

Early Jurassic Insects from the Newark Supergroup, Northeastern United States

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Fossil insects from the Early Jurassic (Hettangian–Sinemurian) of the eastern United States comprise a small fauna that contains two elytra-based genera of beetles, abundant larvae and an adult specimen that may belong to adephagan beetles, other larvae of unknown affinities, a blattoid, and several indeterminate specimens composed of isolated segments and isolated appendages. Beetle elytra include the cupedid *Liassocupes parvus* Zeuner 1962 and the *Holcoptera giebeli* Giebel 1856. *Mormolucooides articulatus* Hitchcock 1858 is interpreted as a coleopteran that includes two morphs distinguished by relative size and degree of sclerotization that represent different stages of instar development. The blattoid is an isolated wing that presently cannot be assigned to a family. These specimens were obtained from playa and shallow lacustrine deposits of the Hartford, Deerfield, and Newark basins of the Newark Supergroup. Except for a single taxon of an aquatic hemipteran from the Middle Jurassic (Callovian) Todilto Formation of the southwestern United States, the fauna described in this chapter constitutes the only record of Jurassic insects from North America.



Lower Mesozoic sedimentary rocks and interbedded basalts of the Newark Supergroup occupy a series of elongate half-graben basins extending from South Carolina to Nova Scotia that formed in response to the crustal extension and rifting associated with the breakup of Pangea (figure 13.1). Strata of Jurassic age are restricted to the northern Newark Supergroup basins, which include the Culpeper, Gettysburg, Newark, Pomperaug, Hartford, Deerfield, and Fundy basins. These Lower Jurassic (Hettangian–Sinemurian) sedimentary rocks represent a broad suite of nonmarine depositional facies, including prominent cyclic dark-gray, laminated siltstones and shales that record deposition in extensive lacustrine environments (Olsen 1986; Smoot 1991). The Newark Supergroup contains well-documented palynomorph, megafossil, fish, and tetrapod records (Cornet 1977; Olsen, Schlische, and Gore 1989; Cornet and Olsen 1990; McDonald 1992; Lucas and Huber, chapter 11 in this volume), but most of the invertebrate groups (mollusks, ostracodes, brachiopods, decapods, insects, trace fossils) have not received rigorous taxonomic analysis. However, studies of the mollusks (Good, Olsen, and McDonald 1994; Good and Huber 1995) and of Triassic age insects (Fraser et al. 1996; Fraser and Grimaldi, chapter 12 in this volume) are in progress.

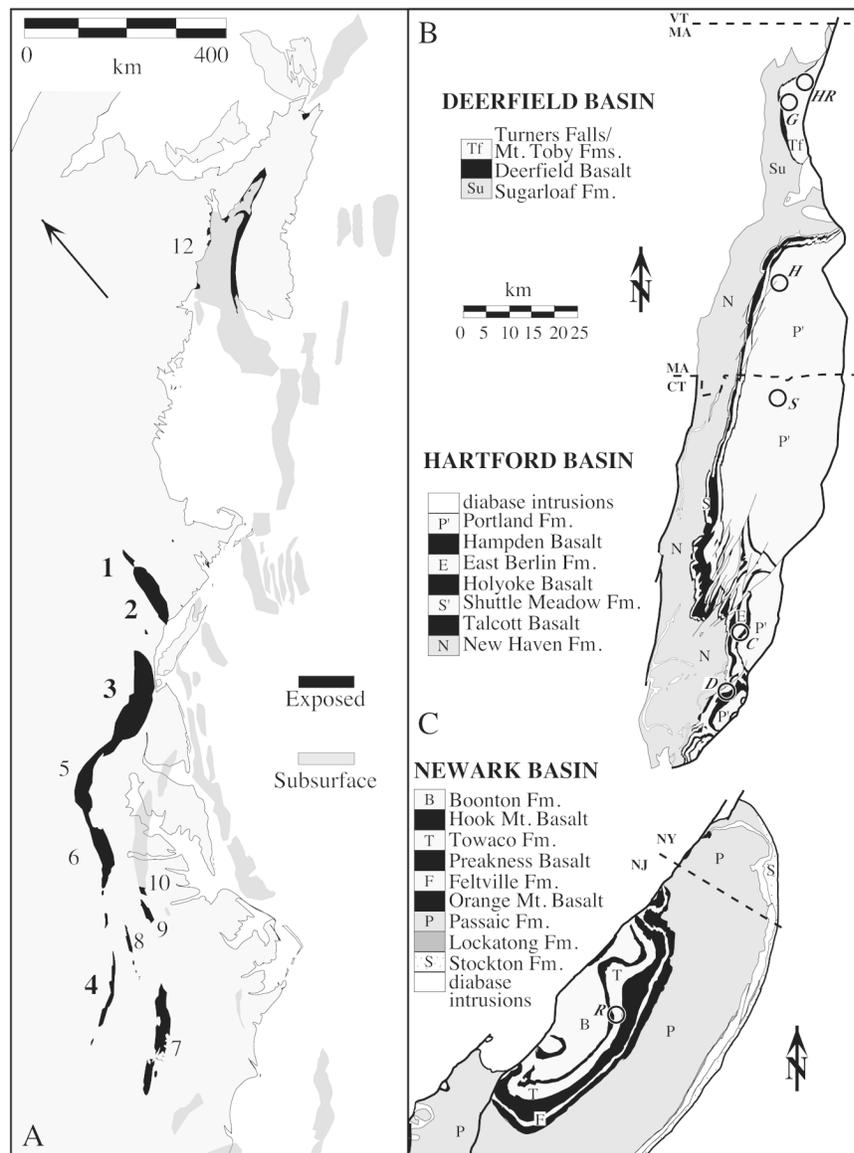


FIGURE 13.1 The Newark Supergroup and details of the Hartford, Deerfield, and Newark basins. (A) Location of the Newark Supergroup basins. (B) Generalized geologic map of the Hartford and Deerfield basins. (C) Generalized geologic map of the northern part of the Newark basin; HR, Horse Race, Montague and Gill, Massachusetts; G, outcrops with *Mormolucooides* (Olsen et al. 1992), Montague, Massachusetts; H, Holyoke Dam, Holyoke, Massachusetts; S, former K-F Quarry, Portland Formation, Suffield, Connecticut; C, Cromwell, Connecticut; D, Durham fish locality, Durham, Connecticut; R, Roseland Quarry, Roseland, New Jersey.

The first specimens of Mesozoic insects collected in North America were abundant larvae discovered on the banks of the Connecticut River during the 1850s by Roswell Field, a local farmer and naturalist of Gill, Massachusetts. Field presented the specimens to Ed-

ward C. Hitchcock, who named them *Mormolucooides articulatus* (Hitchcock 1858) and in turn sent examples of the larvae to Yale geologist James D. Dana for identification. Further collections were made at the site by other residents of the area, including Dexter Marsh

and T. M. Stoughton, and by Yale paleontologist O. C. Marsh, who visited the locality in April 1867. S. W. Loper of Wesleyan University discovered additional examples of these larvae in slightly older beds in south-central Connecticut during the late nineteenth century.

Renewed paleontological investigation of the Hartford, Deerfield, and Newark basins has led us to new insect occurrences (figure 13.1) as well as to the rediscovery of the *Mormolucoides* locality (McDonald and Huber 1995). The most important of our new localities was the now infilled K-F Quarry (Portland Formation) in Suffield, Connecticut (LeTourneau and McDonald 1985). Collecting efforts at this site from 1986 to 1992 yielded approximately 80 beetle elytra, a single blattoid wing, and several fragmentary abdominal segments and appendage elements of uncertain affinities. What we believe to be Roswell Field's *Mormolucoides* beds were found in October 1991, and subsequent efforts yielded approximately 5,000 larvae, several elytra, and an adult beetle. Other larvae were discovered in 1996 in Portland Formation outcrops below the Holyoke Dam in South Hadley, Massachusetts, and in the Shuttle Meadow Formation at Durham, Connecticut (probably Loper's locality mentioned in Lull 1915, 1953). During the course of excavations for fossil fish and dinosaur tracks at the Roseland Quarry in the Newark basin (Towaco Formation), a single elytron was collected that represents the only North American record of a Jurassic age cupedid beetle (Olsen 1995; Huber and McDonald 1996). The combined assemblages from the Hartford, Deerfield, and Newark basins, excepting a single species of aquatic Hemiptera from the Todilto Formation of New Mexico (Kirkland, Denison, and Evans 1995), comprise the only Jurassic insect fauna yet documented from North America. A preliminary description of this fauna is provided in the rest of this chapter.

