

REVISION OF THE LATE OLIGOCENE DWARFED LEPTAUCHENINE OREODONT *SESPIA* (MAMMALIA: ARTIODACTYLA)

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Abstract—*Sespia californica* was a dwarfed leptauchenine oreodont, first described by Chester Stock in 1930, that was common in early Arikareean (late Oligocene) deposits of southern California. However, the type material was fragmentary and the postcranials were never described. Abundant new material, including hundreds of jaws and maxillae, complete skulls, and partial skeletons, were found during excavations for housing developments in the upper Oligocene Otay Formation in San Diego County. Measurements of the relatively undistorted dimensions of skulls and jaws show that *Sespia californica* is a valid taxon (found in both the Otay and Sespe formations) and it is smaller than *Sespia nitida* (senior synonym of *S. marianae*). This suggests that *Sespia californica* migrated from the High Plains (where it first appears in Chron C11n, at 29.5 Ma, in the “brown siltstone” member of the Brule Formation) to California (where it first appears in Chron C10r, or 29.3 Ma). *Sespia ultima* (synonym of *Megasespia middleswarti*) is a valid taxon for the larger *Sespia* from the early and middle Arikareean of the High Plains. *Sespia heterodon* from the early Arikareean of the Deep River beds of Montana is doubtfully valid, because it falls between *S. nitida* and *S. ultima* in size; more complete material is required to fully assess its validity. Measurements of the large samples of *Sespia californica* also show that there is no sexual dimorphism in size, nor was there any evidence of dimorphism in the maxillary “horns,” which some have speculated as dimorphic in leptauchenines. Only the upper canines show a slight indication of sexual dimorphism, which is typical in many other primitive artiodactyls, including pigs, camels, and tragulids.

Key words: *Sespia*, Oligocene, oreodont, Artiodactyla, Arikareean.

INTRODUCTION

Oreodonts (family Merycoidodontidae) are among the most common mammal fossils in the middle to late Eocene, Oligocene, and early Miocene of North America. Their great abundance made them important biostratigraphic indicators of these beds, but they have also been plagued by systematic problems. Early revisers (e.g., Thorpe, 1937; Scott, 1940) tended to be conservative in their definitions of taxa; only three genera and less than a dozen species are recognized in the White River Group by Scott (1940). The most comprehensive revision by Schultz and Falkenbach (1956, 1968) grossly oversplit the group, based on characters that are largely caused by post-mortem deformation, and failed to do any meaningful statistical analysis to determine if taxa were distinct. These problems have been noted by a number of authors over the years (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). The first modern 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 subfamilies of the Merycoidodontidae is the Leptaucheniinae, a group that is very common in the Whitneyan and early to middle Arikareean (late Oligocene). *Leptauchenia decora* is by far the most common fossil in the Whitneyan of South Dakota and Nebraska, so that these deposits have long been known as the “*Leptauchenia* beds.” The distinctive cranial features of the leptauchenines include their very hypsodont (high-crowned) dentition, high-set orbits, inflated auditory bullae, and nasal-facial vacuity. Their skeleton has relatively short limbs and a long midsection and tail. The systematics of the Leptaucheniinae has been revised numerous times since their first description by Leidy (1856). Schultz and Falkenbach (1968) oversplit the leptauchenines into 7 genera and 31 species, based largely on differences in size and stratigraphic position without adequate statistical analysis, and also based on features caused by post-mortem deformation. CoBabe (1996) did a multivariate analysis of most of the

leptauchenines, and retained only two genera: *Leptauchenia* (with two species, *L. decora* and *L. major*) and *Sespia*. CoBabe did not analyze *Sespia*, other than to show that it was easily distinguished from *Leptauchenia* by its small size and other features.

Sespia was a dwarfed leptauchenine with extremely hypsodont teeth. *Sespia nitida* first appears in the “brown siltstone member” of the Brule Formation of Nebraska and the lower Sharps Formation of South Dakota, where its first appearance at 29.5 Ma (Chron C11n), just above the Rockyford Ash and between the second and third Nonpareil Ashes, is an important indicator of the earliest Arikareean (Tedford et al., 1996). It ranges up into the late early Arikareean upper Sharps, Gering, and Monroe Creek formations. *Sespia californica* also first appears around 29.3 Ma (Chron C10r) in the Sespe Formation in Ventura County, California (Prothero et al., 1996), and the same-aged deposits in the Otay Formation of San Diego County, California (Prothero, 1991). *Sespia californica* is important to California stratigraphy because it is the most abundant fossil mammal in the late Oligocene (early Arikareean) faunas of southern California. Past studies have been hampered by a shortage of decent specimens. The type material described by Stock (1930), for example, consists of only a partial palate and jaw (Fig. 1). A recent accumulation of *S. californica* specimens salvaged from housing development sites in the upper Oligocene Otay Formation has greatly improved the size and quality of the sample, allowing us to redescribe the skeleton of *S. californica*, and assess such issues as population variability, sexual dimorphism, and whether or not *S. californica* can be distinguished from *S. nitida*.

METHODS

Specimens were measured with a dial calipers, and photographed with a Nikon 5700 digital camera. Statistics were performed on Excel and Systat version 10 software. We examined almost all the available specimens of *Sespia* in the following collections: AMNH = American Museum of Natural History, New York; ANSP = Academy of Natural Sciences, Philadelphia; F:AM = Frick Collection, now stored in the

