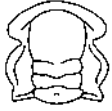# Heterochrony and tooth evolution in hyperodapedontine rhynchosaurs (Reptilia, Diapsida)

MAX C. LANGER, JORJE FERIGOLO AND CESAR L. SCHULTZ

LETHAIA

The tooth arrangement of hyperodapedontine rhynchosaurs shows clear patterns of morphological derivation, which can be summarized as three main apomorphic trends: the increase in the number of tooth rows lateral to the main maxillary groove, the loss of dental structures (medial groove and lingual teeth) medial to the main maxillary groove, and the loss of dental structures (medial crest and lingual teeth) medial to the main dentary crest. The analysis of these trends from a heterochronic viewpoint reveals that acceleration was the most probable process involved in the increase in number of the lateral maxillary tooth rows, while the loss of the medial structures of the maxilla and dentary seem to be related respectively to neoteny and post-displacement. Both peramorphic and paedomorphic processes are, therefore, thought to have directed the main modifications seen in the tooth arrangement of the hyperodapedontine rhynchosaurs. Heterochrony plays an important role in the evolution of the Late Triassic rhynchosaurs, which are differentiated mainly on the basis of their dental morphology. □ *Heterochrony, Hyperodapedontinae, rhynchosaurs, tooth morphology, Triassic.*

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Rhynchosaurs are a well-known group of basal archosauromorphs that were abundant during most of the Triassic period. The first member of the group appeared in the Lower Triassic (Scythian) of South Africa, while the last rhynchosaur was recorded at the Carnian–Norian boundary in southern Brazil. The group was particularly widespread and abundant during the Carnian, when the members of the subfamily Hyperodapedontinae colonized most Pangaean dry-land areas, stabilizing themselves as the dominant first-level consumers in most palaeocommunities in which they occur.

Benton & Kirkpatrick (1989) have been the only authors so far to use a heterochronic approach to analyse rhynchosaur evolution. Their study, which was based mostly on the ontogeny of the Brazilian form usually named 'Scaphonyx fischeri', emphasized the action of peramorphosis (possibly hypermorphosis) in the development of the typical cranial features of this Carnian rhynchosaur. Such features as the deep mandible and the short and broad skull are not unique to 'Scaphonyx fischeri', however, but are found in all hyperodapedontine rhynchosaurs (*sensu* Langer & Schultz 2000). Together with other cranial, dental and appendicular features, those peramorphic traits

differentiate the exclusively Late Triassic Hyperodapedontinae from the typical Middle Triassic rhynchosaurs, such as *Stenaulorhynchus* and *Rhynchosaurus* (Chatterjee 1980; Benton 1990; Dilkes 1998).

The subfamily Hyperodapedontinae includes all rhynchosaurs previously ascribed to the genera *Hyperodapedon* Huxley (Chatterjee 1974; Benton 1983) and 'Scaphonyx' Woodward (Huene 1942; Sill 1970), as well as the primitive form 'Scaphonyx' *sulcognathus* (Azevedo & Schultz 1987). Langer & Schultz (2000) assigned all these forms, with the exception of 'S.' *sulcognathus*, to the genus *Hyperodapedon*, which also includes some poorly known forms such as 'Isalorhynchus' (Buffetaut 1983). The classical Brazilian forms – 'Cephalonia lotziana' and 'Scaphonyx fischeri' – are, along with most of the rhynchosaurs from the Late Triassic of Argentina, grouped in the species *Hyperodapedon sanjuanensis* (Sill).

In spite of being a clearly differentiated group, with world-wide distribution and extreme abundance, hyperodapedontine rhynchosaurs do not exhibit great morphological diversity. The cranial shapes of the various species, for instance, are very similar, the same being true for the appendicular skeleton, in which just a few uncertain discrete differences are present
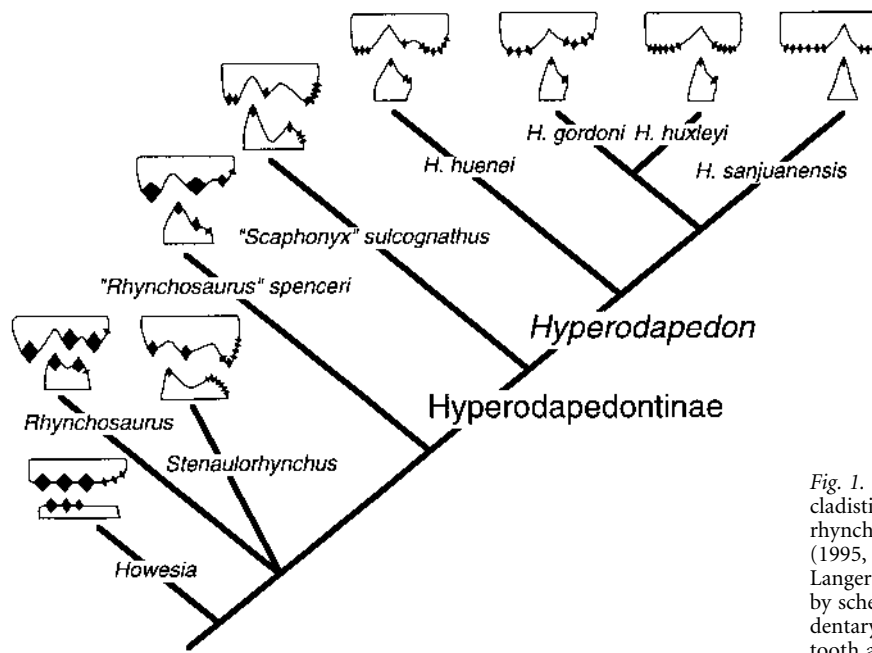
Fig. 1. Strict consensus tree summarizing the cladistic hypotheses for the interrelationships of rhynchosaurs of Benton (1985, 1988, 1990), Dilkes (1995, 1998), Wilkinson & Benton (1995) and Langer & Schultz (1999). Each taxon is represented by schematic transverse sections of the maxilla and dentary (not to the same scale), depicting their tooth arrangement (lateral area towards left).

