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ORIGINAL ARTICLE

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Characters in the book lungs of Scorpiones (Chelicerata, Arachnida) revealed by scanning electron microscopy

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Abstract The fine structure of the book lungs in 29 species representing ten monophyletic taxa of the Scorpiones (Arachnida) was investigated using scanning electron microscopy (SEM). Scorpion lungs are not homogeneous across the group. Here we describe and score three sets of phylogenetically informative characters: (1) the surface ornament of the lung lamellae, (2) the distal margins of the lamellae and (3) the fine structure of the spiracle margin. Provisional results suggest that reticulation on the surface of the lung lamellae is characteristic of the Buthidae. By contrast, non-buthid scorpions maintain the air space between adjacent lamellae using projecting trabeculae. Typically they are simple struts, but the trabeculae are distally branched in all investigated Scorpionidae, plus at least one species belonging to the Liochelidae. Simple thorns on the lamellar margins probably represent the plesiomorphic condition, while more complex, branched, arcuate morphologies appear to be homoplastic, occurring sporadically in numerous scorpion sub-groups. The tightly packed, hexagonal pillars around the posterior margin of the spiracle support a close relationship between Scorpionidae and Liochelidae, to the exclusion of the Urodacidae.

Keywords Book lungs · Spiracles · Lamellae · Scorpiones · Chelicerata · Phylogeny

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Introduction

Book lungs are the characteristic respiratory organs of many species of Arachnida, occurring in the Scorpiones and the Tetrapulmonata (i.e. spiders and their immediate relatives, cf. Weygoldt and Paulus 1979; Shultz 1990). The fine structure of these organs in Aranea is known in some detail thanks largely to light and scanning electron microscopy (SEM) studies (e.g. Moore 1976; Hexter 1982; Strazny and Perry 1987; Reisinger et al. 1990, 1991; Schmitz and Perry 2000). By contrast, scorpion lungs have received rather less attention and most of our present knowledge stems from older descriptions based on dissections and light microscopy only; summarised in Hjelle (1990) and Farley (2001). These are supplemented by brief accounts of *Heterometrus fluvipes* (C.L. Koch, 1837) lungs (Vyas 1974) and various taxa examined by Rödl et al. (1989); both of whom carried out cursory SEM work.

In this paper we offer the first detailed SEM study of book lungs and their associated spiracles in Scorpiones. Scorpion lungs are not homogenous across the group and significant differences can be recognised in terms of: (1) the surface ornament of the lung lamellae, (2) the distal margins of the lamellae and (3) the fine structure of the spiracle margin. Some of these characters have been noted previously (e.g. Berteaux 1889; Laurie 1896a, 1896b; Pavlovsky 1926; Rödl et al. 1989), and even proposed as taxonomic characters. For example Laurie (1896a) provisionally recognised higher taxa defined by ‘spinous’, ‘arcade’ and ‘reticulate’ types of book lung (see Discussion).

With the exception of the reticulate lamellar surfaces in Buthidae (cf. Stockwell 1989), the significance of lung characters for higher level systematics has been largely overlooked in the recent literature (e.g. Prendini 2000, 2003; Soleglad and Fet 2003). The latter authors scored the shape of the lung spiracle, but did not recognise characters in its marginal structure or in the lung lamellae themselves. Here, we identify, describe and figure a series of informative character states for the scorpion lungs and their spiracle margins and present a broad overview of the distribution of these characters based on 29 species in ten monophyletic groups. Further work is evidently needed to score the lungs across all higher taxa in Scorpiones, but our provisional data offers support for a number of monophyletic groupings, while for other taxa potential character conflicts have been recognised.

Materials and methods

SEM was used to compare the book lungs of 28 species taken from the alcohol collections of the Museum für Naturkunde, Berlin (MfN; specimens listed under the repository acronym ZMB) plus one captive-bred example (*Euscorpius carpathicus candiota* Birula, 1903) from the Institut für Biologie, Vergleichende Zoologie (see Table 1).

Sternites were dissected out and the book lungs separated from the overlying midgut diverticulum. Following critical point drying (BAL-TEC CPD 030), the lungs were sectioned sagittally, and sputter-coated up to three times (180 s) with gold (BAL-TEC SCD 005). Specimens of *Brotheas gervaisii* Pocock, 1893, *Cheloctonus jonesii* Pocock, 1893, *Chiromachus ochropus* (C.L. Koch, 1837), *Isometrus maculatus* (DeGeer, 1778), *Lychas scutilus* C.L. Koch, 1845, *Scorpiops petersi* Pocock, 1893 and *Uroplectes occidentalis* Simon, 1876 were sputter-coated using gold-paladium (Polaron SC 7640). Species investigated are listed in Table 1 with familial assignments according to Soleglad and Fet (2003).

Results

Gross morphology

Scorpion book lungs (Fig. 1) occur in pairs on the ventral side of the fourth to the seventh opisthosomal segments and open through narrow spiracles (or stigmata) midway along the sternites (Fig. 1). Each spiracle leads into an atrium (Fig. 1a) with a folded internal surface which is, for the most part, covered by small cuticular projections or warts (Fig. 1d). The main respiratory element of the lungs is made up by many adjacent, leaf-like lamellae projecting from a haemolymph sinus into the atrium (Fig. 1a). These lamellae consist of thin, cuticular epithelia for gas exchange, formed into flat, double-sided sheets.

