized block on a talus slope below steeply dipping cliff exposures. Part or all of this stratigraphic interval, however, appears to correlate with or underlie a sequence in the next drainage south (Río Las Leñas), preliminarily dated at 29.3 ± 0.1 Ma (unpublished $^{40}\text{Ar}/^{39}\text{Ar}$, C.C. Swisher III, personal commun.; Charrier et al., 1997). In addition, the source strata certainly predate stratigraphically higher levels in the Río Las Leñas drainage that have been dated at 16.1 and 20.09 Ma (Flynn et al., 1995; Charrier et al., 2002).

AGE: Indefinite but possibly correlative with, or older than, levels dated elsewhere at ca. 29.3 ± 0.1 Ma (see “Stratigraphic Occurrence”). May be equivalent to the Tinguirirican SALMA in being about earliest Oligocene in age (~31–32 Ma), but the data are also permissive of an even older age.

ETYMOLOGY: In honor of Malcolm C. McKenna, for his remarkable contributions to mammalian systematics, his imaginative integration of geological and biological studies in paleontology, and his collaboration in our early work in Chile.

DIAGNOSIS (BASED, OF NECESSITY, SOLELY ON UPPER DENTAL FEATURES): The taxon is a polydolopine polydolopid; it is conservatively assigned to *Polydolops* as it shares several synapomorphies with other *Polydolops* species, although it differs from all of them in various dental features. Measurements and tooth proportions are presented in tables 6.1

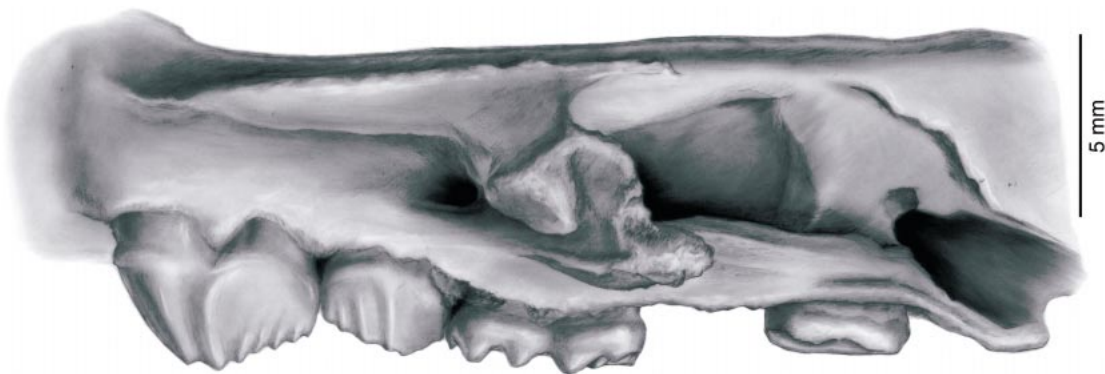


Fig. 6.2. Left lateral view of upper dentition and cranial morphology (partial) of *Polydolops mckennai*.

TABLE 6.1
Dimensions (in mm) for *Polydolops mckennai*

	Left	Right
ANT1 (I?) ^a L	1.37 *(alv)	—
ANT1 (I?) W	1.32 *(alv)	—
ANT2 (C) L	2.30 *(alv)	—
ANT2 (C) W	~1.68 *(alv)	—
ANT3 (P1) L	1.22 *(alv)	—
ANT3 (P1)W	1.18 *(alv)	—
P2 L	5.92	5.99
P2 W	3.14	3.15
P3 L	3.74	2.13 *(alv)
P3 W	2.92	1.73 *(alv)
M1 L	5.61	5.59
M1 Wa	4.00	4.09
M1 Wp	4.38	4.45
M2 L	4.04 *(alv)	3.93 *(alv)
M2 W	3.76 *(alv)	3.59 *(alv)
M3 L	4.27	2.71 *(alv)
M3 W	3.44	2.00 *(alv)
Palate L ^b :	44.71	
Palate W (internal, M1 left to right lingual edges):	11.74	
Braincase W:	28.61	
Skull L ^c :	> 68.94	
Skull W (external, at base of zygoma):	19.73	

Abbreviations: Ant = anterior, I = incisor, C = canine, P = premolar, M = molar, L = length, W = width, Wa = anterior width, Wp = posterior width, *(alv) = alveolus dimension estimates.

