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Stable isotopic evidence for fossil food webs in Eocene Lake Messel

Maia K. Schweizer, Andrew Steele, Jan K. W. Toporski, and Marilyn L. Fogel

Abstract.—Carbon and nitrogen stable isotopic compositions of fossil materials from Lake Messel (47 Ma) in Germany are used to investigate Eocene ecosystem dynamics. Autolithified soft tissues of terrestrial and aquatic vertebrate organisms, as well as plant compression fossils, contain organic material (20–50 wt% C, 1–6 wt% N), which appears to retain precursor compositions. Stable isotopic compositions (δ^{13}C and δ^{15}N) of Messel fossils are similar to those reported for components in modern lacustrine ecosystems. These data show trophically sensible enrichments relative to food sources, reflect multiple feeding strategies for each organism (e.g., omnivory, planctivory, piscivory), and differentiate between benthic and pelagic organic carbon sources. These chemical data broadly confirm existing Messel food web models based on coprolite and gut content analyses. δ^{13}C values for the lacustrine shale range from -30.3 to $-26.3‰$, pointing to mixed terrestrial and aquatic origins for primary producers in the food web. δ^{13}C values for primary consumers such as insects overlap with those for primary producers but are comparatively enriched in ^{15}N. Secondary and higher consumers (fish, crocodiles, and frogs) are associated with even more positive δ^{15}N values and show a more constrained range of δ^{13}C values. Omnivory appears widespread in both low and high trophic level consumers. Hence, the stable isotopic compositions of Messel fossils are complex and overlap, and must be combined with paleontological investigations in order to be conclusive. This study represents the first comprehensive isotopic reconstruction, featuring tens of components, of an ecosystem of Eocene age. A thorough understanding of trophic structure in Eocene Lake Messel contributes to the global databank of ecological history.

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Introduction

Our understanding of modern ecosystems would be incomplete without investigations of fossil ecosystems, which may reveal how organisms adapt to long-term environmental changes. However, of the diversity of tools available to modern ecologists—including stable isotope tracers (e.g., Hecky and Hesslein 1995), biomanipulation experiments (e.g., Mehner et al. 2002), and modeling based on thousands of individual observations (Dunne et al. 2004)—only a few can be applied to ancient ecosystems. The diversity of organisms constituting fossil ecosystems is winnowed by taphonomic processes, and chemical signatures are often not observable because even exquisite fossillagerstätten such as the Burgess shale and Solnhofen limestone seldom preserve significant quantities of organic matter.

Food web analyses of ancient ecosystems therefore rely in large part on paleontological evidence (e.g., Baszio and Richter 2001; Richter and Wedmann 2005), supplemented with limited carbon isotope data. Paleontological food web reconstructions are based on nearest-living-relative comparisons as well as coprolite and gut content analyses. They therefore inevitably oversimplify trophic chains because it is difficult to differentiate between whole and partial trophic levels on the basis of isolated remains. Fossil organisms are typically represented only by their resistant hard parts, which usually contain less than 25 wt% organic carbon in the form of collagen (Gearing 1991; Sillen and Lee-Thorp 1994). δ^{13}C measured from the organic component of fossil bones and teeth (Ostrom et al. 1993; Ostrom et al. 1994; Sillen and Lee-Thorp 1994; Bocherens et al. 1995; Clementz and Koch 2001) has previously been used to reconstruct isolated predator-prey relationships and grazing hab-

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its of fossil organisms (MacFadden et al. 1994, 1999; Wang et al. 1994; Sponheimer and Lee-Thorp 1999). Nitrogen is even less likely to be preserved than carbon, yet is crucial to stable isotopic food web reconstructions.

Eocene Lake Messel in Germany allows us to overcome these obstacles. A complete lacustrine ecosystem and a wide range of terrestrial organisms are exquisitely preserved in the Messel Fossillagerstätte (e.g., Storch and Habersetzer 1988; Lutz 1990; Richter 1992; Schaal and Ziegler 1992), with soft-body materials and organic matter intact. The Messel deposit contains one of the most diverse Eocene biotas in the world. The present study seeks to evaluate paleontological models (Baszio and Richter 2001; Richter and Baszio 2001) of the ecosystem at Lake Messel by using stable isotope compositions of carbon and nitrogen preserved in fossil vertebrate soft tissues, invertebrates, and leaves. Isotope data obtained from a similarly preserved Oligocene ecosystem demonstrate that relative isotope enrichments between organisms may be preserved over geologic time scales, and that it is therefore possible to reconstruct trophic relationships on the basis of the stable isotopic compositions of autolithified soft tissues (Schweizer et al. 2006). If stable isotopic compositions of fossil materials are preserved, do they concur with paleontological data? The data presented here represent a novel approach to decoding ancient ecosystems by applying modern techniques to fossil materials.

The Eocene was a time of fluctuating paleoenvironment (Janis 1993; Torricelli et al. 2006), biome evolution (Blondel 2001; Jacobs 2004; Jacobs and Herendeen 2004) and high-latitude species migrations and turnover facilitated by exceptionally warm temperatures (McKenna 1980, 1983; Hartenberger 1987; Legendre and Hartenberger 1992; Janis 1993; Peters and Sloan 2000; Blondel 2001) and minor latitudinal temperature gradients (Andreasson and Schmitz 1996, 2000; Janis 1993). Interestingly, the Messel shale was deposited at the thermal and mammalian species-diversity maximum of the early middle Eocene (47 Ma), just prior to a major global cooling event that persisted through the remainder of the Eocene and Oligocene (Haq et al. 1987; Zachos et al.

1993; Blondel 2001). This cooling caused a replacement of the tropical forest biome with open forested grasslands and a subsequent turnover of mammals and lower vertebrates adapted to new feeding habits (Janis 1993; Zachos et al. 1993; Blondel 2001). In other words, the Messel shale offers a rare opportunity to take a census of ecosystems that are pre-glacial and hyper-greenhouse in climate.

The fossil record of lakes is persistent and reasonably well known, despite the relatively ephemeral nature of individual lakes. Paleontological reconstructions have traced the evolution of modern-type lake ecosystems from the Paleozoic to today through the appearance of important organisms such as insects and aquatic macrophytes, changing tectonic settings, and substantial terrestrially derived organic input (Gray 1988; Buatois and Mángano 1993; Cohen 2003). Characteristic top-down trophic cascades, where populations of primary producers and consumers are determined by higher predators, were established in lakes by the Mesozoic and appear to have remained dominant throughout the Tertiary with some fluctuations due to the evolution and increasing input of terrestrial and aquatic macrophytes (Gray 1988; Cohen 2003). Reconstructions of specific Eocene lakes (Buchheim 1994; Murray 2001; Melchor et al. 2002; Kvaček et al. 2004; Sasche 2005) as well as widespread lake and terrestrial ecosystem dynamics (Barton and Wilson 1999; Janis 1993; Wilf et al. 2003; Williams et al. 2003; Wilson 1987) have shown that many of the same intertwining factors important to modern ecology, such as temperature and precipitation variation, species richness, and ease of migration controlled Tertiary ecosystems. Specifically, fossil lacustrine food webs appear to have been determined by lake surface area, morphology, longevity, productivity, and stability (Cohen 2003; Gierlowski-Kordesch and Park 2004). Additionally, fossil and modern lakes exhibit major offshore versus nearshore variation in organism assemblages, due to habitat preferences of aquatic organisms and sorting during transportation of allochthonous terrestrial organisms (Roth and Dilcher 1978; Wilson 1980, 1988).

