

## The possible significance of spermathecae in pseudoscorpions (Arachnida)

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Lubbock (1862), Metshnikoff (1871), Cröneberg (1889), Barrois (1896), Schtschelkanovzeff (1898), Kästner (1927) and Chamberlin (1931) have all contributed to our knowledge of the female pseudoscorpion genitalia, but it was Vachon (1938) who first completed a comprehensive survey of their comparative morphology. Recently Legg (1971, 1974a) has made a detailed study of the genitalia of the British species.

The genital atrium is an invagination between sternites 2 and 3 of the opisthosoma. It is divided into four regions: a median (*md*), small posterior (*pvdv*) and two lateral diverticula (*ldv* Fig. 1). A pair of variously developed lateral apodemes (*la*) occur lateral to the median diverticulum. These provide surfaces for muscle attachment and support for the genital atrium. Two pairs of accessory glands are present. The paired median (often fused) and paired lateral glands (*mg*, *lg*) are closely associated with, and open respectively into, the median and lateral diverticula by way of the porous cuticular, median and lateral cribriform plates (*mcp*, *lcp* Fig. 1).

In the British fauna spermathecae are present in species belonging to the families Chernetidae and Cheliferidae, and possibly in a reduced form in the Cheiridiidae (Legg 1971, 1974b). The structures open antero-dorsally into the median diverticulum, dorsal to the opening of the common oviduct (*sp*, *ov* Fig. 1). True spermathecae are absent from the Chthoniidae and Neobisiidae. Chamberlin (1931) believes that the absence of spermathecae in these two families has been brought about by the fusion of the spermathecae to produce a single median structure, which Vachon (1938) terms the median diverticulum of the genital atrium. Since the median diverticulum is part of the genital atrium it seems likely that the spermathecae originated as evaginations of this diverticulum. Scattered glandular cells are found in the epithelium of the cuticle-lined spermathecae (Vachon 1938, Legg

1971).

Reproduction involves the indirect transfer of sperm (Schaller 1965) by means of spermatophores (Kew 1930, Weygoldt 1966). Consequently the female is adapted to picking up and to a greater or lesser extent, adapted to storing the sperm.

In the Chthoniidae, Neobisiidae and Cheiridiidae there is a simple globular packet of sperm at the apex of the peduncular spermatophore. Mechanical rupturing of this packet, involving a swelling mechanism (Weygoldt 1969), liberates the sperm into the female's genital atrium. In the Chernetidae the sperm packet is more complex and M-shaped. This is picked up by the female and sperm are released into her genital atrium (Weygoldt 1969). Extremely complex sperm packets are found in the Cheliferidae. Here mating involves a nuptial dance and the female is guided by the male over the spermatophore. As the sperm packet is positioned in the female's genital aperture, structures associated with the packet forcibly squeeze its contents into the female's spermathecae (Vachon 1938, Weygoldt 1969).

The complexity of the spermatophore is correlated with the type of mating behaviour involved. Weygoldt (1969) classifies pseudoscorpions into four groups depending on the type of mating behaviour they exhibit:

1. Sperm transfer without mating; males and females acting independently both in space and time (Chthoniidae, Neobisiidae and Cheiridiidae).
2. Sperm transfer without mating; one mate acts only in the presence of the other (Olipidae).
3. Sperm transfer with mating; both sexes active:
  - (a) without firm body contact throughout the nuptial dance (Chernetidae);
  - (b) with firm body contact throughout the nuptial dance (Cheliferidae).

This is correlated with the increasing complexity in the type of spermatophore produced and the form of the male genitalia; the former being a function of the latter (Legg 1971). Associated with these developments is the trend towards an increase in complexity of the female genitalia, namely in the development of spermathecae. These morphological and behavioural characteristics, together with other, non-genital characters, have led to the conclusion that the least specialised families include the Neobisiidae, Chthoniidae and Cheiridiidae, whilst the Chernetidae