Specimens discussed in this chapter are in the British Museum of Natural History (BMNH; London), Nicholas G. McDonald collection at the Westminster School (NGM; Simsbury, Connecticut), Shepard and Hitchcock Ichnology Collections at the Pratt Museum of Natural History of Amherst College (PMNH; Amherst, Massachusetts), Virginia Museum of Natural History (VMNH; Martinsville, Virginia), Wesleyan University, Department of Earth and Environmental Sciences collections (WU; Middletown, Connecticut), and Yale Peabody Museum of Natural History (YPM; New Haven, Connecticut).

SYSTEMATIC PALEONTOLOGY

Phylum ARTHROPODA

Class INSECTA

Order COLEOPTERA

Suborder ARCHOSTEMATA Kolbe 1908

Family CUPEDIDAE Lacordaire 1857

Genus *LIASSOCUPES* Zeuner 1962

Liassocupes Zeuner 1962:167, pl. 27 (fig. 4)

Liassocupes (Zeuner 1962) Whalley 1985:66–167, figs. 63–66

Liassocupes (Zeuner 1962) Olsen 1995:169, fig. 7c

Liassocupes (Zeuner 1962) Huber and McDonald 1996:49

Type species: *Liassocupes parvus* Zeuner 1962.

Diagnosis (amended from Zeuner 1962): Cupedid with rounded pronotum and elytra that possess a punctate sculpture arranged in 8 to 12 rows defined by longitudinal veins.

Distribution: Early Jurassic: Flatstones, Black Ven, Charmouth, Dorsetshire, United Kingdom (Sinemurian: obtusem zone); "Member A," Towaco Formation, Roseland Quarry, Essex County, New Jersey (Hettangian).

LIASSOCUPES PARVUS

Holotype: BMNH In64008, lower Lias, Dorsetshire, United Kingdom.

Referred material: YPM 35964.

Diagnosis: Elytra sculptured by 10 rows of longitudinal veins that segregate cells numbering 40+ in each vertical row. Length: 3–7 mm.

Discussion

Liassocupes is an archostematan first established by Zeuner (1962), on the basis of elytral morphology, to contain a single species, *L. parvus*. The holotype and referred materials are part of the Jackson (BMNH) insect collection obtained from the Black Ven at Charmouth, Dorsetshire. At the time of Zeuner's description, the holotype (BMNH In64008) was the only known specimen. Whalley (1985) described an additional specimen (BMNH In49210), an isolated elytron that he referred to this species based on the characteristic sculpture. The holotype of *Liassocupes parvus* is a nearly complete (though poorly preserved) beetle in

dorsal aspect that displays paired elytra missing their posterior margins. As Whalley noted, the head and thorax are detached from the elytra and rotated at a slight angle, but they lack distinguishing characters other than the rounded pronotum. The elytra display cells that are ordered into 10 vertical rows segregated by primary and secondary venation. The other specimen (BMNH In49210), a complete elytron 4.8 mm in length with a rounded posterior end, indicates that each row contains approximately 40 spots.

Whalley (1985) described two additional species and provisionally placed them in this genus. *Liassocupes maculatus* is based on six specimens (holotype BMNH In49577) and differs from *L. parvus* by a greater length of elytra (up to 12.2 mm) that bear 12 vertical rows of cells and lack intermediate, raised subcostal striae. The elytra display flattened costal margins and posteriorly terminate in a pointed apex. *Liassocupes giganteus* possesses elytra that are distinguished from those of other *Liassocupes* species by a sculpture of octagonal cells, an absence of well-defined longitudinal ribbing, and a larger size. Whalley (1985) stated that this taxon bears a resemblance to Permo-Triassic Taldycupedidae with regard to elytra morphology, but he apparently referred the holotype and only known specimen (BMNH In51026) to *Liassocupes* solely on the basis of geologic age. Indeed, although *Liassocupes parvus*, *L. maculatus*, *L. giganteus*, and the Taldycupedidae are united by elytra that display a strongly tuberculate sculpture, *L. giganteus* and the Taldycupedidae lack the well-ordered vertical arrangement of cells (“black spots” of Whalley 1985) that are segregated by strongly parallel venation (cf. Rohdendorf 1961). Furthermore, there is no consensus as to exactly what venation-based characters define the monophyly of the several “families” of cupedid-like Permian and early Mesozoic Archostemata (cf. Carpenter 1992). More often than not, these taxa have been described solely by elytral morphology and hence are organ taxa whose higher-order, phylogenetic relationships are obscure. Because the holotype and only known specimen of *L. giganteus* does not preserve other taxonomically useful characters, we question its placement in both the genus *Liassocupes* and the family Cupedidae and regard it as Archostemata indet.

YPM 35964 (figure 13.2A) is a complete isolated elytron 5 mm in length. The specimen displays 10 vertical rows of cells, 40+ contained in each row, that are defined by subcostal ribbing. As in the holotype of

Liassocupes parvus and the other Dorset specimen, YPM 35964 has a rounded posterior termination but possesses a slightly flattened costal margin. The specimen is identical in all other respects to *Liassocupes parvus*, to which it is referred.

Suborder ?POLYPHAGA Emery 1886

Family *incertae sedis*

Genus *HOLCOPTERA* Handlirsch 1906–1908

(Harpalideous Carabidae) Brodie 1845:101, 124, pl. 6 (fig. 28)

Harpalus Giebel 1856:63

Holcoptera Handlirsch 1906–1908:453, pl. 41 (fig. 64)

Holcoelytrum Handlirsch 1906–1908:453, pl. 41 (fig. 63)

Holcoptera (Handlirsch 1906–1908) Cockerell 1915:480, pl. 61 (figs. 7 and 8)

Holcoelytrum (Handlirsch 1906–1908) Zeuner 1962:170, pl. 27 (fig. 5)

Holcoptera (Handlirsch 1906–1908) Whalley 1985:173, figs. 82–85

Holcoptera (Handlirsch 1906–1908) Olsen, McDonald, Huber and Cornet 1992:495, fig. 7b

Holcoptera (Handlirsch 1906–1908) Huber and McDonald 1996:49

Type species: *Holcoptera schlotheimi* Giebel 1856 (Neotype: BMNH I.59115, elytra and partial prothorax from Flatstones, Charmouth, Dorsetshire, United Kingdom).

Diagnosis: Elytra that range from 5 to 14 mm in length, sculptured by 4 or 5 narrow to broad, straight, and curvilinear stripes that show no surficial relief.

Distribution: Early Jurassic: Flatstones, Stonebarrow, Charmouth, Dorsetshire, United Kingdom (Sinemurian: obtuse zone); middle Portland Formation, Suffield, Connecticut (Hettangian–Sinemurian); Mount Toby Formation, Montague, Massachusetts (Hettangian–Sinemurian).

HOLCOPTERA GIEBELI Handlirsch 1906–1908

Holotype: BMNH I.3581, elytron; lower Lias, Apperley, Gloucestershire, United Kingdom.