Site Description.—The fossiliferous Messel

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oil shale (~8 m thick) was deposited at the anoxic benthic layer of a large maar lake (Franzen 1990; Harms 2002; Robinson et al. 1989; Rolf et al. 2005; Wonik 2005). The lake basin was formed when rising magma came into contact with groundwater, explosively vaporizing the water and leaving behind a steep-sided crater during a period of local volcanism (Müller-Sohnius et al. 1989; Pirrung et al. 2003) at approximately 47 Ma (Mertz et al. 2004; Mertz and Renne 2005) in the middle Eocene. Traces of photosynthetic archaebacteria (Meyers 1997) indicate that even part of the photic zone was anoxic. The lake was therefore strongly stratified. In the Eocene, central Europe was 10° closer to the equator (Schaarschmidt 1992) and mean annual temperature ranged from 20° to 30°C (Andreasson and Schmitz 2000; Mai 1981; Markwick 1996, 2002; Matthes 1968; Schaarschmidt 1992; Sittler 1968; Thiele-Pfeiffer 1988; Wilde 1989) though seasonal variation was similar in magnitude to variation today (Andreasson and Schmitz 2000; Schmitz and Andreasson 2001). Lake Messel was surrounded by a dense paratropical forest (Köhler 1997; Thiele-Pfeiffer 1988; Wilde 1989; Lenz et al. 2005) from which plentiful vegetation and vertebrate carcasses were carried into the lake. Leaves (Collinson 1986), pollen and spores (Schaarschmidt 1992), and seeds and fruit are found at Messel that belong to club mosses, ferns, gymnosperms, and over 200 species of angiosperms dominated by walnuts and laurels. Palynological analysis reveals that floral and faunal composition varied during the deposition of the Messel oil shale because of water table variations, increasing paleotemperatures, and Milankovitch cycles (Lenz et al. 2005). The content of coprolites suggests that the aquatic food web was stable throughout the deposition of the fossiliferous shale, representing some 50 to 100 Kyr (Goth 1990; Richter and Baszio 2001), though there is evidence for different food web compositions lower in the shale sequence (Richter and Wedmann 2005).

Nearest-living-relative comparisons (Schaal and Ziegler 1992) and gut and coprolite content analyses (Schmitz 1991; Baszio and Richter 2001; Richter and Baszio 2001) illuminate possible omnivorous, insectivorous, carnivo-rous, and folivorous diets (Richter 1987; Richter and Baszio 2001) for Messel organisms. A paleontological reconstruction synthesized by Richter and Baszio (2001) describes a six-tiered, linear trophic chain. Aquatic primary producers included pelagic *Tetraedron* and *Botryococcus* (Goth 1990), benthic and floating algae, dinoflagellates, monocellular green algae in blooms, and water lilies (Franzen and Michaelis 1988; Hayes et al. 1989; Robinson et al. 1989; Goth 1990; Meyers 1997; Nix and Feist-Burkhardt 2003). These were consumed by Cladocera, Culicidae, ostracods, caddis flies (Trichoptera), mayflies (Ephemeroptera), and freshwater sponges. Secondary consumers such as water bugs fed on small Crustacea. Juvenile fish and smaller fish species including *Thaumaturus* preyed upon such Arthropoda and constituted the tertiary-level consumers. The fourth level of consumers was composed of large predatory fish that preyed on juveniles, smaller fish species, and large insects (Micklich 1992). Crocodiles, turtles, and piscivorous mammals constituted the fifth and highest level of consumers.

Stable Isotopes as Ecological Tracers.—Stable isotopes of carbon and nitrogen (δ^{13}C and δ^{15}N, respectively) are powerful tools for tracing nutrient flow within ecosystems. The nitrogen isotopic composition of organisms is passed from primary producers to prey to predator with a fractionation of +1‰ to +5‰ δ^{15}N (average +3.4‰) per trophic step (DeNiro and Epstein 1981; Minagawa and Wada 1984; Harrigan et al. 1989; Vander Zanden and Rasmussen 2001) whereas δ^{13}C reflects the source carbon signature with a minimal fractionation of less than ±1‰ (DeNiro and Epstein 1978; Fry and Sherr 1984; Vander Zanden and Rasmussen 2001; McCutchan et al. 2003). Stable isotope analyses of ecosystem components allow the tracing of multiple carbon and nitrogen sources and may therefore yield a nuanced food web instead of a simplified food chain (Cohen et al. 1990; Pimm et al. 1991; Kling et al. 1992; Vander Zanden et al. 1999). For example, consumer isotopic compositions differentiate between benthic algae and pelagic phytoplankton carbon sources (Hecky and Hesslein 1995).

Heterotrophic bacterial reworking of pri-

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mary organic matter in Eocene Lake Messel was undoubtedly widespread (Freeman et al. 1990) and its effect on the stable isotopic composition of fossil materials must be considered. Unlike autotrophic microorganisms, which often produce substantial isotopic fractionations between source carbon (e.g., CO_2) and nitrogen (e.g., N_2) and bacterial biomass (Estep et al. 1978; Macko et al. 1982; Whiticar et al. 1986), heterotrophic bacteria such as those that consumed and replaced Messel vertebrate tissues generally incorporate $\delta^{13}C$ and $\delta^{15}N$ signatures from the substrate without considerable fractionation (DeNiro and Epstein 1978; Coffin et al. 1989; Coffin et al. 1990). Even if replacement is not complete, $\delta^{13}C$ of the bacterial biomass typically falls within 1.0 to 1.5‰ (average $\Delta\delta^{13}C = +1.4$‰) of the substrate (Hullar et al. 1996). Localized variations in stable isotopic composition of individual biomarkers or diagenetic reaction sites tend to balance out and do not substantially affect bulk isotopic compositions of a diverse microbial community (Macko and Estep 1984; Blair et al. 1985; Hayes et al. 1989; Coffin et al. 1990; Boschker et al. 1999; Panacost and Sinninghe Damste 2003). Although heterogeneous preservation and microbial processing may elevate C/N ratios far above what would be expected for living organisms (DeNiro 1985), stable isotopic compositions of C and N components tend to be preserved (Masters 1987).

Estimation of trophic position based on $\delta^{15}N$ values of fossil materials is particularly sensitive to microbial processes because a small amount of fractionation by microbes could significantly affect apparent trophic level. Other microbial processes such as denitrification can greatly influence ^{15}N. Additionally, isotopic trophic shifts between primary producers, primary consumers, and predators can vary. For example, consumers of invertebrates have a lower than average trophic shift relative to their diet ($+1.4 \pm 0.21$‰ $\delta^{15}N$) than do consumers of other high-protein diets ($+3.3 \pm 0.26$‰). Primary consumers feeding on plants and algae exhibit $+2.2 \pm 0.30$‰ enrichment in ^{15}N per trophic step (McCutchan et al. 2003). Furthermore, stable isotope compositions of organism tissues are more likely to reflect the integration of organic carbon and nitrogen sources rather than the ingested materials themselves (Hecky and Hesslein 1995). These uncertainties require a careful evaluation of isotopic data for both modern and ancient food webs.

Taphonomy of Messel Organisms.—Messel leaves and seeds are preserved as compression or impression fossils (Wilde 1989; Manchester et al. 1994). Beetles with chitinous cuticles are the most common insects preserved (Lutz 1992; Wuttke 1992b), while feathers are typically preserved as replicas made by strings of autolithified rod-shaped bacteria, arranged end to end (Davis and Briggs 1995).

Vertebrate carcasses were autolithified by sulfate-reducing and denitrifying bacteria soon after deposition on the bottom of the lake (Wuttke 1983, 1992b,c). By this process, bacteria inhabiting the mostly anoxic bottom waters immediately colonized the carcasses and began releasing metabolic products such as CO_2 and H_2S into sediment pore waters, which already contained CO_2 and iron supplied by weathering of nearby Permian strata (Richter 1992). Siderite reached saturation and precipitated directly onto cell surfaces or within the microorganisms themselves until the rapidly thickening crust exterminated the bacteria (Toporski et al. 2002).

Messel shale contains a significant amount of low-maturity organic carbon. Kerogen and other materials from Messel are known to contain virtually unaltered biolipids (Mycke and Michaelis 1986; Mycke et al. 1987; Robinson et al. 1989) and original albumin (Richter and Storch 1980; von Koenigswald et al. 1981). Reducing conditions in the hypolimnion caused by high productivity in the surface waters (Matthes 1966) prevented thorough decomposition of organic matter, and mild burial conditions ($\leq 40°C$ and 200 m depth [Hayes et al. 1987; Kimble et al. 1974; Matthes 1968]) preserved the organic matter with little alteration. Additionally, autolysis following the death of the organisms may have been inhibited by humic acids associated with organic molecules in runoff (Hummel and Herrmann 1994), by volcanic gases, or by iron from volcanic ash (Ferris et al. 1988; Carson 1991). Fine volcanic ash particles and microbial mats fur-

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TABLE 1. Common vertebrate, invertebrate, and plant fossils analyzed from the Messel Fossillagerstätte.

