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HADROSAURID JAW MECHANICS

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Jaw systems in hadrosaurids can be treated as chewing machines operating in three dimensions. As such, different possibilities of jaw mechanisms can be tested by using kinematic analyses to make predictions about tooth wear for each mechanism, ranging from akinetic monimostylic skulls to kinetic streptostylic skulls. A hadrosaurid jaw mechanism that includes a degree of lateral rotation of the maxilla-premaxilla joint, as well as laterocaudal streptostyly and mobility of other articulations, accounts for tooth wear present in these animals better than the currently-accepted propalinal mechanism. Lateral rotation of the maxilla and concomittant motion of other cranial segments is powered by mandibular adduction, and is best seen as a solution to a transverse power stroke constrained by an isognathous jaw system.

Key words: jaw mechanics, Hadrosauridae, streptostyly, cranial kinesis, kinematics.

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Transverse masticatory motion appears to be a distinctly mammalian characteristic, based on electromyographic and cinefluorographic examinations on Recent forms (see Gans *et. al.* 1978; Hiiemae 1978). Transverse movement tends to be accompanied by development of anisognathous jaws, in which chewing occurs on one side of the mouth at a time. Reptiles, on the other hand, have isognathous jaws, a condition that may prevent any great degree of transverse movement. In fact, such movement has not been observed among Recent reptiles to-date (Throckmorton 1980). Despite such an apparent dichotomy between mammalian and reptilian masticatory mechanics, examination of several cranial modifications in ornithopod ornithischians and manipulation of skulls by computer modeling indicate that members of this reptilian group solved the problem of combining isognathy with a transversely-oriented power stroke in mastication. The following is a preliminary report of masticatory mechanics among hadrosaurid ornithopods, based on research over the entire clade (Weishampel 1981).

Among the more notable features of hadrosaurid crania is the well-developed dental battery, formed of up to 53 tooth positions, with as many as 8 teeth per position. Workers from Cope (1883) and Marsh (1893) to Ostrom (1961) and Hopson (1980) have commented on the functional importance of the arrangement of these teeth which, together with the configuration of the quadrate bone and its potential for mobility, has aroused considerable interest in hadrosaurid jaw mechanics.

Perhaps the earliest comments to be made on cranial functional morphology in hadrosaurids were made by Marsh (1893), who suggested that the quadrate may have been free to move against the squamosal. Lambe (1920), in contrast, rejected quadrato-squamosal movement, postulating instead that chewing consisted solely of simple adduction of the lower jaws, with concomittant shearing of the dentary teeth past those of the maxilla. The hypothesis of jaw adduction as the sole mechanism in hadrosaurids was followed by Lull and Wright (1942) in their monographic treatment of hadrosaurid taxonomy and biology.

Workers in Europe interpreted hadrosaurid jaw mechanics in a vastly different fashion. In 1900, Nopcsa suggested that the quadrate was capable of swinging in a fore and aft direction with considerable freedom of movement at the squamosal-quadrate joint, since he also believed that the joints between the quadrate and palate and cheek region were equally free. Thus, Nopcsa inferred that the hadrosaurid quadrate was capable of swinging in a fore and aft direction. Versluys (1910, 1912) initially rejected quadrate-squamosal movement in hadrosaurids, but later (1923) supported Nopcsa's hypothesis of fore and aft rotation at the quadrate-squamosal joint. Versluys also suggested that the mandibles rotated medially about their long axes during mastication. On reexamination of the material upon which Versluys based his studies on quadrate movement, Kripp (1933) rejected fore and aft mobility of the quadrate, since it was clear to him that several joint restrictions prevented parasagittal quadrate rotation. In contrast to both Nopcsa and Versluys, Kripp hypothesized that jaw mechanics included lateromedial rotation of the quadrate-squamosal articulation, augmented by lateral rotation of the mandibles about their long axes.

Not until 1961 did work on hadrosaurid jaw mechanics continue, when Ostrom produced his large work on the cranial anatomy of these animals. In it, he successfully refuted previous hypotheses of hadrosaurid jaw mechanisms, instead suggesting that the quadrate-squamosal joint was fixed and masticatory movement occurred by means of propalinal translation of the mandibles against the lower head of the quadrate. Recently, Hopson (1980) questioned the mechanism described by Ostrom and suggested that the mandibles moved side-to-side relative to the maxillae, based on several tooth wear characters.