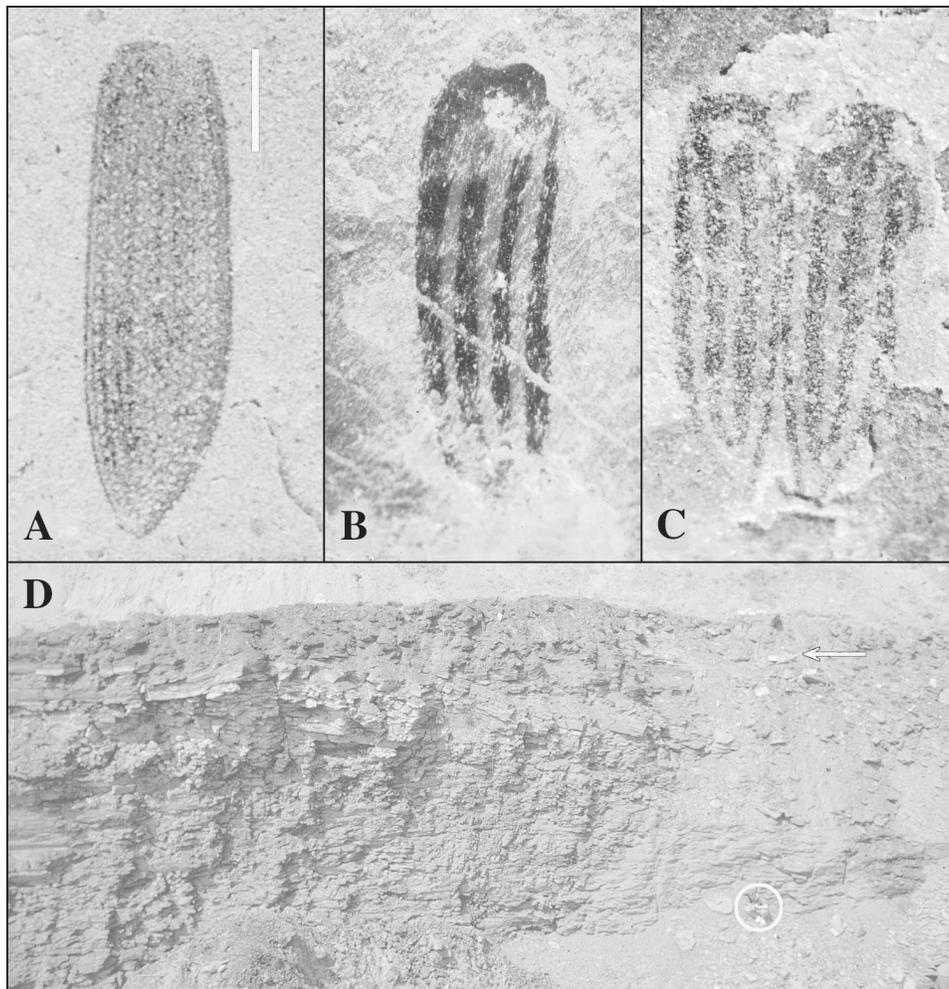


FIGURE 13.2 Jurassic beetles. (A) *Liassocupes parvus* (YPM 35964), elytron from the Roseland Quarry, Towaco Formation, Roseland, New Jersey. (B) *Holcoptera giebeli* (NGM 100), elytron from the Horse Race, Mount Toby Formation, Montague, Massachusetts. (C) Paired elytra (NGM 102) from the K-F Quarry, Portland Formation, Suffield, Connecticut. (D) Outcrop of the insect bed at the former K-F Quarry, Portland Formation, Suffield, Connecticut.

Referred material: YPM 37286, YPM 37287, NGM 99.

Diagnosis: Elytra that differ from those of *H. schloth-eimi* by possessing narrow venation with marginal veins joined at posterior apex and encapsulating the medial veins.

Discussion

Handlirsch (1906) transferred elytra that Giebel (1856) previously described as “*Harpalus schloth-eimi*” to two new genera, each with one species: *Holcoptera schloth-eimi* and *Holcoelytrum giebeli*. Shortly thereafter, Cockerell (1915) reunited these genera and gave pri-

ority to *Holcoptera*. As Whalley (1985) noted, this synonymy was overlooked by Zeuner (1962), who recognized both species under Handlirsch’s name *Holcoelytrum*. Whalley (1985) reinstated Cockerell’s (1915) taxonomy and redescribed the two species.

Previous diagnoses of these species are confusing because of differing terminology. In the descriptions of specimens from the English Lias, the term *stripes* was not used in the sense of the primary venation pattern but referred to the dark-colored, longitudinal interstices on the elytron that are segregated by the venation, which is preserved as light-colored or white

lines (e.g., Zeuner 1962). The reverse is true of all examples from the Newark Supergroup, however, in which the venation is preserved as black lines that encapsulate areas of the light-colored elytron surface. Thus an amended diagnosis for *Holcoptera giebeli* is necessary because it mitigates confusion caused by differing modes of preservation.

The venation of *Holcoptera giebeli* and *H. schlothemi* differs markedly. In *H. giebeli*, the marginal venation extends nearly the length of the elytron and encases medial veins to join at the apex at the posterior margin. A medial vein parallels most of the length of the costal margin and joins a short radial posterolaterally. In contrast, elytra of *H. schlothemi* display wide veins that define equally broad, straight “stripes” that taper and terminate well inward of the posterolateral margin. The only criterion Whalley (1985) used to distinguish *Holcoptera giebeli* from *H. schlothemi* was the larger size of *H. giebeli* in the English Lias sample. Cockerell (1915:480, fig. 8) described an additional species, *H. confluens*, based on material that Brodie collected from an unknown, probably Liassic locality in England. *H. confluens* possesses a wide posteriorly tapering “stripe” that occupies two-thirds of the area adjacent to the medial suture, with 1 or 2 additional very thin and short, dark-colored longitudinal bands adjacent to the costal margin. We have not examined this material, but from Cockerell’s description and figures it appears that this species belongs in a genus.

A total of 85 mostly isolated elytra were collected from two localities: the Horse Race (figures 13.2 and 13.3) in Montague, Massachusetts (Mount Toby Formation, Deerfield basin), and the now filled-in K-F Quarry (figure 13.2C and D) in Suffield, Connecticut (lower to middle Portland Formation, Hartford basin). Of these specimens, only 33 elytra retain more or less complete venation that permits unambiguous identification, though there is little doubt that the remaining specimens belong to the same taxon. The venation of the K-F Quarry specimens is identical to that of the holotype and referred specimens of *Holcoptera giebeli* described by Zeuner (1962) and Whalley (1985), and the only difference is the smaller average length exhibited by the Newark sample (standard elytron length ranges from 4.5 to 9.5 mm). Because slight variation in relative size is not usually a reliable taxonomic criterion, we refer the Newark Supergroup specimens to *Holcoptera giebeli*.

Family *incertae sedis*

MORMOLUCOIDES ARTICULATUS Hitchcock 1858

Mormolucoides articulatus Hitchcock 1858:7, pl. 7 (figs. 3 and 4)

Palephemera mediaeva Hitchcock 1862:452

Mormolucoides articulatus (Hitchcock 1858) Scudder 1868:218

Mormolucoides articulatus (Hitchcock 1858) Packard 1872:1

Mormolucoides articulatus (Hitchcock 1858) Scudder 1886:431, pl. 19

Mormolucoides articulatus (Hitchcock 1858) Scudder 1891:155, 215

Mormolucoides articulatus (Hitchcock 1858) Lull 1915:48, fig. 1

Mormolucoides articulatus (Hitchcock 1858) Olsen, McDonald, Huber and Cornet 1992:497, fig. 4a

Mormolucoides articulatus (Hitchcock 1858) Ponomarenko 1993:185

Mormolucoides articulatus (Hitchcock 1858) Huber and McDonald 1996:49

Lectotype: PMNH 47/11[8], complete, articulated larva.

Other material: PMNH 47/29, 47/36; YPM 27499(A); YPM 27498, 27499, 33019, 33021, 33134, 33144, 33147; VMNH 898, 899, 902, 903; WU uncataloged (three specimens).

Diagnosis: See “Description” in the next discussion section.

Distribution: Late Triassic: Lower Cow Branch Formation, Mayodan, North Carolina (late Carnian); Upper Cow Branch Formation, Virginia Solite Quarry, Cascade, Virginia (late Carnian). Early Jurassic: Mount Toby Formation, Horse Race on north (Gill, Massachusetts) and south (Montague, Massachusetts) banks of Connecticut River; Stoughton footprint quarry and the “Middle beds” of Handy (1976), both in Montague, Massachusetts (Hettangian–Sinemurian); Shuttle Meadow Formation, Durham fish locality, Durham, Connecticut (Hettangian); East Berlin Formation, Cromwell, Connecticut (Hettangian).

