CHINIQUODONTID CYNODONTS: SYSTEMATIC AND MORPHOMETRIC CONSIDERATIONS

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ABSTRACT. Systematic and morphometric reappraisal of most specimens previously assigned to the cynodont clade Chiniquodontidae reveal that the group is diagnosed by two autapomorphies: (1) the distinctive angulation between the posterior portion of the maxillary and the anterior portion of the zygomatic arch and (2) very extended pterygoid flanges, ending in a thin projection; and a combination of features including: posterior postcanines sectorial with principal cusps backwardly recurved, and a long osseous palate. The species *Chiniquodon theotonicus* (including *Belesodon magnificus*, *Probelesodon kitchingi*, *P. lewisi* and *P. minor*) and *C. sanjuanensis* (comb. nov.) were the only recognised members of the family on the basis of qualitative characters. The South American species *Cromptodon mamiferoides*, *Probainognathus jenseni* and *Thrinaxodon brasiliensis* are thus excluded from the group, as are the African taxa *Aleodon brachyrhamphus* and *Cistecynodon parvus*. Allometric analysis of chiniquodontids *sensu stricto* reveals that: (1) all specimens can be confidently arranged in a single growth series, irrespective of their original species assignments; and (2) most of the measurements change isometrically with respect to skull length. Adults are virtually scaled-up juveniles, showing a deepened zygoma, a longer osseous palate, and a wider anterior muzzle in the canine region. Thus, allometric data reinforce the proposed synonymy of all forms, with the specific status of *C. sanjuanensis* supported by qualitative diagnostic traits.

KEY WORDS: non-mammalian cynodonts, South America, Triassic, systematics, allometry.

THE Chiniquodontidae is one of the most distinctive families of the South American non-mammalian cynodonts, marking the earliest large-bodied, sectorial-toothed cynodonts discovered in the continent (von Huene 1935–42). They are represented principally in the Ladinian of southern Brazil and western Argentina (von Huene 1935–42; Romer 1969*a*, *b*; Text-fig. 1), but have been recorded also in the Carnian Ischigualasto Formation, western Argentina (Bonaparte 1966; Martinez and Forster 1996).

Von Huene (1935–42) described the first representatives of the family, two species discovered in outcrops of the Santa Maria Formation at the locality of Chiniquá, Rio Grande do Sul, Brazil. *Chiniquodon theotonicus* was represented by an incomplete skull (Text-fig. 2), and a humerus, while remains of *Belesodon magnificus* consisted of an almost complete but poorly preserved skull (Text-fig. 3), with many postcranial elements. Even though these remains were not well preserved, they were distinct from the African cynodonts then known, and justified the creation of the new family Chiniquodontidae (von Huene 1935–42, p. 156). After these early discoveries and until the end of the 1960s, only poorly preserved and/ or fragmentary representatives of the family were collected from the Ischigualasto and Santa Maria formations (Bonaparte 1966; Romer 1969*a*). This situation changed when Romer (1969*b*) described *Probelesodon lewisi* from the Chañares Formation, in western La Rioja Province, Argentina, represented by extensive, largely complete and well-preserved material. Romer (1970) included a new taxon, *Probainognathus jenseni*, in the chiniquodontids, but he later proposed the family Probainognathidae to include only that species (Romer 1973).

Hopson and Kitching (1972) proposed the inclusion of *Aleodon brachyrhamphus* from the Manda Formation of Tanzania, formerly described as a gomphodont cynodont (Crompton 1955), in the Chiniquodontidae based on unpublished specimens. Teixeira (1982) described the new species *Probelesodon kitchingi*, based on a skull lacking mandibles, collected in the Santa Maria Formation in Brazil.

More recently, Hopson (1991) and Battail (1991*a*) included in the chiniquodontids *Cromptodon mamiferoides*, from the Río Mendoza Formation, Mendoza Province, Argentina. Hopson (1991) pointed out a resemblance between the teeth of this form and a juvenile individual of *Aleodon*. The composition of

TEXT-FIG. 1. Distribution map of Chiniquodontids. 1, Ischigualasto; 2, Los Chañares; 3, Chiniqua; 4, Rinção do Pinhal; 5, Candelaria; 6, Santa Cruz do Sul.

the family was expanded by Battail (1991*a, b*), who included *Cistecynodon parvus* from the Burgersdorp Formation of South Africa and *Thrinaxodon brasiliensis*, from the Santa Maria Formation, Brazil. Abdala (1995, 1996*b*) recognized only three species of chiniquodontids: *Belesodon magnificus*, *Chiniquodon theotonicus* (including as junior synonyms *Probelesodon lewisi* and *Probelesodon minor*), and *Chiniquodon kitchingi* (formerly *Probelesodon kitchingi*). Finally, Martinez and Forster (1996) described *Probelesodon sanjuanensis*, a complete skull with articulated lower jaws and some postcranial material, from the Ischigualasto Formation, Argentina.

Some aspects of chiniquodontid systematics remain to be properly addressed. First, several recognized species lack adequate diagnoses owing to the poor material on which they are based. Second, recent proposals (e.g. Hopson and Barghusen 1986; Battail 1991*a, b*; Hopson 1991) have greatly expanded the conception of the family, including within it species previously regarded as belonging to other cynodont families.

In this contribution, we provide a diagnosis for the family Chiniquodontidae and its species based on a thorough revision of the available material and on comparisons with other cynodont families. After a qualitative examination of chiniquodontid specimens, we performed an allometric study of the specimens included in the family following our revised diagnosis.

Institutional abbreviations. BMNH, The Natural History Museum, London; BPI, Bernard Price Institute for Palaeontology, University of the Witwatersrand, Johannesburg; BS, Bayerische Staatssammlung für Paläontologie und historische Geologie, München; GPIT, Institut und Museum für Geologie und Paläontologie der Universität Tübingen; HMN, Humboldt Museum für Naturkunde, Berlin; MCN-PV, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; MCP-PV, Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil; MCZ, Museum of Comparative Zoology, Harvard
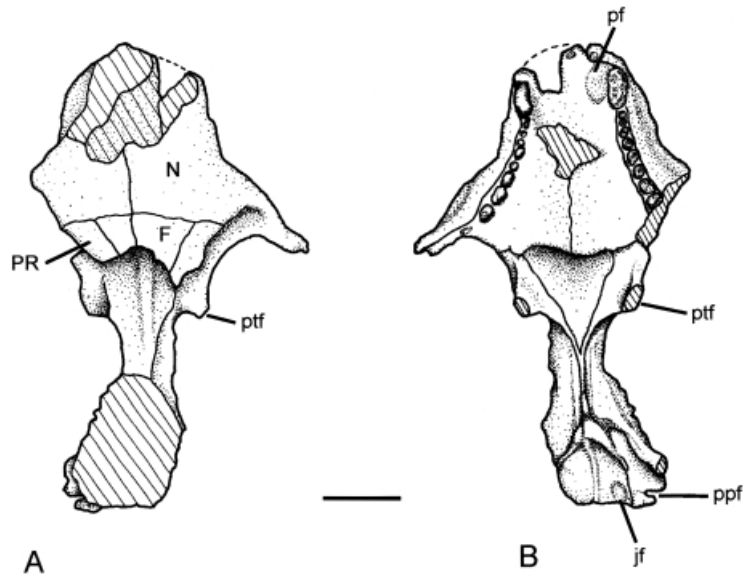
TEXT-FIG. 2. *Chiniquodon theotonicus*, holotype specimen (GPIT 1050) in dorsal (A), and ventral (B) views. Abbreviations: F, frontal; N, nasal; PR, prefrontal; pf, paracanine fossa; ptf, pterygoid flange; ppf, pterygoparaoccipital foramen; jf, jugular foramen. Scale bar represents 20 mm. Cross-hatch pattern indicates broken bone.

University, Cambridge, Massachusetts; PULR, Museo de Antropología, Universidad Nacional de La Rioja, Argentina; PVL, Colección Paleontología de Vertebrados Lillo, Universidad Nacional de Tucumán, Argentina; PVSJ, Museo de Ciencias Naturales, Universidad Nacional de San Juan, Argentina; UFRGS PV, Universidade Federal de Rio Grande do Sul, Porto Alegre, Brazil.

