11 The Leontiniidae (Mammalia, Notoungulata) from the Sarmiento Formation at Gran Barranca, Chubut Province, Argentina

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Abstract

At Gran Barranca, pyroclastic sediments comprising lithostratigraphic units of the Sarmiento Formation include several fossil-bearing levels containing Leontiniidae: three in the Upper Puesto Almendra Member (GBV-19 and GBV-34 in Unit 3, and GBV-35 in Unit 4) and five in the Lower Fossil Zone of the Colhue-Huapi Member (GBV-8, GBV-9, GBV-10, GBV-38, and GBV-43). Two new taxa occur at GBV-19; one of these, *Scarrittia barranquensis* n. sp., also occurs at GBV-34. This new taxon shares with *S. canquelensis* and *S. robusta* enlarged and caniniform incisors I1/i3, but is smaller and the premolar morphology is distinct. The second new taxon is *Henricofilholia vucetichia* n. sp. from GVB-19, much smaller than *S. barranquensis* and lacking labial and lingual cingulids on the premolars and molars. A right dentary fragment from GBV-35 with worn m1–3 is here assigned to cf. *S. canquelensis*. The genus *Scarrittia* is cited for the first time at Gran Barranca. The only leontiniid from the Lower Fossil Zone of the Colhue-Huapi Member (type Colhuehuapian) is *Colpodon distinctus*.

Resumen

La secuencia de sedimentos piroclásticos desarrollada en Gran Barranca se refiere a la Formación Sarmiento y en ella se reconocen tres niveles fosilíferos (GBV-19, GBV-34 y GBV-35) para el Miembro Puesto Almendra Superior y varios (e.g. GBV 8, GBV-9, GBV-10, GBV-38 and GBV-43) para el Miembro Colhue-Huapi. En este trabajo se presenta una revisión del material referido a Leontiinidae exhumado en estas localidades, las que se refieren a las edades Deseadense y Colhuehuapense respectivamente. En la localidad GBV-19 se reconocen dos nuevos taxones, uno de los cuales, *Scarrittia barranquensis* n. sp., también se registra en GBV-34. Este nuevo taxón presenta I1/i3 agrandados y caniniformes al igual que *S. canquelensis* y *S. robusta*, pero es más pequeño en tamaño y difiere en la morfología premolar. El segundo taxón de GBV-19, *Henricofilholia vucetichia* n. sp., es significativamente más pequeño y carece de cingulidos labial y lingual en los premolares y molares. En el nivel GBV-35 se registra un fragmento mandibular derecho con m1–3 muy gastados, y es aqui presentado como cf. *S. canquelensis*. También se discute el registro de *H. lustrata* para niveles deseadenses de Gran Barranca. El género *Scarrittia* es citado por primera vez para Gran Barranca. El único leontínido del Colhuehuapense es *Colpodon* y los materiales registrados en Gran Barranca (GBV-38 y GBV-43) son referidos a *C. distinctus*.

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Introduction

Leontiniidae are endemic South American herbivores of medium to large size with distinctive brachydont to mesodont dentitions. In 1885, Burmeister described *Colpodon propinquus*, which later was included in the family that Ameghino (1895) proposed for notoungulates with enlarged and caniniform upper and lower third incisors (e.g. *Leontinia gaudryi* Ameghino 1895). With more complete material Ameghino (1897) observed that it was actually the second and not the third upper incisor that was enlarged. Over a ten-year period around the turn of the last century, Ameghino (1895, 1897, 1901, 1902, 1904a) described another 12 genera and 30 species for the family.

Martinmiguellia fernandezi Bond and Lopez 1995, a generalized leontiniid of medium size with a complete dental series and brachydont dentition, is the oldest known member of the family and comes from Eocene Casa Grande Formation of northwestern Argentina. Other important older material has been presented by Powell and Deraco (2003), Deraco and Powell (2004), and Deraco *et al*. (2008) from the upper levels of the Lumbrera Formation in Salta Povince, Argentina. The skull and mandible of *Coquenia bondi* present few characters distinct from *M. fernandezi*, and these two taxa are distinct from Leontiniidae elsewhere. Most leontiniids come from Deseadan age deposits in Argentina, Bolivia, Brazil and Uruguay. During the Colhuehuapian, leontiniids are represented only by *Colpodon*. Subsequently, leontiniids disappear from the Argentine fossil record and all younger records come from the Miocene of Colombia and Brazil at more equatorial latitudes.

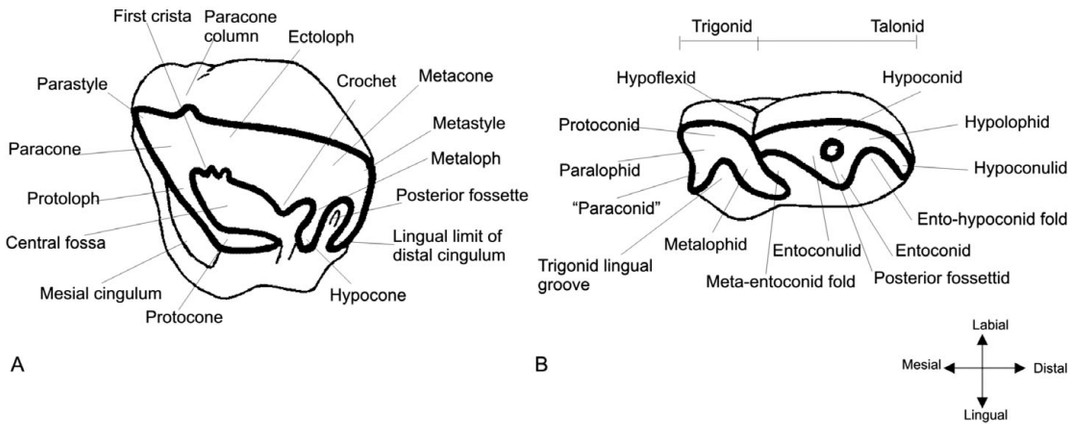

Fig. 11.1. Notoungulate tooth crown nomenclature (from Van Frank 1957; Van Valen 1966; Szalay 1969; Bond 1988). (A) left upper molar; (B) right lower molar.

Much new material of Leontiniidae has been collected at Gran Barranca over the last ten years, with stratigraphic, paleomagnetic, and geochronologic control (e.g. Kay *et al*. 1999; Ré *et al*. 2005; Ré *et al*. Chapter 3, this volume). In this work we describe new material of Leontiniidae from levels at Gran Barranca broadly understood as Colhuehuapian and Deseadan, and compare these with material from other Patagonian and extra-Patagonian localities.

Abbreviations

Institutional

AMNH, American Museum of Natural History, New York; **FMNH**, Field Museum of Natural History, Chicago, Illinois; **MACN**, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Argentina; **MLP**, Museo de La Plata (Departamento Paleontología de Vertebrados), La Plata, Argentina; **MNHN**, Muséum National d'Histoire Naturelle, Paris, France; **MPEF-PV**, Museo Paleontológico "Egidio Feruglio," Trelew, Chubut, Argentina.

