

INTERPTERIGOID VACUITIES IN THE PRIMARY PALATE OF CYNODONTS (THERAPSIDA): HETEROCHRONY AND EVOLUTIONARY SIGNIFICANCE

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“Theory may suggest and predict, but the test must rest upon relative frequencies established by observation.” Stephen J. Gould (1988)

INTRODUCTION

Perhaps, studies on heterochrony are one of the most increasing issue that developed intensely in the last four decades for understanding macroevolutionary mechanisms. Since the revolutionary book titled “*Ontogeny and Phylogeny*” by S. J. Gould (1977), the heterochrony has been intensely explored and the significance of this mechanism in the evolutionary trend of several lineages has been highlighted. **Heterochrony** means evolution via changes in timing and/or rate of developmental events, relative to the same events in the ancestor (e.g., Gould, 1977; Alberch et al., 1979; McNamara, 1982). The modification of developmental timings that alter phenotypes should be tested comparing related forms upon variables such as time, size, and shape (e.g., Alberch et al., 1979; McKinney, 1988). Usually, heterochrony is associated to isolated processes; nonetheless, it is a global phenomena which affect the organisms as a whole (Gould, 1988). Heterochrony include two major processes (Fig. 1): **Paedomorphosis** (i.e., descendant adult morphology resembles juvenile ancestors) that can be achieved by **neoteny** (reduction in rate of morphological development), **progenesis** (earlier offset), or **post-displacement** (delayed onset of growth of particular organs); and **Peramorphosis** (i.e., ancestral adult morphology present in juvenile phase of descendant) that is caused by **acceleration** (increased rate of morphological development), **hypermorphosis** (delayed offset), or **pre-displacement** (earlier onset of growth of particular structures) (Fig. 1; e.g., Gould, 1977; Alberch et al., 1979; McNamara, 1982, 1986).

The cynodonts (Cynodontia) are a monophyletic group of synapsids that include several extinct basal taxa, classically known as non-mammaliaform cynodonts (thereafter

called cynodonts), and the mammals (Mammalia) as the crown group (Rowe, 1988; Hopson, 1991; Hopson and Kitching, 2001). Cynodonts flourished during all the Triassic Period with species occupying varied ecological niches (Hopson, 1991). The fossil record of this lineage has provide exquisite data for macroevolutionary examples in the reptilian-mammalian transition, for example as evidenced the gradual change of the postdentary bones of the lower jaw typical of reptiles to the ossicles of the middle ear of mammals (e.g., Allin & Hopson, 1992).

In this preliminary contribution, I explore the evolutionary meaning of the interpterigoid vacuities, located in the primary palate of the skull, in the lineage of probainognathian cynodonts leading to mammals. The interpterigoid vacuities played a significant role for the establishment of the mammalian skull pattern (Martinelli & Rougier, 2007). The extensive fossil record of the probainognathian lineage (see fig. 2) and the presence of ontogenetic sequences in some fossil taxa permitted the analysis for detecting heterochronic mechanisms in advanced non-mammalian cynodonts and their bearing for the establishment of derived cranial features in basal mammaliaforms. The results presented here are preliminary, pending further studies and a wide analysis of samples. For this study, I follow the phylogenetic hypothesis hold in Martinelli & Rougier (2007).

INTERPTERYGOID VACUITIES IN CYNODONTIA

Morphology

Within cynodonts, the skull suffered several modifications through time. These modifications modeled the typical reptilian pattern through several features that characterized mammals, such as the re-organization of the suspensory apparatus and middle ear, the tooth morphology and replacement, the constitution of the enlarged secondary palate, the modification of the basicranial structure together with the brain growth, among other traits (e.g., Wible, 1991; Luo, 1994).

