AN ATLAS OF BOOK LUNG FINE STRUCTURE IN THE ORDER SCORPIONES (ARACHNIDA)

CARSTEN KAMENZ

Institut für Biologie, Vergleichende Zoologie
Humboldt-Universität zu Berlin Philippstr. 13
D-10115 Berlin, Germany
(CarstenKamenz@gmx.de)

LORENZO PRENDINI

Division of Invertebrate Zoology
American Museum of Natural History
Central Park West at 79th Street, New York, NY
10024-5192, U.S.A.
(lorenzo@amnh.org)

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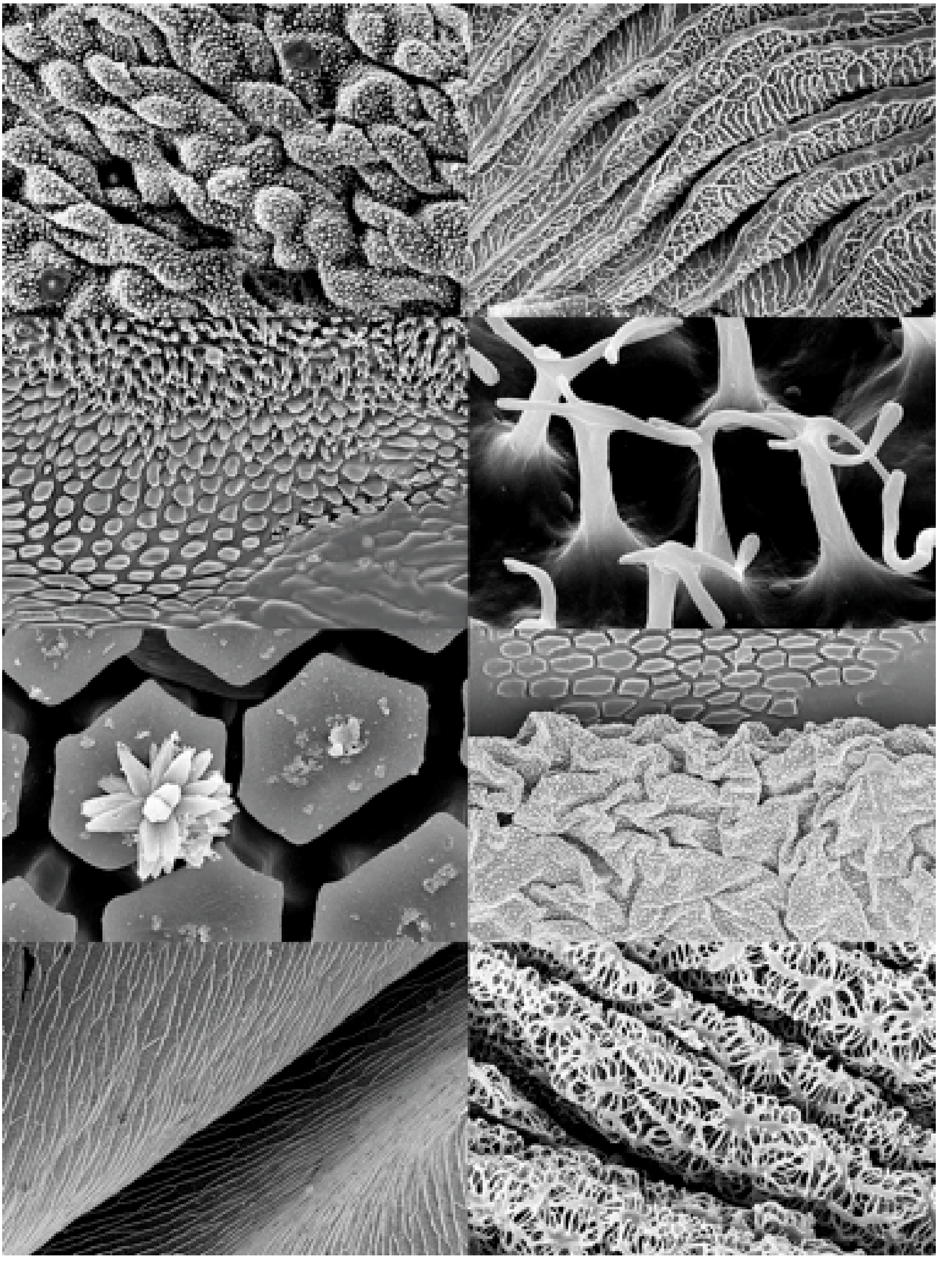

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ABSTRACT

The fine structure of the book lungs of scorpions is diverse and phylogenetically informative, but has not been comprehensively investigated across the major lineages of the order. In this contribution, we present a fully illustrated atlas of the variation in book lung fine structure among 200 exemplars from 100 genera and 18 families of extant scorpions. We document variation in the surface sculpturing of the respiratory lamellae, the edges of the lamellae in the atrial chamber, and the posterior valvelike edges of the spiracles. These data provide insights into the phylogenetic relationships among Recent scorpions at several branches of the tree.

INTRODUCTION

According to Weygoldt and Paulus (1979b), Arachnida Lamarck, 1801, represent the monophyletic terrestrial lineage of Metastomata Weygoldt and Paulus, 1979, which includes the extinct aquatic Eurypterida Burmeister, 1894. With few exceptions (e.g., some Acari Sundevall, 1833 and Araneae Clerck, 1757), all arachnid species occupy terrestrial habitats today. There are several challenges associated with a terrestrial lifestyle, arguably the most severe being the evaporative water loss that results from breathing air. Different solutions for breathing air, in the form of internalized respiratory organs, have evolved among different terrestrial animals. Examples include the lungs of vertebrates, the tracheae of insects, and the gills, modified for air breathing, of terrestrial crustaceans.

The respiratory organs of scorpions, Scorpiones C.L. Koch, 1837, and tetrapulmonate arachnids, Megoperculata Börner, 1902, are called book lungs due to the booklike appearance of the layered, sheetlike lamellae (fig. 1). Book lungs are the primary organs for respiration in arachnids, presumed to have evolved as a consequence of terrestrialization in the stem group of Arachnida (Scholtz and Kamenz, 2006). Book lungs are homologous with, and/or functionally substituted by tracheae in entelegyne spiders and apulmonate arachnids, Apulmonata Firstman, 1973 (Hilken, 1998; Weygoldt and Paulus, 1979a).

The book lungs of Recent scorpions are homologous (Scholtz and Kamenz, 2006). Their similar structural complexity and identical positions within the fourth to seventh opisthosomal segments (fig. 2) are indicative of common ancestry. Several substructures, present in all scorpions examined thus far, are hypothesized to have been present in the common ancestor of arachnids (Scholtz and Kamenz, 2006). For example, bridging trabeculae (cuticular rods) connecting the proximal surfaces of adjacent lamellae and cellular pillars inside the lamellae (fig. 13) occur in all scorpions that have been studied, and also in tetrapulmonates (Scholtz and Kamenz, 2006). Other characters, e.g., spinelike processes on the lamellar edges, are widespread among scorpions and tetrapulmonates. These characters are synapomorphic for Arachnida, but have undergone secondary modifications in Scorpiones and all remaining terrestrial arachnids, called Lipoctena Pocock, 1893 (Scholtz and Kamenz, 2006).

The most obvious feature of the book lungs—their lamellate design (fig. 1)—recalls the book gills of aquatic ancestors. Gills are probably synapomorphic for Euchelicerata Weygoldt and Paulus, 1979. Similar structures are retained in the four species of extant horseshoe crabs, Xiphosura Latreille, 1802. Book lungs are therefore hypothesized to be homologous to the book gills of xiphosurans (Lankester, 1881a, 1881b; Kingsley, 1885) and probably became internalized during the terrestrialization of Arachnida (Weygoldt and Paulus, 1979a).

The importance of book lung morphology for the phylogeny and classification of scorpions was first recognized by Laurie (1896) and Pavlovsky (1926). Pavlovsky (1926) presented a survey of book lung morphology in 35 species from 31 genera and 11 families of scorpions (table 1), based on light microscopy. Except for mention of the shape of the spiracles in various taxonomic and phylogenetic works, no comparative studies of book lung morphology were subsequently conducted until Kamenz et al.

(2005). Using scanning electron microscopy (SEM), Kamenz et al. (2005) confirmed Pavlovsky's (1926) discoveries in an examination of the fine structure of book lungs in 29 species from 28 genera and 10 families of scorpions. Due to limitations on the availability of material and constraints on the number of illustrations that could be published, the study by Kamenz et al. (2005) provided only an overview of variation in the book lung fine structure of scorpions; major lineages were not documented, restricting the utility of the data presented for phylogenetic interpretation. The aim of the study presented here is to expand the work of Kamenz et al. (2005) by providing a more comprehensive, fully illustrated survey of book lung fine structure across all the major lineages of scorpions. Exemplar species representing all scorpion families and as many genera as possible were studied and illustrated in the course of this study, providing a standardized framework that can be used to describe and define characters for phylogenetic analyses at multiple branches of the scorpion tree.

We present one interpretation of the variation observed by describing three characters, defined by Kamenz et al. (2005), which appear to be phylogenetically informative among the taxa studied (table 2): the surface sculpturing of the respiratory lamellae, the edges of the lamellae in the atrial chamber, and processes on the posterior valvelike edge of the spiracles. We chose these three characters because they are readily apparent with the SEM, and appear to be consistent within species as determined by the examination of multiple specimens. Further genetic, cellular, developmental and ultrastructural studies of the book lungs remain to be undertaken. The standardized illustrations provided in this atlas are intended to serve as a reference for further interpretation and provide a foundation upon which future studies of the book lungs of scorpions, and other arachnids, can be built.

MATERIALS AND METHODS

Taxon Sampling

The study presented here applies the "exemplar approach" (Yeates, 1995; Prendini, 2001), according to which an exemplar species represents a supraspecific taxon (usually, but not exclusively, in the context of a phylogenetic analysis). The advantages of this method are obvious: (1) it is impossible to gather data from all species, but the use of exemplars enables the variation to be systematically surveyed in a subsample; (2) exemplar species make no assumptions about the monophyly of the supraspecific taxa they represent, allowing monophyly to be rigorously tested during a phylogenetic analysis; (3) multiple sources of data (anatomy, morphology, behavior, DNA, etc.) are readily combined if gathered from the same exemplar species; (4) the use of exemplars restricts data matrices to manageable sizes for computational purposes.

The exemplar approach is more powerful (i.e., it provides a more rigorous test of the hypothesis of monophyly) when more exemplar species are studied per higher taxon, and when these species are selected to represent the maximum morphological diversity within each higher taxon (Prendini, 2001). In the present study, 200 exemplars in 100 genera were selected to represent all 18 scorpion families (table 2; appendix 1) listed in the status quo classification scheme presented by Prendini and Wheeler (2005). Type species of genera were selected preferentially, when available. Multiple species were sampled from diverse and speciose genera, e.g., *Tityus* C. L. Koch, 1836, to assess the extent of variation among congeners. Contingent on the availability of suitable material, congeneric exemplars were selected to maximize morphological diversity (Prendini, 2001). In this atlas of book lung fine structure, data gathered from the exemplar species selected are presented and discussed by family for operational purposes, with putative phylogenetically related families (e.g., buthoids, chactoids, and scorpionoids) discussed in sequence, rather than in alphabetical order. Within each family, the figures for the species are presented in alphabetical order by genus. This study makes no assumptions about the monophyly or content of these families, however. It serves primarily to document the variation in book lung fine structure and stimulate further investigation into the subject.

TABLE 1

States of the book lung characters recorded by Pavlovsky (1926)

Numbers refer to states defined by Pavlovsky (1926). "Fig." denotes state indicated only in figures

	LAMINAE	LAMINA MARGINS	STIGMA MARGIN
Buthidae C. L. Koch, 1837			
Androctonus australis (Linnaeus, 1758)	reticulate	barbate	(5) barbate
Anomalobuthus rickmersi Kraeplin, 1900	reticulate	barbate	(5) barbate
Centruroides margaritatus (Gervais, 1841)	reticulate	tuberculate	(5) barbate
Compsobuthus acutecarinatus (Simon, 1882)			(3) columellar
Grosphus madagascariensis (Gervais, 1843)		hardly visible spines	(1) smooth-ruffled
Hottentotta eminii (Pocock, 1890)	reticulate	barbate	(5) barbate
Hottentotta hottentotta (Fabricius, 1787)	reticulate	barbate	
Isometrus sp.	transition to barbate-reticulate	(2) tuberculate	
Liobuthus kessleri Birula, 1898	reticulate	barbate	(5) barbate
Lychas mucronatus (Fabricius, 1798)	transition to barbate-reticulate	(2) tuberculate	
Mesobuthus caucasicus (Nordmann, 1840)	reticulate	barbate	(5) barbate
Mesobuthus eupeus (C.L. Koch, 1839)	reticulate	barbate	(5) barbate
Odonturus dentatus Karsch, 1879	reticulate	barbate	(5) barbate
Orthochirus sp.			(5) barbate
Uroplectes lineatus (C.L. Koch, 1844)			(2) tuberculate
Tityus sp.	reticulate		(5) barbate
Chaerilidae Pocock, 1893			
Chaerilus variegatus Simon, 1877	fine reticulate	no spinelets	(5) barbate
Iuridae Thorell, 1876			
Calchas nordmanni Birula, 1899	network on one side + columellae with secondary spines		barbate-columellar
Caraboctonus sp.		arcuate	
Hadrurus sp.		barbate	(5) barbate/ (dentate)
Iurus sp.		arcuate	barbate-columellar
Euscorpiidae Laurie, 1896			
Euscorpius sp.		arcuate	
Scorpiopidae Kraepelin, 1905			
Euscorpiops montanus (Karsch, 1879)	arcuate to barbate?	barbate	(2) tuberculate
Chactidae Pocock, 1893			
Broteochactas sp.		brush of fine setae	(3) columellar
Brotheas granimanus Pocock, 1898		brush of fine setae	(3) columellar
Teuthraustes witti (Kraepelin, 1896)		arcuate	(3) columellar
Vaejovidae Thorell, 1876			
Uroctonus mordax Thorell, 1876		arcuate	(3) columellar
Vaejovis spinigerus (Wood, 1863)		barbate	(4) saw-edge
Bothriuridae Simon 1880			
Bothriurus bonariensis (C.L. Koch, 1842)	columellae (fig.)	barbate (fig.)	barbate
Brachistosternus ehrenbergi (Gervais, 1841)		barbate	(5) barbate
Brachistosternus intermedius Lönnberg, 1902		barbate	(5) barbate
Thestylus glasioui (Bertkau, 1880)		barbate	(5) barbate
Urodacidae Pocock, 1893			
Urodacus yaschenkoi (Birula, 1903)			stumpy (fig.)
Hemiscorpiidae Pocock, 1893			
Hemiscorpius lepturus Peters, 1861		barbate (fig.)	
Scorpionidae Latreille, 1802	columellae with secondary spines	barbate	(6) stumpy

Material, Preparation, and Terminology

Material examined was borrowed from or studied in situ at the following collections: American Museum of Natural History, New York (AMNH); Museum National d'Histoire Naturelle, Paris (MNHN); Museum für Naturkunde, Berlin (MfN), bearing ZMB accession numbers. Available collection data for voucher specimens studied are provided in appendix 1. Mounted SEM stubs are also deposited in these collections.

Standard SEM techniques were used for the preparation and investigation of book lungs. Book lungs were dissected from scorpions preserved in 70–100% ethanol. Several specimens were fixed in Bouin's fluid (15 ml saturated picric acid, 5 ml 35% formaldehyde, and 1 ml acetic acid) or using a method adapted by Karnovsky (1965), in a solution of 0.1 M phosphate-buffered saline (PBS: 10.9 g Na_2HPO_4 [anhydrous], 3.2 g NaH_2HPO_4 [anhydrous], and 90 g NaCl in 1000 ml distilled water, pH 7.2), 3.7% formaldehyde, and 2.5% glutaraldehyde plus postfixation in 2% osmiumtetroxide. Bouin's fluid was washed out with 70% ethanol and Karnovsky's fixatives using PBS first and 40% ethanol in subsequent steps. The ethanol concentration was sequentially increased to 100% for dehydrating the tissues. The ethanol was then removed in critical point dryers, BAL-TEC CPD 030 at the Humboldt-Universität, Berlin (HUB), Emitech K850 (MNHN), or in an oven (AMNH) at 60°C.

After dehydration and prior to examination with the SEM, the lungs were dissected to expose the interior structures before mounting on common stubs. The prepared lungs were then sputter-coated with gold template in a BAL-TEC SCD 005 (HUB), or with gold-paladium in a Polaron SC 7640 (MfN), Joel JFC-1200 Fine Coater (MNHN), or DENTON Desk II (AMNH). The following SEMs were used in the course of the study: a Leo 1540 VP (MfN), a Joel JSM-840 A (MNHN), and a Hitachi S 4700 (AMNH). Images of the book lungs prepared for each species studied were assembled into plates using Adobe Photoshop and Illustrator. Terminology for book lung structures follows Kamenz et al. (2005), a detailed explanation of which follows in the section on Fine Structure of Scorpion Book Lungs.

RESULTS

Gross Morphology and Function of Scorpion Book Lungs

Position of book lungs: The respiratory organs of scorpions occur on the inner surface of the ventral exoskeleton in the mesosoma (fig. 2). A pair of book lungs is situated laterally on the sternites of the third to sixth visible opisthosomal segments (identical to the fourth to seventh embryological opisthosomal segments; Brauer, 1895; Simonnet et al., 2006), following the pectinal segment. A mostly slitlike, in some cases oval or almost circular spiracle (fig. 3) demarcates the posteromedial margin of the book lung. The spiracle is the respiratory opening leading into the atrium of the book lung. The distance from the spiracle to the anterior margin of the sternite is approximately equal to three times the distance between the posterior margin and the spiracle. The longitudinal axis of the spiracle is inclined toward the transverse axis with the medial end lying anteriad.

Lung morphology: Each book lung consists of a stack of leaflike lamellae situated above the ventral sternite (Treviranus, 1812; figs. 1, 4). We define the lamellae as a double layer of cuticle that is flooded by hemolymph and surrounded by air. The adjacent layers of cuticle surrounding the air between the lamellae are saclike in all terrestrial arachnids and are therefore called air sacs (fig. 5). The air sacs are held in place by bandlike ligaments (fig. 6) from an overlying layer of connective tissue in the hemolymph space, called the fenestrated membrane (Farley, 1990; fig. 7). The fenestrated membrane covers the lung from above and is held to the pericard of the heart by the hypocardial ligament (figs. 7, 8).

The lamellae are not in direct contact with the inner cuticular surface of the sternites, but are separated from it by a flat layer of the epidermis and a narrow hemolymph space (fig. 1). The stack of lamellae is slanted dorsoventrally with the medial side of the book lung situated closest to the inner surface

TABLE 2

States of the book lung characters observed in exemplar species of Scorpiones

Lamellar surface (Lam. surf.): simple trabeculae (1); branched trabeculae (2); slender venation (3); ribbed venation (4). Lamellar edge (Lam. edge): bristles (1); spines (2); thorns (3); smooth/wrinkled (4); meandering (5); arcuate bows (6); padded (7). Posterior spiracle edge (Spir. edge): hillocks (1); subconical (2); hairlike (3); flattened (4); scaly (5); chisel-like (6); hexagonal tiles (7); treelike (8); subtree-like (9); polygonal columns (10); clublike (11); spiked macelike (12)

	Lam. surf.	Lam. edge	Spir. edge
Pseudochactidae Gromov, 1998:			
Pseudochactas ovchinnikovi Gromov, 1998	1	2	4
Buthidae C. L. Koch, 1837:			
Ananteris cussinii Borelli, 1910	3	4	?
Androctonus amoreuxi amoreuxi (Audouin, 1826)	3	3	2
Androctonus australis australis (Linnaeus, 1758)	3	3	2
Androctonus bicolor aeneas C.L. Koch, 1839	3	3	2
Anomalobuthus rickmersi Kraepelin, 1900	3	3	2
Apistobuthus pterygocercus Finnegan, 1932	3	3	2
Babycurus buettneri Karsch, 1886	3	4	2
Babycurus jacksoni (Pocock, 1890)	3	4	2
Buthacus arenicola (Simon, 1885)	3	3	2
Buthacus leptochelys (Ehrenberg, 1829)	3	3	1
Butheoloides maroccanus Hirst, 1925	3	3	1
Butheolus gallagheri Vachon, 1980	3	3	2
Buthiscus bicalcaratus Birula, 1905	3	3	2
Buthus ibericus Lourenço and Vachon 2004	3	3	2
Buthus occitanus (Amoreux, 1789)	3	3	2
Caribetityus elii (Armas and Marcano Fondeur, 1992)	4	4	2
Centruroides exilicauda (Wood, 1863)	3	4	2
Centruroides gracilis (Latreille, 1804)	3	4	2
Centruroides m. margaritatus (Gervais, 1841)	3	4	2
Centruroides schmidti Sissom, 1995	3	4	2
Cicileus exilis (Pallary, 1928)	3	3	2
Compsobuthus berlandi Vachon, 1950	3	3	2
Compsobuthus maindroni (Kraepelin, 1900)	3	3	2
Grosphus flavopiceus Kraepelin, 1900	3	4	2
Grosphus grandidieri Kraepelin, 1900	3	4	?
Grosphus hirtus Kraepelin, 1900	3	4	1
Hottentotta conspersus (Thorell, 1876)	3	4	1
Hottentotta hottentotta (Fabricius, 1787)	3	3	2
Hottentotta jayakari (Pocock, 1895)	3	3	1
Isometroides angusticaudis Keyserling, 1885	3	4	1
Isometrus maculatus (DeGeer, 1778)	3	3	1
Karasbergia methueni Hewitt, 1913	3	3	1
Leiurus quinquestriatus hebraeus (Birula, 1908)	3	3	?
Leiurus quinquestriatus quinquestriatus (Ehrenberg, 1828)	3	3	2
Liobuthus kessleri Birula, 1898	3	3	?
Lychas mucronatus (Fabricius, 1798)	3	4	1
Lychas obsti Kraepelin, 1913	3	3	1
Lychas scutilus C.L. Koch, 1845	3	4	1
Lychas tricarinatus (Simon, 1884)	3	4	1
Lychas sp.	3	3	1
Mesobuthus caucasicus parthorum Pocock, 1889	3	3	?
Mesobuthus eupeus thersites (C. L. Koch, 1839)	3	3	2
Mesobuthus gibbosus (Brullé, 1832)	3	3	2
Microtityus rickyi Kjellesvig-Waering, 1966	4	3	2
Odontobuthus doriae (Thorell, 1876)	3	3	2

TABLE 2
(Continued)

	Lam. surf.	Lam. edge	Spir. edge
Buthidae C. L. Koch, 1837:			
Odonturus dentatus Karsch, 1879	3	4	2
Orthochirus innesi Simon, 1910	3	3	1
Orthochirus scrobiculosus scrobiculosus (Grube, 1873)	3	3	1
Parabuthus leiosoma (Ehrenberg, 1828)	3	3	2
Pseudolychas pegleri (Purcell, 1901)	3	3	1
Rhopalurus acromelas Lutz and Mello, 1922	3	4	2
Rhopalurus bonettii Armas, 1999	3	4	1
Rhopalurus junceus (Herbst, 1800)	3	4	1
Rhopalurus laticauda Thorell, 1876	3	4	1
Rhopalurus princeps (Karsch, 1879)	3	4	2
Rhopalurus rochae Borelli, 1910	3	4	2
Tityobuthus baroni (Pocock, 1890)	3	4	1
Tityus asthenes Pocock, 1893	4	4	2
Tityus bahiensis eickstedtae (Lourenço, 1982)	4	4	2
Tityus bolivianus Kraepelin, 1895	4	4	?
Tityus cambridgei Pocock, 1897	4	4	2
Tityus clathratus C. L. Koch, 1844	4	4	2
Tityus confluens Borelli, 1899	4	4	2
Tityus discrepans (Karsch, 1879)	4	4	2
Tityus melanostictus Pocock, 1893	4	4	2
Tityus serrulatus Lutz and Mello, 1922	4	4	2
Tityus silvestris Pocock, 1897	4	4	2
Uroplectes flavoviridis Peters, 1861	3	3	2
Uroplectes occidentalis Simon, 1867	3	4	1
Uroplectes planimanus (Karsch, 1879)	3	3	1
Vachoniolus globimanus Levy, Amitai and Shulov, 1973	3	3	2
Zabius fuscus (Thorell, 1876)	4	4	2
Microcharmidae Lourenço, 1996:			
Microcharmus sp.	3	4	?
Chaerilidae Pocock, 1893:			
Chaerilus truncatus Karsch, 1879	4	7	2
Chaerilus sp.	4	7	?
Iuridae Thorell, 1876:			
Anuroctonus phaiodactylus (Wood, 1863)	1	1	1
Anuroctonus pococki Soleglad and Fet, 2004	1	1	1
Calchas nordmanni Birula, 1899	1	5	6
Caraboctonus keyserlingi Pocock, 1893	1	6	9
Hadruroides charcasus (Karsch, 1879)	1	1	1
Hadrurus concolorous (Stahnke, 1969)	1	1	4
Hadrurus hirsutus (Wood, 1863)	1	2	2
Hadrurus spadix Stahnke, 1940	1	2	2
Iurus dufoureius asiaticus Birula, 1903	1	5	6
Iurus dufoureius dufoureius (Brullé, 1832)	1	5	6
Euscorpiidae Laurie, 1896:			
Euscorpius carpathicus candiota Birula, 1903	1	6	1
Euscorpius flavicaudis (DeGeer, 1778)	1	6	1
Euscorpius italicus (Herbst, 1800)	1	6	1
Megacormus gertschi Díaz Najera, 1966	1	6	1
Megacormus granosus (Gervais, 1843)	1	6	1
Troglocormus willis Francke, 1981	1	1	1

TABLE 2
(Continued)

	Lam. surf.	Lam. edge	Spir. edge
Scorpiopidae Kraepelin 1905:			
Scorpiops hardwickei (Gervais, 1843)	1	1	1
Scorpiops petersii Pocock, 1893	1	1	1
Chactidae Pocock, 1893:			
Broteochactas delicatus (Karsch, 1879)	1	1	6
Broteochactas nitidus Pocock, 1893	1	1	1
Brotheas gervaisii Pocock, 1893	1	1	6
Brotheas granulatus Simon, 1877	1	1	6
Chactas raymondhansi Francke and Boos, 1986	1	6	2
Chactas reticulatus Kraepelin, 1912	1	6	6
Guyanochactas gonzalezspongai (Lourenço, 1983)	1	1	6
Hadrurochactas schaumii (Karsch, 1880)	1	1	6
Nullibrotheas allenii (Wood, 1863)	1	2	2
Teuthraustes atramentarius Simon, 1878	1	6	11
Teuthraustes gervaisii (Pocock, 1893)	1	6	11
Superstitioniidae Stahnke, 1940:			
Alacran tartarus Francke, 1982	1?	5	?
Superstitionia donensis Stahnke, 1940	1	6	1
Troglotayosicidae Lourenço, 1998:			
Belisarius xambeui Simon, 1879	1	1	1
Vaejovidae Thorell, 1876:			
Paravaejovis pumilis (Williams, 1970)	1	2	2
Paruroctonus becki (Gertsch and Allred, 1965)	1	2	10
Paruroctonus boreus (Girard, 1854)	1	2	10
Paruroctonus borregoensis borregoensis Williams, 1972	1	2	10
Paruroctonus gracilior (Hoffmann, 1931)	1	2	10
Paruroctonus stahnkei (Gertsch and Soleglad, 1966)	1	2	10
Pseudouroctonus apacheanus (Gertsch and Soleglad, 1972)	1	1	4
Pseudouroctonus reddelli (Gertsch and Soleglad, 1972)	1	1	4
Serradigitus wupatkiensis (Stahnke, 1940)	1	2	4
Smeringurus vachoni vachoni (Stahnke, 1961)	1	2	4
Syntropis macrura Kraepelin, 1900	1	2	4
Uroctonites huachuca (Gertsch and Soleglad, 1972)	1	1	12
Uroctonus mordax mordax Thorell, 1876	1	6	1
Vaejovis intrepidus cristimanus Pocock, 1898	1	2	2
Vaejovis magdalensis Williams, 1971	1	2	2
Vaejovis mexicanus mexicanus C. L. Koch, 1836	1	1	2
Vaejovis nitidulus C. L. Koch, 1843	1	2	2
Vaejovis spinigerus (Wood, 1863)	1	2	2
Vejovoidus longiunguis (Williams, 1969)	1	1	2
Bothriuridae Simon, 1880:			
Bothriurus bonariensis (C. L. Koch, 1842)	1	2	2
Bothriurus burmeisteri Kraepelin, 1894	1	2	2
Bothriurus chacoensis Maury and Acosta, 1993	1	2	2
Bothriurus coriaceus Pocock, 1893	1	2	2
Brachistosternus ehrenbergii (Gervais, 1841)	1	2	2
Brachistosternus ferrugineus (Thorell, 1876)	1	2	2
Centromachetes obscurus Mello-Leitão, 1932	1	1	9
Centromachetes pocockii (Kraepelin, 1894)	1	1	3
Centromachetes sp.	1	2	2–9

TABLE 2
(Continued)

	Lam. surf.	Lam. edge	Spir. edge
Bothriuridae Simon, 1880:			
Cercophonius sulcatus Kraepelin, 1908	1	2	2
Cercophonius sp.	1	2	?
Lisposoma elegans Lawrence, 1928	1	1	4
Lisposoma josehermana Lamoral, 1979	1	1	4
Orobothriurus alticola (Pocock, 1899)	1	2	2
Pachakutej iskay (Acosta and Ochoa, 2001)	1	1	1
Phoniocercus pictus Pocock, 1893	1	2	2
Phoniocercus sanmartini Cekalovic, 1968	1	2	8
Thestylus glasioui (Bertkau, 1880)	1	1	8
Timogenes dorbignyi (Guérin Méneville, 1843)	1	2	2
Timogenes mapuche Maury, 1975	1	2	9
Urophonius iheringii Pocock, 1893	1	2	8
Urophonius tregualemuensis Cekalovic, 1981	1	2	9
Vachonia martinezi Abalos, 1954	1	2	2
Urodacidae Pocock, 1893:			
Urodacus manicatus (Thorell, 1876)	1	1	1
Urodacus novaehollandiae Peters, 1861	1	1	6
Urodacus yaschenkoi (Birula, 1903)	1	1	4
Urodacus sp.	2	1	2
Heteroscorpionidae Kraepelin, 1905:			
Heteroscorpion opisthacanthoides (Kraepelin, 1896)	1	1	6
Hemiscorpiidae Pocock, 1893:			
Hemiscorpius lepturus Peters, 1861	1	2	7
Hemiscorpius tellinii Borelli, 1904	1	1–2	7
Liochelidae Fet and Bechly, 2001 (1879):			
Cheloctonus anthracinus warreni Hewitt, 1931	1	1	7
Cheloctonus jonesii Pocock, 1892	1	1	7
Chiromachus ochropus (C.L. Koch, 1837)	1	1	7
Hadogenes trichiurus trichiurus (Gervais, 1843)	2	1	7
Hadogenes troglodytes troglodytes (Peters, 1861)	2	1	7
Hadogenes sp.	2	2	7
Iomachus politus Pocock, 1896	2	2	7
Liocheles australasiae (Fabricius, 1775)	1	6	4/6
Liocheles karschii (Keyserling, 1885)	1	6	6
Liocheles waigiensis (Gervais, 1843)	1	6	6
Opisthacanthus africanus Simon, 1876	2	1	7
Opisthacanthus elatus (Gervais, 1844)	2	1	7
Opisthacanthus lecomtei (Lucas, 1858)	1	1	7
Opisthacanthus madagascariensis Kraepelin, 1894	1	1	7
Opisthacanthus validus Thorell, 1876	1	1	7
Palaeocheloctonus pauliani Lourenço, 1996	1	1	7
Diplocentridae Karsch, 1880:			
Bioculus comondae Stahnke, 1968	1	6	7
Cazierius gundlachii (Karsch, 1880)	1	6	7
Didymocentrus lesueurii (Gervais, 1844)	1	6	7
Diplocentrus mexicanus mexicanus Peters, 1861	1	6	7
Diplocentrus tehuacanus Hoffmann, 1931	1	6	7
Diplocentrus whitei (Gervais, 1844)	1	6	7
Diplocentrus zacatecanus Hoffmann, 1931	1	6	7
Heteronebo granti Pocock, 1899	1	6	7
Nebo hierichonticus (Simon, 1872)	1	6	7

TABLE 2
(Continued)

	Lam. surf.	Lam. edge	Spir. edge
Scorpionidae Latreille, 1802:			
Heterometrus fulvipes (C. L. Koch, 1837)	2	1	7
Heterometrus longimanus (Herbst, 1800)	2	1	7
Heterometrus spinifer (Ehrenberg, 1828)	2	1	7
Heterometrus swammerdami Simon, 1872	2	1	7
Heterometrus sp.	2	1	7
Opistophthalmus boehmi (Kraepelin, 1896)	2	2	7
Opistophthalmus capensis (Herbst, 1800)	2	1	7
Opistophthalmus carinatus (Peters, 1861)	2	1	7
Opistophthalmus fitzsimonsi Hewitt, 1935	2	1	7
Opistophthalmus glabrifrons Peters, 1861	2	1	7
Opistophthalmus holmi (Lawrence, 1969)	2	1	7
Pandinus cavimanus (Pocock, 1888)	2	1	7
Pandinus imperator (C.L. Koch, 1841)	2	1	7
Pandinus viatoris (Pocock, 1890)	2	1	7
Scorpio maurus fuliginosus (Pallary, 1928)	2	1	7
Scorpio maurus fuscus (Ehrenberg, 1829)	2	1	7
Scorpio maurus palmatus (Ehrenberg, 1828)	2	2	7
Scorpio maurus subsp.	2	1	7

of the sternite and the uppermost lamella situated on the lateral margin of the sternite (fig. 9). The proximal surfaces of the parallel lamellae are shallowly inclined, each lamella sloping slightly from dorsomedial to ventrolateral, to almost horizontal. The distal edges of the lamellae are more steeply inclined in the same direction. There are fewer lamellae, aligned almost horizontally, in smaller species. The lamellae are more numerous and inclined, to almost vertically aligned, in larger species.

Each air sac (fig. 5) has the shape of an almost straight or bent oval that is distally truncated. The straight distal edge of one lamella merges with the distal edge of the adjacent lamella to form the entrance of an air sac (fig. 1). All the distal lamellar edges together form a grill, merging continuously into the wall of the atrium. The atrial chamber (figs. 1, 4) is lined by cuticle, which is strongly folded and covered with small wartlike cuticular processes (fig. 10). An area of almost unfolded and smooth, wart-free cuticle occurs laterally at the regions of transition (with respect to the axis of the spiracle) where the atrium joins the posterior edge of the spiracle (figs. 1, 11). Cuticular processes, shaped like shallow bars or flat lobes (fig. 11), occur on the central region of transition from the atrial wall to the posterior spiracle edge. The shape of these processes changes closer to the posterior spiracle edge, where they transform into the taxon-specific structures described in more detail below.

LAMELLAE: Each lamella comprises two very thin, parallel layers of epidermal cells on both outer surfaces (Scholtz and Kamenz, 2006). Each layer of epidermal cells is supported by a thin layer of cuticle that separates the inner hemolymph space of the lamellae from the outer air space (figs. 1, 12). The hemolymph space, inside the lamella, is maintained at a uniform width by cellular pillars (figs. 1, 13). These cellular pillars are situated at regular intervals across the inner surfaces of the lamellae, providing a constant space for hemolymph between the inner surfaces of the two adjacent cuticle layers within each lamella. Each pillar comprises two or more cells, which originate on adjacent surfaces and meet each other in the middle, and is filled almost entirely by the nuclei of the pillar cells (Scholtz and Kamenz, 2006).

The cuticular surface of the lamellae is covered with cuticular structures that prevent the air space from collapsing. The

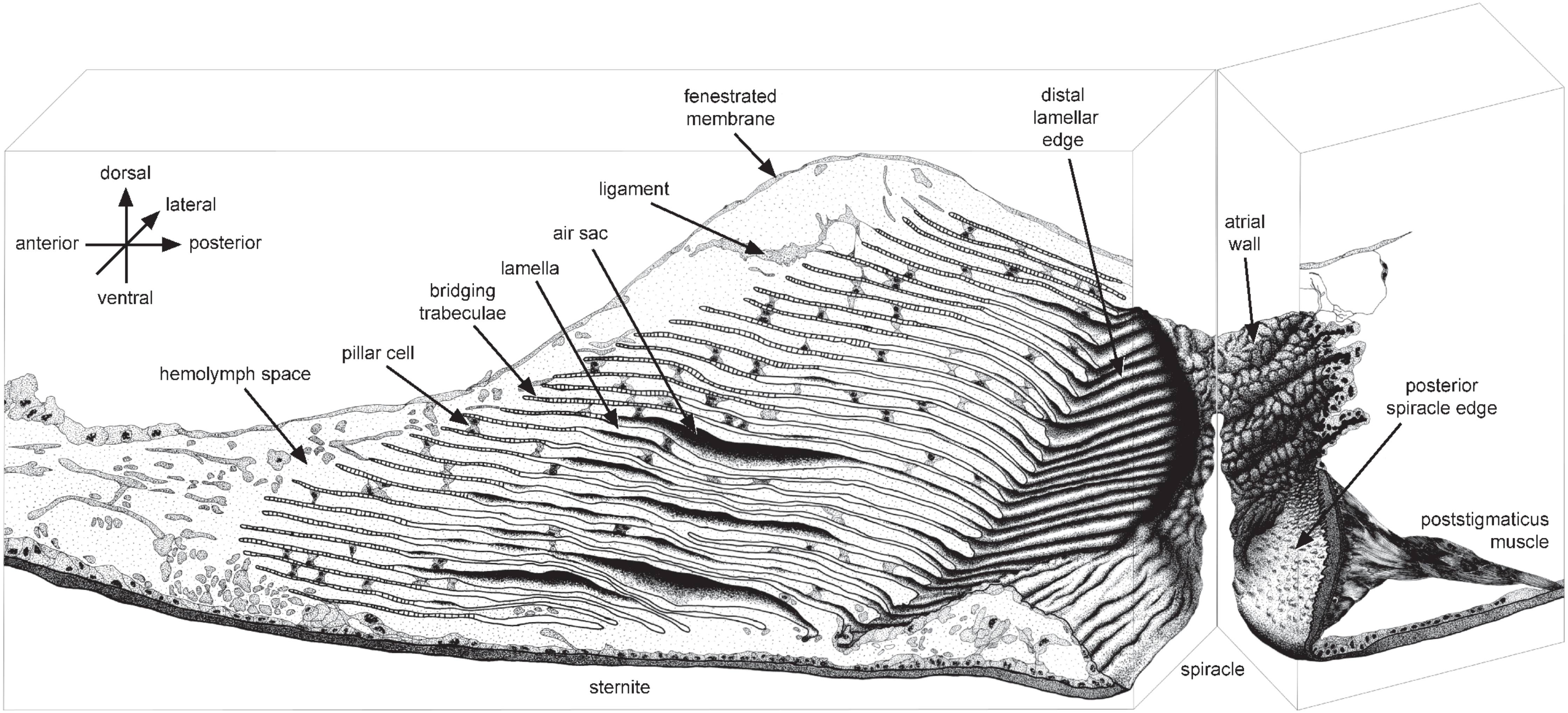


Fig. 1. *Euscorpius carpathicus candota* Birula, 10-3: 1 ♀ (HUB): diagrammatic representation of longitudinal histological section through book lung (foreground), showing cuticular structures in three dimensions.

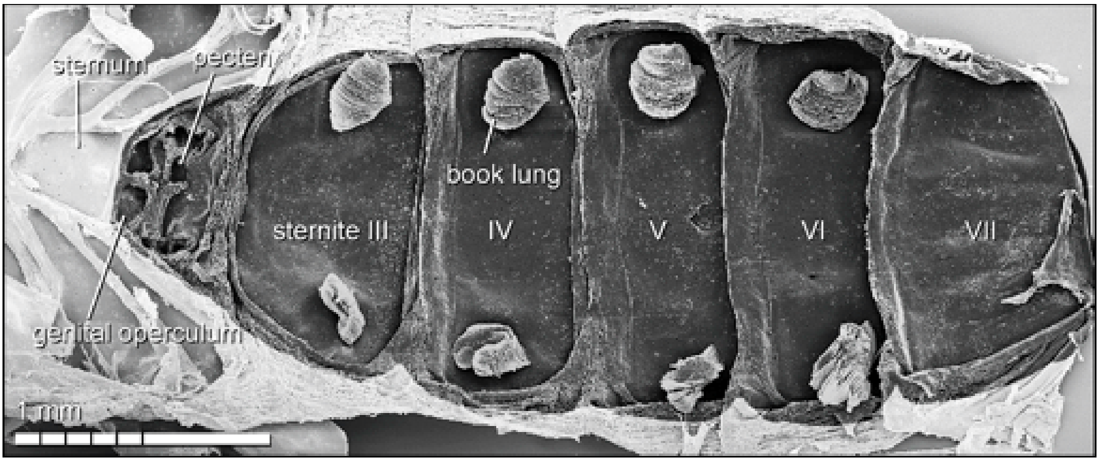


Fig. 2. *Broteochactas delicatus* (Karsch, 1879), 1 juv. ♂ (AMNH), KOH-macerated cuticle: dorsal view of internal aspect of ventral mesosoma, showing location of book lungs.

proximal one-third to one-fifth of the lamellar surface is covered, in all scorpions, with bridging trabeculae (described further below). The distal two-thirds to four-fifths of the lamellar surface are covered with one of two kinds of cuticular structures that are not connected to the adjacent lamellae (Laurie, 1896): reticulate venation or papillate trabeculae. Venation, observed in buthoid scorpions, covers both sides of the lamellae (fig. 15C, D). Papillate trabeculae (fig. 15A, B), observed in non-buthid scorpions, occur only on the ventral surfaces of the lamellae; their free ends are directed toward the adjacent lamellar surfaces.

BRIDGING TRABECULAE: Trabeculae are cuticular processes (figs. 12, 15) that separate adjacent lamellae from one another and prevent collapse of the air space with consequent reduction in the respiratory surface. Bridging trabeculae (fig. 12) are unique in forming continuous columns between adjacent lamellae. Due to their equal size and perpendicular arrangement at regular intervals, bridging trabeculae hold the lamellae at a very constant distance apart, resulting in the parallel appearance of the proximal surfaces of the lamellae.

Bridging trabeculae are present in the book lungs of all arachnids (Scholtz and Kamenz, 2006) and occur on the proximal surfaces of the book lung lamellae of all scorpions (figs. 1, 12), regardless of the presence of venation or trabeculae on the distal surfaces of the lamellae. Bridging trabeculae are situated in a bandlike zone along the anterior to medial margin of each lamella (fig. 5).

GAS EXCHANGE: Air flows through the spiracle into the atrium (figs. 1, 4) of the book lung and from there into the air sacs between the lamellae, where it is separated from the hemolymph only by a single layer of epidermis and cuticle. Gas exchange, by diffusion to and from the hemolymph inside the lamellae, occurs across this extremely thin lamellar surface. Hemolymph flows through the lamellae from the ventral hemolymph sinus to the lateral pneumocardial sinus (fig. 8) receiving oxygen and releasing carbon dioxide along the way. The oxygenated hemolymph is transported dorsally to the heart and then distributed throughout the body.

SPIRACLES AND VENTILATION: Each spiracle (fig. 3) is a small circular, oval or slitlike opening to the book lung in the sternite. The spiracle regulates the influx of gases and can be closed to prevent loss or penetration of gases, liquids, and solid particles. Cuticular processes on the spiracle and the distal edges of the lamellae probably reduce the penetration of dust particles.

Opening of the spiracle is regulated by sensory cells detecting the concentration of carbon dioxide and the pH of the hemolymph (Farley, 1990). The poststigmaticus

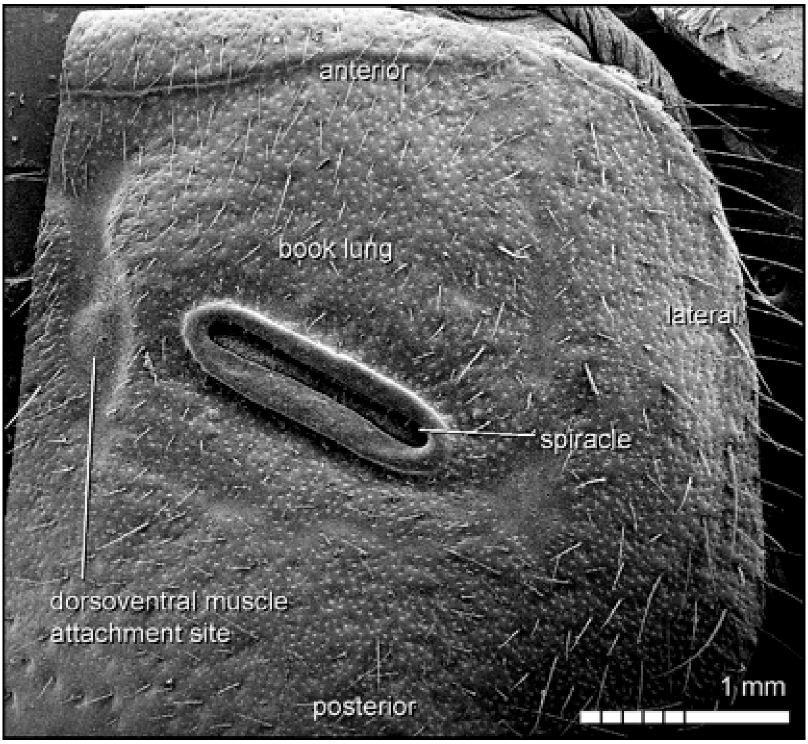


Fig. 3. *Brotheas granulatus* Simon, 1877, 1 ♂ (MNHN RS 8508): ventral view of dextral surface of sternite, showing position of spiracle, slanted with anterior margin (top) toward the midline (left).

muscle (fig. 1), attached to the posterior edge of the spiracle (Fraenkel, 1930; Pavlovsky, 1926; Du Buisson, 1925; Vyas and Laliwala, 1972, 1976; Farley, 1990), connects to the posterior part of the sternite or the posterior intersegmental membrane (fig. 14). The spiracle is opened on contraction of this muscle, which causes the posterior edge to roll or flap back, away from the anterior edge. This mechanism serves to regulate the partial pressure of oxygen and carbon dioxide (Fincke and Paul, 1989). Closure of the spiracle is a passive process. The posterior edge of the spiracle is flexible and closes the spiracle on relaxation.

Whether gas exchange in scorpions occurs by diffusion or active ventilation has not been conclusively demonstrated. Fraenkel (1930) described pumping movements of the book lung due to pulsation of the heart, transmitted via pneumocardial bands, the hypocardial ligaments described by Farley (1990), and ventilation by muscles attached to the posterior spiracle edge and the atrium. However, Fincke and Paul (1989) contradicted the suggestion of effective ventilation. Their physiological investigations on the mygalomorph spider, *Eurypelma californicum* Ausserer, 1871, the entelegyne spider, *Cupiennius salei* (Keyserling, 1877), and the scorpion, *Pandinus imperator* (C.L. Koch, 1841) did not reveal any rapid, rhythmic movements of the spiracle in dormancy or during phases of high activity as occur, for example, in vertebrates. Rhythmic stirring of the hemolymph stream through the book lung, generated by pulsation of the heart, might support gas exchange (Farley, 1990), but this remains to be demonstrated.

Fine Structure of Scorpion Book Lungs

LAMELLAR SURFACES: The distal lamellar surfaces of scorpions may be covered with two distinct kinds of structures (character 1; fig. 15): reticulate venation or cylindrical, rodlike (papillate) trabeculae. Distal, in the sense used here, refers to the main part of the

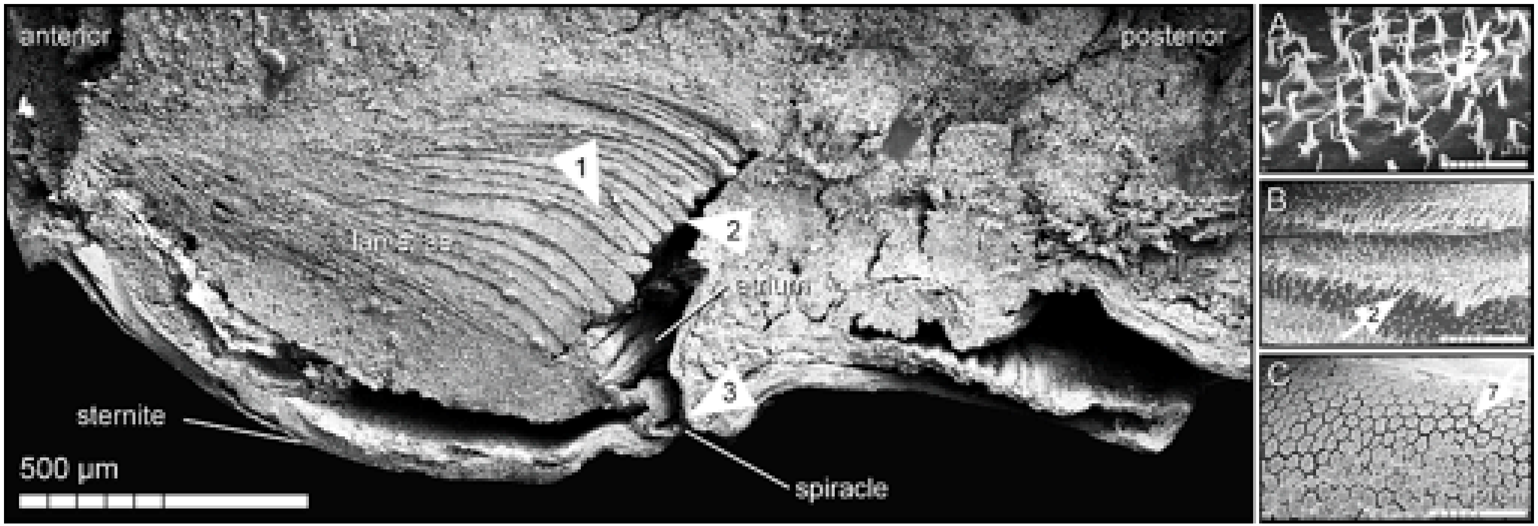


Fig. 4. *Hottentotta jayakari* (Pocock, 1895), 1 subad. ♀ (HUB): lateral view of longitudinal section through book lung, showing position of book lung morphology characters discussed in the atlas (arrowheads): lamellar surface (1); distal lamellar edge (2); posterior spiracle edge (3); (A–C) arrangement of characters in the plates, (A) lamellar surface, (B) distal lamellar edge, (C) posterior spiracle edge; arrowheads and arrows indicate characters and states.

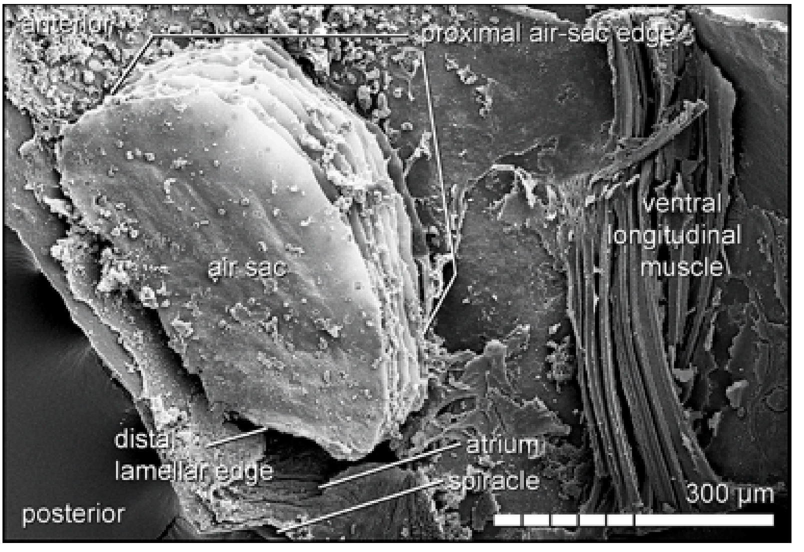


Fig. 5. *Cercophonius sulcatus* Kraepelin, 1908, 1 ♂ (AMNH [LP 1618]): dorsal view of lateral part of sternite, illustrating shape of seven median air sacs of book lung.

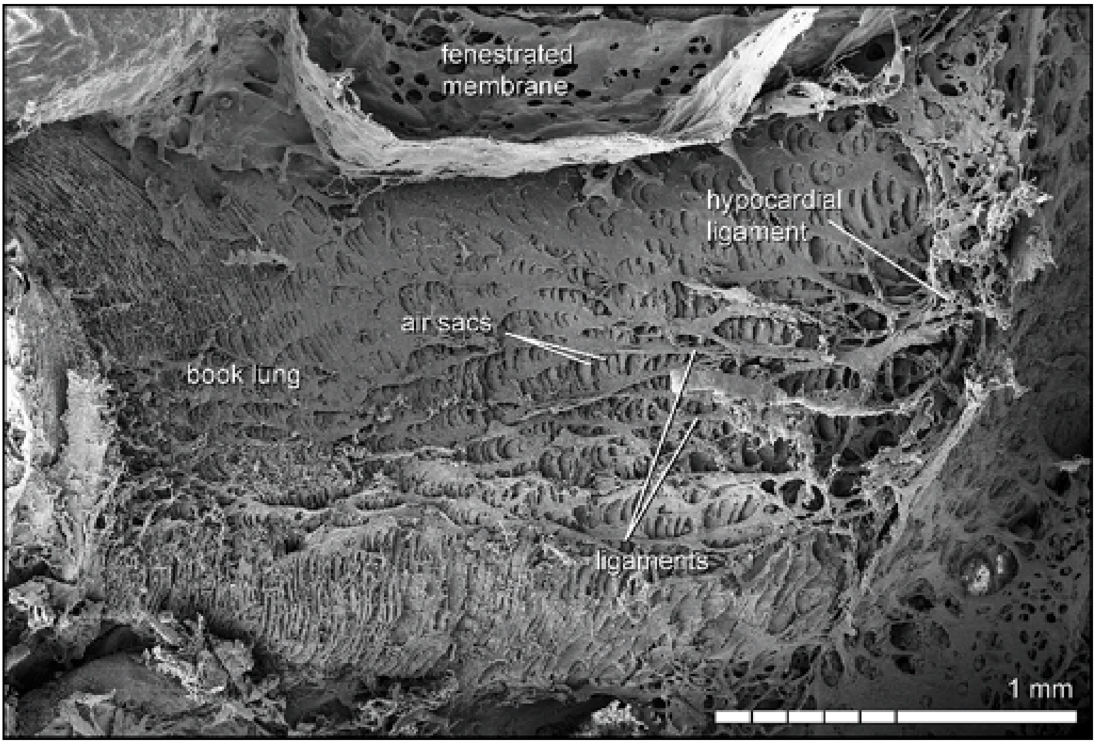


Fig. 6. *Hadogenes* sp., 1 ♂ (HUB): ventral view of book lung, with fenestrated membrane removed, showing ligaments holding air sacs.

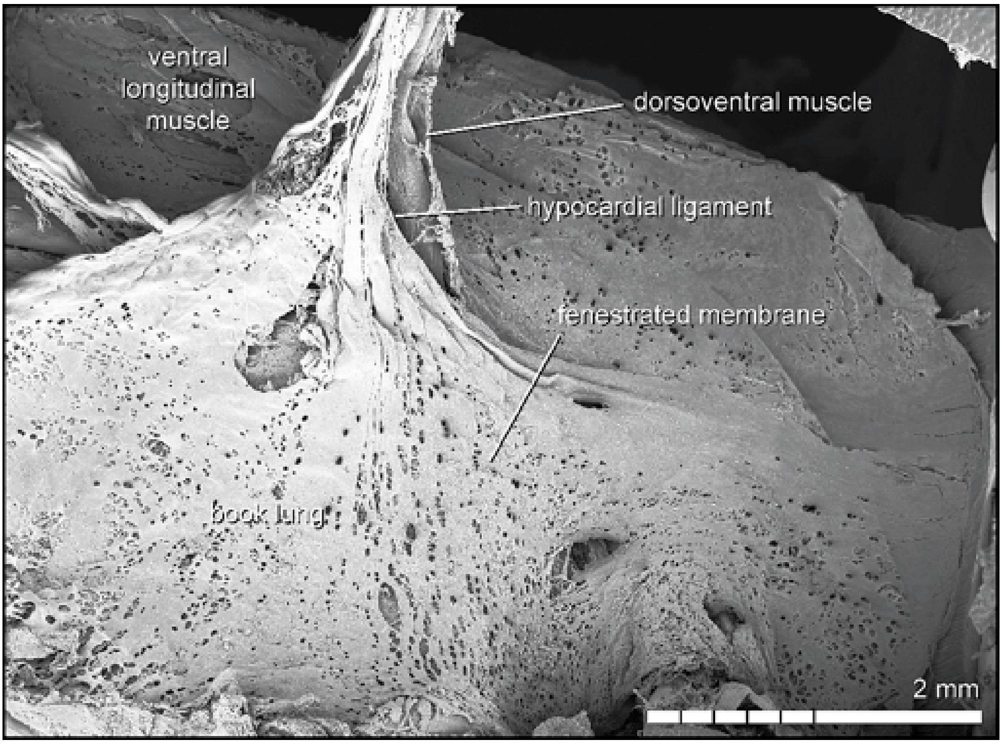


Fig. 7. *Hadogenes* sp., 1 ♂ (HUB): dorsolateral view of fenestrated membrane, covering sternite and book lung.

lamellar surface, distinguishing it from the surfaces along the proximal edges of the air sacs (fig. 5), where adjacent lamellae are connected by bridging trabeculae. There are two distinct states for both structures (reticulate venation and papillate trabeculae), resulting in four states for the character: simple trabeculae (state 1); branched trabeculae (state 2); slender venation (state 3); ribbed venation (state 4).

The two types of papillate trabeculae were previously described by Kamenz et al. (2005). Simple trabeculae (state 1) are observed in most nonbuthid scorpions. These trabeculae are blunt or knoblike apically. Branched trabeculae (state 2) are slender columns with as many as five narrower branches apically.

Slender venation (state 3), first described by Kamenz et al. (2005), consists of branching, reticulate veins that enclose slender areas directed toward the lamellar edges. Ribbed venation (state 4), identified here for the first time, is characterized by veins surrounding polygonal surfaces, which are broader than the surfaces characteristic of state 3 but become consistently more slender near the distal lamellar edges. Each polygonal surface contains up to five parallel ribs, directed toward the distal lamellar edge. Ribbed venation is a new state, not previously mentioned by Kamenz et al. (2005).

Distal edges of lamellae: Structures on the lamellar edges (character 2) differ significantly from those on the lamellar surfaces and are restricted to the immediate edge of the lamella (fig. 16). Although a gradation is sometimes observed from structures on the lamellar surfaces to those on the lamellar edges, the change is usually rather abrupt. Seven different states of structures on the lamellar edge can be distinguished, six of which have already been described by Kamenz et al. (2005): bristles (state 1); spines (state 2); thorns (state 3); smooth/wrinkled (state 4); meandering (state 5); arcuate bows (state 6); padded (state 7). Padded structures are described here for the first time.

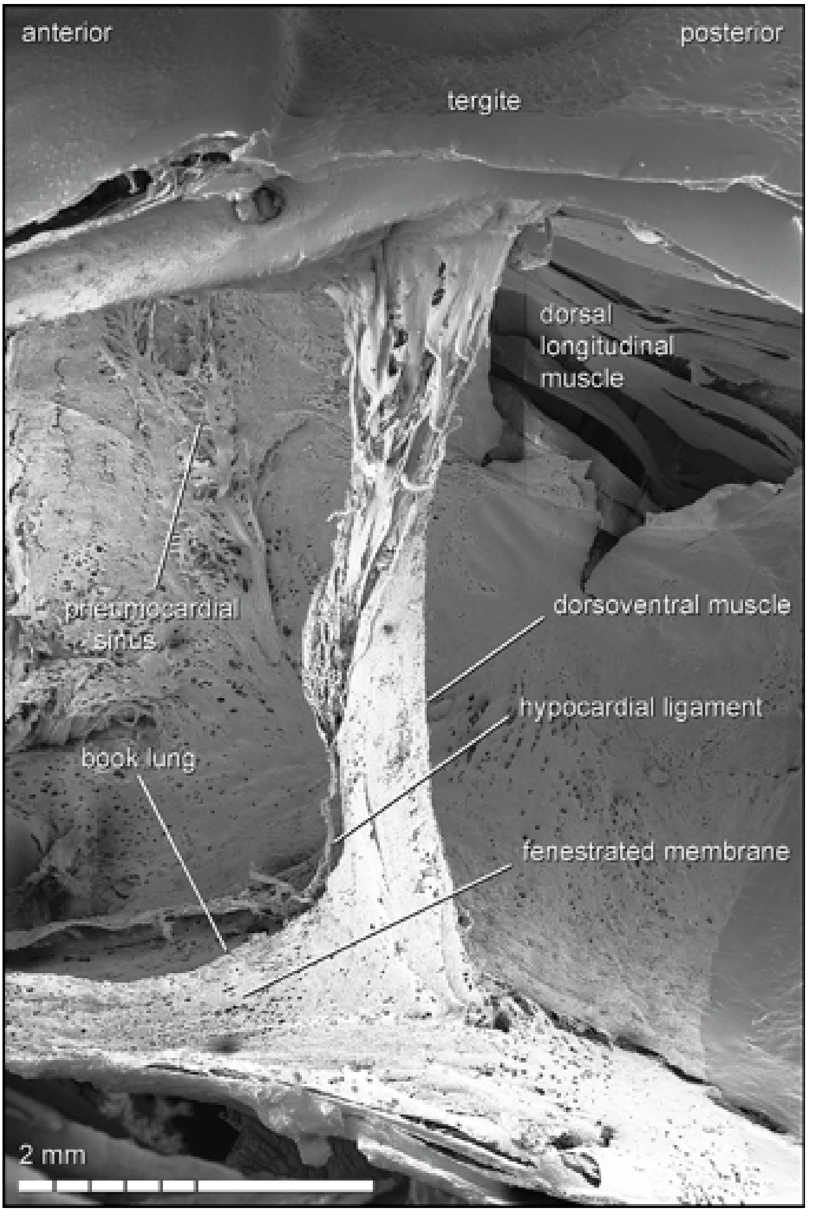


Fig. 8. *Hadogenes* sp., 1 ♂ (HUB): median lateral view of body cavity, with midgut removed.

The first three states of lamellar edge structures are similar. Bristlelike (state 1) and spinelike (state 2) structures have narrow bases, are rather thin, and taper slightly at the ends. Both structures occur on lamellae covered with trabeculae, but are readily distinguished from the latter, which are shorter and more cylindrical in shape. Whereas bristles are soft and flexible, spines are rigid and straight. Bristles point in all directions and often occur side by side around the semicircular (cross section) lamellar edge. Spines are usually arranged almost parallel to one another, projecting away in the same plane as the lamella. The third state of similar structures, thorns (state 3), are rather short and usually exhibit a broad base. Thorns usually arise from wrinkled venation

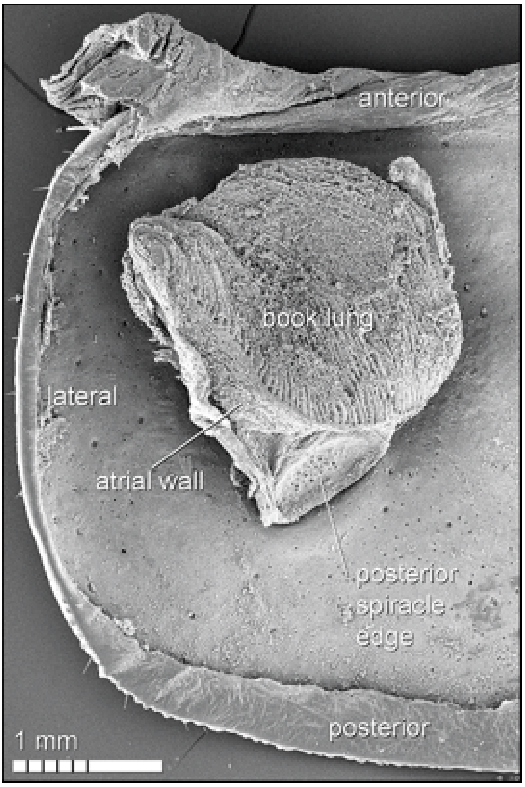


Fig. 9. *Broteochactas delicatus* (Karsch, 1879), 1 ♂ (AMNH), KOH-macerated cuticle: dorsal view of lateral part of sternite, showing cuticular parts of book lung.

Fig. 10. *Didymocentrus lesueurii* (Gervais, 1844), 1 ex. (MNHN): view from lamellae toward atrial wall, showing transition to posterior spiracle edge.

and occur more sporadically along the lamellar edges than spines.

Venation often merges with a smooth or sometimes wrinkled (state 4) lamellar edge. Wrinkles may be very deep but are clearly distinct from meandering structures (state 5), which occur together with trabeculae on the lamellar surfaces. Meandering structures consist of more or less slender areas winding along the lamellar edges, surrounded by winding, raised bulges, sometimes enclosing groups of small spines.

The remaining states of lamellar edges are quite different from one other and from all others. Arcuate bows (state 6), the ends of which merge with the lamellar edge to create a complex, irregular reticulate vault, are always observed together with trabeculae on the lamellar surfaces. Flat or pillowlike pads (state 7), observed only in *Chaerilus* Simon, 1877, cover the lamellar edges with a deeply perforated network.

Posterior edge of spiracle: The posterior spiracle edge (character 3) exhibits the greatest diversity of structures (fig. 17). Twelve character states, five of which (states 8–12) are described here for the first time, can be clearly defined: hillocks (state 1); subconical (state 2); hairlike (state 3); flattened (state 4); scaly (state 5); chisel-like (state 6); hexagonal tiles (state 7); treelike (state 8); subtree-like (state 9); polygonal columns (state 10); clublike (state 11); spiked macelike (state 12). The first three character states are simple processes, the others more complex structures containing distinct substructures.

Kamenz et al. (2005) described simple cuticular processes on the posterior edge of the spiracle, ranging from small, shallow hillocks (state 1), through subconical processes that are higher than wide (state 2), to very long, hairlike processes (state 3). Ka-

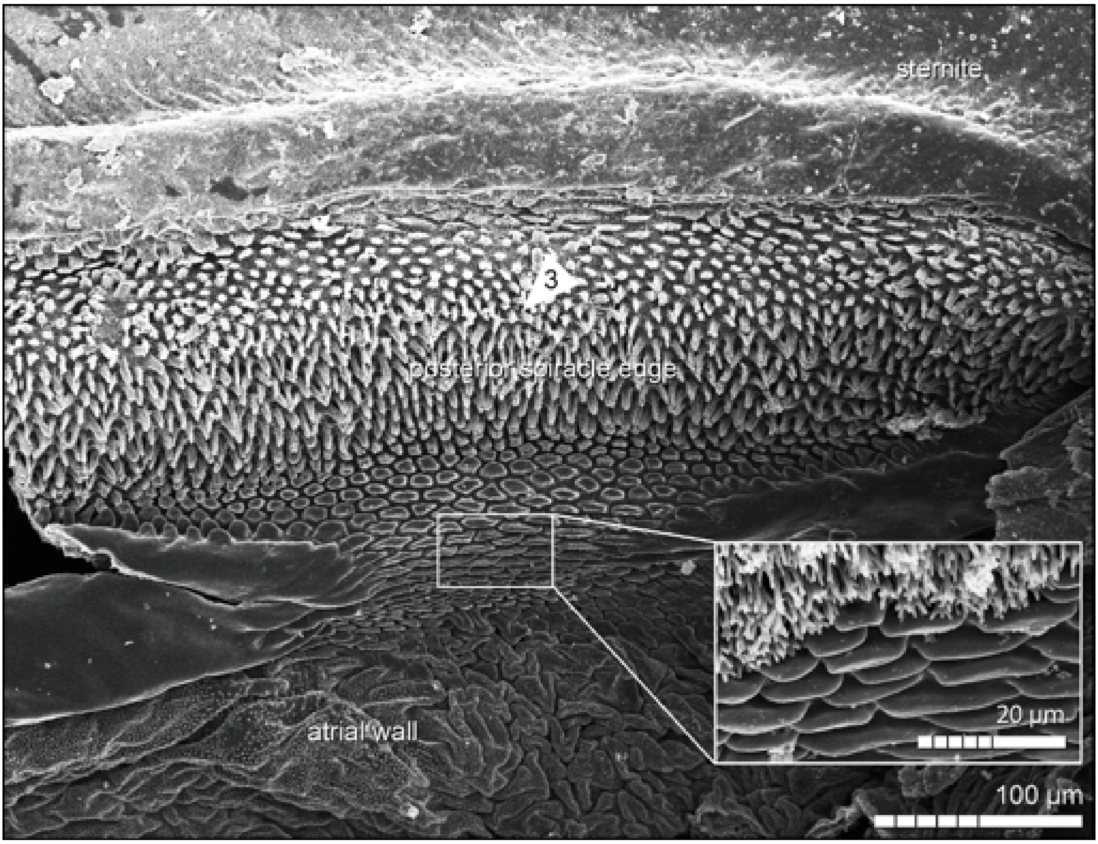


Fig. 11. *Vaejovis spinigerus* (Wood, 1863), 1 ♂ (AMNH [LP 1811]): anterior view of posterior spiracle edge with transition to sternite and wall of atrium, anterior parts of sternite removed. Note change in shape of cuticular processes from flat-oval (box) to subconical structures on spiracle edge (character 3, denoted with arrowhead); a movable flap normally closes the spiracle unless pulled open by contraction of the poststigmaticus muscle. Inset: *Urophonius iheringii* Pocock, 1893, 1 ♀ (AMNH [LP 3457]): magnified posterior view of flat-oval processes on transition from spiracle edge to atrial wall.

menz et al. (2005) described lobelike, flattened processes, the tips of which vary from a single blunt end to several pointed tips, as state 4. The flattened structures described by Kamenz et al. (2005) are sometimes broadened, and overlap one another to a lesser extent than scales (state 5). Chisel-like structures (state 6) are characterised by a nearly cylindrical shaft with a flattened tip, bearing a few distinct teeth. The flattened, scaly and distinct chisel-like structures appear to be points on a continuum of variation.

The hexagonal pillars (state 7), described by Kamenz et al. (2005), are here renamed hexagonal tiles to avoid confusion with the pillar cells inside the lamellae (Scholtz and Kamenz, 2006). This amended term refers to the regular arrangement of each hexagonal plate in a particular surface, and the very regular, jointlike gaps between them. The height of these structures varies from almost zero, when only the hexagonal plates are visible, to about five times the diameter of the plate. The more slender shaft is usually cylindrical to hexagonal.

Treelike structures (state 8), i.e., spinelike to hairlike cuticular processes with several branches, are observed on the posterior spiracle edge of the bothriurid scorpion, *Urophonius iheringii*. Structures on the posterior spiracle edge of the bothriurids, *Centromachetes obscurus* and *Timogenes mapuche*, exhibit similar outgrowths, but the branches on these structures are short and thornlike.

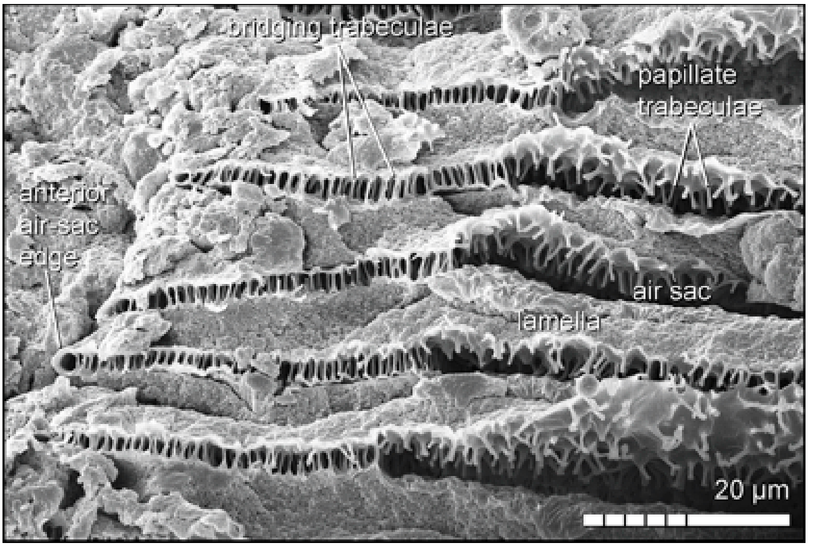


Fig. 12. *Euscorpius carpathicus candiota* Birula, 1903, 1 ♀ (HUB): lateral view of proximal parts of book lung (longitudinal section) showing lamellae and blind ends of air sacs.

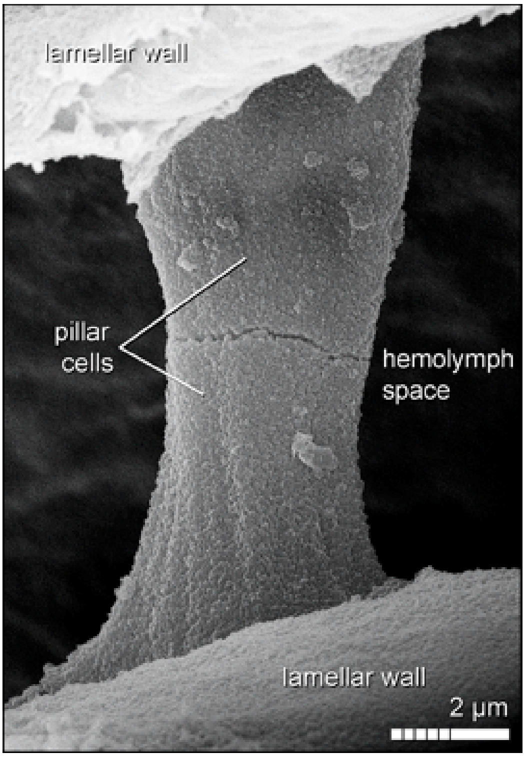


Fig. 13. *Euscorpius flavicaudis* (DeGeer, 1778), 1 ex. (MNHN): internal view into lamella showing cellular pillar in hemolymph space.

These subtree-like structures (state 9) may be an intermediate step in the transformation between subconical and treelike structures.

The structures on the posterior spiracle edge of *Paruroctonus* Werner, 1934 are superficially similar to hexagonal tiles (state 7). However, the apical plates of these structures are smaller, almost as wide as the shaft, irregular in shape, and do not all lie in the same plane. The gaps between the plates are much larger and less regular than in state 7. These structures, not considered to be homologous with the hexagonal tiles, are termed polygonal columns (state 10).

A unique, distally expanded clublike structure (state 11) is observed on the posterior spiracle edge of *Teuthraustes* Simon, 1878. Another unique structure, a spiked mace, shaped somewhat like a flattened hillock, densely covered with subconical thorns (state 12), is observed on the posterior spiracle edge of *Uroctonites huachuca*.

Book Lungs of Pseudochactidae

LAMELLAR SURFACES: Viewed from the air space, the ventral surfaces of the book lung lamellae of *P. ovchinnikovi* are covered with simple, conical trabeculae with a broad base

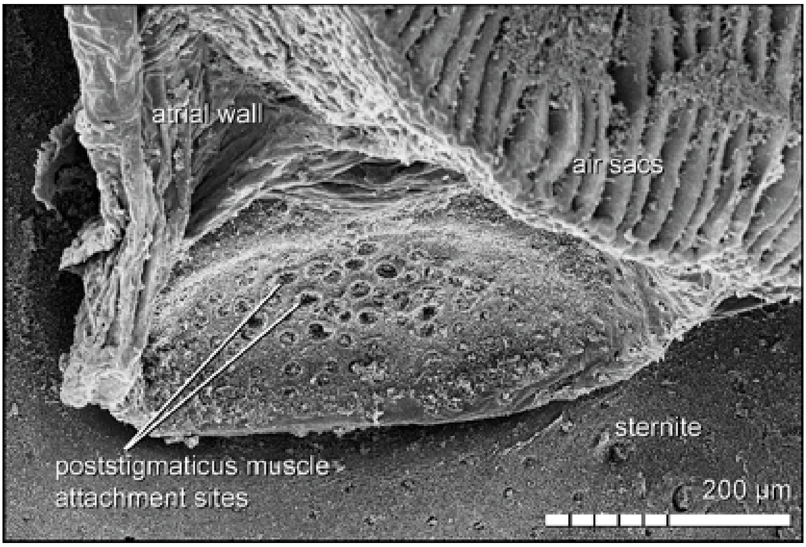


Fig. 14. *Broteochactas delicatus* (Karsch, 1879), 1 ♂ (AMNH), KOH-macerated cuticle: dorsal view of attachment site of poststigmaticus muscle on posterior edge of book lung spiracle. Posterior edge normally closes spiracle unless pulled open by contraction of poststigmaticus muscle.

(pl. 1A). The trabeculae are supported by fold-like ridges merging into the lamellar surface.

DISTAL EDGES OF LAMELLAE: Bristlelike or spinelike processes project into the atrium from the lamellar edges of *P. ovchinnikovi* (pl. 1B). Sail-like cuticular folds are stretched between the lamellar edge and the bases of these spines.

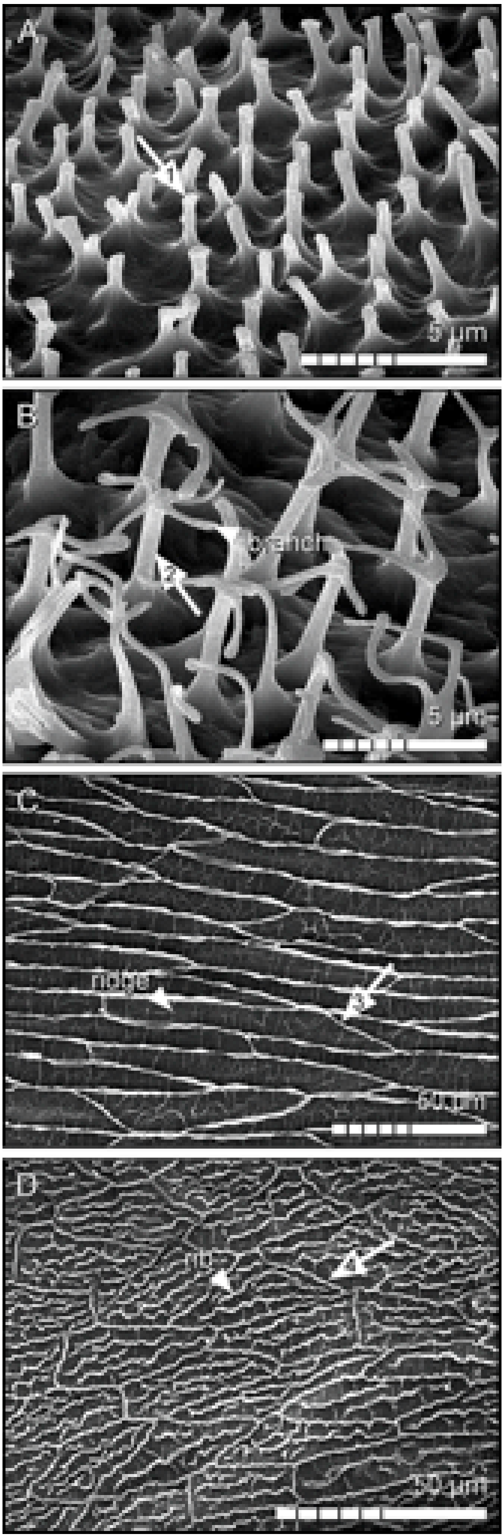
POSTERIOR EDGE OF SPIRACLE: Extremely flattened subconical structures occur along the posterior edges of the spiracles of *P. ovchinnikovi* (pl. 1C). Distal teeth are sometimes also observed.

Book Lungs of Buthidae and Microcharmidae

LAMELLAR SURFACES: Viewed from the air space, the distal lamellar surfaces of all buthoid exemplars (including *Microcharmus* Lourenço, 1995) studied during the present investigation are covered on both sides with reticulate venation (pls. 2–59A). The veins are ridges that branch and fuse, surrounding more or less slender, polygonal surfaces. In some New World buthid exemplars examined (*C. elii*, *M. rickyi*, *Tityus*, and *Z. fuscus*; pls. 12A, 33A, 46–55A, 58A), the surfaces between the veins are usually polygonal and contain up to five parallel striations (ribs), but become more slender toward the distal edges of the lamellae. In all other buthoids, including *Microcharmus*, they are more slender (pls. 2–11A, 23–32A, 34–45A, 56A, 57A, 59A), and often contain folded ridges that branch perpendicularly or wind irregularly from the veins.

DISTAL EDGES OF LAMELLAE: The distal edges of the lamellae of buthoids (including *Microcharmus*) are smooth to wrinkled, with larger veins winding along the edges. Smooth edges are observed in *C. elii* (pl. 12B), *Centruroides* Marx, 1890 (pls. 13–17B), *G. hirtus* (pl. 21B), *R. rochae* (pl. 44B), and *Tityus* (pls. 46–55B). More wrinkled edges, with sporadic thorns, occur in *A. cussinii* (pl. 2B), *B. buettneri* (pl. 7B), *H. conspersus* (pl. 22B), *I. angusticaudis* (pl. 24B), *Lychas* C. L. Koch, 1845 (pls. 30B, 31B), *M. rickyi* (pl. 33B), *O. dentatus* (pl. 35B), *R. bonettii* (pl. 40B), *R. junceus* (pl. 41B), *R. laticauda* (pl. 42B), *R. princeps* (pl. 43B), *T. baroni* (pl. 45B), and *Z. fuscus* (pl. 58B). All other buthid exemplars exhibit short, strong thorns projecting at regular distances along the lamellar edges.

