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Petrodromus tetradactylus (Mammalia, Macroscelidea)

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On the Jaw Musculature and Relationships of *Petrodromus tetradactylus* (Mammalia, Macroscelidea)

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ABSTRACT

The jaw musculature of the elephant shrew, *Petrodromus tetradactylus*, is dissected and compared with rabbits and other mammals. Three derived characters (completely divided internal pterygoid, relatively large pterygoid musculature, and distinct pars reflexa of superficial masseter) are shared by elephant shrews and rabbits. Aardvarks and edentates share large pterygoid muscu-

lature, whereas rodents share a distinct pars reflexa with rabbits and elephant shrews. These characters indicate a close relationship between these groups. Some other placentals also share these derived characters. However, no judgment as to possible relationships with elephant shrews and rabbits is made.

INTRODUCTION

McKenna (1975) has recently hypothesized a close relationship between the macroscelidids and lagomorphs. Both Patterson (1965) and Evans (1942) dealt with the interrelationships of macroscelidids but did not analyze the group cladistically. Patterson tried to segregate primitive and derived characters in his study and concluded that the family was different enough from other insectivores to be placed in its own order. McKenna places these modern mammals and lagomorphs into a new subdivision of the eutheria called the Ernotheria. With these two groups have been added many extinct forms. The ernotheres share the loss of P_3^3 from a plesiomorphic condition of five premolars. Macroscelidids and lagomorphs are also synapomorphous in sharing prismatic teeth.

These characters are easily comparable in both living and extinct taxa for they deal only with hard parts. In the present study an elephant shrew and rabbit are dissected and their jaw muscles compared. Because soft parts are examined, this study can only relate to McKenna's hypothesis of relationship of these two living groups.

Because there are many accounts of rabbit jaw musculature in the literature (Schumacher and Rehmer, 1960; Bensley, 1910), no description is given here. Only similarities and differences of the jaw muscles of *Petrodromus* are mentioned. Only one thorough account of elephant shrew (*Elephantulus*) jaw musculature has appeared (Fiedler, 1953). In addition to *Elephantulus*, Fiedler described many different insectivores so that this work has proved valuable in making

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outgroup comparisons. Turnbull (1970) serves the same purpose but with a wider taxonomic range. I have made all judgments of plesiomorphy and apomorphy on the basis of these works.

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DESCRIPTION

The elephant shrew used for dissection is *Petrodromus tetradactylus*, a young female, AMNH 203328. The specimen is labeled *P. sultani*, but this name has been synonymized by Corbet and Hanks (1968) with *P. tetradactylus*. The illustrations are based on a skull and jaws, also a female, AMNH 203331. The specimens were taken 2½ miles inland from Gedi, Kenya. The collection date is unknown.

A broad aponeurosis covers the entire M. masseter, pars superficialis (figs. 1a; 2a,c). Muscle fibers take origin from this sheet over the dorsal one-third of its height. The sheet gradually thickens toward the zygomatic arch and takes origin laterally on the anterior one-half of arch. The origin is fleshy underneath the tendon sheet and is restricted to the lateral surface of zygomatic arch. The muscle ends anteriorly on the ventral side of the buttress joining the arch to the lateral face of maxilla. Fibers also originate dorsally from a tendon sheet separating pars superficialis from pars profundus.

At the origin fibers run posteroventrally at 45 degrees to the horizontal but run nearly horizontally at the ventral edge of lower jaw. Also the muscle thickens near its insertion to a thick belly.

A combination fleshy and tendinous insertion

runs along the ventralmost lateral surface of jaw from below the midportion of orbit to the tip of angular process posteriorly. The two divisions of masseter are difficult to separate throughout most of their length and are joined by fascia posteriorly from near the arch dorsally to angle of jaw ventrally. The body of the muscle is free of tendinous fibers.

A pars reflexa (fig. 1a) is distinct anteriorly and ventrally but fades into the pars superficialis posteriorly and at its origin under the zygoma-maxilla buttress. The pars reflexa is exposed only laterally. Its fibers run in the same direction as the pars superficialis: 45 degrees posteroventrally near its front and nearly horizontally posteriorly.

The M. masseter, pars profundus (figs. 1b; 2a, c) takes origin only from the lateral surface of zygomatic arch but is restricted to near its ventral edge. The origin extends anteriorly to the zygoma-maxilla buttress and posteriorly to the mid-point of jugal-temporal suture. The origin is entirely fleshy except for a few tendon fibers coming from the anterior one-third of the muscle.

Fiber direction is constant throughout its length, running posteroventrally about 60 degrees from the horizontal. A tendon sheet covers the posteroventral one-half of the muscle. Its border with the fleshy surface extends diagonally near the insertion anteriorly to near the arch posteriorly.

