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SHORT COMMUNICATION

A REVIEW OF THE MOLAR MORPHOLOGY AND PHYLOGENETIC AFFINITIES OF *SILLUSTANIA QUECHUENSE* (METATHERIA, POLYDOLOPIMORPHIA, SILLUSTANIIDAE), FROM THE EARLY PALEOGENE OF LAGUNA UMAYO, SOUTHEASTERN PERU

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The early Paleogene mammalian assemblages known from the red mudstones of the Lower Muñani Formation at Laguna Umayo, southeastern Peru, add significant information on the early phases of the evolution of Metatheria in South America. Two early Cenozoic vertebrate associations have been found from the Laguna Umayo area: localities LU-3 and Chulpas, both including metatherians (Sigé et al., 2004, and literature cited therein). The LU-3 locality yielded *Peradectes austrinum* (Peradectidae; Sigé, 1971, 1972; Crochet, 1980), at least two indeterminate didelphimorphians, and a ?Pediomyidae or ?Microbiotheriidae indet. (Sigé, 1972; Sigé et al., 2004). The Chulpas local fauna includes at least three indeterminate didelphimorphians (Crochet and Sigé, 1993) and three polydolopimorphians: *Chulpasia mattaueri, Chulpasia jimthorselli* (Crochet and Sigé, 1993; Sigé et al., 2009; but see below), and *Sillustania quechuense* (Sillustaniidae; Crochet and Sigé, 1996).

The Laguna Umayo associations have alternatively been referred to the Late Cretaceous or the early Paleogene. Grambast et al. (1967; see also Sigé, 1971) assigned the Chulpas levels to the Vilquechico Formation (Maastrichtian) because it was correlated with deposits containing charophytes and dinosaur eggshells. More recently, Sigé et al. (2004; see also Gelfo and Sigé, 2011) favored a younger age for the LU-3 and Chulpas localities: late Paleocene—early Eocene, probably coincident with the Itaboraian South American Land Mammal Age (SALMA; Gelfo et al., 2009; Oliveira and Goin, 2011). We follow Woodburne et al. (2014) for the calibration of early Paleogene SALMAs.

The highly derived, enigmatic morphology of the only known upper molar of *Sillustania quechuense* led to the recognition of a new family of South American metatherians: Sillustaniidae (Crochet and Sigé, 1996). Crochet and Sigé (1993) preliminarily assumed that *Sillustania* was probably a caenolestoid paucituberculatan, but in their formal description they recognized the Sillustaniidae as a new family belonging to the polydolopoid polydolopimorphians (Crochet and Sigé, 1996).

A review of the holotype and tentatively referred specimen of *Sillustania quechuense* (Figs. 1–3) has led us to reassess its upper molar morphology and homologies, as well as its phylogenetic affinities. The discussion of these aspects constitutes the main aim of this work.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York, U.S.A.; **CHU**, Museo de Historia Natural de Cochabamba, Cochabamba, Bolivia; **MACN A** and **MACN Pv**, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia,' Buenos Aires, Argentina, Ameghino Collection and Museo Collection, respectively; **MLP**, División Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina.

Other Abbreviations and Conventions—**Ma**, mega-annum, one million years in the radioisotopic time scale. **L**, length; **W**, width. **c**, lower canine; **C**, upper canine; **i**, lower incisor; **I**, upper incisor; **m**, lower molar; **M**, upper molar; **p**, lower premolar; **P**, upper premolar; **StA, StB, StC, StD**, and **StE**, stylar cusps A, B, C, D, and E, respectively. Cusp homology follows Chornogubsky et al. (2009).

MATERIALS AND METHODS

Materials

Comparisons for the phylogenetic analysis were made with specimens from MLP, MACN, CHU, and MNHN collections. Most of these specimens are those reviewed by Goin et al. (2009).

Methods

A phylogenetic analysis was carried out using the software TNT 1.1 (Goloboff et al., 2003). The analysis included 25 taxa and 45 characters (Supplementary Data, Appendix S1). All characters were regarded as unordered. Bremer support, consistency index, and retention index were calculated. Minor changes have been included in the data matrix from Goin et al. (2009): character 44 was added; character 33 has a new character state 5 (centrocrista absent) because polydolopids have no centrocrista; character 36 has a new state 2, 'only postmetaconular crest developed'; and character 37 has a new state 4, 'very large metaconule but not hypocone-like' (seen in polydolopiforms). We also included in character 42 the state 2 (fused to StD) and the character 45, 'Position of StB,' both from Forasiepi et al. (2013) (Supplementary Data, Appendix S2).

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In order to analyze which changes could introduce the lower molar tentatively asigned to *S. quechuense* (see below), another phylogenetic analysis was carried out including this locus.

SYSTEMATIC PALEONTOLOGY

Order POLYDOLOPIMORPHIA Archer, 1984
Suborder POLYDOLOPIFORMES Kinman, 1994
Family SILLUSTANIIDAE Crochet and Sigé, 1996

Included Genera—*Roberthoffstetteria* Marshall, Muizon, and Sigé, 1983, and *Sillustania* Crochet and Sigé, 1996.

