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A Generalised Account of the Female 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 female genitalia, with a clarification of the nomenclature.

As with males (Legg, in press) there is confusion over the nomenclature of the various regions of the genitalia. To help clarify the position, table 1 gives a list of synonymous terms used by various authors. In this paper the nomenclature of Vachon (1938) is followed with some variations, stipulated in the following text.

Materials and methods

Specimens of species used by Legg (in press) were also used for this investigation. These included representatives of the five families found in Great Britain (Chthoniidae, Neobisiidae, Cheiridiidae, Chernetidae and Cheliferidae). In addition a few species of the families Feaelidae and Garypidae from West Africa were examined.

The techniques employed were the same as those used by Legg (in press) and included observations of stained, bisected potassium hydroxide cleared specimens and stained serial sections.

Female genitalia

Lubbock (1862), Metschnikoff (1871), Cröneberg (1889), Barrois (1896), Schtschelkanovzeff (1898),

VACHON (1938)	CHAMBERLIN (1931)	SCHTSCHELKANOVZEFF (1898, 1910)	KÄSTNER (1927)	WEYGOLDT (1966, 1969)
female genital atrium*	uterus and genital cavity	uterus	genital atrium*	genital chamber
spermathecae*	spermathecae*	–	spermathecae*	seminal reservoir
cribrillate plates	cribriform plates*	–	–	–
gonopodia*/ gonopods*	gonopods*	–	gonopods*	gonopods*
lateral apodeme*	–	–	–	–
genital armature*	genital armature*	–	–	–
accessory glands*	accessory glands*	–	accessory glands*	accessory glands*

