Are land snails a signature for the Mesolithic-Neolithic transition?

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ABSTRACT – Edible land snails, representing food remains, are frequently very abundant in late Pleistocene and early-middle Holocene archaeological sites throughout the circum-Mediterranean region. As such, they appear to represent a signature for a broad spectrum subsistence base as first conceived by Flannery in 1969, and therefore must be in some way related to the transition from foraging to food production. This paper investigates the implications that can be drawn from the presence of these snails through information on their ecology, biology, behaviour and nutritional value as well as the behaviour of the prehistoric human groups who collected and consumed them.


KEY WORDS – circum-Mediterranean; land snails; Mesolithic-Neolithic transition; diet

If ever there was such a ‘Golden Age’ then surely it was in the early Holocene, when soils were still unweathered and uneroded, and when Mesolithic peoples lived off the fruits of the land without the physical toil of grinding labour. (Roberts 1998.125)

At first hunting, fishing, the collection of fruits, snails, and grubs continued to be essential activities in the food-quest of any food-producing group. (Childe 1951.71)

It is now clear that no recorded modern society has relied primarily on molluscan resources for subsistence. (Waselkov 1987.109)

...one can conclude that while some snail layers of the Pyrenees are natural, others probably represent a casual resource taken from time to time, while a few seem to constitute actual snail-farms; in no case, however, can it be accepted that land molluscs were a staple food. (Bahn 1983.49–50)

INTRODUCTION

Land snails are often abundant in Late Pleistocene and early to mid-Holocene archaeological deposits throughout the circum-Mediterranean region (Fig. 1). The most spectacular examples are the Capsian escargotières of eastern Algeria and southern Tunisia, but archaeological sites containing abundant land snail shells that represent food debris are known from elsewhere in the Maghreb, Cantabria, the Pyrenees, southern France, Italy, southeastern Europe, Cyprus, the Levant, the Zagros region, Ukraine and Cyrenaica (for a full review of these data, see Lubell 2004).
Fig. 1. Approximate location of some sites discussed in the text. Open circles represent sites or levels dated to the late Pleistocene (i.e. older than ~10,000 calBP); filled circles are sites or levels dated to the early and mid-Holocene. The hatched areas, the limits of which are estimated, mostly contain sites that would be represented by filled circles: (A) the main region for Capsian escargotières; (B) the Pyrenean region and southern France in which there are many sites containing abundant land snails; (C) the northeastern Adriatic region which also contains numerous such sites. Individually numbered sites are: (1) the Muge middens – Moita do Sebastião, Cabeço da Arruda, Cabeço da Amoreira – where land snails appear to be found only with human burials; (2) Nerja Cave; (3) Ifri n’Ammar, Ifri-el-Baroud, Taghit Hadouch, Hassi Ouenza; (4) Taforalt; (5) Afaouj bou Rhumel, Tamar Hat; (6) Grotta di Pozzo, Grotta Continenza; (7) Grotta della Madonna, Grotta Paglicci, Grotta di Latronico (8) Grotta dell’Uzzo, Grotta di Levanzo, Grotta Corrucci; (9) Rosenburg; (10) Pupicina Cave and other Istrian sites; (11) Donja Branjevina; (12) Foeni Salas; (13) Cyclope Cave; (14) Maroulas; (15) Franchthi Cave; (16) Hana Felek; (17) Laspi VII; (18) Hoca Çeşme; (19) Ilıpınar; (20) Öküzini Cave; (21) Kissoonerga Mylouthkia; (22) Ksar ‘Akil; (23) Djebel Kafzeh, Hayonim Cave, Erq el-Ahmar, Mugharet ez-Zuitina, Ein Gev; (24) Asiab, Gerd Banahilk, Jarmo, Karim Shahir, Nemrik 9, Paleagaurra, Tepe Sarab, Shanidar Cave layer B, Warwasi, Zawi Chemi Shanidar.

Outside the Mediterranean region the occurrence of land snails as food debris in archaeological deposits is less common. Those instances I am aware of include Peru (Chauchat 1988; Ossa 1974), Texas (Clark 1973; Hester, Hill 1975; Honea 1961; Malof on-line 2001) and perhaps elsewhere in North America (cf. Matteson 1959), the Caribbean (Keegan 2000; Veloz Maggiolo, Vega 1982), East Africa (Mehlman 1979), the Sudan (e.g. Fernández Martínez on-line), Ghana (Stahl 1985), Nigeria (Connah, McMillan 1995) and the Philippines (Katherine Szabo pers. comm. 12.03). There are no doubts (e.g. see Evans 1969; Waseklov 1987 Tab. 3.6; website of the ICAZ Archaeomalacological Working Group at http://triton.anu.edu.au/). There is also evidence for past and modern use of amphibious fresh water snails (Pachychilus and Pomacea) as food amongst the Maya (Emery 1989; Hammond 1980; Healy et al. 1990; Moholy-Nagy 1978), prehistoric (ca. 4200 bp) middens of pond snails of the genus Margarya in Yunnan Province, China (Kira 1999) and apparently abundant aquatic snails at southern Chinese Mesolithic cave sites in the Nanling Mountains dating to perhaps 12,000 years and others in northern China dating to the same time range (Zhang 1999).

What is the significance of land snails as prehistoric food? Fernández-Armesto (2002.56–7) raises several points of interest.

[land snails] together with a few other similar mollusks, ... have – or ought to have – an honored place in the history of food. For they represent the key and perhaps the solution to one of the greatest mysteries of our story: why and how did the human animal begin to herd and breed other animals for food?

Snails are relatively easy to cultivate. ... They are an efficient food, self-packaged in a shell which serves as table as a receptacle. ... The waste is small, the nutrition excellent. Compared with the large and intractable quadrupeds who are usually claimed as the first domesticated animal food sour-
ces, snails are readily managed. ... [They] can be isolated in a designated breeding ground by enclosing a snail-rich spot with a ditch [and] by culling small or unfavored types by hand the primitive snail farmer would soon enjoy the benefits of selective breeding. [Snails] can be raised in abundance and herded without the use of fire, without any special equipment, without personal danger and without the need to select and train lead animals or dogs to help. They are close to being a complete food.

Paleolithic shell mounds ... are so common and in some cases so large that only scholarly inhibitions stop us from assuming that they are evidence of systematic food production. It is hard to break out of the confines of a developmental, progressive model of food history which makes it unthinkable that any kind of food was farmed so early; but snail farming is so simple, so technically undemanding, and so close conceptually to the habitual food-garnering methods of gatherers that it seems pigheadedly doctrinaire to exclude the possibility. In places where shell middens form part of a stratigraphic sequence, it is apparent that societies of snail eaters preceded settlers who relied on the more complex technologies of the hunt.

