A NEW CRAMAUCHENIINAE (LITOPTERNA, MACRAUCHENIIDAE) FROM THE EARLY MIOCENE OF PATAGONIA, ARGENTINA

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ABSTRACT—A new litoptern Cramaucheniinae species, *Pternoconius bondi*, sp. nov., from Colhuehuapian levels of the Sarmiento Formation in Bajada del Diablo (Chubut, Argentina) is described herein. The specimen belongs to an adult animal and preserves the anterior portion of the skull with the maxillary region, some fragments of nasal bones, a small portion of the left zygomatic process, and most of the upper dentition (i.e., left P2–M3, right C, and right P1–M3). It is compared with the Deseadan species ?*Coniopternium primitivum* Cifelli and Soria 1983 and *Pternoconius polymorphoides* Cifelli and Soria 1983, and also with the Colhuehuapian species *Cramauchenia normalis* Ameghino and *Theosodon lydekkeri* Ameghino. Although the hypocone and precingulum development, the paracone and metacone heights, and the connection between paraconule and protocone are singular features, the main characters that diagnose this new species are lack of a mesostyle pillar, soft labial bending of the ectoloph, absence of the metaconule in molars, and the smaller size with respect to other species of the genus. Comparative study leads us to recognize this specimen as a new species that increases the diversity of the Macraucheniidae in the early Miocene of Patagonia.

http://zoobank.org/urn:lsid:zoobank.org:pub:F68802D8-305-45CA-8076-5AEC81B56483.

INTRODUCTION

The Litopterna Ameghino, 1889, is the second largest group of South American native ungulates in abundance and diversity after Notoungulata. They are recorded from the early Paleocene to Pleistocene in South America, and also from the Eocene in West Antarctica (Gelfo et al., 2015). They are characterized by a complete dentition, but some may display a reduction in the number of incisors and of the upper canines. Most litopterns retain primitive brachyodont teeth, and in some groups, a small degree of hypsodonty is observed. They developed different types of occlusal morphology (bunoselenodont, lophoselenodont, or bunodont), and mesaxonic limbs with an odd number of digits (Scott, 1910; Soria, 1981). Most authors (see, for example, Muizon and Cifelli, 2000; Soria, 2001) recognize the families Proterotheriidae Ameghino, 1887, Macraucheniidae Gervais, 1855, Adianthidae Ameghino, 1891, Protolipternidae Cifelli, 1983, Anisolambdidae Soria, 2001, and probably Notonychopidae Soria, 1989, and Sparnotheriodontidae Soria, 1980.

The first remains assigned to Macraucheniidae, all postcranial elements, were collected by Charles Darwin in Puerto San Julian (Santa Cruz, Argentina) in 1834 and described by Owen (1840), under the name of *Macrauchenia patachonica*. The origin and evolutionary history of Macraucheniidae litopterns are unknown, even though proteomic analyses of *Macrauchenia* reveal that litopterns are close allies to the Laurasiatheria, particularly to Perissodactyla (Buckley, 2015; Welker et al., 2015). They were not very abundant in the fossil record, and they had been particularly scarce before the late Oligocene, Deseadan South American Land Mammal Age (SALMA) (Dozo and Vera, 2010). Due to the fact that *Polymorphis lechei* (Roth, 1899) from the late Eocene (Mustersan SALMA) of Patagonia is the only known pre-Deseadan taxon of this family (Cifelli, 1983), the possible phylogenetic relationships among macraucheniids and other litopterns such as Proterotheriidae and Adianthidae, or with the stem-group Didolodontidae, remains uncertain (Muizon and Cifelli, 2000; Gelfo, 2006).

Macraucheniidae are poorly known before the Miocene. The first described Deseadan cramaucheniines were *Coniopternium andinum* Ameghino, 1894, based on one calcaneum, three astragali, and four phalanges (MACN-A 11700–11707), and *Notodiaphorus crassus* Loomis, 1914, represented by a hind limb (ACM 3287). Cifelli and Soria (1983) considered *N. crassus* as a junior synonym of *C. andinum*. They also described two new taxa, ?*Coniopternium primitivum*, based on a fragmentary left dentary with m2–3 (PU 23523) from the Deseadan levels of La Salla-Luribay Basin, Loaza Province in Bolivia, and a new genus and species, *Pternoconius polymorphoides* (AMNH 109619), on the basis of a left p2–m3 and a right p1–m3, recovered from the lowest 9 m of Deseadan sediment and overlying an erosional unconformity with Casamayoran beds (Cifelli and Soria, 1983), which belong to the Upper Puesto Almendra Member of the Sarmiento

Formation, Gran Barranca locality (Bellosi, 2010). In the same locality, but in upper levels, Soria and Hoffstetter (1985) described *P. tournoueri* (MNHN COL 121) based on an almost complete left mandible with a broken p2 and p3–m3, from Colhuehuapian beds (early Miocene) of the Colhue-Huapi Member in the Sarmiento Formation. Ameghino (1902) also described the genus *Cramauchenia* from the early Miocene of Patagonia, and based on their size differences and lower dentition characters, he recognized two species: *C. normalis* and *C. insolita*. In his revision, Soria (1981) made a detailed description of *C. normalis* remains, found in the south cliff of the Gran Barranca locality, and a full comparison with *Theosodon* from the Santacrucian SALMA (late early Miocene). As a consequence, *C. insolita* was considered MNHN a junior synonym of *C. normalis* and could also have shared a common ancestor with *Theosodon*. In 1904, Ameghino described the species *Phoenixauchenia tehuelcha*, based on one astragalus and three metapodial fragments. Although *P. tehuelcha* was still considered a Cramaucheniinae by Schmidt and Ferrero (2014), there have not been any dental remains assigned to it that could serve to reinforce the validity of this species. The last important addition to macraucheniid knowledge was the discovery and description of an almost complete skull and postcranial remains of *Cramauchenia normalis* from Deseadan levels of Cabeza Blanca in Patagonia, which expanded the biochron of the taxon to the late Oligocene (Dozo and Vera, 2010).

The aim of this work is to describe a new species of *Pternoconius*, represented by the anterior portion of a skull that preserves most of the dentition and was found in Colhuehuapian levels of the Bajada del Diablo locality in Chubut Province (central Patagonia, Argentina).

MATERIALS AND METHODS

The specimen studied is the anterior part of a skull, with left P2–M3, right C, and right P1–M3, and was collected in Colhuehuapian levels of the Sarmiento Formation in Bajada del Diablo locality, Chubut Province, Argentina (Ardolino and Franchi, 1996). This specimen (MPEF-PV 2576) is stored in the paleontological collection of the Museo Paleontológico 'Egidio Feruglio,' Trelew (Chubut Province, Argentina).

