

# Chapter 4

## The Paleoecology of the Upper Ndolanya Beds, Laetoli, Tanzania, and Its Implications for Hominin Evolution

Terry Harrison

**Abstract** Evidence from the Pliocene hominin site of Laetoli in northern Tanzania demonstrates that there was a taxonomic turnover of the mammalian fauna between the Upper Laetolil Beds (3.6–3.85 Ma) and the Upper Ndolanya Beds (2.66 Ma). *Paranthropus aethiopicus* was one of the novel species that appeared locally as part of the restructured fauna. This turnover coincides with a major climatic shift at ~2.8–2.5 Ma, which had an important impact on the local environment and the composition of the faunal community. Investigation of the paleoecology of the Upper Ndolanya Beds provides critical evidence about how the vegetation and fauna at Laetoli, including the hominins, responded to these environmental changes. The preponderance of alcelaphin bovids and the reduced frequency of browsing ungulates, in conjunction with evidence from ecomorphology, mesowear and stable isotopes, indicate that the Upper Ndolanya Beds sample drier habitats with a greater proportion of grasslands compared with the earlier Upper Laetolil Beds. However, paleoecological inferences based on ostrich eggshells, rodents, and terrestrial gastropods present a more complicated picture, indicating instead that Upper Ndolanya habitats were more mesic and dominated by dense woodlands. Such confounding results can be reconciled as a consequence of the differential impact of climatic and environmental change on a global, regional and local scale.

**Keywords** Climate change • Fauna • Environment • *Paranthropus* • Pliocene

### Introduction

The Pliocene site of Laetoli in northern Tanzania is well known for the fossil remains of *Australopithecus afarensis* and associated trails of hominin footprints from the Upper Laetolil Beds (ULB) dating to 3.6–3.85 Ma (Fig. 4.1) (Leakey 1987a, b; Harrison 2011a). In addition, *Paranthropus aethiopicus* has been recovered from the younger Upper Ndolanya Beds (UNB) at 2.66 Ma (Harrison 2011a). A major focus of recent research at Laetoli has been to reconstruct the paleoecology of the hominins using evidence from a wide spectrum of different sources, including modern-day ecosystems, sedimentology, paleobotany, stable isotopes, mesowear, ecomorphology, faunal studies and community structure analyses (Kovarovic et al. 2002; Su 2005, 2011; Su and Harrison 2007, 2008; Kingston and Harrison 2007; Kovarovic and Andrews 2007, 2011; Musiba et al. 2007; Andrews and Bamford 2008; Peters et al. 2008; Andrews et al. 2011; Bamford 2011a, b; Bishop 2011; Bishop et al. 2011; Ditchfield and Harrison 2011; Gentry 2011; Harrison 2005, 2011b, c, d, e; Hernesniemi et al. 2011; Kaiser 2011; Kingston 2011; Reed 2011; Reed and Denys 2011; Rossouw and Scott 2011; Tattersfield 2011). Study of the paleoecology provides important contextual evidence that is critical for interpreting hominin habitat preferences, ecology and paleobiology (see Su and Harrison 2008). It is obviously not possible to make deductions about key events that shaped human evolution from the narrow vantage point of individual paleontological sites, but detailed studies of sites such as Laetoli do provide small-scale temporal and spatial snapshots of past ecosystems that can be used to assemble a regional and continent-wide paleoenvironmental montage. The latter can then be used to test macroevolutionary models about hominin speciation, diversification, and extinction. The utility of such models is, however, entirely contingent upon the detail and precision of the paleoecological interpretations of the individual sites. In this regard, Laetoli offers an informative case study.

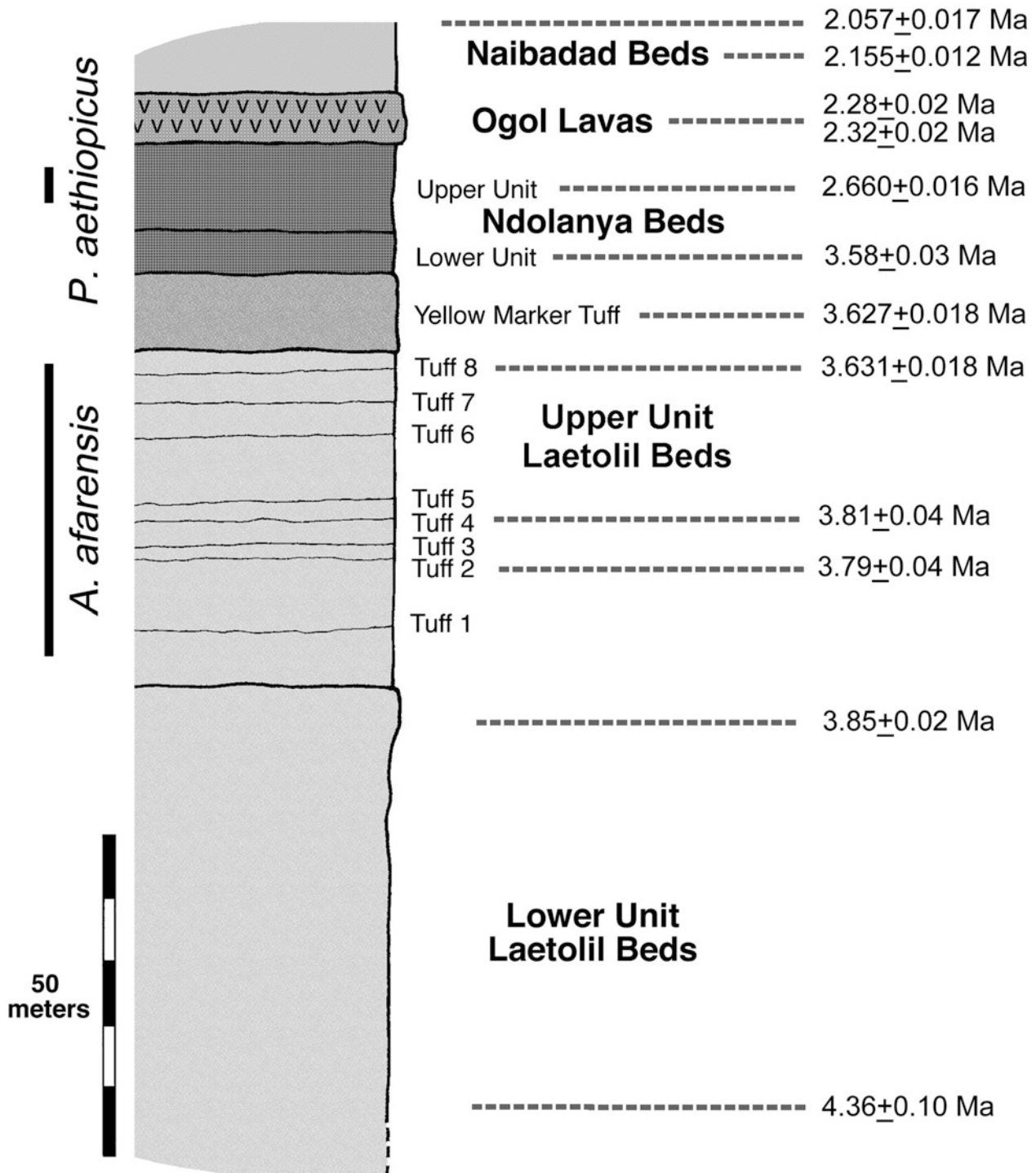
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Conflicting interpretations of the paleoecology at Laetoli can be formulated using different lines of evidence, and possible explanations for these confounding results have implications for understanding the impact of climatic and environmental

changes on hominin evolution at the local and regional scales.