This tendon sheet inserts on jaw as the ventral-most border of the muscle except anteriorly where muscle fibers insert superficially. The muscle inserts on the ventrolateral edge of jaw from below the last molar anteriorly to the jaw angle posteriorly. Insertion is immediately dorsal to the insertion of pars superficialis. Above the angle the pars profundus unites with the zygomaticomandibularis by a raphe. The insertion is fleshy and extends dorsally 2 mm. from near the ventral edge of jaw.

The pars profundus is very hard to separate from zygomaticomandibularis. The zygomaticomandibularis (figs. 1c; 2c) originates from the ventral edge of zygomatic arch and from the entire medial surface of the anterior one-half of the arch. An aponeurosis covers the dorsal half of the muscle and inserts just on the ventrolateral curvature of arch. Muscle fibers run posteroventrally.

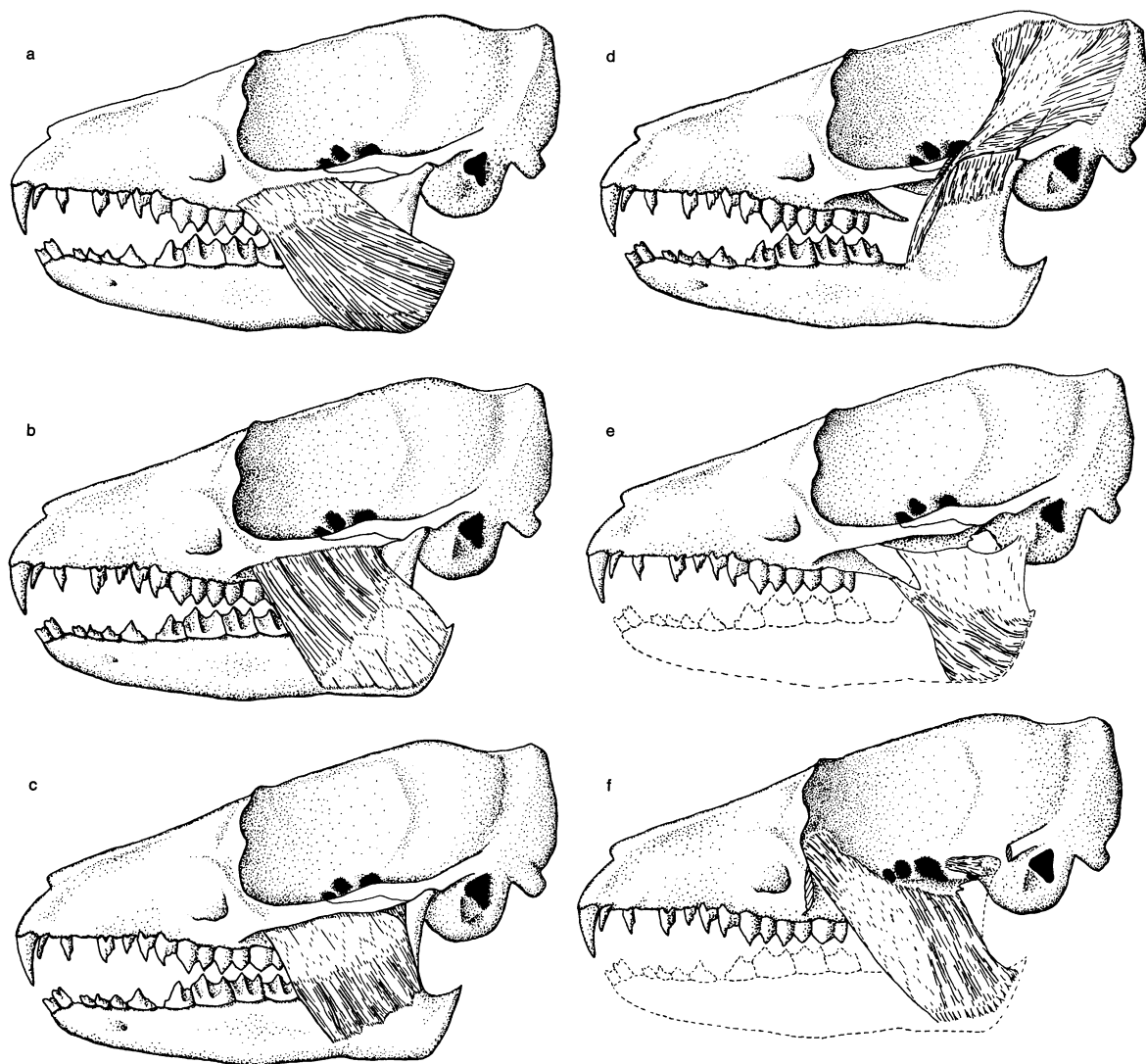


FIG. 1. *Petrodromus tetradactylus* jaw muscles. a. M. masseter, pars superficialis; b. M. masseter, pars profundus; c. M. zygomaticomandibularis; d. M. temporalis, pars superficialis, pars profundus, pars zygomaticus; e. M. pterygoideus internus, internal division; f. M. pterygoideus externus and M. pterygoideus internus, external division.

trally, nearly 60 degrees from the horizontal. Fiber direction is nearly constant throughout the muscle.

