

# Scientific drilling and biological evolution in ancient lakes: lessons learned and recommendations for the future

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**Abstract** Scientific drilling to recover sediment core and fossil samples is a promising approach to increasing our understanding of species evolution in ancient lakes. Most lake drilling efforts to date have focused on paleoclimate reconstruction. However, it is clear from the excellent fossil preservation and high temporal resolution typical of lake beds that significant advances in evolutionary biology can be made through drill core studies coordinated with phylogenetic work on appropriate taxa. Geological records can be used to constrain the age of specific lakes and the timing of evolutionarily significant events (such as lake level fluctuations and salinity crises). Fossil data can be used to test speciation and biogeographic hypotheses and flesh out phylogenetic trees, using a better-resolved fossil record to estimate timing of phylogenetic divergences. The extraordinary preservation of many fossils in anoxic lake beds holds the hope of collecting fossil DNA from the same body fossils that improve our understanding of morphological character evolution and adaptation.

Moreover, fossils allow calibration of molecular clocks, which are currently largely inferential. Lake Malawi Drilling Project results provide some guideposts on what might be expected in a drilling project for studies of evolution. The extreme variability in lake level and environmental history that most ancient lakes experience (exemplified by the Lake Malawi record) demonstrates that no one drilling locality is likely to provide a complete record of phylogenetic history for a radiating lineage. Evolutionary biologists should take an active role in the design of drilling projects, which typically have interdisciplinary objectives, to ensure their sampling needs will be met by whatever sites in a lake are ultimately drilled.

**Keywords** Ancient lakes · Scientific drilling · Speciation · Paleolimnology

## Introduction

Two central issues in the dynamics of speciation in ancient lakes are (1) the timing and (2) the environmental context of evolutionary events. The timing of events determines rates and constrains models of evolution. The environmental context can relate the evolutionary process to an extrinsic driver, such as lake level fluctuations, water chemistry changes or other ecological crises. This provides the most parsimonious approach to inferring evolutionary processes.

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Scientific drilling of ancient lakes is a promising means of collecting data on the timing of environmental change (Brigham-Grette et al., 2007; Walton et al., 2010). Data from drill cores can be used to evaluate hypotheses of when and why a particular lake has undergone major environmental changes, with a precision and resolution that cannot be equaled by other means, such as outcrop-based, geomorphological or geophysical studies. Drill cores have the potential to yield fossils of extinct and extant members of a clade under study, providing information about parts of the stem and crown in an evolutionary radiation that would otherwise be unavailable to us. In this respect, ancient lakes represent unparalleled opportunities for integrating detailed geohistory information into evolutionary studies in ways that are impossible for other model systems of species radiations and extinctions, such as islands, caves, or mountaintop habitats.

Here, I present a brief review of how and where drill cores have been collected in ancient lakes. I will consider some of the prior successes in applying scientific drill core data to understanding lacustrine speciation and extinction. Even lakes which lack significant endemism today may have much to tell evolutionary biologists once a thorough history of the lake is available; why species flocks are absent from some ancient lakes and present in others is a central question. Long core records can also provide a baseline for comparative biodiversity studies, for example for conservation purposes (e.g. Cohen, 2000). Finally, I recommend future scientific drilling studies focused on evolution that might take

advantage of the drilling communities' prior experience in obtaining relevant environmental records and fossils from ancient lakes.

### Drilling in ancient lakes

It may come as a surprise to many biologists interested in ancient lakes that a relatively large number of these bodies of water have been drilled, primarily for paleoclimate studies. If we take as an arbitrary cutoff for "ancient lake" as any continental water body whose history extends back in time at least 500 ka, then at least 15 such lakes have been, or soon will be, investigated through scientific drilling. However, the drill core records do not extend back in time half a million years for all of these (Fig. 1, Table 1). Additionally, there are several dry basins in California that have been drilled, which until the recent geological past held lakes, and which persisted for at least 500 ka. Finally, there are a number of sedimentary basins that have been both drilled and continuously cored (drilling is sometimes accomplished without the collection of a continuous core), which contain the deposits of long-lived lakes of potential interest to evolutionary biologists for their endemic species flocks.

### Why geologists drill lakes

Most of the extant ancient lakes shown in Fig. 1 were originally drilled for the study of regional

**Fig. 1** Map of showing locations of all lakes/lake basins described in text. Numbers refer to list of lakes/basin in Table 1



**Table 1** Ancient lakes that have been or will be drilled in the near future

Lake name/location	Lake age (Ma)	Max. water depth (depth at deepest sub-bottom drilling target)	Max. drilling depth in meters below lake floor or oldest core age at base of drill core)	Objectives	Taxa observed in drill core	Key references
<b>Extant lakes</b>						
1. Bear Lake (USA)	~6?	63 (51)	121 (0.22 Ma)	Test of GLAD-800 system/regional paleoclimate	Diatoms, Ostracodes	Rosenbaum and Kaufman (2009), Bright (2009)
2. Clear Lake (USA)	~0.65	18 (7.5)	177 (0.45 Ma)	Paleoseismology and paleoclimate	Diatoms, Ostracodes, Fish	Sims (1988)
3. Great Salt Lake (USA)	>5 Ma (but evidence for desiccation as recently as Late Pleistocene)	10 (9) based on 1280 m shoreline	121 (0.28 Ma)	Test of GLAD-800/regional paleoclimate	Ostracodes with L. Idaho affinities in selected intervals	Kowalewska and Cohen (1998), Balch et al. (2005)
4. Laguna Potrok Aike (Argentina)	0.77 Ma	100 (95)	101.5 (~85 Ka)	Paleoclimate	Diatoms	Zolitschka et al. (2009)
5. Lake Baikal (Russia)	~25 Ma	1741 (1428 m-discontinuous core)	600 (~8.4 Ma)	Paleoclimate	Diatoms	Colman et al. (2003), Horiuchi et al. (2003), Kuzmin et al. (2000), Kashiwaya et al. (2001)
6. Lake Khubsugul (=Hovsgol) (Mongolia)	Pliocene?	262 (232)	52 (~1.05 Ma)	Paleoclimate	Ostracodes, Diatoms	Poberezhnaya et al. (2006), Prokopenko et al. (2009)
7. Lake Biwa (Japan)	4.5–5.0 Ma	104 (64 m at 200 mbif core site)	1000 (lake margin, ~1.5 Ma; 200 lake center) ~0.5 Ma	Paleoclimate	Diatoms	Horie (1984), TuZino (2010)
8. Lake Bosumtwi (Ghana)	1.07 Ma	81 (74)	294 (lake sediments only) 1.07 Ma	Paleoclimate and Impact Cratering		Koeberl et al. (2007) Scholz et al. (2007)
9. Lake El'gygytgyn (Russia)	3.6 Ma	170 (170)	315 (lake sediment only) 3.6 Ma	Paleoclimate, Impact Cratering and Permafrost studies		Brigham-Grette et al. (2007)

Table 1 continued

Lake name/location	Lake age (Ma)	Max. water depth (depth at deepest sub-bottom drilling target)	Max. drilling depth in meters below lake floor or oldest core at base (estimated age at base of drill core)	Objectives	Taxa observed in drill core	Key references
10. Lake Malawi (Malawi, Tanzania, Mozambique)	>7 Ma (early Late Pleistocene dessiccation)	706 (593)	382 (0.5Ma?)	Paleoclimate	Diatoms, ostracodes, cichlid and cyprinid fish	Scholz et al. (2006, 2007), Cohen et al. (2007)
11. Lake Qinghai (China)	Early Pleistocene? (repeated desiccation)	28	115 m (1109 m at on shore hole but not all lacustrine). Age uncertain	Paleoclimate		Zhisheng et al. (2006)
12. Lake Titicaca (Bolivia, Peru)	2.8	284 (235)	136 (~0.38 Ma)	Paleoclimate	Diatoms	Fritz et al. (2007), Lavenu (1992), Dejoux (1994)
13. Lake Van (Turkey)	~0.8 Ma?	451	Drilling planned for near future for 375 m (est 0.5 Ma)	Paleoclimate		Litt et al. (2007)
14. Lake Ohrid (Macedonia, Albania)	2–5? (poorly constrained)	288	Drilling planned for near future	Evolutionary studies and paleoclimate		Albrecht and Wilke (2008)
15. Dead Sea (Israel, Palestine, Jordan)	Pliocene	308 (300)	Drilling planned for near future for 400 m (est. 0.6–0.8 Ma)	Paleoclimate		Stein (2001)
Currently dry lakes						
16. Owens Lake	? ~5 Ma based on sed. thickness	N/A (64 m when filled to spillway)	323 (0.8 Ma)	Paleoclimate		Smith & Bischoff (1997)
17. Searles Lake	~5 Ma?	N/A (197 m when filled to spillway)	930 (3.2 Ma)	Economic geology and paleoclimate		Phillips et al. (1983), Smith (2000)
Ancient lakes with endemic faunas in ancient (extinct) basins						
18. Paleolake Idaho (USA)	Miocene-Pleistocene. Glenns Ferry Phase ~3.5–2.4 Ma	est. ~380 m for Glenns Ferry lake	301 m (est. ~2.6 Ma)	Paleoclimate	Ostracodes	Malde (1991), Thompson (1996)

