



## 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, *Pelatinus 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, 1947a, 1947b). 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 ( $\approx 8$  square metre) grids, normally excavated in 6 inch ( $\approx 15$  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 5'3 $\frac{3}{4}$ " BD), GJM 295 (5'3 $\frac{3}{4}$ " 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 6'9 $\frac{1}{2}$ " BD), GJM 838 (8'6" to 9' BD). These grids range in depth from 5 to 9 $\frac{1}{2}$  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  $\pm$  600 radiocarbon years B.P. from 6'3 $\frac{3}{4}$ " to 7'1" BD in column L-5 (UCLA-1718) and 32 600  $\pm$  approximately 2800 radiocarbon years B.P. from 7'2 $\frac{1}{2}$ " 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  $\approx 30\ 000$  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  $\approx 8$  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  $\approx 0.8$  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 1941a:59). Berger and Libby (1966:492) dated the flora reported by Mason (1944) at 38 000  $\pm$  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 NE $\frac{1}{4}$  of the NE $\frac{1}{4}$  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 ( $\approx$ .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 ( $\approx$ 1.2 m) near site 3. Pierce designated Bessom’s locality “site 4,” and wrote that the 2 foot ( $\approx$ .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  $\approx$ 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 overlies 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  $\geq$ 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<sup>2</sup>

#### 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.

<sup>2</sup> 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 [ $\approx$ 2740 m], 19 June 1904 (C. A. Richmond:MCZ).

*Apteroloma tenuicorne* (LeConte)*Necrophilus tenuicornis* LeConte 1859a:84*Pteroloma tenuicorne* of Horn 1880:245*Apteroloma tenuicorne* of Hatch 1927b: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 [ $\approx$ 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 1859b: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 1859c: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 [ $\approx$ 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 [ $\delta$ ], C3c, C3d = LACMIP 5722 [ $\varphi$ ?], C3e), \*pronotal fragment; "Bliss 29": 2 complete and 2 partial right elytra (C3f = LACMIP 5723 [ $\delta$ ], C3g = LACMIP 5724 [ $\varphi$ ], 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-

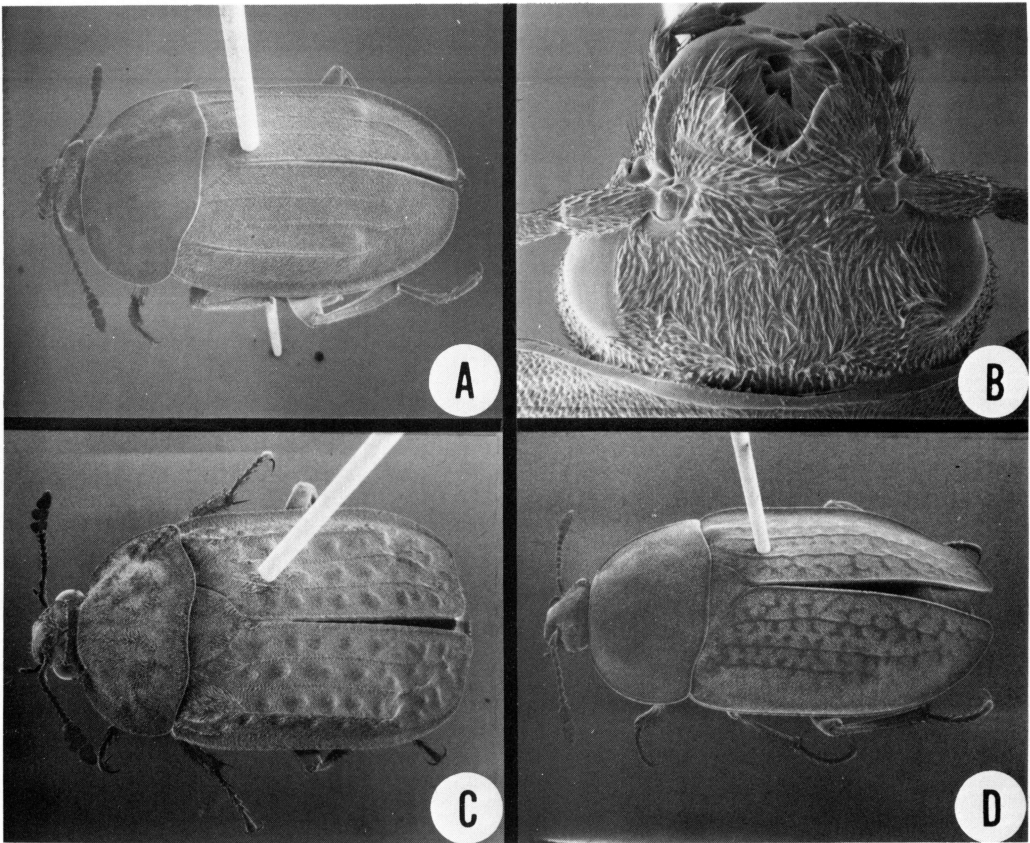


FIG. 1. A–B, *Aclypea bituberosa* (Manitoba, Canada), A, habitus; B, head; C, *Thanatophilus lapponicus*, habitus (Colorado); D, *Heterosilpha ramosa*, habitus (Colorado).

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.

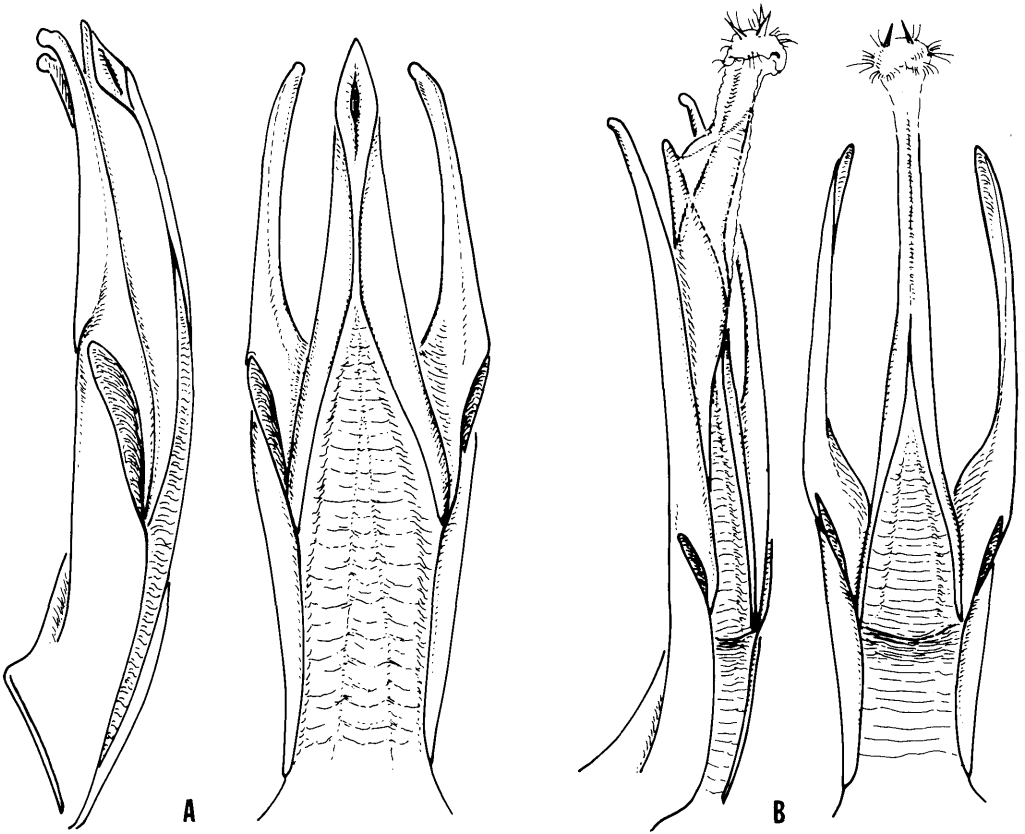


FIG. 2. Male genitalia of *Heterosilpha* species: A, *H. ramosa* (Platteville, Colorado); B, *H. aenescens* with internal sac everted (Alameda County, California). The chord of the arc from the edge of the basal sclerotization to the paramere tips is 2.8 to 3.0 mm in *H. aenescens* and 3.5 to 4.0 mm 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 (1927a, 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 1859d:123). Because of the complete loss of the Say collection (LeConte 1859d, 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/cer-varia/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 apices; 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 (RPL 3247E), CL (RPL 4038E), CR (RPL 4039E); Grid GJM 295: CR (RPL 3303E); Grid GJM 360: CL (RPL 3431E); Grid GJM 364: pronotum (RPL 3486E); Grid GJM 408: BR, CL (RPL 3938E); Grid GJM 568: BL (RPL 27E), pronotum (RPL 28E); Grid GJM 612: CL (RPL 3549E, associated with *Felix atrox* skull); Grid GJM 777: CL (RPL 1180E, associated with *Smilodon californicus* skull); Grid GJM 838: BR (RPL 1824E); Grid GJM 856: CR (RPL 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"),