(Benton 1983; Langer & Schultz 2000). Regarding dental morphology, on the other hand, the hyperodapedontine rhynchosaurs are clearly distinct from each other. This situation was obvious to most authors working on the group, who used the variety of dental arrangements as an important indication of their taxonomic hypotheses (Chatterjee 1969, 1980; Benton 1983, 1990).

The aim of this study is to search for heterochronic processes responsible for the modifications of tooth arrangement acting both in the origin and in the diversification of the hyperodapedontine rhynchosaurs. The exclusive focus on dental morphology does not seem to impose serious problems, since, as pointed out before, the oral region is the area in which the morphological changes of the hyperodapedontines are more evident. Moreover, the use of the dental morphology also fills a gap observed by Benton & Kirkpatrick (1998) in their attempt to study heterochrony in rhynchosaurs: the lack, apart from *Hyperodapedon sanjuanensis*, of completely preserved juvenile skeletons. The robust tooth-bearing elements of rhynchosaurs are, on the other hand, much more commonly preserved. Dentaries and maxillae of various sizes are known for almost all Mid-Late Triassic members of the group, making possible the study of growth series of these bones.

Most tooth-bearing elements are, however, found isolated, and their age – growth stage – is defined solely based on their size in relation to other specimens of the same taxon. Therefore, the size criterion, with all its limitations (Godfrey & Sutherland 1995; Klingenberg 1998), is the only measure of ontogenetic time used in the present study. Hence, some of the determinations of heterochronic processes proposed here may be biased by this relative uncertainty in assigning reliable ages to the analysed specimens.

Institutional abbreviations used in this study are as follows: AMNH, American Museum of Natural History, New York, USA; BGS, British Geological Survey, Nottingham, UK; BMNH, Natural History Museum, London, UK; BSPHG, Bayerische Staatssammlungen für Paläontologie und Historische Geologie, Munich, Germany; BRSUG, Department of Earth Sciences, University of Bristol, Bristol, UK; CAMMZ, Cambridge University Museum of Zoology, Cambridge, UK; EXEMS, Exeter Museum, Exeter, UK; IMGPT, Institut und Museum für Geologie und

Fig. 2. Details of the tooth arrangement of Mid-Late Triassic rhynchosaurs. A–B. Ventral view of *Hyperodapedon sanjuanensis* maxillae; A, juvenile UFRGS PV0047T, right side, ×2.3; B, adult, BSPHG 19.4, right side, ×0.7. C–D. Ventral view of 'Rhynchosaurus' spenceri maxillae; C, juvenile BRSUG 26541, left side, ×1.8; D, adult, BRSUG 26209, right side, ×1.3. E–F. Medial view of *Stenaulorhynchus stockleyi* maxillae; E, juvenile BMNH R9279, left side, ×1.7; F, adult, BMNH R9275, left side, ×0.9. G. Ventral view of adult *Hyperodapedon huenei* maxillae, UFRGS PV 0132T, left side, ×0.7. H–I. Medial view of *Hyperodapedon sanjuanensis* dentaries; H, juvenile, UFRGS PV 0047T, right side, ×1.8; I, adult, BSPHG 19.4, right side, ×0.3. J–K. Medial view of *Hyperodapedon huenei* dentaries; J, juvenile, UFRGS PV 0413T, right side, ×0.6; K, adult, UFRGS PV 0132T, left side, ×0.8. L–M. Medial view of *Rhynchosaurus brodiei* dentaries; L, juvenile, BMNH R2623, left side, ×2.2; M, adult, WARMS G950/1, right side, ×1.2.
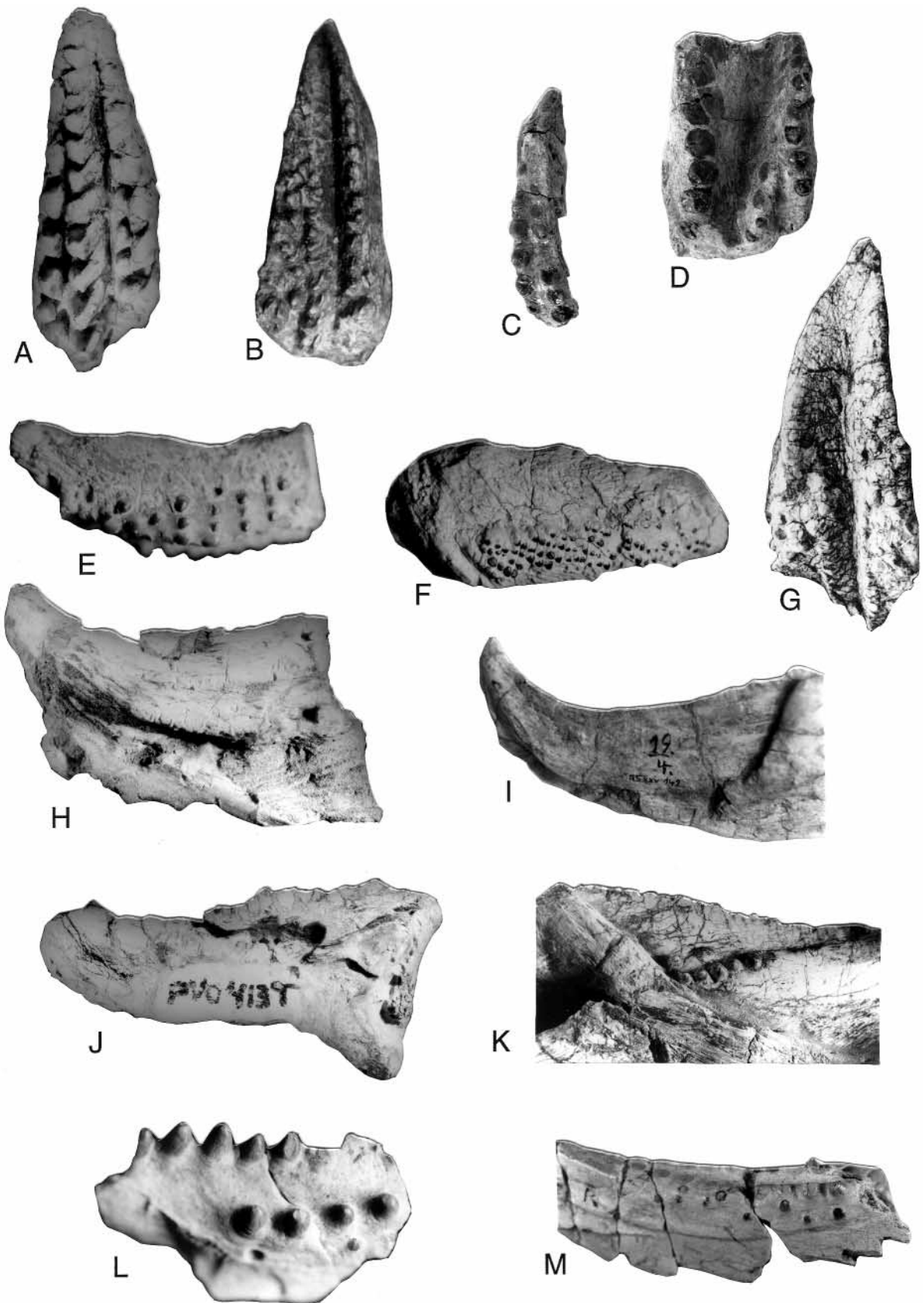
Paläontologie, Tübingen, Germany; ISI, Geology Museum, Indian Statistical Institute, Calcutta, India; MCP, Museu de Ciências e Tecnologia, PUCRS, Porto Alegre, Brazil; MDE, Musée des Dinosaures, Espéraza, France; UA, University of Antananarivo, Antananarivo, Madagascar; UNSJ, Museu de Ciências Naturales, Universidad Nacional de San Juan, San Juan, Argentina; UFRGS, Instituto de Geociências, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; WARMS, Warwick Museum, Warwick, UK.

