

Feeding mechanics in Triassic stem-group sauropterygians: the anatomy of a successful invasion of Mesozoic seas

OLIVIER RIEPPEL FMLS

Department of Geology, The Field Museum, 1400 S Lake Shore Drive, Chicago, IL 606054-2496, USA

Received May 2001; accepted for publication February 2002

The jaw adductor musculature in Triassic stem-group sauropterygians is reconstructed on the basis of a paradigmatic model of muscle architecture (functional equivalence of sarcomeres) and using invariant traits of the anatomy of the trigeminal jaw adductor muscles in extant reptiles. The reconstructed jaw adductor musculature predicts trophic specializations in stem-group sauropterygians. Suction feeding is a component in prey capture for some benthic feeding, as well as for some pelagic feeding taxa. The differentiation of ‘pincer’ jaws is correlated with the potential for rapid, snapping bites. There is some evidence for habitat partitioning among Triassic stem-group sauropterygians with respect to trophic specialization. © 2002 The Linnean Society of London. *Zoological Journal of the Linnean Society*, 2002, **135**, 33–63.

ADDITIONAL KEYWORDS: jaw mechanics – Placodontia – Pachypleurosauria – Nothosauroida – Pistosauroida.

INTRODUCTION

Recent systematic revision of Triassic stem-group sauropterygians has highlighted the morphological diversity of this major clade of secondarily marine Mesozoic reptiles, and also resulted in a well-corroborated hypothesis of phylogenetic interrelationships among basal sauropterygians (Rieppel, 1999, 2000a). The secondary adaptation of primarily terrestrial reptiles to a marine environment has attracted the interest of physiologists (see Seymour, 1982 for a review), as well as of functional anatomists (see Storrs, 1993 for a review). However, the study of adaptive changes to a secondarily marine mode of life (Williston, 1914) has, in recent times, focused mainly on anatomical modifications and changes of skeletal proportions in the appendicular skeleton related to aquatic locomotion (Carroll, 1984, 1985, 1997). Locomotion was, indeed, extensively discussed for some crown-group sauropterygians such as plesiosaurs (J.A. Robinson, 1975, 1977; Taylor, 1981, 1986; Frey & Riess, 1982; Tarsitano & Riess, 1982; Godfrey, 1984; Massare, 1988; Halstead, 1989), whereas Taylor

(1992) provided an in-depth analysis of the functional anatomy of the head in the plesiosaur *Rhomaleosaurus*. Comparable studies of Triassic stem-group sauropterygians are rare.

Some analysis of the mode of life of nothosaurs was offered by Schmidt (1988; see also Schmidt, 1984), while Westphal (1988), and Stein (1995) reviewed the lifestyle of placodonts. Locomotion in pachypleurosaur and nothosaur was discussed primarily with respect to the relative importance of tail undulation and forelimb propulsion by a number of authors (Peyer, 1931; Carroll & Gaskill, 1985; Sues & Carroll, 1985; Kuhn-Schwyder, 1987; Sues, 1987a; Lin & Rieppel, 1998). The use of the forelimbs of pachypleurosaur and, especially, nothosaurs and pistosaurs, either in a paddling action, or as hydrofoils in underwater flight, was discussed by Sanz (1976, 1980), Schmidt (1984, 1985, 1986), and Storrs (1991). Hydrodynamic aspects of locomotion have been studied for the Chinese pachypleurosaur *Keichousaurus* (Lin & Rieppel, 1998). The only studies addressing locomotion in placodonts are those of Pinna & Nosotti (1989) and Renesto & Tintori (1995), both addressing the mode of life of the cyamodontoid *Psephoderma*. The most comprehensive review of functional anatomical aspects of the radiation of Triassic stem-group

Corresponding author. E-mail: rieppel@fieldmuseum.org

Sauropterygia remains that of Storrs (1993), but it, again, focuses mainly on locomotion.

Far less attention has been given to the diversification of feeding mechanics in Triassic stem-group sauropterygians. The biomechanics of the feeding apparatus of some selected placodonts was analysed by Vogt (1983), while a discussion of the feeding mechanics in the pachypleurosaur genus *Serpianosaurus* and in the nothosaurian genus *Simosaurus* was presented by Rieppel (1989). Sanz (1980) recognized two types of trophic specialization among Triassic eosauropterygians based on skull proportions and types of dentition. The prevailing scarcity of information is unfortunate, because feeding under water presents special problems, the solution of which must have been part of the adaptive strategy of the invasion of Early Mesozoic seas by sauropterygians.

Lauder (1985: 210) noted that strategies for underwater feeding have to cope with 'hydrodynamic problems associated with the removal of [relatively] small particles from a dense and viscous medium.' The most widely adapted solution to this problem for macrophagous lower vertebrates is suction feeding. Damme & Aerts, (1997) discuss two strategies for active prey capture under water related to suction feeding: either the sudden expansion of the buccal cavity creates a backward flow carrying the food item into the buccal cavity; or the expansion of the buccal cavity prevents the generation of a significant food-directed water flow as the predator approaches the prey-item.

Suction feeding has been described in elasmobranchs, actinopterygians, lungfishes, the coelacanth, larval and adult salamanders, pipid frogs, caecilians, and chelonians (Lauder, 1985). With respect to suction feeding, Lauder (1985; see also Lauder & Schaffer, 1986; Lauder & Pendergast, 1992) identified two classes of suction feeding designs: unidirectional, as in fishes where water sucked into the buccal cavity is expelled through the gill chamber, and bi-directional, as in salamanders or aquatic chelonians, which lack gill chambers. In aquatic chelonians in particular, buccal and pharyngeal expansion effected by the hyoid skeleton and its associated musculature plays an important role in underwater feeding, as the expanded oesophagus may serve as a water reservoir and hence delay reverse flow until the gape closes and the prey has been secured (Lauder & Pendergast, 1992; Damme & Aerts, 1997).

There are other strategies of feeding in water such as exemplified by crocodylians, which grab prey with a quick snapping bite. This is a feeding strategy mostly applied at the interface between water and air, rather than under water. However, *Crocodylus* was reported to catch fish under water with a quick snapping bite directed laterally by a sideward jerking of the head

(Pooley & Gans, 1976). Werth (2000) categorized marine mammals as filter feeders, suction feeders, raptorial feeders, and grazers. A variety of prey-capture in aquatic feeding was discussed by Taylor (1987) using a paradigm approach. Taylor (1987) characterized underwater predators which secure prey by penetration of teeth (raptorial feeding *sensu* Werth, 2000) as possessing 'pincer' jaws, i.e. a long and narrow snout. The narrowness of the elongated jaws minimizes drag against water during rapid jaw opening and closure. In addition, 'pincer' jaws are usually correlated with a dorsoventrally depressed skull, which in turn minimizes drag against water as the head is jerked sideward to catch prey. A rapid lateral movement of the head with the jaws open prevents the build-up of flow streamlines that would threaten to deflect the prey-item to the side, as would result if the predator approached the prey head-on (Lauder, 1985). As noted by Taylor (1987), a strong dorsoventral compression of the skull may conflict with other functional constraints, however, such as the necessity to withstand bending loads imposed upon the skull through the action of the jaw muscles.

The present paper is designed to investigate possible feeding strategies among Triassic stem-group Sauropterygia as determined by their anatomy as well as by their environment. The primary approach to the analysis of feeding strategies is the reconstruction of the jaw adductor musculature for taxa known from three-dimensionally preserved skulls. Taxon sampling represents all major lineages. Inference of the possible function of the jaw adductors will take into account skull proportions and tooth morphology. The functional interpretation of the jaw mechanics of Triassic stem-group sauropterygians, and its possible palaeoecological implications, will furthermore proceed with reference to a phylogenetic framework (Fig. 1), which has previously been reconstructed for the taxa involved (see Rieppel, 1999, 2000a; for a summary).

Institutional acronyms used in this paper are: SMF, Senckenberg Museum, Frankfurt a.M.; UMO, Umwelt Museum Oberfranken, Bayreuth.

THE JAW ADDUCTOR MUSCULATURE OF EXTANT REPTILES

Reconstruction of complex, multipinnate musculature in fossils is limited by the very nature of the material: soft parts of the anatomy are not preserved, and muscle scars, if visible at all, provide a limited guide to muscle architecture, indicating nothing more than possible sites of insertion for muscle fibres and/or tendons. By comparison with extant reptiles (Haas, 1973; Schumacher, 1973), the jaw adductor musculature must be assumed to have had a complex, multip-

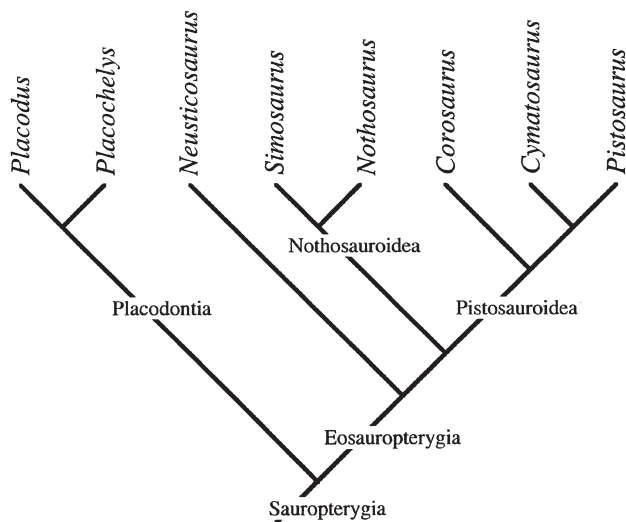


Figure 1. The phylogenetic relationships of Triassic stem-group Sauropterygia (see text, and Rieppel, 2000a for further discussion).

innate architecture in extinct forms as well. The reasons for this are historical, as they result from the phylogenetic inference that the anapsid skull, with a fully closed temporal region, is plesiomorphic for Reptilia (Williston, 1917, 1925). This means that the jaw adductor musculature was originally confined to the finite space of the adductor chamber located between the braincase and the dermatocranial cheek. Muscles packed into a closed space will have a complex pinnate (multipinnate) structure, because pinnation prevents muscles from bulging upon contraction (Alexander, 1968). Pinnation therefore allows the packing of a maximum of muscle fibres into a closed space, hence maximizing the physiological cross section of those muscle(s).

In extant reptiles (Haas, 1973; Schumacher, 1973), the trigeminal jaw adductor musculature is intersected by complex aponeuroses such as the bodenaponeurosis (Fig. 2, bo.ap) inserting into the lower jaw, the pterygoid aponeurosis inserting into the ventral flange of the pterygoid, and the quadrate aponeurosis inserting into the cephalic condyle of the quadrate. Among these, the bodenaponeurosis is usually the largest and most complex, and it has been used by Lakjer (1926) to subdivide the external jaw adductor into separate components.

In Reptilia (including birds), the trigeminal jaw adductors form by cell aggregation around the roots of the trigeminal nerve branches (Fig. 2). They subsequently compartmentalize in the transverse plane of the head, giving rise to the externus rudiment which lies lateral to the maxillary and mandibular branches of the trigeminal nerve, to the medius rudiment which

lies deep to the branches of the trigeminal nerve and is associated with the ascending process of the palatoquadrate, and to the internus rudiment which lies ventral to the palatoquadrate arch (Edgeworth, 1935; see also Song & Board, 1993). From the externus rudiment originates the external adductor (Fig. 2, ame), which is intersected by the bodenaponeurosis. Lakjer (1926) recognized those fibres of the external adductor which insert directly into the lower jaw (surangular) as the adductor mandibulae externus superficialis (Fig. 2, ames); the fibres which insert into the lateral surface of the bodenaponeurosis represent the adductor mandibulae medialis (Fig. 2, amem); and fibres which insert into the medial surface of the bodenaponeurosis are known as the adductor mandibulae profundus (Fig. 2, amep). From the medius rudiment develops the pseudotemporalis muscle (Fig. 2, mps), which originates primarily from the epityergoid (processus ascendens of the palatoquadrate), but which may invade adjacent areas. From the internus rudiment originates the pterygoideus muscle (Fig. 2, mpt). In extant reptiles, a deep and a superficial portion of the pterygoideus muscle are distinguished. The deep pterygoideus muscle originates from the lateral surface of the quadrate ramus of the pterygoid, and inserts into the medial surface of the lower jaw below the medial margin of the adductor fossa. Of greater importance in this context is the much stronger superficial pterygoideus muscle, which originates from the pterygoid aponeurosis attached to the ventrally projecting flange of the pterygoid (ectopterygoid). The muscle wraps around the ventral margin of the posterior end of the lower jaw and inserts into the ventrolateral surface of the latter (Fig. 2, mpt), thus forming a 'masticatory cushion' (Haas, 1973).

The pseudotemporalis and pterygoideus muscles together constitute the internal jaw adductor *sensu* Lakjer (1926; adductor mandibulae internus). The adductor mandibulae posterior (posterior adductor), which lies deep to and posterior to the mandibular branch of the trigeminal nerve (Fig. 2, amp), originates from the externus rudiment in squamates, but from the medius rudiment in chelonians (Rieppel, 1990). The posterior adductor generally originates from the anterior aspect of the quadrate, and inserts directly into the adductor fossa. Its anterior extension into Meckel's canal may result in the formation of an intramandibular muscle.

A final group of muscles to be mentioned is the cid-musculature (constrictor internus dorsalis group) that, apart from eye-lid muscles, also includes the levator, protractor and (if present) retractor pterygoidei muscles of squamates (a protractor quadrati may also be differentiated). This muscle group is mostly related to cranial kinesis (i.e. a movable palatobasal articulation between the pterygoid and the

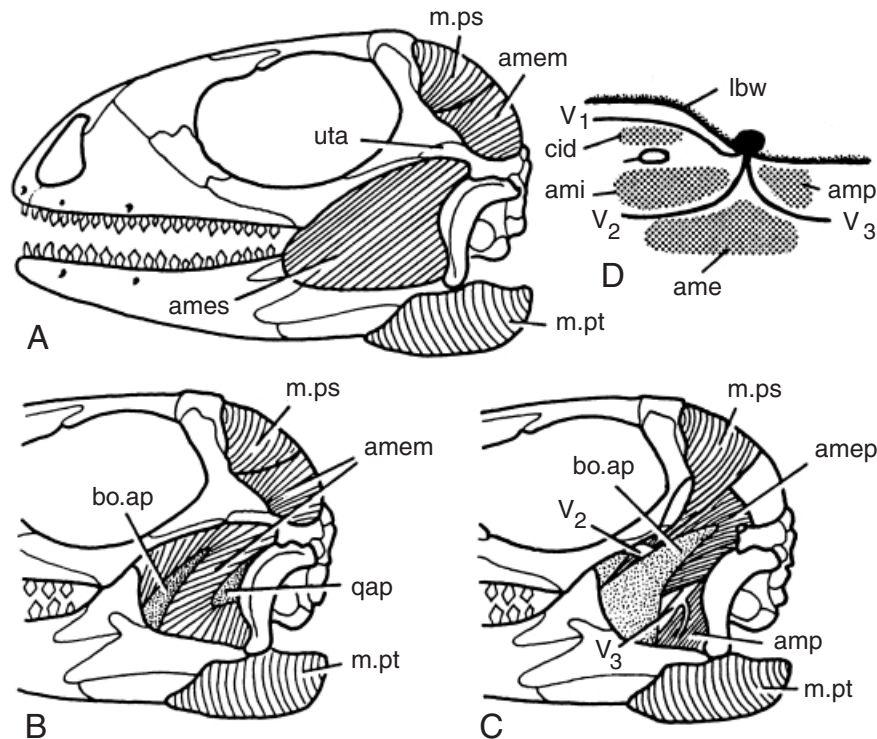


Figure 2. Schematic representation of the trigeminal jaw adductor musculature in extant reptiles (*Iguana*). A–C, Successively deeper layers of dissection. D, Schematic representation of a horizontal section through the left jaw adductor musculature complex at the level of the exit of the trigeminal nerve from the braincase. Abbreviations: ame, m. adductor mandibulae externus; amem, m. adductor mandibulae externus medialis; amep, m. adductor mandibulae externus profundus; ames, m. adductor mandibulae externus superficialis; ami, m. adductor mandibulae internus; amp, m. adductor mandibulae posterior; bo.ap, bodenaponeurosis; cid, constrictor internus dorsalis group; lbw, lateral braincase wall; m.ps, m. pseudotemporalis; m.pt, m. pterygoideus; qap, quadrate aponeurosis; uta, upper temporal arch; V1, profundus branch of trigeminal nerve; V2, maxillary branch of trigeminal nerve; V3, mandibular branch of trigeminal nerve.

basicranium), which is absent in chelonians and crocodylians. Consequently, the cid-muscles are rudimentary in crocodylians, and absent in chelonians (Schumacher, 1973).

In some extant reptiles, most notably in non-ophidian squamates, the superficial part of the external adductor is seen to expand anteroventrally on to the lateral surface of the lower jaw (the 1b-portion of the adductor mandibulae externus superficialis, *sensu* Haas, 1973; Fig. 2, ames). This development is correlated with the loss of the lower temporal arch (Rieppel & Gronowski, 1981). The presence of a restricted, yet appreciable development of the 1b-portion of the superficial jaw adductor in *Sphenodon* may reflect the fact that the complete lower temporal arch is a secondary development in those rhynchocephalians where it occurs (Whiteside, 1986; Rieppel, 1993). A loss of the lower temporal arch has also been recognized to be characteristic of sauropterygians (placodonts: Zanon, 1989; Rieppel, 2000b; eosauropterygians: Jaekel, 1910; Kuhn-Schnyder, 1967), and sauroptery-

gians do, accordingly, show a distinct shoulder on the surangular which suggests expansion of the 1b-portion of the superficial external adductor across the lateral surface of the lower jaw, as will be discussed in more detail below.

The reconstruction of the jaw adductor musculature of sauropterygians discussed below is guided by an attempt to keep structures as simple as possible. The bodenaponeurosis can assume a very complex structure, and together with the quadrate aponeurosis, intersect the external adductor in an extremely complex, multipinnate pattern (Gans *et al.*, 1985) that cannot possibly be reconstructed for extinct forms. By contrast, the areas of origin and insertion of the major parts of the jaw adductor musculature are remarkably constant throughout extant reptiles (Fig. 2; Haas, 1973; Schumacher, 1973), providing a guide towards the reconstruction of the jaw adductors in fossil reptiles such as sauropterygians (based on the method of phylogenetic bracketing described by Witmer, 1997). As a consequence, the jaw adductors of sauroptery-

gians will be reconstructed on the basis of minimal assumptions. Given the akinetic nature of the skull of sauropterygians, the cid-musculature will not be considered, although it is acknowledged that rudiments might have been present.

FUNCTIONAL CONSTRAINTS ON THE JAW ADDUCTOR MUSCULATURE

Pursuing a paradigmatic approach, functional constraints inherent in the design of complex muscles (Gans & Bock, 1965) can provide useful guidance in the reconstruction of jaw adductor muscles in fossils. Functional constraints for muscle action in general primarily result from the length–tension curve and its relationship to the function of sarcomeres (Gans & Bock, 1965). Passive stretching of a muscle fibre, which occurs during jaw opening, should not reduce the overlap of actin and myosin filaments in the individual sarcomeres of that fibre to such a degree that force output at initial contraction is low or minimal. In other words, the action range of a muscle fibre is determined by its absolute length, while the force output of a muscle is determined by its physiological cross-section, i.e. the number of fibres working in parallel.