Within the haeomolymph sinus the lamellae are stabilised by cellular pillars, typically of two epithelial cells, connecting both opposing lamella walls. The air spaces

Table 1 Summary of the occurrence of book lung characters and their states in 29 investigated scorpion species

Supraspecific taxa			investigated species	ZMB-No.	surface of lamellae	edge of lamellae	edge of spiraculum
Buthida	Buthoidea	Buthidae	*Androctonus amoreuxi* (Audouin, 1826)	30909	3	3	2
			Hottentotta hottentotta (Fabricius, 1787)	–	3	3	1
			Isometrus maculatus (DeGeer, 1778)	8199	3	3	1
			Uroplectes occidentalis Simon, 1876	7599	3	4	1
			Lychas scutilus C.L. Koch, 1845	11341	3	4	1
			Centruroides margaritatus (Gervais, 1841)	–	3	4	2
			Tityus cf. *clathratus* C.L. Koch, 1844		3	4	2
			Grosphus flavopiceus Kraepelin, 1900	10383	3	4	2
Iurida	Iuroidea	Iuridae	*Iurus dufoureius* (Brullé, 1832)	7497	1	5	6
		Carboctonidae	*Hadrurus* cf. *hirsutus* (Wood, 1863)	15220	1	1	4
	Scorpionoidea	Scorpionidae	*Scorpio maurus* Linnaeus, 1758	–	2	1	7
			Heterometrus longimanus (Herbst, 1800)	30849	2	1	7
			Opisthophthalmus carinatus (Peters, 1861)	–	2	1	7
			Pandinus viatoris (Pocock, 1890)	15056	2	1	7
		Liochelidae	*Chiromachus ochropus* (C.L. Koch, 1837)	15169	2	1	7
			Opisthacanthus lecomtei Lucas, 1858		1	1	7
			Cheloctonus jonesii Pocock, 1892	35141	1	2	7
			Hadogenes cf. *paucidens* Pocock, 1896	7465	1	2	7
			Liocheles sp.	30838	1	6	6
		Urodacidae	*Urodacus manicatus* (Thorell, 1876)	2392	1	1	1
		Bothriuridae	*Bothriurus* cf. *bonariensis* (C.L. Koch, 1842)	15381	1	2	1
			Bothriurus coriaceus Pocock, 1893	8322	1	1	5
			Timogenes dorbignyi (Guérin Méneville, 1843)	31130	1	2	2
			Centromachetes pocockii (Kraepelin, 1894)	35145	1	1	3
	Chactoidea	Chactidae	*Brotheas gervaisii* Pocock, 1893	15360	1	1	6
			Uroctonus mordax Thorell, 1876	14909	1	6	1
		Euscorpiidae	*Euscorpius carpathicus candiota* Birula, 1903		1	6	1
			Scorpiops petersi Pocock, 1893	3063	1	1	1
		Vaejovidae	*Vaejovis intrepidus cristimanus* Pocock, 1898	15221	1	2	2

Taxonomy follows Soleglad and Fet (2003); ZMS-No. refers to specimens deposited at the Museum für Naturkunde, Berlin)