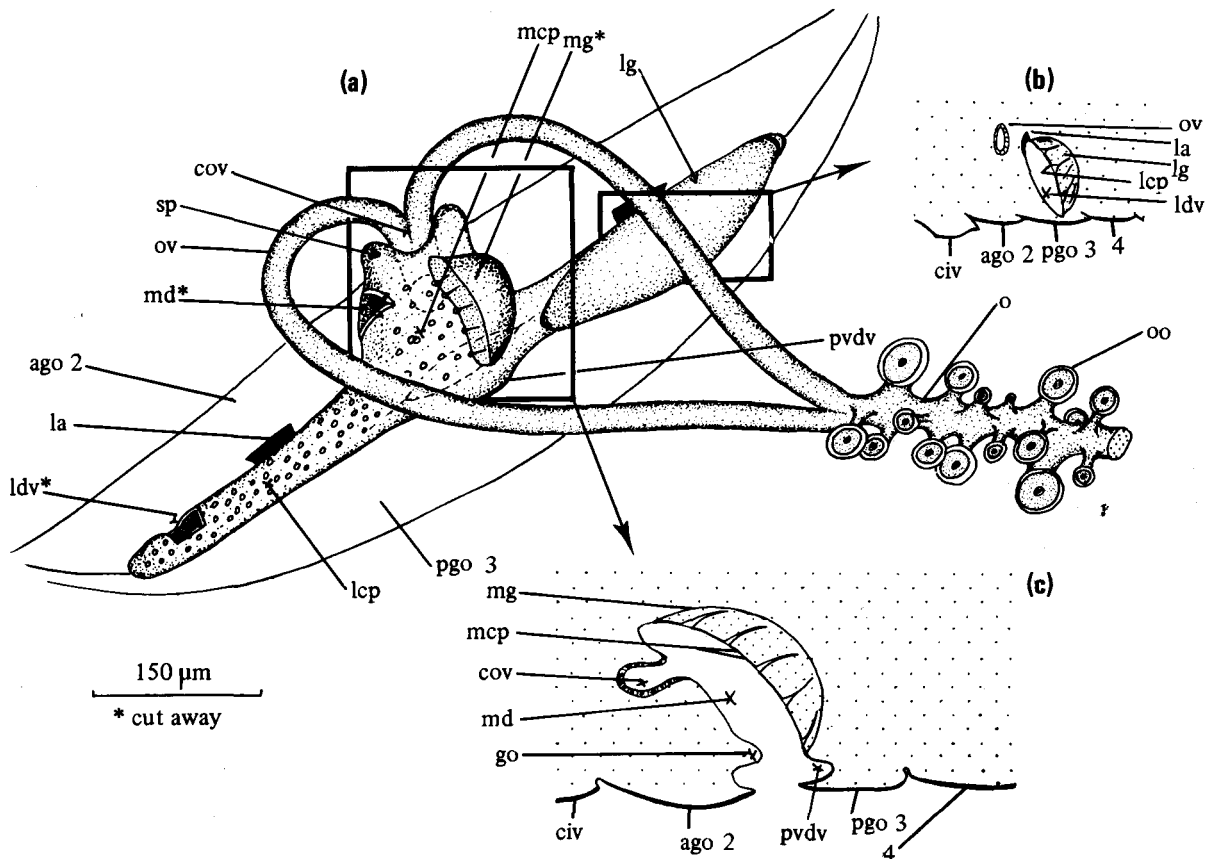


Fig. 1: Generalised female pseudoscorpion genitalia:

(a) Stereogram, latero-dorsal view (\* partly cut away)

(b) Parasagittal section cutting through the lateral diverticulum

(c) Parasagittal section cutting through the median diverticulum.

(anterior genital operculum ago, coxa of leg four civ, common oviduct cov, gonopodium go, lateral apodeme la, lateral cribriform plate lcp, lateral diverticulum ldv, lateral gland lg, median cribriform plate mcp, median diverticulum md, median gland mg, ovary o, oocyte oo, oviduct ov, posterior genital operculum pgo, posterior ventral diverticulum pvdv, spermatheca sp, sternites 2, 3 and 4 of the opisthosoma.)

and Cheliferidae are regarded as being more specialised.

Pseudoscorpions are found in a wide variety of habitats, which can be broadly divided into two major types: the permanent and fairly stable ones of woodland litter and soil (static habitats), and the temporary and less stable habitats of decaying trees, barn refuse and animal nests (non-static habitats). The arrows in Fig. 2 indicate the type of habitat favoured by the various families found in Britain. The

thickness of the arrow indicates, approximately, the relative numbers of species of a particular family using a particular habitat.

The three families Neobisiidae, Chthoniidae and Cheiridiidae lack spermathecae (the latter family possess spermathecal pockets, Legg 1974b), are unable to store sperm for prolonged periods and possess simple mating behaviour. The former two families are found in the more permanent and stable habitats of accumulated vegetable debris and soil.

They are conspicuous by their absence from the temporary and less stable habitats. In contrast, the other two families, Chernetidae and Cheliferidae, especially the former, have exploited both main habitat types.