^aAnterior teeth represented by alveoli only; potential homologies discussed in text.

^bMinimum estimate-posterior edge broken.

^cSignificant underestimate, as posterior portion of the skull is missing.

and 6.2. Upper dental formula tentatively considered 2?.1.3.3.

Differs from all other species of *Polydolops* in having proportionally much more elongate premolars and molars, a longer and more heavily ribbed, arcing, sectorial blade spanning P2 and P3, and apparently fewer and/or less well-developed buccal and stylar cusps on molars. Upper teeth are unknown for all *Polydolops* species except *P. thomasi* and *P. serra*, but proportions of the lower teeth (relative to upper/lower teeth proportions in taxa for which both are known) suggest that those more poorly known taxa also have proportionally much shorter and wider teeth than *P. mckennai*. In absolute size, *P. mckennai* is much larger than *P. serra* (and presumably also other small Riochican-Casamayoran *Polydolops* species not known from upper teeth [*P. winecage*, *P. clavulus*, *P. rothi*, *P. kamektsen*]), and is 10–20% larger and has much longer cheek teeth than *P. thomasi* (and narrower P2–3, but wider M3). Also differs from *P. thomasi* in having more pronounced labial ribs on the anterior half of P2 and a second very large and strong arced rib extending from the anterodorsal edge of P3 to the tip of the crown both lingually and labially.

Differs from *Epidolops* in having P2 and P3 sectorial (rather than only P3), P2 large (P2 tiny or absent in *Epidolops*), axis of P3 in line with molar series (rather than angled about 30° anterobuccally to posterolingually), proportionally and absolutely larger and more cusped molars, narrower and more elongate palate, more gracile skull, and absence of M4.

TABLE 6.2
Dental Proportions for *Polydolops mckennai* and Other Polydolopidae
(*Polydolops serra*, *Polydolops thomasi*, *Amphidolops serrula*, *Eudolops tetragonus*, *Eudolops hernandezi*,
Antarctodolops dailyi, *Epidolops ameghinoi*)^a

	<i>Polydolops</i>			<i>Amphidolops</i>	<i>Eudolops</i>		<i>Antarctodolops</i>	<i>Epidolops</i>
	<i>mckennai</i>	<i>serra</i>	<i>thomasi</i>	<i>serrula</i>	<i>tetragonus</i>	<i>hernandezi</i>	<i>dailyi</i>	<i>ameghinoi</i>
P2	1.90	—	1.14	—	1.59	—	—	—
P3	1.28	—	0.97	—	1.17	—	—	1.13
M1	1.27	0.96	1.03	0.93	1.16	1.36	~1.0	0.68
M2	~1.08	0.86	0.91	0.88	1.07	1.29	1.46	0.67
M3	1.24	1.09	1.0	—	1.16	1.47	—	0.65

^a Dimensions for other species taken from Woodburne and Zinsmeister (1984; *Antarctodolops*) and Marshall (1982; appendices, using species averages calculated by Marshall [*Epidolops*, *P. thomasi*] or averages calculated from measurements on individual specimens).

Differs from *Eudolops* in having smaller molars, absolutely and proportionally (relative to molar size) larger premolars (than *E. tetragonus*, the only species for which these are known), P2 much larger than P3, much less distinct cusps on M3, M2 larger than M3 (rather than subequal in size), M3 much smaller, and less wrinkled enamel in molar basins.