Table 1 continued

Lake name/location	Lake age (Ma)	Max. water depth (depth at deepest sub-bottom drilling target)	Max. drilling depth in meters below lake floor or oldest core at base (estimated age at base of drill core)	Objectives	Taxa observed in drill core	Key references
19. Paleolake Pannon (E. Europe)	Late Miocene-Early Pliocene (~12–4 Ma)		1150 m (Eichorn well in Vienna Basin)	Hydrocarbon exploration	Molluscs, Ostracodes, Dinoflagellates	Magyar et al. (1999), Harzhauser & Mandic (2008) and Harzhauser et al. (2008), Gross et al. (2008)
20. Bohai Basin, E. China	Oligocene		Up to ~4500 m	Hydrocarbon exploration	Ostracodes	Zhencheng (1984)
21. Messel, Germany	Eocene		230 m (lake sediments)	Paleoclimate, volcanic eruptions	Green algae	Lenz et al. (2010)
22. Songliao Basin, Eastern China	Cretaceous		~2,000 m (lacustrine sequences only)	Hydrocarbon exploration	Ostracodes	Ye (1988), Liu et al. (1993, 2010)
23. South Atlantic Paleolake Basins	Early Cretaceous (variable among basins)		Highly variable	Hydrocarbon exploration	Ostracodes	Moura (1988)
24. Newark Basin (USA and Canada)	Late Triassic-Early Jurassic (multiple lake phases)		~4,000 m	Paleoclimate and stratigraphic correlation studies		McCune et al. (1984), McCune (1996), Olsen et al. (1996)

The table includes extant lakes, lakes that are currently dry but retain their original basin morphology, and lake deposits from long-lived basins that are no longer active depositional systems. The column "Taxa observed in drill core" only includes those groups actually described or studied from cores to date, rather than all groups represented in the lake/paleolake

paleoclimates. However, in at least three cases (Baikal, Malawi, and Ohrid) evolutionary studies have either implicitly or explicitly figured in the drilling rationale behind the coring investigations. As we will see, these objectives are not necessarily compatible in terms of the specific scientific objectives and targeting of drilling sites within a given lake.

The attraction of old (and often deep) lakes for paleoclimatological drilling lies in the unique combination of attributes of sediments. In contrast to many other depositional systems, lakes undergo both rapid and relatively continuous sedimentation, making them ideal for obtaining highly resolved records of climate history. In ancient lakes (typically formed as a result of tectonic, volcanic, or meteorite impact processes), the advantages of high sedimentation rates and continuous sedimentation are compounded by the possibility of collecting a highly resolved record that also covers a long interval of time.

Two types of drilling targets have proven particularly interesting for paleoclimate studies (Fig. 2). Most commonly, drilling has been situated in the deepest stratigraphic basin(s) within a lake. This is where the largest amount of sediment has accumulated over a given interval of time, thereby providing greater stratigraphic resolution (i.e. less time represented per meter of sediment), making finer time-step sampling more practical) (column A in Fig. 2). This commonly (but not always) corresponds to the modern hydrologically deepest point in a lake. Since sedimentation is focused toward deeper areas by gravity (Hilton, 1985), deeper locations will tend to fill more rapidly than surrounding areas. Thus, over geological time scales the stratigraphic depocenters are controlled by long term subsidence, given that most ancient lakes have tectonic origins. Characteristically, paleoclimatologists prefer fine-grained muds as they are amenable to the greatest number of analyses for paleoclimatic reconstruction. In some lakes (particularly steep-sided extension basins, like rifts), the thickest accumulations of sediments occur remarkably close to the coastline because of their immediate proximity to a major boundary fault which provides maximal subsidence. These areas, while providing a potentially highly resolved record of sedimentation, are nonetheless undesirable targets for paleoclimate studies because of their large proportions of sand and gravel, much of which probably

undergoes redeposition in underwater channels, especially during periods of lake level fall (e.g. Scholz, 1995; Soreghan & Cohen, 1996; Morley & Wescott, 1999; Cohen et al., 2000 (see Fig. 2)). Sediment that has been disturbed by down-slope slumping, gravitational flows, and other forms of mass wasting, all of which commonly occur on steep slopes close to coastlines, has limited value for paleoclimate analyses, and are typically avoided during site selection.

Drilling targets can be aimed to maximize the time duration of the paleoclimate record rather than the resolution. Cost is a major consideration in determining drilling targets. Drilling is expensive and if the goal is to extend a record further back in time rather than to increase the resolution of that record, then a target that has experienced slow but continuous sedimentation becomes favorable. In large, bathymetrically complex lakes, mid-lake topographic highs provide just such an environment. These areas do not experience sedimentation resulting from down-slope transport by gravity flows that blankets most lake floors. Instead, they only receive sedimentation from the settling of fine (and often biogenic) debris that has previously been suspended in the water column. This process of open-water, suspension-settling sedimentation goes on annually, accumulating watershed materials, organic debris from plankton and fish, and atmospheric dust. But it occurs at a much slower aggregate rate than in locations where gravity flow transport is also involved. Therefore, very time-rich records can be collected from such sites with a relatively shallower drilling depth than that which would be required at the basin's depocenter (e.g. Kashiwaya et al., 2001; Burnett et al., 2010).

For both types of targeting, geologists collaborate closely with geophysicists to obtain relevant subsurface geophysical data (most commonly reflection seismic data) to image the structure and stratigraphy of the lake's sediment below the lake floor and to identify the most promising localities given all of the considerations above. Subsurface geophysics, combined with short cores (typically up to 10–15 m and collected at much less expense and effort than drill cores) provide the information on sedimentation rates, continuity of record and appropriateness of sediments for paleoclimate studies for a prospective drilling site (e.g. see Moernaut et al., 2010 for an excellent

example of this reasoning in the development of a drilling proposal). In fact, a similar approach would be needed for any type of targeting, regardless of objective, including drilling for evolutionary biology targets.

### What evolutionary biologists can learn from drill cores

Several types of information can be gained from drill cores of value to evolutionary biological studies, and these categories of information each dictate their own drilling objectives and targets. To some extent these targets overlap those of paleoclimatologists, a good thing when collaborative funding and team building in support of a particular lake drilling effort is being organized. But evolutionary biologists will also have their own unique objectives which must be clearly framed in the development of a drilling project. If these scientific goals are not clearly articulated the optimal drilling sites for evolutionary biology questions may be abandoned and the value of the drilling effort for understanding evolutionary dynamics will be compromised. The objectives can broadly be grouped into geological and paleobiological goals.

