

SYSTEMATICS OF THE LEPTAUCHENIINE OREODONTS (MAMMALIA: ARTIODACTYLA) FROM THE OLIGOCENE AND EARLIEST MIOCENE OF NORTH AMERICA

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Abstract—The Leptaucheniinae was a subfamily of oreodonts that had eyes and ears high on their skulls, a large nasal-facial vacuity, large auditory bullae, and very hypsodont teeth. They were very common in the Whitneyan and early Arikarean of the High Plains and western Montana, yet vanished in the late Arikarean. Their taxonomy has long been confused by post-mortem deformation and lack of statistical analysis, culminating with oversplitting into the 7 genera and 31 species recognized by Schultz and Falkenbach (1968). CoBabe (1996) employed multivariate analysis and recognized only two genera, *Sespia* and *Leptauchenia*, the latter only containing two species. She did not group her specimens by stratigraphic level, nor address the issue of how much variability is reasonable within a single population. We reanalyzed the problem using both bivariate and multivariate statistics, and compared samples within stratigraphic levels. There seem to be only three species that are statistically supported and diagnosable: the smaller taxon *Leptauchenia decora* (early Orellan to early Arikarean), the intermediate-sized *L. major* (late Whitneyan to late Arikarean), and the large, robust *L. lullianus* (restricted to the early and middle Arikarean). Contrary to previous hypotheses that leptaucheniines were hippo-like aquatic forms or hyrax-like rock dwellers, all the evidence seems to suggest that they lived near the eolian deposits in which they were buried. Their taphonomy is unusual in that very few postcranials are known, and virtually all specimens are isolated skulls found in eolian sands and silts. *Leptauchenia* was restricted to the High Plains and western Montana during the Whitneyan and Arikarean, but is unknown from the similar-looking volcanoclastic deposits in central Oregon, California, and is also absent from the Gulf Coast of Florida or Texas at that time (despite the abundance of other non-leptaucheniine oreodonts in all these deposits).

INTRODUCTION

The family Merycoidodontidae, or the oreodonts, has long been among the most abundant and biostratigraphically important groups of fossil mammals in the middle Cenozoic of North America. Some taxa, such as *Merycoidodon* and *Miniochoerus* (Stevens and Stevens, 1996) are so common in the “turtle-oreodon beds” (lower Oligocene Scenic Member of the Brule Formation of the Big Badlands of South Dakota) that the deposits are named after them, and they are found in rock shops and museums all over the world. Likewise, *Leptauchenia* is by far the most common fossil in the Whitneyan, and so lent its name to the overlying “*Leptauchenia* beds.” Unfortunately, the great abundance of oreodont specimens has been a mixed blessing. In the early history of their taxonomy, nearly every new specimen was designated a new taxon, largely based on subtle differences that did not account for population variation or post-depositional deformation. Some later revisers (e.g., Thorpe, 1937; Scott, 1940) were more conservative in their definitions of taxa. For example, Scott (1940) recognized only three genera and less than a dozen species in the White River Group. The revisions of the oreodonts by Schultz and Falkenbach (1940, 1941, 1949, 1950, 1954, 1956, 1968) grossly oversplit the group, based on characters that are largely caused by post-mortem deformation. Schultz and Falkenbach failed to do any statistical analysis to determine if taxa were distinct, and tended to measure only a few variables on type specimens. In addition, they designated the specimens from each different formation as a separate species, whether or not they actually looked different from those in other formations. These problems have been recognized for a long time (e.g., Harksen and Macdonald, 1969, p. 13; Lander, 1977, 1998; Savage and Russell, 1983, p. 195, footnote 2; Gustafson, 1986, p. 16; Emry et al., 1987, p. 140; Joeckel, 1992; Prothero and Heaton, 1996; MacFadden and Morgan, 2003, p. 383), but the task of revising such a taxonomic mess was daunting, and discouraged immediate revision. The first modern systematic and statistical treatment of the White River merycoidodonts by Stevens and Stevens (1996) reduced dozens of genera and species into just three genera and less than a dozen species.

One of the most distinctive groups of oreodonts was the subfamily Leptaucheniinae, which were very common in the Whitneyan and Arikarean (late Oligocene to earliest Miocene). The leptaucheniines had a very hypsodont (high-crowned) dentition, high-set orbit, inflated auditory bulla, and a large nasal-facial vacuity (Fig. 1). They had relatively short limbs and a long midsection and tail. The systematics of the Leptaucheniinae have been revised numerous times since their first description by Leidy (1856a). Thorpe (1937) considered 8 species in two genera, *Leptauchenia* and *Cyclopidius*, to be valid. Scott (1940) recognized *Leptauchenia decora* and *L. major*, along with “*L.*” (*Sespia*) *nitida*.

Schultz and Falkenbach (1968) oversplit the leptaucheniines into 7 genera and 31 species, based largely on differences in size and stratigraphic position without any statistical analysis, and also based on features caused by post-mortem deformation. They commented (p. 412) that their alleged “six phylogenetic lines” of leptaucheniines would be reduced to two or three without precise stratigraphic data, a remark that reveals how much their species definitions are dependent on stratigraphy rather than morphology. Their oversplitting was apparently also influenced by the fact that they thought the Gering Formation spanned a long period of time. As a result, they tried to name a different species in each generic “lineage” for each level within the Gering, whether or not the specimens were truly distinct. But recent work has shown that many of their “Gering” deposits are actually referable to the “brown siltstone member” of the Brule Formation (Swinehart et al., 1985; Tedford et al., 1996), or to the Sharps Formation of South Dakota, which they refused to recognize (Schultz and Stout, 1961, p. 7; Schultz and Falkenbach, 1968, p. 413). In addition, the restricted Gering Formation spans less than 300,000 years, from 28.0–28.3 Ma (Tedford et al., 1996). The Monroe Creek Formation, on the other hand, appears to span a longer interval (28–26 Ma, *vide* MacFadden and Hunt, 1998), and most of the rest of the Arikarean (26–19 Ma) is represented by the Harrison Formation (Tedford et al., 2004; MacFadden and Hunt, 1998) and by the latest Arikarean Anderson Ranch Formation of Hunt (2002), formerly called the Upper Harrison beds of Peterson (1909) or part of the Marsland Formation of Schultz and Stout (1961). These radical adjustments of the

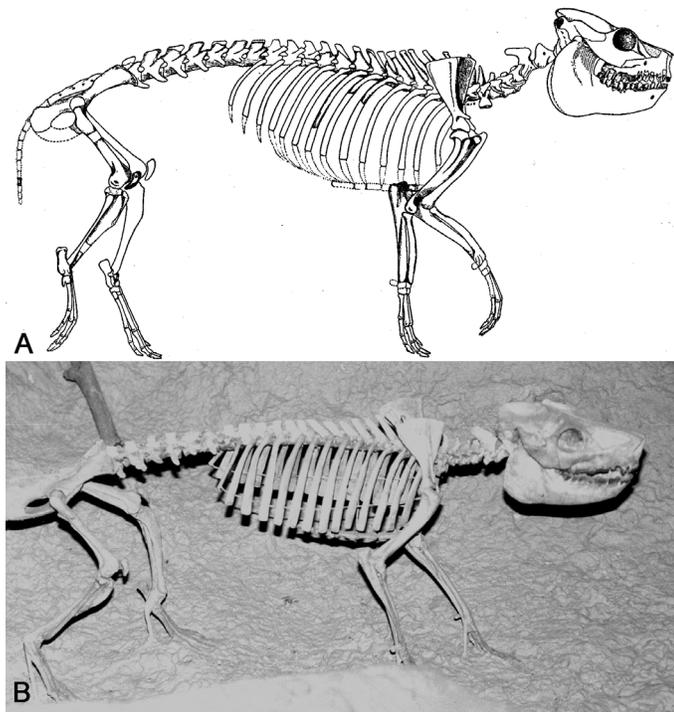


FIGURE 1. *Leptauchenia decora*. A, Restoration of skeleton (from Scott, 1940). B, Photograph of mounted specimen in the South Dakota School of Mines and Technology Museum, Rapid City, South Dakota. The relatively short limbs and long body are apparent in this specimen.

duration of the Arikarean subdivisions invalidate many of the concepts of Wilson (1960), Schultz and Stout (1961), Martin (1975), and Schultz and Falkenbach (1968), who assumed the “Geringian,” “Monroecreekian,” and “Harrisonian” were roughly equal in duration. In addition to these misconceptions, one must remember that these authors thought the entire Arikarean was early Miocene, but Tedford et al. (1987, 2004) showed that it is almost entirely late Oligocene in age.

CoBabe (1996) did a multivariate analysis of most of the leptaucheniines, and retained only two genera: *Leptauchenia* (with two species, *L. decora* and *L. major*) and *Sespia*. Unfortunately, CoBabe did not separate specimens by stratigraphic level, but instead lumped all the materials spanning the entire Whitneyan and Arikarean (19–32 Ma, or 13 million years in duration) into a single data set. Nor did her analysis examine coefficients of variation to see if such an enormous temporal and morphological span of variability can reasonably be attributed to only two species. In addition, CoBabe (1996) failed to adequately justify her large list of synonymies.

Lander (1998) briefly discussed leptaucheniine systematics, but gave a long list of synonymies without adequate justification, discussion, or analysis, so it is not possible to evaluate his systematic decisions. He retained many more of Schultz and Falkenbach’s (1968) species than did CoBabe (1996), but placed all of them (except for *Sespia*) in the genus *Leptauchenia*.

For this reason, we revisited the question of leptaucheniine systematics, measuring and analyzing hundreds of specimens. Our approach differs from that of CoBabe (1996) in that we focused on presumed population samples at each discrete stratigraphic level to see if they are indeed homogeneous, and if their coefficients of variation can be explained as representing a single species.

Part of this study was an analysis of the dwarfed leptaucheniine *Sespia*, which CoBabe (1996) and Lander (1998) recognized as distinct, but did not analyze in detail. That research has now been published (Hoffman and Prothero, 2004). However, most of the large leptaucheniines were not analyzed at that time, so one of us (FS) took on the project as his senior comprehensive project, doing all the measure-

ments and the preliminary analyses. Further statistical and morphological analyses were performed by the senior author, resulting in the present paper.

METHODS

Over 100 specimens from the AMNH and F:AM (mostly complete or nearly complete adult skulls) were measured with digital calipers, and many were photographed with a Nikon 5700 digital camera. Statistics were performed using Excel and SYSTAT version 9 software. A total of 11 measurements were taken (Fig. 2), utilizing most of the 8 variables measured on 127 skulls by CoBabe (1996), who in turn used many of the same landmarks measured by Schultz and Falkenbach (1968). However, we did not use some of the variables in her study. We found that the bullar volume was too difficult to measure reliably (especially on broken, distorted, or unprepared specimens), so we abandoned this feature. Likewise, M1 occlusal area was difficult to measure on enough specimens, because many were still unprepared, or had the mandible still attached, so that the occlusal surface of the upper molars was concealed. Based on the results shown by CoBabe (1996), both of these variables scale largely with size, so we are not convinced that they have any real use in systematics.

Instead, we measured variables that we thought were more useful, or were available on both intact and broken specimens. There is a tendency in some leptaucheniines for the loss (or lack of eruption) of M3 in some individuals, so we added a measurement of M1–2 length (also used by Schultz and Falkenbach, 1968, for the same reason). We wanted to address the possibility of sexual dimorphism in upper canines (found in *Sespia* by Hoffman and Prothero, 2004, and in many other primitive hornless artiodactyls), so we measured the canine length, although the canines were broken in most specimens. We also measured the height of the skull at the occiput, and the skull width at the zygoma, variables used by Schultz and Falkenbach (1968) but not by CoBabe (1996) to assess whether these characters are entirely distorted by post-mortem deformation, or bear useful information.

Institutional abbreviations: ACM = Amherst College Museum, Amherst, Massachusetts; AMNH = American Museum of Natural History, New York; ANSP = Academy of Natural Sciences, Philadelphia; F:AM = Frick Collection, now stored in the AMNH; MCZ = Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; UNSM = University of Nebraska State Museum, Lincoln, Nebraska.; YPM = Yale Peabody Museum, New Haven, Connecticut; YPM-PU = Princeton Collection, now stored at the Yale Peabody Museum, New Haven, Connecticut.

RESULTS

Results of the statistical analysis of the data are shown in Tables 1 and 2. These results are plotted in Figures 4 through 9, and discussed below.

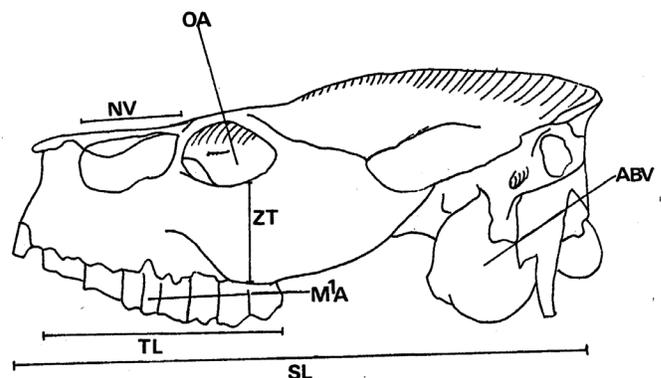


FIGURE 2. Sketch of skull, showing dimensions measured by CoBabe (1996).

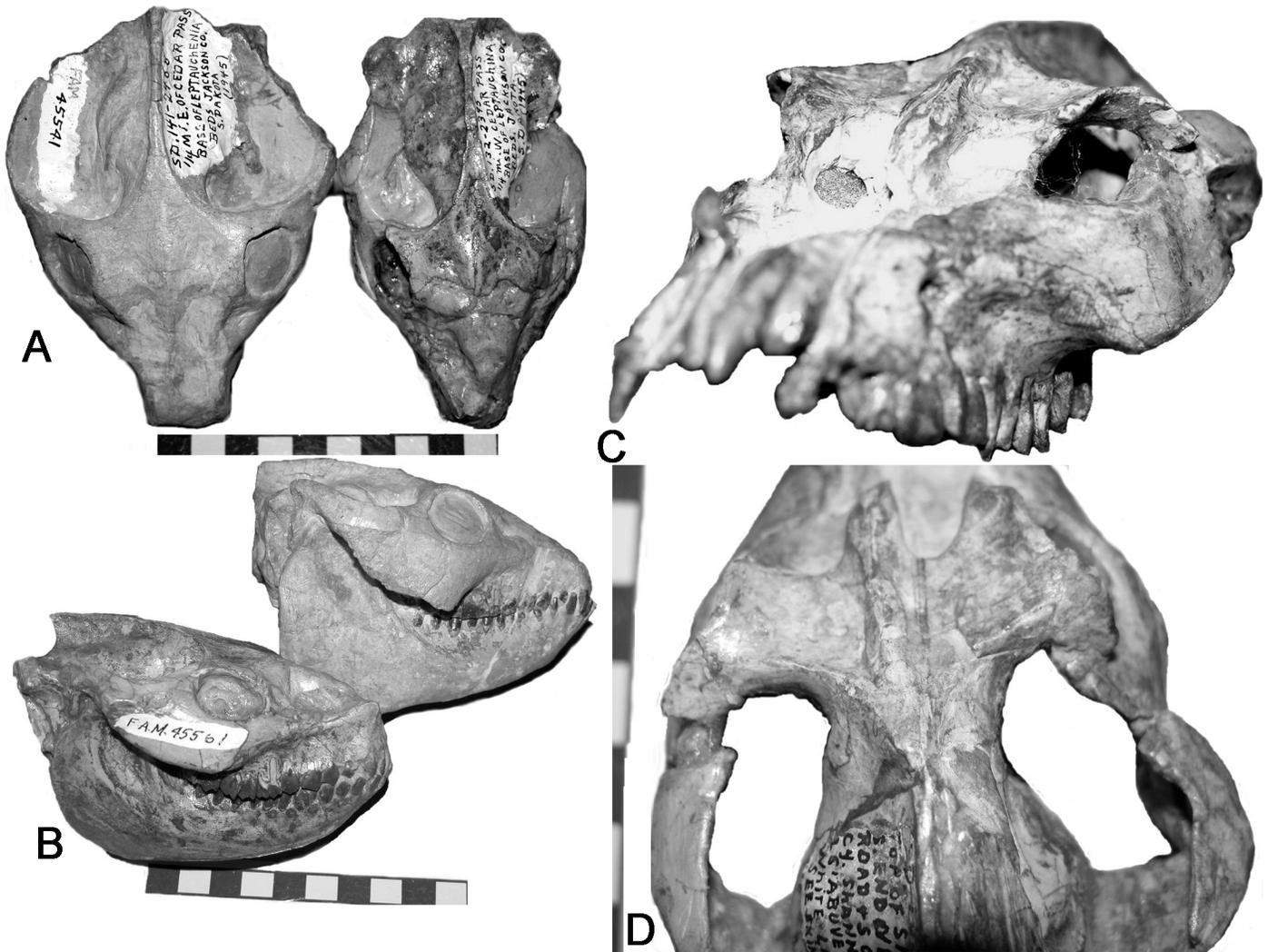


FIGURE 3. **A-B**, Two normal-sized skulls of *L. decora* showing effects of crushing. F:AM 45541 (lighter-colored skull) has been dorsoventrally crushed. F:AM 45561 (mottled skull) has been laterally crushed. In most dimensions of the teeth and the skull length, these skulls are indistinguishable, but they vary widely in shape due to crushing. **C-D**, F:AM 45633, type specimen of “*Pitheciastes mariae*,” showing the specimen in anterior view (**C**) and dorsal view (**D**). This specimen has been dorsoventrally crushed and laterally sheared, so the zygomatic arches are asymmetrical and even restored improperly in this specimen, giving the false impression that it had narrow zygomatic arches and large nasal-facial vacuities. Scale bar in cm.