POSTERIOR EDGE OF SPIRACLE: Low hillocks or subconical spinelike structures are observed along the posterior edges of all buthoid exemplars (pls. 2–58C). These struc-



tures are rounded in *C. exilicauda* (pl. 13C), *C. maindroni* (pl. 20C), *K. methueni* (pl. 27C), *M. eupeus* (pl. 32C), *C. elii* (pl. 12C), and form hillocks in *G. hirtus* (pl. 21C), *H. conspersus* (pl. 22C), *I. angusticaudis* (pl. 24C), *Isometrus* Ehrenberg, 1828 (pls. 25C, 26C), *L. kessleri* (pl. 29C), *Lychas* (pls. 30C, 31C), *Orthochirus* Karsch, 1891 (pls. 36C, 37C), *P. pegleri* (pl. 39C), *R. bonettii* (pl. 40C), *R. laticauda* (pl. 42C), *T. baroni* (pl. 45C), *U. flavoviridis* (pl. 56C), and *V. globimanus* (pl. 57C). The processes on the posterior edges of the spiracles are spinelike and pointed in all other buthoid exemplars. Data for the spiracle edge are unavailable for *A. cussinii*, *T. bolivianus*, and *Microcharmus*.

Book Lungs of Chaerilidae

LAMELLAR SURFACES: The surface structure of the lamellae of *C. truncatus* (pl. 60A) is similar to that observed in the New World buthid exemplars of *Tityus*, *Caribetityus* Lourenço, 1999, *Microtityus* Kjellesvig-Waering, 1966, and *Zabius* Thorell, 1893. It is characterized by reticulate venation surrounding slender to polygonal surfaces with internal striations (ribs) running parallel toward the distal edge of the lamella.

DISTAL EDGES OF LAMELLAE: Irregularly arranged, pillowlike pads, mostly covered with a perforated network of veins, demarcate the distal edges of the lamellae of *C. truncatus* (pl. 60B). The pillowlike sculpturing along the lamellar edges gradually transforms into an extremely dense reticulate network of veins on the lamellar surfaces.

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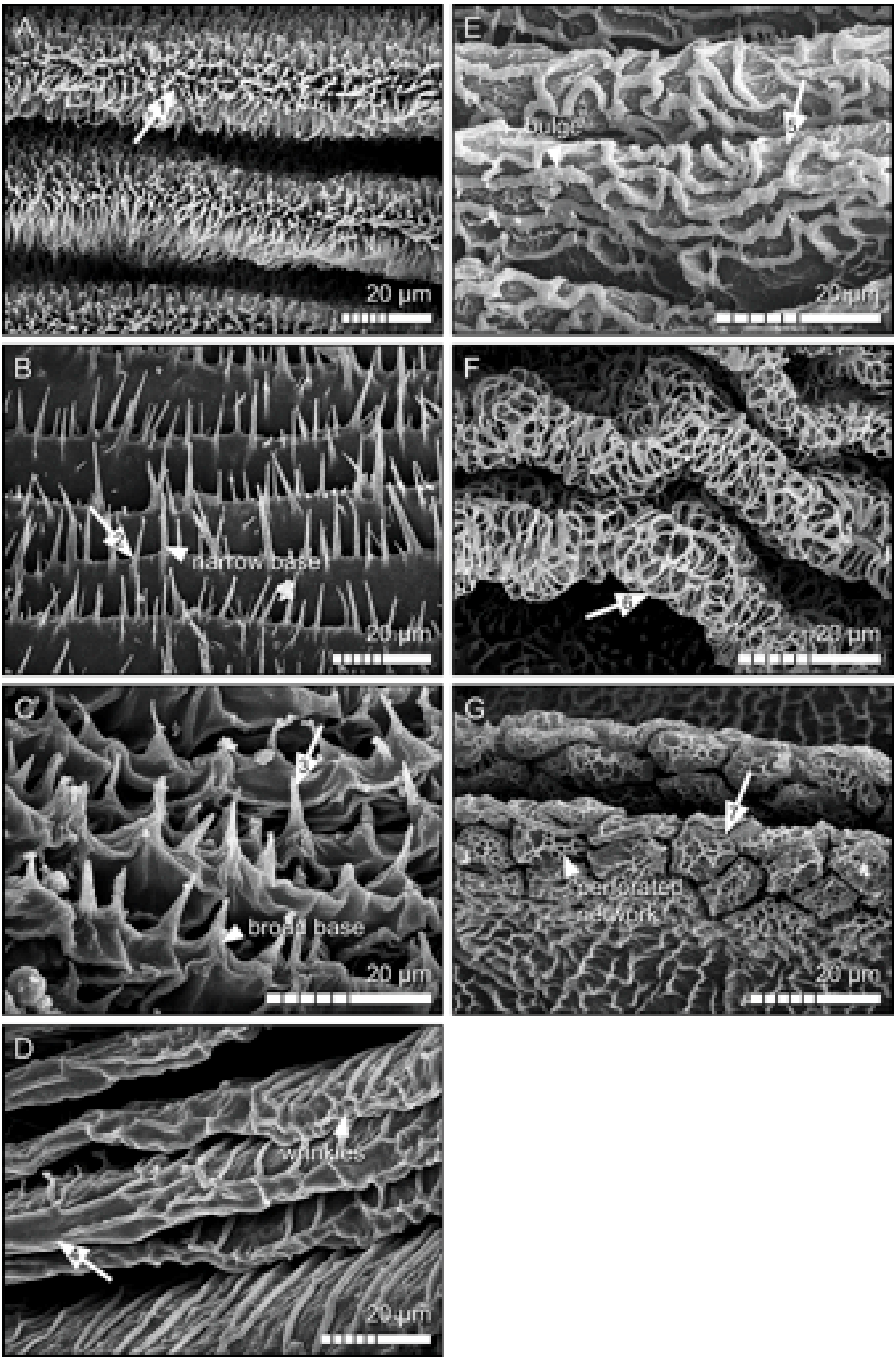
Fig. 15. Book lung, lamellar surface (character 1): **A.** *Paruroctonus becki* (Gertsch and Allred, 1965), 1 juv. ♀ (AMNH [LP 4991]), state 1: simple trabeculae (arrow); **B.** *Pandinus cavimanus* (Pocock, 1888), 1 ♀ (AMNH [LP 3259]), state 2: branching trabeculae (arrow), branch (arrowhead); **C.** *Parabuthus leiosoma* (Ehrenberg, 1828), 1 ♀ (AMNH [LP 1845]), state 3: slender venation (arrow), perpendicular ridge (arrowhead); **D.** *Zabius fuscus* (Thorell, 1876), 1 juv. ♀ (AMNH [LP 1759]), state 4: ribbed venation, polygonal surface (arrow), parallel ribs (arrowhead); numbers in arrows refer to character states.


A
20 µm
B
narrow base
20 µm
C
broad base
20 µm
D
wrinkles
20 µm
E
bulge
20 µm
F
20 µm
G
perforated
network
20 µm

POSTERIOR EDGE OF SPIRACLE: Subconical or spinelike processes are observed on the posterior edges of the spiracles of *C. truncatus* (pl. 60C).

Book lungs of Iuridae

LAMELLAR SURFACES: The lamellae of all iurid exemplars are covered with simple trabeculae on the ventral surfaces (pls. 61–66A). These trabeculae may be very flexible, as in *C. keyserlingi* (pl. 63A).

DISTAL EDGES OF LAMELLAE: The distal lamellar edge exhibits diverse structures in Iuridae (pls. 61–66B). Whereas *A. phaiodactylus* (pl. 61B) and *H. charcasus* (pl. 64B) possess flexible bristles, rigid spines are observed on the lamellar edges of *H. hirsutus* (pl. 65B). The lamellar edges of *C. keyserlingi* (pl. 63B) are covered with arcuate bowlike structures. In the iurine exemplars, *C. nordmanni* (pl. 62B) and *I. dufoureius* (pl. 66B), meandering bulges wind along the lamellar edges and surround slender areas sometimes enclosing small spines.

POSTERIOR EDGE OF SPIRACLE: The structures on the posterior edge of the spiracle are similarly diverse in Iuridae (pls. 61–66C). *Hadruroides charcasus* (pl. 64C) displays low hillocks and subconical processes, *H. hirsutus* spinelike processes (pl. 65C), and *C. keyserlingi* (pl. 63C) spinelike processes with a tendency to branch (subtree-like). The processes along the spiracle edge of *C. nordmanni* (pl. 62C) are broad hillocks or lobes with teeth arranged in irregular rows along the distal margin.

Book Lungs of Euscorpiidae and Scorpiopidae

LAMELLAR SURFACES: The ventral surfaces of the lamellae of all euscorpiid and scorpiopid exemplars studied are covered with regularly spaced, simple trabeculae (pls. 67–70A). The trabeculae are rather short in *T. willis* (pl. 69A), whiplike in *S. hardwickei* (pl. 70A), or end in a knoblike tip in *Euscorpius* Thorell, 1876 species (pl. 67A). The bases of the trabeculae tend to be stabilized by small, foldlike ridges continuously merging into the lamellar surface. Branched trabeculae occur sporadically in *S. hardwickei*.

DISTAL EDGES OF LAMELLAE: The lamellar edges of *S. hardwickei* (pl. 70B) and *T. willis* (pl. 69B) are covered with dense, brushlike bristles. *Megacormus granosus* (pl. 68B) and *Euscorpius* species (pl. 67B) display arcuate bowlike structures along the distal lamellar edges.

POSTERIOR EDGE OF SPIRACLE: All euscorpiid and scorpiopid exemplars investigated exhibit flat hillocks covering the posterior edges of the spiracles (pls. 67–70C).

Book Lungs of Chactidae

LAMELLAR SURFACES: The ventral surfaces of the lamellae of the chactid exemplars studied are covered with simple trabeculae (pls. 71–78A), regularly spaced apart. The trabeculae of most chactid exemplars are flexible and end in a knoblike tip that is at most 1.5 times the narrowest diameter of the

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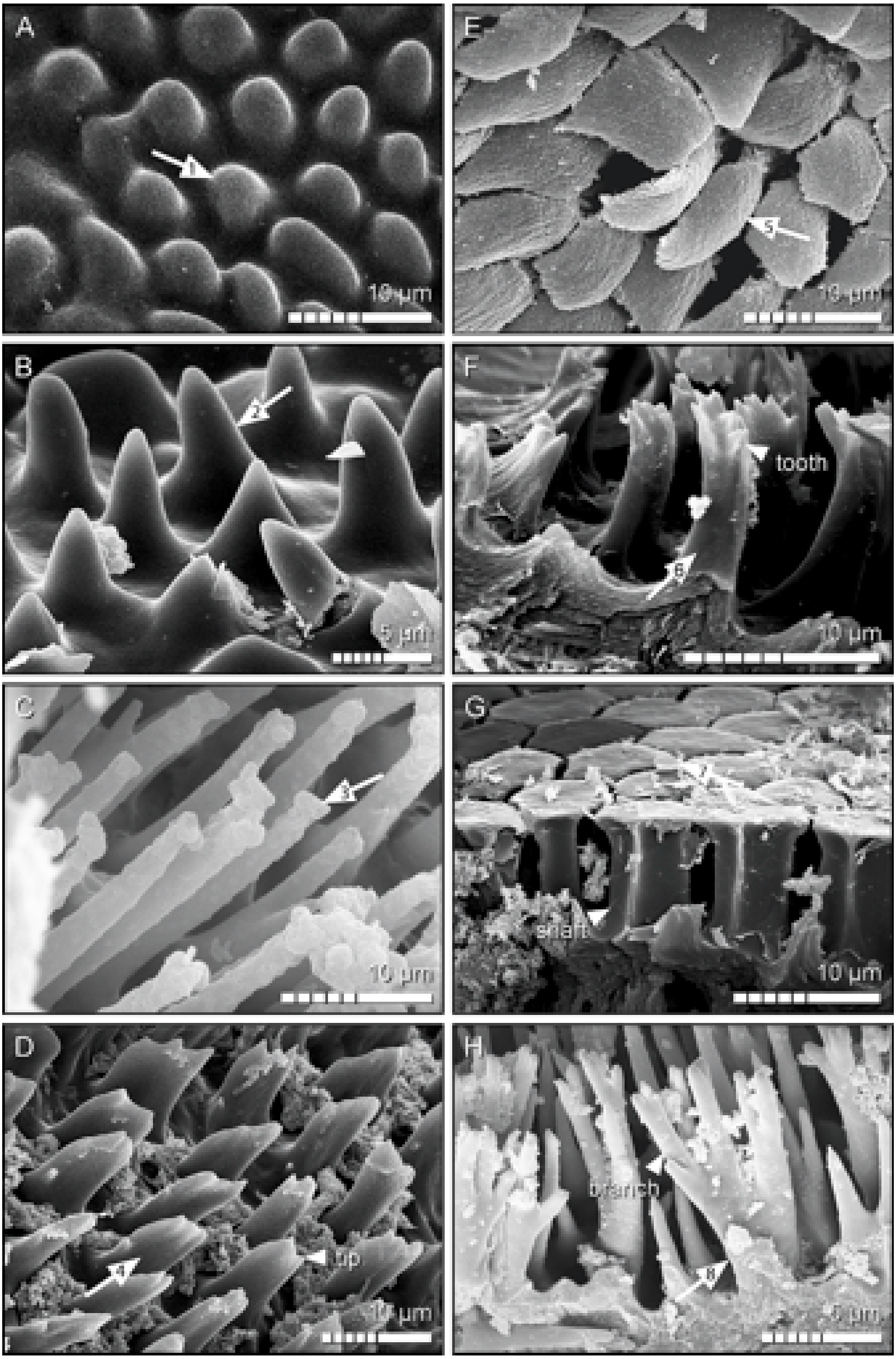
Fig. 16. Book lung, distal lamellar edge (character 2): **A.** *Pandinus cavimanus* (Pocock, 1888), 1 ♀ (AMNH [LP 3259]), state 1: bristles on lamellar edge (arrow); **B.** *Timogenes mapuche* Maury, 1975, 1 ♂ (AMNH [LP 4312]), state 2: spines on lamellar edge (arrow), narrow base of spine (arrowhead); **C.** *Orthochirus innesi* Simon, 1910, 1 ♀ (MNHN RS 5440), state 3: thorns on lamellar edge (arrow), broad base of thorn (arrowhead); **D.** *Rhopalurus princeps* (Karsch, 1879), 1 ♂ (AMNH [LP 1566]), state 4: smooth (arrow) to wrinkled (arrowhead) lamellar edge; **E.** *Iurus dufoureius asiaticus* Birula, 1903, 1 juv. (HUB), state 5: meandering, winding bulges (arrowhead) surrounding winding surfaces (arrow); **F.** *Liocheles waigiensis* (Gervais, 1843), 1 ♀ (AMNH [LP 1502]), state 6: arcuate bows (arrow); **G.** *Chaerilus* sp., 1 ♀ (MNHN RS 0607), state 7: pillowlike pad (arrow), perforated network (arrowhead); numbers in arrows refer to character states.


A
1
10 µm
E
5
10 µm
B
2
5 µm
F
tooth
6
10 µm
C
3
10 µm
G
7
shaft
10 µm
D
4
tip
10 µm
H
branch
8
5 µm

shaft. Compared with the other chactids observed, the trabeculae are rigid in *B. granulatus* (pl. 72A).

DISTAL EDGES OF LAMELLAE: The lamellar edges of most chactid exemplars (pls. 71–78B) display brushlike bristles. However, the bristles are reduced to a sparse, irregular row in *N. allenii* (pl. 77B). *Chactas* Gervais, 1844 (pls. 73B, 74B) and *Teuthraustes* (pl. 78B) possess bow-shaped processes, fusing to form complex arcuate reticulations, along the lamellar edges.

POSTERIOR EDGE OF SPIRACLE: Subconical hillocks are observed along the posterior edges of the spiracles of *B. nitidus* (pl. 71C) and *N. allenii* (pl. 77C). These processes are additionally armed with terminal teeth, often arranged in a row, in *B. granulatus* (pl. 72C), *C. raymondhansi*, *C. reticulatus* (pls. 73C, 74C), *G. gonzalespongai* (pl. 75C), and *H. schaumii* (pl. 76C). These processes are some-

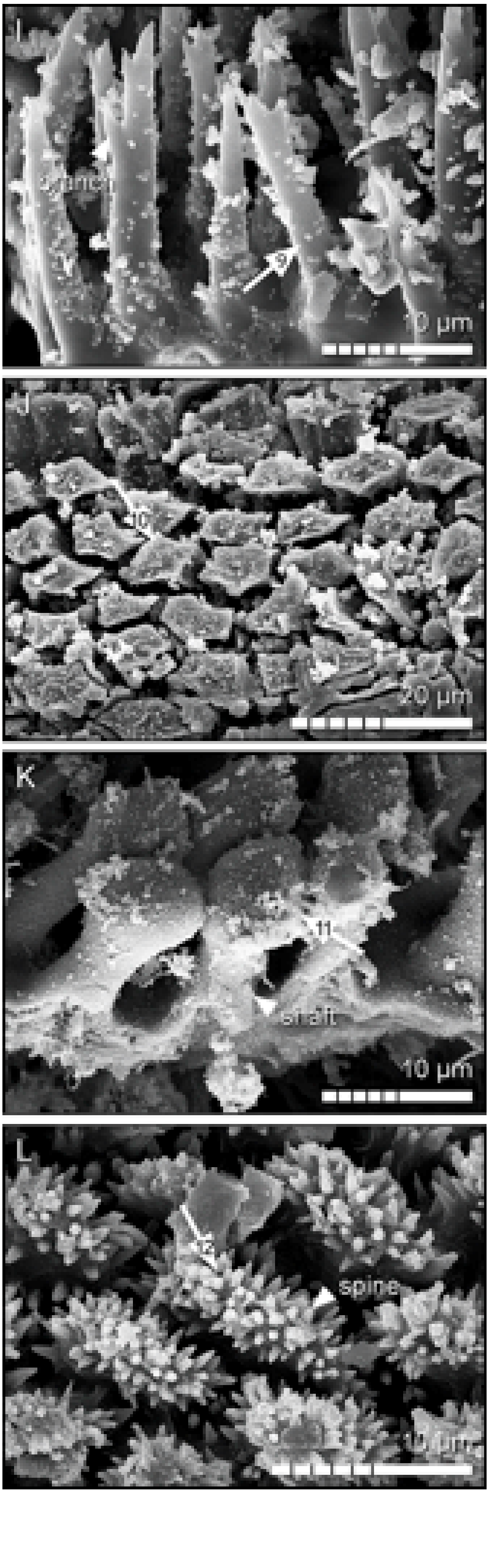


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Fig. 17. Book lung, posterior spiracle edge (character 3): **A.** *Karasbergia methueni* Hewitt, 1913, 1 ♂ (AMNH [LP 1724]), state 1: hillocks (arrow); **B.** *Orthochirus innesi* Simon, 1910, 1 ♀ (MNHN RS 5440), state 2: subconical processes (arrow); **C.** *Centromachetes pocockii* (Kraepelin, 1894), 1 ♀ (ZMB 35145), state 3: hairlike processes (arrow); **D.** *Urodacus yaschenkoi* (Birula, 1903), 1 ♂ (AMNH [LP 1659]), state 4: flattened processes (arrow), pointed tips (arrowhead); **E.** *Bothriurus coriaceus* Pocock, 1893, 1 ♂ (ZMB 8322), state 5: scaly processes (arrow); **F.** *Liocheles waigiensis* (Gervais, 1843), 1 ♀ (MNHN RS 8350), state 6: chisel-like processes (arrow), distinct teeth (arrowhead); **G.** *Scorpio maurus* subsp., 1 ♀ (MNHN), state 7: hexagonal tiles (arrow), columellar shaft (arrowhead); **H.** *Urophonius iheringii* Pocock, 1893, 1 ♀ (AMNH [LP 3457]), state 8: treelike processes (arrow), branches (arrowhead); **I.** *Centromachetes obscurus* Mello-Leitão, 1932, 1 ♂ (AMNH [LP 2436]), state 9: subtree-like processes (arrow), short branches (arrowhead); **J.** *Paruroctonus stahnkei* (Gertsch and Soleglad, 1966), 1 ♂ (AMNH [LP 3566]), state 10: polygonal columns (arrow); **K.** *Teuthraustes atramentarius* Simon, 1878, 1 ♀ (MNHN RS 0784), state 11: clublike processes (arrow), slender shaft (arrowhead); **L.** *Uroctonites huachuca* (Gertsch and Soleglad, 1972), 1 ♀ (AMNH), state 12: spiked macelike processes (arrow), spikes (arrowheads); numbers in arrows refer to character states.

what elongated, with a flat tip, broadened to a chisel shape, in *C. reticulatus* (pl. 74C; Kamenz et al., 2005). Distally expanded, clublike processes are observed in *T. gervaisii* (pl. 78C).

Book Lungs of Superstitioniidae and Troglotayosicidae

LAMELLAR SURFACES: The ventral surfaces of the lamellae of *A. tartarus* (pl. 79A) are folded into small triangular, conelike structures, sometimes fusing into more complex spines. In contrast, the ventral surfaces of the lamellae of *S. donensis* and *B. xambeui* (pls. 80A, 81A) display regularly spaced, simple trabeculae with blunt, rounded ends.

DISTAL EDGES OF LAMELLAE: The distal edges of the lamellae of *A. tartarus* (pl. 79B) are demarcated by meandering bulges, winding along the edges, similar to the structures observed in *Iurus* Thorell, 1876 and *Calchas* Birula, 1899. These bulges leave slender areas, which may contain small spines in between. The edges of the lamellae are covered with arcuate structures, consisting of fused bow-shaped cuticular processes, in *S. donensis* (pl. 80B). Brushlike bristles cover the lamellar edges of *B. xambeui* (pl. 81B).

POSTERIOR EDGE OF SPIRACLE: Flat hillocks are observed on the posterior edges of the spiracles of *S. donensis* (pl. 80C) and *B. xambeui* (pl. 81C). Data are unavailable for the spiracle edge of *A. tartarus*.

Book Lungs of Vaejovidae

LAMELLAR SURFACES: The ventral surfaces of the lamellae of all vaejovid exemplars studied are covered with simple trabeculae (pls. 82–100A), mostly ending in a knoblike tip, which is scarcely wider than the shaft. Single-branched trabeculae are sometimes observed in *P. borregoensis* (pl. 85A), *P. gracilior* (pls. 86A, 87A), *S. wupatkiensis* (pl. 91A), *S. vachoni* (pl. 92A), *S. macrura* (pl. 93A), and *Vaejovis* C. L. Koch, 1836 species (pls. 96–99).

DISTAL EDGES OF LAMELLAE: Several variations of spiny to bristly lamellar edges occur among the vaejovids (pls. 82–100B). Spiny lamellar edges are observed in *P. pumilus* (pl. 82B), *Paruroctonus* (pls. 83–88B), *S. wupatkiensis* (pl. 91B), *S. vachoni* (pl. 92B), *S. macrura* (pl. 93B), *V. nitidulus* (pl. 98B), and *V. spinigerus* (pl. 99B). More bristly projections on the lamellar edges occur in all other vaejovid species, except *U. mordax* (pl. 95B), and may be fused into thicker bundles, e.g., in *V. magdalensis* (pl. 96B). The bristles on the lamellar edges of *P. becki* (pl. 83B), *P. apacheanus* (pl. 89B), and *V. longiunguis* (pl. 100B) are short, and not distinctly different from the trabeculae on the ventral surface. Additionally, they do not cover the lamellar edges, which thus appear smooth. *Uroctonus mordax* is exceptional among vaejovids in possessing arcuate structures (pl. 95B), consisting of fused, bow-shaped cuticular processes, along the lamellar edges.

POSTERIOR EDGE OF SPIRACLE: The posterior spiracle edge displays a diversity of structures among Vaejovidae (pls. 82–100C). Shallow hillocks, observed in *P. pumilus* (pl. 82C), *S. wupatkiensis* (pl. 91C), and *U. mordax* (pl. 95C), are laterally expanded in *S. wupatkiensis* (pl. 91C). *Pseudouroctonus* (pls. 89C, 90C), *S. vachoni* (pl. 92C), *S. macrura* (pl. 93C), *U. huachuca* (pl. 94C), *V. magdalensis* (pl. 96C), *V. mexicanus* (pl. 97C), and *V. nitidulus* (pl. 98C) possess higher, subconical hillocks on the posterior spiracle edges, which are often broadened to round hillocks or lobes. These structures are often secondarily covered with small, regularly spaced wartlike processes, which are larger and thornlike in *P. reddelli* (pl. 90C). Massive subconical thorns without spaces cover the hillocks of *U. huachuca* (pl. 94C) creating a spiked, macelike surface. Primary subconical processes, also covered with secondary wartlike structures, occur on the posterior spiracle edges of *V. spinigerus* (pl. 99C) and *V. longiunguis* (pl. 100C). The secondary structures are arranged in lines or ridges from the base to the tip of the subconical processes in *V. spinigerus*. More complex processes occur on the posterior spiracle edges of all *Paruroctonus* exemplars studied (pls. 83–88C). These processes are columellar and irregular in cross section, from oval to irregular polygons with sharp or rounded corners. The distal end of these processes form irregular polygons with planar surfaces in *P. gracilior* (pls. 86C, 87C) and *P. stahnkei* (pl. 88C). The processes are fairly regularly spaced apart and superficially resemble the hexagonal tiles observed in diplocentrids, liochelids and scorpionids, but their irregular polygonal cross section suggests that they are not homologous with the tiles observed in these scorpionoid families.

Book Lungs of Bothriuridae

LAMELLAR SURFACES: All bothriurid exemplars studied possess rigid, simple trabeculae, regularly spaced apart, on the ventral surfaces of the book lung lamellae (pls. 101–119A). In cross section, the trabeculae are constant throughout most of their length, becoming broader at the base, which merges gradually into the lamellar surface. The tip of each trabecula is also expanded into a knoblike disc, the diameter of which is not greater than twice the diameter of the narrowest point of the trabecula, in *L. elegans* (pl. 109A). The trabeculae of all other bothriurids possess blunt, somewhat rounded tips.

DISTAL EDGES OF LAMELLAE: The bothriurid exemplars *L. elegans* (pl. 109B), *P. pictus* (pl. 113) and *U. tregualemuensis* (pl. 118B) exhibit an abrupt change from a ventral surface covered with trabeculae to a smooth dorsal surface. However, in most other bothriurid exemplars, the trabeculae on the edge change gradually into elongated and conical spines or attenuated bristles (pls. 101–108B, 110–112B, 114–117B, 119B). At one extreme on the morphological continuum, the spines of psammophilous species such as *T. mapuche* (pl. 116) and *B. ehrenbergii* (pl. 105B) are regularly spaced in a single row, and project straight into the atrium. At the other extreme, a bristly lamellar edge is observed in silvicolous species such as *C. obscurus* (pl. 107B) and *T. glasioui* (pl. 115B), where the softer, bent bristles form a dense, brushlike surface along the lamellar edges. The lamellae of most bothriurid exemplars exhibit spination somewhere between the two extremes. The bases of the spines may also be fused to restricted ridges along the edge, as observed in *B. burmeisteri* (pl. 102B). Branched spines occur sporadically on the lamellae of a few species, e.g., *C. sulcatus* (pl. 108B).

POSTERIOR EDGE OF SPIRACLE: The posterior edge of the spiracle is covered primarily with spinelike processes in all bothriurid exemplars studied (pls. 101–119C), except the two species of *Lisposoma* Lawrence, 1928. These spines may be rather short, as in *B. ferrugineus* (pl. 106C) and *V. martinezi* (pl. 119C), or elongated and hairlike, as in *C. pocockii* (Kamenz et al., 2005). In many cases, e.g., *B. chacoensis* (pl. 103C), *B. coriaceus* (pl. 104C), *C. obscurus* (pl. 107C), *C. sulcatus* (pl. 108C), and *T. mapuche* (pl. 116C), the long spines display a tendency to branch. Well-developed, branched treelike structures occur along the posterior spiracle edges of *P. sanmartini* (pl. 114C), *T. glasioui* (pl. 115C), and *U. iheringii* (pl. 117C). The structures on the posterior spiracle edge of *P. iskay* (pl. 112C) are flat, and form low hillocks or lobes. *Lisposoma* species (pls. 109C, 110C) display rigid, flattened or lobelike processes that are strengthened by lateral bulges.

Book Lungs of Urodacidae

LAMELLAR SURFACES: Simple, flexible trabeculae cover the ventral surfaces of the lamellae in the *Urodacus* Peters, 1861 exemplars studied (pls. 120A, 121A). Most trabeculae end in a knoblike tip, but some possess a single distal, perpendicular branch, the diameter of which is narrower than the shaft.

DISTAL EDGES OF LAMELLAE: The lamellar edges of *Urodacus* species are covered with brushlike bristles (pls. 120B, 121B).

POSTERIOR EDGE OF SPIRACLE: Elongated flattened to chisel-like structures occur along the posterior spiracle edges of *Urodacus* species (pls. 120C, 121C). These structures display irregular teeth, arranged in a single row, distally.

Book Lungs of Heteroscorpionidae

LAMELLAR SURFACES: The ventral lamellar surfaces of *H. opisthacanthoides* (pl. 122A) are covered with simple trabeculae. The trabeculae are mostly cylindrical, constant in diameter, and end in a blunt tip. Some trabeculae possess single branches of smaller diameter than the shaft. These branches arise perpendicularly from the shaft of the trabecula. The trabeculae rarely exhibit multiple branches.

DISTAL EDGES OF LAMELLAE: Brushlike bristles cover the distal edges of the lamellae of *H. opisthacanthoides* (pl. 122B).

POSTERIOR EDGE OF SPIRACLE: Polygonal columns or chisel-like processes occur on the posterior edge of the spiracles of *H. opisthacanthoides* (pl. 122C). The polygonal plates on top of the processes are often inclined, such that one side of the plate is fused to the shaft and the opposite side presents a sharp, chisel-like edge. All transitional states between the extremes described above, may be observed side by side along one spiracle edge.

Book Lungs of Hemiscorpiidae

LAMELLAR SURFACES: Rigid erect, simple trabeculae with a cylindrical, rodlike shape cover the ventral surfaces of the lamellae of *H. lepturus* (pl. 123A) and *H. tellinii* (not shown). The tips of the trabeculae are blunt and slightly rounded.

DISTAL EDGES OF LAMELLAE: The cuticular projections on the distal lamellar edges of *Hemiscorpius* Peters, 1861, e.g., *H. lepturus* (pl. 123B), are rigid, almost conical, sharply pointed spines, often branching apically. At the base, these spines appear to have pierced through the lamellar edges from inside, and abruptly give way to a smooth edge.

POSTERIOR EDGE OF SPIRACLE: The posterior spiracle edge of *Hemiscorpius*, e.g., *H. lepturus* (pl. 123C), is covered with hexagonal columns, the distal ends of which are expanded to closely aligned, hexagonal plates (tiles), leaving gaps of constant dimension across the surface.

Book Lungs of Liochelidae

LAMELLAR SURFACES: Regularly spaced, simple trabeculae, each with a knoblike tip, occur on the ventral surfaces of the lamellae of all liochelid exemplars studied (pls. 124–138A). As many as three (maximum five) perpendicular branches occur on the distal ends of the trabeculae in *Hadogenes* Kraepelin, 1894 (pls. 127–129A), *I. politus* (pl. 130A), *O. elatus* (pl. 135A), and *P. pauliani* (pl. 138A). The branches are narrower in diameter than the shaft of the trabeculae and, in most cases, fairly short. The tips of the branches may be clublike or knoblike.

DISTAL EDGES OF LAMELLAE: The lamellar edges of all liochelid exemplars studied, except *Liocheles* Sundevall, 1833 species, are densely covered with brushlike bristles (pls. 124–138B). The bristles on the lamellar edges of *Hadogenes* (pls. 127–129B) and *I. politus* (pl. 130B) are more rigid and spinelike. *Liocheles* species (pls. 131–134B), in contrast, display arcuate structures formed by the fusion of bent cuticular processes covering the lamellar edges.

POSTERIOR EDGE OF SPIRACLE: All liochelid exemplars, except *Liocheles*, possess hexagonal columns on the posterior edges of the spiracles (pls. 124–138C). The distal ends of the columns are expanded into hexagonal plates (tiles) which may be so closely aligned that they form an almost closed surface of facets, separated only by a regular, narrow network of gaps. *Liocheles* species (pls. 131–134C), however, display chisel-like structures with a broad, flat tip bearing several teeth in one or more irregular rows. The base of these structures is rounded and the tips may be bent posteriorly.

Book Lungs of Diplocentridae

LAMELLAR SURFACES: More or less rigid, simple trabeculae cover the ventral surfaces of the lamellae of all diplocentrid exemplars studied (pls. 139–144A). The trabeculae of *B. comondae* (pl. 139A) are rather short compared with those of *D. lesueurii* (pl. 141A) and *D. mexicanus* (pl. 142A), the tips of which are broadened into a knob, at most twice the diameter of the shaft.

DISTAL EDGES OF LAMELLAE: The lamellar edges of all diplocentrid exemplars studied are covered with a complex arcuate structure comprising fused, bow-shaped cuticular processes (pls. 139–144B).

POSTERIOR EDGE OF SPIRACLE: All diplocentrid exemplars display columns with a hexagonal cross section along the posterior spiracle edges (pls. 139–144C). These columns vary in height from almost flat to three times their average diameter. The distal ends of the columns are expanded into hexagonal plates (tiles), often arranged side by side to form an almost closed surface of facets, separated only by a regular, narrow network of gaps.

Book Lungs of Scorpionidae

LAMELLAR SURFACES: The ventral lamellar surfaces of the scorpionid exemplars studied are covered with trabeculae with up to five narrower branches (pls. 145–156A). These branched trabeculae vary from robust rodlike shapes to thinner whiplike structures.

DISTAL EDGES OF LAMELLAE: The lamellar edges of the scorpionid exemplars (pls. 145–156B) are densely covered with brushlike bristles, which are more sparsely distributed on the lamellar edges of the psammophilous *O. holmi* (pl. 151B) and more rigid in *O. boehmi* (pl. 148B).

POSTERIOR EDGE OF SPIRACLE: Columns, which are hexagonal in cross section, cover the posterior spiracle edges of the scorpionid exemplars (pls. 145–156C). The distal ends of these columns are expanded into hexagonal plates (tiles), which may be so closely aligned that they form an almost closed surface of facets, separated only by a regular, narrow network of gaps across the posterior spiracle edge.

DISCUSSION

Historical Context

During the course of a century, only two studies, by Laurie (1896) and Pavlovsky (1926), investigated and compared the morphology of scorpion book lungs across a range of families, while a few earlier workers (e.g., Lankester, 1883; Berteaux, 1889) studied the morphology of the book lungs in a more limited sample of taxa. Laurie (1896) studied 22 species in 21 genera, whereas Pavlovsky (1926) expanded Laurie's taxon sample to 35 species in 31 genera (table 1). Although these studies were in many ways at the cutting edge of research for their time, the extent to which they can be compared with the results of the present study is, unfortunately, rather limited. Obviously, both authors were dependent on the optical equipment of the time. Many of the character states revealed in the present study cannot be observed, adequately or at all, with standard histological techniques and light microscopy, and it is not surprising that new character states have been discovered, and/or interpretations revised, with the application of SEM. Laurie and Pavlovsky were also limited by the availability of specimens and taxa for observation, necessitating generalizations about characters and their distribution in taxa. Compared with previous studies, the use of multiple exemplars for determining the distribution of character states across higher taxa in the present study is vastly superior to making assumptions based on one or a few representatives.

In spite of these advances and their implications for comparison with earlier literature on the subject, we are nevertheless able to confirm several observations made by previous authors. For example, the general observation by early workers of the occurrence of reticulated lamellae in all buthid scorpions was confirmed in the present study. Lankester (1883: pl. 81) was the first to demonstrate these "reticulate ornaments" in precise illustrations. The reticulation was subsequently reported sporadically in the literature (e.g., Berteaux, 1889; Kaestner, 1940; Rödl et al., 1989), misinterpreted by Peters (1969), in transverse sections, as papillate trabeculae covering both sides of the lamellae, and appeared finally in the first quantitative analysis of scorpion phylogeny, the unpublished Ph.D. dissertation of Stockwell (1989). The two distinct types of reticulation on the lamellar surfaces of buthoids and chaerilids (figs. 15C, D, pls. 2–60A) were not recognized prior to the present study, however.

Trabeculae were first described by Lankester (1883: 378), who observed the combination of reticulation with "punctate ornament in the periphery of the … lamella". Lankester (1883) was probably referring to the bridging trabeculae (fig. 12), which appear as points in the view from above, but it is unclear what he referred to by "periphery of the lamella". We prefer the use of "proximal" to emphasize the occurrence of bridging trabeculae primarily in the anterior to medial areas of the lamellae (fig. 5), where the booklike respiratory organs of all chelicerates, including xiphosurans, are flooded with hemolymph. We follow Scholtz and Kamenz (2006) in interpreting this proximal region to be plesiomorphic for arachnids.

Berteaux (1889) was the first to identify and distinguish branched trabeculae (fig. 15B), projecting into the air space, in a scorpionid, *Heterometrus cyaneus* (C.L. Koch, 1836), as *Scorpio indicus* (Karsch, 1884), from the simple unbranched trabeculae of other species (fig. 15A). This character state was not noted again until the present study, where it was confirmed in a broader group of scorpionoid taxa, including scorpionids (pls. 145–156A), liochelids (pls. 127–130A, 135A, 138A), and urodacids (pls. 120A, 121A). Pavlovsky's (1926) observations of the occurrence of reticulation (''chitinous network'') on one side and trabeculae (''chitinous columellae'') on the other side of the lamellae of *Calchas nordmanni* could not be confirmed in our investigations: only the usual covering of trabeculae was observed.

We also disagree with some of the terminology and observations proposed by Laurie (1896) and accepted by Pavlovsky (1926). The terms ''spinous lamella'' (sensu Laurie, 1896) or ''barbate lamina'' (sensu Pavlovsky, 1926) are too imprecise to be informative. The distinct kinds of cuticular processes on the lamellar edges were not mentioned by these authors, nor was a distinction made between the trabeculae (fig. 15) and the structures on the lamellar edges (fig. 16), as we have recognized in the present contribution. The terms ''barbate'' lamellar edges and ''spinelets'' were applied as vague, all-encompassing descriptors of diverse bristles (fig. 16A), spines (fig. 16B) and thorns (fig. 16C), some of which are probably not homologous structures, and were compared with ''arcade'' (sensu Laurie, 1896) or ''arcuate'' (sensu Pavlovsky, 1926) lamellar edges (cf. fig. 16F). The edges of the reticulated lamellae were also poorly characterized by Laurie (1896), although his documentation of arcuate structures was, with one exception, confirmed in the present study. The ''arcade'' structures on the lamellar edges of *Iurus dufoureius* (Brullé, 1832), noted by Laurie (1896), are probably misinterpretations of histological sections.

The importance of the cuticular protuberances on the ''posterior margin of the stigmata'' (posterior spiracle edge, character 3 in Kamenz et al., 2005) was first recognized by Pavlovsky (1926: 135), who defined six distinct states of this character: (1) ''smooth margin … [to] slightly ruffled''; (2) ''tuberculate margin''; (3) ''columellar margin''; (4) ''saw-edge, in section resembling a picket-fence with triangular protuberances''; (5) ''barbate margin with fine sharp spines''; (6) ''stumpy margin with chaetoids in the shape of columellae widening toward the end''. Unfortunately, such precise definitions were not provided for the surfaces and the edges of the lamellae. A smooth edge was not observed in the present study. However, Pavlovsky's (1926) ''ruffled'' (1) and ''tuberculate'' (2) states, and probably also his ''saw-edge'' (4) state, are comparable to the ''hillocks'' state (fig. 17A) described in the present contribution and previously, as state 1 of character 3, by Kamenz et al. (2005). Pavlovsky's (1926) ''columellar margin'' (3), ''saw-edge'' structures (4), and probably his ''barbate margin'' (5), correspond to the larger ''subconical'' state described in the present contribution (state 2 of character 3; fig. 17B). We do not distinguish more rounded ''subconical'' structures from pointed spines in the present study (fig. 17B). Our attention is focused on secondary structures like teeth on the ''chisel-like'' processes (state 5 of character 3; fig. 17F), which could not have been observed in histological sections with light microscopy, but are clearly visible using SEM. Pavlovsky's character state (5) ''barbate margin with fine sharp spines'' also corresponds to the ''hairlike'' structures described by Kamenz et al. (2005) as state 3 of character 3 (fig. 17C). It is not clear whether Pavlovsky (1926) recognized the hexagonal tiles of scorpionids and liochelids, but we presume that his character state (6), ''stumpy margin'', is synonymous with our state 6, ''hexagonal tiles'' (fig. 17G), which are only recognizable as hexagonal in the transverse section of the so-called ''chaetoids'', missed in Pavlovsky's (1926) studies.

In conclusion, although our observations and interpretations of character states on the posterior edge of the spiracle depart somewhat from those of earlier workers, there is much overlap. Our advances in the documentation and interpretation of these structures would not be possible without the aid of modern techniques such as SEM, allowing visualization of the complete three-dimensional structure which was not possible 80–120 years ago.

New Phylogenetic Insights

LAMELLAR SURFACES: Two distinct types of reticulate venation (ribbed vs. slender; figs. 15C, D) occur on the lamellar surfaces of Buthidae (table 2). The presence of both types of venation in the diverse New World buthid genus *Tityus* (pls. 46–55A) suggests that this genus and, hence, the New World buthids may be basal and paraphyletic with respect to the Old World buthids, a possibility suggested by others (Fet et al., 2003; Coddington et al., 2004). Two species of *Tityus* studied during this investigation (*T. bahiensis* and *T. serrulatus*, pls. 47A, 54A) possess a state that appears to be intermediate between the two types of lamellar venation in Buthidae (pls. 2–59A), implying a transformation series from ribbed to slender venation. These species of *Tityus* may share a more recent common ancestor with the Old World buthids than with the other *Tityus* species studied, which show a ribbed venation pattern similar to that of the New World buthid exemplars of *Caribetityus*, *Microtityus*, and *Zabius* (e.g., pls. 12A, 33A, 58A).

Slender venation (fig. 15C) is observed in all Old World buthids, for which it is hypothesized to be synapomorphic. Slender venation also occurs in *Microcharmus* (pl. 59A), confirming a widely held opinion that Microcharmidae renders Buthidae paraphyletic (e.g., Coddington et al., 2004; Prendini and Wheeler, 2005) and should be synonymized with the latter (Volschenk et al., in press).

Chaerilus, often considered to be the sister group of all nonbuthid scorpions (Lamoral, 1980; Coddington et al., 2004), possesses the same ribbed venation (pl. 60A) as the New World buthid exemplars of *Caribetityus* (pl. 12A), *Microtityus* (pl. 33A), and *Zabius* (pl. 58A), and most *Tityus* exemplars (pls. 46A, 48–53A, 55A). This observation suggests that ribbed venation may be plesiomorphic in Buthidae and lends further support to the hypothesis that the New World buthid assemblage may be basal and paraphyletic with respect to the Old World buthids. The presence of ribbed venation in *Chaerilus* may also support Stockwell's (1989) hypothesis that *Chaerilus* is the sister group of Buthidae or "Buthoidea". Alternatively, *Chaerilus* must have acquired this venation independently from Buthidae. A sister-group relationship between Chaerilidae and Buthidae, based on lamellar venation, would exclude the enigmatic *Pseudochactas* Gromov, 1998, however, for the lamellar surface of *Pseudochactas* (pl. 1A) bears no similarity to either type of buthid venation. The structures on the ventral lamellar surfaces of *Pseudochactas* resemble the typical trabeculae of nonbuthid scorpions and probably represent the plesiomorphic condition for scorpions, based on their occurrence in other arachnids. As with several other characters (Prendini et al., 2006), the lamellar surface structure of *Pseudochactas* neither confirms nor refutes Soleglad and Fet's (2003) proposal that pseudochactids are the sister group of all other Recent scorpions.

Viewed from the air space, the ventral lamellar surfaces of the remaining nonbuthid scorpion families (Bothriuridae, Chactidae, Diplocentridae, Euscorpiidae, Hemiscorpiidae, Heteroscorpionidae, Iuridae, Liochelidae, Scorpionidae, Scorpiopidae, Superstitioniidae, Troglotayosicidae, Urodacidae, and Vaejovidae) are covered with branched or simple trabeculae. Although truly branched trabeculae occur only in Scorpionidae and Liochelidae (pls. 145–156A, 127–130A, 135A, 138A), a tendency for the trabeculae to branch occurs in all Scorpionoidea sensu stricto, i.e., excluding Bothriuridae, (pls. 120–156A) suggesting that branched trabeculae are synapomorphic for Scorpionoidea s.s. Alternatively, branched trabeculae may be plesiomorphic in Scorpiones or in nonbuthid scorpions. Branched trabeculae may have evolved from trabeculae that interconnect or bridge the air space between adjacent lamellae, and are retained in the proximal region of the book lung, while detaching from one lamellar surface in the distal region of the book lung. Folds or ridges on the ventral sides of the trabeculae could be retained as branches. Similar conditions are observed in mygalomorph spiders (Reisinger et al., 1990) and uropygids (Börner, 1904), where the branched trabeculae develop a network of ridges between them. The position of the papillate trabeculae of scorpions differs from that of tetrapulmonate arachnids, however, in which the trabeculae occur on the dorsal surfaces of the lamellae. It remains unknown as to whether the trabeculae on one major surface of the lamellae are plesiomorphic in Arachnida, requiring rotation of the book lung in scorpions or tetrapulmonates, or evolved convergently in both arachnid lineages.

LAMELLAR EDGES: Considerable variation is observed in the shape of the lamellar edges (table 2). Thorny and/or smooth to wrinkled lamellar edges (fig. 16C, D) occur in buthids, almost always coincident with venation. Although thorns are observed only in buthids with slender venation, it is difficult to identify a group for which this state might be apomorphic. Smooth and wrinkled edges (e.g., fig. 16D), with a gradation of intermediates, are observed in all buthid species with ribbed surface venation (e.g., pls. 12A, 33A, 46–55A, 58A), but also in some buthids with slender venation (pls. 2A, 7A, 13–17A, 21A, 44A). The smooth to wrinkled lamellar edges appear to be plesiomorphic in buthids. The lamellar edges of Chaerilidae, a potential sister group of Buthidae, are exceptional in possessing pillow- or pad-shaped structures (figs. 16G, pl. 60B), unlike those of other scorpions, and apparently autapomorphic. However, dense reticulation, close to the lamellar edges (pl. 60B) of chaerilids, resembles similar venation in New World buthids such as *C. elii* and *T. asthenes* (pls. 12B, 46B), further evidence of a basal position for New World buthids and particularly *Tityus* species within the buthid clade, and also for a potential sister-group relationship between *Chaerilus* and the buthids.

Bristles and spines on the lamellar edges (e.g., fig. 16A, B) are longer, more slender, and have a weaker, narrower base than thorns. Bristles are typically more curved and flexible than spines, which are rather straight and rigid. These structures occur in most nonbuthid scorpions, including all exemplars of Bothriuridae, Hemiscorpiidae, Heteroscorpionidae, Pseudochactidae, Scorpionidae, Scorpiopidae, Troglotayosicidae, and Urodacidae, and have also been observed in mesothele spiders (Haupt, 2003; C. Kamenz, personal obs.), mygalomorph spiders (C. Kamenz, personal obs.), amblypygids, and uropygids (Scholtz and Kamenz, 2006). Bristles and spines are therefore probably plesiomorphic in scorpions. Bristles or spines on the lamellar edges are present in all liochelids except *Liocheles* (pls. 124–130B, 135–138B), and in all vaejovids except *Uroctonus* Thorell, 1876 (pls. 82–94B, 96–100B). The absence of spines may be autapomorphic in both genera. The absence does not support Soleglad and Fet's (2003, 2004) transferral of *Uroctonus* (pl. 95B) to Chactidae, however, as spines/bristles are present in most Chactidae, and also in *Anuroctonus* Pocock, 1893 (pl. 61B), Soleglad and Fet's (2003, 2004) putative sister group of *Uroctonus*. Although most chactid and iurid exemplars possess spines or bristles on the lamellar edges (e.g., pls. 69–72B, 75–77B, 61B, 64B, 65B), two euscorpiid genera, *Euscorpius* and *Megacormus* Karsch, 1881, do not (pls. 67B, 68B). The affinities of *Troglocormus* Francke, 1981 with Scorpiopidae, pointed out by several authors (Soleglad and Sissom, 2001; Soleglad and Fet, 2003) are confirmed by the similarity of the structures on their lamellar edges (pls. 69B, 70B).

Meandering lamellar edges (fig. 16E) are observed in only three genera among the taxon sample investigated for this study: *Alacran* Francke, 1982 (Supersitioniidae) (pl. 79B), *Calchas* (pl. 62B) and *Iurus* (pl. 66B) (Iuridae). These structures may be synapomorphic for *Calchas* and *Iurus* and evolved independently in *Alacran*, or synapomorphic for all three genera.

The lamellar edges of all diplocentrid exemplars (pls. 139–144B), most euscorpiid exemplars (pls. 67B, 68B), some chactid exemplars (pls. 73B, 74B, 78B), *Caraboctonus* Pocock, 1893 (pl. 63B) (Iuridae), *Liocheles* (pls. 131–134B) (Liochelidae), *Superstitionia* Stahnke, 1940 (pl. 80B) (Superstitioniidae), and *Uroctonus* (pl. 95B) (Vaejovidae) are covered with arcuate structures (fig. 16F), which appear to have evolved independently several times, perhaps in association with a developmental constraint. Little is known about the development and regulation, from transcription of the encoding genes to outgrowth, of cuticular structures like spines or bristles on the lamellar edges. Sanetra et al. (2005) provide a few models of how such processes could be regulated. Epigenetic effects in book lung development have not been described either. Accordingly, all explanations for the distribution of such characters in scorpions are speculative. The possibility that such structures might be associated with environmental conditions like the relative humidity of the microhabitat is also plausible, but remains to be tested.

POSTERIOR EDGE OF SPIRACLE: The processes observed along the posterior spiracle edge are often variable. Different types may occur with transitional stages along a single edge. The character must therefore be scored for the state that is observed at the center of the posterior edge and contacts the anterior edge of the spiracle on closing.

The most typical structures on the posterior spiracle edge of scorpions are simple, cuticular processes, the shape of which varies from shallow hillocks to subconical or pointed spines (table 2; pls. 3–47C, 49–58C, 64C, 65C, 67–71C, 78C, 80–82C, 91C, 95C, 101–108C, 111C, 113C 116C, 119C). Such processes are absent in *Pseudochactas* (pl. 1C), suggesting that they may be synapomorphic for other scorpions, and hence that *Pseudochactas* may be basal in Scorpiones, as proposed by Soleglad and Fet (2003). On the other hand, their widespread occurrence in all other scorpion families may suggest that they are plesiomorphic, and absence (“loss”) autapomorphic in *Pseudochactas*.

Elongated hairs (e.g., fig. 17C) and other, more complex structures (e.g., fig. 17D–L) occur less often, and are probably derived from this generalized condition. One extreme shape among the structures observed on the posterior spiracle edge is the very regular hexagonal tiles (fig. 17G) that occur in all examined scorpionids, diplocentrids, hemiscorpiids, and liochelids (except *Liocheles*) (pls. 123–130C, 135–156C). The chisel-like structures (fig. 17F) observed in urodacids and *Liocheles* (pls. 120C, 121C, 132–134C) may represent intermediate states in a transformation between the simple subconical or spinelike structures (fig. 17B) of other scorpions and the hexagonal tiles of other scorpionoids, whereas the chisel-like structures of *Heteroscorpion* Birula, 1903 (pl. 122C) appear to be very similar to the hexagonal tiles, and may represent the penultimate step in a transformation series. If that were the case, hexagonal tiles would represent a synapomorphy for all scorpionoid families excluding Heteroscorpionidae and Urodacidae, following Prendini (2000, 2003) and Volschenk and Prendini (2008), with an autapomorphic reversal in *Liocheles*.

The sporadic occurrence of flattened and chisel-like structures is enigmatic. Flattened structures (fig. 17D) may be derived from chisel-like or simple, subconical processes (fig. 17F, B). Treelike or precursor states (e.g., fig. 17H, I) may be apomorphic in Bothriuridae, but their appearance in the family is inconsistent. For example, different states occur in the bothriurid genera, *Phoniocercus* Pocock, 1893 and *Urophonius* Pocock, 1893 (pls. 114C, 117C, 118C). A distant relative, *Caraboctonus* (Iuridae), also possesses these subtree-like structures (pl. 63C), otherwise unknown outside Bothriuridae.

CONCLUSIONS

The importance of the book lung morphology of scorpions was underestimated in the past. The tremendous diversity of structures documented in the present study is matched only by the respiratory organs of air breathing crabs (Farrelly and Greenaway, 1992). Although structural variation in the book lungs of scorpions has long been known (Laurie, 1896; Pavlovsky, 1926), modern SEM techniques reveal a much greater diversity of structures and enable them to be described and documented in more detail. It is clear that these structures contain phylogenetically informative variation at multiple branches in the scorpion tree.

One striking example is the surface sculpturing of the respiratory lamellae (Stockwell, 1989). Reticulate venation is observed only in buthoids and chaerilids, whereas papillate (simple or branched) trabeculae occur on the ventral surface of the lamellae of all other scorpion families. Both conditions of the lamellar surface structure show further variation, which may be informative at lower levels in the taxonomic hierarchy. Which of these and other structures described above are apomorphic, and which plesiomorphic, remains to be tested in a phylogenetic analysis by congruence with other characters from diverse sources (internal anatomy, external morphology, behavior and DNA). We hope that the data presented in this atlas will be incorporated into such analyses, and will also stimulate further investigations on the book lungs of scorpions and other arachnids. Future studies should build upon this work, by enlarging the taxon sample investigated, refining the homology statements proposed, defining new ones, and investigating the functionality of the diverse structures identified in the different taxa.

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APPENDIX 1

Scorpion Taxa and Material Examined in the Present Investigation

Abbreviations for collections as follows: American Museum of Natural History, New York, U.S.A. (AMNH); Humboldt-Universität, Berlin, Germany (HUB); Museum National d'Histoire Naturelle, Paris, France (MNHN); Museum für Naturkunde, Berlin, Germany (ZMB).

Bothriuridae Simon, 1880:

Bothriurus bonariensis (C. L. Koch, 1842): 1 ♀ (AMNH [LP 2165]), Argentina: ex J.O. Rein, 1.X.2002

Bothriurus burmeisteri Kraepelin, 1894: 1 ♀ (AMNH [LP 4258]), Argentina: Río Negro Province: Las Grutas: road to Cerro Banderita [40°45′18.3″S 65°2′38″W], M. Magnanelli and E.G. López, 11.I.2005

Bothriurus chacoensis Maury and Acosta, 1993: 1 ♀ (AMNH [LP 1913]), Argentina: ex F. Somma, VII.1998; 1 ♀ (ZMB 15381), Paraguay: Fiebrig

Bothriurus coriaceus Pocock, 1893: 1 ♂ (ZMB 8322), Chile: Coquimbo, IX.1893; 1 juv. ♂ (AMNH [LP 2391]), Chile: Region IV (Coquimbo): Choapa Province: Los Vilos, 1 km S [31°55.468′S 71°29.202′W], L. Prendini, C. Mattoni and J. Ochoa, 3.XI.2003, collected at night with UV light

Brachistosternus ehrenbergii (Gervais, 1841): 1 ♂ (AMNH [LP 3066]), Peru: Arequipa Departament: Islay Province: Arenales de Iberia, cerca de las lagunas de Mejma, R. Gutierrez and J.A. Ochoa, 2.III.2004

Brachistosternus ferrugineus (Thorell, 1876): 1 ♀ (MNHN RS 0619), Argentina: Presidente Peron Province: Charata, M. Rayano, X.1951

Centromachetes obscurus Mello-Leitão, 1932: 1 ♂ (AMNH [LP 2436]), Chile: Region IX (La Araucanía): Malleco Province: Parque Nacional Nahuelbuta, near campsite [37°49.744′S 73°00.418′W], L. Prendini, C. Mattoni and J. Ochoa, 14.XI.2003, collected at night with UV light and burrow excavation

Centromachetes pocockii (Kraepelin, 1894): 1 ♀ (ZMB 35145), Chile: Schönemann

Centromachetes sp.: 1 ♀ (MNHN RS 6333), Chile: Concepcion Province: Pinares, T. Cekalovic, 30.IX.1967

Cercophonius sulcatus Kraepelin, 1908: 1 ♂ (AMNH [LP 1618]), Australia: Western Australia: Jarrahdale, E.S. Volschenk, 24–25.II.1998, under stone; 1 ♂ (AMNH [LP 2117]), Australia: Western Australia: Perth escarpment [31°35′14.2″S 116°12′14.2″E], E.S. Volschenk and J. Warden, V.1999, collected with UV light in leaflitter

Cercophonius sp.: 2 ♀ (MNHN RS 0571), [Australia]: J. d'Albans, 1888

Lisposoma elegans Lawrence, 1928: 1 ♂ (AMNH [LP 1636]), Namibia: Namib-Naukluft Park, Volstruishoogte, L. Prendini and E. Scott, 18.I.1998

Lisposoma josehermana Lamoral, 1979: 1 juv. ♀ (AMNH [LP 2524]), Namibia: Oshikoto Region: Tsumeb District: Farm Varianto on Elandshoek 771 [19°22.773′S 17°44.456′E], L. Prendini, E. Scott, T. and C. Bird, Q. and N. Martins, 4.I.2004

Orobothriurus alticola (Pocock, 1899): 1 subad. ♂ (AMNH [LP 4309]), Argentina: San Juan Province: between Paso de Agua Negra and Aduana, vega and surrounds [30°17′33.1″S 69°46′45.6″W], C. Mattoni and A. Ojanguren, 27.I.2005, collected with UV light

Pachakutej iskay (Acosta and Ochoa, 2001): 1 subad. ♂ (AMNH [LP 3061]), Peru: Apurmmac Departament: Abancay, Tamburco, J. Achicahuala and J.A. Ochoa, 28.I.2004

Phoniocercus pictus Pocock, 1893: 1 ♀ (MNHN), Chile: Calbuco, 7.XI.1937

Phoniocercus sanmartini Cekalovic, 1968: 1 ♀ (AMNH [LP 1994]), Chile: Valdivia Province: Parque Oncol, Sendero Punucapa, T. Cekalovic, 13.IV.2001

Thestylus glasioui (Bertkau, 1880): 1 ♂ (AMNH [LP 1965]), Brazil: Parque Nacional da Serra dos Órgãos, Teresópolis, Rio de Janeiro, Pinto-da-Rocha, Dietz and Rosa, 23–28.XI.1999

Timogenes dorbignyi (Guérin Méneville, 1843): 1 ♂ (ZMB 31130), Bolivia: Villa Montes, Eisentraut, 5.X.1930; 1 ♂ (MNHN), H. Krieg, 1931

Timogenes mapuche Maury, 1975: 1 ♂ (AMNH [LP 4312]), Argentina: Neuquén Province: Picún Leufú [39°32′13.5″S 69°13′21.8″W], M. Magnanelli and E.G. López, 25.I.2005

Urophonius iheringii Pocock, 1893: 1 ♂ (MNHN RS 4305), Uruguay: Montevideo: Sayago: Bajo Madera, P.R. San Martín, 17.VI.1943; 1 ♀ (MNHN RS 4306), Uruguay: Maldonado Departament: Cerro de las Animas, P.R. San Martín, 9.VIII.1959, bajo piedro; 1 ♀ (AMNH [LP 3457]), Argentina: Buenos Aires Province: Villa Ventana, near Municipal Camping and Arroyo Belisario [38°05′37″S 61°56′10.2″W], C. Mattoni and M. Magnanelli, 13.VII.2004, collected with UV light

Urophonius tregualemuensis Cekalovic, 1981: 1 juv. ♂ (AMNH [LP 5165]), Chile: Region VII: Talca Province: Parque Nacional Altos del Lircay, A. Ojanguren and P. Korob, 16.II.2005

Vachonia martinezi Abalos, 1954: 1 juv. ♀ (AMNH [LP 2441]), Argentina: Balneario El Condor, M. Magnanelli, 5.V.2003

Buthidae C. L. Koch, 1837:

Ananteris cussinii Borelli, 1910: 1 ♂ (AMNH [LP 1716]), Trinidad and Tobago: Trinidad: Mt. St. Benedict [10°39′49″N 61°23′56″W], L. Prendini, 9.VII.1999, collected at night with UV light

Androctonus amoreuxi amoreuxi (Audouin, 1826): 1 ♀ (ZMB 30909), Mauretania: M. Bout and P. Spatz; 1 ♀ (MNHN RS 2034), Algeria: M. Vachon

Androctonus australis australis (Linnaeus, 1758): 1 ♀ (AMNH [LP 1970]), Egypt: ex R. MacInnes, 6.VI.2002; 1 ♀ (MNHN RS 3081), Sahara, Kef el Dor, Sidi bel Abbés, Denier

Androctonus bicolor aeneas C.L. Koch, 1839: 1 ♀ (MNHN), Tunisia: 10.X.1977

Anomalobuthus rickmersi Kraepelin, 1900: 1 ♂ (AMNH [LP 3772]), Kazakhstan: Almaty Area: Zhambyl District: Taukum Desert, S edge, 12 km NNE of Aidarly [44°17′57″N 75°54′40″E], L. Prendini and A.V. Gromov, 27.VI.2003, collected with UV light at night

Apistobuthus pterygocercus Finnegan, 1932: 1 ♀ (AMNH [LP 1795]), United Arab Emirates: ex T. Gearheart, IX.2000

Babycurus buettneri Karsch, 1886: 1 ♂ (AMNH [LP 1744]), Gabon: Province Ogooue-Maritime: Reserve Monts Doudou, 25.2 km 304° NW Doussala [2°13′36″S 10°23′12″E], M. Burger, 14.III.2000

Babycurus jacksoni (Pocock, 1890): 1 ♂ (MNHN RS 1415), Zanzibar: Mrogoro, P. Leroy, 1889

Buthacus arenicola (Simon, 1885): 1 ♀ (AMNH [LP 1973]), Egypt: ex R. MacInnes, 6.VI.2002

Buthacus leptochelys (Ehrenberg, 1829): 1 ♂ (MNHN RS 5456), Morocco: Ouzzina, 27 km S Taouz, 17.V.1970

Butheoloides maroccanus Hirst, 1925: 1 ♂ (MNHN RS 5264), Morocco: 17.V.1955

Butheolus gallagheri Vachon, 1980: 1 ♂ (AMNH [LP 2280]), Oman: ex R. MacInnes, IV.2003

Buthiscus bicalcaratus Birula, 1905: 1 ♂ (MNHN RS 1721), Algeria: Lallanda, El Oued, L. Balozet, XII.1953

Buthus ibericus Lourenço and Vachon, 2004: 1 ♀ (MNHN RS 8198), Spain: Geróna

Buthus occitanus (Amoreux, 1789): 1 ♂ (AMNH [LP 4595]), Senegal: Ndiass, 7 km W [14°41′14.6″N 17°08′37.0″W], J. Huff and V. Vignoli, 10.VII.2005, collected with UV light at night

Caribetityus elii (Armas and Marcano Fondeur, 1992): 1 ♀ (AMNH [LP 3277]), Dominican Republic: La Vega Province: Loma Casabito, Reserva Científica Ebano Verde, alongside road to transmitter station [19.0375°N 70.5186°W], E.S. Volschenk and J. Huff, 18.VII.2004, 1478 m, pine forest to humid montane forest, hand collected from under stones and logs, and with blacklights

Centruroides exilicauda (Wood, 1863): 1 ♀ (AMNH [LP 4477]), Mexico: Baja California Sur: Municipio Loreto: Loreto, S, ca. 8 km along gravel road to San Javier, from junction with Route 1 [25°59.733′N 111°25.116′W], L. Prendini, E. González, R. Mercurio and W.E. Savary, 8.VII.2005, collected with UV light at night

Centruroides gracilis (Latreille, 1804): 1 ex. (MNHN RS 1077), Colombia: Gervais and Simon; 1 ♀ (AMNH [LP 2306]), Mexico: Tamaulipas: La Pilita, Area Aldama, P. Sprouse, 3.I.2003; 2 ♀ (AMNH [LP 2051]), Mexico: San Luis Potosí: Antena de Microondas de Ciudad Valles [21°58′55″N 99°08′58″W], L. Prendini, J. Soriano and E. Gonzalez, 2.VIII.2002, collected with UV light at night

Centruroides margaritatus margaritatus (Gervais, 1841): 1 ♂ (AMNH [LP 1787]), Honduras: ex R.D. Gaban, III.2001; 1 ♀ (ZMB)

Centruroides schmidti Sissom, 1995: 1 ♀ (AMNH [LP 2070]), Mexico: Veracruz: Estacion de Biologia 'Los Tuxtlas', UNAM, J. Ponce and O. Francke, 19.VII.2002, collected with UV light at night

Cicileus exilis (Pallary, 1928): 1 ♀ (MNHN RS 1273), Algeria: Tamanrasset; 1 ♀ (MNHN RS 3223), Central Sahara: Gara Assekrem, Hoggar

Compsobuthus berlandi Vachon, 1950: 1 ♀ (MNHN RS 4910), Algeria: Djanet (Tassili), W border, 29.I.1967

Compsobuthus maindroni (Kraepelin, 1900): 1 ♂ (AMNH [LP 3765]), United Arab Emirates: Ruus Al Jibal Mtn. Range, ca. 12 km WSW of Al Fujayrah, canyon near Hayl Fort [25°05′14″N 56°13′14″E], A.V. Gromov, 30.III.2003, collected with UV light at night

Grosphus flavopiceus Kraepelin, 1900: 1 ♀ (ZMB 10383), Madagascar: Tukar, S.G. Voeltzkow

Grosphus grandidieri Kraepelin, 1900: 1 ♀ (MNHN RS 1336), Madagascar: Valleé de Tiberenova

Grosphus hirtus Kraepelin, 1900: 1 ♀ (AMNH [LP 2774]), Madagascar: Antsiranana Province: Nosy Be, Parc National de Lokobe, 4.95 km 125° ESE Hellville [13°24′56″S 48°18′27.3″E], D. Andriamalala, C. Griswold, H. Ratsirarson and D. Silva, 13.II.2003

Hottentotta conspersus (Thorell, 1876): 1 juv. (AMNH [LP 2627]), Namibia: Kunene Region: Opuwo District: Hartmann's Valley, ca. 39 km N of Orange Drum [17°26.396′S 12°15.868′E], L. Prendini, E. Scott, T. and C. Bird, Q. and N. Martins, 14.I.2004

Hottentotta hottentotta (Fabricius, 1787): 1 subad. ♂ (AMNH [LP 4822]), Benin: Tanogou: Cascade de Tanogou [10°48.12′N 01°26.26′E], V. Vignoli, VI.2005; 1 ♀ (ZMB 10274), Cameroon: Lake Chad, Duma, S.G. Riggenbach, 17–20.VI.1909

Hottentotta jayakari (Pocock, 1895): 1 subad. ♀ (HUB), Yemen: 2004

Isometroides angusticaudis Keyserling, 1885: 1 ♀ (AMNH [LP 2110]), Australia: South Australia: Coolton National Park [34°12′40.5″S 140°37′42.2″E], E.S. Volschenk and J. Tregear, 9.XII.1998, collected with UV light

Isometrus maculatus (DeGeer, 1778): 1 ♀ (AMNH [LP 1788]), São Tomé and Principé: São Tomé: Praia du Mutamba [00°23′45.5″S 006°36′19.1″E], J.M. Ledford, 2.IV.2001; 1 ex. (MNHN RS 0952), Liberia: Monrovia; 1 ♀ (ZMB 8199), Jahuit, Bartels, 7.II.1900

Karasbergia methueni Hewitt, 1913: 1 ♂ (AMNH [LP 1724]), South Africa: Northern Cape Province: Lekkersing, G.J. Müller et al., 16.I.1999, collected with UV light at night

Leiurus quinquestriatus hebraeus (Birula, 1908): 1 ♀ (MNHN RS 6484), Oman: Masirah Island, R.J. Parker, 17.XII.1972

Leiurus quinquestriatus quinquestriatus (Ehrenberg, 1828): 1 ♀ (AMNH [LP 1530]), Egypt: ex B. Capiz, VII.1998

Liobuthus kessleri Birula, 1898: 1 ♂ (AMNH [LP 3790]), Kazakhstan: South Kazakhstan Area: Chardara District: 3 km W of Chardara [41°16.106′N 67°53.228′E], L. Prendini and A.V. Gromov, 20.VI.2003, collected with UV light at night

Lychas mucronatus (Fabricius, 1798): 1 ♀ (MNHN RS 1437), Indonesia: Java; 1 ♀ (MNHN RS 1474), China: Baie d'Alones, Dawydoff, X.1934

Lychas obsti Kraepelin, 1913: 1 ♂ (AMNH [LP 1797]), Kenya: ex J. Ove Rein

Lychas scutilus C.L. Koch, 1845: 1 ♀ (ZMB 11341), Indonesia: Heinroth, 28.VIII.1902

Lychas tricarinatus (Simon, 1884): 1 ex. (MNHN RS 1440), India: North Arkof, Maindron

Lychas sp.: 1 ♀ (AMNH [LP 1646]), Australia: Queensland: Undara National Park [18°12′32.2″S 144°38′30.6″E], E.S. Volschenk, T. Heslin and C. Berridge, 26.III.1999, collected with UV light in leaflitter

Mesobuthus caucasicus parthorum Pocock, 1889: 1 ex. (MNHN RS 4666), Iran: Chahpuze (Asarhaydjan), Habibi, 1968

Mesobuthus eupeus thersites (C. L. Koch, 1839): 1 ♂ (AMNH [LP 3810]), Kazakhstan: South Kazakhstan Area: Chardara District: 3 km W of Chardara [41°16.106′N 67°53.228′E], L. Prendini and A.V. Gromov, 20.VI.2003, collected with UV light at night

Mesobuthus gibbosus (Brullé, 1832): 1 ♀ (MNHN RS 7010), Greece: Aegean Sea: Arkos Is., Pili, Constantinos, 12.VIII.1972

Microtityus rickyi Kjellesvig-Waering, 1966: 1 ♀ (AMNH [LP 1717]), Trinidad and Tobago: Trinidad: Gaspar Grande Island, L. Prendini, 7.VII.1999, collected with UV light at night

Odontobuthus doriae (Thorell, 1876): 1 ♀ (MNHN RS 1823), Iran: Kashan; 1 ♀ (AMNH [LP 2908]), Iran: Yazd Province: Ardakan, 10 km E [32°18.626′N 54°15.133′E], V. Vignoli and P. Crucitti, 11.IV.2004

Odonturus dentatus Karsch, 1879: 1 ♂ (AMNH [LP 1578]), Tanzania: ex R.D. Gaban, XI.1999

Orthochirus innesi Simon, 1910: 1 ♀ (MNHN RS 5440), Morocco: Taouz (environs), 27.III.1970; 1 ♀ (AMNH [LP 4407]), Oman: ex A. Tietz, VIII.2005

Orthochirus scrobiculosus scrobiculosus (Grube, 1873): 1 ♀ (AMNH [LP 3775]), Kazakhstan: South Kazakhstan Area: Chardara District: 3 km W of Chardara [41°16.106′N 67°53.228′E], L. Prendini and A.V. Gromov, 20.VI.2003, collected with UV light at night

Parabuthus leiosoma (Ehrenberg, 1828): 1 ♀ (AMNH [LP 1845]), Kenya: Nguruman, Rift Valley, X.1999

Pseudolychas pegleri (Purcell, 1901): 1 ♀ (AMNH [LP 1326]), Swaziland: Mlawula Nature Reserve: Sara Camp [26°11′44″S 31°59′24″E], L. Prendini, G. Giribet and R. Boycott, 2.IV.2001, collected with UV light at night

Rhopalurus acromelas Lutz and Mello, 1922: 1 ♀ (MNHN), Brazil: Brasilia, Barreiras, W.R. Lourenço, 3.X.1975

Rhopalurus bonettii Armas, 1999: 1 juv. ♂ (AMNH [LP 3267]), Dominican Republic: Pedernales Provence: Parque Nacional Jaragua, Cabo Rojo [17.8958°N 71.6600°W], E.S. Volschenk and J. Huff, 9.VII.2004, collected with UV light

Rhopalurus junceus (Herbst, 1800): 1 ♀ (MNHN RS 3288), Cuba: Etangra Samorrostra, J. Négre, 21.V.1950; 1 juv. (AMNH [LP 1517]), Cuba: Santiago de Cuba Province: La Socapa, 10 km SW of Santiago de Cuba, R. Teruel, 9.IV.1999

Rhopalurus laticauda Thorell, 1876: 1 ♀ (AMNH [LP 2462]), Venezuela: Caracas, C. Siederman, 2001

Rhopalurus princeps (Karsch, 1879): 1 ♂ (AMNH [LP 1566]), Dominican Republic: Pedernales Province: Manuel Goja, 3.9 km N, D. Huber, 9.V.1998

Rhopalurus rochae Borelli, 1910: 1 ♂ (AMNH [LP 1582]), Brazil: Paraiba: Soledade [7°02.118′S 36°27.311′W], A. Kury and A. Giupponi, 16.III.1999

Tityobuthus baroni (Pocock, 1890): 1 ♂ (AMNH [LP 1941]), Madagascar: Antsiranana Province: Nosy Be, Réserve Naturelle Intégrale de Lokobe, 6.3 km 112° ESE Hellville [13°25′10″S 48°19′52″E], B.L. Fisher, C.E. Griswold et al., 19.III.2001

Tityus asthenes Pocock, 1893: 1 ♀ (AMNH [LP 1831]), Ecuador: Sarayacu, Rio Bobonaza and Capahuari, M. Peprný, VI.1999

Tityus bahiensis eickstedtae (Lourenço, 1982): 1 ♀ (AMNH [LP 1596]), Brazil: ex Instituto Butantan via R. Pinto-da-Rocha, VIII.1999

Tityus bolivianus Kraepelin, 1895: 1 ♂ (AMNH [LP 4249]), Bolivia: Potosí Department, Comunidad Phalapaya, 10 km E of Betanzos [19°36′21.6″S 65°23′54.7″W], C. Mattoni, A. Ojanguren and J. Ochoa, 9.I.2005, collected with UV light

Tityus cambridgei Pocock, 1897: 1 ex. (MNHN RS 5252), French Guiana: Saul, A.S. Balachowsky, 27.X.1969; 1 ♀ (AMNH [LP 3649]), French Guiana: Maripasoula: Saul, Chez Fred's [3°37′42.0″N 53°12′40.0″W], J. Huff, 14.XII.2004, collected with UV light; 1 ♂ (AMNH [LP 3434]), French Guiana: Roura District: Kaw Mountains, NE slopes, R.C. West, 24.IX.2004

Tityus clathratus C. L. Koch, 1844: 1 ♀ (AMNH [LP 1567]), Trinidad and Tobago: Trinidad: Gaspar Grande Island, L. Prendini, 7.VII.1999, collected with UV light at night

Tityus confluens Borelli, 1899: 1 ♀ (AMNH [LP 2938]), Argentina: Chaco: Parque Nacional Chaco, A. Ojanguren, F. Labarque, C. Grismado and L. Compagnucci, 26.II.2004

Tityus discrepans (Karsch, 1879): 1 ♀ (AMNH [LP 1547]), Venezuela: Caracas, M.A. Gonzalez-Sponga, XI.1998

Tityus melanostictus Pocock, 1893: 1 ♀ (AMNH [LP 1504]), Trinidad and Tobago: Trinidad: Gaspar Grande Island, L. Prendini, 7.VII.1999, collected with UV light at night

Tityus serrulatus Lutz and Mello, 1922: 1 ♀ (AMNH [LP 1597]), Brazil: ex Instituto Butantan via R. Pinto-da-Rocha, VIII.1999; 1 ♀ (MNHN), Brazil: Butantan, W. Bücherl, 13.XII.1961

Tityus silvestris Pocock, 1897: 1 ♂ (AMNH [LP 3643]), French Guiana: Maripasoula, Saul, Campsite Chez Fred's [03°37′42.0′N 53°12′40.0″W], J. Huff, 14–15.XII.2005, manicured landscape surrounded by primary tropical rainforest, hand collected using UV light at night; 1 ♀ (ZMB), Surinam: Paramaribo, S.V. Heller, I.1908

Uroplectes flavoviridis Peters, 1861: 1 ♀ (AMNH [LP 1707]), Zimbabwe: Highlands, Harare, M. Cumming, 24.I.1999

Uroplectes occidentalis Simon, 1867: 1 ♀ (ZMB 7599), Cameroon: Jaunde, Zenker

Uroplectes planimanus (Karsch, 1879): 1 ♀ (MNHN [ANG 1839-1]), Angola

Vachoniolus globimanus Levy, Amitai and Shulov, 1973: 1 ♂ (AMNH [LP 3767]), United Arab Emirates: Rub' Al Khali Desert, ca. 17 km SE of Dubai [25°10′04″S 55°28′07″E], A.V. Gromov, 28.III.2003
Zabius fuscus (Thorell, 1876): 1 juv. ♀ (AMNH [LP 1759]), Argentina: Córdoba: La Quebrada, M. López, 8.XI.1999

Chactidae Pocock, 1893:
Broteochactas delicatus (Karsch, 1879): 1 ♂ (MNHN RS 3392), French Guiana: Camopi, Valleé de l'Oyapock, 18.XII.1948; 1 ♂, 1 ♀, 1 juv. ♂ (AMNH), French Guiana, 2005
Broteochactas nitidus Pocock, 1893: 1 ♀ (AMNH [LP 1511]), Trinidad and Tobago: Trinidad: Mt. St. Benedict [10°39′49″N 61°23′56″W], L. Prendini, 28.VI.1999, collected with UV light at night
Brotheas gervaisii Pocock, 1893: 1 ♂ (MNHN RS 8508]), French Guiana: Rive droite de l'Arataye en aral du Sant Parané, J.P. Gasc, I.1981; 1 ♀ (ZMB 15360), Surinam: Paramaribo, Heller, 1909; 1 ♀ (MNHN RS 7389); 1 ex. (MNHN)
Brotheas granulatus Simon, 1877: 1 ♂ (MNHN RS 8508]), French Guiana: Rive droite de l'Arataye en aral du Sant Parané, J.P. Gasc, I.1981; 1♀ (AMNH [LP 3439]), French Guiana: Roura District: Kaw Mountains, NE slopes, R.C. West, 24.IX.2004; 1 ex. (MNHN)
Chactas gestroi Kraepelin, 1912: 1 ♀ (MNHN RS 0760), Colombia: Merida, Simon
Chactas raymondhansi Francke and Boos, 1986: 1 subad. ♀ (AMNH [LP 1586]), Trinidad and Tobago: Trinidad: Mt. El Tucuche summit, L. Prendini, 8.VII.1999
Chactas reticulatus Kraepelin, 1912: 1 ♀ (MNHN RS 0775), Colombia: Angelopolis, L. Fuhrmann, 1910; 1 ex. (MNHN), Colombia: Angelopolis, II.1998
Guyanochactas gonzalezspongai (Lourenço, 1983): 1 ♀ (AMNH [LP 3435]), French Guiana: Roura District: Kaw Mountains, NE slopes, R.C. West, 24.IX.2004; 1 ex. (MNHN)
Hadrurochactas schaumii (Karsch, 1880): 1 ♀ (AMNH [LP 3680]), French Guiana: Approuague-Kaw: Kaw mountains, area around Amazone Nature Lodge [4°33′35.0″N 52°12′25.3″W], J. Huff, 21.XII.2004; 1 ex. (MNHN)
Nullibrotheas allenii (Wood, 1863): 1 juv. ♂ (AMNH [LP 2869]), México: Baja California Sur: El Tecolote [24°20.259′N 110°18.580′W], R. Mercurio, M. Nishiguchi, et al., 21.V.2004, collected with UV light
Teuthraustes atramentarius Simon, 1878: 1 ♀ (MNHN RS 0784), Ecuador: Riobamba, G. Rivet, 1901
Teuthraustus gervaisii (Pocock, 1893): 1 ♀ (AMNH [LP 1855]), Ecuador: Guyallabamba, M. Peprný, VI.1999

Chaerilidae Pocock, 1893:
Chaerilus truncatus Karsch, 1879: 1 ♂ (AMNH [LP 2197A]), Nepal: Naudanda, Kaski, Gandaki (west Nepal), Tillack, Grossmann and Tillack, VII.1999
Chaerilus sp.: 1 ♀ (MNHN RS 0607), Indonesia

Diplocentridae Karsch, 1880:
Bioculus comondae Stahnke, 1968: 1 juv. ♀ (AMNH [LP 4738]), Mexico: Baja California Sur: Municipio Loreto: Loreto, S, ca. 8 km along gravel road to San Javier, from junction with Route 1 [25°59.733′N 111°25.116′W], L. Prendini, E. González, R. Mercurio and W.E. Savary, 8.VII.2005, collected with UV light at night
Cazierius gundlachii (Karsch, 1880): 1 ♂ (AMNH [LP 1779]), Cuba: Santiago de Cuba Province: Quintero, Santiago de Cuba, R. Teruel, 15.IV.1999
Didymocentrus lesueurii (Gervais, 1844): 1 ♀ (AMNH [LP 3638]), Martinique: E of Anses-d'Arlet, 6.5 km W of Le Diamant [14°29′37.6″N 61°04′16.0″W], J. Huff, 7.XII.2004; 1 ex. (MNHN), Martinique
Diplocentrus mexicanus mexicanus Peters, 1861: 1 ♀ (AMNH [LP 2055]), Mexico: Oaxaca: 3.7 km N El Moral [17°30.134′N 96°56.091′W], L. Prendini, O. Francke, E. Gonzalez and J. Ponce, 23.VII.2002
Diplocentrus tehuacanus Hoffmann, 1931: 1 ♂ (MNHN RS 4281), Mexico
Diplocentrus whitei (Gervais, 1844): 1 ♂ (MNHN RS 3350), Mexico: Genin, 1922
Diplocentrus zacatecanus Hoffmann, 1931: 1 ♂ (MNHN RS 4284), Mexico: Zacatecas: Mazapil, A. Diaz N., 4.IX.1963
Heteronebo granti Pocock, 1899: 1 juv. ♀ (AMNH [LP 1634]), Yemen: Abd-al-Kuri Island, W. Wranik, II.1999
Nebo hierichonticus (Simon, 1872): 1 juv. ♂ (AMNH [LP 1561]), Israel, Mitrani Center for Desert Ecology, ex Y. Lubin, VI.1998; 1 ♂ (MNHN RS 4541), Jordan, D. Wahbek, III.1966; 1 ♀ (MNHN), Israel: Ein Geddi, J. Wahrman, 8.IV.1951

Euscorpiidae Laurie, 1896:
Euscorpius carpathicus candiota Birula, 1903: 3 ♀ (HUB), Greece: Crete, 1999
Euscorpius flavicaudis (DeGeer, 1778): 1 ex. (MNHN)
Euscorpius italicus (Herbst, 1800): 1 juv. ♀ (HUB), Italy, 2006
Megacormus gertschi Díaz Najera, 1966: 1 ♂ (MNHN RS 0787) Mexico: Muyoapan
Megacormus granosus (Gervais, 1843): 1 ♀ (AMNH [LP 2074]), Mexico: Veracruz: Camino a Cañada Blanca [18°55.707′N 96°51.434′W], E. Gonzalez Santillan, 18.VII.2002, collected with UV light at night
Troglocormus willis Francke, 1981: 1 juv. ♂ (AMNH), Mexico: Tamaulipas: Cueva del Brinco, P. Sprouse, VII.1978

Hemiscorpiidae Pocock, 1893:
Hemiscorpius lepturus Peters, 1861: 1 ♀ (AMNH [LP 4343]), Iran: Khouzestan Province: Andimeshk, H.R. Goodarzi, V.2005
Hemiscorpius tellinii Borelli, 1904: 1 ♀ (MNHN RS 0560), Ethiopia; 1 ♀ (MNHN RS 0607)

Heteroscorpionidae Kraepelin, 1905:
Heteroscorpion opisthacanthoides (Kraepelin, 1896): 1 subad. ♂ (AMNH [LP 2706]), Madagascar: Antsiranana Province: Montagne de Français,

7.2 km 142° SE Antsiranana (= Diego Suarez) [12°19′22″S 49°20′17″E], B.L. Fisher, C.E. Griswold et al., 22.II.2001; 1 ♀ (MNHN RS 4813), Madagascar: Nossi-Komba, Millot, 1945

Iuridae Thorell, 1876:

Anuroctonus phaiodactylus (Wood, 1863): 1 subad. ♀ (AMNH [LP 4970]), U.S.A.: California: Inyo County: Death Valley National Park: South Pass, junction of Saline Valley Road and Hunter Mountain Road [36°31.441′N 117°32.894′W], R. Mercurio and L. Prendini, 4.IX.2005, burrow excavation

Anuroctonus pococki Soleglad and Fet, 2004: 1 ♂ (MNHN RS 6207), U.S.A.: California: San Diego: Mount Soleglad, S.C. Williams, 21.III.1965

Calchas nordmanni Birula, 1899: 1 ♀ (MNHN RS 6452), Turkey: Biledjik, 23.IV.1971; 1 ♀ (AMNH [LP 2246]), Turkey: Artvin: Ardanug, A. Karataş, 26.VIII.2001; 1 ♂ (AMNH [LP 4333]), Turkey: Antep-Sehitkamil: Incesu Köyü, E. Aydin, 7.V.2005

Caraboctonus keyserlingi Pocock, 1893: 1 ♀ (MNHN RS 8561), Chile: Coquimbo Province: Bajada El Teniente, km 330, T. Cekalovic, 13.IX.1964; 1 ex. (AMNH [LP 3686]), Chile: Aguas Claras, near Zapallar, J.S. Ascher, 1.XII.2004; 1 ♂ (MNHN RS 8571), 5.IX.1968

Hadruroides charcasus (Karsch, 1879): 1 ♀ (MNHN RS 714), Peru: Baños, P.O. Simons; 1 ♀ (AMNH [LP 1555]), Peru: ex R.D. Gaban, VI.1999; 1 ♀ (AMNH [LP 1575]), Peru: ex T. Gearheart, 16.V.2000

Hadrurus concolorous Stahnke, 1969: 1 ♀ (ZMB 15220), Mexico: Baja California: San José, v. Blücher

Hadrurus hirsutus (Wood, 1863): 1 ♂ (AMNH [LP 3131]), Mexico: Baja California Sur: La Paz, 75 km NW [24°05′56.2″N 110°45′41″W], O. Francke, E. González and A. Valdez, 7.VII.2004, collected with UV light at night

Hadrurus spadix Stahnke, 1940: 1 ♀, 1 ♂ (MNHN RS 6194), U.S.A.: California: Inyo County: Saline Valley: Grapevine station 44 Canyon road, B. Banta, 4.VI.1960, collected with a pit trap

Iurus dufoureius asiaticus Birula, 1903: 1 ♂ (MNHN RS 5168), Turkey: B.H. Lamoral, 1980; 1 juv. (HUB), Turkey: Silifke, Turkish Riviera, Cennet Sinkhole [36°27′08.2″N 34°06′22.3″E], S. Huber, 4.IV.2005

Iurus dufoureius dufoureius (Brullé, 1832): 1 ♂ (ZMB 7497), Cyprus: Rolle; 1 ♀ (MNHN RS 2977]), Greece: Crete, K. Lindberg, 1979

Liochelidae Fet and Bechly, 2001 (1879):

Cheloctonus anthracinus warreni Hewitt, 1931: 1 ♀ (MNHN RS 0374 [NM 700]), South Africa: KwaZulu-Natal Province: Trurence

Cheloctonus jonesii Pocock, 1892: 1 ♂ (ZMB 35141), South Africa: Limpopo Province: Lekgalameetse, Koch, 18.XII.1995; 1 juv. ♀ (AMNH [LP 1558]), South Africa: Kwazulu-Natal Province: Weenen Nature Reserve, L. Prendini and E. Scott, 6.XII.1998, burrow excavation; 1 ex. (MNHN RS 6612), Republic of South Africa: Ubombo, J.P. Gasc, 5–7.X.1973

Chiromachus ochropus (C.L. Koch, 1837): 1 ♂ (ZMB 15169), Seychelles, Brauer; 1 ♀ (MNHN RS 0383]), Seychelles; 1 juv. ♀ (AMNH [LP 2189]), Seychelles: Fregate Island, J. Gerlach, 1.X.2002

Hadogenes trichiurus trichiurus (Gervais, 1843): 1 ♂ (AMNH [LP 3402]), South Africa: Eastern Cape Province: Graaff-Reinet District: Ouberg Pass, J. Visser, 26.IV.2004

Hadogenes troglodytes troglodytes (Peters, 1861): 1 ♂ (AMNH [LP 1315]), South Africa: Limpopo Province: Kruger National Park, Tshanga Lookout Point [23°13.73′S 31°14.28′E], L. Monod and B. Striffler, IV.2001; 1 ♀ (MNHN)

Hadogenes sp.: 1 ♀ (AMNH [LP 1794]), Tanzania: ex T. Gearheart; 1 ♀ (ZMB 7465); 1 ♂ (HUB)

Iomachus politus Pocock, 1896: 1 ♂ (AMNH [LP 1514]), Tanzania: ex T. Gearheart, 4.VI.1999

Liocheles australasiae (Fabricius, 1775): 1 ♀ (AMNH [LP 1854]), India: Andaman Islands: Havelock Island, III.1999; 1 ♀ (AMNH [LP 4764]), Malaysia: Selangor, Batu Caves area [3.244°N 101.695°E], W. Maddison, D. Li, I. Agnarsson and J.X. Zhang, 19.V.2005; 1 ♀ (MNHN RS 0454), Mariana Islands, 5–6.III.1888; 1 ♀ (MNHN RS 3236)

Liocheles karschii (Keyserling, 1885): 1 ♂ (ZMB 30838), Papua New Guinea: Kaiserins.

