Chapter 15

The Present and the Past: The Interpretation of Sub-Fossil Molluscan Assemblages and the Relevance of Modern Studies, with Specific Reference to Wet-Ground Contexts in the UK

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INTRODUCTION

The interpretation of sub-fossil Mollusca from archaeological contexts and Holocene soils and sediments has always relied upon there being a relationship between the present and the past. It is possible to reconstruct past environments and landscapes, since virtually all of the species found as Holocene sub-fossils are still to be found in the British Isles. A standard uniformitarianist approach can readily be adopted, where the modern ecologies (or aspects of the modern ecologies) of species (or groups of species) can be applied back through time. While this is not without its difficulties, many of which are outlined below, Thomas (1985, 149) correctly noted that sub-fossil analysis has worked ‘because the data generally make ecological sense’.

This paper will consider some of the general theoretical difficulties of a uniformitarian approach to the interpretation of sub-fossil Mollusca, in particular concentrating on the issues surrounding the theoretical problem of non-analogue communities (Gee and Giller 1991). Attention will then turn to wetlands, with a discussion of assemblages recovered from Holocene overbank alluvial deposits and modern floodplain faunas, although the implications of the demonstrated relationships between present and past are wider. This will be followed by discussion of the interpretation of sub-fossil molluscan assemblages recovered from early-mid Holocene tufa deposits, and how modern ecological work might help improve the level at which we can reconstruct the environments in which such deposits formed.

MODERN ECOLOGIES AND ECOLOGICAL GROUPS

Although snail shells were recognised as being present in archaeological contexts and Holocene sediments over a century ago (Evans 1972), the development of sub-fossil molluscan analysis as a powerful tool for environmental reconstruction can in essence be traced back to two seminal papers. These, by A. E. Boycott

(1934, 1936), synthesising knowledge of modern ecologies of land snails and freshwater snails, respectively (freshwater snails are not further considered here). Both papers made a number of important observations. First, it was recognised that while many species of Mollusca had very broad ecologies and could tolerate a wide variety of conditions, a number were rather more exacting in their requirements. For land snails, Boycott (1934) proposed that species could be grouped into several major categories:

Obligate hygrophiles – species restricted to damp places
Facultative hygrophiles – other species found in damp places but not restricted to them
Xerophytes – species restricted to dry places
Facultative xerophytes – other species found in dry places but not restricted to them
Synanthropes – species showing a liking for sites associated with human activity
Anthropophobes – species avoiding sites associated with human activity
Rupestrals – species particularly associated with stone walls
Woodland – species found in woodlands
Woodland 'restricted' – species usually found only in woodland
Non-woodland – species not normally found in woodlands

While the groups were not necessarily mutually exclusive (*i.e.* one particular species of snail might belong to more than one group), some of the groupings were much better defined than others – the 'woodland restricted' group, for example. The value of this to sub-fossil studies was quickly recognised, and Sparks (1961) was able to apply a modified version of these groupings to quantitatively-based fossil studies, recognising four ecological groups (marsh, dry land, woodland and *Vallonia* sp.) as being useful for interpreting past environments. The difficulties, however, were still recognised, with Sparks (1961, 77) reporting that 'these groups must not in any way be considered final, as the variations in the groups have so far been little studied'.

The following ten years saw a tremendous increase in the application of molluscan analysis to archaeological contexts and Holocene sedimentary sequences, particularly by M.P. Kerney and J.G. Evans. Evans (1972) was able to provide a major synthesis on the use and interpretation of Mollusca recovered from archaeological sites, and to propose the following ecological groupings as useful in interpretation:

Woodland species
Pomatias elegans
Intermediate (or catholic) species
Open-country species
Marsh species –amphibious
  obligatory marsh
  characteristic but not confined
  others with no special affinity
Freshwater slum
Alien species – those introduced to the British Isles in the historic period
Burrowing species
Anthropophobic species
Synanthropic species

The synthesis described which species should go into which group, and also summarised the literature on species ecology and their sub-fossil occurrences. The link between known ecology and palaeoecology was made explicitly apparent for each species present in British Holocene deposits, and limitations (as well as potential) were recognised. Subsequently, other ecological groupings have been used. Preece (1980), for example, has used ‘swamp’ (obligate hygrophiles), ‘terrestrial A’ (catholic/generalist) and ‘terrestrial B’ (more shade-demanding) groupings in interpreting Mollusca recovered from tufa deposits (see below), but to some extent these are variants on the themes already established by Sparks and Evans.