Discussion

Deerfield Basin Material. The first Mesozoic insect specimens found in North America were collected by

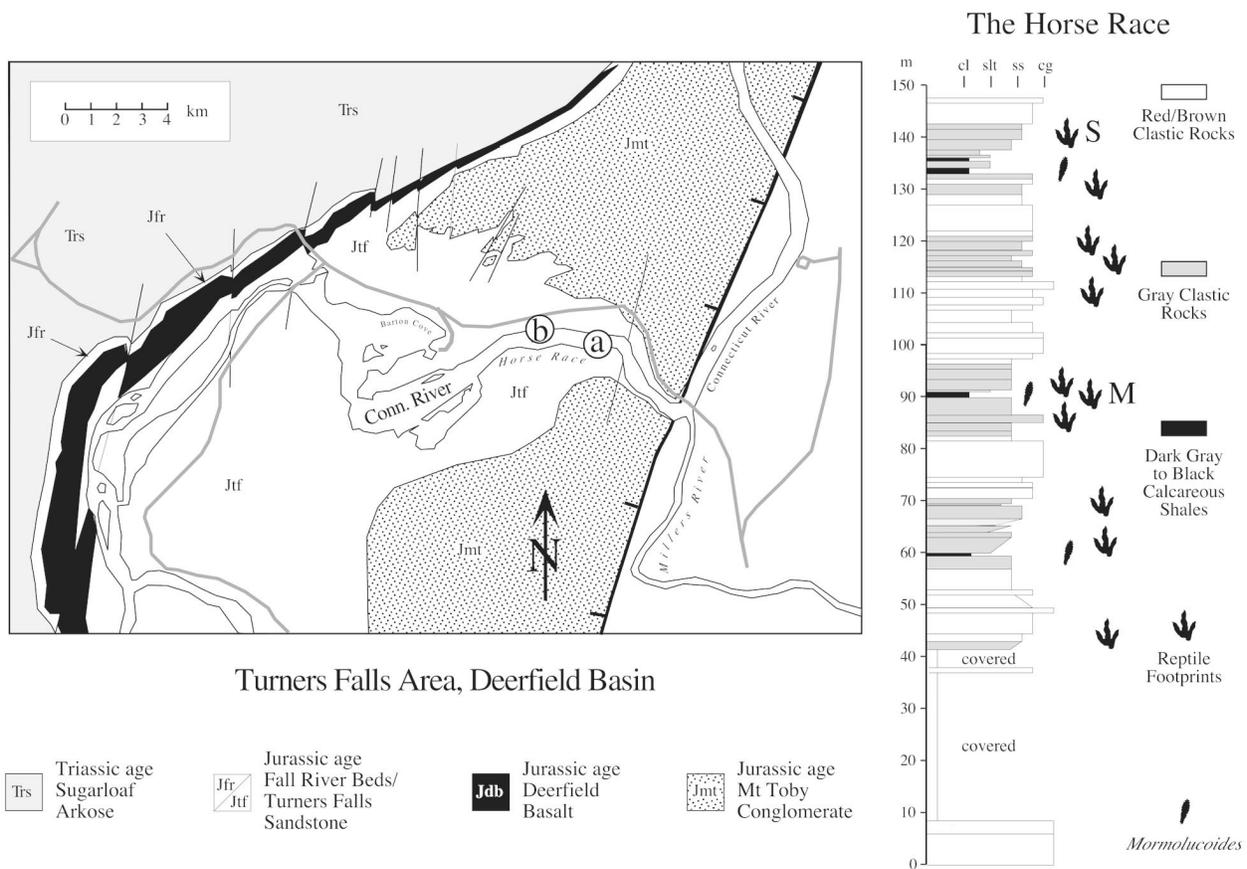


FIGURE 13.3 *Mormolucoides* localities in the northern Deerfield basin. (Left) Location of lacustrine cycles that produce *Mormolucoides* larvae; a, locality on south bank of the Connecticut River at the Horse Race, Montague, Massachusetts, the type locality for *Mormolucoides*; b, *Mormolucoides*-producing outcrops on the north bank of the Connecticut River, Gill, Massachusetts. (Right) Measured section of the Horse Race outcrops, Montague, Massachusetts, Deerfield basin; M, the lacustrine cycle that contains the type locality of *Mormolucoides*; S, position of the Stoughton Quarry. (Modified from Olsen et al. 1992)

Roswell Field, probably during the 1850s, in the Deerfield basin of north-central Massachusetts. These larvae were presented to Edward Hitchcock, who named them *Mormolucoides articulatus* (Hitchcock 1858). Subsequent collections made by O. C. Marsh and T. M. Stoughton during the 1860s are at YPM. We collected more than 5,000 *Mormolucoides* between 1991 and 1995 but have not yet cataloged these specimens. Similar larvae have been discovered in the Dan River basin of Virginia and North Carolina and are of interest because they are of late Carnian age, predating the New England occurrences by at least 25 million years.

Examination of all the PMNH and YPM specimens and of the majority we recently obtained confirms that most are derived from a single bed of dark-gray shale and siltstone exposed along the Horse Race in Gill and Montague, Massachusetts. Before construction of the

Turners Falls dam, the Horse Race stretch of the Connecticut River (from 1 to 2 km upstream) consisted of extensive outcrops on both the north and south banks and ledges exposed at low water levels in the bed of the river. In his field notebook, Marsh (1867) stated that “there are five layers [that contain *Mormolucoides*],” but it is not clear whether this description refers to five gray shale beds or to five productive horizons contained within one bed. A measured section of this stratigraphic interval located three dark shale beds that contain larvae (figure 13.3). However, only the middle of the three beds produces abundant, articulated *Mormolucoides*, and larval occurrences in the others are restricted to isolated segments or to rare partially articulated specimens. Marsh (1867) also noted that “many plants” were present at the main locality, but well-preserved conifer stems and foliage are common

in all the gray shale units in the area. Labels for the YPM specimens also indicate that they were taken from outcrops on both the north and south banks of the Connecticut River, but do they not mention if the specimens are from the same bed.

Marsh's (1867) field notes and the contemporaneous *Atlas of Franklin County, Massachusetts* (Beers 1871), provide a potential solution to the problem of identifying the type locality. Marsh states that the main locality he visited was on land formerly owned by Field and later sold to Stoughton. Field's land holdings along the Horse Race originally encompassed both sides of the river, but the 1871 map shows land on the south bank (containing the locality we excavated) as belonging to Stoughton. This information and the fact that abundant, articulated larvae occur in only one of the three lacustrine units currently exposed in the area strongly suggest that the type locality is contained in the middle lacustrine bed currently exposed on the south bank of the Connecticut River in the town of Montague.

At present, only seven slabs with *Mormolucoides* are preserved in collections at the Pratt Museum. PMNH 47/11 contains several larvae from the Horse Race at Gill, including the specimen that Scudder (1886:fig. 6) indicated to be the holotype described and figured by Dana (in Hitchcock 1858). Another slab containing five larvae (catalog no. 47/29) has a Horse Race locality label attached, and some of the larvae were figured by Scudder (1886:pl. 19, fig. 14). PMNH 47/19 is marked as coming from the Horse Race at Gill, but the specimens contained by it are indistinct. PMNH 47/86 is a large slab that displays several well-preserved larvae (Scudder 1886:figs. 7, 9, 13), but it lacks locality data, as does another slab with no catalog number that contains six poorly preserved larvae. Scudder (1886:figs. 5, 11, 12) also illustrated several specimens from a slab in the Shepard Collection (no. 1405) at PMNH. It bears a badly torn and incomplete locality label that states "Turners Falls," though the larvae on the slab, numbering around 30, are poorly preserved graphitic smears that do not compare favorably with Scudder's detailed illustrations. Two other specimens from the Shepard Collection (nos. T.A. 3 and T.A. 5) have a similar preservation, and the larvae are indistinct.

