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Fossil carrion beetles of Pleistocene California asphalt deposits, with a synopsis of Holocene California Silphidae (Insecta: Coleoptera: Silphidae)

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Abstract. Fossil Silphidae occur in three late Pleistocene asphalt deposits in California: Rancho La Brea in Los Angeles County, McKittrick in Kern County, and Carpinteria in Santa Barbara County. Pierce's 1949 *Nicrophorus* taxa from Rancho La Brea and McKittrick are all new junior synonyms: *Nicrophorus guttula labreae, Nicrophorus mckittricki, Nicrophorus obtusiscutellum,* and *Nicrophorus investigator latifrons* = *Nicrophorus marginatus* Fabricius; *Nicrophorus guttula punctostriatus* = *Nicrophorus guttula* (Motschoulsky); *Nicrophorus investigator alpha* = *Nicrophorus nigrita* (Mannerheim). Lectotypes are designated for *N. g. labreae* and *N. i. alpha.* The following resurrected generic combinations are used: *Thanatophilus lapponicus* (Herbst), *Heterosilpha ramosa* (Say), *Heterosilpha aenescens* (Casey). A neotype is designated for *Heterosilpha ramosa. Heterosilpha aenescens* is a valid species and a lectotype is designated for it. The fauna of each deposit includes: Rancho La Brea: *T. lapponicus, H. ramosa* (and perhaps *H. aenescens*), *N. marginatus, N. guttula,* and *N. nigrita*; McKittrick: *N. guttula* and *N. marginatus*; Carpinteria: *N. guttula* and *N. nigrita. Nicrophorus marginatus* is the best represented species of *Nicrophorus* in the asphalt, although it is the least common species of the genus in the modern southern California fauna. Possible reasons for this apparent faunal change include real faunal changes and biased preservation. Due to limited knowledge of silphid ecology, detailed paleoecological conclusions cannot be made at the present time. All silphid species presently known from California are reviewed, and a key is given. *Aclypea bituberosa* (LeConte) (new combination) occurs in the Sierra Nevada Mountains, *Thanatophilus sagax* (Mannerheim) (new combination) is raised from synonymy, *Pelatines latus* (Mannerheim) is recorded from northern California, a lectotype is designated for *Nicrophorus hecate* (Bland), and several other geographic ranges are extended.

Introduction

Pierce (1949) recognized 6 species and 5 subspecies of Silphidae from the Rancho La Brea and McKittrick asphalt deposits. Two of these species and 4 subspecies were described as new. This study reevaluates Pierce's (1949) taxa and records newly found specimens. In order to place the fossils properly, we review the taxonomy and distribution of the Holocene Silphidae of California.

Although most of Pierce's basic concepts (Pierce 1961) regarding fossil insects were valid, his publications and taxonomic procedures were replete with errors. Serious identification problems result from his erection of taxa based on fragmentary specimens. In addition to poor descriptions, some of his drawings were inaccurate (e.g., Carpenter 1968, Matthews and Halffter 1968). Our study was hampered by past improper labeling by Pierce and some errors in cataloging many type specimens by Sphon (1973).

All the Pleistocene specimens studied represent Holocene species and fall within reasonable ranges of morphological variation. The use of subspecific names is not

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justified, because the fossil forms are not geographic races and there is no morphological basis upon which to found chronosubspecies. Studies by other workers indicate that almost all Pleistocene insect fossils represent extant species (Coope 1970, Matthews 1977).

There is confusion regarding proper application of generic and specific names in the Silphidae. Members of the Silphini discussed here usually have been included in *Silpha* Linnaeus 1758. However, we are presenting several resurrected and new combinations, in agreement with R. B. Madge's (*personal communication*) as yet unpublished review of the world Silphini.

Our synonymies cite only original descriptions and important references; more complete synonymies are given by Hatch (1928) and Madge (1958). All fossil silphids we examined are listed in the text, along with appropriate specimen numbers (LACMIP type number, RLP entomology number, and/or Pierce's number [with "C" or "McK" prefix]). All are in LACM, except those from UCMP localities 2051 and 7139. Those not cited by Pierce (1949) are preceded by an asterisk (*).