SILLUSTANIA QUECHUENSE Crochet and Sigé, 1996
(Figs. 1–3)

Holotype—CHU 33, an isolated left M2 (Figs. 1, 2A).

Tentatively Referred Specimen—CHU 34, an isolated left lower molar (Figs. 2B, 3).

Provenance—Both specimens come from the upper levels of the red mudstone unit of the lower Muñani Formation, Chulpas locality and local fauna, Laguna Umayo area, southeastern Peru (Sigé et al., 2004:figs. 1–3).

New Diagnosis—Polydolopiformes more similar to *Roberthoffstetteria nationalgeographica* than to any other taxon of the clade. It differs from *Roberthoffstetteria* in the following features of the upper molars: postmetaconular crest not contacting the posterior cingulum; preparaconular crest not reaching the StA; StB large and aligned with the paracone; and StC larger than StD.

Description—The holotype of *Sillustania quechuense* is an isolated, worn M2 broken at its posterolabial and anterolabial corners (Figs. 1, 2A). In lingual view, the margin of the crown is rounded (not bi- or trilobed). In occlusal view (Figs. 1A, B, 2A), it has three almost anteroposteriorly aligned cusps: the paraconule (mesial), the metaconule (distal), and the protocone (intermediate). The protocone is the largest of the lingual cusps; it occupies most of the center of this margin, and is slightly more lingual than the para- and metaconule, with its apex mesially projected. It is further away from the metaconule than from the paraconule. There is no cingulum or crest at the base of the protocone. The paraconule is heavily worn and labiolingually compressed. The preparaconular crest extends labially, reaching the anterior cingulum (Figs. 1A, C, 2A). The metaconule lies distal to the protocone and is separated from it by a shallow furrow. (Figs 1A, B, 2). This cusp is bulbous like the protocone, but shorter, and its lingual face protrudes from the lingual face of the crown. Although large, it is not hypocone-like in size, as in bonapartheriiforms. The postmetaconular crest is well developed and almost at the same level as the trigon basin, mesiodistally expanding surface of the latter. The postmetaconular crest reaches the metacone, ending distal to it (Fig. 1D).

The paracone and metacone are labially placed in the crown (Figs. 1A, B, 2A). They are robust and large. Judging from the preserved bases, they were the tallest cusps of the tooth. The paracone is more lingually placed, set closer to the paraconule than the metacone is to the metaconule, buccolingually wider than the metacone, and the preparacrista is directed towards StA. The postparacrista contacts the premetacrista, forming a short and straight centrocrista (the straightness of the centrocrista is not evident because of wear on the paracone and metacone, which gives the impression that it is 'V'-shaped). The postmetacrista is incomplete, longer than the preparacrista and curved in occlusal view.

The stylar region of the tooth is eroded and partially broken (Figs. 1A, B, 2A). Anteriorly, StA is small. The StB is large and appears to be aligned with, and compressed to, the paracone. At the labial margin, and aligned with the paracone and the StB, there is another cusp. At the middle of the mesiodistal length of the stylar

