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A Generalised Account of the Male Genitalia and Associated Glands of Pseudoscorpions (Arachnida)

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Introduction

The present paper includes a review of the literature and a general account of the male genitalia of pseudoscorpions which are concerned with the production of spermatophores. Detailed studies of families and genera are reserved for later papers.

Representatives of five families, Chthoniidae (*Chthonius ischnocheles* (Hermann), *C. tenuis* (L. Koch), *C. tetrachelatus* (Preyssler), *C. orthodactylus* (Leach), *C. kewi* (Gabbutt)); Neobisiidae (*Neobisium muscorum* (Leach), *N. maritimum* (Leach), *N. carpenteri* (Kew), *Roncus lubricus* (L. Koch), *Microcreagris cambridgei* (C. L. Koch)); Cheiridiidae (*Cheiridium museorum* (Leach)); Chernetidae (*Chernes cimicoides* (Fabricius), *Dendrochernes cyrneus* (L. Koch), *Allochernes dubius* (O-P. Cambridge), *A. wideri* (C. L. Koch), *A. powelli* (Kew), *Lamprochernes nodosus* (Schrank), *L. godfreyi* (Kew), *Toxochernes panzeri* (C. L. Koch)); Cheliferidae (*Chelifer cancroides* (Linn.), *Dactylochelifer latreillei* (Leach), *Withius subruber* (Simon)), from Britain were examined. In addition four species from West Africa (Sierra Leone) were examined, three unidentified species of the family Garypidae and a single unidentified species of *Fealla* (Ellingsen) (Feaellidae).

There is confusion over the nomenclature of the different parts of the genitalia. To help clarify the situation Table 1 shows a list of synonymous terms used by different authors. In general the nomenclature of Vachon (1938) is followed, with some variations stipulated in the following text.

Materials and methods

The techniques employed included two main techniques used by previous authors.

Cuticular structure

1. The cuticular structure of all species was examined after the following treatment.

Individuals were fixed in Bouin, bisected (transverse, horizontal, longitudinal section) cleared in 5% aq. potassium hydroxide, stained in acid fuchsin and mounted in balsam. Both Vachon (1938) and Chamberlin (1931) have used a comparable technique with successful results. If the treatment with KOH is done with restraint even very delicate cuticular structures remain intact (0.5 μm thick). Staining greatly enhanced contrast and phase-contrast microscopy was only used to resolve the occasional doubtful case.

2. Four species, *C. ischnocheles, N. muscorum, R. lubricus* and *M. cambridgei,* particularly the first named, were examined following bisection and clearing in KOH, in a Cambridge Stereo Scan electron microscope. Despite the occasional distortion of some delicate cuticular structures (consequent upon vacuum or air-drying) the use of the stereo-scan permitted a clear view of the surface features of the cuticular parts of the genitalia and their spatial relationships with each other.

Internal anatomy

1. (a) Various fixatives (commonly Bouin) were used depending on the staining technique employed. The material was then dehydrated by an ethanol series, double embedded in celloidine and paraffin wax, sectioned at 10 μm in three different planes and stained in a variety of histochemical and histological stains. For the majority of species haemotoxylin and eosin, and Mallory's trichrome provided the best preparations.

1. (b) Some material (*C. ischnocheles, N. muscorum, Ch. museorum, T. panzeri* and *D. latreillei*) was cut fresh on a freezing-microtome prior to histochemical treatment (Legg 1973).

It was possible using these two techniques subsequently to construct three-dimensional models of the genitalia and to have some understanding of the histochemistry of the various tissues involved in spermatophore formation.