Study of the time-successive faunas at Laetoli demonstrates that there was a taxonomic turnover of the



**Fig. 4.1** Stratigraphic column and radiometric dating of the lower part of the sequence at Laetoli (adapted from Harrison 2011a). The temporal distribution of the Pliocene hominins is shown (left). Data from Hay (1987); Drake and Curtis (1987); Ndessokia (1990); Manega (1993); Mollel et al. (2011); Deino (2011); Harrison (2011a)

mammalian fauna between the ULB and the UNB. *Paranthropus aethiopicus* was one of the new species that appeared locally as part of the restructured faunal community. This turnover coincides with a major climatic shift in eastern Africa at ~2.8–2.5 Ma. Climate change at this time has been associated with increased intensification of northern hemisphere glacial cycles and greater aridity in eastern Africa (Bobe and Behrensmeyer 2004; Bonnefille et al. 2004; deMenocal 2004, 2011; Feakins et al. 2005; Sepulchre et al. 2006; Feakins and deMenocal 2010; Bonnefille 2010). However, recent work on lake-levels in East Africa has shown that climate change at 2.6 Ma coincides with 400 kyr eccentricity maxima, which resulted in greater climate variability and relatively high moisture levels (Deino et al. 2006; Kingston et al. 2007; Trauth et al. 2005, 2007, 2009, 2010; Maslin and Trauth 2009).

A number of lines of evidence indicate that the UNB fauna is associated with a shift from a woodland-bushland-grassland mosaic in the ULB to habitats that were somewhat drier, with a greater proportion of grasslands (Kovarovic et al. 2002; Kovarovic 2004; Kingston and Harrison 2007; Kovarovic and Andrews 2007, 2011; Gentry 2011; Harrison 2011b, c; Hernesniemi et al. 2011; Kaiser 2011; Kingston 2011; Rossouw and Scott 2011; Su 2011; Barboni 2014). Given the length of the hiatus between the ULB and the UNB (almost 1 myrs), it is possible that the change in the ecology was the result of multiple shifts over an extended period of time. Such an ecological transition between the ULB and UNB would be fully consistent with expectations of increased aridity as a result of global climate change during the mid-Pliocene. However, alternative lines of evidence point to the UNB being more comparable to the ULB, with habitats that continued to be dominated by woodland mosaics. This latter scenario fits better with an inferred period of increased moisture availability, rather than increased aridity.

Accurate reconstruction of the paleoecology of the UNB and a better understanding of the nature of the ecological changes at Laetoli during the Pliocene are important because the UNB samples a key period in human evolution that witnessed the local extinction of *Australopithecus* and the origin and divergence of *Paranthropus*. The ecological changes that took place at Laetoli and at other localities in eastern Africa during this time period potentially provide valuable clues to understanding what environmental factors may have contributed to these major evolutionary events. This chapter aims to critically examine the evidence available to reconstruct the paleoecology of the UNB, and to offer a possible explanation for how contradictory lines of evidence might be reconciled. It provides a more nuanced and synthetic approach to understanding possible paleoecological change at Laetoli. The findings also have implications for contemporary debates about the relationship between climatic change and cladogenesis among Pliocene African

hominins (Potts 1998, 2013; deMenocal 2004, 2011; Bobe and Behrensmeyer 2004; Maslin and Trauth 2009; Reed and Russack 2009; Bobe and Leakey 2009; Trauth et al. 2010; Harrison 2011a; Macho 2014).

## Paleoecology of the Upper Ndolanya Beds

The consensus view, based on multiple lines of evidence, is that the ULB was dominated by a mosaic of closed woodland, open woodland, shrubland and grassland, with riverine woodlands and forests along ephemeral watercourses (see Harrison 2011c). It was certainly more densely wooded and more mesic than the modern-day Laetoli ecosystem (Andrews and Bamford 2008; Andrews et al. 2011). Changes in the vertebrate fauna between the ULB and the UNB provide clear evidence of a shift in the ecology, but the precise nature of what those changes mean in terms of the overall structure of the habitat is less evident.

The greater preponderance of bovids (especially alcelaphins) and the reduced frequency of large browsing herbivores in terms of number of specimens, in conjunction with evidence derived from ungulate ecomorphology, mesowear and stable isotopes, suggests that the UNB samples drier habitats with a greater predominance of grasslands compared with the ULB (Kovarovic et al. 2002; Kovarovic 2004; Kovarovic and Andrews 2007, 2011; Hernesniemi et al. 2011; Kaiser 2011; Bishop et al. 2011; Gentry 2011; Su 2011). However, stable isotope data from ostrich eggshells (Kingston and Harrison 2007; Kingston 2011) and the community structure of the rodents (Reed and Denys 2011; Denys 2011) and terrestrial gastropods (Peters et al. 2008; Tattersfield 2011) indicate that the picture is much more complicated, and that the UNB was a relatively mesic habitat dominated by woodlands.

The evidence supporting an ecological shift in the UNB towards drier habitats dominated by open woodlands and grasslands comes from a number of independent avenues of investigation. The taxonomic and paleobiological composition of the large mammal fauna provides one such important line of evidence. Of the 24 large mammal taxa from the UNB identified to the species level (including those identified as cf. and aff.), 62.5% also occur in the younger ULB (Table 4.1). Only 9 large mammal species make their first appearance at Laetoli in the UNB (i.e., *Paranthropus aethiopicus*, *Eurygnathohippus cornelianus*, *Ceratotherium simum*, *Metridiochoerus andrewsi*, *Giraffa pygmaea*, *Parmularius altidens*, *Parmularius parvicornis*, *Megalotragus kattwinkelilisaaci* and *Antidorcas recki*). Using a combination of stable isotopes, dental mesowear and ecomorphology (Kingston 2011; Kaiser 2011; Bishop 2011), all of the new