Anatomical

Dental terminology follows the convention of using uppercase letters for the upper incisors, canines, premolars, and molars and lower-case for the lower series. Deciduous teeth are prefixed with "d." Notoungulate tooth crown nomenclature used to describe Leontiniidae in this work is illustrated in Fig. 11.1.

Systematic paleontology

Order **NOTOUNGULATA** Roth 1903
Suborder **TOXODONTIA** Owen 1853
Family **LEONTINIIDAE** Ameghino 1895
Genus *Scarrittia* Simpson in Chaffee 1952

Scarrittia Simpson 1934, p. 2; Chaffee 1952, p. 517, plates 7, 8, 9 (Figs. 1, 2, 3, 4, 5), 10 (Figs. 1, 2), 11 (Figs. 1, 2), and 12 (Figs. 1,2); Simpson 1945, p. 127; Ubilla, Perea and Bond 1994, p. 94; McKenna and Bell 1997, p. 458.

Type species *Scarrittia canquelensis* Simpson in Chaffee 1952, p. 517

Referred species *Scarrittia canquelensis* Simpson in Chafee 1952; *S. robusta* Ubilla, Perea and Bond 1994; *S. barranquensis* n. sp.

Revised diagnosis Large Leontiniidae with a complete dental formula without diastema; I1 and i3 enlarged and compressed mesiodistally; small I2; continuous mesiolingual cingulum on the upper premolars; lacking a lingual groove on the P2–4 protocone; short mandible with narrow symphyseal region.

Geographic and chronologic distribution Argentina and Uruguay, Deseadan SALMA.

Scarrittia barranquensis n. sp.
Fig. 11.2.

Holotype MPEF-PV 7753, an incomplete skull with right I3–C, P2–M2 and alveoli of I1–2, C, and P1; left P2–4 and alveoli for I1–3, C, and P1.

Referred material MPEF-PV 6108, right M3; MPEF-PV 6109, right M1; MPEF-PV 6125, left maxilla fragment with P2–4; MPEF-PV 6126, left dentary fragment with p3–m3; MPEF-PV 6131, right P2; MPEF-PV 6132, right dentary fragment with p3–m1; MPEF-PV 6133, left fragment dentary with p4–m2 and m3 broken; MPEF-PV 6134, right P3; MPEF-PV 6137, left M1; MPEF-PV 6139, right P1; MPEF-PV 6141, left dentary fragment with m1–3; MPEF-PV 6144, right M3; MPEF-PV 6143, left P2–4; MPEF-PV 6149, left M1; MPEF-PV 6152, left p2 and P2; MPEF-PV 6227, right m3; MPEF-PV 6229, right

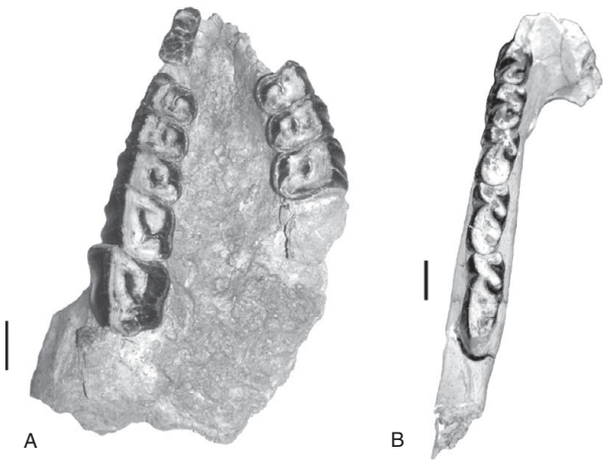

Fig. 11.2. *Scarrittia barranquensis* n. sp. (A) MPEF-PV 7753 (holotype), skull in palatal view with right I3–C, P2–M2 and I1–2, C, P1 alveoli; left P2–4 and I1–3, C, P1 alveoli; (B) MPEF-PV 6609, left mandible with p3–m3 in occlusal view. Scale bar 2 cm.

dentary fragment with p2–m2, MPEF-PV 6231, right dentary fragment with p4–m2; MPEF-PV 6232, left m3; MPEF-PV 6244, right p3; MPEF-PV 6245, right P4; MPEF-PV 6250, left P4; MPEF-PV 6252, right P2; MPEF-PV 6258, right I3; MPEF-PV 6259, right i1 and p3; MPEF-PV 6266, right P1; MPEF-PV 6267, fragmentary left maxilla with P3–4; MPEF-PV 6270, right M3; MPEF-PV 6271, isolated right and left I3 and C; MPEF-PV 6276, right I3 and left P4; MPEF-PV 6609, left mandibular ramus with p3–m3; MPEF-PV 6611, fragmentary right maxilla with P3–M2 and M3 broken; MPEF-PV 6620, right M1; MPEF-PV 6684, mandibular ramus with left i1,c, p1–m1 and right i1–3, p3–m1; MPEF-PV 6858, right p4; MPEF-PV 6953, left p4; MPEF-PV 6955, right P2–3; MPEF-PV 7082, right I1 and I3; MPEF-PV 7086, partial right mandibular ramus with m1–3, and left p3–m3; MPEF-PV 7346, left P3–4; MPEF-PV 7697, fragmentary right maxilla with P2–4; MPEF-PV 7701, right maxilla fragment with M1–3; MPEF-PV 7708, right maxilla fragment with M1–3; MPEF-PV 7718, left maxilla fragment with P2–3; MPEF-PV 7723, partial right mandibular ramus with p4–m3; MPEF-PV 7728, left dentary fragment with m3; MPEF-PV 7730, fragmentary right premaxilla with I2–3, left I3, right maxilla with P2–3; left maxilla with P2–4, M2–3, and right dentary fragment with m1–2; MPEF-PV 7736, right dentary fragment with p4–m3; MPEF-PV 7739, right dentary fragment with p3, m1–3; MPEF-PV 7752, right maxilla fragment with P2–4; MPEF-PV 7944, right maxilla fragment with P4-M3.

Diagnosis Smaller than *S. canquelensis* and *S. robusta*; the molars with mean occlusal areas 22% smaller than in *S. canquelensis*; dentition more brachydont than in *S. canquelensis*, hypocone absent on P1–3, and much reduced on P4, premolars with a distinct paracone column and an indistinct metacone column, labial face relatively flat.

Type locality Gran Barranca Vertebrate locality GBV-19 "La Cantera," Stratigraphic Profile A, and GBV-34, both in Unit 3 of the Upper Puesto Almendra Member, Sarmiento Formation at Gran Barranca, Chubut Province, Argentina.

Etymology In reference to geographic provenance.

