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THE SYSTEMATICS AND BIOLOGY OF PSEUDOSCORPIONS

MARK S. HARVEY

Biological Survey Department, Museum of Victoria, 71 Victoria Crescent, Abbotsford, Vic. 3067.

ABSTRACT

Previous pseudoscorpion classifications are reviewed and the present subordinal scheme devised by Chamberlin is analysed. Following, and expanding on previous work, it is suggested that this classification should be abandoned, and preliminary notes on character states that may be useful in a new classification are presented. Characters presently used at various levels in pseudoscorpion systematics are reviewed, and deficiencies are highlighted. A general life cycle if presented, and life histories and phoresy are discussed.

INTRODUCTION

The Pseudoscorpionida is a medium sized chelicerate order, with nearly 3000 described species in over 400 genera in 22 families throughout the world. Its members are generally small animals but the giants such as *Garypus titanius* Beier attain a body length of 12 mm. Pseudoscorpions, along with most other chelicerates, are predators, and members of most families possess venom glands in one or both chelal fingers. They feed on small arthropods such as springtails, thrips, mites, beetle larvae and flies. Despite their small size, or perhaps because of it, pseudoscorpions are fascinating animals, leading Hooke (1665) to note that "... Nature had crowded together into this very minute Insect, as many, and as excellent contrivances, as into the body of a very large Crab, for as to all the apparent parts, there is a greater rather than a less multiplicity of parts and the like may be in all the other visible parts; and 'tis very likely, that the internal curiosities are not less excellent".

The objectives of this review are to examine critically the existing subordinal classification and the characters used at various levels in the taxonomy of the order, as well as to review our knowledge of life histories and other aspects of pseudoscorpion ecology.

REVIEW OF SUBORDINAL CLASSIFICATION

Simon (1879) provided the first extensive subdivision of the order and recognised 3 subfamilies within the single family Cheliferidae. While his key indicates that he may consider the Garypinae and the Cheliferinae closer to each other than to the Obisiinae, this cannot be taken for granted and I have simply portrayed his classification as a trichotomy (Fig. 1). Balzan (1892) basically recognised the same system, but grouped what are now the Garypoidea, Cheiridoidea and Cheliferoidea into the suborder Panctenodactyli and the Chthonioidea and Neobisioidea into the suborder Hemictenodactyli (Fig. 1). These were based primarily on the degree of fusion of the serrula exterior to the moveable cheliceral finger. The feaellids were not described until 1906 (Ellingsen 1906) so do not figure in either Simon's or Balzan's scheme. Balzan's suborders were

supported by all subsequent authors until 1929, when Chamberlin (1929) presented a novel subordinal scheme that was fully expounded in Chamberlin (1931). He divided the order into 3 suborders based upon the number of tarsal segments of the legs. The first group, The Heterosphyronida, was treated as the sister-group of the remaining taxa. This group contained pseudoscorpions in which legs I and II possess a single tarsus, while legs III and IV possess 2 tarsi. The remaining 2 suborders, Diplosphyronida and Monosphyronida, were placed together in the Group Homosphyronida which was characterised by the presence of equal numbers of tarsi on all 4 pairs of legs. As their names suggest, pseudo-scorpions of the Diplosphyronida possess 2 tarsi per leg, while those of the Monosphyronida possess 1 tarsus per leg. Chamberlin divided these 3 suborders into 6 superfamilies as follows: Heterosphyronida (Chthonioidea); Diplosphyronida (Garypoidea, Neobisioidea); and Monosphyronida (Feaelloidea, Cheiridioidea, Cheliferoidea).

Beier (1932a, 1932b) subsequently adopted Chamberlin's classification and the only major change he made was transferring the monotarsate Feaelloidea to the Diplosphyronida, apparently on the basis of its members' resemblance to garypids.

Apart from a few cosmetic changes, such as the elevation of some subfamilies to families, and the description of 2 new families, Chamberlin's classification has largely gone unchallenged. However, Muchmore (1982) rejected the subordinal ranks and simply recognised the 6 superfamilies that were proposed by Chamberlin, stating that "recent studies ... have cast some doubt on the usefulness of this classification". I heartily concur with this statement and provide notes on the most obvious misclassification, the details of which may be found in Harvey (1986). The monotarsate Feaelloidea (Feaelidae and Pseudogarypidae) have been treated as members of the Monosphyronida by Chamberlin (1931) and of the Diplosphyronida by Beier (1932a). Yet it is apparent that they share several synapomorphies with the heterotarsate Chthonioidea (Chthoniidae and Tridanchthoniidae). All 4 families possess a pair of accessory trichobothria arising from a contiguous pair of areoles, on the tip of the fixed chelal finger, and all possess coxal spines (although the latter are lost in 1 or 2 chthonioid genera). Furthermore, the developmental sequence of the chelal trichobothria is relatively similar (Weygoldt 1969; Mahnert 1981), and the male genital atrium bears a number of internal spines in all 4 families.