2. Specimens of male *C. ischnocheles* were suitably prepared, sectioned and examined under an AEI 801

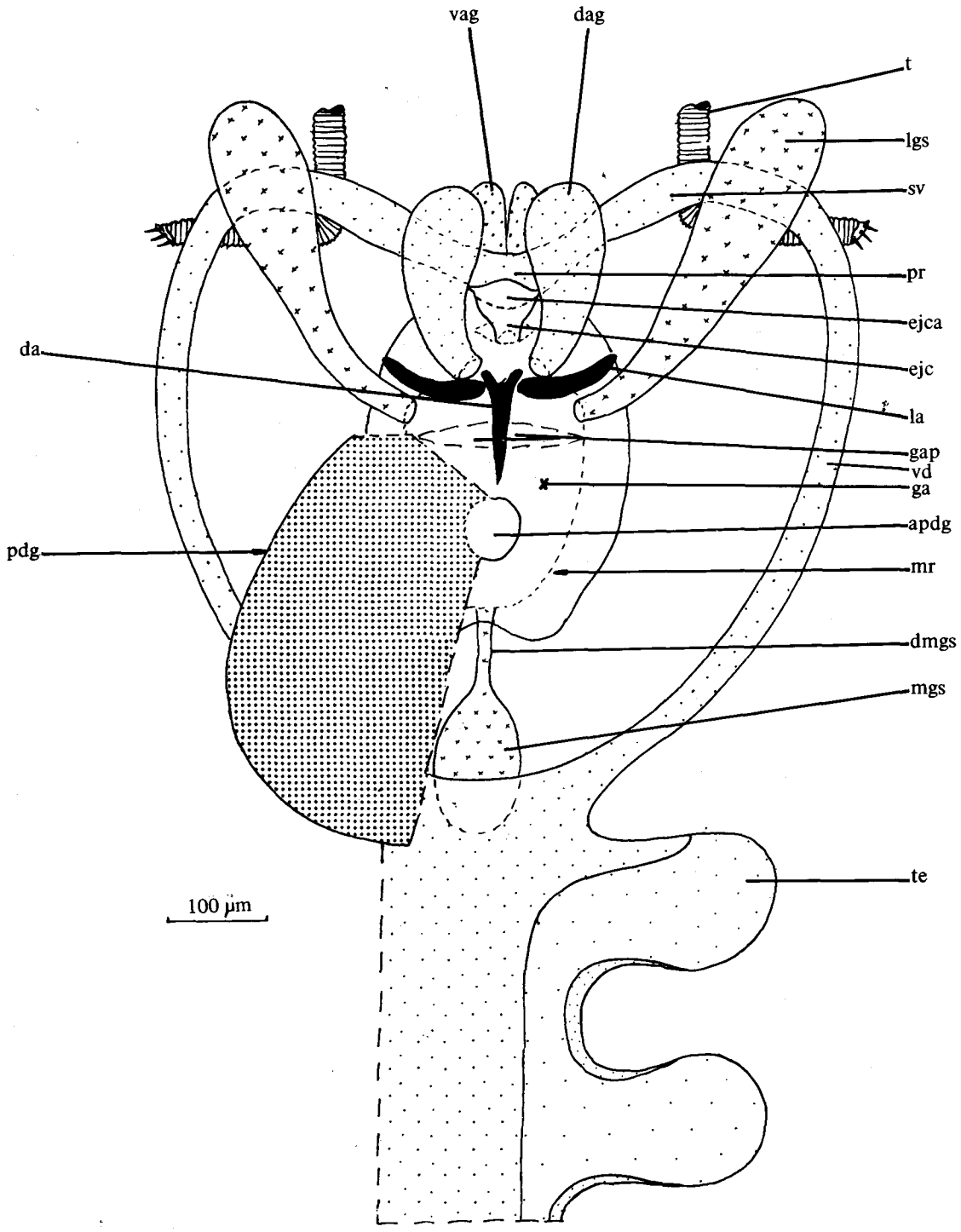

Fig. 2. Dorsal view of the generalised male genitalia and associated glands (modified after Vachon, 1938).

complex ones in the Chthoniidae and Chernetidae, and extremely elaborate genital atria are found in the Cheliferidae.

Genital armature

Associated with the genital atrium are a number of apodemes which constitute the genital armature (Vachon 1938). The use of the term apodeme in this context is probably incorrect, since it refers not only to a thickened region of cuticle forming part of the genital atrium but also to structures which should really be referred to as apophyses. Strictly speaking an apodeme is an invagination or inflexion of the cuticle which is hollow, whilst an apophysis is solid, both being used for muscle attachment (Richards 1951). However, the terms used by Vachon (1938) will be adhered to, to avoid additional complications. A medial thickening extends laterally on either side of the ejaculatory canal in the sagittal plane. This is the dorsal apodeme *(da)* (Figs. 1, 2 and 3c) and although bilobed its form varies in the different families, for example it might be bi-saccate as in the Neobisiidae and Cheiridiidae, or bifid and elongate as in the Chthoniidae and Cheliferidae. A pair of lateral apodemes *(la)* extend laterally and to some extent ventrally around the anterior region of the genital atrium (Figs. 1, 2 and 3c). These apodemes serve for the attachment of muscles and support the medial and dorsal diverticula. A third pair of thickenings, the lateral rods, which support the ejaculatory canal, are found in the Chernetidae and particularly in the Cheliferidae.

