Chapter 11
The Mesozoic Lacustrine Revolution

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11.1 Introduction

The Mesozoic lacustrine revolution (MLR) represents a major evolutionary event in the continental realm (Cohen 2003). The decline in taxic diversity at the family level in lacustrine environments that took place during the late Paleozoic–Middle Triassic was reversed later in the Mesozoic, with diversification seeming to have continued to the Quaternary, although potential biases may have affected this trend (Cohen 2003). Major novelties and innovations that took place in lacustrine

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settings during the mid-Mesozoic include the diversification and increase in morphological disparity of aquatic macrophytes, aquatic insects, and teleosts. By the mid Cretaceous (125–90 Ma), the basic ecologic structure of the MLR was well established, defined by an ecologically significant increase of herbivory within ecosystems which previously had been overwhelmingly composed of detritivores and predators. This trophic readjustment was minimally altered by the end-Cretaceous global crisis and the subsequent ecologic rearrangement of the Paleogene world (Dunne et al. 2014).

It is a basic premise of this chapter that a review of this formative interval from a comparison of the body- and trace-fossil records will illuminate our understanding of the MLR. Although direct links between individual ichnotaxa and producers commonly are not possible, a comparison of the trace-fossil and body-fossil records through time is valuable in detecting the timing of large-scale ecologic changes in lacustrine ecosystems. Consequently, in this chapter we review the trace- and body-fossil record of lake and related continental aquatic deposits to establish and assess the importance of the MLR. As part of our examination, we discuss how ichnologic evidence may provide insights into major evolutionary innovations within lacustrine ecosystems. To do so, we provide an extensive summary of the available ichnologic information for Mesozoic–Cenozoic lacustrine successions. In addition, a review of the paleoecologic structure of Eurasian paleolakes in particular provide important evidence for understanding the impact this event had on trophic relationships throughout the water column (Zherikhin et al. 1999; Sinitshenkova 2002) as well as the lacustrine benthos and associated sediments during this formative interval (Buatois et al. 1998a; Mángano and Buatois 2007; Voigt and Hoppe 2010). Although this chapter is focused on the evolutionary novelties and innovations that took place during the Mesozoic, in order to place these changes within a broader context, we briefly outline the basic features of lacustrine ecosystems prior to the MLR (see Chap. 6 for a detailed discussion on the ichnology of Silurian-Permian lakes). A more complete context for understanding the MLR involves a search for the roots of Mesozoic MLR novelties and innovations in older deposits to establish relevant ichnological, biotic, and physical contrasts between the late Paleozoic and the Mesozoic worlds. Similarly, we provide a discussion of the post-Mesozoic record in order to evaluate the aftermath of the MLR.

11.2 Methods and Terminology

For this study, all ichnotaxonomic determinations have been checked and adjusted based on a reevaluation of the available literature. Because the literature essentially provides two contrasting trace fossil-assemblages, a distinction is made between lake-margin settings and fully subaqueous lacustrine conditions. Lake-margin settings are characterized by periodic fluctuations of the water table, leading to highly variable conditions in substrate consistency. Typically, a characteristic zonation from softgrounds near the edge of the water body to drier substrates outward from the lake develops (Scott et al. 2012a). Lake-margin ichnofaunas commonly display activity of a combined terrestrial to shallow subaqueous biota. The degree of consolidation of the substrate plays a major role for preservation of biogenic structures in lake-margin deposits (Buatois and Mángano 2004, 2009). Ichnofaunas from lake-margin settings typically comprise the *Scoyenia* Ichnofacies (Buatois and Mángano 1995, 2004, 2009) and less commonly the *Camborygma* Ichnofacies (see Chaps. 1 and 13).

Fully lacustrine settings (i.e. the permanent subaqueous zone), particularly in hydrologically open systems, may host a relatively diverse benthic fauna. In this zone a where a lake experiences a high degree of environmental stability and appropriate ecologic conditions, particularly high levels of oxygenation, low energy, constant food supply, the presence of freshwater, and cohesive substrates (Buatois and Mángano 1995, 2004, 2009; Miller and White 2007; Scott et al. 2012a). Oxygenation is a first-order limiting factor, because in lakes with year-round thermal stratification the hypolimnion becomes anoxic or dysoxic and bioturbation is precluded in the lake bottom below the mixolimnion. Low-energy turbidity and underflow currents may provide oxygen and food to lake bottoms. Colonization by macrobenthos and preservation of their trace fossils are both unfavorable in soupy substrates and, accordingly, some degree of substrate cohesion is required to allow the passage of discrete biogenic structures through the fossilization barrier. Ichnofaunas from fully lacustrine settings typically form the *Mermia* Ichnofacies (Buatois and Mángano 1995, 2004, 2009; see Chap. 1).

At the scale of the basin, we commonly refer to the scheme developed by Bohacs et al. (2000), who recognized three different types of lake basins, namely overfilled, balanced-fill, and underfilled. Overfilled-lake basins occur if the rate of sediment/water input exceeds the rate of formation of potential accommodation. These systems are typically hydrologically open, and form deposits of fluvio-lacustrine, siliciclastic sediments that display parasequences resulting from shoreline progradation and delta-channel avulsion. Balanced-fill lake basins are formed when rates of sediment/water supply are in balance with the formation of potential accommodation. These lakes tend to shift periodically from hydrologically open to closed and vice versa, producing both carbonate and siliciclastic deposits which display parasequences that record both progradational parasequences and aggradation of chemical sediments during periods of desiccation. Underfilled-lake basins are characterized by rates of accommodation formation that exceed the rate of supply of sediment/water. These are typically hydrologically closed lakes, dominated by evaporite deposits which display parasequences that record vertical aggradation. This scheme has been successfully used to frame both ichnologic (Buatois and Mángano, 2004, 2007, 2009) and paleobiologic (Gierlowski-Kordesch and Park, 2004) information.

In order to frame the major ecosystem changes discussed in this chapter, we have used the distinction between novelties and innovations outlined by Erwin and Krakauer (2004) and Erwin (2012). According to these authors, invention is the creation of something new, whereas innovation is a successful development of an invention. Evolutionary novelties only result in innovations when they drive ecologic transformation (Erwin 2012).

For better clarity in specifying the immatures of non-holometabolous versus holometabolous insects, we employ the standard entomological terminology used in North America (China et al. 1958). For those insects possessing egg to naiad/nymph to adult development, the term "naiad" is used for an aquatic immature instar that lacks holometabolous development (Snodgrass 1954). Immatures consisting of naiads occur in the Ephemeroptera (mayflies) and Odonata (dragonflies and damselflies), the extinct archaeorthopteroid Chresmodida, Plecoptera (stoneflies), and some groups of Heteroptera (true bugs) within the Hemiptera. A terrestrial immature of these non-holometabolous insects is termed a "nymph" (Snodgrass 1954; Davies 1958), and nymphs commonly occur within the same major groups as species with naiad immatures. Examples of taxa with nymphs include the terrestrial Orthoptera (grasshoppers, crickets), Blattodea (cockroaches), Isoptera (termites), and Mantodea (mantids). We restrict the term "larva" solely to insects with holometabolous development, consisting of egg to larva to pupa to adult development (Snodgrass 1954). Holometabolous taxa that have aquatic larvae include certain groups within the Coleoptera (beetles); the Megaloptera (alderflies and dobsonflies); a few groups of Neuroptera such as spongillaflies; certain, especially nematocerous, Diptera (true flies); and the Trichoptera (caddisflies). Restriction of the term, larva, to holometabolous insects offers more precision than application of the term broadly to multiple developmental modes that would encompass developmental stages such as aquatic naiads, terrestrial nymphs, and probably forms that lack developmental change. The distinction used herein generally has been accepted by a broad spectrum of evolutionary developmental biologists (Gilbert 2014).

The body-fossil record of ancient lacustrine basins is strongly biased as a result of the distribution of fossil *Lagerstätten*. Fortunately, these spectacular deposits are quite common in lacustrine successions (see Table 14.1 in Cohen 2003). However, integrating body-fossil evidence from fossil Lagerstätten with ichnologic information frequently is problematic because many of the former records accumulated as event beds under anoxic conditions, preventing bioturbation, and therefore having a sparse trace-fossil record. Notwithstanding this limitation, there are a number of Mesozoic examples where exceptional body-fossil accumulations have been recovered in association with trace fossils, most notably the Madygen (Voigt and Hoppe 2010), El Montsec (de Gibert et al. 2000) and Las Hoyas (Buatois et al. 2000a; de Gibert et al. 2016) biotas.

11.3 Lacustrine Ecosystems in Deep Time

Exploration of lacustrine ecosystems in deep time is a challenging enterprise because lakes are geologically ephemeral (Cohen 2003). However, the long-term evolution of organisms in freshwater settings provides continuity, allowing reconstruction, albeit tentative, of secular changes in lacustrine biotas (Anderson and Dean 1988; Buatois et al. 1998a; Labandeira 1999; Park and Gierlowski-Kordesch 2007). Because of the patchiness and lack of connection between individual lakes in space and time, as opposed to the more continuous record of oceans, the fossil record of lacustrine organisms is sporadic (Cohen 2003).

As with other depositional settings, lakes are affected by a number of taphonomic megabiases (Behrensmeyer and Kidwell 1985; Behrensmeyer et al. 2000).

Taphonomic megabiases are defined as "largescale patterns in the quality of the fossil record that affect paleobiologic analysis at provincial to global levels and at timescales usually exceeding ten million years" (Behrensmeyer et al. 2000). In particular, the fossil record of lacustrine basins is strongly affected by both intrinsic changes and extrinsic abiotic and biotic changes. The former results from the evolution of new body plans and the impact of behavior on fossilization potential (Behrensmeyer et al. 2000). As in the archetypal case of marine environments, development of mineralized hard parts is one of the intrinsic factors in lake settings, as is the establishment of fossorial behavior by vertebrates. The increased depth and extent of bioturbation through time exhibited by the lacustrine infauna is certainly one of the most important, extrinsic biotic factors contributing to taphonomic megabiases in these settings (see Sect. 11.8.2). Finally, tectonic and climatic controls on the establishment and evolution of lacustrine basins are prime examples of extrinsic, abiotic factors in the generation of taphonomic megabiases. These interpretive limitations notwithstanding, our understanding of this record are informed by several key observations.

(1) **Lacustrine habitats have experienced a history of regular and repeated formation, isolation, and destruction**. Because of the combined effects of climate variability and change as well as sediment infill, most individual lakes only persist over timescales of ~10^2–10^4 yrs, with only a small percentage of lakes, generally those originating from tectonic, volcanic, and meteoritic impact processes, persisting over longer intervals of time (Cohen 2003; Cohen et al., 2015). Most of the processes that create lakes, such as fluvial diversion from damming, glacial blockage of drainage systems and delta-plain subsidence, are also predilect for the eventual destruction of these same habitats. The creation and destruction of lakes often occur at quasi-predictable tempos scaled by the lake formation process, including determining potential sediment accommodation space, coupled with the typical range of sediment accumulation rates associated with lacustrine systems.

(2) **The need for dispersal of organism populations among lakes is a primary driver of both evolutionary innovations and constraints on the lacustrine biota**. The excellent dispersal adaptations of organisms are a hallmark characteristic of most lacustrine systems. Organisms have evolved adaptations for dispersal as well as for the constraints emplaced on them by the "typical" lacustrine environment mentioned above. These features include adaptations for flight, such as active flight by aquatic insects, and passive carriage by birds, fish, and wind (Boag 1985; Bilton et al. 2001; Green and Figuerola 2005; Van Bocxlaer et al. 2011); active parasitism on animal dispersal vectors (Graf and Cummings 2006); and desiccation resistance (Watanabe et al. 2002; Watanabe 2006). Conversely, the very adaptations for dispersal between ephemeral waterbodies also promote gene exchange between populations and reduce the likelihood of population isolation and speciation (Bilton et al. 2001). These adaptations inherently constrain and scale the rates of lacustrine evolution to the stability and persistence of their waterbodies, with the faunas of shorter-lived lakes (better migrants or desiccation survivors) associated with slower evolutionary rates and overall lower diversity. Morphological novelties arising from new functional and behavioral modifications take advantage of changing lacustrine

food resources, of which herbivory on aquatic plants or tiered detritivory exploiting deeper substrates are prime examples. These novelties become innovations when in the case of dispersal, the spread of disseminules is severely impeded by a periodic scarcity of quasipersistent lakes, and the energetic requirements of adaptations for exploiting lacustrine resources run up against the competing need to migrate to new habitats.

(3) **Lacustrine evolution in long-lived lakes is highly iterative and lacustrine habitats can act as refugia for evolutionary novelties and innovations.** Comparative studies of the living and fossil faunas of long-lived Neogene African Great Lakes and early Mesozoic Newark Supergroup paleolakes show that speciation and diversification trends often are highly iterative. The iteration of homologous morphological novelties in lacustrine clades evolve repeatedly in space and time whenever lakes persist sufficiently long for the results of diversification to be expressed (McCune 1996; Salzburger et al. 2014). Particular body plans and evolutionary novelties have been observed resulting from the convergence of lineages within isolated lakes. One such convergence is the iconic example of cichlid fish pharyngeal jaw mechanics and overall body structure converging among species populations in Lakes Tanganyika and Malawi (Kocher et al. 1993). Perhaps even more remarkable, trophic interactions have also been observed to converge among long-lived lakes, albeit occasionally with slightly different players. One example involves patterns of escalatory predator–prey coevolution (West and Cohen 1996; Van Damme and Pickford 2003). Occasionally, the resulting species of these radiations are themselves later dispersed into other lake systems, providing the beginnings for more widespread spatial diversification of the original clade (Van Damme and Pickford 1999; Anderson et al. 2010).

(4) **The tempo of evolutionary innovation related to trophic interactions in lakes is probably modulated by the history of geochronologically long-lived lakes**. If long-lived lakes can serve as incubators for diversification and evolution of key innovations and interactions in aquatic organisms, then it is likely that during times of such lake abundance, the most favorable opportunity exists for large scale trophic “revolutions” within lacustrine biotas. The mid-Mesozoic breakup of Pangaea probably represented the peak period of long-lived lake formation. These lakes were coupled with an ever increasing provinciality as they were progressively rafted on different continental land masses around the planet (Cohen 2003).

11.4 The Lacustrine World Prior to the Mesozoic Revolution

In this section we provide a brief review of the basic features of lacustrine communities that immediately preceded those of the Mesozoic world. Evidence of Proterozoic lacustrine biotas is scarce, to say the least, essentially being restricted to stromatolites most likely formed by cyanobacteria (e.g. Hoffmann et al. 1980) and leiosphaeridian acritarchs that may have been adapted to freshwater, although this is a contentious issue (Martín-Closas 2003). There is a paucity of evidence for body-fossils in Cambrian through mid-Silurian continental aquatic habitats (Labandeira 2005a). Tasmanitids (green algae) were abundant during the early Paleozoic, but most likely inhabited brackish rather than fresh water (Martín-Closas 2003). The Cambrian-Ordovician evidence for the incipient colonization of land originates from trace fossils of arthropods that were able to foray into intertidal areas, coastal dunes and ponds (see Chap. 5), and stromatolites that were similar in structure to, but commonly more diminutive than those of the Precambrian (Ponomarenko 2009). In addition, the occurrence of a diverse cryptospore assemblage in Lower to Middle Ordovician deposits represents the earliest evidence of land plants, suggesting an early origin of embryophytes (Rubinstein et al. 2010). Chlorophytes were represented mainly by the Chlorococcales, which became dominant in lacustrine plankton by the Ordovician (Martín-Closas 2003), and the closely related Charophytes that were present in freshwater bodies at by the Late Silurian, if not earlier (Feist et al. 2005). The presence of liverwort and embryophyte-grade spores toward the end of this interval, and continuing into the Early Devonian, signals the establishment of an incipient subaerial plant cover, probably adjacent to bodies of brackish and freshwater inland and along coastlines (Strother 2000). These developments, in conjunction with the presence of lacustrine (and fluvial) sediments, particularly during the Late Ordovician and Silurian, indicate the emergence of a depauperate lacustrine biota consisting of transient and permanent microorganisms, plants, fungi, and invertebrate animals. The fossil history of lacustrine zooplankton is notably poor. However, molecular clocks may help to provide some constraints. For example, cladoceran crustaceans are thought to have originated by the Devonian (Sacherová and Hebert 2003). The Silurian-Devonian lacustrine trace-fossil record is restricted to lake-margin settings, and is dominated by arthropod trackways (Buatois and Mángano 1993a; Buatois et al. 1998a; see Chap. 6). The restriction of biogenic structures to lake margins and the apparent absence of fully lacustrine ichnofaunas are consistent with extremely inefficient nutrient delivery in the absence of an extensive upland plant cover (Cohen 2003). These lakes may have been ultraoligotrophic and limited in phosphorous (Cohen 2003), precluding the establishment of a lacustrine benthos.

With few exceptions (Grenier 1974; Clarkson et al. 1993; Rolfe et al. 1993; Jeram and Selden 1993; Shear 1993), the Lower Carboniferous (Mississippian) lacks a significant record of well-documented lake deposits and associated biotas. During the Late Carboniferous (Pennsylvanian), two major types of ecosystems appeared that were displaced by differing environmental conditions. The Wet Biome emerged during the earlier Pennsylvanian and included a wide variety of wetlands, notably coal-swamp communities that consisted of water-tolerant lycopods, sphenopsids, medullosan seedferns, and arborescent marattialean ferns, occupying much of humid equatorial Euramerica (Gastaldo et al. 1996). By contrast, evidence for a Dry Biome appears toward the latter half of the Pennsylvanian, and included communities dominated by a desiccation-tolerant biota, such as cordaites, noeggeranthialeans, conifers, gigantopterids, peltasperms, and probably cycads that occupied more continental, extra-tropical environments (Opluštil et al. 2013). Regarding zooplankton, copepods were already present by the Mississippian in glacial lakes of

Gondwana (Selden et al 2010). During the Permian, the tropical to paratropical Wet Biome diminished significantly, at least in North America and Europe, although it survived largely intact in China (D'Rozario et al. 2011). By contrast, the Dry Biome, which first appeared during the latter half of the Pennsylvanian (Opluštil et al. 2013), temporally overlapped with the Wet Biome, and became prominent in more inland, drier basins of the Permian as it assumed a distinctive biotal character in many habitats. Aquatic herbivory was still absent, in contrast to a pulse of significant herbivory that had evolved on land by the Late Pennsylvanian (Labandeira 2006). In addition to ichnofaunas in lake-margin deposits, Mississippian and Pennsylvanian trace fossils also are present in fully subaqueous lacustrine deposits, indicating a significant environmental expansion of the benthic fauna (Buatois and Mángano 1993a; Buatois et al. 1998a) (see Chap. 6). These lacustrine deposits were colonized by a moderately diverse, mobile, detritus-feeding epifauna. This expansion was probably linked to the rapid diversification, and increase in abundance of land plants, attributable to vegetational changes that introduced abundant organic detritus into previously nutrient-poor, lacustrine habitats (Maples and Archer 1989). Also, ichnologic information suggests a major diversification event during the Mississippian and Pennsylvanian, which parallels the diversification of freshwater organisms, such as arthropods, annelids, fish, and mollusks (Maples and Archer 1989; Buatois et al. 1998a). The ichnologic evidence of the Dry Biome during the subsequent Permian consists of a high abundance and moderate diversity of arthropod trackways emplaced in subaerially exposed sediment of playa-lake systems (see Chap. 6). By the Permian, the presence of meniscate trace fossils (e.g. *Scoyenia*) records the establishment of a mobile, shallow- to mid-tier, infauna in firm, desiccated substrates. However, these structures still were relatively rare and for the most part have been recorded in overbank environments rather than in lake-margin settings that are overwhelmingly dominated by arthropod and tetrapod trackways.

11.5 The Mesozoic Lacustrine Revolution

The Mesozoic trace-fossil record of lacustrine successions is uneven in time and space. The Lower Triassic ichnologic record of lake-margin environments is remarkably poor, and we are not aware of well-documented, fully lacustrine, Early Triassic ichnofaunas. In contrast, Middle to Late Triassic lacustrine ichnofaunas have been documented in great detail. The Jurassic ichnologic record is uneven, with a number of detailed studies documenting both Early and Late Jurassic ichnofaunas, but less information is available for the Middle Jurassic. The Early Cretaceous record is relatively good, but the record of Late Cretaceous fully lacustrine ichnofaunas is particularly poor.

Unsurprisingly, body fossils of the MLR are unevenly distributed as well. Triassic paleontologic information is essentially based on Eurasian localities and, to a lesser extent, eastern North America and South Africa. The Jurassic body-fossil record, particularly for aquatic insects, is still significantly centered in Eurasia, but includes a few localities in western North America as well. In contrast, the Early Cretaceous tends to show a more widespread distribution of lacustrine fossiliferous localities, but still is heavily represented by Eurasian lake deposits, most likely resulting from extensional tectonics during the breakup of Gondwana. However, information from the Late Cretaceous is patchy.

11.5.1 Early Triassic Denouement

After the ecologic crisis at the Permian–Triassic boundary, the short-lived, five million-year-long Early Triassic represents a period that ranges from biotal stasis to subtle increases in the diversity of aquatic and terrestrial communities (Looy et al. 1999). The ichnology of Lower Triassic lake-margin deposits has been documented in a few places, namely Germany (Knaust and Hauschke 2004, 2005) and the western United States (Lovelace and Lovelace 2012). A moderate diversity of invertebrate trace fossils has been recorded in marginal facies of an underfilled playa-lake system in Germany (Knaust and Hauschke 2005). The playa-lake ichnofauna contains arthropod trackways and trails (*Diplichnites*, *Stiallia*, *Diplopodichnus*), arthropod bilobate structures (*Cruziana*, *Rusophycus*), vertical burrows (*Skolithos*), bivalve burrows (*Lockeia*), branching burrow systems (*Phycodes*), and the horizontal J-shaped ichnogenus *Fuersichnus*. Pseudofossils, such as *Aristophycus*, are present in the same deposits (Knaust and Hauschke 2004). Body fossils have been recovered from these deposits, including conchostracans, notostracans, and xiphosurids, as well as indeterminate fish remains (Knaust and Hauschke 2005). The arthropod trackway *Diplichnites* and the bivalve dwelling/resting structure *Lockeia* also occur in Lower Triassic shallow-lacustrine deposits of the western United States (Lovelace and Lovelace 2012).

In contrast to younger lake-margin ichnofaunas, meniscate, backfilled trace fossils are absent in these Lower Triassic examples, and arthropod trackways seem to be relatively common. In this respect, Lower Triassic lake-margin ichnofaunas apparently are more similar to those from the Permian (see Chap. 6) than to the archetypal Mesozoic suites, revealing the persistence of Paleozoic types of animal–substrate interactions. Also, as is commonly the case for Paleozoic lacustrine ichnofaunas, shallow tiers were dominant and penetrative structures, such as those responsible for ichnofabric formation, were absent (Knaust and Hauschke 2005).

The Early Triassic continental body-fossil record is sparse as well (Shcherbakov 2008a). Freshwater insects originate mostly from Eurasian localities and generally consist of mayfly wings (Sinitshenkova 2013), archaeorthopteran and related orthopteroid taxa (Shcherbakov 2008b), cockroaches (Żyla et al. 2013), a few basal hemipteran lineages (Shcherbakov 2008a), and isolated elytra of schizophorid and permosynid beetles and related lineages (Ponomarenko 2004, 2008). Many of these fossil taxa preferentially are represented by immatures, especially naiads, that when compared to conspecific adults, occur at frequencies greater than is typical of the Permian (Shcherbakov 2008b). As with Early Triassic plants (Looy et al. 2001), contemporaneous insect faunas are characterized by four major changes when compared to their Late Permian precursors (Shcherbakov 2008b). These shifts are: (1) the evolution of new, Early Triassic dominant groups at the expense of earlier Late Permian dominants; (2) movement into the high-latitude Triassic by groups that formerly occurred at Permian low latitudes; (3) preferential survival of small-sized, generalist feeding taxa; and (4) emergence of lineages that were aquatic or otherwise tied to water bodies such as lakes. Although these changes promoted diversity, it was not until the Anisian stage of the early Middle Triassic, 5–11 m.yr. after the end-Permian crisis, when insect taxa, including aquatic forms, and their interactions with plants approached the diversity that had existed during the Late Permian (Gall 1996; Labandeira 2005b).

Another important component of the Triassic benthos was charophytes, which are particularly well known in lacustrine carbonates and marls (Martín-Closas 2003). *Isoetes*-related, nonflowering vascular plants were present in the littoral zone (Cohen 2003; Moisan et al., 2012b). As in the Paleozoic, lacustrine phytoplankton was still dominated by Chlorococcales, but an increase in diversity is apparent (Brenner and Foster 1994; Martín-Closas 2003).

11.5.2 Rediversification During the Middle to Late Triassic

Ichnofaunas have been documented in detail in Middle to Upper Triassic lake-margin deposits (including those of playa lakes) from the eastern (Metz 1995, 1996, 2000; Szajna and Hartline 2003) and western (Gillette et al. 2003; Lucas et al. 2010) United States, Argentina (Melchor et al. 2003, 2006; Melchor 2004; Genise et al. 2009; Marsicano et al. 2010), Greenland (Bromley and Asgaard 1979), England (Porter and Gallois 2008), Germany (Schlirf et al. 2001), Morocco (Hminna et al. 2015), and China (Shi et al. 2007; Li et al. 2014). These lake-margin deposits commonly contain a relatively wide variety of vertebrate and invertebrate trace fossils.