Abbreviations for collections consulted and cited in the text are:

ANSP Academy of Natural Sciences of Philadelphia;
CAS California Academy of Sciences;
CDA California Department of Food and Agriculture;
CIT California Institute of Technology (VP collection now housed at LACM);
CMNH Carnegie Museum of Natural History;
LACM Natural History Museum of Los Angeles County;
LACMIP LACM Invertebrate Paleontology collection;
MCZ Museum of Comparative Zoology, Harvard University;
RLP Rancho La Brea Project (current LACM excavation of Pit 91);
SBMNH Santa Barbara Museum of Natural History;
UCMP University of California Museum of Paleontology, Berkeley;
UCR University of California at Riverside;
USNM United States National Museum of Natural History.

We also examined Holocene silphids from the American Museum of Natural History, British Museum (Natural History), California Insect Survey (University of California at Berkeley), Field Museum of Natural History, Peabody Museum (Yale University), San Diego Natural History Museum, University of California at Davis, and our personal collections. Records from the California Channel Islands, compiled in ongoing SBMNH research, are included in the Holocene distribution summaries.

Other abbreviations used in the text are:

BD below datum (for depths within Pit 91, Rancho La Brea);
B.P. before present (in radiocarbon dating, present calculated as 1950);
loc. locality number;
VP vertebrate paleontology.

Localities

Pierce (1949) studied fossil silphids only from the Rancho La Brea and McKittrick asphalt deposits (Pierce 1946, 1947*a*, 1947*b*). We studied silphids from these localities and the Carpinteria asphalt deposit. Additional vertebrate fossil bearing asphalt deposits near Maricopa in Kern County (Macdonald 1967) have yielded no silphids.

RANCHO LA BREA

The Rancho La Brea asphalt deposits are located in Hancock Park, Los Angeles, Los Angeles County, California. More than 100 individual excavations or "pits" have been made since 1905. Most of these were unproductive test holes and fewer than 15 were major sources of fossil vertebrates (Howard 1962, Marcus 1960, Stock 1956). Before the reopening of Pit 91 in 1969, emphasis was placed on large vertebrates;

insects and other small fossils were neglected by the early excavators. In addition to Pierce's material, we have studied silphids salvaged from miscellaneous unsorted material from several original excavations and silphids recovered in the modern excavation of Pit 91.

Most of the silphids from older LACM excavations were studied by Pierce (1949). Silphids from Pits 9, 28, 37, and 81 (excavated between 1913 and 1915) bear no further data than pit number. Pits A and B were excavated in 1929, and Pierce's "Bliss 29" specimens were collected in 1929 by W. Bliss from Pits A, B and C after the official LACM excavation ended. The age of "Bliss 29" insects is questionable due to unknown locality and possible contamination. Pierce's "Pit X" consisted of "mixed material lacking data" (Pierce 1954), and may not be fossil. We have also seen silphids from UCMP loc. 2051, a large excavation made in 1912 (Stoner 1913).

Pit 91, partially excavated in 1915, was reopened in 1969 by the Rancho La Brea Project of LACM. The current excavation is laid out on the basis of 3 foot square (≈.8 square metre) grids, normally excavated in 6 inch (≈15 cm) layers (each assigned a grid number), within a coordinate system, lettered from south to magnetic north and numbered from east to west. Once separated from the surrounding matrix (G. Miller 1971), the insects are cleaned with 1,1,1-trichloroethane (other solvents such as xylene may also be used) in ultrasonic cleaners. Each insect fragment (or conspecific specimens with the same data) is assigned an RLP entomology catalog number and is stored dry in a gelatin capsule housed in a glass vial.

