

# Comparative anatomy of the mesosomal organs of scorpions (Chelicerata, Scorpiones), with implications for the phylogeny of the order

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We present a review and reassessment of anatomical variation in the ovariterus (and associated follicles), digestive gland, and lateral lymphoid organs of scorpions, and discuss the contribution of these character systems to the understanding of scorpion phylogeny. New data, obtained using light microscopy, are presented from an examination of 55 scorpion species, representing most scorpion families, and are collated with observations from the literature. Six distinct types of ovariterine anatomy are identified: five in the family Buthidae and one in the remaining (nonbuthid) families. The buthid genera *Lychas* C.L. Koch, 1845 and *Rhopalurus* Thorell, 1876 are exceptional in possessing multiple types of ovariterine anatomy among the congeneric species studied. The presence or absence of lateral lymphoid organs appears to be phylogenetically informative: the organ is absent in buthids, chaerilids and *Pseudochactas* Gromov, 1998. Embryo follicle morphology appears to be phylogenetically informative within the superfamily Scorpionoidea Latreille, 1802, where it supports the controversial sister-group relationship between *Urodacus* Peters, 1861 and *Heteroscorpion* Birula, 1903. The mesosomal anatomy of *Microcharmus* Lourenço, 1995 (Microcharmidae Lourenço, 1996) is consistent with that of Buthidae C.L. Koch, 1837, and we therefore propose the following new synonymy: Microcharmidae Lourenço, 1996 = Buthidae C.L. Koch, 1837. © 2008 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2008, 154, 651–675.

**ADDITIONAL KEYWORDS:** digestive gland – follicle – lymphoid organs – ovariterus – reproduction – systematics.

## INTRODUCTION

Scorpion systematics is currently based almost entirely on characters of the external morphology (Sissom, 1990), despite an extensive body of literature documenting phylogenetically informative character systems from the internal anatomy (particularly the mesosoma) of scorpions. The mesosoma contains most of the scorpion's organ systems, including the intestine and glands of the digestive system, the reproduc-

tive system, the respiratory system, the circulatory system, and lymphoid organs (Hjelle, 1990). Phylogenetically informative characters from the mesosomal anatomy were first reported a century ago (Laurie, 1890, 1891, 1896a, b; Pavlovsky, 1913, 1915a, b, c, d, 1917, 1924a, b, c, d, 1925, 1926), and, with the notable exception of characters from the male reproductive system, the subject has since received little attention from scorpion systematists. For example, the three family-level phylogenetic analyses of scorpions presented to date included numerous characters from the male reproductive system (23 in Stockwell, 1989; 12 in Prendini, 2000; 8 in Soleglad & Fet, 2003), but only three characters from the female reproductive system. A further problem concerns the limited number of taxa in which the mesosomal anatomy has been studied in detail. Most observations in the early literature were reported from a limited sample of

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taxa, and have not been subsequently confirmed. These observations were nevertheless incorporated into recent phylogenetic analyses, and in some cases were extrapolated to other taxa in which they had not been observed. Other organ systems (e.g. the digestive gland and lateral lymphoid organs) have never been studied in a comparative manner across a diversity of taxa, and the variation and phylogenetic content of these structures are largely unknown.

The present contribution aims to reinvestigate the mesosomal anatomy, focusing specifically on the patterns of connection and branching of the ovariueterine tubules; the lobular formation of the digestive gland; the presence and development of the lateral lymphoid organs; and the morphology of the diverticulae in katoikogenic scorpions. We examine a broad sample of taxa representing all scorpion families, and collate and reassess the observations of previous authors, providing an up-to-date synthesis of the literature.

## HISTORICAL CONTEXT

### OVARIUTERUS

The female reproductive system (ovariuterus) of scorpions comprises a network of tubules that emanate from a pair of variably developed spermathecae (or seminal receptacles *sensu* Pavlovsky, 1925; Millot & Vachon, 1949), which connect to the genital atrium, and open at the genital operculum (Hjelle, 1990; Sissom, 1990). The basic ovariueterine network comprises two lateral longitudinal tubules, connected to a median longitudinal tubule by two, four, or five paired transverse tubules (or anastomoses *sensu* Matthiesen, 1970; Francke, 1982) on either side of the median longitudinal tubule, thereby forming a network of two, six, or eight roughly quadrilateral 'cells' (Matthiesen, 1970; Francke, 1982; Hjelle, 1990; Sissom, 1990). More complex variations involve the development of a pair of submedian longitudinal tubules, forming a median 'cell'; however, for reasons unknown to us, this median 'cell' has never been considered in the overall 'cell' count.

Laurie (1896a, b), Pavlovsky (1913, 1915a, b, c, d, 1924a, b, c, d, 1925, 1926) and Pavlovsky & Zarin (1926) provided the earliest and most extensive contributions on the comparative anatomy of scorpions. Pavlovsky (1915d, 1917, 1924a) was the first to discuss the now widely recognized importance of the male paraxial organ and hemispermatophore for scorpion systematics, which will be addressed elsewhere.

Pavlovsky's (1924b, 1925) contributions remain the most detailed on the patterns of branching and connectivity of the ovariueterine tubules. Pavlovsky (1925) illustrated the ovariueterus of six buthids, one bothriurid, one euscorpoid, and two scorpoidids (Table 1).

Pavlovsky (1924b, 1925) was the first to observe a difference between the eight-celled ovariueterus of buthids and the six-celled ovariueterus of nonbuthids. Pavlovsky (1924b, 1925) also noted the enlarged spermathecae of some nonbuthids. Pavlovsky (1925) illustrated four different patterns of branching and connectivity of the ovariueterine tubules of Buthidae C.L. Koch, 1837, but did not comment on this surprising diversity (and neither have subsequent authors): (1) median cell closed by anterior fusion of the submedian tubules, *Lychas variatus* (Thorell, 1876); (2) median cell closed anteriorly by a short transverse tubule, *Parabuthus planicauda* (Pocock, 1889); (3) median cell open anteriorly, *Lychas tricarinatus* (Simon, 1884); (4) median cell absent, *Anomalobuthus rickmersi* Kraepelin, 1900, *Liobuthus kessleri* Birula, 1898, and *Lychas marmoreus* C.L. Koch, 1844.

Later contributions to the understanding of the female reproductive anatomy of scorpions supported most of Pavlovsky's (1924b, 1925) observations, but either added few new observations (Francke, 1982; Sissom, 1990), or focused on one or a few species: *Leiurus quinquestriatus* (Ehrenberg, 1828), Warburg & Elias (1998), Warburg & Rosenberg (1990); *Hottentotta judaicus* (Simon, 1872) (as *Buthotus judaicus*), Warburg & Rosenberg (1992b); *Rhopalurus rochae* Borelli, 1910, *Tityus bahiensis* (Perty, 1833), *Tityus cambridgei* Pocock, 1897, *Tityus serrulatus* Lutz & Mello, 1922, *Tityus stigmurus* (Thorell, 1876), Matthiesen (1970); *Nebo hierichonticus* (Simon, 1872), Warburg & Rosenberg (1990, 1992a); *Heterometrus scaber* (Thorell, 1876), Mathew (1956); *Pandinus imperator* (C.L. Koch, 1841), Mahsberg & Warburg (2000); *Scorpio maurus fuscus* (Ehrenberg, 1829), Warburg & Rosenberg (1990, 1993); *Urodacus manicatus* (Thorell, 1876), Mathew (1968), Warburg & Rosenberg (1994); and *Pseudochactas ovchinnikovi* Gromov, 1998, Prendini *et al.* (2006). Notable among these contributions were those of Mathew (1960, 1962), who redescribed and confirmed the unusual ovariueterine anatomy of *L. tricarinatus*, first illustrated by Pavlovsky (1925); the contribution of Matthiesen (1970), who discovered the two-celled pattern in two species of *Tityus* C.L. Koch, 1836 (Table 1), contradicting Pavlovsky's (1924b, 1925) reports of an eight-celled ovariueterus in this genus, and reported the eight-celled pattern in *R. rochae*; and the contribution of Prendini *et al.* (2006), who illustrated the six-celled ovariueterus of *P. ovchinnikovi*.

The eight-celled and two-celled patterns have only been observed in Buthidae; however, relatively few buthids have been examined in the literature (Table 1), and a broader sample from this diverse family must be studied to confirm whether these observations are more general. The six-celled ovariueterus

uterus, documented only in nonbuthid scorpions, is based on equally few observations. Prendini *et al.* (2006: 238, table 7) provided the most recent summary of published observations on variation in the ovariuterine anatomy of scorpions, which we enlarge upon in the present contribution.

#### SPERMATHECAE

The spermathecae, which facilitate sperm storage and maintenance after mating (Hjelle, 1990; Peretti & Battán-Horenstein, 2003; Peretti, 2003), are the swollen anterior extensions of the lateral longitudinal tubules. Although little is known about variation in the spermathecal anatomy within the order Scorpiones, it is clear that considerable variation exists, ranging from only a slight anterior swelling of the ovariuterine tubules in some buthids, to the formation of large sac-like structures in some bothriurids (Pavlovsky, 1925).

#### LOCATION OF EMBRYONIC DEVELOPMENT

Differences in the type of embryonic development (katoikogenic vs. apoikogenic development) have been studied in many scorpion species, and were first summarized by Polis & Sissom (1990: 184–187, table 4.2); however, few attempts have been made to analyse and summarize the data comparatively (Laurie, 1890, 1891, 1896a, b; Francke, 1982; Polis & Sissom, 1990; Farley, 2001). Laurie (1896a) first recognized two distinct types of embryonic development in scorpions: apoikogenic, in which embryonic development occurs inside the ovariuterine tubules, and the embryos are nourished by yolk; and katoikogenic, in which development occurs inside diverticulae of the ovariuterus, and the embryos are nourished via a placenta-like organ. Apoikogenic and katoikogenic development are among the few characters from the female reproductive system to have been included in phylogenetic analyses of the higher phylogeny of Scorpiones (Stockwell, 1989; Prendini, 2000; Soleglad and Fet, 2003).

Francke (1982) clarified several misconceptions concerning the development of scorpions, and concluded that all are viviparous, but with some important differences in the morphology and development of the ovarian follicles and embryos, first noted by Laurie (1896a, b), and discussed further below. Warburg (2001) described a putative third type of development in *Vaejovis spinigerus* (Wood, 1863) and *Compsobuthus werneri schmiedechnehti* Vachon, 1949 (as *C. werneri judaicus* Levy *et al.*, 1973), in which the oocytes apparently mature inside the ovarian tubes, rather than inside follicles on the outer surface.

#### FOLLICLES

The oocytes are located in follicles that are variably situated on the exterior of the ovariuterine tubules. Three types of follicles have been recognized (Francke, 1982; Sissom, 1990; Lourenço, 2002): (1) sessile and in direct contact with the ovariuterus (Bothriuridae Simon, 1880; Buthidae, Chactidae Pocock, 1893; Chaerilidae Pocock, 1893); (2) connected to the ovariuterus by a short stalk or pedicel (Iuridae Thorell, 1876; Vaejovidae Thorell, 1876); (3) oocytes located within diverticulae that arise from the ovariuterine tubules (Diplocentridae Karsch, 1880; Hemiscorpiidae Pocock, 1893; Liochelidae Fet and Bechly, 2001; Scorpionidae Latreille, 1802; Urodacidae Pocock, 1893). The ovariuterus of *Smeringurus mesaensis* (Stahnke, 1957) is unusual in that the follicles are initially sessile and in direct contact with the ovariuterus, but, during early embryology, a trophic layer of cells develops and completely covers the maturing follicles (Farley, 1998, 2001).

The size and shape of the follicles are directly related to the type of embryonic development. Sessile and stalked follicles are characteristic of scorpions with apoikogenic development (Laurie, 1896a; Francke, 1982; Polis & Sissom, 1990; Farley, 2001). Follicles of apoikogenic scorpions are oval or rounded, whereas those of katoikogenic scorpions are more elongated (Laurie, 1896a, b; Francke, 1982; Polis & Sissom, 1990; Farley, 2001), which may be related to the development of the follicle into the diverticulum in katoikogenic scorpions.

Stalked follicles (with a pedicel) were once thought to be uniquely present in and potentially synapomorphic for Iuridae and Vaejovidae (Laurie, 1896a; Francke, 1982; Stockwell, 1989; Sissom, 1990); however, stalked follicles have also been reported in the buthids *Lychas tricarinatus* (Mathew, 1962: 348, fig. 1), *Tityus bahiensis* and *T. serrulatus* (Matthiesen, 1970: 628, figs. 3, 5), *Hottentotta judaicus* (Warburg & Rosenberg, 1992b: 34, figs. 3, 4, 7), and *Leiurus quinquestriatus* (Warburg, Elias & Rosenberg, 1995), and in the euscorpiids, *Euscorpius italicus* (Herbst, 1800) (Laurie, 1890) and *Euscorpius flavicaudis* (DeGeer, 1778) (Lourenço, 2002: 73, fig. 3b).

