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# ENVIRONMENTAL CONTROLS ON SHELL-RICH FACIES IN TROPICAL LACUSTRINE RIFTS: A VIEW FROM LAKE TANGANYIKA'S LITTORAL

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## ABSTRACT

**Lake Tanganyika, the world's largest tropical rift lake, is unique among its counterparts in East Africa for the remarkable diversity of mollusk-rich sediments in its littoral zone. Molluscan shell beds are, however, a common feature of ancient lacustrine rift deposits and thus a better understanding of their spatial and temporal development is important. Targeted surveys across the littoral region of the Kigoma Basin reveal three surficial shell-rich facies that differ widely in depositional style and geometry. A unifying characteristic of these deposits is the volume of shells of *Neothauma tanganyicense*, a large, viviparous gastropod endemic to the lake. Reservoir-corrected radiocarbon dating indicates that *Neothauma* deposits in these surficial sediments are time averaged over at least the last ~1600 calendar years BP. Preservation of fossil *Neothauma* shells in the littoral zone depends on both environmental conditions and on post-mortem shell modifications. Interaction between shells and mobile siliciclastic grains, facilitated by wave action and storms, represents a particularly destructive taphonomic process in the study area. Rank scoring of damage to *Neothauma* suggests that stromatolitic encrustations or early calcite coatings may help mitigate shell destruction caused by hydraulic fragmentation and abrasion. Persistence of *Neothauma* in littoral beds has important implications for the structuring of specialized communities of shallow-water benthos, as well as for improving analog models for hydrocarbon reservoirs in lacustrine carbonates.**

## INTRODUCTION

The inland waters of tropical East Africa have been a subject of curiosity since the mid-19th century, when explorers commissioned by the Royal Geographical Society (RGS) in London began searching for the source of the Nile River. The second RGS expedition, famously led by R.F. Burton and J.H. Speke, introduced the western world to several of the Great Rift Valley lakes, including Lake Tanganyika (LT). Since that time, LT has been the subject of many decades of rich scientific inquiry, spanning such diverse fields as evolutionary biology, limnogeology, and paleoclimatology. Today, the lake is recognized as one of the most biologically diverse fresh-water ecosystems found anywhere on Earth (Kawanabe et al., 1997). LT is especially noted for its endemic fauna, which includes species flocks of cichlid fish, crabs, and gastropods (Coulter, 1994; Cumberlidge et al., 1999; West et al., 2003).

Due to their sediment-producing potential, organisms with carbonate hardparts lie at an important interface between bio- and geosystems in lake basins. In LT's littoral zone, endemic mollusks produce conspicuous biogenic carbonate accumulations. Cohen and Thouin (1987) first documented the presence of these nearshore coquinas, while subsequent expeditions mapped similar surficial deposits in water depths up to ~70 m (Tiercelin et al., 1992; Soreghan and Cohen, 1996). In most cases, these deposits are dominated in biomass by shells of the gastropod *Neothauma tanganyicense* Smith, 1880. Hereafter, we will refer to this snail by its generic name alone for convenience. The species is relatively well known to ichthyologists, as numerous fish utilize these gastropod shells as their breeding substrate (Sato and Gashagaza, 1997; Gordon and Bills, 1999; Koblmüller et al., 2007). From a geologic perspective, however, many important questions regarding *Neothauma* and the accumulations they help form remain unanswered. For instance, detailed facies and taphonomic analyses have not been attempted. Studies focusing on geochronology are likewise absent. As a consequence, little is known about the accumulation history of these deposits. This knowledge gap is striking considering the importance of lacustrine shell beds in the rock record, both as archives of paleobiologic information and as hydrocarbon reservoir rocks in continental rifts (Williamson, 1981; Abrahão and Warme, 1990; Chang et al., 1992; van Damme and Pickford, 1999).

The goal of this study is to provide a thorough analysis of *Neothauma* shell accumulations found in the littoral zone of the Kigoma Basin, western Tanzania. Our approach has been threefold. First, field data were used to refine facies characterizations of these deposits. Second, radiocarbon dating was done on *Neothauma* shells from each newly defined facies to provide preliminary constraints on the extent of time averaging within accumulations. Finally, we performed taphonomic analyses on *Neothauma* in order to evaluate post-mortem damage across different littoral environments. Whereas numerous taphonomic studies have been conducted on invertebrates in marine environments (e.g., Davies et al., 1989; Meldahl and Flessa, 1990; Best and Kidwell, 2000), similar studies on lacustrine systems are comparatively rare. Our integrated assessment brings new focus on the mechanisms of shell-bed development and preservation in the littoral zones of continental rift lakes. Post-mortem *Neothauma* shell survival appears to influence, and potentially structure, a number of specialized benthic communities within LT—a far-reaching implication for future biodiversity, conservation, and paleobiologic studies in the basin.

## BACKGROUND

### Geologic Setting

Lake Tanganyika, situated between 3°S and 9°S in East Africa, is the world's largest tropical rift lake (Fig. 1). Most geologic evidence suggests that LT formed during the middle Miocene (9–12 Ma; Cohen et al., 1993; Nyblade and Brazier, 2002). At present, the lake occupies several linked half-graben basins and acts as a mixed carbonate-siliciclastic depositional

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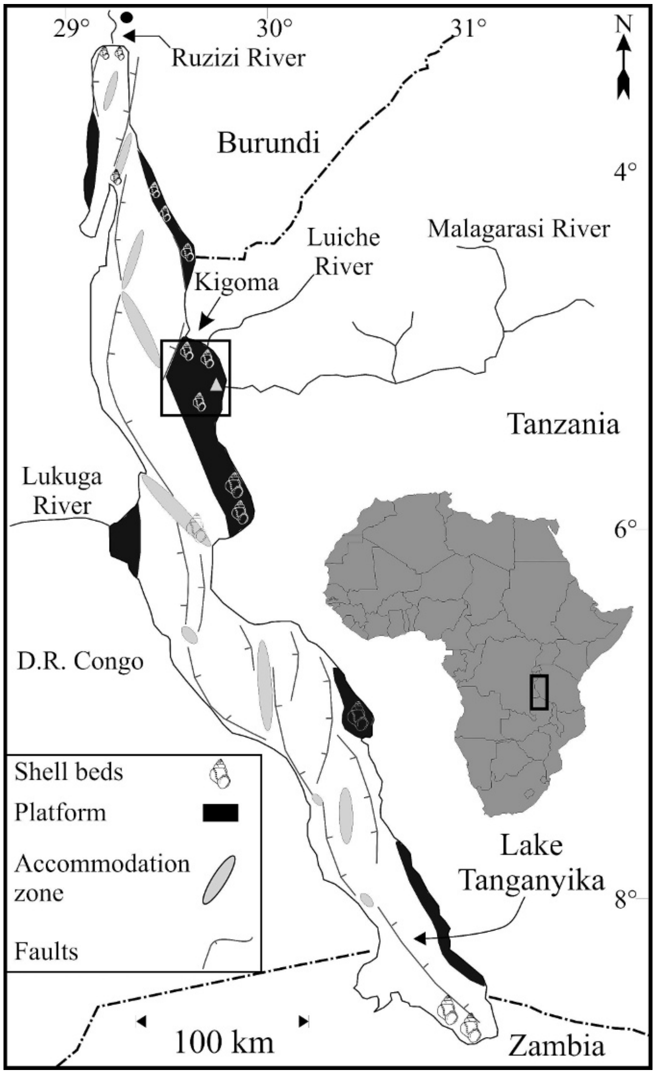

**FIGURE 1**—Overview map of Lake Tanganyika, tropical East Africa. The study area (outlined in box) is located near the town of Kigoma, Tanzania. Known shell beds are combined from the authors' research experiences and records from Leloup (1953). Allochemical sandstone samples (see Fig. 5 and text for details) were collected from paleo-highstand deposits on the Ruzizi River plains (dot at top). Triangle in study area is the location of core T97-1VC (see Fig. 8).

system strongly influenced by both tectonics and climate (e.g., Soreghan and Cohen, 1996). Lake Tanganyika has a volume of ~19,690 km$^3$ and reaches a maximum depth of ~1470 m in its southern basin (Rosendahl, 1988; McGlue et al., 2008). The lake is hydrologically open, draining to the west via the Lukuga River (Fig. 1). Lake waters are slightly conductive due to the warm monsoonal climate (20–24 °C mean annual temperature [MAT]) and significant yearly losses due to evaporation. Lake Tanganyika is saturated with respect to carbonate due to cation-rich input from the Ruzizi and Malagarasi Rivers (Haberyan and Hecky, 1987; Casanova and Hillaire-Marcel, 1992). Small hydrothermal vents in northern LT indicate the potential importance of groundwater to the lake's ionic composition and alkalinity, but extensive datasets from other coastal regions are lacking (Tiercelin et al., 1993). Southerly wind-driven waves impact the lake's littoral zone during the dry season (May–September), and wind speeds over historic times have ranged up to ~11 m/s (O'Reilly et al., 2003).

