JAWS AND MUSCLES

A) Introduction

Mammals evolved within the **synapsid** radiation (Figure 1). In turn, synapsids were part of the amniote radiation, a separate evolving lineage distinct from another group of amniotes, the diapsids. Synapsid evolution included changes in many structural and physiological systems. The locomotor system exhibited changes in posture wherein the limbs were brought from a sprawled stance to one in which the limbs were carried under the body. The lumbar region became more distinct, reflecting accommodation of dorsoventral flexions of the vertebral column during locomotion. Endothermy would evolve late in synapsids, and with it the appearance of related correlated characters such as hair.

In this section, we examine the evolution of jaws and jaw muscles within the synapsids. We begin by noting significant changes within jaw suspension.

- JAWS (Figures 2, 3). In basal synapsids, the jaw articulation is established between articular (lower jaw) and quadrate (braincase). But in derived groups, suspension is via dentary (lower jaw) and squamosal (braincase), see Figure 2a. In particular, the articular and quadrate bones become reduced in size, and join the stapes (=columella) in the middle ear so that in derived synapsids (mammals) they now function in sound transmission, and no longer in jaw suspension, see Figure 2b. Accompanying this change in jaw suspension, the postdentary bones are reduced and some lost from the lower jaw along with the formation of a tall coronoid process.

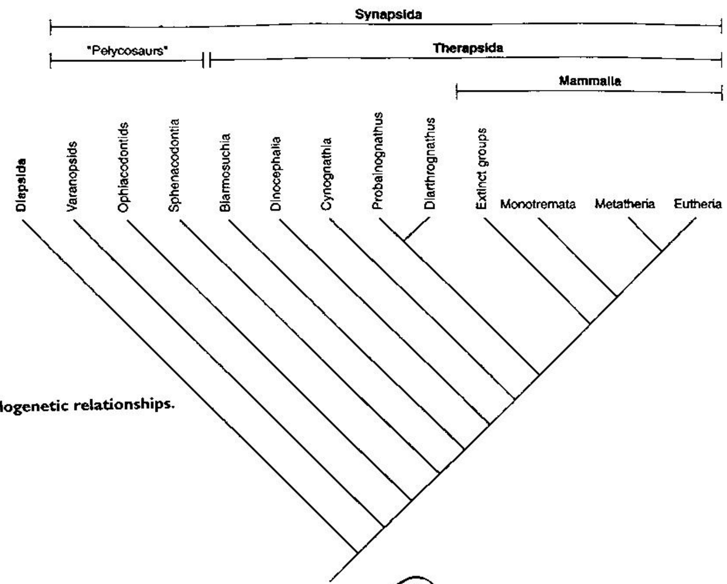

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FIGURE (3.40) Synapsida, phylogenetic relationships.