Description *Skull* The holotype MPEF-PV 7753 (Fig. 11.2A) preserves the rostrum and from this it can be inferred that *Scarrittia barranquensis* n. sp. had a skull slightly smaller than that of *S. canquelensis* and *Leontinia gaudryi* and a facial region shorter that *L. gaudryi*. The anterior foramen of the infraorbital canal is located at the level of M1. The osseous palate is elongate, concave, and probably extended to the level of M3. The area of attachment of the masseter muscle is prominent (see also MPEF-PV 7730, MPEF-PV 7944) and situated ventrolaterally as in *S. canquelensis*, *L. gaudryi*, and *Taubatherium paulacoutoi*, but differs from *Ancylocoelus frequens and Colpodon propinquus*, wherein this attachment area has a more ventral position.

Mandible MPEF-PV 6229, 6684, 7730, and 6609 present a mandibular corpus about 54 mm deep at the level of m1, while *Scarrittia canquelensis* is about 65 mm and *Leontinia gaudryi* about 60–62 mm. The inferior margin of the corpus in *S. barranquensis* n. sp. is nearly horizontal and the symphyseal region is wider and relatively more elongate than in *S. canquelensis*, about 50 mm in length and extending to the level of p4. A mental foramen appears beneath p2. The posterior margin of the ascending ramus is vertical, similar to *S. canquelensis*, and differing from *L. gaudryi* and *Ancylocoelus frequens* where it is more rounded. As in *A. frequens* and *S. canquelensis* the coronoid process is vertical, differing from *L. gaudryi* where it projects anteriorly.

Upper dentition The upper teeth (Fig. 11.2A) are brachydont but become more mesodont in M1–3. The dentition is complete (3.1.4.3), without diastema. General crown morphology is similar to *Scarrittia canquelensis*. I1 (MPEF-PV 7082) is enlarged and slightly caniniform, triangular in cross-section, with a convex labial face much higher than the lingual, and a distolingual wear facet. Because the material is fragmentary, no labial or lingual cingula can be observed. I2 is not preserved, but its alveolus is smaller than that of I1. I3 (MPEF-PV 7753) is very much smaller than I1 and similar in shape to C in that

both present a convex labiolingual cusp with strong labial and lingual cingula. Premolars are more brachydont than those of *S. canquelensis*. In MPEF-PV 6139, P1 is much smaller than P2–4 and has a single root. There is a strong protocone and labial and lingual cingula. The labial face is slightly convex in P1, flat in P2–4, differing from *S. canquelensis* wherein it is more convex. In MPEF-PV 7753, P2 is smaller than P3, of rectangular aspect, and narrower mesiodistally. The paracone column is well delineated by a median groove. A parastyle and a labial cingulum are both present. The strong protocone is united to the metaconule and in turn to the ectoloph, thereby forming a metaloph. The small paraconule also is united to the ectoloph. The central fossa is open and only closes in advanced wear. Mesial and lingual cingula are shallow, continuous, and separated from the distal cingulum by the protocone crest. P3 and P4 are larger than P2. Paraconule becomes united to the ectoloph and protocone by wear, thereby forming a protoloph that closes the central fossa mesially. The hypocone is absent on P2–3 and much reduced on P4; the parastyle and both labial and distal cingula are present, and the mesial and lingual cingula are continuous.

The molars of *Scarrittia barranquensis* n. sp. are similar to those of *S. canquelensis*, but more brachydont and the labial face is flatter. Both species present a variable lingual cingulum that is strong when present. M2 is larger than M1, with a proportionally larger protocone and smaller hypocone separated by the lingual aperture of an oblique central fossa that becomes obliterated with wear. Parastyle is also stronger on M2. At the lingual limit of the ectoloph the crests formed by enamel folds disappear quickly with wear. There is a persistent mesial cingulum. The distal cingulum becomes united to the hypocone very early in wear, forming a posterior fossette that is deeper on M2. The labial cingulum is absent. M3 (e.g. MPEF-PV 7944) has a reduced hypocone and the aperture of the central fossa is in a more distal position. M3 has a conspicuous parastyle and metastyle, a variable lingual cingulum mesially, and no labial cingulum.

Lower dentition In MPEF-PV 6684 the i1–2 are small and of similar size, with convex labial and lingual faces. Labial and lingual cingula are present. The i3 is larger than i1–2 and its root more compressed mesiodistally. The labial and lingual faces are convex, with a labial cingulum and very strong lingual cingulum. The i2 and i3 display a strong median ridge on the lingual face. In *Scarrittia canquelensis* the i3 is three times larger than the i1–2, whereas in *S. barranquensis* n. sp. it is only twice as large. In the available material the lower canine was not preserved.

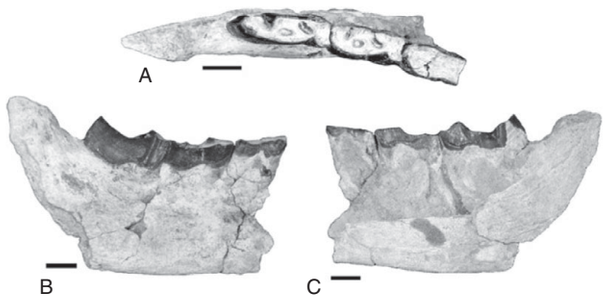

Fig. 11.3. *Scarrittia* cf. *S. canquelensis* Simpson in Chafee 1952. MPEF-PV 6207, right mandibular ramus fragment with m1–3 in occlusal (A), labial (B), and lingual (C) views. Scale bar 2 cm.

The premolars and molars are morphologically similar to those of *Scarrittia canquelensis*, but much smaller in size. The p1 presents the premolar pattern, but the talonid is short and simple, and the labial and lingual cingulids are strong. The p2–4 have protoconids and an elongate distolingually directed metaconids. On each tooth, a small entoconid unites distally with the hypolophid to form a short entolophid and meta-entoconid fold mesially. There is a strong hypoflexid, and labial and lingual cingulids. The p3 and p4 display a small mesiolingual cusp that forms a delicate paralophid. With regard to the molars in MPEF-PV 6609, the m1–3 trigonids are much shorter than the talonids and the metaconid is elongate distolingually. The lingual groove of the trigonid and the meta-entoconid fold are deeper in m3, while the ento-hypoconid fold and hypoflexid are shallower. A posterior fossettid is present. The labial cingulid is only weakly developed in the m2–3. The lingual cingulid of m1–3 sometimes extends to the distal end of the crown.

Scarrittia cf. *S. canquelensis* Simpson in Chaffee 1952 Fig. 11.3.

Referred material MPEF-PV 6207, right mandibular ramus fragment with m1–3; MPEF-PV 6689, left M1.

Locality and stratigraphic horizon GBV-35, Unit 4 of the Upper Puesto Almendra Member, Profile J, Sarmiento Formation at Gran Barranca, Chubut Province, Argentina.