### Study Area

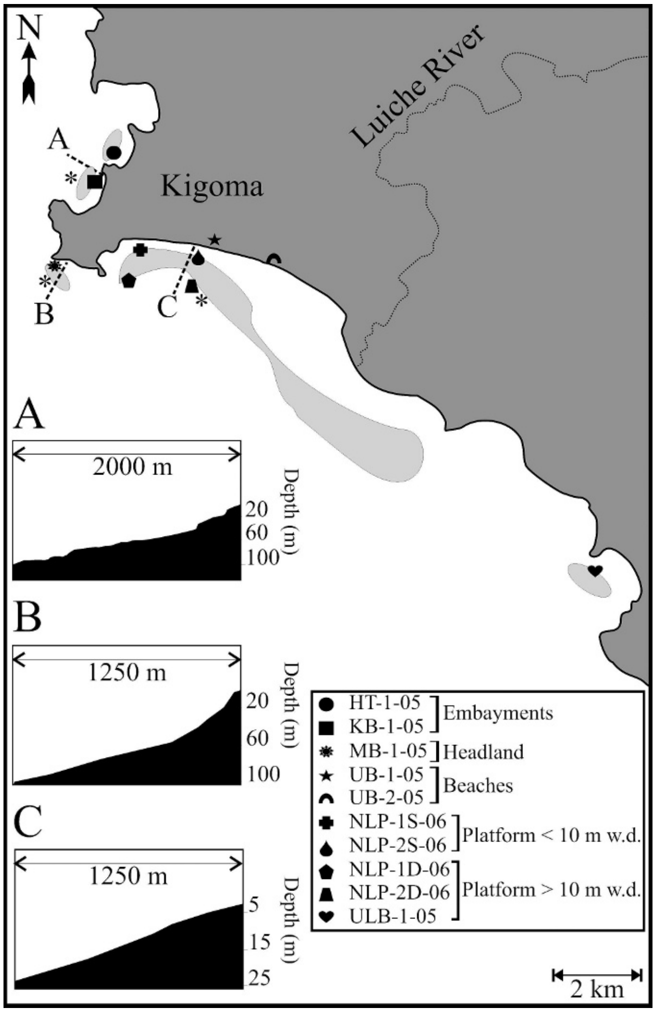

**FIGURE 2**—Study area enlarged from box in Figure 1. Symbols used for sites are the same as those used for ternary taphograms (Fig. 7). Bathymetric profiles A, B, and C illustrate the difference in lake-floor gradient across the littoral zone. Pale gray areas denote approximate known extents of *Neothauma*-rich facies. Asterisks denote locations where samples of well-indurated equivalents of modern unconsolidated facies were discovered. w.d. = water depth.

The study area is situated along the shoaling margin of the lake's central basin near the town of Kigoma, Tanzania (Fig. 2) and along the flexural margin of the Kigoma basin. Kigoma's nearshore region displays four geomorphic environments: (1) fault-controlled headlands, (2) embayments, (3) beaches, and (4) a delta. Headlands are characterized by steep outcrops of Proterozoic quartzite and cobble-dominated beaches. Embayments are typically narrow (<2 km in breadth) cuspate environments with sand to cobble beaches. Commonly, bays are separated from one another by promontories with significant (>50 m) topographic relief. The lake floor associated with headlands and embayments exhibits stepped or ramp-like morphologies with high gradients (Fig. 2). Conversely, the bathymetry of the Luiche River delta resembles a platform; the lake floor has a low gradient over ~3 km from the river mouth, but abruptly ends at a westward dipping slope. Beaches located northwest of the Luiche delta are moderately wide (~50–150 m), sandy, and lack significant vegetation.

### Target Taxon

*Neothauma tanganyicense*, the most common large bioclast in littoral shell carbonates, is a species of viviparous gastropod endemic to LT (Fig. 3). Van Damme and Pickford (1999) have proposed that the genus evolved early in the Miocene, based on fossil occurrences in the Lake Albert Basin. *Neothauma* is considered a relict endemic of a more

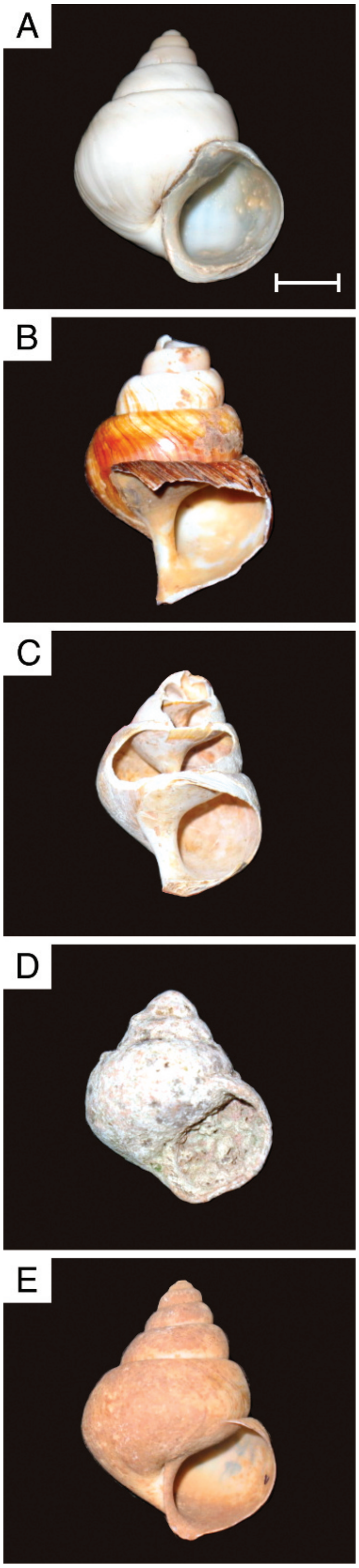

**FIGURE 3**—Examples of *Neothauma* and different damage states. Scale bar = 1 cm. A) Undamaged, dead *Neothauma*. B) Heavy mechanical fragmentation damage (score = 2). C) Heavy abrasion damage (score = 2) typical of samples encountered in beach ridges. D) Shell sample from the headland site with heavy stromatolitic encrustations (score = 2). E) Oxidation patina on sample collected along the 20 m isobath on the Luiche River deltaic platform (score = 2).

widespread, diverse clade, but it is closely related to *Bellamya*, which includes a number of extant African species (van Damme and Pickford, 1999; Sengupta et al., 2009). *Neothauma* is thought to comprise a single living species and thus contrasts with the highly diverse cerithioid snail clades in LT, some of which occur in shell-rich facies but generally account for a trivial proportion of the total biomass.

*Neothauma* are recognizable by their smooth, globose shells with rounded whorls, sinuous growth lines, dextral coiling, and obtuse protoconch (Brown, 1980). Shells display determinate growth and typical adult heights range between 35 and 65 mm (Leloup, 1953). Shells of live animals range in color from white to light brown to gray (Fig. 3A). *Neothauma* distribution is patchy but lakewide, with known shell beds indicated in Fig. 1. Although few published data exist on *Neothauma* ecology, early dredge surveys and recent SCUBA sampling have encountered live *Neothauma* in water depths up to 50 m on a wide range of sandy, muddy, and shelly substrates (Leloup, 1953; E. Michel and G. Kazumbe, personal observations, 2006). *Neothauma*-rich facies are absent beneath LT's chemocline (80–150 m water depth), as anoxia and alkalinity limit snail habitat and enhance corrosion of shell carbonate, respectively.

## METHODS

Dead *Neothauma* shells were collected from lake-floor substrates using SCUBA and a variety of hand-operated devices, including scoop samplers and box cores. Divers described deposits in the field following the methods outlined in Kidwell et al. (1986) and Kidwell and Holland (1991). Modern facies nomenclature follows the recommendations of Schnurrenberger et al. (2003) for lake sediments. In some cases, lithified *Neothauma* deposits occur just beneath unconsolidated lake-floor deposits or in older outcrops on the lake plain. Samples of this kind were sectioned for microfacies analysis and examined using a Leitz Ortholux petrographic microscope with a Luminoscope ELM2A cathodoluminescence (CL) adapter.

At each site, shell collections were made from the upper 10 cm of the lake floor in order to complete a comparative biostratinomic analysis (Table 1). Sampling along the Luiche River delta was accomplished by swimming depth transects orthogonal to the shoreline (NE to SW; Fig. 2). Depth transects provided the opportunity both to evaluate the spatial extent of shell-rich accumulations, as well as to collect shells from representative sites in both shallow and deeper water. Presence-absence counts of erect sponges, which commonly grow on shell beds, were also collected during these transects. Because *Neothauma*-rich accumulations along headlands and bays are spatially restricted, shells were collected along lines that crossed several isobaths at these sites. At beach sites, shells were retrieved from representative deposits. In all cases, shell samples were labeled and securely packaged to minimize damage during transport. Prior to analysis, shells were gently washed with deionized water and dried at 40 °C. Eight nicely preserved *Neothauma* shells from surficial collections were selected at random for radiocarbon dating. Handling and pretreatment followed standard procedures for shell carbonate. Radiocarbon dates were corrected for LT's old carbon reservoir using the curve developed by Felton et al. (2007) and converted to calendar years using CalPal07 (Table 2; Weninger et al., 2008).