Differs from *Amphidolops* in its much larger overall size, having P3 roots more equal in size, presence of large P2 (apparently absent in *Amphidolops*) and thus P2 and P3 both sectorial (rather than just P3), having M3 longer than wide, and possessing less wrinkled enamel in molar basins.

Differs from *Antarctodolops* in being smaller (based on *Antarctodolops* P3 alveoli size estimates, M1 length and width, and M2 length [based on *P. mckennai* alveolus minimum measurements]), having a proportionally larger P3 (compared to M1 dimensions), having P2 broader (posteriorly) than P3 (the reverse was inferred by Woodburne and Zinsmeister, 1984, from alveoli in *Antarctodolops*), having higher L/W ratio for M1 and a slightly lower ratio for M2, and possessing many fewer labial and stylar molar cusps.

Differs from *Eurydolops* (a taxon known only from a single P3) in having a P3 that is much larger, much more elongate, double-rooted, and possessing more and better-developed serrations, a labial cingulum, and a more expanded posterolingual shelf.

DESCRIPTION: The specimen is well preserved, but is crushed in various parts, es-

pecially through dorsoventral flattening. The animal was a mature adult, as all the teeth appear to have been erupted and moderately worn, and sutures are not readily observable on the skull.

Although anterior teeth are not preserved, alveoli are present on both sides (better on the left). These alveoli provide the first evidence of the anterior upper dentition for a polydolopine, allowing comparison to the conditions in their nearest outgroup, *Epidolops*. There likely was one large, laterally compressed tooth near the anterior end of the snout, with two smaller alveoli flanking it. The smaller alveoli are closely appressed to the alveolus for the enlarged central tooth, being separated from the latter by a bony transverse partition (the posterior alveolus is more pronounced on the left side, appearing as a shallower and more laterally constricted pit on the right side). In general form and position, these alveoli in *P. mckennai* are very similar to those in *Epidolops ameghinoi* (see Paula Couto, 1952: fig. 2, and Marshall, 1982: fig. 62), suggesting comparable morphology of the anterior tooth battery.

The posteriormost of these three anterior alveoli almost certainly held P1, given its position in the tooth row, the ancestral marsupial premolar complement, and the presence of two premolars posterior to it. Judging from alveolar size and position, this tooth was quite small and sat tightly against its enlarged anterior neighbor. This is the first demonstrated occurrence of P1 in a polydol-

opine (as *P. abanicoi* from Chile had earlier shown for p1; Flynn and Wyss, 1999).

The middle of the alveolus for the large tooth appears laterally constricted, although this is much more pronounced on the left than the right side probably due to post-depositional distortion. We interpret this as a single alveolus for an enlarged tooth, given the left-right asymmetry in the apparent constriction, lack of a transverse bony partition within the alveolus on either side, and the continuous smooth rim of the alveolus. This interpretation seems much more likely than the alternative of two subequally-sized teeth, given the above observations, the complementary enlarged procumbent lower tooth (canine) in polydolopids, and similarity to the morphology of the anterior upper dentition in *Epidolops* (in which there is an almost identical elongate and compressed alveolus for a single enlarged tooth, also flanked by closely appressed and much smaller alveoli for incisors and P1). The enlarged tooth in *Polydolops mckennai* is interpreted as the canine; as the premaxillary-maxillary suture is not visible, this is based on its occurrence well posterior to the anterior end of the snout, its position immediately anterior to the tooth identified as P1, the morphology of the anterior upper dentition (especially the canine) in *Epidolops*, and the additional homology arguments presented by Marshall (1982). The orientation of the alveoli suggests that the canine would have been vertical or only slightly procumbent.

At least one and possibly two teeth (incisors) were present anterior to the enlarged tooth. These are on the buccal border of the palate and well posterior to the anterior rim of the snout (within which no alveoli are obvious).

A very long diastema (nearly 15 mm) separates the canine/P1 from P2.

