Cave and Karst Science

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BCRA

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Subterranean aquatic Crustacea
Victoria Cave, Yorkshire, UK
Stone money in Micronesia
Planinska jama, Slovenia

Cave and Karst Science

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Cave and Karst Science

TRANSACTIONS OF THE BRITISH CAVE RESEARCH ASSOCIATION

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Cover photo:

Androniscus dentiger Verhoeff, 1908 (Crustacea: Isopoda), commonly known as the Rosy Woodlouse. This animal is a troglophile and is one of the commonest woodlice to be found in British caves. It is a detritivore, which means that it can exist on food from diverse sources. No studies of this species have been carried out to determine its exact ecological status in British caves. However, extensive work by Gentile and Sbordoni in Italian caves (e.g. *Evolution,* Vol.52, 432–442, 1998) has demonstrated clearly that individual populations of this species, in separate caves, are very distinct genetically, and do not exchange genes with other cave populations or with surface populations. Thus, each population is effectively troglobitic and effectively a separately evolving taxon. Given the findings of this study, it seems very likely that many populations of cave animals (and perhaps especially terrestrial ones) will be found to be independently evolving entities. In British caves and groundwater it is highly likely that many genetically distinct populations exist. It is equally likely that British populations are distinct genetically from those in mainland Europe. This topic is discussed in a Paper by Proudlove *et al.* in this Issue.

Photograph by Phil Chapman.

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EDITORIAL

John Gunn and David Lowe

This Issue contains a Paper that is the first of what we hope will be several on related topics, so we have asked the lead author, Graham Proudlove, to write a Guest Editorial explaining the background and also presenting some potentially controversial thoughts on the future direction for biospeleology in Great Britain.

GUEST EDITORIAL

Graham Proudlove

This Issue of *Cave and Karst Science* carries a Paper on some aspects of the biology of cave and groundwater animals. This is not unique. In recent years there have been numerous biological papers in *Cave and Karst Science*, but this one is notable. It is based on data collected during the heyday of cave biology in Britain and Ireland and is the first of a number using a remarkable and very valuable dataset The editors asked me to write a Guest Editorial on subterranean biology to introduce this Paper. I will say a few things about the history of subterranean biology in the British Isles, about our current level of knowledge, and about how we progress from here. Some of what I say may be controversial. Thanks to Dave Lowe and John Gunn for giving up this space.

The study of subterranean biology in Britain and Ireland has a long and distinguished history. In 1938 a small group of cavers started to collect animals from caves, the main impetus being provided by E A Glennie and Mary Hazelton. It was Hazelton who took on two vital tasks: getting the animals accurately and authoritatively identified, and publishing the information so that it became a useable resource. These publications, termed the *Biological Records*, were published by the Cave Research Group of Great Britain and later by the BCRA. The 16 parts contain a 38-year dataset, the accumulated work of over a hundred individuals during thousands of person-hours of work, often in uncomfortable conditions. The final part (1978) saw the retirement of Mary Hazelton as Biological Recorder. A few significant studies were carried out in the post-Hazelton era, but they were the exception, rather than the rule.

Biological studies were re-started in 1998, with the work of Paul Wood and John Gunn in the Limestone Research Group at the University of Huddersfield. In 2000 I took over the post of Biological Recorder within BCRA from Mick Day. When I took over, the largest single job remaining from the Hazelton period was the creation of a computer-readable (digital) version of the *Biological Records*. With financial assistance from BCRA this job was completed in 2003. The digital version is named *Hazelton* in honour of its main architect. The paper by Proudlove *et al.* in this issue is the first to use the *Hazelton* dataset (with additional records from elsewhere) to examine the distribution of subterranean organisms at the species level. Previous studies, by Hazelton and Glennie, by Jefferson, and by Chapman, have described the biota principally at the phylum, class and order levels. Further analyses using the *Hazelton* database are now in progress. A copy of the full *Hazelton* database will be available on the BCRA biology web page within a few months.

The completion of a digital version of the *Biological Records*, and its subsequent analysis, sees the culmination of the general data gathering period. Randomly collected data, such as form the core of *Hazelton*, are no longer required for several reasons: 1. A dataset of >6000 records from a 38 year period is quite adequate, and further similar data would add little, if anything, to knowledge. 2. Although Mary Hazelton managed to get all of the specimens sent to her properly identified this is not so easy today. The experts who can identify difficult animal groups have neither time nor resources to devote to "our"" samples. Notwithstanding this problem, it cannot be over-emphasised that accurate identifications are crucial to any sort of biological study. Organisms that are not identified (ideally to species), or, worse, are identified wrongly, have no place in modern biology. Great damage would result from any conclusions drawn using misidentified organisms. 3. It is probably true to say that such random collection is contrary to the principles of conservation.

The main conclusion we draw from these data are: Britain and Ireland have very few obligate subterranean animals (troglobites and stygobites) and we hypothesize that this results from the effects of the Pleistocene glaciations. A large proportion of records are of accidentals, those animals that have no place in the subterranean habitat. Another large proportion are troglophiles, which are viable in both surface and subterranean habitats Some of these will be active colonizers and we can characterize the current subterranean fauna as an early post-glacial one One intriguing possibility, suggested in the Crustacea data presented later, is that some stygobites may have survived Pleistocene glacials in caves beneath the ice – sub-glacial refugia. We are currently examining this with DNA profiles.

To assist in determining the directions of future work we can use the *Hazelton* data to pinpoint areas where we are lacking knowledge, and areas that are of obvious importance within the British subterranean realm. We can thus plan and implement targeted studies. For example, it is a surprising fact that terrestrial areas of Peak Cavern are almost unstudied. This large, old and diverse cave would form an ideal site for a whole cave study. Ogof Draenen also comes to mind and is rather better preserved than Peak Cavern. The *Hazelton* data also demonstrate that Collembola are among the most important of all animals within British caves. These small to minute animals require a determined approach but any study would be very worthwhile, especially as there is currently a major study of this group under way at Reading University. A further insight from *Hazelton* is that we know quite a lot about caves but rather less about an equally significant subterranean environment, the groundwater. This suite of habitats covers much greater areas than do caves. Very recently one major water company, whose supplies come predominantly from groundwater, have begun active study of the groundwater organisms found in their boreholes. I expect some major advances in knowledge of the groundwater fauna to come from this collaborative project.

As with every aspect of modern life, subterranean biology gets more complex by the year. Although the time of the *"Gentleperson-Amateur"* is not yet passed, it is quickly receding. Current studies in progress require, among other things, deep borehole sampling, DNA analysis and stable isotope analysis. These are not kitchen-sink activities. I predict that progress in subterranean biology in future will rely very heavily on University or similar research facilities. Of course, this is no different to many other aspects of scientific endeavor.

So to summarize my position on where we go from here: No random collections, no collection of accidentals, collection of targeted taxa only, collections in targeted sites only. It is perhaps too early to ask for hypothesis-driven research and in any case I do not believe that this should entirely supplant observational activities.

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A review of the status and distribution of the subterranean aquatic Crustacea of Britain and Ireland.

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Abstract: Britain and Ireland do not support many obligate subterranean organisms (troglobites and stygobites) compared to mainland Europe. The largest group of stygobitic taxa is the Amphipoda with seven representatives. In addition, there is one isopod, one syncarid and one copepod. This paper examines the distribution of these animals based on samples taken over 150 years. There is also a number of stygophilic taxa (Copepoda, Cladocera, Ostracoda and Amphipoda) that may be common and even abundant in some caves. Several taxa previously identified as stygobites in Britain and Ireland are shown to be stygophilic. Most stygobitic taxa appear to be restricted to an area south of the maximum limit of the Devensian glaciation. However there are exceptions, the most significant of which is the presence of a syncarid in central Scotland. Dispersal from southern European refugia, and survival in the glaciated areas in tundra or sub-glacial refugia are discussed. It is concluded that both mechanisms may have played a part in influencing the current distribution of the fauna. Much additional research on these animals is clearly required. In particular, a modern systematic survey of subterranean habitats (hyporheic, hypotelminorheic and deep phreatic groundwaters) and a phylogeographical analysis to examine the relationship of the British and Irish fauna with that of mainland Europe.

Dedication: To the memory of Mary Hazelton (1905 – 1987) without whose tireless work, as the Biological Recorder of the Cave Research Group of Great Britain, this paper could not have been written.

(Received 19th March 2003; Accepted 10th November 2003)

INTRODUCTION

The islands of Great Britain and Ireland (including the Isle of Man and the Channel Islands) have few obligate subterranean species (troglobites in the terrestrial realm, stygobites in the aquatic). From extensive recording over 60 years, a relatively small number of insects, arachnids and Crustacea are known to live permanently in a variety of subterranean habitats (Jefferson, 1976; Chapman, 1993). The most widely distributed and diverse of these is the crustacean group Amphipoda and in particular the families Niphargidae (*Niphargus aquilex* Schiodte, 1855, *N. fontanus* Bate, 1859, *N. glenniei* Spooner, 1952, *N. kochianus kochianus* Bate, 1859, *N. kochianus irlandicus* Schellenberg, 1932 and *N. wexfordensis* Karaman, Gledhill and Holmes, 1994) and Crangonyctidae (*Crangonyx subterraneus* Bate, 1859). In addition, there is one isopod from the family Asellidae (*Proasellus cavaticus* (Leydig, 1871) *sensu* Henry, 1971) and one (or more) syncarids from the family Bathynellidae (*Antrobathynella stammeri* (Jakobi, 1954) and possibly *Bathynella natans* Vejdovsky, 1882). Although subterranean amphipods, "well shrimps" as they were once known, were first observed and described in the mid 19th Century, it was between the mid-1930s and 1970s that the majority of sampling of subterranean habitats was undertaken. A pattern of distribution emerged that echoed the perceived knowledge that subterranean amphipods were found no further north than the maximum extent of the Devensian ice sheet. This theory was first proposed by Ruffo (1956) and advanced for British caves most vigorously by Glennie (1967). However, even by the time of Glennie's paper it was known that the Syncarida were found as far north as Scotland, and Glennie himself (1968) describes the finding of a juvenile *Niphargus aquilex* west of the Devensian limit in the River Teme at Gwerneirin in Wales. Since this seminal paper no major departures from this widely accepted view have been advanced for Britain and Ireland.

N. aquilex has been recorded in riverine gravels near the River Humber, much farther north than previous records, but still relatively close to the Devensian glacial limit in that area. Clearly, the picture of stygobitic Crustacea being limited by the Devensian glacial limit is simplistic, even for Amphipoda and especially so for Syncarida. Most recent accounts of post-glacial colonisation (e.g. Bilton, 1994; Yalden, 1999) discount any refugial contributions, suggesting that dispersal is the only re-colonisation mechanism However, the distribution of some of these Crustacea suggests otherwise.

This paper reviews the status of all Crustacea from Britain and Ireland that have been recorded in the literature as stygobites or stygophiles. We have three aims: first to identify those organisms that are stygobitic and stygophilic based on all available data; second, to re-analyse the distributional data for these animals in the light of more detailed knowledge of the geological and geomorphological history of the region; and third to identify key areas where further research is required.

The main references for the fauna inhabiting subterranean habitats in Britain and Ireland are: Hazelton and Glennie (1953, 1962), Hazelton (1955, 1956a,b, 1958, 1959, 1960a,b, 1961, 1963a, 1965, 1967, 1968, 1970, 1971, 1972, 1974, 1978 – the "Biological Records", appended with BR in the reference list), Jefferson (1976), Chapman (1993), Jefferson (1994) and Juberthie and Decu (1994). An account of the systematics and distribution of Malacostracan Crustacea is provided by Gledhill *et al.* (1993). A large bibliography of works on the British and Irish subterranean environment is maintained on the BCRA web site (www.bcra.org.uk/biology). The following aquatic groups are considered in this review: "Entomostraca" – Ostracoda, Copepoda, and "Cladocera"; Malacostraca – Syncarida, Amphipoda and Isopoda.

The discovery of subterranean aquatic Crustacea in Britain and Ireland

The first hypogean animal recorded from England was discovered around 1812, when a blind amphipod was obtained from a well in the grounds of St. Bartholomew's Hospital in London. It was subsequently named *"Gammarus subterraneus"* (Leach, 1814). The next documented record was from Westwood (1853), who recorded "*Niphargus stygius*" from a well near Maidenhead (Berkshire), where they were *"...found in great numbers* [and] *the water ... was in consequence rendered unfit to use."* Hogan (1859) suggests that these specimens were in fact *Niphargus aquilex*. No further specimens of subterranean amphipods were reported in the scientific literature until 1857, when E H Mullins collected some specimens in Corsham (Wiltshire) (these were the then undescribed, *N. fontanus*). A R Hogan examined these animals and in 1858 discovered additional specimens at Ringwood (Hampshire). At this remarkable site he discovered three unknown species (*Niphargus fontanus*, *Niphargus kochianus* and *Crangonyx subterraneus*, all described by Bate (1859) (see also Hogan, 1859, 1860), and *Niphargus aquilex*. Even more remarkably the same site, or at least a site in Ringwood, also proved to be the first known locality in Britain for *Proasellus cavaticus*, recorded as early as 1925 (Calman, 1928; Tattersall, 1930; Moon and Harding, 1981), and the only true stygobitic copepod, *Acanthocyclops sensitivus* (Harding and Smith, 1974). By 1860 the known distribution of *N. aquilex* had widened to Corsham and Warminster (Wiltshire) and *C. subterraneus* to Warminster (Hogan, 1860).

At the end of the nineteenth century a number of important discoveries were made. The first Irish subterranean amphipod species, *Niphargus kochianus irlandicus*, was collected in the outskirts of Dublin in 1899, and at three other sites up to 1910, including at the bottom of Lough Mask (Kane, 1904). However, subterranean Crustacea were not recorded in Ireland again until 1956. In England specimens of "*Niphargus subterraneus*" were collected by R J House in a well at West Hartlepool (Durham) around 1893 (Norman and Brady, 1893) and *N. aquilex* was recorded at Cringleford, near Norwich (Norfolk) (Harmer, 1899) In addition, *N fontanus* was recorded in Jersey from two wells at St Helier (Walker and Hornell, 1896).

The inter-war years saw further records of *Proasellus cavaticus*, as well as Lowndes' (1932a,b) discovery of the first British syncarid, which was recorded together with *Proasellus cavaticus* and *"...at least two species of Niphargus"* in Pickwick Quarry, one of the Corsham Stone quarries (David Pollard pers. comm.). From the late 1930s onward the group led by Aubrey Glennie and Mary Hazelton, of the Cave Research Group of Great Britain (CRG), greatly increased our knowledge of the distribution of subterranean Crustacea. It is principally upon these collections, and the records kept by Hazelton, that this review is based. Additional valuable records were collected by TG, when working at the River Laboratory of the Freshwater Biological Association.

The first attempt to describe the distribution of British hypogean Crustacea (specifically Amphipoda) was undertaken by Glennie (1956), and this was subsequently expanded in a later publication (Glennie, 1967). The distribution of *Proasellus cavaticus* was compiled by Moon and Harding (1981) and Harding (1989). Very little is known about the discovery of any of the possibly stygobitic Ostracoda or Copepoda and there is very little literature covering Britain and Ireland (Fabio Stoch pers. comm.)

METHODS

Most of the distribution records result from the work of a group of individuals acting under the auspices of the CRG. The main contributors to the early records were Aubrey Glennie, who did much of the sampling, and Mary Hazelton, who kept records of the collections. Later collectors, including Bill Maxwell and Marjorie Railton, also contributed many records. These were published as the Biological Records of the CRG in 16 parts between 1955 and 1978 (see above for references). The majority of the data for subterranean Crustacea relate to the distribution of hypogean amphipods and these were computerized, validated and analysed at the Biological Records Centre in 1986 for the then Nature Conservancy Council (Harding *et al.*, 1986). In 1988 this work was updated and extended to include *Bathynella* spp., *Proasellus cavaticus*, two species of Aranaea and two species of Diptera (Harding and Greene, 1988). Other major contributions were made by Terry Gledhill and Stephanie Ham both working for the Freshwater Biological Association (Gledhill *et al.*, 1993 and references therein; Ham, 1982). The distribution records have been summarized rather than providing lengthy lists of individual records (of which there are several hundred), other details have been taken from the literature. The full list of recorded sites can be found at the National Biodiversity Network Gateway (www searchnbn org) The *"Coded Checklist of Animals Occurring in Fresh Water in the British Isles"* (found at http://www.ceh.ac.uk/subsites/eic/ddc/furselist/index.htm) has been very useful for tracking down literature and references for some of these poorly-studied animals. The methods used to collect samples from groundwaters are variable. Glennie used baited traps, a plankton net and a Gilson Well Pump, developed by H C Gilson of the Freshwater Biological Association specifically for this task (Driver, 1964). The Karaman – Chappuis and Bou-Rouch methods (Pospisil, 1992, p.113), were used to collect syncarids from groundwaters in riverine gravels.

BRITISH AND IRISH SUBTERRANEAN CRUSTACEA

OSTRACODA

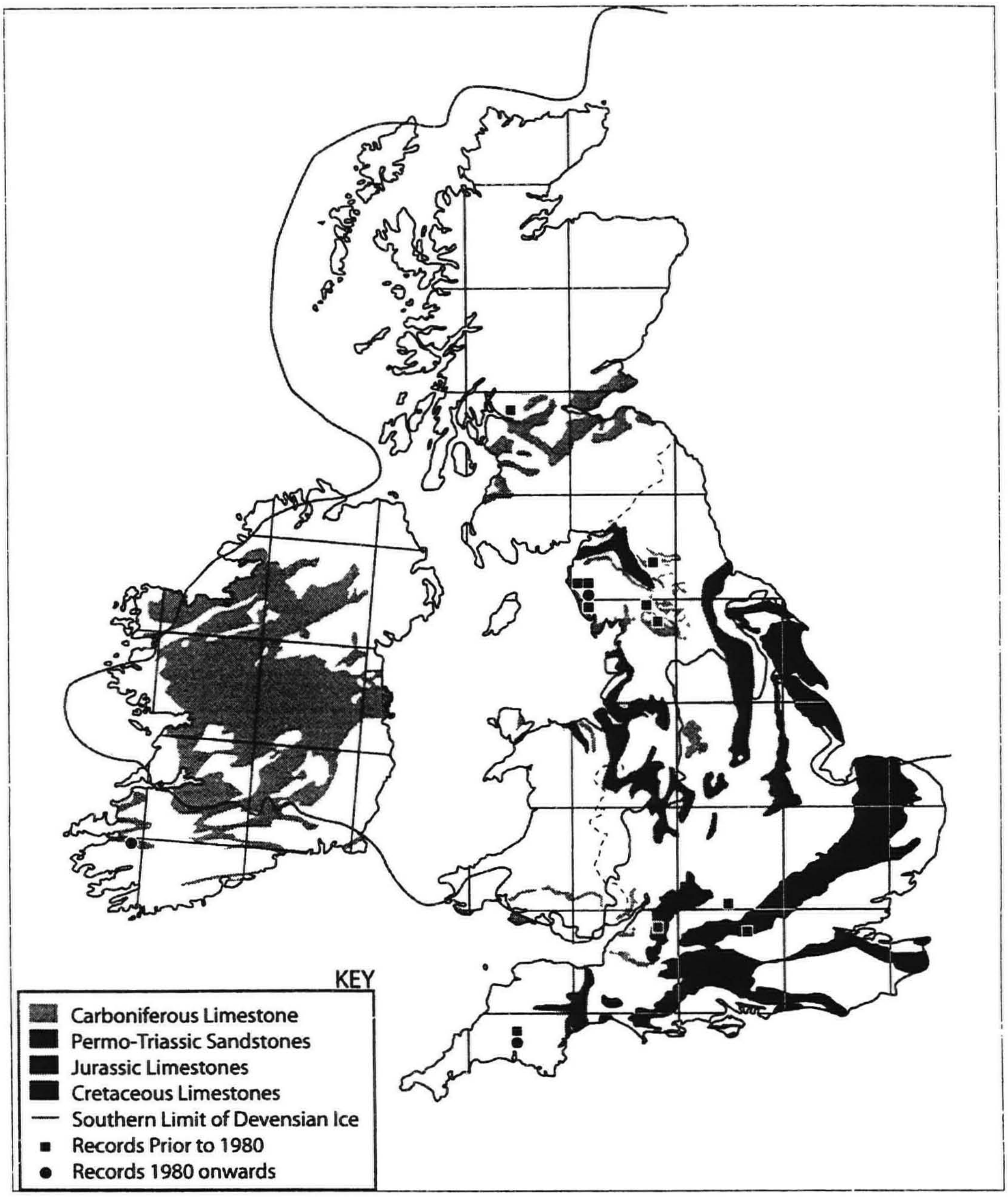
There are very few published records of hypogean species. Of more than 50 ostracod species mentioned by Meisch (2000) as being stygobitic or stygophilic in Europe, only about half have been recorded in Britain (and not always in groundwater habitats). *Potamocypris fallax* was recorded in Ingleborough Cave (Yorkshire) by Fox (1967), *Cavernocypris subterranea* in the Ogof Ffynnon Ddu System (Glamorgan, Wales) (Fox, 1967; Marmonier *et al.*, 1989), but both of these are stygophilic rather than stygobitic species and are found more commonly in springs. *Candona candida* and *Potamocypris variegata* were recorded from groundwater (wells) at Nantgarw in Wales by Griffiths and Evans (1991).

Jefferson (1976, p.383) and Chapman (1993, p.156) both consider several species of ostracod to be stygobitic, or phreatobitic, in England although neither provide literature references to support their statements. They identify the following species.

Eucypris anglica Fox, 1967

Described by Fox (1967) from specimens collected in a temporary pool in a meadow due to high groundwater. No mention is made by Fox of the subterranean habitat. Jefferson (1976, p.383) says "... Eucypris anglica... *appears in bourne springs* [and is] *no doubt* [an] *underground form which* [is] *occasionally carried to the surface."* Chapman (1993, p.156) says that this species is *"almost certainly cavernicol*[ous]." Neither says where this information comes from and there appears to be little justification for such statements. Henderson (1990, p.142) gives no details of habitat but Meisch (2000, p.292) describes it being found in three sites in southern England, all in temporary pools (details from Fox, 1967 and Ham, 1982). Griffiths and Evans (1995a) conclude that the species is distinct from other European *Eucypris* and is therefore an English endemic. It remains possible that this species normally resides in hypogean waters, coming to the surface at times of high

Figure 1. The distribution of Syncarida in Britain and Ireland by 10km squares.



groundwater. However, this seems unlikely given the relatively large size (approx. 2.0mm long) of the animal in question. Furthermore, species of *Eucypris* are common in temporary surface waters but virtually unknown in groundwaters. The only English species found commonly in springs and seepages is *E. pigra* (Fischer, 1851), which is relatively small for the genus (0.8 – 1.0mm long). We must concur with Jefferson (1976, p.383) who comments that *"...our information is so sparse that little can be said with assurance on this topic."*

***Herpetocypris palpiger* Lowndes, 1932**

This species was originally described by Lowndes (1932c) from Corsham, the same general locality as *Candona wedgewoodii* (see below). Chapman (1993, p.156) suggests that it is *"now considered to be* [a] *troglobite..."*. The species is not mentioned by Henderson (1990) or Griffiths and Evans (1995a). Meisch (2000) considers it to be a synonym of *Herpetocypris helenae* Muller, 1908, which is widely distributed in continental Europe in small stagnant water bodies, the littoral zone of lakes, swamps and slow flowing streams and rivers. Lowndes (1932c, p.157) actually found it living in *"a large disused tank at Corsham"*; he makes no mention of it being found underground. No other species of *Herpetocypris* lives in groundwaters. There seems to be no justification, therefore, for regarding *H. palpiger* as either a distinct species or an inhabitant of subterranean waters.

***Candona wedgewoodii* Lowndes, 1932**

This species was described by Lowndes (1932d) from Pickwick Quarry, one of the Corsham Stone quarries (Wiltshire), where he found it to be abundant in puddles formed by the outflow from a tub that contained *"Bathynella chappuisi"* (= *Antrobathynella stammeri*, see below). It has apparently been overlooked by most subsequent workers and is not mentioned by Henderson (1990), Griffiths and Evans (1995a) or Meisch (2000). Chapman (1993, p.156), however, suggests that it is *"now considered to be* [a] *troglobite"*. In terms of size and carapace shape it is very close to *Fabaeformiscandona breuili* (Paris, 1920) a stygobitic species found elsewhere in western and central Europe (Meisch, 2000). *F. breuili* has not previously been reported living in Britain, although fossil valves have been recorded from Holocene deposits in Wiltshire and Hampshire (Griffiths and Evans, 1995b). Lowndes' illustrations of limbs are, however, inadequate to confirm this identification and we have been unable, so far, to locate any of his original material. Recently, a few specimens collected by one of us (DJH) from a small stony stream near Inchnadamph (Assynt, northwest Scotland) have been identified as *F. breuili*. However, confirmation of possible synonymy with *C. wedgewoodii* awaits the collection and study of additional material.

***Cavernocypris subterranea* (Wolf, 1920)**

Originally placed in the genus *Cypridopsis* (Marmonier *et al.*, 1989). Described originally from Switzerland, this species was first found in Britain by Fox (1967) who records it from five localities:

1 A spring in Lower Greensand, Paines Hill, Surrey (TQ 412513),

2 In a stream flowing from a spring at the base of the Chalk,

Candona candida (O. F. Müller, 1776)
Candona cf. *neglecta* Sars, 1887
Candonopsis kingsleii (Brady & Robertson, 1870)
Candonopsis scourfieldi Brady, 1910
Cavernocypris subterranea (Wolf, 1920)
Cryptocandona reducta (Alm, 1914)
Cryptocandona vavrai (Kaufmann, 1900)
Cyclocypris ovum (Jurine, 1820)
Cypria ophtalmica (Jurine, 1820)
Cypridopsis lusatica Schafer, 1943 (syn *Cypridopsis bamberi* Henderson, 1986)
Cypridopsis vidua (O. F. Müller, 1776)
Eucypris pigra (Fischer, 1851)
Fabaeformiscandona breuili (Paris, 1920) (?syn *Candona wedgewoodii* Lowndes, 1932)
Heterocypris salina (Brady, 1868)
Ilyocypris inermis Kaufmann, 1900
Nannocandona faba Ekman, 1914
Potamocypris fallax (Fox, 1967) (syn *P Wolfi* Brehm, 1920)
Potamocypris fulva (Brady, 1868)
Potamocypris pallida Alm, 1914 (syn *P thienemanni* Klie, 1925)
Potamocypris variegata (Brady & Norman, 1889)
Potamocypris villosa (Jurine, 1820)
Potamocypris zschokkei (Kaufmann, 1900)
Pseudocandona albicans (Brady, 1864)
Pseudocandona eremita (Vejdovsky, 1882)
Pseudocandona pratensis (Hartwig, 1901)
Pseudocandona rostrata (Brady & Norman, 1889)
Pseudocandona sarsi (Hartwig, 1899)
Psychrodromus olivaceus (Brady & Norman, 1889)
Psychrodromus robertsoni (Brady & Norman, 1889)

Table 1. Checklist of stygophilic ostracod species recorded in the British Isles (not necessarily in groundwater habitats). Data from Fox (1964, 1967) and Meisch (2000).

Newtimber Place, Sussex (TQ 272139);

3 In a Chalk spring, Dagnall, Buckinghamshire (SP 990175);

4 A spring in Carboniferous limestone, east of Malham Tarn, Yorkshire (SD 898670);

5 Ogof Ffynnon Ddu system, Breckonshire, South Wales (SN 848153), Chapman (1993, p.156) states that "Cypridopsis subterranea *is quite numerous in the mesocavernous seepage water running over flowstone slopes in caves such as Ogof Ffynnon Ddu in South Wales and is otherwise known only from springs.*" However, in a thorough faunistic survey of this cave, Jefferson and Chapman (1979) did not record this species.

Fryer (1993, p.281) indicates that these five sites are still the only known localities. Henderson (1990, pp.212-213) does not mention localities, but provides a map with five points, probably the same five sites indicated by Fryer (1993). Meisch (2000, p.386) records that it is widely distributed throughout Europe, excluding Ireland. In Eurasia males are unknown and the species is fully parthenogenetic. It is therefore possible that the British populations are distinct from those on the continent.

The records to date suggest that there are no true stygobitic ostracods in Britain or Ireland. *Cavernocypris subterranea* is certainly a stygophile and may qualify as a local stygobite in places (e.g. Ogof Ffynnon Ddu, South Wales), if isolated from epigean populations. It is also possible that the individuals collected in streams downstream of springs were washed out of hypogean habitats.

Published records from Britain and Ireland: stygophilic ostracods

A list of stygophilic species recorded in Britain which, according to Meisch (2000), are found in Europe living in such habitats as springs, caves, interstitially in sediments (including hyporheic stream habitats), is given in Table 1 with some additional species recorded from British springs. However, not all of these British records are actually from groundwater habitats. The list is based primarily on the NODE database (see Horne *et al.*, 1998 for details of this database). This list also includes new records discussed below.

Of particular interest is *Psychrodromus robertsoni*, a British endemic first described from the Isle of Skye by Brady and Norman (1889). This large (approx. 1.7mm-long) ostracod is common in springs and seepages in the English Lake District and in northwest Scotland including the Hebridean islands (DJH, unpublished data), as well as being recorded in southern England (Henderson, 1990) and Ireland (Douglas and McCall, 1992). Fryer (1993) may well have found it in Yorkshire but does not consider it to be distinct from *Psychrodromus olivaceus* (Brady and Norman, 1889), which is widespread elsewhere in Europe. We disagree with Fryer; *P. robertsoni* is consistently larger and has a more dorsally arched carapace, with maximum height farther back, than *P. olivaceus*, and although the two are commonly found in the same sample they are not difficult to separate with confidence. Fox (1964, 1967) recorded *Cryptocandona vavrai*, *Ilyocypris inermis*, *Cavernocypris subterranea*, *Potamocypris fallax*, *Potamocypris zschokkei*, *Psychrodromus olivaceus* and *Psychrodromus robertsoni* in springs in England and Wales. Fryer (1993) lists *Candona candida*, *Candona* cf *negelecta*, *Cryptocandona vavrai*, *Eucypris pigra*, *Psychrodromus olivaceus*, *Potamocypris pallida*, *Potamocypris zschokkei*, *Potamocypris fallax* and *Potamocypris villosa* from springs in Yorkshire. *Cypridopsis lusatica* was reported (as *C. bamberi* n. sp.) from a spring at Trethin, near Camelford, Cornwall, by Henderson (1986).

New British records of stygophilic ostracods

To the above published records can be added several new records, mainly of spring-dwelling ostracods, based on the collections of one of us (DJH) (awaiting more detailed study prior to publication).

In springs on the Isle of Skye and in the Assynt region of northwest Scotland the following have been recorded: *Candona candida*, *Cryptocandona reducta*, *Cryptocandona vavrai*, *Cyclocypris ovum*, *Cypria ophtalmica*, *Eucypris pigra*, *Potamocypris zschokkei*, *Potamocypris pallida*, *Psychrodromus robertsoni*, *Psychrodromus olivaceus*. A new record of *Fabaeformiscandona breuili* in this region has already been mentioned.

In the English Lake District (Cumbria), Brownrigg Well, a spring near the summit of Helvellyn, has yielded *Potamocypris pallida*, whereas *Psychrodromus robertsoni* is common in slow-flowing seepages associated with springs and small streams having been recorded in several localities in the Windermere, Ullswater and Coniston catchments.

Finally, the minute interstitial species *Nannocandona faba* has been found in slow seepages associated with springs in the English Lake District and on the island of Eriskay in the Outer Hebrides. It is common in British Quaternary deposits, but there are no previously published living records from Britain (Griffiths and Evans, 1995a), although Douglas and Healey (1991) record an unidentified species of *Nannocandona* from Ireland. Meisch (2000) states that it inhabits both epigean and hypogean habitats; Marmonier and Danielopol (1988) found it living interstitially in the bed of a stream in Austria, being rare at the surface and most abundant 40 to 100cm deep in the sediment.

During a thorough faunistic study of Peak and Speedwell caverns in Derbyshire, PJW collected *Candona candida* in Speedwell Cavern but not in the streams feeding the caves, nor in the resurgences draining them. It seems very likely that this species is stygophilic within this cave system (Wood, 1999; Wood and Gunn, 2000; Gunn *et al.*, 2000).