The analysis is based on morphometric description of the specimen and comparative study with other Macraucheniidae stored in collections from Argentina, the United States of America, and France (Tables 1 and 2). Dental morphology follows the terminology used by Soria (1981, 2001), Cifelli and Soria (1983), and Gelfo (2006). Measurements (all in millimeters) were taken using an Essex 0–150 mm digital caliper, and the specimen was photographed using a Nikon D90 digital camera with an AF-S NIKKOR DX 18–105 mm f/3.5–5.6G ED VR lens.

Occlusal area of each tooth was calculated by multiplying the mesiodistal length with the labiolingual width. The results were then log_{10}-transformed and statistics calculated using Microsoft Excel 2007. With this information, the profile of the dental series (PDS) was plotted in order to compare taxa, following methodology developed in Gelfo (2016). In the present work, PDS indicates the occlusal area of each tooth of the upper series (Table 3). The PDS for each taxon was built using the measurements in Table 2.

Institutional Abbreviations—**ACM**, Beneski Museum of Natural History, Amherst, Massachusetts, U.S.A.; **AMNH**, American Museum of Natural History, New York, U.S.A.; **CENPAT**, Centro Nacional Patagónico, Puerto Madryn, Chubut, Argentina; **MACN-A**, División Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia,' Ameghino collection, Buenos Aires, Argentina; **MLP**, División Paleontología de Vertebrados, Museo de La Plata, La Plata, Argentina; **MNHN**, Muséum national d'Histoire naturelle, Paris, France, **DES**, Deseadan collection and **COL**, Colhuehuapian

collection; **MPEF-PV**, Museo Paleontológico 'Egidio Feruglio', Trelew, Chubut, Argentina; **YPM PU**, Princeton University collection, Yale Peabody Museum of Natural History, Yale University, New Haven, Connecticut, U.S.A.

Anatomical Abbreviations—**C**, upper canine; **ccr**, centrocrista; **dia**, diastema; **ecr**, entocrista; **hyp**, hypocone; **M**, upper molar; **mcn**, metaconule; **me**, mesostyle; **mt**, metacone; **mts**, metastyle; **P**, upper premolar; **pacn**, paraconule; **par**, paracone; **popc**, postparacrista; **prc**, precingulum; **prmc**, premetacrista; **prpc**, preparacrista; **prpcc**, preparaconular crista; **prptc**, preprotocrista; **prt**, protocone; **pst**, parastyle; **pstpc**, postprotocrista; **ptc**, postcingulum; **ptmc**, postmetacrista.

GEOGRAPHIC AND STRATIGRAPHIC CONTEXT

At the Bajada del Diablo locality (42°51′32.3″S and 67°27′23.9″W), Chubut Province, Argentina (Fig. 1A), the continental sediments of the Sarmiento Formation crop out (Ardolino and Franchi, 1996; Lema et al., 2001). This formation represents one of the most expressive units in terms of geologic events and fossil remains from the Paleogene of extra-Andean Patagonia. Its paleontological richness allows us to distinguish different mammal ages, from Casamayoran to Colhuehuapian SALMAs (Pascual et al., 1965, 1996; Ré et al., 2010). In Bajada del Diablo, southwest from the Telsen locality, the Somun Curá and Sarmiento formations interleave (Ardolino and Franchi, 1996) (Fig. 1B). Thus, tuffs of the Sarmiento Formation under- and overlie basalt mantles from the Somun Curá Formation. One basalt sample from this site gave an isotopic age of 27 Ma. They are also covered in the same locality by a basalt mantle, named Basalto La Mesada, with an age of about 17 to 16 Ma. Following this, sediments beneath the Somun Curá Formation may be correlated with those representing a Deseadan SALMA, with the ones above it (upper parts of the Sarmiento Formation) belonging to Colhuehuapian SALMA.

The specimen here studied (MPEF-PV 2576) derives from a zone of white tuffs and fine sandstones, slightly stratified, belonging to the upper part of the Sarmiento Formation (Colhuehuapian SALMA, early Miocene), located a few meters above the basalt mantle corresponding to the Somún Curá Formation (late Oligocene) (Fig. 1C). At this locality, and in contrast to others (e.g., Gran Barranca), this is the only portion of the Sarmiento Formation where fossil remains have been found. Over it, there are a few meters of tuffs and stratified sandstones, with filling channels and large conglomerate clasts. According to Ardolino and Franchi (1996), the paleoenvironment was an open plains region, slightly undulating, with freshwater ponds and shallow riverbeds, with intermittent volcanic activity and removal, reworking, and resedimentation of older material.

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758
LAURASIATHERIA Waddell et al., 1999
PANPERISSODACTYLA Welker et al., 2015
LITOPTERNA Ameghino, 1889
MACRAUCHENIIDAE Gervais, 1855
CRAMAUCHENIINAE Ameghino, 1902
PTERNOCONIUS Cifelli and Soria, 1983

Type Species—*Pternoconius polymorphoides* Cifelli and Soria, 1983.

Geographic and Stratigraphic Distribution—Argentina, Chubut and Santa Cruz provinces. Deseadan to Colhuehuapian SALMAs (late Oligocene to early Miocene).

