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Dicynodont jaw mechanisms reconsidered: the *Kannemeyeria* (Anomodontia Therapsida) masticatory cycle

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Abstract. The unique feature of the dicynodont masticatory apparatus is the double-convex jaw articulation, which permitted free antero-posterior movement. Since Crompton and Hotton's demonstration of the jaw articulation, most subsequent work has argued either for or against true propaliny of the lower jaw. It has been generally agreed that food was processed by shearing. Grinding or crushing was not viewed as an integral part of the masticatory cycle. Examination of undistorted cranial material of *Kannemeyeria* Weithofer revealed that there may well be an alternative jaw action to that of the classic antero-posterior one. A functional study of the jaw morphology of this taxon yields evidence to support a specific adaptive specialisation of the sliding double condyle, to accommodate a predominantly crushing and grinding action. This action is described and investigated using a model that recognises a single, fixed pivot point. Traction lines represent muscle forces acting around a bell-crank curve, and can be described using simple motion laws. Such evidence has several implications for the interpretation of the total cranial structure of the animal in functional terms.

Key words. Dicynodontia. *Kannemeyeria*. Jaw articulation. Mastication. Triassic.

Introduction

The skull structure of dicynodonts, specialised for herbivory, made the largest contribution to the great success of the Dicynodontia in the Permian, as well as their Triassic resurgence after the global Permian-Triassic extinction events (King *et al.*, 1989). Although Pearson (1924) alluded to the unique dicynodont jaw articulation in *Kannemeyeria* Weithofer (1888), this mechanism was first described by Watson (1948), who stressed that the large apparently sliding jaw articulation in dicynodonts must have enabled the lower jaw to move freely backwards and forwards through a considerable distance. He thus envisaged dicynodonts employing propalinal movements to process plant material. Crompton and Hotton (1967) argued that dicynodonts did not exhibit true propaliny and that the anterior muscular action was merely a recovery stroke, but it has been convincingly shown that propaliny was a definite possibility in some large dicynodonts (Cluver and King, 1983; King *et al.*, 1989). The critical elements involved in the production of the dicynodont masticatory cycle include the condylar surfaces and characteristics of the quadrate and articular, the contact areas on the dentary symphysis and palate, the origins, insertions and orientations of the jaw adductor musculature, and the cranial modifications made to accommodate both muscle action and jaw function.

Masticatory apparatus of *Kannemeyeria*

Although the masticatory apparatus and cycle of dicynodonts have been extensively examined in the past (Crompton and Hotton, 1967; Cluver, 1974; King *et al.*, 1989), no work has been conducted on any of the Triassic dicynodonts and certainly not on *Kannemeyeria*. The cranium of *Kannemeyeria* is characterised by an elongate preorbital region, an obliquely orientated occiput, and in particular a narrow and high intertemporal crest drawn-out postero-dorsally. *Kannemeyeria* exhibits a continuous set of features which can be closely associated to a specific jaw action, and in particular are related to a more dorsal origin of the external adductor musculature. Such an origin allows for the potential of a greater vertical component to the force applied by the adductor musculature. Although the action of such a muscular moment arm is largely associated with a greater force at the alveolar border, it also provides for an alternative masticatory cycle other than the classic antero-posterior one employed by many Permian and Triassic dicynodonts.

Crompton and Hotton (1967) demonstrated that dicynodonts often employed some degree of vertical component to the force exerted by the external adductor musculature, which was then translated into

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an overall horizontal force by the morphological characteristics of the articular condyle and articular recess. In *Kannemeyeria*, however, the articular condyle and recess have a definite vertical orientation (Renaut, 2000), indicating a dorso-ventral action at the jaw joint instead of the typical antero-posterior one. Such an action results in a vertical crushing action by the lower jaw against the palate. The more dorsal origin of the external adductor muscles in *Kannemeyeria* has been suggested by Keyser and Cruickshank (1979) as well as King (1990), but the current study has demonstrated that the articulation, itself, has a vertical orientation and thus action. The articular recess has a high anterior wall and the depression has a marked vertical orientation, and yet occurs slightly anterior to the dorsal rim of the lateral condyle. Consequently, the jaw joint probably performed two distinct sets of operations: a primary action where the articular is moved up and down the quadrate (phase 1 of the masticatory cycle), and a secondary action where the quadrate is slotted into and out of the articular recess (phase 2 of the cycle). Such a configuration also means that in *Kannemeyeria*, a muscle employing any horizontal component will have most of its force converted into a vertical action by the jaw articulation. The condition in *Kannemeyeria* may thus be envisaged to employ more crushing and grinding actions than the typical shearing actions reconstructed for large Permian dicynodonts.