Gans *et al.* (1985; see also Gans & deVree, 1987) developed the paradigm of ‘functional equivalence’ in their analysis of the complex structure of the jaw adductor musculature in squamates. ‘Functional equivalence’ is achieved when all sarcomeres of parallel-fibred or regularly pinnate muscles have equivalent properties and will, at any one time, occupy equivalent positions on the length–tension curve (Gans *et al.*, 1985: 232). This means that individual fibre length in parallel-fibred or regularly pinnate muscles will have to be adjusted to the relative degree of passive stretching. In rotational movements, a muscle fibre will be stretched to a degree that is proportional to the distance of its insertion from the centre of rotation (Gans & deVree, 1987). For jaw adductors this means that the further anteriorly a muscle fibre inserts into the lower jaw, the more it will be stretched upon jaw opening. In the simplest case of a parallel-fibred muscle inserting at a right angle to the long axis of the element undergoing rotation (such as the lower jaw rotating around the mandibular joint), the muscle will assume a wedge-shape, the height of the wedge increasing with increasing distance from the centre of rotation (mandibular joint). It is intriguing to note in non-ophidian squamates that the complex intersections of the external adductor by the bodenaponeurosis does result in the impression of a number of wedge-shaped muscle compartments packed into the confined space of the temporal region of the skull (Gans *et al.*, 1985). However, the degree of

relative stretching of a muscle fibre will also be determined by the angle of insertion: the smaller the angle of insertion relative to the long axis of the mandible, the lesser the degree of relative stretching of a muscle fibre (Rieppel & Gronowski, 1981). Along with the noted conservatism of areas of origin and insertion of jaw adductors in extant reptiles, the paradigm of ‘functional equivalence’ provides important guidance in the reconstruction of the jaw adductor musculature in fossils.

The antagonist of the jaw adductors is the depressor mandibulae, which originates high up at the posterolateral corner of the occiput (formed by the squamosal in sauropterygians), and which inserts into the posterior end of the lower jaw (retroarticular process if present). Since this muscle lies outside and behind the skull, it can bulge upon contraction and hence is generally parallel-fibred in extant reptiles. If a tympanic membrane is present in extant reptiles, it is attached to the posterior margin of the lower jaw, and the depressor mandibulae is located behind it. It should be noted, however, that the opening of the mouth in ‘lizards’ not only includes the depression of the lower jaw, but also the elevation of the upper jaw (Rieppel, 1979). Contraction of the epaxial neck muscles will therefore contribute to mouth opening (Gans *et al.*, 1985).

THE JAW ADDUCTOR MUSCULATURE IN TRIASSIC STEM-GROUP SAUROPTERYGIANS

THE PHYLOGENETIC RELATIONSHIPS OF THE PLACODONTIA

The Placodontia have been recognized as sister group of all other Sauropterygia, collectively referred to as Eosauropterygia (Zanon, 1989; Rieppel, 1994a, 2000a). The Placodontia have in turn been divided into two clades, the Placodontoidea (with the genera *Paraplacodus* and *Placodus*), and the Cyamodontoidea (Rieppel & Zanon, 1997; references therein). But whereas the monophyly of Cyamodontoidea is highly corroborated (Rieppel, 2001a), evidence from the recent re-description of *Paraplacodus* indicates paraphyly of the Placodontoidea (Rieppel, 2000b). Instead, *Placodus* and *Paraplacodus* are successive sister-taxa of the Cyamodontoidea.

JAW MECHANICS IN *PLACODUS*

The cranial anatomy of *Placodus* was recently reviewed by Rieppel (1995). The skull is relatively high and narrow by comparison to cyamodontoids (accordingly, *Placodus* was referred to the Macrocephali by Meyer, 1863). There are several more-or-less three-dimensionally preserved skulls, the best one being the excellent specimen UMO BT 13

first described by Sues (1987b; see also Rieppel, 1995, 2000a). Phylogenetic analysis indicates that the relatively complete covering of the cheek by dermal bone resulted from secondary expansion of the upper temporal arch (Sues, 1987b; Zanon, 1989; Rieppel, 2000b). Mazin (pers. comm.; see also Taylor, 2000) suggested that pachyostosis, which affects the skull in *Placodus*, might have served to increase its weight in adaptation to benthic feeding habits. Indeed, the strongly procumbent and chisel-shaped premaxillary and (symphyseal) dentary teeth suggest that *Placodus* picked hard-shelled sessile invertebrate prey from the substrate, which it subsequently crushed between the enlarged posterior dentary, maxillary and palatal tooth plates (Westphal, 1988).

A stapes is preserved in the skull of *Placodus* (SMF R-1035; Drevermann, 1933), showing the distal end of the shaft to articulate with the medial surface of the quadrate, as is also the case in cyamodontoids. The posterior margin of the relatively short shaft of the quadrate is strongly concave, suggesting the presence of a powerful depressor mandibulae muscle.

There is only one mandible with a completely preserved coronoid process available for *Placodus* (SMF R-1035; Drevermann, 1933). The coronoid process is very high, and terminates dorsally in an irregular margin suggesting the insertion of muscle fibres and/or tendons. For its greater part, the coronoid process is formed by a posterodorsally ascending process of the dentary. Lateral and posterior to the posteriormost crushing tooth plate, the dentary develops a broad lateral shelf for the insertion of the superficial 1b-portion of the external adductor. The posterior-most dentary tooth plate is partially hidden in lateral view by the coronoid process. The deep and wide adductor fossa opens medial to the coronoid process and behind the posterior-most dentary tooth plate. A distinct, longitudinal bony ridge projects dorsally from the dorsal surface of the angular into the bottom of the adductor fossa. It must have facilitated the attachment of an insertional tendon for muscle fibres which entered deeply into the adductor fossa and which may have extended anteriorly into Meckel's canal.

Other than the dentition, there are a number of morphological correlates of durophagy to be observed in the skull of *Placodus*. Placement of the posterior-most tooth plates at a level just anterior and medial to the coronoid process minimizes the load arm relative to the effort arm during crushing action. The high coronoid process increases the moment arm of muscular forces (DeMar & Barghusen, 1972) for those adductor fibres that slant in a posterodorsal direction (rather than being positioned vertically relative to the long axis of the lower jaw). The skull and mandible are sturdy and deep to resist strong bending loads created

by the action of the jaw adductors. The deeply concave posteroventral margin of the lower jaw must have accommodated a massive superficial pterygoideus muscle. The latter may have originated from a pterygoid aponeurosis that must have attached to the well-developed, longitudinally orientated and ventrally projecting pterygoid–ectopterygoid flange.

Muscle reconstruction (Fig. 3) takes into account the facet on the lateral surface of the posterior end of the dentary as an insertion site for the 1b-portion of the superficial external adductor (Fig. 3A, ames-1b). The extension of the muscle onto the lateral surface of the lower jaw may have been restricted, however, by the expanded temporal arch that provides a dermal cover for the ventral cheek region. Fibres of deeper parts of the external adductor may have inserted into the lateral and medial surfaces of the high coronoid process. Anteriorly positioned fibres that originated from the anterolateral and anterior margins of the upper temporal fossa would have been positioned vertically, and hence would have had to be relatively long, extending down to the base of the coronoid process (Fig. 3B, amem). Fibres inserting into the apex of the coronoid process would have had to be inclined posterodorsally in order to prevent excessive stretching during jaw opening. The bodenaponeurosis (Fig. 3C, bo.ap) may have been attached to the longitudinal ridge projecting upwards from the floor of the adductor fossa. As is true for the coronoid process, muscle fibres would have had to become progressively inclined posterodorsally and medially the higher they would have inserted into the bodenaponeurosis. This affects primarily the medialis (Fig. 3B, amem) and profundus portions of the external adductor, as they originate from the tendon covering the upper temporal fossa (medialis) and from the paroccipital process and circumference of the post-temporal fenestra (profundus), respectively (Fig. 3C, amep). The pseudotemporalis is assumed to have originated from the lateral surface of the antero-posteriorly flaring epipterygoid (see Broili, 1912; pl. 14, fig. 6), with superficial fibres possibly invading the anteromedial corner of the upper temporal fossa (Fig. 3C, m.ps). It would have inserted deep in the anterior part of the adductor fossa, perhaps with a separate insertional tendon. The posterior adductor would have originated from the deep, antero-medially extending flange of the quadrate (which broadly overlaps the equally deep, medially positioned quadrate ramus of the pterygoid: Broili, 1912; pl. 14, fig. 6), and it would have inserted deep in the more posterior parts of the adductor fossa. The pseudotemporalis, and particularly the posterior adductor, may have extended anteriorly into Meckel's canal as in crocodylians and some nonophidian squamates, thus forming an intramandibularis muscle (Fig. 3D, amp, m.ps).

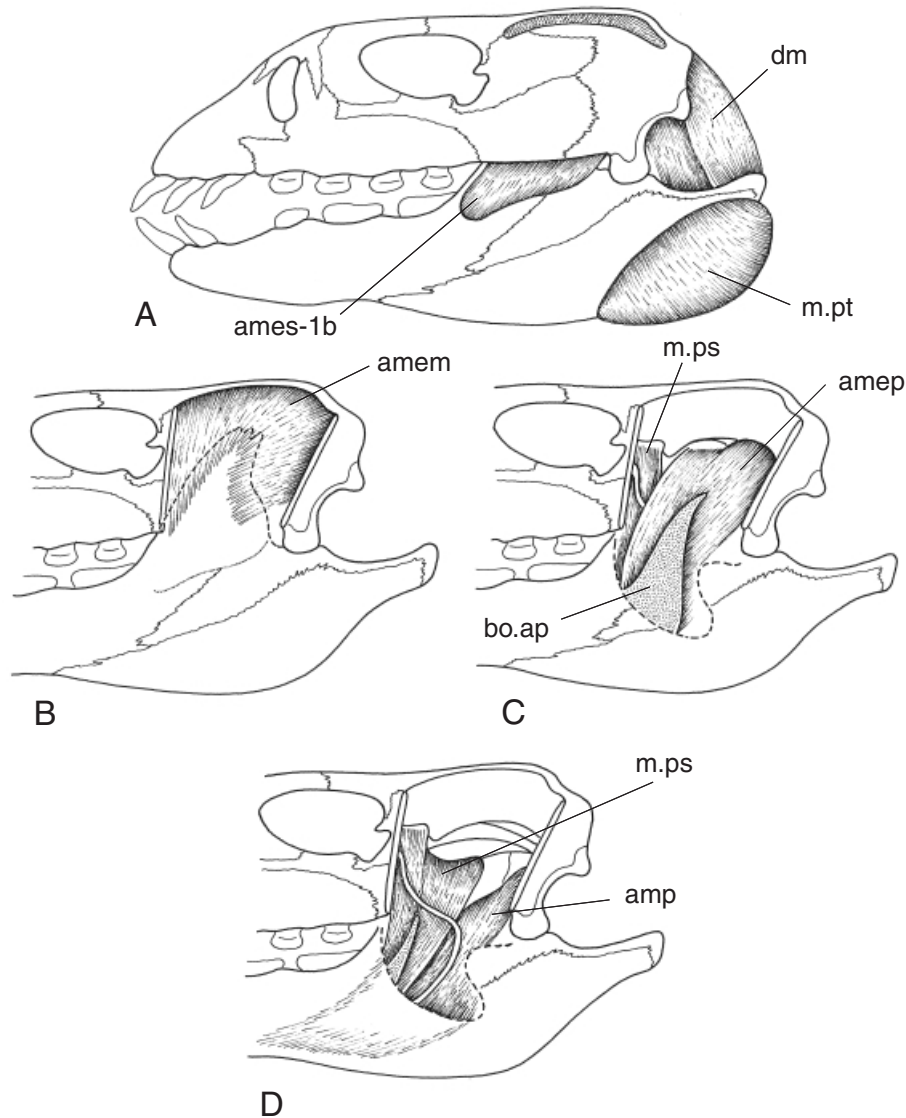


Figure 3. Hypothetical reconstruction of the jaw adductor musculature in *Placodus gigas*. A–D, Successively deeper layers of dissection. Abbreviations: amem, m. adductor mandibulae externus medialis; amep, m. adductor mandibulae externus profundus; ames-1b, 1b-portion of m. adductor mandibulae externus superficialis; amp, m. adductor mandibulae posterior; bo.ap, bodenaponeurosis; dm, depressor mandibulae; m.ps, m. pseudotemporalis; m.pt, m. pterygoideus.

The generally high skull of *Placodus* would have imparted few constraints on muscle architecture except for those fibres that inserted into the apices of the coronoid processes and of the bodenaponeuroses. The proportions of the temporal region, as well as the relative position of the orbit, indicate that the bulk of the jaw adductor muscle fibres were relatively steeply orientated. The mechanical advantage of the jaw adductors other than the pterygoideus would have increased with decreasing gape, reaching its maximum with the jaws near to closure. By contrast, the mechanical advantage of the pterygoideus muscle would have been greatest with the jaws wide open.

Depending on the size of the prey item, the pterygoideus may have been instrumental during initial phases of jaw closure, while the significance of the jaw adductor would have increased during later phases of jaw closure (crushing).

It is conceivable that *Placodus* could have manipulated a prey item such as to position it far back in the buccal cavity, between the much-enlarged posterior palatine and dentary tooth plates, for crushing. Although this necessitates a greater degree of jaw opening at the beginning of the crushing phase (loss of mechanical advantage of the jaw adductors other than the pterygoideus muscle), it minimizes the load

arm relative to the effort arm, and hence increases the efficiency of the crushing action. The model developed by Druzinsky & Greaves (1979) to determine the posterior limit of the bite point in reptiles provides a useful approach to a better understanding of the jaw mechanics in *Placodus*. The most important assumptions inherent in this model are that symmetrical muscle activity is maintained on both sides, that the resultant vector of the combined force generated by the jaw adductors passes through the apex of the coronoid process (F_1 in Fig. 4), and that this vector is orientated vertically relative to the long axis of the lower jaw (i.e. relative to the plane of the drawing, F_1 in Fig. 4). Application of the model (Druzinsky & Greaves, 1979) to *Placodus* (Fig. 4) is based on the use of the undistorted skull UMO BT 13 to determine the divergence of the mandibular rami (CA and CB, respectively, in Fig. 4). The location of the centre of the posteriormost tooth plate (bp in Fig. 4), and of the apex of the coronoid process (E in Fig. 4), relative to the long axis of the mandibular ramus is reconstructed using the well preserved right mandible of the specimen described and figured by Drevermann (1933). Assuming a vertically orientated resultant force vector, as would result from symmetrical contraction of jaw adductors that insert vertically into the coronoid process relative to the long axis of the lower jaw (F_1 in Fig. 4A, orientated at a right angle relative to the

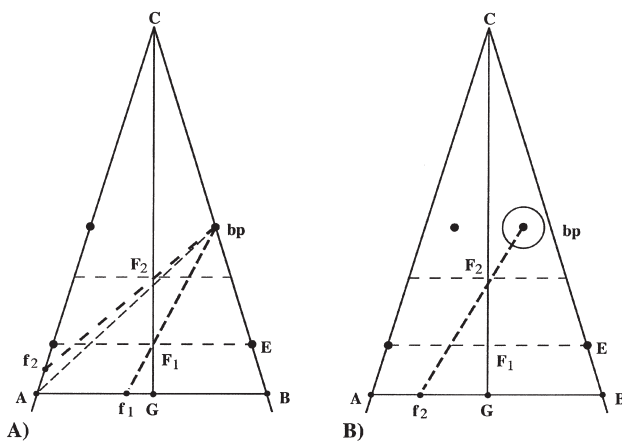


Figure 4. Analysis of the jaw mechanics in *Placodus* on the basis of the model derived by Druzinsky & Greaves (1979). For further discussion see text. Abbreviations: A, B, location of the mandibular joints; E, location of the apex of the coronoid process; bp, bite point in the centre of the posterior dentary tooth plate; F_1 , f_1 , resultant vertical muscle force (F_1 , acting perpendicular to the plane of the drawing) and fulcrum (f_1); F_2 , f_2 , adductive component of the resultant muscle force generated by posterodorsally inclined muscles (F_2 , acting perpendicular to the plane of the drawing), and fulcrum (f_2)

plane of the drawing), the posterior-most tooth plates of *Placodus* lie in front of the theoretically posterior-most bite point. Resistance forces to the pull of the jaw adductors will build up at the bite point (crushing the prey item) and at the mandibular joints. As a result of the location of the fulcrum f_1 closer to joint A (Fig. 4A), the reaction force will be larger at the mandibular joint A by comparison to the joint of the lower jaw ramus that is engaged in crushing (B in Fig. 4A).

However, even a moderate posterodorsal inclination of the resultant muscle force vector for the jaw adductors changes the situation dramatically. Several factors would contribute to the posterodorsal orientation of the resultant vector of jaw adductor muscle forces. These are the posterodorsal inclination of the fibres inserting into the apex of the coronoid process and/or of the bodenaponeurosis, the posterodorsal inclination of the fibres inserting into the posterior margin of the coronoid process and of the bodenaponeurosis (particularly the profundus layer of the external adductor), the orientation of the posterior adductor and the possible extension of the pseudotemporalis and posterior adductor into Meckel's canal. The well-preserved right lower jaw ramus of *Placodus* illustrated by Drevermann (1933) shows in lateral view that the surface of the posterior dentary tooth plate lies at the same level as the articular facet of the mandibular joint. If the resultant muscle force vector passing through the apex of the coronoid process is assumed to be inclined posterodorsally, it will intersect the long axis of the lower jaw at the horizontal plane defined by the posterior tooth plate and mandibular articulation in a more forward position, i.e. more closely behind the posterior dentary tooth plate (F_2 in Fig. 4A). Because the effective fulcrum (f_2 in Fig. 4A) cannot physically move lateral to joint A, the lever resulting from the biting action will correspond to the line bp-A in Fig. 4(A). Because the adductive force vector F_2 in Fig. 4(A) (orientated perpendicular to the plane of the drawing) cannot lie on the line bp-A, a rotational moment will build up, threatening the disarticulation of that mandibular ramus which is engaged in crushing (joint B in Fig. 4). Disarticulation of the respective jaw joint must be prevented either by asymmetric muscle action, or by resistance generated by contraction of the massively developed superficial pterygoideus muscle, along with activity of the depressor mandibulae. Simultaneous activity of the superficial pterygoideus muscle and depressor mandibulae was, indeed, recorded in the agamid lizard *Uromastix* during bites on tough food items (Throckmorton, 1978).