Taxon	Description	Size
Thaumaturus intermedius	Small modern fish	15 to 50 mm long
Cyclurus kehreri	Medium-sized bowfin	10 to 60 cm long
Atractosteus strausi	Large-sized plated garfish	15 to 90+ cm long
Formicium giganteum	Giant ant	10 to 30 mm long
Elateridae (family)	Click beetles	Widely varied
Buprestidae (family)	Jewel beetles	Widely varied
Scarabaeidae (family)	Dung beetles	Widely varied
Curculionidae (family)	Weevils	2 to 10 mm long
Trichoptera (order)	Caddis fly	4 to 12 mm long
Blattodea (order)	Cockroach	5 to 25 mm long
Ephemeroptera (order)	Mayfly	5 to 20 mm long
Nymphaeaceae (family)	Water lily	Up to 10 cm wide

ther preserved the structure of organisms by physically isolating them and protecting them from disruption by turbulence (Zimmerle 1993; Harding and Chant 2000; Meyer et al. 2001).

Methods

Material Collection.—Material from the Messel Fossillagerstätte was collected in July and September 2003 from the Messel pit, located 20 km southeast of Frankfurt. Fossils were excavated from a 1-m-thick exposure of shale, the bottom of which is approximately 80 cm above the α horizon (Franzen et al. 1982). The majority of fossils were subsampled in the field. A hand-held digital microscope with a $100\times$ lens (Scalar DG2) was used to investigate the quality of preservation prior to sampling in instances where the amount of material preserved was unclear. Several milligrams of macroscopically representative material were loosened with cleaned and sterilized micropicks and placed in aluminum foil bags, which had previously been cleaned by heating them to 500°C in a muffle furnace. Shale was collected from within a few millimeters of each fossil to provide a comparison with the fossil material. All samples were quickly refrigerated to restrict fungal growth on the organic-rich material, and remained refrigerated during transport. Upon reaching the laboratory, the fossil material was kept frozen at -20°C.

Seeds were pried whole from the shale, and foliar material could be peeled from the shale with little or no sediment contamination. Bacterial biofilms preserving soft tissues in vertebrate fossils were scraped from the shale and from bone surfaces as a fine powder. The detailed morphological preservation of the specimens allowed different tissue types to be distinguished and extracted. Sample material from vertebrate fossils was classified as pure ''soft tissues'' consisting of muscle and internal organs or occasionally as a specific morphological feature (such as an eye). These terms are based on anatomy and are used throughout this paper for simplification, though it should not be forgotten that the original organic material of the soft tissues has been preserved by bacterial biofilms. A selection of the fossils we sampled are listed and described in Table 1.

Trophic webs for the terrestrial and aquatic ecosystems at Messel were reconstructed based primarily from relationships between stable isotopic compositions of fossil organisms and secondarily from paleontological data from previous studies.

Stable Isotope Analysis.—An aliquot between 400 and 2000 μg of each sample was weighed into a 3.5 $\times$ 5 mm tin capsule. The tin capsules were sealed and introduced into an elemental analyzer where they were combusted and reduced prior to analysis of stable isotope ratios using continuous-flow, stable isotope ratio mass spectrometry, as previously described for similar samples (Schweizer et al. 2006). Both N_2 and CO_2 samples were analyzed relative to gas standards and the results are presented in standard notation, defined:

$$\delta^h X = \left(\frac{{}^h X_{\text{sample}} / {}^l X_{\text{sample}}}{{}^h X_{\text{std}} / {}^l X_{\text{std}}} - 1 \right) \times 1000.$$

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Precision was calculated from triplicate measurements of the same acetanilide (C_8H_9NO) standard at the beginning of each run of 50 samples, as well as at ten-sample intervals during the runs: $\delta^{15}N \pm 0.24‰$ (%N by weight = ± 0.80) and $\delta^{13}C \pm 0.33‰$ (%C by weight = ± 3.30).

Testing of Isotope Measurement Validity.—We used two bulk isotopic tests to evaluate the quality of C and N isotopes as biosignatures in Messel materials: first, a test for significant diagenetic alteration, which might be expected to produce uniformly or randomly distributed stable isotope signatures, instead of clustered data; and second, a test for stable isotopic compositions of the shale matrix, which should be unrelated to the composition of embedded fossil material.

Shale was sampled several centimeters away from each fossil specimen, within approximately the same lamina. This revealed no clear correlation between shale and fossil isotopic variation. Additionally, for several vertebrate fossils, shale was sampled at increments of 2 to 5 mm from the fossil, up to 5 cm away to determine the extent of carbon and nitrogen exchange between the fossil material and the shale. There was, again, no significant correlation between $\delta^{13}C$, $\delta^{15}N$, wt% C, or wt% N and distance from the fossil. Both tests indicate that carbon and nitrogen have not diffused outward from the fossil into the surrounding sediments sufficiently to affect the stable isotopic signatures. Plant fossils, beetles, and vertebrate soft tissues were found to be characterized by relatively high C (27 to 43

wt%) and N (1 to 4 wt%) content (Table 2). Caddis fly larva cases, which were originally composed of silk from the insect and clinging sedimentary particles, have distinctly lower C and N contents, as do fish hard parts such as scales and bones (typically 3% to 8% C and 0.1% to 0.3% N). These patterns are consistent with good-quality preservation of the original precursor materials.

Results

Primary Producers.—Stable isotope ratios for shale and each of the primary producer categories (fruits, seeds, terrestrial and aquatic leaves, and wood) cluster together on a $\delta^{13}C$ and $\delta^{15}N$ bi-plot (Fig. 1). Messel shale and leaf $\delta^{15}N$ values are statistically similar (average $\Delta\delta^{15}N = 0.28‰$, single-factor ANOVA with $p > 0.05$) and elevated with respect to modern atmospheric nitrogen values ($\delta^{15}N_{atm} \cong 0‰$). Water lilies were abundant primary producers in the aquatic food web of the Messel lake and are depleted in ^{15}N compared to terrestrial leaves (average $\Delta\delta^{15}N = -1.26‰$, ANOVA with $p \ll 0.05$), although average $\delta^{13}C$ values of water lily and terrestrial leaves are statistically indistinguishable ($\Delta\delta^{13}C = 0.22‰$, ANOVA with $p = 0.32$). The $\delta^{13}C$ values of shale are depleted in ^{13}C relative to terrestrial and water lily leaves ($\Delta\delta^{13}C = 1.73‰$, single-factor ANOVA tests with $p \ll 0.005$) (Table 2). These compositional differences between fossil leaves, which are particularly sensitive to contamination and diagenetic alteration owing to their large surface area-to-volume ratio, and the shale matrix seems to confirm that isotopic

TABLE 2. Summary of average isotope values, and C and N content (± 1 SD) of the most common sample types.