**Table 4.1** List of the mammalian taxa from the Upper Laetoli Beds (ULB) and Upper Ndolanya Beds (UNB) (after Harrison 2011c)

| Order                         | Family                             | Genus and species                                 | ULB | UNB |
|-------------------------------|------------------------------------|---|-----|-----|
| Macroscelidea                 | Macroscelididae                    | <i>Rhynchocyon pliocaenicus</i>                   | X   |     |
| Tubulidentata                 | Orycteropodidae                    | <i>Orycteropus</i> sp.                            | X   |     |
| Proboscidea                   | Deinotheriidae                     | <i>Deinotherium bozasi</i>                        | X   | ?   |
|                               |                                    | <i>Anancus ultimus</i>                            | X   |     |
|                               | Stegodontidae                      | <i>Stegodon</i> sp. cf. <i>Stegodon kaisensis</i> | X   |     |
|                               |                                    | <i>Loxodonta exoptata</i>                         | X   | X   |
| Primates                      | Galagidae                          | <i>Laetolia sadimanensis</i>                      | X   |     |
|                               | Cercopithecidae                    | <i>Parapapio ado</i>                              | X   | X   |
|                               |                                    | Papionini indet.<br>cf. <i>Rhinocolobus</i> sp.   | X   | X   |
|                               |                                    | <i>Cercopithecoides</i> sp.                       | X   |     |
|                               | Hominidae                          | <i>Australopithecus afarensis</i>                 | X   |     |
|                               |                                    | <i>Paranthropus aethiopicus</i>                   |     | X   |
| Rodentia                      | Sciuridae                          | <i>Paraxerus meini</i>                            | X   | X   |
|                               |                                    | <i>Xerus</i> sp.                                  | X   |     |
|                               |                                    | <i>Xerus janenschii</i>                           | X   | X   |
|                               | Cricetidae                         | <i>Gerbilliscus satimani</i>                      | X   |     |
|                               |                                    | <i>Gerbilliscus winkleri</i>                      |     | X   |
|                               |                                    | <i>Gerbilliscus</i> cf. <i>inclusus</i>           | X   |     |
|                               |                                    | <i>Dendromus</i> sp.                              | X   |     |
|                               |                                    | <i>Steatomys</i> sp.                              | X   |     |
|                               |                                    | <i>Saccostomus major</i>                          | X   | cf. |
|                               |                                    | <i>Saccostomus</i> sp.                            |     | X   |
|                               | Muridae                            | <i>Aethomys</i> sp.                               | X   |     |
|                               |                                    | <i>Thallomys laetoliensis</i>                     | X   | X   |
|                               |                                    | <i>Mastomys cinereus</i>                          | X   |     |
|                               |                                    | <i>Mus</i> sp.                                    | X   |     |
|                               | Thryonomyidae                      | <i>Thryonomys wesselmani</i>                      |     | X   |
|                               | Bathyergidae                       | <i>Heterocephalus quenstedti</i>                  | X   |     |
|                               | Hystricidae                        | <i>Hystrix leakeyi</i>                            | X   |     |
| <i>Hystrix makapanensis</i>   |                                    | X   | X   |     |
| <i>Xenohystrix crassidens</i> |                                    | X   |     |     |
| <i>Pedetes laetoliensis</i>   |                                    | X   |     |     |
| Pedetidae                     | <i>Pedetes</i> sp.                 |   | X   |     |
|                               | <i>Serengetilagus praecapensis</i> | X   | X   |     |
| Lagomorpha                    | Leporidae                          |   |     |     |
| Soricimorpha                  | Soricidae                          | ? <i>Crocidura</i> sp.                            |     | X   |
| Carnivora                     | Canidae                            | ? <i>Nyctereutes barryi</i>                       | X   |     |
|                               |                                    | cf. <i>Canis</i> sp. A                            | X   |     |
|                               |                                    | cf. <i>Canis</i> sp. B                            | X   |     |
|                               |                                    | aff. <i>Otocyon</i> sp.                           | X   |     |
|                               |                                    | <i>Propoecilogale bolti</i>                       | X   | X   |
|                               | Mustelidae                         | <i>Mellivora</i> sp.                              | X   |     |
|                               |                                    | Mustelidae indet.                                 | X   |     |
|                               |                                    | <i>Viverra leakeyi</i>                            | X   |     |
|                               | Viverridae                         | <i>Genetta</i> sp.                                | X   |     |
|                               |                                    | aff. Viverridae                                   | X   |     |
|                               |                                    | <i>Herpestes palaeoserengetensis</i>              | X   |     |
|                               | Herpestidae                        | <i>Herpestes ichneumon</i>                        | X   |     |
|                               |                                    | <i>Galerella</i> sp.                              | X   |     |
|                               |                                    | <i>Helogale palaeogracilis</i>                    | X   | X   |
|                               |                                    | <i>Mungos dietrichi</i>                           | X   | X   |
| <i>Mungos</i> sp. nov.        |                                    | X   |     |     |

(continued)

Table 4.1 (continued)

| Order                                 | Family                       | Genus and species                                   | ULB  | UNB  |
|---------------------------------------|------------------------------|---|------|------|
| Perissodactyla                        | Hyaenidae                    | <i>Crocuta dietrichi</i>                            | X    | X    |
|                                       |                              | <i>Parahyaena howelli</i>                           | X    |      |
|                                       |                              | <i>Ikelohyaena</i> cf. <i>I. abronia</i>            | X    | ?    |
|                                       |                              | <i>Lycyaenops</i> cf. <i>L. silberbergi</i>         | X    |      |
|                                       |                              | ? <i>Pachycrocuta</i> sp.                           | X    |      |
|                                       | Felidae                      | <i>Dinofelis petteri</i>                            | X    | X    |
|                                       |                              | <i>Homotherium</i> sp.                              | X    | X    |
|                                       |                              | <i>Panthera</i> sp. aff. <i>P. leo</i>              | X    |      |
|                                       |                              | <i>Panthera</i> sp. cf. <i>P. pardus</i>            | X    | X    |
|                                       |                              | <i>Acinonyx</i> sp.                                 | X    |      |
|                                       |                              | <i>Caracal</i> sp. or <i>Leptailurus</i> sp.        | X    | X    |
|                                       |                              | <i>Felis</i> sp.                                    | X    | X    |
|                                       | Equidae                      | <i>Eurygnathohippus</i> aff. <i>hasumense</i>       | X    |      |
|                                       |                              | <i>Eurgnathohippus</i> aff. <i>cornelianus</i>      |      | X    |
|                                       |                              | <i>Ancylotherium hennigi</i>                        | X    |      |
|                                       | Chalicotheriidae             | <i>Ceratotherium efficax</i>                        | X    | X    |
|                                       | Rhinocerotidae               | <i>Ceratotherium</i> cf. <i>simum</i>               |      | X    |
| <i>Ceratotherium</i> sp.              |                              |   | X    |      |
| <i>Diceros</i> sp.                    |                              | X   |      |      |
| Artiodactyla                          | Suidae                       | <i>Notochoerus euilus</i>                           | X    |      |
|                                       |                              | <i>Notochoerus jaegeri</i>                          | X    |      |
|                                       |                              | <i>Nyanzachoerus kanamensis</i>                     | X    |      |
|                                       |                              | <i>Potamochoerus afarensis</i>                      | X    |      |
|                                       |                              | <i>Kolpochoerus heseloni</i>                        | X    | X    |
|                                       |                              | <i>Metridiochoerus andrewsi</i>                     |      | X    |
|                                       | Giraffidae                   | <i>Giraffa stillei</i>                              | X    | aff. |
|                                       |                              | <i>Giraffa jumae</i>                                | aff. |      |
|                                       |                              | <i>Giraffa pygmaea</i>                              |      | aff. |
|                                       | <i>Sivatherium maurusium</i> | X   | aff. |      |
|                                       | Camelidae                    | <i>Camelus</i> sp.                                  |      | X    |
|                                       | Bovidae                      | <i>Tragelaphus</i> sp.                              | X    |      |
|                                       |                              | <i>Tragelaphus</i> sp. cf. <i>T. buxtoni</i>        |      | X    |
|                                       |                              | <i>Simatherium kohllarseni</i>                      | X    |      |
|                                       |                              | <i>Brabovus nanincisus</i>                          | X    |      |
|                                       |                              | Bovini sp. indet.                                   | X    | X    |
|                                       |                              | Cephalophini sp.                                    | X    | ?    |
|                                       |                              | <i>Hippotragus</i> sp.                              | X    |      |
|                                       |                              | <i>Hippotragus</i> sp. aff. <i>cookei</i> ?         |      | X    |
|                                       |                              | <i>Oryx deturi</i>                                  | X    |      |
|                                       |                              | <i>Oryx</i> sp.                                     |      | X    |
|                                       |                              | <i>Parmularius pandatus</i>                         | X    |      |
|                                       |                              | <i>Parmularius altidens</i>                         |      | X    |
|                                       |                              | <i>Parmularius parvicornis</i>                      |      | X    |
|                                       |                              | Alcelaphini, larger sp. indet.                      | X    |      |
|                                       |                              | Alcelaphini, small sp.                              | ?    |      |
|                                       |                              | <i>Megalotragus kattwinkeli</i> or <i>M. isaaci</i> |      | X    |
| ? <i>Connochaetes</i> sp.             |                              |   | X    |      |
| Reduncini sp. indet.                  |                              | X   | X    |      |
| <i>Madoqua aviflumini</i>             |                              | X   | X    |      |
| ? <i>Raphicerus</i> sp.               |                              | X   | X    |      |
| <i>Aepyceros dietrichi</i>            | X                            |   |      |      |
| <i>Aepyceros</i> sp.                  |                              | X   |      |      |
| " <i>Gazella</i> " <i>kohllarseni</i> | X                            |   |      |      |
| <i>Gazella janenschi</i>              | X                            | X   |      |      |
| <i>Gazella granti</i>                 | ?                            | ?   |      |      |
| <i>Gazella</i> sp.                    |                              | X   |      |      |
| <i>Antidorcas recki</i>               |                              | X   |      |      |

