Early development of the mammalian superficial masseter muscle in cynodonts

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The masseter muscle is a hallmark of the jaw-closing mechanism of modern mammals, acting in concert with other mandibular adductor muscles to fine-tune oral food processing. The model explaining the origin of this muscle within non-mammalian therapsids involves the differentiation of a masseter-like muscle from a primitive external adductor, a downward migration of the masseter insertion on the mandible, and a division and distribution of the muscle to a condition that is similar to that in living mammals. The presence of a suborbital process of the jugal, which is interpreted as the site of origin for the superficial masseter, has been previously regarded as the earliest putative morphological evidence used to infer masseteric division. The suborbital process is first recorded in late Early Triassic (*c.* 245 Ma) cynognathian cynodonts. Here it is shown that primitive galesaurid cynodonts of earliest Triassic age (*c.* 251 Ma) display a distinct angulation of the zygomatic arch below the orbit, indicating the presence of a divided masseter amongst more basal cynodonts. This alters the timing of masseter muscle evolution by showing that the downward migration and division of the masseter occurred simultaneously, prior to the evolution of advanced cynodonts (=eucynodonts).

Keywords: masseter muscle, occlusion, Galesauridae, angular process.

INTRODUCTION

A suite of features present in late therapsids ('mammal-like reptiles'), especially non-mammaliaform cynodonts, is recognized as being unequivocally related to the acquisition of a feeding system typical of mammals. An outstanding feature of this system is the crown-to-crown postcanine occlusion (Crompton 1995) that results in the extensive mechanical reduction of food in the oral cavity (Hiiemae & Crompton 1985; Smith 1993). The most important modifications towards the mammalian system of feeding documented in late therapsids can be broadly summarized as follows: (1) a marked differentiation of the marginal teeth into incisors, canines and postcanines, with the acquisition of a more complex crown pattern in the latter; (2) the expansion of the temporal opening of the skull; (3) the enlargement of the dentary bone of the mandible with a concomitant elaboration of the angular, coronoid and articular processes of that bone, intimately associated with which is (4) the notable reduction of the postdentary bones and the quadrate/quadratojugal complex, resulting ultimately in the establishment of the craniostylic mandibular joint typical of mammals (Kemp 1982; Crompton 1995). The changes outlined in (2) through (4) are correlated with the development of the jaw adductor musculature, including the temporal and masseter muscles, and (4) is also linked with the elaboration of the auditory system (Allin 1975; Allin & Hopson 1992; Luo & Crompton 1994).

Adams (1919) carried out a detailed study on the jaw muscles in vertebrates. He interpreted the arrangement of the jaw-closing muscles in the cynodont *Cynognathus* as close to the mammalian pattern, with a large temporalis filling the temporal opening and a masseter originating from the zygomatic arch. Watson (1948) and Parrington (1955) proposed that a similar, mammal-like arrangement of the occlusal musculature was already present in basal synapsids such as *Dimetrodon,* a hypothesis supported by Crompton (1963). However, in a landmark study, Barghusen (1968) demonstrated that in *Dimetrodon* and basal therapsids the jaw-closing musculature filling the temporal fossa consisted of an adductor mandibulae externus, as in living reptiles. According to the widely accepted model for the origin and development of the masseter muscle proposed by Barghusen (1968), the earliest evidence indicating a superficial masseter muscle separated from the adductor mandibulae externus is the suborbital process of the jugal. This structure constitutes the origin for the superficial masseter and is present in advanced cynodonts such as *Trirachodon, Diademodon* and *Cynognathus* (Barghusen 1968).

In this paper we present new morphological evidence from basal galesaurid cynodonts which shifts our knowledge of the timing of origin of the superficial masseter muscle to earlier in the history of cynodonts, prior to the divergence of Cynognathia and Probainognathia, the major subclades of advanced cynodonts (=eucynodonts). We also discuss the possible homology of the pseudangular process of non-mammaliaform cynodonts and early mammaliaforms with the angular process of mammals.