The muscle inserts fleshily over a large area of the lateral surface of ascending ramus. A few tendon fibers insert anterodorsally near the anterior

border of the muscle. The insertion extends ventrally to just below the ascending ramus and runs back to the concavity formed by the jaw angle. Dorsally the insertion extends halfway up the ascending ramus and inserts all along the length of the process.

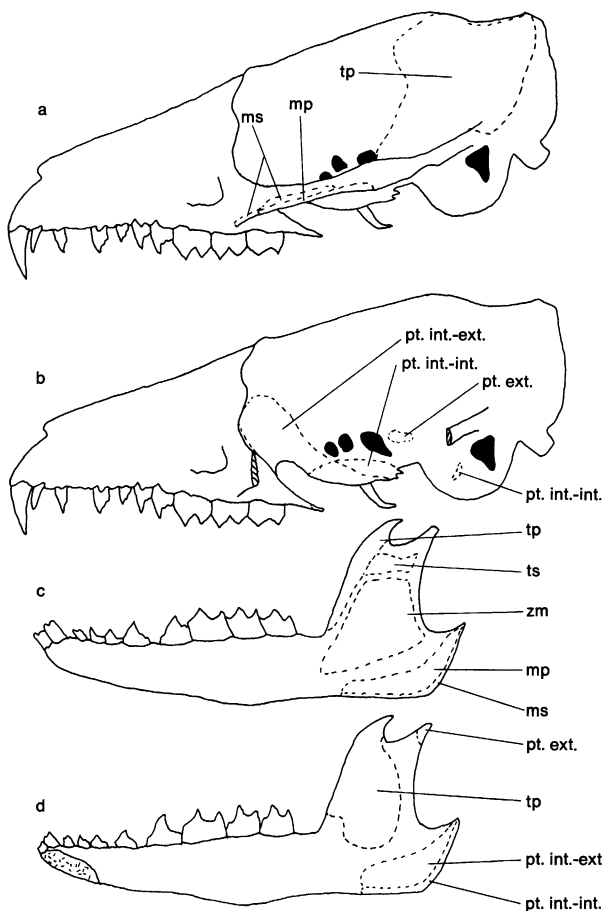


FIG. 2. Outlines of origins and insertions of jaw muscles of *Petrodromus tetradactylus*. a. and b. are lateral views of skull; c. lateral view of lower jaw; d. medial view of lower jaw. *Abbreviations:* ms, *M. masseter, pars superficialis*; mp, *M. masseter, pars profundus*; pt. ext., *M. pterygoideus externus*; pt. int.-ext., *M. pterygoideus internus, external division*; pt. int.-int., *M. pterygoideus internus, internal division*; tp, *M. temporalis, pars profundus*; ts, *M. temporalis, pars superficialis*; zm, *M. zygomaticomandibularis*.

Fascia is common throughout the muscle and allows easy separation of most of the muscle into fine layers. The muscle is very difficult to separate from the underlying *M. temporalis, pars superficialis*.

The *M. temporalis, pars superficialis* (figs. 1d; 2c) originates from the medial surface of zygomatic arch from just anterior to the jugal-temporal suture to a point immediately anterior to the glenoid fossa. Fibers run anteroventrally, lying 80 degrees from the horizontal. In frontal

view the fibers are nearly horizontal as they come off the arch. External fibers turn vertically as they insert on the lower jaw, whereas more medial fibers insert almost horizontally.

There is little tendinous material in the muscle. Posteriorly, at the insertion, tendon fibers are prominent and firmly anchor the muscle to the ascending ramus. Everywhere else the insertion is fleshy. The insertion is restricted to the upper one-third of the ascending ramus. The *pars zygomatica*, as it descends past the zygomatic

arch, fuses with pars superficialis on the laterally facing ridge which runs down the front edge of ascending ramus. Because this muscle is completely fused with pars superficialis, its distal half is weighed with pars superficialis.

