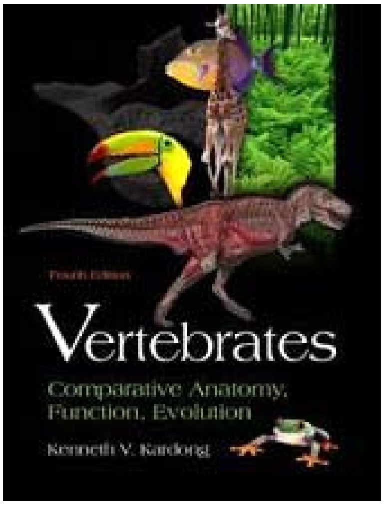


Taking the Bite Out of Evolution:

Synapsid Jaws and Muscles

Follow up in Textbook: pp. 275-277; 281-282

A. Objectives:

1. Explain how stresses at jaw joints have changed in synapsids.
2. Describe the functional consequences of the heightened coronoid on the jaw joint.
3. Explain how the appearance of a superficial masseter in derived synapsids increases the bite force without adding large stresses at the jaw joint.

B. Textbook Reference:

No textbooks are needed for this exercise.

C. 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 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.

JAW MUSCLES (Figure 4). There is differentiation of the jaw-closing musculature. In basal synapsids, the major jaw-closing muscle is the *adductor mandibulae* (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 *temporalis* and *massete*r. 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 *deep masseter* originates on the zygomatic arch and inserts on the lower jaw; the *superficial masseter* part arises beneath the eye, passes across the deep masseter, to insert on the angle of the dentary.

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 jaw bones and muscles reflect shifts in functional demands. To explore what these might be, we are going to model the primitive and derived conditions.

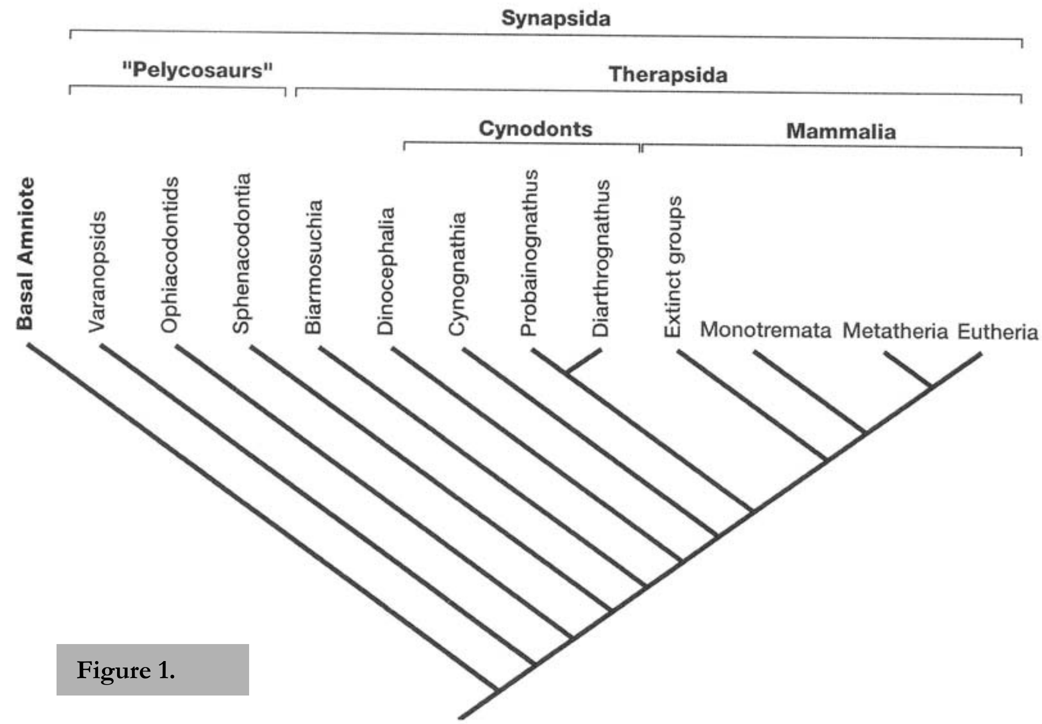


Figure 1.