Institutional abbreviations: AMNH, American Museum of Natural History, New York; BP, Bernard Price Institute for Palaeontological Research, Johannesburg; NMQR, National Museum, Bloemfontein; RC, Rubidge Collection, Wellwood, Eastern Cape Province, South Africa; SAM, Iziko Museums (South African Museum), Cape Town; TM, Transvaal Museum, Pretoria.

MATERIAL

The following galesaurid specimens were examined for this study: AMNH 2223 (described as *Glochinodontoides gracilis* by Boonstra 1935) and 2227; BP/1/4602 and 5064; NMQR 860 (described as *Platycraniellus elegans* by Brink 1954b), 1451 (referred to *Glochinodontoides gracilis* by Brink

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1954a) and 3340; RC 845; SAM PK-K-1119, K-9954 (holotype of *Progalesaurus lootsbergensis* Sidor & Smith 2004) and K-9956.

EVOLUTION OF THE TEMPORAL FENESTRA, MASSETER MUSCULATURE, AND LOWER JAW IN CYNODONTS

Temporal fenestra

The reduction of the skull roof in the temporal region in late therapsids resulted in the development of a mammal-like temporal opening, first established in the Therocephalia-Cynodontia clade (Eutheriodontia), and subsequently expanded in non-mammaliaform cynodonts (Barghusen 1972). In basal cynodonts, such as the Late Permian *Procynosuchus* and *Dvinia,* widening of the temporal opening is achieved by an outward flaring of the zygomatic arch in the middle of the temporal region (Broom 1938, 1948; Tatarinov 1968). This basic temporal morphology appears to be highly conservative in the more advanced Probainognathia (e.g. *Lumkuia* and *Chiniquodon*), the group that ultimately gave rise to mammals. Departures from this basic pattern include the slightly smaller temporal opening present in the small-sized Early Triassic genera *Thrinaxodon* and *Galesaurus,* and the extensive flaring of the jugal along the entire temporal opening in the Middle Triassic *Probainognathus* (Crompton & Hylander 1986). On the other hand, members of the Cynognathia, the sister group of the Probainognathia, display a large temporal opening with the zygomatic arches diverging backward instead of flaring outward in the middle of the temporal region (Hopson 1991). In summary, the expansion of the temporal openings in a mammal-like fashion appeared in the latest Permian – minimally, 251 million years ago – and remained virtually unchanged in later probainognathians, basal Mammaliaformes (i.e. morganucodontids and other extinct taxa that are closely related to mammals; Luo *et al.* 2001), and even many extant mammals (for example *Didelphis*; Hiiemae & Jenkins 1969).

Masseter musculature

Masseter muscles derive from the reptilian mandibulae externus muscle (Barghusen 1968, see below) and are usually sub-divided in superficial and deep parts in extant mammals, although a more complex pattern can also be recognized (see Hiiemae & Jenkins 1969: 4). The superficial masseter generally extends along the ventral margin of the anterior portion of the zygomatic arch and, in some cases (e.g. *Ovis, Equus*), continue in front of the arch, attaching on the rostrum. The deep masseter has its origin along the entire ventral edge, or ventral and lateral facet (e.g. *Didelphis*; Turnbull 1970) of the lower edge of the zygomatic arch. Both muscles insert along the ventral border of the masseteric fossa, with the superficial attachment generally more ventrally and/or posteriorly located (Turnbull 1970).