Table 1

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

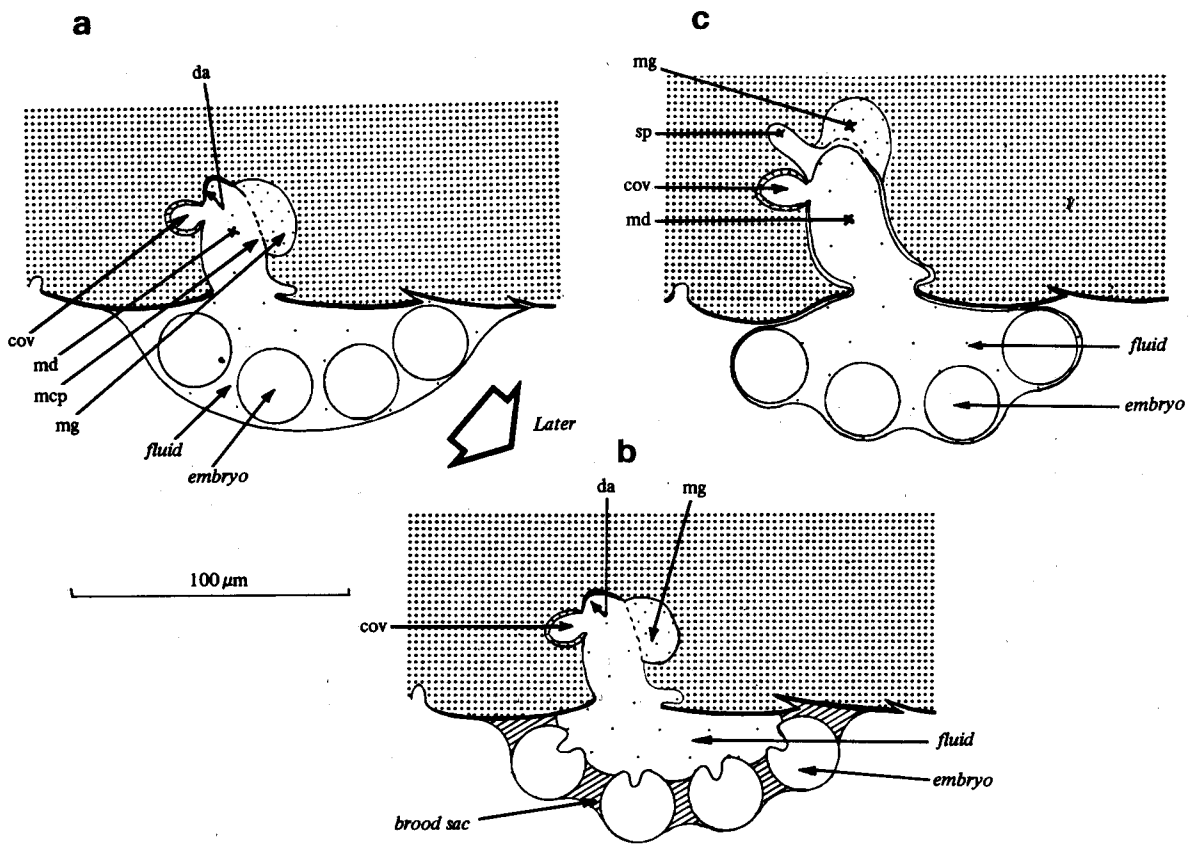

Figure 3. Sagittal sections through various female pseudoscorpions bearing brood sacs (modified after Weygoldt, 1966): (a) and (b) *Chthonius* species, (c) *Chelifer cancroides.*

enter the median diverticulum (*md*) (figs. 1 and 2a, c).

Gonopodium

The gonopodium (*go*) is formed by the evagination of the anterior-ventral wall of the genital atrium (fig. 2c) (Lubbock, 1862; Vachon, 1938; Weygoldt, 1966). Vachon (1938) assumes that the gonopods are vestigial appendages, since he argues that the genital opercula are derived from fused opisthosomal appendages. However, Chamberlin (1931) considers that the genital opercula are derived directly from the sternites of the opisthosoma. Weygoldt (1966) favours this latter origin and consequently used the term "erectile body" instead of gonopodium, thus avoiding any association of the structures with segmental appendages. Although the present author accepts the view that the genital opercula have originated from sternites, Vachon's (1938) term gonopodium will continue to be used on the grounds that it is an adequately descriptive term. The gonopodium is probably everted by haemocoelic pressure and retracted by its associated musculature (*m*) (fig. 2c). It is present in most species so far examined. However, Makioka (1970) found that the gonopodium of *Garypus japonicus* was a temporary structure, the muscles of which atrophied after the young had left their mother.

Brood sac

Pseudoscorpions carry their embryos in a brood sac, attached to the genital opercula, which opens into the genital atrium (fig. 3) and is supported by the gonopodia (Lubbock, 1862; Vachon, 1938; Weygoldt, 1966). Makioka (1970), however, suggests that the gonopodia not only support the brood sac but are concerned with the control of nutritive fluid supplied by the ovary to the embryos in the brood sac.

During reproduction Vachon (1938) and Weygoldt (1966) believe that the accessory glands are responsible for formation of the brood sac. Weygoldt has shown that there are two types of brood sac. In the Chthoniidae the eggs are at first carried in a fluid droplet, derived from the ovary (fig. 3a). After a few days a substance is secreted, probably by the accessory glands, which binds the eggs together (fig. 3b). Weygoldt (1966 and 1969) has found that in other families the brood sac or brood pouch possesses very elastic walls derived from the large accessory glands. This type of sac contains the eggs and later the embryos (fig. 3c).

Review

Thus the ovary is a source of eggs and, at certain times, nutritive fluid for the developing eggs and young. The eggs travel down the oviduct into the genital atrium where they are fertilized by sperm. Sperm are either temporarily stored in the median diverticulum (Wood, 1971), or prolonged storage occurs in the species with spermathecae. The secretory cells of the spermathecae probably provide either nutrients for the stored sperm, or a secretion to breakdown the encysted sperm wall. After fertilization the zygotes are carried in a brood sac which in some species is primarily derived from ovarian secretions, while in others is predominantly derived from accessory gland secretions.