Emended Diagnosis—Cramaucheniinae with relatively low crowned cheek teeth, robust and less molariform premolars than later taxa. Anterior p1–2 lanceolated, with paracristid
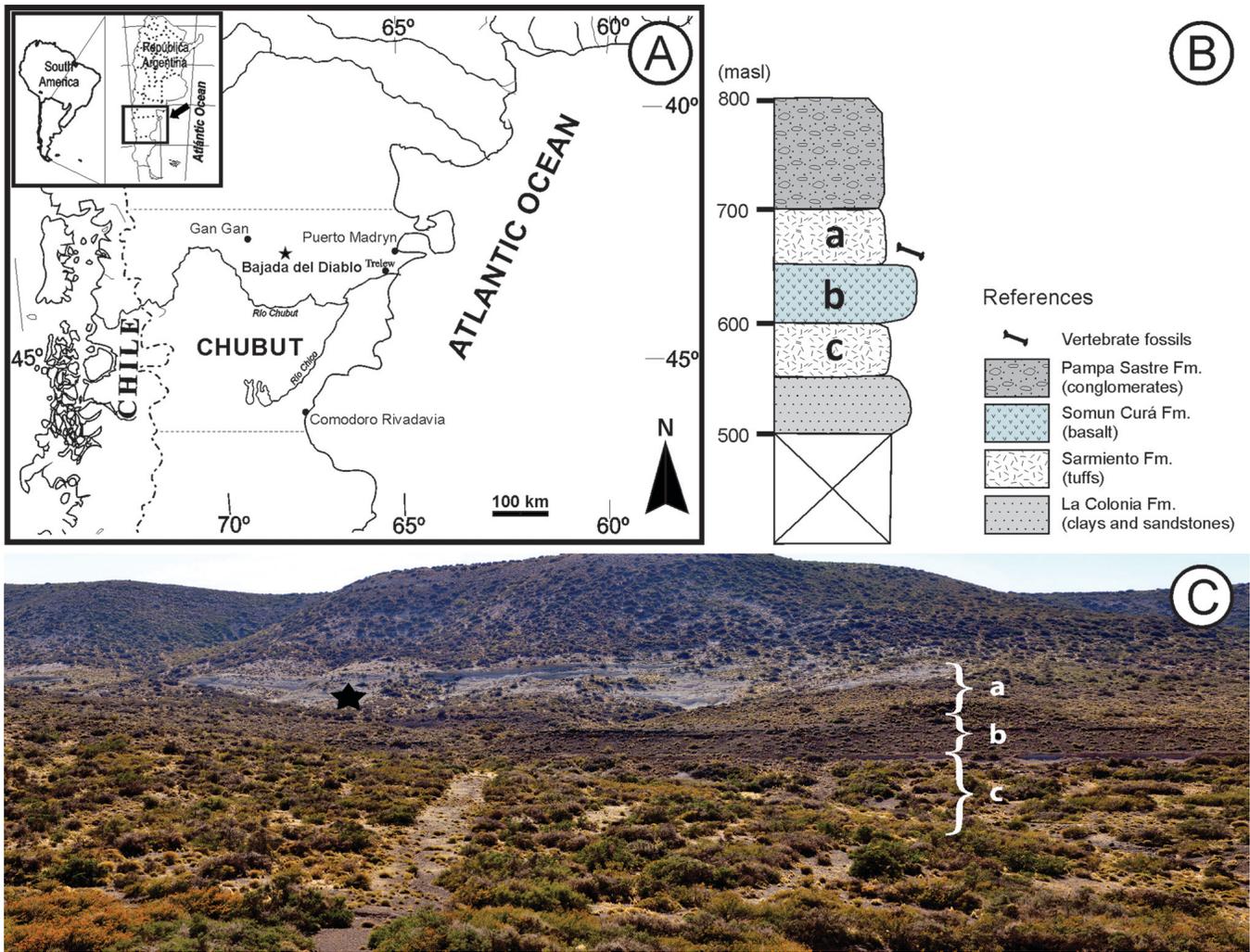
FIGURE 1. **A**, map with the geographic location of Bajada del Diablo locality where *Pternoconius bondi* (MPEF-PV 2576) was found; **B**, stratigraphic profile of the site, drawn from Ardolino and Franchi (1996); **C**, panoramic photograph showing Sarmiento and Somun Curá formations and the stratigraphic location of the fossil (black star). **Abbreviations**: **a**, Colhuehuapian levels of Sarmiento Formation; **b**, Somun Curá Formation; **c**, Deseadan levels of Sarmiento Formation.

descending mesially from the protoconid and straight, not curved as in *Coniopternium*; without paraconid or metaconid in p1; and p2 at least in *Pternoconius tournoueri* with an incipient metaconid. The talonid increases in size from p2 to p4. Paraconid relatively weak on p3 and absent on p4. Lower molars with distolabial cingulid and transverse entolophid. The M1–3 with strong precingulum but not extended through the lingual base of the protocone as in ?*Coniopternium primitivum*; parastyle weaker than *Theosodon* but similar to *Cramauchenia*; hypocone strong with a robust entocrista projected to the postprotocrista, and wide entoflexus.

PTERNOCONIUS BONDI, sp. nov.

(Figs. 2–4)

Holotype—MPEF-PV 2576, anterior portion of skull with maxilla and fragments of nasal bones, part of the left zygomatic process, left P2–M3, right C, and right P1-M3.

Type Locality—The holotype comes from Bajada del Diablo, 42°51′32″S and 67°27′23″W, Chubut Province, Argentina.

Age and Stratigraphy—Early Miocene of the Sarmiento Formation, Colhuehuapian SALMA.

Etymology—For Mariano Bond, in recognition of his contributions to the knowledge of South American native ungulates.

Diagnosis—Differs from *Pternoconius polymorphoides* in smaller size, and absence of metaconule and mesostyle labial pillar in molars. Metaconule in premolars very reduced and always smaller than paraconule. Diastema mesial and distal to P1.

Description

Skull—The specimen MPEF-PV 2576 corresponds to the anterior portion of a skull that has a pronounced breakage in the dorsal region, where only the maxillary and some fragments of the nasal bones are preserved (Fig. 2A). It is also distorted by slight lateral and dorsoventral crushing. In ventral view, the palate is broken and incomplete and the zygomatic processes that are located at the level of the M2 are visible. The specimen preserves left P2–M3, right C, and right P1–M3 (Fig. 2B). Tooth wear and bone structure indicate that the skull belonged to an adult animal. The inferred total length would be slightly smaller than that of *Cramauchenia normalis* (Table 1).

The nasal bones are almost entirely destroyed, except the posterior portion of the left one, which despite its poor preservation and due to the height of maxillary bones at P2–3 level, has a
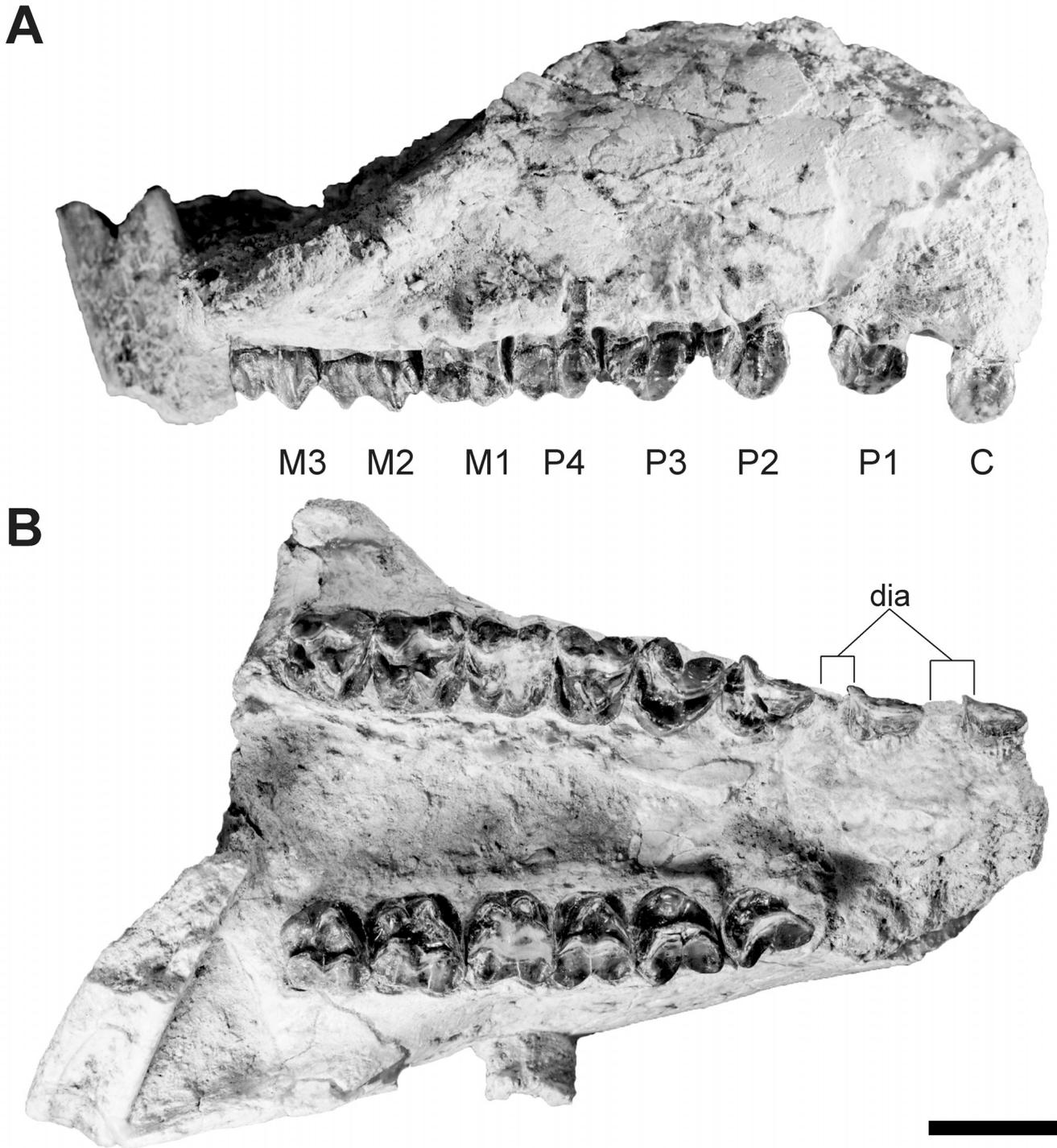
FIGURE 2.   Anterior portion of skull of *Pternoconius bondi* (MPEF-PV 2576). **A**, right view; **B**, ventral view. **Abbreviations**: see Anatomical Abbreviations. Scale bar equals 20 mm.