ungulate taxa, with the exception of *Giraffa pygmaea*, can be deduced to be mixed feeders (*Ceratotherium simum*, *Metridiochoerus andrewsi*, *Parmularius parvicornis*, *Antidorcas recki*) or grazers (*Eurygnathohippus cornelianus*, *Megalotragus kottwinkeli/isaaci*, *Parmularius altidens*). At the same time, many of the large browsing mammals in the ULB, such as *Anancus ultimatus*, *Deinotherium bozasi*, *Ancylotherium hennigi*, *Diceros* sp., *Giraffa jumae*, *Simatherium kohllarseni* and *Brabovus nanincisus*, are no longer present in the UNB. Consequently, the UNB witnessed a significant shift in its large herbivore dietary guild to one with a greater emphasis on taxa that included a significant proportion of grasses in their diets. In the ULB, only 41% of ungulate species are grazers or mixed feeders, whereas the proportion increases to 59% in the UNB. A further indicator of the decline in large browsing mammals in the UNB is provided by the reduction in the number of giraffids. Giraffids comprise only 4.6% of the ruminant specimens in the UNB, compared with 15.7% in the ULB (Harrison 2011b, c; Robinson 2011).

Differences in the taxonomic composition of the bovid fauna provide further support for an ecological difference between the UNB and ULB. The UNB has a much higher proportion of alcelaphin and antilopin bovids (77.4% of bovid specimens), which are predominantly mixed feeders and specialist grazers (Gagnon and Chew 2000), compared with the ULB (only 50.1%) (Table 4.2). The small gazelle in the ULB, *Gazella janenschi*, continues into the UNB, but is replaced as the dominant antilopin by the medium-sized and more hypsodont *Antidorcas recki* (Gentry 2011). Similarly, the dominant alcelaphin in the ULB, the medium-sized *Parmularius pandatus*, is replaced by a greater diversity of alcelaphins in the UNB, ranging in size from the small *Parmularius parvicornis* to the large *Megalotragus* sp., with most species having more hypsodont molars.

Stable carbon isotope data (Kingston and Harrison 2007; Kingston 2011) confirms a shift towards a greater emphasis on C<sub>4</sub> diets among equids and alcelaphin bovids in the UNB

compared with the ULB (Fig. 4.2). The mean  $\delta^{13}\text{C}_{\text{enamel}}$  for UNB alcelaphins is 0.1‰, which is significantly higher than the -2.4‰ in the ULB (Student's t-test,  $p = 0.01$ ). The hipparionine equid *Eurygnathohippus* exhibits a similar trend, although less pronounced, with a shift in mean  $\delta^{13}\text{C}_{\text{enamel}}$  from -1.0‰ to 0.2‰ from the ULB to the UNB (Student's t-test,  $p = 0.05$ ). None of the other mammals demonstrate a significant difference in carbon isotopic signatures between the ULB and UNB.

Analyses of ungulate dental mesowear provide complementary results (Kaiser 2011). Mesowear scores are an indication of the degree of abrasiveness of the diet of large herbivores and they provide a guide to overall dietary behavior. The mesowear scores for the ULB are much lower than for the UNB, which Kaiser (2011) interprets as a shift to a predominance of grazing species in the UNB (57%) compared with that in the ULB (6%). However, few species are sampled from the UNB ( $n = 7$ ) and the overall mesowear score is heavily influenced by the high scores for alcelaphin bovids and equids, which fall within the specialist grazer end of the spectrum.

Kovarovic et al. (2002) and Andrews (2006), using an ecological diversity approach (including all mammals, except bats), conclude that the UNB is predominantly a semi-arid bushland-grassland that was distinctly drier and more open than the ULB. This is due to the high proportion of terrestrial taxa and grazing herbivores, and the low incidence of frugivores. Ecomorphological studies of bovid postcranials (Kovarovic and Andrews 2007; Bishop et al. 2011) indicate that, although woodland and forest habitats continued to be present at Laetoli during the UNB, the majority of UNB bovids had a preference for open or lightly vegetated habitats (65.4% in the UNB versus 23.3% in the ULB).