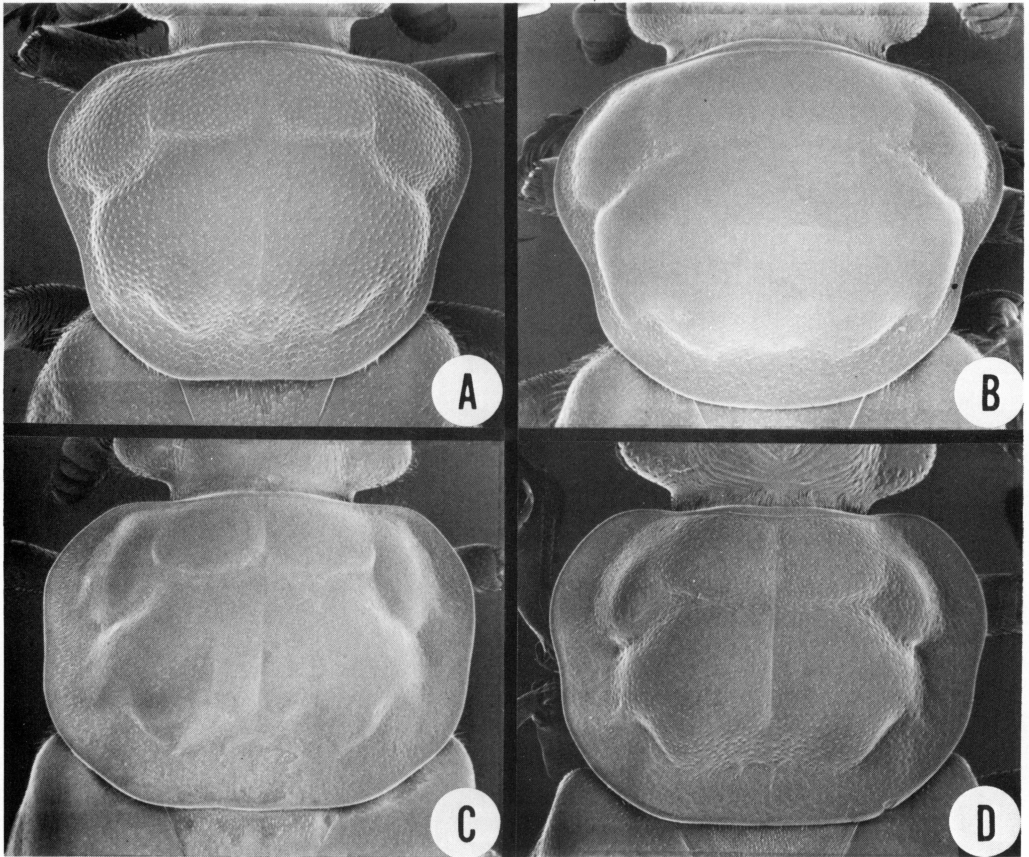


FIG. 3. Pronota of *Nicrophorus* species: A, *N. guttula* (Santa Barbara, California); B, *N. marginatus* (New Mexico); C, *N. nigrita* (Santa Barbara, California); D, *N. defodiens* (Northwest Territories, Canada).

“CASEY/bequest/1925,” red type label “TYPE USNM/48743,” and our lectotype label. The lectotype and 7 paralectotypes (4 males and 3 females, all with same labels as lectotype, but red type labels “aenescens/paratype USNM/48743”) were all examined. The USNM type labels were placed on the assumed types during curation of the Casey collection at the USNM (Buchanan 1935). Casey’s locality code indicates these specimens came from “San Francisco and immediate vicinity as far south as Redwood City and Purissima.” Seven other specimens from “Alameda/Co. Cal.” and “Cal” are assigned to *H. aenescens* in the Casey collection, but these were not considered part of the type series by Buchanan and do not bear paratype labels.

*Pleistocene*.—As discussed above, *H. aenescens* may be represented by Rancho La Brea fossils, but cannot be differentiated from *H. ramosa* at this time.

*Holocene*.—*Heterosilpha aenescens* ranges at least from Baja California, Mexico through California into southern Oregon.

Tribe Nicrophorini  
Genus *Nicrophorus* Fabricius 1775

The proper spelling is *Nicrophorus*, not *Necrophorus* Illiger 1798 (Herman 1964). Arnett (1944) and Madge (1958) treat the North American species, and a revision is in preparation by R. B. Madge (*personal communication*).

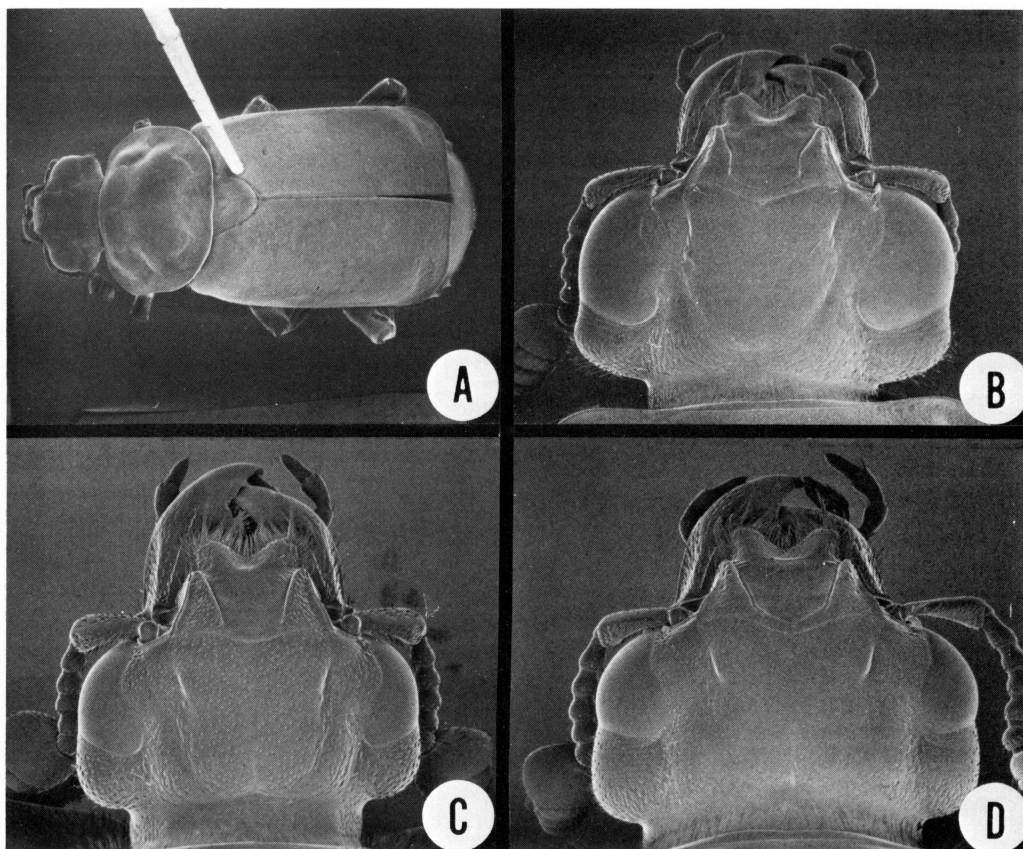


FIG. 4. *Nicrophorus* species: A–B, *N. nigrita* (Santa Barbara, California), A, habitus; B, head; C, *N. guttula*, head (Santa Barbara, California); D, *N. marginatus*, head (New Mexico).