Among the skull changes, the presence of interpterygoid vacuities in adult specimens of advanced cynodonts (such as *Brasilodon*, *Brasilitherium*, and ictidosaur; see Fig. 2) is significant *per se*. The interpterygoid vacuities are always constituted by the same bones (see *Procynosuchus* in Fig. 2), regardless of the ontogenetic stage. The vacuities are flanked mostly by the pterygoids with a contribution of the parasphenoid-basisphenoid complex in the posterior edge. A median projection of the parasphenoid-basisphenoid complex, the cultriform process, incompletely divides the space in two lateral vacuities. Dorsal to the

cultriform process, the vacuities are expansive and fully connected to each other, to the caudal regions of the nasal cavity and the open orbitotemporal space rostral to the epipterygoid (e.g., Fourie, 1974). A more complete division into right and left realms of the space was probably effected by soft tissue. The size and position of the vacuities with respect to the transverse flange of the pterygoids, and the system of ridges and troughs in the posterior portion of the primary palate, vary slightly among cynodonts. Some minor differences could be artificial because in many cases the vacuities are only partially known and the reconstruction of this portion of the skull is therefore tentative.

Interpterygoid vacuity among cynodonts

Interpterygoid vacuities appear in the Late Permian *Dvinia* (Tatarinov, 1968) and *Procynosuchus* (Kemp, 1979; Fig. 2), therefore the presence of these structures in basalmost non-eucynodont cynodonts (see Fig. 2) is considered symplesiomorphic for the group (Hopson & Bargushen, 1986; Hopson & Kitching, 2001).

In galesaurids (e.g., Sidor & Smith, 2004), *Thrinaxodon* (e.g., Fourie, 1974; Fig. 2), non-tritylodontid gomphodonts (e.g., Crompton & Ellenberger, 1957; Bonaparte, 1962; Hopson & Barghusen, 1986; Abdala et al., 2002), and basal probainognathians (e.g., Romer, 1970; Martínez et al., 1996; Abdala & Giannini, 2002), the vacuities are absent and the posterior portion of the pterygoids contacts each other in the sagittal plane, together with the ventral extension of the cultriform process of the parasphenoid, to constitute a narrow and sharp antero-posteriorly oriented ridge (marked in Fig. 2 with an arrow). Among members of these lineages, open vacuities only often occur in juvenile specimens. This is the case for ‘*Nanictosaurus*’ (Van Heerden, 1976), *Thrinaxodon* (Estes, 1961), *Probelesodon* (Bonaparte, 1980), and possibly *Lumkuia* (Hopson & Kitching, 2001).

In Tritylodontidae, the interpterygoid vacuities are usually absent in adult specimens (Kühne, 1956; Clark & Hopson, 1985; Sues, 1986), but present in juvenile specimens (e.g., *Kayentatherium*; Sues, 1986) and randomly in some adult specimens (e.g., *Yunnanodon* and *Dianzhongia*).

Interpterygoid vacuities have also been reported in both immature and mature individuals of *Brasilodon* and *Brasilitherium* (Bonaparte et al., 2005; Fig. 2), and in all ictidosaurids (at least those whose primary palate is known; Fig. 2) (Crompton, 1958; Bonaparte, 1980; Hopson & Kitching, 2001; Bonaparte et al., 2001; Sidor & Hancox, 2006).

In basal mammaliaforms, the interpterygoid vacuities are absent, and the floor of the skull posterior to the choana is relatively broader than in cynodonts (e.g., Kermack et al., 1981; Fig. 2).

Heterochrony

Based on the phylogenetic hypothesis obtained (Martinelli & Rougier, 2007), the interpterygoid vacuities occur in two separate groups, being lost in adult specimens of eucynodontians including cynognathians and basal probainognathians (such as *Lumkuia*, *Ecteninion*, *Chiniquodon*, and *Probainognathus*).

The re-acquisition of interpterygoid vacuities in derived non-mammaliaform cynodonts, which have high resemblance with the pattern present in basal-most forms and immature individuals of more derived forms, could be the result of heterochronic processes (Gould, 1977; Alberch et al., 1979). The fact that the descendant adult morphology resembles that of the juvenile ancestor suggests that the re-appearance of vacuities in these derived non-mammaliaform cynodonts could be explained by paedomorphosis. This feature possibly has been achieved in advanced non-mammaliaform cynodonts either by a neotenic slowing down of growth rate or by a progenetic earlier onset of maturity, truncating the growth period.