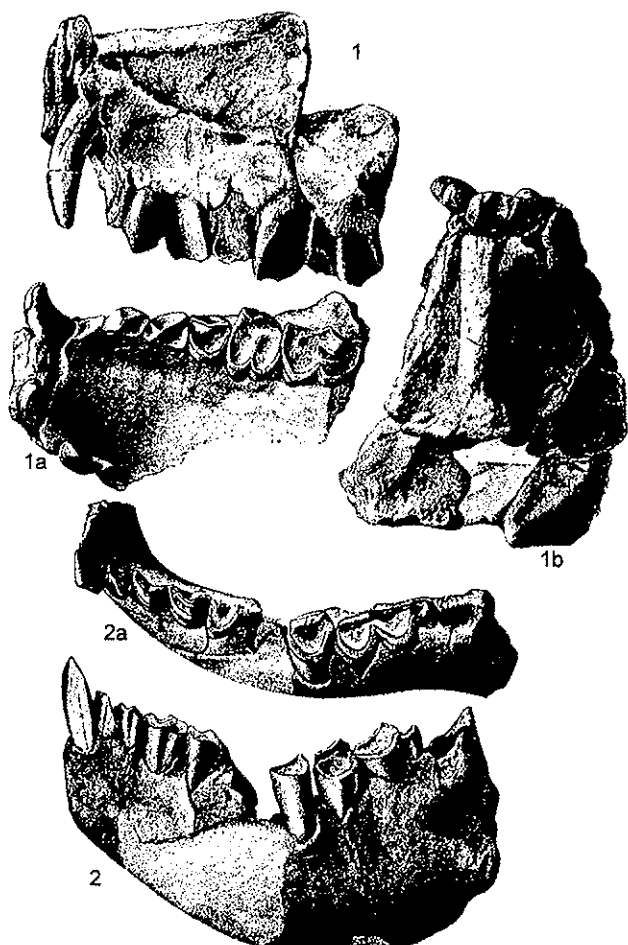


FIGURE 1. Stock's (1930) illustration of the type specimen of *Sespia californica* (UCMP 27720).

AMNH; LACM = Natural History Museum of Los Angeles County; LACM(CIT) = California Institute of Technology collections (now stored at the LACM); MCZ = Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; SDNHM = San Diego Natural History Museum, San Diego; UCMP = University of California Museum of Paleontology, Berkeley; UNSM = University of Nebraska State Museum, Lincoln, Nebraska.

SYSTEMATIC PALEONTOLOGY

Order ARTIODACTYLA Owen, 1848

Family MERYCOIDODONTIDAE (Leidy, 1848)

Subfamily LEPTAUCHENIINAE Schultz & Falkenbach, 1940

Sespia Stock, 1930

Leptauchenia Leidy, 1869:129 (in part)

Cyclopidus Cope, 1878:222 (in part)

Pithecistes Cope, 1884:559 (in part)

Leptauchenia: Thorpe, 1921:410 (in part)

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

Leptauchenia? (*Sespia*): Stock, 1930:38

Cyclopidus: Schlaikjer, 1935:161 (in part)

Sespia: Schultz and Falkenbach, 1968:239; MacDonald, 1970:77; Lander, 1977:94

Megasespia: Schultz and Falkenbach, 1968:255

Type species—*Sespia nitida* (Leidy, 1869).

Included species—*S. californica* (Stock, 1930); *S. ultima* Schultz and Falkenbach, 1968

Distribution—Early to late Arikareean, High Plains, Montana, and California.

Diagnosis—Small-sized leptauchenines with extremely hypsodont cheek teeth. Because of their smaller size relative to *Leptauchenia*, they also have a smaller facial vacuity, a shallower malar, and a smaller tympanic bulla. The paroccipital process, however, is more inflated than in *Leptauchenia*. The styles on M1-3 and the ribs and stylids on m1-3 are much less prominent than in *Leptauchenia*. M3 is lost in many specimens.

Discussion—The first known *Sespia* specimen (ANSP 10870) was a fragmentary skull collected from the Arikareean (presumed Gering equivalent) of Nebraska at White Earth Creek in the White River drainage by the Hayden Expedition in 1856. It was originally described as *Leptauchenia nitida* by Leidy in 1869. In 1878, Cope described a tiny maxilla with worn teeth (AMNH 8131) from the early Arikareean Deep River beds, Smith River Valley, Meagher County, Montana, as *Cyclopidius heterodon*, assigning it to his much larger genus of High Plains leptauchenines. In 1884, Cope transferred *C. heterodon* to another leptauchenine genus, *Pithecistes*. Matthew (1899) argued that Cope's *P. heterodon* was simply the juvenile dentition of *Pithecistes decedens*, but this has since been disproved, since the type of *C. heterodon* is clearly an adult dentition. In 1925, Loomis combined *Cyclopidius* and *Pithecistes* to call the taxon *Cyclopidius* (*Pithecistes*) *heterodon*.

In 1930, Chester Stock described the type specimen of *Leptauchenia?* (*Sespia*) *californica* from the upper Oligocene South Mountain Sespe beds and referred *L. nitida* to his subgenus *Sespia*. The type material of *Leptauchenia?* (*Sespia*) *californica* described by Stock consisted only of a left jaw fragment and a partial palate. The postcranials were unknown. Loomis (1937) did not recognize Stock's (1930) subgenus, but referred the Nebraska specimens to *Leptauchenia nitida*, and the California specimens to *Cyclopidius californicus*. Schultz and Falkenbach (1968) oversplit *Sespia* into six species in two genera. CoBabe (1996) recognized only one genus, *Sespia*, but did not include California specimens in her sample, so she did not deal with the issue of how many species of *Sespia* were valid. Lander (1998) considered all the specimens of *Sespia* referable to one species, *S. nitida*, but provided no justification or detailed analysis for this decision.

Sespia californica (Stock, 1930)

Figures 1-2, Tables 1-2

Leptauchenia? (*Sespia*) *californica* Stock, 1930

Cyclopidius californica: Schlaikjer, 1935

Cyclopidius californicus: Thorpe, 1937

Sespia californica: Schultz and Falkenbach, 1968

Sespia nitida Lander, 1998 (in part)

Holotype—UCMP 27720, partial skull and mandible (Fig. 1), from the South Mountain l.f. (early Arikareean), upper Sespe Formation, Ventura County, California (Prothero et al., 1996).

Hypodigm—From the type locality: UCMP 58038, 58039, 58040, 29991; LACM(CIT) 7327, 3488, 3484, 3490, 3487, 3489, 3491, 3492, 3485, 3486, 12664. From San Marcos Pass, Santa Barbara County, California: UCMP 52421. From Bee Canyon (LACM loc. 7326, 7327), Ventura County, California: LACM 145850, 145844, 145851, 18852, 14840, 148415. From the Sespe Formation (various localities): 145852, 148405, 148404. From the Otay Formation, San Diego County, California: SDNHM 31243, 28216, 28160, 42889, 47889, 43441, 43438, 28579, and hundreds of additional specimens not listed here.

Distribution—Earliest Arikareean (late Oligocene), Ventura, Santa Barbara, and San Diego counties, California.

Diagnosis—Smallest known species of *Sespia*; infraorbital foramen above anterior border of P4.

