

## GOMPHODONT CYNODONTS OF THE CHAÑARES FORMATION: THE ANALYSIS OF AN ONTOGENETIC SEQUENCE

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**ABSTRACT**—A revision of gomphodont cynodonts from the Chañares Formation of Argentina, is presented. Four species in two genera: *Massetognathus pascuali*, *M. teruggii*, *M. major*, and *Megagomphodon oligodens* were originally described by Romer in 1967 and 1972. Qualitative characters proposed originally as diagnostic of the species were revised, and a bivariate analysis of allometry of 17 linear skull measurements was performed upon 31 specimens. Allometry relationships account for most of the differences among specimens. There are neither size gaps nor systematic trends across the sample. The temporal region scales with a 'positive' allometry, whereas components of the neurocranium and muzzle show 'negative' or isometric scaling. This results in a change from short, stocky skulls with large muzzles in small specimens, to slender skulls with small muzzles and large temporal fossae characteristic of large individuals. The reduction and ontogenetic loss of the parietal foramen in a cynodont is reported for the first time. Consideration of qualitative characters together with the allometric results lead us to conclude that all forms belong to a single species in a growth series. Consequently, *Massetognathus pascuali* is recognized as the only valid entity, an idea previously suggested but without a justification based upon extensive analysis.

### INTRODUCTION

Gomphodont cynodonts are among the dominant Middle and Late Triassic vertebrates in South America (Bonaparte, 1982; Arcucci et al., 1994; Abdala, 1996). A distinctive representative is *Massetognathus*, found in the Middle Triassic of the Chañares and Santa Maria formations of Argentina and Brazil, respectively (Romer, 1967, 1972; Barberena, 1981).

The genus was created by Romer (1967) who recognized the type species *Massetognathus pascuali*, and a second species *M. teruggii* (Fig. 1A, B). The former was diagnosed as a small form with a mean skull length of 87 mm (ranging 82 to 95 mm); a flat triangular dorsal area formed by the posterior portion of the frontals and the anterior part of the parietals, extending back to a parietal foramen of modest size; postorbitals also extending close to the foramen; angular process of the lower jaw forming approximately a right angle with the ventral margin of the dentary. Finally, the presence of 12 upper and 11 lower postcanines was emphasized.

For *Massetognathus teruggii*, Romer (1967) recognized as diagnostic: a skull length with a mean of 125 mm (ranging 115 to 138 mm); a more restricted flattened dorsal area of the frontals and parietals; a parietal foramen reduced to a tiny slit, with the postorbitals extending to a point well back of the foramen; an angular process forming an obtuse angle with the ventral margin of the dentary; and 13 to 15 upper and 11 to 13 lower postcanines. Romer (1967) had five skulls of the species available at the time of his description.

Later, Romer (1972) described *Massetognathus major*, based on a single skull without lower jaw (Fig. 1C), diagnosed by its large size (205 mm); forward extension of the orbits; narrow antorbital region; and postcanine series less divergent posteriorly than others members of the genus. Other features mentioned by Romer (1972) were the presence of 13 postcanines, and the weaker development of the labial platform lateral to the postcanine series as consequence of the relative narrowness of the muzzle.

Based on two specimens, Romer (1972) also erected *Mega-*

*gomphodon oligodens* (Fig. 1D), a form he considered close to *Massetognathus*, with skull length of 180 mm and 17–18 relatively small postcanines (especially the anterior ones). He also pointed out that this taxon has a more slender skull than *Massetognathus*.

Several authors have cast doubt on the existence of four separate species with such similar morphologies, the same geological age and found within a limited geographic area. Romer (1967, 1972) himself speculated about the possibility that all the Chañares gomphodonts might belong to a single growth series, but he finally recognized all of them as valid. Hopson and Kitching (1972) considered *M. teruggii* a junior synonym of *M. pascuali*. More recently, Battail (1991) recognized *M. pascuali* as the only valid species of Chañares gomphodont, but did not discuss any evidence in favor of his conclusion.

