

## SOME ASPECTS OF THE AUSTRALIAN CAVERNICOLOUS FAUNA

by

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### Introduction

The South Australian Museum has given particular recognition to the significance of research on cave-dwelling fauna. Although some speleologists will already be familiar with the programme on which I am engaged for the Museum, others will no doubt be interested to know the details of it. Firstly, specimens collected from caves are curated as a separate collection with its own register. This ensures their ready accessibility and makes an overview of the cave fauna much easier than would be the case if the specimens were incorporated into the massive general collections. Secondly, as specimens come to hand, every effort is made to identify these or to pass them on to specialist taxonomists for study, identification and, if necessary, description of new species. When new species are described from the collection, then the holotypes are transferred to the relevant section of the general collection for the safe-keeping accorded to holotypes as part of normal Museum practice. Thirdly, two indices have been established in which all available data, both on this collection and on any other available information on Australian cave fauna, is recorded. One index is arranged according to the identity of species and the other according to the locality from which species have been recorded. It is thus easy to find all available data on any specific category of fauna or on the total fauna of any specific cave or cave area. Fourthly, a comprehensive library of material on biospeleology has been established and indices to relevant literature are maintained.

This programme is readily available for the assistance of speleological societies or individual speleologists throughout Australia (subject only to my own time limitations). Specimens forwarded will be identified or passed on for identification wherever possible and the results notified. Although we will be glad if such specimens can be retained, they will always be returned if this is requested. However, I would emphasise the importance of placing specimens either in a State museum or in the National collections held by C.S.I.R.O. Material in private collections is inaccessible and subject to considerable risk of loss.

I would also like to comment briefly on the difficulty in providing rapid identification of specimens. Many families of Australian invertebrate animals have not been studied at any depth and are very imperfectly known. In many cases, such a family is not currently being studied by anyone and so no specialist can be found to provide an accurate determination. Even if a family is currently being studied, it is often necessary to carry out an immense amount of further research before a particular specimen can be accurately identified or described as new. This can be, and often is, intensely frustrating to the collector. At the same time, there has been an immense increase in basic zoological research in Australia during recent years; the cavernicolous fauna has attracted particular attention and it is probably true to say that the cave-dwelling fauna is now better-known than that of many other comparable limited habitats. The South Australian Museum programme alone has resulted in a number of taxonomic papers describing new species of cave-dwellers. A number of papers have also been published summarising the cave fauna of specific areas or dealing with special aspects of biospeleology.

The present paper describes some conspicuous characteristics of the Australian mainland cave fauna and discusses the implications of these for thinking about the origin and history of this fauna. Let me stress at this point that Australian biospeleology is still at a very early stage of development and further that the history of a cave fauna can only be fully understood within a framework of geological and climatic history which in Australia is far from clear. So only extremely tentative hypotheses can be advanced, but I believe it is useful to try and do so as even a tentative hypothesis provides some sort of framework within which we can test the significance of our knowledge and seek further data.

### Ecological classification and history

Most speleologists will be familiar with the traditional Schiner-Racovitza ecological classification of cave fauna into the three categories of Trogloxenes, Troglophiles and Troglobites. The way in which this classification has been used has often been far from satisfactory. Some categories of fauna e.g., parasites, do not fit readily into these three divisions and their placement therein confuses rather than clarifies their ecological status. I have proposed elsewhere (1971) a revised scheme of classification which attempts to resolve some of the problems in use of the Schiner-Racovitza system and although there is neither time nor need to fully outline this here, one aspect of it is important to the argument of this paper. The troglotic category is traditionally reserved for those species which show some clear morphological modification in keeping with their cave-dwelling habit. The troglaphiles thus include both species which also live on the surface and those which are confined to the caves but have not developed morphological modi-

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fications. Attention has been drawn to this problem by others, e.g., Barr (1963, 1968), and I have proposed that the troglaphiles can more usefully be divided into two categories, which I have labelled first and second level troglaphiles. I believe this distinction is not only useful from an ecological viewpoint, but that it makes possible a clearer relationship between ecological classification and the history of a fauna.

