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Several million years of stability among insect species because of, or in spite of, Ice Age climatic instability?

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There is a curious paradox in the evolutionary legacy of Ice Ages. Studies of modern species suggest that they are currently evolving in response to changing environments. If extrapolated into the context of Quaternary Ice Ages, this evidence would suggest that the frequent climatic changes should have stimulated the evolutionary process and thus increased the rates of change within species and the number of speciation events. Extinction rates would, similarly, be high. Quaternary insect studies call into question these interpretations. They indicate that insect species show a remarkable degree of stability throughout the Ice Age climatic oscillations. The paradox arises from the apparent contradiction between abundant evidence of incipient speciation in insect populations at the present day and the evidence that, in the geological past, this apparently did not lead to sustained evolution.

Keywords: Quaternary; Coleoptera; ecology; evolution; biogeography

1. INTRODUCTION

Insects are by far the most diverse of all terrestrial animals and are adapted to most habitats apart from the fully marine. Their remains are remarkably abundant in Quaternary freshwater deposits that have accumulated under anaerobic conditions, for example at the bottom of ancient ponds or peat bogs. They occur commonly in archaeological contexts wherever there are waterlogged sediments. They are also found in permanently frozen ground or in dry places where desiccation ensures long-term preservation. They are not usually recovered from deposits that have been oxidized because the fossils easily decompose in these circumstances where they are attacked by fungi and bacteria.

The most robust group of insects are the Coleoptera (beetles) whose tough exoskeletons survive in large numbers in all manner of waterlogged deposits. Furthermore, in terms of the number of known species, they are extremely varied so that they comprise approximately one-quarter of all the species of animals and plants combined and actually outnumber the flowering plants (Southwood 1978).

These beetle fossils present a wide range of intricate morphological features that are often specifically consistent. Since, for the most part, entomologists studying modern insects use characteristics of the exoskeleton to identify and differentiate between species, and since these same features are available on the fossils, the palaeoentomologist can use exactly the same criteria to identify species. Our respective species' concepts are thus identical and the same nomenclature can be used for both modern and fossil species. This is in contrast to so many other branches of palaeontology where the fossils only possess a small selection of the characteristics available to the present-day taxonomist.

Much of classical palaeontology deals with fossils that date from millions of years ago whose strangeness and remoteness in time makes their interpretation difficult to relate to present-day organisms and evolutionary processes. Palaeontological events occur in 'geological time' whereas modern biology takes place in 'ecological time'; in what is, by comparison, a single instant. Quaternary time spans these two positions, dealing with the direct precursors of the modern biota. Many of the fossils are either identical to living species or closely related to them, so that their ecological preferences can be more precisely understood and their taxonomy related to well-understood living relatives.

These insect fossils should be excellent subjects for the investigation of the course and process of evolution by bridging the gap between studies of living animals and their direct ancestors. Since insect species are highly specialized, being precisely adapted to their habitats, they would seem to have been vulnerable to past environmental changes. Furthermore, their high reproductive rate (on average, they produce one generation per year) would give natural selection ample opportunity to alter the proportions of the alleles in the gene pools as living conditions altered. It would seem that insects provide an excellent model with which to check evolutionary and biogeographical hypotheses.

2. QUATERNARY INSECT FAUNAS

One of the most interesting results of the resurgence of interest in Quaternary entomology has been the discovery that almost all fossil specimens match precisely their modern equivalents. These similarities even extend to the intimate intricacies of their male genitalia, which can be

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dissected out of compressed abdomens frequently found in the fossil assemblages (e.g. Coope & Angus 1975). Species morphologically identical with those of the present day can be traced back to the earliest Quaternary and even into the uppermost Tertiary, namely several million years ago (Elias & Matthews 2002).