*Nicrophorus defodiens* (Mannerheim)

Figure 3D

*Nicrophorus defodiens* Mannerheim 1846:513

*Nicrophorus defodiens* of Hatch 1927a:355

*Nicrophorus conversator* of Leech 1934:36 (misidentification)

*Nicrophorus defodiens* long has been confused with *Nicrophorus vespilloides* (Herbst 1784). Despite the work of Leech (1937), unpublished studies by R. B. Madge indicate that *N. defodiens* is a distinct species.

*Pleistocene*.—Unknown from California.

*Holocene*.—This species occurs along the Pacific Coast of North America from Alaska into central California. Leech (1934) discussed its natural history, but misidentified the beetles as *N. conversator* (Walker 1866).

*Nicrophorus nigrita* (Mannerheim)

Figures 3C, 4A, B

*Nicrophorus nigrita* Mannerheim 1843:251

*Nicrophorus investigator nigritus* of Hatch 1927a:357

*Nicrophorus nigrita* of Arnett 1944:15

*Nicrophorus investigator alpha* Pierce 1949:67, fig. 13 (specimen LACMIP 3048),  
NEW SYNONYMY

This species was once considered a subspecies of *N. investigator* (Zetterstedt 1824), but it is specifically distinct. True *N. investigator* has not been recorded in California. Pierce's *N. investigator alpha* is *N. nigrita*, which was not considered a valid species by Hatch (1927a), upon which Pierce based his work. *Nicrophorus investigator alpha* was described from 6 syntype pronota (LACMIP 3048–3052, 5263; C121a–f) all from Pit A, Rancho La Brea. Pierce labeled syntype LACMIP 3048 (C121d) as holotype, although it was published (Pierce 1949) as a syntype. We are hereby designating 3048 as **lectotype** because it was labeled as holotype by its author, it was illustrated (Pierce 1949: Fig. 13), and it is the syntype in best condition. Specimen LACMIP 3048 was mistaken by Sphon (1973) as the holotype of *N. investigator latifrons* Pierce and bears a notation to that effect.

*Pleistocene*.—Eleven specimens as follows: RANCHO LA BREA: Pit A: LACMIP 3048–3052, 5263 (*N. i. alpha* type series); \*Pit 91: Grid GJM 295: head (RLP 3339E) and pronotum fragment (RLP 4034E); Grid GJM 408: head fragment (RLP 3944E); \*CARPINTERIA: pronotum fragment and right elytron fragment.

*Holocene*.—This distinctive large black species is the most common *Nicrophorus* in southern California today. It ranges along the Pacific Coast from California (including Santa Rosa, Santa Cruz, West Anacapa, Santa Barbara and San Clemente Islands) to British Columbia and inland to Nevada.

*Nicrophorus marginatus* (Fabricius)  
Figures 3B, 4D

*Nicrophorus marginatus* Fabricius 1801:334

*Nicrophorus marginatus* of Hatch 1927a:360

*Nicrophorus guttulus labreae* Pierce 1949:63, Figs. 4–10, NEW SYNONYMY

*Nicrophorus mckittricki* Pierce 1949:66, Fig. 11, NEW SYNONYMY

*Nicrophorus investigator latifrons* Pierce 1949:67, Fig. 14, NEW SYNONYMY

*Nicrophorus obtusiscutellum* Pierce 1949:67, Fig. 12, NEW SYNONYMY

*Nicrophorus guttulus labreae* was described from 166 syntypes from Rancho La Brea as follows: Pit A: 31 heads (LACMIP 2950, 2951, 4339, 5633–5660), 31 pronota (2953–2979, 4334, 4353, 4354, 5270), 2 right elytra (2952, 4336), left elytron (4348), 6 scutella (4337, 4341, 4343, 4345, 4351, 4352), and 8 tibia (4335, 4338, 4340, 4342, 4344, 4346, 4349, 4350); Pit B: head (4355), 2 pronota (2980, 2981); “Bliss 29”: 2 heads (4370, 4371), 9 pronota (4362–4369, 4374), left elytron (4372); Pit 28: pronotum (3045); Pit 37: pronotum (3046); Pit 81: 3 tibia (4357–4359), elytral fragment (4361); “Pit X”: 34 heads (3011–3044), 28 pronota (2982–3010), left elytron (4356); unknown pit: head (4374). Syntype 4351, an elytral fragment from Pit 81, is apparently not a silphid. Syntype 2952 (C2a1, a complete right elytron from Pit A) was labeled by Pierce as holotype, but this designation is invalid as the taxon was published on the basis of syntypes. We are hereby designating 2952 **lectotype** (Pierce 1949: Fig. 4). Unpublished notes and specimen labels indicate that Pierce first considered this a subspecies of *N. marginatus*, but published it under *N. guttula*. *Nicrophorus mckittricki* was described from the holotype pronotum (LACMIP 3054 = McK3a) and 2 paratype elytra (5733 and 5734; McK3b and McK3c) from site 3, depth 2 feet [≈0.6 m] at McKittrick, 6 paratype elytra (5735–5740; McK3d–McK3i) from site 4, depth 4 feet [≈1.2 m] at McKittrick, and 8 “tentatively associated” specimens (not paratypes) from Pits A, B, “X”, 28, and “Bliss 29”, Rancho La Brea (C120a–c and unnumbered). One “tentatively associated” specimen has not been located, and may not be *N. marginatus*. Although the holotype does have characteristics that tend toward *N. guttula*, it is a specimen of *N. marginatus*. *Nicrophorus investigator latifrons* was described from the holotype head (LACMIP 3053 = C120d) from “Pit X”, Rancho La Brea. *Nicrophorus obtusiscutellum* was described from the holotype scutellum (LACMIP 3055 = C120e) from Pit A, Rancho La Brea. Although it is possible that this specimen represents a distinct taxon, there is not enough evidence to convince us at present. We consider it *N. marginatus* because it falls within the range of variation of this species.

*Pleistocene*.—Two hundred forty-four specimens and 1 literature record: RANCHO LA BREA: Pits A, B, 28, 37, 81, “Bliss 29”, “Pit X”, and an unknown pit; LACMIP 2950–3046, 4334–4359, 4361–4374, 5270, 5633–5660 (type series of *N. g. labrae*); Pit A: LACMIP 3055 (holotype of *N. obtusiscutellum*), head, pronotum (C120a), \*2 complete and 2 fragmentary pronota, \*5 complete and 3 fragmentary heads, \*scutellum, \*6 elytral fragments (elytral determinations questionable); Pit B: head; “Bliss 29”: pronotum (C120c); Pit 28: pronotum (C120b); Pit 81: \*head fragment; “Pit X”: head, \*head, 3 fragmentary pronota, LACMIP 3053 (holotype of *N. i. latifrons*), 3 heads (1 recorded by Pierce but now missing); \* Pit 91: Grid GJM 295: right and partial left elytra (RLP 3314E), 2 pronotum fragments (RLP 4035E); Grid GJM 408: pronotum fragment (RLP 3941E); \*UCMP loc. 2051: 10 complete and 1 fragmentary heads, 13 pronota; McKITTRICK: Pierce’s Site 3, depth 2 feet: LACMIP 3054, 5733, 5734 (holotype and paratypes of *N. mckittricki*); Pierce’s Site 4, depth 4 feet: LACMIP 5735–5740 (paratypes of *N. mckittricki*); \*CIT VP loc. 138: 7 heads.