**First-level troglaphiles** are those species which are able to live their total life cycle within the cave but which may also be found outside of caves. **Second-level troglaphiles** are those which are apparently confined to caves, but which do not show the morphological modifications which distinguish the troglabites. They are species which have been isolated in caves by the extinction of their surface-dwelling ancestral populations. It is likely that this extinction has occurred too recently to permit the development of troglabitic modifications. Barr (1963, 1968) suggests that they are potential progenitors of troglabitic species and that, given favourable conditions over sufficient time, they may well evolve into troglabites.

**Troglabites** are species which have become obligate cavernicoles, are thus confined to the cave environment, and show clear morphological modification accordingly. It is not clear what minimum period of isolation within caves is necessary to permit the evolution of troglabitism, but the most generous estimates generally correspond with that of Barr (1968) when he says "Many troglabites apparently colonized caves during the Pleistocene, some of them at least as late as the Sangamon (Riss-Wurm) interglacial, about 300,000 years ago". Others adopt a more conservative approach, e.g., Vandel (1964, tr.1965), who makes statements such as "Terrestrial cavernicoles are for the most part descendents of a tropical fauna which populated Europe and North America during the first part of the Tertiary". Various kinds of climatic or other change may cause the extinction of surface-dwelling populations and consequent isolation of species, and Vandel (op.cit.) refers to troglabites as being relicts of thermophilic, glacial, hydrophilic or marine populations.

If climatic change proceeded in the same direction and at a constant rate of change, we could expect to find a complete range of stages in cave colonization in any cave fauna. However, it is well known that climatic change has not only been subject to changes in direction, but that some changes have been relatively sudden. We find that any particular cave fauna may comprise various elements which can be related to particular stages in cave colonization and similarly to specific climatic or other changes. In many cases, of course, we lack the detailed knowledge to establish clear historical patterns in the development of a cave fauna, but evidence is accumulating that the origin of troglabites seems to be related to sudden and dramatic changes, rather than gradual ones. Barr (pers. comm.) has referred to the idea of "catastrophe" as being fundamental to the isolation of cave-dwelling populations.

Another important and related aspect of historical biospeleology is the speciation which occurs in isolated populations. If a widely distributed population is suddenly to be extinguished from all but a few isolated sites, which may be caves, then each such isolated population is likely to evolve in a distinctive way, developing its own peculiar characteristics and ultimately forming a number of distinct species. However, in addition to this mechanism, it must be emphasized that most widespread species show considerable variation from point to point within their distributional range. Although it may not be possible to separate neighbouring forms from each other, forms chosen from widely separated parts of the geographical range may be very different from each other. So, if such a species suffers general extinction, leaving a few isolated and widely separated relict populations, these may well be immediately readily separable from one another.

#### Previous discussion on the origin of Australian cavernicoles

Moore (1964) pointed out that the Australian cave beetles known at that time were troglaphilic and derived from weakly hygrophilous groups. He suggested that earlier cave inhabitants may have suffered secondary extinction, probably as a result of hot dry inter-glacial or post-glacial periods, leaving the cave environment vacant for fresh invasion during the post-glacial.

I suggested (1967b, 1969), without elaboration, that structural factors leading to flooding and later dehydration of cave systems may have also played a significant part in the secondary extinction of earlier cave faunas. When discussing the fauna of the Nullarbor caves, I proposed that the presence of the troglabitic cockroach *Troglablattella nullarborensis* indicated the isolation of this species since the Tertiary, and hence gave support to the suggestions of Jennings that cave genesis may have been initiated at the close of the Tertiary and that climatic conditions on the Nullarbor have not undergone major change. This line of reasoning was rejected by Richards and Lane (1969) but followed by Main (1969) when describing *Troglodiplura lowryi*. I also divided the remaining species into three categories: second-level troglaphiles, first-level troglaphiles which although still living in surface habitats do not appear to do so on the Nullarbor, and first-level troglaphiles which are still prevalent on the Nullarbor Plain surface. It was suggested that this indicated past climates had probably been slightly wetter than the present.

The other significant discussion has centred about the specific issue of the North-West Cape fauna (Mees 1962, Richards, 1963) but has largely been concerned with the distinctive characteristics of that fauna.