MATERIAL AND METHODS

Family diagnosis

Specimens of all the cynodont families were examined by one of us (FA) in the museums noted above. The following references were consulted for each family: Procynosuchidae (Brink 1963; Kemp 1979); Thrinaxodontidae (Parrington 1946; Fourie 1974); Galesauridae (Broom 1932*b*; Boonstra 1935); Cynognathidae (Broili and Schröder 1934, 1935*a*; Brink 1955*b*; Abdala 1996*a*); Diademodontidae (Broili and Schröder 1935*b*; Brink 1955*a*), Trirachodontidae (Crompton 1955) Traversodontidae (Bonaparte 1962; Romer 1967, 1972; Crompton 1972; Barberena 1974; Hopson 1984; Goñi and Goin 1988, 1990); Tritylodontidae (Kühne 1956; Hopson 1964; Clark and Hopson 1985; Sues 1986); Probainognathidae (Romer 1970), and Tritheledontidae (Crompton 1958, 1963*a*; Gow 1980). Synthetic works, and various phylogenetic analyses were also sources of data, e.g., Broom (1932*a*); Hopson and Kitching (1972); Kemp (1982); Hopson and Barghusen (1986); Rowe (1986, 1993); Hopson (1991, 1994); Wible (1991); Luo (1994) and Martinez *et al*. (1996).

Besides the chiniquodontids from South America (Table 1), material of *Aleodon brachyrhamphus* in the BMNH, the holotypes of *Cromptodon mamiferoides* in the PVL, *Cistecynodon parvus* in the BPI, and *Thrinaxodon brasiliensis* in the UFRGS PV, as well as specimens of *Probainognathus jenseni* in the MCZ, PULR and PVL were examined. At the beginning of this study, one of us (FA) was able to measure the holotypes of *Probelesodon lewisi* and *P. minor*, then in the Museum of the Universidad Nacional de La Rioja. Recently, this material was shamefully stolen from that institution, but their measurements are included here.
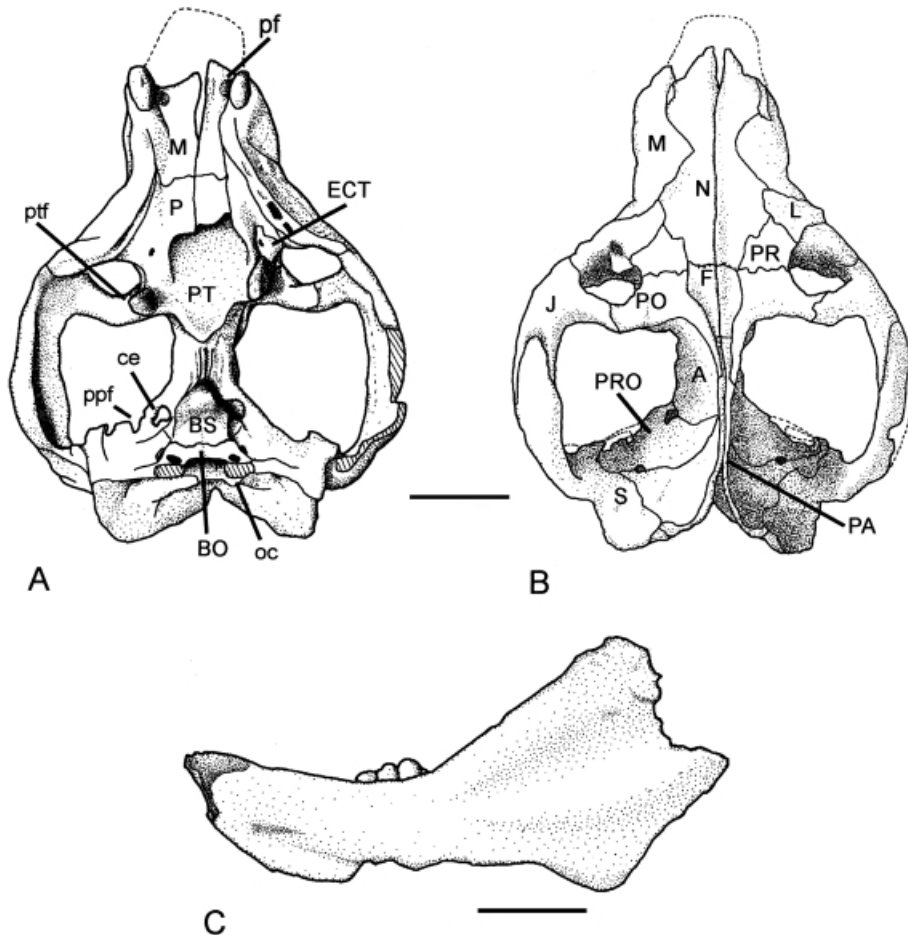
TEXT-FIG. 3. *Belesodon magnificus*, holotype specimen (GPIT 40). Skull in ventral (A) and dorsal (B) views; right dentary in lateral view (C). Abbreviations: BO, basioccipital; BS, basisphenoid; ECT, ectopterygoid; F, frontal; J, jugal; L, lacrimal; M, maxilla; N, nasal; P, palatine, PA, parietal; PO, postorbital; PR, prefrontal; PT, pterygoids; S, squamosal; ce, cavum epiptericum; oc, occipital condyle; pf, paracanine fosa; ptf, pterygoid flange; ppf, pterygopar-aoccipital foramen. Scale bars represent 40 mm. Cross-hatch pattern indicates broken bone. Modified from von Huene (1935–42).

Allometry

Fifteen measurements of the skull, intended to represent skull shape in all relevant dimensions (Text-fig. 4), were used in the analysis of allometry to investigate growth responses of different parts of the skull to the overall increase in size. Most of these measurements were used previously by Abdala and Giannini (2000) for the study of allometry in *Massetognathus*. We used only skull dimensions because most specimens lack postcranial material. All measurements were taken with a sliding vernier caliper, and recorded to the nearest millimetre. The specimens used for the measurements varied widely in quality of preservation; sample size for each analysis varied between 12 and 20. We included specimens of all six previously described chiniquodontids (as that group is defined here) in the analysis of allometry, ignoring their original species assignments. This represents a null hypothesis of there being a single chiniquodontid species. Thus, if all specimens are adequately described by the allometry functions (without outliers, systematic trends in residuals or size gaps), they must be considered a growth series of one taxon. The
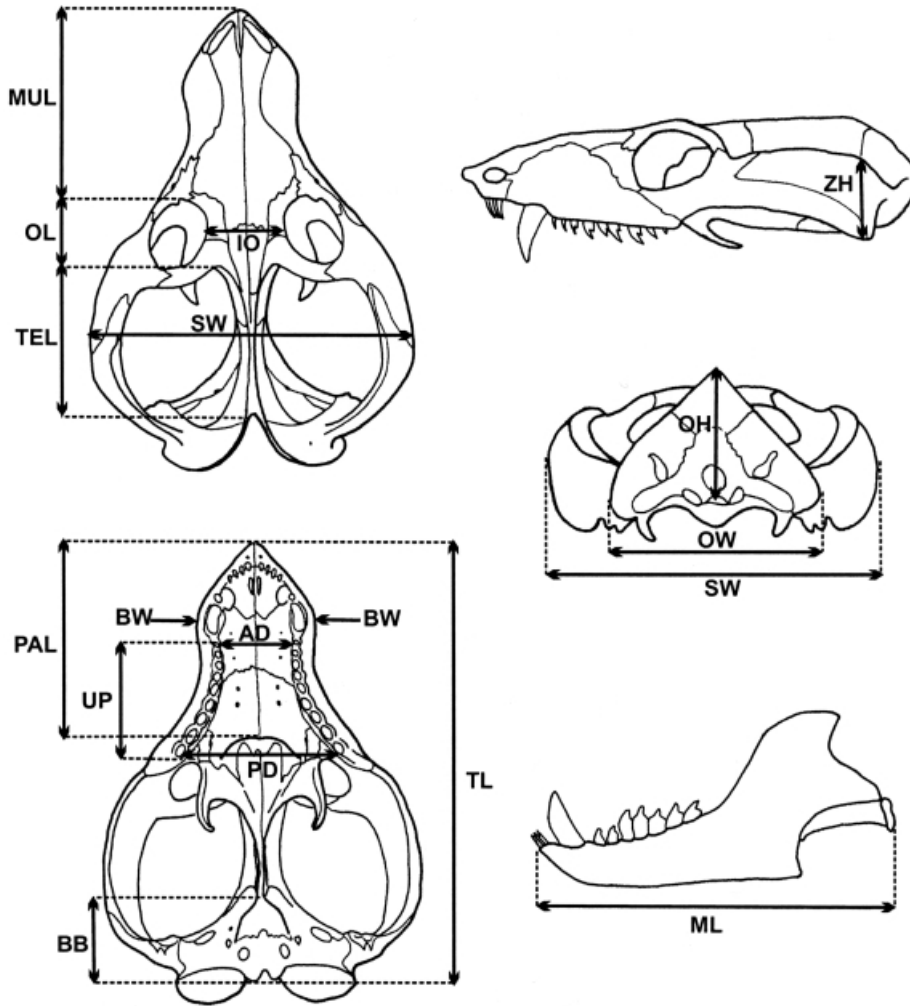
TEXT-FIG. 4. Chiniquodontid skull measurements. Muzzle length (MUL), temporal region length (TEL), maximum skull width (SW), maximum height of zygomatic arch (ZH), interorbital distance (IO), maxillary bicanine width (BW), anterior postcanine distance (AD), posterior postcanine distance (PD), palate length (PAL), upper postcanine row length (UP), dentary length (DL), occipital plate width (OW), height of the occipital plate (OH), basicranial length (BB), orbital length (OL).

holotypes of *Belesodon magnificus*, *Chiniquodon theotonicus*, *Probelesodon kitchingi*, *P. lewisi*, *P. minor*, and *P. sanjuanensis* were included in most analyses. Analysis of allometry was done in parallel with the species diagnosis reappraisal based upon qualitative traits.