The M. temporalis, pars profundus (figs. 1d; 2a,c,d) takes origin from the lateral side of skull roof. The origin extends dorsally to the sagittal crest, posteriorly to the occipital crest, ventrally to a level just dorsal to the external auditory meatus, and anteriorly forms the posterior orbital rim. The origin all along the periphery is by a narrow tendinous band. More internal to this tendon ring is a strong fleshy origin. Tendon fibers intermingle with the fleshy origin. An aponeurosis covers only the median part of the muscle externally.

Fibers converge toward the anterior edge of ascending ramus. More ventral fibers run nearly horizontally, whereas more dorsal fibers (on sagittal crest) run down vertically. The average fiber direction is anteroventral, running 45 to 50 degrees from the horizontal.

The external aponeurosis converges ventrally into a narrow tendon band, inserts on the dorsal edge of coronoid process, and runs down the front edge of ascending ramus. There is also a tendinous insertion in the trough separating the coronoid process from the jaw condyle. The muscle inserts fleshily on the medial side of ascending ramus. The medial insertion is wide, covering the entire area from the mandibular foramen ventrally to the coronoid process dorsally. Only a narrow 3 mm. strip along the back edge of ascending ramus is free from any muscle insertion. The fiber direction is nearly vertical with a slight anteroventral trend.

The dorsal half of pars zygomatica (fig. 1d) is only an anteroventrally trending bulge of the pars profundus and has no separate origin on the skull roof. However, the pars zygomatica does take origin from the dorsal surface of zygomatic arch for a length of 4 or 5 mm. The fibers run horizontally and dip down to fuse with pars profundus as it inserts on the leading edge of ascending ramus.

The pterygoideus externus (figs. 1f; 2b,d) is a small muscle compared with pars internus. The muscle originates fleshily on alisphenoid just dorsal to foramen ovale and foramen rotundum.

A few strong tendon fibers lie within the muscle and assist in its origin.

In side view the muscle passes 10 degrees from the horizontal posterodorsally toward its insertion. In frontal view the muscle runs nearly straight laterally out toward the joint capsule of lower jaw. The muscle fibers are nearly parallel but diverge slightly as they near the lower jaw. There is no tendinous material within the body of the muscle or on its surface.

Very near the insertion, however, some muscle fibers run into a very strong tendon sheath which in turn fuses with the joint capsule. Immediately ventral to the joint capsule, muscle fibers insert directly on the medial surface of jaw.

The pterygoideus internus is very well developed and has a complex origin. The muscle is easily divided into distinct divisions that are joined posteriorly. The external division (figs. 1f; 2b,d) is the more massive of the two and its origin covers the entire orbital exposure of palatine bone. The origin is fleshy and roughly outlines the suture of palatine with the surrounding orbital bones. The origin continues posteriorly and ventrally onto the lateral and medial sides of the lateral pterygoid wing. Tendons take origin from the edge.

The external division has almost no slope in frontal view except for the more ventral fibers which run 30 degrees from the horizontal ventrolaterally. In side view the fibers run posteroventrally at 30 degrees from the horizontal.

A strong tendon sheet surrounds this division of the muscle. This sheet continues down the lateral, dorsal, and ventral surface of the muscle to insert on lower jaw. Only a few tendon fibers are present in the body of this division.

The external division of internus inserts by a series of very strong separate tendons which receive muscle fibers from the body of the muscle. Insertion begins anteriorly midway between front and back of ascending ramus and reaches to the jaw angle posteriorly. The muscle inserts fleshily on the tip of the jaw angle. Dorsal to the tendinous insertion, muscle fibers insert directly for a height of 2 mm.

The internal division of the internus (figs. 1e; 2b,d) takes origin from the ventromedially directed hooklike process of palatine, from the

bullae at the tympanic-entotympanic suture, and from the pterygoid fossa. The origin is entirely tendinous. The muscle is quite thin throughout and tapers proximally into a very thin tendon sheet.

Muscle fibers run posteroventrally, are nearly horizontal at their insertion, but lie 30 degrees from the horizontal at their origin. In frontal view the muscle runs 45 degrees from the horizontal near its origin but runs nearly vertically at its insertion.

This division inserts very near the ventral edge of jaw. The insertion extends anteriorly to the same point as external division. Posteriorly and dorsally the insertion reaches the tip of jaw angle.

The midportion of the internal division of pars internus is free of tendinous material.

The M. digastricus is unusual in the poor development of the ventral belly. A strong tendon sheet covers the entire ventral belly and inserts on the ventral edge of lower jaw. Internal to this tendon sheet, muscle fibers insert directly on lower jaw. The insertion extends anteriorly only to the second molar and 3 mm. posterior to the point below the leading edge of ascending ramus.