Liocheles waigiensis (Gervais, 1843): 1 ♀ (AMNH [LP 1502]), Australia: Queensland: Connondale National Park [26°41′50.0″S 152°33′12.4″E], E.S. Volschenk and P.A. Aitken, 17.III.1990, collected with UV light; 1 ♀ (MNHN RS 8350), New Caledonia: Ova Tom, P. Boachet, 16.IX.1979

Opisthacanthus africanus Simon, 1876: 1 ♀ (MNHN RS 0550), French Congo: Brazzaville, Roubond and Weiss, 15.III.1907

Opisthacanthus elatus (Gervais, 1844): 1 ♂ (MNHN RS 0301), 1922; 1 ♀ (AMNH [LP 1837]), Panama: Soberalie National Park, M. Makovec, 15.X.2000

Opisthacanthus lecomtei (Lucas, 1858): 1 ♀ (ZMB), Cameroon

Opisthacanthus madagascariensis Kraepelin, 1894: 1 ♀ (AMNH [LP 2799]), Madagascar: Mahajanga Province: Mahavavy River, 6.2 km 145° SE Mitsinjo [16°03′06″S 045°54′30″E], B.L. Fisher, C.E. Griswold et al., 1.XII.2002; 1 ♀ (MNHN RS 0256), Madagascar: Mahafaly, M. Bastard

Opisthacanthus validus Thorell, 1876: 1 juv. ♀ (AMNH [LP 3379]), South Africa: Eastern Cape Province: Humansdorp District: Swart River [34°04′S 24°54′E], J. Visser, 23.VII.2004

Palaeocheloctonus pauliani Lourenço, 1996: 1 ex. (MNHN RS 3970), Madagascar: Concession Wilmain, Tulear, Emerit, 30.XI.1962

Microcharmidae Lourenço, 1996:

Microcharmus sp.: 1 ♀ (AMNH [LP 1769]), Madagascar: Antsiranana Province: Réserve Spéciale Manongarivo, 10.8 km SW Antanambao [13°57.7′S 48°26.0′E], B.L. Fisher, 8.XI.1998

Pseudochactidae Gromov, 1998:

Pseudochactas ovchinnikovi Gromov, 1998: 1 juv. ♂ (AMNH [LP 2303]), 1 juv. (AMNH), Uzbekistan:

Surkhandarya Area: Dikhana Canyon, ca. 5 km WSW Akmechet (Oqmachit) village, foothills on E slopes of Babatag Mtn. Range [38°01.638′N 68°15.198′E], L. Prendini and A.V. Gromov, 20.V.2003, collected with UV light

Scorpionidae Latreille, 1802:
Heterometrus fulvipes (C. L. Koch, 1837): 1 ♀ (AMNH [LP 4324]), India: Tamil Nadu: Kancheepuram District: Nemmali, 45 km from Chennai, on the eastern coastline, H.A. Vadivelu, A. and R. Ali and F. Paul, 30.V.2005
Heterometrus longimanus (Herbst, 1800): 1 ♀ (ZMB 30849), Indonesia: Sumatra: Padang, Tiefsee, 1914
Heterometrus spinifer (Ehrenberg, 1828): 1 ♂ (AMNH [LP 1604]), Singapore, K. Wee, IX.1998
Heterometrus swammerdami Simon, 1872: 1 ♂ (AMNH [LP 1607]), India: ex T. Gearheart
Heterometrus sp.: 1 ex. (MNHN)
Opistophthalmus boehmi (Kraepelin, 1896): 1 ♀ (AMNH [LP 1827]), Tanzania: ex K. Suzusaki, 27.II.2000
Opistophthalmus capensis (Herbst, 1800): 2 ♀ (AMNH [AH 1266, 1268]), South Africa: Western Cape Province: Strand District: Base of Koeëlberg, 20 km S Strand, A. Harington, 13.I.1979
Opistophthalmus carinatus (Peters, 1861): 1 ♀ (ZMB 14951), Namibia; 1 juv. ♂ (MNHN), Kalahari, B. Le Bret.
Opistophthalmus fitzsimonsi Hewitt, 1935: 1 juv. (MNHN), Kalahari
Opistophthalmus glabrifrons Peters, 1861: 1 ♀ (AMNH [LP 1074]), South Africa: Northern Province: Soutpansberg District: Crystal Salt Works, near firing range [22°58′S 29°20′E], L. Prendini and J. Laing, I.1996
Opistophthalmus holmi (Lawrence, 1969): 1 ♀ (AMNH [LP 1082]), Namibia: Karas Region: Lüderitz District, Diamond Area 1: Namib-Naukluft Park, Koichab riverbed, dunes on northern bank [26°13.41′S 15°59.24′E], L. Prendini, E. Scott and P. Swiegers, 3.I.1998
Pandinus cavimanus (Pocock, 1888): 1 ♀ (AMNH [LP 3259]), Tanzania
Pandinus imperator (C.L. Koch, 1841): 1 ♀ (AMNH [LP 4836]), Benin: Bemberekè: Riviere Dere, Foret classe d'Ouenou-Benou, Gando village [10°12.09′N 02°39.05′E], V. Vignoli and S. Tchibozo, 3.VI.2005; 1 ♂ (MNHN), Sudan: Delami, W. Ruttledge, 20.V.1927
Pandinus viatoris (Pocock, 1890): 1 ♀ (ZMB 15056), Mozambique: Tiesler
Scorpio maurus fuliginosus (Pallary, 1928): 1 ♂ (AMNH [LP 1930]), Morocco: Haha Mountains (western outliers of Atlas), ca. 10 km N Isk/Immouzer, ca. 60 km N Agadir, S. Huber, 21.VII.2000; 1 ex. (MNHN RS 1200), Morocco: Kasba d'Asni, J. de Lépiney, 31.V.1939
Scorpio maurus fuscus (Ehrenberg, 1829): 1 ♂ (AMNH [LP 1556]), Israel: Mitrani Center for Desert Ecology, ex Y. Lubin, VI.1998
Scorpio maurus palmatus (Ehrenberg, 1828): 1 ♀ (AMNH [LP 1532]), Egypt: ex D. Taylor, X.1997
Scorpio maurus subsp.: 1 ♀ (MNHN), Algeria: Manoc; 1 ex. (ZMB)

Scorpiopidae Kraepelin, 1905:
Scorpiops hardwickei (Gervais, 1843): 1 ♀ (MNHN RS 0722), Himalaya: Rhala, G. Babault, 1915; 1 ♀ (MNHN RS 0725), India: Himalaya: Calcutta, Simon
Scorpiops petersii Pocock, 1893: 1 ex. (ZMB 3063), India: Himalaya, Trochnow

Superstitioniidae Stahnke, 1940:
Alacran tartarus Francke, 1982: 1 ♀ (AMNH [LP 3499]), México: Oaxaca: Municipio San Miguel: Cueva de Escorpion [18.1065°N 96.7982°W], A. Gluesenkamp, P. Sprouse and C. Savvas, 18.IX.2004
Superstitionia donensis Stahnke, 1940: 1 ♂, 2 ♀ (AMNH [LP 3420]), U.S.A.: Arizona: Piñal County: Superstition Mountains, D. Vernier, XI.2003

Troglotayosicidae Lourenço, 1998:
Belisarius xambeui Simon, 1879: 1 ♀ (MNHN RS 7743), Spain: Mataro, J. Nègre, 31.VIII.1948; 1 ♀ (MNHN RS 0801), Spain: Gerona: Camprodon, J. Mateu, IX.1954

Urodacidae Pocock, 1893:
Urodacus manicatus (Thorell, 1876): 1 ♀ (ZMB 14909), Australia: Germantown, Oschatz, 1910
Urodacus novaehollandiae Peters, 1861: 1 ♂ (AMNH [LP 1658]), Australia: Western Australia: Jarrahdale, E.S. Volschenk, 25.II.1998
Urodacus yaschenkoi (Birula, 1903): 1 ♂ (AMNH [LP 1659]), Australia: South Australia: Berri, N.A. Locket and E.S. Volschenk, 24.IX.1997
Urodacus sp.: 1 ♂ (MNHN RS 8352), Australia: Western Australia: S.D. Bradshaw, IV.1980

Vaejovidae Thorell, 1876:
Paravaejovis pumilis (Williams, 1970): 1 ♂ (AMNH), México: Baja California Sur: Ciudad Constitucion, 32 km W [24°55′17″N 111°58′5.5″W], O. Francke, W. Savary, A. Valdez and E. Gonzalez, 11.VII.2004, 26 m, UV light detection at night
Paruroctonus becki (Gertsch and Allred, 1965): 2 juv. ♀ (AMNH [LP 4991]), U.S.A.: California: Inyo County: Alabama Hills Recreational Area, 7 mi. W Lone Pine [36°35.991′N 118°11.005′W], L. Prendini and R. Mercurio, 5.IX.2005, collected with UV light
Paruroctonus boreus (Girard, 1854): 1 ♂ (AMNH [LP 4388]), U.S.A.: Washington: Yakima County: Humphrey Road, Tieton [46°41′15″N 120°46′25″W], H. Leochelt, 24.VIII.1996
Paruroctonus borregoensis borregoensis Williams, 1972: 1 ♀ (AMNH [LP 4530]), Mexico: Sonora: Municipio Puerto Peñasco: Reserva de la Biosfera and Parque Nacional El Pinacate: 95 km NW Sonoyta off Route 2, W of Microondas Cerro Lava [32°06.175′N 113°47.105′W], R. Mercurio and E. González, 28.VI.2005, collected with UV light at night
Paruroctonus gracilior (Hoffmann, 1931): 1 ♀ (AMNH [LP 2152]), U.S.A.: New Mexico: Eddy

County: White's City, roadside 0.1 mi. S, K.J. McWest, 21.VI.2002; 1 ♀ (AMNH [LP 2213]), U.S.A.: Texas: Loving County: Wink, ca. 4 mi. NW at junction TX 302 and TX 1232 [31°48′55.08″N 103°12′11.43″W], WTAMU Arachnology Class, 5.X.2002

Paruroctonus stahnkei (Gertsch and Soleglad, 1966): 1 ♂ (AMNH [LP 3566]), U.S.A.: Arizona: Pima County: Tucson, near Bopp Road and Continental Road, B.R. Tomberlin and S.J. Burchfield, 15.IX.2004

Pseudouroctonus apacheanus (Gertsch and Soleglad, 1972): 1 ♀ (AMNH), U.S.A.: Arizona: Southwestern Research Station, 5 mi. W Portal, W.J. Gertsch, VII.1962

Pseudouroctonus reddelli (Gertsch and Soleglad, 1972): 1 ♀ (MNHN), U.S.A.: Texas: Travis County: Tooth Cave, Mitchell, 9.VI.1967; 1 ♀ (AMNH [LP 2155]), U.S.A.: Texas: Hays County: 0.5 mi. S Hays City, B. McMinn, 29.V.2002

Serradigitus wupatkiensis (Stahnke, 1940): 1 ♂ (AMNH [LP 3216]) U.S.A.: California: Inyo County: Inyo National Forest: White Mountains, roadside of 168 [37°15′45.0″N 118°09′19.1″W], W. Savary, R. Mercurio, K. Bamba and M. McCoy, 15.VIII.2004

Smeringurus vachoni vachoni (Stahnke, 1961): 1 ♂ (AMNH [LP 2684]), U.S.A.: California: San Bernardino County: Desert Studies Center, Soda Dry Lake, W.E. Savary and P.R. Craig, 5.VII.2003

Syntropis macrura Kraepelin, 1900: 1 juv. ♂ (AMNH [LP 4729]), Mexico: Baja California Sur: Municipio Comondú: San José de Comondú [26°03.542′N 111°48.985′W], L. Prendini, R. Mercurio, E. González, and W.E. Savary, 7.VI.2005, collected with UV light at night

Uroctonites huachuca (Gertsch and Soleglad, 1972): 1 ♀ (AMNH), U.S.A.: Arizona: Cochise County: Huachuca Mts, Cary Peak Trail, J. Burkhart, 20.IX.1969, 11:00 am, elev. 7000 ft, under rock slabs, deep pine needles

Uroctonus mordax mordax Thorell, 1876: 1 ♂ (AMNH [LP 1595]), U.S.A.: California: Contra Costa County: Clayton Road, near Clayton, W. Savary and L. Prendini, X.1997; 1 ♂ (ZMB 2392), U.S.A., California, Forrer; 2 ♀ (MNHN RS 0732), U.S.A.: California, M. Lourquin, 1953

Vaejovis intrepidus cristimanus Pocock, 1898: 1 ♂ (ZMB 15221), Mexico: San José, v. Blücher

Vaejovis magdalensis Williams, 1971: 1 ♀ (AMNH [LP 3155]), Mexico: Baja California Sur: La Paz, 50 km NW [24°5′56.2″N 110°43′41″W], O. Francke, E. González, and A. Valdez, 7.VII.2004, collected with UV light at night

Vaejovis mexicanus mexicanus C. L. Koch, 1836: 1 ♂ (AMNH [LP 1826]), Mexico: Estado de México: Municipio Atizapan de Zaragoza: Casa habitacion, O. Francke, X.2001

Vaejovis nitidulus C. L. Koch, 1843: 2 ♂ (AMNH [LP 2052]), Mexico: Hidalgo: Antena de Microondas de Zimapan [20°44′47″N 99°20′54″W], L. Prendini, O. Francke, E. Gonzalez, and J. Ponce, 3.VIII.2002, collected with UV light at night

Vaejovis spinigerus (Wood, 1863): 1 ♂ (AMNH [LP 1811]), U.S.A.: Arizona: Maricopa County: Buckeye Hills Recreation Area [33°17.039′N 112°38.754′W], J. and J. Bigelow, 24.VIII.2000

Vejovoidus longiunguis (Williams, 1969): 1 ♂ (AMNH [LP 3147]), Mexico: Baja California Sur: Guerrero Negro, 12 km S [27°56′5.8″N 113°54′23.1″W], O. Francke, W. Savary, E. González, and A. Valdez, 15.VI.2004, collected with UV light at night

PLATES

Plate 1. *Pseudochactas ovchinnikovi* Gromov, 1998, 1 juv. ♂ (AMNH [LP 2303]): **A.** surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** wrinkled distal edges of book lung lamellae covered with spines (arrow), posterior view; **C.** movable posterior edge of spiracle with flattened structures (arrow), anterior view. Numbers in arrows refer to character states.

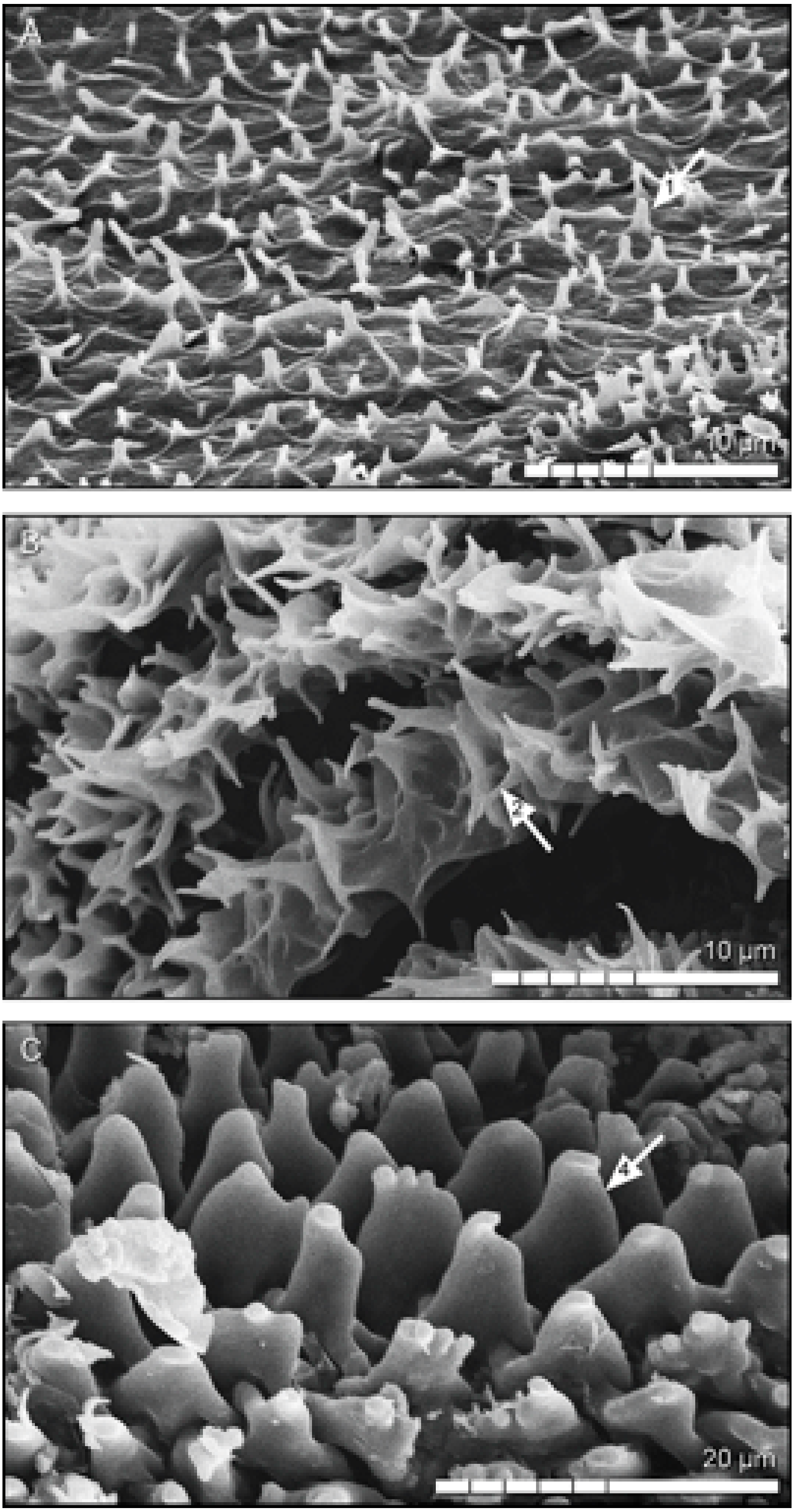
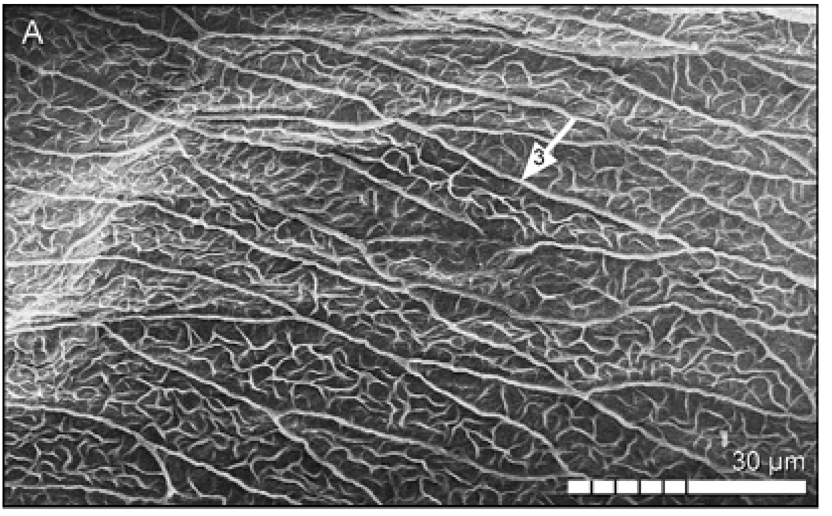

A
10 µm
B
10 µm
C
4
20 µm

Plate 2. *Ananteris cussinii* Borelli, 1910, 1 ♂ (AMNH [LP 1716]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas, directed to distal lamellar edge, and with irregular foldlike ridges, viewed from air space; **B.** smooth to creased distal edges of book lung lamellae (arrow), posterior view. Numbers in arrows refer to character states.


A
3
30 µm

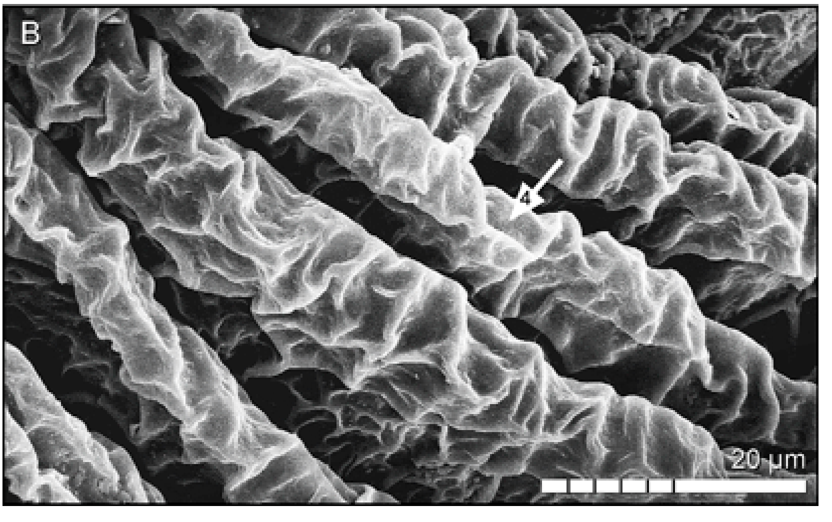

B
4
20 µm

Plate 3. *Androctonus amoreuxi amoreuxi* (Audouin, 1826), 1 ♀ (MNHN RS 2034): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas, directed to distal lamellar edge, and with almost perpendicular foldlike ridges, viewed from air space; **B.** distal edges of book lung lamellae densely covered with rigid thorns (arrow), posterior view; **C.** movable posterior edge of spiracle with subconical structures (arrow), anterior view. Numbers in arrows refer to character states.

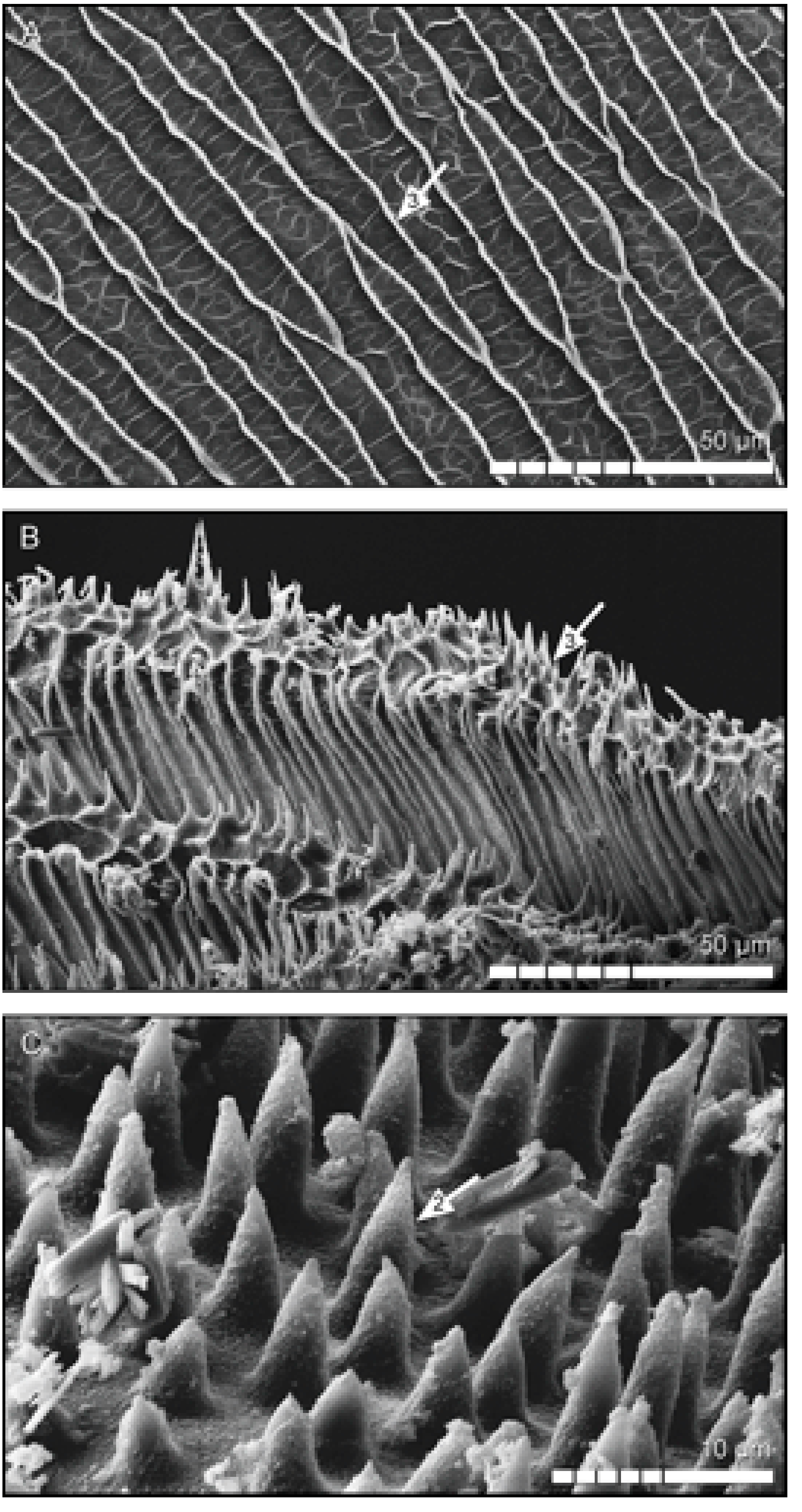

A
3
50 µm
B
3
50 µm
C
2
10 µm

Plate 4. *Androctonus australis australis* (Linnaeus, 1758), 1 ♀ (AMNH [LP 1970]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas, directed to distal lamellar edge, viewed from air space; **B.** distal edge of lamella with rigid thorns (arrow), posterior view; **C.** movable posterior edge of spiracle with subconical structures (arrow), anterior view. Numbers in arrows refer to character states.

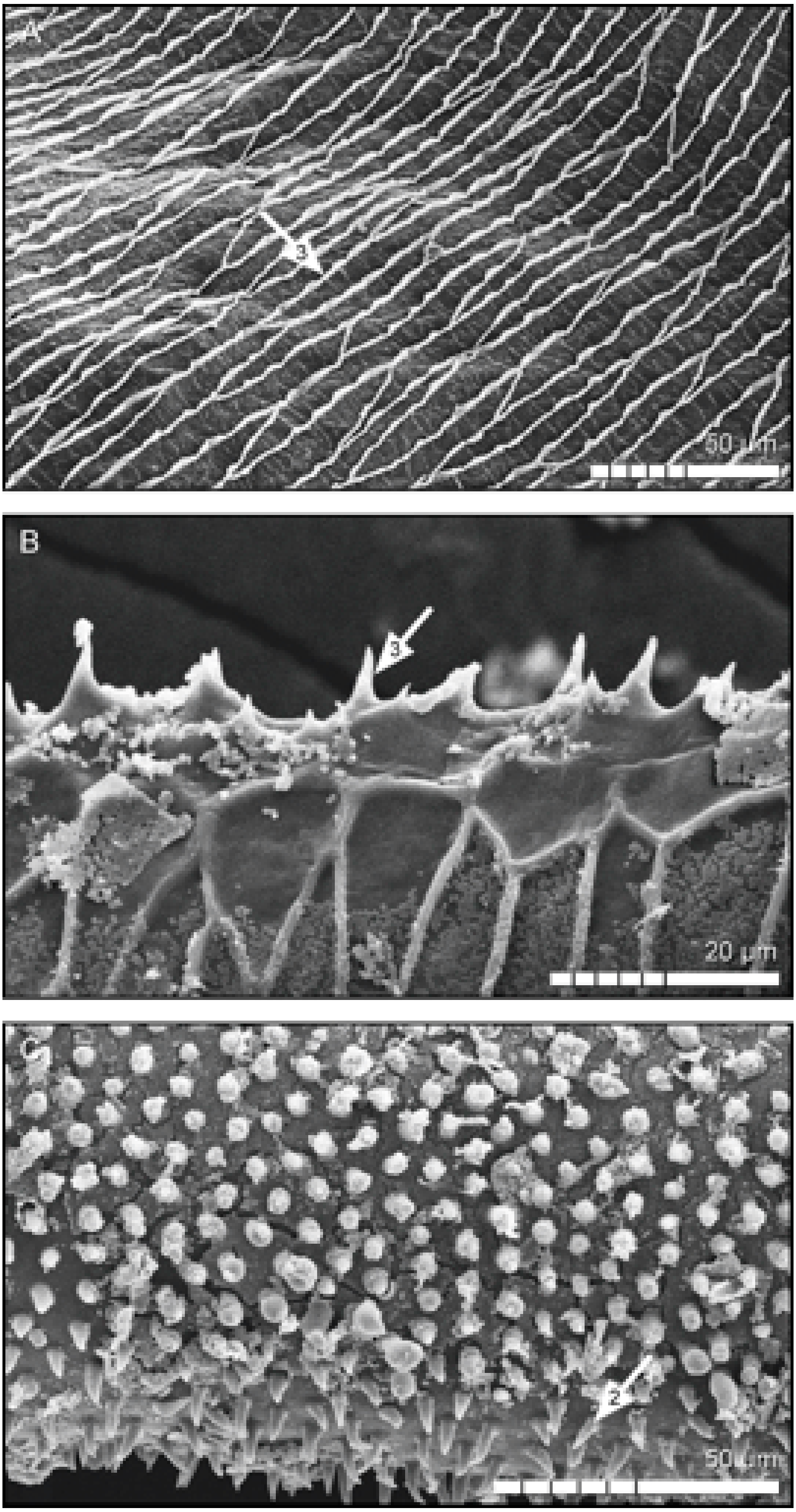

A
3
50 µm
B
3
20 µm
C
2
50 µm

Plate 5. *Anomalobuthus rickmersi* Kraepelin, 1900, 1 ♂ (AMNH [LP 3772]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas, directed to distal lamellar edge, and with irregular foldlike ridges, viewed from air space; **B.** distal edges of book lung lamellae covered with rigid thorns (arrow), posterior view; **C.** movable posterior edge of spiracle with subconical structures (arrow), anterior view. Numbers in arrows refer to character states.

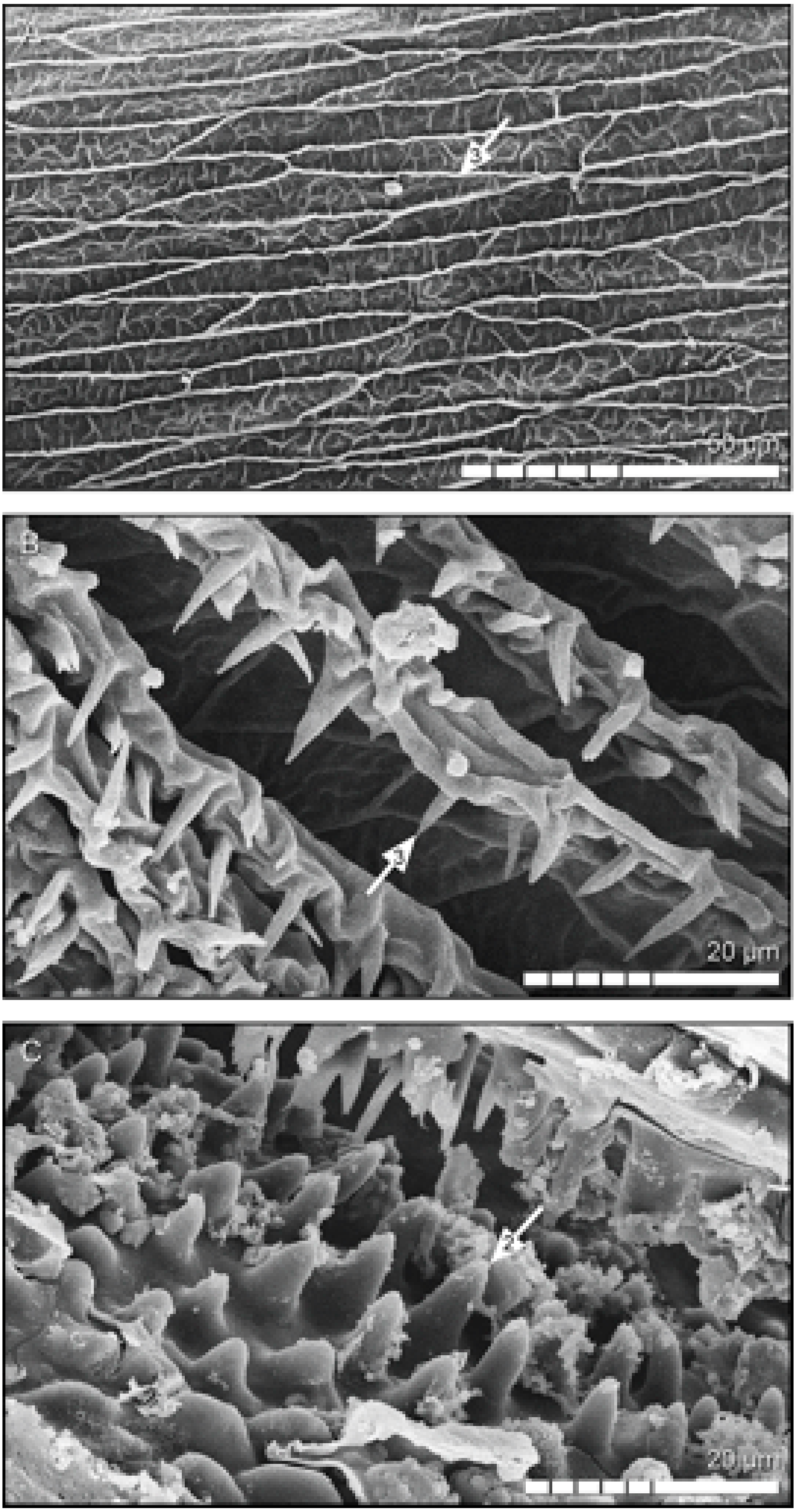

A
50 µm
B
20 µm
C
20 µm

Plate 6. *Apistobuthus pterygocercus* Finnegan, 1932, 1 ♀ (AMNH [LP 1795]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas, directed to distal lamellar edge, and with perpendicular foldlike ridges, viewed from air space; **B.** distal edges of book lung lamellae densely covered with rigid thorns (arrow), posterior view; **C.** movable posterior edge of spiracle with subconical thornlike structures (arrow), anterior view. Numbers in arrows refer to character states.

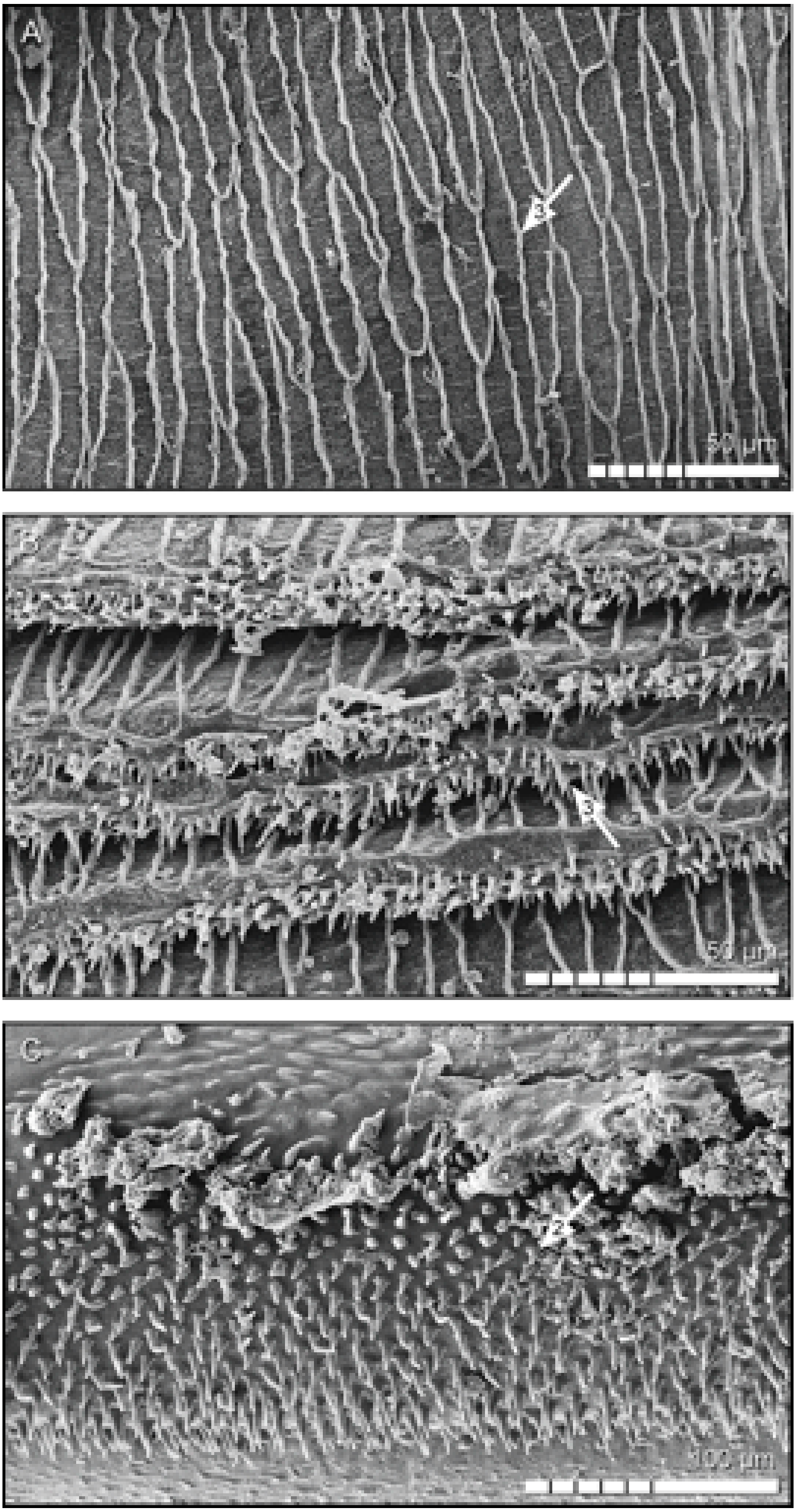

A
50 µm
B
50 µm
C
100 µm

Plate 7. *Babycurus buettneri* Karsch, 1886: 1 ♂ (AMNH [LP 1744]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas, directed to distal lamellar edge, distally, and with fewer slender areas and bridging trabeculae (broken), proximally, viewed from air space; **B.** wrinkled distal edges of book lung lamellae (arrow) covered with reticulate veins, posterior view; **C.** movable posterior edge of spiracle with subconical thornlike structures (arrow), anterior view.

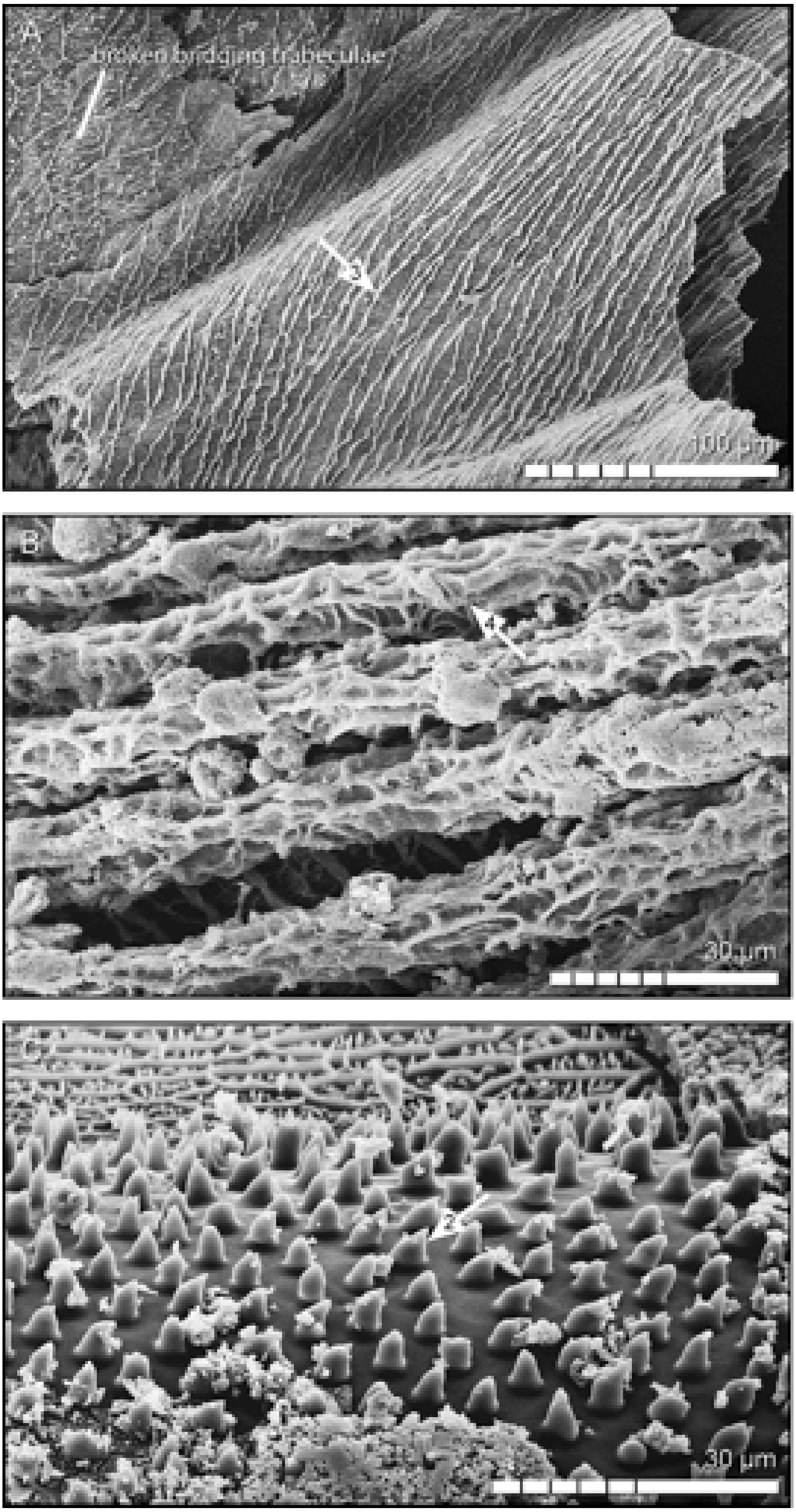

A
broken bridging trabeculae
100 μm
B
30 μm
C
30 μm

Plate 8. *Buthacus arenicola* (Simon, 1885): 1 ♀ (AMNH [LP 1973]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas, directed to distal lamellar edge, and with irregular foldlike ridges, viewed from air space; **B.** distal edges of book lung lamellae covered with rigid thorns (arrow), posterior view; **C.** movable posterior edge of spiracle with subconical structures (arrow), anterior view. Numbers in arrows refer to character states.

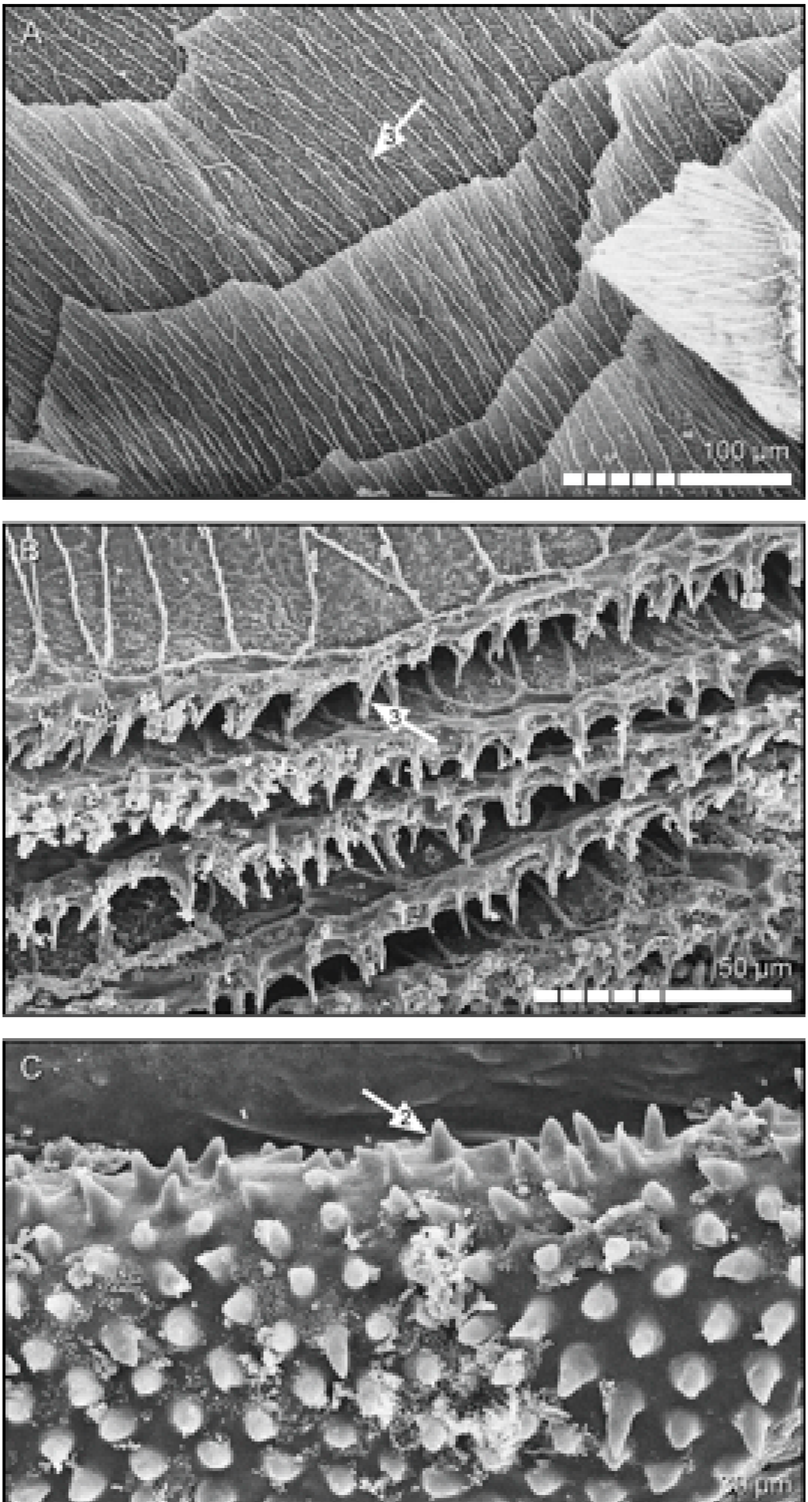

A
100 µm
B
50 µm
C

Plate 9. *Butheolus gallagheri* Vachon, 1980: 1 ♂ (AMNH [LP 2280]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas, directed to distal lamellar edge, and with irregular foldlike ridges, viewed from air space; **B.** distal edge of book lung lamella covered with rigid thorns (arrow), posterior view; **C.** movable posterior edge of spiracle with subconical structures (arrow), anterior view. Numbers in arrows refer to character states.

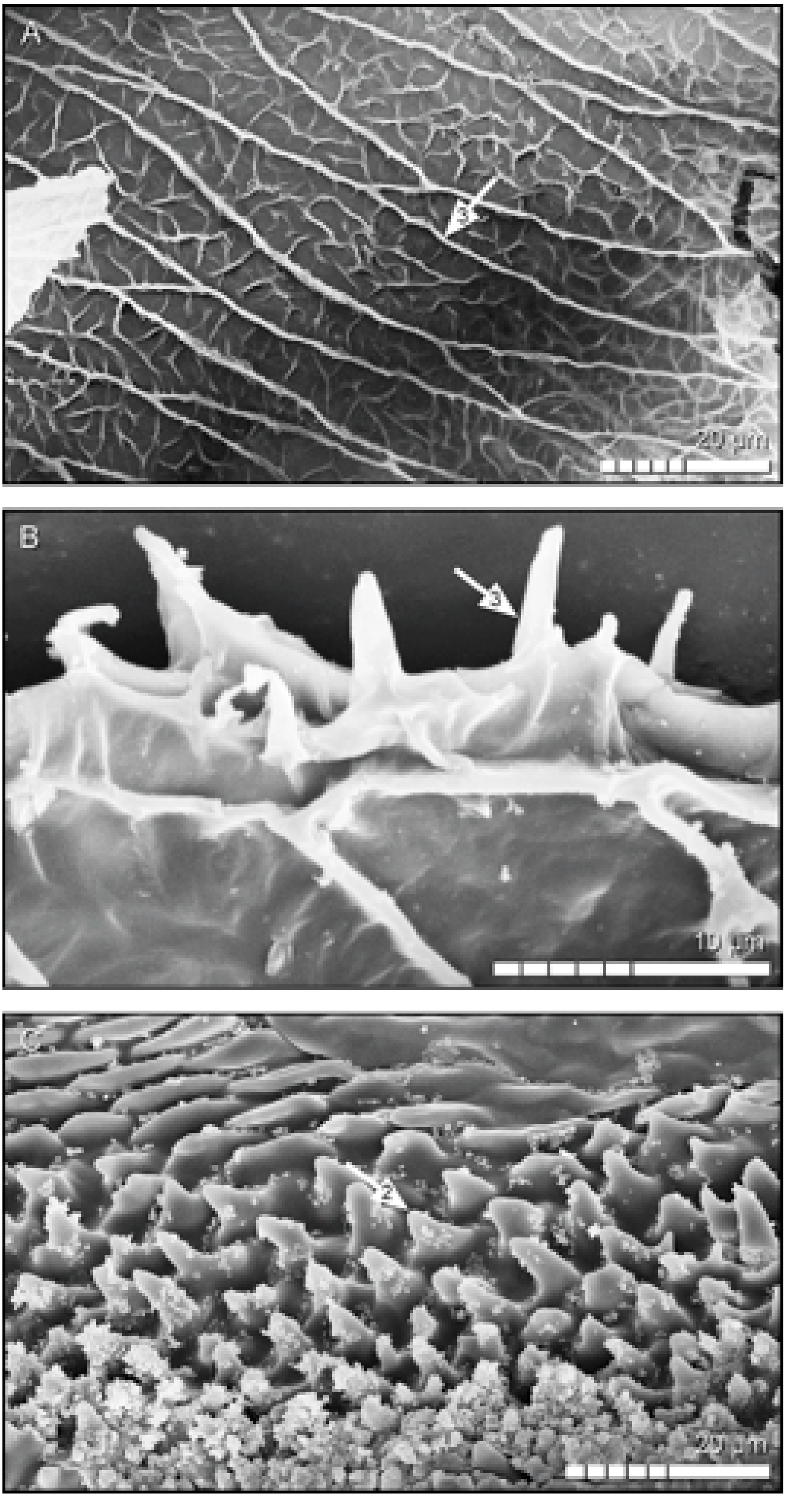

A
20 µm
B
10 µm
C
20 µm

Plate 10. *Buthiscus bicalcaratus* Birula, 1905: 1 ♂ (MNHN RS 1721): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas, directed to distal lamellar edge, and with perpendicular and irregular foldlike ridges, viewed from air space; **B.** distal edges of book lung lamellae covered with rigid thorns (arrow), posterior view; **C.** movable posterior edge of spiracle with subconical structures (arrow), anterior view. Numbers in arrows refer to character states.

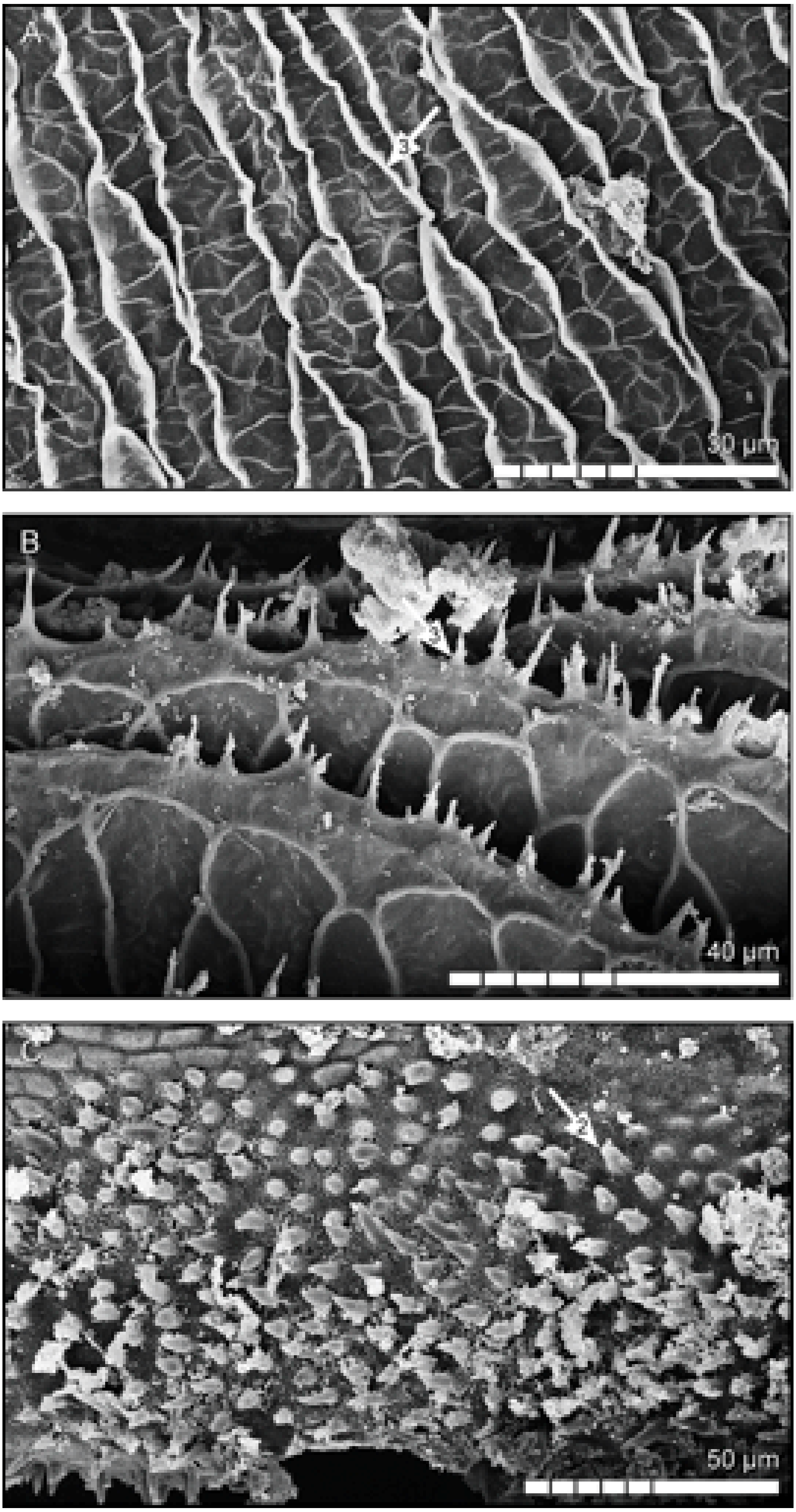

A
30 µm
B
40 µm
C
50 µm

Plate 11. *Buthus occitanus* (Amoreux, 1789): 1 ♂ (AMNH [LP 4595]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas, directed to distal lamellar edge, and with perpendicular and irregular foldlike ridges, viewed from air space; **B.** distal edges of book lung lamellae covered with rigid thorns (arrow), posterior view; **C.** movable posterior edge of spiracle with subconical structures (arrow), anterior view. Numbers in arrows refer to character states.

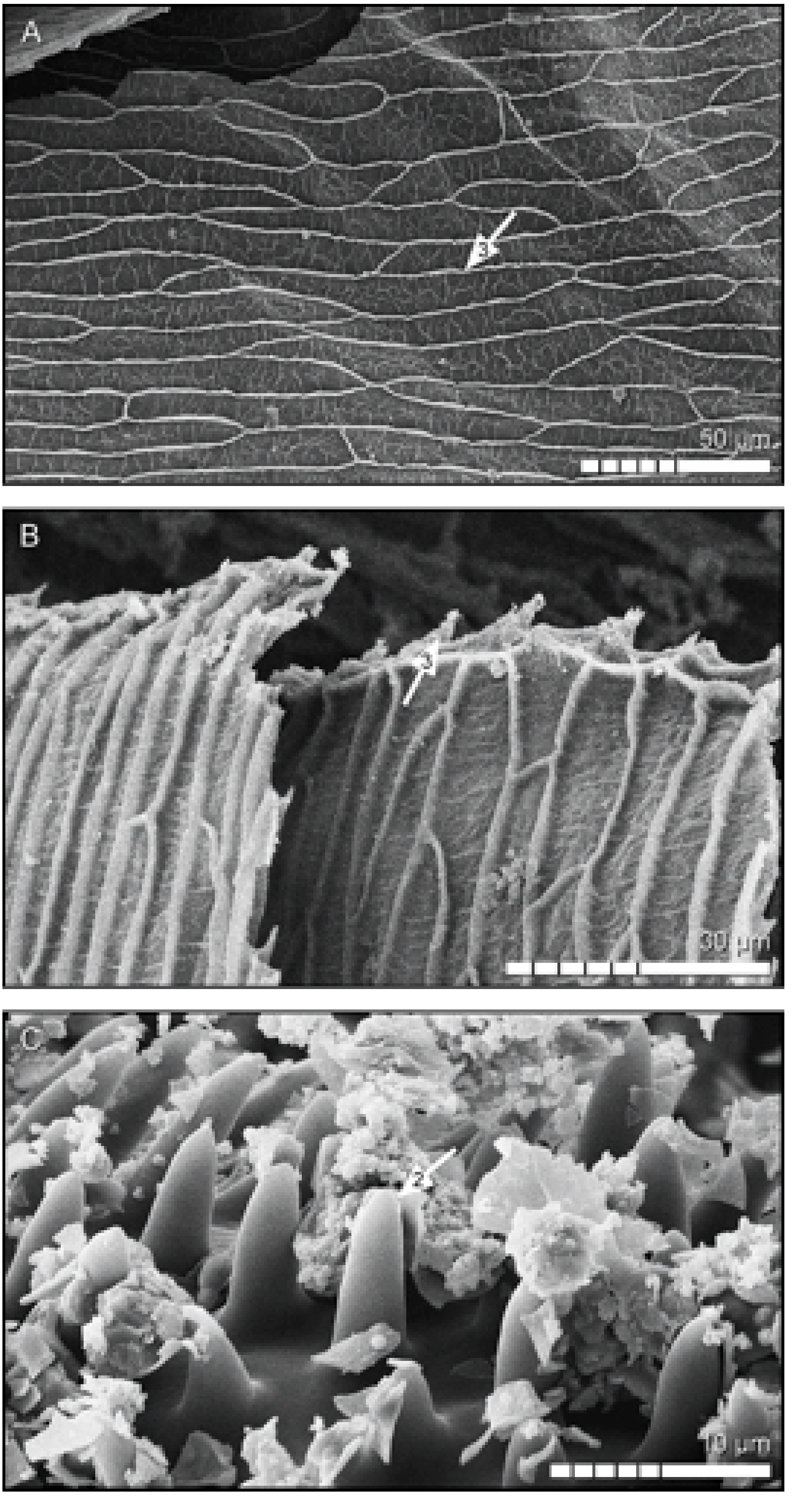

A
3
50 µm
B
1
30 µm
C
2
10 µm

Plate 12. *Caribetityus elii* (Armas and Marcano Fondeur, 1992): 1 ♀ (AMNH [LP 3277]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding polygonal areas with parallel veins (ribs), directed to distal lamellar edge, and with perpendicular foldlike ridges, viewed from air space; **B.** smooth distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with subconical structures (arrow), anterior view. Numbers in arrows refer to character states.

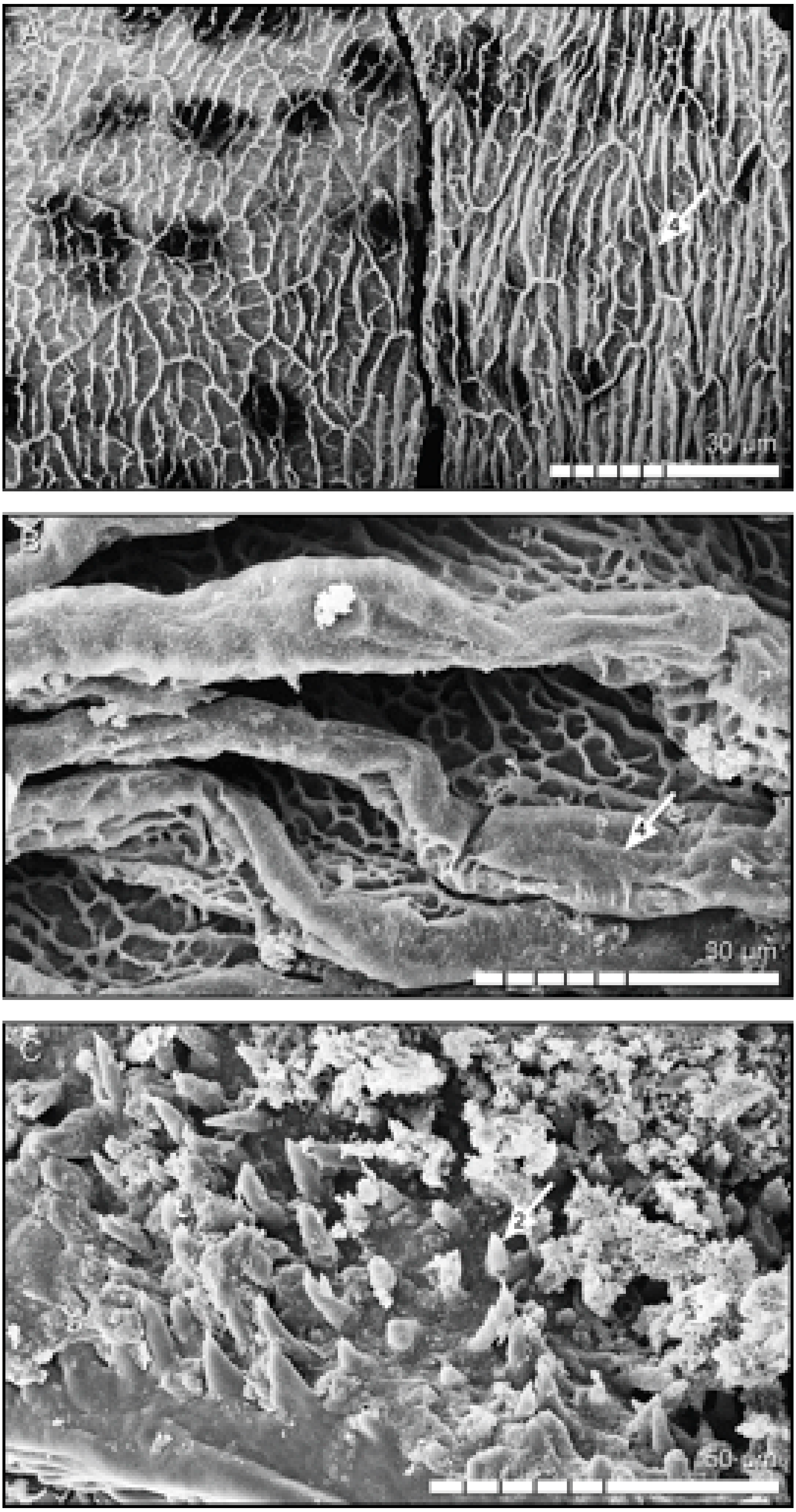

A
4
30 µm
B
4
30 µm
C
2
50 µm

Plate 13. *Centruroides exilicauda* (Wood, 1863): 1 ♀ (AMNH [LP 4477]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas, directed to distal lamellar edge, viewed from air space; **B.** smooth distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with subconical structures (arrow), anterior view. Numbers in arrows refer to character states.

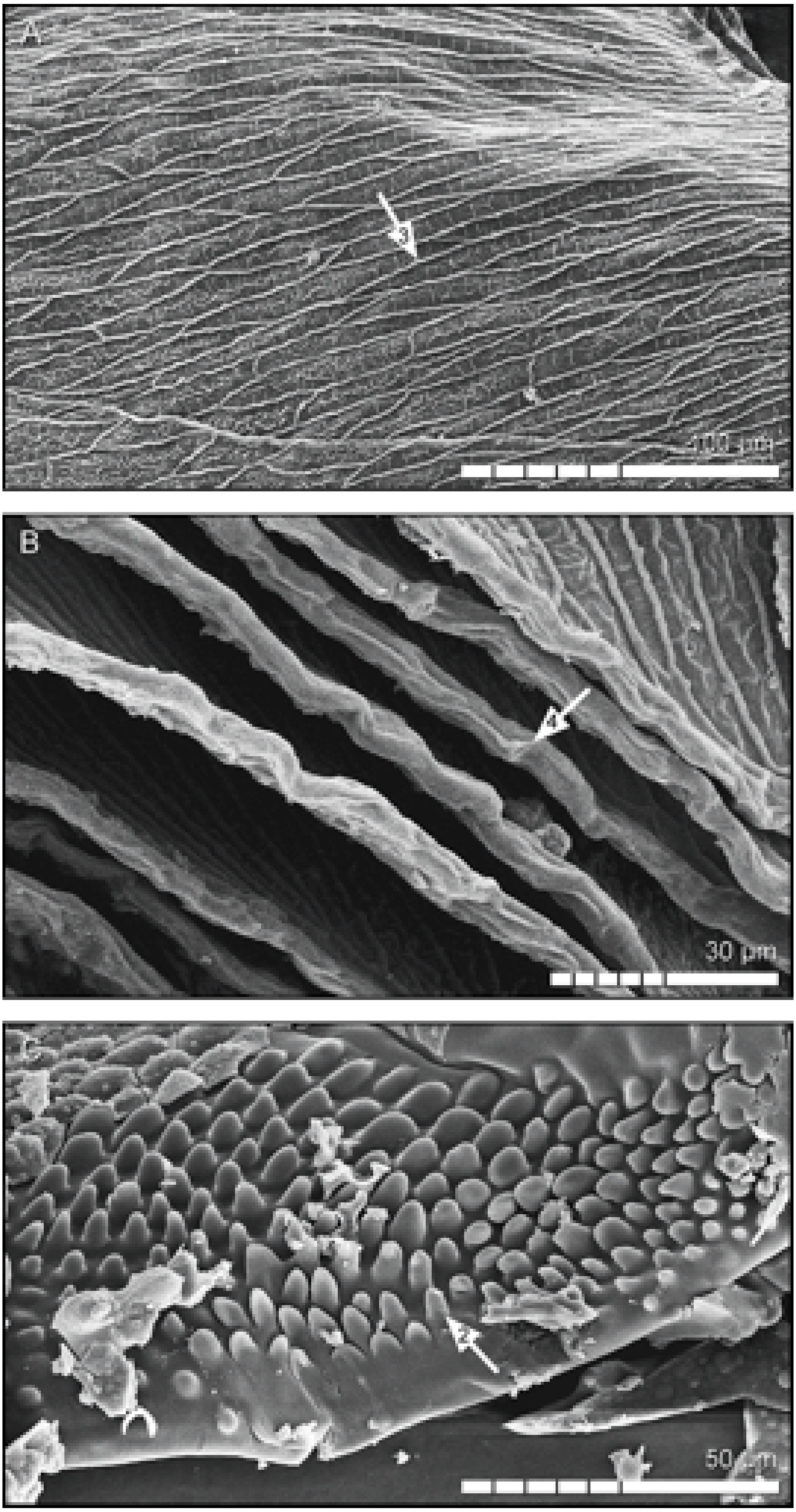

A
100 µm
B
30 µm
C
50 µm

Plate 14. *Centruroides gracilis* (Latreille, 1804), 1 ♀ (AMNH [LP 2051]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas, directed to distal lamellar edge, and with irregular foldlike ridges, viewed from air space; **B.** smooth distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with subconical structures (arrow), anterior view. Numbers in arrows refer to character states.

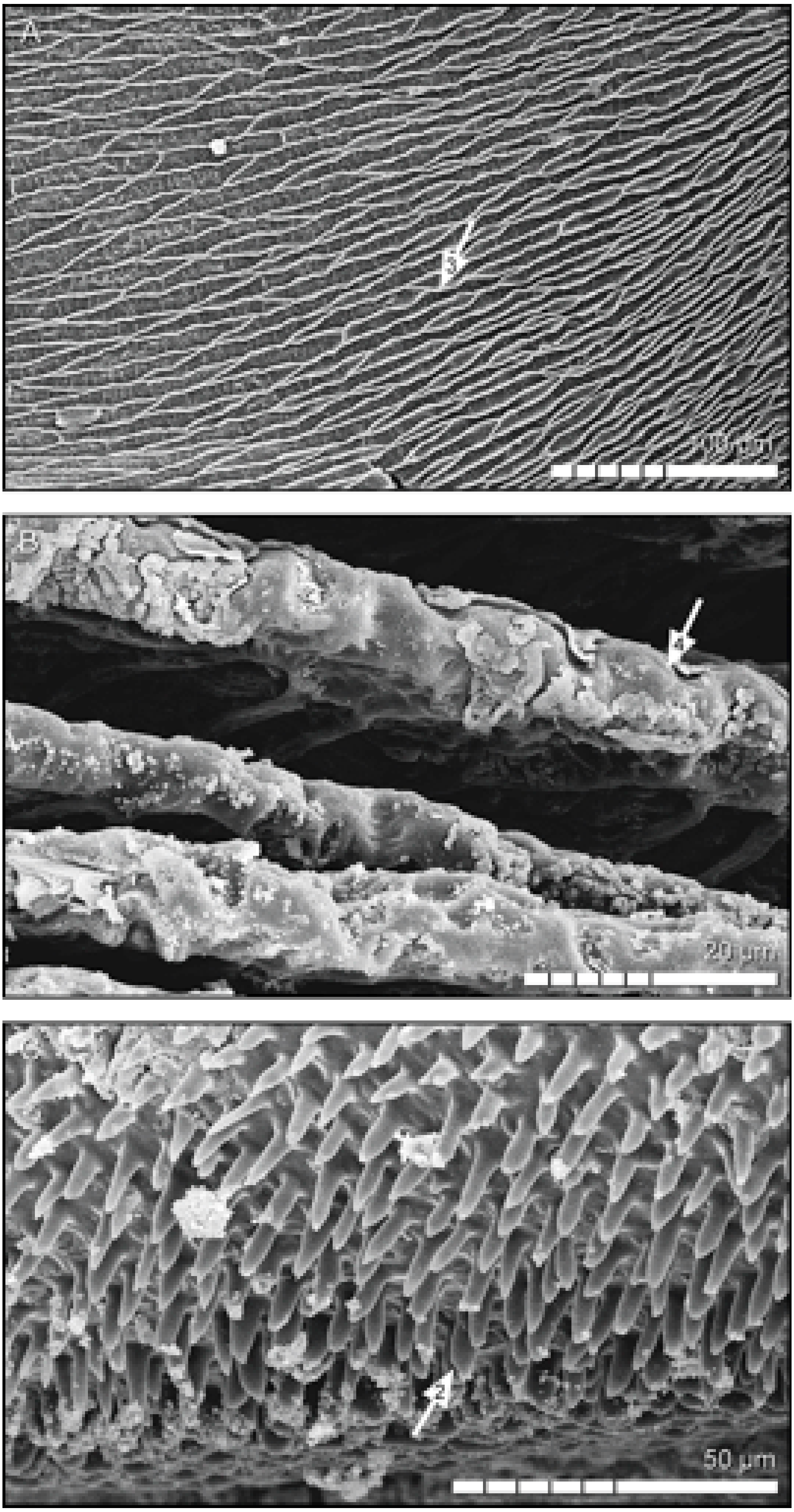

A
B
20 µm
C
50 µm

Plate 15. *Centruroides gracilis* (Latreille, 1804), 1 ♀ (AMNH [LP 2306]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas, directed to distal lamellar edge, and with perpendicular foldlike ridges, viewed from air space; **B.** wrinkled distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with subconical structures (arrow), anterior view. Numbers in arrows refer to character states.

