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Late Quaternary Insects of Rancho La Brea, California, USA

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Abstract

Asphalt-impregnated sediments at Rancho La Brea, Los Angeles County, California, provide a rich Quaternary insect record. Ages of various sites at Rancho La Brea range from more than 40,000 ^{14}C yr B.P. to modern. The major palaeoecological insect groups are: (1) ground dwellers, (2) aquatics, (3) scavengers, and (4) miscellaneous. Only two apparent terminal Pleistocene extinctions are recognized, both dung beetles (Coleoptera: Scarabaeidae).

KEYWORDS: Coleoptera, Quaternary, asphalt, Rancho La Brea, California, Extinction, Palaeoecology.

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Appreciation

In the late 1970s, I noticed that while studies by Russell Coope and his students in Europe and North America showed no recognizable extinction of insects at the end of the Pleistocene, many supposedly extinct insect species had been described from the asphalt deposits at Rancho La Brea. The combination of Professor Coope's reinterpretation of the temporal stability of insect species with a revolution in understanding of the taphonomy of the asphalt deposits catalyzed by Leslie Marcus, stimulated my interest in Rancho La Brea insects. Therefore, I am very pleased to contribute this review of Rancho La Brea insects to this volume honouring Professor Coope.

Introduction

The Rancho La Brea asphalt deposits are among the world's most renowned Late Pleistocene vertebrate localities (Stock & Harris 1992), but the associated abundant invertebrate and plant fossils have received little attention. Most of the early entomological papers contained significant errors in identifications and interpretations. Preliminary studies were made on limited samples from the early excavations by the University of California Museum of Palaeontology (Grinnell 1908; Blaisdell 1909; Essig 1931). W.D. Pierce published a series of papers from 1946 to 1957 on insects from excavations by the Natural History Museum of Los Angeles County. Pierce was among the first workers in North America to appreciate the significance of Quaternary insects and their potential as palaeoecological indicators, but his publications and taxonomic procedures were replete with errors (see Miller 1983). Rancho La Brea insects were reviewed by Miller (1983), which culminated a series of papers evaluating the previously described taxa (Moore & Miller 1978; Miller & Peck 1979; Doyen & Miller 1980; Miller *et al.* 1981; Gagne & Miller 1982; Miller 1983; Nagano *et al.* 1983). The present paper reviews this body of knowledge again and suggests directions for future research.

The popular conception of fossil accumulation at Rancho La Brea presents a picture of great pools of continuously active liquid asphalt ("tar pits") that trapped unwary animals, which in turn attracted scavengers that also became trapped. However, recent studies (see Marcus & Berger 1983; Stock & Harris 1992) indicate 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. The "pits" at Rancho La Brea were artifacts of excavation, and did not represent naturally occurring deep pools of liquid asphalt. While the larger and more continuous fossil accumulations probably represent areas where animals were mired in flows or small pools of asphalt, many of the smaller accumulations probably represent localized fluvial concentration of bones in stream channels or ponds. Once buried, the fossils were impregnated by asphalt permeating upward and laterally.

Over eighty species of insects in over thirty-one families have been recorded from Rancho La Brea, along with largely unidentified millipedes, centipedes, spiders, harvestmen, and isopods (Miller 1983; Larew 1987; Stock & Harrris 1992). Many more families and species will be recognized as material already excavated is analysed in detail. Almost all Rancho La Brea insect specimens are considered conspecific with Holocene species and fall within reasonable ranges of geographic variation. While studies by other workers indicate that almost all Pleistocene insect fossils represent extant species (Elias 1994; Coope

1995), two Rancho La Brea species appear to be extinct.