It is suggested that the species of the families Chernetidae and Cheliferidae have been able to increase their distribution range because:

1. Fertilization of the female is ensured since both sexes act only in the presence of each other (Weygoldt 1969). This also reduces sperm and spermatophore wastage which otherwise occurs in those which mate indirectly at random.
2. A complex spermatophore is produced to aid fertilization.
3. Females possess specialised regions of the median diverticulum of the genital atrium, the spermathecae, in which sperm can be stored for *prolonged periods*. The presence of secretory cells in the spermathecal epithelium might, in addition to the secretion from the median glands, help to nourish the stored encysted sperm.

Because of their temporary nature, habitats such as dead trees and animal nests are highly unlikely to be exploited by pseudoscorpions unable to store sperm for prolonged periods, unless such a habitat is in close proximity to a stable and permanent one. The development of spermathecae and efficient fertilization mechanisms has enabled the Cheliferidae and in particular the Chernetidae to utilise these habitats. A single fertilized female reaching a suitable but isolated habitat can initiate a population.

How does a suitably fertilized female with spermathecae reach a new habitat? Since it is unlikely that individuals will leave for example a bird's nest and move "on foot" in the hope that a suitable new habitat will be found, then another mechanism must operate to facilitate their dispersal.

It is well known that many pseudoscorpions demonstrate the association called *phoresy*. This association has received a great deal of attention, particularly from Vachon (1940, 1954), Beier (1948) and Muchmore (1971a, b). It was generally considered that the phoretic behaviour was an aid in dispersal, in fact, Muchmore (1971b) gives a dictionary definition of the phenomenon as "a non-parasitic association of one kind of animal with another in order to obtain transport" (Webster's Third New International

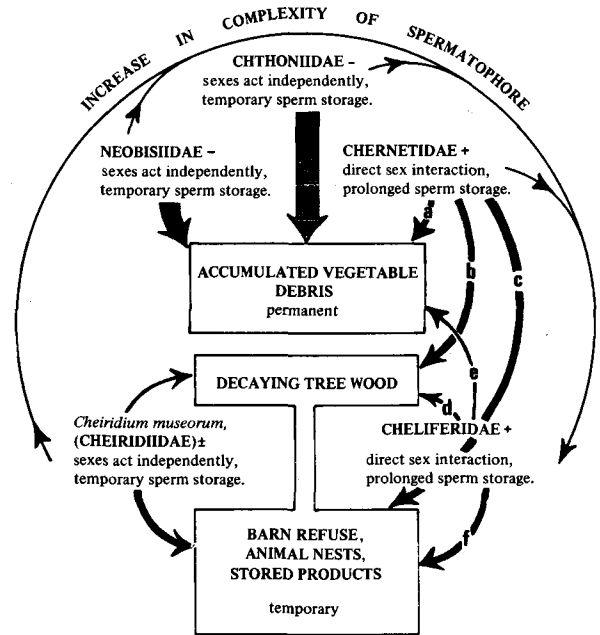


Fig. 2: Some habitats exploited by pseudoscorpions.

- a *Allochernes dubius*, *Lamprochernes* spp., *Pselaphochernes* spp.  
 b *A. wideri*, *Toxochernes panzeri*, *Chernes cimicoides*, *Dendrochernes cyrneus*  
 c *A. wideri*, *T. panzeri*, *Chernes cimicoides*  
 d *Dactylochelifer latreillei*  
 e *Chelifer cancrivorus*  
 f *Chelifer cancrivorus*, *Withius subruber*  
 - spermatheca absent  
 ± spermatheca absent and/or spermathecal pockets present  
 + spermatheca present

Dictionary). However, Muchmore goes on to say that phoresy is not primarily concerned with dispersal but is a phenomenon which has simply resulted from the *predacious* habits of pseudoscorpions. On this basis he redefines phoresy as a "non-parasitic association of one kind of animal with another which results in transportation of the smaller by the larger", thus avoiding any reason for the association and leaving open the question of whether or not dispersal is involved. It is perhaps useful to note here that pseudoscorpions are not alone in the use of phoretic behaviour. Entirely obligate insect parasites, such as the Mallophaga, which are secondarily wingless and thus have a restricted dispersal mechanism (Askew

1971) are faced with the equivalent problems of the Chernetidae and Cheliferidae. To overcome the dispersal problem (Askew 1971) many parasitic insects have developed phoretic behaviour. On dying the host attracts flies some of which visit live hosts. The lice attach themselves to the flies either accidentally or as an outcome of their *parasitic* habits and are transported to a new host.