For the biostratinomic analysis, all shells (n = 1547) were examined under 10× stereoscopic magnification. Only shells and identifiable shell fragments >4 mm from lake-floor collections were considered in the analysis. Each *Neothauma* shell was compared to a reference set and scored for four taphonomic variables: (1) fragmentation, (2) abrasion, (3) encrustation, and (4) oxidation patinas (Table 3). The scoring system recognized three damage states per variable: no damage (score = 0), low damage (score = 1), and high damage (score = 2). A single evaluator (McGlue) was employed for the analysis in order to maintain internal consistency. Following Kidwell et al. (2001), results were

**TABLE 1**—Description of sites studied on Lake Tanganyika's littoral margin near Kigoma, Tanzania. Sample size includes the number of *Neothauma* shells scored for taphonomic variables.

| Site name | Environment | Water depth | Lake-floor gradient | Sample size |
|---|---|---|---|---|
| HT-1-05 | Bay; base of slope | 17–22 m | 8% | 148 |
| KB-1-05 | Bay; base of slope | 13–21 m | 11% | 150 |
| MB-1-05 | Wave-exposed headland | 12–15 m | 16% | 150 |
| UB-1-05 | Platform beach | Swash zone | <3% | 168 |
| UB-2-05 | Platform beach | Swash zone | <3% | 151 |
| NLP-1S-06 | Deltaic platform | 8 m | <3% | 152 |
| NLP-1D-06 | Deltaic platform | 20 m | <3% | 168 |
| NLP-2S-06 | Deltaic platform | 8 m | <3% | 150 |
| NLP-2D-06 | Deltaic platform | 20 m | <3% | 160 |
| ULB-1-05 | Bay on deltaic platform | 10 m | <3% | 150 |

presented as high-threshold damage profiles with 95% confidence intervals and ternary taphograms (Kowalewski et al., 1995) of full-frequency data.

## RESULTS

### Sedimentology

*Embayments (Sites HT-1-05 and KB-1-05).*—Accumulations encountered in bays are parautochthonous, poorly-sorted beds of gravelly mollusk hash. These deposits are restricted to 15–22 m water depth and form wedge-shaped aprons along slope fronts (Fig. 4A). Compositionally, the deposits consist of whole and fragmented bioclasts and coarse lithoclasts. The bioclasts include multiple species of mollusks, but *Neothauma* and the small (<25 mm long) unionid clam *Coelatura burtoni* Woodward are dominant in the size fraction that is >4 mm. Box cores and trenching reveal densely packed sediments lacking preferential arrangement of skeletal material in cross section. Beds are internally complex and up to 20 cm thick; modern sediments overlie well-indurated equivalents. In thin section, large well-preserved fragments of *Neothauma* aragonite are conspicuous, marked by green CL. These fragments are cemented with smaller mollusks and coarse clasts of sandstone, quartzite, and quartz (Fig. 5A). Calcite cement is dominant, marked by bright orange-red CL.

*Headland (Site MB-1-05).*—Accumulations encountered at the headland site are parautochthonous, well-sorted patches of gravelly mollusk hash. Individual patches are restricted to the hollows created between stromatolite pillars and typically cover <5 $m^2$ (Fig. 4B). Compositionally, the deposits consist of *Neothauma* with shells of *Pleiodon spekii* Woodward (a robust, endemic unionid mussel) and gravel- to cobble-sized sandstone lithoclasts present in lesser abundances. Patches are densely packed with highly variable thicknesses, in some instances exceeding 0.5 m. Thin sections from indurated deposits display microbial carbonate (patchy pink CL) with a massive to crudely laminated microstructure (Fig. 5D).

*Beaches (Sites UB-1-05 and UB-2-05).*—Accumulations encountered along beaches are allochthonous, well-sorted ridges of sandy mollusk hash. Individual ridges are elongate and narrow, typically <2 m wide and tens to hundreds of meters long with multiple semi-parallel ridges occurring in certain locations (Fig. 4C). The ridges are polytypic, consisting of *Neothauma* shells with other larger mollusks, including *Coelatura burtoni*, *Pila ovata* (Olivier), and *Melanoides admirabilis* (Smith). Sediments are loosely packed and lack preferential arrangement of skeletal material along bedding planes and in cross section. Beds are internally simple, grading from sand to pure shell material; individual ridges can reach up to 10–15 cm thick.

*Deltaic Platform.*—This environment includes sites of varying water depth: sites NLP-1S-06 and NLP-2S-06 (both 8 m water depth), sites NLP-1D-06 and NLP-2D-06 (both 20 m deep), and site ULB-1-05, with 10 m water depth. Accumulations studied along the Luiche River delta cover at least 8 $km^2$, although spot-grab samples suggest the deposit is likely more extensive. Our transect-based observations allow us to differentiate two subenvironments based on water depth. Deposits in <10 m of water are allochthonous beds of bioturbated, sandy-silty mollusk hash (Fig. 4D). In contrast, accumulations in deeper water (~20 m) are parautochthonous beds of pure mollusk hash. Beds in both subenvironments are polytypic, dominated by *Neothauma*, with varying abundances of *Coelatura* shells and other smaller bioclasts. The bioclasts do not display any discernable preferred orientation. Beds in shallow water are loosely packed and mixed up to 50% by weight with sand and silt, whereas the accumulations in deeper water display dense packing of shells, less siliciclastic material, and many erect sponges (Fig. 4E). Trenching along the depth transects indicates that beds thicken with increasing water depth up to a maximum thickness of ~15–20 cm.

An ancient example of the shallow-water hash was retrieved from outcrops north of the lake, along the plains of the Ruzizi River (Fig. 1). In thin section, large fragments of heavily pitted, recrystallized *Neothauma* (dull CL) are conspicuous, cemented with calcite to sand-sized grains of angular to sub-rounded quartz (Fig. 5E). A lithified equivalent of the deep water hash was discovered in association with the modern facies on the Luiche platform. In thin section, high-Mg calcite exhibiting dark red CL thickly coats well-preserved gastropod aragonite (Fig. 5H).

### Geochronology

Results of radiocarbon dating are summarized in Table 2. Age data reveal an admixture of late Holocene shell material across the study area. *Neothauma* from the embayment and headland sites (n = 4) are

**TABLE 2**—Radiocarbon data from *Neothauma* shells collected near Kigoma, Tanzania. Ages are adjusted for Lake Tanganyika's old carbon reservoir using a correction curve developed in Felton et al. (2007). Shells from the headland and embayment sites (HT-1-05, MB-1-05) are centered on the late 19th century, whereas samples from the delta region are time averaged over ~1600 calendar years. CE = common era.

| Lab accession number | Site | $^{14}C$ age | Error $^{14}C$ yrs | Reservoir-corrected $^{14}C$ age | Calibrated age (yrs BP) | 2 sigma range (yrs BP) | Calendar years CE |
|---|---|---|---|---|---|---|---|
| AA84619 | HT-1-05 | 1045 | 45 | 110 | 139 ± 100 | 38–239 | 1811 ± 100 |
| AA84620 | HT-1-05 | 1078 | 44 | 148 | 143 ± 105 | 37–248 | 1807 ± 105 |
| AA84621 | MB-1-05 | 1043 | 36 | 110 | 141 ± 98 | 42–239 | 1809 ± 98 |
| AA84622 | MB-1-05 | 1092 | 36 | 167 | 147 ± 115 | 32–262 | 1803 ± 115 |
| AA84623 | NLP-1D-06 | 2296 | 44 | 1686 | 1613 ± 60 | 1553–1673 | 337 ± 60 |
| AA84624 | NLP-2D-06 | 986 | 35 | 36 | modern | modern | modern |
| AA84625 | NLP-1S-06 | 1045 | 36 | 110 | 141 ± 98 | 42–239 | 1809 ± 98 |
| AA84626 | UB-1-05 | 1768 | 36 | 1023 | 946 ± 21 | 925–967 | 1004 ± 21 |
| AA4772[a] | Malagarasi Delta | 1260 | 70 | 375 | 415 ± 73 | 341–488 | 1535 ± 73 |

[a] Data point from Cohen et al. (1997)

TABLE 3—Taphonomic variables and scoring system used in this study. See text for details.

| Variable | No damage (0) | Low damage (1) | High damage (2) | Remarks |
|---|---|---|---|---|
| **Fragmentation** | None | Minor chips to apertural lip | Large angular fragments | Environmental energy indicator |
| **Abrasion** | None; original luster | Dull luster | Heavy pitting, chalky, eroded | Environmental energy indicator |
| **Encrustation** | None | Covering <10% of shell | Covering >10% of shell | Coverage by encrusting organisms |
| **Oxidation patina** | None; original color (white-cream-gray) | Covering <10% of shell | Covering >10% of shell | Proxy for lake-bottom exposure |

similar in age, clustering around the early 19th century (median age of 1807 ± 105 CE [common era] reservoir-corrected calendar years). Radiocarbon ages on shells collected from the Luiche delta (n = 4) exhibit a wider variation. Two shells collected along the ~20 m isobath date to 337 ± 60 CE and the present, respectively. A shell collected from the ~8 m isobath yielded an age of 1809 ± 98 CE, whereas a shell collected up-dip along the beach returned an age of 1004 ± 21 CE. These data, together with a reservoir-corrected shell age from a previous study (Cohen et al., 1997), demonstrate a mixed temporal range spanning more than 1600 calendar years at the two-sigma level.