Comments Although MPEF-PV 6207 is very fragmentary, molars present the typical leontiniid posterior fossettid in the talonid, the mandibular corpus is 63 mm deep at the level of m1, similar to *Scarrittia canquelensis* and *Leontinia gaudryi*, but differs from the latter in being thinner or delicate, as in *S. canquelensis.*

Genus *Henricofilholia* Ameghino 1901

Henricofilholia Ameghino 1901, pp. 404–405; *Parastrapotherium* McKenna and Bell 1997, p. 467 (*partim*).

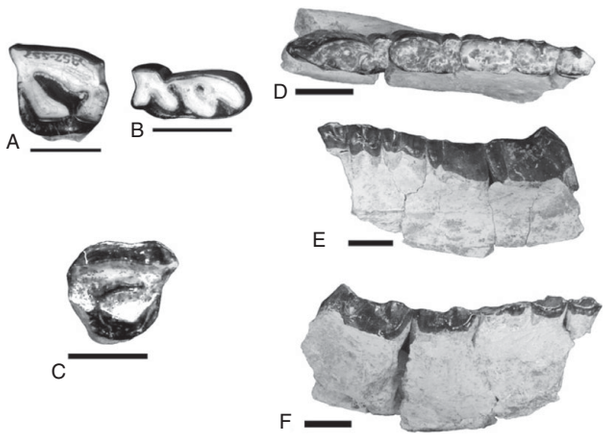

Fig. 11.4. *Henricofilholia lustrata* Ameghino 1901. (A) MACN A52–557 (lectotype), left upper molar, possibly M1, occlusal view; (B) MACN A52–538 (paralectotype), right lower molar, possibly m2, occlusal view. H. *vucetichia* n. sp. (C) MPEF-PV 6129 (holotype), right upper M1, occlusal view; (D–F) MPEF-PV 7717 (paratype) left mandibular fragment with p3–m3 in occlusal (D), labial (E), and lingual (F) views. Scale bar 2 cm.

Type species *Henricofilholia lustrata* Ameghino 1901, p. 405

Referred species *Henricofilholia lustrata* Ameghino 1901; *H. vucetichia* n. sp.

Revised diagnosis Smaller than *Ancylocoelus frequens* and *Taubatherium paulacoutoi*, lacking the first crista on the maxillary molars.

Geographic and chronologic distribution Patagonia, Argentina, Deseadan SALMA.

***Henricofilholia lustrata* Ameghino** 1901

Fig. 11.4A, B.

Henricofilholia lustrata Ameghino 1901, p. 405.

Lectotype MACN A52–557: left upper molar, possibly M1.

Paralectotype MACN A52–538: right lower molar, possibly m2.

Revised diagnosis Leontiniidae having maxillary molars with a reduced parastyle, a mesial cingulum, and no labial or lingual cingula; and with the lower molar lingual cingulid extending to the entolophid.

Type locality *Pyrotherium* beds ("Piso Pyrotheriense"), Sarmiento Formation, Gran Barranca "Barranca Sur del Colhue-Huapi"), Chubut Province, Argentina.

Description The upper molar (MACN A52–557, possibly an M1) of *Henricofilholia lustrata* displays a protoloph larger than the metaloph separated by an oblique central fossa that is open lingually, parastyle is reduced, the mesial cingulum present but not a labial cingulum. The lower molar (MACN A52–538, m1 or m2) presents a lingual cingulid that extends distally to the entolophid. The upper molar differs from those of *Ancylocoelus frequens* by being smaller, and lacking a first crista projecting into the central fossa from the ectoloph; it also lacks a strong mesiolingual cingulum.

***Henricofilholia vucetichia* n. sp**.

Fig. 11.4C–F.

Holotype MPEF-PV 6129, right upper M1.

Paratype MPEF-PV 7717, left dentary fragment with p3–m3.

Referred material MPEF-PV 6135, right lower m2–3; MPEF-PV 6248, left m2; MPEF-PV 6269, right dentary fragment with m2–3; MPEF-PV 7700, associated right lower p2–m1.

Diagnosis Similar to *Henricofilholia lustrata* in size and in lacking a first crista, but differs by displaying a strong parastyle and mesial and lingual cingula in the upper molars; weakly developed or no labial and lingual cingulids on the lower premolars and no labial or lingual cingulids in the lower molars.

Type locality Gran Barranca Vertebrate locality GBV-19 "La Cantera," Profile A, Unit 3 of the Upper Puesto Almendra Member, Sarmiento Formation at Gran Barranca, Chubut Province, Argentina.

Etymology In honor of Dr. María Guiomar Vucetich (MLP).

Description The M1 (MPEF-PV 6129, Fig. 11.4C) is small, and the first crista and labial cingulum are absent as in *Henricofilholia lustrata*. This tooth differs from *H. lustrata* by the presence of a strong mesiolingual cingulum, whereas in *H. lustrata*, this cingulum is very weak and restricted to the mesial aspect, as in *Taubatherium paulacoutoi*. It also differs from *Leontinia gaudryi, Scarrittia barranquensis* n. sp., *S. canquelensis* and *Ancylocoelus frequens* by being very much smaller.

The lower premolars (e.g. MPEF-PV 7717, Fig. 11.4D) are rectangular in outline, with the trigonid and talonid having the same mesiodistal diameter. The entoconid on p2 is much reduced, but in p3–4 becomes united with the hypolophid labially and to the hypoconulid distolingually, forming a false fossettid that eventually disappears with wear. The lingual and labial cingulids are very weak (MPEF-PV 7717, Fig. 11.4E, F), and the latter is restricted to the base of the crown and does not have the same conformation observed in *Leontinia gaudryi, Scarrittia canquelensis* or *Ancylocoelus frequens*, where it is strong and extends across the labial face of the crown. The m1–3 trigonids are much shorter mesiodistally than the talonids; the metaconid is elongate distolingually and the meta-entoconid fold is deeper than the

ento-hypoconid fold. The posterior fossettid is present and hypoflexid shallow. The lingual cingulid of the molars (MPEF-PV 6135, MPEF-PV 6269, and MPEF-PV 7717, Fig. 11.4F) is absent, and in this regard *Henricofilholia vucetichia* differs from the type of *H. lustrata* (MACN A52–538), where the lingual cingulid is evident, crenulated, and runs along the base of crown to the entolophid. In *H. vucetichia* the labial cingulid is absent as in *Taubatherium paulacoutoi* and *Huilatherium pluriplicatum*, but it differs from *H. lustrata, Leontinia gaudryi, Scarrittia barranquensis* n. sp., *S. canquelensis*, and *Ancylocoelus frequens* where the labial cingulid extends across the entire labial face of m1, although is reduced on the talonid of the m2–3.