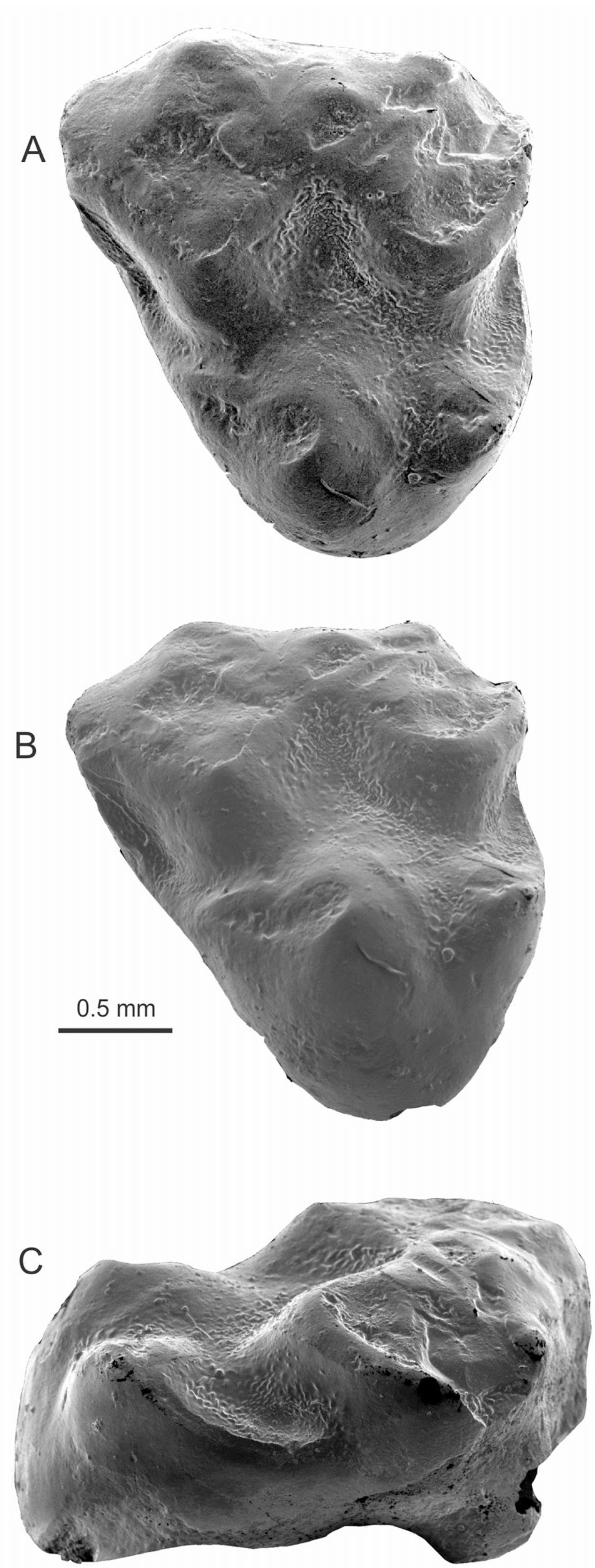

FIGURE 1. SEM photographs of the holotype of *Sillustania quechuense*, CHU 33. **A**, occlusal view; **B**, occlusolingual view; **C**, distal view.

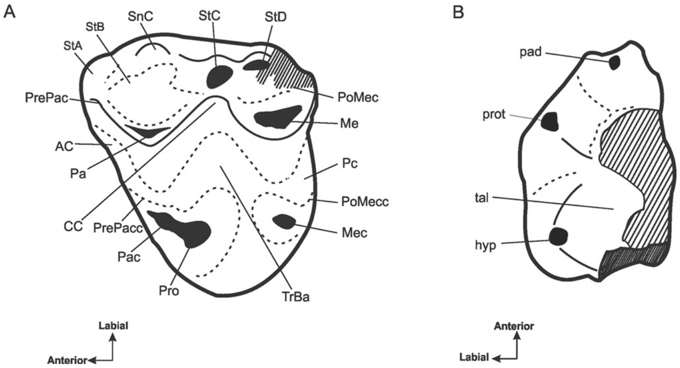

FIGURE 2. Schematic drawings. **A**, holotype of *Sillustania quechuense*, CHU 33; **B**, referred material, CHU 34. **Abbreviations**: **Ac**, anterior cingulum; **CC**, centrocrista; **hyp**, hypocone; **Me**, metacone; **Mec**, metaconule; **Pa**, paracone; **Pac**, paraconule; **pad**, paraconid; **Pc**, posterior cingulum; **PoMeC**, postmetacrista; **PoMecc**, postmetaconular crest; **PrePaC**, preparacrista; **PrePacc**, preparaconular crest; **Pro**, protocone; **prot**, protoconid; **SnC**, supernumerary stylar cusp; **StA**, **StB**, **StC**, **StD**, stylar cusps A, B, C, and D, respectively; **tal**, talonid; **TrBa**, trigon basin. Oblique lines indicate that the area is broken.

shelf, a robust StC is present, more lingually placed than the StB. The StD is large and labiolingually aligned with the metacone.

An isolated left lower molar (CHU 34; Figs. 2B, 3) has been tentatively assigned to this species (Crochet and Sigé, 1996; see also Remarks). The tooth is lingually broken (Figs. 2B, 3A, C), and the metaconid, hypoconid, and hypoconulid are missing. The trigonid is more labially salient than the talonid. The protoconid is the largest cusp of the crown and is not mesiodistally compressed; however, because of its quite flat posterior wall, it is not as conical as in *Roberthoffstetteria*. A notched paracristid joins the paraconid and protoconid. The metacristid is obliquely set, as is also the case in the m1 of *Roberthoffstetteria* and many microbiotherians and paucituberculatans. The metaconid is broken; however, judging from the orientation and preserved base of the metacristid, it seems that it was posteriorly placed with respect to the protoconid.

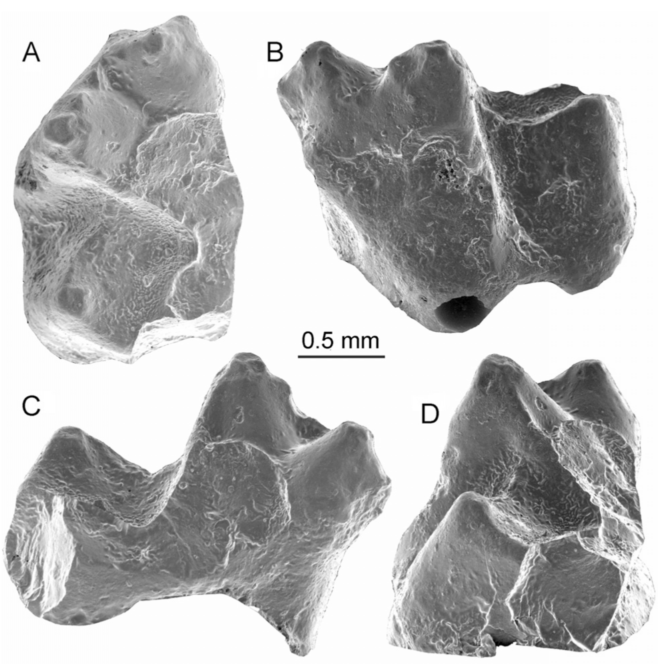

FIGURE 3. SEM photographs of lower molar, CHU 34. **A**, occlusal view; **B**, labial view; **C**, lingual view; **D**, distal view.