The entire cheek-tooth series is elongate and aligned anteroposteriorly, parallel to the midline. The second and third upper premolars are both enlarged, sectorial teeth, whereas the molars are flattened crushing teeth, consisting of large enamel-rimmed basins. The cheek-tooth-bearing portion of the palate is somewhat longer and significantly broader than the rostral part. The palate extends posteriorly to M3 and does not vary

appreciably in breadth posterior to P2; a distinct foramen or vacuity occurs near the posterobuccal corner of the palate.

The second upper premolar is the longest cheek tooth, being slightly longer than M1 (M2 represented only by alveoli). It is anteroposteriorly elongate, laterally compressed, and generally ovoid in outline. The second upper premolar is significantly larger than P3, especially in length and crown height. Like P3, however, P2 is dorsoventrally elaborated into slicing "blades", with the axial ridges on both forming a continuous, gently S-curved, arcing ridge. On P2 the axial ridge is strong, serrated, and slightly concave buccally. The ridge is marked by six distinct cusps, from which climb a series of dorsoventral ribs forming the serrations on the labial face of the tooth. The posterior four serrations extend dorsally only about one-fourth the height of the tooth crown. The two anterior cusps and rib serrations are the most prominent, both extending from the dorsal base of the crown to its ventral tip, with the second forming the highest cusp on the tooth and its rib creating a marked rim separating the anterior third of the tooth from the posterior two-thirds. A shallow depression exists on the posterobuccal side of this rim. A series of shallow grooves is present on the anterior face of the tooth, as is a slight antero-dorsal cingulum.

The third upper premolar is irregularly triangular in outline, with a distinct and slightly basined posterolingual lobe. As on P2, an axial ridge runs the entire length of the tooth, but it is less well developed, slightly convex buccally, and located more lingually on the crown. On the anterior half of the tooth, four weak cusps and associated dorsoventral serrations mark the crest of the axial ridge. The posteriormost serration is the strongest, extending almost to the base of the tooth, while the other serrations become progressively weaker anteriorly.

The molars decrease progressively in size posteriorly ($M1 > M2 > M3$). The crowns are fairly heavily worn, making it difficult to determine the number and positions of all the distinct cusps and cuspules on an unworn tooth.

The first upper molar is quadrate in outline. Both the lingual and buccal edges are

pinched by shallow grooves near the middle of the tooth, dividing it into distinct anterior and posterior lobes. On the crown surface the basins of the two lobes are continuous, with a bordering enamel rim. Buccal cusps appear to be obliterated early in wear, although at least four large cusps were present (two on each lobe). The two anterior cusps are widely separated by a deep valley, whereas the two posterior cusps are more proximate, with a small "pocketed" enamel basin forming between them on the posterobuccal corner of the tooth.

The second upper molar is not preserved on either side of the specimen, but the general shape and size of the alveoli indicate that the tooth would have been smaller than, but similar in shape, proportions, and morphology to M1.

The third upper molar is preserved on the left side of the skull; it is a gently rounded, isosceles triangle in outline. The triangle's most acute angle forms the posteromedial end of the tooth, and the anterior edge of the tooth represents the triangle's base, making the tooth much wider anteriorly than posteriorly. A continuous rim of enamel surrounds a central basin. No distinct cusps are present, but there are indications of two closely appressed cuspules at the anterobuccal corner and at least one at the posterobuccal end of the buccal rim.

The palate posterior to M3 is complete enough to indicate that no M4 was present in this animal.

The skull clearly is crushed, but most of the distortion appears to be dorsoventral flattening rather than lateral or oblique distortion, allowing approximate estimates of lengths and widths of some features. Overall, the skull appears quite gracile, with a very long but generally narrow form. The snout is elongate and narrow, but the palate broadens significantly across the cheek-tooth region, being broadest near the anterior base of the zygomatic arches. There are slight lateral constrictions just anterior to P2, at the anterior base of the zygoma (P3-M1 junction), and posterior to the cheek-tooth row (separating an expanded braincase from the rostral part of the skull). The anterior root of the zygomatic arch is moderately robust, form-

ing a strong bridge extending buccally from the area lateral to M1-M2.