In order to test whether the group may represent a growth series, we considered here, as null hypothesis, that all Chañares specimens of *Massetognathus* and *Megagomphodon* belong to a single species represented by individuals of different ages. If allometry accounts for the trends across individuals, irrespective of species assignment, the null hypothesis should be accepted and, therefore, all species described must be subsumed into the first-named species. However, this outcome still needs to be confirmed by the absence of clear qualitative traits defining the entities. In this work we present a revision of the characters considered as diagnostic of the four recognized species of the gomphodonts from the Chañares Formation and consider the implications of a bivariate analysis of allometry using skull measurements.

### MATERIALS AND METHODS

#### Specimens Examined

Thirty-one skulls were examined. The material belongs to the paleontological collections of the Universidad Nacional de La Rioja (PULR), the Universidad Nacional de Tucumán (PVL), both in Argentina; the Museum of Comparative Zoology (MCZ), Harvard University; and the Natural History Museum

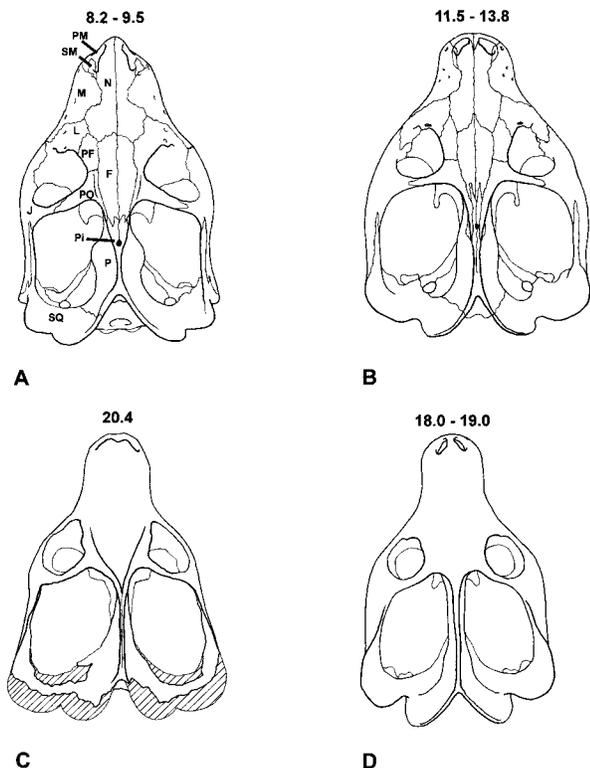


FIGURE 1. Dorsal views of the skull of the four nominated species of gomphodont cynodonts from the Chañares Formation. **A**, *Massetognathus pascuali* (modified from Romer, 1967, composite illustration). **B**, *Massetognathus teruggii* (modified from Romer, 1967, composite illustration). **C**, *Massetognathus major* (PULR 11). **D**, *Megagomphodon oligodens* (modified from Romer, 1972, composite illustration based on the holotype and MCZ 4138). **Abbreviations:** F, frontal; J, jugal; L, lacrimal; M, maxilla; N, nasal; P, parietal; Pi, pineal foramen; PF, prefrontal; PM, premaxilla; PO, postorbital; SM, septomaxilla; SQ, squamosal. Length of the skull (TL) in cm for each species is shown.

(BMNH), London. The list of specimen is as follows: PULR 10 (*Massetognathus pascuali* holotype), PULR 11 (*Massetognathus major* holotype), PULR 13 (*Massetognathus teruggii* holotype), PULR without/number<sub>a</sub> (*Megagomphodon oligodens* holotype); PULR w/n<sub>a</sub>; PVL 3901–3904, 3906, 4613, 4726–4729, w/n<sub>a</sub>; MCZ 3691, 3786, 3798, 3801, 3804, 3806, 3807, 4021, 4138, 4208, 4215, 4216, 4258, 4265; BMNH R8430.

### Allometry

Seventeen measurements of the skull were used in the analysis of allometry (Fig. 2). A vernier caliper was used and the measurements were recorded to the nearest millimeter. When some kind of deformation was present (especially in transversal dimensions) a careful approximation was attempted; otherwise the measurement was discarded.