Due to the enormous quantity of fossil insects recovered and the limited support available for processing them, most of the Pit 91 insects are not available for study at present. Thus, our treatment of Pit 91 silphids is only preliminary, and we hope to continue our research. We have specimens from 13 grids in 7 columns in the northeast corner of the excavation, as follows: column G-3: grid GJM 360 (5′4″ to 7′ BD); J-6: GJM 346 (8′8″ to 9′6″ BD); L-4: GJM 408 (6′ to 6′6″ BD), GJM 612 (7′ to 7′6″ BD), GJM 856 (7′6″ to 8′ BD); L-5: GJM 364 (5′4″ to 5′10″ BD), GJM 568 (6′4″ to 7′ BD); M-3: GJM 275 (5′ to 5′3¾″ BD), GJM 295 (5′3¾″ to 6′3″ BD), GJM 550 (7′ to 7′6″ BD); M-4: GJM 777 (7′ to 7′6″ BD); and N-3: GJM 273 (5′ to 6′9½″ BD), GJM 838 (8′6″ to 9′ BD). These grids range in depth from 5 to 9½ feet BD, with most between 6 and 8 feet BD. Two radiocarbon dates from the northeast corner of the excavation can be approximately correlated with the silphids. The dates, both from bone collagen of *Smilodon californicus* Bovard, are (Berger and Libby, *in press*): 30 800 ± 600 radiocarbon years B.P. from 6′¾″ to 7′1″ BD in column L-5 (UCLA-1718) and 32 600 ± approximately 2800 radiocarbon years B.P. from 7′2½″ to 7′6″ BD in columns M-3 + 4 (UCLA-1738D). These dates and others (L. F. Marcus, *personal communication*) from elsewhere in Pit 91 indicate that most of our silphids are probably ≈30 000 radiocarbon years old. Higher grids (GJM 273, 275, 295) should be younger and the deeper grids (especially GJM 838) older. The silphid-bearing deposit in the northeast corner was generally a productive deposit for vertebrates (mostly small) that terminated at a depth of ≈8 feet 6 inches [2.59 m] (A. Tejada-Flores, *personal communication*). Silphids may be present in other sectors of Pit 91, in material which has not yet been sorted.

McKITTRICK

The McKittrick asphalt deposit is ≈0.8 km south of McKittrick, Kern County, in the southern San Joaquin Valley. The biota is considered late Pleistocene, although there is some "admixture of a later (Recent, but not present-day) assemblage" (DeMay 1941*a*:59). Berger and Libby (1966:492) dated the flora reported by Mason (1944) at 38 000 ± 2500 radiocarbon years B.P. (UCLA-728) based on UCMP plant material which lacked specific excavation data (D. I. Axelrod, *personal communication*). However, the age of Pierce's material is questionable and it may be subfossil.

The described fossil localities are all in the NE¼ of the NE¼ of Section 29, Township 30 South, Range 22 East (Mount Diablo base line and meridian). The original 1921 excavation (UCMP loc. 4096) was on the southeast side of the present northern

fork of State Highway 58, but the 1925–1927 excavations (UCMP loc. 7139 and CIT VP loc. 138 = LACMIP loc. 5103) were across that road on the southeast side. The CIT VP loc. 138 "comprises essentially the same area as U.C. locality 7139" (Schultz 1938:130). Pierce's sites 3 and 4 (LACMIP loc. 260) were southeast of the original localities, on the east side of the present State Highway 33 about 1.2 km south of McKittrick. In 1945, Pierce excavated matrix from a depth of 2 feet (≈.6 metres) below the surface in a fracture in the recently exposed bank, designating this "site 3" (Pierce 1947*b* and unpublished notes). In 1947, Leonard Bessom of LACM collected from a depth of 4 feet (≈1.2 m) near site 3. Pierce designated Bessom's locality "site 4," and wrote that the 2 foot (≈.6 m) depth at site 3 would correspond to the 24 to 30 inch (.6–.76 m) layer at site 4. Pierce believed site 3 was younger than site 4, and that the insects from site 3 indicated drier conditions than those from site 4. Stratigraphic and age relationships of Pierce's localities to the CIT and UCMP localities have not been determined, but Pierce's localities appear to be much younger.

CARPINTERIA

The Carpinteria asphalt deposit is located on a seaside bluff overlooking the Pacific Ocean ≈1.5 km southeast of Carpinteria, Santa Barbara County, California. Fossils were discovered in the Carpinteria asphalt quarry in February 1927, and paleontological excavations were undertaken by the SBMNH, CIT and UCMP (CIT VP loc. 139 = LACMIP loc. 5102). The quarrying operation was later abandoned and the site was used as a refuse dump beginning in the 1940s. Natural topography at the site has been so drastically changed by human activities that the locations and depths of the fossil excavations can only be approximated.

