ISOPODA: PHREATOICIDEA

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One would expect with such a name that some species at least of the sub-order Phreatoicidea Stebbing, 1893 would inhabit the Stygal, and indeed the first phreatoicid found was collected from a well near Christchurch, New Zealand, in September 1882 and formally described shortly afterwards as *Phreatoicus typicus* (Chilton, 1882). Later, Chilton (1894) recounted the history of the discoveries of subterranean amphipods and isopods in New Zealand. The notion based on morphological criteria that phreatoicids must be an ancient group, advanced by Chilton (1882) and repeated by several eminent carcinologists who have expressed their interest in the group (for example K. H. Barnard, G. E. Nicholls, O. A. Sayce and G. W. Smith), has been borne out by more recent studies on Paleozoic and early Mesozoic fossils. *Hesslerella shermani* was described from Mid Pennsylvanian near shore marine deposits of what is now Illinois, USA (Schram, 1970, 1981), and Permian fossils from several localities of Laurasia, and *Protamphisopus wianamattensis* from the Triassic of Australia, indicate an evolutionary sequence from marine ancestors through brackish to freshwater inhabitants. Phreatoicids now are restricted to predominantly fresh surface waters of Australia, India, New Zealand and South Africa, with stygobionts on all except South Africa of these Gondwana fragments.

Numerous species descriptions were published during the six decades following Chilton's discovery, culminating in the publication in 2 parts of Nicholls (1943, 1944) taxonomy of the Phreatoicidea — a work that remains the authoritative statement on the taxonomy of the group. Nicholls recognised 2 families within the Phreatoicidea, the Amphisopidae Nicholls (with 5 sub-families; 18 species including 1 fossil), and the Phreatoicidae Stebbing (with 3 sub-families; 34 species). Basically the families are separated by one feature, namely, that in members of the Amphisopidae, both mandibles bear a *lacinia mobilis* whereas in the Phreatoicidae, the *lacinia mobilis* is absent from the right mandible. Nicholls acknowledged his Amphisopidae to be a very heterogeneous assemblage and possibly not a monophyletic group. Subsequent publications include descriptions of 2 species of extant stygobionts from India, *Nichollsia kashiense* (Chopra & Tiwari, 1950) and *N. menoni* (Tiwari, 1955a) for which the family Nichollsidae was erected (Tiwari, 1955b) and of 3 fossil species (Birstein, 1962; Glaessner & Malzahn, 1962; Schram, 1970). Birstein (1962) also erected the family Palaeophreatoicidae for his new genus and species *Palaeophreatoicus sojanensis.*

In his study, however, Nicholls did not survey adequately within and between population character variation, nor did he heed the problems posed by allometry. These criticisms are particularly pertinent to the subterranean forms. The fault is not entirely Nicholls'. Phreatoicids inhabit many areas which even now are very difficult of access, and subterranean forms are rarely collected in large numbers, so it may well be he was unaware of the extent of character variation shown by members of the sub-order. A difficulty which Nicholls should not have had to anticipate was the loss of the bulk of his collection rendering it impossible to check now the accuracy of his descriptions.

A revision of the sub-order is being undertaken by the present author, and although significant changes were suggested in an interim report (Knott, 1975), the study is only now nearing completion. However, it is pertinent to briefly mention the several changes relevant to subterranean phreatoicids mooted by Knott, namely, that each sub-family of the Amphisopidae be elevated to full familial status, and that the genus *Hyperoedesipus* be grouped with the genera *Hypsimetopus* and *Phreatoicoides* in a separate family tentatively named Hypsimetopidae. The latter 2 genera are probably synonymous, with *Phreatoicoides* being the senior synonym. Despite this possibility, the name Hypsimetopidae (recognising an elevation in taxonomic ranking of Nicholls' subfamily (Hypsimetopinae) is retained in this paper simply for convenience: there is already defined a family Phreatoicidae. Isopods clearly assignable to the *Phreatoicoides — Hypsimetopus* generic complex exhibit considerable character variation, and characters regarded by Nicholls to have generic significance are not consistently associated or expressed: for example, the presence of epipodites on pleopods 3, 4 and 5 and of plumose setae on the endopodite of pleopod 1 in *Hypsimetopus*; and their absence in *Phreatoicoides*. Nor are the proportionate lengths of pereonite 1 to pereonite 2 (1.0 in *Hypsimetopus*, 0.67 in *Phreatoicoides*) consistent. Values on a range of specimens from Tasmania measured by the present author varied from 0.49 to 1.34, the last on an individual from the remnants of the Nicholls' collection lodged in the

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Western Australian Museum. The difficulty of resolving the question of synonymy is exacerbated by the loss of Nicholls' specimens, and inconsistencies in the published descriptions. From what is now building to an extensive collection of hypsimetopids from western Tasmania, the present author distinguishes 5 species, but their nomenclatural status remains unresolved.