During the Quaternary period (the past 2.4 Myr), there have been drastic changes in the world climates reflected, notably, in the extent of continental ice sheets. Traditionally these oscillations between glacials and interglacials would have been expected to lead to numerous extinctions, as well as new opportunities for speciation, as small populations were isolated in refuges or colonized newly available ground as the ice retreated. Yet these expectations are not borne out by the ample evidence of Quaternary insect fossil species in which stasis appears to have prevailed for millions of years despite this climatic instability.

This paradox, in part, accounts for the natural reluctance shown by many entomologists to become involved in what was seen to be of only marginal importance: after all, they had the whole spectrum of modern species to deal with and they are legion. There were two widely held, but erroneous, beliefs that lay at the bottom of this reluctance. The first of these was that insect species were hard to identify from isolated fragments by those accustomed to looking at the whole animal. Furthermore, keys to identification could not be used on fossil specimens from which the diagnostic features were frequently absent. These problems are very real but do not make the task impossible, just rather difficult. The second belief that impeded progress in Quaternary entomology was that, since there are so many insect species living today, many of which are restricted to relatively small geographical areas, they would appear to be evolving very rapidly at the present time and might have been expected to have changed significantly during this period. Consequently, because of these expectations little concerted attempt was made to investigate Quaternary insect fossils.

The use of the word fossil in this context needs some qualification here. Quaternary insect remains are not mineralized in the manner of classical palaeontological specimens. The exoskeletons are often beautifully preserved in their original chitin, though much of this apparently superb preservation is rather illusory since their component proteins, waxes and other vulnerable organic molecules have long since decomposed. Attempts have been made to recover DNA from them but, so far, without success. It is possible that better prospects for DNA recovery will come from desiccated specimens.

Ample evidence is available from studies of present-day insect species to show that incipient speciation appears to be occurring at the present time in the form of geographical variants in morphology, physiology and genetics adapting them to local environmental conditions. There is no need to explore the wealth of literature on this subject since it is very well known, complex and convincing.

In the past, this evidence frequently led to the belief that Quaternary fossils were the evolutionary ancestors of living species and could be viewed as extinct. Thus, they were entitled to be given new, often fanciful, names (see, for example, Scudder (1900) and some of the identifications by Lomnicki (1914)). In the few instances where the specimens are still available, it has become clear on re-examination that these new names were unwarranted and that the fossils could be matched precisely with modern forms (see revision of W. D. Pierce's original identifications of the Rancho La Brea coleoptera by Miller (1983, 1997)). It is important to note, however, that some early entomologists did recognize that the fossils were in fact identifiable as modern species (e.g. Henriksen 1933; Lindroth 1948). However, in some of these investigations, the stratigraphy and chronology of the fossil sites were poorly understood and consequently difficult to set in a modern context.

Although recognition of morphological stability among insect species is now demonstrable from the fossil record, the question arises as to the extent to which physiological evolution might have taken place under cover of morphological stasis. This question cannot be answered directly. However, the ecological preferences of a species can be taken as some indication of its physiology. If we assume that a species in a fossil assemblage had, in the past, the same environmental requirements as those of the present day, the picture that emerges makes good ecological sense. In the past, species occurred in the same company as they do today. This does not mean that all past assemblages of species have precise present-day analogues. Their different temporal and spatial contexts may have prevented the coming together of exactly the same groups of species as are found today even if their respective environments are identical. Differences of this kind are particularly evident after periods of sudden and intense climatic change, when the whole flora and fauna were temporarily thrown out of harmony with the physical environment, as each species responded individually, or in small interdependent groups, to the new conditions at their own rate. Whole ecosystems did not respond immediately *en bloc* to climatic changes. The long-term ecological consistency of individual species suggests that morphological stability was accompanied by a similar degree of physiological stasis.