Finally, paleobotanical remains are scarce in the UNB (no pollen or macrobotanical remains are known), but phytoliths have been recovered (Rossouw and Scott 2011). Although the abundance of phytolith in grasses can lead to an over-estimation of the extent of grassland habitats in

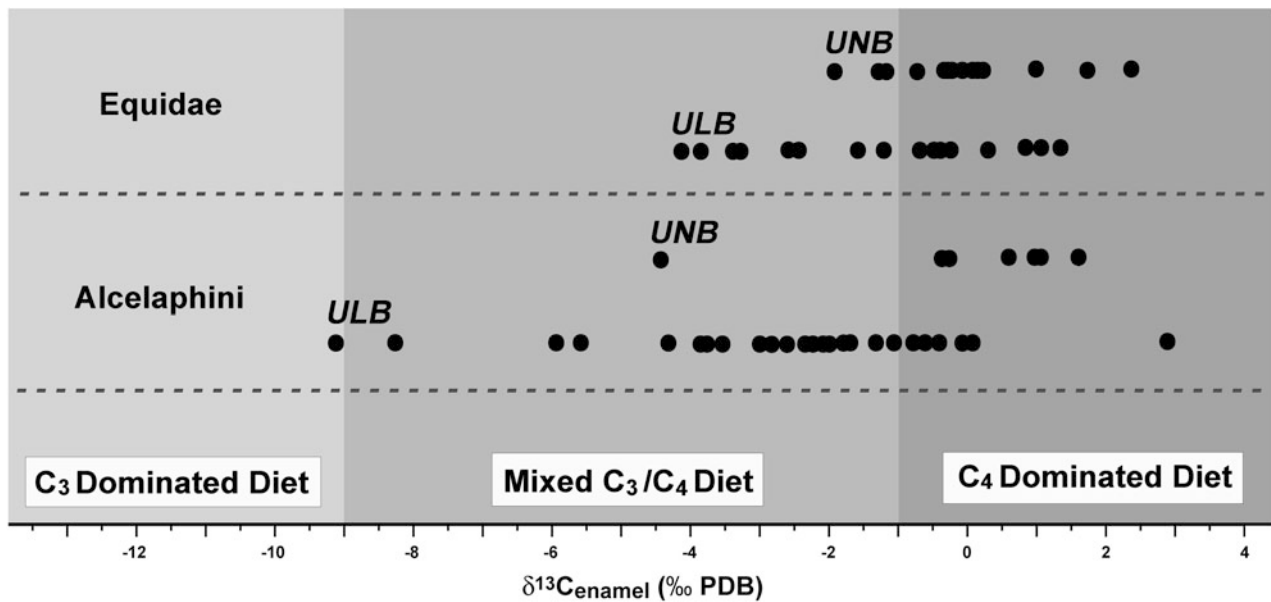
**Table 4.2** Relative proportions of bovid tribes in the Upper Laetolil and Upper Ndolanya Beds

| Taxon (Tribe) | Upper Laetolil Beds |              | Upper Ndolanya Beds |              |
|---------------|---------------------|--------------|---------------------|--------------|
|               | NISP <sup>a</sup>   | %            | NISP <sup>a</sup>   | %            |
| Alcelaphini   | 561                 | 28.1         | 171                 | 49.6         |
| Antilopini    | 440                 | 22.0         | 96                  | 27.8         |
| Bovini        | 14                  | 0.7          | 8                   | 2.3          |
| Cephalophini  | 12                  | 0.6          | 2                   | 0.6          |
| Hippotragini  | 332                 | 16.6         | 6                   | 1.7          |
| Neotragini    | 629                 | 31.5         | 41                  | 11.9         |
| Reduncini     | 2                   | 0.1          | 0                   | 0.0          |
| Tragelaphini  | 7                   | 0.4          | 21                  | 6.1          |
| <b>Total</b>  | <b>1997</b>         | <b>100.0</b> | <b>345</b>          | <b>100.0</b> |

Data from Gentry and Su (2011)

<sup>a</sup>NISP, number of individual specimens





**Fig. 4.2** Stable carbon isotope analysis of the dental enamel of hipparionine equids and alcelaphin bovids from the Upper Laetoli Beds (*ULB*) and the Upper Ndolanya Beds (*UNB*). The data points represent values for individual specimens. The dietary categories (in different shades of grey) correspond to browser (left), mixed feeders (middle), and grazers (right), respectively. Note that the *UNB* values are more strongly skewed towards the  $C_4$  dominated end of the spectrum. (data from Kingston 2011)

paleoenvironmental reconstructions, a critical interpretation of the evidence indicates that grasses were ubiquitous in the *ULB* and *UNB*, but were never the dominant vegetation cover. Instead, the phytoliths indicate that the vegetation was heterogeneous throughout the sequence, and included a combination of  $C_3$  and  $C_4$  grasses. Even so, the phytoliths do indicate that there was a relatively higher frequency of  $C_4$  grasses in the *UNB* compared with the upper part of the *ULB*. This is supported by stable carbon isotope analyses of soil carbonates that indicate a shift from woodland in the *ULB* to grassy woodland or grassy bushland habitats that were dominated by  $C_4$  grasses in the *UNB* (Cerling 1992).

In summary, the combined evidence from multiple proxies indicates that there was a shift (or probably multiple shifts) in the paleoecology at Laetoli during the depositional hiatus between the *ULB* and *UNB*. Data from stable isotopes, mesowear, ecomorphology, phytoliths and the mammalian community structure all provide support for the conclusion that the paleoecology of the *UNB* was somewhat drier with a greater proportion of grassland than in the *ULB*.

However, it is important to emphasize that this evidence does not indicate that woodland gave way to grassland. Rather, the *ULB* and *UNB* both represent a spectrum of woodland-bushland-grassland habitats, in which the *ULB* is inferred to be at the mesic and more wooded end of that range, while the *UNB* is inferred to be slightly more arid with a somewhat greater coverage of grasses. As noted by Kovarovic and Andrews (2007), the types of habitats in the area did not change between the *ULB* and *UNB*, only the

relative proportions of vegetation types. This relationship is reflected in the marked continuity in the large mammal faunas between the *ULB* and *UNB*, with 62.5% of *UNB* species also occurring in the *ULB*, despite the substantial temporal gap. Another important point to note is that the evidence in support of a significant ecological change in the *UNB* is driven to a large extent by taxonomic and paleobiological changes in the bovids and equids. The *UNB* witnessed the arrival of just a few new species of antilopine and alcelaphin bovids, as well as a replacement species of hipparionine equid, many of which were more specialized for grazing (based on hypsodonty, mesowear and stable isotopes), and presumably better adapted postcranially for increased cursoriality in open country settings (based on ecomorphology) than their earlier counterparts in the *ULB*. The significance of these observations will be made apparent in the concluding discussion.

As noted above, other lines of evidence run counter to the interpretation that the *UNB* was characterized by drier and more open habitats compared with the *ULB*. Ostrich eggshells are ubiquitous throughout the sequence at Laetoli (Harrison and Msuya 2005), and can be attributed to two time-successive species – *Struthio kakesiensis* in the Lower Laetoli Beds and lower part of the *ULB* and the extant *Struthio camelus* in the upper part of the *ULB* and *UNB* (Harrison and Msuya 2005). Studies of the carbon and oxygen isotopes from the ostrich eggshells provide evidence that contradicts the conclusion that the *UNB* samples drier and more open habitats than the preceding *ULB*.