Accessory glands

Associated with the male reproductive system are a number of glands and sacs some of which are now known to be implicated in the production of the spermatophore (Legg 1973).

(a) *Anterior glands*

The bilobed dorsal anterior glands *(dag)* are situated anterior to the genital atrium. They open by two ducts into the left and right anterior regions of the anterior dorsal diverticulum, on either side of the ejaculatory canal (Figs. 1, 2 and 3b). The glandular epithelium is thick and folded and a porous cuticular plate covers the apertures of the glands into the genital atrium. In some families, such as the Cheiridiidae, these glands are absent.

Two ventral anterior glands *(vag)* (Figs. 1, 2, and 3b) open by two ducts, on either side of the mid-line into the anterior ventral diverticulum. They have a similar form to that of the dorsal anterior gland. Frequently the two ventral anterior glands are so closely associated that they form a single bilobed median gland (e.g. Chthoniidae) and open by a single cuticular duct into the anterior ventral diverticulum.

(b) *Posterior dorsal gland*

The posterior dorsal gland *(pdg)* lies close to the genital atrium (Fig. 1) and extends anteriorly and posteriorly (Fig. 3b, c and d). This gland is composed of club-shaped masses, the ducts from which open into a median atrium. The atrium of the posterior dorsal gland *(apdg)* is an invagination in the mid-line from the roof of the genital atrium, posterior to the ejaculatory canal. The actual opening of the atrium is in the region of the posterior medial diverticulum (Figs. 1, 2 and 3d). Cröneberg (1889) termed the posterior dorsal gland the "spinning gland" or "cement gland". These are unsatisfactory terms since the gland neither spins (material) nor does it produce cement. The more descriptive terminology of Vachon (1938) is favoured in this case. The posterior dorsal gland is common to all the species of pseudoscorpion examined and represents the most prominent accessory gland.

(c) *"Posterior lateral glands"*

Although these glands differ in their morphology, position and function in three known families (author's unpublished work) in which they occur, Vachon (1938) has termed them all "posterior lateral glands". Boissin (1970) when describing the genitalia of *Hysterochelifer meridianus* (L. Koch) (Cheliferidae) has continued to use the terminology adopted by Vachon. To help clarify this situation it is proposed to call the "posterior lateral glands of the Chthoniidae, the lateral glands; those of the Cheliferidae, the glands of the ram's horn organ; and to retain the term posterior lateral gland only for the Chernetidae. The Neobisiidae and Cheiridiidae lack "lateral glands". In the Chthoniidae the lateral glands open via four pairs of cuticular papillae along the posterior ventral ridges of the genital atrium. The glands of the ram's horn organs of the Cheliferidae occur close and lateral to the ram's horn organs (folded evaginations of the posterior ventral