#### DIGESTIVE GLAND

The digestive gland is the largest organ in the scorpion's body, comprising most of the contents of the mesosoma. The organ is formed by six pairs of glands connected to the intestine by means of fine ducts. The first pair of diverticulae are situated in the prosoma; the remaining five are in each of the first five mesosomal segments. The digestive gland contains cells that produce enzymes for degrading ingested materials, and cells that absorb and store digested materials

**Table 1.** Summary of ovariuterine anatomy from Prendini et al. (2006) with new data

Family	Species	LC	MC	Citations
<b>Bothriuridae</b> Simon, 1880	<i>Bothriurus bonariensis</i> (C.L. Koch, 1842)	6	–	Pav24b, Pav25
	<i>Brachistosternus intermedius</i> Lönnberg, 1902	6	–	Pav24b, Pav25
	<i>Lisposoma josehermana</i> Lamoral, 1979	6	–	
	<i>Timogenes elegans</i> (Mello-Leitão, 1931)	6	–	
	<i>Urophonius granulatus</i> Pocock, 1898	6	–	
<b>Buthidae</b> C.L. Koch, 1837	<i>Ananteris platnicki</i> Lourenço, 1993	9	B	
	<i>Androctonus amoreuxi</i> (Audouin, 1826)	8	–	
	<i>Androctonus australis</i> (Linnaeus, 1758)	8	–	Pav24b, Pav25
	<i>Anomalobuthus rickmersi</i> Kraepelin, 1900	8	–	Pav24b, Pav25
	<i>Babycurus buettneri</i> Karsch, 1886	9	O	Pav24b, Pav25
	<i>Babycurus jacksoni</i> (Pocock, 1890)	9	O	
	<i>Butheoloides monodi</i> Vachon, 1950	8	–	
	<i>Buthus occitanus</i> (Amoureux, 1789)	8	–	Pav24b, Pav25
	<i>Centruroides elegans</i> (Thorell, 1876)	8	–	Pav24b, Pav25
	<i>Centruroides exilicauda</i> (Wood, 1863)	8	–	
	<i>Centruroides gracilis</i> (Latreille, 1804)	8	–	
	<i>Centruroides margaritatus</i> (Gervais, 1841)	8	–	Pav24b, Pav25
	<i>Compsobuthus acutecarinatus</i> (Simon, 1882)	8	–	Pav24b, Pav25
	<i>Grosphus flavopiceus</i> Kraepelin, 1900	9	B	
	<i>Grosphus madagascariensis</i> (Gervais, 1843)	9	B	Pav24b, Pav25
	<i>Hottentotta eminii</i> (Pocock, 1890)	8	–	Pav24b, Pav25
	<i>Hottentotta hottentotta</i> (Fabricius, 1787)	8	–	Pav24b, Pav25
	<i>Hottentotta judaicus</i> (Simon, 1872)	8	–	Pav24b, Pav25
	<i>Hottentotta saulcyi</i> (Simon, 1880)	8	–	Pav24b, Pav25
	<i>Isometrus maculatus</i> (DeGeer, 1778)	9	F	Pav24b, Pav25; Mat62
	<i>Leiurus quinquestriatus</i> (Ehrenberg, 1828)	8	–	Pav24b, Pav25
	<i>Liobuthus kessleri</i> Birula, 1898	8	–	Pav24b, Pav25
	<i>Lychas marmoreus</i> (C.L. Koch, 1844)	8	–	Pav24b, Pav25
	<i>Lychas mucronatus</i> (Fabricius, 1798)	8	?	Pav24b, Pav25
	<i>Lychas tricarinatus</i> (Simon, 1884)	9	O	Pav24b, Pav25; Mat62
	<i>Lychas variatus</i> (Thorell, 1876)	9	F	Pav24b, Pav25
	<i>Mesobuthus caucasicus</i> (Nordmann, 1840)	8	–	Pav24b, Pav25
	<i>Mesobuthus eupeus</i> (C.L. Koch, 1839)	8	–	Pav24b, Pav25
	<i>Microcharmus pauliani amber</i> Lourenço, 2006	9	O	
	<i>Microtityus consuelo</i> Armas & Marciano Fondeur, 1987	2	–	
	<i>Odonturus dentatus</i> Karsch, 1879	9	O	Pav24b, Pav25
	<i>Orthochirus scrobiculosus</i> (Grube, 1873)	8	–	Pav24b, Pav25
	<i>Parabuthus granulatus</i> (Ehrenberg, 1831)	9	B	
<i>Parabuthus leiosoma</i> (Ehrenberg, 1828)	8	?	Pav24b, Pav25	
<i>Parabuthus planicauda</i> (Pocock, 1889)	8	?	Pav24b, Pav25	
<i>Rhopalurus abudi</i> Armas & Marciano Fondeur, 1987	8	–		
<i>Rhopalurus princeps</i> (Karsch, 1879)	8	–		
<i>Rhopalurus rochae</i> Borelli, 1910	9	B	Matt70	
<i>Tityus bahiensis</i> (Perty, 1833)	2	–	T-P39b; Matt70	
<i>Tityus cambridgei</i> Pocock, 1897	2	–	Matt70	
<i>Tityus serrulatus</i> Lutz & Mello, 1922	2	–	T-P39a; Matt70	
<i>Tityus stigmurus</i> (Thorell, 1876)	2	–	Matt70	
<i>Uroplectes fischeri</i> (Karsch, 1879)	8	?	Pav24b, Pav25	
<i>Uroplectes formosus</i> Pocock, 1890	8	?	Pav24b, Pav25	
<i>Uroplectes lineatus</i> (C.L. Koch, 1844)	8	?	Pav24b, Pav25	
<i>Uroplectes planimanus</i> (Karsch, 1879)	8	–		
<i>Uroplectes t. triangulifer</i> (Thorell, 1876)	8	–	Pav24b, Pav25	
<i>Zabius fuscus</i> (Thorell, 1876)	9	B		
<b>Chactidae</b> Pocock, 1893	<i>Broteochactas delicatus</i> (Karsch, 1879)	6	–	
	<i>Broteochactas gollmeri</i> (Karsch, 1879)	6	–	Pav24b, Pav25
	<i>Brotheas amazonicus</i> Lourenço, 1988	6	–	
	<i>Brotheas subgranosus</i> Pocock, 1898	6	–	Pav24b, Pav25
	<i>Chactas aequinoctialis</i> (Karsch, 1879)	6	–	
<i>Teuthraustes witti</i> (Kraepelin, 1896)	6	–	Pav24b, Pav25	

Table 1. *Continued*

Family	Species	LC	MC	Citations
<b>Chaerilidae Pocock, 1893</b>	<b><i>Chaerilus granosus</i> Pocock, 1900</b>	6	–	
	<i>Chaerilus variegatus</i> Simon, 1877	6	–	Pav24b, Pav25
	<i>Chaerilus</i> sp.	6	–	Pav24b, Pav25
<b>Diplocentridae Karsch, 1880</b>	<b><i>Bioculus comondae</i> (Stahnke, 1968)</b>	6	–	
	<b><i>Diplocentrus whitei</i> (Gervais, 1844)</b>	6	–	
	<b><i>Nebo flavipes</i> Simon, 1882</b>	6	–	
	<i>Nebo hierichonticus</i> (Simon, 1872)	6	–	W&R92a
<b>Euscorpiidae Laurie, 1896</b>	<b><i>Euscorpius concinnus</i> (C.L. Koch, 1837)</b>	6	–	
	<i>Euscorpius flavicaudis</i> (DeGeer, 1778)	6	–	Pav24b, Pav25
<b>Hemiscorpiidae Pocock, 1893</b>	<b><i>Hemiscorpius lepturus</i> Peters, 1861</b>	6	–	
<b>Heteroscorpionidae Kraepelin, 1905</b>	<b><i>Heteroscorpion goodmani</i> Lourenço, 1996</b>	6	–	
<b>Iuridae Thorell, 1876</b>	<b><i>Caraboctonus keyserlingi</i> Pocock, 1893</b>	6	–	
	<b><i>Hadruroides charcasus</i> (Karsch, 1879)</b>	6	–	
	<b><i>Hadrurus a. arizonensis</i> Ewing, 1928</b>	6	–	Sis90
	<b><i>Iurus dufourei</i> asiaticus Birula, 1903</b>	6	–	
	<i>Iurus d. dufourei</i> (Brullé, 1832)	6	–	Pav24b, Pav25
	<b><i>Hadogenes hahni</i> (Peters, 1862)</b>	6	–	
<b>Liochelidae Fet &amp; Bechly, 2001</b>	<i>Iomachus politus</i> Pocock, 1896	6	–	Pav24b, Pav25
	<b><i>Liocheles australasiae</i> (Fabricius, 1775)</b>	6	–	Pav24b, Pav25
	<b><i>Liocheles waigiensis</i> (Gervais, 1843)</b>	6	–	
	<b><i>Opisthacanthus validus</i> Thorell, 1876</b>	6	–	
	<b><i>Pseudochactas ovchinnikovi</i> Gromov, 1898</b>	6	–	Pre06
<b>Pseudochactidae Gromov, 1998</b>				
<b>Scorpionidae Latreille, 1802</b>	<i>Heterometrus cyaneus</i> (C.L. Koch, 1836)	6	–	Pav24b, Pav25
	<i>Heterometrus scaber</i> (Thorell, 1876)	6	–	Mat56
	<b><i>Opisthophthalmus cavimanus</i> Lawrence, 1928</b>	6	–	
	<i>Pandinus imperator</i> (C.L. Koch, 1841)	6	–	M&W00
	<i>Scorpio maurus fuscus</i> (Ehrenberg, 1829)	6	–	W&R90, W&R93
	<i>Scorpio maurus</i> subsp.	6	–	M&V49
<b>Scorpiopidae Kraepelin, 1905</b>	<b><i>Euscorpiops longimanus</i> (Pocock, 1893)</b>	6	–	
	<i>Euscorpiops montanus</i> Karsch, 1879	6	–	Pav24b, Pav25
	<i>Scorpiops leptochirus</i> Pocock, 1893	6	–	Pav24b, Pav25
	<b><i>Superstitionia donensis</i> Stahnke, 1940</b>	6	–	
<b>Superstitioniidae Stahnke, 1940</b>				
<b>Troglotayosicidae Lourenço, 1998</b>	<b><i>Belisarius xambeui</i> Simon, 1879</b>	6	–	
<b>Urodacidae Pocock, 1893</b>	<i>Urodacus manicatus</i> (Thorell, 1876)	6	–	Mat68, W&R94
	<b><i>Urodacus planimanus</i> Pocock, 1893</b>	6	–	
	<b><i>Urodacus spinatus</i> Pocock, 1902</b>	6	–	
	<i>Urodacus</i> sp.	6	–	
<b>Vaejovidae Thorell, 1876</b>	<b><i>Smeringurus mesaensis</i> (Stahnke, 1957)</b>	6	–	
	<b><i>Uroctonus mordax</i> Thorell, 1876</b>	6	–	Pav24b, Pav25
	<i>Vaejovis intrepidus cristimanus</i> Pocock, 1898	6	–	Pav24b, Pav25
	<b><i>Vaejovis spinigerus</i> (Wood, 1863)</b>	6	–	Pav24b, Pav25

The species examined in this study are set in boldface.

Abbreviations: B, bridged; F, fused; LC, lateral cell number; MC, median cell form; O, open.

Citations: M&V49, Millot & Vachon 1949; M&W00, Mahsberg & Warburg, 2000; Mat56, Mathew 1956; Mat62, Mathew 1962; Mat68, Mathew 1968; Mat70, Matthiesen 1970; Pav24b, Pavlovsky 1924b; Pav25, Pavlovsky 1925; Pre06, Prendini *et al.* 2006; Sis90, Sissom 1990; T-P39a, Toledo-Piza 1939a; T-P39b, Toledo-Piza 1939b; W&R90, Warburg and Rosenberg, 1990; W&R92a, Warburg and Rosenberg, 1992a; W&R93, Warburg and Rosenberg, 1993; W&R94, Warburg and Rosenberg, 1994.

Unknown state (?) is assigned to taxa for which the MC has not been described.

(Pavlovsky & Zarin, 1926; Snodgrass, 1952; Hjelle, 1990). Anatomical variation in the digestive gland was first observed by Pavlovsky (1925: fig. 1, plates VII and VIII), who illustrated the compact digestive gland of *Centruroides margaritatus* (Gervais, 1841), and the markedly lobate digestive gland of *Scorpio maurus* Linnaeus, 1758 in dorsal aspect. Pavlovsky & Zarin (1926) subsequently reported a less lobate digestive gland in Chactidae and Vaejovidae, but unfortunately provided no identification of the species examined.

#### LATERAL LYMPHOID ORGANS

These organs consist of a pair of large, two-cell-thick tubular structures connected anteriorly to the diaphragm dividing the prosoma from the mesosoma. Laurie (1896b) first noticed the variation of the tubes, and considered them to be associated with the coxal glands, part of the excretory system of scorpions, located in the prosoma (Hjelle, 1990). Laurie (1896b) also noted the absence of these tubes in the buthids he examined. Pavlovsky (1924c) provided a more detailed description of these structures and named them 'lymphoid organs', believing them to be associated with the lymphatic system. Additional components of the scorpion lymphatic system comprise strand-like lymphatic glands, extending along the dorsal surface of the ventral nerve cord in the mesosoma, that are referred to as the supraneural glands (Pavlovsky, 1924c; Millot & Vachon, 1949); Farley, 1984, 1999; Hjelle, 1990).

Pavlovsky (1924c) described two kinds of lymphatic system in scorpions: (1) simple lymphatic system, without lateral lymphoid organs; (2) complex lymphatic system, with lateral lymphoid organs. Pavlovsky (1924c) observed the simple system in Buthidae and the complex system in other families (Bothriuridae, Chactidae, Euscorpiidae Laurie, 1893, Iuridae, Liochelidae, Scorpionidae, Scorpipidae Kraepelin, 1905, Urodacidae, and Vaejovidae), and noted that the form and size of the tubes varied, from short ovoid to long tubes. Unfortunately, Pavlovsky (1924c) provided no further details about the differences observed.

The function of these organs was largely unknown until recently (Farley, 1984; Hjelle, 1990). Previous researchers reported the presence of phagocytic cells, which eliminate foreign substances (Pavlovsky, 1924c; Millot & Vachon, 1949), but Nayar (1966) suggested that they may serve an endocrine function. Farley (1984, 1999) demonstrated the hematocytopenic function of the lateral lymphoid organs by means of ultrastructural studies.

The lateral lymphoid organs have been identified in the following families: Bothriuridae (Pavlovsky,

1924c); Chactidae (Pavlovsky, 1924c); Euscorpiidae (Pavlovsky, 1924c, as Chactidae); Iuridae (Pavlovsky, 1924c, as Vaejovidae and Chaerilidae); Liochelidae (Laurie, 1896b, as Ischnuridae Simon, 1879; Pavlovsky, 1924c, as Scorpionidae); Scorpionidae (Laurie, 1896b; Pavlovsky, 1924c); Scorpipidae (Pavlovsky, 1924c, as Chactidae); Urodacidae (Pavlovsky, 1924c, as Scorpionidae); and Vaejovidae (Pavlovsky, 1924c). The absence of these organs has only been confirmed in Buthidae (Laurie, 1896b; Pavlovsky, 1924c), whereas the presence or form of these organs has not been reported in the remaining scorpion families, including Chaerilidae and Pseudochactidae Gromov, 1998.

