Coxal glands of spiders of the genera *Bymainiella, Atrax* and *Namea* (Hexathelidae, Dipluridae, Mygalomorphae)

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Abstract – Knowledge of coxal glands in mygalomorph and liphistiomorph spiders is reviewed. The hexathelid species *Bymainiella terraereginae* (Raven) has vesicles and coxal gland outlets associated with coxae I, II, and III – the most plesiomorphic state in any known arachnid. *Bymainiella lugubris* Raven, *Atrax* (Hexathelidae) and *Namea* (Dipluridae) have coxal gland outlets on at least coxae I and III.

INTRODUCTION

Coxal glands are the prosomal excretory organs of arachnids. Their structure is discernible only through histological sectioning. By the early 20th century many studies on coxal glands of arachnids had been made. However, those studies were found inconsistent by Buxton (1913, 1917, 1924) who reviewed them and systematically examined coxal glands of representatives of all living arachnid orders. In most arachnid groups, one saccule occurs in either coxae I (Solifugae, Mygalomorphae, Araneomorphae and Amblypygi) or in coxae III (Scorpionida and Opilionida) (Buxton 1913). The outlets of spider coxal glands are of two states: 1, most mygalomorph spiders and the plesiomorphic genus *Liphistius* have two outlets, one each on coxae I and III; 2, most Araneomorphae and a diplurid mygalomorph have an outlet only on coxae I.

Since Buxton's definitive three works (1913, 1917, 1924), the gross morphology of coxal glands of other spiders has almost been ignored. Todd (1942, unpublished M.Sc. thesis) examined the internal anatomy and described coxal glands of all five New Zealand mygalomorph genera. Petrunkevitch (1933) succeeded only in misreporting Buxton's findings. Millot (1933) also examined coxal glands of *Liphistius* and confirmed Buxton's findings. Marples (1968) examined only hypochiloids. Gabe (1968) noted the cytology and histochemistry of coxal glands of four araneid species including the nemesiid, *Nemesia caementaria*. Platnick and Gertsch (1976) used the number of coxal gland outlets to support their hypothesis of the relationships of spider suborders. Also, Lopez (1983) remarked upon the extensiveness of what he regarded as modified coxal glands in *Metepeira* (Araneidae).

The initial object of this study was to determine whether the small posterior book-lungs of *B. terraereginae* (Raven) were functional. In fact, those book-lungs have as many leaves as the anterior pair. Because the sections were of good quality, I sought to elucidate other structures of interest.

This paper recognises the contributions of Dr Barbara York Main to arachnology and its directions in Western Australia.

MATERIALS AND METHODS

The results are based upon serial sections of *Bymainiella terraereginae* (Raven, 1976), *B. lugubris* Raven, 1978, and unnamed species of *Atrax* and *Namea*. All spiders were immature (not embryonic), as were those of Buxton (1913). Specimens of both *Bymainiella* species were pre-penultimate or older. Spiders were fixed either in Bouin's fixative, 10% formalin, or a mixture of ethanol, 2% glacial acetic acid, water, and glycerol. Specimens were impregnated in a methyl-benzoate celloidin solution and embedded in wax. Sagittal sections were cut at 8–15m. They were stained with Mann's methyl blue-eosin for 1–2 hours; the "blue" was then fixed with water or a 1% solution of ammonium hydroxide. Sections were counterstained by immersion of *ca*. 20 seconds in 70% ethanol with 10 drops of Orange G per 100ml. The specimen of *B. terraereginae* was subadult with carapace length of 3mm; the carapace of adult females were 3.68–5.63mm long (Raven 1976).

