PARTIAL SKULL OF *PALEOSINOPA SIMPSONI* (MAMMALIA, INSECTIVORA), LATEST PALEOCENE HOBACK FORMATION, CENTRAL WESTERN WYOMING, WITH SOME GENERAL REMARKS ON THE FAMILY PANTOLESTIDAE

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Abstract.— A newly discovered, nearly complete skull and upper dentition of latest Paleocene *Paleosinopa simpsoni* is described. The University of Michigan specimen is the oldest known relatively complete pantolestid skull. It is compared with older pantolestid dentitions and with known skulls and dentitions of younger forms, especially middle Eocene *Pantolestes natans* and *P. longicaudis* and early Oligocene *Chadronia margaretae*. Some primitive features of the upper dentition appear to have been retained from a late Cretaceous or early Paleocene proteutherian ancestry, especially the large upper canines with well developed posterointernal wear facets indicating a relatively large P_1 and the markedly transverse M^3 with distinct parastylar "hook." Non-trenchant P^{1-3}, partially molariform P^4, and still transverse but decidedly quadrangular, low cusped M^{1-2} were capable of crushing. The lineage *Propaleosinopa* (middle Paleocene) — *Paleosinopa* (late Paleocene and early Eocene) — *Pantolestes* (middle Eocene) — *Chadronia* (early Oligocene) appears reasonable. Pantolestids increased in both absolute size (in some taxa) and in size diversity from the middle Paleocene to the middle Eocene, suggesting progressive niche partitioning. Relatively abrupt change in skull proportions occurred between the late Paleocene and middle Eocene. Relative shortening of the muzzle and cheek tooth battery, and relative lengthening of the posterior part of the cranium, especially in the anterior part of the orbitotemporal fossa, was correlated with strengthening and redirection of the anterior portion of M. temporalis profunda and other changes in skull morphology and jaw closing musculature. The net effect, in middle Eocene pantolestids, was to increase the effort force exerted, through the mandible, on the crushing cheek tooth battery. This and other evidence strengthens the earlier conclusions of others that pantolestids specialized for an aquatic or semiaquatic mode of life and a malacophagous diet. Some of the resulting features can be viewed as convergent on those of seals and sea otters. Stratigraphic and sedimentologic evidence and the nature of mollusks found in association with the UM skull suggest that the paleoecology of the late Paleocene, particularly at the Dell Creek Quarry site, was conducive to such an adaptive shift. It is suggested that in late Paleocene pantolestids that adaptive shift was primarily behavioral, morphological adaptation following rapidly thereafter in the Eocene. Pantolestids first appear in the middle Paleocene of North America. In the late Paleocene to early Eocene they occur in both North America and Europe when they are much alike at the generic level. By the middle Eocene they had diverged, possibly due to plate tectonic breakup of the North Atlantic land bridge.

INTRODUCTION

Well preserved and relatively complete cranial material other than dentitions is rare for small Paleocene mammals. The partial pantolestid[1] skull described here for the first time will help fill that gap. Hereafter it will be referred to as the UM skull (University of Michigan). The specimen, University of Michigan Museum of Paleontology V-55122, comes from the Dell Creek Quarry, University of Michigan-Sublette County-Wyoming (UM-Sub-Wy) Locality 1, Hoback Formation, Hoback Basin, central western Wyoming. Detailed maps and descriptions of this locality, discussions of the geology, and lists of the associated vertebrate fauna are given in earlier papers (Dorr, 1952, 1958; Dorr and others, 1977). My original conclusion (1952) that the age of the associated fauna is Tiffanian (late Paleocene) has generally been accepted although the assemblage now appears to be late Tiffanian rather than middle Tiffanian in age. Gingerich (1975, p. 146, fig. 2 and 1976, p. 55, fig. 16) recently has placed the Dell Creek Local Fauna in the late Tiffanian on the basis of his zonation of the middle Paleocene to early Eocene plesiadapid primates, specimens of which occur in the collection from that quarry. The Dell Creek assemblage of mammals clearly is older than Clarkforkian (earliest Eocene, Gingerich, 1975, 1976) but younger than the early Tiffanian Scarritt Quarry mammal assemblage from Montana from which came the type and referred specimens of *Paleosinopa simpsoni* Van Valen, 1967 (p. 222), the genus and species to which I refer the UM skull. The species was erected by Van Valen to receive referred specimens from *P. "senior"* (Simpson, 1937, *nomen nudem* per Van Valen, 1967, p. 222).

Detailed measurements of the specimen are given in Table 1. On text-figure 1, the natural size stereopairs are in natural shades of black and white, where bone appears dark gray to black, matrix medium to light gray, and water soluble cement (White Glue) a shiny, milky white. Text-figure 1 also includes a stereopair palatal view of the specimen enlarged to times 1.5. On this view, the specimen was whitened with ammonium chloride to facilitate inspection of the upper dentition, consequently bone, matrix and adhesive are difficult to distinguish.

The specimen suffered post-depositional deformation along with the rock matrix from which it came. Consequently it was broken into small fragments within the matrix. The fragments were carefully left in place during preparation, but their margins obscure the positions of skull bone sutures. Thus I am unable to distinguish or describe individual bone shapes, sizes or relationships. Fortunately, the original shape of the skull can still be seen, although there has been extensive crushing of the lachrymal region and a displacement toward the midline of a portion of the right maxillary bearing P^{2-3}. The specimen was found by mechanical quarrying. The blow which exposed it fractured it along two parasagittal planes, one passing through the palate just linguad of the left upper cheek tooth series, the other along the approximate midline of the left upper molar series. All recoverable fragments were cemented back into position first. Then the three portions of the specimen were cemented back together. This left the specimen completely embedded again in a matrix of dense, tough limestone from which it was extricated by a combination of mechanical, chemical and airbrasive methods. Removal of tightly adhering matrix inevitably caused local minor damage to the surface of the bone. Anyone who subsequently may examine this specimen should know that water, acetone and alcohol soluble cements all had to be used sequentially at several different stages of preparation. Therefore, any further attempt to chemically clean or prepare this specimen might seriously damage it.

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[1] Throughout this paper, I use the term pantolestid to exclude pentacodontids and "pantolestoids," following Van Valen (1967), not Coombs (1971) or certain other earlier workers.

TABLE 1 – Measurements (in millimeters) of partial skull of *Paleosinopa simpsoni*, University of Michigan Museum of Paleontology specimen number V55122. (* signifies dimension approximate due to post-depositional rock and specimen deformation.)

Skull

*Anterior edge of canine alveolus to anterior edge of orbit 18.0

*Anterior margin of orbit to anterior edge of posterior base of zygomatic arch. 21.0

*Anterior edge of canine alveolus to anterior edge of posterior base of zygomatic
    arch (minimum). 38.5

*Depth of facial region above M^3 . . . . 23.0

*Width of facial region at M^3 . . . . 28.0

*Width of cranium at postorbital constriction. 10.0

Teeth (Average where both right and left sides present. Observed difference 0.01 or less in such
    cases.)

*Anterior edge of canine alveolus to posterior edge of M^3 . . . . 28.0 (min.)

P^4-M^3, inclusive, average of two sides 16.2

M^1-M^3, inclusive, average of two sides 12.4

Canine at alveolus
    Anteroposterior 4.5
    Transverse 2.8
P^2, A-P 3.1
    Tr 2.2
P^3, A-P 3.6
    Tr 3.3
P^4, A-P 4.2
    Tr . . . . 5.7 approx.
M^1, A-P 4.6
    Tr 6.3
M^2, A-P 5.0
    Tr 7.6
M^3, A-P 3.5
    Tr 7.5

The type specimen of *Paleosinopa simpsoni* Van Valen, 1967, is a right M^1, American Museum of Natural History (AMNH) No. 33991. Van Valen also referred a right M^2, AMNH 33828, to that species. I have seen both specimens. In addition to utilizing the literature descriptions, I also made direct comparisons between the UM specimen and other North American pantolestid materials as follows:

1) *Propaleosinopa albertensis*, as redefined by Van Valen, 1967, including "*Bessoecetor diluculi*" (Torrejonian, Gidley Quarry, Montana) and "*B. thomsoni*" (early Tiffanian, Scarritt Quarry, Montana).   Referred specimens are in the AMNH and the U. S. National Museum
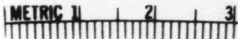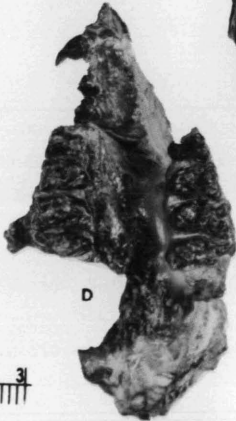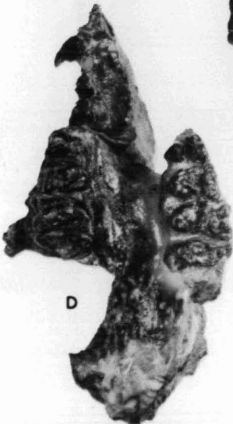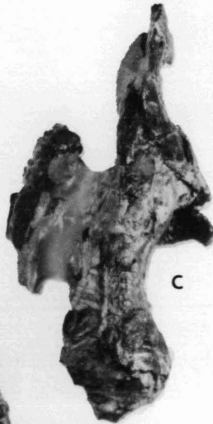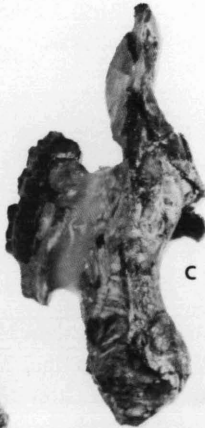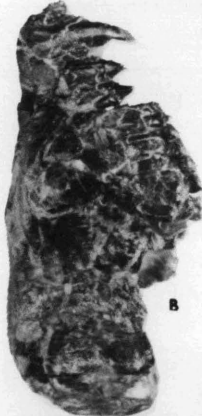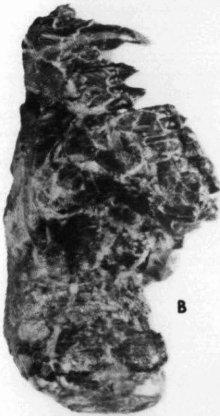
(USNM); for synonymy see Van Valen, 1967, p. 226-227. Unfortunately, the type of *P. albertensis* consists only of an isolated P_4.

2) *Paleosinopa veterrima*, Wasatchian, Bighorn Basin, Wyoming, specimens in the AMNH.

3) *Paleosinopa didelphoides*, including specimens from (a) Wasatch Formation, Elk Creek, Bighorn Basin, Wyoming, specimens in the AMNH; (b) Wasatchian (Graybull) Willwood Formation, Bighorn Basin, Wyoming, specimens in the Yale Peabody Museum (YPM) and University of Michigan Museum of Paleontology (UMMP) collections; (c) Earliest Eocene (Clarkforkian according to Gingerich, 1976), Bear Creek, Montana, specimens possibly referrable to this taxon in the AMNH. *P. didelphoides* originally was described by Matthew (1901, p. 23) from the "Wind River Beds" of Wyoming as well, but I have seen only the literature on this material.