The braincase is missing its posterior portion, and is ventrally flattened; nonetheless, it is clear that the braincase was fairly expanded and globular. Although it is uncertain whether the breakage of the braincase resulted from postmortem transport or predation/scavenging, it is reminiscent of the damage done to mammal skulls preyed on by modern birds (e.g., owls) and the breakage of the posterior ends of the only other polydolopoid skulls known (Polydolopidae: *Epidolops ameghinoi*, Itaboraí, Brazil, Itaboraian SALMA, Paula Couto, 1952, Marshall, 1982; Bonaparthiidae: *Bonaparthium hinakusijum*, Lumbrera Formation, Salta, Argentina, Casamayoran SALMA, Pascual, 1981).

DISCUSSION

The skull of *Polydolops mckennai* is the first recovered for a polydolopine and only the second for any polydolopid, providing evidence bearing on questions of polydolopid monophyly, basal diversification, and the features typifying the group and subclades ancestrally. A full revision of polydolopid phylogenetics would be worthwhile, especially in light of advances in systematic methods, description of many new taxa since Marshall's (1982) review of polydolopids, and proposals that some taxa currently recognized may not be monophyletic or that the important Antarctic taxa (*Antarctodolops* and *Eurydolops*) may be nested within various species assigned to *Polydolops*. Although outside the scope of this brief initial report, such an analysis will yield better understanding of patterns of morphological evolution within the clade and of early Cenozoic biogeographic relationships among "Gondwanan" continents. For example, *Eurydolops* is a taxon known only from a single tooth (considered P3 by Case et al., 1988). Although this taxon has reasonably been considered to be a polydolopine, the shape and morphology of the available tooth has many resemblances to the P2 of *Epidolops*; if *Eurydolops* is in fact an epidolopine rather than polydolopine, this would have important biogeographic and temporal ramifications.

Polydolops mckennai is readily distinguishable from the other taxon known from a skull (*Epidolops ameghinoi*), as well as other non-*Polydolops* polydolopines, in a variety of features (see diagnosis). In overall size, *P. mckennai* is smaller than *Epidolops* and *Eudolops*, but larger than most other polydolopines.

It is more difficult to distinguish *P. mckennai* from other species of *Polydolops*, as many of them are known from less complete or noncomplementary material (e.g., P2–3 known only for *P. thomasi*; upper molars known only for *P. thomasi* and *P. serra*), but it is larger than almost all of them (see diagnosis) and differs in cheek-tooth proportions. The largest species of *Polydolops*, *P. mckennai* and *P. mayoi*, are represented by material that is not directly comparable (i.e., skull and upper dentition versus lower dentition only), so the approximate sizes can only be inferred through relative sizes of upper and lower teeth in closely related taxa for which both are known. Upper cheek teeth of *P. mckennai* are ~10–20% larger than those of *P. thomasi*, and the lower cheek teeth in the holotype of *P. mayoi* are 2–26% longer and 20–35% wider than the average for *P. thomasi*. Thus, among *Polydolops* species, *P. mckennai* may most closely approximate *P. mayoi* in size (and possibly in having elongate cheek teeth), although they likely differ in shape and proportions, particularly in *P. mckennai* having proportionally larger and more elongate P2–3. The most distinctive autapomorphy of *P. mckennai*, distinguishing it from all other species of *Polydolops*, is the extreme elongation of all the cheek teeth (table 6.2). In *P. mckennai* all cheek teeth are at least 15% longer than they are wide, and P2 is almost twice as long as it is wide. In other species of *Polydolops* the upper cheek teeth are squared (approximately equal in length and width) or wider than long, except P2, which is much less elongate in those other species. The extreme elongation of both P2 and P3 appears to be a diagnostic autapomorphy for *P. mckennai*, distinguishing the species from all other polydolopids. Although *Eudolops tetragonus* also has an elongate P2 and slightly elongate P3, they are not nearly so elongate as in *P. mckennai* (e.g., P2: 60% versus 90% longer than broad)