Total skull length was considered the independent variable reflecting overall size (Simpson *et al.* 1960; Radinsky 1981*a, b*; Emerson and Bramble 1993; Abdala and Giannini 2000). We studied the relation of each cranial variable in relation to total skull length through the allometry equation:

$$\log y = \log b_0 + b_1 \log x + \log e$$

which derives from the power growth equation $y = b_0 x^{b1} e$ by the calculation of (base 10) logarithms in both members. Here b_0 is the y-intercept, b_1 is the slope of line (coefficient of allometry), and e represents

the error term that is assumed to be multiplicative (i.e. it may interact with the independent term, for instance, by increasing variance with size). Significance of slopes was assessed via one-tailed *t*-tests. We also evaluated deviations from isometry (unequal rate of change of the independent and dependent variables) with one-tailed *t*-tests. This was accomplished by setting the null coefficient equal to the value expected under geometric similarity, i.e. unity for linear measurements (see Alexander 1985). 'Negative' and 'positive' coefficients of allometry are significantly less or greater than those expected by isometry (Emerson and Bramble 1993), i.e. statistically different from unity.

The analysis described above meets ordinary least squares criteria assuming, among other points, that (1) there is a dependence relationship, and (2) the independent variable is measured without error. Although the first assumption is more likely to be met, since all variables are expected to change as a function of overall size, the second assumption is certainly less realistic. Therefore, we complemented ordinary least squares parameter estimation by computing coefficients via reduced major axis regression method (RMA). The latter is an alternative approach for these types of data since it does not assume a dependence relationship between variables and allows variation in both *x*- and *y*-axes (Radinsky 1981*a, b*; Niklas 1994; Abdala and Giannini 2000).

DIAGNOSIS OF THE FAMILY CHINIQUODONTIDAE

Carnivorous eucynodonts with an overall cranial morphology similar to that of *Thrinaxodon*, but showing a more robust zygomatic arch, which is also conspicuously more flared laterally; characteristic angulation (*c.* 110 degrees or more) between the ventral edge of the maxillary zygomatic process and the anteroventral margin of the jugal; pterygoid flanges greatly elongated, ending in a thin projection, directed posteroventrally; osseous secondary palate posteriorly expanded; and the posterior sectorial postcanine teeth with backwardly recurved principal cusps, lacking cingula or with tiny lingual cingular cusps (Text-fig. 5).

Comments on the family diagnosis. The most important problems that have hindered a detailed diagnosis of the Chiniquodontidae are the fragmentary nature and, in some cases, poor preservation of the specimens described by von Huene (1935–42), Bonaparte (1966) and Romer (1969*a*). In some specimens of this family, as in the type of *Belesodon magnificus*, the secondary osseous palate does not reach the posterior end of the postcanine series. For this reason, we prefer to use elongate palate, but not necessarily extending to the end of the postcanine series (see Hopson and Barghusen 1986). An elongate secondary palate is also present in probainognathids and tritheledontids plus Mammaliaformes (Hopson and Barghusen 1986) and similar sectorial teeth with backwardly recurved principal cusps occur in the posterior (sectorials) postcanines of *Diademodon* (Abdala, pers. obs.; HMN R1004). Therefore, this diagnosis includes two autapomorphic features: (1) marked angulation of zygomatic root; (2) enlarged pterygoid flanges, ending in a thin projection. Other features here included in the Chiniquodontidae diagnosis, although not autapomorphic, are also useful when considered jointly.
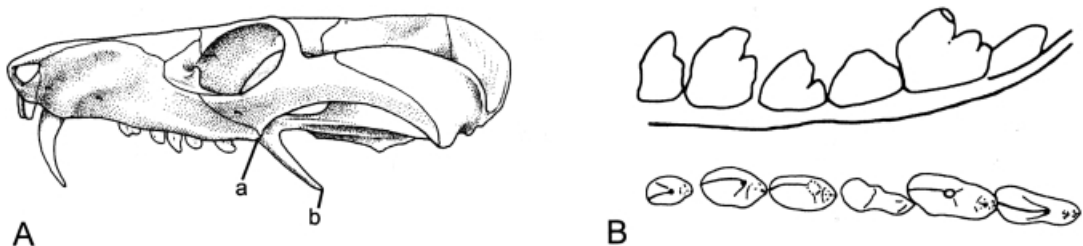
TEXT-FIG. 5. Chiniquodontid diagnostic features. A, lateral view of a chiniquodontid skull showing the angulation (a) between the posterior portion of the maxilla and the anterior base of the zygomatic arch, and the elongated pterygoid flanges (b). B, labial and occlusal view of the chiniquodontid sectorial, postcanine series (PVL 4444).

## SPECIES EXCLUDED FROM THE FAMILY CHINIQUODONTIDAE

Based on our diagnosis, the following species are excluded from the chiniquodontids: *Aleodon brachyrhamphus* Crompton, 1955; *Cistecynodon parvus* Brink and Kitching, 1953; *Cromptodon mamiferoides* Bonaparte, 1972; *Probainognathus jenseni* Romer, 1970; and *Thrinaxodon brasiliensis* Barberena, Bonaparte and Teixeira, 1987.

Aleodon brachyrhamphus from the Manda Formation, East Africa is represented by fragmentary skulls and lower jaws; the most complete specimen is a muzzle with dentition (BMNH 9390; Text-fig. 6A). *Cromptodon mamiferoides* from the Rio Mendoza Formation, Argentina, is a tiny lower jaw with some postcanines (PVL 3858; Text-fig. 6D). Both species share bucco-lingually expanded postcanines, with well-developed cingular platforms (Text-fig. 6, cp), a condition noticeably different from that regarded here as diagnostic of the Chiniquodontidae. Hopson (1991) and Battail (1991a) considered *Aleodon* and *Cromptodon* to be chiniquodontids without specifying, however, the dental morphology substantiating this familial assignment. As Hopson (1991) stated, the resemblance between the postcanines of *Aleodon* and *Cromptodon* is very striking. Although a small lingual cingulum is present in postcanines of some Brazilian specimens (MCZ 3165 and MCN PV 2755), we consider chiniquodontid postcanines to be sectorial without broad cingular platforms, thus removing *Aleodon* and *Cromptodon* from the family. Additional material is required to provide a definite taxonomic placement for these two genera.

Probainognathus jenseni has been excluded from the chiniquodontids by nearly all recent authors except Battail (1991a). Abdala (1996b) proposed numerous craniodental and postcranial autapomorphies for *Probainognathus* that support its inclusion in the monotypic Probainognathidae as proposed by Romer (1973). We should mention that the only chiniquodontid diagnostic feature shared with *Probainognathus* is the elongated posterior extension of the palate. As an example of noteworthy differences between probainognathids and the other cynodont families, Text-figure 7 presents the proportion of three skull regions (muzzle, orbital region, and temporal region) in different cynodont genera, all of them with postorbital bars; note that only in *Probainognathus* is there an inversion of skull proportions, with the temporal region being longer than the muzzle.