### Taphonomy

The rank-order importance of the four taphonomic variables evaluated in this study varies with littoral subenvironment (Fig. 6). Qualitative evaluation of high-threshold damage profiles suggests three groups among the sites in terms of their overall taphonomic signature. Shells accumulating along beaches and those in shallow water on the deltaic platform exhibit a characteristic pattern wherein abrasion ≥ fragmentation > oxidation patina ≥ encrustation damage (Fig. 6). *Neothauma* collections from beds at depths ≥10 m along the deltaic platform and at the headland site exhibit a different taphonomic signature in which encrustation ≥ oxidation patina > fragmentation > abrasion damage. Encrustations at the headland site are heavy and stromatolitic (Fig. 3D), whereas oxidation patinas are generally thin stains and cover <30% of the shell exterior. In contrast, oxidation patinas on samples collected along the 20 m isobath on the deltaic platform commonly cover ≥50% of the exterior surface (Fig 3E). Encrustations at these sites are patchy and probably algal in origin. The final group, where *Neothauma* shells exhibit damage with a pattern of encrustation > fragmentation > oxidation patina > abrasion, typify accumulations in embayments (Fig. 6). Encrustations on shells from embayments are commonly stromatolitic.

Pair-wise tests using the confidence limits presented in Figure 6 provide a means for quantitative comparison among the sites (Table 4). In many cases, sites with dissimilar bathymetry exhibit statistically significant differences in damage state. For example, shells along shallow to deep transects on the deltaic platform are commonly statistically different from each other for all taphonomic variables evaluated. Shallow-water samples on the delta are statistically similar to shells collected along the platform beach; only site NLP-2S-06 exhibits statistically different abrasion patterns than the other three locales. Shallow-water delta and beach samples are strongly dissimilar from the headland site and mostly dissimilar in comparison to the two bay sites (Table 4). In these cases, similarity among sites occurs most commonly for the fragmentation variable. Samples from all sites in ≥10 m of water, regardless of lake-floor gradient, are statistically similar for abrasion.

Ternary taphograms provide a full-frequency perspective on damage states among sites. Fragmentation frequency is inversely related to water depth (Fig. 7A). Shells situated in deep water plot towards the no-damage and low-damage poles, whereas shells situated <10 m sub-bottom are almost invariably heavily fragmented. A strong spread is likewise evident on both the abrasion and encrustation taphograms. Abrasion data also exhibit an inverse relationship with water depth; samples at ≥10 m water depth typically group along the no-damage pole (Fig. 7B). Encrustation patterns exhibit a positive relationship with water depth (Fig. 7C). *Neothauma* shells collected from sites in <10 m of water depth rarely display encrustation on more than 10% of the shell exterior. Frequency data for oxidation patina coverage are more complicated, especially on the deltaic platform (Fig. 7D). Shells located in ~20 m water depth group near the high-damage pole, whereas samples from shallow water group towards the low-damage pole. Along the platform beach, shells commonly show little evidence of oxidation patinas and plot near the no-damage pole. The bay sites likewise group near the no-damage pole, as does site ULB-1-05. Damage patterns from ULB-1-05 are intriguing because they commonly plot relatively close to the embayment sites for all variables. This site is a bay south of the Luiche River delta, but the lake-bottom gradient at this site more closely resembles other sites on the deltaic platform. Pair-wise comparisons of damage indicate that ULB-1-05 is statistically indistinguishable from HT-1-05 for abrasion and KB-1-05 for fragmentation and abrasion (Table 4).

## INTERPRETATIONS

### Embayment and Headland Sites

We interpret the *Neothauma* shell beds encountered at the embayment (HT-1-05 and KB-1-05) and headland (MB-1-05) sites as relict parautochthonous assemblages (*sensu* Kidwell et al., 1986) due to: (1) the absence of live animals, despite extensive SCUBA surveys; (2) repeated radiocarbon ages centered on the early 19th century; and (3) shell erosion patterns implying minimal long-distance transport (Fig. 6; Table 2). *Neothauma* shells in these locales probably reflect populations that existed at a time when environmental conditions allowed for the accumulation of fine-grained sedimentary organic matter, providing the snails with a readily available food source. Today, net sedimentation in embayments and along headlands is low, and dead *Neothauma* shells commonly far outnumber living specimens (live-dead disagreement). Living populations of *Neothauma* are known to inhabit clear shallow waters marked by sandy and silty substrates (E. Michel, personal observations, 2006). Following this analog, the extant lake bottom at embayments and headlands near Kigoma likely does not support large populations of live *Neothauma*. Sedimentation along the flexural margins of rift lakes, however, is inherently subject to change, especially considering the frequency of base-level variations associated with climate change in the tropics. Remarkably consistent radiocarbon data on *Neothauma* from embayments and headlands, coupled with low abrasion damage, provide compelling evidence for the concentration of a local population of animals sometime between the early 18th and early 20th centuries. During this interval, modest lake-level fluctuations were common due to regional shifts in precipitation associated with the Little Ice Age (~1550–1850 CE) as well as a ~10 m regression associated with a breach of LT's sediment-filled outlet channel in the late 1800s (Alin and Cohen, 2003; Cohen et al., 2005). We conclude that relative shifts in the paleoshoreline during this interval periodically allowed more hospitable conditions for *Neothauma* in these environments.

We interpret shell bed formation in embayments to be linked with mass-transport processes. Structureless bedding and chaotic arrangement of bioclasts suggest slope-front, gravelly mollusk hash beds may be the remains of shallow sublacustrine slides. Slides were probably

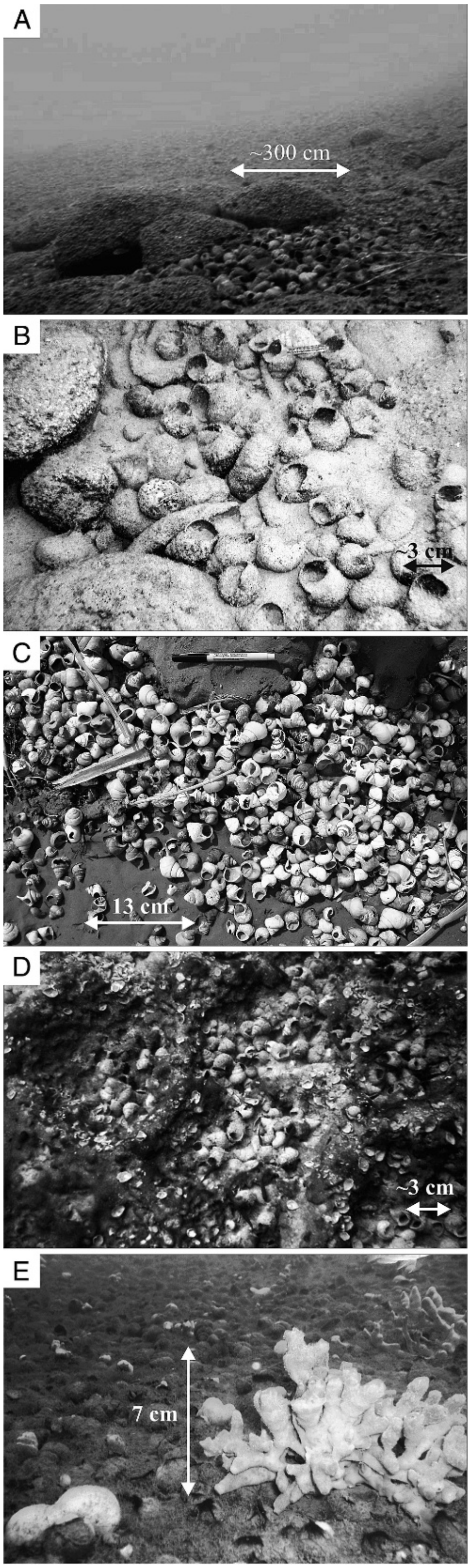

**FIGURE 4**—Field photographs of representative facies. *Neothauma* shell collections used in biostratinomic analyses were made from the upper 10 cm of these lake-floor substrates. A) Slope-front gravelly mollusk hash from embayment sites. B) Gravelly mollusk hash from the headland site. C) Beach ridges composed of sandy gastropod hash. D) Sand- and silt-rich mollusk hash from ~8 m below lake surface on the deltaic platform. Note cratered appearance due to fish bioturbation. E) Pure gastropod hash found along the 20 m isobath on the deltaic platform. Branching sponges are common in this locale and appear to utilize shell beds exclusively as their substrate.