4) *Paleosinopa lutreola*, Wasatchian, Coon Creek, Bighorn Basin, Wyoming, specimens in the Harvard University Museum of Comparative Zoology (MCZ).

I have not personally examined specimens of European pantolestids, relying only on the discussions of Russell (1964, 1966), Van Valen (1967) and Jaeger (1970) to support my remarks on those forms.

All of the foregoing taxa are represented only by isolated parts of dentitions and lower jaw or skull fragments. However, three reasonably complete skulls of other pantolestid taxa exist, as follows:

1) *Pantolestes natans* Matthew, 1909 (p. 533), AMNH type specimen 12153, middle Eocene, "Upper Bridger," Wyoming. Relatively complete skeletal material of a referred specimen (AMNH 12152) led Matthew to conclude that this species was an aquatic predator. Dr. Malcolm C. McKenna, AMNH, kindly loaned me the type skull and jaws for study (see text-fig. 2).

2) *Pantolestes longicaudis* Cope, YPM No. 13525. The label on the specimen box indicates that this skull was collected by B. D. Smith in 1872 from the "Lower Bridger" at "Bridger Station," Wyoming and probably is early middle Eocene in age, although the species also has been recorded from the "Upper Bridger." So far as I know, this specimen has never been formally described because it was only recently recognized in the YPM collection. Dr. McKenna, who had it on loan from Yale, called it to my attention. I am grateful to both Dr McKenna and Dr. John Ostrom at Yale for allowing me to borrow it. Although it originally had been identified as *Pantolestes* cf. *P. natans*, I am accepting a subsequent reference of it (on the tray label) to *P. longicaudis*. I shall not describe this specimen completely, but shall compare it to a limited extent with the UM skull (see text-fig. 3).

3) *Chadronia margaretae* Cook, 1954, early Oligocene ("Lower Chadron"), Nebraska. I have not directly examined this skull, which is the type specimen, having seen only the photograph accompanying the type description. The specimen, along with the rest of the Harold J. Cook collection, is now at the AMNH. However, Mr. Kenneth D. Rose of the University

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(Opposite Page)

TEXT-FIG. 1 — *Paleosinopa simpsoni*. University of Michigan Museum of Paleontology V-55122. Latest Paleocene (late Tiffanian), Dell Creek Quarry, Hoback Formation, central western Wyoming. Stereopair A, X 1.5, is whitened with ammonium chloride. Stereopairs B-D, X 1.0, natural tones.

TEXT-FIG. 2 – *Pantolestes natans*, American Museum of Natural History specimen 12153, middle Eocene, Bridger Formation, Wyoming, X 1.0. A – Lateral, B – Dorsal, C – Palatal.
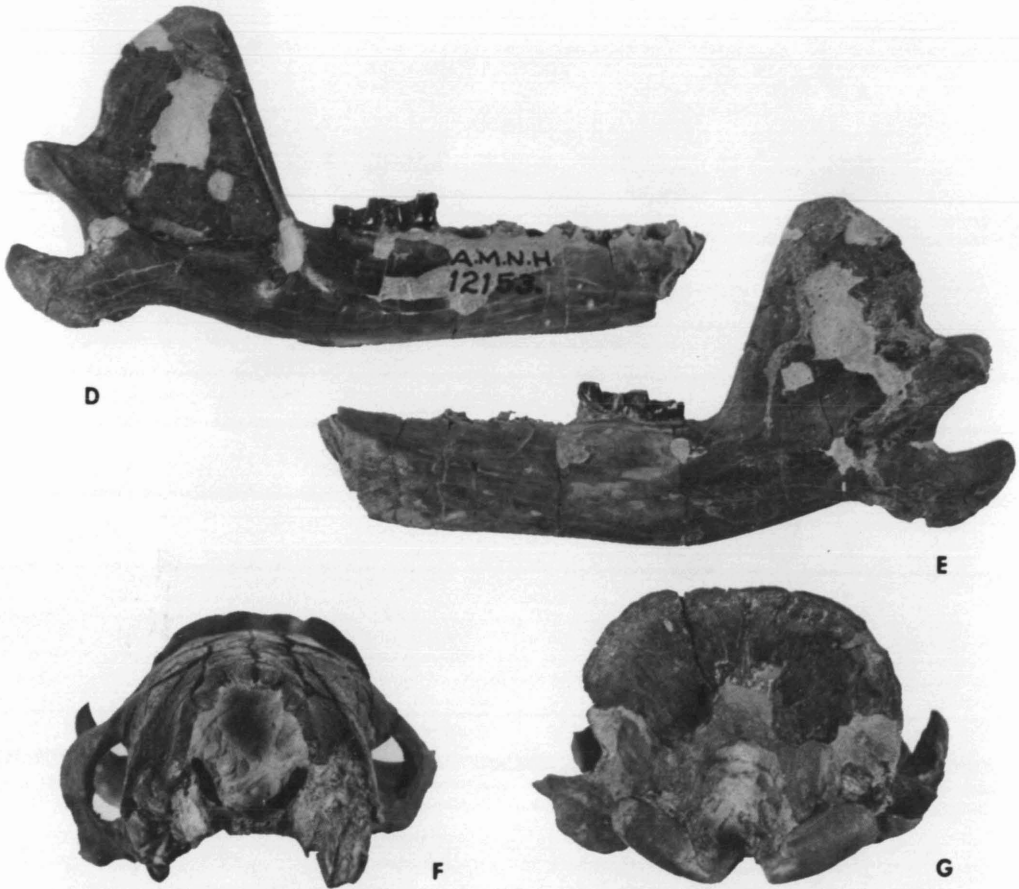
TEXT-FIG. 2 – Cont'd. D – External, E – Internal views of right mandible, F – Anterior, G – Posterior views of skull.

of Michigan was helpful by obtaining the measurements of this specimen for me, which I use in another section of this paper. I also am grateful to Dr. Richard H. Tedford of the AMNH who sent me squeeze casts of the upper and lower cheek teeth.

Thus reasonably complete pantolestid skulls are known from the late Paleocene (UM skull), middle Eocene and early Oligocene.

DENTITION

That portion of the upper dentition which is preserved on the UM skull consists of the right canine, an alveolus for a single-rooted right P^1, right P^{2-3}, and right and left P^4-M^3. The postero-external corner of RM^3, the hypoconal heel of RM^2, the protocone of RP^4, and portions of the central parts of LP^4-LM^2 were lost when the matrix block was cracked out of the quarry. Other-
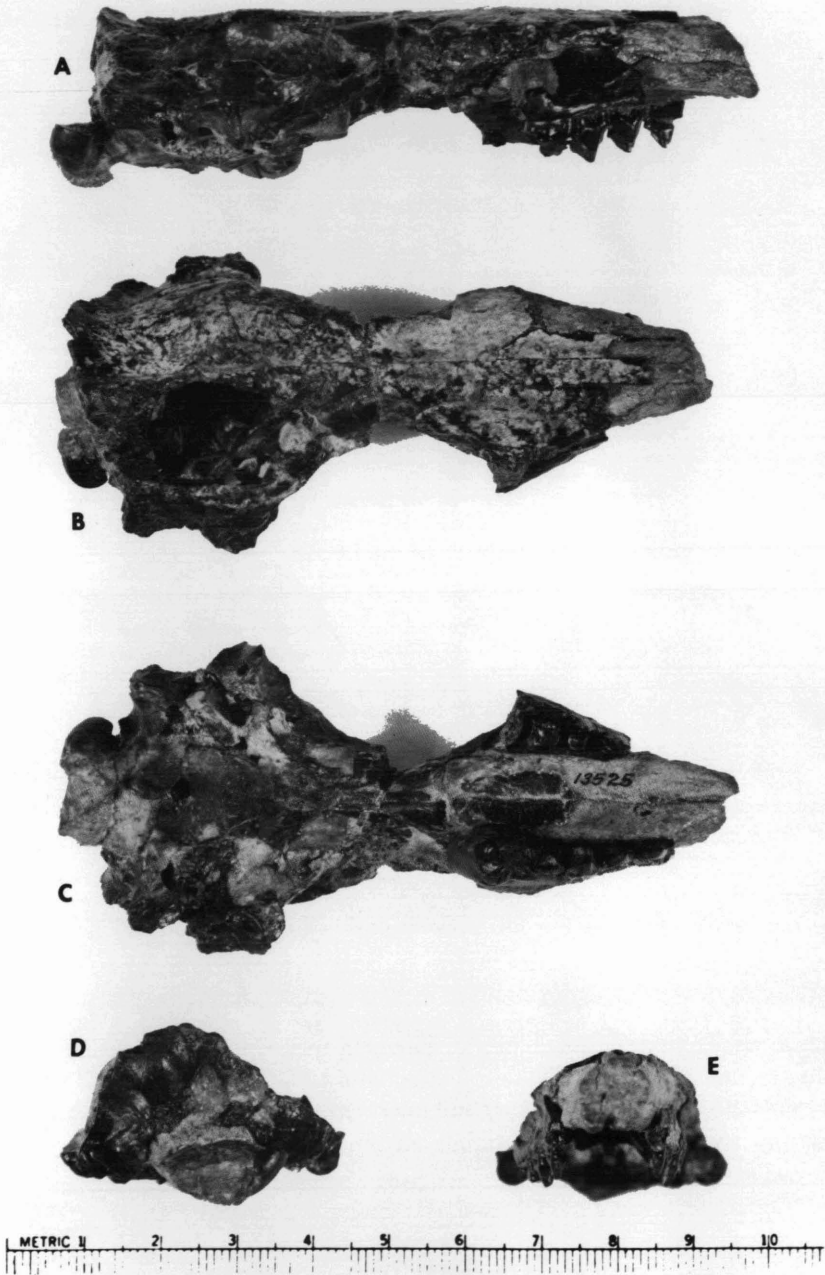
TEXT-FIG. 3 – *Pantolestes longicaudis*, Yale Peabody Museum specimen 13525, middle Eocene, Bridger Forma-
tion, Wyoming, X 1.0. A – Lateral, B – Dorsal, C – Palatal, D – Posterior, E – Anterior views of
skull.

wise the remaining dentition is intact. RP^{2-3} and a fragment of the maxillary containing them, were displaced dorsally and lingually. The right upper canine and P^1 appear to have been rotated slightly posteroventrally, and the remaining left upper cheek teeth were shifted dorsally by tectonic deformation of the strata from which the matrix block came. The observable upper dental formula of this specimen is ?-1-4-3, but a specimen of *Paleosinopa veterrima* (Matthew, 1901, p. 22) shows that early Eocene pantolestids had three upper incisors on each side. Probably this was also true for *P. simpsoni.* I^3 in *P. veterrima* was inset linguad, apparently to allow space for a large lower canine. Cook (1954) describes I^3 as missing in *Chadronia margaretae*, apparently for further accommodation of a larger, more recurved lower canine.