#### Geological goals

##### Age of lake basin

An obvious goal of a lake drilling effort from an evolutionary biologist's point of view might be to establish the timing of the initial formation of a lake. This could be critical, for example, in defining a maximum age for what appear (or independent, phylogenetic evidence demonstrates) to be intralacustrine radiations (e.g. Salzburger et al., 2002; Seehausen, 2006). Obtaining this information generally requires drilling to the base of the lacustrine deposits within the basin and dating those sediments, although there are special cases where independent evidence may provide a relatively precise age estimate in the absence of drilling (for example, in the ancient meteorite impact crater Lakes Bosumtwi (Ghana) and El'gygytyn (Russia), where ages of ejecta were already known long before the lakes were

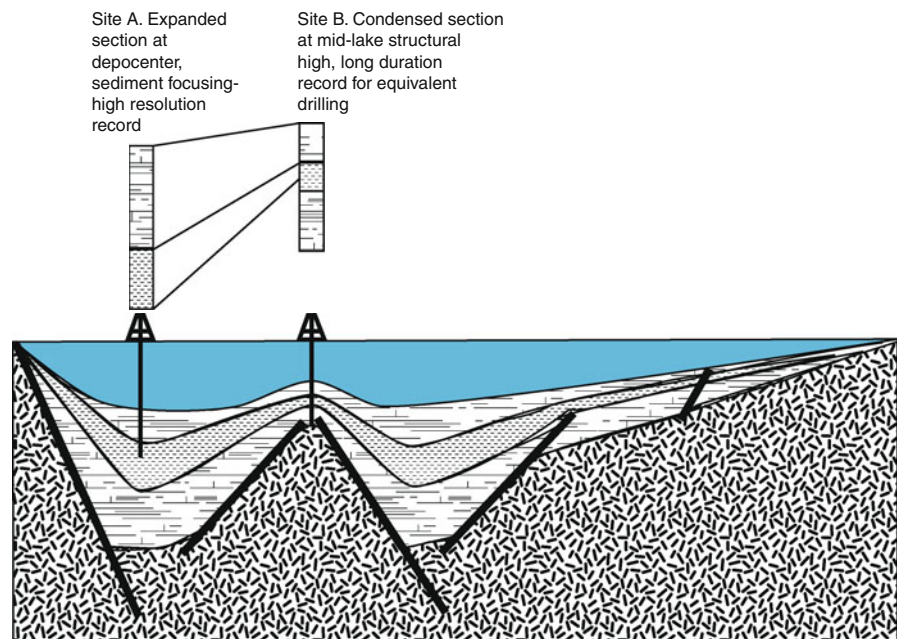
drilled (Koeberl et al., 1997; Layer, 2000). Drilling to the base of the lacustrine deposits has been achieved in several prior drilling projects (e.g., Lakes Bosumtwi and El'gygytyn mentioned above, as well as Lake Biwa) and is practical in even the oldest lakes by using an appropriate drilling strategy (for example in a condensed section on a mid-lake structural high-see Fig. 2, site B).

##### History of forcing events relevant to evolution

Sediment core records have proven extraordinarily valuable in determining the timing of important environmental forcing events, especially desiccation events, which can have the effect of either totally eliminating or severely reducing the diversity of an intralacustrine radiation. This would have direct bearing for example, in tests of evolutionary models such as the Founder-Flush Hypothesis (e.g. Schultheiss et al., 2009), which posits a bottleneck event in the diversity of a clade caused by some extinction-causing ecological crisis. An example of the power of such information to reshape our thinking about evolutionary histories lies in the discovery from sediment cores and reflection seismic data that Lake Victoria either completely or nearly completely dried up during the Late Pleistocene (Johnson et al., 1996). Although some systematists had suspected that the Lake Victoria cichlid radiation might be relatively young, at least in relation to those of the other African Great Lakes, this demonstration that cichlids must have largely repopulated Lake Victoria in the past 15,000 years profoundly influenced thinking within the "speciation in ancient lakes" community (e.g. Seehausen, 2002). This finding was quite controversial at the time among some evolutionary biologists, with some systematists vigorously arguing against the desiccation hypothesis (e.g. Fryer, 2001), albeit in the face of very strong geological evidence otherwise (Stager & Johnson, 2008). Arguably, the discoveries concerning Lake Victoria's geological history have also led to more nuanced and geologically complex hypotheses about the history of this lake's cichlid superflock (e.g. Verheyen et al., 2003), for example the demonstration using molecular genetic data that a refugia for the present Lake Victoria cichlid diversity probably existed in Lake Kivu (Elmer et al., 2009).



**Fig. 2** Typical drilling targets for paleoclimate history targets in a tectonically controlled (rift) ancient lake. Drilling at Site A, where fine-grained sediment accumulation is concentrated yields a thick sequence, where the highest temporal resolution sampling is possible. Site B, on a structural high, yields a longer temporal record for an equivalent drilling depth (and cost) but with slower sedimentation rates and lower temporal resolution



Just as the demonstration of desiccation events can place constraints on maximum ages for particular radiations, drill core records can also downgrade the probable importance of hypothesized forcing events of a particular age when the paleoenvironmental evidence points otherwise. Given Lake Victoria's near-total desiccation in the Late Pleistocene (toward the end of the Last Glacial Maximum-LGM), it might seem reasonable that similarly profound lake level falls would have also fundamentally impacted the other African Great Lakes, resulting in mass extinctions or at least severe diversity bottlenecks within various clades. In fact, it had been well established for over 30 years that aridification and lake level drops were widespread in tropical Africa during the Latest Pleistocene (e.g. Gasse & Street, 1978; Beuning et al., 1997; Barker & Gasse, 2003; Felton et al., 2007), roughly contemporaneous with the one documented for Victoria, and evidence of lake level declines had been documented for both Lakes Malawi and Tanganyika, although the exact magnitude of those lake level falls was not well constrained. The recovery of drill cores from Lake Malawi clearly demonstrated that LGM aridification and its consequent lake level fall (~100 m) had little impact on the lake's physical and ecosystem processes (Cohen et al., 2007; Stone et al., 2010), although population structure in littoral communities could certainly have

been affected by such changes (e.g., Peyreyra et al., 2004). Furthermore, the series of megadroughts which did profoundly affect Lake Malawi's level and chemistry during the early Late Pleistocene (~135–70 ka) had a much more muted effect on neighboring Lake Tanganyika (McGlue et al., 2007). The clear message from these findings is the occurrence of regional heterogeneity in both climate events and lake consequences; there is a danger in extrapolation from one lake's known history to another's unknown one.

In addition to lake level fluctuations driven by climate variability, there are other types of forcing or catastrophic events which could affect lake ecosystems and conceivably be recorded in drill cores. In regions that experience large and/or frequent volcanic eruptions, ejecta can have profound impacts on nearby lakes, from outright infilling of a basin by volcanic ash, to less severe or protracted ecological impacts (for example Spirit Lake, Mt St Helens; Larson, 1993). In ancient lakes that have formed adjacent to volcanic terrains, such as Pliocene paleolake Idaho (with its rich endemic fauna, existing on the fringe of the Yellowstone volcanic hotspot, e.g., Smith, 1987) a comparison could readily be made between paleobiological and volcanic tephra records, conceivably even from the same drill cores. Additionally, some meromictic ancient lakes



(especially in geothermally active rifts such as Lake Kivu, or lakes of volcanic origin) have episodic hydrothermal gas discharges from deep water, resulting in massive die-offs of animals in the epilimnion. Again, the record of such events is likely to be recorded in trace element or isotopic geochemical records retrievable from sediment cores (Haberyan & Hecky, 1987; Bernard & Symonds 1989; Couthures, 1989; Johnson & Scholz, 2010).