However, the posterior dentary tooth plates of *Placodus* are displaced medially relative to the outer margin of the lower jaw, biting against the palatine tooth plates that are located medial to the maxillary

tooth row (Rieppel, 1995). It must therefore be assumed that *Placodus* would have manipulated a potential prey item to a more medial location, to be crushed between the posterior dentary and palatine tooth plates. If this medial shift of the posterior-most bite point is accounted for in the application of Druzinsky & Greaves's (1979) model to the jaw mechanics of *Placodus*, the build-up of a rotational moment is prevented. Assuming the same resultant adductive force vector (orientated vertically to the long axis of the lower jaw) generated by posterodorsally slanting adductor muscles (F_2 in Fig. 4B) as was previously postulated (F_2 in Fig. 4A), but moving the posterior-most bite point medially (Fig. 4B), will result in the location of the fulcrum f_1 (that develops as a consequence of reaction forces that build up at the bite point and at the mandibular joints) medial to the jaw joint A (in Fig. 4B). The reaction force will consequently be larger at the mandibular joint A by comparison to joint B (in Fig. 4A), but no rotational momentum results.

JAW MECHANICS IN *PLACOCHELYS*

Placochelys is here used as a 'paradigm' for cyamodontoid jaw mechanics other than *Henodus*. The cyamodontoid skull in general (see Rieppel, 2000a; see Rieppel, 2001a; for a detailed description of cyamodontoid skulls) is much more depressed than that of *Placodus* (hence Meyer's (1863) characterization of the group as Platycephali). At the same time, there is a tendency to expand the temporal area posteriorly by the development of posterodorsally projecting squamosals. This tendency is least expressed in basal representatives of the group, such as *Cyamodus*, and most strongly expressed in the relatively apomorphic taxa *Placochelys* and *Psephoderma*. The premaxillary rostrum shows correlated morphoclineal changes within the cyamodontoid lineage. It is relatively short and rounded, and carries procumbent premaxillary teeth in basal taxa such as *Cyamodus*, in which it must have been used to pick up hard-shelled invertebrates from the substrate. Elongation of the rostrum is correlated with a reduction of its dentition, until the rostrum becomes an edentulous, elongate and narrow structure in the apomorphic representatives of the clade (*Placochelys*, *Psephoderma*). Cyamodontoids other than *Henodus* retain large crushing tooth plates. The posterior palatine and posterior dentary tooth plates are very prominent indeed, and the posterior palatine tooth plates can be shown to be subject to positive allometric growth in *Psephoderma* (Rieppel, 2001a; references therein). These large tooth plates, together with the high coronoid process, indicate the potential for forceful crushing activity in cyamodontoids.

In very general terms, depression of the skull in cyamodontoids together with the relatively high coronoid process must have imposed functional constraints on the arrangement of the jaw adductor muscle fibres in order to allow them to maintain an efficient fibre length. However, the skull of cyamodontoids is not only depressed, but its temporal region is also expanded both laterally, with the flaring temporal arches and the wide upper temporal fossae, and posteriorly, with the posterodorsally projecting squamosals. These allow a pronounced inclination of muscle fibres both in a posterodorsal direction (fibres originating from the posterior part of the temporal fossa) as well as in a latero-medial (fibres originating from the lateral margin of the upper temporal fossa) or medio-lateral (fibres originating from the medial margin of the upper temporal fossa) direction. Inclination of those fibres inserting high into the coronoid process or into the bodenaponeurosis is critical as it reduces the degree of passive stretching upon jaw opening.

The posterior concavity of the shaft of the quadrate is not as strongly expressed in cyamodontoids as in *Placodus*, and a distinct facet to receive the distal end of the stapes can be identified on the anteromedial aspect of the shaft (Nosotti & Pinna, 1998; Rieppel, 2001a). A tympanic membrane is therefore again assumed to have been absent in cyamodontoids, which allowed for expansion of the depressor mandibulae. Development of this muscle is further enhanced by the posterodorsal expansion of the squamosals, from the ventral surface of which the depressor mandibulae originated (Fig. 5A, dm).

By contrast to *Placodus*, the coronoid process of cyamodontoids is formed by the coronoid bone only, which extends far down on the lateral surface of the lower jaw, approaching its ventral margin (not in *Henodus*). The lateral surface of the coronoid shows a shallow yet distinct and extensive depression that must have accommodated the well-developed 1b-portion of the external adductor (Fig. 5A, ames-1b). This muscle portion must have emerged from below the temporal arch which shows a much more distinctly embayed ventral margin compared to *Placodus*, and it seems to have invaded the lateral surface of the coronoid up to a level lateral to the posterior dentary tooth plate (the latter is again partially concealed by the coronoid process).

The arrangement of deeper layers of the jaw adductors would have corresponded to the general pattern outlined for *Placodus*. Anteriorly and more-or-less vertically positioned muscle fibres would have had to insert into the basal parts of the coronoid process and/or bodenaponeurosis in order to preserve a functional fibre length. The higher up muscle fibres inserted into the coronoid process and/or bode-

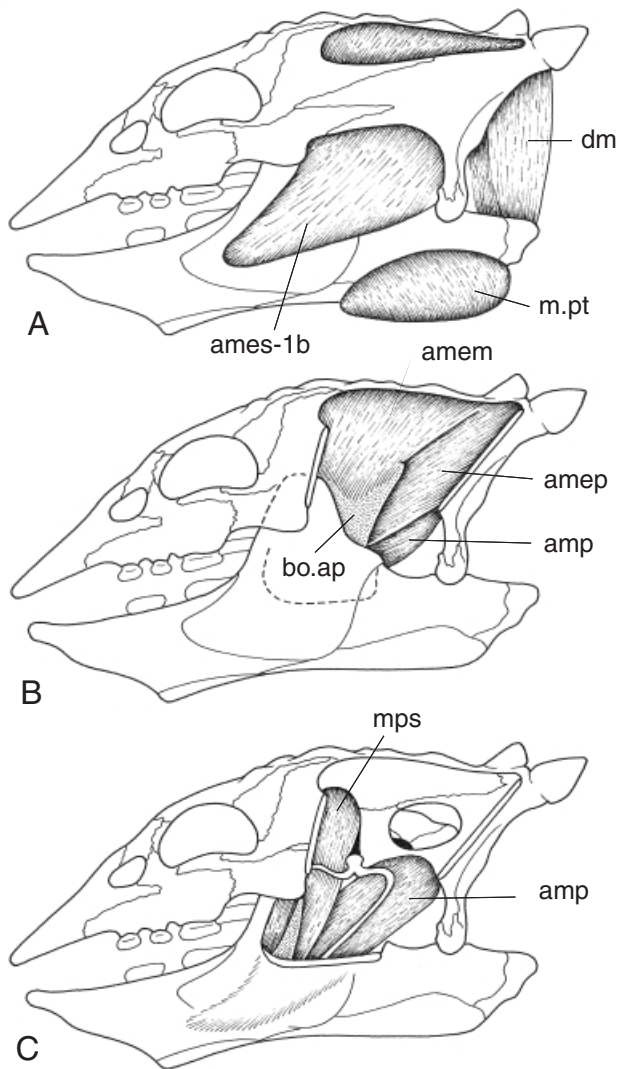


Figure 5. Hypothetical reconstruction of the jaw adductor musculature in *Placochelys placodonta*. A–C, Successively deeper layers of dissection. Abbreviations: amem, m. adductor mandibulae externus medialis; amep, m. adductor mandibulae externus profundus; ames-1b, 1b-portion of m. adductor mandibulae externus superficialis; amp, m. adductor mandibulae posterior; bo.ap, bodenaponeurosis; dm, depressor mandibulae; m.ps, m. pseudotemporalis; m.pt, m. pterygoideus.

naponeurosis, the more inclined they would have had to be relative to the long axis of the lower jaw in order to reduce relative stretching during jaw opening (Fig. 5B, amem, amep). The adductor fossa again is deep and wide in cyamodontoids, and would have allowed the pseudotemporalis muscle (originating from the anteriorly positioned, broad epipterygoid, and perhaps from neighbouring areas of the laterally descending flange of the parietal), as well as the

posterior adductor (originating from the anteromedially flaring flange of the quadrate overlapping the quadrate ramus of the pterygoid), to enter deeply into the adductor fossa and, possibly, to expand anteriorly into Meckel's canal as an intramandibularis muscle (Fig. 5C, mps, amp).

Longitudinally orientated, ventrally projecting flanges of the pterygoid are prominently developed in cyamodontoids, which indicates a strong development of the superficial pterygoideus muscle (Fig. 5A, m.pt). Given its orientation relative to the long axis of the lower jaw, this muscle would again have worked with the greatest mechanical advantage during initial phases of jaw adduction, while the other jaw adductors would have gained mechanical advantage with progressive jaw closure (crushing).

As noted by Vogt (1983), cyamodontoids differ from *Placodus* in the general geometry of the lower jaw relative to the position of the coronoid process, posterior dentary tooth plate, and mandibular articulation. The essential difference is a more anterior position of the coronoid process relative to the posterior-most dentary tooth plate in *Cyamodus*. This accentuates the problem, discussed for *Placodus* above, of a bite point located far posterior relative to the insertion of the posterodorsally inclined jaw adductor musculature. But cyamodontoids realized the same solution as did *Placodus* (Fig. 4), which is a shift of the posterior-most bite point medially on the posterior dentary tooth plates, biting against the posterior palatine tooth plates. In fact, just as the coronoid process is located more anterior relative to the posterior tooth plate in cyamodontoids, the medial shift of the posterior-most bite point is accentuated by a much more distinctive enlargement of the posterior dentary and palatine tooth plates compared to *Placodus*.

Hard-shelled invertebrate prey must first be secured, however, before it can be processed. Plesiomorphic cyamodontoids, with their relatively short and rounded rostrum carrying strongly procumbent premaxillary teeth, may be assumed to have picked up their prey from the substrate much like *Placodus*. More derived cyamodontoids, such as *Placochelys* and, especially, *Psephoderma*, have an elongate and slender rostrum deprived of premaxillary teeth, and also lack anterior dentary teeth. They would therefore have had to pick up their prey with their slender and, especially in *Psephoderma*, delicately built rostra. Advanced cyamodontoids with edentulous rostra have previously been portrayed as predators on endobiotic shelled invertebrates (Pinna & Nosotti, 1989; Stefani *et al.*, 1992; Mazin & Pinna, 1993). Mazin & Pinna (1993) in particular, drew an analogy between *Psephoderma* and myliobatids (eagle rays), which are described as inhabitants of littoral environments and lagoons, digging through the soft sea-floor with their rostrum

in search of hard-shelled invertebrates. An analogous lifestyle for *Psephoderma* has been disputed by Renesto & Tintori (1995) with reference to the absence of a 'shelled' endofauna in the Calcare di Zorzino, a deposit that yielded several specimens of *Psephoderma*.

In the context of this controversy it should be noted that the delicate and slender rostrum of *Psephoderma* seems ill-suited to pick up sessile bivalves securely fastened to the substrate (such as bivalves attached by a byssum) as postulated by Renesto & Tintori (1995). There is also no evidence for an abundance of bivalves in the Calcare di Zorzino (A. Garassino, pers. comm.) as was assumed by Renesto & Tintori (1995), nor is there an abundance of gastropods, and echinoderms are very rare (Stefani *et al.*, 1992). Instead, the invertebrate fauna of the Calcare di Zorzino is dominated by epibenthic as well as free-swimming decapod crustaceans (Stefani *et al.*, 1992). The morphocline development of an elongated and slender rostrum without dentition among cyamodontoids is also correlated with the development, on the ventral (palatal) surface of the rostrum, of distinct grooves that extend from the tip of the rostrum to the internal nares (Rieppel, 2000a, figs 24–26; see also Rieppel, 2001a). This suggests that more derived cyamodontoids such as *Placochelys* and *Psephoderma* would have sucked in water in search of olfactory clues. As postulated by Mazin & Pinna (1993), the animals may well have been probing the soft substrate along the slopes of the basin(s) in search of invertebrate prey, using sucking action in response to olfactory cues. The heavy dermal armor of cyamodontoids suggests a benthic lifestyle (Mazin & Pinna, 1993), and because endobiotic invertebrate prey would not be securely fastened to the substrate, it would have been possible to pick it up with the rostrum and/or to get it between the jaws by suction. As was discussed above, suction feeding is accomplished by aquatic chelonians without major morphological changes (Lauder & Pendergast, 1992; Damme & Aerts, 1997), and it may well have been a component of the feeding strategy in advanced cyamodontoids.

A prerequisite for the creation of efficient suction, be that in search of olfactory clues or as a means to secure prey, is a rapid opening of the buccal cavity. The principal muscle responsible for jaw opening is the depressor mandibulae, and it must have been very well developed in cyamodontoids, as the posterior expansion of the squamosals provides an increased area of origin for this muscle. Its insertion was concentrated on the retroarticular process, perhaps through insertional tendons. The retroarticular process is much more massively built and deeper in cyamodontoids than in *Placodus*, indicating its potential to withstand stronger bending moments.

JAW MECHANICS IN *HENODUS*

Although highly autapomorphic, *Henodus* was found to be the sister-taxon of the genus *Cyamodus*, and hence placed rather basally in the hierarchy of cyamodontoids by comparison to placocheleids (Rieppel, 2000a, 2001a). The skull of *Henodus* is broad and dorsoventrally depressed. The upper temporal fenestrae are roofed over by an expansion of neighbouring elements, in particular of the parietal. The lower jaw is very deep and massive. Yet the crushing dentition of *Henodus* is much reduced. The only crushing teeth that persist are a small posterior palatine and dentary tooth plate. However, distinct grooves line the lateral margin of the upper (maxilla, perhaps extending onto the jugal) and lower (dentary) jaw, which according to Huene (1936) would have carried baleen-like structures. Huene (1936) claimed to have observed non-ossified structures creating a striated pattern in one of the jaw grooves, but this material was removed through preparation. A similar observation was reported with respect to a different specimen more recently, however (Reif & Stein, 1999). Even more importantly, Reif & Stein (1999) observed a row of minute denticles lining the anterior, transversely orientated margin of the premaxilla (but not of the dentary). These denticles could only have had a cutting or scraping function, while the presence of baleen-like structures certainly suggests some degree of either suction feeding (in the benthic mode), or – less likely – ram feeding (in the suspension mode) (Collin & Janis, 1997).

The reconstruction of the jaw adductor musculature in *Henodus* (Fig. 6) is subject to many uncertainties, given the highly unusual skull proportions. The skull is very low indeed, but so is the coronoid process on the otherwise very deep mandible, which indicates a reduced degree of durophagy. The same is suggested by the reduced crushing dentition. The coronoid process is furthermore set fairly far back relative to the anterior corner of the temporal adductor chamber, suggesting that fibres originating from the anterior part of the adductor chamber (anterior parts of the external jaw adductor, and probably the pseudotemporalis muscle) must have ascended from the coronoid process in an anterodorsal direction. Conversely, fibres originating from the posterior part of the adductor fossa (posterior parts of the external jaw adductor and the posterior adductor) must have ascended in a posterodorsal direction. In fact, there is no other possibility to preserve a functional muscle fibre length for all parts of the jaw adductor musculature than to assume that *Henodus* is convergent upon the Eusauropterygia in the development of a dual jaw adductor system (see below for a more detailed discussion). The anterior part of the external adductor

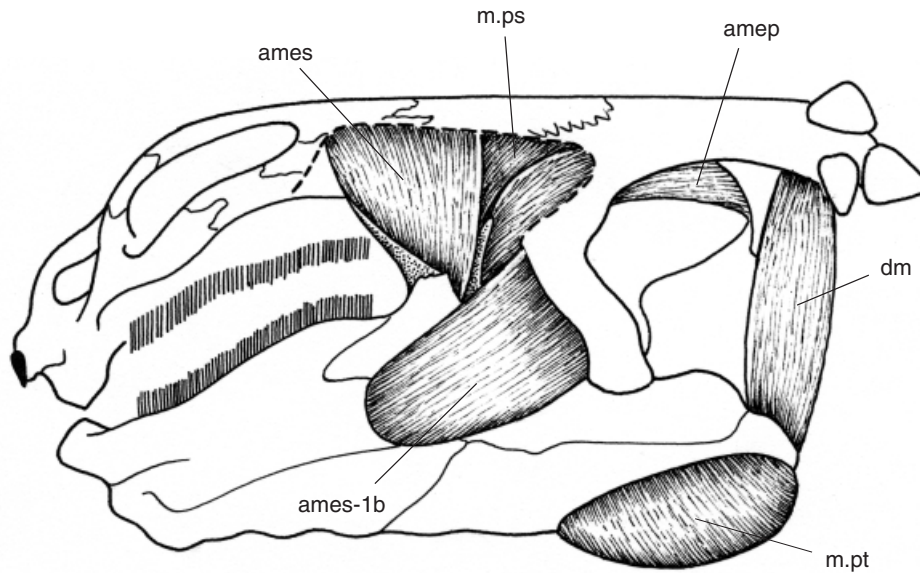


Figure 6. Hypothetical reconstruction of the jaw adductor musculature in *Henodus chelyops*. Superficial view of jaw adductor musculature. Abbreviations: amem, m. adductor mandibulae externus medialis; amep, m. adductor mandibulae externus profundus; ames-1b, 1b-portion of m. adductor mandibulae externus superficialis; bo.ap, bodenaponeurosis; dm, depressor mandibulae; m.pt, m. pterygoideus.

would thus have inserted into an anterior sheet of the bodenaponeurosis (Fig. 6, ames), whereas the posterior part of the external adductor inserted into a posterior sheet (Fig. 6, amep).

As was noted in the morphological description of the skull (Rieppel, 2001a; see also Rieppel, 2000a, fig. 19), the jaw suspension is again highly autapomorphic in *Henodus*. The cephalic condyle of the quadrate is drawn out posteriorly, its posterior tip abutting against a ventrally descending flange of the squamosal. Between the dorsal expansion of the quadrate, the skull roof, and the descending flange of the squamosal there persists, in all specimens of *Henodus*, a gap that leads into the temporal adductor chamber of the skull. This morphology suggests that the fibres of the deep portion of the external adductor (adductor mandibulae externus profundus) extended posteriorly across the paroccipital process to gain access to the anterior surface of the descending flange of the squamosal (Fig. 6, amep), which hence provided an expanded area for their origin (Vogt, 1983). With this arrangement of posterodorsally expanded jaw adductors (Fig. 6), *Henodus* – the ‘false turtle’ (Gregory, 1946: 315) – provides yet another striking analogy to chelonians which develop a similar pulley-system for the jaw adductors (Gaffney, 1975).

A distinct shoulder on the lateral surface of the surangular furthermore suggests the development of a strong anteroventral 1b-portion of the external adductor (Fig. 6, ames-1b). By comparison to other cyamodontoids, the ventrally projecting pterygoid

flange is weakly developed in *Henodus*. Yet it is still differentiated, and from it must have originated the pterygoid aponeurosis giving rise to the superficial pterygoideus muscle.

The depressor mandibulae muscle must have originated from the posterior surface of the ventrally descending flange of the squamosal, and inserted into the deep retroarticular process (Fig. 6, dm). It remains unknown, however, whether the origin of the depressor mandibulae muscle extended onto the lateral surface of the ventrally projecting flange of the squamosal and of the cephalic condyle of the quadrate. Finally, it may be important for a better understanding of the feeding mechanics of *Henodus* to note that well ossified elements of the hyoid apparatus are preserved in several specimens (Huene, 1936; personal observation).

