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Phylogenetic Systematics of the Primate Genus Aotus,
Based on Hyoid Morphology

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Senior Honors Thesis
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April 18, 1997

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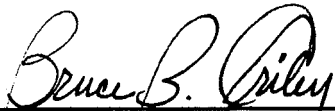
A Senior Research Honors Paper Presented
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April 18, 1997

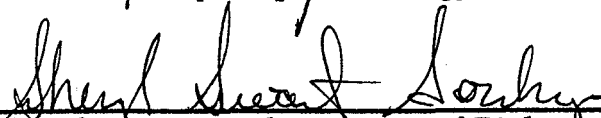
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Abstract

Dissection of a specimen of the South American primate genus Aotus was performed, focusing on the morphology of the hyoid apparatus and surrounding musculature within the hyoid region (the ventral side of the throat). Data collected from this dissection, along with data from published descriptions of primate genera from both primate suborders Haplorhini and Strepsirhini, were analyzed using the computer software program PAUP (Phylogenetic Analysis Using Parsimony). This analysis generated four equally probable phylogenetic trees (cladograms) depicting possible phylogenetic relationships of Aotus to other primates. While the cladograms differ in minor detail, they all show that Aotus appears to be more closely related to the more apomorphic suborder Haplorhini than to the Strepsirhini, and that it is a relatively plesiomorphous member of the haplorhine group. This suggests that the ancestor of the New World monkeys arrived in South America at about the time when haplorhine primates were beginning to diverge in the rest of the world, about 28 million years ago.

Introduction

Traditionally, primates have been divided into two taxa, the prosimians and anthropoids, with the tarsier group included as prosimians. More recent investigations have supported the hypothesis that tarsiers are more closely related to the anthropoids. This arrangement was first proposed by Pocock (1918) and supported by Goodman (1975) and Erickson (1996). With this change in grouping, there is a consequent change in nomenclature. Therefore, the prosimian group without the tarsiers is known as the suborder Strepsirhini and the anthropoids along with the tarsiers comprise the suborder Haplorhini. Members of the suborder Strepsirhini are considered relatively plesiomorphous and include such groups as the lemurs, aye-ayes, and lorises (Goodman 1975). The suborder Haplorhini includes the primate groups like the Old World monkeys (e.g. rhesus monkeys, baboons) and the apes (Goodman 1975). New World (South American) monkeys have traditionally been included with the haplorhines (Simpson 1945). However, it is not known exactly where they fit in: closer to the anthropoids or to the tarsiers.

The origin of South American primates has long been a mystery to primatologists, both where they came from (Africa and North America each contained possible ancestors, Carroll 1988) and when they arrived in South America. One way to examine these questions is to use the fossil record. The earliest fossil primates found in South America have been classified as members of the suborder Haplorhini that lived approximately 27-28 million years ago (mya), during the Upper Oligocene epoch (Carroll 1988). The earliest haplorhine fossils from Africa have been dated to the Middle Oligocene epoch, about 28-30 mya (Carroll 1988). This suggests that New World monkeys arrived in South America at about the time when haplorhines began to diverge from the more plesiomorphous strepsirhine group in Africa. According to Carroll (1988), New World monkeys are a monophyletic group. Therefore, all extant and extinct species are the result of a

single invasion and in this analysis it is assumed that findings for the representative genus (Aotus) are consistent with those for the rest of the South American taxa.

The genus Aotus contains species that are collectively referred to as "owl monkeys." They are the only strictly nocturnal anthropoid group (not including tarsiers) that exist (Ford 1994). There is some debate as to how many species of Aotus exist (Nowak 1991); however, it is herein assumed that all Aotine species (if there is more than one) are similar with regard to hyoid morphology.

The morphology of the primate hyoid region seems to be relatively stable, evolutionarily (Griffiths pers. comm.). As a result, differences in this anatomical region among primate groups should indicate evolutionary divergence. The purpose of this project was to describe the morphology of the Aotine hyoid region and compare it with that of other previously described primate groups in order to determine the relationships between this South American primate genus and those other groups. This information may shed light on the questions of when and from where New World monkeys originated.

Materials and Methods

The specimen of Aotus examined was that of a newborn male, preserved in formalin and ethanol, from the Illinois Wesleyan University fluid-preserved primate collection. The species of the specimen could not be determined with certainty because the original color patterns in the fur were altered due to the long-term formalin preservation. Dissection of the hyoid region was performed using a Bausch & Lomb dissecting microscope, twin fiber optic light sources, and standard microscope dissecting technique. Pencil drawings were made of each muscle layer exposed by the dissection. The drawings most relevant to the subsequent analysis were inked and labeled for inclusion into this paper. Written descriptions were made of all hyoid muscles for comparison with similar descriptions of the hyoid

regions of other primates (lemurs, Hill 1953; aye-ayes, Hill 1953; tarsiers, Erickson 1996; rhesus monkeys, Geist 1961, Howell and Straus 1961, Huber 1961; and humans, Williams et al. 1989) along with that of a closely related non-primate, the tree shrew (Griffiths in manuscript). Variations in hyoid morphological traits from all of these groups were assigned character state values in a MacClade data matrix table. The computer program PAUP (Phylogenetic Analysis Using Parsimony, Swofford 1993) was used to perform the analysis. Character state data from tree shrews, a group of mammals considered to be related to the ancestor of primates, were designated as the "outgroup" (a group of organisms that are considered equally dissimilar to each of the other ingroups analyzed). PAUP calculated the amount of dissimilarity between the organisms in question and translated that into phylogenetic trees (cladograms). Cladograms are diagrams of theoretical evolutionary paths depicting the relationships between organisms. The goal of this analysis is to find the most parsimonious cladograms (those with the fewest number of evolutionary steps involved) to explain the variation seen among these organisms.