### Three major characteristics of Australian cave fauna

#### 1. The Paucity of Troglobites

Australia's first troglobite was the fish *Milyeringa veritas* described from North-West Cape by Whitley (1945). From the same locality, Holthuis (1960) described the two shrimps *Stygiocaris lancifera* and *S. stylifera* and Mees (1962) described an eel, *Anommatophasma candidum*. Despite further investigation, summarised by Richards (1963), no further species have been collected from this area. Williams (1964) has since described two further shrimps, *Parisia unguis* and *P. gracilis*, from the Katherine Caves. These six species, as is typical of tropical troglobites, are all aquatic marine relict species.

Four troglobites so far have been recorded from the Nullarbor caves. These are the cockroach *Trogloblattella nullarborensis* described by Mackerras (1967), the remarkable trapdoor spider *Troglodiplura lowryi* described from dead material by Main (1969) and not yet seen as a living specimen, and two currently undescribed spiders, both of which are briefly discussed by Lowry (1970).

Some other species which are currently being studied may prove to be truly troglobitic, but it would be premature to comment on their ecological status at this point. However, several are apparently relicts of considerable antiquity, e.g., a Phreatoicid from Wee Jasper, N.S.W. and two species of Millepede from Buchan, Victoria, and these will be taken into account in the discussion below.

It is also necessary to comment at this stage on the Pseudoscorpions. Beier (1967) refers to several of these as "true cave-dwelling species" and others, including myself (1967b) have referred to them as troglobitic. In view of the lack of significant morphological modification (absence of eyes is not unusual in this order, even being the normal condition in many genera, and cannot be construed as a result of cavernicolous habit) and the association of most mainland cave-dwelling species with bat guano, it seems preferable at this point to adopt the conservative approach and treat these as troglaphiles.

Thus, at this stage, we can only with certainty list 10 troglobites for mainland Australia. This contrasts markedly with many other countries, and although up-to-date figures are not readily available for comparison, various published figures suffice to demonstrate the relative paucity of our own fauna in this regard. Barr (1960) noted approximately 250 species from U.S.A.; Nicholas (1962) listed 170 from Central America; Ueno (1964) refers to at least 150 species; Strinati (1969) lists approximately 60 from Switzerland; and in all of these countries (with the possible exception of Switzerland) new troglobites are being discovered and described at frequent intervals.

#### 2. The Abundance of Second-level Troglaphiles

Although some species which have as yet only been collected from caves prove to also live in other habitats, it is striking to note the number of second-level troglaphiles so far recorded from our caves, some of which enjoy an extremely wide distribution. It has already been mentioned that Barr (1963, 1968) has referred to the occurrence of such species in the U.S.A. but it would appear that they are relatively few in number compared with the proportion occurring in the Australian fauna. My own knowledge of the Japanese cave fauna indicates that in that country, second-level troglaphiles are relatively unusual while troglobites are extremely diversified and numerous.

I sometimes reflect that Australian biospeleology may be in a position analogous with mammalogy. It has been said that the classification of the placental mammals into 16 orders with the lumping of all marsupials into one order is not so much a reflection of the validity of the classification, but a comment on the fact that mammal classification was based on European experience by zoologists who were placental mammals. If mammalogy had been established first in Australia (and by zoologists who were themselves marsupials) we might well have a very different pattern. Perhaps if biospeleology had fifty years of development in Australia before any serious study was made of cave fauna elsewhere, we would find considerable significance attached to the second-level troglaphile rather than to the troglobite. Perhaps the incredible fauna of Japanese caves would be seen as impoverished! More seriously, I suspect that studies of our cave fauna may tell us a great deal more about the process of cave colonization than might be learnt from other countries.

Rather than merely cataloguing the second-level troglaphiles, it will probably be of more value to example their occurrence in a couple of well-known groups. Twelve pseudoscorpions have so far been recorded from caves on the Australian mainland. None of these have been recorded from any other habitat. Their distribution is tabulated in Table 1, and it will be seen that 9 species have each only been taken from a single cave. In several cases, caves in close proximity to each other have yielded quite different species. A particularly interesting pattern is demonstrated by

*Protochelifer cavernarum*, of which the nominate sub-species occurs across the whole of Southern Australia, while the sub-species *P. c. aitkeni* is confined to Abrakurrie Cave.