Vertebrate ichnofaunas in Middle to Upper Triassic lake-margin deposits typically are dominated by tetrapod trackways (e.g. *Brachychirotherium*, *Brasilichnium*, *Dicynodontipus*, *Characichnos*, *Evazoum*, *Grallator*, *Gwyneddichnium*, *Rhynchosauroides*, *Tetrasauropus*) and, more rarely, lungfish burrows (*Redondarefugium*) (Melchor et al. 2006; Lucas et al. 2010). Typical invertebrate trace fossils in lake-margin deposits are shallow-tier, ornamented, meniscate, unbranched (*Scoyenia*), and branched (*Spongeliomorpha*) structures, as well as meniscate structures lacking bioglyphs (*Taenidium*), arthropod bilobate structures (*Cruziana*, *Rusophycus*), and simple horizontal (*Palaeophycus*, *Planolites*) and vertical (*Skolithos*) burrows (Bromley and Asgaard 1979; Metz 1995, 1996; Schlirf et al. 2001; Gillette et al. 2003; Melchor et al. 2003, 2006; Melchor 2004; Shi et al. 2007; Porter and Gallois 2008; Lucas et al. 2010; Li et al. 2014; Hminna et al. 2015). In some cases, great densities of the bivalve burrow *Lockeia* (Lucas et al. 2010) and the ichnogenus *Fuersichnus* (Bromley and Asgaard 1979) have been documented, typically forming monospecific trace-fossil suites. Arthropod trackways, although extremely common in Paleozoic lake-margin settings (Buatois and Mángano 1993a; Buatois et al. 1998a; see Chap. 6), and are quite rare in Middle to Upper Triassic deposits that were formed in similar environments, typically represented as isolated occurrences (Melchor 2004; Melchor et al. 2006). Horizontal, nonspecialized grazing trails, such as *Helminthopsis* and *Cochlichnus*, may be present (Melchor 2004; Shi et al. 2007; Li et al. 2014; Hminna et al. 2015), but they are never dominant and tend to reflect emplacement in substrates that did not experience periodic desiccation. Three-dimensional branching burrow systems (*Treptichnus*) may be present, but are uncommon (Porter and Gallois 2008). These structures were typically emplaced close to the sediment surface, the only exception being those produced by crayfish, referred to the ichnogenus *Camborygma*, which display variations in architecture as a response to the depth of the water table. Complex architectures with many branches and chambers were constructed by primary burrowers in areas of high water table, whereas deep and simple burrows are dominant in areas of low and/or highly fluctuating water table (Hobbs 1981; Hasiotis and Mitchell 1993).

Middle to Late Triassic, fully lacustrine ichnofaunas are known from the eastern United States (Metz 1995, 1996, 2000), Argentina (Melchor et al. 2003, Melchor 2004), Kyrgyzstan (Voigt and Hoppe 2010), England (Porter and Gallois 2008), and Greenland (Bromley and Asgaard 1979). Ichnofaunas in low-energy deposits are essentially represented by invertebrate trace fossils, with a dominance of very shallow-tier, simple, horizontal trails of deposit and detritus feeders (e.g. *Helminthopsis*, *Helminthoidichnites*, *Cochlichnus*, *Mermia*) and of shallow-tier, three-dimensional, branching burrow systems (*Treptichnus*) (e.g. Metz 1995, 1996, 2000; Melchor et al. 2003; Melchor 2004; Porter and Gallois 2008). Vertebrates are represented by the fish trail *Undichna* (Melchor 2004).

One of the first lacustrine ichnofaunas studied in detail is that of the Fleming Fjord Formation of Greenland (Bromley and Asgaard 1979) (Fig. 11.1a–f). Integration of ichnologic and sedimentologic information indicates that three main trace-fossil assemblages are present in these ephemeral lacustrine deposits (Bromley and Asgaard 1979, 1991; Dam and Stemmerik 1994; Bromley 1996). *Skolithos*, *Arenicolites,* and *Polykladichnus* occur in tempestites, whereas *Fuersichnus* (Fig. 11.1a–b) and *Lockeia* (Fig. 11.1c) are present in fair-weather deposits. *Scoyenia* (Fig. 11.1d–f) and *Skolithos* (Fig. 11.1d–f) occur in marginal-lacustrine deposits.

Upper Triassic ichnofaunas preserved in deposits of the Newark Supergroup, which record sedimentation in lakes within an extensive rift system in eastern North America, formed during the initial breakup of Pangaea (Olsen 1989; Schlische 2003). These ichnofauna have been analyzed in detail (e.g. Olsen and Flynn 1989; Metz 1995, 1996, 2000) (Fig. 11.2a–g). One of these units, the Lockatong Formation, records sedimentation in a balanced-fill lake characterized by recurrent base-level fluctuations. As a result, successions show well-defined, vertically stacked, transgressive–regressive cycles (Olsen 1980). The invertebrate ichnofauna consists of a combination of feeding (*Planolites montanus*, *Scoyenia gracilis, Treptichnus pollardi*), dwelling (*Spongeliomorpha milfordensis*), grazing (*Cochlichnus anguineus*), resting (*Lockeia siliquaria*), and locomotion (an undetermined arthropod trackway)

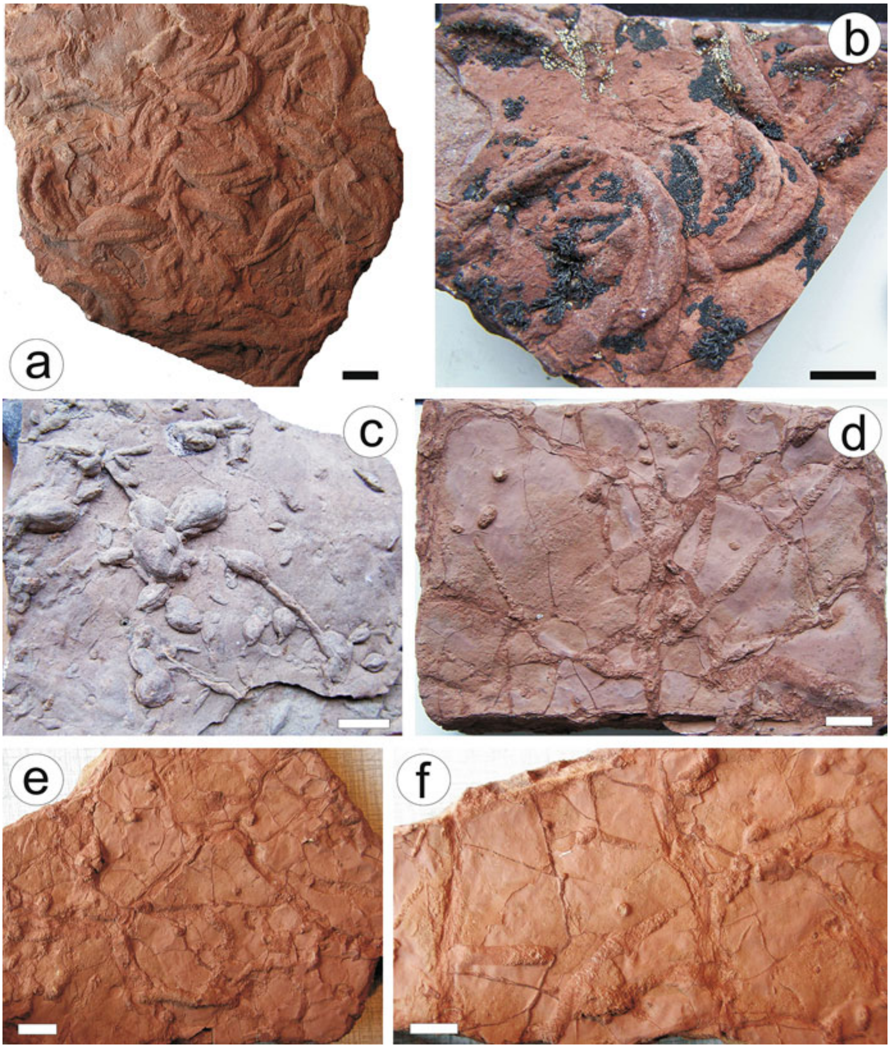


Fig. 11.1 Characteristic trace fossils from Upper Triassic ephemeral lacustrine deposits of the Flemming Fjord Formation of Greenland. (**a**) General view of a surface displaying a high density of *Fuersichnus communis*; (**b**) Close-up of *Fuersichnus communis* showing its characteristic banana shape; (**c**) The almond-shape trace fossil *Lockeia amygdaloides*. The associated horizontal burrows may be referred to the ichnogenus *Ptychoplasma*; (**d**) General view of a surface showing several specimens of the meniscate ichnotaxon *Scoyenia gracilis*. Note the presence of circular cross-section of vertical *Skolithos* isp.; (**e**) *Scoyenia gracilis* with less developed meniscate infill and bedding-plane expression of *Skolithos* isp.; (**f**) Close-up of *Scoyenia gracilis* and *Skolithos* isp. All scale bars are 1 cm long

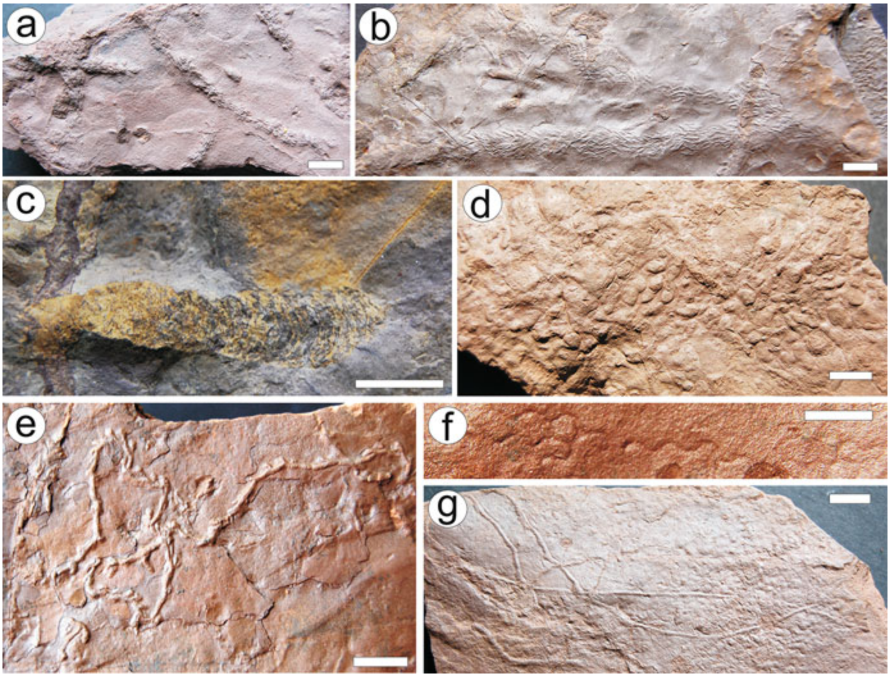


Fig. 11.2 Characteristic trace fossils from Upper Triassic lake-margin deposits of the Newark Supergroup of eastern United States. (**a**) General view of a surface with *Scoyenia gracilis*, Passaic Formation; (**b**) Close-up showing bioglyphs in *Scoyenia gracilis*, Passaic Formation; (**c**) Close-up showing meniscate infill in *Scoyenia gracilis*, Lockatong Formation; (**d**) General view of a surface with high density of *Lockeia amygdaloides*, Passaic Formation; (**e**) *Treptichnus bifurcus*, Passaic Formation; (**f**) *Cochlichnus anguineus*, Passaic Formation; (**g**) *Helminthoidichnites tenuis*, Passaic Formation. All scale bars are 1 cm long. Photographs courtesy of Robert Metz

structures (Metz 1995). The reptile trackway *Gwyneddichnium* is present as well (Olsen and Flynn 1989). Trace fossils are almost invariably restricted to lake-margin deposits. Whereas some of these structures most likely were emplaced in wet substrates (e.g. *Treptichnus pollardi*, *Lockeia siliquaria*), other ichnotaxa, such as *Scoyenia gracilis* and *Spongeliomorpha milfordensis*, support their formation in firm substrates resulting from desiccation (Metz 1995). Under extremely dry conditions, all other ichnotaxa disappear, and only *Spongeliomorpha* and *Scoyenia* are present. Collectively, the Lockatong ichnofauna represents the *Scoyenia* Ichnofacies (Metz 1995). A slightly more complicated picture is revealed by the Passaic Formation. Overall, this unit displays similar ichnologic characteristics to the Lockatong Formation, namely the widespread presence of the *Scoyenia* Ichnofacies in lake-margin deposits, and the presence of *Spongeliomorpha* and *Scoyenia* as the only ichnotaxa present in sediments deposited under extremely arid conditions (Metz 1996). However, some elements of the *Mermia* Ichnofacies are present in this unit as well, illustrating transitions from subaqueous portions during the initial phase of lake regression (Metz 1996).

Another extensively studied continental unit, containing well-exposed lacustrine intervals and represented by abundant trace fossils, is the Middle to Upper Triassic Agua de la Peña Group of the Ischigualasto–Villa Unión Basin of western Argentina (Melchor et al. 2003; Melchor 2001, 2004, 2007). As in the case of the Newark Supergroup, this rift basin developed during the breakup of Pangea (Uliana and Biddle 1988; Milana and Alcober 1994). In particular, the most abundant and diverse ichnofaunas occur in the Los Rastros Formation, which represents sedimentation in a shallow, overfilled lake characterized by successive prograding delta deposits (Melchor 2007). Deposits are typically arranged in coarsening-upward parasequences encompassing prodelta, delta-front, and delta-plain facies. The highest ichnodiversity occurs in the distal delta-front deposits, which are dominated by grazing trails (*Helminthoidichnites tenuis*, *Gordia marina*, *Archaeonassa fossulata*, *Cochlichnus anguineus*) and fish trails (*Undichna britannica*, *U. bina*, *U.* cf. *insolentia*). Also present are feeding (*Treptichnus pollardi*), dwelling (*Palaeophycus tubularis*), locomotion (*Bifurculapes* isp., *Cruziana problematica*, *Diplopodichnus biformis*, *Didymaulichnus lyelli*, *Diplichnites* isp., *Protichnites* isp.) and resting (*Rusophycus stromnessi*, *Avolatichnium* isp.) structures (Melchor 2001). Middle delta-front deposits display a similar ichnologic composition to distal delta-front deposits, being dominated by grazing trails (*Helminthoidichnites tenuis*, *Helminthopsis abeli*, *Gordia indianaensis*, *Archaeonassa fossulata*, *Cochlichnus anguineus*), with fish trails (*Undichna britannica*) and dwelling structures (*Palaeophycus tubularis*) also present (Melchor et al. 2003). Upper delta-front to lower delta-plain deposits reflect a decrease in ichnodiversity that parallels a shallowing of the lake, with only *Palaeophycus tubularis*, *Skolithos* isp., and *Cochlichnus anguineus* recorded. Upper delta-plain deposits contain dwelling trace fossils, some of which contain striations (e.g. *Palaeophycus striatus*) and vertebrate trackways (*Rhynchosauroides* isp.). Collectively, the Los Rastros ichnofauna reflects the vertical transition from the *Mermia* to the *Scoyenia* Ichnofacies as a result of shallowing caused by deltaic progradation.

The Middle to Upper Triassic Madygen Formation of Kyrgyzstan contains abundant trace fossils formed in an overfilled lake (Voigt and Hoppe 2010; Voigt et al. 2016). Lake-margin deposits are characterized by pervasive root trace fossils (Voigt et al. 2016) (Fig. 11.3a). The most abundant trace fossils in this unit occur in permanent subaqueous deposits, and consist of horizontal networks of multiple-branched burrows (Voigt and Hoppe 2010) (Fig. 11.3b–e). These structures have been compared with *Thalassinoides* by Voigt and Hoppe (2010), but were placed in the ichnogenus *Virgaichnus* by Knaust (2010). Further work is required to unravel the ichnotaxonomic affinity of these burrows. Regardless of these ichnotaxonomic complexities, these trace fossils represent feeding structures of worm-like deposit feeders. These burrows occur at their highest densities in deposits formed around the sublittoral–profundal boundary, probably coincident with the paleo-thermocline and chemocline (Voigt et al. 2016). It has been speculated that the producers of these burrows may have been able to tolerate dysoxic conditions, allowing them to colonize deeper parts of the lake which may have acted as a refugium from predators (Voigt et al. 2016). Other structures documented in these deposits are the grazing trail

Helminthoidichnites tenuis (Fig. 11.3f), unidentified sand-filled radiating burrow systems, and ribbon-like burrows with transverse segmentation, which have been interpreted as branchiopod locomotion traces (Voigt and Hoppe 2010; Voigt et al. 2016).

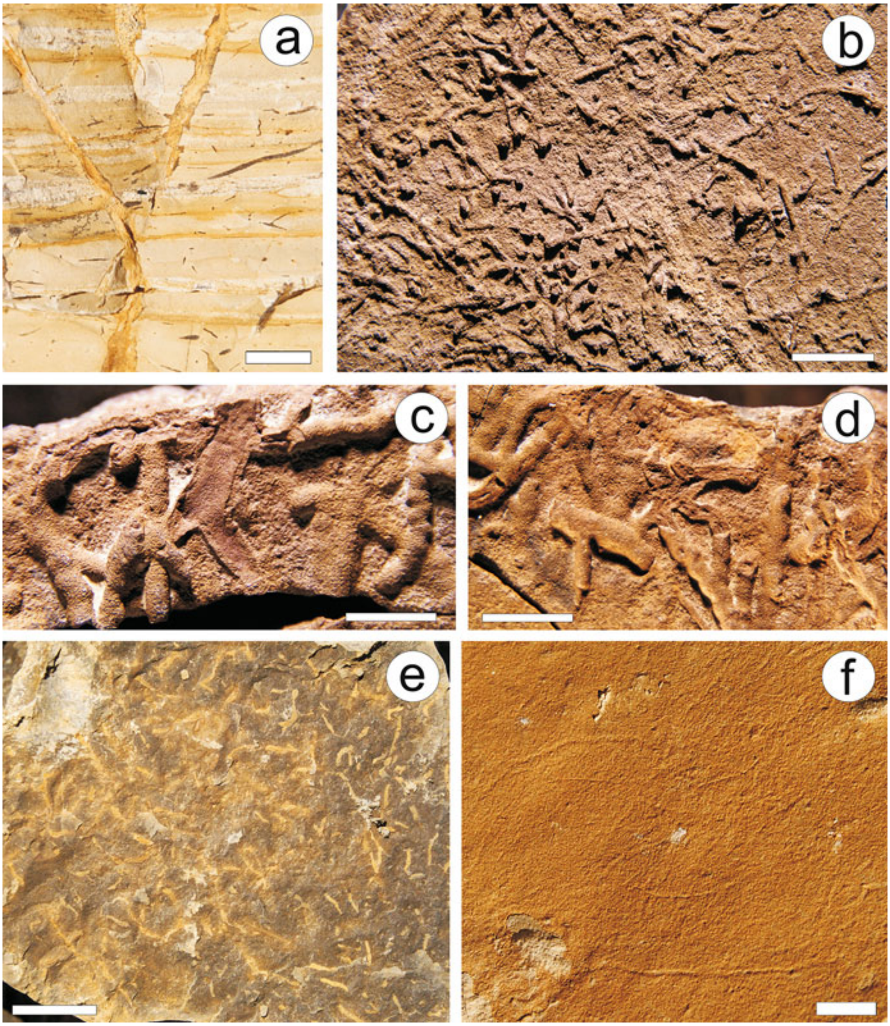


Fig. 11.3 Characteristic trace fossils from Middle to Upper Triassic lacustrine deposits of the Madygen Formation of Kyrgyzstan. (**a**) Root trace fossils in lake-margin deposits; (**b**) General view of a sandstone surface with horizontal networks of multiple-branched burrows in permanent subaqueous lacustrine deposits; (**c**) and (**d**) Close-up of networks showing branching patterns; (**e**) Preservational variation of horizontal networks as cleavage relief in mudstone; (**f**) *Helminthoidichnites tenuis* in lacustrine deltaic deposits. All scale bars are 1 cm long, with the exception of **c** and **d**, which are 0.5 cm long

Globally, Middle to Late Triassic ichnofaunas from lake-margin deposits are of modern aspect and record the widespread establishment of the *Scoyenia* Ichnofacies. In addition, the presence of trace-fossil suites dominated by the crayfish burrow *Camborygma* records the appearance of the homonymous ichnofacies (see Chap. 13). Middle to Late Triassic, fully lacustrine ichnofaunas resemble trace-fossil assemblages described from similar, late Paleozoic settings (Buatois and Mángano 1993a; Buatois et al. 1998a; see Chap. 6). However, more penetrative trace fossils occur, as revealed by the presence of networks of irregularly branched burrows in the Madygen deposits (Voigt and Hoppe 2010). In addition, higher-energy sandy, storm, and mouth-bar deposits tend to contain relatively deep vertical burrows, such as *Skolithos*, *Arenicolites,* and *Polykladichnus* (Bromley and Asgaard 1979; Mángano et al. 1994; Bromley 1996) (Fig. 11.4), representing freshwater equivalents of the *Skolithos* Ichnofacies (Buatois and Mángano 2004, 2009).

In short, ichnologic data seem to support Sinitshenkova's (2002) view that the Triassic is a time of significant evolutionary innovation in lacustrine communities. This is particularly evident in lake-margin settings which exhibit trace-fossil assemblages that would dominate these environments for the rest of the Phanerozoic. The picture in fully lacustrine settings is slightly different because central lake deposits display some ichnofaunas reminiscent of the late Paleozoic, with the addition of more penetrative burrows typical of the rest of the Mesozoic and Cenozoic.

During the late Middle to Late Triassic there was a major, qualitative increase in the abundance of lacustrine insect taxa. Fossil assemblages of this age contain a prevalence of immature over adult aquatic insects, such that in many deposits immature stages (naiads and larvae) outnumber adult specimens (Sinitshenkova 2002)—a situation that reverses that of the Permian. For this, and other reasons, Sinitshenkova (2002) mentions that "…the Triassic [is] a starting point of a new, Mesozoic evolutionary stage of lacustrine biocoenoses." This novelty may be

Fig. 11.4 *Arenicolites* isp. in deltaic mouth bar deposits of the Upper Triassic Tanzhuang Formation of central China. Scale bar is 1 cm long

attributable to greater stability of the hydrological and water-chemistry conditions in the physical environment of Eurasian, Late Triassic lakes (Kalugina 1980). Also, part of the diversification event may be attributed to increased provinciality from the breakup of Pangaea or to sizable increases in number and persistence of long-lived lakes associated with the breakup (Cohen 2003).

Late Triassic aquatic taxa included new lineages representing a diversity of functional feeding groups. For crustaceans, the major lineages were detritivorous ostracods, conchostracans, notostracans and the bizarre central Asian lineage, Kazakharthra. Dasyleptid bristletails were holdovers from the Permian, and persisted until the Late Triassic along bodies of water. Mayflies diversified, with benthic naiads assuming nektonic, epifaunal and infaunal filter-feeding strategies; some benthic forms constructed U-shaped burrows, representing potential producers of the biogenic structures typically found in lacustrine deposits of this age (e.g. Bromley and Asgaard 1979; Mángano et al. 1994) (Fig. 11.4). Odonatans are represented by fewer fossil occurrences of naiads than adults, and all of the mostly benthic naiads possessed a prominent, raptorial labial mask. The Plecoptera were represented by obligately aquatic, benthic naiads, as were their Permian counterparts, and included the extinct benthic–lentic taxa of the Euxenoperlidae, *Mesoleuctra* and *Siberioperla* (Sinitshenkova 2002). Grylloblattids (rock crawlers), a surviving lineage from the Permian, may have inhabited lakeshores or even shallow-aquatic habitats.

Most of the trophically dominant predators were streamlined, agile nectic heteropteran bugs and adephagan beetles. A few lineages of dominantly predatory, aquatic heteropteran bugs appeared during or just before the Late Triassic, consisting of the dominant naucoroid lineages of the extinct Triassocoridae, and the extant Notonectidae (backswimmers) and Belostomatidae (giant water bugs) (Popov 1980). Aquatic adephagan lineages, such as the extinct Schizophoridae, Ademosynidae, Colymbothetidae, and the extant Dytiscidae (predaceous diving beetles) had similar dietary habits. The extant algivorous Haliplidae (crawling water beetles) and its extinct Triassic relative, the Triaplidae, occurred on bottom substrates and in aquatic plant entanglements (Fraser et al. 1996). Both adults and larvae of the nectic Coptoclavidae were major predators, and had agile, active life habits based on legs equipped for rapid movement and raptorial mouthparts, likely feeding on small vertebrates and large insects. Megalopteran larvae are very similar to present-day alderflies (Marchal-Papier 1998). A few taxa of Mecoptera (scorpionflies) have been encountered, such as liassophilids that resemble modern aquatic Nannochoristidae. The earliest, definitive, aquatic Trichoptera (caddisflies) are from the Late Triassic, and include adults of the basal lineages Prorhyacophilidae and Necrotaulidae, but also immatures that likely were predatory (Sinitshenkova 2002).

These lacustrine biotas still lacked a significant herbivore component, which emerged later in the Mesozoic. Supporting this observation is the absence of submerged or emergent aquatic macrophytes, which did not occur in significant abundance until the Early Cretaceous. There is limited evidence, however, for a flora fringing lakes and pools during the earlier Mesozoic, as indicated by the presence of aquatic quillworts such as *Isoetes*, and *Azolla*-related ferns (Retallack 1997; Moisan et al. 2012a, 2012b; Sun et al. 2014). In any case, the contribution was overwhelmingly dead plant matter for detritivores rather than live plant tissues. For herbivores as in the Early Triassic, charophytes continued to be the dominant macrophytes and Chlorococcales the dominant phytoplankton (Martín-Closas 2003).

Six major community types have been recognized in Triassic Eurasian freshwater deposits (Sinitshenkova 2002). These community types are characterized by distinctive groupings of major taxa that occur in particular types of lakes and habitats. Although Sinitshenkova's (2002) general trophic analysis of lake ecosystems demonstrated significant partitioning of available lotic and lentic resources, evidently the herbivore guild was largely absent.