Given the above developments it can be seen that interpretation of sub-fossil assemblages can potentially proceed in two ways, either through an autecological approach (based upon individual species ecology), or a synecological approach (where present and past communities can be compared). In reality it is somewhat artificial to separate these fully, since, as will become apparent, there is overlap. To do so, however, is useful heuristically. In relation to Mollusca, the approaches and their difficulties have previously been outlined by Evans (1972, 1991), Cameron (1978a) and Thomas (1985), upon whose work much of the following two sections is based.

Interpretation difficulties – autecology

At its most basic level an autecological approach can assign each recovered species to an ecological group based upon its present day habitat preferences, *i.e.* the classic uniformitarianist approach. The changing percentages of these groups through a sequence can then be used to indicate environmental change, for example from shaded to open-country. While Harris and Thomas (1991) point out that this tends to reduce interpretation to a summation of micro-habitats, they also recognise the value in that it avoids matching past and present *communities* (see below). Nevertheless, as for other macro- or micro-fossil analyses where there is a continuation into the present, autecological uniformitarianism leads to a number of difficulties which can be summarised as follows:

Identicality of ecology between past and present is often assumed rather than demonstrated. Indeed, identicality of *species* is also assumed, not proven, based upon identicality of shell morphology, which conceivably may not be a reliable guide.

Specificity of ecology is also problematic. In reality, very little detail is known about molluscan species ecology. Distributions are controlled by a large number of interacting variables, both biotic and abiotic, most of which are unknown or unpredictable for most species. The modern work that has been done seems to make it increasingly difficult even to assign species to an appropriate habitat group. Basically, poor knowledge of modern ecologies leads to weak and generalised interpretation of sub-fossil material, and this can be particularly true when it comes to wetlands (see below). Even if we had very detailed modern ecological data, for example on tolerances to environmental variables, this does not get around the potential problem of identicality of species (see above), nor serve to demonstrate that the same variables acted in the same way upon the species, either singly or in concert, in the past. The species that seem to be very restricted in their distributions (stenotopic species), and may therefore be good candidates for status as indicator species, may, to some extent, have become more restricted in their distributions through the Holocene, not least because of the increasing effects of human modification of the landscape.

Finally, the degree to which we can accept identicality of environments is also problematic. Modern grasslands are not, in detail, like Neolithic or Bronze Age grasslands, modern woodlands are not, in detail, like prehistoric ‘wildwoods’, and modern, managed wetlands are not, in detail, like unmanaged wetlands. The extent to which we can use individual species’ present habitat requirements and project this back in time is potentially uncertain. As well as relating to the above, this also relates to the problems of non-analogue communities (see below).

Interpretation difficulties – synecology

A synecological approach to interpretation may in part be considered as the summation and synthesis of the autecology of each species within the assemblage – in effect treating it as akin to an ecological community. An extra dimension can be given, however, by the use of analogy at the community level. Autecology uses *individual* ecologies analogously between present and past, while synecology matches, or attempts to match, present communities with past *representations* of communities (the fossil assemblages recovered). Sometimes the assemblages recovered may represent an amalgamation of several past communities, both spatially, for example when post-mortem transport brings shells from a wide area together at one point, or temporally, where the recovered assemblage represents an accumulation of several successive communities that occupied a given spot through time. In such circumstances a synecological approach may be problematic. At other times, however, for example from the surfaces of buried soils, or within overbank alluvial or tufa deposits, the recovered assemblage may be very closely representative of the once living community (Evans 1991), and the principle of one-to-one community matching between past and present becomes theoretically possible. An example is the work of Bush (1988), which utilised numerical analysis techniques in matching past and present wetland molluscan samples and used this as a basis for legitimising the interpretations offered for the fossil samples and for tracking the direction of environmental change. Nevertheless, this analogue community approach is open to criticism, summarised briefly as follows (note again that there is overlap between some of the arguments and with some of the autecological arguments):