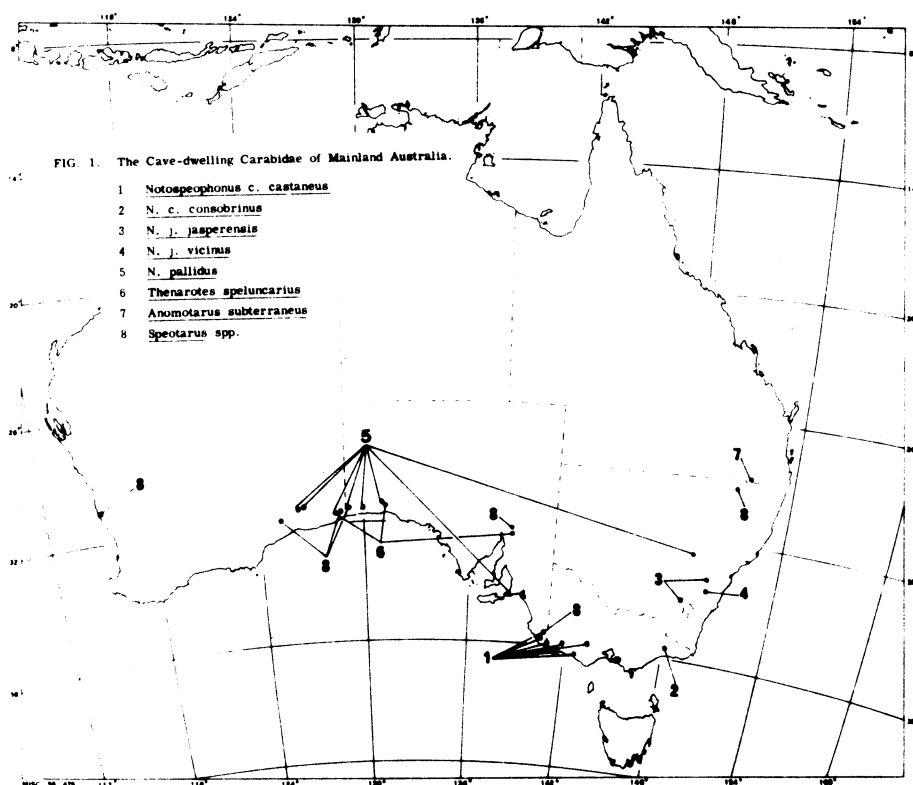
<p><b>Family CHTHONIIDAE</b>  <i>Austrochthonius cavicola</i> Beier  <i>Sathrochthonius teuna</i> Chamberlain</p> <p><i>Pseudotyrannochthonius jonesi</i> Chamberlain  <i>P. hamiltonsmithi</i> Beier  <i>P. gigas</i> Beier  <i>Morikawa cavicola</i> Beier</p> <p><b>Family CHERNETIDAE</b>  <i>Sundochernes guanophilus</i> Beier  <i>Troglochernes imitans</i> Beier</p> <p><b>Family CHELIFERIDAE</b>  <i>Protochelifer naracoortensis</i> Beier  <i>Protochelifer cavernarum cavernarum</i> Beier</p> <p><i>Protochelifer cavernarum aitkeni</i> Beier</p> <p><b>Family CHEIRIDIIDAE</b>  <i>Cryptocheiridium australicum</i> Beier</p>	<p>Cathedral Cave, Naracoorte, S.A.  Southern Limestone, Jenolan, N.S.W.  Basin Cave, Wombeyan, N.S.W.  Punchbowl Cave, Wee Jasper, N.S.W. (?)  Cave, 'probably in the Blue Mountains'  Mt Widderin Cave, Skipton, Victoria  Byaduk Caves, Victoria (2 caves)  Grill Cave, Bungonia, N.S.W.</p> <p>Fig Tree Cave, Wombeyan, N.S.W.  Dingo Cave, Nullarbor, W.A.</p> <p>Bat Cave, Naracoorte, S.A.  Murder Cave, Cliefden, N.S.W.  Belfrey Cave, Timor, N.S.W.  (also caves unspecified, Cliefden and Timor)  Ashford Cave, N.S.W.  Clogg's Cave, E. Buchan, Victoria  Murrarwijinee n.3 Cave, Nullarbor, S.A.  Lynch Cave, Nullarbor, W.A.  Mullamullang Cave, Nullarbor, W.A.  Super Cave, Nambung River, W.A.  Gooseberry Cave, Jurien Bay, W.A.  Abrakurrie Cave, Nullarbor, W.A.</p> <p>Murra-el-elevyn Cave, Nullarbor, W.A.</p>
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**Table 1:** Cave-dwelling Pseudoscorpions of the Australian mainland.