Genus *Colpodon* Burmeister 1885

Colpodon Burmeister 1885, pp. 161–169, est. III, Fig. 46; Burmeister 1891, pp. 389–399, est.VII, Figs. 4–10; Ameghino 1902, pp. 108–109; Ameghino 1904a, pp. 232–233; Ameghino 1904b, p. 437; Ameghino 1904c, p. 239, Fig. 316; Simpson 1945, p. 127; Soria and Bond 1988, p. 36; McKenna and Bell 1997, p. 459.
Baenodon Ameghino, 1892, p. 461. *Syn. n.*

Type species *Colpodon propinquus* Burmeister 1885, pp. 161–169.

Revised diagnosis Leontiniidae presenting a combination of characters including: concave area of origin of the masseter in a ventral position as in *Ancylocoelus frequens*; upper canine vestigial or absent, lower canine absent, but without diastema; in the premolars, the paraconule is close to protocone and labiodistal fossette; the maxillary molar fossettes by union of the first crista, second crista, and crochet.

Geographic and chronologic distribution Patagonia, Argentina, Colhuehuapian SALMA.

Colpodon distinctus Ameghino 1902

Fig. 11.5.

Colpodon distinctus Ameghino 1902, pp. 108–109; Ameghino 1904b, p. 437; Patterson, 1952, *in litteris*.
Colpodon divisus Ameghino 1904a, p. 232 (*error*)
Colpodon plicatus Ameghino 1904a, pp. 232–233; Ameghino 1904c, p. 239, Fig. 316; Patterson 1952, *in litteris* (*sin.*).

Lectotype MACN A52–574, premaxilla and maxilla fragments with right and left I1–3; right P1, right and left P2–M3, mandible with right and left i1–3, left p1, right and left p2–m3.

Referred material MACN A52–576, maxilla fragment with left DM2–4 (holotype of *Colpodon plicatus*); AMNH 29688, left dentary fragment with p2–m3; AMNH 29721, right dentary fragment with dm2–m2; FMNH-13304, anterior region of skull fragment; FMNH-13310, skull fragment with left P2–M3; FMNH-13316, dentary fragment with right p2–m3; FMNH-13591, MACN A52–579, right and left maxilla fragments with P1–4; MACN A52–580, right maxilla fragment with M1–3; MACN A52–581, left maxilla fragment with M1–3; MPEF-PV 6346, left dentary fragment with m1–2; MPEF-PV 6448, left isolated dp4?; MPEF-PV 7014, left maxilla fragment with worn P3–4, M1; MPEF-PV 7080, left maxilla fragment with P4; MPEF-PV 7134, two associated teeth, MPEF-PV 7306, lower premolar; MPEF-PV 7465, maxilla; MPEF-PV 7837, upper molar fragment; MLP 82-V-2–40, right and left maxilla fragments with P4–M3 and temporal region; left P4–M3; MNHN 1900–18, three specimens: left P3–M2; right P1–M2; left M3.

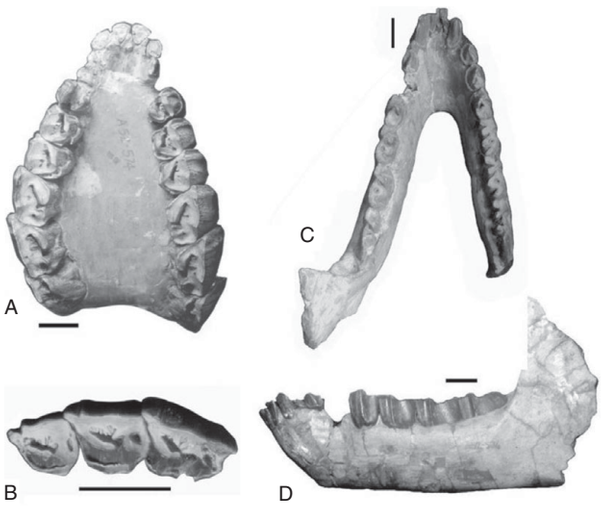

Fig. 11.5. *Colpodon distinctus* Ameghino 1902. (A, C, D) MACN A52–574, (lectotype); (B) MACN A52–576 (type of C. *plicatus*). (A) skull in palatal view with right I1–3, P1–M3 and left I1–3, P2–M3; (B) left DM2–4 in occlusal view; (C–D) mandible with left i1–3, p1–m3, and right i1–3, p2–m3 in occlusal (C) and lateral (D) views. Scale bar 2 cm.

Locality and stratigraphic horizon Gran Barranca, "*Colpodon* beds," GBV-8 (level A), GBV-9 (level B), GBV-10 (level C), GBV-38 (level Z), and GBV-43 (level 16), Lower Fossil Zone, Colhue-Huapi Member, Sarmiento Formation, Chubut Province, Argentina. The biostratigraphic range of *Colpodon distinctus* encompasses the full thickness of local magnetozone N2 of Profile A-1, interpreted as Chron C6An.1n (20.0 and 20.2 Ma) (Ré *et al*. Chapter 4, this book).

Revised diagnosis *Colpodon distinctus* is smaller than C. *propinquus*; with molar mean occlusal area 32% smaller than in C. *propinquus;* P2–4 protocone proportionally larger than in *C. propinquus*; P2 central fossa opens mesiodistally, and mesially in P3.

Description *Mandible* MACN A52–574 (Fig. 11.5C, D) displays a delicate horizontal corpus that is 42.4 mm deep at the level of p4, and that differs from the robust mandible of *Colpodon propinquus* (MPEF-PV 1104, Gaiman) that is 45 mm deep at the level of p4. The mandible is synostosed; and relatively narrow symphyseal region extends nearly to the level of p3.

Upper dentition All teeth are mesodont.

Deciduous upper dentition In MACN A52–576 (Fig. 11.5B), in size, dM2 < dM3 < dM4. The protocone is united to the paraconule and the ectoloph to form a protoloph. DM2 metaloph evident in advanced wear. Multiple crista are present along the lingual margin of the ectoloph. The parastyle is strong and separated from the paracone by a deep groove. The oblique central fossa is open lingually but closes with wear. The posterior fossette appears distally and there is a mesiolingual cingulum.

