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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

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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

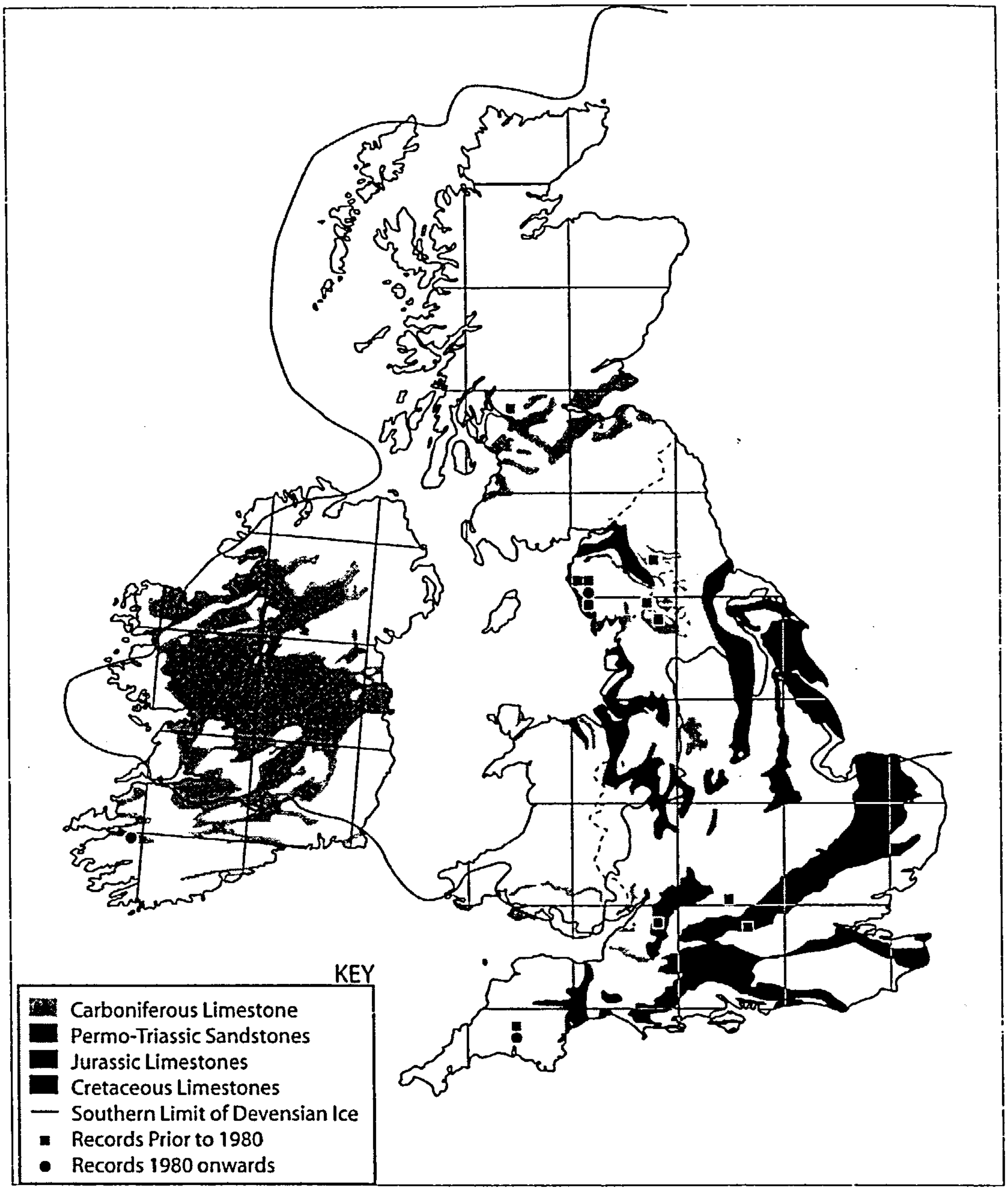
There are very few published records of hypogean species Of more than 50 ostracod species mentioned by Meisch (2000) as being stygobitic or stygophilic in Europe, only about half have been recorded in Britain (and not always in groundwater habitats) *Potamocypris fallax* was recorded in Ingleborough 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