Notwithstanding Scudder's (1886) comment that PMNH 47/11 "appears to be the original type" described by Dana in Hitchcock (1858:7–8, pl. 7, figs. 3

and 4), it is difficult to determine which of the PMNH specimens is the holotype because no catalog number was provided with the original description. Scudder admitted the difficulty he had in matching any of the *Mormolucoides* specimens to Hitchcock's figure and to Dana's description, and he noted that the most likely candidate had been "tooled to some extent and bears no small resemblance to the figures in Hitchcock's plate." Dana's brief description (Hitchcock 1858:7–8) refers to a single larva, yet the slab Scudder thought contained the holotype includes at least eight individuals. Of these, PMNH 47/11[8] corresponds well with Hitchcock's (1858) illustration on plate 7, figure 4, especially in the slight curve of the body and presence of posteriorly directed lateral structures that project from abdominal terga. However, Dana and Hitchcock were astute observers, and we find it strange that both failed to document the presence of more than one larva in their respective comments, though two different specimens were illustrated. No mention was made of the other slabs in the Pratt Museum collections, and because it is possible that they were obtained subsequent to publication of the original description, we cannot consider faithfully any of the PMNH specimens as syntype, other than the larvae contained on PMNH 47/11. Therefore, we designate PMNH 47/11[8] as the lectotype of *Mormolucoides articulatus* (figure 13.4A). Because of the poor preservation common to most of the PMNH specimens, we designate as holotypes PMNH 47/29 and 47/36 and the YPM specimens described by Scudder (1868, 1886) and listed by White (1995). The description in the next paragraphs is based on these specimens and on the larvae contained by YPM 27497, 36241, 36242, 36243, and 36244.

Description. *Mormolucoides* are endopterygotan larvae that consist of nine dorsoventrally flattened abdominal and three thoracic sclerites. From the generally rectangular abdominal terga extend posteriorly directed, triangular pleurites (figure 13.4B). The width to length ratio of the terga is maintained as the abdomen tapers posteriorly. Abdominal segment T9 is reduced to a small, bar-shaped plate from which project short, thin, straight urogomphi. At least one specimen (figure 13.4C) also preserves paired, short projections inside the larval urogomphi that may be pupal urogomphi, a phenomenon that variably occurs in modern representatives of the Staphylinidae (Crowson

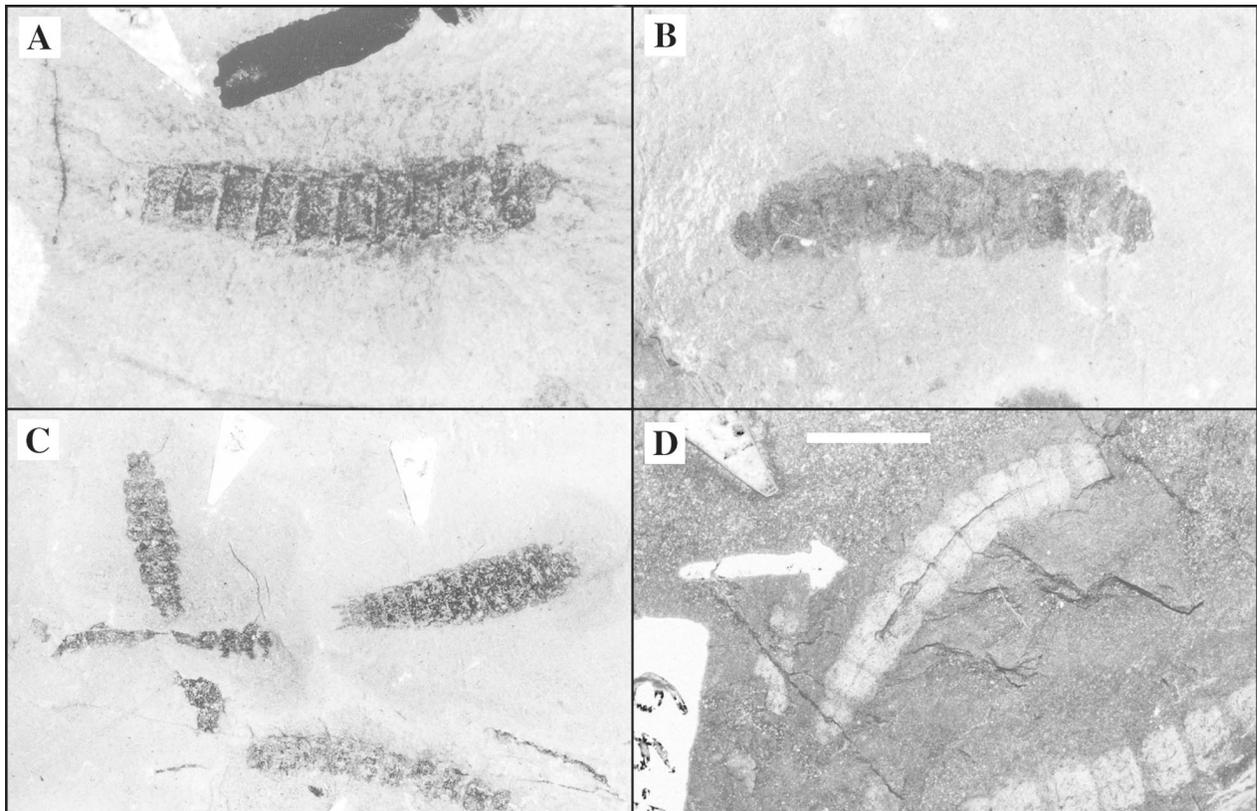


FIGURE 13.4 *Mormolucoides articulatus*. (A) Lectotype (PMNH 47/11[8]), complete larvae. (B) Larvae displaying lateral sclerites (PMNH 47/29). (C) Larvae with paired larval and pupal urogomphi (PMNH 47/36[2]). (D) Articulated larvae preserving the gut tract (YPM 27499).

1981). Clearly defined appendages are not apparent on abdominal and thoracic segments. Scudder (1868, 1886) claimed the presence of thin, short “bristles” projecting from the posterolateral margin of abdominal segments on several YPM specimens, but careful examination of these specimens and of the entire collection has not confirmed this observation.

Most of the larvae are preserved in dorsal aspect, but several are laterally compressed. No individuals that preserved thoracic appendages were found among the many thousands of specimens we examined. Two size morphs are represented that correspond to immature and mature instars. The dorsal surface of the abdominal segments on more mature individuals is divided into three sections, with a short, median tergal ridge that is flanked by concave ridges of equal length. Many specimens preserve the alimentary canal, the trace of which is defined by parallel, slightly raised longitudinal structures that apparently represent the peritrophic membrane (figures 13.4D and 13.5). The

meta- and mesothorax are narrowly ovate and nearly identical in size and shape, with laterally expanded margins that extend beyond the prothorax. The prothorax is less rounded and usually smooth, with anteriorly projecting pleural processes that extend a short distance beyond the cervix for reception of the small, retracted head. Details of the cranial morphology are obscured severely by the graphitic mode of preservation to the extent that the occipital sutures, eyes, and labrum cannot be distinguished. The trace of the coronal suture is visible on only a few of the thousands of available specimens, but several examples display broadly U-shaped frontal sutures and also preserve blunt, triangular, hook-shaped mandibles (figure 13.5B and C). Anatomical features on early instars are not well developed, though preservation of these morphs is not very good. Sclerotization of terga is weak, and though the apical segment is well developed, no indications of urogomphi have been seen. On a few specimens, the frontal suture is clearly developed, but



FIGURE 13.5 Specimens of *Mormolucoides* from the Horse Race, Mount Toby Formation, Montague, Massachusetts. (A) Mass-mortality layer of larvae interpreted as early instars (YPM 36241). (B) Larvae showing blunt, triangular-shaped mandibles (YPM 36244). (C) Close up of YPM 36244, showing mandibles.

no examples clearly display the mandibles. The only other element visible is the faint trace of the alimentary canal. It should be noted that even though individuals of this morph occur in mass-mortality layers by the hundreds, their weak sclerotization and smaller size do not serve to enhance the quality of preservation (figures 13.4 and 13.5).

Affinities. The taxonomic position of *Mormolucoides* is difficult to determine because of its poor state of preservation at all the localities from which it is known. Dana (in Hitchcock 1858) considered these larvae to be neuropteran, a view endorsed by LeConte (in Hitchcock 1862), who referred them to the Ephemeraeidae. Scudder (1868) examined the Yale specimens and initially concluded that they pertained to aquatic coleopterans, but he later changed his opinion (Scudder 1886, 1891) and agreed with Dana's original diagnosis (in Hitchcock 1858). Packard (1872) also examined *Mormolucoides* and thought the collective material pertained to "aquatic coleopterus larvae" allied to the Heteroceridae. Lull (1915, 1953) provided a

useful summary of the distribution and taxonomic history of this genus and concurred with Dana's original diagnosis. Ponomarenko (1993:185) examined a number of specimens that F. M. Carpenter sent to him and postulated a dipteran affinity, though this opinion was based solely on the "great density of deposition" rather than on morphological grounds.