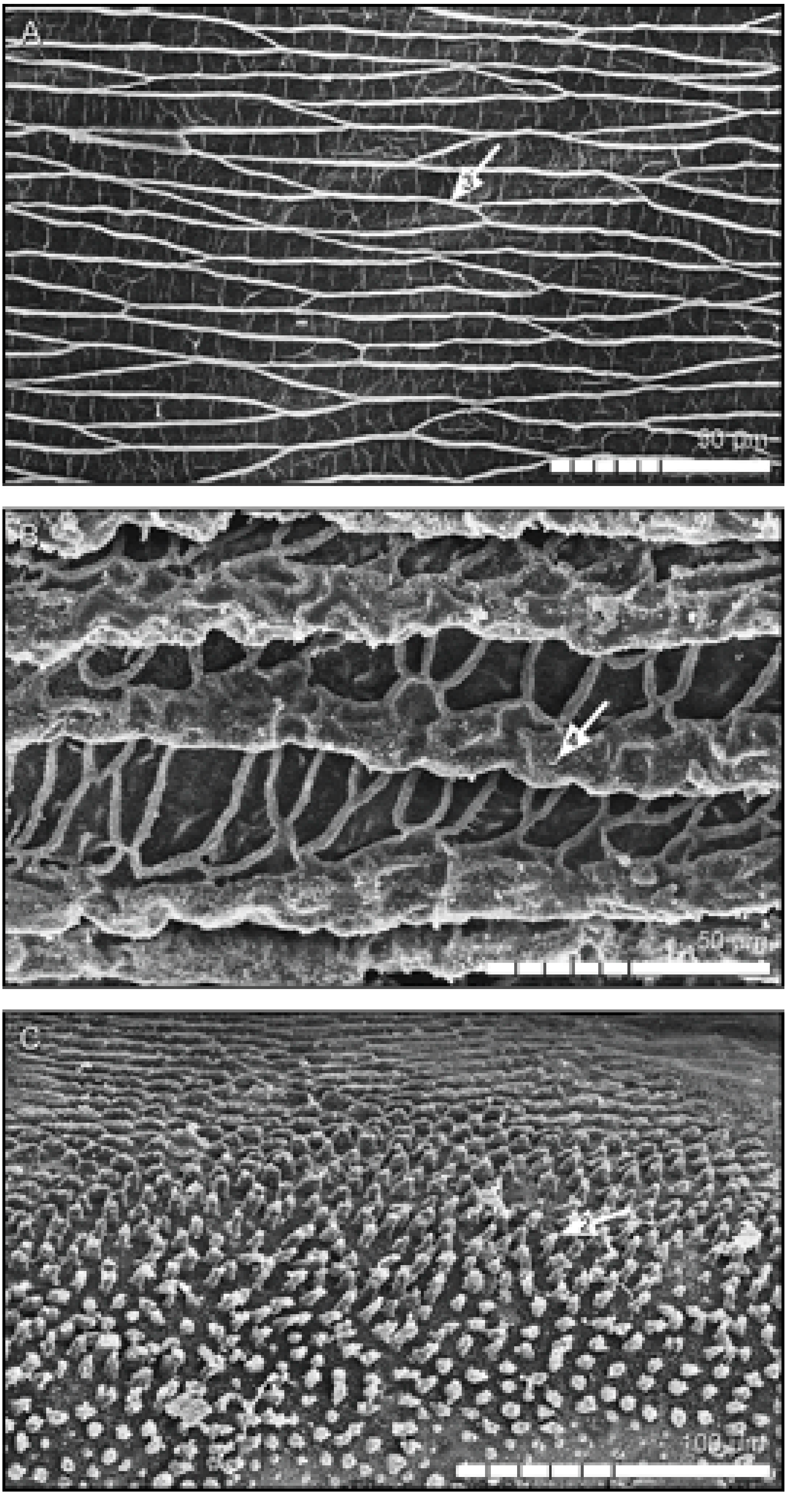

A
50 µm
B
50 µm
C
100 µm

Plate 16. *Centruroides margaritatus margaritatus* (Gervais, 1841), 1 ♂ (AMNH [LP 1787]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas, directed to distal lamellar edge, viewed from air space; **B.** smooth distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with subconical structures (arrow), anterior view. Numbers in arrows refer to character states.

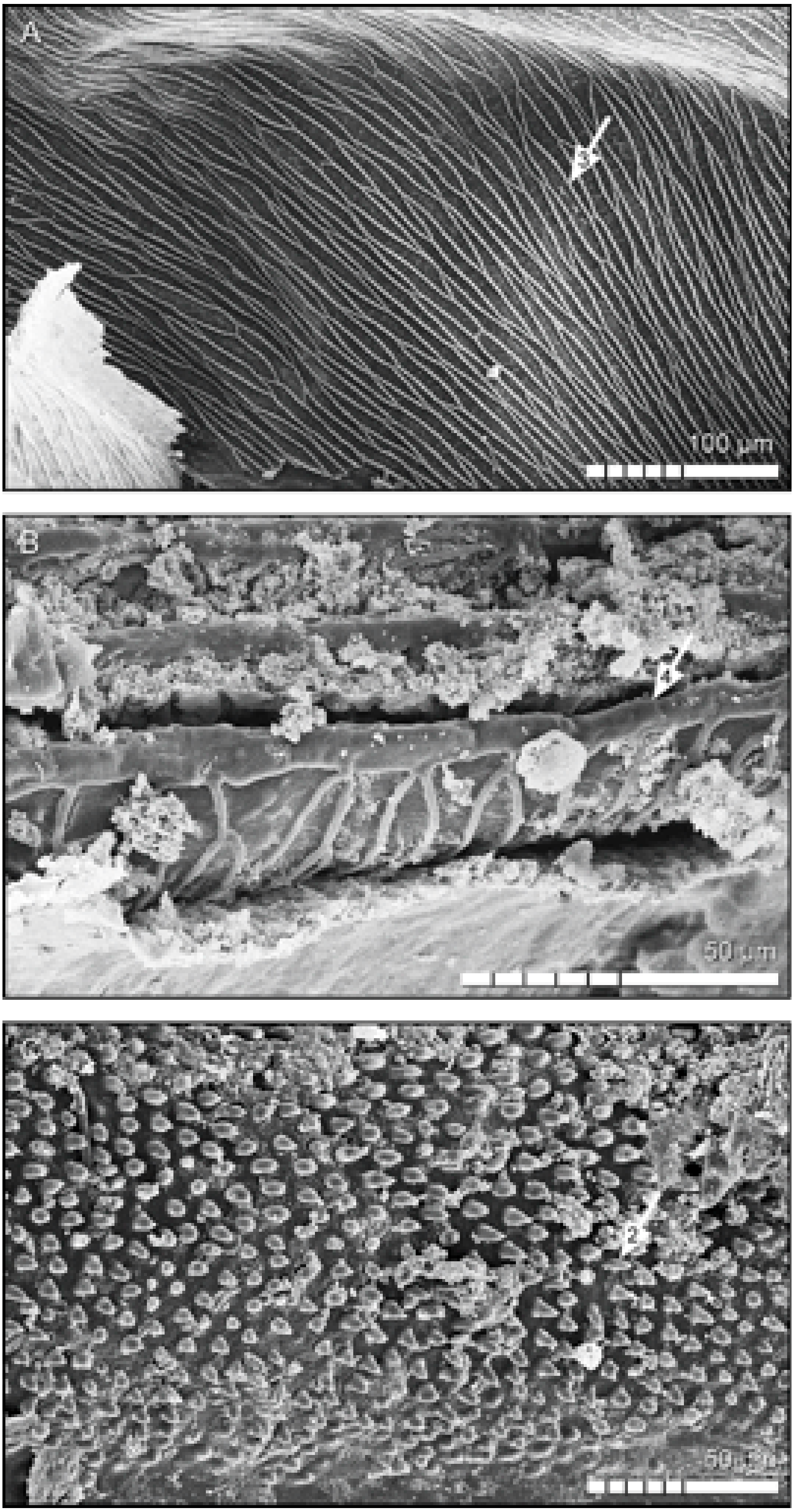

A
100 µm
B
50 µm
C

Plate 17. *Centruroides schmidti* Sissom, 1995, 1 ♀ (AMNH [LP 2070]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas, directed to distal lamellar edge, and with irregular foldlike ridges, viewed from air space; **B.** smooth to slightly wrinkled distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with subconical structures (arrow), anterior view; numbers in arrows refer to character states.

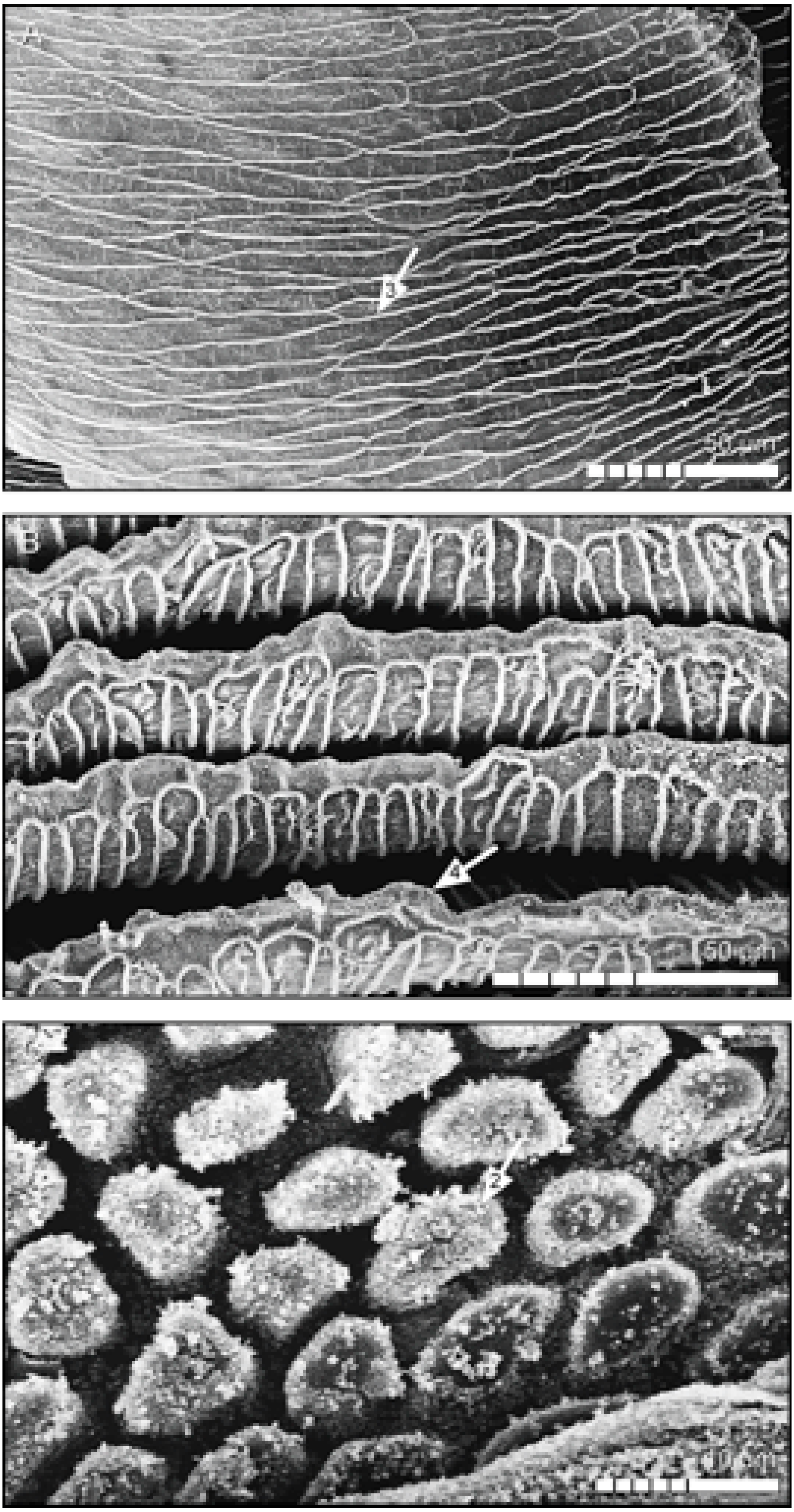

3
B
4
50 µm

Plate 18. *Cicileus exilis* (Pallary, 1928), 1 ♀ (MNHN RS 1273): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas, directed to distal lamellar edge, and with irregular foldlike ridges, viewed from air space; **B.** distal edges of book lung lamellae covered with small thorns (arrow), posterior view; **C.** movable posterior edge of spiracle with subconical structures (arrow), anterior view. Numbers in arrows refer to character states.

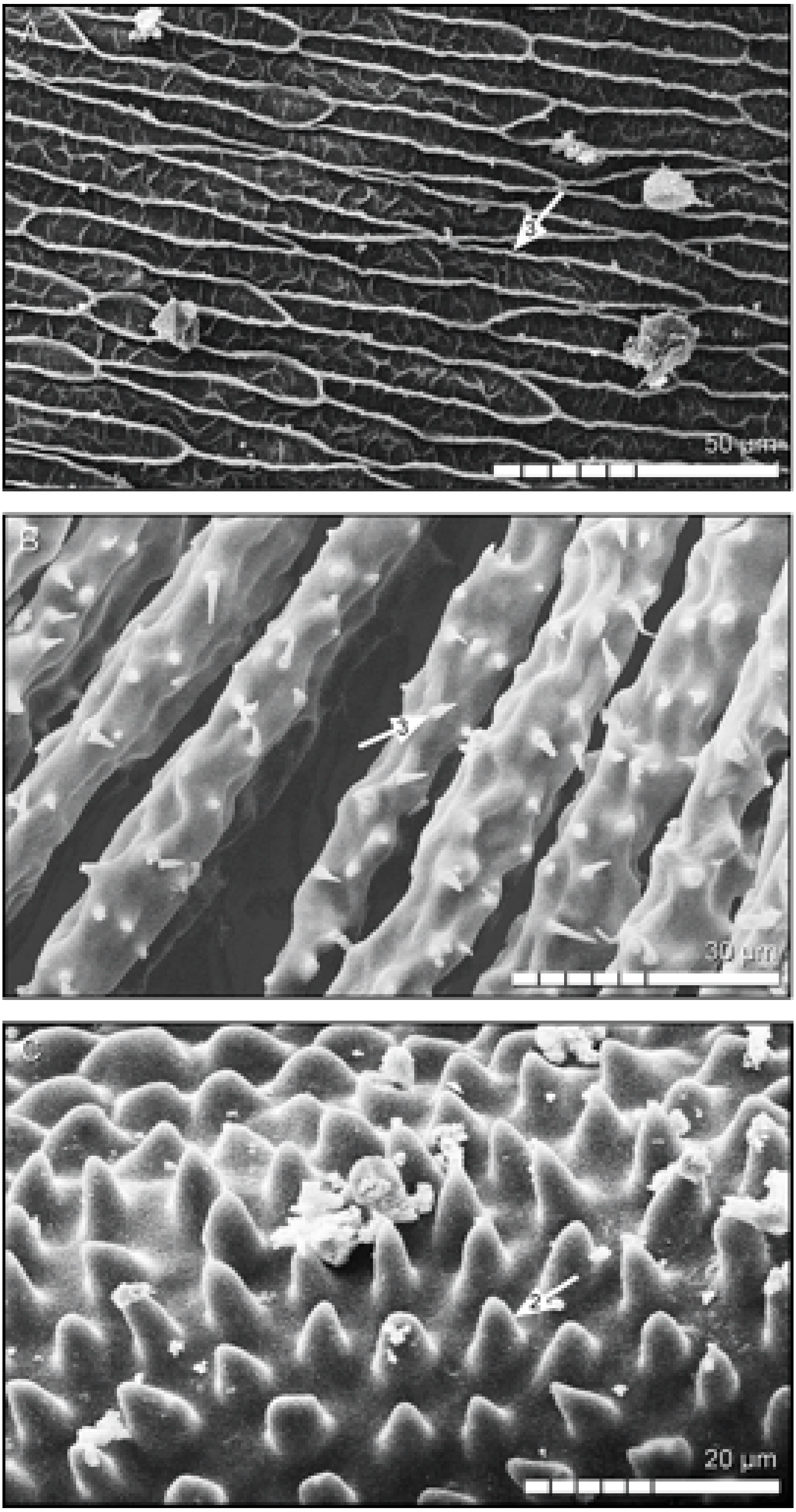

A
50 µm
B
30 µm
C
20 µm

Plate 19. *Compsobuthus berlandi* Vachon, 1950, 1 ♀ (MNHN RS 4910): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas, directed to distal lamellar edge, and with irregular foldlike ridges, viewed from air space; **B.** distal edges of book lung lamellae covered with thorns (arrow), posterior view; **C.** movable posterior edge of spiracle with subconical structures (arrow), anterior view. Numbers in arrows refer to character states.

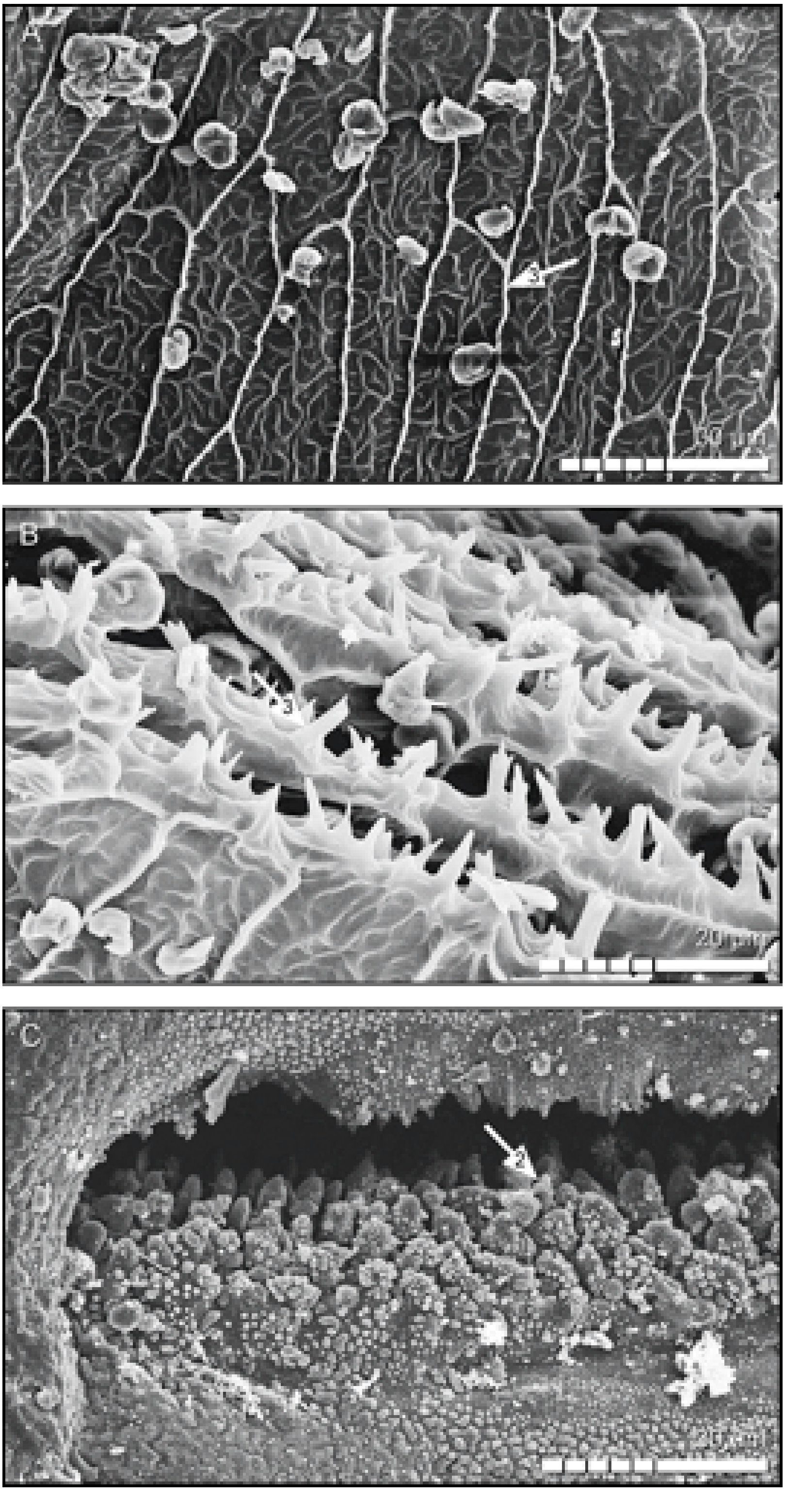

A
B
20 μm
C

Plate 20. *Compsobuthus maindroni* (Kraepelin, 1900), 1 ♂ (AMNH [LP 3765]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas, directed to distal lamellar edge, and with irregular foldlike ridges, viewed from air space; **B.** distal edges of book lung lamellae covered with thorns (arrow), posterior view; **C.** movable posterior edge of spiracle with subconical structures (arrow), anterior view. Numbers in arrows refer to character states.

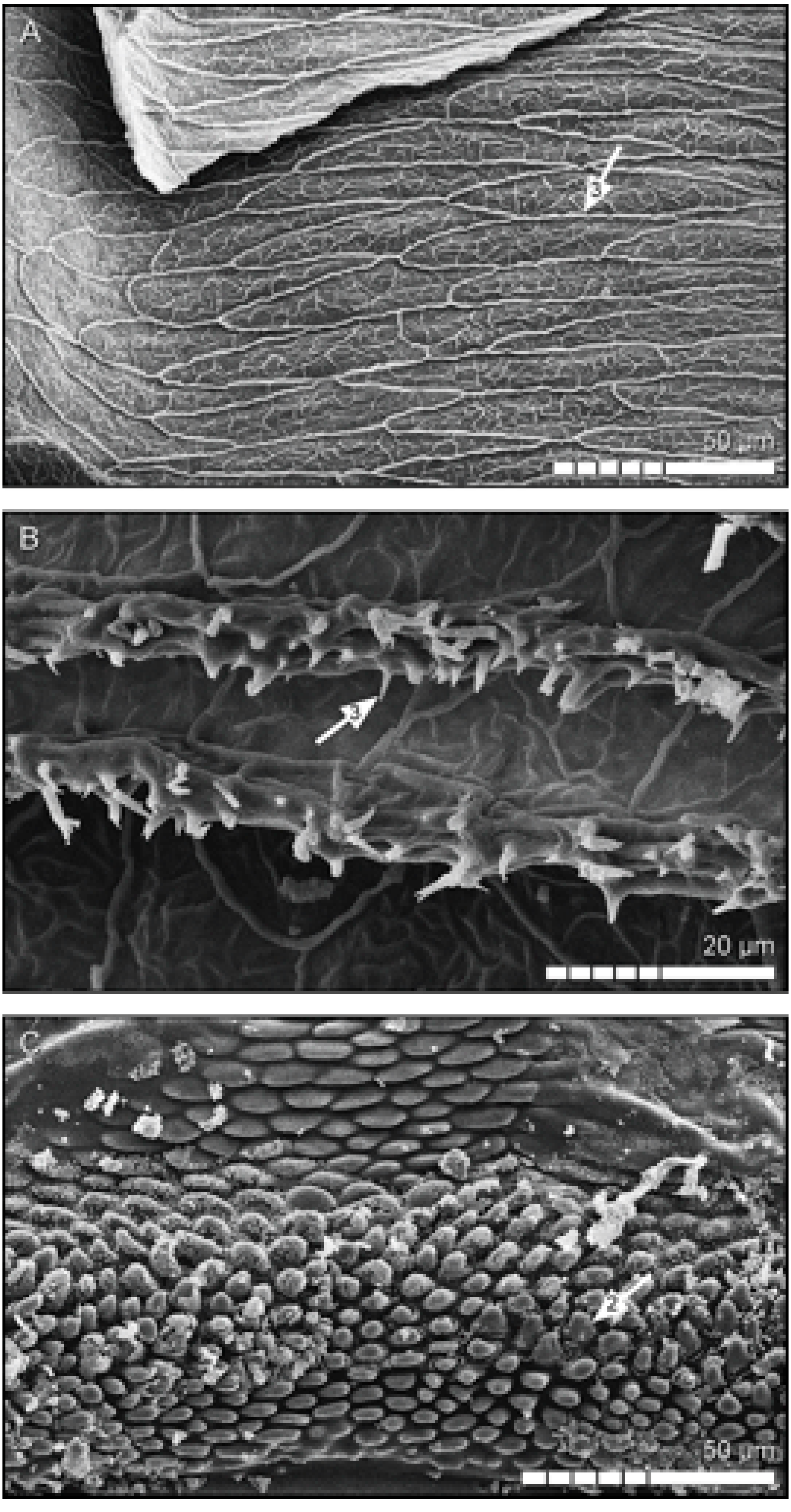

A
50 µm
B
20 µm
C
50 µm

Plate 21. *Grosphus hirtus* Kraepelin, 1900, 1 ♀ (AMNH [LP 2774]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas, directed to distal lamellar edge, viewed from air space; **B.** smooth distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with hillocklike structures (arrow), anterior view. Numbers in arrows refer to character states.

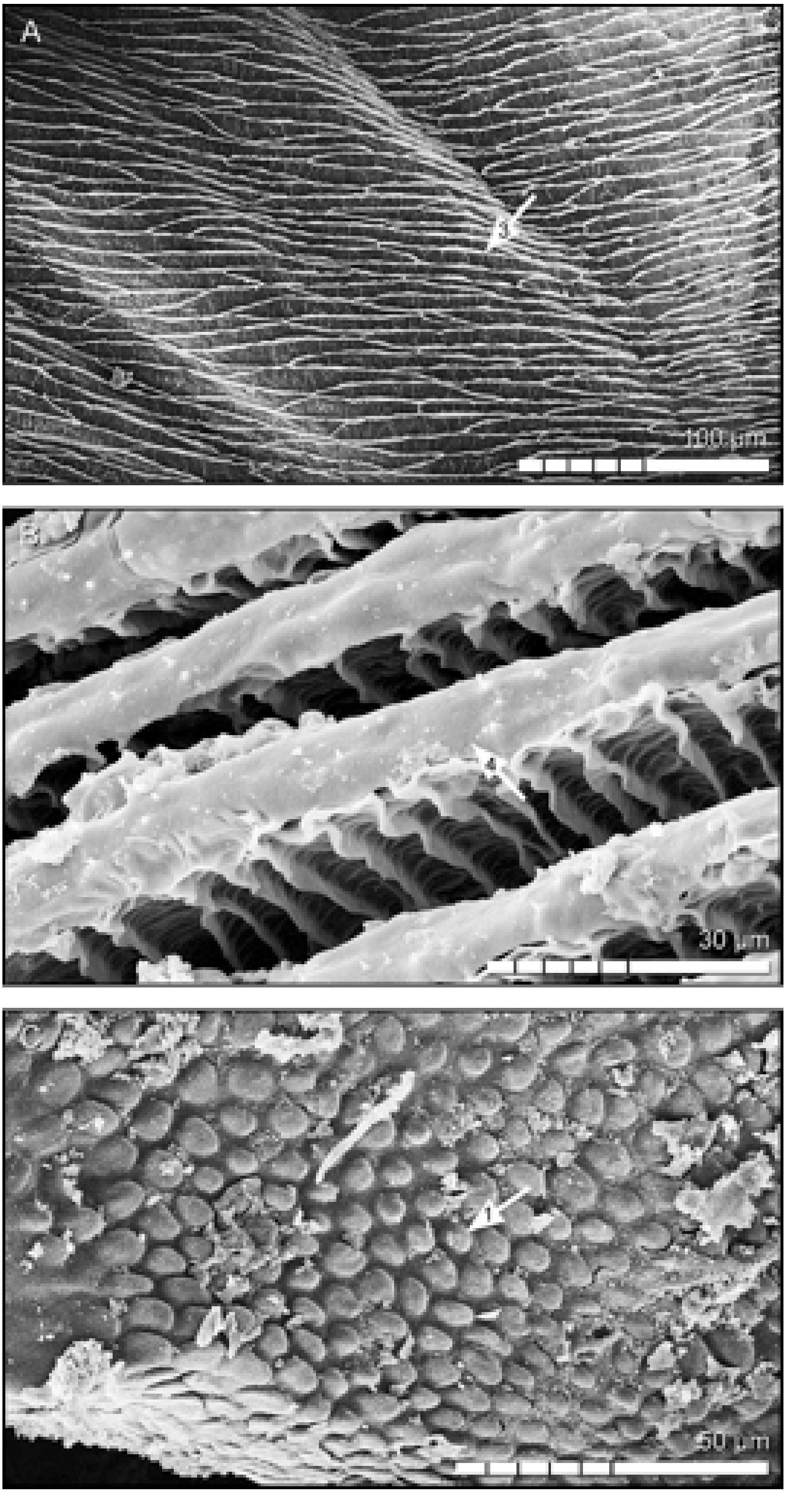

A
100 µm
B
30 µm
C
50 µm

Plate 22. *Hottentotta conspersus* (Thorell, 1876), 1 juv. (AMNH [LP 2627]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas, directed to distal lamellar edge, and with irregular foldlike ridges, viewed from air space; **B.** smooth distal edges of book lung lamellae (arrow) with a few small thorns, posterior view; **C.** movable posterior edge of spiracle with hillocklike structures (arrow), anterior view. Numbers in arrows refer to character states.

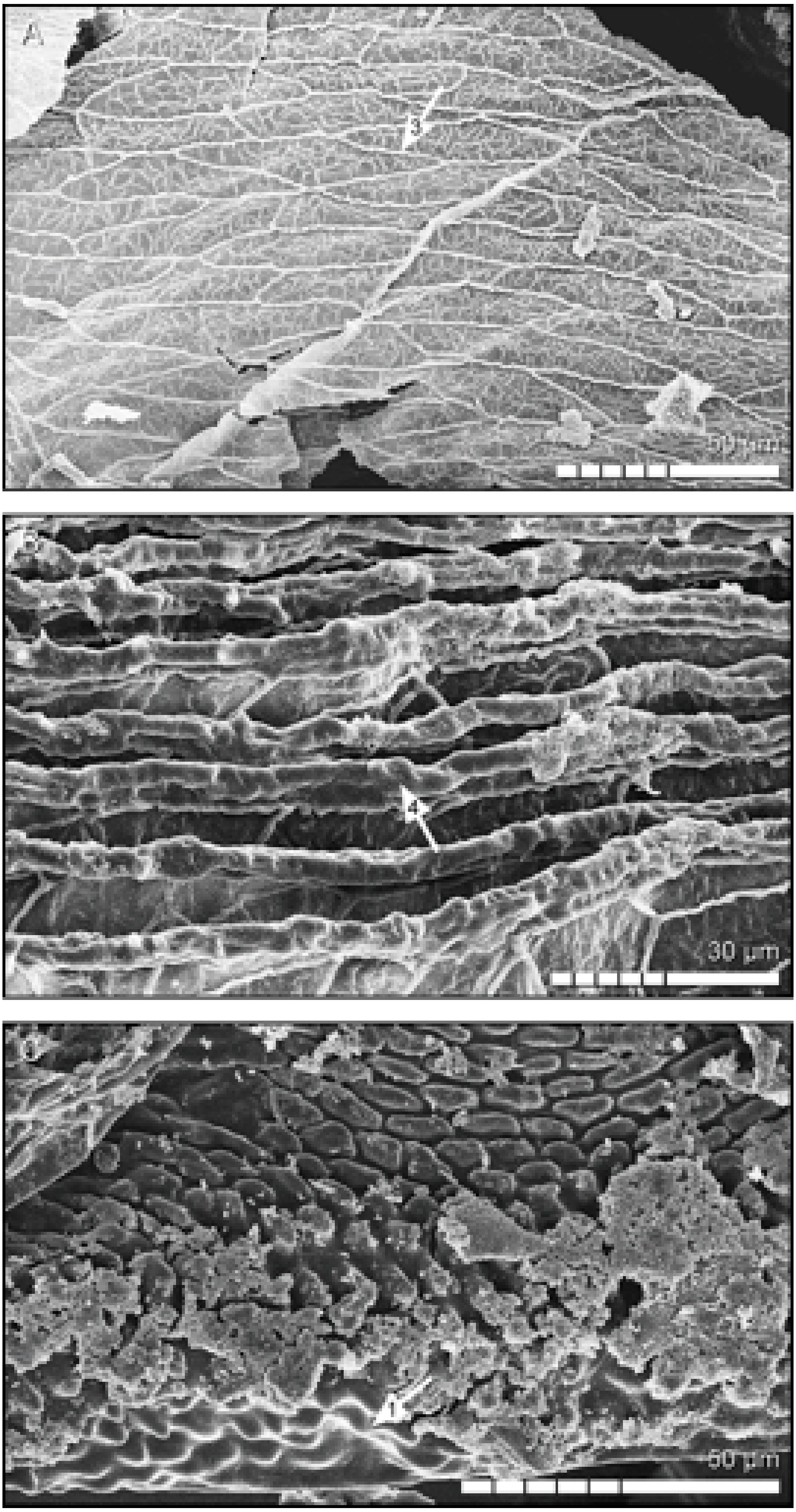

A
3
50 µm
4
30 µm
1
50 µm

Plate 23. *Hottentotta hottentotta* (Fabricius, 1787), 1 subad. ♂ (AMNH [LP 4822]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas, directed to distal lamellar edge, and with irregular, perpendicular foldlike ridges, viewed from air space; **B.** distal edges of book lung lamellae covered with rigid thorns (arrow), posterior view; **C.** movable posterior edge of spiracle with spinelike structures (arrow), anterior view. Numbers in arrows refer to character states.

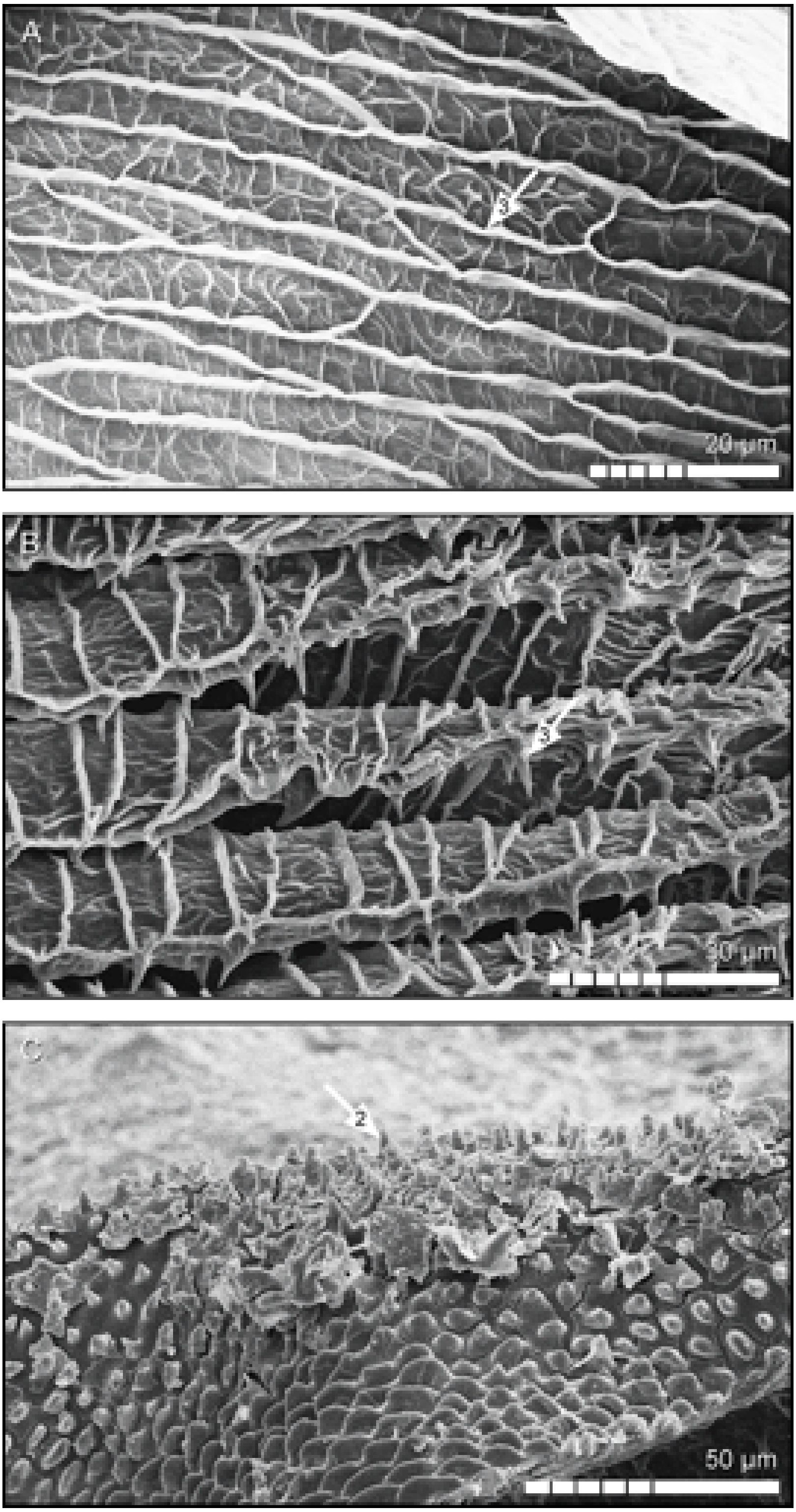

A
3
20 µm
B
3
C
2
50 µm

Plate 24. *Isometroides angusticaudis* Keyserling, 1885, 1 ♀ (AMNH [LP 2110]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas, directed to distal lamellar edge, and with irregular foldlike ridges, viewed from air space; **B.** smooth to slightly wrinkled distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with hillocklike structures (arrow), anterior view. Numbers in arrows refer to character states.

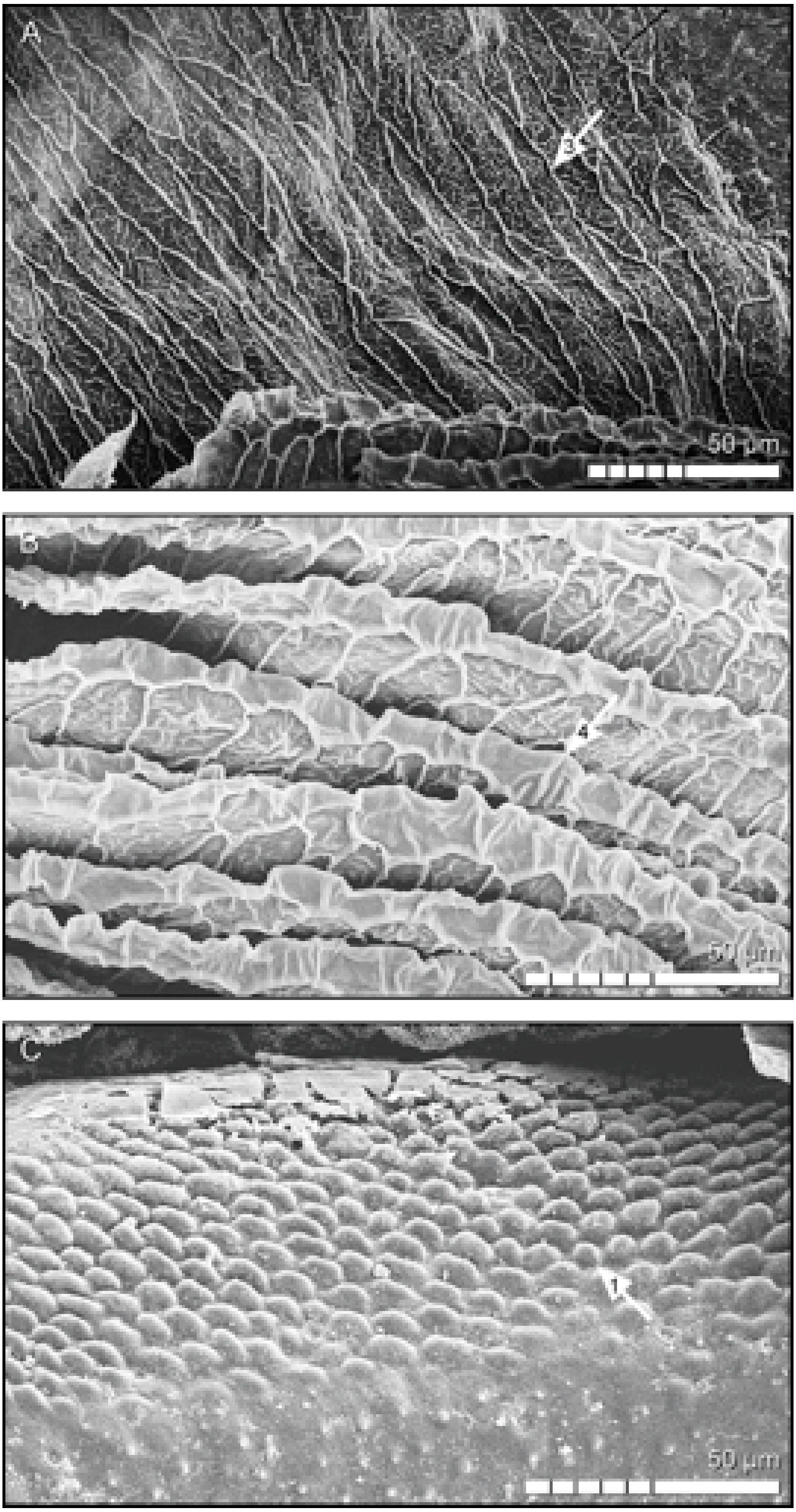

A
3
50 µm
B
4
50 µm
C
1
50 µm

Plate 25. *Isometrus maculatus* (DeGeer, 1778), 1 ♀ (AMNH [LP 1788]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas, directed to distal lamellar edge, and with irregular foldlike ridges, viewed from air space; **B.** smooth to slightly wrinkled distal edges of book lung lamellae with some small thorns (arrow), posterior view; **C.** movable posterior edge of spiracle with hillocklike structures (arrow), anterior view. Numbers in arrows refer to character states.

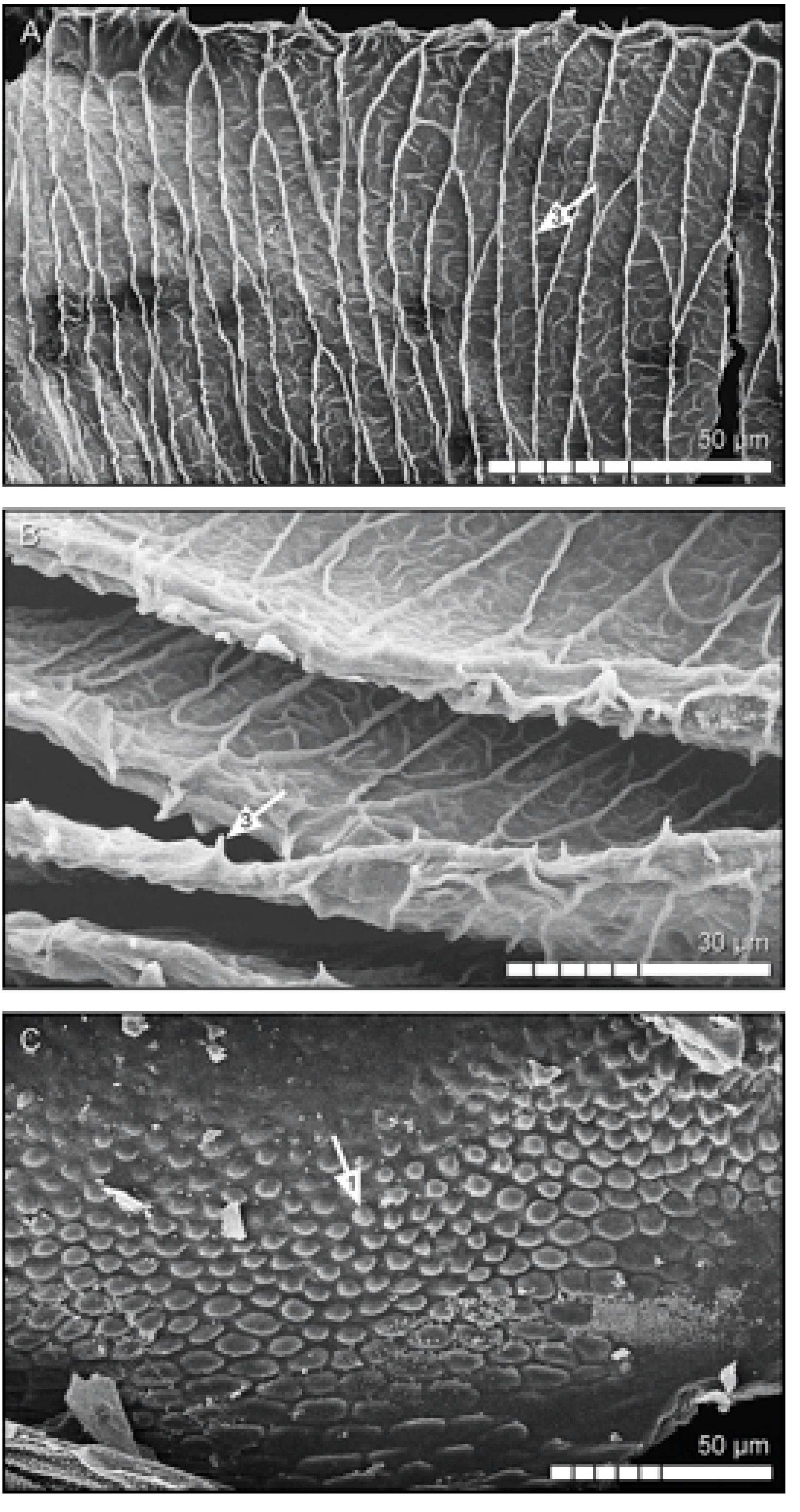

A
50 µm
B
30 µm
C
50 µm

Plate 26. *Isometrus maculatus* (DeGeer, 1778), 1 ♀ (MNHN RS 0952): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas, directed to distal lamellar edge, and with perpendicular foldlike ridges, viewed from air space; **B.** smooth to slightly wrinkled distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with hillocklike structures (arrow), anterior view. Numbers in arrows refer to character states.

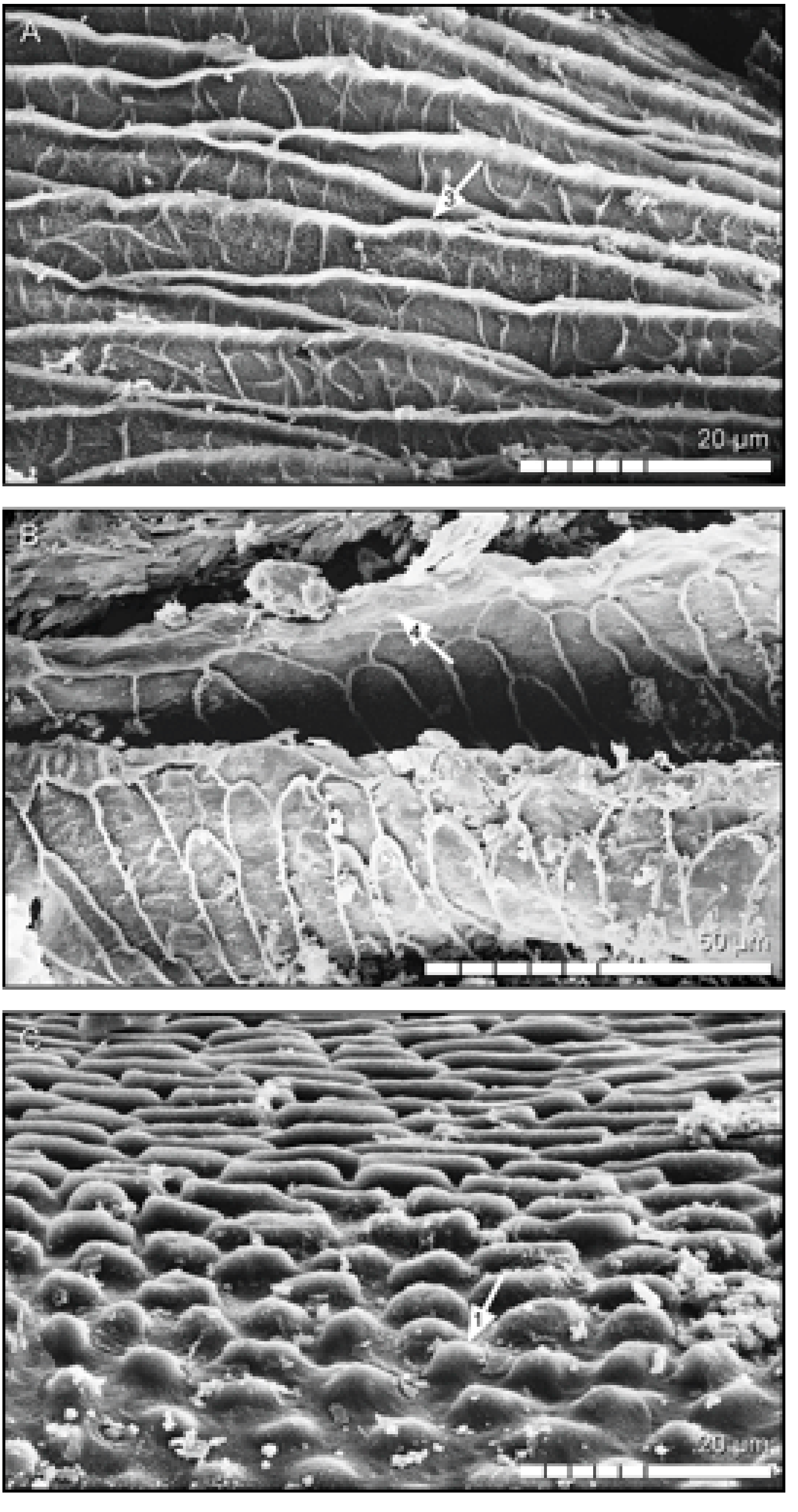
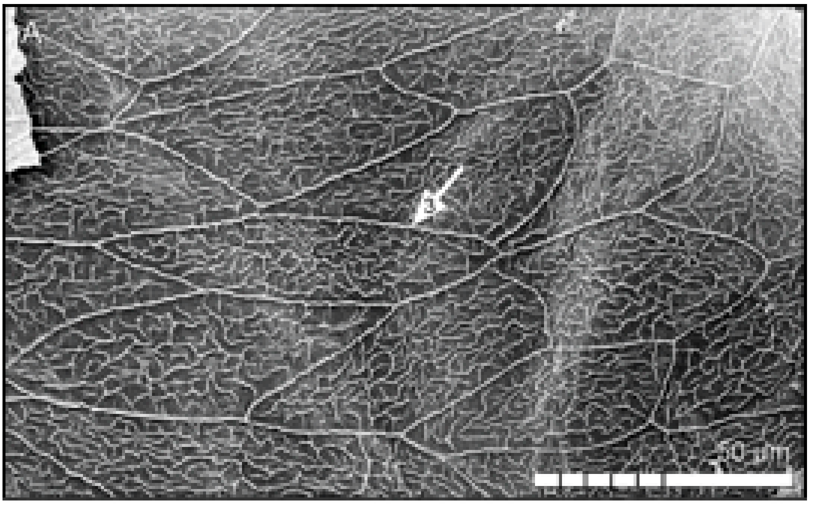
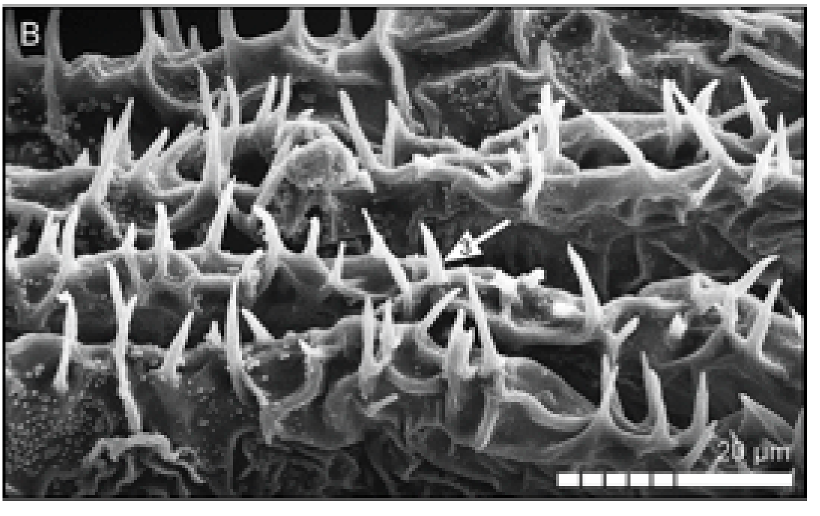

A
3
20 µm
B
4
2
50 µm
C
1
20 µm

Plate 27. *Karasbergia methueni* Hewitt, 1913, 1 ♂ (AMNH [LP 1724]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas, directed to distal lamellar edge, and with irregular foldlike ridges, viewed from air space; **B.** distal edges of book lung lamellae covered with rigid thorns (arrow), posterior view; **C.** movable posterior edge of spiracle with hillocklike structures (arrow), anterior view. Numbers in arrows refer to character states.


A
10 µm
3


B
20 µm
3

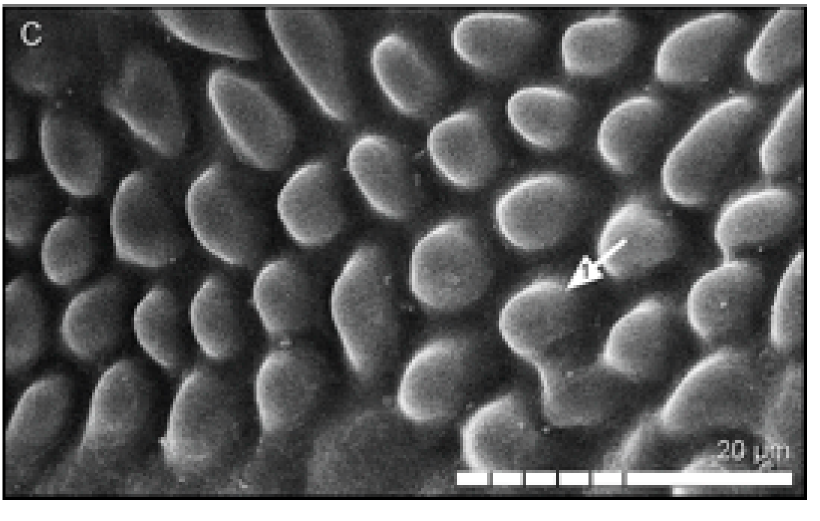

C
20 µm
1

Plate 28. *Leiurus quinquestriatus quinquestriatus* (Ehrenberg, 1828), 1 ♀ (AMNH [LP 1530]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas, directed to distal lamellar edge, and with perpendicular foldlike ridges, viewed from air space; **B.** distal edges of book lung lamellae covered with rigid thorns (arrow), posterior view; **C.** movable posterior edge of spiracle with spinelike structures (arrow), anterior view. Numbers in arrows refer to character states.

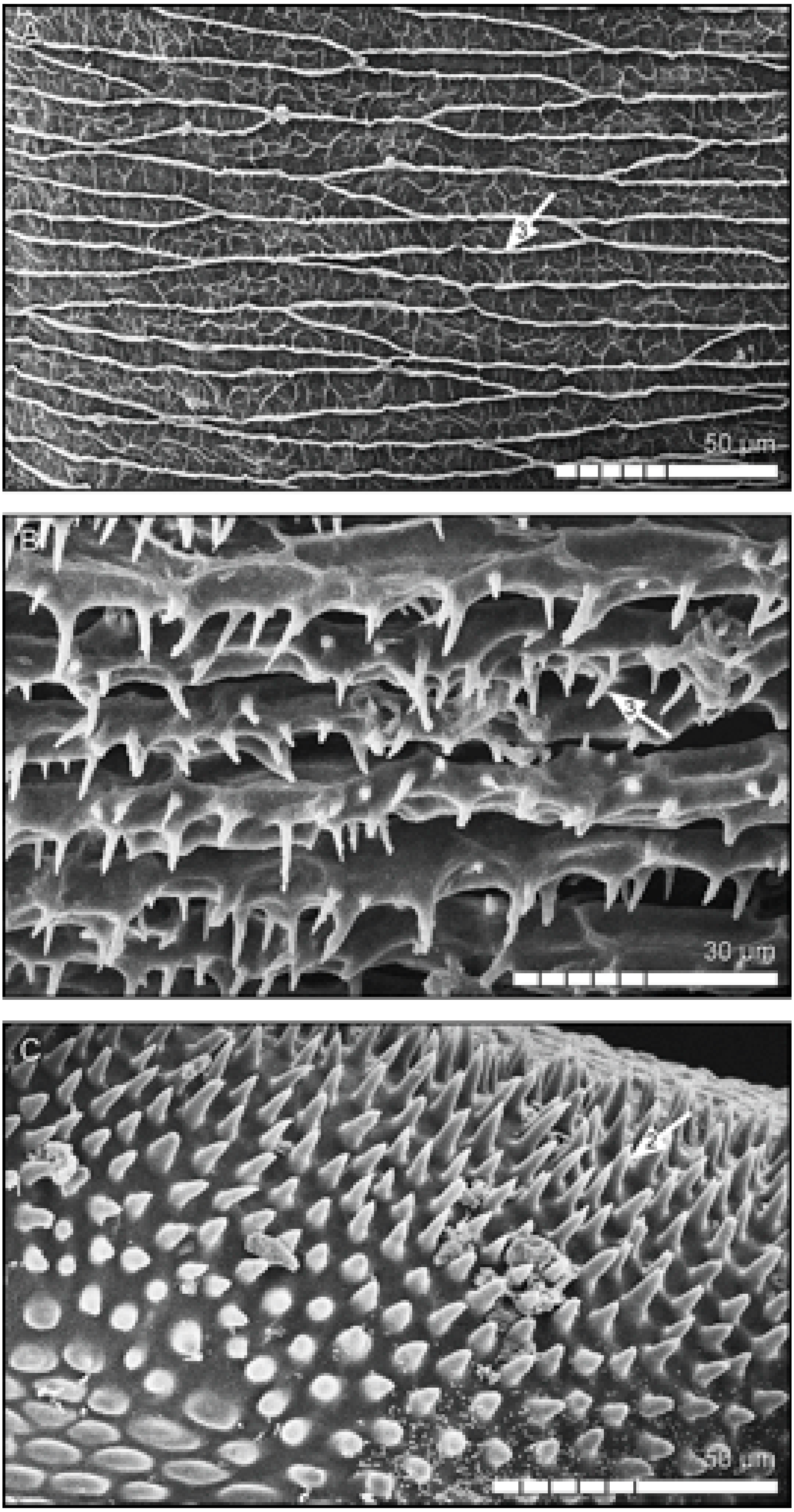

A
50 µm
B
30 µm
C
50 µm

Plate 29. *Liobuthus kessleri* Birula, 1898, 1 ♂ (AMNH [LP 3790]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas with irregular foldlike ridges, viewed from air space; **B.** distal edges of book lung lamellae covered with rigid thorns (arrow), posterior view. Numbers in arrows refer to character states.

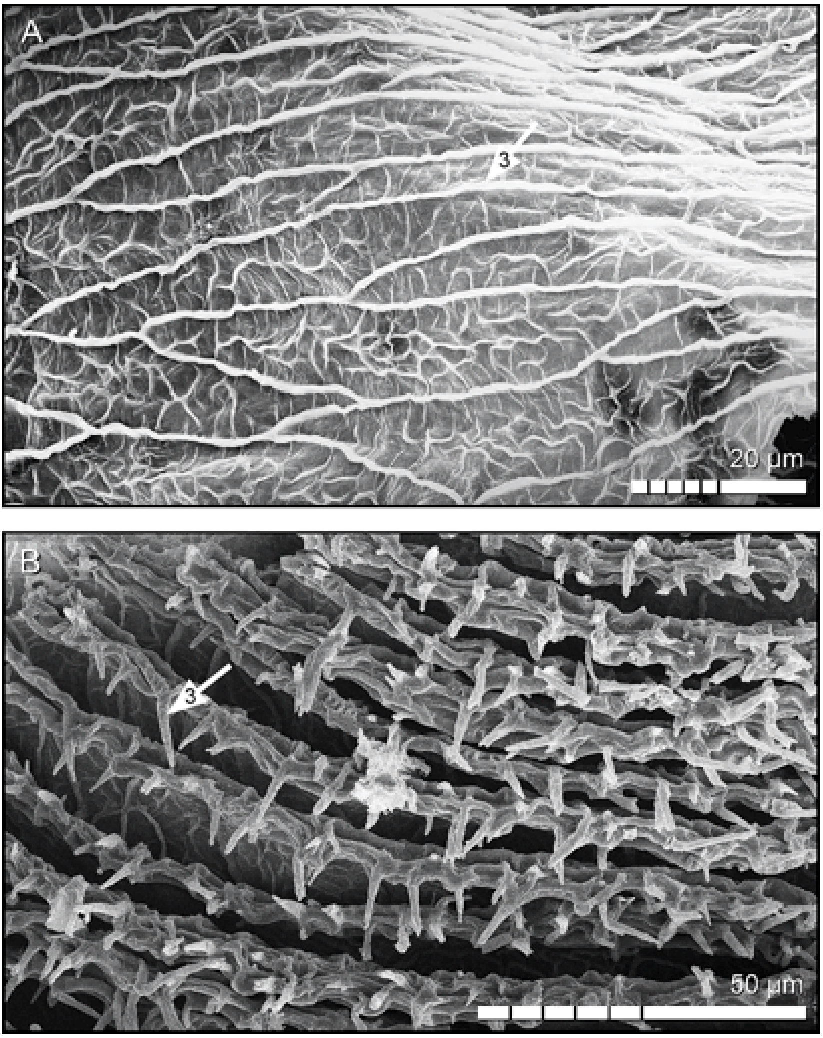

A
3
20 µm
B
3
50 µm

Plate 30. *Lychas obsti* Kraepelin, 1913, 1 ♂ (AMNH [LP 1797]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas with irregular foldlike ridges, viewed from air space; **B.** smooth to wrinkled distal edges of book lung lamellae (arrow) with a few thorns, posterior view; **C.** movable posterior edge of spiracle with hillocklike structures (arrow), anterior view. Numbers in arrows refer to character states.

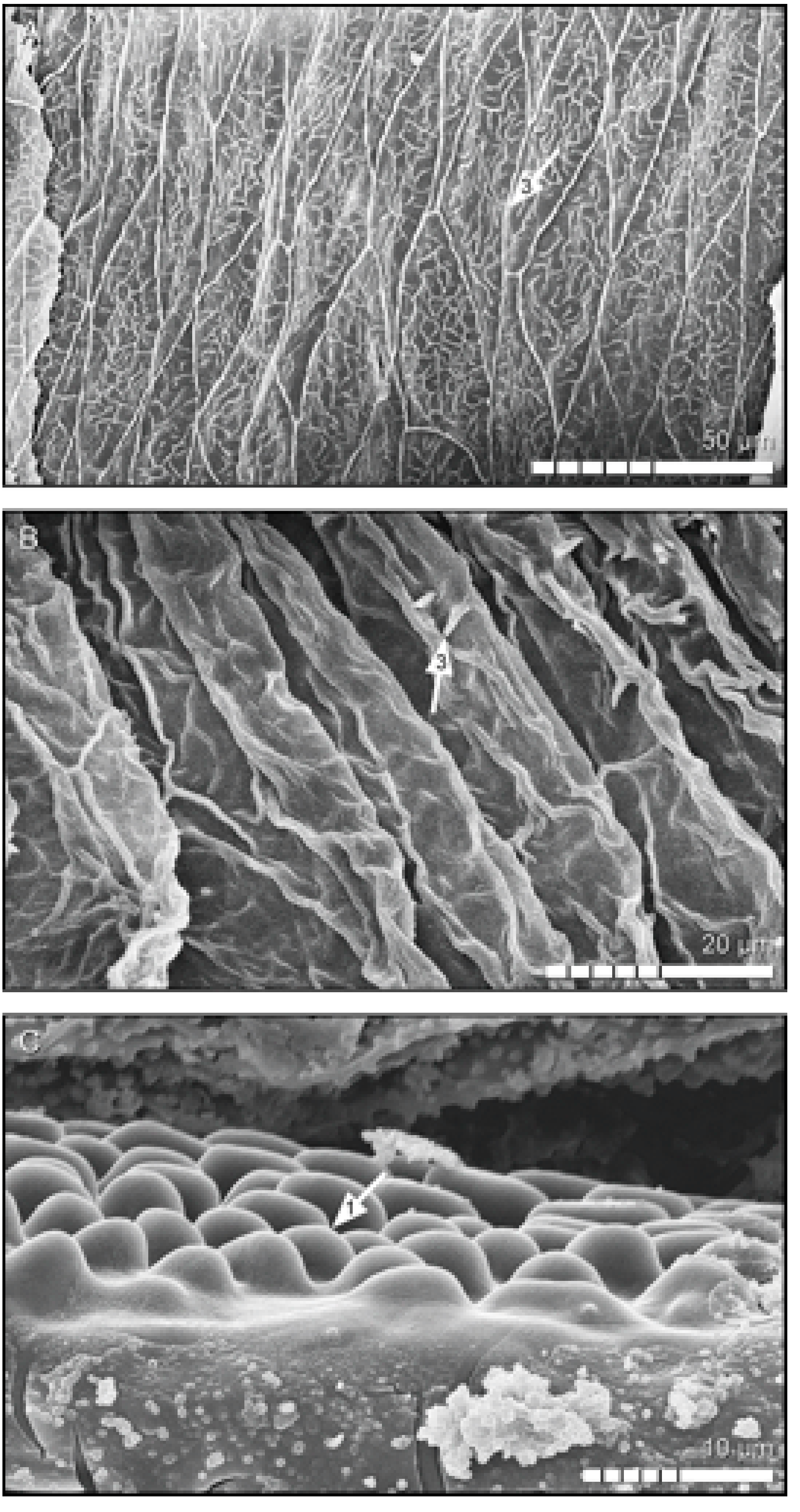

A
3
50 μm
B
3
20 μm
C
1
10 μm

Plate 31. *Lychas* sp., 1 ♀ (AMNH [LP 1646]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas with irregular foldlike ridges, viewed from air space; **B.** wrinkled distal edges of book lung lamellae (arrow) with reticulation along edge, and with a few thorns, posterior view; **C.** movable posterior edge of spiracle with hillocklike structures (arrow), anterior view. Numbers in arrows refer to character states.

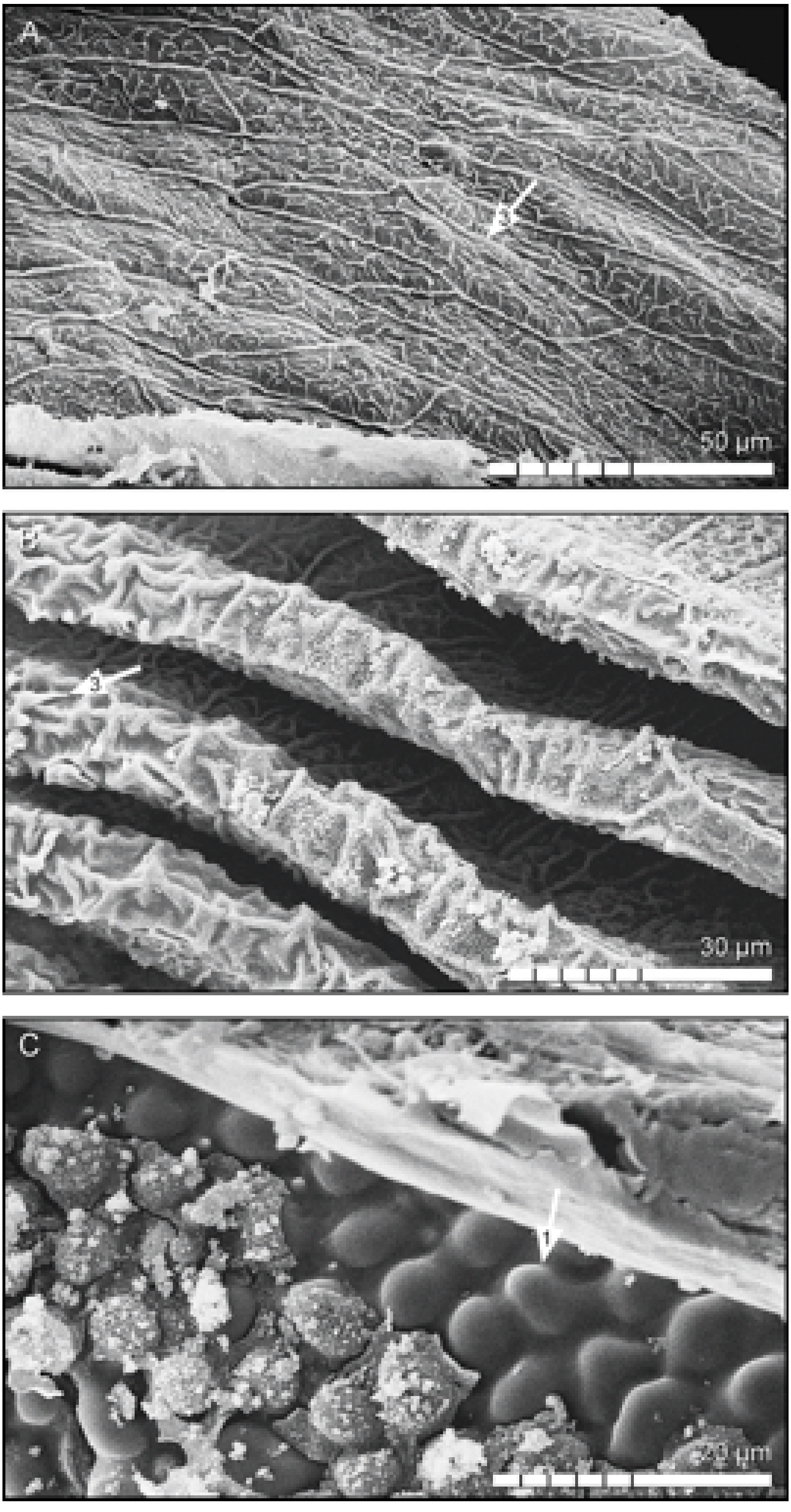

A
50 µm
B
30 µm
C

Plate 32. *Mesobuthus eupeus thersites* (C. L. Koch, 1839), 1 ♂ (AMNH [LP 3810]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas with irregular foldlike ridges, viewed from air space; **B.** distal edges of book lung lamellae covered with rigid thorns (arrow), posterior view; **C.** movable posterior edge of spiracle with subconical structures (arrow), anterior view. Numbers in arrows refer to character states.

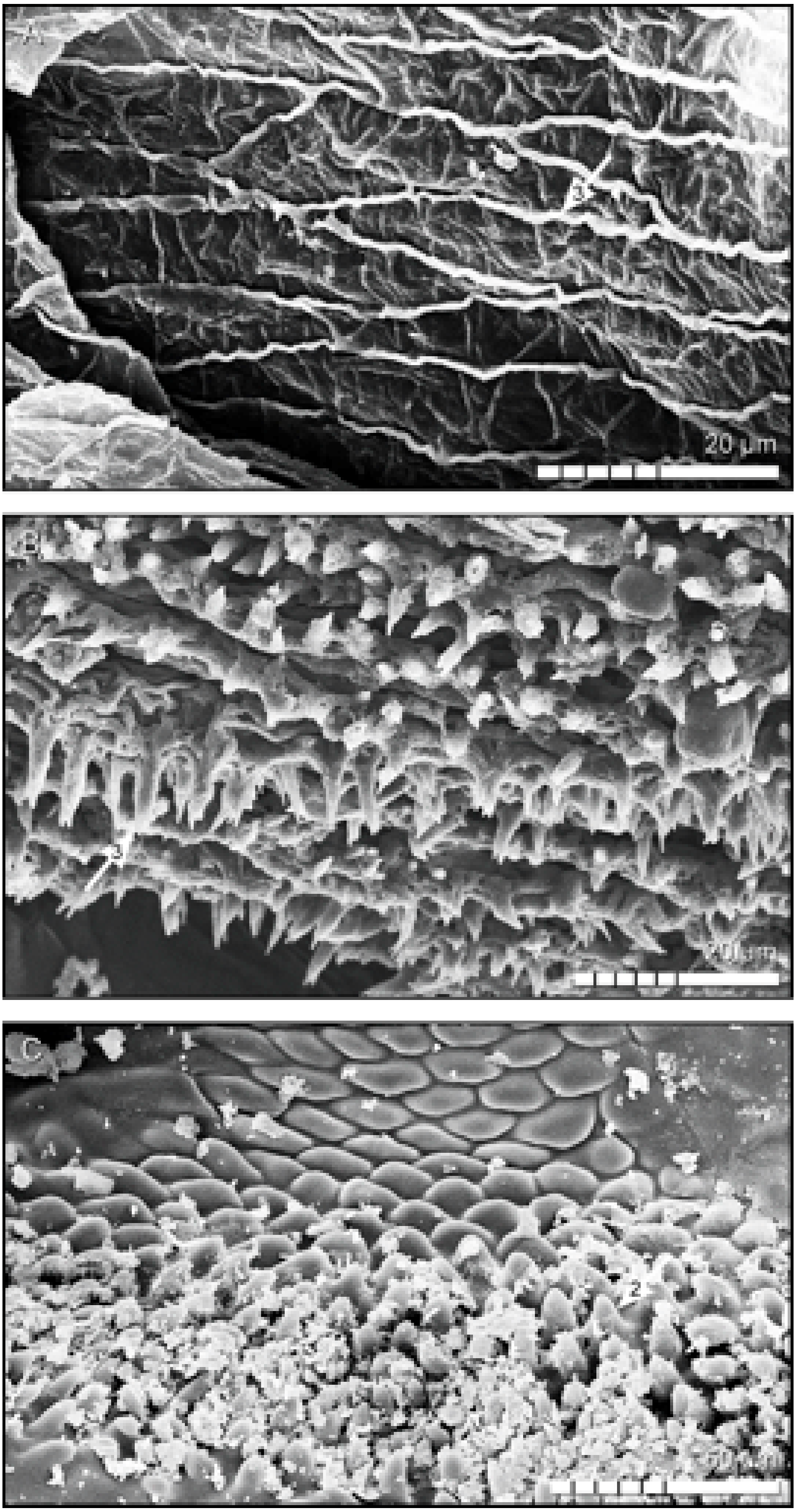

20 µm

Plate 33. *Microtityus rickyi* Kjellesvig-Waering, 1966, 1 ♀ (AMNH [LP 1717]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding polygonal areas with parallel veins (ribs), directed to distal lamellar edge, viewed from air space; **B.** smooth to wrinkled distal edges of book lung lamellae covered with rigid thorns (arrow), posterior view; **C.** movable posterior edge of spiracle with subconical structures (arrow), anterior view. Numbers in arrows refer to character states.

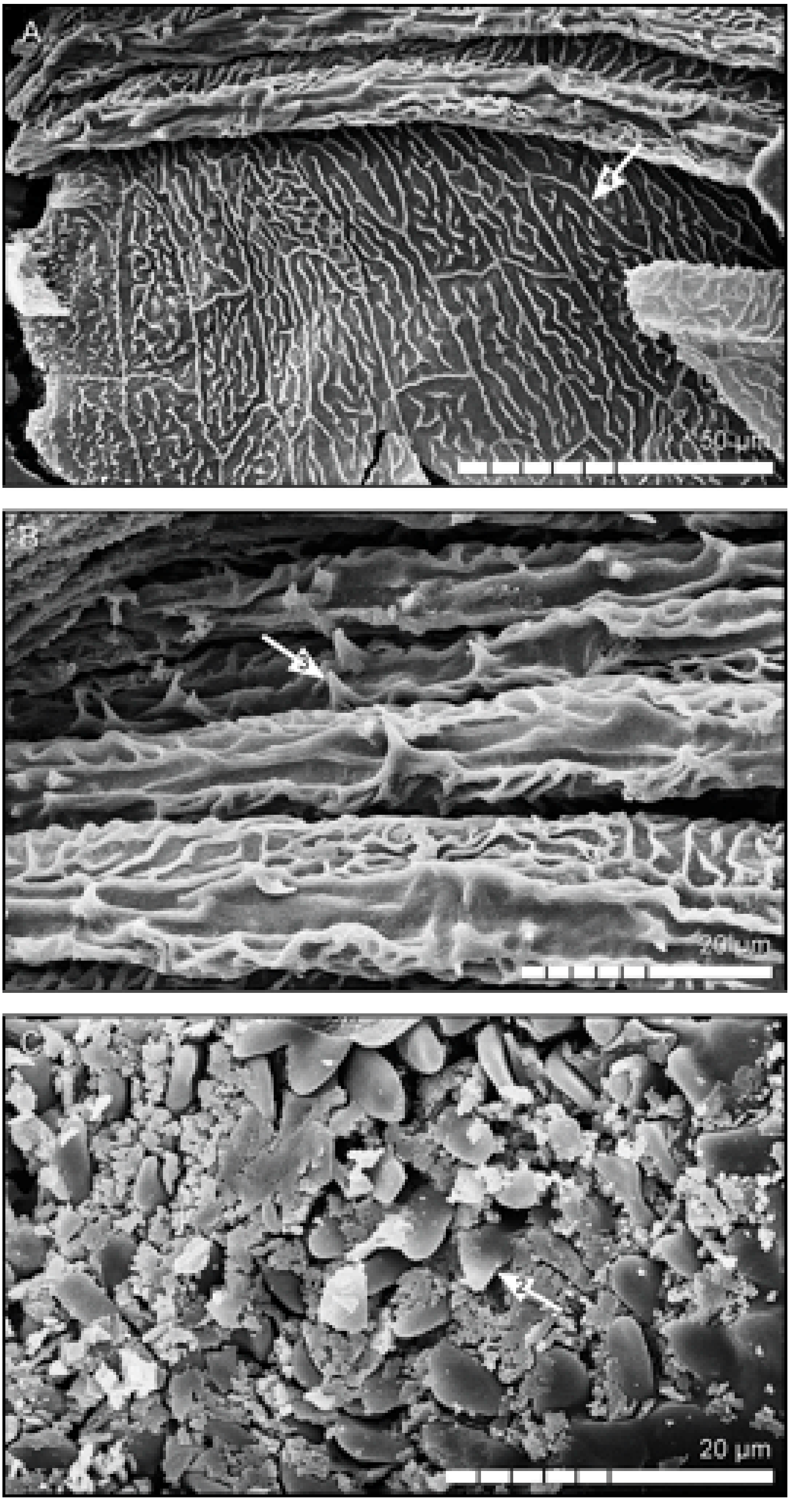

A
50 µm
B
20 µm
C
20 µm

Plate 34. *Odontobuthus doriae* (Thorell, 1876), 1 ♀ (MNHN RS 1823): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas with perpendicular foldlike ridges, viewed from air space; **B.** distal edges of book lung lamellae covered with rigid thorns (arrow), posterior view; **C.** movable posterior edge of spiracle with spinelike structures (arrow), anterior view. Numbers in arrows refer to character states.

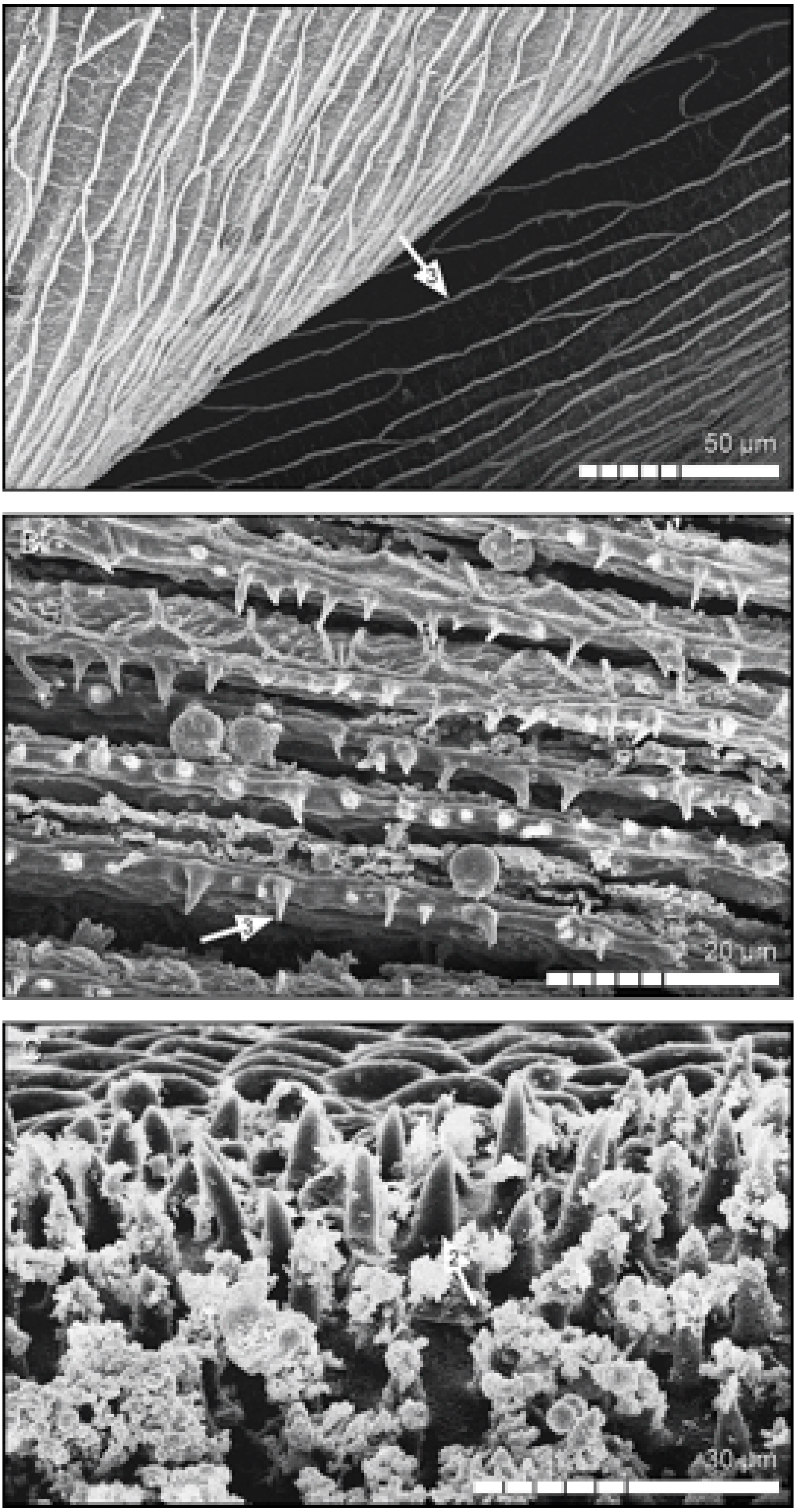

50 µm
20 µm
30 µm

Plate 35. *Odonturus dentatus* Karsch, 1879, 1 ♂ (AMNH [LP 1578]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas with perpendicular to irregular foldlike ridges, viewed from air space; **B.** wrinkled distal edges of book lung lamellae (arrow) with reticulation, posterior view; **C.** movable posterior edge of spiracle with spinelike structures (arrow), anterior view. Numbers in arrows refer to character states.