and although both teeth are sectorial in both taxa, their morphologies are quite distinct. The primitive condition for molar shape in polydolopids appears to be either squared (as in most polydolopines) or broader than long (as most marked in the polydolopine proximal outgroup *Epidolops*). Although the elongate molars in *Eudolops hernandesi* make inferences about the ancestral molar shape in polydolopids and polydolopines a bit problematic, clear distinction of this taxon from *Polydolops* and the roughly squared or relatively broad molars in all other polydolopids (including the other species of *Eudolops*) support the proposed reconstruction. Thus, the very elongate molars in *P. mckennai* appear to be diagnostic autapomorphies. Peculiarly, *P. mckennai* appears to have many fewer buccal and stylar cusps on the upper molars than do other species of *Polydolops*. This distinction, as well as the very elongate cheek teeth, might be used to argue for exclusion of *mckennai* from a *Polydolops* clade. However, currently lacking complementary material for many of the other polydolopine taxa (e.g. skulls for all, anterior dentitions for most, and any upper teeth in some), and given the apparent synapomorphies in P2–3, cheek-tooth row orientation, and other molar morphology, we conservatively choose to ally the new species with other species of *Polydolops*.

The anterior teeth (and consequently dental formulas) are poorly known in polydolopids, owing to the dearth of specimens with a preserved anterior mandibular ramus or rostrum; indeed, until recently this region of the dentition was reasonably well known in just a single taxon, *Epidolops ameghinoi*. Preservation of almost the entire rostrum and mandibular ramus in taxa from the Abanico Formation, *Polydolops mckennai* (this paper) and *P. abanicoi* (Flynn and Wyss, 1999), providing the first evidence of the anterior upper dentition in any polydolopid other than *Epidolops*, strengthens homology inferences for the anterior teeth in polydolopids (particularly identification of P1/p1 and the enlarged tooth) and supports the conclusion that these are synapomorphic in all polydolopids (see below).

P. mckennai documents the occurrence of upper incisors (at least one, and possibly two

or more) in *Polydolops*; *Epidolops* had three upper incisors (Paula Couto, 1952; Marshall, 1982). As in *Epidolops*, the incisor(s) were not located on the anterior rim of the snout, however, but rather were set more posteriorly on the buccal rim of the palate, closely appressed to several other teeth. The lateral position and development of a battery of anterior upper teeth [incisor(s), canine, P1] seem congruent with the great enlargement and procumbency of the lower canine (located near the midline and symphysis of the mandibular rami), and associated great reduction or loss of all lower incisors. In addition, this specimen establishes the expected, but previously undocumented, presence of a large, vertically oriented upper canine. The clear presence of P1 in *P. mckennai* contradicts the earlier inference that P1 and p1 were both absent in *Polydolops* (Marshall, 1982), and is consistent with the evidence from *P. abanicoi* of a small, anteriorly positioned p1 in the clade (Flynn and Wyss, 1999). Thus, the presence of P1 in *P. mckennai* and p1 in *P. abanicoi* (also likely in *P. clavulus*, as noted by Ameghino, 1903; see Flynn and Wyss, 1999), and similar P1/p1 in the polydolopine outgroup *Epidolops*, suggests that a small P1/1, located far anteriorly on the ramus or maxilla (close to the canine and separated from P2/2 by a long diastema), was the ancestral condition for polydolopids and polydolopines. The homology of this suite of modifications (very large upper and lower canines; procumbency of the lower anterior teeth, particularly the canines; great reduction or loss of upper and lower incisors; reduction of P1/p1; and long P1/p1–P2/p2 diastema separating the anterior dental battery from the cheek-tooth row) between *Epidolops* and polydolopines strengthens the hypothesis of polydolopid monophyly supported by these synapomorphies (in addition to those in the cheek-tooth battery).