common along bathymetric slopes during the Little Ice Age, as gravitational instabilities and changes in interstitial pore pressures along slope crests likely resulted from regressions >20 m (Cohen et al., 2005). Massively bedded lithified sediments underlying the modern hash beds are bioclastic hybrid arenites. In thin section, these rocks exhibit poor size sorting, consistent with a mass-transport origin (Fig. 5A). Calcite cement (Fig. 5B) observed in bioclastic hybrid arenites may result from input of calcium- and bicarbonate-rich fluids along coastal faults, but extensive data on the geohydrology of LT are absent. Relict *Neothauma* shells in these deposits appear to be most affected by processes resulting in fragmentation and encrustation (Fig. 6). Fragmentation of mollusk shells is often difficult to interpret, given the vast number of processes that result in shell breakage (e.g., Zuschin et al., 2003). Our data suggest mechanical processes outweigh biologic processes as the primary cause of shell fragmentation in the bays we studied. In embayments, the maximum distance shells can be transported by currents is limited by lake-bottom physiography. Nevertheless, reworking of shells is common, given the high instantaneous current velocities achieved in each half-wave cycle during storms (e.g., Allen, 1985). Saltation of *Neothauma* shells along the lake floor during storms may provide an effective means of producing cracking along weak points on the shell. Alternatively, fragmentation may result from biologic processes, but we consider such damage less likely. Molluscivorous crabs abound in LT, but experimental studies demonstrate that shell microstructure and size makes adult *Neothauma* strongly resistant to predation (e.g., West and Cohen, 1996). Transport of dead *Neothauma* by nesting cichlids seems unlikely to contribute to significant fragmentation, but maintenance of shell middens does keep *Neothauma* shells at the lake bottom and thus subject to more continuous physical destruction. In order for these processes to effectively operate, *Neothauma* shells must remain exposed on the lake floor; heavy coverage by encrusting sponges and bryozoans suggests this is indeed the case (Fig. 7).

Gravelly patches of mollusk hash discovered at the headland site are interpreted as mixed origin (sedimentologic and extrinsic biogenic) concentrations. Accumulations at MB-1-05 are similar in some aspects to cichlid nests described by Sato and Gashagaza (1997) but a number of differences suggest concentration is not accomplished solely through biogenic means. Observations of *Lamprologous callipterus* show that these cichlids build substantial so-called clump nests along the fringes of rocky substrates at many locales in Lake Tanganyika (Sato and Gashagaza, 1997). Although empirical data on transport distances are lacking, observations suggest these fish do not ordinarily move shells more than 10 m when constructing nests (M. Taborsky, personal communication, 2008). Since stromatolitic reefs along headlands span several tens of meters in the dip direction, hash patches may represent abandoned nests that were subsequently reworked into the inter-reef accumulations by wave- and storm-driven currents. Such reworking explains the admixture of *Neothauma* with materials not directly useful for brooding, such as sandstone cobbles and disarticulated valves of the unionid mussel *Pleiodon spekii* (Fig. 4B). Ultimately, these sediments are cemented together to form gastropod-rich stromatolite boundstones (Fig. 5C).

Taphonomic processes resulting in encrustation and the development of oxidation patinas dominate along headlands (Fig. 7). Cryptic irregular laminations revealed in CL images and XRD-based mineralogy indicate encrustations are aragonitic with minor biogenic calcite and probably stromatolitic in origin (after Mazzoleni et al., 1995). We suggest these features contribute to shell preservation in this environment. Wilson (1975) noted that encrustations reduce post-mortem destruction of chambered hollow skeletons along high-energy marine shelves. Headland environments in rift lakes are also high-energy environments where the potential for shell preservation through burial in fine-grained sediment is low. Rapid encrustation of *Neothauma* shells likely abates the mechanical processes that would otherwise lead to shell loss due to fragmentation or abrasion. As noted above, extensive data on groundwater flows into LT

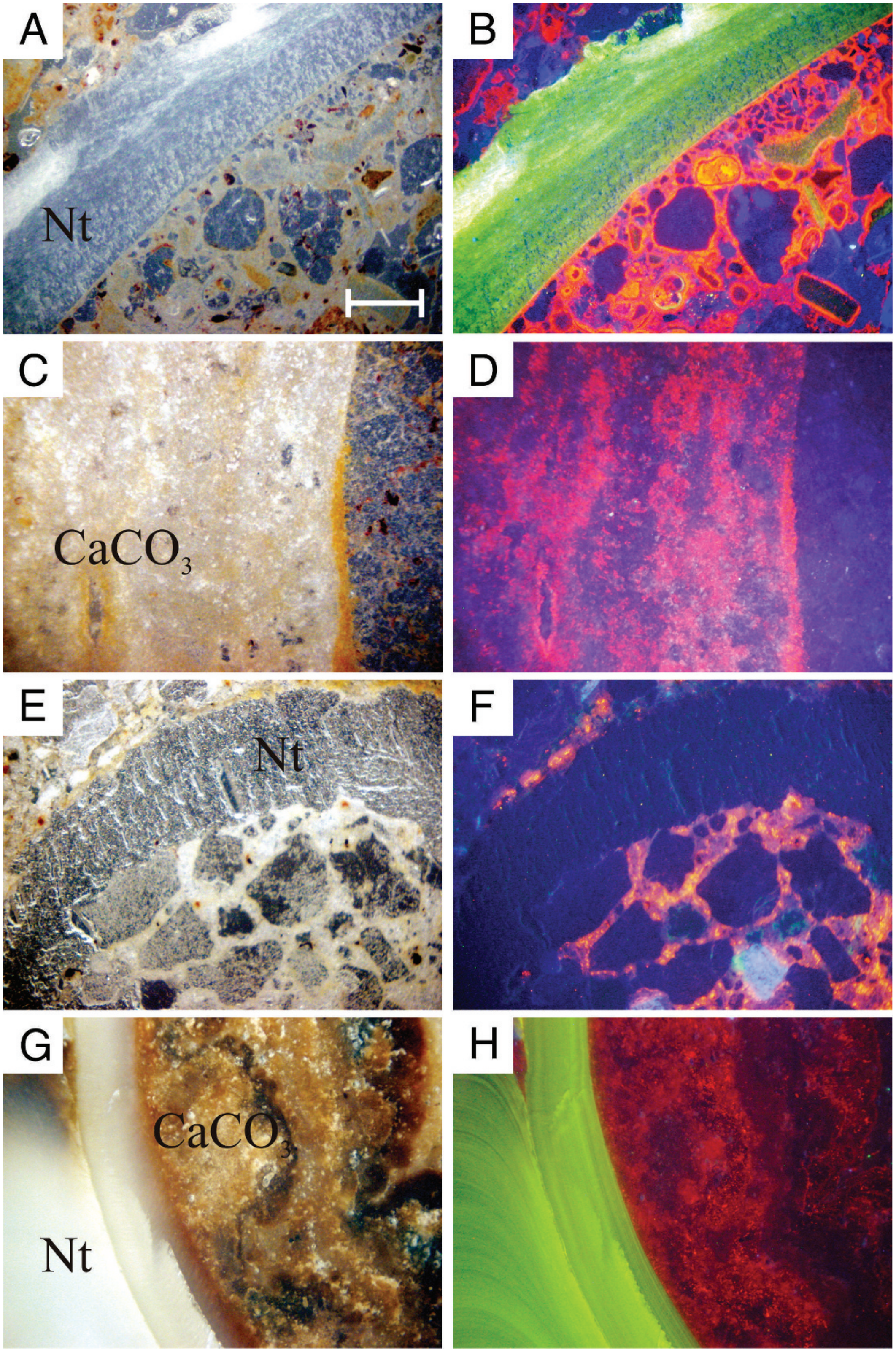

**FIGURE 5**—Photomicrographs of representative facies under plane light (left-hand images: A, C, E, G) and cathodoluminescence (CL; right-hand images: B, D, F, H). Primary aragonite produces apple-green CL, whereas biogenic calcite ranges from pink to red. Quartz and quartz-rich sediments commonly exhibit blue or purple CL. A–B) Bioclastic hybrid arenite sample from an embayment site. C–D) Gastropod-rich boundstone sample from headland site. E–F) Allochemical sandstone sample from paleoforeshore deposits, Ruzizi plains. G–H) Gastropod grainstone from ~20 m below the lake surface on the Luiche River deltaic platform. Scale bar = ~3 mm. Nt = fragments of *Neothauma* shell.