The most diverse Triassic insect assemblage is in an upper-Middle to lower-Upper Triassic lacustrine deposit near the village of Madygen, in Kyrgyzstan, central Asia, whose ichnofauna has been summarized above. In particular, one locality, Dzhailoucho, and nearby outcrops have provided some of the best insights into later Triassic aquatic and terrestrial life, including a diverse assemblage of 20 orders and ca. 106 family-ranked lineages of insects, such as the earliest definitive occurrences of Diptera (true flies) and Hymenoptera (sawflies, wasps, ants, and bees) (Shcherbakov 2008c). The Madygen Biota consists of typical, early Mesozoic plant groups, including cryptogams, sphenopsids, lycopsids, filicalean ferns, broadleaved conifers, diverse peltasperms, corystosperms, a variety of ginkgophytes and rare bennettitaleans (Dobruskina 1995). Aquatic invertebrates include several microconchids, bivalves, gastropods, bryozoans, and a spectrum of crustaceans consisting of phyllopods, ostracods, conchostracans, kazakharthrans, and malacostracan decapods (Voigt et al. 2006). The vertebrate fauna is rather diverse, and is comprised of a broad variety of fishes, such as lungfish, coelacanths, hybodontid, and xenacanthid sharks, and ray-finned fish, including palaeoniscids, evenkiids, perleidids, and a saurichthyid (Sytchevskaya 1999; Kogan et al. 2009; Fischer et al. 2011). The fauna also includes six genera of lake-margin tetrapods, notably an early urodelan, basal reptiliomorph, primitive cynodont, and three small diaspids including tree-climbing, gliding, and insectivorous reptiles (Voigt et al. 2006; Schoch et al. 2010; Alifanov and Kurochkin 2011). The lacustrine aquatic food web consisted of a variety of lakeside plants, numerous insects and other aquatic invertebrates, fish and occasional tetrapods (Shcherbakov 2008c). The aquatic portion of the biota included eight orders of insects and ca. 25 families of primarily aquatic or amphibiotic insects, of which a fifth of the lineages are extant. The Ephemeroptera included only the single, extant family, Siphlonuridae (small minnow mayflies); by contrast, ten families of Odonata were present, none of which are extant. Extinct Miomoptera constituted one family, and Plecoptera were represented by two extinct families. The Hemiptera included one family, the extant Ochteridae (velvet shore bugs). As for holometabolous insects, aquatic Coleoptera were represented by five, early to mid-Mesozoic, structurally streamlined families, but only one lineage, the Hydrophilidae (water scavenger beetles) are extant, likely appearing as large, black, and shining species. Similarly, the Trichoptera was represented by the basal and extant Philopotamidae (fingernet caddisflies). Likewise, the Diptera consisted of two new taxa, notably the diverse, extant Limoniidae (short-palped crane flies).

Neoichnologic data suggest that dipterans, in particular larval Limoniidae, produce zigzag burrows that in the fossil record may be referred to the ichnogenus *Treptichnus* (Muñiz-Guinea et al. 2014). This ichnogenus is quite common in Middle to Upper Triassic lacustrine deposits (Fig. 11.2e), which is consistent with paleoentomologic information on the earliest definitive occurrences of Diptera. However, *Treptichnus* is known in late Paleozoic lacustrine to fluvio-estuarine deposits as well (Buatois and Mángano 1993b, c; Buatois et al. 1998b). Interestingly, a molecular analysis placed the origin of crown group Diptera in the middle Permian (Bertone et al. 2008).

11.5.3 Continued Jurassic Diversification and Increased Infaunalization

Lower Jurassic, lake-margin ichnofaunas have been documented in both eastern (Gierlowski-Kordesch 1991; Metz 1992; Collette et al. 2011) and western (Lucas et al. 2006; Tanner and Lucas 2008) United States, whereas Upper Jurassic equivalents are widespread only in the latter (Hasiotis 2004; Foster and Lockley 2006; Hunt and Lucas 2006). Among invertebrate trace fossils, shallow-tier, meniscate, backfilled structures with striated walls (*Scoyenia*) or without bioglyphs (*Taenidium*) are typical, as are striated, branched burrows (*Spongeliomorpha*) (Gierlowski-Kordesch 1991; Hasiotis 2004). Simple horizontal (*Planolites*, *Palaeophycus*) and vertical (*Skolithos*) structures, together with crayfish burrows (*Camborygma*) and banana-shaped structures (*Fuersichnus*), also are common (Gierlowski-Kordesch 1991; Hasiotis 2004; Tanner and Lucas 2008). Grazing trails (*Helminthoidichnites*) and arthropod trackways (*Diplichnites*, *Kouphichnium*) are only abundant locally (Lucas et al. 2006). Borings in stromatolites have been mentioned, but it is uncertain if these were formed in lacustrine or marine coastal settings (Hasiotis 2004).

Although the earliest body-fossil record of dinosaurs is Late Triassic, dinosaur tracks are known at least since the Middle Triassic (Marsicano et al. 2007; see Chap. 10). However, it is by the Early Jurassic that dinosaur tracks (e.g. *Grallator*, *Eubrontes*) become the dominant vertebrate-generated structures in lake-margin deposits (Hunt and Lucas 2006). Dinosaur tracks also occur in Lower Jurassic deposits where the first megatracksites are recorded (Hamblin et al. 2006). These megatracksites include trampled surfaces, although these seem to occur in wet interdunes, rather than in lake margins (Seiler and Chan 2008). However, by the Late Jurassic spectacular megatracksites are known from lake-margin deposits of the Morrison Formation (Lockley et al. 1986; Jennings and Hasiotis 2006), among other sites. The Morrison tracksites are associated with intense bioturbation and the development of trampled surfaces (Lockley et al. 1986; Jennings and Hasiotis 2006). These Jurassic trampled surfaces are significant because, as demonstrated by studies in Quaternary and modern lake-margin deposits (e.g. Laporte and Behrensmeyer 1980; Ashley and Liutkus 2002), activities by large vertebrates play a major role in disturbing primary sedimentary fabric.

Fully lacustrine ichnofaunas have been documented in the Lower Jurassic of the eastern United States (Metz 1992) and China (Wu 1985; Buatois et al. 1995, 1996; Hu et al. 1998; Uchman et al. 2011), the Middle Jurassic of England (Whyte et al. 2007), and the Upper Jurassic of the western United States (Hasiotis 2004). These ichnofaunas show a combination of shallow-tier, simple trails and burrows (*Helminthopsis*, *Helminthoidichnites*, *Palaeophycus*, *Diplopodichnus*, *Paracanthorhaphe*) and deeper-tier, branching burrow systems (*Vagorichnus*) (Metz 1992; Buatois et al. 1996; Uchman et al. 2011). Vertical U-shaped burrows (*Arenicolites*) (Hasiotis 2004) and bivalve burrows (*Lockeia*) (e.g. Whyte et al. 2007) are present as well. As in the case of earlier assemblages, the fish trail *Undichna* is the typical vertebrate ichnotaxa in this setting (Whyte et al. 2007).

The Lower Jurassic Anyao Formation of central China is arguably the most studied deep-lacustrine succession of this age, providing valuable insight into the colonization of a fully lacustrine setting (Wu 1985; Buatois et al. 1995, 1996; Hu et al. 1998; Uchman et al. 2011). This formation represents deposition in a deep overfilled lake system developed in a pull-apart basin (Buatois et al. 2000b). The Anyao trace fossils are mostly present in thin-bedded turbidites which were formed in lobe-fringe areas of lacustrine turbidite systems. This ichnofauna is relatively diverse, encompassing both pre- (open burrows casted by the incoming turbidite sand) and post- (burrows penetrating from a colonization surface at the top of the turbidite sand) turbidite suites (Buatois et al. 1996) (Fig. 11.5a–i). The pre-event suite consists of *Helminthopsis abeli* (Fig. 11.5a), *Helminthoidichnites tenuis* (Fig. 11.5b), discrete specimens of *Tuberculichnus vagans* (Fig. 11.5c–d), *Monomorphichnus lineatus*, *Paracanthorhaphe togwunia* (Fig. 11.5e–f), and thin irregular trails. The post-event suite consists of *Vagorichnus anyao* (Fig. 11.5g–h), *Cochlichnus anguineus* (Fig. 11.5i) and *Helminthopsis hieroglyphica*. Specimens of *Gordia marina* and *Tuberculichnus vagans* intergrading with *V. anyao* also are part of this suite. The ichnofauna is dominated by feeding and grazing trace fossils produced by deposit feeders. From an evolutionary perspective, the Anyao ichnofauna is significant because it is dominated by infaunal burrows that reflect the activity of invertebrates that were able to penetrate into discrete sandy layers for subsequently expanding along sand–mud interfaces, a behavior unknown in older deposits in similar environmental settings. The producer of these burrows is uncertain, although it has been noted that in modern environments oligochaetes construct structures that radiate from a surface tube and branch horizontally within the sediment (Chamberlain 1975; Buatois et al. 1995). Amphipods and isopods may potentially construct similar structures, but the paucity of modern analogues precludes further evaluation (Buatois et al. 1995). In addition, this behavior shows the appearance of more organized branching patterns, such as *Paracanthorhaphe togwunia*, that reveal an increase in complexity with respect to Paleozoic lacustrine ichnofaunas.

Overall, the taxonomic composition of invertebrate ichnofaunas in lake-margin Jurassic deposits is quite similar to that of the Middle to Upper Triassic. No major evolutionary novelties or innovations are apparent in these settings from the perspective of invertebrate ichnnology. However, the appearance of megatracksites and trampled surfaces represents a major change with respect to older deposits, implying substantial sediment reworking and modification by dinosaurs. This was probably the first time in the history of the biosphere that lake-margin landscapes were significantly transformed at a large scale by biogenic activity.

In addition, trace-fossil information from fully lacustrine environments provides a different picture to that of older deposits. Ichnodiversity levels are similar

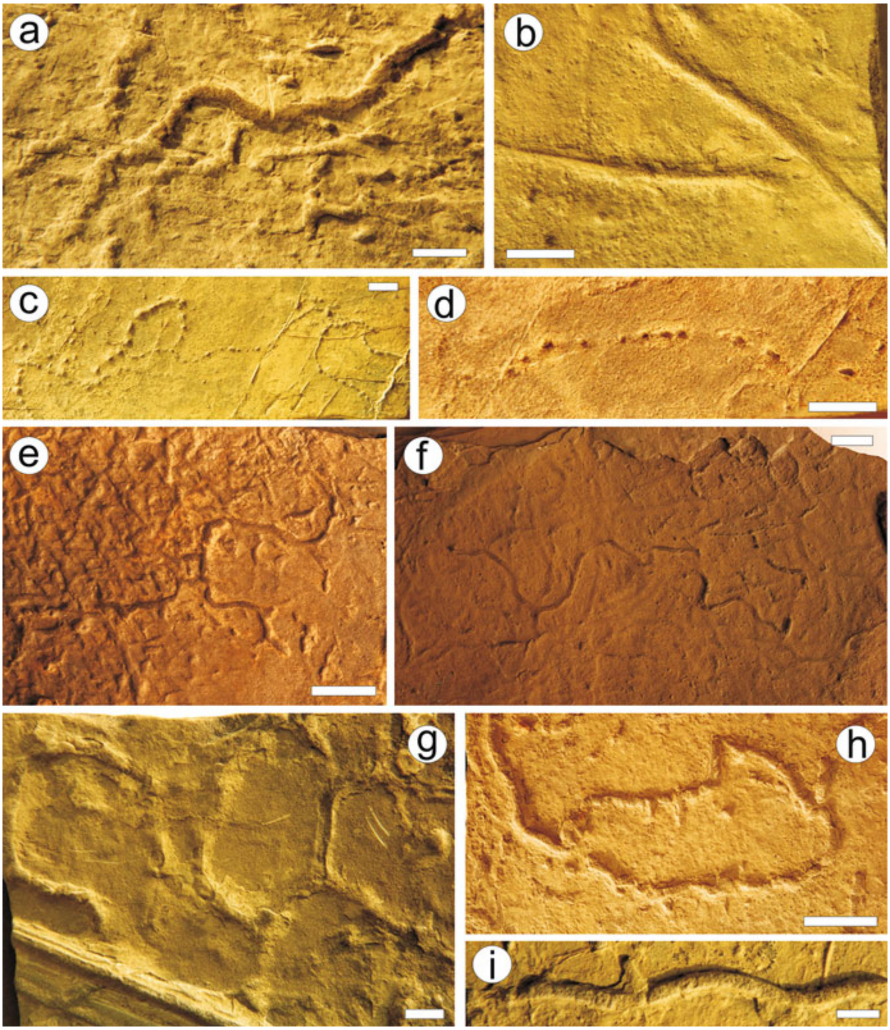


Fig. 11.5 Characteristic trace fossils preserved at the base of Lower Jurassic lacustrine turbidites of the Anyao Formation of central China. (**a**) *Helminthopsis abeli*; (**b**) *Helminthoidichnites tenuis*; (**c**) General view of *Tuberculichnus vagans* displaying a meandering pattern; (**d**) Close-up of *Tuberculichnus vagans*; (**e**) and (**f**) *Paracanthorhaphe togwunia*; (**g**) *Vagorichnus anyao* cross-cutting and inorganic sole mark; (**h**) Close-up of *Vagorichnus anyao*; (**i**) *Cochlichnus anguineus*. All scale bars are 1 cm long

to those of the Middle to Late Triassic, and even to those of the late Paleozoic, but the principal difference is the degree of infaunalization, as revealed by the widespread occupation of mid tiers in deep lacustrine sediments.

During the Early Jurassic there was further taxonomic, morphologic, and ecologic diversification of continental aquatic biotas. Much of the Jurassic zooplankton was represented by diverse cladoceran crustaceans, indicated by fossil occurrences (Zherikhin and Kalugina 1985), supported by molecular-clock data from phylogenetic analyses (Colbourne and Hebert 1996). One of the more distinctive differences from Triassic aquatic insect assemblages was the greater presence of immature stages (naiads, larvae) in Jurassic deposits, a consequence of a different preservational mode. The opposite situation of adult stages predominating over immature stages was much less common, and may have been attributable to poor preservation in habitats frequented by adults or the presence of adults in distant, more upland environments that have low preservation potential. Another distinction is the absence of virtually all Permian insect faunal elements and the first occurrences of many modern family-level lineages (Sinitshenkova 2002).

The dominant insect groups of Jurassic lotic and lentic ecosystems represent a spectrum of lineages that would occur in the same habitats today, although not necessarily with the same ecologic tolerances or proportional abundances as their present-day descendants. Ephemeropterans and odonatans were significantly more speciose than their Triassic equivalent taxa. Ephemeropterans experienced a major diversification, with the naiads of many groups, such as the Siphlonuridae and extinct Mesonetidae and Epeorominidae having laterally positioned abdominal gills and reaching considerably larger sizes than their Triassic confamilial antecedents. Currently, ephemeropterans occur in high numerical abundance at local scales, are present at significant diversities, and apparently were the major collector and filter-feeding functional feeding groups (Merritt and Cummins 1984) in many Jurassic localities. The Jurassic mayfly fauna is found in almost every aquatic environment, in streams ranging from cascade-like rhythral settings, to calm water sites on floodplains such as oxbow lakes and overbank ponds, to lowland playas, and highland graben-formed lakes. Like ephemeropterans, odonatans were diverse, best illustrated by several, large, dragonfly genera which co-occur in the Solnhofen Formation of southern Germany, including a relict lineage of late Paleozoic meganeurid forms. Jurassic odonatan naiads typically resemble modern damselfly naiads with a narrow body and three, flap-like, heavily sclerotized, and terminal abdominal structures, the cercus and paracerci. The formidable labial-masks of naiads indicate predation on other larger aquatic insects and small vertebrates, such as fish and tadpoles. In some lacustrine environments odonatan naiads likely were top predators in the absence of fish (Sinitshenkova 2002).

Plecopteran nymphs occur commonly in Lower Jurassic deposits and are represented by three life-habit groups that are different from their modern representatives taxa. The Mesoleuctridae possessed unusually long and slender legs, suggesting an unusual detritivorous feeding habit. By contrast, the Platyperlidae bore an opposite, flat habitus, with exceptionally squat, wide legs indicating a benthic insectivorous diet. The Siberioperlidae, judging from robust mouthparts unusual for the Plecoptera, were consumers of fibrous or otherwise indurated plant tissues (Sinitshenkova 2002). An unrelated group is the extinct Chresmodidae of the Archaeorthoptera. The family Chresmodidae includes large, water-strider-like insects presumably occurring on water surfaces. Chresmodids have had a checkered history of being taxonomically poorly resolved and having equally contentious dietary preferences. Some specimens display mouthparts designed for active predation but possess external, sawtooth ovipositors that functioned for insertion of eggs into substrates such as aquatic plant stems (Delclòs et al. 2008). Based on ovipositional lesions on preangiospermous Mesozoic plants associated with lake deposits, the most likely hosts for ovipositing chresmodids were lycopsids (Moisan et al. 2012b) and horsetails (Kräusel 1958), or less likely a seed plant such as a bennettitalean (Pott et al. 2008).

Jurassic lotic and lentic biotal assemblages commonly are dominated by aquatic heteropteran bugs or adephagan beetles, or both. Heteropteran aquatic bugs included the dominant nepomorph taxa of Corixidae (water boatman) and Nepidae (water scorpions), as well as giant water bugs, backswimmers, and the Mesoveliidae (mesoveliid water striders), distant relatives of modern Gerridae (water striders) that likely skimmed the water surface of lakes and streams. These taxa were predaceous, except for mostly algivorous corixids and shurabellids (Popov 1971). Based on mouthpart structure that employed a triturating device (Cobben 1978), these microvorous corixid and shurabellid microvores filter fed on unicellular or very small multicellular algae. Some heteropterans inhabited hypersaline playas and coastal brackish lagoons or estuaries (Santiago-Blay et al. 2001). Like heteropteran bugs, aquatic adephagan beetles were ecologically diverse and mostly predaceous, although some were scavengers and microvorous consumers of algae. There is no indication of macrovorous herbivorous forms.

During the Early Jurassic the dominant beetle clade is the Schizophoridae, but its diversity and abundance decreases towards the latest Jurassic (Ponomarenko 1995). During this time extinct aquatic lineages include large, predaceous Coptoclavidae with active, nektonic larvae, the Liadytidae, possessing benthic larvae, and the Parahygrobiidae, of unknown feeding habits. The extant, large Gyrinidae (whirligig beetles) appear in significant numbers in Jurassic lentic deposits, consisting of predaceous larvae and detritivorous adults. The Parahygrobiidae are known only from larvae of mid-Mesozoic lake deposits and are presumed predaceous. In contrast to the commonness of beetle taxa, alderfly and dobsonfly larvae of the Megaloptera are rare and confined to lotic habitats.

Other holometabolan taxa are the larvae of scorpionflies, caddisflies, and true flies which typically were rare at most sites. The extinct Liassophilidae belongs to a scorpionfly lineage that survived into the Early Jurassic, and whose modern close relatives are the primitive, aquatic Nannochoristidae (Novokshonov 1997). Caddisflies are represented primarily by the Necrotaulidae and the larger complex of families constituting the Phryganeina. The Phryganeina appeared during the Late Jurassic (Sukatcheva 1991) and their presence is indicated by some of the earliest caddisfly cases in the fossil record. Caddisflies were mostly microvores, and likely were algivorous, detritivorous, or omnivorous, commonly occurring in eutrophic environments (Zherikhin and Kalugina 1985). Unlike other abundant holometabolan groups, true flies represent a major radiation throughout the Jurassic, particularly involving several nematocerous lineages, principally the Limoniidae, Chironomidae (midges), Chaoboridae (phantom midges), Psychodidae (moth flies), Simuliidae (black flies), Dixidae (nonbiting midges), and the extinct Eoptychopteridae, a clade related to modern phantom crane flies (Kalugina 1980). These seven dipteran lineages included disparate mouthpart modifications for passive and active filter feeding, net sieving, collecting, and mandible-assisted chewing, indicating that they were dominantly microvores. Microvory in nematocerous Diptera is typically achieved by the pumping of water currents into a specialized mouthpart filter or sieve for capture of small particulate matter such as diatoms, protists, ostracods, and a variety of other microorganisms.

The Jurassic also witnessed the appearance of major lineages of teleost fish, frogs, crocodilians, and aquatic birds (Cohen 2003). These lineages represent evolutionary novelties that may have been conducive to key innovations, mostly increased predation in freshwater settings, which in turn may have resulted in the disappearance of large-bodied branchiopods and other slow moving crustaceans from many lacustrine settings (Webb 1979; Cohen 2003). Since the Jurassic, these taxa seem to have been displaced to more marginal habitats, such as saline lakes and vernal pools, characterized by low diversity of predators. Also, the coincidence of increased predation and infaunalization of the lacustrine benthos may be significant. As indicated by Vermeij (1987), the infaunal environment typically is regarded as a haven from predation and, therefore, infaunalization may be regarded as an adaptive response to increased predation.

Relatively little is known about aquatic vegetation during the Jurassic. The dominance of charophytes is apparent, with porocharaceans and nitellaceans occurring in Early to Middle Jurassic Chinese basins (Wang et al. 1976), probably reflecting accommodation to ephemeral lakes (Martín-Closas and Serra-Kiel 1991). By the Late Jurassic, two charophyte families underwent diversification, the Characeae and the Clavatoraceae, which were associated with oligotrophic and alkaline lakes (Martín-Closas and Serra-Kiel 1991). This may have resulted in the displacement of porocharaceans to higher latitudes and brackish-water settings (Martín-Closas 2003). Nonflowering vascular plants were represented by relatives of *Azolla* ferns along littoral zones (Cohen 2003). An incipient colonization of ponds by ferns also is apparent by the Late Jurassic (Martín-Closas 2003), particularly the Hymenophyllaceae (filmy ferns), that preferred hydric habitats (Hennequin et al., 2008). Lacustrine phytoplankton retained its ancestral condition, with Chlorococcales remaining dominant (Martín-Closas 2003).

Beginning toward the end of the Early Jurassic, and culminating during the Middle to Late Jurassic, a distinctive, fluvio-lacustrine ecosystem is recognized in Eurasia. This ecosystem represents a continuation of earlier, similar, Late Triassic ecosystems, but is characterized by a suite of physical, chemical, and biological features that were distinct from other contemporaneous and later ecosystems (Table 11.1). The overwhelmingly Jurassic biotas that occupy this ecosystem are the "Assemblage B" of Sinitshenkova and Zherikhin (1996), characterized by a detritivore-based food web, in which primary production consisted of coarse and fine detritus and dead benthic algae. These sources of food were channeled to filter-feeding and shredding invertebrates, particularly insects, but also crustaceans, mollusks, and bryozoans (Table 11.1 and Fig. 11.6). Although this biota persisted into the Early Cretaceous, the geochronologic acme of this community type was during the Middle to Late Jurassic.

A prime example of an Assemblage B community is the *Mesoleuctra–Mesoneta* assemblage at Ust'-Balei, in Transbaikalian Russia, representing a lacustrine deposit from uppermost Lower Jurassic strata (Sinitshenkova and Zherikhin 1996). The *Mesoleuctra–Mesoneta* assemblage was more productive, through the fixation of organic carbon by chemotrophic and autotrophic organisms, than those from coexisting Assemblage A lakes. However, the *Mesoleuctra–Mesoneta* assemblage was considerably less productive than Assemblage C lakes of the Early Cretaceous (Table 11.1 and Fig. 11.6). This assemblage type may have occurred in several Gondwanan sites, although documentation is poor. The dominant biotal features of the *Mesoleuctra–Mesoneta* assemblage at Ust'-Balei was an epibenthic fauna that consisted dominantly of mayfly and stonefly taxa, the absence of chaoborid dipteran larvae, and the general presence of some algae, bivalves, and fish. Deposits containing an Assemblage B biota are associated with lignitic and coal-bearing strata, paleobotanical indicators suggesting oxygen depletion (Samylina 1988), and a setting in which microbial activity was strongly suppressed. At Ust'-Balei, the *Mesoleuctra–Mesoneta* assemblage inhabited an aquatic environment similar to a modern, disaerobic peat lake wherein bacterial metabolic activity is limited by water acidity (Kuznetsov 1970).

Jurassic lacustrine deposits are present in North America as well (see review of ichnologic literature above), but unlike those in Eurasia, they have been less studied in a paleoentomological context, typically lacking body fossils, notably insects. Deposits such as the deep, graben-fill deposits of the Late Triassic (Theismeyer 1939) and the more laterally persistent, epicontinental strata of the Late Cretaceous–Early Paleogene temporally bracket the Middle Jurassic (Callovian) Sundance and Late Jurassic (Tithonian) Morrison Formations. The Morrison Formation evidently included a series or large, relatively shallow alkaline lakes, most of which were intermittent and lacked significant freshwater input due to water limitation within an arid, subtropical belt (Turner and Fishman 1991; Demko and Parrish 1998; Engelmann et al. 2004). Although much is known of the vertebrates of landscapes surrounding Morrison lakes, little is understood of their aquatic invertebrate faunas. Lacustrine insects are unknown, and the only significantly studied invertebrates are lacustrine ostracods (Schudack 1998) and bivalves occurring in associated fluvial, floodplain and pond environments (Good 2004).

The Sundance Formation perhaps provides the sole exception of a Jurassic, North American lacustrine biota on par with numerous Eurasian examples of the same period (Fig. 11.7). The Sundance Formation occurs along the central-northern Wyoming and central-southern Montana border, and provides paleoentomologically the best documented Jurassic lacustrine ecosystem in North America (Santiago-Blay et al. 2001; Grimaldi and Engel 2005). In particular, the thinly laminated, interbedded paper shales of the Hulett Sandstone Member provide considerable evidence for a modestly diverse lacustrine fauna. The deposit was formed from

Table 11.1 Biological features of Mesozoic lakes before and after the Mesozoic Lacustrine Revolution (MLR) based on aquatic insect data. Modified slightly from Sinitshenkova and Zherikhin (1996), with brown indicating more detritivore-based and green more herbivore-based lacustrine assemblages

	Pre Mesozoic lacus trine revolution lake structure		Post Mesozoic lacustrine revolution lake structure		
Assemblage Type[a]	A	B	C	D	E
Age:	Upper Lower J—Lower K	Upper Lower J—Lower K[a]	Lower K[a]	Lower K	Lower K
1. Algal production	Low	Low	High	?Moderate	High
2. Macrophyte production	Very low	Moderate	Low	Low	Low
3. Allochthonous detritus	Low	High	Low	?Low	?Variable
4. Turnover rate	Low	High	High	High	High
5. Microbial activity	Low	Low, suppres-sed by antibio-tic leaf litter	Moderate, high in deep-water zone	Unknown	?High
6. Dominating trophic chain	Detritivorous	Detritivorous	Herbivorous	Herbivorous	Herbivorous
7. Trophic web complexity	Low	Low	High	Low	Moderate
8. Dominating strategy	K	K	?r	?r	r
9. Shredders[b]	Common	Common	Uncommon	?Uncommon	?Uncommon
10. Scrapers[b]	Common	Common	Uncommon	Uncommon	Uncommon
11. Grazers[b]	Rare	Rare	Common	Common	Common
12. Filtrators[b]	Very rare	Rare	Uncommon	Common	Common
13. Planktonivores[b]	Moderately common	Rare	Very abundant	Very abundant	Very abundant
14. Predators[b]	Common	Common	Common	Rare	Common
15. Modern analogues	Cold, clear-water oligo-trophic lakes	None	None	Unknown	None
16. Ecosystem type	Montane; oligotrophic to ultraoligotrophic	Hypotrophic (non-acid dystrophic)	Pseudoligo-trophic (productive nonsaprobic)	?Mesoligo-trophic	?Pseudoligo-trophic.