FIG. 2

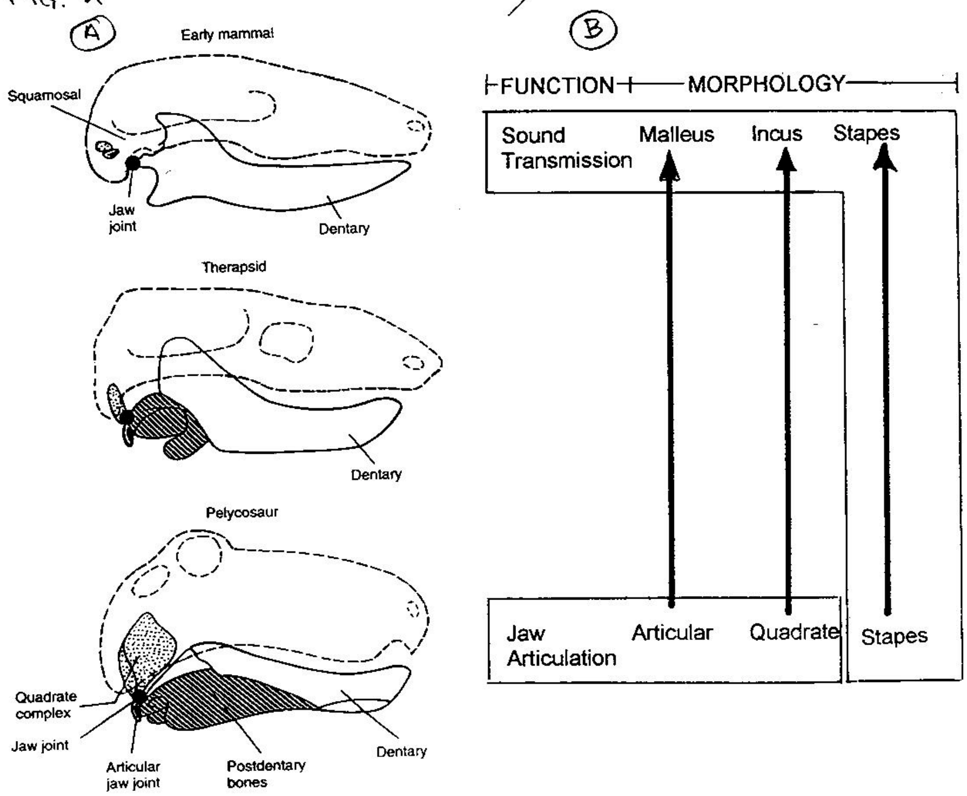
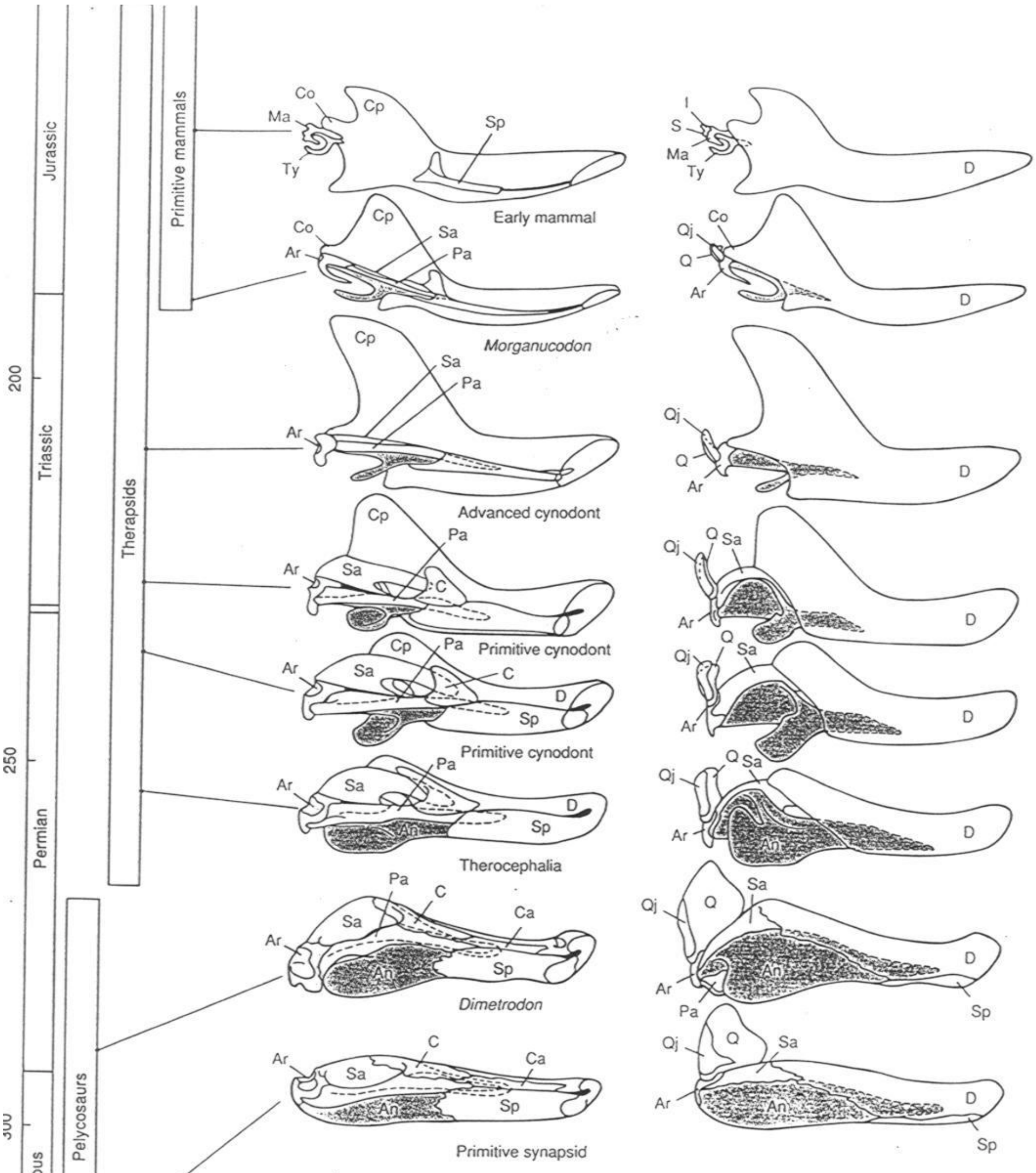


Figure 1 Synapsida, phylogenetic relationships

Figure 2. Synapsid Jaw Articulation, early ("pelycosaurs") to therapsids to mammals. (a) Note loss of postdentary bones, and loss of quadrate and articular bones from jaw articulation. (b) The articular and quadrate join the columella in the middle ear of mammals becoming the tiny malleus, incus, and stapes.



Figure(7.55) Evolution of the mammalian middle ear bones. From primitive pelycosaurs, to therapsids, to the first mammals, changes in the postdentary bones are indicated along with incorporation of the quadrate (incus) and articular (malleus) into the middle ear. The fossil species used to follow these changes are shown in relationship to their occurrence in the geological record. Abbreviations: angular (An), articular (Ar), coronoid (C), anterior coronoid (Ca), condyle of dentary (Co), coronoid process (Cp), dentary (D), incus (I), malleus (Ma), prearticular (Pa), quadrate (Q), quadratojugal (Qj), stapes (S), surangular (Sa), splenial (Sp), tympanic annulus (Ty).
Based on the research of James A. Hopson and Edgar F. Allin.

FIGURE 3

(3)

Figure 3. Evolution of mammalian middle ear bones.

- JAW MUSCLES (Figure 4). There is differentiation of the jaw-closing musculature. In basal synapsids, the major jaw-closing muscle is the <u>adductor mandibulae</u> (externus). It originates from the back of the skull and inserts on the posterior end of the lower jaw. In derived synapsids, the adductor mandibulae divides into two major sets of jaw-closing muscles, the <u>temporalis</u> and <u>masseter</u>. The temporalis originates from the skull roof near the sagittal crest and inserts on the coronoid process. The masseter in turn divides into two parts. The <u>deep</u> <u>masseter</u> originates on the zygomatic arch and inserts on the lower jaw; the <u>superficial</u> <u>masseter</u> part arises beneath the eye, passes across the deep masseter, to insert on the angle of the dentary.