Results

Branchiomic Musculature

Extrahyoid Muscles

M. digastricus anterior (Figs. 1 & 2)

Origin: This muscle has a double origin from the digastric tendon and the ventral surface of the basihyal (mostly from the tendon).

Insertion: Fibers insert onto the medial surface of the mandibular body from a point approximately 1 mm posterior to the mandibular symphysis to a point 10 mm posterior to the symphysis.

Comments: This muscle is indirectly connected at its origin to the omohyoid and the sternohyoid through fascia. There is no direct connection between the two

anterior digastrics except that they are connected to the basihyal. There is not a typical arcuate tendon present. Instead there is what is herein referred to as a vestigial arcuate tendon. This tendon is deep to the anterior digastrics and has associated muscle fibers which pass perpendicularly to the sagittal plane connecting the posterior digastrics. Some fibers run from the deep surface of the anterior digastric into the vestigial arcuate tendon.

M. digastricus posterior (Figs. 1, 2 & 3)

Origin: This band-like muscle originates from the paraoccipital bone just posterior to the auditory bulla, immediately posterior to and in common with the connective tissue fibers of the stylohyal ligament.

Insertion: Fibers run anteromedially to insert into the intermediate tendon and the vestigial arcuate tendon.

Mylohyoid Group

Muscles of this group are innervated by branches of the mylohyoid nerve, which is a branch of the mandibular nerve which, in turn, is a branch of the trigeminal (fifth cranial) nerve.

M. mylohyoideus (Figs. 2 & 3)

Origin: This muscle originates from the ventro-medial surface of the mandibular body to a point approximately 10 mm posterior to the mandibular symphysis.

Insertion: Most fibers run postero-medially. Those fibers that originate from the mandibular symphysis to a point approximately 3.5 mm posterior to it run perpendicular to the sagittal plane. Fibers insert into a midline connective tissue

raphe and onto the ventral surface of the basihyal, deep to the origin of the anterior digastrics.

M. mylohyoideus profundus

This muscle is absent.

M. mandibulo-hyoideus

This muscle has been recently determined to be the same muscle as the anterior digastric (Griffiths, in manuscript). The anterior digastric was previously described in this paper.

Hyoid Constrictor Group

Muscles of this group are innervated by branches of the facial nerve (seventh cranial nerve).

M. stylohyoideus (Figs. 1 & 2)

Origin: This muscle originates from a short tendon which in turn takes origin from the same paraoccipital connective tissue that gives rise to the stylohyal ligament and the posterior digastric.

Insertion: Fibers run antero-medially to insert near the insertion of the anterior digastrics and superficial to the insertion of the omohyoid onto the basihyal.

Comments: This muscle does not insert onto the basihyal.

M. jugulohyoideus

This muscle is absent.

M. sphincter colli profundus

This muscle is absent.

Glossopharyngeal Group

Muscles of this group are innervated by branches of the glossopharyngeal nerve (ninth cranial nerve).

M. stylopharyngeus (Figs. 3 & 4)

Origin: This muscle originates from the medial surface of the stylohyal ligament at a point approximately opposite from the origin of the styloglossus.

Insertion: Fibers insert into the lateral pharynx just anterior to the thyropharyngeus.

Comments: This muscle is extremely reduced in the specimen examined.

M. ceratohyoideus (Fig. 4)

Origin: From the anterior surface of the entire length of the thyrohyal.

Insertion: Fibers insert on the entire posterior surface of the two ossified anterior cornua elements: the ceratohyal and epihyal.

Pharyngeal Constrictor Group

Muscles of this group are innervated by branches of the vagus (tenth cranial) nerve.

M. hyopharyngeus (superior constrictor muscle - not illustrated)

Origin: This origin of this muscle is the pterygoid region of the inferior surface of the skull and the fascia of the lateral styloglossus region.

Insertion: Fibers run dorsally and insert onto the dorsal midline raphe of the pharynx.

M. thyropharyngeus (middle constrictor muscle - Fig. 4)

Origin: This muscle originates from the dorsal surface and tip of the thyrohyal at a point deep to the lateral fibers of the hyoglossus.

Insertion: Fibers pass dorsally, overlapping the anterior part of the cricopharyngeus, to insert onto the dorsal pharyngeal midline and intermingle with the fibers of the antimeres.