Thus a monotarsate superfamily is the sister group of the heterotarsate superfamily. However useful they may have been in the past, Chamberlin's sub-orders do not validly reflect the evolutionary pathways within the Pseudoscorpionida.

While it is obvious that these suborders must be discarded, what shall replace Chamberlin's system? Muchmore's use of the 6 superfamilies without ranking them in a hierarchical fashion is an intermediate stage and we should attempt to group these superfamilies into higher categories whenever possible. As a proponent of the cladistic system of classification, I feel that any new classification should be based on the recognition of undoubtably monophyletic clades by the identification of apomorphic character states. While it is relatively simple to identify autapomorphies for some taxa, there are large gaps in our knowledge for certain groups, especially in vital areas such as genitalia. At this stage a new classification would be premature, but there are several apomorphies which should be useful in any future scheme. These include 1) the monophyly of the feaelloids and chthonioids mentioned above; 2) the occurrence of spermathecae and a mating dance in the Withiidae, Cheliferidae, Chernetidae and Atemniidae; 3) the oblique femoral junction of legs I and II in the latter 3 families; 4) the smooth, or virtually smooth, moveable cheliceral finger in the Feaelloidea, Garypoidea, Cheiridioidea and Cheliferoidea (independently evolved in the feaelloids); 4) the reduction from 4 corneate eyes to 2 corneate eyes or eye spots in the Cheiridioidea and Cheliferoidea; and 5) the monotarsate legs in

the Feaelloidea, Cheiridioidea and Cheliferoidea.

Problems include the apparent lack of apomorphies for the Garypoidea and Cheiridioidea, and perhaps their constituent families need to be accommodated in other ways.

CHARACTERS OF TAXONOMIC IMPORTANCE

Virtually all parts of the pseudoscorpion body, including internal organs, may yield information that could be used at various levels in systematics. Yet I shall restrict this discussion of taxonomic characters to those that appear to be of critical importance in delimiting species, or that may be useful at higher levels in the classification.

Chelae

(i) Venom apparatus

Croneberg (1888) first noted the presence of a venom apparatus in the chelal fingers of pseudoscorpions, and Chamberlin (1924a) extended the observations and noted its presence and absence in several taxa. He later (Chamberlin 1929, 1930, 1931) used it to distinguish between families, and it is still used as a major character today. Of the 22 families currently recognised, 11 possess the venom apparatus in both chelal fingers, 5 possess it in only the fixed finger, 3 possess it in only the moveable finger, and 3 lack it altogether, while minor variation occurs in the Cheiridiidae and Chernetidae (Chamberlin 1938; Judson 1985). A venom apparatus occurring in both chelal fingers would appear to be the primitive state (due to its wider distribution), and it has since been lost independently in several lineages. The presence in both fingers is plesiomorphic and cannot be used as a character to define groups.

Unfortunately nothing is known of the biochemical nature of pseudoscorpion venom. Moreover, little is known of the mode of action of the venom apparatus, apart from Muchmore's (1981) supposition that the lamina defensor, a modified seta typically associated with a functional fang, "might act as a trigger for the release of venom".

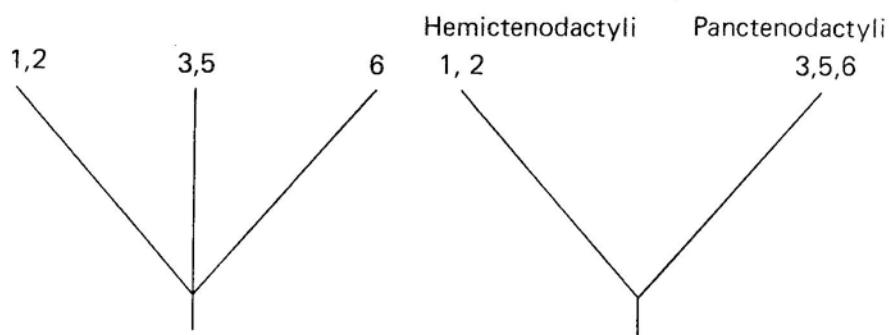
(ii) Trichobothria

The pedipalpal chela is provided with several sets of sense organs, the most obvious and probably most important being the trichobothria. Spider trichobothria have been shown to be "touch-at-a-distance" receptors involved in detection of air currents and low-frequency sound waves (Foelix 1982), but no experimental work on pseudoscorpions has been attempted. It is probable that pseudoscorpion trichobothria act in essentially the same manner as those of spiders.