A relatively large, long, well developed right upper canine is well preserved in the UM specimen. I have not seen the canines equally well preserved in any other Paleocene or early Eocene pantolestid specimens, but the canine bases are present in the middle Eocene skull of *Pantolestes natans* and in the type skull of early Oligocene *Chadronia margaretae*. The nature of the upper canines and their relationship to the lower teeth, particularly P_1, are not known in possible middle Paleocene pantolestids such as *Propaleosinopa*. Moreover, I found no lower teeth referrable to *Paleosinopa* in the Dell Creek Quarry from which the UM skull came. Therefore, although the following description of the upper canine in the UM specimen adds to knowledge of that tooth in Paleocene forms, the reasons for its peculiarities must in part be inferred from reference to closely related, non-pantolestid proteutherians. At the level of the alveolus, the tooth is much longer than P^1 and as long as or slightly longer than P^2 or P^3. It has a broad but anteroposteriorly elongated oval cross-section at that level. The basal one third above the alveolus is about the same diameter throughout, but the distal two thirds taper rapidly to a sharp, backwardly recurved tip. There is a small, anteroexternal wear facet, probably produced by shear past the lower canine, which in Eocene and Oligocene pantolestids is large and locks tightly against the upper canine. The most striking feature of the upper canine is a large, posterointernal wear facet which is responsible for the abrupt tapering of the tooth. I believe that this facet was produced by shear past a relatively large P_1, the latter set closely against the lower canine. A relatively large P_1 occurs in early Eocene *Paleosinopa didelphoides*. The alveoli in the lower jaws associated with the type skull of middle Eocene *Pantolestes natans* also show that a relatively large, possibly double-rooted P_1 was present, closely pressed between the lower canine and P_2. *Buxolestes hammeli*, a middle Eocene form from France, is close to *Pantolestes longicaudis* of the same age in North America and had a large, but single-rooted P_1 (Jaeger, 1970, p. 71). Early Oligocene *Chadronia* not only retained P_1 but strengthened it with a second root. The UM specimen suggests that a similar P_1 was present in late Paleocene *Paleosinopa simpsoni*. Middle Paleocene pantolestid specimens are too fragmentary to show exactly what the condition was, but *Propaleosinopa albertensis* ("*Bessoecetor thomsoni*") shows a large, single-rooted P_1 alveolus (Simpson, 1936, p. 9). A large upper canine, larger than $P_{\overline{1}}^1$ or $I_{\overline{3}}^3$, and a large P_1 closely packed between the lower canine and P_2 are known in other proteutherian insectivores. Amongst the middle Paleocene paleoryctids, *Avunculus* had such a relatively large, single-rooted P_1, and the large P_1 in *Acmeodon* could be either single- or double-rooted (Van Valen, 1966, p. 28-29). A relatively large P_1 which sheared past the posterointernal face of the upper canine was also present in such middle Paleocene to early Eocene leptictids as *Prodiacodon* and *Diacodon*. Traced farther back in time, a relatively large, single-rooted P_1 occurred directly behind a large canine in latest Cretaceous *Protungulatum*, an arctocyonid condylarth from Montana (Sloan and Van Valen, 1965). Those authors suggest that *Procerberus*, possibly a leptictid insectivore, from the same deposits might be a structural ancestor of *Protungulatum*, but they also suggest that *Procerberus* might be a pantolestid. Whatever the case may be, it appears to me that the features of the upper canine and those inferred for P_1 in the UM specimen probably were carried into pantolestids from a nexus of ancestral traits in the late Cretaceous proteutherian stock from which,

among others, arose leptictids, pantolestids and arctocyonids. A functional P_1 persists even in the modern Malaysian Hairy Hedgehog or Moonrat (*Echinosorex gymnurus*). In University of Michigan Museum of Zoology (UMMZ) specimen No. 117117, a small female, the P_1 is relatively small, does not directly contact the upper canine, and therefore does not produce a posterointernal facet on the canine. However, Dr. W. D. Turnbull (written comm., 1977) informs me that on Field Museum of Natural History (FMNH) specimen No. 32673, a much larger female of that species, P_1 and the canine do contact one another and show opposing wear facets.

P^1 in the UM skull is single-rooted, P^{2-3} are double-rooted, and P^4 is triple-rooted as in early Eocene pantolestids, but P^1 appears to have been double-rooted in middle Eocene *Pantolestes natans* and early Oligocene *Chadronia*. The upper premolars in the UM specimen increase in size progressively from front to rear. They appear more crowded than in the type of *Paleosinopa veterrima* Matthew, 1901, being more as in *Pantolestes natans*, but post-burial fracturing and offset of RP^{2-3}, and backward rotation of the canine in the UM specimen may account for the apparent absence of space between the premolars and the canine. P^3 is larger and more inflated than the preceding premolars. P^4 is even larger, more inflated and more transverse than the other premolars, but smaller than M^1. The alveolus suggests that P^1 had a simple, approximately circular base. This first premolar was smaller than the others, as is the case in late pantolestids. P^2 is somewhat trenchant, but not so much so as in the Yale skull of *Pantolestes longicaudis*, being relatively broader posteriorly. P^2 has a single main cusp and no accessory cuspules, but there is a barely perceptible anterior cingulum and a somewhat stronger posterior cingulum.' There are barely perceptible connections along both sides of the tooth between the anterior and posterior cingula. Similar but even less well developed cingula occur on P^2 of *Pantolestes longicaudis*.

P^3 also is single-cusped. It is nearly as wide as long, and is encircled by a weak cingulum which broadens posterointernally. These features make P^3 in late Paleocene *Paleosinopa simpsoni* less trenchant than in middle Paleocene *Propaleosinopa albertensis* (cf. "*Bessoecetor thomsoni*," AMNH 33812, from Scarritt Quarry).

P^4 is enlarged, triangular and moderately transverse, being slightly wider than long, with a single, high, outer cusp and a strong and distinct but somewhat lower medial cusp. There is a well developed posterointernal cingulum but no suggestion of a hypocone. It has a complete but weak external cingulum. The outer cusp is elongate anteroposteriorly, but less so relative to the medial cusp than in either *Paleosinopa didelphoides* or *Pantolestes longicaudis*, thus it too appears less trenchant. P^4 is relatively smaller than in pentacodontid insectivores.

There is a small carnassial pocket formed by the posterior placement of the protocone on M^1 and the lack of a hypocone on P^4.

M^2 is the largest of the three molars in both length and width. M^1 is narrower but longer than M^3. Both M^1 and M^2 are moderately transverse and subquadrate. The external length of each is only slightly greater than its internal length. There is a moderate posteroexternal extension of the metastylar corner of these two molars. Their subequal paracones and metacones are distinct but closely spaced. The protocone is large and distinct. Each has a rudimentary but distinct hypocone on a well developed posterointernal cingular shelf, as in *Pantolestes*. There is a complete but narrow external cingulum. Anterior and posterior cingula are present but weak and incomplete. There are no mesostyles, but minute cuspules are present on both teeth on the slightly elevated parastylar and metastylar corners of the cingular crest. The closely placed para- and metacones and very weak conules appear more as in proteutherian insectivores than in arctocyonids.

M^3 is markedly transverse, being about twice as wide as long. Both the right and left teeth are partially broken on the specimen. Paracone and protocone are present but the metacone is absent. A very weak, narrow cingulum encircles the protocone and bears a minute cuspule directly linguad

from that cusp. The most distinctive feature on M^3 is an extension of the parastylar corner. This extension arcs anteroexteriorly and anterointernally to form a distinct "hook" which meets the moderately extended metastylar corner of M^2. Thus those two teeth are joined at their adjacent external corners, but there is a distinct pocket which widens linguad between them. The alveoli of M^{2-3} on the AMNH skull of *Pantolestes natans* suggest that a similar condition existed in that species. M^{2-3} are not preserved on the Yale skull of *Pantolestes longicaudis* so cannot be compared. Matthew (1901, p. 22) described M^3 in *Paleosinopa veterrima* as transverse, but his type figure does not show the "hook"-like feature on that tooth and I have not seen a specimen of that species which does. A similar, but perhaps even more exaggerated "hook" is shown on M^3 on the type figure of middle Paleocene *Pantomimus leari* Van Valen (1967, p. 229), an early possible pantolestid. This feature is well developed in "*Bessoecetor diluculi*" which Van Valen (1967) synonymized with *Propaleosinopa albertensis*. Thus it appears to be an old feature retained from middle Paleocene pantolestids along with the markedly transverse shape of M^3.

A small paraconule and slightly larger metaconule are present on M^{1-2}, and a paraconule on M^3. These conules are represented by slight flaring of the wear-exposed dentine tracts on the pre- and post-crista of the protocone.

SUMMARY OF DENTAL DISTINCTIONS FROM OTHER PANTOLESTID OR RELATED TAXA

The UM specimen of *Paleosinopa simpsoni* clearly is larger than *Pantinomia ambigua* Van Valen, 1967 (middle Paleocene) for which the skull and upper dentition are unknown, but the latter species probably is an arctocyonid, not a pantolestid (Van Valen, 1967, footnote, p. 225).

In contrast with *Pantomimus leari* Van Valen, 1967 (middle Paleocene), the UM specimen is larger, has hypocones on the upper molars, and the infraorbital foramen opens above M^1, not above P^3. Moreover, *P. leari* bears a striking resemblance to *Coriphagus montanus*, currently classified as a pentacodontid (Van Valen, 1967, p. 230), and may not be a pantolestid.

Middle Paleocene *Propaleosinopa albertensis*, including "*Bessoecetor diluculi*" and "*Bessoecetor thomsoni*," is a smaller form, with more trenchant P^{2-3}. The hypocone on M^{1-2} is located relatively farther labiad in the "*B. thomsoni*" material. Compared with the USNM specimen 9553 paratype of "*B. diluculi*," M^1 on the Michigan specimen is slightly less transverse, with a more fully developed hypocone and less distinctly extended para- and metastylar corners.

Early Eocene *Paleosinopa veterrima* and *P. didelphoides* appear to have been slightly larger than *P. simpsoni*. The overall lengths for M^{1-3} given by Matthew (1918, p. 590) are 13.7 mm for *P. veterrima* and 15.0 mm for *P. didelphoides*, compared with 12.4 mm for the UM specimen of *P. simpsoni*. The hypocone on M^{1-2} in *P. simpsoni* is closer to the protocone and thus more clearly distinct from the posterointernal cingulum. The external cingulum on those teeth is narrower in *P. simpsoni*. Both teeth are more quadrate in *P. didelphoides* and the posterointernal cingulum is wider. Posterolinguad migration of the hypocone and broadening of the posterointernal cingulum, from *Propaleosinopa* to *Paleosinopa didelphoides*, squared off the molars of the latter. Both P^3 and P^4 in the UM specimen are smaller and shorter anteroposteriorly (hence less trenchant) than in early Eocene specimens I have seen referred to *P. didelphoides*. The external and internal cusps on P^4 are more distinctly separated in *P. veterrima*.