We studied the relation of each cranial variable with overall size through the equation of allometry

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

which derives from the exponential growth equation  $y = b_0 x^{b_1}$  (Alexander, 1985) by the calculation of base 10 logarithms in both members. Here  $b_0$  is the y-intercept and  $b_1$  is the slope of the line or coefficient of allometry. Significance of slope values was assessed with a *t*-test. Deviations from isometry were assessed by comparing the allometry coefficient with the one expected under geometric similarity (see Alexander, 1985). Our

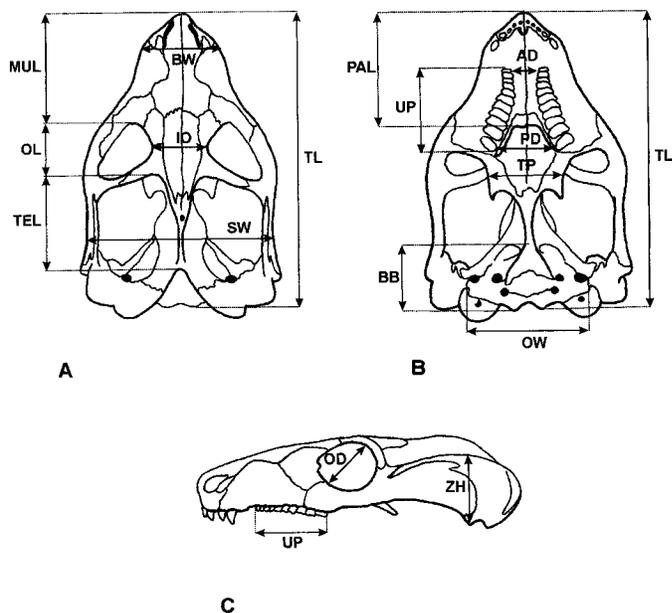


FIGURE 2. Schematic drawing of a *Massetognathus* skull showing measurements and abbreviations used in this study (modified from Romer, 1967). Dorsal (**A**), ventral (**B**) and lateral (**C**) views of the skull. Measurements were grouped into several regions categories: overall skull, muzzle, orbital region, temporal region and braincase. **Abbreviations:** **Skull:** TL, total length of the skull, from the anterior tip to the occipital condyles. **Muzzle:** MUL, muzzle length; BW, maxillary bicanine width; PAL, palate length; AD, anterior postcanine distance; PD, posterior postcanine distance; TP, transverse process width; UP, upper postcanine tooth row length. **Temporal region:** TEL, total temporal region length; SW, maximum skull width; ZH, maximum height of the zygomatic arch. **Orbital region:** OL, orbital length; IO, interorbital distance; OD, orbital diameter. **Braincase:** BB, basicranial length; OH, height of the occipital plate; OW, occipital plate width.

estimator of overall size was, as usual, the total skull length (Simpson et al., 1960; Emerson and Bramble, 1993; Radinsky, 1981a, b). The expected coefficient under isometry is 1.0 for all the variables measured in this study. We used *t*-tests with the null coefficient set equal to 1.0 to assess significant deviations from isometry. A coefficient significantly less than expected by isometry is referred to as 'negative' allometry and one significantly higher than expected as 'positive' (Emerson and Bramble 1993).

Least squares regression was also used to assess the relation of tooth number and overall size. Some specimens show a slightly different number of teeth in left and right upper rows, so the average was used. The expected coefficients under isometry for a dimensionless variable such as a number is zero; then a conventional *t*-test provides both the significance of the regression line and the deviation from isometry.

Least squares regression assumes that there is a clearly identifiable independent variable, and that it has neither measurement error nor natural variation (Hair et al., 1995; Zar, 1996). These assumptions do not hold in our study, although it can be argued that all variables are size-dependent. Consequently we have also calculated reduced major axis (RMA) coefficients of allometry for all variables (see Radinsky, 1981a, b; Niklas, 1994). The RMA method allows variation in both dimensions; therefore residuals are oblique, representing also variation in size. We compared least squares coefficients with the more appropriate RMA coefficients to ensure reliability of the estimators of the relation of each variable with overall size (total length of the skull).

TABLE 1. Results of regressions on the total length of the skull. Expected coefficient of allometry under isometry is 1.0 for all variables. **Abbreviations:** n, sample size;  $b_0$ , y-intercept;  $b_{1(LS)}$ , coefficient of allometry calculated via least squares; t, t-value for  $b_{1(LS)}$ ;  $R^2$ , adjusted coefficient of determination;  $t_{ISO}$ , calculated t-value for isometry; r, product moment correlation coefficient;  $b_{1(RMA)}$ , coefficient of allometry calculated via reduced major axis method. Abbreviations for variables as in Figure 1.