Paucity of applicable data is one of the major problems. Although the number of modern studies, and thus our knowledge of modern communities, continues to increase, the applicability of the data to the past is usually somewhat limited. Many modern studies have been conducted on woodland faunas from a variety of woodland types (*e.g.* Wardhaugh 1997), but interpretation of fossil assemblages still tends not to go beyond 'woodland' as a generic habitat classification for an environment dominated (at least in terms of the most obvious vegetation) by trees. Even then (see below) there can still be an element of doubt in some cases. Part of the problem is that modern ecological studies are not asking questions of relevance to palaeoecological interpretations (Davies 2003a). Another problem is that many of the modern studies are from geographical areas different to those of most of the fossil material they could potentially help to interpret. This is problematic since molluscan faunas are geographically dependent (see, for example, Cameron and Redfern 1972, Cameron 1978b). A further potential problem is that modern studies have tended to concentrate on established, stable habitats, whereas many of the fossil assemblages may derive from transient, unstable ones (see below).

Similarity of past and present faunas may, of course, also be purely coincidental, *i.e.* the match does not necessarily imply similarity of habitat (in detail) between past and present. This has already surfaced as a problem above, and serves to compound the problem of ending up with 'limp' environmental reconstructions (grassland, woodland, marsh *etc.*), rather than detailed discussion of the habitat structure and other characteristics.

The treatment of *past assemblages as communities* can also be questioned. As mentioned above, except in defined circumstances (Evans 1991), two of which are expanded upon below, recovered assemblages are often not representative of past communities – they have suffered additions, removals and amalgamation. The use of an analogous community approach is therefore best restricted to those exceptional circumstances where autochthony is more certain.

In short, most of the problems relate to non-analogue communities. Some molluscan communities today may not be represented in the past, and some in the past may not be represented in the present. Even if there are real similarities between past and present, they may not be recognisable due to one or more of the factors detailed above.

Interpretation difficulties – summary and caution

It is time, perhaps, to remember the earlier comment of Thomas (1985), that notwithstanding its difficulties, sub-fossil molluscan analysis does work. It is vital to appreciate that some of the above difficulties are theoretical, which is not the same thing as saying they are actually real and apply at all times. Indeed, much of the 'art' of interpretation involves assessing the difficulties and making informed decisions as to which do or do not apply. This is particularly true of the autecological difficulties; just because one cannot prove identicality of ecology through time does not mean that one cannot assume it. When assumptions are made and they seem to be consistent with other evidence (either molluscan or not) then the assumptions are strengthened. Proof is an unobtainable goal in such analyses. Similarly, while it may not be possible to prove identicality of environment through time, that does not prevent a consideration of general environmental parameters such as vegetation characteristics, for example shaded or open, structured or unstructured, grazed or ungrazed, or hydrological characteristics, for example wet versus dry, or seasonally flooded as compared to catastrophically flooded. The general features of the environment will have an effect on the molluscan species present irrespective of the actual habitat-type as we would classify it. Of course, it helps to know how terms like wooded, open, wet, dry *etc.* relate to molluscan faunas; that, above all, is where appropriate modern ecological work has a real value.

The synecological difficulties are more 'real'. This has led, with exceptions (*e.g.* Bush 1988) to something approaching reluctance in wholeheartedly adopting such an approach and seeing what happens. Nevertheless, it is clear that sometimes the sub-fossil record can preserve molluscan assemblages that ought to be fairly close (in terms of species and abundance) to the molluscan communities from which they were derived (Evans 1991 and above). In such cases, at least some of the difficulties are removed. Furthermore, if in such cases there are closely comparable modern communities from narrowly defined environments similar to that which one would expect to be represented in the fossil sequence, the comparability must mean something, particularly if the relationship is replicated elsewhere. Such closely related sub-fossil assemblages and modern communities have been demonstrated recently with respect to the Mollusca of floodplains. In central southern England the assemblages recovered from overbank alluvial deposits within Holocene floodplain fills show a high degree of comparability with faunas from modern floodplain environments. Some of the similarities have been detailed elsewhere (Davies *et al.* 1996, Davies and Grimes 1999, Davies 2003a), and recently synthesised (Davies 2003b). To date, the implications of the work for other appropriate contexts have not been articulated. Here I wish to outline briefly the major points and then discuss their relevance to assemblages recovered from another type of wet-ground deposit – tufa.