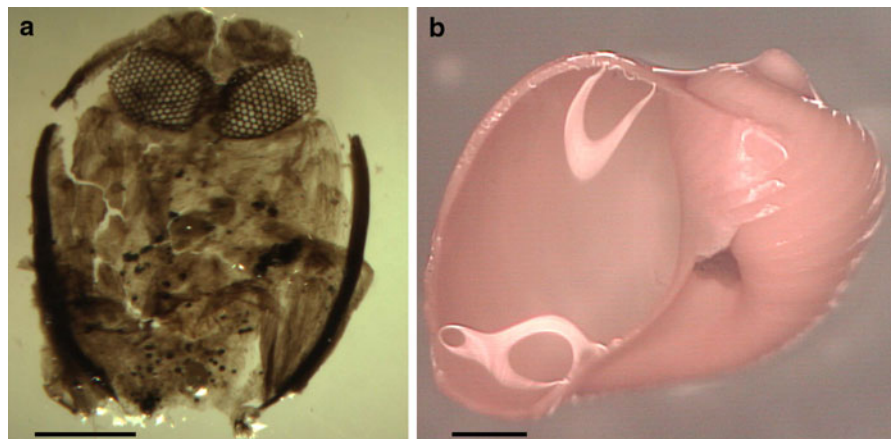
### Paleobiological goals

Besides providing a paleoenvironmental/paleoclimatic context for interpreting evolutionary history, drill cores can yield direct fossil evidence of that history. Most groups of organisms with recorded, important intralacustrine radiations are widely reported as fossils from lake drill cores, including diatoms, sponges, ostracodes, mollusks and fish, and even the skeletons of weakly sclerotized crustaceans and insects can be well preserved in fine-grained, anoxic lake sediments (e.g. Balch et al., 2005; Cohen et al., 2007). Typical drill core diameters (50–70 mm) dictate that only smaller organisms can be recovered as intact within a core. Thus, complete, articulated fish fossils are rarely encountered. However, during the initial core description of the Lake Malawi drill cores, intact or nearly intact specimens of the small endemic cyprinid *Engraulicypris sardella* were occasionally found by core describers. Mitigating against this recovery is the fact that since cores are typically cut and observed perpendicular to bedding planes, this

type of preservation is likely to be overlooked by casual observers and would need to be actively sought out by specialists.

As illustrated by the preceding examples, fossil preservation in lacustrine cores (particularly those from deep or meromictic lakes) can be extraordinary. Lake deposits have long been known for their exceptional examples of fossil preservation, called *Konservat Lagerstätten* (Seilacher, 1970), with many famous examples from the Eocene Green River Formation (Grande & Buchheim, 1994; Grande, 2001), Messel paleolake deposits (Franzen, 1985; Richter & Wedmann, 2005), and the Miocene Clarkia Formation (Smiley, 1985; Niklas et al., 1985; Logan & Eglinton, 1994; Yang & Huang, 2003). In most cases, the preservation of intact body fossils, soft tissues, and biomolecules as compression fossils on the bedding planes of extremely fine-grained sediments, make them less likely to be noted in drill cores, although non-compression lacustrine lagerstätten (inside concretions) are also known (Park, 1995). Features and body parts that are rarely preserved have been documented from drill core specimens. Examples include preserved shell color in gastropods (Malawi), soft tissues, and eyes in insects and crustaceans (Malawi and Great Salt Lake) and even lightly sclerotized fossil brine shrimp eggs (Great Salt Lake) (Fig. 3). This exceptional preservation opens the possibility of greatly expanding the suite of characters amenable for comparative phylogenetic analysis between living and fossil members of a clade. A remarkable example of extraordinary preservation specifically retrieved from drill core

**Fig. 3** Examples of extraordinary preservation in drill core fossils from Lake Malawi. **a** Nearly intact head from an insect, with muscle fibers evident and perfectly preserved compound eyes, age ~123 ka. Scale bar 0.25 mm. **b** *Lanistes* sp. juvenile showing preserved shell color, age ~135 ka. Scale bar 1mm



specimens is documented from the paleolake Messel oil shales (Richter & Wedmann, 2005). Coprolites (fossilized fish and mammalian feces) from this formation have yielded a wide array of lacustrine invertebrates and delicate body parts that are rarely preserved in sediments of this age, including fossilized cladoceran ephippia, respiratory horns of chaoborid pupae and mouthparts (ligulae), and eggs from chironomids.

#### Direct evidence of phylogenetic history from fossils

Drill cores can provide continuous chronological sequences of fossils that have the potential to be used to estimate times of divergences, reconstruct phylogenetic trees and infer tempo and mode of evolution. Fossils are useful in clarifying phylogenetic relationships because they can provide information on the direction of character evolution and convergence (Donoghue et al., 1989), and can be particularly useful in constraining ancestral character conditions and subdividing long branches (Donoghue et al., 1989; Huelsenbeck, 1991). The clarification of a clade's fossil record within a lake can reduce the uncertainty associated with the ages of divergence events, and, when used in conjunction with molecular data, better resolve phylogenetic relationships and the accuracy of evolutionary hypotheses based on these trees. Biomolecules and stable isotopes preserved in drill core fossils can also provide direct evidence of habitat preferences and diet for members of a species flock at various times (e.g. Reinthal et al., 2010), thereby potentially constraining ecological hypotheses of speciation and diversification.

Thick lacustrine sediment sequences, drilled primarily for petroleum exploration purposes, especially in Eastern China (Late Cretaceous-Paleogene), around the margins of the South Atlantic (early Cretaceous) and in Central/Eastern Europe (Mio-Pliocene Pannonian Basin) commonly yield abundant and diverse fossil ostracodes and molluscs, evidence of enormous species flocks in very large and long-lived lakes (e.g. Ye, 1988; Moura, 1988; Harzhauser & Mandic, 2008; Harzhauser et al., 2008). Similar biostratigraphic records of endemic diatoms have been assembled for Lake Baikal (e.g. Khursevich et al., 2005), holding out the additional promise of integrating modern and fossil species in a phylogenetic analysis. Studies of the

modern distribution of species within clades of readily fossilized organisms in lakes also suggest that it may be possible to infer the evolution of patterns of habitat specialization/niche partitioning from paleobiological records in drill cores (e.g. Park et al., 2000, 2002). In most cases, however, the documentation of these fossils has been for biostratigraphic purposes and only limited attempts have been made to develop explicit phylogenetic hypotheses regarding the species recovered.

Oceanic drill cores have provided microfossil records that have been extensively used to tests of models of speciation by documenting morphological shifts within lineages (e.g. Kellogg, 1975; Kucera & Widmark, 2000). By combining close interval sampling with careful morphometric measurements, of a single or small number of taxa, the timing and mode of morphological change, and in some cases selectional forcing, can be inferred. However, the temporal resolution of such studies has always been limited by the very slow rates of sediment accumulation in the deep sea (typically 0.01–0.1 mm year<sup>-1</sup>), coupled with the natural background sediment mixing processes (bioturbation in the upper few cm and sediment transport), which impose absolute limits on achievable temporal resolution of population changes. Microfossils in lake sediments could provide better temporal records for investigating fine-scale morphological evolution, since annual, or near annual-scale resolution in sampling can be readily achieved in many lake deposits (e.g. Bell et al., 2006; Hunt et al., 2008). Given this fact, it is all the more surprising that few studies have attempted to duplicate this approach in lacustrine drill cores. A striking example of what might be accomplished in understanding an evolutionary event using drill core records comes from a diatom study of Yellowstone Lake (Theriot et al., 2006). The authors conducted an analysis of the evolution of the endemic centric diatom *Stephanodiscus yellowstonensis* from its presumed ancestral morphospecies (the regionally common *S. niagarae*), using a ~8.5 m Küllenberg piston core, collected from the central part of the lake. The fossil record, spanning the last ~14,000 years was sampled at ~200 year time steps (16 cm increments), demonstrated the rapid evolution of *S. yellowstonensis* between 13.7 and 10.0 ka. This change corresponded closely to other paleolimnological changes evident in the record (diatom species

assemblage, biogenic silica concentration, lithology, and pollen), suggesting that the directional change observed in the diatom lineage had a selective origin.

The distribution of lacustrine endemic species in drill cores can also be used to record the biogeographic connectivity of ancient lakes. In a study of fossil ostracodes from drill cuttings (fragments of drilled material brought to the surface during drilling activity when continuous core is not being collected) from the Great Salt Lake Basin (GSLB, Utah, USA), Kowalewska and Cohen (1998) recovered cytherideid ostracodes that are closely related to species only otherwise known from Paleolake Idaho, which at the time lay ~150 km to the north of the GSLB. We showed that the temporal occurrence of these species in GSLB sediments (Latest Pliocene–Early Pleistocene) were concurrent with the history of Lake Idaho. Furthermore, we were able to demonstrate through stable isotope evidence that the direction of flow for the connecting waterway was from Lake Idaho to the south, with GSLB being a terminal lake basin at the time. This is particularly interesting from a paleohydrological standpoint because today the Snake River Plain lies at a lower elevation than GSLB. However, during the period when Lake Idaho was in existence, the passage of the Yellowstone Hotspot under the area had inflated and elevated the crust to the point that the topographic relationships and drainage interconnections were extremely different from today.