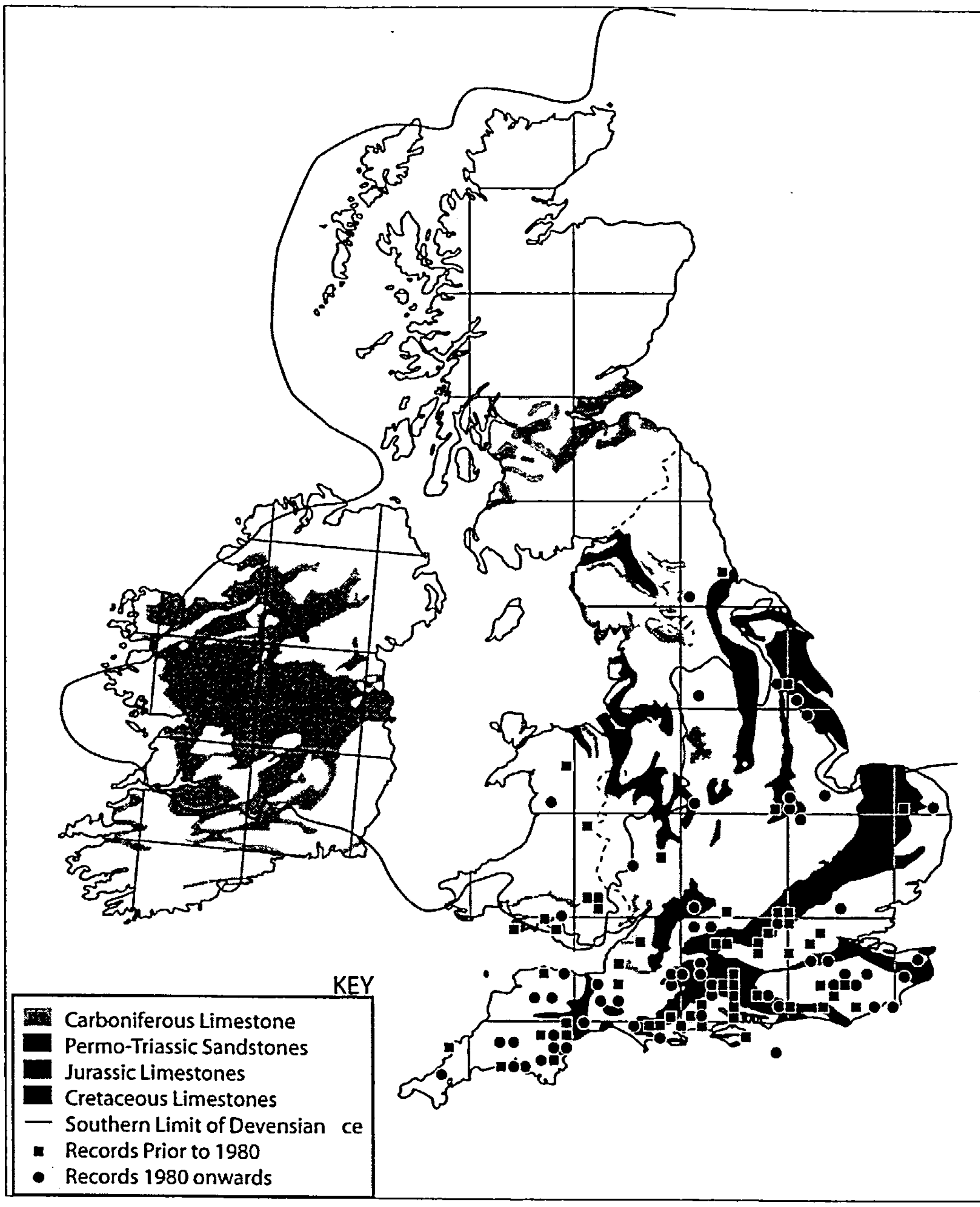


Figure 2. The distribution of Niphargus aquilex *by 10km squares*

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)

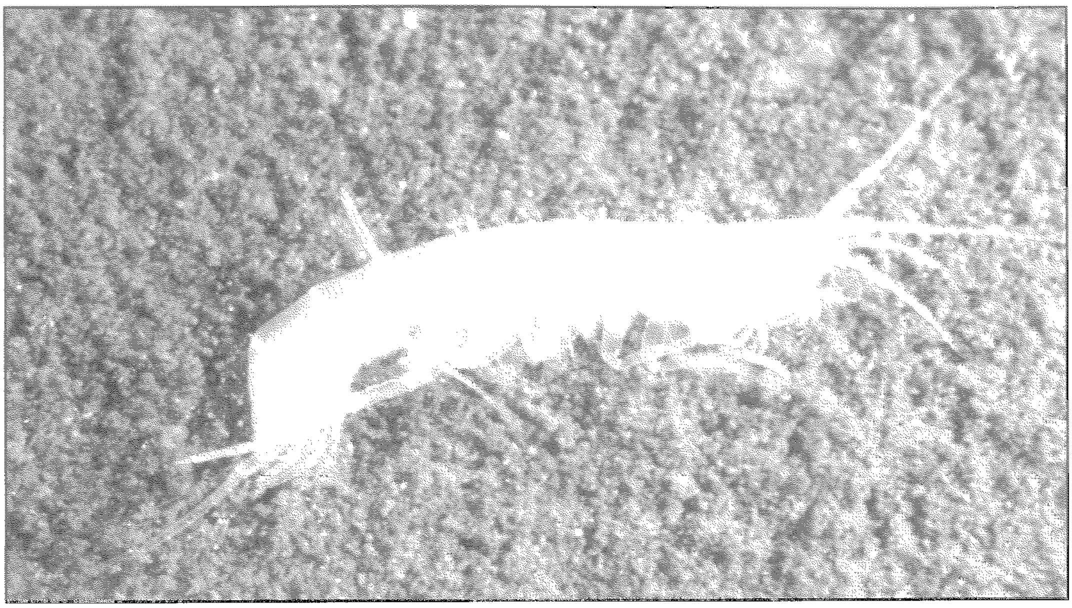
***Niphargus fontanus* Bate, 1859** (Fig 3 and Fig 4)

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



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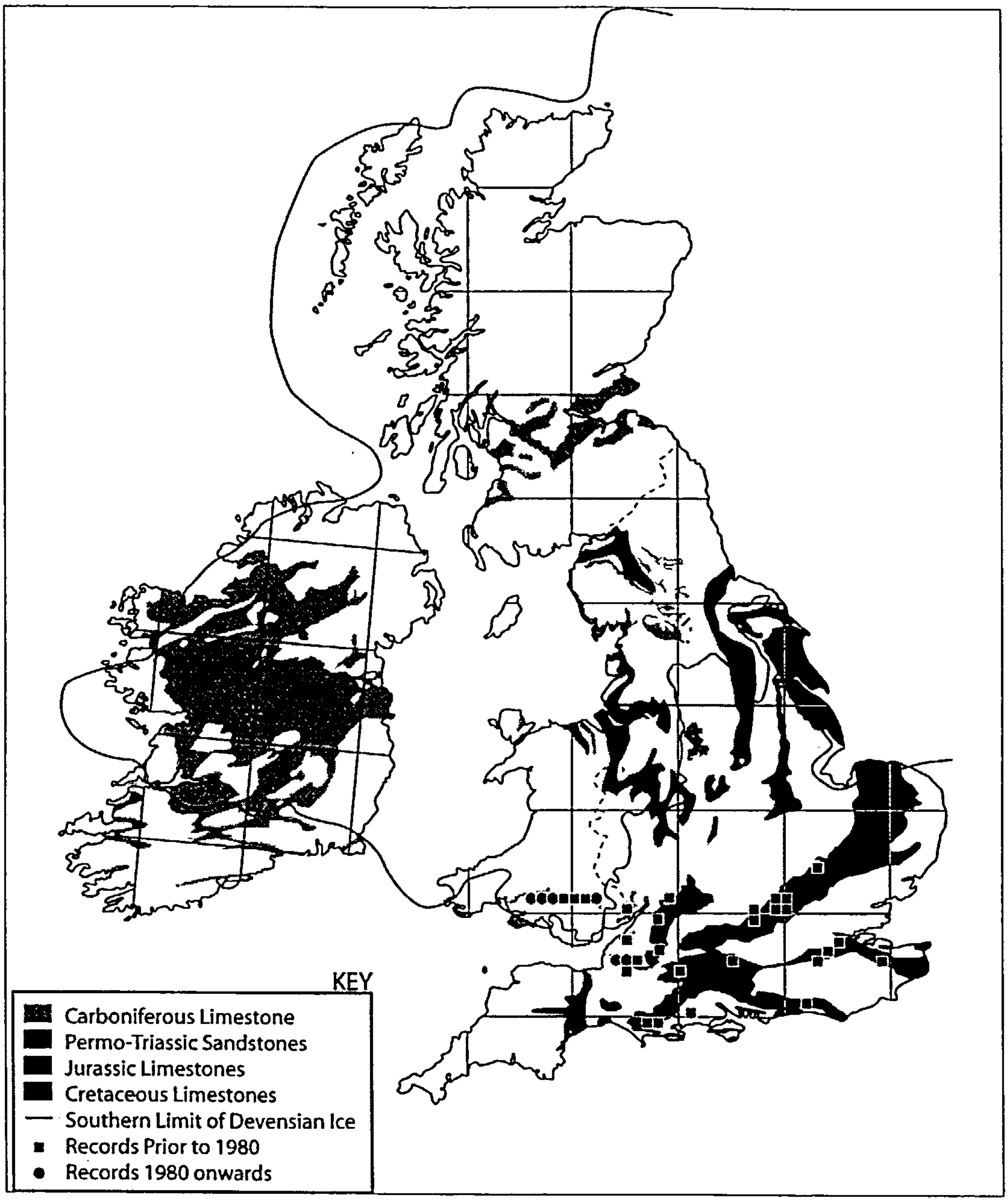