Cistecynodon parvus, represented by a single skull from the Burgersdorp Formation of South Africa (BPI 2520; ex BPI 318), was included in chiniquodontids by Battail (1991a, b) on the basis of an elongated secondary palate and a more dorsal position of the inferior border of the zygomatic arch in relation to the alveolar margin of the maxilla. Abdala (1996a) noted, however, that its palate is shorter than in chiniquodontids, extending back only to the level of the fourth postcanine. It also lacks the characteristic angulation of the zygomatic arch, with the jugal less extended ventrally than in chiniquodontids. A recent first-hand examination of the holotype, shows that a key feature thought to characterize the taxon, osseous palate not formed posteriorly by palatines (Brink and Kitching 1953), is not distinctly present in the specimen. Hence, the Family Cistecynodontidae as proposed by Abdala (1996a) would be non-existent. Furthermore, traits such as the small size, the expanded basicranium and the complete absence of a parietal crest, hint that this is a juvenile specimen, probably of *Cynognathus*, as suggested by Hopson and Kitching (1972).

Thrinaxodon brasiliensis, represented by a fragmentary skull, lower jaws and postcranial skeleton (UFRGS PV 248T; Text-fig. 8A–D), was included in chiniquodontids by Battail (1991a, b) based on its elongate secondary palate and the shape of its dentary. This species illustrates the mosaic distribution of features in non-mammalian cynodonts. The lower postcanines closely resemble those of *Thrinaxodon liorhinus* in the number and form of cusps (Crompton 1963b), as well as in a strongly developed lingual cingulum (Text-fig. 8C–D). This similarity goes even further; the lower postcanines in the Brazilian species are clearly similar to the A, M and P types defined by Osborn and Crompton (1972) for the African species. Upper postcanines in the Brazilian species are simpler than lowers with two tiny labial cingular cusps in the base of the posterior accessory cusps and isolated anterior and posterior lingual cusps. Other structures suggesting thrinaxodontid affinity are the low and inclined coronoid process (although this trait is variable in specimens of *Thrinaxodon liorhinus*; Abdala, pers. obs.) and the lesser differentiation of the angle of the dentary (Barberena *et al.* 1987; Text-fig. 8C). Some puzzling features were pointed out as diagnostic of *Thrinaxodon brasiliensis* by Barberena *et al.* (1987). The presence of five upper and four lower incisors is an unusual condition, considering that a synapomorphy of the thrinaxodontid plus eucynodont level is the
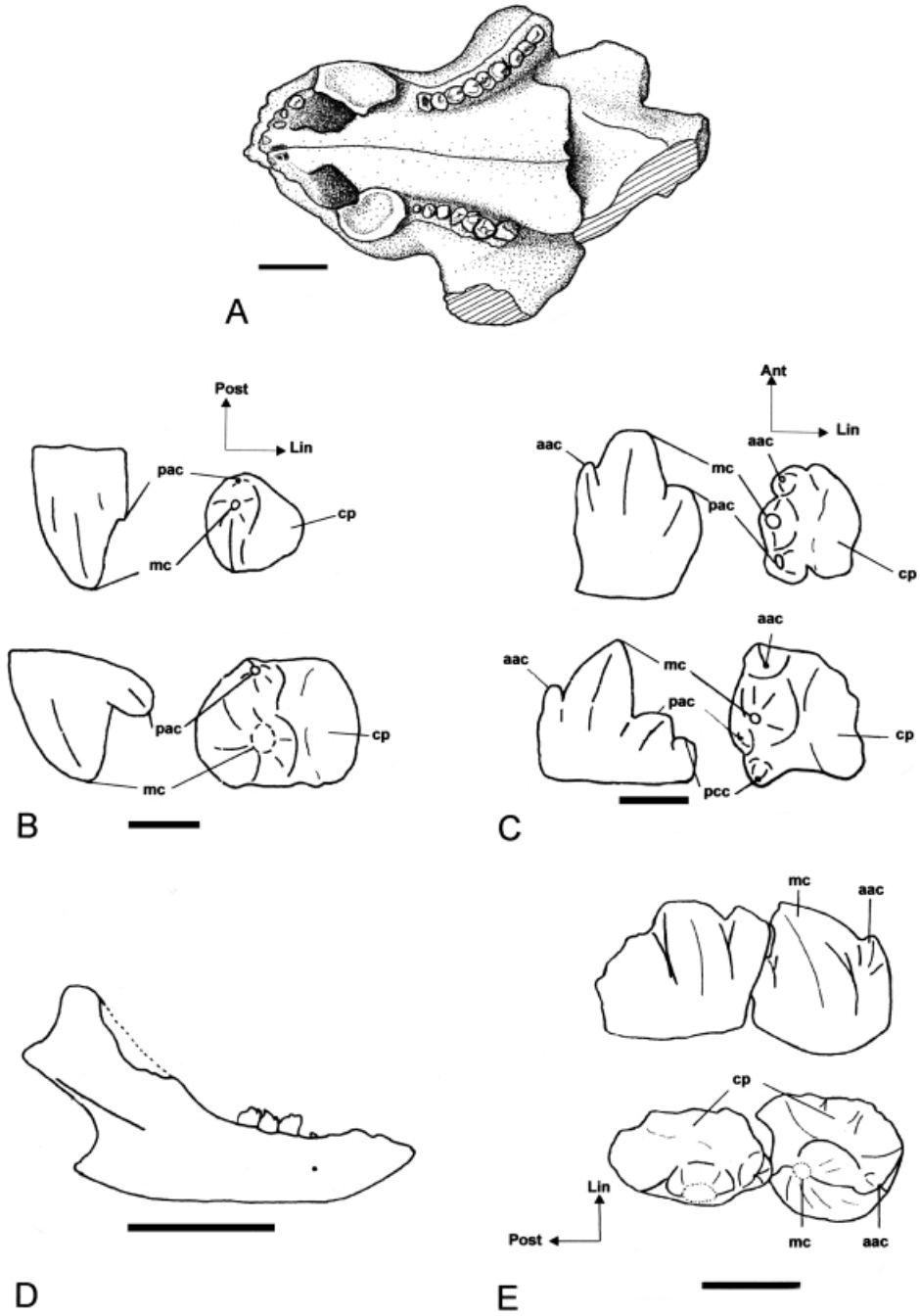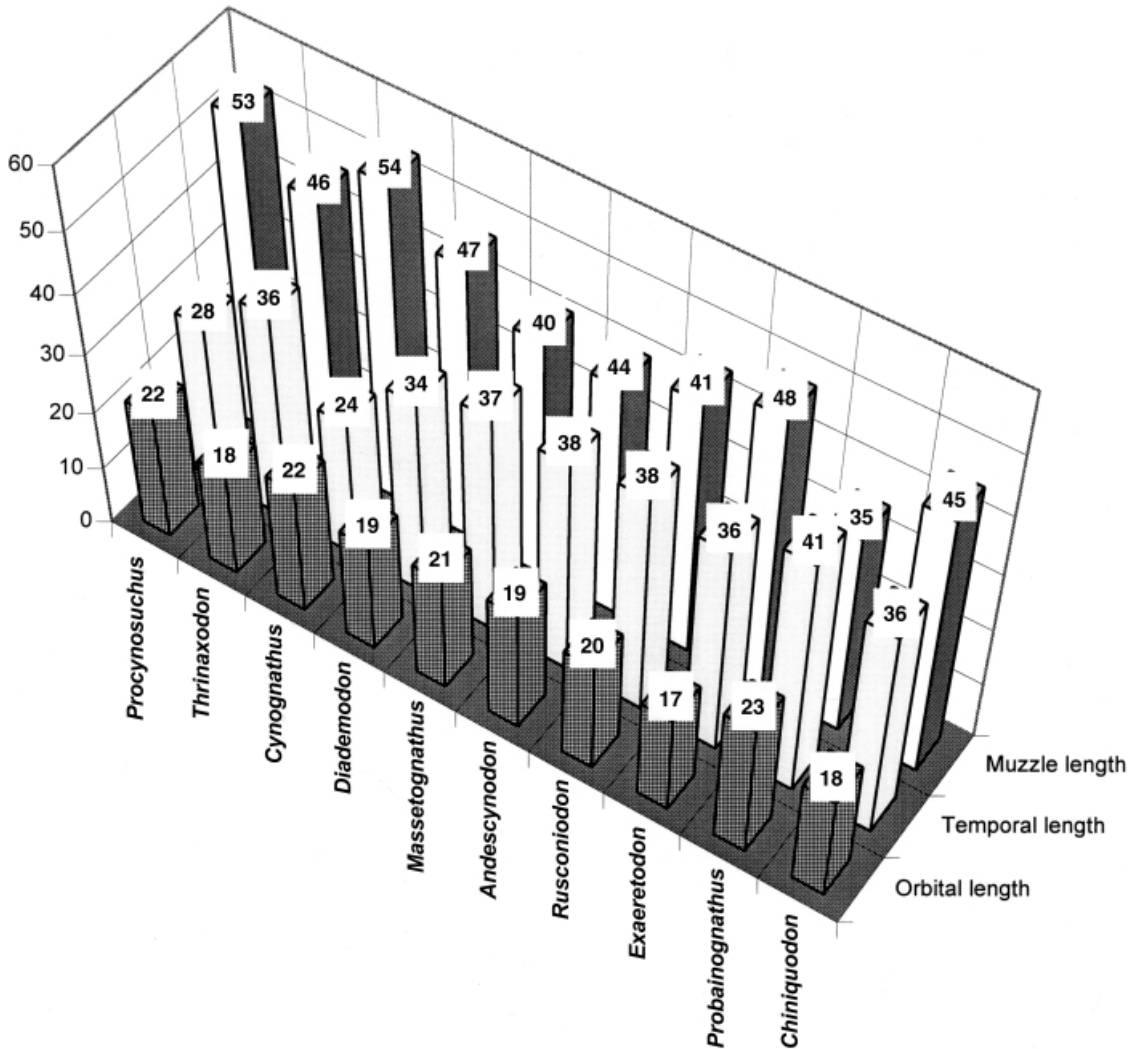
TEXT-FIG. 7. Percentage proportions of three skull regions in different non-mammalian cynodont groups.