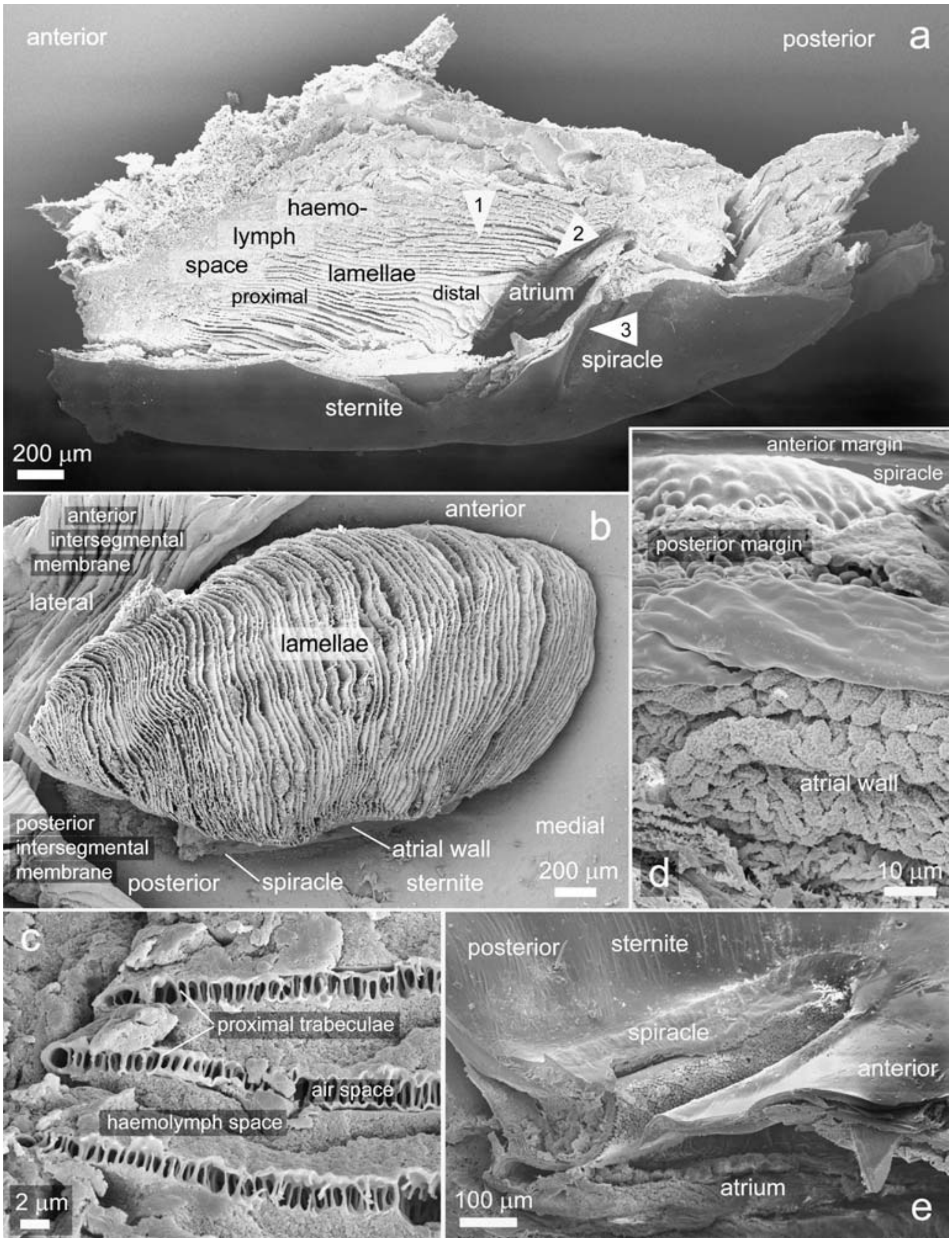

Fig. 1 Gross morphology of scorpion book lungs, SEM-images. **a** Overview of a scorpion lung showing the positions of the three characters (*arrowed*: 1-distal lamellar surface, 2-lamellar margin, 3-posterior spiracle margin) investigated here—longitudinal section, **b** dorsal view onto the cuticular parts of the book lung, **c** proximal region of the lamella showing the interconnecting trabeculae between the lamellae, **d** view onto posterior atrial wall and spiracle, **e** spiracle, **a** and **e** *Opistophthalmus carinatus*, **b** *Iurus dufoureius*, **c** and **d** *Euscorpius carpathicus candiota*

between the lamellae connect to the atrium and are protected from collapsing by diverse cuticular structures (spines or veins; see below). However, in all scorpions investigated the proximal regions of the lamellae, are protected from collapsing by cuticular spines, or trabeculae, which stand at a regular distance from each other. These proximal trabeculae are attached perpendicularly to the opposing sides of adjacent lamellae, such that the distance between the lamellae remains constant. The two ends of these proximal trabeculae are equal in size, and broadly merge into the lamellar surface (Fig. 1c). Together, this mass of trabeculae forms a rigid composite at the proximal region of the lung in order to maintain the air space.

Distal lamellar surface

Character states: 1—simple trabeculae, 2—branched trabeculae, 3—reticulate veins

In non-buthid scorpions the entire surface of the lamellae—and not just the proximal region (see above)—is covered by spine-like trabeculae (Fig. 2a, b). At regular distances these spines hang nearly perpendicular down into the air space from the ventral surface of each lamella, separating adjacent lamellae from one another. Their shape is consistently thin and rodlike and at their base the trabeculae merge smoothly into the cuticle of the lamellae from which they originate. Thin folds running from the base of the trabeculae onto the lamella surface appear as tiny struts or stabilising buttresses. Except in buthids (see below), the dorsal surface of the lamellae is almost smooth to lightly folded and lacks sculpture or ornament.

Most of the investigated scorpions (Table 1) have ‘simple trabeculae’ (character state 1) which take the form of thin rods with a more or less distinctive knob-like terminus (Fig. 2a). However, in all Scorpionidae studied and in *Chiromachus ochropus* (Liochelidae), the trabeculae are distally ‘branched’ (character state 2, Fig. 2b). Two to five branches, approximately equal in length to the trabecula itself, radiate almost perpendicularly from the tip; the whole structure resembling the supports of an umbrella.

In all studied Buthidae there are proximal trabeculae as in other scorpions, but distal trabeculae are lacking. Instead, both the dorsal and ventral sides of the buthid lamellae are covered by an uneven system of branching and merging ‘reticulate veins’ (character state 3; Fig. 2c). The main orientation of these veins is from the proximal region towards the distal margin of the lamellae.

Lamellar margins

Character states: 1—bristly, 2—spiny, 3—thorny, 4—smooth, 5—meandering, 6—arcuate bows

The distal margins of the lamellae in scorpions are mostly covered by thorn-like spines. When present, these marginal spines are generally more than 1.5 times longer than the trabeculae on the lamellar surfaces and in the material studied six different types of marginal ornament could be recognised. In all studied species of Scorpionidae, the one species of Urodacidae, and in some species of the Bothriuridae, Chactidae and Euscorpiidae investigated, the lamellar margins are ‘bristly’ (character state 1: Fig. 3a), and the projections can be relatively soft and slightly curving. In two Liochelidae, two Bothriuridae and the one Vaejovidae investigated the margins are ‘spiny’ (character state 2: Fig. 3b) where, by contrast, the projections form highly rigid spikes. In general, weakly bent spines stand much more densely at the lamellar margin compared to rigid ones.