Several lines of evidence favor placement of *Mormolucoides* within the Coleoptera. The retracted head, robust mandibles, and distinctive, U-shaped frontal suture—when taken together with the earlier description of the dorsal postcrania—are strongly suggestive of coleopterans rather than of neuropterans, mecopterans, or dipterans. The mode of occurrence of the larvae as mass-death assemblages spread across single bedding planes (figures 13.5A and 13.6) and the fact that the only other arthropod taxa from the locality are coleopterans support the speculation that *Mormolucoides* might represent the larval form from which *Holcoptera* elytra were derived. The single adult beetle specimen found at the locality is unfortunately a lateral

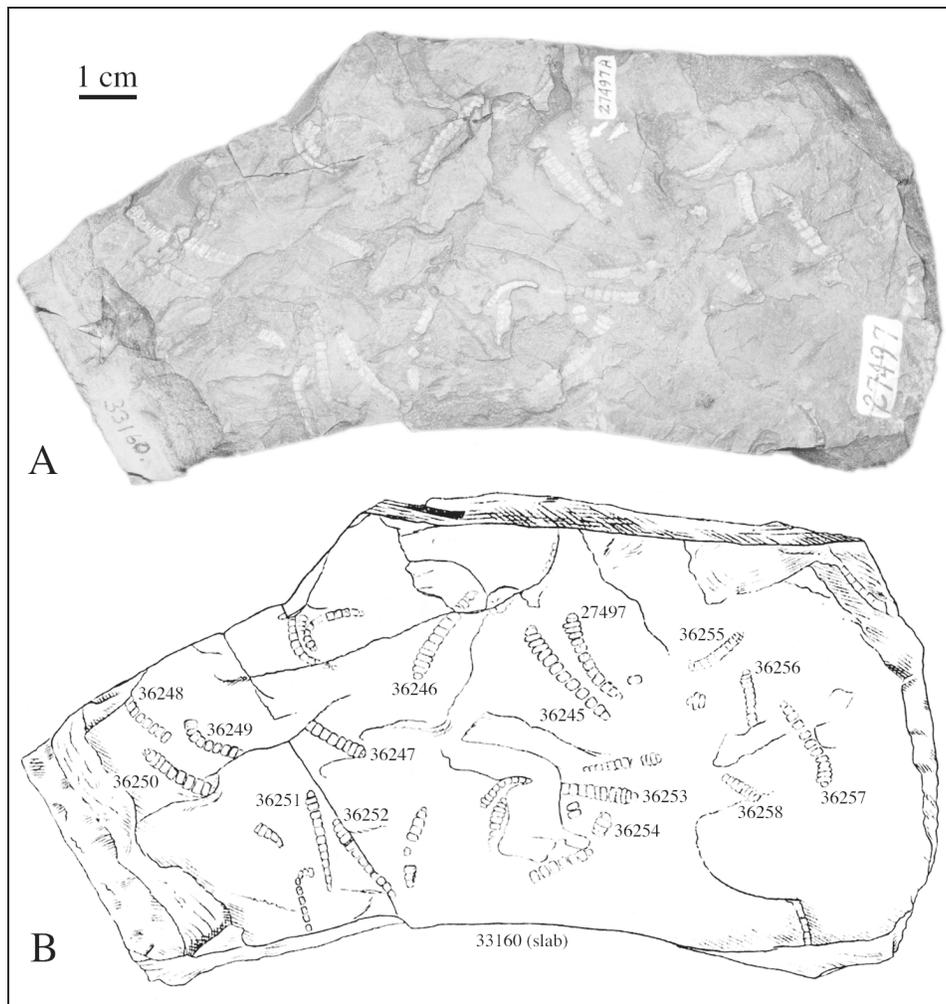


FIGURE 13.6 *Mormolucoides articulatus*. (A) Hypotypes (YPM 27497, 36245–36258 on slab cataloged separately as YPM 33160), collected by O. C. Marsh in April 1867 from the Horse Race locality. (B) Reproduction of Scudder's (1886:pl. 19) engraving that illustrates the same slab.

compression on which elytra are not visible, and poor preservation prohibits identification. Larvae representing several groups of aquatic beetles, particularly the Dysticidae, are known from fossilized mass-death assemblages (e.g., Ponomarenko 1993), which are taphonomic analogs to the *Mormolucoides* beds discussed earlier.

Material from Other Basins. Several examples of *Mormolucoides* larvae were collected recently from two localities in the Dan River basin of Virginia. The stratigraphically oldest of these larvae occurs in the lower lacustrine sequence of the Cow Branch Formation at Mayodan, North Carolina. Larva (e.g., VMNH 902, 903) from the locality occur in massive to laminated

black silty shale and include three semiarticulated specimens and abundant, isolated sclerites, all of which represent early instars. Fossil insects from the Virginia Solite Quarry (Upper Cow Branch Formation) occur in at least four separate beds of lacustrine black shale. Three of these lakebeds contain diverse assemblages (Fraser et al. 1996), and the fourth produces an assemblage similar to that at the Horse Race locality by containing an abundance of *Mormolucoides* larvae (e.g., VMNH 898, 899), complete adult beetles, and isolated elytra.

S. W. Loper collected several examples of *Mormolucoides* during the late nineteenth century from the Shuttle Meadow and East Berlin Formations in south-

central Connecticut. The Shuttle Meadow Formation specimens apparently were obtained from a bed of dark-gray laminated siltstone located approximately 3 m below the famous Durham fishbed, as indicated by our collecting efforts. Specimens from the East Berlin Formation consist of two larvae on a small slab that reportedly was collected from a now abandoned railway cut in Cromwell, Connecticut (cf. Lull 1915, 1953). The outcrop in question includes the lithology identical to that of the slab that contains the larvae, but additional specimens were not found.

Other larvae have been found in beds downstream from the Holyoke Dam in the middle Portland Formation in central Massachusetts. Preservation is very poor, and the material consists of a single mass-death layer of larvae that display faint outlines of body segments surrounded and almost obliterated by discoloration halos, though the gut track is well defined (figure 13.7B). The larvae are consistently larger than the more robust examples of *Mormolucoides* by a factor of 2.5 to 1. They occur in the middle of an unusually thick sequence of lacustrine limestone and shale that is riddled with evaporate pseudomorphs (Parnell 1983), which may indicate the mechanism that triggered the mass-mortality event.

Order BLATTARIA
Family *incertae sedis*

A well-preserved, isolated blattoid wing (YPM 37284) was recovered from a reddish-brown claystone horizon at the former K-F Quarry, developed in the Portland Formation at Suffield, Connecticut. No attempt has been made to identify the specimen to genus (figure 13.8A), though it shows broad similarities with early Mesozoic cockroaches from Europe and Asia, all of which have been placed in the paraphyletic Mesoblattinidae (Handlirsch 1906–1908; Fujiyama 1973; Whalley 1985). An additional specimen from Turners Falls, Massachusetts, resides in the YPM collections but is too fragmentary for identification more precise than Blattoidea indet. Fragmentary insects that consist of isolated abdominal segments and a single articulated hindleg were found in association with the blattoid and *Holcoptera* elytra at the K-F Quarry. The isolated segments cannot be identified, although we note their resemblance to isolated, abdominal segments of *Mormolucoides*. The hindleg (YPM 37285) has not been

studied but might be referable to the Orthoptera (figure 13.8B).

Order *incertae sedis*

A remarkable, undescribed larval specimen collected by B. K. Emerson in 1901 from the Portland Formation near Holyoke, Massachusetts, was recently found in the PMNH collections. This scarabaeiform larva is 4.5 cm in length and is preserved in dorsolateral aspect with the body slightly coiled (figure 13.7A). No ornamentation is visible on the abdominal segments, except for anteriorly placed, dorsoventrally expanded dark stripes between each segment that apparently represent small intersegmental folds. Sutures and other structures of the broad head are not preserved. The affinities of this specimen cannot be determined readily, though there is a remarkable, albeit superficial, resemblance to certain genera of extant Curculionoidea (Crowson 1981:fig. 127).