Material (n)	$\delta^{13}C$	$\delta^{15}N$	%C (wt)	%N (wt)	C/N (wt)
Shale (159)	-28.54 ± 2.71	6.76 ± 1.06	20.94 ± 4.02	0.62 ± 0.10	33.77
Terrestrial leaves (63)	-26.81 ± 0.83	7.04 ± 0.89	38.84 ± 6.42	1.46 ± 0.38	26.60
Terrestrial seeds (4)	-25.81 ± 1.17	7.00 ± 0.81	32.90 ± 4.05	1.12 ± 0.19	29.38
Wood (14)	-26.21 ± 1.02	7.12 ± 0.50	36.60 ± 5.28	1.58 ± 0.35	23.16
Palm fruits (8)	-25.30 ± 0.51	6.76 ± 0.77	33.05 ± 4.02	1.42 ± 0.23	23.27
Water lily leaves (16)	-27.03 ± 0.75	5.78 ± 1.23	43.26 ± 6.55	0.95 ± 0.33	45.54
Beetles (20)	-26.69 ± 1.63	6.44 ± 1.43	33.16 ± 5.90	1.64 ± 0.43	20.22
Caddis fly larvae (8)	-28.90 ± 1.39	7.03 ± 1.63	3.32 ± 2.77	0.12 ± 0.09	27.67
Other insects (9)	-26.87 ± 1.58	7.44 ± 1.49	32.63 ± 8.86	1.53 ± 0.53	21.33
Thaumaturus soft tissue (14)	-26.95 ± 1.55	8.07 ± 1.87	28.86 ± 7.97	1.77 ± 0.54	16.31
Cyclurus soft tissue (4)	-26.99 ± 0.41	11.78 ± 2.19	35.57 ± 7.94	3.76 ± 0.98	9.46
Atractosteus soft tissue (3)	-26.53 ± 1.54	8.57 ± 0.71	26.99 ± 13.83	1.71 ± 1.02	15.78
Cyclurus hard parts (25)	-19.51 ± 3.58	6.39 ± 2.26	4.38 ± 2.54	0.13 ± 0.08	33.69

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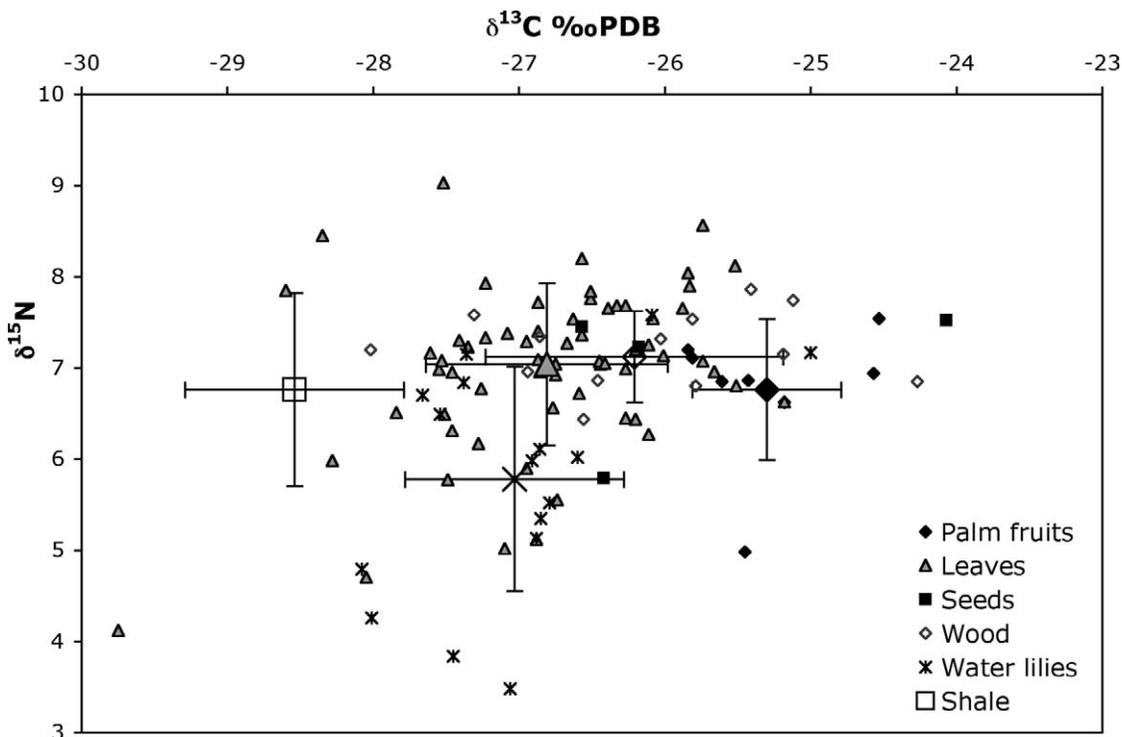
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FIGURE 1.   Fossil primary producer and background (shale) stable isotope measurements. Error bars represent one standard deviation from mean for the symbol grouping. Individual shale measurements ($n = 159$) have been omitted for clarity.

exchange between fossils and substrate was not so extensive that it obscures distinct isotopic ranges.

Consumers.—All varieties of fossil insects from Messel share a similar $\delta^{15}N$ range, from approximately $+4‰$ to $+10‰$, whereas $\delta^{13}C$ values differ between taxonomic groups (Fig. 2). Messel beetle $\delta^{13}C$ values range from approximately $-24‰$ to $-29‰$, which may reflect a number of carbon sources. Note that invertebrates sampled were amalgamated on the basis of gross morphology. This limits the taxonomic resolution of trophic data; for example, the grouping denoted ''Beetles'' (Fig. 2) may include detritivorous, herbivorous, omnivorous, and carnivorous specimens from various taxa (Table 1). However, because the material sampled was often fragmented, a specific taxonomic identification was rarely possible. Caddis fly larvae are aquatic primary consumers and their larval cases are generally more depleted in ^{13}C than the exoskeletons of beetles and other terrestrial insects (by 2.21‰ on average, single-factor ANOVA with $p <$

0.005), though their $\delta^{15}N$ values are statistically similar ($p > 0.05$).

The fish population in Lake Messel was dominated by three species (Table 1). *Thaumaturus*, the smallest of the three, has the widest range of stable isotope compositions (Fig. 3; $\delta^{13}C = -23‰$ to $-29‰$, $\delta^{15}N = +5‰$ to 10.5‰). *Thaumaturus* fossils were sampled as follows: eye material, often the most obvious and greatest quantity of soft tissue material in a specimen; and muscle and soft tissues scraped from the body of the fish, usually from between the delicate ribs. The stable isotope compositions of eye material overlap significantly with muscle compositions ($\delta^{13}C$ and $\delta^{15}N$, single-factor ANOVAs with $p \gg 0.05$). On the basis of this observation, we placed eye material with muscle in the ''soft tissue'' category for *Atractosteus strausi*, which is found much less frequently in the shale, to provide sufficient numbers of samples for robust data analysis.

Bones and scales from fish and higher consumers were analyzed (Table 2), though their

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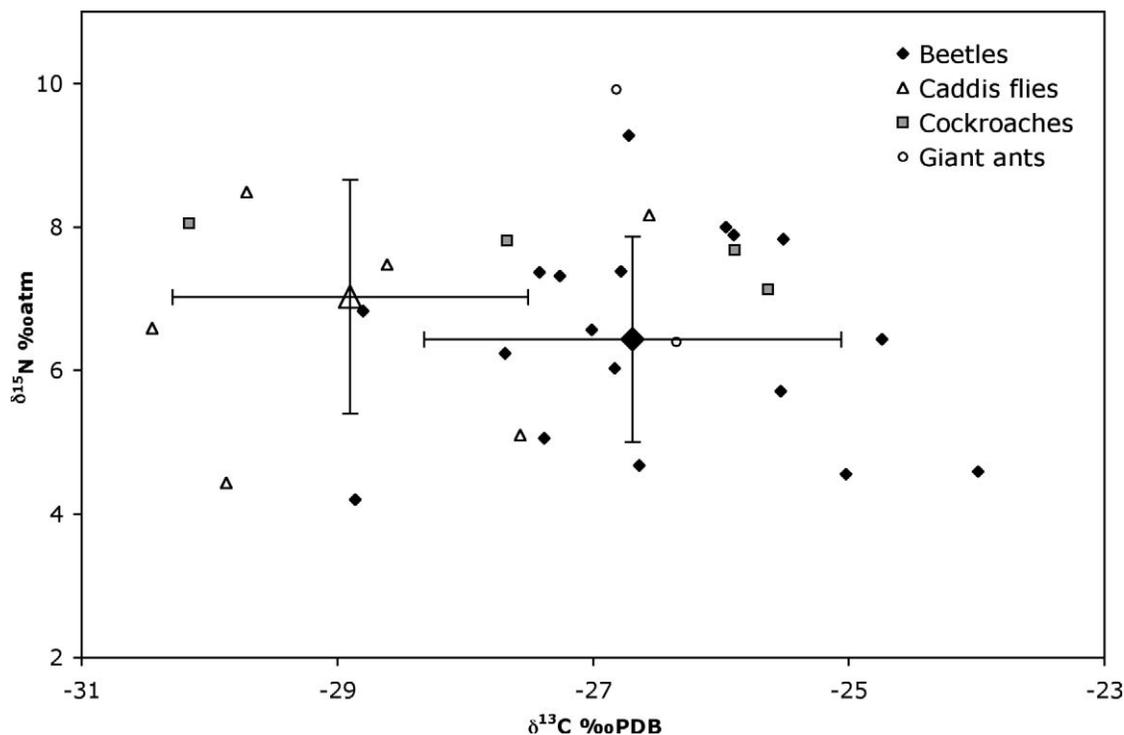
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FIGURE 2. Summary of invertebrate stable isotope compositions. Caddis flies represent the aquatic food web, as do most beetles. Cockroaches and giant ants represent the terrestrial ecosystem. Error bars represent one standard deviation from mean.

isotopic compositions cannot be directly compared to fossilized soft tissue values. Soft tissues are typically 35 to 45 wt% C and 1.5 to 2.5 wt% N, while bones are 5 to 15 wt% C and 0.05 to 0.2 wt% N. The length of *Thaumaturus* specimens used in this study ranged from 15 to 50 mm. δ^{15}N (i.e., degree of carnivory) does not vary strongly with *Thaumaturus* length (slope of linear regression: 0.013‰ δ^{15}N per mm length, $r^2 = 0.0079$).