presence of four upper and three lower incisors (Hopson and Barghusen 1986; Rowe 1993). In the holotype, nine upper and seven lower incisors are present, with the first right and fifth left upper, and the fourth left lower, being remarkably smaller. In addition, the right lower jaw shows three incisors and an erupting fourth one. We interpret the large number of incisors in *T. brasiliensis* as the retention of an older tooth in the process of being replaced alongside the recently emerged new one in last upper and lower left

TEXT-FIG. 6. A, palatal view of *Aleodon brachyrhamphus* (BMNH 9390), with the osseous palate extended posteriorly; scale bar represents 10 mm. B, labial and occlusal views of the upper postcanines II and V of *Aleodon brachyrhamphus* (BMNH 10048); scale bar represents 2 mm. C, labial and occlusal views of the lower postcanines II and III of *Aleodon brachyrhamphus* (BMNH 10048); scale bar represents 2 mm. D, lateral view of the lower jaw of *Cromptodon mamiferoides* (PVL 3858); scale bar represents 10 mm. E, labial and occlusal views of the lower postcanines IV and V of *Cromptodon mamiferoides*; scale bar represents 1 mm. Abbreviations: aac, anterior accessory cusp; cp, cingular platform; mc, central cusp; op, osseous palate; pac, posterior accessory cusp; pcc, posterior cingular cusp.
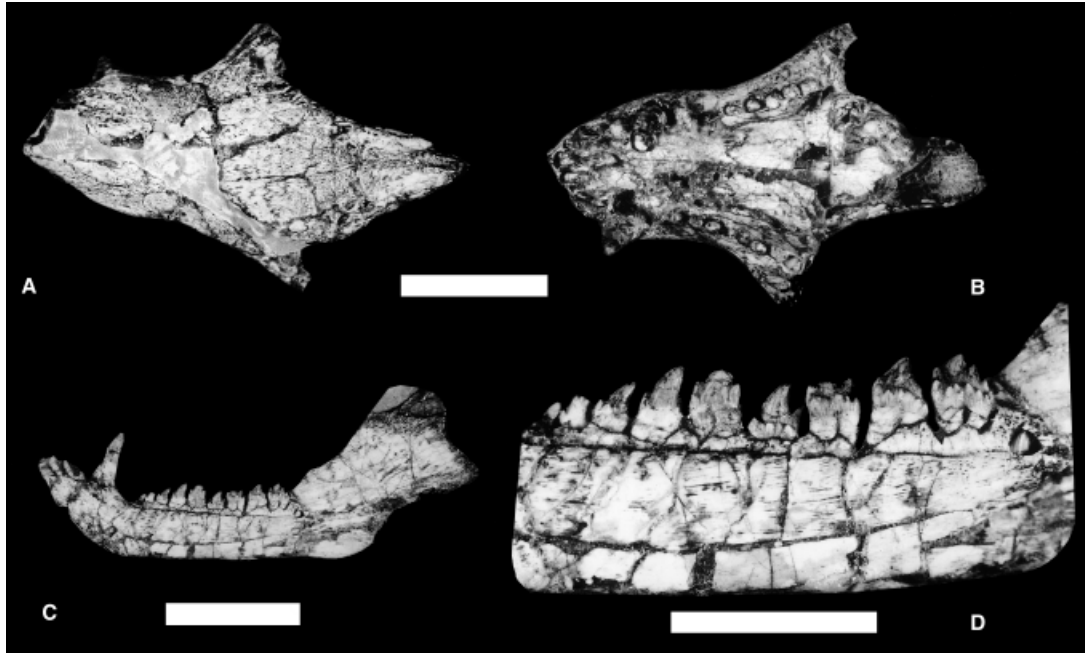
TEXT-FIG. 8. Dorsal (A) and ventral (B) views of the skull, lingual view (C) of the lower jaw, and lingual view (D) of the lower postcanines of *Thrinaxodon brasiliensis* (UFRGS PV 248T). Scale bars represent 20 mm (A–C) and 10 mm (D).

positions. Another cited diagnostic trait was a notable difference in the number of upper and lower postcanines (seven upper and ten lower). Examination of the specimen however, shows a high variability in postcanine number: seven plus one in eruption on the upper right and six plus one in eruption on the upper left (Text-fig. 8A), and nine plus a bud on the lower right (Text-fig. 8C–D) and eight plus a bud on the lower left. In sum, *T. brasiliensis* has a mixture of features of different non-mammalian cynodonts. On the one hand, its postcanines are similar to those of *T. liorhinus* and thus to morganucodontids (Crompton and Jenkins 1968), and on the other hand, it shares synapomorphies, such as the extended osseous palate (Text-fig. 8B), with late eucynodonts.

SYSTEMATIC PALEONTOLOGY

Order THERAPSIDA Broom, 1905
Infraorder CYNODONTIA Owen, 1861
Family CHINIQUODONTIDAE von Huene 1935–42

Genus CHINIQUODON von Huene 1935–42

Chiniquodon theotonicus von Huene, 1935–42, emend.

Text-figure 2

1935–42   *Chiniquodon theotonicus* von Huene, p. 93, pl. 11, fig. 1
1935–42   *Belesodon magnificus* von Huene, p. 96, fig. 20a–b; pl. 11, fig. 2; pls 12–14; pl. 15, fig. 1.
  1969   *Probelesodon lewisi* Romer, p. 1, figs 1–7.
  1973   *Probelesodon minor* Romer, p.1, figs 1–2.
  1982   *Probelesodon kitchingi* Teixeira, p. 1, pls 1–4.

Holotype. GPIT 1050 (Text-fig. 2).

Referred specimens. GPIT 40; UFRGS PV 66T, 66Tg, 122T, 274, 275T; MCN PV 2755; MCP PV 1600; MCZ 1533, 3035, 3614, 3615, 3776, 3777, 3779, 3781, 4002, 4020, 4100, 4296, 8823; PVL 4167, 4444, 4448, 4674, 4675; PULR 12, 18, 100, 101, 102; BM (NH) 8429.

Localities and horizons. Chiniqua (São Pedro do Sul), Candelaria, and Santa Cruz do Sul, Rio Grande do Sul State, southern Brazil; and Los Chañares locality, La Rioja Province, western Argentina. Brazilian specimens are from the Ladinian *Dinodontosaurus* Biozone (Barberena *et al.* 1985), and a new, also probably Ladinian, traversodontid Biozone in the Santa Maria Formation (Abdala *et al.* 2001). Specimens from Argentina are from the lower lithosome of the Ladinian Chañares Formation (Rogers *et al.* 2001). The holotype comes from the Cynodontier Sanga, west of the town of Chiniquá (von Huene 1935–42).

Emended diagnosis. Chiniquodontid cynodont showing a zygomatic arch with a slightly arched ventral border, reaching the level of the ventral orbital rim; sectorial postcanine teeth having no, or very reduced, cingula; cusps of the postcanines lacking serrated edges.

Remarks. Two specimens assigned to this species, the skull MCZ 3615 from Candelária, described by Romer (1969*a*), and the lower jaw MCN PV 2755 from the new locality of Santa Cruz do Sul (Abdala *et al*. 2001), bear posterior postcanines with small lingual cingula consisting of two tiny cusps. These specimens may represent a different species, but considering their poor preservation and fragmentary nature we include them in *C. theotonicus* until more complete material is discovered. Moreover, wide variation in postcanine morphology, including the presence and absence of cingula in different tooth positions, occurs in *Thrinaxodon liorhinus* (Crompton 1963*b*; Crompton and Jenkins 1968).