DISCUSSION

Variability Due to Post-Mortem Deformation

Are some of the characters used in systematic diagnoses by Schultz and Falkenbach (1968) simply due to post-mortem deformation that they failed to recognize, and/or are they due to simple scaling from small individuals to large ones? Such deformation is apparent in visual inspection (Fig. 3), and previous authors (e.g., Phleger and Putnam, 1942; Bader, 1955; Lander, 1977, 1998) have informally filtered out taphonomic effects, and rarely used crushing-susceptible features in their diagnoses. Stevens and Stevens (1996) addressed this question directly by molding an oreodont skull in soft latex, then deformed the mold as the plaster set within the mold. This produced the “brachycephalic” and “dolichocephalic” versions of the same mesocephalic original. They found that many of the “diagnostic features” of merycoidodontine taxa erected by Schultz and Falkenbach (1956, 1968) were taphonomic, making them “taphotaxa” *sensu* Lucas (2001). For example, among the miniochoerines, the genus *Miniochoerus* was represented by undeformed skulls, *Playtochoerus* (literally translated as “flat pig”) was based on dorsoventrally crushed specimens, and *Stenopsochoerus* (“narrow pig”) was based on laterally crushed specimens. In all other dimensions not affected by crushing, the

measurements were nearly identical for specimens from the same stratigraphic level, so Stevens and Stevens (1996) synonymized the latter two genera under *Miniochoerus*. They found similar problems with specimens of *Merycoidodon* that were identical in size and from the same stratigraphic horizon, but differed only in crushing.

There are other ways to address this issue. We recorded as we measured each specimen if there was obvious post-mortem deformation (Fig. 3), and compared those notes to the results of our statistical analysis. Unlike *Miniochoerus* skulls, which might be crushed dorsoventrally if they landed on their dorsal surface or palate, or laterally if they landed on their side when they were buried, we found that the shape of the *Leptauchenia* skull is such that it usually came to rest on the dorsal side or palate as it was buried. This is especially true if no mandible was attached. Consequently, *Leptauchenia* skulls are typically crushed dorsoventrally, and rarely crushed laterally. This is apparent in the coefficients of variation for the different variables (Table 1). The largest values all occur on measurements that are likely to be affected by dorsoventral crushing (occipital height of skull, which is shortened in dorsoventral crushing; skull width at zygoma, which is expanded during dorsoventral crushing; thickness of zygoma, which can be either compacted or expanded due to crushing) and by other aspects of deformation (e.g., nasal-

TABLE 1. Statistics of leptaucheniine specimens analyzed in this study (mm). N = number of specimens; M = mean; SD = standard deviation; CV = coefficient of variation.

CHARACTER	Total sample N = 103			E. Whitneyan N = 24			Lt. Whitneyan N = 23			E. Arikareean N = 43			Lt.E. Arikareean N = 16			Lt. Arikareean N = 11		
	M	SD	CV	M	SD	CV	M	SD	CV	M	SD	CV	M	SD	CV	M	SD	CV
M1-2 length	21.8	5.0	23.1	18.4	2.4	13.0	19.3	3.5	18.3	25.5	4.4	21.0	20.0	3.6	18.0	22.2	3.5	15.6
P2-M3 length	51.3	8.1	15.7	42.8	2.3	6.9	46.7	7.2	15.5	57.1	7.1	12.4	50.9	4.9	9.7	54.1	4.1	7.5
M1-3 length	33.7	5.5	16.5	27.9	2.5	8.9	30.7	3.7	11.9	37.5	4.8	12.7	33.1	4.5	13.7	36.9	4.0	10.9
C1 length	8.9	2.4	27.0	8.5	2.5	28.9	7.2	2.1	29.0	9.4	2.7	28.6	8.3	2.0	24.0	10.2	1.1	10.6
Malar thickness	18.5	5.0	26.8	13.7	1.9	14.1	15.2	1.9	12.6	21.5	4.2	19.4	19.9	3.4	17.0	22.8	4.9	21.5
Orbital height	17.6	2.7	15.2	18.1	1.3	7.4	16.9	2.2	13.0	17.4	2.9	16.9	18.5	3.9	21.0	17.6	3.2	17.9
Orbital length	20.9	2.6	12.4	19.0	1.4	7.3	19.1	1.8	9.3	22.0	2.6	11.8	20.9	2.7	13.1	22.2	2.1	9.5
NFV length	31.9	6.6	20.6	24.1	3.6	14.7	26.6	3.0	11.4	36.2	5.7	15.6	34.7	3.9	11.1	33.3	4.3	13.0
Skull length	112.6	18.8	16.7	96.3	7.2	7.5	105.7	11.9	11.3	124.7	19.5	15.6	110.3	14.8	13.5	120.9	13.5	11.1
Skull width	81.6	16.0	19.6	71.3	8.3	11.7	71.5	11.3	15.7	93.3	13.8	14.8	76.6	11.8	15.4	78.4	13.5	17.3
Skull height	37.4	7.5	20.0	32.4	5.3	16.4	37.6	10.3	27.3	40.3	4.8	11.9	39.9	5.8	15.4	41.2	6.5	15.8

facial vacuity length, especially vulnerable to crushing and distortion, since it represents a weak spot in the skull). Upper canine length was also highly variable, but we believe this is due to sexual dimorphism (see below). By contrast, the lowest CV values occur in the relatively less deformable cheek tooth row (M1-3 length; P2-M3 length; M1-2 length). As noted by Phleger and Putnam (1942, p. 58) and Stevens and Stevens (1996, p. 499), the skull length is unlikely to be changed by crushing (only by breakage), and was low in variability. The orbit itself is a fairly robust ring of bone, so the CVs of orbit height and orbit length were also low. A similar hierarchy of CV values in merycoidodontine skulls was observed by Stevens and Stevens (1996, Table 1).

Another way to address the issue of the variability of measurements when the sample size is large with many variables is with multivariate analysis. A principle components analysis (PCA) and factor analyses using varimax and equimax rotations were performed on the data matrix to identify the major components of variability in multivariate hyperspace (Cooley and Lohnes, 1971; Harris, 1975; Neff and Marcus, 1980). As in most PCA and factor analyses of specimens with significant size ranges, the first PC and first factor primarily reflect the size component of the data. In our study (Table 2), it explained 65.6% of the variance in the PCA and the same percentage in factor analyses run with either equimax or varimax rotations. This is to be expected, since all of these methods are fitting the first PC to the longest axis of variability of the multivariate ellipsoid, so rotations do not change this result. The second PC, and the second factor, explained 10.2% of the variability, and represent the axis of next greatest variability in the hyperspace ellipsoid of the multivariate data. PCA automatically fits the second PC orthogonal to the first in this direction of next greatest variability, while the different types of factor analysis allow the vector of the second factor to rotate at any angle to the first factor to explain the greatest variability. In our analysis, the PCA and factor analyses obtained the same result. The second PC or second factor tended to load most heavily on variables such as the nasal-facial vacuity length and the height of the orbit, both of which are prone to distortion during dorsoventral crushing (Table 2; Fig. 4A), although the occipital height of the skull, which should be similarly affected, did not show such high loadings (Table 2). The third, fourth, fifth principal components and factors explained much less than 10% of the variability (Fig. 4B), so there is no indication that they are significant. There is no evidence of a component of shape in these data that cannot be explained simply by size or by post-mortem deformation.

It is interesting to compare our multivariate analysis with that performed by CoBabe (1996). In her factor analysis, the first factor loaded heavily on zygomatic arch thickness, nasal-facial vacuity length, and tooth row length. All of these variables load heavily on the first factor due to size, of course, but we did not find (Table 2) that the

zygomatic arch thickness or tooth row length stood out, as she did. Her second factor loaded heavily on orbital area, whereas ours loaded more heavily on nasal-facial vacuity length and orbital height, but not orbital length. Thus, the orbital area does not separate out in our analysis as it did for CoBabe (1996).

In short, if we wish to filter out the variability due to post-mortem deformation as much as possible, we will focus on the least variable measurements. Such measurements give us the potential to discriminate size differences more finely than do measurements that have additional non-biological variability due to distortion. Thus, most of the plots in this study that focus on size differences plot various tooth row variables, plus skull length; orbital dimensions are discussed below. In the discussions of systematic decisions below, we will rely on this analysis to discount characters that are prone to distortion.

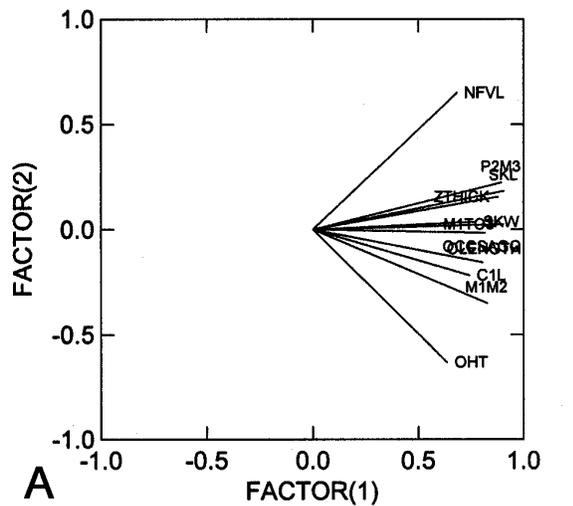
Variability Due to Sexual Dimorphism

Another possible source of the scatter in our data is sexual dimorphism. For hornless artiodactyls, the most obvious difference between the sexes is canine size, with males having larger canines, while there is little body size difference between males and females. Among living artiodactyls, this is especially noticeable in groups such as the camelids, suids, hippopotamids, and tayassuids, and also in the hornless ruminants such as cephalopids, tragulids and moschids (Janis, 1982; Nowak, 1991). Upper canine dimorphism (with little or no size dimorphism) has also been documented in extinct camels (Prothero, 1996) and in protoceratids (Patton and Taylor, 1971, 1973; Ludtke and Prothero, 2004). In a natural biological sample of West Texas peccaries, Stevens and Stevens (1996, Appendix A) found no significant differences in most size variables, despite the fact that male peccaries have much larger upper canines than do females.

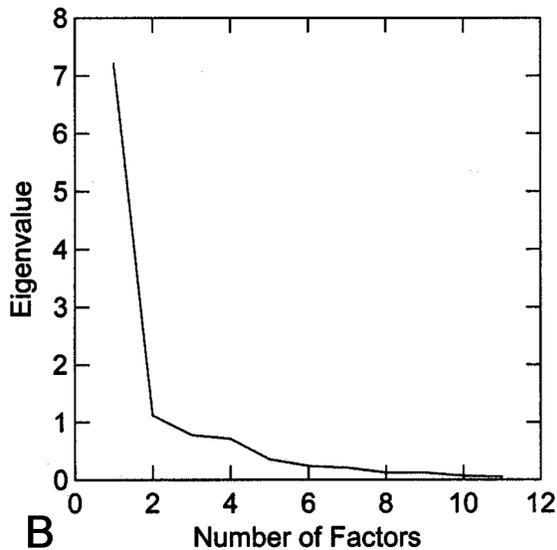
The sample of *Sespia* from the upper Oligocene (early Arikareean) Otay Formation of San Diego County, California, allowed Hoffman and Prothero (2004) to measure dozens of skulls and palates with well-preserved upper canines. This study showed that there were no statistically significant (as evaluated by t-tests) differences in size associated with large (presumed male) and small (presumed female) canines. Unfortunately, the sample of leptaucheniine (other than *Sespia*) skulls with well-preserved canines is much smaller than we expected. The early Whitneyan sample (Fig. 5A) only had 9 skulls, and the late Whitneyan sample (Fig. 5B) only contained 6 skulls that had both measurable upper canines and another useful proxy of body size (e.g., M1-3 length). Nonetheless, there are general trends that can be observed. There is no strong positive correlation between canine length and body size (as measured by M1-3 length), so canine size is not simply a function of increase in body size. Instead both plots show a number of skulls with shorter

TABLE 2. Component loadings of principal component analysis (PCA) of leptaucheniine skulls (see Figure 4). Measurements as in Figure 2 and Table 1.

CHARACTER	Component 1	Component 2
M1-2 length	0.827	-0.350
P2-M3 length	0.894	0.223
M1-3 length	0.902	0.025
C1 length	0.743	-0.218
Malar thickness	0.877	0.155
Orbital height	0.637	-0.631
Orbital length	0.815	-0.016
NFV length	0.682	0.648
Skull length	0.905	0.183
Skull width	0.772	0.036
Skull height	0.805	-0.157

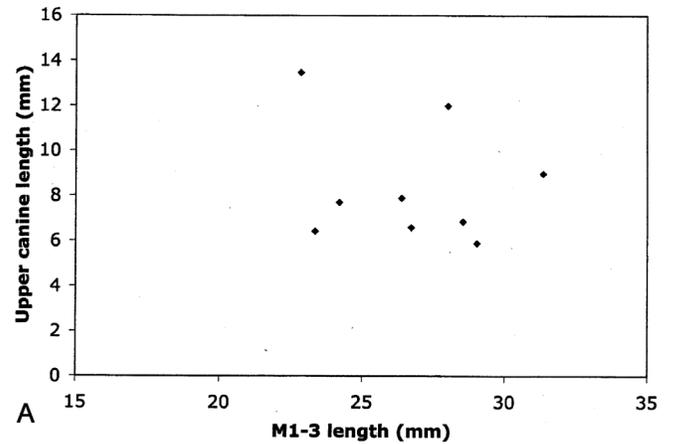


A

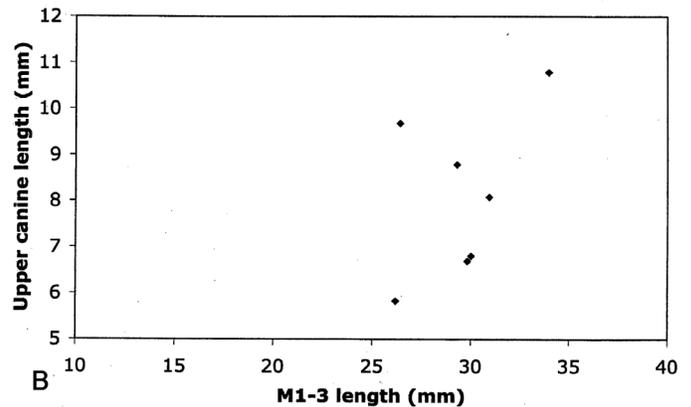


B

FIGURE 4. A, Factor loadings plot of the second PC, showing that the nasal-facial vacuity (NFVL) length and orbital height (OH) load most heavily on the second PC, probably because they are the most frequently distorted on most specimens. B, Scree plot of the loadings of each factor on the eigenvectors, showing that most of the variation is explained by the first PC, and some by the second PC, and the remaining PCs explain very little variability and are probably not significant.