The importance of mollusks as probably the first creatures herded and bred by men has never been broached, much less investigated or acknowledged. So what little can be said about it has to be tentative, commended as much by reason as evidence.

Fernández-Armesto is only partly correct. Yes, archaeologists have tended to ignore the issue; the emphasis has been on the palaeoenvironmental information that can be obtained from study of archaeological land snail assemblages rather than on the role of land snails in human subsistence (e.g. Abell 1985; Bobrowsky 1984; Drake 1960–1962; Eiseley 1937; Evans 1972; Goodfriend 1988; 1991; 1992; Margaritz, Kaufman 1983; Margaritz, Goodfriend 1987; Rousseau et al. 1992; Sparks 1969). Even work dealing with molluscs as food in archaeological sites ignores any mention of land snails (Meighan 1969), while other papers have been more focussed on non-food uses (Biggs 1969). However, there have been a few studies with a different emphasis: Lubell et al. (1976) attempt to test the ideas first advanced by Pond et al. (1938) on the contribution of land snails to prehistoric diet in the Holocene Maghreb; Bahn (1983:47–49) constructs an interesting argument in favour of Mesolithic snail farming in the Pyrenees; Guilaine (1979), Chenorkian (1989) and Girod (2003) discuss various aspects of the dietary importance of land snails in prehistory.

In this paper I will take up Fernández-Armesto’s theme and attempt to better understand whether the presence of abundant land snails represents part of a signature for the “broad spectrum revolution” (Flannery 1969; Stiner 2001). By doing so, I hope to be able to determine whether there is some hitherto unrealized correlation between the consumption of land snails and the transition to a diet based on herded animals and cultivated plants, perhaps analogous (but certainly not identical) to that proposed for marine and fresh-water aquatic foods and the appearance of anatomically modern Homo sapiens (Broadhurst et al. 1998; 2002).

ARCHAEOLOGICAL EVIDENCE

This paper complements my review of the archaeological evidence (Lubell 2004), and I will refer here to those data only as required. It is appropriate, however, to first set out the criteria that allow us to decide whether or not the land snail shells found in an archaeological deposit do, or do not, represent the remains of prehistoric meals.

There have been several arguments made against interpreting land snails as food remains, especially in Cantabrian cave deposits (de Barandiaran 1947; Straus 1992:212; Aparicio, Escorza 1998; Arias 2002). While these may, in certain instances, be correct, I find the counter arguments of Bahn (1982; 1983), Guilaine (1979) and Miracle (1995) more compelling. When considering open-air sites such as those in the Maghreb or the Zagros, the sheer quantities of shells found, and their consistent association with cultural materials, argues incontrovertibly for their anthropogenic origin and, in most cases, for their interpretation as food debris. There are certain species, such as Rumina decollata, which are known to be carnivorous and may thus have colonized the organic rich deposits themselves, but the majority of species are herbivorous and unlikely to colonize abandoned archaeological sites in such large numbers as are found (Lubell et al. 1982–83). Under some conditions today, land snails are known to be the prey of rodents which then accumulate the shells in substantial middens (Yom-Tov 1970), but these are devoid of any cultural associations. I suppose it might be possible that some prehistoric accumulations were formed in this way, given the ap-
parent alternation of human and rodent activity in some open-air land snail shell middens (Lubell et al. 1982–83), but the frequency and size of the accumulations we find, argue strongly against this as an explanation for more than a very few.

The most convincing evidence for prehistoric land snail consumption is found in the Maghreb, beginning in the Iberomaurusian by 20,000 BP and continuing through the Capsian to at least 6000 BP (Guilaine 1979; Pond et al. 1975; 1976). That came from mammals such as au-rochs (Bos primigenius), hartebeest (Alcelaphus buselaphus), zebra (Equus marnaicus), mouflon (Ammotragus lervia), gazelle (Gazella dorcas, G. cuvieri), two lagomorphs (Lepus capensis, Oryctolagus cuniculus) and perhaps ostrich eggs (Struthio camelus) since the shells were used for both containers and ornaments. Other than the charred bulbs of Allium sp. found in the collections at the Logan Museum (Lubell et al. 1976.919), there is no direct evidence for the vegetal component in the diet. Analyses of charcoal from archaeological deposits (Couvert 1972; 1975; 1976) suggest that nuts (pine, pistachio, oak) and some fruits (carob, juniper) would have been available on a seasonal basis (see also Roubet 2003).

This subsistence reconstruction is similar to those from other parts of the Mediterranean region in which land snails are often found in abundance: for example, the Pyrenees (Bahn 1982; Boone 1976; Guilaine 1979), the Italian peninsula, (Mussié et al. 1995), the northern Adriatic (Girod 2003; Miracle 2002), the Aegean (Sampson 1998; Sampson et al. 2002) and the Zagros (Braidwood 1983; Reed 1962; Solecki 1981). It is consistent with the concept of a “broad spectrum” pattern as first proposed by Flannery (1969).

WHY LAND SNAILS?

Archaeological evidence cannot tell us who was eating snails, how they were prepared, or whether or not they were part of an ‘haute cuisine’ or common fare... (Hyman 1986.23)

Hyman overstates the uncertainties involved, as the archaeological evidence makes clear (Lubell 2004). The more interesting questions to ask are: Why are land snails such a common item of food refuse in archaeological sites throughout the Mediterranean region that date just prior to the appearance of agricultural economies in the early post-Glacial period of rapid climatic and environmental change? Were
they a necessity, a luxury or merely an appetizer? Was their use as food restricted by age or gender? Might they have had ritual significance? An examination of data on late Pleistocene and early to middle Holocene paleoenvironments in the circum-Mediterranean may assist in answering such questions.

**PALAEENVIRONMENTAL EVIDENCE**

Several recent publications deal with late Pleistocene and Holocene environmental changes in the Mediterranean region. While there are identifiable long-term trends (Marchal et al. 2002, van Andel 2000), the situation is far from uniform and there is sometimes fundamental lack of agreement on how to interpret the available data (Jalut et al. 1997 vs Pons, Quezel 1998). There has also been considerable debate as to whether or not identified changes should be ascribed to anthropogenic or natural causes (Bintliff 2002). Those studies I have found to be the most useful for my purposes here are Macklin et al. (2002) and Magny et al. (2002), several of the articles in a special issue of The Holocene (vol. 11, no. 6, 2001) and the summary treatment in Roberts (1998).