***Figure 4.** The distribution of* Niphargus fontanus *by 10km squares*

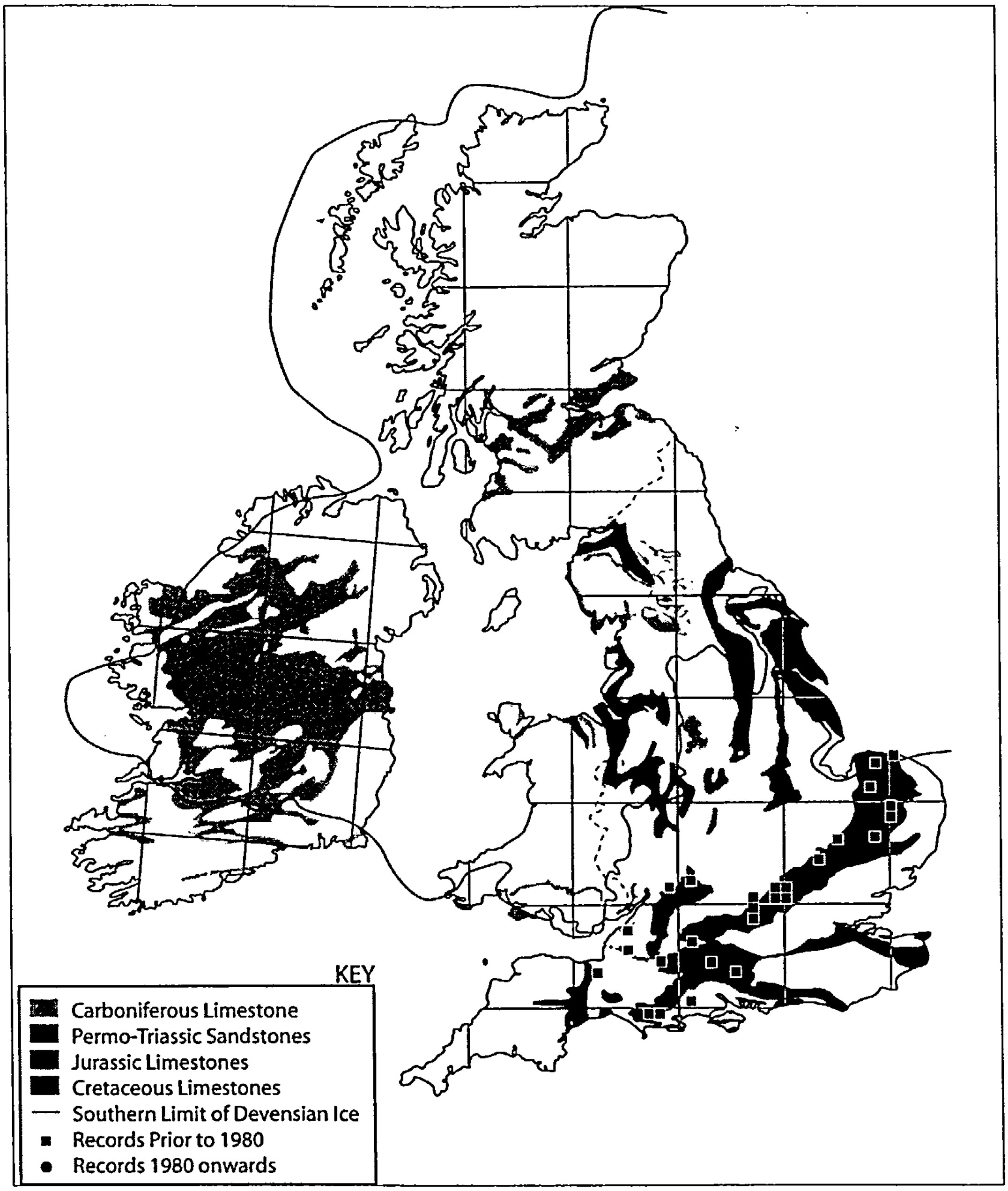
numbers have been collected near Puddletown in Dorset c 40km away (Gledhill, 1977; Stock and Gledhill, 1977) It would be sensible to look for this species in the North and South Downs In the light of the records of *N aquilex* in northern Lincolnshire it would also be sensible to look in the Cretaceous 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)