HOLOCENE OVERBANK ALLUVIAL ASSEMBLAGES AND MODERN FAUNAS

Evans (1991) and Evans *et al.* (1992) recognised that a number of distinct species groupings could be identified as recurrent within assemblages recovered from Holocene overbank alluvium within river valleys of the central southern chalklands of England. Davies (1992, 1998) also demonstrated that these could be defined numerically using multivariate techniques. The recurrent groups (termed taxocenes; WGT = wet-ground taxocene) and their environmental interpretations are as follows:

WGT-1 – A low diversity assemblage with mainly open-country species, *Vallonia pulchella, Trichia hispida, Cochlicopa lubrica* and Limacidae being the predominant species. Amphibious and marsh species at low abundance or absent. This taxocene most likely represents an open, structurally simple, low diversity, relatively dry-ground environment, akin to grazed pasture or meadow which is only occasionally flooded.

WGT-2 – As WGT-1 but with marsh/swamp species well represented, principally *Lymnaea truncatula, Carychium minimum* and Succineidae. This taxocene represents an open but wetter and more structurally diverse environment than taxocene 1, such as lightly grazed pasture or winter flooded meadow.

WGT-3 – Marsh and/or woodland species predominant, often high diversity. The marsh species *Zonitoides nitidus* and *Carychium minimum* are usually characteristic, as is a paucity of *Vallonia pulchella* and Succineidae. This most probably represents a winter flooded environment of high structural diversity such as fen/marsh or, when woodland species are predominant, woodland.

WGT-4 – A low diversity taxocene, principally *Lymnaea truncatula* although Succineidae may also be well represented. Likely to represent a low diversity and perhaps transient environment such as a mudflat.

WGT-5 – The amphibious *Anisus leucostoma, Lymnaea truncatula* and *Pisidium personatum* are distinctive, although land species (either open-country or woodland) may also be abundant. This represents an environment akin to those outlined as WGT- 2 or 3, but flooded for longer periods and possibly with permanent pools of water.

WGT-6 – Taxocene 1 plus abundant *Pupilla muscorum*. It is difficult to know what environment this represents, since *Pupilla* is typically xerophilic although it can presently live in marshes and was a marsh species during the Late-glacial (Kerney *et al.* 1964). Either this represents an environment in which alluvial material has rapidly accreted and dried, providing a baked fissured surface (which the species favours as a xerophyte), or it is some sort of long, rank grassland with a thick thatch. A recent study undertaken at Kingsmead Bridge in Wiltshire suggested that the former was more likely at that site (Davies 1996, but see below also).

WGT-7 – *Lymnaea peregra* distinctive, with other amphibious species and a land component that can either be open-country or wooded. This taxocene is as yet geographically restricted to the upper Kennet valley (Evans *et al.* 1988). At the moment, it remains possible that *Lymnaea peregra* is allochthonous, brought in by flooding, and environmental interpretation is therefore uncertain.

WGT-8 – Freshwater species, particularly *Valvata cristata* and *Pisidium casertanum.* This taxocene represents the transition from wetland to aquatic habitats or *vice versa*. The environment indicated is permanently wet and subject to stagnation.

It should be noted that the term taxocene is in itself interpretative. It implies an ecological relationship between the species, in other words it accepts them as being representative of a past community (it does not imply interaction between the species). This does not preclude the fact that other species might be represented in the assemblage too; taxocenes and assemblages are not the same. Further details of the geographical occurrences of the taxocenes can be found in Davies (2003b).

The environmental interpretations offered for the taxocenes were based, in effect, upon general faunal characteristics and the autecology of some of the species or groups of species involved. One of the key faunal characteristics is diversity. Modern studies (and fossil ones where there is corroborating evidence) suggest that low diversity taxocenes are likely to be characteristic of simple, relatively unstructured environments, such as pasture or mudflat. High diversity taxocenes are much more likely to represent environments with more structural diversity, for example tussocky fen, marsh or woodland. Further discussion of interpretative issues relating to taxocenes can be found in Evans *et al.* (1992).