The general consensus seems to be that until at least the latter part of the mid-Holocene (i.e. long after the establishment of agricultural economies in most of the region), any changes observed can be ascribed to globally observed climatic events rather than anthropogenic causes.

Macklin et al. (2002.1639–1640) show that three alluviation events dated 21±0.8–26±2, 16±5–19±1 and 12.5±1.5–13±2 ka. can be correlated with abrupt decreases in sea surface temperature in the northeast Atlantic, thus providing evidence “that rapid and high frequency climate change in the North Atlantic during the Last Glacial period had a profound effect not only on the vegetation of the Mediterranean region, but also on catchment erosion and river alluviation” and for “a high degree of synchrony in major river aggradation events across the Mediterranean in catchments with very different tectonic regimes and histories”.

Gvirtzman and Wieder (2001) studied sequences of palaeosols at seventeen localities along the coastal plain of Israel, and identify six episodes of pedogenesis (indicating wetter conditions) interspersed with seven episodes of sedimentation or accumulation (indicating drier conditions) during the past 53k years.

While these two sets of terrestrial sequences are not entirely congruent in terms of chronology – perhaps due in part to time lag as a result of distance from the ice sheets as well as meteorological and oceanic circulation patterns – the number and characteristics of arid episodes seem to me sufficiently similar to corroborate the scenario of Macklin and colleagues. I note the similarities of Holocene climatic variability as seen in marine records from the Mediterranean, the North Atlantic, the GISP2 ice record and elsewhere (Casford et al. 2001.Tab. 4).

Magny et al. (2002) use palaeohydrological and other data to show that the Holocene in the Mediterranean region can be divided into an earlier period of cooler and moister conditions and a later one which is warmer and drier (and see also van Andel 2000). The change occurred at ~5000 BP and is reflected in the pollen record, numbers of lakes and lake levels, distribution of radiocarbon dates as a reflection of settlement density, and Sapropel event 1 which indicates an increase in discharge of fresh water into the Mediterranean between 8000 and 6000 BP when lake levels were at their highest (see Magny et al. 2002.Fig. 1).

Reviewing the record from lake cores in Turkey and Iran as well as other data from the eastern Mediterranean, Roberts et al. (2001b.734) conclude: “All of these proxy-climate data sources are therefore in agreement that the hydroclimatic environment in the Eastern Mediterranean altered significantly during the mid-Holocene from relative water surplus to water deficit.”

Roberts et al. (2001a.633) show that Holocene climates and environments across the Mediterranean region were neither uniform nor synchronous, and that the available palynological and palaeohydrological data: ...suggests that a complex rather than a simple patterning of Holocene climate change occurred across the circum-Mediterranean region, which is potentially explicable in terms of meridional or longitudinal shifts in atmospheric circulation. In any case, many records indicate rather marked climatic differences between the two halves of the Holocene [the main point of Magny et al. 2002], and this adds convincing weight to the argument that climates in the Mediterranean Basin have been modulated by precessional forcing during the Holocene.

In another paper, Roberts et al. (2001b.734) stress the complexity of the overall picture and the likeli-
hood that ‘modern’ climatic conditions were not estab-
lished in the Mediterranean Basin until after 6000 cal.
yr BP, presumably linked – directly or otherwise – to
changes in the net receipt of solar radiation as a
result of precessional forcing”.

Despite all these uncertainties, which I expect will
be resolved as further data are collected and ana-
lized, I think we can probably accept the generali-
zed picture presented by Roberts et al. (2001a, 632; see
also Roberts 1998, 104): The herb-steppe which
surrounded most of the Mediterranean Sea during the
late Pleistocene was replaced during the early and
mid-Holocene by sub-humid forest, sometimes
dominated by conifers, more usually by broad-
leaved deciduous trees. Typically Mediterranean
formations of xeric evergreen forests, shrub and
heathland are only rarely represented in early to
mid-Holocene pollen diagrams.

It must, however, be acknowledged that there is no clear
relation between palaeovegetation patterns and
the occurrence of sites with abundant land snails.
Plotting the distribution of sites shown in Figure 1
against the vegetation patterns which can be recon-
structed from the Review and Atlas of Palaeoveg-
etation: Preliminary land ecosystem maps of the world
since the Last Glacial Maximum (Adams et al. on
line), indicates no consistent overall associations.
Admittedly, this is only a very rough approximation of
what would have been complex local patterns, but
the lack of any clear correlation between major ve-
getation zones and site distributions is curious. Other
variables (elevation? soil type? edaphic conditions?
diurnal temperature ranges?) must not doubt be con-
sidered, but that is beyond the scope of this paper.

The Maghreb

Perhaps the only consistent association is the distribu-
tion of Maghreb sites within the zone of Mediterra-
nean scrub, and so it may be useful to look briefly at
conditions in the Maghreb, since that is where land
snails are most abundant in the archaeological record.

During the end of the Iberomaursian and the begin-
ing of the Capsian (i.e., the Younger Dryas), North
Africa experienced a relatively arid phase, evidenced in
part by lowered water levels in Lake Chad. After
10 000 BP, humidity increased again and vegetation
zones of the Sahara appear to have had limits similar
to modern ones. Moist conditions continued, rea-
hing a maximum between ca. 9000 and 8000 BP
when they were interrupted by a short but severe
arid phase found worldwide and dated to 8200 BP
(Alley et al. 1997). The effects of this event may
have lasted until 7500 BP in North Africa. From ca.
6500 to 5500 BP, conditions became even more arid
but were still more humid than today (Adams et al.
on-line; Vernet 1995). Ballais (1995), interprets allu-
vial Holocene terraces in the eastern Maghreb as
indicating greater humidity between about 8500 and
5000 BP, which is somewhat at odds with other (ad-
mittedly incomplete) evidence.

Analyses of charcoal (Couvert 1972, 1975, 1976;
Renault-Miskovsky 1985), faunal remains (Bouchud
1975; Lubell 1984; Lubell et al. 1975, 1976, 1982–
1983; 1984; Morel 1974; Pond et al. 1938) pollen
and other data (Lamb et al. 1989; 1995; Ritchie
1984), provide a relatively good idea of the climatic
and ecological conditions during the Capsian. Vege-
tation cover was open woodland savanna, probably
not too different in many respects from modern East
African environments, with Mediterranean forests
and maquis at upper elevations and/or where humid-
ity was higher. The 8200 BP event mentioned above
is correlated with a change in Capsian technology
that has been identified at several sites (Lubell et al.
1984, 182–184; Rahmani 2003; Sheppard 1987;
Sheppard and Lubell 1990).