THE STRUCTURE AND POSITION OF COXAL GLANDS

Coxal glands consist essentially of three components: 1, the labyrinth; 2, the saccule; and 3, the exit tubule. The labyrinth is a highly convoluted tube lying beside and above the endosternite (16, Fig. 1). Anterior to and above each exit tubule the laby-
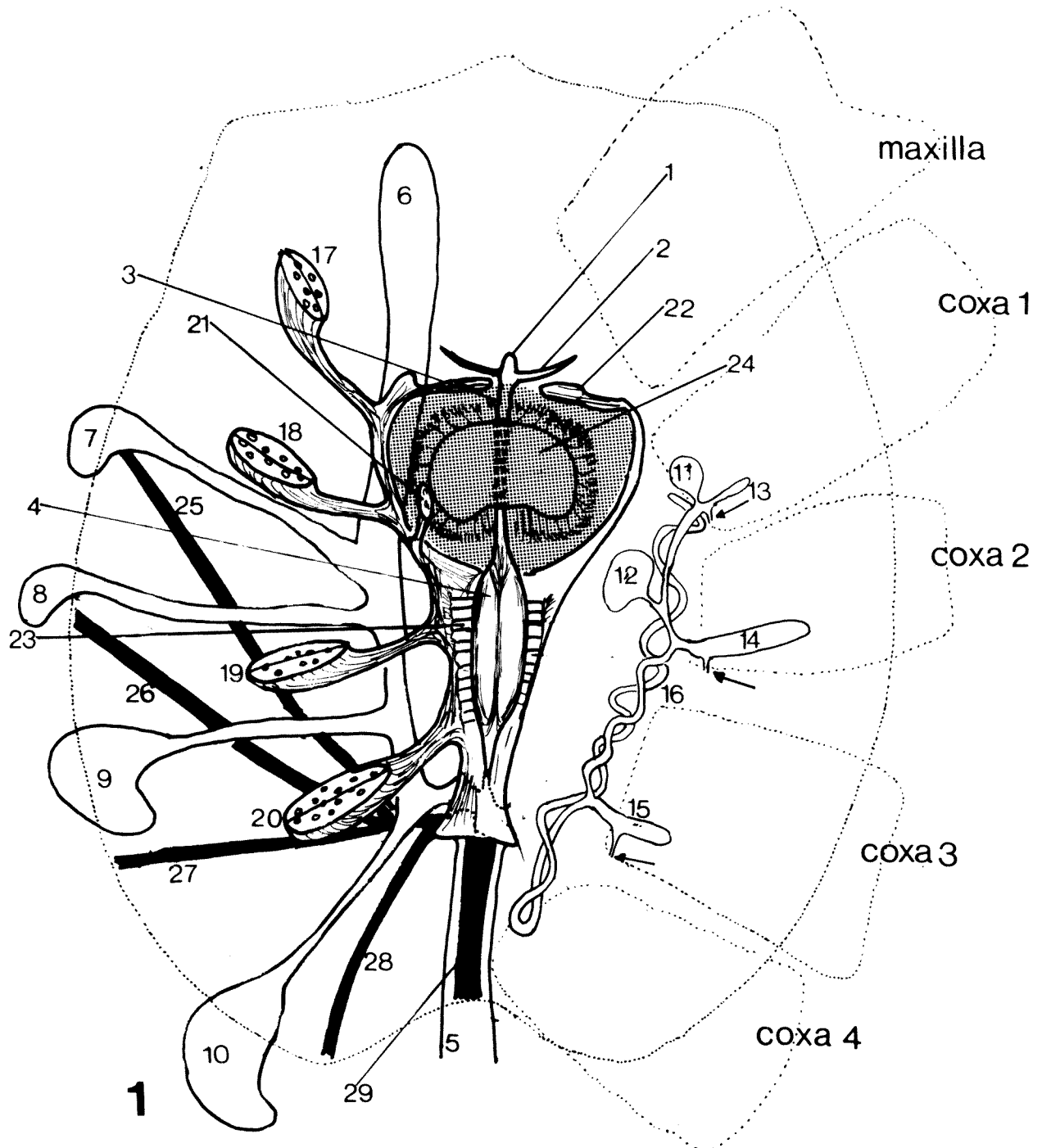
Figure 1 *Bymainiella terraereginae*, prosoma: 1–10, Digestive system. 1, anterior pharyngeal horn; 2, pharynx; 3, oesophagus; 4, sucking stomach; 5, midgut; 6, anterior branch of midgut diverticula; 7–10, lateral branches of midgut diverticula to coxae I–IV, respectively. 11–16, coxal glands: 11, 12, saccules; 13–15, vesicle and outlet (arrow) on coxae I–III; 16, coxal gland labyrinth. 17–23, endosternite and associated muscles: 17–20, suspensor I–IV respectively; 21, Suspensor centralis; 22, Protractor endosterni(?); 23, Dilator proventriculi lateralis. 24, dorsal ganglionic nerve mass. 25–29, Arterial system; 25–28, latertal aortae to coxae I–IV respectively (maxillary aorta omitted); 29, anterior aorta.

rinth enlarges into a vesicle (V, Fig. 4). From there it narrows and becomes the exit tubule (ET, Figs. 3, 4) that opens into the posterior upper corner of either coxae I, II or III. Posterior to coxae II, the coxal glands curve entally and thus it is not possible to show the three outlets in one section. Large, thin-walled cells with darkly stained nuclei (NC,

Fig. 4) are presumably nephrocytes.