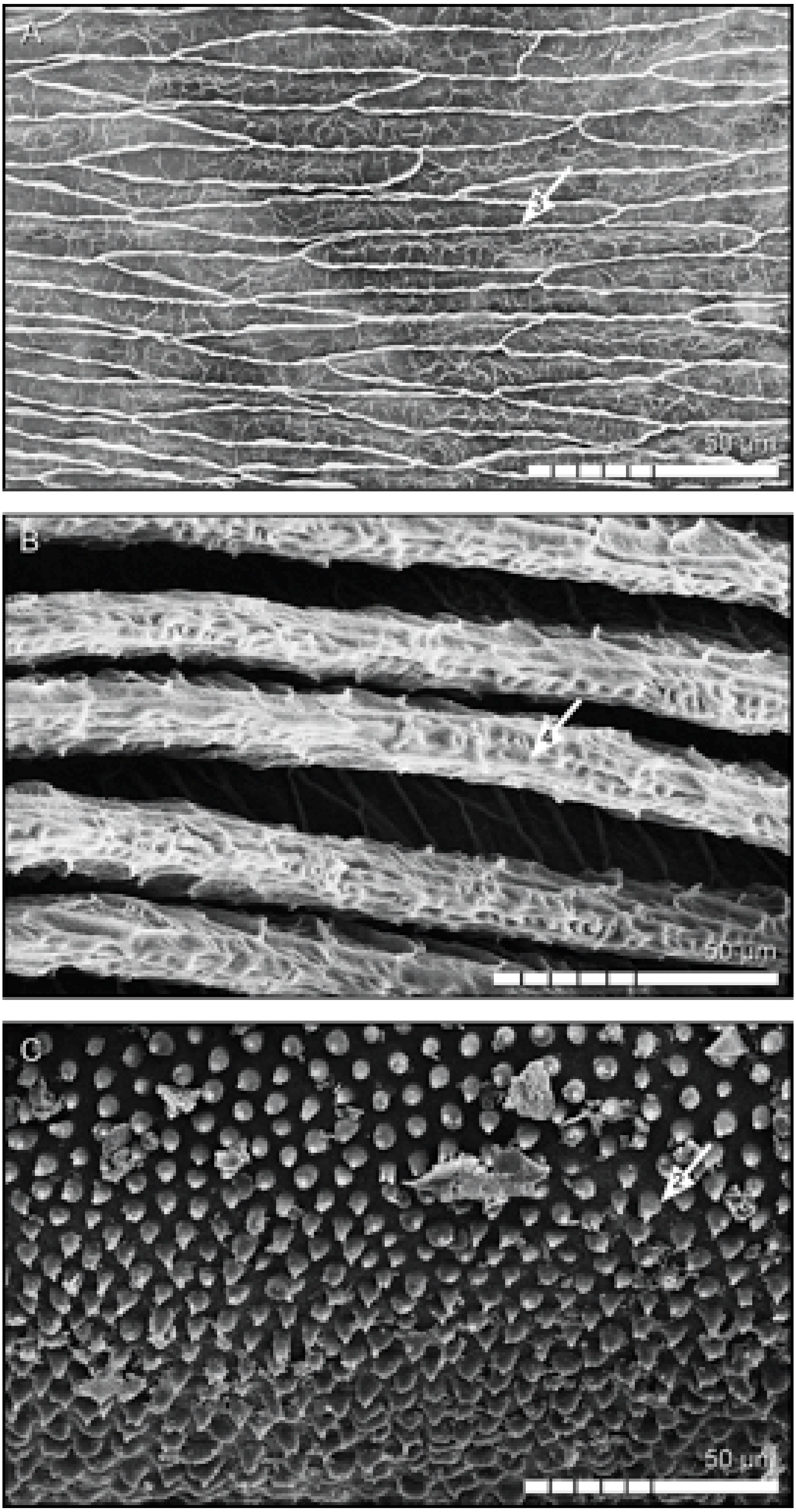

A
50 µm
B
50 µm
C
50 µm

Plate 36. *Orthochirus innesi* Simon, 1910, 1 ♀ (MNHN RS 5440): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas with irregular foldlike ridges, viewed from air space; **B.** distal edges of book lung lamellae covered with rigid thorns (arrow), posterior view; **C.** movable posterior edge of spiracle with hillocklike structures (arrow), anterior view. Numbers in arrows refer to character states.

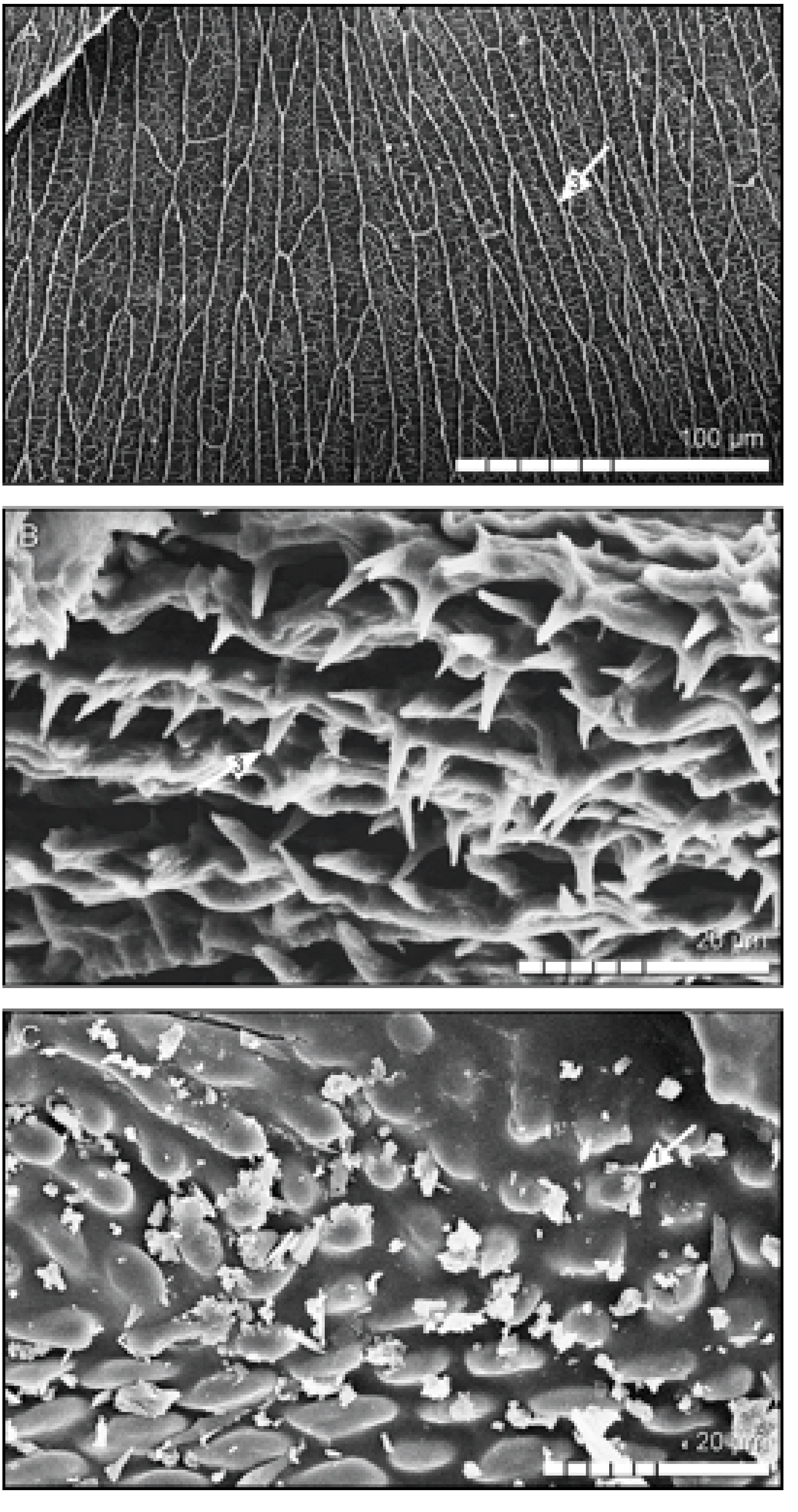

A
100 µm
B
20 µm
C

Plate 37. *Orthochirus scrobiculosus scrobiculosus* (Grube, 1873), 1 ♀ (AMNH [LP 3775]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas with irregular foldlike ridges, viewed from air space; **B.** wrinkled distal edges of book lung lamellae covered with rigid thorns (arrow), posterior view; **C.** movable posterior edge of spiracle with hillocklike structures (arrow), anterior view. Numbers in arrows refer to character states.

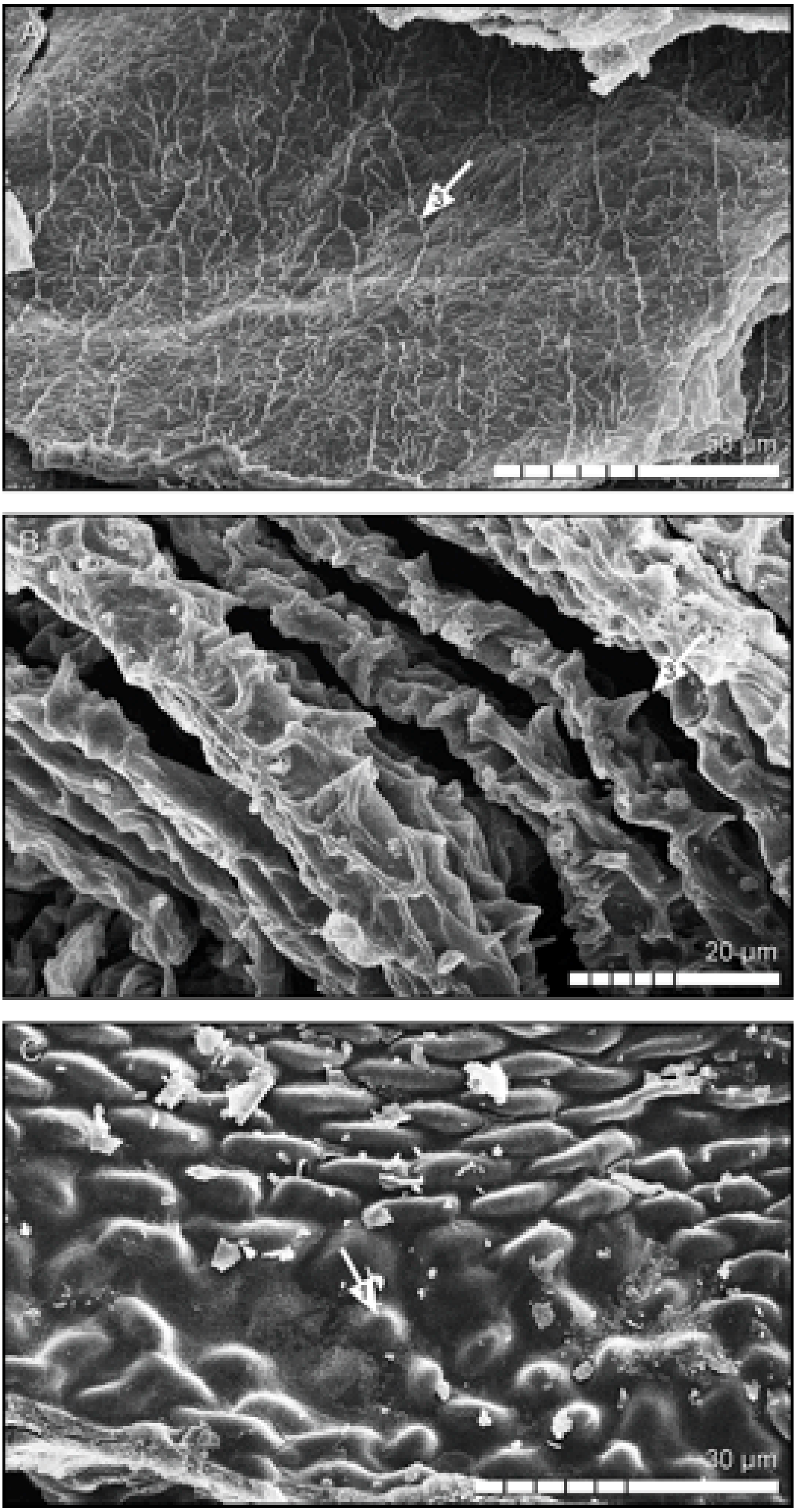

20 µm
30 µm

Plate 38. *Parabuthus leiosoma* (Ehrenberg, 1828), 1 ♀ (AMNH [LP 1845]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas with perpendicular and irregular foldlike ridges, viewed from air space; **B.** distal edges of book lung lamellae covered with rigid thorns (arrow), posterior view; **C.** movable posterior edge of spiracle with subconical to spinelike structures (arrow), anterior view. Numbers in arrows refer to character states.

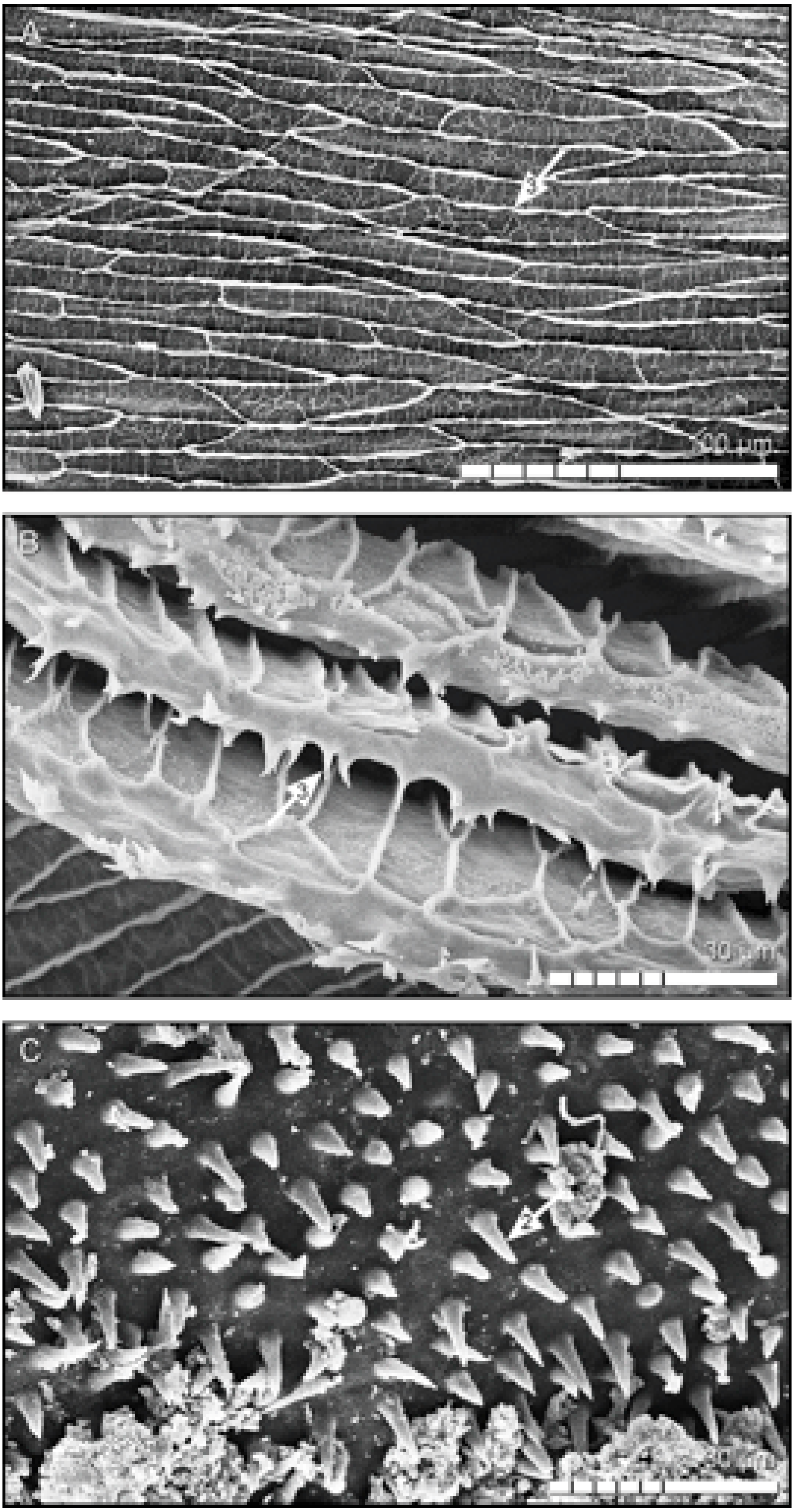

A
B
30 µm
C

Plate 39. *Pseudolychas pegleri* (Purcell, 1901), 1 ♀ (AMNH [LP 1326]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding polygonal, slender areas with irregular foldlike ridges, viewed from air space; **B.** wrinkled distal edges of book lung lamellae covered with rigid thorns (arrow), posterior view; **C.** movable posterior edge of spiracle with hillocklike structures (arrow), anterior view. Numbers in arrows refer to character states.

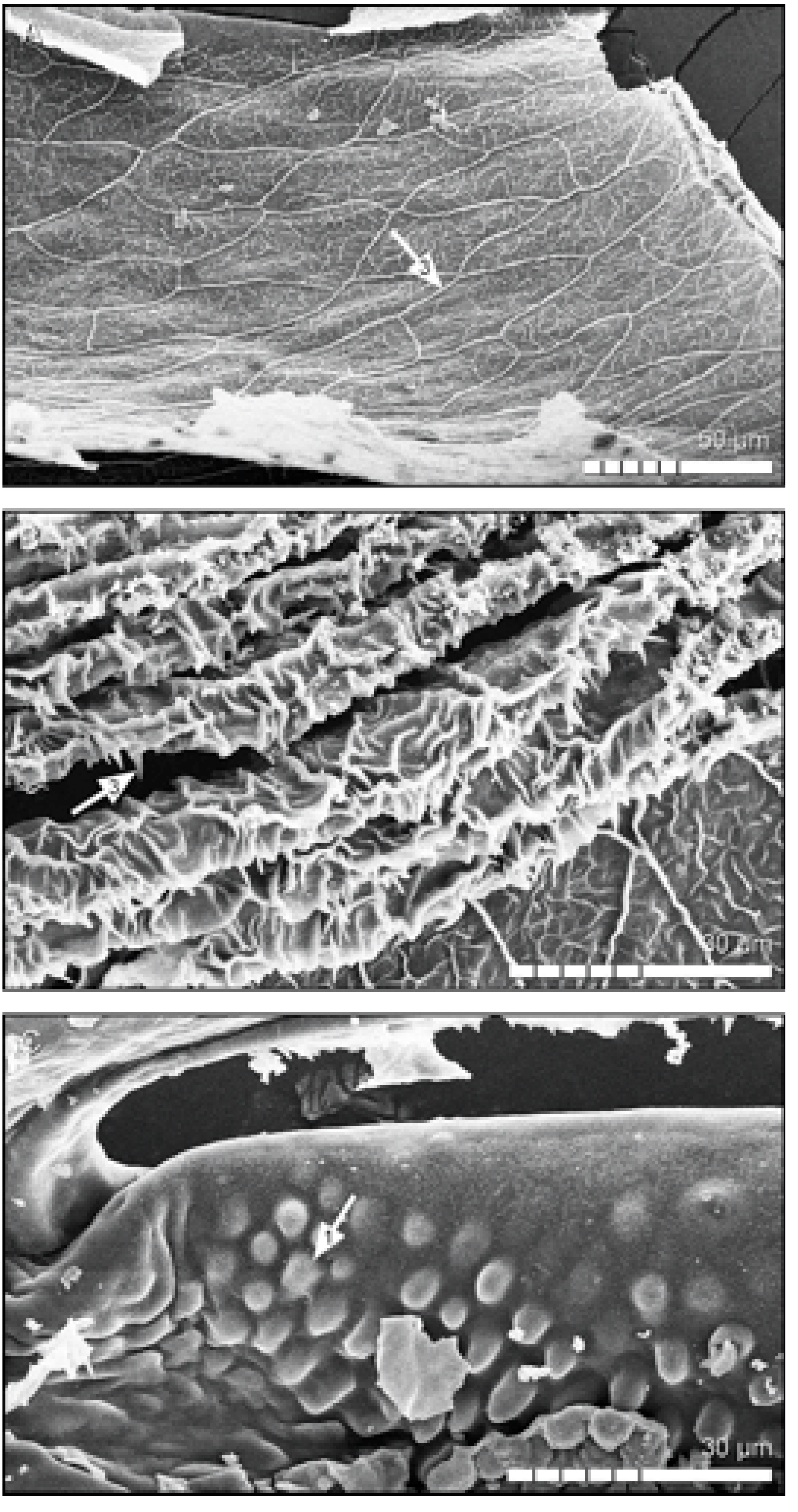

50 µm
30 µm
30 µm

Plate 40. *Rhopalurus bonettii* Armas, 1999, 1 juv. ♂ (AMNH [LP 3267]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding polygonal, slender areas with irregular foldlike ridges, viewed from air space; **B.** wrinkled distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with hillocklike structures (arrow), anterior view. Numbers in arrows refer to character states.

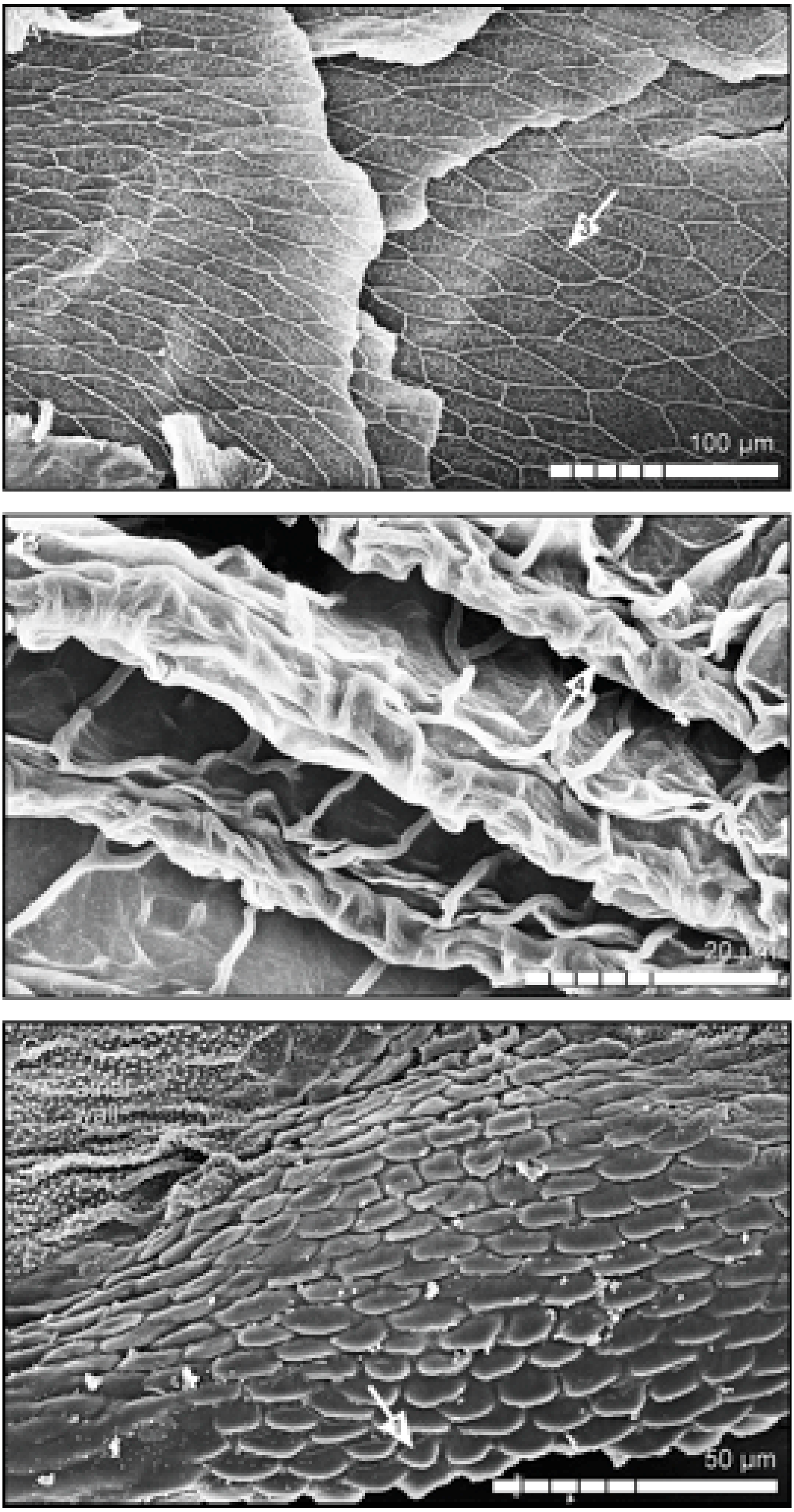

100 µm
50 µm

Plate 41. *Rhopalurus junceus* (Herbst, 1800), 1 ♀ (MNHN RS 3288): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding polygonal, slender areas with irregular foldlike ridges, viewed from air space; **B.** wrinkled distal edges of book lung lamellae (arrow), fusing with one another and with atrial wall, posterior view; **C.** movable posterior edge of spiracle with hillocklike structures (arrow), anterior view. Numbers in arrows refer to character states.

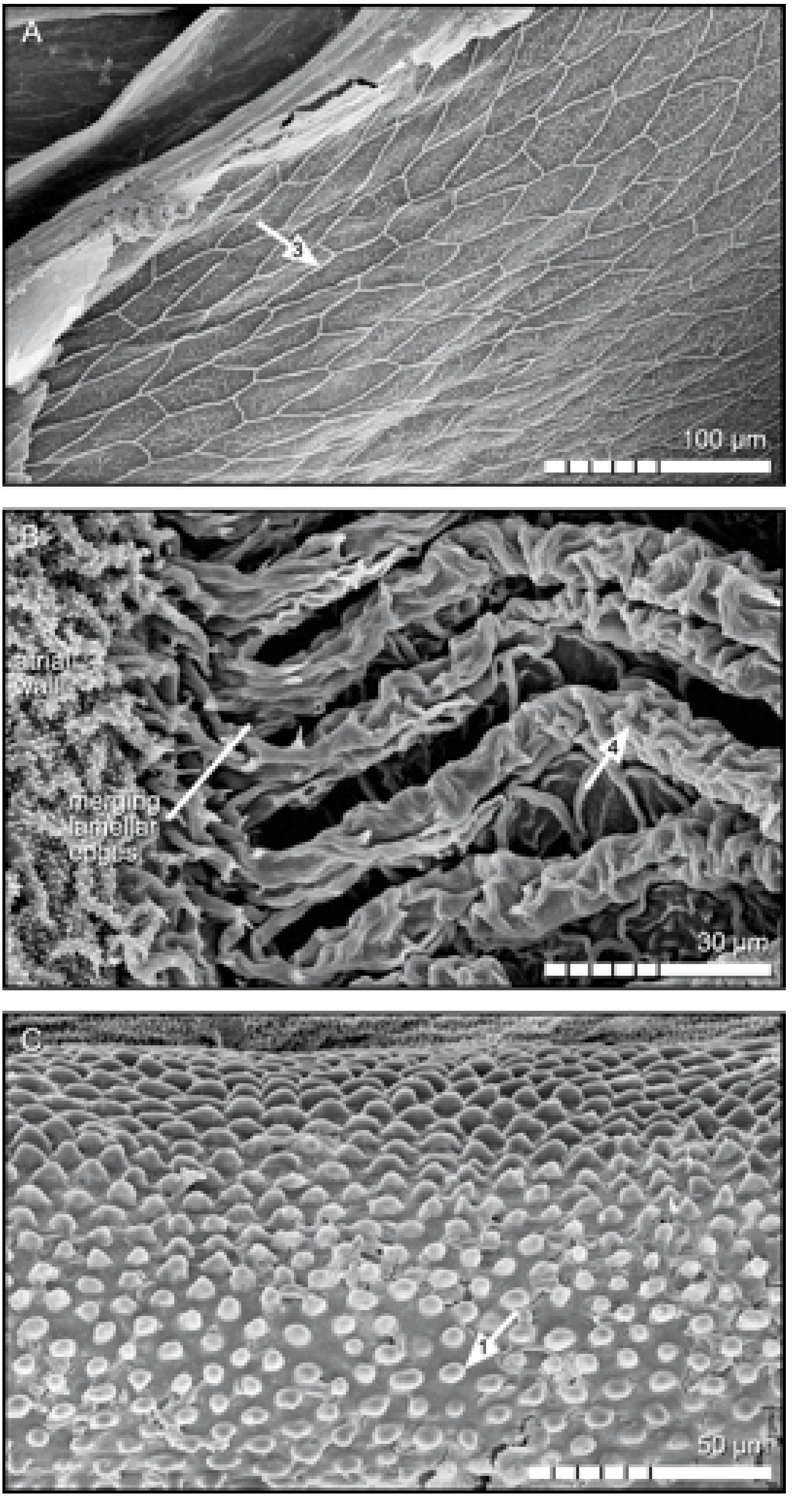

A
3
100 µm
B
atrial wall
merging lamellar edges
4
30 µm
C
1
50 µm

Plate 42. *Rhopalurus laticauda* Thorell, 1876, 1 ♀ (AMNH [LP 2462]): **A.** surface of book lung lamella with reticulate veins (arrow), viewed from air space; **B.** wrinkled distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with hillocklike structures (arrow), anterior view. Numbers in arrows refer to character states.

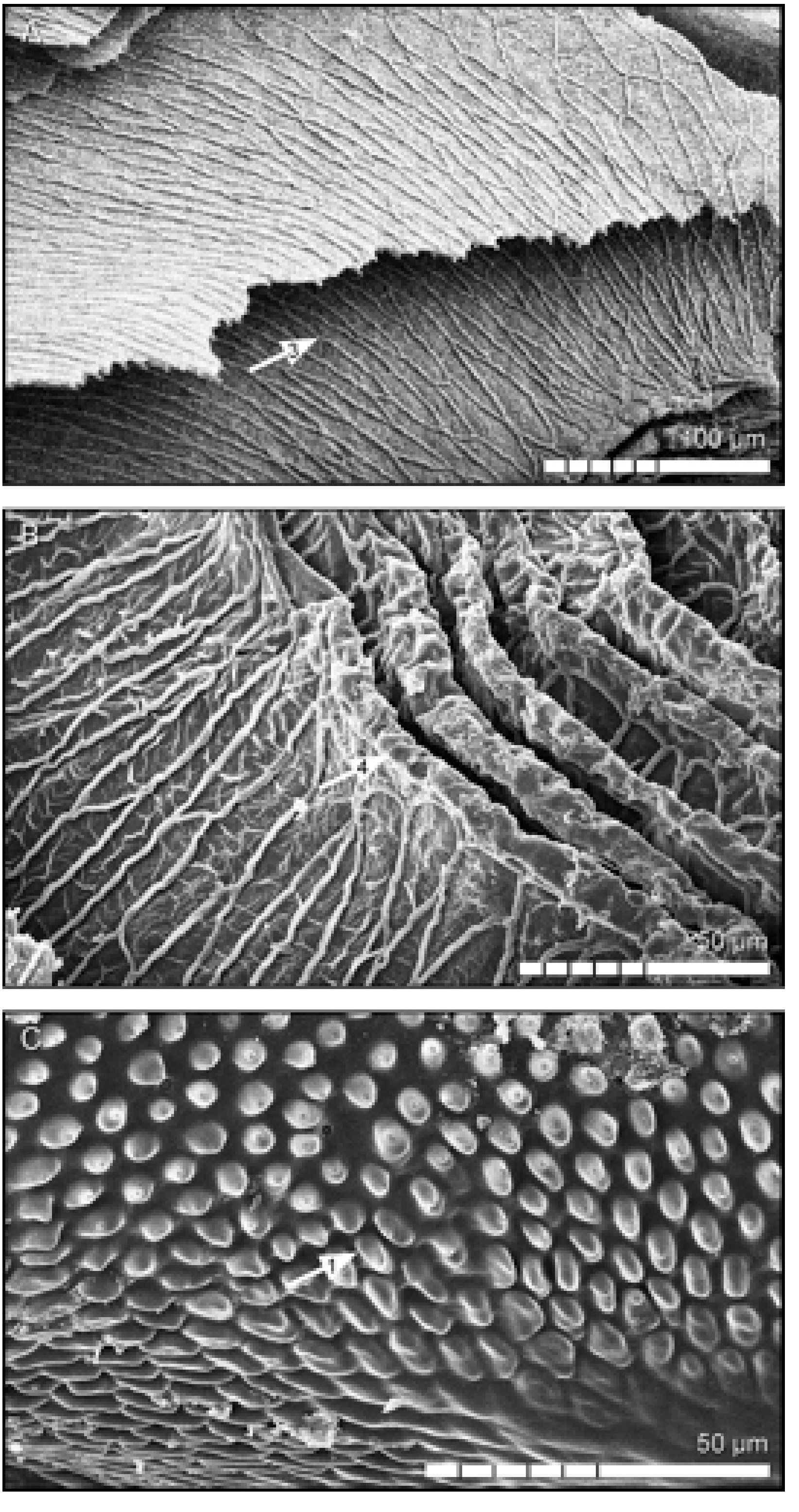

B
C
100 µm
50 µm
50 µm
3
4
1

Plate 43. *Rhopalurus princeps* (Karsch, 1879), 1 ♂ (AMNH [LP 1566]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas with irregular foldlike ridges, viewed from air space; **B.** wrinkled distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with subconical structures (arrow), anterior view. Numbers in arrows refer to character states.

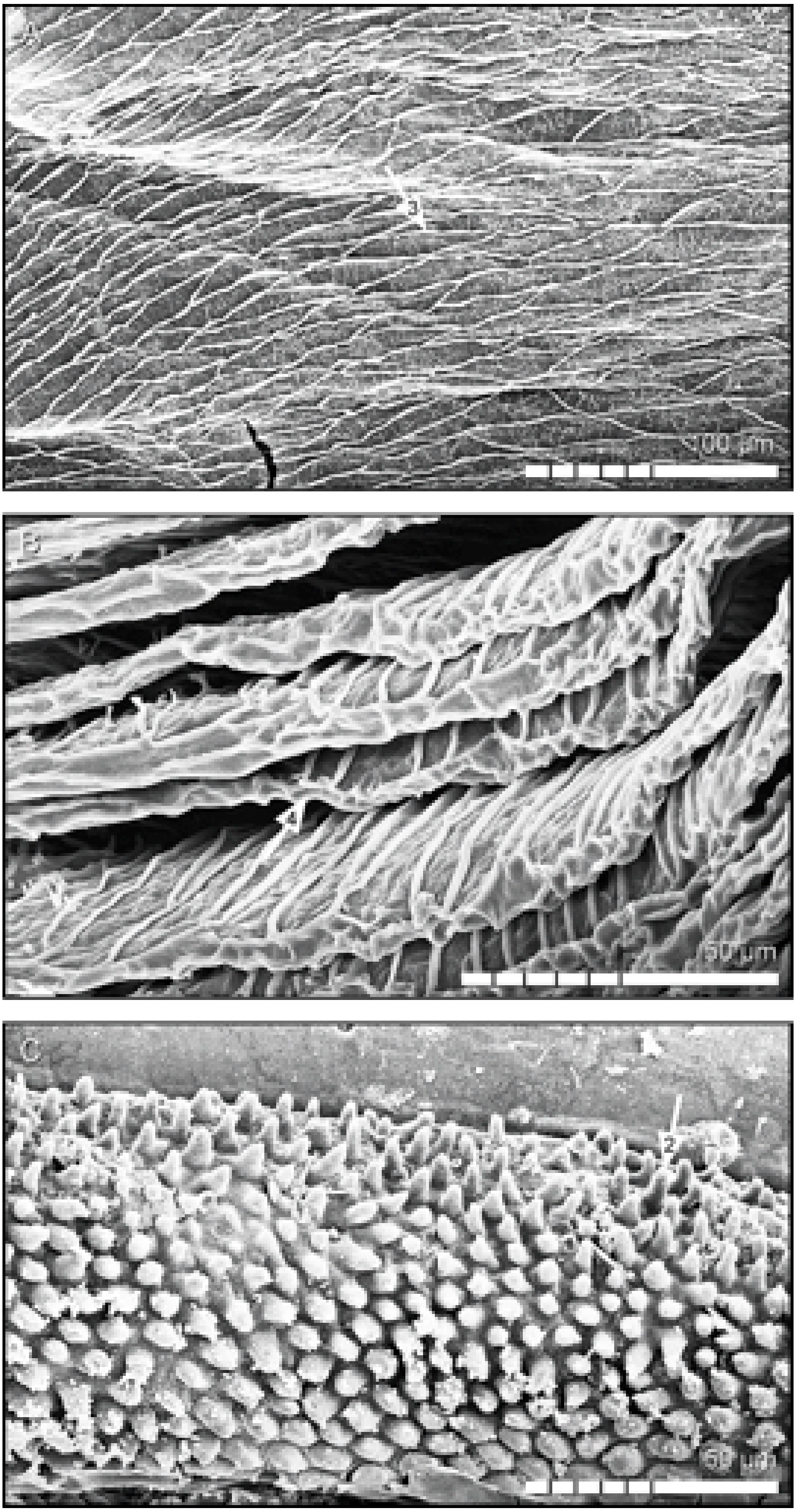

100 µm
50 µm
50 µm

Plate 44. *Rhopalurus rochae* Borelli, 1910, 1 ♂ (AMNH [LP 1582]): **A.** surface of book lung lamella with reticulate veins (arrow), viewed from air space; **B.** smooth distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with spinelike structures (arrow), anterior view. Numbers in arrows refer to character states.

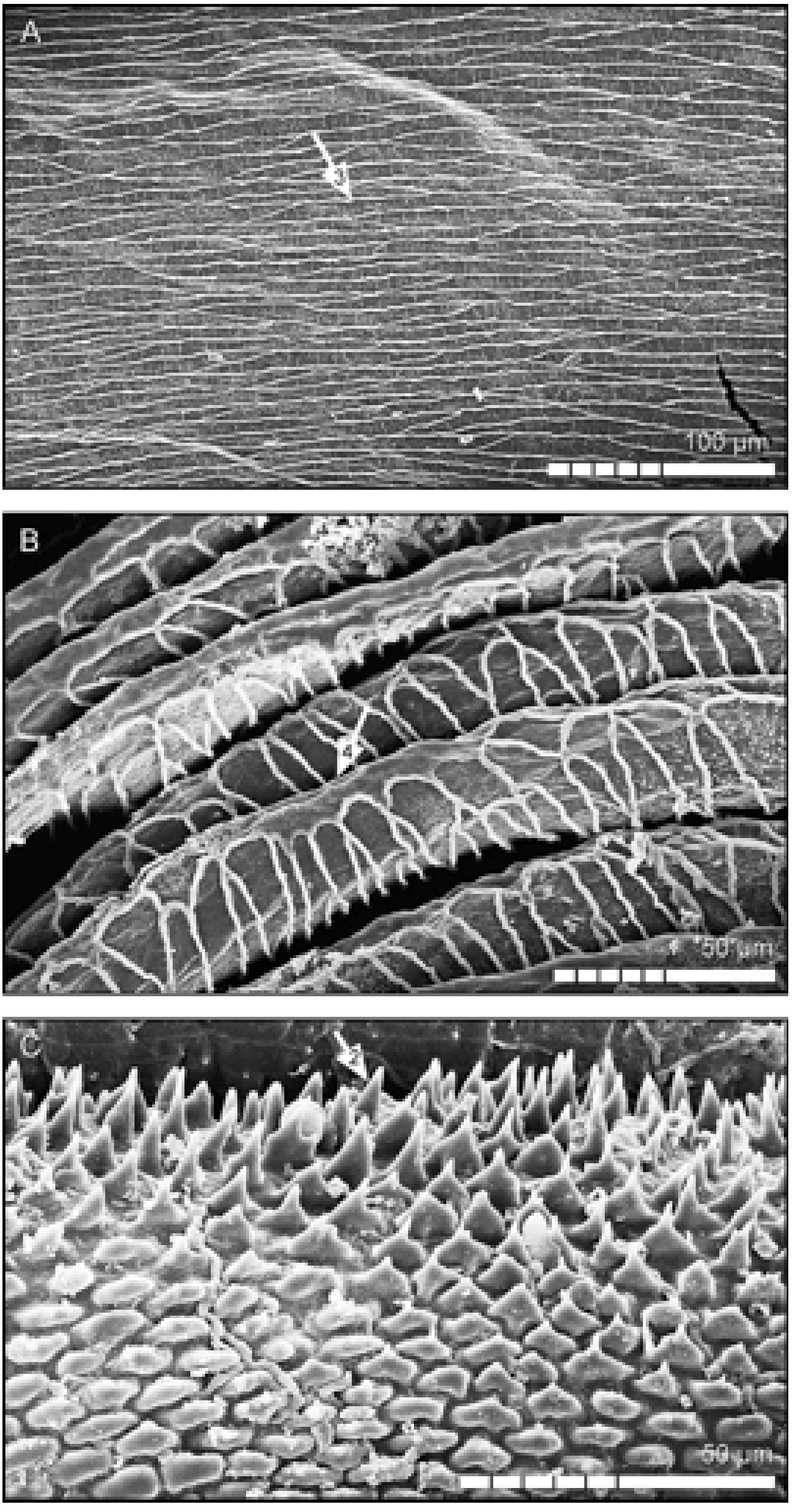

A
100 µm
B
50 µm
C
50 µm

Plate 45. *Tityobuthus baroni* (Pocock, 1890), 1 ♂ (AMNH [LP 1941]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas with irregular foldlike ridges, viewed from air space; **B.** wrinkled distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with hillocklike structures (arrow), anterior view. Numbers in arrows refer to character states.

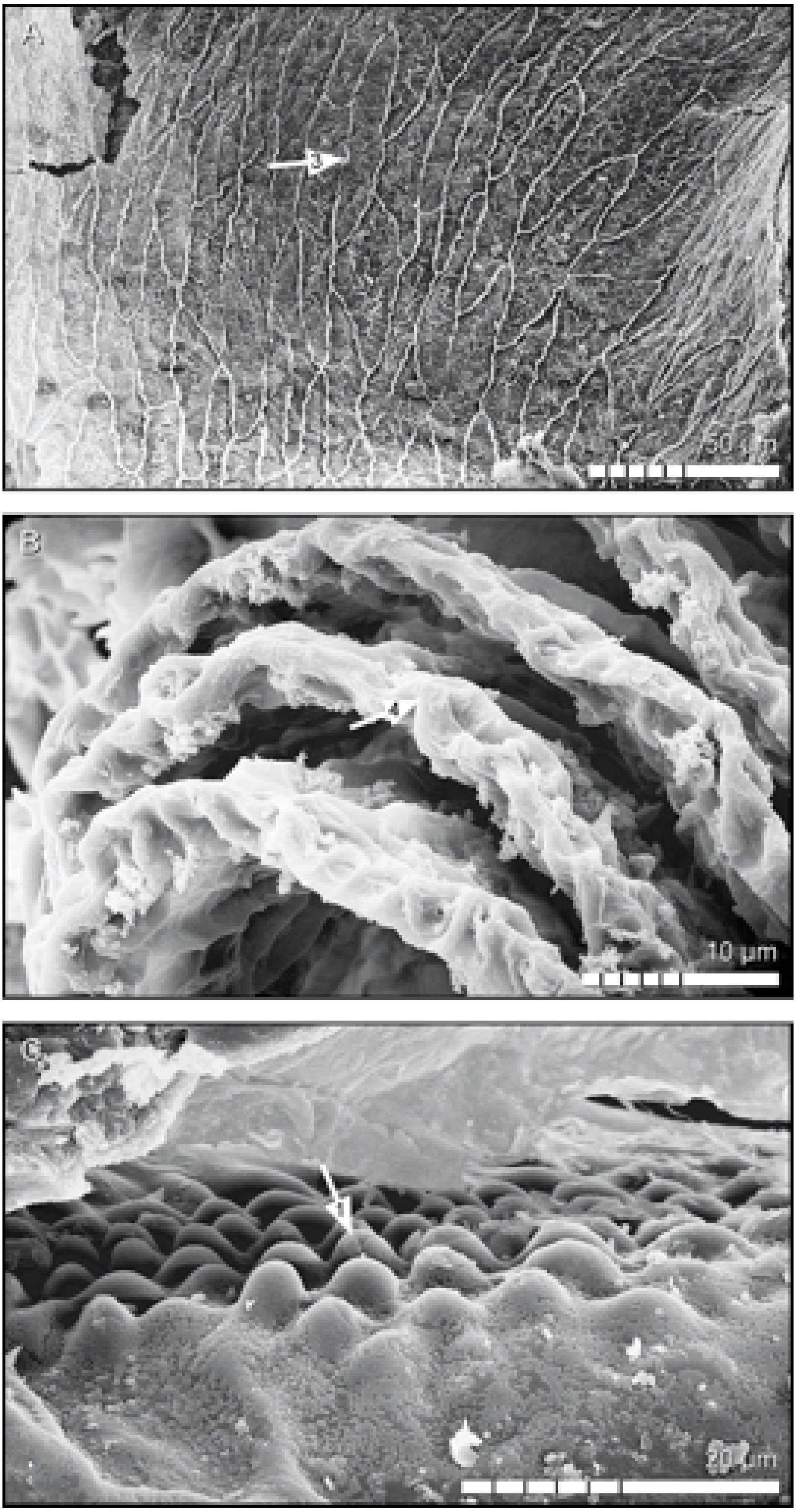

A
B
10 µm
C
20 µm

Plate 46. *Tityus asthenes* Pocock, 1893, 1 ♀ (AMNH [LP 1831]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding polygonal areas with parallel veins (ribs), directed to distal lamellar edge, viewed from air space; **B.** smooth distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with spinelike structures (arrow), anterior view. Numbers in arrows refer to character states.

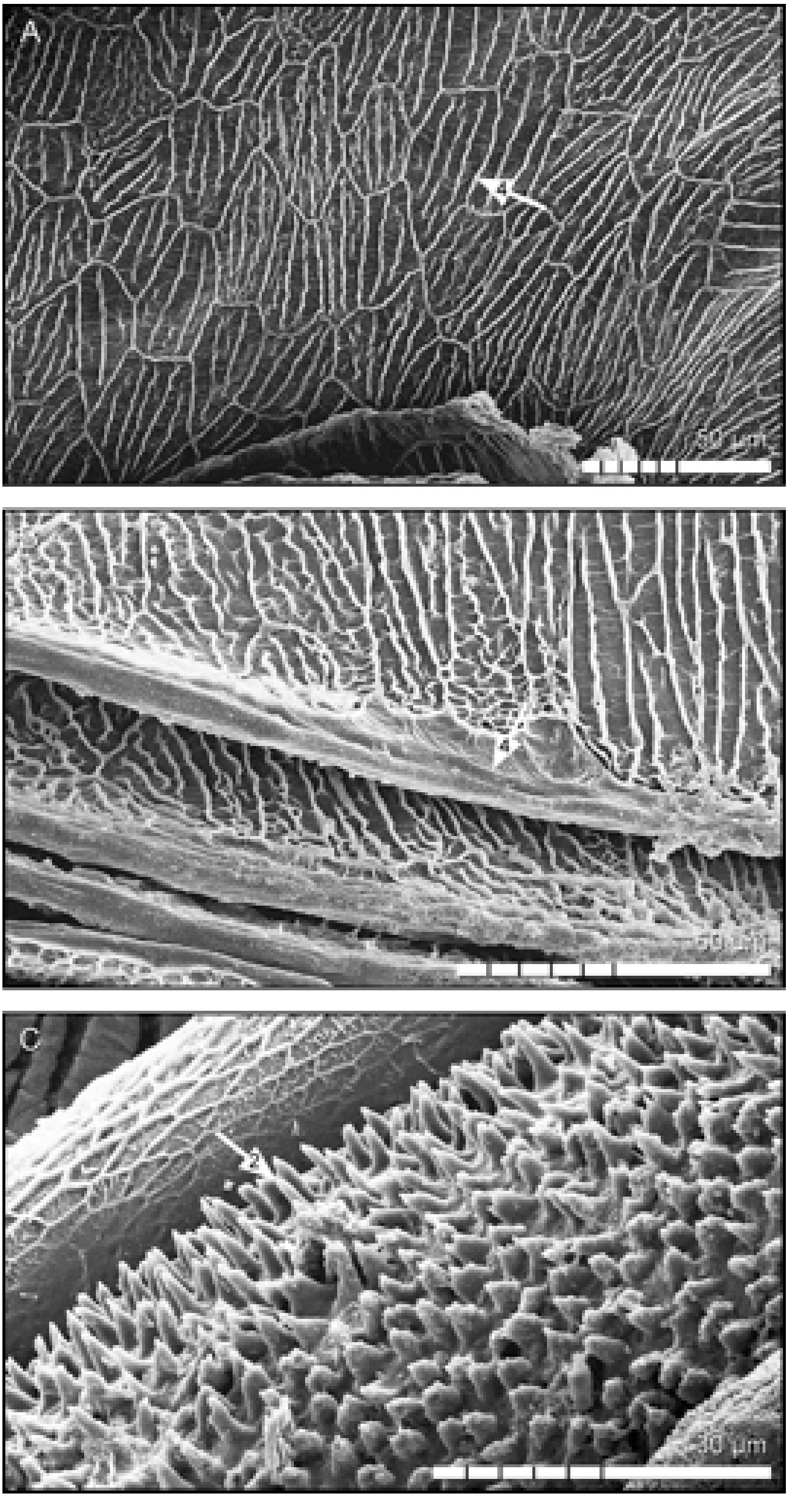

A
50 µm
50 µm
C
30 µm

Plate 47. *Tityus bahiensis eickstedtae* (Lourenço, 1982), 1 ♀ (AMNH [LP 1596]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding polygonal areas with veins (ribs), directed to distal lamellar edge, viewed from air space; **B.** smooth distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with subconical structures (arrow), anterior view. Numbers in arrows refer to character states.

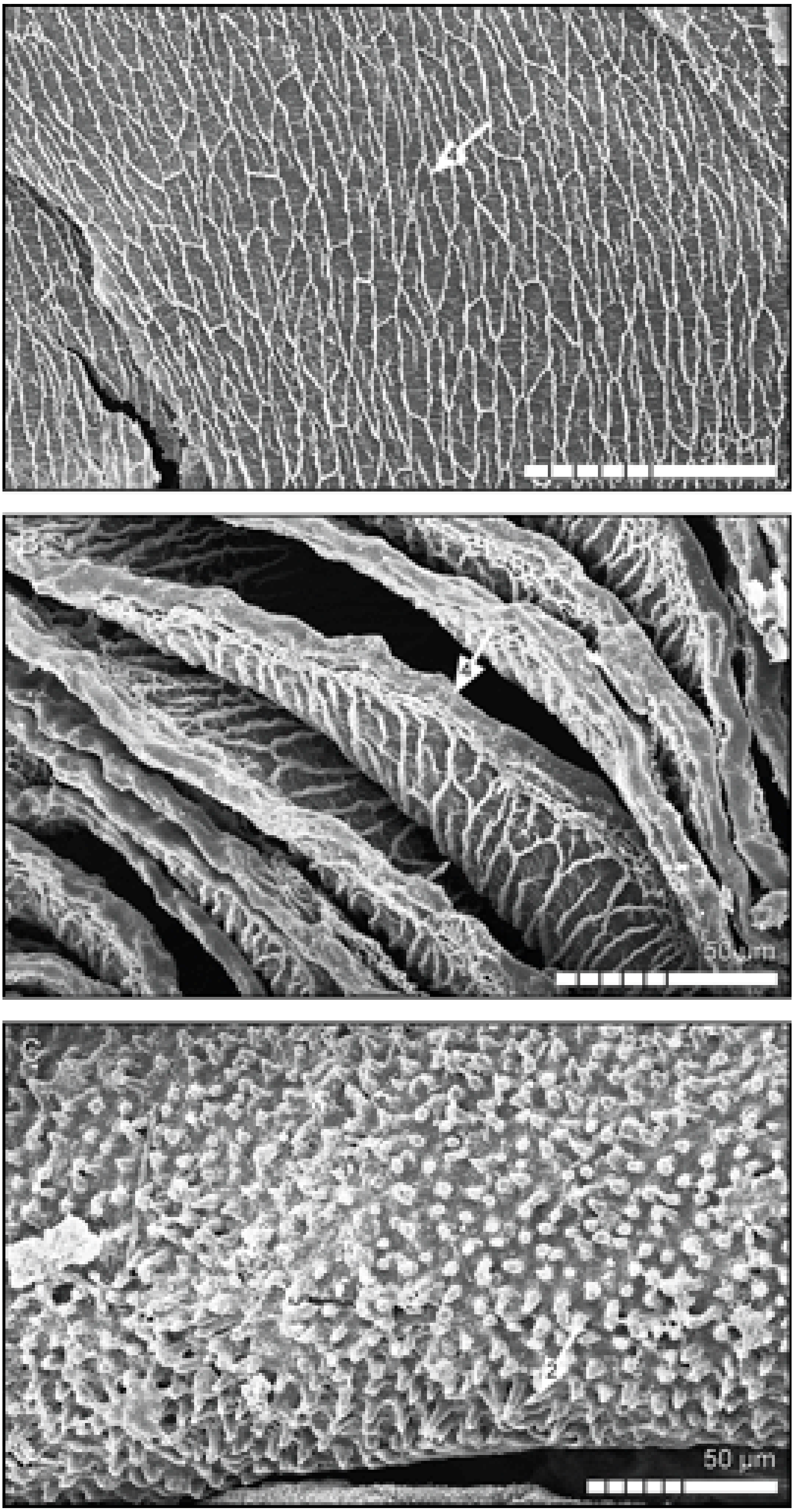

50 µm
50 µm

Plate 48. *Tityus bolivianus* Kraepelin, 1895, 1 ♂ (AMNH [LP 4249]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding polygonal areas with parallel veins (ribs), viewed from air space; **B.** wrinkled distal edges of book lung lamellae (arrow), posterior view. Numbers in arrows refer to character states.

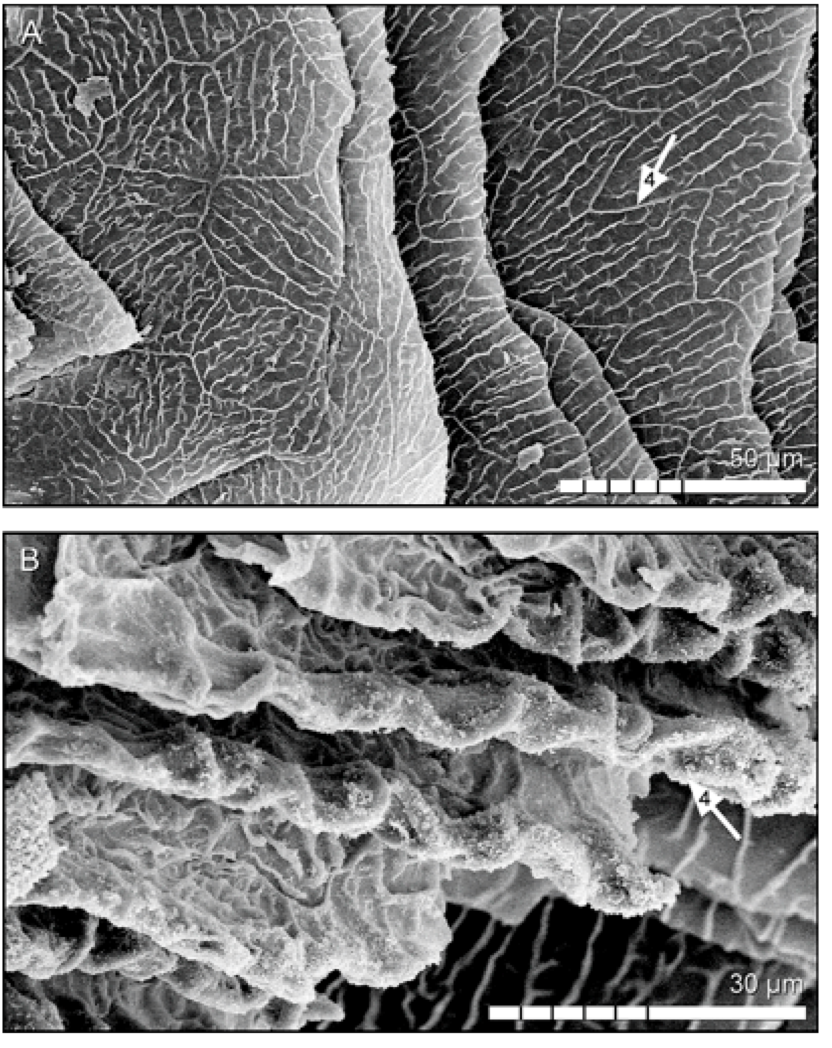

A
4
50 µm
B
4
30 µm

Plate 49. *Tityus cambridgei* Pocock, 1897, 1 ♀ (AMNH [LP 3649]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding polygonal areas with parallel veins (ribs), directed to distal lamellar edge, viewed from air space; **B.** smooth distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with subconical structures (arrow), anterior view. Numbers in arrows refer to character states.

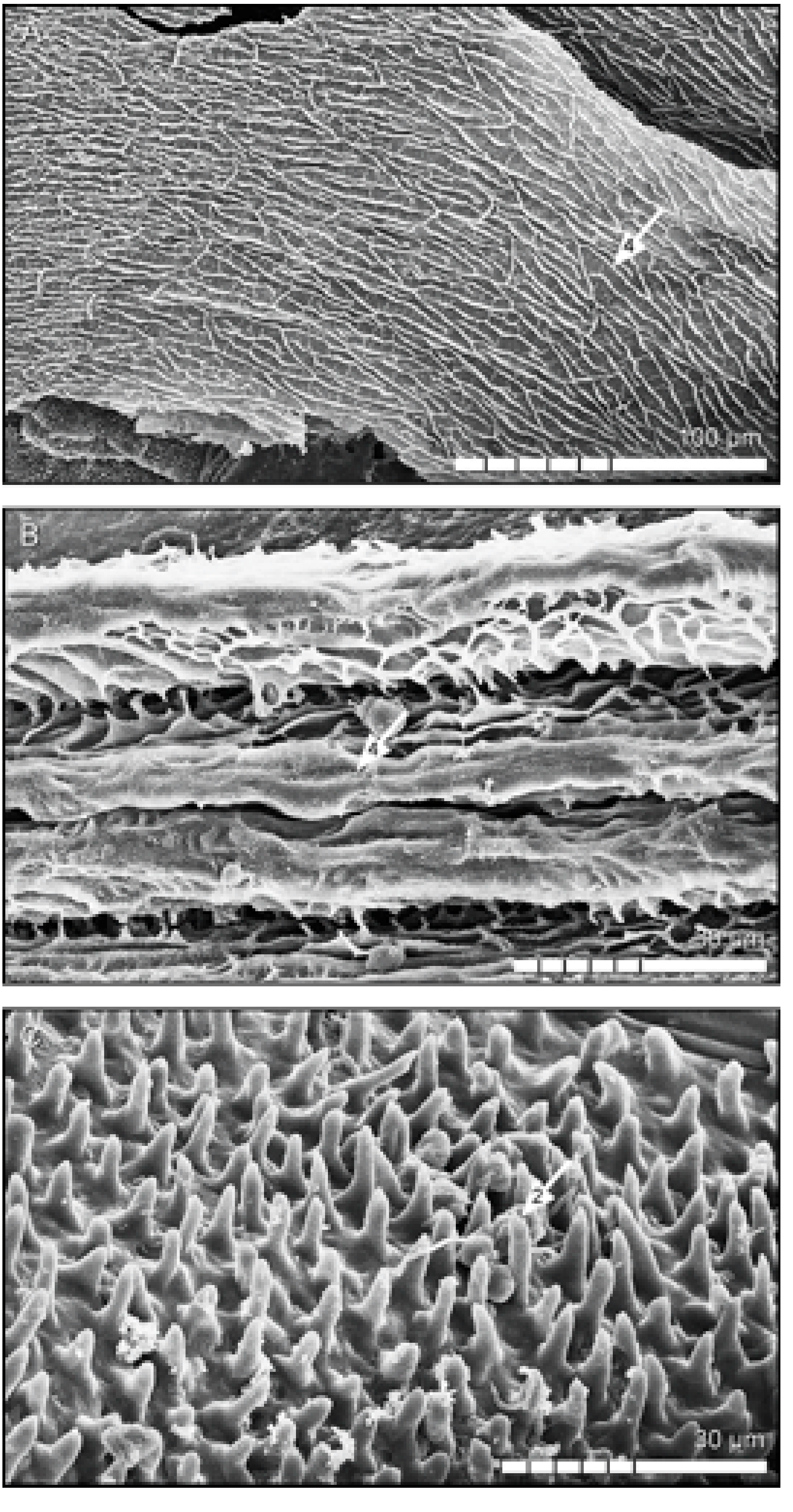

4
100 µm
B
2
30 µm

Plate 50. *Tityus clathratus* C. L. Koch, 1844, 1 ♀ (AMNH [LP 1567]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding polygonal areas with parallel veins (ribs), directed to distal lamellar edge, viewed from air space; **B.** smooth to wrinkled distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with subconical structures (arrow), anterior view. Numbers in arrows refer to character states.

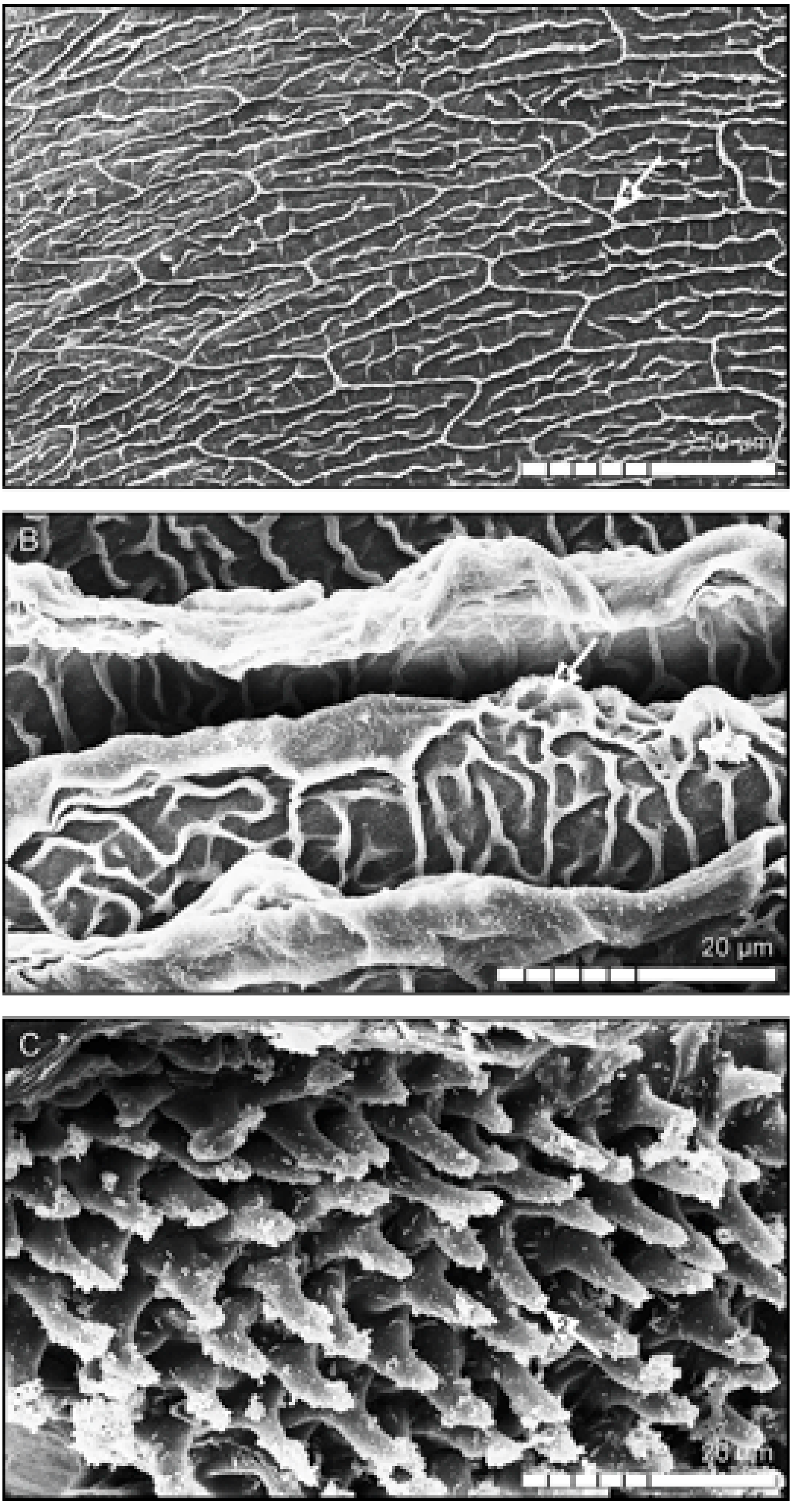

B
20 µm
C

Plate 51. *Tityus confluens* Borelli, 1899, 1 ♀ (AMNH [LP 2938]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding polygonal areas with parallel veins (ribs), directed to distal lamellar edge, viewed from air space; **B.** smooth to wrinkled distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with spinelike structures (arrow) branched, anterior view. Numbers in arrows refer to character states.

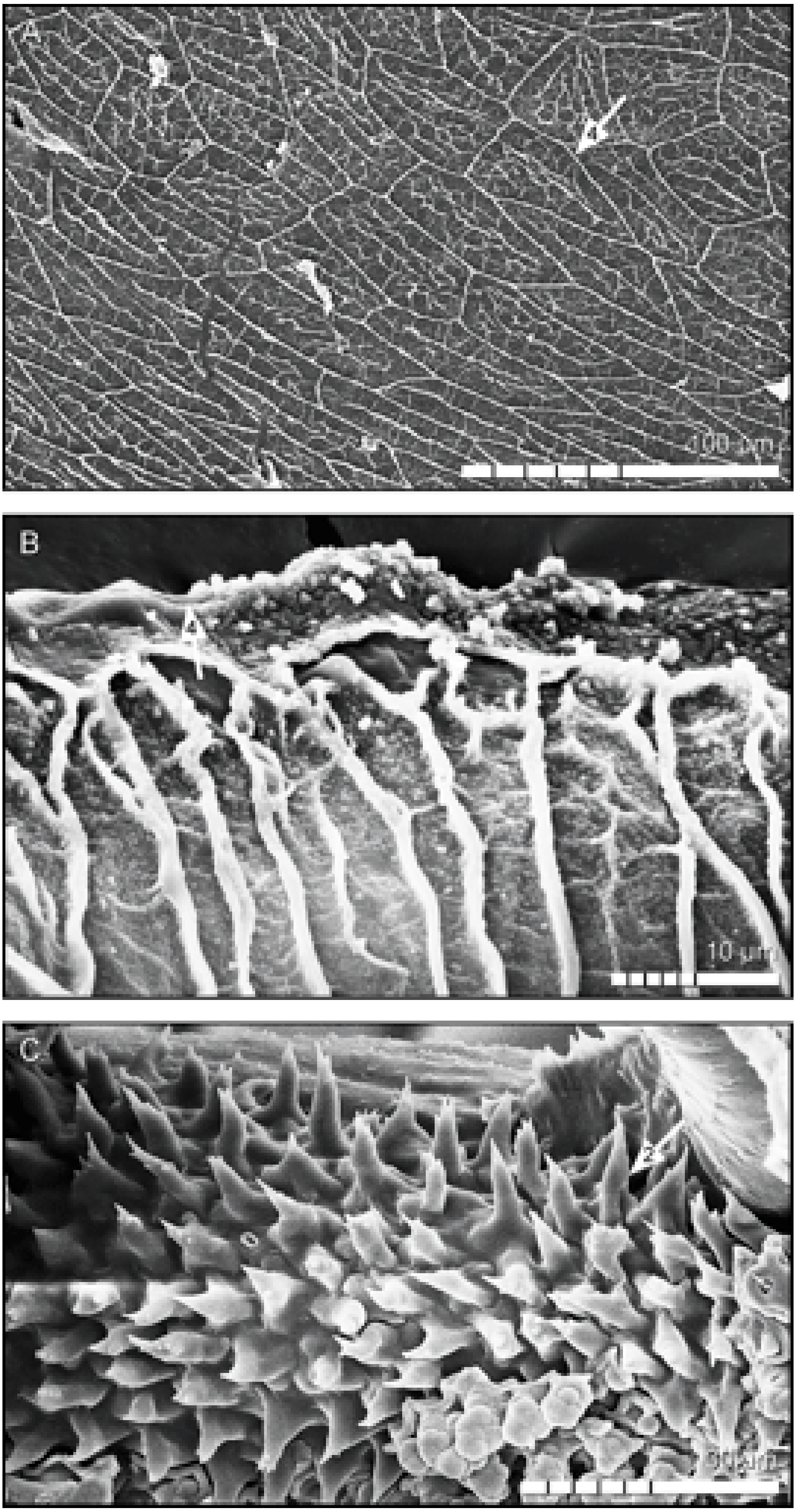

A
100 µm
B
10 µm
C

Plate 52. *Tityus discrepans* (Karsch, 1879), 1 ♀ (AMNH [LP 1547]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding polygonal areas with parallel veins (ribs), directed to distal lamellar edge, viewed from air space; **B.** smooth distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with subconical structures (arrow), anterior view. Numbers in arrows refer to character states.

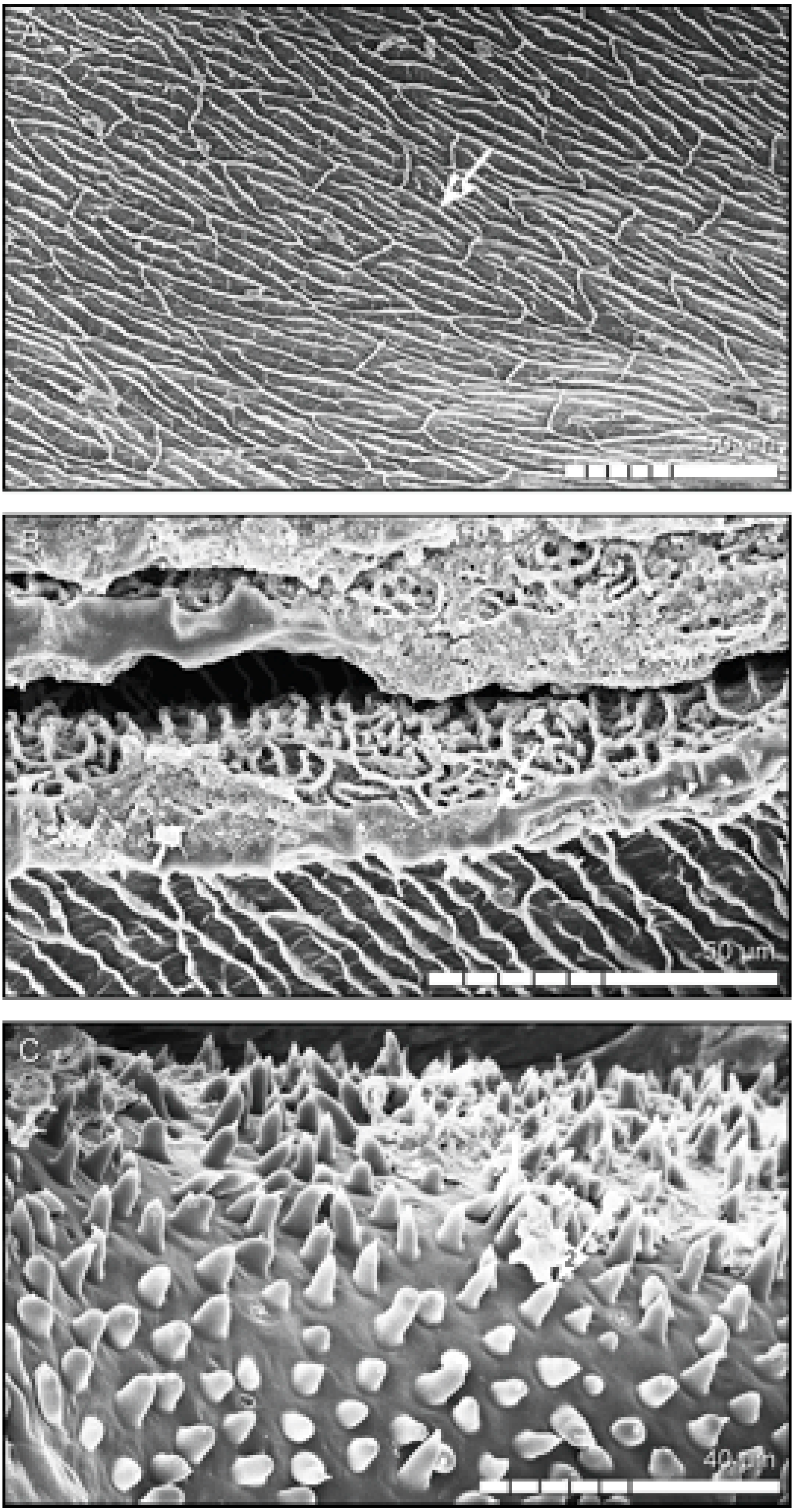

B
50 µm
C
40 µm

Plate 53. *Tityus melanostictus* Pocock, 1893, 1 ♀ (AMNH [LP 1504]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding polygonal, slender areas with veins (ribs), directed to distal lamellar edge, viewed from air space; **B.** smooth to wrinkled distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with subconical structures (arrow), anterior view. Numbers in arrows refer to character states.

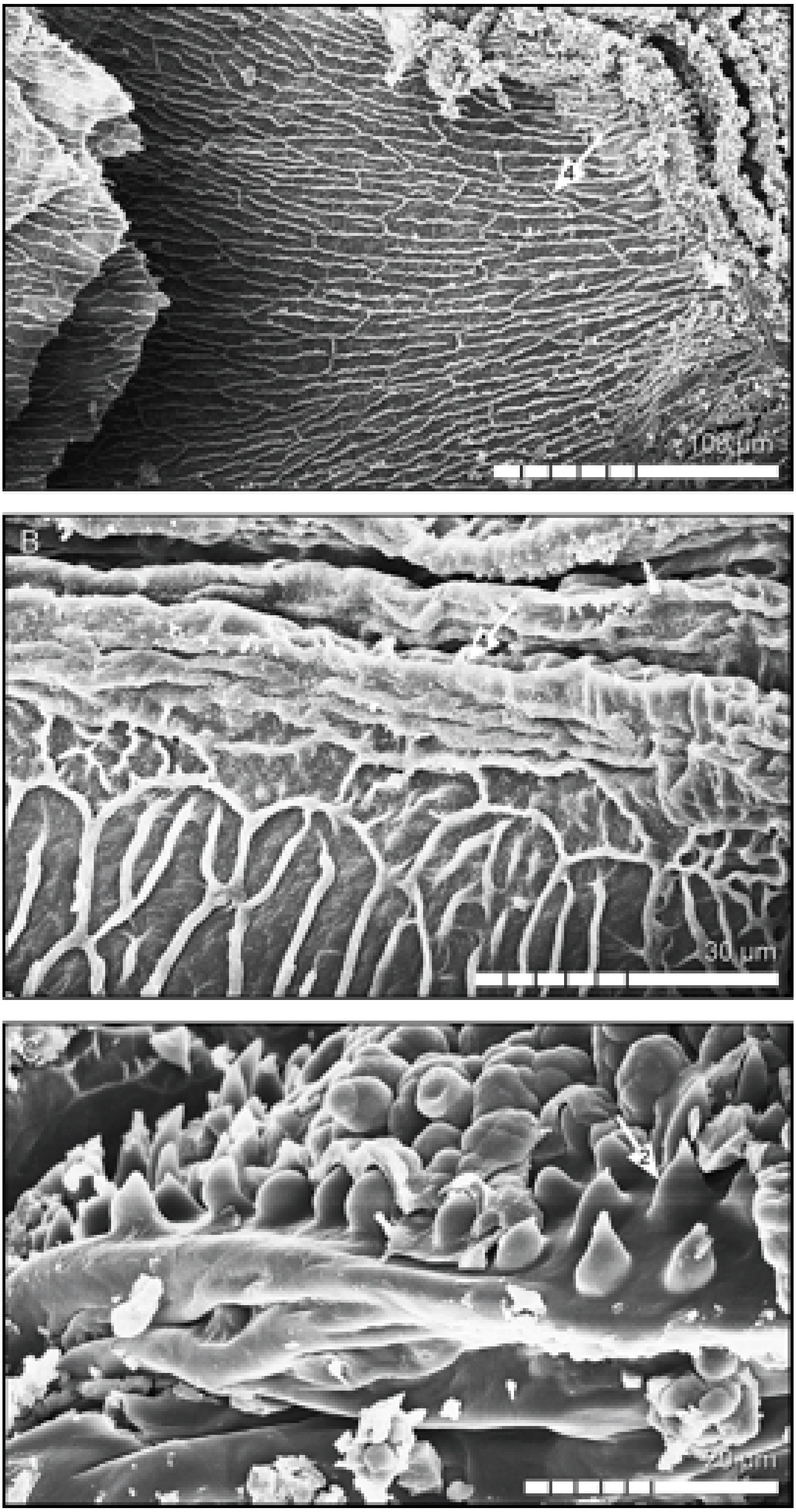

4
B
30 µm
2

Plate 54. *Tityus serrulatus* Lutz and Mello, 1922, 1 ♀ (AMNH [LP 1597]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding polygonal, slender areas with veins (ribs), directed to distal lamellar edge, viewed from air space; **B.** smooth distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with subconical structures (arrow), anterior view. Numbers in arrows refer to character states.

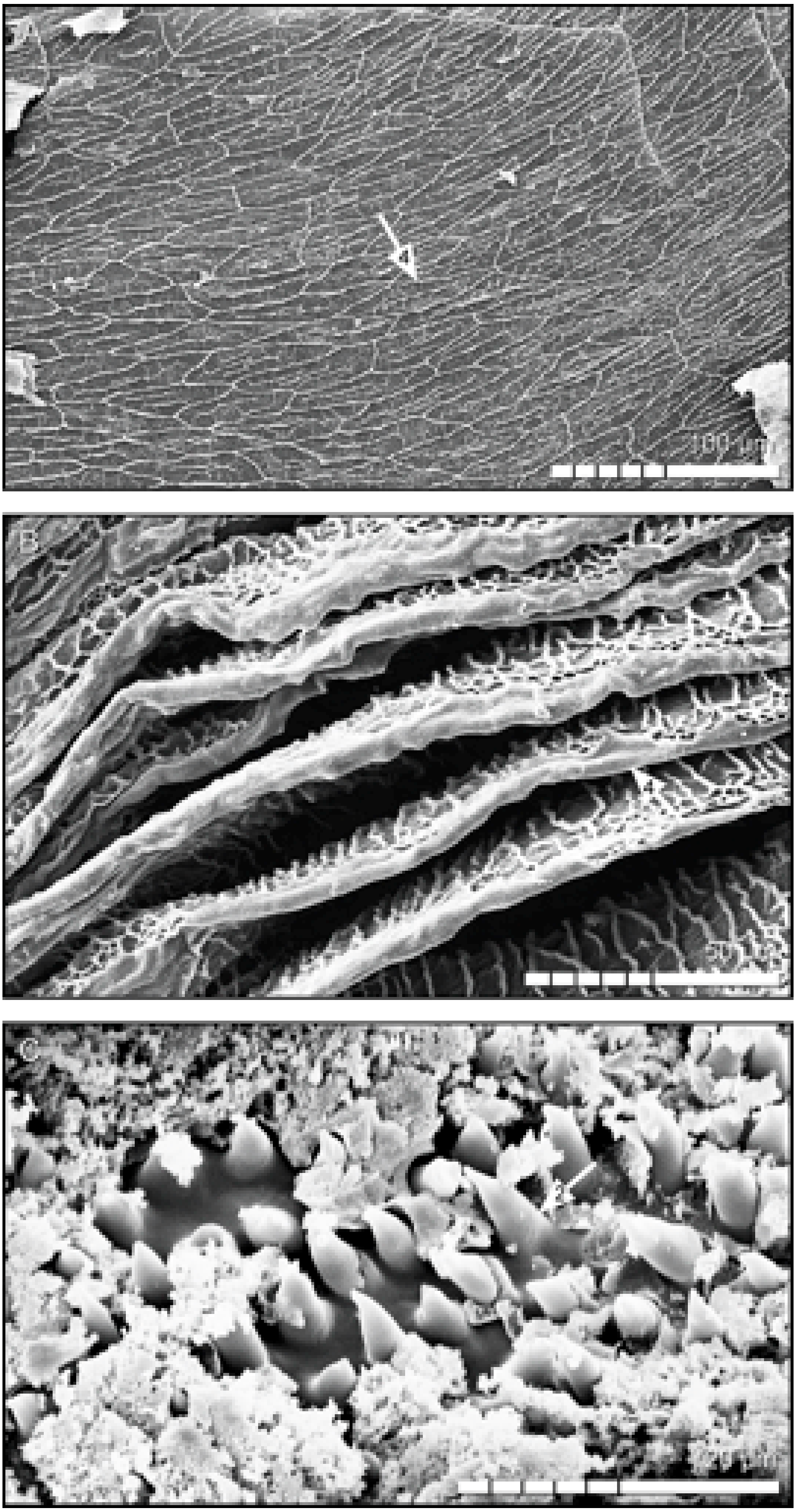

100 µm

Plate 55. *Tityus silvestris* Pocock, 1897, 1 ♂ (AMNH [LP 3643]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding polygonal areas with parallel veins (ribs), directed to distal lamellar edge, viewed from air space; **B.** smooth distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with subconical structures (arrow), anterior view. Numbers in arrows refer to character states.