COPEPODA

Copepods are small crustacea (0.1-5mm) frequently found in meiobenthic and hyporheic habitats. These habitats grade into true groundwaters and it seems likely that many species are inhabitants of all three (see discussion in Dole-Olivier *et al.*, 2000).

Stygobitic species

Jefferson (1984) indicates a number of copepod species that are stygobitic in Britain. Lescher-Moutoué (1986) and Rouche (1986) also identify some stygobitic species for Britain and Ireland. However, the names used by these authors are not in agreement and are in any case out of date. Fabio Stoch (pers. comm.) has provisionally indicated that the following species are potential stygobites here:

CYCLOPOIDA

***Acanthocyclops sensitivus* (Graeter and Chappuis, 1914)**
Originally described from Switzerland, the first record from Britain was by Gurney (1933, pp.215-218). It was collected from wells at Ringwood (Hampshire) together with *Proasellus cavaticus*, *Niphargus* sp., and three other copepods. As late as 1974, Harding and Smith (1974, p.50) were only able to report this record and describe it as *"Colourless. Subterranean."* Outside of Britain it is known from Switzerland, France, Austria and Germany (Leruth, 1939).

***Graeteriella unisetigera* (Graeter, 1908)**
Gurney (1933, pp.278-281) records this species in only two places, both epigean, and comments that *"It has been found abroad only in caves or spring waters, but in this country hitherto in surface waters"*. Harding and Smith (1974, p.53) record it from *"Wet peat or moss. Subterranean."* In a study of this species in Belgium, Fiers and Ghenne (1990) also found it to be epigean. Fabio Stoch (pers. comm.) suggests that it may only be stygobitic in southern Europe.

***Speocyclops demetiensis* (Scourfield, 1932)**
First described by Scourfield (1932) from a seepage in a cliff face at Tenby, Wales. Scourfield notes that the animal was seen above ground only under certain conditions and was probably hypogean. His species was placed in the genus *Speocyclops* in 1937 along with other, similar hypogean species. It is now known from four other sites:

1. A muddy seepage on the southern slopes of Great Shunner Fell, Yorkshire (SD 862958, altitude 600m) (Fryer, 1982);
2. Among sodden *Sphagnum* at Gorple, Yorkshire (SD 922317) (Fryer, 1982);
3. A small acidic stream in the Upper Twyi Valley, mid Wales, where it is very abundant (Rundle, 1993);
4. An acidic stream in Cornwall (Burton *et al.*, 2001).

These records suggest that this species may be stygophilic or even epigean in this country although it is exclusively hypogean in continental Europe.

In summary, it appears that *Acanthocyclops sensitivus* is the only true stygobitic cyclopoid in the Britain and that even this designation is based on very limited information.

HARPACTICOIDA

***Parastenocaris phyllura* Kiefer, 1938**
Collected from fine sand at the source of a spring at Rosneigr, Anglesey (Wales) (Geddes, 1972).

***Parastenocaris vicesima* Klie, 1935**
Collected from fine sand at the source of a spring at Rosneigr, Anglesey (Wales) (Geddes, 1972). Rouch (1986, p.351) records it from the estuary of the River Ythan, Scotland.

It would appear from these limited data that these two harpacticoids are psammobitic species at the sites where they were recorded in Britain. Studies of these two *Parastenocaris* species have been made in mainland Europe by Glatzel (1990, 1991, 1992) and Glatzel and Schminke (1996). Enckell (1969) recorded both species from various sandy habitats in fresh and brackish water in northern Europe. Thus the data suggest that there are no true stygobitic harpacticoid copepods in Britain or Ireland.

Stygophilic species

CYCLOPOIDA

***Eucyclops serrulatus* (Fischer, 1851)**
This species was recorded as a stygophile in Ireland by Juberthie and Decu (1994) and from Peak Cavern, Derbyshire by Wood *et al.*, (2002).

***Paracyclops fimbriatus* (Fischer, 1853)**
Chapman (1979) records this cyclopoid deep in Otter Hole, Chepstow, and considers it a stygophile.

***Megacylops viridis* (Jurine, 1820)**
Recorded as a stygophile in Ireland by Juberthie and Decu (1994) and from Peak and Speedwell Caverns, Derbyshire by Wood *et al.*, (2002).

***Acanthocyclops venustus* (Norman and Scott, 1906)**
Gurney (1933, pp.210-215) shows that this species is widespread in *Sphagnum* spp. but also says *"In acute contrast to these habitats is its occurrence in caves and in wells, in both cases apparently in limestone districts"*. Galassi (2001) describes this species as a generalist stygophile. Juberthie and Decu (1994) mistakenly record this species as a stygobite in Ireland and Wood *et al.* (2002) record it within Peak and Speedwell caverns, Derbyshire. This is probably a species complex and there are several stygobitic subspecies in continental Europe (Fabio Stoch, pers. comm.).

***Diacyclops bicuspidatus* (Claus, 1857)**
This species has been collected in many wells in Chalk remote from surface water and in association with *Niphargus fontanus* and *N kochianus kochianus* (Hazelton, 1963b, p 40) It may be a stygophile Fabio Stoch (pers comm) suggests that the animals from wells may in fact be the subspecies *D b lubbocki* (Brady, 1869)

***Diacyclops hypnicola* (Gurney, 1927)**
Although clearly an epigean species in places, it has also been collected from wells at Walsingham, Norfolk and Ringwood, Hampshire. Both well samples also had *Niphargus* spp. and the site at Ringwood *Proasellus cavaticus* (Gurney, 1933, pp.242-246).

During a thorough faunistic study of Peak and Speedwell Caverns in Derbyshire six species of copepod were recorded:

- Peak Cavern only: *Diacyclops bicuspidatus lubbocki* and *Eucyclops serrulatus*;
- Speedwell Cavern only: *Megacyclops gigas;*
- Peak and Speedwell Caverns: *Acanthocyclops venustus, Acanthocyclops vernalis* (Fischer, 1853) and *Megacyclops viridis.*

However, none of these species was found in the streams feeding the caves, nor in the resurgences draining them. It seems very likely that these are stygophilic species within both cave systems (Wood, 1999; Wood and Gunn, 2000; Gunn *et al.*, 2000; Wood *et al*, 2002).

CLADOCERA

This group of micro Crustacea (1–2mm) is not noted for its association with subterranean environments and worldwide only 94 species and subspecies have been recorded from hypogean habitats. Of these only 12 are stygobitic (Dumont and Negrea, 1996). Wood and Greenwood (2001) record large numbers of *Alona quadrangularis* (Muller, 1776) (Chydoridae) from various parts of the streamway in Speedwell Cavern, Derbyshire. They consider it to be stygophilic. It seems likely that other detailed studies of fine sediments will reveal further cladoceran species.

SYNCARIDA

With the exception of several Australian species, syncarids are microscopic animals, c.1mm long, normally only found in interstitial and phreatic habitats. The British and Irish faunas are poorly known and studied. Five names relating to syncarids recorded from subterranean habitats in Britain and Ireland have been reported in the

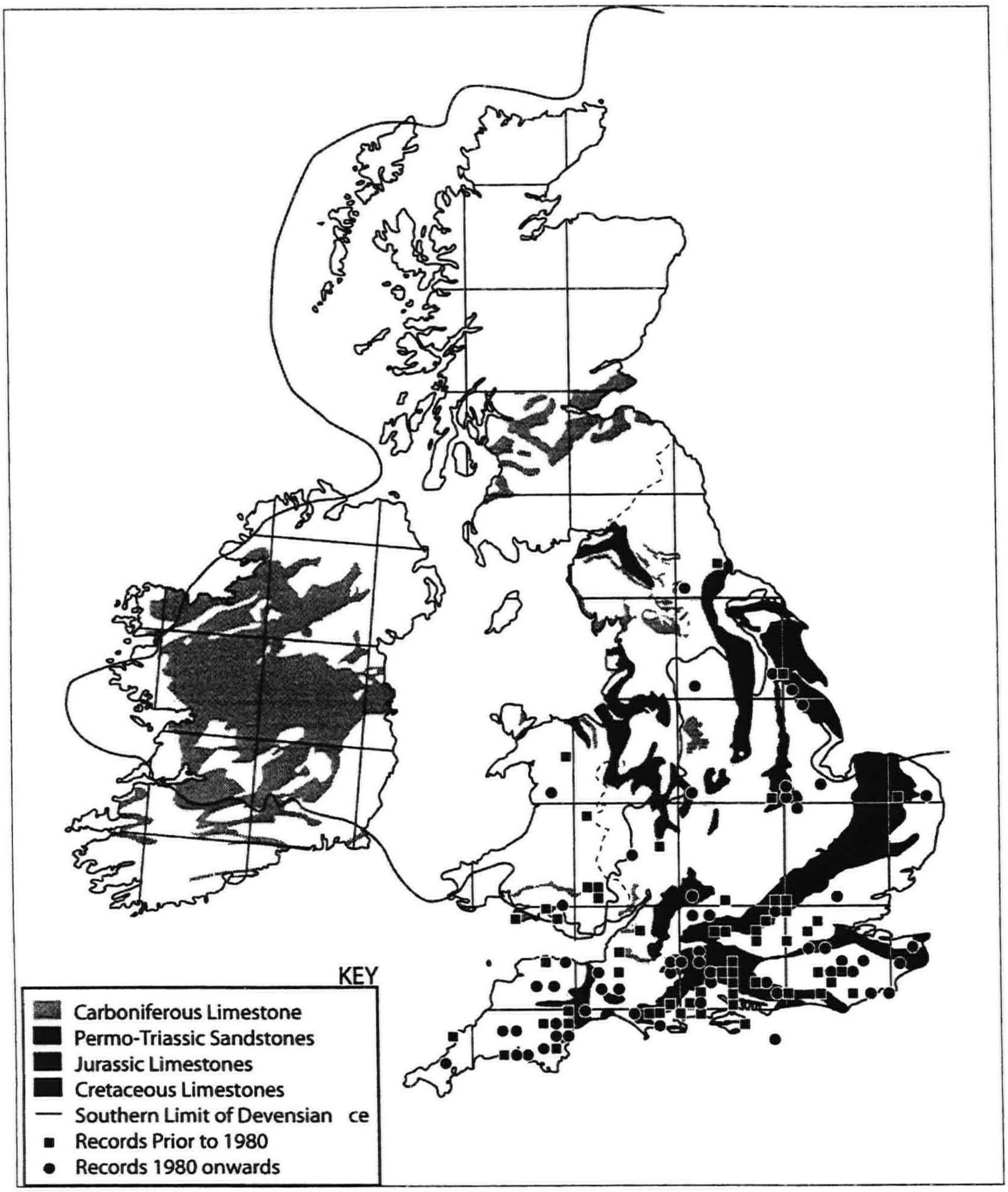


Figure 2. *The distribution of* Niphargus aquilex *by 10km squares.*

literature:

1 *Bathynella chappuisi* Delachaux, 1920 (Lowndes, 1932a,b; Calman, 1932; Efford, 1959);

2 *Bathynella natans* Vejdovsky, 1882 (Spooner, 1961; Maitland, 1962, 1966; Gledhill and Driver, 1964);

3 *Bathynella natans stammeri* Jakobi, 1954 (Serban and Gledhill, 1965);

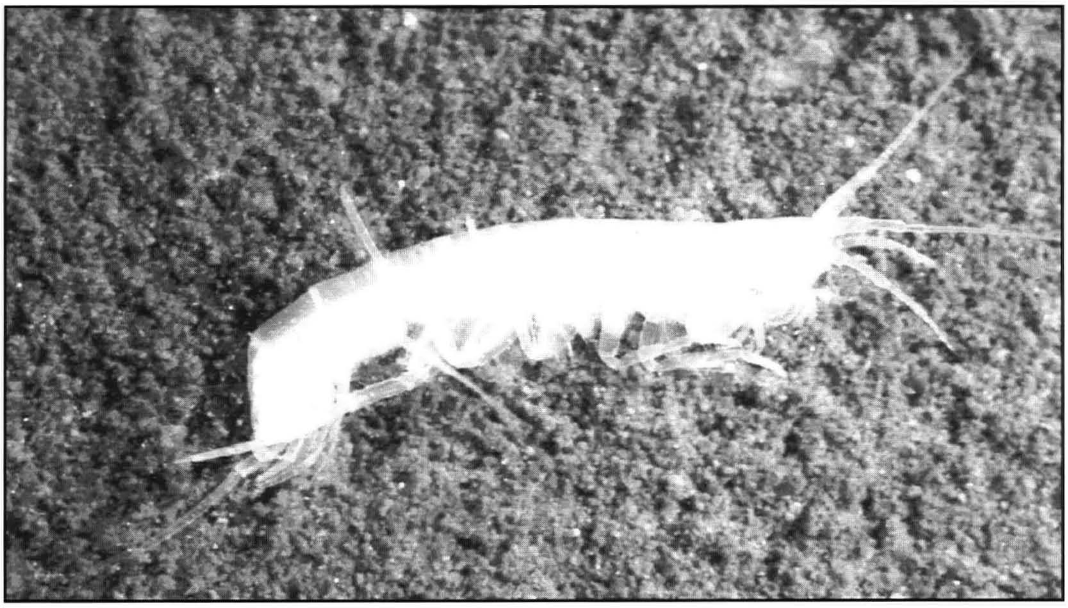
4 *Bathynella stammeri* Jakobi, 1954 (Gledhill and Gledhill, 1984);

5 *Antrobathynella stammeri* (Jakobi, 1954) (Gledhill *et al*, 1993).

The first of these names (*B. chappuisi*) is easily dealt with, as it is a synonym of *B. natans*. Gledhill *et al.* (1993, pp.96–98) discuss the other names. They suggest that all recent (post-1966) records are of the species *stammeri*. This species was transferred from the genus *Bathynella* to *Antrobathynella* by Serban (1973). We (TG and GSP) have recently examined specimens of the pre-1966 records of the species referred to *chappuisi* and *natans* kept in the Natural History Museum, London. The specimens from Corsham, collected by Lowndes in 1931 (BMNH 1931.12.29:1-3) (Lowndes, 1931a,b), and the specimens collected from Scotland by Maitland in 1961 (no BMNH accession number) (Maitland, 1962), both appear to be the species *stammeri*. This is based on the presence of four, rather than five to seven, spines on the uropodal protopod. A second diagnostic character, the number of mandible teeth (seven in *natans*, six in *stammeri*), is too difficult to see without dissection and we were unwilling to do this on valuable museum material. The Natural History Museum also has a bottle with a label suggesting it contains specimens collected by Efford in Oxfordshire in 1959, but it appears to be empty. The specimens collected by Spooner in various localities appear to be lost. Despite a search of the collections of the Natural History Museum, and the Marine Biological Association, no material has been found. No mention is made of syncarid specimens in an examination of Spooner's material by Costello (1991). The supposition of Gledhill *et al.* (1993, p.98), that *B. natans* is not present in Britain and Ireland, is thus supported. There is currently only one representative of the Syncarida, *Antrobathynella stammeri*, in Britain and Ireland.

Syncarids were first recorded in Britain by Lowndes (1932a,b; see also Calman, 1932) from Pickwick Quarry, one of the Corsham Stone quarries, Wiltshire, and rediscovered in Berkshire in 1959 (Efford, 1959). Spooner (1961) records *B. natans* from Oxfordshire, Berkshire and Devon. Syncarids were collected from the Altquhur Burn, a tributary of the River Endrick, which flows into Loch Lomond, in Scotland by Maitland (1962, 1966) and from Yorkshire in 1964 (Gledhill and Driver, 1964; Schofield, 1964; Serban and Gledhill, 1965). Gledhill and Gledhill (1984) discovered syncarids in the River Flesk, Killarney, Ireland in 1982. Gledhill *et al.* (1993, p.98) report them from riverine gravels in the Rivers Derwent, Duddon, Liza, Lune and Tees, all in Cumbria (Fig.1). There are 41 records, collected from 16 sites in fourteen 10km squares (11 squares from pre-1980 records and three squares from post-1980 records.). Two of the sites are caves: White Scar Cave and Great

Figure 3. Niphargus fontanus *in Ogof Ffynnon Ddu Photograph by Phil Chapman.*



Douk Cave (Yorkshire). Outside of Britain and Ireland this species is known from Germany, Austria, Italy, Romania and the Czech Republic (Delamare Deboutteville, 1960; Pesce, 1985; Schminke, 1986).

AMPHIPODA

Stygobitic species

***Niphargus aquilex* Schiödte, 1855** (Fig.2).

Originally recorded in Britain by Westwood (1853) from a well near Maidenhead (Berkshire) (as *Niphargus stygius*) and described from British material by Schiödte (1855). The first probable cave records were from Dan-yr-Ogof and Porth yr Ogof, South Wales in April 1946 (Hazelton, 1956a, p.8, 1956b, p.1). The first confirmed cave record is from Holwell Cave (Somerset) in November 1951 (Hazelton, 1960a, p.12). There are 208 records of this species collected from 137 sites in eighty-six 10km squares (54 squares from pre-1980 records, 32 squares from post-1980 records) (Fig.2). The majority of these sites are interstitial in nature and the species is known from only 14 caves. Ten of these caves are in Devon and it is possible that it is commoner there than elsewhere because there is less competition with other Niphargids. However, it does coexist with *N. glenniei*.

There are several records north of the Devensian glacial limit. Two dating from 1863 (Henwick) and 1893 (West Hartlepool) cannot now be confirmed. Those modern enough to be reliable are from:

1. the Afon Hirnant, a tributary of the Welsh River Dee, collected by Noel Hynes in 1961;
2. the River Teme at Gwerneirin in Wales (1964, Glennie, 1968), 20km west of the limit;
3. Barton Upon Humber (1969) and South Ferriby Cliff (1986), both on the River Humber just a few kilometres north of the limit; and
4. Ogof Agen Allwedd (Crickhowell, Powys).

This species is the most superficial of the British *Niphargus* and has been found in streams, although probably washed out from shallow gravels (e.g. Townsend *et al.*, 1983; Ham, 1982; LK personal observations). In recent years the number of records for all species of stygobitic amphipods has fallen as older collectors gave up collecting. The superficial nature of this species means that it has been sampled more often than the other species. Gledhill and Ladle (1969) made observations on the life history of this species (see below). Karaman (1980) designated a specimen from Crowborough (east Sussex) as the neotype of *Niphargus aquilex* (male, 6.8mm, BMNH 1980:140). Outside of Britain the species is known from central and southern Europe, including Italy and the Balkans (Karaman, 1982; Pesce, 1985; Karaman and Ruffo, 1986).

***Niphargus fontanus* Bate, 1859** (Fig.3 and Fig.4)

Originally described by Bate (1859) from Ringwood (Hampshire) this species was recorded only seven times prior to 1938. All pre-Glennie records are from wells, and the first cave record was from Swildons Hole in May 1946 (Hazelton, 1956b, p.2) There are 147 records of this species, collected from 62 sites in thirty-three 10km squares (27 squares from pre-1980 records, 6 squares from post-1980 records). The sites comprise 23 interstitial sites, 12 caves in the Mendip Hills, 17 caves in South Wales and 3 mines. It has also been recorded from two wells on the outskirts of St Helier, Channel Islands (Walker and Hornell, 1896) (Fig.4). It was recorded only once in a thorough, and detailed, study of Otter Hole, near Chepstow (Chapman, 1979). Jefferson and Chapman (1979, p.9) record this species from 8 sites in Ogof Ffynnon Ddu II in South Wales and comment *"Widespread in trickle-fed pools and small streams, often in crevices, under stones or in mud cracks. Predator/detritivore, may supplement diet with bacteria-rich silt."* In Pen Park Hole near Bristol it is found in the lake with *N. kochianus kochianus* (Glennie, 1963; Hazelton, 1963b) though in smaller numbers. It is of note that specimens from interstitial sites (e.g. the Waterston Cress Beds) are routinely smaller than those from caves (e.g. Ogof Ffynnon Ddu). This may be an adaptation to small cavity size or it may be that the food supply is poorer in interstitial habitats. During a systematic study of various *Niphargus* species in northern Europe Gledhill (1980) found it necessary to erect a lectotype for this species (BMNH 1978:190). Outside of Britain *N. fontanus* is found in eastern France, Belgium (the Ardennes), Germany and Austria (Karaman and Ruffo, 1986).

***Niphargus kochianus kochianus* Bate, 1859** (Fig.5)

Originally described by Bate (1859) from a single specimen from a pump in a house at Ringwood, Hampshire. The first modern record was from a well at Rossway House, Berkhamsted in April 1947 (Hazelton, 1958, p.7). The first cave record was from Holwell Cave in February 1951 (Hazelton, 1960a, p.9). There are 76 records of this species, collected from 39 sites in twenty-seven 10km squares (all records pre-1980). The sites comprise 30 interstitial sites and 3 caves, St Cuthberts Swallet in the Mendip Hills, Holwell Cave in the Quantock Hills and Pen Park Hole near Bristol. At the latter site it is found in great numbers in the lake together with *Niphargus fontanus* (Glennie, 1963; Hazelton, 1963b). There is a very close correlation between the distribution of this species and the outcrops of Cretaceous limestones (Chalk), in the south of England (Fig.5), an association previously reported for this subspecies in France by Vonk (1988). Outside the Chalk areas there are two records from Jurassic limestones, two from Carboniferous limestones and two from other sites: the no longer existent Town Well at Ringwood and Holwell Cave. *N. kochianus kochianus* was collected twice in Holwell cave in 1951 (Hazelton, 1960a, p.9) but recently only *N. aquilex* has been seen there (LK personal observations). The species has not been collected from Ringwood since 1928, although large

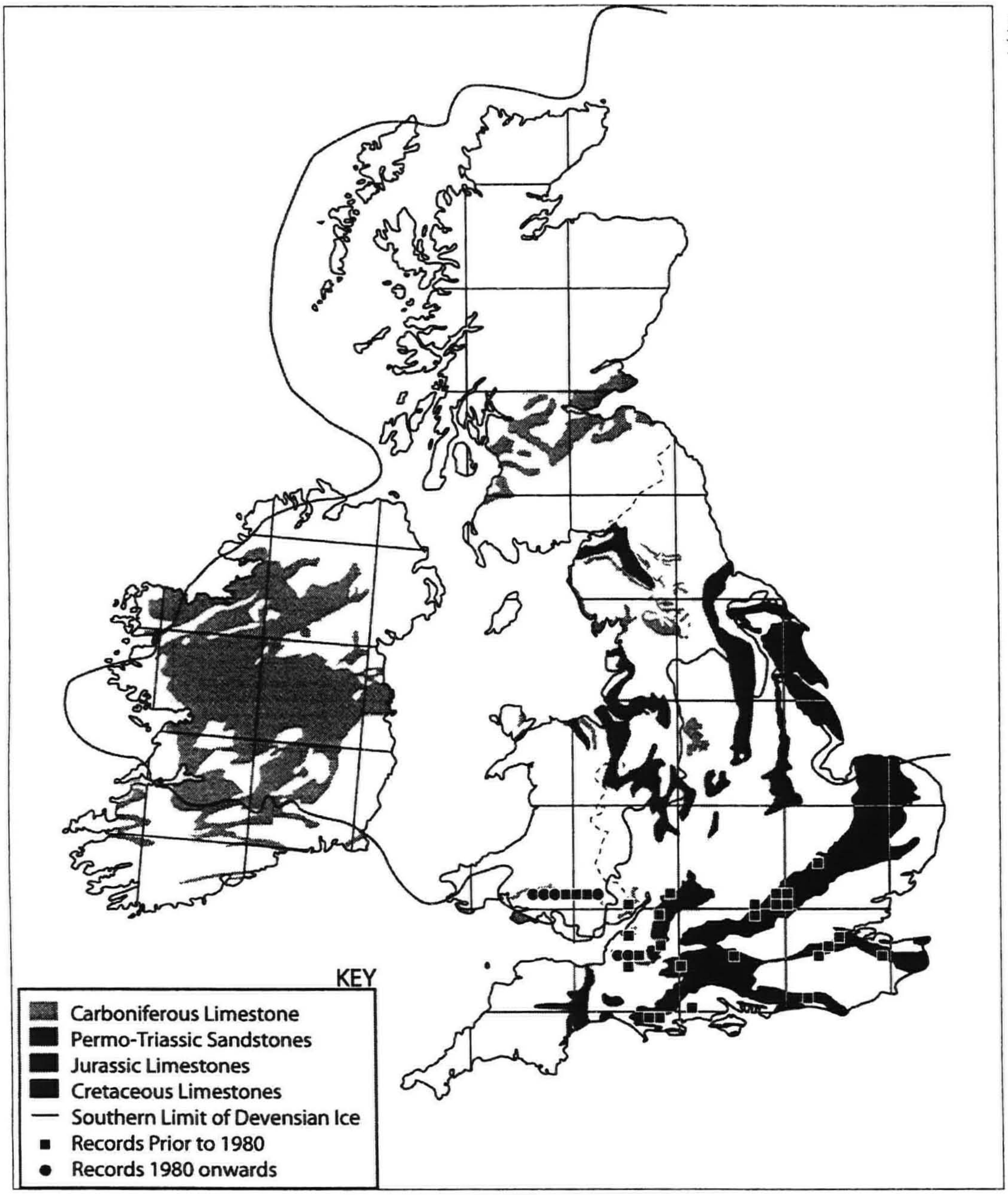


***Figure 4.** The distribution of* Niphargus fontanus *by 10km squares.*

numbers have been collected near Puddletown in Dorset c.40km away (Gledhill, 1977; Stock and Gledhill, 1977). It would be sensible to look for this species in the North and South Downs. In the light of the records of *N. aquilex* in northern Lincolnshire it would also be sensible to look in the Cretaceous limestone areas of the Lincolnshire and Yorkshire Wolds. Stock and Gledhill (1977) and Karaman and Ruffo (1986) consider this subspecies to be endemic to England, though Vonk (1988) and Ginet (1996) record it from France. Other members of the *kochianus* group (*kochianus dimorphopus*, *kochianus petrosani*, *kochianus polonicus* and *N. pachypus*) are found throughout Europe from northern France to Romania and Russia (Karaman and Ruffo, 1986).

Stock and Gledhill (1977) provide details of the taxonomy and systematics of this (sub)species and other members of the *kochianus* species group. They found that the *kochianus* and *irlandicus* taxa are morphologically very similar, and proposed retention of subspecific status for both. However, these taxa have been completely isolated from one another by the marine Irish Sea for at least 10,000 years, and probably much longer, and are clearly not in genetic continuity. It is perhaps time to recognize them as separate species. In a similar case in France, Mathieu *et al.* (1997) found that there was marked genetic divergence between geographically close, in one case hydrologically connected, populations of *Niphargus rhenorhodanensis*. This strongly suggests that morphology is very conservative and therefore a poor means of discriminating between taxa.

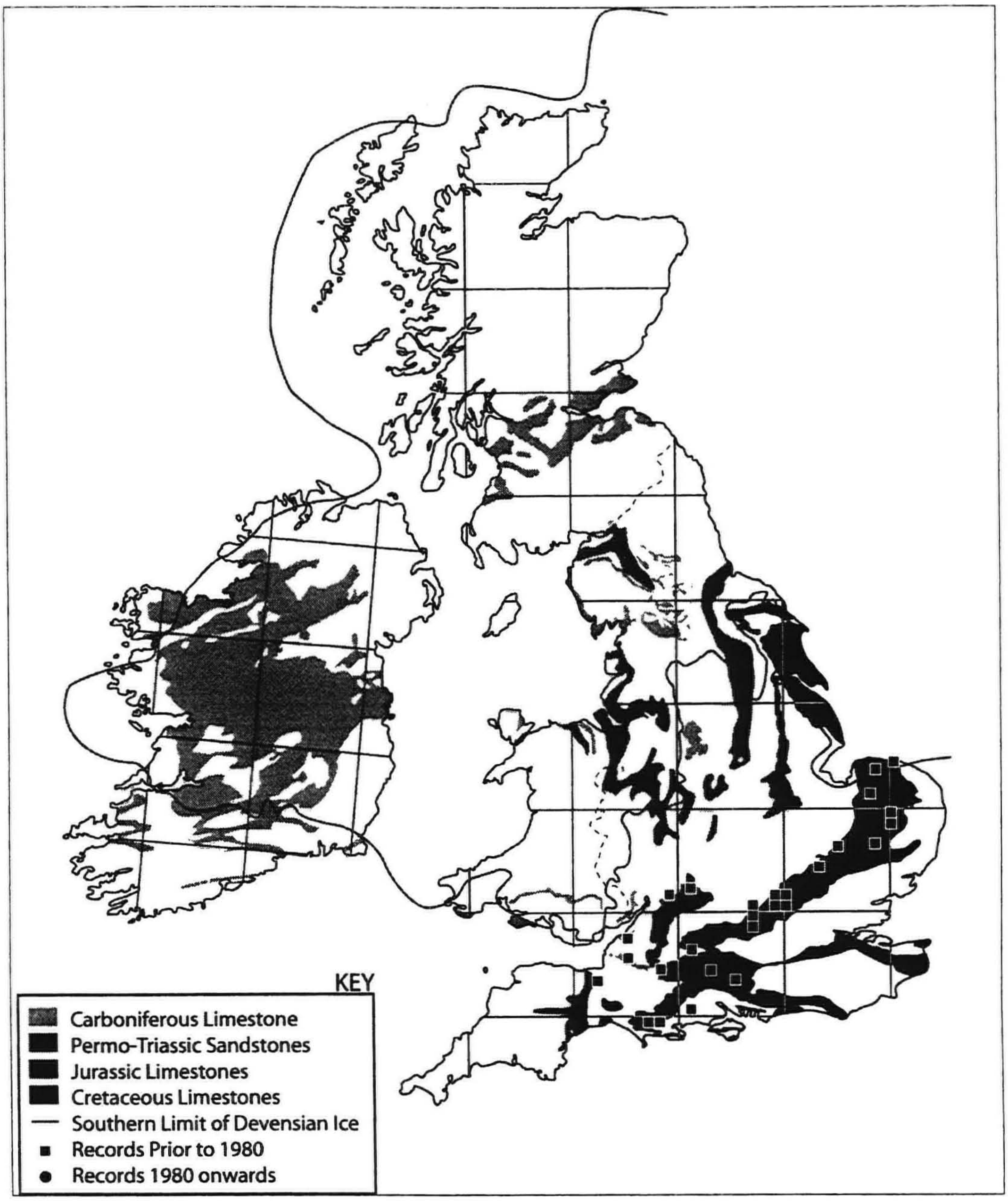
***Niphargus kochianus irlandicus* Schellenberg, 1932** (Fig.6)

First recorded from Templeogue, Dublin, in 1899 as *N. kochianus*. The species was recorded again in 1904 from the bottom of Lough Mask (Kane, 1904) and from Mullingar in 1910. Schellenberg (1932) differentiates the Irish taxon as a separate subspecies, *N. kochianus irlandicus,* a decision upheld by Stock and Gledhill (1977) in a detailed modern study. There were no additional records until 1956 when it was collected from Gragan West Cave (Hazelton, 1960b, p.19). There are 51 records of this species, collected from 35 sites in twenty-eight 10km squares (27 squares from pre-1980 records, 1 square from post-1980 records). The records comprise 25 interstitial sites, 9 caves and Lough Mask (Fig.6). This subspecies is endemic to Ireland, and its distribution differs markedly from that of *Niphargus* species in Britain. Where most British records are distributed no further north than the southern limit of the Devensian ice, this subspecies is found in areas fully glaciated in Midlandian (= Devensian) times. Costello (1993) suggests that it may be pre-glacial, relict, species having survived glaciation below ground (see below). The Lough Mask and Mullingar records (53°30'N), together with the South Ferriby record of N. *aquilex* (53°40'N), and a record of N. *aquilex* in Helgoland, Germany (54°N) are the most northerly records of the genus *Niphargus* (Stock and Gledhill, 1977). Ireland is the westernmost location for the genus *Niphargus*.

***Niphargus glenniei* Spooner, 1952** (Fig.7)

Niphargus glenniei was first observed on 19th April 1948 by Aubrey Glennie, in company with Mary Hazelton, who actually captured the

Figure 5. *The distribution of* Niphargus kochianus kochianus *by 10km squares.*



first specimen. Six specimens were seen in a small, shallow, mud-lined pool, about 100m from the entrance of Pridhamsleigh Cavern (Devon). The young female captured by Hazelton is now the holotype for the species and is deposited at the Natural History Museum, London. The "co-type" is a young female collected from the Deep Well in Pridhamsleigh on 21st June, 1948. The species was first described by Spooner (1952) in the genus *Niphargus*, following his examination of specimens collected from Pridhamsleigh and Reed's caves near Buckfastleigh (south Devon).