Three buthid taxa, *Androctonus amoreuxi* (Audouin, 1826), *Hottentotta hottentotta* (Fabricius, 1787) and *Isometrus maculatus* (DeGeer, 1778), have ‘thorny’ (character state 3: Fig. 3c) margins in which short, robust thorns with a distinctly broad base are strung out along the lamellar margins. Of these, *I. maculatus* shows spines at the lamellar margins which are shortened and appear only infrequently. The remaining buthids (Table 1) lack spines altogether and their ‘smooth’ (character state 4: Fig. 3d) lamellar margins show at best a undulating morphology. In buthid lungs the surface veining (see below) frequently merges into a single vein that winds its way along the lamellar margin.

Iurus dufoureius (Brullé, 1832) has a uniquely ‘meandering’ (character state 5: Fig. 3e) morphology in which cuticular bulges wind their way along the lamellar

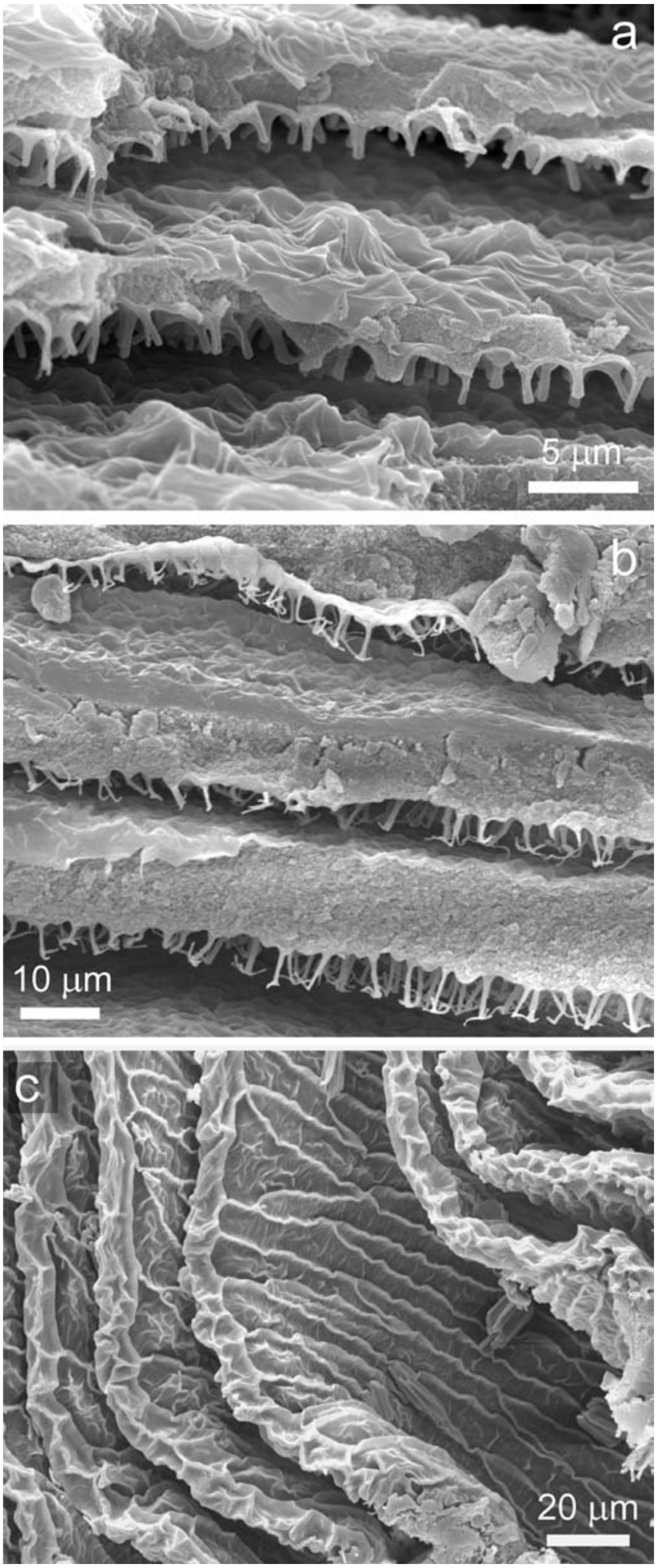

Fig. 2 Distal surface of book lung lamellae, SEM-images. **a** character state 1- ‘simple trabeculae’ *Euscorpius carpathicus candiota*, ventral lamella surface. **b** character state 2- ‘branched trabeculae’ *Opistophthalmus carinatus*, view of sectioned lamellae, trabeculae on the ventral side. **c** character state 3- ‘reticulate veins’ *Lychas scutilus*, view of some lamellae