A



B

FIGURE 5. Upper canine length (measured from base to tip) vs. M1-3 length in early Whitneyan (A) and late Whitneyan (B) samples of *L. decora*. Note that for the same range of body sizes (M1-3 length), there are both large and small (male and female) canines.

canines (between 6 and 8 mm long in the early Whitneyan sample; between 5 and 7 mm long in the late Whitneyan sample) that vary widely in body size; these might represent female individuals. There are also a few specimens (both larger and smaller in overall size) with much larger canines (greater than 8 mm in both samples); these are presumed to be male specimens. Unfortunately, the sample size is too small to statistically test this hypothesis, but it is consistent with the results of Hoffman and Prothero (2004), and apparent on visual inspection as well (Fig. 6).

Janis (1982; also in Lander, 1998) argued that some male leptaucheniine skulls had small bosses on the nasals that suggested they might have had horns. Hoffman and Prothero (2004) found no evidence of nasal horn bosses in *Sespia*, and we looked for the same characters in the American Museum sample of leptaucheniines. Instead, we found that the specimens which Janis thought had horn bosses (Fig. 7) are simply large, robust skulls that have been dorsoventrally crushed, so the nasal bone is broken along its suture with the maxillary and the narrow dorsal nasal process of the maxillary sticks up to resemble a "horn boss." This is to be expected, since the large nasal-facial vacuity is an area of weakness in the dorsal side of the skull, and any dorsoventral crushing will break the thin strut of bone along the nasal-premaxillary suture that supports the anterior rim of the vacuity. We found no evidence of a true rugose area for horn attachment, comparable to that found in rhinoceroses, and doubt that leptaucheniines had horns.

Population Variability and Species Limits

Once variation due to post-mortem distortion and sexual dimorphism has been assessed, we can look at the remaining variation and see whether it is within the expected limits of a single species, or too great for

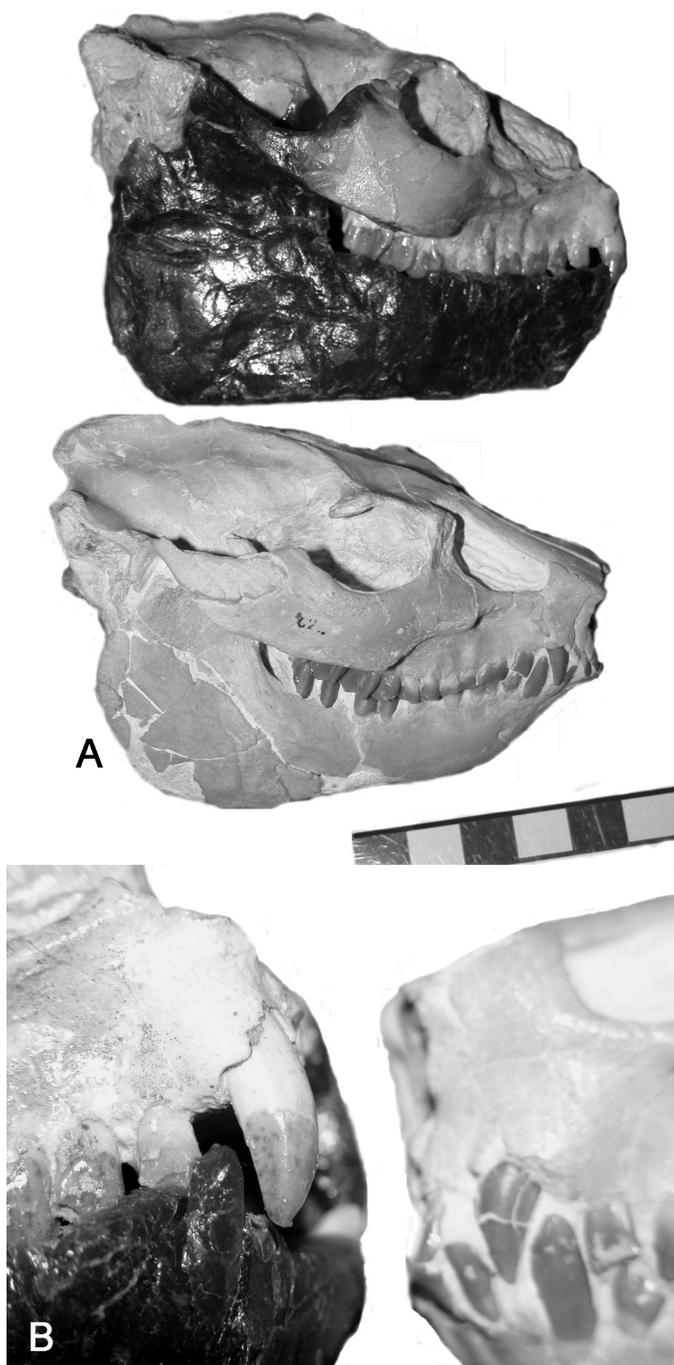


FIGURE 6. A, Specimens of presumed male (AMNH 622, top, with lower jaw reconstructed in dark wax) and female (AMNH 1328, bottom) *L. decora*, showing similar overall size. B, Close-up of the anterior dentition of the large upper canine specimen (presumed male) on left, and small upper canine specimen (presumed female) on right. Scale bar in cm.

one species. CoBabe (1996) lumped nearly all the specimens over 13 million years of the Whitneyan and Arikarean into just two species. *Leptauchenia decora* and *L. major*, without regard to their stratigraphic level. We have clustered the samples by stratigraphic level (most from a very limited stratigraphic interval in a few localities) to see if the variability in our fossil population samples is consistent with that of a single population, or requires more than one species, as measured by conventional statistics such as coefficient of variation.

The “rule of thumb” in mammalian systematics has long been that

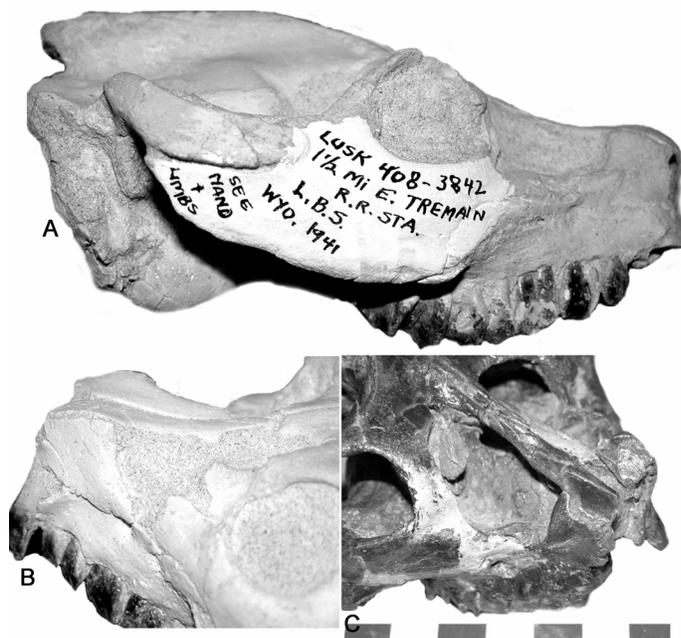


FIGURE 7. A-B, Close-up of a *L. major* skull (Lusk 408-3842) showing the buckling of the nasal-premaxillary suture due to dorsoventral crushing, giving the appearance of “horns” in lateral views. C, Close-up of AMNH 8115, type specimen of “*Cyclopidius emydidianus*”, showing the “nasal horn bosses.” As can be seen, the specimen is dorsoventrally crushed, and the anterodorsal process of the premaxillary has been broken upward and separated from the nasal bones, giving the false impression of a “horn boss.”

living mammal populations rarely show CV values in excess of 10 for most common variables that are not strongly sexually dimorphic (Kurtén, 1953; Simpson et al., 1960; Yablokov, 1974). For samples of living peccaries (among the closest living relatives to oreodonts, other than camels), Stevens and Stevens (1996, table 1 and appendix A) found only one CV (malar depth) that approached 10, and most were less than 5. Stevens and Stevens (1996, table 1) looked at merycoidodont and miniochoere samples from limited stratigraphic horizons, and found that most variables had CVs much less than 10, except for a few skull variables that were susceptible to crushing. Phleger and Putnam (1942) and Bader (1955) found similar results of their calculations of CVs in oreodonts.

Within our own data, the coefficients of variation of the entire pooled Whitneyan and Arikarean sample (Table 1) are clearly too large to belong to a single natural population. Values of CV range from 12.35 for orbit length to 27.06 for upper canine length, and most values are between 15 and 26. If the biological criteria mentioned above are valid, this sample of skulls cannot belong to a single species, and probably not even two species, as suggested by CoBabe (1996). Put another way, the skull lengths of these specimens range from as small as 80 mm to as large as 177 mm, more than a two-fold size increase (equivalent to about 20 to 40 kg in body weight). If there were evidence of sexual dimorphism, such a huge range of sizes might be accommodated into one species. As we have just outlined, however, there is only a slight range of sizes in samples at restricted stratigraphic levels, and no evidence that males are larger than females. Thus, a two-fold size increase seems too large to attribute to one species, or probably even two.

The next step is to examine samples taken from restricted stratigraphic horizons, which, in the absence of quarry samples, is our best proxy for a natural population sample. For example, the CVs of 24 well-preserved specimens from the early Whitneyan (primarily the lower Poleslide Member of the Brule Formation in the Big Badlands of South Dakota) are much more reasonable, with most values being under 10, and all of them under 14; only the CV of the upper canine (28.9) is large, and

(as discussed above) this is probably due to sexual dimorphism. Thus, the CVs of the early Whitneyan sample are comparable to those observed by Stevens and Stevens (1996, table 1) and Bader (1955) for merycoidodontine samples from limited stratigraphic horizons in the same deposits, and this sample is one of our best candidates for a likely biological sample. On the other hand, the late Whitneyan sample of 23 well-preserved skulls (almost all from the upper Poleslide Member "Leptauchenia beds" of the Big Badlands of South Dakota) yields CV values that are almost all larger than 10 (mostly between 11 and 18), suggesting that this sample is composed of more than one species.

Bivariate plots of these same specimens (Fig. 8) confirm these interpretations. The early Whitneyan specimens tend to form a smaller, more tightly confined cluster (especially apparent in Figs. 8A and 8B) in which the P2-M3 length does not exceed 50 mm, the M1-2 length is less than 22 mm, the M1-3 length is shorter than 34 mm, and the skull length is less than 105 mm. This cluster is referred to *Leptauchenia decora* in the discussion that follows. By the late Whitneyan, there are not only many specimens of this smaller size, but also a number of much larger specimens, suggesting a new, larger species (here referred to *L. major*) has been added to the sample (Fig. 8). By size criteria, this larger species might be characterized by having P2-M3 lengths between 51 and 62 mm, M1-3 lengths between 34 and 42 mm, M1-2 lengths between 22 and 29 mm, and skull lengths between 105 and 125 mm. The taxonomy of Schultz and Falkenbach (1968) would recognize as many as four different genera and four species in the late Whitneyan, but there is no evidence from the size data to support more than two genera with a single species each.

Similar reasoning can be applied to the Arikareean specimens (Fig. 9). The early Arikareean sample is much larger (43 well-preserved skulls), and mostly derived from the Gering Formation equivalent at Little Muddy Creek, Goshen County, Wyoming (Schultz and Falkenbach, 1968). The CV of this sample is again very large, ranging from 11 to as high as 28, so it appears that at least two species must be present. Most of the specimens are in the same size range (P2-M3 length = 51-62 mm, M1-3 lengths = 34-44 mm, M1-2 lengths = 22-27 mm, and skull lengths = 105-125 mm) as the late Whitneyan cluster we identified as *Leptauchenia major*, and, on size alone, that would be the only reasonable assignment. However, during the early Arikareean (but not the late Arikareean) there was a cluster of much larger specimens (P2-M3 length = 62-71 mm, M1-3 lengths = 42-48 mm, M1-2 lengths = 27-35 mm, and skull lengths = 125-185 mm) that are distinct and non-overlapping with any other Arikareean assemblage, and appear to die out by the late Arikareean; these are referred to *L. lullianus* below. Thus, the simplest interpretation is that there are two species in the early Arikareean, *L. major* and the larger *L. lullianus*, and the smaller *L. decora* is rare.

By the late Arikareean, the CV values on most variables are again close to 10, suggesting that only a single species population may be present. This sample is still within the size range (P2-M3 length = 51-62 mm, M1-3 lengths = 34-44 mm, M1-2 lengths = 22-27 mm, and skull lengths = 105-125 mm) we recognize as *L. major*. We interpret this pattern to mean that most of the specimens are *L. major*. In Figure 9, it appears that *L. lullianus* has died out, but there are actually a few poor specimens of *L. lullianus* (called "*Pseudocyclopidius lullianus expiratus*" by Schultz and Falkenbach, 1968) that could not be measured and included in the plots. These specimens establish the persistence of *L. lullianus* into the Monroe Creek Formation, before the entire group vanishes in the late Arikareean.

Dealing with the boundaries between fossil species is typically a complicated problem that seldom gives simple, unambiguous solutions, especially when the sample size is this large and so strongly affected by factors such as post-mortem distortion. Nonetheless, using the most reasonable biological criteria available to us, this solution seems most parsimonious and best supported by the quantitative data. The systematic treatments below reflect the analyses we have just discussed.

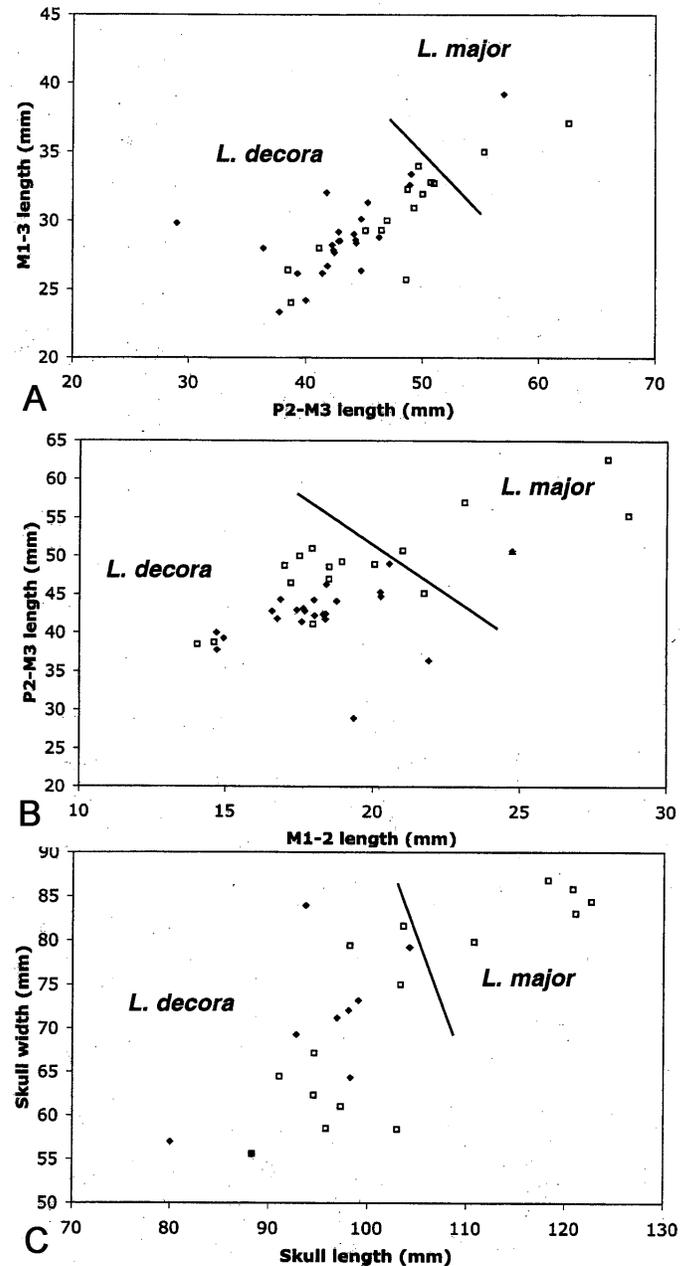


FIGURE 8. A-C, Bivariate plots of dimensions of *Leptauchenia* specimens from the early Whitneyan (solid diamonds) and late Whitneyan (open squares).