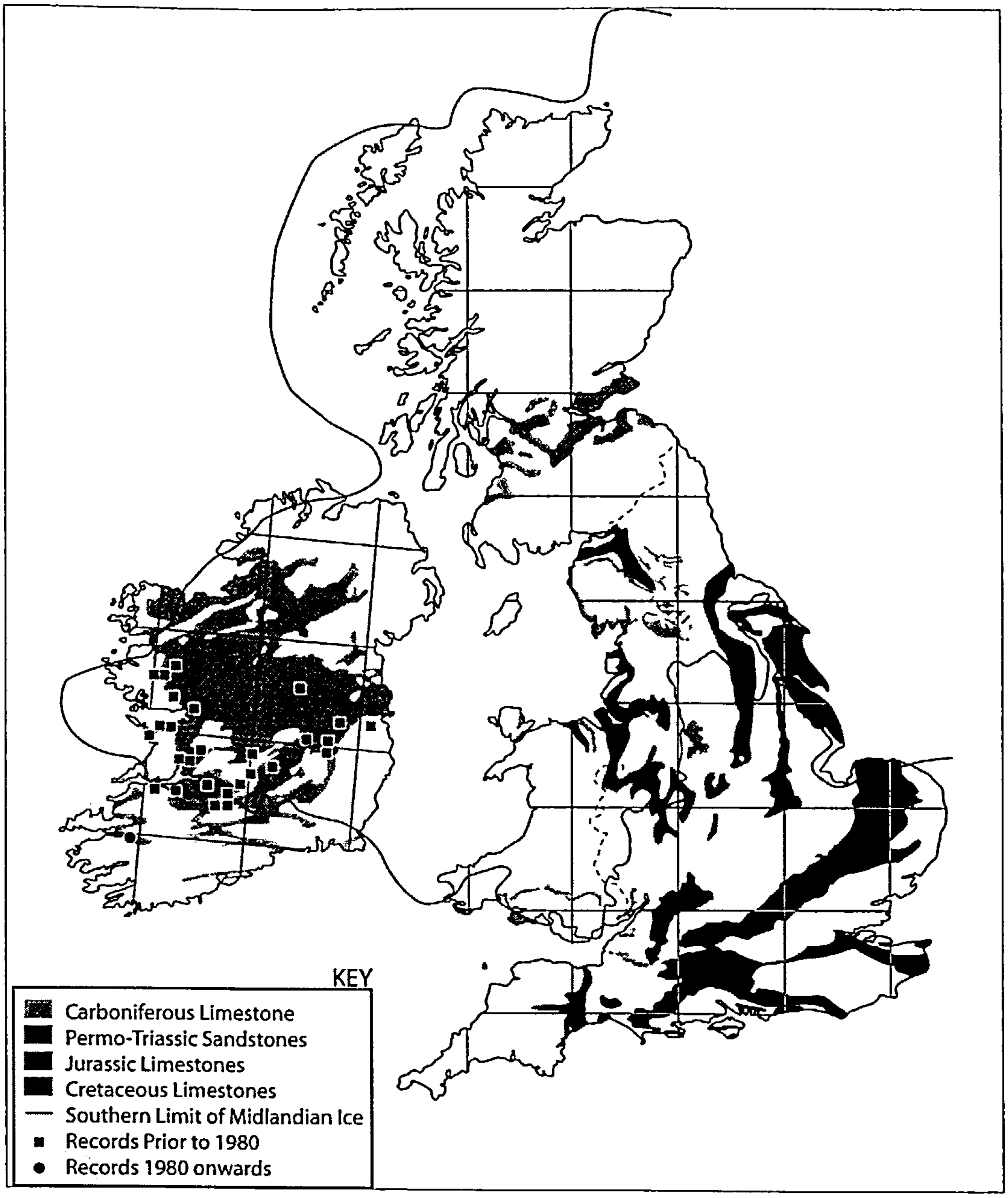


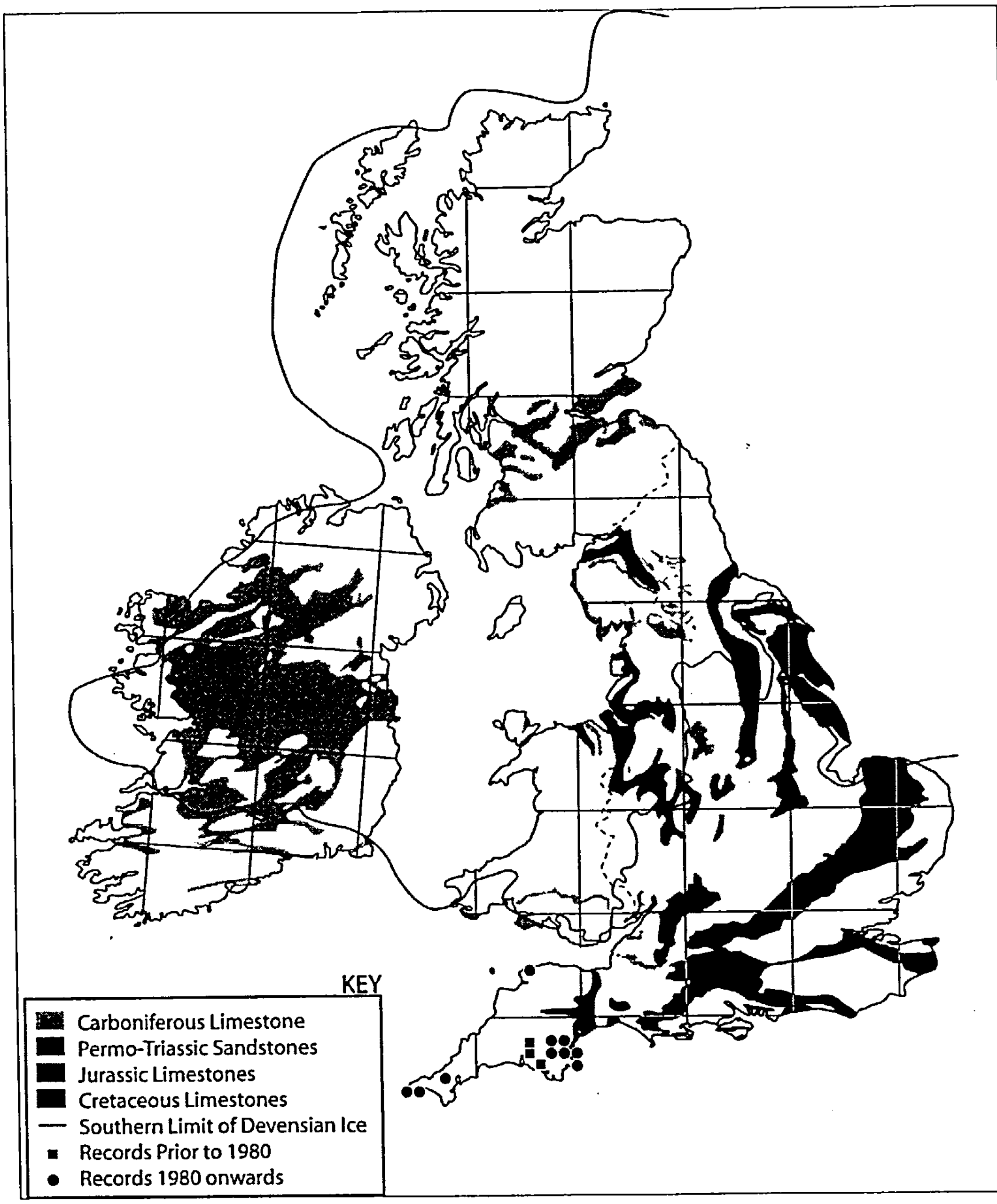
Figure 6. The distribution of Niphargus kochianus irlandicus *by 10km squares*