The entire habitus of *Henodus*, including the dorsoventrally flattened carapace and the low skull with its massive lower jaw, suggest benthic habits, or at least a benthic-feeding lifestyle. Opening the jaws would have been as much an effect of dropping the mandible as of elevating the skull. The muscles responsible for jaw opening would be the depressor mandibulae as well as the epaxial neck muscles. Given the very massive structure of the lower jaw, one might expect gravity (much reduced in water, however) to represent some additional factor in the depression of the lower jaw, unless it was resting on the substrate. In this case, elevation of the skull would have been the major component of the jaw opening mechanism of

Henodus. Indeed, by comparison to the lower jaw, the skull appears to be of much lighter structure (see Reif & Stein, 1999, fig. 1b). Elevation of the skull can be achieved by the combined action of the depressor mandibulae and epaxial neck muscles. The dorsal surface of the retroarticular process of *Henodus* distinctly slopes posteroventrally, which not only allows for longer muscle fibres of the depressor mandibulae, but also increases the mechanical advantage of these fibres (Gans, 1966). Collectively, the lightly built skull, the massive lower jaw subject to the pull of gravity (Reif & Stein, 1999, fig. 1b), and a well developed depressor mandibulae working at an improved mechanical advantage, suggest the potential for rapid jaw opening.

The relatively posterior position of the coronoid process reduces the length of the effort arm relative to the possible load arm, which again reflects the reduced capacity of durophagy in *Henodus*, but also indicates that more emphasis is placed on maintaining speed (against the drag caused by water) rather than force in jaw closure (P.L. Robinson, 1973). Initial phases of jaw closure would have been effected by the mechanically advantageously placed anterior parts of the external adductor, the pseudotemporalis muscle and the pterygoideus muscle. Posterior parts of the external jaw adductor, as well as the posterior adductor, would have acted at an increased mechanical advantage with increasing jaw closure. As noted by Huene (1936), and Reif & Stein (1999), the only invertebrates present in the sediments that yielded *Henodus* are crustaceans (estherias). It is for this reason that Reif & Stein (1999) interpreted *Henodus* as herbivorous. It might indeed have used its premaxillary cutting edge to cut off plant material, or to scrape plant material (algae) off the substrate. Once free, the plant material or, alternatively, any other possible food item (such as small crustaceans), would have been sucked into the buccal cavity by rapid jaw opening occurring simultaneously with a depression of the (well ossified) hyoid apparatus, as is known from modern aquatic chelonians (Lauder & Schaffer, 1986; Damme & Aerts, 1997). Closure of the jaws would have trapped food-items within the baleen-like structures that would nevertheless have allowed water to be expelled. It is even conceivable that *Henodus* was an omnivore, sieving through fine grained substrate (analogous to grey whales: Collin & Janis, 1997). Should a captured food-item need to be crushed or reduced in size, this could have been accomplished by the use of the small posterior tooth plates (Huene, 1936).

The position of the posterior-most tooth plate relative to the apex of the coronoid process is different in *Henodus*, compared to both *Placodus* and *Placochelys*. The coronoid process is relatively lower in *Henodus*, but the posterior-most dentary tooth plate lies imme-

diately medial to the anteriorly placed apex of the coronoid process. The simultaneous activation of the anterior and posterior divisions of the dual jaw adductor system would have provided a vertically orientated resultant vector that, passing through the apex of the coronoid process, would have worked at a maximal mechanical advantage. On the basis of the model developed by Druzinsky & Greaves (1979), use of the posterior dentary and palatine tooth plates in a crushing bite would invariably require asymmetrical muscle activity and/or stabilization of the opposite mandibular articulation by the action of the pterygoideus muscle and the depressor mandibulae. However, the biting forces generated by *Henodus* must have been limited, given its diminished potential for durophagy and the small size of the rudimentary posterior dentary and palatine tooth plates.

THE PHYLOGENETIC RELATIONSHIPS OF PACHYPLEUROSAURIA

In many aspects of their generalized skeletal anatomy, the Pachypleurosauria may represent the plesiomorphic condition for sauropterygians in general. While pachypleurosauria are a well corroborated monophyletic clade (Rieppel & Lin, 1995; Rieppel, 1998a), their phylogenetic position within the Eosauropterygia remains unresolved. The closed occiput, and other shared derived characters, tend to place pachypleurosauria as the sister group of the Nothosauroida (Rieppel, 1998b). However, the recent inclusion (Rieppel, Sander & Storrs, in press) of *Augustasaurus* (Sander *et al.*, 1997) in the analysis of phylogenetic interrelationships of stem-group Sauropterygia showed the pachypleurosauria (represented by *Neusticosaurus* in Fig. 1) to be the sister-taxon of all other Eosauropterygia, collectively referred to as Eusauropterygia (Tschanz, 1989).

JAW MECHANICS IN PACHYPLEUROSAURIA

As a group, the lizard-like pachypleurosauria are among the smallest sauropterygians, their total length rarely exceeding 50 cm (Rieppel & Lin, 1995). *Neusticosaurus edwardsii* is the notable exception, reaching a maximum length of 120 cm (Carroll & Gaskill, 1985). Although some species are known from a large number of individuals (Sander, 1989), there is only one three-dimensionally preserved pachypleurosaur skull in a public repository, i.e. a skull of *Anarosaurus heterodontus* (Rieppel & Lin, 1995, fig. 10; Rieppel, 2000a fig. 37). The proportions of this specimen correspond closely to the three-dimensional reconstruction of the skull of *Neusticosaurus edwardsii* by Carroll & Gaskill (1985), which is here used as paradigmatic representative of its clade.

Pachypleurosaurs were characterized by Sanz (1980) as mesorostral, as compared to the 'microrostral' (i.e. brevirostrine) *Simosaurus*, or the 'macrorostral' (i.e. longirostrine) nothosaurs. The relative rostrum length in pachypleurosaurs is, indeed, somewhat larger than in the short-snouted *Simosaurus*, but the tooth row is restricted to a level in front of the orbit in pachypleurosaurs, whereas it extends backwards to a level behind the orbit in *Simosaurus*. The snout of the pachypleurosaur skull is broad, blunt and rounded, and without a rostral constriction. By comparison to other Triassic stem-group sauropterygians, pachypleurosaurs are characterized by relatively large orbits, and a relatively short postorbital region in a skull that is not distinctly depressed (Rieppel & Hagdorn, 1998). Pachypleurosaurs are the only Triassic stem-group sauropterygians to retain sclerotic ossicles. There are a number of three-dimensionally preserved skulls of stem-group sauropterygians that have been carefully prepared, some with acid (*Placodus*: Sues, 1987b; *Cyamodus*: Nosotti & Pinna, 1998; *Nothosaurus*, specimen SMNS 56618; *Cymatosaurus*: Rieppel & Werneburg, 1998), which document the genuine absence of sclerotic ossicles in those clades. Sclerotic ossicles are known to occur, however, in crown-group sauropterygians such as *Plesiosaurus*

(Storrs, 1997). The differentiation of a ring of sclerotic bones is correlated in reptiles (including birds) with the development of a powerful, lens-squeezing mechanism of accommodation (Walls, 1942).

In a recent paper, Motani *et al.* (1999) related the relative size of the eyeball in ichthyosaurs to diving capacities. Species with larger eyeballs are presumed to have been able to hunt at greater depths. Deep diving in pachypleurosaurs appears to conflict with middle ear structure, however (Rieppel, 1989). The posterior margin of the quadrate is deeply concave, suggesting the presence of a relatively large tympanic membrane (Fig. 7). Furthermore, the mandibular condyle of the quadrate is drawn out to form a posterior process that must have supported the ventral margin of the tympanic membrane. This process fits into a deep trough on the dorsal surface of the retroarticular process with the jaws open, thus preventing a folding of the tympanic membrane that would otherwise occur between the quadrate and the retroarticular process (Rieppel, 1979). The presence of a relatively large tympanic membrane, suggesting an air-filled middle ear cavity, would not have been compatible with rapid dives to greater depths (Rieppel, 1989). Pachypleurosaurs are therefore believed to have inhabited shallow coastal, lagoonal,

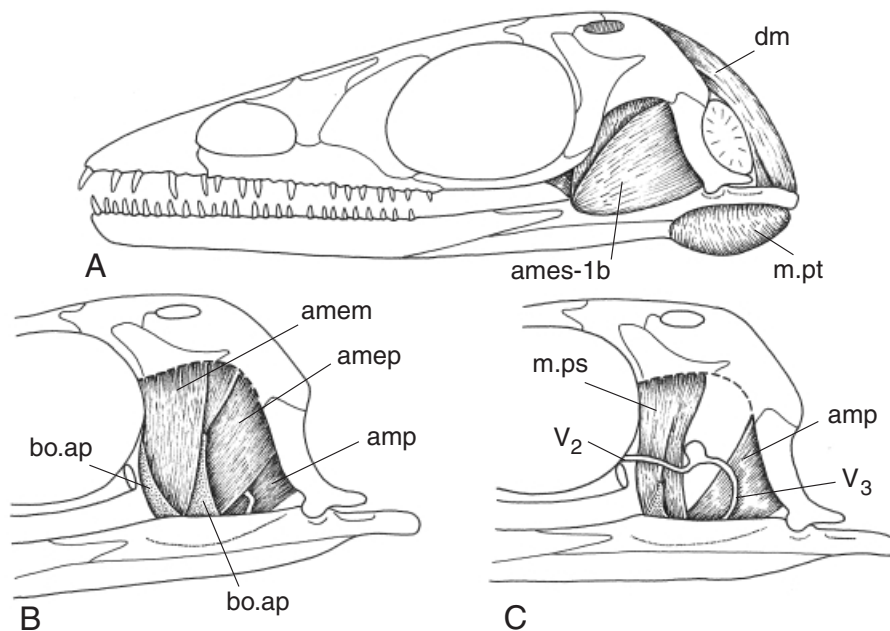


Figure 7. Hypothetical reconstruction of the jaw adductor musculature in *Neusticosaurus edwardsii*. A–C, Successively deeper layers of dissection. Abbreviations: amem, m. adductor mandibulae externus medialis; amep, m. adductor mandibulae externus profundus; ames-1b, 1b-portion of m. adductor mandibulae externus superficialis; amp, m. adductor mandibulae posterior; bo.ap, bodenaponeurosis; dm, depressor mandibulae; m.ps, m. pseudotemporalis; m.pt, m. pterygoideus; V₂, maxillary branch of trigeminal nerve; V₃, mandibular branch of trigeminal nerve.

and eustarine waters (Sander, 1989), as is also indicated by the limited development of bone ballast (Taylor, 2000).

The development of relatively large eyeballs infringes on the space available for jaw adductor musculature (Rieppel & Hagdorn, 1998). The upper temporal fossa is relatively larger in plesiomorphic representatives of the clade compared to more apomorphic species such as those of the genus *Neusticosaurus* (Rieppel & Lin, 1995; Rieppel, 1998a), but its longitudinal diameter is always much shorter than the longitudinal diameter of the orbit. The temporal arch again is relatively narrower in plesiomorphic representatives of the clade, while in advanced members it becomes broadened, which adds to the reduction of the size of the upper temporal fossa, and to the dermal covering of the dorsal cheek region. Finally, the development of a relatively large tympanic membrane restricts the size of the depressor mandibulae muscle.

The lower jaw of pachypleurosaurs is a rather delicate structure. There is no elongation of the mandibular symphysis, as is seen in other Triassic stem-group Sauropterygia. A coronoid process is absent. The dentition of pachypleurosaurs is homodont, consisting of a row of relatively small, at best slightly recurved, conical teeth. The only indication of heterodonty is the relative enlargement of the anterior premaxillary and dentary teeth in *Anarosaurus heterodontus* (Rieppel & Lin, 1995). The anterior premaxillary and dentary teeth of pachypleurosaurs may be slightly procumbent, but never to the extent seen in other Triassic stem-group Sauropterygia.

A shallow insertional facet on the surangular indicates the differentiation of an anteroventral 1b-portion of the external adductor, which expanded onto the dorsolateral shoulder of the mandible (Fig. 7A, ames-1b). Deeper layers of the external adductor would have inserted into a bodenaponeurosis. Fibres located in the anterior part of the adductor chamber, immediately behind the eyeball, would have been vertically orientated. Deeper and more posteriorly located fibres of the external adductor may have inserted into a bodenaponeurosis in a pattern similar to that seen in extant reptiles (Fig. 7B, amep). Posterodorsal inclination would have reduced relative stretching during jaw opening of those fibres inserting into the apex and posterior margin of the bodenaponeurosis. The pseudotemporalis muscle would again be located in the anteromedial part of the adductor chamber. It was vertically orientated, and most probably inserted into the lower jaw with its own insertional tendon (Fig. 7C, m.ps). The posterior adductor originated from the anterior slope of the quadrate, and inserted into the adductor fossa (Fig. 7C, amp). The dermal palate of pachypleurosaurs is flat throughout, without even a

rudimentary development of a ventrally descending pterygoid flange. Although the pterygoideus muscle must have been present, its superficial portion in particular would not have been very strongly developed. By contrast, pachypleurosaurs are exceptional among stem-group sauropterygians by the frequent preservation of well ossified elements of the hyobranchial skeleton, indicative of a well differentiated hyobranchial apparatus that may have supported feeding (the frequent occurrence of hyobranchial elements in pachypleurosaurs may also be related to the large number of specimens found in articulation: Zangerl, 1935; Carroll & Gaskill, 1985; Rieppel, 1989; Sander, 1989).

The adductor chamber of pachypleurosaurs was confined anteriorly by the posterior wall of the large eyeball. Although pinnate muscles, with fibres arranged between tendinous sheets, do not bulge upon contraction (Alexander, 1968), some pressure on the posterior wall of the eyeball might have developed as a consequence of the contraction of the long-fibred, vertically orientated anterior portions of the external adductor which would be expected to insert directly into the dorsal margin of the lower jaw (coronoid process absent) and/or into the anteroventral part of the bodenaponeurosis. The build-up of any such pressure on the posterior wall of the eyeball can easily be prevented by the development of a tendinous sheath wrapping around the anterior portions of the external adductor, separating the latter from the eyeball, and preventing all possible bulging of the muscle towards the eyeball upon constriction (Fig. 7B, amem). If reconstructed as a special anterior addition to the bodenaponeurosis, the latter would have assumed a more complex, dual partition by comparison to the plesiomorphic pattern of its differentiation. An anteriorly ascending tendinous plate would have sheathed the external adductor anteriorly, while a posteriorly ascending tendinous plate would have served as site of insertion for the medial and deep portions of the external adductor (Fig. 7B, amem, amep). The adductor musculature would thus have been neatly confined to the adductor chamber, not entering into any competition for space with the eyeball.

Given the large eyeball, the concomitant reduction of the temporal region of the skull, the mildly elongated, yet blunt and rounded rostrum, and the restriction of the tooth row to a level in front of the orbit, the load-arm would always be long relative to the effort arm no matter where the bite point is placed. A geometrical configuration of jaws that results in a short effort arm relative to a long load arm is not a very efficient design to subdue vigorous prey, and the diet of pachypleurosaurs has been suggested to have been composed of soft-bodied invertebrates (cephalopods) and small or juvenile fish (Sander, 1989). The frequent

preservation a well developed hyobranchial skeleton suggests that it may have played an important role in securing prey. Opening of the jaws followed by rapid depression of the hyobranchial apparatus would have created the suction necessary to draw a potential prey item into the buccal cavity, which would then have been secured by a rapid ('snapping') closure of the jaws during the initial phases of which the oesophagus may have acted as a water reservoir to prevent redirection of the water flow, in a manner analogous to aquatic chelonians.

THE PHYLOGENETIC RELATIONSHIPS OF NOTHOSAUROIDEA

The Nothosauroidae constitute one of the major clades of Eusauropterygia, sister group of the second major clade, the Pistosauroidae (Rieppel, 1998b). The Nothosauroidae include four well-known genera with resolved phylogenetic interrelationships. *Simosaurus* is the relatively most plesiomorphic representative of the group, sister-taxon to the Nothosauria (Fig. 1). Within the Nothosauria, *Germanosaurus* is the sister-taxon of the Nothosauridae, which in turn include the two sister-taxa *Nothosaurus* and *Lariosaurus*. The tree for the Nothosauroidae therefore reads: (*Simosaurus* (*Germanosaurus* (*Nothosaurus*, *Lariosaurus*))). *Shingyisaurus* and *Sanchiaosaurus* from the Middle Triassic of China are nothosauroids *incertae sedis* (Rieppel, 1998c).

JAW MECHANICS IN *SIMOSAURUS*

Simosaurus is known from several three-dimensionally preserved skulls (Rieppel, 1994a). In a preliminary discussion of the jaw adductor musculature of *Simosaurus*, Rieppel (1989) hypothesized the presence of a dual jaw adductor system, which is also characteristic of crown-group sauropterygians (Taylor, 1992). The necessity to differentiate a dual jaw adductor muscle system results from the constraints to preserve a functional jaw adductor muscle fibre length in a clade characterized by an increasingly dorsoventrally depressed skull.

The skull of *Simosaurus* is brevirostrine, characterized by a short and broad, rounded rostrum without rostral constriction (Sanz, 1980). However, *Simosaurus* drastically differs from pachypleurosaur by a relative elongation of the temporal region in a dorsoventrally depressed skull (Fig. 8). The longitudinal diameter of the upper temporal fossa is much larger than the longitudinal diameter of the orbit. Furthermore, the maxilla, along with the jugal, is extended backwards along the ventral margin of the cheek region to a level below the midpoint of the longitudinal diameter of the upper temporal fossa. The

posterior extension of the maxilla carries the maxillary tooth row to a level well beyond the posterior margin of the orbit and below the anterior part of the upper temporal fossa. As a consequence, the anterior margin of the subtemporal fossa, through which the jaw adductors gain access to the lower jaw, lies at a level well behind the anterior margin of the upper temporal fossa (Rieppel, 1994a, figs 8,9), i.e. below the midpoint of the longitudinal diameter of the upper temporal fossa. Given this skull geometry, those parts of the external (and perhaps internal) adductor which originate in the anterior part of the upper temporal fossa slant in an anterodorsal–posteroventral direction, and must glide across the dorsal surface of the anterior margin of the subtemporal fossa upon contraction (Fig. 8B,C, amem, m.ps).

The lower jaw of *Simosaurus* again lacks a coronoid process, and the dentary tooth row extends backwards to match the extent of the maxillary tooth row. The adductor fossa of the lower jaw is restricted in its longitudinal extent to the level behind the anterior margin of the subtemporal fossa. The retroarticular process is well developed, and a tympanic membrane is assumed to be absent in *Simosaurus*, given the very shallow concavity on the posterior margin of the posteriorly slanting quadrate (Rieppel, 1989). The teeth of *Simosaurus* have a characteristic bulbous shape, suggesting some degree of durophagy. The anterior premaxillary and dentary teeth are not, or only very slightly, procumbent.