Chiniquodon sanjuanensis (Martinez and Forster, 1996) comb. nov. emend.

1996   *Probelesodon sanjuanensis* Martinez and Forster, p. 285, figs 1–4.

Holotype. PVSJ 411.

Referred materials. PVL 2076, 2077, 2115, considered to be *Chiniquodon* cf. *theotonicus* by Bonaparte (1966).

Localities and horizon. The holotype is from the north side of the Cancha de Bochas area, Ischigualasto Provincial Park, lower half of the Ischigualasto Formation, San Juan Province, Argentina (Martinez and Forster 1996). The exact provenance of the referred material is not known. Following the timescale of Gradstein and Ogg (1996), it is dated as earliest Carnian (Rogers *et al.* 1993).

Emended diagnosis. Chiniquodontid cynodont similar in overall morphology and general skull proportions to *C. theotonicus*, but differing in its highly arched zygomatic arch, with its ventral border strongly curved and extending to a level above the middle of the orbit; with a serrated posterior edge of the main cusp of at least the last postcanine (and probably also the anterior ones).

Remarks. The lower jaws of the holotype are in occlusion, obscuring whether the lingual cingula occur on the postcanines. The referred material, originally described by Bonaparte (1966), was found in Ischigualasto Provincial Park; its inclusion in this species is tentative owing to its poor state of preservation.

Comments on the diagnosis of the species in the family Chiniquodontidae

One aspect of Chiniquodontidae systematics that needs emphasis is the absence of diagnostic or autapomorphic features for the species previously recognised within the family. Von Huene (1935–42) described *Chiniquodon theotonicus* and *Belesodon magnificus* without providing a diagnosis for either or a distinction between the two species except size. However, he (von Huene 1935–42, pp. 156–157) did provide a diagnosis or a characterization of the Chiniquodontidae, pointing to postcanine morphology and palate extension, among other traits. Bonaparte (1966, p. 166) provided the first diagnosis for the genus

Chiniquodon, but considered symplesiomorphies shared with different groups of non-mammalian cynodonts, together with traits diagnostic for the Chiniquodontidae. Bearing in mind that Bonaparte (1966) regarded the Chiniquodontidae as monotypic, it is not surprising that diagnostic traits of the family were also useful for the genus. The lack of diagnoses for chiniquodontid species went unaddressed until the description of *Probelesodon lewisi*. This taxon was diagnosed by Romer (1969*b*, p. 2) based on general size differences from *Belesodon* as well as on palate length and tooth morphology, the last two characters actually being useful for a family diagnosis. This situation was not unexpected since specimens of *Probelesodon lewisi* were well preserved and provided a wealth of new information about chiniquodontid morphology. By contrast, previously described material was either fragmentary, poorly preserved, or both, practically precluding clear comparisons with *P. lewisi*. This picture did not change with the description of *Probelesodon minor*, which was differentiated from *P. lewisi* simply on the basis of size (Romer 1973, p. 1). Thus, this family came to include three genera and four species, all lacking proper diagnoses. Two other species were erected more recently. Most of the characters said to be diagnostic of *Probelesodon kitchingi* (Teixeira 1982; Text-fig. 9A–C)) are found as variations in the extensive sample of *P. lewisi*. The sole potentially valid distinction of the former taxon is the lateral expansion of the frontal in dorsal view (Text-fig. 9A) and the presence of ten postcanines (Teixeira 1982; Text-fig. 9C). The last trait, however, also occurs in one specimen (MCZ 3777) out of many nine-toothed individuals from the Chañares Formation (Table 1), showing that there is a modest variation in the postcanine number above nine teeth. On balance, however, skull morphology of *Probelesodon kitchingi*, including the form of most of the sutures, is markedly similar to that of *P. lewisi*. Diagnostic features of the last species described, *Chiniquodon sanjuanensis*, are a highly arched zygomatic arch, with its ventral border strongly curved and reaching the middle of the orbit, and the presence of serrations on the posterior edge of the main cusp of the sixth postcanine. Other features proposed as diagnostic for *C. sanjuanensis*, such as the well-developed squamosal-surangular articulation or the long retroarticular process (Martinez and Forster 1996) are also found in Chañares specimens. Characters such as the postorbitals widely separated along the midline are features typical of juvenile cynodonts as observed in *Thrinaxodon* (Estes 1962) and *Massetognathus* (Abdala, pers. obs.). Given that the specimen is a juvenile, a condition also inferred from cranial expansion as reflected in the parietals being wide in dorsal view, we do not regard the presence of six postcanines as diagnostic of this taxon. Nevertheless, considering the number of postcanines in relation to skull length of the holotype (see Table 1) it is probable that adults of *C. sanjuanensis* had fewer postcanines than species from the Chañares and Santa Maria formations.

Considering chiniquodontid diversity altogether, three different morphologies seem apparent. Two morphologies are distinguished by just one difference, postcanine structure. Most chiniquodontids have postcanines lacking cingular cusps. This is the condition in the holotypes of *Chiniquodon theotonicus*, *Probelesodon kitchingi*, and all the specimens from the Chañares Formation for which postcanines are known. The second morphotype is marked by tiny lingual cingular cusps present on some posterior postcanines in two specimens of the Santa Maria Formation (MCZ 3615 and MCN-PV 2755). The third morphology is that represented by *Chiniquodon sanjuanensis*, as outlined in the diagnosis presented above. Omitted from discussion on postcanine structure are all the specimens previously assigned to *Belesodon*, which either lack postcanines or are so poorly preserved that the presence of cingula cannot be confidently determined.

CRANIAL ALLOMETRY OF THE CHINIQUODONTIDS

All variables significantly responded to the increase in overall size as estimated by the total length of the skull, showing a tight relationship (P values for slopes <0·001, R^2 values >0·88; Table 2). Neither outliers nor systematic trends were evident in residuals. Coefficients obtained via least squares were comparable to those obtained via reduced major axis, the latter slightly larger, as is usual (Niklas 1994). Considering least squares results, four variables evinced a significant ($P \leq 0.05$) deviation from unity, but only the maximum height of the jugal (ZH) was strongly different from unity (Table 2). Two other variables showed 'positive' deviations, namely the length of the palate (PAL), and the maxillary bicanine width (BW). The height of the occipital plate (OH) was the only variable with a 'negative' allometry.
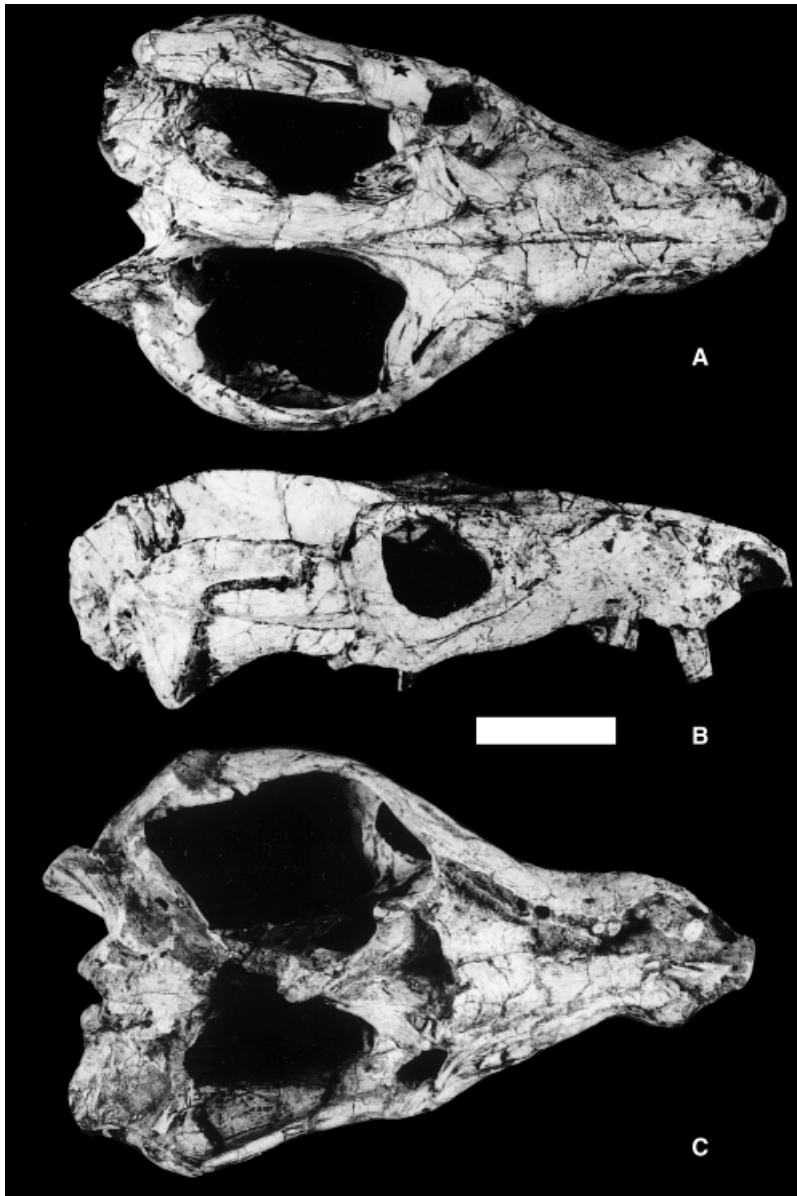
TEXT-FIG. 9. Dorsal (A), right lateral (B) and ventral (C) views of *Probelesodon kitchingi* (MCP 1600 PV). Scale bar represents 40 mm.