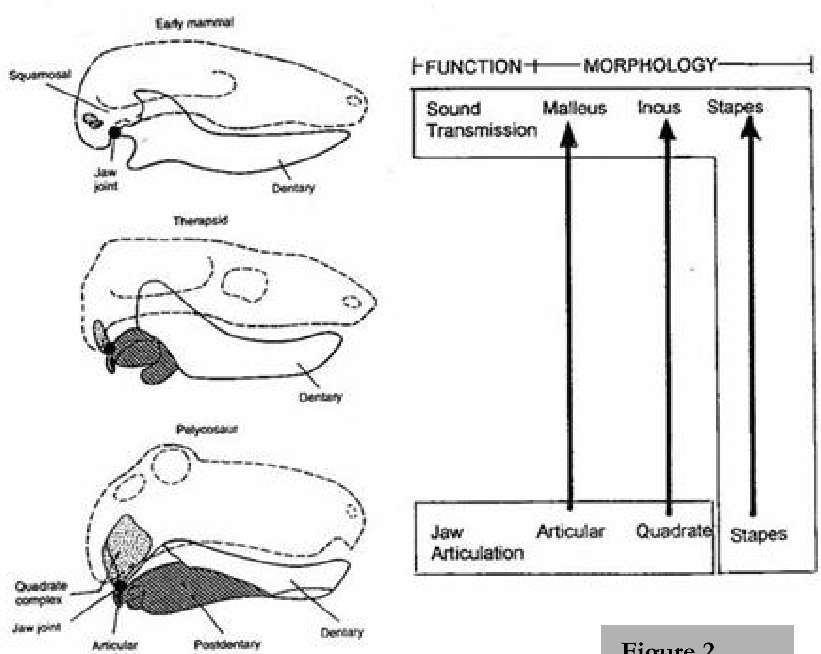


Figure 2.

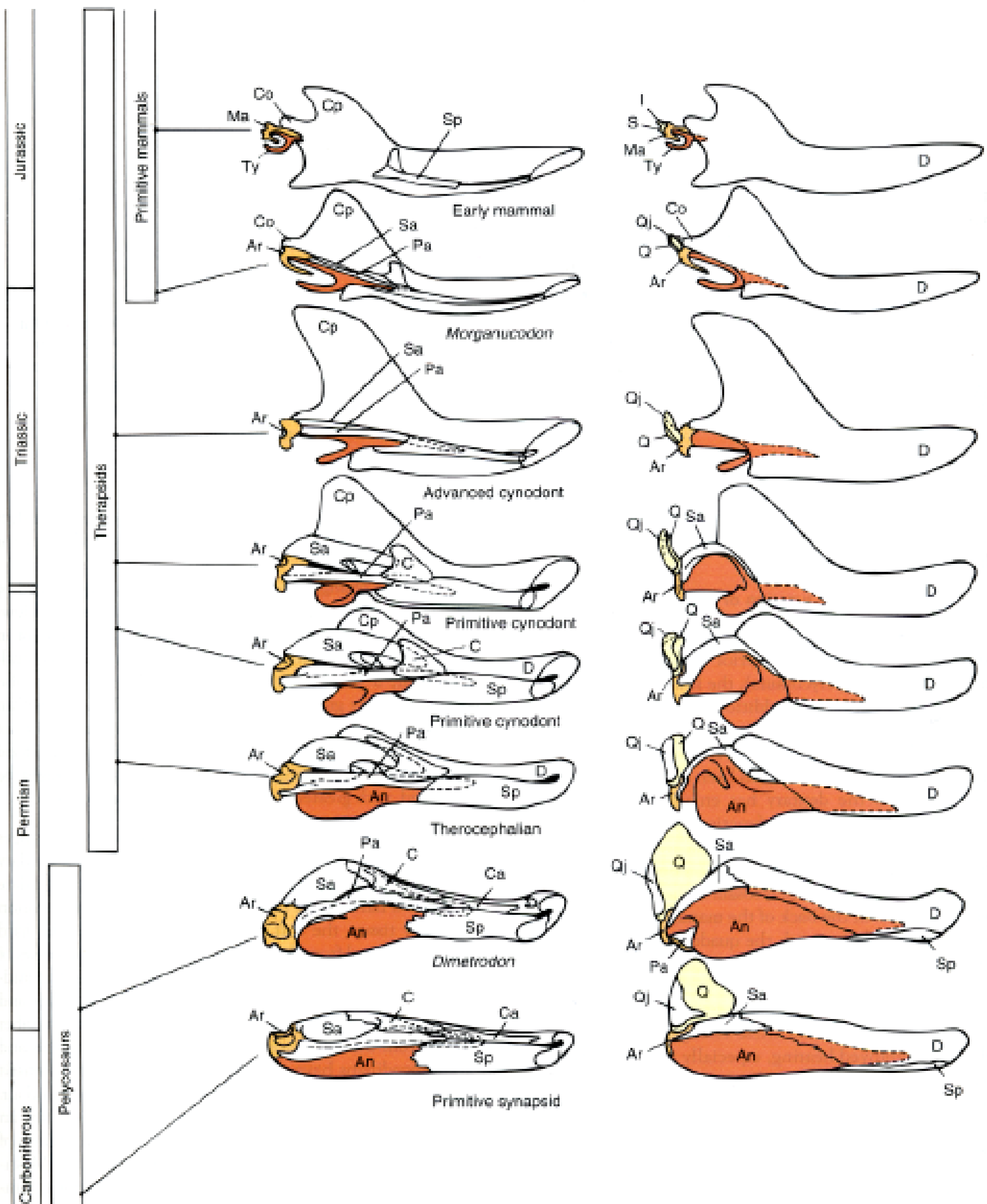
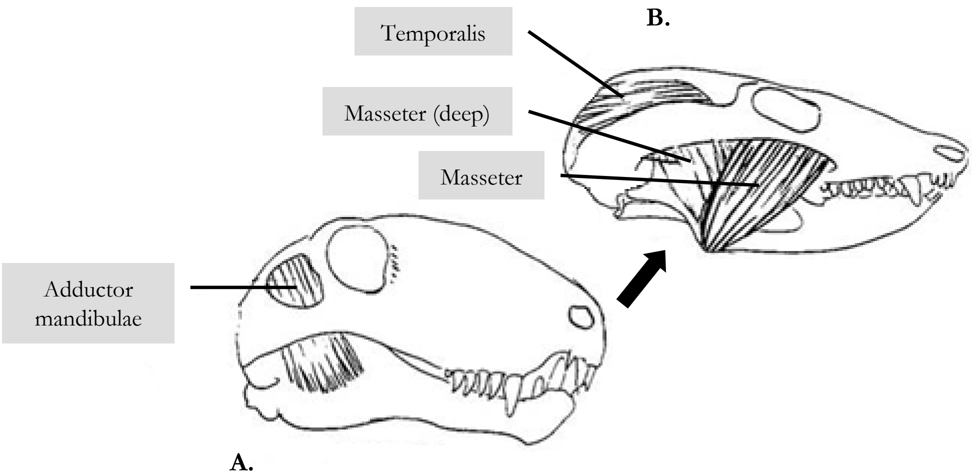