Stable isotopic compositions of *Cyclurus kehreri* are strongly enriched in ^{15}N (Fig. 3; δ^{13}C = -27‰ to -28‰, δ^{15}N = $+10$‰ to 15‰). This species is significantly larger than *Thaumaturus*, allowing for greater distinction between sample materials from a single specimen (e.g., gut contents). As with *Thaumaturus*, there appears to be no relationship between *Cyclurus* fish length and δ^{15}N. However, in the case of *Cyclurus*, the limited size range of fish sampled may be insufficient to reveal such a pattern. Because soft tissues are often difficult to isolate beneath *Cyclurus* scales, we were un-

able to sample soft tissue of both a 45-cm adult and a 12-cm juvenile.

Atractosteus strausi stable nitrogen isotope values mostly fall between *Thaumaturus* and *Cyclurus* values (Fig. 3). Soft tissue δ^{13}C and δ^{15}N range from -25‰ to -28‰ and 7.5‰ to 9‰, respectively. Several higher vertebrates were sampled and analyzed (Table 3). Stable isotopic compositions of the ribs from a 70-cm-long pipe snake skeleton are comparable to values from hard parts of other Messel fossil organisms, such as fish (Table 2). The organic-rich crocodile gut material yielded stable isotope ratios and elemental compositions characteristic of soft tissue (Table 3).

Discussion

The Aquatic Food Web.—The data presented above represent the first isotopic investigation of fossilized soft tissue material of Eocene age, to our knowledge. The isotopic compositions of Messel fossil organisms will be discussed here in order of increasing trophic position,

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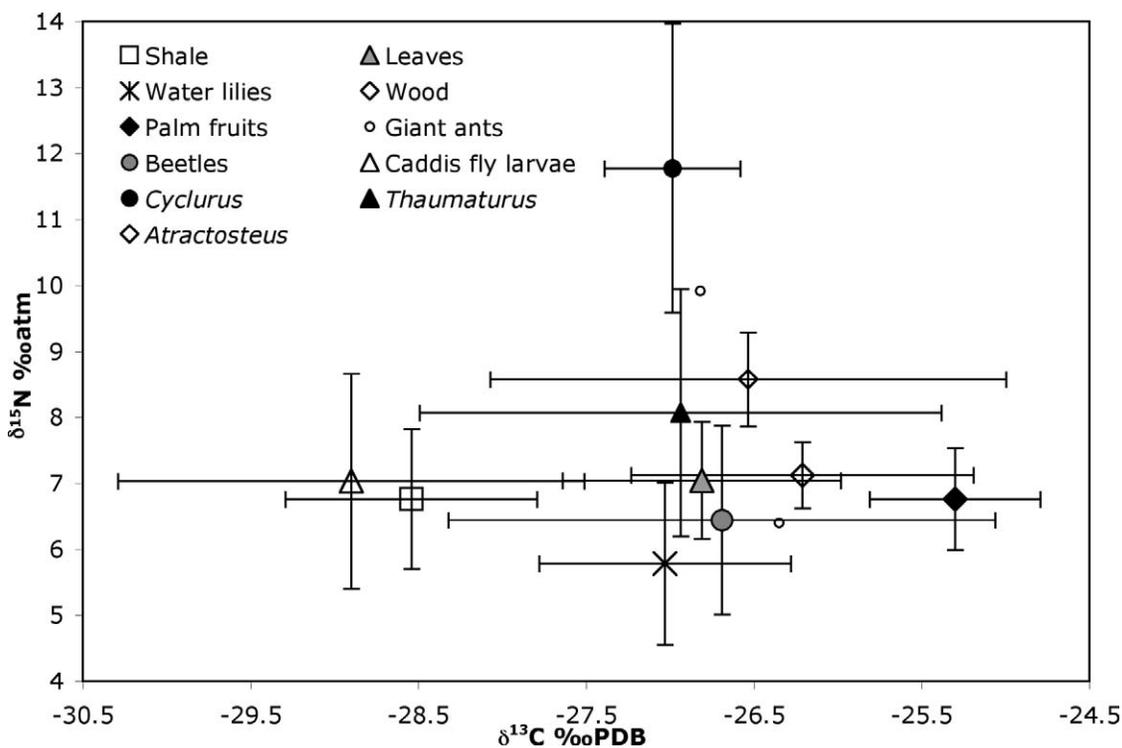598   MAIA K. SCHWEIZER ET AL.

FIGURE 3.   Average stable isotope compositions from the most common aquatic and terrestrial fossil materials. Error bars represent one standard deviation from mean.

and then tested against existing paleontological models. Variation in Messel bulk sediment (shale) $\delta^{13}C$ is similar in magnitude to variation seen among primary producers in modern lacustrine ecosystems, where benthic primary producers are typically depleted in ^{13}C by 2‰ to 10‰ (average 6.5‰, Post et al. 2000) relative to pelagic primary producers in the littoral regions (France 1995; Hecky and Hesslein 1995; Vander Zanden and Rasmussen 1999; Post et al. 2000; Post 2002). The average $\delta^{13}C$ for Messel shale (−28.5‰) is nearly 6‰ lower than the −23.4‰ previously reported for isolated aquatic photosynthesizers at Messel (Hayes et al. 1987, 1989; Freeman et al. 1990). This difference arguably arises from extensive terrestrial input, though isotopically light methane (as low as −60‰, [Whiticar et al. 1986]) produced by fermenting methanogens may contributed to depleted ^{13}C in the

TABLE 3.   Stable isotopic and elemental compositions of fossil materials from rare vertebrates at Messel.

Organism	Species	Sample type	$\delta^{15}N$	$\delta^{13}C$	%C	%N	C/N
Pipe snake	Boidae, subfamily Erycinae	Ribs	5.14	−20.38	4.70	0.15	31.64
Frog	*Eopelobates wagneri*	Muscle	9.23	−28.17	39.06	1.57	24.88
		Bone	4.41	−20.81	3.85	0.08	47.45
Crocodile	*Diplocynodon* sp.	Gut biofilm	7.80	−24.70	18.60	1.36	13.67
		Foreleg bone	4.36	−15.74	2.31	0.06	39.44
Bird	Unknown	Feather	6.47	−26.57	26.34	1.27	20.82
Bird	Unknown	Feather	7.99	−27.52	25.06	1.08	23.23
Bird	Unknown	Feather	9.41	−27.76	33.55	1.25	26.67
Bat	*Archaeonycteris trigonodon*	Muscle	5.85	−26.36	26.96	1.85	14.56
		Bone	3.38	−21.82	4.48	0.12	37.88
Bat	*Archaeonycteris trigonodon*	Skin	8.80	−27.93	30.08	2.40	12.54
		Bone	n.d.	−21.80	3.58	0.10	35.51
Mammal?	Unknown	Gut cord	10.60	−27.03	19.41	1.42	13.69

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sediment (Chappe et al. 1982; Freeman et al. 1990; Goossens et al. 1985; Michaelis and Albrecht 1979). Two dramatically lighter shale values from this study ($\delta^{13}C = -36.01$‰, and -60.28‰) with typical $\delta^{15}N$, %C, and %N may correspond to localized high concentrations of methanogenic activity.