The presence of well-developed sagittal and occipital crests in the large temporal opening of therocephalians and cynodonts indicate that the adductor mandibulae

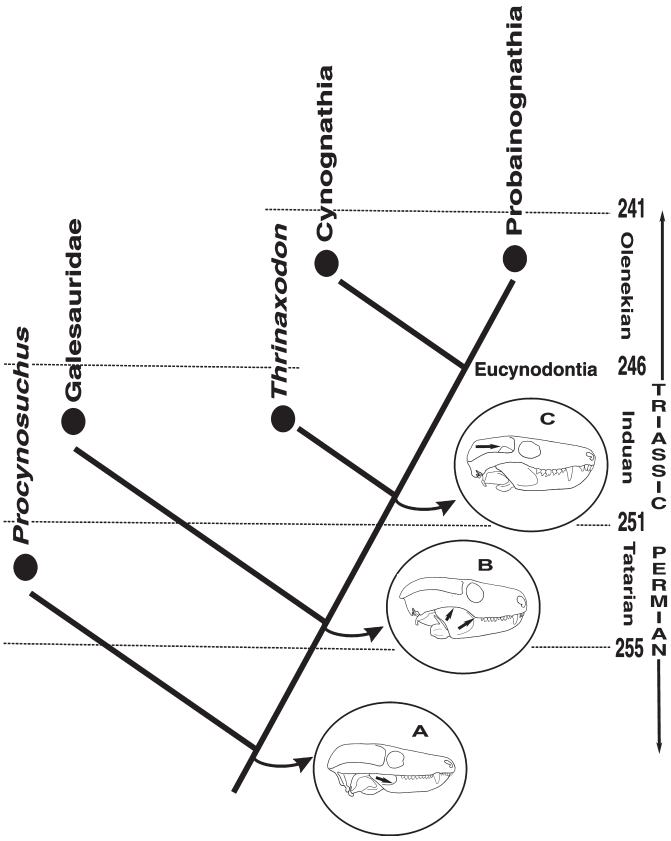

Figure 1. Phylogenetic relationships and morphological changes in the temporal region of the skull in basal cynodonts. Inset circles depict key morphological changes in the temporal region. **A**, In *Procynosuchus,* the zygomatic arch is straight and the masseteric fossa high on the dentary; **B**, in galesaurid cynodonts, the zygomatic arch shows an upward flexure and the development of a suborbital angulation; the masseteric fossa extends to the base of the dentary; **C**, In *Thrinaxodon,* the coronoid process of the mandible is significantly taller. Phylogeny follows Hopson & Kitching (2001); the clade Probainognathia includes mammals. *Procynosuchus* and *Thrinaxodon* modified from Hopson (1994).

externus muscle originated from a temporal aponeurosis attached to the aforementioned crests (Barghusen 1968). In the Late Permian *Procynosuchus,* a lateral fossa is present high on the coronoid process of the dentary (Crompton 1963; Figs 1 & 2). The presence of this fossa on the mandible indicates a division of the adductor mandibulae externus muscle, and it was interpreted as an initial stage in the differentiation of the masseter, which originated on the temporal aponeurosis (Barghusen 1968). In lateral view, the zygomatic arch of *Procynosuchus* is oriented horizontally, whereas in the earliest Triassic (i.e. Induan) *Galesaurus* and *Thrinaxodon,* it displays an upward flexure (Figs 1, 2 & 3). Concomitant with this flexure in the zygoma is a notable increase in the size of the dentary, with a larger coronoid process, an extension of the lateral fossa (= masseteric fossa) to the base of the dentary, and the beginning of the development of the angular process. As a result of these changes, the masseter muscle extended its insertion, reaching the angle region in *Galesaurus* and *Thrinaxodon,* while its origin was located along the internal surface of the zygomatic arch (Barghusen 1968, 1972; DeMar & Barghusen 1972; Bramble 1978).