The evolutionary dilemma outlined here may be briefly set out as follows. If incipient speciation, both morphologically and physiologically, can be extensively recognized among insects at the present day, and there is every reason to believe that this is true, what inhibited this process continuing to full speciation; what process set back the evolutionary clock to its 'default' position? Furthermore, it is likely that, in the Quaternary past, there was a similar degree of local geographical incipient speciation to that of the present day. For long-term stasis to have been maintained, the evolutionary clock must have been set back repeatedly throughout the whole of this period.

Traditionally it has been claimed that the frequency, rapidity and intensity of climatic changes during the Quaternary period had profound evolutionary significance, leading to widespread speciation events and large-scale extinctions as cold phases alternated with warm ones. During glacial episodes ice sheets expanded over many of the continental masses at middle latitudes. At such times, vast areas of land adjacent to the ice sheets were covered with tundra-type vegetation and inhabited by mammals and insects that are now largely confined to Arctic regions. Between these glacial periods, the interglacials were characterized, in lowland mid-latitudes, by landscapes with rich forests in which lived animals that, today, live in temperate conditions. Many other lesser climatic oscillations, termed stadials and interstadials, were superimposed on the major fluctuations and these also had considerable effects on both the flora and fauna of the time. In lower latitudes the glacial/interglacial cycles were also represented by temperature oscillations and, in many regions, by large-scale changes in precipitation, though these do not always coincide precisely with the climatic changes elsewhere. All these climatic events would also have had serious biological consequences.

Faced with these severe climatic changes, a species has three possible options: (i) it may become extinct; (ii) it may evolve by natural selection *in situ* to fit the new conditions; or (iii) it can move out of trouble by altering its geographical range to track the locations of acceptable conditions.

It is curious that, in spite of these dramatic climatic events, there is so little evidence among Quaternary fossil insects for widespread extinction (Coope 1995*a*) especially as, intuitively, we should expect that it would have been a common fate of many species in such circumstances. There is ample fossil evidence that many species became locally extinct but little or no evidence of any species becoming globally extinct at this time. This is a common problem when dealing with all negative evidence, which must always be circumstantial. Initially, there were specimens that, though distinctive enough, persistently defied identification and were, hopefully, looked upon as possibly extinct species. However, many of these eventually proved to be extant species living today far from the fossil site where they were found. There are many other fossil specimens that cannot yet be identified, either because their remains are too fragmentary or because they are too nondescript and devoid of any diagnostic characters.

There are, nevertheless, one or two Quaternary fossil beetle species (out of over 2000) belonging to small, well-known, genera that may indeed represent new species (Angus 1997). Yet, even here they do not appear to be the ancestors of any living ones. As with all small and cryptic organisms the possibility is always present that the fossils represent living species whose existence has formerly been overlooked. Thus, evidence for evolutionary change among the Quaternary fossil beetles is remarkably rare.

In contrast to the other two options considered above there is abundant evidence to indicate that the most usual response of insect species to climatic change was to alter their geographical ranges; they simply tracked the whereabouts of acceptable climatic conditions as these changed their locations on the continents (e.g. Coope 1970, 1979, 1995*b*). This has led to some unexpected records. Thus, during the glacial periods many species were abundant in the British Isles that are, currently, exclusively Asiatic. Today, some of these species live in extremely limited areas. For example, *Tachinus caelatus* is currently found only in the mountains near Ulan Bator in Mongolia (Ullrich 1975) but was widespread in Europe right up to the closing stages of the Last Glaciation (Taylor & Coope 1985; Coope & Elias 2000). One of the most abundant dung beetles in Britain during the same glaciation is now confined to the high plateau of Tibet and adjacent western China (Coope 1973). A species of water beetle, *Ochthebius figueroi*, found in deposits laid down at least 43 000 radiocarbon years ago in central England, is now confined to the headwaters of the river Ebro in Spain (Angus 1993). Many other southern species extended their ranges further north into Britain during the warm intervals, including some that today have exclusively Mediterranean distributions (Coope 1990).