At the mesial side of the tooth, a small basal cingulid is present. The talonid was probably wide, the hypoconid being the only preserved cusp. It is large, mesiodistally long, and about half the height of the protoconid. The cristid obliqua ends at the midpoint of the posterior face of the protoconid.

Remarks—Our interpretation of the cusp homologies of the upper molar of *Sillustania quechuense* differs in several aspects from Crochet and Sigé (1993, 1996). On the lingual edge of the holotype, these authors stated that conules are absent, and that the large, lingual cusp distal to the protocone is a hypocone. On the contrary, we interpret that there is a thick preprotocrista, a heavily worn paraconule in association with its preparaconular crest, and a hypocone-like metaconule, similar to most ‘pseudodiprotodont’ metatherians (Ride, 1964; Goin et al., 2009); the preparaconular crest, as well as the postmetaconular one, develops long, high, shelf-like cingula. In addition, we interpret the centrally placed cusp at the labial edge of the holotype to be homologous to the StC of other metatherians. This cusp is more lingually placed on the labial edge than StB and StD. In all these features (presence and development of conules; high, cingular pre- and postconular crests, and lingually placed StC), *Sillustania quechuense* resembles the polydolopiform polydolopimorphian *Roberthoffstetteria nationalgeographica* more than it does any other metatherian, living or extinct (see also Goin et al., 2003).

The assignment of the lower molar to the same species as the holotype was justified by Crochet and Sigé (1996) because of their size compatibility, comparably massive aspect, similar crest development, and the orientation of the cristid obliqua and ‘paralophid,’ in accordance with antagonist structures of the upper molar. Specimen CHU 34 may correspond to an m1: the metaconid is set well apart from the protoconid, and the latter cusp is located slightly posterior with respect to the protoconid base. Both features are present in m1s of several metatherians, such as *Roberthoffstetteria*, microbiotherians, and many Paucituberculata. In *Roberthoffstetteria*, m2—4 have closely twinned paraconid and metaconid.

PHYLOGENETIC ANALYSIS

After a cycle of *tree bisection* and *reconnection* (TBR) with 1000 replications and saving 10 trees per replication, the algorithm found seven equally parsimonious trees of 124 steps. The consistency (CI = 0.54) and retention (RI = 0.79) indices were calculated for all trees. Bremer support was low for most nodes in the Polydolopimorphia group and in almost all Paucituberculata nodes (Fig. 4A).

The general topology of the consensus tree of the first analysis (Fig. 4A) is similar to the one obtained by Goin et al. (2009), except that *Chulpasia* and *Sillustania* were now included. *Chulpasia* forms a polytomy with Polydolopimorphia, *Glasbius*, and *Microbiotherium*. On the other hand, S*illustania quechuense* is nested within Polydolopiformes, along with *Roberthoffstetteria* and *Polydolops*. The absolute Bremer support is 1, whereas the relative one is 14. Three synapomorphies support this grouping: (1) anterobasal and posterior cinguli of M1–3 expanded and level with the trigon basin; (2) presence of supernumerary cuspules on the stylar shelf; (3) anteroposterior alignment of the protocone, paraconule, and metaconule. The analysis shows no resolution within the Polydolopiformes.

A second analysis was conducted under implied weighting. The one tree obtained was stabilized for K values higher than 10 (Fig. 4B) with a fit of 39.46. It shows *Chulpasia* as basal to Polydolopimorphia + *Glasbius*. One extra synapomorphy characterizes Polydolopiformes: the presence of a large but not hypocone-like metaconule (character 37[4]). *Sillustania* is the sister taxon to *Roberthoffstetteria* in the already named family Sillustaniidae, which forms a monophyletic group together with *Polydolops*.