Because several statistical tests were applied to the same sampling units (i.e. the same skulls), a Bonferroni correction of the nominal *P*-value may be advisable (Hair *et al.* 1995). If Bonferroni correction is applied, the *P*-level for rejecting the null hypothesis of isometry must be reset equal to 0·003; i.e. 0·05/16, or the nominal *P*-value (0·05) divided by the number of tests (16) applied to the same sampling units (Hair *et al.* 1995), which are the 16 different regressions performed over measurements taken from the same skulls. Only the maximum height of the jugal (ZH) can be retained as allometric under this constraint ($P < 0.001$).

TABLE 1. Specimens included in the study. Abbreviations: (e), estimated; H, holotypes; N, information not available; PN, upper postcanine number; TL, length from the muzzle tip to the occipital condyle; U, unpublished; *, specimens stolen from the museum.

Specimen	Country	Formation	Original assignment	TL (mm)	PN	References
MCZ 3035	Brazil	Santa Maria	*Chiniquodon* or *Belesodon*	65	7?	Romer (1969*a*)
PV 0066 T	Brazil	Santa Maria	U	105	N	
PV 0066 Tg	Brazil	Santa Maria	U	130	N	
GPIT 1050	Brazil	Santa Maria	*Chiniquodon theotonicus* (H)	145 (e)	8 + 1	von Huene (1935–42)
MCZ 3615	Brazil	Santa Maria	*Chiniquodon*	150 (e)	9	Romer (1969*a*)
MCZ 3614	Brazil	Santa Maria	*Chiniquodon*	152	N	Romer (1969*a*)
MCP PV1600	Brazil	Santa Maria	*Probelesodon kitchingi* (H)	164	10	Teixeira (1982)
MCZ 1533	Brazil	Santa Maria	*Belesodon*	224	11?	Romer (1969*a*)
PV 0274	Brazil	Santa Maria	U	255	10	
GPIT 40	Brazil	Santa Maria	*Belesodon magnificus* (H)	260	9?	von Huene (1935–42)
PV 0122 T	Brazil	Santa Maria	U	310	N	
PV 0275T	Brazil	Santa Maria	U	N	N	
PVL 2076	Argentina	Ischigualasto	*Chiniquodon* cf. *theotonicus*	N	8?	Bonaparte (1966)
PVL 2077	Argentina	Ischigualasto	*Chiniquodon* cf. *theotonicus*	N	N	Bonaparte (1966)
PVL 2115	Argentina	Ischigualasto	*Chiniquodon* cf. *theotonicus*	N	N	Bonaparte (1966)
PVSJ 411	Argentina	Ischigualasto	*Probelesodon sanjuanensis* (H)	80	6	Martinez and Forster (1996)
MCZ 4296	Argentina	Chañares	U	50 (e)	5?	
PVL 4675	Argentina	Chañares	U	55 (e)	N	
PULR 12*	Argentina	Chañares	*Probelesodon minor* (H)	70	6-7	Romer (1973)
MCZ 4100	Argentina	Chañares	*Probelesodon minor*	73	8	Romer (1973)
PVL 4444	Argentina	Chañares	U	85	8+1	
PVL 4674	Argentina	Chañares	U	101	9	
PULR 18*	Argentina	Chañares	*Probelesodon lewisi* (H)	110	8-9	Romer (1969*b*)
PVL 4448	Argentina	Chañares	U	113	9	
PVL 4167	Argentina	Chañares	U	116	9	
MCZ 3779	Argentina	Chañares	U	116	9	
MCZ 3777	Argentina	Chañares	*Probelesodon minor*	121	10	
PULR 0101	Argentina	Chañares	U	129 (e)	9	
PULR 0100	Argentina	Chañares	U	134	9	
MCZ 4002	Argentina	Chañares	*Probelesodon lewisi*	137	9	Romer and Lewis (1973)
PULR 0102	Argentina	Chañares	U	138	9	
MCZ 3776	Argentina	Chañares	U	145	N	
BM(NH) R 8429	Argentina	Chañares	U	145	8	
MCZ 4020	Argentina	Chañares	U	200 (e)	8	
MCZ 8823	Argentina	Chañares	U		6?	
MCZ 3781	Argentina	Chañares	*Probelesodon lewisi*	N	N	Romer and Lewis (1973)

Small sample sizes may be in part responsible for this result ($12 \leq N \leq 20$), since rejection of the null hypothesis of isometry partially depends on sample size, but strong allometry was detected with a sample size as small as in the height of the zygoma ($N = 15$). Thus, only minor deviations from isometry could be missed.

Results from RMA regressions were concordant with least squares in ZH, BW, and PAL (Table 2). However, the method also found significant 'positive' allometry in the length of the temporal region (TEL), skull width (SW), and basicranial length (BB), and failed to detect allometry in OH. Therefore, unambiguous (i.e. consistent in all methods) allometric growth was found in three splanchnocranial components (ZH, BW, and PAL) and they were all of a 'positive' sign.

TABLE 2. Summary of regressions on the total length of the skull in Chiniquodontidae. Abbreviations: n, sample size; $R^2_{adj.}$, adjusted coefficient of determination; b_0, y-intercept; b_1, coefficient of allometry (least squares); t, one-tailed Student's t-value for b_1 (d.f. $= n - 2$); P (t_{ISO}), P-values for one-tailed t-values (not shown) under null hypothesis of isometry, calculated upon least squares coefficients (expected coefficient of allometry under isometry is unity; d.f. $= n - 2$); b_{RMA}, coefficient of allometry (reduced major axis); P ($b_{RMA\ ISO}$), P-values for one-tailed t-values (not shown) under null hypothesis of isometry, calculated upon RMA coefficients.

Variables	n	$R^2_{adj.}$	$\log b_0$	b_1	t_{b1}	P (t_{ISO})	b_{RMA}	P ($b_{RMA\ ISO}$)
Muzzle length (MUL)	18	0·92	-0·88	0·98	14·50[a]	0·401	1·02[b]	0·364
Temporal region length (TEL)	17	0·94	-1·25	1·09	16·38	0·101	1·12	0·042
Maximum skull width (SW)	13	0·95	-0·48	1·10	16·17	0·086	1·12	0·047
Maximum height of zygomatic arch (ZH)	14	0·98	-2·13	1·23	24·05	<0·001	1·24	<0·001
Interorbital distance (IO)	16	0·87	-1·42	1·02	10·89	0·420	1·09	0·187
Maxillary bicanine width (BW)	16	0·91	-1·78	1·18	12·72	0·034	1·24	0·011
Anterior postcanine distance (AD)	13	0·88	-1·85	0·98	9·44	0·435	1·04	0·349
Posterior postcanine distance (PD)	12	0·82	-0·70	0·90	7·16	0·234	0·99	0·467
Palate length (PAL)	17	0·98	-0·93	1·07	28·09	0·037	1·08	0·021
Upper postcanine row length (UP)	16	0·97	-0·98	0·92	22·77	0·036	0·93	0·062
Dentary length (DL)	13	0·98	-0·18	1·01	23·06	0·374	1·03	0·284
Occipital plate width (OW)	12	0·91	-0·97	1·06	10·44	0·270	1·11	0·148
Height of the occipital plate (OH)	14	0·88	-1·00	0·88	9·81	0·108	0·94	0·244
Basicranial length (BB)	16	0·85	-2·12	1·19	9·60	0·074	1·28	0·019
Orbital length (OL)	16	0·81	-1·52	0·88	8·05	0·140	0·97	0·385