#### Fossil DNA from drill core?

The excellent preservation of organic matter in fine-grained lake sediments has allowed various research groups to extract intact or only slightly degraded biomolecules from these sediments, including fossilized DNA (e.g. Suyama et al., 1996; Coolen & Gibson, 2009). Although most studies to date on lake sediments have been focused on obtaining sequence information from lacustrine prokaryotes, fossil lacustrine metazoans as old as 10 ka have also been successfully amplified and sequenced. In a study of an Antarctic lake core, Bissett et al. (2005) sequenced DNA fragments from fossil copepod DNA preserved in bulk sediment and were able to successfully place these sequences in a phylogenetic tree constructed from living copepods found in nearby Antarctic lakes. Most work thus far has involved the extraction and amplification of DNA from bulk lake sediments.

However, DNA has been extracted and amplified from plant body fossils (pollen grains and leaves) preserved in lake deposits as old Early Miocene (Suyama et al., 1996; Golenberg et al., 1990). In most cases where DNA has been successfully collected and identified from lake sediments the host sediments are organic rich, derived from low-oxygen depositional environments such as deep lake, fine-grained muds or peat bog deposits, settings where organic matter degradation (especially pyrimidine oxidation) is minimized. In this regard, drill core samples are probably superior targets for molecular sampling over outcrops because oxidation and hydrolytic damage to organic compounds in the near-surface weathering zone is common (Petsch et al., 2000). A stratigraphic sequence of an endemic lineage that yielded both body fossils and DNA is possible from a drill core and could yield extraordinary new insights into the pace and drivers of intralacustrine evolution!

#### Observations from the Lake Malawi drill cores

Lake Malawi was drilled at two locations in 2005 (Scholz et al., 2006). Although the primary objectives were for paleoclimate studies, from the drilling project's inception evolutionary biological implications had been identified as an important secondary goal of the project (Cohen et al., 2000), given the important role the Lake Malawi cichlid fish fauna has played in our understanding of evolutionary biology.

Both drill sites were located in very deep water (592 and 359 m for central basin Site 1 and north basin Site 2, respectively) well below the modern oxicleine of this meromictic lake (Scholz et al., 2007). A planned site in the southern basin in much shallower water (which would be more frequently saturated with respect to calcium carbonate) unfortunately had to be eliminated from the project as a result of mounting costs. However, cores from both sites yielded extraordinary records of periods in the past when lake levels were much lower than present and littoral or even exposed conditions prevailed at both core sites. The most remarkable of these low lake stands known to date occurred during the early Late Pleistocene in several discrete events between 135 and 90 ka (Cohen et al., 2007). Evidence from fossil pollen, diatoms, charcoal, and elemental geochemistry (Cohen et al., 2007; Beuning et al., 2010;

Brown, 2010; Stone et al., 2010) all supported the idea that these low stands resulted from severe and protracted megadroughts, which also severely impacted other lakes in East Africa (McGlue et al., 2007; Burnett et al., 2010; Moernaut et al., 2010).

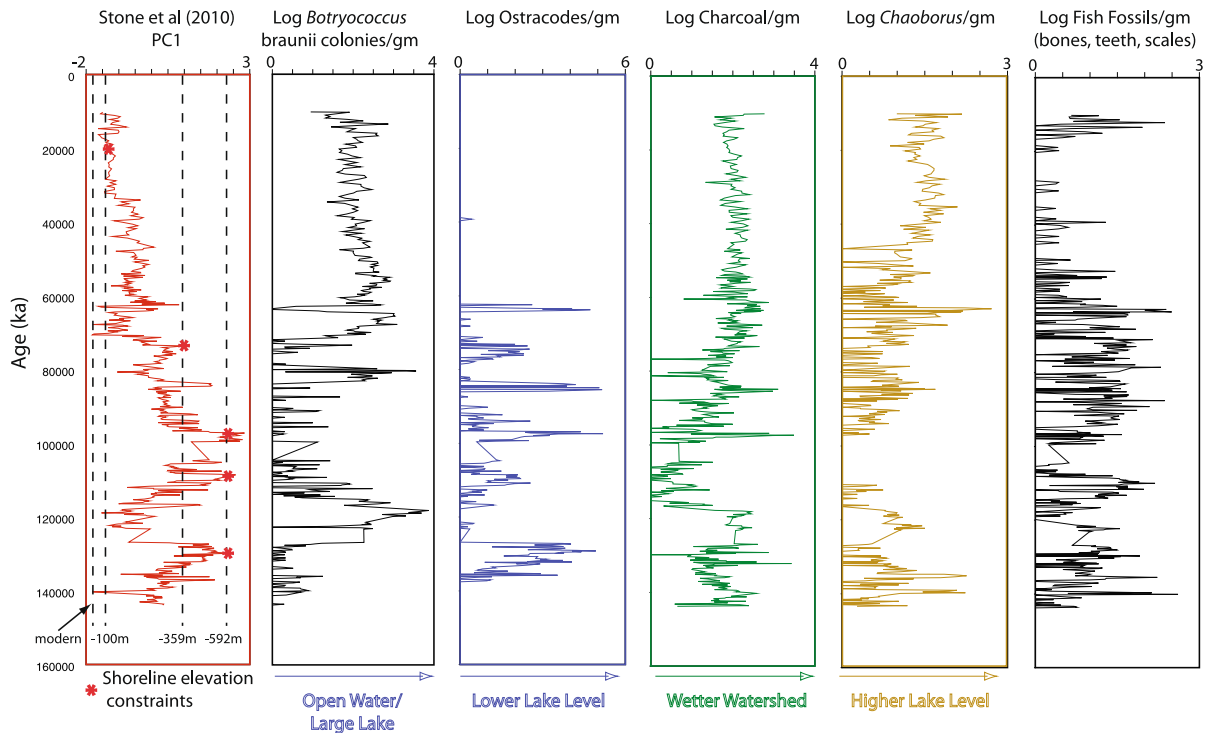
Paleobiological studies have been concentrated at central basin Site 1. The drill core sediments are richly fossiliferous, with diatoms, insects (mostly chaoborid lake flies but occasionally terrestrial insects as well), pollen, plant macrofossils and fish fossils found throughout, and benthic invertebrates (mostly ostracodes with occasional mollusks and sponges) occurring during the low lake stand intervals (Beuning et al., 2010; Park & Cohen, 2010; Reinthal et al., 2010; Stone et al., 2010) (Fig. 4). Fossils recovered also include numerous endemic diatoms and ostracodes, none of which have yet been subjected to detailed phylogenetic studies. However, the paleolimnological variables such as changes in lake level, water quality, and benthic habitat all have important implications for the evolutionary biology of this lake. During the megadrought phases of the early Late Pleistocene, Lake Malawi was reduced to a ~100 m deep body of water, with a tiny fraction of its current surface area. Importantly from the standpoint of its *mbuna* (rock dwelling) cichlid fauna, rocky habitat during this phase would have been nearly or completely eliminated from the lake's littoral fringe. Furthermore, the water quality of this much-reduced lake was very different than at present, with relatively eutrophic and turbid water prevailing. Given the demonstrable importance of water clarity for cichlid reproductive success and in preventing hybridization (Seehausen et al., 1997) these eutrophic soft substrate conditions can be expected to have radically altered cichlid communities, perhaps leading to widespread extinctions at this time. It is clear, however, from the presence of 130,000 year old tricuspid cichlid teeth (predating the later and most severe megadrought stages), that *mbuna* inshore benthic feeding strategies had evolved by at least that time and were not completely eliminated during the limnological reorganization that accompanied the megadrought (Reinthal et al., 2010). This is consistent with independent nuclear (0.7 ma) and mitochondrial (0.57–1.0 ma) molecular clock estimates of the timing of the origin of the *mbuna* (Won et al., 2006; Sturmbauer et al., 2001, respectively). Given that bedrock substrates were effectively eliminated

during the 115–90 ka period in Lake Malawi, perhaps some alternative hardground substrate existed in the littoral zone that would have supported the remaining *mbuna*, such as stromatolite-algal reefs, as occur in Lake Tanganyika today.