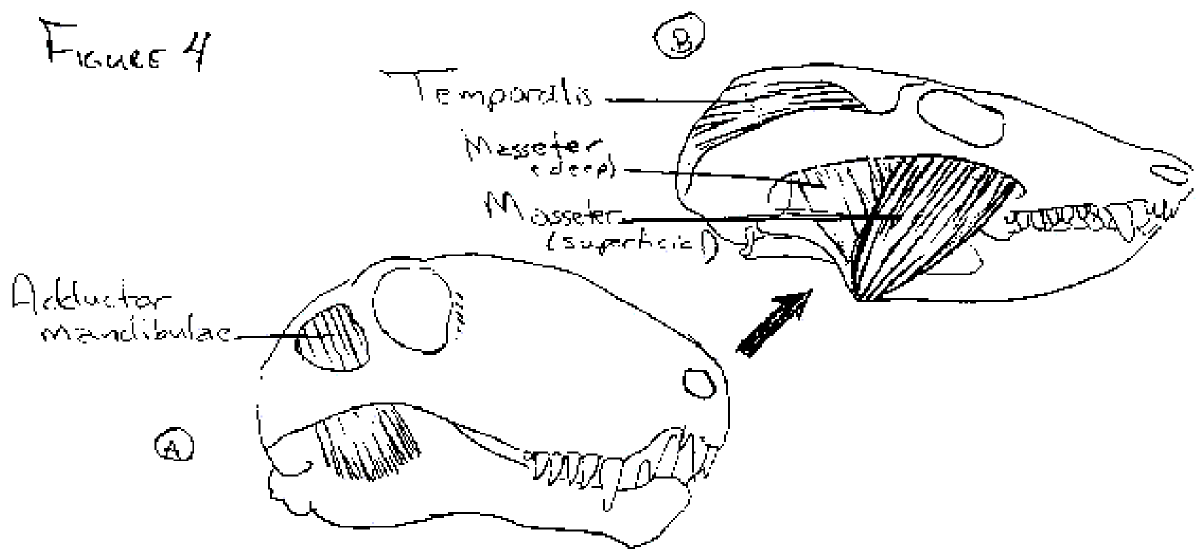


Figure 4. Evolution of Synapsid jaw adductor muscles.

Other changes occur as well:

- A secondary palate develops across the roof of the mouth (Figure 5a).
- Teeth become much more specialized and thereby more distinct in their particular morphologies (Figure 5b).
- A zygomatic arch, “cheek bone”, becomes prominent (Figure 5).

Functional Significance. The changes in the jaws and jaw muscles reflect changing functional demands. To explore what these might be, we are going to model the two conditions, primitive and derived conditions.

B) Objectives

1) Determine how stresses at the jaw joint, positive and negative, have changed in synapsids?
2) Determine the functional consequences of the heightened coronoid on the jaw joint?
3) Determine how the appearance of a superficial masseter in derived synapsids increases the bite force but without adding large stresses at the jaw joint?

C) Procedures

Method of General Procedure

1) Work within your seminar teams. At the end of each exercise, switch participants so that each member applies the input forces (muscles) and then experiences the output forces (jaws).

2) Discuss the questions posed as you meet them during the exercise. When agreed, write the answer on the sheet, then proceed.

3) Keep in mind that the exercises simulate real and hypothesized conditions in fossils. Your experimental outcomes will vary slightly depending upon how closely your tests match the real conditions.