***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

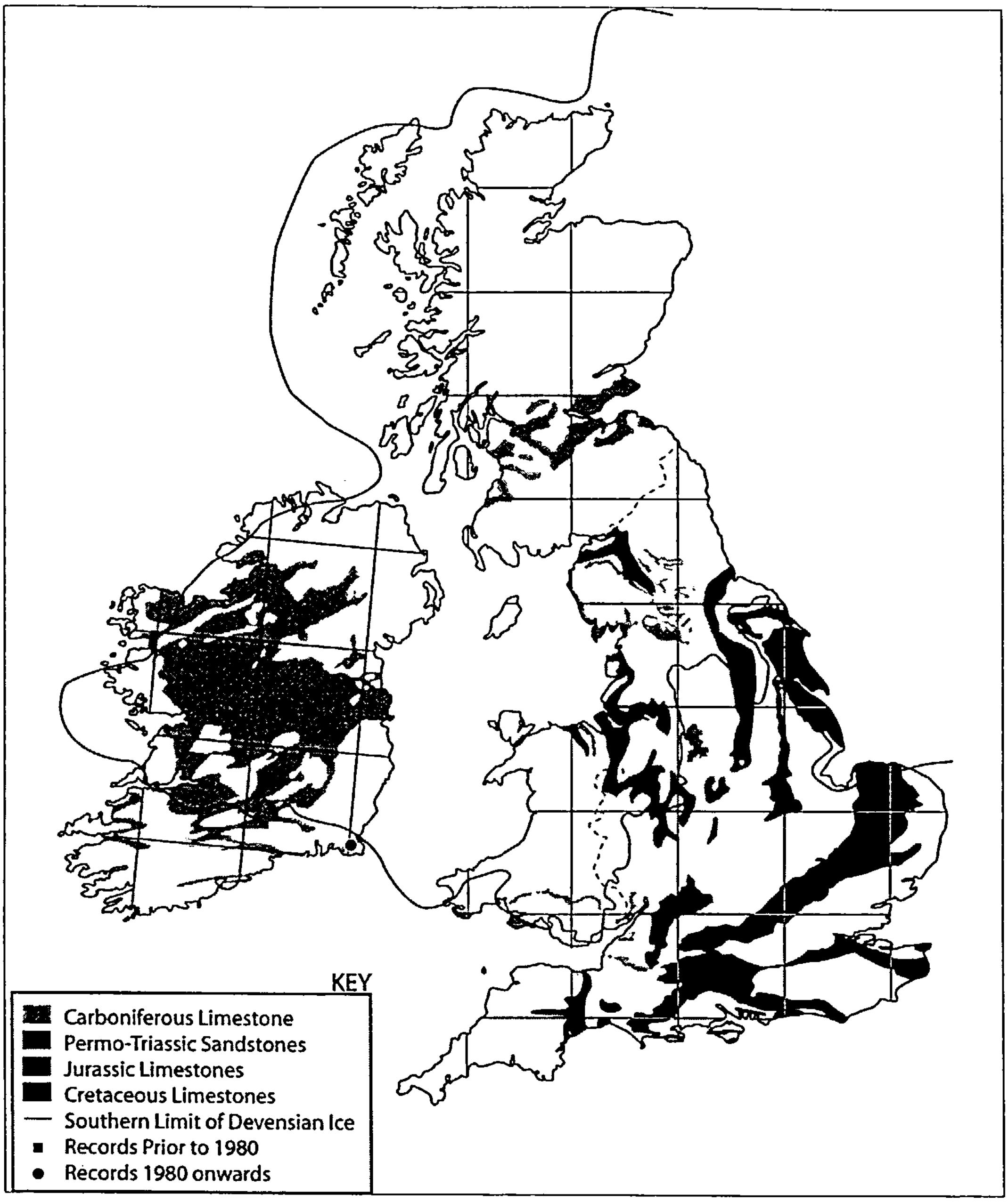


Figure 8. *The distribution of* Niphargus wexfordensis

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)

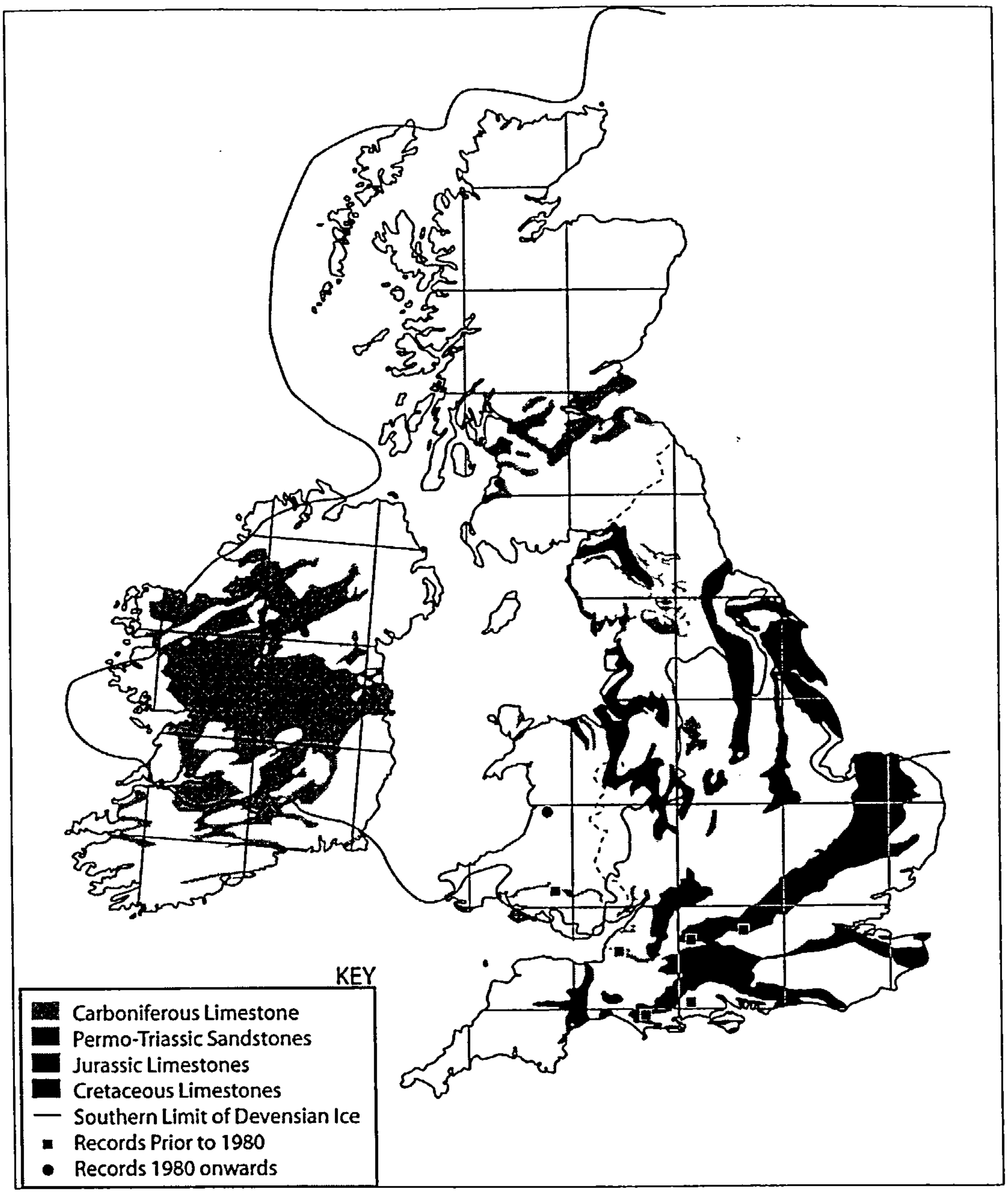
[A note on the generic name *Rivulogammarus* In many of the records of *G pulex* published in the Biological Records (see above for references), and derived works (e g Dixon, 1974), the generic name used is *Rivulogammarus* rather than *Gammarus* Stock (1969) has shown that *Rivulogammarus* is an invalid 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