## MATERIAL AND METHODS

### MATERIAL EXAMINED

Taxon sampling for this study aimed primarily at sampling exemplar species of most families currently recognized in Scorpiones (classification follows Prendini & Wheeler, 2005), and secondarily at corroborating previous observations, particularly those of Pavlovsky (1924b, 1925). Owing to the destructive procedures required to obtain observations on the mesosomal anatomy, we selected specimens with no locality data, which were thus of limited systematic utility, or specimens from large series, wherever possible.

The broad scope of taxon sampling (representatives of almost every family and a large sample of the family Buthidae), from an equally broad distribution of habitats around the world, necessitated the use of museum specimens. All specimens were preserved in 75% ethanol. Whereas most of the specimens are known to have been fixed in ethanol, some specimens were originally fixed in formalin, causing the digestive gland and muscles to be very brittle. The material examined is listed in the Appendix.

### DISSECTIONS

In order to examine the mesosomal organs, particularly the ovariterus, a careful dissection is required. Dissections were conducted using fine-tipped forceps, dissection needles, iris scissors (Miltex 18-1620) and Nikon SMZ-1500 dissection stereomicroscopes. Dissections were conducted in glass or plastic Petri dishes, and specimens were either immersed in 75% ethanol or placed in a plastic Petri dish without ethanol.

Using the iris scissors, a shallow incision was made through the pleural membrane, between the tergites and sternites of the mesosoma, starting beneath tergite VI and cutting anteriorly around the lateral and

anterior carapace margins of the prosoma, then posteriorly between tergite VII and sternite VII, and finally through the membrane connecting tergite VII and metasomal segment I. The opisthosomal terga were then carefully removed by cutting through the dorsoventral muscles that restrain the dorsal sclerites and carapace. Once the tergites were removed, the dorsal aspect of the digestive gland was completely exposed for examination, prior to being carefully dissected away. Dissections usually commenced anteriorly, in the area covered by tergites I and II, and proceeded posteriorly after the anterior branches of the ovariuterus were located. The ovariuterine tubules run through the digestive gland, the removal of which must be undertaken carefully to avoid damaging the ovariuterus.

The preservation of specimens available for dissections was variable. Near complete exposure of the ovariuterus was obtained by careful dissection of softer and fresher specimens. Brittle specimens were soaked in 20% ethanol or distilled water for 2–5 days to soften the digestive gland, and increase the elasticity of the ovariuterine tubules, thus significantly increasing the ease of dissection and reducing the damage to the ovariuterus. In a few cases, soaking only slightly improved the specimens, and dissections removed just enough of the digestive gland to confidently make observations. Specimens satisfactorily dissected were returned to 75% ethanol, and were later photographed using a Microptics™ ML1000 digital imaging system, or a Nikon Coolpix 4500 digital camera attached to a Nikon SMZ-1500 microscope. Suitable images were then used to render line drawings of the ovariuterus.

Measurements were taken directly from the digital photographs using the software UTHSCSA IMAGE TOOL 3.00 (1996–2002), which was developed at the University of Texas Health Science Center at San Antonio, TX, USA, and is available from <http://ddsdx.uthscsa.edu/dig/itdesc.html>. The body width was measured at diaphragm level. The length and width of the lymphoid organ represent the maximum distances observed on the specimen.

#### TERMINOLOGY

This study is concerned with anatomy, the ‘science of internal morphology, as revealed by dissection’ (Torre-Bueno *et al.*, 1989: 38). Anatomical terminology mostly follows Hjelle (1990); however, the following terms were developed based on our observations.

The lateral longitudinal tubules (LT; Figs 1J, 3E, 6B) are the primary longitudinal tubules, leading directly from the spermathecae and extending posteriorly to mesosomal segment VI, where they curve inwards towards each other, and in so doing become

the fifth pair of transverse tubules. The lateral longitudinal tubules are usually situated slightly above the intestine in the body cavity.

The median longitudinal tubule (MT; Figs 1J, 3B) is located below the intestine, and is usually lower in the body cavity than the LTs. The MT divides anteriorly, forming the anteriormost pair of transverse tubules. All nonbuthids and some buthids exhibit complete development of the MT. Francke (1982) and Hjelle (1990) considered this tubule to be the result of fusion of the submedian longitudinal tubules.

Submedian longitudinal tubules (ST; Fig. 2E) occur only in some buthids. These tubules run parallel to one another and to the lateral longitudinal tubules. The right and left STs usually converge anteriorly with the lateral tubule on corresponding sides of the mesosoma. In two taxa, *Isometrus maculatus* (DeGeer, 1778) and *L. variatus*, the submedian tubules fuse anteriorly to form a median longitudinal tubule that divides slightly more posteriorly, as described for the MT (Fig. 1). The STs of all buthids possessing these tubules converge posteriorly to form a short MT, usually between the fourth and fifth LTs.

The transverse tubules (TT; Figs 1E, 2E, 3B) extend transversely between the lateral tubules and either the MT or ST. There are usually five transverse tubules in buthids (Fig. 1J). Representatives of *Microtityus* Kjellesvig-Waering, 1966 and *Tityus* possess only the anteriormost and posteriormost transverse tubules (Fig. 2H, I).

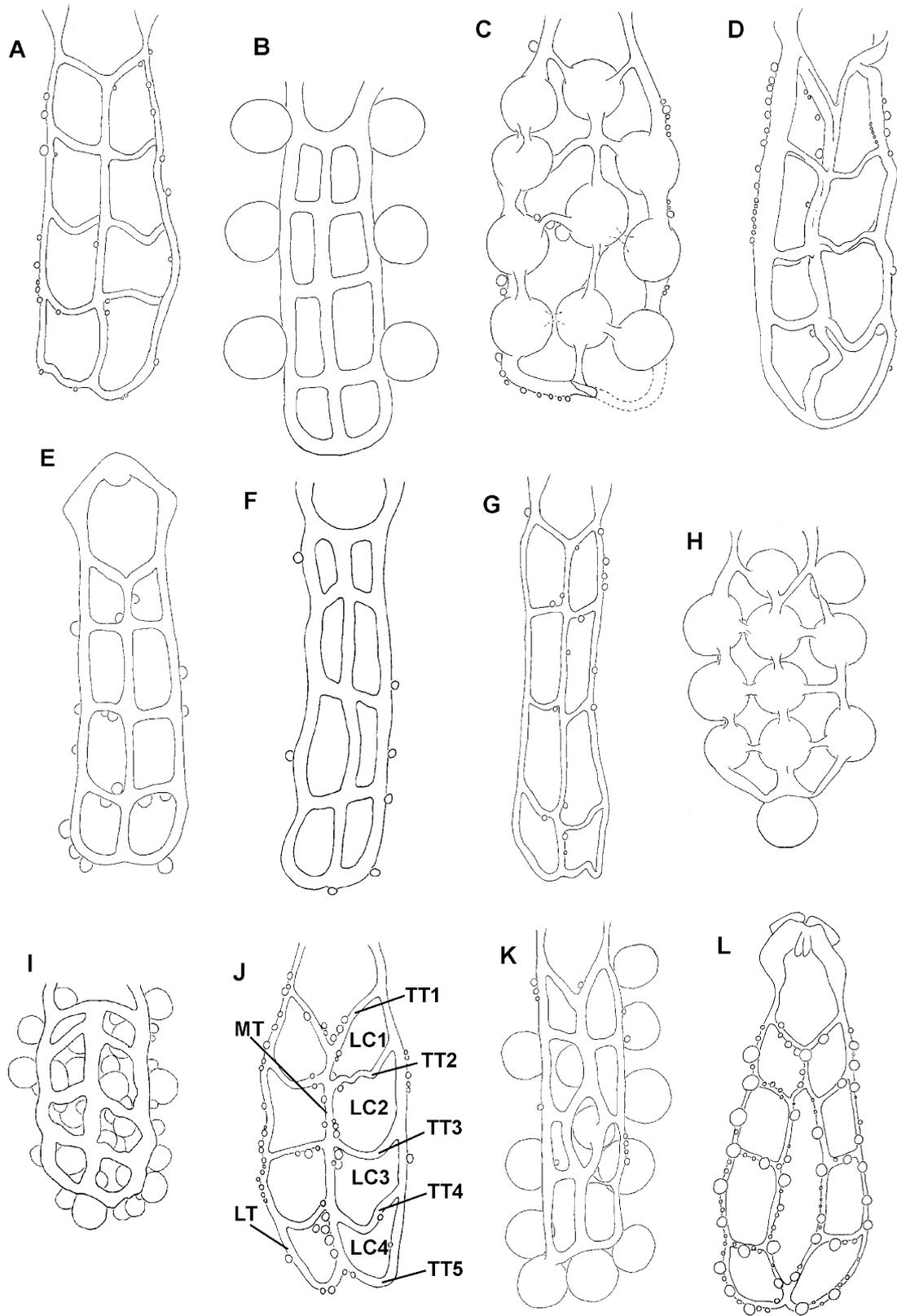
Lateral cells (LC; Figs 1–3, 6D, 7B) are the quadrilateral ‘cells’ in the ovariuterine network. The median cell (MC; Figs 1K, L, 2A–G) is the single, large ‘cell’, and is bounded by the STs. The MC is closed anteriorly by fusion of the STs (Fig. 1K, L), or by a short transverse tubule (Fig. 2A–D), in most taxa observed; however, the MC is open, without any form of anterior closure (Fig. 2F, G), in *L. tricarinatus*, *Odonturus dentatus* Karsch, 1879 and *Microcharmus pauliani ambre* Lourenço & Goodman, 2006.

## RESULTS

### OVARIUTERUS

We observed six different patterns in the branching and connectivity of the ovariuterine tubules. Five of these occur in the Buthidae: (1) simple, eight-celled (Fig. 1A–J); (2) simple, two-celled (Fig. 2F, G); (3) complex-bridged (Fig. 2A–D); (4) complex-fused (Fig. 1K, L); (5) complex-open (Fig. 2F, G). All nonbuthids possessed a similar six-celled ovariuterus.

The simple eight-celled ovariuterus (Fig. 1A–J) comprises a single MT to which the TTs are fused. The simple two-celled ovariuterus (Fig. 2H, I) lacks all but the anteriormost and posteriormost TTs.



**Figure 1.** Eight-celled (A–J) and nine-celled (K, L) ovariuteri of selected buthid scorpion species, depicting variation in the simple ovariuterus (A–J) and the complex-fused ovariuterus (K–L). Ovariuteri display embryos developing within tubules (C, H) or follicles containing mature, or nearly mature, oocytes on ovariuterine walls (B, I, K). A, *Hottentotta hottentotta* Fabricius, 1787. B, *Rhopalurus princeps* Karsch, 1879. C, *Centruroides gracilis* (Latreille, 1804). D, *Rhopalurus abudi* Armas & Marcano Fondeur, 1987. E, *Lychas marmoreus* (C.L. Koch, 1844) (after Pavlovsky, 1925: plate VI, fig. 8). F, *Butheoloides monodi* Vachon, 1950. G, *Uroplectes planimanus* (Karsch, 1879). H, *Orthochirus scrobiculosus* (Grube, 1873). I, *Anomalobuthus rickmersi* Kraepelin, 1990 (after Pavlovsky, 1925: plate VI, fig. 12). J, *Androctonus amoreuxi* (Audouin, 1826). K, *Isometrus maculatus* DeGeer, 1778. L, *Lychas variatus* (Thorell, 1876) (after Pavlovsky, 1925: plate VII, fig. 9) Abbreviations: LC, lateral cell; LT, lateral longitudinal tubule; MT, median longitudinal tubule; TT, transverse tubule.

The complex ovariuterus is defined by the formation of an MC or mesial branches, according to Francke (1982). In our opinion, the MC should be added to the 'cell' count, and these ovariuterine patterns are in fact 'nine-celled', not 'eight-celled' as is usually reported in the literature (Table 1). The complex ovariuterus may be subdivided into three types, depending on whether or not the MC is closed, and on the manner of the closure. All types of complex ovariuterus examined are eight-celled. The complex-bridged ovariuterus (Fig. 2A–E) possesses a closed MC formed by a short TT bridging the STs.

The complex-fused ovariuterus (Fig. 1K, L) possesses a closed MC, formed by anterior fusion of the STs. The complex-open ovariuterus (Fig. 2F, G) is most similar to the complex-bridged form, but lacks the anterior bridging tubule, leaving the MC incomplete, or open.

The simple six-celled ovariuterus (Fig. 3) lacks the anteriormost TTs, and may be planar in cross section, the TTs situated almost level with the MT (in katoikogenic taxa), or W-shaped, the TTs forming two ventrally directed arcs between the MT and the LTs (in apoikogenic taxa) (Table 2). The planar ovariuterus of katoikogenic taxa is situated between the dorsal and ventral sections of the digestive gland, and does not extend ventrally as in apoikogenic taxa (Fig. 6D). The diverticulae mostly emanate from the lateral and ventral surfaces of the ovariuterine tubules, in between the lobes of the digestive gland, with the appendices (when present) directed randomly outwards. The tubules of apoikogenic taxa are usually rounded in cross section, whereas those of katoikogenic taxa are dorsoventrally compressed.