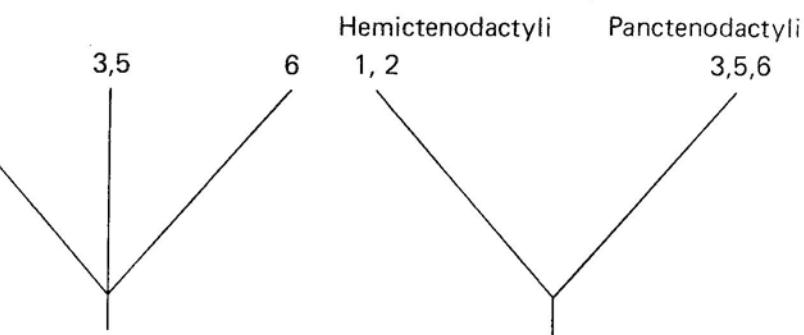
Adult pseudoscorpions typically possess 12 chelal trichobothria, but variation does occur and some taxa possess extra trichobothria (Ideoroncidae and Menthidae), while others have reduced numbers (e.g. Cheiridiidae, Sternophoridae, many Garypidae, and some Neobiidae, Olpiidae and Chernetidae). Chamberlin (1924b) provided a trichobothrial naming system that is still in use today, and began to describe routinely the trichobothriotaxies in each species or genus he treated. The position and number of trichobothria have often been useful at the generic level, but Harvey (1985b) cautioned against the maintenance of genera based solely upon the presence or absence of trichobothria, especially when the remaining trichobothria are in identical positions.

Vachon (1934) was the first to document the post-embryonic changes in trichobothrial number, and thus to recognise that 4 post-embryonic stages occur. Mahnert (1981) has recently summarised our knowledge of post-embryonic development.

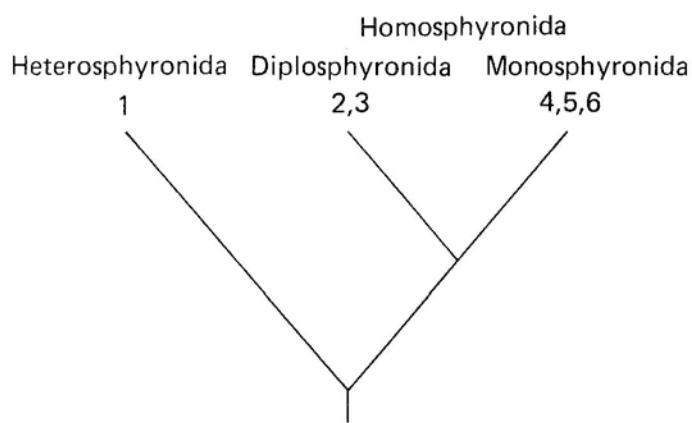
SIMON, 1879



BALZAN, 1892



CHAMBERLIN, 1929-1931



BEIER, 1932a, 1932b

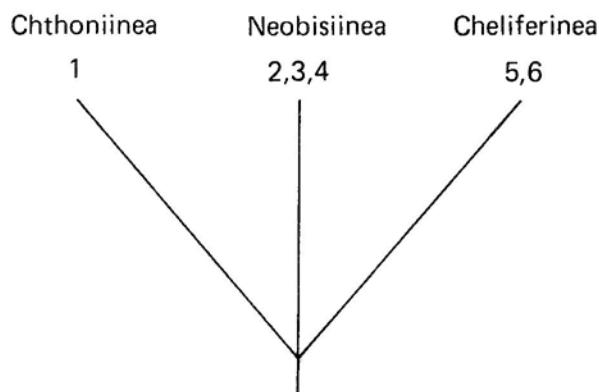


Fig. 1. Pseudoscorpion classifications proposed by various authors. The numbers refer to the superfamilies as currently recognised, even though Simon and Balzan did not recognise such categories.