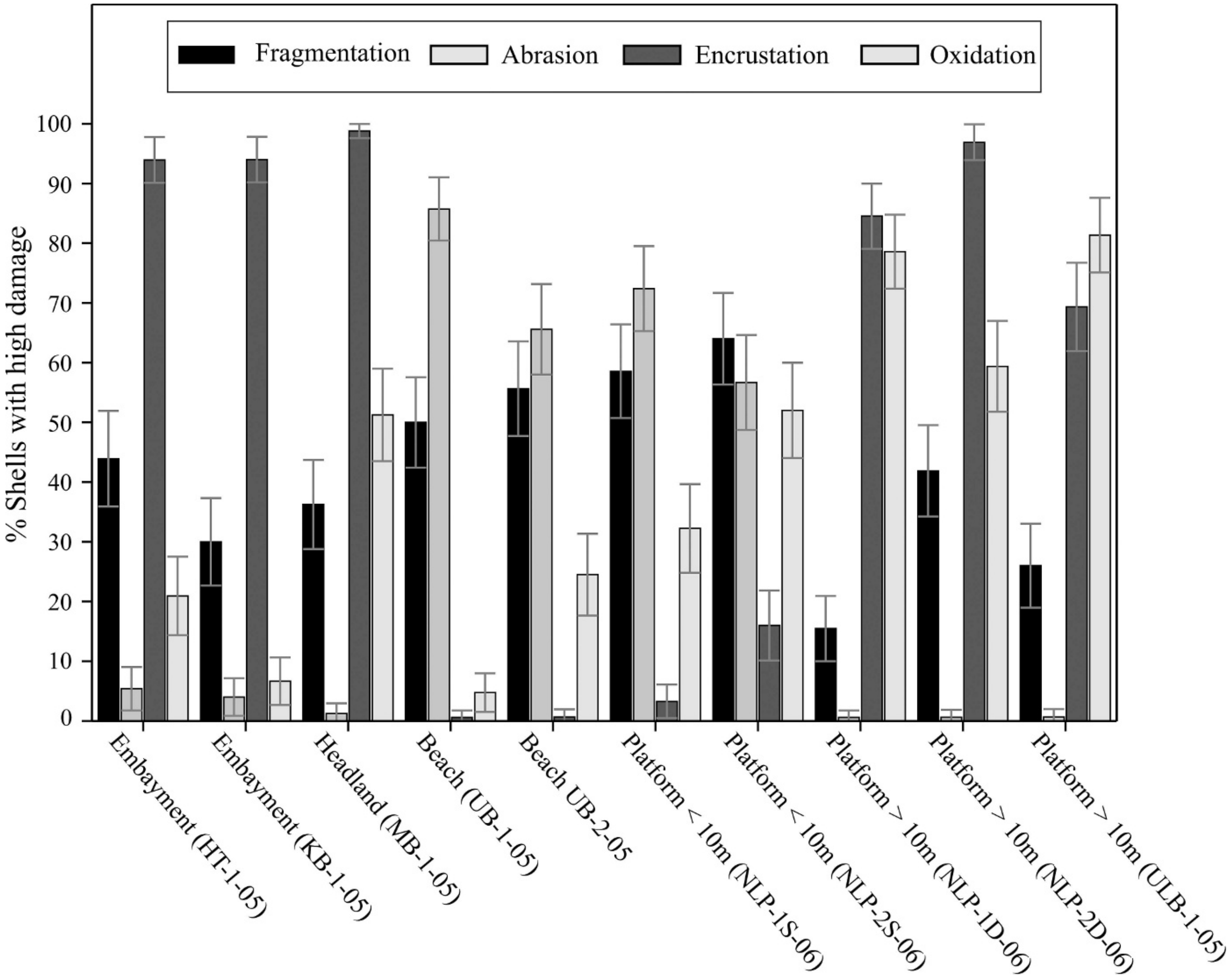

**FIGURE 6**—High-frequency damage threshold diagrams for all sites evaluated in this study. Error bars represent 95% confidence limits for the data. See text for details.

are lacking, but Rosen et al. (2004) noted the importance of concentrated seeps for the accelerated growth of lake-margin microbial carbonates and a similar process may be influencing shell beds situated near coastal faults near Kigoma.

### Delta Sites

Mollusk hash deposits encountered along the deltaic platform, from ~20 m below the lake surface to the ridges encountered along beaches, are interpreted as sedimentological concentrations with heavy extrinsic biogenic modification at shallow-water sites. Damage patterns suggest that at present fossil and subfossil shells from ~20 m of water are transported by storm currents into ~8 m of water and form sandy and silty mollusk hash beds. Radiocarbon ages on shells from the 8 m isobath and the platform beach (1809 ± 98 CE and 1004 ± 21 CE, respectively) demonstrate temporal mixing of older *Neothauma* populations in the pure mollusk hash beds situated in deeper water. Bioturbation by fish strongly controls depositional style along the ~8 m isobath, as evidenced by numerous mounds, depressions, and scattered nests observed during diver surveys (Fig. 4D). Ultimately, many of

**TABLE 4**—Site-by-site comparison of taphonomic data using 95% confidence intervals. In each cell, the results are listed (in order) as a string for the four test variables: fragmentation, abrasion, encrustation, and oxidation patinas. n = statistical similarity at the 95% level; * = statistically different damage.

| Site | KB-1-05 | MB-1-05 | UB-1-05 | UB-2-05 | NLP-1S-06 | NLP-2S-06 | NLP-1D-06 | NLP-2D-06 | ULB-1-05 |
|---|---|---|---|---|---|---|---|---|---|
| HT-1-05 | nnn* | nnn* | n*** | n**n | n**n | **** | *n** | *nn* | *n** |
| KB-1-05 |  | nnn* | ***n | **** | **** | **** | *n** | nnn* | nn** |
| MB-1-05 |  |  | n*** | **** | **** | ***n | *n** | *nnn | *n** |
| UB-1-05 |  |  |  | n*n* | n*n* | n*** | **** | n*** | **** |
| UB-2-05 |  |  |  |  | nnnn | nn** | **** | n*** | **** |
| NLP-1S-06 |  |  |  |  |  | n*** | **** | **** | **** |
| NLP-2S-06 |  |  |  |  |  |  | **** | ***n | **** |
| NLP-1D-06 |  |  |  |  |  |  |  | *nn* | nn*n |
| NLP-2D-06 |  |  |  |  |  |  |  |  | *n** |

these shells are transported onto the platform beach to form ridges. Shells accumulating in beach ridges and at ~8 m below the lake surface on the platform exhibit pronounced abrasion and fragmentation damage (Fig. 7). Pitting from impacts of mobile sand grains and the oscillatory rolling of shells along the lake bottom due to waves produce characteristic damage to *Neothauma*, resulting in complete loss of external growth lines, luster, and shell density (Fig. 3C). Although shell survival in the foreshore area is difficult, preservation in paleo-highstand deposits does occur. Allochemical sandstones encountered along the lake plain attest to the preservation of such deposits, albeit with alteration from meteoric diagenesis commonly observed (Fig. 5F).

We interpret the pure mollusk hash encountered along the ~20 m isobath to have accumulated by sedimentologic processes. Radiocarbon data on shells from this locale are time averaged and include the youngest (modern) and oldest (337 ± 60 CE) shells in the study area. These data are important because they confirm that samples of *Neothauma* are parautochthonous in these locales, and demand a concentration mechanism that allows for temporal mixing. Presently, sedimentation rates northwest of the Luiche River appear to be low, probably as the result of sub-lacustrine channels that divert deltaic sediments to the south (e.g., Soreghan et al., 1999). Modern *Neothauma* are not limited by food resources in this environment, but our surveys and initial radiocarbon data indicate that ancient shells are more abundant than subfossil shells in these deposits. Taphonomic data reveal a dominance of damage associated with prolonged lake-floor exposure, expressed as encrustation and oxidation patina coverage on shell surfaces (Fig. 7). In contrast, heavy shell fragmentation is low to moderate and abrasion damage is virtually absent. Well-preserved gastropod aragonite observed in hardground grainstones suggests that these deposits have remained submerged, as dissolution associated with meteoric diagenesis is absent (Fig. 5H). In concert with inferences from sediment core studies, we interpret these data to reflect a complex accumulation history that is probably typical of low-gradient littoral zones in tropical rift basins. In ocean basins, shell lags develop as sea level rises and wave ravinement reworks nearshore sediments (e.g., Cattaneo and Steel, 2003). Commonly, shell lags develop as thin but regionally extensive units overlying sediments with evidence of shoreface erosion and inundation (Van Waggoner et al., 1990; Cattaneo and Steel, 2003). Figure 8 illustrates the recent stratigraphy of *Neothauma* hash beds north of the Malagarasi River delta, ~30 km south of the Luiche River delta (Parson, 2001). At this locale, pure mollusk hash beds overlie sandy units with abundant shell fragments and a muddy transgressive surface. We interpret this stacking pattern as evidence for recent landward migration of the shoreline. Radiocarbon data, though limited, place live *Neothauma* along the Malagarasi delta near the beginning of the Little Ice Age (~1535 ± 73 CE) and thus local death assemblages would have been subject to concentration by wave action. Given their proximity, we conclude the same process acted to concentrate mollusk hash beds offshore of the Luiche River delta. The role of hydraulic and biogenic processes associated with lake-level lowstands, however, cannot be discounted in the development of the deposits we observed. For example, Cohen (1989) noted that phenotypic deviance among *Paramelania damoni* (Smith) shells could be reconciled by time averaging of populations solely through winnowing of vertically stacked shell beds. Winnowing does not seem to be the dominant process affecting mollusk-hash bed formation along the Luiche delta, as the majority of our samples lack black reduction patinas characteristic of prior burial in oxygen-deficient sediments (e.g., Owen et al., 1996). Reworking by a change in wave base associated with the post–Little Ice Age transgression (mid-19th century) provides an alternate mechanism for the admixture of diachronous *P. damoni* described by Cohen (1989) and fits more robustly with data from this study. We suggest that winnowing and biogenic activities probably play secondary roles in concentrating *Neothauma* during periods of relative lake-level lowstand.