#### SPERMATHECAE

The spermathecae of most Buthidae (*O. dentatus* appears to be an exception), Pseudochactidae, Vaejoidea, Liochelidae, Hemiscorpiidae, and Urodacidae are weakly developed, and are usually visible as a slight expansion of the anteriormost part of the LTs of the ovariuterus. The spermathecae are enlarged and sac-like in Bothriuridae, Chactidae, *O. dentatus*

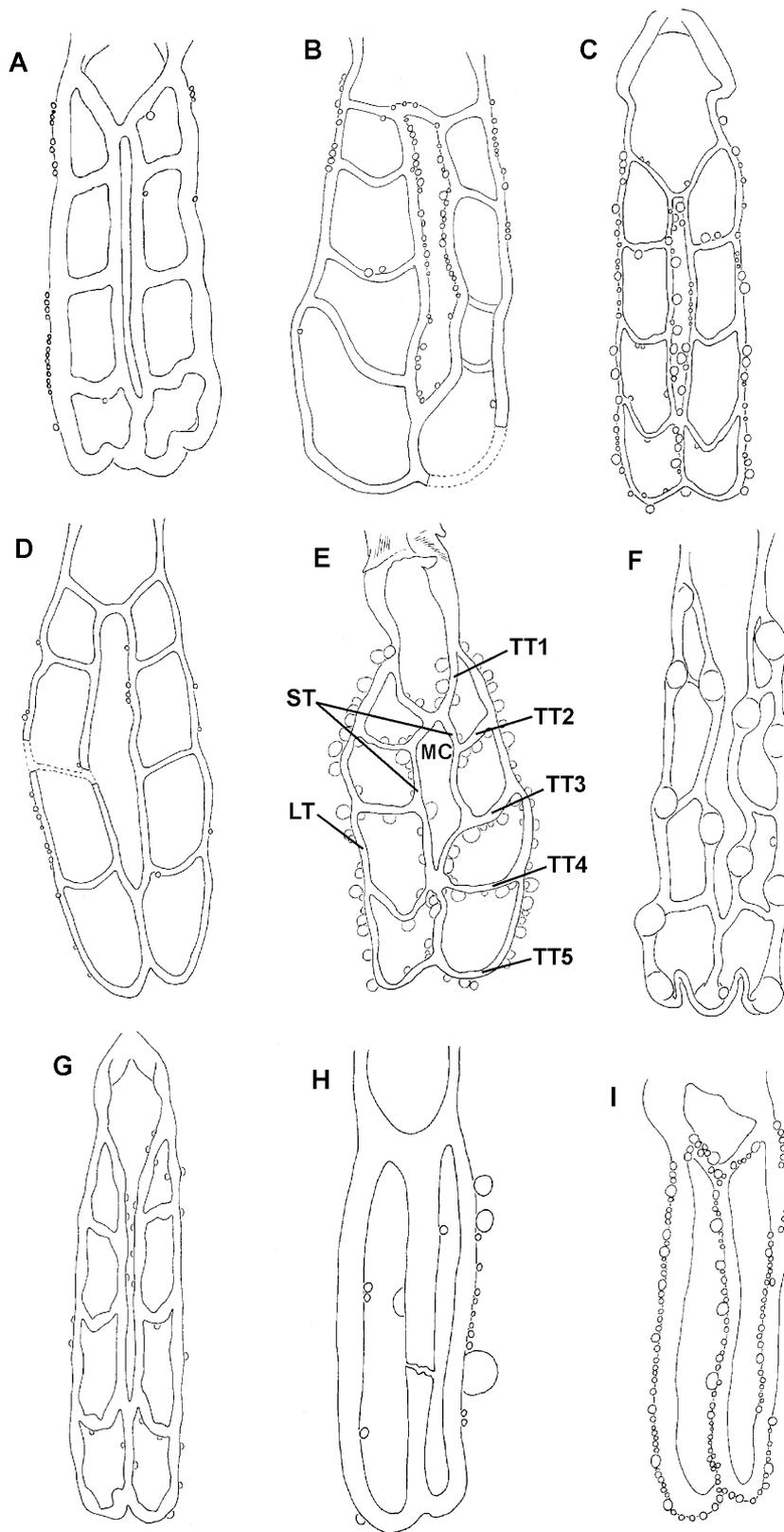
(Buthidae), *Caraboctonus keyserlingi* Pocock, 1893 and *Hadrurus a. arizonensis* Ewing, 1928 (Iuridae). The LTs of the ovariuterus attach medially to the internal side of the spermathecae (Fig. 3G) in all bothriurids except *Lisposoma josehermana* Lamoral, 1979, and at the posterior end of the spermathecae (Fig. 3E) in all other taxa examined (including *L. josehermana*). The spermathecae of *H. a. arizonensis* (Iuridae) are extremely large and attached almost posteriorly, but the first section of the ovariuterine tubule (oviduct, according to Hjelle, 1990) forms an anteriorly-directed 'handle' close to the spermathecal wall, creating the impression that it is attached medially (as in Sissom, 1990: 80, fig. 3.13D).

#### FOLLICLES AND LOCATION OF EMBRYONIC DEVELOPMENT

The shape of the follicle is related to the type of embryonic development. Rounded or oval follicles are characteristic of apoikogenic taxa, whereas elongated follicles are characteristic of katoikogenic taxa. The mature follicles of chactids, euscorpids, scorpionids, and most iurids are oval (as in Fig. 5A), whereas the follicles of the remaining apoikogenic families are rounded (as in Fig. 5B).

The follicles of all taxa examined arise predominantly from the ventral and lateral surfaces of the ovariuterine tubules. All apoikogenic taxa examined, including *V. spinigerus*, display small, rounded, or oval follicles, with a well-developed stalk or pedicel (Fig. 5A, B). The only exception was observed in *S. mesaensis* (Vaejoidea), in which the follicles are surrounded by a trophic layer (Figs 3F, 5C). We did not observe stalked follicles in this species, although they were illustrated by Sissom (1990: 80, fig. 3.13E). The follicles of katoikogenic scorpions are more elongated, forming broad-based, thumb-like processes (Fig. 3H, I; Fig 5D).

The appendix of the diverticula was observed in all katoikogenic taxa except for *Urodacus* Peters, 1861 (Urodacidae) and *Heteroscorpion goodmani* Lourenço, 1996 (Heteroscorpionidae Kraepelin, 1905), in which the diverticula possess only a rounded distal end



**Figure 2.** Nine-celled (A–G) and two-celled (H–I) ovariuteri of selected buthid scorpion species, depicting variation in the complex-bridged ovariuterus (A–E), the complex-open ovariuterus (F, G), and the simple two-celled ovariuterus (H, I). The following developmental stages are illustrated: embryos developing within tubules (F); early stage follicles (A–E, G–I); nearly mature follicle (H). A, *Zabius fuscus* (Thorell, 1876). B, *Parabuthus granulatus* (Ehrenberg, 1831). C, *Parabuthus planicauda* (Pocock, 1889) (after Pavlovsky, 1925: plate VII, fig. 10). D, *Grosphus flavopiceus* Kraepelin, 1900. E, *Rhopalurus rochae* Borelli, 1910 (after Matthiesen, 1970: 627, fig. 2). F, *Odonturus dentatus* Karsch, 1879; G, *Lychas tricarinatus* (Simon, 1884) (after Pavlovsky, 1925: plate VII, fig. 8). H, *Microtityus consuelo* Armas & Marcano Fondeur, 1987. I, *Tityus bahiensis* (Perty, 1833) (after Matthiesen, 1970: 628, fig. 5). Abbreviations: LT, lateral longitudinal tubule; MC, median cell; ST, submedian longitudinal tubule; TT, transverse tubule.

(Fig. 4A). Considerable variation was observed in the shape of the appendix, from the long, narrow tube of *Opisththalmus cavimanus* Lawrence, 1928 (Fig. 4D), to the bottle-shaped distal end (Fig. 4B, C) of Hemiscorpiidae and most Liochelidae (except for *Opisthacanthus validus* Thorell, 1876, in which it is straight, and ends helicoidally), or the distal 'button' of Diplocentridae (Fig. 4B).

#### DIGESTIVE GLAND

We identified three types of digestive glands in this study: (1) compact (Fig. 6A); (2) digitiform (Fig. 6B); (3) a new, perhaps intermediate, hemidigitiform digestive gland (Fig. 6C, D). All apoikogenic scorpions examined possess a compact digestive gland (Table 2). Although dorsal and ventral divisions are evident in the compact digestive gland, longitudinal divisions are difficult or impossible to identify. The lateral tubules of the ovariuterus are situated between the dorsal and ventral portions, and the transverse tubules are situated in between the ventral lobes of each segment.

The digitiform digestive gland was observed in all katoikogenic taxa, excepting *Urodacus*, which possess a hemidigitiform digestive gland. The digitiform digestive gland displays well-developed lobes on both the dorsal and ventral portions; however, there appears to be no obvious association between the 'digits' and particular mesosomal segments (Fig. 6B). The dorsal portion of the hemidigitiform digestive gland is extremely compact, and is slightly narrower than the ventral portion, the lateral sides of which are visible in dorsal aspect (Fig. 6C). The ventral portion of the hemidigitiform digestive gland has thickened lobes (Fig. 6D).

#### LATERAL LYMPHOID ORGANS

These organs were absent in all buthids and chaerilids examined, as well as in *P. ovchinnikovi* and *M. pauliani ambre*. All remaining species examined possess lateral lymphoid organs. We observed considerable variation in the shape and size of these organs. Some taxa, e.g. *C. keyserlingi* and *Hadruroi-*

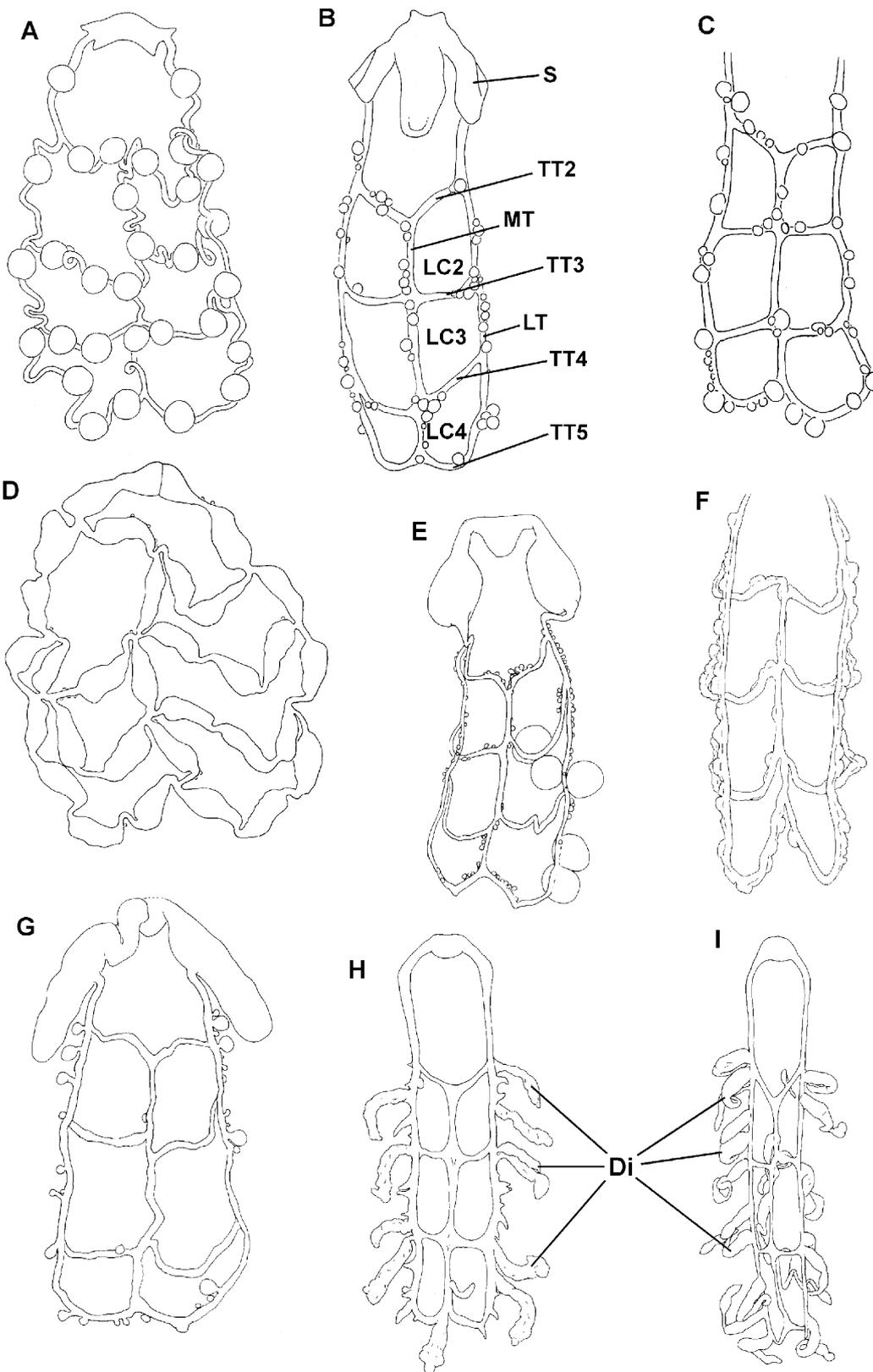
*des charcasus* Pocock, 1900 (Iuridae), *Superstitionia donensis* Stahnke, 1940 (Superstitioniidae Stahnke, 1940), and the Diplocentridae, exhibit small, sac-like structures that do not extend beyond mesosomal segment II, with a length/width ratio of less than 4.5 (Table 2). Others, e.g. *Urodacus*, exhibit narrow tubes, which may extend as far as segment IV, with a length/width ratio up to 16.67 (Table 2, Fig. 7A, B). The lateral lymphoid organs are straight in most cases, extending slightly to the ventral surface, and lie between the ovariuterine LTs. The lateral lymphoid organs of *Urodacus planimanus* Pocock, 1893 are very long (organ length/body width ratio of 1.22), and become tortuous distally (Table 2, Fig. 7B). *Superstitionia donensis* has the smallest lymphoid organ observed, with an organ length/body width ratio of 0.15 (Table 2).

## DISCUSSION

### OVARIUTERUS

All nonbuthid scorpions described in the literature, and examined in the present study, possess a six-celled ovariuterus. Two distinct types of six-celled ovariuterus were identified, conforming to taxa with apoikogenic and katoikogenic development. Apoikogenic taxa possess a generally broader, often W-shaped arrangement of tubules, in which the TTs form two ventrally directed arcs between the MT and the LTs (Fig. 3A–G). Katoikogenic scorpions possess a planar, more elongated arrangement, in which the TTs are almost level with the MT in cross-section (Fig. 3H–I). As discussed further in the section on embryonic development, katoikogeny is restricted to the scorpionoid families, excluding Bothriuridae, and is apomorphic relative to apoikogeny (Stockwell, 1989; Prendini, 2000, 2003).