The land snails found in such abundance at Maghreb
archaeological sites provide less than satisfactory
data about past climate and environment. The major
species are Helix aspersa, H. melanostoma, Leuco-
chroa candissima, Helicella setifensis and Otala
sp., and since all still occur in the region today, we
have a reasonable idea about the local environmental/
ecological conditions they represent. H. aspersa,
H. melanostoma (the two largest) and Otala prefer
shady, moister habitats, and are known to burrow.
L. candissima and H. setifensis are much smaller,
have greater tolerance for light and heat, and are of-
ten found clustered on the stalks of vegetation, far
enough off the ground to avoid excessive heat build
up within the shell. However, because all five spe-
cies are adapted to semi-arid conditions and can aes-
tivate for long periods of time, they are able to sur-
vive through periods of adverse conditions and are
therefore less than perfect indicators of past climate.
While their abundance in the sites might suggest
that climate was more humid in the past than now,
I suspect that modern conditions are more an arti-
fact of environmental degradation brought on by
mono-cropping and poor land conservation practi-
ces, a pattern well documented elsewhere in the cir-
cum-Mediterranean (e.g. Labaune, Magnin 2002).
In sum, from the late Pleistocene through to the mid-Holocene, the Maghreb was a very good place to be a hunter-gatherer. As I have suggested before (Lubell 1984), I view the abundance of easily available food resources as a key factor in the late arrival and adoption of Neolithic economic practices, late compared to the rest of the circum-Mediterranean region (but see Roubet 2003). However, this does not tell us why land snails were such a common component in sites elsewhere in the Mediterranean just prior to the appearance of food production and, in some areas, after it was well established.

SNAILS AS FOOD

Nutritional value

There are few comprehensive data available, but the best review I have seen is by Elmslie (n. d.) which confirms the generally held view that snail meat is high in protein and low in fat, with the majority of the fats in the form of polyunsaturates.

Despite the high consumption of snails in France (estimates cited by Elmslie are on the order of 30 000 tonnes per annum), the New Larousse Gastronomique is far from complimentary: *From a nutritional point of view, snails' flesh has little food value and is rather indigestible. However, it does contain a large quantity of both Vitamin C and mineral salts (calcium, magnesium, etc.).* (Montagné 1977.849–850).

Snails can also be a fairly labour intensive food source, because in addition to collection, they must be purged before being consumed.

To avoid the risk of poisoning, snails must be deprived of food for some time before they are eaten, for they may have fed on plants harmless to themselves but poisonous to humans. Furthermore it is advisable only to eat snails which have sealed themselves into their shells to hibernate. (ibid. 849)

This is why it appears that aestivating/hibernating snails, with a sealed operculum, are preferred by modern producers and consumers (Elmslie 1982). Since they do not need to be “purged before eating, they are cooked with the epiphragm in place (i.e. they are not woken up first as the gut seems to be emptied before they go into diapause, and the rate of metabolism in that condition is extremely slow” (Elmslie, pers comm 12/03/2004).

Dr. M. Charrier (pers comm. 06/03/2004) contradicts this statement. She says that during dormancy hibernating snails accumulate excretory products in the kidney and the digestive gland and these have such a bad taste that the organs must be removed before cooking the flesh. Therefore, French farmers cook the snails at the end of the growth stage, and those kept during winter are intended to reproduce at the next season.

There is a long history of snail consumption in Europe, and especially in France as noted by Davidson (1999) and Hyman (1986), neither of whom mention nutritional value in any meaningful sense. Nor does Mayle (2001) although he provides some useful gastronomical data. Barrau (1983.91) makes only passing mention, while in Hagen (1995.173) we find the interesting anecdote that, “Helix aspersa ... was apparently eaten in Romano-British times, and was still sold in Bristol markets at the beginning of this [the 20th] century under the name ‘wall fish’.”

Bar (1977) provides archaeological, ethnohistorical and ethnographic examples of land snail consumption in the Levant (though not, of course, by either Muslims or Jews). This should be in no way surprising, for the abundance of land snails in semi-arid regions can be truly astonishing, and farmers consider them a crop pest. Even deep in the Sahara and other hot deserts, land snails can be remarkably abundant (e.g. Schmidt-Neilsen et al. 1971), so much so that experimental evidence has shown them to be useful as a survival food (Billingham 1961). The modern and much-touted “Mediterranean diet” especially as found in Crete (e.g. Galanidou pers. comm. 2/2004; Simopoulos on-line) often includes land snails, but there is as yet no reliable data on their contribution to the overall nutritional makeup.

Miracle (1995) interprets the land snails found in Istrian late Pleistocene and early Holocene sites as a low-ranked resource, compared to large ungulates such as giant deer, horse or elk, and argues that they would “enter the diet only in response to extreme shortage of other resources”, although he al-

2 Dr. Nena Galanidou (Dept. of History and Archaeology, University of Crete) is beginning a research program on the ethnoarchaeology of modern land snail collection and consumption in Crete where “they form a vital part of modern rural diet and their collection has certain seasonal traits” (pers. comm. 2/2004).
lows that season may have an effect (pp. 271–2). He goes on to say that “the significant accumulations of land snails at sites like Badanj [in Levels 2a/2b, younger than 12 000 bp, pp. 64, 493–4] and Kopačina [ca. 9000 bp, pp. 76–7] indicate either extreme resource depletion and subsistence hardship for hunter-gatherers, or environmental shifts that forced snails to increasingly seek the shade and moisture of rockshelters...[but that] we lack the detailed taphonomic data needed to test these alternative hypotheses” (see also pp. 487–88).

Miracle’s interpretation of the overall contribution of land snails to the animal protein component of the diet is congruent with the one we reached for Capsian escargotières in Algeria (Lubell et al. 1976), a view echoed by Morel (1974; 1977; 1978; 1980) for the Maghreb and by Girod (2003) for the northern Adriatic region. However, none of us has as yet looked carefully into the nutritional value of land snails or their importance in the evolution of human diet as has been done for other molluscs (e.g. Ackman 1989; Broadhurst et al. 1998; 2002; Chernorukian 1989; Crawford et al. 1999; Meehan 1982; Nestle 1999; Wasek 1987).

Appendix 1 provides data on the carcass composition of land snails which has been culled from a number of sources. Unfortunately, these data are rather uneven, only two of the analyses (G; and I) are based on populations that can be considered to have been “wild”, and the units of measurement used are not always easy to compare.