Fibers run longitudinally except where they begin to rise to meet the posterior belly of digastric. The two divisions meet each other by a dividing tendon. From the dividing tendon the posterior belly reaches up to the mastoid process where it takes a tendinous origin. The fiber direction of this belly is vertical and parallel.

Both bellies are connected tendinously to stylohyoid, geniohyoid, and mylohyoid.

DISCUSSION

The jaw muscle data of *Petrodromus* and *Sylvilagus* are condensed into two tables. Table 1 lists all the shared characters between the two plus other mammals in which these characters also occur. From this outgroup comparison with other mammals the character is assigned plesiomorphic or apomorphic status.

A few comments should be made concerning some of the shared derived characters of *Petrodromus* and *Sylvilagus*. Characters 2, 14, and 15 are judged to be apomorphic. Well-developed pterygoideus musculature (character 2) occurs

in many different mammals but is distinctly different in *Didelphis*, *Centetes* (Fabian, 1925), and *Echinosorex*. In these three forms the pterygoideus musculature takes up roughly 10 percent or less of the total trigeminal muscle weight. Table 3 shows the relative weights of the jaw muscles of *Petrodromus*. The pars reflexa division of M. masseter, pars superficialis (character 14) is very distinct in the rabbit and elephant shrew and has a large superficial exposure. The pars reflexa is not completely comparable in the two, however. There is a wide raphic union with M. pterygoideus pars internus in the rabbit while the pars reflexa is completely restricted to the lateral side of jaw in *Petrodromus*. From the table we see that rodents also share this character, but the pars reflexa is not so distinct. The M. pterygoideus, pars internus (character 15) is distinctly divided in *Sylvilagus* and *Petrodromus*, the two divisions being only slightly joined posteriorly by a common raphe. A comparable condition occurs only in *Felis*. However *Odocoileus* has many divisions and all the others listed for this character have only a poor separation into superficial and deep parts. Character 8 is judged to be apomorphic but *Elephantulus*, another elephant shrew, lacks this character. Its usefulness is therefore questioned.

Table 2 is a list of differences in jaw musculature in *Sylvilagus* and *Petrodromus*. Most of the character assignments are self explanatory, but one character is left unassigned with respect to plesiomorphy or apomorphy. From character 1 of table 2 we see that many different mammals share this character and yet it is absent among carnivores and insectivores of the preptotheres and *Didelphis* of the marsupials.

Here we see three new synapomorphous characters that can be added to McKenna's (1975) list which unite elephant shrews and rabbits together as a monophyletic group. These characters are present in other types of mammals but might be due to convergence in these other forms. The only available means of testing homology (and thus convergence) here is by constructing a relationship having the most parsimonious distribution of shared derived characters (Wiley, 1975). That is, the hypothesis of relationships with the least number of independently

TABLE 1
Similarities Between Elephant Shrews and Rabbits

	Character Shared With	Apomorphous (A)	Plesiomorphous (P)
1. M. temporalis, pars profundus has aponeurosis covering only mid-portion of muscle	Many insectivores, <i>Didelphis</i> , <i>Ovis</i> , <i>Odocoileus</i>		P
2. Large pterygold muscles relative to the rest of trigeminal musculature (data from Fabian, 1925, Turnbull, 1970, Schumacher, 1961)	Some primates, <i>Orycteropus</i> , <i>Myrmecophaga</i> , <i>Euphractus</i> , <i>Sus</i> , kangaroo species? <i>Camelus</i> , <i>Odocoileus</i> , <i>Ovis</i>	A	
3. Origin of M. masseter, pars superficialis restricted to anterior part of zygomatic arch	<i>Didelphis</i> , <i>Felis</i> , <i>Odocoileus</i> , <i>Hystrix</i> , some insectivores		P
4. Aponeurosis covers dorsal part of M. masseter, pars superficialis	<i>Didelphis</i> , <i>Felis</i> , <i>Equus</i> , <i>Odocoileus</i> , <i>Ovis</i> , <i>Sciurus</i> , <i>Rattus</i>		P
5. Fiber direction M. masseter, pars superficialis is 45° postero-ventrally at origin and near horizontal at insertion	<i>Didelphis</i> , <i>Felis</i> , <i>Equus</i> , <i>Odocoileus</i> , <i>Sciurus</i>		P
6. M. masseter, pars superficialis inserts broadly on lower jaw	<i>Didelphis</i> , <i>Echinosorex</i> , <i>Odocoileus</i> , <i>Ovis</i> , <i>Sciurus</i> , <i>Rattus</i> , <i>Hystrix</i>		P
7. M. masseter, pars profundus has very wide origin on zygomatic arch	<i>Didelphis</i> , <i>Echinosorex</i> , <i>Felis</i> , <i>Sciurus</i> , <i>Rattus</i> , <i>Hystrix</i>		P
8. Tendon sheet covers ventral part of M. masseter, pars profundus	<i>Odocoileus</i> , <i>Ovis</i> , <i>Sciurus</i>	A?	
9. Insertions of M. masseter, pars profundus and zygomaticomandibularis cover the entire back portion of horizontal ramus	<i>Didelphis</i> , <i>Echinosorex</i> , <i>Felis</i> , <i>Rattus</i>		P
10. Fibers of M. temporalis, pars superficialis run slightly anteroventrally	<i>Didelphis</i> , <i>Echinosorex</i> , <i>Felis</i> , <i>Equus</i>		P
11. M. temporalis, pars profundus inserts on medial surface of jaw covering almost the entire medial surface of ascending ramus	<i>Didelphis</i> , <i>Echinosorex</i> , <i>Felis</i> , <i>Odocoileus</i> , <i>Ovis</i>		P