Variations in Orbital Area

CoBabe (1996) argued that *Leptauchenia decora* and *L. major* could be distinguished by the area of the orbit, overall body size, and auditory bulla volume. We addressed the final two characteristics earlier, but it is worth examining the issue of orbital area as a taxonomic character. CoBabe's (1996, fig. 4) plot of orbital area versus M1 area only weakly discriminates the two groupings, and her plot (CoBabe, 1996, fig. 2) of factor loadings even more weakly separates specimens with larger orbital areas (large second factor loadings) from those without. Visual inspection of specimens suggests that orbital area simply scales up with larger skulls, except in cases where crushing has distorted the orbit. We saw no evidence visually that the orbits of bigger leptaucheniine skulls were much larger than would be expected from scaling for increased size.

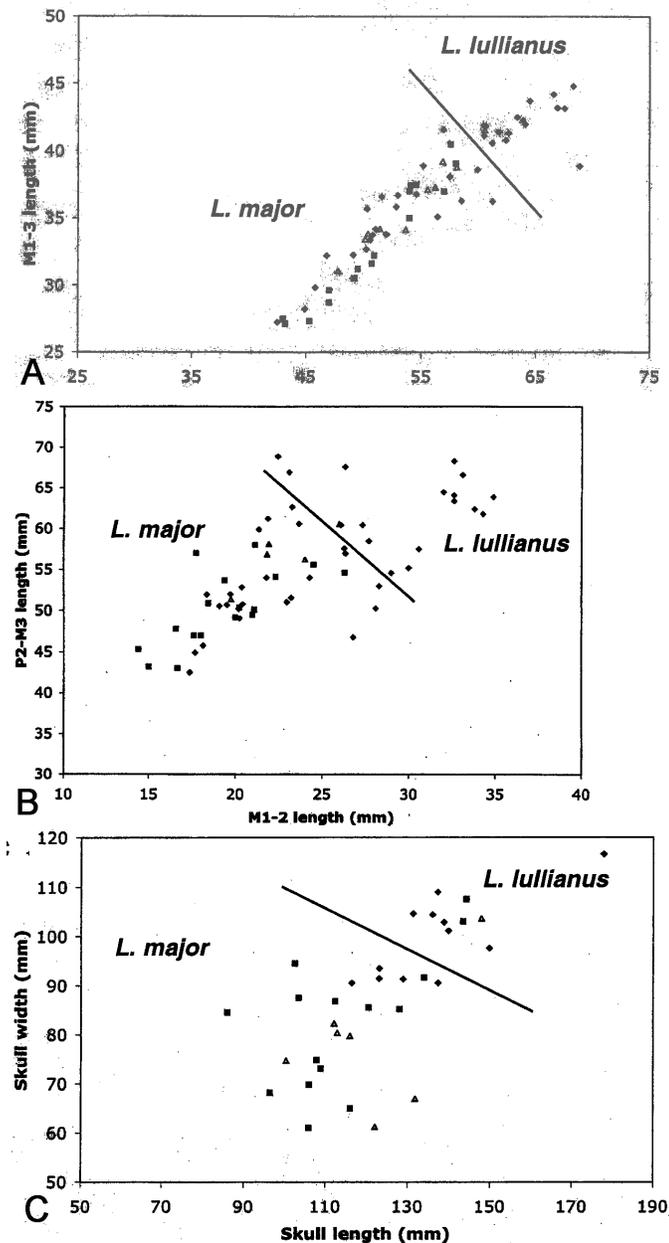


FIGURE 9. A-C, Bivariate plots of dimensions of *Leptauchenia* specimens from the early Arikareean (solid diamonds), middle Arikareean (solid squares), and late Arikareean (open triangles).

To evaluate this hypothesis, we did both bivariate and multivariate analyses. As discussed above, our multivariate analyses did not obtain the same result as did hers, and showed no heavy loadings on orbital area in the second PC or second factor. In a simpler bivariate analysis, we computed the orbital area (by multiplying orbital height by orbital length) for the sample from the Whitneyan, and plotted it against one of the least variable and most commonly available size proxies, M1-3 length. The results are striking (Fig. 10). Except for one extreme outlier that probably represents a highly distorted specimen, the early Whitneyan sample (which we argued above represents just one species, *L. decora*) has a wide range of orbital areas (300-400 square mm). The late Whitneyan sample (which we argued above contains two species, *L. decora* and *L. major*) has many specimens with longer M1-3 lengths (which would be *L. major*) as well as some within the M1-3 range of *L. decora*. Yet both the larger and smaller specimens show the full range of orbital area values. In fact, a number of the large *L. major* specimens of the late

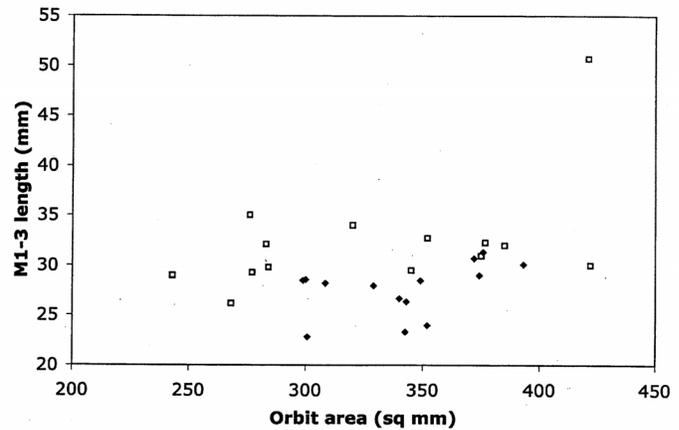


FIGURE 10. Comparison of orbital area between early Whitneyan specimens (solid diamonds) and late Whitneyan specimens (open squares). Both the early Whitneyan population (all *L. decora*, smaller in size), and the late Whitneyan population (*L. decora* plus *L. major*, slightly larger in size) have a similar large range of orbital areas. Orbital area does not systematically increase through time, as suggested by CoBabe (1996), but remains highly variable.

Whitneyan have orbital values that are smaller than any early Whitneyan *L. decora* (Fig. 10). Clearly, there is no clear distinction in orbital area between *L. decora* and *L. major*. In fact, there is no obvious trend in larger orbital area for larger skulls, which is the more conservative prediction. Instead, it appears that orbital area is highly variable and not a good predictor of other variables, and thus probably not a good taxonomic character as well. This is surprising, given that the values of orbital height and length have some of the lowest coefficients of variation in this study (Table 1), so it would be expected that they should be less variable, and would not be distorted due to crushing.

SYSTEMATIC PALEONTOLOGY

Order Artiodactyla Owen, 1848

Family Merycoidontidae (Leidy, 1848)

Subfamily Leptaucheninae Schultz & Falkenbach, 1940

Leptauchenia Leidy, 1856a

Leptauchenia Leidy, 1856a:88

Pitheciastes Cope, 1878:219

Brachymeryx Cope, 1878:220

Cyclopidus Cope, 1878:221

Leptauchenia Thorpe, 1921:410 (in part)

Cyclopidius (*Chelonocephalus*) Thorpe, 1921:410

Cyclopidius (*Pitheciastes*) Loomis, 1925:248 (in part)

Cyclopidus Schlaikjer, 1935:161 (in part)

Hadroleptauchenia Schultz and Falkenbach, 1968:323

Pseudocyclopidius Schultz and Falkenbach, 1968:303

Type species: *Leptauchenia decora* Leidy, 1856

Included species: *L. major* Leidy, 1856b, and *L. lullianus* (Thorpe, 1921)

Distribution: Late Orellan to late Arikareean, High Plains (primarily Wyoming, South Dakota, Nebraska), and western Montana.

Revised diagnosis: (modified from CoBabe, 1996, and Lander, 1998) Small to moderate-sized oreodonts with a greatly enlarged pair of nasal-facial vacuities enclosed by the nasal, frontal, premaxillary, and maxillary bones; fan-shaped occipital region; orbit elevated high on the skull; inflated auditory bullae; external auditory meatus tube long, large, elevated and posteriorly directed; deep zygomatic arch and malar bone; teeth hypsodont to extremely hypsodont, with thin occlusal enamel. I1 reduced or absent; P1-3 anteriorly shortened, nearly square, with central

fossette; M1-3 lingual selenes rounded, closely appressed, broadly continuous, forming a single crest extending toward the mesostyle, and offset posteriorly relative to labial selenes. Differs from *Sespia* in having a larger body size, wider and thicker zygomatic arch (malar bone) than *Sespia*, and teeth which are not as hypsodont, but have more prominent styles on M1-3 and stylids on m1-3.

Discussion: Leidy (1856) erected the genus *Leptauchenia* based on a number of specimens collected by F.V. Hayden in 1855 from “the valley of the White River, Nebraska [now considered to be Big Badlands of South Dakota] consisting of fragments of upper and lower jaws with teeth”. He did not designate a type specimen, so Schultz and Falkenbach (1968, p. 278) designated ANSP 10878, a partial right maxilla with P4-M3, as the lectotype (Fig. 11A-B). Leidy recognized that the hypsodont dentition resembled that of a camelid (*Auchenia* was the old generic name for the llama, now genus *Lama*), but that it was tinier and more slender (“leptos” in Greek). Leidy (1869) illustrated a partial skull and mandible, ANSP 10765, further illuminating the peculiar anatomy of *Leptauchenia*.

Cope (1878) named the genus *Cyclopidius* for large “Miocene” (mostly late Oligocene) leptaucheniines with only two incisors from the early Arikareean “Deep River beds” of Meagher County, Montana. (These deposits are now known as the Fort Logan Formation of Koerner, 1940, according to Tedford et al., 2004). Schultz and Falkenbach (1968, p. 296) pointed out that there is no evidence of only two lower incisors in any leptaucheniine, including the material Cope referred to *Cyclopidius*. Many of the Arikareean leptaucheniines have only two upper incisors, but this is highly variable, and also independently occurs in the *Sespia* lineage. In practical terms, the incisors are rarely preserved in most specimens, so it is difficult to use this criterion for diagnosis, even if it were consistent. Schultz and Falkenbach (1968, p. 296) restricted the concept of *Cyclopidius* to early Arikareean forms from Montana that were smaller in size and more gracile than contemporary Great Plains forms.

On the previous page in the same paper, Cope (1878) erected the taxon *Brachymeryx feliceps* based on a partial skull with a canine and dP2-M2 (AMNH 8126), mistaking the milk dentition for adult teeth. In 1884 Cope recognized his mistake, and synonymized this taxon with *Cyclopidius*. That synonymy was followed by Thorpe (1937, p. 241) and Schultz and Falkenbach (1968, p. 298).

Cope (1878) named yet another leptaucheniine, *Pithecistes brevifacies*, based on a partial mandible (AMNH 8129, Fig. 11C-D) from the same Arikareean deposits (Fort Logan Formation of Koerner, 1940) in Meagher County, Montana, that yielded *Cyclopidius* and *Brachymeryx*. Cope based *Pithecistes* on material that he thought had only one lower incisor on each side, a non-incisiform lower canine, and no p1. Matthew (1899) showed that there are actually alveoli for three incisors on each side, that the canine (mistaken for an incisor by Cope) is worn to a stump, and that the p1 (mistaken for the canine) is present and caniniform in shape. Matthew (1899) regarded *Pithecistes* as a junior synonym of *Cyclopidius*, as did Schlaikjer (1935) and Thorpe (1937). Schultz and Falkenbach (1968, p. 259), however, resurrected this genus for specimens with a short face and many features due to lateral crushing, and added four additional species to the taxon, based on additional specimens from the High Plains.

Thorpe (1921) named a new subgenus of *Cyclopidius*, *Chelonocephalus*, based on a skull (YPM 10123) with extreme shortening of the basicranial region and muzzle, proportionally larger bullae, and deeper intrusion of the nasal-facial vacuity into the frontals. It was supposedly from the “Sheep Creek beds” (late Hemingfordian) of Hermosa, South Dakota, which would make it far younger than any other leptaucheniine (which died out in the late Arikareean). Loomis (1925) regarded this specimen as simply an extreme form of *Cyclopidius*. Schultz and Falkenbach (1968, p. 278, 281) regarded YPM 10123 as simply an unusually brachycephalic example of Whitneyan *Leptauchenia decora*. They cited work by Morris Skinner to show that there were no “Sheep Creek beds” near Hermosa, South Dakota, but there were late Whitneyan deposits. Apparently, Thorpe’s (1921, 1937) mistaken idea

that the specimen was from the Hemingfordian fooled him into believing it was different from typical Whitneyan forms.

Schultz and Falkenbach (1968, p. 303) erected the genus *Hadroleptauchenia* for specimens that were larger than contemporary *Leptauchenia* but smaller than *Pseudocyclopidius* from the same deposits. They performed no statistical analysis to support this three-fold split of contemporary oreodont samples by size classes, and cited very few other characters to distinguish the three genera. It is interesting that they mention that all three genera undergo parallel evolution in the development of various characters, which should have been a clear indicator that the genus was oversplit. In this regard, their thinking resembles that of Osborn, who viewed his grossly oversplit taxa as evolving in multiple contemporary but unrelated lineages with extensive parallel evolution (Rainger, 1991).

Schultz and Falkenbach (1968, p. 323) named yet another new genus, *Pseudocyclopidius* for the largest, most robust skulls from a given level in the Orellan, Whitneyan, or Arikareean. Most of the characters they used to define this genus are simply related to the greater size of the skulls compared to *Hadroleptauchenia* or *Leptauchenia*, or to the greater robustness of the skull. As in the case of *Hadroleptauchenia*, no statistics were performed to justify the separation of the three genera.

Lander (1998) and CoBabe (1996) rejected all of these genera and subgenera except *Leptauchenia*, although they did not provide adequate justification or discussion of this synonymy.

Leptauchenia decora Leidy, 1856

Figures 1, 11-13; Table 3

- Pithecistes brevifacies* Cope, 1878: 219
Pithecistes decedens Cope, 1884:558
Cyclopidius decedens Matthew, 1899:73
Cyclopidius (Chelonocephalus) schucherti Thorpe, 1921: 415
Pithecistes breviceps [sic] Loomis, 1925:248
Leptauchenia minora Schlaikjer, 1935: 119.
Cyclopidius loganensis Koerner, 1940:856
Pithecistes tanneri Schultz and Falkenbach, 1968: 261
Pithecistes mariae Schultz and Falkenbach, 1968: 264
Pithecistes atageringensis Schultz and Falkenbach, 1968:265
Pithecistes copei Schultz and Falkenbach, 1968: 269
Leptauchenia harveyi Schultz and Falkenbach, 1968: 276
Leptauchenia martini Schultz and Falkenbach, 1968: 288
Leptauchenia parasimus Schultz and Falkenbach, 1968: 291
Hadroleptauchenia eiseleyi Schultz and Falkenbach, 1968: 306
Hadroleptauchenia primitiva Schultz and Falkenbach, 1968:307
Pseudocyclopidius orellaensis Schultz and Falkenbach, 1968: 327
Leptauchenia eiseleyi eiseleyi Lander, 1998
Leptauchenia eiseleyi orellanensis Lander, 1998
Leptauchenia major schucherti Lander, 1998

Lectotype: ANSP 10878, a partial right maxilla with P4-M3. Precise locality data are unknown, but Schultz and Falkenbach (1968) argue that it is from the upper Whitneyan “*Leptauchenia* beds” (their “Zone D”) of the Big Badlands of South Dakota.