Localities

The Rancho La Brea asphalt deposits are located in Hancock Park, Los Angeles, Los Angeles County, California (Fig. 1). More than one hundred individual excavations or "pits" have been made since 1905. Most of these were unproductive test holes and fewer than fifteen are considered major sources of vertebrate fossils. The most important site for insect fossils is Locality (Pit) 91 (=LACM Vertebrate Paleontology Locality 6909). No insects were available from the original partial excavation of Locality 91 in 1915, but the renewed excavation starting in 1969 and continuing to the present (Shaw 1982), has yielded a vast assemblage of insects. Before the reopening of Locality 91, emphasis was placed on large vertebrates; insects and other small fossils were neglected by early excavators. Pierce's specimens were largely salvaged from the miscellaneous material associated with the vertebrate collections, including matrix inside the skull cavities of large vertebrates.

Almost all the insect fossils from Rancho La Brea are housed at the George C. Page Museum, a branch of the Natural History Museum of Los Angeles County (LACM). An estimated 100,000 insect specimens have been sorted and catalogued in some 13,500 catalogue numbers at LACM. Of these, over 9,000 catalogue numbers and the bulk of the individual specimens are from Locality 91. At least another 100,000 insect specimens, predominantly from Locality 91, remain uncatalogued (C.A. Shaw, personal communication). Only a small percentage of the Locality 91 specimens have received detailed analysis and identification. The University of California Museum of Paleontology (UCMP) houses a small amount of Rancho La Brea insect material, most of which represents vouchers for the earliest studies by Grinnell (1908), Blaisdell (1909), and Essig (1931).

Pierce (1946a; 1947) mentioned the occurrence of insects from the following Localities (Pits) at Rancho La Brea: A, B, 2, 3, 4, 9, 10, 13, 16, 28, 29, 36, 37, 51, 60, 61, 67, 77, 81, 101, "Academy", "Bliss 29" and "Pit X". Original matrix was available to Pierce only from Localities A, 81, 101, and presumably "Bliss 29" and "Pit X". Insects from Localities 3, 4, 13, 60, 61, 67, and 77 were recovered from the brain cavities of *Smilodon* skulls. Although material from such skulls is probably contemporaneous with the skulls, it may not be (*e.g.* Harington 1980, 197). Miller (1983) described the insect fossil localities within Rancho La Brea in greater detail (see also Marcus & Berger 1983; Stock & Harris 1992). It is worth noting that the age of some of Pierce's material is questionable, especially his "Bliss 29" and "Pit X".

Palaeoecology

Interpretation of accumulation and preservation in asphaltic matrix is difficult, and much remains to be learned about insect palaeoecology in general (Elias 1994). Two distinct processes appear to be involved: direct preservation (entrapment in viscous asphalt) and indirect preservation (impregnation with asphalt subsequent to death and burial). Accumulation of asphalt deposits occurs in two major ways (Campbell 1979): the horizontal flow (forming thin, radiating layers), and the filling of natural depressions (forming lense-like deposits). The latter appears to have been more common at Rancho La Brea. Viscous asphalt flows or pools can trap animals by (1) appearing as water, (2) having sticky, melted surfaces at high temperatures (solid at lower temperatures), and/or (3) being camouflaged with a covering of dirt, leaves or debris.

Insects can be attracted to asphaltic sediments in the following three ways, but they can also simply be accidentally trapped, without attraction, by crawling or falling into asphalt and not being able to free themselves. (1) Attraction to carrion or other material already trapped or otherwise in contact with the asphalt, expected among the scavenging insects. (2) Attraction, especially of aquatic species, to pools of oil and water which appear to be water (Hanna 1924; Miller 1930; Pierce 1946b, fig. 6; 1957; Kennedy 1917). Many aquatic insects locate water visually and appear to have poor sense of smell. "For insects that see in the ultraviolet, oil surfaces closely mimic the polarization and reflectivity characteristics of water" (Horáth & Zell 1996). Some water beetles will "land on the shiny tops of cars, mistaking them for water" (Leech & Chandler 1956, 309), and even water itself is an effective trap for many terrestrial insects (Kenward 1978, 40). (3) Attraction to warmth or perhaps chemicals, versus visual attraction to the asphalt itself. Some insects appear to be attracted to the fresh tar coating on roads (Saylor 1933; Borell 1936; Hubbs & Walker 1947), although this attraction may result from the warmth of the roads because some beetles (e.g., *Melanophila* spp.) have infrared sense organs (Evans 1966). In practice, taphonomy is a product of all these processes, each of which occur at modern asphalt seeps, but the relative importance of each process is not known. The physical characteristics of the asphalt seep and the circumjacent microhabitat(s) are also important; some species may have been more attracted than others to the particular microhabitat(s) present. A special case of preservation has been observed at asphalt deposits near Maricopa, Kern County (Miller & Peck 1979, 101), where modern insects and debris appear to be incorporated into Pleistocene matrix by accumulating in the bottoms of natural cracks and rodent burrows which penetrate into the matrix.