B. terraereginae has vesicles and associated gland outlets in coxae I and III, as do most mygalomorphs known. However, an additional outlet and vesicle is associated with coxa II (Figs 2, 3, 4). The thin-walled saccules associated with coxae I and II are evident; however, no saccule was

observed near coxa III. The labyrinth passes posterior to ental coxae IV (Fig. 1). Moreover, the ental limb of the labyrinth lying dorsal to the endosternite is not highly convoluted and a much longer vesicle extends ectally into coxae II.

In sagittal sections of *B. lugubris*, coxal gland outlets and vesicles associated with coxae I and III are evident. However, the poor quality of available sections did not allow either the confirmation or falsification of the presence of outlets and associated vesicles in coxae II. Also, in good quality sagittal sections of *Atrax* and *Namea*, coxal gland outlets and vesicles are associated only with coxae I and III.

DISCUSSION

Buxton (1913) sectioned the spiders of nine mygalomorph genera (as given by Buxton) of four families: an unidentified theraphosid genus; two species of *Rhechostica* (as *Eurypelma rusticum* Simon, 1890 and *Dugesiella hentzi* (Girard, 1854)), *Eurypelma* (=*Euathlus*) *vagans* (Ausserer), *Hapalopus pentaloris* (Simon, 1888) and *Ischnocolus* in the Theraphosidae; *Neocteniza mexicana* F.O.P.-Cambridge, 1897 (Idiopidae); *Ischnothele* (Dipluridae); and *Atypus affinis* (Eichwald, 1830) (Atypidae). Later, he (1924) also sectioned *Liphistius batuensis*. Buxton found that all of those genera, save *Ischnothele*, have coxal gland outlets on each of coxae I and III. *Ischnothele* has coxal gland outlets only on coxae I (Buxton 1913). Todd (1942) found similarly that *Cantuaria* (=*Misgolas*, Idiopidae), *Hexathele* and *Porrhothele* (Hexathelidae), *Aparua* (=*Stanwellia*, Nemesiidae) and *Migas* (Migidae) have coxal gland outlets also on coxae I and III. Totally thus far, 15 mygalomorph genera have been studied since Buxton (1913), prior to which results were inconsistent.

The occurrence of a third coxal gland outlet in a mygalomorph spider raises a number of questions, but the occurrence of three states varying from the most plesiomorphic state known for spiders (as in *B. terraereginae*) to a third but apomorphic state (as in *Ischnothele*) simplifies those questions. The third coxal gland outlet must be regarded as the most plesiomorphic condition in the arachnids by outgroup comparison with the Xiphosura, which have four outlets. Also, in *Heptathela*, Yoshikura (1955) reported that mesodermal ducts, ectodermal exit ducts and paired coelomic end sacs, the origins of coxal glands, arise in the coxae of the palp and legs I–III. The palpal sacs degenerate after hatching. The sacs in legs I–III are associated with ectodermal ducts but the duct on leg II later closes leaving the common condition in mygalomorphs. [The putative sister group of spiders, the Amblypygi, are known to have only one outlet or two, as in most mygalomorphs.] Hence, both by outgroup comparison and embryology, the most plesiomorphic condition in spiders is that reported here for *B. terraereginae*.

Platnick and Gertsch (1976) hypothesized that the Liphistiidae were the most plesiomorphic spiders and used the one outlet condition (as one of five characters) of araneomorphs to support their monophyly. Clearly, the findings of Buxton and those presented here support neither araneomorph monophyly nor the plesiomorphic state of the Mesothelae. Although *B. terraereginae* has six spinnerets, a plesiomorphic number for the Mygalomorphae, it lacks other unequivocally plesiomorphic characters of the Liphistiidae. Therefore, unless a reversal is hypothesized several alternatives are possible and few are parsimonious. A reversal is more parsimonious but only if the reacquisition of a complex gland and associated ducts is treated as a single character. There are far too few data yet to definitively proclaim anything, as Anderson (1973) also concluded. More attention needs to be given to Antrodiaetidae, Atypidae, and Mecicobothriidae–taxa that are putatively basal on a mygalomorph cladogram (Raven 1985; Goloboff 1993).