Phylogenetic framework

The current orthodoxy regarding rhynchosaur phylogeny has been built by a series of cladistic works, focusing either on the whole group (Benton 1985, 1988, 1990; Wilkinson & Benton 1995; Dilkes 1995, 1998) or specifically on Late Triassic forms (Langer & Schultz 2000). A strict consensus tree (Sokal & Rohlf 1981; Swofford 1992) from these cladistic hypotheses (Fig. 1) is used here as a phylogenetic framework for the heterochronic study.

In all those attempts to reconstruct the evolutionary story of rhynchosaurs by cladistic methods, as well as in pre-cladistic works (Chatterjee 1969, 1980; Benton 1983), special attention was always given to dental morphology. Various morphological trends based on tooth arrangement were suggested as apomorphic/derived within Mid-Late Triassic rhynchosaurs, namely:

1. Increase in the number of occlusal tooth rows in the lateral part of the maxilla (Langer & Schultz 2000).
2. Increase in width of the lateral area of maxilla in relation to the medial area (Benton 1983, 1990; Langer & Schultz 2000).
3. Reduction in the number of occlusal tooth rows in the medial part of the maxilla (Chatterjee 1969).
4. Loss of the secondary medial maxillary groove (Chatterjee 1980; Benton 1983, 1985, 1988, 1990; Dilkes 1995, 1998; Langer & Schultz 2000).
5. Loss of maxillary lingual teeth (Chatterjee 1980; Benton 1983, 1985, 1988, 1990; Dilkes 1995, 1998; Langer & Schultz 2000).
6. Reduction in the number of tooth rows in the dentary (Benton 1983, 1985, 1988; Dilkes 1998).
7. Loss of medial dentary cutting blade (Benton 1988, Langer & Schultz 2000).
8. Reduction in the number of occlusal tooth rows in the medial side of the dentary (Chatterjee 1969; Chatterjee 1980; Benton 1990).
9. Loss of dentary lingual teeth (Chatterjee 1980; Benton 1990; Langer & Schultz 2000).

Taking into consideration the changes in tooth arrangement listed above, it is possible to observe that only a few general trends were responsible for most of the morphological changes seen in the dentition of the Mid-Late Triassic rhynchosaurs. Both the maxilla and dentary of more derived taxa tend to present less complex medial tooth-bearing areas, while the lateral maxillary area becomes more complex (Fig. 1). These modifications can be summarized in three apomorphic trends: (1) increase in the number of tooth rows lateral to the main maxillary groove; (2) loss of dental structures (medial groove and lingual teeth) medial to the main maxillary groove; (3) loss of dental structures (medial crest and lingual teeth) medial to the main dentary crest. In order to search for the processes acting upon these changes, each of the trends will be analysed from a heterochronic viewpoint.