The deposit is situated in a raised marine terrace of beach sands, considered middle to late Pleistocene in age (R. S. Gray, *personal communication*), that disconformably overlie shales of the Monterey Formation of Miocene age. However, the terrestrial fossil-bearing zone (not to be confused with the underlying marine zone of Grant and Strong 1934), which apparently graded into the beach sands, is considered late Pleistocene in age. Two cones of *Pinus radiata* Don, which were among the first fossils collected at the site in early 1927, yielded dates ≥44 500 (QC-468), >41 000 and >53 000 (QC-467B) radiocarbon years B.P. The differences in the maximum ages of the 2 portions of QC-467B are due to differences in the statistics of separate counting in different vials (R. R. Pardi, *personal communication*). Asphalt-impregnated wood collected in 1962 from a roadcut in the asphaltic sands near the original fossil sites yielded dates >38 000 radiocarbon years B.P. (UCLA-180 and UCLA-181 in Fergusson and Libby 1964), but their stratigraphic relationship to the original excavations is unknown.

Synopsis of California Silphidae

Family Silphidae[2]
Tribe Pterolomini
Genus *Apteroloma* Hatch 1927

These small beetles (length 5–7 mm) are found under stones and debris, especially at stream margins. We are giving *Apteroloma* generic status rather than subgeneric status under *Pteroloma* Gyllenhal 1827 in accordance with studies by R. B. Madge and A. F. Newton. Papers by Van Dyke (1928), Hatch (1957), and Bolivar y Pieltain and Hendrichs (1972) are useful for identification of species. The genus has no known fossil record in California.

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[2] According to a study in preparation by A. F. Newton, the tribes Pterolomini and Agyrtini should be removed from the Silphidae and combined into a distinct family. Awaiting this change, we will follow the traditional inclusion of these tribes in the Silphidae.

Apteroloma caraboides (Fall)

Pteroloma caraboides Fall 1907:235
Apteroloma caraboides of Hatch 1928:70
Pteroloma (*Apteroloma*) *caraboides* of Hatch 1957:6

Ranges from British Columbia and Idaho to northern California. Only one specimen (a syntype) is known from southern California: Mount San Antonio [="Old Baldy"], 9000 feet [≈2740 m], 19 June 1904 (C. A. Richmond:MCZ).

Apteroloma tenuicorne (LeConte)

Necrophilus tenuicornis LeConte 1859*a*:84
Pteroloma tenuicorne of Horn 1880:245
Apteroloma tenuicorne of Hatch 1927*b*:12
Pteroloma (*Apteroloma*) *tenuicorne* of Hatch 1957:6

Ranges from British Columbia, Montana and Colorado to northern California. Only one specimen is known from southern California: Mill Creek, San Bernardino Mountains, 4800 feet [≈1460 m], 15 April 1965 (CDA).

Apteroloma tahoecum (Fall)

Pteroloma tahoeca Fall 1927:136
Apteroloma tahoeca of Hatch 1928:70
Pteroloma (*Apteroloma*) *tahoeca* of Hatch 1957:6

Found primarily in the Sierra Nevada Mountains, but also in other areas of northern California and Oregon. Several old and questionable records exist for Nevada and Utah.

Tribe Agyrtini
Genus *Pelatines* Cockerell 1906

The following is the first record of the genus in California; it has no known fossil record in the state.

Pelatines latus (Mannerheim)

Necrophilus latus Mannerheim 1852:331
Pelates latus of Horn 1880:244
Pelatines latus of Cockerell 1906:240

This small (3–4 mm long) species ranges from southeastern Alaska to northern California. In California, it is known from Alameda, Del Norte and El Dorado counties (specimens in ANSP, CDA, CMNH, and MCZ).

Genus *Agyrtes* Froelich 1799

The small (length 3–5 mm) and little known North American species of *Agyrtes* were reviewed by Peck (1975). The genus has no known fossil record in California.

Agyrtes longulus (LeConte)

Necrophilus longulus LeConte 1859*b*:282
Agyrtes longulus of Horn 1880:246

Ranges from central California northwards through coastal mountains to southern Alaska and inland to Idaho, presumably associated with forest habitats.

Agyrtes similis Fall

Agyrtes similis Fall 1937:29

Known only from a few specimens from the coastal ranges of central and southern California.