development similar to the one observed in *Cramauchenia normalis* and different from that in *Theosodon*, where the same bones are shorter and with less development (Scott, 1910).

   Dentition—The dentition of MPEF-PV 2576 is not completely preserved, but as in *Cramauchenia normalis*, the first premolar is well separated from the canine and the second premolar by regular spaces (Dozo and Vera, 2010; Fig. 2). These diastemata are larger than those observed in other Cramaucheniinae. The rest of the dental series, from P2 to M3, is continuous and with a clear contact between each contiguous tooth. As in *C. normalis* according to Dozo and Vera (2010), premolars and molars are brachyodont, bunoselenodont, and gradually increasing in size mesiodistally from P1 to M2. In *C. normalis*, P2 and P3 are mesiodistally longer, whereas from P4 to M3 the teeth are transversally wider. A similar pattern in premolar and molar sizes is present in *P. bondi*, with a similar area of P2 and P3 as indicated
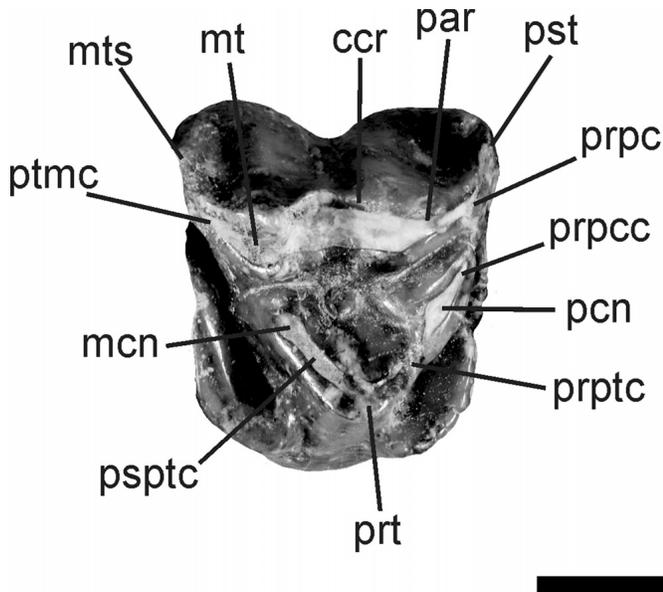
FIGURE 3. Right P4 of *Pternoconius bondi* (MPEF-PV 2576) showing occlusal cristae. **Abbreviations**: see Anatomical Abbreviations. Scale bar equals 5 mm.

in the PDS (Fig. 5). The main differences are in the smaller area of the rest of the loci and particularly of C and P1. The measurements of M2–3 of *P. polymorphoides* are larger than those in *C. normalis* and *P. bondi* but follow the same proportional pattern due to the usual reduction in size of M3 (Table 2). The comparative PDS shows a significant difference in occlusal area between the C and P1 of *P. bondi* and *C. normalis* (Fig. 4).

The right upper canine is the only one preserved. It is incisiform, laterally flattened, and with a rounded paracone. The preparacrista and the postparacrista run slightly labially, and in lateral view, they make a rounded outline. The lingual side is concave, and the labial one is relatively flat but slightly convex in the central portion. These characters are very different from the ones described by Dozo and Vera (2010) in *C. normalis*, where the canine has two lobes separated by a central furrow and with a triangular outline and an acute point.

The P1 is transversely compressed as in *C. normalis* (Soria, 1981; Dozo and Vera, 2010), and similar to the canine, but larger and wider (Table 2; Fig. 2B). The paracone and a metastyle zone are better developed. There is a short but wide rim located distolingually, but no trace of protocone or lingual cuspule is observed. As previously noted, P1 is separated from the canine and P2–M3 by diastemata that are longer than in *C. normalis*.

The left P2 is better preserved than the right one, in which a mesial fracture is projected into the distal part of the paracone. The labial side is concave, with a well-marked ectoflexus. The occlusal surface is triangular and is wider than in P1, mainly labiolingually. The paracone is the main cusp, forming a high labial ridge with the preparacrista projected mesially to the parastyle zone and the postparacrista distolabially up to the metastyle zone. The preparacrista reaches the base of the crown and continues with a short cingulum of lingual projection. The postparacrista descends at a lower angle than the preparacrista. There is no connection between the postparacrista and the postcingulum. The latter ends at the base of the former. The parastyle zone is a lingual and marked projection from the preparacrista, and the metastyle from the postparacrista. There is a distolingual shelf formed by the expansion of the lingual cingulum, lower than the

labial ridge formed by the paracone and associated cristae. This lingual cingulum forms a sharp ridge, curved from the distolingual base of the postparacrista to a small knob in the most lingual sector, which is the only trace of a protocone. The lingual cingulum continues mesiolabially in a shorter segment, with a protuberance formed by three weak cuspules that could be serially homologous to the paraconule present in the P4 and molars.