Studies of the bone microstructure in advanced non-mammaliaform cynodonts have revealed a relatively rapid growth rate during early ontogeny and then a slower rate in later stages, suggesting that the overall body growth was slowing down (Chinsamy & Hurum, 2006). These data support both mechanisms (neoteny or progenesis) for interpreting the re-acquisition of interpterygoid vacuities in advanced non-mammaliaform cynodonts.

Evolutionary significance

The presence of interpterygoid vacuities in basal-most and derived cynodonts results in transversely wide pterygoids, and consequently a broad floor of the mesocranial portion of the skull (mesocranium) similar to that of basal mammaliaforms (e.g., *Morganucodon* and *Sinoconodon*, Kermack et al., 1981; Crompton & Luo, 1993; Fig. 2), although mammaliaforms lack interpterygoid vacuities.

The interpterygoid vacuities and the mesocranium are in fact a crossroads of two developmental territories. The vomer, ectopterygoid, pterygoid, and palatine form from tectoseptal mesoderm of the maxillary process, whereas the parasphenoid from prechordal mesoderm (De Beer, 1937; Parrington & Westoll, 1940; Presley & Steel, 1978). A developmental way to explain the presence of the vacuity is that this area is a growth zone

where the intramembranous pterygoid finalizes its ossification relatively late in development, allowing for an easy way to increase skull length and width. This idea accords with allometric studies in gomphodont cynodonts which show that the posterior portion of the skull grows at a different rate than the rostrum (e.g., Abdala & Giannini, 2000).

In advanced non-mammaliaform cynodonts, the simultaneous reduction of postdentary bones (part of them to be included ultimately in the cranial middle ear; e.g., Allin, 1986) and the backward enlargement of the secondary palate are related to the reduction and reorganization of the reptilian pterygoideus musculature (Parrington & Westoll, 1940; Presley & Steel, 1978) as well as the posterior movement of the nasopharyngeus and oropharyngeus systems (because of the reduction of the posterior floor of the primary plate). From this point of view, wide pterygoids (with the re-appearance of interpterygoid vacuities) in ictidosaur, *Brasilodon*, and *Brasilitherium* are related to the modification of the secondary palate and the extreme reduction of postdentary bones. Moreover, in these species the posterior enlargement of the dentary is notable, possibly reaching the squamosal (Crompton, 1963; Luo, 1994; Bonaparte et al., 2003, 2005). Therefore, the presence of interpterygoid vacuities represents an ancestral condition that facilitated the development of the mammalian basis cranii constituted by the reduced pterygoids, the basisphenoid, and posteriorly, the development of the presphenoid by the ventral extension of the braincase (e.g., Parrington & Westoll, 1940; Moore, 1981; Novacek, 1993). Possibly, the main factors in the remodelling of this area are the forward and ventral expansion of the cranial cavity and the subsequent development of the sphenoid sinus. This is a major transformation of the skull architecture of the mesocranial region.

FINAL REMARKS

This short contribution deal with the significance of interptergoid vacuities in cynodonts and its possible re-adquisition in derived forms due to heterochronic processes. These processes possible affected the cynodont skull shape and deep studies on this matter will open new windows for interpreting the mechanisms that occurred in the cynodont-mammalian transitions.

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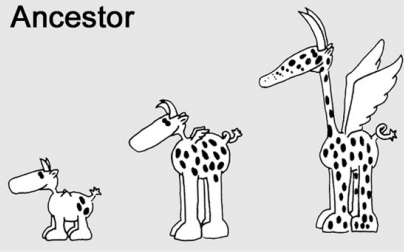
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FIGURE CAPTIONS

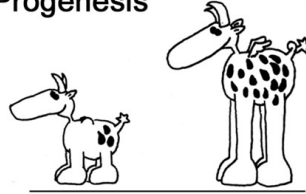
Figure 1. Heterochronic mechanisms: Paedomorphosis (i.e., descendant adult morphology resembles juvenile ancestors) can be achieved by neoteny (reduction in rate of morphological development), progenesis (earlier offset), or post-displacement (delayed onset of growth of particular organs); and Peramorphosis (i.e., ancestral adult morphology present in juvenile phase of descendant) is caused by acceleration (increased rate of morphological development), hypermorphosis (delayed offset), or pre-displacement (earlier onset of growth of particular structures). Modified from McNamara (1986, 1997).