M. cricopharyngeus (inferior constrictor muscle - not illustrated)

Origin: This muscle originates from the lateral cricoid cartilage and from the posterior most cornu on the thyroid cartilage.

Insertion: Fibers insert into the dorsal pharyngeal midline and into the fibers of the antimeres.

Myotomic Musculature

Lingual Group

Muscles of this group are innervated by branches of the hypoglossal (twelfth cranial) nerve.

M. genioglossus (not illustrated)

Origin: This muscle originates from the posteromedial surface of the mandible, immediately lateral to the mandibular symphysis.

Insertion: Fibers pass posteriorly to two distinct insertions. One insertion is into the posterior one-third of the tongue (these fibers become part of the intrinsic

tongue musculature). Some fibers continue posteriorly to the other insertion, onto the anterior surface of the basihyal.

M. hyoglossus (Fig. 3)

Origin: This muscle originates from the lateral basihyal, lateral to the origin of the geniohyoid, and from the ventral thyrohyal.

Insertion: Fibers run antero-laterally and deep to the styloglossus to insert into the lateral tongue.

Comments: The hyoglossus is a very broad, unbroken, fan-shaped muscle.

M. styloglossus (Figs. 3 & 4)

Origin: This muscle originates from the posterolateral surface of the stylohyal ligament. The origin is about 4-5 mm anterior to the dorsal attachment of the stylohyal ligament.

Insertion: Fibers are anterior and run parallel to the hyoglossus nerve to insert along and into the lateral tongue surface.

Medial Ventral Cervical Group

Muscles of this group are innervated by the ansa cervicalis, a complex of nerves originating in the anterior cervical region, except for the geniohyoid which is innervated by the hypoglossus (twelfth cranial) nerve.

M. geniohyoideus (Fig. 3)

Origin: From the medial surface of the mandible, lateral and posterior to the mandibular symphysis.

Insertion: Fibers pass posteriorly to insert onto the anterior surface of the basihyal.

Comments: The geniohyoid is a broad strap which covers the genioglossus ventrally.

M. sternohyoideus (Figs. 1 & 2)

Origin: The sternohyoid originates from the dorsal surface of the entire width of the manubrium of the sternum.

Insertion: This muscle inserts onto the postero-ventral surface of the basihyal.

Comments: The two antimeres of this muscle are fused at the midline. The origin extends laterally along the manubrium out to the sternoclavicular articulation. No fibers originate from the clavicle.

M. sternothyroideus (Figs. 1 & 2)

Origin: The sternothyroid originates from the dorsal surface of the lateral-most part of the manubrium of the sternum.

Insertion: Fibers insert onto the lateral surface of the thyroid cartilage of the larynx.

Comments: This muscle is fused at its origin to the lateral sternohyoid with which it forms a continuous sheet across the posterior end of the trachea. As fibers of these muscles pass anteriorly, the sternothyroid separates from the sternohyoid so that the medial sternothyroid passes deep to the lateral sternohyoid (from a ventral viewpoint).

M. omohyoideus (Figs. 1& 2)

Origin: This muscle originates by a very short tendon from the midpoint of the superior border of the scapula, just medial to the scapular notch.

Insertion: Fibers pass antero-medially, emerging from deep to the sternomastoid and insert onto the basihyal lateral to the insertion of the sternohyoid.

M. thyrohyoideus (Figs. 2, 3 & 4)

Origin: The thyrohyoid originates from the entire lateral surface of the thyroid cartilage.

Insertion: This muscle inserts into the entire posterior surface of the thyrohyal.

Comments: This muscle is very broad.

Hyoid Apparatus (Fig. 4)

The hyoid apparatus of Aotus is made up of several elements. In this specimen, the basihyal, the largest component, has a roughly rectangular shape with two projections (cornua) that extend from it laterally. The more anterior cornu (termed the lesser cornu by human anatomists) has two fused bony constituents, the more medial ceratohyal and the more lateral epihyal. These, in turn are attached to the stylohyal ligament which extends laterally around the auditory bulla to the paraoccipital region of the skull. The more posterior cornu originating from the basihyal (the greater cornu of human anatomists) has only one bony element, the thyrohyal, which is strongly fused to the basihyal.

Results and Discussion

The data used for the PAUP analysis (collected from the literature search and dissection) are presented in Table 1. Four equally parsimonious cladograms (Fig. 5, A-D) were generated by PAUP delineating possible placements of Aotus in the primate evolutionary tree. Differences between the cladograms are relatively

minor, but indicate the need for more data to help reduce the number of most parsimonious cladograms down to one or two. However, all four cladograms show three consistent groupings: the aye-ayes with the lemurs (supporting their traditional placement in the taxonomic group Strepsirhini); the tarsiers with rhesus monkeys, humans, and Aotus (supporting their classification in the haplorhine group); and finally, the tree shrews (separate because they are the outgroup). The consistent placement of the divergence of Aotus near that of tarsiers (a plesiomorphic haplorhine) suggests that this particular New World monkey is also a plesiomorphic member of the haplorhine group. This implies that the ancestor of the New World monkeys arrived in South America at about the time that haplorhine primates were beginning to diverge in other parts of the world (about 28 mya), providing independent confirmation of what the fossil record evidence seems to suggest.