Paleosinopa lutreola appears to have been a smaller form, although a specimen referred to *P. lutreola* in the MCZ (No. 19508) is nearly as large as the Michigan specimen. In *P. lutreola* the hypocone on M^{1-2} is smaller and thus those teeth are less quadrate than in *P. simpsoni*. In this respect, *P. lutreola* is more like *P. veterrima*.

Pantolestes natans and *P. longicaudis* both are distinctly larger than *Paleosinopa simpsoni*. P^1 appears to have been double-rooted in *Pantolestes natans*; single-rooted in *Paleosinopa simpsoni*. M^{1-2} are more transverse and less inflated in the UM specimen than in *Pantolestes natans*. The skull between M^3 and the posterior base of the zygomatic arch is longer relative to the muzzle in both *P. natans* and *P. longicaudis*.

Comparable skull materials are not available, but the UM specimen dentition is only about one half or less the size of other described species of *Pantolestes* such as Upper Bridger *P. phocipes* and *P. intermedius* (Matthew, 1909, p. 532-533). "*Pantolestes elegans*" ("*Anisacodon*") is indeterminate and not comparable.

The type skull of early Oligocene *Chadronia margaretae* is close to the same size as *Pantolestes natans* and the skull posterior to M^3 similarly elongated. P^1 is double-rooted. M^1 is larger than M^2 in *Chadronia*, whereas the reverse is true in *Pantolestes* and *Paleosinopa*. The molar cusps of *Chadronia* are even lower and more enlarged than in Eocene pantolestids, presumably in further adaptation for crushing.

DESCRIPTION AND COMPARISONS OF SKULL

The left side of the UM skull is missing except for a portion of the maxillary with P^4-M^3. The surviving portion of the right side, however, is more complete, extending from the sagittal midline downward to include the teeth from the canine through M^3, and from a point on the snout about 2mm ahead of the anterior edge of the canine backward to about 5 mm behind the anterior edge of the posterior base of the zygomatic arch. The zygomatic arch itself is not preserved. Sutures between individual bones cannot be distinguished amongst the many post-depositional fractures, but the general proportions of the skull can be observed.

The skull is long and low. Viewed from above, the cranium (exclusive of zygomatic arches) was widest at about the posterior edge of M^3, as in *Pantolestes natans*. The snout region, including incisors, is not preserved, but in both *Pantolestes* and *Chadronia* was relatively long; presumably the same was the case in the UM skull when it was complete. There is a distinct postorbital constriction of the cranium as in later pantolestids. The same constriction is present but less pronounced in modern *Echinosorex*. The sagittal crest is very low and weak, also as in later pantolestids, and is less pronounced than in *Echinosorex*. The muzzle region, from the canine back to the anterior margin of the orbit is wide and deep as in *Pantolestes* and *Chadronia*, but it is longer relative to the remaining posterior portion of the skull than in those two genera. Although the specimen is incomplete posterior to the zygomatic arches, the facial region is deep and the skull has a flat-topped profile with no perceptible "stop" to the forehead, as in later pantolestids but also as in *Echinosorex*. The external nares appear to have been large and deep as in later pantolestids, but their width cannot be determined. As in *Echinosorex*, the orbital region is separated from the muzzle by a distinct ridge between the maxillary and lachrymal bones and there is a small lachrymal foramen immediately behind the ridge. There is a well developed infraorbital foramen which appears to have been relatively large and which opens anteriorly above M^1 as in later pantolestids. The specimen is badly fractured and distorted in this region, however, so the original shape of the foramen cannot be determined exactly. There is no indication of a postorbital process on the frontal, thus the orbit appears to have been completely confluent with the temporal fossa, as in other primitive insectivores including pantolestids. The widely flaring bases of the zygomatic arches which are preserved suggest that the arches themselves were wide spreading laterally, but relatively thin and delicate as in *Echinosorex*. Together with the confluent orbitotemporal fossa and the marked postorbital constriction of the cranium,

this suggests that the creature had relatively powerful jaw closing musculature, particularly the anterior portion of M. temporalis pars profunda, for operation of the relatively short but massive and powerful, low-cusped cheek tooth battery. This can be interpreted as an adaptation for crushing as will be discussed in more detail later. The eyes apparently looked effectively upward and sideward as well as forward. Matthew was the first to suggest that pantolestids were aquatic or semiaquatic, comparing them with pinnipeds. His aquatic interpretation (1909, p. 531-532) was based upon his analysis of the limbs and tail of a skeleton which he referred to *Pantolestes natans*. In this connection it is interesting to note that the shape and position of the confluent orbitotemporal fossa (without postorbital processes), marked postorbital constriction, long, low, flat-topped profile, relatively short muzzle and large infraorbital foramen all resemble features found in seals such as *Phoca* and to some extent also in the modern sea otter (*Enhydra*). I elaborate on this later.

It is not possible to compare all features and dimensions on the presently known well preserved series of pantolestid skulls. Not all are equally or equivalently complete. In particular, the posterior portion of the UM skull is missing, and the position of M^3 in the Yale skull of *Pantolestes longicaudis* is uncertain. Moreover, the upper canine and P^1 are missing from the latter. Nevertheless, text-figure 4 shows (read figures giving actual dimensions) that the latest Paleocene UM skull of *Paleosinopa simpsoni* is smaller than that of middle Eocene *Pantolestes natans* for both dimension A (C-M^3 inclusive, *P.s.* = 60.6% of *P.n.*), and for dimension B (C-posterior base of zygomatic arch, *P.s.* = 47.5% of *P.n.*). The UM skull is incomplete behind the zygomatic arches so its dimension C (overall skull length, C-occipital condyle) cannot be compared with the other skulls. Text-figure 4 indicates *P. simpsoni* was about the same size and had about the same proportions as a female of modern *Echinosorex gymnurus*, the Malaysian Moonrat or Hairy Hedgehog, UMMZ (Mammalogy) Cat. No. 117117. Text-figure 4 also shows that there are negligible size or proportion differences between *Pantolestes natans* and *Chadronia margaretae* (*P.n.* = 95.7, 97.2 and 96.4% of *C.m.* for dimensions A, B and C, respectively). If *P. simpsoni, P. natans* and *Chadronia* are members of a single lineage, then it would appear the increase in size and modification of skull proportions in large pantolestids had almost entirely culminated in *P. natans*. The UMMZ specimen of *Echinosorex gymnurus* used in this comparison appears to be a small individual, as does another UMMZ specimen of the same size. In contrast, a FMNH skull tagged as a female of the same species (measurements provided by W. D. Turnbull) is about 27 percent larger. I have not made a thorough study of size variation in *E. gymnurus* so am not able to say whether this variation is individual, or stems from local population difference, or results from mistaken identification of species or sex. Whatever the case may be, however, dimension B of the U of M skull of *Paleosinopa simpsoni* falls within the range of that dimension for the *E. gymnurus* skulls mentioned when the dimensions of the latter are scaled down in proportion to *P. simpsoni* as in text-figure 4.

The marked change in skull proportions in pantolestids occurred some time between the late Paleocene and middle Eocene. This is best seen on text-figure 4 where the C-M^3 lengths of other skulls are scaled down to 28 mm, the minimum of that dimension in the UM skull of *Paleosinopa simpsoni*[2], and other dimensions reduced proportionately. The zygomatic arch region is proportionately longer compared with the muzzle in *P. natans* than in *Paleosinopa simpsoni*, thus making

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[2] The actual or original length of C-M^3 in the UM skull no doubt exceeded the measureable 28 mm because the specimen was post-depositionally deformed, but if the specimen were to be restored, and the tooth row thus lengthened, the net effect would be to decrease the relative post-M^3 length of the UM skull. This in turn, in the scaled comparisons on text-figure 4, would result in an even greater proportional lengthening of the post-M^3 portion of the skulls of later pantolestids, thus strengthening my conclusions regarding changes in skull proportions in middle Eocene pantolestids.

Echinosorex gymnurus, female,
Modern Malaysian Moonrat,
Univ. Mich. Mus. Zool. 117117.

Paleosinopa simpsoni,
Univ. Mich. Mus. Paleo. V55122,
Latest Paleocene.

Pantolestes longicaudis,
Yale Peabody Mus. 13525,
Middle Eocene,
(dimensions estimated, see text).

Pantolestes natans,
Amer. Mus. Nat. Hist. 12153,
Middle Eocene.

Chadronia margaretae,
Amer. Mus. Nat. Hist.
Cook Coll. HC750,
Early Oligocene.
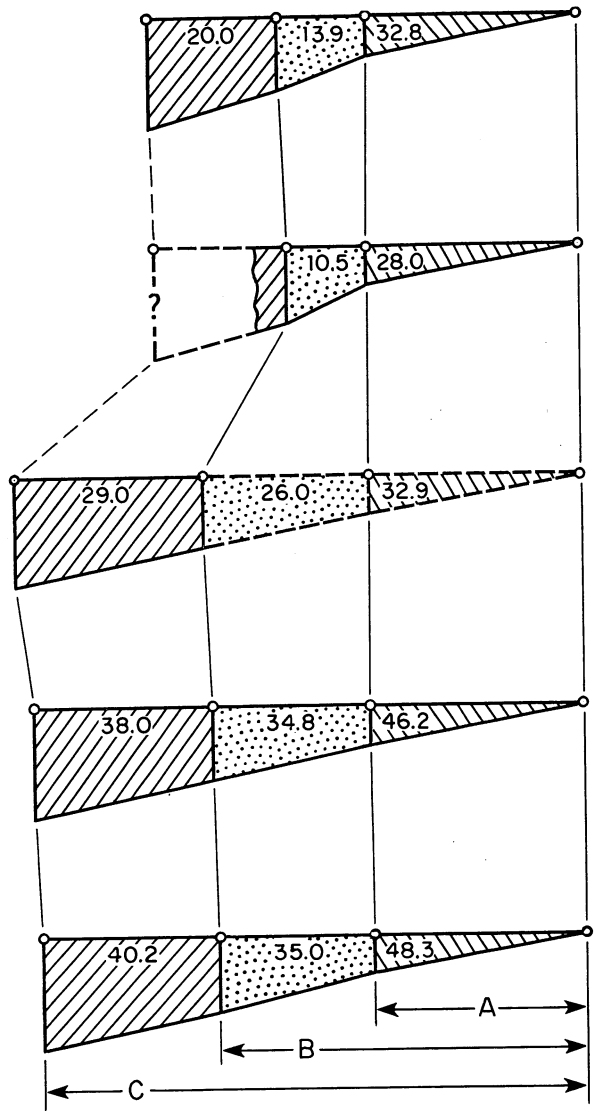
TEXT-FIG. 4 — Comparison of pantolestid skull proportions. Dimension A for all skulls was set at 28.0 mm (the actual measurement on the University of Michigan skull of *Paleosinopa simpsoni*). Other dimensions on other skulls reduced proportionately. Numerical values are actual dimensions in mm. Dimension A is from anterior margin of upper canine alveolus to posterior margin of M^3. Dimension B is from anterior margin of canine alveolus to anterior margin of posterior base of zygomatic arch. Dimension C is from anterior margin of canine alveolus to posterior margin of occipital condyle.

the dental battery of *Pantolestes* shorter relative to overall skull length and also in proportion to total mandibular length. The scaled comparisons on text-figure 4 also show that the proportions of *Paleosinopa simpsoni* are about the same as those of modern *Echinosorex* whereas those of *Pantolestes* are closely matched by those of *Chadronia*. It appears in the three fossil genera that pantolestid

skull proportions changed most some time between late Paleocene *Paleosinopa* and middle Eocene *Pantolestes*. It is unfortunate that there is not yet known a good skull of an early Eocene pantolestid. If this paper had included a thorough restudy of all available pantolestid material and a revision of that family, I would have been tempted, on this skull evidence, to suggest that in spite of dental differences, such as the later enlargement and inflation of M^3, *Chadronia* should be reduced to congenery with *Pantolestes*.