Summary

The ' genitalia of the female pseudoscorpion are concerned with receiving sperm and carrying the brood sac containing the young. The genital atrium is complex but less variable than that of the male. It consists of an invagination between sternites 2 and 3 of the opisthosoma which is divided into four regions: median, two lateral and a posterior diverticulum. The median diverticulum opens to the exterior via the genital aperture while antero-dorsally the oviduct opens into it. Two sets of accessory glands, median and lateral glands, are present which open into the median and lateral diverticula via median and lateral cribriform plates, respectively.

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Kästner (1927) and Chamberlin (1931) have all contributed to our knowledge of the female genitalia, but it was Vachon (1938) who first completed a comprehensive survey of their comparative morphology.

Genital aperture, opercula and atrium

The genital aperture and transverse, crescent-shaped genital opercula of the female, representing sternites 2 and 3 of the opisthosoma, are far less distinct than they are in the male (*ago, pgo*) (fig. 2a).

The genital atrium of the female is much less complicated than that of the male. The atrium is divided into four regions: a large median (*md*), small posterior ventral (*pdv*) and two lateral diverticula (*ld*) (figs. 1 and 2a). Makioka (1970) refers to the genital atrium as the "median chamber of the oviduct". This is incorrect since the atrium is not part of the mesodermal oviduct, but is ectodermal in origin (Wood, 1971) and lined by cuticle.

Genital armature

Lateral to the median diverticulum are a pair of lateral apodemes (*la*) (fig. 2a), the form of which slightly varies between the families. They are generally present as small thickened regions close to the lateral diverticula (*ld*); however, in the Chthoniidae they form a complete frame which may or may not surround the median diverticulum (Legg, 1971). These apodemes provide surfaces for muscle attachment and support for the genital atrium. All authors regard the lateral apodemes of the male and female as homologous.

Accessory glands and cribriform plates

Two pairs of accessory glands are present. The paired median (*mg*) (often fused) (figs. 1 and 2c) and paired lateral glands (*lg*) (figs. 1 and 2b) are closely associated with, and open respectively into, the median and lateral diverticula by means of the median and lateral cribriform plates (*mcp, lcp*) (fig. 1). Each plate is cuticular and is perforated by pores (figs. 1 and 2a, b, c). The cribriform plates may be restricted in area (fig. 1) or more extensive (fig. 2). Variations occur between and within families in the pattern of the cribriform plates. Each pore receives a fine intracellular ductule, similar in form to those found in the defence glands of certain Coleoptera (Forsyth, 1970).

The lateral glands in the Chthoniidae and Cheliferidae occur on the posterior walls of the lateral diverticula and thus the lateral cribriform plates are posterior. By contrast the lateral glands of the Neobisiidae, Cheiridiidae and many of the Chernetidae are on the anterior walls of the lateral diverticula, and thus the cribriform plates are anterior.

Spermathecae

Spermathecae (*sp*) (figs. 1 and 2a) are present in the Chernetidae, either as coiled tubular structures or blind mushroom-like diverticula (their form being used by Vachon (1957) to distinguish generically the British species) and in the Cheliferidae as short tubular structures. The spermathecae form distinct antero-dorsal cuticle lined evaginations from the median diverticulum, above the opening of the common oviduct (*cov*) (fig. 1). True spermathecae are absent in the Chthoniidae and Neobisiidae. However, the sub-family Ideobisiinae of the Neobisiidae and the family Cheiridiidae (Legg, 1974) possess distinct dorsally bilobed median diverticula. No details are available about the other pseudoscorpion families. Chamberlin (1931) believes that the absence of spermathecae in the two families Chthonidiidae and Neobisiidae has been brought about by the fusion of the spermathecae to produce a single median structure, which Vachon (1938) terms the median diverticulum. Since the median diverticulum is part of the genital atrium it seems likely that in fact the spermathecae are evaginations of this diverticulum. Chamberlin was in error in believing that the median cribriform plate(s) occurred at the openings of the spermathecae instead of being associated with the median accessory gland(s). Scattered glandular cells occur in the epithelium of the spermathecae (Vachon, 1938).