It is well accepted that the critical dicynodont jaw adductor muscles would have been comparable to those found in extant reptilian grade amniotes, and can be differentiated into external and internal adductor groups (King *et al.*, 1989). The external adductor group can be divided into lateral and medial external adductor muscle units, responsible for the major jaw closing action, as well as the power strokes of the masticatory cycle. The interior adductor group is usually represented by the pterygoideus muscle units. Using a pattern of main muscle groups outlined by King *et al.* (1989) and examining the abundance of well preserved and relatively undistorted specimens at the Bernard Price Institute, it is possible to accurately reconstruct the generalised positions of the essential muscle groups responsible for the masticatory cycle.

Masticatory cycle of *Kannemeyeria*

The two phases of jaw action (figure 1) combine to form a complete masticatory cycle composed of four main stages. To achieve the position of maximum gape, stage 1, at the end of jaw depression, the articular condyles were moved anteriorly along the quadrate condyles a maximum distance, to reach their extreme ventral rim. This caused the lower jaw to open, an action largely produced by gravity acting on the dentary symphysis with a simultaneous action on the jaw articulation by the m. depressor mandibulae. From this stage the lower jaw was elevated to produce the beak-bite, and the resting position of stage 2. Elevation was primarily accomplished by the external adductor musculature (AEM and AEL). Once the external adductor musculature was engaged, it exerted an extremely powerful force on the lower jaw, translated at the jaw articulation into an almost entirely vertical direction. Since the vertical force exerted by this muscle group was applied at the lower jaw and by transferred energy to the articulation the beak-bite was very powerful. The lateral articular condyle was moved, indirectly, downwards so that the quadrate condyle came to rest against the upper end of the lateral articular condylar surface. The upward motion of the jaw was controlled at the jaw articulation by the pterygoideus musculature and the posterior adductor muscle, and simultaneously guided at the dentary symphysis by the tusks and caniniform processes.

From stage 2 the masticatory cycle entered its second phase characterised by a crushing and grinding action between the opposing jaw surfaces, while the jaws were effectively closed. This was achieved by moving the articular condyle postero-ventrally, stage 3, so that the quadrate rested in the articular recess, followed by stage 4 where the articular condyle was pulled antero-dorsally, so that the quadrate condyle was moved out of the recess and onto the dorsal rim of the lateral articular condyle. The action at stage 3 was produced by the vertical action of the external adductor muscles pulling the dentary pad and table directly against the palatal pad and palate, whereas that at stage 4 was produced by the pterygoideus musculature pulling the articular condyle upwards and forwards. This action secondarily forced the posterior end of the dentary pad against the palatal surfaces. Further contraction by the pterygoideus musculature, with greater relaxation of the external adductor muscles, brought the lower jaw back to a resting state, and represented the recovery stroke of the lower jaw.

It is evident that the horizontal force model used by Crompton and Hotton (1967) to describe the jaw action of Permian dicynodonts can not be applied to *Kannemeyeria*. We are not, in this case, interested in the occlusal force of the lower jaw, but rather in a descriptive interpretation of the observed jaw and articulation morphology. Consequently, an alternative description of the jaw mechanism may be constructed which includes the singular joint morphology and jaw action, and is based on the recognition that all jaw articulations behave as rigid levers pivoting