The comparison of proportions cannot, for reasons of nonequivalence of specimens, be exact for the Yale skull of *Pantolestes longicaudis*. There are no teeth preserved ahead of P^2 in that specimen, it lacks RM^3, and the upper molar fragment inserted in plasticene in the position of LM^3 may not be M^3 and may not be properly located. Nevertheless, the UM specimen is only about 67% the size of the Yale specimen measured from the anterior margin of P^2 to the anterior edge of the posterior base of the zygomatic arch. Thus the Yale specimen is larger than the UM specimen but smaller than either *Pantolestes natans* or *Chadronia margaretae*. I roughly estimated the C-M^3 length of the Yale specimen by comparing P^2-M^1 length in that specimen with that of the UM skull and calculating C-M^3 length in *Pantolestes longicaudis* to the same proportion. Using the latter dimension and scaling it down to 28 mm I contrived a comparison with the measureable length of the anterior portion of the temporal fossa in that species and show that on text-figure 4. For what this rough approximation may be worth, it appears to suggest that post-M^3 elongation in *Pantolestes longicaudis* (over *Paleosinopa*) was as great as in *Pantolestes natans*. If this is correct, and in view of the fact that *P. longicaudis* is substantially smaller than *P. natans*, then this could mean that post-M^3 cranial elongation in middle Eocene and later pantolestids was not simply an allometric effect. *P. longicaudis* appears to be simply a smaller version of *P. natans*. The smaller species has been recorded from both the "Lower" and "Upper" Bridger (Matthew, 1909, p. 532), hence both preceded and was contemporaneous with *P. natans*.

In the four known pantolestid skulls, the permanent molars are fully erupted and partially worn, indicating that all four were mature adults. The limited available material is statistically inadequate to reveal the extent to which skull and tooth dimensions and proportions of all pantolestids might approach or overlap one another if the degree of individual variation within each group were known, but certain genera and species have been distinguished taxonomically from one another on the basis of morphology, dental size and proportions. On present evidence, I suggest the following with regard to size and proportion changes or both through time in pantolestids.

1) All suggested predecessors of *Paleosinopa simpsoni*, including *Propaleosinopa*, *Pantinomia* and *Pantomimus*, were smaller than *P. simpsoni* in tooth dimensions. Whatever the ancestry may have been, there was a size increase in pantolestids from middle to latest Paleocene time.

2) In the early Eocene (?Clarkforkian and Wasatchian), pantolestids are represented by two size clusters, (a) *Paleosinopa didelphoides* and *P. veterrima*, both similar in size and only slightly larger than *P. simpsoni*, and (b) *P. lutreola*, distinctly smaller than *P. simpsoni*. Cranial material is not yet available for these early Eocene forms, but tooth dimensions show that marked size differentiation had occurred between certain described taxa at least by the early Eocene.

3) Next in the temporal sequence, the Yale skull of *Pantolestes* is recorded as having come from the "Lower" Bridger, but the species has also been recorded from the "Upper" Bridger. This middle Eocene form is intermediate in size between the taxa listed in 2(a), above, on the one hand, and contemporary and younger taxa listed in 4, below. Its skull shape and proportions appear to have resembled those of *P. natans*.

4) *Pantolestes intermedius* from the "Upper" Bridger is intermediate in size between *P. longicaudis* on the one hand, and *P. natans* and *P. phocipes* on the other, the latter two being similarly sized. A fourth "Upper" Bridger species, *P. elegans* is poorly known but may be smaller than

all other middle Eocene forms. Although I suspect that a thorough study of all existing panto-lestid materials from this country might show that some of these named species are invalidly distinguished on type specimen size alone, nevertheless there is evidence that most of the known middle Eocene forms were larger than those of the Paleocene and early Eocene, and there was some size differentiation amongst them.

5) Early Oligocene *Chadronia margaretae* is nearly the same, if not identical with *P. natans* in skull size and proportions.

In summary, most but not all North American pantolestids increased in size from the middle Paleocene to the latter part of the middle Eocene. Thereafter there was little size increase in known taxa. Pantolestid taxa can be differentiated into large and small sizes in the early Eocene and into larger, intermediate and small sizes in the middle Eocene, but the relationships of these through time cannot yet be established with certainty. The degree of size differentiation, if any, in the latest Eocene is not yet known, but only a single, large form is known to have survived into the early Oligocene. The progressive increase in size in some taxa and increasing size differentiation amongst taxa could be interpreted as a case of progressive partitioning of their aquatic or semiaquatic mollusk feeding niche. Adaptive morphological specialization for this niche, discussed in detail later in this paper, appears to have occurred most rapidly some time between the latest Paleocene and the middle Eocene, with relatively little change thereafter.

PANTOLESTID RELATIONSHIPS

The dentition of pantolestids is much like that of leptictids, palaeoryctids and some early arcto-cyonids, a fact which Van Valen (1967) has already noted. The resemblance amongst all these is particularly marked in the cases of the enlarged canines and the decidedly transverse M^3 with its "hook"-like parastylar extension. Van Valen (1967, p. 225) was unable to conclude with certainty whether the immediate ancestry of the various species of late Paleocene and early Eocene *Paleosinopa* lay (1) entirely in middle to late Paleocene *Propaleosinopa*, or (2) in middle Paleocene *Pantinomia*, or (3) in some closely related complex of those two genera, or (4) separately in both *Propaleosinopa* (giving rise to ?Clarkforkian and Wasatchian *Paleosinopa didelphoides*) and in *Pantinomia* (giving rise to Wasatchian *Paleosinopa veterrima*). The absence of a hypocone in *Pantomimus*, a small middle Paleocene form which he was unable to assign to a family, but which he suggested might be a pantolestid, makes that genus, if it is valid, an unlikely progenitor for approximately contemporaneous *Paleosinopa*, particularly in view of the fact that *Propaleosinopa*, a form whose dental morphology was closer to *Paleosinopa*, also was a contemporary of *Pantomimus*. Van Valen tentatively expressed a preference for the first of his four hypotheses listed above, for the dubious reasons that *Propaleosinopa* is better known than *Pantinomia* and because he could see nothing about *Propaleosinopa* which would exclude it from direct ancestry to *Paleosinopa*. After that, in a prepublication footnote in the same paper, he concluded that *Pantinomia* really was an arctocyonid condylarth, thus demolishing the second, third and fourth of his hypotheses as listed above. In my opinion, the new and more complete specimen of *Paleosinopa simpsoni* described here strengthens Van Valen's own original preference for his first hypothesis that *Propaleosinopa* was directly ancestral to all the later species of *Paleosinopa*. Both the UM specimen and the type of *P. simpsoni* are temporally intermediate between *Propaleosinopa* and the Eocene species of *Paleosinopa*. The UM specimen is intermediate in size as well. The structure of the teeth in *P. simpsoni* is much like that in both *Propaleosinopa* and later species of *Paleosinopa*. M^3 in the specimen is primitive and is close to that in *Propaleosinopa*, but M^{1-2} differ only in very minor details from those teeth in the early Eocene

species of *Paleosinopa*. The transverse character of M^3, with its "hook"-like parastylar extension and the relationship of that tooth to M^2 and the latter's metastylar extension is particularly close to the condition in *Propaleosinopa*. I see no need for the unnecessarily complex suggestion that *Propaleosinopa* and *Pantinomia* were paired in some closely related complex and separately ancestral to different species of later *Paleosinopa*. That might equally well mean that *Pantinomia* is a synonym of *Propaleosinopa*, or, as Van Valen's footnote admitted, more likely a condylarth convergent toward but not directly related to pantolestids. Moreover, *Paleosinopa didelphoides* and *P. veterrima* are structurally so close to one another and to *Paleosinopa simpsoni* that I see no need to invoke a complex explanation for their origins separately through parallelism. All that recommended this, even to Van Valen, was in his own words, "a lack of evidence to the contrary in poorly known *Pantinomia*."

The even earlier fundamental stock for pantolestids may have been a leptictid insectivore such as latest Cretaceous *Procerberus*. The distinctive dental morphology of pantolestids appears to have been well established in the middle Paleocene, but at that time it was not far removed from that found in contemporaneous leptictids such as *Prodiacodon* and *Diacodon*. Between the time of the Paleocene-early Eocene pantolestids and middle Eocene species of *Pantolestes* there was a tendency for M^{1-2} to become more inflated, but M^2 remained larger than M^1; also, P^1 became enlarged and strengthened by a second root. In early Oligocene *Chadronia*, I^3 was lost to make room for the enlarged lower canine and M^1 became larger than M^2.

The late Paleocene skull described here extends the fossil record of pantolestid cranial morphology farther back in time than any previously recorded specimen from this family. Until now, it was conceivable that although pantolestid dental features, particularly the omnivorous or crushing character of the cheek teeth, originated at least as early as the late Paleocene, all of the distinctive cranial features might have been middle Eocene acquisitions. This appears not to have been the case entirely. Instead, the UM skull shows a mixture of primitive and advanced features. The absence of postorbital processes and thus the ill-defined character of the orbit and confluent nature of the large orbitotemporal fossa are primitive or generalized insectivore characters. On the other hand, the deep, broad muzzle, large external nares, relatively large infraorbital foramen, especially marked postorbital constriction (more so than in more generalized insectivores), especially weak sagittal crest and flat-topped skull profile found in middle Eocene *Pantolestes natans* and *P. longicaudis* also occur in the UM skull of late Paleocene *Paleosinopa simpsoni*. If these latter traits are characteristic of the family, then they extend nearly as far back in time as does the first certain (middle Paleocene) record, based on teeth alone, of the entire family. The principal post-Paleocene cranial change that can be detected in the presently known series of skulls is post-M^3 elongation of the cranium and enlargement of the anterior part of the orbitotemporal fossa to accommodate stronger and mechanically more efficient Temporalis musculature, a subject discussed in detail in the following section. It remains for future discoveries of cranial material to show whether or not any of the distinctive pantolestid cranial features were present in the middle Paleocene or perhaps even earlier.