Although many of the taxocenes have been recognised in overbank alluvial deposits dating to the Neolithic and Bronze Age (Davies 2003b), some of the deposits discussed by Evans *et al.* (1992) and Davies (1998) consisted of relatively recent overbank alluvium, certainly Roman or post-Roman. In addition, the same recurrent assemblages have been found in very recent (either late-Medieval or post-Medieval) overbank alluvial deposits within the Bristol Avon and Wellow Brook, Somerset valleys (Davies unpublished). Logically, therefore, it is reasonable to enquire as to whether such recurrent groupings have

Fig. 15.1 Fen at Bossington, Hampshire.

any modern analogues. Several modern studies have been undertaken recently within the same geographical area (the central southern chalklands), and the details can be found in the published papers, but one or two points are worth restating here as an indication of the value of comparative modern studies.

Davies *et al.* (1996) discussed wet-ground molluscan faunas recovered from reedswamp pasture, rank grassland, fen and carr. They found, unsurprisingly perhaps, that the less complex the vegetation structure, the less was the faunal diversity. In addition however, while in the context of their particular study the carr fauna could be separated from those of fen and rank grassland (both tussocky), due to several species which only occurred in the carr, none of those species could be considered as indicator species of carr more generally, all having been found in other wetland habitats in other published studies. The implication, not stated at the time, is that it is most likely impossible to differentiate between highly structured non-wooded and wooded wet-ground environments in the sub-fossil record. Further work where large tussocks within the fen were actually dissected and sampled (Davies unpublished) confirmed that even the strongest of the so-called 'woodland' species (*e.g. Acanthinula aculeata* and *Clausilia bidentata*) were present. As far as the Mollusca were concerned, fen and carr offer more or less identical conditions (Figs 15.1 and 15.2), and WGT-3 as detailed above ought just to be considered representative of highly-structured environments which may or may not be wooded.

Davies and Grimes (1999) demonstrated that small-scale spatial variation in hydrological and vegetation characteristics had a significant effect on molluscan fauna. By assessing the fauna of sheep-grazed relic carrier and drain features of an abandoned floodplain water-meadow system on the River Wylye, Wiltshire, they showed that each had unique faunal characteristics. Furthermore, the fauna of the carriers (*Vallonia-Trichia-Cochlicopa*) were identical to those of WGT-1 (above), and those of the drains (carrier fauna plus *C. minimum, L. truncatula*) were identical to those of WGT-2. Clearly, modern analogue faunas could be found.

Further work (Davies 2003b) found that relic water-meadow drains within cattle-grazed pasture on the floodplain of the River Test, Hampshire (Fig. 15.3), contained a fauna (*Vallonia-Trichia-Cochlicopa-Pupilla*)

Fig. 15.2 (left) Carr at Bossington, Hampshire. The molluscan fauna is similar to that of the fen in Fig. 15.1.
Fig. 15.3 (above) Relic water meadow system, River Test, Hampshire.

identical to that of WGT-6 (above). This contrasted with the sheep-grazed pasture of the River Wylye (above) and suggested that it might be possible to distinguish between cattle-grazed and sheep-grazed floodplain pasture in the sub-fossil record.

In summary, therefore, some basic ecological surveys have shown that there are modern analogues for WGT-1, 2, 3 and 6. This is somewhat ironic, since the interpretive approach used in designating taxocenes was intended from the outset not to be reliant on species-based analogy (Evans *et al.* 1992). Nevertheless, of crucial importance here is the fact that all of these modern studies were in part designed in order to demonstrate whether the wet-ground taxocenes previously proposed had any modern analogues, though that was sometimes subordinate to other research questions. Geographic areas and precise sites were targeted because they were most likely to have analogous faunas. There was a clear link between the modern and sub-fossil work, and there is a clear benefit in designing modern ecological work explicitly (though not necessarily wholly) to consider palaeoecological questions. The other taxocenes may also have modern parallels, but finding them will depend upon surveying carefully chosen locations.