La Brea fossil insects can be crudely classified as: (1) aquatic and semiaquatic species that lived in water overlying the tar or were attracted to tar appearing as water, (2) scavenging species that lived on or were attracted to carrion or dung, (3) ground-dwelling beetles and other

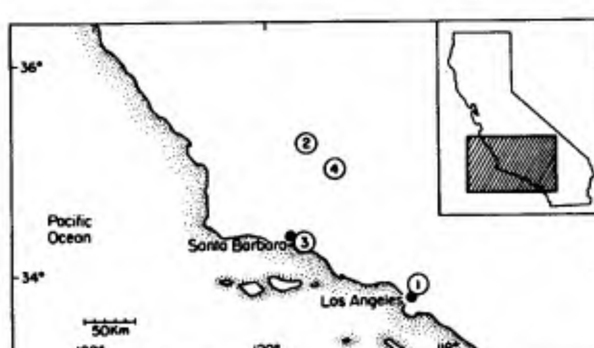

Figure 1. Map showing the location of Rancho La Brea (1) and other fossil-bearing asphalt deposits in California: McKittrick (2), Carpinteria (3), and Maricopa (4) (drawing by L. Meszoly).

Table 1. Beetle families recorded from asphalt deposits around the world. See text for references.

	Rancho La Brea, California	McKittrick, California	Carpinteria, California	Talara, Peru	Fyzabad, Trinidad	Binagady, Caucasus
Carabidae	X	X	X	X	X	X
Haliplidae	X	X		?		
Dytiscidae	X	X	X	X	X	X
Gyrinidae				X		X
Histeridae	X			?		X
Hydrophilidae	X	X	X	X	X	X
Staphylinidae	X	X	X			X
Silphidae	X	X	X			X
Scarabaeidae	X	X	X	X	X	X
Buprestidae		X			X	X
Elateridae	X		X			
Heteroceridae		X				
Dermestidae	X			?		X
Cleridae						X
Tenebrionidae	X	X	X	X	X	X
Zopheridae	X					
Coccinellidae	X					X
Anthicidae	X					
Cerambycidae	X			?		X
Chrysomelidae	X					X
Scolytidae	X					
Curculionidae (s.l.)	X		X	X		X

terrestrial crawling species, (4) miscellaneous stray individuals of herbivorous and other species which are not preserved in significant numbers, and (5) fragments of insects from faeces or gut contents of vertebrates. Members of the last category are minor and cannot now be distinguished from the others, but careful studies of vertebrate feeding habits (e.g. Dodson & Wexler 1979) should eventually allow differentiation.

Detailed understanding of La Brea insects has been held back by the following problems: (1) Conclusions of early authors clouded understanding of ecological and extinction patterns. These conclusions have been largely reevaluated (e.g. Miller 1983), providing a new foundation for research. (2) More data needs to be accumulated from sorting and identification of fossils, especially from Locality 91. This is hampered by the tremendous diversity of the modern California fauna, as well as the paucity of identification aids in the literature (e.g., keys and illustrations). The modern California insect fauna includes over 30,000 species, many of which are poorly understood or characterized (Powell & Hogue 1979). Studies of Quaternary insects of northern North America have prospered in recent years in large part because the modern fauna is less diverse and better known. In contrast to works like Lindroth (1961–1969), no modern review exists for Carabidae or Tenebrionidae of California. Over 90 years have passed since the last general review of southern California beetles (Fall 1901), and it contained no keys or illustrations! (3) More data needs to be accumulated on the ecology of living insects. Progress is being made, however, especially in areas such as aquatic insects (e.g. Merritt & Cummins 1996) and forensic entomology (Smith 1986).