The P3 is somewhat larger than P2, with a trapezium-like shape, more molariform and a bit wider than long. The labial side is triangular with a central ectoflexus. The parastyle and metastyle are well developed. The paracone is the central and highest cusp, and it is associated with a lower metacone with slight wear (much more visible in the right P3; Fig. 2B). Both cusps join together in a tall ectoloph, mesially and distally projected to the parastyle and metastyle, respectively. Lingually, there is a slightly compressed protocone, lower than the main labial cusps, that is part of a lingual crest. This crest is similar to the one observed in P2 and encloses a large enamel fossa, joining the intersection of the metastyle with the postmetacrista. A small paraconule is located near the protocone, and its base contacts the mesiolingual side of the paracone. The preparaconular crista contacts the parastyle and mesially encloses a slumped area, limited labially by the paracone and lingually by the paraconule.

The P4 is molariform (Fig. 3). Compared with the P3, it is larger and more quadrangular, due to the strong development of the pre- and postcingulum. Although most of the occlusal areas in the PDS indicate that *P. bondi* is smaller than *Cramauchenia normalis*, they share similar surface area for P2–3 (Fig. 4). In contrast to the description of Soria (1981) for *C. normalis*, no mesostyle pillar is present, either in P4 or in the molars. The parastyle and metastyle are associated with a conspicuous ectoloph, with evident labial folds of the paracone and metacone. On the other hand, as seen in *C. normalis*, the precingulum and postcingulum are well-developed and delimit deep fossae. Both cingula are projected lingually at the base of the protocone but without contact between them. The precingulum is projected from the mesiolingual base of the protocone to the parastyle, slightly expanding in the lingual sector. The postcingulum projects from the distolingual side of the protocone to the metastyle. Because of the later eruption of P4 with respect to the M1, the distolingual portion of the postcingulum is placed below the precingulum and the parastyle of M1. In occlusal view, the paracone and metacone are more separated than in P3, but similar to M1. The preparacrista and the postmetacrista are labially projected, whereas the portion belonging to the centrocrista is slightly labially projected, but with no evidence of a mesostyle column like those present in *Pternoconius polymorphoides* (Cifelli and Soria, 1983). This is a notable feature of this new taxon. As in the molars, the wear over the middle portion of the centrocrista strengthens the middle labial projection of the ectoflexus in occlusal view (Fig. 4A). There is no labial pillar, fold, or cusp present between the paracone and the metacone that could be interpreted as a mesostyle, which is particularly evident in teeth with little wear. The protocone is lower than the labial cusps and is connected with the paraconule and a little metaconule through the preprotocrista and postprotocrista, respectively. Both conules are separated from the ectoloph by a deep furrow. The trigon is wide, and in the right P4, there is a small, low round hump in the center. The paraconule is located mesiolingual to the paracone and projects a preparaconular crista on the way to the parastyle. There is no evidence of other cristae associated with any of the conules.

The molars all preserve the same pattern, apart from locus-specific variations. The styles and labial cusps are higher than the lingual ones, and together form an ectoloph. The protocone is the highest lingual cusp, followed by the hypocone, which is developed as a lingual structure of the postcingulum. The entocrista connects the hypocone to the postprotocrista. No
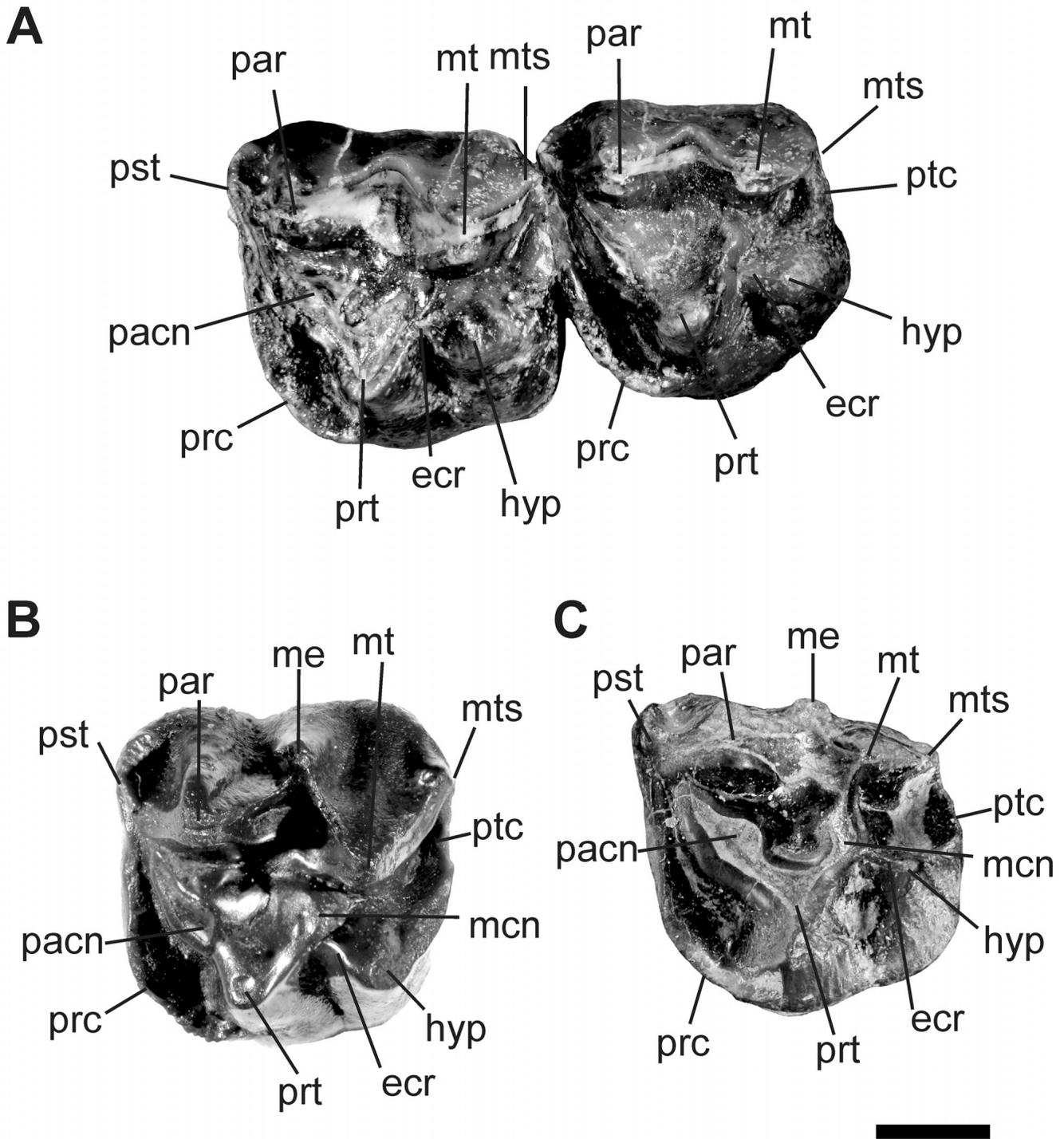
FIGURE 4. Comparison between *Pternoconius bondi* and *Pternoconius polymorphoides*. **A**, M2–3 of *P. bondi* (MPEF-PV 2576); **B**, M2 of *P. polymorphoides* (MLP 61-IV-11-103); **C**, M3 of *P. polymorphoides* (MNHN DES 161). **Abbreviations**: see Anatomical Abbreviations. Scale bar equals 5 mm.

metaconule is present in M2–3, and it should be also absent in M1 where the wear has obscured most of the trigon features, exposing dentine. This absence contrasts with what is observed in P4, but is expected because premolars belong to a different dental generation than molars. The metaconule is present in the premolars as a very smooth structure that is never as well developed as the paraconule. It could be inferred that in the deciduous premolars, the metaconule should also be absent. In contrast to the P4, the precingulum and postcingulum are less developed on the lingual side.