N. glenniei is much smaller than the other British *Niphargus*, with the exception of *Niphargus wexfordensis*, attaining sexual maturity at 3 to 3 5mm. The other species are sexually mature at a minimum size of 4 to 6mm, with most specimens being at least 8mm (Spooner, 1952).

Schellenberg (1938) established the genus *Niphargellus* with the species *Niphargellus arndti* (Schellenberg, 1938) and *Niphargellus nolli* (Schellenberg, 1938). Differences between the two genera are slight, with *Niphargellus* differing from *Niphargus* only in the extremely reduced setation of the mandibular palp (Karaman *et al*, 1994). Because of the reduced setation of mandibular palp article 3 in *N. glenniei*, 4 E-setae and 1 D-seta, some authors consider this taxon to belong to *Niphargellus*, e.g. Gledhill *et al* (1976) and Karaman and Ruffo (1986). However, with the discovery of *Niphargus wexfordensis*, another small species with reduced mandibular setation, Karaman *et al* (1994) conclude that the genus *Niphargellus* should be retained only for *Nipargellus arndti* and *Niphargellus nolli* They also postulate that the *N. glenniei* group of species (with *N boulangei* Wichers, 1964 and *N wexfordensis*), all with a low number of D-setae, represents a link between the genus *Niphargus*, with numerous D-setae, and the genus *Niphargellus*, with none.

There are 62 records of this species, collected from 24 sites in thirteen 10km squares (3 squares from pre-1980 records, 10 squares from post-1980 records). The sites comprise 11 caves and 5 mines in Devon, 3 interstitial sites in Devon and 3 wells in Cornwall (Fig 7). The caves are in the Buckfastleigh, Chudleigh, Torquay and Brixham Devonian limestone outcrops (Knight, 1999, 2001).

The species is thought to be a highly interstitial form, being washed into pools in caves and mines after heavy rainfall. It is probably much more widespread within the hypogean domain than is currently known. It has not yet been found in association with similar strata elsewhere in southwest England. A preliminary search of Holwell Cave in 1998 recorded only *Niphargus aquilex* *N. glenniei* is endemic to England and is currently afforded a RDB K / 5 (Red Data Book listed: insufficiently known / endemic) conservation status (Bratton, 1991).

Niphargus wexfordensis **Karaman, Gledhill and Holmes, 1994** (Fig 8)

A species described from a well at Kerloge, County Wexford, Ireland (T0519) by Karaman *et al.* (1994). This is still the only known locality for this species, which is endemic to Ireland (Fig 8).

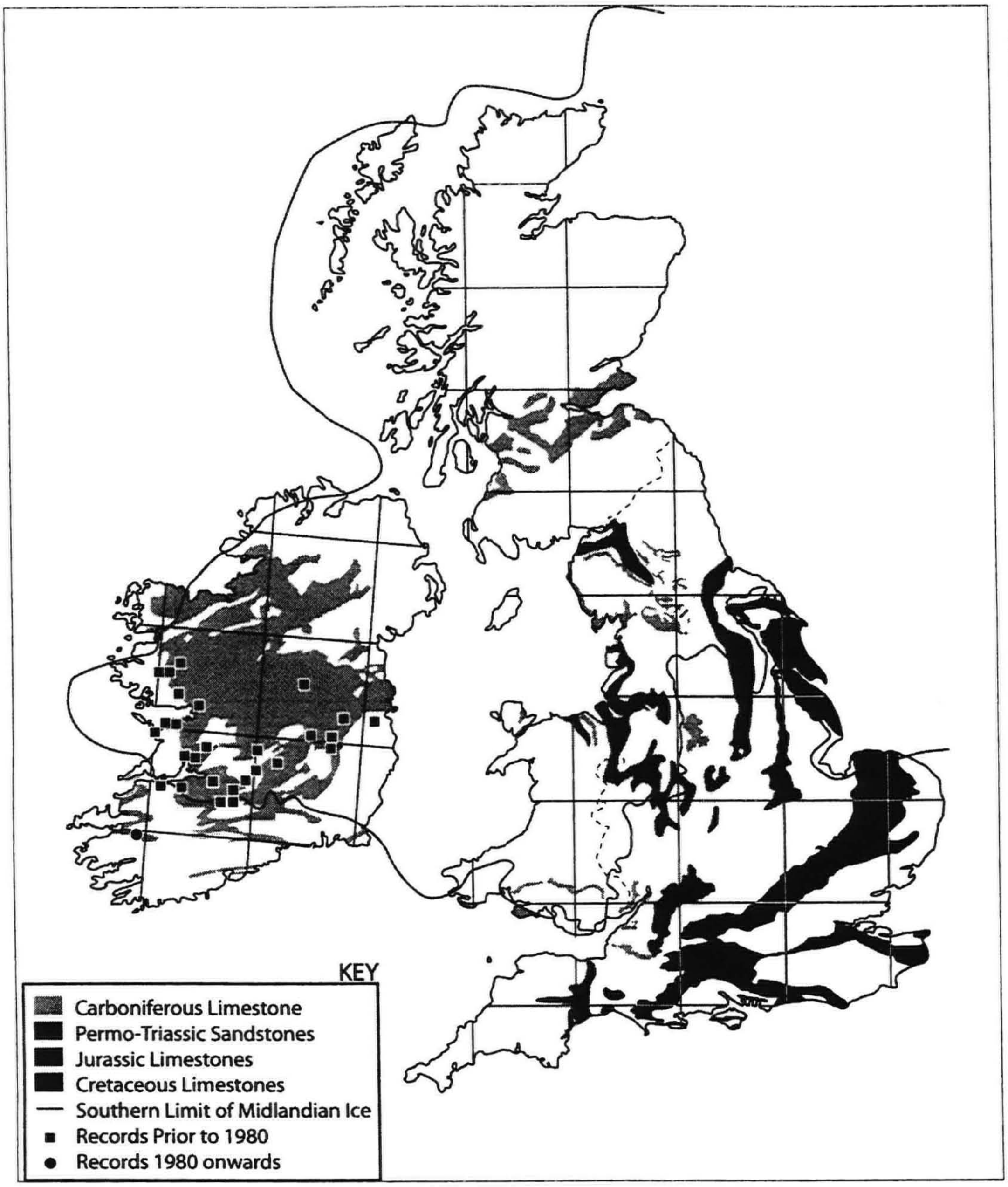


Figure 6. *The distribution of* Niphargus kochianus irlandicus *by 10km squares.*

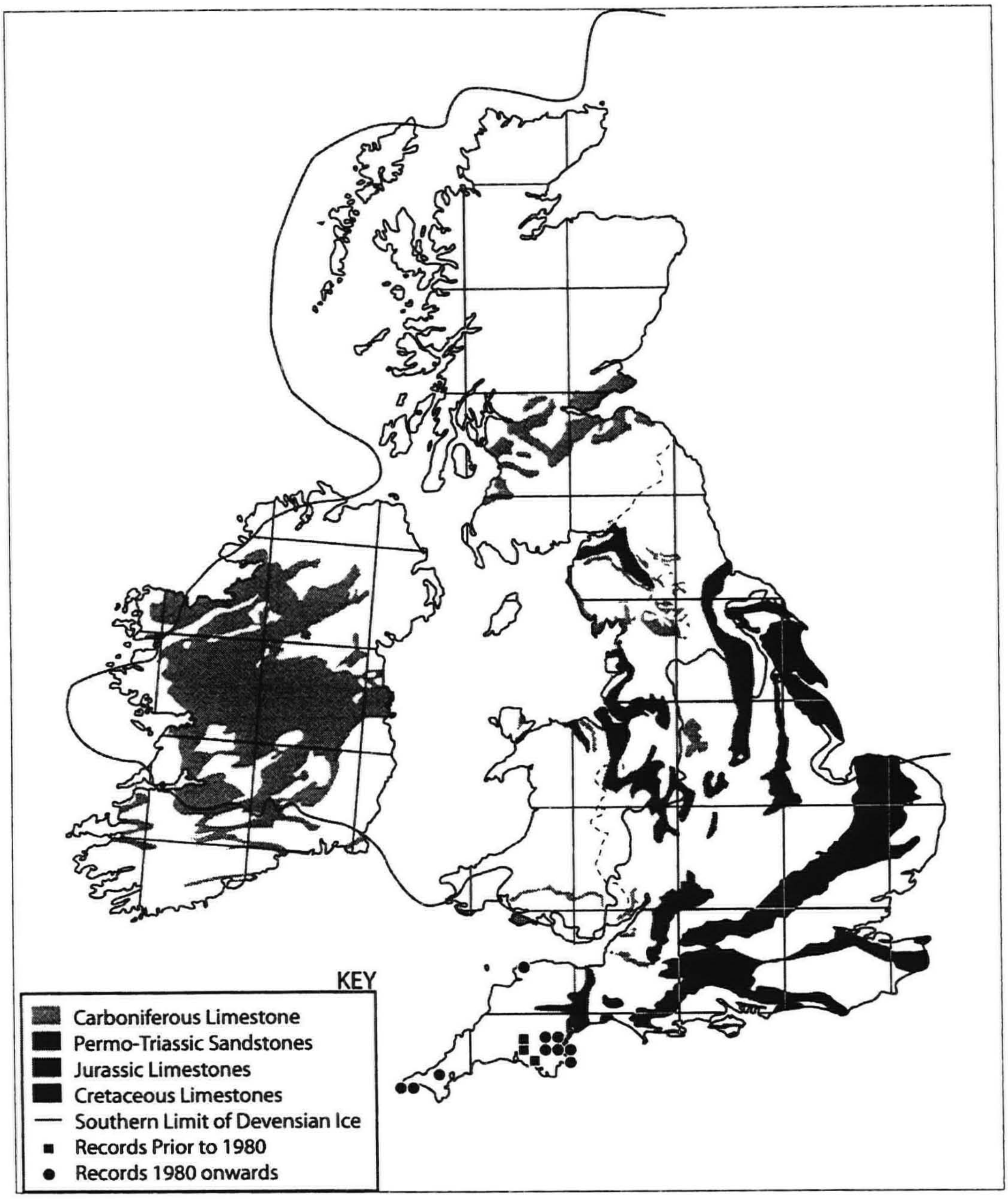
Crangonyx subterraneus **Bate, 1859** (Fig 9)

Originally described by Bate (1859) from a well at Ringwood, Hampshire (in association with *Niphargus kochianus kochianus* and *Niphargus fontanus*), and then found in a well at Marlborough, Wiltshire in 1900 (Glennie, 1967). It was recorded again at Ringwood in 1920 and 1928. It was not until 1951 that it was collected from a cave – Ogof Pant Canol, part of the Ogof Ffynnon Ddu system (Powys) – in one pool in association with *Niphargus fontanus* and *Proasellus cavaticus* (Hazelton, 1960a, p 8; Hazleton and Glennie, 1953, p 271). It was recorded by Spooner (1961) in the Thames Valley near Pangbourne (Berkshire), and from the Waterston Cress Beds (Dorset) by Gledhill (1977), who collected it regularly between 1969 and 1974. The only other cave record, from Goughs Cave, Mendip (Somerset), was made in 1966 (Hazelton, 1967, p 173). The most recent record, from 1998, is the most striking of any for subterranean amphipods. It was collected from river gravels in the Afon Lluestgota (part of the R Rheidol catchment (Ceredigion), Wales) at over 350m altitude in the hills northeast of Aberystwyth. This site is 100km north of the Devensian limit in south Wales and 100km west of the limit in the Wales / England border area. If this record is confirmed it has significant implications for the colonisation history of the country after the end of the last glaciation (see below). At present this record is unconfirmed because the specimen was not retained for examination and we await further specimens (Fig.9). There are 26 records of this species, collected from 7 sites in seven 10km squares (6 squares from pre-1980 records, 1 square from post-1980 records). The sites comprise 2 caves and 5 interstitial sites Outside of Britain *C. subterraneus* is recorded from western and central Europe (Holsinger, 1986).

Notes on stygobitic amphipods

Gledhill (1977) records numerical fluctuations of four species of amphipods from the same site, the Waterston Cress Beds, Dorset. Over a 5-year study period the relative species abundances were: *Niphargus aquilex* 53.64%, *Niphargus kochianus kochianus* 29.09%, *Crangonyx subterraneus* 12.86% and *Niphargus fontanus* 4.38% *N aquilex* was recorded throughout the year, as was *N. fontanus*, but in much smaller numbers *C. subterraneus* was more common in the first half of the year *N. kochianus kochianus* was also common in the first half of the year but totally absent from samples in the second half. Gledhill (1977) argues that the fluctuations in numbers of these four amphipod species was closely related to variations in water level within the site, and thus to the amount of water entering from subterranean sources. Gledhill and Ladle (1969) examined the life history details of *Niphargus aquilex* from superficial gravels of the R Oberwater in Hampshire. Overwintering adults began to grow in the spring and they released young in mid summer These matured in the autumn and bred from October onwards.

Figure 7. The distribution of Niphargus glenniei *by 10km squares.*



Stygophilic species

***Gammarus pulex* (Linnaeus, 1758)** (Fig.10 and Fig.11)

Gammarus pulex is an extremely common and widespread epigean amphipod that has been recorded many times in caves. There have been no detailed ecological studies of this species in caves in Britain and Ireland to determine its status with certainty, but it seems clear that many populations in active stream passages are most likely to have arrived there in the drift (Elliott, 2002). Their feeding behaviour, as generalist shredders and predators (Kelly *et al.*, 2002), means that they can make use of any water-borne food supplies (e.g. detritus, leaf fragments and micro- and macroinvertebrates) Male / female amplexus pairs are common, as are juveniles, and it is almost certain that *G. pulex* is able to feed and breed in the absence of light. A four-year study in the Peak-Speedwell System (Derbyshire) strongly supports this supposition (Wood *et al.*, 2002) Many individuals arriving in the cave with the drift will also leave by the same means, and it is likely that the "population" seen in any individual stream segment is of transitory individuals These individuals may be considered as transitory stygophiles. In contrast to these are individuals found in static pools of two types: pools filled by floodwater from a cave stream and pools above flood level fed by percolation water. The former are probably transitory stygophiles with a longer residence time, and the population may become extinct if there is too little food in the pool or if the flood return time is too long Individuals recorded within percolation water fed systems are potentially the most interesting because of the mode of colonization of subterranean habitats and isolation of individual populations. Chapman (1993, p.159) has no doubt that some populations are stygophilic, having studied a population high above the stream level in Swildons Hole. These animals are depigmented and have white eye facets (Fig.10 and Fig.11), conditions noted also by Holsinger (pers. comm) in stygophilic amphipods in North America.

The mechanism of colonization of these percolation pools has never been studied, but it is possible that amphipods are small enough to travel through the micro- and mesoporous spaces with percolation water, although this relies on permanent water bodies in epigean habitats. It is also possible that they actively migrate into the cave where predation pressure may be reduced (but see below). Harris *et al* (2002) demonstrated that the North American epigean amphipod *Crangonyx pseudogracilis* migrates through groundwater to reach temporary ponds. The problem of their food supply has similarly not been studied. Detritus may also enter with water, although percolation pools are often remarkably clear and lacking any obvious coarse particulate organic matter. In the absence of this type of food it is probable that amphipods can obtain energy from fine particulate organic matter in the sediments that often line such pools. It is known that silt is an important part of the diet of some *Niphargus* and *Crangonyx* species (e g Dickson, 1979). Another potential source of food would be other individuals of *G. pulex* and other macro- and microinvertebrates utilizing the percolation water. These populations can be considered true stygophiles, successfully

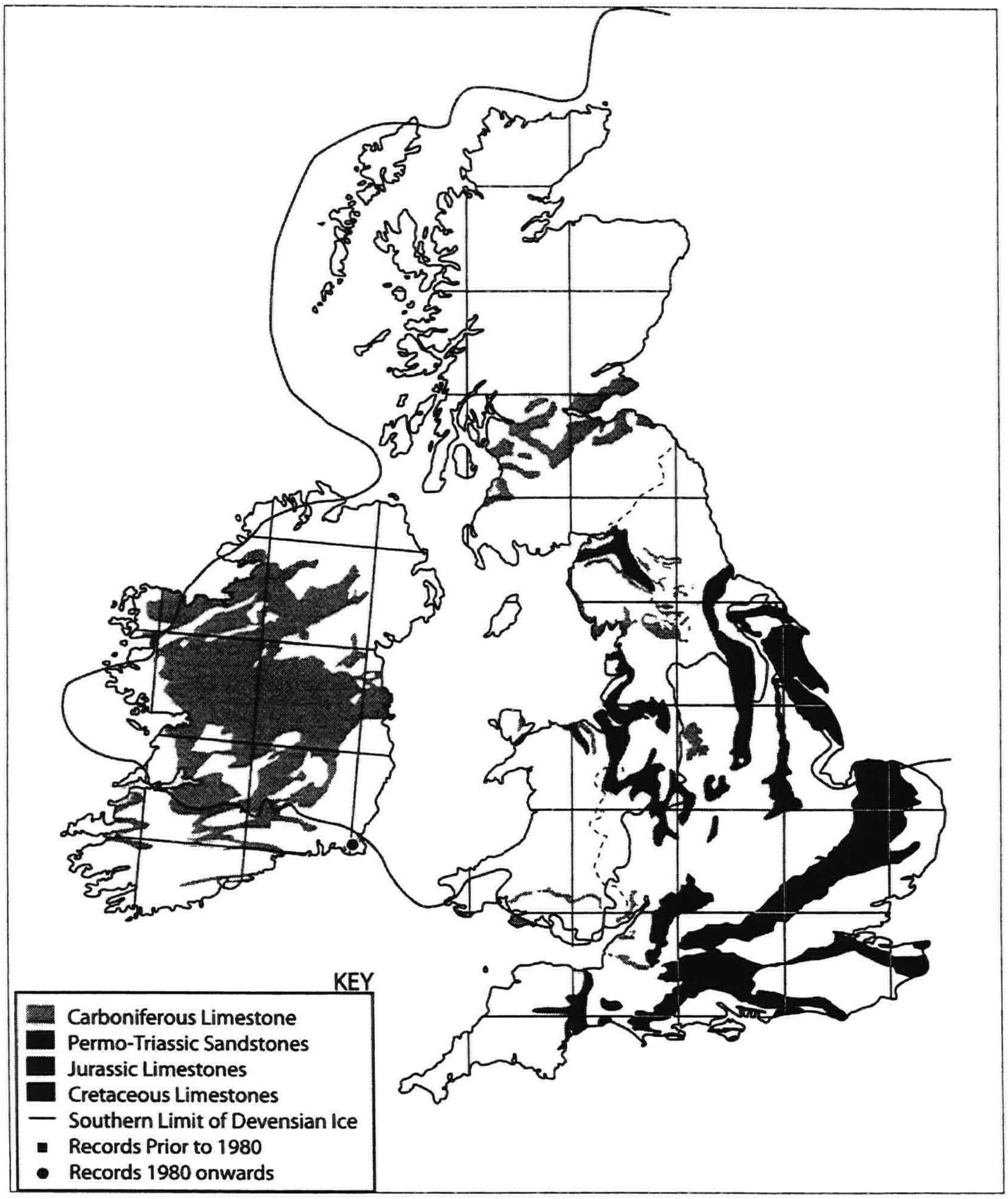


***Figure 8.** The distribution of* Niphargus wexfordensis.

living and reproducing within caves. However, much has yet to be learnt from the study of these populations.

The most comprehensive studies of this species to date are those of Piearce and co-workers (Piearce, 1975; Piearce and Cox, 1977a,b) and Gidman (1975) who studied a population in Ingleborough Cave, Yorkshire (the downstream end of the Gaping Gill System). They discovered two colour morphs (pale yellow/orange (unpigmented) and grey/grey-brown (pigmented)) with disjunct distributions. In the stream feeding the system (Fell Beck) all animals were pigmented. In the resurgent stream (Clapham Beck) up to 80% of animals were unpigmented. Furthermore, unpigmented animals were abundant in Ingleborough Cave up to 1km upstream from the resurgence No intermediate morphs were found. Laboratory studies indicated that the unpigmented animals do not develop pigment if kept in daylight for 6 months. The implication of this study is that a population of unpigmented animals exists within the Gaping Gill System and further studies of this interesting situation are required.

In Bulgaria and Poland there are taxa within the species G. *pulex* that are, apparently, restricted to caves. They are accorded subspecific status by Karaman and Pinkster (1977) as G. *pulex cognominis* Karaman and Pinkster, 1977 and G. *pulex polonensis* Karaman and Pinkster, 1977 respectively. The former has eyes but the latter is totally without them Karaman and Pinkster (1977, p.21) say of *G. pulex polonensis "Since this subspecies was found within the distribution area of* G. pulex *and no reproductive isolation is proved so far we must consider this form an ecologically isolated subspecies of* G. pulex". This account gives us an indication that ecologically isolated taxa of *G. pulex* do exist and that it is perfectly possible for the Bulgarian and Polish examples to be repeated here. Indeed, eyeless *G. pulex* have been collected from Lathkill Head Cave by one of us (PW) though the ecological status of the population from which they came is not known A subspecies of *G. pulex, G. pulex* subterraneus Schneider, 1885, was described from caves in Germany. However Karaman and Pinkster (1977) consider that the individuals allocated to this subspecies are in fact probably juvenile *G. fossarum.* A number of additional studies have been undertaken of cave populations of *Gammarus pulex* in some detail in Germany (Schneider, 1885; Muhlmann, 1938; Anders, 1953; 1956a, b; Michel and Anders, 1954).

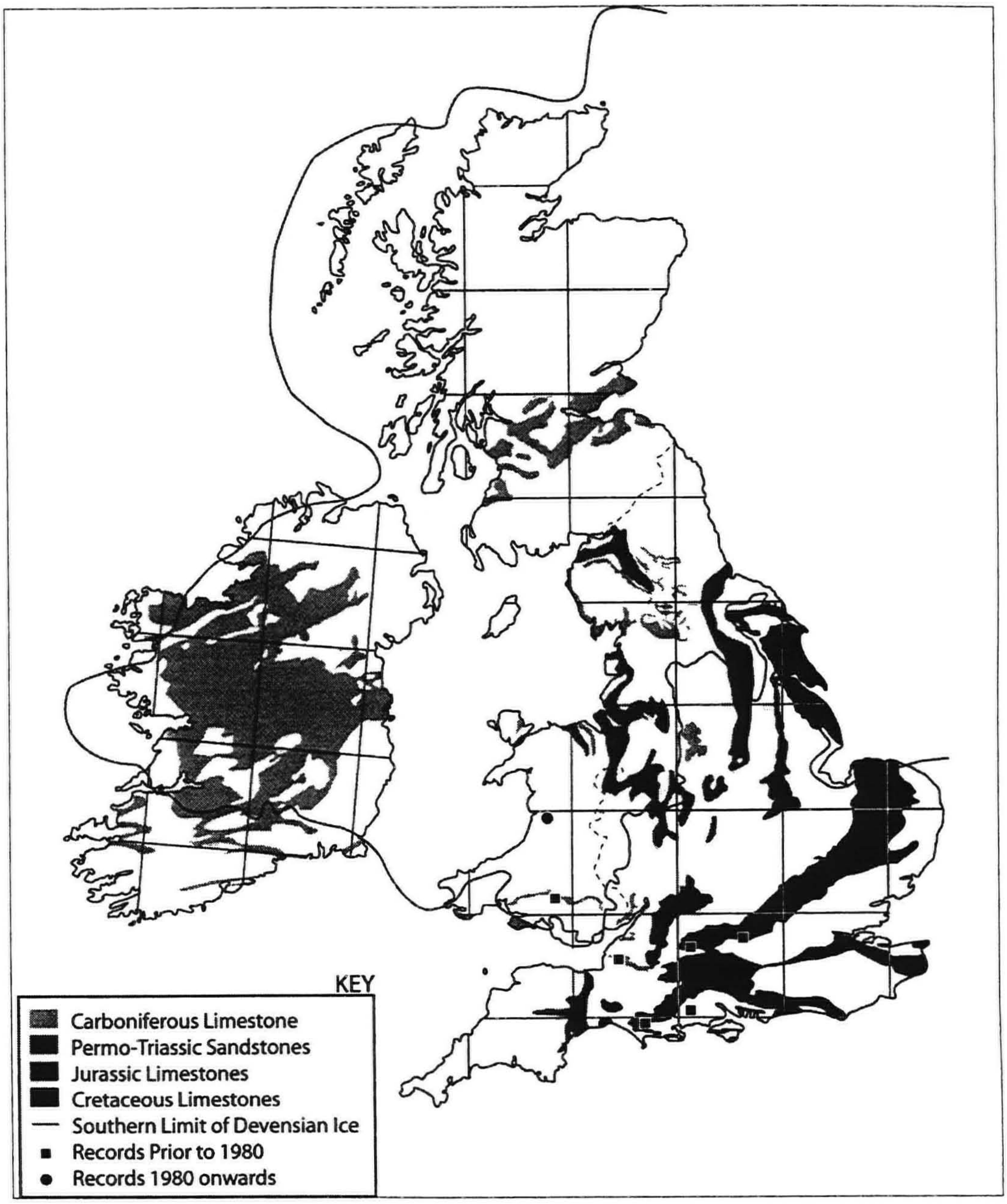
[A note on the generic name *Rivulogammarus*. In many of the records of *G pulex* published in the Biological Records (see above for references), and derived works (e.g. Dixon, 1974), the generic name used is *Rivulogammarus* rather than *Gammarus*. Stock (1969) has shown that *Rivulogammarus* is an invalid name and should not be used. More recent works (e.g. Moseley, 1997) also use this generic name and the same applies.]

ISOPODA

***Proasellus cavaticus* (Leydig, 1871) *sensu* Henry, 1971** (Figs 12, 13 and 14)

Originally recorded in Britain by Calman (1928), and described in

Figure 9. The distribution of Crangonyx subterraneus *by 10km squares.*



detail by Tattersall (1930), from a well at Ringwood (Hampshire) where it was discovered in 1925 by a Miss Lucas. Next recorded by Lowndes (1932a,b) in Pickwick Quarry, one of the Corsham Stone Quarries (Wiltshire). The first South Wales cave record was from Dan-yr-Ogof (Powys) in 1939 (Hazelton, 1955, p 9), and the first Mendip cave record from Swildons Hole (Somerset) in 1946 (Hazelton, 1956, p 7). There are 88 records of this species, collected from 35 sites in twenty-one 10km squares (16 squares from pre-1980 records, 5 squares from post-1980 records). The sites comprise 12 caves in South Wales, 8 caves in the Mendip Hills (Somerset), Otter Hole Cave near Chepstow (Monmouthshire) (Chapman, 1979), Spratts Barn Mine in Oxfordshire and 7 interstitial sites (Fig 14) Ormerod and Walters (1984) collected this species in an epigean stream in Breconshire, Wales It is possible, however, that it was washed out from a spring in the area. This is the most northerly record and is 50km north and west of the Devensian limit in this area Jefferson and Chapman (1979, p 9) recorded it from 12 sites in Ogof Ffynnon Ddu II (Powys) in South Wales and comment: *"Widespread and common in water films on flowstone, in shallow gour pools, under rocks in larger trickles Frequent where flowstone is covered with slimy brown (? bacterial) film Diet probably consists largely of filamentous bacteria/fungi."* Further details of the biology of this species are provided by Jefferson and Chapman (1979, pp.45–46).

Animals collected from the vadose zone of Mendip caves are about 4mm in length (Hazelton and Glennie, 1962; Jefferson, 1976), whereas those from the phreatic zone in Wookey Hole and the Cheddar River Cave are 8mm (Chapman, 1993, p.157) South Wales examples are also 8mm Chapman (1979) observed a large population in Otter Hole, which is situated between these two areas, and found that adults from this population were also 8mm. The Ringwood animals are also the larger morph. We do not know the size of animals from the easternmost record, at Wilmington near Dartford (Kent), as the Natural History Museum specimen has not been found Neither do we know the size of animals from Spratts Barn Mine (Oxfordshire) nor the Stone Quarries at Corsham, (Wiltshire). In continental Europe the maximum size of *P. cavaticus* is 8mm (Henry *et al.*, 1986). If the size difference is shown to be genetically controlled it may be considered that the Mendip population is a separate taxon If the smaller individuals are an ecotype it is hard to see why they are only found in one cave region. The origin and age of British *P. cavaticus* are discussed by Henry (1977). He suggests that colonization took place when sea levels were lower than today and the Thames was a tributary of a proto-Rhine. This species is also recorded from The Netherlands, Germany, Belgium, Switzerland, Austria and France (Henry, 1976), with the northern and western limits in Wales, the southern limit in the Alps and the eastern limit provided by the Hartz Mountains and the Danube. As in Britain it is found in karstic and non-karstic rocks and alluvial sediments.

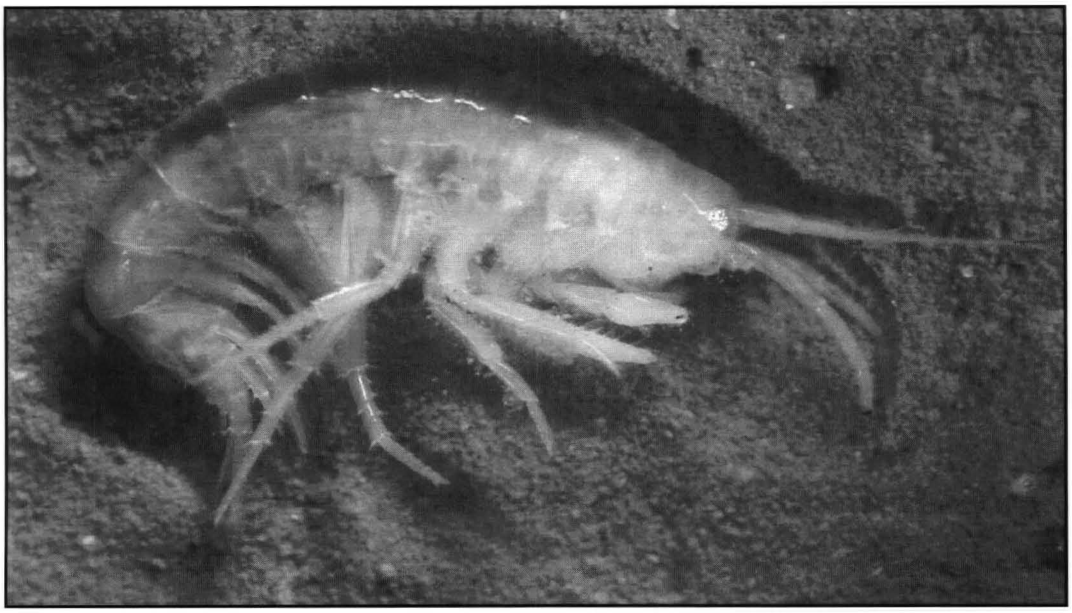


Figure 10 Depigmented and white eyed Gammarus pulex *Photograph by Phil Chapman.*

GEOLOGICAL, GEOMORPHOLOGICAL AND HISTORICAL EXPLANATIONS FOR THE DISTRIBUTION OF BRITISH SUBTERRANEAN CRUSTACEA

It is generally accepted that the British fauna is impoverished as a result of the last glaciation (named the Devensian in Great Britain, Midlandian in Ireland, Würm in the Alps, Weichselian in northern Europe and Wisconsinan in North America). At its maximum, between 25,000 and 15,000 years ago, the ice advanced south to cover most of Ireland, all of Wales and Scotland and northern and northwestern England (Fig.15). Central England and all of the southeast and southwest were ice-free but in these areas permafrost conditions would have prevailed It is usually assumed that the ice would have sterilized the environment beneath it and that the permafrost areas would be nearly as badly affected. Yalden (1999, p.23, p.25) explains that in the case of mammals *"South of the ice sheet was a very bare tundra with sparse vegetation and probably few animals ... Very few of the extant species could have survived such glacial conditions even in the extreme south of England or Ireland".* However, it is possible that small groundwater animals fared differently (see below). If the last ice age removed, or severely reduced, any pre-existing subterranean fauna, as is usually supposed, then the current populations must be descended from animals that arrived here from unglaciated areas. Alternatively, it is possible that some animals survived one or more stadials in particularly favourable areas (refugia). These two, not exclusive, possibilities are examined below.