The question of "Where did South American monkeys come from?" can be addressed by examining the details of the cladograms. However, there is not a definitive answer. Figure 5A depicts Aotus and tarsiers as more closely related to each other than to any of the other primate groups. This suggests that tarsiers and Aotus share a common ancestor. It has been hypothesized that a fossil group of tarsiers (family Omomyidae) was ancestral to New World monkeys based on dentition comparison (Gazin 1958). Fossil evidence exists of these omomyid tarsiers living in North America around the time of the primate arrival in South America (Carroll 1988). Given this fossil evidence and the degree of similarity between the tarsier and Aotine hyoid regions, these data support the hypothesis that the ancestor of New World monkeys was a tarsier-like organism that migrated south from North America. Although the majority of tarsier fossils come from North America, there is one fossil tarsier (family Tarsiidae) found in northern Africa from this same

time period (Carroll 1988). Therefore, it is still possible that the ancestor to New World monkeys may have been a tarsier group that came from Africa.

Figure 5B depicts Aotus as the earliest lineage of the haplorhine group included in this study. This suggests that the ancestor of the New World monkeys diverged from the strepsirhine lineage before any other group did. This implies that the ancestor of New World monkeys must have diverged in Africa from other primates before the tarsiers split off (and thus before they could appear in North America). Therefore, according to Figure 5B it would appear that a very early African origin for South American monkeys is probable.

Figure 5C is identical to 5B except that the evolutionary placements of tarsiers and Aotus are switched relative to each other. Consequently, this implies that tarsiers diverged from the Strepsirhini line before any other strepsirhine group. It also depicts a closer relationship between Aotus and the human-rhesus group than between Aotus and tarsiers. Therefore, from this cladogram it would seem more likely that the ancestral New World Monkey came from African haplorhines and not the widespread tarsiers.

The final cladogram, Figure 5D, shows a close relationship between Aotus and tarsiers as does Figure 5A. However, the difference is in the timing of the human divergence from the other haplorhines. Therefore, it does not discount the possibility of a tarsier origin for the South American primates.

Although the "When" question of origins can be addressed by my analysis, some uncertainty remains surrounding the question of "From where?" The hyoid data can be interpreted to support either an African or North American origin for South American primate species. Further study is necessary to address this question.

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Table 1: Summary of character states in the MacClade matrix used by PAUP to generate the most parsimonious cladograms.

Aotus data		1	2
		stylohyoid course	genioglossus
1	Aye-ayes	superficial to digastric	strongly attached to basihyal
2	Lemurs	superficial to digastric	strongly attached to basihyal
3	Tarsiers	deep to digastric	reduced, attached to basihyal
4	Rhesus monkeys	deep to digastric	strongly attached to basihyal
5	Humans	superficial and deep to digastric	strongly attached to basihyal
6	Tree shrews	superficial and deep to digastric	no connection to basihyal
7	Aotus	superficial to digastric	reduced, attached to basihyal
Aotus data		3	4
		styloglossus from	stylopharyngeus from:
1	Aye-ayes	tympnum	tympnum
2	Lemurs	tympnum	tympnum
3	Tarsiers	stylohyal ligament	stylohyal ligament
4	Rhesus monkeys	stylohyal ligament	stylohyal ligament
5	Humans	stylohyal ligament	stylohyal ligament
6	Tree shrews	tympnum	stylohyal element & tympnum
7	Aotus	stylohyal ligament	stylohyal ligament
Aotus data		5	6
		length of cornua	* elements ant. cornua
1	Aye-ayes	anterior longer	three complete elements
2	Lemurs	anterior longer	three complete elements
3	Tarsiers	anterior longer	two complete elements
4	Rhesus monkeys	posterior longer	one fused element, long tendon
5	Humans	posterior longer	one fused element, long tendon
6	Tree shrews	anterior longer	three complete elements
7	Aotus	posterior longer	two complete elements
Aotus data		7	8
		shape of hyoid	anterior digastric: tendon
1	Aye-ayes	curved transverse bar	arcuate tendon across midline
2	Lemurs	curved transverse bar	NO tendon or midline connect
3	Tarsiers	rectangular transverse body	arcuate tendon across midline
4	Rhesus monkeys	rectangular transverse body	arcuate tendon across midline
5	Humans	rectangular transverse body	intermed. tendon, not cross mid
6	Tree shrews	curved transverse bar	arcuate tendon across midline
7	Aotus	rectangular transverse body	red. arc. tend. across midline

Figure 1: First in the hyoid dissection series (the most superficial layer exposed). Drawing is 3.5X natural size.