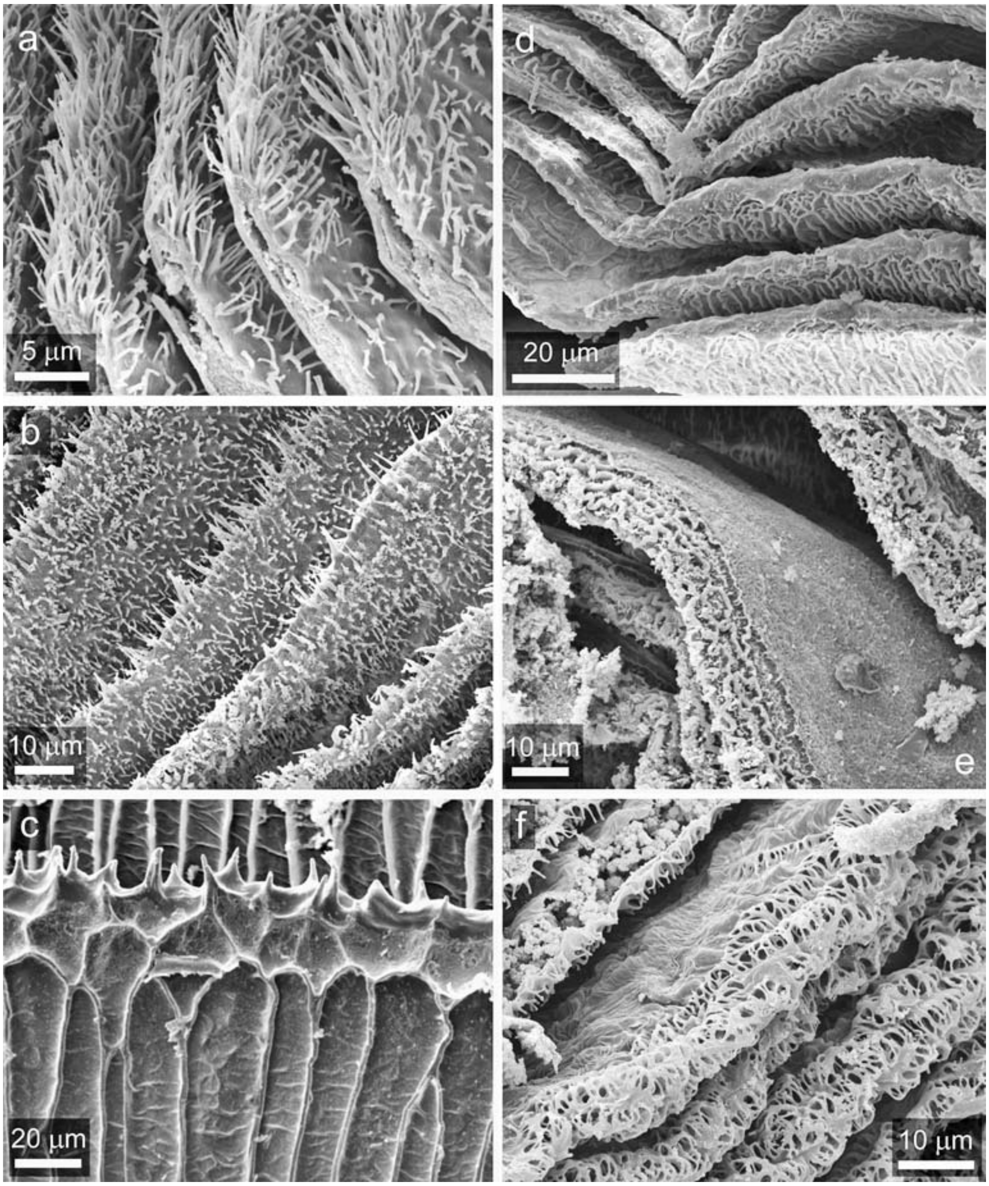

Fig. 3 Margins of book lung lamellae, SEM-images. **a** character state 1- 'bristly' *Opistophthalmus carinatus*, lateral view of sectioned book lung, lamella margins are directed to the atrium. **b** character state 2- 'spiny' *Timogenes dorbignyi*, ventral view of lamella margins. **c** character state 3- 'thorny' *Androctonus amoreuxi*, ventral view of one lamella margin. **d** character state 4- 'smooth' *Tityus cf. clathratus*, view of book lung lamellae directed towards the atrium. **e** character state 5- 'meandering' *Iurus dufoureius*, view of lamella margins. **f** character state 6- 'arcuate bows' *Euscorpius carpathicus candiota*, view of lamella margins

margin, surrounding slender areas with small cuticular spines in the central regions. In this species, thin folds form struts from the bulges to the basal surface. Finally, in *Liocheles* sp. Sundevall, 1833, *Uroctonus mordax* Thorell, 1876 (Chactidae) and *Euscorpius carpathicus candiota* (Euscorpiidae) the cuticular spines grow outwards and merge together into distinctive 'arcuate bows' (character state 6: Fig. 3f). These anastomosing branches interconnect to form a complex vault system, extending all the way along the lamellar margin.