Another useful example is the Carabid beetles, which include 9 second-level troglophiles along with a number of first-level species. The distribution of the second-level troglophiles is mapped in Fig. 1 and demonstrates some intriguing patterns of relict distribution and speciation. The five described species and sub-species of *Notospeophonus* provide an interesting problem in the relative chronology of their development and the mechanism responsible for speciation in this instance. The genus *Speotarus*, with species described from Naracoorte, South Australia and Ashford, N.S.W., but in which the overall pattern of speciation remains unclear, at least to me, (but see Moore, this volume) has a remarkably wide scatter of apparently isolated populations, typical of a relict species.

### 3. Australian cavernicoles may belong to different sections of major taxa from similar species in other countries

Moore (1964) first drew attention to this characteristic in relation to the cave Carabidae. Of our second-level troglophiles in this family, 6 belong to the Harpalinae and 3 to the Lebiinae, both of which rarely occur in caves elsewhere. On the other hand, the sub-family Trechinae which is generally dominant in cave faunas is only represented in Australian mainland caves by *Trechimorphus diemenensis*, a first-level troglophile from Bungonia, Jenolan and Buchan. I pointed out in earlier papers (1966, 1967b) that a somewhat similar pattern could be demonstrated in the mites. It is now possible to cite two further examples of particular interest.



Of the twelve pseudoscorpions listed above, 6 belong to the Chthoniidae which are commonly cavernicolous in other countries; 2 to the Chernetidae and 3 to the Cheliferidae, both of which are only very rarely recorded from caves elsewhere, and 1 to the Cheiridiidae, of which I can trace no previous record from a cave. In this instance, it must be noted that the family Neobisiidae, which contains some 60% of the cavernicolous pseudoscorpions of the world, is confined to the Northern hemisphere and is hence not available to colonise Australian caves.

The other more striking example is afforded by the beetle family Cryptophagidae. One species has been named from an Australian cave (in Tasmania) but I have currently in preparation descriptions of a further two forms. In addition, I have specimens which probably belong to three further distinct forms (but am lacking male specimens of these, so am unable to be certain of their identity). All of these belong to the genus *Atomaria* of the sub-family Atomariinae. All Cryptophagids taken from caves elsewhere belong to the genus *Cryptophagus*, sub-family Cryptophaginae. Both these genera are widely distributed throughout the world, and so both appear to be equally available as potential colonists of the cave habitat in Australia and elsewhere.

## Discussion

In spite of considerable research, the general geochronology and climatic history of the Australian Quaternary and Recent remains unclear (Brown et al 1968). This is even more so in the Northern parts of the continent (Jennings 1969). Jennings (e.g. 1967, 1968a) has continually emphasised our lack of knowledge about these aspects when discussing the genesis and development of Australian caves, and the lack of this data is equally a problem in reaching some understanding of the history of cave fauna.

The present evidence indicates that a relatively hot and wet Tertiary was followed by a cooler Quaternary, in which there was negligible glaciation and in which wet and dry periods alternated, although the timing, sequential and geographical relationships or actual climate of these periods remains unclear. This in turn has been succeeded by a more arid Recent. It is also generally accepted that considerable uplifting of the Eastern Highlands occurred during the Quaternary, but this was probably initiated during the Tertiary and continued over an extended period (see discussion by Jennings 1968a).