TUFA DEPOSITS – THE SUB-FOSSIL RECORD AND POTENTIAL OF MODERN WORK

Late-Glacial and Holocene tufa deposits are widespread in the chalk and limestone dominated areas of Britain, principally in the south of England but also in areas adjacent to the Yorkshire and Lincolnshire Wolds, in South Wales and elsewhere (Evans 1972, Pentecost 1993). Paludal tufas, forming as a result of calcium carbonate precipitation from spring-flushes or groundwaters rising to surface level (Ford and Pedley 1996), have been particularly useful. These tufas have often formed over long periods of time (thousands of years) and contain well preserved and abundant molluscan remains that can furnish detailed terrestrial environmental sequences (*e.g.* Kerney *et al.* 1980, Preece 1980, Evans and Smith 1983, Preece and Robinson 1984). They are of particular value since many have been obtained from parts of the UK where pollen is not readily preserved and vegetation history is otherwise largely unknown. Detailed molluscan bio-chronozones are now well established for southern England (see Kerney 1977, Kerney *et al.* 1980 and recent re-assessments by Preece and Bridgland 1998, 1999). Furthermore, the tufa deposits often seal, or are interstratified with, palaeosols representing early to mid-Holocene land surfaces. It is particularly noticeable that such British tufa deposits often have associated *in-situ* Mesolithic archaeology, for example at Blashenwell, Dorset (Preece 1980), Cherhill, Wiltshire (Evans and Smith 1983), Cwm Nash (Evans *et al.* 1978), Bossington (Davies 1992, Davies and Griffiths 2005). Other such sites are listed in Evans (1972).

Associated Mesolithic material is also evident at several Irish sites (Preece and Robinson 1982, Preece *et al.* 1986). In a number of studies some of the molluscan evidence obtained has been interpreted as suggestive of Mesolithic interference with woodland vegetation (*e.g.* Evans *et al.* 1978, Preece 1980, Preece *et al.* 1986, Davies 1992; Davies and Griffiths 2005), although whether such clearings were in fact purposefully created rather than naturally created and opportunistically utilised (Brown 1997) is impossible to assess. Nevertheless, the importance of tufa deposits as repositories of both environmental and cultural material is clear.

Generally, the environmental histories that emerge from tufa deposits are in good agreement, both with each other and with respect to what is known about the Late-Glacial and Holocene periods from other environmental evidence. Broadly they show cold, open Late-Glacial conditions giving way as the Holocene progresses to warmer and eventually fully wooded habitat. This is very clearly shown at Sidlings Copse, Oxfordshire, where the molluscan evidence was complemented by pollen data (Preece and Day 1994). Extensive tufa deposition seems to have ceased by around 4000 BP, the cessation most often being explained as a result of changing hydrological conditions consequent upon increasing human impact and landscape openness (*e.g.* Preece and Robinson 1982). Further discussion of the 'tufa decline' can be found in Griffiths and Pedley (1995) and Goudie *et al.* (1993).

The woodland fauna generally found in mid-Holocene tufa deposits are extremely species-rich in comparison with fauna documented from modern woodland habitat (Meyrick and Preece 2001), reflecting the ideal conditions offered to Mollusca in warm, damp, shaded and undisturbed habitat. This difference is attributable in part to the lack of modern analogue habitat (warm, damp, shaded, undisturbed *and* calcium carbonate forming conditions), and perhaps also in part to the lack of quantitative studies from wet woodland. Most modern studies have been of relatively dry woodlands (*e.g.* Bishop 1976, Wardhaugh 1997) although of course there is usually some inherent spatial variability in the dampness of the sites studied. There have been few studies of wet-woodlands (carrs, or more particularly marsh woodland – based on mineragenic rather than organic substrates), and even fewer within the same general geographic area as substantial tufa deposits; in short, there are limited appropriate modern data. It is worthy of note that in terms of numbers of species some of the modern samples from fen and carr at Bossington, Hampshire (Davies *et al.* 1996), an area where there are also substantial tufa deposits (Pentecost 1993), approached the richness found by Meyrick and Preece (2001) in fossil tufa deposits, although the species composition was different.