Messel shale bulk sediment is enriched in ^{15}N relative to nitrogen fixed by terrestrial vegetation or aquatic primary producers, which typically has $\delta^{15}N$ values between $+1$‰, and $+2$‰ (Kohl and Shearer 1980). Active recycling of nitrogen by ammonia-oxidizing bacteria in anaerobic regions and sediment pore waters is here regarded as the likely cause for this enrichment (see Freeman et al. 1990). The $\delta^{15}N$ of the primary producers may therefore have been lower than the bulk shale measurement, perhaps within the range of water lily values (Fig. 1), which are isotopically lighter because water lilies fixed nitrogen directly from the atmosphere. Average shale $\delta^{15}N$ is also likely to represent a mixture of benthic and pelagic contributions.

The carbon isotope fractionations between different terrestrial plant materials (e.g., between leaves and wood) at Messel are similar to those observed in Oligocene Enspel fossil material (Schweizer et al. 2006). $\delta^{15}N$ of other terrestrial plant materials (i.e., wood, seeds, and palm fruits) overlap significantly or entirely with leaf values (Fig. 1; single-factor ANOVAs with $p > 0.05$).

The isotopic compositions reported here, as well as observations of fossil caddis fly larvae attached to water lily stems and leaves (Lutz 1991, 1992), indicate that Messel caddis fly larvae consumed water lily parts. Specimens with lower $\delta^{13}C$ values likely incorporated more terrestrial detritus in their diets, as modern caddis flies do (Hutchens et al. 1997). Caddis fly $\delta^{13}C$ values are similar to cockroach (terrestrial detritivore) compositions. Other aquatic insects are greatly underrepresented in the shale, either because insect carcasses were eaten before they could sink or because of a genuinely undersized insect population (e.g., Rietschel 1988).

Most *Thaumaturus* fish $\delta^{15}N$ values are approximately one trophic step more positive than the broad cluster of insect values (Table 2), judging from an average enrichment of 1.4‰ in modern organisms with invertebrate diets (McCutchan et al. 2003). Specimens with outlying stable isotopic compositions may have incorporated more algae, carcasses of other vertebrates, juvenile fish, or all of these into their diets. Unlike many modern piscivorous fishes, *Thaumaturus* does not exhibit increasing $\delta^{15}N$ values with specimen length, which would point to the growing importance of piscivory to maturing fish diets (Fig. 3). The many small coprolites containing insects and minute bones described from Messel (Schmitz 1991; Micklich 1992; Baszio and Richter 2001) therefore confirm that *Thaumaturus* was a lifelong opportunistic feeder that did not pass through a insectivore-to-piscivore transition.

Three *Atractosteus* fish soft tissue samples show wide variation in $\delta^{13}C$ values but reasonably uniform $\delta^{15}N$ values. These $\delta^{15}N$ are trophically sensible for a diet of mostly insects and some *Thaumaturus*, given an enrichment of between 1.4‰ and 3.3‰ ^{15}N for modern organisms that consume invertebrates and other animals, respectively (McCutchan et al. 2003). *Atractosteus* specimens may also have consumed sufficient primary producers during algal blooms (Richter and Baszio 2001) to enrich their $\delta^{13}C$ values to just under -25‰ (Fig. 3). It should be noted that the *Atractosteus* specimens analyzed in this study are at the lower end of the size range for the species, and thus are likely to reflect juvenile diets. *Atractosteus* could therefore have matured to a completely piscivorous diet with time, as has been suggested by paleontological reconstructions (Micklich 2002; Richter and Wedmann 2005).

Cyclurus fish specimens (Table 1) have the highest $\delta^{15}N$ values of any organism analyzed. Three *Cyclurus* soft tissue $\delta^{15}N$ measurements fell between $+10$‰ and 12‰, one trophic shift above insects and some *Thaumaturus* and *Atractosteus* values. Though medium to large coprolites at Messel are difficult to assign to a source organism owing to the plethora of candidates, nearest-living-relative comparisons suggest that *Cyclurus* was a formidable predator (Micklich 1992; Richter and Baszio 2001). Stable isotopic data confirm this hypothesis. The highest *Cyclurus* $\delta^{15}N$ value of $+15$‰ is consistent with a completely carnivorous diet.

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Cyclurus δ^{13}C values are also much less variable than those measured for other organisms. This channeling phenomenon is frequently observed in stable isotopic compositions of the highest trophic element of modern ecosystems, presumably because these predators reflect the mean δ^{13}C value of the scattered prey in all lower trophic levels (Post 2002).

Black biofilm material sampled from the 40-cm-long crocodile may preserve either the internal organs of the crocodile or partially digested flesh from its last meal. If the former is the case, then the biofilm stable isotopic composition (Table 3) indicates a nitrogen source relatively depleted in ^{15}N, such as terrestrial invertebrates. If the biofilm represents partially digested flesh in the crocodile's gut, then the stable isotopic composition of this material reflects the actual composition of the diet. In this case, the crocodile, similar to alligators and modern caimans, probably consumed fish and, occasionally, invertebrates (Berg 1966; Keller and Schaal 1992b).

Variations among the stable isotope compositions of individuals belonging to one species may result from a number of factors. First, the ecosystem in and surrounding Lake Messel was complex enough to provide a number of nutrient sources for each organism. Varied eating habits can rapidly and significantly affect an organism's soft tissue stable isotopic composition, for example by up to 2‰ δ^{15}N in seven days (Adams and Sterner 2000) and by n‰ δ^{13}C in n days (e.g., 3‰ in three days; Olive et al. 2003). Additionally, as discussed above, the diet-to-tissue nitrogen isotope fractionation is not constant between organisms with different diets (McCutchan et al. 2003; Pearson et al. 2003; Robbins et al. 2005). The variability in trophic step fractionation (3‰ or more) is itself at least one trophic step. Furthermore, different soft tissues from the same organism may have slightly different stable isotope compositions. For example, lipid synthesis discriminates against ^{13}C, producing depleted fatty tissues (Pinnegar and Polunin 1999), whereas muscle, heart tissue, and liver tissue from the same fish typically fall within ±1‰ δ^{15}N and ±2‰ δ^{13}C (Bocherens et al. 1996). These uncertainties constrain the potential accuracy of stable isotopic studies of
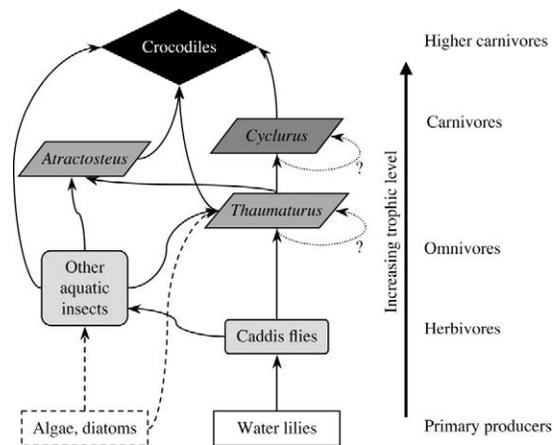

FIGURE 4. Flowchart constructed from stable isotopic evidence for trophic structure of the Eocene aquatic ecosystem of Lake Messel. Additional trophic levels, such as primary consumers (e.g., microscopic zooplankton) or additional carnivorous organisms may exist but were either not available for study or not recorded in the stable isotopic measurements. Solid arrows represent relationships that are recorded in stable isotopic compositions; dashed arrows represent likely relationships according to paleontological and nearest-living-relative comparisons that were not tested using stable isotopes in the present study.

ancient ecosystems, particularly given that the behavior of the organisms cannot be observed directly. However, the present data provide a trophic ranking based on δ^{15}N and a broad differentiation between benthic and pelagic habitats.