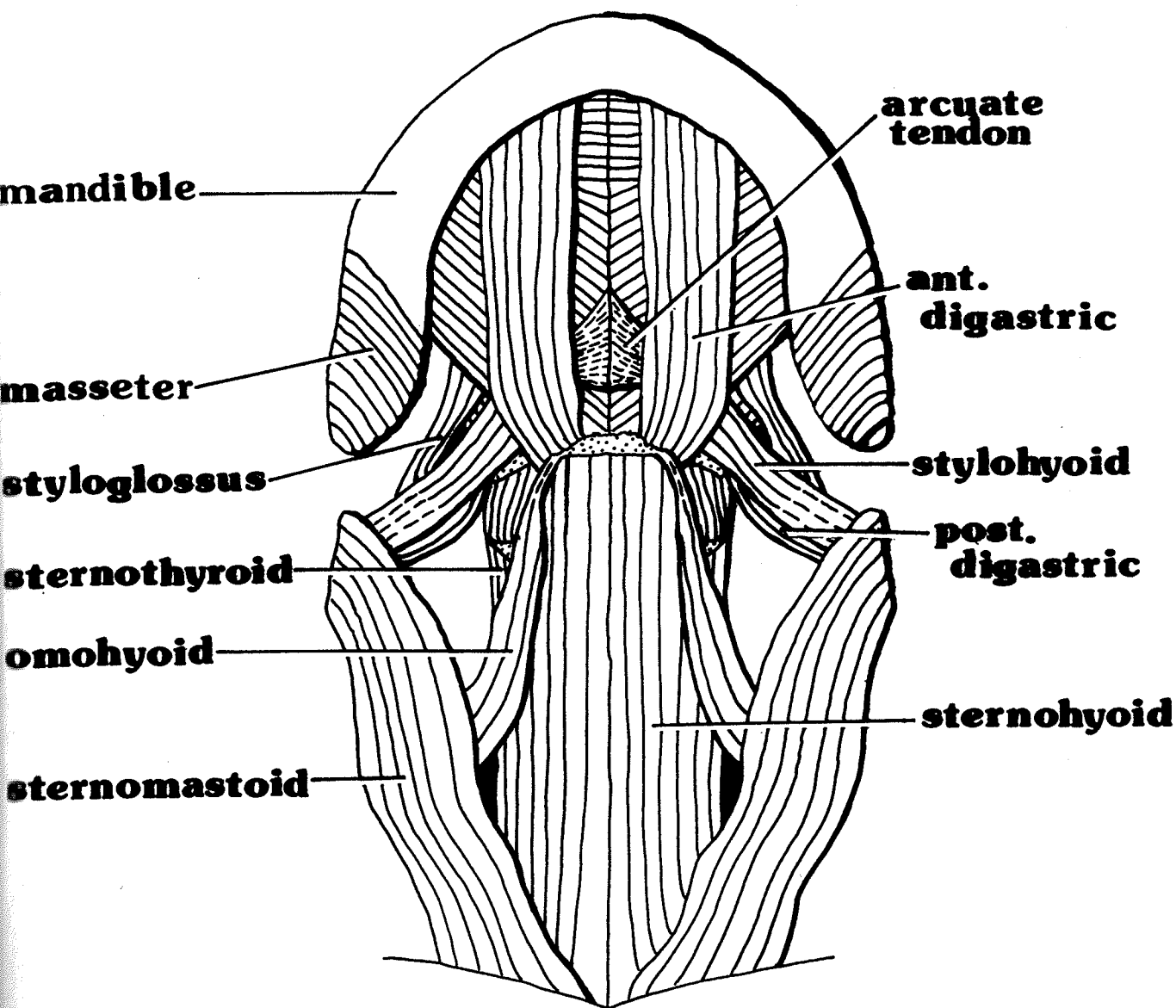


Figure 2: Second in the hyoid dissection series (both the superficial layer and the one exposed deep to it). Drawing is 3.5X natural size.