Genus *Necrophilus* Latreille 1829
Necrophilus hydrophiloides Mannerheim

Necrophilus hydrophiloides Mannerheim 1843:253

Adults (length 9–11 mm) and larvae are found on carrion and decomposing vegetable matter from southeastern Alaska to southern California (extension of published range south into Los Angeles County). The species has no known fossil record in California.

Tribe Silphini
Genus *Aclypea* Reitter 1885

We are using *Aclypea* as it was used by Seidlitz (1888:311), whom we regard as the first reviser in accordance with article 24(a)(i) of the International Code of Zoological Nomenclature. These species have often been placed in *Blitophaga* Reitter 1885. The genus has no known fossil record in California.

Aclypea bituberosa (LeConte), **comb. nov.**
Figure 1A, B

Silpha bituberosa LeConte 1859*c*:6

The occurrence of *A. bituberosa* in the Sierra Nevada Mountain region has been confused and unconfirmed since Horn's misidentified record of *Silpha opaca* "near Mono Lake" (Horn 1880), based on a single specimen (now in MCZ). California occurrence of *A. bituberosa* is now well documented by these additional specimens: Alpine County: Ebbetts Pass, 8 July 1970 (F. G. Andrews: CDA), Sonora Pass, 24 June 1937 (N. W. Frazier: CAS), 27 June 1951 (E. L. Silver: LACM); El Dorado County: Echo Lake (7400 feet [≈2260 m]), 15 July 1933 (A. E. Michelbacher: CAS), [Mount] Tallac, July (A. Fenyes Colln.: CAS); Tuolumne County: no further data (A. Koebele Colln.: CAS); and Yosemite National Park: Mount Lyell, 7 August 1935 (E. C. Van Dyke Colln.: CAS). The species is also known from Colorado and Manitoba to Alberta and Oregon; its biology is discussed by Cooley (1917). The primarily Palearctic species *Aclypea opaca* (Linnaeus 1759), which is often confused with *A. bituberosa,* occurs in North America only in Alaska.

Genus *Thanatophilus* Leach 1815
Thanatophilus lapponicus (Herbst)
Figure 1C

Silpha lapponica Herbst 1793:209, plate 52: Fig. 4
Thanatophilus lapponicus of Portevin 1926:33
Silpha (Thanatophilus) lapponica of Pierce 1949:59, Figs. 1, 2 (specimens LACMIP 5722–5724)

Pleistocene.—12 specimens as follows: RANCHO LA BREA: Pit A: 2 complete and 2 partial left elytra (C3b [♂], C3c, C3d = LACMIP 5722 [♀?], C3e), *pronotal fragment; "Bliss 29": 2 complete and 2 partial right elytra (C3f = LACMIP 5723 [♂], C3g = LACMIP 5724 [♀], C3h, C3i); "Pit X": broken left elytron (C3a); *Pit 91: Grid GJM 346: complete left elytron (RLP 3366E); Grid GJM 273: elytral fragment (RLP 4040E); Grid GJM 550: broken left elytron (RLP 4041E).