The M1, with a quadrangular contour, has a nearly straight mesial face, while the distal one is a little convex; the lingual side is shorter than the labial side. An advanced wear stage is observed on the occlusal surface, exposing a continuous dentine

TABLE 1. Measurements (in mm) of the skulls of *Pternoconius bondi* (MPEF-PV 2576), *Cramauchenia normalis* (MPEF-PV 2524), and *Theosodon lydekkeri* (MACN-A 9269-88).

Dimension	MPEF-PV 2576	MPEF-PV 2524	MACN-A 9269-88
Total length		270.4	322.0
Rostrum length		115.0	150.0
Cranium length		155.0	172.0
Basicranium length		105.0	109.0
Maxillary length	103.35	109.6	166.0
Condylobasal length		238.5	287.0
Snout width		34.4	28.0
Palatal width in P2	21.38	48.6	29.61
Nasals width		34.0	27.8
Supraorbital foramen width		65.5	74.0
Maximum supraoccipital width		36.0	36.0
Minimum supraoccipital width		21.9	35.0
Facial height	35.96	60.7	73.72
Maximum zygoma height		19.1	18.31
Minimum zygoma height		10.9	15.6
Nasal height		34.4	69.22
Orbital height		39.4	43.24
Orbital width		37.9	49.05
P1–M3 length	89.52	88.24	
P2–M3 length	73.41	73.68	

Modified from Dozo and Vera (2010).

surface from the labial wall of the ectoloph to the enamel edge of the lingual cusps. As in the description of the M2 assigned to *Pternoconius polymorphoides* (MLP 61-IV-11-103), and in contrast to *C. normalis*, there is no trace of a mesostyle pillar but only a slightly labial bend of the centrocrista portion of the ectoflexus. Most of the metastylar portion is masked by tooth wear, but it seems to be smaller than the parastylar one. The parastyle forms the mesiolabial angle of the molar and is separated by a lingual flexus from the paracone. The precingulum encloses a small fossa mesial to the protocone. Particularly well seen in the right M1, the degree of wear leaves a small distal fossa surrounded by enamel, formed by the lingual base of the postmetacrista and part of the postcingulum.

The M2 is the biggest tooth in the molar row (Table 2; Figs. 2B, 4A, 5), with a subquadrangular contour and with its labiolingual diameter slightly longer than the mesiodistal one. The surface development of the M2 contrasts with those in the PDS of *Cramauchenia normalis* where M1, and not M2, is the tooth with the larger occlusal area (Fig. 5). The paracone and the metacone are clearly identified from the ectoloph, the paracone being higher and in a more labial position. The protocone is bulky and occupies most of the lingual sector. It is linked to the hypocone through a short entocrista, more evident in the left M2. This crista contacts the edge of the postprotocrista near the center of the occlusal area. The precingulum is lingually expanded up to the mesial base of the protocone, forming a low fossa. Even though there are some similarities with YPM-PU 23529 (?*Coniopternium primitivum*), in shape and size of the molar, the main differences are in a smaller hypocone and a shorter precingulum. The moderate wear of the M2 allows a better interpretation of the main features present on it. As mentioned previously for the M1, and in contrast to *P. polymorphoides* (MLP 61-IV-11-103) and *C. normalis*, the mesostyle column is absent, the centrocrista is slightly labially curved, and the metastyle is barely developed. The parastyle, as in the preceding molar, forms the mesiolabial angle and is separated from the paracone by a flexus. The paraconule is developed and connected to the protocone by a low and rounded preprotocrista. A short and worn preprotocrista has a continuous dentine surface with the protocone and paraconule. A short postprotocrista is projected from the protocone, pointing to the metacone and separated from the base of the ectoloph by a deep furrow. The distal side of this molar is almost filled by the postcingulum; it is short and limited labially by the metacone and lingually by the hypocone.
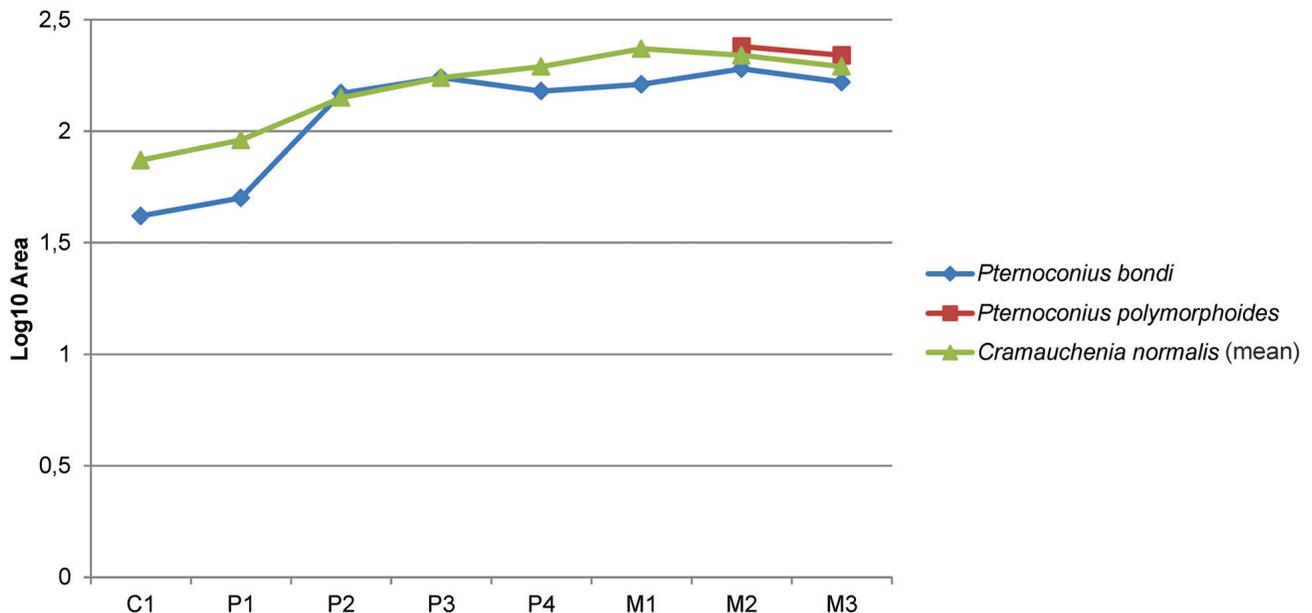

FIGURE 5. Profile of the dental series (PDS) of the occlusal area of *Pternoconius bondi* (MPEF-PV 2576) and compared taxa: *P. polymorphoides* (MLP 61-IV-11-103; MNHN DES 161) and *Cramauchenia normalis* (MACN-A 52-219; MPEF-PV 2524).