Variables	n	R <sup>2</sup>	log b <sub>0</sub>	b <sub>1(LS)</sub>	SE	t	t <sub>ISO</sub>	r	b <sub>1(RMA)</sub>
MUL	31	0.92	-0.68	0.90	0.05	18.89***	-2.06 <sup>m</sup>	0.96	0.94
BW	31	0.89	-1.14	0.94	0.06	15.65***	-1.01 <sup>ns</sup>	0.95	0.99
PAL	25	0.96	-0.42	0.81	0.04	22.94***	-5.23*	0.98	0.83
AD	16	0.8	-2.08	0.97	0.13	7.72***	-0.27 <sup>ns</sup>	0.90	1.07
PD	16	0.77	-1.11	0.73	0.10	7.22***	-2.68*	0.89	0.82
TP	22	0.72	-0.29	0.52	0.07	7.37***	-6.82*	0.85	0.61
UP	26	0.88	-0.64	0.78	0.06	13.87***	-3.88*	0.94	0.83
TEL	29	0.95	-1.55	1.22	0.05	23.47***	4.22*	0.98	1.25
SW	28	0.95	-1.03	1.27	0.05	23.81***	5.10*	0.98	1.30
ZH	24	0.8	-1.65	1.10	0.12	9.54***	0.90 <sup>ns</sup>	0.90	1.23
IO	29	0.88	-1.47	1.02	0.07	14.59***	0.33 <sup>ns</sup>	0.94	1.09
OL	30	0.76	-1.15	0.80	0.08	9.70***	-2.46*	0.88	0.91
OD	27	0.76	-0.72	0.64	0.07	9.15***	-5.20*	0.88	0.73
BB	28	0.81	-1.15	0.79	0.07	10.95***	-2.90*	0.91	0.87
OH	27	0.88	-1.22	0.95	0.07	13.68***	-0.68 <sup>ns</sup>	0.94	1.01
OW	28	0.81	-1.19	1.01	0.09	10.90***	0.12 <sup>ns</sup>	0.91	1.12

\*\*\*Significant ( $P < 0.001$ ), \*significant ( $P < 0.05$ ); <sup>m</sup>marginally significant; <sup>ns</sup>non-significant ( $P > 0.05$ ).

RESULTS

All variables are significantly related to overall size estimated as the total length of the skull (Table 1). The empirical models found explain a large fraction of total variation in dependent variables, with R<sup>2</sup> values ranging from 0.72 to 0.97 (most >0.80). Examination of residuals in all variables shows neither outliers nor particular trends across individuals, nor systematic trends across the sample—an example is shown in Figure 3. In other words, small deviations from the corresponding regression lines can be easily attributed to random variation. Coefficients of allometry calculated via least squares and reduced major axis show little differences but, as expected, RMA values are slightly larger (Niklas, 1994). Because of the constraints of least squares regression (see Methods), RMA values must be considered a better approximation to the true coefficients of allometry for these relationships (Radinsky, 1981a, b; Niklas, 1994).

Nine variables (plus muzzle length, marginally significant) deviate from isometry (Table 1). Of these, all but two scale with a ‘negative’ allometry; the two ‘positive’ variables are dimensions of the temporal region—temporal region length (TEL) and maximum skull width (SW). Thus, the facial, orbital, and braincase components grow slower than, or at the same

rate as the skull as a whole, whereas the temporal region grows faster both longitudinally and transversely.

The number of postcanine teeth increases with total skull length ( $t = 13.87$ ,  $p < 0.001$ ; see model in Fig. 4), representing a ‘positive’ deviation from isometry (null  $b_1=0$ ). The model fit less well than in the case of linear dimensions ( $R^2 = 0.41$ ), having greater variation, and being accompanied by asymmetry in some individuals. The specimen PVL 4613 has 12 right and 13 left upper postcanines and 13 right and 14 left lower ones. Variation was also recorded for larger specimens such as PVL 3902 (14–13 upper and 14–15 lower postcanines) and PVL 3904 (14–13 upper and 13–11? lower postcanines). It is worthwhile to note that this asymmetry is not caused by poor preservation.