In the Middle Triassic chiniquodontid probainognathians, there is a characteristic angulation below the orbit,

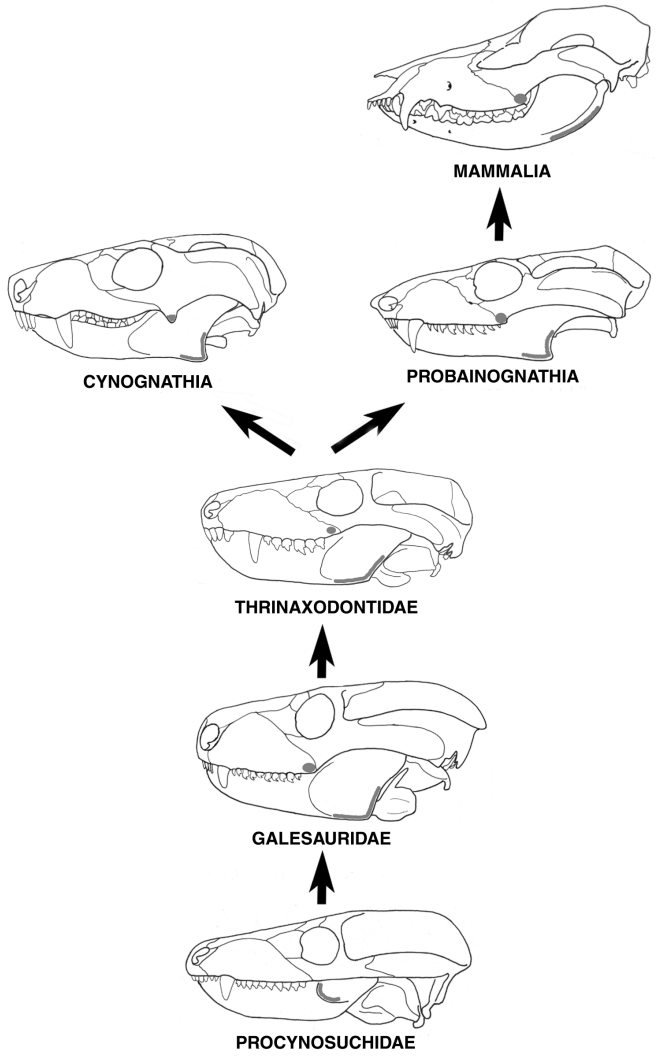

Figure 2. Evolution of the superficial masseter muscle in non-mammaliaform cynodonts and mammals. The origin and insertion points of the superficial masseter in the Galesauridae, *Thrinaxodon, Trirachodon* (representing the condition in Cynognathia), *Chiniquodon* (sensu Abdala & Giannini 2002; representing the condition in Probainognathia), and the extant mammal *Didelphis,* are depicted. In *Procynosuchus* the entire masseter, in its initial phase of differentiation, was inserted on the lateral fossa of the dentary. *Procynosuchus* modified from Hopson (1991), *Trirachodon* modified from Hopson & Barghusen (1986), and *Chiniquodon* modified from Romer (1969).