Hypodigm: Materials listed in Schultz and Falkenbach (1968) under the above synonyms.

Distribution: Early Orellan to earliest Arikareean, High Plains and western Montana.

Diagnosis: Relatively small leptaucheniines (P2-M3 length = 30-50 mm; M1-2 length = 14-22 mm; M1-3 length = 21-34 mm; skull length = 80-105 mm) with less robust zygomatic arches and smaller orbits; teeth subhypsodont to hypsodont; styles on M1-3 and stylids on m1-3 well developed.

Description: A full description was given by Scott (1940) and Schultz and Falkenbach (1968), so no further detail is required here.

Discussion: As discussed above, there seems to be a single homogeneous cluster of morphologies in the early Whitneyan (Fig. 8), with

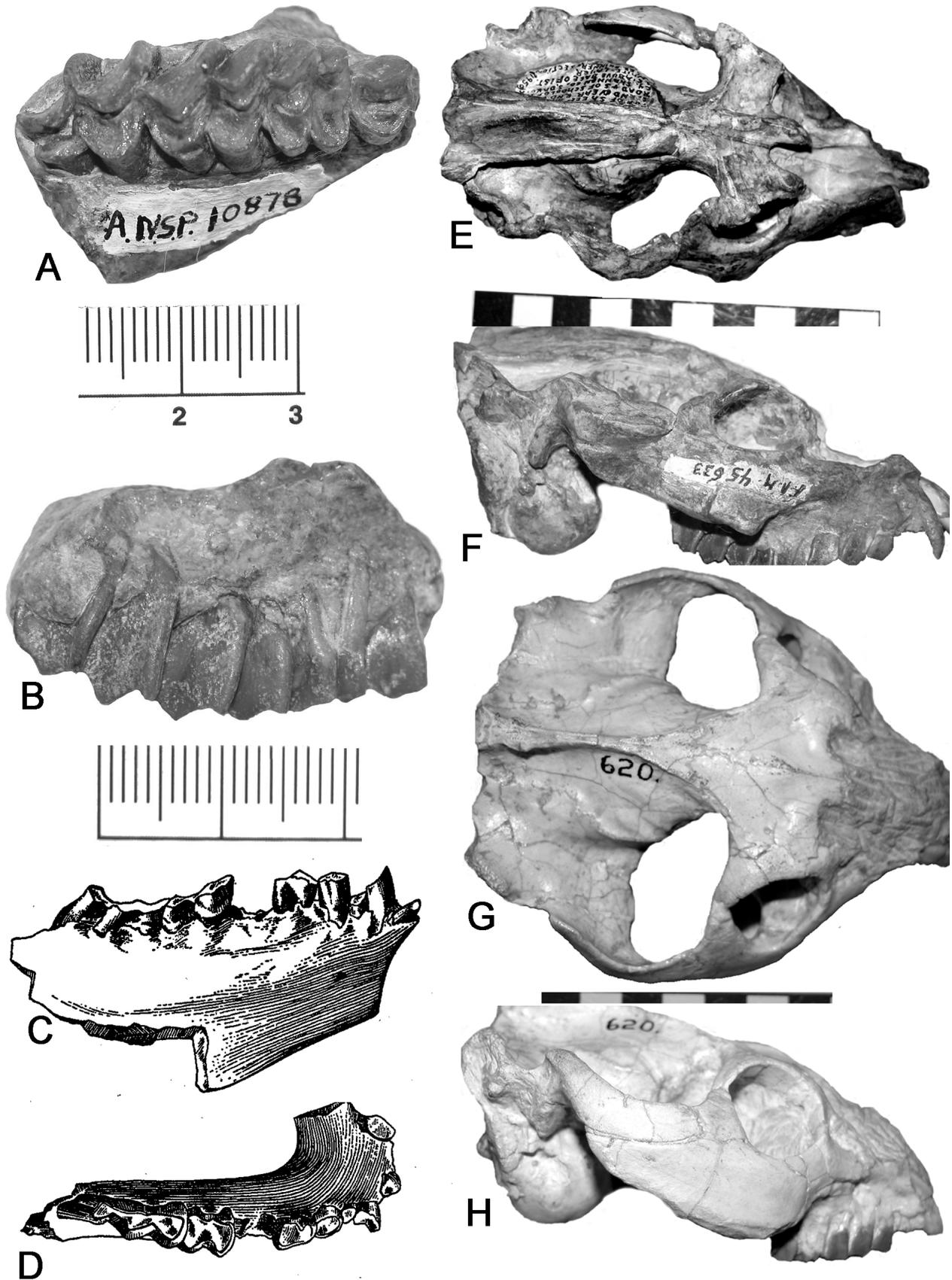


FIGURE 11. Specimens referred to *L. decora*. A-B, Type specimen of *L. decora*, ANSP 10878. C-D, Type specimen of "*Cyclopidius brevifacies*" (AMNH 8129) (after Cope, 1888). E-F, Type specimen of "*Pitheciestes mariae*" (F:AM 45633) in dorsal and right lateral views. (See also Fig. 3C-D). G-H, Type specimen of *Leptauchenia "harveyi"* (AMNH 620) in dorsal and right lateral views. Scale bar in cm.

size variables that have no CV greater than 10, and we feel that this is strong evidence of a single early Whitneyan species, which would bear the name *Leptauchenia decora*. Specimens of this size and morphology continue into the late Whitneyan and the earliest Arikareean. In addition, the relatively poorly preserved Orellan specimens (discussed below) fall within this size range, and so are synonymized with *Leptauchenia decora*.

Having set reasonable diagnoses and size limits on *Leptauchenia decora* based on the total sample, we must review the various type materials of the taxa we regard as invalid, and justify their synonymy. *Pithecistes brevifacies* was named by Cope (1878) based on a broken mandible (AMNH 8129; Fig. 11C-D) from the early Arikareean Fort Logan Formation of Meagher County, Montana. In 1888, Cope mentioned it as *Pithecistes facies*, a *lapsus calami*. As discussed above, Matthew (1899) corrected the mistakes that Cope made in identifying teeth and alveoli, and regarded *Pithecistes brevifacies* as a synonym of *Cyclopidius simus*. Schlaikjer (1935) referred *Pithecistes brevifacies* to *Cyclopidius brevifacies*, and Loomis (1925) incorrectly called it *Pithecistes breviceps*. Schultz and Falkenbach (1968, p. 268) retained *Pithecistes brevifacies* as a valid taxon, but their only diagnostic features were the short and narrow facial region and a few other characters that can be attributed to deformation. Other than Koerner's (1940) *Cyclopidius loganensis* (which Schultz and Falkenbach, 1968, p. 268, showed was a junior synonym of *Pithecistes brevifacies*), and one additional Cope specimen (AMNH 8119), no additional material has been found that can be attributed to this species. Nevertheless, it appears to fall entirely within the size range of *Leptauchenia decora*. Nor is the "short face" that diagnostic. Comparison with many other *L. decora* mandibles (see figures 32, 33, and 34 in Schultz and Falkenbach, 1968) shows that the symphysis is only slightly more upturned and elevated than other similar specimens. Given that there are only a total of three specimens known, it is far more likely that this taxon is based on older individuals with slightly shorter jaws, possibly as a result of age or pathology.

Cope (1884) named *Pithecistes decedens*, also from the Arikareean Fort Logan Formation of Montana, based on a maxilla (AMNH 8130) with a dP3-M1, and most of its "diagnostic" characters are based on the deciduous dentition. Matthew (1899) regarded this specimen as a juvenile *Cyclopidius*, and Loomis (1925) synonymized it with *C. simus*. However, comparison of the type specimen shows that it is within the size range of *Leptauchenia decora*, not "*Cyclopidius simus*" (= *L. major*).

As discussed above, *Cyclopidius (Chelonocephalus) schucherti* (Thorpe, 1921) was based on a badly preserved skull that was named as a new taxon because it was erroneously attributed to the Hemingfordian "Sheep Creek" beds near Hermosa, South Dakota. Schultz and Falkenbach (1968, p. 278, 281) argued that it is actually Whitneyan in age, and should be referred to *Leptauchenia decora*.

Schlaikjer (1935) named a new species, *Leptauchenia minor*, based on a juvenile palate with I3, dP2-4, and M1-2 (MCZ 2841), from the "lower Miocene" (probably early Arikareean) of Goshen County, Wyoming. Thorpe (1937, p. 239) argued that the specimen was not valid, because it was largely based on juvenile characters, but that it was probably a synonym of *Leptauchenia decora*. Schultz and Falkenbach (1968) and Lander (1977, 1998) assigned *Leptauchenia minor* to *Sespia nitida*, but we found that it is too large for *Sespia*, and its morphology is more like that of *L. decora*.

Following Cope's concept of *Pithecistes* as a small leptaucheniine with a slightly shorter, narrower face and more gracile features, Schultz and Falkenbach (1968) named four additional species of *Pithecistes*, each distinguished primarily by its stratigraphic level and little else. *P. tanneri* was based on specimens from the late Whitneyan of South Dakota and Nebraska. The type specimen (UNSM 28451) is at the smaller end of the size range (Fig. 12) of *L. decora* (see Schultz and Falkenbach, 1968, table 11), and a side-by-side comparison of referred specimens (see Schultz and Falkenbach, 1968, figures 32 and 33) shows that the taxon is based on specimens that happen to be smaller and more gracile than

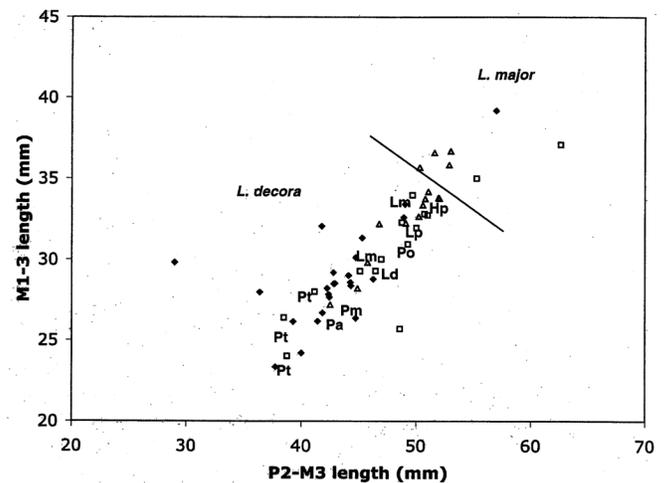


FIGURE 12. Plot of M1-3 length vs. P2-M3 length for specimens of *Leptauchenia*, showing the clusters referred to *L. decora* and *L. major*. Early Whitneyan = solid diamonds; late Whitneyan = open squares; early Arikareean = open triangles. Symbols for type or referred specimens as follows: Hp = type of "*Hadroleptauchenia primitiva*"; Ld = type of *L. decora*; Lm = type and referred skull of *L. "martini"*; Lp = type of *L. "parasimus"*; Pa = type of "*Pithecistes altageringensis*"; Pm = type of "*Pithecistes mariae*"; Po = type of "*Pseudocyclopidius orellaensis*"; Pt = type and referred skulls of "*Pithecistes tanneri*."

typical *L. decora*, and (in many cases) look "narrow" because they are laterally crushed. The upturned symphysis is also invalid as a generic character, because comparison between specimens from the late Whitneyan *L. decora* sample shows that this feature is highly variable (and also susceptible to post-mortem deformation).

Pithecistes mariae (Figs. 3C-D, 11E-F) was based on specimens from the earliest Arikareean lower Gering Formation in Nebraska, and lower Sharps Formation in South Dakota, and was supposedly larger, more robust, and more hypsodont than *P. tanneri* (Schultz and Falkenbach, 1968, p. 264). Although it may be slightly larger than *P. tanneri*, all of its measurements fall within the range of *L. decora* (Fig. 12; see also Schultz and Falkenbach, 1968, table 11), and all of the "diagnostic features" can be seen on specimens of *L. decora* as well. Most of the specimens show extensive dorsoventral crushing (especially the type specimen), which accounts for the differences in shape. The "shortening" of the premolar row and face relative to the total tooth row length is completely within the small end of the typical range of variation of leptaucheniines (Fig. 12).

Pithecistes altageringensis was based on specimens from the upper Gering Formation in Nebraska and Wyoming (as the name implies) and upper Sharps Formation in South Dakota (a unit that Schultz and Falkenbach, 1968, and Schultz and Stout, 1961, refused to recognize). Although *P. altageringensis* is supposedly larger and more robust than *P. mariae*, in reality all of its measurements overlap those of *P. mariae* and *L. decora* (Fig. 12; see also Schultz and Falkenbach, 1968, table 11), and in side-by-side comparison, the typical material of *P. altageringensis* is actually smaller than that of *P. mariae*. The shortened face, as mentioned above, is also highly variable within leptaucheniines, and not diagnostic. This is a clear-cut example of two samples that are indistinguishable, but since they come from lower and upper parts of the "Geringian" (which Schultz and Falkenbach, 1968, thought spanned a long period of time), they were named different species, and never compared with Whitneyan *L. decora*.

Schultz and Falkenbach (1968, p. 273) also finely subdivided the *Leptauchenia* lineage, restricting *L. decora* to specimens from the late Whitneyan. They separated out the early Whitneyan samples (Fig. 11G-H) as a new species, *Leptauchenia harveyi* (Schultz and Falkenbach, 1968, p. 276), based on their supposedly smaller and more gracile ap-

pearance than *L. decora*, but as shown in Figure 12 (and also apparent in Schultz and Falkenbach, 1968, table 12), its measurements fall entirely within the homogeneous range of variation of early Whitneyan leptaucheniines. As argued above, these data only support the hypothesis of one species, based on coefficients of variation.

Leptauchenia martini (Schultz and Falkenbach, 1968, p. 288) was erected for specimens (Fig. 13A-B) from the lower Gering Formation and equivalents, but as Schultz and Falkenbach (1968, p. 288) confess in the diagnosis, it is “within the size range of that of *Leptauchenia decora*,” and this is borne out by our own data (Fig. 12; see also Schultz and Falkenbach, 1968, table 12). The only other “diagnostic” property is that the skull is supposedly “more depressed,” but examination of the material shows that this is clearly due to dorsoventral crushing (Fig. 13B). This is yet another example of perfectly good specimens of *Leptauchenia decora* being given another name because they came from a different formation, even though the diagnosis itself reveals that almost nothing distinguishes the two species.

Likewise, *Leptauchenia parasimus* (Schultz and Falkenbach, 1968, p. 291) was distinguished from *L. martini* primarily by its occurrence within the upper Gering Formation and equivalents. It is supposedly slightly larger (Fig. 13C-D) and more robust than *L. martini*, but again this falls entirely within the normal range of variation of early Arikareean *L. decora* (Fig. 12; see also Schultz and Falkenbach, 1968, Table 12).

Hadroleptauchenia primitiva (Schultz and Falkenbach, 1968, p. 308) was based on specimens (Fig. 13E-G) from the upper Whitneyan that are slightly larger than most examples of *L. decora*, but fall within the upper part of its range of variation (Fig. 12). Contrary to the assertions of Schultz and Falkenbach (1968, p. 308), the premolars are not measurably shorter than those of *L. decora*. The “short muzzle,” “oblong orbits,” and most of the features that they considered diagnostic are simply due to the fact that the type specimen (F:AM 45577) and most of the referred skulls are badly crushed dorsoventrally.