Table 1 summarizes basic nutritional data values derived from Appendix 1 and adds data from two other studies. Land snails have a high water content (80% or more in all but one case), confirming the experimental observations of Billingham (1961). Protein value fluctuates widely, perhaps because of what the snails are eating (especially in those cases where commercial feeds are used), but the method of sample preparation and analysis may also have an effect on this. Total fat (i.e. lipid) content tends to be quite low and is apparently independent of size since the values given here are similar to those for the giant African land snail Archachatina marginata (Ajayi et al. 1978; Imevbore, Ademosun 1988) and for another giant snail (Achatina fulica) and the apple snail (Ampullarius insularis) in Korea (Lee et al. 1994). Land snails contain more crude protein and less fat than chicken (Elmslie 1982.24, Elmslie n.d.), and are therefore a lower source of energy (measured in cals/100 g) for humans than chicken (and presumably ruminant) flesh. Land snails contain all the essential amino acids required by humans, but in amounts so small that a diet based largely or entirely on land snails for animal protein would not provide sufficient amounts for adequate nutrition (Grandi, Panella 1978; Imevbore, Ademosun 1988.81). Land snails also contain the five essential unsaturated fatty acids (Grandi, Panella 1978), but again in rather small amounts and with much less of the ω-3 group (considered so important to development of brain and vision function in utero and during the first two years of life) than the ω-6 group although unpublished data cited by Elmslie (n.d.) may, if confirmed, require revision of this interpretation.

Whether or not the nutritional value of land snails is affected by season of collection seems to be uncertain. In those regions where they are collected intensively (e.g. Greece and Bulgaria), there are government regulations that restrict the season of collection to ensure adequate population replacement (Elmslie n.d.). It is also uncertain whether or not the fatty acid composition of land snails changes seasonally: one study, conducted in the Netherlands (van der Horst, Zandee 1973) says they do not, whereas another conducted on Italian land snails suggests they do (Cantoni et al. 1978).

I interpret these data as confirmation that land snails could not have been a primary food resource, and certainly not a major source of animal flesh for for-

3 Erlandson (1988.106), discussing the role of shellfish in prehistoric economies, suggests that “In mixed economies (both agricultural and hunter-gatherer), therefore, a protein perspective suggests that there may be nothing inconsistent with large shell middens reflecting relatively sedentary occupations where shellfish [and therefore I would argue, land snails] served as a long-term dietary protein staple”.

4 In other molluscs, e.g. the Australian abalone Haliotis rubra, there may be marked differences in polysaturated fatty acid content of the flesh between wild and cultured specimens depending on the source and type of nutrients (Su et al. 2004).

5 For a review on the “essential” aspect of fatty acids, see Cunnane (2003). Imevbore and Ademosun (1988.83), writing about the giant African land snail Archachatina marginata, say that “since snail meat appears to be intermediate in essential and polysaturated fatty acids, it may not possess any outstanding nutritional and physiological characteristics much different from the other samples tested along with it”. These were beef, chicken, goat, mutton, pork and two species of fish (Tilapia macraccephala and Clarias lazera).
aging populations. They would not supply sufficient nutrition or energy, even in the enormous quantities apparently consumed by groups in the Maghreb, and they would have been a seasonal rather than a year-round resource. As with other molluscs, their visibility in the archaeological record is high, but the food value represented by the mass of empty shells is not always commensurate with appearances – a point made especially by Paul Bahn (1982; 1983).

Nonetheless, if we accept the characterization of the “paleolithic diet” of Eaton and Eaton (2000. Tab. 2), land snails, if consumed in sufficient quantities, could have provided a significant amount of low fat protein as well as the minerals, amino acids and fatty acids required for human nutrition (Appendix 1, Table 1, and the data in Grandi, Panella 1978). Because they were almost certainly eaten cooked (see Wandsnider 1997 for a discussion of prehistoric cooking methods), water content is probably not a particularly important variable, and the low lipid content means that they would have had to be supplemented by other resources to achieve sufficient caloric input.

LAND SNAILS AND THE BROAD SPECTRUM REVOLUTION

However, are we to interpret the consistent presence, and indeed abundance, of land snails in circum-Mediterranean archaeological sites dating just prior to the advent of agriculture? The generally held view is that when large numbers of land snails occur in late Pleistocene and early Holocene sites they are best seen as one component, normally a minor one, in a subsistence strategy that incorporated what had previously been “less preferred resources” (Gebauer, Price 1992.3; see also Flannery 2000.6) But this leaves unanswered questions as to whether or not land snails were a controlled and harvested resource (Fernández-Armesto 2002) or more an indicator of feasting events than of everyday diet (Miracle 2002).

### Biology and ecology of land snails

To investigate such questions we need to know something about the biology and ecology of land snails. In this section I have relied heavily on The Biology of Terrestrial Molluscs (Barber 2001) and several of the papers cited by the contributors to that volume.

There are thousands of species of land snails, each with its own characteristics, but there are a series of general traits that we can focus on here.

Because they have no physiological means of controlling intake or loss of moisture other than sealing themselves in their shell, and are relatively intolerant of extreme cold or heat (with certain significant exceptions – see, e.g. Schmidt-Nielsen et al. 1972), land snails have evolved physiological responses to deal with cold (hibernation) and heat or drought (aestivation) that allow them to survive extended periods without taking in nourishment. This, combined with the fact that they are also hermaphrodites and can on occasion self-fertilize, means that land snail evolution has been rather slow and polymorphism is quite common. Cooke (1913.37–39) cites a number of examples of land snails that survived up to five years of aestivation after which, in one 19th century instance, a single *Helix lactea* placed in an herbarium, reproduced offspring. However, both Gomot de Vaufleury (2001.343) and Heller (2001a)

### Tab. 1. Nutritional composition of land snails.

<table>
<thead>
<tr>
<th></th>
<th>Appendix 1</th>
<th>Grandi and Panella (1979)</th>
<th>Lee et al. (1994)</th>
</tr>
</thead>
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<tr>
<td>H₂O</td>
<td>78.9 ± 9.2</td>
<td>79.46 – 80.50</td>
<td>81.20 – 82.36</td>
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<td>Protein</td>
<td>38.6 ± 24.1</td>
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<td>Carbohydrates</td>
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<td>1.25 – 1.39</td>
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<td>Essential amino acids</td>
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<tr>
<td>Essential PUFAs</td>
<td>0.4 ± 0.1</td>
<td>13.8 – 18.1</td>
<td></td>
</tr>
</tbody>
</table>

a Data are g/100g raw.
b Data are percentage ranges for *Helix aspersa*, *H. lucorum* and *H. pomatia* except for minerals and PUFAs which are only for *H. aspersa* and *H. lucorum* and the latter is the percentage of all fatty acids.
c Data are g/100g edible portion for cultivated *Achatina fulica* and *Ampullarius insularus*.
d 41.9% of all amino acids
e 34.6% of all fatty acids

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6 Flannery cites the evidence for land snails in the Mousterian levels at Devil’s Tower, Gibraltar (in Garrod et al. 1928) as indicating even earlier broad spectrum patterns. As with the Pre-Aurignacian deposits at Haua Fteah (Klein and Scott 1986; Hey 1967), I believe the case for subsistence use at such an early date has yet to be demonstrated.
make it clear that the majority of pulmonate land snails breed by mating and outcrossing.