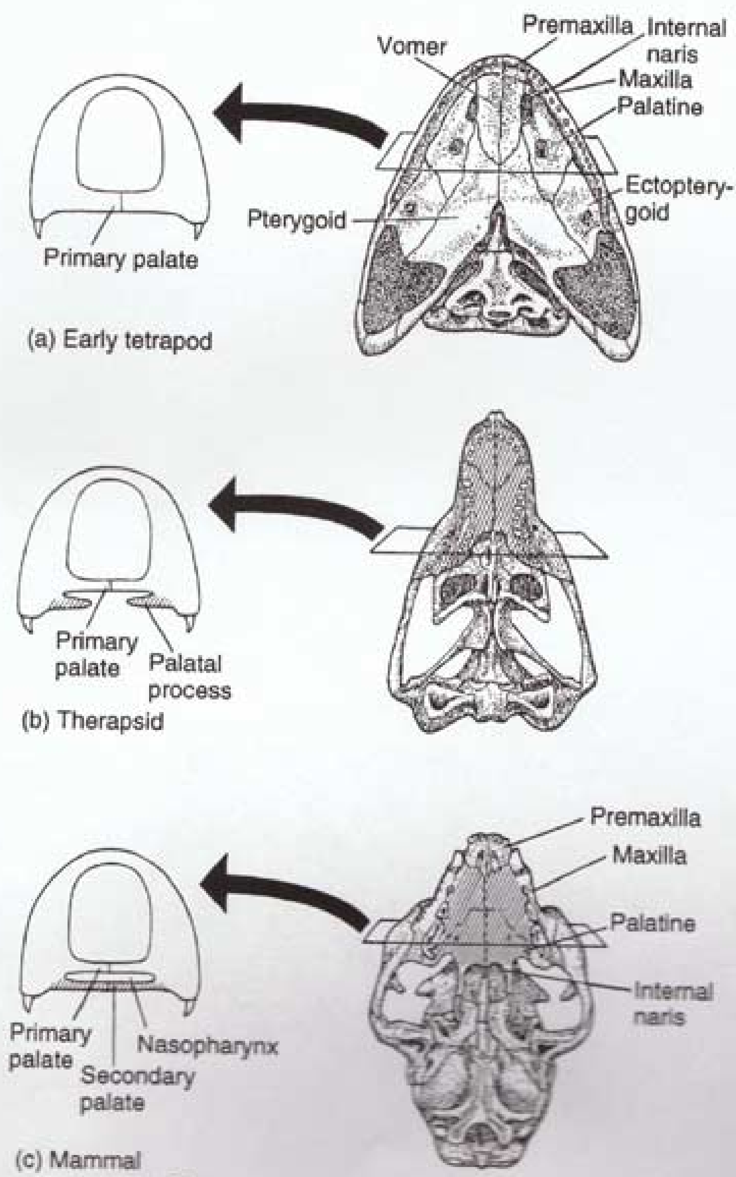
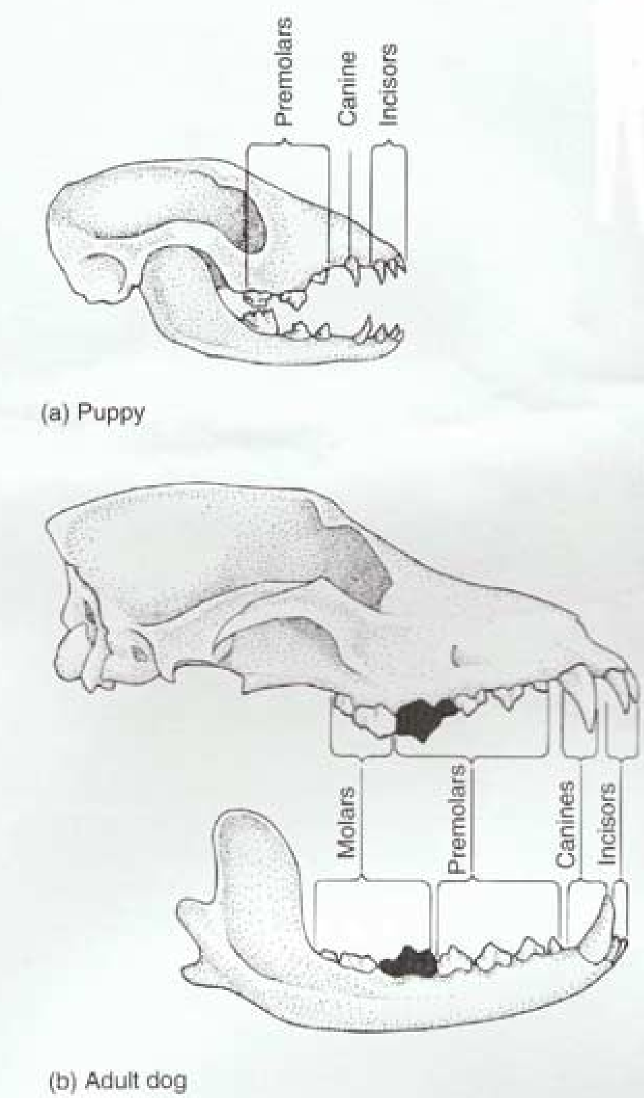


FIGURE (7.58) 5A Evolution of the secondary palate. (a) Early tetrapod with a primary palate in cross section (left) and ventral (right) views. (b) Therapsid with a partial secondary palate formed by the medial extension of the premaxilla and maxilla. (c) Mammal with a secondary palate that, in addition to extensions of the premaxilla and maxilla, includes part of the palatine bone.

After Smith.



5B
FIGURE 13.7 **Deciduous (a) and permanent teeth (b) in a dog.** The carnassials (shaded teeth) are specialized carnivore teeth derived from last premolar (upper) and first molar (lower).

Figure 5. Other changes in Synapsid skull. (a) Secondary Palate. (b) Heterodont teeth.

Exercise 1: Height of Coronoid

Assumptions: When biting, food in the mouth acts mechanically as an occlusal fulcrum about which the jaw tends to rotate (Figure 6). When the adductor mandibulae muscle contracts, it exerts a force on the lower jaw tending to close the jaw. How this force is experienced by the jaw joint depends upon the line of action of the adductor mandibulae and the location of the occlusal fulcrum established by the food. Increased mechanical stress on the jaw joint is positive (+), decreased stress is negative (-) or stays about the same, neutral (o).