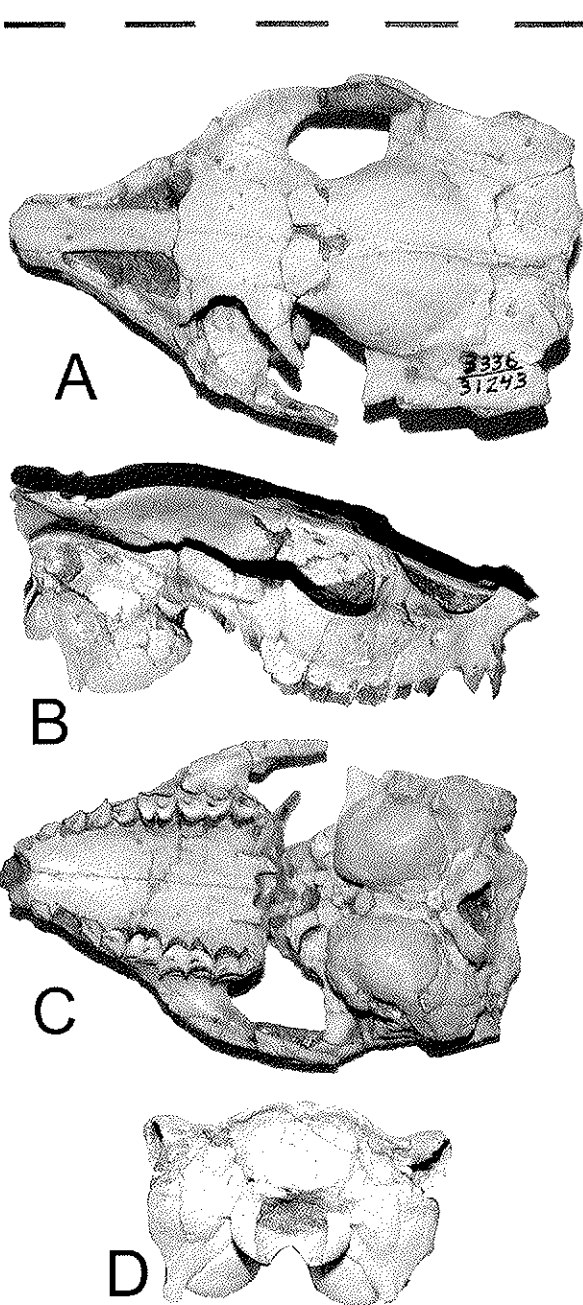


FIGURE 2. Referred skull of *Sespia californica* from the Otay Formation, San Diego County (SDNHM 31243) in (A) dorsal; (B) lateral; (C) palatal; and (D) occipital views. Scale bar in cm.

Description—Stock (1930) provided a description of the known material of *S. californica*, which consisted of only a partial maxilla and mandible (Fig. 1). Schultz and Falkenbach (1968, p. 241) provided no additional descriptions, and even wrote that “the posterior portion of the skull is unknown,” since no new material was known to them. However, the Otay collections in the SDNHM yield many excellent specimens, including a number of uncrushed palates, maxillae and jaws, and one or two excellent skulls (Fig. 2). These form the basis for the description below.

SDNHM 31243 (Fig. 2A-D) is a complete uncrushed skull of *S. californica* from the Eastlake locality (SDNHM loc. 3336) in the Otay Formation (early Arikarean) of southern San Diego County (Walsh and



FIGURE 3. Postcranials of *Sespia californica* from the Otay Formation, San Diego County. (A) Partial articulated skeleton with forelimb (SDNHM 42852). (B) Humerus, ulna, femur, tibia (SDNHM 31317). Scale bars in cm.

Deméré, 1991; Prothero, 1991). This is a considerable improvement over the fragmentary type material (Fig. 1), which consists of broken pieces of the maxilla and mandible. SDNHM 31243 has a broad, posterodorsally-flaring lambdoid crest, and a weak sagittal crest. Judging from the small canines, it appears that this individual is a female, so the sagittal crests (which are larger on other specimens from this locality on male specimens) might be relatively weak due to sexual dimorphism. The sagittal crest splits into a triangular area as it joins the lambdoid crest, and also divides anteriorly into two crests that merge with the supraorbital ridges. The frontal bones are gently concave between the orbits, with a number of small foramina. The facial vacuities are large, with a broad triangular posterior end narrowing toward the anterior direction, and with a broad nasal bone between them. Their suture with the anterior end of the maxilla is slightly broken, giving the appearance of nasal “horns” as discussed elsewhere.

In lateral view (Fig. 2B), the anterior process of the maxilla is large and broad where it contacts the nasals, and there is a deep dorsal indentation for the facial vacuity. There is a large pre-orbital foramen in the middle of the maxilla just above the P2. The zygoma is broad and outwardly curved, and the orbit, although slightly dorso-ventrally crushed, is large and slightly upward facing. The periotic region is robust, with a long tube-like auditory meatus typical of leptauchenines. The auditory bullae are large, as in all leptauchenines.

In ventral view (Fig. 2C), the palate is broad and concave, with

TABLE 1. Measurements of skulls and jaws of *Sespia californica* (in mm). Conventions follow Schultz and Falkenbach (1968, table 10). (M) and (F) are skulls with male and female canines. L = length; W = width.