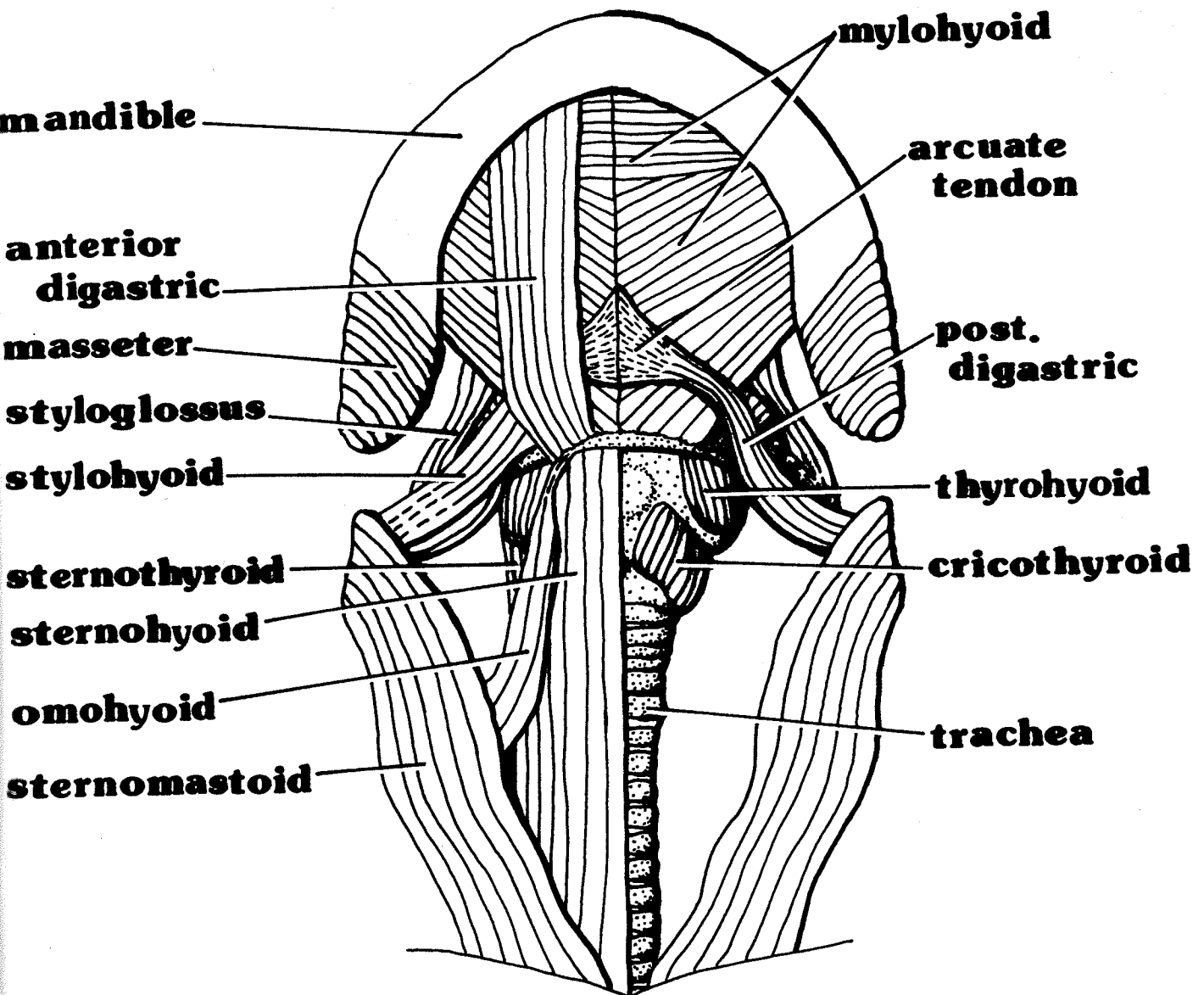


Figure 3: Third in the hyoid dissection series with a deeper layer exposed. Drawing is 3.5X natural size.