Goin and Candela (1995) suggested that Polydolopidae might not be monophyletic, given the highly modified lower first molar of polydolopines and the difficulty in deriving them from a hypothesized epidolopine (= *Epidolops*) ancestry. *Epidolops* represents a lineage that diverged from the remaining polydolopids (a clade termed the Polydolopinae) at least as early as the Itaboraian SAL-

MA. Although *Epidolops* (*E. ameghinoi*) represents the earliest known occurrence of a polydolopid (polydolopines are first recorded in the somewhat younger [Flynn and Swisher, 1995] Riochican SALMA), and does have some quite different aspects of molar morphology, it is the proximal outgroup of the polydolopines (with its own autapomorphies) rather than an ancestor. Therefore, one should not necessarily expect to be able to derive every feature seen in polydolopines from the condition in *Epidolops*, but rather from a more generalized condition that marked the common ancestor of both lineages.

Epidolops is distinguished from polydolopines by marked differences in P2/p2 and some aspects of molar morphology, loss of M4/m4 (in polydolopines), and significant rotation of the greatly expanded P3/p3 blades in *Epidolops*. With discovery of the first polydolopine skull (*Polydolops mckennai*), comparison to the other available polydolopid cranium (*Epidolops ameghinoi*, Paula Couto, 1952; Marshall, 1982) reveals differences in several distinctive features between the two lineages, although caution must be exercised in interpreting these differences (due to dorsoventral crushing of both specimens), and understanding their distribution in other polydolopids and phylogenetic implications awaits discovery of crania for other taxa. The cheek-tooth row is straight in *P. mckennai*, rather than V-shaped or arcuate (P3 is angled sharply outward and the tooth rows converge posteriorly in *E. ameghinoi*), proportionally much longer, and with more similarly sized cheek teeth (contra the dominance of a huge P3 in *E. ameghinoi*). The skull of *Epidolops ameghinoi* appears to be markedly more robust than *P. mckennai*, with a very broad rostrum and massive zygomatic arches. The anterior root of the latter is much broader (forming a flattened shelf) and more anteriorly placed relative to the cheek-tooth row (spanning the anterior edge of P3 to the posterior end of M2) in *E. ameghinoi*. In contrast, the anterior zygomatic root in *P. mckennai* spans only the anterior edge of M1 to the middle of M2. The snout is narrower and less flattened anteriorly in *P. mckennai*, and the canine alveolus is less robust and more laterally compressed.

The basicranial portion of the skull and the braincase appear to be much smaller, proportionally, in *E. ameghinoi* than in *P. mckennai*.

All polydolopids share a large suite of unusual, and apparently homologous, dental and gnathic features, including inflexion of the portion of the mandibular ramus bearing the anterior dentition relative to that bearing the cheek teeth, great enlargement of upper and lower canines, procumbency of the enlarged lower canine, reduction of P1/p1, elongate diastema between the canine and cheek teeth, greatly enlarged and bladelike sectorial P3/p3, and quadrate and highly cusped molars. The two available skulls suggest polydolopids are characterized by elongate snouts, broad and relatively flat (dorsoventrally) skulls, and robust zygomatic arches, although crushing of both of the known skulls makes interpretation of these as synapomorphies of the clade tentative. Although similar conditions for some of these appear sporadically among other marsupial taxa, some of these resemblances can be clearly shown to be nonhomologous (e.g., see discussions in Ride, 1962; Marshall, 1982). For example “diprotodont” procumbent anterior teeth, or “plagiaulacoid” shearing blades, occur in other marsupials, but these generally are in different tooth loci than in polydolopids. Similarly, quadrate cheek teeth (sometimes accompanied by a diastema from the anterior tooth battery) occur in other taxa, but anterior and cheek teeth typically are aligned linearly along the ramus. Given their close correspondence in form and apparent homology, we consider this suite of features as synapomorphies indicative of the unique common ancestry of all polydolopids, and thus we conservatively regard *Epidolops* and polydolopines as constituting a monophyletic group (see also Flynn and Wyss 1999).