Most land snails are iteroparous (several reproductive periods, usually one each year for a number of years) although some are semelparous (only one reproductive period, after which the organism dies). They lay eggs in clutches, most often in holes excavated into the ground, and almost always during periods (seasons?) of increased moisture. Clutches vary widely in size – from as few as ten to as many as several hundred eggs – depending on the species and on soil and moisture conditions. Desiccation has a marked effect on rates of egg mortality, and studies show that location with reference to prevailing climate can be critical. For example, in the Negev the rate of hatching was 100% for eggs laid on a northern slope, but less than half (46%) for those laid on a southern slope and thus more exposed to the sun.

Tompa (1984:124–125) provides some data on the time from egg laying (oviposition) to hatching. There appears to be considerable variability, depending on size of snails, size of clutch, season and temperature. In temperate climates, eggs laid in autumn may overwinter and not hatch until the following spring. In other cases, eggs may hatch in autumn but the animals are not mature until the following summer. Chevallier (1979:Fig. 14) suggests that although adult size is attained within one year, it takes an average of two years for Helix to reach maturity, whether raised under controlled or “natural” conditions. These estimates are corroborated by papers on modern snail farming (Elmslie et al.1986) which provide additional data on controlled breeding and raising. I have been unable to find anything equivalent for “wild” land snails.

Temperature is also an influence. While reproduction can occur in a range from 5°–25°C, much higher rates occur in the range of 20°–25°C. Furthermore, maturation takes place far more rapidly in temperatures above 15°C with a long-day photoperiod.

Land snails living in temperate regions often hibernate during the winter, and during this time gametogenesis may cease completely and then resume prior to the end of the hibernation cycle: “the longer the hibernation period (up to 18 months evaluated), the sooner the mating behaviour occurred at the break of hibernation and the higher the reproductive output.” (ibid. 335)

Gomot de Vaufleury (2001) reviews growth and reproduction in land snails. She points out that photoperiod length influences reproduction: the fewer hours of daylight, the lower the rate of egg laying, spermatogenesis and reproductive output. There are inter-specific differences, but the general principle obtains for all.

Many species live less than two years, but a number of the larger ones and especially the Helicidae which include the edible species most often found in archaeological deposits, can live between five and 15 years (Heller 1990:Tab. 3). To some extent, but especially amongst those species that inhabit unpredictable environments such as the semi-arid and desertic regions of North Africa and the Levant, the less favourable the environmental conditions the longer-lived the land snails (ibid. 270). Thus, reconstruction of palaeoenvironmental conditions (using species lists of land snails in addition to other proxy data), may be key to understanding how human populations relied on land snails as a food resource. A series of studies by Goodfriend (1988; 1991; 1992; Margaritz, Goodfriend 1987) have made a start in this direction, but more needs to be done.
Heller (2001a; see also Heller 1988), reviewing life history strategies, points out that predation affects survival, as does cannibalism of eggs by hatchlings. Predation by rodents, especially in arid and semi-arid regions, may lead to the accumulation of substantial middens of shell (Yom-Tov 1970), and at least one documented instance of massive predation by wild boar (Sus scrofa) reduced the adult snail population by 50% (Heller and Ittiel 1990). This allowed smaller individuals to grow to adult size whereas previously competition had kept them small. Heller and Ittiel suggest that the mucus left behind as a result of snail locomotion is a factor in reducing competition for resources by keeping down the number of adolescent individuals. This may have implications for human predation and control of land snails as a resource, especially if snails were kept in an enclosure prior to consumption – either bred there or collected and conserved there.

This leads to a whole range of possible considerations on the taphonomy of land snail shell middens such as those found in the Maghreb, where rodent burrows are ubiquitous. In almost all the instances I have observed, the presence of modern macrobotanical materials in the burrows argues against anything other than disturbance of the archaeological deposits by rodents. Nonetheless, some disturbance may be very ancient, if (as seems likely) sites were recolonized by snails and rodents during periods of non-occupation by humans (see Lubell et al. 1982–1983). We did, at one time, consider the possibility that abandoned escargotières would have been attractive habitats for land snails, thus leading to the large numbers of sites – occupation of one by a group who then collected snails at neighbouring sites. Unfortunately, the resolution of the archaeological record (or at least our data) is too coarse to test this hypothesis. The idea would, in any case, really only apply to the Maghreb where there are hundreds of contiguous, coeval open-air sites (Grébénart 1975; Lubell et al. 1976. Fig. 1) that could have functioned as “snail farms”. It is not applicable in areas such as the Pyrenees or the northern Adriatic where sites are in rockshelters or caves, in neither of which would there be naturally occurring concentrations of land snails of the size and density found in archaeological deposits despite some suggestions to the contrary (Bahn 1982; Girod 2003; Guilaine 1979 vs. Aparicio 2001; de Barandiarian 1947). Reviewing land snail ecology, Cook (2001.453) makes the point that: "In population studies of terrestrial gastropods, many species have been found to exhibit a decline in abundance in both the summer and winter. In some cases, this probably represents a genuine decline in numbers, but in others it is best interpreted as substantial proportions of the population becoming inactive and therefore not being sampled."

The onset and termination of both hibernation and aestivation are controlled largely by prevailing weather conditions rather than endogenously (ibid. 456), however diurnal activities (i.e. circadian rhythm) are controlled by both endogenous factors and external ones such as length of day and amount of humidity (ibid.). Thus, “while the relationship between activity and weather is an important aspect of the control of behaviour, it is not a simple one” (ibid. 457).

Nor is the relationship between land snail populations and the environments in which they are found. LaBaune and Magnin (2002) studied land snail communities in overgrazed Mediterranean uplands and make some observations of interest here.

The number of xerophilic open-ground snails decreases when the grassland remains ungrazed, but a homogeneous grazed herb layer significantly reduces snail diversity and abundance.