<u>Skulls</u>	UCMP 27720 (M) (type)	SDNHM 31243(M)	SDNHM 28216(F)	SDNHM 28160	SDNHM 42889(M)	SDNHM 47889(F)
L supraoccipital to incisors	—	85.0	—	—	82.0	90.5
Basal L	—	73.0	77.0	—	77.0	84.5
Maximum W	—	52.5	57.0	53.2	51.7	45.0
W at braincase	—	41.3	42.5	—	—	32.0
W interorbital	—	17.7	16.0	—	15.0	15.0
Anterior orbit to canine	—	27.7	26.4	—	26.0	29.0
Anterior orbit to supraoccipital	—	55.3	50.7	—	54.2	57.0
W muzzle at infraorbital foramen	21.5	21.5	17.0	17.6	19.9	16.5
W across canines	12.0	12.0	11.5	12.4	11.8	11.5
L C-M2	—	34.4	32.2	31.2	29.1	31.1
L C-M3	40.0	39.3	40.2	38.0	39.4	43.1
L P1-M2	28.7	31.4	29.7	26.3	34.1	27.5
L P1-M3	35.0	36.1	36.7	33.0	40.0	39.0
L P1-4	15.5	17.6	17.4	14.0	19.2	14.0
L M1-2	12.5	13.9	12.3	14.2	16.0	14.5
L M1-3	—	20.6	19.2	18.2	21.5	21.5
W M3	—	5.5	4.5	4.8	5.5	—
Depth malar below orbit	—	7.9	—	10.0	9.1	7.0
<u>Lower jaw</u>	UCMP 27720 (type)	SDNHM 43442	SDNHM 43438	SDNHM 28574	SDNHM 47889	
Jaw L	—	64.0	63.8	62.0	69.5	
L canine to condyle	—	60.0	54.5	55.0	67.1	
Depth at coronoid	—	21.0	22.0	20.0	17.5	
Depth at anterior m3	15.0	17.0	14.5	14.5	12.0	
L c-m3	—	43.0	36.5	41.7	39.0	
L p1-m3	39.0	40.0	37.0	38.0	36.5	
L p1-4	14.5	14.3	12.5	15.0	14.0	
L m1-3	—	24.3	22.0	22.6	24.8	

well-developed midline sutures. There is a well-marked internal narial opening, but much of the basisphenoid region is broken in this specimen. Except for the huge auditory bullae, very little of the rest of the basicranium is well enough preserved for detailed description. However, there are large, pointed triangular paroccipital processes that wrap around the posterolateral surfaces of the bullae. The teeth are described elsewhere, but show the typical extreme hypsodonty of all leptauchenines.

In posterior view (Fig. 2D), the long paroccipital processes are striking, as are the large bullae. The broad lambdaoid crest can be seen, as can the large tube-like auditory meatuses. There is a broad foramen magnum, with well-developed occipital condyles. Numerous mandibles and rami are known from the SDNHM collections but they provide no additional features not already described by Stock (1930) and Schultz and Falkenbach (1968).

Partial skeletons and postcrania are known from a variety of SDNHM *Sespia californica* specimens from the Otay Formation, and are illustrated in Figure 3. In most respects, they differ little from other leptauchenine postcrania described by Scott (1940) and Schulz and Falkenbach (1968), except that they are smaller. Measurements of the postcrania are given in Table 2, and discussed further below.

Discussion—The tiny size of *S. californica* (it is the smallest of

all known leptauchenines) has always tended to support the validity of this taxon, and the only question is whether it could be distinguished from High Plains *L. nitida*. The specimens from the Otay Formation and the Sespe Formation are within the same size range in almost every variable (Table 1, Fig. 4), so the two California samples are the same species.

Whenever size is a criterion for taxonomic distinctions, the question naturally arises as to whether size differences could be due to sexual dimorphism. In the case of *S. californica*, we can rule this out because all the smaller specimens are found only in the Arikareean of California, while the larger specimens (here referred to *S. nitida*) are restricted to the High Plains. In addition, there is some evidence of sexual dimorphism within the *S. californica* sample from the Otay Formation. The sample of palates and maxillae seem to have two discrete sizes of upper canines: noticeably larger than the adjacent P1 or P2, or about the same size as the P1 or P2. (Due to wear, it is difficult to get reliable measurements of this size difference, but visually it is striking and easily recognized). These two non-overlapping clusters of canine types suggest sexual dimorphism, which is common in many other hornless artiodactyls, such as hippos, pigs, peccaries, camels, tragulids, moschids, and many extinct groups. However, there is no evidence with the Otay sample that there is any dimorphism of size or any other feature.

TABLE 2. Measurements of postcrania of *Sespia californica* (in mm). Conventions follow Schultz and Falkenbach (1968). L = length; W = width; SD = standard deviation.

	MEAN	SD	N
Scapula olecranon W	11.1	3.2	5
Scapula maximum W of blade	27.8	5.0	3
Scapula maximum L	44.5	2.8	4
Humerus L	66.0	4.8	10
Humerus midshaft anteroposterior W	7.5	1.7	10
Humerus midshaft transverse W	6.6	1.6	10
Radius L	61.8	3.4	6
Radius midshaft anteroposterior W	5.6	1.3	6
Radius midshaft transverse W	5.8	2.7	6
Ulna L	75.3	2.8	8
Ulna midshaft anteroposterior W	7.0	1.7	8
Ulna midshaft transverse W	5.1	1.8	8
Metacarpal III L	24.4	3.2	5
Metacarpal III transverse width	4.9	0.9	5
Femur L	64.9	2.7	12
Femur midshaft anteroposterior W	5.5	1.3	12
Femur midshaft transverse W	6.8	0.5	12
Tibia L	68.1	4.5	6
Tibia midshaft anteroposterior W	5.9	0.8	6
Tibia midshaft transverse W	6.0	0.6	6
Metatarsal III L	29.0	2.7	3
Metatarsal III transverse W	5.0	0.6	3

Both large-canine and small-canine individuals plot with overlapping size distributions in every variable. To test for the significance of this result, a student's t-test was performed (Fig. 5). For M1 length, M1 width, M1-M3 length, and P2-M3 length the probabilities were 0.894, 0.875, 0.617, and 0.687, respectively, that the large-canine and small-canine samples come from the same statistical population. These values support the acceptance of the null hypothesis that there is no statistical difference between the grouped distributions of canine size and the rest of the dentition.

Janis (1982; also in Lander, 1998) suggested that there might be sexually dimorphic "horns" on the tips of the nasals and maxillaries of leptaucheniines. We examined all the specimens with well-preserved nasal regions, and found no association between rugose nasal bones and canine size. We also examined this feature in all the leptaucheniine skulls in the AMNH collection from which Janis made her observations. We find that the supposed "horns" are simple rugose areas on the nasal-maxillary suture, just in front of the facial vacuity. They are probably due to the fact that this suture is a point of weakness in the skull, due to the large area of the facial vacuity behind it. In many specimens, it was apparently robust and heavily ossified to support this weak, narrow suture. In addition, post-mortem dorsoventral crushing has caused this suture to buckle, giving the appearance of a horn-like protuberance. During crushing, the anterodorsal process of the maxilla protrudes upward as it breaks away from the suture with the nasal bones. However, we found no evidence of a rugose nasal boss that might have supported horns, as is found in rhinoceroses or a number of artiodactyls.