*Holocene*.—Ranges over much of the United States and southern Canada, but is less common in California than *N. nigrita*. This species seems to prefer open woodland or grassland situations to dense forests.

*Nicrophorus guttula* (Motschoulsky)

Figures 3A, 4C

*Nicrophorus guttula* Motschoulsky 1845:53

*Nicrophorus guttulus* of Hatch 1927a:359

*Nicrophorus guttulus punctostriatus* Pierce 1949:66, NEW SYNONYMY

*Nicrophorus guttulus guttulus lajollae* Hatch of Pierce 1949:66

*Nicrophorus guttula* has been confused with *N. hecate* (Bland 1865), a questionably distinct species (see below). We see no justification to consider *N. g. punctostriatus*, described from holotype left elytron from Pit A, Rancho La Brea (LACMIP 3947 = C132b), a distinct subspecies.

*Pleistocene*.—Twenty-eight specimens as follows: RANCHO LA BREA: Pit A: LACMIP 3947 (holotype of *N. g. punctostriatus*), 3 elytra (C131a, C131b, C132a), \*head fragment; \*Pit 9: head (C2bu); \*\*\*Bliss 29”: 1 complete and 1 fragmentary right elytron; \*Pit 91: Grid GJM 275: head (RLP 3338E), pronotum (RLP 3101E), 3 pronotum fragments (RLP 3315E); \*UCMP loc. 2051: 2 heads, pronotum; \*McKITTRICK: UCMP loc. 7139: 2 complete and 4 fragmentary elytra, 3 heads; CIT VP loc. 138: 2 heads, 1 pronotum; \*CARPINTERIA: 3 heads (bearing grid notation 6B3 ± 8’), left elytron.

*Holocene*.—The species is primarily limited to California (including San Clemente Island) and Oregon.

*Nicrophorus hecate* (Bland)

*Nicrophorus hecate* Bland 1865:382

*Nicrophorus guttulus hecate* of Hatch 1927a:360

*Nicrophorus hecate* of Arnett 1944:15

*Nicrophorus hecate* was described from an unspecified number of specimens collected in the Colorado Territory by James Ridings (Bland 1865). Two specimens are placed as syntypes in the ANSP, with labels “Col.,” “LectoTYPE/3283”, “TYPE/N. hecate/Bland” and “Col.,” “PARATYPE/3283”. The lectotype and paratype labels were apparently placed on the specimens in routine curation and are not valid designations. We hereby designate the first, and larger, specimen **lectotype**.

Some populations from central California to southern Oregon show an intergradation of the characteristics of *N. guttula* into those of *N. hecate*. We do not presently have adequate material to document the nature of this intergradation. These are probably the same species (R. B. Madge, *personal communication*), but we lack adequate data to formally synonymize *N. hecate* under *N. guttula*.

*Pleistocene*.—Unknown from California.

*Holocene*.—Ranges from central California to British Columbia and east through the Rocky Mountains to the western Great Plains.

#### *Dubious California Records*

Several species have been recorded in literature or are represented in collections by specimens labeled California. Some of these represent introductions of Palearctic species which are not established in North America. Most, however, are old specimens from "California" which we think are mislabeled, as follows: *Necrodes surinamensis* (Fabricius 1775): "Cal." (LACM)—does not occur in California (Ratcliffe 1972); *Nicrophorus germanicus* (Linnaeus 1758): "California" (holotype of *Nicrophorus grandior* Angell 1912; Hatch 1927a)—Palearctic; *Nicrophorus humator* (Gleditsch 1767): "California" (paratype of *N. grandior*; Hatch 1927a)—Palearctic; *N. investigator* (Zetterstedt 1824): "Cal." (F. C. Bowditch Collection: MCZ); *Nicrophorus orbicollis* (Say 1825): San Jacinto Mountains (Madge 1958), "Cal." (MCZ); *Nicrophorus pustulatus* (Herschel 1807): "Cal." (Hatch 1927a); *Nicrophorus tomentosus* (Weber 1801): Trabuco Canyon, Orange County, 10 July 1963 (D. Hubbard: LACM); *Oxelytrum discicolle* (Brulle 1840): "Southern California" (Hatch 1927a); *Silpha tristis* Illiger 1798: Santa Ana, in soil 9 March 1959 (J. L. Bath: UCR)—Palearctic.

Two species that live in adjacent regions may range into California. These are *Oxelytrum discicolle* (Brulle 1840) known from northern South America to northern Mexico and *Thanatophilus truncatus* (Say 1850), occurring from Arizona and western Mexico northward and eastward through the Rocky Mountain chain to the prairies of Colorado and Kansas.

#### KEY TO CALIFORNIA SILPHIDAE

1. a. Elytra with 3 longitudinal ridges or smooth; generally large beetles (usually >10 mm) ..... 8
- b. Elytra with 9 longitudinal depressed lines, rarely becoming indistinct; generally small beetles (usually <10 mm) ..... 2
2. (1) a. Antennae filiform; 7th antennal segment twice as long as wide, or nearly so ..... (*Apteroloma*) 3
- b. Antennae clavate; 7th antennal segment nearly as wide as long .... (*Agyrtini*) 5
3. (2) a. Pronotum distinctly narrowed posteriorly, much narrower at base than base of elytra, somewhat cordate ..... *Apteroloma caraboides*
- b. Pronotum only slightly narrowed posteriorly, almost as broad at base as base of elytra, not cordate ..... 4
4. (3) a. Hind angles of pronotum sharp cornered ..... *Apteroloma tahoecum*
- b. Hind angles of pronotum rounded ..... *Apteroloma tenuicorne*
5. (2) a. Maxillary palpi with terminal segment about same width as penultimate segment; terminal antennal segment subequal or more than twice as long as penultimate segment ..... 6
- b. Maxillary palpi with terminal segment much wider than penultimate segment; terminal antennal segment less than twice as long as penultimate segment ..... (*Agyrtes*) 7
6. (5) a. Length 8 mm and greater ..... *Necrophilus hydrophiloides*
- b. Length <5 mm ..... *Pelatines latus*
7. (5) a. Antennal club of 4 segments; 3rd antennal segment appreciably longer than the 2nd; aedeagus in side view with a pronounced bend . . .  
..... *Agyrtes longulus*
- b. Antennal club of 5 segments; 3rd antennal segment only slightly longer than the 2nd; aedeagus in side view relatively straight *Agyrtes similis*
8. (1) a. Elytra truncate, exposing at least tip of abdomen; general shape elongate (as in Fig. 4A) ..... (*Nicrophorus*) 9

- b. Elytra covering most or all of abdomen; general shape oval (as in Figs. 1A, 1C, 1D) ..... 13
9. (6) a. Pronotum (Figs. 3C, 3D) sides feebly sinuate; pronotum base nearly as wide as apex; pronotum not cordate ..... 10
- b. Pronotum (Figs. 3A, 3B) sides strongly sinuate; pronotum base much narrower than apex; pronotum cordate ..... 11
10. (9) a. Elytra black; 3 terminal segments of antennae orange; metasternal pubescence brown ..... *Nicrophorus nigrita*
- b. Elytra with red fascia (sometimes faint); 3 terminal segments of antennae black; metasternal pubescence golden ... *Nicrophorus defodiens*
11. (9) a. Basal segment of antennal club black or orange; anterior face of procoxae with very long hairs on basal half ..... 12
- b. Basal segment of antennal club orange; anterior face of procoxae with only short hairs on basal half ..... *Nicrophorus marginatus*
12. (11) a. Basal segment of antennal club black; no elytral fascia; elytral epipleuron red at humerus ..... *Nicrophorus guttula*
- b. Basal segment of antennal club red; red elytral fascia present; elytral epipleuron usually predominantly red ..... *Nicrophorus hecate*
13. (8) a. Clypeus broadly and shallowly emarginate; eyes normal, comparatively large ..... 14
- b. Clypeus sharply and deeply emarginate (Fig. 1B); eyes comparatively small (Fig. 1B) ..... *Aclypea bituberosa*
14. (13) a. Elytral intervals with reticulate sculpturing (Fig. 1D); labrum narrowly emarginate; pronotum not tomentose ..... (*Heterosilpha*) 15
- b. Elytral intervals with isolated tubercles (Fig. 1C) or smooth; labrum broadly emarginate; pronotum usually tomentose .... (*Thanatophilus*) 16
15. (14) a. Not sexually dimorphic, ♂♂ and ♀♀ superficially alike; male genitalia as in Fig. 2B ..... *Heterosilpha aenescens*
- b. Sexually dimorphic, elytral apex of ♀♀ elongated, front and middle tarsi of ♂♂ dilated; male genitalia as in Fig. 2A .... *Heterosilpha ramosa*
16. (14) a. Intervals between elytral striae with 8–10 tubercles; common species (Fig. 1C) ..... *Thanatophilus lapponicus*
- b. Intervals between elytral striae without tubercles; rare species ..... *Thanatophilus sagax*