Dispersal hypotheses - they walked back

If Britain and Ireland were totally sterilized by glacial and permafrost conditions, the current populations must have arrived here from unglaciated areas. It is likely that the majority of animals dispersed here from refugia in the south, particularly the Balkans (Hewitt, 1999, 2000; Rundle *et al.*, 2000, Bilton *et al.*, 1998, Taberlet *et al*, 1998). When the ice sheet was at its maximum, sea level was up to 100m lower than today and Britain was connected to mainland Europe, and for a time, the Thames, Scheldt, Maas and Rhine rivers were part of the same system (Gibbard, 1988). After the ice started to melt, sea level began to rise. Given that the English Channel formed between 15,000 – 9500 years ago, freshwater, obligate subterranean animals must have colonized Britain before this time. Of the 28 species of *Niphargus* recognized in France (Ginet, 1996) only three (*N aquilex*, *N fontanus* and *N kochianus kochianus*) reached Britain in post-Devensian times. Three other niphargid taxa, *N. glenniei* in Devon and Cornwall and *N. wexfordensis* and *N. kochianus irlandicus* in Ireland, are endemic and must have evolved from one or more of the other three species. How the Irish freshwater subterranean taxa colonized Ireland is far from clear. Yalden (1999) described a 100m-deep channel that separated Ireland from Great Britain and there is little evidence of the necessary land bridge to facilitate colonization. The postulated Inishowen (Northern Ireland) to Islay (Scotland) landbridge, which may have existed for 1200 years around 11,000 years ago, cannot be invoked as a colonization route for subterranean amphipods as it is unlikely they have ever occurred as far north as Islay to utilise it. The other potential colonization route centres on a mobile and northward moving landbridge caused by ice recession (see e.g Devoy, 1995 and Wingfield, 1995). This would almost certainly have been low-lying and possibly tidal. Other epigean freshwater taxa, such as the dytiscid water beetle *Hydroporus glabriusculus*, would also have required a land bridge to enter Ireland (Bilton, 1994). In common with this beetle, but perhaps even more pronounced, subterranean animals disperse via active dispersal (i.e by their own energy). Passive dispersal (i.e carried by some other animal(s) or by the wind) is almost impossible in the case of obligate hypogean species, though there may be a very slight chance for some coastal species living on pilgrimage and trading routes (see Bilton *et al.*, 2001 and Griffiths and Evans, 1995b for discussions of these mechanisms).

Refugial hypotheses - they never went away

If dispersal mechanisms cannot simply account for the present distribution patterns, perhaps a glacial refugial model can be invoked The known distribution of amphipods in England and Wales seems to parallel the ice margin of the last glacial maximum, suggesting that any pre-existing population north of that line were extirpated but that populations continued living to the south of it (Figs 2, 4, 5, 9, 14, 15). Some populations are now found in areas that were glaciated. There are two possible refuge types: those in unfrozen groundwater within the tundra (tundral refugia) and those in groundwater below the ice sheet (sub-glacial refugia).

Tundral refugia

There is a growing realisation that some cryptic refugia existed in glaciated areas. Stewart and Lister (2001, p.608) document some epigean examples and propose that they *"would have been in areas of sheltered topography that provided suitable stable microclimates".* Caves and other subterranean environments match this description perfectly Hanfling *et al.* (2002, p.1727) studied the epigean fish *Cottus gobio* (the bullhead) using microsatellite DNA markers and showed that *"bullhead populations most probably persisted throughout the last major glaciation within the British Isles.*

Such observations provide the first genetic evidence for a glacial refugium in such close proximity to the European glacial margins" (see also Volckaert *et al*, 2002) Groundwater habitats may have been relatively favourable locations for many taxa. They can exist at depth in rock formations and thereby benefit from geothermal warming, and this warming would be insulated by a

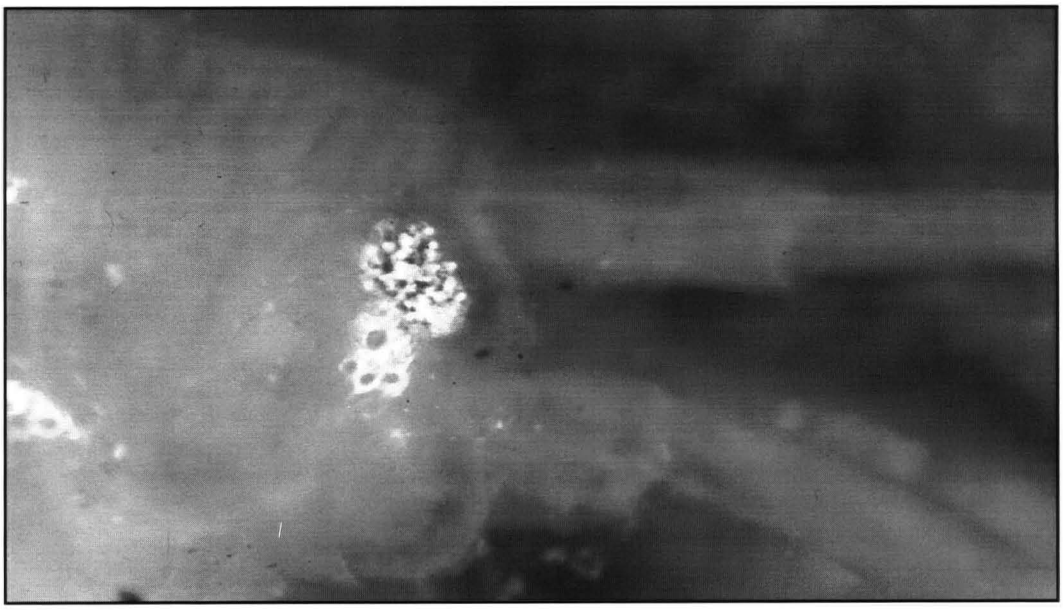


Figure 11. A close up view of the eye of the white eyed Gammarus pulex *Photograph by Phil Chapman.*

layer of snow or ice above it. If epigean fish and other animals managed to survive close to the ice then it seems reasonable to hypothesize that hypogean animals could exist in cave and groundwater habitats if sufficient energy resources (food) were available.

Sub glacial refugia

There is a mounting body of evidence that suggests that some terrestrial and aquatic species survived in refugia beneath the ice during the last glacial period. Holsinger (1978, 1980, 1981), Holsinger *et al.* (1983) and Koenemann and Holsinger (2001) provide good evidence for the survival of amphipod Crustacea at various glaciated sites in the northern USA and Canada. The most remarkable of these sites is Castleguard Cave, which is 500km north of the last glacial limit, and there are many others closer to the margin. This cave has been relict and ice-free for at least 700,000 years and may therefore have provided refugial conditions for much of the latter half of the Pleistocene when glacial conditions were most pronounced. A second stygobitic amphipod, *Stygobromus secundus* (Bousfield and Holsinger, 1981), and a troglobitic mite, *Robustocheles occulta* (Zacharda and Pugsley, 1988), are also found in these areas and support the hypothesis. Survival of groundwater taxa in sub-glacial refugia is reported by Strayer *et al.* (1994), who collected polychaet annelids and syncarid crustaceans from a spring outflow of a large aquifer well north of the glacial limit. Other examples from North America are provided by Lewis and Bowman (1981), Smith (1985) and Holsinger and Shaw (1987). In Europe, Christian (2002, p.264) collected Collembola from *"caves below the ice mantle* [which] *have obviously served as shelters for a number of arthropods two locally endemic* Pseudosinella *species [Collembola] are considered to have endured the last Würm glaciation in the large cave systems where they are found today, in spite of the ice cover"* Further support for sub-glacial refugia is reported by Fabel *et al* (2002, p.397) They record ancient landscape features persisting for up to 845,000 years and suggest that *"These relict areas also have significance as potential long-term subglacial biologic* [sic] *refugia".*

The distribution of *Niphargus fontanus* and *Proasellus cavaticus* suggests that these Crustacea may have survived beneath ice sheets in pre-existing caves. Both of these species are common in the North Crop limestone of South Wales, which was certainly covered by Devensian ice. Many of the caves in this area (e.g. Ogof Ffynnon Ddu, Dan Yr Ogof and the caves of Mynydd Llangattwg) are very old and were in existence long before Devensian times. Few absolute dates are known but one flowstone from Ogof Ffynnon Ddu II was deposited c 267,000 years ago (during the Hoxnian interglacial). Calculations of vadose entrenchment rates in the deep streamway of Ogof Ffynnon Ddu III suggest that this passage is 750,000 years old, and the cave system may have been developing for over a million years (Gascoyne *et al*, 1983; Smart and Christopher, 1989) The two size morphs (in Mendip and South Wales) of *Proasellus cavaticus* (see above) have some relevance here If they are separate taxa, i.e. the 4mm Mendip morph is apomorphic with respect to the 8mm morph found elsewhere, it is unlikely that the caves of South Wales were colonized from the unglaciated Mendip area once the ice retreated. This lends weight to the sub-glacial survival of the South Wales populations (Jefferson, 1976, p 414). Further debate requires some hard, probably DNA, evidence to ascertain the nature, and timing, of the 4mm/8mm dichotomy.

Sub-glacial refugia in non-karstic groundwater are also possible. There is some evidence that the base of large ice sheets melt into permeable and porous strata below them. For example, Boulton and Dobbie (1993), Boulton and Caban (1995), and Boulton *et al.* (1994, 1995, 1996) provide detailed discussions of groundwater recharge and flow below the Weichselian ice sheet in northeastern Europe.

The syncarid *Antrobathynella stammeri* is found in the Midland Valley of Scotland, in an area that is not only many hundreds of kilometres north of the Devensian limit, but was also subject to the Loch Lomond re-advance during the Younger Dryas c 11,000 years ago. It has also been recorded in the glaciated areas of Cumbria and the northern Pennines. If any species survived in sub-glacial refugia this is the best candidate. The Syncarida have little capacity for dispersal (Guil and Camacho, 2000) and therefore it seems unlikely that they colonized Scotland during the Holocene Other possible instances of syncarid survival in sub-glacial refugia are provided by Strayer *et al.* (1994, see above) and Shaw (pers. comm), who has collected syncarids from glaciated areas in western Canada. The distribution of *Niphargus kochianus irlandicus* (Fig.6) is also suggestive of sub-glacial survival, at least through the Nahanagan stadial (= Loch Lomond, = Younger Dryas) after colonization of Ireland during the Woodgrange (= Windermere) interstadial via a landbridge.

Any discussion of the long term survival of animals below ice must address the problem of energy resources (food supply). Downstream of the ice margin there is some possibility that plant material from the tundra vegetation entered groundwater habitats, although closer to it this is less likely. Until recently this was a major stumbling block for the sub-glacial refugia hypothesis. However, the discovery of several caves with proven autochthonous, chemoautotrophic, nutrient supplies (e.g. Kinkle and Kane, 2000; Sarbu, 2000) demonstrates that allochthonous supplies are not always required and that some organisms could have survived in sub-glacial refugia utilising autochthonous energy resources.

At present there is no consensus on which of these explanations, or combination of both, is correct. It is possible that elements of both hypotheses have resulted in the current distribution of subterranean Crustacea, although the mechanisms involved for different species may have varied.

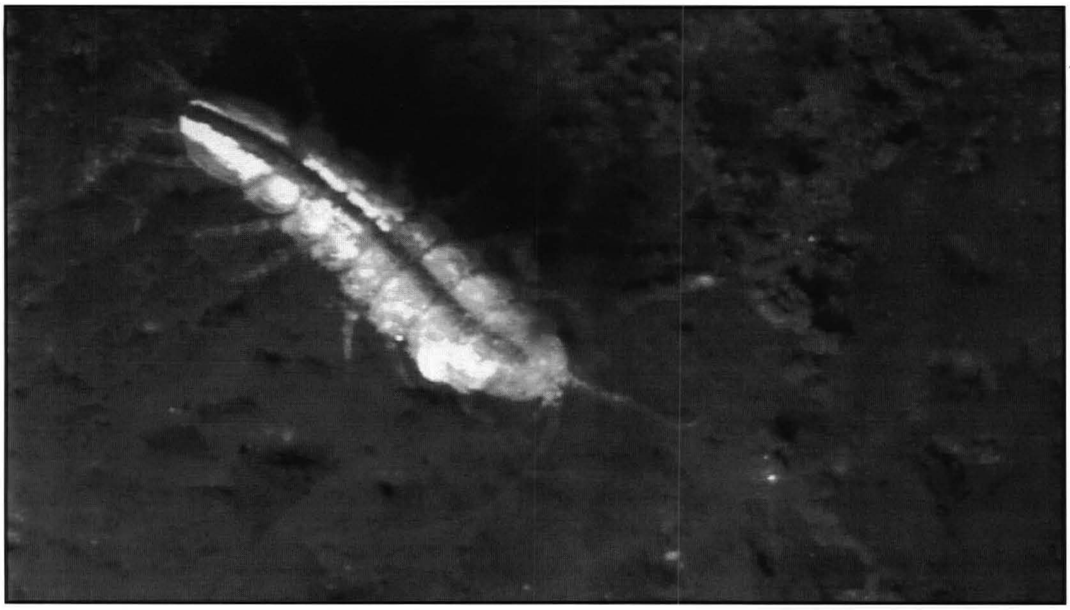


Figure 12. Proasellus cavaticus *on a flowstone wall in Ogof Ffynnon Ddu Photograph by Phil Chapman.*

DISCUSSION

Phylogeography. Relationships of British and Irish to European stygobitic Crustacea

The genus *Niphargus* is distributed throughout Europe and contains over 200 species (Karaman and Ruffo, 1986). Of these Britain and Ireland have two species found in Europe (*N. aquilex*, and *N. fontanus*) and four endemic taxa (*N. kochianus kochianus* [though Vonk (1988) and Ginet (1996) suggest that this taxon is also found in France], *N. glenniei* in Devon and Cornwall and *N. wexfordensis* and *N. kochianus irlandicus* in Ireland). In addition, the amphipod *Crangonyx subterraneus*, the isopod *Proasellus cavaticus* and the syncarid *Antrobathynella stammeri* have also been recorded in Britain and Ireland. These latter two species have unexplained distributional anomalies. In addition to understanding how these taxa arrived here we also need to know how and when the endemic taxa evolved Jefferson (1976) postulated a series of islands during a time of high sea level during the Tertiary. It is possible that *N. glenniei* colonized the Devon region before the sea level rise and then speciated once isolated by the sea. The Irish taxon *N. kochianus irlandicus* is considered a subspecies of *N. kochianus* on morphological grounds. However it seems very likely that it will have diverged genetically from the nominate subspecies, *kochianus kochianus*, and that it may merit full specific status once adequately studied. One such study, in France (Mathieu *et al*, 1997) identified major genetic divergences between populations of *N. rhenorhodanensis* despite geographical proximity and, in one case, hydrological connectivity between the populations studied. Taberlet *et al.* (1998) and Hewitt (1999, 2000) have clearly demonstrated that the Alps have been a major barrier to the northern dispersal of animals from refugia in Italy. Tabarlet *et al.* (1998) also demonstrate that Italian populations of some organisms are genetically distinct from conspecifics in other European areas. This then casts some doubt on the monophyly of Italian and other populations of *Niphargus aquilex* (Karaman, 1982). However, there is growing evidence that significant speciation took place during the Pliocene (see Taberlet *et al.* 1998) If this is correct the clades of *N. aquilex* are morphologically conservative (see Jarman and Elliott (2000) for a discussion of this in the Syncarida). The isopod *Proasellus cavaticus* has two size morphs, a small 4mm morph found only in the Mendip area, and a "normal" 8mm morph found in the rest of its range (including mainland Europe, Henry *et al.*, 1986). There is a suggestion that the Mendip morph is genetically distinct and may be a separate taxon. A study of *Proasellus* populations in Sardinia (Ketmaier *et al.*, 2001) revealed unexpectedly high levels of genetic divergence, and allowed recognition of genetically distinct taxa (probably species) currently subsumed under one name (*Proasellus coxalis*). The syncarid *Antrobathynella stammeri* has a disjunct distribution, being known from the south of England, the north of England and central Scotland. This is most probably a sampling artefact since this very small (0 5mm) animal has been very poorly studied Nonetheless the Scottish record is highly intriguing How this species relates to conspecifics in Europe is not known Jarman and Elliott (2000) demonstrated that Anaspidacean syncarids in Tasmania are morphologically similar while being very distinct genetically. They identified three cryptic species (and perhaps one cryptic genus) using mitochondrial DNA methods. If there is similar genetic distinction in Bathynellacean syncarids we can expect there to be many more taxa than we currently recognize (Proudlove and Wood, 2003). Only a detailed phylogeographic study, using mitochondrial or microsatellite DNA, will elucidate these relationships. Such a study is underway in Europe as part of the PASCALIS project (www.pascalis-project.org). This aims to characterize the groundwater fauna of Europe using many techniques and the phylogeography of *Niphargus* is one of its work packages. It is possible that molecular clock data, timing the divergence of the endemic Irish taxa (*N. kochianus irlandicus* and *N. wexfordensis*) from others, may even help to elucidate the timing of a land bridge between Great Britain and Ireland.

The need for further research

During the period 1938 – 1976, when the majority of the data presented here were collected, wells were still commonly in use and many were sampled by Glennie and others They provided a convenient random sample of otherwise inaccessible groundwaters. However, in the past two decades many wells have been filled in, or otherwise fallen into disrepair, and even where still extant they are no longer used or noticed. A modern survey would need to use as many wells as could be identified, together with samples from riverine gravel aquifers. An additional, and potentially very powerful, method would be to sample deep aquifers using the extensive array of groundwater monitoring wells and boreholes maintained by the Environment Agency. These are used principally for monitoring water depth and chemistry in potable water supplies from groundwater aquifers in several rock types. They would allow a stratified random sampling program to be devized and implemented. Details of these wells can be found at www nwl ac uk/ih/nrfa/ groundwater Additionally, it would be sensible to target specific areas that potentially contain suitable habitats but which currently have few or no known records Examples include:

- the North and South Downs and the Lincolnshire and Yorkshire Wolds (all Cretaceous limestone areas);
- the Jurassic limestones of the East Midlands and North Yorkshire;
- the Carboniferous limestones of North Wales and the Midland Valley of Scotland;
- the Permo-Triassic sandstones of the vales of York and Eden and those underlying Cheshire, and
- the Permian (Magnesian) limestones of Yorkshire and Durham

Fig.15 plots the distribution of 10km squares where any stygobitic Crustacea have been recorded Clearly there are many gaps that have never been sampled.

Figure 13. Proasellus cavaticus *feeding (?) on fungal hyphae in Otter Hole Photograph by Phil Chapman.*

Conservation

The UK has recently signed up to the EC Water Framework Directive, which means that it must implement many provisions for the improvement of water quality and the amelioration of pollution (e g Sutcliffe, 2001). Although for groundwaters there is no provision to sample fauna (only chemical and water level parameters are mandatory) it seems sensible to write into the UK protocols that, as well as chemistry, groundwater fauna, particularly stygobites, should be monitored. Not only would this provide additional quality data but it would allow a continuous assessment of the conservation status of these animals that spend their whole lives underground. We need to protect this hidden fauna just as much as many more prominent and well-known organisms. Several key sites that have provided a substantial number of the subterranean crustacean records may require special protection. These include:

1 ***The Old Town Well at Ringwood (Hampshire)***
This remarkable site is in the Hampshire Basin It is, or has been, the home to six stygobitic species, a unique occurrence (Amphipoda: *Niphargus aquilex*, *Niphargus fontanus*, *Niphargus kochianus*, *Crangonyx subterraneus*, Isopoda: *Proasellus cavaticus*, and Copepoda: *Acanthocyclops sensitivus*). Given this apparent richness it would be advisable to examine the Hampshire Basin in much more detail. It may be significant that this area escaped glaciation both during the Devensian and during the earlier and more widespread Anglian stadial. However, it seems that the well itself no longer exists.

2 ***The Waterston Experimental Station of the Freshwater Biological Association (the Waterston Cress Beds) (Dorset)***
Gledhill (1977) collected four stygobitic amphipods here on a regular basis for 5 years (*Niphargus aquilex*, *N. kochianus kochianus*, *N. fontanus* and *Crangonyx subterraneus*). During this study the otherwise rare *Crangonyx subterreaneus* was four times as common as *Niphargus fontanus*. This may support the hypothesis that the former is commoner in interstitial habitats whereas the latter prefers caves. In addition to these amphipods, there are several records of *Proasellus cavaticus* from this site and others in the vicinity. This site is now privately owned and known as Waterston Springs.

3 ***Holwell Cave (Somerset)***
This cave is notable for its records of *Niphargus kochianus kochianus* (in the Holy Spring, pH 8.5) (Hazelton 1960a, pp 9,10) and *Niphargus aquilex* in a muddy pool overflowing into the spring stream (vadose water, pH 6.7) (Hazelton 1960a, p.12; see also Glennie, 1967) *N. k. kochianus* is known from only three caves and *N. aquilex* from only 15, and both of these species are more common in interstitial and phreatic waters (see above). However, recently only *N. aquilex* has been recorded from this site (LK personal observations).

4 ***Afton Red Rift (Devon)***
Both the endemic *Niphargus glenniei* and *N. aquilex* have been collected from this cave in Devon (Hazelton 1972, p 226) The latter species was abundant and was observed on the surface of a pool eating Collembola. In recent observations *N. aquilex* was less common than *N. glenniei* and the latter species maintains a permanent cave population in gour pools supplied with detritus (LK personal observations). These two species have also been observed together in Rift Cave, Bunkers Hole and Pridhamsleigh Cavern

5. ***Pen Park Hole (Bristol)***
The lake in this cave contains both *Niphargus fontanus* and *N. kochianus kochianus*, the latter in great abundance (Glennie, 1963). This lake is part of a large body of phreatic groundwater that rises and falls, though the timing and magnitude of this is not understood. This site requires both protection and further research.

It is important to stress that three (possibly four) of the taxa considered here are endemic taxa *N. glenniei* is known only from England and *N. wexfordensis* only from Ireland. The Irish subspecies *N. kochianus irlandicus*, is endemic to Ireland, and is probably an independent species. The English subspecies *N. kochianus kochianus*, is reported also from the Aquitane basin in France (Vonk, 1988) but it seems likely that the English and French taxa will be found to be independent once sufficiently studied Great Britain and Ireland have very few endemic taxa and it is important to highlight their status. Perhaps they could function as keystone species in conservation assessments and thus provide overall protection to many other species.

The data on which this review is based were largely collected before 1980 and it is certainly time for a systematic nationwide re-survey, both to discover unknown populations (and species ?) and to assess the current status of those reported here However, any sampling scheme must be designed and implemented with regard for the principles of conservation. Minimal impact methods are recommended, so as to cause as little disturbance as possible to the subterranean environment and the organisms it supports.

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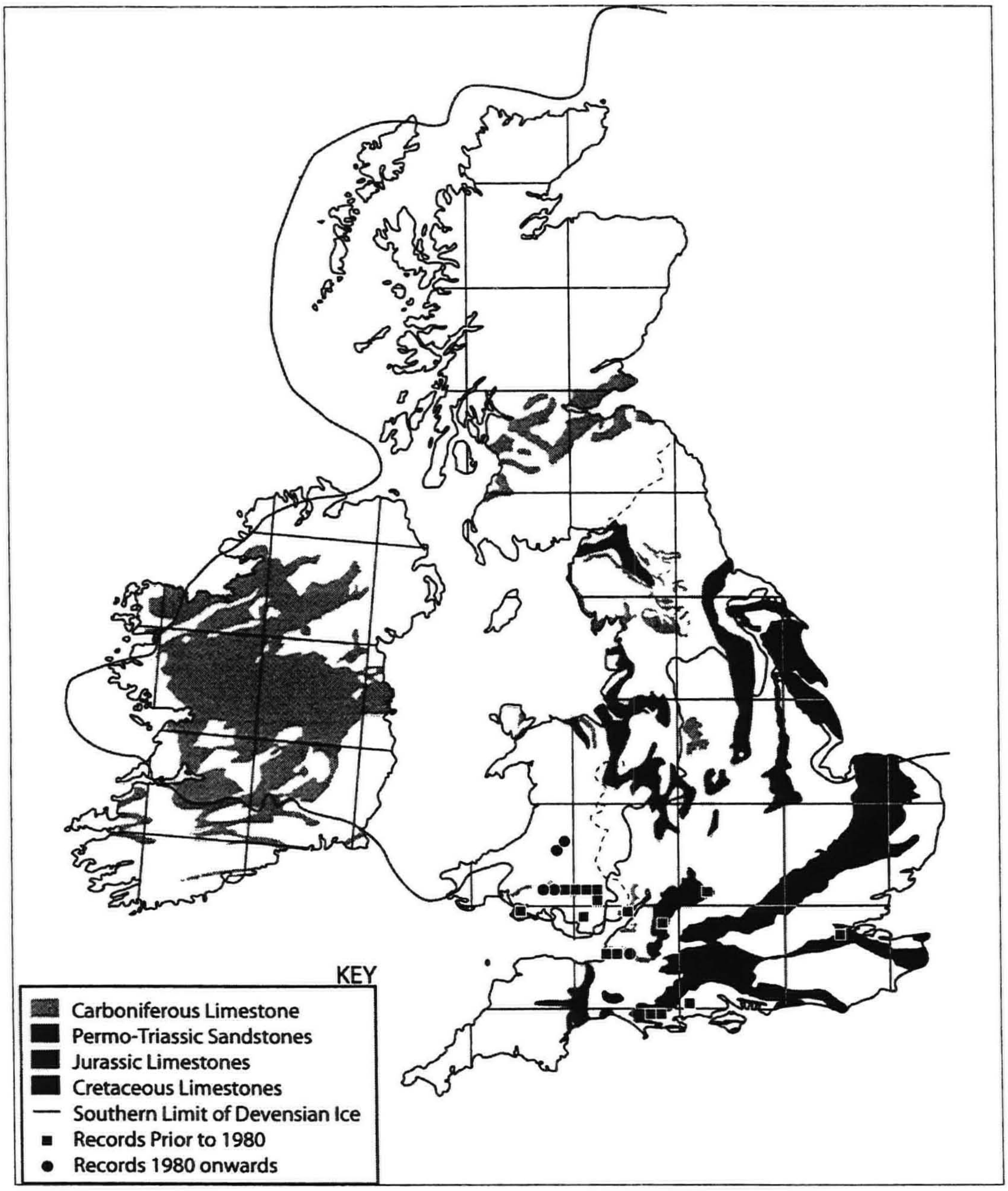

Figure 14. The distribution of Proasellus cavaticus *by 10km squares.*

their loan to GSP. John Bishop of the Marine Biological Association searched, in vain, for the Spooner material. John Holsinger provided valuable comments on an earlier version of the text.

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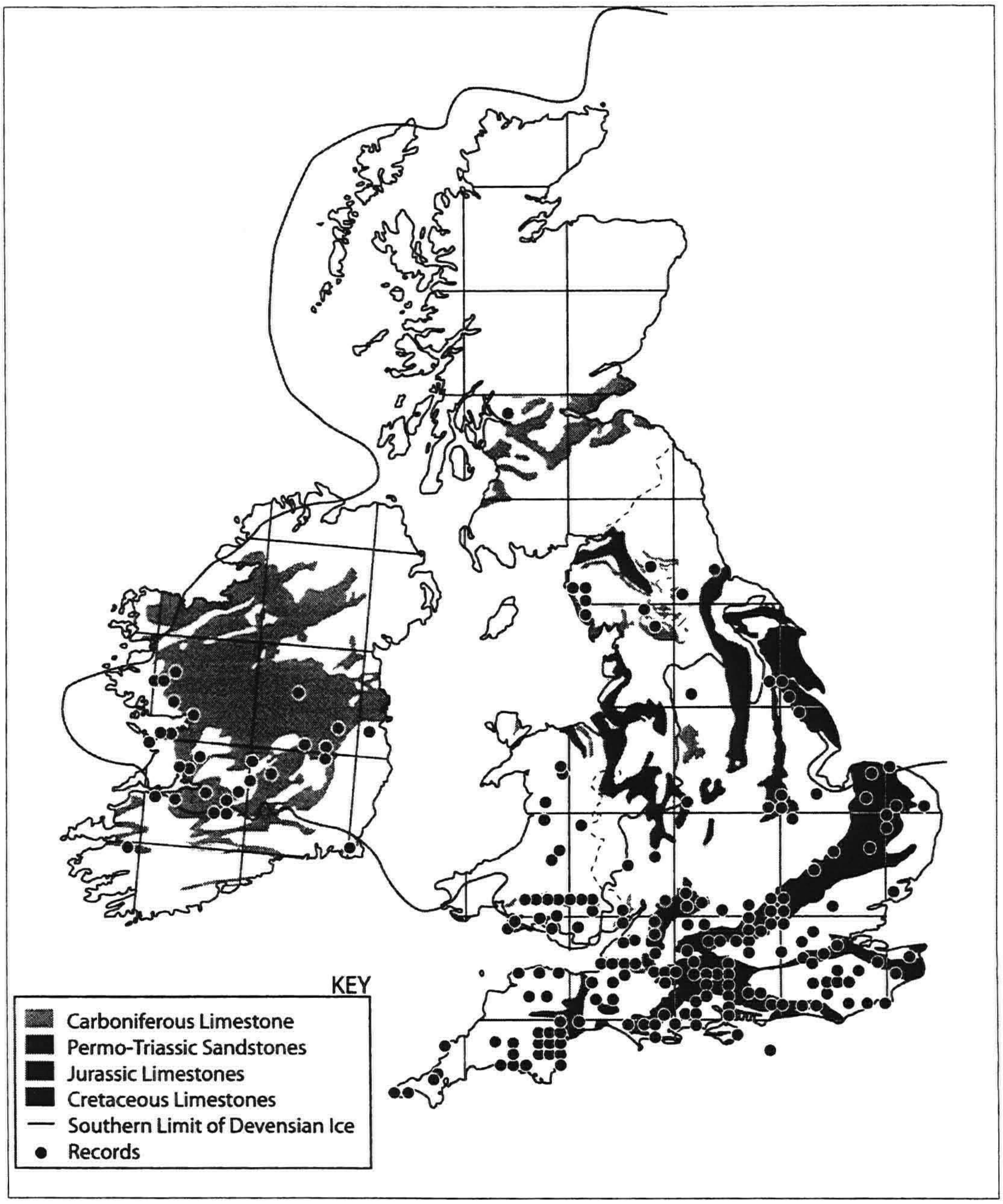
Figure 15. Total records of all stygobitic Crustacea (by 10km squares) to show coverage. There are many gaps where no recording has taken place.



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An archaeological study on the extraction of flowstone from caves and rockshelters for producing stone money in Western Micronesia.

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Abstract:For centuries, Yapese Islanders in western Micronesia traveled 400km south to the Palauan archipelago to carve their famous stone money from speleothem found in caves and rockshelters. Ethnohistorical accounts and oral traditions provide some information regarding the manufacture of stone money, but a lack of archaeological data has prevented a better understanding of how limestone was quarried, the residuals from carving stone money, and the mineralogical composition of carbonates used in production. In this paper, the first archaeological evidence for speleothem quarrying in Palau by the Yapese is presented. Macroscopic and mineralogical analysis of speleothem debitage and stone money disks indicate that 1) the material quarried was culturally produced and not natural detritus, and 2) it was calcite and not any other material type commonly cited by historians and archaeologists.

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INTRODUCTION

For archaeologists, stone represents some of the most visible traces of human settlement and interaction (Ayres, 1998). In the Pacific, native islanders are well known for having exploited a wide variety of stone resources for making objects, tools, residential structures and ceremonial statues such as the famous "moai" of Easter Island. Frequently documented rock types include obsidian in Melanesia (White, 1996), basalt in Polynesia (Clark, 1993; Weisler, 1993, 1998; Weisler *et al.*, 1994), and various volcanic glasses (Weisler, 1990; Clark and Wright, 1995). The analysis of these stone resources has significantly improved our understanding of tool manufacture, political relationships, village organization, trade and exchange systems, and the rise of social complexity, among other social processes (e.g. Kirch, 1990; Baker, 1993; Green, 1996).