Heterochrony in hyperodapedontine rhynchosaurs: analysis of the dental morphological trends

Increase in the number of tooth rows lateral to the main maxillary groove

An ontogenetic trend towards the increase in the number of tooth rows in the lateral area of the maxilla is seen in rhynchosaurs in general. All juvenile *Stenaulorhynchus* (e.g. BMNH R9279; see also Benton 1984, fig. 7c) and *Rhynchosaurus* (e.g. WARMS Gz955) possess a single lateral tooth row, while some of the adults of these animals, though not all of them, possess extra teeth lying lateral to that row, sometimes making up a secondary row (Benton 1984, fig. 9, 1990, fig. 47c). This ontogenetic trend is much more clearly seen in Late Triassic rhynchosaurs. Among the specimens of *Hyperodapedon huxleyi* described by Chatterjee (1974, figs 13, 14), the smaller maxillae present two to three longitudinal tooth rows in their lateral area, while a larger one presents up to six rows. In the South American *Hyperodapedon* species the pattern is similar. Juvenile individuals (fig. 2A; see also Huene 1942, fig. 56) usually present two lateral tooth rows, medium-sized ones (e.g. MCP 1693PV, IMGPT 19.2; see also Fig. 2B) present three to four rows, while larger ones (e.g. UFRGS PV0408T, AMNH 7800) up to seven rows.

This trend towards an ontogenetic increase in the number of lateral tooth rows in the maxilla attests to the peramorphic nature of the higher number of those
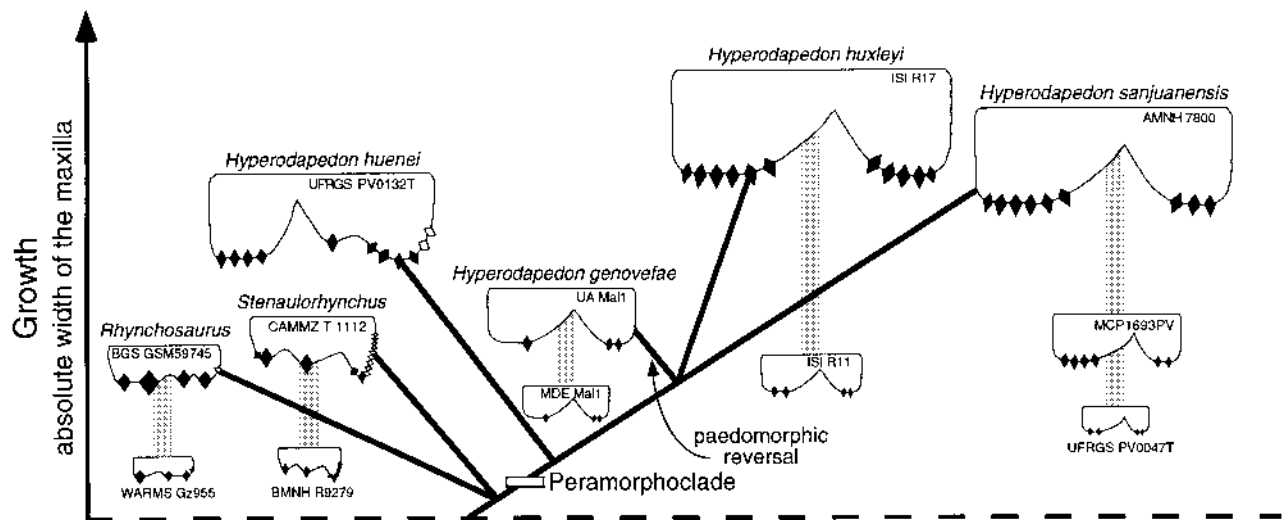
Fig. 3. Phylogenetic relationships (black lines) and ontogeny (grey lines) of Mid-Late Triassic rhynchosaurs depicting the peramorphic increase in the number of lateral maxillary tooth rows in *Hyperodapedon*. Specimens (with collection number indicated) are represented by schematic transverse sections of the maxilla (lateral area towards left) drawn at approximately the same scale (×0.8).

tooth rows seen in *Hyperodapedon* (*sensu* Langer & Schultz 2000), when compared with less derived rhynchosaurs (Fig. 3). The development of the lateral area of the maxilla is clearly extended in the species of that
genus, going beyond what is seen in more primitive forms such as *Rhynchosaurus* and *Stenaulorhynchus*. *Hyperodapedon* is the only rhynchosaur that has more than two lateral tooth rows in the maxilla, an apomorphic condition that characterizes this peramorphoclade.

It would be tempting to relate this peramorphic modification of the maxillary tooth arrangement to the general hypermorphic trend present in Late Triassic rhynchosaurs (Benton & Kirkpatrick 1989). This is not the case, however, since these two heterochronies took place at different times of rhynchosaur evolutionary history. The hypermorphic changes in the shape of the skull and mandibles described by Benton & Kirkpatrick (1989) are related to the origin of Hyperodapedontinae (*sensu* Langer & Schultz 2000), one of them (skull broader than long) even being present in '*Rhynchosaurus*' *spenceri*, a Middle Triassic non-hyperodapedontine rhynchosaur. The increase in the number of lateral maxillary tooth rows, on the other hand, characterizes the genus *Hyperodapedon*, a less inclusive peramorphoclade.

There are three ways in which the peramorphic increase in the number of lateral maxillary tooth rows could have arisen: hypermorphosis, acceleration and pre-displacement (McNamara 1986). In hypermorphosis, derived forms show a delayed offset in the development of certain structures and the early stages of the development of these structures are similar in both peramorphic and 'primitive' taxa. Acceleration acts to increase the rate of development of a structure during the ontogeny of the peramorphic forms (McNamara 1986). In such a case, the morphological differences between the derived and 'primitive' taxa (regarding the structure in question) are more marked when later stages of development are compared. Predisplacement, on the other hand, promotes ontogenetic disturbances (an earlier onset of the development of some structures) that affects mostly early stages of development of the peramorphic forms, and the morphological difference between 'primitive' and derived taxa does not increase significantly during later stages of ontogenetic growth.