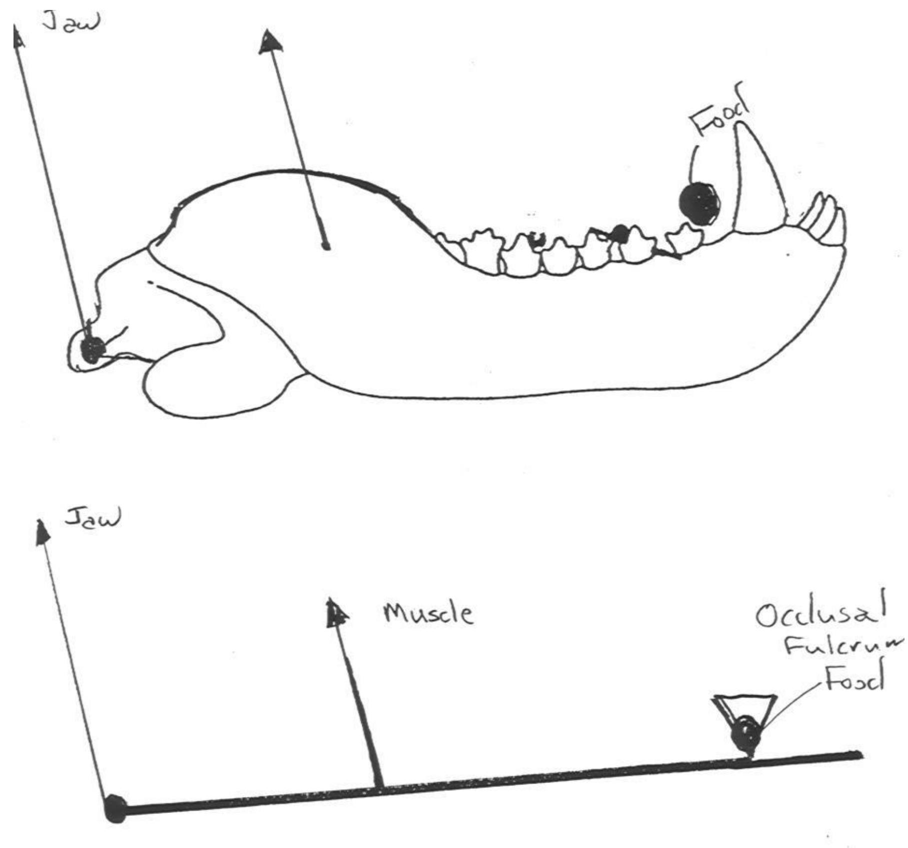


FIGURE 6. Occlusal Fulcrum

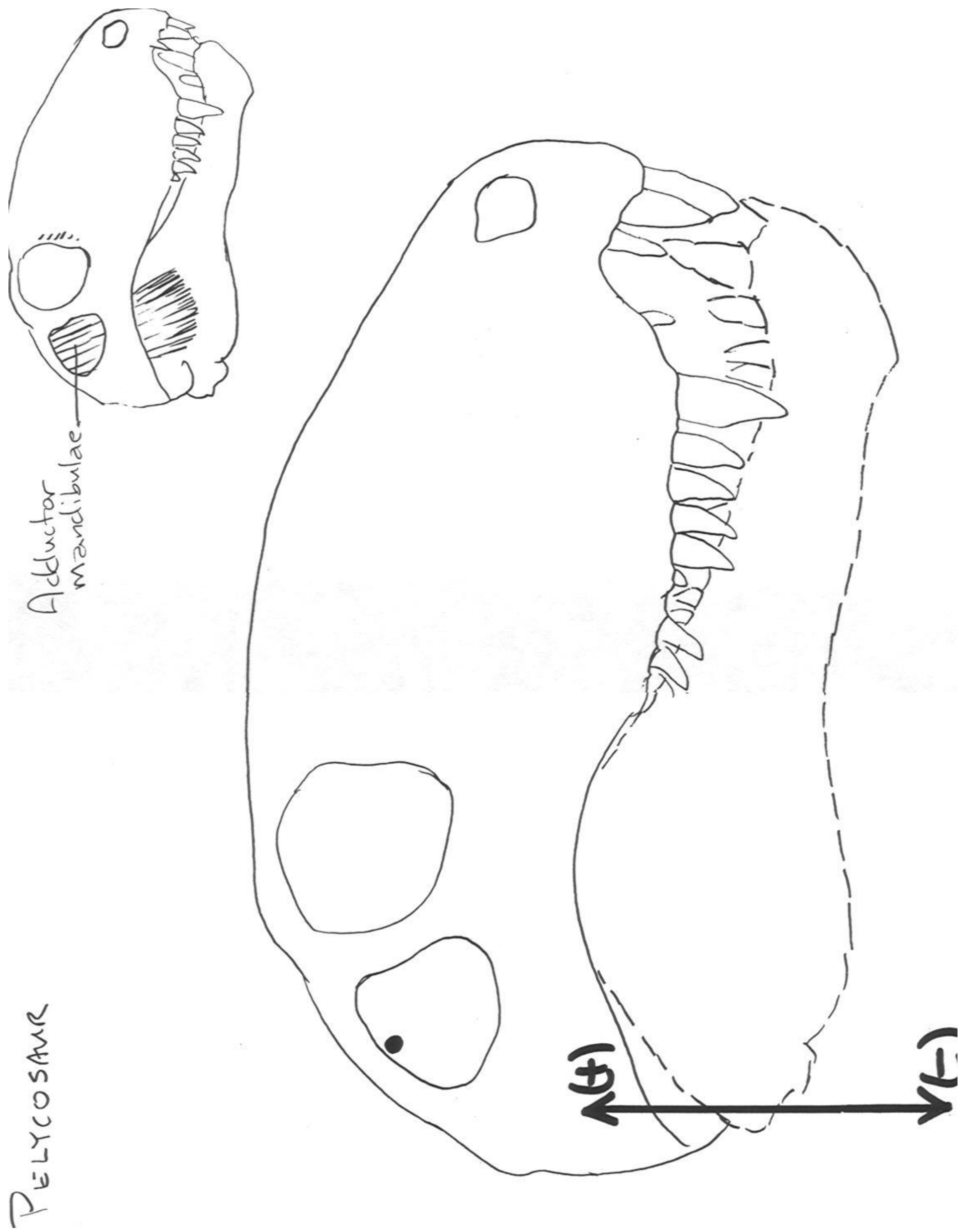
Figure 6. Occlusal Fulcrum.