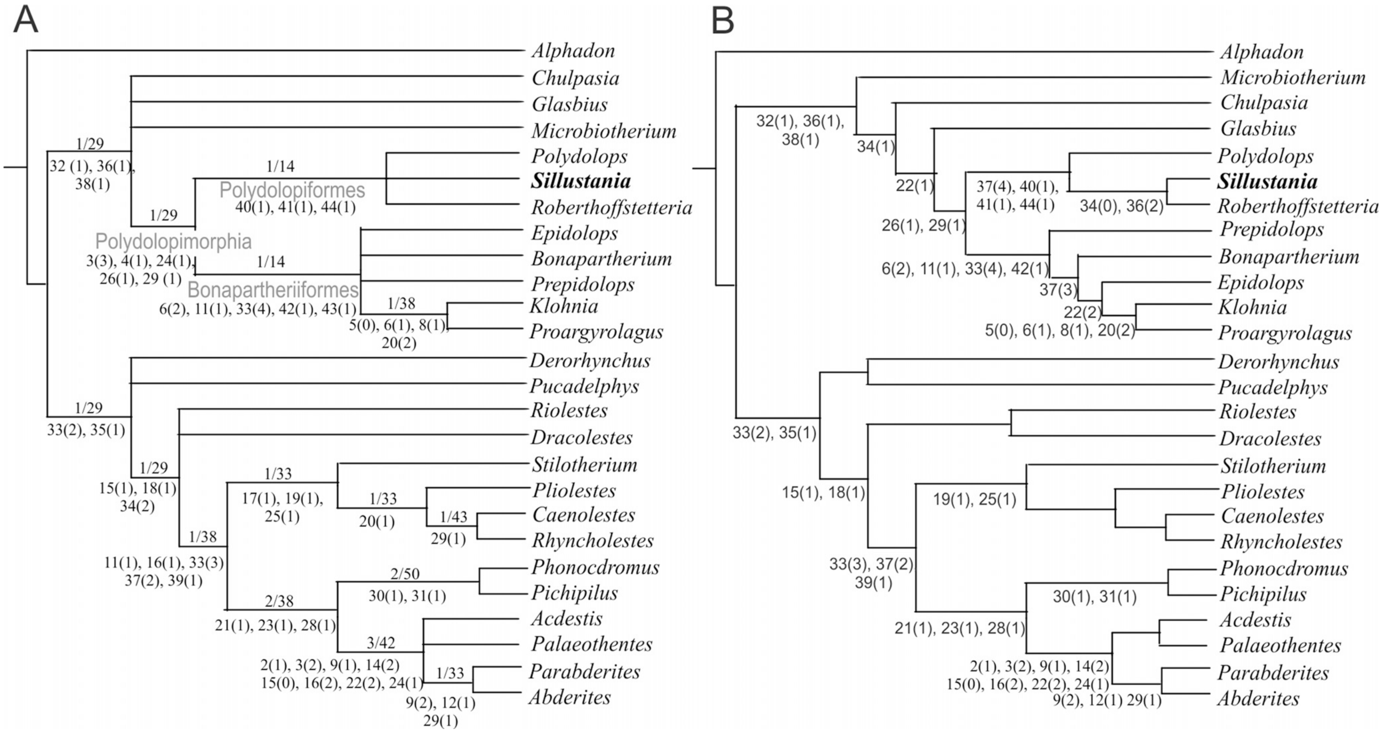

FIGURE 4. Results of phylogenetic analyses. **A**, Strict consensus of seven trees obtained under equal weights; **B**, single tree obtained under implied weighting. Numbers above branches correspond to absolute/relative Bremer support. Numbers below branches correspond to synapomorphies as listed in Goin et al. (2009) with additions/corrections made in this work (see text).

The Sillustaniidae is supported by two synapomorphies: (1) para- and metaconule are larger than stylar cusps B and D (character 34[0]), and (2) the metaconule has only the postmetaconular crest developed (character 36[2]).

The analysis including the lower molar (Supplementary Data, Appendix S3) shows results similar to the other analyses, although *Riolestes* groups both with Polydolopimorphians and Paucituberculatans, obscuring the results. This topology may be related to the fact that the characters corresponding to the lower molar of *S. quechuense* are a few and plesiomorphic, due to the poor preservation of this tooth.

DISCUSSION AND CONCLUSIONS

Affinities of *Sillustania quechuense*

The large size of the hypocone-like metaconule of *Sillustania* was originally noted by Crochet and Sigé (1996) when *S. quechuense* was formally described. For this reason, comparisons were made with the Australian taxa Peramelina and Diprotodonta, and the South American Paucituberculata, Bonpartheriidae (*Bonapartherium*), and some Polydolopimorphia (*Epidolops* was then regarded as a polydolopid, but see Goin and Candela, 1995, who consider Polydolopinae as the sole subfamily included in the family). These comparisons led Crochet and Sigé (1996) to conclude that *S. quechuense* had characters similar to, but more primitive than, *Bonapartherium* and *Epidolops* because of their bunodont cusps and selenodont tendency, presence of stylar cusps (although variable in number), elevated crowns, and presence of a furrow between the paracone and 'hypocone.' Crochet and Sigé (1996) concluded that *S. quechuense* has an morphology intermediate between Prepidolopinae and Polydolopinae.

The results of our study support the affinities of *Sillustania* with Polydolopimorphia as proposed by Crochet and Sigé (1996), and within this group, closer relationships are with the Polydolopiformes *Roberthoffstetteria* and polydolopids (*Polydolops* and allies). A further analysis with implied weighting shows a sister-group relationship of *Sillustania* and *Roberthoffstetteria*, supporting the family Sillustanidae. Summarizing, we regard the Sillustanidae, including *Roberthoffstetteria* and *Sillustania*, as members of the Suborder Polydolopiformes, Order Polydolopimorphia.