Permanent upper dentition The upper incisor is not markedly enlarged as in *Leontinia gaudryi*, but I2 is the largest. The incisors in MACN A52–574 (Fig. 11.5A) are somewhat fractured, but I1 has a triangular outline and a weak labial cingulum; I2 is larger than I1, with a subtriangular outline, a labial cingulum on the distal portion of labial face, and a lingual cingulum. I3 is smaller than I1–2, with a smaller labiolingual diameter, and strong labial and lingual cingula. There is no alveolus for the upper canine in MACN A52–574, nor in other material from Gran Barranca, but MLP 49-XI-21–15 (from Punta Magagna, Chubut, ?Trelew) displays small roots between I3 and P1, suggesting that the upper dental formula of *Colpodon* in this specimen was complete, including a vestigial C. P1 is small and in MACN A52–579 and presents little wear compared with the other premolars. P1 has a rudimentary protocone united to the mesial and distal cingula, a mesiodistally short ectoloph, and a central fossa, wide and open both mesially and distally, convex labial face, and labial and lingual cingula. P2–4 are rectangular in outline. P2 is smaller than P3 and slightly narrower mesiodistally. The P2 protocone is united lingually to the distolingual cingulum and distally to the metaconule: a "metaloph" forms in advanced wear. The paraconule is much reduced and united to the protocone. Mesiodistally the central fossa is open. There is a strong paracone column. The mesiolingual cingulum is continuous, a parastyle is present, as are distal and labial cingula. The P3–4 protocone is united to the paraconule to form an oblique protoloph, which when heavily worn in P3 becomes united to the ectoloph, closing the central fossa mesially. The P3 hypocone is united to the metaconule and this in turn to the ectoloph thereby forming a metaloph. There is a strong paracone column. The labiodistal fossette is formed by the union of the crochet with the lingual end of the ectoloph; enamel folds in the ectoloph form isolated enamel fossettes with wear similar to those observed in *Huilatherium pluriplicatum* and *Purperia cribatidens*. There is a strong mesiolingual cingulum near the base of the crown. The deeper distal cingulum is separated from the mesiolingual cingulum by a crest that projects from the hypocone. A parastyle is present, as are lingual and distal cingula. The labial cingulum is present only on the mesial portion of the labial face. The premolar protocone of *Colpodon* differs from that of other leontiniids. This morphology may be a consequence of the closer approximation between paraconule and protocone. The mesiolingual cingulum is continuous, as in *Scarrittia*, but very different from *Leontinia* and *Ancylocoelus*. The labiodistal fossa is observed only in *Colpodon*. The premolars of *C. distinctus* are similar to the *C. propinquus*, but differ in more rectangular outline, and presenting a larger protocone more separated from the hypocone.

M1 and M2 are quadrangular in outline and with wear become mesiodistally shortened. The protocone is larger than the hypocone and separated by the lingual opening of the oblique central fossa. There is a strong parastyle. The first and second crests are observed on the ectoloph lingually; a strong crochet projects from the metaloph; crests form small enamel fossettes, the posterior fossette is conspicuous and the lingual cingulum is tenuous or absent; a labial cingulum is absent. M3 has a strong protoloph and much reduced hypocone and a central fossa that opens lingually; first and second crests are united to the crochet of the metaloph forming small fossettes with wear. Parastyle and metastyle are strong, the mesiolingual cingulum is tenuous or absent. There is no labial cingulum; a distal cingulum forms the posterior fossette. In the upper molars the crochet and second crest form conspicuous fossettes, differing in this regard to other Oligocene leontiniids and more nearly resembling *Huilatherium pluriplicatum* and *Purperia cribatidens*.

Permanent lower dentition The i1 and i2 are similar in size and much smaller than i3. The incisor crowns are narrow and high, with the labial face slightly flat and with a labial cingulid. A narrow longitudinal crest and cingulid appear on the lingual face. The i3 is enlarged and turned lingually; its labial and lingual faces are convex, the latter with a longitudinal crest medially. There are labial and lingual cingulids. The incisors are similar to those of *Colpodon propinquus*, but more delicate and smaller, mesiodistally narrow, and mesodont. The c1 is absent, as in *Ancylocoelus frequens*. The p1 is very

small, smaller than i1–2, and has a triangular and pointed crown with strong labial and lingual cingulids. The check teeth do not present significant morphological differences when compared with *C. propinquus* or the other leontiniids. The p2 trigonid is distinct from the talonid. A protoconid is present. There is a short groove between the trigonid and metaconid lingually and a strong hypoflexid labially. A small entoconid is present on the talonis and labial and lingual cingulids are present. The p3 is larger than p2. The p2 talonid slightly larger than trigonid; the entoconid is united with the hypolophid distally, the hypoflexid is deep, smaller meta-entoconid fold; labial and lingual cingulids present. The p4 is larger than p3. The p4 talonid slightly larger than trigonid; the entoconid is connected to the medial portion of the hypolophid; labial and lingual cingulids are present. The m1–3 trigonids are narrower mesiodistally than the talonid; metaconid slightly elongate distolingually, trigonid groove shallow; deep meta-entoconid fold; ephemeral ento-hypoconid fold on m1, persistent on m2, open and deep on m3; elongate hypoconulid and more mesodont crown; posterior fossettid present; shallow hypoflexid; no labial cingulid; lingual cingulid on m1–3 at the level of the entolophid.

Discussion

Systematics

Five taxa of Leontiniidae occur at Gran Barranca, two at GBV-19 (Unit 3, Upper Puesto Almendra Member) and GBV-34 (Unit 3, Upper Puesto Almendra Member), a third taxon at GBV-35 (Unit 4, Upper Puesto Almendra Member), and another purportedly from the "*Pyrotherium* beds" (Ameghino 1901, 1906), and the fifth in the Lower Fossil Zone of the Colhue-Huapi Member (GBV-8, 9, 10, 38, and 43).

Two new taxa occur at GBV-19 and GBV-34 (Unit 3) that are of different size and morphology. The larger taxon, *Scarrittia barranquensis* n. sp., presents many diagnostic characters that refer it unequivocally to *Scarrittia*. This Gran Barranca species is smaller of *S. canquelensis* from Chubut Province and *S. robusta* from Uruguay, with cheek teeth that are shorter mesiodistally (Fig. 11.6). Morphologically, it is very similar to the other species of *Scarrittia*, except in having more brachydont premolars and molars, and maxillary premolars with a more marked paracone column, a reduced hypocone, and a flatter labial face. By contrast, maxillary premolars in *S. canquelensis* display a well-marked metacone column, stronger hypocone (on P3–4), and a convex labial face.

The fragmentary material MPEF-PV 6207 from locality GBV-35 (Unit 4, Upper Puesto Almendra Member) is