DISCUSSION

Allometry results suggest that the specimens studied belong to a continuous growth series. The very good fit of the models also implies a high reliability of prediction of missing values in partially preserved material within the range of measurements. No gap was evident along the range of sizes spanned by the sample and no systematic trends were found by examining residuals. This clearly suggests a remarkably homoge-

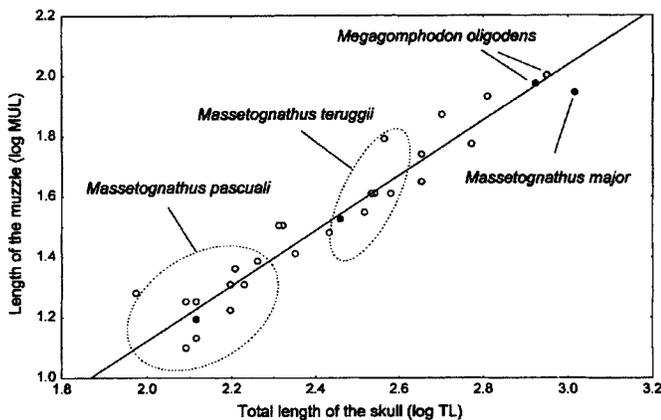


FIGURE 3. Regression of muzzle length (log MUL) on total skull length (log TL), with indications of specific assignments following Romer (1967, 1972). See Table 1 for regression model. Solid circles indicate holotypes of the species.

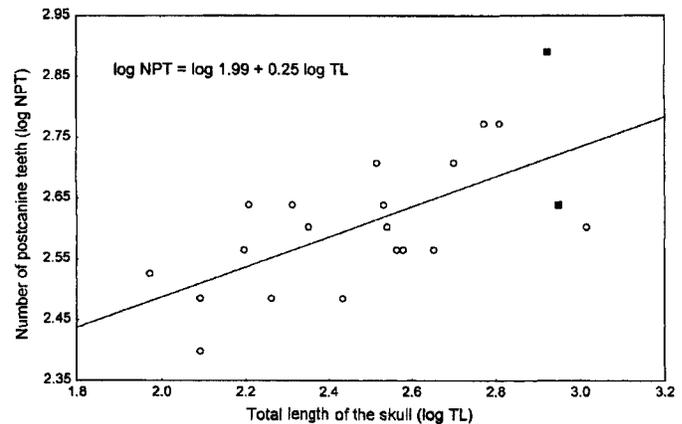


FIGURE 4. Regression of (log) number of upper postcanine tooth on total skull length (log TL). Solid squares indicate *Megagomphodon oligodens* specimens. Inset: regression models for the number of postcanine tooth.

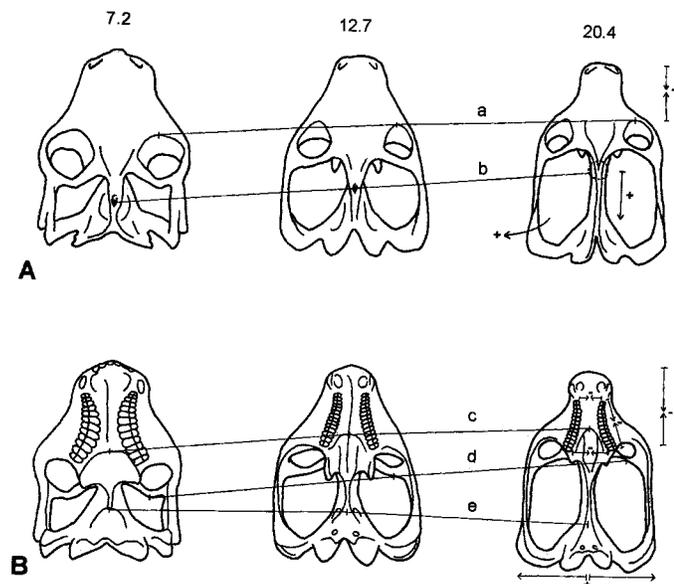


FIGURE 5. Schematic drawings (represented to the same skull length) of three size stages of *Massetognathus* skulls. **A**, dorsal view; **B**, ventral view. Actual length of the skull (TL) is shown above each example in cm. From left to right, specimens are PVL4613, PVL3902 and PULR11. Lines connect reference points across the specimens in order to show changes in proportion. **Abbreviations:** a, posterior limit of muzzle; b, pineal foramen position (note that in the third specimen location is approximated); c, posterior end of secondary palate; d, anterior end of temporal region; e, anterior end of the basicranial axis.