Acceleration seems to be the case for the studied morphological trend. A juvenile *Hyperodapedon* possesses two lateral tooth rows in the maxilla, while a same-size juvenile of a 'primitive' taxon such as *Stenaulorhynchus* possesses a single one. The lateral maxillary area is, thus, already more developed (more peramorphic) in juveniles of derived rhynchosaurs (Fig. 3), precluding the sole action of hypermorphosis in this peramorphosis. The morphological difference, however, is much greater if the lateral maxillary area of adult Stenaulorhynchus that barely possesses a second lateral row (some individuals do not have it) is compared with the same area of *Hyperodapedon* maxillae of the same size, which usually possesses about four well-developed lateral tooth rows. This shows that the increase in the number of lateral maxillary tooth rows during later stages of development was higher in the more derived rhynchosaur taxa, indicating acceleration as the most probable peramorphic process in action (Fig. 4).
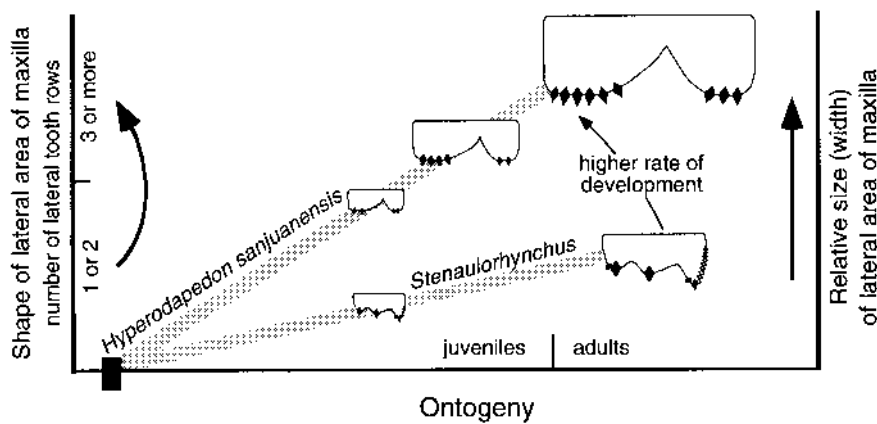
Fig. 4. Ontogenies of *Stenaulorhynchus stockleyi* and *Hyperodapedon sanjuanensis* compared (same growth series in Fig. 3), depicting the action of acceleration in the increase in number of lateral tooth rows in the maxilla of the species of *Hyperodapedon*. Larger arrows indicate the direction of the phylogenetic changes. Other symbols as in Fig. 3.

It would be tempting to explain the increase in width of the lateral maxillary area seen in *Hyperodapedon* as the size effect (Klingenberg & Spence 1993) of the peramorphic change in the morphology of this area (increase in the number of tooth rows). There is, however, no observable ontogenetic change in the relative width of the lateral and medial maxillary areas in any known rhynchosaur, and these changes cannot be directly related to heterochrony.

The independence between the enlargement of the lateral area of the maxilla and the increase in its number of tooth rows is corroborated by the study of *Hyperodapedon genovefae* (Buffetaut 1983). Both adults and juveniles of this rhynchosaur possess a wide lateral maxillary area that, however, bears only a single row of teeth. All known individuals of other *Hyperodapedon* species present at least two lateral tooth rows in the maxilla, along with the already discussed ontogenetic trend towards increase in their number. The adults of *H. genovefae*, therefore, retain a character that is seen only in juvenile specimens of primitive rhynchosaurs, such as *Stenaulorhynchus* and *Rhynchosaurus*. This is not only an autapomorphic reversal within the genus *Hyperodapedon*, but a clear case of paedomorphosis within the *Hyperodapedon* peramorphoclade (Fig. 3).

Loss of dental structures (medial groove and lingual teeth) medial to the main maxillary groove

The presence or absence of a secondary maxillary groove is a well-explored character in rhynchosaur phylogeny (Chatterjee 1980; Dilkes 1998). Furthermore, Benton (1990, figs 35, 36) could identify some ontogenetic changes regarding this character in rhynchosaurs from the Middle Triassic of England. In fact, the medial maxillary area of juvenile specimens of '*Rhynchosaurus*' *spenceri* (e.g. BRSUG 26541, EXEMS 7/1986.3; see also Fig. 2C) presents just one

or two rows of occlusal teeth, and no subsidiary groove is seen. Adults of this taxon (e.g. BRSUG 26209, EXEMS 60/1985.292; see also Fig. 2D), however, have a clearly developed secondary medial groove. A similar situation also seems to occur in *Rhynchosaurus brodiei* (Benton 1990, fig. 35), though it is not as clear as in '*R.*' *spenceri*. *Stenaulorhynchus*, on the other hand, shows no clear ontogenetic changes regarding this feature, and both juveniles and adults have two well-developed maxillary grooves (Benton 1984).

A similar ontogenetic pattern is seen for the maxillary lingual teeth. Juveniles of *Stenaulorhynchus* (e.g. BMNH R9279; see also Fig. 2E) possess about four rows of these teeth in the maxilla, while adults present a clear increase in this number, always showing more than six lingual tooth rows (e.g. BMNH R9275, IMGPT 312; see also Fig. 2F). This trend is not so evident in rhynchosaurs from the English Middle Triassic, with *Rhynchosaurus brodiei* showing no clear ontogenetic changes in this respect (Benton 1990). '*Rhynchosaurus*' *spenceri*, on the other hand, shows subtle modifications, with juveniles usually possessing a single row of maxillary lingual teeth (e.g. BRSUG 26541, EXEMS 7/1986.3), and larger individuals two or more of those rows (e.g. EXEMS 69/1985.292, 65/1984, 7/1986.4).

Hyperodapedon shows no observable ontogenetic changes regarding the presence of the medial groove or lingual teeth in the maxilla. All known juveniles (e.g. UNSJ 0065, MDE Mal 1, UFRGS PV0047T; see also Huene 1942, fig. 56; Chatterjee 1974, fig. 14) lack these elements, a morphology that is retained in the adults of most species of that genus. An exception is *H. huenei*, which has lingual teeth as well as a vestigial medial groove on the maxilla (Fig. 2G), and for which no juvenile maxilla is known.