The Lake Malawi core record has another major implication for interpretation of evolutionary events in lakes. The cores show that for the past ~70 ka there have been no major lake level fluctuations of the magnitude that occurred in the early Late Pleistocene. For example, lake level decline during the Last Glacial Maximum (~35–15 ka), a period of known aridity in East Africa, were on the order of 50–100 m in Lake Malawi. Furthermore, diatom and other paleolimnological evidence suggest no major trophic or biogeochemical reorganizations of the water column or turbidity changes comparable to those observed for the megadrought period. This suggests that molecular clock calibrations that tie major cichlid diversification events to presumptive lake habitat expansion after the LGM in Lake Malawi are unlikely to be correct, since no major ecological event occurred at that time. Furthermore, the differential responses of the three largest African Great Lakes (Victoria, Tanganyika, and Malawi) to early Late Pleistocene and LGM aridity imply that alternative explanations aside from lake level fluctuations are required to understand the apparent synchronicity of molecular evolutionary rates observed in the three lakes (e.g. Sturmbauer et al., 2001; see Cohen et al., 2007, Supplementary Documents for further discussion). These results from Lake Malawi highlight the fact that molecular dating methods for phylogenies are very sensitive to the sources of calibration used, whether fossil or other, such as vicariance, events (e.g. Yang & Rannala, 2006). To the extent that future drill core environmental or fossil records can improve these calibrations, they will greatly improve subsequent tree reconstructions.

### Optimal drilling strategies for evolutionary biology studies

Given the wide range of potential evolutionary biology research objectives that might be pursued in future scientific drilling projects in ancient lakes, along with the demonstrable results from the Lake Malawi Drilling Project, how might we best design



**Fig. 4** Key paleobiological variables from Lake Malawi MAL-05-1C drill core (central basin, 592 m water depth) covering the last ~145 ka. See Cohen et al. (2007), Reinthal et al. (2010), and Stone et al. (2010), for details and methods. Over-penetration of the drill core resulted in a loss of the record for the last ~10 ka Stone et al. PC1 is the first principal component of the following data: relative abundance of seven diatom functional groups (periphyton, tychoplankton, littoral plankton, deep-water meroplankton, shallow-water/upwelling meroplankton, saline euplankton, and freshwater euplankton) plus the Shannon Index of diatoms, % vivianite, % terrigenous minerals, and log ostracodes  $g^{-1}$ . Planktonic diatoms are present throughout the core record. For horizons where absolute water depth data is available PC1 is highly correlated with depth, with lower PC1 scores (left) corresponding to higher lake levels (see *asterisked* lake level constraints with corresponding modern water depths). *Botryococcus braunii* is a colonial green algal phytoplankton species commonly found in core samples and in Lake Malawi today. Its abundance is strongly correlated with lake level and elsewhere it is considered a paleoecological indicator of open-water, large lake conditions (Jankovská & Komáraek, 2000). Ostracodes are absent from the core record for the last ~60 ka, since the lake floor at the drill site became too deep and anoxic to support benthic invertebrates. Benthic invertebrates only enter

future drilling projects to obtain the most informative records of evolutionary history? There is no simple answer because each ancient lake is unique and will present its own opportunities and challenges. However, there are some observations and

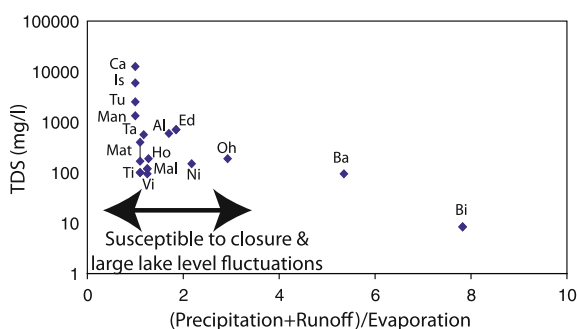
the fossil record at this deep-water drill site when lake level is very low and the ecosystem is stressed by high salinity. Charcoal abundance provides a record of fire activity in the watershed. During the peak megadrought interval (~115–95 ka), when lake area was reduced to <5% of modern, watershed vegetation was converted to semidesert conditions, with disconnected vegetation that could not sustain continuous fire (probably ~300–400 mm year<sup>-1</sup> or a third to a quarter of modern precipitation). *Chaoborus* sp. (probably *C. edulis*) or phantom midges are vertically migratory (diel migration) zooplankton and one of the dominant zooplankters in Lake Malawi today. Their modern abundance is associated with nocturnal feeding in surface waters and diurnal return to deep-water (anoxic) refugia. In the shallow southern basin of the modern lake, where anoxic refugia are less extensive, *Chaoborus* are less abundant than in the deeper water northern basin. Thus, the paleoecological pattern can be interpreted as indicating an elimination or near elimination of deep-water (anoxic) habitats during the megadrought period. Fish fossil abundance generally appears to reflect more extensive fish populations and higher numbers when littoral conditions prevailed at the drill site and conversely low abundances when the drill site was far offshore, although the top of the record is clearly anomalous in this regard

guiding principles of drilling relevant to all ancient lakes that are worth considering in developing such a project.

First, it is important to note the inherent environmental variability, especially in terms of lake level



and salinity, which exists in most of the extant ancient lakes of the world. Most lie in hydrologic/climatic regions where the ratio of precipitation + runoff to evaporation is low, and consequently most water is lost through evaporation, leading to high or potentially high salinities (Fig. 5). The only major exceptions to this generalization are Lakes Biwa and Baikal. As a result, most ancient lakes are highly susceptible to hydrologic closure and can be expected to experience large dynamic ranges of lake level over their history. Consequently, there is no single water depth where drilling is likely to capture the whole history of biodiversity in an ancient lake.