Figure 3 **Evolution of the mammalian middle ear bones.** Left column a medial view of the left mandibular ramus; right column lateral view of right mandibular ramus and quadrate. No teeth are shown to make comparisons clear. From primitive pelycosaurs, to therapsids, to the first mammals, changes in 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 4.



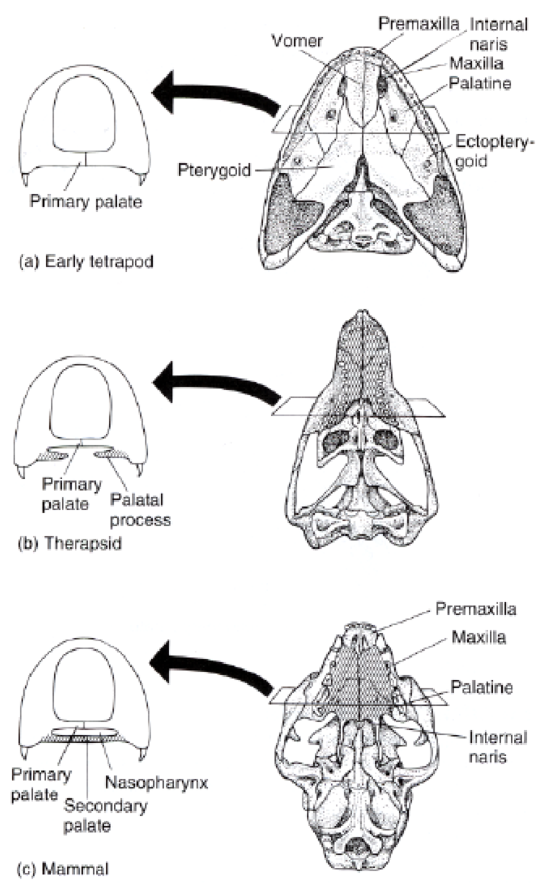


Figure 5a **Evolution of the secondary palate.**
(a) Early tetrapod with a primary palate in cross section (left) and ventral (right) views. (b) Therapsid with a partial secondary palate formed by the medial extension of the premaxilla and maxilla. (c) Mammal with a secondary palate that, in addition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

After Smith.