In addition, Knott (1975) presented the first description of a cavernicolous phreatoicid — *"Lakeamphisopus trogloendemicus"* from Mersey Hill Cave in northern Tasmania.

It is appropriate at this juncture to mention two discoveries of phreatoicids about which accounts have yet to be published. 1). In Western Australia, isopods clearly assignable to the genus *Hyperoedesipus* have been found very recently in three headwater streams flowing through jarrah (*Eucalyptus marginata*) forest. The specimens morphologically are quite variable, and show some expressions new to *H. plumosus*. However a paucity of adult specimens (juveniles comprise the bulk of the samples) has prevented a proper evaluation being carried out to determine whether they belong to *H. plumosus* or to a new species. On first impressions those specimens from Finlay Brook (part of the North Dandalup River catchment) appear to be *H. plumosus*; those from Little Dandalup Creek (part of the South Dandalup River Catchment) and McKnoe Brook (near Wagerup) are possibly *Hyperoedesipus* sp. nov. 2). Dr L. P. Gupta (Zoological Survey of India) kindly informed the author of the discovery of subterranean phreatoicids during deep drilling operations for the installation of tube wells in Andhra Pradesh. The specimens are apparently in the possession of Professor P. J. Sanjeeva Raj (Madras Christian College, Tambaram) but as yet no description of these southern Indian forms has been published.

The subterranean phreatoicids are defined by their habitat and morphology. *P. typicus* was taken from a shallow well reaching approximately 5 m into a gravel substratum (Chilton, 1882) and most of the stygobionts from New Zealand (including *Phreatoicus orarii* and *Neophreatoicus assimilis*) were originally collected from wells fitted with suction or cylinder pumps reaching to depths of about 10 m; none were recovered from another two water bearing strata in the same area at depths exceeding 18 m (Chilton, 1894). *Nichollsia* spp. are collected from wells approximately 10 m deep on the Ganges Plain. *Hyperoedesipus plumosus* is also associated with springs which flow only after prolonged, heavy rain.

Subterranean phreatoicids are blind; white; their body attenuated, vermiform; short abdominal epimera scarcely cover the base of the pleopod (with the possible exception of *N. assimilis*). The palm of the gnathopod often develops to massive size, and there may be an elongation of the post-maxillipedal portion of the head, especially in large males. Other so-called subterranean characters are not so obvious and must be treated with caution: elongation of antennae; slender pereopods with limited broadening of the basis in pereopods 5, 6 and 7; shortening of the penial stylets; relative shortness of the pleon. Indeed comparison between relative length or proportions of body parts in stygobionts and surface benthic forms is unsatisfactory for two reasons: firstly, somites in the latter forms tend to overlap, so measurement becomes at best difficult; and secondly, the question of whether increases in, say, antennal length in stygobionts are real, a reflection of allometry or due to lower nutritional levels in groundwaters, has still to be resolved. Nor is the lack of eyes confined to stygobionts: surface dwelling species of *Notamphisopus* from New Zealand, and an undescribed species of *Synamphisopus* from Victoria are blind. The several forms of *Hypsimetopus* and *Phreatoicoides* inhabit not only subterranean waters of western Tasmania where they constitute an element of the pholeteros*, but also they are frequently collected from surface waters on the more or less permanently wet button grass (*Gymnoschoenus sphaerocephalus*) plains and runnels of the cool temperate *Nothofagus* rainforests. Indeed, Richardson and Swain (1978) recovered one form much more frequently from interstitial water within the ground bed of riffle zones of the Gordon River and its major tributaries than from interstitial waters of the nearby sedgelands and forests. Nevertheless, *Hypsimetopus intrusor* and *Phreatoicoides* spp. from western Tasmania and southern Victoria are classified here as stygobionts because they exhibit the subterranean facies described above. It is perhaps more appropriate they be considered as opportunistic subterraneans in reverse rather than stygophiles: stygobionts utilising suitable surface waters. The same categorisation undoubtedly applies (and for the same reason) to the populations of *H. plumosus* and/or *Hyperoedesipus* sp. nov. from the Dandalup and Wagerup sites mentioned previously. In each instance, the phreatoicids were collected (in low numbers) from interstitial water of the gravel bed during Surber sampling of a riffle zone: a potential subterranean source has not been discovered (S. Bunn, pers. comm. March 1983). *"L. trogloendemicus"* is blind and only lightly pigmented, but resembles a surface dwelling phreatoicid in other aspects of external morphology. *Phreatoicopsis terricola* could possibly be included in the Tables, for the first accounts of its habits describe the species as burrowing strongly in river banks above the water table. However this species lacks the subterranean morphotype, and the present author found specimens under rocks and leaf litter in streams of the Grampian and Otway Mountains in Victoria. It is probably more accurately classified as a stygophile.