Comparison between Laguna Umayo and Tiupampa Localities

It has already been mentioned that Tiupampa is currently regarded as early Paleocene in age (Puercan 3; see Gelfo et al., 2009; Gelfo and Sigé, 2011), whereas the age of the Laguna Umayo faunas (LU-3 and Chulpas localities) is arguable, both variously regarded as middle to late Paleocene or even early Eocene in age (Sigé et al., 2004). More recently Gelfo et al. (2009) considered the Chulpas and Laguna Umayo localities as probably coincident with the Itaboraian SALMA. If the latter is proved true, there would be no less than 10 Ma in age between them. However, several aspects suggest to us that the Laguma Umayo fauna is actually much older.

The main result of this work is the close affinity found between *Sillustania quechuense* and the Tiupampian-aged *Roberthoffstetteria nationalgeographica*. Both taxa are regarded by us as sillustaniid polydolopiforms. Similarities between *Roberthoffstetteria* and *Sillustania* add to those between the Peradectidae already described from the Bolivian and Peruvian faunas: *Peradectes austrinum* from LU-3 (Sigé, 1971) and *Peradectes* cf. *austrinum* from Tiupampa (Muizon, 1991). However, the tooth from Tiupampa originally referred to *Peradectes* cf. *austrinum* has more recently been regarded as probably belonging to a new species, different from *P. austrinum* (Muizon, 1991; Sigé et al., 2004). If the specimen regarded as 'Family ?Pediomyidae or ?Microbiotheriidae' by

Sigé (1972:392; see also Sigé et al., 2004) proves to be referable to *Khasia* Marshall and Muizon, 1988, this would constitute a third closely related metatherian taxon in common between the Bolivian and Peruvian faunas. However, it still needs to be carefully compared with *Khasia* in order to determine if it is closer to the Tiupampian taxon than to the Itaboraian *Monodelphopsis*. The extremely fragmentary evidence at hand makes it impossible, for the moment, to obtain any secure determination. Gelfo and Sigé (2011) described a new didolodontid condylarth, *Umayodus raimondii*, from Laguna Umayo. The taxon is clearly more derived than the Tiupampa kollpaniids while belonging to the same clade as *Raulvaccia* and *Escribania*, two Punta Peligro taxa. *Umayodus* seems to have no close affinities with Itaboraian-aged condylarths.

In conclusion, several elements suggest that the Laguna Umayo faunas are probably closer in age to the Peligran SALMA than to the Itaboraian SALMA. Taking into account the recent dating of Itaboraian-aged levels of the Las Flores Formation, in central Patagonia (Woodburne et al., 2014), as well as the updated age of the Peligran SALMA (Clyde et al., 2014), a middle to late Paleocene age for Laguna Umayo seems the most reasonable hypothesis. This would reduce, probably by half (5 Ma), the age hiatus between Laguna Umayo and Tiupampa, as compared with the conclusions of Sigé et al. (2004).

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APPENDIX S1. Character-taxon matrix used for the phylogenetic analyses.

Taxon	10	20	30	40	45
Alphadon	?000000000	0000000000	0000000000	0000000000	00-00
Pucadelphys	0000000000	0001000000	0000000000	0010101000	00?00
Derorhynchus	?10200?00?	????000000	0000000000	0020101000	00?00
Dracolestes	????????0?	????1?1100	0??????0?0	0022101000	0??0?
Riolestes	????????01	0010100100	0??????0?0	0?????????	?????
Stilotherium	?011000100	1011111110	0100101000	0032102010	02000
Rhyncholestes	1011000102	1011111111	0100101010	0032102010	0200-
Caenolestes	1011000102	1011111111	0100101010	0032102010	0200-
Pliolestes	?1112??102	1011111111	0110101000	0?????????	?????
Pichipilus	?011000102	1001110100	1110001101	1032102010	02000
Phonocdromus	?0110??102	1001110100	1110001101	1032102010	02000
Palaeothentes	0121000111	1002020100	1211001100	?0?2102010	02000
Acdestis	0121201111	1002020100	1211001100	00?2102010	02000
Abderites	?121220121	?1??020100	1211001110	00?2102010	0200-
Parabderites	?0210??121	?1?0020100	1211001110	00?2102010	0200-
Microbiotherium	0100000000	0001000000	0001000000	0100011?0	0??0-
Glasbius	?0??001000	0001000000	0110000000	0101011100	00?00
Prepidolops	?1??121000	1001000000	0100010010	0141011100	01?00
Bonapartherium	01??121001	?0?1000000	0101010010	0141013100	01100
Proargyrolagus	01?1011100	?0?1010002	02?1??0010	00???131?0	0110-
Klohnia	?131011100	?0?10??0?2	02?12?0010	0140003100	01100
Roberthof.	?0??0???00	0011000000	0101010010	0100024101	10010
Sillustania	????????0?	??????????	???????0??	?100023101	10110
Polydolops	?131101102	?0??030000	0201210110	0151114101	1001-
Epidolops	0122121011	1000030000	0211110010	0141013100	01100
Chulpasia	????????0?	????000002	1000?0?000	0131011100	00000

APPENDIX S2. List of characters based in the order from Goin et al. (2009). References include the ones present in recent, similar analyses. More references in the references mentioned below.

