VENTRAL MESOSOMAL CHANGES IN EMBRYOS FROM THREE SCORPION FAMILIES: IURIDAE, BUTHIDAE AND VAEJOVIDAE

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ABSTRACT. The scanning electron microscope was used to examine embryos at a stage when booklungs and spiracles are forming. Earlier studies with scorpion fossils suggest there was ventral mesosomal transition from gills or booklungs above ventral plates to sternites, booklungs and spiracles. In Hadrurus arizonensis (Iuridae), ventral plates and then sternites are formed on the ventral surface of mesosomal segments before spiracles appear. Bilateral invaginations in body segments XII–XV apparently give rise to the booklungs, with spiracles formed lateral to the site of invagination. Sternites with bilateral depressions were also present before spiracles in embryos of the buthid Centruroides exilicauda. In the developmental stages herein examined, spiracles were formed in embryos of Paruroctonus mesaensis (Vaejovidae); but there was no indication of ventral plates or sternites on the ventral mesosoma. Spiracles appear in the intersegmental area posterior to body segments XIII–XV. Booklungs may form later from primordia associated with bilateral depressions observed in a later stage in these segments.

METHODS

The composition of physiological saline and the procedures for collection and maintenance of specimens were described in an earlier publication (Farley 1987). Specimens of Paruroctonus mesaensis Stahnke 1957 were collected in the Colorado Desert near Indio and Palm Springs, California. Specimens of Hadrurus arizonensis Ewing 1928 (Williams 1970; Francke & Soleglad 1981) and Centruroides exilicauda Wood 1863a (Wood 1863b; Ewing 1928; Williams 1980) were collected in Arizona. Specimens of all three species are in the California Academy of Science, San Francisco.

Tissues were flushed with saline to remove debris as animals were dissected with microscissors and forceps. The ovariuterine tubules were opened and embryos removed. Surrounding membranes (amnion, serosa) were pulled away with microprobe and forceps.

Tissues were fixed (6–10 h, 23–25 °C) with 4% glutaraldehyde in 0.1 M cacodylate buffer with one drop of calcium chloride for each 10 ml of solution (Lane et al. 1981). The tissues were washed in cacodylate buffer-NaCl solution and postfixed (2 h, 23–25 °C) in 1% osmium tetroxide in 0.2 M cacodylate buffer with NaCl. The concentrations of these solutions were adjusted to approximate the os-
molarity of scorpion blood (630 mOsm; Yokota 1984). Tissues were dehydrated in acetone, critically-point dried (Balzers, CDD 020) and sputter-coated (EMscope SC500) with 20 nm thickness of gold/palladium. Tissues were examined at 12–15 KV with a Philips 15 scanning electron microscope (SEM).

RESULTS
At a stage before spiracle and booklung formation, embryos of H. arizonensis have plates demarcated on the ventral surface of mesosomal segments. Initially, only a narrow ridge outlines the ventral plates, with the delineated region much smaller than the ventral surface of the segment. The outlined region becomes a flap-like structure (Fig. 1) fused to the body wall anteriorly but free at the lateral and posterior margins. The early ventral plates do not extend the full width of the mesosoma nor overlap antero-posteriorly. Embryos were not sectioned, but no indications of an opening or gill-like structures were observed at the posterior margin of the ventral plates. Paired indentations in body segments XII–XV (Hjelle 1990) are presumably booklung primordia.

In later stages, the invaginations in segments XII–XV become more prominent (Fig. 2), and the ventral cuticle increases in length and width, forming structures that resemble adult sternites with the perimeter joined to pleural or intersegmental integument. The sternites extend the full width of the mesosoma and overlap in the longitudinal axis. Intrasternal spiracles eventually form at the adult location (Farley 1990a, b), just lateral to the site of booklung invagination. Booklungs do not develop in segment XVI; paired indentations in body segments XII–XV (Hjelle 1990) are presumably booklung primordia.

DISCUSSION
In H. arizonensis and C. exilicauda, booklung and spiracle formation appears to be like that described by earlier workers in species from the families Buthidae (Abd-el Wahab 1951), Chactidae (Laurie 1890; Brauer 1895) and Scorpionidae (Metschnikoff 1871; Laurie 1892). The bilateral depressions evident in mesosomal segments in Figs. 1–3 appear to be sites of invagination, and spiracles are later formed here at the location seen in adults (Farley 1990a, b). The early demarcation of flap-like structures (Fig. 1) supports the notion that ventral plates preceded (Kjellesvig-Waering 1986) or occurred with booklungs in ancient scorpions (Selden & Jeram 1989; Jeram 1990).