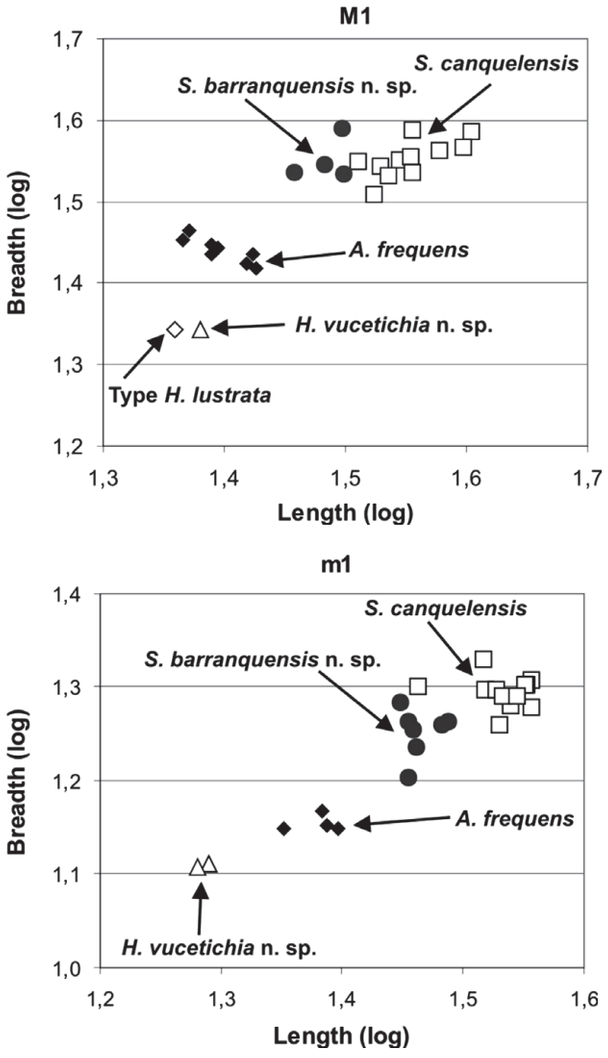

Fig. 11.6. Plot of upper and lower M1/m1 length and breadth measurements for specimens of *Scarrittia barranquensis* n. sp. from Gran Barranca (GBV-19 "La Cantera" and GBV-34), *S. canquelensis* from Scarritt Pocket, Los Búlgaros, Laguna Payahilé localities, *Henricofilholia vucetichia* n. sp. from GBV-19, *H. lustrata* from Gran Barranca, and *Ancylocoelus frequens* from La Flecha.

tentatively refered to *Scarrittia* cf. *S. canquelensis* on the basis of its large size and dentary morphology. The discovery of *Scarrittia* at Gran Barranca is noteworthy, especially given that the Ameghino collection includes no material of this genus.

Three species of smaller Deseadan leontiniid were proposed by Ameghino (1895, 1901), *Leontinia garzoni* in 1895, and *Ancylocoelus minor* and *Henricofilholia lustrata* in 1901. *Leontinia garzoni* was described on the basis of two specimens from La Flecha (MACN A52–599

and MACN A52–600bis) analyzed by Patterson (1952) and revised by Ribeiro (2003), who considered both specimens very similar to *Ancylocoelus frequens*. *Ancylocoelus minor* was based on a right maxillary fragment with M2–3 (MACN A52–551) and left M3, both from La Flecha. According to the original diagnosis (Ameghino 1901) this species is smaller than *A. frequens* with molars shorter mesiodistally and a continuous lingual cingulum around the protoloph. As the molars are only slightly smaller than *A. frequens* and the occlusal morphology differs only in the absence of the first crista in the central fossa of M3, Patterson (1952) and Ribeiro (2003) referred it to *A. frequens*. Finally, *Henricofilholia lustrata* was proposed by Ameghino (1901). Five additional species were eventually described (*H. circumdata*, *H. cingulatum*, *H. inaequilatera, H. intercincta, H. lemoinei*) (Ameghino 1901, 1904a). Patterson (1952) and Ribeiro (2003) synonymize *H. circumdata* from Cabeza Blanca with *Leontinia gaudryi*. They consider *H. cingulatum* and *H. inaequilatera* from La Flecha and *H. intercincta* from Monte Espejo as junior synonyms of *A. frequens*. *Henricofilholia lemoinei* is an Astrapotheriidae. *Henricofilholia lustrata* from Gran Barranca differs in size and morphology and is therefore considered a valid taxon. AMNH 29607 from Scarritt Pocket with M1 morphology similar to the *H. lustrata* (described by Chaffee 1952, p. 518, Fig. 3 as cf. Leontiniidae indet.) may also belong to *H. lustrata*.

Henricofilholia lustrata was collected by Carlos Ameghino at the "*Pyrotherium* beds" of Gran Barranca, and it differs from the small leontiniid from GBV-19 in important details: on M1 there is a strong mesiolingual cingulum; the lingual cingulid of the lower molars is weak or absent and there is no labial cingulid. On the basis of these features, we conclude that the small leontiniid from GBV-19 belongs to another new species, *Henricofilholia vucetichia* n. sp.

Leontiniids are solely represented in the Colhuehuapian by *Colpodon*. Ameghino (1902) claimed that the labial roots are bifurcate, well separated and divergent in *C. propinquus*, whereas P1–2 in *C. distinctus* present single convex labial roots and P3 a single labial and another lingual root. Restudy of the original material reveals that premolar roots are not preserved in MACN A-967 and the premolar roots of the type of *C. distinctus* (MACN A52–574) are poorly preserved. Nevertheless, while the more proximal portion in *C. distinctus* is unique in structure, without benefit of further preparation or radiography, Ameghino (1902) could not have excluded the possibility that the roots were bifurcate within the alveolus (other specimens in the Ameghino collection preserve bifurcate roots on P2–3, e.g. MACN A52–579). One must conclude then that this character (single labial root in the maxillary premolars) of Ameghino (1902) is not observable in the

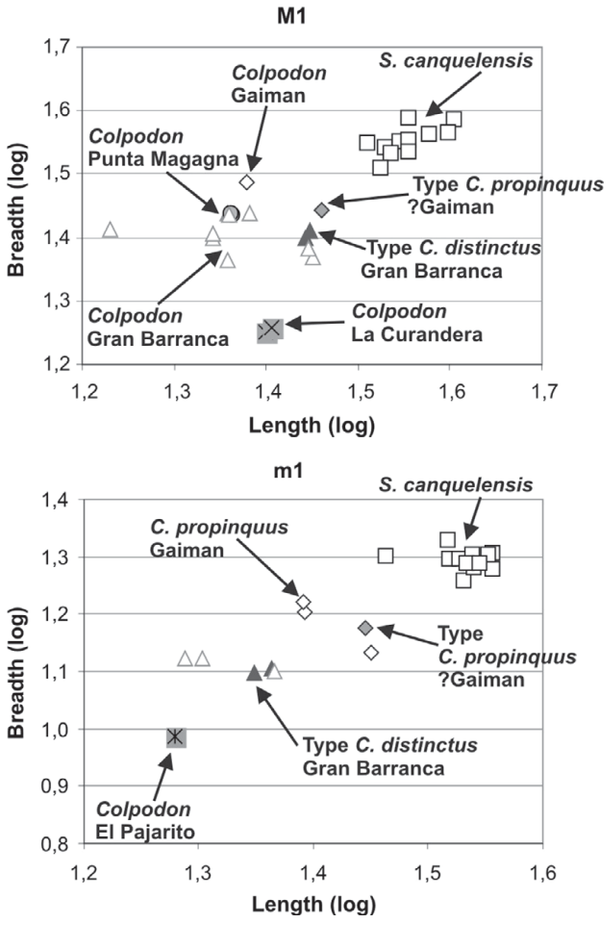

Fig. 11.7. Plot of upper and lower M1/m1 length and breadth measurements for specimens of *Scarrittia canquelensis* from Scarritt Pocket, Los Búlgaros, Laguna Payahilé localities, *Colpodon propinquus* from Gaiman, *C. distinctus* from Gran Barranca, *Colpodon* from Punta Magagna, and *Colpodon* sp. from La Curandera and El Pajarito.