Testing the Paleontological Model.—A flowchart showing the path of carbon and nitrogen sources through the Messel food web based on stable isotope data (Fig. 4) can be compared with the existing paleontological model (Richter and Baszio 2001). Stable isotope data show that Messel organisms engaged in complex and varied feeding habits beyond those indicated by their coprolites. Some trophic level components as described in the Richter and Baszio's linear trophic chain might be reclassified as partial trophic levels in light of the stable isotope data. For example, *Atractosteus*, with its combined diet of insects, smaller fish, and even algae (Fig. 4), might belong to the second or third trophic level instead of the fourth, depending on the importance of each of these components to its overall diet. The stable isotope reconstruction is broadly compatible with the paleontological model, in that

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none of the trophic links are reversed. Although Richter and Baszio incorporated certain organisms for which there are no stable isotope data (e.g., sponges, crustaceans, and higher consumers such as piscivorous mammals), the isotope data presented here provide an independent and nuanced reconstruction of feeding strategies, even accommodating changes in diet with time or maturation. Conversely, in some cases the isotopic data represent averages for an entire clade of organism (e.g., ''other insects''), whereas paleontological observations (e.g., of gut contents) may be tied to specific species and even individuals. The resulting flowchart (Fig. 4) presents possible trophic connections suggested by the isotopic data, but departs from convention in that it does not take into account paleontological information unless specifically noted. Isotopic reconstructions such as the one presented here are therefore most effective when used in conjunction with more traditional techniques.

The Terrestrial Food Web.—This study represents the first formal reconstruction of the terrestrial food web at Messel. However, terrestrial vertebrates, including obligate carnivores such as *Messelogale kessleri*, are extremely rare and were not available for sampling. Thus the uppermost trophic level (top consumers), and presumably several lower levels (other omnivorous, detritivorous, and carnivorous vertebrates), are not represented by these data. The placement of each component of the terrestrial ecosystem will be discussed in order of increasing trophic level.

Messel leaf $\delta^{13}C$ values fall within the $-36‰$ to $-22‰$ range typical for modern C_3 vegetation (Farquhar et al. 1989). Variation among the fossil stable isotope measurements is similar in magnitude to variation among modern primary producers from a single location (Smith and Epstein 1971; Leavitt and Long 1986). These observations are consistent with evidence for comparable levels of atmospheric CO_2 in the middle Eocene and today (Royer et al. 2001) and also with previous stable isotopic measurements of Eocene plant fossils, for example $\delta^{13}C = -27.5‰$ from North America (Hayes et al. 1987).

Messel leaf $\delta^{15}N$ is enriched above the range of expected values ($0‰$ to $+6‰$) based on the fixation of atmospheric nitrogen (Delwiche et al. 1979; Kohl and Shearer 1980; Shearer and Kohl 1989). However, nitrogen is typically in excess as a nutrient in tropical forests (Keller et al. 1986; Vitousek and Sanford 1986; Vogt et al. 1986; Niell et al. 1995), which allows plants to lose nitrogen through a more ''open'' nitrogen cycle (Martinelli et al. 1999). As a result of fractionating pathways along the cycle, combined with the greater turnover of nitrogen, plants thereby become enriched in ^{15}N. Average foliar $\delta^{15}N$ under these conditions has been estimated at $4.7 \pm 2.1‰$, with some species approaching $+10‰$ (Martinelli et al. 1999), similar to Messel values. Water lily leaves are therefore not similarly enriched, because the plants did not live in terrestrial soils. The average wt% N is similar between modern tropical leaves (1.9 ± 0.8 [Martinelli et al. 1999]) and Messel fossil leaves (Table 2). Like modern plant components (Evans et al. 1996), Messel wood and leaves share similar ^{15}N compositions (Fig. 1).

Messel beetles with high $\delta^{15}N$ values typically belong to terrestrial taxa (Table 1) whose extant relatives consume dung, leaves, detritus, pollen, and other insects (Lutz 1990, 1992). Beetles with lower $\delta^{15}N$ and higher $\delta^{13}C$ ($-24‰$ to $-26‰$) probably consumed components of the aquatic ecosystem such as caddis fly larvae and water lily leaves with their associated algae.

Messel giant ants have high $\delta^{15}N$ values consistent with their active hunting strategies, as hypothesized by Lutz (1986, 1992). Depending on the species, they may also have consumed leaves, fungi, carcasses of other insects, or all of the above (Lutz 1992). Insect stable isotopic compositions change to reflect varying diet on a short time scale (Olive et al. 2003), so the highest giant ant $\delta^{15}N$ value ($+9.92‰$, Fig. 2) may reflect consumption of a vertebrate or invertebrate carcass.

The muscle $\delta^{15}N$ of a 6-cm-long terrestrial frog (Wuttke 1992a) also implies a high trophic level (Table 3). The sole known *Eopelobates* specimen with preserved gut material had consumed a small reptile before its death (Wuttke 1992a). This paleontological datum is consistent with its enrichment in ^{15}N, which indicates a tertiary consumer status (i.e., pri-

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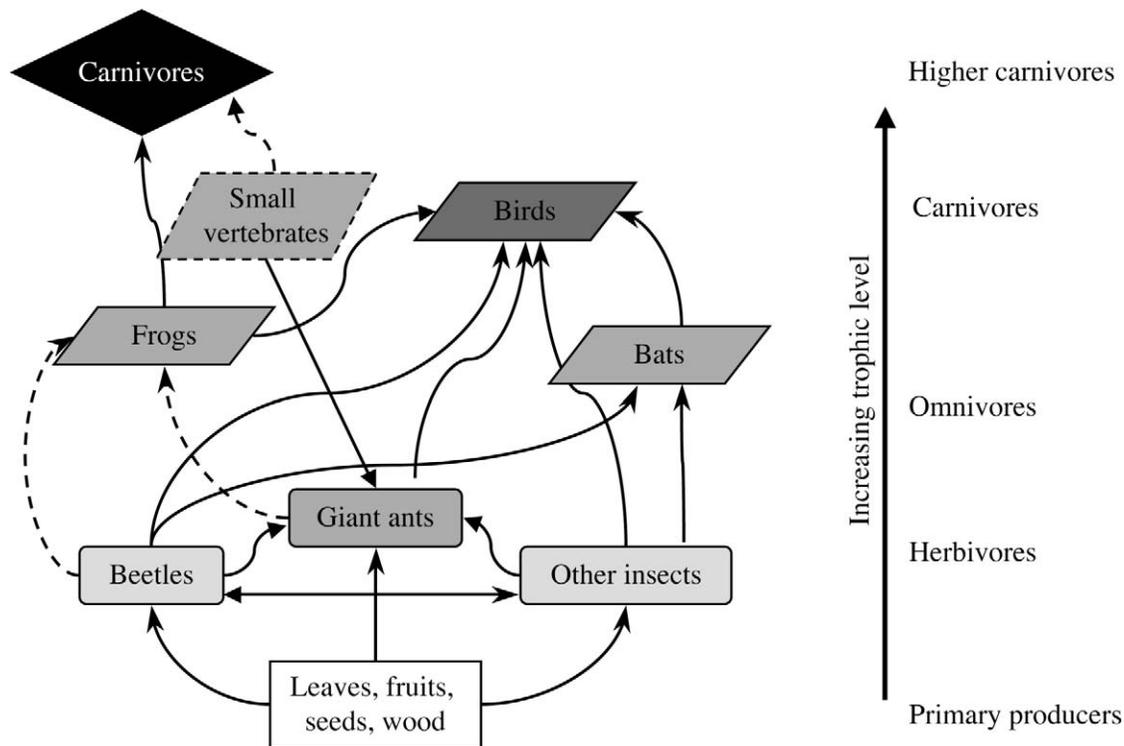File # 06TQ

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FIGURE 5. Flowchart based on stable isotopic evidence for trophic structure of the terrestrial ecosystem surrounding Lake Messel. Additional trophic components might include primitive horses and other such rare finds. Solid arrows represent relationships that are reflected in stable isotopic compositions; dashed arrows represent likely relationships according to paleontological and nearest-living-relative comparisons that were not tested using stable isotopes.

mary producer → insect → small lizard, amphibian, or mammal → *Eopelobates*).