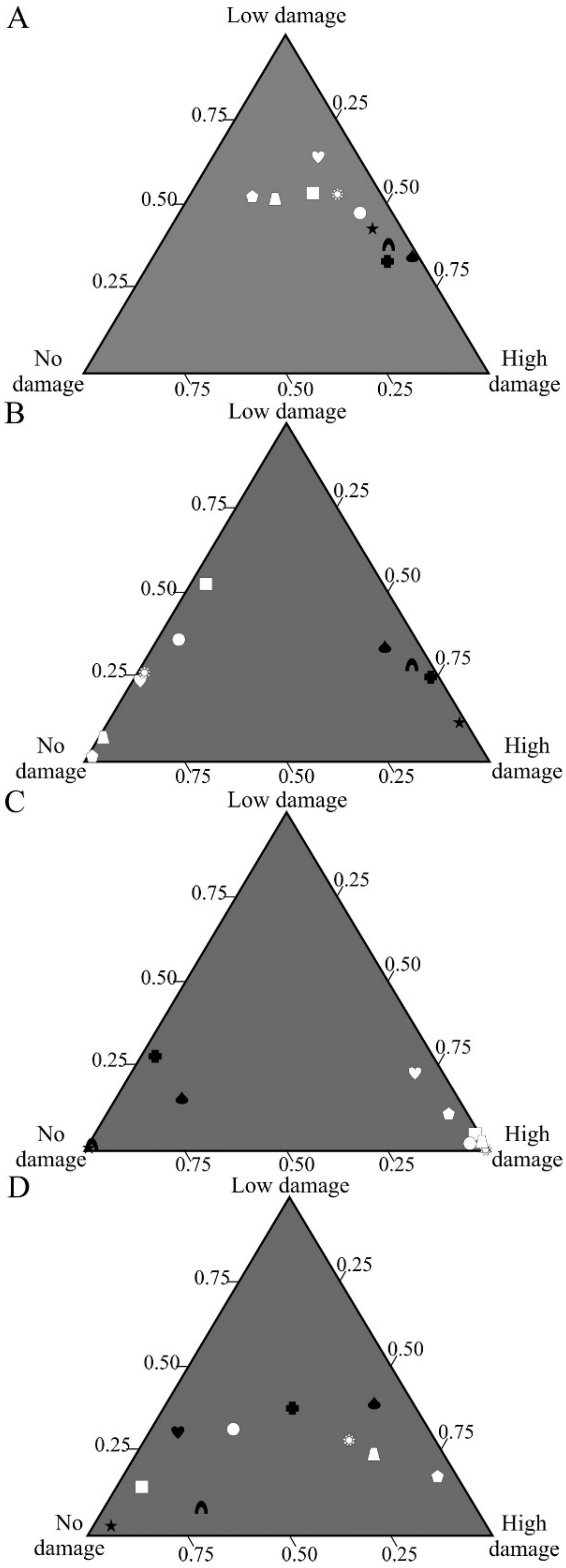

FIGURE 7—Ternary taphograms for all sites evaluated in this study. Symbols representing sites are the same as in Figure 2. Dark symbols signify shell collections made in water <10 m deep and light symbols those from deeper (>10 m) water. A) Fragmentation. B) Abrasion. C) Encrustation. D) Oxidation patina.

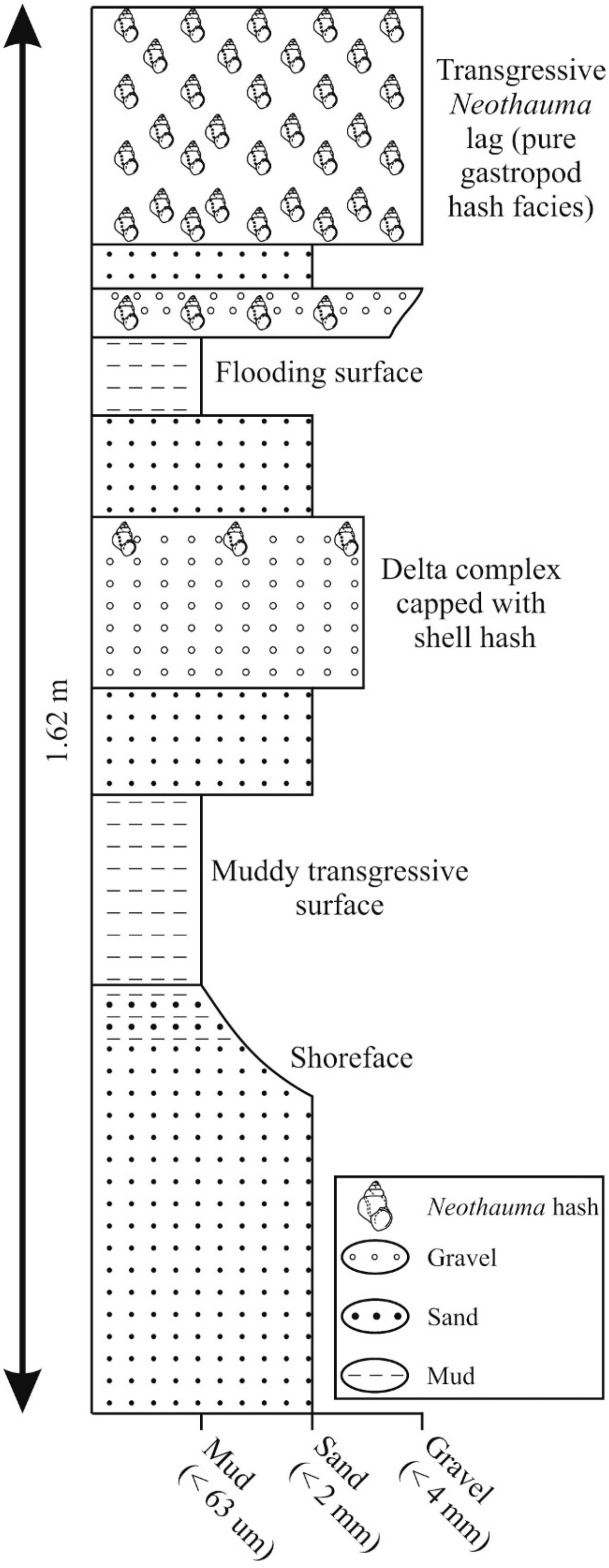

**FIGURE 8**—Stratigraphic log of vibracore T97-1VC, collected at 26 m water depth north of the Malagarasi River delta (modified after Parson, 2001). Note the presence of a *Neothauma* shell lag near the top of the core, capping a paleodelta complex and a muddy transgressive unit. *Neothauma* shells from this lag are heavily fragmented, consistent with erosion through wave ravinement.

## DISCUSSION

Examples of *Neothauma*-rich facies in the recent rock record at LT confirm preservation across a variety of littoral subenvironments (Fig. 9). Water depth clearly influences depositional style, patterns of damage, and in some instances, processes of preservation. Our analysis indicates shell survival in Lake Tanganyika's littoral zone hinges on post-mortem shell modifications that abate mechanical taphonomic processes, as adult *Neothauma* shells show little indication of biologically induced damage. The most destructive taphonomic zone in LT, and probably in most mixed carbonate-siliciclastic rift lakes, is the foreshore of low-gradient deltaic platforms (Fig. 9). Here, mobile sand grains induce heavy taphonomic damage as bioclasts are abraded and fragmented. Mitigation of damage in this environment is difficult, but at greater water depths, shell preservation is possible in spite of prolonged exposure on the lake bottom. Shells at sites NLP-1D-06 and NLP-2D-06 are currently developing into hardgrounds due to heavy post-emplacement calcite cementation (Fig. 3D). Early diagenetic cements increase both shell diameter and density, which in turn increase the environmental energy required for shoreward transport. These processes create a preservation feedback loop that extends taphonomic half life (*sensu* Cummins et al., 1986) along deltaic platforms, as residence in deeper water below wave base ultimately delays transport into the taphonomically active foreshore. The origins of early diagenetic cements in LT are speculative, given the dearth of data on coastal hydrology, but mixing of lake water with shallow groundwater aquifers may provide the conditions necessary for early cementation. It is important to note that the climatic sensitivity of lake systems may also play a role in littoral zone shell preservation. Frequent deltaic avulsions and lobe switching prompted by changes in effective precipitation can promote preservation through rapid burial of shell-rich accumulations.

*Neothauma*-rich accumulations detailed in this study suggest a wider diversity of littoral zone carbonate facies than has previously been documented for rift lakes. The rock record in East Africa exhibits shell-rich accumulations mostly in low-gradient littoral environments. For example, Betzler and Ring (1995) reported the existence of bivalve-rich accumulations from the Chiwondo beds of Lake Malawi that are similar to the hash deposits encountered on the Luiche River delta. Lake Turkana's famous mollusk-rich facies of the Plio–Pleistocene Koobi Fora Formation (Brown and Feibel, 1986; Lepre et al., 2007) and shore-zone accumulations from Lake Bogoria (Renaut and Owen, 1991) are broadly similar to the sandy mollusk hash deposits found at shallow depths on the Luiche platform. Intriguingly, few studies have noted the potentially important contributions of fish towards shaping the depositional style of shell-rich accumulations. Cichlids play a clear role in concentrating shells at headland and embayment sites as well as at 8-m-water depth on the Luiche Platform, where fish and nest counts were high along our transects (Castañeda and O'Connell, 2006). Feibel (1987) noted the existence of fossil fish nests in the bioclastic sandstones and packstones in the Koobi Fora, providing supporting evidence that extrinsic biogenic processes play at least an accessory role in the development of some rift-lake nearshore carbonates.