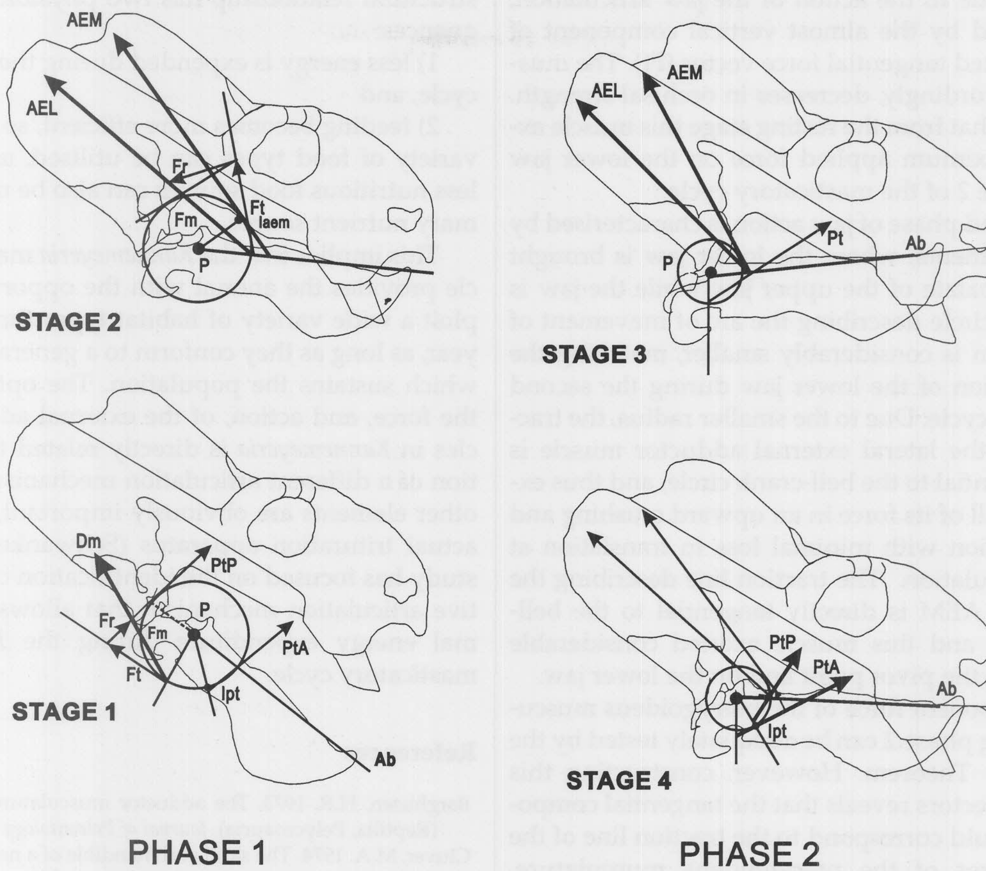

Figure 1. *Kannemeyeria* masticatory cycle. Circle - radius of bell-crank curve, Dm - depressor mandibulae, Ab - alveolar border, P - pivot point. Traction lines AEM - medial external adductor muscle, AEL - lateral external adductor muscle PtP - posterior pterygoideus fibres, PtA - anterior pterygoideus fibres, Iaem - interception point of the medial external adductor muscle. Ipt - interception point of the anterior pterygoideus muscle fibres, Fm - applied muscular force, Ft - tangential force component, Fr - resultant force.

about a fixed point. Although every jaw articulation employs both rotational and translational movement, it is possible to apply a broad and generalised principle that the jaw muscles act on or about a bell-crank curve describing the rotation about a single pivot. This curve exactly reflects the arc of action ascribed at the alveolar border of the lower jaw. From the above interpretation it is clear that the lower jaw action in *Kannemeyeria* is described via a single pivot point, which approached the original "primitive" position of the jaw hinge in basal therapsids (Barghusen, 1973).

The pivoting point of the lower jaw is not at the point of contact between the quadrate and articular condyles, but rather occurs further anteriorly, slightly ventral to the articular recess. This point is stable in respect to the anterior end of the symphysis, but changes relative to the changing contact area between the quadrate and articular. The force diagram produced (figure 1) reveals that, for depression in this case, the moment arm of the anterior-most fibres of the pterygoideus musculature are tangential to the bell-crank circle, indicating that most of its force is concerned with medially orientated elevation. To further test the validity of the described event, and since the diagram shows that the pivot point mechanism is acting as a class-1 lever, it is possible to express it mathematically by the law of moments (Crompton and Hotton, 1967): (Ipt - P Pab) + Fm.