Although leptaucheniines are extremely rare in the Orellan compared to the hundreds of merycoidodontines, a total of six specimens have been found. Consistent with their other practices, Schultz and Falkenbach (1968) placed this handful of specimens into two different taxa, and did not adequately compare them with Whitneyan forms. As discussed above, Schultz and Falkenbach (1968, p. 303) erected the genus *Hadroleptauchenia* for specimens that were intermediate in size between typical *Leptauchenia* and *Pseudocyclopidius*. They named the species *Hadroleptauchenia eiseleyi* based on a fragmentary maxilla (UNSM 28208) and an additional maxilla and left ramal fragment from the early Orellan deposits 6 miles east of Lyman in Scottsbluff County, Nebraska. Although this material is very incomplete, the size (e.g., M1-3 length = 28.5 mm) is actually within the larger end of the range of *Leptauchenia decora*, yet this material was never compared to Whitneyan specimens. Visual inspection of the type material shows that there are no features that can be used to distinguish it from *L. decora*, and indeed, Schultz and Falkenbach (1968, p. 306) cite no “diagnostic features” except size and stratigraphic level.

The other Orellan material was referred to *Pseudocyclopidius*, because the skulls were larger and more robust than most others of the same formation, and their dorsoventral crushing exaggerated these proportions. Three specimens (Fig. 13E-G) from the early Orellan deposits of Douglas, Wyoming (Evanoff et al., 1992) were referred to their new species, *Pseudocyclopidius orellaensis* (Schultz and Falkenbach, 1968, p. 328). The type skull (F:AM 45528) is juvenile and probably also a female specimen. Only two additional specimens, a partial skull (F:AM 45637) and a left ramus (UNSM 28230) are known. Nonetheless, comparison of the measurements (see Schultz and Falkenbach, 1968, table 14) shows that the available dimensions are completely within the size range of *L. decora* (Fig. 12). *P. orellaensis* was never compared with other Orellan specimens such as *Hadroleptauchenia eiseleyi*, let alone Whitneyan taxa such as *L. decora*, but only with its supposed descendant, *Pseudocyclopidius major* (here referred to *Leptauchenia major*). Naturally, it is smaller and more gracile than that species.

TABLE 3. Statistics of *Leptauchenia* species analyzed in this study (mm). Abbreviations as in Table 1.

CHARACTER	<i>L. decora</i>			<i>L. major</i>			<i>L. lullianus</i>		
	M	SD	CV	M	SD	CV	M	SD	CV
M1-2 length	18.4	2.4	13.0	22.2	3.5	15.6	28.8	4.2	14.4
P2-M3 length	42.8	2.3	6.9	54.1	4.1	7.5	60.6	5.9	9.7
M1-3 length	27.9	2.5	8.9	36.9	4.0	10.9	39.8	3.2	8.1
C1 length	8.5	2.5	28.9	10.2	1.1	10.6	10.5	3.0	28.9
Malar thickness	13.7	1.9	14.1	22.8	4.9	21.5	23.6	3.5	15.0
Orbital height	18.1	1.3	7.4	17.6	3.2	17.9	18.4	3.2	17.6
Orbital length	19.0	1.4	7.3	22.2	2.1	9.5	22.9	2.4	10.4
NFV length	24.1	3.6	14.7	33.3	4.3	13.0	40.0	3.6	9.0
Skull length	96.3	7.2	7.5	120.9	13.5	11.1	136.2	16.1	11.9
Skull width	71.3	8.3	11.7	78.4	13.5	17.3	41.4	5.4	13.1
Skull height	32.4	5.3	16.4	41.2	6.5	15.8	28.8	4.2	14.4

Leptauchenia major Leidy, 1856b

Figures 14-16; Table 3

Cyclopidius simus Cope, 1878:211
Brachymeryx feliceps Cope, 1878:220
Cyclopidius emydinus Cope, 1884: 553
Cyclopidius incisivus Scott, 1893:661
Leptauchenia densa Loomis, 1925:245
Cyclopidius densa Schlaikjer, 1935: 161
Pitheciastes copei Schultz and Falkenbach, 1968:269
Leptauchenia margeryae Schultz and Falkenbach, 1968: 294
Hadroleptauchenia densa Schultz and Falkenbach, 1968:316
Hadroleptauchenia shanafeltae Schultz and Falkenbach, 1968:311
Hadroleptauchenia extrema Schultz and Falkenbach, 1968: 322
Pseudocyclopidius frankforteri Schultz and Falkenbach, 1968:328
Pseudocyclopidius major Schultz and Falkenbach, 1968:331
Leptauchenia major brevifacies Lander, 1998
Leptauchenia major loganensis Lander, 1998

Lectotype: ANSP 10941 (Fig. 14A-B), a left maxilla with C-M3. Precise locality data are unknown, but Schultz and Falkenbach (1968, p. 332) argue that it is from the “Gering Formation” (actually lower Sharps Formation, a unit that Schultz and Falkenbach refused to recognize) near Eagle Nest Butte, Washabaugh County, South Dakota.

Hypodigm: Specimens listed under the above synonyms by Schultz and Falkenbach (1968).

Distribution: Late Whitneyan to late Arikareean, High Plains and western Montana.

Diagnosis: Medium to large leptaucheniines (P2-M3 length = 51-62 mm, M1-3 lengths = 34-44 mm, M1-2 lengths = 22-27 mm, and skull lengths = 105-125 mm) with relatively more robust zygomatic arches and larger orbits; teeth hypsodont to very hypsodont; styles on M1-3 and stylids on m1-3 well developed. Contrary to CoBabe’s (1996, p. 578) diagnosis, the presence or absence of the M3 is highly variable in both this species and *L. decora*.

Description: A full description was given by Schultz and Falkenbach (1968, p. 333), so no further detail is required here.

Discussion: In the late Whitneyan (Fig. 8), the smaller leptaucheniine cluster (here identified as *L. decora*) is augmented by a larger size cluster, greatly increasing the variability and CVs of the late Whitneyan sample. As discussed above, this is good evidence that a second species has emerged, which is larger in most variables and slightly more robust than typical *L. decora*. The first available name for leptaucheniines of this size range is *Leptauchenia major* Leidy, 1856b, and so we identify all specimens in this size range as that taxon (as did CoBabe, 1996). *L. major* persists into the Arikareean (Fig. 9), where it flourishes in the early Arikareean, together with relict *L. decora* and even larger *L. lullianus*. Both *L. major* and *L. lullianus* occur in the samples from the Monroe Creek Formation (Fig. 9), before the subfamily dies out altogether as the early Miocene begins.

We have already discussed above the reasons for Cope’s (1878) naming of *Cyclopidius*, based on mistaken identifications of incisor counts

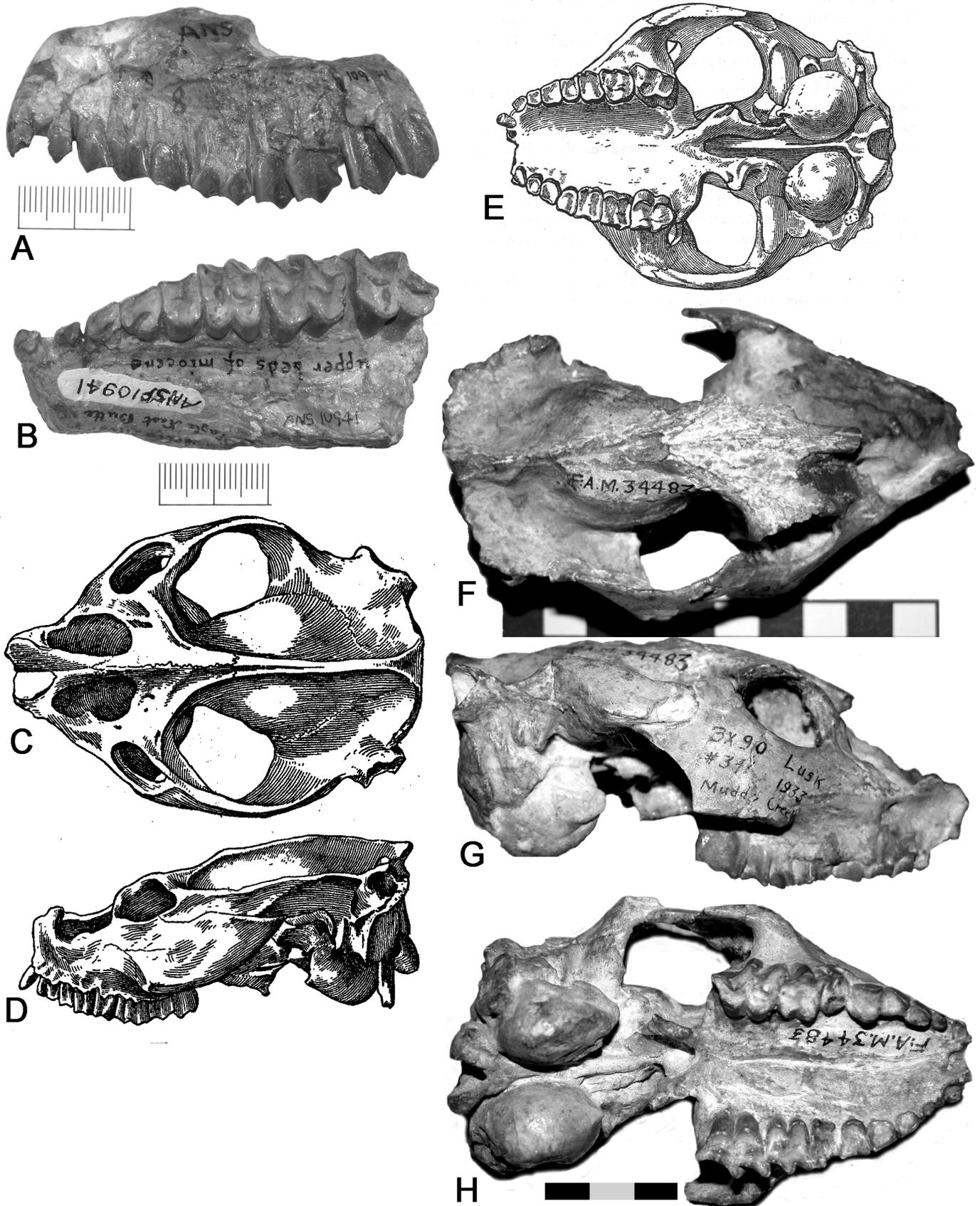


FIGURE 14. Specimens referred to *L. major*. A-B, Type specimen of *L. major* (ANSP 10941). C-E, Type specimen of "*Cyclopidius emydianus*" (AMNH 8115) in dorsal, left lateral, and ventral views (after Thorpe, 1937) (see also Fig. 7C). F-H, Type specimen of "*Pitheciastes copei*" (F:AM 34487) in dorsal, left lateral, and ventral views. Scale bar in cm.

of specimens from the Arikarean Fort Logan Formation (“Deep River beds”) of Meagher County, Montana. *Cyclopidius simus* (Cope, 1878) was based on a specimen (AMNH 8116) with “short, broad skulls” (largely due to extensive dorsoventral crushing). In the same paper, Cope also named *Brachymeryx feliceps*, which (as discussed above) Cope (1884), Matthew (1899) and later authors realized was based on a deciduous dentition. In 1884, Cope named *Cyclopidius emydinus*, based on a skull (AMNH 8115; Fig. 14C-E) that is larger and more robust with a longer snout than the type of *C. simus*. Matthew (1899) and Loomis (1925) upheld the distinction between *C. simus* and *C. emydinus*, but Schlaikjer (1935, p. 166) was “unable to observe any character or characters in *C. emydinus* which distinguish it specifically from *C. simus*,” and Thorpe (1937, p. 252) agreed that the two taxa were probably the same. Schultz and Falkenbach (1968, p. 299), however, argued that the greater length of the basicranium in *C. emydinus* justified its separation from *C. simus*. Close examination of the specimens, however, shows that they are identical in tooth dimensions, which are least likely to be distorted by crushing (Fig. 15). Each skull has undergone extensive crushing, so that the basicranium is flattened and rotated posteriorly in *C. emydinus*, enlarging the distance between the M3 and the auditory bulla, while it is rotated ventrally and anteriorly in *C. simus*, shortening that distance. Because these specimens are the same size in their undistorted tooth measurements and come from the same beds, it is very likely that they are the same species. Both species are within the size range of *L. major*, so they are junior synonyms of Leidy’s taxon.

Scott (1893) named *Cyclopidius incisivus*, based on the anterior portion of a skull with I2-M3 (YPM-PU 10473) from the Arikarean of Smith River Valley, Montana. Scott (1893) diagnosed the taxon based on supposedly small incisors in the twisted premaxillary, but Loomis (1925), Schlaikjer (1935), Thorpe (1937), and Schultz and Falkenbach (1968) all agreed that these characters were misinterpreted and this specimen was indistinguishable from either *C. emydinus* or *C. simus*. Because we regard these two forms as synonyms of *L. major*, the difference is moot.

Loomis (1925) described a partial skull (AC 8695) from the early Arikarean Horse Creek basin, Goshen County, Wyoming as *Leptauchenia densa*. This taxon was transferred to *Cyclopidius densa* by Schlaikjer (1935), and then corrected to *Cyclopidius densus* by Thorpe (1937), before being transferred again to *Hadroleptauchenia densa* by Schultz and Falkenbach (1968, p. 316). The distinction between *L. densa* and other species was again based on the questionable identification of fewer than three upper incisors in the type specimen, and other differences based on the robustness of the type skull. However, the teeth are entirely within the size range of *L. major* (Fig. 15), and the remaining differences in the skull can easily be attributed to post-mortem deformation. The supposed “high sagittal crests” cited by Schultz and Falkenbach (1968, p. 316) are simply due to the fact that these specimens are slightly larger and more robust, and along with their “more rounded orbits,” not as dorsoventrally crushed as other skulls from the same deposits.

Schultz and Falkenbach (1968, p. 269) named *Pithecistes copei* for the largest and last member (late Arikarean Monroe Creek Formation) of their supposed “*Pithecistes*” lineage, a group largely defined by their relatively small size, short upturned symphysis, and other features that are due to crushing or more gracile skull characters (Fig. 14F-H). The type specimen (F:AM 34483) is badly crushed dorsoventrally, and bears small (probably female) upper canines. However, in all its measurements (Fig. 15; Schultz and Falkenbach, 1968, table 11), it is indistinguishable from the cluster of specimens that we recognize as *Leptauchenia major*.

In the same manner, Schultz and Falkenbach (1968, p. 294) designated the largest and last (Monroe Creek Formation) member of their *Leptauchenia* lineage as *Leptauchenia margeryae* (Fig. 16A-C). Their diagnosis of the taxon focuses on the fact that it is the “largest, widest, and latest” of the species in this supposed lineage, but the type specimen (F:AM 45632) and most of the referred specimens are badly dorsoventrally crushed, and some are even plastically deformed. In most undeformed measurements (Fig. 15; Schultz and Falkenbach, 1968, table

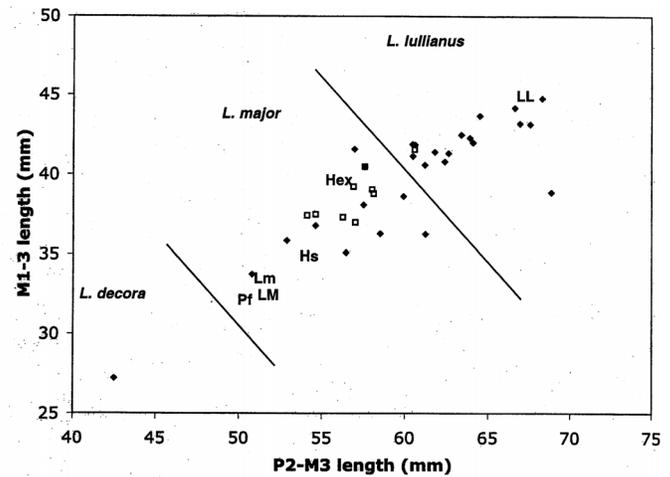


FIGURE 15. Plot of M1-3 length vs. P2-M3 length for specimens of *Leptauchenia*, showing the clusters referred to *L. decora*, *L. lullianus*, and *L. major*. Early Arikarean = solid diamonds; late Arikarean = open squares. Symbols for type or referred specimens as follows: Hex = type specimen of “*Hadroleptauchenia extrema*”; Hs = type specimen of “*Hadroleptauchenia shanafeltae*”; LL = type specimen of *L. lullianus*; LM = type specimen of *L. major*; Lm = referred specimen of *L. major*; Pf = type specimen of “*Pseudocyclopidius frankforteri*.”