Examination of the cave fauna itself enables one to make some assumptions about the relative age of particular components. On this basis, I believe it is possible to distinguish five major groups and it is then possible to propose tentative hypotheses about some aspects of their origin.

The marine relicts of Northern Australia are possibly the most ancient, as all are widely separated from their nearest relatives. Both the fish have been placed in distinctive genera, the affinities of which are far from clear (Mees 1962), while the shrimps, although closely related to other living species, have their near relatives in Madagascar (Holthuis 1960, Williams 1964). However, it must be pointed out that their origin as cavernicoles is not necessarily related to the time of their colonization of brackish or fresh (*Parisia* spp.) water from the ocean. All belong to families which have been adapted to freshwater for a very long period and Vandel (1964, tr. 1965) cites the example of Atyid shrimps from Oligocene freshwater deposits, although he is in error in stating that all Atyids are fresh-water species (Holthuis 1963).

The zoological evidence suggests that the cockroach and spiders of the Nullarbor can be attributed to the late Tertiary. I still believe that this gives support to the suggestion that cave genesis on the Nullarbor was initiated at this time, although I realise that more direct evidence would be essential for confirmation of this suggestion.

At this stage, I would like to spend a little time on the question of our paucity of other troglobites. It must be emphasized that many of our caves are of relatively recent origin and would not have been available for colonization at a sufficiently early point in time. The caves of the aeolian limestones are mainly of Pleistocene or even Recent genesis (Jennings 1968b) and it is extremely doubtful if they are sufficiently ancient to have developed a troglobitic population. The caves in the Miocene limestones of South-eastern South Australia may well have been initiated, but faced considerable fluctuations in sea-level during the Pleistocene (Blackburn et al 1965) and so again, would not have been available. In the Eastern Highlands a large proportion of the caves occur in relatively small areas of "Karst Barre" limestone, that is, with morphological and hydrological development being dependent upon erosional levels in the surrounding and relatively impermeable rocks (Jennings 1967, Sweeting 1960). In these areas, cave genesis can be related to Pleistocene water levels (Sweeting 1960) or to various stages in the erosion of surrounding rocks (Jennings 1964) and in at least some cases, to the orogenetic movements of the Eastern Highlands (Jennings 1967). Thus, some of these caves are of relatively recent origin, while others have been subject to extremely wet conditions and to vadose development followed by dehydration as the erosion of the surrounding landscape has lowered the water levels (Jennings 1964).

Some of these caves contain a fauna which includes species of considerable antiquity, whose status remains unclear. These include the Phreatoicid of Wee Jasper and the Millepedes of Buchan referred to above. At Wee Jasper, Jennings (1964) has shown that the stream responsible for the development of the Punchbowl-Signature system now flows through the Dogleg Cave within which the Phreatoicid occurs. This species has probably followed the down-cutting of the stream, even though this has involved migration between what are now separate caves. The millepedes at Buchan both occur in caves which have obviously maintained a continuing relationship to the stream responsible for their development over an extremely long period. The available evidence suggests that these species may have colonised the caves concerned since at least the early Pleistocene.

The fourth group are the Second-level Troglophiles. These are not uncommonly found in caves which have only been available for colonization during the mid-recent, and so it seems reasonable to date their period of colonization as during the late Pleistocene and early Recent. Assuming the validity of the "catastrophe" concept referred to earlier, this would suggest some drastic change in climatic or other conditions during the mid-Recent which led to the extinction of the surface-dwelling ancestral populations.

It not only seems likely that this change was one of increasing aridity, but it is interesting to note similar indications from other fields of research. Crocker (1949), in discussing the history of Australian vegetation, suggests an onset of aridity during the mid-Recent and that this was "sudden and drastic". Wakefield (in press) as a result of studying fossil mammals from the Pyramids Cave at Murrindal, Victoria, proposes that the earlier mammal fauna of wet sclerophyll forest "collapsed dramatically" and was replaced by the modern dry forest fauna.