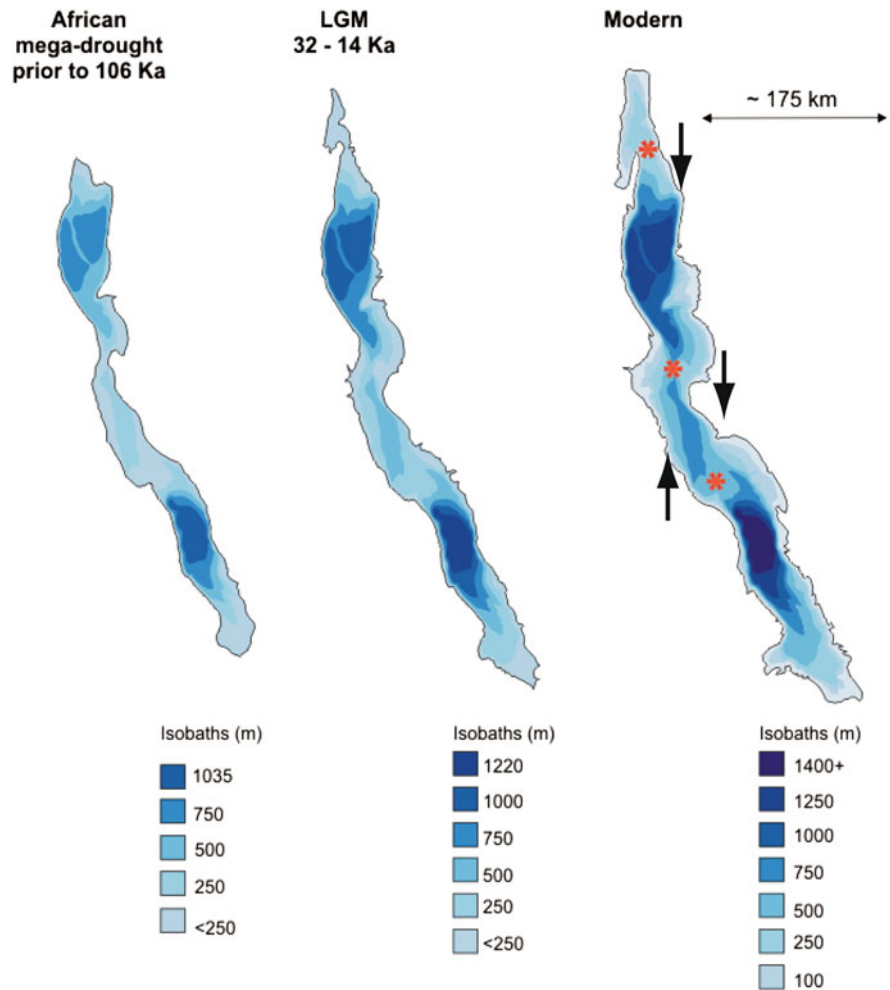
**Fig. 5** Precipitation + Runoff to evaporation ratio compared with total dissolved solids (salinity) for selected ancient lakes. The low (P + R)/E ratios and highly variable TDS for most ancient lakes is symptomatic of their susceptibility to both lake level swings and changes in salinity during periods of climate change, as most occupy deep structural basins. Abbreviations and data sources: *Al* Albert (<http://www.ilec.or.jp/database/afr/afr-11.html>; Lehman, 1996; Mohamed et al., 2004; Sutcliffe and Parks, 1999; <http://iahs.info/bluebooks/SP005.htm>, <http://www.iwmi.cgiar.org/wetlands/pdf/africa/contents.pdf>), *Ba* Baikal (Peeters et al., 1997; [http://www.eawag.ch/organisation/abteilungen/wut/schwerpunkte/umweltisotope/projekte/Salt\\_Budget\\_of\\_Lake\\_Baikal.pdf](http://www.eawag.ch/organisation/abteilungen/wut/schwerpunkte/umweltisotope/projekte/Salt_Budget_of_Lake_Baikal.pdf); Hohmann et al., 1997), *Bi* Biwa (Taniguchi et al., 2000; <http://www.ilec.or.jp/database/asi/asi-01.html>; Aota et al., 2002; Endoh & Tsujii, 2008), *Ca* Caspian Sea (Peeters et al., 2000; Clauer et al., 2000; Ghadiri et al., 2006), *Ed* Edward (Russell & Johnson, 2006; Lehman, 1996; Russell and Werne, 2007; Lehman, 2002; Beuning & Russell et al., 2004), *Ho* Hovsgul (<http://www.ilec.or.jp/database/asi/dasi51.html>); Fedotov et al., 2004), *Is* Issyk Kul (Meybeck, 1995; Garcia-Castellanos, 2006), *Mal* Malawi (Patterson & Kachinjika, 1995; Spigel & Coulter, 1996), *Man* Managua (Montenegro-Guillen, 2003; Huete, 1987), *Mat* Matano, (Lehmusluoto et al., 1999; D. Haffner, pers. comm), *i* Nicaragua (Montenegro-Guillen, 2003; Huete, 1987), *Oh* Ohrid (Matzinger et al., 2006, 2007), *Ta* Tanganyika (Branchu & Bergonzini, 2004), *Ti* Titicaca (Fritz et al., 2006; Delclaux et al., 2007), *Tu* Turkana (Spigel & Coulter, 1996; Cerling, 1996; Lehman, 1996), *Vi* Victoria (Spigel & Coulter, 1996; Lehman, 1996; <http://www.fao.org/docrep/005/t0473e/T0473E09.htm>)

For example, the deep-water Malawi drill sites, although appropriately sited for understanding paleoclimate history, do a relatively poor job of informing us about littoral conditions (where the diversity is highest) during high stands of the lake, such as the present. Conversely, had we drilled in a shallow-water location at Lake Malawi rather than the deep-water sites ultimately chosen we would have obtained a highly punctuated record of the lake's history, with relatively complete records during times of high lake stands separated by major unconformities marking the periods when the lake fell below the drill site elevation. The larger the lake's *dynamic range* of potential depths (a consequence of both the (P + R)/E ratio and the tectonically controlled accommodation space of its basin, the depth from lake floor to spillway elevation the more this becomes a problem). In larger lakes with multiple structural basins, such as Lake Tanganyika, the problem is further complicated by the fact that each basin will have its own unique spillway elevation. During lowered lake stands this could result in a possible combination of hydrologically open basins feeding into downstream closed basins (Fig. 6). Fortunately, determining the lake's dynamic range is a relatively straightforward exercise if good seismic stratigraphic data is available from pre-drilling surveys. Skilled interpreters of seismic reflection data can frequently infer sedimentary indications of both the highest and lowest levels reached by the lake during its fluctuations (e.g. McGlue et al., 2007; Scholz et al., 2007; Moernaut et al., 2010). This emphasizes the critical importance for evolutionary biologists to work in close consultation with seismic stratigraphers in developing a drilling plan to optimize fossil and relevant paleoenvironmental record recovery.

Given that no single drill site will tell the whole story we seek, what are the advantages/disadvantages of each different type of site? For rift basins (which make up the majority of ancient lakes globally), some generalities can be drawn by considering the depositional characteristics of these basins. The broad concepts discussed below, although focused on rift lakes, are generally applicable to any type of lake, once adjusted for basin morphometry, bathymetry, and sediment delivery patterns.

Most rift basins, at least during their earlier stages of development, consist of single or linked half-grabens, where one side or the other of the basin

**Fig. 6** Bathymetry and paleobathymetry of Lake Tanganyika at various water depths, including the modern lake (*right*), arid period of Last Glacial Maximum (*center*) and the early Late Pleistocene megadrought, modified from McGlue et al. (2007). The *asterisks* indicate points of potential hydrological basin separation based on modern tectonic and bathymetric thresholds. *Arrows* indicate probable direction of overflow for periods when sufficient runoff entered the upstream basin based on the inflow volume of modern rivers entering each sub-basin's catchment



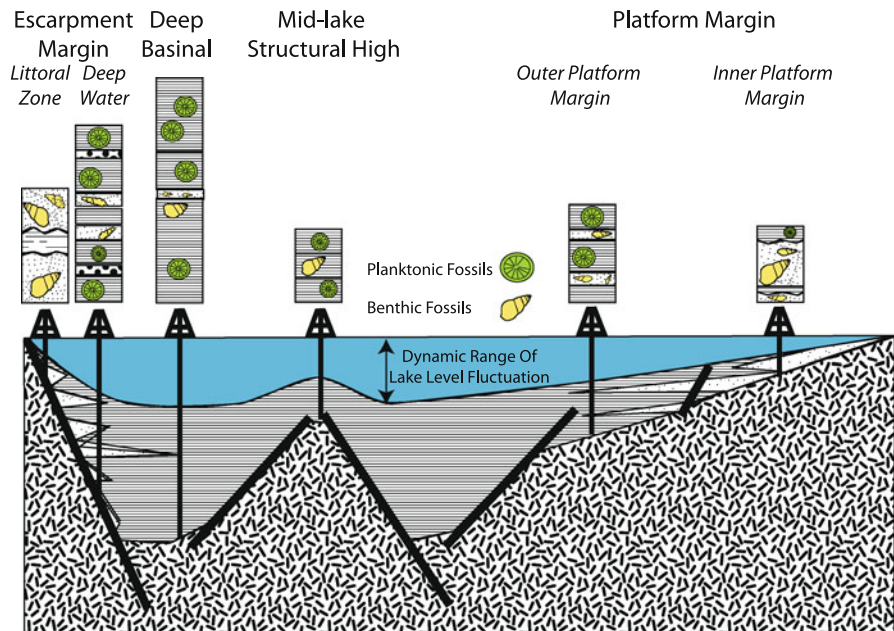
experiences the majority of the crustal extension being applied to the region (Rosendahl et al., 1986; Morley, 1999; Gawthorpe & Leeder, 2000). Typically that highly faulted margin of the basin (hereafter referred to as an escarpment margin) is opposed by a less faulted, structurally, and topographically gentler platform margin. The steepest slopes, deepest water depths, and greatest amount of sediment slumping are typically associated with escarpment margins, reflecting the underlying basin structure, whereas the platform margins tend to display shallower water depths and gentler slopes for a given distance offshore. Furthermore, large rift lakes are commonly comprised of several half-graben basins, which often alternate in their polarity along the axis of the rift valley (typically on scales of  $\sim 100$  km), such that a shoreline may alternate between escarpment and platform conditions. This tectonic

asymmetry imposes a depositional asymmetry in a rift lake, that in turn regulates the thickness and depositional continuity of fossil-bearing deposits that will be laid down as a lake cycles through its dynamic range (Cohen, 1990) (Fig. 7).