Sespia nitida (Leidy, 1869)

Figures 6-7, Table 3

Leptauchenia nitida Leidy, 1869

Leptauchenia (Sespia) nitida: Stock, 1930

Leptauchenia minora Schlaikjer, 1935

Leptauchenia nitida: Thorpe, 1937

Otay vs. Sespe

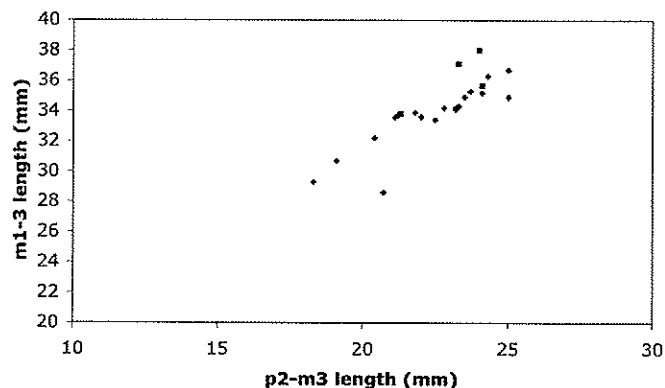


FIGURE 4. Comparison of lower tooth dimensions of jaws of *Sespia californica* from the Otay Formation (diamonds) and from the Sespe Formation (squares), showing overlap in size range.

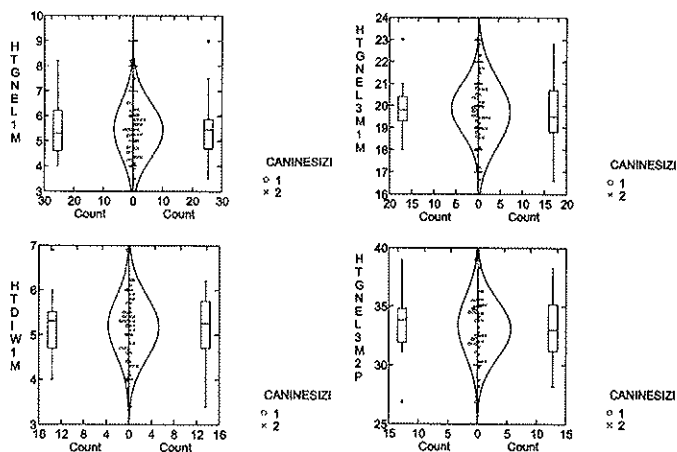


FIGURE 5. Student's t-test comparing dimensions of specimens of *Sespia californica* from the Otay Formation with large (presumed male) canines (circles) and small (presumed female) canines (x symbols). In all four variables, the size distributions of presumed male and female samples are statistically indistinguishable. (Upper left) M1 length; (Upper right) M1-3 length; (lower left) M1 width; (lower right) P2-M3 length. These plots show that presumed male and female specimens do not differ in size or in any other variable except upper canine size.

Sespia nitida: Schultz and Falkenbach, 1968

Sespia marianae Schultz and Falkenbach, 1968

Sespia nitida: Lander, 1998 (in part)

Holotype—ANSP 10870, partial female skull, from the early Arikarean, White Earth Creek, White River drainage, Sioux County, Nebraska (Fig. 6).

Hypodigm—Schultz and Falkenbach (1968, p. 249) provided a detailed list of dozens of *S. nitida* specimens in the F:AM, MCZ, and AMNH collections, so this will not be repeated here. The hypodigm also includes numerous F:AM and UNSM specimens referred to *S. marianae*.

Distribution—Early-middle Arikarean of the High Plains (Sharps Formation in South Dakota; "brown siltstone" member of the Brule Formation and Gering Formation and equivalents in western Nebraska, northeastern Colorado, and eastern Wyoming).

Diagnosis—Medium-sized specimens of *Sespia* (see Tables 1, 2); infraorbital foramen above anterior P3 to anterior P4.

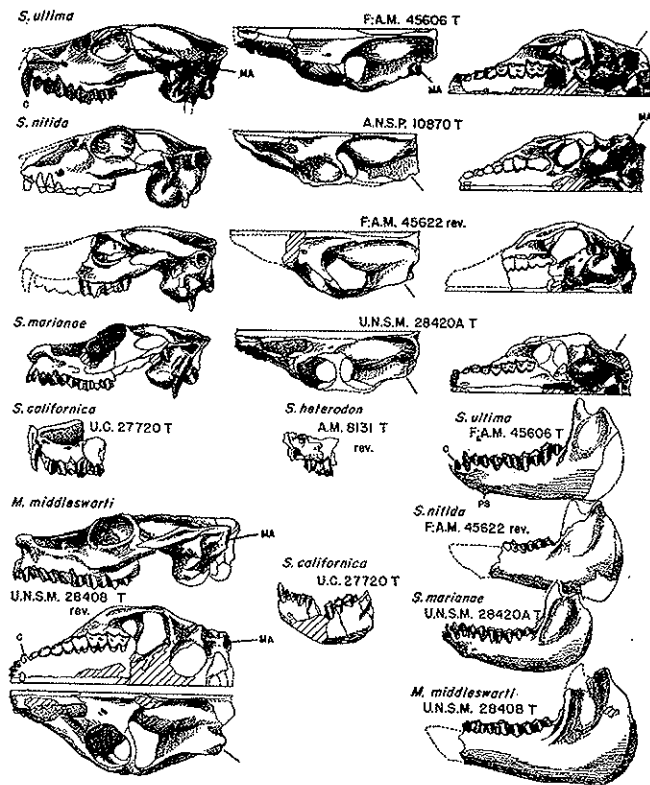


FIGURE 6. Holotypes of the species of *Sespia*, all drawn to the same scale, and shown in lateral, dorsal, and palatal views of skulls, and lateral views of mandibles. After Schultz and Falkenbach (1968, Fig. 31).

Description—No new material of *S. nitida* has appeared since Schultz and Falkenbach (1968), so there is no need for additional description here.