*Pseudochactas ovchinnikovi* also possesses a six-celled ovariuterus, yet this enigmatic scorpion also exhibits numerous buthid-like characters (Prendini *et al.*, 2006). Although its phylogenetic position remains to be rigorously tested, the evidence suggests that *Pseudochactas* Gromov, 1998 is the sister group of Buthidae (Prendini *et al.*, 2006). If this is the case,



**Figure 3.** Six-celled ovariuiterus of nonbuthid scorpion species, depicting variation in apoikogenic (A–G) and katoikogenic (H, I) patterns. The following developmental stages are illustrated: embryos developing within tubules (A, D); follicles containing early to mid-stage oocytes (B, C, E–G); five nearly mature oocytes (E); embryos developing within diverticulae (H, I). Note the enlarged spermathecae close to the genital atrium (B, E, G). A, *Euscorpions montanus* (Karsch, 1879) (after Pavlovsky, 1925: plate VII, fig. 5). B, *Brachistosternus intermedius* Lönnberg, 1902 (after Pavlovsky, 1925: plate VII, fig. 11). C, *Pseudochactas ovchinnikovi* Gromov 1998 (after Prendini *et al.*, 2006: 239, fig. 46). D, *Scorpiops leptochirus* Pocock, 1893. E, *Lisposoma josehermana* Lamoral, 1979. F, *Smeringurus mesaensis* (Stahnke, 1957). G, *Urophonius granulatus* Pocock, 1898. H, *Heteroscorpion goodmani* Lourenço, 1996. I, *Liocheles waigiensis* (Gervais, 1843). Abbreviations: Di, diverticula; LC, lateral cell; LT, lateral longitudinal tubule; MT, median longitudinal tubule; S, spermatheca; TT, transverse tubule.

and likewise if *Pseudochactas* is the sister group of all other Recent scorpions, as proposed by Soleglad & Fet (2003), the eight-celled ovariuiterus found in most Buthidae must be apomorphic.

Among the buthid genera examined during the present investigation, *Androctonus* Ehrenberg, 1828, *Anomalobuthus* Kraepelin, 1900, *Hottentotta* Birula, 1908, *Liobuthus* Birula, 1898, and *Orthochirus* Karsch, 1891, representing the Old-World Palaeartic buthid clade (Fet, Soleglad & Lowe, 2003, 2005; Coddington *et al.*, 2004), all possess the simple eight-celled ovariuiterus, suggesting that it may be synapomorphic for this clade.

The complex eight-celled ovariuiterus has apparently evolved several times independently from the simple condition. All buthids in which the complex eight-celled ovariuiterus was observed, originate from parts of the former Gondwanaland (Australia, India, Madagascar, southern Africa, and South America). In the present study, *Uroplectes planimanus* Karsch, 1879 and *Uroplectes t. triangulifer* Thorell, 1876 were found to possess the simple eight-celled ovariuiterus, whereas representatives of *Grosphus* Simon, 1880 and *Parabuthus* Pocock, 1890 were found to possess a complex-bridged eight-celled ovariuiterus. Prendini (2004) proposed that *Uroplectes* Peters, 1861 is the sister group of *Parabuthus*, and that the two African genera form a monophyletic sister group of the Malagasy *Grosphus*. Prendini's (2004) hypothesis implies that the simple eight-celled ovariuiterus was independently derived in *Uroplectes* and the Palaeartic buthids, which are not closely related (Fet *et al.*, 2003).

Two notable cases of variation in ovariuiterine anatomy were observed among congeners. *Rhopalurus princeps* (Karsch, 1879) and *R. abudi* from the Dominican Republic both exhibit the simple eight-celled ovariuiterus. In contrast, the Brazilian *R. rochae* displays the complex-bridged ovariuiterus, first observed by Matthiesen (1970), and confirmed in the present study. *Rhopalurus* Thorell, 1876 is discontinuously distributed in the Caribbean and Brazil (Lourenço, 1986, 2000a; Lourenço & Pinto-da-Rocha, 1997; Armas, 1999; Armas, Ottenwalder & Guerrero,

1999). The observed differences in ovariuiterine anatomy suggest that it may contain informative characters for the systematics of the genus. The phylogenetic relationships of *Rhopalurus* are currently unknown, but it is possible that the genus may be paraphyletic with respect to *Centruroides* Marx, 1890, with which its component species share several synapomorphies (Sissom, 1990; Fet & Lowe, 2000). We examined *Centruroides exilicauda* (Wood, 1863) and *Centruroides gracilis* (Latreille, 1804) in the present study, both of which possess the simple eight-celled ovariuiterus.

Pavlovsky (1925) illustrated three different types of ovariuiterine anatomy in the buthid genus *Lychas* C.L. Koch, 1845. *Lychas marmoreus* exhibits the simple eight-celled ovariuiterus (Fig. 1E), *L. variatus* exhibits the complex-fused ovariuiterus (Fig. 1L), and *L. tricarinatus* exhibits the complex-open ovariuiterus (Fig. 2G). If Pavlovsky's (1925) illustrations correctly depict the anatomy of these species, then these observations suggest that this widespread genus (distributed in Africa, Australasia, and India) may also be paraphyletic. The ovariuiterine anatomy of *L. tricarinatus* was independently confirmed by Mathew (1960, 1962), and the anatomy of the other *Lychas* species illustrated by Pavlovsky (1925) was verified during the present study. The taxonomy of the Australian *Lychas* (particularly *L. marmoreus*, *L. variatus*, and their respective synonyms) is chaotic (Kraepelin, 1916; Glauert, 1925; Koch, 1977; Kovařík, 1997). Additional species of *Lychas* should be examined to illuminate the patterns observed by Pavlovsky (1925). All other buthid genera examined during the present investigation, except *Rhopalurus*, possess the same ovariuiterine anatomy among congeners.

Our observations on the ovariuiterine anatomy also support mounting evidence that the genus *Microcharmus* Lourenço, 1996, currently placed in a unique family, Microcharmidae Lourenço, 1996, is a buthid (Coddington *et al.*, 2004). We observed the complex open form of the eight-celled ovariuiterus in *M. pauliani ambre* and two buthids, *Babycurus jacksoni* (Pocock, 1890) and *L. tricarinatus*. *Microcharmus*

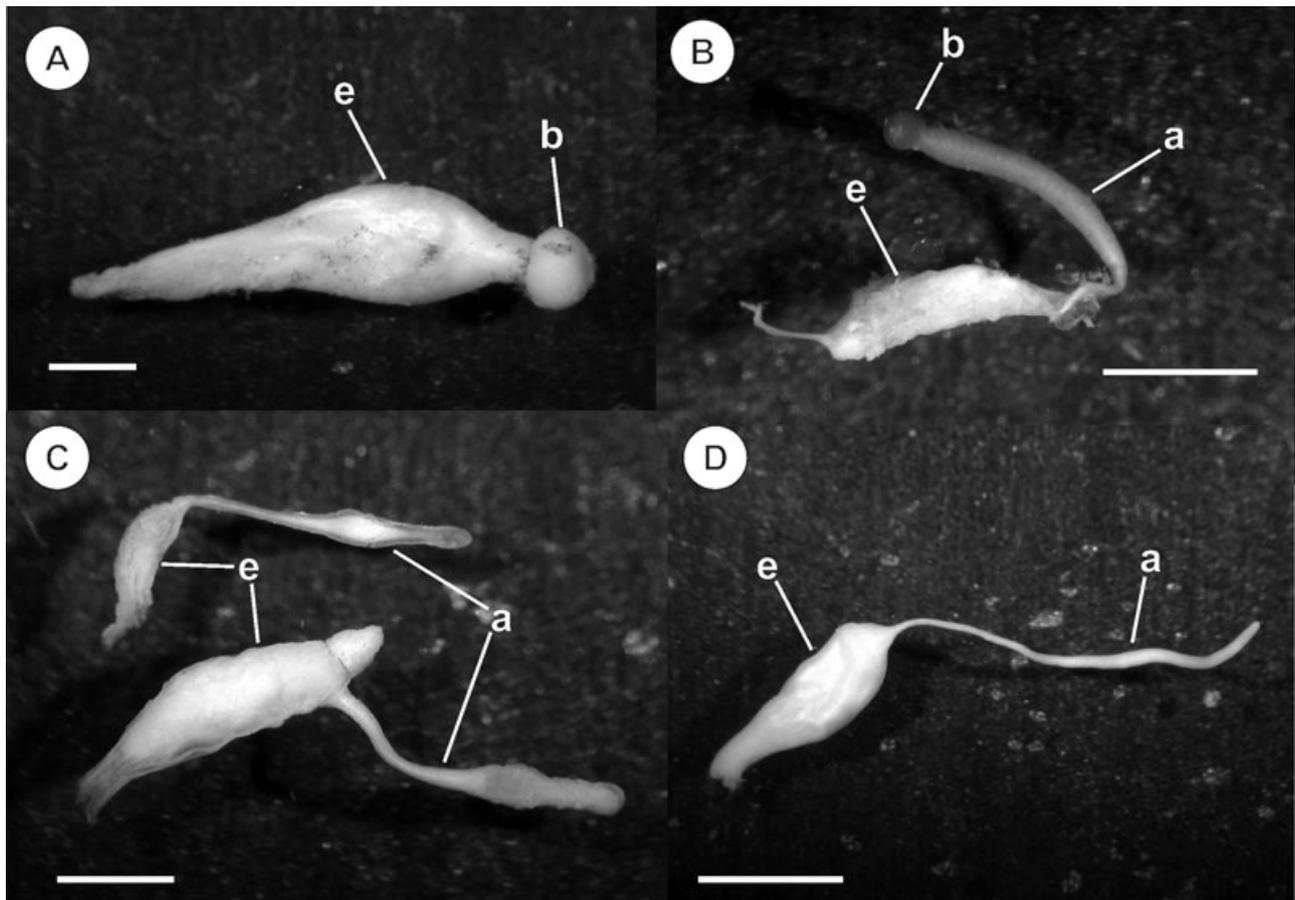
**Table 2.** Summary of embryological observations on the ovariole, digestive gland, and lateral lymphoid organs for taxa examined in the present study

Family	Species	Follicles				Spermatheca			Lateral Lymphoid Organs	
		Development	Appendix	Shape	Pedicle	Connection to ovarian tube	Digestive gland form	Shape	Length/body width	Length/width
<b>Bothriuriidae</b>	<i>Brachistosternus intermedius</i>	apokogenic	–	round	present	medial	compact	tube	0.48	4.6
	<i>Lisposoma josehermana</i>	apokogenic	–	round	present	distal	compact	tube	0.46	7.92
	<i>Timogenes elegans</i>	apokogenic	–	round	present	medial	compact	tube	0.63	9.4
	<i>Urophonius granulatus</i>	apokogenic	–	round	present	medial	compact	?	?	?
	<i>Ananteris platnicki</i>	apokogenic	–	round	?	distal	compact	absent	–	–
	<i>Androctonus amoreuxi</i>	apokogenic	–	round	?	distal	compact	absent	–	–
	<i>Androctonus australis</i>	apokogenic	–	round	?	distal	compact	absent	–	–
	<i>Babycurus jacksoni</i>	apokogenic	–	round	?	distal	compact	absent	–	–
	<i>Butheoloides monodi</i>	apokogenic	–	?	?	distal	compact	absent	–	–
	<i>Buthus occitanus</i>	apokogenic	–	round	present	distal	compact	absent	–	–
<b>Buthidae</b>	<i>Centruroides exilicauda</i>	apokogenic	–	round	?	distal	compact	absent	–	–
	<i>Centruroides gracilis</i>	apokogenic	–	round	?	distal	compact	absent	–	–
	<i>Grosphus flavopiceus</i>	apokogenic	–	round	?	distal	compact	absent	–	–
	<i>Hottentotta hottentotta</i>	apokogenic	–	round	present	distal	compact	absent	–	–
	<i>Isometrus maculatus</i>	apokogenic	–	?	?	distal	compact	absent	–	–
	<i>Microharmus pauliani ambre</i>	apokogenic	–	round	present	distal	compact	absent	–	–
	<i>Microtityus consuelo</i>	apokogenic	–	round	?	distal	compact	absent	–	–
	<i>Odonturus dentatus</i>	apokogenic	–	round	present	distal	compact	absent	–	–
	<i>Orthochirus scrobiculosus</i>	apokogenic	–	round	?	distal	compact	absent	–	–
	<i>Parabuthus granulatus</i>	apokogenic	–	round	?	distal	compact	absent	–	–
<b>Chactidae</b>	<i>Rhopalurus abudi</i>	apokogenic	–	round	?	distal	compact	absent	–	–
	<i>Rhopalurus princeps</i>	apokogenic	–	round	present	distal	compact	absent	–	–
	<i>Rhopalurus rochae</i>	apokogenic	–	round	?	distal	compact	absent	–	–
	<i>Uroplectes planimanus</i>	apokogenic	–	round	?	distal	compact	absent	–	–
	<i>Uroplectes t. triangulifer</i>	apokogenic	–	round	?	distal	compact	absent	–	–
	<i>Zabius fuscus</i>	apokogenic	–	round	?	distal	compact	absent	–	–
	<i>Brotheas amazonicus</i>	apokogenic	–	oval	present	distal	compact	?	?	?
	<i>Brotochactas delicatus</i>	apokogenic	–	?	?	distal	compact	tube	0.41	4.71
	<i>Chactas aequinoctialis</i>	apokogenic	–	?	?	distal	compact	tube	0.52	8