The vertical line separating Assemblages B and C indicates the timing of the MMLR transition

[a] The five assemblages (A–E) are further detailed in Sinitshenkova and Zherikhin (1996)

[b] Macroinvertebrate functional feeding groups (after Merritt and Cummins 1984)

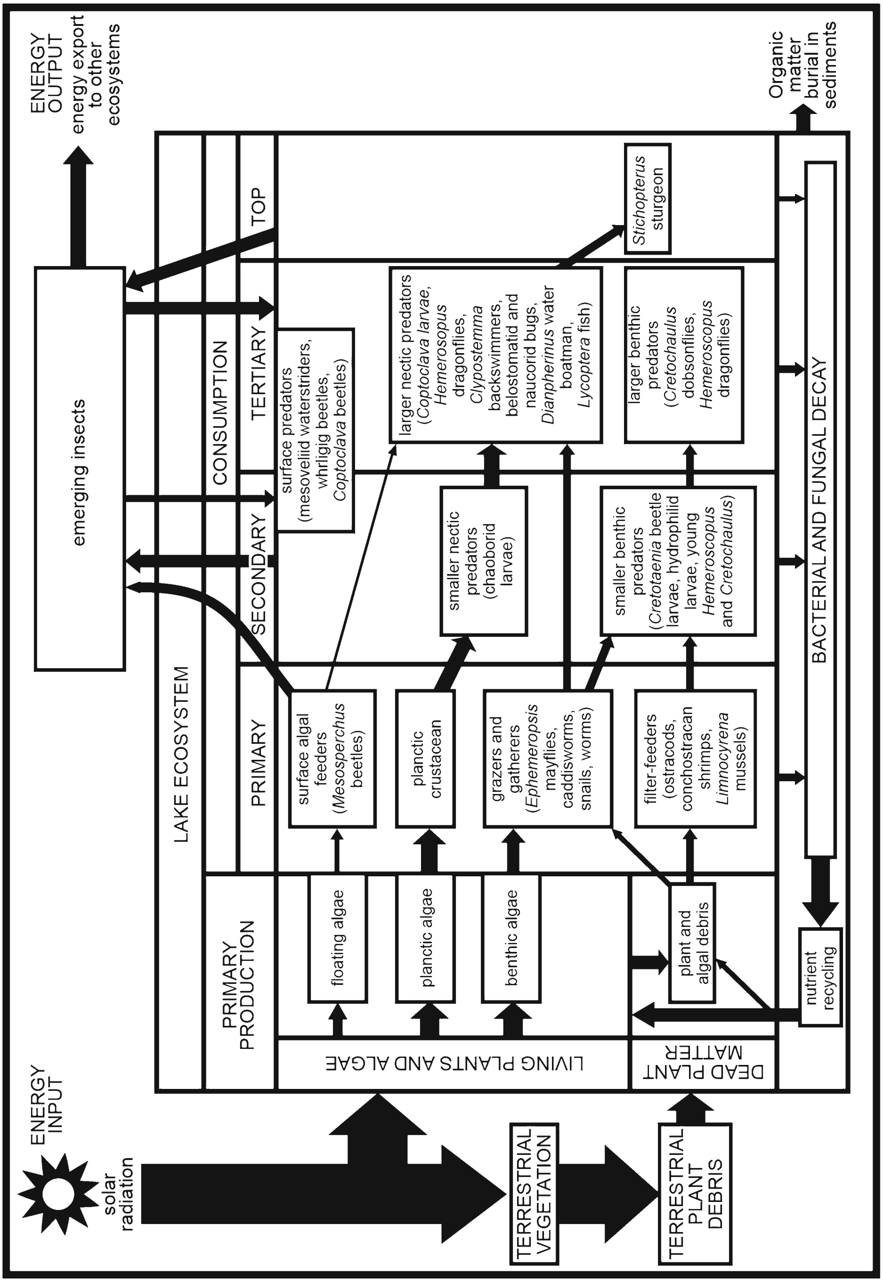


Fig. 11.6 Trophic structure reconstruction for primary producers and arthropods of a Middle Jurassic hypotrophic lake (Zherikhin and Kalugina 1985). This lake represents the *Mesoleuctra–Mesoneta* biotal assemblage typifying Lake Ust'Balei, in the Irkutsk Region of northern Siberia, Russia. This trophic reconstruction corresponds to the Type B lake biotal assemblage of Sinitshenkova and Zherikhin (1996). See Assemblage B in Table 11.1 for additional physical, chemical and biological details. Redrawn, with modification, from Sinitshenkova and Zherikhin (1996)

freshwater to brackish water input and includes locally a back-barrier shoal and tidal inlet consistent with a more estuarine environment during certain time intervals (Uhlir et al. 2006; Stone and Vondra 2013). Vertebrate footprints and bone material have been found in other strata of the Sundance Formation. The biota of the Hulett Sandstone Member consists of pollen, land-plant fragments, aquatic insects, and a leptolepid fish, presumably of continental provenance (Fig. 11.7a–p). The insects are modestly diverse, consisting minimally of about 15 species, and include a variety of typically freshwater nepomorph heteropterans, especially notonectids, corixids, belostomatids, and possibly the extinct Enicocoridae. Adephagan beetles include dytiscids and possible parahygrobiids, and elytra assigned to *Holcoptera* are suggestive of a polyphagan lineage (Santiago-Blay et al. 2001; Grimaldi and Engel 2005). Other faunal constituents are very rare caddisfly cases. Whereas much of these strata, particularly those containing the insects, indicate lacustrine deposition, other strata indicate a more marine influence, suggesting harsh, occasionally hypersaline conditions and an uninhabitable benthic environment. Palynomorph and mesofossil land-plant material reveal a xerophytic coastal vegetation of cheirolepidiaceous and araucariaceous conifers and possible gnetaleans indicated by *Eucommiidites* pollen. A similar, approximately coeval lacustrine deposit, the Todilto Formation, occurs in central New Mexico, is less diverse but has a similar depositional environment with periodic influxes of fresh and brackish water alternating with marine incursions from the east, and has a similar lacustrine biota (Bradbury and Kirkland 1966; Anderson and Lucas 1996; Ulmer-Scholle 2005).

11.5.4 Persistence of Previous Trends During the Early Cretaceous

Early Cretaceous lake-margin ichnofaunas have been documented in England (Goldring et al. 2005), Spain (Moratalla et al. 1995; Moratalla and Hernán 2009), Mongolia (Johnson and Graham 2004) and Korea (Kim and Paik 1997; Kim et al. 2002, 2005, 2012a,b,c; Paik et al. 2012; Lockley et al. 2012). Dinosaur (e.g. *Ornithopodichnus*, *Dromaeosauripus*, *Caririchnium*, *Minisauripus*), bird (e.g. *Koranornis*, *Jindongornipes*, *Uhangrichnus*, *Ignotomis*), crocodile, turtle (*Emydiphus*), and pterosaur (e.g. *Pteraichnus*, *Haenamichnus*) tracks are extremely common, in many cases forming megatracksites (Moratalla et al. 1995; Meyer et al. 2001; Moratalla and Hernán 2009; Lockley et al. 2012; Kim et al. 2012a,b,c).

As is the case for their earlier Mesozoic counterparts, Early Cretaceous lake-margin invertebrate ichnofaunas are dominated by shallow-tier striated or nonstriated meniscate, backfilled structures (*Scoyenia*, *Taenidium*), and simple horizontal (*Planolites*, *Palaeophycus*) and vertical simple or U-shaped (*Skolithos*, *Diplocraterion*) features (Zhang 1987; Kim and Paik 1997; Kim et al. 2002, 2005; Johnson and Graham 2004; Goldring et al. 2005). Arthropod trackways (*Diplichnites*), simple grazing trails (*Helminthopsis*, *Cochlichnus*), and branching burrows (*Thalassinoides*) occur locally (Kim et al. 2002, 2005; Goldring et al. 2005).

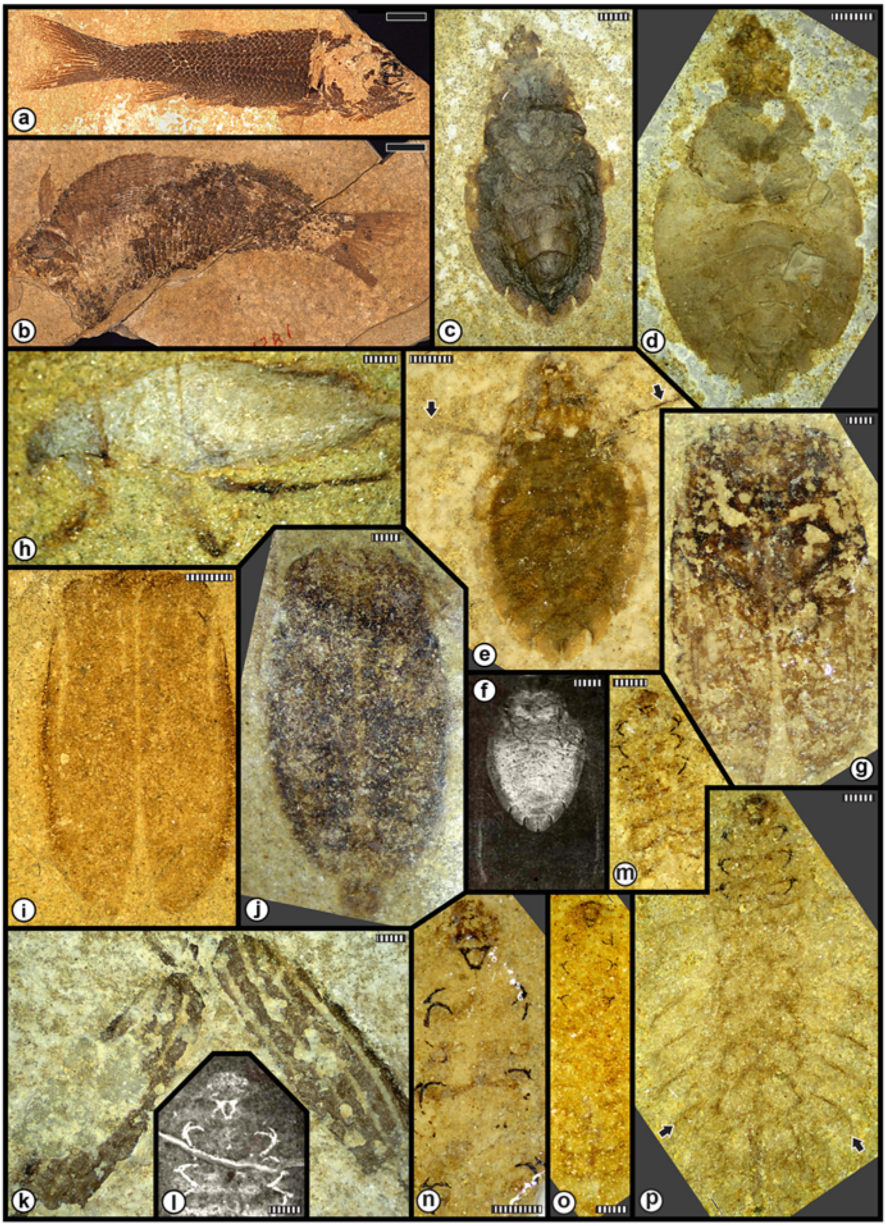


Fig. 11.7 The late Middle Jurassic (Callovian, 165 Ma) Sundance Biota from the lacustrine Sundance Formation, central-northernmost Wyoming and adjacent central-southernmost Montana, United States (Santiago-Blay et al. 2001). (**a**) Leptocerid fish (USNM-597438, Specimen 605); (**b**) Leptocerid fish (USNM-597439, Specimen 1281); (**c**) Hemiptera: ?Belostomatidae (USNM-597440, Specimen 554–39); (**d**) Hemiptera: Belostomatidae (USNM-597441, Specimen 775); (**e**) Hemiptera: Corixidae (USNM-597442, Specimen 1377A); (**f**) Hemiptera: Corixidae (USNM-597443, Specimen 1801); (**g**) Hemiptera: ?Notonectidae (USNM-597444, Specimen 2688B); (**h**) Hemiptera: Enicocoridae (USNM-597445, Specimen 2194); (**i**) Coleoptera: undetermined family (USNM-597446, Specimen 24); (**j**) Coleoptera: undetermined family (USNM-597447, Specimen 2443); (**k**) Coleoptera: (USNM-597448, Specimen 2501); (**l**) (USNM-597449, Specimen 1936B); (**m**) (USNM-597450, Specimen 2398B); (**n**) (USNM-597451, Specimen 2260); (**o**) (USNM-597452, Specimen 2906); (**p**) Coleoptera: (USNM-597453, Specimen 2149). Scale bars: solid, 10 mm; striped, 1 mm

Early Cretaceous examples of fully lacustrine ichnofaunas have been recorded in Spain (de Gibert et al. 1999, 2000, 2016; Buatois et al. 2000a) and Brazil (Buatois and Mángano 1998). Information is sparse, and examples are known from quite different lacustrine settings, further complicating the establishment of general patterns. The Spanish paleolake deposits are carbonates, and their ichnofaunas are dominated by very shallow-tier trails and burrows (*Gordia*, *Cochlichnus*, *Steinsfjordichnus, Cruziana, Helminthoidichnites, Palaeophycus, Treptichnus, Planolites*), with a very minor contribution of arthropod trackways (*Hamipes*) (de Gibert et al. 2000, 2016; Buatois et al. 2000a) (Fig. 11.8a–d). The vertebrate component of the subaqueous biota is represented by the fish trail *Undichna* (de Gibert

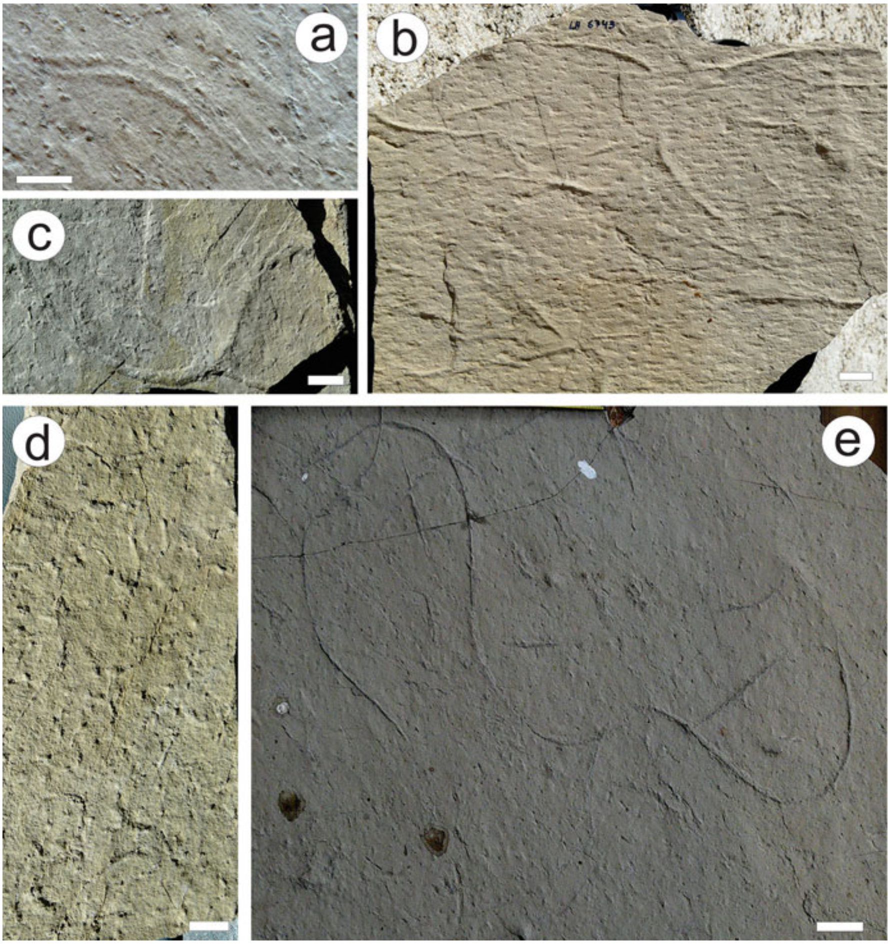


Fig. 11.8 Characteristic trace fossils from Lower Cretaceous fully subaqueous lacustrine carbonate deposits of Las Hoyas, Spain. (**a**) *Cruziana* isp.; (**b**) *Helminthoidichnites tenuis*; (**c**) *Palaeophycus tubularis*; (**d**) Surface containing high density of poorly developed *Treptichnus pollardi*; (**e**) *Undichna unisulca.* All scale bars are 1 cm wide, with the exception of **e**, which is 2 cm long

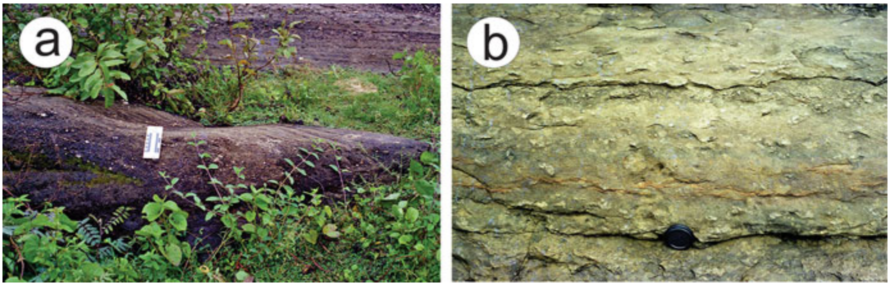


Fig. 11.9 Ichnofabrics from the Lower Cretaceous lacustrine shoreface deposits of the Coqueiro Seco Formation of northeast Brazil. (**a**) General view of cross-bedded pebbly very coarse-grained sandstone (foreground) interbedded with intensely bioturbated fine-grained sandstone (background); (**b**) Close-up of intensely bioturbated sandstone displaying mottled texture. Lens cap diameter is 5.5 cm long

et al. 1999) (Fig. 11.8a–e). In contrast, the Brazilian ichnofauna is derived from intensely bioturbated, lacustrine, clastic shoreface deposits, and displays mottling attributable to *Planolites* (Buatois and Mángano 1998) (Fig. 11.9a–b).

Lower Cretaceous shallow-lake deposits present within the nonmarine Sindong Group of South Korea are useful to illustrate the major characteristics of lacustrine ichnofaunas from this age (e.g. Kim and Paik 1997; Kim et al. 2002, 2005; Paik et al. 2012). In particular, the Jinju Formation has been the object of several ichnologic studies (e.g. Kim et al. 2002, 2005, 2012c). This unit was deposited in a shallow lake periodically affected by immersion and desiccation. The ichnofauna contains a variety of feeding (*Beaconites antarcticus*, *B. coronus*, *Planolites annularis*, *P. beverleyensis*, *Taenidium barretti*), locomotion (*Octopodichnus* cf. *didactylus*, *Diplichnites* ispp., unassigned sauropod trackways), dwelling (*Palaeophycus sulcatus*, *P. tubularis*, *Skolithos magnus*), and grazing (*Cochlichnus anguineus*, *Helminthopsis hieroglyphica*) traces (e.g. Kim et al. 2005). The vast majority of these ichnotaxa are common in the *Scoyenia* Ichnofacies, which is consistent with the lake-margin interpretation for these deposits. The sharply defined margins of the trackways suggest firm substrates. However, Kim et al. (2005) noted that some of the grazing trails may have been emplaced in softgrounds, implying colonization under subaqueous conditions and transition to the *Mermia* Ichnofacies. Potential producers include several groups of dipterans as well as nematodes and spiders. Overall, the Early Cretaceous, South Korean lake ichnofaunas show a similar trace-fossil distribution to those ichnofaunas recorded in shallow-lacustrine deposits of the Newark Supergroup. In both cases, colonization by benthic organisms reflects changes in the degree of consolidation of the substrate as a result of progressive subaerial exposure.

Early Cretaceous lotic and especially lentic insect taxa are derived from the same taxonomic families as those of the Late Jurassic (Martínez-Delclòs et al. 1995; Delclòs et al. 2008). Representatives of this faunal assemblage are a lentic, ephemeropteran fauna that consists of siphlonurids, hexagenitids and mesonetids.

Hexagenitid naiads, as well as ephemeroid naiads, are very common in some Early Cretaceous lentic assemblages (Sinitshenkova 2002), including taxa that produced the bioerosion ichnogenus *Asthenopodichnium* subaqueously in woods (Thenius 1989). Most of the Early Cretaceous mayfly genera did not survive into the Late Cretaceous (Sinitshenkova 2002), and only one lineage, the Australiephemeridae, became extinct at the end-Cretaceous (K-Pg) boundary.

The Early Cretaceous aquatic odonatan fauna is quite different from that of the Jurassic. The diversification of modern anisopteran (dragonfly) and zygopteran (damselfly) lineages appear for the first time. Curiously, the Pseudomyrmeleontidae, interpreted by some as related to the Paleozoic Meganeuroidea, were still present as a relict group. Unlike ephemeropteran assemblages, odonatan assemblages appear to have most of their evolutionary development in lotic habitats. The dominant Early Cretaceous odonatan lineages are the Isophlebioidea, Heterophlebioidea, Calopterygoidea, and other anisopteran clades. Among these lineages are a few specialized types, such as naiads of the Eurasian Hemeroscopidae and Sonidae (Pritykina 1986), which include a morphotype with long legs possessing paddling locomotion and a nectic, predatory existence. By contrast, other taxa, such as the Nothomacromyiidae lacked swimming structures but retained actively cursorial, long legs, indicating predatory pursuit habits. Another ecomorph is represented by the short-legged, burrowing Gomphidae (Bechley 1998). The labial-mask mouthpart structure has been examined for a select few species of these lineages, and no conclusions could be made regarding prey-specific relationships (Sinitshenkova 2002).

Plecopteran family-level diversity increased during the Early Cretaceous. Jurassic plecopteran clades persisted into the Early Cretaceous and were supplemented by the earliest occurrences of several, modern, family-level lineages. All of the modern, plecopteran functional feeding groups were present during the Early Cretaceous, such as collectors and shredders engaged in detritivory, algal herbivory and insect predation. In addition, chresmodids are still present in some lacustrine settings, but probably became competitively excluded by emerging, Early Cretaceous gerrid lineages.

True bugs of the Hemiptera are ubiquitous and diverse throughout the Early Cretaceous, and with the exception of the Shurabellidae, are continuations of Jurassic lineages (Sinitshenkova 2002). By contrast, the Gerridae and Mesoveloidea (water treaders) initially appear during the Early Cretaceous, ecologically supplementing and replacing an earlier convergent ecotype, the orthopteroid Chresmodidae, which had affinities to orthopteroid insects (Martínez-Delclòs et al. 1995). This replacement included larger-sized, surface-skimming gerrids during the Late Cretaceous that approached in size many of the medium-sized Jurassic chresmodids, the latter of which had legspans of up to 16 cm (Labandeira pers. observ.). Corixids, notonectids, mesotrephids and notably large, predaceous belostomatids continued into the Early Cretaceous (Delclòs et al. 2008). Although there are some evolutionary novelties between Jurassic and Early Cretaceous aquatic bug faunas, it appears that all of the Jurassic ecologic feeding types were present during the Early Cretaceous and encompassed surface water and neuston-zone feeders on dead or dying arthropods, nectic algivores, nectic predators and epibenthic predators.

There are minimal taxonomic and ecologic differences between Late Jurassic and Early Cretaceous beetle faunas. Archostematan schizophorids became very rare; the largely aquatic Adephaga retained a similar spectrum of major taxa as before, although the proportions of major lineages change. The major shifts are that the Parahygrobiidae become more abundant; the Coptoclavidae become dominated by a newly emerging, advanced clade, the Coptoclavinae; the Gyrinidae increase in diversity; the Liadytidae become rarer; the Dytiscidae remain rare; and the Haliplidae have their earliest occurrence (Ponomarenko 1969). The dominantly terrestrial Polyphaga are represented by the same families in the Early Cretaceous as during the Jurassic, including the Scirtiidae (marsh beetles), but especially the detritivorous Hydrophilidae, represented by new taxa such as *Cretotaenia*.

Other holometabolous insect clades with aquatic stages include the Megaloptera, Neuroptera (lacewings, antlions, and related forms) and Mecoptera. These clades express a similar pattern of mostly lotic-based diversity, as do their descendants in modern ecosystems. The predaceous larvae of megalopterans, such as the Corydalidae (dobsonflies), neuropterans such as the Osmyloidea (net-winged lacewings and relatives) and the detritivorous mecopteran larvae of the Nannochoristidae occur in Lower Cretaceous deposits of Eurasia and Australia (Zherikhin 1978; Jell and Duncan 1986). These lineages currently reside in the same habitats, although they have been overshadowed by more derived Cenozoic lineages that entered the same aquatic niches.

During the Early Cretaceous, caddisflies experienced major evolutionary novelties, as new family-level lineages emerged, other groups assumed dominance, and a profusion of larval case-making activity ensued. Evidence from adult caddisflies indicate that the earliest Mesozoic caddisflies, necrotaulids, became rare; others, such as the extinct phryganeoid families Dysoneuridae, Vitimotaulidae, and Baissoferidae were common, as were the extant Phyganeoidea, the Calamoceratidae (flat-case caddisflies), Lepidostomatidae (lepidostomatid casemaker caddisflies), Plectrotarsidae (plectrotarsid caddisflies), and Helicopsychidae (snail-case caddisflies) (Sinitshenkova 2002). Of these, the Vitimotaulidae were the most numerically abundant, or at least were common across most Eurasian localities. There was significant differentiation of the Vitimotaulidae at the generic level across Eurasia, and the dominance of particular local genera occurred throughout the region.