An examination of the distribution of the species which have *so far* been shown to demonstrate phoresy shows that approximately 55% of the species belong to a single family, the Chernetidae and 12% to the Cheliferidae. The remaining 33% represent the rest of the 18 pseudoscorpion families. Fig. 2 shows that the Chernetidae is a particularly successful family in that it contains many species which have exploited a very large range of both permanent and temporary habitats. Gabbutt (1969) points out that the long duration of the life-cycle of *Pselaphochernes scorpioides* (Hermann), together with phoretic behaviour, facilitates dispersal. Weygoldt (1969) suggests that phoresy is important in the dispersal of the chernetid pseudoscorpion *Lasiochernes pilosus* (Ellingsen) a European species found in the nests of moles.

Gilyarov (1947, 1956) produced a controversial hypothesis on the evolution of terrestrial invertebrates. With particular reference to the insects he considered that the soil provides an ideal environment for many invertebrates of aquatic origin, which can obtain oxygen from the air without danger of desiccation. The derivation of winged forms from apterous soil living ancestors then enabled the insects to exploit the air, for dispersal, thus increasing their range of habitats. It is perhaps possible to extend this idea to pseudoscorpion evolution. Thus, the development of both a complex mating behaviour to ensure fertilization of the female and a sperm store, the spermathecae, has enabled the pseudoscorpions to escape from the stable, static and humid habitat of soil and decaying vegetable debris and to exploit less favourable, isolated, non-static and temporary habitats.

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## A Taxonomic Revision of the Genus *Erigonoplus* Simon 1884 (Araneae: Linyphiidae: Erigoninae)

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The genus *Erigonoplus* was created by E. Simon in 1884 (p. 724) for the following species:

*Erigonoplus inclarus* (Simon 1882)

*E. nigerrimus* (Simon 1884) – later (Simon 1926) synonymized with *E. inclarus*

*E. nigrocaeruleus* (Simon 1882)

*E. globipes* (L. Koch 1874)

*E. turriger* (Simon 1882)

*E. justus* (O. P.-Cambridge 1875)

*E. castellanus* (O. P.-Cambridge 1875)

*E. inclarus* is the type species under the "first species" rule.

The genus was defined in 1884 by the size and arrangement of the eyes, and by the presence on the undersides of the anterior femora of two rows of long spines or bristles, often longer in the distal half. The males usually had a cephalic lobe, but not in the type species.

In 1894 (p. 617) Simon synonymized the genus *Erigonoplus* with *Caracladus* Simon 1884, but in his posthumous treatise (1926, p. 485) the genus was resurrected for the type species *inclarus* alone. The remaining species, except *castellanus*, were transferred to *Trichopterna* Chyzer and Kulczynski 1894, while *castellanus* was placed in a new genus, *Cotyora* Simon 1926. In 1943, Miller rightly decided

that *globipes* did not fall in *Trichopterna*, and created for it a new genus *Erigonopterna*, in which he placed also his new species *jarmilae* Miller 1943. In 1965, Denis placed *justus* rather doubtfully in *Acartauchenius* Simon 1884.

The author has recently re-examined as many as possible of the species originally placed by Simon in *Erigonoplus*, and in addition the species *Erigonopterna jarmilae*. These were as follows:

*Erigonoplus inclarus*: 3♂ (2 labelled *E. nigerrimus*) loaned from Paris (MNHN), rather depilated but the palpal organs still in good condition; ♀ unknown.

"*Trichopterna*" *nigrocaerulea*: ♂ loaned from Paris (MNHN), in good condition but slightly depilated; ♀ unknown.

"*T.*" *turrigera*: ditto.

"*T.*" *justa*: ♂ loaned from Oxford (Hope Department), in relatively good condition; 2♂ and immature ♀ in good condition loaned from Brussels (Institut Royal des Sciences Naturelles de Belgique). Adult ♀ unknown.

"*Erigonopterna*" *globipes*, "*E.*" *jarmilae*: Both sexes very kindly donated by Professor Miller (Brno).

"*Erigone*" *castellana*: ♀♂ loaned by Oxford (Hope Department), in good condition.

These species are figured in Figs. 1-36.

It has not been possible to obtain from Paris any specimens of *Trichopterna krueperi* (Simon) which Simon (1926, p. 484 footnote) says is similar to *T. turrigera*. It is to be noted that with the exception of *globipes* and *jarmilae* the species are all of extreme rarity, and that four of them appear not to have been re-taken since their original captures some 90-100 years ago.