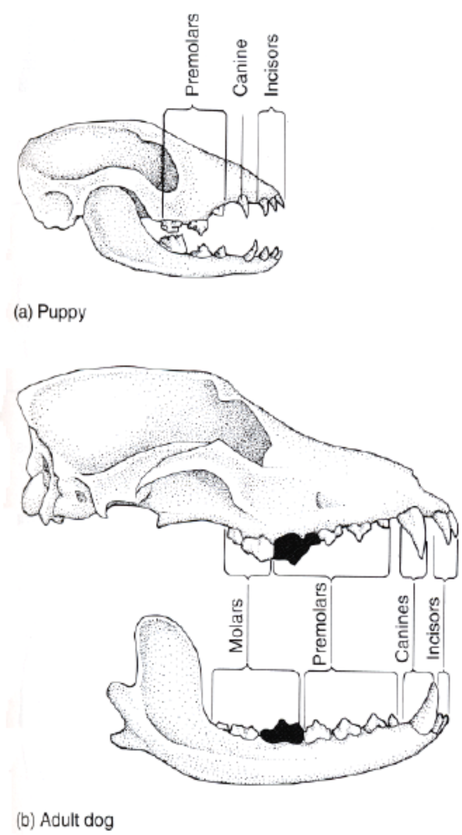


Figure 5b **Deciduous (a) and permanent teeth (b) in a dog.** The carnassials (shaded teeth) are specialized carnivore teeth derived from last premolar (upper) and first molar (lower).

D. Preparation & 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 a group consensus is reached, write the answer on the sheet, and then proceed to the next step.
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.

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 the jaw joint experiences this force 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).

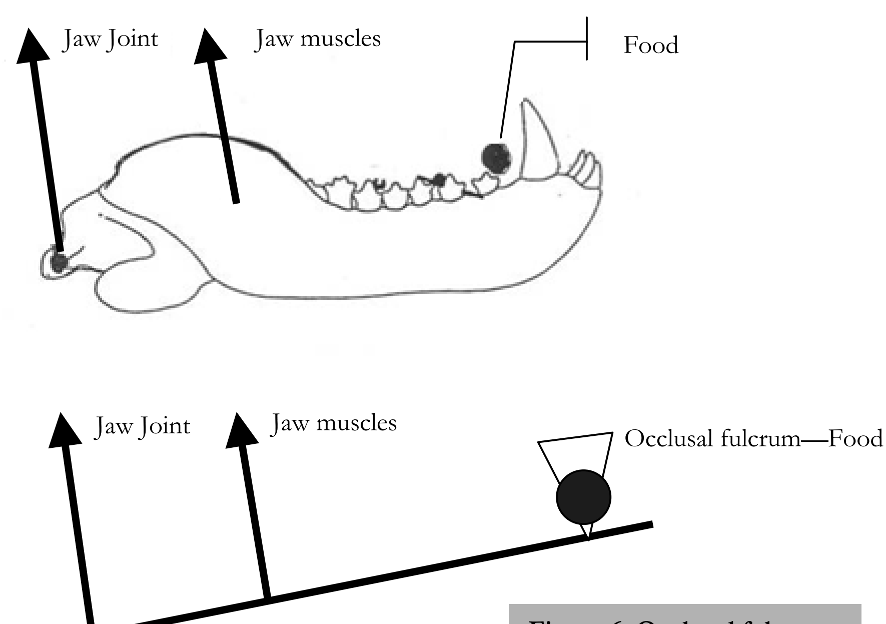


Figure 6. Occlusal fulcrum

Part A: Basal Synapsid ("pelycosaur")

Modeling. Obtain a model of a "pelycosaur" lower jaw from your instructor. Place the lower jaw in its outline (see page 13). 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 insertion of the Adductor mandibulae (**Am** $_i$). The other end of the rubber band should pass through the origin, marked on the skull with a dot " • ", the origin of the Adductor mandibulae (**Am** $_o$).