1. Antorbital vacuities: absent (0), present (1).
References: Goin et al. (2009); Abello (2013; character 1).
2. Relative height of the dentary: moderate to low (0), high (1).
References: Goin et al. (2009); Forasiepi et al. (2013; character 1).
3. Number of incisors: 4 (0), 3 (1), 2 (2), 1 (3).
References: Goin et al. (2009).
4. Size and orientation of the first incisor: small and subvertical (0), hypertrophied and procumbent (1), large but not hypertrophied and procumbent (25. *Size of p3:* p3 normal in size or moderately larger than p2 and m1 (0), hypertrophied (1), reduced (2).
References: Goin et al. (2009), Forasiepi et al. (2013; characters 3 and 4); Abello (2013; character 2).
5. Size of p3: p3 normal in size or moderately larger than p2 and m1 (0), hypertrophied (1), reduced (2).
References: Goin et al. (2009), Abello (2013; character 5).
6. Size of P3: moderately developed (0), reduced (1), enormous (2).
References: Goin et al. (2009); Forasiepi et al. (2013; character 5); Abello (2013; character 48). Character 48 in Abello (2013) with only two states: not hypertrophied (0) and hypertrophied (1).
7. Length-width ratio of P3. length-width ratio of P3 higher than 1.5 (0), length-width ratio of P3 less than 1.5 (1).

References: Goin et al. (2009); Forasiepi et al. (2013; character 32).
8. Size of the lower canine: normally developed (i.e., larger than any lower permolar) (0), reduced or absent (1).
References: Goin et al. (2009), Forasiepi et al. (2013; character 6).
9. Presence/absence of transverse lophs: upper and molars without transverse lophs (0), with incipient transverse lophs (1), with well-developed transverse lophs (2).
References: Goin et al. (2009); Forasiepi et al. (2013; character 30); Abello (2013; character 68).
10. Relative length of trigonid and talonid of m1: subequal (0), long trigonid (i.e., longer than talonid) (1), short trigonid (i.e., shorter than talonid) (2).
References: Goin et al. (2009); Forasiepi et al. (2013; character 10).
11. Form of the paracristid in m1: m1 paracristid normal (0), without notch, forming a continuous blade between proto- and paraconid (1).
References: Goin et al. (2009); Forasiepi et al. (2013; character 8).
12. Presence of ribs in the trigonid of m1: ribs absent (0), ribs present (1).
References: Goin et al. (2009).
13. Notch in the metacristid of m1: metacristid with a deep or moderate notch (0), metacristid notch poorly or not developed (1).
References: Goin et al. (2009); Forasiepi et al. (2013; character 9).
14. Orientation of the cristid obliqua in m1: toward the protoconid or slightly labial respect to the metacristid notch (0), toward the notch or midpoint between the protoconid and metaconid (1), in contact with the metaconid (2)
References: Goin et al. (2009); Forasiepi et al. (2013; character 10); Abello (2013; character 21).
15. Development of the hypoconid in m1–2: poorly developed (0), quite developed and labially salient (1).
References: Goin et al. (2009); Forasiepi et al. (2013; character 12, only for m2).
16. Hypoconulid shape in m1–3: well developed (0), somewhat reduced, with certain anteroposterior compression (1), disc-shaped, very broad, occupying most of the posthypocristid edge (2), forming a cingulum posterior to the talonid (3).
References: Goin et al. (2009); Forasiepi et al. (2013; character 13, only for m1); Abello (2013; character 45 with only three states).
17. Distal height of the entocristid in m1–3: low (0), high (1).
References: Goin et al. (2009); equivalent to Forasiepi et al. (2013; character 11).
18. Shape of the entoconids of m1–3: conical (0), laterally compressed (1).
References: Goin et al. (2009); Forasiepi et al. (2013; character 15); Abello (2013; character 35).
19. Orientation of the pre-entocristid in m1–3: straight (0), curved (1).
References: Goin et al. (2009); Forasiepi et al. (2013; character 16).
20. Position of the entoconid: normally placed, opposed to the hypoconid at the lingual edge of the talonid (0), more posteriorly located, at least in the m1 (1), more anteriorly located (2).
References: Goin et al. (2009); Forasiepi et al. (2013; character 17).
21. Crest-like expansion posterior to the metaconid in m1–3: absent (0), present (1).
References: Goin et al. (2009); Forasiepi et al. (2013; character 18); Abello (2013; character 29).
22. Height of the protoconid in m2-3: protoconid higher than the para- and metaconid (0), protoconid subequal in height to the paraconid and metaconid (1), protoconid lower than the paraconid and metaconid (2).
References: Goin et al. (2009); Forasiepi et al. (2013; character 19).