TABLE 1 – (Continued)

	Character Shared With	Apomorphous (A)	Plesiomorphous (P)
12. Internal pterygoid originates from both lateral and medial surfaces of lateral pterygoid wing	<i>Echinosorex, Equus, Ovis, Sciurus</i>		P?
13. Internal pterygoid inserts tendinously on lower jaw	<i>Echinosorex, Felis, Equus, Ovis, Hystrix</i>		P?
14. Pars reflexa of M. masseter, pars superficialis present	<i>Sciurus, Rattus, Hystrix</i>	A	
15. Internal pterygoid has two distinct divisions	<i>Equus</i> (partial separation), <i>Odocoileus</i> (many divisions), <i>Didelphis</i> (partial separation), <i>Felis</i> (complete separation), <i>Hystrix</i> (partial separation)	A	

TABLE 2
Differences Between Elephant Shrews and Rabbits

	Character Shared With	Apomorphous (A) or Autapomorphous (AA)	Plesiomorphous (P)
1. <i>Petrodromus</i> : M. masseter and M. temporalis equal in weight relative to the other jaw muscles (data from Fabian, 1925; Kuhlhorn, 1939) <i>Sylvilagus</i> : M. temporalis much smaller than M. masseter in relative weight (data from Turnbull, 1970)	some primates, <i>Orycteropus</i> , <i>Tolypeutes</i>		?
	<i>Sciurus, Rattus, Hystrix</i> , and other rodents	A or AA	
2. <i>Petrodromus</i> : M. masseter, pars reflexa restricted to lateral surface of jaw <i>Sylvilagus</i> : M. masseter, pars reflexa extends to medial side of jaw	none	AA	
	<i>Sciurus, Rattus, Hystrix</i>		P
3. <i>Petrodromus</i> : M. masseter, pars superficialis inserts on lateral side of jaw <i>Sylvilagus</i> : M. masseter, pars superficialis inserts medially into M. pterygoideus, pars internus	<i>Equus, Odocoileus, Ovis, Hystrix</i>	A or AA	
	<i>Echinosorex, Didelphis, Sciurus, Felis</i>		P
4. <i>Petrodromus</i> : tendon sheet covers dorsal half of M. zygomaticomandibularis	none	AA	

TABLE 2 – (Continued)

	Character Shared With	Apomorphic (A) or Autapomorphic (AA)	Plesiomorphous (P)
<i>Sylvilagus</i> : tendon sheet covers ventral half of M. zygomaticomandibularis	none	AA	
5. <i>Petrodromus</i> : M. temporalis, pars superficialis takes origin from posterior two-thirds of zygomatic arch	<i>Didelphis</i>		P
<i>Sylvilagus</i> : M. temporalis, pars superficialis restricted more posteriorly	<i>Echinosorex</i>	A or AA	
6. <i>Petrodromus</i> : wide insertion of M. temporalis, pars superficialis	<i>Didelphis</i> , <i>Echinosorex</i> , <i>Felis</i>		P
<i>Sylvilagus</i> : narrow insertion of M. temporalis, pars superficialis	none	AA	
7. <i>Petrodromus</i> : M. temporalis, pars superficialis inserts fleshily	<i>Didelphis</i> , <i>Echinosorex</i>		P
<i>Sylvilagus</i> : M. temporalis, pars superficialis inserts tendinously	none	AA	
8. <i>Petrodromus</i> : M. temporalis, pars zygomatica present	<i>Didelphis</i> , <i>Felis</i> , <i>Echinosorex</i>		P
<i>Sylvilagus</i> : M. temporalis, pars zygomatica absent	<i>Ovis</i> , <i>Sciurus</i> , <i>Rattus</i> , <i>Hystrix</i>	A or AA	
9. <i>Petrodromus</i> : M. temporalis, pars profundus originates from both lateral and dorsal surfaces of skull roof	<i>Didelphis</i> , <i>Echinosorex</i> , <i>Felis</i> , <i>Equus</i> , <i>Sciurus</i> , <i>Hystrix</i>		P
<i>Sylvilagus</i> : M. temporalis, pars profundus originates from lateral side of skull roof only	<i>Odocoileus</i> , <i>Ovis</i>	A or AA	
10. <i>Petrodromus</i> : M. pterygoideus internus takes extensive origin from palatine in orbital wall	none	AA	
<i>Sylvilagus</i> : M. pterygoideus internus takes origin from pterygoid and not from palatine	<i>Didelphis</i> , <i>Echinosorex</i> , <i>Felis</i> , <i>Equus</i> , <i>Odocoileus</i> , <i>Ovis</i> , <i>Sciurus</i> , <i>Rattus</i> , <i>Hystrix</i>		P
11. <i>Petrodromus</i> : midportion of M. pterygoideus internus free of tendinous material	<i>Didelphis</i> , <i>Sciurus</i> , <i>Rattus</i>		P
<i>Sylvilagus</i> : tendon sheet covers medial surface of M. pterygoideus internus	<i>Echinosorex</i> , <i>Equus</i> , <i>Odocoileus</i> , <i>Ovis</i>	A or AA	