QUESTION: 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?

Group hypothesis:

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). A second person should put their finger on the jaw joint of the lower jaw to hold it. A third person in your group should now pull on the rubber band along this line of action. Partners should now exchange roles, try this again, and then other members should take their turns.

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

What was the result?

Part B: Derived Synapsid (therapsid)—Deep Masseter, (Md)

Modeling. Obtain a model of a therapsid lower jaw from your instructor. Place the jaw in its outline on the paper (see page 14). Use a rubber band to represent the line of action of the deep masseter. Do this by affixing the rubber band with tape to the insertion (**Md** $_i$) of this muscle on the lower jaw. The other end of the rubber band should pass through the origin, marked on the skull with a dot " • ", (**Md** $_o$). [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**$_o$ ". Although off the skull, this point is along the line of action of the deep masseter. Thus, for our purposes it can be used to simulate the origin of the muscle.]

Note that this therapsid muscle has the same line of action as the Adductor mandibulae of the pelycosaur in Part A.

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

Group hypothesis:

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). A second person secures the jaw joint of the lower jaw. A third 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)?

What was the result?:

Part C: Derived Synapsid (therapsid)—Temporalis

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 Temporalis muscle, but this time simulate the line of action from a heightened coronoid process. Do this by affixing this rubber band with tape to the top of the coronoid process ($\mathbf{T}_i$) the actually insertion as occurs in derived therapsids. The other end of the rubber band should pass through the origin, marked on the skull with a dot " • ", ($\mathbf{T}_o$) .

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?

Group hypothesis:

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). A second person secures the jaw joint of the lower jaw. A third 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)?

What was the result?:

OVERVIEW of Exercise 1:
Notice how your simulations of forces generated by jaw closing muscles on the lower jaw impart forces on the food and at the jaw joint. With a change in insertion and line of action, Deep Masseter to Temporalis, 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: Therapsid Jaw Muscles—adding it up

Part A: Derived Synapsid (therapsid): Temporalis + Superficial Masseter

Assumptions. Same.
Modeling. Use the same setup for the derived therapsid jaw. Keep the Temporalis inserted "high" and its line of action running through its origin, marked on the skull with a dot " • " ($\mathbf{T}_o$). 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 ($\mathbf{Ms}_i$) and its line of action runs through the origin marked on the skull with a dot " • " ($\mathbf{Ms}_o$).

QUESTION: 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? Will these be positive, negative, or about neutral?

Group hypothesis:

PROCEED to test your hypothesis: One person should be food in the mouth; a second secure the jaw joint; and a third 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.

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

What was the result?:

QUESTION: Did the force on the food increase or decrease?

What was the result?:

Part B: Derived Synapsid (therapsid): All three jaw adductor muscles

Assumptions. Same.
Modeling. Use the same setup as was just used in Part 2A, but now we will add the third jaw adductor, the Deep Masseter to the actions of the Temporalis and Superficial Masseter.

If you have the lower jaw properly fitted, there will be three rubber bands, each simulating one of the three major adductor muscle—Temporalis, Superficial Masseter, and Deep Masseter. Check to make sure this is set up correctly.

QUESTIONS: When there is food in the mouth (occlusal fulcrum) and ALL THREE muscles contract together (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?

Group hypothesis:

b) will the force on the food increase, decrease, or stay about the same?

Group hypothesis:

PROCEED to test your hypotheses: One person should be food in the mouth; a second secure the jaw joint; and a third and maybe additional person should now pull on ALL THREE rubber bands along their lines of action. Partners should exchange roles and run this again. Other members should also take their turns.

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

Group consensus:

Did the force on the food increase or decrease?

Group consensus:

OVERVIEW of Exercise 2
In therapsids, notice how adding muscles with new lines of action (Superficial Masseter and Temporalis) changes the forces. When all three jaw adductor muscles now contract, notice how forces on the food increase 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 try to duplicate the forces of the three major jaw muscles. However, that is difficult to do from fossils alone. Because modern day mammals evolved as a later stage in therapsid radiation (Figure 1), we can turn to carefully selected mammalian species as representatives of the fossil condition.

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

E. Synthesis:

Coronoid Height
What is the functional significance of a change in the height of the coronoid plus a Temporalis that acts on it (see Figure 3)?

Superficial Masseter + Temporalis
What is the functional significance of a Superficial Masseter plus Temporalis, compared to just a single jaw adductor muscle as in basal synapsids (pelycosaurs)?