The use of limestone by Pacific Islanders for producing tools, objects or structures, however, is rare. In the Marianas (Micronesia), columns and capstones called *latte* were quarried from upraised reef limestone and used for supporting house structures as early as AD 1000 (Kirch, 2000, p.184-86). In Tonga, limestone slabs and beachrock blocks (sand and beach debris cemented by calcium carbonate) were used as chiefly backrests and sitting platforms, in certain earthen and burial mounds, and to define the perimeter of monumental features (Sand and Valentin, 1991; Burley, 1998; Kirch, 2000, p.227–228). Beachrock was an exotic resource that was transported between islands and used by peoples within the Tongan archipelago (Burley, 1993). But one of the only other instances of native Pacific Islanders manipulating carbonate rock, and the only example of the finished product being quarried and transported to another island by a culturally and linguistically distinct group, is the Yapese quarrying of their famous stone money in the Palauan archipelago of western Micronesia.

The characteristics of stone money and reasons surrounding its use are described first. The mineralogical characteristics of carbonate materials and the geological context of the limestone islands in Palau are then reviewed. Archaeological research at stone money quarry sites since 1999 puts into context the extent to which the Yapese quarried limestone and how lithic debitage found at quarries is the result of quarrying activities, not natural karst formation processes. I then discuss the first examination of carbonate materials used in stone money production, indicating that other researchers previously misidentified the mineralogy.

Figure 1. A stone money disk (Feature 1) at the Metuker ra Bisech site in Palau. This disk weighs in excess of 7.6 metric tons and was apparently abandoned after it broke during transport (note broken edge in foreground).

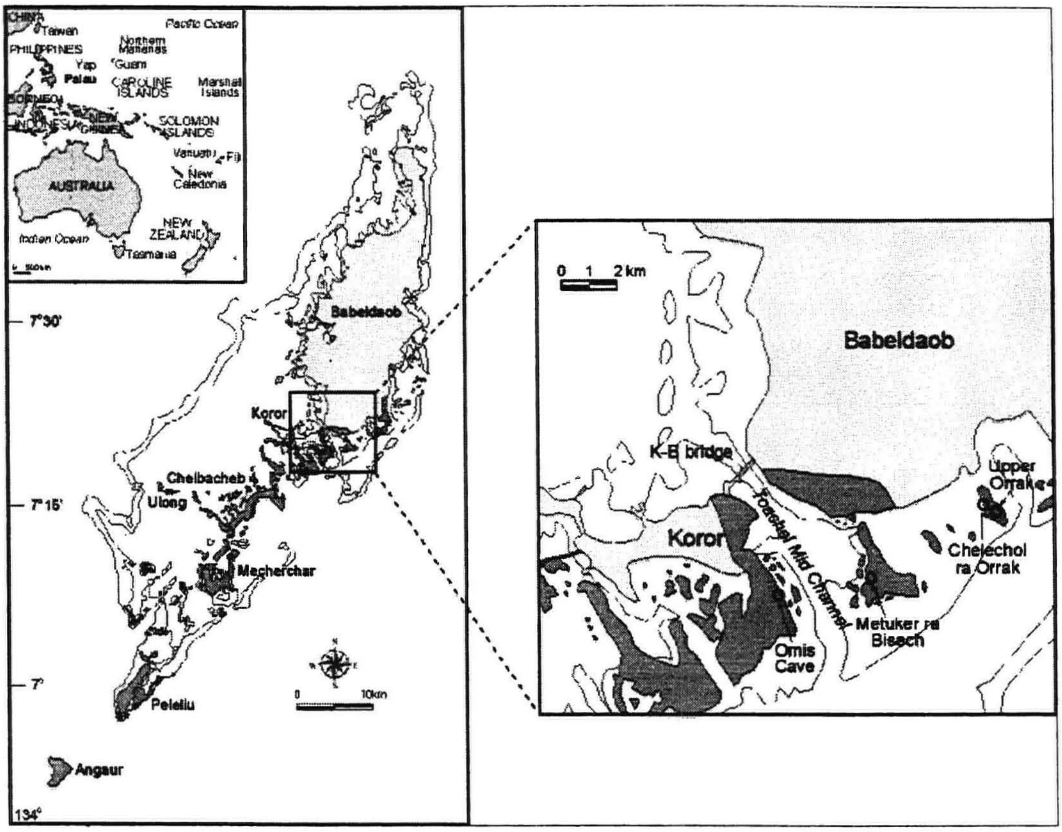

Figure 2. Map of the main Palauan archipelago with inset of sites investigated in this study. Neogene limestone (shaded) unconformably overlies the eroded Paleogene stratocone of Babeldaob (running NNE-SSW through the centre of the island) and neighbouring islets. The Rock Islands south of Babeldaob (Chelbacheb, Mecherchar, and associated island clusters) are remnants of subsided karsted limestone. Peleliu and Anguar are a result of annular accretion of uplifted limestone terraces (see Corwin et al., 1956; Fitzpatrick et al., 2003 for further descriptions).

Ultimately, I add a previously undocumented archaeological dimension to the carving of limestone by Pacific Islanders. This investigation allows for the development of methodologies for investigating other limestone quarries in the Palauan archipelago and is a critical step for documenting how and why the quarrying of stone money took place.

YAPESE STONE MONEY QUARRYING

The quarrying of stone money by Yapese Islanders in western Micronesia is one of the most archaeologically dramatic, but least understood instances of "portable" artifact exchange in the Pacific (Fitzpatrick, 2003). Stone money disks (also referred to as *rai* or *fei* by the Yapese and *balang* in Palauan) up to 4.5m in diameter and weighing over nine metric tons, were carved almost exclusively from the many natural limestone caves around the Palauan archipelago and transported by ocean-going canoes or European trading ships sailing back to Yap Island almost 400km away (Fig.1).

Oral history and ethnohistorical accounts report that the Yapese traveled to Palau in canoes, and carved disks of stone inside limestone caves by splitting off rock slabs using fire and shell adzes. Le Hunte (1883, p.25) noted in his report that he found "*no less than a hundred Yap natives at Pelew*" (Palau) occupied in cutting these stones and preparing them for transport. They then drilled a hole in the center using a reef stone with a fire drill (de Beauclair, 1971, p 188). The stone money was then moved by placing timbers through a hole in the centre of the disk and transported back to Yap on rafts, canoes, or ships. "*Many exceeded six feet in diameter and were proportionally thick, having a large hole in the centre through which a log of wood is passed and this when laid across two canoes is sufficient to support the stone in transit*" (LeHunte, 1883, p.25).

Palauan oral traditions suggest that the Yapese had access only to those quarries that were under the control of specific Palauan villages with which they had some affiliation. They were able to arrange this access with gifts of exotic foodstuffs, glass beads (Florencio Gibbons, 1998, pers. comm.), which were part of the standard Palauan "monetary" system (de Beauclair, 1963; Smith, 1997), and other valuables such as shanks of sennit cord made from coconut husk.

Einzig (1966, p.37) reported that the scarcity (non-indigenous to Yap), cost of production (i.e., Yapese labour and tribute to Palauans), and risk (heavy loads transported overseas) all influenced the value of stone money and that it also "*...depends largely on its size measured in spans, which in Yap means the stretch of the index finger and thumb.*" Whether this last statement was true prior to European contact is unknown, although it is clear that size was one factor in determining value. De Beauclair (1971, p.187) noted that "*a piece of stone money is valued according to its material, size, shape, history, and mode of transportation.*" In general, the evidence suggests that the final worth of a stone money disk was determined by a combination of scarcity, shape, size, quality, effort expended (i. e., lives lost, amount of labour, and risk involved), and method of transport.

Stone money today is still considered valuable and used as a medium for exchange in Yap, although the disks themselves are not always moved; only ownership may be transferred. Disks are often placed in front of stone platforms (*dayif*), young men's houses (*faluw*), community meeting houses (*pebaey*), or along trails (see Hunter-Anderson, 1983, pp.45–47, 50, 58). "*Transactions using stone money were, and are today to some degree, connected with almost every phase of social life*" and it is important to note that exchanges involving pieces of rai are always given from the mother's side (de Beauclair, 1971, p.196).

The production of these exotic valuables is known, in part, from European explorers who participated in the transport of the disks back to Yap in the 1800s (Tetens, 1958, p.12; Hezel, 1983). A rich collection of ethnographical data and oral traditions suggests that stone money manufacture took place prior to European contact (de Beauclair, 1971; Gillilland, 1975). This makes these megaliths the heaviest portable objects ever moved over open ocean by Pacific Islanders. Radiocarbon dates from stratified deposits at quarry sites support the oral history and ethnohistorical accounts, suggesting that stone money manufacture was taking place prior to European contact, perhaps as early as 600 years ago (Fitzpatrick, 2002, 2003).

According to oral traditions, ethnohistorical accounts, and archaeological investigations in Palau (Fitzpatrick 2001, 2003), the sequence of manufacturing a stone money disk involved several stages, probably not dissimilar to those used by other stone carvers worldwide. These included the following:

1 **Selection** – After obtaining quarrying rights from Palauan chiefs, Yapese quarry workers searched for and located flowstone deposits in the Rock Islands. Large speleothems could be found in the many caves and rockshelters on the coast or in the interior valleys of the limestone islands prevalent throughout the Palauan archipelago.

2 **Preform carving** ("roughing out") – After a suitable deposit of flowstone was chosen, the general shape was "roughed out." The Yapese did not split speleothems into workable blocks and move them to other areas for finer carving. Stone money found at Omis Cave (Feature 1; Fitzpatrick, 2001), Metuker ra Bisech (Feature 2; Fitzpatrick, 2002), and Chelechol ra Orrak (Feature 1; Fitzpatrick, 2003) suggest that the disk's general shape was carved from the deposit *in situ*. The first stages of shaping a preform were probably done with picks, hammers or hammerstones, axes, and wedges used as pitching tools for breaking off edges. Iron tools such as an iron pick and axe found at Metuker ra Bisech (Fitzpatrick 2003) would have been ideal for this first stage of carving.

3 **Detailed carving** – As the desired shape of a stone money disk emerged, gouges or chisels were probably used to create a flat and relatively smooth surface. This could have been achieved by working from the top down, or by making parallel grooves and striking them with a point chisel to remove smaller sections of stone one at a time. Tool markings on unfinished stone money disks at Metuker ra Bisech (Feature 2) and Chelechol ra Orrak (Feature 1) indicate this stage took place even before the disk had been separated from the limestone deposit (Fitzpatrick, 2003).

4 **Abrasion or flattening** – After the shape of the disk was complete, the surface was then abraded or "flattened," using a chisel made from shell, stone, or iron.

5 **Perforation** – Once the disk was nearly complete, it was perforated through the centre using a reef (coral) stone and a fire drill (de Beauclair, 1971, p.188) before iron tools came into use during the historical period. Stone money disks found at Omis Cave and Chelechol ra Orrak (Fitzpatrick, 2001, 2003) suggest that they were removed from the flowstone deposit and propped against a wall or mound of rocks prior to perforation.

6 **Polishing** – The final stage of stone money production was the polishing of the stone using an abrader, perhaps in conjunction with water. According to oral traditions, prior to European contact this was done using pumice, although it is likely that other materials such as sand were used; during historical times wire brushes or scrubbers, sand, and/or whet stones may have replaced these traditional techniques. Examples of stone money from Metuker ra Bisech indicate that the Yapese were able to overcome the crumbly nature of the stone and polish even larger crystal facets to a smooth finish (Fitzpatrick, 2003).

Multiple data sources provide important clues into how stone money was manufactured. Questions still remain, however, as to the exact material used for producing stone money, why certain locations were chosen for quarrying, and the ability of Yapese carvers to shape limestone.

GEOGRAPHICAL SETTING

Palau is located in the Western Caroline Islands, roughly 600km equidistant from the Philippines to the west and Irian Jaya to the south (Fig.2). The main archipelago is situated at 7° 30' north of the equator, 134° 30' east, and is over 160km long, 25km across, and oriented in a northeast–southwest direction. The Palauan archipelago is a remnant of the highest peaks of the Kyushu Range that stretches from Japan to New Guinea. The West Caroline Ridge extends north to south and curves southwestward through Yap and Ngulu Atoll toward the Palau Islands. The Palau Ridge is the southwesternmost of a series of long submarine ridges separating the basins of the Pacific Ocean and the Philippine Sea (Corwin *et al.*, 1956). This ridge extends from Kyushu southward as a broad upwarp surmounted elsewhere only by Parece Vela Reef, but which becomes ridge-like near the Palau Islands and curves southwestward. The ridge and the trench comprise the Palau Arc.

The several hundred islands in Palau are comprised of four major geological formations: volcanic, coral reef and atoll, low platform limestone, and high limestone. These islands form a land area of almost 400km^2. Volcanic islands comprise about 80% of Palau and

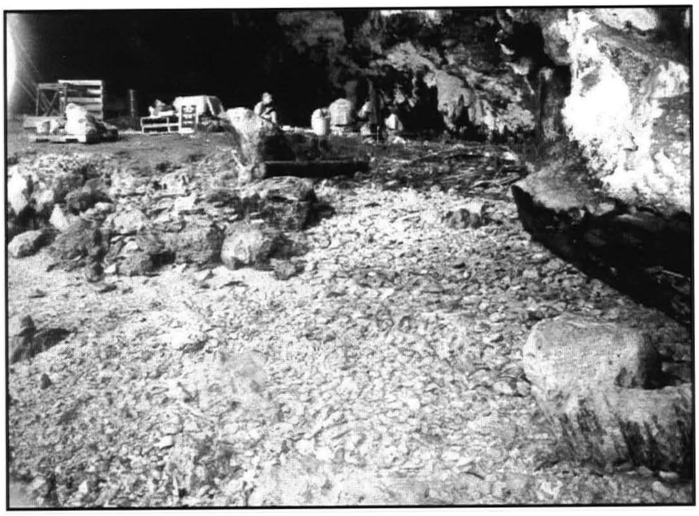

Figure 3. Limestone debitage refuse on the beach and at the entrance to Omis Cave (note people in background).

include Babeldaob, Meiuns, Malakal, and the western portion of Koror (Babeldaob is the largest, more than 330km^2 in area). Kayangel and Ngaruangel are small atolls north of Babeldaob (Corwin *et al.*, 1956). The Southwest Islands, a political addition to the Republic, but linguistically and culturally distinct, are comprised of low platform islands and atolls, while Peleliu and Angaur are considered low platforms. The karstic "Rock Islands," as they are known locally, are the most abundant island type and extend 30 kilometers in length primarily between Peleliu and Koror. The major formations include Ngemelis, Ngerkersil, Ngeruchubtang, Ngaretelin, and Ngerechong, nearly all of which contain caves and rockshelters with speleothem formations.

Sites where the Yapese quarried their stone money are all in island localities where valley margins have eroded back to intersect former underground caverns or where karstic springs and subterranean streams emerge. Three of the four quarries researched (Metuker ra Bisech, Chelechol ra Orrak and Upper Orrak; see inset Figure 2), are found within small valleys where several caves, rockshelters and/or overhangs contain large dripstone and flowstone formations. Such sites are ideal for habitation and for production of large quantities of stone money disks (Omis Cave, the fourth site, is a small coastal cave). It is important to note that there is no evidence that the karstic bedrock was ever used for producing stone money. Because of its jagged nature and non-malleability, the bedrock would have been highly unsuitable for carving. However, smaller chunks of karstic bedrock were often used for building stone architectural features at quarry sites (Fitzpatrick, 2001, 2003).

Of the four stone money quarry sites investigated, Omis Cave and Metuker ra Bisech are the most well known and have the best evidence collected thus far for intensive quarrying activity. Omis Cave is located in the Rock Islands north of Koror Island, the main government and commercial centre in Palau. The site is approximately 3km south of the Koror-Babeldaob "Friendship" bridge, oval in plan view, and 780m^2 in size. A large speleothem outcrop runs north-south along the eastern portion of the cave. A shallow pool lies directly below the outcrop and contains an abundant amount of refuse material including pottery and limestone debitage. Three stone money disks were recorded at the site in 1999 along with several stone architectural features (Fitzpatrick, 2001).

Metuker ra Bisech is a large inland site about 4km across the Toachel Mid Channel from Omis Cave in Airai State. Surface survey indicates that it is quite large (~2,500–3,000m^2), although the exact site boundaries have not been fully determined. The site has extensive architectural features including stone platforms, walls/ alignments, and mounds made from coral and limestone rock. One finished and two unfinished stone money disks were recorded in 2000. Another finished disk was located during survey near the site, but away from the main quarry area.

During excavations at these sites, a substantial amount of flowstone fragments was recovered. A major research question was whether these fragments were in fact a result of Yapese quarrying of

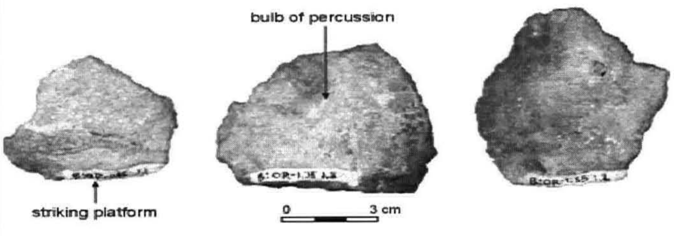

Figure 4. Limestone debitage flakes recovered from Omis Cave.

the speleothem deposits or if they were natural detritus. Another question was whether there where any differences in the quality of limestone chosen by Yapese carvers that would suggest why these quarries might have been chosen over others? Some of the mineralogical characteristics of speleothems, macroscopic examination of the fragments, and the natural processes that could potentially affect interpretation of lithic specimens are examined below to help answer these questions.

SPELEOTHEM EXPLOITATION

Why was carbonate rock from Palauan caves preferred by the Yapese for constructing stone money disks? Along with the lack of limestone in Yap, the risk and labour associated with traveling to Palau and back, colour, translucency, and the greater malleability of carbonate minerals compared to other rock types (e.g. basalt, andesite) were all probably important factors (Gillilland, 1978; Fitzpatrick, 2003). It is important to be able to determine differences in the mechanical and mineralogical properties of carbonate material from various quarries, which help in determining intra- and inter-source compositional variation and establishing the exact nature of the stone used. Of particular interest was examining whether there were mineralogical differences in the carbonate minerals that the Yapese exploited for stone money quarrying. If so, was this a conscious effort or was stone money produced from carbonates regardless of their true mineralogical composition?

One of the many advantages of working in stone money quarries is that the excellent preservation of artifactual and ecofactual remains in the protected and carbonate environment is conducive for examining and interpreting quarry activities. However, as in other depositional settings, many sedimentary processes are involved in creating the materials that fill the caves or rockshelters (e.g., bioturbation from crabs, aeolian deposition, rock fall, solution deposits, and human-induced impacts). Despite the complex sedimentary processes, archaeological excavation suggests that it is possible to analyze quarrying production processes in these sites by carefully recording the stratigraphy and closely examining stone money disks and surrounding speleothem deposits for tool markings and breakage patterns.

The abundance of speleothem fragments observed on the surface and in excavation at quarry sites presented some interesting questions. Were these fragments natural detritus or remains from quarrying activity, and were the speleothems calcite or aragonite, the two minerals most commonly described by other researchers as being the material stone money was carved from? Answering these questions can be accomplished by examining the physical properties of speleothems (e.g. rock strength, hardness), the processes by which

Test Unit	size	depth (cmbs)	volume (m^3)	debitage	density measure
1	2.0 m x 1.0 m	40 cm	0.80	1,858	2.32
2	2.0 m x 1.0 m	60 cm	1.20	3,599	2.99
3	1.0 m x 0.6 m	70 cm	0.42	1,662	3.96
Total	---	---	2.42	7,119	---

Table 1. Test unit data from Omis Cave.

natural cave breakdown occurs, close inspection of speleothem fragments found in association with stone money quarrying (e.g. disks, tools), and analyzing the samples using both X-Ray Diffraction and thin-section petrography.

On the Mohs relative hardness scale commonly used by geologists for basic field description (where talc = 1, quartz = 7, diamond = 10), calcite is 3.0 and aragonite is 3.5 to 4.0. It should also be noted that calcite is geologically considered to fracture in a "brittle-conchoidal" way, i.e. with fractures that produce very small, conchoidal fractures. Aragonite is considered to fracture in a "sub-conchoidal" way and to be brittle, characterized by semi-curving fracture surfaces (Jennings, 1985). When taking samples for analysis at Omis Cave, it was clear that the flowstone was fine-grained. It was possible to break chunks off from speleothems with just a few blows from a hammer, especially if a narrow crevice was gouged and the loose rock pried away. To obtain samples from a stone money disk at Metuker ra Bisech, pieces only needed to be pried off with a knife. This suggested that there was a significant difference in the mineralogical properties of speleothems between these sites, the rock in general could easily be manipulated, and that it was generally friable. These and other field observations including macroscopic identification, indicated that there was a wide range in the mineralogical characteristics of speleothems at these sites and that they were soft and structurally weak. But, just because the rock appeared suitable for breaking and carving, was it still possible that the rock fragments found at quarry sites were a result of natural causes? To determine the differences in speleothems between sites in more detail, carbonate samples from Omis Cave, Metuker ra Bisech, and Chelechol ra Orrak were examined for evidence of purposeful flaking, breaking, and other culturally related effects.

Speleothem fragments: natural detritus or culturally produced?

Rockfalls, block slides, and rock slides are common occurrences in karst environments because soils are usually thin, the rock is soft and erodes readily, dissolution occurs both vertically and laterally, and streams effectively undercut slopes (Jennings, 1985, p.28). There are also permanent stresses on the rock – gravity, tectonics, and the load of overlying rocks (lithostatic load; Jennings, 1985, p.28). All of these features in karst terrain serve to open up joints in the rock, induce rockfall, and cause cave roof collapse. Of these natural processes, could any of them have created the masses of rock fragments found at stone money quarry sites?

Cavern breakdown, or the *"detachment of masses of rock of various sizes from the roof and walls of a cave,"* is usually angular in nature (White and White, 1969; Warwick, 1976, p.92) and produces a rough jumble of fragments that are unsorted and highly permeable (White, 1988, p.229). White and White (1969) classified these "breakdowns" into *block breakdown* (masses of rock fragments consisting of more than one bed that remain as a coherent unit), *slab breakdown* (fragments of a single mass), and *chip breakdown* (rock fragments from the disintegration of a unit; see Warwick [1976, p.93] and White [1988, p.229-231]). Warwick (1976, p.92) noted that fresh rockfalls in Britain, for example, were rare, although large piles of blocks could be found, many of which were cemented together with flowstone. Breakdown talus piles, which can range from scattered slabs of bedrock to "mountains" tens of metres high, also can occur, albeit infrequently (White, 1988, p.236).

In general, although rockfall and cavern breakdown are known to occur in Palau (personal observation), this does not explain the masses of smaller chips, flakes, and chunks commonly found on the surface and in excavation units of Yapese stone money quarries (see Fig.3). Surface remains of rock fragments were covered in a greenish-black coating of coralline algal growth, guano, and other sediment (usually on one side only), whereas those found in excavation were typically characterized by a lack of this growth and were a shiny, milky yellowish-white. Because the use of speleothems as a raw material is not well documented in the Pacific or elsewhere, this presented an obstacle for identification and classification. Not only was there a lack of references for comparison, but the crystalline stone when flaked, did not appear to show the clear morphological characteristics typical of other rock types like obsidian or basalt (e.g., striking platforms and bulbs of percussion). Nevertheless, with careful observation of surface and excavated limestone fragments, it became apparent that they were not natural, but were caused by human activities and that standard lithic categories could be applied to these specimens because: 1) they were found in concentrated masses adjacent to stone money disks, both on the surface and in excavation (this was found at every Palauan cave where the Yapese quarried stone money and absent where they did not (Masse, 1989; personal observations); 2) the majority consisted of smaller flakes and chunks (≤ 3-6cm in length), atypical of other rocks at the sites which were from natural cavern breakdown; 3) subsurface material was frequently characterized by a lack of surface coloration (from coralline algae growth, guano deposition, etc.) which would not be expected if occasional rockfall had occurred and remained stationary on the surface for a period of time; masses of smaller rock chips building up over time would have protected them from other wind-blown or natural deposits; 4) there was evidence of tool marks on numerous flakes and chunks (Clifford Ambers, pers. comm. 1998; personal observation); 5) gouge marks from purposeful chipping were present on the surface of flowstone deposits and unfinished stone money disks; and 6) "flakes", although mineralogically coarse compared to other rock types commonly used for producing tools in the Pacific and elsewhere, exhibited some of the same morphological characteristics as these rock types including striking platforms, bulbs of percussion, and cortex.

Speleothem fragments typically ranged from about 3 to 10cm in length, but it should be noted that thousands of smaller chips (flakes and chunks <2cm) were also found, but not quantified; however, bulk samples were collected for comparison. "Flake" specimens were usually semi-triangular or sub-rectangular in shape and had a rough bulb of percussion and striking platform (Fig.4). Specimens separated into "chunks" did not exhibit these characteristics, although many had surfaces that were pecked or chipped. Because the speleothems were relatively crumbly, areas struck by a tool could easily be seen where crystals were crushed from a striking blow (Clifford Ambers, pers. comm. 1998).

Debitage was classified typologically by the presence of "cortex." Cortex on speleothems is the exterior or skin of a dripstone or flowstone formation in which a fresh deposit of calcium carbonate comes into contact with the existing crystal structure of the solid, usually forming a smooth surface with no visible crystal terminations (Gonzalez and Lohmann, 1988, pp.84–86; Fig.5). For analysis, the material was sorted into standard lithic categories of *primary* (cortex covered one whole side of specimen), *secondary* (some cortex visible) and *tertiary* (no cortex visible) flakes or chunks. The cortex on limestone is typically smooth and darker in colour with hues of yellow, green, brown, or red from wind blown sediments and coralline algal growth. To provide an archaeological context for limestone exploitation and stone money quarrying, two sites where excavation were conducted are discussed – Omis Cave and Metuker ra Bisech. As noted before, these sites had good evidence for extensive stone money manufacture and the most substantial lithic debitage assemblages from excavation.

ARCHAEOLOGICAL INVESTIGATIONS

Omis Cave

A total of 7,119 pieces of flowstone debitage were collected during excavations of three test units at Omis Cave (see Fitzpatrick, 2001, 2003 for a more detailed description of the site). All debitage specimens were measured (length, width, thickness) and weighed (weights were taken from collection bags that contained numerous flakes and chunks; weight was not tallied for each individual specimen).

Of the total debitage assemblage at Omis Cave, 1,077 (15.1%) were primary, 398 (5.6%) secondary, and 5,644 (79.3%) tertiary (Table 1). In Test Unit 3 (located directly adjacent to an unfinished piece of stone money, debitage was predominantly tertiary. The proximity of the disk (Feature 3; Test Unit 3) to another unfinished piece (Feature 1) and a rock wall, and its upright placement, makes it likely this area was used in the finishing stages of carving and abrasion. The density of debitage volumetrically in Test Unit 3 compared to Units 1 and 2 (3.96/10 cm^3 versus 2.32 and 2.99, respectively) and average weight per specimen (TU1=61.9 g; TU2=91.8 g; TU3=60.8 g) suggest this area was used for completing stone money using smaller pieces of tertiary debitage from detailed carving as fill to support the disk.

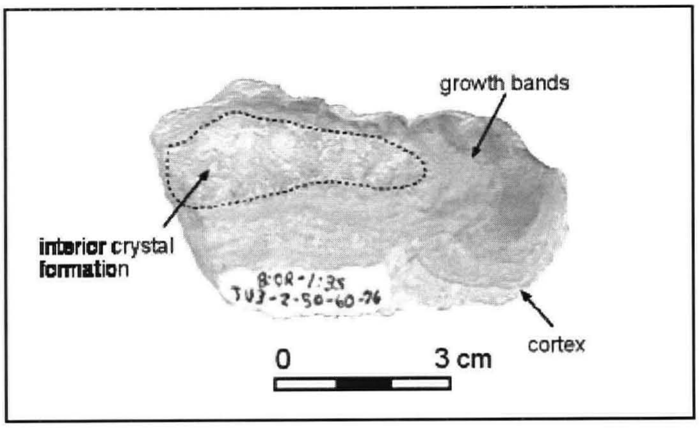

Figure 5. Limestone debitage showing exterior cortex, growth bands, and interior crystal formation.

Metuker ra Bisech

Four test units at Metuker ra Bisech were excavated to find evidence of stone money quarrying activities (see Fitzpatrick, 2002, 2003). Test units were placed in areas that were adjacent to obvious remnants of limestone carving (Test Units 1–3) or where an abundance of surface faunal material was present (Test Unit 4).

A total of 5,927 pieces of flowstone debitage were found in test excavations at the site. The total debitage assemblage consisted of 3,006 flakes and 2,921 chunks Of these, 368 (6.2%) were primary, 174 (2.9%) secondary, and 5,385 (90.9%) tertiary (Table 2). At Omis Cave I measured (length, width, height) and calculated weights for debitage specimens, which was extremely time consuming. Due to time constraints and the vast amount of data on limestone debitage already collected, the recording procedures at Metuker ra Bisech were changed slightly. Each specimen collected during excavation was placed on a centimeter measuring grid in the field and separated into categories based on length only (< 5, 5-8, 8-11, 11-14, 14-17, 17-20, and 20+cm) and catalogued as primary, secondary, or tertiary Weights were not taken.

Comparisons between Omis Cave and Metuker ra Bisech

The percentages of debitage types are somewhat different at Metuker ra Bisech than Omis Cave, where primary and secondary flakes are more common and tertiary flakes make up about 80% of the assemblage (Fig.6). One explanation for these differences might be that the areas excavated at Metuker ra Bisech were used by quarry workers who focused more heavily on the finishing stages of stone money carving (e.g. gouging away the exterior to create the final shape) and not on the early stages of rock selection and pre-form carving. Test Units 1 and 2 both had evidence for detailed carving activities including an unfinished stone money disk (Feature 2) adjacent to Test Unit 1, iron tools, and a subsurface coral rock foundation in Test Unit 2, which may support this conclusion.

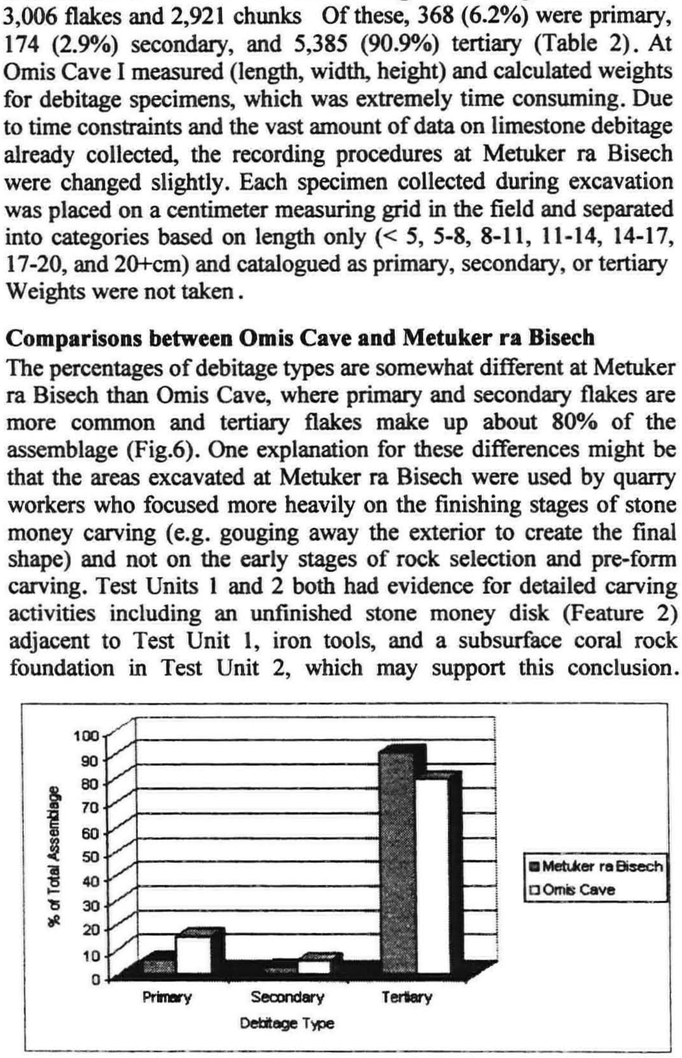

Figure 6. Comparison of limestone debitage found at Metuker ra Bisech and Omis Cave as a percentage of each site's total assemblage.