Palaeoecological conclusions that can be drawn from Rancho La Brea insects are limited at present, but further study of the modern and fossil faunas promises to yield significant contributions to palaeoecology. La Brea insects offer data not only on Quaternary climatic changes, but also on changes in community composition, which may allow evaluation of postulated terminal Pleistocene changes in community ecology (e.g. FAUNMAP 1996).

Insects are also known from other Quaternary asphalt deposits in California (Fig. 1): Carpinteria, Santa Barbara County (Miller 1978; Moore & Miller 1978; Miller & Peck 1979; Doyen & Miller 1980; Miller, unpublished data); Maricopa, Kern County (Doyen & Miller 1980); and McKittrick, Kern County (Miller 1983). Similar deposits also occur near Talara, Peru (Churcher 1966), Fyzabad, Trinidad (Blair 1927), and Binagady, in the Caucasus Region (Bogachev 1948; Burchak-Abramovich & Dzhafarov 1955; Vereschagin 1967). Although the faunas of most of these remain incompletely known, comparison of the beetle families recorded from them shows distinct similarity (Table 1). The major paleoecological groups are: (1) ground dwellers (Carabidae, Tenebrionidae); (2) aquatics (especially Dytiscidae, Hydrophilidae, with other families); (3) scavengers (especially Scarabaeidae), and (4) miscellaneous families. A detailed analysis of these deposits is beyond the scope of the present paper, but there are certainly similarities between these deposits in their Late Quaternary ages, taphonomy, palaeoecology, and faunal composition (see also Akersten 1980). Churcher (1966) also questionably listed Silphidae from Talara, but S.B. Peck (personal communication) was unable to locate any Silphidae in Churcher's samples at the Royal Ontario Museum. Zopheridae has only recently been recognized as separate from Tenebrionidae, so may yet be recorded from the other deposits.

Extinction

The causes of extinctions among large vertebrates at the end of the Pleistocene remain a topic of debate (Beck 1996 and references therein). Axelrod (1967) and Martin and Neuner (1978) suggested that low seasonality of

Figure 2. Holotype head of *Onthophagus everestae* from Locality 81, Rancho La Brea (width about 2 mm; LACM IP 3057; scanning electron micrograph by L.E.C. Ling, Carleton University).

Pleistocene environments permitted the establishment of very complex communities that lack modern analogs, and that the inception of Holocene seasonal environments was a major cause of terminal Pleistocene extinctions. Despite the potential data at Rancho La Brea and elsewhere, relatively little remains known about the Quaternary climatic and vegetational history of southern coastal California (Johnson 1977; Cole & Liu 1994). Many birds and mammals recorded from Rancho La Brea are now extinct (Stock & Harris 1992). Terrestrial and aquatic invertebrates other than insects have not been adequately studied, but none have been recognized as extinct. No extinct plants are known from any of the California asphalt deposits (Warter 1976; Miller 1979).

At Rancho La Brea, the extinction picture for insects was clouded by Pierce's many supposedly extinct taxa. Most of these have now been placed in synonymy of extant taxa, two have been recognized as being extinct, and others are impossible to identify because of the nature of the type specimens and the taxonomic condition of the groups concerned (Miller 1983).

The scarab beetles *Copris pristinus* Pierce and *Onthophagous everestae* Pierce (Figure 2) appear to be extinct. The most closely related species occur today in Mexico (and in Texas for *Copris*) and are associated with mammal dung. Probably the reduction of dung availability due to terminal Pleistocene mammal extinctions, as well as direct effects of the changing climate, caused the demise of these scarabs. However, even if the large mammal fauna had survived into the Holocene, the scarabaeine fauna of California might not have survived the present seasonal dry periods, since their successful reproduction requires adequate moisture (Miller *et al.* 1981). Of course, possibly one or both of these species still lives in inadequately collected regions of Mexico and remain to be rediscovered.