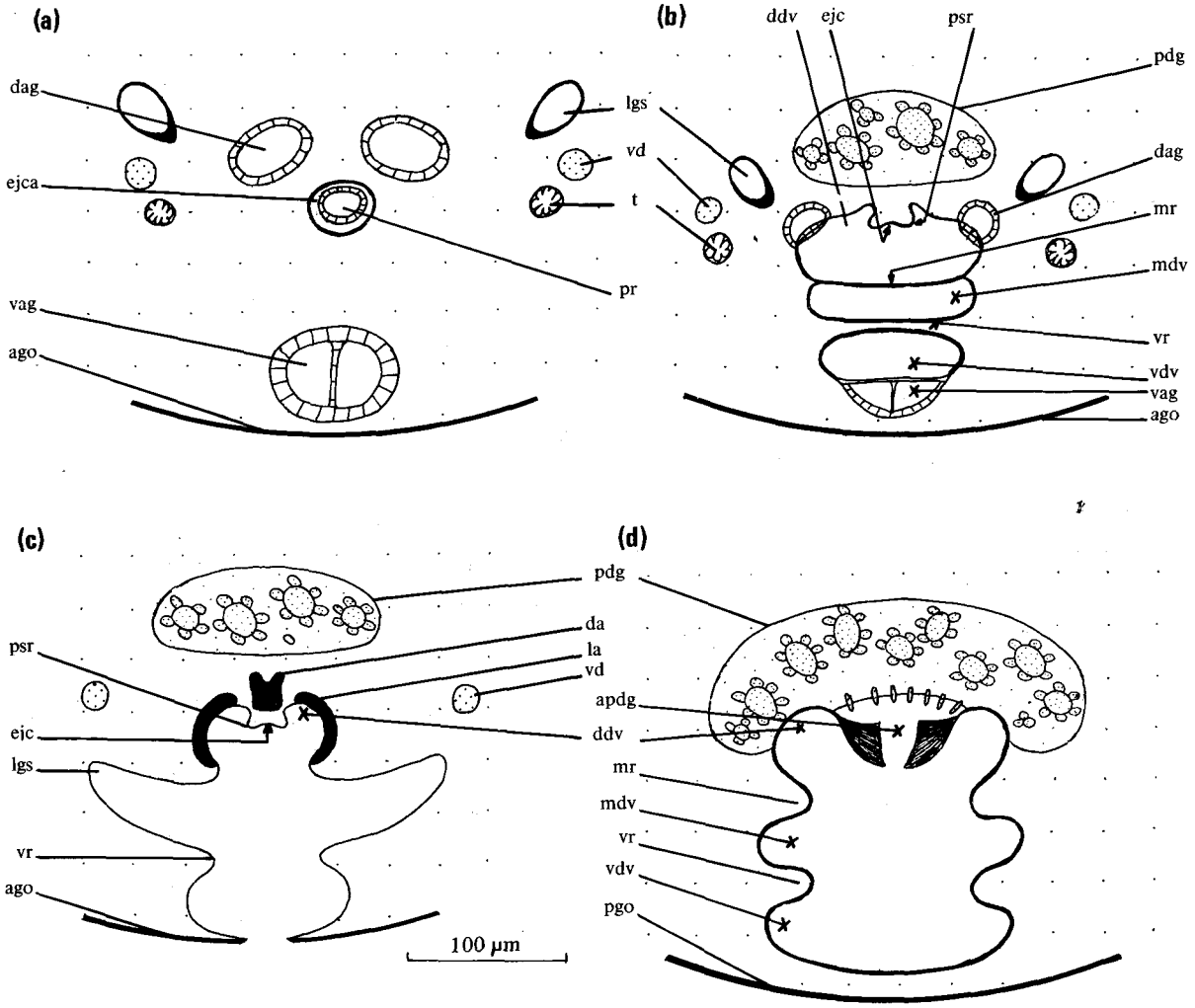

Fig. 3. Serial transverse sections through the generalised male genitalia and associated glands (testis omitted from (d)). Positions shown in Fig. 1.

diverticulum) opening near their bases. Finally, the posterior lateral glands of the Chernetidae lie close to the posterior dorsal gland and open into the atrium of that gland.

Genital sacs

(a) *Lateral genital sacs*

The lateral genital sacs *(lgs)* are a pair of gas-filled, non-glandular, chitinous sacs opening into the medial diverticula on the anterior ventral ridge, below the lateral apodemes (Figs. 1, 2 and 3b, c). They are considered to be evaginations of the walls of the medial diverticula (Vachon 1938, Weygoldt 1966) and are well developed in the Chthoniidae, Neobisiidae and Cheiridiidae and apparently absent or very reduced in the Cheliferidae. Their morphology indicates that they are capable of considerable extension.

Chamberlin (1931) compares these lateral genital sacs with the apparently similar air sacs described by Michael (1897) in the mite *Bdella* (Latreille). Chamberlin (1931) has no objection to the views of Oudemans (1906) and Schtschelkanovzeff (1910) who consider that the sacs are of tracheal origin and

suggests that this would account for the fate of the derivatives of the primitive paragenital respiratory organs which persist as the pectens in the scorpions. Support for the tracheal origin of the lateral genital sacs would come from Chamberlin's (1931) suggestion that the internal genitalia were derived from an invagination of the third opisthosomal segment. Since it is more likely that the genitalia are derived from an invagination between the second and third opisthosomal sternites, and since the lateral genital sacs are not striated like tracheae (Chamberlin 1931) but are instead thrown into transverse folds, it therefore seems unlikely that the sacs are of tracheal origin. The sacs vary in size and shape and possess a distinct, but thin, epithelium, with cuticle on the inner surface.