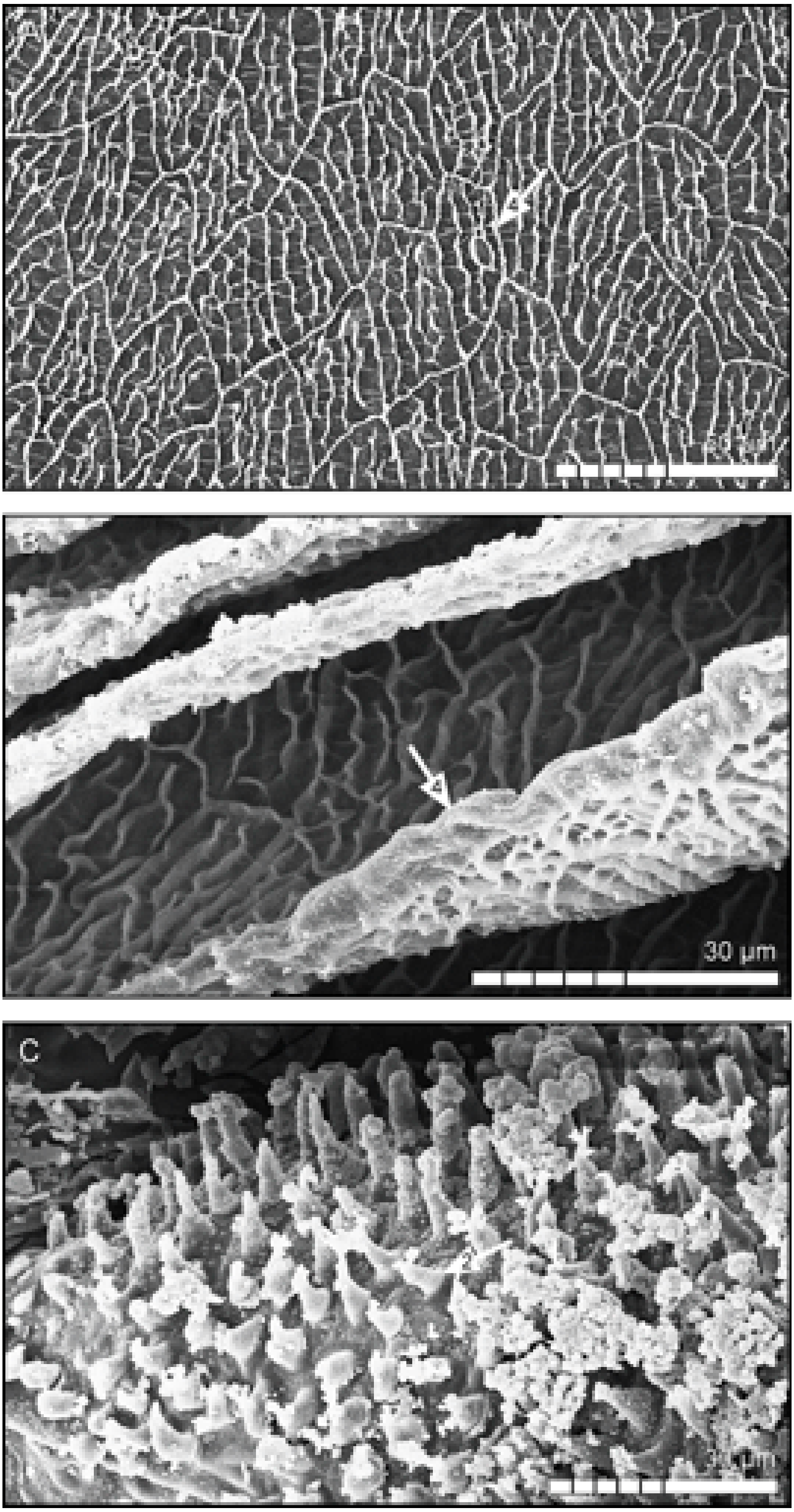

30 µm
C

Plate 56. *Uroplectes flavoviridis* Peters, 1861, 1 ♀ (AMNH [LP 1707]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas with irregular foldlike ridges, viewed from air space; **B.** distal edges of book lung lamellae covered with thorns (arrow), posterior view; **C.** movable posterior edge of spiracle with hillocklike structures (arrow), anterior view. Numbers in arrows refer to character states.

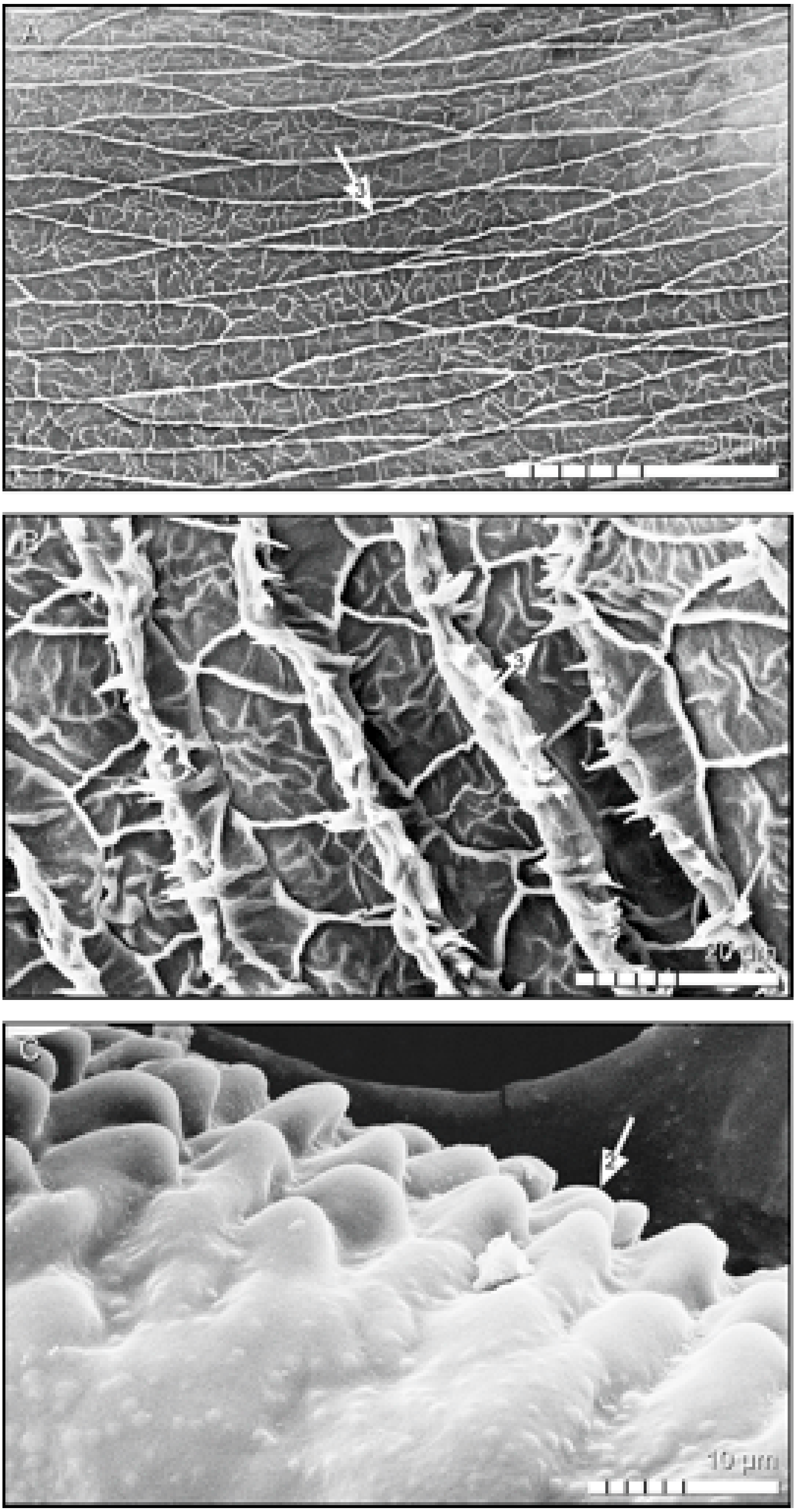

10 µm

Plate 57. *Vachoniolus globimanus* Levy, Amitai and Shulov, 1973, 1 ♂ (AMNH [LP 3767]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas, directed to distal lamellar edge, and areas with bridging trabeculae (broken) proximally, viewed from air space; **B.** distal edges of book lung lamellae covered with thorns (arrow), posterior view; **C.** movable posterior edge of spiracle with thornlike subconical to hillocklike structures (arrow), anterior view. Numbers in arrows refer to character states.

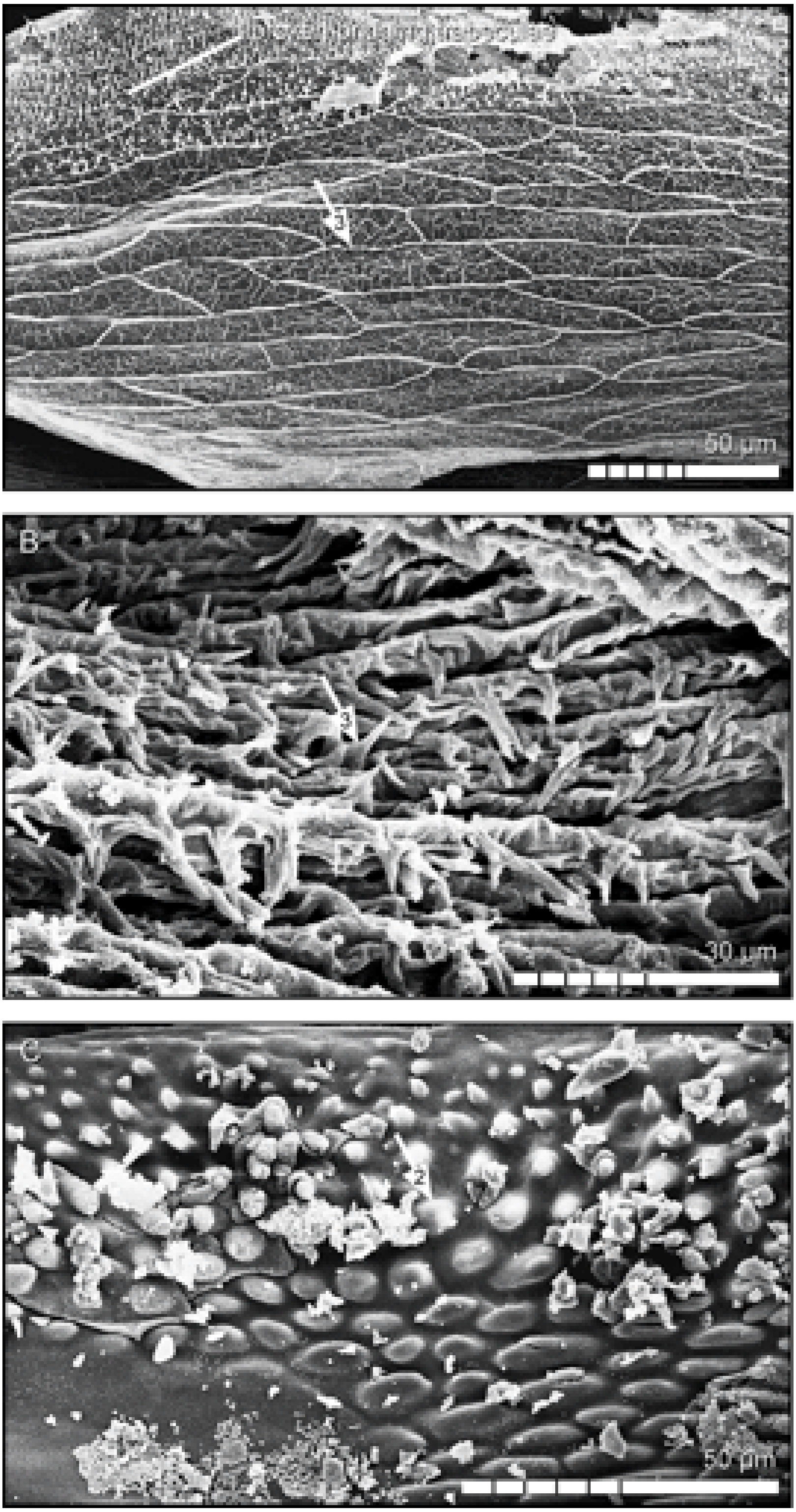

3
50 µm
B
3
30 µm
C
2
50 µm

Plate 58. *Zabius fuscus* (Thorell, 1876), 1 juv. ♀ (AMNH [LP 1759]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding polygonal areas with parallel veins (ribs), directed to distal lamellar edge, viewed from air space; **B.** wrinkled distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with spinelike structures, anterior view. Numbers in arrows refer to character states.

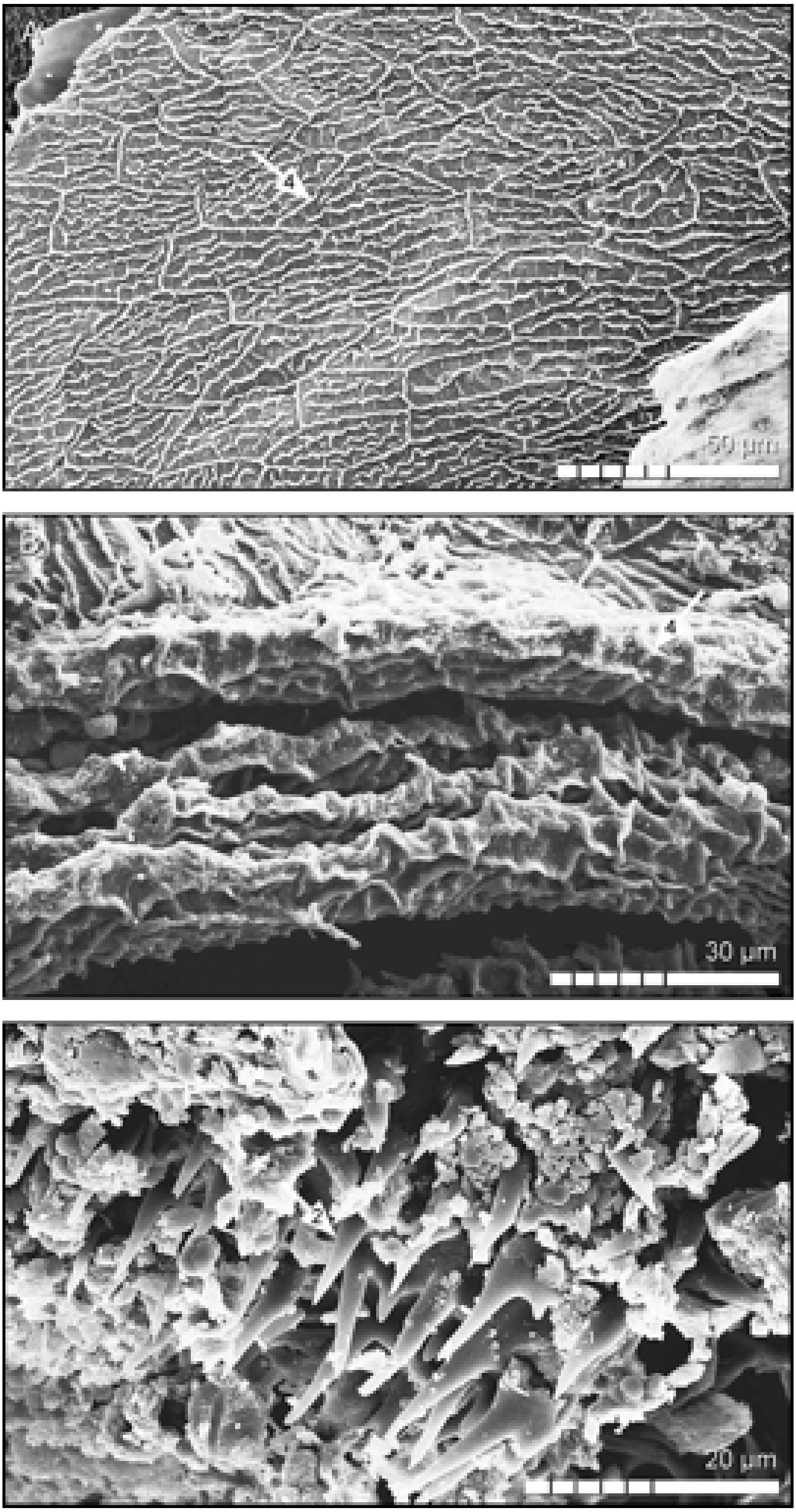

4
50 µm
4
30 µm
2
20 µm

Plate 59. *Microcharmus* sp., 1 ♀ (AMNH [LP 1769]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding slender areas with irregular foldlike ridges, viewed from air space; **B.** smooth to wrinkled distal edges of book lung lamellae (arrow), posterior view. Numbers in arrows refer to character states.

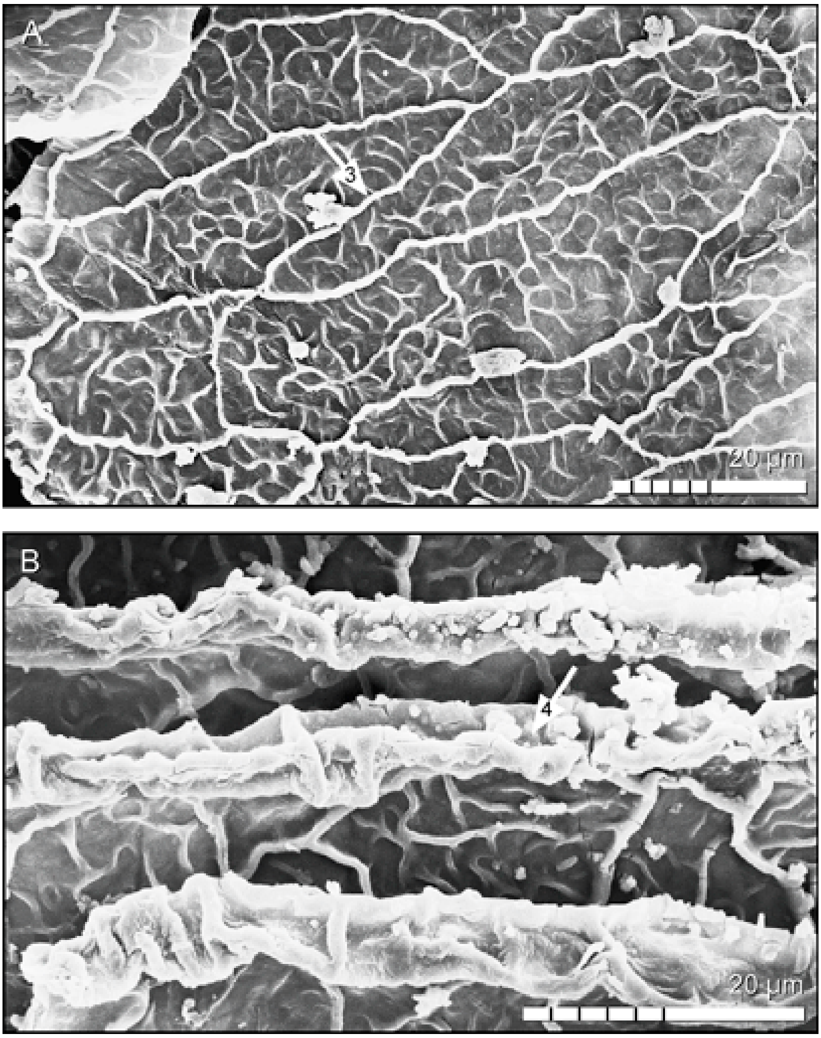

A
3
20 µm
B
4
20 µm

Plate 60. *Chaerilus truncatus* Karsch, 1879, 1 ♂ (AMNH [LP 2197A]): **A.** surface of book lung lamella with reticulate veins (arrow) surrounding polygonal areas with parallel veins (ribs), directed to distal lamellar edge, and with perpendicular foldlike ridges, viewed from air space; **B.** distal edge of book lung lamella with pillowlike structures (arrow) covered with reticulate veins, posterior view; **C.** movable posterior edge of spiracle with subconical structures (arrow), anterior view. Numbers in arrows refer to character states.

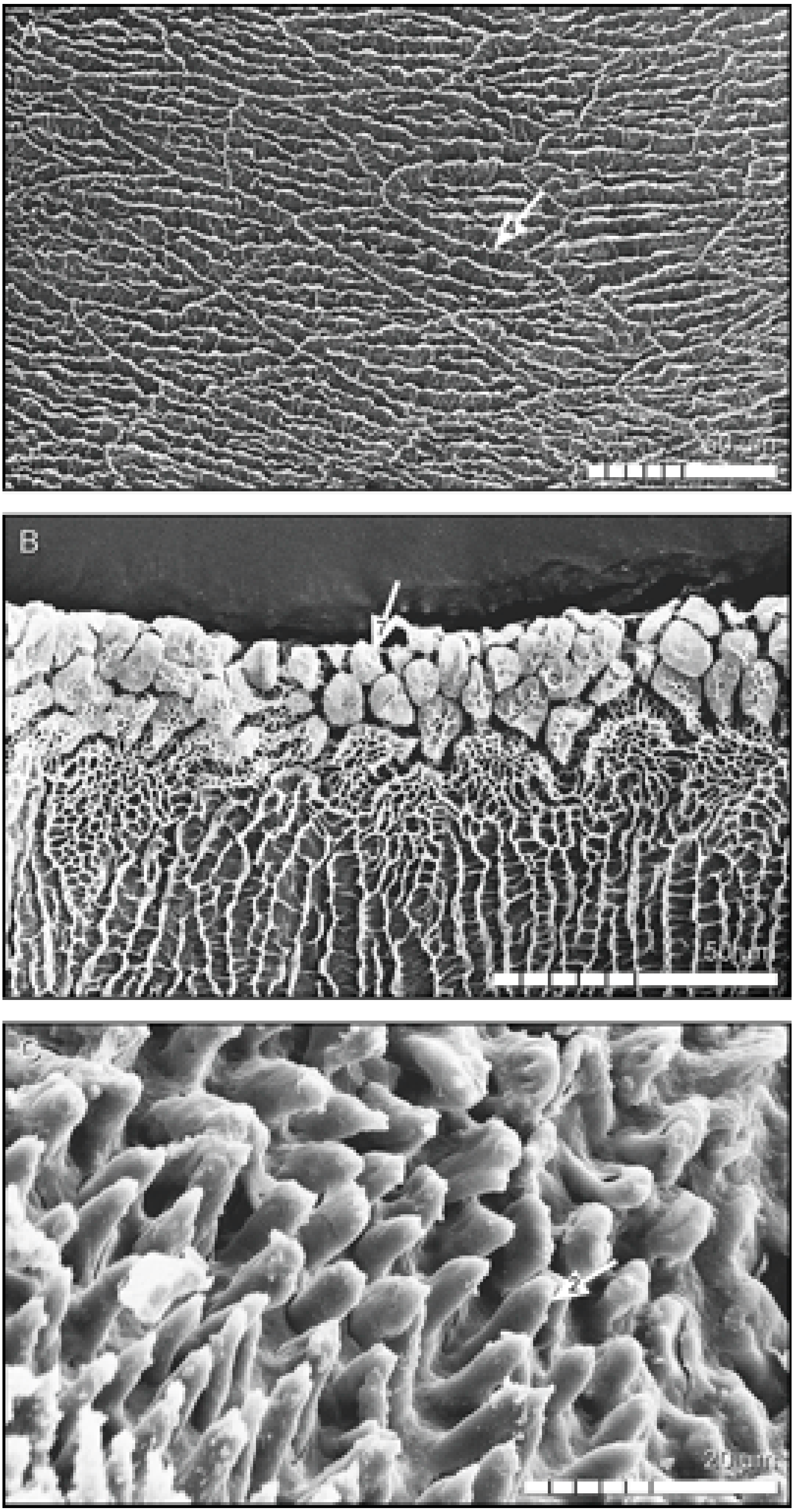

B

Plate 61. *Anuroctonus phaiodactylus* (Wood, 1863), 1 subad. ♀ (AMNH [LP 4970]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae densely covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with flat hillocklike structures (arrow), anterior view. Numbers in arrows refer to character states.

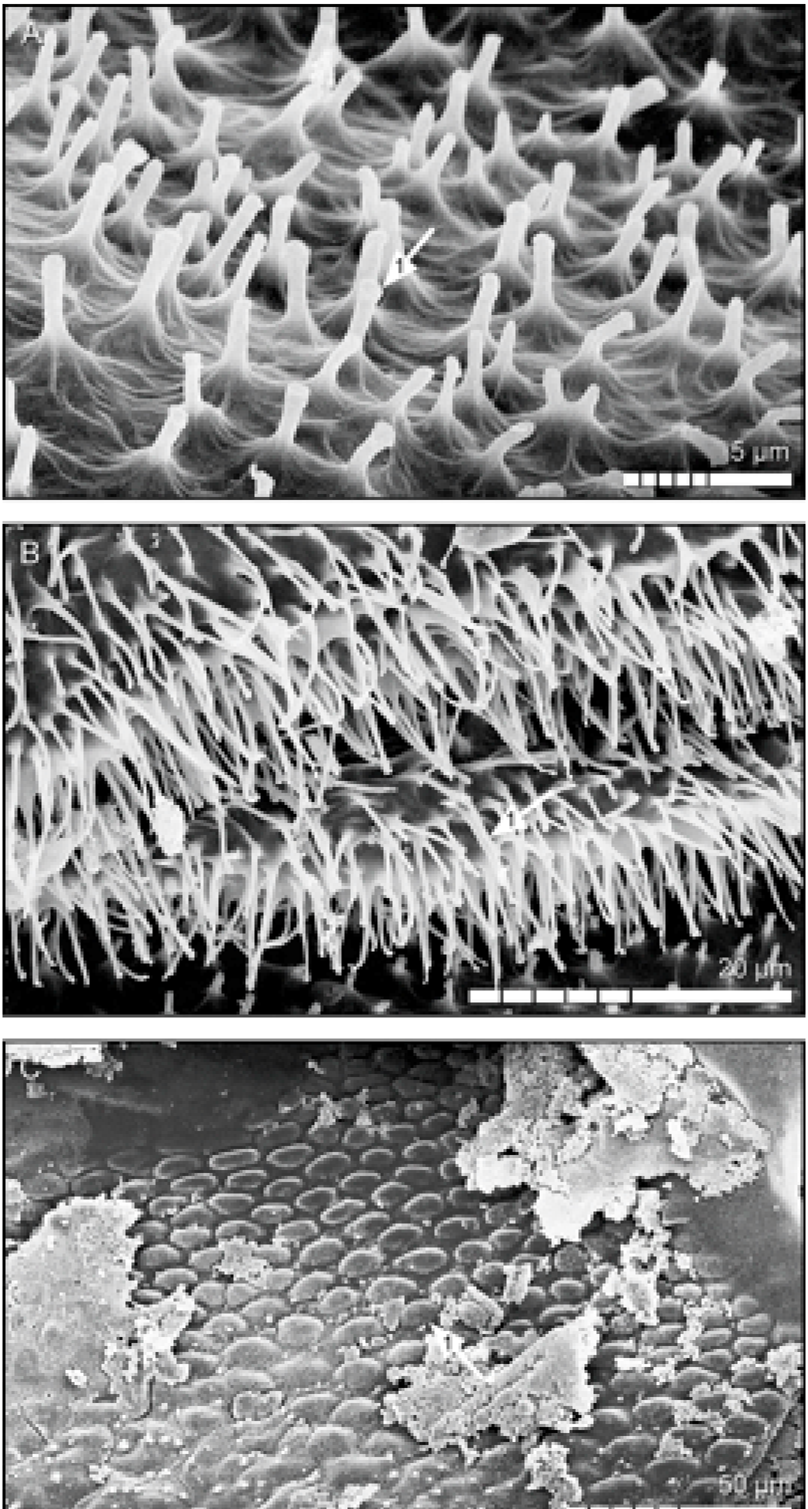

A
1
5 µm
B
1
20 µm
C
1
50 µm

Plate 62. *Calchas nordmanni* Birula, 1899, 1 ♀ (AMNH [LP 2246]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae with meandering bulgelike structures (arrow) winding along edge, posterior view; **C.** movable posterior edge of spiracle with broadened subconical structures with teeth (arrow), anterior view. Numbers in arrows refer to character states.

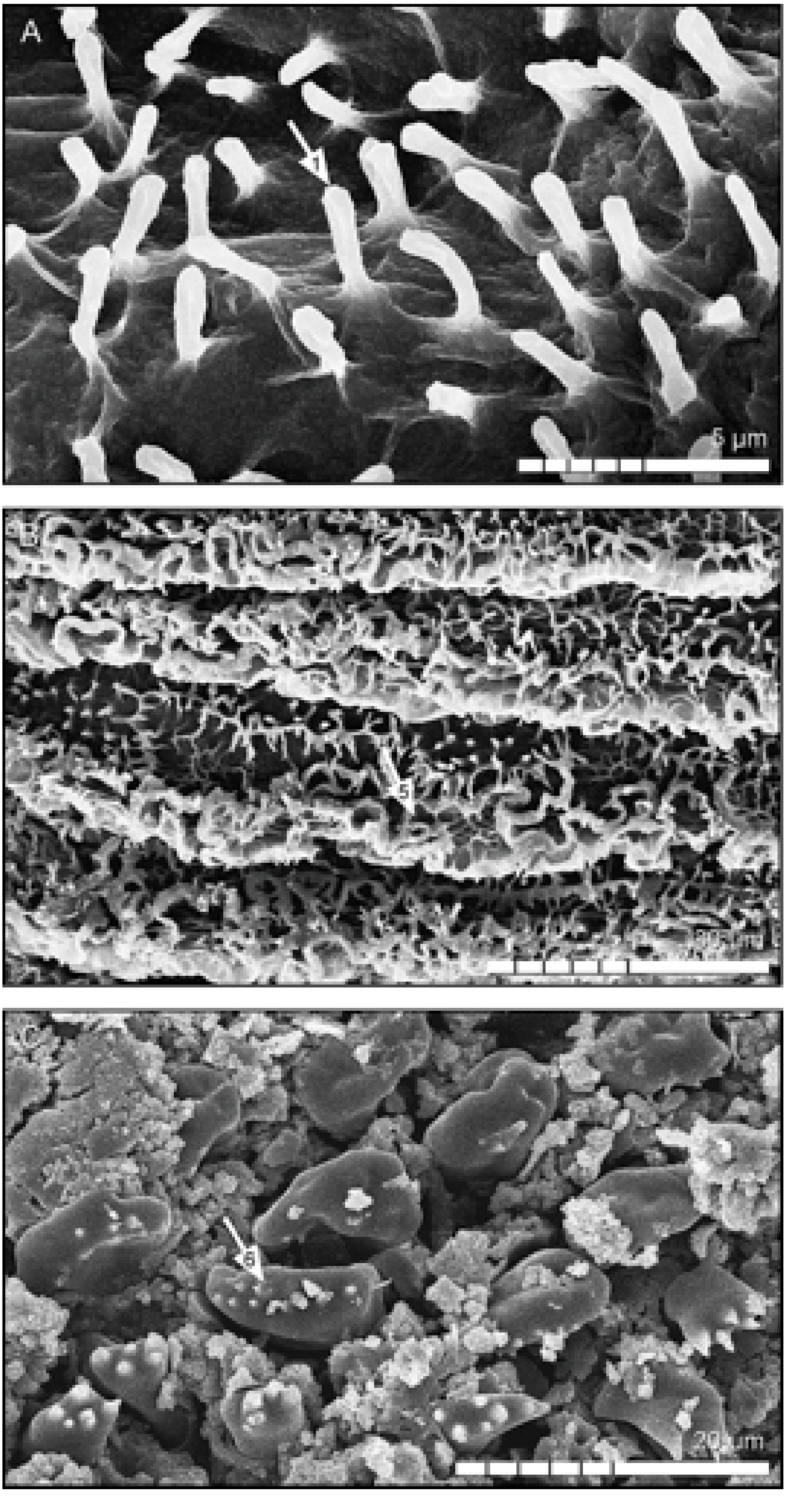

A
5 µm
B
C
20 µm

Plate 63. *Caraboctonus keyserlingi* Pocock, 1893, 1 ex. (AMNH [LP 3686]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** arcuate distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with branched spinelike structures (arrow), anterior view. Numbers in arrows refer to character states.

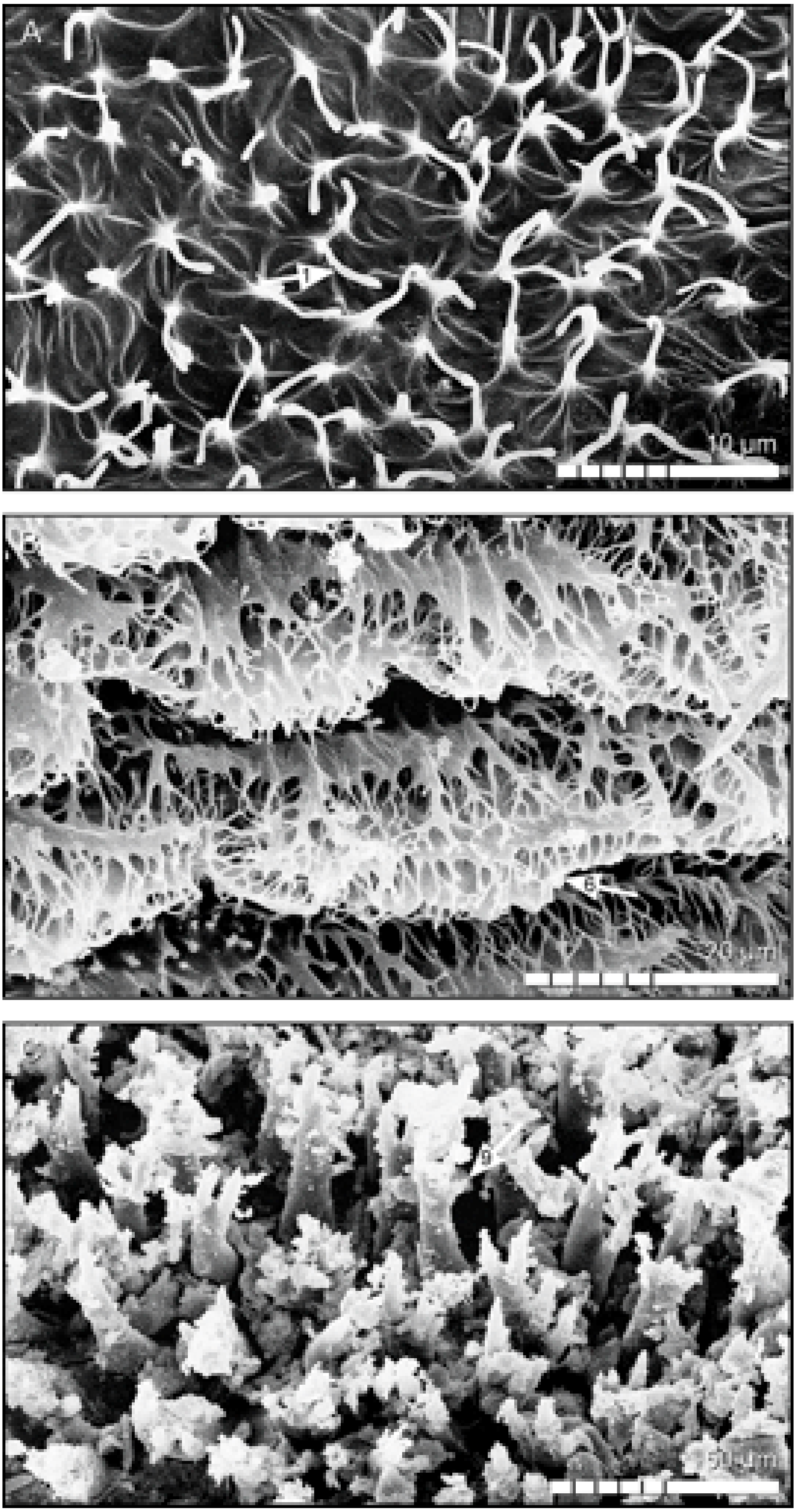

A
10 µm

Plate 64. *Hadruroides charcasus* (Karsch, 1879), 1 ♀ (AMNH [LP 1555]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with bent bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with hillocklike structures (arrow), anterior view. Numbers in arrows refer to character states.

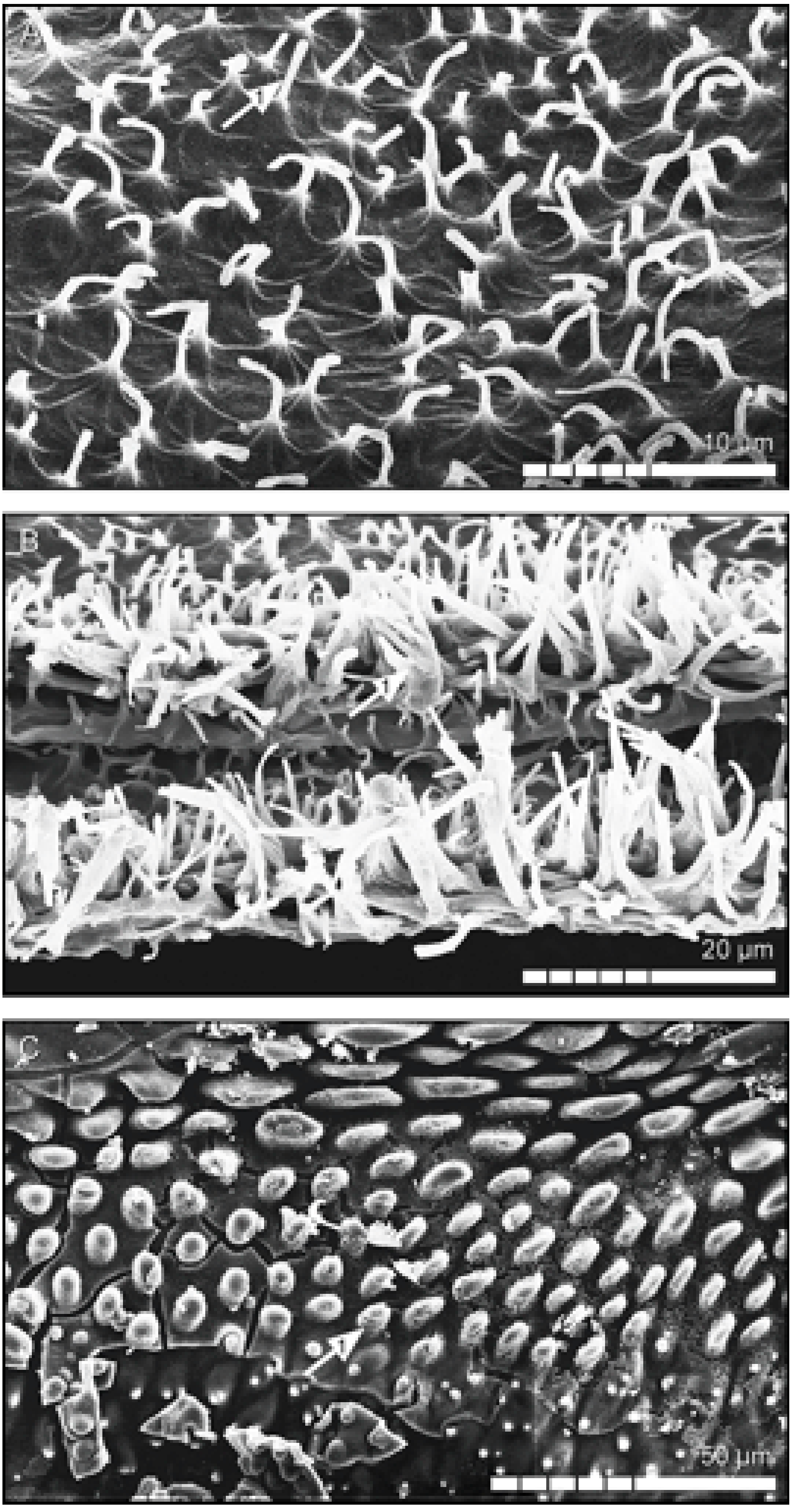

A
10 µm
B
20 µm
C
50 µm

Plate 65. *Hadrurus hirsutus* (Wood, 1863), 1 ♂ (AMNH [LP 3131]): **A.** ventral surface of book lung lamella with bristlelike trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with rigid spines (arrow), posterior view; **C.** movable posterior edge of spiracle with spinelike structures (arrow), anterior view. Numbers in arrows refer to character states.

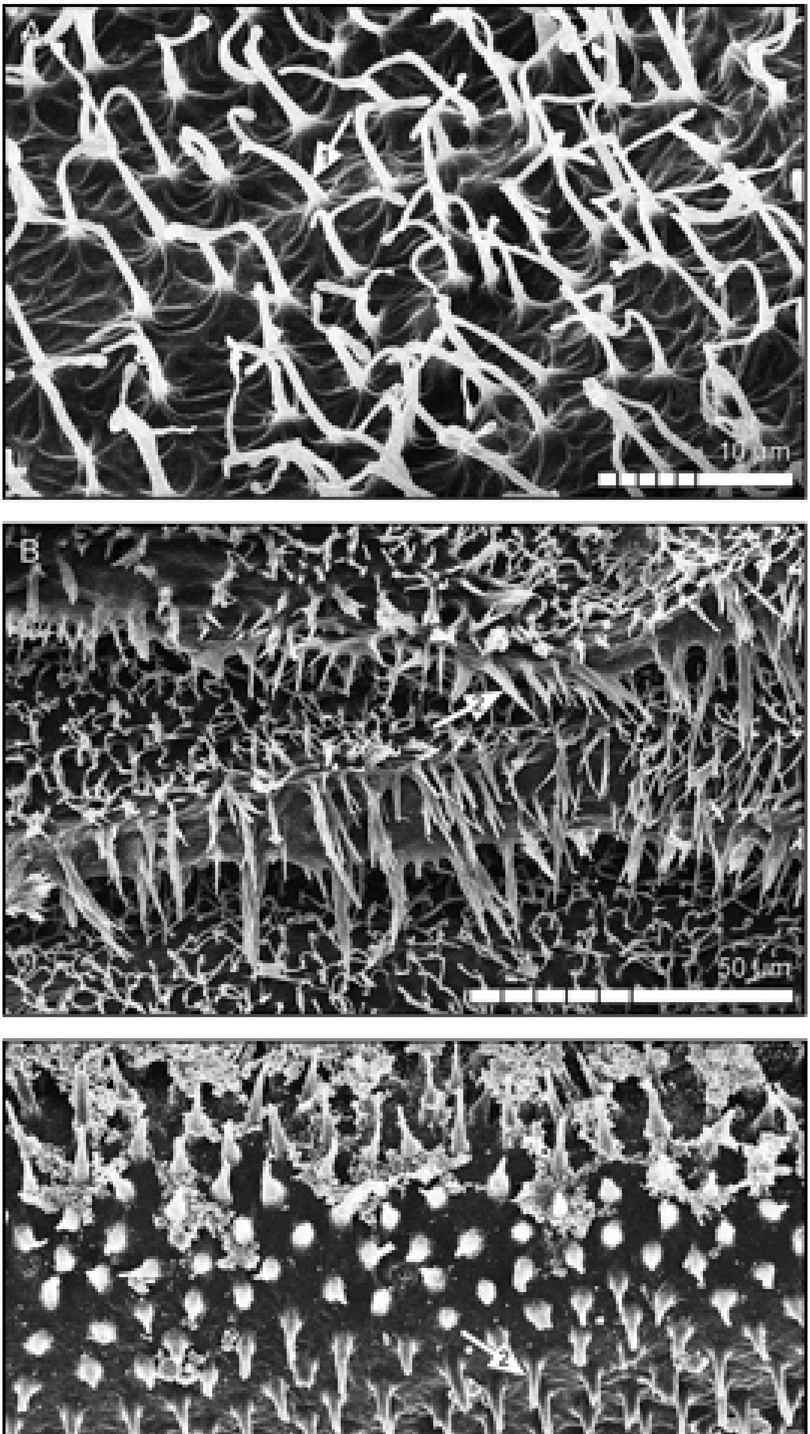

A
10 µm
B
50 µm
50 µm

Plate 66. *Iurus dufoureius dufoureius* (Brullé, 1832), 1 ♀ (MNHN RS 2977), 1 ♂ (ZMB 7497): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae with meandering bulgelike structures (arrow) winding along edge, posterior view; **C.** movable posterior edge of spiracle with chisel-like structures (arrow), anterior view. Numbers in arrows refer to character states.

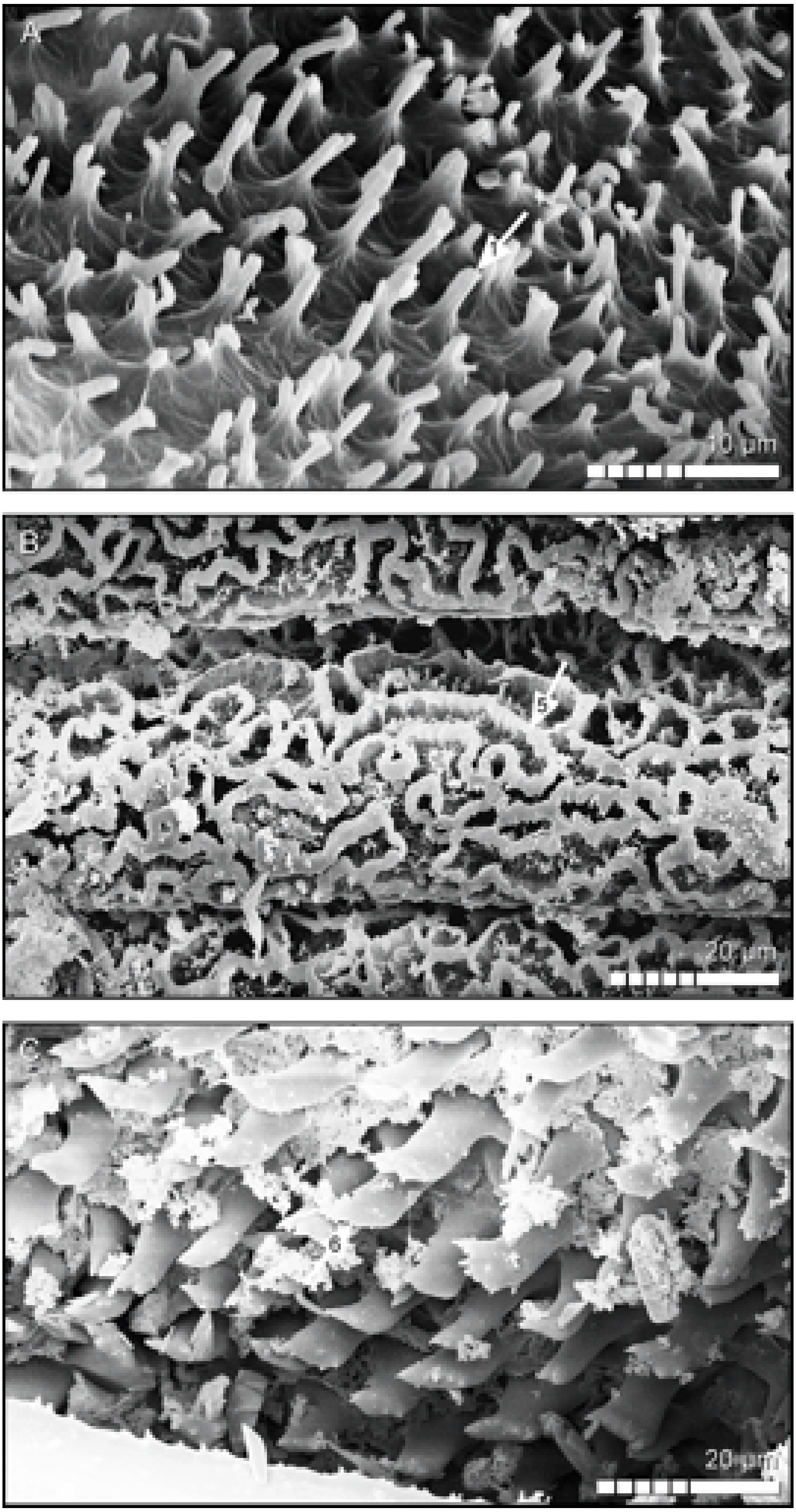

A
10 µm
B
5
20 µm
C
6
20 µm

Plate 67. *Euscorpius carpathicus candiota* Birula, 1903: 3 ♀ (HUB): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** arcuate distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with hillocklike structures (arrow), anterior view. Numbers in arrows refer to character states.

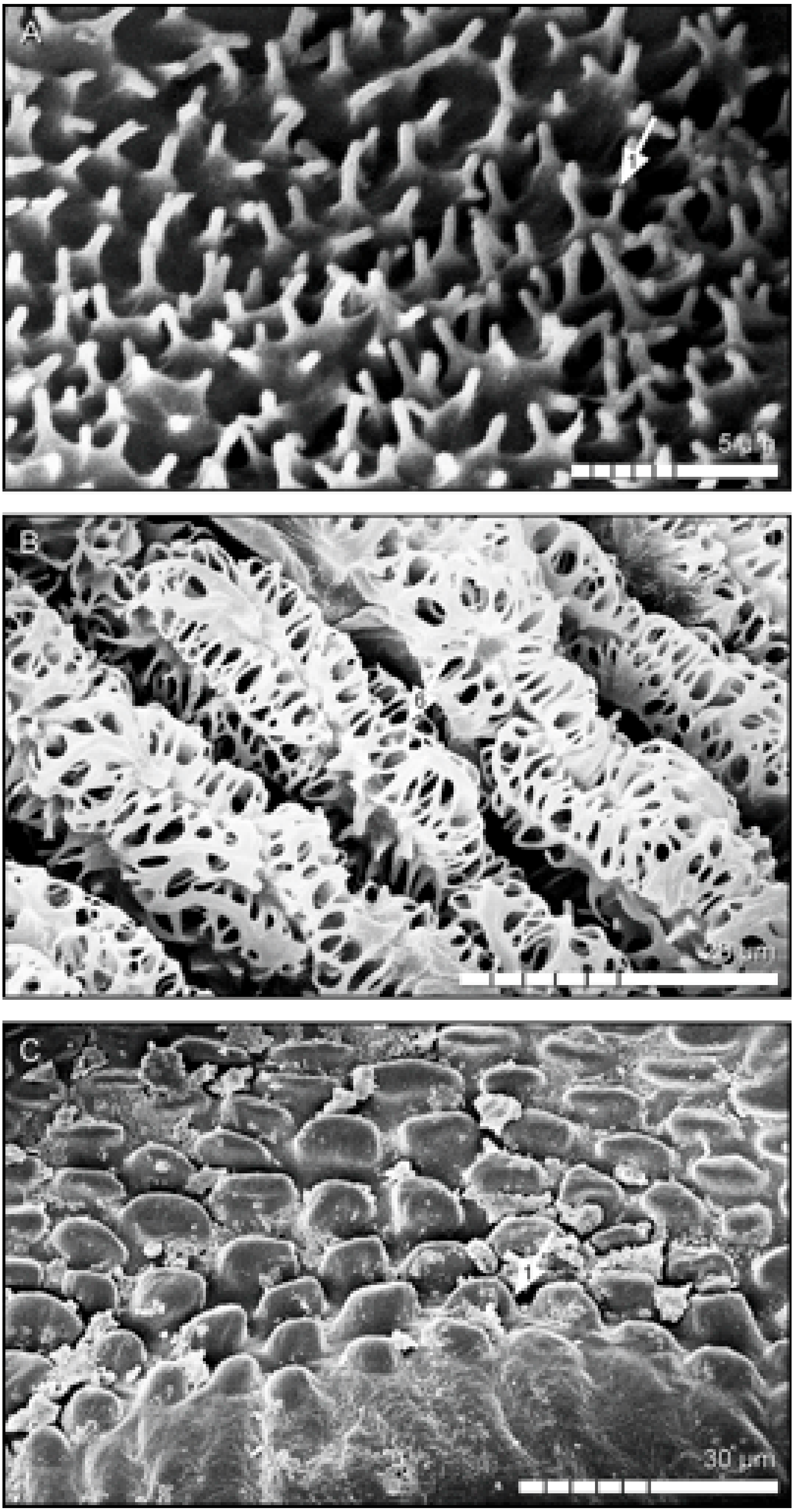

A
B
C
30 µm

Plate 68. *Megacormus granosus* (Gervais, 1843): 1 ♀ (AMNH [LP 2074]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** arcuate distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with hillocklike structures (arrow), anterior view. Numbers in arrows refer to character states.

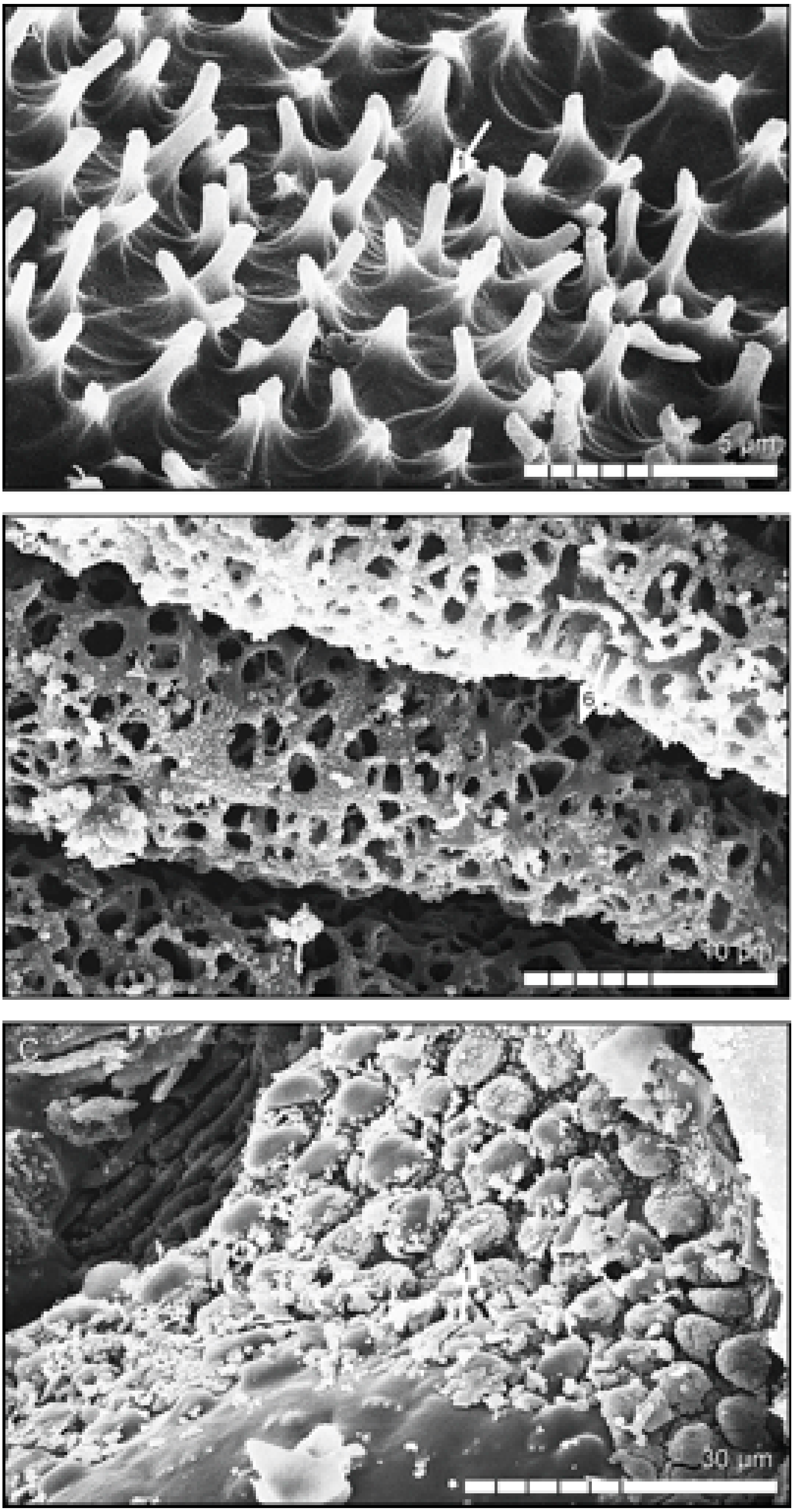

A
5 µm
10 µm
C
30 µm

Plate 69. *Troglocormus willis* Francke, 1981, 1 ♂ (AMNH): **A.** ventral surface of book lung lamella with short simple trabeculae (arrow), viewed from air space; **B.** distal edge of book lung lamella covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with hillocklike structures (arrow), anterior view. Numbers in arrows refer to character states.

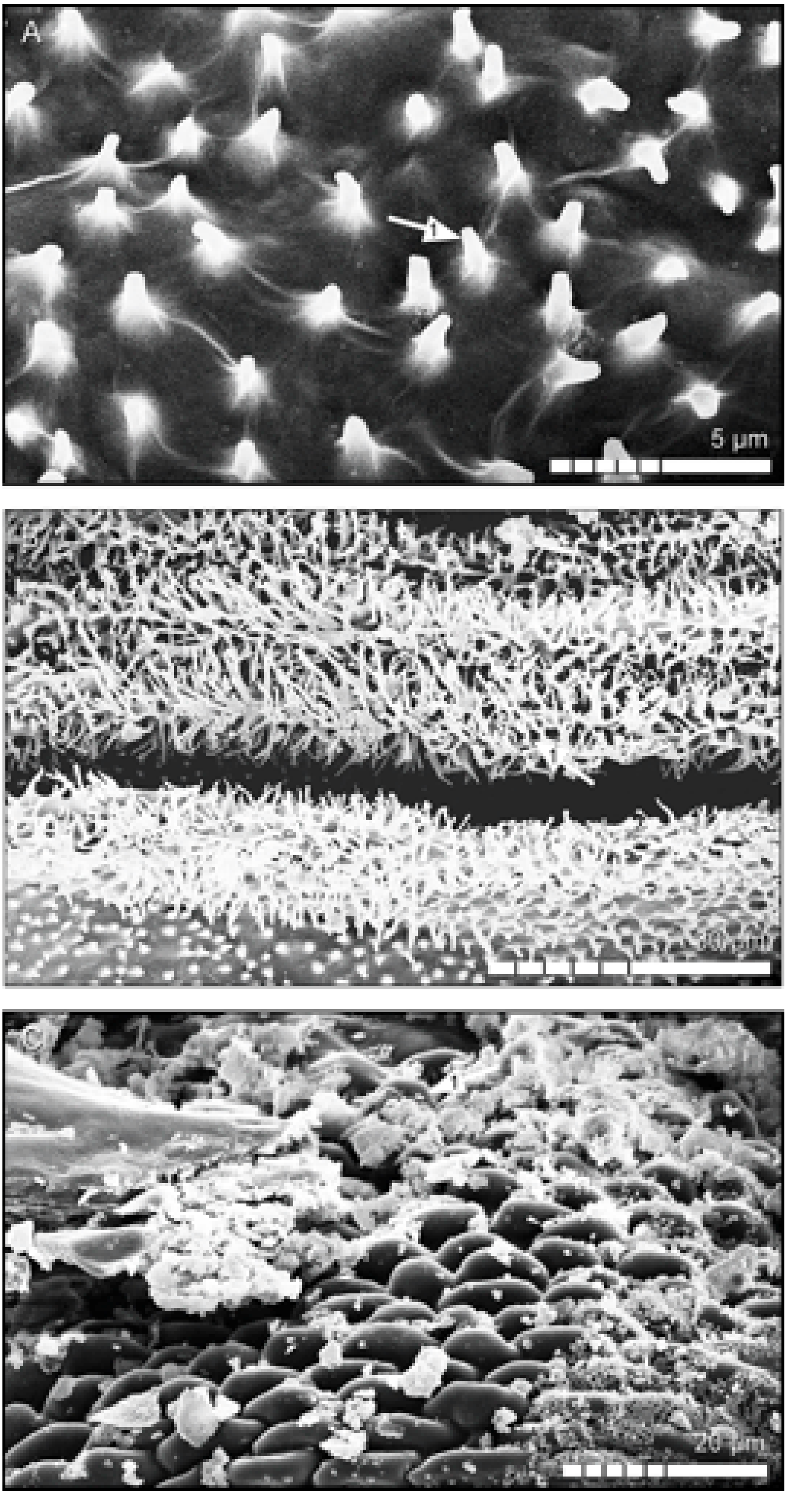

A
5 µm
20 µm

Plate 70. *Scorpiops hardwickei* (Gervais, 1843), 1 ♀ (MNHN RS 0722): **A.** ventral surface of book lung lamella with bristlelike trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with hillocklike structures (arrow), anterior view. Numbers in arrows refer to character states.

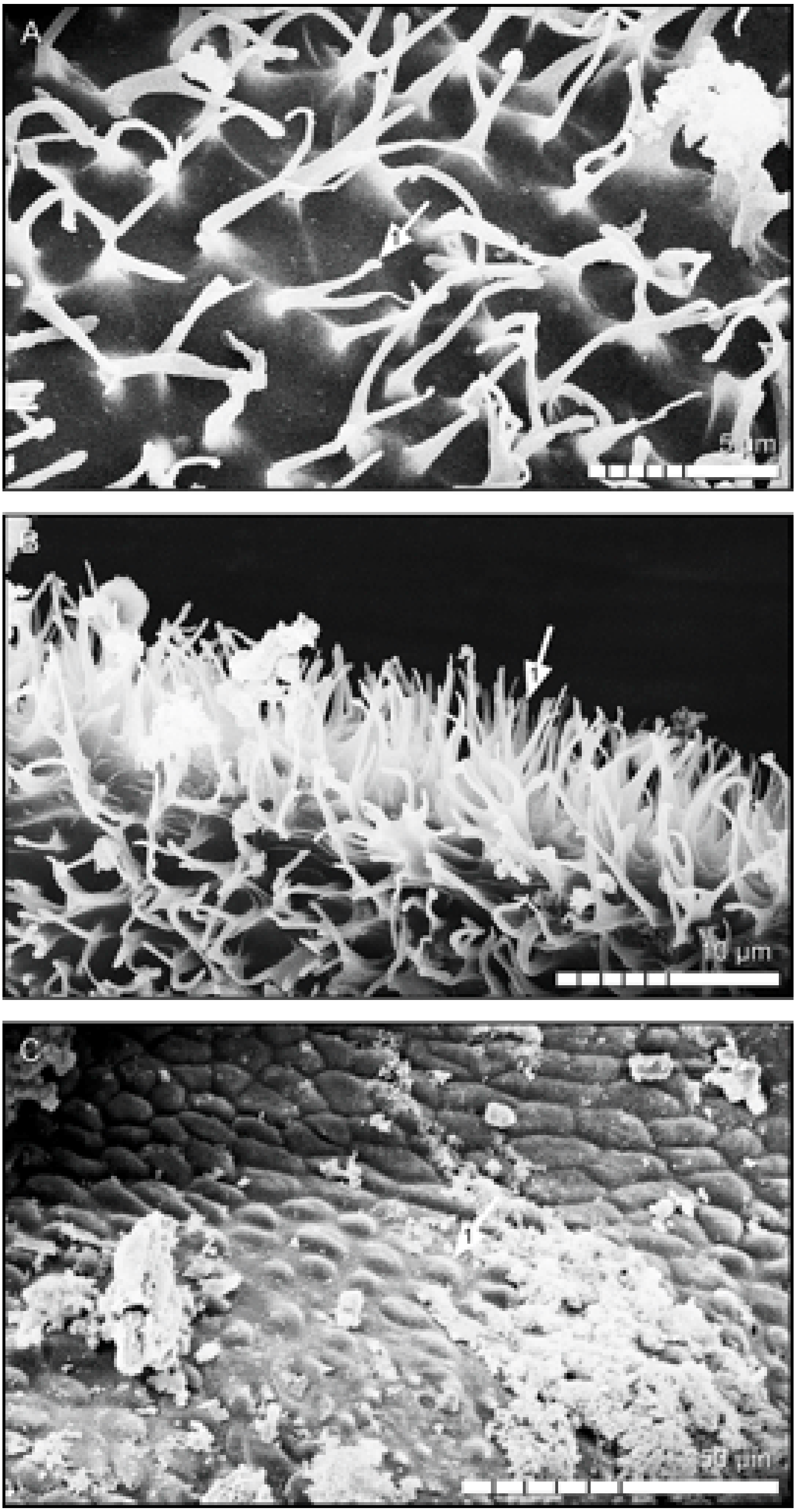

A
B
10 µm
C
50 µm

Plate 71. *Broteochactas nitidus* Pocock, 1893, 1 ♀ (AMNH [LP 1511]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae densely covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with flat hillocklike structures (arrow), anterior view. Numbers in arrows refer to character states.

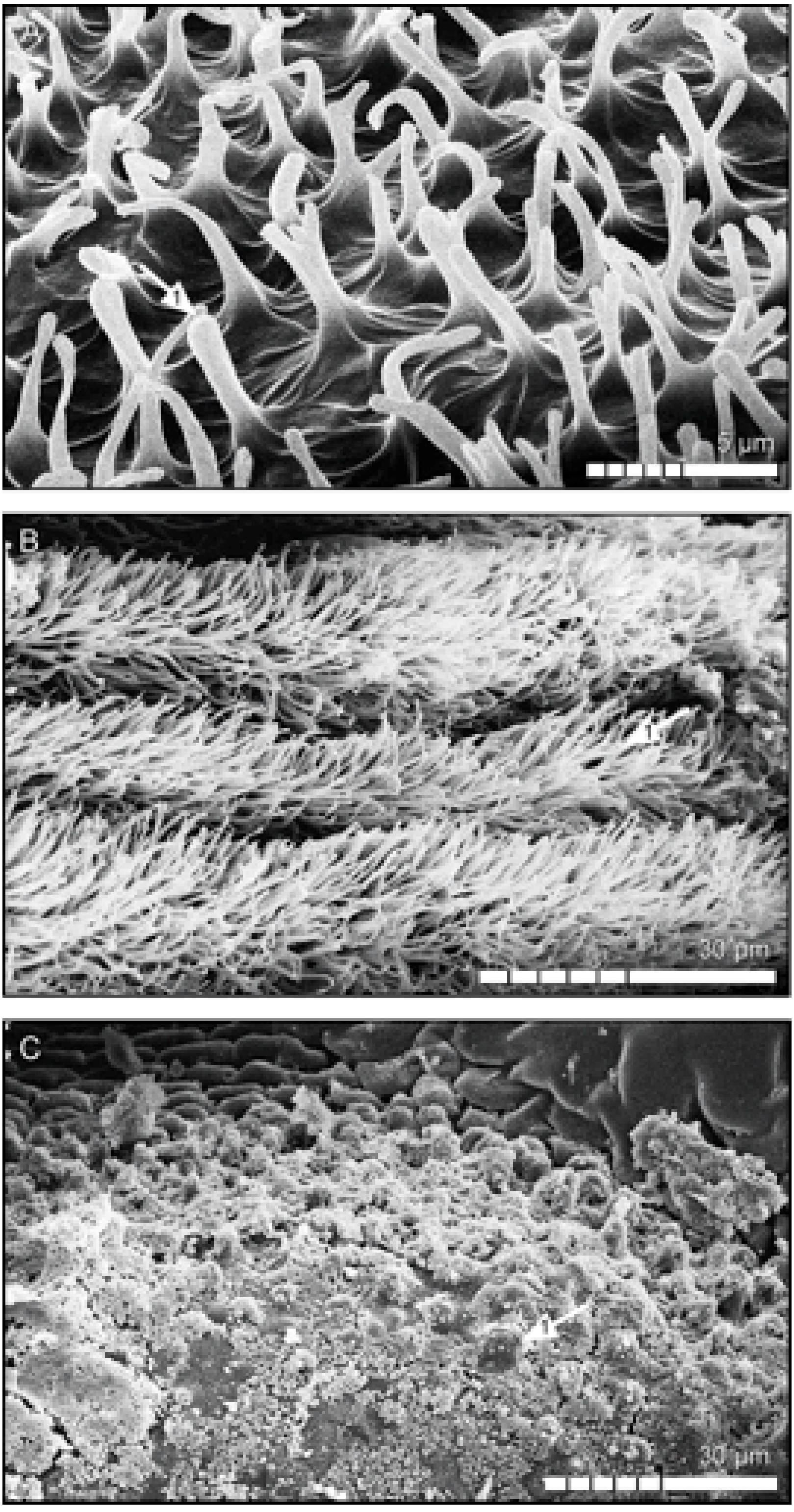

5 µm
B
30 µm
C
30 µm

Plate 72. *Brotheas granulatus* Simon, 1877, 1 ♂ (MNHN RS 8508): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae densely covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with flat hillocklike to subconical structures (arrow) with apical teeth, anterior view. Numbers in arrows refer to character states.

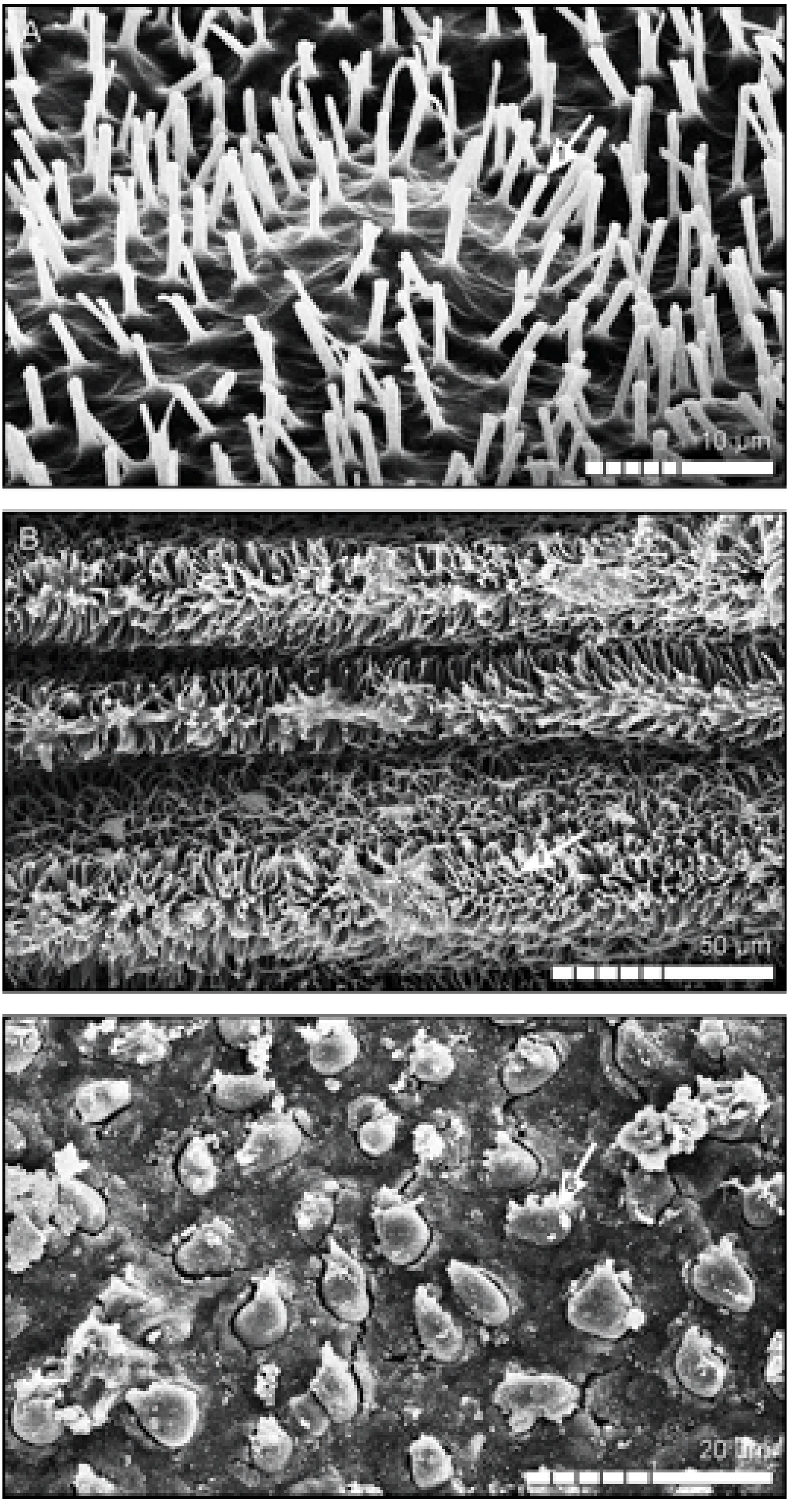

A
10 µm
B
50 µm
20 µm

Plate 73. *Chactas raymondhansi* Francke and Boos, 1986, 1 subad. ♀ (AMNH [LP 1586]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** arcuate distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with subconical structures (arrow), anterior view. Numbers in arrows refer to character states.

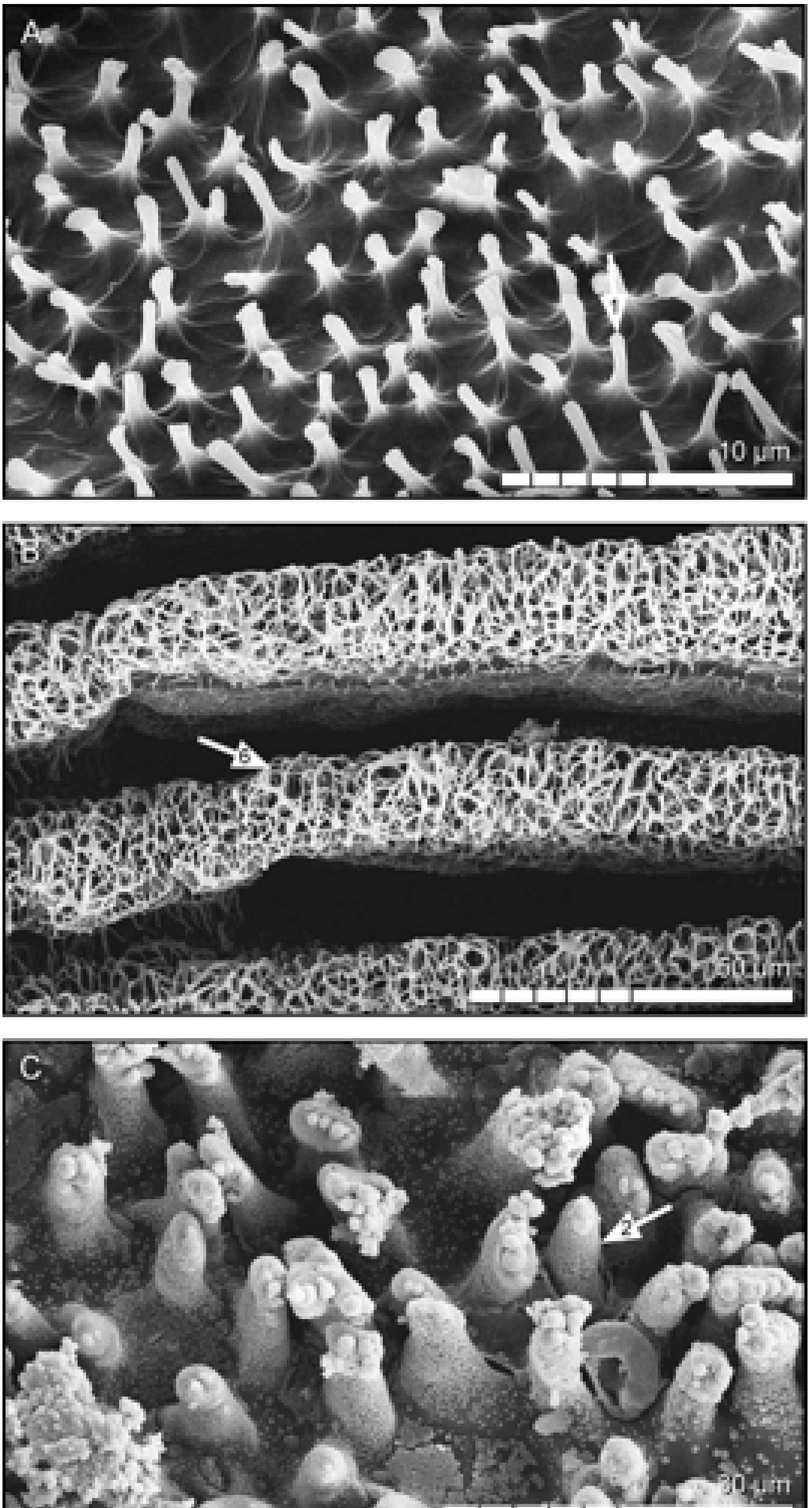

A
10 µm
B
C

Plate 74. *Chactas reticulatus* Kraepelin, 1912, 1 ♀ (MNHN RS 0775): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** arcuate distal edge of book lung lamella (arrow), posterior view; **C.** movable posterior edge of spiracle with chisel-like structures (arrow), anterior view. Numbers in arrows refer to character states.

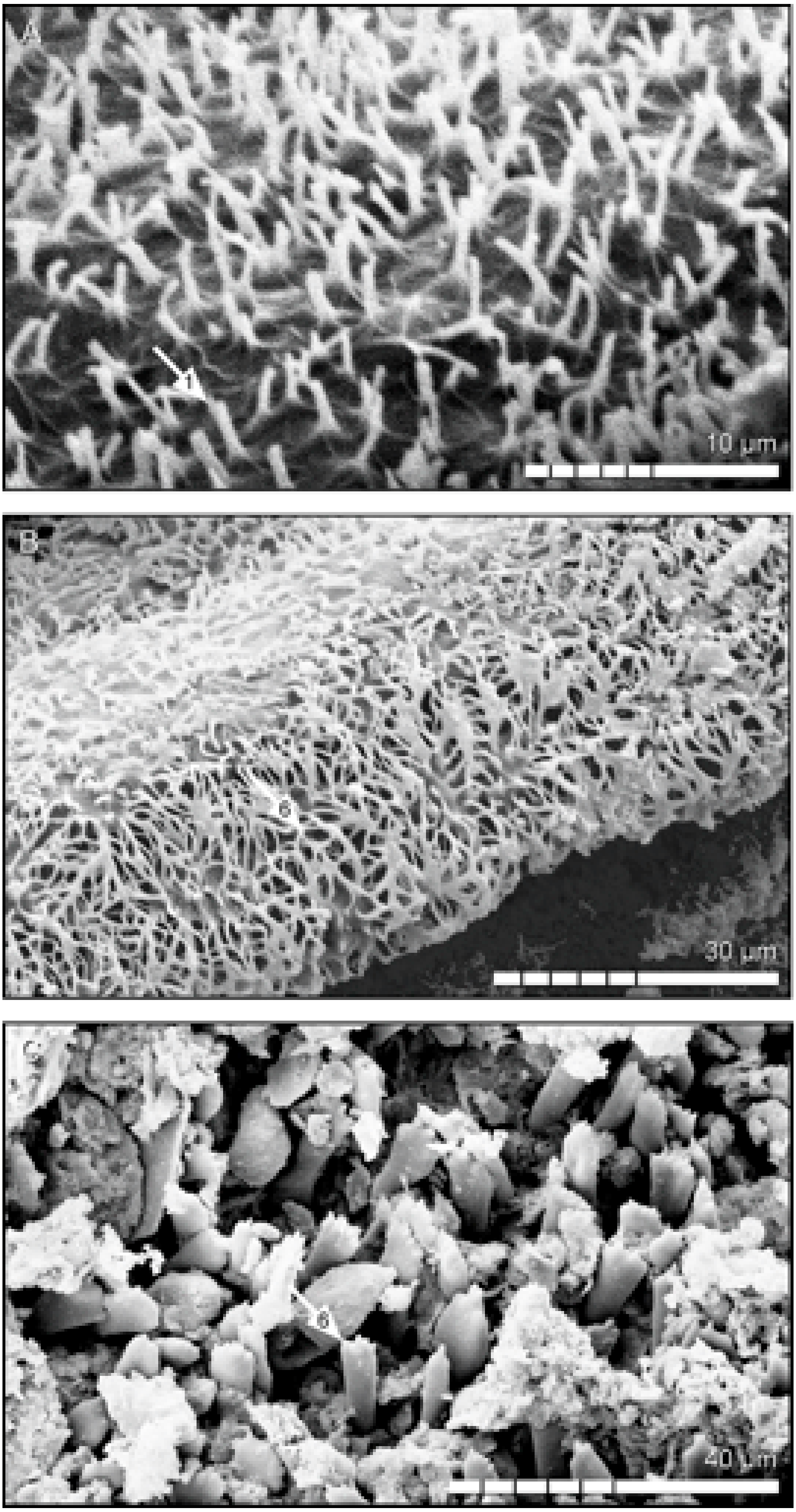

A
10 µm
B
30 µm
C
40 µm

Plate 75. *Guyanochactas gonzalezspongai* (Lourenço, 1983), 1 ♀ (AMNH [LP 3435]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae densely covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with hillocklike structures (arrow) with small teeth, anterior view. Numbers in arrows refer to character states.