Figure 2. Most parsimonious tree of eucynodont relationships obtained by Martinelli & Rougier (2007) illustrating the condition of the posterior primary palate and pterygoid vacuities in a few cynodonts. The arrow indicates the condition in which posterior portion of the pterygoids constitute a narrow and sharp antero-posteriorly oriented ridge. Gray areas indicate the cavum epiptericum. Not to scale. Anatomical Abbreviations—bs, basisphenoid; e, ectopterygoid; ep, epipterygoid; iv, interpterygoid vacuity; j, jugal; m, maxilla; mf, mental foramen; pa, palatine; pt, pterygoid; v, vomer.

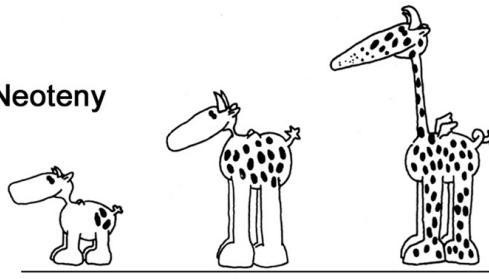
Ancestor



Progenesis

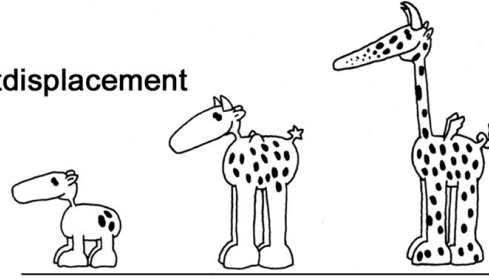


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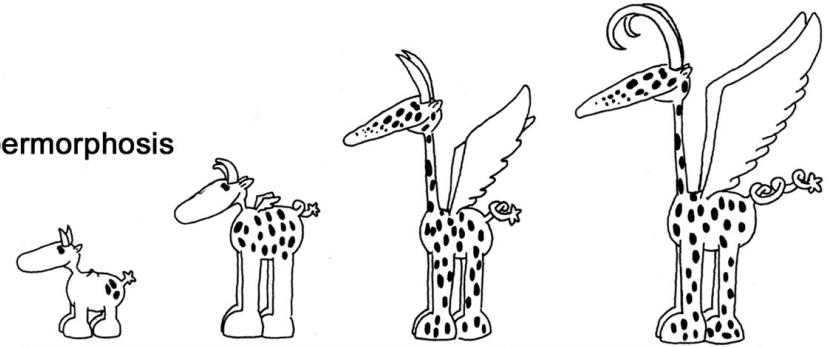
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Postdisplacement

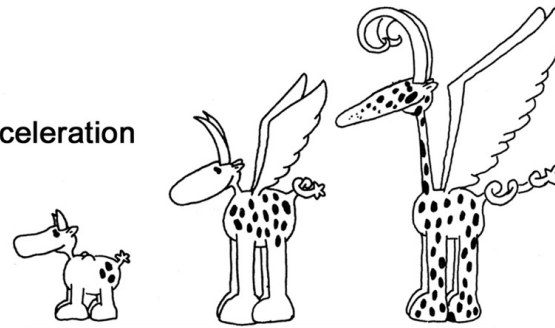


HETEROCHRONY

Hypermorphosis

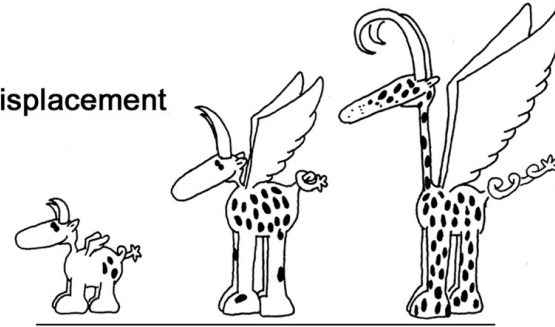


Acceleration



Peramorphosis

Predisplacement



Tree Length: 170
 Consistency Index (Ci): 0.68
 Retention Index (Ri): 0.77