Summarising the above discussion, I am suggesting that the paucity of troglobites is due primarily to the fact that Australia has few caves which were (1) available for colonization during the Tertiary or early Pleistocene and (2) have enjoyed relatively stable conditions since that time. However, many of these caves became available during the later Pleistocene, and were colonised by various species, some of which have been isolated as second-level troglophiles, probably by aridity during the mid-Recent. There has not been space in this paper to deal with other than a few cave areas, but evidence to support this proposal is available in respect of many other Southern cave areas.

Finally, there are the first-level Troglophiles, which in fact are actively colonizing the cave environment at this point in time. We can see some interesting examples where change in environment is occurring and isolation of cave populations may in fact be in progress. I have already referred to the Nullarbor species which appear to have vanished

from the surface in that area, even though widespread elsewhere. A second instance is the beetle *Mystropomus subcostatus*, normally a dweller in the leaf-litter of dense rain-forest (Britton 1970), which is abundant in the Mt Etna Caves of Queensland, but is rare and probably vanishing from surface environments in that area. I have also described elsewhere (1968) a different kind of "catastrophic" change which has occurred in the Mt Widderin Cave of Victoria. In this case, the desertion of a cave by what was apparently a nursery colony of the bent-winged bat has drastically changed the environmental conditions of the cave, but a few of the former guanophile species have survived within the cave.

Only one aspect of our cave fauna remains for comment in this discussion and that is the extent to which Australian cavernicoles are derived from different sections of major taxa from those of other countries. I would suggest that we cannot fully elucidate this problem without a much more detailed understanding of the biology of the taxa concerned, but that this characteristic of our fauna is probably related in some way to its relatively recent origin compared with the troglotic forms from elsewhere.

### Acknowledgments

An overall review paper of this kind obviously owes its existence to the work and co-operation of an immense number of people. The list of references below gives some indication of this, but in addition, many of these authors and others have assisted by personal discussion of the issues dealt with here. Many cavers have contributed either by collecting specimens or by assisting the author on his own fieldwork. The fact that a paper of this kind is possible at all is an indication of the level and quality of co-operation throughout Australian speleology.

Two organizations must, however, be specifically named. The South Australian Museum (Director, Dr W.G. Inglis) has assisted immensely through the provision of facilities and support for the study of Australian cave faunas. The Speleological Research Council Inc. (Sydney) has provided financial assistance.

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## DISCUSSION

- Q You mentioned the pseudoscorpions in Australia as being both on the surface and underground. Have the underground ones no modifications?
- A These twelve species are only known in the caves and I don't believe any of them are significantly modified for cave conditions.
- C I don't think you can validate your point about caves not being available for colonization. In some areas there are caves which started early and have continued ever since. This would include Mt Etna which I think is a residual probably dating from some time in the Miocene and standing up in a sea which I think was developed in the Pliocene. Another point indicated by this karst barre feature is that many of the areas have been wiped out at various periods e.g. Cooleman. It is quite recognizably not a cave system at all. We are rather lucky to have so many of our limestone areas bearing caves right now. Let's say there is some small act on the part of providence considering the paucity of limestone. The position is that the caves are periodically wiped out as each knick point creeps up the river. These knick points are steadily moving up river. They have been doing so continuously but each time it involves the obliteration of the cave area between the time that one knick point arrives to give you rejuvenation and the time of eventual destruction. Few of them have remained continuous. Colong for example is entirely a late system. Jenolan shows more evidence of continuity as a river system. This suggests that it is not universally applicable, but I think it is applicable to sufficient of the cave areas to make your point valid. The mid-Recent break is marked by the very widespread occurrence of river terraces and marine benches right around the coast in which the previous river channel system has changed from one that is reasonably well fit to the valley to the present one where most streams are strongly underfit. I think this means that a very drastic change did occur and the evidence for that is very good.
- C I suspect several places where we might in fact look for troglotic fauna in the mainland. Where in fact we generally haven't looked, are the high level caves which may by chance have a very, very long period of stability as relatively dry. There has been a quite interesting paper from Switzerland recently where one such cave yielded something like nine troglotites to everybody's utter astonishment. It is a tin pot little cave which has been sitting high up on the mountain apparently for an extremely long time and I sometimes wonder about some of the high level caves in our eastern cave areas. It might be worth devoting a lot more attention to these from the biological point of view.