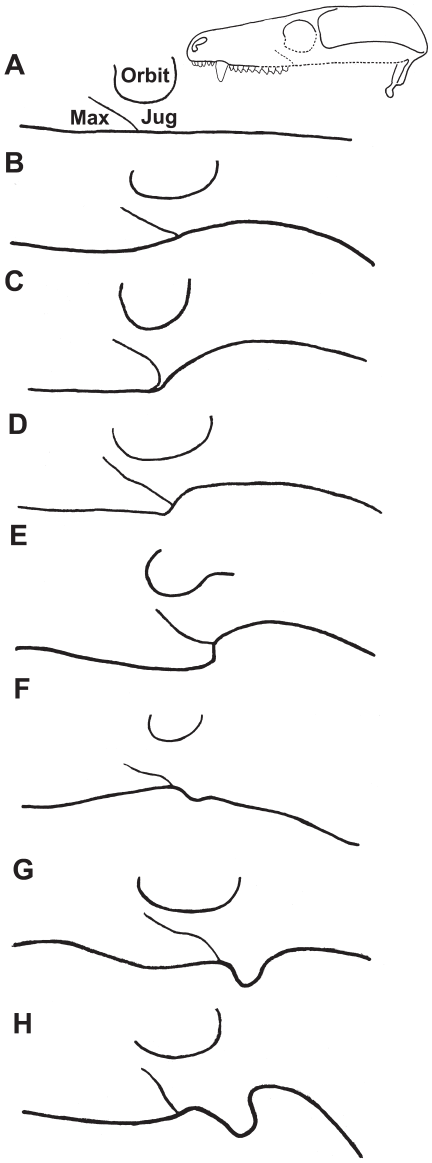

Figure 3. Lateral view of the suborbital region in different cynodonts. **A**, *Procynosuchus*; **B**, *Thrinaxodon*; **C**, Galesauridae; **D**, *Chiniquodon*; **E**, *Didelphis*; **F**, *Cynognathus*; **G**, *Trirachodon*; **H**, *Diademodon.* C, D, and E show the suborbital angulation; F, G and H show the suborbital process of the jugal. Abbreviations: Jug, jugal; Ma**x**, maxilla. Outline of *Procynosuchus* skull based on Hopson (1994).

hereafter termed the suborbital angulation. This feature is located at the junction between the anteroventral margin of the jugal and the zygomatic process of the maxilla (Hopson & Barghusen 1986; Hopson 1991; Hopson & Kitching 2001: character 41; Abdala & Giannini 2002; Figs 2 & 3), and seems a by-product of a higher upward flexure of the jugal (but see Hopson & Kitching 2001: fig. 2). A similar suborbital angulation is recognized in didelphid marsupials, and is manifested as a boss at the junction of the maxilla and the jugal on the anteroventral edge of the zygomatic arch (Hiiemae & Jenkins 1969; Figs 2 & 3). In both of these groups, the angulation is in a roughly similar position to the suborbital process of the jugal, a structure typical of late Early/early Middle Triassic cynognathian cynodonts (e.g. *Trirachodon, Cynognathus, Diademodon*). The suborbital process of the jugal in cynognathian cynodonts has been regarded as the earliest evidence of an independent origin for the superficial masseter muscle, according to the accepted model of evolution of the adductor musculature in therapsids (Barghusen 1968, 1972; DeMar & Barghusen 1972; Bramble 1978; Figs 2 & 3). However, a suborbital angulation identical to that of chiniquodontid cynodonts and didelphid marsupials is also present in large-sized galesaurid cynodonts of earliest Triassic age (Abdala 2003; Table 1, Figs 2 & 3). This evidence indicates that the differentiation of the superficial masseter muscle occurred first in members of the Galesauridae, some five million years earlier than currently recognized and prior to the evolution of advanced cynodonts (i.e. eucynodonts; Hopson & Kitching 2001; Figs 1 & 2). The differentiation of the superficial masseter in cynodonts thus occurred simultaneously with the downward expansion of the masseter insertion to the angular region of the lower jaw. Previously, these processes were considered to represent consecutive stages in the evolution of the mammalian

Table 1. Skull lengths in various galesaurid specimens, showing a correlation between larger skull size and the presence of a suborbital angulation.

Specimen	Skull length (mm)	Suborbital angulation
RC 845	69	Absent
SAM PK-K-1119	72	Absent
SAM PK-K-9956	73	Absent
AMNH 2227	79	Absent
BP/1/4602	82	Absent
NM QR1451	90	Present/Absent*
SAM PK-K-9954	92	Present
AMNH 2223	100	Present
NM QR3340	101	Present
BP/1/5064	103	Present
NM QR860	114	Present

*Angulation presents on the left zygoma but absent in the right.

occlusal complex (Barghusen 1968, 1972; Bramble 1978).