neous group, in contrast with Romer's (1967, 1972) opinion that four different species are recognizable within *Massetognathus* and *Megagomphodon*. The existence of intermediate specimens filling the proposed size gaps between the species erected by Romer (1967, 1972) is seen in Figure 3. Likewise, bivariate and multivariate studies performed upon an extensive sample of skulls of diademodontine cynodonts from South Africa and Zambia, (Grine and Hahn, 1978; Grine et al., 1978; Bradu and Grine, 1979) subsumed 24 species into *Diademodon tetragonus*. Romer also disregarded possible sexual dimorphism, when comparing *Massetognathus pascuali* and *M. teruggi*, arguing that 'the difference in size is considerably greater than that expected by sex differences, and it is hence reasonable to believe that we are dealing with two distinct species' (Romer 1967:2). We believe that there is no basis for such statement in light of the allometry results, and because there are plenty of far more extreme examples of sexual dimorphism in size among vertebrates (Macdonald, 1984:7; McMahon and Bonner, 1986; Pough et al., 1996).

Deviations from isometry indicate that muzzle components are comparatively large in juveniles and grow at a slower rate than the rest of the skull during ontogeny, while the temporal region grows faster, probably to accommodate larger adductor muscles that become increasingly important towards adulthood. Lengthening of the temporal region apparently occurs at the basicranial girder and zygomatic arches, because basicranium length coefficient of allometry is 'negative' and therefore does not contribute to the 'positive' allometry of the total temporal length. These aspects can be seen in Figure 5.

Comparatively, allometry in *Massetognathus* skull is rather particular. According to Radinsky (1981a), neurocranial components tend to scale with a negative allometry, whereas splanchnocranial components tend to scale isometrically or with a slight positive allometry. This generalization, that seems to

hold in mammals, does not hold in the Chañares' *Massetognathus*. The variables related to the neurocranium (orbital and posterior parts of the skull) are isometric or scale 'negatively', but most of the elongation of the temporal region occurs at the basicranial girder (Fig. 5), whose internal component is a part of the neurocranium. Splanchnocranial components do not scale uniformly, muzzle measurements are negative or isometric whereas zygomatic length and width are positive. This leads to large and slender skulls with relatively small muzzles and enormous temporal fossae as the individual grows.

Postcanine tooth number increases with body size, but its variation is larger than that of linear measurements of the skull. This is an important point because among the characters defining *Megagomphodon oligodens*, one is the presence of 17–18 postcanines in comparison with 14 or less in *Massetognathus* specimens of similar or larger size. By examining the distribution of specimens along the regression line (Fig. 4), it seems clear that variations occur in both directions (animals with more or less teeth than expected by their size) and therefore they could be random deviations from the number predicted by size. Another point is that the second specimen assigned by Romer (1972) to *Megagomphodon oligodens* (MCZ 4138) has 13 or at most 14 upper postcanines, thus differing also from the number of postcanines of the holotype (Fig. 4).

The other two characters mentioned in the diagnosis of *Megagomphodon oligodens* are a relatively slender, large skull, and relatively small teeth, especially the anterior ones (Romer, 1972). Both can be refuted in terms of allometry. First, it was shown that the muzzle grows at a slower rate than the rest of the skull, and that the temporal region grows faster. Consequently, small animals should have comparatively robust muzzles and short temporal regions, giving the impression of stocky skulls, whereas large ones should appear to be slender because of the elongation of the temporal region, the separation of the zygomatic arches, and the proportionately small muzzles (compare extremes in Fig. 5). Second, allometry of the size of individual teeth was not measured in our work but can be inferred from the allometry of tooth number and upper tooth row length. Tooth number is dimensionless and therefore must scale with overall size with a zero coefficient. However, although variation is large, teeth number does increase with size, which implies that individual tooth size changes with a 'negative' allometry in order to arrange more teeth along the row while growing, as observed. Then, it is not surprising that teeth are proportionally smaller in larger animals. The tooth replacement in diademodontids, traversodontids and the mammaliaform *Sinoconodon* involves the eruption of postcanines only at the posterior end of the series and the loss of the anterior elements (Crompton, 1955, 1972; Hopson, 1971; Goñi and Goin, 1988; Crompton and Luo, 1993). Thus, an alternative interpretation for the differences in postcanines number could be that the anterior postcanines in the holotype of *Megagomphodon oligodens* could be retained later than usual (as in other cases teeth could be lost unusually early due to random variation) and are of a small absolute size. Differing from the replacement patterns of *Diademodon* (Hopson, 1971; Crompton, 1972), *Scalenodon* (Crompton, 1955) and *Sinoconodon* (Crompton and Luo, 1993), the erupted tooth in *Massetognathus* was added at the end of the series of postcanines without replacement of old elements.