#### PALEOECOLOGY *Silphid ecology*

Silphids are found mostly on carrion and occasionally on decaying vegetation. Some feed on the carrion or plant matter, whereas others are predaceous on maggots and other animals present on the carrion. Adults of *Nicrophorus* species bury carrion such as mice and reptiles (Milne and Milne 1976).

Pierce (1949) considered silphids to be characteristic inhabitants of carrion in "ammoniacal fermentation" (his fifth period of decomposition), occurring in the 4th to 8th months following death. His conclusion, based on forensic studies of insects associated with human corpses, is excessive, as silphids inhabit carrion much sooner after death. In some cases, silphids find carrion within an hour after death (Milne and Milne 1944). Shubeck (1969) found that "Carrion seemed to be most attractive to carrion beetles from the fifth to the tenth days when it was in the fresh-bloated, bloated, and decay stages. Since this is the period of time during which the maggots were present . . . , it is possible that they are in some way involved in making the carrion habitat attractive to carrion beetles." Illingworth (1927), at Upland, California, found adult *Nicrophorus nigrita* "feeding on maggots" under a cat dead 3 days. He found *Thanatophilus lapponicus* under the cat after 7 days. After 27 days, "Many fat silphid larvae were present. They had destroyed a large percentage of the dipterous larvae." The ecology of the California silphids is poorly known, although most are large, con-

spicuous, and easy to attract (Newton and Peck 1975) and capture. Until such information is obtained, silphids can contribute only a fraction of their potential to an understanding of California Pleistocene paleoecology.

#### *Accumulation and Preservation of the Fossils*

The popular generalization regarding accumulation of fossils at Rancho La Brea presents a picture of great pools of continuously active liquid asphalt which trapped unwary animals, which in turn attracted scavengers which also became trapped (Stock 1956 and others). However, recent studies (Woodard and Marcus 1973) indicate that such great "death traps" had little role in the accumulation of fossils. Reinterpretation of stratigraphy and radiocarbon dating indicates that the fossil deposits were formed at the sites of discontinuously active asphaltic seeps during the accumulation of alluvium from the late Pleistocene to the present. Most deposits are stratified and can be correlated with facies of surrounding sediments which are not oil impregnated. The "pits" at Rancho La Brea were artifacts of excavation, and did not represent naturally occurring deep pools of liquid asphalt. Woodard and Marcus (1973) further state that "While the larger and more continuous pockets may represent areas of asphaltic quicksand in which animals became mired, it is apparent from the abundance of coarse, stream-worn debris that many of the smaller pockets more likely represent localized fluvial concentrations of bones in stream channels or ponds. Once buried, the abraded and fragmented fossils were enveloped in asphalt permeating upwards and laterally into the sediments from active vents and fissures." Penetration by asphalt was prompt in some cases, preserving fragile specimens such as leaves. Some trapping of small animals may have taken place in shallow pools of asphalt concealed by leaves, dirt or water and/or covered with a thin and weak layer of hardened asphalt.

Deposition at McKittrick was discussed by Shultz (1938): "During late Pleistocene time sedimentation was active in the area, and as the oil reached the surface [from numerous small discontinuously active petroleum seeps] and spread out in sheets of a fraction of an inch or so in thickness it became intercalated with clay, sand, gravel, and windblown material. The resulting product is a rudely stratified material consisting of fine and coarse sediments more or less uniformly saturated with petroleum. The upper layers which contain a Recent vertebrate fauna seem to be somewhat better stratified than the lower levels which contain the Pleistocene vertebrates. Vander Hoof (1934) . . . contends that it was mainly during the summer months that the oil became fluid enough to spread over large areas; while the winter rains carried in most of the clastic material." The result is a breia belt representing a complicated sequence of events.

The geology of the Carpinteria asphalt deposit also indicates fluvial deposition of the fossils (Putnam 1942). Many plant fossils (especially wood) are water worn and partially decayed, indicating stream alluvium subsequently impregnated with asphalt (Chaney and Mason 1933, Mason 1940, Webber 1933). Ralph Hoffman wrote (unpublished letter to R. W. Chaney, 4 June 1932) that "the steam shovel at the asphalt beds has struck a tangle of stumps and logs so dense that they had to stop work at that point . . . ." This "tangle" was probably flood debris similar to one found in Pit 91 at Rancho La Brea.

Interpretation of accumulation and preservation by asphaltic matrix is difficult, especially in light of our present poor knowledge of and problems inherent in insect paleoecology (Kenward 1976, Coope 1977). Research in progress at Rancho La Brea eventually may provide more definitive answers, but 2 distinct processes appear to be involved: direct preservation (trapping in viscous asphalt) and indirect preservation (impregnation with asphalt subsequent to death and burial). Entrapment of insects occurs in 4 ways. (1) Insects can be attracted to carrion or other material already trapped or otherwise in contact with asphalt. (2) Insects, especially aquatic species, can be attracted to pools of oil and water which appear as water, but this probably has little effect on silphids. (3) Insects can be attracted to the asphalt itself. Some insects



are attracted to fresh tar coating roads (Saylor 1933, Hubbs and Walker 1947), but we are not aware of any silphids being attracted to asphalt. (4) Insects can be accidentally trapped, without being attracted, by crawling, flying, or falling into asphalt and not being able to free themselves. In practice, preservation/entrapment is a product of all these processes, all of which have been observed to occur at modern asphalt seeps, but the relative importance of each process is not known. Also, some species may have been more attracted than others to the particular microhabitats present.

A special case of preservation has been observed at the Maricopa deposit. At this site, asphaltic outcroppings occur in large mounds which are often penetrated by large cracks and rodent burrows. Tenebrionid beetles (Coleoptera: Tenebrionidae) often live in and about these orifices, and their remains, apparently only several seasons old, are found along with seeds and other debris in low points in these holes. Although not presently impregnated with asphalt, future changes in the activity of the asphalt could easily mix this Holocene material into surrounding Pleistocene matrix. This should especially be considered when evaluating Pierce's McKittrick fossils. These cracks may also be responsible for movement of fossils within the deposit (similar to a Vertisol, *see* Johnson and Hester 1972).

#### *Late Pleistocene Environments*

At Rancho La Brea, several apparently contemporaneous late Pleistocene plant communities existed in the vicinity of the site of deposition now known as Pit 91 (Warter 1976). A cool, moist coastal closed-cone pine forest was probably dominant near the site, whereas chaparral and foothill woodland occurred inland on warmer, drier sites at higher elevations. Stream-drifted wood of *Sequoia sempervirens* (D. Don) Endlicher suggests the occurrence of coast redwood forest in sheltered canyons in nearby mountain foothills. Riparian woodland and aquatic plants are also represented from Pit 91, as are herbs from drier situations. Plants recovered from the silphid-bearing grids indicate the presence of nearby standing water at the time of preservation (J. K. Warter, *personal communication*). Thus, the silphids were apparently deposited in a placid pool in a slow stream or a pond margin.