A general ontogenetic trend towards an increase in complexity of the medial area of the maxilla is, therefore, present in Middle Triassic rhynchosaurs.
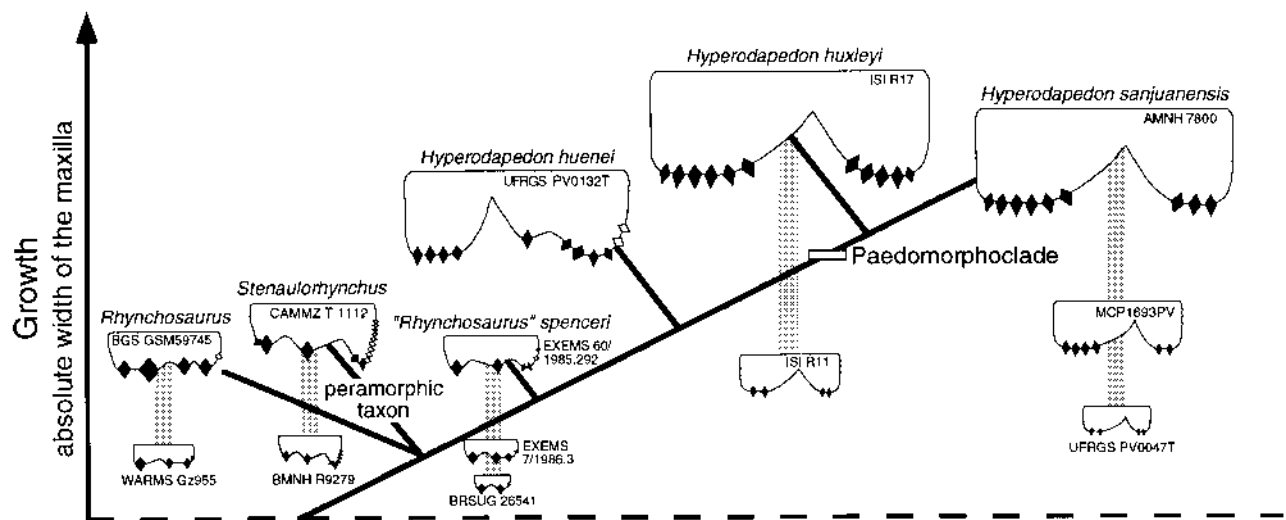
Fig. 5. Phylogenetic relationships and ontogeny of Mid-Late Triassic rhynchosaurs depicting the paedomorphic loss of maxillary structures (medial groove and lingua teeth) in the more derived species of *Hyperodapedon*. Symbols as in Fig. 3.

This indicates the paedomorphic nature of the loss of the medial groove and lingual teeth in the maxilla of more derived species of *Hyperodapedon*, defining a paedomorphoclade that includes all species of that genus except *H. huenei* (Fig. 5). The ontogeny of the medial maxillary area in those derived *Hyperodapedon* is clearly truncated in relation to that of more primitive rhynchosaurs, with the lingual teeth and the medial groove totally failing to appear.

Progenesis (= hypomorphosis) acts promoting a precocious termination in the development of certain structures of the paedomorphic forms (Reilly *et al.* 1997). Therefore, as in the case of hypermorphosis, both derived and 'primitive' taxa have similar early stages of development. In the case of the loss of structures in the medial maxillary area of rhynchosaurs, however, juveniles of the paedomorphoclade are already more derived (paedomorphic) than juveniles of more 'primitive' forms (Fig. 5), precluding progenesis as responsible for those changes.