Holocene.—This 11–14 mm long carrion feeder is widely distributed through Arc-

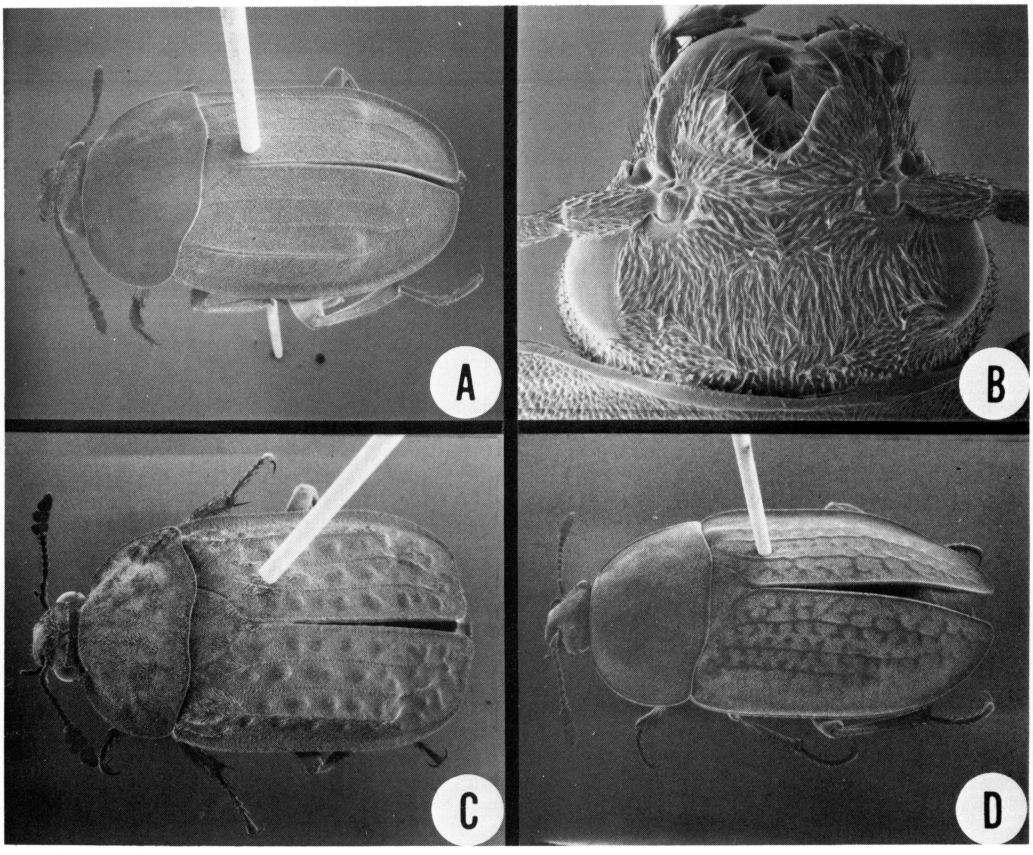

FIG. 1. A–B, *Aclypea bituberosa* (Manitoba, Canada), A, habitus; B, head; C, *Thanatophilus lapponicus*, habitus (Colorado); D, *Heterosilpha ramosa*, habitus (Colorado).

tic Europe and Asia, and in North America from Alaska and Greenland to the District of Columbia, Pennsylvania, Michigan, Iowa, Kansas, New Mexico, California and northern Mexico. *Thanatophilus lapponicus* was recorded from Santa Rosa Island, California by Fall (1897), but we have seen no specimens (which may have been destroyed in the 1906 CAS fire). It occurs more commonly in arctic and arctic alpine tundra, grassland, or open woodland habitats than in heavily forested habitats.

Thanatophilus sagax (Mannerheim), **comb. nov.**

Silpha sagax Mannerheim 1853:173

This 9–11 mm long species is poorly known, as *T. sagax* long has been considered a junior synonym of *Thanatophilus trituberculatus* (Kirby 1837). The distinguishing characteristics are as follows: In *T. sagax* the intervals between elytral striae lack tubercles, but the middle elytral stria has a single broad tubercle two thirds of the way to the apex. This tubercle slightly elevates the outer stria, which continues into the posterior quarter of the elytron. In *T. trituberculatus*, the outer stria terminates at the tubercle, with a small disjunct tubercle in the posterior quarter of the elytron.

Pleistocene.—Unknown from California.

Holocene.—*Thanatophilus sagax* ranges from northern California (Brockway, Placer County, 15 July 1941, G. S. Mansfield in CAS) through British Columbia to Alaska (Kenai Peninsula) and eastward to the Northwest Territories and Manitoba. We have seen *T. trituberculatus* from only the Northwest Territories and Manitoba.