Discussion—Schultz and Falkenbach (1968) provided justification for the validity of *S. nitida*, and showed that *Leptauchenia minor* (Schlaikjer, 1935) is a junior synonym of *S. nitida*. However, they erected a new taxon, *Sespia marianae*, based on specimens from the lower Gering Formation (many of which are now known to come from the “brown siltstone member” of the Brule Formation, as redefined by Tedford et al., 1996), which they claimed was smaller and less robust than *S. nitida*. However, they provided no rigorous quantitative or statistical justification for this distinction, and most of the characters listed in their diagnosis (p. 244) are clearly due to the fact that these specimens are slightly less robust than typical *S. nitida*. In most size measurements, specimens of *S. marianae* fall well within the size range of typical *S. nitida* (Fig. 7), so there is no size distinction between the two species, as claimed by Schultz and Falkenbach (1968, p. 244). We suspect that they erected *S. marianae* to separate the specimens from the lower Gering Formation from *S. nitida* of the upper Gering Formation, but this distinction is not based on any valid morphological criterion, so has no relevance to species diagnoses.

Lander (1998) suggested that *S. nitida* and *S. californica* are synonyms. However, in most size variables (Tables 1, 3; Fig. 7), nearly all specimens of *S. nitida* are larger than those of *S. californica*, with only slight overlap, so it is possible to make the distinction between the two species, and uphold their validity. In addition, *S. nitida* does not occur in California, nor does *S. californica* occur in the High Plains, so there appears to be a clear geographic separation between them as well, which further justifies the species separation.

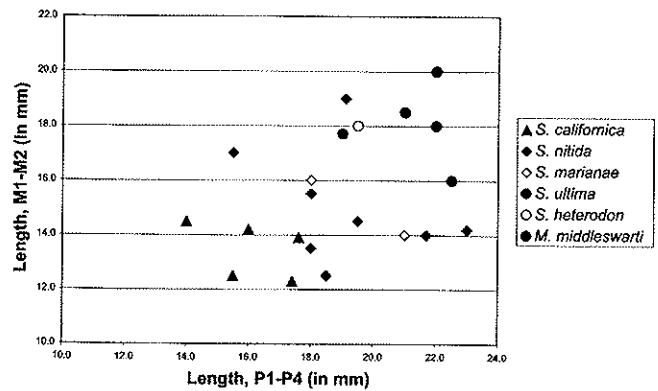


FIGURE 7. Plot of M1-2 length versus P1-4 length of the best skulls of different *Sespia* species, showing the small individuals of *S. californica* (solid triangles), the intermediate individuals of *S. nitida* (gray diamonds), and the large individuals of *S. ultima* (solid circles). The position of other proposed species within these size clusters is shown by other symbols.

Sespia ultima Schultz and Falkenbach, 1968

Figures 6-7, Table 3

Sespia ultima Schultz and Falkenbach, 1968

Megasespia middleswarti Schultz and Falkenbach, 1968

Sespia nitida CoBabe, 1996 (in part)

Sespia nitida: Lander, 1998 (in part)

Holotype—F:AM 45606, partial skull from the Monroe Creek Formation, Muddy Creek area, North Platte River drainage, Niobrara County, Wyoming (Fig. 6).

Hypodigm—19 F:AM specimens listed by Schultz and Falkenbach (1968:254); 10 F:AM and UNSM specimens of *Megasespia middleswarti* recorded by Schultz and Falkenbach (1968:256).

Distribution—From the early Arikarean (upper Gering Formation and equivalents) and the middle Arikarean (Monroe Creek Formation) of Niobrara and Laramie counties, Wyoming, and Banner, Sioux, and Morrill counties, Nebraska.

Diagnosis—Largest and most hypsodont species of *Sespia*; infraorbital foramen between P3 and P4.

Description—No additional specimens have been discovered since Schultz and Falkenbach (1968), so no further descriptions are possible.

Discussion—Schultz and Falkenbach (1968) erected the taxon *Sespia ultima* for the middle Arikarean (youngest) members of the *Sespia* lineage, and pointed out that they were also larger and more hypsodont than specimens of *S. nitida* from the early Arikarean. This distinction still holds (Table 3; Fig. 7), so we tentatively retain *S. ultima* for these large specimens of *Sespia*. Although the sample size is still small, nearly all specimens of *S. ultima* are larger than any specimen of *S. nitida*, so they can be objectively recognized by their size.

Schultz and Falkenbach (1968, p. 255) erected the new genus *Megasespia*, with one species, *M. middleswarti*, for large individuals of *Sespia* from the upper Gering Formation and equivalents in Nebraska and Wyoming. Their justification for the new taxon was that they are larger than typical *S. nitida* from the Gering Formation, but they did not compare *M. middleswarti* to *S. ultima* because they were from different (but successive) stratigraphic levels. Their diagnosis includes no valid criteria other than size; most of their “diagnostic features” are due to the fact that the specimens of *M. middleswarti* are dorsoventrally flattened, so they “include forms with broad, flat skulls.” When they are plotted with other materials, *M. middleswarti* falls within the range of *S. ultima* (Fig. 7). We suspect that Schultz and Falkenbach (1968) erected this taxon because throughout their publications all of

TABLE 3. Measurements of skulls and jaws of *Sespia* (in mm). Conventions follow Schultz and Falkenbach (1968, Table 10). L = length; W = width.