In the absence of the fossil record, many of these species with restricted distributions would have been considered 'endemic species' with the associated implication of 'native and originating' where they now live. Their existence as fossils in Britain, at sites so far from their present-day range, casts considerable doubt on the value of using the restricted geographical ranges of the present-day species, as indicators of their evolutionary history. Thus, the Quaternary fossil record can show that the legacy of the Ice Age is much more dynamic than anything that can be inferred from present-day biogeography; reconstructing evolutionary history on the basis of present-day distribution alone is rather like trying to reconstruct the plot of a film from its last few frames.

Our knowledge of biogeographical history is most complete during the last glacial/interglacial cycle, during which many insect species can be shown to have undergone changes in their geographical distributions involving several thousand kilometres. However, there is accumulating evidence that, throughout the Quaternary period, insect species responded to each of the numerous and intense climatic oscillations in a similar manner. It is evident that complex assemblages of temperate insects spread northwards during each of the interglacials and, during each of the cold periods, assemblages of Arctic and continental species extended their distributions well to the south and west of their modern ranges. Thus movements of species in response to Quaternary climatic oscillations involved range changes in all directions and not just northern extensions from southern refugia as studies of present-day, post-glacial, geographical distribution patterns might suggest.

It is important to recognize that tracking appropriate thermal climatic conditions often involves a change of latitude with the associated changes in, for example, photoperiod. All species that can be shown to have moved from one latitude to another must either have been able to adjust to such latitudinal changes or else have been indifferent to them. It is likely that any thermally sensitive species that was tied to a specific latitude, for whatever reason, was unlikely to survive the onslaught of the first glacial cooling. Thus, any search for fossils of extinct species should logically be made among Late Tertiary or earliest Pleistocene assemblages, that is, before the extinction of these latitudinally dependent species.

Of course, the stratagem of tracking acceptable climates only works when there is somewhere to go. On oceanic islands, the option of avoiding trouble is not available and any changes must be endured on the spot. Evolving out of trouble by natural selection may well have been the only option in these circumstances. Moreover, it is likely that climatic oscillations on remote islands may have been damped by the ameliorating effect of the surrounding ocean. Evolution in these circumstances may be more rapid than the more 'normal' rates of change found on the continental masses.

The frequent large-scale movement of insect species in response to Ice Age climatic fluctuations leaves another evolutionary legacy. With each oscillation, populations become isolated from one another as thermophilous ones flee to lower latitudes from the advancing ice sheets during glacial periods, or cold-adapted species find refuge on mountains during the interglacials. Refuges such as these are classical 'evolutionary traps' in which evolution might be expected to have been atypically rapid. However, these traps are readily sprung at the time of the next climatic change when their occupants are freed to associate with other populations released from neighbouring traps. It is likely that these frequent movements in response to climatic changes led to the amalgamation of isolated populations resulting in the eventual mixing of the gene pools and the undoing of all the genetic consequences resulting from their original isolation. This process of separation and recombination would have naturally recurred with every climatic fluctuation but since the mixing may be more or less incomplete each time, populations may carry biogeographical and genetic vestiges of the previous glacial/interglacial cycle. Nevertheless, ultimately, with the large number of climatic oscillations that occurred during the Quaternary, this process was continuous so that a thorough mixing of populations was inevitable. It is suggested that this repeated stirring of the gene pools resets the evolutionary clock to zero each time the climate changes. If this explanation is true, evolutionary stasis should be viewed as a direct consequence of Ice Age climatic instability. As Sheldon (1996) so elegantly points out, 'plus ça change, plus c'est la même chose' is a relevant model for many groups of fossils throughout the entire palaeontological record.

3. PRE-GLACIAL INSECT FAUNAS

Several insect faunas have recently been investigated that pre-date the major onset of the glacial/interglacial cycles. So far, most of these originate from North America but there is no reason why Late Tertiary terrestrial deposits in Europe should not also yield fossil insect assemblages. There is evidence from these faunas for both evolutionary change and extinction of species.