An important event in lotic and especially lentic environments was the global diversification of caddis larval-case morphotypes (Sukatcheva 1982). This expansion of domicile morphotypes that used a variety of mineral, plant, and animal resources evidently commenced during the earliest Cretaceous in northern Asia, and penecontemporaneously in Europe, South America and Australia (Sinitshenkova 1999). Circumstantial evidence indicates that the Vitimotaulidae were the dominant fabricators of these cases. In localities where adult body fossils and larval cases are both abundant and diverse, it appears that each case morphotype likely is associated with one adult species. Apparently, each case morphotype was made by an adult species that was restricted to a particular lotic or lentic habitat, partly reflected by use of building materials that were available for case construction. Cases were variously fabricated from conchostracan shells, *Karkenia* ginkgoalean seeds, conifer needles, plant twigs, quartz grains, mica flakes, and other available materials (Sukatcheva 1982).

The dominant lacustrine lineages of the Diptera during the Early Cretaceous were the same as for the Late Jurassic. Planktivorous chaoborids were more abundant but less speciose during the Early Cretaceous when compared to the Late Jurassic, whereas chironomids had an opposite trend. Both groups are represented primarily by adult and pupal fossils; larvae are relatively rare and poorly preserved. This pattern of differential preservation of developmental stages also exists for limoniids, eoptychopterids and other nematocerous fly lineages. Not only compression deposits capture this pattern, but this pattern also is found in amber occurrences, such as Lebanese Amber. In Lebanese Amber the most common families are, in decreasing rank: Chironomidae, Ceratopogonidae, Psychodidae, and Eoptychopteridae (Kalugina 1980). However, in Paleolake Baissa deposits, chaoborids were very abundant and likely were a major food resource for consumers that sustained much of the upper tier of the food-web. One interesting development in Early Cretaceous lakes was the emergence of brachyceran fly larvae, including the Stratiomyiidae (soldier flies), Empididae (dance flies), other asilomorphs, and possibly the Sciomyzidae (snail-eating flies) (Whalley and Jarzembowski 1985).

Arguably, one of the major innovations by the Early Cretaceous is the appearance of aquatic angiosperms which, together with ferns (Schneider et al. 2004), started to replace charophytes as the dominant macrovegetational elements in lacustrine ecosystems (Martín-Closas 2003; Friis et al. 2003, 2010; Gandolfo et al. 2004; Coiffard et al. 2007). The presence of freshwater species representing among the first angiosperms documented in the fossil record is hard to interpret, because it may reflect an initial evolution and diversification in aquatic habitats or a taphonomic bias (Martín-Closas 2003). Regardless of these alternatives, the appearance of angiosperms was an evolutionary breakthrough that may have had a considerable impact on aquatic life in ponds and lakes (Ponomarenko 1998; Friis et al. 2010). Specifically, aquatic angiosperms (Sun et al. 2002; Friis et al. 2003; Dilcher et al. 2007) would have been instrumental in providing substrates for epiphytic organisms, increasing the release of phosphorous by decaying macrophytes, promoting light attenuation, steepening of the vertical temperature gradient, retarding of water flow and enhancing fine-grained sediment deposition, among other processes (Carpenter and Lodge 1986; Granéli and Solander 1988; Ponomarenko 1998; Cohen 2003). Paralleling this pattern, aquatic ferns experienced further diversification (Schneider et al. 2004), but lycophytes remained abundant (Martín-Closas 2003). With respect to phytoplankton, although Chlorococcales were still abundant, the appearance of freshwater dinoflagellates is a major evolutionary innovation which signaled the demise of green algal dominance in freshwater phytoplankton (Martín-Closas 2003; Leliaert et al. 2011).

As with the Triassic and Jurassic, Cretaceous lotic and lentic insect faunas have been divided into distinctive lacustrine assemblages, each characterized by specific dominant and ecologically important insect species occurring in a particular environmental setting (Zherikhin 1978; Sinitshenkova and Zherikhin 1996; Sinitshenkova 1999; Sinitshenkova 2002). For the Cretaceous, 18 such assemblages have been described (Sinitshenkova 2002), one of which is Assemblage 5A, or the *Ephemeropsis melanurus–Hemeroscopus baissicus* Assemblage, whose environmental conditions and trophic structure have been examined in detail (Table 11.1 and Fig. 11.10). This

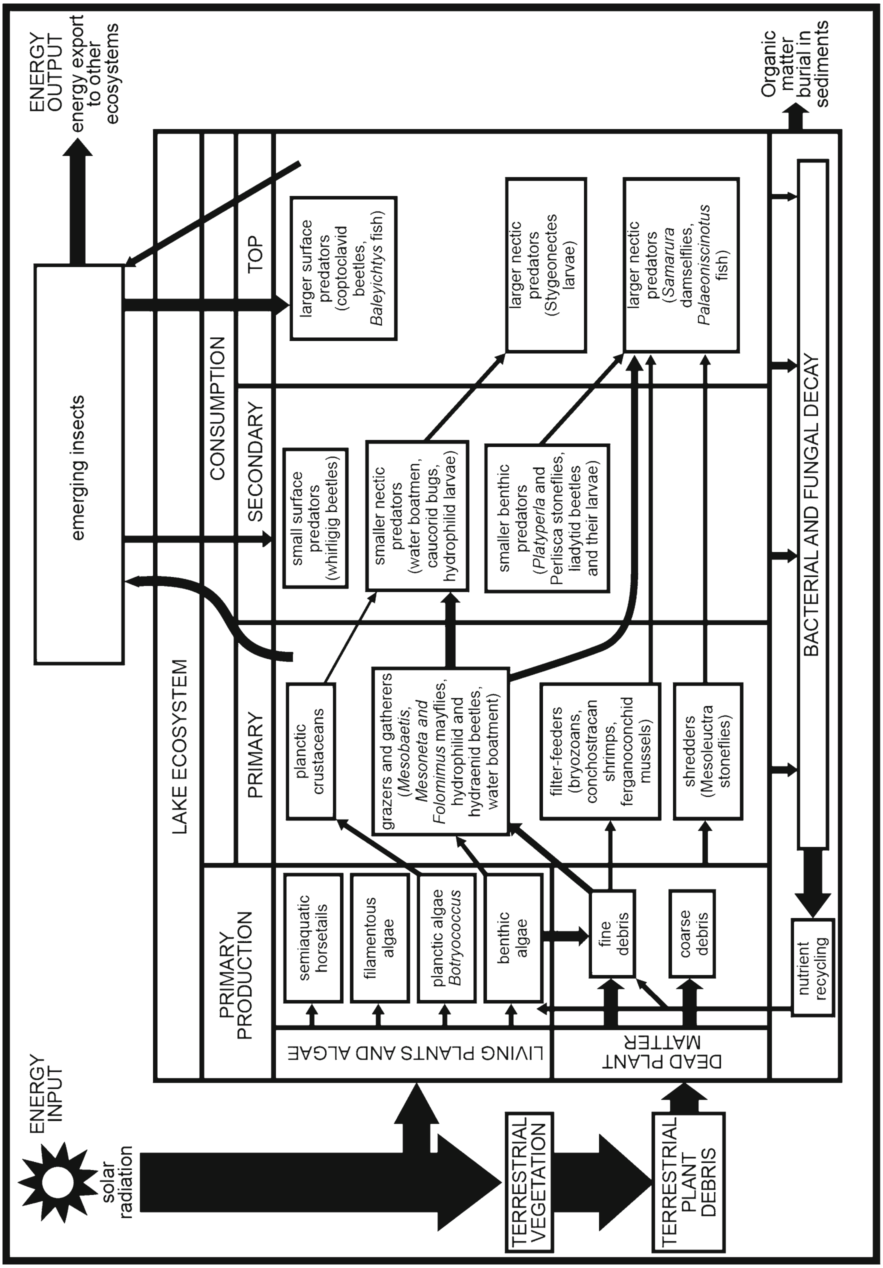


Fig. 11.10 Trophic structure reconstruction of an Early Cretaceous pseudoligotrophic lake (Zherikhin et al. 1999). This lake represents the *Ephemeropsis melanurus–Hemeroscopus bassicus* biotal assemblage typifying Paleolake Baissa in southern Siberia, Russia. This trophic reconstruction corresponds to the Type C lake biotal assemblage of Sinitshenkova and Zherikhin (1996). See Assemblage C in Table 11.1 for additional physical, chemical and biological details. Redrawn, with modification, from Sinitshenkova and Zherikhin (1996)

assemblage, from Paleolake Baissa, occurs in the Zaza Formation, Buryat Republic, in Transbaikalian Russia, and was deposited in a deep, intermontane, meromictic lake. Paleolake Baissa periodically dried out in shallower regions, indicated by mass mortality occurring as dense accumulations of the same instar of large coptoclavid larvae that became locally confined to a few bedding surfaces. Accumulations of chaoborid larvae are present at more widespread event horizons and at small unconformities or possibly diastems separating adjacent beds (Zherikhin et al. 1999).

The *Ephemeropsis melanurus–Hemeroscopus bassicus* Assemblage is more taxonomically and ecologically diverse than earlier Jurassic Eurasian paleolakes. This assemblage includes tetrapods, birds, and osteoglossomorph fish such as *Lycoptera*, and a rare *Stychopterus* sturgeon; phyllopod, conchostracan and ostracod crustaceans, gastropods, bivalves and freshwater bryozoans (Vinogradov 1996). Most of the estimated 1000 species of insects in the fauna are terrestrial and allochthonous in origin (Zherikhin et al. 1999). The autochthonous lacustrine component of the biota consists of ca. 80–120 species of lake residents, and was dominated by the aquatic immatures of odonatans, heteropterans, coleopterans, dipterans and numerous caddisflies (as cases). Insect fossils typically are shed exuviae rather than whole, dead individuals. The surrounding vegetation consisted of *Pseudolarix* forest, a *Podozamites–Czekanowskia* shrubland, and groundcover of horsetails, ferns, and very rare angiosperms of uncertain affiliation (Zherikhin et al. 1999). Although this assemblage represents one of the earliest occurrences of angiosperms in an Eurasian lake deposit, the effect of angiosperms were insignificant, and it was toward the end of the Early Cretaceous, during the Aptian and Albian Stages, during which the role of angiosperms were manifest in terrestrial ecosystems (Labandeira, 2014; Labandeira et al. 2016) and likely in freshwater ecosystems as well.

In most Mesozoic deposits intraspecific links between growth stages, such as naiads and adults in nonholometabolous insects and larvae and adults in holometabolous insects are not possible (Zherikhin and Sinitshenkova 2002). However, in the *Ephemeropsis melanurus–Hemeroscopus bassicus* Assemblage, some larval and adult taxa are associated based on a variety of evidence. Strong associations include the dragonfly adult of the hemeroscopid *Hemeroscopus baissicus* and a very common species of an aeschnidiid naiad, and similarly the hydrophilid beetle adult *Hydrophilopsia baissensis* with the hydrophilid larva *Cretotaenia pallipes*. Adults and larvae of the dobsonfly *Cretochaulus lacustris* and the adephagan beetle *Coptoclava longipoda* are also found in this assemblage, although the latter may be a complex of several species (Zherikhin et al. 1999). It appears that most of the caddisfly cases were constructed by various species of Vitimotaulidae. However, many of these fossils are immature individuals of lentic taxa whose adults are associated with nearby, lotic, especially rhythral, habitats that were allochthonously transported into Paleolake Baissa. The transported lotic taxa are represented by rare odonatans, plecopterans, simuliid dipterans, and nannochoristid mecopterans. These connections between immatures and adults in different aquatic habitats within lakes and rivers indicate a greater autecologic partitioning within species by life stage, as well as among species. This twofold, intraspecific and interspecific subdivision of resources can be interpreted as a maturation of terrestrial aquatic habitats that became more widespread during the Early Cretaceous (Zherikhin et al. 1999).

11.5.5 The Late Cretaceous Biotal Replacement

Ichnologic information from Late Cretaceous paleolakes is remarkably scarce, precluding a detailed discussion. Late Cretaceous examples of lake-margin ichnofaunas are known from the southern United States (Montgomery and Barnes 2012), western Canada (Rylaarsdam et al. 2006), Botswana (Du Plessis and Le Roux 1995), Bolivia (Meyer et al. 2001), China (Zhang 1987), and Korea (Paik et al. 2012; Lockley et al. 2012; Minter et al. 2012). However, most of these studies do not address the ichnofaunas in a comprehensive fashion. As for fully lacustrine deposits, we are aware of only one study documenting Late Cretaceous ichnofaunas in this setting, namely perennial lake deposits in Botswana (Du Plessis and Le Roux 1995).

The crayfish burrow *Camborygma* is present in lake-margin deposits (Montgomery and Barnes 2012), indicating the persistence of this deep tier throughout the Mesozoic. Vertical burrows (e.g. *Skolithos*) and branching structures (e.g. *Thalassinoides*) occur as well (Zhang 1987; Du Plessis and Le Roux 1995). Arthropod trackways (*Lithographus*) have been recorded locally (Minter et al. 2012). Dinosaur and bird tracks preserved along lacustrine paleoshorelines also are known (Meyer et al. 2001; Rylaarsdam et al. 2006; Paik et al. 2012; Lockley et al. 2012). In particular, intense bioturbation by dinosaurs continued to have an impact on the sedimentary fabric of lake-margin deposits throughout the Late Cretaceous (Rylaarsdam et al. 2006).

A complex mosaic of lacustrine deposits is preserved in Upper Cretaceous grabens, whose infill is recorded in the Kalahari Group of Botswana (Du Plessis and Le Roux 1995). The succession includes deposits of ephemeral and perennial alkaline lakes. In both systems, an irregular network of tunnels, showing Y-shaped bifurcations, attributed to *Thalassinoides*, has been recorded (Du Plessis and Le Roux 1995). In the ephemeral lake deposits, these structures are present in sand and mud flats flanking the lake system. In the perennial lake deposits, *Thalassinoides* occurs in fully lacustrine deposits in great abundances, commonly forming intensely bioturbated fabrics, which most likely record less saline conditions in relatively deeper water environments (Du Plessis and Le Roux 1995). In these deposits, *Thalassinoides* commonly occurs in association with vertical shafts that have lateral tunnels, which have been compared with the poorly known vertical burrow *Lennea* (Du Plessis and Le Roux 1995), but this attribution needs further confirmation. In short, the sparse information available suggests continuation in lake-margin environments of the same trends evidenced earlier in this setting. As well, the presence of intensely bioturbated, fully lacustrine deposits resembles similar deposits of the Lower Cretaceous.

Much less is known about Late Cretaceous lacustrine biotas when compared to those of the Early Cretaceous. Most likely this is a reflection of limited outcrop that resulted from the end of the broad extensional-tectonic regime that dominated the mid-Mesozoic continental breakup, which promoted the formation of widespread lacustrine rifts (Cohen 2003). The fossil record of aquatic insects documents mid-Cretaceous extinction of some lineages that were thriving during the Early Cretaceous but are not present during the Late Cretaceous. This event included the extinction of about 20 family- and superfamily-level lineages (Zherikhin 1978; Sinitshenkova and Zherikhin 1996). Of ephemeropterans, none became extinct; for odonatans, the latest meganeuroid lineage, the Protomyrmeleontidae, became extinct, as did the Isophlebioidea and Heterophlebioidea. For plecopterans, the family Oecanthoperlidae is extinguished, as was the Chresmodida, a major Jurassic clade of aquatic Archaeorthoptera. With the exception of the Shurabellidae, apparently no lineage of hemipterans became extinct, as early originating lineages such as corixids, notonectids, belostomatids, and mesoveliids survive to the present day. Coleopterans experienced several major extinctions, such as the Ademosynidae, Parahygrobiidae, Schizophoridae, Coptoclavidae, and Liadytidae. No major extinctions are known for the major lineages of the relatively undiverse neuropteroid groups Megaloptera, Raphidioptera, or Neuroptera, or for the Mecoptera, of which the extant Nannochoristidae is an aquatic representative. For the Trichoptera, major extinctions of family-level taxa were the Dysoneuridae, Necrotaulidae, Baissoferidae, and Vitimotaulidae, the latter of which produced a high diversity of caddisfly case morphologies. The Diptera remained unaffected by the mid-Cretaceous extinction events; evidently the nematocerous Eoptychopteridae and possibly the Hennigmatidae are the only family-level lineages that became extinct (Zherikhin 1978; Sinitshenkova and Zherikhin 1996).

Perhaps more important are the originations of new aquatic insect lineages during the mid Cretaceous, almost all of which survive to the present and essentially form the modern lentic and lotic aquatic insect fauna. Approximately 19 family- and superfamily-level lineages have their first fossil occurrences during the mid Cretaceous, consisting of approximately the same number of lineages that go extinct. For the Ephemeroptera, only the earliest Heptagenoidea is known to occur close to the Early–Late Cretaceous boundary. In odonatans, modern family-level lineages of the Zygoptera (damselflies) may have originated during this interval, but geochronological timing is poorly constrained. No known major lineages of plecopterans originated during the mid Cretaceous. As for hemipterans, the diverse clade Gerromorpha had its earliest major bout of diversification during the mid Cretaceous, including some of the first occurrences of sublineages within the Gerridae, Hydrometroidea (water measurers), probably the Hebroidea (velvet waterbugs and relatives), and the extinct Mesotrephidae. Of coleopterans, only the Haliplidae and Scirtiidae have their earliest occurrences during the mid Cretaceous. Five lineages of the Trichoptera have their first occurrences at this time, including the Hydrobiosidae (pincer-clawed caddisflies), Sericostomatidae (bushedtailed caddisflies), Odontoceridae (mortarjoint casemakers), Calamoceratidae (comblipped casemakers), and Leptoceridae (long-horned caddisflies). The origin of these lineages curiously is associated with a significant decline in case morphotype diversity, as early Cretaceous cases range from 10–15 morphotypes in a typical assemblage, to ca. 5 per assemblage in the Late Cretaceous (Sukatcheva 1991). This decline may be attributable to the disappearance of the diverse Vitimotaulidae which became extinct at this time. Several nematocerous lineages of dipterans with aquatic larvae diversified during the mid Cretaceous, particularly the Ptychopteridae (phantom crane flies), Culicidae (mosquitoes), Chaoboridae (phantom midges), Corethrellidae (frog-biting midges), and Ceratopogonidae (biting midges). Interestingly, while the number of known aquatic insect extinctions and originations for the mid Cretaceous appear to balance out with ca. 20 lineages in each category, the totals of insect herbivore turnover is much greater for the mid-Cretaceous terrestrial realm (Labandeira 2014).

The biologies of these aquatic insect lineages indicate that, whereas the aquatic immatures (naiads, larvae) were well integrated into aquatic ecosystems, the adults became more removed from aquatic habitats than in previous freshwater biotas. For example, whereas the naiads of damselflies were major aquatic predators, their adults preyed on aerially winged insects. The adults of aquatic heteropterans became predators on other aquatic insects (Anderson 1998). Almost all dipteran lineages were comprised of larvae that were aquatic filter-feeders whereas their adults—at least the females—were obligate blood feeders on vertebrates (Labandeira 2002). As the aquatic larvae of caddisflies increasingly became herbivorous, their terrestrial adults targeted angiosperm nectar or similar nutritive sources (Porsch 1958), or lacked feeding capabilities altogether. The disjunction of habitats between immatures (naiads, larvae) and adults increased during the Late Cretaceous, exhibiting an even more profound separation between the life habits of immatures and adults than ever before.

The Late Cretaceous witnessed the continuation of the radiation of aquatic angiosperms and ferns (Martín-Closas 2003; Gandolfo et al. 2004; Schneider et al. 2004), the former showing increased interaction with modern insect families. The shift from gymnosperm-dominated floras to angiosperm-dominated floras was accompanied by a major turnover in their terrestrial insect associates (Labandeira 2014; Labandeira et al. 2016). This transition occurred during the angiosperm radiation, and included episodes of extinction and origination that paralleled a similar pattern characterizing the MLR, although it appears that there is a time shift between the two major events. By contrast, no such pattern is seen in freshwater algal groups. Charophyte assemblages became dominated by the Characeae (Martín-Closas 2003). During the Late Cretaceous, lacustrine phytoplankton displays a similar composition to that of the Early Cretaceous, as indicated by the presence of Chlorococcales and freshwater dinoflagellates (Martín-Closas 2003). However, evidence of diatoms is known from the Late Cretaceous, suggesting early diversification, albeit playing a limited role as lacustrine plankton (Chacón-Bacca et al. 2002). Chrysophytes also are documented from the Cretaceous (Cornell 1979; Adam and Mahood 1981), but as with diatoms, they radiated later in the Cenozoic when they became an important phytoplankton component (Leliaert et al. 2011). In any case, the major changes in the plankton composition involved the diversification of freshwater diatoms and chrysophytes.

11.6 The Aftermath of the Revolution

An examination of the trace- and body-fossil records, as well as the ecological structure of Cenozoic lakes, provides a picture of the aftermath of the MLR, thereby revealing whether additional evolutionary novelties or innovations took place. Interestingly, the biological response to the MLR is not straightforward.

A review of the Cenozoic lacustrine trace-fossil record shows that Cenozoic lake-margin invertebrate ichnofaunas are similar in composition to those of the Late Cretaceous (Table 11.2). Apparently there was minimal effect of the Cretaceous–Paleogene (K-Pg) events on the MLR (see Chap. 12). This is in sharp contrast, for example, with the ongoing rapid diversification of insect nesting structures in paleosols that took place during the Cenozoic (see Chap. 13).

Little is known of complete inventories of bulk aquatic insect faunas from amber and compression–impression deposits during the Late Cretaceous and Paleocene, unlike the significantly better documented terrestrial fossil insect record (Zherikhin and Sinitshenkova 2002; Labandeira 2005b). Perhaps more importantly, paleoecological data indicate that the modern ecologic structure from one, well-documented lake was well established by the early–middle Eocene boundary interval at Paleolake Messel (Fig. 11.12), and resembled in all measured food-web indices that of a variety of modern lake ecosystems (Dunne et al. 2014). This study proposes that earlier, well preserved lake deposits that postdate the MLR but predate Messel (and straddling the K-Pg boundary) also be examined to determine how far back in geologic time modern lacustrine food-web structure extends (Dunne et al. 2014). Until food-web studies that use similar analytical techniques and trophic measurement indices as those used for Messel are applied to well-preserved lake deposits before and after the MLR, analytical detection of the trophic shift left by the MLR may be difficult. Nevertheless, studies of ichnofaunas and insect biotas, particularly those from the Paleogene may provide robust results in lieu of detailed food-web analyses of lake deposits using modern ecological techniques. One particular approach that may be useful is to attempt an associational approach in the freshwater, especially lacustrine realm that has been done for the terrestrial realm (Labandeira et al. 2002; Wilf et al. 2006). In lieu of more complete knowledge of aquatic, arthropod body-fossil faunas during this time interval, analyses of interactions may provide an another approach for detecting the trophic shift toward herbivore-dominated aquatic communities following the MLR.