A hypothesized drill site from the littoral zone along the escarpment margin (where biodiversity is typically highest in most rift lakes) can be expected to reflect that diversity during periods of high lake stand. Furthermore, we can expect relatively good preservation of shelly ( $\text{CaCO}_3$  bearing) fossils, deposited above any local carbonate compensation depth (below which chemical corrosion of the fossils will occur). Weighed against these positive features, such a site will provide a very discontinuous stratigraphic record, highly affected by episodic gravity-driven transport of sediments (including fossils) with only high-stand conditions recorded and erosion



**Fig. 7** Model of probable fossil distribution and preservation patterns for a series of potential drill sites across a half-graben basin, based on the author's prior experience in drilling and short coring studies in North American and African ancient lakes



occurring during low lake levels. Gravity-driven transport at these locations will also result in relatively low resolution geological records, because of extensive time averaging of the deposits. Furthermore, from a technical drilling perspective this type of area is unfavorable because of its steep and unstable slopes. For full-graben lakes, this type of deposystem will exist along the fault-bounded escarpment margins on both sides of the basin,

A deepwater drill site along the escarpment margin would eliminate the problem of numerous stratigraphic gaps present in the littoral site record and would give a continuous record of planktonic species and potentially of benthic ones as well. Those benthic fossils, however, would include a significant proportion of transported material from upslope with locally derived fossils. Furthermore, during high-stand conditions, shelly fossils from a deep-water site may be subject to corrosion (below CCD). As a result, fossils from shallow-water at this site may be abraded and corroded. Conversely this type of site could produce a well-preserved record of low stand fossils formed under more stressed (higher salinity) conditions. Finally, sand and gravel from gravity transport off the escarpment margins may make this area problematic for drilling (and obtaining continuous core recovery), and because of its potentially coarse-

grained texture is unlikely to be a high priority for concurrent paleoclimate studies.

A deep basinal site (between sediment delivery sources from the two margins) is generally optimal for comparative paleoclimate studies and many lake drilling sites (such as Malawi Site 1) have been located in this setting. Such a site can yield a continuous record for planktonic fossils, especially diatoms. Benthic organisms on the other hand will be limited to low stand (and therefore stressed) conditions in warm water lakes, or to profundal communities in higher latitude/hardwater lakes with seasonal mixing. Drilling and coring conditions in this setting are optimal because of the fine-grained texture of the sediments, although in very deep lakes these sites may be more expensive to drill because of additional technical complications associated with operations in greater water depths.

A site on the outer (i.e. deep water) part of the platform margin, centered within the lake's dynamic range of lake level fluctuations, might provide a good choice for an evolutionary biology-focused study. The stratigraphic record here would be relatively complete and would capture the most interesting littoral communities at the middle of the dynamic lake level fluctuation range, where the community is less stressed than would be the case for the

basin-floor site. Core-based studies in this type of environment (e.g. Palacios-Fest et al., 2005) indicate that benthic invertebrates as well as planktonic fossils are likely to be preserved. Some complications may arise in these sites because of dynamic shifts in nearby deltas but these can often be foreseen with careful planning and review of available seismic data. This type of site would be a good choice for evolutionary biologists if they are limited to a single site for drilling. Similar records might be obtained from mid-lake structural highs, depending on their actual elevation within the dynamic lake level range of the lake, but will have lower sedimentation rates and stratigraphic resolution for reasons discussed previously (although this may be a plus if the goal is to obtain a very long temporal record).

An inner platform site, like the littoral escarpment site, would produce a discontinuous record of high-stand communities with no low stand record. However, this record would be superior stratigraphically to the escarpment site since platform margins are areas of greater sediment delivery and what records do come from these areas would be of higher resolution. In fact, fossil assemblages from this type of rift lake setting are often spectacular and have generated much interest (and controversy) for evolutionary biology studies in the past (e.g. Williamson, 1981; Cohen & Schwarz, 1983; Cohen, 1989). Fossils from this setting can be very well preserved (although coating and abrasion is common in hardwater lakes). Records may be more discontinuous for planktonic fossils because of shallow-water reworking. Again, drilling in very sandy deposits may be problematic.

Clearly, no single drill core location can provide a complete record of biodiversity in an ancient lake. Therefore, evolutionary biologists interested in obtaining these types of records must either plan to drill multiple cores in different settings, or, if that proves impractical, be prepared to modify their objectives to address specific questions appropriate to the selected drill core site. Prior experience shows that successful drilling projects in lakes often have multiple objectives, including studies of paleoclimate, meteorite impact, and environmental hazards (e.g. Koeberl et al., 2007; Brigham-Grette et al., 2009 and [http://www.geo.umass.edu/lake\\_e/pdfs/May2009PressRelease.pdf](http://www.geo.umass.edu/lake_e/pdfs/May2009PressRelease.pdf)). While this strengthens the argument for drilling a particular lake, it also weakens the case for any single one of these objectives, whose

drilling needs may not be (and typically are not) identical. Thus, the development of any drilling project invariably involves compromises between the objectives of its different proponents. Paleobiologists and evolutionary biologists would do well, therefore, to come to the bargaining table well-prepared in terms of identifying and articulating their drilling needs as the project planning itself evolves from a good idea to an executed drilling project.

## Conclusions

Most scientific drilling in lakes to date has been directed primarily at obtaining high resolution paleoclimate records. However, the attributes of long sedimentary records, coupled with potentially detailed and continuous fossil records, make ancient lakes particularly attractive targets for studies in evolutionary biology. Both geological and paleobiological information from drill cores is likely to be useful to biologists and paleobiologists studying ancient lakes.

Relevant geological information includes determining the age of the lake basin itself (for example placing a maximum age on any intralacustrine radiations). Geological data (here including paleoecological data) may also be useful in determining the history of environmental forcing events, such as lake level fluctuations, salinity crises, volcanic eruptions, and habitat availability, etc. which may have severely altered ecological conditions in the lake, and promoting speciation or extinction events.

Paleobiological information encompasses the morphological and biogeochemical record of the endemic species/species flock(s) being studied. The exceptional preservation often found in lacustrine fossils (including soft tissues in some cases) has long suggested that important questions in evolution might be attacked by sampling continuous stratigraphic sequences. For modern lakes, where outcrops are absent, drilling provides the only means of recovering such fossils, and even in cases where extinct “ancient lakes” are being studied, drill core samples provide preservational characteristics (notably lack of prior weathering) that makes them superior to outcrop-derived samples. Drill cores can yield a direct record of the evolutionary and ecological history of a clade at a sample site, including the timing and rates of

changing preferred habitat, diet, speciation, and extinction, and when coupled with paleoenvironmental data provides possible explanatory mechanisms for those events. The possibility of integrating morphological data with fossil DNA from the same specimens could open up an entirely new arena in phylogenetic investigations and tree reconstructions; in ancient lakes this would likely be better achieved than in almost any other imaginable depositional environment, given their combination of duration and potential for preserving intact DNA.

Prior studies at Lake Malawi and from other drilling projects suggest potential strategies for obtaining high quality core records relevant to both the geological and paleobiological goals mentioned above. Many geological and limnological settings might be promoted as drilling targets within a lake and none are perfect in all respects. The advantages and disadvantages of shallow versus deep-water sites or sites near steeply sloping rocky coasts (with their typically high diversity) versus sites away from these areas all need to be weighed against the specific scientific objectives of the evolutionary study envisioned. Compromise with other scientists promoting drilling the same lake but with different objectives is a certainty and evolutionary biologists would do well to clearly articulate their drilling needs early in the process of drilling project development.

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### Author Biography



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