Pedipalpal morphometrics

Pseudoscorpion species have long been distinguished on the relative sizes of the various pedipalpal segments, but little statistical work has been attempted to quantify these presumed differences. Heurtault (1980) used regression analyses to separate 2 species of *Rhacochelifer* (Cheliferidae) based upon the length and width of the pedipalpal femur. Harvey (1987) used multivariate discriminant functions analyses to examine groups of closely related species of *Synsphyronus* (Garypidae). Harvey (1984, 1985b, 1987) provided graphs of chela length versus chela width of several taxa which portrayed specific differences much more effectively than simply listing series of measurements and length/width ratios.

Eyes

Most pseudoscorpions possess at least 1 pair of eyes, although some species lack eyes altogether. Members of the superfamilies Chthonioidea, Feaelloidea, Neobisioidea and Garypoidea usually possess 2 pairs of eyes, and these are mostly corneate. The remaining 2 superfamilies, the Cheiridioidea and Cheliferoidae, at most possess 1 pair of eyes, sometimes corneate, but usually represented by eye-spots. It would appear that corneate eyes are primitive for the order and that several independent reductions to eye-spots or complete blindness have occurred.

As it appears that eyes may be a useful taxonomic tool at higher levels in the ordinal classification, it is unfortunate that little histological work, and apparently no comparative histological work, has been attempted. The best study is that of Callaini (1981) who recently examined the eyes of *Blothrus muscorum* (Leach).

Female genitalia

The genitalia of female pseudoscorpions are relatively simple, but structures of taxonomic importance do occur. The most notable are the spermathecae and the cribiform plates.

Spermathecae are present in only 4 families, the Withiidae, Cheliferidae, Chernetidae and Atemnidae, where they attain a variety of shapes which may be useful at the generic level, especially in the Chernetidae (Vachon 1957; Muchmore 1975). Even though several cheliferid genera apparently lack spermathecae, the presence of spermathecae is a shared apomorphic character for these 4 families. Those cheliferids that lack spermathecae possess character states that immediately associate them with other cheliferids that possess spermathecae (e.g. presence of statumen convolutum and often coxal sacs or ram's-horn organs in males).

The female cribiform plates were first utilised in systematics by Chamberlin (1931-1932) who used them to distinguish between the Cheliferini and Dactylocheliferini (as Lissocheliferini). Recently, Harvey (1985b) was able to distinguish the 3 sternophorid genera only on the basis of the number and structure of the median cribiform plates.

Given the high potential of female genitalia for pseudoscorpion taxonomy it is regrettable that these have been documented for only a small proportion of the species. The best accounts are those of Legg (1974a, 1974c, 1975a, 1975b), and a review of the genital musculature is given by Legg (1974b).

Male genitalia

The genitalia of male pseudoscorpions are even more poorly known than those of females, presumably due to their greater complexity. Chamberlin (1923) made

the first comparative observations, and Vachon (1938) and Legg (1974a, 1975a, 1975b, 1975c) examined several species. Legg also stabilised the nomenclature (Legg 1975c) and examined the genital musculature (Legg 1974b). Male genitalia may be quite useful at the alpha level (e.g. Heurtault 1971; Mahnert 1982; Harvey 1985b), but in some genera no variation occurs (Harvey 1987).

GENERAL BIOLOGY

Life histories

Few life history analyses have been determined for pseudoscorpions, and these are all restricted to northern hemisphere species (Gabbutt and Vachon 1963, 1965, 1967, 1968; Gabbutt 1969; Nelson 1973, 1982; Goddard 1976, 1979; Sato 1978, 1980). The problems involved in the sampling of pseudoscorpion populations in leaf litter are discussed by Gabbutt (1970).

A generalised life-cycle (Fig. 2) is as follows. The protonymph hatches from the brood-sac, becomes free-living for usually 1 year, constructs a silken chamber and moults into a deutonymph (see Levi (1948) for a description and figures of the moulting sequence of *Chelifer cancroides* (L.) (Cheliferidae)). The silk is spun from a gland in the cephalothorax that is excreted via the galea on the moveable cheliceral finger. It is spun into an igloo or disc shaped chamber that is often embedded with particles of wood, sand or discarded insect remains. The deutonymph then abandons the chamber and becomes free-living until it constructs a silken chamber and moults into a tritonymph. This process is repeated once again and it becomes an adult. Adults do not moult. The species examined by Gabbutt (1969) and Nelson (1982) are univoltine, but populations of *B. muscorus* may be bivoltine in more favourable environments (Gabbutt 1969).