Posterior spiracle margin

Character states: 1—hillocks, 2—sub-conical, 3—hair-like, 4—flattened, 5—scaly, 6—chisel-like, 7—hexagonal pillars

To open the spiracle the posterior margin is drawn away from the anterior by two muscles (Fraenkel 1930), although proactive ventilation of the lungs has not been reported (e.g. Farley 1990). In most scorpions this posterior spiracular margin is strengthened by a somewhat thicker, modified cuticle (Rödl et al. 1989). In detail, this region is covered by minute projections, of which seven different microstructures could be recognised here in the taxa studied (Table 1).

Half the Buthidae studied, both the investigated Euscorpiidae, *Uroctonus mordax*, *Bothriurus* cf. *bonariensis* (C.L. Koch, 1842) and *Urodacus manicatus* (Thorell, 1876) have spiracle margins bearing flat to slightly rounded structures which we term 'hillocks' (character state 1; Fig. 4a). In the remaining buthids, in *Timogenes dorbignyi* (Guérin Méneville, 1843) and *Vaejovis intrepidus cristimanus* Pocock, 1898 slender, tapering 'sub-conical' (character state 2; Fig. 4b) projections cover the posterior margin. The precise shape of these varies across and along the spiracle margin. *Centromachetes pocockii* (Kraepelin, 1894) (Bothiuridae) uniquely expresses

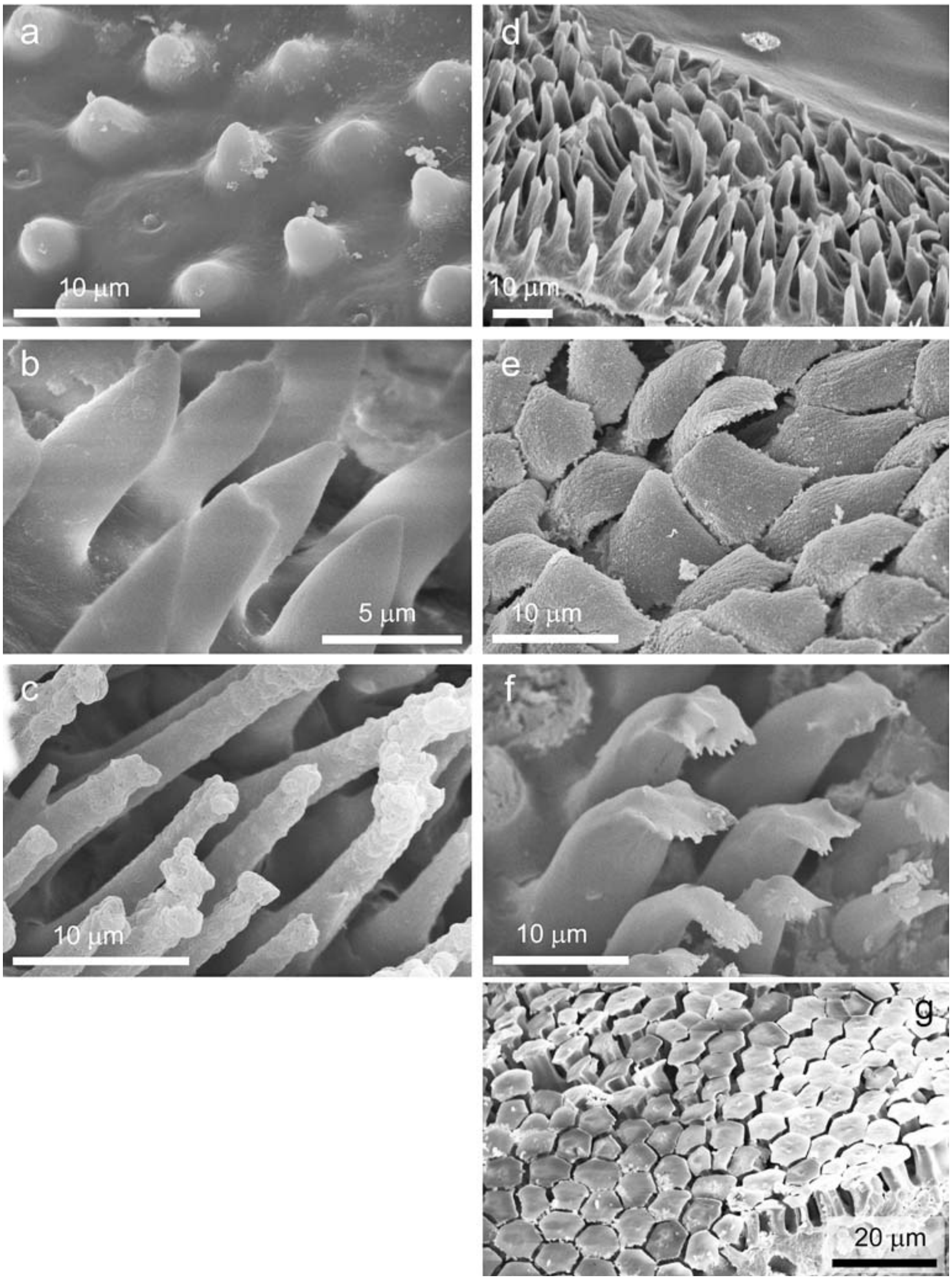

Fig. 4 Posterior margins of the spiracles, SEM-images. **a** character state 1- 'hillocks' *Hottentotta hottentotta*, cuticular structure on the posterior margin of the spiracle. **b** character state 2- 'sub-conical' *Centruroides margaritatus*, structures of the posterior margin of the spiracle. **c** character state 3- 'hairlike' *Centromachetes pocockii*, view of the spiracle. **d** character state 4- 'flattened' *Hadrurus cf. hirsutus*, cuticular structure on the posterior margin of the spiracle. **e** character state 5- 'scaly' *Bothriurus coriaceus*, structures of the posterior margin of the spiracle. **f** character state 6- 'chisel-like' *Liocheles* sp., structures of the posterior margin of the spiracle. **g** character state 7- 'hexagonal pillars' *Opistophthalmus carinatus*, cuticular structure on the posterior margin of the spiracle