A distinctly developed, laterally projecting shelf on the surangular suggests the presence of a well-developed anteroventral 1b-portion of the external adductor (Fig. 8A, ames-1b). The organization of the other parts of the external adductor must have reflected the development of the dual jaw adductor system, and may hence be divided into an anterior and a posterior, instead of a medial and deep portion (Rieppel, 1989). Whether the pachypleurosaur are considered the sister group of the Nothosauroidae to the exclusion of the Pistosauroidae [(Pistosauroidae (Pachypleurosauria, Nothosauroidae))], or whether the Pachypleurosauria are considered to be the sister group of the Eusauropterygia [Pachypleurosauria (Pistosauroidae, Nothosauroidae)], it is conceivable that *Simosaurus* shared the dual partition of the bodenaponeurosis which is characteristic of pachypleurosaur, and which may have been present in the hypothetical ancestor shared by pachypleurosaur and Nothosauroidae or Eusauropterygia, respectively. The dorsal surface of the anterior tendinous sheet of the bodenaponeurosis would have been the site of insertion for those fibres of the external adductor which originate from the anterior part of the adductor fossa, it would have separated the anterior part of the external adductor from the deeper pterygoideus muscle,

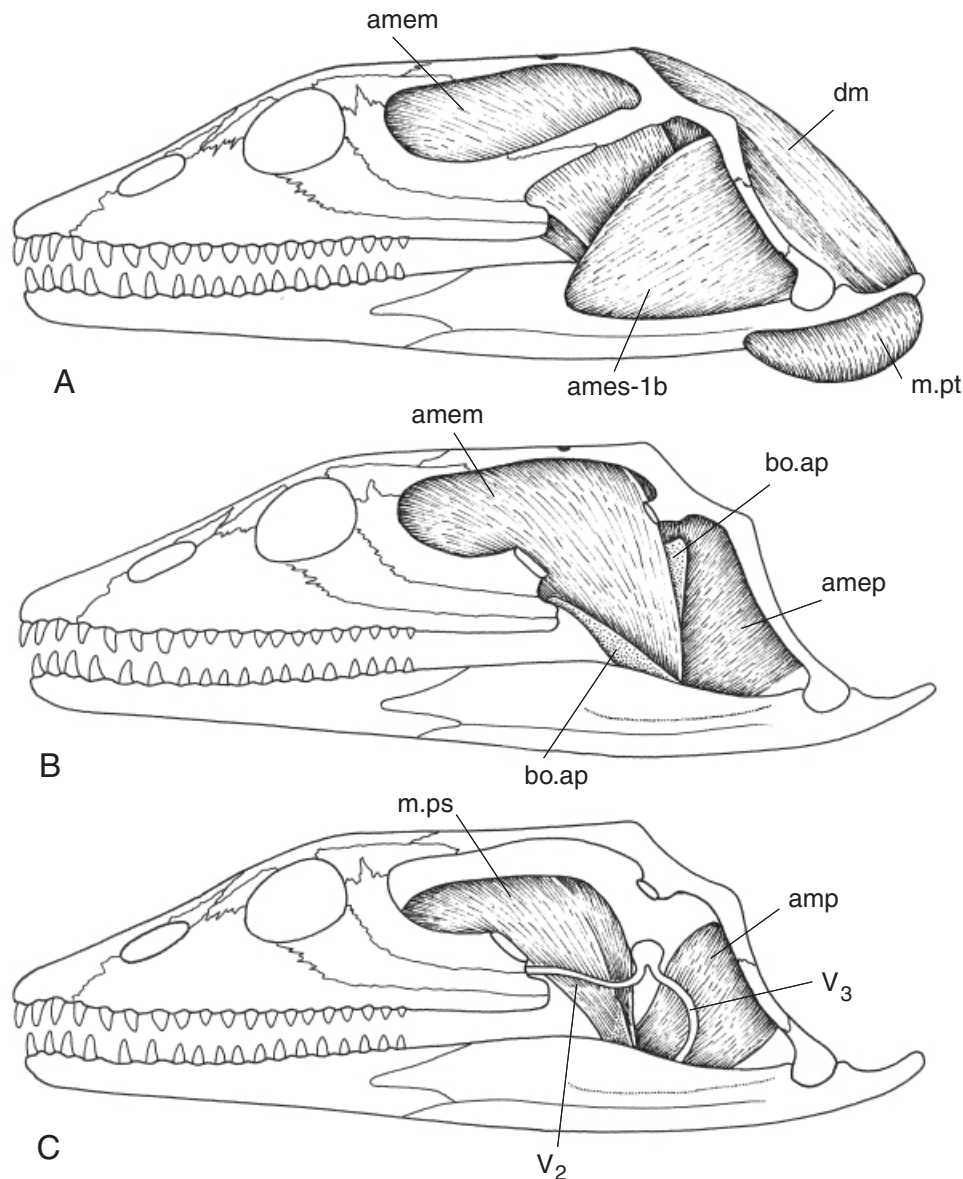


Figure 8. Hypothetical reconstruction of the jaw adductor musculature in *Simosaurus gaillardoti*. A–C, Successively deeper layers of dissection. Abbreviations: amem, m. adductor mandibulae externus medialis; amep, m. adductor mandibulae externus profundus; ames-1b, 1b-portion of m. adductor mandibulae externus superficialis; amp, m. adductor mandibulae posterior; bo.ap, bodenaponeurosis; dm, depressor mandibulae; m.ps, m. pseudotemporalis; m.pt, m. pterygoideus; V₂, maxillary branch of trigeminal nerve; V₃, mandibular branch of trigeminal nerve.

and it would have provided a protective sheath for the anterior part of the external adductor as it glides across the anterior margin of the subtemporal fossa during jaw opening and closure (Fig. 8B, amem). Such an anterior insertional tendon is also the optimal geometrical solution to preserve a functional fibre length for the anterodorsally–posteroventrally slanting fibres of the external adductor.

The posterior part of the external adductor would in turn insert into the posteromedial sheet of the bode-

naponeurosis. Its fibres would show a variable degree of posterodorsal inclination that would again reduce their relative stretching during jaw opening (Fig. 8B, amep).

In the absence of an epipterygoid, the pseudotemporalis muscle must be assumed to have originated from the ventral margin of the laterally descending flange of the parietal in front of the prootic and anterior to the trigeminal complex. This places the muscle again in an anterior position, resulting in an inclina-

tion of the fibres along an anterodorsally–posteroventrally sloping trajectory. The muscle must have inserted into the anterior corner of the adductor fossa, most likely with its own insertional tendon (Fig. 8C, m.ps). Given its position and orientation, the pseudotemporalis muscle would have complemented the action of the anterior part of the external adductor in jaw adduction. The posterior adductor must have originated from the anterior slope of the quadrate, and it must have inserted into the posterior part of the adductor fossa.

As in pachypleurosaurs, the ventral surface of the dermal palate is flat in *Simosaurus*. There is no distinct, ventrally projecting pterygoid (ectopterygoid) flange. Nevertheless, a pterygoid aponeurosis must be assumed to have attached to the ventral surface of the pterygoid and ectopterygoid along the anterior margin of the subtemporal fossa, giving rise to a moderately developed superficial pterygoideus muscle which would have wrapped around the posterior ventral margin of the lower jaw to insert into its ventrolateral surface (Fig. 8A, m.pt). Unlike the condition in pachypleurosaurs, however, the quadrate ramus of the pterygoid carries a distinct, ventrally projecting flange along the anterior part of its ventromedial margin, from which must have originated the deep pterygoideus muscle (Rieppel, 1994b). The latter would have inserted into the medial surface of the lower jaw below the adductor fossa, i.e. into the prearticular.

With the elongated tooth row, and the concentration of the insertion of the jaw adductors into the posterior part of the mandible, the jaw mechanism of *Simosaurus* is again characterized by a short effort arm relative to a potentially long load arm. This indicates the capacity for a snapping bite (P.L. Robinson, 1973), which is further enhanced by the dual jaw adductor system. Slanting along an anterodorsally–posteroventrally orientated trajectory, the anterior part of the external adductor, along with the pseudotemporalis and pterygoideus muscles, work at their greatest mechanical advantage with the jaws open. By contrast, the mechanical advantage of the anteroventral 1b-portion and other posterior parts of the external adductor, as well as of the posterior adductor, increases with decreasing gape.

The closed occiput of *Simosaurus*, a trait shared with pachypleurosaurs and nothosaurs, indicates a strong development of the epaxial neck muscles. The elongate retroarticular process, along with the absence of a tympanic membrane, suggests an equally strong development of the depressor mandibulae. Together, the epaxial neck muscles and the depressor mandibulae would have been able to effect rapid jaw opening. If coupled with hyoid depression, suction may have been created that was strong enough to capture

free-swimming, shelled, yet agile invertebrates such as ammonites, as well as fish. Rapid jaw closure may have been essential in securing the prey item. The pharyngeal cavity (through depression of the hyolaryngeal skeleton), and the oesophagus of the elongated neck would have to have acted as a water reservoir during feeding in order to prevent a reverse water flow during jaw closure. Instead of, or in addition to, performing suction feeding in analogy to aquatic chelonians, it is also conceivable that *Simosaurus* could have effected a rapid sideward motion with its head following rapid jaw opening, securing prey in a sideward directed snapping bite.

JAW MECHANICS IN *NOTHOSAURUS*

The trends that become apparent in the modification of the jaw mechanics of *Simosaurus* as compared to pachypleurosaurs become even more accentuated in the Nothosauridae, which include the sister-taxa *Nothosaurus* and *Lariosaurus*. No three-dimensionally preserved specimens of *Lariosaurus* are known (Rieppel, 1998d), but their general skull proportions may be assumed to be closely similar to those of *Nothosaurus*, of which several well-preserved, three-dimensional skulls are known (Rieppel & Wild, 1996; Rieppel, 2000a). If anything, specialization of the jaw adductors is carried to a greater degree in *Nothosaurus* than in lariosaurs.

Morphological specializations in *Nothosaurus* as compared to pachypleurosaurs and *Simosaurus* are numerous, and include further dorsoventral compression of the skull (Fig. 9). The skull in general becomes very narrow and elongate. Elongation not only affects the postorbital part of the skull, but also, and in particular, the preorbital area of the skull. The skull becomes longirostrine, developing a rostrum of variable relative length (Rieppel & Wild, 1996), which is distinctly set off from the remainder of the skull by a rostral constriction.

As in *Simosaurus*, the maxillary tooth row extends to a level below the anterior part of the temporal region in *Nothosaurus*, indeed to a level below the midpoint of the longitudinal diameter of the upper temporal fossa in the most derived species of the genus (Rieppel & Wild, 1996). The dentition becomes markedly heterodont in *Nothosaurus*. The premaxillary rostrum carries four to five much elongated and strongly procumbent fangs. These are separated by smaller anterior maxillary teeth from two enlarged maxillary fangs located immediately in front of the orbits (Fig. 9).

The lower jaw of *Nothosaurus* again lacks a well developed coronoid process. The mandibular symphysis is elongated, and carries enlarged and strongly procumbent anterior dentary fangs interlocking with

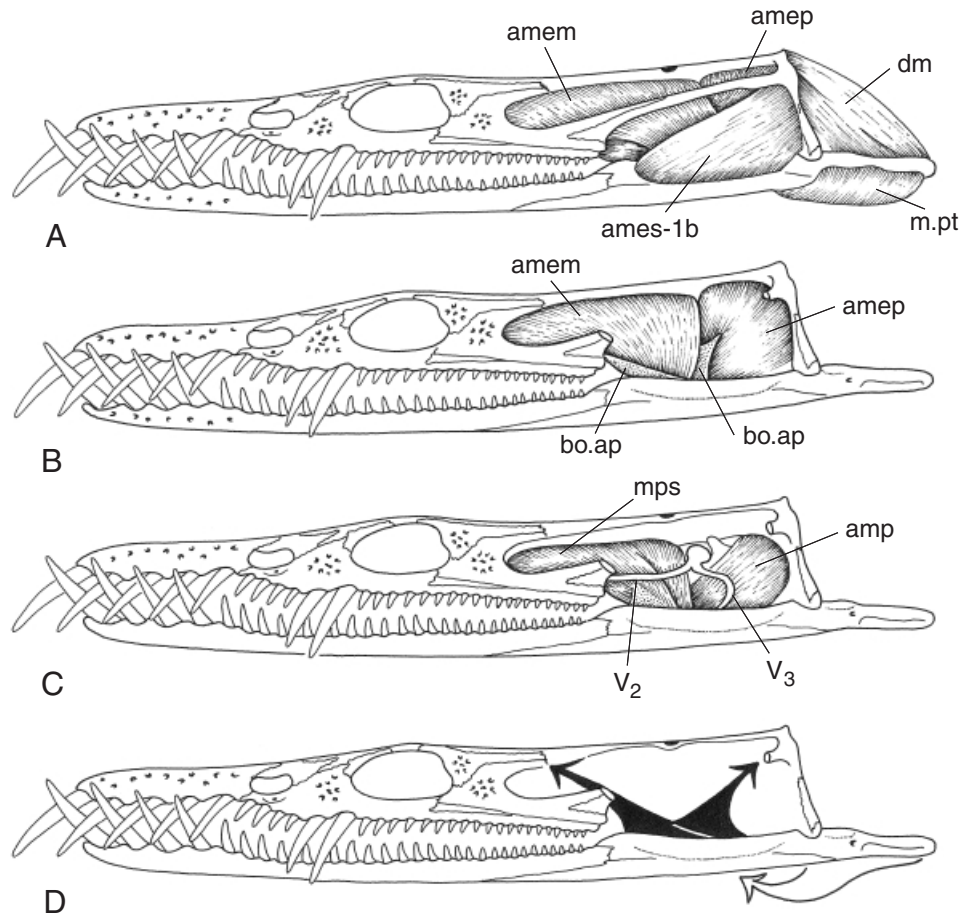


Figure 9. Hypothetical reconstruction of the jaw adductor musculature in *Nothosaurus mirabilis*. A–D, Successively deeper layers of dissection. Abbreviations: amem, m. adductor mandibulae externus medialis; amep, m. adductor mandibulae externus profundus; ames-1b, 1b-portion of m. adductor mandibulae externus superficialis; amp, m. adductor mandibulae posterior; bo.ap, bodenaponeurosis; dm, depressor mandibulae; m.ps, m. pseudotemporalis; m.pt, m. pterygoideus; V₂, maxillary branch of trigeminal nerve; V₃, mandibular branch of trigeminal nerve.

those of the premaxillae. Again, the anterior margin of the subtemporal fossa lies behind the anterior margin of the upper temporal fossa, i.e. below the midpoint of the longitudinal diameter of the upper temporal fossa, and the adductor fossa of the lower jaw is restricted in its longitudinal extent to the level behind the anterior margin of the subtemporal fossa. The retroarticular process is elongate, very distinctly so in some species (Rieppel, 2001b), and a tympanic membrane is assumed to be absent in *Nothosaurus* in view of the straight posterior margin of the strongly posteroventrally sloping quadrate. This suggests a strong development of the depressor mandibulae, complemented by strongly developed epaxial neck muscles inserting into the closed occiput.

The skull proportions of *Nothosaurus*, in particular the enhanced elongation of the postorbital region coupled with a strong dorsoventral depression, must have accentuated the differentiation of the dual jaw

adductor system (Fig. 9D). The surangular carries a very distinct, laterally projecting shelf indicating a well developed anteroventral 1b-portion of the external adductor (Fig. 9A, ames-1b). The anterior portion of the external adductor, originating from the anterior part of the upper temporal fossa, would again have inserted into the dorsal surface of an anterior sheet of the bodenaponeurosis. This tendinous sheet would have separated the external adductor from the deeper pterygoideus muscle, and would have glided across the anterior margin of the subtemporal fossa during jaw opening and closing cycles (Fig. 9B, amem). The posterior part of the external adductor would have inserted into the posteromedial sheet of the bodenaponeurosis with fibres more or less inclined in a posterodorsal direction (Fig. 9B, amep). In one species of *Nothosaurus*, i.e. *N. edingeriae*, the development of a low sagittal crest (Rieppel & Wild, 1994) might have allowed for some expansion of the posterior division of

the external adductor in a posterodorsal direction. As in *Simosaurus*, the pseudotemporalis muscle, originating from the lateral surface of the epipterygoid and the adjacent ventral margin of the descending parietal flange, would have complemented the action of the anterior part of the external adductor, while the posterior adductor would originate from the anterior slope of the quadrate and insert into the posterior part of the adductor fossa (Fig. 9C, m.ps).

The ventrally projecting pterygoid (ectopterygoid) flange is relatively weakly developed in *Nothosaurus* except for very large individuals, such as adults of *Nothosaurus giganteus* (Rieppel & Wild, 1996). A superficial pterygoideus muscle must be assumed to have been present, wrapping around the ventral margin of the posterior part of the lower jaw. Ventrally projecting flanges are developed along the entire length of the lateral and medial margins of the quadrate ramus of the pterygoid (Rieppel, 1994b), indicating a strong development of the deep pterygoideus muscle which would have inserted into the medial surface of the lower jaw ventral to the adductor fossa (prearticular).

Nothosaurus is characterized by an elongated yet narrow 'pincer' jaw as discussed by Taylor (1987). Given the strong dorsoventral compression of the skull, it is difficult to understand how a functional muscle fibre length could be maintained in *Nothosaurus* other than by the accentuated development of the dual jaw adductor system (Fig. 9D). This is especially true for those adductor fibres that originate from the middle section of the upper temporal fossa, for which a more or less vertical orientation relative to the long axis of the lower jaw must be assumed. Inclination in the transverse plane relative to the long axis of the lower jaw may have reduced the relative degree of stretching, but the effect cannot have been a major one given the narrowness of the skull. It should be kept in mind, however, that with the much elongated shape of the nothosaur skull, including the differentiation of an elongated rostrum, even a small degree of depression of the lower jaw will result in an appreciable gape at the front end of the jaws.

The differentiation of the heterodont dentition of nothosaurs suggests piscivorous habits, although smaller pachypleurosaurs (Sander, 1989) as well as small cyamodontoid placodonts (Tschanz, 1989) are known as stomach contents of *Lariosaurus*. Soft-bodied invertebrates (cephalopods) may also have been part of the diet of nothosaurs. Given their absolute size, some nothosaurs, in particular *Nothosaurus giganteus* and *Lariosaurus calcagnii*, must have been at the top of the food chain in their respective habitats. The low profile of the dorsoventrally compressed skull would have minimized drag

against water during rapid sideward movements of the head, generated by the elongated neck characteristic of nothosaurs. It is therefore conceivable that *Nothosaurus* secured prey by rapid, laterally directed snapping bites. Rapid opening of the jaws would have been effected by the strongly developed depressor mandibulae and the epaxial neck muscles. Given the narrowness of the skull of *Nothosaurus*, it is questionable that rapid jaw opening would have displaced enough water to create an efficient suction action. Instead, the head would have been moved laterally in a quick motion generated in the elongated neck. In addition to the general dorsoventral depression of the skull, keeping the jaws open at least to some degree during this lateral motion would have further prevented the buildup of a significant food-directed water stream alerting the prey-item or even carrying it away. Rapid closure of the jaws would have been effected by the anterior division of the external adductor contracting synchronously with the pseudotemporalis and the pterygoideus musculature. By contrast, the posterior compartments of the external adductor, along with the posterior adductor, would have gained mechanical advantage during jaw closure (Fig. 9D). The enlarged and strongly procumbent premaxillary and anterior dentary fangs must have functioned as a fish-trap, preventing the prey item to escape from the buccal cavity, rather than being used to puncture the prey. Once secured, the prey must have been swallowed whole using kinetic inertial feeding (Gans, 1969).