Soft tissue isotopic compositions of two 8-cm (anterioposterior body length) bats span a whole trophic level and are consistent with a secondary or tertiary consumer's variable diet (Table 3). Messel *Archaeonycteris* bats are thought to have specialized in hunting insects in the midlevel trees of the tropical forest surrounding Lake Messel (Habersetzer et al. 1992), and their isotopic compositions presumably reflect the diets of the beetles and other insects they consumed (Table 2).

Nitrogen isotope ratios measured for three feathers (Table 3) span at least one trophic level and are consistent with any number of feeding strategies used by these birds. With an enrichment of 2.5‰ to 3.6‰ in $\delta^{13}C$ and 3.7 ‰ to 5.6‰ in $\delta^{15}N$ relative to diet (Peters 1992), two feathers can be traced back to a diet of beetles and other insects (Table 3). The highest feather $\delta^{15}N$ (+9.41‰) may have belonged to

a bird of prey, which fed on frogs or bats as well as insects. The avian fauna of Messel included birds of prey, ibises, fowl, cranes, rails, owls, woodpeckers, and even flamingoes and ostriches (Mizutani et al. 1992; Mayr 2005).

An isolated section of intestine, probably from a rare carnivorous terrestrial mammal (Schaal and Ziegler 1992), has the highest terrestrial $\delta^{15}N$ value in this study (+10.60‰). Given this value, the unknown organism may have hunted or scavenged frogs, birds, insects, or bats. Like the aquatic food web, the terrestrial ecosystem is characterized by interrelationships and mixed feeding strategies (Fig. 5).

Messel Ecosystem Dynamics.—The stable isotopic data record two nuanced, intertwining ecosystems associated with the Eocene Lake Messel: one in the lake itself and one inhabiting the surrounding rainforest. The trophic structure of this 47-Ma environment shares many characteristics with modern environ-

ments, including trophic isotopic enrichments, flexible, adaptive feeding strategies, and fractionation between tissues from a single organism. Paleontological studies confirm that many Messel fossil organisms were highly specialized and adapted to their paratropical lacustrine environment (e.g., Habersetzer and Storch 1987). Our stable isotopic data support paleontological evidence for symbiotic and parasitic relationships, for example, between caddis fly larvae and water lily leaves, and flowering plants and pollinating beetles (Schaarschmidt 1992).

Network structure parameters (see Dunne et al. 2002, 2004) extrapolated from the two flowcharts depicting generalized trophic relationships (Figs. 4, 5) are also comparable to those calculated for modern ecosystems. The connectance values (trophic links per species^2) of the terrestrial and aquatic food webs are $L/S^2 = 0.22$ and 0.23, respectively. These values fall within the upper end of the range reported for diverse modern ecosystems (approximately 0.05 to 0.3 [Dunne et al. 2004]). Link densities (trophic links per species) in Messel terrestrial ($L/S = 2$) and aquatic ($L/S = 1.85$) ecosystems are also within the range of modern networks, although at the lower end of the range. These parameters vary widely between modern lacustrine ecosystems (Williams and Martinez 2000, 2004; Dunne et al. 2002), and so it is possible that the values calculated for Messel's ecosystems accurately reflect their network structures. However, the absence of data for some species and entire groups no doubt skews the connectance upward because our trophic ''species'' in fact represent generalized groups encompassing some degree of variation, and some trophic species are not represented at all. The degree of omnivory (i.e., fraction of organisms feeding from more than one trophic level) observed in Messel food webs ($\sim$0.3 for both food webs) is also similar to modern values for terrestrial and lacustrine ecosystems (Dunne et al. 2002, 2004).

However, some puzzles remain. For example, Messel appears to have fewer trophic levels than expected for a lake of its size. In modern lacustrine ecosystems, the maximum trophic level depends more on lake volume than nutrient availability or primary production levels (Post et al. 2000). According to best-fit data on highest-trophic-level organisms in 25 North American lakes (Post et al. 2000), a lake of Messel's volume ($\sim$10^7 m^3) should have a maximum trophic level between 3.7 and 3.9, where

$$\text{maximum trophic level}$$
$$= \frac{\delta^{15}N_{\text{highest organism}} - \delta^{15}N_{\text{primary producers}}}{3.4\text{\textperthousand (avg. enrichment)}}.$$

For Messel,

$$\delta^{15}N_{\text{Cyclurus}} - \delta^{15}N_{\text{water-lily}} = 11.78\text{\textperthousand} - 5.78\text{\textperthousand}$$
$$= 6.00\text{\textperthousand},$$

corresponding to approximately two trophic steps of +3.4‰ each (Vander Zanden and Rasmussen 2001). There are several possible explanations for this discrepancy. As discussed above, trophic fractionation between organisms is determined by diet, and there may be substantial deviations from the canonical +3.4‰ enrichment. For example, the majority of Messel's organisms incorporated varying proportions of insects into their diets (Figs. 4, 5), where the fractionation between consumer and insect is typically +1.4‰ $\delta^{15}N$ (McCutchan et al. 2003). Additionally, extremely rare aquatic organisms such as turtles, crocodiles, and the less common fish species, which were not available for sampling, are all thought to be mostly or purely piscivorous, and may therefore constitute another partial or whole trophic level.

Finally, the elevated $\delta^{15}N$ values for primary producers at Messel may have condensed the apparent fractionation between bottom and top trophic levels. These high values may be due to original microorganism compositions or post-deposition alteration by continued nitrogen cycling. If the former is correct, then we would expect a food web with overall elevated $\delta^{15}N$ but sensible trophic separations, whereas if the latter is correct (and the sedimentary nitrogen cycling affected primary producer values but not fossil macroorganism values) we would expect only the bottom trophic levels to be condensed while the top trophic levels show typical fractionations. The data (Fig. 1) suggest that the latter is the case. The stable

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isotope data exhibit a sensible trophic ranking based on $\delta^{15}N$, although the lowest levels, composed of shale, terrestrial plants, insects, and even some *Thaumaturus*, overlap significantly. Despite these limitations, however, the stable isotopic compositions here reported for 47-Ma fossil organisms seem to broadly reflect trophic position and provide a tantalizing example of what stable isotopic reconstructions of ancient food webs may reveal.

Conclusions

Messel fossils contain sufficiently well preserved carbon and nitrogen compounds to allow stable isotopic decoding of ecosystem structure. A diverse aquatic ecosystem inhabited the lake, including primary producers (water lilies and algae), invertebrate consumers (insects and their larvae), and vertebrates (fish, turtles, and crocodiles). The stable isotopic compositions of many of these components show trophically sensible enrichments relative to food sources, enabling the reconstruction of a flow-chart food web that takes into account multiple feeding strategies for each organism. This food web, although in some cases based on average values for a large group of organisms (e.g., insects), is broadly compatible with existing paleontological models based on coprolites and gut contents. These data highlight the potential of stable isotopic studies to unravel ancient food webs and their ecosystems.

Trophic structure relates to aspects of ecosystem dynamics, including species diversity, biomass, biogeochemistry, and stability, all of which are critical to a thorough understanding of ecosystems in the past. The Messel flora and fauna share genera with other Eocene fossil deposits around the world, including *Diplocynodon* crocodiles and avian communities in Europe and North America (Peters 1991; Keller and Schaal 1992a). The biota is also similar to extant organisms in subtropical regions, including India (Habersetzer and Storch 1987) and South America (Storch and Schaarschmidt 1992). Indeed, modern Southeast Asian lakes have been proposed as the most appropriate modern analogues to Messel on the basis of environmental parameters (Rabenstein et al. 2004). Stable isotopic studies of the same, or related, species in these other locations would yield insights into their behavioral adaptations to distant and different environments to complement the paleontological studies of evolutionary morphological features. The apparent fidelity of stable isotopic signatures at Messel raises the possibility of further investigations into older fossillagerstätten, especially those with soft tissue preservation such as the Ordovician Soom shale of South Africa or any of several Early Cambrian sites.

Although carbon and nitrogen stable isotope compositions of Messel fossils broadly reflect those of the living organisms, basing an ecosystem reconstruction solely on isotopic data is not possible even at this exceptionally preserved site. Paleontological clues such as gut contents, coprolites, plant-insect associations, functional morphology, and nearest living relatives are essential for decoding the complex and overlapping isotopic values just as observations of organism behavior are supplemental to modern isotope studies.

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