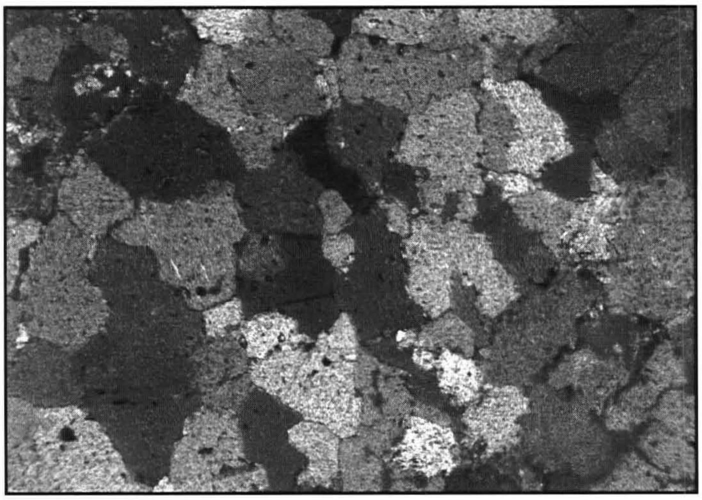

Figure 7. Petrographic thin section of fine-grained limestone from Omis Cave (sample no. B:OR-1:35_SM2.6[n1]; scale = 3mm across).

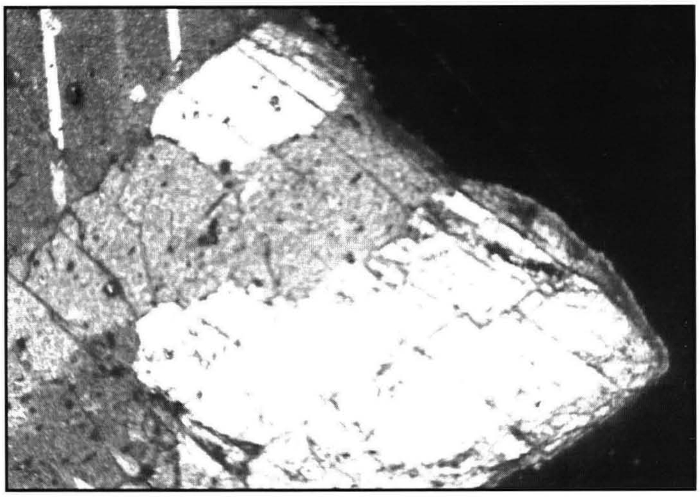

Figure 8 Petrographic thin section of coarse-grained limestone from Metuker ra Bisech (sample no. B:IR-2:24_SM2.4; scale = 3mm across).

Because Metuker ra Bisech is considerably larger than Omis Cave, it is also possible that the flowstone deposits were more extensive here and that the outer cortex was removed early in the quarrying process using shell, stone, or iron tools (accounting for a lower percentage of primary and secondary debitage). Further research is needed to determine whether these are in fact real possibilities or if it is an artifact of sampling.

The density of debitage volumetrically in Test Unit 3 at Metuker ra Bisech compared to Test Units 1, 2W, 2E, and 4 (5.58/10cm^3 versus 3.67, 2.93, 3.16, and 1.61 respectively) suggests this area was heavily quarried, as was Test Unit 1. This is similar to what is found in Test Unit 3 at Omis Cave (Feature 3) where higher concentrations of debitage were found directly adjacent to an unfinished stone money disk and quarried limestone deposits. Very few pieces of debitage were found in Test Unit 4. The density of surface shell and lack of debitage here support the conclusion that this was primarily an area of habitation and not flowstone carving (Fitzpatrick, 2003).

It is clear that both sites were exploited by the Yapese for producing stone money. How do the flowstone deposits at these two sites compare in terms of mineralogy?

PETROGRAPHICAL AND X-RAY DIFFRACTIONANALYSIS OF FLOWSTONE FRAGMENTS

To help determine the mineralogical characteristics of flowstone flake material at quarry sites, over 400 specimens from Omis, Metuker ra Bisech and Chelechol ra Orrak for collected for analysis. These samples included flowstone fragments from excavation units and small chips from individual stone money pieces. Determining the exact mineralogy of flowstone was important geologically, because aragonite has typically been identified by historians and archaeologists as the predominant mineral present in the Palau quarries (deBeauclair, 1971; Einzig, 1966; Bellwood, 1979; Berg, 1992; Descantes, 1998; Kirch, 2000; Morgan, 1996:35; D'Arcy, 2001, p.169), despite no previous studies having been done on the subject and calcite being a far more common carbonate rock.

For analysis, thin-section petrography and X-ray Diffraction (XRD) were used to determine the mineralogy of carbonate fragments and archaeological features found at quarry sites. Only

Test Unit	size	depth (cmbs)	volume (m^3)	debitage	density measure
1	1.0 m x 0.5 m	80	0.4	1,466	3.67
2W	1.0 m x 1.0 m	60	0.6	1,759	2.93
2E	1.0 m x 1.0 m	40	0.4	1,265	3.16
3	1.0 m x 0.5 m	40	0.2	1,115	5.58
4	1.0 m x 0.5 m	40	0.2	322	1.61
Total	n/a	n/a	1.8	5,927	---

Table 2. Test unit data from Metuker ra Bisech.

samples of stone money disk and flowstone fragments from Palau were collected and analyzed. Due to the high social and economic value placed on stone money disks located in Yap, samples from here were not taken for comparative analyses. In the future, I hope to collect samples from stone money in Yap using a technique such as micro-coring to minimize visible impact to the specimens.

Petrographical analysis of 110 (~25%) randomly selected flowstone fragments (n=100) and stone money disk specimens (n=10) suggested they were calcite with little aragonite present. XRD analysis of 67 of the same 110 (61%) samples (stone money n=5; 7.5%) confirmed these results, demonstrating that calcite is the predominant material found at these quarry sites. Petrography indicated that the stone money disks and debitage found at Omis Cave and Chelechol ra Orrak were composed of crystalline structures that range from fine- to medium-grained (Fig.7), whereas samples from Metuker ra Bisech are predominantly medium- to coarse-grained (Figs 8 and 9). This shows that the Yapese carved stone money disks from speleothem deposits that had a high degree of granulometric variability. These crystalline structures also showed bands of coralline algal growth and other inclusions. It may be possible to determine the provenance of flowstone from one quarry to another using these bands. Accurately determining the provenience and ownership of stone money disks and quarry sites traced along ancestral lines could reveal differential access to resources (i.e. quarries) by certain clan groups and whether there were certain qualities of flowstone that would suggest preference for quarrying. However, this has not yet been tested in Palau.

Overall, results from flowstone samples analyzed using XRD (see Figs 10 and 11) and thin-section petrography indicate that the carbonates from these quarries were calcite spars with little or no aragonite present. These findings contradict previous descriptions of stone money mineralogy by historians and archaeologists in which aragonite was reported as the material quarried (Müller, 1917; Einzig, 1966; de Beauclair, 1971, p.185; Bellwood, 1979; Alkire, 1980, p.234; Berg, 1992; Descantes, 1998; Kirch, 2000; Morgan, 1996, p.35; D'Arcy, 2001, p.169)

CONCLUSIONS

Although carbonate rock (e.g. carbonate cement, beachrock, uplifted reef limestone) is extremely common in Oceania, it rarely occurs in the quality and quantity that would promote its use as a resource for building structures, objects or tools as it does in Palau (i.e. dripstone or flowstone deposits). Archaeological research in the Pacific has provided a wealth of data concerning the use of stone by prehistoric peoples in Oceania. However, only in a few cases was limestone used for cultural purposes. The quarrying of speleothems by the Yapese is not only unusual, but is a testament to their ability at finding and shaping friable stone and transporting the heavy masses across the sea (Fitzpatrick, 2003).

Debitage was the most common artifact type found in excavations at the Yapese stone money quarries. Petrographical and

XRD analysis of speleothem debitage and stone money disk specimens is important for determining the mineralogy (i.e. is it aragonite, calcite, or some other rock type?) and examining whether different speleothem deposits were preferred by the Yapese over others (i.e. if some formations were more easily carved or less susceptible to breakage). The analyses of over 100 samples indicate that the limestone used for producing stone money at Omis Cave, Metuker ra Bisech, and Chelechol ra Orrak was calcite. Growth bands in the flowstone matrix suggested that carbonates within the quarries can be distinguished based on the presence of highly microcrystalline structures in the carbonates (most likely coralline algae growth) that occur in bands. However, these structures may also be highly localized even within individual quarries, and it is unclear whether they can be used satisfactorily for determining provenance.

The analysis of debitage helped to determine the behavior of these materials and examine the variability within specific quarries using compositional analysis procedures. Future research should be dedicated to discovering whether growth bands can provide an adequate "fingerprint" for the source material to answer questions regarding differential access to quarries placed on various Yapese groups by Palauan chiefs.

The karst environments of the Rock Islands provided numerous locales where the Yapese could extract and carve speleothems. Such abundance of carbonate deposits is rare in Micronesia, although islands in the Marianas, including Guam, Saipan and Tinian, are known to have extensive flowstone deposits and cave formations (Young, 1989; Hoffmann *et al.*, 1998; Mylroie *et al.*, 2001). Ethnohistorical accounts report that limestone caves in Guam may have been exploited by the Yapese for stone money quarrying, although there is no archaeological evidence yet to support this claim. In general, it is clear that the Yapese had good knowledge of these kinds of environments and were capable of finding and selecting materials conducive to carving. Although all of the quarries identified so far are found in the Rock Islands between Koror and Babeldaob, it is likely that other quarries exist in the southern parts of the archipelago where there are more and larger limestone islands. The ability to find other quarry sites in the hundreds of islands in Palau hinges on developing a survey strategy that takes into account the presence of karst formation processes such as collapse, inland marine lakes, cave and rockshelters, and intersecting valleys. Although a comprehensive survey of the archipelago to locate other Yapese stone money quarries has not yet been attempted, existing topographical maps, aerial photographs, satellite imagery, and low altitude reconnaissance should help in eventually identifying those islands with a good possibility for speleothem deposits and hence, quarrying activity.

There has been little geological research conducted on limestone caves in the Palauan Rock Islands and so it is difficult to assess the mineralogical variability of speleothems throughout the archipelago and how this might be related to patterns of procurement by the Yapese. I have demonstrated that the debitage found in stone money quarries is cultural and identifiable based on morphological characteristics and evidence for quarrying activities such as dense debitage deposits, carving tools, and architectural features. Determining the mineralogical composition of speleothems used in stone money production is important for understanding what stone money was made from (they have often been referred to as being made from various carbonates such as aragonite, calcite or even, erroneously, sandstone), whether there was a preference by the Yapese for certain flowstone deposits, if there are characteristics useful for provenance study, how the rock was manipulated through carving, and if the speleothem flake material is the result of natural or cultural processes. This research is the first of its kind dedicated to archaeologically examining Yapese stone money quarrying in Palau. It is hoped that continued analysis of speleothem deposits and investigations of quarry sites throughout the archipelago can shed further light on this fascinating exchange system and improve our understanding of indigenous technologies and stone resource procurement in the Pacific Islands.

Figure 9. *Macrophoto of calcite crystal formation along the broken edge of a stone money disk (Feature 1) at Metuker ra Bisech (photo is approximately 4cm across).*

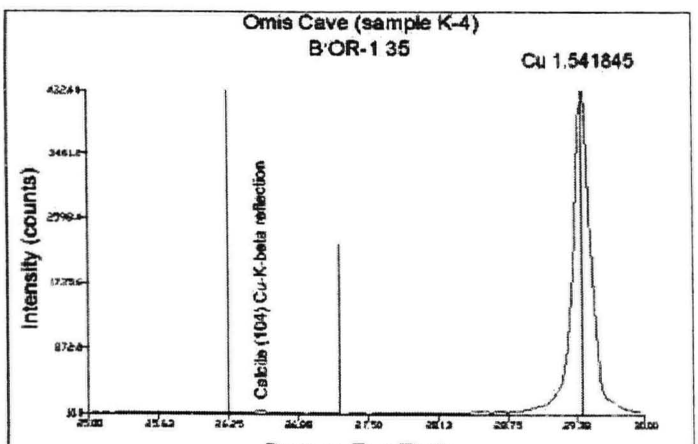

Figure 10. *X-Ray Diffraction plot of a limestone debitage sample from Omis Cave.*

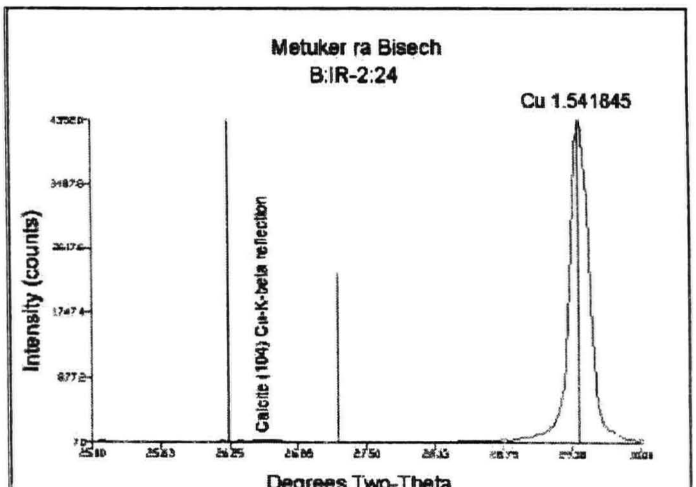

Figure 11. *X-Ray Diffraction plot of a limestone debitage sample from Metuker ra Bisech.*

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Victoria Cave, Yorkshire, UK: new thoughts on an old site.

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Abstract: A re-examination of the *'laminated clays'* overlying the Ipswichian strata in Victoria Cave suggests an origin as a cave interior deposit rather than a pro-glacial deposit coincidentally located within a cave. These sediments pre-date the second phase of the Late Glacial Interstadial. The sequence exposed outside the cave mouth shows that the area was glaciated post-dating OIS 5e then subjected to a prolonged period of periglacial weathering pre-dating the Late Glacial Interstadial.

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INTRODUCTION

Victoria Cave, on the limestone uplands northeast of Settle (Yorkshire, United Kingdom), contains an extended sequence of Quaternary cave sediments with evidence for clastic sediment deposition and stalagmite formation beginning more than 350,000 years ago (Gasgoyne *et al.,* 1983). It is well known for a Last Interglacial 'hippopotamus fauna' overlain by stalagmite dated to about 120,000 years ago (Gascoyne *et al.,* 1981), a small suite of Late Upper Palaeolithic organic artefacts dated by the AMS radiocarbon technique to the second phase of the Late Glacial Interstadial about 11,800BC – 10,800BC (Hedges *et al.,* 1992), and a rich assortment of Romano-British artefacts.(Dearne and Lord, 1998). The clastic sediments at the site are still largely unstudied, however, and for key parts of the sequence little work has been done since the nineteenth century.

Victoria Cave was subjected to large-scale excavations from 1870–1878, based on the early scientific methods developed by William Pengelly at Kent's Cavern, Devon. (Lord, 1997a and 1997b). Professional geologists directed the excavations, first William Boyd Dawkins from 1870–1873, then Richard H Tiddeman from 1874 until 1878, when a lack of funds brought the excavations to an abrupt end.

Dawkins was already a national authority on caves and on the Quaternary before these excavations began. Clearly ambitious, Dawkins aimed to consolidate his reputation in 1874 with the publication of *"Cave Hunting, Researches on the Evidence of Caves respecting the Early Inhabitants of Europe"*. This provided a lucid summary of modern human development and the Quaternary in Europe, based largely on evidence from caves, including results from the Victoria Cave excavations up to 1873. However, Dawkins' model of Quaternary events presented in *"Cave Hunting"*, especially his views on climate, were already regarded as outdated by some of his contemporaries. Crucially, they were not accepted by Richard Tiddeman. Even before Tiddeman took over the Victoria Cave excavations both men were openly critical of each other. Tiddeman worked for the Geological Survey and was engaged in fieldwork in glaciated areas In 1872 he published evidence for glaciation in northwest England, which included descriptions of the movement of ice-sheets in the region (Tiddeman, 1872a).

Tiddeman was clearly influenced by the cyclical model of Quaternary climate change based on the early astronomical theory of William Croll and taken up by the geologist James Geikie (Imbrie and Imbrie, 1979). Geikie's seminal book *"The Great Ice Age"*, advocating glacial–interglacial cycles, was first published in 1874, the same year as Dawkins's *"Cave Hunting"*. Once in charge of the Victoria Cave excavations, Tiddeman was well placed to interpret the long Quaternary sequence there to support a cyclical model of climate change. Dawkins, probably mindful to protect his reputation, mounted a vigorous rebuttal, which ultimately damaged the scientific value of Tiddeman's excavations. The Dawkins versus Tiddeman dispute was also responsible for the sometimes confusing and often-conflicting publications about the 1870s excavations. Nevertheless, there is sufficient published information about the excavations to put together a basic stratigraphy of the main Quaternary deposits.

Dawkins was a very competent faunal specialist and when he was in charge of the excavations he identified all the finds, including the bones. After Tiddeman took over Professor George Busk, a physical anthropologist and faunal specialist based at the Royal College of Surgeons, London, identified the bones. Recent reappraisal of the substantial archive from the 1870s excavations has

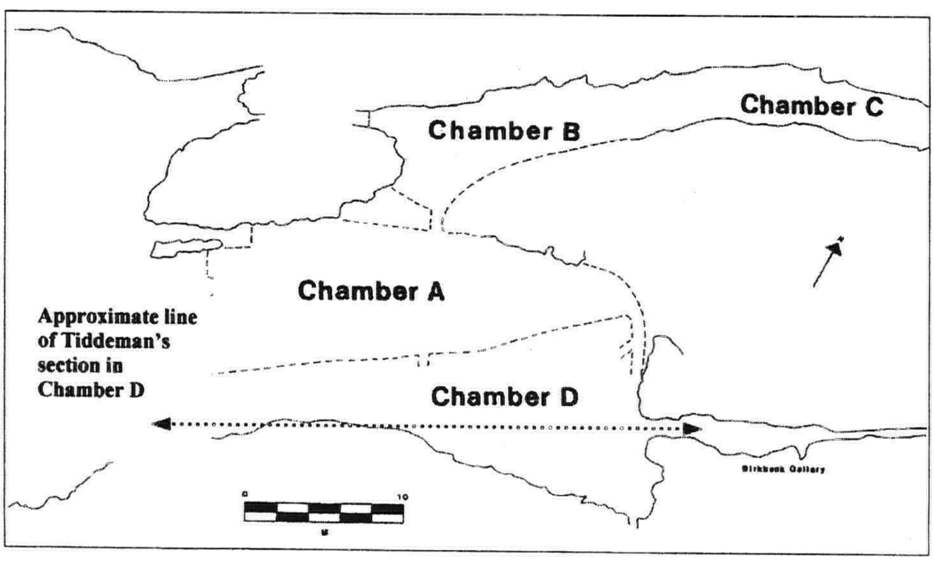

Figure 1: *Ground plan of Victoria Cave showing the names used in the 1870-78 excavation reports for the different chambers. The arrow shows the approximate line of Tiddeman's section of the deposits in Chamber D, as shown in Fig.2 below (After Dearne and Lord, 1998).*

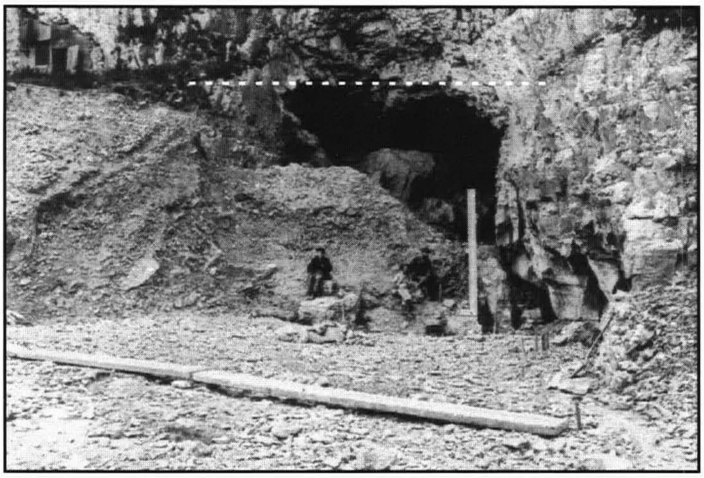

Plate 1: Excavations in progress outside Victoria Cave in 1874. The figures sit at the base of thick scree directly above a Late Devensian diamicton. Joseph Jackson, the figure on the left, sits on an erratic and rests his feet on a limestone boulder in the diamicton beneath the scree. Richard Tiddeman is possibly the bearded figure in Geological Survey uniform on the right. The large blocks of limestone visible in the cave have fallen from the cave roof. Such blocks were a major component of the cave earth containing the last interglacial 'hippopotamus fauna' dated to about 120,000 years ago, OIS 5e. The white dashed line represents the surface of the deposits outside the cave before the 1870s excavations began.

revealed that, surprisingly, Dawkins misidentified a number of critical specimens. Dawkins' species lists for Victoria Cave are unreliable. The faunal identifications made by Busk, included with Tiddeman's reports, stand up much better to modern re-examination. Nonetheless, a modern, comprehensive account of the various Quaternary faunas from Victoria Cave would add significantly to our understanding of the site.

Despite the scale of the nineteenth century excavations, a considerable amount of intact stratigraphy remains at the site, leaving scope for further research to integrate the historical excavation accounts into our modern knowledge of Quaternary events. In this paper we consider possible reinterpretations for the origin of sediments within the cave and the sequence exposed in the hill slope below.

THE BEDS INSIDE THE CAVE

In considering the nineteenth century descriptions of the excavations, it is important to realise that the cave consisted of a number of large interconnected chambers each with somewhat different topography and floor deposits (Fig.1). For the purpose of this review attention will focus on the deposits in Chamber A and Chamber D. The excavation of Chamber A took place under the direction of Dawkins then latterly under Tiddeman, whereas Chamber D was excavated entirely under the direction of Tiddeman. The excavations in Chamber D provide the more detailed records of the clastic sediments reviewed in this paper.

Tiddeman conducted extensive excavations in Chamber D to demonstrate that the bone bed in the *Lower Cave Earth* contained a wholly interglacial or 'warm' mammal fauna, in contradiction of Dawkins' descriptions of it as a mixture of 'warm' and 'cold' species (Dawkins, 1873, 1874). Examination of extant specimens from the *Lower Cave Earth* has confirmed that the interglacial assemblage reported by Tiddeman is an example of Sutcliffe's (1960) aptly termed 'hippopotamus fauna'. It is a key biostratigraphical horizon in the British Quaternary sequence. It was correlated with OIS 5e for the first time by ASU dates of about 120,000 years old on stalagmite encrusting bones excavated by Tot Lord in 1937 from the Victoria Cave *Lower Cave Earth* (Gascoyne, *et al.*, 1981). Dawkins' claim (Tiddeman, 1877) that reindeer was found in the *Lower Cave Earth* when he was in charge of the excavations was possibly based on misidentified fallow deer *(Dama dama)* bones, which are present in the extant 1870s collection from this deposit (Lord, *in prep*). Fallow deer is one of the characteristic large mammal species in 'hippopotamus faunal' assemblages (Sutcliffe, 1985; Currant and Jacobi, 2001).

Overlying the *Lower Cave Earth* in Chamber D Tiddeman recorded a thick bed of *laminated clays* (Fig.2). He called the deposits above the *laminated clay bed* the *Upper Cave Earth*. In Tiddeman's scheme, the *laminated clay bed* represented a glacial event separating deposits formed during the last warm or interglacial episode from those formed at the onset of the present interglacial. Near the south wall of the cave in Chamber D, he reported pieces of reindeer antler directly on top of the *laminated clay bed*. These he took to indicate a period of still cold climate prior to the warming of the present interglacial (Tiddeman, 1876a, 1876b). Tiddeman reported the *laminated clay bed* reached a thickness of 12 feet (3.6m) in Chamber A, thinning out in Chamber D especially towards the back (Tiddeman, 1875).

Tiddeman described the *laminated clay bed* in several accounts and thought it to be a result of fine material being brought into the cave by glacial melt water when ice covered the cave entrance (Tiddeman, 1873a, 1873b, 1875, 1876a, 1876b). Dawkins initially accepted that a glacier might be involved, but only as providing the dam at the cave mouth behind which water in the cave might pond up. He suggested that the deposit accumulated in still water, because *"...the even stratification, and the lines of calcareous matter, by which it is separated into layers as thin as the leaves of a book, show that it was the deposit of water more or less in a state of rest*". (Dawkins 1872). Latterly, Dawkins rejected Tiddeman's explanation that the deposit was glacial in origin.(Dawkins, 1873, 1874). An opportunity to re-examine part of these sediments was provided by an investigation carried out by Lancaster University Archaeological Unit on behalf of the Yorkshire Dales National Park Authority in 1997.(Quartermaine and Newman, 1997).

Grainsize analysis of the deposit showed all particles were below 63μm and an alternation between fine and coarser laminae was identified.(Quinn, 1997). Analysis (for this paper) of a sample from the 1870–78 excavations, preserved in the Lord collection, showed no material coarser than 56μm and the grain-size distributions are skewed towards the fines. The paler (coarser, silty clay) layers are pale yellowish orange (10YR 8/6) and grade to the darker layers, commonly with an intermediate layer of greyish orange (10YR 7/4). The darker (finer, clay grade) layers are light brown (5YR 6/4) and have sharply defined tops, though the bases are gradational with the paler material, so each pale to dark colour change is a fining upward sequence. The mineralogy of the silt grains is dominated by quartz, with minor amounts of mica, calcite and some heavy minerals. The fine-grained layers consist of iron-rich clay minerals. This material also forms the groundmass in the coarser layers. The mineralogy of the coarse and fine layers is consistent through the sample available for this study.

A number of features of the deposit suggest that it is a true cave interior deposit rather than a proglacial deposit coincidentally located within a cave. The layers within the deposit follow the contours of the cave passage and in places the cave passage is filled to the roof. These features are both described by Tiddeman, and shown on the section of the deposits in Chamber D (Fig.2). This is typical of cave interior deposits such as those described by Bull (1981) from the cap muds of Agen Allwedd in South Wales Bull records sediments (all less than 63μm diameter) that accrete parallel to the underlying surface, even on slopes exceeding 70° from the horizontal. This is a feature not seen in layered fine-grained sediments deposited in proglacial lakes such as those described by Gilligan (1914) from a deposit in the Aire Valley near Leeds.

Layered clastic sediments from a cave in direct contact with an ice mass have been described by Schroeder and Ford (1983) from Castleguard Cave in Canada. Although the cave contains extensive layered fine-grained deposits, they are horizontally bedded. An origin due to either injection from the base of the ice or back flooding due to blocking of the groundwater exits from the system has been proposed. For the sediments described from South Wales Bull proposed a mechanism of translatory flow, through fissures in the overlying limestone, carrying fine sediment in pulses into ponded water in a cave passage. A process of parallel deposition on

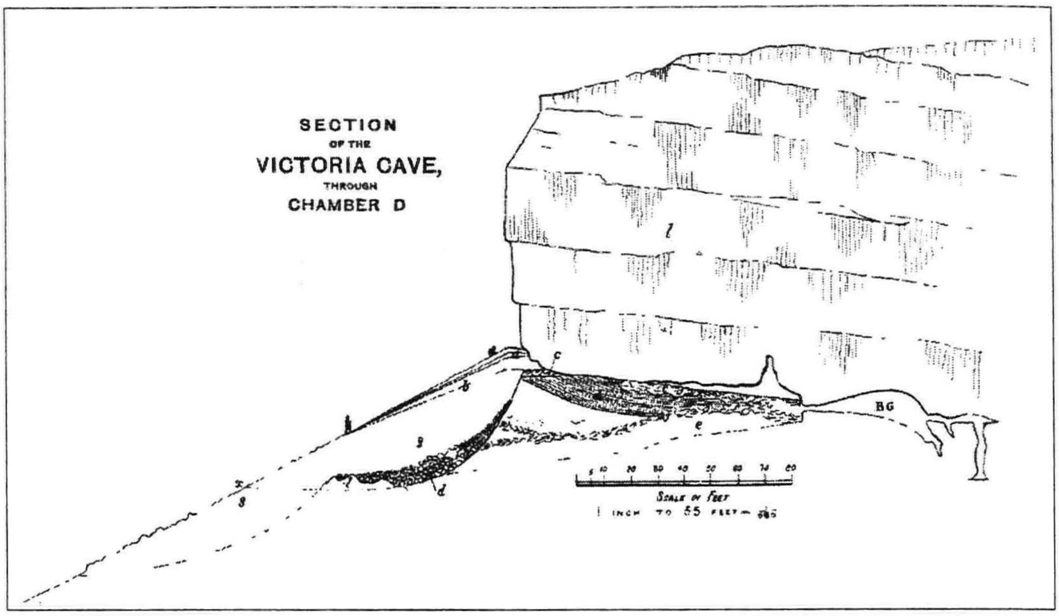

Figure 2. Tiddeman's published section of the excavations in Chamber D in December 1875 ***a*** *= Romano-British layer,* ***b*** *= The horizon wrongly described as Neolithic by Dawkins and Tiddeman (at the entrance to Chamber A this contained AMS radio-carbon dated Late Glacial Interstadial specimens),* ***c*** *= Upper Cave Earth,* ***d*** *= Laminated clay bed with some layers of stalagmite;* ***d'*** *= diamicton,* ***e*** *= Lower Cave Earth with a last interglacial 'hippopotamus fauna' dated at about 120,000 years ago,* ***S*** *= scree or talus,* ***l*** *= limestone bed rock. Section and legend amended after Tiddeman (1876b).*

the underlying bed topography produces the layering. The laminated deposits in Victoria Cave occur in the lowest part of the cave passage, and this would be consistent with deposition into ponded water. The deposits in Victoria Cave fill part of the cave to the roof, a feature also described for cave interior deposits by Bull (1981), which would be very difficult to explain by unidirectional fluvial deposition.

Laminated sediments are described by Gale and Hunt (1985) from Kirkhead Cave in the Morecambe Bay karst. They are similar to the '*laminated clay*' of Victoria Cave because they are also parallel the cave floor and fill the lowest part of the cave passage. The sediments contain no material coarser than 50µm but they are otherwise identical in grain-size distribution to loessic deposits from the area. This lack of coarse material in the sediment is also a feature of the '*laminated clay*' from Victoria Cave, where no material coarser than 63µm was recorded by Quinn (1997) and none coarser than 56µm from analyses undertaken for this paper. This lack of any coarse material appears to be a feature of sediments deposited in caves by a process of translatory flow through the bedrock and the recycling of loess deposits, as demonstrated by Gale and Hunt (1985). The parallel-accreted laminations are explained as being due to transportation by percolation water flowing down the cave walls in a subaerial environment. It does not require the presence of ponded water. However, the laminations described from Kirkhead Cave are not true time-plane laminae but are extremely small trough cross beds (C Hunt, University of Huddersfield, pers.com.). This is not the case in Victoria Cave, where the laminae are much more consistent, suggesting an origin closer to that proposed by Bull (1981) than to that proposed by Gale and Hunt (1985).

Sediments interpreted as glacial rock flour that has been washed into caves through fissures while the caves were filled with sub-glacial meltwater have been described from Assynt, Scotland (Lawson, 1995), and Chapel-le-Dale, North Yorkshire (Murphy, 1999). In both these cases there is very little evidence of layering within the sediments. The presence of laminations suggests that the sediments in Victoria Cave were not emplaced while the passage was filled by sub-glacial meltwater.

Tiddeman reported that the *laminated clay bed* in Chamber A was deposited against a series of massive fractured limestone blocks fallen from the cave roof for a distance of about 60 feet (18m) (see Plate 2). In turn the fallen limestone blocks rested on the bone bed containing the last interglacial mammal fauna (Tiddeman, 1877).

The LUAU survey found a surviving part of the *laminated clay bed* deposited against the fallen limestone block shown in Plate 2 (Lord, 1997a). It clearly demonstrates that the layered sediments post-date substantial roof collapse. The ponding of water into which the layered sediments were deposited may have been due to blocking of water movement in the passage by extensive roof fall debris.