In addition, the upper tooth row shape was considered as diagnostic in separating small and larger forms (Romer, 1967, 1972), the former with strongly curved, divergent series, the latter with more subparallel series. However it, can be seen from the corresponding coefficients of allometry that anterior palate width (AD, anterior inner postcanine distance) is isometric, and posterior palate width (PD, posterior inner postcanine distance) is 'negative' (Table 1). Thus, posterior diver-

gence of the tooth row would be expected to decrease with age, giving less curved series in older specimens.

Features of the cranial roof that Romer (1967) proposed to differentiate *M. pascuali* from *M. teruggii* could be interpreted alternatively as ontogenetic modifications in the cranial architecture, that also involve the parietal foramen. In small specimens parietals surface are more exposed dorsally, especially the portion anterior to the parietal foramen. In larger specimens, this area is usually less developed because of the anterior extension of the parietal crest (due to increase in mass of adductor muscles) and the close apposition of (the posterior projection of) the postorbital bones over the parietal crest. Therefore, size-related ossification in the triangular area formed by frontals and parietals could explain the differences between *M. pascuali* and *M. teruggii* in the skull roof.

In connection with this modifications, there is a change in the relative position and a gradual decrease in size of the parietal foramen, until its complete loss in larger specimens (Fig. 5). In specimens of small size (e.g., PULR 10, skull length 88 mm) the parietal foramen is in the middle of the temporal region and is laterally bordered only by the parietals. In larger specimens (e.g., PULR 13, skull length 121 mm), the parietal foramen is vestigial, located in the anterior third of the temporal region, and also laterally bordered by the enlarged posterior extension of the postorbital. The reduction and closure of the parietal foramen was observed in large-sized, probably old specimens of the squamates *Anolis carolinensis*, *Cyclura cornuta*, and *Iguana iguana* (Roth et al., 1986). Based on their ontogenetic analysis in these lizards, the authors argued that Late Permian scaloposaurs could have been misdiagnosed if the presence-absence of the parietal foramen was used as the single character to distinguish species. In fact, the opening would be present in smaller, possibly young individuals and absent in larger, probably adult ones of the same species. This is precisely the condition found in the skull series of *Massetognathus* analyzed here, and therefore we disregard the presence or absence, and degree of constriction of the parietal foramen, as a diagnostic character.

We also found that the braincase of the small specimens is comparatively large and bulbous below the parietal crest, but shows a gradual change towards a slender, only slightly expanded, braincase in larger individuals.

Finally, the diagnosis of *Massetognathus* species using the angle formed by the angular process and the ventral margin of the dentary (Romer, 1967) does not seem justified. Most angles in our sample are slightly obtuse, but a right angle is also present in some specimens. This morphology apparently does not correlate with size.

### CONCLUSION

We argue that in order to recognize closely-related entities as different, even if they follow the same rules of growth (same slopes), they must show either different y-intercepts (implying different sizes of particular structures) or clear qualitative characters that can be used to argue for phylogenetic distinctness. We consider that this is not the case in our study, suggesting the existence of a single taxon within which specimens can be convincingly arranged in an ontogenetic sequence. Allometric relationships account for most of the trends shown among specimens, and our revision failed to reveal clear qualitative characters to separate proposed species. Therefore, we recognize *Massetognathus pascuali* as the only valid species for Chañares gomphodonts, and consider *M. teruggii*, *M. major*, and *Megagomphodon oligodens* as junior synonyms. This is coincident with Battail's (1991) opinion, but we have now provided a clear argument to justify this viewpoint.

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