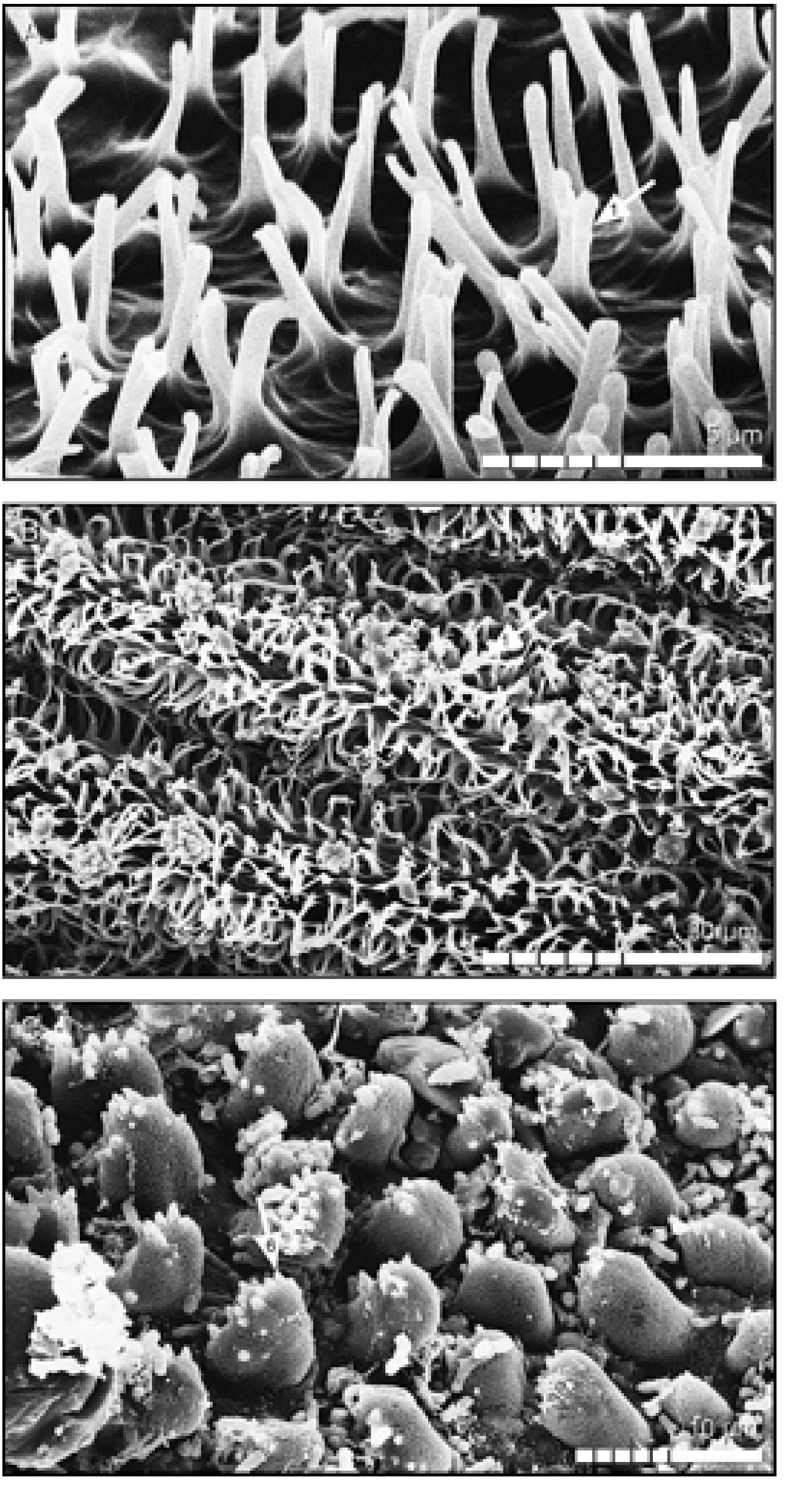


Plate 76. *Hadrurochactas schaumii* (Karsch, 1880), 1 ♀ (AMNH [LP 3680]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae densely covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with hillocklike structures (arrow) with small teeth, anterior view. Numbers in arrows refer to character states.

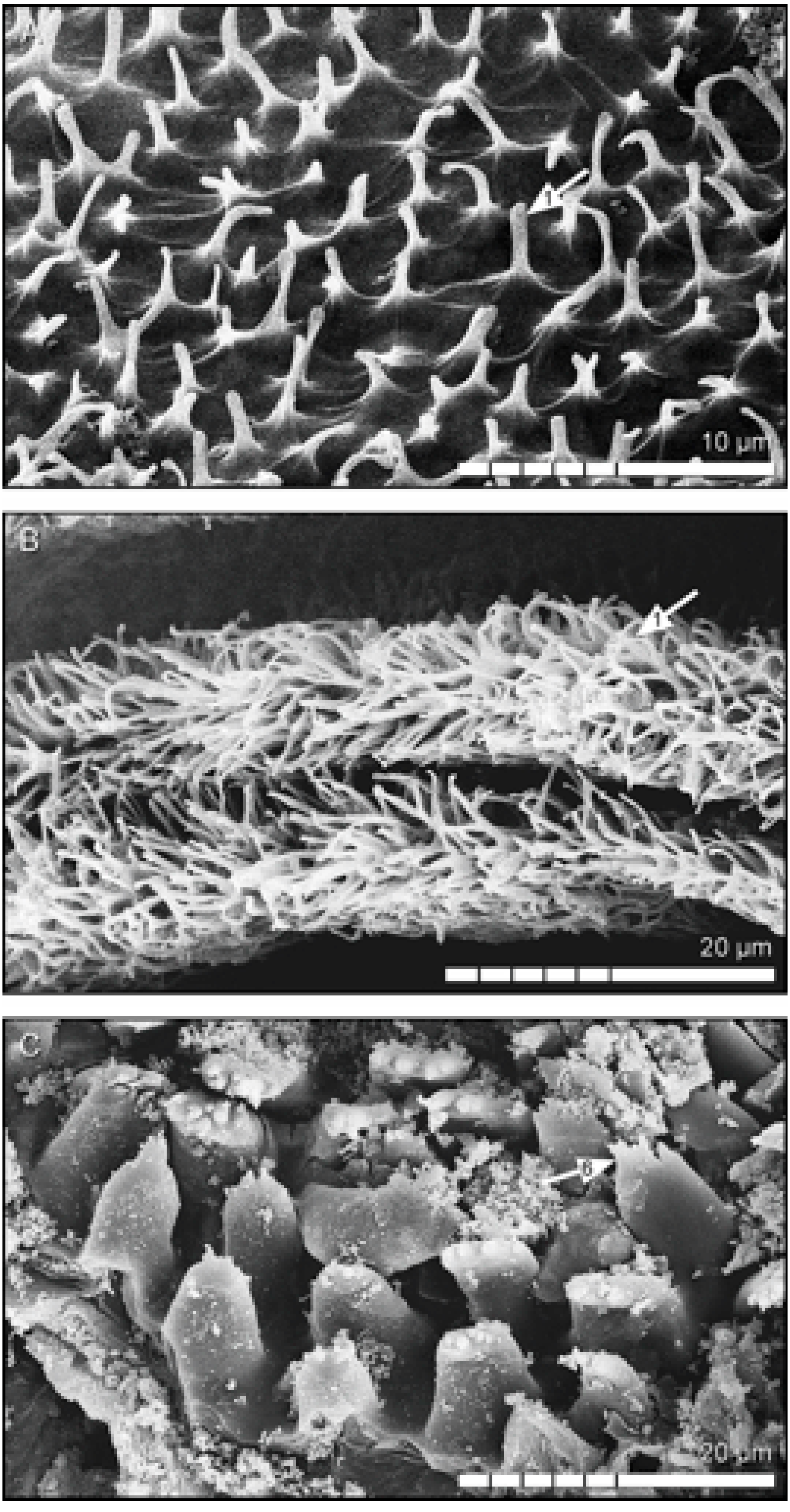

1
10 µm
B
1
20 µm
C
20 µm

Plate 77. *Nullibrotheas allenii* (Wood, 1863), 1 juv. ♂ (AMNH [LP 2869]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with spines (arrow), posterior view; **C.** movable posterior edge of spiracle with subconical structures (arrow), anterior view. Numbers in arrows refer to character states.

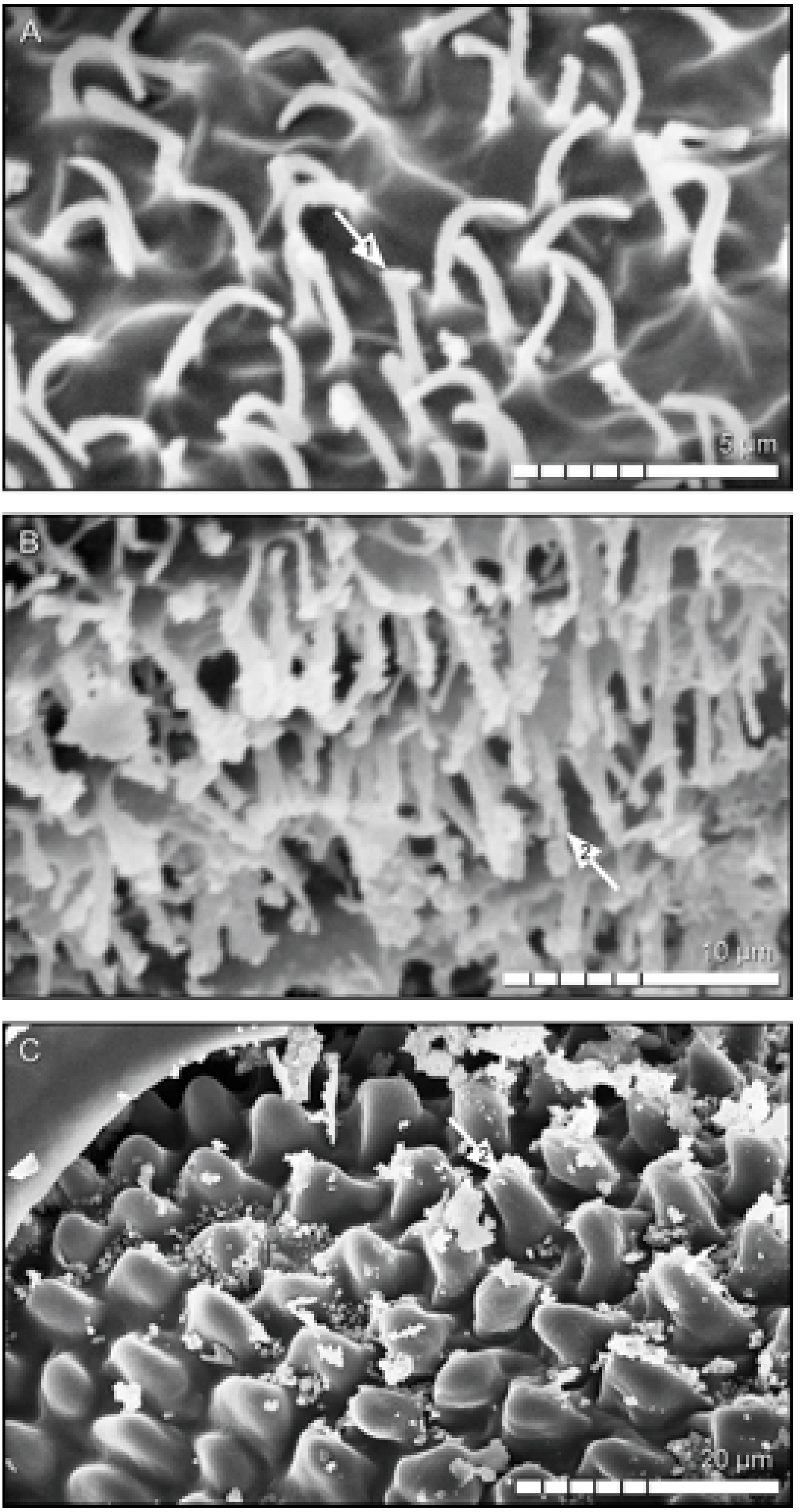

A
5 µm
B
10 µm
C
20 µm

Plate 78. *Teuthraustes gervaisii* (Pocock, 1893), 1 ♀ (AMNH [LP 1855]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** arcuate distal edge of one book lung lamella (arrow), posterior view; **C.** movable posterior edge of spiracle with clublike structures (arrow), anterior view. Numbers in arrows refer to character states.

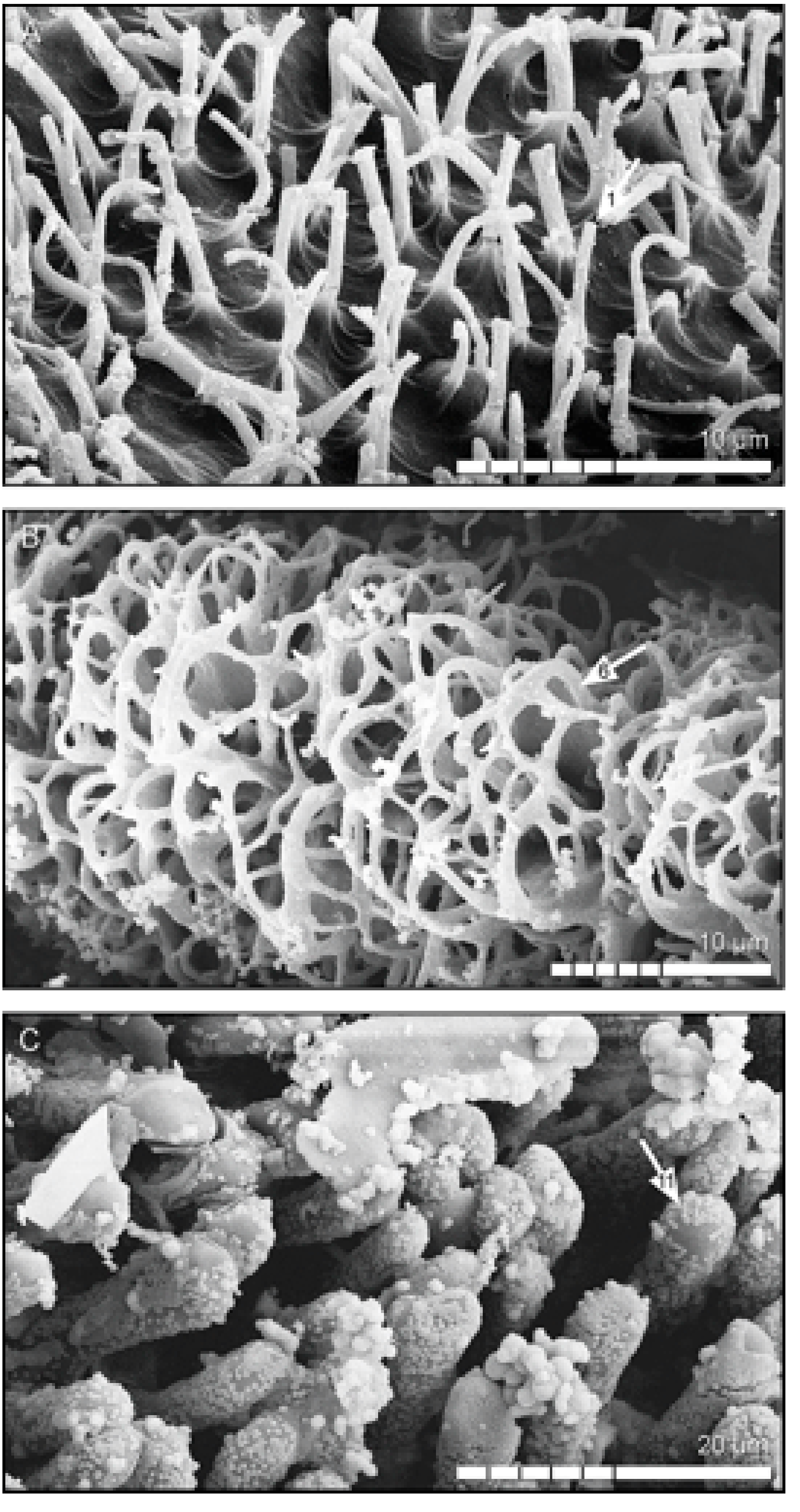
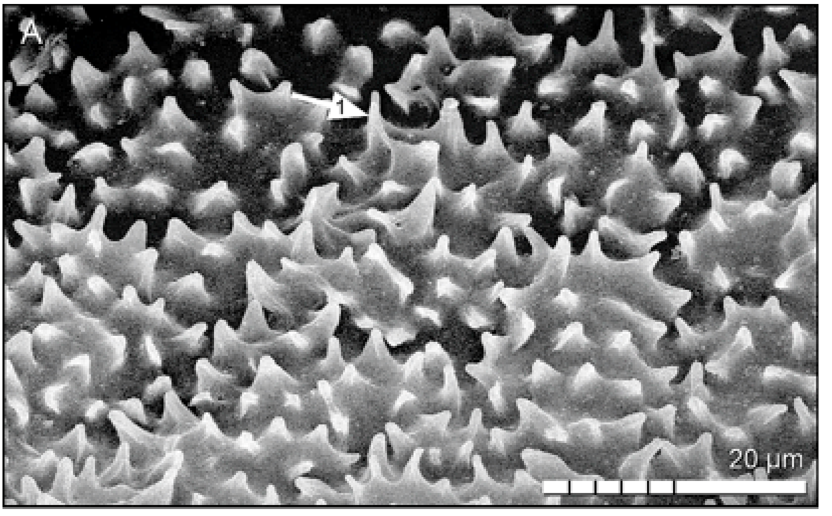

A
1
10 μm
B
6
10 μm
C
11
20 μm

Plate 79. *Alacran tartarus* Francke, 1982, 1 ♀ (AMNH [LP 3499]): **A.** ventral surface of book lung lamella covered with subconical to thornlike structures (arrow), viewed from air space; **B.** distal edges of book lung lamellae with meandering bulgelike structures (arrow) winding along edge, posterior view. Numbers in arrows refer to character states.


A
1
20 µm

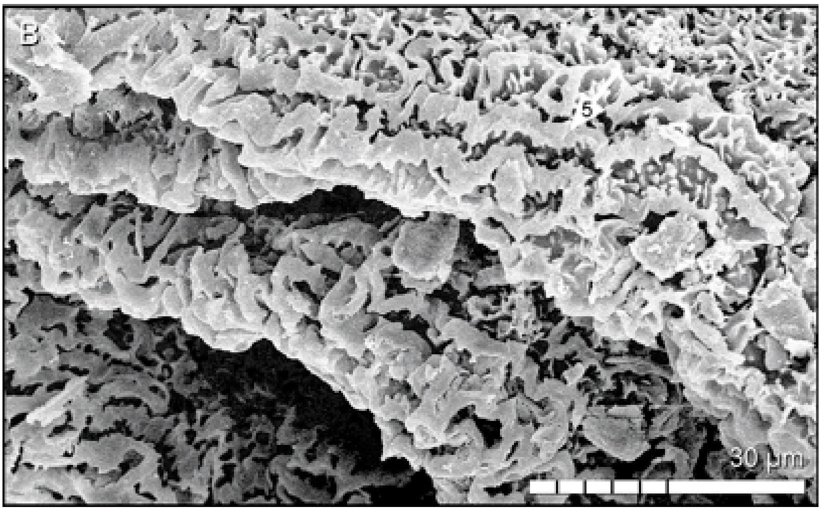

B
5
30 µm

Plate 80. *Superstitionia donensis* Stahnke, 1940, 1 ♀ (AMNH [LP 3420]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** arcuate distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with hillocklike structures (arrow), anterior view. Numbers in arrows refer to character states.

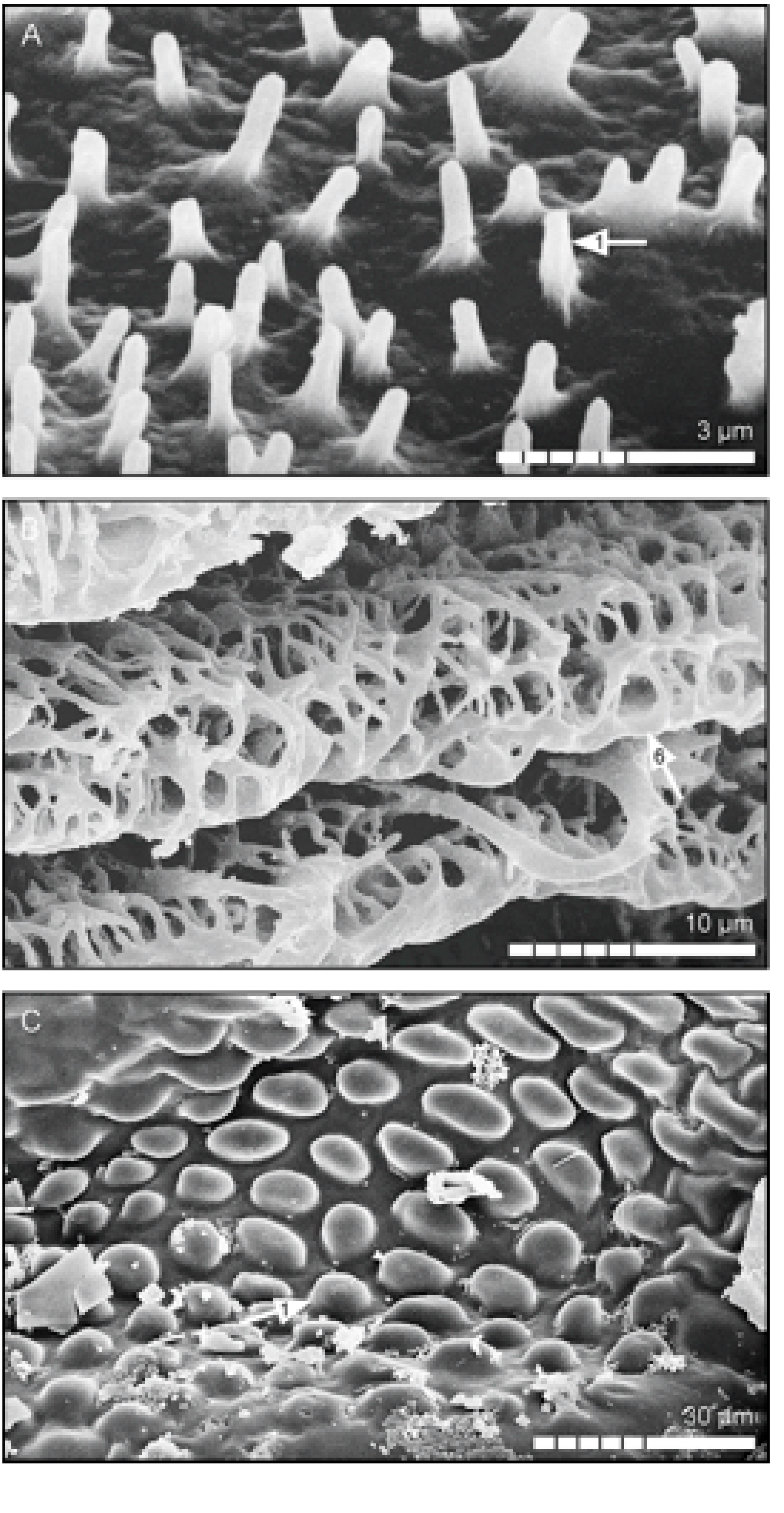

A
1
3 µm
B
6
10 µm
C
1
30 µm

Plate 81. *Belisarius xambeui* Simon, 1879, 1 ♀ (MNHN RS 7743): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae densely covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with flat hillocklike structures (arrow), anterior view. Numbers in arrows refer to character states.

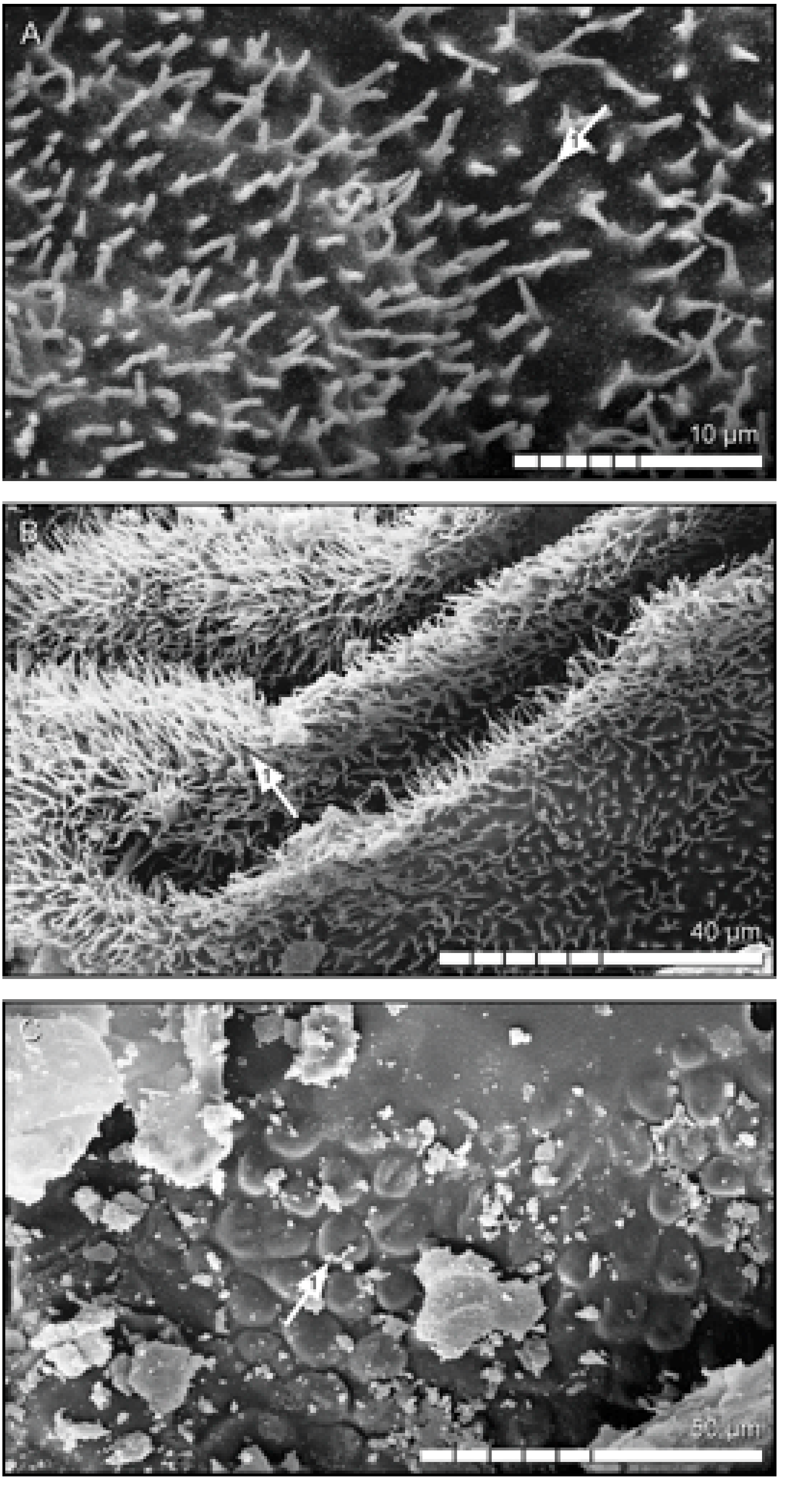

A
10 µm
B
40 µm
C
50 µm

Plate 82. *Paravaejovis pumilis* (Williams, 1970), 1 ♂ (AMNH): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with spines (arrow) and fused with atrial wall, posterior view; **C.** movable posterior edge of spiracle with hillocklike structures (arrow), anterior view. Numbers in arrows refer to character states.

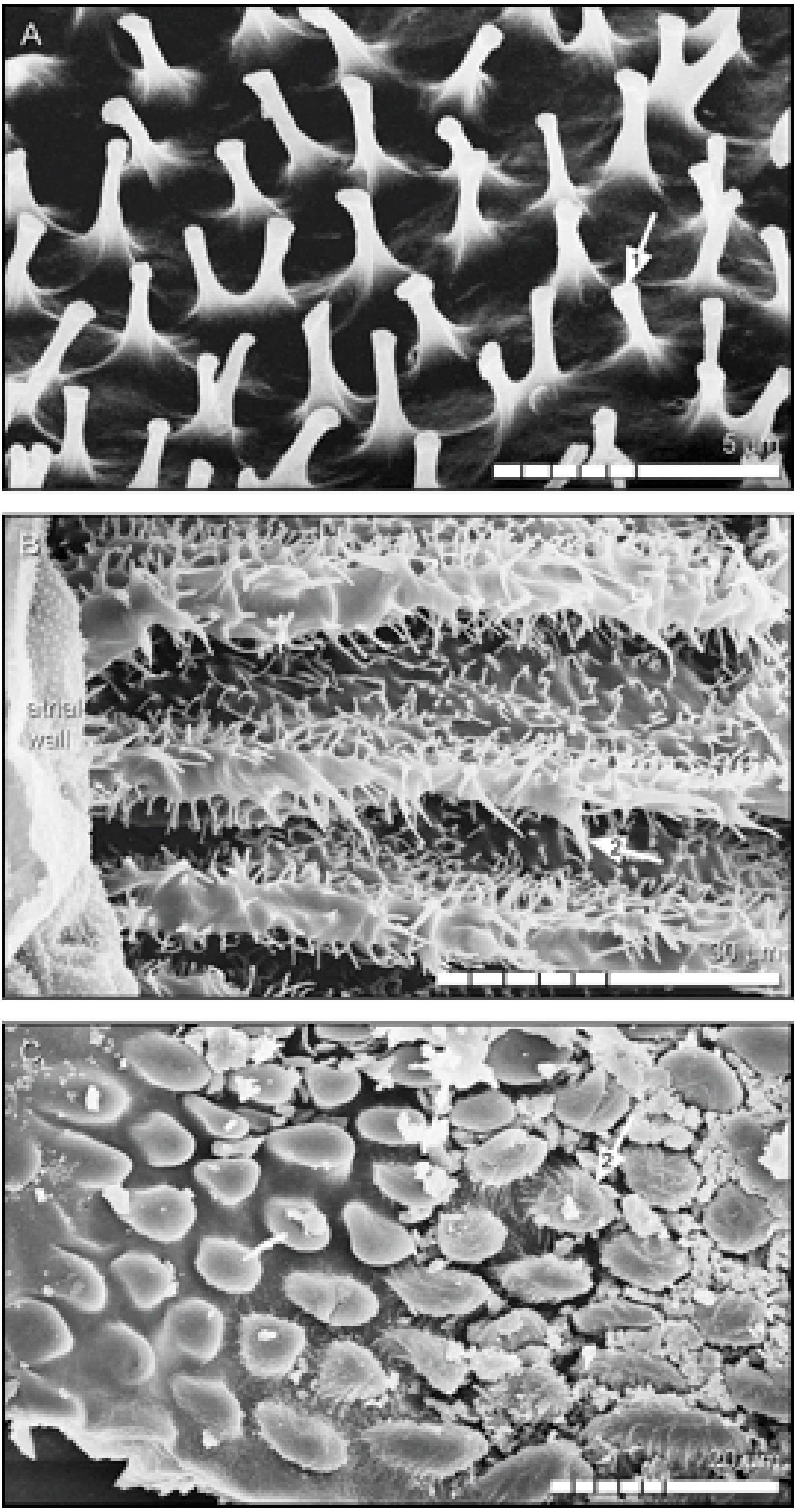

A
1
5 µm
B
atrial
wall
2
C
2

Plate 83. *Paruroctonus becki* (Gertsch and Allred, 1965), 1 juv. ♀ (AMNH [LP 4991]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with spines (arrow), posterior view; **C.** movable posterior edge of spiracle with polygonal columns (arrow), anterior view. Numbers in arrows refer to character states.

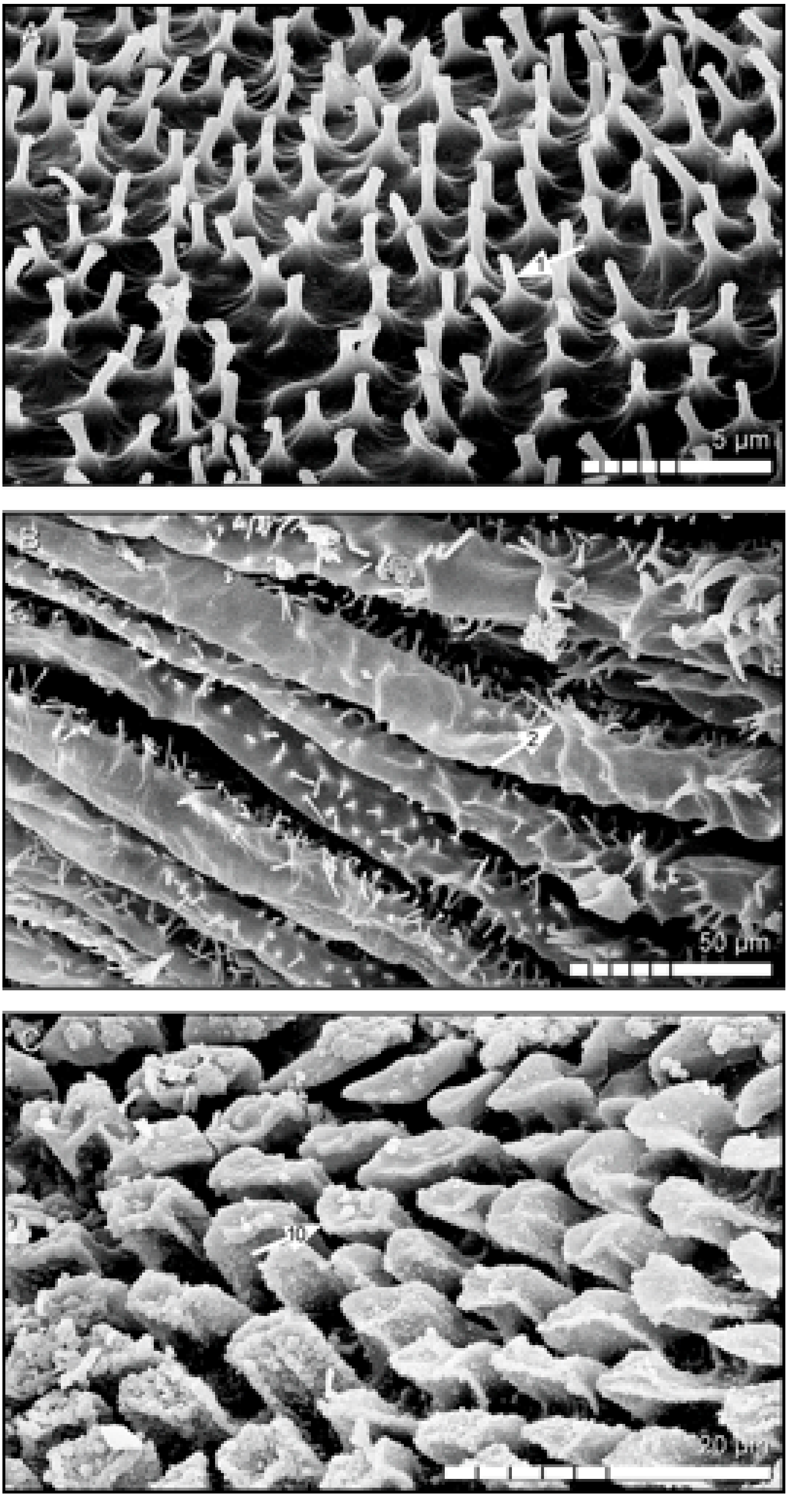

1
5 µm
2
50 µm
10
20 µm

Plate 84. *Paruroctonus boreus* (Girard, 1854), 1 ♂ (AMNH [LP 4388]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with spines (arrow), posterior view; **C.** movable posterior edge of spiracle with polygonal columns (arrow), anterior view. Numbers in arrows refer to character states.

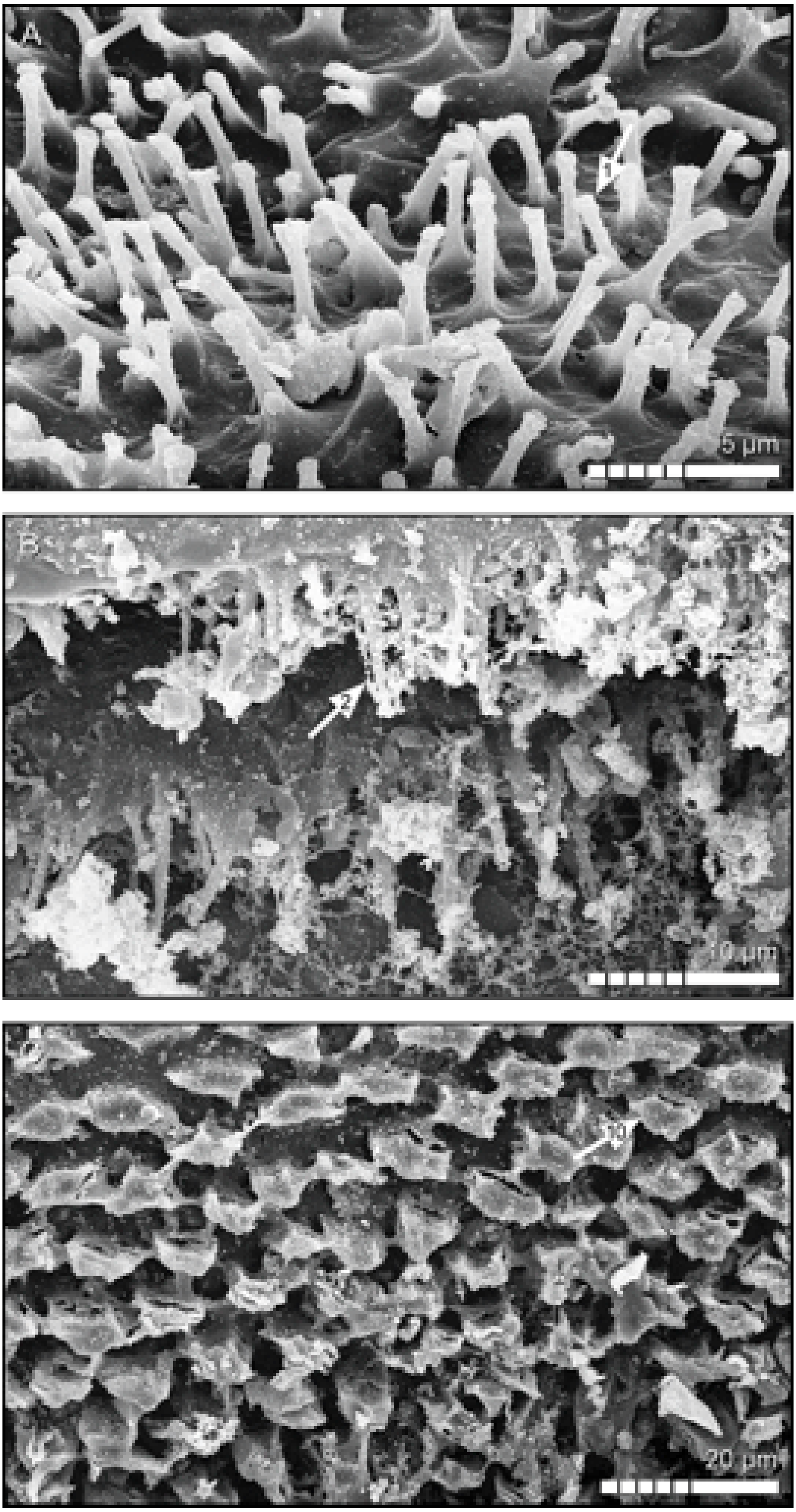

A
5 µm
B
10 µm
20 µm

Plate 85. *Paruroctonus borregoensis borregoensis* Williams, 1972, 1 ♀ (AMNH [LP 4530]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with spines (arrow), posterior view; **C.** movable posterior edge of spiracle with polygonal columns (arrow), anterior view. Numbers in arrows refer to character states.

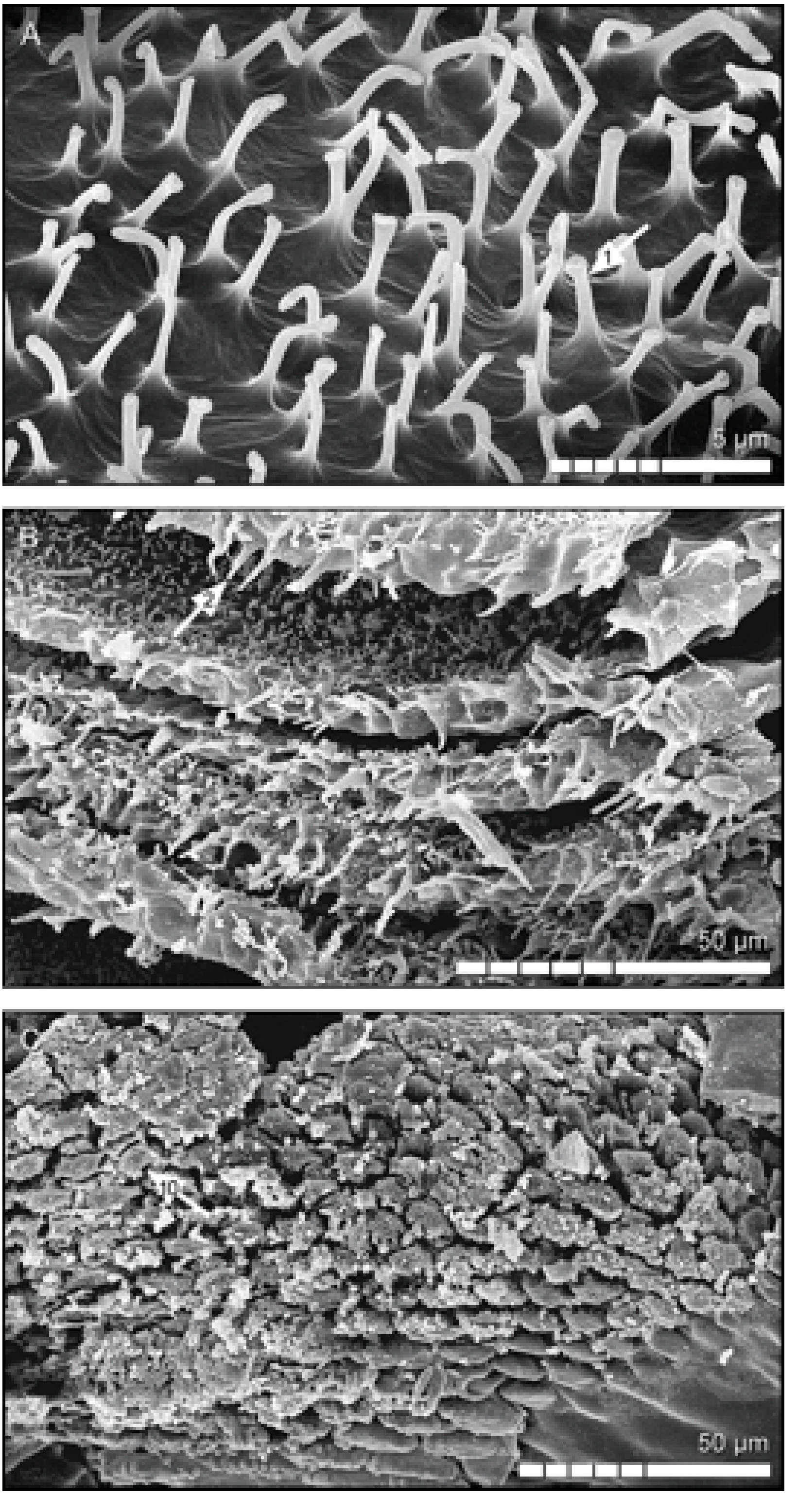

A
5 µm
B
50 µm
C
50 µm

Plate 86. *Paruroctonus gracilior* (Hoffmann, 1931), 1 ♀ (AMNH [LP 2213]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with spines (arrow), posterior view; **C.** movable posterior edge of spiracle with polygonal columns (arrow), anterior view. Numbers in arrows refer to character states.

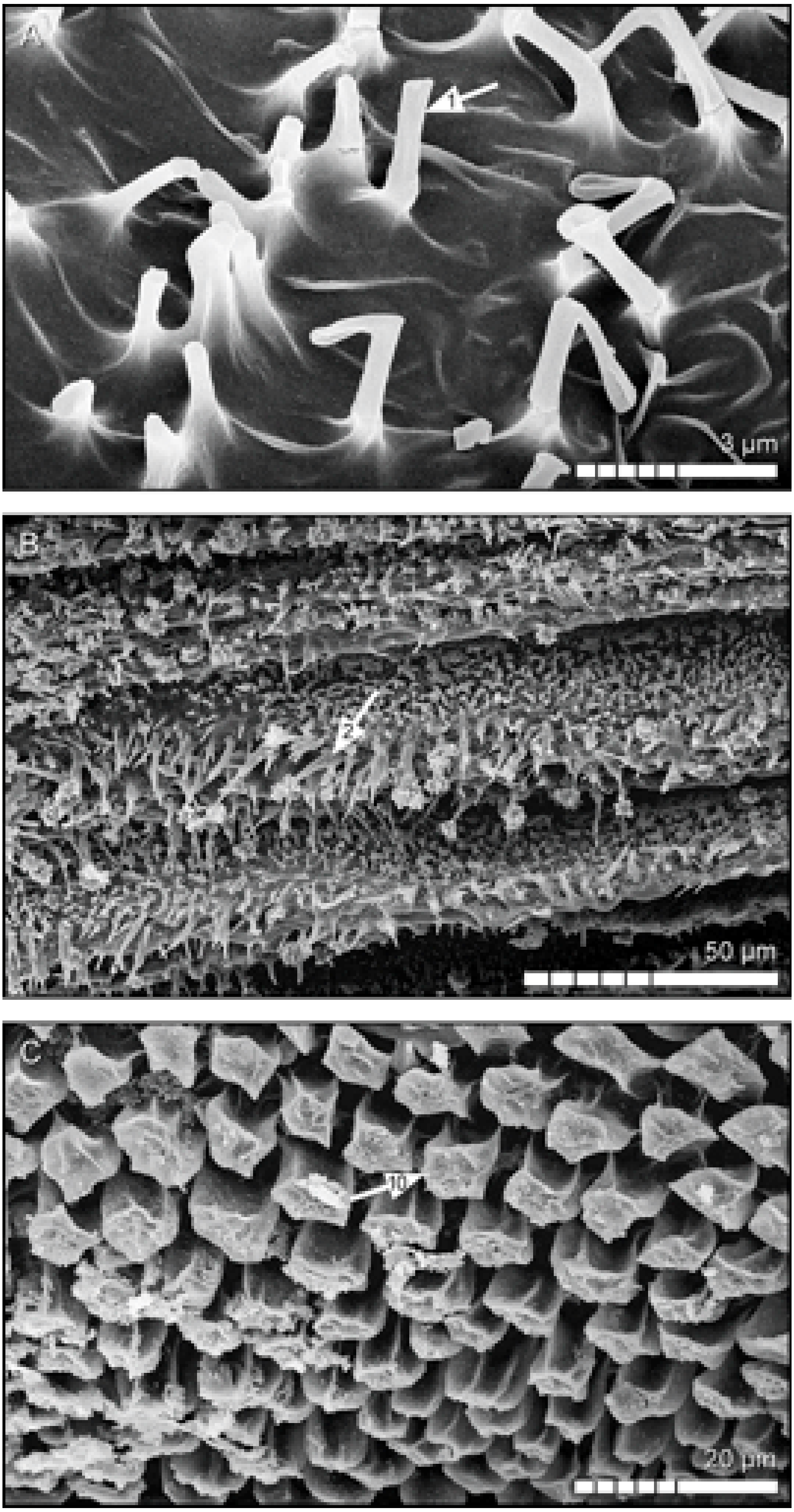

A
1
3 µm
B
2
50 µm
C
10
20 µm

Plate 87. *Paruroctonus gracilior* (Hoffmann, 1931), 1 ♀ (AMNH [LP 2152]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with spines (arrow) and fused with atrial wall, posterior view; **C.** movable posterior edge of spiracle with polygonal columns (arrow), anterior view. Numbers in arrows refer to character states.

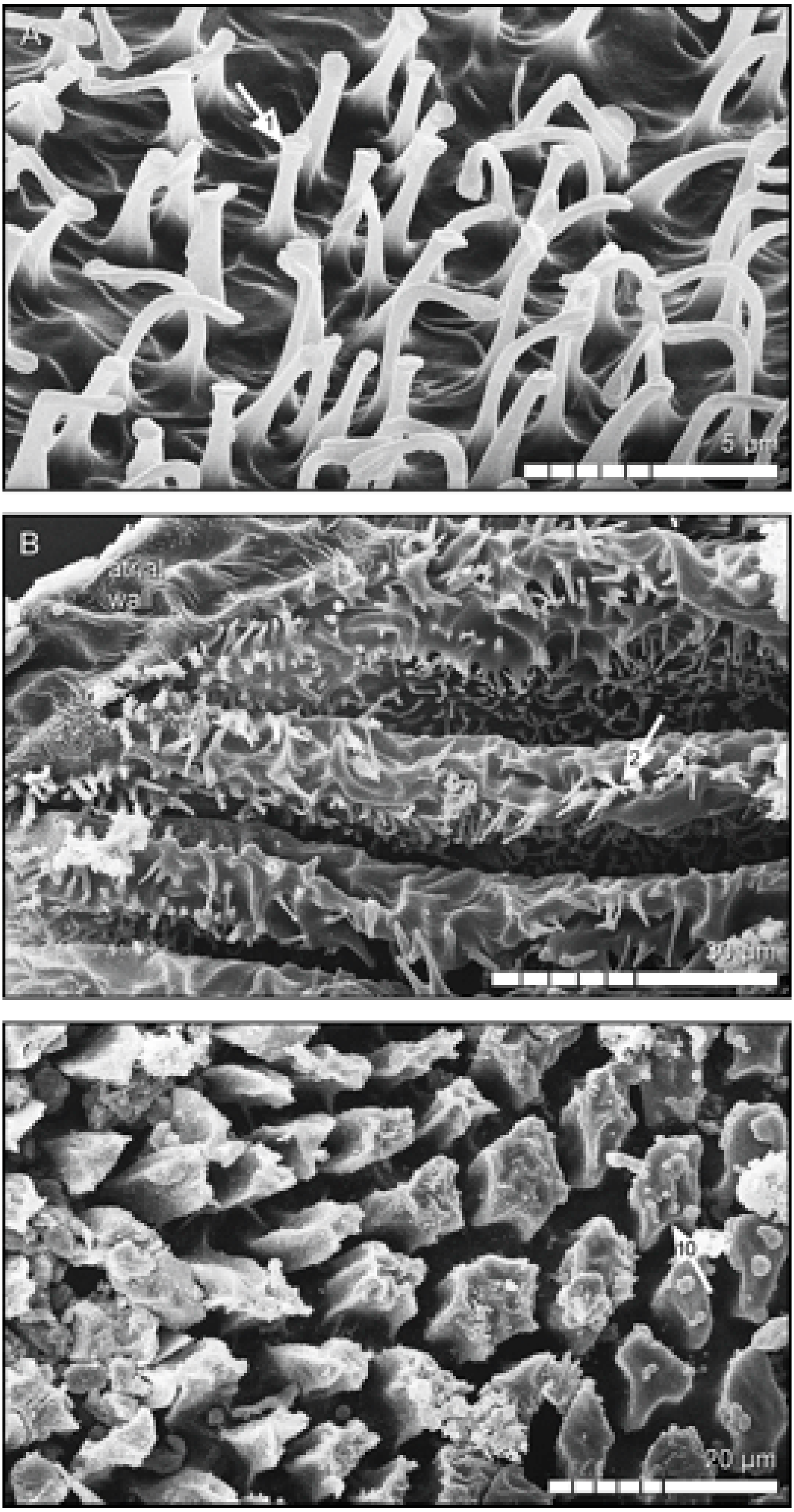

A
1
5 µm
B
atrial
wall
2
10
20 µm

Plate 88. *Paruroctonus stahnkei* (Gertsch and Soleglad, 1966), 1 ♂ (AMNH [LP 3566]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with spines (arrow), posterior view; **C.** movable posterior edge of spiracle with polygonal columns (arrow), anterior view. Numbers in arrows refer to character states.

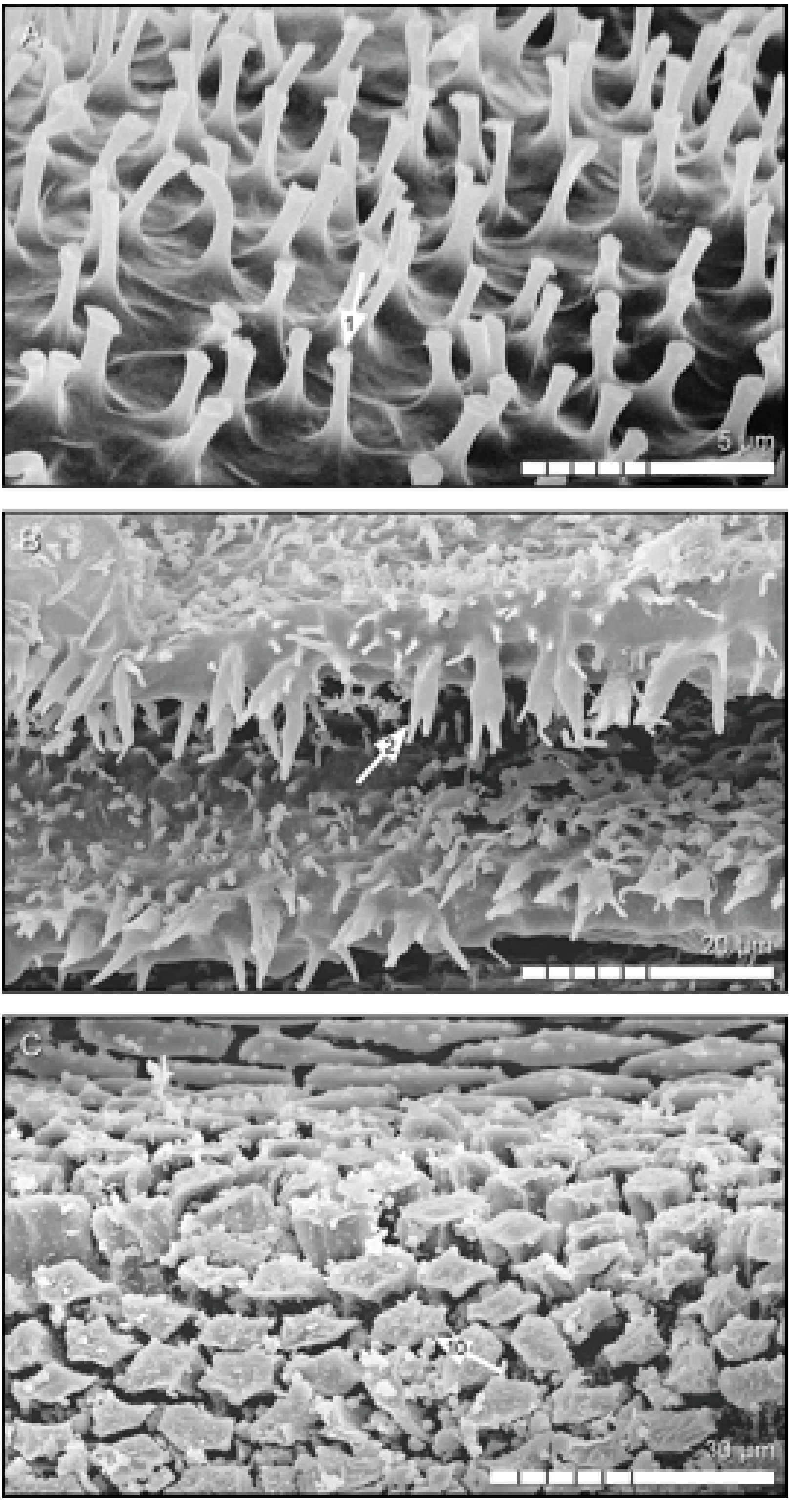

A
1
5 μm
B
20 μm
C
30 μm

Plate 89. *Pseudouroctonus apacheanus* (Gertsch and Soleglad, 1972), 1 ♀ (AMNH): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with broad, flattened lobelike structures (arrow), anterior view. Numbers in arrows refer to character states.

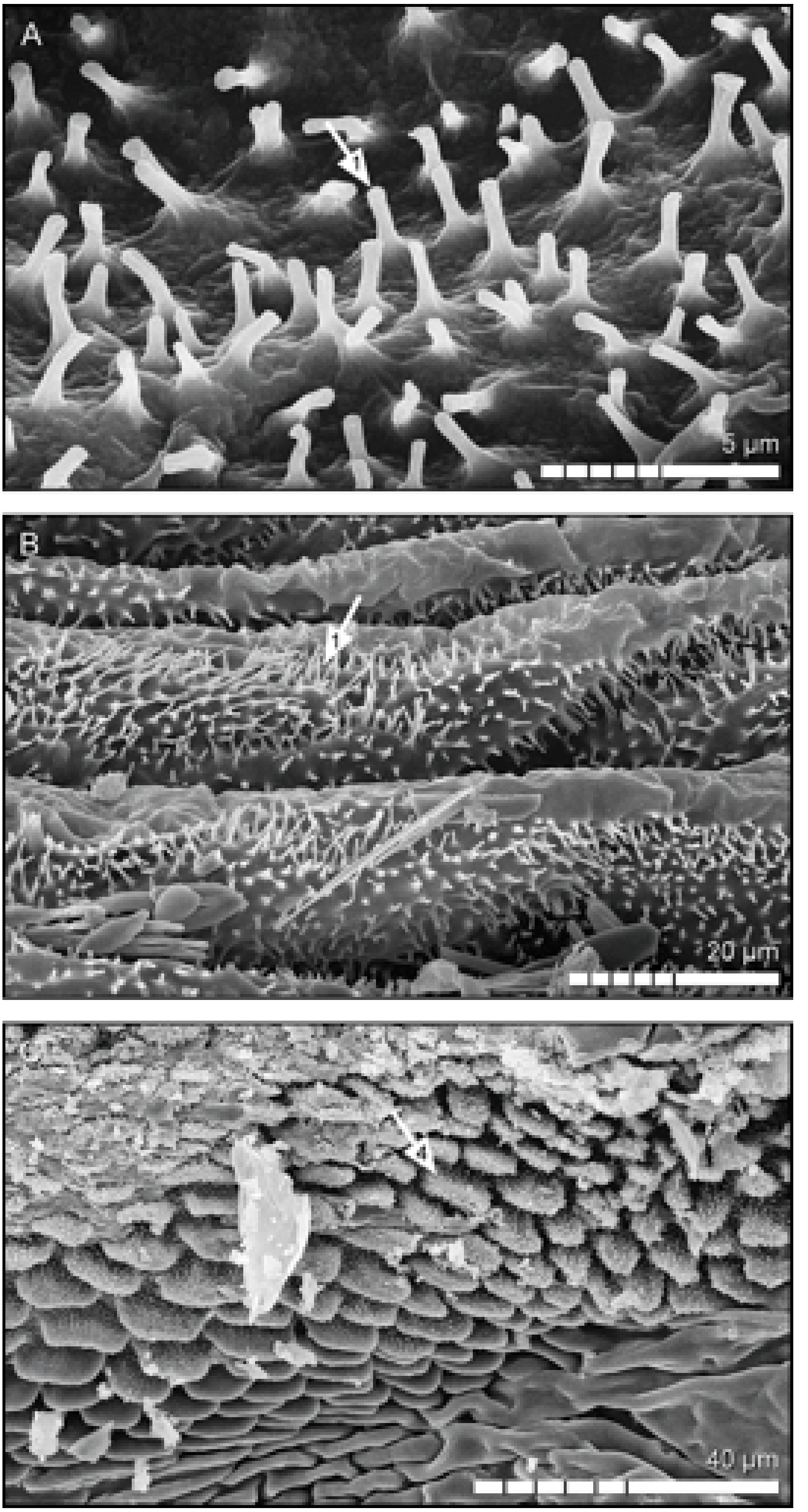

A
5 µm
B
20 µm
40 µm

Plate 90. *Pseudouroctonus reddelli* (Gertsch and Soleglad, 1972), 1 ♀ (AMNH [LP 2155]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** wrinkled distal edges of book lung lamellae covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with broad, flattened hillocklike structures (arrow), covered with wartlike spines, anterior view. Numbers in arrows refer to character states.

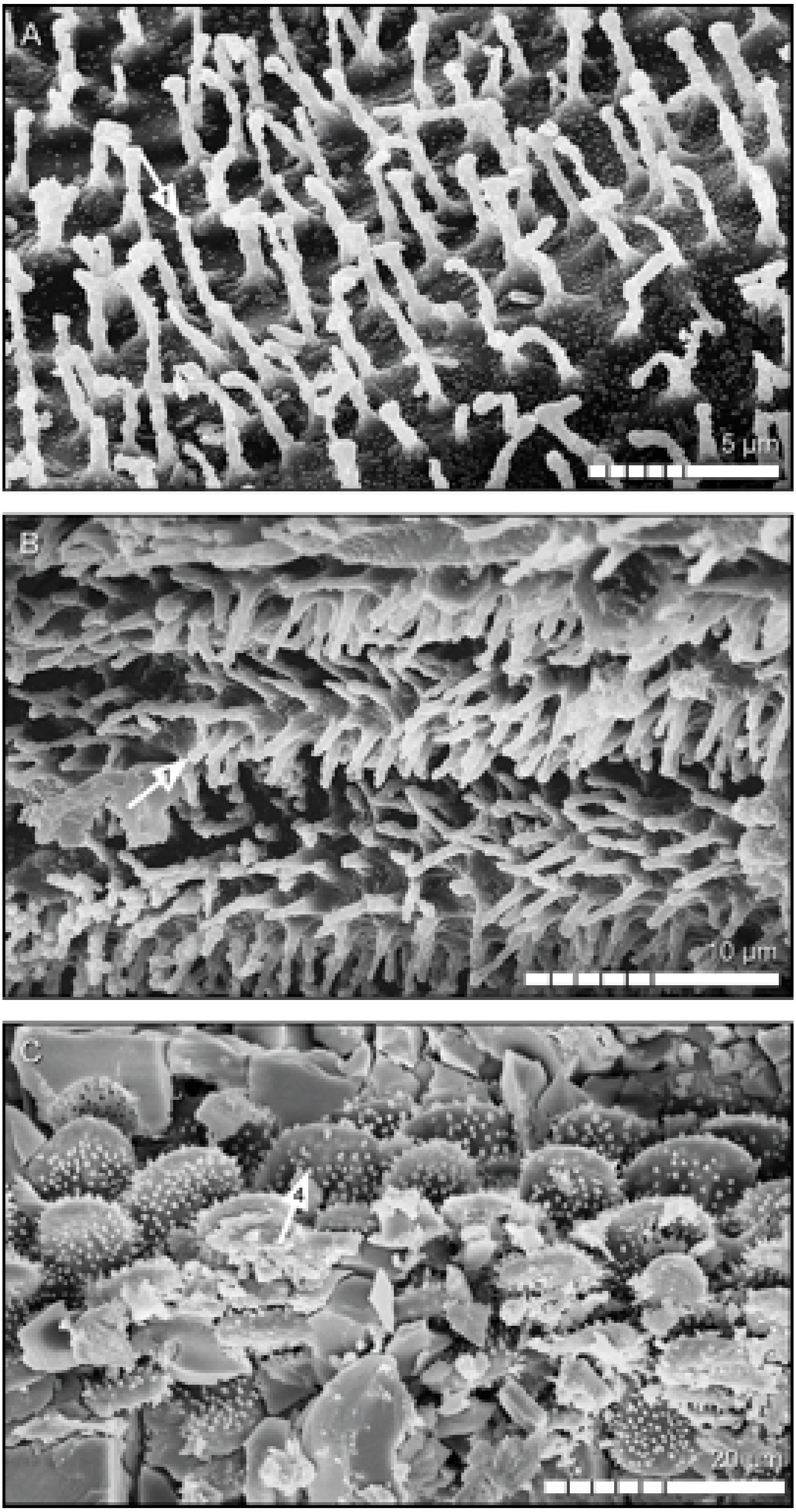

A
1
5 µm
B
1
10 µm
C
4
20 µm

Plate 91. *Serradigitus wupatkiensis* (Stahnke, 1940), 1 ♂ (AMNH [LP 3216]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with spines (arrow) and fusion of adjacent lamellae at edges of air sacs, posterior view; **C.** movable posterior edge of spiracle with broad, hillocklike structures (arrow), anterior view. Numbers in arrows refer to character states.

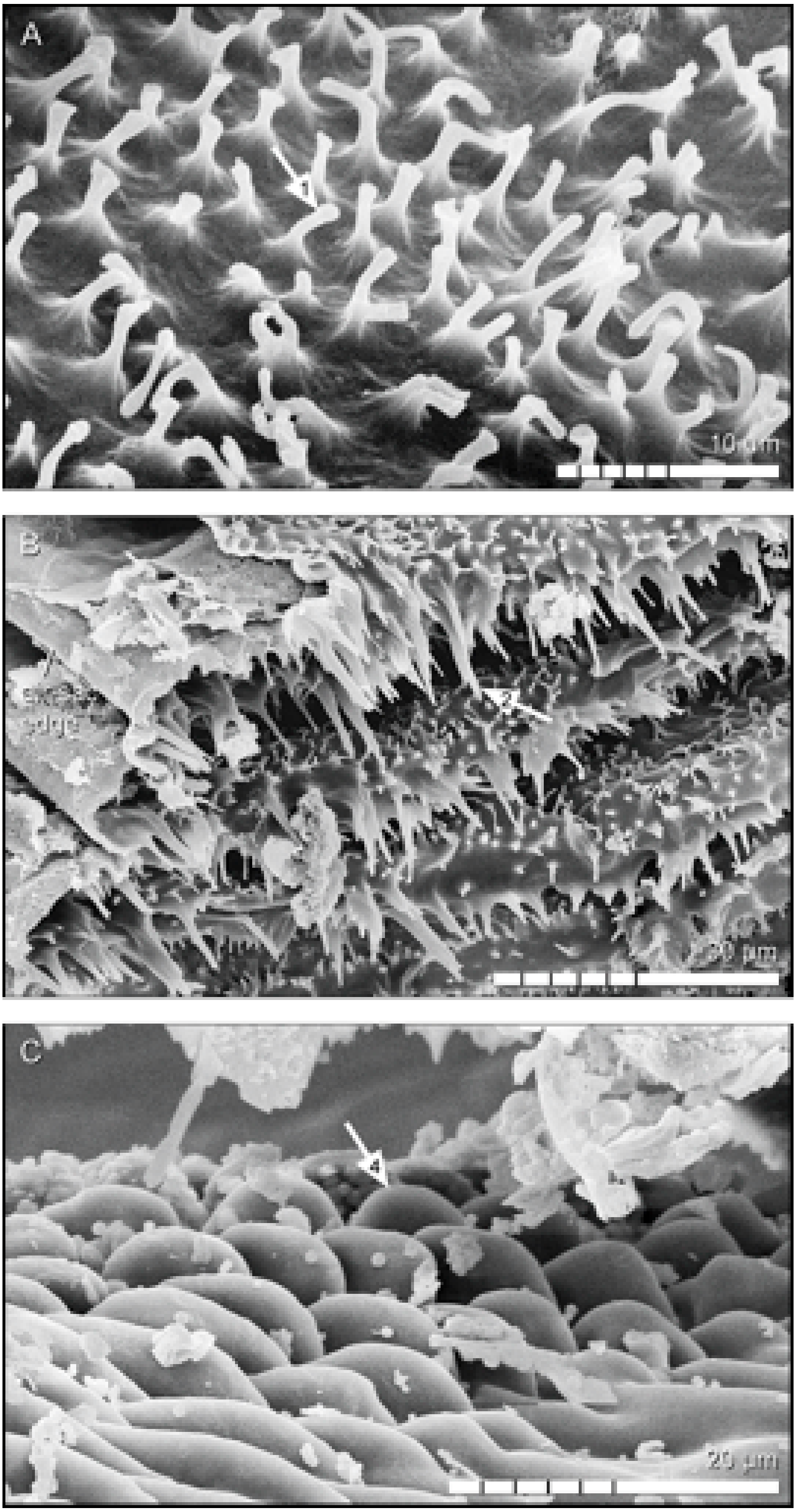

A
10 µm
B
20 µm
C
4
20 µm

Plate 92. *Smeringurus vachoni vachoni* (Stahnke, 1961), 1 ♂ (AMNH [LP 2684]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with spines (arrow), sometimes with single branch, posterior view; **C.** movable posterior edge of spiracle with broad, flattened lobelike structures (arrow), anterior view. Numbers in arrows refer to character states.

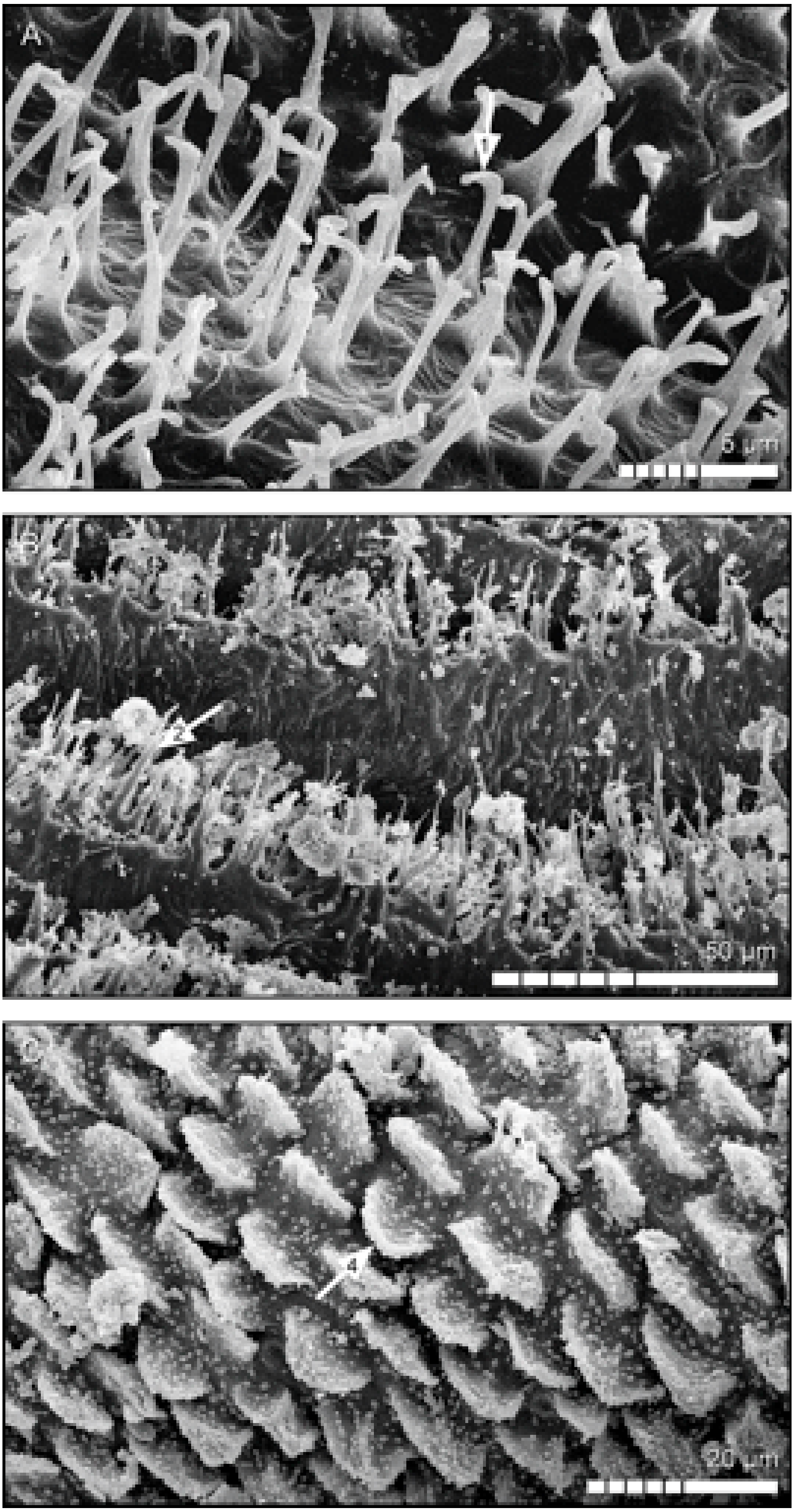

A
5 µm
B
2
50 µm
C
4
20 µm

Plate 93. *Syntropis macrura* Kraepelin, 1900, 1 juv. ♂ (AMNH [LP 4729]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with spines (arrow), posterior view; **C.** movable posterior edge of spiracle with broad, flattened lobelike structures (arrow), anterior view. Numbers in arrows refer to character states.

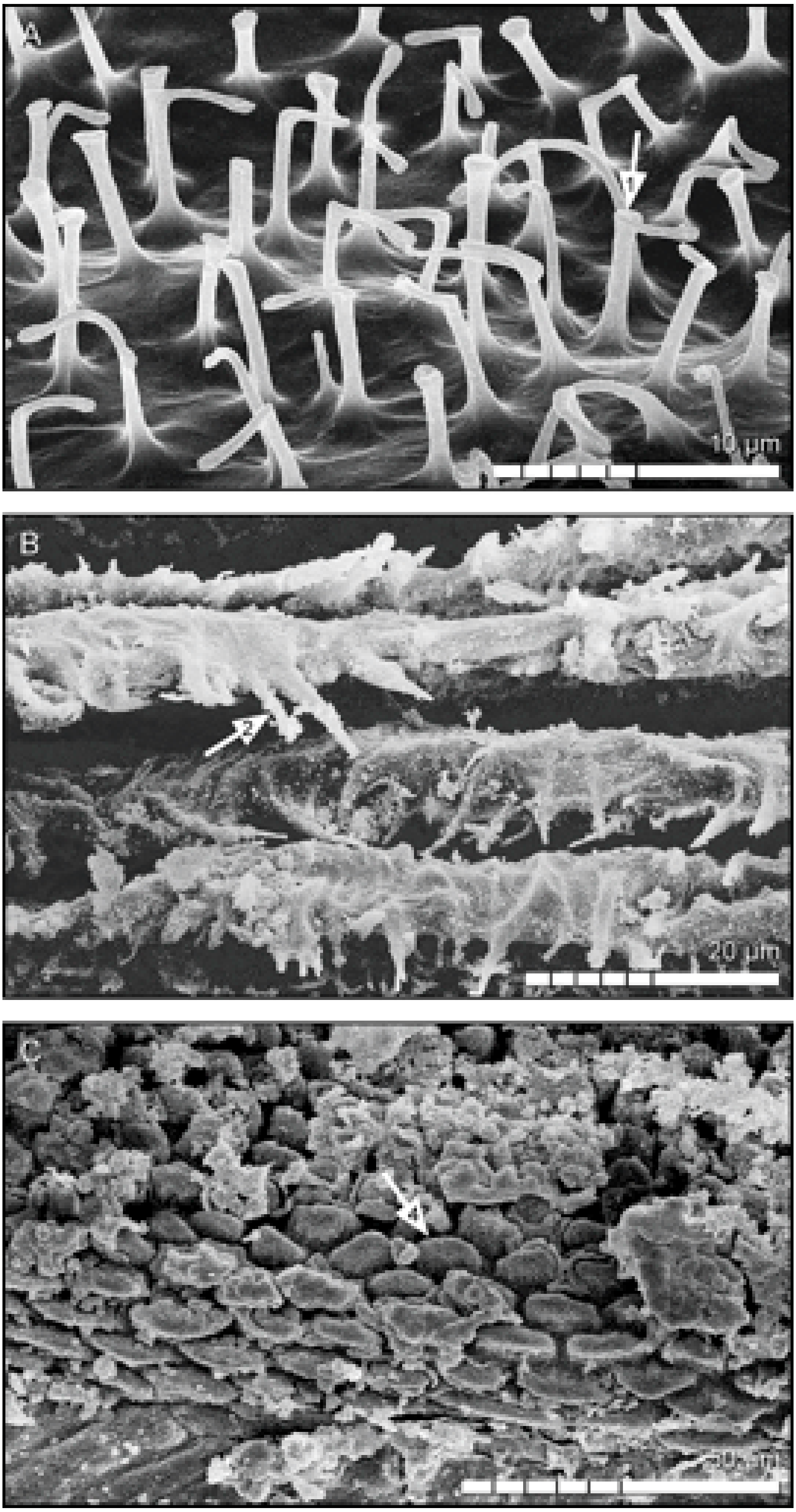

A
10 µm
B
20 µm
C

Plate 94. *Uroctonites huachuca* (Gertsch and Soleglad, 1972), 1 ♀ (AMNH): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with broad, thorny hillocklike structures (arrow), posterior view. Numbers in arrows refer to character states.

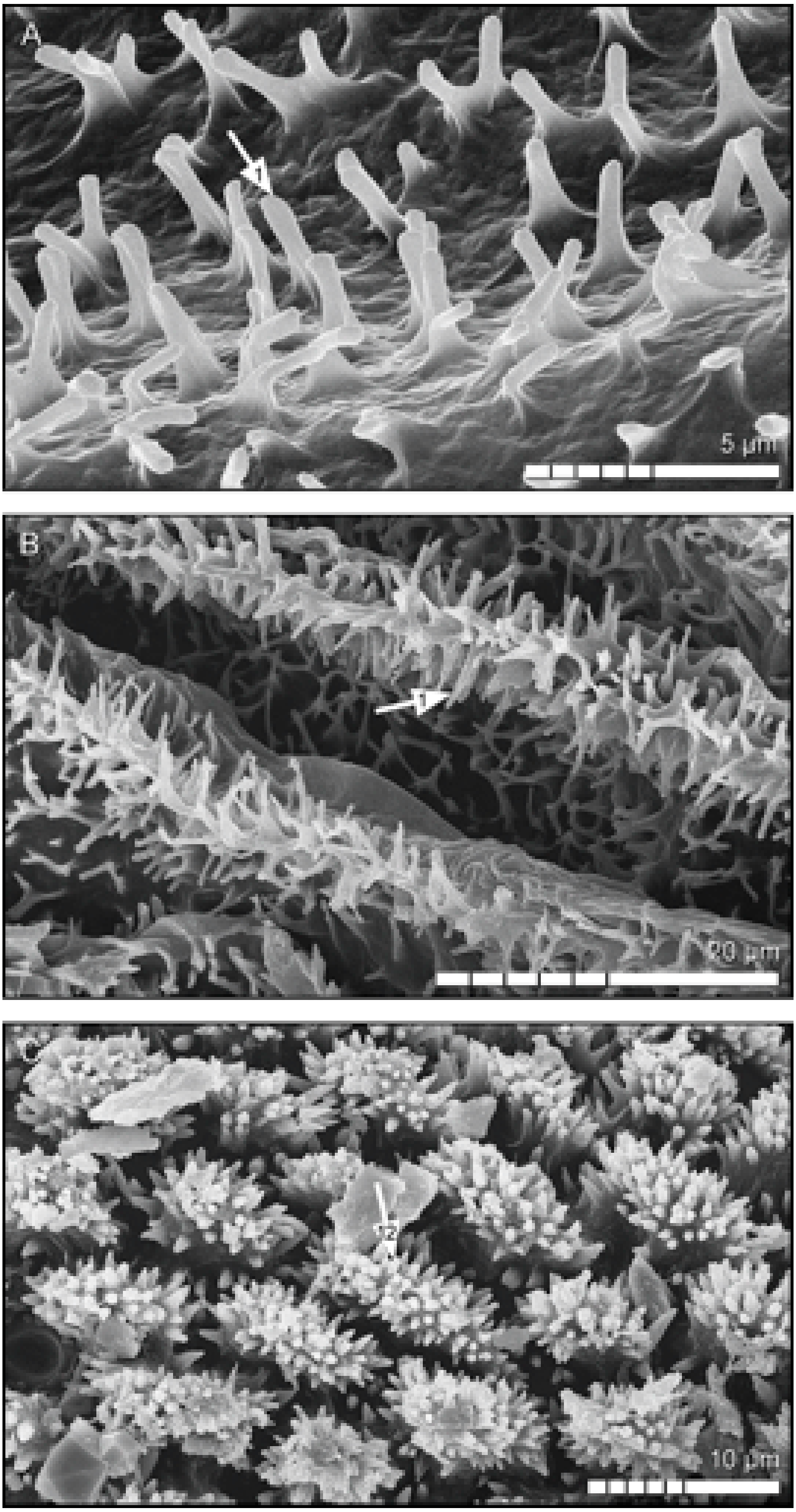

A
5 µm
B
20 µm
C
10 µm

Plate 95. *Uroctonus mordax mordax* Thorell, 1876, 1 ♂ (AMNH [LP 1595]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** arcuate distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with hillocklike structures (arrow), anterior view. Numbers in arrows refer to character states.