P. mckennai is the first specimen described from new localities in the Abanico Formation of the Río Cachapoal drainage. It is not yet clear whether the material collected from the Cachapoal locality represents a single fauna/horizon, or several horizons, as our initial collection from this area (currently numbering several dozen specimens) was recovered both in situ and in blocks rolled from the steep valley slopes. The holotype of *P.*

mckennai, as most of the other fossils obtained from this drainage, was found in a block derived from an uncertain stratigraphic horizon within the Abanico Formation. Preliminary assessment of the stratigraphic, structural, and topographic (from analysis of aerial photos) data, relative to more intensively studied sequences only a few kilometers to the south (the Río Las Leñas drainage; Flynn et al., 1995; Charrier et al., 1997, 2002; work in progress by R. Charrier and the authors), suggests that the very steeply dipping strata in this area likely represent only a relatively short interval of time, predating 16.1 Ma and 20.09 Ma levels (the latter containing a fossil platyrrhine, among other taxa; Flynn et al., 1995; Charrier et al., 2002) along the Río Las Leñas. Much or all of the stratigraphic interval at the Cachapoal locality appears to correlate with or underlie strata exposed at Río Las Leñas, which have been preliminarily dated at 29.3 ± 0.1 Ma ($^{40}\text{Ar}/^{39}\text{Ar}$, unpublished, C.C. Swisher III, personal commun.). We thus tentatively consider the material and localities in the immediate vicinity of the polydolopid skull find as representing a single faunal interval, herein termed the Cachapoal locality, although the presence of a mixed fauna from strata of several ages within the suite of material collected from rolled blocks must remain a viable alternative (Charrier et al., 1997). Continuing study of the fauna, geology, and geochronology by R. Charrier and the authors may provide stronger support for interpretation of a single fauna or further evidence for multiple horizons (and their ages).

The youngest previously known polydolopid, *P. abanicoi*, is from the pre-Deseadan, post-Mustersan Tinguiririca Fauna (Flynn and Wyss, 1999). Thus, the Cachapoal locality from which *P. mckennai* derives is no younger than earliest Oligocene (Tinguirirican SALMA, Flynn and Swisher, 1995; Flynn et al., 2003), or this taxon marks an age extension (Deseadan or younger) for the last appearance of polydolopids; the available evidence suggests that the former interpretation is more likely. The Cachapoal locality strata seem to lie within the core of a major anticline, with even more tightly folded anticlinal strata to the east (Charrier et al., 2002). Radioisotopic and new biochronol-

ogic data suggest that deposition in this area initiated by the earliest Oligocene (if not earlier, within the Eocene), and that compression and uplift postdated the early Miocene. Alternatively (but unlikely), if the Cachapoal locality strata (earliest Oligocene or older) are shown not to lie at the core of an anticline, but instead to overlie the 16–29 Ma sequence, it would document eastward thrusting of older strata after the middle Miocene. Such thrusting, although of uncertain timing relative to that in the Las Leñas/Cachapoal area, has been documented in the Abanico Formation along the Río Tinguiririca valley well to the south (Wyss et al., 1994, 1996; Charrier et al., 1994, 1996; see also Godoy and Lara, 1994; Sempere et al., 1994; Godoy et al., 1999). More robust information on the age and tectonostratigraphic relations of the Cachapoal locality strata will be essential to refining the model for basin development under an initial extensional tectonic regime and the timing of subsequent tectonic deformation, compression, and uplift (Charrier et al., 2002).

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