Surface dwelling phreatoicids inhabit a wide variety of habitats, including temporary head-water runnels and swamps, and in suitable areas respond to seasonal dry conditions by burrowing into the substrate. Benthic phreatoi-

*Pholeteros — a term coined by P. S. Lake in 1977 for the faunal assemblage associated with burrows of freshwater crayfish, which often burrow to depths of 2-3 m.

cids from lakes in south eastern Australia and Tasmania may burrow into superficial lacustrine sediments. These phreatoicids could be regarded as stygophiles, with burrowing being basically an opportunistic exploitation of some resource where there is complete continuity between surface and ground waters, or an avoidance response to lethal conditions.

In Knott's revision, 46 species of extant Phreatoicidea are recognised, 12 of them being subterraneans (about 26%). The phylogeny of the stygobiontic component has not yet been elucidated, but it appears that each of the groups Nichollsidae — Hypsimetopidae — *Phreatoicus/Neophreatoicus* — *Lakeamphisopus* represents a separate invasion of the underground. What are the conditions which facilitate invasion of the underground? Does an invasion such as this require stable contact over a long span of time between surface and subterranean waters? It is a reasonable suggestion that landform stability and reliably wet climate during a long geological period up to the present has characterised the areas now inhabited by *Hyperoedesipus* and hypsimetopids. Alternatively, would changing surface conditions trigger this invasion? — such as the onset during the Tertiary and subsequent expansion across much of Australia of arid conditions. However, phreatoicids are unknown from any subterranean waters in desert areas. [*Phreatomerus latipes* is described from surface waters of mound springs in the arid area about the southern end of Lake Eyre, South Australia]. Elsewhere, subterranean phreatoicids occur in alluvial plains of geologically recent formation: the Holocene river gravels, sands and silts of the Cantebury Plain in New Zealand, and the unconsolidated recent alluvium of the Gangetic Plain between Varanasi and Monghyr in India.

Again somewhat inexplicably, phreatoicids are rarely encountered in cave streams although such habitats in Australia are now known to harbour a diverse crustacean fauna, serving both as refuge for ancient species showing relictual, highly discontinuous or extremely localised distributions, and as a habitat being invaded by recent forms undergoing incipient speciation.

The spectre is raised, therefore, that for phreatoicids invasion of the underworld may not be a viable long term solution to avoid the evolutionary stakes to extinction. Escape into the underground may present a feasible short term solution for forms contending with an increasingly hostile surface environment, but their chances for long term survivorship are enhanced if suitable epigean habitats subsequently become available again.