Chamberlin (1931) and Weygoldt (1969) refer to the lateral genital sacs of the Cheliferidae as the ram's horn organs or protrusible genital sacs. In fact these structures are not synonymous. The ram's horn organs are lateral evaginations from the posterior ventral diverticulum, not from the anterior medial diverticulum. These remain collapsed, except during courtship, when they are engorged and extended to such an extent that they are protruded through the genital aperture.

(b) *Median genital sac*

The median genital sac *(mgs)* has a similar form to that of the lateral genital sacs, but it is not distinctly gas filled. The sac opens via a short duct *(dmgs)* into the posterior ventral diverticulum (Figs. 1 and 2). Vachon (1938) regards this sac as a direct evagination of the posterior ventral diverticulum. The epithelium is thick and folded with a lining of thin cuticle. Muscles are attached to the duct and to sternite 3.

Review

The genitalia of the male pseudoscorpion and its associated glands form a complex arrangement of reproductive organs. The testis is the source of sperm and also nutritive fluid for the sperm. These two products are conveyed by the vasa deferentia to the seminal vesicles which act as temporary sperm stores. The work of Legg (1973) indicates that prior to release of the sperm, the large posterior dorsal gland secretes the spermatophore stalk and, if present, its apical modifications. Following the spermatophore stalk's secretion the sperm and seminal fluid (possibly slightly augmented by that of the prostatic reservoir, (Legg 1973)) are ejaculated via the ejaculatory canal atrium, into the genital atrium and encapsulated by the secretions from the anterior glands. The encapsulated sperm and fluid are then deposited on the apex of the spermatophore stalk. Where lateral glands occur, as in the Chthoniidae, these appear to secrete a pheromone which is deposited on the spermatophore stalk as a droplet (Legg 1973).

Summary

The genitalia of the male pseudoscorpion are concerned with the production of spermatophores. The genital atrium is complex and varied among pseudoscorpions. It consists basically of a cuticular invagination between sternites 2 and 3 of the opisthosoma, associated with which are accessory glands and a number of thickenings of the cuticle. Anteriorly the vasa deferentia are modified into seminal vesicles, which open into a prostatic reservoir. This in turn is surrounded by a cup-shaped antero-dorsal evagination from the genital atrium, the ejaculatory canal atrium. This ejaculatory canal atrium opens into the anterior region of the genital atrium via an ejaculatory canal. Paired cuticular evaginations, the lateral genital sacs, are also associated with this anterior region. These gas-filled sacs open lateral to the ejaculatory canal. Two sets of accessory glands are associated with the genitalia. Opening into the anterior region are the anterior glands. Associated with the posterior region of the genital atrium is the posterior dorsal gland, which opens via a dorsal cuticular invagination in the mid-line of the atrium. Also associated with the posterior region is the cuticle-lined median genital sac.

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References

BOISSIN, L., 1970: Gametogenèse au cours du developpement post-embryonnaire et biologie de sa reproduction chez *Hysterochelifer meridianus* (L. Koch). Ph.D. thesis, Univ. of Paris.

CHAMBERLIN, J. C., 1931: The arachnid order Chelonethida. *Stanford Univ.Publs (Biol).* **7**: 1-284.

CRÖNEBERG, A., 1889: Beitrag zur Kenntnis des Baues der Pseudoscorpione. *Bull.Soc.Imp.Nat.Moscou.* **2**: 416-461.

KÄSTNER, A., 1927: Pseudoscorpions. After-oder Mousskorpione. *Biologie Tiere Dtl.*, **18**: 1-68.

LEGG, G., 1973: Spermatophore formation in the pseudoscorpion *Chthonius ischnocheles* (Chthoniidae). *J.Zool., Lond.* **170**: 367-394.

MICHAEL, A. D., 1897: The internal anatomy of *Bdella*. *Trans.Linn.Soc.Lond.* (2) **6**: 477-523.

OUDEMANS, A. C. 1906: Ueber Genitaltracheen bei Chernetiden und Acari. *Zool.Anz.* **30**: 135-140.

RICHARDS, A. G., 1951: *The integument of arthropods.* Univ. of Minnesota Press, Minneapolis.

SCHTSCHELKANOVZEFF, J. P., 1898: Bau der weiblichen Genital-organe der Pseudoscorpione. *Nachr.Ges.Fr.Nat.Moscou.* **86**: 1.