A low richness and diversity of land snail communities is associated with large patches of grazed grassland, mainly with a continuous herb layer 5- cm high. On the other hand, the highest diversity is observed for communities living in scrublands or in smaller patches of grassland. Thus, heterogeneity seems to favour snail diversity both at the local and landscape scales. At the local level, the heterogeneity of vegetation (horizontal and vertical) and a complex cover of the soil surface enable more species to co-exist. At the landscape level, heterogeneity has an effect on land snail dispersal and on microclimate (LaBaune, Magnin 2002.243).

I take all these observations to mean that under prehistoric conditions, in which overgrazing is unlikely to have been a problem, both diversity and abundance of land snails would have been sufficient to enable extensive, and at times intensive, collection by humans without seriously impairing the survival of land snail populations as a predictable natural resource. However, a question remains.

**How “productive” are land snails?**

If we are going to consider seriously the proposition that prehistoric groups cultivated land snails as op-
posed to harvesting them as a wild resource, we need to look more carefully at questions of population control, breeding and productivity.

Fernández-Armesto (2002 56) proposes that: “Land varieties can be isolated in a designated breeding ground by enclosing a snail-rich spot with a ditch. By culling small or unfavored types by hand the primitive snail farmer would soon enjoy the benefits of selective breeding. Snails are grazers and do not need to be fed with foods which would otherwise be wanted for human consumption. They can be raised in abundance and herded without the use of fire, without any special equipment, without personal danger and without the need to select and train lead animals or dogs to help.”

The literature on snail farming suggests to me that this is an oversimplification (Elmslie n.d.). As an example, Elmslie (1982 23) draws a distinction between “part life-cycle farming” and “complete life-cycle farming”. In the former, wild snails are collected when abundant, kept in paddocks formed by simple wire fencing (in which the ground is carefully prepared), and fed on either natural vegetation or a mixture of salad vegetables and brassicas until market conditions are right for maximum profit. I suppose something similar to this scenario might, in a few instances, be a plausible approximation of what took place in the prehistoric past (and I admit the Capsian escargotières could be one such possibility), but in reality I believe it is far more likely that land snails were sometimes an intensively harvested, rather than a cultivated, resource. The key to resolving this may be modern data on population biology for both wild and captive modern populations.

Some data are available for wild populations in the Mediterranean region (e.g. André 1982; Cameron et al. 2003; Heller 2001b; Iglesias, Castillejo 1999; Kiss, Magnin 2003; Staikou et al. 1988) and elsewhere (Greenwood 1974; 1976; Lange, Mwinzi 2003). However, other than the papers by Greenwood and by Staikou et al., they are not that helpful in this instance because most are concerned with species diversity rather than with actual population numbers and densities of single species or a limited number of edible species.

Greenwood (1974; 1976) studied populations of Cepea nemoralis, a species analogous to the edible snails found in archaeological sites, in the Derbyshire Dales of the north midlands of England. He estimates that for populations with densities of 0.1, 1.5 and 10/m², neighbourhood sizes (an expression of population) would be 190, 2850 and 12 000 respectively. Given his estimates for a generation interval of about four years, relatively constant annual production of juveniles, an average adult lifespan of approximately 2.4 years, mean lifetime production of young of 99.6 with a variance of 10 811 (!), and survivorship of at least 50%, it is clear that a population of 3000 adults (some of which would breed hermaphroditically) can produce an enormous number of offspring.

Staikou and colleagues (1988) spent four years studying a population of wild land snails in a 400 m² fenced off area in northern Greece. Four helicid species were present: Helix lucorum, Monacha cartusiana, Bradybaena fruticum and Cepea vindobonensis. Although only H. lucorum is considered an edible snail today, B. fruticum and C. vindobonensis are within the size range, and have some of the ecological characteristics, of the smaller species found in Capsian sites. Mean population densities (number of individuals/m² ± 1sd) over a three year period were: H. lucorum (4.95 ± 2.12) M. cartusiana (6.94 ± 2.77), B. fruticum (6.36 ± 1.25) and C. vindobonensis (1.42 ± 0.06). It is not clear from the publication how many of the individuals were mature (i.e. of edible size), nor were densities uniform across the entire sampling area. Nonetheless, if we use very conservative figures and say that only 50% could be considered mature at any one time, the total average numbers available to collect would be on the order of: 1000 H. lucorum, 1200 B. fruticum and 300 C. vindobonensis for a total of 2500 snails. For H. lucorum only, Staikou and colleagues estimate the mean annual crop (biomass) at 4.04gm⁻² and an annual production of 5.02gm⁻². These hardly seem values high enough to provide anything like sufficient protein annually for a group of foragers.

In this light, I am dubious about the sort of figures one finds on websites devoted to snail farming. The following is only one of many possible examples.

Using a control group of 200 Helix aspersa (Brown Garden) snails, under ideal conditions, we created a large number of market size snails in a three-year period. The following figures are based on this three-year study.

Taking the 200 snails with a laying capacity of 150 eggs each during the spring and summer months we figured on having approx. 30 000 snails at the end of our first year of production. With a rea-
Are land snails a signature for the Mesolithic-Neolithic transition?

zation that we should expect a normal mortality of 40–50% from all causes we should then have something around 15,000 snails survive with half of these ready to produce 75 eggs each. This produces 562,500 snails if all survived. We again figured a 50% mortality rate, by the end of the third cycle something like 17 million snails would be produced if all lived. A more realistic figure of those growing to maturity would be something like 1/16th, or 1,000,000 plus. (www.frescargot.com/expect.htm)

Studies of species diversity and population biology for land snail populations on Crete (Cameron et al. 2003) and for Helix aspersa in north-western Spain (Iglesias et al. 1996) do not provide data equivalent to those found in Greenwood (1974; 1976), but they do suggest that his estimates are applicable to populations in semi-arid Mediterranean environments and even in arid ones (e.g. Heller 2001b) as do those of Staikou et al. (1988) discussed above.

Given these data, and the fact that most land snail species prefer dead plant material to fresh and herbs to grasses (e.g. Williamson, Cameron 1976), I am not convinced that raising land snails would have been all that more advantageous in most instances than relying simply on their natural fecundity to provide sufficient numbers to meet human dietary requirements.

I believe this is also borne out by the data available for captive, “domesticated” modern populations (e.g.

Elmslie 1982; n.d.; www.lumache-elic.com; links found at www.manandmollusc.net) which show that raising snails is a far more complex activity than the procedures discussed by Fernández-Armesto, and far more prone to failure.

For example, this is from the U.S. Department of Agriculture website www.nalusda.gov/afsic/AFSIC_pubs/srb96-05.htm*.