From a hydrocarbon systems perspective, rift lakes hold significant value for their potential to develop organic-rich source intervals (e.g., Talbot, 1988). Reservoir intervals in rift lakes have received less attention from industry, most likely because of size limitations and poor reservoir quality associated with flexural-margin sand bodies (Katz, 2001). Cretaceous coquina reservoirs in rift lakes are an important exception to this trend, as prolific fields offshore of Brazil and the Congo demonstrate (e.g., Abrahão and Warme, 1990; Harris et al., 1994; Carvalho et al., 2000). Our study highlights at least two new rift-lake reservoir facies: bioclastic hybrid arenites and gastropod-rich stromatolitic boundstones. Vertical stacking juxtaposes both facies types with stromatolite reefs, which together may represent significant

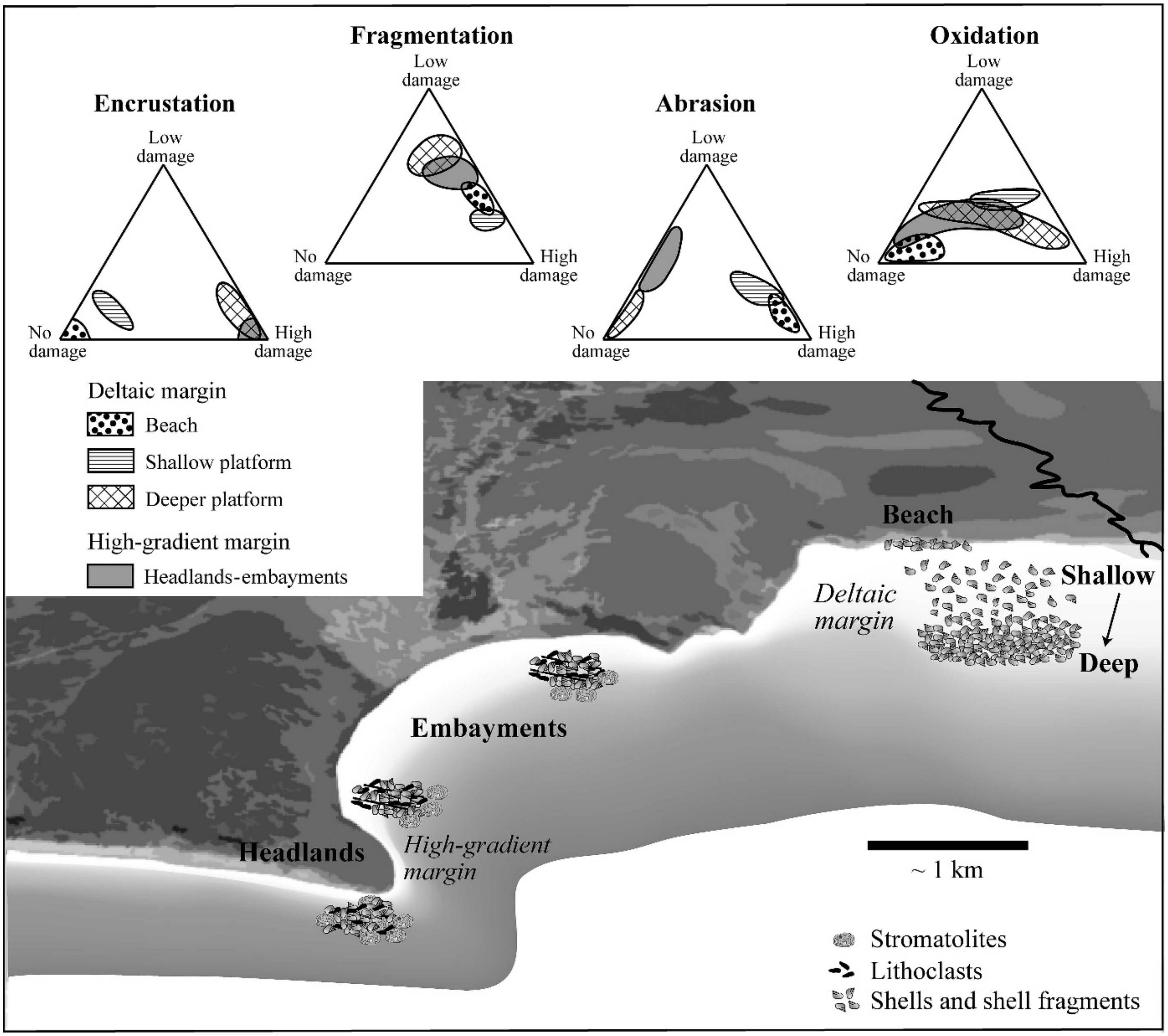

**FIGURE 9**—Summary diagram of taphonomic processes and *Neothauma*-rich carbonates along LT's flexural margin. Gravelly mollusk hash beds developing along high gradient lake floors are commonly juxtaposed with stromatolite reefs, helping to form a potential hydrocarbon reservoir facies. Shell hash beds on the deltaic platform support abundant benthic life, especially sponges, crabs, and fish along the ~20 m isobath.

prospective reservoir intervals over geologic time. Both facies develop along high-gradient depositional surfaces down dip of significant paleorelief (faulted promontories), which could aid identification in subsurface datasets.

The implications of shell survival in long-lived lacustrine systems are intriguing. In terms of rift lakes, studies of cichlid fish bear on this topic. Ribbink (1990) noted that the species richness of fish communities inhabiting hard lake-floor substrates (i.e., boulders, cobbles) exceeds those associated with fine-grained substrates. The preservation of shells in LT's littoral zone helps create a unique suite of intermediate-hardness substrates that helps to structure several specialized benthic communities. Ecological surveys across LT's littoral zone have noted certain taxa living in association with *Neothauma* shell beds. Cichlid utilization of empty *Neothauma* shells is well documented, but other fish including *Auchenoglanis occidentalis* (Valenciennes), a bagrid catfish, appear to utilize shells in nest-building activities as well (Ochi et al., 2001). Certain crab species, including *Platythelphusa maculata* Cunnington, also appear to be restricted to *Neothauma*-rich substrates (Marijnissen et al., 2008). The small, rounded bodies of *P. maculata* and their marked substrate preference suggest a potential evolutionary adaptation reliant on the presence of *Neothauma* shell beds. Additionally, Michel (2004) encountered the endemic cerithioid snail *Vinundu westae* Michel living on shell beds, as well as their better-documented rocky habitats. Census work conducted during our sampling transects noted an abundance of fresh-water erect sponges living on the shell beds, particularly at ~20 m water depth on the deltaic platform (Fig. 4E). Mean sponge abundances at sites NLP-1D-06 and NLP-2D-06 exceeded several hundred individuals of varying morphotypes (Castañeda and O'Connell, 2006). Although research on LT's sponges is in its infancy, the limited data available suggest that some species exclusively utilize *Neothauma* shell beds as habitat (Weier, 2005). Taken in concert, these observations suggest that the preservation of dead *Neothauma* may directly contribute to the structuring of shallow benthic communities in LT's littoral zone.

## CONCLUSIONS

1. Actualistic analyses of *Neothauma*-rich accumulations in Lake Tanganyika's littoral zone reveal three modern facies types: gravel-rich mollusk hash, sandy and silty mollusk hash, and pure mollusk hash. Depositional style varies with lake-floor gradient and water depth, ranging from slope-front aprons and patches (embayments and headlands, respectively) to beach ridges and expansive beds (low-gradient deltaic platform). Vertical stacking of gravel-rich, mollusk hash beds with stromatolitic reefs constitutes a prospective reservoir facies in ancient lacustrine rift basins.

2. Reservoir-corrected radiocarbon data on *Neothauma* from the study area suggest that mollusk hash beds on the Luiche River delta are time averaged over at least the latest Holocene. Pure mollusk-shell beds on the Luiche delta are interpreted as transgressive lags, consistent with stratigraphic inferences from the Malagarasi River delta. Radiocarbon data on *Neothauma* shells from embayment and headland sites center on the early 19th century and are consistent with fluctuating paleoenvironments of the Little Ice Age.

3. Evaluation of four taphonomic variables suggests relatively high preservation potential for *Neothauma* shells across the littoral subenvironments encountered near Kigoma. Preservation is lowest at shallow ($<$10 m) water depths on deltaic platforms, where abrasion and fragmentation damage from interaction with waves and sand grains are pronounced. Rapid development of stromatolitic encrustations and early cement coatings may help reduce post-mortem shell destruction by mechanical processes.

4. Shell survival in the littoral zone may have important implications for structuring specialized benthic communities within Lake Tanganyika. Gastropod-rich shell-hash beds constitute a key intermediate hardness substrate that seems to be exclusively used by a number of specialized organisms, including several species of fish, crabs, and sponges. Biogenic feedback of this kind is uncommon in fresh-water systems and is probably limited to long-lived lakes where the processes of evolution and diagenesis have time to operate.

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