Intriguingly, the development of the suborbital angulation appears to be linked with the size of the animal. For instance, the suborbital angulation is absent in the small-sized cynodonts *Thrinaxodon* and *Probainognathus* with skull lengths up to approximately 80 mm, and in small individuals of the Galesauridae. An exception to this is the presence of the suborbital angulation in the small *Platycraniellus elegans* (TM 25; basal skull length 84 mm), which may be due to the remarkable development of the temporal opening in both longitudinal and transverse directions. In fact, this species exhibits the most widened temporal region amongst non-mammaliaform cynodonts (approximately 88% with respect to the basal skull length). In contrast, the suborbital angulation is present in large individuals of the Galesauridae with skull lengths above 90 mm (Table 1, Fig. 4), and in chiniquodontids with skull lengths up to 310 mm (Abdala & Giannini 2002). Evidence from ontogeny also supports a correlation between size and the suborbital angulation/suborbital process of the jugal. Tiny juveniles of *Trirachodon berryi* (BP/1/4534 and 4535) lack a suborbital process, whereas this process is well developed in adults. A similar ontogenetic trend is observed in the extant marsupial *Didelphis albiventris,* in which the maxillary boss, the homologue of the suborbital angulation in non-mammaliaform cynodonts, is absent in juveniles of *c.* 3.5 months (Abdala *et al.* 2001).

As a corollary of the evidence discussed above, we support the hypothesis of the presence of a differentiated superficial masseter in all epicynodonts (a monophyletic group including the common ancestor of Galesauridae and mammals, and all its descendants; Hopson & Kitching 2001). This hypothesis is favoured by the widely distributed suborbital process/angulation in non-mammaliaform cynodonts (Fig. 3), indicating that the superficial masseter remained differentiated in both Cynognathia and Probainognathia. Consequently, *Thrinaxodon,* which is phylogenetically placed between galesaurids and eucynodonts (Fig. 1), also possessed a differentiated superficial masseter. This hypothesis was advanced in muscular reconstructions of *Thrinaxodon* by Allin & Hopson (1992: figure 28.10C) and Crompton (1995: figure 4.4), although they did not provide supportive

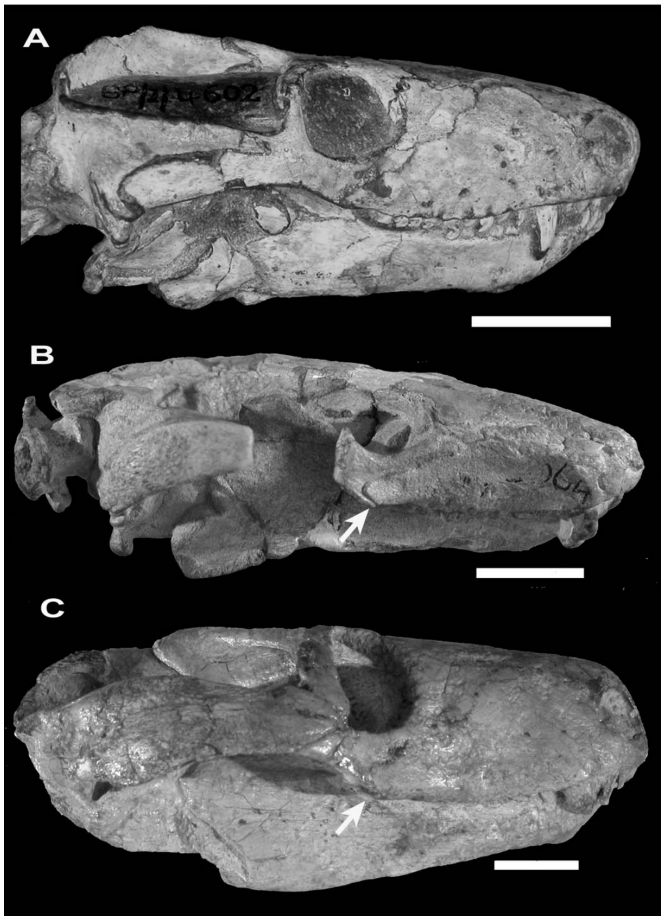

Figure 4. Lateral view of the skull of three specimens of Galesauridae. **A**, BP/1/4602 (skull length, 82 mm); **B**, BP/1/5064 (skull length 103 mm); **C**, NM QR860 (skull length 114 mm). Arrows in B and C indicate the suborbital angulation. Scale bars = 2 cm.

evidence to depart from the model proposed by Barghusen (1968).