Tiddeman's section through Chamber D, Fig.2, labels the sediments as "*Laminated clay, with some layers of stalagmite*". (Tiddeman, 1876b). The presence of stalagmite in the sequence provides evidence of groundwater movement but also shows that the area did sometimes dry out to allow stalagmite growth. Glacial ice does not necessarily prevent groundwater movement: Ford, Smart and Ewers (1983) describe the occurrence of groundwater flow in karst directly adjacent to the base of an icefield, including speleothem growth within 150m of an ice plug injected into a cave.

Tiddeman (1873) reported that the *laminated clay bed* in Chamber A was overlain by stony clay with angular limestone clasts in turn overlain by silts, a sequence confirmed by the recent LUAU survey. (Lord, 1997a). Although not identified at the time, two refitting pieces of a Late Upper Palaeolithic antler implement were found at the rear of Chamber A in deposits contiguous with those overlying the *laminated clay bed*. The AMS radio-carbon date for this implement OxA 2455 11,750 ± 120 BP (Hedges *et al.*, 1992) lies in the second phase of the Late Glacial Interstadial. It provides a minimum age for the deposition of the *laminated clay bed*.

A reconsideration of the origin of the laminated sediment from Victoria Cave suggests it may have been emplaced by a mechanism of translatory flow through fissures in the rock mass into a subterranean lake. The layering would then relate to surface climatic fluctuations rather than to diurnal meltwater pulses from the base of a glacier covering the cave entrance (as proposed by Tiddeman). It shows there was significant groundwater in the area at times during the Devensian. This agrees with uranium series speleothem dates from the region, which show that speleothem growth occurred at various times in the Devensian (Gascoyne et al, 1983; Sutcliffe *et al.*, 1984; Atkinson *et al.*, 1986; Baker *et al.*, 1993; Murphy and Latham, 2001).

The probable source for the fine-grained material is from loessic deposits. Loess of possible Late Glacial age is described from the Morecambe Bay karst (Vincent and Lee, 1981; Gayle, 2000), from the limestone pavements around Great Asby (Vincent, 1996) and from the Malham area (Bullock, 1971). Such deposits are believed to be widespread but of limited thickness on the limestone uplands of the Yorkshire Dales, (Catt, 1977). One possible explanation for the distribution pattern is that some of the loess originally deposited in the region has been removed from the land surface by the efficient karst drainage network, leaving only a patchy layer over much of the area. The probable loess in the Victoria Cave *laminated clay bed* appears to demonstrate this process, but most likely taking place sometime earlier in the Devensian.

THE BEDS AT THE CAVE MOUTH

The discovery of the *Lower Cave Earth* bone bed by means of a shaft dug in Chamber A in May 1872 encouraged more large scale excavations. (Tiddeman, 1872b). Sections of these deposits

Plate 2: *Chamber A, Victoria Cave, August 1898. A party from the Lancashire and Cheshire Antiquarian Society stand in front of a fallen limestone block uncovered during the 1870–78 excavations. Part of the laminated clay bed survives in the crevice immediately behind and to the left of the gentleman standing with his legs wide apart. Sediments here were examined by the LUAU in 1996.*

illustrated by Tiddeman (1873b) and Dawkins (1874) show the *Lower Cave Earth* and its contained bone deposits overlain by a diamicton at the cave entrance. In a later section showing the deep excavations in Chamber D (Fig.2) the diamicton is clearly shown as truncating the *Lower Cave Earth* (Tiddeman, 1876b). Details of the cave entrance deposits were also photographed between 1874 and 1876 (Plates 1 and 3). On all the published sections it is clear that the diamicton is younger than the *Lower Cave Earth,* but no section shows an unequivocal stratigraphical relationship between the diamicton outside the cave and the *laminated clay bed* inside the cave.

The diamicton described by Tiddeman consists of rounded and striated clasts contained within a matrix of "tenacious" clay. He interpreted the deposit as glacial till (Plate 3). The clasts included limestone and erratics, especially from the Lower Palaeozoic rocks exposed to the north, which Tiddeman called Silurian, as well as some gritstone and conglomerate from the base of the Great Scar Limestone. The diamicton shown on the Chamber D section reached a maximum thickness of about 8 feet (2.4m) (Fig.2).

The extensive sheet of boulder clay that covers much of the Settle area has an upper limit at about 490m AOD, above which there are large areas of periglacial deposits and any extant boulder clay deposits are patchy (Arthurton *et al.,* 1988). This suggests that at least for some of the time during the last glacial, Victoria Cave (at 440m AOD) could have been, if not above, at least very close to the upper limits of the ice.

Overlying the diamicton was a thick scree, which Tiddeman reported as being up to 25 feet (7.5m) thick.(Tiddeman, 1876a). The existence of this quite remarkable thickness of scree is supported by the deposits shown in the Chamber D section, which is drawn to scale, and by photographs of the outside of the cave at different stages of the excavations. The boundary between the diamicton and scree was photographed, for example Plates 1 and 3, and is clearly defined.

A composite bone assemblage believed to represent a mixture of bones weathered out of the *Lower Cave Earth* and subaerial accumulation on the till surface was identified by George Busk. (Tiddeman, 1876a). The bone assemblage from the diamicton/scree boundary suggests a possible hiatus between the formation of the two units. An especially intriguing record is a large bird bone, which George Busk provisionally identified as a species of swan, a potential seasonal migrant and early coloniser of a deglaciated habitat.

Scree is a common feature below the glacially over-steepened scars of the Craven uplands but has received very little serious study (Arthurton *et al.,* 1988). The section at Victoria Cave is a rare view through a scree slope in the area. Scree slopes appear to be mainly relict features today, as shown by the vegetated state of many and the fact that early photographs taken around Victoria Cave show no discernable down slope movement of clearly recognisable blocks between the 1870s and today. Below Victoria Cave some material appears to be retained on the upslope side of a pre-seventeenth century drystone wall line, showing some movement has occurred in historical times.

Tiddeman's section (Fig.2) shows a substantial accumulation of scree between the diamicton and a fossiliferous horizon wrongly called Neolithic by Dawkins and Tiddeman in all their published reports. Recent examination of extant specimens from the so-called Neolithic horizon at the entrance to Chamber A has identified a number of reindeer bones, all of them missed by Dawkins (Lord *in prep*). Had Dawkins identified the reindeer he would have assigned the deposit to the end of the Palaeolithic. Dawkins assumed the faunal material in the deposit belonged to a single event, but it contained intrusive domestic cattle bones, and these probably led him to believe it was Neolithic.(Dawkins, 1872, 1874). AMS radio-carbon dates on three specimens from it have been published (Hedges *et al.,* 1992). The results cluster within the second half of the Late Glacial Interstadial (Table 1).

Tiddeman (1876a) reported that of the 25 feet- (7.5m) deep scree outside the cave about 19 feet (5.7m) had accumulated between the diamicton and the so-called Neolithic horizon, now known to include AMS radio-carbon dated Late Glacial specimens. A similar amount is shown in the Chamber D section (Fig.2). Tiddeman's records indicate that by far the greater part of the scree outside Victoria Cave must have formed before the end of the Late Glacial Interstadial, and certainly before the Younger Dryas cold event.

Some sixty years ago, the palaeontologist Wilfrid Jackson commented on the fact that the greater part of the scree outside Victoria Cave had formed before the biserially barbed harpoon (Table 1) was left there. He reasoned that this scree formation indicated a period of prolonged cold with severe frosts after the disappearance of the ice sheet that had deposited the diamicton (Jackson, 1938). The timing of this cold event is difficult to reconcile with a simple climate model in which the Late Glacial Ice Maximum is followed by a warming event leading to the Late Glacial Interstadial beginning at c 13,000BP. Nor can the formation of thick scree be explained by accelerated scree formation immediately following deglaciation. In the Alpine karst of the Castleguard-Columbia Icefield, Canada, Ford (1971) observed that deglacierized limestone surfaces are especially resistant and there is no glacier pressure-release cracking. Photographs of the scree immediately above the diamicton outside Victoria Cave (Plates 1 and 3) show the limestone clasts are generally quite small.

A considerable body of environmental evidence is now available for the Late Glacial Interstadial event in Britain. The data suggest some climatic fluctuations and a decline in temperatures as the Late Glacial Interstadial progressed (Jacobi, 2000; Currant and Jacobi, 2001). However, Jackson's period of prolonged cold with severe frosts does not fit this record, especially as the AMS radio-carbon dates from Victoria Cave indicate that the major phase of scree formation took place before the second half of the Late Glacial Interstadial.

Victoria Cave lies in the Ribble Valley catchment, which drains westwards into the Irish Sea. It seems reasonable to explore the possibility that the deposits at the entrance to Victoria Cave might reflect the climatic events now known in some detail for the region of the north Irish Sea Basin. Here there is now considerable evidence for a pronounced warm-cold-warm climatic oscillation associated with the Heinrich event 1 cold episode after the Late Glacial Ice Maximum (McCabe *et al.,* 1998).

We make the following suggestions to explain the deposits outside Victoria Cave. The diamicton is a Late Glacial Maximum Ice Sheet deposit and part of the high-level boulder clay that reaches altitudes of about 490m AOD in the Settle area (Arthurton *et al.,* 1988). The composite bone assemblage identified by George Busk from the surface of the diamicton represents a climatic amelioration equivalent to the Cooley Point Interstadial in the north Irish Sea Basin McCabe *et al.,* 1998). The build-up of scree outside Victoria Cave might begin at this time. We suggest, however, that the main phase of scree accumulation took place in the subsequent stadial, the Killard Point Stadial of the north Irish Sea Basin Researchers working on these sediments suggest that the Killard Point Stadial is coeval with the Dimlington Stadial of the Late Devensian type site (McCabe *et al.*, 1998). This stadial witnessed a major ice readvance in the northern Irish Sea basin, associated with the Heinrich event 1 cold episode (McCabe *et al.*, 1998).

In our scenario, the record of scree accumulation outside Victoria Cave demonstrates a major phase of periglacial weathering during the Heinrich event 1 cold episode. We believe this is Jackson's (1938) period of prolonged cold and severe frosts Following the sequence of events now established for the northern Irish Sea basin, the Heinrich 1 event scree outside Victoria Cave shows that the Ribble Valley glacier failed to overrun the cave entrance at an altitude of 440m AOD during the Dimlington Stadial. This might be a result of fast ice flow transporting ice volume away from the higher ground. Fast flow appears to characterise the ice advance associated with the Heinrich event 1 cold episode in the northern Irish Sea basin (McCabe *et al.*, 1998). Fast ice flow is a key factor in drumlin formation, and it is possible that the drumlinization of the Settle area, which is limited to altitudes below about 350m (Arthurton *et al.*, 1988) took place at this time.

We also suggest the possibility that Dimlington Stage glaciers did not generally reach the plateau-like surface of the Great Scar Limestone at an altitude of 300 to 400m AOD. It is possible that periglacial weathering rather than glacial erosion was the dominant process acting on the Dales karst plateau during the Dimlington Stadial. We propose that the main phase of scree accumulation at Victoria Cave shows that karst landforms in the Dales underwent intense periglacial weathering during the Heinrich event 1 cold episode.

THE RELATIONSHIP BETWEEN THE BEDS AT THE CAVE MOUTH AND THE BEDS INSIDE THE CAVE

If the *laminated clay* deposits overlying the *Lower Cave Earth* with its last interglacial 'hippopotamus fauna' are, as proposed in this paper, a true cave interior deposit then they must have been deposited away from the entrance zone of the cave. In the nineteenth century excavations they were exposed at the mouth of the cave, suggesting there has been a significant retreat of the cliff since they were deposited. This inference is supported by the truncated profile of the *Lower Cave Earth* and its contained bone bed (Fig.2). The large rounded stalagmite block photographed in the diamicton in 1875 might represent debris from the retreating cave entrance (Plate 3).

It appears that the entrance to Victoria Cave was blocked by fallen limestone debris shortly after the formation of the bone bed containing the 120,000 years old, OIS 5e, 'hippopotamus fauna'. Despite deep and extensive excavations no reliable evidence was found in the *Lower Cave Earth* of a 'bison-reindeer fauna' (Currant and Jacobi, 1997) recorded during the later part of OIS 5, by about 83,000 years ago, at Stump Cross Cavern in the Yorkshire Dales (Sutcliffe *et al.*, 1985). However, species such as reindeer and bear reported from above the *laminated clay bed* have yet to be dated. These animals were present in Britain at various times during the Devensian and are, of course, major elements in Early Devensian 'bison reindeer' faunal assemblages. Reliable dating is needed for this part of the Victoria Cave sequence. Correlation with the Devensian clastic sediments interbedded between the dated stalagmite horizons at Stump Cross Cavern (Sutcliffe *et al.*, 1985; Baker *et al*, 1996) might elucidate the timing of the climatic pulse responsible for the formation of the *laminated clay bed*.

It seems that Victoria Cave remained sealed until extensive erosion occasioned by the Last Glacial Ice maximum unblocked the cave entrance. It is likely that this event preceded the Heinrich event 1 cold episode, which is dated regionally from about 14,700BP to 13,700BP (McCabe *et al.*, 1998). Although this points to a considerable time lag between re-opening the entrance and the beginning of faunal inputs as suggested by the published AMS radio-carbon dates for Late Glacial specimens (Hedges *et al.*, 1992), the dated specimens in Table 1 were recovered from sediments close to the cave entrance. It is located above a steep slope of potentially

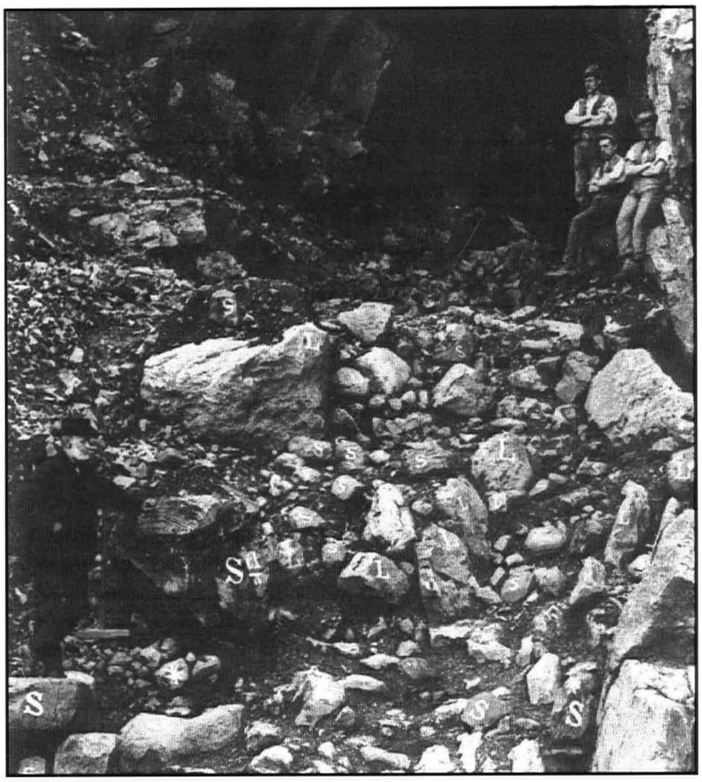

Plate 3: *Clasts in the diamicton outside Victoria Cave exposed in 1875. Joseph Jackson, on the left, stands against a rounded block of stalagmite, marked* ***Stlm****, possibly derived from cave deposits at the entrance destroyed by glacial erosion. The key for the other boulders in the picture is* ***S*** *for Silurian erratics;* ***L*** *for limestone. The contact between the diamicton and the scree may be seen in the area behind Jackson. Note that large fractured pieces of limestone in the scree are rare immediately above the diamicton. The level of the last interglacial bone bed containing the 'hippopotamus fauna' is shown by the crow bar to the left of the three excavators.*

unstable cave deposits (Fig.2) and susceptible to erosion and mass movement during an event of periglacial weathering. This possibility is suggested by a section at the entrance to Chamber A that appears to show a steep sheer face in the sediments against which the deposits containing the dated specimens in Table 1 were formed (Dawkins, 1872, Fig.1, 1874, Fig.20). Older Late Glacial faunal material might survive inside the cave, perhaps the large bear remains identified by Busk from Chamber D (Tiddeman, 1876a).

CONCLUSIONS

A review of evidence from Victoria Cave shows that the depositional mechanism proposed by Tiddeman for the *laminated clays* may not be correct. An alternative explanation proposed in this paper is emplacement by a mechanism of translatory flow through the rock mass into a subterranean lake. It is suggested that this was driven by a climatic pulse that might be detectable in Devensian cave sediments elsewhere in the region.

The section recorded through the extensive scree slope outside the cave suggests a complex sequence of climate change after the Late Glacial Ice Maximum Before the Late Glacial Interstadial there is evidence of a prolonged cold event with severe frosts, which we believe represents the Heinrich event 1 cold episode. Confirmation

Lab	*Age (14C BP)*	*Material*
OxA-2457	11.590 ± 130	Partial left radius adult reindeer
OxA-2454	10.970 ± 120	Partial right mandible juvenile reindeer
OxA-2607	10.810 ± 100	Biserially barbed harpoon

Table 1. *AMS radio-carbon dates on organic specimens excavated in 1870 from the so-called Neolithic horizon at the entrance to Chamber A, Victoria Cave From Hedges et al., 1992. These dates are uncalibrated. The calibrated age range would lie approximately from 11,600BC to 10,800BC*

of fast ice flow and intense periglacial weathering suggested for the Heinrich event 1 would greatly help in understanding the development of landforms in the area. New work on the Victoria Cave sediments is clearly vital to understanding the Glacial and Late Glacial history of the southern margin of the Craven Uplands.

A program of AMS radio-carbon dating is needed on specimens from Victoria Cave, to test for the arrival of animals after the Last Glacial Maximum. This will help determine more precisely when complex ecological communities were able to colonise deglaciated habitats in the Yorkshire Dales.

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The Late Quaternary dynamics of Planinska jama, south-central Slovenia.

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Abstract: During the last 100ka cave development in Planinska jama has been very "vigorous", but it has not essentially modified the pre-existing layout of bedrock channels. Spatial interpretation of the sediments in Planinska jama has revealed that only the Pivka river can be proven to have flowed through the cave in the Early Quaternary. Its outlet switched between the present cave "entrance" and the Malni Valley. After Würm I the Cerkniščica river entered Cerkniško Polje. Gradual elimination of the polje's main vertical ponors by its growing alluvial cone deflected the main stream westwards. This water found its way to Planinska jama, up to this time penetrated only by the Pivka. Newly arrived waters pushed the Pivka from the Eastern Branch of Planinska Jama and made the river reopen a long-choked outlet in the area of the present cave "entrance" before the end of Würm II. Consequently, the Western and Eastern branches of Planinska jama were washed clear of older sediments and eventually the present flow pattern was established.

Key words: Karst of Slovenia, Planinska jama, speleogenesis, cave sediments.

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INTRODUCTION

Planinska jama consists of three known main branches. Considered simply, the Eastern Branch carries water that flows through the Rakov Škocjan Valley (the Rak) from Cerkniško Polje. At the Confluence (Slovene: Sotočje) it joins the Western Branch, through which the Pivka arrives from the direction of Postojna. After the Confluence the combined river acquires the name Unica and leaves the cave through the Northern Branch (Fig.1). The completely phreatic Javorniki stream, entering from the south, is connected with the Eastern Branch by a c.30m-deep phreatic shaft. It drains directly to the Malni Spring, which is also fed partly by water from the Rak (Jenko, 1959; Habič, 1969; Morel, 2000, 2001). The details of the interplay between the Javorniki and Rak streams are as follows:

1 During drought periods the Rak does not reach Planinska jama. At such times the top of the phreatic shaft resembles a small lake, and the Javorniki stream passes 30m below, flowing directly to the Malni Spring. Under these conditions the Rak in the Rakov Škocjan valley is insignificant and all of it flows directly to the Malni without reaching the known passages of Planinska jama.
2 During periods of "normal" water level only part of the Rak can flow directly to the Malni Spring and the surplus water enters the Eastern Branch of Planinska jama. At the same time, most of the Javorniki stream maintains its flow to the Malni, while the surplus penetrates upwards through the phreatic shaft and joins the Rak. This upward flow is only a fraction of the whole Javorniki stream, and the Rak component – which enters the known Eastern Branch and joins the partial Javorniki stream's contribution – is perhaps half of the volume of the full Rak stream's flow. The other half passes by and flows directly to the Malni Spring. In summary – only surplus quantities of both streams "overflow" into the Eastern Branch whereas the rest flows directly to the Malni Spring through channels that are currently mostly unknown.
3 During high water periods the Rak increases to such an extent that most of it enters the Eastern Branch. The rest of it – which has become only a fraction of the whole – keeps flowing into the Malni Valley. The Javorniki stream does not increase significantly, as it is a completely karstic system drain. Consequently, though it is to be expected that a fraction of it still enters the Eastern Branch, its contribution becomes undetectable.

Recent complex dye tests (Kogovšek, 1999) have revealed that a swarm of minor streams, originating from the Javorniki mountains and the southern part of the Pivka Basin, join the cave's Eastern Branch in the stretch between Rakov Škocjan and the Western Branch. The Pivka enters the cave system and then enters the polje, concentrated into its extreme southwestern corner. In contrast, at the

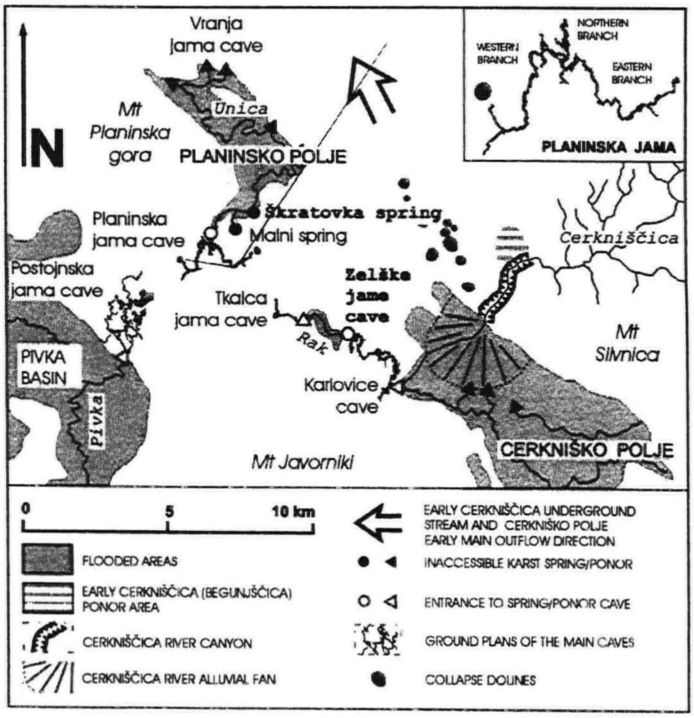

Figure 1. *Major features of the area around Planinska jama, south-central Slovenia.*

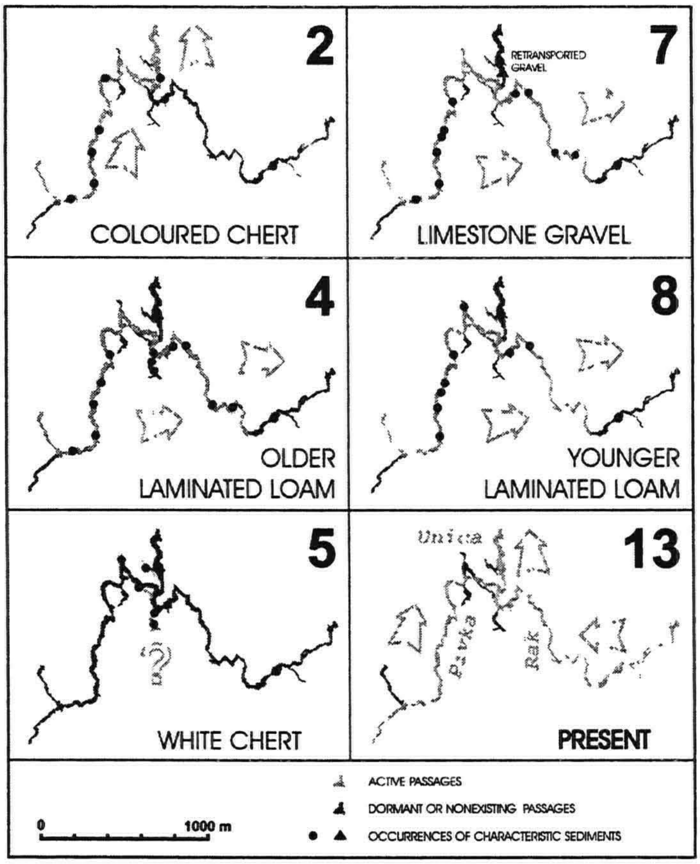

Figure 2. *Distribution of main sediment types in Planinska jama (numbered according to Table 2).*

highest water level, the Rak enters the polje dispersed along a nearly 2km-long stretch between Planinska jama, the Malni and the Škratovka springs. In the cave, it joins the Pivka to form a single river, the Unica.

This paper will demonstrate:

- that the Rak, as a clearly indentifiable steam, penetrated into Planinska jama relatively late in the cave's development, during the Mid Würm[1];
- that formation of the Rak is a direct consequence of Mid Würmian developments in Cerkniško Polje, and in its catchment;
- that the Late Pleistocene situation in Planinska jama was far from being stable, even before the formation of the Rak;
- that, during all this ongoing activity, the bedrock channels have hardly changed.

The study primarily concerns the latest changes of flow direction, as reflected by the evidence of preserved sediments. It is anticipated that – at least as far as the cave pattern identified within the present Planinska jama is concerned – water flowing through the Western Branch arrived from the Pivka Basin.

INTERPLAY OF THE UNDERGROUND RIVERS

To a large extent this work is based on previous research by the late Professor Dr Rado Gospodarič (1933 - 1988), who had collected various crucial material data. It appears that only his untimely death prevented him from synthesizing his findings about the underground karst in the area between Postojna, Planina and Cerknica.

In his comprehensive treatise (Gospodarič, 1976) he provides extensive information about Late Quaternary development in Planinska and Postojnska jama caves. He recognized and described the main clastic sediment types and fitted them into an appropriate time frame. He stated that most of the present cave (considering it as voids in the bedrock) must have existed at the time of deposition of the oldest known sediment (*coloured chert*), though some passages had not achieved their ultimate dimensions.

It is clear from his Plate 3A (Gospodarič, o.c., 128–129) that the original large elliptical phreatic passages of the Western Branch are so well preserved that significant mechanical erosion before deposition of the *coloured chert* cannot be hypothesized. Gospodarič (o.c., 134, Table 3) also provides a clear overview of the general sedimentary events in Planinska jama. Applying his basically stratigraphical findings to the plan of the cave (Fig.2), and omitting less significant details for simplicity, the Late Quaternary history shown in Table 1 can be extracted.

That changes of water level accompanied important development phases in the cave is clearly evident on simplified profiles (Fig.3a, b). When considered in combination with Figure 2 this reveals that the sediment locations are not scattered randomly, but that sediments were deposited in regular patterns at different times and within specific cave channels, which the sediments themselves identify and confirm unequivocally. Careful observation and recording has enabled relationships to be established between the clear patterns that emerge. For this reason, Gospodarič's original information and numbered phases require some additional discussion.

Phase 2

Coloured chert pebbles were deposited throughout the cave in a layer no thicker than 1m (Gospodarič, o.c., 58). Considering that the layer is thin and uniformly inclined along the bedrock channel floor, this indicates that the Pivka flowed without great obstacles through the Western and Northern branches, in the general direction of the present outlet (cave entrance). The Eastern Branch, which currently carries floodwater from Rakov Škocjan and, indirectly, from Cerkniško Polje, appears to have been inactive but not choked at this time. Otherwise it could not have become sediment-filled (*older laminated loam*) during the next phase.

Gospodarič was firmly convinced that the Rak was present in the Eastern Branch during this period, so he did not even discuss the topic. Present knowledge does not permit such a conclusive judgement, though the general circumstances make it appear highly unlikely. An alternative explanation would be that during deposition of the *coloured chert* the Northern Branch was choked, but that it was completely emptied immediately afterwards. However, no evidence in support of this possibility has been found.

Phase 4

The existence of sediments of comparable appearance in many caves in the wider area and even on the surface in the vicinity, made Gospodarič consider deposition of the *older laminated loam* to be an event of paramount regional importance (o.c., 61), though there was no conclusive proof that all loams were the same age or even had the same mineralogy. He viewed these deposits as an outcome of a general "sedimentation phase", following an "erosion phase". However, this assumption is not inevitable. In principle, increased production of loamy material is possibly a regional event, triggered, say, by climate change (o.c., 60). On the other hand, the actual deposition is an immediate consequence of a decrease in the water's transport capacity, which primarily reflects a local change in stream velocity at a particular location.

The comparable elevations of the highest known (*older*) *laminated loam* deposits throughout the cave indicate that a uniform water body once existed. This can be related to the withdrawal of the Pivka from the Northern Branch and its redirection into the Eastern Branch. An as yet unknown event at the outlet of the Northern Branch choked the outflow and forced the river to reactivate the then dormant Eastern Branch.

The difficulties that the river had to overcome at its alternative outlets were somewhat different. An obstacle in the area of the Malni Spring restricted the flow, yet it remained sufficiently transmissive for the river to overcome the resistance by an increase of water level. On the other hand, flow through the Northern Branch was completely eliminated, and the water that deposited the *older laminated loam* in the Western and Eastern branches did not penetrate there.

Past failure to correlate lamination patterns in the loam at various locations (o.c., 60–61), indicates either that deposition was

2	Mid Quaternary		Deposition of *coloured chert*	Western and Northern branches active, Eastern Branch dormant	Input close to the present inlet to the Western Branch; output through the Northern Branch towards the present "cave entrance" (i.e. outlet)
4		before c.80ka b.p.	Deposition of *older laminated loam*	Flooding of the Western and Eastern branches to elevation of c.475m a.s.l ; Northern Branch dormant	Stream direction unknown the most likely input close to the present "inlet" to the Western Branch; output through Easter Branch towards present Malni Spring
5	Riss		Deposition of *white chert*	Only relatively small passages active close to the Confluence; the rest of the cave dormant	Stream direction equivocal; in both possible cases the inlets and outlets were away from the present main conduits
6	Riss-Würm		Flowstone growth dated at 80ka b.p.		General data about the location of stalagmite insufficient. Perhaps too high to be related to "fluvial" phases
7	Early Würm And Mid Würm	Before c.30ka b.p.	Deposition of *limestone gravel*	The Western and Eastern branches active, the Northern Branch dormant	Input through "Paradise" near the present "inlet" to the Western Branch; output through the Eastern Branch towards the present Malni Spring
8			Deposition of *younger laminated loam*	Western and Eastern branches active and flooded	
9			*Limestone gravel* removed from the Western and Eastern branches	All three main branches active, limited sedimentation of reworked material in the Northern Branch	Stream flow direction comparable to present day; input through the Western and Eastern branches; inflow from the east increasing, outflow through the Northern Branch
12	Late Würm		Emplacement of *Flood Loam* to an elevation of c.490m a.s.l		Hydrological situation generally comparable to present day; possibly greater discharge along the Rak; ephemeral flooding of most of the cave
13	Present day		Erosion through most of the Western and branches; probable sediment accumulation in the central part of the Eastern Branch		All three main branches active Water enters through the Western and Eastern branches and leaves the cave through the Northern Branch

Table 1. *Main sedimentary events in Planinska jama; numbering follows that in Table 2 (data extracted and rearranged after Gospodarič, 1976, tables 1 and 3).*

not fully contemporaneous at different locations, or that local influences prevailed. So, it seems more feasible to interpret deposition of the *older laminated loam* as a local event, occurring only in Planinska jama and its immediate area of influence. The occurrence elsewhere of loams that appear similar to the naked eye should not be related to this event without substantial additional evidence.

The absence of *older laminated loam* in the dormant Northern Branch is somewhat surprising, but could be related to extensive collapse near the outlet, or to choking by materials produced by slope processes on the facing Mt Planinska gora. Yet, in either of these cases, some loam-laden water could be expected to penetrate into the Northern Branch, and *older laminated loam,* even if only minute traces, should exist in remote corners. Gospodarič's explanation that the loam was totally removed during subsequent extensive widening of the passage is not convincing.