SCHTSCHELKANOVZEFF, J. P., 1910: Der bau der Männlichen Geschlechtsorgane von *Chelifer* und *Chernes.* Zur Kenntnis der stellung der Chelonethi im system. *Fest.Sech Geb.R.Hertwig* **2**: 1-38.

VACHON, M., 1938: Recherches anatomiques et biologiques sur la réproduction et le développement des pseudoscorpions. *Annls Sci.nat.(Zool).* (11) **1**: 1-207.

WEYGOLDT, P., 1966: Vergleichende Untersuchungen zur Fortpflanzungs-biologie der Pseudoscorpione: Beobachtungen über das Verhalten, die Samenübertragungsweisen und die Spermatophoren einiger einheimischer Arten. *Z.Morph.Ökol.Tiere* **56**: 39-92.

WEYGOLDT, P., 1969: *The biology of pseudoscorpions.* Harvard University Press.

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Araneid Types in Liverpool Museums

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The collections in the department of invertebrate zoology of the City of Liverpool Museums divide themselves naturally into two parts. They are, those specimens which survived the bombing damage and ensuing fire in May 1941, and those which were accessioned after this time (even though the collections may predate it). The very few arachnids which survive from pre-war accessions fortunately include three holotypes, but others do not now exist. Post-war accessions of this Class include only one collection containing type material, namely the donation of William Falconer's collection by Miss M. Falconer, his daughter, following his death in 1943 at Waterloo, Liverpool.

It has been very difficult to ascertain what type material this museum did possess before the second world war. The cryptic descriptions of incoming material recorded in the stock books are not very helpful. In many cases specimens have been used for original description after they had been accessioned, but these facts were not recorded alongside the original entry. Hence, reliance has been made on old correspondence, requests for types on loan and the answers made to these enquiries. The result has been poor for spiders. Although it may be possible that type material other than that noted below came to Liverpool Museums, it is certain that none of it exists now.

The nineteenth century types all originate from the Reverend Nendick Abraham of South Africa and were presented to the museum by Mr. Frederick Taylor of Rainhill, near Liverpool. Abraham studied spiders and their behaviour and although a very poor man, who claimed in one letter that he could barely raise the postage for that parcel of specimens, he managed to send large numbers of spiders to Taylor. The latter had produced standard printed requests for trap-door spiders which he sent to correspondents all round the world and Abraham was the most

VACHON (1938)	CHAMBERLIN (1931)	SCHTSCHELKANOVZEFF (1898, 1910)	KÄSTNER (1927)	WEYGOLDT (1966, 1969)
accessory glands*	accessory glands*	–	accessory glands*	accessory glands*
anterior glands*	–	–	–	–
lateral glands*	–	–	–	–
posterior dorsal gland*	–	–	–	–
median gland	–	–	–	–
prostatic reservoir*	seminal receptacle	–	prostatic reservoir*	prostatic reservoir*
seminal receptacle	seminal receptacle	–	–	–
ventral diverticulum*	–	vestibulum	–	–
anterior and posterior genital plates	genital opercula*	genital plates	genital opercula*	genital plates
genital aperture*	genital slit	genital aperture*	genital aperture*	gonopore
ejaculatory canal* and ejaculatory canal atrium*	inner chamber of uterus externus	uterus masculinus internus	ductus ejaculatus	ductus ejaculatorius
genital atrium*	atrium and uterus externus (+ inner atrium also outer atrium = diverticulum	uterus masculinus externus	–	–
cylindrical organs	ram's horn organ*	–	–	ram's horn organ*
lateral genital sacs* or anterior lateral glands	lateral genital sac*	–	lateral genital sac*	–
median genital sac* or posterior ventral gland	posterior genital sac	–	–	–
dorsal apodeme*	–	–	–	–
lateral apodeme*	–	–	–	–
genital armature*	genital armature*	–	cuticular armature	–

Table 1: List of synonymous terms for the male genitalia used or mentioned by different authors (those used by the present author are marked with an asterisk)

electron microscope (see Legg 1973). This technique permitted a detailed study of the genital organs and tissues.

Male genitalia

Introduction

Schtschelkanovzeff (1898, 1910), Kästner (1927), Chamberlin (1931) and Vachon (1938) have all made contributions to our knowledge of the genitalia of pseudoscorpions. The last author in particular clarified the nomenclature (Table 1) and undertook the first comprehensive survey of the genitalia, mainly in terms of their taxonomic importance.