Many innovations associated with the feeding system in late non-mammaliaform cynodonts and early mammaliaformes are interpreted as safety devices that allow the postdentary bones and the quadrate to reduce in size while maintaining a viable, but weak, craniomandibular joint (CMJ). Modifications in the lower-jaw are related to increasing complexity of the external adductor musculature in the temporal fossa, which reduced mechanical stress exerted on the CMJ of non-mammaliaform cynodonts (Bramble 1978; Crompton & Hylander 1986). In this context, the anteriorly oriented fibres of the superficial masseter may have reduced compressive loading on the CMJ produced by the temporalis and deep masseter fibers (see Crompton & Hylander 1986: figs 5–9). The superficial masseter in non-mamaliaform cynodonts and early mammaliaformes seems to be shorter and dorsoventrally more obliquely orientated than in generalized mammals with relatively unspecialized masticatory apparatus such as *Didelphis* (Turnbull 1970), as a result of the anterior location of the angle of the dentary (see Fig. 2). The orientation and short fibres of the superficial masseter are also probably related to decreasing the stress on the weak CMJ by preventing exposure to anteroposteriorly directed tensile forces that could displace the joint. This sort of arrangement in the

superficial masseter evidently restricted the muscle capacity in relation to mandibular protraction.

Lower jaw

Modifications to the temporal region of the skull in relation to the evolution of adductor musculature were initiated in the Late Permian therocephalians and basal cynodonts, leading to a basic mammal-like temporal design in the Early Triassic galesaurids. With the expansion of the temporal opening in basal cynodonts, the incipient coronoid process of the lower jaw was repositioned in the middle of that opening, increasing the space for adductor (i.e. masseter) musculature between the zygomatic arch and the lateral surface of the lower jaw (Barghusen 1968). Besides a repositioning of the coronoid process, modifications of the lower jaw towards the mammalian condition seem to have been somewhat delayed with respect to the skull transformations. Galesaurids share with *Thrinaxodon* a similar degree of development of the angle of the dentary. However, only *Thrinaxodon* shows the more mammal-like condition of a higher coronoid process and a slight reduction in the size of the postdentary bones and of the reflected lamina of the angular (Hopson & Kitching 2001; Figs 1 & 2). The morphology of the lower jaw attained in the Early Triassic *Thrinaxodon* was the basic pattern from which further modifications to the mandible were derived. These include an increase in the height of the coronoid process, an elaboration of the angular process, and a further reduction of the postdentary bones. The development of this 'derived' plan of the lower jaw has generally been interpreted as acquired independently in the Cynognathia and Probainognathia (Allin & Hopson 1992; Hopson & Kitching 2001).