The presence of outlets on coxae III and/or on coxae I in mygalomorphs (as in *Ischnothele*) does not falsify Platnick and Gertsch's (1976) hypothesis. However, the outlet in coxae II in *Bymainiella terraereginae* indicates that the hypothesis concerning coxal glands must be re-framed. In *Atrax* (Macrothelinae, the putative sister group of the Hexathelinae: Raven 1980) only two outlets are present. Therefore, unless the hypotheses of Raven (1980) and of Platnick and Gertsch (1976) are false, then the second coxal gland outlet was lost more than once – a quite unparsimonious alternative.

Another possibility, if Platnick and Gertsch (1976) are correct, is that the two-outlet conditions in Mesothelae and most mygalomorphs are not homologous. Alternatively, their cladogram may be incorrect, in which case the Mygalomorphae may be polyphyletic – a highly unparsimonious and readily falsifiable alternative.

Because coxal glands of only 15 genera of seven families (out of 16 families and 263 genera) are known broad conclusions about the phylogenetic significance of coxal glands in mygalomorph spiders are not warranted. When the coxal glands of more mygalomorph taxa are known I suggest that they will be of low informative value to classifications. An alternative is that the polyphyletic nature of a number of mygalomorph families is obscuring an otherwise informative pattern. Finally, Buxton (1913) suggested that the reduced coxal glands in *Ischnothele* had developed because much of the excretory products are utilised in the production of silk for the expansive webs. If valid, many
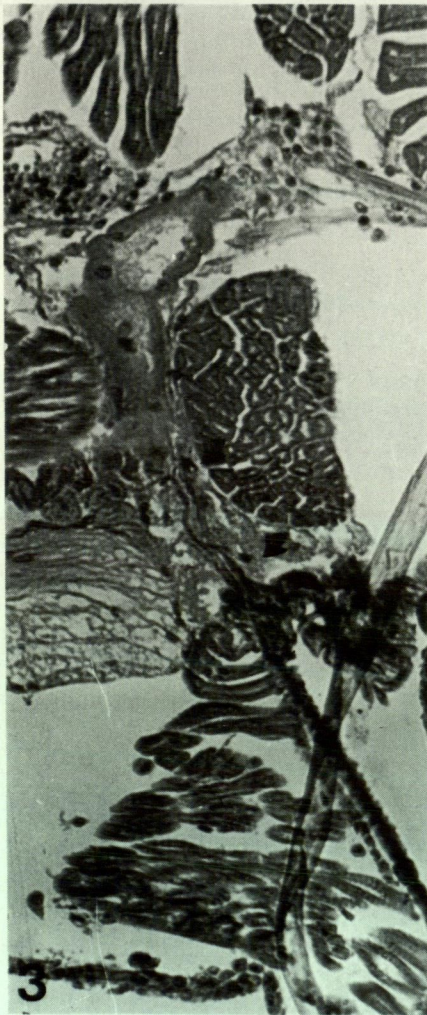
Figures 2–4   *Bymainiella terraereginae*, prosoma, sagittal section: 2, Maxillae to coxae III, coxal glands discharging onto posterior edge of coxae I and II (arrows); 3, 4 Coxal gland outlet and exit tubule on coxae I (3) and coxa II (4). Abbreviations: A, artery; CL, coxal labyrinth; ET, exit tubule; M, muscle; MD, midgut diverticula, lateral branch; N, nerve; NC, nephrocytes(?); O, outlet; S, saccule; V, vesicle.

Ischnothelinae and the long spinnereted *Diplura*-like genera should also have reduced coxal glands.

The extra outlet in *Bymainiella terraereginae* is not a result of the immaturity of the specimen because the sectioned individual was subadult (see Material and Methods). Juvenile stages are effectively embryological in some characters. However, although the specimen here sectioned was within two moults of maturity, independent evidence suggests that some embryological conditions of the coxal glands are no more plesiomorphic than that of the mature spider. Schimkevitch and Schimkevitch (1911) were able to discern only one coxal gland outlet in segment III of the embryo of *Ischnocolus* and yet Buxton (1913) found that *Ischnocolus* has outlets on segments III and V (coxae I and III). That Schimkevitch and Schimkevitch (1911) could not see an outlet on segment V may indicate that their entire observation was doubtful. However, I consider that if more than two outlets were present, it is highly unlikely that they would have seen only one.

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