Although Ostrom's is the last word on intracranial and quadrate mobility as they relate to jaw mechanics in hadrosaurids, I have examined the full range of these phenomena by treating the hadrosaurid skull as a chewing machine in order to make predictions about tooth wear. To test alternative jaw mechanisms, each can be reduced to its component parts and modeled as a kinematic linkage system by means of three-dimensional computer simulation. A significant feature of computer modeling is in making predictions independent of the data used in constructing the model, i.e. tooth-to-tooth wear for each mechanism. Thus, any modeled mechanism, based on an actual specimen, can provide a domain of possible tooth wear configurations that can be compared with tooth wear actually found in that specimen. This domain is limited by constraints on movement imposed by each joint, as well as by linear dimensions between joints. Predicted *versus* actual tooth wear can then be used to confirm or reject hypotheses of jaw mechanics that generate appropriate or inappropriate tooth wear.

Data gathered from osseous structures include: i. joint type, ii. rotational or translational freedom of movement, and iii. joint position. Both positional and morphologic data were then applied to Integrated Mechanisms Program (IMP; Sheth and Uicker 1971), in order to model each skull as a three-dimensional mechanism for mastication. In particular, IMP requires the three-dimensional positions for all movable joints, assignment of joint types (for example, hinge/revolute, planar, spheroidal), and axes of rotation or planes of translation. Manipulation of different segments of the mechanism and propagation of displacement through the linkage network makes possible the prediction of various tooth wear characters indicating movement between occluding teeth during chewing.

The propalinal jaw mechanism proposed by Ostrom (1961) maintains that all cranial joints with the exception of the quadrate-mandible joint were rigid, and that quadrate-mandibular translation produced fore and aft movement of the lower jaw during the power stroke (fig, 1). Predictions about tooth wear include:

1. Wear facet angulation can be steep or shallow, but cannot vary between the two over the length of the tooth row.

2. The occlusal surfaces of upper and lower tooth rows need not be the same length and are only constrained by the fore-aft translatory distance of the jaw joint.

3. Thickened enamel must have a dominant buccolingual disposition to insure contact between enamel in the upper and lower tooth rows.

4. If the tooth rows are parallel and the mandible moves rostrally during the power stroke, the mesial edge of the dentary occlusal surface becomes the leading edge and thus the enamel-dentine interface is flush; the distal edge bears a step enamel-dentine interface (the converse in