Ovary and oviduct

The ovary (*o*) (fig. 1) lies posterior and dorsal to the genitalia. It is unpaired (like the testis) with numerous egg follicles. Two oviducts (*ov*) (figs. 1 and 2a) pass anteriorly and then curve ventrally to fuse in the mid-line as a common oviduct (*cov*) where they

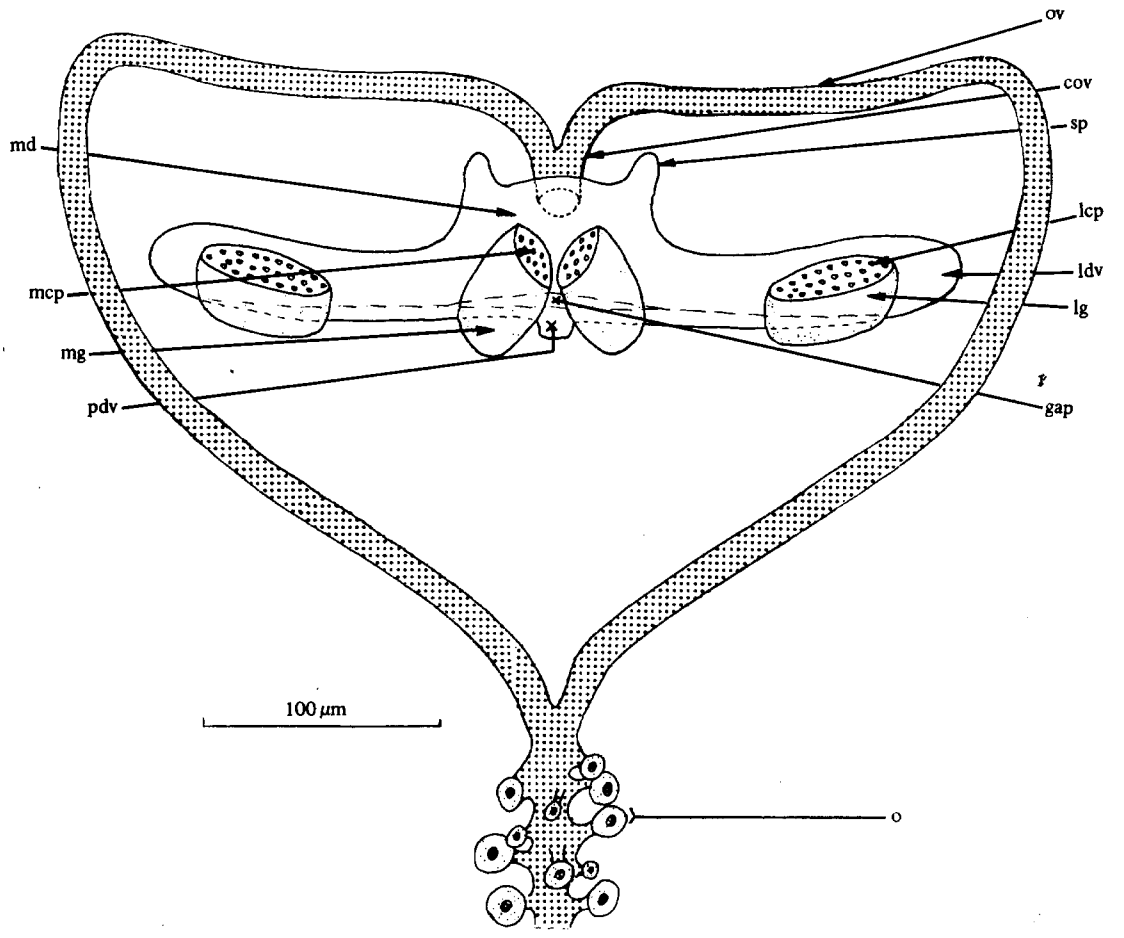

Figure 1. Dorsal view of generalised female genitalia and associated glands (modified after Vachon, 1938).