As happens in the peramorphosis discussed before, the morphological differences between more derived species of *Hyperodapedon* and 'primitive' rhynchosaurs (regarding the medial area of the maxilla) are more marked when adults rather than juveniles are compared. The development from juvenile to adult of primitive rhynchosaurs such as '*Rhynchosaurus*' spenceri includes not only the appearance of the medial groove, but also the increase in the number of lingual teeth. On the contrary, the development from juvenile to adult in the members of the discussed paedomorphoclade shows neither of these transformations. This indicates that the paedomorphic taxa present heterochronic disturbances even in later stages of development, precluding post-displacement (which affects mostly early ontogenetic stages) as the process responsible for such paedomorphosis. In other words, during its ontogeny, the medial area of the maxilla of the paedomorphic rhynchosaurs shows a reduced degree of allometric growth (morphological modifica-
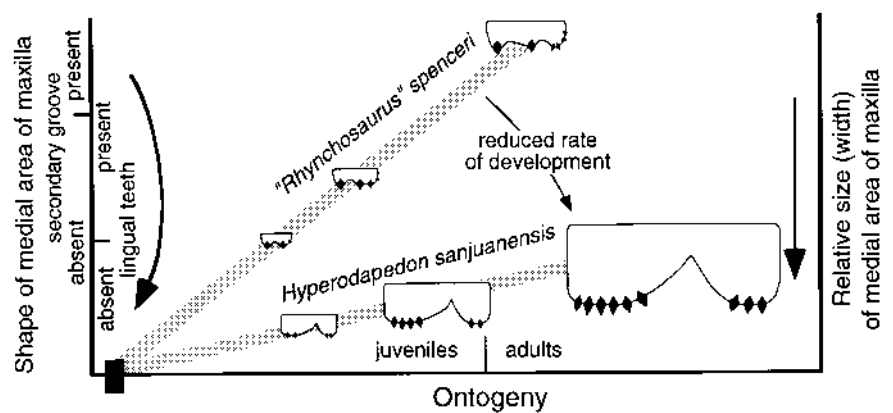
Fig. 6. Ontogenies of '*Rhynchosaurus*' *spenceri* and *Hyperodapedon sanjuanensis* compared (same growing series of Fig. 5), depicting the action of neoteny in the loss of the medial maxillary structures of the more derived species of *Hyperodapedon*. Symbols as in Fig. 4.
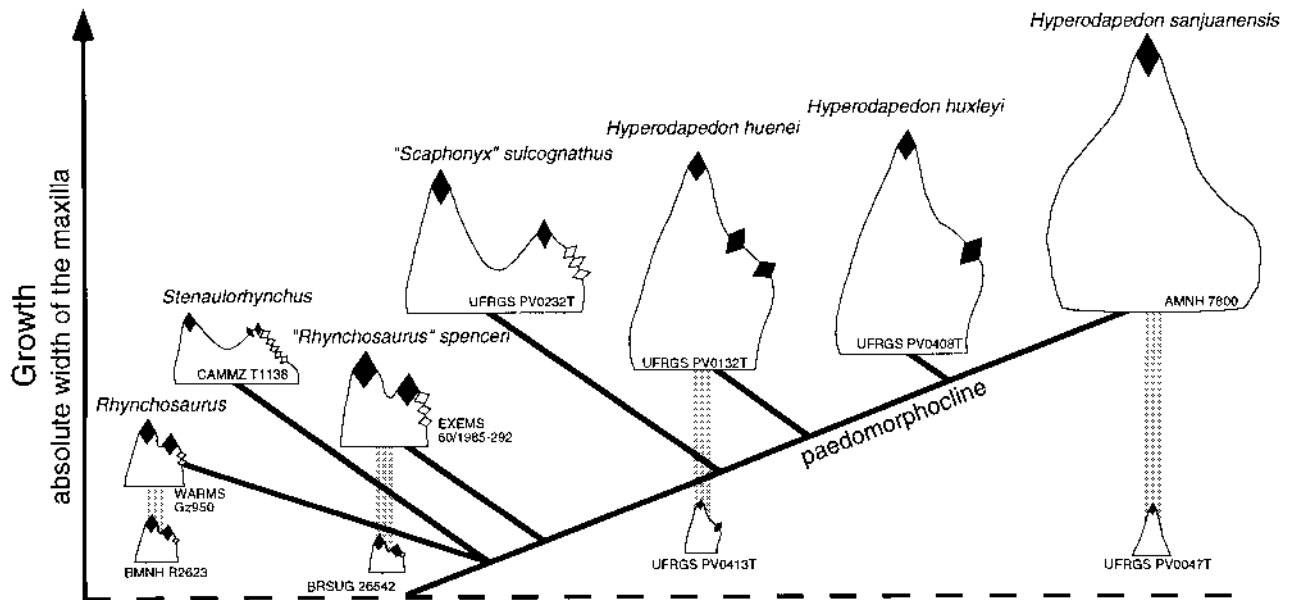
Fig. 7. Phylogenetic relationships and ontogeny of Mid-Late Triassic rhynchosaurs depicting the paedomorphic reduction of the medial dental structures of the dentary of *Hyperodapedon*. Specimens are represented by schematic transverse sections of the dentary (primary lingual teeth in white). Other symbols as in Fig. 3.

tion) compared to 'primitive' forms. This condition is associated by McNamara (1988) with neoteny (= deceleration), which is probably the process responsible for the discussed paedomorphosis (Fig. 6).

In the Middle Triassic *Stenaulorhynchus*, an inverse situation is seen. This rhynchosaur possesses a well-developed medial maxillary groove since early juvenile stages, and both adults and juveniles have more lingual teeth than any other member of the group. The medial part of the maxilla of this taxon is clearly peramorphic (Fig. 5), with its juveniles showing the typical adult features of other rhynchosaurs.

Loss of dental structures (medial crest and lingual teeth) medial to the main dentary crest

Most species of the genus *Hyperodapedon* does not present observable ontogenetic changes in the morphology of the medial area of the dentary. Juveniles of *H. sanjuanensis* (UFRGS PV0047T; see also Fig. 2H), for example, do not have any kind of medial dentition, a condition that is maintained in adults of that species (e.g. IMGPT 19.2, AMNH 7800; see also Fig. 2I). A juvenile possibly related to the primitive form *H. huenei* (Fig. 2J), on the other hand, has a single row of teeth on the medial area of the dentary, while an adult specimen (Fig. 2K) presents a row plus some scattered teeth lateral to it.

Among the rhynchosaurs from the Middle Triassic of England, some ontogenetic trends can also be

traced. Juveniles of *Rhynchosaurus brodiei* (Fig. 2L) present only a main medial tooth row on the dentary along with some scattered lingual teeth. Adults of this taxon (e.g. WARMS G959; see also Fig. 2M), however, usually have two clear medial rows, plus scattered teeth. Juveniles of '*Rhynchosaurus*' *spenceri* (e.g. BRSUC 26542) also have only one tooth row on the medial side of the dentary, while adult individuals present three to four (e.g. BMNH R9190, EXEMS 65/1984-313, 65/1985-292) of those rows.

An ontogenetic trend towards an increase in the number of tooth elements in the medial area of the dentary is, therefore, present in Mid-Late Triassic rhynchosaurs in general. Accordingly, the gradual reduction of these elements seen in the phylogeny of the Hyperodapedontinae (Fig. 1) represents a clear paedomorphocline (Fig. 7). Primitive members of the group, such as '*Scaphonyx*' *sulcognathus*, share with Middle Triassic forms the presence of a toothed medial secondary crest along with lingual teeth. In the genus *Hyperodapedon*, the development of this area of the dentary is truncated, with the medial crest and the primary lingual teeth (Langer & Schultz 2000) failing to appear. *H. sanjuanensis* shows a further reduction in the development of this area, and no teeth at all are present medial to the main cutting crest.