As shown by differences in faunal composition (Howard 1962, Marcus 1960, Stock 1956) and radiocarbon dates (L. F. Marcus, *personal communication*), the many Rancho La Brea "pits" are not equivalent accumulations representing the same time periods and ecological conditions. Unfortunately, most of the pits from which insects are available are not among the important vertebrate-bearing pits, and have not been included in papers analyzing paleoecology, age, or vertebrate faunal composition. Also, many of the faunal differences may be attributable to selective entrapment and/or selective preservation due to differences in the physical characteristics of the individual asphalt seeps and their methods of accumulating organic material. Because of differences between periods of activity of the Rancho La Brea asphalt seeps, several environments and associated biotas are represented. Thus, older conclusions about the Pleistocene environment and climate at Rancho La Brea (i.e., Stock 1956), most of which assumed that the pit faunas were contemporaneous, must be used with caution. Even more recent conclusions must be used with care due to new data from the current excavation of Pit 91. However, the general conclusions of Brattstrom (1953a) seem safe. He suggested "that from Late Pleistocene to Recent there was a local transition from a moist climate of *Pinus* and *Cupressus* through a stage of decreasing rainfall and a vegetation of *Quercus agrifolia* and *Juniperus californica*, to the present-day climate and vegetation of Oakwoodland Savanna and Coastal Sage-scrub with subsequent changes in the fauna." Available radiocarbon dates indicate that asphalt seeps at Rancho La Brea have been active over most of the last 40 000 yr (Woodard and Marcus 1976). Further information on late Pleistocene climate and fauna can be found in Johnson (1977b) and W. Miller (1971).

At McKittrick, the late Pleistocene climate and environment were similar to those of the region today, except that there was probably more rainfall and perhaps a nearby

TABLE 1. Occurrence of silphids in California Pleistocene deposits

Taxa	Rancho La Brea	McKittrick	Carpinteria
<i>Heterosilpha ramosa</i>	X		
<i>Thanatophilus lapponicus</i>	X		
<i>Nicrophorus nigrita</i>	X		X
<i>Nicrophorus guttula</i>	X	X	X
<i>Nicrophorus marginatus</i>	X	X	

lake or marsh (Brattstrom 1953b, DeMay 1941a, Mason 1944, and Schultz 1938). DeMay (1941a) reconstructed the environment as “. . . sparsely timbered mountain slopes giv[ing] way to brush-covered hills and arid or semi-arid plains lying adjacent to a desert lake.” The flora was a pinyon–juniper woodland similar to that presently occurring in the foothills of the Sierra Madre Mountains bordering the Cuyama Valley in northeastern Santa Barbara County, about 50 km south of McKittrick (Mason 1944).

At the Carpinteria deposit, the fossil assemblage indicates that the environment in the immediate vicinity of the site was more moist than at present (Chaney and Mason 1933, DeMay 1941b, Wilson 1933). Most components of the assemblage indicate an environment similar to that now present on the Monterey Peninsula (320 km northwest), although with less oceanic influence. However, xeric components indicate the presence of a drier environment nearby, or perhaps at a different time. DeMay (1941b) suggested, due to the scarcity of aquatic bird fossils, that the site was more remote from the seacliff than it presently is, and that no large body of freshwater, such as apparently was present at McKittrick, existed in the vicinity. The few studies on insects of this deposit agree with these conclusions (Lance 1946, Miller 1978, Moore and Miller 1978).

#### *Silphid Faunal Composition*

The fossil record indicates that the composition of the southern California silphid fauna during the Pleistocene differed from that of the region today, although the fossil record may not be a representative sampling of Pleistocene populations. Of the 16 Holocene California silphids, only 6 are important to the fossil study: *Thanatophilus lapponicus*, *Heterosilpha aenescens*, *H. ramosa*, *Nicrophorus nigrita*, *N. guttula*, and *N. marginatus*. *Nicrophorus nigrita* is the most abundant species of *Nicrophorus*, followed by *N. guttula*, with *N. marginatus* being found only occasionally. The habitat preferences of these species are poorly known.

The fossil record (Table 1) shows that *Thanatophilus lapponicus* and *Heterosilpha ramosa* were present in Pleistocene southern California. *Heterosilpha aenescens* may have been present, but cannot be distinguished from *H. ramosa* on the basis of elytra. Fossils of *Nicrophorus marginatus* are most abundant, but *N. guttula* and *N. nigrita* are also present. Pierce's Rancho La Brea material is dominated by *N. marginatus* (90%), with a small percentage of *N. guttula* and even less *N. nigrita*. The UCMP loc. 2051 at Rancho La Brea yielded mostly *N. marginatus* (87%) with some *N. guttula* (13%). Overall, the current excavation of Pit 91 has produced similar numbers of *N. marginatus* and *N. guttula* with slightly fewer *N. nigrita*. *Nicrophorus marginatus* and *N. guttula* have not been found in the same grids in Pit 91. Grid GJM 275 yielded only *N. guttula*, but grids GJM 295 and GJM 408 yielded only *N. marginatus* and *N. nigrita* in almost equal numbers. At Carpinteria, only *N. guttula* and *N. nigrita* are found, with the former more abundant. At McKittrick, UCMP loc. 7139 yielded only *N. guttula* whereas Pierce's sites 3 and 4 yielded only *N. marginatus*. The CIT VP loc. 138 yielded both *N. guttula* and *N. marginatus*, but considerably more *N. marginatus*. This apparent change in faunal composition could be due to (1) the inadequacy of the fossil record and/or to (2) true differences in faunal composition due to climatic shifts.

True changes in faunal composition could be due to (1) alterations in the relative abundances of populations *in situ* over time and/or (2) movement of new populations

into the region, replacing the previous populations. Such changes, initiated by the climatic shifts associated with glaciation, could have occurred multiple times during the late Pleistocene. With these climatic shifts came variations in vegetation and the kinds of carrion available, including extinction of the large mammals that were present in the region during the Pleistocene. This extinction was probably largely due to sudden climatic changes, with perhaps some influence from human hunting (Axelrod 1967, Johnson 1977a). At least some *Nicrophorus* species show no interest in carrion too large for them to bury (Milne and Milne 1944), so the Pleistocene *Nicrophorus* may not have utilized large mammal carrion. Climatic variations would have also affected the rate of decomposition of carrion, changing its insect fauna. These factors could have favored certain species over others, thus modifying the relationships of populations present in the region, or they could have favored species not previously present in the region, thereby allowing new populations to displace the previous resident species. Research at Rancho La Brea, Searles Lake (Smith 1968, 1976), and other places may eventually correlate late Pleistocene climatic shifts with floral and faunal changes.