Even among Late Tertiary insect faunas, the evidence for evolutionary change among the fossil beetles is remarkably rare. The best-documented examples have been described by Matthews (1976) from Late Tertiary (Late Miocene and Pliocene) sites in Alaska and Arctic Canada. He illustrated statistically the reduction of the already vestigial wings and the elytra of *Tachinus apterus* in a succession of fossil assemblages (Matthews 1974). A second example of apparent evolutionary change concerns the alterations in sculpture on the elytra of Late Miocene precursors of *Helophorus tuberculatus* (Matthews 1976). However, in another study on the genus *Micropeplus*, a suggested ancestral type (Matthews 1970) has recently been discovered living in Siberia under the name *Micropeplus dokuchaevi* Rjabukhin (opinion of M. J. Campbell in Elias (1994)); a cautionary tale that stems from working with small, cryptic species.

Insects that lived at a time before the onset of the Quaternary climatic oscillations generally show a remarkable degree of species constancy, most of the fossils representing extant species. It has recently been shown that even as far back as upper Miocene times (about 5.8 Ma) beetle assemblages indicate patterns of climatic changes, estimated by the Mutual Climatic Range method (Atkinson *et al.* 1987). They suggest large-scale climatic variations that are in agreement with inferences drawn from the associated fossil floras (Elias & Matthews 2002). Major climatic fluctuations would seem to have been taking place millions of years before the Quaternary Ice Age. The ecological consistency of the evidence from both fossil plants and insects from these sites suggests that physiological stability, as well as morphological constancy, can be traced back to long before the Quaternary climatic oscillations.

One of the most unusual of these early insect faunas has been described by Böcher (1995) from Kap København, eastern Peary Land, north of Greenland, within latitude 7° of the North Pole. Here, a rich assemblage of 155 fossil insects has been obtained that dates from latest Pliocene/earliest Quaternary *ca.* 2.5–2.0 Ma, i.e. from near the period of the first climatic oscillation that ushered in the Quaternary glacial cycles. This assemblage included tree-dependent species as well as wood fragments bored by long-horned beetles, indicating that trees or even small forests similar to those near to the northern timber limit at the present-day grew there at that time. Almost all the insect species represent living forms, though three of them appear to belong to extinct species. One of these species, *Diacheila* named *matthewsi*, is also found as a fossil in Alaska. The climate of north Greenland at the time was clearly considerably warmer than it is today.

Undoubtedly, other examples of evolutionary change and extinctions among insects will be found, but they should be sought within fossil assemblages from other regions in deposits that date from several million years ago. Present-day species would seem to have a long pre-Quaternary history. Ice Age climatic instability was not alone in maintaining species stasis.

4. EVOLUTIONARY LEGACY OF ICE AGES: A SUMMARY

There is now a large and complex literature on the possible origins of evolutionary stasis and it would be inappropriate to enter this discussion. Long-term stasis remains an interesting but rather intractable problem when viewed entirely from the point of view of living species. Its satisfactory resolution can be approached only by a combination of palaeontological, biogeographical and genetic enquiry. This problem is invariably avoided by current evolutionary texts, which concentrate on the role of environmental change and on natural selection as the mainspring of evolutionary change. While few would doubt that this is indeed true, the abundance of examples of evolutionary change in the literature perhaps results from a bias in their favour; there are no accolades for those who show that evolution did not happen. Traditionally, evolutionary stasis is seen as marginal and exceptional. However, the evidence from Quaternary fossil insects suggests that stasis is in fact the norm. Certainly, in the temperate zones, there is abundant evidence that millions of years (= generations) of species stability appear to be the usual state of affairs in the natural environments on the continental masses. Unfortunately, there are currently no data available on the Quaternary history of insect species in the tropics, though this may be available in high-altitude peat accumulations. The classical examples of evolutionary changes on remote islands provide excellent models of the evolutionary processes but these are atypically rapid and, fascinating though these examples are, they have only a limited relevance to our understanding of the rates of change and evolutionary history of mainland populations.