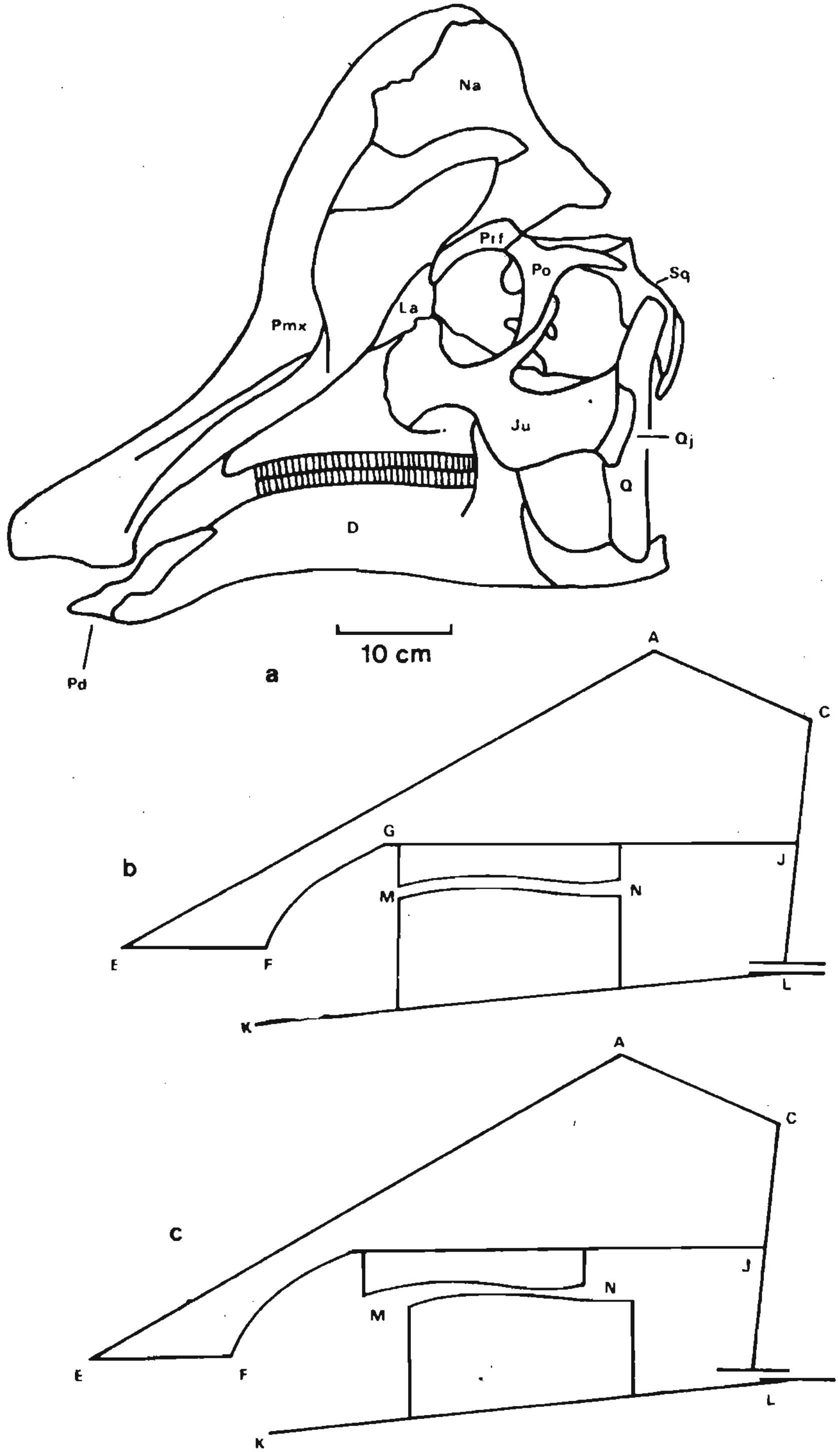

Fig. 1. *a* Skull of *Corythosaurus casuarius*, National Museum of Canada (NMC 8676); *b* kinematic diagram of *Corythosaurus casuarius*, with cranial movement solely at the quadrate-mandibular joint; *c* propalinal movement of the mandible through quadrate-mandible translation.

true of maxillary teeth). If the mandible moves distally during the power stroke, the form of the enamel-dentine interface is reversed between mesial and distal edges of each tooth. However, if the tooth rows converge rostrally, propalinal movement of the lower jaws drives the dentary teeth outward relative to maxillary teeth. Thus, the leading edge of dentary teeth (flush morphology) occurs buccally, while the trailing edge (step morphology) is lingual.

5. Wear striae are mesiodistally-oriented under conditions of parallel tooth rows, but highly oblique when tooth rows are convergent.

6. Grooves may occur mesiodistally, but no transverse curvature is expected to occur. Wear between adjacent teeth is expected to be confluent.

7. The tooth rows may been parallel or show lateromedial curvature.

8. The tooth rows may show dorsoventral curvature or may be planar.

Computer modeling has also been used to assess the mobility of two other cranial joints (fig. 2*a*, *b*): lateral rotation of the caudodorsally-inclined maxilla-premaxilla joint (continuing caudally between the jugal-maxilla complex and the lacrimal) and caudolateral rotation of the quadrate-squamosal joint (streptostyly). Combined movement of the maxilla and quadrate implies a form of intracranial mobility not seen in other tetrapods, involving several other cranial joints: 1. translation between the postorbital and jugal (fig. 2c), 2. rotation between the quadratojugal and quadrate (fig. 2d), 3. cylindrical movement (rotation plus translation) between the basipterygoid process of the basisphenoid and the pterygoid (fig. 2e), 4. symphyseal rotation of the mandibles, and 5. rotation between the pterygoid and palatine-ectopterygoid-maxilla complex (fig. 2f). Mandibular adduction powers the mechanism, driving the maxillae laterally along the hinge joint with the premaxillae, and this movement in turn propels the movement at the other cranial joints outlined above.

The mechanism of streptostyly and lateral motion of the maxilla (fig. 3) makes the following eight prediction about tooth wear:

1. Wear facet angulation is variable along the tooth row: slightly steeper mesially and shallower distally.

2. The occlusal surfaces of the upper and lower tooth rows need not be the same length, but the difference between lower and upper tooth rows must be no greater than the difference between fore-aft excursion of the dentary and maxilla, related to laterocaudal quadrate rotation.

3. Thickened enamel occurs either buccally or lingually.

4. Since mandibular adduction and consequent lateral movement of the maxillae comprise the basis of masticatory movement, the buccal edge of maxillary teeth forms the leading (flush morphology) edge of the power stroke, while the lingual edge of these teeth have a step morphology. The converse is true of dentary teeth.