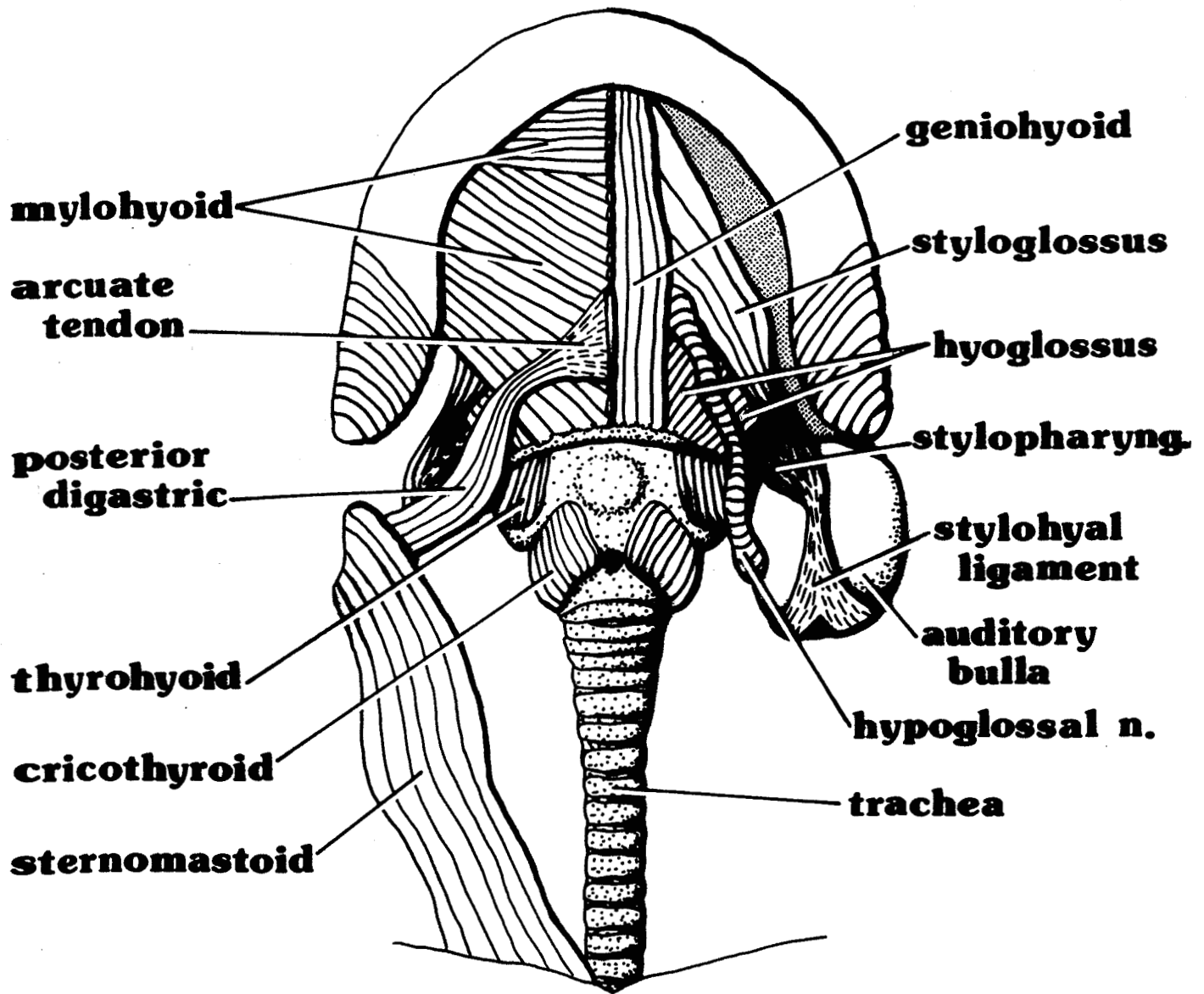


Figure 4: Fourth in the hyoid dissection series (the hyoid apparatus-the deepest layer dissected).
Drawing is 3.5X natural size.

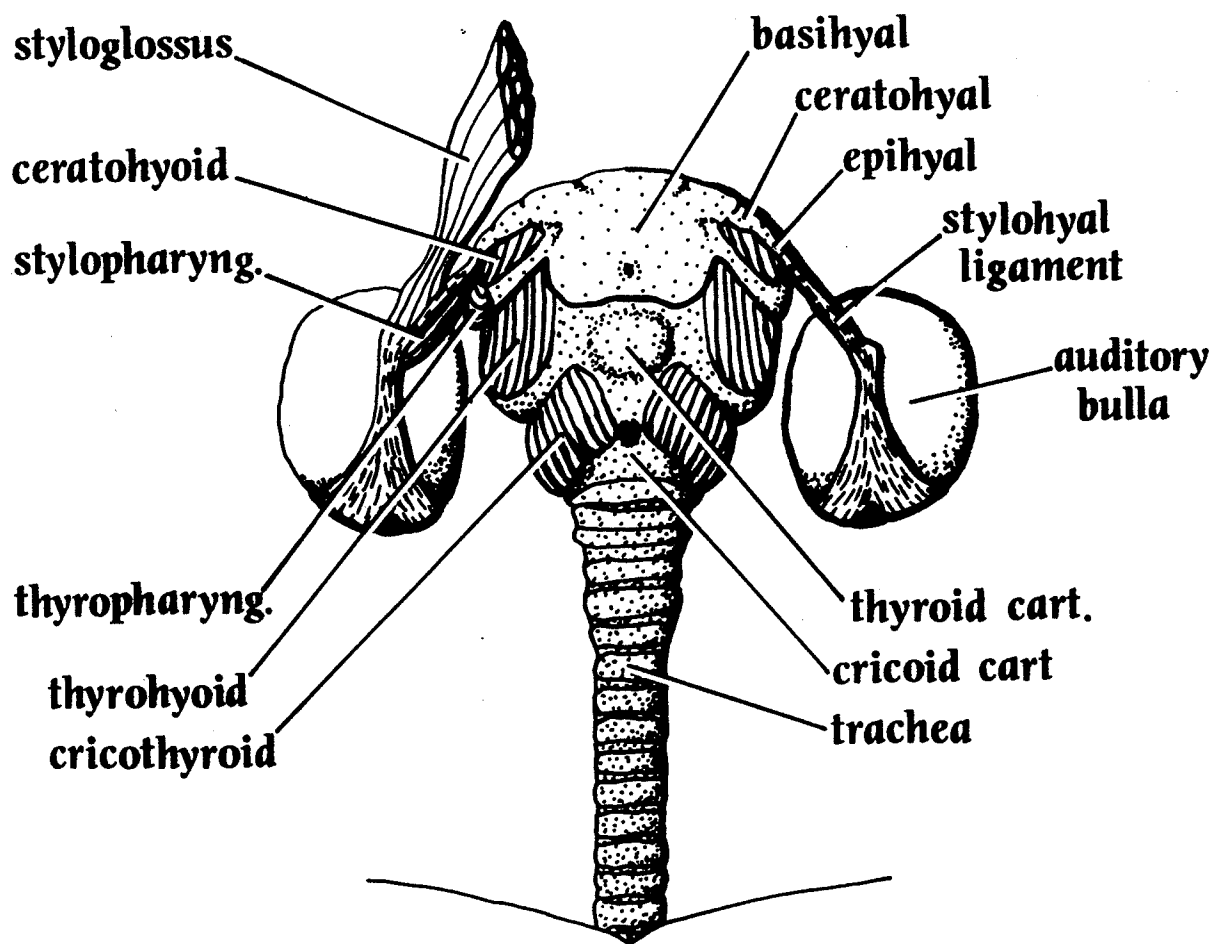
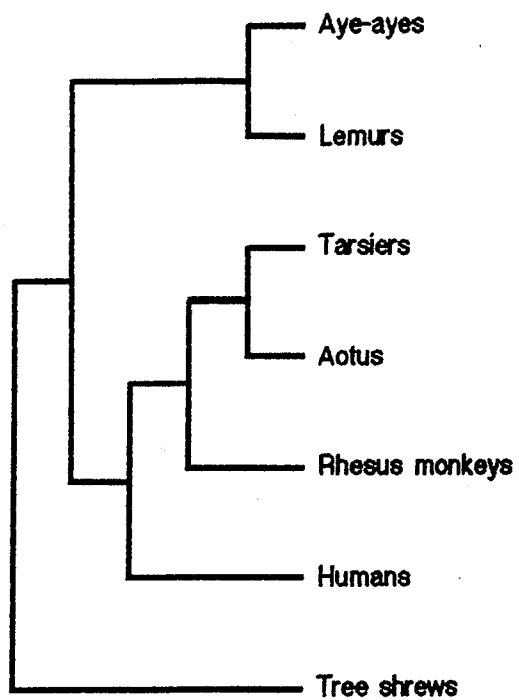
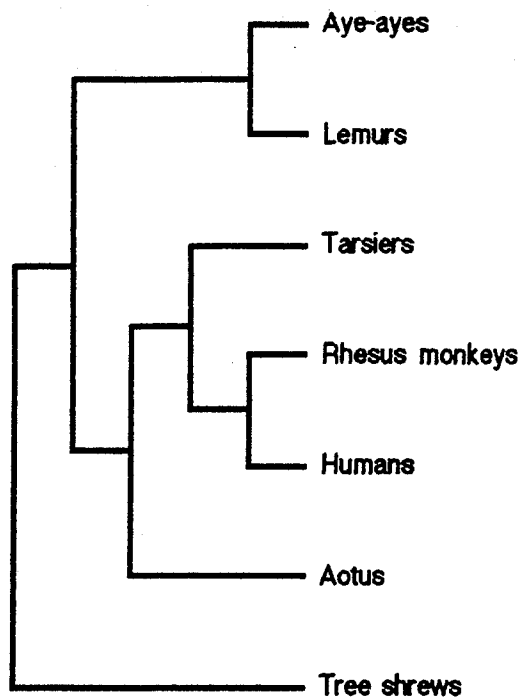