TABLE 2 – (Continued)

	Character Shared With	Apomorphic (A) or Autapomorphic (AA)	Plesiomorphous (P)
12. <i>Petrodromus</i> : digastric originates from mastoid process <i>Sylvilagus</i> : digastric originates from paroccipital process	none <i>Didelphis, Echinorex, Equus, Odocoileus, Ovis, Sciurus, Rattus</i>	AA	P
13. <i>Petrodromus</i> : digastric inserts under ascending ramus <i>Sylvilagus</i> : digastric inserts anterior to ascending ramus	none <i>Didelphis, Ovis, Echinorex, Equus, Odocoileus, Sciurus, Rattus</i>	AA	P
14. <i>Petrodromus</i> : M. pterygoideus externus has fleshy origin <i>Sylvilagus</i> : M. pterygoideus externus has tendinous origin	<i>Echinorex, Ovis</i> <i>Didelphis, Sciurus</i>	A or AA	P

TABLE 3
Muscle Weights and Percentages for the Jaw Muscles of *Petrodromus tetradactylus*

	Weight in Grams (dry weights)	% of Weight excluding M. digastricus	
M. Masseter:			
pars superficialis	.08	19	29
pars profundus	.04	10	
M. zygomaticomandibularis	.04	10	10
M. temporalis:			
pars superficialis and distal half of pars zygomaticus	.02	5	
pars profundus and proximal half of pars zygomaticus	.13	31	36
M. pterygoideus internus:			
internal division	.02	5	22
external division	.07	17	
M. pterygoideus externus	.02	5	5
M. digastricus	.01		
Total		102	

derived characters is the most parsimonious. Most of these derived characters are shared with advanced members of a group of mammals called the Preptotheria by McKenna (1975). The preptotheres are united by the common loss of M₃³ and the retention of dP₅⁵. These derived jaw mus-

cle characters might be homologous in preptotheres and in rabbits and elephant shrews. Therefore some of these derived characters may indicate nothing more than preptotheres being a closer sister group to ernotheres than either one is to marsupials (fig. 3a). However, all these de-

rived jaw muscle characters occur in only a few preptotheres. Another alternative hypothesis (fig. 3b) would be that only those preptotheres sharing these derived jaw muscle characters are related to elephant shrews and rabbits. In effect

these preptotheres may really be mistaken ernotheres.

The merits of this hypothesis must rest on a parsimony test. However, this will not be attempted here for two reasons. First, the prepto-