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#### LITERATURE CITED

- Angel, J. W. 1912. Two new North American species of *Nicrophorus* (Coleop.). *Entomological News* 23(7):307.
- Arnett, R. H., Jr. 1944. A revision of the Nearctic [sic] Silphini and Nicrophorini based upon the female genitalia (Coleoptera, Silphidae). *Journal of the New York Entomological Society* 52(1):1-25.
- . 1946. Coleoptera notes I: Silphidae. *Canadian Entomologist* 78(7-8):131-134.
- Axelrod, D. I. 1967. Quaternary extinctions of large mammals. *University of California Publications in Geological Science* 74:1-42.
- Berger, R., and W. F. Libby. 1966. UCLA radiocarbon dates V. *Radiocarbon* 8:467-497.
- . *In press*. UCLA radiocarbon dates X. *Radiocarbon*.
- Bland, J. H. B. 1865. Descriptions of several new species of North American Coleoptera. *Proceedings of the Entomological Society of Philadelphia* 4:381-384.
- Bolivar y Pieltain, C., and J. Hendrichs. 1972. Distribucion en Norteamerica del genero holarctico *Pteroloma* Gyllenhal, 1827 y estudio de tres nuevas formas mexicanas (Col. Silph.). *Ciencia [Mexico]* 27(6):207-216.
- Brattstrom, B. H. 1953a. The amphibians and reptiles from Rancho La Brea. *Transactions of the San Diego Society of Natural History* 11(14):365-392.
- . 1953b. Records of Pleistocene reptiles from California. *Copeia* 1953(3):174-179.
- Brewer, J. W., and T. R. Bacon. 1975. Biology of the carrion beetle *Silpha ramosa* Say. *Annals of the Entomological Society of America* 68(5):786-790.
- Buchanan, L. L. 1935. Thomas Lincoln Casey and the Casey Collection of Coleoptera. *Smithsonian Miscellaneous Collections* 94(3):1-15.
- Carpenter, F. M. 1968. The affinities of the genus *Sobobapteron* Pierce. *Bulletin of the Southern California Academy of Sciences* 67(4):263-265.
- Casey, T. L. 1886. Descriptive notices of North American Coleoptera. I. *Bulletin of the California Academy of Sciences* 2(6):157-264.
- Chaney, R. W., and H. L. Mason. 1933. A Pleistocene flora from the asphalt deposits at Carpinteria, California. *Carnegie Institution of Washington, Publication* 415(3):45-79.
- Cockerell, T. D. A. 1906. Preoccupied generic

- names of Coleoptera. *Entomological News* 17:240-244.
- Cooley, R. A. 1917. The spinach carrion beetle: *Silpha bituberosa* Lec. *Journal of Economic Entomology* 10:94-102.
- Coope, G. R. 1970. Interpretations of Quaternary insect fossils. *Annual Review of Entomology* 15:97-120.
- . 1977. Quaternary Coleoptera as aids in the interpretation of environmental history. Pages 55-68 in Shotton, F. W., editor. *British Quaternary Studies/Recent Advances*. Clarendon Press, Oxford.
- DeMay, I. S. 1941a. Quaternary bird life of the McKittrick asphalt, California. *Carnegie Institution of Washington, Publication* 530(3):35-60.
- . 1941b. Pleistocene bird life of the Carpinteria asphalt, California. *Carnegie Institution of Washington, Publication* 530(4):61-76.
- Fabricius, J. C. 1801. *Systema eleutheratorum secundum ordines, genera, species: adiectis synonymis, locis, observationibus, descriptionibus*. Kiliae: Impensis Bibliopolii Academici Novi. 2 Volumes. [reprint 1970, Vaals: Asher and Company].
- Fall, H. C. 1897. A list of the Coleoptera of the southern California islands, with notes and descriptions of new species. *Canadian Entomologist* 29:233-244.
- . 1907. New Coleoptera from the southwest-III. *Canadian Entomologist* 39:235-243.
- . 1927. New Coleoptera XII. *Canadian Entomologist* 59:136-141.
- . 1937. Miscellaneous notes and descriptions (Coleoptera). *Canadian Entomologist* 69:29-32.
- Fergusson, G. J., and W. F. Libby. 1964. UCLA radiocarbon dates III. *Radiocarbon* 6:318-339.
- Grant, U. S., and A. M. Strong. 1934. Fossil mollusks from [below] the vertebrate-bearing asphalt deposits at Carpinteria, California. *Bulletin of the Southern California Academy of Sciences* 33(1):7-11.
- Hatch, M. H. 1927a. Studies on the Silphinae. *Journal of the New York Entomological Society* 35:331-370.
- . 1927b. Studies on the carrion beetles of Minnesota, including new species. *University of Minnesota Agricultural Experiment Station Technical Bulletin* 48:1-19.
- . 1928. Fam. Silphidae II. *Coleopterorum Catalogus* 7(95):1-154.
- . 1946. Mr. Ross H. Arnett's "Revision of the Nearctic Silphini and Nicrophorini." *Journal of the New York Entomological Society* 54:99-103.
- . 1957. The beetles of the Pacific Northwest: Part II: Staphyliniformia. *University of Washington Publications in Biology* 16:i-ix, 1-384.
- Herbst, J. F. W. 1793. *Natursystem aller bekannten in- und ausländischen insecten als eine fortsetzung der von Buffonschen naturgeschichte. Der Kafer*. Volume 5. Pauli: Berlin.
- Herman, L. H., Jr. 1964. Nomenclatural consideration of *Nicrophorus* (Coleoptera: Silphidae). *Coleopterists' Bulletin* 18(1):5-6.
- Horn, G. H. 1880. Synopsis of the Silphidae of the United States with reference to the genera of other countries. *Transactions of the American Entomological Society* 8:219-322.
- Howard, H. 1962. A comparison of avian assemblages from individual pits at Rancho La Brea, California. *Los Angeles County Museum Contributions to Science* 58:1-24.
- Hubbs, C. L., and B. W. Walker. 1947. Abundance of desert animals indicated by capture in fresh road tar. *Ecology* 28(4):464-466.
- Illingworth, J. F. 1927. Insects attracted to carrion in Southern California. *Proceedings of the Hawaiian Entomological Society* 6:397-401.
- Johnson, D. L. 1977a. The California ice-age refugium and the Rancho La Brea extinction problem. *Quaternary Research* 8:149-153.
- . 1977b. The Late Quaternary climate of coastal California: evidence for an ice age refugium. *Quaternary Research* 8:154-179.
- Johnson, D. L., and N. C. Hester. 1972. Origin of stone pavements on Pleistocene marine terraces in California. *Proceedings of the Association of American Geographers* 4:50-53.
- Kenward, H. K. 1976. Reconstructing ancient ecological conditions from insect remains; some problems and an experimental approach. *Ecological Entomology* 1:7-17.
- Lance, J. F. 1946. Fossil arthropods of California. 9. Evidence of termites in the Pleistocene asphalt of Carpinteria, California. *Bulletin of the Southern California Academy of Sciences* 45(1):21-27.
- LeConte, J. L. 1854. Synopsis of the Silphales of America, north of Mexico. *Proceedings of the Academy of Natural Sciences of Philadelphia* 6: 274-287.
- . 1859a. Catalogue of the Coleoptera of Fort Tejon, California. *Proceedings of the Academy of Natural Sciences of Philadelphia*, pages 69-90.
- . 1859b. Additions to the Coleopterous fauna of Northern California and Oregon. *Proceedings of the Academy of Natural Sciences of Philadelphia*, pages 281-293.
- . 1859c. The Coleoptera of Kansas and Eastern New Mexico. *Smithsonian Contributions to Knowledge* 11(6):1-66 + 3 plates.
- , editor. 1859d. The complete writings of Thomas Say on the entomology of North America. S. E. Cassino and Company, Boston. Two volumes, xxiv + 412 pp. + 54 plates and iv + 814 pp.
- Leech, H. B. 1934. The family history of *Nicrophorus conversator* Walker. *Proceedings of the Entomological Society of British Columbia* 31:36-40.
- . 1937. Notes on certain names in use in the *vespilloides* group of *Nicrophorus* Fab. (Coleoptera: Silphidae). *Bulletin of the Brooklyn Entomological Society* 32(4):156-159.
- Lindroth, C. H., and R. Freitag. 1969. North American ground-beetles (Coleoptera, Carabidae, excluding Cicindelinae) described by Thomas Say: designation of lectotypes and neotypes. *Psyche* 76(3):326-361.
- Linsley, E. G. 1942. Notes on the habits of some beetles from the vicinity of Yosemite National