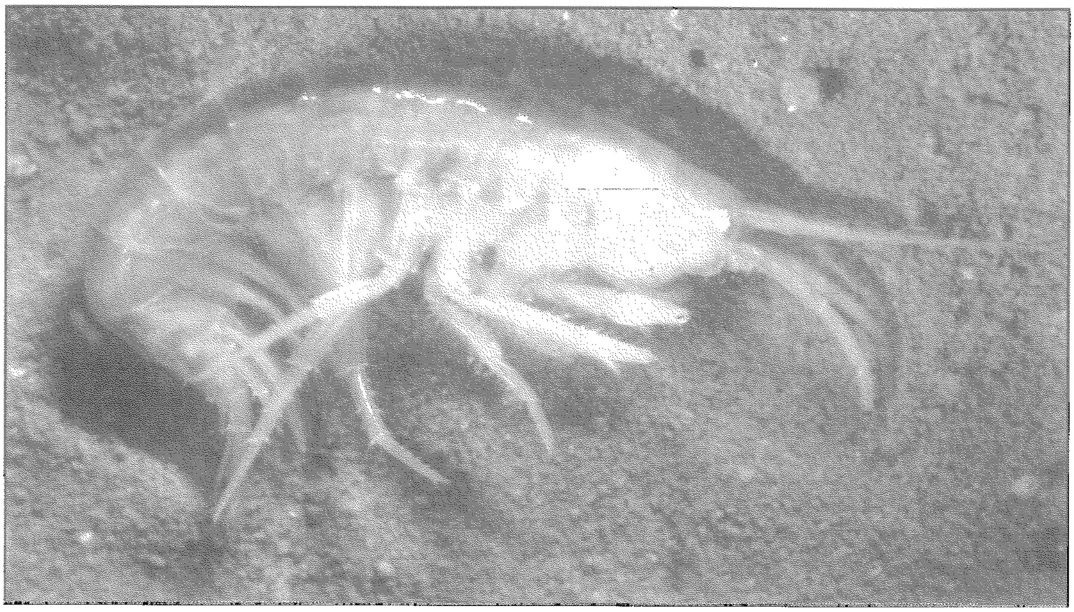
If Britain and Ireland were totally sterilized by glacial and permafrost conditions, the current populations must have arrived here from unglaciated areas It is likely that the majority of animals dispersed here from refugia in the south, particularly the Balkans (Hewitt, 1999, 2000; Rundle *et al*, 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



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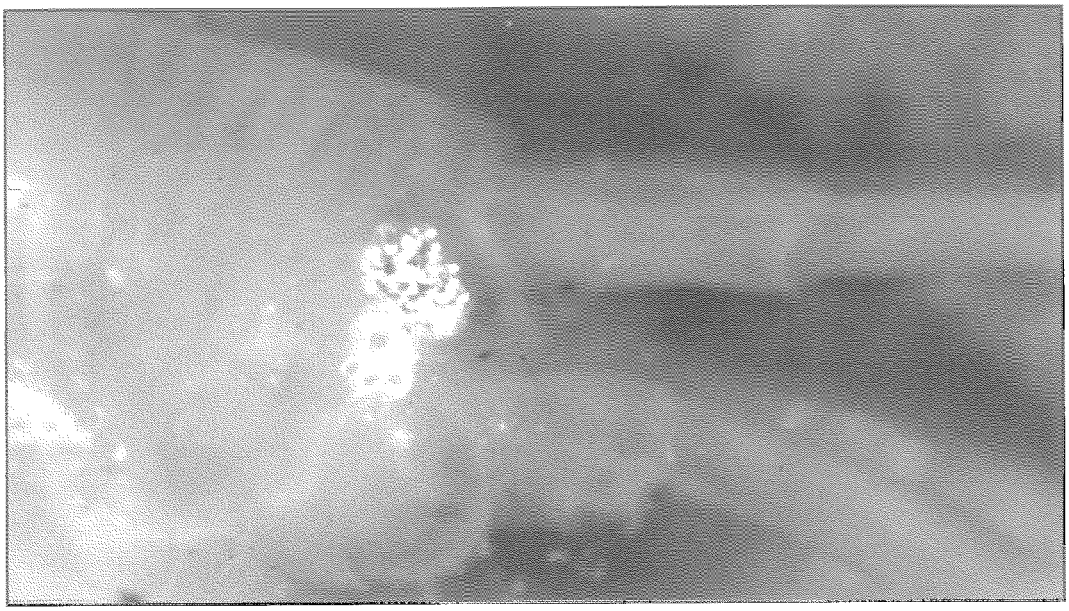

layer of snow or ice above it If epigean fish and other animals managed to survive close to the ice then it seems reasonable to hypothesize that hypogean animals could exist in cave and groundwater habitats if sufficient energy resources (food) were available