The adults and nymphs of some species build silken chambers in which they overwinter (Wood and Gabbutt 1979a, 1979b; Gabbutt and Aitchison 1980), but males of *B. muscorus* lack silk glands and associated ducts and are thus incapable of building silken chambers (Wood and Gabbutt 1979a).

Males adopt a number of mating strategies, but all involve the deposition of spermatophores. Sperm transfer has been reviewed by Weygoldt (1969), who recognised 3 methods; 1) both sexes acting independently of each other where the male deposits a spermatophore which the female searches for, steps over and takes up for insemination (Chthoniidae, Tridenchthoniidae, Pseudogarypidae, Neobisiidae, some Olpiidae, Garypidae and Cheiridiidae); 2) the male deposits a spermatophore only in the presence of a female, but without physical contact (some Olpiidae); and 3) with physical contact where the male grasps the female's pedipalps and performs a short ritualised dance before he deposits a spermatophore which the female, often with guidance from the male, takes up for insemination - this being somewhat similar to the mating dance of scorpions (Withiidae, Chernetidae, Atemniidae and Cheliferidae). Spermatophore morphology and transfer is also reviewed by Weygoldt (1969), and once again the most complex forms are found amongst the Cheliferoidea.

Inseminated females usually then construct a silken chamber several days before the brood-sac is formed. The brood-sac, which is formed by the hardening of a secretion from the accessory glands, remains attached to the female gonopore. Five to 30 eggs are laid into the brood-sac and development of the embryo begins. Weygoldt (1969) recognises 2 embryonic instars before the development of the protonymph which then hatches out of the brood-sac and, after a few days, leaves the silken chamber.

Habitat preferences

Apart from the data gleaned from collection labels, we have little detailed

information on habitat preferences. Hoff (1959) critically examined the micro-distribution of the pseudoscorpions of New Mexico, U.S.A. and Weygoldt (1969) provided a cross-section through an island off the coast of North Carolina, U.S.A., showing habitat partitioning of 9 pseudoscorpion species. There appears to be a distinct littoral fauna in many parts of the world and Lee (1979) examined the littoral pseudoscorpions of Baja California, Mexico, noting habitat preferences of several species on the beach.

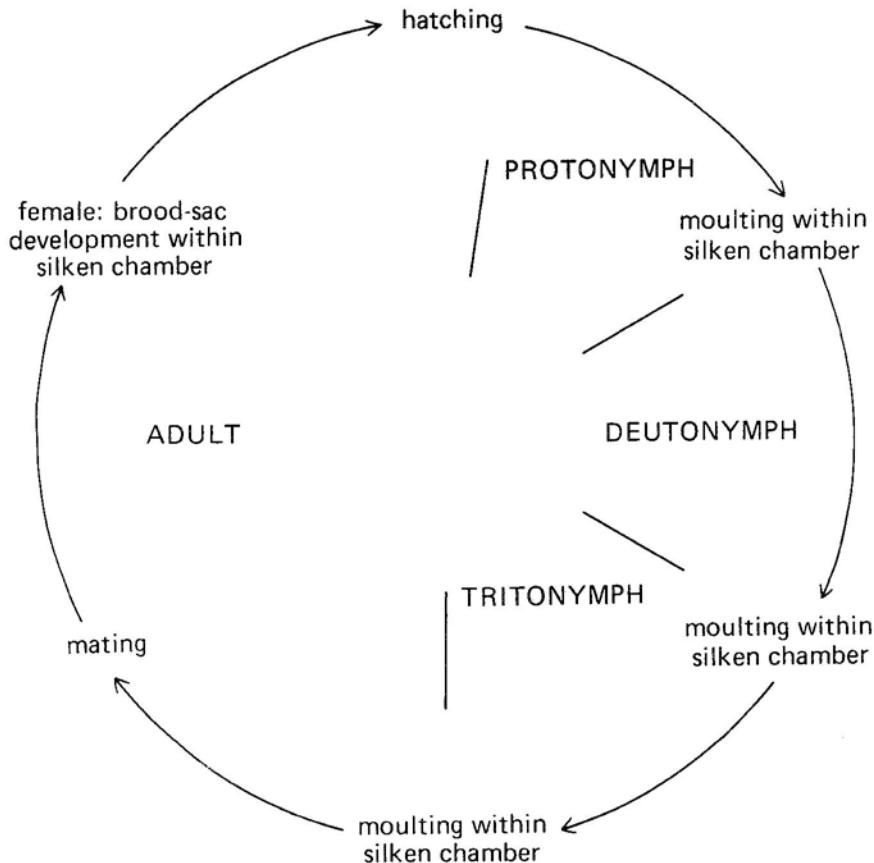


Fig. 2. A generalised life cycle of a pseudoscorpion.