THE PHYLOGENETIC RELATIONSHIPS OF PISTOSAUROIDEA

Triassic Pistosauroidea includes four genera, viz. *Corosaurus*, *Cymatosaurus*, *Augustasaurus*, and *Pistosaurus*. The recent inclusion of *Augustasaurus* into the phylogenetic analysis of Triassic stem-group Sauropterygia (Rieppel, Sander & Storrs, in press) showed *Corosaurus* to be the most basal representative of the group, sister-taxon of all other pistosauroids. *Cymatosaurus*, in turn, is the sister-taxon of the remaining pistosaurs (Fig. 1). *Augustasaurus* was found to be the sister-taxon of *Pistosaurus*, the two taxa constituting the family Pistosauridae. The Pistosauridae, finally, are the sister group of Jurassic and Cretaceous crown-group sauropterygians. The pistosauroid tree therefore reads (*Corosaurus* (*Cymatosaurus* ((*Augustasaurus*, *Pistosaurus*) (crown-group Sauropterygia such as plesiosaurs)))).

JAW MECHANICS IN *CYMATOSAURUS*

The most basal pistosauroid, *Corosaurus*, is known from a single, incompletely preserved and dorsoven-

trally compressed skull (Storrs, 1991; Rieppel, 1998b). The three-dimensional reconstruction of the skull by Storrs (1991) suggests, by its geometry, a subdivision of the external adductor into an anterior and posterior division as is also characteristic of nothosauroids (Fig. 10). By comparison to nothosaurs, the dual jaw adductor system is less distinctly differentiated in *Corosaurus*, as is also the case in *Cymatosaurus* (Fig. 11).

The genus *Cymatosaurus* is known from skulls only. A lower jaw fragment has tentatively been referred to the genus (Rieppel, 1994a). Most of the known skulls of *Cymatosaurus* have been dorsoventrally compressed during fossilization (Rieppel, 1997) with two exceptions: 'specimen P' of *Cymatosaurus 'silesiacus'* (a subjective junior synonym of *C. latifrons* Gürich: Rieppel, 1997), described and illustrated by Schrammen (1899; this skull can no longer be located), and the holotype of *Cymatosaurus minor* Rieppel & Werneburg (1998). These two specimens were used as a template to reconstruct the lateral view of a *Cymatosaurus* skull on which to reconstruct the jaw adductor musculature (Fig. 11).

The skull of *Cymatosaurus* shares some striking yet convergent similarities with that of *Nothosaurus*, especially its elongate, narrow and dorsoventrally depressed shape, the development of a distinct premaxillary rostrum set off from the remainder of the skull by a rostral constriction, the heterodont dentition with enlarged and strongly procumbent premaxillary teeth, and the presence of two maxillary fangs located immediately in front of the orbit. However, important differences also exist. The temporal region is relatively less elongated in *Cymatosaurus* as compared to *Nothosaurus*, the postorbital arch is narrower, and the maxillary tooth row extends backwards to a level below the posterior margin of the orbit only. As a consequence, the anterior margin of the subtemporal fossa is located only a short distance behind the level of the anterior margin of the upper temporal

fossa. Furthermore, the ventrally projecting flange formed by the pterygoid and ectopterygoid for the attachment of the pterygoid aponeurosis is much more distinctly developed in *Cymatosaurus*, suggesting a more strongly developed superficial pterygoideus muscle. The quadrate is more vertically orientated in *Cymatosaurus* as compared to *Nothosaurus*, but its posterior margin is straight, suggesting the absence of a tympanic membrane. The occiput of *Cymatosaurus*, as indeed of all pistosauroids, retained wide open post-temporal fossae, which may indicate a somewhat lesser degree of development of the epaxial neck muscles in *Cymatosaurus* as compared to nothosauroids.

Some aspects of the reconstruction of *Cymatosaurus* must necessarily remain hypothetical, as no complete lower jaw is known. The general similarity to *Nothosaurus* suggests, however, that the mandibular symphysis must have been elongated to some degree at least, and must have carried enlarged and procumbent anterior dentary fangs to match the fangs of the premaxillary rostrum. By analogy to *Nothosaurus*, it is further assumed that the coronoid process was absent or very poorly developed, and that a retroarticular process was present.

As other sauropterygians, *Cymatosaurus* is reconstructed as having a well developed anteroventral 1b-portion of the external adductor (Fig. 11A, ames-1b). Phylogenetic bracketing (Witmer, 1997) also suggests that *Cymatosaurus* shared the dual nature of the bodenaponeurosis, present in pachypleurosaurs, nothosauroids, and crown-group sauropterygians (Taylor, 1992). The anterior raphe of the bodenaponeurosis would again have served as the insertion area of the anterior division of the external adductor. This raphe would also have separated the external adductor from the deeper pterygoideus muscle, and it would have provided a tendinous sheet gliding across the anterior margin of the subtemporal fossa and across the lateral surface of the well devel-

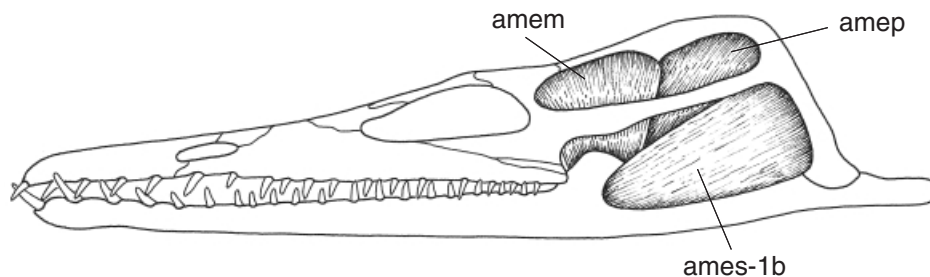


Figure 10. Hypothetical reconstruction of the jaw adductor musculature in *Corosaurus alcovensis* (skull reconstruction after Storrs, 1991 fig. 8). Superficial view of jaw adductor musculature. Abbreviations: amem, m. adductor mandibulae externus medialis; amep, m. adductor mandibulae externus profundus; ames-1b, 1b-portion of m. adductor mandibulae externus superficialis.

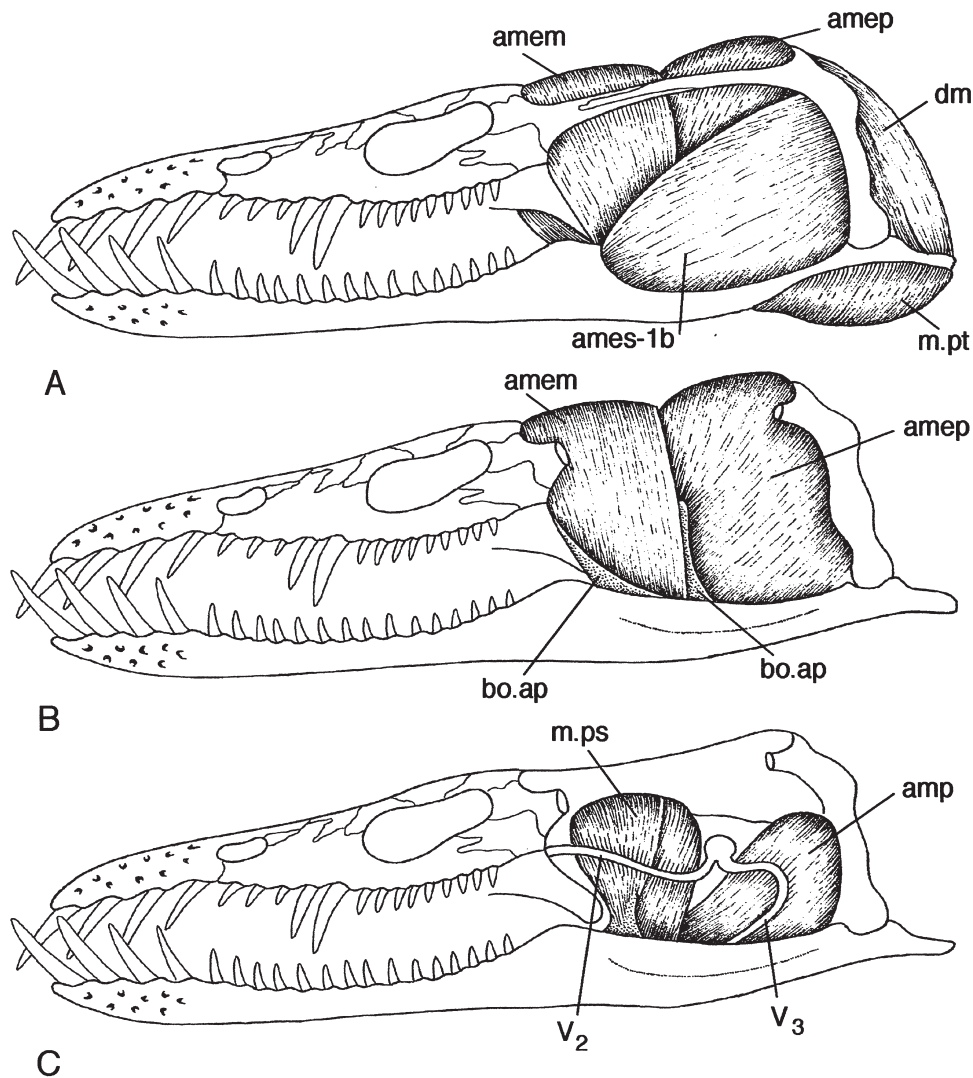


Figure 11. Hypothetical reconstruction of the jaw adductor musculature in *Cymatosaurus* sp. A–C, Successively deeper layers of dissection. Abbreviations: amem, m. adductor mandibulae externus medialis; amep, m. adductor mandibulae externus profundus; ames-1b, 1b-portion of m. adductor mandibulae externus superficialis; amp, m. adductor mandibulae posterior; bo.ap, bodenaponeurosis; dm, depressor mandibulae; m.ps, m. pseudotemporalis; m.pt, m. pterygoideus; V₂, maxillary branch of trigeminal nerve; V₃, mandibular branch of trigeminal nerve.

oped pterygoid–ectopterygoid flange during jaw opening and closing cycles (Fig. 11B, amem). Given the geometry of the skull of *Cymatosaurus*, the anterior division of the external adductor would be less inclined along an anterodorsally–posteroventrally slanting trajectory than is the case in *Nothosaurus*. The posterior division of the external adductor would be inserting into the posteromedial sheet of the bodenaponeurosis with fibres inclined to a greater or lesser degree in a posterodorsal direction (Fig. 11B, amep). The lateral braincase wall remains incompletely known, but a narrow epipterygoid appears to have slanted in an anterodorsal direction (Rieppel & Werneburg, 1998).

This places the pseudotemporalis muscle into the anterior division of the adductor chamber, where the muscle origin may have spread farther anteriorly along the ventral margin of the laterally descending flange of the parietal (Fig. 11C, m.ps). The muscle would have inserted into the anterior part of the adductor fossa of the lower jaw, perhaps with its separate tendon. The posterior adductor would have originated from the anterior slope of the quadrate, and inserted into the posterior part of the adductor fossa (Fig. 11C). Due to the well developed ventrally projecting pterygoid–ectopterygoid flange, the superficial portion of the pterygoideus muscle can be assumed to

have been strongly developed. The deep portion of the pterygoideus muscle would have originated from the quadrate ramus of the pterygoid, and inserted into the medial surface of the lower jaw ventral to the adductor fossa.

Given the lesser elongation of the temporal region of the skull, and the lesser posterior extent of the tooth-row in *Cymatosaurus* as compared to *Nothosaurus*, the effort arm will be longer relative to the load arm in *Cymatosaurus*. This suggests a relatively stronger bite in *Cymatosaurus*. The same is suggested by the more vertical orientation of the anterior division of the external adductor and of the pseudotemporalis muscle. Again, a relatively small degree of rotation of the lower jaw joint around the mandibular articulation will result in an appreciable gape at the anterior end of the jaws.

Although characterized by a potentially stronger bite, the general feeding strategy of *Cymatosaurus* must have corresponded rather closely to that described for *Nothosaurus* above. The 'pincer' jaw of *Cymatosaurus*, furnished with a heterodont dentition, was most probably operated in rapid, laterally directed bites. A similar prey may also be assumed between corresponding size classes of each genus (*Cymatosaurus* never gets as large as the largest species of *Nothosaurus*, such as *N. mirabilis* and, especially, *N. giganteus*).

JAW MECHANICS IN *PISTOSAURUS*

The skull of *Augustasaurus* and *Pistosaurus* are closely similar in general morphology. Two skulls of *Pistosaurus* are known (one of them now lost), both in three-dimensional preservation (Edinger, 1935; Meyer, 1847–1855), which allows the reconstruction of the jaw adductor musculature (Fig. 12). No lower jaw is known for *Pistosaurus*, but the lower jaw is preserved in *Augustasaurus*, and is here used to complete the muscle reconstruction for *Pistosaurus*.

The skull of *Pistosaurus* shows important differences compared to the skull of *Nothosaurus* and *Cymatosaurus*. It is not dorsoventrally compressed, but rather elevated, particularly in its posterior part where the parietals form a prominent sagittal crest (Fig. 12C). As in *Cymatosaurus*, the temporal region of the skull is less elongated compared to *Nothosaurus*, and the maxillary tooth-row does not extend posteriorly to a level beyond the posterior margin of the orbit. Flanges projecting from the postorbital, frontal, and parietal form a sloping platform that separates the anteromedial corner of the upper temporal fossa from the orbit (Edinger, 1935). This platform provides an extended site of origin for anterior and deep jaw adductor muscle fibres in the anteromedial corner of the upper temporal fossa. The ventrally projecting

pterygoid–ectopterygoid flange is prominent in *Pistosaurus*.

The premaxillary rostrum of *Pistosaurus* is more elongated and narrower than that of *Cymatosaurus* or *Nothosaurus*. Its shape must have been matched by the elongated mandibular symphysis, as is seen in *Augustasaurus*. *Pistosaurus* thus developed the most highly differentiated 'pincer' jaw (Taylor, 1987) among Triassic stem-group eosauropterygians (i.e. excluding plesiosaurs such as *Rhomaleosaurus*: Taylor, 1992) and although the dentition retained some degree of heterodonty, expressed in enlarged anterior premaxillary teeth and the presence of maxillary fangs, the heterodonty is much less expressed by comparison to *Cymatosaurus* and *Nothosaurus*, because the posterior premaxillary and remaining maxillary teeth are relatively larger. The anterior premaxillary (and dentary) teeth are less procumbent than in *Cymatosaurus* and *Nothosaurus*, and the teeth in general are not only larger, but also less numerous and more widely spaced, which suggests their use in puncturing prey. The use of the teeth in puncturing prey is also indicated by the capability to generate stronger bite forces as is suggested by the reconstruction of the jaw adductor musculature.

A laterally projecting shelf on the surangular of *Augustasaurus* indicates a well developed anteroventral 1b-portion of the external adductor in this genus, as is also assumed for *Pistosaurus* (Fig. 12A, ames-1b). Deeper layers of the external adductor are again reconstructed on the model of the dual nature of the bodenaponeurosis. The anterior raphe would have received the insertion of the anterior division of the external adductor, originating from the anterior part of the upper temporal fossa. As in *Cymatosaurus*, the raphe would have separated the external adductor from the pterygoideus muscle, and would have glided across the lateral surface of the extensive pterygoid–ectopterygoid flange during jaw opening and closure (Fig. 2B, amem). Again, the anterior division of the external adductor would be in a more vertical position than is the case in *Nothosaurus*, made possible by a lesser degree of dorsoventral depression of the skull. The posterior division of the external adductor, which would have inserted into the posteromedial sheet of the bodenaponeurosis, may be expected to have been very strongly developed, as it expanded in a posterodorsal direction to reach the upper limit of the sagittal crest and the posterior margin of the upper temporal fossa (Fig. 12B, amep). Given the skull geometry of *Pistosaurus*, the posterior division of the external adductor is again more vertically orientated than is the case in *Cymatosaurus* and *Nothosaurus*, made possible by the dorsal expansion of the temporal region of the skull in its posterior part.

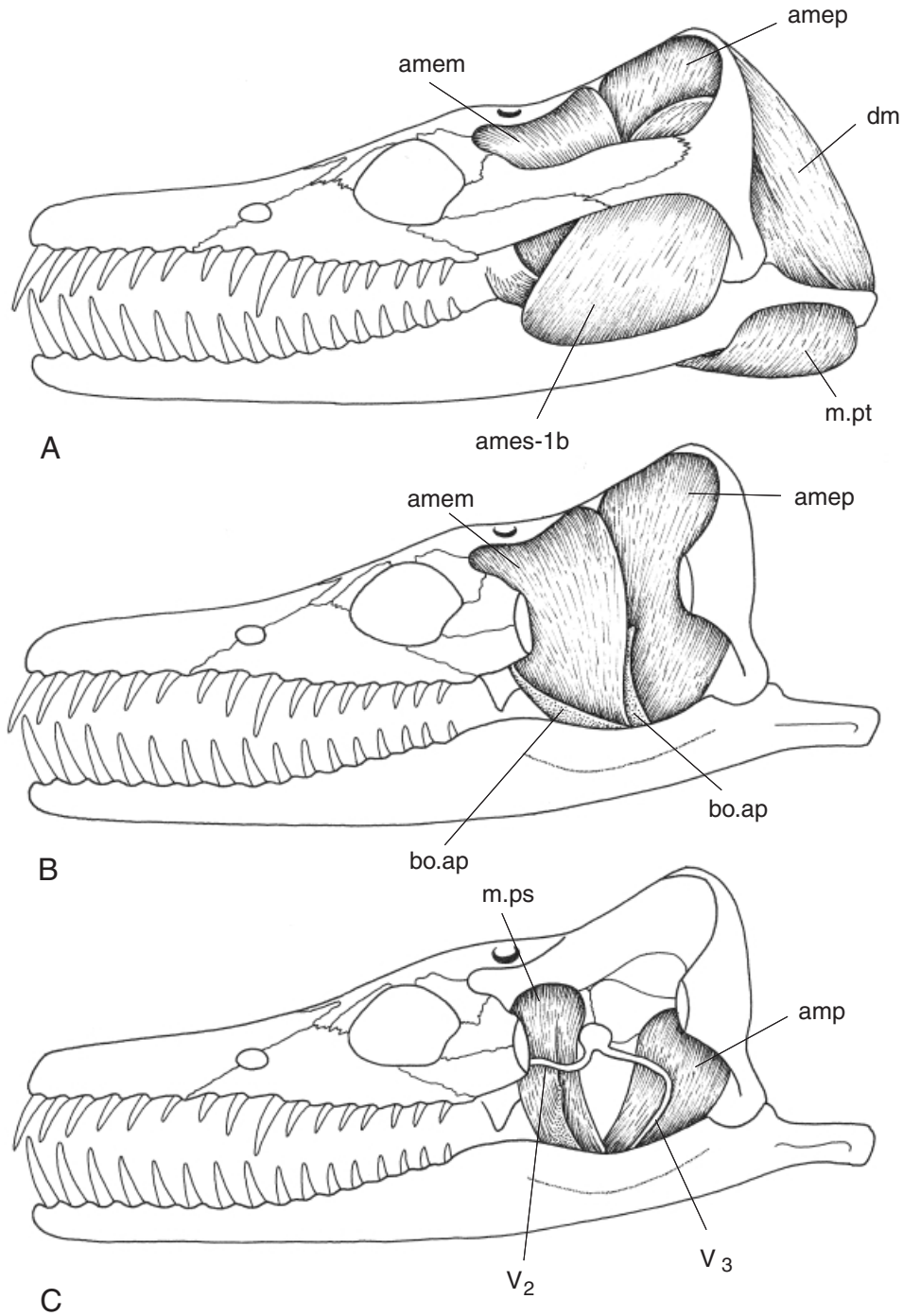


Figure 12. Hypothetical reconstruction of the jaw adductor musculature in *Pistosaurus longaevus*. A–C, Successively deeper layers of dissection. Abbreviations: amem, m. adductor mandibulae externus medialis; amep, m. adductor mandibulae externus profundus; ames-1b, 1b-portion of m. adductor mandibulae externus superficialis; amp, m. adductor mandibulae posterior; bo.ap, bodenaponeurosis; dm, depressor mandibulae; m.ps, m. pseudotemporalis; m.pt, m. pterygoideus; V₂, maxillary branch of trigeminal nerve; V₃, mandibular branch of trigeminal nerve.