FUNCTIONAL MORPHOLOGY OF THE PANTOLESTID SKULL

Matthew (1909, p. 531-532) concluded from his study of the type skull of *Pantolestes natans* (AMNH 12153) and of skeletal material of a referred specimen (AMNH 12152) that the species "appears to be an aquatic Insectivore of predatory habits, with marked analogy and some degree of affinity to the Pinnipedia. Its food may have been fish or turtles, or, . . . fresh water clams . . . ." Most subsequent authors, most recently including Van Valen (1967, p. 226) have accepted the "aquatic

predator" part of the proposal, but not the "pinniped affinity" part. I certainly favor the idea of a malacophagous diet, and add the following observations which may give strength to that argument.

P^4-M^3 in the skulls of *Paleosinopa simpsoni, Pantolestes longicaudis, P. natans* and *Chadronia margaretae* are distinctly low-cusped and inflated. Even P^{1-3} are relatively large and inflated compared with earlier and most contemporary eutherians. Thus the increased capability for a crushing function appears in the pantolestid dentition at least as early as the late Paleocene.

Certain features of advanced pantolestid skulls, especially well seen in *Pantolestes natans*, suggest that the crushing function of the pantolestid dentition had become markedly enhanced by the middle Eocene. The paper by Turnbull (1970) on the mammalian masticatory apparatus was especially helpful in the analysis that follows, although I must accept entire responsibility if I have misunderstood his work. The more or less constant depth of skulls of pantolestids, from the anterior nares back to the abruptly flaring occipitolambdoidal crest, gives them a flat-topped (streamlined) profile. Although this profile is enhanced by the fact that the sagittal crest is very low and weak, this does not necessitate a weakening of the temporal and other jaw closing musculature. Turnbull (1970, p. 299, 342) notes that the generalized masticatory apparatus of primitive ("menotyphlan") insectivores already had at least a partial capability for crushing. This certainly appears to be the case in the modern but primitive Moonrat (*Echinosorex gymnurus*). Although Tate (1947, p. 36) notes that the stomach contents of dead gymnures show that they feed on roaches, termites and other insects, the lingual halves of their quadrangular M^{1-3} clearly show flattened cusp wear patterns that result from and further facilitate crushing in addition to the shear that predominates in the upper premolars and along the lingual faces of the para- and metacones of the upper molars. Turnbull suggests that, given appropriate alterations within the large temporal fossa of such mammals in the early Tertiary, a generalized jaw muscle pattern, with M. temporalis predominating, could accomplish some very advanced, specialized masticatory functions. The molar teeth of late Paleocene *Paleosinopa simpsoni* appear already to have possessed considerable capability for crushing and thus were preadapted for an extension and specialization of that capability in later pantolestids of the middle Eocene and early Oligocene. Not only did the exaggerated postorbital constriction of the cranium increase the space available in the anterior part of the orbitotemporal fossa to accommodate an enlarged anterior portion of M. temporalis pars profunda, but the absence of a sagittal crest for origin of the muscle in that area was compensated for in *Pantolestes natans* (text-fig. 2) by the presence of five or more rugose ridges on each side of, parallel with and just below the sagittal line. Since the thus strengthened anterior portion of M. temporalis profunda originated relatively far forward on the cranium and inserted relatively far forward of the condyle (fulcrum) on the massive coronoid process of the mandible, the effort force of this portion of M. temporalis would have been more efficiently directed, that is exerted more nearly perpendicular to the mandibular lever arm, instead of partially backward toward the condyle as is the case with the remainder of the temporal musculature. The effect, convergently of course, would have been similar to that which in rodents results from increased emphasis on anterodorsally directed effort of M. masseter. This, coupled with the shortened cheek tooth battery relative to temporal fossa length, served to increase the effort force of the lower jaw relative to the resistance force of the shortened but enlarged crushing dentition. Other, more posterior portions of the jaw closing apparatus were strengthened as well. The abruptly flaring, enlarged and rugose anterior face of the occipitolambdoidal crest on the skull and the rugose medial face of the relatively massive coronoid process of the mandible suggest a strong posterior portion of M. temporalis profunda. For other muscle origins, the zygomatic arch as seen in *Pantolestes natans* is stout for insectivores, flares widely outward, and its posterior base is broad anteroposteriorly and shelves relatively far outward from the cranium. Correlatively for insertions, the masseteric fossa is deep, rugose and strongly rimmed, and the distal tip of the angle is much enlarged, rugose and

deeply pitted. These features suggest that, compared with more generalized insectivore musculature, M. temporalis zygomatica, M. masseter (pars superficialis and profunda), M. zygomaticomandibularis and M. pterygoideus internus all were exceptionally strong as well. Strengthening of the more posteriorly directed jaw musculature effort would also have had the secondary advantage of offsetting the more anteriorly directed effort of the anterior portion of M. temporalis, thus decreasing the likelihood of dislocation of the mandible anteriorly from the glenoid inasmuch as the articulation of the condyle at that fossa was weak. These adaptations for crushing mastication were slightly further exaggerated in early Oligocene *Chadronia*.

Coombs (1971, p. 25) compares the specializations of *Simidectes*, a late Eocene "pantolestoid" from the western United States, with those of *Ursus*, suggesting that certain features of the mandible and teeth of the former imply a grinding tooth function and an omnivorous diet.

The pantolestid skull is flattened dorsoventrally, being broader than high. The facial region is wider just ahead of the orbits than is the braincase at any place behind. This is because not only is there a marked postorbital constriction, but the braincase does not broaden out again behind the constriction to its width ahead of the constriction. The apparently greater breadth of the skull posterior to M^3 is due to a marked outward shelving of the squamosals to meet the posterior ends of the widely spaced zygomatic arches. Thus the pantolestid skull appears wedge shaped when viewed from above and is streamlined in both profile and dorsal views. This streamlined shape is in many respects similar to that seen in the skulls of seals and it is achieved in much the same way except that in seals a larger brain must be accommodated. *Phoca*, for example, is short faced, has a long, flat-topped skull with weak sagittal crest but with rugose temporals, widely flaring zygomatic arches with broadly shelving squamosals, and a marked postorbital constriction. The modern sea otter (*Enhydra*) couples a streamlined skull with a powerful crushing dentition. In that form, too, there is a postorbital constriction and a flat-topped profile, and the widely spreading zygomatic arches impart a wedge shaped appearance to the skull viewed from above. However, the braincase of the pantolestid skull expands relatively little behind the postorbital constriction, whereas the expansion in *Phoca* and *Enhydra* is great to accommodate their larger brains. The similarly shaped skull outlines in these forms can be interpreted to represent coupled convergent adaptations for both swimming and strengthened jaw musculature. A prominent feature on the skulls of both *Pantolestes natans* and *P. longicaudis* is the abruptly flaring, much enlarged, rugose and pitted occipitolambdoidal crest which forms a distinct frill at the posterior end of the skull. A similar feature is present in modern *Echinosorex*, but it is less rugose or deeply pitted. Matthew's figure of *P. natans* (1909, p. 524) does not adequately portray the exaggerated size and strength of this feature, although one of his views (figure 108) does illustrate well the rugosity of its posterior face. Here again there is a similarity to both *Phoca* and *Enhydra*, suggesting that, as in those forms, there was a powerful M. erector capitis on a thick but streamlined neck, the latter merging with little break into the well muscled posterior portion of the wedge shaped head. The short muzzle, inflated cheek teeth and powerful jaw musculature, large external nares and infraorbital foramen, and the absence of postorbital processes on the frontals all are duplicated in *Enhydra*, and in *Phoca* and some other pinnepeds as well. Although the absence of postorbital processes may have been a primary insectivoran character in pantolestids, its combination with the exaggerated postorbital constriction and the large, open, upwardly directed orbital region suggests that the eyes were not only relatively large and sensitive, but also were capable of looking relatively far upward as well as forward and to the side. This also is the condition in both *Phoca* and *Enhydra* and is what might be expected in an aquatic predator which sought its food both in relatively dim light at depth and in the water above. The large infraorbital foramen suggests a tactile snout for underwater feeding in poorly lighted conditions. As noted by Matthew, the relatively large canines suggest predaceous feeding habits. Although large,

interlocking canines were present in other middle and late Paleocene insectivores, they were capital-
ized upon by pantolestids at least as early as the late Paleocene and became progressively more
exaggerated in middle Eocene and early Oligocene forms. When I first considered the possible origin
of the large, posterointernal wear facets on the upper canines of *Paleosinopa simpsoni*, I thought
they might have been caused by abrasion against hard food substances such as shells or carapaces,
and it still seems possible that this may partially have been the cause. The upper canines of old
individuals of modern, shell crushing and crustacean eating *Enhydra* that I have examined show a
similar facet, as do the upper canines of certain modern pinnipeds such as the California sea lion
(*Zalophus californianus*). However, as noted earlier, the fossil evidence from other pantolestids
and closely related proteutherians suggests that a relatively large P_1 which sheared past the upper
canine also could have produced that facet.

PALEOECOLOGY AND ADAPTATIONS

Geological studies of the Hoback Formation (Dorr, 1952, 1958; Spearing, 1969; Dorr and others,
1977) and especially of the stratigraphic section at the Dell Creek Quarry from which the UM skull
came, together with evidence from associated vertebrates, invertebrates and plants from that quarry,
afford some interesting insights into the possible life habits of pantolestids of the late Paleocene.
The stratigraphic section at the quarry is similar to that at many other sites and levels in the forma-
tion. The main productive fossil zone is immediately underlain by a 60 cm thick but lensing sand-
stone which contains large fragments of fossil wood and relatively rare mollusk shell fragments.
This drab colored sandstone is gray, weathering to tan, medium and angular to subangular grained,
feldspathic, calcareous and massive, with crossbeds present but ill defined. The sandstone has yielded
a single mammal specimen, a nearly complete lower jaw of the primate *Phenacolemur frugivorus*.
The most productive zone overlies the sandstone, and is a thin (about 18 cm), gray, lensing, impure
argillaceous limestone with some pods of pure limestone. Carbonized small plant fragments are
common in the limestone as well as occasional larger pieces of stems and twigs. The fragmentary
nature of the woody material and the absence of in-place root structures suggest that the plant re-
mains fell and drifted into the deposit from the margin of an open pond. The limestone lens extends
for about 70 meters along the outcrop but the mammal specimens were found concentrated in a
local "pocket" about 4 meters long and extending about 2 meters back into the outcrop. The lime-
stone grades upward through about 30 cm of coal and highly carbonaceous shale into about 25
meters of dark gray shale with numerous small, thin, lensing coal stringers. A few mammals and
invertebrates were found in the lower part of the transition zone between the limestone and shale.
All of this sedimentary sequence is drab in color, as is most of the Hoback Formation, indicating
deposition under reducing conditions in a moist, poorly drained region (Hanley, 1976, p. 255).
The pantolestid skull came from the limestone itself, where it was found in association with small
mammals of other kinds. Fossil remains of the latter include abundant multituberculates, other
insectivores, small carnivores, small condylarths, and especially abundant plesiadapid primates.
Small alligators and a small lizard also were found. All of the mammals were quarried, not collected
from a weathered surface, and had to be painstakingly extricated from the limestone matrix by hand
under a binocular microscope, so their condition at the time of deposition could be determined.
All are fragmentary, but show no signs of subaerial weathering or abrasion by transport, and their
sizes range from that of a pinhead or smaller to several centimeters in length, without evidence of
size sorting. I believe the fossil mammals accumulated in wet sediment, not in a burrow complex
or on a subaerial surface. This, together with the size and shape of this localized pocket of fossil

remains, suggests to me that the vertebrate remains fell in an already fragmentary condition from above, possibly from some predaceous bird or mammal perch or nest. They clearly are not a biocoenose, and probably represent a selected sample of relatively small vertebrates from a considerable distance around the site.