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

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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

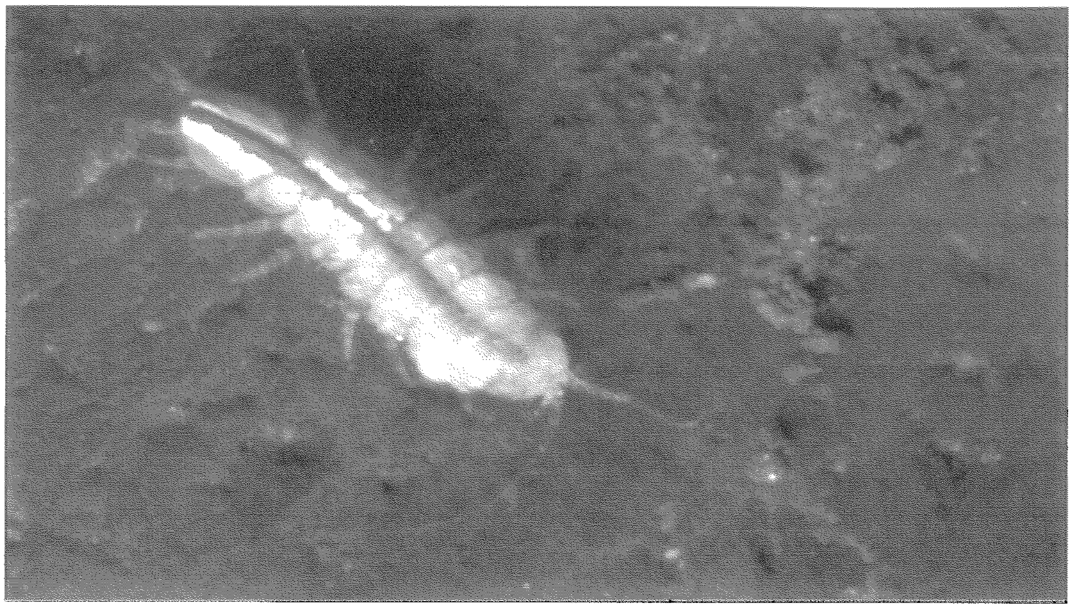
The genus *Niphargus* is distributed throughout Europe and contains over 200 species (Karaman and Ruffo, 1986) Of these Britain and Ireland have two species found in Europe (*N aquilex*, and *N fontanus*) and four endemic taxa (*N kochianus kochianus* [though Vonk (1988) and Ginet (1996) suggest that 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



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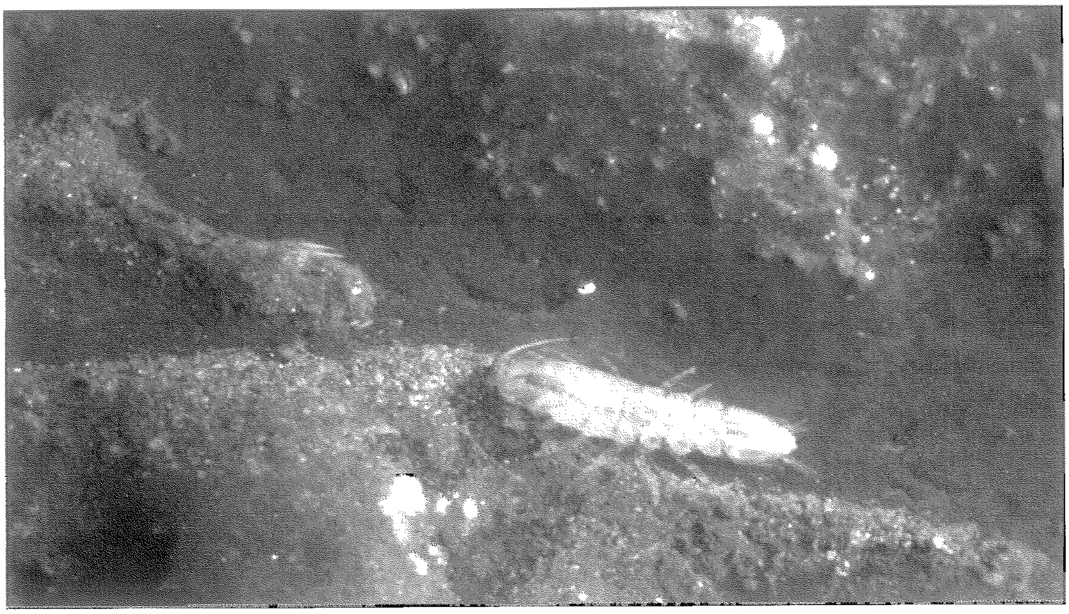

Figure 13. Proasellus cavaticus *feeding (?) on fungal hyphae in Otter Hole Photograph by Phil Chapman*