extremely long, 'hairlike' (character state 3; Fig. 4c) outgrowths.

In *Hadrurus* cf. *hirsutus* (Wood, 1863) the projections are uniquely lobe-like and 'flattened' (character state 4; Fig. 4d). The posterior spiracular margin of *Bothriurus coriaceus* Pocock, 1893 is covered by adjacent, overlapping 'scaly' (character state 5; Fig. 4e) cuticle. In *Iurus dufoureius*, *Liocheles* sp. Sundevall, 1833 and *Brotheas gervaisii* there are slender, tapering projections which are flattened at the top to form a broad 'chisel-like' (character state 6; Fig. 4f) margin in which the flattened region is angled slightly downwards. Finally, in all Scorpionidae and almost all Liochelidae (except our *Liocheles* sp.) investigated the cuticular projections are upright prisms with a clearly hexagonal base. These 'hexagonal pillars' (character state 7; Fig. 4g) generally have flat, broadened tops, which together build up an almost closed, facetted surface; resembling a honeycomb.

Discussion

Lung characters and scorpion phylogeny

Relationships among recent Scorpiones, or Orthosterni, are still largely in a state of flux (cf. Lamoral 1980; Stockwell 1989; Soleglad and Fet 2003). There has been a substantial increase in the number of suprageneric taxa recognised in recent years and Soleglad and Fet (2003), in particular, proposed a number of quite significant changes to scorpion higher systematics. The typical characters used to resolve scorpion relationships, such as sternum shape, trichobothria, pedipalp and pectine morphology, etc., are detailed in appendix A of their analysis. The changing number of monophyletic groups and the lack of a stable internal phylogeny for scorpions makes it difficult to map our results onto a single tree. Nevertheless, we are able to recognise some patterns within our provisional data and we encourage further investigations to score these characters more widely, such that they can be incorporated into high-level systematic analyses in the future.

Gross morphology and non-informative lung characters

In general, all scorpions express a similar gross morphology of the lung. Based on our data, the atrium wall showed no significant difference between the species studied. Furthermore, trabeculae in the proximal regions of the lung connecting the opposing lamellae walls occur in all the scorpion taxa investigated. Both these characters appear uninformative for resolving relationships within extant Scorpiones.

Distal lamellar surface

Both Laurie (1896a, 1896b) and Pavlovsky (1926) described reticulate surface structures on the lamellae of buthid scorpions. Rödl et al. (1989) called them ribs. Stockwell (1989) scored this reticulation as an apomorphic character state, as opposed to the "spiny" trabeculae. This is the only previous use of lung lamellae in a phylogenetic analysis and curiously this rather straightforward character was not picked up in subsequent investigations. Our studies support reticulation as a distinctive character state characterising the lung lamellae of Buthidae. We have scored it in eight genera so far (Table 1) and predict that it occurs more widely in the buthids. We have no data for Microcharmidae, which was raised for two buthid genera to a separate group by Lourenço (1998). We also note that Laurie (1896b, p. 122) reported reticulation in the 'aberrant' species [his description] *Chaerilus variegatus* Simon, 1877 (Chaerilidae), but we have not been able to confirm this observation. Pavlovsky (1926) described the *Chaerilus* 'network' as untypical for Buthidae, and further noted that *Calchas nordmanni* Birula, 1899 (Iuridae) expresses both reticulation *and* trabeculae. Reticulation differs from the lung surfaces of other scorpions—and those of tetrapulmonate arachnids (e.g. Moore 1976 for spiders; Weygoldt 2000 and personal observations for Amblypygi and Uropygi)—which have the more typical trabeculae spread across the entire lung surface.

With respect to the polarity of the character, buthids do have proximal trabeculae—like other scorpions—and Laurie (1896a) regarded 'spiny' lungs as the plesiomorphic character state. Nevertheless, Shear et al. (1996) described cuticle fragments from the Early Devonian of Canada which included lung lamellae picked from a scorpion macrofossil. These lamellae are the oldest unequivocal evidence for terrestrial scorpions; although the specimen hosting them has not been assigned taxonomically. These fossil lung fragments appear to lack distal trabeculae, but express marginal ribs on the lamella surface which at least superficially resemble buthid reticulation. Furthermore, although the relationship between scorpions and the fossil Eurypterida (sea scorpions) remains controversial (see e.g. Shultz 1990), we also note Laurie's (1893, pl. 1, Fig. 6) description of putative respiratory structures in the branchial region of the large eurypterid *Slimonia acuminata* (Salter, 1856), which show a distinctly veined surface.