Skulls	ANSP 10870 (type of <i>S. nitida</i>)	F:AM 45611A (<i>S. nitida</i>)	LACM 18845 (<i>S. nitida</i>)	UNSM 28420A (type of <i>S. marianae</i>)	F:AM 45606 (type of <i>S. ultima</i>)	UNSM 28408 (type of <i>Megasespia</i>)
L supraoccipital to incisors	90.0	92.0	81.5	87.0	96.0	108.0
Basal L	81.0	83.0	73.5	72.5	81.0	—
Maximum W	50.0	65.0	44.3	52.5	53.5	73.0
W at braincase	24.0	33.0	36.0	27.5	29.0	34.0
W interorbital	24.0	—	17.7	21.5	24.0	25.5
Anterior orbit to canine	36.0	43.0	30.0	32.0	37.0	39.0
Anterior orbit to supraoccipital	62.0	—	—	56.0	66.0	—
W muzzle at infraorbital foramen	22.0	—	22.0	22.0	25.0	32.0
W across canines	—	—	15.9	13.5	14.0	18.0
L C-M2	—	40.0	32.5	39.0	45.0	43.0
L C-M3	—	49.0	39.5	39.0	50.0	53.0
L P1-M2	—	34.0	28.5	—	40.5	39.0
L P1-M3	40.5	43.0	37.0	—	45.0	48.5
L P1-4	18.5	18.0	15.5	18.0	21.0	22.0
L M1-2	12.5	15.5	—	16.0	18.5	18.0
L M1-3	22.0	25.0	19.5	—	26.0	28.0
W M3	6.5	6.5	6.6	6.0	6.5	8.5
Depth malar below orbit	10.0	12.0	16.6	10.0	11.0	11.5
Lower jaw	ANSP 10870 (type of <i>S. nitida</i>)	F:AM 45611A (<i>S. nitida</i>)	LACM 18845 (<i>S. nitida</i>)	UNSM 28420A (type of <i>S. marianae</i>)	F:AM 45606 (type of <i>S. ultima</i>)	UNSM 28408 (type of <i>Megasespia</i>)
Jaw L	—	81.0	—	71.0	79.0	—
L canine to condyle	—	78.0	—	66.0	74.0	—
Depth at coronoid	—	44.0	29.0	37.0	41.0	—
Depth at anterior m3	—	19.0	21.0	17.0	18.0	23.0
L c-m3	—	—	—	48.5	54.0	—
L p1-m3	—	—	36.2	45.5	50.0	—
L p1-4	—	17.0	16.0	17.0	18.0	—
L m1-3	—	27.0	25.0	28.5	32.0	32.0

their species are restricted to one stratigraphic level, so that if these specimens were larger than contemporary *S. nitida*, they had to be a new taxon; in their minds, they could not possibly be the same taxon as the slightly younger *S. ultima*.

CoBabe (1996) and Lander (1998) suggested that *S. ultima* and *S. nitida* are synonyms, but provided no detailed justification for this synonymy. Although these species are very similar in most features, they can be clearly distinguished in size, so we consider both taxa to be valid.

Sespia heterodon (Cope, 1878)

Figures 6- 8

Cyclopidius heterodon Cope, 1878

Pithecostes heterodon: Cope, 1884

Cyclopidius (Pithecostes) decedens: Matthew, 1899 (in part)

Cyclopidius (Pithecostes) heterodon: Loomis, 1925

Cyclopidius simus Thorpe, 1937 (in part)

Sespia heterodon: Schultz and Falkenbach, 1968

Sespia nitida: CoBabe, 1996 (in part)

Sespia nitida: Lander, 1998 (in part)

Holotype—AMNH 8131, from the early Arikareean Deep River

beds, Smith River Valley, southeast of Fort Logan, Meagher County, Montana (Figs. 6, 8).

Hypodigm—AMNH 21328, the anterior portion of a skull, from the same locality as the type specimen (Schultz and Falkenbach, 1968: 253).

Discussion—*Sespia heterodon* was erected by Cope (1878) as *Cyclopidius heterodon* based on a fragmentary maxilla with very hypsodont teeth and no styles (Fig. 9), so it is clearly related to *Sespia* and not to other leptauchenines. In the years following Cope's (1878) original description, the specimen had been reassigned to *Pithecostes*, *Cyclopidius (Pithecostes)*, and then to *Sespia*, thanks to the enormous taxonomic confusion in the oreodonts. Unfortunately, only one additional specimen has been recovered, and it is not much better than the type specimen. Most of the skull, and all of the jaw and postcranials, are still unknown.

In size (Fig. 7), the teeth of the type specimen of *S. heterodon* fall in the overlap between *S. nitida* and *S. ultima*, so it is not possible to clearly assign it to one taxon or the other based on the size of the teeth. If more of the skull were known, it might be possible to use other skull measurements to determine whether it is a synonym of one of these taxa, or something that is truly distinct. Until better material is recovered, we retain *Sespia heterodon* as a doubtfully valid taxon.

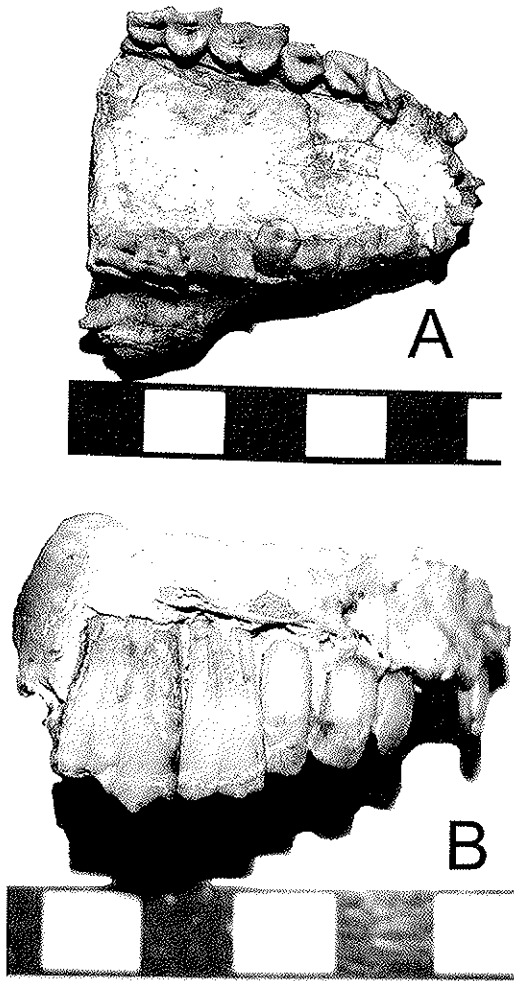


FIGURE 8. Type specimen of *Sespia heterodon* (AMNH 8131), showing the extreme hypsodony and the poor preservation of this questionable taxon.

LIMB BONE ALLOMETRY

Any time dwarfing or size reduction occurs in a lineage, it is worth asking whether there are interesting allometric trends in limb scaling (McMahon, 1975; Alexander et al., 1979; Prothero and Sereno, 1982). The large sample of limb bones from the SDNHM collections of *Sespia californica* (Table 2) provides the first good set of measurements of a single large population of leptauchenine limbs, and allows us to test these hypotheses. To facilitate this analysis, we measured all the available postcrania of the remaining leptauchenine population samples in the AMNH, so that there would be comparable data.