Several Pierce taxa remain problematic, but it is best to assume they are extant until contrary evidence is found (Miller 1983). It is presently impossible to identify properly *Serica kanakoffi* Pierce, but there is no good reason to assume that it is not conspecific with an extant (but unidentified) species. *Serica* is a large, poorly understood genus of plant feeding beetles (Miller *et al.* 1981). Likewise, the specific identity of the scarab *Phanaeus labreae* (Pierce) also cannot presently be determined due to the broken and distorted condition of the holotype, although it probably is assignable to an extant species (Miller *et al.* 1981; Edmonds 1994, 91). The millipede *"Spirobolus" australis* Grinnell (Figure 3) is another unidentifiable taxon, known only from the fragmentary types. It is probably a *Hiltonius* or *Tylobolus* (Miller 1983, 96). The tenebrionid beetle *Coniontis remnans* Pierce is not conspecific with any described species (Doyen & Miller 1980), but this does not mean it is extinct. *Coniontis* is a genus of numerous poorly understood species, probably including at least several undescribed species. *C. remnans* probably still lives in southern California, but has yet to be recognized (most *Coniontis* in museum collections are unidentified or misidentified).

Figure 3. Holotype of *"Spirobolus" australis* from Rancho La Brea (width about 7 mm; UCMP Invertebrate specimen 10008).

Directions for future research

The high quality of preservation, both in physical characteristics and geochemistry (e.g. McMenamin *et al.* 1982), as well as the large numbers of individuals available for study, make Rancho La Brea fossils excellent subjects for many kinds of research. This presents the possibility of evaluating 40,000 years of change in morphology, genetics, and isotopic composition in individual insect species!

The high quality of data associated with specimens from Locality 91 will allow palaeoecological studies. These could be especially illuminating if undertaken as part of multidisciplinary research including analysis of plants, vertebrates, and sediments. The availability of computer data processing and storage now allows correlation of data from many sources. Any further research will require a major program of sorting and identification. For some taxa, this will require reevaluation of the modern California fauna to place the fossils in a context (e.g. Miller & Peck 1979). Plant fossils should also be examined for signs of insect damage, such as the gall illustrated in Figure 4, and other phytopathological data for comparison to modern studies such as Gagne (1989), Keifer *et al.* (1982), and Opler (1974).

Recent developments in isotopic and molecular analysis techniques open new horizons on the information that can be extracted from Rancho La Brea insect specimens. These insects have already been used in carbon isotope studies of climatic change (QC-1049, QC-1050; L.F. Marcus & S.E. Miller, unpublished data). La Brea specimens should be suitable for other isotopic studies (e.g. R. Miller 1991; R. Miller *et al.* 1993). Accelerator radiocarbon dating techniques now being applied to bone can be extended to insects as well (Elias & Toolin 1990; Stafford *et al.* 1991). Likewise, some of the techniques of nucleic acid extraction and analysis now being applied to population genetics and systematics of insects (Hillis *et al.* 1996) should be applicable to Rancho La Brea specimens (see also Janczewski *et al.* 1992).

Conclusion

Asphalt-impregnated sediments at Rancho La Brea, Los Angeles County, California, provide a rich fossil record spanning the last 40,000 years. The abundance of insect specimens and their excellent preservation, especially at Locality 91, provide tremendous but untapped opportunities for palaeoecological and climate change studies. The resolution of basic questions about apparent terminal Pleistocene extinctions provides a foundation for

Figure 4. Unidentified cynipid gall (Hymenoptera: Cynipidae) on *Quercus* (?) sp. (Fagaceae) from Pit A, Rancho La Brea (length about 20 mm; specimen LACM RLP 4308).

further work on this and other asphalt deposits.

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