The  $\delta^{13}\text{C}_{\text{OES}}$  demonstrates that ostriches throughout the Laetoli sequence were foraging predominantly on  $\text{C}_3$  plants (Kingston 2011) (Table 4.3). However, the UNB ostrich eggshells show more depleted  $^{13}\text{C}$  values than those from the ULB, implying that habitats were likely more mesic in the UNB. In addition, the eggshells of *Struthio camelus* from the UNB are significantly thicker (14% thicker on average) than those from the upper part of the ULB (Harrison and Msuya 2005). It is known that extant ostriches with access to better quality food and those living in areas of higher rainfall produce eggs with relatively thicker shells (Sauer 1968; Harrison and Msuya 2005). These inferences are further supported by studies of oxygen isotopes in the eggshells (Kingston 2011). The  $\delta^{18}\text{O}_{\text{OES}}$  values are significantly lower in the UNB than in the ULB, suggesting that conditions in the UNB were cooler and more humid than in the ULB (Kingston 2011) (Table 4.3).

The rodent fauna from the Upper Ndolanya Beds is dominated by the ground squirrel, *Xerus janenschii* (58.8% of the rodent fauna) and the gerbil, *Gerbilliscus winkleri* (20.0%) (Denys 2011) (see Table 4.1). Modern-day *Xerus* occurs in semi-arid open woodland, wooded grassland and subdesert habitats (Kingdon 1997; Waterman 2013), while *Gerbilliscus* has broad habitat tolerances, ranging from forest edge mosaics to woodlands and grasslands (Kingdon 1997; Campbell et al. 2011; Reed 2011; Granjon and Dempster 2013). In addition to the greater frequency of *Xerus* in the UNB compared with the ULB (where *Xerus* represents less than 1% of the rodent fauna), the absence of *Heterocephalus*, the rarity of *Pedetes* and the appearance of *Thryonomys* in the UNB represent important differences (Reed and Denys 2011). Today, the naked mole-rat, *Heterocephalus*, and the spring hare, *Pedetes*, have minimal geographical overlap, but they both prefer dry grassland and open woodlands with firm, well-drained soils. The occurrence of *Thryonomys*, the cane rat, in the UNB (comprising 11.3% of the rodent fauna) is indicative of habitats with dense grass cover and reliable precipitation, such as open woodlands, wooded grasslands, reed beds and swamps (Kingdon 1997; Happold 2013). Overall, the rodent fauna from the UNB implies open woodlands and sparsely wooded grasslands that were more mesic than those in the ULB (Reed and Denys 2011).

Terrestrial gastropods, which are common at all localities and horizons throughout the ULB and UNB (Table 4.4), provide an extremely valuable source of information on the paleoecology of Laetoli (Peters et al. 2008; Tattersfield 2011). This is because modern analogs commonly have relatively narrow environmental requirements and preferences (i.e., vegetation, humidity, precipitation, temperature and altitude) and because they have not moved or been transported far from the locations where they lived, died and were fossilized. As a consequence, fossil gastropod communities are likely to provide fine-grained and highly accurate indicators of local habitats, especially when compared with vertebrate taxa that tend to range more widely over the landscape and have a greater chance of being transported (as entire or partial carcasses) by mammalian carnivores and avian raptors (Su and Harrison 2008).

The terrestrial snail community changes during the course of the ULB sequence (Peters et al. 2008; Tattersfield 2011) (Table 4.5; Fig. 4.3). Below Tuff 7, *Subulona*, *Kenyaella*, and *Achatina* are the dominant taxa, which indicate the presence of woodland and forest habitats. Above Tuff 7, *Gittenedouardia* and *Trochonanina* indicate a less mesic period, with a predominance of woodland and wooded grassland. However, the rare occurrence of *Halolimnolix* and *Subulona* suggest that forest and dense woodland habitats continued to persist. The gastropod fauna confirms that the ULB was more mesic than present-day Laetoli, and indicates that the ULB ecosystem was heavily vegetated with extensive woodland and forest habitats.

The common genera of terrestrial snails represented in the UNB fauna, especially *Kenyaella* and *Subuliniscus*, are restricted today to forest and closed woodland habitats with relatively high levels of precipitation (Table 4.5). This is inconsistent with inferences based on the large mammal fauna that the UNB was a relatively dry open woodland-grassland mosaic. A possible explanation for these contradictory results could be that the fossil gastropods are being sampled from heavily vegetated microhabitats that are patchily distributed across the local landscape, and are not representative of the wider ecosystem. However, if this were the case, one would expect to find marked heterogeneity in the gastropod communities between different localities, reflecting both the dominant vegetation type and the mosaic of different

**Table 4.3** Comparison of carbon and oxygen isotopes from ostrich (*Struthio camelus*) eggshells from the Upper Laetolil Beds and Upper Ndolanya Beds

|                                    | Upper Laetolil Beds |        |       |               | Upper Ndolanya Beds |        |       |               | p     |
|------------------------------------|---------------------|--------|-------|---------------|---------------------|--------|-------|---------------|-------|
|                                    | n                   | Mean ‰ | SE    | Range ‰       | n                   | Mean ‰ | SE    | Range ‰       |       |
| $\delta^{13}\text{C}_{\text{OES}}$ | 45                  | -7.8   | 0.267 | -4.1 to -12.1 | 12                  | -9.6   | 0.570 | -6.1 to -11.7 | 0.003 |
| $\delta^{18}\text{O}_{\text{OES}}$ | 45                  | 3.7    | 0.328 | -1.8 to 9.1   | 12                  | 1.7    | 0.570 | -2.2 to 4.7   | 0.007 |

Data from Kingston (2011)



**Table 4.4** List of gastropod taxa from the Upper Laetoli Beds (ULB) and Upper Ndolanya Beds (UNB) (after Tattersfield 2011; Harrison 2011c) (see Fig. 4.3)

| Family             | Genus and species                                  | ULB | UNB |
|--------------------|--|-----|-----|
| Cerastidae         | <i>Gittenedouardia laetoliensis</i>                | X   |     |
| Subulinidae        | <i>Subulona pseudinvoluta</i>                      | X   |     |
|                    | <i>Pseudoglessula (Kempioconcha) aff. gibbonsi</i> | X   |     |
|                    | <i>Kenyaella leakeyi</i>                           | X   |     |
|                    | <i>Kenyaella harrisoni</i>                         |     | X   |
|                    | <i>Subuliniscus</i> sp. A                          |     | X   |
| Streptaxidae       | <i>Streptostele (Raffraya) aff. horei</i>          | X   | X   |
|                    | <i>Streptostele</i> sp. A                          | X   |     |
|                    | <i>Gulella</i> sp. A                               | X   |     |
| Achatinidae        | <i>Burtoa nilotica</i>                             | X   |     |
|                    | <i>Limicolaria martensiana</i>                     | X   |     |
|                    | <i>Achatina (Lissachatina) indet.</i>              | X   |     |
|                    | <i>Trochonanina</i> sp. B                          | X   | X   |
| Urocyclidae        | Urocyclinae sp. A                                  | X   | X   |
|                    | Urocyclinae sp. B                                  | X   | X   |
|                    | Urocyclinae sp. C                                  | X   | X   |
|                    | Urocyclinae sp. D                                  | X   | X   |
|                    | Urocyclinae sp. E                                  | X   | X   |
|                    | Urocyclinae sp. F                                  | X   | X   |
| Halolimnohelicidae | <i>Halolimnohelix rowsoni</i>                      | X   |     |