Population density also affects successful snail production. Pens should contain no more than six to eight fair-sized snails per square foot, or about four large H. pomatia; or figure one kilogram per square meter (about .2 pounds of snail per square foot), which automatically compensates for the size of the snails. If you want them to breed, best results will occur with not more than eight snails per square meter (.8 snails per square foot). Some sources say that, for H. pomatia to breed, .2 to .4 snails per square foot is the maximum.

Snails tend not to breed when packed too densely or when the slime in the pen accumulates too much. The slime apparently works like a pheromone and suppresses reproduction. On the other hand, snails in groups of about 100 seem to breed better than when only a few snails are confined together. Perhaps they have more potential mates from which to choose. Snails in a densely populated area grow more slowly even when food is abundant, and they also have a higher mortality rate. These snails then become smaller adults who lay fewer clutches of eggs, have fewer eggs per clutch, and the eggs have a lower hatch rate.

CONCLUDING REMARKS

This enquiry is a work-in-progress. I cannot honestly say that I have so far been able to answer satisfactorily many of the questions initially asked although I am convinced that the answer to the question posed in the title – Are land snails a signature for the Mesolithic-Neolithic transition? – is an unequivocal “yes”; a point made in a humorous fashion by the late Pierre Lau-
An essay such as this, in which one ventures far outside one's area of expertise, requires the cooperation of many colleagues. For their gracious responses to my ill-informed enquiries about the lipid chemistry of molluscs, I am indebted to Robert Ackman (Dalhousie University), C. Leigh Broadhurst (22nd Century Nutrition, Inc.), Bernard Fried (Lafayette College), Kenneth Storey (Carleton University) and Annette de Vaufleury (Université de Franche-Comté). Joseph Heller (Hebrew University) and R.A.D. Cameron (University of Sheffield) both provided insight into land snail ecology. Leslie J. Elmslie (Rome) generously allowed me to see his unpublished data and provided copies of Italian publications on land snail carcass composition that I would have otherwise missed. Dr. Maryvonne Charrier (UMR EcoBio 6553, Université de Rennes 1) provided several helpful comments on an earlier draft. For their prompt responses to my many enquiries, I am grateful to Pablo Arias (Universidade de Cantabria), Paul Bahn (Hull, UK), Robert Chenorkian (Economies, Sociétés et Environnements Préhistoriques, Aix-en-Provence), Josef Eiringer (Deutschen Archäologischen Instituts, Bonn), Kitty Emery (Florida Museum of Natural History), William Farrand (University of Michigan), Alberto Girod (Laboratorio di Malacologia Applicata, Milano), Haskel Greenfield (University of Manitoba), Eva Lenneis (Universität Wien), Andrew Malof (Austin, TX), Preston Miracle (Cambridge University), Marcel Otte (Université de Liège), Noura Rahmani (Montreal, PQ), Adamantios Sampson (University of the Aegean), Janet Ridout-Sharpe (CABI Inc.), Dominique Sacchi (CNRS Carcassone), Ralph and Rose Solecki (Columbia University), Lawrence Straus (University of New Mexico), Laurens Thissen (Amsterdam) and Xiaohong Wu (University of Beijing). None of those mentioned above can be held responsible for what are no doubt my numerous errors and mis-statements.

I am grateful for suggestions made by colleagues attending the two conferences at which preliminary versions of these ideas were presented and to the organizers of those conferences: Jean-Philip Brugal and Jean Desse (CÉPAM, Sophia Antipolis, Valbonne) – XXIVe Rencontres Internationales d’Archéologie et d’Histoire d’Antibes ‘Petits Animaux et Sociétés Humaines’; Mihael Budija (University of Ljubljana), 10th International Neolithic Seminar – ‘The Neolithization of Eurasia: Paradigms, Models and Concepts Involved’. My participation in both was in part made possible by a grant from the HFSRR Fund, University of Alberta.

This paper began in 1966 when Ralph Solecki assigned me a seminar project to find out if the land snails occurring in the upper levels at Shanidar Cave could be used for palaeoenvironmental reconstruction. He could never have suspected where this would take us! I owe a debt I can now never repay to the late Alonzo Pond whose research in North Africa formed the basis from which my own began. Achiel Gautier (Rijksuniversiteit-Gent) started that quest with me and we have continued to share ideas ever since. As always, I thank Mary Jackes for her encouragement and help over almost that many years.

Finally, I thank the Inter-Library Loan Services of the University of Alberta Library for never failing me. Figure 1 is slightly modified from an original prepared by Michael Fisher, Department of Earth and Atmospheric Sciences, University of Alberta for Lubell (2004). Laurens Thissen pointed out errors which have been rectified in the version used here. Figure 2 is reproduced by permission of Professor Jean Guilaine (Collège de France).
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### Appendix 1: Composition of land snail flesh

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<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
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<td>Stearic 18:0</td>
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<td>docosahexaenoic 22:6 ω-3*</td>
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<tr>
<td>other after 18:0</td>
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<tr>
<td>unidentified</td>
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A Scherz et al. (2000). Helix pomatia L., 100g edible portion. Units of measure as per column α.

B Hui (1996 Tab. 13.6). Steamed or poached: contents/100g. Units of measure as per column α.


D Zhu, N et al. (1994). Average for Helix sp. + Haplotrema sportella + Vespericola columbiana. Units of measure are mean % of total fatty acids.

E Salvini et al. (on-line). H. pomatia per 100g edible. Units of measure as per column α.

F Fineli Food Composition Database (1999–2002) National Public Health Institute, Finland (http://www.ktl.fi/fineli/). Units of measure as per column α.

G1 Gomot (1998 Tab. 2). Values are g/100g for “natural” (i.e., not fed on commercial meal) H. pomatia and H. lucorum, calculated on dry matter. Units of measure as per column α.

G2 Gomot (1998 Tabs. 2 and 4). Values are averages of foot and viscera combined in g/100g for H.a.aspersa, H. aspersa maxima, H. lucorum and H. pomatia fed on E3–2 commercial meal, calculated on dry matter. Units of measure as per column α.

H Bonomi et al. (1986). Industrially raised H. pomatia maior. Units of measure as per column α.

I van der Horst and Zandee (1973). Wild Cepea nemoralis. Average of seven monthly values in mol per cent (the amount of each fatty acid present as a percentage of the total fatty acids recovered).

J Thiele and Kröber (1963) as given in Voogt (1972 Tab. XII). Values are free fatty acids expressed as %. For C17:0 this is 17:0 + 16:2.

* Data from Grandi and Panella (1978) are not included because they are expressed in a way that makes it difficult to compare with the values reported here. They are summarized in Table 1 and discussed in the text.