Well preserved snail shells are common in the limestone. Moore (1955) identified the five most common, relatively large forms as *Campeloma* (Viviparidae, closely related to *Viviparus*), *Physa* (Physidae), *Discus* (Endodontidae), *Grangerella* (Grangerellidae) and *Oreohelix* (Oreohelicidae). The most abundant of these five, and also the largest, is *Oreohelix* which reaches 49 mm in width and 20 mm in height. The next largest is *Campeloma* which reaches 32 mm in height and 21 mm in width. I estimate that these two constitute at least one half of the biomass of the collected mollusk assemblage. There are in addition many smaller snail shells, some as yet unidentified, plus juveniles of the larger, more common forms. The small snails range down to pinhead size. Snail shells are far more abundant than mammal remains and the shells are more widely distributed within the limestone than are the mammals. Hundreds of specimens of the many species of snails were found during quarrying as well as during subsequent preparation of the matrix.

Moore noted that the modern hypsometric range of *Viviparus* falls below about 380 meters ASL, the genus being most numerous between about 50-200 m. The hypsometric range of *Campeloma* falls below 430 m. Thus these viviparids suggest that the late Paleocene Hoback Basin surface in western Wyoming stood much closer to sea level than does that surface today after late Cenozoic regional uplift of about 1600 m.

Recent studies of late Paleocene paleobotany (Hickey, 1972; Wolfe and Hopkins, 1967) suggest that the late Paleocene in this area was a time of humid but Warm Temperate climate, in contrast with humid but warmer Subtropical conditions in the preceding middle Paleocene and succeeding early Eocene.

Hanley (1976) published an excellent analysis of the paleosynecology of some slightly younger nonmarine mollusk associations from the Green River and Wasatch formations (Eocene) of southwestern Wyoming. His work is relevant to an interpretation of the snail assemblage from the Dell Creek Quarry, because many of the same families and even genera occur in both places in similar lithologies. Thus the·taphonomic bases for his ecological interpretations (Hanley, 1976, p. 240-241) appear to me to be applicable at the generic and family level to the Dell Creek Quarry mollusk assemblage. In Hanley's terms, the Dell Creek collection is a "mixed assemblage" because it is ecologically heterogeneous, containing both aquatic (*Campeloma, Physa*) and terrestrial (*Discus, Grangerella, Oreohelix*) forms. The aquatic element qualifies as "in place" because whole shells predominate over fragments. Even the terrestrial shells commonly are whole and evidently arrived at the site of deposition after minimal transport from the adjacent moist terrestrial fringe of the pond or shallow lake in which the aquatic forms lived and where the limestone was being deposited.

Combining the stratigraphic, sedimentologic and biologic evidence, and interpreting it in part in Hanley's terms, I suggest the following:

1) The drab sandstone is a lowland floodplain channel sandstone. The terrestrial (*Oreohelix*) and aquatic (*Campeloma*) snail fragments comprise a mixed assemblage carried into the deposit over very short distances from the moist fringes and relatively quiet water oxbows and sloughs of the immediately adjacent floodplain.

2) The argillaceous limestone represents a succeeding, quieter water phase of deposition, probably in an oxbow lake or slough which was cut off from a meander bend of the preceding stream channel. Snails were abundant. The autochthonous aquatic forms thrived in the open, ponded water or shallow lacustrine environment of the site. The terrestrial forms occupied the fringe of the well watered and heavily vegetated adjacent floodplain. Remains of a sample of the small mammal fauna of the area fell into the margin of the pond where some predator fed

above. Large plants, some tree sized, fringed the open water, possibly growing along a natural levee bordering the recently shifted stream channel. The pantolestid insectivore skull, which is the most complete mammal specimen yet recovered from the site, may have arrived there more directly than did the other mammal remains.

3) As the oxbow or slough filled with calcareous sediment it was converted into a heavily vegetated swamp, as indicated by the succeeding thin transition zone of coal and highly carbonaceous but fissile, dark shale. Mollusk shells are present near the base of this zone but clearly are less abundant than in the limestone below, perhaps because fewer snails occupied this environment, but perhaps also because the low pH in this paludal environment tended rapidly to dissolve their shells after death.

4) Filling of the swamp initiated the next phase of deposition of drab but less carbonaceous, poorly bedded, fine grained argillaceous sediments which accumulated as periodic overbank or crevasse splay deposits on the floodplain. Moist, poorly drained, low pH soil conditions continued to prevail on this low, vegetated plain.

It seems unlikely that *Paleosinopa simpsoni*, with its relatively small jaws and gape, could have grasped and crushed the largest of the associated mollusks whole. The maximum shell dimensions of *Campeloma* and *Oreohelix* are equal to or even double the length of the entire cheek tooth row of that pantolestid. But if such shells were penetrated locally, perhaps in some cases through an inoperculate aperture (as in *Oreohelix*), the creature might then have fed piecemeal upon the fleshy parts of those large forms. It seems just as likely, however, that this early pantolestid might initially have added mollusks as a supplement to its primitively insectivorous diet beginning with the abundant "bite sized" smaller varieties of snails and juvenile individuals of the larger forms. The adaptive shift from capturing relatively mobile insects such as roaches and crushing their tough exoskeletons to the supplemental capture and crushing of abundant and far less mobile, fragile-shelled snails probably was behavioral at the outset and would have required little if any morphologic change because, as discussed earlier, the generalized masticatory apparatus of primitive insectivores, especially that of Paleocene pantolestids, was preadaptively capable of some shell crushing. Two modern examples of a similar, opportunistic behavioral shift to a supplementary diet of mollusks are noted by Van der Schalie (1970, p. 52). He states that mink and muskrats, both semiaquatic but members of entirely different mammalian orders and the latter normally an herbivore, feed occasionally on clams in the Duck and Buffalo river drainages of Tennessee. This behavior on their part appears even more opportunistic because they now feed upon *Corbicula*, a foreign clam which since its introduction in historic time has largely replaced the formerly abundant native mussel fauna of that area. The Muskrat, not even a predator in the normal sense, apparently is unable to open the mussels directly, but has accommodated its behavior to fit the opportunity in an ingenious way. According to E. G. Kauffman (1977, oral comm.), it carries the mussels from the water to a mud flat where aerial exposure kills its prey, allowing the abductor muscles to relax and the shell automatically to open, thus exposing the edible contents. There are, of course, numerous other well known examples of the assumption of mollusk feeding habits and attendant morphological adaptation amongst the mammalian and other orders of vertebrates. The presence of such a gratuitous food supply seems almost to guarantee multiple solutions for its utilization.

What the pantolestids appear to have done in the course of their specialization was to become successfully aquatic, to diverge into a range of small, intermediate and large sizes, to improve their shell crushing capabilities through additional modification of the masticatory apparatus, and thus to become successful, as a family, in the exploitation of the full spectrum of freshwater mollusk feeding opportunities. The reason for their extinction, apparently at the end of the early Oligocene, is not clear. Certainly it was not for lack of a molluscan food supply. Perhaps they were replaced by con-

vergent adaptive types derived from some newer and more successful mammalian order such as the Carnivora. The mustelids in the latter appear in the early Oligocene and some later became morphologically adapted for a malacophagous diet, although even less specialized mustelids feed to some extent upon shellfish.

PALEOBIOGEOGRAPHY OF PANTOLESTIDS

Text-figure 5, with its accompanying notes, documents the discussion which follows and provides detailed references to the literature cited.

The oldest presently known record of pantolestids comes from the middle Paleocene of the United States. *Propaleosinopa albertensis* is the only certain record of that age; *Pantomimus* and *Pantinomia* probably are not pantolestids. Thus it is possible that the family originated in North America. *Propaleosinopa* also occurs in the late Paleocene of both North America and Europe, so faunal interchange evidently was possible at that time. Since *Propaleosinopa* appears to have been ancestral to North American *Paleosinopa*, it may also have been ancestral to the Eocene and later pantolestids of Europe, although *Paleosinopa* may also occur in Europe and thus might have been the more immediate ancestor of later European forms. The solution of this problem awaits resolution of questions, mentioned below, regarding the taxonomy of the European forms.

Two distinct genera and species, *Propaleosinopa albertensis* and *Paleosinopa simpsoni*, occur in the early Tiffanian (early late Paleocene) of North America and, as discussed earlier, I believe the line of familial descent there was from *Propaleosinopa* to the various late Paleocene and early Eocene species of *Paleosinopa*, to the middle Eocene species of *Pantolestes*, and ultimately to its termination in early Oligocene *Chadronia*.

The situation in the late Paleocene and early Eocene of Europe is less clear, primarily because recent students differ on matters of taxonomy. Russell (1964, 1966) recognizes four distinct late Paleocene forms. He refers two of these to *Pagonomus*, another to "*Bessoecetor*," and leaves the fourth unidentified. He also assigns part of the early Eocene fossil material once referred to *Paleosinopa osborni* to *Pagonomus* instead, and leaves the remainder of that material unassigned. Van Valen (1967), on the contrary, suggests that late Paleocene *Pagonomus* may be *Paleosinopa* although he leaves *Pagonomus* to stand as valid in his formal classification (1967, p. 259). Also, he synonymizes North American "*Bessoecetor*" with *Propaleosinopa*, thus transferring Russell's "*Bessoecetor*" *levei* (from the late Paleocene of France) to *Propaleosinopa*. If Van Valen's suggestions are correct, then the late Paleocene pantolestids were congeneric between North America and Europe and may have remained so into the early Eocene. By either interpretation, however, it seems clear that the late Paleocene and possibly the early Eocene pantolestids of the two continents were very similar. This close similarity, if not actual generic identity, further suggests that Europe and North America were intimately connected geographically, thus allowing unrestricted faunal interchange, a conclusion which previously has been reached by others on the basis of similarity of whole faunas of middle Paleocene to earliest Eocene age on the two continents.