<b>Chaeriliidae</b>	<i>Chaerilus granosus</i>	-	round	present	distal	compact	absent	-	-
<b>Diplocentridae</b>	<i>Bioculus comondae</i>	present	thumb	absent	distal	digitiform	sac	0.42	2.88
	<i>Diplocentrus whitei</i>	present	?	?	distal	digitiform	sac	0.24	2.3
	<i>Nebo flavipes</i>	present	?	?	distal	?	?	?	?
<b>Euscorpidae</b>	<i>Euscorpis concinnus</i>	-	oval	present	distal	compact	tube	0.47	8.66
<b>Hemiscorpiidae</b>	<i>Hemiscorpius lepturus</i>	present	thumb	absent	distal	digitiform	tube	0.44	4.65
<b>Heteroscorpionidae</b>	<i>Heteroscorpion goodmani</i>	absent	cone	absent	distal	digitiform	?	?	?
<b>Iuridae</b>	<i>Caraboctonus keyserlingi</i>	-	oval	present	subdistal	compact	sac	0.44	4.43
	<i>Hadruroides charcasus</i>	-	oval	present	distal	compact	sac	0.34	3.1
	<i>Hadrurus a. arizonensis</i>	-	round	present	subdistal*	compact	tube	0.31	8.05
	<i>Iurus dufouraei asiaticus</i>	-	oval	present	distal	compact	tube	0.35	4.55
<b>Liochelidae</b>	<i>Hadogenes hahni</i>	present	thumb	absent	distal	digitiform	tube	0.35	6.36
	<i>Liocheles australasiae</i>	present	thumb	absent	distal	digitiform	?	?	?
	<i>Liocheles waigiensis</i>	present	?	absent	distal	digitiform	tube	0.46	13.75
	<i>Opisthacanthus validus</i>	present	thumb	absent	distal	digitiform	tube	0.47	5.63
<b>Pseudochactidae</b>	<i>Pseudochactas ovchinnikovi</i>	-	round	present	distal	compact	absent	-	-
<b>Scorpionidae</b>	<i>Opistophthalmus cavimanus</i>	present	thumb	absent	distal	digitiform	?	?	?
<b>Scorpiopidae</b>	<i>Euscorpis longimanus</i>	-	oval	present	distal	compact	tube	0.33	8.25
<b>Superstitionidae</b>	<i>Superstitionia donensis</i>	-	round	present	distal	compact	sac	0.15	1.5
<b>Troglotayosicidae</b>	<i>Belisarius xambeui</i>	-	?	?	distal	compact	tube	?	?
<b>Urodactidae</b>	<i>Urodacus planimanus</i>	absent	thumb	absent	distal	hemidigitiform	tube	1.22	15.28
	<i>Urodacus spinatus</i>	absent	thumb	absent	distal	hemidigitiform	tube	?	?
	<i>Urodacus</i> sp.	absent	thumb	absent	distal	hemidigitiform	tube	0.77	16.67
<b>Vaejovidae</b>	<i>Smeringurus mesaensis</i>	-	thumb	absent	distal	compact	tube	0.38	6.71
	<i>Uroctonus mordax</i>	-	-	absent	distal	compact	tube	0.68	9.5
	<i>Vaejovis spinigerus</i>	-	round	present	distal	compact	tube	0.41	6.5

Unknown state (?) is assigned to taxa for which the information could not be scored, because of poor preservation or inappropriate developmental stage, and as the appendix is only present in katoikogenic species, this state is scored as inapplicable (-) in apoikogenic species.

\*The medial connection of ovarium to seminal receptacle illustrated by Sissom (1990: 80, fig. 3.13D) may be incorrect.



**Figure 4.** Diverticular anatomy of katoikogenic scorpions, depicting variation in appendices: obsolete appendix with well-developed terminal 'button' (A); well-developed appendix (B–D), with terminal 'button' (B); two diverticulae in different stages of embryonic development (C), top, illustrating early-stage embryo, bottom, illustrating larger and more advanced embryo. A, *Urodacus spinatus* Pocock, 1902. B, *Nebo flavipes* Simon, 1882. C, *Hadogenes hahni* Peters, 1862 (two stages of development). D, *Opisththalmus cavimanus* Lawrence, 1928. Abbreviations: a, appendix; b, terminal 'button'; e, embryo developing within diverticula. Scale bars: 1 mm.

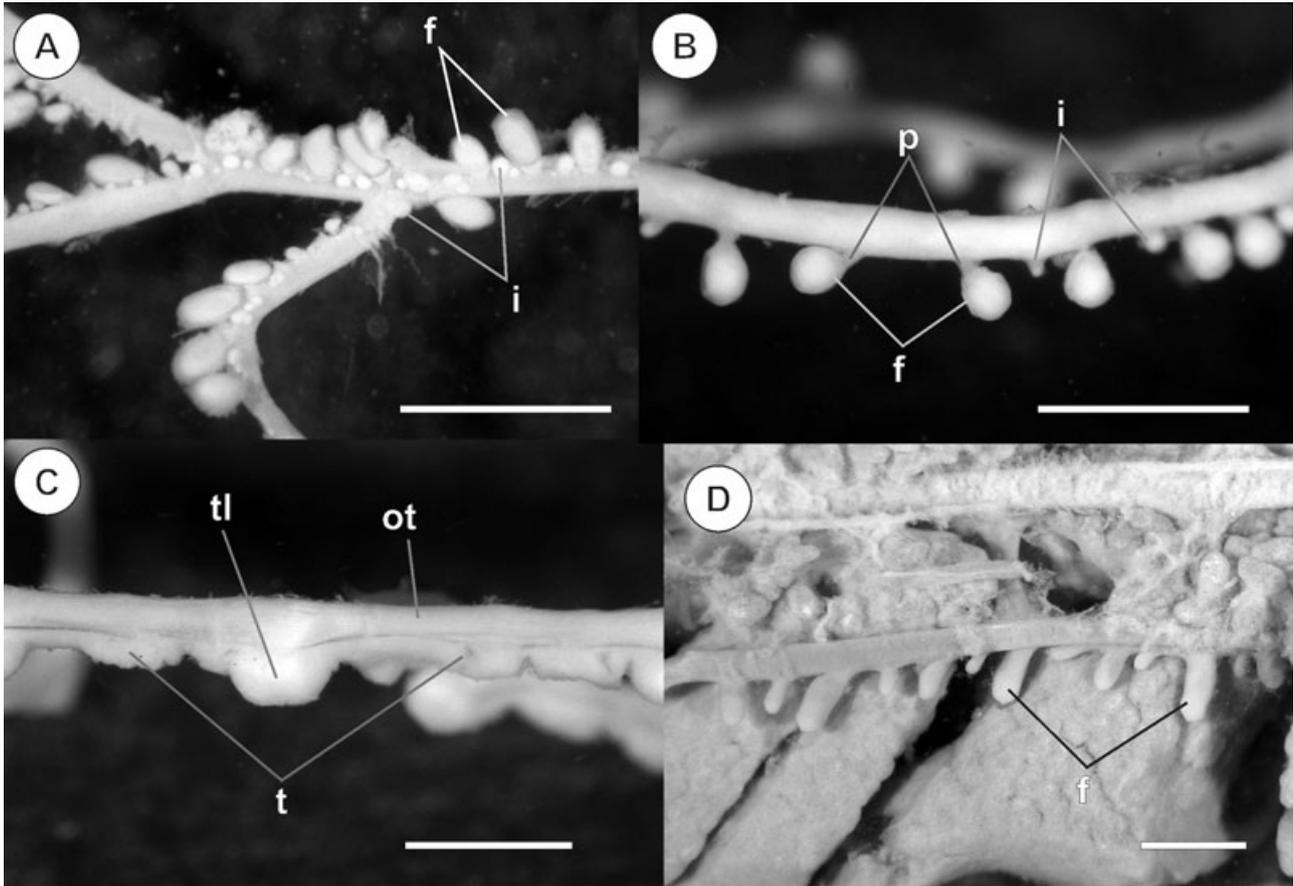
also lacks lateral lymphoid organs, which is another buthid characteristic. These anatomical characters support numerous external morphological characters (e.g. the presence of the type-A trichobothrial pattern on the pedipalps) otherwise unique to Buthidae, from which Microcharmidae is separated principally on the basis of size and ecology (Lourenço, 2000b). The balance of evidence does not, in our opinion, warrant continued recognition of Microcharmidae, which renders Buthidae paraphyletic (E. S. Volschenk & L. Prendini, unpubl. data). We therefore propose the following new synonymy: Microcharmidae Lourenço, 1996 = Buthidae C.L. Koch, 1837.

#### SPERMATHECAE

The spermatheca is an elastic structure, which is probably subject to slight changes in size depending

on the quantity of sperm contained within; however, several characters of this organ may be phylogenetically informative. Knowledge of the extent of variation in the spermathecae is limited, as spermathecal size is probably dependent on time elapsed since the last mating, as well as on the stage of the reproductive cycle. Three independent studies observed enlarged spermathecae in the iurid, *H. a. arizonensis* (Sissom, 1990; Farley, 2001; this study). Spermathecal size may also be phylogenetically informative in the other iurids, bothriurids, and chactids, in which enlarged spermathecae have been observed. The absence or small size of the spermathecae of most other scorpions, including Buthidae and *Pseudochactas*, suggests that enlarged spermathecae are apomorphic.

The extremely enlarged spermathecae observed in some taxa (e.g. *H. a. arizonensis* and *Urophonius*



**Figure 5.** Ovariuterine follicles, depicting variation in shape: round follicles of apoikogenic scorpions (A–C); more elongated, thumb-like follicles of katoikogenic scorpions (D). A, *Hadruroides charcasus* (Karsch, 1879). B, *Timogenes elegans* (Mello-Leitão, 1931): ventral view showing small immature follicles and larger maturing follicles. C, *Smeringurus mesaensis* (Stahnke, 1961): showing the trophic network attached to ovariuterine tubule and completely covering the maturing follicle with the trophic lobe. D, *Urodacus* sp.: mature follicles. Abbreviations: f, maturing follicles; i, immature follicles; ot, ovariuterine tubule; p, pedicel; t, trophic network; tl, trophic lobe. Scale bars: 1 mm.

*granulatus* Pocock, 1899) probably contain sperm from multiple inseminations, because the quantity of sperm contained in a single spermatophore from these species is a small fraction of the volume of the spermatheca (A.V. Peretti, pers. comm.). The purpose of this accumulation of sperm is unknown, but is presumed to facilitate the production of multiple broods.

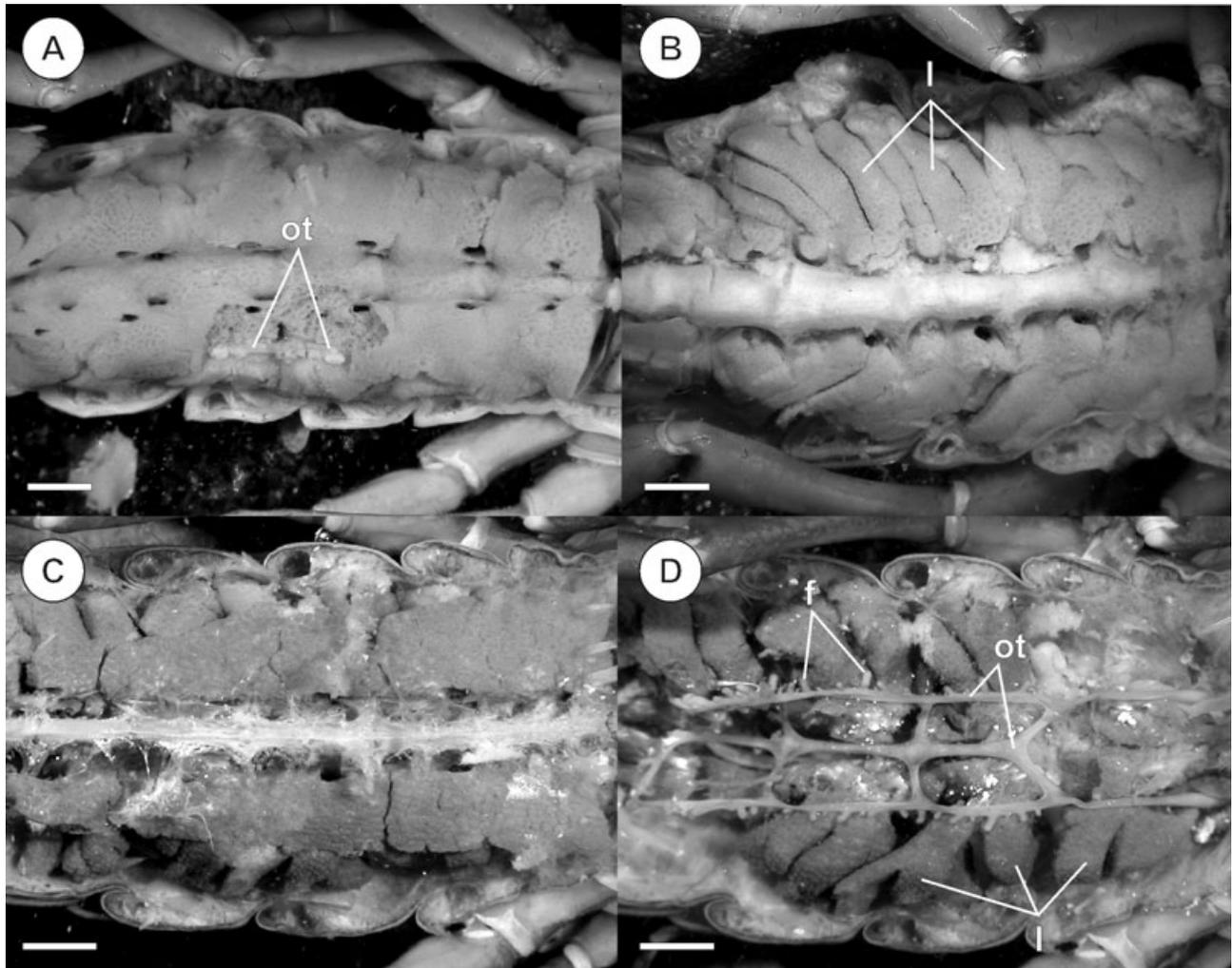
The point of attachment of the ovariuterus to the spermathecae also varies. The ovariuterus of most scorpions possessing spermathecae is attached posteriorly, and it is likely that, during parturition, any sperm retained in the spermathecae will be expelled as the first of the brood pass through to the exterior. The ovariuterus of all bothriurids (except *L. josehermana*) examined in the present study attaches interolaterally to the spermathecae. Lateral attachment to the spermathecae creates a broad pocket that may facilitate the storage of large quantities of sperm. The extreme size of the spermathecae observed in iurids

and bothriurids may thus serve not only to store a large mass of sperm, but also to prevent its expulsion during parturition.