Part A: **Basal Synapsid (“pelycosaur”)**

<u>Modeling</u>. Place the “pelycosaur” lower jaw in its outline on the paper. Use a rubber band to represent the line of action of the adductor mandibulae. Do this by affixing the rubber band with tape to the point of insertion on the lower jaw, marked with an “X“. The other end of the rubber band should pass through the origin, marked on the skull with a dot “ • “.

QUESTION: <u>Hypothesis</u> 1: When there is food in the mouth (occlusal fulcrum) and the adductor muscle contracts, will the posterior of the mandible exert significant stresses at the jaw joint? Positive or negative or neutral?

<u>Answers</u>:



<u>PROCEED to test your hypothesis</u>: One person should place their finger on the tooth row just posterior to the tallest tooth representing food in the mouth (occlusal fulcrum). Another person in your group should now pull on the rubber band along this line of action. Partners should now exchange roles and run this again, then other members should take their turns.

Did the jaw joint move up (+) or down (-) or neutral (o)?

Answer:

Part B: **Derived Synapsid (therapsid)—LOW Coronoid Process**

Modeling. Place the therapsid lower jaw in its outline on the paper. Use a rubber band to represent the line of action of the adductor. Do this by affixing the rubber band with tape to the “low” point, representing an insertion of this muscle on the lower jaw at a point similar to its insertion in basal synapsids (Part A, above). The other end of the rubber band should pass through the origin, marked on the skull with a dot “ • “.

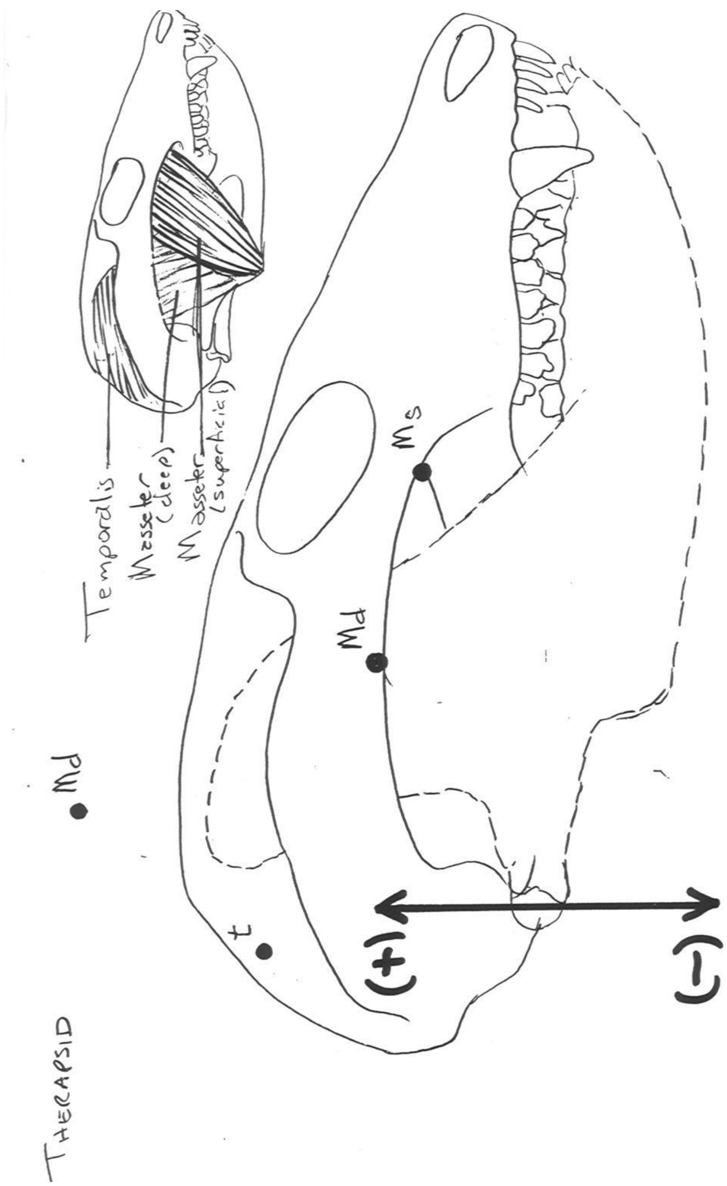
QUESTION: Hypothesis 2: When there is food in the mouth (occlusal fulcrum) and the adductor muscle contracts, will the posterior of the mandible exert significant stresses at the jaw joint? Positive or negative or neutral?

Answers:

PROCEED to test your hypothesis: One person should place their finger on the tooth row just posterior to the tallest tooth representing food in the mouth (occlusal fulcrum). Another person in your group should now pull on the rubber band along this line of action. Partners should now exchange roles and run this again, then other members should take their turns.

Did the jaw joint move up (+) or down (-) or neutral (o)?

Answer:


THERAPSID
Temporalis
Masseter (deep)
Masseter (superficial)
Md
Ms
Md
t
(+)
(-)

Part C: **Derived Synapsid (therapsid)—HIGH Coronoid Process**

Modeling. Again place the therapsid lower jaw in its outline on the paper. Leave the previous rubber band taped to the lower jaw, but add another rubber band to represent the line of action of the jaw adductor, but this time simulate the line of action from a heightened coronoid process. Do this by affixing this rubber band with tape to the “high” point, representing an insertion of this muscle on the lower jaw as it actually occurs in derived therapsids. The other end of the rubber band should pass through the origin, marked on the skull with a dot “ • t“.

QUESTION: Hypothesis 3: When there is food in the mouth (occlusal fulcrum) and the adductor muscle contracts, will the posterior of the mandible exert significant stresses at the jaw joint? Positive or negative or neutral?