**Table 4.5** Stratigraphic distribution and inferred habitat preferences of fossil terrestrial gastropods from the Upper Laetoli Beds and Upper Ndolanya Beds

| Stratigraphic unit  | Horizon             | #1 Ranked taxon              | #2 Ranked taxon           | #3 Ranked taxon                               | Paleoecological inference   |
|---------------------|---------------------|------------------------------|---------------------------|---|---|
| Upper Ndolanya Beds |                     | <i>Kenyaella</i> (72%)       | <i>Subuliniscus</i> (16%) | <i>Streptostele</i> (4%)                      | Closed woodland and forest<br>Rainfall: 760–1500 mm                       |
| Upper Laetoli Beds  | Above Tuff 7        | <i>Gittenedouardia</i> (45%) | <i>Trochonanina</i> (30%) | <i>Subulona</i> (10%)                         | Woodland and wooded grassland;<br>forest patches<br>Rainfall: 500–1270 mm |
|                     | Between Tuffs 5 & 7 | <i>Subulona</i> (50%)        | <i>Achatina</i> (23%)     | <i>Trochonanina</i> & <i>Burtoa</i> (both 6%) | Woodland and forest<br>Rainfall: 760–1500 mm                              |
|                     | Between Tuffs 3 & 5 | <i>Subulona</i> (44%)        | <i>Kenyaella</i> (41%)    | <i>Achatina</i> (10%)                         | Closed woodland and forest<br>Rainfall: 760–1500 mm                       |
|                     | Below Tuff 3        | <i>Kenyaella</i> (77%)       | <i>Achatina</i> (6%)      | <i>Pseudoglessula</i> (6%)                    | Woodland and forest<br>Rainfall: 700–1200 mm                              |

See Fig. 4.1 for reference to stratigraphic units, horizons and radiometric dating

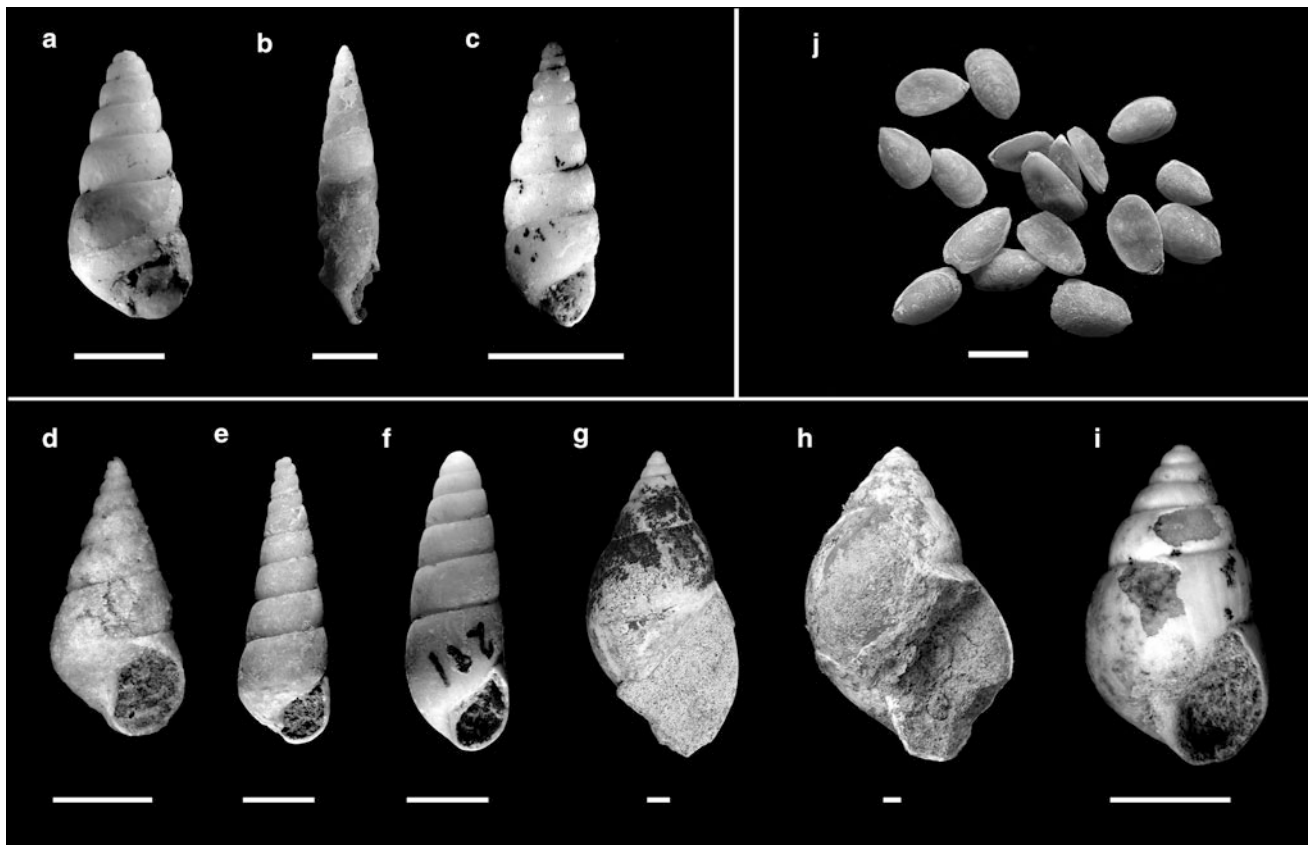
Data on Laetoli gastropods from Harrison (unpublished) and Tattersfield (2011)

Data on habitat preferences and rainfall from Verdcourt (1963, 1987), Pickford (1995, 2004, 2009) and Tattersfield (2011)

microhabitats. This is not the pattern observed. The same gastropod community occurs uniformly at all of the UNB localities, implying that woodland-forest habitats were widespread rather than patchily distributed. Additional support for this inference comes from urocyclid slugs, which are particularly sensitive to humidity and precipitation (Fig. 4.3). Slugs do occur in the Laetoli area today, but they are active only during or immediately following the rainy season and they are ecologically restricted to densely vegetated areas where leaf-litter and fallen tree trunks offer suitable habitats for estivation during the dry season. The ubiquitous

occurrence of fossil slugs at UNB localities (they comprise 88.8% of all fossil gastropods recovered from the UNB) offers incontrovertible evidence that woodland habitats were present and relatively widespread.

The conflicting paleoecological evidence presented above for the UNB is not easily reconciled. The evidence derived primarily from the large mammal fauna suggests that the faunal turnover between the ULB and UNB was associated with increased aridity and a change in the composition of the woodland-shrubland-grassland mosaic in favor of a greater representation of grassland. In contrast, the stable isotope



**Fig. 4.3** Representative shells of the most common fossil terrestrial gastropods at Laetoli. Upper Ndolanya Beds: (a) *Kenyaella harrisoni*; (b) *Subuliniscus* sp. A; (c) *Streptostele* aff. *horei*. Upper Laetoli Beds: (d) *Gittenedouardia laetoliensis*; (e) *Subulona pseudinvoluta*; (f) *Kenyaella leakeyi*; (g) *Achatina* (*Lissachatina*) indet.; (h) *Burtoa nilotica*; (i) *Pseudoglessula* aff. *gibbonsi*. Urocyclid slugs: (j) assorted shells. a–j at approximately the same shell height. Scale bars = 5 mm. Images a–i courtesy of P. Tattersfield

data from ostrich eggshells, the rodent fauna, and the composition of the gastropod communities, indicate that the UNB was relatively more mesic in comparison to the ULB, and that woodlands persisted as the dominant habitat type.