MASSETERIC INSERTION AND ANGULAR PROCESS OF THE DENTARY

In our interpretation of the non-mammaliaform cynodont angle, and the angular process as a site of insertion of the superficial masseter, we concur with Luo *et al.* (2002: character 8) in recognizing them as homologous with the angular process of mammals. We would like to address here some aspects of the debate about the homology of the angle (pseudangular process of Patterson 1956) of therapsids and basal mammaliaforms (e.g. *Morganucodon, Sinoconodon*), and the angular process of late mammals. The initial proposal that a pseudangular process existed in late cynodonts and early mammaliaforms (Patterson 1956; see also Patterson & Olson 1961) was based on the comparatively long distance separating the angle from the CMJ in these groups. In contrast, Patterson & Olson (1961) indicated that the true angular process in therian mammals was at the same level as the CMJ. The functional correlate to this hypothesis was the suggestion that the pseudangular process was the insertion site for the mandibular depressor, based on the presence of a similar process in the lower jaw of the monotreme *Tachyglossus* (Patterson & Olson 1961). This muscular insertion was also suggested by the presence of a large, backwardly projecting process on the tip of the angle in cynodonts from the Ischigualasto Formation, concurrent with the supposed disappearance of the retroarticular process in these cynodonts. Two factors weaken the hypothesis of Patterson and Olson (1961): (1) the fact that only *Tachyglossus,* with the skull and lower-jaw highly modified, presents a structure 'homologous' to the pseudangular region/process of late therapsids and early mammaliaforms, supporting the putative insertion of the mandibular depressor; (2) a well-developed retroarticular process was later documented in advanced cynodonts, including those from the Ischigualasto Formation (Allin 1975, 1986), while the posteriorly projecting tip of the angle is known in quite a few non-mammaliaform cynodonts, including some traversodontids and tritylodontids (Bonaparte 1962; Kemp 1980; Sun 1984; Sues 1985; Flynn *et al.* 2000).

More recently, the presence of both the pseudangular and the 'true' angular processes have been documented in the mammaliaforms *Dinnetherium* from the United States (Jenkins *et al.* 1983) and *Megazostrodon* from South Africa (Gow 1986). Jenkins *et al.* (1983) interpreted the angular flange (true mammalian angle) as a neomorphic downward extension of the dentary for insertion of a part of the masseter, probably the superficial portion. They do not make any claim about the muscle attaching to the pseudangular process, but considering previous studies by these authors (e.g. Crompton & Jenkins 1979) it is clear that they interpret this process as a site for masseter attachment as well. This functional interpretation obviously indicates different homologies for the pseudangular process of these authors and that of Patterson & Olsen (1961). In contrast, Hopson (1994, see also Crompton & Luo 1993: fig. 4.4) has interpreted the pseudangular process of *Dinnetherium* as a reduced angular process, and the angular flange as a neomorphic lateral ridge behind the angular region. With respect to *Megazostrodon,* Gow (1986) also considered the 'true' angular process as a ventral extension of the lateral ridge of the dentary. Some early mammaliaforms such as *Hadrocodium* (Luo *et al.* 2001: fig. 3), and some specimens of *Morganucodon* (Crompton & Luo 1993: fig. 4.7), show the angular process (= pseudangular process of Patterson, 1956) closer to the CMJ when compared with non-mammaliaform cynodonts and other early mammaliaforms. In addition, an ontogenetic series of *Sinoconodon* shows the angular process clearly located more posteriorly in large specimens (Crompton & Luo 1993: fig. 4.2; Zhang *et al.* 1998: fig. 2). This evidence supports the homology between the angle and angular process of basal cynodonts and early mammaliaforms, and that of late mammals, as advanced by Hopson (1994). In addition, the evidence supports Parrington's (1959) hypothesis regarding the posterior migration of the angular process from the condition known in non-mammaliaform cynodonts and early mammaliaforms (morganucodonts in Parrington's view), to that present in 'typical pantotheres' (e.g. *Amphitherium,* Parrington 1959) and therian mammals.

CONCLUSION

The subdivision of the reptilian external adductor musculature into masseter and temporal muscles is linked with a strengthening of the mandible and with the more

complex movements involved in mammalian mastication (Walker 1987). The presence of a differentiated superficial masseter in galesaurids implies that the morphology of the adductor musculature was already sophisticated in cynodonts lacking postcanine occlusion. This indicates that the first stages in the division of the adductor musculature (i.e. differentiation of the superficial masseter) was a prerequisite for crown-to-crown postcanine occlusion, albeit in a rudimentary fashion as in gomphodont cynodonts (Crompton 1972), or a more precise occlusion with consistent relationships between upper and lower molars, as later developed in Mammaliaformes (Crompton & Luo 1993).

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