List of abbreviations used in the figures

ago	anterior genital operculum
clV	coxa of leg four
cov	common oviduct
gap	genital aperture
go	gonopodium
la	lateral apodeme
lcp	lateral cribriform plate
ldv	lateral diverticulum
lg	lateral gland
mcp	median cribriform plate
md	median diverticulum
mg	median gland
o	ovary
ov	oviduct
pdv	posterior diverticulum
pgo	posterior genital operculum
sp	spermatheca
st2, st3, st4	sternites two, three and four of the opisthosoma

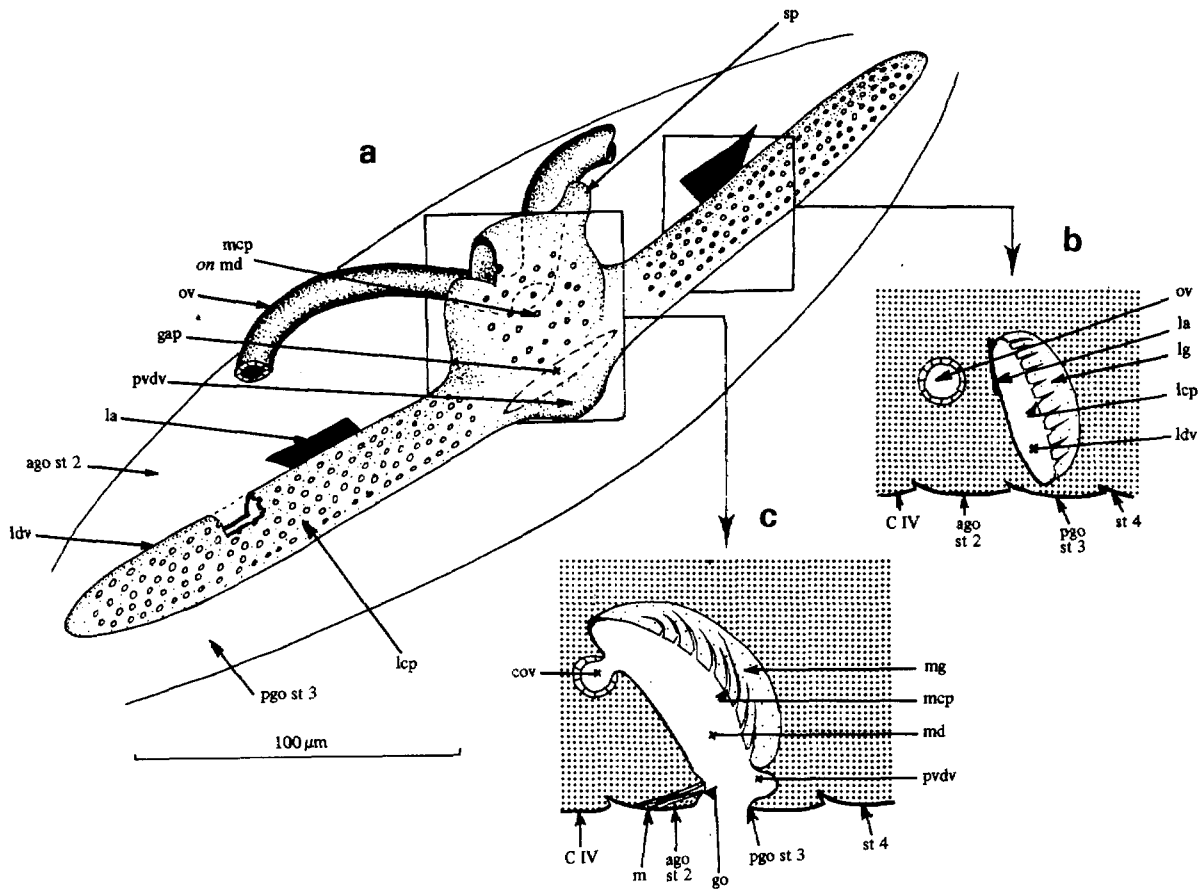

Figure 2. Views of the generalised female genitalia:

(a) Antero-lateral view of the genitalia after clearing in potassium hydroxide (the oviducts have been included);

(b) Transverse section through the lateral diverticulum;

(c) Transverse section through the median diverticulum.