## Discussion and Conclusions

These contradictory findings appear, at first glance, to be difficult to reconcile. However, a more critical assessment of the nature of the evidence, along with a more nuanced appreciation of the significance of spatial scale and evolutionary processes, may offer the possibility to develop a unified and coherent paleoecological model that is consistent with all available lines of evidence. The solution to the problem may have implications for how one perceives the relationship between paleoecological reconstruction of fossil sites and hominin evolution.

There is near-universal agreement that the ULB and UNB represent a mosaic of woodland, shrubland and grassland. What is less certain is the relative proportion of grasslands

that were represented in these mosaic habitats, and whether or not there were significant shifts in the paleoecology between the ULB and UNB. The consensus view, based mainly on evidence derived from the large mammal fauna, is that the ULB ecosystem was composed predominantly of closed and open woodlands with large tracts of grassland, while the UNB was more arid with a higher proportion of grassland. However, contradictory evidence implies that the UNB was relatively mesic and that woodlands continued to be the dominant habitat type.

Two key questions need to be answered to settle the impasse. Which of the two alternative scenarios is most likely given the nature of the evidence? If one scenario is preferred over the other, how can the contradictory evidence be reconciled? First, it is important to highlight that the different lines of evidence offer insights into the paleoecology of Laetoli on different spatial scales. For example, ostrich eggshells, terrestrial snails and micromammals have a limited capacity for dispersal and/or transportation, and modern gastropods and rodents are often characterized by relatively narrow habitat preferences. As a consequence, these sources of evidence tend to reflect fine-grained

ecological differences over relatively small spatial scales, and they are likely to provide a high-precision and reliable indicator of local environmental conditions. Large mammals, on the other hand, tend to range more widely across the landscape, with a greater capacity to traverse and occupy a broad range of different habitats, including those that are marginal or lie outside what would be considered their preferred habitats. As such, paleoecological interpretations based on large mammals tend to be more coarse-grained and applicable over larger spatial scales. The graininess of the environment is clearly dependent on the size of the organism. A small patch of dense vegetation represents a complex ecosystem for a small gastropod, whereas to an elephant the same patch is likely an inconsequential component of a much larger ecosystem. If one accepts the validity of this general premise, then it follows that the evidence derived from ostrich eggshells, rodents and gastropods should be given the greatest weight and has the potential to provide the most accurate reading of the local ecology. In this case, the most likely interpretation of the paleoecology is that the UNB was dominated by woodland and was not substantially different, at least in the general composition of the major vegetation types, from the ULB. This is not to imply that there was no discernable difference in the ecology between the ULB and UNB, but the differences may have been far subtler than has been proposed previously based on analyses of the large mammal fauna.

If this is the preferred scenario, then one has to account for the contradictory evidence that indicates a profound ecological shift in the UNB. It is important to reiterate two points made earlier: (1) many of the species of large mammals in the ULB continued unchanged in the UNB; (2) the main difference in the dietary and locomotor profiles of the large mammals is principally a consequence of the reduced diversity of the browsing ungulates and the appearance of new species of equids and bovids that were more specialized for cursoriality and grazing. However, the temptation is to presume a close correspondence between changes in the composition of the fauna at Laetoli and the local ecology, but this does not take into account the broader paleoenvironmental and evolutionary changes that were taking place across eastern Africa at this time. As noted above, the UNB coincides with a major global climatic shift associated with increased intensification of northern hemisphere glaciation, and this likely led to greater aridity and the expansion of grasslands in eastern Africa (deMenocal 2004, 2011; Bonnefille 2010; Barboni 2014). However, the impact of global climate change was modulated and amplified to a greater or lesser degree by synchronous regional and local influences on the environment (Bobe and Behrensmeyer 2004; Feakins et al. 2005; Trauth et al. 2005, 2009, 2010; Kingston 2007; Kingston et al. 2007; Bobe and Leakey 2009; Bailey et al. 2011; Levin et al. 2011; Barboni 2014). For example, the

complex interplay between regional climatic variability, tectonic activity and lake formation, produced a diversity of ecological settings regionally that presumably represented important loci for speciation and endemism (Potts 1998, 2013; Trauth et al. 2005, 2009, 2010; Maslin and Christensen 2007; Bailey et al. 2011; Macho 2014). It is important, therefore, to place Laetoli in a broader regional context when attempting to interpret the ecological implications of faunal change.

It could be argued that changes in the composition of the large mammal fauna in the UNB has been influenced more by biotic responses to environmental change at a regional level than it has at the local level. In other words, climate change and the accompanying expansion of grasslands in eastern Africa at ~2.8–2.5 Ma was associated with extinctions and speciation events in mammalian lineages across the region in response to local environmental changes and varied selection pressures. Successful new species capable of extending their geographical ranges beyond the confines of their original centers of endemism were potentially able to occupy new areas with somewhat different environments and become new constituent members of previously established local faunal communities. Of the changes that took place in the UNB fauna, it is the appearance of a new species of *Eurygnathohippus* and of several new alcelaphins and antilopins that had the greatest impact on the stable isotope, mesowear and ecomorphology results. These taxa, many of which were more specialized for exploiting more open country environments than their ULB counterparts, had presumably originated elsewhere in eastern Africa in response to regional climatic and environmental changes. These more sophisticated specialists were better able to take advantage of the availability of the grasslands that existed within the woodland-grassland mosaic at Laetoli. The best interpretation of the faunal evidence suggests that the overall ecology remained broadly similar between the ULB and UNB (although it is likely that there was a slight increase in aridity and the proportion of grassland in the UNB), but the composition of the large mammal fauna changed with the arrival of more advanced and specialized herbivores that were better adapted for exploiting the grassland component of the Laetoli ecosystem. Such a model implies that changes in the community structure of local faunas may not necessarily be indicative of significant changes in local ecosystems, but potentially reflect speciation and evolutionary events operating on a broader regional scale.

Testing these ideas and understanding their relationship to hominin evolution will require much more data from many more sites in eastern Africa, but the conclusions presented here do allow us to question whether the appearance of *Paranthropus* in the UNB was directly related to ecological change at Laetoli. The evidence suggests that *Paranthropus* occupied habitats at Laetoli that were not substantially

different from those of *Australopithecus afarensis* earlier in time. We can conclude from this case study that there is not a simple correspondence between the local appearance of new hominin species and changes in the immediate ecology. Attempts to model the causal factors driving hominin speciation events using paleoenvironmental evidence obtained at the local level are highly unlikely to lead to meaningful interpretations and conclusions. One has to look to broader regional environmental changes to understand the nature of the underlying factors that led to the extinction of *A. afarensis* and the origin of the *Paranthropus* lineage.

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