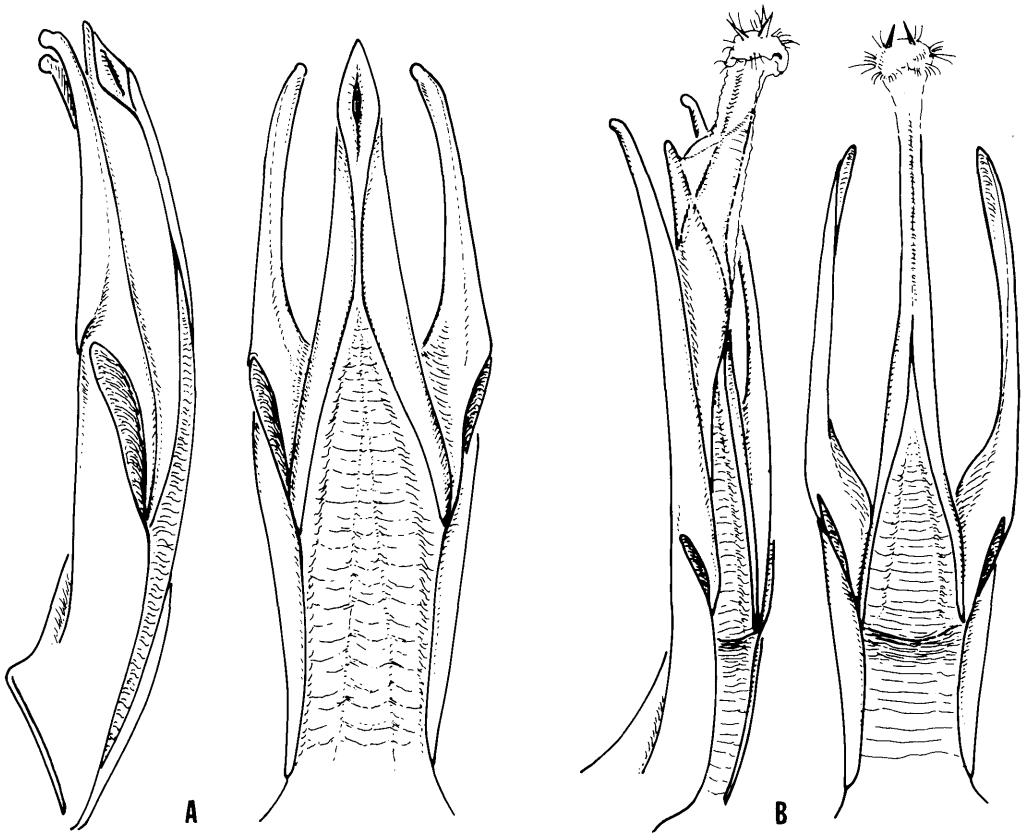

FIG. 2. Male genitalia of *Heterosilpha* species: A, *H. ramosa* (Platteville, Colorado); B, *H. aenescens* with internal sac everted (Alameda County, California). The chord of the arc from the edge of the basal sclerotization to the paramere tips is 2.8 to 3.0 mm in *H. aenescens* and 3.5 to 4.0 mm in *H. ramosa*.

Genus *Heterosilpha* Portevin 1926

Two superficially similar species, *Heterosilpha ramosa* (Say 1823) and *Heterosilpha aenescens* (Casey 1886), occur throughout most of California. *Heterosilpha aenescens* has been considered a synonym of *H. ramosa* (Arnett 1944, 1946). However, as stated by Hatch (1927*a*, 1946) and Portevin (1926), they are distinct species. Distinguishing characters (in decreasing order of reliability) are found in the male genitalia, secondary sexual characters and color. The male genitalia (Fig. 1 A, B) are distinct and offer the most reliable identification characteristics. *Heterosilpha ramosa* is sexually dimorphic in the elytral apex of females and in the tarsi of males, but it is nearly impossible to distinguish the sexes of *H. aenescens*, except by reference to the genitalia. In females of *H. ramosa* the apex of the elytra is prolonged, rather than gradually rounded as in *H. ramosa* males and both sexes of *H. aenescens*. The anterior and middle tarsi of *H. ramosa* males are strongly dilated, but there is no such tarsal dilation in male *H. aenescens*. Except for minor color and tarsal differences, *H. ramosa* males look very similar to both sexes of *H. aenescens*. The external distinguishing characteristics of *H. aenescens* are the aeneous lustre and coarser elytral sculpture. Adults of both species are 12–15 mm long.

Heterosilpha ramosa (Say)
Figures 1D, 2A

Silpha ramosa Say 1823:193
Heterosilpha ramosa of Portevin 1926:85 (as synonym, in error, of *Heterosilpha cervaria* [Mannerheim 1843]).