Ichnofaunas from lake-margin deposits are known from the Paleogene of the western United States (Melchior and Erickson 1979; Lamond and Tapanila 2003; Bohacs et al. 2007; Scott and Smith 2015), Spain (Rossi 1992; de Gibert and Sáez 2009), China (Hsiao et al. 2010), Antarctica (Yang and Shen 1999; Perea et al. 2001), the Neogene of the western United States (Toots 1975; Smith et al. 1982; Squires and Advocate 1984; Scrivner and Bottjer 1986; Lucas et al. 2002), Spain (Rodriguez-Aranda and Calvo 1998; Uchman and Álvaro 2000; Ortí et al. 2003) and Kenya (Laporte and Behrensmeyer 1980; Cohen 1982; Ekdale et al. 1989; Cohen et al. 1991, 1993; Lamond and Tapanila 2003). Shallow-tier, horizontally striated or non-ornamented, meniscate, backfilled structures (*Scoyenia*, *Taenidium*, *Beaconites*), simple horizontal structures (*Planolites*, *Palaeophycus*), vertical burrows (*Arenicolites*, *Polykladichnus*), and striated or non-ornamented branching burrows (*Spongeliomorpha, Labyrintichnus*) are the dominant elements (Toots 1975; Smith et al. 1982; Squires and Advocate 1984; Rodriguez-Aranda and Calvo 1998; Uchman and Álvaro 2000; Ortí et al. 2003; Bohacs et al. 2007; de Gibert and Sáez 2009; Hsiao et al. 2010). The crayfish burrow *Camborygma* has been locally recorded (Hsiao et al. 2010). Vertical burrows with a terminal chamber, ascribed to the ichnotaxon *Liticuniculatus erectus,*

Table 11.2 Summary of ichnologic, paleontologic, and paleoecologic information on the Mesozoic Lacustrine Revolution (MLR)

Evolutionary phases	Aquatic insect body fossils (representative families)[a]	Other benthos	Aquatic plants	Nekton/plankton	Lake-margin trace fossils	Permanently subaqueous trace fossils	Ecosystem characteristics
Pre-Mesozoic Backdrop to Diversification	Dasyleptidae, Protereismatidae, Misthodotidae, Syntonopteridae, Jarmilidae, Oboriphlebiidae, Eraspteriidae, Meganeuridae, Protomyrmeleontidae, Permagrionidae, Kennedyidae, Perlopseidae, Tschekardiperliidae, Palaeonemouriidae	Chelicerates, conchostracans, leperditocopid crustaceans, shrimp-like crustaceans, oligochaetes, bivalves, gastropods, amphibians, reptiles	Charophytes, water-tolerant lycopods, sphenopsids, medullosan seedferns and arborescent marattialean ferns in wetlands; cordaites, noeggeranthialeans, conifers, gigantopterids, and peltasperms in dry settings	Chlorophytes (mostly Chlorococcales), agnathan, acanthodian, placoderm, chondrichthyan, and osteichthyan fish	Arthropod and tetrapod trackways dominant	Superficial grazing trails and shallow-tier feeding trace fossils dominant, fish trails present	Colonization of lake-margin settings by the Silurian-Devonian and of permanently submerged lake bottoms by the Carboniferous. Limited to no colonization of the infaunal ecospace. Poorly developed food webs driven by detritivores and top predators as near-exclusive consumers; herbivory was absent
Early Triassic Denouement	Protomyrmeleontidae, Batkeniidae, Naucoridae, Belostomatidae, Permosynidae, Schizophoridae, Liassophilidae, Tipulidae	Decline in family-level biodiversity. Conchostracans, shrimp-like crustaceans, bivalves, gastropods, oligochaetes, amphibians, reptiles	Charophytes and *Isoetes*-related nonflowering vascular plants	Chlorophytes (mostly Chlorococcales), osteichthyan fish	Arthropod trackways dominant	No data	Persistence of Paleozoic styles of animal–substrate interactions in lake-margin settings. Poorly developed food webs driven by detritivores and top predators as near-exclusive consumers; herbivory was absent

(continued)

Table 11.2 (continued)

Evolutionary phases	Aquatic insect body fossils (representative families)[a]	Other benthos	Aquatic plants	Nekton/plankton	Lake-margin trace fossils	Permanently subaqueous trace fossils	Ecosystem characteristics
Middle-Late Triassic Rediversification	Triassolestidae, Saxonagrionidae, Triadophlebiidae, Siphloneuridae, Euxenoperlidae, Ochteridae, Triassocoridae, Notonectidae, Belostomatidae, Schizophoridae, Ademosynidae, Colymbothetidae, Hydrophilidae, Dytiscidae, Triaplidae, Philopotamidae, Prorhyacophilidae, Nannochoristidae	Biodiversity recovery. Conchostracans, shrimp-like crustaceans, ostracods, kazacharthrans, phyllopods, bivalves, gastropods, oligochaetes, bryozoans, amphibians, reptiles	Charophytes and *Isoetes*- and *Azolla*-related nonflowering vascular plants	Chlorophytes (mostly Chlorococcales), osteichthyes fish	Meniscate trace fossils dominant, crayfish burrows common, reptile trackways and lungfish burrows present	Superficial grazing trails and shallow-tier feeding trace fossils dominant, fish trails present, mid-tier feeding burrows locally present. Vertical dwelling burrows in higher-energy settings	Increase in depth and extent of bioturbation in lake-margin sediments Persistence of Paleozoic styles of animal-substrate interactions in permanent subaqueous lake settings, but incipient colonization of the infaunal ecospace locally. More complex food webs, albeit still driven by detritivores and top predators with herbivory absent
Jurassic diversification and infaunalization	Tarsophlebiidae, Siphlonuridae, Mesonetidae, Epeorominidae, Mesoleuctridae, Siberioperlidae, Chresmodidae, Belostomatidae, Gyrinidae, Mesoveliidae, Shurabellidae, Coptoclavidae, Haliplidae, Liadytidae, Parahygrobiidae, Necrotaulidae, Limoniidae, Chironomidae Eoptychopteridae, Chaoboriodae	Conchostracans, shrimp-like crustaceans, ostracods, phyllopods, bivalves, gastropods, oligochaetes, bryozoans, amphibians, reptiles	Charophytes dominant (radiation of Characeae and the Clavatoraceae), *Azolla*-related nonflowering vascular plants, ferns, porocharaceans and nitellaceans locally	Chlorophytes (mostly Chlorococcales), osteichthyes fish	Meniscate trace fossils dominant, dinoaur trackways present (including trampled surfaces)	Shallow-tier feeding and grazing trace fossils and deeper-tier feeding burrows dominant, fish trails present, mid-tier feeding burrows locally present. Vertical dwelling burrows in higher-energy settings	Persistence of Middle to Late Triassic styles of animal-substrate interactions in lake-margin settings, but with the addition of intense bioturbation by dinosaurs. Widespread occupation of mid tiers in deep lacustrine deposits, but limited sediment reworking.Increase in predation pressures. Initial transformation from detritivore-driven to herbivore-driven trophic networks of the mesolimnion and epilimnion

Early Cretaceous Persistence	Petaluridae, Libellulidae, Hemeroscopidae, Hexagenitidae, Chresmodidae, Clypostemmatidae, Mesotrephidae, Gerridae, Mesoveliidae, Hydrophilidae, Dytiscidae, Coptoclavidae Scirtiidae, Corydalidae Vitimotaulidae, Baissoferidae Calamoceratidae	Conchostracans, shrimp-like crustaceans, ostracods, phyllopods, bivalves, gastropods, oligochaetes, bryozoans, amphibians, reptiles	Aquatic angiosperms and ferns common, charophytes present	Chlorophytes (mostly Chlorococcales), dominant, dinoflgellates, osteichthyan fish	Meniscate trace fossils dominant, crayfish burrows common, dinosaur, pterosaur, bird, reptile and turtle trackways present	Shallow-tier feeding and grazing trace fossils, mid-tier pervasive burrow mottlings, fish trails present	Establishment of the lacustrine mixed layer. Transformation from detritivore-driven to herbivore-driven trophic networks of the mesolimnion and epilimnion
Late Cretaceous biotal replacement	Gomphidae, Petaluridae, Aeshnidae, Libellulidae Coenagrionidae Gerridae, Hebridae, Hydrometridae, Mesotrephidae, Hydrobioscidae, Sericostomatidae, Leptoceridae Culicidae, Ptychopteridae, Chaoboridae Ceratopogonidae	Conchostracans, shrimp-like crustaceans, ostracods, phyllopods, bivalves, gastropods, oligochaetes, bryozoans, amphibians, reptiles	Aquatic angiosperms and ferns dominant, charophytes present.	Chlorophytes (mostly Chlorococcales), and dinoflgellates dominant, osteichthyan fish	Crayfish burrows, and dinosaur and bird trackways present	Deeper-tier feeding burrows present	Persistence of previous trends in styles of animal–substrate interactions

(continued)

Table 11.2 (continued)

Evolutionary phases	Aquatic insect body fossils (representative families)[a]	Other benthos	Aquatic plants	Nekton/plankton	Lake-margin trace fossils	Permanently subaqueous trace fossils	Ecosystem characteristics
Cenozoic Aftermath to MLR	Sieblosiidae, Zacallatidae, Dysagrionidae, Baetidae, Hydrophilidae, Dytiscidae, Hydropsychidae, Leptoceridae, Limnephilidae, Hydroptilidae, Phryganeidae, Culicidae Tipulidae, Cylindrotomidae Chironomidae	Conchostracans, shrimp-like crustaceans, ostracods, phyllopods, bivalves, gastropods, oligochaetes, bryozoans, amphibians, reptiles and mammals	Aquatic angiosperms and ferns dominant.	Chlorophytes (mostly Chlorococcales), and dinoflgellates dominant, freshwater diatoms and chrysophytes, osteichthyan fish	Meniscate trace fossils dominant, crayfish burrows common, insect nests and borings locally, bird and mammal trackways present	Shallow-tier feeding and grazing trace fossils and deeper-tier feeding burrows dominant, fish trails and nests present, mid-tier feeding burrows locally present. Shallow-tier trails in glacial settings. Vertical dwelling burrows in higher-energy settings	Persistence of previous trends in styles of animal–substrate interactions. Strong impact of diatoms starting in early Neogene on the biogeochemical cycling of silica, promotion of more complex trophic webs and probable overall increase of lacustrine productivity

[a] This column provides the more important aquatic forms or inhabitants of wet habitats adjacent to lakes for at least one stage in their life cycle (naiad, larva, adult)

were compared with similar structures produced by decapods (Melchior and Erickson 1979). This is a poorly known ichnotaxon that may elicit comparisons with *Camborygma*. Simple grazing trails (*Archaeonassa*, *Cochlichnus*) are very rare (Smith et al. 1982; de Gibert and Sáez 2009).

In some cases lake-margin deposits are overprinted by a suite of insect nests (*Celliforma, Roselichnus*; Uchman and Álvaro 2000), which are particularly common in Cenozoic terrestrial settings (see Chap. 13). Spectacular examples of surfaces and beds containing several overprinted suites from fully aquatic to transitional and fully terrestrial facies are known from a number of Quaternary localities in Kenya (Scott et al. 2009; Owen et al. 2009). Borings (*Trypanites*, *Sertaterebrites*) and embedment cavities have been documented in lacustrine stromatolites (Ekdale et al. 1989; Lamond and Tapanila 2003; but see Corsetti and Grotzinger 2005 for an alternative interpretation). Evidence of insects capable of burrowing in highly stressed, hypersaline environments of underfilled lakes are observed for the first time in some of the Neogene basins of Spain (e.g. Rodriguez-Aranda and Calvo 1998; Uchman and Álvaro 2000; Ortí et al. 2003).

Vertebrate trace fossils in Cenozoic lake-margin deposits include bird (e.g. *Gruipeda*) and mammal tracks (Scrivner and Bottjer 1986; Yang and Shen 1999; Perea et al. 2001; Lucas et al. 2002; de Gibert and Sáez 2009). A wealth of information has been produced on how vertebrates modify lake-margin surfaces. Large mammals (e.g. hippos) are known to produce trampled surfaces, actively modifying lake-margin landscapes (Laporte and Behrensmeyer 1980; Cohen et al. 1991, 1993; Ashley and Liutkus 2002; Deocampo 2002; Scott et al 2007, 2008) (Fig. 11.11a–c). Additionally, flamingos produce nest mounds and alter lake-margin deposits by trampling and churning wet clayey sediments (Scott et al. 2009, 2012b). These authors documented that these nests may be so compacted that they contribute to the stability of deltaic distributary channels in lake margins, leading to channelization of flow by water diversion around the mounds. Indeed, the impact of flamingos on lake-margin sediments results in the development of a distinctive mounded topography that qualifies as an ichnolandscape (*sensu* Buatois and Mángano 2011a), which can be preserved in the fossil record (Fig. 11.12a–b).

Ichnofaunas from fully lacustrine deposits have been recorded nearly worldwide in Cenozoic deposits. They have been documented from the Paleogene of the western United States (Moussa 1968, 1970; Melchior and Erickson 1979; Loewen and de Gibert 1999; Bohacs et al. 2007; Martin et al. 2010; Scott and Smith 2015), Antarctica (Yang and Shen 1999; Perea et al. 2001), the Neogene of the eastern (O'Brien and Pietraskek-Mattner 1998; Benner et al. 2009; Knecht et al. 2009) and western (Smith et al. 1982) United States, eastern Canada (Gibbard and Dreimanis 1978), Hungary (Babinszski et al. 2003; Magyar et al. 2006; Cziczer et al. 2009), Slovakia (Starek et al. 2010; Hyžný et al. 2015), England (Gibbard and Stuart 1974), Lithuania (Uchman et al. 2008, 2009), Finland (Gibbard 1977), Sweden (Uchman and Kumpulainen 2011), Germany (Walter 1985; Walter and Suhr 1998), Greece (Owen et al. 2011), Turkey (Price and McCann 1990; Uchman et al. 2007), China (Yang 1996), Indonesia (Whateley and Jordan 1989), Thailand (Gibling et al. 1985; Flint et al. 1989), Japan (Allison et al. 2008), Kenya (Feibel 1987) and New Zealand (Lindqvist 1994).

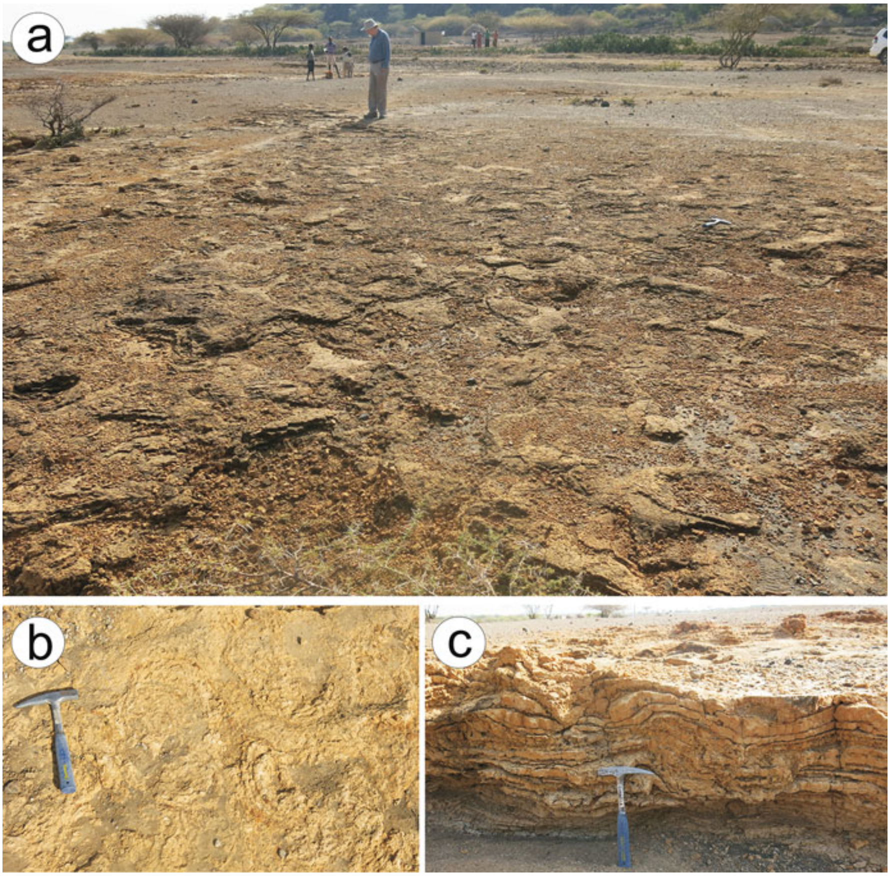


Fig. 11.11 Fossilized trampled surface consisting of a high-density of hippopotamus tracks, Pleistocene, Ilosowuani horst near Logumukum, Lake Bogoria Basin, Kenya. (**a**) General view of the trampled surface; (**b**) Close-up of one of the tracks; (**c**) Cross-section view showing intense disturbance of the primary sedimentary fabric

Ichnofaunas from fully lacustrine, Cenozoic deposits are known from both nonglacial and glacial settings. Nonglacial lake deposits that accumulated under low energy conditions tend to be dominated by a combination of very shallow-tier grazing trails (*Cochlichnus*, *Helminthopsis*), shallow-tier mottlings attributed to *Planolites*, and deeper-tier branching burrows (*Vagorichnus*) (Moussa 1968, 1970; Smith et al. 1982; Gibling et al. 1985; Feibel 1987; Flint et al. 1989; Whateley and Jordan 1989; Yang and Shen 1999; Perea et al. 2001; Bohacs et al. 2007; Uchman et al. 2007; Owen et al. 2011). *Oligichnos limnos*, an ichnotaxon erected by Melchior and Erickson (1979) and suggested to have been made by oligochaetes, needs re-evaluation and may become a junior synonym of *Helminthopsis*. Also, the presence of the bivalve burrow *Lockeia* has been mentioned (Feibel 1987). Interbedded sandstone tempestites and dolomites contain deeper-tier vertical burrows (*Skolithos*, *Arenicolites Polykladichnus*) (Price and McCann 1990; Magyar et al. 2006). Vertical burrows similar to *Trichichnus* have been

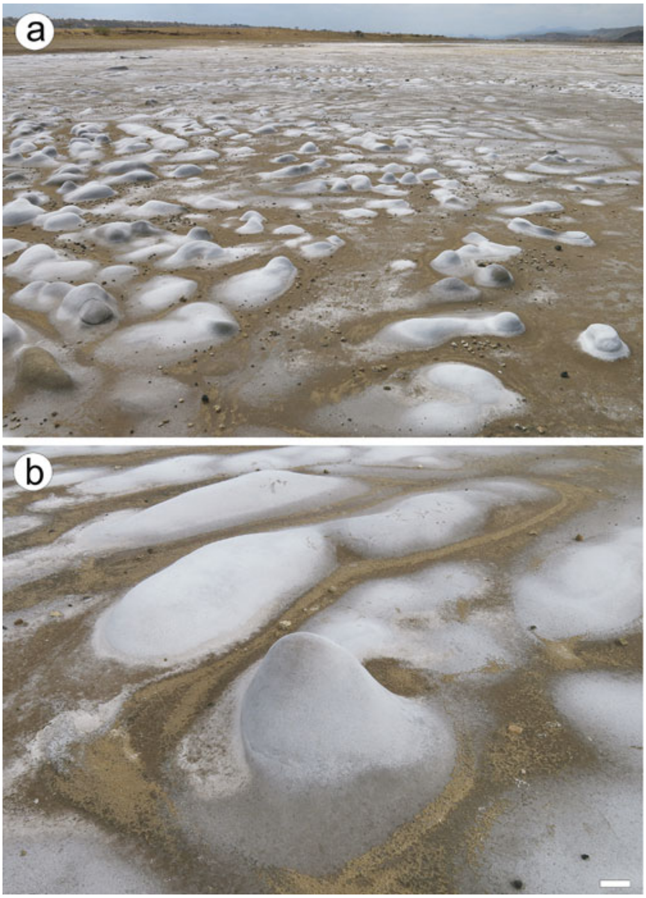


Fig. 11.12 Fossilized flamingo nests, Pleistocene, High Magadi Beds, Lake Magadi, Kenya. (**a**) General view of the nest-bearing surface showing a spectacular biogenic topography (i.e. ichnolandscape); (**b**) Close-up of nests. Scale bar is 10 cm long

mentioned in lacustrine shales (Lindqvist 1994). Burrow systems from long-lived brackish- to freshwater fossil Paleolake Pannon have been attributed a new ichnotaxon, *Egbellichnus jordidegiberti* (Hyžný et al. 2015). These burrows have been interpreted to have been produced by ghost shrimps, indicating that these marine organisms were able to survive for a long time after the closure of the seaway connecting this water body with the central Paratethys sea (Hyžný et al. 2015). Vertebrates are represented by the fish trail *Undichna* (Loewen and de Gibert 1999; Martin et al. 2010) and the fish nest *Piscichnus* (Feibel 1987).

Glacial lakes are dominated by very shallow-tier grazing trails (*Cochlichnus*, *Gordia*, *Helminthoidichnites*) and arthropod trackways (*Glaciichnium*, *Warvichnium*, *Dendroichnites*, *Lusatichnium*), with the branching burrow *Treptichnus* and the conchostracan resting trail *Surculichnus* locally present (Gibbard and Stuart 1974; Gibbard 1977; Gibbard and Dreimanis 1978; Walter and

Suhr 1998; O'Brien and Pietraskek-Mattner 1998; Uchman et al. 2009; Benner et al. 2009; Knecht et al. 2009; Uchman and Kumpulainen 2011). Vertebrates are represented by the fish ichnotaxa *Undichna*, *Broomichnium* and *Piscichnus* (Benner et al. 2009; Uchman and Kumpulainen 2011). The ichnofaunas of Pleistocene glacial lakes are somewhat unusual in that they closely resemble those that are typical of the Paleozoic, displaying a dominance of very shallow-tier ichnotaxa and an underutilized infaunal ecospace. The anachronistic nature of Pleistocene glacial lacustrine ichnofaunas may represent another example of the so-called *déjà vu* effect (Buatois and Mángano 2011b). The dominance of very shallow-tier structures in Pleistocene glacial deposits may reflect very limited burial of organic matter in highly oligotrophic lakes, restricting the habitable zone to a few millimeters below the sediment–water interface.

It should be noted, however, that suppressed bioturbation is not restricted to these types of settings, but also occur in highly productive lakes having oxygenated bottom waters, as evidenced in Lake Turkana (Cohen 1984). In this lake, primary productivity is extremely high toward the lake shore, but phytoplankton populations are markedly less productive offshore. As a result, food content is quite low in offshore lake bottoms and the invertebrate fauna essentially consists of epibenthic detritivores which do not disturb the primary sedimentary fabric. In addition, the lack of sediment mixing results in a redox discontinuity surface very close to the sediment–water interface, further restricting infaunalization (Cohen 1984). This pattern may be regarded as reminiscent of Paleozoic settings displaying limited colonization of infaunal ecospace.

To summarize, a review of the Cenozoic lacustrine trace-fossil record fails to show the appearance of any major evolutionary novelty or innovation from an ichnologic perspective. The spectacular trampled surfaces produced by large mammals that characterize Neogene and modern lake margins were preceded by equally extended and bioturbated surfaces produced by dinosaurs in the Mesozoic. Cenozoic ichnofaunas suggest a continuation of trends that started during the MLR. However, these extensive ichnologic studies need to be linked with examination of body-fossil assemblages from lacustrine and other aquatic environments, particularly during the Paleogene, to more comprehensively document the effects of the MLR. It is notable that, as discussed below, aquatic organisms and ecosystems were better buffered from extinction and ecological reorganization than terrestrial ecosystems during and after the K-Pg crisis (also see Chap. 12). This buffering has multiple sources, including (1), behavioral modifications of lacustrine organisms, including infaunalization, encystment, and planktotrophic larvae that would predispose organisms toward avoiding major environmental vicissitude (Chap. 12); (2), more generalized and less specialized food webs occurring in lakes than for coexisting, surrounding terrestrial communities, at least known for the middle Eocene (Dunne et al. 2014); and (3), the temporally ephemeral nature of lake communities that require considerable dispersal mechanisms for continuity of lake biotas (Cohen 2003), Additionally, the responses to the K-Pg event were variable by the taxonomic group involved, by their occupied habitat, by where they occurred in regional landscapes and in their worldwide distribution, and were variably dampened by the effects of time.

A major effect of the end-Cretaceous global crisis (see Chap. 12) was not only extensive taxonomic extinction and subsequent origination for many non-arthropodan terrestrial lineages, but equally important, trophic pruning of ecosystem structure. On land, the consequences of this event meant the demise of numerous lineages, particularly vertebrates (Archibald and Bryant 1990) and plants (Nichols and Johnson 2008), but this extinction only minimally affected arthropod groups, when evaluated as body-fossil taxa at the family level (Labandeira 2005b). However, when plant–insect interactions are examined at the K-Pg boundary interval, the consequences were important, and hit especially specialized insects such as gallers and leaf miners, while leaving taxa with generalized feeding habits relatively intact (Labandeira et al. 2002; Wilf et al. 2006). In aquatic ecosystems, there was less of an effect (but see Bailey et al. 2005 for possible taphonomic biases). Aquatic insects were minimally affected, at least at the family level (Labandeira 2005b), although there may have been significant changes in food-web structure that persisted well into the Paleogene (Dunne et al. 2014). One important pattern documented for aquatic invertebrates was the differential effects that the K-Pg event had on organisms that inhabited the benthos of water bodies (Twitchett 2006). Detritivorous organisms in or on the sediment were considerably more buffered both from extinction and destruction of their food resources than those trophic networks subsisting on food resources derived from photosynthetic organisms such as algae, diatoms, or aquatic vascular plants (Sheehan and Hansen 1986). This immunity was enhanced for those aquatic invertebrates, such as many detritivorous arthropodan groups, that had planktic immature stages and thus were more able to withstand extinction. For aquatic, especially lentic and lotic–potamic habitats, there was a reduced effect from the end-Cretaceous crisis, particularly for local trophic networks whose dietary resources were not dependent on the herbivory of photosynthetic organisms.

The history of Paleogene insects in aquatic ecosystems is poorly known outside of Central Europe and North America. Most aquatic insect orders have been minimally documented, and many assemblages are woefully deficient in species-level descriptions and revisions. The number of autochthonous lentic taxa is poorly known. Better documented are exceptionally well preserved compression deposits that include the Green River, Messel, Kishenehn, and Menat paleolakes (Nel and Roy 1996; Smith ME et al. 2008b; Greenwalt and Labandeira 2013; Dunne et al. 2014). These well-documented deposits represent only a broad outline of Paleogene aquatic insect history, even though their temporal proximity to the modern fauna should allow easier identification and ecological interpretation of the insect taxa present (Zherikhin and Sinitshenkova 2002). These and almost all Paleogene aquatic taxa are assigned to extant families. The only significant exceptions to this generalization lie within the Odonata, in which the families Sieblosiidae (which disappeared during the Pliocene) and Zacallatidae (Paleogene only) and the subfamilies Dysagrioninae (Paleogene only) and Eodichrominae (Paleogene only) are absent from the modern fauna (Zherikhin and Sinitshenkova 2002). The overwhelming majority of modern lotic and lentic aquatic families extend at least to the Paleogene, and occur in compression and amber deposits. There are many cases of extant aquatic genera extending to the middle Eocene, and apparently living species present in sediments as old as the Eocene (Askevold 1990; Murray 1976; Kluge 1986).

The naiads of ephemeropterans are uncommon in Paleogene compression deposits. Some amber deposits, such as Baltic Amber have provided the overwhelming majority of known mayfly adults. A common, modern epibenthic form, the Baetidae, is virtually absent from Paleogene aquatic faunas. Paleogene odonatan assemblages exhibit minimal similarity with those of today when compared to other aquatic insect lineages (Zherikhin and Sinitshenkova 2002). The relative rarity of Lestidae (spreadwing damselflies), Coenagronidae (narrow-winged damselflies), Corduliidae (emerald dragonflies) and Libellulidae (darner dragonflies) are in stark contrast to the abundance of these lineages in extant aquatic faunas. Naiads are rare in Paleogene aquatic deposits, whereas they are much more common in Neogene faunas, a pattern mirrored by ephemeropterans and attributable to styles of preservation in lacustrine deposits rather than any intrinsic biologic cause.

Paleogene Plecoptera are represented principally by adults in resins and are referable to extant genera. These fossil Plecoptera probably were confined to lotic habitats, consistent with the rarity of their naiad stages in lentic deposits. Apparently, stoneflies do not exhibit any shift in taxonomic proportions between the Paleogene and Neogene (Zherikhin and Sinitshenkova 2002), and display a dominance similar to corixids and notonectids. Aquatic bugs (Hemiptera), unlike paleopterous taxa, are common in Paleogene deposits, where they are often numerically dominant. Similarly, aquatic beetles are diverse in the Paleogene, but are marked by the absence of the algivorous Haliplidae and the overwhelmingly presence of the Hydrophilidae and Dytiscidae, particularly during the Oligocene. Aquatic megalopterans and neuropterans are represented only by extinct genera, and aquatic mecopterans have not been documented.