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

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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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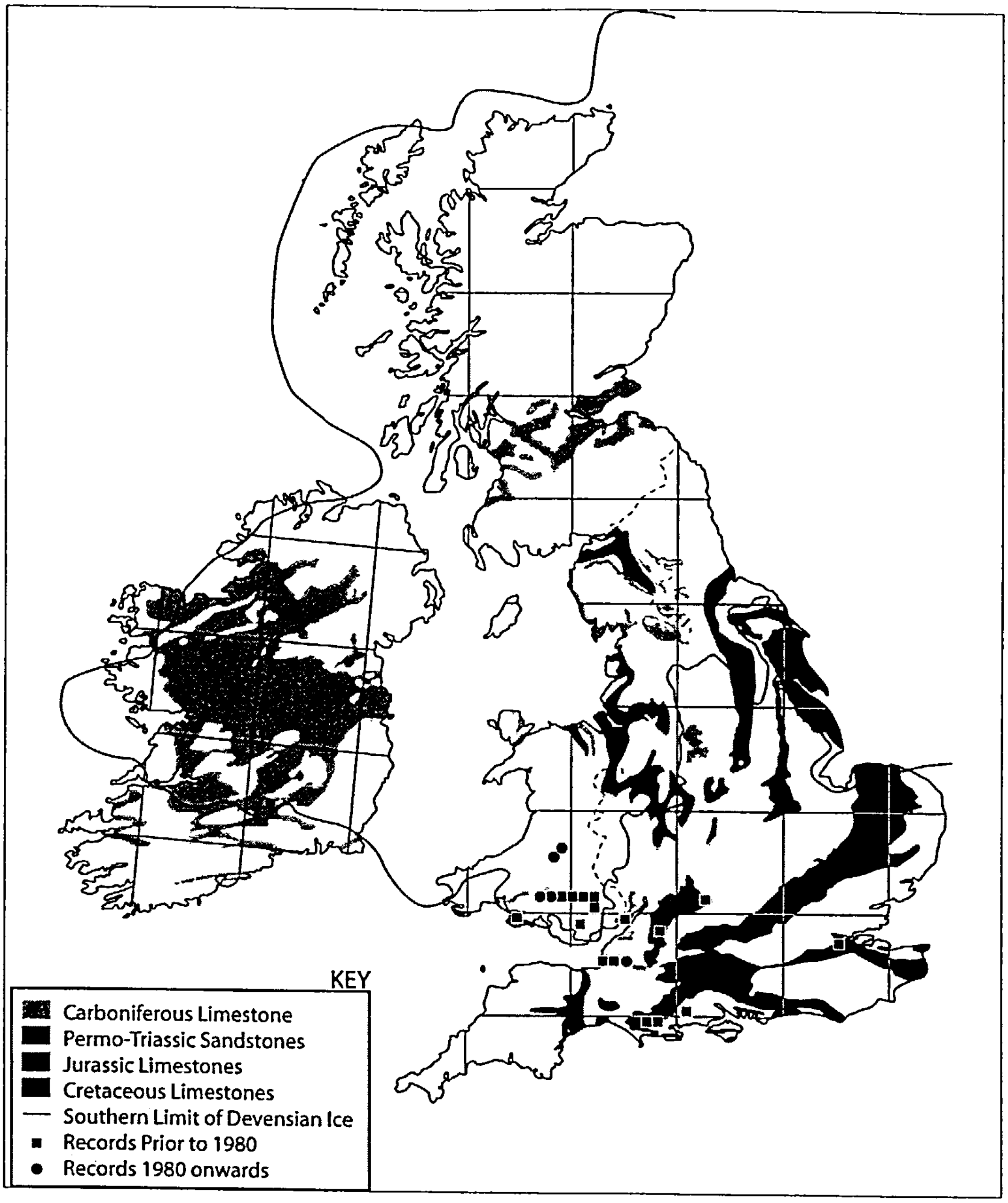

Figure 14. The distribution of Proasellus cavaticus *by 10km squares*

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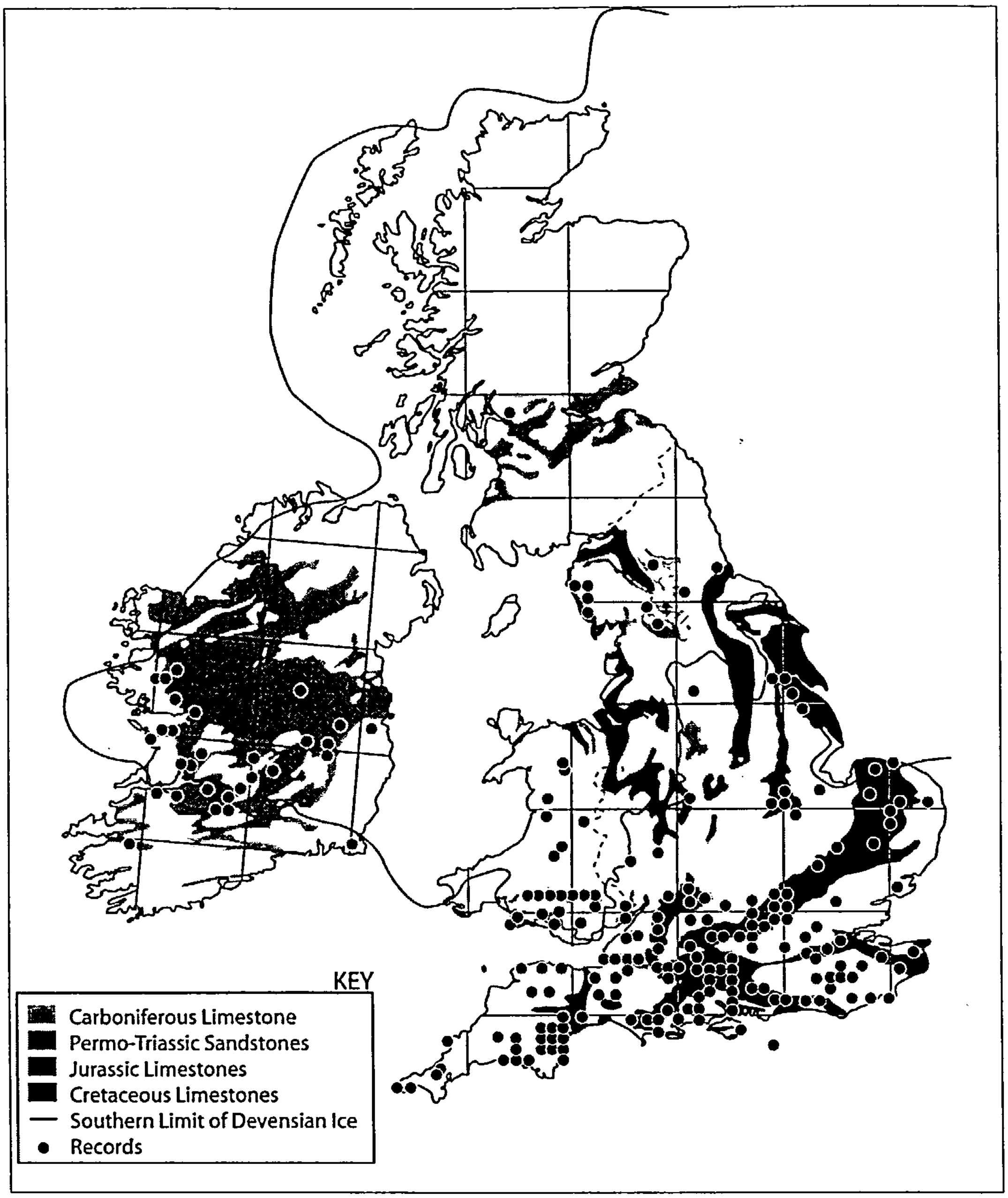
Figure 15 Total records of all stygobitic Crustacea (by 10km squares) to show coverage There are many gaps where no recording has taken place



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