Differences were reported among scorpion species in the shape and texture of the cuticle of adult booklung lamellae (Lankester 1885; Berteaux 1889; Laurie 1896a, b). These were proposed as taxonomic criteria, but other features subsequently found acceptance (Stock-
Figures 1, 2.—SEMs of ventral surface of mesosoma of embryos of *Hadrurus arizonensis*. 1. Flap-like ventral plates (P) are fused to the body wall anteriorly and free at the posterior margin. Bilateral invaginations (arrows) are present where spiracles and booklungs will eventually form. Teeth (T) are evident at the posterior edge of the pectines. XIV, body segment; 2. Later stage. The ventral cuticle of each segment has broadened and is now a sternite (S) attached around the entire perimeter. Bilateral invaginations (black arrows) have deepened. Shallow depressions occur in body segment XVI, but booklungs do not develop in this segment. The white arrow indicates a pair of small, transitory appendages of unknown significance between gonopore and pectine. A, remnants of amnion not removed during preparation; T, pectinal teeth. Scales, 0.5 mm.
Figures 3, 4.—SEMs of ventral surface of mesosoma of embryos. 3, *Centruroides exilicauda*. Each segment has a sternite (S) like that of the irurid embryo of Figure 2. Bilateral invaginations (arrows) are presumably the site of booklung formation. Depressions are evident in body segment XVI although booklungs do not form in this segment. L, fourth walking leg. T, pectinal teeth. Scale, 0.5 mm; 4, *Paruroctonus mesaensis*, left side of ventral mesosoma. No ventral plates or sternites are evident, but spiracles (arrows) are present at the posterior margin of body segments XIII–XV. The spiracles are at the medial end of an invaginated intersegmental region (⋆) with vertical striations. L, fourth walking leg. Scale, 0.2 mm.
well, 1989, 1992; Sissom 1990). Developing booklungs were previously described as bilateral invaginations in the ventral mesosoma (Metschnikoff 1871; Laurie 1890, 1892; Brauer 1895; Abd-el Wahab 1951). Tissue sections showed that sac-like invaginations extend anteriorly in the segment from the initial site of ingress, which remains open to become the spiracle. A few lamellae are initially formed in the horizontal plane. These later rotate 90° to the dorso-ventral axis, along with development of many more lamellae (Laurie 1890, 1892).

There may be absence or delay of ventral plates, and sternites may form late in embryos of *P. mesaensis* in comparison with the iurid and buthid embryos. Among scorpion families, heterochrony occurs in embryogenesis in relation to the mode of maternal nourishment of the embryos (Matthew 1959; Farley 1999a, b). All extant scorpions have adaptations for terrestrialization (*i.e.*, oral tube, booklungs, latterly compressed podomeres), but may be polyphyletic with convergent evolution (Jeram 1994). The possibility of a different vaejovid derivation is raised in the present studies by the delay or absence of ventral plates (Fig. 4) and the development of spiracles at the medial end of lateral intersegmental specializations that may be indicative of ancestral respiratory structures. Fossils of British Triassic scorpions have slit-like spiracles in the intersegmental membrane of mesosomal segments or in the latero-posterior margin of the abdominal plates (Wills 1947).

Tissue sections are needed to determine if booklung formation is also distinctive in *P. mesensis*. The lack of tissue invagination at the place where spiracles first appear in the intersegmental area (Fig. 4) suggests this is not the site of booklung primordia. These spiracles may migrate from the intersegmental area to the adult position more anterior and lateral in the segment (Farley 1990a, b). Another possibility is that the early spiracles in Fig. 4 are transitory, and new spiracles form later with booklungs more anterior in the segments.

Kjellesvig-Waering (1986) proposed that ventral plates were abdominal flaps or appendages that overlay the body wall beneath, and sternites developed as the abdominal plates were reduced and eventually lost. From their review of fossil evidence, Selden & Jeram (1989) considered it more likely that ventral plates later became sternites by fusion with the body wall. The latter proposal is supported in the present study in embryos of *H. arizonensis*. Small regions, initially outlined by a ridge on the ventral surface of mesosomal segments, become flap-like plates (Fig. 1) and then the ventral cuticle is broadened to form sternites (Fig. 2). There was no indication of reduction or loss of the ventral plates, resulting in exposure of overlying sternites.

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**LITERATURE CITED**