Whatever the outcome of the debate about the mechanism of evolutionary stasis, the Ice Age imposed its own special potentialities and limitations on the evolutionary process. Contrary to intuitive expectations, rapid and intense changes in Ice Age climates did not lead to rapid evolution among insects, nor did they lead to large-scale extinctions. It is true that they led to the extermination of local populations of both animals and plants and their replacement by different suites of species, which had clearly survived elsewhere to recolonize the old area when climates reverted once again to their former condition. Movements of populations often meant that species changed their geographical distributions by thousands of kilometres even within a single glacial/interglacial cycle. It is now possible to allocate these faunal changes to their precise stratigraphical position and to set them in a reliable time framework.

The evolutionary significance of this dynamic view of recent faunal history is threefold. First, if species track acceptable thermal climates across the continents, the conditions in which they live may have remained largely the same; in a sense, it was the geography that changed. There would be little imperative for any evolutionary change. In these circumstances, species could be honed to precise adaptive relationships over many generations despite the intense climatic changes, and stabilizing selection could operate to increase specialization in species in spite of climatic variability. Second, the large-scale movements of populations under the pressure of climatic changes ensured that formerly isolated populations would be amalgamated frequently (gene pools were kept well stirred) and the genetic consequences of isolation broken down. As suggested above, it is this mechanism that repeatedly set back the evolutionary clock to its ‘default’ position. Third, since climatic zones are, to a large extent, determined by latitude, only those species populations that can change their latitude as the conditions vary would be able to adjust as the climate fluctuated. Those species that could not make such an adjustment would have become extinct at the beginning of glacial/interglacial cycles, i.e. in Late Tertiary times. The species that cleared the first fence of the climatic hurdle race could similarly clear all the rest. Thus the species of the fauna (and presumably also the flora) that are living today are already a selected assemblage of the geographically mobile and latitudinally independent. When the next major climatic change takes place, these species will simply adopt the same stratagem to avoid the climatic changes (unless human activities preclude such an option) that served them so well in the past.

On the negative side, the fossil evidence of great changes in species distribution in the geologically recent (and evolutionarily relevant) past means that present-day distributions are not necessarily a reliable indication of evolutionary or biogeographical history. It provides a cautionary tale that endemism, by itself, should be used with great care as an indicator of the location of evolutionary origins. If we are to look for evidence of evolution among insects, the fossil record, derived as it is solely from temperate latitudes, may not be the place to look. Paradoxically, Quaternary fossil insect assemblages from tropical latitudes, where the climatic oscillations may not have been so extreme, may produce evidence of both phyletic change and extinctions. Thus, on a final cautionary note, the extensive fossil records so far available are from the Northern Hemisphere only and may themselves, ultimately, transpire to be atypical.

At the beginning of this paper, the question was posed: was species constancy among insect species a result of, or in spite of, Ice Age climatic inconstancy? In the light of what has been discussed above, a small change of wording now seems necessary. The word ‘or’ could be replaced by ‘and’ since it now seems likely that both factors were involved. Much species stasis apparently predates the Quaternary period but it was maintained by the frequent genetic mixing resulting from the numerous and intensive climatic oscillations of the Quaternary Ice Age.

REFERENCES

Angus, R. B. 1993 Spanish ‘endemic’ *Ochthebius* as a British Pleistocene fossil. *Latissimus* **2**, 24–25.

Angus, R. B. 1997 Challenges and rewards in the identification of Pleistocene fossil beetles, with the description of a new species of *Hydraena* Kugelann (Coleoptera; Hydraenidae) from the Hoxnian interglacial. *Quatern. Proc.* **5**, 5–14.