The internal genitalia of the male are extremely complex, resulting from their functions of producing sperm and producing and depositing spermatophores. The genital aperture (*gap*, Fig. 1) opens between sternites 2 and 3 of the opisthosoma (anterior and posterior genital opercula) into a spacious cavity, the genital atrium *(ga)*. The anterior genital operculum (*ago* = sternite 2) is a curved transverse plate whilst the posterior genital operculum (*pgo* = sternite 3) might be similarly curved or deeply cleft. The genital atrium is separated from an inner region, the ejaculatory canal atrium *(ejca)* and ejaculatory canal *(ejc)* (Figs. 1 and 2) by means of folds. The genital atrium, ejaculatory canal atrium and ejaculatory canal are all lined with thin cuticle. These three structures together form the "uterus masculinus externus" of Schtschelkanovzeff (1910) (Table 1). This is rather an unsatisfactory term, as Chamberlin (1931) points out, for the term "uterus" should be reserved for females and not males. Vachon's (1938) nomenclature does not include a term to cover both the genital atrium and ejaculatory canal atrium since any such term would be unnecessary and redundant in any morphological description.

Testis, vasa deferentia, seminal vesicles and prostatic reservoir

The position of the single, much lobed and variable ventral testis *(te)* and associated ducts are shown in Figs. 1 and 2.

A pair of vasa deferentia *(vd)* arise anteriorly from the ventral testis and are dilated anteriorly as seminal vesicles *(sv)* (= the seminal receptacles of Chamberlin (1931) and Vachon (1938), an unsatisfactory term since it applies to a female structure) which open into a common prostatic reservoir *(pr)* (Figs. 1 and 2) close to a pair of tracheal trunks *(t)*. The prostatic reservoir is invaginated into the ejaculatory canal atrium *(ejca)*, folds of which extend around the prostatic reservoir (Fig. 3a). An evagination from the genital atrium forms the dorso-cephalad, cup-shaped ejaculatory canal atrium (Fig. 1). Posteriorly the ejaculatory canal atrium extends as either a short duct or as a canal *(ejc)* (Fig. 1), the grooves of which are termed the parasagittal ridges *(psr)* (Figs. 1 and 3b, c). This canal, together with the ridges, extends posteriorly as far as the invagination in the mid-line of the atrium of the posterior dorsal gland *(apdg)* (Figs. 1 and 3d). There is considerable variation in the form and degree of development of the ejaculatory canal atrium, ejaculatory canal and parasagittal ridges, being poorly developed in the Chthoniidae, and extremely elaborate in the Cheliferidae.

Genital atrium

The genital atrium receives the products from the testis and accessory glands.

The walls of the genital atrium are thrown into a number of folds, the most dorsal of these, the parasagittal ridges, having already been described. The remaining two folds almost circumscribe the genital atrium (Fig. 1) horizontally and are termed the medial *(mr)* and ventral ridges *(vr)* respectively. The term "lateral ridges" was used by Vachon (1938) for the medial ridges but this term is misleading since they are continuous, except anteriorly. The spaces between the ridges are described as follows:

(a) dorsal diverticulum *(ddv)* between the parasagittal *(psr)* and medial ridges *(mr)* (Figs. 1 and 3b, c, d).

(b) medial diverticulum *(mdv)* between the medial *(mr)* and ventral ridges *(vr)* (Figs. 1 and 3b, d).

(c) ventral diverticulum *(vdv)* between the ventral ridges *(vr)* and genital opercula *(ago, pgo)* (Figs. 1 and 3b, c, d).

The terms anterior and posterior have been prefixed to each of the above diverticula in the following text. They are used in a topographical context to aid description, no precise anatomical significance being intended. Anterior, refers to those structures which lie adjacent or anterior to the openings of the lateral genital sacs; posterior, to those