The epipterygoid has a narrow dorsal process that is located in a rather anterior position in *Pistosaurus*. This places the pseudotemporalis muscle into the anteromedial corner of the adductor chamber, and its fibres would have slanted slightly posteroventrally on their way to the anterior corner of the adductor fossa in the lower jaw (Fig. 12C, m.ps). It is possible that the pseudotemporalis invaded part of the sloping surface formed by flanges from the postorbital, frontal and parietal as described above. The posterior adductor originated from the anterior surface of the quadrate, and its fibres extended in an anteroventral direction to insert into the posterior part of the adductor fossa (Fig. 12C, amp). The prominent pterygoid–ectopterygoid flange suggests a strong development of the superficial pterygoideus muscle.

The retroarticular process is well developed in *Augustasaurus*, and is assumed to have been similar in *Pistosaurus*. The differentiation of a box-like squamosal encasing the quadrate renders the presence of a tympanic membrane in *Pistosaurus* impossible, but suggests a strong development of the depressor mandibulae instead. Unlike in other Triassic stem-group sauropterygians, but as in crown-group taxa such as plesiosaurs, the squamosals meet each other in the midline of the skull behind the parietal sagittal crest, providing the site of insertion for superficial epaxial neck musculature. Deeper epaxial neck muscles must have inserted into the U-shaped supraoccipital, and into neighbouring braincase elements (posterior surface of the paroccipital processes).

With its narrow and elongated ‘pincer’ jaw, *Pistosaurus* was certainly ill-equipped for any kind of suction feeding. Instead, the size of the teeth, and their relatively widely spaced arrangement, suggest that *Pistosaurus* used its teeth to puncture prey. The same is suggested by the arrangement of the jaw adductor musculature. Given the degree of elongation of the rostrum, the effort arm may have been short rel-

ative to the load arm, especially if prey was caught with the anterior end of the jaw. The lesser dorsoventral depression of the skull allowed for a greater degree of vertical orientation of the jaw adductor muscle fibres other than the pterygoideus muscle, whereas the posterodorsal expansion of the temporal region of the skull into a parietal sagittal crest allowed an increase of the physiological cross-section of the posterior part of the external adductor. By contrast, the strongly developed pterygoideus muscle may have initiated rapid jaw closure. The postcranial skeleton of *Pistosaurus* remains incompletely known (Sues, 1987a), yet the neck of *Augustasaurus* is distinctly longer than in other stem-group Sauropterygia. If a similar length of the neck is assumed for *Pistosaurus*, it may be concluded that *Pistosaurus* secured prey by rapid yet powerful snapping bites correlated with rapid and far-reaching lateral movements of the head.

DISCUSSION AND CONCLUSIONS

The characterization of jaw mechanics in stem-group Sauropterygia allows the prediction of a number of basic adaptational strategies (Tables 1 and 2). However, a number of caveats must be considered when general predictions are made with respect to feeding strategies in fossils. First, prey size will vary relative to the absolute size of the predator. The absolute size of the predator is, however, subject to both ontogenetic as well as taxonomic variation. Immature individuals will prefer relatively smaller prey items compared to adults of the same taxon, just as an adult of a small size taxon will prefer relatively smaller prey than an adult of a large size taxon. When assigning different classes of (preferred) prey size to different taxa, ontogenetic variation of relative prey size preference must be kept in mind. Second, preference for relatively larger prey by adults of a large size

Table 1. Benthic feeders amongst Triassic stem-group Sauropterygia and their potential prey

Type and size of prey	Method of prey capture	Method of processing prey	Taxon
Small to large size epibenthic and sessile hard shelled invertebrates	Securing prey with procumbent premaxillary and dentary teeth	Crushing and swallowing	<i>Paraplagodus</i> , <i>Placodus</i> basal cyamodontoids (<i>Cyamodus</i>)
Small to medium size epibenthic or endobenthic non-sessile hard shelled invertebrates	Securing prey by suction feeding	Crushing and swallowing	Derived cyamodontoids (<i>Placochelyidae</i>)
Small, endo- or epibenthic, nonsessile soft-shelled invertebrates or plant material	Suction and sieving	Weak crushing and swallowing	<i>Henodus</i>

Table 2. Pelagic feeders amongst Triassic stem-group Sauropterygia and their potential prey

Type and size of prey	Method of prey capture	Method of processing prey	Taxon
Small size pelagic soft-shelled invertebrates (cephalopods)	Suction feeding	Swallowing by kinetic inertial feeding	Pachypleurosaurs
Small to large size hard-shelled pelagic invertebrates	Suction feeding	Crushing and swallowing	<i>Simosaurus</i>
Small to large size soft-shelled pelagic invertebrates, fish	Fish-trap dentition on pincers jaw	swallowing by kinetic inertial feeding	<i>Nothosaurus</i> <i>Cymatosaurus</i>
Small to large size soft-shelled pelagic invertebrates, fish	Puncturing dentition on pincers jaw	Swallowing by kinetic inertial feeding	Pistosaurus

taxon does not exclude the possibility that such an animal will not secure a smaller prey item should the opportunity arise. Third, there can be no doubt that the presence of a well-developed crushing dentition indicates a preference for hard-shelled invertebrates. In the absence of a well-developed crushing dentition, however, soft-shelled (or soft-bodied) invertebrates may have formed as much a part of the diet of an animal as would fish. On the other hand, some Triassic actinopterygians were characterized by a heavy scale covering.

A first distinction that can easily be drawn is that between benthic feeders and pelagic feeders (Tables 1 and 2). Placodonts qualify as benthic feeders, whereas eosauroptrygians qualify as pelagic feeders. Beyond this simple distinction, it can be concluded that suction feeding was characteristic for the feeding strategies of some Triassic sauropterygians. This concerns mostly those taxa characterized by a broad skull such as cyamodontoid placodonts (placochelyids and *Henodus*), pachypleurosaurs, and *Simosaurus*. These taxa are generally characterized by the lack of procumbent premaxillary and anterior dentary teeth that can be used to pick up prey items from the substrate or to catch free-swimming prey, and, in the case of the eosauroptrygian pachypleurosaurs and *Simosaurus*, by a homodont dentition. Taxa characterized by slender and elongate 'pincer' jaws are ill-equipped for suction-feeding, and must have caught their prey with a sideward directed snapping bite. Their dentition is either of the 'fish-trap', or of a puncturing type.

A general depression of the skull, including the temporal region, is characteristic for those taxa that secure prey with a sideward directed snapping bite. This imposes functional constraints on the jaw adduc-

tor musculature. A dual system of jaw adductors appears to have been the solution to that problem. Although the currently available hypotheses of sauropterygian interrelationships certainly do not allow unequivocal optimization of this character, it is possible that a bipartite bodenaponeurosis differentiated in the hypothetical ancestor of pachypleurosaurs and eusauropterygians in correlation with the presence of relatively large eye-balls and a short temporal region of the skull. This bipartite bodenaponeurosis would have allowed the differentiation of a dual jaw adductor system in more derived sauropterygians with a strongly depressed yet elongated temporal region of the skull.

The capture of prey – either through suction or a laterally directed snapping bite – is followed by the swallowing of prey. Swallowing of the prey most likely involved a component of kinetic inertial feeding, especially in nothosaurs and pistosaurians, the skulls of which are characterized by an elongate and narrow rostrum that would have made intraoral food processing using the tongue an awkward procedure. The effectiveness of kinetic inertial feeding under water has been questioned by Russell (1964, 1967), but as discussed by Gans (1969), it may be quite effective. Kinetic inertial feeding essentially depends on the density of the prey item relative to the density of the medium, and given that soft-shelled pelagic invertebrates and fish are hypothesized as the main prey items of nothosaurs and pistosaurians, kinetic inertial feeding would seem not to have been a problem. Other stem-group sauropterygians with broad and short skulls like placodonts or *Simosaurus* (and possibly also pachypleurosaurs) may have relied more heavily on their tongue for intraoral food transport.

As far as benthic feeders are concerned (Table 1), hard-shelled invertebrate prey is the obvious choice except for *Henodus*. Taxa with well developed and procumbent premaxillary and anterior dentary teeth (*Paraplocodus*, *Placodus*, *Cyamodus*, *Protenodontosaurus*) may be assumed to have used those to pick up sessile invertebrates from the substrate. Taxa that lacked such dentition (placochelyids) may be assumed to have secured nonsessile invertebrates, either epibenthic or endobenthic, by suction feeding.

Among the pelagic feeders (Table 2), pachypleurosaur and *Simosaurus*, characterized by a relatively short, broad and rounded snout, and a homodont dentition, may be assumed to have secured prey by suction feeding. The only possible exception is *Anarosaurus heterodontus* (Rieppel & Lin, 1995), which developed enlarged puncturing premaxillary and anterior dentary teeth potentially used for prey capture. Prey items of pachypleurosaur will have been relatively small and soft-bodied. The durophagous dentition of *Simosaurus* by contrast suggests a diet composed of shelled invertebrates.

Nothosaurs have elongate 'pincer' jaws furnished with a 'fish-trap' type dentition designed to capture prey with a quick, sideward directed snapping bite. The same appears to hold for *Cymatosaurus*, whereas pistosaurs have 'pincer' jaws furnished with a puncturing dentition, probably again used in a sideward directed snapping bite.

Triassic stem-group sauropterygians show relatively little overlap of hypothesized feeding strategies at the generic level, but some overlap still exists (Tables 1 and 2). There is overlap first among *Paraplocodus*, *Placodus*, and *Cyamodus*; second, among derived cyamodontoids (placochelyids); and third, among *Nothosaurus* and *Cymatosaurus*. Interestingly, the temporal and spatial distribution of the genera in question indicates some degree of habitat partitioning.

Placodus has so far never been reported in association with *Paraplocodus*, unless it is accepted that *Saurosphargis* from the lower Muschelkalk of Upper Silesia is a subjective synonym of *Paraplocodus* (Rieppel, 2000a). The overlap in temporal and spatial distribution of *Placodus* and *Cyamodus* is, however, frequent in localities of the Germanic Basin (Hagdorn & Rieppel, 1999), both in the lower Muschelkalk (*Cyamodus tarnowitzensis*) and in the upper Muschelkalk (mo1: *Cyamodus rostratus*, *Cyamodus muensteri*; mo2: *Cyamodus kuhnschnyderi*). Conversely, both *Cyamodus* and placochelyids are reported from several localities of the Alpine Triassic of late Anisian through early Carnian times, which contrasts with the exceedingly rare occurrence of *Placodus* in the Alpine Triassic. In fact, only two teeth of *Placodus* are known from the lower upper Anisian of the Alpine Triassic

(Rieppel & Dalla Vecchia, 2001). The *Placodus* tooth plate reported by Bassani (1892, not figured) from Dogna, north-eastern Italy, could easily be one of a cyamodontoid placodont, as these occur at that locality (Pinna, 1990). Conversely, cyamodontoid placodonts do show an extensive temporal and spatial overlap in their distribution, most notably at the Middle Triassic Makhtesh Ramon locality in Israel (Haas, 1959, 1975; Rieppel, work in progress), but the diversity of rostrum morphology (see Rieppel, 2000a for a summary) may well indicate trophic divergence within this clade at a finer scale than was possible to capture on the basis of a reconstruction of their jaw musculature and mechanics.

Finally, there is also a notable lack of overlap in the temporal and spatial distribution of the morphologically very similar genera *Cymatosaurus* and *Nothosaurus*, again suggesting some significant degree of habitat partitioning (Rieppel & Werneburg, 1998). Indeed, the varied trophic opportunities offered by near-shore habitats, with lagoonal basins interspersed among reef complexes, as well as those of shallow epicontinental seas, may well account for the taxic diversity of Triassic stem-group sauropterygians.

Finally, the crown-group Sauropterygia from the Jurassic and Cretaceous (plesiosaurs, pliosaurs and elasmosaurs) will evidently have to be classified as pelagic feeders, as they are obligatory marine organisms with limbs transformed into hydrofoils. A review of the feeding strategies throughout the crown-group Sauropterygia is beyond the scope of this study, but it is evident that different feeding strategies have been realized among them. Many taxa show skulls which in general proportions, rostrum shape and dentition resemble the pattern discussed for *Pistosaurus* (Taylor, 1992; Carpenter, 1996), suggesting functional analogy. Other taxa, such as *Plesiosaurus* (Storrs (1997) and *Thalassiodraco* (Storrs & Taylor, 1996) resemble *Simosaurus* more closely, with a short and rounded rostrum, but with jaws furnished with numerous needle-shaped teeth. As for *Simosaurus*, suction feeding may have been an important factor for these taxa in securing soft-bodied pelagic prey, the palisade of teeth forming a ratchet that retained the prey item inside the buccal cavity while the excess water was expelled.

ACKNOWLEDGEMENTS

This review of Triassic stem-group Sauropterygia would not have been possible without the generous help and hospitality of numerous colleagues and their respective institutions (listed in Rieppel, 2000a). H. Hagdorn, A. Garassino and G. Teruzzi deserve special credit for sharing their knowledge of Middle Triassic

stratigraphy and palaeoecology. Michael A. Taylor and Glenn W. Storrs provided much appreciated input which greatly improved the content of this paper. Karen Nordquist offered invaluable help with the preparation of the figures. Financial support for the research that built the basis for this study came from the U.S. National Science Foundation grants DEB-9220540, DEB-9419675 and DEB-9815235.

REFERENCES

- Alexander R, Mc. 1968.** *Animal Mechanics*. London: Sidgwick & Jackson.
- Bassani F. 1892.** Avanzi di vertebrati inferiori nel calcare marnoso triasico di Dogna in Friuli. *Rendiconti della Regia Accademia dei Lincei* **1**: 284–287.
- Broili F. 1912.** Zur Osteologie des Schädels von *Placodus*. *Palaeontographica* **59**: 147–155.
- Carpenter K. 1996.** A review of the short-necked plesiosaurs from the Upper Cretaceous of the Western Interior, North America. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **201**: 259–228.
- Carroll RL. 1984.** The emergence of marine reptiles in the Late Paleozoic and Early Mesozoic. In: Reif WE, Westphal F, eds. *Third Symposium on Mesozoic Terrestrial Ecosystems, Short Papers*. Tübingen: Attempto Verlag, 41–46.
- Carroll RL. 1985.** Evolutionary constraints in aquatic diapsid reptiles. *Special Papers in Palaeontology* **33**: 145–155.
- Carroll RL. 1997.** Mesozoic marine reptiles as models of long-term, large-scale evolutionary phenomena. In: Callaway JM, Nicholls EL, eds. *Ancient Marine Reptiles*. San Diego: Academic Press, 467–489.
- Carroll RL, Gaskill P. 1985.** The nothosaur *Pachypleurosaurus* and the origin of plesiosaurs. *Philosophical Transactions of the Royal Society of London* **B309**: 343–393.
- Collin R, Janis CM. 1997.** Morphological constraints on tetrapod feeding mechanisms: why were there no suspension-feeding marine reptiles. In: Callaway JM, Nicholls EL, eds. *Ancient Marine Reptiles*. San Diego: Academic Press, 451–466.
- Damme Jv Aerts P. 1997.** Kinematics and functional morphology of aquatic feeding in Australian snake-necked turtles (Pleurodira: *Chelodina*). *Journal of Morphology* **133**: 113–125.
- DeMar R, Barghusen HR. 1972.** Mechanics and evolution of the synapsid jaw. *Evolution* **26**: 622–637.
- Drevermann F. 1933.** Die Placodontier. 3. Das Skelett von *Placodus gigas* Agassiz im Senckenberg-Museum. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* **38**: 319–364.
- Druzinsky RE, Greaves WS. 1979.** A model to explain the posterior limit of the bite point in reptiles. *Journal of Morphology* **160**: 165–168.
- Edgeworth FH. 1935.** *The Cranial Muscles of Vertebrates*. Cambridge: Cambridge University Press.
- Edinger T. 1935.** *Pistosaurus*. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Abhandlungen* **B74**: 321–3459.
- Frey E, Riess J. 1982.** Considerations concerning plesiosaur locomotion. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **164**: 193–194.
- Gaffney ES. 1975.** A phylogeny and classification of the higher categories of turtles. *Bulletin of the American Museum of Natural History* **155**: 387–436.
- Gans C. 1966.** The functional basis of the retroarticular process in some fossil reptiles. *Journal of Zoology, London* **150**: 273–277.
- Gans C. 1969.** Comments on inertial feeding. *Copeia* **1969**: 855–857.
- Gans C, Bock WJ. 1965.** The functional significance of muscle architecture: a theoretical analysis. *Advances in Anatomy, Embryology, and Cell Biology* **38**: 115–142.
- Gans C, deVree F. 1987.** Functional bases of fiber length and angulation in muscle. *Journal of Morphology* **192**: 63–85.
- Gans C, deVree F, Carrier D. 1985.** Usage pattern of the complex masticatory muscles in the shingleback lizard, *Trachydosaurus rugosus*: a model for muscle placement. *American Journal of Anatomy* **173**: 219–240.
- Godfrey SJ. 1984.** Plesiosaur subaqueous locomotion: a reappraisal. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **1984**: 661–672.
- Gregory WK. 1946.** Pareiasaurs versus placodonts as near ancestors to turtles. *Bulletin of the American Museum of Natural History* **86**: 275–326.
- Haas G. 1959.** On some fragments of the dermal skeleton of Placodontia from the Trias of Aari en Naga, Sinai Peninsula. *Kunglita Svenska Vetenskapsakademiens Handlingar* **4**: 1–19.
- Haas G. 1973.** Muscles of the jaws and associated structures in the Rhynchocephalia and Squamata. In: Gans C, Parsons TS, eds. *Biology of the Reptilia*, Vol. 4. London: Academic Press, 285–490.
- Haas G. 1975.** On the placodonts of the Wadi Ramon area Muschelkalk. *Colloque International du Centre National de la Recherche Scientifique* **218**: 451–456.
- Hagdorn H, Rieppel O. 1999.** Stratigraphy of marine reptiles in the Triassic of Central Europe. *Zentralblatt für Geologie und Paläontologie, Teil I (1998)*: 651–678.
- Halstead LB. 1989.** Plesiosaur locomotion. *Journal of the Geological Society of London* **145**: 37–40.
- Huene Fv. 1936.** *Henodus chelyops*, ein neuer Placodontier. *Palaeontographica A* **84**: 99–148.
- Jaekel O. 1910.** Über das System der Reptilien. *Zoologischer Anzeiger* **35**: 324–341.
- Kuhn-Schnyder E. 1967.** Das Problem der Euryapsida. *Colloques Internationaux du Centre National de la Recherche Scientifique Paris* **163**: 335–348.
- Kuhn-Schnyder E. 1987.** Die Triasfauna der Tessiner Kalkalpen. XXVI. *Lariosaurus lavizzarii* n.sp. (Reptilia, Sauropterygia). *Abhandlungen der Schweizerischen Paläontologischen Gesellschaft* **110**: 1–24.
- Lakjer T. 1926.** *Studien über die Trigemini-Versorgte Kaumuskulatur der Sauropsiden*. Copenhagen: C.A. Reitzel.