[a] All t-values highly significant ($P < 0·001$)·
[b] All t-values calculated upon b_{RMA} highly significant ($P < 0·001$)

Allometry and systematics in chiniquodontids. The bivariate plots showed a size gap between the two specimens assigned to *Belesodon magnificus* and the rest of the sample (e.g. Text-fig. 10). The small-sized group included specimens with a skull length that varied between 50 and 164 mm, whereas the large-sized group ranged from 255 to 310 mm. However, in the absence of clear qualitative characters for the differentiation of *B. magnificus* as a distinct form (see discussion above), this size gap may well be merely a result of lack of specimens, given the high linear fit of all regressions. This argument can be tested in the presence of new material. For instance, there exists an incomplete specimen, MCZ 4020 from the Chañares fauna, for which the total length of the skull is unknown, with a palate length of 90 mm. If the size of this individual is to be inferred from the length of its palate (which is reasonable given the extremely high fit of this regression model: adjusted $R^2 = 0·98$; Table 2), this individual would have measured 203 mm in total skull length, partially filling the gap between *B. magnificus* and the rest of the specimens (Text-fig. 10). It also shows that sizes larger than those commonly recorded were attained by chiniquodontids encountered in the Chañares Formation. This fact is not trivial if we consider that larger sizes in the Chañares fauna are attained by specimens not fossilized in concretions. Meanwhile, nearly all the vertebrate fossils in this fauna are recorded within concretions, showing a counter-intuitive bias against the preservation of large-bodied specimens (Rogers *et al.* 2001). There-fore, all individuals can be arranged in a continuous growth series irrespective of their original species assignation, suggesting the existence of a single form. The lack of clear qualitative traits useful for diagnosing the species brings additional support to this contention. This idea, which derives from regression results, is reinforced by the fact that specimen MCZ 4020 could be confidently placed between *B. magnificus* and the rest of the sample. The position of the holotype of *C. sanjuanensis* in the regression plots (e.g. Text-fig. 10) is also concordant with the growth model, given that it contributed very little to the error term (i.e. the specimen is close to the fitted regression lines, implying a small residual value). However, in this case diagnostic traits were identified in order to keep the species separated.
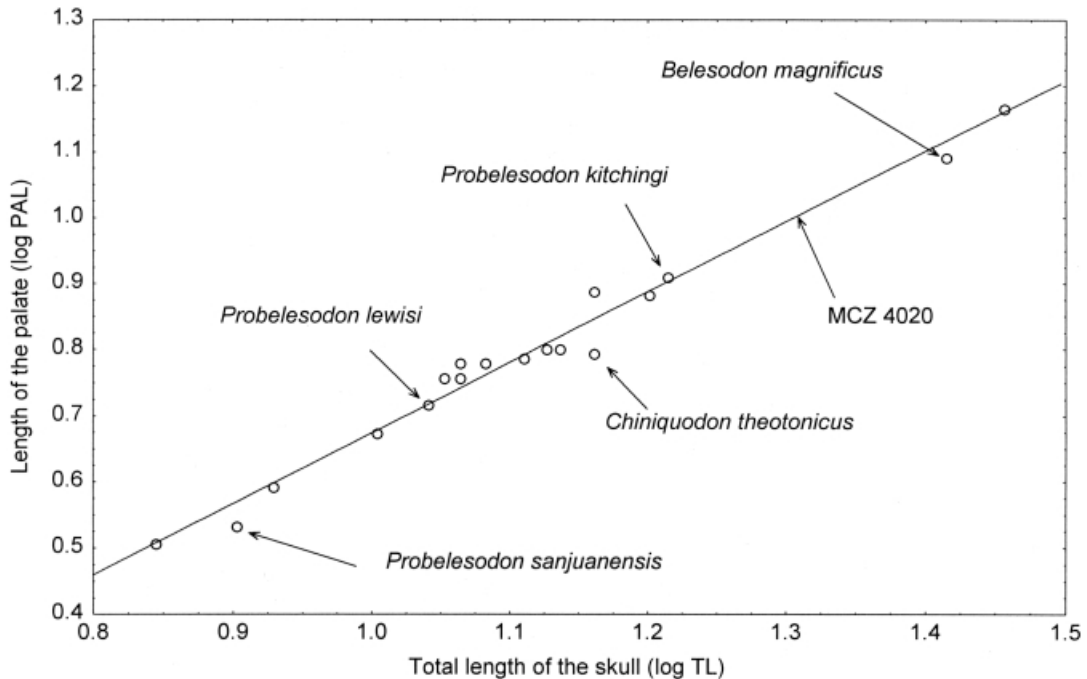
TEXT-FIG. 10. Regression of length of the palate (log PAL) on total length of the skull (log TL), with indications of the holotypes of the different species proposed for the family Chiniquodontidae. The expected position of the specimen MCZ 4020 from the Chañares Formation in the bivariate plot, based on the length of the palate, is indicated.

Comparative allometry. Allometry of skull components was also studied in the gomphodont cynodonts *Diademodon* (Grine *et al.* 1978) and *Massetognathus* (Abdala and Giannini 2000). In the first case, most coefficients of allometry indicated isometric or nearly isometric trends, probably a reflection of a small sample size ($6 < N > 11$) or specimen distortion (Grine *et al.* 1978). Negative allometry was recorded in seven of 33 variables, most of which are related to neurocranial components (eyes and brain). In *Massetognathus*, Abdala and Giannini (2000) measured virtually the same variables as in *Chiniquodon* with larger sample sizes ($16 < N > 31$). The last species shows fewer variables that clearly deviate from isometry (three variables against nine of *Massetognathus* or 12 per cent versus 56 per cent). In addition, unambiguous allometry in *Chiniquodon* is 'positive' and associated with splanchnocranial components, whereas in *Massetognathus* allometric variables are either 'negative' or 'positive' and related to splanchnocranium and neurocranium. Particular differences included, for instance, the palate length ('negative' in *Massetognathus*, 'positive' in *Chiniquodon*) and the height of zygomatic arches ('isometric' in *Massetognathus*, 'positive' in *Chiniquodon*). Modelling of the skull in *Massetognathus* involved facial, orbital, and braincase components that grew slower or at the same rate as the skull as a whole, in contrast with the temporal region that grew faster both longitudinally and transversally. This resulted in skulls with relatively small muzzles and enormous temporal fossae in adulthood (Abdala and Giannini 2000). In *Chiniquodon*, skull shape developed in a far less spectacular fashion, with very few deviations from isometry. Adults were approximately scaled-up juveniles, except for the relatively wider muzzle, heavier zygoma, and longer palate.

SUMMARY

We provide a diagnosis of the family Chiniquodontidae based on a thorough revision of nearly all the specimens previously assigned to Chiniquodontidae, and a comparison with representatives of the

remaining non-mammalian cynodonts. Two autapomorphic features and a combination of other characters diagnose Chiniquodontidae, a family exclusively represented in South America.

Species previously assigned to Chiniquodontidae in recent proposals, such as *Cromptodon mamiferoides*, *Probainognathus jenseni* and *Thrinaxodon brasiliensis* from South America, and *Aleodon brachyrhamphus* and *Cistecynodon parvus* from South Africa, are excluded from the family following the diagnosis provided here.

Two species are recognized in the Chiniquodontidae: *Chiniquodon theotonicus* von Huene, 1935–42, including *Belesodon magnificus*, *Probelesodon kitchingi*, *P. lewisi* and *P. minor* as junior synonyms, and *C. sanjuanensis* (Martinez and Forster, 1996), a new combination that includes the holotype, as well as specimens described as *C.* cf. *theotonicus*.

Analysis of allometry performed on skulls of chiniquodontids (as defined here) shows that all specimens can be arranged in a continuous growth series independent of their original assignment, indicating the existence of a single form. The location of the holotype of *C. sanjuanensis* in the regressions is also concordant with the growth model, but the species is recognized because of qualitative characters identified as autapomorphies.

Only three variables related to the splanchnocranium were unambiguously allometric in chiniquodontids: the maximum height of the zygoma (ZH), the length of palate (PAL) and the maxillary bicanine width (BW), all of them being 'positive'. This scaling is modest if compared with that of *Massetognathus*, which showed nine allometric variables, either 'positive' or 'negative', related to splanchnocranium and neurocranium.

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