Answers:

PROCEED to test your hypothesis: One person should place their finger on the tooth row just posterior to the tallest tooth representing food in the mouth (occlusal fulcrum). Another person in your group should now pull on the rubber band along this line of action. Partners should now exchange roles and run this again, then other members should take their turns.

Did the jaw joint move up (+) or down (-) or neutral (o)?
Answer:

REVIEW of Exercise 1:

Notice how your simulations of forces generated by adductor muscles on the lower jaw impart forces on the food as well as at the jaw joint. With a change in insertion (high coronoid process) these jaw joint forces diminish and even become negative. This relieves jaw joint forces and reduces the mechanical role played by the articulating bones, articular and quadrate.

But also notice that the single large adductor mandibulae of basal synapsids becomes divided into several major jaw closing muscles with different lines of action in derived therapsids (Figure 4). We explore the consequences of these changes in the next exercise.

Exercise 2: Jaw Muscles

Part A: **Derived Synapsid (therapsid): Superficial Masseter**

Assumptions. Same.

Modeling. Use the same setup, the derived therapsid jaw, keeping the temporalis inserted "high" and its line of action running through the origin, marked on the skull with a dot " • t". Now add another rubber band representing the line of action of the superficial masseter. Its line of action is at about right angles to that of the temporalis. Insertion is on the corner of the mandible and its line of action runs through the origin marked on the skull with a dot " • Ms".

QUESTION: Hypothesis 4: When there is food in the mouth (occlusal fulcrum) and BOTH muscles contract (temporalis and superficial masseter), will the posterior of the mandible exert significant stresses at the jaw joint? Positive or negative or about neutral?

Answers:

PROCEED to test your hypothesis: One person should place their finger on the tooth row just posterior to the tallest tooth representing food in the mouth (occlusal fulcrum). Another person in your group should now pull on BOTH rubber bands along their lines of action. Partners should now exchange roles and run this again, then other members should take their turns.

Did the jaw joint move up (+) or down (-) or neutral (o)?

Answer:

Did the force on the food increase or decrease?

Answer:

Part B: **Derived Synapsid (therapsid): Deep Masseter**

Assumptions. Same.

Modeling. Use the same setup as in Part A, but now we will simulate the contraction of the third jaw adductor muscle, the deep masseter to that of the other two, the superfician masseter and temporalis. Add yet another rubber band, taping it to the insertion on the lower jaw and allowing it to run through its origin marked Md on the zygomatic arch. NOTE that the coronoid of the therapsid lower jaw falls across this point on the zygomatic arch in the simulation. To compensate for this, use the virtual point above the skull marked with a dot " • Md". Although off the skull, this point is along the line of action of the deep masseter so for our purposes here can be used as the simulate origin of the muscle.

If now you have the lower jaw properly fitted, there will be three rubber bands, each simulating one of the three major adductor muscle—temporalis, supericial masseter, deep masseter. Check to make sure this is set up correctly.

QUESTION: Hypothesis 5: When there is food in the mouth (occlusal fulcrum) and ALL THREE muscles contract (temporalis superficial masseter, and deep masseter), a) will the posterior of the mandible exert significant stresses at the jaw joint? Positive or negative or about neutral? And b) will the force on the food increase, decrease, or stay about the same?

Answers:

PROCEED to test your hypothesis: One person should place their finger on the tooth row just posterior to the tallest tooth representing food in the mouth (occlusal fulcrum). Another person in your group should now pull on ALL THREE rubber bands along their lines of action. Partners should now exchange roles and run this again, then other members should take their turns.

Did the jaw joint move up (+) or down (-) or neutral (o)?

Answer:

Did the force on the food increase or decrease?

Answer:

REVIEW of Exercise 2

Notice how adding muscles (superficial and deep masseters) changes the force on the food without producing large stresses on the jaw joint, as was the case in basal synapsids.

Also notice, especially in Part B, how differences in the three relative forces (how hard you pull on individual rubber bands) between the three simulated muscles affects the outcome of biting forces and affects forces at the jaw joint. At this point in our simulation of muscle forces, we should really try to duplicate the forces of the three major jaw muscles, but that of course is difficult from fossils alone. Because modern day mammals evolved as a later stage in therapsid radiation (Figure 1), we would turn to carefully selected mammalian species as representatives of the fossil condition.

Lets turn to several thought questions that tie together the work you have just completed and perhaps give us some understanding of synapsid evolution and accompanying changes in jaw structure and function.

Seminar Teams:

Summary and Conclusions

Evolution of JAWS and JAW MUSCLES in Synapsids

1) Coronoid Height
   What is the functional significance of a change in the height of the coronoid (Figure 3)?

2) Superficial Masseter
   What is the functional significance of a superficial masseter plus temporalis, compared to just a single jaw adductor muscle?

3) Evolution
   Considering the changes in stresses on the jaw joint (pelycosaur to therapsid), how might this help to explain the loss of postdentary bones (Figure 3)?

References

This exercise is based on theoretical work by D. Bramble.

Bramble, D. 1978. Origin of the mammalian feeding complex: models and mechanisms. Paleobiology 4:271-301.

Crompton, A. W. and P. Parker. 1978. Evolution of the mammalian masticatory apparatus. Amer. Sci. 66: 192-201.