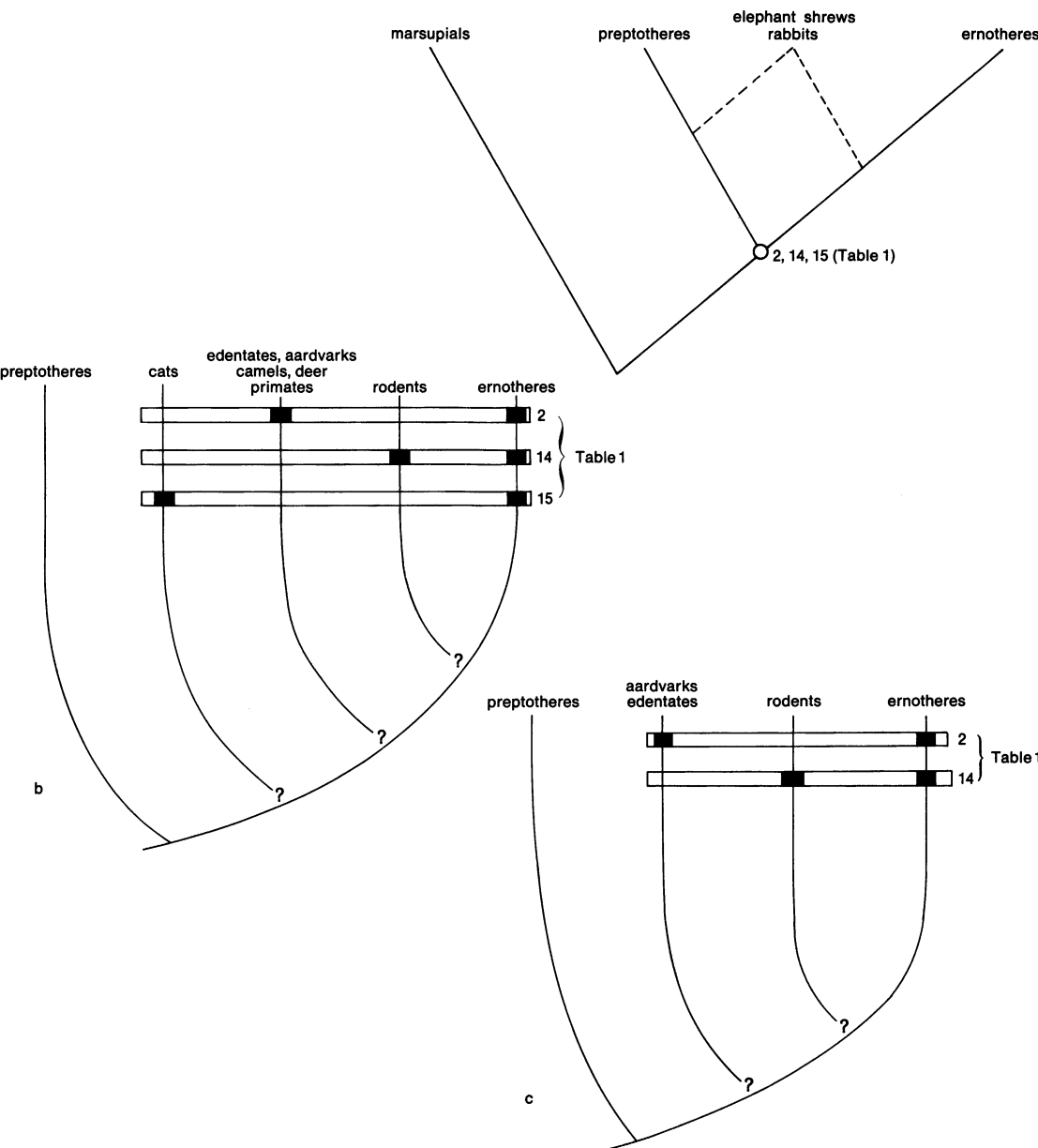


FIG. 3. Three hypotheses of relationship between elephant shrews, rabbits, and other mammals. See text for explanation.

theres have yet to be analyzed cladistically. Second, few of these preptotheres share more than one of these characters with elephant shrews and rabbits. Because of the paucity of characters now available, a parsimony argument would be extremely tenuous.

Some of these derived jaw muscle characters are shared with aardvarks, edentates, and rodents. McKenna (1975) did not attempt to unite these groups with any other mammals using shared derived characters. This study points toward ernotheres being a closer sister group to these groups than to preptotheres (fig. 3c).

This study also reveals many differences in jaw musculature between rabbits and elephant shrews. In many cases, through outgroup comparisons, the difference was shown to be autapomorphic or plesiomorphic in both the rabbit and elephant shrew or autapomorphic in one and plesiomorphic in the other. In most cases where a character is shared with another mammal group, it is shared with rodents. However, an apomorphic character is frequently shared with preptotheres. For the same reasons given above no judgment will be made concerning the homology of these characters between elephant shrews or rabbits and these preptotheres. If no character homology can be established, then the data presented here cannot be used to disprove elephant shrews and rabbits being more closely related to one another than either is to preptotheres. Hence, no corroboration of McKenna's hypothesis of relationships can be given.

More derived characters shared among the mammals called preptotheres by McKenna (1975) are needed. This would support the hypothesis that these mammals are a monophyletic group. Characters 2 and 14 (table 1) would then be derived in parallel in the preptotheres and ernotheres (elephant shrews and rabbits). The derived jaw muscle characters shared between elephant shrews and rabbits would then corroborate McKenna's hypothesis.

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