All non-buthid scorpions investigated have 'spiny' lamellae, that is, trabeculae across the whole surface, but these can be differentiated into two character states: simple and branched. The latter is clearly a more complex structure and represents a putative apomorphy. Based on our data it is restricted to Scorpionidae and at least one liochelid: *Chiromachus ochropus*. Does this render the character homoplastic? Details of characters supporting the monophyly of Liochelidae—a replacement name for the preoccupied Ischnuridae (see Fet and Bechly 2001)—can be found in Prendini (2000) and relate to various aspects of the carapace and ocular tubercle, the chelae and their trichobothria and the venom glands.

Our data offer some previously unrecognised character conflicts with respect to liochelids. Not only does *C. ochropus* exhibit 'scorpionid' branched trabeculae, our *Liocheles* sp. has 'chisel-like' structures (see above) instead of the hexagonal *pillars* around the spiracles seen in all other scorpionids and liochelids. These features are interesting to assess the homogeneity of lung morphology within the Liochelidae and, perhaps, its monophyly. At least one author (Kraepelin 1905) inferred the descent of Scorpionidae from among the probably paraphyletic Ischnuridae (= Liochelidae), but further discussion is beyond the scope of this paper.

Lamellar margins

In many scorpion species the lamellar margins differ little from the surface structure of the lamella itself. Often the trabeculae at the margins are simply outgrown into slightly longer thorns or spines and the gradation in the rigidity of these structures observed here makes it difficult to establish robust and mutually exclusive character definitions. Lamellar margins thus emerge as the least informative of the three characters here, at least for higher systematics. Some morphologies do, however, represent potential autapomorphies: that is, meandering margins in *Iurus dufoureius*.

The complex, interconnected arcuate bows (Fig. 3f)—a condition recognised as a regular 'arcade' in *Euscorpius* by Berteaux (1889)—has also been observed in *Diplocentrus* Peters, 1861, *Nebo* Simon, 1878 and *Caraboctonus* Kraepelin, 1905 (cf. Laurie 1896a) and in *Liocheles* sp. and *Uroctonus mordax* (this study). Its presence across genera from multiple taxa tends to suggest homoplasy, and there are also comparable structures in the lungs of some araneomorph spiders (Comstock 1912; Moore 1976; Hexter 1982). One could argue that this arcuate margin is part of the arachnid ground pattern, but we find this explanation unlikely. Thorny lamellar margins occur not only in some buthid scorpions—Buthidae traditionally resolves as the most basal living scorpion clade—but also in Amblypygi and Uropygi (personal observations) and the basal mesothelid spiders (Haupt 2003). These more complex arcuate margins occur in scorpions which according to most phylogenies resolve as derived groups, and might be correlated to specific ecological conditions (Victor Fet, personal communication). This hypothesis must be tested against a wider taxonomic spectrum.

Posterior spiracular margin

We suggest that the plesiomorphic character state for the posterior margin of the spiracles is the presence of ‘hillocks’, since these rather uncomplicated, raised structures occur sporadically across at least five scorpion taxa: Buthidae, Urodacidae, Bothriuridae, Chactidae and Euscorpiidae. Although we lack data to resolve the direction of evolutionary change, the more complex spiracular ornaments observed (spines, hairs, scales, etc.) could conceivably have been derived as outgrowths from simple, hillock-like bases. With one exception, the distribution of alternative patterns of ornamentation does not suggest a clear phylogenetic signal, and some morphologies may offer autapomorphies for individual genera or species, for example hairs in *Centromachetes pocockii*, flattened lobes in *Hadrurus* cf. *hirsutus* and scales in *Bothriurus coriaceus*. Further data are needed to test these hypotheses. We suspect that structures like hairs or angled projections might act as filters, trapping particles in front of the spiracular opening (see also Rödl et al. 1989). Functional investigations and/or ecological correlations would be welcome. We did not investigate the shape of the spiracle in any detail and refer to Soldeglad and Fet (2003: character 101) for scorings and distribution of this character.

Of greatest phylogenetic interest are the tightly packed, hexagonal pillars observed in all investigated species of the Scorpionidae and, except for one *Liocheles* sp., all investigated species of the Liochelidae. This highly distinctive morphology (Fig. 4g) is a putative synapomorphy of Scorpionidae and Liochelidae; with a possible reversal in *Liocheles*. Most authors have regarded these taxa as closely related. Prendini (2000) recovered a clade of the form ((Diplocentridae + Scorpionidae) (Hemiscorpiidae + Liochelidae)). No diplocentrid or hemiscorpiid material was available to us to test whether the character supports the entire clade *sensu* Prendini. By contrast, Soleglad and Fet (2003, fig. 126) recovered a provisional tree more like that of Stockwell (1989) of the form (Heteroscorpionidae (Liochelidae + Hemiscorpiidae)), itself sister-group to a clade (Urodacidae (Diplocentridae + Scorpionidae))—see these authors for details of synapomorphies. We also lack data for heteroscorpionids, but our urodacid (*Urodacus manicatus*) has simple ‘hillocks’ rather than complex, hexagonal pillars. Thus, this distinctive hexagonal morphology would be rendered homoplastic by the Soleglad and Fet model.

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