12), it is completely within the limits of *L. major* as we have redefined it, so we consider it to be a junior synonym.

As discussed above, *Hadroleptauchenia* was defined by Schultz and Falkenbach (1968, p. 303) as a lineage slightly larger than *Leptauchenia* and smaller than *Pseudocyclopidius*. The earliest members of that supposed lineage, *H. eiseleyi*, and *H. primitiva*, fall within the morphological and size range of *L. decora*. Specimens from the lower Gering were named *Hadroleptauchenia shanafeltae* by Schultz and Falkenbach (1968, p. 311). In size (Fig. 15; see also Schultz and Falkenbach, 1968, table 13), the specimens fall in the lower part of the range of *L. major*. Many of the supposed diagnostic features (e.g., orbit more rounded) appear different simply because the specimens in their hypodigm are not as dorsoventrally crushed as others from the same beds. Still other features (e.g., “muzzle broader”) are simply not true, and cannot be substantiated either by visual examination or statistical analysis.

Just as Schultz and Falkenbach (1968) gave distinct names to the Monroe Creek specimens they referred to their supposed *Pithecistes* and *Leptauchenia* lineages, so too were the Monroe Creek specimens of their alleged *Hadroleptauchenia* lineage recognized as a distinct species, *Hadroleptauchenia extrema* (Fig. 16C-D). Interestingly, Schultz and Falkenbach (1968, p. 316, and table 13) confess that its size range (especially the dentition) is completely within the range of *H. densa*, and differentiate the two largely by the elongated post-orbital and basicranial portions of the referred skulls (which happen to be crushed differently than in *H. densa*). The type specimen of *H. extrema* (F:AM 45602) happens to be very badly dorsoventrally crushed, elongating its posterior skull region (Fig. 16D), but other than this difference, it is just a large specimen of *Leptauchenia major*. Because the uncrushed dental dimensions (Fig. 15) are completely within the range of *H. densa* (and thus *L. major*), and there are no valid differences in the skulls that cannot be attributed to crushing, we synonymize both of these taxa with *L. major*. Once again, the apparent reason for the existence of this taxon is Schultz and Falkenbach’s (1968) practice in naming a new species for every formation, regardless of whether the specimens can be objectively distinguished.

Finally, Schultz and Falkenbach’s (1968) *Pseudocyclopidius* lineage is based on the largest, most robust specimens at each level. Clearly, that includes the type material of *Leptauchenia major* from the lower Gering (which they called *Pseudocyclopidius major*), and also the largest

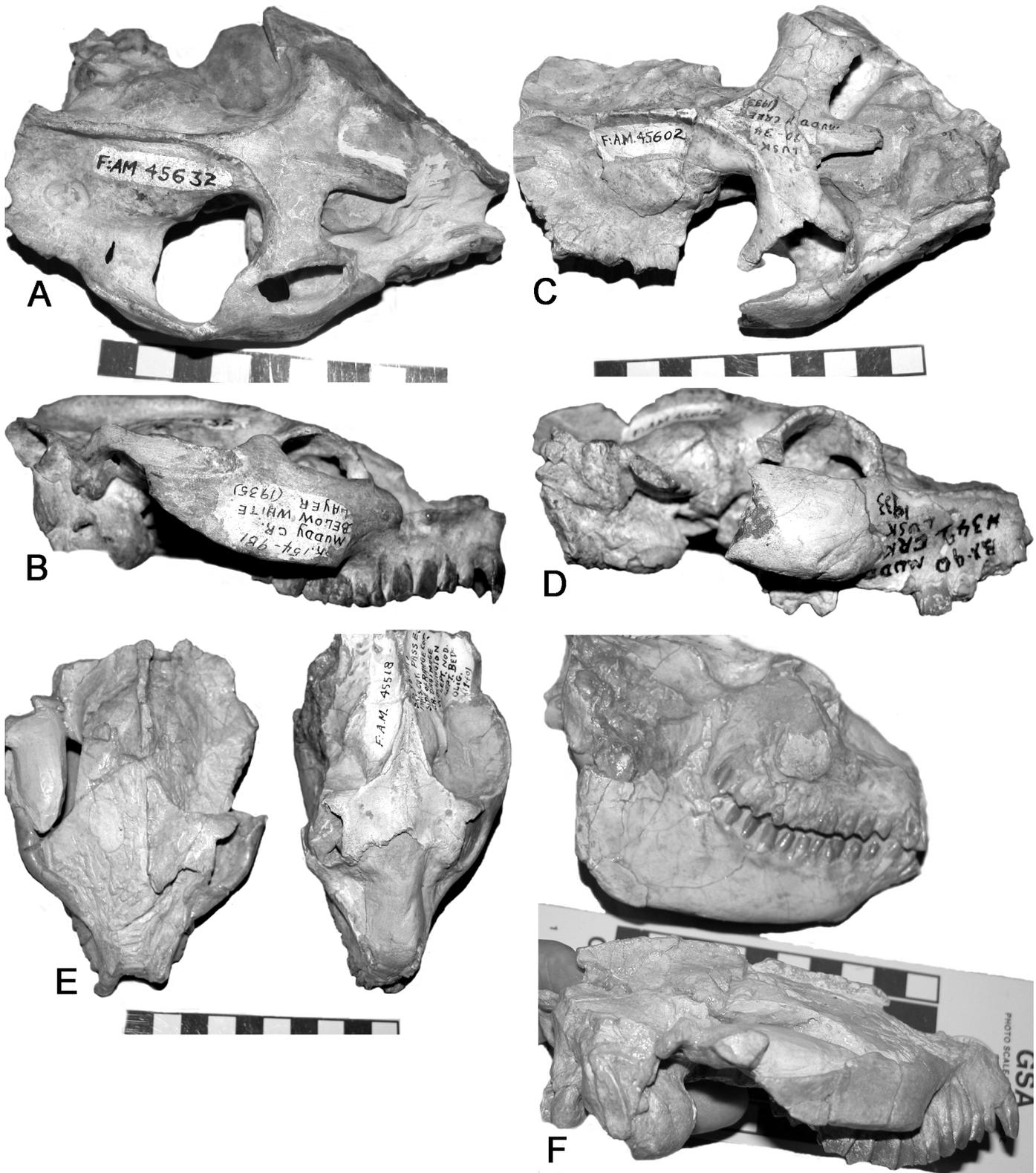


FIGURE 16. Specimens referred to *L. major*. **A-B**, Type specimen of *L. "margeryae"* (F:AM 45632) in dorsal and right lateral views. **C-D**, Type specimen of "*Hadroleptauchenia extrema*" (F:AM 45602) in dorsal and right lateral views. **E-F**, Specimens referred to "*Pseudocyclopidius frankforteri*", showing variation due to crushing. F:AM 45573 (left in E, top in F) and F:AM 45518 (right in E, bottom in F). Scale bar in cm.

late Whitneyan specimens (Fig. 8). Schultz and Falkenbach (1968, p. 328) referred most of these specimens to *Pseudocyclopidius frankforteri*. According to their diagnoses, *P. frankforteri* is smaller and less robust than typical *L. major*, but they are still within the size range (Fig. 15;

Schultz and Falkenbach, 1968, table 14) of *L. major*, and the other features of the skull are also within the range of the species after factoring out differences due to size, allometry, and post-mortem deformation (Fig. 16E-F).

Leptauchenia lullianus (Thorpe, 1921)

Figure 17, Table 3

Cyclopidius lullianus Thorpe, 1921:413*Cyclopidius quadratus* Koerner, 1940: 857*Pseudocyclopidius quadratus* Schultz and Falkenbach, 1968:345*Pseudocyclopidius lullianus* Schultz and Falkenbach, 1968: 336*Pseudocyclopidius lullianus expiratus* Schultz and Falkenbach, 1968: 342

Holotype: YPM 10117, a skull (Fig. 17B-C) with I2-M3 and mandible with c-m3, from the upper Gering Formation equivalent, Muddy Creek area, "Spanish Mines," Niobrara County, Wyoming.

Hypodigm: Specimens listed under the synonyms above by Schultz and Falkenbach (1968).

Distribution: Early to middle Arikareean, High Plains and western Montana.

Diagnosis: Large leptaucheniines (P2-M3 length = 62-71 mm, M1-3 lengths = 42-48 mm, M1-2 lengths = 27-35 mm, and skull lengths = 125-185 mm) with very robust zygomatic arches and larger orbits; snout relatively flattened and shovel-like; malar relatively deep; teeth very hypsodont.

Description: A full description was given by Thorpe (1921, 1937), Loomis (1925), and Schultz and Falkenbach (1968, p. 337), so no further detail is required here.

Discussion: As discussed above, the early and late early Arikareean sample contains a large size cluster that does not occur in the Whitneyan or the late Arikareean, and seems to be a distinct, short-lived large species. Close examination of the skulls show that they bear both small, presumed female (e.g., F:AM 57084, 45600, 56993, 45597, 47014) and large, presumed male (e.g., F:AM 57088, 57013, 57005, 57015, 57016, 57009, 3486) upper canines, so this large cluster is not composed only of large robust male skulls. Adding this sample to the sample of *L. major* from the early Arikareean makes the variability of the sample unacceptably large (Table 1), so we consider this larger size group a valid species, both for statistical reasons and also for its limited distribution in space and time. To test for the significance of the differences of these two clusters, we performed t-tests on them. In most measurements that are low in variability and not prone to distortion (especially tooth dimensions), t-tests indicate that the means are significantly different. For example, the means of the P2-M3 length are significantly different with a probability of 5.98×10^{-11} . The means of the M1-3 lengths are significantly different with a probability of 6.67×10^{-8} . This is not surprising, given that the two distributions are almost completely non-overlapping and easily separated by a size gap (Fig. 8A).

The first valid name for this species is *Cyclopidius lullianus* (Thorpe, 1921), based on YPM 10117, a partial skull and mandible from the early Arikareean at "Spanish Mines" (Muddy Creek area) in eastern Wyoming. This species was transferred to the robust, large *Pseudocyclopidius* lineage by Schultz and Falkenbach (1968, p. 336), and many more specimens were added to the hypodigm. As discussed above, we find no defensible reason for retaining either *Cyclopidius* or *Pseudocyclopidius* as a valid genus, so we place Thorpe's species in the only valid genus, *Leptauchenia*. It turns out that these large oreodonts are very common in the Gering, Monroe Creek, and Sharps formations and their equivalents, and easily distinguished from the smaller, less robust *L. major*.

Koerner (1940) described the anterior portion of a skull (YPM 13960) from the "Deep River beds," near White Sulphur Springs, Meagher County, Montana, as *Cyclopidius quadratus*. As the trivial name implies, his diagnosis focused largely on the equidimensional crowns of M1. As Schultz and Falkenbach (1968, p. 345) noted, however, the shape of the crown of M1 varies largely with wear. Based on its dimensions (M1-2 length = 29.9 mm), it is probably a junior synonym of *L. lullianus*.

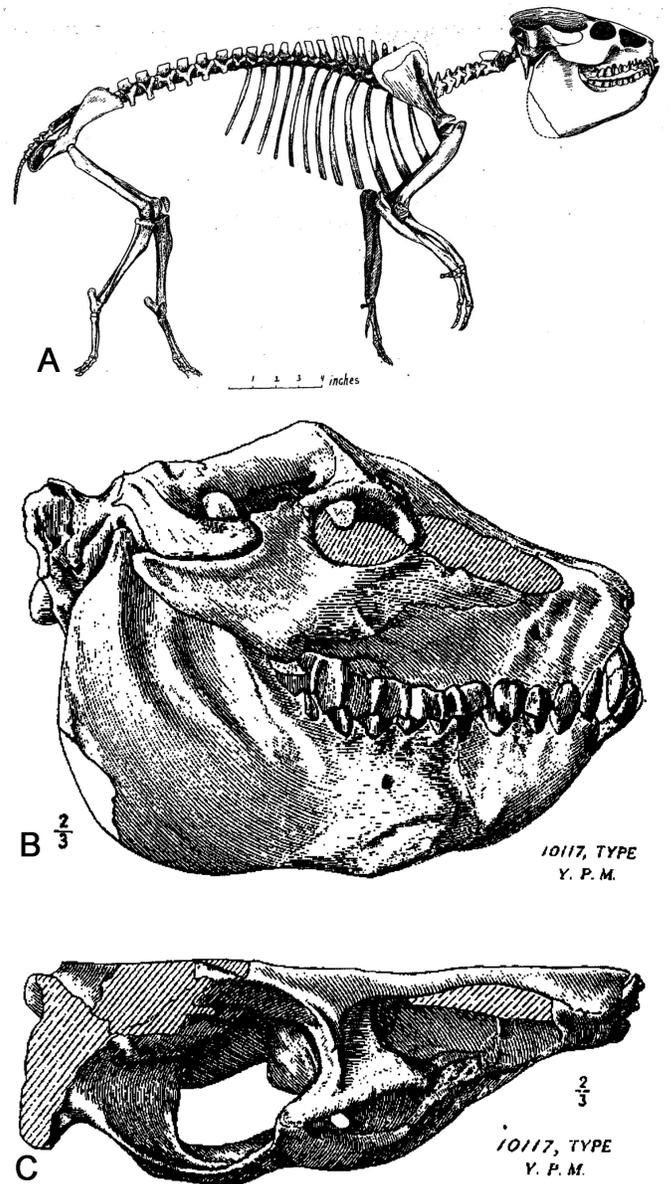


FIGURE 17. *Leptauchenia lullianus*. A, Mounted skeleton (ACM 7679) (after Loomis, 1925, fig. 1). B-C, Type skull (YPM 10117) in lateral and dorsal views (after Thorpe, 1921).

Pseudocyclopidius lullianus expiratus was a "new geologic subspecies" designated by Schultz and Falkenbach (1968, p. 342) for specimens from the Monroe Creek Formation. However, their diagnosis (p. 342) and discussion essentially admit that there are no differences from the skulls of the Gering Formation, and imply that the only basis for the name is the different formation from whence the specimens came. Although none of these specimens were complete enough to be plotted in Figures 9 or 16, the existence of these large skulls of *L. lullianus* in the Monroe Creek Formation suggests that this species did straggle on into the late early Arikareean.

Loomis (1925) briefly described a nearly complete skeleton of "*Cyclopidius*" *lullianus* (ACM 7679; Fig. 17A) that shows the size and proportions of this animal. The striking feature of this specimen is how disproportionately large the skull is relative to the small, short-limbed body. Although the limbs are slightly larger and more robust than those of *L. major*, they apparently did not increase in size as rapidly as did the head of this taxon.