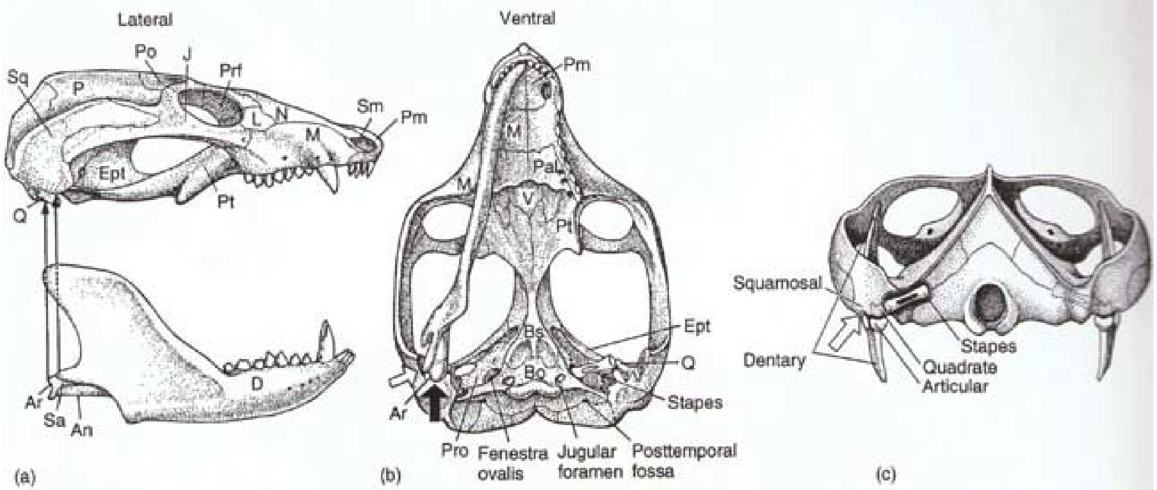


FIGURE 7.64 **Double jaw articulation.** Skull of *Probainognathus*, a late cynodont (therapsid) shown in lateral (a) and ventral (b) views, double jaw articulation occurs between the quadrate and articular (solid arrow), the primitive condition, and another articulation occurs between dentary and temporal (squamosal) (open arrow) that came to predominate in later mammals. (c) Posterior view, with window cut to show the stapes and its contact with the reduced quadrate. The new articulation, dentary-temporal (via squamosal), open arrow, as well as the primitive jaw articulation, quadrate-articular, are present. Abbreviations: angular (An), articular (Ar), basioccipital (Bo), basisphenoid (Bs), dentary (D), epipterygoid (Ept), jugal (J), lacrimal (L), maxilla (M), nasal (N), parietal (P), prefrontal (Prf), premaxilla (Pm), prootic (Pro), postorbital (Po), pterygoid (Pt), quadrate (Q), surangular (Sa), septomaxilla (Sm), squamosal (Sq), vomer (V).

After Carroll; After Romer.

Instructor's Manual

Purpose: Analysis of mammalian lower jaw.

Background:

Mammals are part of the synapsid lineage, a lineage that included some of the most extraordinary tetrapods ever to evolve. Synapsids date to the Carboniferous, and were later contemporaries of the dinosaurs, but a distinct clade from those Mesozoic diapsids.

Formerly known as "mammal-like reptiles", the basal synapsids have often been overlooked, in anticipation of the mammals to come. But within them major changes occur within the locomotor and feeding systems, as well as later changes in physiology (endothermy). Changes in bones of the lower jaw alone are truly remarkable. Postdentary bones are lost or moved to new locations with new functions. The movement of articular and quadrate bones into the middle ear would test credibility were it not for a remarkable fossil record that makes such a transformation undeniable.

Goals:

Without resorting to vector diagrams or complicated mathematics, this exercise is intended to provide students with an insight into the changes in forces brought about by a heightened coronoid and by division of the adductor mandibulae into additional jaw muscles. With this in hand, students are invited to consider the evolutionary significance of basal (pelycosaur) to derived (therapsid) changes in forces exerted at the jaw joint.

Facilitation:

a) Coronoid Height—Lengthening the coronoid changes the position of the insertion of the temporalis muscle, a derivative of the adductor mandibulae. The consequence is to change the stresses exerted on the lower jaw joint.

b) Masseter Muscle—Although the superficial masseter, also derived from the adductor mandibulae, increases bit forces, it does not do so by returning increased stresses (+) on the jaw joint. Thus bit force increases, but forces on the jaw joint do not increase.

c) Basal to Derived Conditions—A problem Cuvier would have enjoyed comes to light within this evolution of the synapsid jaw joint. In basal synapsids, the jaw joint is formed between articular and quadrate bones. Students have seen this type of joint in diapsids (e.g. alligators) and in parareptilia (e.g. turtles). But in derived synapsids, this jaw joint is between two different bones, the dentary and the squamosal. How could such a change in structure occur without disrupting function??

A partial answer is suggested by this exercise. The changes in jaw design (tall coronoid, splitting of adductor mandibulae) result in reduced forces at the primitive (articular-quadrate) jaw joint. Bones could be reduced in size and prominence without compromising function. The robust articular and quadrate articulation would be less of a constraint.

Further, *Diarthrognathus*, a late therapsid in which this condition was first discovered, may be a structural and functional intermediate. In this therapsid, both joints are present, suggesting one way the dentary-squamosal joint could take over the function of jaw articulation without disrupting function. A more complete late therapsid fossil exhibiting this condition is *Probainognathus*.

Practical Matters:

a) Preparing materials—Looped rubber bands can be cut making a short "string" used to make lines of muscle action. Insertion is held in place with masking tape. Outlines of lower jaws can be cut with scissors in tag board or cut with a bandsaw from plexiglas.