



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 Despite the work of Leech (1937), unpublished studies by R. B. Madge indicate that *N. defodiens* is a distinct species.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 brea 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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