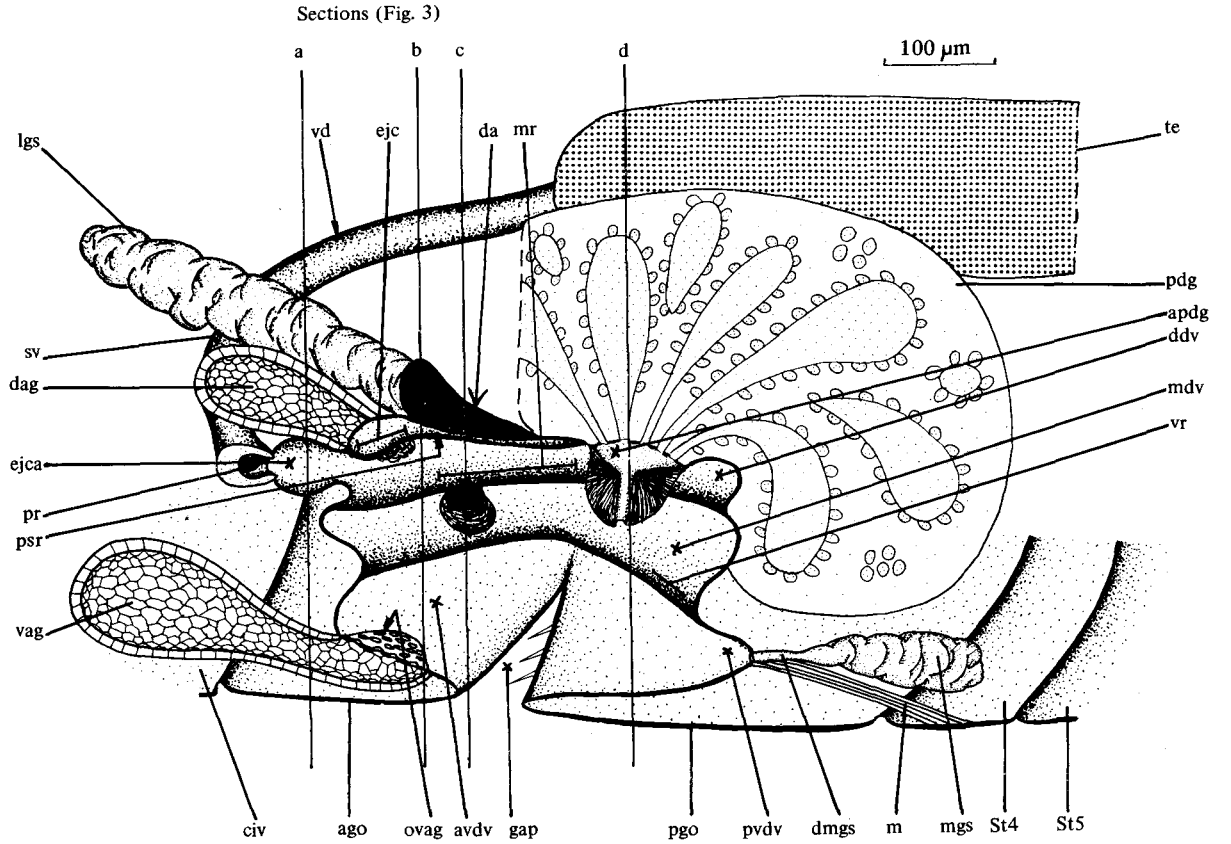

Fig. 1. Half lateral view of the generalised male genitalia and associated glands (most muscles omitted).

List of abbreviations used in the figures

ago	anterior genital operculum
apdg	atrium of posterior dorsal gland
avdv	anterior ventral diverticulum
civ	coxa of leg IV
da	dorsal apodeme
dag	dorsal anterior gland
ddv	dorsal diverticulum
dlgs	duct of lateral genital sac
dmgs	duct of median genital sac
ejc	ejaculatory canal
ejca	ejaculatory canal atrium
ga	genital atrium
gap	genital aperture
la	lateral apodeme
lgs	lateral genital sac
m	muscle
mdv	medial diverticulum
mgs	median genital sac
mr	medial ridge
ovag	opening of ventral anterior gland
pdg	posterior dorsal gland
pgo	posterior genital operculum
pr	prostatic reservoir
psr	parasagittal ridge
pvdv	posterior ventral diverticulum
sv	seminal vesicle
t	tracheal trunk
te	testis
vag	ventral anterior gland
vd	vasa deferentia
vdv	ventral diverticulum
st1 – st5	sternites one to five of the opisthosoma

structures posterior to the openings of the lateral genital sacs.

Considerable variations occur in the form of the genital atrium and its associated ridges and diverticula. Simple atria, with few clearly defined ridges occur in the Neobisiidae and Cheiridiidae, more