In contrast to several modern aquatic groups that were uncommon during the Paleogene, the Trichoptera were quite common in local assemblages. All Paleogene taxa have been assigned to modern lineages, many which consist of extant genera (Sukatcheva 1982; Wichard and Weitschat 1996). However, there is a significant difference in family-level dominance between the Paleogene and Neogene assemblages, and in compression versus resin deposits, with the Oligocene being a transitional interval. During the Paleogene, the currently dominant families, the Hydropsychidae (net-spinning caddisflies), Leptoceridae, and Limnephilidae (northern caddisflies) are either rare or absent. Similarly, the diversity of caddisfly cases are rare when compared to the Cretaceous or present-day levels (Zherikhin and Sinitshenkova 2002). Some of these taxa may have colonized floating algal mats (Ponomarenko 1996) or dwelled amid the floating leaves, as appears to be the case for fossils from earliest middle Eocene Paleolake Messel (Lutz 1991).

The Paleogene aquatic dipteran fauna is particularly depauperate in culicids, chironomine chironomids (nonbiting midges), and higher brachyceran taxa. However, the abundance of the enigmatic botfly-like larvae of *Lithohypoderma* continues to elude taxonomic placement and ecologic understanding (Stokes 1978; Sinitshenkova 2002). Culicids (mosquitoes) and brachyceran taxa became more abundant during the Oligocene. Toward the Oligocene–Miocene boundary, the aquatic fauna attained an even more modern cast than in the previously described Paleogene assemblages.

Paleogene aquatic angiosperms continued to be dominant in ponds and lakes, forming diverse assemblages and displaying increased provincialism (Martín-Closas 2003). Aquatic ferns also exhibited further diversification (Schneider et al. 2004), whereas taxonomic turnover within the Characeae took place during the Paleogene (Martín-Closas 2003). Further extinctions and replacements occurred within the charophytes later in the Cenozoic. Aquatic bryophytes became common in shallow lakes and swamps (Mai 1995). The most significant changes, however, are those experienced by lacustrine phytoplankton, essentially by expansion of freshwater diatoms and chrysophytes during the Eocene (Martín-Closas 2003; Wolfe and Edlund 2005; Sims et al. 2006; Leliaert et al. 2011). During the Neogene, diatoms clearly dominated over the Chlorococcales (Martín-Closas 2003; Sims et al. 2006). The overall ecologic impact of the colonization of freshwater bodies by diatoms cannot be overemphasized. In particular, diatoms typically exert a significant effect on the biogeochemical cycling of silica, promote a diversion of other nutrients into other trophic pathways and increase overall lacustrine productivity (Cohen 2003).

One of the most highly investigated Cenozoic lacustrine deposits is the series of four major paleolake basins that form the Green River Formation in the Western Interior of the United States. The Green River Formation is dated from ca. 54.0–43.5 Ma (Smith ME et al. 2008b), and consists of a mixture of open lacustrine, lake-margin lacustrine, shallow playa, carbonate mudflat, fluvial, deltaic and alluvial deposits (Ferber and Wells 1995; Chetel and Carroll 2010; Aswasereelert et al. 2013). The Green River Formation is assigned to Cenozoic Lake Assemblage Type 8 (Zherikhin and Sinitshenkova 2002), dominated by brachyceran fly larvae with few, if any, other aquatic insects (Zherikhin and Sinitshenkova 2002). Green River fossils overwhelmingly preserve land-based organisms, especially plants, insects, and vertebrates, to the near exclusion of autochthonous aquatic organisms (Wilson 1978), which likely was taphonomically modulated by depositional biases favoring terrestrial taxa (Smith, 2000, 2008). The insect fauna is very diverse, consisting of about 26 of the ca. 35 modern recognized orders for the Piceance Creek Basin of the Green River Formation (Pribyl et al. 1996). The apparently under-represented aquatic insect fauna is autochthonous, but only consists of several major lineages of mostly nematocerous Diptera, principally tipulids, cylindrotomids, culicids, chironomids, and the occasional aquatic beetle. In spite of the extensive geographic coverage and numerous fossiliferous strata, there is only minor representation of lotic and lentic fossils from the Green River Formation. Nevertheless, three families of dragonflies are represented (Wilson 1978; Petrulevičius et al. 2007), two families of Hemiptera, two families of beetles, four families of nematocerous Diptera and the enigmatic *Lithohypoderma* "botfly" (Pribyl et al. 1996; Sinitshenkova 2002). The Trichoptera includes the Hydropsychidae, Hydroptilidae (micro caddisflies), Limnephilidae, and Sericostomatidae. The particular reason for such an under-representation of the lentic and lotic fauna, especially when adjacent terrestrial insects are exceedingly abundant by comparison, is likely attributable to the role of size in the formation of live versus death assemblages of insects. In the Green River biota, death assemblages that become incorporated in the fossil record are smaller sized and more robust than live equivalents (Smith 2000). Although the role of size and robustness applies to beetles (Smith 2000), it is unclear if such a relationship also applies to softer-bodied, more gracile insects that are often disarticulated prior to sediment burial.

The taxonomic composition and ecologic structure of Neogene paleolakes is very similar to that of modern lakes (Zherikhin and Sinitshenkova 2002). Many modern aquatic species occur throughout the Neogene. A few extinct insect clades are known, such as the subfamily Electrobatinae of the Gerridae and the coral bug species *Halovelia electrodominica*, both from early Miocene Dominican Amber; the coeval dytiscid genus *Palaeogyrinus* from Germany; several extinct aquatic taxa of the Megaloptera and Neuroptera, including the species *Sialis strausi* from the Pliocene of Germany; and several new caddisfly case morphotypes that are difficult to attribute to potential modern or extinct genera (Illies 1967; Galewski and Glazek 1997; Sukatcheva 1982; Anderson 1998). Throughout the Miocene, these occurrences do not represent any significant change in aquatic insect community characterization, a conclusion buttressed by the similarity of overall lake ecologic structure between the middle Eocene and the present (Dunne et al. 2014), indicated in Fig. 11.13.

There is evidence for an increase in lentic habitats and their biotas at the beginning of the Neogene. This extension is indicated by greater submergent and emergent angiosperm vegetation that increased habitat structural complexity, resulting in an expansion of herbivory, greater constancy of O_2 levels and nutrient cycle stability (Zherikhin

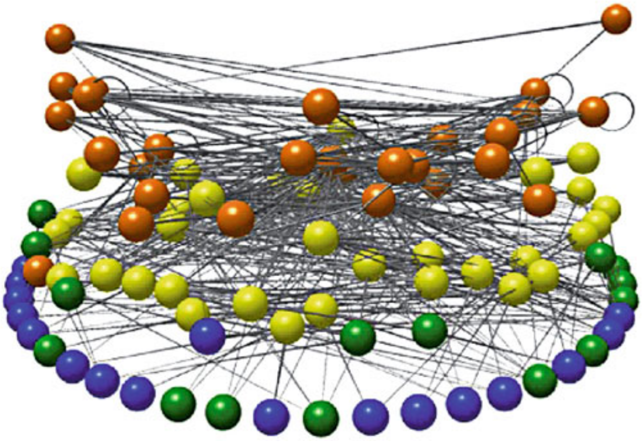


Fig. 11.13 Visualization of the middle Eocene (48 Ma) food web of Paleolake Messel, in central-west Germany, representing a post MLR lake. Spheres designate trophic taxa and lines represent feeding links. A trophic taxon is a species or group of species (in the case of microorganisms) that have links to organisms that consume it and to other organisms that it consumes. Plants have links only to their consumers. Looped links refer to cannibalism. The vertical axis corresponds to short-weighted trophic level, with autotrophic taxa and detritus at the bottom. The colors of nodes indicate the taxonomic assignment of species: green = plants, algae and diatoms; blue = bacteria, fungi and detritus; yellow = invertebrates; orange = vertebrates. This image was produced with Network 3D software (Williams 2010), and reprinted with permission from the Royal Society

1978; Kalugina 1980). Nevertheless, special sedimentary environments occupying spatially small areas could have hosted aquatic communities of distinctive taxonomic composition and ecologic structure. Examples of these biotic microcosms include small bodies of water associated with sinter structures, ponds in asphaltum depressions, karst sinkholes, impact craters, and pits created by subsurface diatreme explosions. Such deposits are typically spatiotemporally ephemeral and constitute a very minor part of the lacustrine record that is represented preferentially toward the recent.

11.7 Discussion

There are four issues about the MLR that necessitate further discussion. The first issue is whether the MLR is indirectly or directly connected to other obvious, major biotic events during the mid Mesozoic, such as the Mesozoic marine, parasitoid, angiosperm, and Cretaceous terrestrial revolutions. The second issue is to what extent did the MLR involve not only a change in the diversity and abundances of participating fossil groups, but also their effect on the sedimentological record through the increased variety of ichnotaxa and bioturbation intensities recorded from well sampled sections. A third issue is how modern lacustrine trophic webs were established. These trophic webs are recorded in a well-examined Paleogene lake deposit, but also should be present in earlier, mid-Mesozoic food webs. Finally, what is the role of behavioral convergence in shaping the aquatic marine and continental trace fossil records, and to what extent should ichnotaxonomic nomenclature be applied across the marine/continental divide to very similar trace fossils that involve convergent morphologies (and presumably behaviors).

11.7.1 Possible Connections to Other Mesozoic, Biotal Revolutions

Other than the MLR, four other, major biotic revolutions occurred during the mid to late Mesozoic: the Mesozoic marine revolution in the marine realm and the parasitoid, angiosperm and Cretaceous terrestrial revolutions in the continental realm. These mid-Mesozoic, global ecologic shifts may have had an effect on the MLR that may be relevant to the development of lacustrine food webs throughout the later Mesozoic. The possible connections among these five prolonged events may shed light on the shift of detritivore- to herbivore dominated ecosystems in lacustrine and other freshwater habitats during the mid Mesozoic.

One of the aspects involved in the Mesozoic marine revolution (see Chap. 9) was the notable increase in mechanical sturdiness and increased robustness of other structural features that promoted the resistance of shells, principally gastropods, to crushing by predators (Vermeij 1977; Stanley 1977). Major structural transformations favored durable shell architecture of molluscan prey, and involved new modes by mostly arthropods and teleost predators of pursuing, capturing, and overcoming the mechanical defenses of their prey. Another aspect of the Mesozoic marine revolution was intensification of marine herbivory, such as grazing on algae at relatively shallow and subsurface depths. Added to the expansion of durophagy and grazing pressure was increased predation in benthic communities that led to infaunalization of many former epibenthic groups, as well as a significant reduction of the sessile life habit (Stanley 2008). The major consequence of these innovations has been the relegation of their certain life forms to extinction or to refugial habitats (Oji 1996), and the occupation of their adaptive zones by competitively superior, new, predatory groups (Vermeij 1977; Stanley 1977). This worldwide marine reorganization has been linked to continental breakup, widening of latitudinal belts, and the emergence of angiosperms on land (Vermeij 1977).

The parasitoid revolution is based on an observation that the first appearances of several major clades of parasitoid insect clades occur primarily during the mid Jurassic (Labandeira 2002). Parasitoids are a distinctive type of carnivore in which a small, invading organism attaches to or lives on or in an animal and slowly feeds on internal tissues and organs of their relatively long-lived but still alive host. The much smaller parasitoid feeds on host such that the most vital organs are consumed immediately before the host dies, followed by its emergence from the host as an adult parasitoid (Vinson and Barbosa 1987). Parasites, by contrast, such as mosquitoes do not kill the host, but use host tissues such as blood to feed on. For insects, the actively feeding parasitoid stage is always a holometabolous larva, overwhelmingly a parasitoid wasp, and less frequently a brachyceran fly. Parasitoids may feed on their hosts internally (endoparasitoids) or externally (ectoparasitoids) and attack arthropod hosts, such as myriapods, arachnids, especially insects, and some vertebrates (Godfray 1994). The earliest appearance of the parasitoid guild was the mid Early Jurassic, during which several clades of parasitoid wasps appear. This was followed and supplemented by more modest brachyceran dipteran diversification and the massive radiation of several parasitoid superfamilies during the Late Jurassic, and continued with the addition of occasional neuropteran, beetle, and lepidopteran parasitoid lineages into the Paleogene (Labandeira 2002).

A major consequence of the parasitoid revolution was the increased complexity of food webs by insertion of a significant more efficient mode of carnivory. This greater efficiency resulted from the targeting of particular species of prey by a host-specific parasitoid using specific chemical, behavioral, visual, and other cues emanating from prey. With the proliferation of the host-specialist, parasitoid feeding guild that originated during the mid Mesozoic, carnivory became considerably more targeted than was the case for food webs earlier in time based solely on diffuse generalist predation patterns (Labandeira 2002). This ecological shift resulted in consumer-driven, top–down regulation of herbivores, rather than bottom–up, resource-driven regulation, based on modern food-web studies (Dunne et al. 2002). In modern ecosystems, parasitoid loads on insect herbivores are elevated (Memmott and Godfray 1993), and are much more efficient at assimilating prey biomass into consumer biomass than either predators such as dragonflies or parasites such as fleas or lice (Eggleton and Belshaw 1992). In lacustrine systems, unionacean and mytilacean bivalves are dispersed in their larval stages as ectoparasites on fish; some copepod and isopod crustaceans are also parasitic on fish, as well as certain flatworms and trematodes (Cohen 2003). One of the major effects of the parasitoid revolution on lake biotas was to further separate immature aquatic stages of insects from their adult terrestrial counterparts. Additional work needs to be done to properly address the importance of parasitoids in lacustrine food webs.

The angiosperm revolution consists of the early, major diversification interval of flowering plants, ranging during the mid Cretaceous from 125 to 90 million years ago (Crane et al 1995). The angiosperm revolution had a major effect on terrestrial ecosystem structure (Wing and Boucher 1998). The emergence of numerous clades of angiosperms over a ca. 35 million-year interval resulted in a major replacement of fern- and gymnosperm dominated floras by angiosperms in most habitats globally (Crane 1987), including aquatic settings (Wing and Boucher 1998).

The Cretaceous terrestrial revolution is directly connected to and may be a consequence of the angiosperm revolution because it encompasses not only the evolutionary radiation of land-dwelling organisms, but involves the replacement of ferns and gymnosperms by angiosperms (Lloyd et al. 2008). Therefore, the comments outlined for the angiosperm revolution are prefatory to the Cretaceous terrestrial revolution. Together with the rapid expansion of flowering plants, the Cretaceous terrestrial revolution includes the diversification of herbivorous and social insects (see Chap. 13), squamates, birds, and mammals (Lloyd et al. 2008). However, these authors (Lloyd et al. 2008) questioned the notion that dinosaur evolution was driven directly by angiosperm diversification. From an ichnologic standpoint, the appearance of trampled surfaces is a direct consequence of the expansion of dinosaur faunas that significantly altered lake-margin landscapes.

Both the Mesozoic marine revolution and the parasitoid revolution provided a greater efficiency in the conversion of prey biomass into consumer biomass. The angiosperm and Cretaceous terrestrial revolutions expanded the amount of photosynthetic biomass created by a new group of primary producers that had a major global impact. The MLR was characterized by increased infaunalization and a major trophic shift from detritivore-based to herbivore-based foodwebs in lacustrine and other terrestrial aquatic ecosystems. However, the detritivore to herbivore shift occurred much earlier in terrestrial ecosystems than in aquatic ones (Vermeij and Lindberg 2000; Miller and Labandeira 2002) – a shift that was already noticeable during the Permian (Labandeira 2006). This is not surprising, as in the continental realm, aquatic ecosystems always have been lagging behind terrestrial ecosystems in other features such as species diversity, trophic relationships, and food-web development (Vermeij and Lindberg 2000; Sinitshenkova 2002). Nevertheless, it is unclear whether there are satisfactory explanations invoking cause-and-effect links among any of these four major revolutions to lacustrine ecosystems.

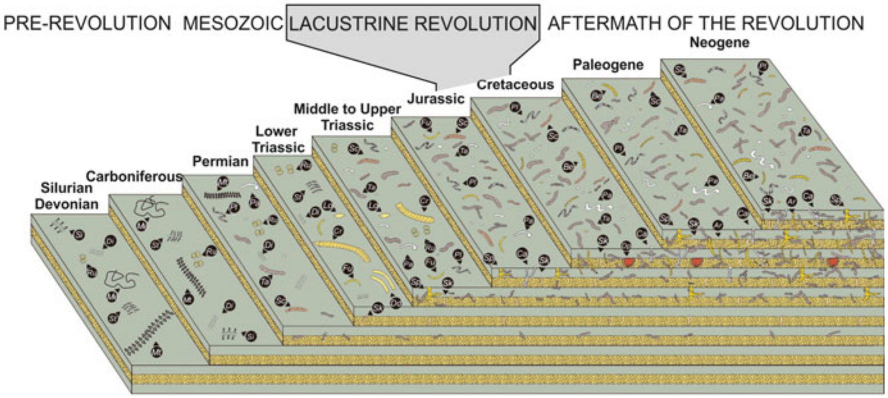
11.7.2 Secular Changes in Global Ichnodiversity and Bioturbation

A systematic review of the ichnologic record indicates that the MLR is expressed not only by body-fossil data. Ichnologic evidence demonstrates that colonization of freshwater habitats has been a protracted process (Buatois and Mángano 1993a;

Buatois et al. 1998a), with the MLR representing a pivotal point (Cohen 2003) (Table 11.2). Freshwater colonization may have been delayed due to the need to develop complex osmoregulatory systems and innovative styles of reproduction and dispersal (Miller and Labandeira 2002).

Unlocking the evolutionary significance of the lacustrine trace fossil record requires integration of several conceptual and methodological tools. Patterns of change in global ichnodiversity may be misleading, and should not be analyzed in isolation (Buatois and Mángano 2013; see Chap. 16). Mesozoic global invertebrate ichnodiversity in lacustrine environments does not show any significant increase with respect to late Paleozoic levels (Buatois and Mángano 1993a; Buatois et al. 1998a), in contrast to what may have been expected by diversity curves based on body fossils (Labandeira 2005b). Indeed, whereas global ichnodiversity levels for fully lacustrine environments have remained more or less constant since the Carboniferous, global ichnodiversity of lake-margin settings is actually higher in the late Paleozoic than in the Mesozoic. However, it often has been suggested that the Permian ichnodiversity peak reflects at least in part splitting tendencies in arthropod trackway taxonomy (see discussion in Buatois et al. 1998a and Chap. 6). Also, the fact that diversity trajectories for body and trace fossils are markedly dissimilar is not unexpected. The three groups that diversified the most – aquatic insects, aquatic macrophytes, and teleosts – are unevenly represented in the ichnologic record. Aquatic insects are thought to have been widespread tracemakers; some fish (e.g. cichlids) may contribute locally to sediment disturbance (Feibel 1987; Martin et al. 2010; Abbate et al. 2012); and aquatic macrophytes are represented by root structures but technically do not contribute to ichnodiversity. (No formal ichnotaxonomic names are given to root trace fossils.) In addition, it long has been recognized that equating ichnodiversity with biological diversity is fundamentally misleading, and one-to-one correspondences between ichnotaxa and biotaxa is simply not possible (Bromley 1996). This is particularly true for very simple structures (Buatois and Mángano 2011a), which tend to be dominant in lacustrine settings.

However, an evaluation of changes of ichnodiversity that parallel changes in intensity and depth of bioturbation may be illuminating. In both lake-margin and fully lacustrine deposits, an increase in extent and depth of bioturbation long has been recognized (Miller 1984; Buatois and Mángano 1993a; Buatois et al. 1996, 1998a; Miller and Labandeira 2002; Miller et al. 2002) (Fig. 11.14). In lake-margin settings, trace fossils of the *Scoyenia* ichnoguild became more abundant, leading to increased sediment mixing since the Middle Triassic (Buatois et al. 1998a). In addition, a stationary deep crayfish infauna , referred to as the *Camborygma* ichnoguild, was established by the Triassic, further contributing to destruction of primary sedimentary fabric. This is in sharp contrast with the situation of Paleozoic lake-margin deposits, which overwhelmingly are dominated by very shallow-tier trace fossils, mostly arthropod trackways (Buatois and Mángano 1993a; Buatois et al. 1998a; see Chap. 6). Arthropod trackways, although locally present in Mesozoic lake-margin deposits, are never dominant components, and they essentially disappeared from the Cenozoic lacustrine trace-fossil record with the exception of glacial lakes, where they tend to occur in distal facies rather than in lake-margin deposits (Uchman et al. 2009). Seilacher (2008) underscored the importance of bioglue for trackway preservation, Lake margin



Fully lacustrine

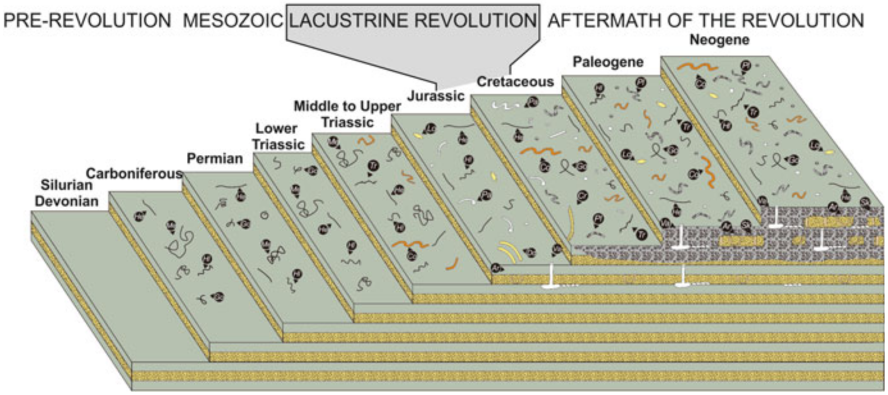


Fig. 11.14 Secular changes in bioturbation in lake-margin and fully subaqueous lacustrine deposits. Note progressive colonization of the infaunal ecospace through time

suggesting that the scarcity of trackways in post-Paleozoic lake-margin deposits may have resulted from the appearance of a bioturbating meiofauna, therefore precluding the formation of coherent biofilms. In any case, it is clear that there is a negative correlation between diversity of shallow-tier trace fossils and intensity and depth of bioturbation. This trend also has been noted for tidal flats, which display high diversity during the late Paleozoic due to a richness of shallow-tier structures and decreased ichnodiversity during the Mesozoic–Cenozoic, with ichnofaunas characterized by deeper-tier structures (Mángano et al. 2002; Mángano and Buatois 2015). This decrease in tidal-flat global ichnodiversity is arguably a taphonomic product resulting from increased colonization of infaunal ecospace (Mángano et al. 2002; Buatois and Mángano 2011a; Mángano and Buatois 2015). A similar argument can be posited to explain the post-Paleozoic decrease in global ichnodiversity in lake-margin deposits.

In fully lacustrine settings, a similar increase in intensity and depth of bioturbation is apparent throughout the Mesozoic, although changes seem to have been slightly more gradual, lagging behind those in lake-margin environments. During the Middle to Late Triassic, assemblages dominated by very shallow-tier grazing trails, not unlike those of the late Paleozoic, were still common (Metz 1995, 1996, 2000; Melchor et al. 2003; Melchor 2004). However, the simultaneous appearance of penetrative trace fossils is evidenced by systems of irregularly branched burrows, most likely produced by oligochaetes or insect larvae (Voigt and Hoppe 2010). The high density of these burrows contributed locally to disruption of the primary fabric, generating patches of intense bioturbation in lacustrine mudstones. Branching burrows occur in Lower Jurassic turbidites as well, reflecting the establishment of the *Vagorichnus* ichnoguild, which represents the activity of a mobile, mid-tier, deposit-feeding infauna (Buatois et al. 1995, 1996). These mid-tier trace fossils persisted in Cenozoic lacustrine deposits (Uchman et al. 2007). Interestingly, although Lower Jurassic turbidites contain many ichnotaxa (e.g. *Cochlichnus*, *Helminthopsis*) common in older deposits, these are more robust and produced infaunally, reflecting penetration into the sediment and unlike those of the late Paleozoic. In the example of the *Vagorichnus*-bearing deposits, the increase in maximum bioturbation depth is not associated with an increase in bioturbation intensity. The decoupling of bioturbation depth and intensity of bioturbation results from the observation that these burrow systems were emplaced at lithologic interfaces without causing major disturbance of the primary sedimentary fabric (Buatois et al. 1995, 1996).

This pattern contrasts with Cretaceous ichnofaunas, which include pervasive mottlings reflecting establishment of a shallow-tier deposit-feeding infauna, referred to as the *Planolites* ichnoguild. The high density of these structures caused major disruption of lacustrine sedimentary fabrics (Buatois and Mángano 1998; Buatois et al. 1998a). These observations may suggest that the establishment of the mixed layer in these settings is a result of the MLR. Although further work needs to be done to detect the exact timing of formation of the mixed layer, sparse data suggest that this sediment zone was already incipiently developed in lake bottoms by the Middle to Late Triassic and well established by the beginning of the Cretaceous. As is the case of lake-margin deposits, the appearance of these active bioturbators was detrimental for the preservation of very shallow-tier structures. In any case, biogenic homogenization of the lacustrine bottom sediments is not a universal phenomenon, as indicated by the dominance of very shallow-tier trace fossils, in pristinely preserved, sedimentary fabrics of other Lower Cretaceous lacustrine deposits (de Gibert et al. 2000, 2016; Buatois et al. 2000a), as well as in modern glaciolacustrine varves (Gibbard and Stuart 1974; Uchman et al. 2009). Studies in other modern lakes, such as the Great Lakes in North America, indicate up to 10 cm of deep reworking by insects, oligochaetes, bivalves, and amphipods (McCall and Tevesz 1982; Miller and Labandeira 2002), suggesting a well-established mixed layer.