#### LOCATION OF EMBRYONIC DEVELOPMENT

Several studies (e.g. Stockwell, 1989; Prendini, 2000, 2003) demonstrated that apoikogenic development is plesiomorphic, and katoikogenic development apomorphic, in scorpions. Katoikogenic scorpions include all Scorpionoidea Latreille, 1802 (*sensu* Prendini, 2000) except Bothriuridae, which are apoikogenic. Katoikogeny appears to have evolved only once (Prendini, 2000, 2003).

Lourenço (2002) speculated that *Lisposoma* would possess well-developed diverticulae like other scorpionoid taxa, contrary to Stockwell (1989) and Prendini (2000). We confirmed the presence of a typical,



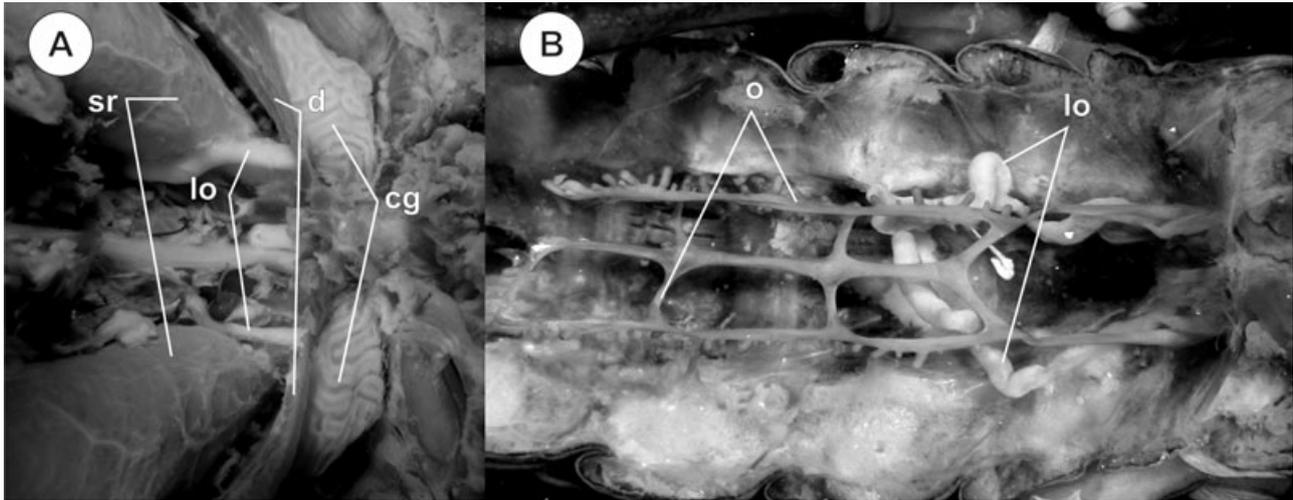
**Figure 6.** Variation in digestive gland: compact digestive gland (A); digitiform digestive gland (B); hemidigitiform digestive gland, showing compact dorsal part (C), and with compact dorsal part removed, showing ovary lying over lobate ventral portion of gland (D). Developmental types: apoikogenic development (A); katoikogenic development (B–D). A, *Smeringurus mesaensis* (Stahnke, 1957): with part of digestive gland removed to expose ovary. B, *Opisththalmus cavimanus* Lawrence, 1928. C, D, *Urodacus* sp. Abbreviations: f, follicles; l, lobules of digestive gland; ot, ovary tubule. Scale bars: 2 mm.

apoikogenic ovary in *L. josephiana* (Fig. 4E), as reported by Stockwell (1989) and Prendini (2000, 2003).

The alleged 'third type' of embryonic development reported for *V. spinigerus* and *C. werneri judaicus* (Warburg & Rosenberg, 1996; Warburg, 2001) appears to be a misinterpretation of an advanced stage in the development of the embryos inside the ovary. We observed regular follicles in *V. spinigerus*, conforming to typical apoikogenic development.

The typical, elongated diverticular appendix is not present in all katoikogenic taxa (Laurie, 1896b). We did not observe elongated appendices on the diverticulae of *H. goodmani* (Heteroscorpionidae) or *Urodacus spinatus* Pocock, 1902 (Urodacidae), which

was the only urodacid with developing embryos that we examined in the course of this study. We instead observed a thickened structure, on a short pedicel (perhaps a rudimentary appendix), situated distally on the embryos (Fig. 4A) of these taxa. Laurie (1896b) and Mathew (1968) documented similar structures in the early embryos of *Urodacus novaehollandiae* Peters, 1861 and *U. manicatus*, respectively. Mathew (1968) conducted a detailed investigation of the internal structure of the follicles of *U. manicatus*, and demonstrated that the thick, button-like structure is an accumulation of gland cells, which may secrete nourishment for the developing embryo. This secretory structure is located at the distalmost part of the elongated appendices that are characteristic of other



**Figure 7.** Lateral lymphoid organs of selected scorpion species. A, *Hadrurus a. arizonensis* Ewing, 1928: seminal receptacle, coxal glands, and tubes arising from diaphragm. B, *Urodacus planimanus* Pocock, 1893: enlarged tubes and planar ovariuterus. Abbreviations: cg, coxal glands; d, diaphragm; lo, lymphoid organs; sr, seminal receptacle (spermathecae); o, ovariuterus.

katoikogenic scorpions (Laurie, 1896b; Mathew, 1968; Fig. 4B).

Laurie (1896b) considered the short 'appendix' of *U. novaehollandiae* to be nonfunctional and plesiomorphic, compared with the elongated appendices observed on the diverticulae of other katoikogenic taxa. Our observation of a similar structure in *Heteroscorpion* Birula, 1903 is significant, as it contributes evidence to the debate concerning the relative phylogenetic positions of Urodacidae and Heteroscorpionidae, which have been contentious since Prendini (2000) first proposed a sister-group relationship for these families (Soleglad & Sissom, 2001; Prendini, 2003; Soleglad & Fet, 2003; Coddington *et al.*, 2004; Prendini & Wheeler, 2005; Soleglad, Fet & Kovařík, 2005; Lourenço & Goodman, 2006; Volschenk & Prendini, 2008). According to the alternative hypothesis, first proposed by Stockwell (1989), but also obtained in some analyses by Prendini (2000) and a reanalysis of Prendini's (2000) data by Soleglad *et al.* (2005), Heteroscorpionidae is sister to Hemiscorpiidae and Liochelidae, whereas Urodacidae is sister to Diplocentridae and Scorpionidae. The new observations reported here are consistent with Prendini's (2000) hypothesis that Urodacidae and Heteroscorpionidae form a monophyletic sister group to the other katoikogenic scorpion families.

#### FOLLICLES

The pedicel of the follicle, repeatedly claimed to be present only in Iuridae and Vaejovidae (Laurie, 1891; Francke, 1982; Stockwell, 1989; Sissom, 1990), was observed in all of the apoikogenic species studied in

the course of the present investigation (Table 2). The pedicel appears to be nothing more than a stage in the development of the follicle and the oocyte it contains. Follicles in the early stages of development are smaller in size and possess a pedicel that is not always present (or obvious) in larger, more mature follicles.

We presume that the original observations of Laurie (1896b) and Pavlovsky (1926) were based on very early stage oocytes. This misconception has persisted for more than a century, despite the clearly illustrated examples of other scorpion taxa (at least six buthids and two euscorpiids) with stalked follicles (Laurie, 1890; Mathew, 1962; Matthiesen, 1970; Warburg & Rosenberg, 1992b; Warburg *et al.*, 1995; Lourenço, 2002), and illustrates the importance of checking observations in specimens, rather than uncritically recycling data in the literature (Prendini, 2001).

#### DIGESTIVE GLAND

We observed three different types of digestive glands in the present investigation: compact, hemidigitiform, and digitiform. The function of the digitiform digestive gland is unknown, and we suggest two possibilities.

The digitiform and hemidigitiform digestive glands are only known in katoikogenic scorpions, suggesting that they may be associated with this type of embryonic development. The elongated katoikogenic diverticulae occupy the spaces between the lobes of the digestive glands. The diverticular appendices, when present, often extend deep into the mesosoma. It is

thus possible that the diverticulae may require additional space in the mesosoma for growth and development.

The digitiform and hemidigitiform digestive glands may also increase the surface area that is exposed to the haemolymph. Although the appendix of the diverticula is known to channel nutrients to the embryo at its base (Mathew, 1968), the mechanism by which these nutrients enter the appendix is unknown. On the assumption that this process occurs by diffusion from the haemolymph, the increased surface area of the digitiform and hemidigitiform digestive glands would increase the rate at which nutrients could diffuse from the glands into the haemolymph.

Contrary to Pavlovsky & Zarin (1926), we did not observe a digitiform digestive gland in the chaetids and vaejovids we examined, all of which possessed a compact digestive gland.

The digestive gland does not appear to be sexually dimorphic. The same anatomy has been observed in males and females in all species possessing a compact digestive gland. Similarly, the digitiform digestive gland was observed in both sexes in at least two katoikogenic scorpions (*Bioculus comondae* Stahnke, 1968 and *O. validus*).

#### LATERAL LYMPHOID ORGANS

The absence of lateral lymphoid organs in *P. ovchinikovi*, Buthidae, and Chaerilidae is congruent with all hypotheses concerning the possible placement of Pseudochaetidae in the phylogeny of scorpions: sister group of all recent scorpions, sister group of Buthidae, or sister group of Chaerilidae (Prendini *et al.*, 2006). Considering the most recent hypothesis of scorpion phylogeny (Coddington *et al.*, 2004), the presence of lateral lymphoid organs may be apomorphic in the order. The morphology and degree of development of these organs is quite variable (Table 2), but is consistent within some taxa (e.g. *Urodacus*), and may carry phylogenetic information. Further physiological research is needed to completely clarify the function of these organs (Farley, 1999).

#### CONCLUSIONS

Phylogenetically informative characters from the mesosomal anatomy of scorpions were first reported a century ago (Laurie, 1896a, b; Pavlovsky, 1913, 1915a, b, c, d, 1917, 1924a, b, c, d, 1925, 1926; Pavlovsky & Zarin, 1926), and have received little attention since. Many of the observations in these early studies were reported from a limited sample of taxa, and few were subsequently confirmed. These observations were nevertheless incorporated into the anatomical literature and into recent phylogenetic

analyses, and, in some cases, were extrapolated to other taxa in which they had not been observed. Some organ systems (e.g. the digestive gland and lateral lymphoid organs) have never been studied comparatively across diverse taxa, or from a systematic perspective, and their reference in the literature is limited to their original discovery.

Here, we summarized existing data on these organs, reassessed the original observations as far as possible, augmented the set of observations across a sample of taxa representing most scorpion families, and revised the terminology to accommodate the range of variation observed. In so doing, we confirmed most of the original observations of previous workers and also identified a few misconceptions. In spite of these advances, the mesosomal anatomy of scorpions remains poorly known. Further study is needed to assess the extent of intraspecific variation in these organs, and to further enlarge the taxon sample at the generic level. Just as male hemispermaphores are increasingly included in taxonomic descriptions and phylogenetic analyses on scorpions, we hope that this contribution will inspire the inclusion of more characters from the internal anatomy of scorpions.

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- York, NY, USA; AVG, Alexander V. Gromov Private Collection, Almaty, Kazakhstan; CAS, California Academy of Sciences, San Francisco, CA, USA; ESV, Erich S. Volschenk Private Collection, Brisbane, Australia; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA; QM, Queensland Museum, Brisbane, Australia; USNM, US National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; WAM, Western Australian Museum, Perth, Australia; ZMB, Museum für Naturkunde der Humboldt-Universität, Berlin, Germany.

## BOTHRIURIDAE SIMON, 1880

*Brachistosternus intermedius* Lönnberg, 1902: 1 ♀ AMNH (ESV7135), 19 km N Humahuaca, Jujuy Province, Argentina, 23°02'15.4"S 65°22'53.7"W, 3150–3500 m a.s.l., 5.i.2005, C. Mattoni & A. Ojanguren.

*Lisposoma josehermana* Lamoral, 1979: 1 ♀ AMNH (ESV7628), Farm Variante on Elandshoek 771, Tsumeb District, Oshikoto Region, Namibia, 19°22.773'S 17°44.456'E, 1500 m a.s.l., 4.i.2004, L. Prendini, E. Scott, T. & C. Bird, Q. & N. Martins.

*Timogenes elegans* (Mello-Leitão, 1931): 1 ♀ AMNH, Camping Oasis, Las Grutas, Río Negro Province, Argentina, 40°46'8.9"S 65°2'21.4"W, 14 m a.s.l., 11.i.2005, M. Magnanelli & E.G. Lopez.

*Urophonius granulatus* Pocock, 1898: 1 ♀ AMNH (ESV7338), Destacamento Policial Las Sierras, SW Pico Truncado, Santa Cruz Province, Argentina, 47°18'14.2"S 68°31'57.7"W, 232 m a.s.l., 16.i.2005, M. Magnanelli & E.G. Lopez.

## BUTHIDAE C.L. KOCH, 1837

*Ananteris platnicki* Lourenço, 1993: 1 ♀ AMNH (LP 6100), Reserva Biológica 'Hitoy Carere', Limón, Cahuita, Limón Provincia, Costa Rica, 09°40'18"N 83°01'30"W, 95 m a.s.l., 17–18.v.2006, V. Vignoli, C. Viquez & H. Ajuria.

*Androctonus amoreuxi* (Audouin, 1826): 1 ♀ AMNH (ESV7321), 22 km N Ourosogui, Senegal, 15°47'59.3"N 13°26'30.6"W, 52 m a.s.l., 6.vii.2005, J. Huff & V. Vignoli.

*Androctonus australis* (Linnaeus, 1758): 1 ♀ AMNH (ESV7137), Medira, Algeria, Spring 1969.

*Babycurus jacksoni* (Pocock, 1890): 1 ♀ AMNH (ESV7437), East Usambara Mt., Amani, Tanzania, xi.2006, J. Beraducci.

*Butheoloides monodi* Vachon, 1950: 1 ♀ AMNH (ESV7944), Riverzoo Farm, Bambadinca, Guinea-Bissau, 12°00'09"N 14°53'25.9"W, 28 m a.s.l., 29.vi–2.vii.2005, J. Huff & V. Vignoli.