type specimen of *C. distinctus*, and thus, not a diagnostic character of the species. Other than the fact that *Colpodon distinctus* premolars are more rectangular in outline (they have a larger protocone and somewhat more separated hypocone), the cheek teeth of *C. distinctus* do not present important morphological differences from *C. propinquus*. So similar are they, in fact, that Soria and Bond (1988) considered *C. distinctus* conspecific with *C. propinquus*, but noted that the type material of *C. propinquus* was somewhat larger. Dental measurements of the types and all material subsequently assigned to *Colpodon* from Gran Barranca, Gaiman, La Curandera, and El Pajarito, confirm that the type of *C. propinquus* is larger than the type of *C. distinctus*. However, this size difference is not always observed in the upper molars, as these teeth change size with occlusal wear (Fig. 11.7).

Table 11.1. *Localities of Deseadan age in Argentina (Patagonia and Mendoza province), Bolívia (Salla) and Brazil (Tremembé Formation) where the Leontiniidae are represented*

	Gran Barranca				Other localities							
	UPA				Argentina					Uy	Bol	Bz
Taxon	GBV-19	GBV-34	GBV-35	PB	SP	CB	EP	QF	LF			
Scarrittia canquelensis					x							
Scarrittia cf. *S. canquelensis*			x					x				
Scarrittia barranquensis	x	x										
S. robusta										x		
Leontinia gaudryi						x	x		x			
Henricofilholia vucetichia	x											
H. lustrata				x								
Ancylocoelus frequens						x	x		x			
Taubatherium paulacoutoi												x
Anayatherium fortis											x	
Anayatherium ekecoa											x	

Notes: LF, La Flecha.
UPA, Upper Puesto Almendra.
PB, "*Pyrotherium* beds"
SP, Scarritt Pocket.
CB, Cabeza Blanca.
EP, El Pajarito.
QF, Quebrada Fiera.
Uy, Uruguay, Fray Bentos Formation.
Bol, Salla, Bolivia.
Bz, Taubaté, Tremembé Formation, Brazil.

While most of the material of *C. distinctus* from Gran Barranca consists of lower molars, some have been found in association with maxillary teeth, and these associations lead us to conclude that the species at Gran Barranca is indeed *C. distinctus*.

Finally, in passing, we note that material of *Colpodon* from the Colhuehuapian localities at El Pajarito and La Curandera are demonstrably smaller than material from either Gran Barranca or Gaiman.

Biogeography, biostratigraphy, and paleoecology

Leontiniidae are represented in many localities of Deseadan age in Argentine Patagonia and in Mendoza Province, and elsewhere in South America at Salla in Bolívia and the Tremembé Formation of Brazil (Table 11.1). The largest number of Deseadan taxa occur in Patagonia and include *Leontinia gaudryi*, *Ancylocoelus frequens*, *Scarrittia canquelensis*, *Henricofilholia lustrata*, and the two new species described herein, *S. barranquensis* n. sp. and *H. vucetichia* n. sp.

The geographic distribution of these Deseadan species is remarkable. Whereas *Henricofilholia lustrata* and *H. vucetichia* n. sp. are leontiniids of relatively small size and occur only at Gran Barranca and possibly Scarritt Pocket (Chubut Province), *Leontinia gaudryi* and *Ancylocoelus frequens* (larger leontiniids) are restricted to the northern part of Santa Cruz Province (La Flecha, Cerro Alto, Piedra Negra, Monte Espejo, Estancia 8 de Julio) and central Chubut Province (Cabeza Blanca, Rincón del Zampal, Las Cascadas) to as far north in Patagonia as El Pajarito. *Scarrittia* is the best-known leontiniid, and occurs in localities extending from the latitude of central Chubut (*S. canquelensis*) to as far north as Mendoza (*S.* cf. *S. canquelensis*) and Uruguay (*S. robusta*).

It is noteworthy that *Leontinia gaudryi* and *Ancylocoelus frequens* do not occur at any localities or levels where *Scarrittia* occurs, whether *S. barranquensis* n. sp., *S. canquelensis*, or *S. robusta*.

Scarrittia canquelensis comes from the Scarritt Pocket locality along with a faunal assemblage assigned to the Deseadan SALMA. *Scarrittia canquelensis* and the rodent *Platypittamys brachyodon* are the only taxa occurring in the Scarritt Pocket quarry (Locality I of Marshall *et al.* 1986) in

stratigraphic relationship with basalts that were dated to between 23.4 Ma and about 21.0 Ma.

This contrast in composition may indicate differences in the age of these faunas, although most of these localities remain undated. What can be established is that *S. barranquensis* n. sp. occurs at two localities or levels at Gran Barranca, GBV-19 "La Cantera" and GBV-34 that are between 33.7 and 29.5 Ma in age, whereas GBV-34 occurs in Unit 4 of the Upper Puesto Almendra Member on a discontinuity surface that postdates basalts dated between about 29.2 and 26.3 Ma. The material assigned to *S.* cf. *S. canquelensis* is higher-crowned and somewhat larger and occurs at GBV-35 in a laterally extended lenticular fossil-rich homeoconglomerate bed (Ré *et al.* Chapter 3, this volume). Neither *L. gaudryi* nor *A. frequens* occur at these localities or levels at Gran Barranca. The only dated locality where *L. gaudryi* and *A. frequens* occur is at La Flecha where as yet unpublished dates are between 21.5 and 23.4 Ma (R. Madden, personal communication).

During the Colhuehuapian, leontiniids are represented only by *Colpodon* in a distribution restricted to central Patagonian localities in Chubut (Gran Barranca, Gaiman, Punta Magagna, and Sacanana) and Rio Negro provinces (Paso Córdoba, Chichinales Formation).

The most outstanding features of leontinids include their canine-like incisors and low-crowned, brachydont to mesodont cheek teeth. The Deseadan leontinids were herbivores of medium (smaller than a tapir) to large (smaller than a rhinoceros) size with large, brachydont cheek teeth and for *S. canquelensis* Chaffee (1952) described broadly splayed digits with flat hooves, a combination of morphologies suggesting a browsing habitus on soft substrate. The Colhuehuapian *Colpodon* is mesodont, having somewhat higher crowns than other known Leontiniidae. In general, while the diversity of Colhuehuapian ungulates is less than in the Deseadan, browsing forms like *Colpodon* are more common (Bond 1986).

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