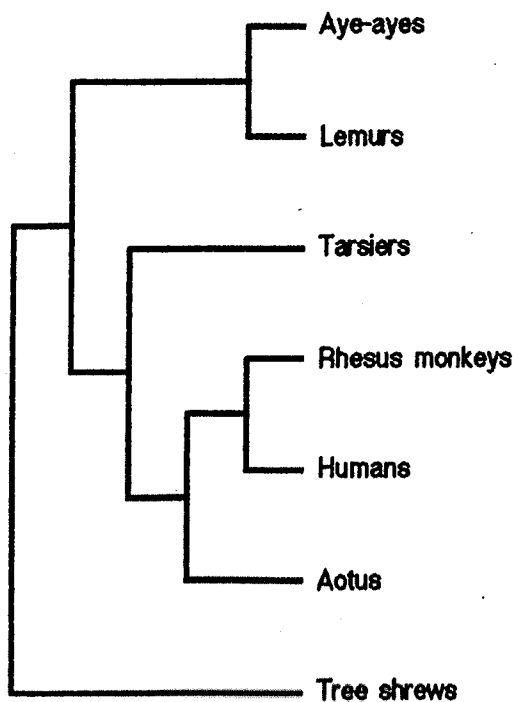
Figure 5, A-D: The four most parsimonious cladograms generated by the PAUP analysis (using the data in Table 1).



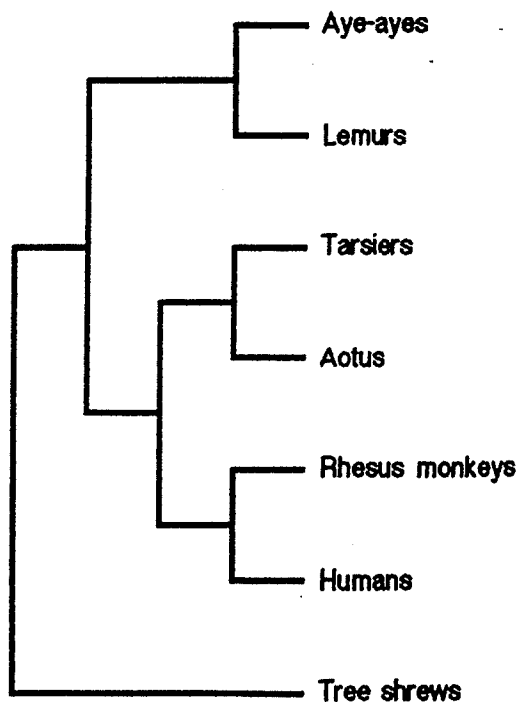
A



B



C



D