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)?

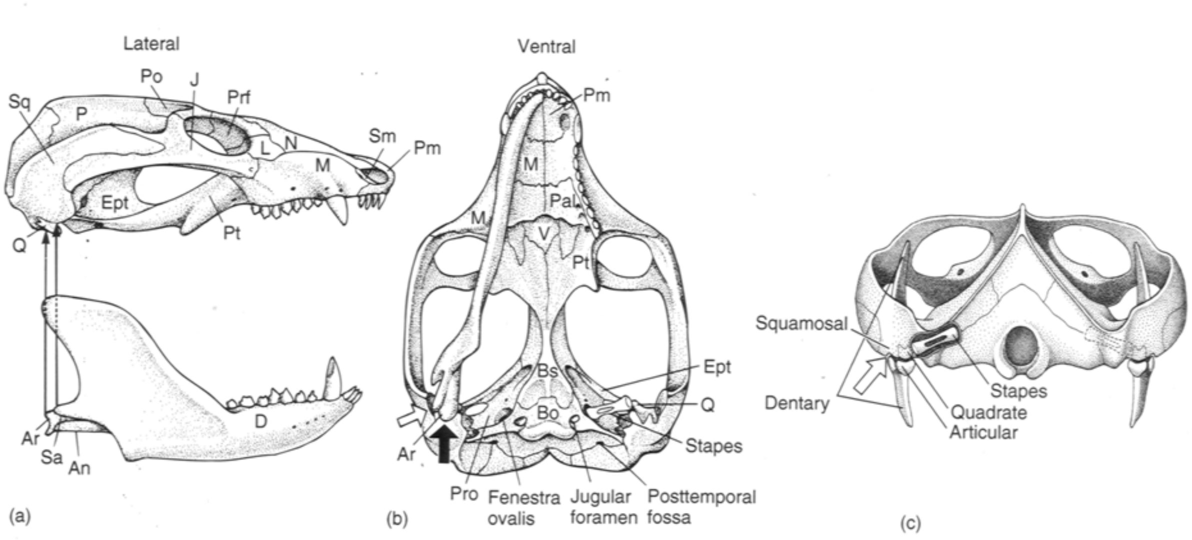
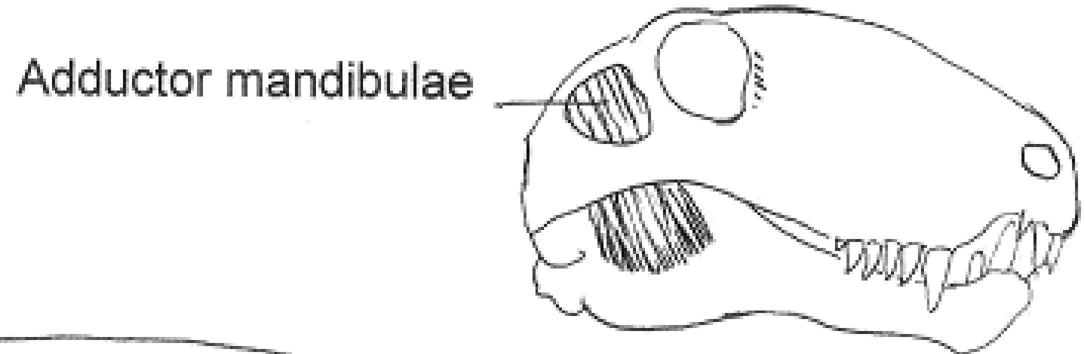
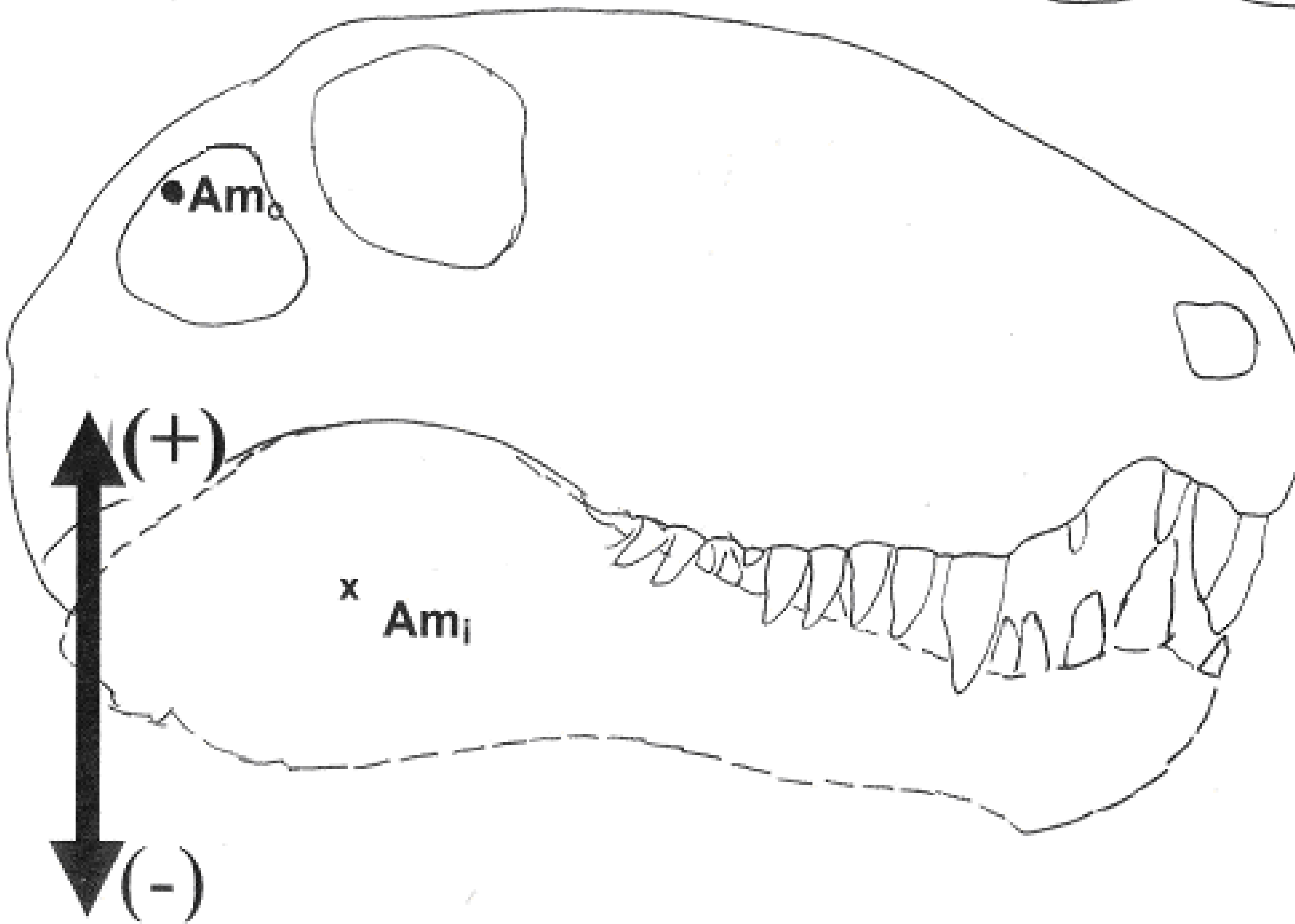