- Lauder GV. 1985.** Aquatic feeding in lower vertebrates. In: Hildebrand M, Bramble DM, Liem KF, Wake DB, eds. *Functional Vertebrate Morphology*. Cambridge MA: The Belknap Press of Harvard University Press, 210–229.
- Lauder GV, Pendergast T. 1992.** Kinematics of aquatic prey capture in the snapping turtle *Chelydra serpentina*. *Journal of Experimental Biology* **164**: 55–78.
- Lauder GV, Schaffer HB. 1986.** Functional design of the feeding mechanism in lower vertebrates: unidirectional and bidirectional flow systems in the tiger salamander. *Zoological Journal of the Linnean Society* **88**: 277–290.
- Lin K, Rieppel O. 1998.** Functional morphology and ontogeny of *Keichousaurus hui* (Reptilia, Sauropterygia). *Fieldiana (Geology)* n.s. **39**: 1–35.
- Massare JA. 1988.** Swimming capabilities of Mesozoic marine reptiles: implications for methods of predation. *Paleobiology* **14**: 187–205.
- Mazin JM, Pinna G. 1993.** Paleoecology of the armoured placodonts. *Paleontologia Lombarda* n.s. **2**: 83–91.
- Meyer Hv. 1847–1855.** *Zur Fauna der Vorwelt. Die Saurier des Muschelkalkes mit Rücksicht auf die Saurier aus buntem Sandstein und Keuper*. Frankfurt a. M.: Heinrich Keller.
- Meyer Hv. 1863.** Die Placodonten, eine Familie von Sauriern der Trias. *Palaeontographica* **11**: 175–221.
- Motani R, Rothschild BM, Wahl W. 1999.** Large eyeballs in diving ichthyosaurs. *Nature* **402**: 747.
- Nosotti S, Pinna G. 1998.** Osteology of the skull of *Cyamodus kuhnschnyderi* Nosotti and Pinna 1993 (Reptilia, Placodontia). *Paleontologia Lombarda* n.s. **6**: 1–42.
- Peyer B. 1931.** Die Triasfauna der Tessiner Kalkalpen. IV. *Ceresiosaurus calcagnii* nov. gen. nov. spec. *Abhandlungen der Schweizerischen Paläontologischen Gesellschaft* **51**: 1–68.
- Pinna G. 1990.** *Protenodontosaurus italicus* n.g., n.sp., un nuovo placodonte del carniio italiano. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* **131**: 5–12.
- Pinna G, Nosotti S. 1989.** Anatomie, morfologia funzionale e paleoecologia del rettile placodonte *Psephoderma alpinum* Meyer, 1858. *Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* **25**: 1–50.
- Pooley AC, Gans C. 1976.** The Nile crocodile. *Scientific American* **234**: 114–124.
- Reif WE, Stein F. 1999.** Morphology and function of the dentition of *Henodus chelyops* (Huene, 1936) (Placodontia, Triassic). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **1999**: 65–80.
- Renesto S, Tintori A. 1995.** Functional morphology and mode of life of the Late Triassic placodont *Psephoderma alpinum* Meyer from the Calcare di Zorzino (Lombardy, N Italy). *Rivista Italiana di Paleontologia e Stratigrafia* **101**: 37–48.
- Rieppel O. 1979.** A functional interpretation of the varanid dentition (Reptilia, Lacertilia, Varanidae). *Gegenbaurs Morphologisches Jahrbuch* **125**: 797–817.
- Rieppel O. 1989.** A new pachypleurosaur (Reptilia: Sauropterygia) from the Middle Triassic of Monte San Giorgio, Switzerland. *Philosophical Transactions of the Royal Society of London* **B323**: 1–73.
- Rieppel O. 1990.** The development of the jaw adductor musculature in the turtle *Chelydra serpentina*. *Zoological Journal of the Linnean Society* **98**: 27–62.
- Rieppel O. 1993.** Patterns of Diversity in the Reptilian Skull. In: Hanken J, Hall BK, eds. *The Skull*, Vol. 2. Chicago: The University of Chicago Press, 344–390.
- Rieppel O. 1994a.** Osteology of *Simosaurus gaillardoti*, and the phylogenetic interrelationships of stem-group Sauropterygia. *Fieldiana (Geology)* n.s. **28**: 1–85.
- Rieppel O. 1994b.** The braincases of *Simosaurus* and *Nothosaurus*: monophyly of the Nothosauridae (Reptilia: Sauropterygia). *Journal of Vertebrate Paleontology* **14**: 9–23.
- Rieppel O. 1995.** The genus *Placodus*: Systematics, Morphology, Paleobiogeography, and Paleobiology. *Fieldiana (Geology)* n.s. **31**: 1–44.
- Rieppel O. 1997.** Revision of the sauropterygian reptile genus *Cymatosaurus* v. Fritsch, 1894, and the relationships of *Germanosaurus* Nopsca, from the Middle Triassic of Europe. *Fieldiana (Geology)* n.s. **36**: 1–38.
- Rieppel O. 1998a.** The systematic status of *Hanosaurus hupehensis* (Reptilia, Sauropterygia) from the Triassic of China. *Journal of Vertebrate Paleontology* **18**: 545–557.
- Rieppel O. 1998b.** *Corosaurus alcovensis* Case, and the phylogenetic interrelationships of Triassic stem-group Sauropterygia. *Zoological Journal of the Linnean Society* **124**: 1–41.
- Rieppel O. 1998c.** The status of *Shingyisaurus unexpectus* from the Middle Triassic of Kweichow, China. *Journal of Vertebrate Paleontology* **18**: 541–544.
- Rieppel O. 1998d.** The status of the sauropterygian reptile genera *Ceresiosaurus*, *Lariosaurus* and *Silvestrosaurus* from the Middle Triassic of Europe. *Fieldiana (Geology)* n. S. **38**: 1–46.
- Rieppel O. 1999.** Phylogeny and Paleobiogeography of Triassic Sauropterygia: problems resolved and unresolved. *Paleogeography, Paleoclimatology, Paleoecology* **153**: 1–15.
- Rieppel O. 2000a.** Sauropterygia I: Placodontia, Pachypleurosauria, Nothosauroida, Pistosauroida. In: Wellnhofer P, ed. *Encyclopedia of Paleoherpology*, Vol. 12A. Munich: Pfeil, 1–134.
- Rieppel O. 2000b.** *Paraplacodus* and the phylogeny of the Placodontia (Reptilia: Sauropterygia). *Zoological Journal of the Linnean Society* **130**: 635–659.
- Rieppel O. 2001a.** The cranial anatomy of *Placochelys placodonta* Jaekel, 1902, and a review of the Cyamodontoidea (Reptilia, Placodontia). *Fieldiana (Geology)* n.s. **45**: 1–104.
- Rieppel O. 2001b.** A new species of *Nothosaurus* (Reptilia: Sauropterygia) from the upper Muschelkalk (lower Ladinian) of southwestern Germany. *Palaeontographica A* **263**: 137–161.
- Rieppel O, Dalla Vecchia FM. 2001.** Marine reptiles from the Triassic of the Tre Venezie Area, northeastern Italy. *Fieldiana (Geology)* n.s. **44**: 1–25.
- Rieppel O, Gronowski RW. 1981.** The loss of the lower temporal arcade in diapsid reptiles. *Zoological Journal of the Linnean Society* **72**: 203–217.

- Rieppel O, Hagdorn H. 1998.** Fossil Reptiles from the Spanish Muschelkalk (Mont-ral and Alcover, Province Tarragona). *Historical Biology* **13**: 77–97.
- Rieppel O, Lin K. 1995.** Pachypleurosaur (Reptilia: Sauropterygia) from the Lower Muschelkalk, and a review of the Pachypleurosauridae. *Fieldiana (Geology)* n.s. **32**: 1–44.
- Rieppel O, Sander PM, Storrs GW. 2002.** The skull of the pistosaur *Augustasaurus* from the Middle Triassic of northwestern Nevada. *Journal of Vertebrate Paleontology*, in press.
- Rieppel O, Werneburg R. 1998.** A new species of the sauropterygian *Cymatosaurus* from the lower Muschelkalk of Thuringia, Germany. *Palaeontology* **41**: 575–589.
- Rieppel O, Wild R. 1994.** *Nothosaurus edingeri* Schultze, 1970: diagnosis of the species and comments on its stratigraphical occurrence. *Stuttgarter Beiträge für Naturkunde B204*: 1–13.
- Rieppel O, Wild R. 1996.** A revision of the genus *Nothosaurus* (Reptilia, Sauropterygia) from the Germanic Triassic, with comments on the status of *Conchiosaurus clavatus*. *Fieldiana (Geology)* n.s. **34**: 1–82.
- Rieppel O, Zanon RT. 1997.** The interrelationships of Placodontia. *Historical Biology* **12**: 211–227.
- Robinson PL. 1973.** A problematic reptile from the British Upper Trias. *Journal of the Geological Society* **129**: 457–479.
- Robinson JA. 1975.** The locomotion in plesiosaurs. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **149**: 286–332.
- Robinson JA. 1977.** Intracorporal force transmission in plesiosaurs. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **153**: 86–128.
- Russell DA. 1964.** Intracranial mobility in mosasaurs. *Postilla* **86**: 1–19.
- Russell DA. 1967.** Systematics and morphology of American mosasaurs. *Peabody Museum of Natural History, Yale University, Bulletin* **23**: 1–240.
- Sander PM. 1989.** The pachypleurosaurids (Reptilia: Nothosauria) from the Middle Triassic of Monte San Giorgio, (Switzerland), with the description of a new species. *Philosophical Transactions of the Royal Society of London B325*: 561–670.
- Sander PM, Rieppel O, Bucher H. 1997.** A new pistosaurid (Reptilia: Sauropterygia) from the Middle Triassic of Nevada and its implications for the origin of plesiosaurs. *Journal of Vertebrate Paleontology* **17**: 526–533.
- Sanz JL. 1976.** *Lariosaurus balsami* (Sauropterygia, Reptilia) de Estada (Huesca). *Estudios Geológicos* **32**: 547–567.
- Sanz JL. 1980.** Algunas precisiones morfofuncionales en Nothosauria y Pachypleurosauria (Sauropterygia, Reptilia). *Estudios Geológicos* **35**: 421–426.
- Schmidt S. 1984.** Paleoecology of nothosaurs. In: Reif W, Westphal F, eds. *Third Symposium on Mesozoic Terrestrial Ecosystems, Short Papers*. Tübingen: Attempto Verlag, 215–219.
- Schmidt S. 1985.** Biomechanics of *Nothosaurus*. In: Riess J, Frey E, eds. *Konstruktionsprinzipien Lebender und Ausgestorbener Reptilien. Konzepte SFB 230, Heft 4*. Stuttgart and Tübingen: University of Stuttgart and University of Tübingen, 193–198.
- Schmidt S. 1986.** *Lokomotion und Lebensweise der Nothosaurier (Diapsida, Sauropterygia, Trias)*. PhD Thesis, Tübingen: Eberhard-Karls-University.
- Schmidt S. 1988.** Die Nothosaurier des Crailsheimer Muschelkalks. In: Hagdorn, H, ed. *Neue Forschungen zur Erdgeschichte von Crailsheim*. Korb (Stuttgart): Goldschneck, 144–150.
- Schrammen A. 1899.** 3. Beitrag zur Kenntnis der Nothosauriden des unteren Muschelkalkes in Oberschlesien. *Zeitschrift der Deutschen Geologischen Gesellschaft* **51**: 388–408.
- Schumacher GH. 1973.** The head muscles and hyolaryngeal skeleton of turtles and crocodylians. In: Gans C, Parsons TS, eds. *Biology of the Reptilia*, Vol. 4. London: Academic Press, 101–199.
- Seymour RS. 1982.** Physiological adaptations to aquatic life. In: Gans C, Pough FH, eds. *Biology of the Reptilia*, Vol. 13. London: Academic Press, 1–51.
- Song J, Boord RL. 1993.** Motor components of the trigeminal nerve and organization of the mandibular arch muscles in vertebrates. *Acta Anatomica* **148**: 139–149.
- Stefani M, Arduini P, Garassino A, Pinna G, Teruzzi G, Trombetta GL. 1992.** Paleoenvironment of extraordinary fossil biotas from the Upper Triassic of Italy. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* **132**: 309–335.
- Stein F. 1995.** Pflasterzahnsaurier (Placodontia). In: Hungerbühler A, Maisch MW, Westphal F, eds. *Schwimm-saurier*. Tübingen: Attempto Verlag, 35–44.
- Storrs GW. 1991.** Anatomy and relationships of *Corosaurus alcovensis* (Diapsida: Sauropterygia) and the Triassic Alcova Limestone of Wyoming. *Bulletin of the Peabody Museum of Natural History* **44**: 1–151.
- Storrs GW. 1993.** Function and phylogeny in sauropterygian (Diapsida) evolution. *American Journal of Science* **293A**: 63–90.
- Storrs GW. 1997.** Morphological and taxonomic clarification of the genus *Plesiosaurus*. In: Callaway JM, Nicholls EL, eds. *Ancient Marine Reptiles*. San Diego: Academic Press, 191–216.
- Storrs GW, Taylor MA. 1996.** Cranial anatomy of a new plesiosaur genus from the lowermost Lias (Rhaetian / Hettangian) of Street, Somerset, England. *Journal of Vertebrate Paleontology* **16**: 403–420.
- Sues HD. 1987a.** Postcranial skeleton of *Pistosaurus* and interrelationships of the Sauropterygia (Diapsida). *Zoological Journal of the Linnean Society* **90**: 109–131.
- Sues HD. 1987b.** On the skull of *Placodus gigas* and the relationships of the Placodontia. *Journal of Vertebrate Paleontology* **7**: 138–144.
- Sues HD, Carroll RL. 1985.** The pachypleurosaurid *Dactylosaurus schroederi* (Diapsida: Sauropterygia). *Canadian Journal of Earth Sciences* **22**: 1062–1608.
- Tarsitano S, Riess J. 1982.** Plesiosaur locomotion – underwater flight versus rowing. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **164**: 188–192.

- Taylor MA. 1981.** Plesiosaurs – rigging and ballasting. *Nature* **290**: 628–629.
- Taylor MA. 1986.** Lifestyle of plesiosaurs. *Nature* **319**: 179.
- Taylor MA. 1987.** How tetrapods feed in water: a functional analysis by paradigm. *Zoological Journal of the Linnean Society* **91**: 171–195.
- Taylor MA. 1992.** Functional anatomy of the head of the large aquatic predator *Rhomaleosaurus zetlandicus* (Plesiosauria, Reptilia) from the Toarcian (Lower Jurassic) of Yorkshire, England. *Philosophical Transactions of the Royal Society of London* **B335**: 247–280.
- Taylor MA. 2000.** Functional significance of bone ballast in the evolution of buoyancy control strategies by aquatic tetrapods. *Historical Biology* **14**: 15–31.
- Throckmorton GS. 1978.** Action of the pterygoideus muscle during feeding in the lizard *Uromastyx aegyptius* (Agamidae). *Journal of Morphology* **190**: 217–222.
- Tschanz K. 1989.** *Lariosaurus buzzii* n. sp. from the Middle Triassic of Monte San Giorgio (Switzerland), with comments on the classification of nothosaurs. *Palaeontographica* **A208**: 153–179.
- Vogt C. 1983.** *Evolutive Palökologie der Placodontier* (Placodus, Henodus; *Euryapsida*, *Trias*). PhD Thesis, Tübingen: Eberhard-Karls-University.
- Walls GL. 1942.** *The Vertebrate Eye*. Bloomfield Hills, MI: The Cranbrook Institute of Science.
- Werth A. 2000.** Feeding in marine mammals. In: Schwenk K, ed. *Feeding, Form, Function, and Evolution in Tetrapod Vertebrates*. San Diego: Academic Press, 487–526.
- Westphal F. 1988.** Pflasterzahnsaurier (Placodonten) aus dem süddeutschen Muschelkalk (Mitteltrias). In: Hagdorn H, ed. *Neue Forschungen zur Erdgeschichte von Crailsheim*. Korb (Stuttgart): Goldschneck. 151–165.
- Whiteside DI. 1986.** The head skeleton of the Rhaetian sphenodontid *Diphydontosaurus avonensis* gen. et sp. nov. and the modernizing of a living fossil. *Philosophical Transactions of the Royal Society of London* **B312**: 379–430.
- Williston SW. 1914.** *Water Reptiles of the Past and Present*. Chicago: The University of Chicago Press.
- Williston SW. 1917.** The phylogeny and classification of reptiles. *Journal of Geology* **25**: 411–421.
- Williston SW. 1925.** *The Osteology of the Reptiles*. Cambridge MA: Harvard University Press.
- Witmer LM. 1997.** The evolution of the antorbital cavity of archosaurs: a study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. *Society of Vertebrate Paleontology Memoir* **3**: 1–73.
- Zangerl R. 1935.** Die Triasfauna der Tessiner Kalkalpen. 9. *Pachypleurosaurus edwardsi* Cornalia sp., Osteologie – Variationsbreite – Biologie. *Abhandlungen der Schweizerischen Paläontologischen Gesellschaft* **56**: 1–80.
- Zanon RT. 1989.** *Paraplacodus* and the diapsid origin of Placodontia. *Journal of Vertebrate Paleontology* **9**: 47A.