23. Position of the metaconid in m3: at the same level than the protoconid (0), anteriorly placed and frequently twinned or fused to the paraconid (1).
References: Goin et al. (2009); Forasiepi et al. (2013; character 20).
24. Development of the anterobasal cingulum in m2-4: normally developed (i.e., reaching at least the base of the protoconid) (0), vestigial or absent (1).
References: Goin et al. (2009); Forasiepi et al. (2013; character 22); Abello (2013; character 32 but with 5 states).
25. Size and roots of m4: m4 double-rooted and subequal in size to m3 (or, if smaller, representing the extreme size of a gradient from m1 to m4) (0), m4 single-rooted and greatly reduced in relation to m3 (1).
References: Goin et al. (2009); Forasiepi et al. (character 24).
26. Size and location of the paraconid of m2–3: normal (i.e., aligned with metaconid) (0), reduced and placed labially to the metaconid (1).
References: Goin et al. (2009); Forasiepi et al. (2013; character 25).
27. p3-m1 contact: mostly contiguous (0), p3 talonid supports most or all of the m1 trigonid (1).
References: Goin et al. (2009); Forasiepi et al. (2013; character 26); Abello (2013; character 11).
28. Enamel thickness in the molars: uniform throughout the entire surface of the tooth (0), markedly different thickness between the lateral and occlusal faces (1).
References: Goin et al. (2009); Forasiepi et al. (2013; character 27); Abello (2013; character 12).
29. Depth of the metacristid in m2–3: Relatively deep (0), little or not developed (1).
References: Goin et al. (2009); Forasiepi et al. (2013; character 28, similar but for m2-4).
30. Crest posterior to the protoconid in m1–3: absent (0), present (1).
References: Goin et al. (2009); Abello (2013; character 30).
31. Posterior entoconid crest: absent (0), present (1).
References: Goin et al. (2009); Forasiepi et al. (2013; character 29).
32. Size and shape of the protocone: moderately sized (0); large and bulky (1
References: Goin et al. (2009); Forasiepi et al. (2013; character 33).
33. Shape of the centrocrista: straight (0), slightly "V"-shaped (1), deeply "V"-shaped (2), open, with the premetacrista and postparacrista basally fused to the lingual slopes of StD and StB respectively (3), open, with the premetacrista and postparacrista connected to the anterior edge of StD and posterior edge of StB, respectively (4).
References: Goin et al. (2009); Forasiepi et al. (2013; character 34). Abello (2013; character 66). In Forasiepi et al. (2013) only character states 0 to 3 with the latter being ‘open’. We added character state 5 In this work.
34. Relative sizes of the paracone and metacone with respect to stylar cusps B and D: para- and metacone larger (0), approximately subequal (1), StB, or StB and StD, much larger (2).
References: Goin et al. (2009); Forasiepi et al. (2013; similar to character 35).
35. Relative size of paracone and metacone: subequal (0), metacone larger (1).
References: Goin et al. (2009); Forasiepi et al. (2013; character 36).
36. Metaconule shape: ‘winged’ (with pre- and postmetaconular cristae) (0), not "winged" (without such cristae) (1); only postmetaconular crest developed (2).
References: Goin et al. (2009); Forasiepi et al. (2013; character 37). We added character state 2 in this work.
37. Relative size of the metaconule: subequal to the paraconule (0), larger than the paraconule (1), very large, ‘hypocone’-like, but without reaching lingually to the level of the protocone (2), very large, ‘hypocone’-like, lingually reaching the protocone (3); large metaconule but not ‘hypocone’-like (4).

References: Goin et al. (2009); Forasiepi et al. (2013; character 37); Abello (2013; character 56). Forasiepi et al. (2013) only character states 0 to 2, with the latter being ‘very large, hypocone-like’. Abello (2013) only include as character states small, moderately sized, and large. We added character state 4 in this work.
38. Width of the stylar shelf: not reduced labio-lingually (0), labio-lingually reduced (1).
References: Goin et al. (2009); Forasiepi et al. (2013; character 39).
39*:* Degree of labiolingual compression of StB and StD: not compressed (i.e., almost circular in cross section) (0), compressed (i.e., oval in cross section) (1).
References: Goin et al. (2009); Forasiepi et al. (2013; character 40); Abello (2013; character 62).
40. Anterobasal and posterior cinguli of M1–3: not elevated and expanded (0), expanded and at a level with the trigon basin (1).
References: Goin et al. (2009); Forasiepi et al. (2013; includes part of character 44).
41. Supernumerary cuspules on the stylar shelf: absent (0), present (1).
References: Goin et al. (2009).
42. Stylar cusp C: present (0), absent (1), fused to StD (2).
References: Goin et al. (2009, without character state 2); Forasiepi et al. (2013; character 41).
43. Lingual flex in the upper molars: absent (0), present (1).
References: Goin et al. (2009); Forasiepi et al. (2013; character 42).
44. Alignement of paraconule, protocone, and metaconule: not aligned (0); aligned or almost aligned (1).
References: this character was added in the present work.
45. Position of StB: in front of the paracone (0), posterior to the paracone (1).
References: Forasiepi et al. (2013; character 43).

APPENDIX S3. Characters of *Sillustiania quechuense* when including the tentatively assigned lower molar.

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Taxon                       10         20         30         40    45
Sillustania        ?????????0? 00?00????? ???????0?? ?100023101 10110
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