As with the medial area of the maxilla, progenesis is not responsible for the paedomorphic reduction of the medial area of the dentary. In juveniles of *Hyperodapedon*, this area is already more paedomorphic than in juveniles of 'primitive' taxa (Fig. 7), indicating that

Fig. 8. Ontogenies of 'Rhynchosaurus' spenceri, Hyperodapedon huenei and H. sanjuanensis compared (same growth series as Fig. 7), depicting the action of post-displacement in the reduction of the medial dental structures of the dentary of Hyperodapedon. Other symbols as in Fig. 4.
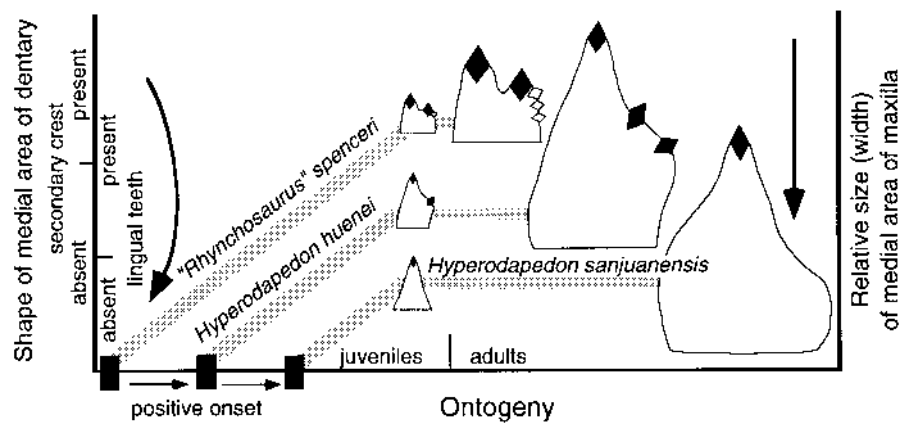
they do not share common early stages of development.

The decision between neoteny and post-displacement is less straightforward. The morphological differences between the medial dentary area of derived and 'primitive' rhynchosaurs is approximately the same if adults or juveniles are taken into account. Neither adults nor juveniles of *Hyperodapedon* possess a secondary medial crest or primary lingual teeth in the dentary, while forms such as *Stenaulorhynchus* and *Rhynchosaurus* possess both traits. The same occurs in *H. sanjuanensis*, in which neither adults nor juveniles possess any tooth element in the medial area of the dentary. In this circumstance, the later stages of development of the medial area of the dentary are supposed to be undisturbed by heterochrony, growing at the same rate in 'primitive' and derived rhynchosaurs. The differences in their final morphology are, thus, attributed to disturbances occurring in the early stages of development of the structure, most probably a late time of onset.

Post-displacement is, therefore, the most probable paedomorphic process involved in the origin of these morphological changes in the dentary (Fig. 8). Moreover, it affects both morphology and size, since it produces a paedomorphic medial dentary area that is relatively narrower in comparison to the primitive condition.

Final considerations

The shift of the main maxillary groove from a more lateral to a more medial position (Fig. 1) during the evolution of the Mid-Late Triassic rhynchosaurs has been well documented (Chatterjee 1980), but poorly explained in terms of the processes that caused it. In this study we have shown how heterochronic processes

could have affected this shift, promoting increases and reductions of complexity in the lateral and medial tooth-bearing areas, respectively. Some modifications, however, remain unexplained, and further clarification is necessary.

1. It is clear that the shift in the main maxillary groove of Late Triassic rhynchosaurs was not produced by an enlargement of the lateral tooth-bearing area, or a reduction of the medial area, alone. Both modifications had to take place together for this shift to occur. Medial structures of the maxilla, such as the medial groove and the lingual teeth, would not have been lost during hyperodapedontine evolution if just an enlargement of the lateral area had occurred. On the other hand, the increase in the number of lateral tooth rows makes it clear that an enlargement has indeed taken place in this maxillary area, creating space for these teeth to appear. Moreover, neither a reduction nor an increase in the relative width of the maxilla is seen in the evolution of the Late Triassic rhynchosaurs, indicating that the enlargement of the lateral area and the reduction of the medial counterbalanced each other.

2. Benton (1984, 1990) showed that the grooves of the rhynchosaur maxilla are an intrinsic feature of this bone, and not caused by wear during occlusion with the dentary. However, its origin may also be related to a stimulus from the dentary during embryological time. Under such an epigenetic approach, a shift in the occlusal position could produce a shift in the location of the maxillary groove. That occlusal shift could arise from the paedomorphic reduction of the medial area of the dentary or even from structural modifications related to the hypermorphic positive allometry of the temporal region of the skull of hyperodapedontines (Benton & Kirkpatrick 1989). In this case, the medial shift of the maxillary groove would be simply an apomorphy, and not directly related to heterochronic processes.

This phenomenon could explain the enlargement of the lateral area and reduction of the medial area of the maxilla, and even the loss of the medial secondary groove, which tends to disappear along with the medial crest of the dentary. It fails, however, to explain key changes in the dental evolution of the Late Triassic rhynchosaurs, such as the appearance of additional lateral tooth rows in the maxilla, the loss of maxillary lingual teeth, as well as all the modifications in the dentary.

Heterochrony can explain those changes with a peramorphic increase in the number of lateral maxillary rows and a paedomorphic loss of structures in the medial area of maxilla and dentary. It is a current belief (Alberch *et al.* 1979; Klingenberg 1998) that combinations of heterochronic processes occur commonly in nature, acting in the morphological differentiation that leads to the evolution of a group. McNamara (1997) explained this phenomenon in terms of developmental trade-offs, showing its occurrence in several vertebrate groups such as theropod dinosaurs, horses and ratite birds. The same seems to occur in Late Triassic rhynchosaur evolution, in which heterochrony plays an important role, since the peramorphic and paedomorphic changes of tooth arrangement are the main morphological modifications observed in the group.

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