There are no immediate threats to the survival of the hypsimetopids from western Tasmania and southern Victoria, although destruction wrought by man through mining, logging, land clearance and other activities affecting drainage patterns have lead undoubtedly to the demise of local populations, and retraction in geographical range of others. It is possible that *Phreatoicoides gracilis* recorded from one location has long been extinct (Nicholls, 1943, p. 135), but until the taxonomic issues alluded to above are resolved, the question of survival of each species must be held in abeyance. *Nichollsia* spp. are known from a number of isolated localities in Uttar Pradesh and Bihar (L. P. Gupta, pers. comm. Jan, 1983) but are likely to have a much wider distribution across the Ganges Plain in India. Stygobionts from New Zealand were collected by Chilton in a narrow zone of the Canterbury Plain stretching from Eyreton to Winchester. The phreatoicids were never abundant but more readily collected when water levels were falling (Chilton, 1894); a recent general text (Chapman & Lewis, 1976), makes no mention on their present abundance. Until the commencement in 1981 of Mr. Bunn's faunal studies on jarrah forest streams just south of Perth, *H. plumosus* was known to occur at but two sites, both springs which flow only after prolonged heavy rain: one at Lesmurdie near the Darling Scarp to the east of Perth, the other in the Avon Valley some 40 km north. Given the increasing salinity level of groundwater in the area about both sites, and the fact that the last successful collection was made in 1955 (from the latter locality) despite intensive searching during the last 6 years, it is quite possible the species is now extinct. An unnecessarily gloomy view if some at least of the specimens from the McKnoe Brook and two Dandalup River sites conform to *H. plumosus*. Nevertheless, whatever their specific identity, the prospects for survival in the long term of *Hyperoedesipus* populations in headwater streams of the jarrah forests cannot be viewed with confidence. Just how commonly they occur in these streams remains to be seen, but if Bunn's data (from his main study area and excluding spot samples from other locations — pers. comm. March 1983) is an accurate guide, they are not common, occurring at one out of twelve study sites on six streams. Significant tracts of land encompassing jarrah forest with headwater streams which potentially may harbour *Hyperoedesipus* sp. are under lease for future strip mining for alumina. If carried out, strip mining will undoubtedly cause irreversible destructive changes to the present faunal composition of streams within the mined area, with the phreatoicid highly susceptible to the changes.

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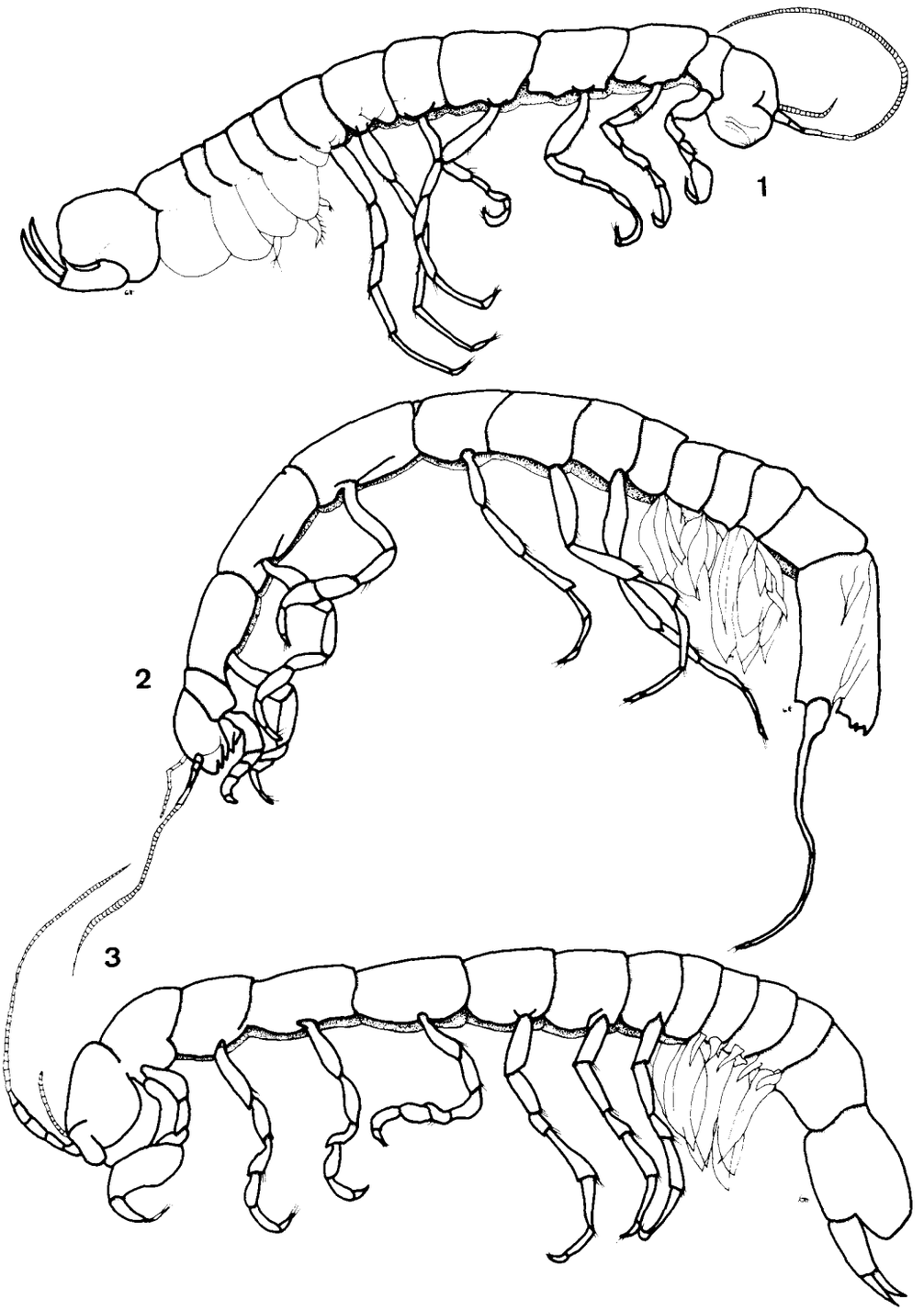