5. Wear striations are predominantly buccolingually-oriented.

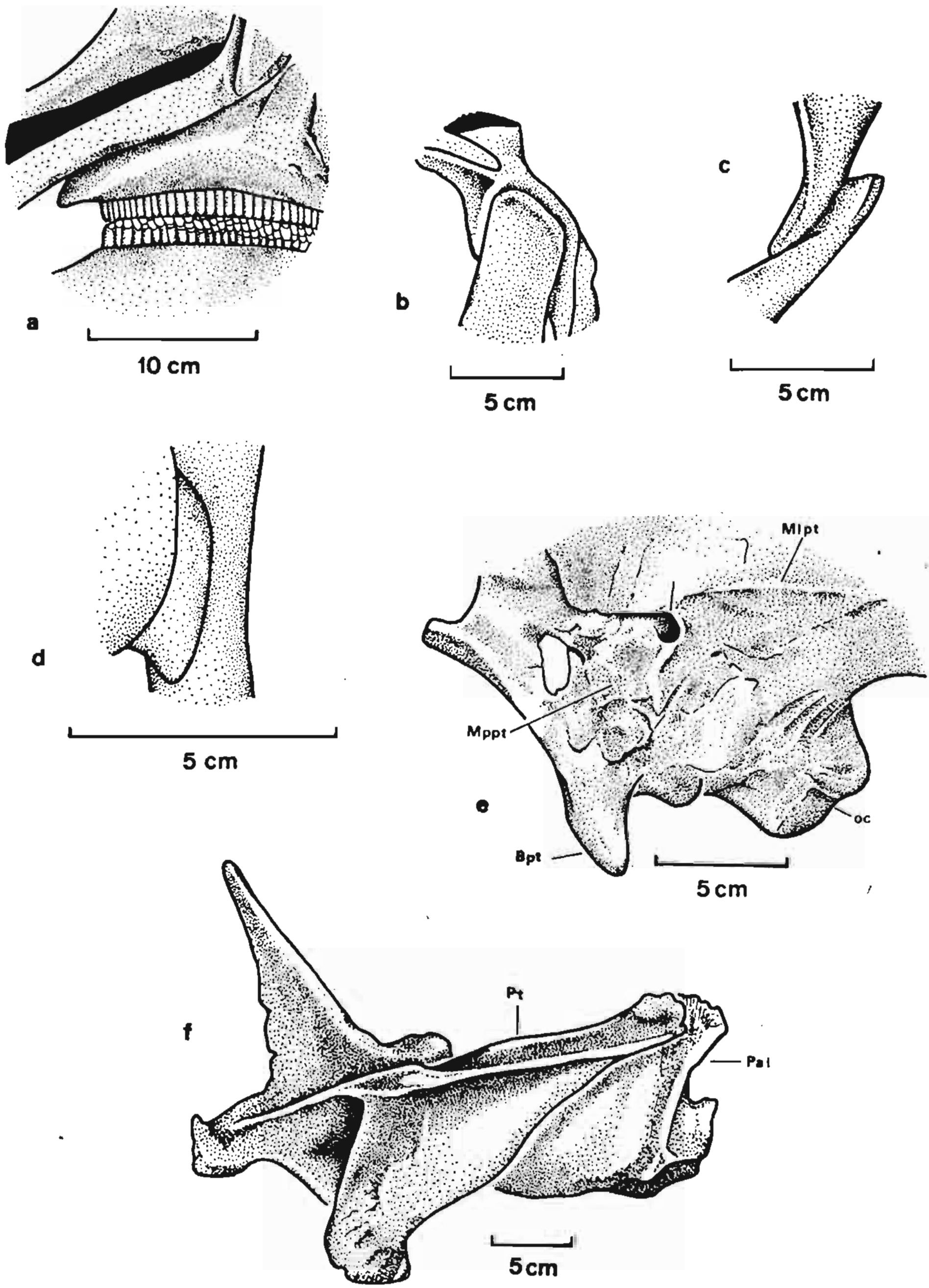

Fig. 2. *a* Maxilla-premaxilla joint in *Corythosaurus casuarius* (NMC 8676); *b* quadrate-squamosal joint; *c* postorbital-jugal joint; *d* quadratojugal-quadrate joint; *e* basipterygoid-pterygoid joint; *f* pterygoid-palatine joint.