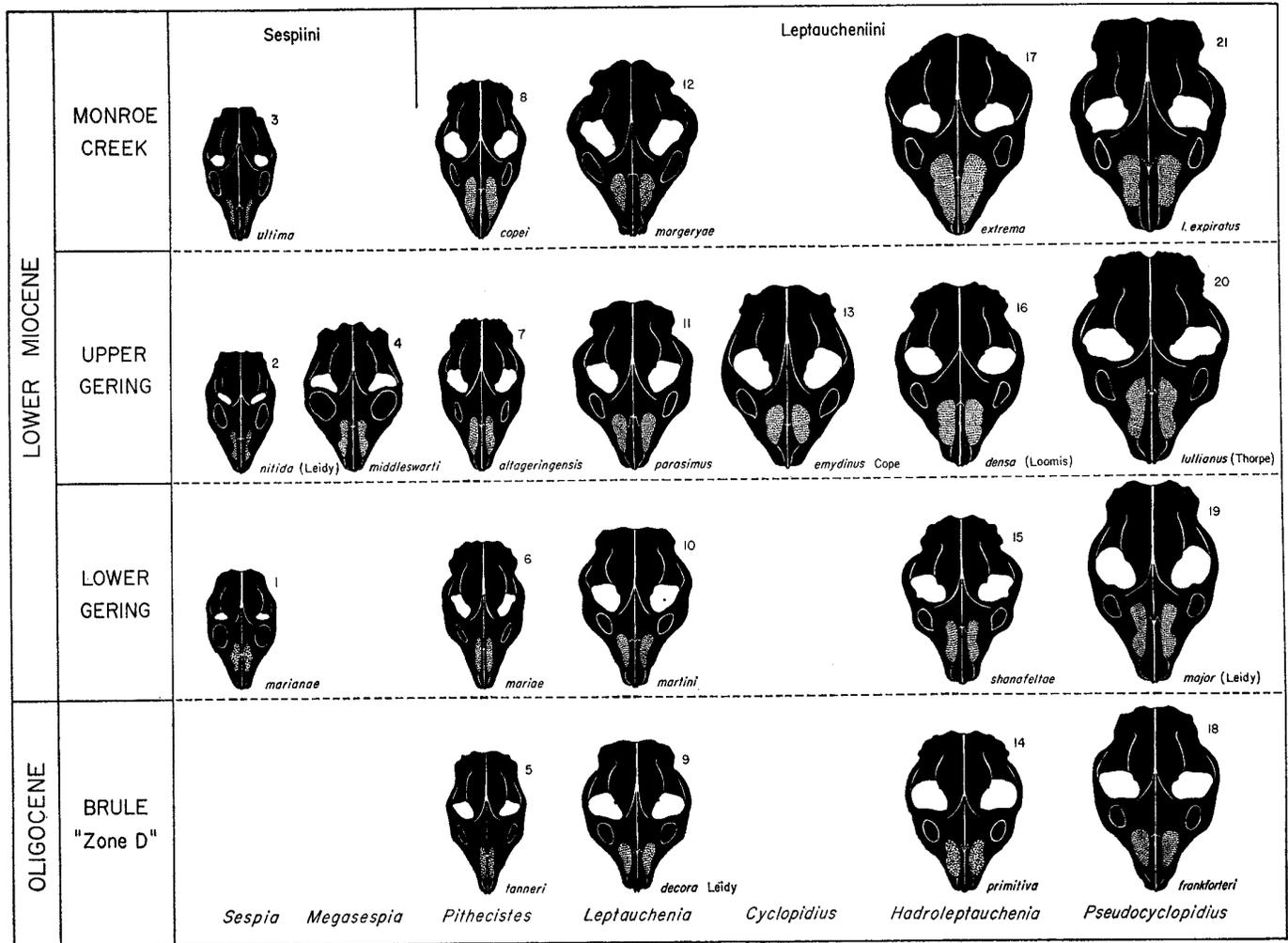


FIGURE 18. Schultz and Falkenbach's (1968, chart 19, p. 431) supposed seven generic lineages of leptaucheniines, each assigned to different species at each level. All specimens are drawn to the same scale, and shown in dorsal view. Despite their attempt to split out and name all these taxa, even a casual glance (once crushing has been accounted for) reveals that there are tiny specimens referred to *Sespia*, plus three clusters of *Leptauchenia*: smaller forms (the "*Pithecistes*" lineage, plus *Leptauchenia decora* through *L. "parasimus"*); an intermediate-sized group (all of the "*Hadroleptauchenia*," plus the two early species of "*Pseudocyclopidius*," *L. "margeryae*," and "*Cyclopidius emydinus*"), and the large robust forms they referred to "*Pseudocyclopidius*" *lullianus* (two skulls in upper right).

Summary

Interestingly, our one-genus, three-species arrangement is apparent even within the oversplit concepts presented by Schultz and Falkenbach (1968). Their Chart 19 (Fig. 18 in this paper) shows the "six phylogenetic lines" of their 7 genera and 31 species. But a glance at the figure actually reveals the clusters that we advocate here (Fig. 19). In addition to the obviously discrete dwarfed *Sespia* lineage, there is a smaller more gracile lineage (largely placed in their concept of *Pithecistes* and *Leptauchenia*) that does not change much in size or shape, other than due to the effects of post-mortem deformation. (*Pithecistes* skulls are often laterally compressed). We place all these specimens in *L. decora*. A larger lineage (composed mainly of their concept of *Hadroleptauchenia*, *Cyclopidius*, and the earlier species of *Pseudocyclopidius*) is also apparent from Chart 19, and visually they can be seen to be nearly identical; these we place in *L. major*. Finally, the disjunctly large and robust *L. lullianus* (which they placed in *Pseudocyclopidius*) also stand out visually, and corroborate our interpretations.

PALEOECOLOGY, TAPHONOMY, AND BIOGEOGRAPHY

The peculiar leptaucheniines, with their high-set eyes and ears, large nasal-facial vacuities, huge auditory bullae, and hypsodont teeth

(among the most hypsodont artiodactyls of their time, along with camels and the ruminant *Hypisodus*), have long inspired speculation as to their mode of life. Cope (1884) was the first to advocate the aquatic hippopotamus analogue for leptaucheniines, largely based on the high placement of the eyes, ears, and presumably nostrils on the head. This hypothesis was also supported by Matthew (1899) and Scott (1937, 1940), although Sinclair (1910) and Thorpe (1937) were not convinced that the aquatic interpretation was the only reasonable one for their anatomy. Schultz and Falkenbach (1968, pp. 230-231) argued that the leptaucheniines were specialized for a desert mode of life. They based this largely on the fact that the Whitneyan and Arikareean deposits of the High Plains are largely eolian deposits (and this has been confirmed by Swinehart et al., 1985 and Hunt, 1990), with few or no river channels. Indeed, where channel facies are known (such as the "*Protoceras* channels" of the upper Whitneyan in South Dakota), leptaucheniines are rare or absent, while other fossils (especially the presumed moose analog, *Protoceras*) are common. Although they did not point it out, the fact that leptaucheniines are very hypsodont, with highly worn tooth crowns (the crown pattern is nearly always worn off, except in juveniles), and a deep jaw and thick, heavy zygomatic regions for jaw muscles, suggests that they lived on a much more abrasive, grittier diet than most contemporary mammals. Schultz and Falkenbach (1968) also pointed out that

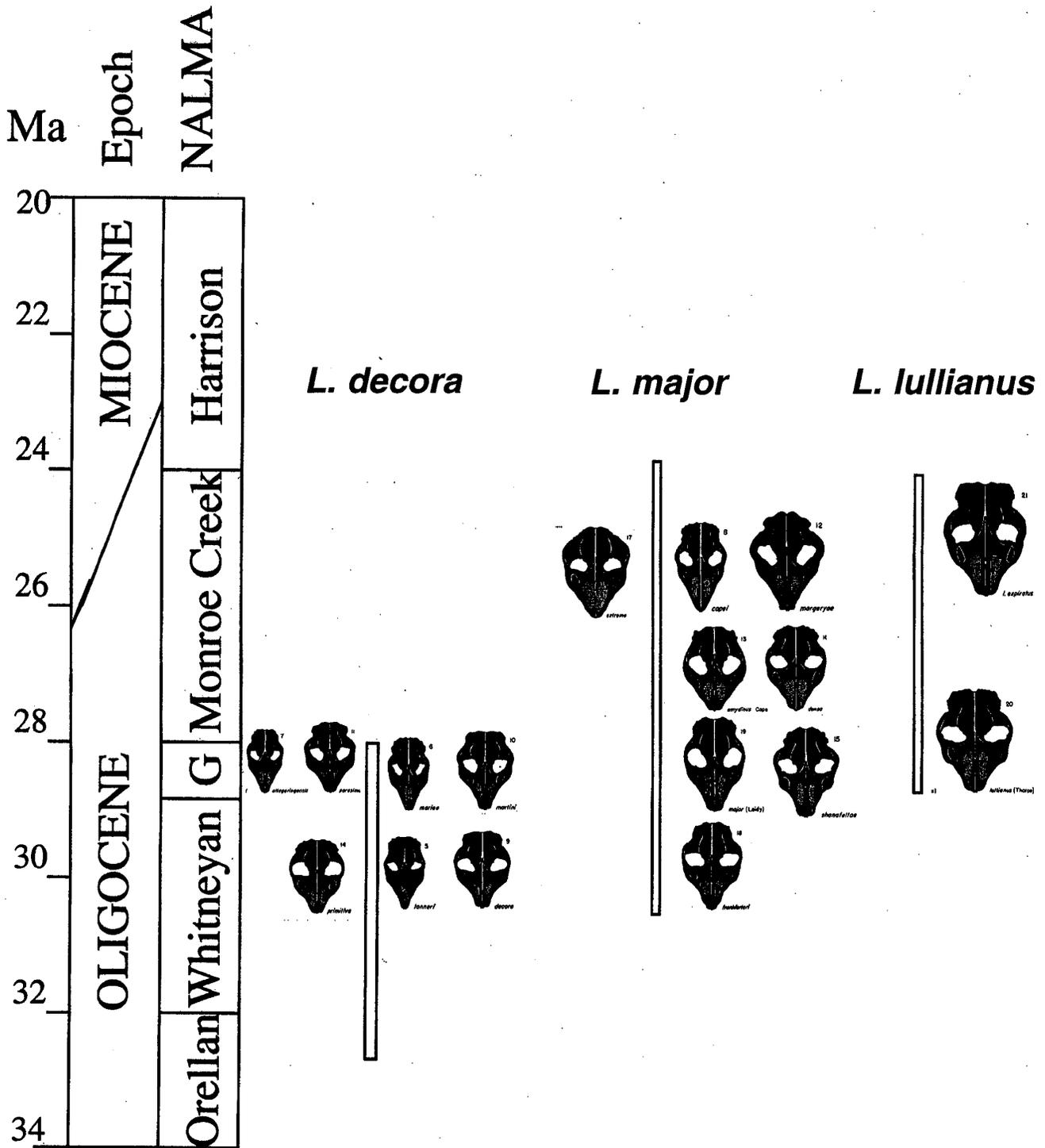


FIGURE 19. Our rearrangement of leptacheniines, using modern time scales and modern concepts of systematics. The dorsal views of leptacheniine skulls are reproduced from Schultz and Falkenbach (1968, chart 19, p. 431—see our Fig. 18) but preserve the relative sizes. Time ranges of each species shown by open bars. Time scale after Tedford et al. (1996, 2004). Note that the “Geringian” (G) is reduced to only 300,000 years (28.0-28.3 Ma, according to Tedford et al., 1996), which collapses down the nine different species (see Fig. 18) recognized by Schultz and Falkenbach (1968) into a very short time. There are also specimens known from the late Orellan and early Whitneyan, but they were not illustrated by Schultz and Falkenbach (1968, chart 19). NALMA = North American Land Mammal Age.

many desert bovids have comparable conditions of large bullae, large facial vacuities, and specialized nasal areas. Finally, Schultz and Falkenbach (1968) cited work by Webster (1962) that showed kangaroo rats also have large auditory bullae, which help them with low-frequency hearing (for detecting approaching predators) in open habitats, such as deserts.

Joeckel (1992) analyzed the ear region of leptacheniines in detail, and found that the issue was not so simple as this, because some desert rodents and bovids lack large bullae, but some taxa not living in arid climates had large bullae. Nevertheless, he concluded that the large bullae of leptacheniines were most likely an adaptation to open, arid habitats. Certainly, their fossilization in eolian deposits, and almost never in

fluvial deposits of the same age in the High Plains, is strong corroboration of this hypothesis. Where fluvial deposits do occur in the early Arikareean (such as the Sespe or Otay formations of California), we find *Sespia* but no larger leptaucheniines.

Janis (*in* Lander, 1998), on the other hand, felt that hyraxes were a better analogue for leptaucheniines. She suggested that their body proportions resembled that of hyraxes, better suited for a rock-climbing mode of life in arid lands. This would also be consistent with their capabilities for low-frequency hearing in open terrain. Although this seems plausible, the fact remains that most leptaucheniine skulls are found in unquestioned eolian deposits, not in conglomeratic sandstones close to rock outcrops. In addition, the Arikaree Group has very few conglomerates (most of which are largely clay gall conglomerates reworked from muddy floodplains, *vide* Swinehart et al., 1985; Hunt, 1990), so there is little evidence that large rocky outcrops, such as the African *kopjes* that shelter hyraxes, were nearby. Indeed, geologic evidence from the northern Rocky Mountain region (Love, 1970; McKenna and Love, 1972; Prothero, 1998) suggests that most of the Rockies were deeply buried by the Arikareean, so there were few uplifted rocky areas to provide conglomerates, let alone shelter hyrax-like animals.

In addition to this taphonomic fact, another phenomenon is apparent, whether one collects them in the field or examines museum specimens. More than any other group of oreodont, leptaucheniines are rarely known from even partial skeletons, but largely consist of isolated skulls (and occasional jaws). Hoffman and Prothero (2004) attempted to compare the postcrania of a wide spectrum of leptaucheniines, and found that most had no known postcranial bones. A glance through the lists of postcranial bones in Schultz and Falkenbach (1968) confirms this, as did our examination of every drawer in the collections of the AMNH. This is not an artifact of collecting bias, because the Frick collectors were diligent about obtaining partial or complete skeletons when they were available, and were not simply “headhunters.” It is unclear why preservation in eolian deposits preferentially favored fossilization of skulls, and rarely or never trapped complete animals, but that is the fact, nonetheless. Indeed, the postcranials of *Sespia*, which are known primarily from fluvial deposits (such as the Sespe and Otay formations in California) are far more abundant and better known (Hoffman and Prothero, 2004), and this is probably due to the change of facies and taphonomic factors.

Finally, the leptaucheniines show a very peculiar pattern of biogeography and abundance. They are extremely abundant in the volcaniclastic

eolian deposits of the Whitneyan of the High Plains (often making up more than 50% of the fossils collected), and remain so in the windblown ash deposits (Hunt, 1990) of the Gering and Monroe Creek formations and their equivalents (along with a few specimens of *Sespia nitida* and *Sespia ultima*—see Hoffman and Prothero, 2004). However, they are still unknown from the Arikareean volcaniclastic rocks of the John Day Formation, even though nearly all the other oreodonts of the Arikareean are found there (as are most other mammals known from the High Plains, including rhinos, horses, camels, entelodonts, rodents, and especially hypertragulids). Why they were abundantly preserved in the High Plains volcaniclastics but not the similar sediments in Oregon is a mystery, especially when the oreodonts and nearly all other large mammals, are largely the same. In the fluvial Arikareean deposits of California (Sespe and Otay formations), *Leptauchenia* is absent, but *Sespia* is by far the most abundant fossil. Finally, in the Arikareean deposits of the Gulf Coast of Florida and Texas (Albright, 1998), leptaucheniines are absent, even though other types of oreodonts are known, as are most of the rhinos, horses, camels, and ruminants species common in the High Plains. Clearly, there is some sort of biogeographic filter operating here that restricted *Leptauchenia* to the High Plains and Montana, but had no such effect on the rest of the common large mammals.

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