The pattern of increased infaunalization during the MLR is empirically well supported, but the underlying causes remain more speculative. As a first approach, the increase in sediment penetration and disruption during the MLR is connected with the expansion and diversification of certain groups of benthic aquatic organisms, most likely dipterans (such as chironomids), which together with oligochaetes, are among the key bioturbators in modern lacustrine settings (McCall and Tevesz 1982; Duck and McManus 1984; Wootton 1988; Evenhuis 1994; Buatois et al. 1998a). At a deeper explanatory level, one may invoke protection from environmental disturbance, escape from predators and increased rates of buried organics as potential causes of infaunalization. It long has been known that burrowing is a key strategy intended to minimize environmental stress, such as salinity variations and sediment disturbance by currents or waves (see Buatois and Mángano 2011a for discussion). However, environmental disturbance may only work as an explanation for infaunalization at a local scale. In a situation such as the MLR, infaunalization occurred globally and no overarching disturbance factor can be associated with this macroevolutionary trait, therefore precluding protection from environmental disturbance as a likely causal factor of infaunalization. In contrast, the link between increased predation pressure and infaunalization seems to be a more robust explanation because the former is considered a driving force in macroevolution, with the infaunal ecospace serving as refugium for predation. As discussed above, the coincidence between increased predation and infaunalization during the MLR is consistent with a causal link. The possibility that infaunalization can be linked to exploitation of increasing amounts of organic matter buried within the sediment cannot be disregarded. Higher quantities of food supply may have resulted from increased eutrophication in lacustrine systems combined with increased delivery of terrestrially derived and aquatic organic matter resulting from macrophyte diversification. Indeed, nutrient availability may be regarded as an overarching factor controlling lacustrine ecospace utilization in deep time (Cohen 2003). The ultraoligotrophic conditions predominant during the early Paleozoic were most likely the key limiting factor preventing colonization of lacustrine bottoms, a situation that started to change during the late Paleozoic, albeit with colonization limited to a narrow inhabitable zone close to the sediment–water interface (Buatois and Mángano 1993a; Buatois et al. 1998a). Finally, it may be argued that invoking complex geobiologic feedbacks between bioturbation and a wide range of abiotic to biotic factors (e.g. Mángano and Buatois 2014) probably is more realistic than strict causal linkage. In the case of the MLR, the timing of events suggests that the interplay of increased predation pressures and food availability may have been the casual drivers forces in lacustrine infaunalization.

To summarize, whereas the Paleozoic is characterized by an increase in global ichnodiversity as a result of the progressive colonization of continental environments (Buatois and Mángano 1993a; Buatois et al. 1998a; see Chap. 6), the ichnologic expression of the MLR is one of increased colonization of infaunal ecospace (Table 11.2). This is reflected by an increase in both degree and depth of bioturbation, although these increases occurred first in lake margins and subsequently in fully lacustrine settings. In addition, the increased intensity of bioturbation lagged behind greater penetration in burrowing depth in both settings. For further evaluation of the evolutionary significance of the MLR, we turn now our attention to trophic webs.

11.7.3 The Establishment of Modern Lacustrine Trophic Webs

Biotic interactions are of fundamental importance to understand ecosystem structure and function in lakes. In particular, deciphering food webs, the complex networks among predators, herbivores, autotrophs, and detritus/deposit feeders is a central issue in reconstructing the biotic dynamics of lakes. Experimental studies show that lacustrine food webs reflect an interplay of both bottom–up and top–down selective pressures. Bottom–up processes involve food/nutrient resource availability and competition for those resources whereas top–down processes involve trophic cascades in which predation and selective consumption are the main regulators of community structure (Carpenter and Kitchell 1993). Various groups of benthic invertebrates, including crustaceans, mollusks, annelids, and larval insects play important roles in mediating energy flow, nutrient cycling, and the ingestion of organic and inorganic detritus and fecal production (reflected to some extent by bioturbation) that is a central component of lacustrine food webs (Charbonneau and Hare 1998; Covich et al. 1999; Voigt and Hoppe 2010). However, from an energetic point of view, the importance of planktonic and nektonic components of the lacustrine food web is probably much greater (Schweitzer et al. 2007).

Accordingly, exploring the timing of the establishment of the modern lacustrine food web and its potential connection with the MLR may yield insights into the evolutionary history of lake ecosystems. There is little known about Early Triassic lakes or their fossils. Late Middle–early Late Triassic Paleolake Madygen, discussed earlier (Voigt et al. 2006), included organisms representing at least five trophic levels (Fig. 11.15). Phytoplankton (of which there is no fossil evidence as yet) and macrophytes (e.g., *Ricciopsis*, *Neocalamites*, and some lycopsids) were presumably the major primary producers. An important external source of food must have been dead

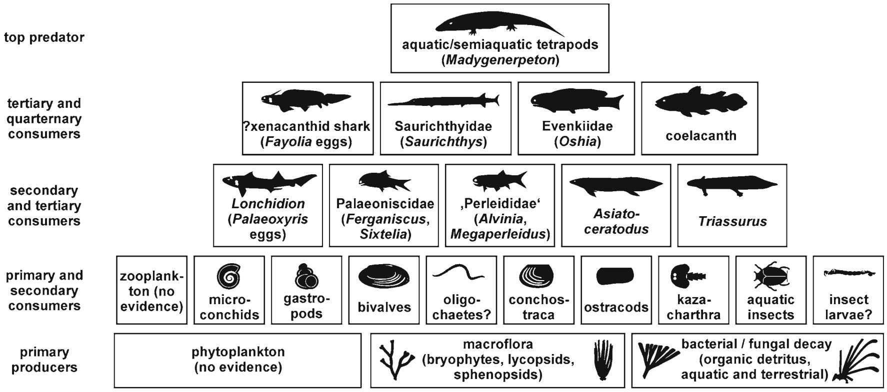


Fig 11.15 Ecosystem of the Madygen Formation of Kyrgyzstan. Trophic levels and their respective constituents as proposed for the Triassic Madygen lake environment. Note the absence of macro herbivores After Voigt et al. (2006, 2016)

organic matter (e.g., plants, insects, tetrapods) transported from the land into lakes. Zooplankton (of which there is no fossil evidence as yet), microconchids, gastropods, bivalves, conchostracans, ostracods, kazakharthrans, certain insects (schizophorid beetles), and wormlike aquatic invertebrates such as oligochaetes or particular insect larvae, based on indirect evidence from trace fossils, are interpreted as primary consumers. These organisms in turn served as food for a variety of fishes including actinopterygians (Palaeoniscidae, "Perleididae"), dipnoans (*Asiatoceratodus*), and durophagous sharks (*Lonchidion*). Four large carnivorous fishes – *Saurichthys*, *Oshia*, a currently unknown xenacanthid (suggested by *Fayolia*-type egg capsules), and coelacanths – can be considered tertiary consumers. The semi-aquatic reptiliomorph *Madygenerpton* may have been the apex predator of Paleolake Madygen. This system shows clear evolutionary innovations when compared to Paleozoic lakes, as it represents among the earliest known record of a well-developed, deep lacustrine infauna (Voigt and Hoppe 2010), and documents a quantitatively important pattern of macrophytic colonization of the shoreline (Moisan et al. 2012a).

Although energy-flow diagrams have not been constructed for a Late Triassic lake, coarse-grained trophic webs have been estimated for the biota of a hypotrophic (low primary production, high O_2) Middle Jurassic lake (Fig. 11.6; Sinitshenkova and Zherikhin 1996), and for a pseudoligotrophic (high O_2 but with an active herbivore guild) Early Cretaceous lake (Fig. 11.10; Zherikhin et al. 1999). These data indicate that there was a major shift in lacustrine productivity and biotal complexity later in the Mesozoic (Table 11.1). However, it appears that these changes likely began during the Late Triassic. The trophic structure of the Jurassic *Mesoleuctra–Mesoneta* Assemblage (Sinitshenkova and Zherikhin 1996) occurred throughout the warm temperate region of Siberia and other Eurasian and perhaps Gondwanan Jurassic localities (Sinitshenkova 2002). In the lowlands at temperate latitudes, particularly in Eurasia, these shallow, hypotrophic (type B) lakes of the Jurassic consisted of depauperate lentic and lotic faunas that allowed high O_2 levels to accumulate, and with a near exclusive trophic emphasis on detritivory (Fig. 11.6). The high abundance of O_2 throughout these hypotrophic lakes, and particularly the benthos, is attributable to the absence of respiring organisms to sufficiently take up the O_2 that was being produced by autotrophic microorganisms (Sinitshenkova and Zherikhin 1996). In addition, Sinitshenkova and Zherikhin (1996) state that these lakes were littered with incoming ginkgoalean and czekanoskialean plant detritus that exerted a negative control on productivity of the lake by having an antimicrobial effect on decomposers, judging by the negative effect that modern *Ginkgo biloba* litter has on modern lake productivity (Samylina 1988). Consequently, productivity in these lakes had two, related features: there was poor development of a detritivore base, in part likely hindered by the dominant terrestrial vegetation of the time that favored build-ups of O_2. In addition, there was absence of large, especially vascular, hydric plants that would allow herbivores to expand herbivory, as seen in later Cretaceous lakes (Fig. 11.10). The subsequent changeover is notable, particularly establishment of a guild of grazing herbivorous organisms, present in pseudoligotrophic Paleolake Baissa, a type C lake but also with high O_2 levels, is notable. This shift during the mid Early Cretaceous from a detritivore-based to herbivore-driven food web, occurred in the switch from Type A and B to Type C to E lakes, documented in Eurasia, and is probably the single most important event associated with the MLR. The ecologic structure of Early Cretaceous Paleolake Baissa differs significantly from that of its predecessor lacustrine biotas during the Jurassic (Table 11.1).

The basic trophic structure of Cretaceous Paleolake Baissa was a highly productive, pseudo-oligotrophic lake in which there were relatively low levels of dissolved nutrients supporting an abundant and diverse standing crop of green plants, especially algae. Paleolake Baissa apparently is a lake type without a clear modern analog. The algae was limited by high consumption levels, but promoted a complex, herbivore-based food web within an ecosystem of de-emphasized detritivore food chains (Sinitshenkova 2002). The elevated O_2 levels were sufficiently depressed to allow a diverse, detritivorous insect fauna (Zherikhin et al. 1999) at greater depths in the water column, the hypolimnion. At intermediate depths, in the mesolimnion, but below the surface-water layer of the epilimnion, there was an herbivore community of grazing and algivorous gastropods and insects, including case-bearing caddisflies, which were supported by abundant and diverse benthic, planktonic, and floating algae (Sinitshenkova 2002). Paleolake Baissa was an early lake ecosystem where aquatic invertebrate herbivory played a significant trophic role. Other coeval deposits of similar origin are the lacustrine beds of the Yixian Formation in China (Barrett 2000; Pan et al. 2011) and the Las Hoyas wetland deposits of Spain (Buscalioni et al. 2016 and references therein).

In particular, the Las Hoyas fossil site, which is now interpreted as a freshwater carbonatic, lentic wetland, has been analyzed recently from a trophic-web approach (Buscalioni et al. 2016). According to this study, hydrophytic vegetation is dominated by charophytes and aquatic angiosperms. The large mass of hydrophytic plants allowed the presence of abundant grazers, such as ostracods, gastropods, spelaeogryphaceans, and aquatic insects, pointing to the importance of herbivory in this trophic web, as is the case of Paleolake Baissa. Various worm-like organisms have been regarded as feeding on phytoplankton and zooplankton, whereas unionid bivalves were suspension feeders and crayfish are considered omnivorous scavengers. Some large aquatic insects may have preyed on fish larvae and medium-sized fish consumed various aquatic insects. Buscalioni et al. (2016) also emphasized the importance of insects and fish in lake productivity, which is consistent with data from modern wetlands.

During the Cretaceous, physical and chemical lake conditions exhibit a major shift favoring development of certain lake types based on a variety of physiochemical conditions. These features were increased aridity, greater topography, more unstable and variable lake levels, enhanced variability in annual temperature, greater water-column stratification, and higher water turbidity. Chemical indicators show elevated nutrient levels, a tendency toward alkaline over acidic water *p*H’s, and more variable and lower dissolved oxygen levels. These physiochemical shifts provided an opportune environment for biotal changes, such as less allochthonous plant detritus as input, much greater turnover rates, higher microbial activity, and considerably higher algal production, but anomalously, lower macrophyte production. For food-web development, there was a shift from detritivore to herbivore processing of primary productivity (via more intensive levels of herbivory), greater complexity of food webs, and an emphasis from K-selected to r-selected evolutionary strategies. Among benthic insects there was a trophic shift from shredders and scrapers to filter-feeding and live-plant ingesters as the dominant feeding types (Sinitshenkova and Zherikhin 1996).

Finally, a recent examination of the 48 million-year-old deposit of Paleolake Messel, near Darmstadt, in central Germany, produced an exhaustive food-web analysis that was made for 94, well-documented organisms, including amphibious taxa, that constituted the lake portion (Fig. 11.13) of the total food web (Dunne et al. 2014). This study provides valuable information on food webs in the aftermath of the MLR. The Messel lacustrine web was constructed by using highly-resolved, well-documented data of feeding relationships among all taxa. The lacustrine food-web data from Messel indicate an ecologic structure very similar to modern lake webs, and notably, a stability of trophic relationships that were likely in place shortly after the K-Pg extinction (Dunne et al. 2014). However, the fact that Chlorococcales dominated over diatoms in Paleolake Messel represents a departure from the situation in modern lakes.

11.7.4 Behavioral Convergence Between Marine and Continental Benthic Fauna

A comparison between marine and lacustrine ichnofaunas suggests that use of freshwater infaunal ecospace may have been less complete than in marine environments (Miller and Labandeira 2002). In addition, levels of ichnodiversity and complexity of biogenic structures are significantly lower in lakes than in marine settings (Buatois and Mángano 1998). Evaluation of the extent and limitations of behavioral convergence on both sides of the salinity barrier may help to understand evolutionary constraints on the lake colonization process.

Ichnotaxonomic problems undoubtedly prevented an adequate recognition of the similarities and differences between the marine and continental realms. There are two sides to this problem: uncritical use of marine ichnotaxa in continental settings and unsupported erection of new ichnotaxa apparently exclusive to continental settings. Whereas the former has contributed to the overemphasis of behavioral convergence, the latter promoted its lack of appreciation. This is essentially an issue with freshwater, rather than terrestrial trace fossils. The vast majority of the latter (e.g. *Coprinisphaera*, *Termitichnus*, *Vondrichnus*, *Celliforma*, *Eatonichnus*, *Castrichnus, Quirogaichnus*) are exclusively found in paleosols, and their ichnotaxonomic intricacies have been clarified by extremely detailed and solid work (e.g. Genise 2000, 2004; Laza 2006).

Freshwater trace fossils tend to be characterized by relatively simple morphologies, typically including facies-crossing ichnotaxa that occur in marine environments (e.g. *Gordia*, *Helminthoidichnites*, *Cochlichnus*). In contrast, there are many ichnotaxa that are restricted to marine environments, including the typical elements of the *Nereites* and *Zoophycos* Ichnofacies and a considerable number of those in the *Cruziana* Ichnofacies (Buatois and Mángano 2007). Arguably, the best example of this confusion is *Scolicia*. This ichnogenus consists of bilobate or trilobate horizontal structures displaying a complex meniscate backfill and two parallel strings, representing the feeding and locomotion activities of irregular echinoids (Smith and Crimes 1983; Uchman 1995; Bromley et al. 1997), which are restricted to the marine realm. Although *Scolicia* has been the subject of a number of taxonomic revisions and is well understood among ichnologists, surprisingly the name continues to be applied for continental, simple epirelief furrows that lack the complex morphology of this ichnogenus (Turner 1978; Hasiotis 2002, 2004; Lovelace and Lovelace 2012). Less commonly, other typical marine ichnotaxa, such as *Paleodictyon*, *Nereites,* and *Chondrites*, are used for much simpler freshwater trace fossils. Structures included in *Paleodictyon* from freshwater settings (e.g. Archer and Maples 1984; Wu 1985; Pickerill 1990) are quite simple, and do not display the regular pattern that characterizes this ichnogenus in marine turbidites. A feeding trace referred to as *Nereites* in lacustrine turbidites (Hu et al. 1998) lacks the internal, complex backfill structure of this ichnogenus, displaying only superficial similarities with *Nereites*. Feeding traces doubtfully assigned to *Chondrites* in lacustrine deposits (Smith et al. 1982; Kim et al. 2005) may superficially resemble this ichnogenus, although the dichotomous, primary successive branching that is diagnostic of *Chondrites* has never been documented in continental settings.

By contrast, some names that have been introduced for freshwater trace fossils fail to pass ichnotaxonomic validation. The classic example is *Isopodichnus*, a combination of short, bilobate resting traces and more continuous bilobate trails. Although *Isopodichnus* was frequently used in the past for continental bilobate trace fossils, recently its use essentially has been abandoned, following convincing demonstration that it is a junior synonym of *Rusophycus* and *Cruziana* (Bromley 1996). More recently, however, meniscate trace fossils present in continental deposits, previously referred informally as “adhesive meniscate burrows” (Hasiotis 2004), were subsequently included in a new ichnogenus, *Naktodemasis* (Smith JJ et al. 2008). However, *Naktodemasis* clearly falls within the diagnosis of *Taenidium* (Krapovickas et al. 2009; Díez-Canseco et al. 2016), an ichnogenus known from marine environments as well.

Behavioral convergence may also be evaluated by examining categories of ichnodisparity (architectural designs) rather than ichnotaxa. Of the 58 architectural design categories defined for invertebrate bioturbation structures (see Chap. 16), none are exclusive to freshwater settings, six are only present in terrestrial settings (vertical to oblique simple ornamented burrows; isolated, clustered, or interconnected cells; chambers with discrete thick linings; excavated chambers with thin linings undetachable from rock matrix; interconnected chambers and boxworks; and Holes, pits and galleries in walls and fillings), and one is shared by terrestrial and marginal-ichnofaunas (Simple to complex burrows with terminal chambers). Indeed, the only ichnogenus in the latter present in both marine and continental environments is *Macanopsis*, which actually occurs in backshore coastal areas, rather than in fully marine settings.

Freshwater ichnofaunas are represented by twenty architectural design categories, all of which also occur in marine environments: (1) simple horizontal trails (*Archaeonassa, Circulichnis, Cochlichnus, Gordia, Helminthoidichnites, Helminthopsis, Herpystezoum, Mermia*); (2) trails with undulating transverse bars and furrows (*Steinsfjordichnus*); (3) bilobate trails and paired grooves (*Cruziana, Didymaulichnus, Diplopodichnus*); (4) trackways and scratch marks (e.g. *Diplichnites, Hamipes, Keircalia, Lithographus, Siskemia, Stiallia, Stiaria, Tasmanadia, Umfolozia*); (5) bilaterally symmetrical short, scratched impressions (e.g. *Avolatichnium, Rotterodichnium, Tonganoxichnus*); (6) bilaterally symmetrical short, scratched burrows (e.g. *Rusophycus*); (7) passively filled horizontal burrows (*Palaeophycus*); (8) simple actively filled (massive) horizontal burrows (e.g. *Planolites*); (9) simple actively filled (meniscate) horizontal burrows (e.g. *Scoyenia, Taenidium, Beaconites*); (10) simple actively filled (pelletoidal) horizontal burrows (e.g. *Edaphichnium, Sphaerapus*); (11) complex actively filled (meniscate) horizontal burrows (*Scolecocoprus*); (12) horizontal branching burrow systems (*Labyrintichnus, Paracanthorhaphe, Shanwangichnus, Vagorichnus)*; (13) horizontal burrows with horizontal to vertical branches (*Ctenopholeus*, *Treptichnus*); (14) burrows with horizontal spreiten (*Fuersichnus, Rhizocorallium*); (15) isolated and serial almond-shaped burrows (*Calceoformites, Lockeia, Ptychoplasma*); (16) vertical simple burrows (e.g. *Skolithos*); (17) vertical U- and Y-shaped burrows (e.g. *Arenicolites, Diplocraterion*); (18) vertical multiple U- and Y-shaped burrows (*Polykladichnus*); (19) Simple to complex burrows with terminal chambers (*Camborygma, Castrichnus, Katbergia, Macanopsis, Platicytes)*; and (20) mazes and boxworks (*Thalassinoides*, *Spongeliomorpha, Virgaichnus*)

The common feature of this list is that these freshwater biogenic structures collectively represent relatively simple behaviors. Miller and Vokes (1998) categorized trace fossils as incidental and deliberate. Incidental trace fossils are those that record a single or dominant behavioral activity, and typically are structurally simple. Deliberate trace fossils are those that represent restructuring of habitats, modulation of disturbances, and control of food resources, and are typically structurally complex. Freshwater trace fossils tend to fall within the first category. In some cases, the same groups of producers were involved (*Lockeia* produced by both marine and freshwater bivalves). In other cases, true behavioral convergence can be invoked. The U-shaped burrow *Arenicolites* in marine environments is produced by a wide variety of organisms, such as polychaetes, echiuran worms, crustaceans, holothurians, and enteropneusts (e.g. Bromley 1996; Mángano et al. 2002), whereas in freshwater settings insects and oligochaetes are involved (e.g. McCall and Tevesz 1982; Scott et al. 2012a). Amphipods produce U-shaped burrows in both freshwater and marine settings. Behavioral convergence on both sides of the salinity barrier seems to have occurred only with the simplest ethologic types. The most complex architectural categories, such as burrows with helicoidal spreiten, dichotomous branching burrows, and those included within graphoglyptids, do not have a freshwater counterpart. This is clearly illustrated by the contrasting trace-fossils suites present in lacustrine and marine turbidites (Buatois and Mángano 1998).

Although the term "salinity barrier" has been commonly used to contrast the nature of freshwater and marine ichnofaunas, the term is somewhat misleading. Differences between ichnodiversity levels and the degree of morphologic complexity of trace fossils most likely are explained by the stability-time hypothesis developed by Sanders (1968), rather than salinity per se. According to this hypothesis, species diversity – and parallel to this, the degree of complexity of biogenic structures – is a function of environmental stability or predictability of the environment. Because lakes are considerably shorter-lived than oceanic basins, they tend to display lower taxonomic diversity (and ichnodiversity) levels and more simple structures than marine settings (Buatois and Mángano 1998). In addition, this line of reasoning can be applied to understand contrasting ichnodiversity levels in different lakes. For example, lakes from recently glaciated regions exhibit lower diversity levels than those from the long-lived, large, and deep lakes such as Lakes Baikal and Tanganyika (Saunders 1968).

Finally, regardless of the specifics of the MLR and lacustrine ecosystems in general, there are at least two common themes between the macroevolutionary aspects of marine and lacustrine settings. First, the overall trend in increased infaunalization discussed above also took place in marine basins, albeit with very different timing, because infaunalization in lacustrine basins lagged behind the same process in marine settings (Buatois and Mángano 1993a; Buatois et al. 1998a). Second, an analogue of the onshore – offshore pattern recognized in marine communities seems to be apparent in freshwater settings as well. An onshore origination of novelties and subsequent migration or expansion into deeper water has been proposed in marine settings based on body fossils (e.g. Jablonski et al. 1983; Sepkoski and Miller 1985; Jablonski 2005; Sepkoski and Sheehan 1983) and trace fossils (Crimes and Anderson 1985; Bottjer et al. 1988; Jensen and Mens 1999). In freshwater settings, an analogue of the onshore-offshore pattern is indicated by increases in the depth and extent of bioturbation that took place progressively through time, expanding from fluvial and lake-margin settings to permanent subaqueous lacustrine environments (Buatois et al. 1998a). These commonalities between the continental and marine trace-fossil records suggest the existence of recurrent macroevolutionary patterns of animal–substrate interactions through time (see Chap. 16).

11.8 Conclusions

Our review of the trace-fossil and body-fossil histories of the continental aquatic record suggests that the Mesozoic Lacustrine Revolution (MLR) represents a significant evolutionary event for lacustrine ecosystems that took place in a protracted fashion in time and space. Although ichnologic data demonstrate that both lake-margin and fully lacustrine deposits were colonized prior to the MLR, benthic activity essentially was restricted to a very narrow zone at the sediment–water interface, leaving the overwhelming portion of infaunal ecospace empty or underutilized. This situation commenced first in lake-margin environments during the Middle to Late Triassic, as shown by widespread presence of mid-tier meniscate trace fossils and deep-tier crayfish burrows. Colonization of the infaunal ecospace in these deposits resulted in more intense sediment reworking, typically precluding preservation of superficial trace fossils such as arthropod trackways. Although incipient penetration of the substrate in fully lacustrine settings has been recorded locally during the Middle to Late Triassic, ichnofaunas from these settings are typically reminiscent of those from the Paleozoic, suggesting that colonization of lacustrine bottoms was delayed in comparison with lake margins. Deeper penetration into the substrate became more common during the Early Jurassic, but the intensity of bioturbation remained low. The lacustrine mixed layer seems to have become well-established by the Early Cretaceous, as indicated by intense bioturbation mottlings.

The MLR also is recorded by examination of the record of body-fossils, particularly arthropods and angiosperms, and by trophic interactions at both the interorganismic and entire-lake foodweb levels. From an ecosystem perspective, prior to the MLR, lacustrine primary production by microorganisms was low and the depressed level of invertebrate consumption was overwhelmingly detritivorous. After the MLR, lakes are characterized by the appearance of macrophytes and a significantly more robust herbivore guild of microorganisms and increasingly larger arthropods and vertebrates, especially grazers on plants other than microscopic and small algae. This transition occurred during elevated lake oxygen levels, attributable to the insufficiency of detritivorous microorganisms before the MLR and detritivorous plus dominant herbivorous organisms after the MLR to use all available O_2 for respiration. Given this context, the MLR actually represents the incremental trophic shift from a detritivore-based to an herbivore-based lacustrine biota and concomitant food-web adjustments. But this change also represents a shift toward infaunalization that results from predatory escalation, also seen in other parts of the lake environment postdating the MLR. Perhaps related to predatory escalation is the distinct evolution of insect species in which their immature aquatic stages become increasingly more environmentally decoupled from their conspecific, exclusively terrestrially occurring adult stages. Based on the arthropod body-fossil record, this switch took place during the Late Jurassic to Early Cretaceous, but may have had a variable spatiotemporal occurrence in other mid-Mesozoic continents. Information from both trace fossils and body fossils suggests that this shift to more mixed trophic strategy consisting of detritivores, herbivores, predators, and other macroguilds that form animal communities has persisted to the present since initiation of the MLR, as demonstrated by the Paleolake Messel food web.

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