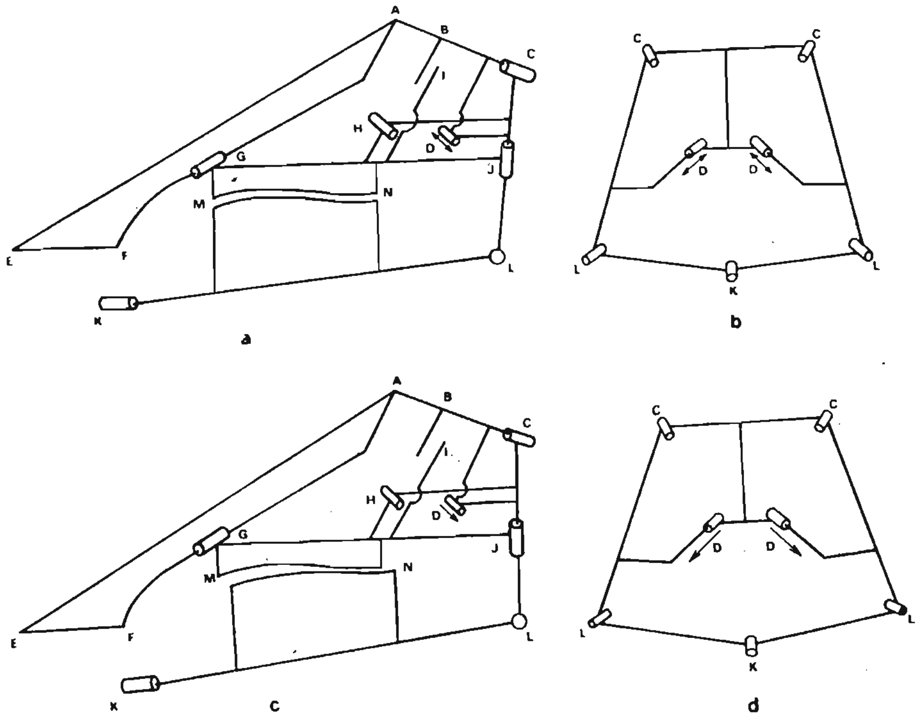

Fig. 3. *a* Kinematic diagram of *Corythosaurus casuarius* (NMC 8676), lateral view; *b* caudal view; *c* streptostylic movement of *a*, lateral view; *d* caudal view.

6. Longitudinal grooves are not expected. However, the occlusal surface of the maxillary tooth row is expected to be convex transversely, while that of the dentary tooth row is expected to be concave transversely. Reciprocal curvature is produced by rotation between the maxilla and premaxilla. Wear may be confluent between adjacent teeth, but need not be.

7. Both maxillary and dentary tooth rows are expected to be slightly buccally concave along their length.

8. The dentary tooth rows are expected to be dorsally concave along their length, with reciprocal ventral convexity to the maxillary tooth rows.

Only four of these predictions from the propational and streptostyly mechanism differ enough to be of any real value in choosing between the two mechanisms. These are: transverse *versus* lingual or buccal enamel, mesial or distal *versus* lingual or buccal enamel-dentine interface, mesiodistal *versus* buccolingual wear striations, and transversely flat *versus* curved tooth rows (in each of these predictions, those for the propalinal mechanism are given first, the streptostyly mechanism, second).

Reference to actual hadrosaurid specimens indicates the following tooth wear characters:

1. Enamel is disposed along the buccal side of each maxillary tooth and along the lingual side of each dentary tooth (fig. 4*a*). Such a placement makes sense only when the power stroke is transverse, insuring total intersection between enamel of the maxillary and dentary tooth