All limb data were measured to the nearest millimeter, averaged for each species sample (so the plots do not mix interspecific with intraspecific allometry) and plotted on Excel spreadsheets, and their slopes calculated by both least squares and reduced major axis methods. As is apparent from Figure 9, the sample size is still not large, since surprisingly few postcrania are available for most leptauchenine taxa. In addition, the range of sizes of individuals is not large. It is only about half an order of magnitude in linear dimensions, or about 3 to 26 kg in body weight estimated from tooth dimensions. Thus, we do not have the wide range of body sizes ("mouse to elephant") necessary to obtain the most robust allometric data.

Nevertheless, there are some interesting results (Fig. 9). McMahon (1975) predicted that limb bones lengths should scale with a slope of

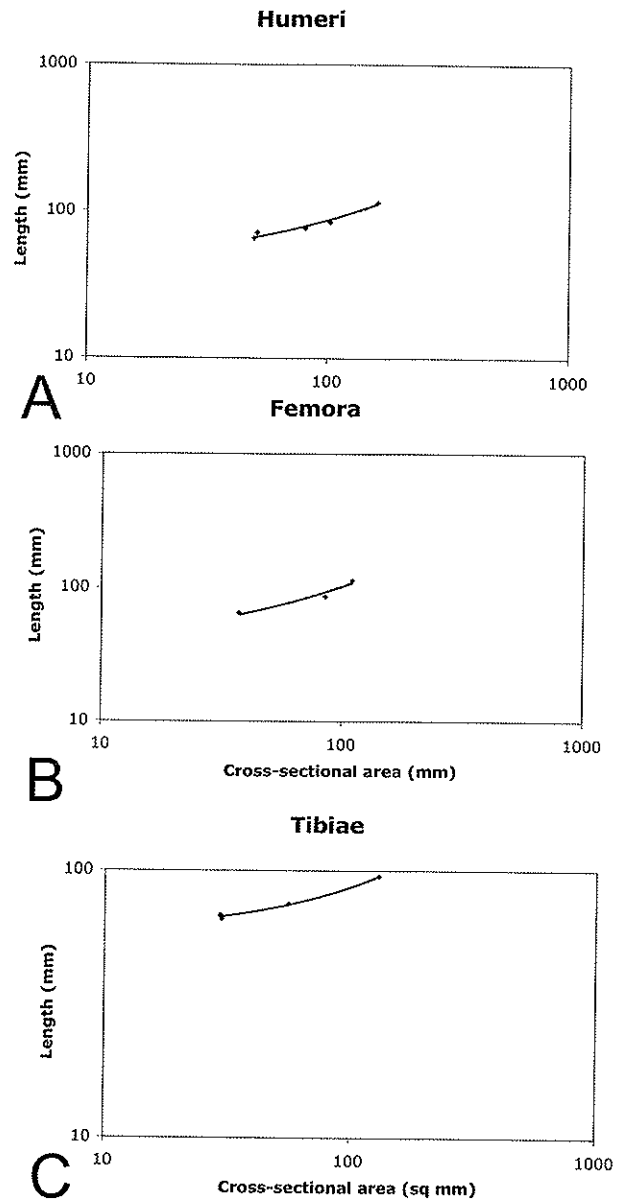


FIGURE 9. Allometric plots of leptauchenine limb length versus cross sectional area for (A) humeri; (B) femora; and (C) tibiae. Each diamond is the mean of a different species sample of leptauchenine; the smallest diamond is *Sespia californica*.

0.67 relative to limb diameters. In actuality, within the non-dwarfed Artiodactyla he found slopes of 0.66 for humeri, 0.75 for the femora, and 0.65 for the tibiae. Prothero and Sereno (1982, table 2) found that in non-dwarfed ceratomorphs, the slope was actually between 0.48-0.61 for the humerus, femur, and tibia, but that the dwarfed rhinos and hippos were significantly more robust. For the leptauchenine humerus, we find a slope of 0.89; for the femur, the slope is 0.88; and for the tibia, the slope is 0.42. On this metric, the slope appears steeper for the humerus and femur, and shallower for the tibia. This suggests that the dwarf *Sespia* humeri and femora are more robust than predicted by simple allometric scaling (consistent with earlier studies), but the tibia is less robust (not previously reported).

To check this result, we looked at the predicted allometric slope for plots of a linear dimension (limb length) versus cross-sectional area, which is 0.38 (Prothero and Sereno, 1982, table 2). For humeri, the slope

was 0.27, and for femora, the slope was 0.36, and for tibia, the slope was 0.38, which are probably not significantly different from predictions given the small sample size and limited range of sizes (Fig. 9). Prothero and Sereno (1982) found that the limbs of dwarfed rhinoceroses and dwarf hippopotami were significantly more robust in cross-sectional area than predicted for their body size within the trends of their non-dwarfed relatives. In our results of length versus area, none of the limbs of *Sespia* are significantly more or less robust than predicted. This is probably due to the fact that *Sespia* is not as extreme an example of dwarfing as the dwarf rhinos or hippos, and also that it was a relatively small animal with unspecialized limbs, not a huge graviportal animal where there would be a noticeable change in limb proportions with significant dwarfing.

CONCLUSIONS

Analysis of new specimens of *Sespia* from the Otay Formation gives a fuller picture of *Sespia californica*, and supplements the material from the Sespe Formation. *Sespia californica* shows some sexual dimorphism in the upper canines, but in no other feature, and does not show any "horns" on the nasals as claimed by Janis (1982). After statistical analysis, only three *Sespia* species (of the six originally recognized by Schultz and Falkenbach, 1968) can be statistically distinguished: *Sespia californica*, *Sespia nitida*, and *Sespia ultima*. *S. marianae* Schultz and Falkenbach, 1968, is a junior synonym of *S. nitida* (Leidy, 1869), and *S. ultima* (Schultz and Falkenbach, 1968) includes *Megasespia middleswarti*.

The poorly known taxon *Sespia heterodon* from Montana is doubtfully valid, pending more complete specimens.

This reduction in valid species strengthens the biostratigraphic importance of *S. nitida* and *S. ultima* as diagnostic fossils for the Arikareean North American land-mammal "age" (NALMA). These two species can be used more confidently as part of the early Arikareean assemblage of terrestrial mammals present in the northern Great Plains region. Additionally, any *Sespia* samples found in southern California (in either San Diego or Ventura counties) can be confidently used as early Arikareean index fossils.

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