Atkinson, T. C., Briffa, K. R. & Coope, G. R. 1987 Seasonal temperatures in Britain during the past 22 000 years, reconstructed using beetle remains. *Nature* **325**, 587–592.

Böcher, J. 1995 Palaeoentomology of the Kap København Formation, a Plio-Pleistocene sequence in Peary Land North Greenland. *Meddelelser om Grøland* **33**, 1–82.

Coope, G. R. 1970 Interpretations of Quaternary insect fossils. *A. Rev. Entomol.* **15**, 97–120.

Coope, G. R. 1973 Tibetan species of dung beetle from Late Pleistocene deposits in England. *Nature* **245**, 335–336.

Coope, G. R. 1979 Late Cenozoic fossil Coleoptera; evolution, biogeography and ecology. *A. Rev. Ecol. Syst.* **10**, 247–267.

Coope, G. R. 1990 The invasion of northern Europe during the Pleistocene by Mediterranean species of Coleoptera. In *Biological invasions in Europe and the Mediterranean basin* (ed. F. di Castri, A. J. Hansen & M. Debussche), pp. 203–215. Dordrecht, The Netherlands: Kluwer.

Coope, G. R. 1995*a* Insect faunas in Ice age environments: why so little extinction? In *Extinction rates* (ed. J. H. Lawton & R. M. May), pp. 55–74. Oxford University Press.

Coope, G. R. 1995*b* The effects of Quaternary climatic changes on insect populations: lessons from the past. In *Insects in a changing environment* (ed. R. Harrington & N. E. Stork), pp. 30–49. London: Academic Press.

Coope, G. R. & Angus, R. B. 1975 An ecological study of a temperate interlude in the middle of the last glaciation, based on fossil Coleoptera from Isleworth, Middlesex. *J. Anim. Ecol.* **44**, 365–391.

Coope, G. R. & Elias, S. A. 2000 The environment of upper Palaeolithic (Magdalenian and Azilian) hunters, interpreted from coleopteran remains. *J. Quatern. Sci.* **15**, 157–175.

Elias, S. A. 1994 *Quaternary insects and their environments*. Washington, DC: Smithsonian Institution Press.

Elias, S. A. & Matthews Jr, J. V. 2002 Arctic North American seasonal temperatures from the latest Miocene to the Early Pleistocene, based on mutual climatic range analysis of fossil beetle assemblages. *Can. J. Earth Sci.* **39**, 911–920.

Henriksen, K. L. 1933 Undersøover Danmark-Skanes kvartaere Insectfauna. *Vidensk. Medd. dansk naturh. Fören. Kbh.* **96**, 77–355.

Lindroth, C. H. 1948 Interglacial insect remains from Sweden. *Sverig. geol. unders.* **C41**, 1–29.

Lomnicki, A. M. 1914 The invertebrates from the mammoth shaft. *Wydaw. Muz. Dzieduszyck.* **15**, 37–98. [In Polish.]

Matthews Jr, J. V. 1970 Two new species of *Micropeplus* from the Pliocene of western Alaska with remarks on the evolution of Micropeplinae (Coleoptera: Staphylinidae). *Can. J. Zool.* **48**, 779–788.

Matthews Jr, J. V. 1974 Quaternary environments at Cape Deceit (Seward Peninsula, Alaska): evolution of a tundra ecosystem. *Bull. Geol. Soc. Am.* **85**, 1357–1384.

Matthews Jr, J. V. 1976 Evolution of the subgenus *Cyphelophorus* (genus *Helophorus*, Hydrophilidae, Coleoptera): description of two new fossil species and discussion of *Helophorus tuberculatus* Gyll. *Can. J. Zool.* **54**, 652–673.

Miller, S. E. 1983 Late Quaternary insects from Rancho La Brea and McKittrick, California. *Quatern. Res.* **20**, 90–104.

Miller, S. E. 1997 Late Quaternary insects of Rancho La Brea, California, USA. *Quatern. Proc.* **5**, 185–192.