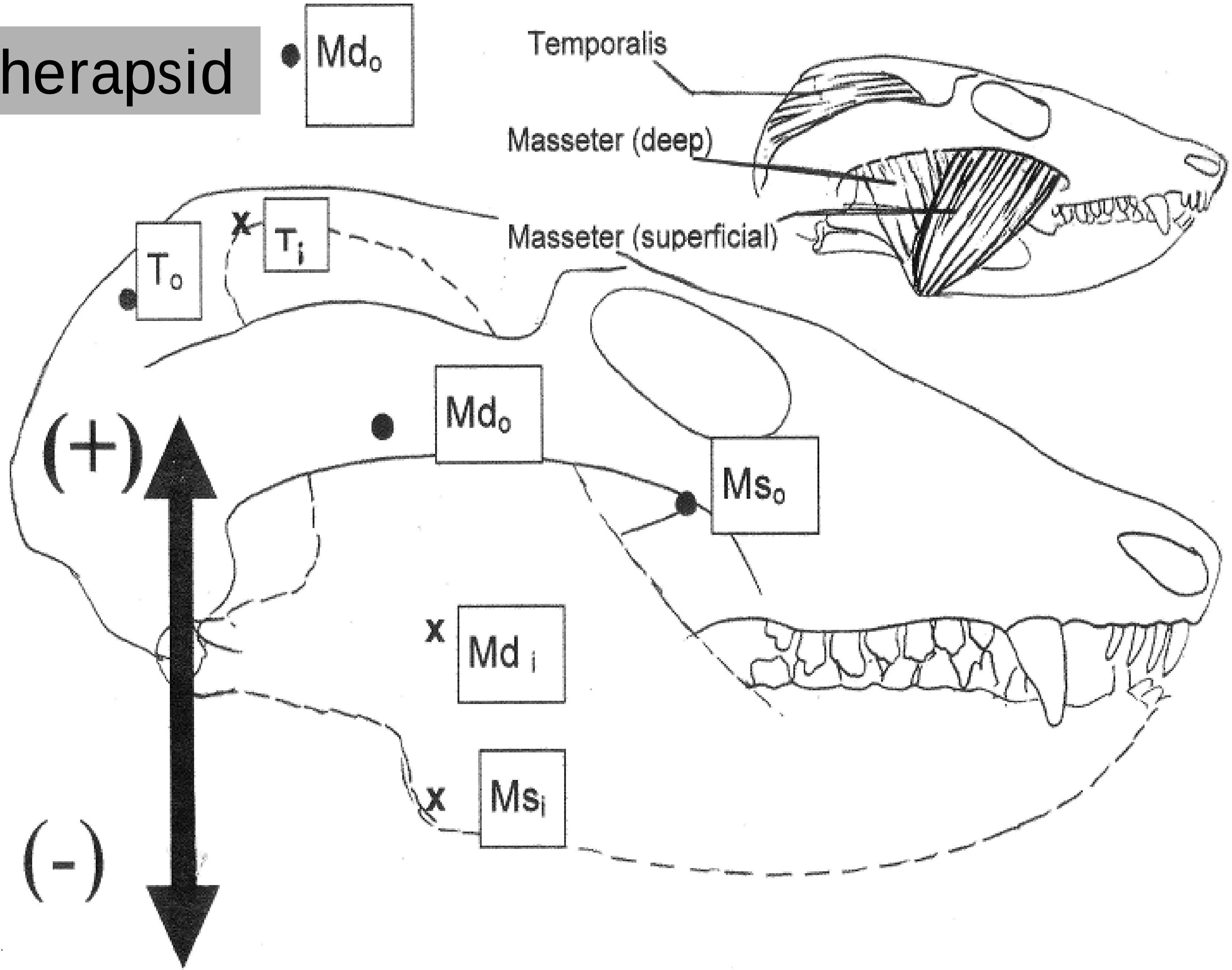
Figure 7. Double jaw articulation of *Probainognathus*.