TABLE 2. Tooth measurements (in mm) of *Pternoconius bondi* (MPEF-PV 2576) and compared taxa: *P. polymorphoides* (MLP 61-IV-11-103; MNHN DES 161) and *Cramauchenia normalis* (MACN-A 52-219; MPEF-PV 2524).

Tooth	Dimension	MPEF-PV 2576 Left	MPEF-PV 2576 Right	MLP 61-IV-11-103 Left	MNHN DES 161 Left	MPEF-PV 2524 Left	MPEF-PV 2524 Right	MACN-A 52-219 Left
I1	MD							
	LL							
I2	MD					—	6.49	
	LL					—	5.56	
I3	MD					7.33	7.29	
	LL					6.24	6.63	
C	MD	—	9.81			10.02	12.86	10.86
	LL	—	4.28			6.93	7.02	5.81
P1	MD	—	11.41			12.47	—	11.58
	LL	—	4.42			8.21	—	6.82
P2	MD	13.01	13.39			13.28	—	12.5
	LL	11.38	11.31			10.87	—	10.99
P3	MD	12.58	12.62			13.97	—	11.76
	LL	14.17	13.59			13.29	—	13.99
P4	MD	11.48	11.57			12.49	—	13.64
	LL	13.26	13.31			14.54	—	14.66
M1	MD	12.56	11.86			12.45	—	15.6
	LL	13.29	13.23			15.22	—	15.47
M2	MD	13.62	12.79	15.4		14.33	—	16.36
	LL	14.67	14.27	15.7		16.19	—	17.37
M3	MD	12.48	12.49		14.0	14.24	—	14.31
	LL	13.34	13.13		15.6	15.14	—	15.34

Abbreviations: **LL**, labiolingual; **MD**, mesiodistal.

The M3 is the smallest of the molars, with a 'trapezoidal' shape. The paracone is the highest cusp. The protocone and the hypocone are present on the lingual side, the latter in a more distal position, compared with that in M2. The hypocone is more labial than the protocone. The ectoloph presents a weak paracone labial fold. The metacone is placed in a more lingual position and is lower than the paracone. The parastyle, small and low, forms a weak labial fold where the preparacrista of the ectoloph portion and the precingulum converge. In contrast to the parastyle, no metastylar fold is observed in a labial position, but the metacrista zone tends to be slightly labially curved. The precingulum contacts the mesiolingual side of the protocone and encloses a wide fossa, as in M2. Through the labial section, this fossa gets narrower, forming only a deep furrow separating the paraconule and preparaconular crista from the precingulum. In the right M3, the protocone is broken. It contacts the paraconule through a preprotocrista and projects a rounded postprotocrista that does not contact the lingual base of the metacone, which is separated by a furrow, and encloses a wide trigon basin, mesially closed by a wide paraconule. The hypocone is lower than the protocone and is linked to the postprotocrista by a short entocrista. In the left M3, an accessory cusp can be observed, low and more lingually located, which probably is part of the lingual continuity of the postcingulum. A short postcingulum contacts the distal portion of the ectoloph and the hypocone and encloses a small but deep fossa, distal to the metacone. In contrast to *C. normalis*, the parastyle and metastyle are less developed and no mesostyle pillar is present labially to the ectoloph.

DISCUSSION

The taxonomic reviews of the family Macraucheniidae proposed by Soria (1981) and Cifelli and Soria (1983) considered two subfamilies, Cramaucheniinae (including Theosodontinae as defined by Ameghino, 1902) and Macraucheniinae. Cramaucheniinae included the primitive Oligocene and Miocene forms based on small or medium size, the anterior position of the nasal opening, the normal development of the nasal bones, maxillary

not dorsally projected, orbits posteriorly opened, and brachyodont teeth. Macraucheniinae, in contrast, includes late Miocene to Pleistocene forms, with medium or large body size, a posterodorsal position of the nasal opening, reduced nasal bones, maxillary dorsally projected, orbits posteriorly closed, and with protohypsodont teeth. The recent phylogeny of Schmidt and Ferrero (2014) corroborated the monophyly of Macraucheniidae but failed to clearly differentiate the subfamilies, because Cramaucheniinae is part of an unresolved polytomy.

The specimen MPEF-PV 2576 can be included within the Cramaucheniinae sensu Soria (1981) due to the presence of brachyodont, bunoselenodont molars, similar tooth sizes to those species included in the subfamily, P3 to M3 without any fossettes nor cementum in the trigon basin, no mesostyle in P3, a crest that links the hypocone with the metaconule in upper molars, and upper incisors and P1 separated from canine and second premolar by short, regular spaces. In addition, although not a taxonomic argument, it is important to emphasize that MPEF-PV 2576 was collected in Colhuehuapian levels (early Miocene) of

TABLE 3. Profile of the dental series of *Pternoconius bondi* (MPEF-PV 2576), *P. polymorphoides* (MLP 61-IV-11-103; MNHN DES 161), and *Cramauchenia normalis* (MACN-A 52-219; MPEF-PV 2524). MD and LL measurements in mm. Area values expressed as Log10.

Tooth	*Pternoconius bondi* MD	LL	Area	*Pternoconius polymorphoides* MD	LL	Area	*Cramauchenia normalis* (mean) MD	LL	Area
C1	9.81	4.28	1.62				11.25	6.59	1.87
P1	11.41	4.42	1.70				12.02	7.51	1.96
P2	13.2	11.34	2.17				12.89	10.93	2.15
P3	12.6	13.88	2.24				12.86	13.64	2.24
P4	11.52	13.28	2.18				13.58	14.40	2.29
M1	12.21	13.26	2.21				14.97	15.77	2.37
M2	13.20	14.47	2.28	15.4	15.7	2.38	14.95	14.86	2.34
M3	12.48	13.23	2.22	14.0	15.6	2.34	13.66	14.38	2.29

Abbreviations: **LL**, labiolingual; **MD**, mesiodistal.

the Bajada del Diablo locality, where only members of the sub-family Cramaucheniinae have been found.