In the middle Eocene, if not before, the pantolestids on the two continents appear to diverge. According to Jaeger (1970), *Buxolestes* in Europe is similar to, but distinct from, North American *Pantolestes*, and I reach the same conclusion from his figures. He suggests that the similarity of those two genera resulted in part from their common ancestry and in part from parallel but separated evolution following their earlier common origin. My suggestion is that this common origin would have been in the *Paleosinopa*-?=*Pagonomus* complex of closely similar species which ranges from the late Paleocene into the earliest Eocene (Clarkforkian, and early Wasatchian or Graybull=Sparnacian)

GEOLOGIC TIME (North American Land Mammal Ages in parentheses)	WESTERN UNITED STATES AND CANADA				
Later times					
Early Oligocene (Chadronian of North America)	Chadronia margaretae (9)				
Late Eocene (Uintan and Duchesnean)	?	?	?	?	?
Middle Eocene (Bridgerian)	Pantolestes longicaudis (7)	Pantolestes natans (8)	Pantolestes phocipes (8)	Pantolestes intermedius (8)	?Pantolestes elegans (8)
Early Eocene (Wasatchian of North America)		Paleosinopa veterrima (6)	Paleosinopa lutreola (6)	Paleosinopa "sp. E" (6)	
(Clarkforkian of North America)	Paleosinopa didelphoides (5)				
Late Paleocene (Tiffanian of North America)		(4) Paleosinopa simpsoni (3)	(2)		
Middle Paleocene (Torrejonian of North America)	(Pantinomia ambigua) *	(Pantomimus leari) **	Propaleosinopa albertensis (1)		

TEXT-FIG. 5 — Pantolestid temporal and geographic distribution (not including pentacodontids).

* — Probably an arctocyonid, not, as Van Valen originally thought, a pantolestid (Van Valen, 1967, footnote p. 225).

** — Probably not a pantolestid, possibly a pentacodontid, but see Van Valen (1967, p. 228-230). (1) Includes "*Bessoecetor*" *diluculi*, Gidley Quarry, Montana, see Van Valen, 1967, for synonymy; (2) Includes "*Bessoecetor*" *thomsoni*, Scarritt Quarry, Montana and Paskapoo Formation, Alberta, see Van Valen, 1967, for synonymy; (3) Scarritt Quarry, Montana; (4) Dell Creek Quarry, Wyoming; (5) ?Clarkforkian and Wasatchian; (6) Wasatchian (Graybull), see Van Valen, 1967, p. 225 (left); (7) "Lower" and "Upper" Bridger according to Matthew, 1909, p. 532. The "Upper" Bridger Formation may extend temporally into the late Eocene; (8) "Upper" Bridger, may extend into the late Eocene. These named species may not all be valid, but see Matthew, 1909, p. 532-533; (9) Lower Chadron according to Cook, 1954.

on both continents, although divergence from more primitive *Propaleosinopa* is possible if *Paleosinopa* does not equal *Pagonomus*. It is of special interest in this connection that West and Dawson (in press and written comm., 1977) have reported *Pantolestes natans* from the Eureka Sound Formation on Ellesmere Island in the northeastern Canadian Arctic. They say that on present evidence

ELLESMERE ISLAND, northeastern CANADA	EUROPE				AFRICA	
						Kelba (24)
	Androconus verlindeni (20)	Dyspterna woodi (21)	(22)-? →			Qarunavus meyeri (23) Ptolemaia lyonsi (23)
	Cryptopithecus sideroolithicus (18)	Cryptopithecus major (18)	Galethylax blainvillei (19)			
	Buxolestes hammeli (16)		pantolestid indet. (17)			
Pantolestes natans (25) ? ↕ ?	? Pagonomus osborni (may be Paleosinopa) (14)		pantolestid indet. (15)			
	?Pagonomus sp. (10)	Pagonomus dionysi (may be Paleosinopa) (11)	small pantolestid (?Propaleosinopa) (12)	Propaleosinopa (="Bessoecetor") levei (13)		

(The Africa column is labeled vertically "Ptolemaiidae".)

TEXT-FIG. 5 – Cont'd.   (10) Walbeck, Germany, Russell, 1964, p. 69-70. *Pagonomus* may be a synonym of *Paleosinopa* according to Van Valen, 1967, p. 227; (11) Cernay, France, Russell, 1964, p. 66-69, but see note 10 above; (12) Cernay, France, Russell, 1964, p. 70-71.   May be *Propaleosinopa* according to Van Valen, 1967, p. 227; (13) Berru, France. Russell and others, 1966, p. 848-850, assigned this species to "*Bessoecetor*" which Van Valen, 1967, p. 226-227, synonymized with *Propaleosinopa*.   Whichever is correct, the same genus appears to be present in North America and Europe; (14) Late Ypresian (Cuisian), Epernay, France. Includes "*Paleosinopa*" *osborni* in part, see Russell, 1966, p. 849-850 and Jaeger, 1970, p. 76-77; (15) Same as note 14 above; (16) Bouxwiller, France, Jaeger, 1970. Size of *Pantolestes longicaudis*; (17) Bouxwiller, France, Jaeger, 1970; (18) Includes "*Opsiclaenodon*," see Van Valen, 1966, p. 87 and 1967, p. 227. *Cryptopithecus sideroolithicus*-Germany, *Cryptopithecus major*, England; (19) Phosphorites, Quercy; (20) Hoogbutsel, Belgium; (21) Isle of Wight, England; (22) See Van Valen, 1966, p. 89 and 1967, p. 228 regarding possible origin of Ptolemaiidae from Pantolestidae; (23) Fayum, Egypt, Simons and Gingerich, 1974; (24) Miocene, Africa; (25) Ellesmere Island, Canadian Arctic, West and Dawson (written communication, 1977, and in press), exact age uncertain.

the age of the associated faunal assemblage is uncertain and may prove to be either late early or early middle Eocene. Whatever the exact age may be, it appears that *Pantolestes* ranged from western to northeasternmost North America, but did not reach Europe, probably because by the late early

or middle Eocene the land connection across the proto-North Atlantic had broken.

Thereafter, the family appears to have followed separate ways in North America and Europe. It appears to have become extinct at about the same time, the end of the early Oligocene, in both places, although Van Valen has suggested that the early Oligocene Ptolemaiidae of Africa may have been derived from European pantolestids before the latter became extinct.

ACKNOWLEDGMENTS

LITERATURE CITED

COOK, H. J. 1954. A remarkable new mammal from the lower Chadron of Nebraska. The American Midland Naturalist, 52(2): 388-391.

COOMBS, M. C. 1971. Status of *Simidectes* (Insectivora, Pantolestoidea) of the Late Eocene of North America. American Museum of Natural History Novitates, no. 2455, 41 p.

DORR, J. A., JR. 1952. Early Cenozoic stratigraphy and vertebrate paleontology of the Hoback Basin, Wyoming. Geological Society of America Bulletin, 63: 59-94.

_____ 1958. Early Cenozoic vertebrate paleontology, sedimentation and orogeny in central western Wyoming. Geological Society of America Bulletin, 69: 1217-1244.

DORR, J. A., JR., D. R. SPEARING and J. R. STEIDTMANN. 1977. Deformation and deposition between a foreland uplift and an impinging thrust belt, Hoback Basin, western Wyoming. Geological Society of America Special Paper 177, 82 p.

GINGERICH, P. D. 1975. New North American Plesiadapidae (Mammalia, Primates) and a biostratigraphic zonation of the middle and upper Paleocene. University of Michigan Museum of Paleontology Contributions, 24(13): 135-148.

_____ 1976. Cranial anatomy and evolution of early Tertiary Plesiadapidae (Mammalia, Primates). University of Michigan Museum of Paleontology Papers on Paleontology, no. 15, 141 p.

HANLEY, J. H. 1976. Paleosynecology of nonmarine Mollusca from the Green River and Wasatch formations (Eocene), southwestern Wyoming and northwestern Colorado. p. 235-261 in Scott, R. W. and West, R. R., Structure and classification of paleocommunities; Dowden, Hutchinson and Ross, Inc.

HICKEY, L. J. 1972. Stratigraphic summary of the Golden Valley Formation (Paleocene-Eocene) of western North Dakota. p. 105-122 in Ting, F. T. C. (Ed.), Depositional environments of the lignite-bearing strata in western North Dakota; Miscell. Series No. 50, North Dakota Geological Survey.

JAEGER, J. J. 1970. Pantolestidae nouveaux (Mammalia, Insectivora) de l'Eocène moyen de Bouxwiller (Alsace): Palaeovertebrata, 3(3): 63-82, 3 pls.

MATTHEW, W. D. 1901. Additional observations on the Creodonta. American Museum of Natural History Bulletin, 14(1): 1-38.

_____ 1909. Carnivora and Insectivora of the Bridger Basin, middle Eocene. American Museum of Natural History Memoirs, 9: 289-567.

_____ 1918. A revision of the lower Eocene Wasatch and Wind River faunas. Part 5. Insectivora (continued), Glires, Edentata. American Museum of Natural History Bulletin, 38(15): 565-657.

MOORE, R. G. 1955. Mollusks from the Hoback Formation. University of Michigan Dept. of Geology, Ann Arbor, Michigan, Master's thesis, 26 p., unpublished.

RUSSELL, D. E. 1964. Les Mammifères Paléocenes d'Europe. Mém., Mus. Natl. d'Hist. Nat., new ser., ser. C, v. 13, 324 p., 16 pls.

RUSSELL, D. E., P. LOUIS and M. POIRIER. 1966. Gisements nouveaux de la faune cernaysienne (Mammi-
     fères paléocènes de France). Bull. Soc. géol. de France, (7), VIII, p. 845-856.
SIMONS, E. L. and P. D. GINGERICH. 1974. New Carnivorous mammals from the Oligocene of Egypt. Geo-
     logical Survey of Egypt Annals, 4: 157-166.
SIMPSON, G. G. 1936. A new fauna from the Fort Union of Montana. American Museum of Natural History
     Novitates, no. 873, 27 p.
SLOAN, R. E. and L. VAN VALEN. 1965. Cretaceous mammals from Montana. Science, 148(3667): 220-227.
SPEARING, D. R. 1969. Stratigraphy and sedimentation of the Paleocene-Eocene Hoback Formation, western
     Wyoming. Wyoming Geological Association Guidebook, 21st Annual Field Conference, p. 65-76.
TATE, G. H. H. 1947. Mammals of eastern Asia. The Macmillan Co., New York, 366 p.
TURNBULL, W. D. 1970. Mammalian masticatory apparatus. Fieldiana-Geology, 18(2): 356 p.
VAN DER SCHALIE, H. 1973. The mollusks of the Duck River drainage in central Tennessee. Sterkiana, no. 52,
     p. 45-55.
VAN VALEN, L. 1966. Deltatheridia, a new order of mammals. American Museum of Natural History Bulletin,
     132(1): 1-126, 8 pls.
_____ 1967. New Paleocene insectivores and insectivore classification. American Museum of Natural History
     Bulletin, 135(5): 217-284.
WEST, R. M. and M. R. DAWSON. 1977. Mammals from the Paleocene of the Eureka Sound Formation, Ellesmere
     Island, Canada. Geobios, in press.
WOLFE, J. A. and D. M. HOPKINS. 1967. Climatic changes recorded by Tertiary land floras in northwestern
     North America. Symposium Pacific Sci. Congress, 25: 67-76.