Silpha (Heterosilpha) ramosa of Pierce 1949:61, Figs. 3a, 3b (specimens LACMIP 5720 [rounded tip due to breakage] and 5721)

Heterosilpha ramosa was described from a specimen collected by Thomas Nuttall on "the upper Missouri" (Say 1823:193, reprinted by LeConte 1859*d*:123). Because of the complete loss of the Say collection (LeConte 1859*d*, Lindroth and Freitag 1969), we designate as **neotype** a male (MCZ 32444) in the LeConte collection bearing the following labels on its pin: a greenish disk; a handwritten label "S. ramosa/Say/cervaria/Mann."; and our neotype label.

It is generally accepted (Lindroth and Freitag 1969) that LeConte had the opportunity to compare his specimens with those in Say's collection, and that LeConte's collection is the most reliable indication of Say's concepts of his species. The greenish disk is LeConte's locality code for the area including the upper Missouri River and its tributaries, so the type locality is unchanged. In accordance with Article 75 of the International Code of Zoological Nomenclature, this neotype designation is in the interest of stability of nomenclature, is in connection with the revisionary work necessary to establish the identity of the asphalt deposit fossils, and characters differentiating the taxa are given. Our proposed designation has been discussed with other specialists on North American Silphidae and does not arouse objections.

Pleistocene.—Pierce (1949) apparently did not consider the possibility that some of his *Heterosilpha* specimens may have been *H. aenescens*. On the basis of elytra and pronota, it is impossible to separate *H. aenescens* from male *H. ramosa* with present knowledge. At least some of Pierce's Rancho La Brea elytra are *H. ramosa*, as they show female sexual dimorphism. However, *H. aenescens* elytra may be mixed with the male *H. ramosa*. Although 8 of the 11 *Heterosilpha* elytra from Pit 91 have broken tips, the 3 with the apex intact are rounded, so *H. ramosa* cannot be positively recorded from this excavation. Only future study of the morphology of Holocene *Heterosilpha* and additional *Heterosilpha* specimens from Pit 91 will resolve this question.

Heterosilpha is represented by 20 elytra and 2 pronota. The elytra fall into 3 categories: (A) female *H. ramosa*, (B) elytra with rounded apexes; which could be male *H. ramosa* or either sex of *H. aenescens*, and (C) elytra with broken or damaged tips which cannot be placed in the 2 former groups; the category and side (R = right, L = left) of each is noted below. RANCHO LA BREA: Pit A: CR (C1d); *Pit 9: AR (C1i); "Bliss 29": CL (C1a = LACMIP 5720), CR (C1b), AR (C1c = LACMIP 5721), two AL (C1e, C1f), CR (C1g), CL (C1h); *Pit 91: Grid GJM 273: BL (RLP 3247E), CL (RLP 4038E), CR (RLP 4039E); Grid GJM 295: CR (RLP 3303E); Grid GJM 360: CL (RLP 3431E); Grid GJM 364: pronotum (RLP 3486E); Grid GJM 408: BR, CL (RLP 3938E); Grid GJM 568: BL (RLP 27E), pronotum (RLP 28E); Grid GJM 612: CL (RLP 3549E, associated with *Felix atrox* skull): Grid GJM 777: CL (RLP 1180E, associated with *Smilodon californicus* skull); Grid GJM 838: BR (RLP 1824E); Grid GJM 856: CR (RLP 2164E).

Holocene.—Literature records of *H. ramosa* cannot be trusted, due to past confusion with *H. aenescens*. *Heterosilpha ramosa* occurs in much of western North America (including Santa Rosa, Santa Cruz, and San Miguel islands). Brewer and Bacon (1975) have treated the biology of *H. ramosa* in Colorado. Linsley (1942) gives additional ecological notes on *H. ramosa*, but these may refer to *H. aenescens* (we have been unable to locate voucher specimens).

Heterosilpha aenescens (Casey)
Figure 2B

Silpha aenescens Casey 1886:171
Heterosilpha aenescens of Portevin 1926:85

Heterosilpha aenescens was described from an unspecified number of specimens from San Francisco, California (Casey 1886). A **lectotype** is hereby designated as a male in the USNM bearing the labels "Cal." (with black dot in middle of the "C"),