DISCUSSION

The fauna described in this chapter is important because it helps to fill stratigraphic and biogeographic gaps in the record of Mesozoic insect diversity and distribution. A number of Triassic age (Carnian) insect assemblages have been collected from the Newark Supergroup. Perhaps the most spectacular of these assemblages is from the Upper Cow Branch Formation (late Tuvallian) at the Solite Quarry in the Danville–Dan River basin of North Carolina. The Solite assemblage contains the highest diversity of insects known from any single Triassic age locality in the Western Hemisphere and was summarized by Olsen et al. (1978), Fraser et al. (1996), and Fraser and Grimaldi (chapter 12 in this volume) to contain blattoids, odonatans, heteropterans, schizophorid, dysticid and staphylinid beetles, and dipterans, in addition to one or more arachnids and undescribed possible malacostracans. As already mentioned, one of the lakebeds at the quarry contains an association of *Mormolucoides* larvae and fragmentary to complete adult beetles. The newly discovered insect fauna from the slightly older Lower Cow Branch Formation is also diverse, but, unlike the complete body fossils from the Solite Quarry, most of the specimens are isolated wings and elytra. Preliminary sampling has revealed the presence of one or more blattoids (wings); odonatans (wings); at least

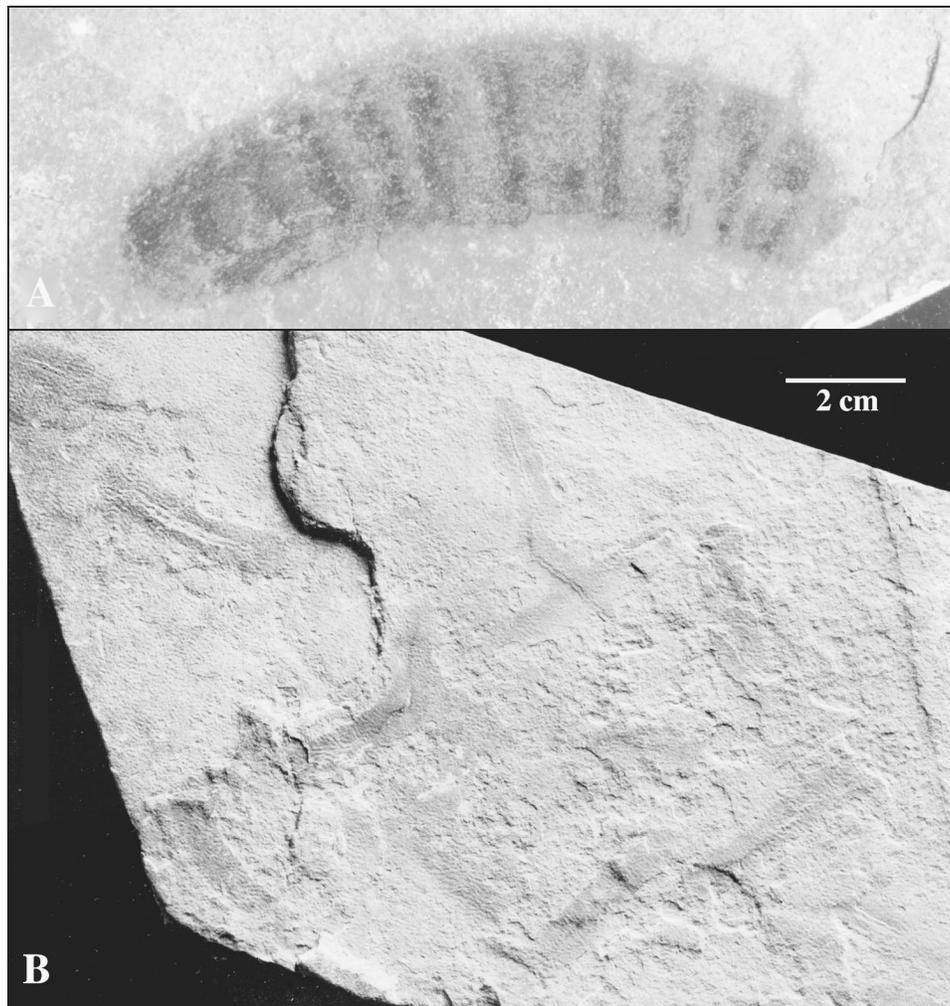


FIGURE 13.7 Jurassic insects. (A) Unidentified larva (PMNH T.A. 6), collected by B. K. Emerson in 1901 near Holyoke, Massachusetts. (B) Unidentified larvae (YPM 36419), downstream from the Holyoke Dam, Portland Formation, South Hadley, Massachusetts.

three orthopterans (wings); homopterans (complete specimens); abundant beetle elytra, including several archostematan; and one neuropteran (wings). Coleopteran elytra are relatively common at several other sites—including the Triangle Brick Quarry in the Durham subbasin of the Deep River basin (early Norian), North Carolina (e.g., YPM 34642 [Olsen and Huber 1997:fig. 3.41]); two localities in the Briery Creek basin, Virginia (early Carnian); and the type section of the Stagg Creek Formation in the Taylorsville basin, Virginia (Cornet and Olsen 1990:pl. 12)—though these specimens have not been described.

Newark Supergroup Jurassic Insecta occur in three characteristic depositional environments and facies that correspond to the ecological habits of their con-

stituent taxa. The former K-F Quarry at Suffield, Connecticut, exposed a sandstone-dominated sequence of mostly fluvial origin (LeTourneau and McDonald 1985). Red-brown sandstones at the locality contain a variety of trace fossils, including invertebrate trails and burrows and grallatorid dinosaur tracks. Gray-to buff-colored sandstones at the quarry are remarkable for the preservation of bornite- and chalcocite-replaced coalified wood, articulated conifer foliage (Cornet and McDonald 1995), and semionotid fish remains. A 0.5 m thick lenticular zone of intercalated, ripple cross-laminated to finely laminated, gray to red siltstone and claystone near the top of the quarry wall (figure 13.2D) produced most of the invertebrates known from the locality, including several conchostracan taxa (*Cyzicus*

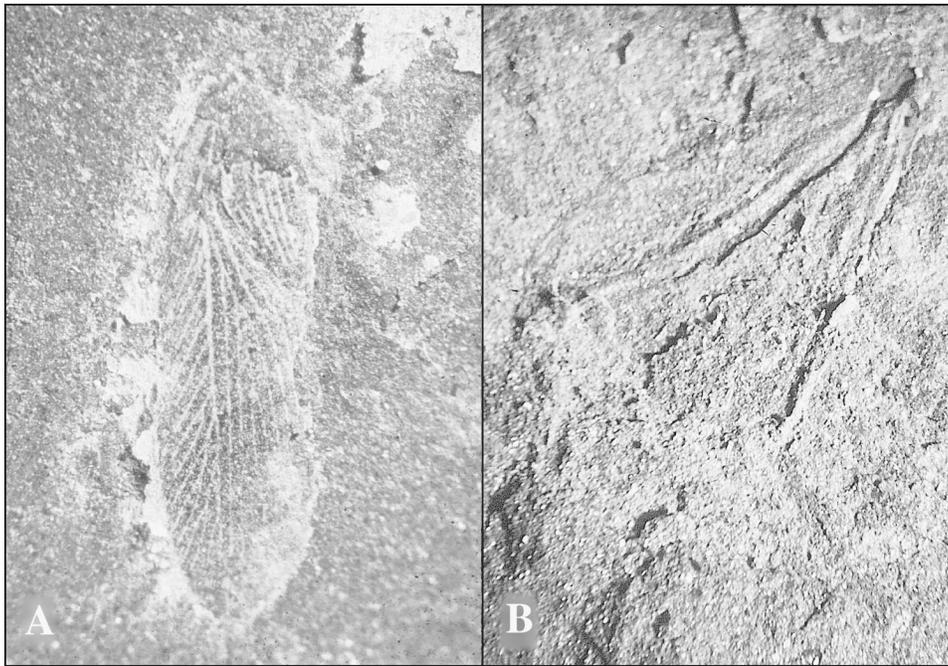


FIGURE 13.8 Specimens from the former K-F Quarry, Portland Formation, Suffield, Connecticut. (A) Blattoid wing (NGM 98). (B) ?Orthopteran hind leg (NGM 99).

sp., cf. *Cornia* sp.), the blattoid wing, *Holcoptera giebeli*, and indeterminate insect body parts (LeTourneau and McDonald 1985; McDonald 1992). Exoskeletons of the insects are preserved as thin, calcified cuticles that display the venation patterns of *Holcoptera* elytra and the blattoid wing. Based on the color, bedding, lenticular geometry, and association with fluvial sandstone, we interpret the K-F Quarry insect bed as an ephemeral floodplain pond or shallow lake deposit.