- Park. Bulletin of the Southern California Academy of Sciences 41(3):164-166.
- Macdonald, J. R. 1967. The Maricopa brea. Los Angeles County Museum of Natural History Quarterly 6(2):21-24.
- Madge, R. B. 1958. A taxonomic study of the genus *Necrophorus* in America north of Mexico (Coleoptera, Silphidae). Master's thesis. University of Illinois, Urbana.
- Mannerheim, C. G. 1843. Beitrag zur kaefer-fauna der aleutischen inseln, der insel sitkha und new-californiens. Bulletin de la Societe Imperiale des Naturalistes de Moscou 16(2):175-314.
- . 1846. Nachtrag zur kaefer-fauna der aleutischen inseln und der insel sitkha. Bulletin de la Societe Imperiale des Naturalistes de Moscou 19:501-516.
- . 1852. Zweiter nachtrag zur kaefer-fauna der Nord-Amerikanischen laender des russischen reiches. Bulletin de la Societe Imperiale des Naturalistes de Moscou 25(1):283-387.
- . 1853. Dritter nachtrag zur kaefer-fauna der Nord-Amerikanischen laender des russischen reiches. Bulletin de la Societe Imperiale des Naturalistes de Moscou 26:95-273.
- Marcus, L. F. 1960. A census of the abundant large Pleistocene mammals from Rancho La Brea. Los Angeles County Museum Contributions to Science 38:1-11.
- Mason, H. L. 1940. A Pleistocene record of *Pseudotsuga macrocarpa*. Madrono 5:233-235.
- . 1944. A Pleistocene flora from the McKittrick asphalt deposits of California. Proceedings of the California Academy of Sciences (series 4) 25(8):221-234.
- Matthews, E. G., and G. Halffter. 1968. New data on American *Copris* with discussion of a fossil species (Coleopt., Scarab.). Ciencia [Mexico] 26(4):147-162.
- Matthews, J. V., Jr. 1977. Tertiary Coleoptera fossils from the North American arctic. Coleopterists' Bulletin 31(4):297-308.
- Miller, G. J. 1971. Some new and improved methods for recovering and preparing fossils as developed on the Rancho La Brea Project. Curator 14(4):293-307.
- Miller, S. E. 1978. A fossil of *Scaphinotus interruptus* from the Pleistocene Carpinteria asphalt deposit, Santa Barbara County, California (Coleoptera, Carabidae). Pan-Pacific Entomologist 54(1):74-75.
- Miller, W. E. 1971. Pleistocene vertebrates of the Los Angeles basin and vicinity (exclusive of Rancho La Brea). Natural History Museum of Los Angeles County Science Bulletin 10:1-124.
- Milne, L. J., and M. J. Milne. 1944. Notes on the behavior of burying beetles (*Necrophorus* spp.). Journal of the New York Entomological Society 52:311-327.
- . 1976. The social behavior of burying beetles. Scientific American 235(2): 84-89.
- Moore, I., and S. E. Miller. 1978. Fossil rove beetles from Pleistocene California asphalt deposits (Coleoptera: Staphylinidae). Coleopterists' Bulletin 32(1):37-39.
- Motschoulsky, V. de. 1845. Remarques sur la collection de Coleopteres Russes. Bulletin de la Societe Imperiale des Naturalistes de Moscou 18(1):1-127.
- Newton, A. F., Jr. and S. B. Peck. 1975. Baited pitfall traps for beetles. Coleopterists' Bulletin 29(1):45-46.
- Peck, S. B. 1975. A review of the *Agyrtes* (Silphidae) of North America. Psyche 81(3-4):501-506 ("1974").
- Pierce, W. D. 1946. Fossil arthropods of California. 10. Exploring the minute world of the California asphalt deposits. Bulletin of the Southern California Academy of Sciences 45(3):113-118.
- . 1947a. Fossil arthropods of California. 13. A progress report on the Rancho La Brea asphaltum studies. Bulletin of the Southern California Academy of Sciences 46(3):136-138.
- . 1947b. Fossil arthropods of California. 14. A progress report on the McKittrick asphalt field. Bulletin of the Southern California Academy of Sciences 46(3):138-143.
- . 1949. Fossil arthropods of California. 17. The silphid burying beetles in the asphalt deposits. Bulletin of the Southern California Academy of Sciences 48(2):55-70.
- . 1954. Fossil arthropods of California. No. 18. The Tenebrionidae-Tentyriinae of the asphalt deposits. Bulletin of the Southern California Academy of Sciences 53(1):35-45.
- . 1961. The growing importance of paleoentomology. Proceedings of the Entomological Society of Washington 63(3):211-217.
- Portevin, G. 1926. Les grands Necrophages du globe. Encyclopedie Entomologique 6:1-270.
- Putnam, W. C. 1942. Geomorphology of the Ventura Region, California. Bulletin of the Geological Society of America 53:691-754.
- Ratcliffe, B. C. 1972. The natural history of *Necrodes surinamensis* (Fabr.) (Coleoptera: Silphidae). Transactions of the American Entomological Society 98:359-410.
- Say, T. 1823. Descriptions of coleopterous insects collected in the late expedition to the Rocky Mountains, performed by order of Mr. Calhoun, Secretary of War, under the command of Major Long. Journal of the Academy of Natural Sciences of Philadelphia 3:139-216 [reprinted in LeConte 1883].
- Saylor, L. W. 1933. Attraction of beetles to tar. Pan-Pacific Entomologist 9(4):182.
- Schultz, J. R. 1938. A Late Quaternary mammal fauna from the tar seeps of McKittrick, California. Carnegie Institution of Washington, Publication 487(4):111-215.
- Seidlitz, G. 1887-1891. Fauna Baltica. Die Kafer (Coleoptera) der Deutschen Ostseeprovinzen Russlands. Zweite neu bearbeitete Auflage. Konigsberg: Hartungsberg Verlagsdruckerei. (Silphidae issued in 1888.)
- Shubeck, P. P. 1969. Ecological studies of carrion beetles in Hutcheson Memorial Forest. Journal of the New York Entomological Society 77(3):138-151.
- Smith, G. I. 1968. Late-Quaternary geologic and climatic history of Searles Lake, southeastern California. Proceedings, VII Congress of the

- International Association for Quaternary Research 8:293–310.
- . 1976. Paleoclimatic record in the upper Quaternary sediments of Searles Lake, California, USA. Pages 577–604 in Horie, S., editor. Paleolimnology of Lake Biwa and the Japanese Pleistocene, volume 4. University of Kyoto, Kyoto, Japan.
- Sphon, G. G. 1973. Additional type specimens of fossil Invertebrata in the collections of the Natural History Museum of Los Angeles County. Natural History Museum of Los Angeles County Contributions to Science 250:1–75.
- Stock, C. 1956. Rancho La Brea: a record of Pleistocene life in California. Natural History Museum of Los Angeles County Science Series 20:1–81.
- Stoner, R. C. 1913. Recent observations on the mode of accumulation of the Pleistocene bone deposits of Rancho La Brea. University of California Publications, Bulletin of the Department of Geology 7(20):387–396.
- Vander Hoof, V. L. 1934. Seasonal banding in an asphalt deposit at McKittrick. Proceedings of the Geological Society of America, page 332.
- Van Dyke, E. C. 1928. The American species of *Pteroloma* (Coleoptera-Silphidae) and a new Japanese species. Bulletin of the Brooklyn Entomological Society 23(1):19–27.
- Warter, J. K. 1976. Late Pleistocene plant communities—evidence from the Rancho La Brea tar pits. Pages 32–39 in Latting, J., editor. Plant communities of southern California. California Native Plant Society Special Publication No. 2, Berkeley.
- Webber, I. E. 1933. Wood in the Carpinteria deposits. Pages 66–69 in R. W. Chaney and H. L. Mason. A Pleistocene flora from the asphalt deposits at Carpinteria, California. Carnegie Institution of Washington, Publication 415(3):45–79.
- Wilson, R. W. 1933. Pleistocene mammalian fauna from the Carpinteria asphalt. Carnegie Institution of Washington, Publication 440(6):59–76.
- Woodard, G. D., and L. F. Marcus. 1973. Rancho La Brea fossil deposits: a re-evaluation from stratigraphic and geological evidence. Journal of Paleontology 47(1):54–69.
- . 1976. Reliability of Late Pleistocene correlation using C-14 dating: Baldwin Hills—Rancho La Brea, Los Angeles, California. Journal of Paleontology 50(1):128–132.

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