Cramaucheniinae from Patagonia are represented in the Oligocene–Miocene by *Coniopternium* from the Deseadan SALMA (Cifelli and Soria, 1983), *Pternoconius* and *Cramauchenia* from the Deseadan and Colhuehuapian SALMAs (Soria, 1981; Cifelli and Soria, 1983; Soria and Hoffstetter, 1985; Dozo and Vera, 2010), and *Theosodon* in the Miocene (Soria, 1981; Tauber, 1997). During this period, *Coniopternium* and *Pternoconius*, considered the most primitive genera of the Cramaucheniinae, are little known and scarce. The former is represented by postcranial elements, mandibular fragments, and a few upper teeth, whereas *Pternoconius polymorphoides* was described based on a jaw (AMNH 109619), one isolated lower molar, and two isolated upper molars (Cifelli and Soria, 1983). The upper molars are an M2 (MLP 61-IV-11-103) from Deseadan levels of the El Pajarito locality (also in Chubut Province) and an M3 of the Tournouër Collection (MNHN DES 161), from Deseadan levels of the Río Deseado estuary (Santa Cruz Province). This last molar is tentatively referred by Cifelli and Soria (1983) to *P. polymorphoides* due to indirect association with an isolated m3 (MNHN DES 160) by direct occlusion between them and also because the latter has the same occlusal characters as the m3 of the species' holotype. *Pternoconius tournoueri* was described by Soria and Hoffstetter (1985) from an almost complete left mandible (MNHN COL 121) collected in the Colhue-Huapi Member of the Sarmiento Formation at the Gran Barranca locality (Chubut Province). When described, the age of the carrier level was considered to be late Oligocene and referred to the Colhuehuapian SALMA (Soria and Hoffstetter, 1985), but it was later properly assigned by isotopic dates to the early Miocene (Dunn et al., 2013); therefore, *P. tournoueri* and *P. bondi* are coetaneous but allopatric.

Considering the above-mentioned diversity of Cramaucheniinae, the smaller size of MPEF-PV 2576, the presence of an evident diastema between the upper canine and first premolar, the canine and first premolar with a flat labial side, the absence of a well-defined mesostyle column in the molar row, and the presence of molars with lophodont morphology in the labial side, we reject its belonging to *Cramauchenia* or *Theosodon*, whose molars have a more bunoselenodont shape and where the mesostyle is a conspicuous structure in the labial side of each molar.

Although it shows some similarities, particularly in molar shape and size, with YPM PU 23529 (M2–3 of ?*Coniopternium primitivum*) from the Deseadan SALMA, the main differences are a straight mesial side in M2, the lesser development of the hypocone, the absence of the mesostyle pillar, and the lack of lingual continuity of the precingulum, which does not reach the hypocone (Fig. 4A).

The M2 (MLP 61-IV-11-103) from El Pajarito (Fig. 4B) resembles the specimen here studied in the development of the parastyle and metastyle, and in the precingulum, which runs from the parastyle and ends with a soft, mesially concave curve on the mesial side of the protocone. But it differs due to its larger dimensions, the more lingual position of the metacone, the presence of an evident mesostyle column, and a greater development of the hypocone.

The M3 of *Pternoconius polymorphoides* (MNHN DES 161) from Río Deseado (Fig. 4C) has moderate wear, but the occlusal features are clearly distinguishable. The occlusal area of the molars is greater than that of *P. bondi*, but it is important to note that they follow almost the same slope from M2 to M3 in the PDS (Fig. 5). In contrast to *P. bondi*, the parastyle and metastyle have the same development, but other features, such as the mesostyle labial column and the metaconule, are only present in *P. polymorphoides*. The paracone and metacone, although very worn in MNHN DES 161, have similar development in *P. bondi*. The precingulum

has the same expansion in both species, but it reaches a more lingual position in *P. bondi*.

Pternoconius bondi shares with *P. polymorphoides* M2 (MLP 61-IV-11-103) and M3 (MNHN DES 161) the following characters: (1) hypocone weakly developed; (2) short precingulum, surrounding only the mesial half of the protocone, and postcingulum in the same position; and (3) paraconule linked to protocone by a low preprotocrista. However, *P. bondi* differs by the time span where it was found, the absence of the mesostyle column in the molars, the lack of a metaconule, and its smaller size.

Pternoconius tournoueri, also from the Colhuehuapian SALMA, is only known from a left jaw with alveoli of c and p1, a broken p2, and the series p3–m3. Although a direct comparison between the two is therefore not possible, there are some inferences that allow us to justify the allocation to different taxa. The mesiodistal length of the preserved tooth row (p2–m3) in *P. tournoueri*, which belongs to an adult specimen, is 107 mm (Soria and Hoffstetter, 1985), much longer than the same measurement for the P2–M3 row in *P. bondi*, which is only 75.31 mm length. Even though there are no complete measurements of the dental series, it is evident that *P. bondi* represents a smaller taxon. Another important evidence for taxonomic differentiation rests on the presence of a conspicuous diastema before and after the P1 of *P. bondi*. These spaces resemble those present anterior and posterior to the P1/1 in *Theosodon* (e.g., AMNH 9230), in which, in addition, short diastemata are present, separating the canines and each of the incisiforms, which are placed in a more lateral than frontal position. This configuration is related to the elongation of the rostrum in *Theosodon*. It can be inferred from this comparison that the skull of *P. bondi* was also probably anteriorly elongated and with a diastema between i, c, and p1. In contrast, from the close position of the alveoli of c and p1, and also the placement of p2, in *P. tournoueri* (MNH COL 121) it is evident that the p1 was in contact mesially and distally with the c and the p2, respectively.

To summarize, even though the upper dentition of *P. tournoueri* and the lower dentition of *P. bondi* are still unknown, and both were found in levels assigned to the Colhuehuapian SALMA, we are confident in considering them as separate taxa of different sizes and, probably, distinct rostral elongation.

CONCLUSIONS

The specimen here studied (MPEF-PV 2576) is assigned to a new species of Cramaucheniinae: *Pternoconius bondi*, from the Colhuehuapian SALMA, in Bajada del Diablo locality (Chubut Province, Argentina). The general morphology in the occlusal features of the molars resembles that of the Deseadan SALMA taxon *Pternoconius polymorphoides*. This is particularly evident in several characteristics such as the hypocone or precingulum development, the paracone and metacone heights, and the connection between paraconule and protocone. In contrast, there are important differences, such as the absence of a mesostyle column and metaconule, and the smaller general size, that justify the recognition of a new taxon. Although the characters mentioned are few, they are very strong in order to diagnose and differentiate MPEF-PV 2576 from *P. polymorphoides* and *P. tournoueri*. Although it is also important to note that, considering that neither the lower dentition of *P. bondi* nor a complete upper series for *P. polymorphoides* and *P. tournoueri* is known, a more accurate formal differentiation at the generic level is, for the moment, unwarranted. This specimen is very useful in order to describe better the main features of the genus, due to its more complete status.

The species here described represents a new lineage of Cramaucheniinae, the third species of *Pternoconius* and the second for the Colhuehuapian SALMA (early Miocene). The specific diversity of the Macraucheniidae for the Colhuehuapian

SALMA in Patagonia was already discussed by Soria and Hoffstetter (1985), as well as the possible geographic differences between local faunas from Gran Barranca and those from the Trelew and Gaiman localities, all of them in Chubut Province (see also Soria, 1981). The available knowledge is not enough to evaluate properly if at the same time there was a geographic segregation between *Pternoconius* species, *P. bondi* in the northern and *P. tournoueri* in the south.

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