Phoresy

Pseudoscorpions have long been known to be phoretic, and the current definition, coined by Muchmore (1971), is a "nonparasitic association of one kind of animal with another which results in transportation of the smaller by the larger". Phoretic pseudoscorpions have been found in many families (see reviews by Vachon 1940; Beier 1948; Muchmore 1971), and they usually are phoretic on insects, even though opiliones or, less occasionally spiders, may be utilised.

Reports of phoretic pseudoscorpions, however, must be treated with a moderate amount of caution, especially when the mode of collection of the insect and the pseudoscorpion may not permit the determination of true phoresy. For example, I have noticed that placing a pseudoscorpion into a vial with another small invertebrate such as an insect sometimes causes the pseudoscorpion to grasp hold of the insect on which the pseudoscorpion then appears phoretic, especially if the collection is then preserved and transferred to a museum collection.

Nevertheless, numerous authentic cases of phoresy have been observed.

While phoresy appears to have the effect of dispersing pseudoscorpions to preferred habitats, there has been no experimental work to prove or disprove the hypothesis. Pseudoscorpions are found on small oceanic islands of recent origin, and one must assume that they reach the islands by either phoresy or rafting. Simberloff and Wilson (1969) found a species of *Tyrannochelifer* (Cheliceridae) on a previously fumigated mangrove islet 370 days after fumigation. Guilmette *et al.* (1970) reported a pseudoscorpion collected 5 km from Santa Catalina Island, California, U.S.A., during a survey of air-borne insects. The specimen (lodged in the Bishop Museum and examined courtesy of Dr J.A. Tenorio) is a chelicerid protonymph. Presumably, it was phoretic on 1 of the 4 flies (of 3 different families) collected at that time. Recent field work on Krakatau, an island group that was totally denuded of life in 1883 by a volcanic eruption, has uncovered 11 species in 7 families (Harvey, unpubl. data).

THE AUSTRALIAN FAUNA

Only 120 species of pseudoscorpions in 43 genera and 13 families have been described to date from Australia and its territories [Harvey (1985a) provided the most recent catalogue; see Harvey (1981) for the superfamilies into which the Australian families are currently placed], and many of these are known only from 1 or 2 localities. Compared with a world total of 3000 species, this appears to be disproportionately small. Obviously many Australian species await description and much work needs to be undertaken before a realistic picture of the Australian fauna can be obtained. I would estimate that several hundred undescribed species are present in museum collections, and relatively unsampled areas such as Cape York are bound to reveal a further wealth of new forms. Nevertheless, we must not be solely preoccupied with new species, because the bulk of the previously described species are still poorly known: genitalia have not been examined, nymphal stages are virtually unrecorded, and distributions have yet to be ascertained. Life history work is non-existent, and should prove to be extremely interesting when compared with the life histories of the northern hemisphere species mentioned above. Ecological work is restricted to general studies such as that of Richards (1971).

THE FUTURE

What, then, is in store for the study of pseudoscorpions? With larger collections amassing in museums around the world, especially from poorly studied areas such as South America, southeast Asia and Australia, there is an exciting time ahead in taxonomy. Yet many of the so-called well-known faunas, such as in Europe, are still far from perfectly known and we should not ignore the problems there. I also feel that the stage is now set for revisions on a world basis. It is all very well to describe new forms from here and there (who hasn't?), but a synoptic view must be taken, especially at the generic level for which it is apparent that more and more genera are not endemic to continents, but are widespread across various geographical zones.

The use of Tullgren funnels and other extraction devices such as the Winckler apparatus will continue to uncover many litter and soil dwelling forms. The availability and application of modern techniques, such as the scanning electron microscope, will enhance our knowledge of the fine detail of surface and internal sclerotised structures. Biochemical work, such as the use of electrophoresis in detecting and analysing sister species has not been attempted, and cytological studies are limited to the work of Boissin and Manier (1966) who examined *Hysterochelifer meridianus* (L. Koch).

The perception of Robert Hooke (1665, quoted in the introduction) has been

shown to be correct - the "internal curiosities are not less excellent" (italics added) than the external features he could examine. But 200 years after his observations we still have a long way to go, not only in the study of the internal organs but in many other aspects of their biology and morphology.

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