Pelycosaur

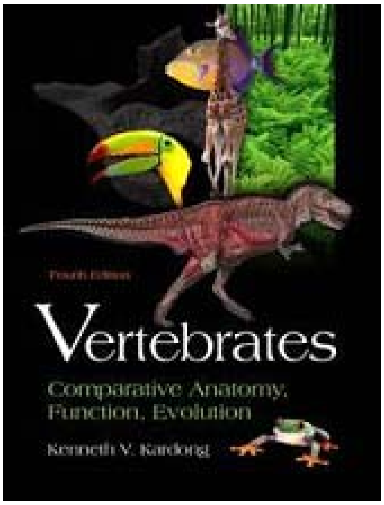




Therapsid



Md$_o$
Temporalis
Masseter (deep)
Masseter (superficial)
T$_o$
T$_i$
Md$_o$
Ms$_o$
Md $_i$
Ms$_i$
(+)
(-)



Instructor's Guide

Taking the Bite Out of Evolution: Synapsid Jaws and Muscles

Follow up in Textbook: pp. 275-277; 281-282

A. 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, and 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.

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.

B. Materials Preparation

Material List

- Rubber bands: Looped rubber bands can be cut making a short "string" used to make lines of muscle action.
- Masking tape: Insertions can be held in place with masking tape.
- Lower jaw models of a pelycosaur and therapsid: Outlines of lower jaws can be cut with scissors from heavy cardboard or cut with a bandsaw from Plexiglas.

Tape rubber band to the point of insertion and pull it through the point of origin as indicated. For instance, $\mathbf{Am_o}$ and $\mathbf{Am_i}$ in the Pelycosaur, origin and insertion respectively.

C. Facilitating and Assessment Tips

Suggested responses to the final synthesis questions.

1. 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.

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

3. Evolution—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*.

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.