*Buthus occitanus* (Amoreux, 1789): 1 ♂, 1 ♀ AMNH (ESV7139), 22 km SW Kidira, Senegal, 14°32'22.9"N 12°21'90.6"W, 61 m a.s.l., 5.vii.2005, J. Huff & V. Vignoli.

## APPENDIX: MATERIAL EXAMINED

Where specimens possess a museum catalog number, that number is documented. For specimens without institutional catalog numbers, an Erich S. Volschenk registration (ESV) number, corresponding to the first author's database of material examined, is provided in parentheses following the institutional abbreviation. ESV numbers without parentheses are from specimens in the private collection of ESV. All specimens given ESV numbers possess the same number printed on a small card with the specimens.

The museum abbreviations used are as follows: AMNH, American Museum of Natural History, New

*Centruroides exilicauda* (Wood, 1863): 1 ♀ AMNH (ESV7025), 15 mi. W San Ignacio, Baja California Sur, Mexico, 200 ft, 28.vi.1974, T. Lutz & H.L. Stahnke; 1 ♂, 2 ♀ AMNH (ESV7526), Middle March Canyon Road, 2.1 mi. from turnoff to Pearce, towards China Peak, Middle March Canyon, Dragoon Mountains, Coronado National Forest, Cochise County, Arizona, USA, 31°53.644'N 109°58.769'W, 1976 m a.s.l., 23.vi.2006, R. Mercurio & W.E. Savary.

*Centruroides gracilis* (Latreille, 1804): 1 ♀ AMNH (ESV7324), vicinity Cuevos de los Savinos, near Valles, San Luis Potosí, Mexico, 8.iii–4.iv.1946, B.J. Dontzin & E. Runda; 1 ♀ AMNH (ESV7005), 2 mi. NE Comalcalco, Tabasco, Mexico, ii–v.1956, G. Ekholm.

*Grosphus flavopiceus* (Kraepelin, 1900): 1 ♀ AMNH (ESV7339), Nosy Lava, Madagascar.

*Hottentotta hottentotta* Fabricius, 1787: 1 ♀ AMNH (ESV7304), 21 km W Thies, Senegal, 14°46'35.9"N 16°59'16.9"W, 90 m a.s.l., 26.vi.2005, J. Huff & V. Vignoli.

*Isometrus maculatus* (DeGeer, 1778): 1 ♀ CAS (ESV5110), Maui, Hawaii, 12.viii.1972, L. Gomez.

*Microcharmus pauliani ambre* Lourenço, 2006: 1 ♂, 1 ♀ AMNH (ESV7419), Réserve Spéciale d'Ambre, 3.5 km 235° SW Sakaram, Antsiranana Province, Madagascar, 12°28'08"S 49°14'32"E, 26–31.i.2001, B.L. Fisher, C.E. Griswold, *et al.*

*Microtityus consuelo* Armas & Marcano Fondev, 1987: 1 ♂, 1 ♀ AMNH (ESV6087), Parque Nacional Del Este, Track between Ranger Station at Bayahibe and La Tortuga, La Altagracia Province, Dominican Republic, 8.5 m, 18°19'41"N 68°48'10.4"W, 13.vii.2004, E.S. Volschenk & J. Huff.

*Odonturus dentatus* Karsch, 1879: 1 ♀ CAS (ESV5054), 11 mi. N Kajiado, Kenya, 1550 m a.s.l., 20.x.1957, E.S. Ross & R.E. Leech.

*Orthochirus scrobiculosus* (Grube, 1873): 1 ♀ AMNH (ESV7305), c. 10 km E Lebap (Turkmenistan), c. 19 km N Turpakkala, Uchizak Hills, Kyzylkum Desert, Hazorasp District, Uzbekistan, 41°01.673'N 62°00.361'E, 227 m a.s.l., 31.v.2003, L. Prendini & A.V. Gromov.

*Parabuthus granulatus* (Ehrenberg, 1831): 1 ♂, 1 ♀ AMNH (ESV7323), Marienfluss, Opuwo District, Kunene Region, Namibia, 512 m a.s.l., 17°34.637'S 12°33.900'E, 10.i.2004, L. Prendini, E. Scott, T. & C. Bird, Q. & N. Martins.

*Rhopalurus abudi* Armas & Marcano Fondev, 1987: 1 ♀ AMNH (ESV6039), 1 ♀ AMNH (ESV6010), Parque Nacional Del Este, Track between Ranger Station at Boca de Yuma and Punta Faustino, La Altagracia Province, Dominican Republic, 18°21'17.2"N 68.36'52.3"W, 3.25 m a.s.l., 15.vii.2004, E.S. Volschenk & J. Huff.

*Rhopalurus princeps* (Karsch, 1879): 1 ♀ AMNH (ESV6033), Parque Nacional Sierra de Baoruco on road between Rabo de Gato and Duverge, Independencia Province, Dominican Republic, 18°19'37.8"N 71°33'55.4"W, 447 m a.s.l., 7.vii.2004, E.S. Volschenk & J. Huff.

*Rhopalurus rochae* Borelli, 1910: 1 ♀ AMNH (ESV7210), 18 km Exu, Pernambuco, Brazil, 5.iii.1977, L.J. Vitt.

*Uroplectes planimanus* (Karsch, 1879): 1 ♂, 1 ♀ AMNH (ESV7147), Munutum riverbed, at junction with road Orange Drum–Orupembe, Opuwo District, Kunene Region, Namibia, 18°10.882'S 12°24.186'E, 576 m a.s.l., 16.i.2004, L. Prendini, E. Scott, T. & C. Bird, Q. & N. Martins.

*Uroplectes triangulifer triangulifer* (Thorell, 1876): 1 ♀ AMNH (ESV7345), South Africa.

*Zabius fuscus* (Thorell, 1876): 1 ♀ ESV7915, La Granja, Alta Gracia, Córdoba, Argentina, 15–30.i.1924.

#### CHACTIDAE POCOCK, 1893

*Broteochactas delicatus* (Karsch, 1879): 1 ♀ AMNH (ESV7123), Guyana, i.1932, Kamakusa; 1 ♀ AMNH (ESV7641), Manaus, Brazil, 1943, T. Gilliard.

*Brotheas amazonicus* Lourenço, 1988: 1 ♀ AMNH (ESV7136), Manaus, Brazil, ii.1943.

*Chactas aequinoctialis* (Karsch, 1879): 1 ♀ AMNH (ESV7131), Laguna Herrera, Dabana de Bogota, Colombia, 2650 m a.s.l., iv.1958, F. Medem.

#### CHAERILIDAE POCOCK, 1893

*Chaerilus granosus* (Pocock, 1900): 2 ♀ MCZ (ESV7048), Kooloo, Himalaya Mts., India, Carleton.

#### DIPLOCENTRIDAE KARSCH, 1880

*Bioculus comondae* Stahnke, 1968: 1 ♂, 1 ♀ AMNH (ESV7335), c. 10 km SE La Paz on BCS 286 to San Juan de Los Planes, Baja California Sur, Mexico, 24°08.433'N 110°15.333'W, 106 m a.s.l., 9.vii.2005, L. Prendini & R. Mercurio.

*Diplocentrus whitei* (Gervais 1844): 2 ♀ AMNH (ESV7334), Dry Lake Bed, 2.2 mi. NE Punta San Marcos, 5 mi. SW Cuatro Ciénegas, Coahuila, Mexico, 13.viii.1968, M.A. Cazier *et al.*

*Nebo flavipes* Simon, 1882: 1 ♀ AMNH (ESV7212), Wadi Quatam, Jabal Harra, Hatim al Khalidi, Saudi Arabia, 18°12'N 44°05'E, 1500 m a.s.l., 1982, J. Gasparetti.

#### EUSCORPIIDAE LAURIE 1896

*Euscorpius concinnus* (C.L. Koch, 1837): 1 ♀ AMNH (ESV7307), Italy, J.D. Nopp.

## HEMISCORPIIDAE POCOCK, 1893

*Hemiscorpius lepturus* Peters, 1861: 1 ♀ USNM 2035782, 35 km E Gach Saran, Khuzistan Province, Iran, 6.ii.1964, J. Neal.

## HETEROSCORPIONIDAE KRAEPELIN, 1905

*Heteroscorpion goodmani* (Kraepelin, 1896): 1 ♀ AMNH (ESV7211), S.E. Madagascar, ix.1932.

## IURIDAE THORELL, 1776

*Caraboctonus keyserlingi* (Pocock, 1893): 1 ♀ AMNH (ESV7947), Quebrada Huaquen, 2 km from Huaquen, Provincia de Petorca, Region V (Valparaiso), Chile, 32°19.758'S 71°24.954'W, 21 m a.s.l., 11.xi.2003, C. Mattoni, L. Prendini & J. Ochoa.

*Hadruroides charcasus* (Karsch, 1879): 1 ♀ AMNH (ESV7942), Top of Quebrada Honda, c. 1/2 mi. above and below Oky Well, near Talara, Peru, 10.v.1981, J. Boos.

*Hadrurus arizonensis arizonensis* Ewing, 1928: 1 ♀ AMNH (ESV7231), Crater Mts., 20 mi. NW Ajo, Yuma County, Arizona, USA.

*Iurus dufourei asiaticus* (Brullé, 1832): 1 ♀ ZMB (ESV7928), Turkey.

## LIOCHELIDAE FET AND BECHLY, 2001

*Hadogenes hahni* (Peters, 1862): 1 ♀ AMNH (ESV7240), Farm Uisib 427, 15 km NW Otavi, Grootfontein District, Otjozondjupa Region, Namibia, 19°33.132'S 17°14.124'E, 1293 m a.s.l., 2.ii.2004, L. Prendini, E. Scott, T. & C. Bird, Q. & N. Martins.

*Liocheles australasiae* (Fabricius, 1775): 1 ♀ AMNH (ESV7810), Wandumi, Wau Valley, Morobe District, NE New Guinea, 15.xii.1968, R.C.A. Rice.

*Liocheles waigiensis* (Gervais 1843): 1 ♀ AMNH (ESV7337), New Caledonia, iii-iv.1939, L. Macmillan.

*Opisthacanthus validus* Thorell, 1876: 1 ♂ AMNH (ESV5713), 1 ♀ AMNH (ESV7922), South Africa.

## PSEUDOCHACTIDAE GROMOV, 1998

*Pseudochactas ovchinnikovi* Gromov, 1998: 3 ♀ AMNH (ESV7331, ESV7919, and ESV7608), Dikhana Canyon, foothills of E slope of Babatag Mountain range, c. 5 km WSW Ochmachit (Akmechet) Village, Uzun District, Surkhandarya Area, Uzbekistan, 38°01.638'N 68°15.198'E, 722 m a.s.l., 20-24.v.2003, L. Prendini & A.V. Gromov; 2 subad. ♂ AVG (ESV7601), Dikhana Canyon, foothills of E slope of Babatag Mountain range, 5-6 km WSW Akmechet Village, Uzun District, Surkhandarya Area, Uzbekistan, 38°02'01"N 68°14'03"E, 730-870 m a.s.l., 4.v.2002, A.V. Gromov.

## SCORPIONIDAE LATREILLE, 1802

*Opisthophthalmus cavimanus* Lawrence, 1928: 1 ♀ AMNH (ESV7333), 4 km W Rooidrum, Opuwo District, Kunene Region, Namibia, 17°48.131'S 12°30.584'E, 896 m a.s.l., 11.i.2004, L. Prendini, E. Scott, T. & C. Bird, Q. & N. Martins.

## SCORPIOPIIDAE KRAEPELIN, 1905

*Euscorpions longimanus* Pocock, 1893: 1 ♀ AMNH, Thailand, B. & A. Steele.

## SUPERSTITIONIIDAE STAHNKE, 1940

*Superstitionia donensis* Stahnke, 1940: 1 ♀ AMNH (ESV7328), Upper Campground, Molino Basin Station, Catalina Mts., 4400 ft, Pima County, Arizona, USA, 29-30.iii.1975, E. Minch.

## TROGLOTAYOSICIDAE LOURENÇO, 1998

*Belisarius xambeui* Simon, 1879: 1 ♀ AMNH (ESV6007), Haut Vallespir, D54 to Montferrer, Klein Geröllhalde, 24°27.120'N 2°36.191'E, 1305 ft, Pyrenées-Orientales, France, 5.vii.2003, S. Huber.

## URODACIDAE POCOCK, 1893

*Urodacus planimanus* Pocock, 1893: 1 ♀ ESV7920, Jarrahdale, near Alcoa mine site, Western Australia, Australia, ix.1999, E.S. Volschenk & K.E.C. Brannan.

*Urodacus spinatus* Pocock, 1902: 1 ♀ ESV7946, James Cook University Campus, Townsville, Queensland, Australia, 5.v.1996, E.S. Volschenk.

*Urodacus* sp.: 1 ♀ QM S48432, Oakwells, W of Injune, Queensland, Australia, 21.ix.2002, C. Eddie & B. Cosh.

## VAEJOVIDAE THORELL, 1876

*Smeringurus mesaensis* (Stahnke, 1957): 1 ♀ AMNH (ESV7925), Algodones Dunes, Junction of Ogilby Rd (S34) and Interstate Hwy 8, Imperial County, California, USA, 32°45.454'N 114°50.203'W, 50 m a.s.l., 31.viii.2005, R. Mercurio & L. Prendini; 1 ♀ AMNH (ESV7145), City Dump, 2.5 mi N Sumer-ton, Yuma County, Arizona, 14.viii.1969, J. Bigelow.

*Uroctonus mordax* Thorell, 1836: 1 ♀ AMNH (ESV7325), McAllister Soda Spring, Jackson County, Oregon, 3000 ft, 4.vii.1946, B. Malkin & V.E. Thatcher; 1 ♀ AMNH (ESV 7442), Ashland, Oregon, 17.vii.1943, H.A. Scullen.

*Vaejovis spinigerus* (Wood, 1863): 1 ♀ AMNH (ESV7207), Canyons, Sonoita Ranch, 4 mi. S Patago-nia, Santa Cruz County, Canyon, Arizona, USA, 24.iii.1970, 4000 ft, O.F. Francke, M.A. Cazier & J. Bigelow.