Scudder, S. H. 1900 Canadian insect fossils. *Contrib. Can. Palaeontol.* **2**, 67–92.

Sheldon, P. R. 1996 Plus ça change—a model for stasis and evolution in different environments. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **127**, 209–227.

Southwood, T. R. E. 1978 The components of diversity. In *Diversity of insect faunas* (ed. L. A. Mound & N. Waloff), pp. 19–40. Oxford: Blackwell Scientific.

Taylor, B. J. & Coope, G. R. 1985 Arthropods in the Quaternary of East Anglia—their role as indices of local palaeoenvironments and regional palaeoclimates. *Mod. Geol.* **9**, 159–186.

Ullrich, W. G. 1975 Monographie der Gattung Tachinus Gravenhorst (Coleoptera Staphylinidae) mit bermkungen zur Phylogenie und verbreitung der arten. Dissertation, Christian-Albrechts Universität zu Kiel.

Discussion

G. Larson (*Jesus College, University of Oxford, Oxford, UK*). Does the speed at which beetles migrate in the fossil record violate expectations of potential beetle dispersal rates based upon knowledge of their modern-day capabilities? In other words, is there an analogue to Reid's paradox in beetles?

G. R. Coope. Unfortunately, the Quaternary fossil record gives us only the arrival time of species at a particular locality. Without knowing where it started from it is impossible to know the speed at which its range changed. However, at times of sudden climatic change such as the beginning of the Lateglacial Interstadial, the episode of local extinction of the original population of thermally sensitive species is followed immediately by the appearance in our sedimentary sequences of thermally sensitive species equipped to live under the new regime. I think that flying species of beetle arrive ahead of the pedestrians. Nevertheless, the response time for many of them is very fast and apparently more rapid than the response time of the trees.

P. R. Sheldon (*Department of Earth Sciences, Open University, Milton Keynes, UK*). The plus ça change model (Sheldon 1996) proposes that many of today's species are relatively inert to environmental change because they have come through so much of it. They are generalists in a long-term, non-ecological, sense, and persistent, wide physical fluctuations have damped down their morphological response to environmental change. The model predicts that continuous evolution is more likely in relatively stable environments such as the interior of a tropical rainforest, which have a very poor fossil record. Are there any such tropical deposits with well-preserved insects to test whether stasis is less prevalent there than in the temperate latitudes where your samples come from?

G. R. Coope. I am most grateful to Peter Sheldon for putting our understanding of stasis of Quaternary insect species in a longer-term and more general context. As I have frequently pointed out, the phenomenon of stasis is a more intractable problem than evolutionary change. With regard to his specific comment about the lack of work on tropical deposits: I agree absolutely. Work on peat from more equatorial deposits (in Kenya for instance) would be most instructive in our understanding of the role of environmental instability in maintaining stasis or stimulating evolutionary change. Careful selection of fossiliferous montane sites might also help to elucidate problems of the origin of endemic species.

J. Stewart (*Anthropology Department, University College London, London, UK*). Does the existence of non-analogue communities refute the notion that beetles have lived in constant environments until the present day?

G. R. Coope. Most examples of 'non-analogue' communities refer to the lack of geographical analogues for some of our fossil assemblages. However, non-analogue geographical assemblages do not necessarily imply non-analogue environments. The role of the accidents of space and time introduce a stochastic element into the composition of all present-day communities. Thus, we do not expect every fossil assemblage to have a precise present-day analogue. For the most part, however, fossil assemblages make good ecological sense in terms of environmental analogues and these can be traced back to assemblages from the uppermost Tertiary, suggesting that most species also show stasis in their environmental requirements over several millions of years. After periods of sudden and intense climatic change, it is true that curious species assemblages have been found that have no present-day equivalent, but these are best understood as the dynamic response of species adjusting individually to the new conditions prior to the eventual establishment of a harmonious relationship with their physical environment.