The traction line of the m. depressor mandibulae is not exactly tangential to the circle of rotation (bell-crank curve) around the lower jaw pivot point. However, it is only the tangential component (Ft) which actually produces any action (Crompton and Hotton, 1967) and this reflects the greater degree of translation of the muscular force at the jaw joint with the consequent loss of some its energy. Therefore, the components of force exerted by the m. depressor mandibulae have to be described by reference to the Pythagorean Theorem: $Ft^2 + Fr^2 = Fm^2$.

A similar set of circumstances describe the action of the muscles during elevation and are of particular importance when the jaw has reached the 'resting stage'. During the entire process of elevation the traction line of the AEL is never tangential to the radius of the bell-crank circle describing the arc of action of this phase of the masticatory cycle. The translated force of the AEL became almost directly vertically orientated due to the action of the jaw articulation, demonstrated by the almost vertical component of the constructed tangential force vector (Ft). The muscle force, accordingly, decreases in occlusal strength. This means that from the resting stage this muscle exerted its maximum applied force on the lower jaw during phase 2 of the masticatory cycle.

The second phase of jaw action is characterised by orthal movements, where the lower jaw is brought against the palate of the upper jaw while the jaw is closed. The circle describing the arc of movement of the lever arm is considerably smaller, matching the range of action of the lower jaw during the second phase of the cycle. Due to the smaller radius, the traction line of the lateral external adductor muscle is nearly tangential to the bell-crank circle, and thus exerts almost all of its force in an upward crushing and grinding action with minimal loss to translation at the jaw articulation. The traction line describing the force of the AEM is directly tangential to the bell-crank curve and this muscle exerted considerable force at both the pivot point and on the lower jaw.

The component force of the pterygoideus musculature during phase 2 can be adequately tested by the Pythagorean Theorem. However, constructing this set of force vectors reveals that the tangential component (Ft) would correspond to the traction line of the anterior fibres of the pterygoideus musculature. Further, the intercept the traction line of the anterior fibres makes with the bell-crank curve (Ipt) lies at exactly the same point as the point of maximum action of the posterior fibres. This interplay of these two traction lines during the anterior stroke of Phase Two supports the recognition of these muscle fibres as a single pterygoideus muscle unit.

Conclusions

The primary anatomical pattern of the genus *Kannemeyeria* involves its masticatory cycle, where adaptive changes in the skull and lower jaw can be attributed to a more vertical action of the adductor musculature. This produces a concentrated and powerful crushing and grinding action of the jaws during the second phase of mastication. Cardinal to this function is the realignment of the cranial structures so as to produce a single pivot point about which the lower jaw is rotated. The use of a single pivot in conjunction with the characteristic dicynodont sliding jaw articulation mechanism, resulted in an almost circular crushing and grinding action of the lower jaw against the upper jaw. This, in turn, facilitated the *Kannemeyeria* jaw mechanism to be both highly efficient and effective. Little or no energy is lost during the cycle to translation of the muscle forces at the jaw articulation. This functional and structural relationship has two physiological consequences:

1) less energy is expended during the masticatory cycle, and

2) feeding becomes more efficient, so that a larger variety of food types can be utilised, and tough or less nutritious food sources can also be used as a primary nutrient source.

This implies that the *Kannemeyeria* masticatory cycle provides the animal with the opportunity to exploit a wide variety of habitat types throughout the year, as long as they conform to a generalised system which sustains the population. The optimisation of the force, and action, of the external adductor muscles in *Kannemeyeria* is directly related to the evolution of a different articulation mechanism. Although other elements are obviously important, such as the actual trituration apparatus (Schwanke, 1998), this study has focused on the identification of an alternative articulation mechanism that allows for a maximal energy expenditure during the *Kannemeyeria* masticatory cycle.

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