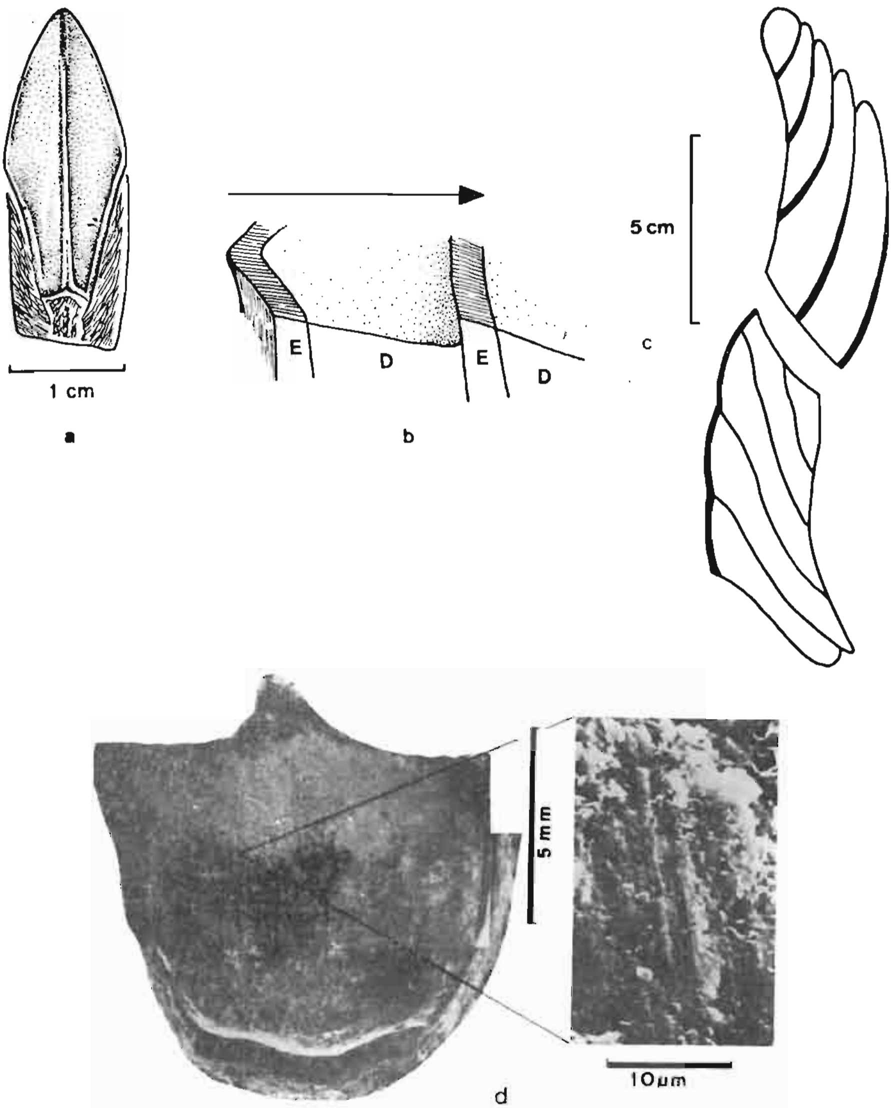

Fig. 4. *a* Hadrosaurid dentary tooth, lingual view, showing enamel surface of the crown; *b* close-up of the enamel-dentine interface in two successive dentary teeth: *D* dentine, *E* enamel; arrow shows direction of movement of maxillary teeth during the power stroke; *c* cross-section of maxillary and dentary teeth in place within reciprocal alveoli. Note concavity and convexity to the dentary and maxillary occlusal surfaces, respectively; *d* electron micrograph of the occlusal surface of a dentary tooth of *Corythosaurus casuarius* (left) and buccolingual wear striations along the occlusal surface of the same tooth (right).

rows. Such transverse motion of the jaws is predicted by the streptostyly mechanism through lateral rotation of the maxilla. In the propalinal mechanism, contact between enamel on maxillary and dentary teeth is rare and dependent upon the relative wear of the maxillary teeth.

2. The enamel-dentine interface (buccal for maxillary teeth, lingual for dentary teeth) is flush, indicating that the leading edge of dentary teeth is lingual, the leading edge of maxillary teeth is buccal, and the maxillae moved laterally relative to the dentaries (fig. 4*b*).

3. The dentary teeth exhibit transversely concave wear confluent over all wearing teeth in each tooth position, while maxillary teeth show reciprocally convex or flat wear (fig. 4*c*).

4. Wear strations occur predominantly buccolingually (fig. 4*d*).

All four tooth wear characters conform to predictions made by the streptostyly mechanism and not by the propalinal mechanism; thus, the propalinal mechanism can be confidently rejected.

Mastication in hadrosaurids can be characterized as follows. Vertical adduction of the lower jaws brings the dentary teeth into occlusion with those of the maxilla. Both right and left sides of the dentition meet at the same time (isognathy, as in all other reptile groups). Following tooth--tooth contact, the maxillae are forced apart by the continue vertical movement of the dentary teeth, producing a transverse power stroke. Laterocaudal mobility of the quadrate on the squamosal is consequent upon maxillary movement, as is the spheroidal movement of the jaw joint. The transverse power stroke consists of lateral movement of the maxillary teeth relative to dentary teeth. The jaw mechanism for hadrosaurids outlined here is unlike that in other vertebrates that grind their food by a transverse power stroke and probably results from constraints placed by an originally isognathous jaw system on the ways in which a grinding mechanism can be assembled.

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