The break between deposition of *coloured gravel* and of *older laminated loam* was caused by the Pivka's reversal towards the Malni Spring and cessation of flow in the general direction of the present cave outlet. Whereas the presence or absence of waters from Rakov Škocjan in the Eastern Branch during Phase 2 cannot be confirmed, during Phase 4 it was close to nil.

Phase 5

Gospodarič (o.c., 61) noted: "*Sinking* (i.e. underground[2]) *river deposited the sediment* (i.e. white chert gravel) *into the* (nearly completely) *in-filled Planinska jama, into the upper third of its* (main) *branches, under the ceiling, or into independent, (minor,) higher lying channels, which had been formed around the Confluence above the elevation of 475m a.s.l.*" The highest known location is 490m a.s.l. At most locations small quantities of *white chert* appear in "pockets" in the cave walls, whereas at just one location (480m a.s.l.) it lies on top of *older laminated loam*. The vertical range of 15m within an approximate distance of 500m is not negligible, and the vertical distribution reveals no spatial pattern. These observations raise the question of whether the deposits are in their primary position.

Putting this doubt aside, only one explanation offered by Gospodarič (o.c., 46-47), is possible. During *white chert* deposition, most of the cave's main branches were completely sediment filled (perhaps choked with *older laminated loam*) and water had to re-use "parallel" passages that had become inactive a long time before. Thus, the present authors prefer the view that the *white chert gravel* is indicative of a less important episode, when the main channels were almost totally inactive.

The river must predominantly have by-passed the presently known cave passages, and the flow direction remains uncertain. Gospodarič (o.c., 62) stated that the presence of the *white chert gravel* is an indicator of an increase in the velocity of the river to at least 0 5m s^{-1} and its ability to carry a heavier load, as "*...the river could flow faster towards Planinsko polje*" (o.c., 62). Reading between the lines it may be that Gospodarič assumed a lowering of the erosional base level within the Planinsko Polje basin.

Gospodarič (o.c., 62) confirmed the source area of the *white chert gravel* as the southern part of the Pivka Basin. Hypothetically, when the Pivka began to carry it into the cave, its catchment area must have been expanded dramatically. Assuming channel sections were not adapted to the presumably larger discharge, increased velocity would inevitably result in augmented gravel entrainment.

Phase 5a

During deposition of *limestone gravel* (Phase 7), the Western and Eastern branches must initially have been sediment free. Thus, a major erosional event must have taken place after deposition of the *white chert gravel* Gospodarič was aware of that, but in Table 1 (o. c., 69 [126]), he groups sedimentation and evacuation of the *white chert gravel* together, evidently believing that the processes went on hand-in-hand.

However, it is difficult to recognize a direct logical connection between *white chert gravel* in some high, remote, smaller, passages, and the massive scouring that swept the main passages clear of about 1 Mm^3 of material. Considering the flow pattern indicated by *white chert gravel* distribution, the erosional mechanism would require a radical change of general circumstances, just to make it operate. Thus, the two effects should not be considered contemporaneous without strong material proof.

The flow direction during the erosional phase following deposition of the *white chert gravel* can be estimated only indirectly. As during the next phase (7) the river followed a highly transmissive route from the Pivka inlet, through the Western Branch and farther eastwards through the Eastern Branch towards the Malni Spring, this direction is at least probable. If so, after some tens (or even hundreds) of thousands of years, the obstacle in

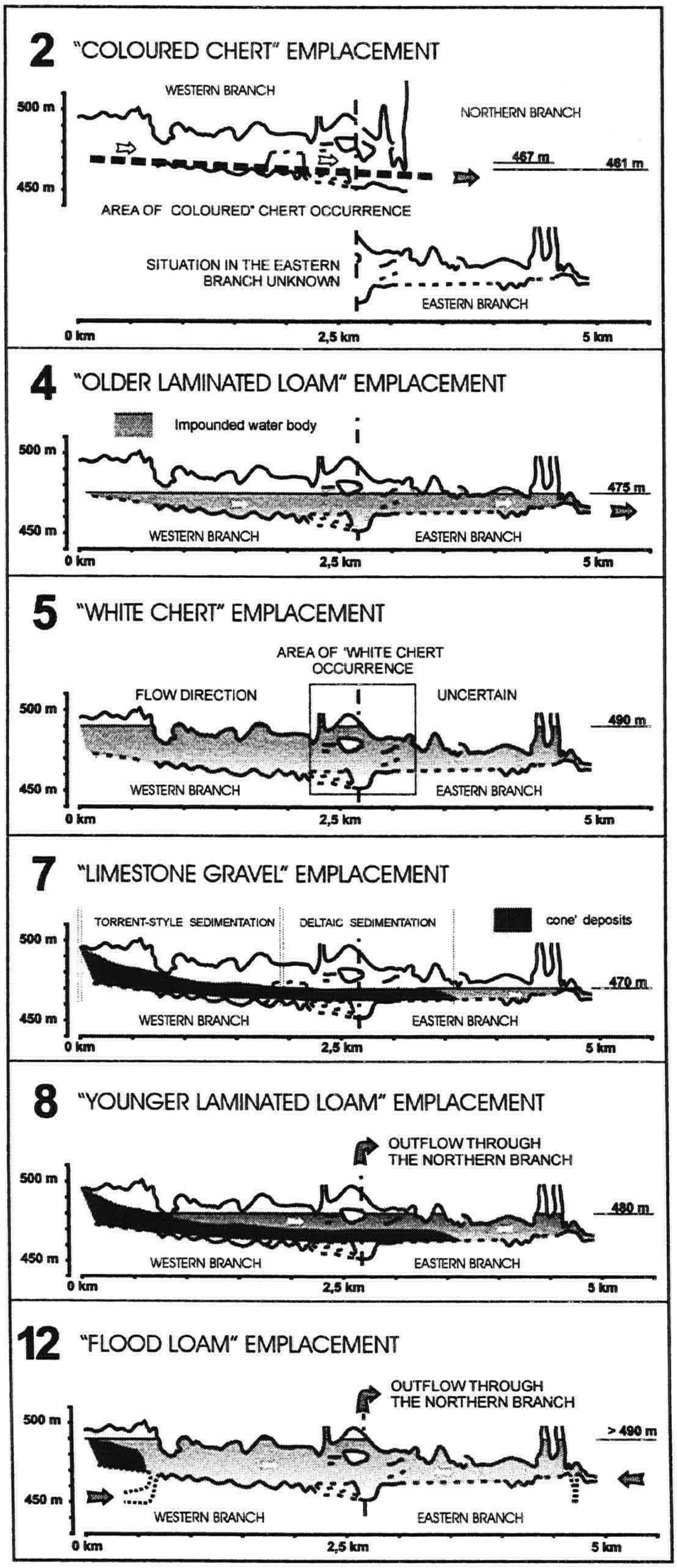

Figure. 3a, b: *Water levels during some characteristic "stages".*

the Malni Spring area vanished and the general hydrogeological regime of the *older laminated loam* deposition period was restored. Evacuation did not include the Northern Branch, which remained inactive, and in all likelihood the present (cave entrance) outlet remained blocked.

It appears that until the second half of the Würm the flow direction of the Pivka through to the Malni Spring was the fundamental arrangement, and that temporary deviations were just the consequences of internal or external interruptions.

Phase 6

Due to lack of data events during this episode remain unclear. The only dated samples are at elevations of 488m and 495m (Gospodarič, (o.c., Fig.9, p.40). The former lies immediately on the *older laminated loam*, within the vertical range of the *white chert* sedimentation. Indirectly it indicates that general evacuation of the *white chert gravel* happened before the flowstone deposition.

Phase 7

Emplacement of *limestone gravel* in the Western and Eastern branches appears to be one of the most dramatic events in Planinska jama's known history Gospodarič (o.c., 62–65) gives well-supported information about the origin and geometry of the cone-like pile in the cave. Micropalaeontological study (Gospodarič and Pavlovec, 1974) confirmed that the gravel originates from the Planinska koliševka collapse doline. The length of the longitudinal section of the gravel pile totals about 3.5km.

Two parts can be distinguished within it. In nearly the whole of the Western Branch the profile of the gravel bank decreases exponentially, which is characteristic of high flow velocities, indicating a free water surface. Its apex is at almost 495m elevation and its toe at about 470m, only a few hundred metres before the Confluence (observed Pivka-downstream). From there the elevation remains virtually constant for the next kilometre and a quarter (in the Eastern Branch), before suddenly dropping down and wedging out after another 100m. This is typical of deltaic sedimentation[4], implying that the Eastern Branch water level was more or less stable at 470m for a longer period.

Gospodarič (o.c., 65) believed the the extreme part of the Eastern Branch was evacuated by backwards erosion. The present authors, however, favour the explanation that this reflects two stages in the "cone" development. During the first one, the entire Pivka flowed through the base of the collapse, washing out gravel and rolling cobbles and boulders, as large as its transport capability allowed. It deposited its load when it came upon the stagnant, dammed water body, and its velocity (and, consequently, transport ability) reduced almost instantaneously. The river extended its sedimentary pile in the form of a pro-grading alluvial fan or delta.

On the other hand, the younger, "torrent-cone-like" part was deposited by extremely high waters, not all of which could pass through the newly formed by-pass channels. The pulses grew less frequent and weaker, and the transport capability of the current through the collapse base decreased. Input through "Paradise" (Figs 2, 3) near the present "inlet" to the Western Branch, and output through the Eastern Branch towards the Malni Spring is beyond any doubt (Gospodarič and Pavlovec, 1974). Possible simultaneous Northern Branch activity, indicated by Gospodarič (o c , 62) – to be discussed below – remains, at best, questionable. So, the Western and Eastern branches were not only active, but they even permitted unimpeded transport of coarse sediment.

Phase 8

Younger laminated loam appears in the Western Branch and in adjacent parts of the Eastern Branch Gospodarič (o.c., 65) noted that *"...it must have been eroded from the other parts of the Eastern Branch"*. It has not been detected elsewhere in the cave, including the Northern Branch. The sediments reach elevations of about 480m, which yields some important information:

- the Pivka still flowed eastward, i e towards the Malni Spring;
- the cave outlet was impeded, but not blocked;
- flow through the cave was relatively slow;
- the Northern Branch was still inactive.

Transmissivity in the direction of the Malni Spring was stable until an obstacle appeared there that increased the watertable elevation by about 10m. Evidently *limestone gravel* emplacement had ceased. As the dynamics of the collapse doline do not imply any intrinsic cause, the most feasible explanation is that the Pivka found a by-pass to Planinska koliševka. There is little doubt that this was the present inflow siphon. Relatively rapid by-pass formation corresponds to the theoretical expectations of Dreybrodt and Eisenlohr (2000) and their team. However, the possibility that water might reactivate pre-existing, sediment filled, channels, must not be overlooked.

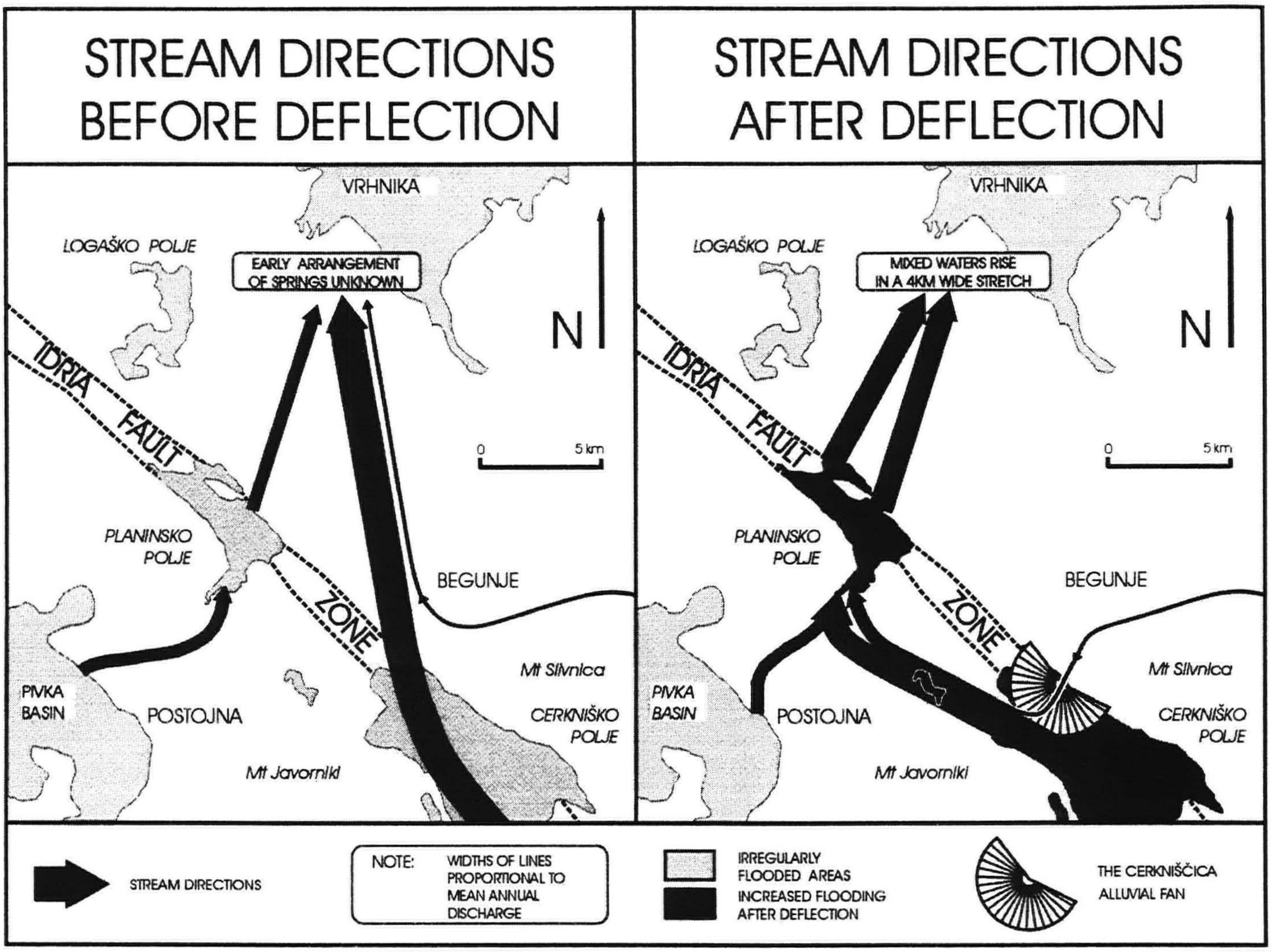

Figure 4. *Stream directions in the Planinsko polje area before and after deflection by the Cerkniščica alluvial fan.*

Phase 9

Gospodarič focused his interest primarily upon sedimentation within the cave and he unwillingly underestimated the importance of the extensive erosion following the 8th phase. In the context of the present paper the most important effect was the reversal of flow in the Eastern Branch, from the earlier eastward to the present westward direction. The agent of the reversal was the newly formed Rak, as an immediate consequence of the great changes in the Cerkniško Polje area (Table 2). Before the reversal the Pivka flowed from west to east from the Western Branch and then along the Eastern Branch, by-passing the Northern Branch Subsequently, the flow of the Rak (currently >$10m^3s^{-1}$) entering the cave from the east became significantly stronger than that of the Pivka (4 $8m^3s^{-1}$). A probably relatively short period of back-up and flooding is assumed Soon after this the combined waters of the two streams re-opened the Northern Branch and flowed northwards together towards the present entrance (Figs.2, 3).

When discussing phase 7, Gospodarič (o.c., 62) wrote: *"The* (i. e. limestone)[5] *gravel layer shows most evidence of erosional rounding between the Confluence and the cave entrance"* (i.e. in the Northern Branch). He wondered (o.c., 56) why – in the only occurrence he found – " *the pebbles are the most rounded among all of the studied samples in the cave"*. If considering the distance from the source one would expect less rounded and coarser pebbles. An obvious explanation is that these more-rounded pebbles are now in a secondary position. If so, first the Pivka deposited the gravel far up the Eastern Branch. Later, the Rak entrained it again and brought it into the newly reactivated Northern Branch During the renewed transport from the Eastern Branch to their present position in the Northern Branch the clasts suffered additional rounding.

Phase 12

After the flow reversal in the Eastern Branch – which in effect indicates inrush by the Rak –the flow directions in the cave since the Late Würmian have remained essentially the same as today. Thus, it is somewhat surprising that during the Late Würmian some floods reached an elevation of 490m or perhaps even higher (Fig.2, 12), i.e. 10m higher than the highest flood triggered by the inrush of the newly formed Rak. Gospodarič (o.c., 65–66) alludes to similar development in the caves in the wider area including at Cerkniško Polje (Karlovice Cave) and Postojnska jama, concluding (o.c., 66): " *...that the underground karst of* (the) *Postojna region was flooded during one of* (the) *younger periods"*.

If this is reality, and not just premature generalization, it is an indication of a catastrophic event that excedes all of those previously mentioned. Evidently it was not just a choke that raised the water table about 40m or more above the level of Planinsko Polje. The absence of laminations indicates:

- that elevation of the water table took place in a short time;
- that enormous quantities (compared to other similar events) of loam were deposited, and these must have been washed in from somewhere in a very short time;
- that all possible paths from the flooded underground to Planinsko Polje were impeded to such an extent that water could not force the formation of new ones (alternatively, this may be explained by total flooding of the polje to the same elevation: however, this alternative invokes a still greater "catastrophe").

Such a development is not *"a priori"* impossible, but it is so highly unfeasible that any further discussion without additional information would be fruitless.

Epoch	Time	Cerkniško polje			Planinska jama		
		Situation on the polje floor	Begunjščica / Cerkniščica	Outflow from the polje	General situation	Flow direction	
		1.1	1.2	1.3	2.1	2.2	
Mid Quaternary					Phreatic conditions (1 / 2.1)	Unknown (1 / 2.2)	1
		The floor is predominantly dry. During cold periods a sedimentary load of mass flow material originating from the neighbouring slopes is deposited (2 – 6 / 1.1)	The Begunjščica sinks near the present Begunje village In cold periods it brings pebbles ("Cerkniščica sediment" in the present sense of its meaning) into the "Ravnik" cave system (2 – 6 / 1.2)	Most flow probably disappears into the northern ponors (towards Vrhnika) Cave ponors divert surplus towards Malni (Planinsko Polje) (2 – 6 / 1.3)	Coloured chert is deposited in the Western and Northern branches; the Eastern Branch is inactive (2 / 2.1)	Through the Western and Northern branches towards the present "entrance" (outlet) (2 / 2.2)	2
					An outlet in the broad area of the present "entrance" is blocked (3 / 2.1)	Reversal of the Pivka from the Northern to the Eastern Branch (3 / 2.2)	3
	before 80ka b.p.				Stagnant water in the Western and Eastern branches; sedimentation of the older laminated loam (4 / 2.1)	Possibly through the Western and Eastern branches towards Malni (4 / 2.2)	4
Riss					Most of the cave is "dead" and filled with clastic sediments. Deposition of *white chert* in "side" passages (5 /2.1)	Unknown Most of the discharge is by-passing the presently kienown "main" galleries (5 / 2.2)	5
Riss/Würm	Before 78 ± 8.4ka b.p.				Growth of the *older flowstone* (6 / 2.1)		6
Early Würm	Cold period	Loam and quartz sand are deposited in the NE of the basin (inverse succession if compared to the one in the unroofed caves of the Brezje and Ravnik cave systems) (7 / 1.1)	The Begunjščica flows (at least partly) through reactivated caves in the Brezje system and washes them out Floods begin to appear in the polje basin, and the discharge gradually increases (7 / 1.2)	Most probably disappears into the northern ponors (torards Vrhnika) and ponor caves are gradually activated (direction to Malni) (7 / 1.3)	Water in the Eastern Branch is stagnant and its level increases. Limestone gravel is deposited in the Western and Eastern branches (7 / 2.1)	Through the Western and Eastern branches towards Malni (7 / 2.2)	7
	Brorup inter-stadial	The river brings extensive fluvial dolomite gravel into the polje basin for the first time; alluvial cone formation begins (8 / 1.1)	The whole of the Cerkniščica (Begunjščica) almost certainly flows into the polje basin (8 / 1.2)	The northern ponors grow weak and the stream switches from them into the cave ponors (8 / 1.3)	In the Eastern Branch the water level keeps increasing; the *younger laminated loam* is deposited in the Western Branch (8 / 2.1)	Through the Western and Eastern branches towards Malni; it gradually turns into the Northern Branch (8 / 2.2)	8
Mid Würm	Cooling just after the end of the Brörup inter-stadial	Massive dolomite gravel production in the upper Cerkniščica catchment (9 / 1.1)	Rapid growth of the alluvial fan gradually eliminates the northern ponors (9 / 1.2)	The northern ponors are predominantly eliminated, flow into the cave ponors increases (9 / 1.3)	The present "entrance" (outlet) is reopened, working as the outlet of the Northern Branch. First the Northern, then the Western and Eastern branches are emptied of early sediment deposits. Resedimentation reaches the northern rim of Planinsko polje (9 – 11 / 2.1)	The Rak inundates the Eastern Branch and diverts the Pivka. Both rivers flow together through the Northern Branch (9 – 10 / 2.2)	9
	Cold period	The unimpeded Cerkniščica brings an alluvial load into the polje basin The alluvial cone totally obliterates the northern ponors (10 – 11 / 1.1)	Reactivated caves of the Brezje system collapse completely and the canyon-like Kurja dolina forms (10 – 11 / 1.2)	Permanent lake compensates for the still insufficient transmissivity of the ponor caves (10 / 1.3)			10
	Near the end of Mid Würm			Cave ponors become able to divert the entire outflow, so the permanent lake disappears (11 / 1.3)			11
Late Würm	Cooling	Massive dolomite gravel production in the upper Cerkniščica catchment. Probable formation of new vertical ponors as by-passes towards the channels of the Cerknica cave system (12 / 1.1)	Filling-in of vertical ponors impedes low water outflow, making seasonal flooding last longer (formation of seasonal lake) (12 / 1.2)	Primary transmissivity of ponor caves is restored, but their openings are too high to receive low level water in the polje (12 / 1.3)	Stabilised under new conditions [1] (12-13/2.1	The Pivka, which emerges from the Western Branch, and the Rak, which enters via the Eastern Branch, merge at the "Confluence". The newly formed Unica leaves the cave through the present "entrance" (11-13/2.2)	12
Holocene		Gravel production is unimportant (13-/1.1)	The Cerkniščica corrodes and erodes its own alluvial fan (13-/1.2)	Vertical ponors make permanent progress into the alluvial cone and undermine it; cave channels behind the Northern ponors are partially reactivated (13-/1.3)			13
Note:	Only a few of the event times are confirmed by absolute dating. Most of the development has been interpolated logically between these "milestones". Consequently, timing is – in detail – only approximate. Numbers in the boxes and along the top and right-hand margins, are intended to facilitate orientation within the table and they have no other significance.						

Table 2. *Comparative timetable of events in Cerkniško polje and in Planinska jama (compiled after M Pleničar, 1953; A Šercelj, 1974; R Gospodarič, 1976; R Gospodarič and P Habič, 1979 and S Šušteršič, 2002).* [1] *Flood loam sedimentation extended to an elevation of 490m during this period (Fig.3, 12), indicating that the deposits were emplaced by a catastrophic event "par excellence". However, it is difficult to frame this event within the general context of the cave's sub-recent history. So, speculation about this must be postponed until more abundant field data can be assembled and considered.*

KEY EVENTS

Despite local variations, induced by changes to the Pivka catchment area, Late Quaternary development in Planinska jama is mostly a string of events that follow one another logically. Straightforward development has been disturbed by three events[6] when the situation changed radically, and which can be viewed as catastrophes:

- Mid Quaternary redirection of the Pivka from the Northern Branch to the Eastern Branch;
- formation of the Planinska Koliševka collapse doline and resedimentation of the collapsed material in the Western and Eastern branches during the Early Würm;
- inrush of the Rak into the Eastern Branch, formation of the Unica and redirection of the outflow through the Northern Branch immediately afterwards.

Due to the current lack of information, discussion of the first point is postponed until the future.

On the other hand, formation of the gravel "cone" can readily be related to the dynamics of the collapse doline. Gospodarič (o.c., 64) proposed that abundant production of gravel was a consequence of increased mechanical weathering in one of the cold periods of the Pleistocene. He (o.c., 64) believed that massive gravel production was a result of the cold Pleistocene climate (Early Würm [Table 3]). Nevertheless, his photographs (Plates 4B, 7A and 7B) and sieving diagrams (Fig.24, 63) do not support this idea. The gravel contains a relatively small proportion of pebbles of dimensions characteristic of Pleistocene gelifractional products, and too many very coarse particles. This implies that the gravel was washed out from the base of the collapse in the cave, without direct influence from the surface. The Pivka had been undercutting the obstacle until it excavated a "by-pass". However, this does not actually preclude that the process culminated during a cold period, but it would be mere coincidence.

One can conclude that in spite of unique and even spectacular events, in the wider context, it is just an isolated occurrence that is only indirectly related to the general history of the cave system. Reversal of the stream direction in the Eastern Branch is, however, quite a different story. During the previous episode (deposition of *limestone gravel*) the water in the Eastern Branch was dammed at an altitude of 470m. This is only 2m higher than the presently lowest elevation of the water surface in the final syphon in the Eastern Branch. One can readily imagine that this obstacle did not differ greatly from those that presently prevent humans from entering the underground hinterland behind the Malni Spring.

During the next stage, when the *younger laminated loam* was deposited, the elevation increased by 10m. Evidently, in the Malni, or in its immediate background, an obstacle appeared, whose efficiency gradually increased. Two hypotheses are at hand:

- transmissivity of the actual springs decreased due to physical obstacles (such as collapse);
- new quantities of water began to flow into the catchment of the springs, so that the outlets could not cope with them.

In the Malni (pocket) Valley one can hardly imagine collapses considerably larger than the present ones. Additionally, there is no source area from which much greater masses could be derived by slope processes So, it is worth giving serious consideration to the latter option, that the water table close behind the Malni Spring would rise due to increased discharge. This idea becomes even more attractive when considering that it is certain that, not much later, such a stream did exist, and it evacuated the Eastern Branch completely and also reopened the Northern Branch.

The reason for the flooding of the cave (and washing clear of the main channels immediately afterwards) must be searched for in an essentially fluvial event that has, in all likelihood, been damped. The route to the answer is not very long. The only noteworthy surface stream in the catchment of the Rak (Eastern Branch) is the Cerkniščica. Its Late Quaternary development was studied extensively by S Šušteršič (2002a, b), F Šušteršič *et al*. (2002), and F and S Šušteršič (2003). They confirmed an older observation (Pleničar, 1953) that before the Würm (Šercelj, 1974) Cerkniško Polje had no surface inflow and was at the most flooded to a lesser extent than presently. Most – if not all – of the water that entered the polje drained through the *Northern ponors*, and was directed straight to the sources of the Ljubljanica near Vrhnika. The situation changed partially by the end of Würm I, when the Begunjščica/Cerkniščica[7] found its way into the polje basin (S Šušteršič, 2002a).

As a direct consequence of increased gravel production in the upper part of its basin during the colder period of Würm II, the Cerkniščica's extensive alluvial cone covered and eventually eliminated the *Northern ponors*. Consequently, the greater part of the inflow into the Cerkniško Polje basin turned northwestwards, through the Rakov Škocjan Valley, towards the Malni Spring at Planinsko Polje.

It is difficult to estimate the increase of discharge towards the Malni directly. The volumes of the collapse dolines behind the area of the Cerkniško Polje *Northern ponors* indicate that flow there was abundant and, at a given moment, all the polje waters could escape through them, avoiding Planinsko Polje. When deflected, a flow of $14.40 m^3s^{-1}$ (F Šušteršič *et al.*, 2002b; F Šušteršič and S Šušteršič, 2003) might have turned towards Rakov Škocjan, i.e. into the immediate hinterland of the Malni. Even if only half of this quantity penetrated the present conduits of Planinska jama, the Pivka (its average discharge is $4\ 84 m^3s^{-1}$ / Žibrik *et al.*, 1976, 49, Tab.2) would be unable to cope with it, the Rak could have pushed its way through wherever it found it most suitable.

Timing of the reversal can be estimated fairly well. Coarse material within the Cerkniščica alluvial cone must have been deposited after 55ka b.p. as this is the age of a spruce cone found in its base (Šercelj, 1974; Gospodarič and Habič, 1979). On the other hand, Planinska jama must have been finally washed clear of most of its gravel (originating from Planinska koliševka) before the end of Würm II (30ka b.p.), because bones of *Ursus spelaeus* (which become extinct at this time) lie above the re-transported gravel in Vranja jama (F Šušteršič *et al.*, 2002a).

CONCLUSIONS

Some statements can be made in line with the title of the present paper:

- The present general passage layout in Planinska jama had existed before the Late Pleistocene (statement by Gospodarič, 1976).
- At that time, only the Pivka can be proven to have flowed through the cave.
- Before Würm II, all of the three main branches of the cave, i.e. the Western, Eastern and Northern branches, had been used, in various combinations, by the Pivka only.
- The outlet position swapped between the present cave "entrance" and the Malni Valley, perhaps due to random choking of the springs.
- After Würm I the Begunjščica/ Cerkniščica inundated Cerkniško Polje.
- Growth of the alluvial fan gradually eliminated the main vertical ponors and eventually deflected the main stream westwards, ultimately into the Eastern Branch of Planinska jama.
- Increased inflow from the Eastern Branch stemmed the Pivka and forced it to re-open a long-choked outlet in the area of the present cave "entrance" (and eventually, to reactivate the Northern Branch).
- The river now known as the Unica was created at this time.
- Simultaneously, the inflow into Planinsko Polje might have increased by up to 5 times [8].
- Before the end of Würm II, the newly formed Rak washed the Eastern Branch of Planinska jama clear of older sediments.
- Consequently, the Pivka's local erosional base level subsided and the river could wash the Western Branch clear, through the Northern Branch, in a similarly way to the Rak.
- In the Northern Branch some limestone gravel, re-transported from the Eastern Branch, remained preserved in remote corners.

- Before the end of Würm II redeposition of sediments (conditionally) originating from Planinska jama reached across Planinsko Polje, i.e. into Vranja jama.

And more generally:

- The development in Planinska jama during the last 100ka was very "vigorous", but it did not essentially affect the layout of pre-existing bedrock channels.
- Catastrophic events in cave history are more common than generally expected, and ongoing effects can be very far reaching.
- The present floods in Cerkniško Polje and, indirectly, in Planinsko Polje are consequences of a catastrophic event during Würm II. So, they reflect an unstable transient situation, and they are not a feature inherent in poljes, at least not in these poljes.

The main issues have become clear, though available data do not cover all of the details, and some of them may require revision. Events in Cerkniško Polje directly influenced the development of Planinska jama An apparently independent inundation of Cerkniško Polje by the Cerkniščica and an until-now rather enigmatic flow reversal in the Eastern Branch of Planinska jama are closely related. Clearly the active stream routes that comprise the currently known parts of Planinska jama are only a fraction of the system as a whole. The system would appear completely different, and far more complex, if all of the component passages, many of which must be blocked or completely filled by sediment at present, were known.

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End Notes

1 Würm is the approximate equivalent of the British Devensian Stage.

2 Due to the subtle undertones inherent in the words originally used by Gospodarič, "literal" translation from Slovene into English is not appropriate. To give readers a more accurate impression of the original idea, the present authors have added the expressions shown in (brackets).

3 This follows from Gospodarič's (o.c., Table 3, 112 [134]) estimation that sedimentation of *older laminated loam* is Rissian, and sedimentation of *coloured chert gravel* pre-Rissian.

4 Unfortunately, the presently known gravel occurrences are not large enough to confirm the expected existence of the dipping bed forms that are characteristic of deltaic sedimentation.

5 To give a more accurate impression of the original ideas the present authors have again added the expressions in (brackets).

6 Being somewhat enigmatic, the "fourth catastrophe" (**12**), i.e. the occurrence of *flood loam* in Würm III (Fig.3, 12), is ignored in the ensuing discussion.

7 The pre-reversal river – which did not flow through the present town of Cerknica that gave the present river its name – has been termed the Begunjščica since the time of the pioneer investigations (Melik, 1928; Rus, 1925).

8 This paper is not intended to discuss the wider consequences of the development history that is presented In any case, the floods in Planinsko Polje augmented (if they appeared at all, before) and reactivated the caves in its extreme northern corner (Zötl, 1989; F Šušteršič, 2002).

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