At the Horse Race and other localities, horizons that contain *Mormolucoides* larvae are beds of dark-gray, finely laminated silty claystone sometimes intercalated with 1 to 10 cm beds of massive, light-gray siltstone. The claystone is composed of alternating silt and organic-rich lamina with occasional interspersed laminae of dolomitic carbonate. The base of the most productive 1 m thick lacustrine cycle at the Horse Race begins with olive-brown, massive-bedded silty sandstone with upper bedding surfaces that display symmetrical ripples and contain grallatorid dinosaur and *Batrachopus* footprints and macerated plant debris. The basal unit is upwardly gradational, with dark-gray claystone and siltstone that contain most of the *Mormolucoides* larvae collected to date. The lower and upper portions of the productive unit are wavy to finely

laminated, lack interspersed layers of dolomitic carbonate, and contain horsetail stem fragments, conifer shoots, grallatorid and crocodylomorph footprints, and numerous, isolated segments of *Mormolucoides* and rare *Holcoptera* elytra. The central 0.3 m thick portion of the sequence is well indurated and finely laminated and contains thousands of partially and fully articulated larvae. Although single individuals are distributed randomly throughout this interval, the majority of specimens occur on four or more bedding surfaces that represent mass-kill layers (figures 13.4–13.6), possibly Marsh's (1867) "five layers." Preservation of larvae is highly variable and ranges from detailed compressions to three-dimensional individuals that preserve sclerite structures on abdominal segments to graphitic smears with a slickensided appearance. Some of the mass-kill layers are riddled with small, probable halite crystal casts. The top of the *Mormolucoides* zone grades upward into medium-gray siltstone with abundant plant debris and small reptile footprints.

Based on color, bedding style, lithology, and association with encasing sediments that contain abundant footprints of terrestrial vertebrates, we interpret the Horse Race *Mormolucoides* beds as forming in shore-

ward areas of a shallow, perennial lake. The complete absence of conchostracan, ostracode, and fish remains throughout this lacustrine sequence is important. The occurrence of alternating silt- and organic-rich and dolomitic carbonate laminae indicates the possibility of seasonal (i.e., wet–dry) climatic influence over deposition. This interpretation finds further support from the association of mass-kill layers with probable evaporite hopper casts. Thus we envision a paleoecologic model in which silt-rich laminae and thicker units were deposited by increased clastic input during the wet phase of a monsoonal climatic regime. At the onset of the dry season, clay-size particles and organic matter settled from suspension and beetle eggs hatched and colonized parts of the shallowing lake. Although we have no information on the life-cycle duration of these larvae, the association of mass-kill layers and evaporates on individual bedding surfaces suggests that the shoreward portions of the lake became periodically hypersaline and caused mass mortality of some of the *Mormolucoides* larvae before they entered the pupal stage. Such a scenario also explains the absence of conchostracans and darwinulid ostracodes and of fish, for the larvae would have provided an optimal nutrient resource for omnivorous genera such as *Redfieldius* and *Semionotus*, taxa that are common in other broadly correlative lacustrine sequences of the Hartford and Deerfield basins.

This model also explains the paucity of *Mormolucoides* and other insects in the classic “deep-water,” fish-bearing lacustrine deposits of the Newark, Hartford, and Deerfield basins. Although these fishbeds have been the focus of extensive excavations and study for well more than 150 years, the only insect records they contain are the single elytron of *Liassocupes* and scant examples of *Mormolucoides*. Thus the singular occurrence of *Liassocupes* in a gray, thin-bedded, lacustrine shale of the Towaco Formation leads to the speculation that the elytron was transported offshore by subaqueous or wind-carried suspension. The *Liassocupes* elytron probably escaped predation by macrofaunal and microbial scavengers because of its durable proteinaceous structure and small size, as well as the influence of dysoxic substrate conditions.

Invertebrate trace fossils are found also in playalacustrine red to grayish siltstones that represent well-oxygenated, shallow-water depositional environments. These facies occur as single cycles or encase offshore

deposits of gray microlaminated mudrocks. They contain at least 17 morphotypes of arthropod trace fossils, divisible into three generalized categories that represent burrow, feeding, and walking traces. Hitchcock (1858) named the Hartford and Deerfield basin occurrences of these traces to comprise what we consider to be a grossly oversplit ichnofauna of some 27 genera and 52 species (Lull 1915, 1953; Olsen et al. 1992). Burrows can be referred to *Scoyenia*, *Planolites*, *Fucoides*, and *Skolithus* or are clearly unionid mollusk escape traces (McDonald and LeTourneau 1988). The organisms responsible for the feeding traces are enigmatic but probably included a number of vermiform and crustacean detrital herbivores that constructed horizontal and subhorizontal furrows across sediment surfaces. The walking traces include eight morphologies, all of which are likely referable to insects, arachnids, and myriapods, although assignment to lower taxonomic levels is not possible at present (Hitchcock 1858; Lull 1915, 1953). In spite of this severe limitation, the ichnofauna does indicate the presence of diverse insect assemblages in the Hartford, Deerfield, and Newark basins during the Early Jurassic.

The Newark Supergroup is one of the few regions that preserves thick sequences of fossiliferous mudrocks that bracket the Triassic–Jurassic boundary and represent substantial amounts of Late Triassic and Early Jurassic time. Recent biostratigraphic and correlation studies indicate that these rocks collectively span the ?Anisian–Ladinian through Sinemurian–Pliensbachian (Lucas and Huber 1993, chapter 11 in this volume; Olsen 1997). We believe that the Newark Supergroup offers the potential to help fill the time-stratigraphic gap in the fossil record of insect evolution and diversity during the early Mesozoic. Insect assemblages of Late Triassic age that show a significant measure of diversity are known from Gondwanan faunas in Australia and South Africa, although most of the South African taxa (Molteno Formation: ?Carnian) have not been described. Relatively diverse assemblages that have been assigned a Late Triassic age were described from Central and eastern Asia (Ponomarenko 1969; Fujiyama 1973), but aside from associated megaflores (Dobruskina 1994) there is no independent age control for most of these assemblages, which may be Early to Middle Triassic or even Jurassic in age.

Significant insect faunas of Early Jurassic age have been long known from Europe and Central Asia, and

at least most of the European localities have been tied directly to the standard ammonite-based timescale, whereas the ages of most of the Central Asian localities have not been determined accurately. Many of these faunas are quite diverse (Handlirsch 1906–1908; Bode 1953; Whalley 1985), and some show broad similarity to the Newark Supergroup Early Jurassic fauna in that they are dominated by coleopterans (Ponomarenko 1969, 1993; Whalley 1985). Of particular significance is the mutual occurrence of *Liassocupes* and *Holcoptera* in the Newark Supergroup and in the broadly contemporaneous strata of Europe (dated as Sinemurian by ammonites). *Holcoptera* has a broad temporal range that extends below the Triassic–Jurassic boundary in England to the Rhaetian. The range of *Mormolucoides* spans the late Carnian (late Tuvanian) through the Liasic, a period of approximately 25 million years. Because *Mormolucoides* is a form genus, the possibility exists that these larvae might represent more than one genus or numerous species or both. It is difficult to draw any meaningful conclusions from this distribution because of the limited diversity of Jurassic age Newark Supergroup insects. However, this distribution does not contradict nonmarine, biogeographic models for the Pangaean Early Jurassic, which demonstrate a high degree of stability and homogeneity among low-to midlatitude palynofloras, macrofloras, and fish and tetrapod assemblages (Olsen and Sues 1986).

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