1: *"Lakeamphisopus trogloendemicus"*, lateral view of male, 15 mm body length, from Mersey Hill Cave, Mole Creek, Tasmania; 2: *Nichollsia kashiense*, lateral view of male, 25 mm body length, from Varanasi, Uttar Pradesh, India; 3: *Hyperoedesipus plumosus*, lateral view of male, 7 mm body length, from Moondyne Spring, Avon Valley, Western Australia. Original figures drawn by C. M. Hanley.

	Amphisopidae Nicholls, 1943		
	Mesamphisopinae Nicholls, 1943		
	Hyperoedesipus Nicholls & Milner, 1923		
1	plumosus Nicholls & Milner, 1923	VI 3a: 2 springs near Perth, and headwater streams just S. of Perth, Western Australia.	S
	Hypsimetopinae Nicholls, 1943		
	Hypsimetopus Sayce, 1902		
2	intrusor Sayce, 1902	VI 3b: crayfish burrows near Zeehan, Tasmania.	β
	Phreatoicoides Sayce, 1900		
3	gracilis Sayce, 1900	VI 3b: tributary of the Narracan River, Victoria.	β
4	longicollis Nicholls, 1943	VI 3b: swampy country near Queenstown, Tasmania.	β
5	wadhami Nicholls, 1943	VI 3b: from Beechforest, Otway Mountains, Victoria.	β
	Phreatoicidae Stebbing, 1893		
	Phreatoicinae Nicholls, 1943		
	Phreatoicus Chilton, 1882		
6	orarii Nicholls, 1944	VI 4: wells near Ashburton and Orari Valley, South Island.	K
7	typicus Chilton, 1882	VI 4: wells on Canterbury Plain, South Island.	K
	Neophreatoicus Nicholls, 1944		
8	assimilis Chilton, 1884	VI 4: wells near Winchester, South Island.	K
	Paraphreatoicinae Nicholls, 1944		
	Lakeamphisopus Knott, 1975 (MS name!)		
9	trogloendemicus Knott, 1975 (MS name!)	VI 3b: Mersey Hill Cave and Marakoopa II Cave, in northern Tasmania.	C

	Nicholllsidae Tiwari, 1955		
	Nichollsia Chopra & Tiwari, 1950		
10	kashiense Chopra and Tiwari, 1950	V 2: a number of localities in Uttar Pradesh and Bihar, in the Gangetic Plains (Uttar Pradesh: deep wells at Lohagara, Varanasi = Benares, and Rainnagar; Bihar: Chapra and Patna).	K
11	menoni Tiwari, 1955	V 2: Well at Monghyr, Bihar.	K

NOTES

2-5: reasons for including these species in the Tables as stygobionts are presented in the text. Briefly, the species all show morphotypes strongly suggestive of a subterranean existence and indeed these "hypsimetopids" may be found in groundwater and as a component of the pholeteros. They also are frequently collected from surface waters.

Hyperoedesipus: see Introduction for information concerning a possible second species.

Nichollsia: following data in a MS by L. P. Gupta (prepared for publication in the Memoirs of the Zoological Society of India) "It appears that diligent surveys in the Gangetic Plains are likely to reveal that this genus may be more widespread in the subterranean waters". Some additional information on the distribution of *N. kashiense* (see Tables) was extracted from this manuscript.