Recently, it has been noted that modern tufa deposition is most likely severely underestimated, at least in some areas (Baker and Simms 1998). Although deposition of large quantities of tufa in any one location is not likely to approach that normal in early-mid Holocene deposits, the actual number of tufa deposition points within suitable geological areas (the limestone of the Mendips and the Wessex area, Somerset) was demonstrated to be potentially much higher than previously estimated. Subsequent visits by the author and colleagues to some of the sites mentioned by Baker and Simms (1998) have confirmed tufa deposition. Additionally, survey of other likely sites has added to the list of both modern and fossil deposits. Crucially, some of the more substantial modern deposition is occurring in woodland with the type of ground conditions often inferred in sub-fossil interpretation, principally wet, tussocky, and herb- and calcium carbonate-rich (Fig. 15.4). The undisturbed analogy is less secure, in that the woodlands do not necessarily have a demonstrably long history, although they are certainly not heavily impacted upon by human activity. Deposition at other sites is in open conditions with vegetation ranging from short to long and tussocky. Relevant too is the fact that substantial early-mid Holocene deposition in the Test Valley, Hampshire, has recently been documented as having formed largely in open-conditions, although a woodland 'phase' is apparent (Davies and Griffiths 2005).

Fig. 15.4 Modern tufa deposition site within woodland, Mendip.

Given that there are now potentially some useful modern analogue sites within the same geographical area (southern Britain), it would seem an ideal opportunity to test sub-fossil inferences which have often been internally-derived, *i.e.* with relation to the sub-fossil Mollusca alone. It has already been outlined how the fauna of fen-type habitat closely resemble those from carr or wet-woodland-type habitat, and it would seem that the possibility that some of the 'woodland' fauna of fossil tufa deposits might not in fact represent woodland, but other highly structured wet-ground environments, ought to be tested. The interpretations offered may well be correct, but will obviously be strengthened by being 'tested' via analogous comparison. Certainly, species composition will vary between past and present, some species common to Holocene tufa deposits now being either absent from the UK or national rarities (Meyrick and Preece 2001). Nonetheless, it is true to say that the degree to which analogous comparisons can be made can only be established after the fact.

WETLANDS AND MOLLUSCA – FUTURE DIRECTIONS

The lack of modern faunal studies that are appropriate for analogous comparison with sub-fossil assemblages has already been highlighted, and this clearly needs addressing. The fact that neither the studied habitats nor the species involved may be identical with fossil counterparts is to some extent irrelevant or, as in the case of alluvial fauna above, needs demonstrating in any case. Similar habitat (and this means similar as far as the Mollusca are concerned) will result in similar general faunal characteristics (see above). More narrowly, the following two aspects would seem worthy of study.

Fig. 15.5 River Wylye, overbank flood conditions.

First, seasonal variation of molluscan fauna has been outlined as a possibility on the basis of sub-fossil studies in English river valleys (*e.g.* Robinson 1988, Davies 1996) and recently demonstrated in modern studies elsewhere (Valero *et al.* 1998). Research into the temporal variation of active molluscan communities on floodplains subject to seasonal inundation (Fig. 15.5) would perhaps help further in the interpretation of sub-fossil wet-ground taxocenes (see above), although finding floodplains that flood in a manner similar to that which would have occurred prior to recent flood management regimes may be difficult.

Second, the spatial variation of molluscan fauna in spatially complex habitat needs to be further addressed. As mentioned above, one of the reasons why there may not be any published modern studies demonstrating the same level of species richness as some mid-Holocene tufa assemblages may relate to the fact that similar habitats (wooded, tussocky, wet, carbonate-rich) have yet to be adequately studied. The modern floodplain study of Davies and Grimes (1999) has demonstrated a high degree of spatial separation of species over relatively small distances due to minor variations in hydrology and vegetation structure, a feature that has also been demonstrated elsewhere (Vareille-Morel *et al.* 1999). Separation is likely to be much more marked in spatially complex habitats (Fig. 15.4), particularly if they are also subject to seasonal change. The death assemblages, and future sub-fossil assemblages, will reflect this complexity.

Finally, and by way of summary, it is worthwhile reiterating that improving the interpretation of sub-fossil molluscan sequences is most likely to be dependent upon more modern studies, a point also made by Evans and O'Connor (1999). Further, it is important that future modern studies are designed specifically with the aim of furthering palaeoecological interpretation.

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