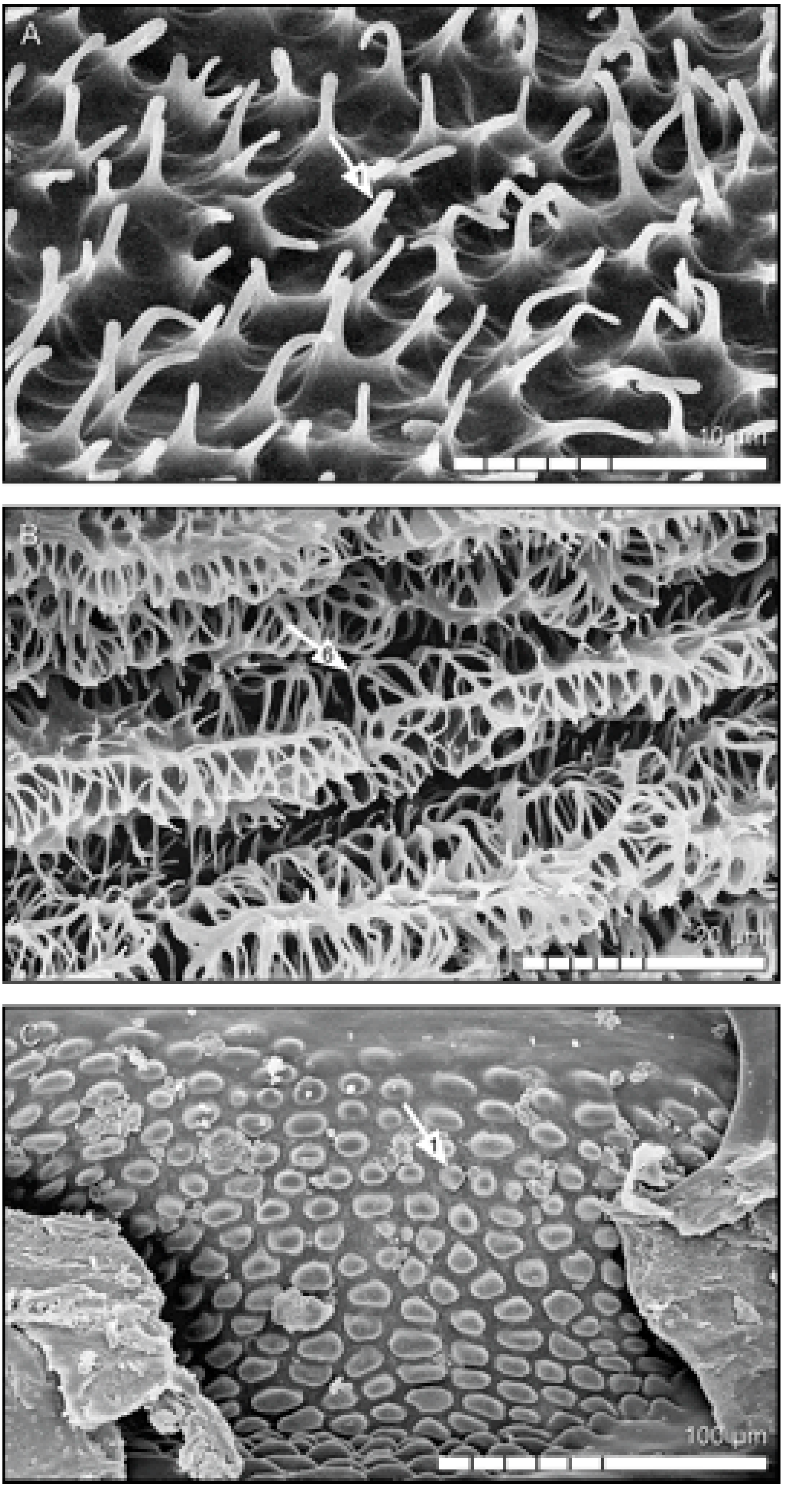

A
1
10 µm
B
6
20 µm
C
1
100 µm

Plate 96. *Vaejovis magdalensis* Williams, 1971, 1 ♀ (AMNH [LP 3155]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), sometimes with single branch, viewed from air space; **B.** distal edges of book lung lamellae covered with spines (arrow), sometimes branched, posterior view; **C.** movable posterior edge of spiracle with subconical structures (arrow), anterior view. Numbers in arrows refer to character states.

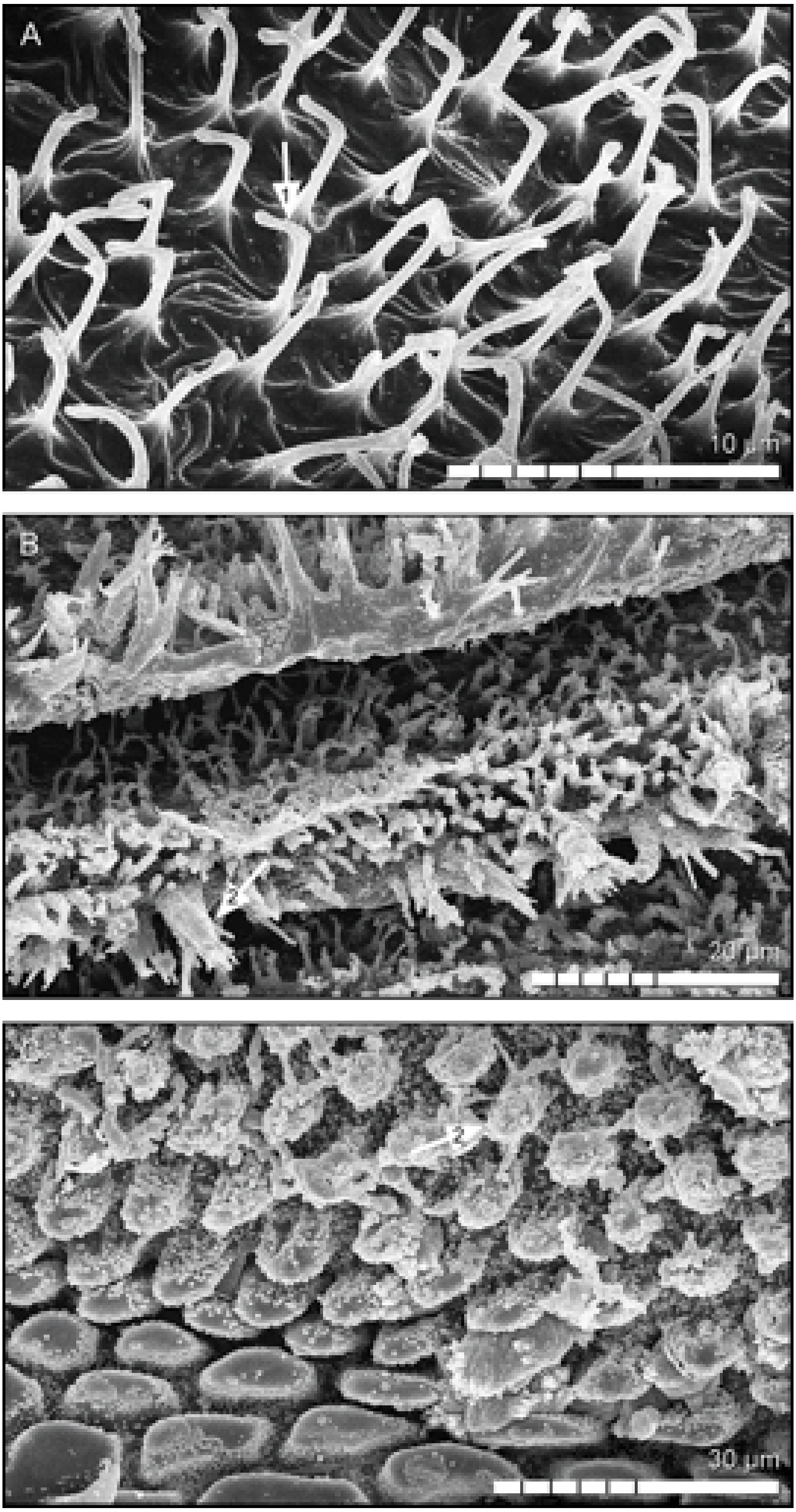

A
10 µm
B
20 µm
30 µm

Plate 97. *Vaejovis mexicanus mexicanus* C. L. Koch, 1836, 1 ♂ (AMNH [LP 1826]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), sometimes with single branch, viewed from air space; **B.** distal edges of book lung lamellae covered with spines (arrow), posterior view; **C.** movable posterior edge of spiracle with hillocklike structures (arrow), anterior view. Numbers in arrows refer to character states.

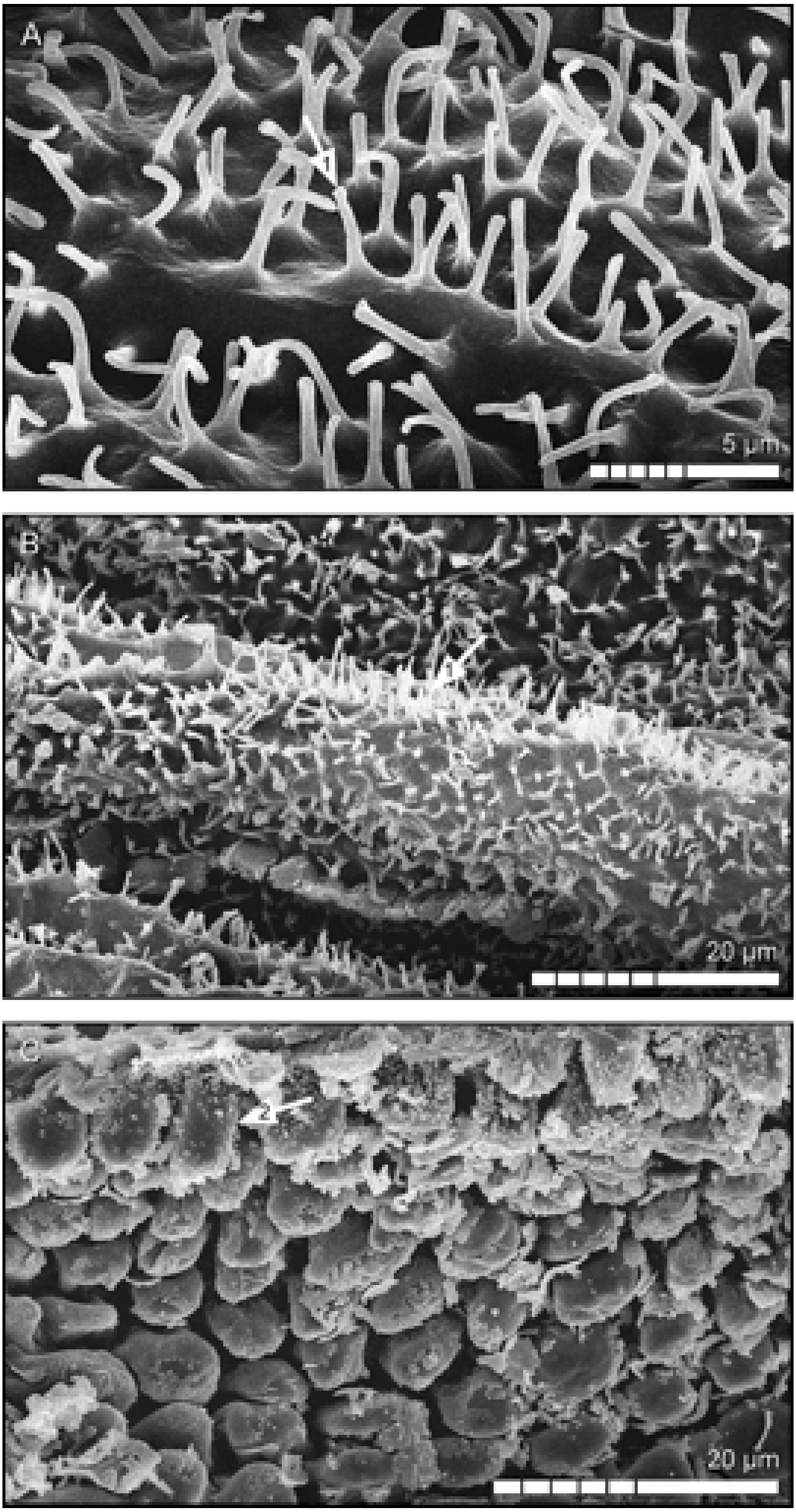

A
5 µm
B
20 µm
C
20 µm

Plate 98. *Vaejovis nitidulus* C. L. Koch, 1843, 1 ♂ (AMNH [LP 2052]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), sometimes with single branch, viewed from air space; **B.** distal edges of book lung lamellae covered with spines (arrow), posterior view; **C.** movable posterior edge of spiracle with broad hillocklike structures (arrow), anterior view. Numbers in arrows refer to character states.

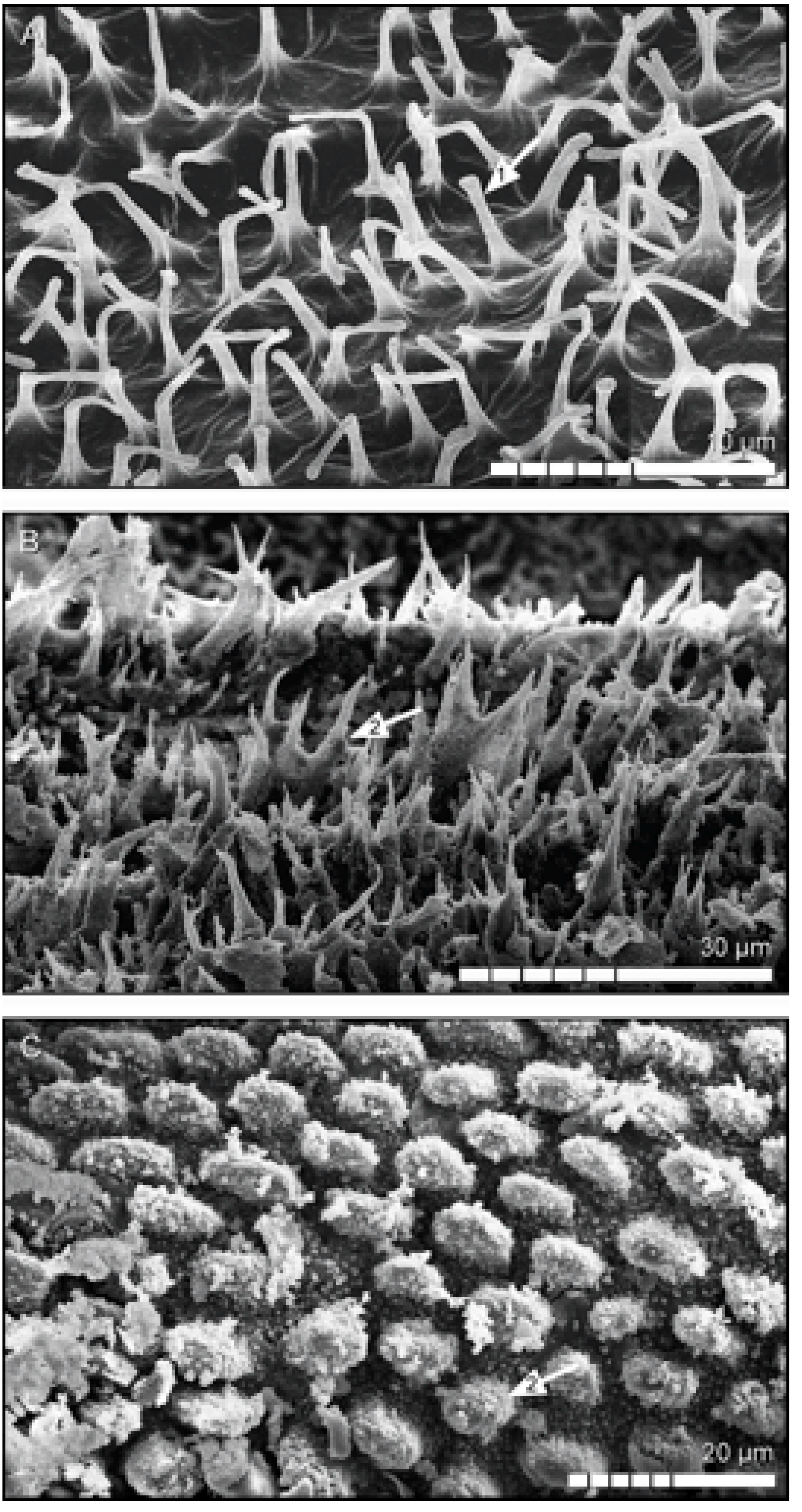

A
B
30 µm
C
20 µm

Plate 99. *Vaejovis spinigerus* (Wood, 1863), 1 ♂ (AMNH [LP 1811]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), rarely with single branch, viewed from air space; **B.** distal edges of book lung lamellae covered with spines (arrow), posterior view; **C.** movable posterior edge of spiracle with ridged subconical structures (arrow), anterior view. Numbers in arrows refer to character states.

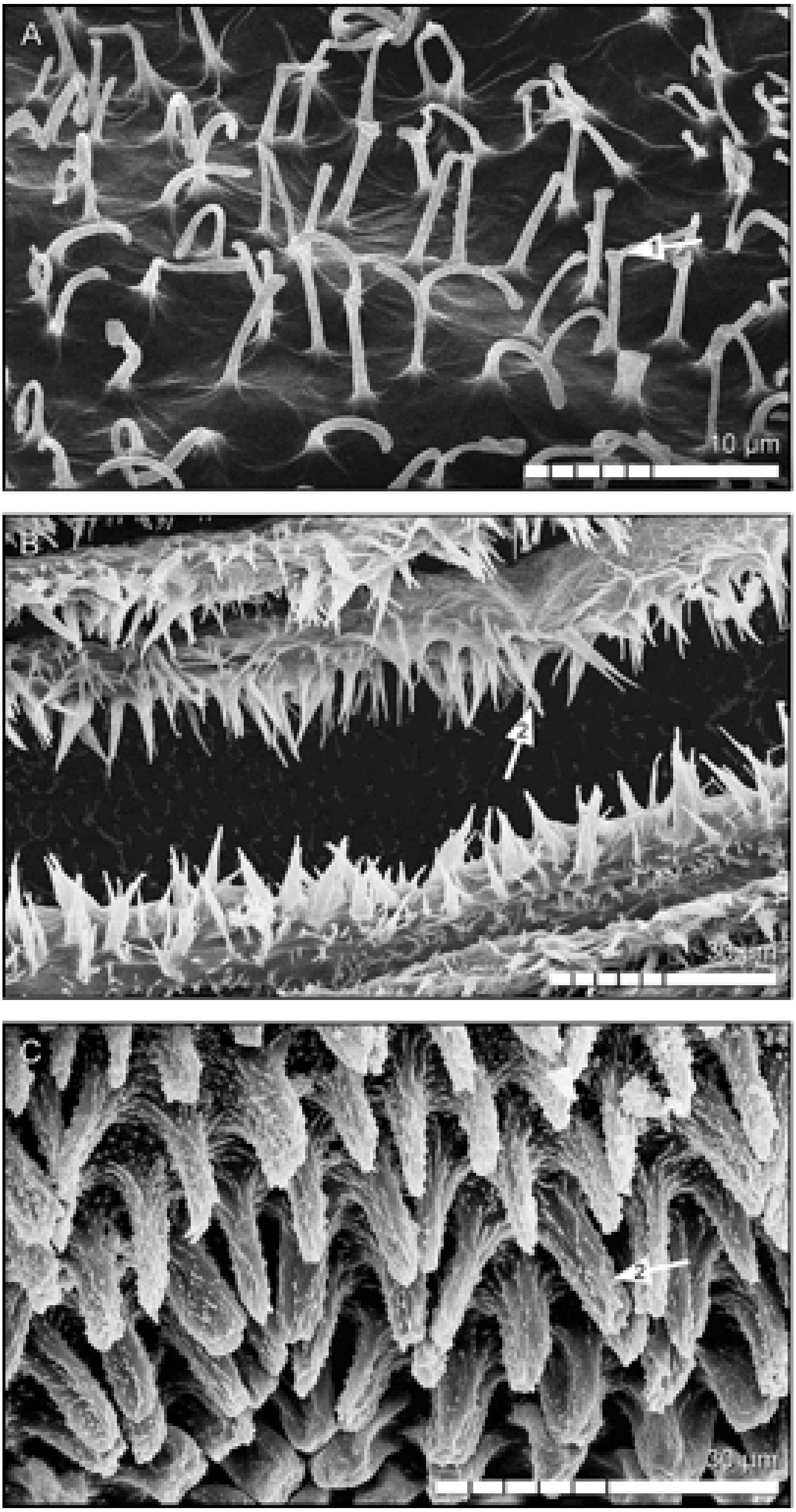

A
1
10 µm
B
2
C
2
30 µm

Plate 100. *Vejovoidus longiunguis* (Williams, 1969), 1 ♂ (AMNH [LP 3147]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with spines (arrow), posterior view; **C.** movable posterior edge of spiracle with subconical structures (arrow), anterior view. Numbers in arrows refer to character states.

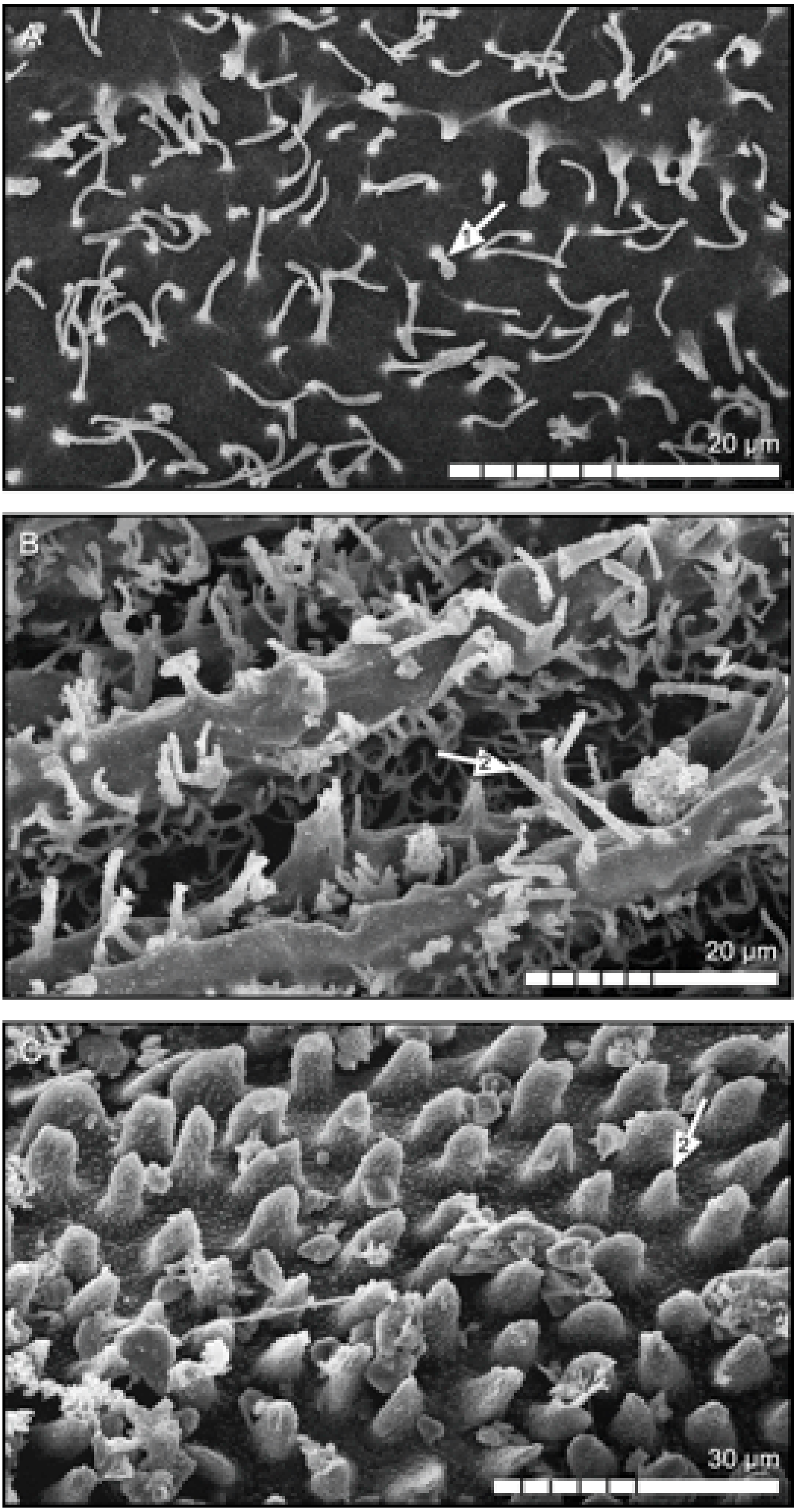

A
1
20 μm
B
2
20 μm
C
2
30 μm

Plate 101. *Bothriurus bonariensis* (C. L. Koch, 1842), 1 ♀ (AMNH [LP 2165): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae densely covered with rigid spines (arrow), posterior view; **C.** movable posterior edge of spiracle with subconical to spinelike processes (arrow), anterior view. Numbers in arrows refer to character states.

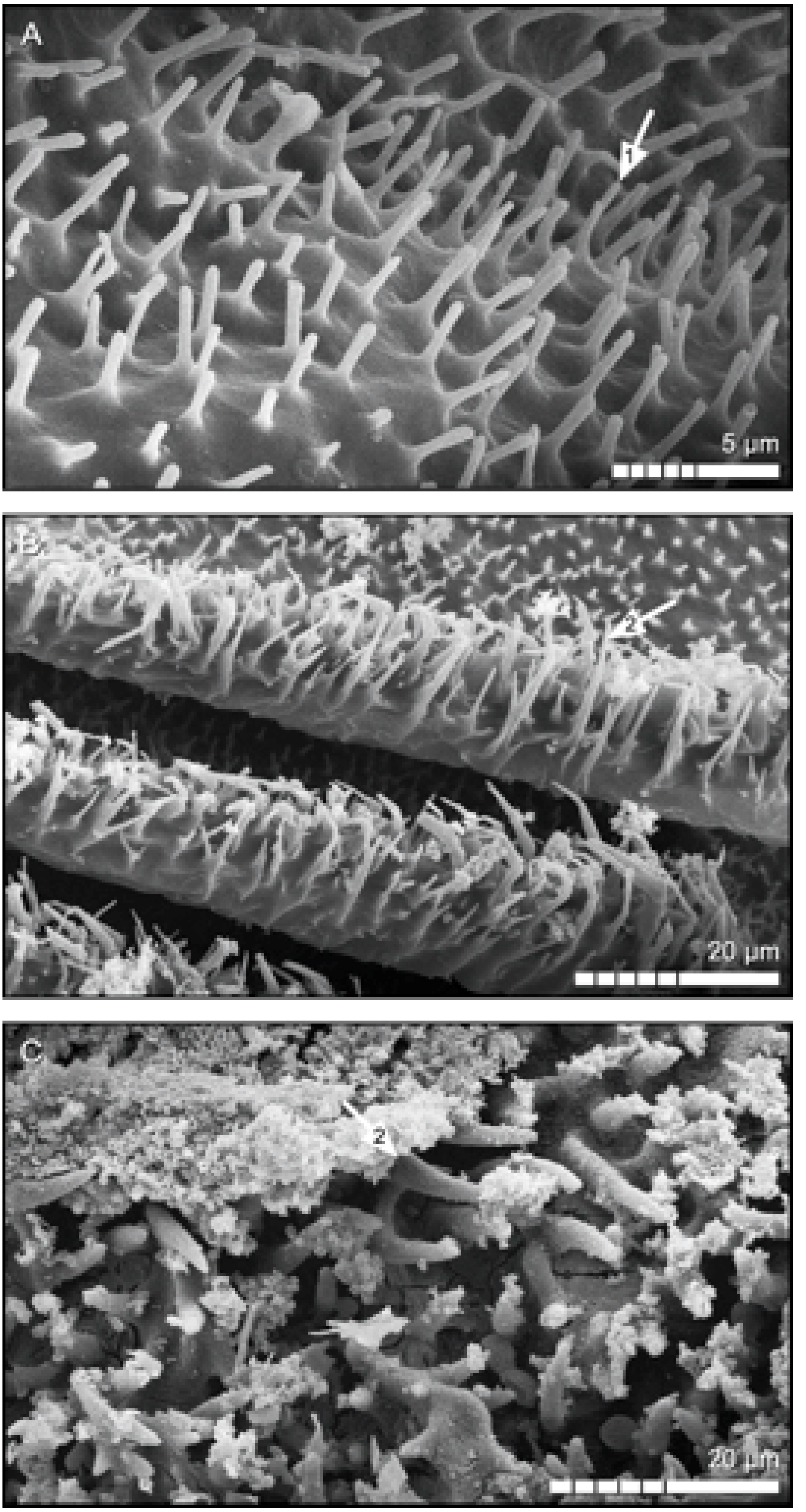

A
1
5 µm
B
2
20 µm
C
2
20 µm

Plate 102. *Bothriurus burmeisteri* Kraepelin, 1894, 1 ♀ (AMNH [LP 4258]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae densely covered with rigid spines (arrow), posterior view; **C.** movable posterior edge of spiracle with spinelike processes (arrow), anterior view. Numbers in arrows refer to character states.

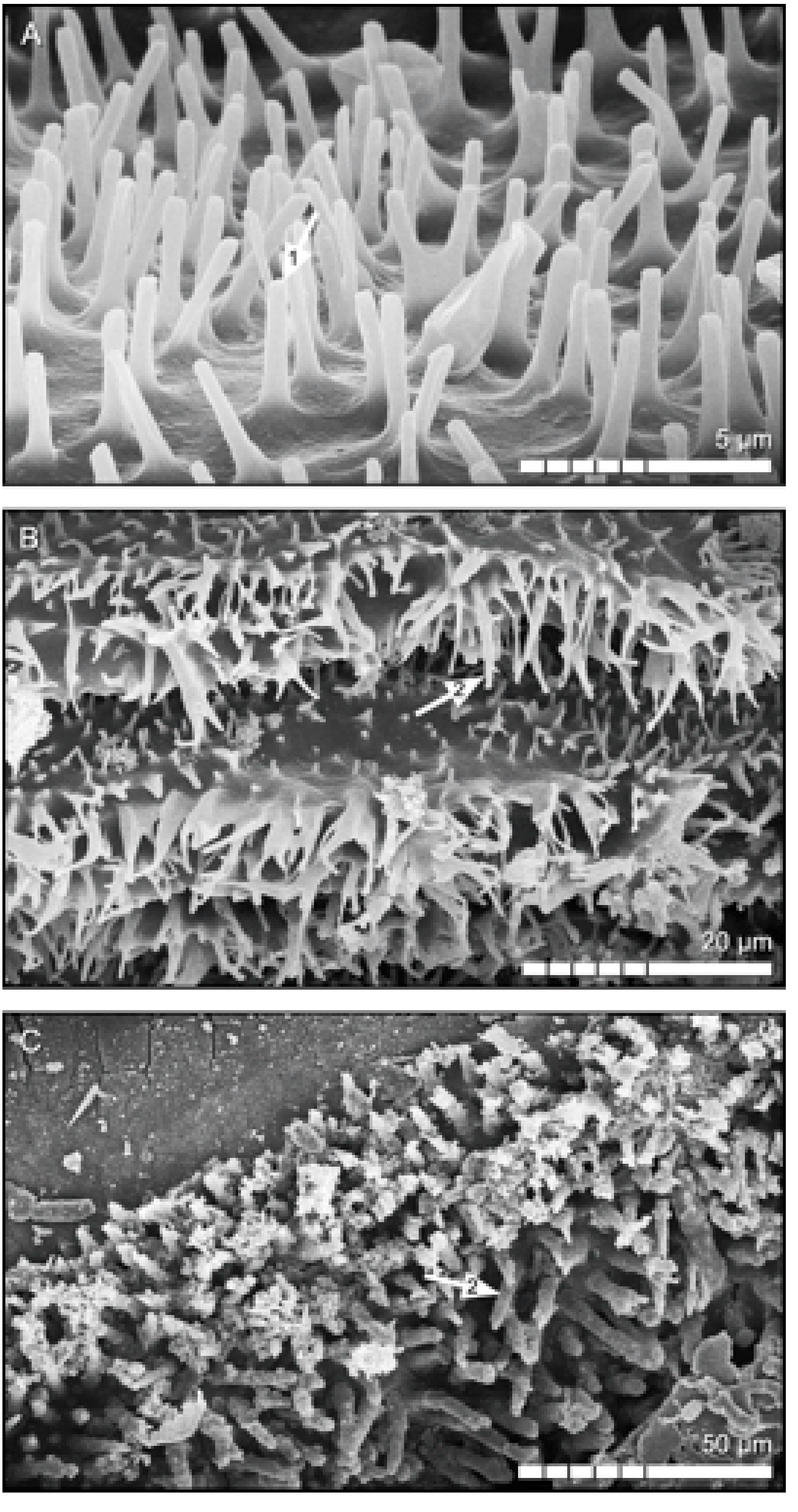

A
1
5 µm
B
2
20 µm
C
2
50 µm

Plate 103. *Bothriurus chacoensis* Maury and Acosta, 1993, 1 ♀ (AMNH [LP 1913]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae densely covered with rigid spines (arrow), posterior view; **C.** movable posterior edge of spiracle with spinelike processes (arrow), sometimes branched, anterior view. Numbers in arrows refer to character states.

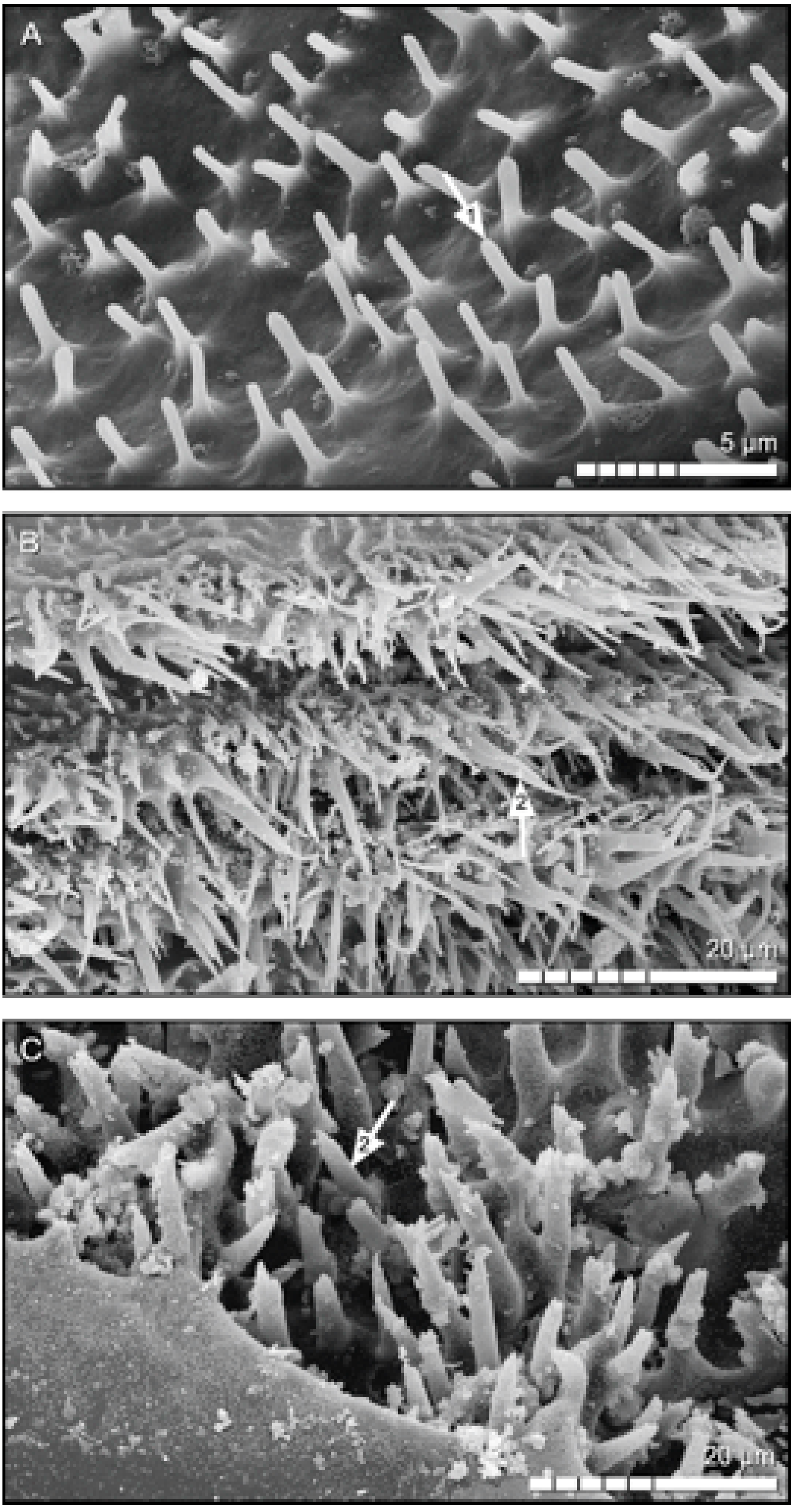

A
1
5 µm
B
2
20 µm
C
2
20 µm

Plate 104. *Bothriurus coriaceus* Pocock, 1893, 1 juv. ♂ (AMNH [LP 2391]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with rigid spines (arrow), posterior view; **C.** movable posterior edge of spiracle with spinelike processes (arrow), sometimes branched, anterior view. Numbers in arrows refer to character states.

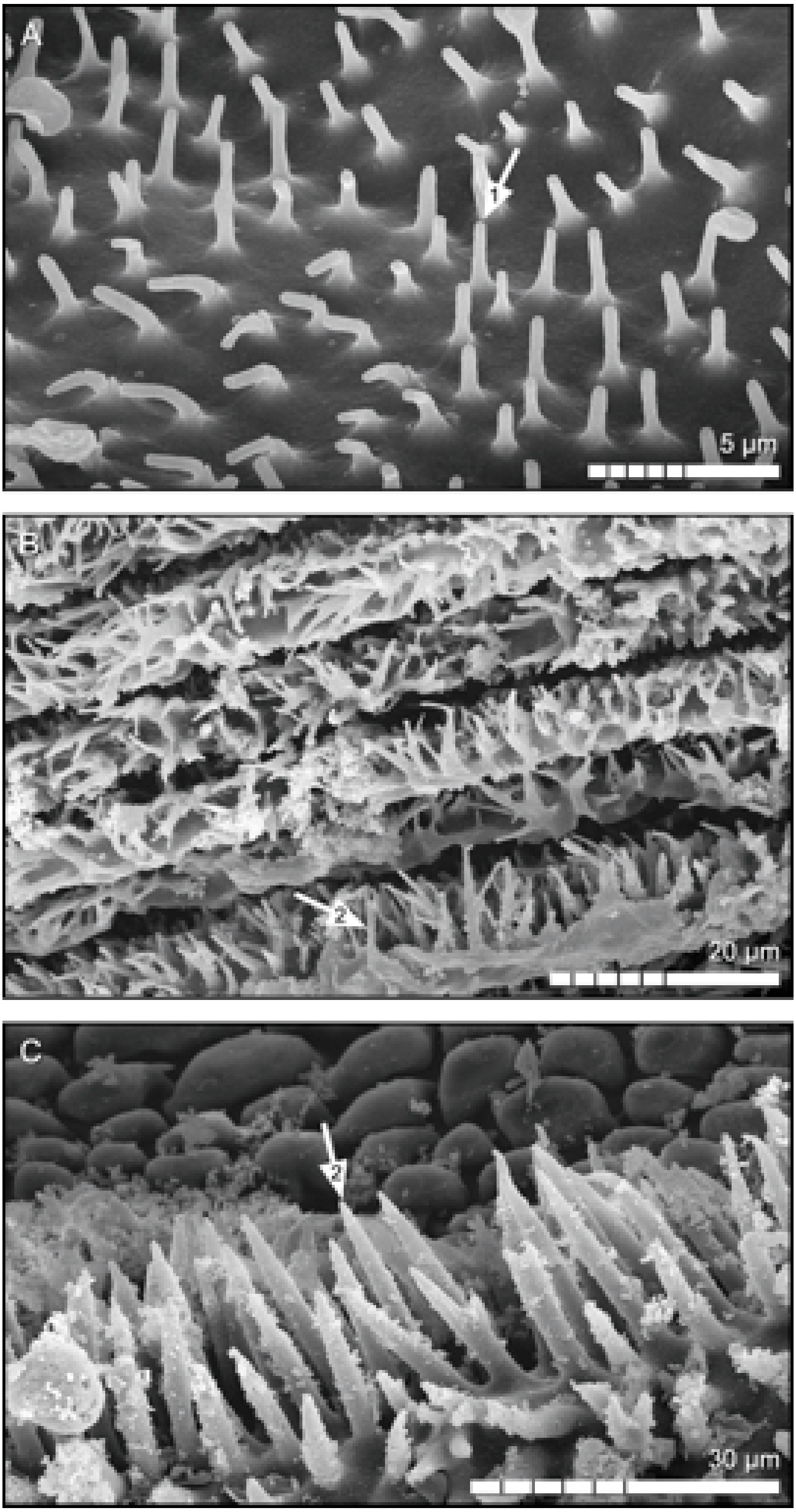

A
1
5 µm
B
2
20 µm
C
2
30 µm

Plate 105. *Brachistosternus ehrenbergii* (Gervais, 1841), 1 ♂ (AMNH [LP 3066]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with rigid spines (arrow), posterior view; **C.** movable posterior edge of spiracle with spinelike, subconical processes (arrow), anterior view. Numbers in arrows refer to character states.

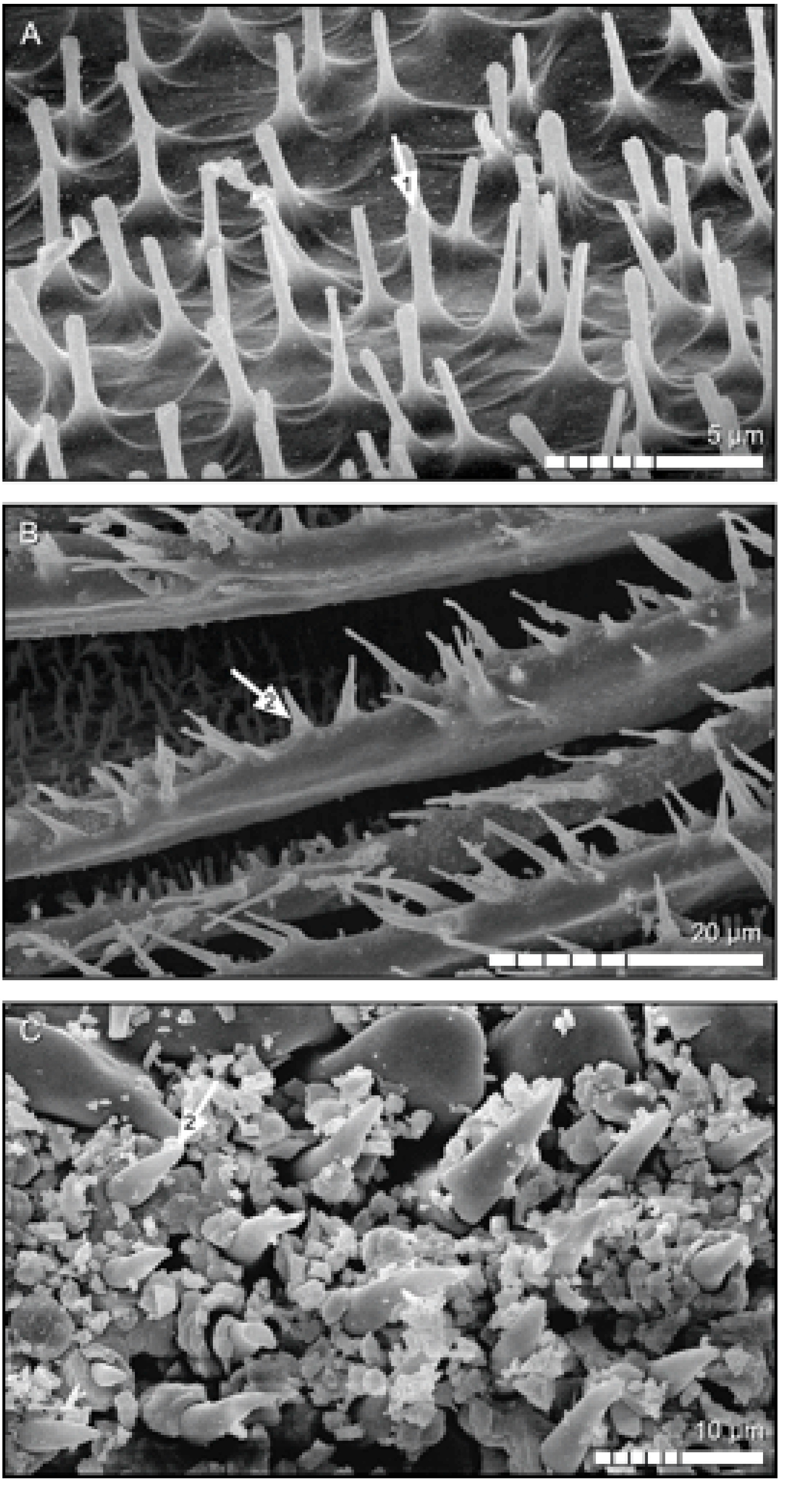

A
1
5 µm
B
2
20 µm
C
2
10 µm

Plate 106. *Brachistosternus ferrugineus* (Thorell, 1876), 1 ♀ (MNHN RS 0619): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae densely covered with rigid spines (arrow), posterior view; **C.** movable posterior edge of spiracle with subconical processes (arrow), anterior view. Numbers in arrows refer to character states.

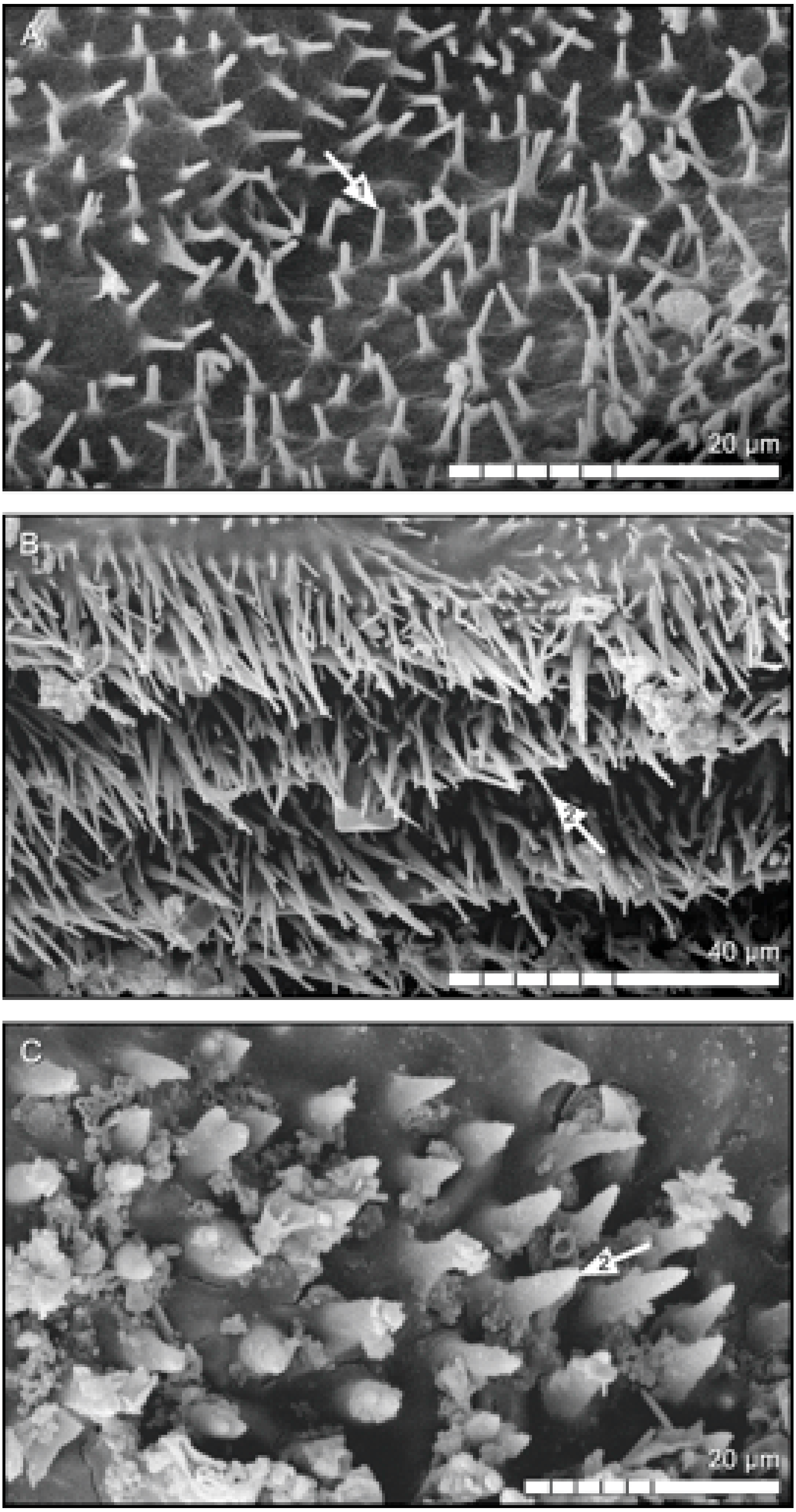

A
20 µm
B
40 µm
C
20 µm

Plate 107. *Centromachetes obscurus* Mello-Leitão, 1932, 1 ♂ (AMNH [LP 2436]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae densely covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with spinelike processes (arrow), sometimes branched, anterior view. Numbers in arrows refer to character states.

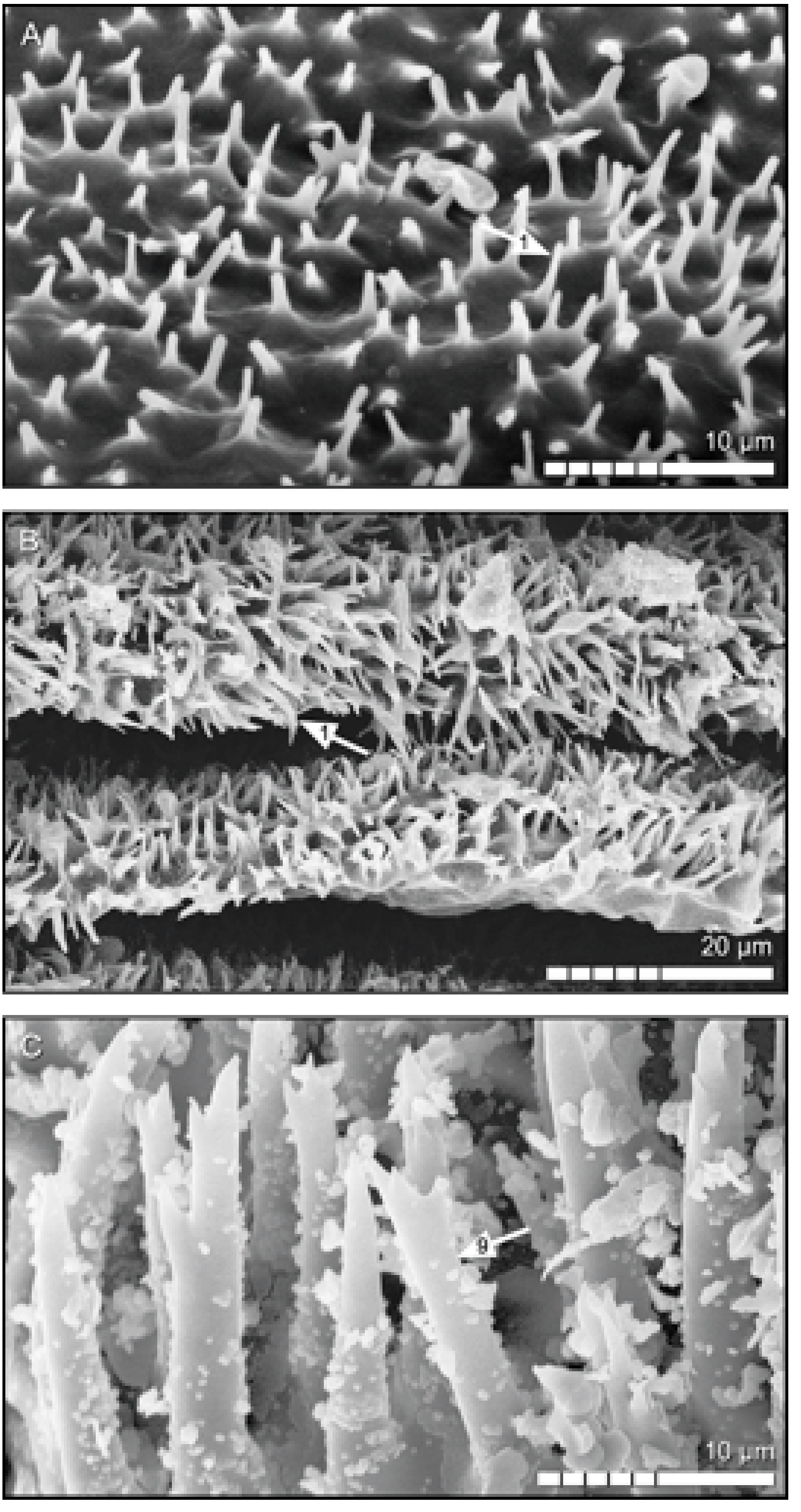

A
1
10 µm
B
1
20 µm
C
9
10 µm

Plate 108. *Cercophonius sulcatus* Kraepelin, 1908, 1 ♂ (AMNH [LP 1618]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with short branched spines (arrow), posterior view; **C.** movable posterior edge of spiracle with spinelike structures (arrow), sometimes branched, anterior view. Numbers in arrows refer to character states.

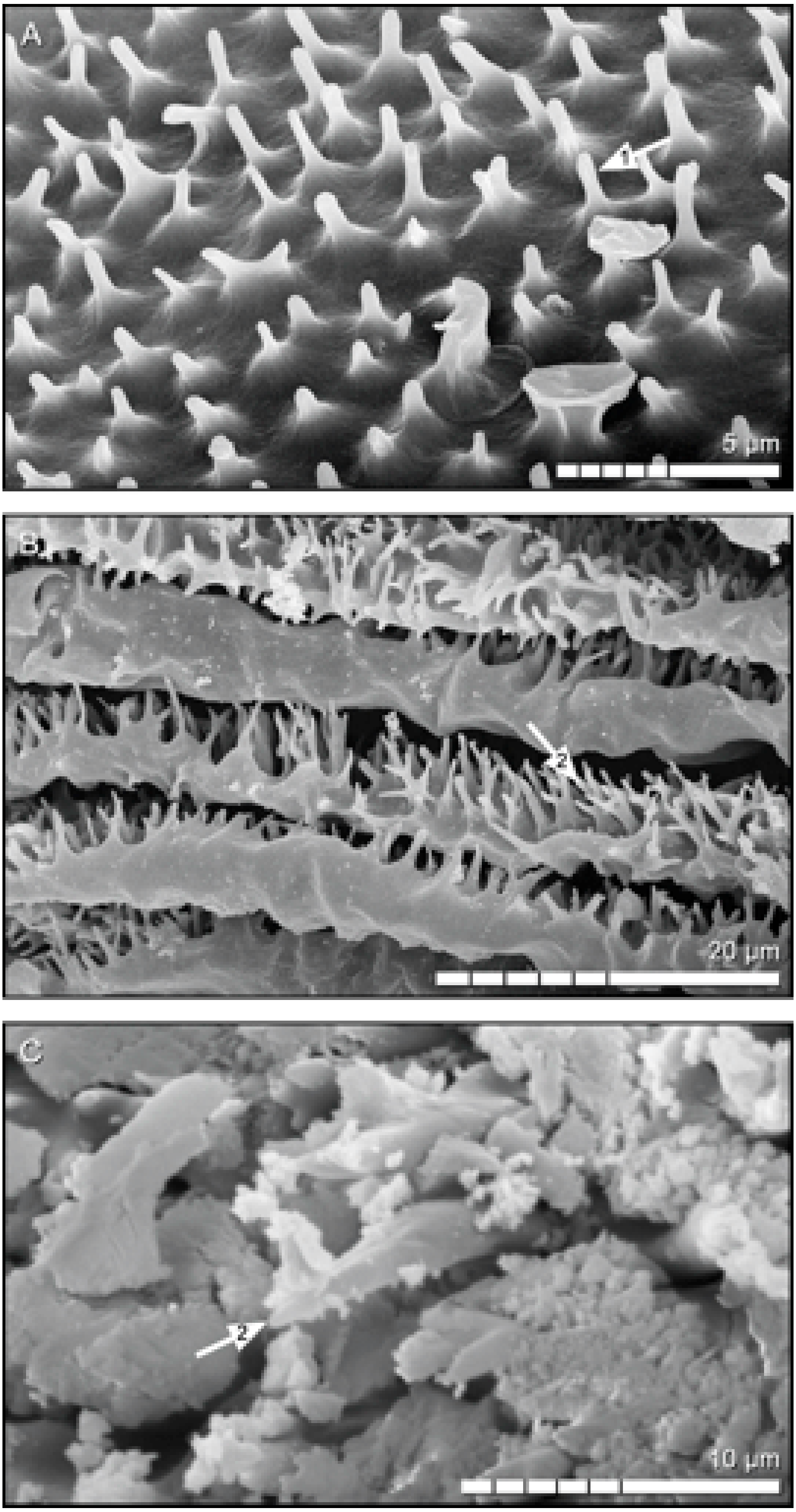

A
1
5 µm
B
2
20 µm
C
2
10 µm

Plate 109. *Lisposoma elegans* Lawrence, 1928, 1 ♂ (AMNH [LP 1636]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with short bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with flattened structures (arrow), anterior view. Numbers in arrows refer to character states.

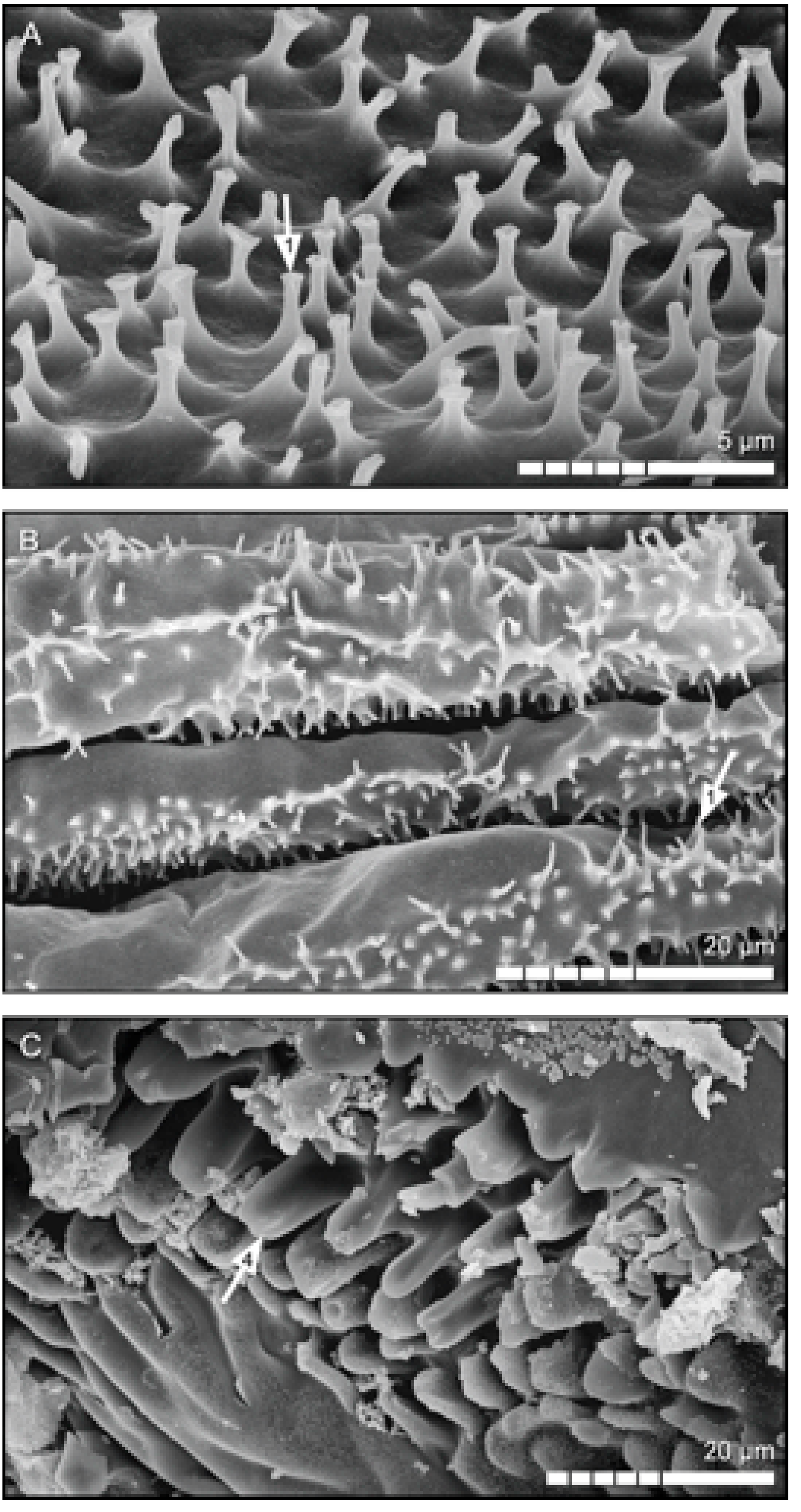

A
5 µm
B
20 µm
C
20 µm

Plate 110. *Lisposoma josehermana* Lamoral, 1979, 1 juv. ♀ (AMNH [LP 2524]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with flattened structures (arrow), anterior view. Numbers in arrows refer to character states.

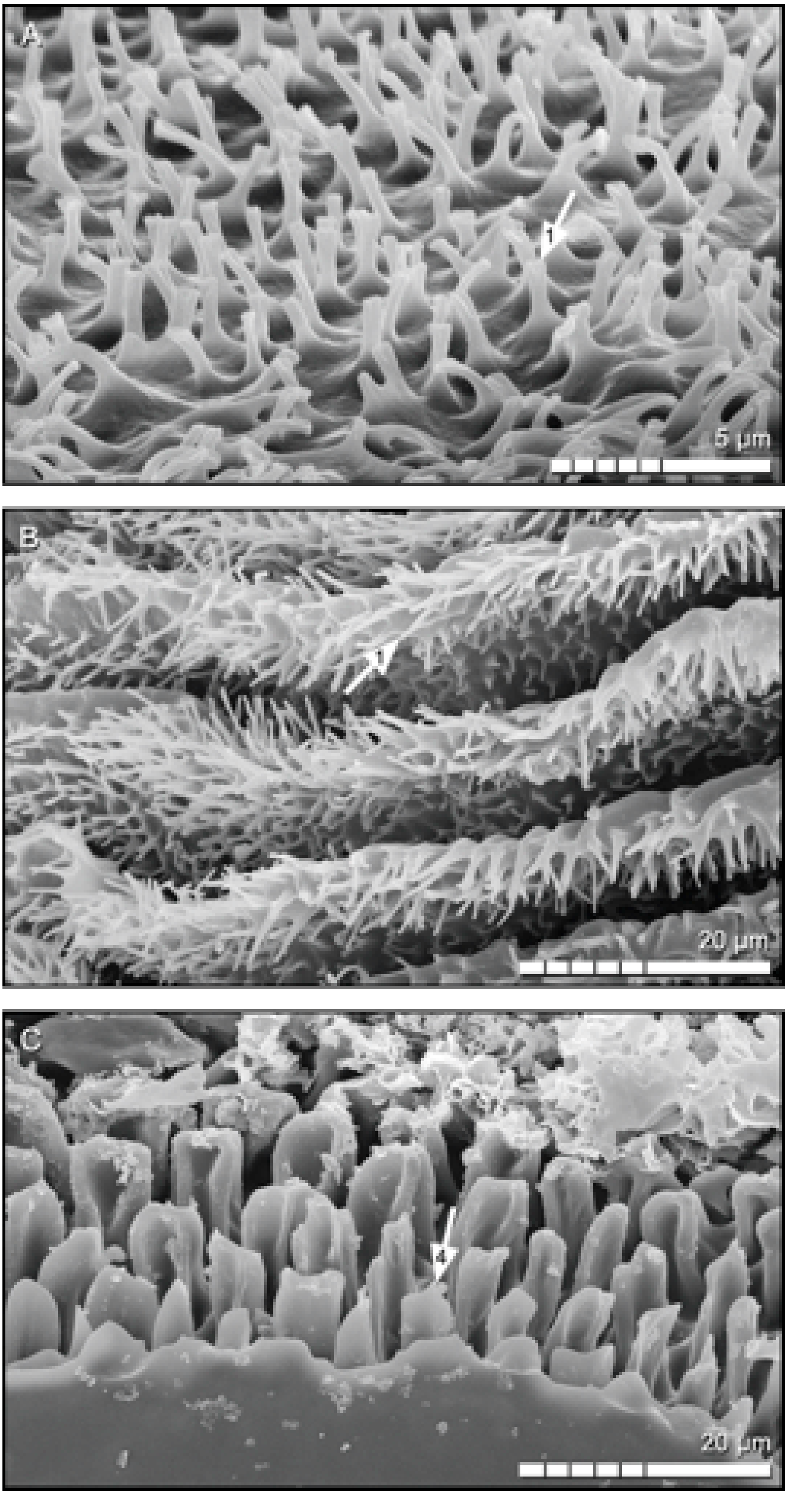

A
1
5 µm
B
1
20 µm
C
4
20 µm

Plate 111. *Orobothriurus alticola* (Pocock, 1899), 1 subad. ♂ (AMNH [LP 4309]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae densely covered with spines (arrow), posterior view; **C.** movable posterior edge of spiracle with spinelike structures (arrow), anterior view. Numbers in arrows refer to character states.

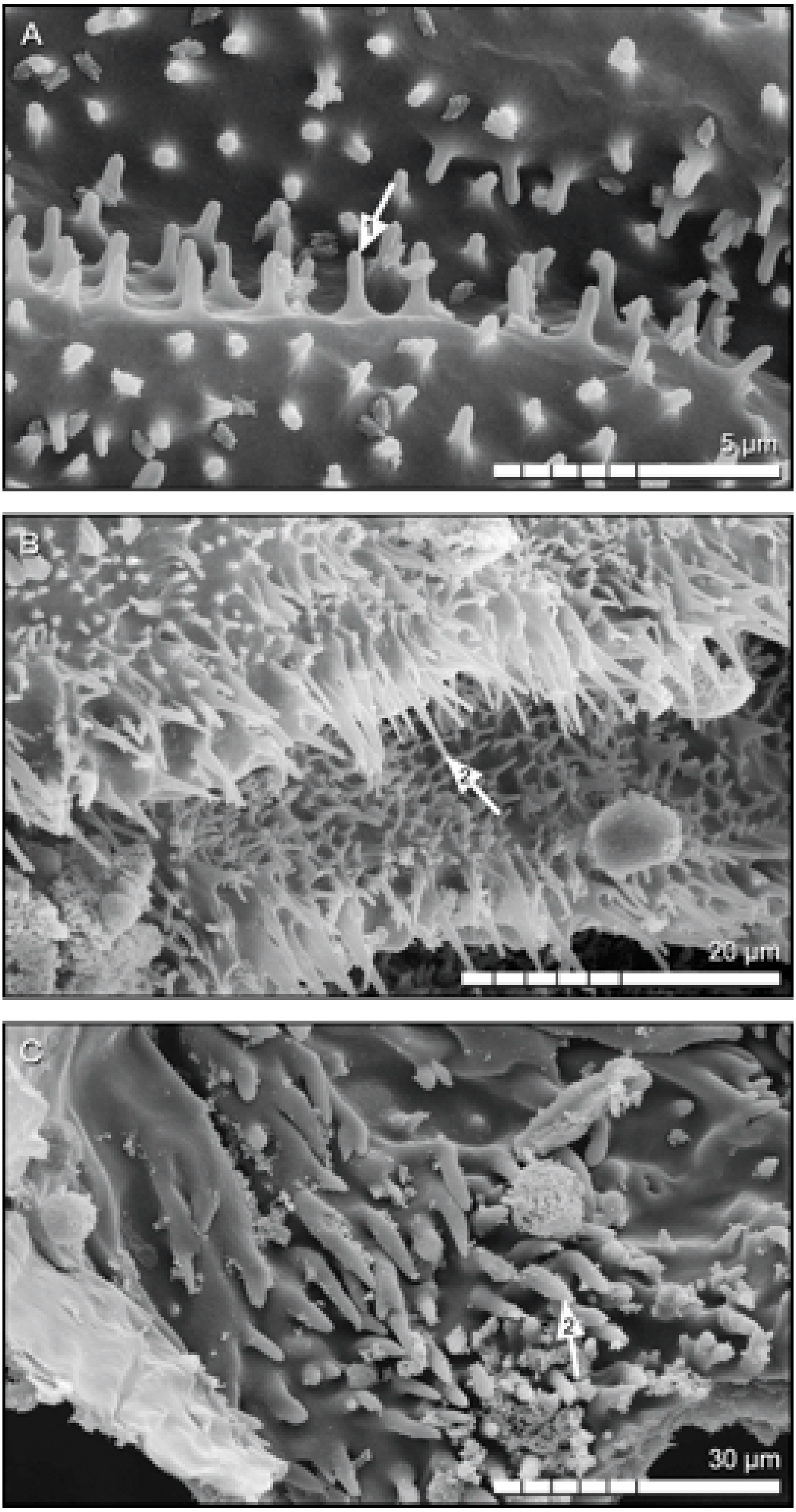

A
5 µm
B
20 µm
C
2
30 µm

Plate 112. *Pachakutej iskay* (Acosta and Ochoa, 2001), 1 subad. ♂ (AMNH [LP 3061]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with bristles (arrow), fusion of lamellar edges with atrial wall, posterior view; **C.** movable posterior edge of spiracle with hillocklike structures (arrow), anterior view. Numbers in arrows refer to character states.

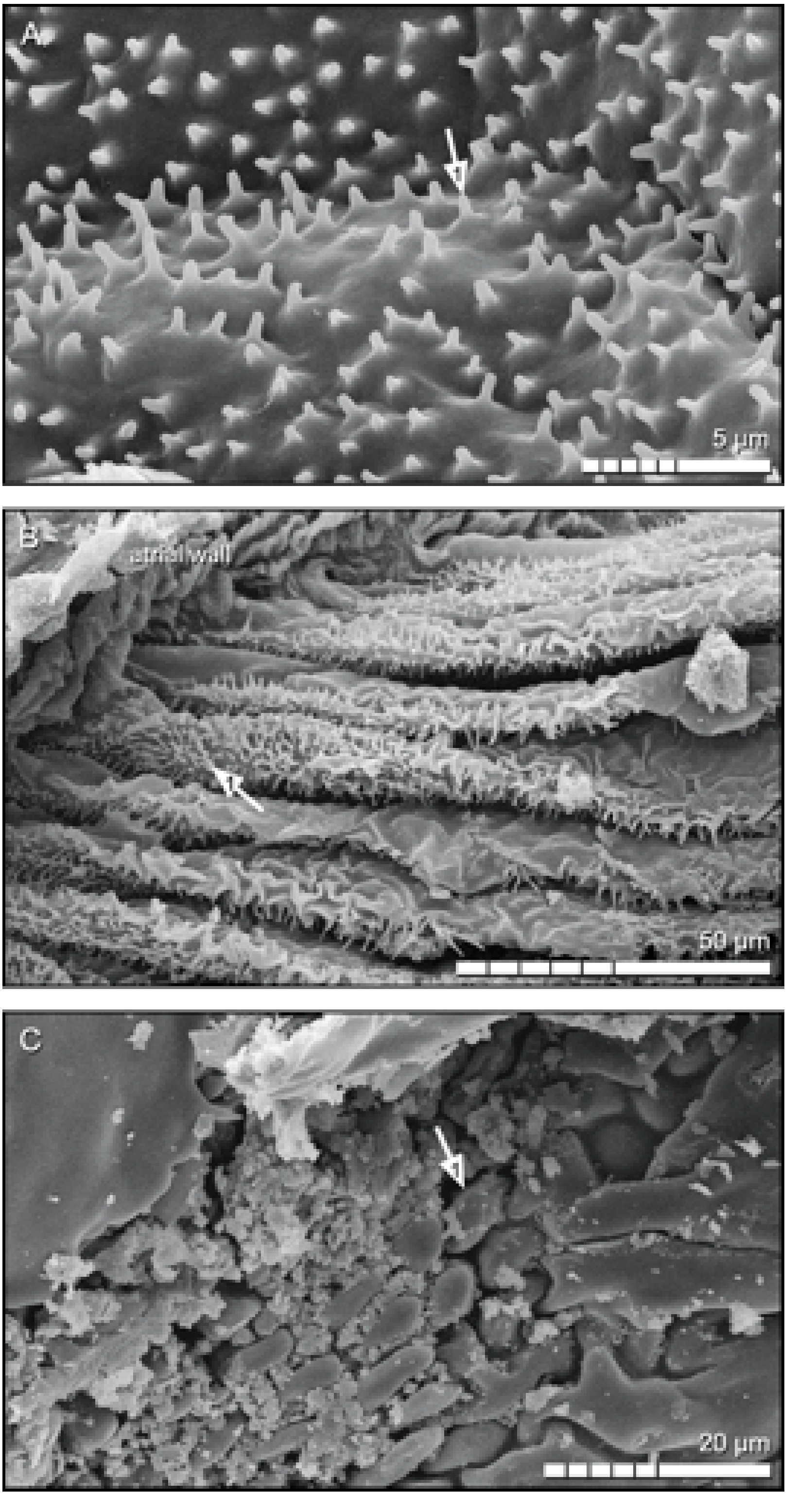

A
5 µm
B
atrial wall
50 µm
C
20 µm

Plate 113. *Phoniocercus pictus* Pocock, 1893, 1 ♀ (MNHN): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** wrinkled distal edges of book lung lamellae covered with spines (arrow), posterior view; **C.** movable posterior edge of spiracle with spinelike structures (arrow), sometimes branched, anterior view. Numbers in arrows refer to character states.

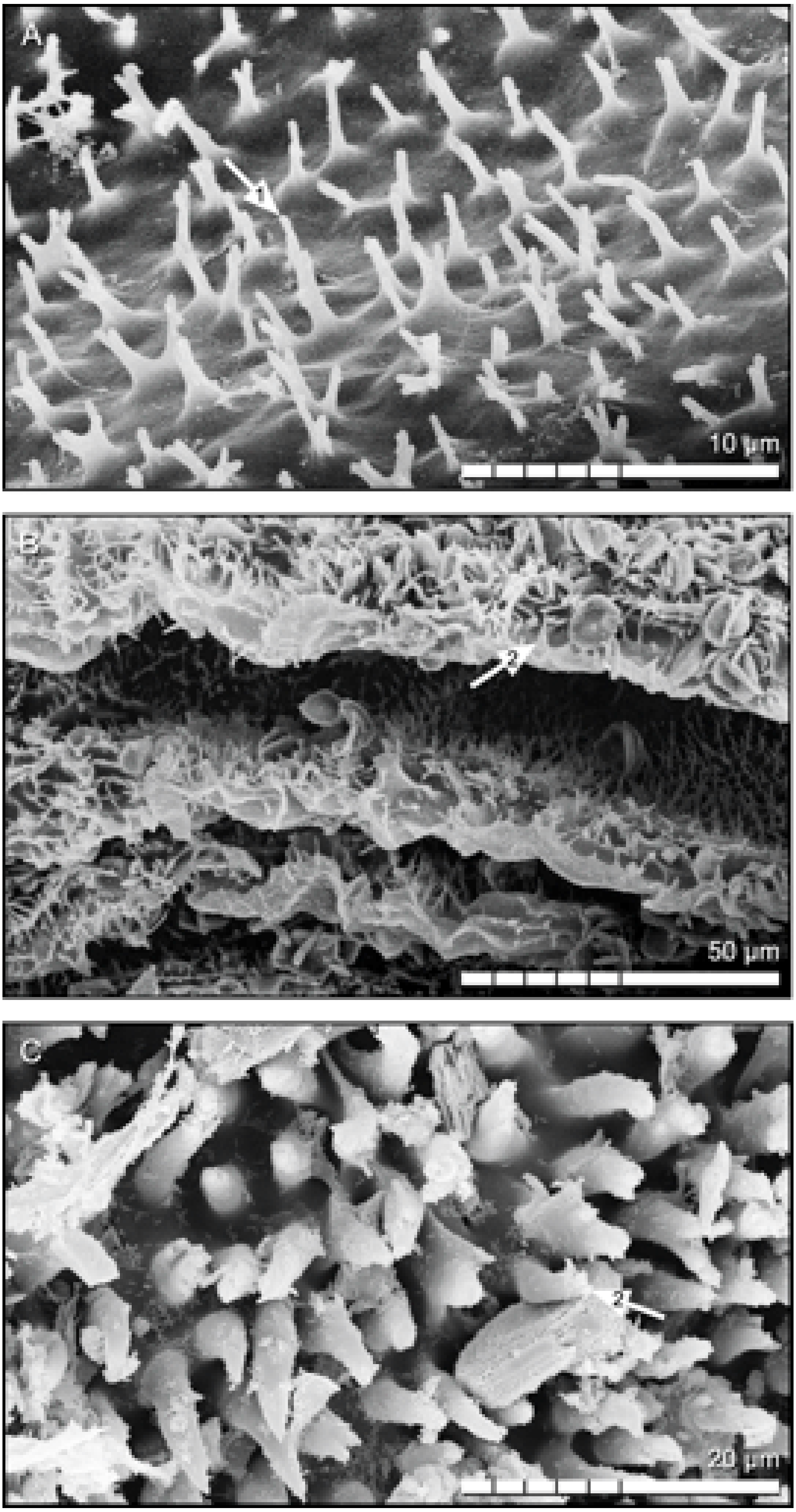

A
10 µm
B
50 µm
C
20 µm

Plate 114. *Phoniocercus sanmartini* Cekalovic, 1968, 1 ♀ (AMNH [LP 1994]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** wrinkled distal edges of book lung lamellae covered with trabecula-like spines (arrow), posterior view; **C.** movable posterior edge of spiracle with branched treelike structures (arrow), anterior view. Numbers in arrows refer to character states.

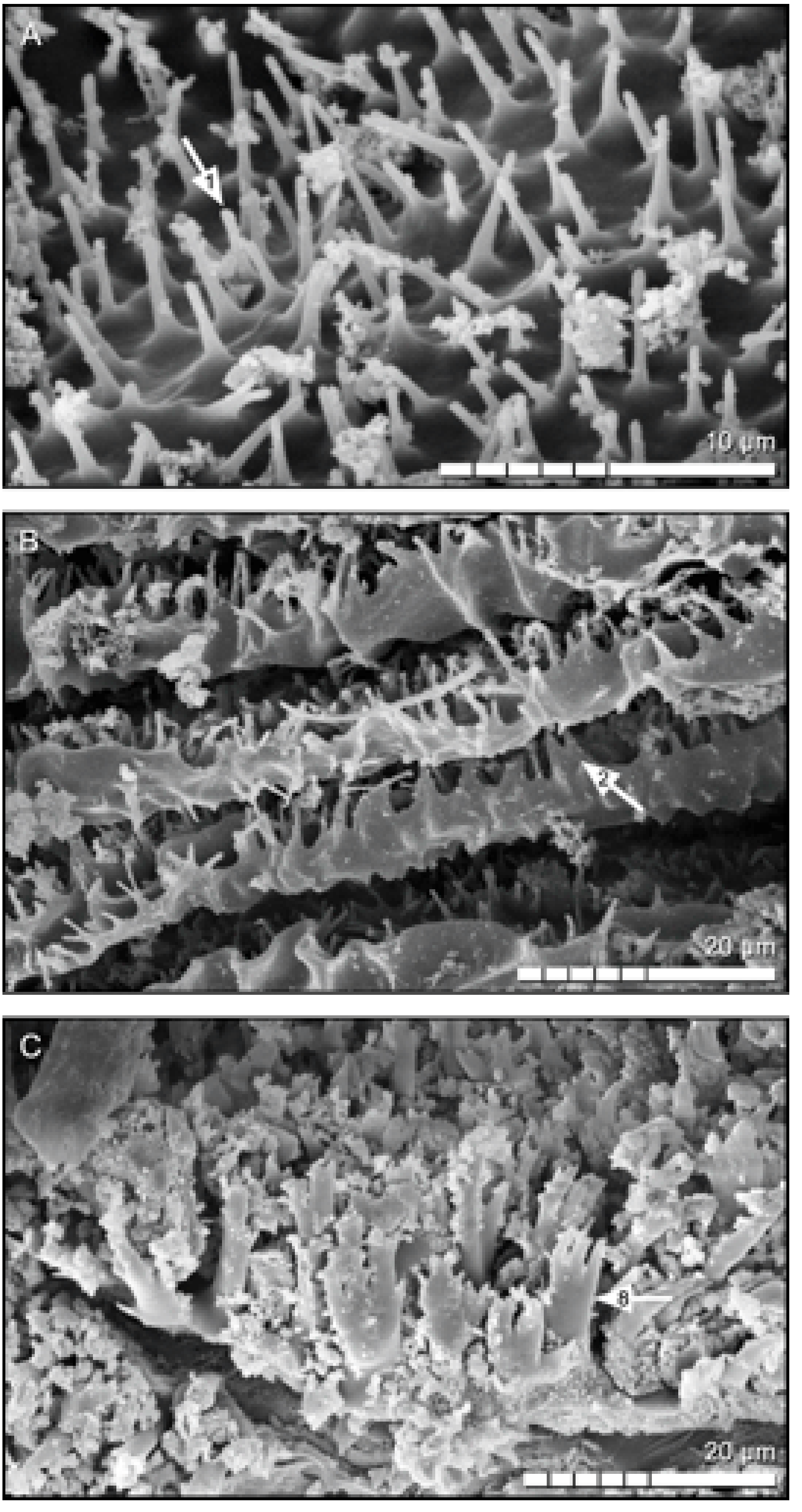

A
10 µm
B
20 µm
C
8
20 µm

Plate 115. *Thestylus glasioui* (Bertkau, 1880), 1 ♂ (AMNH [LP 1965]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with branched structures (arrow), anterior view. Numbers in arrows refer to character states.

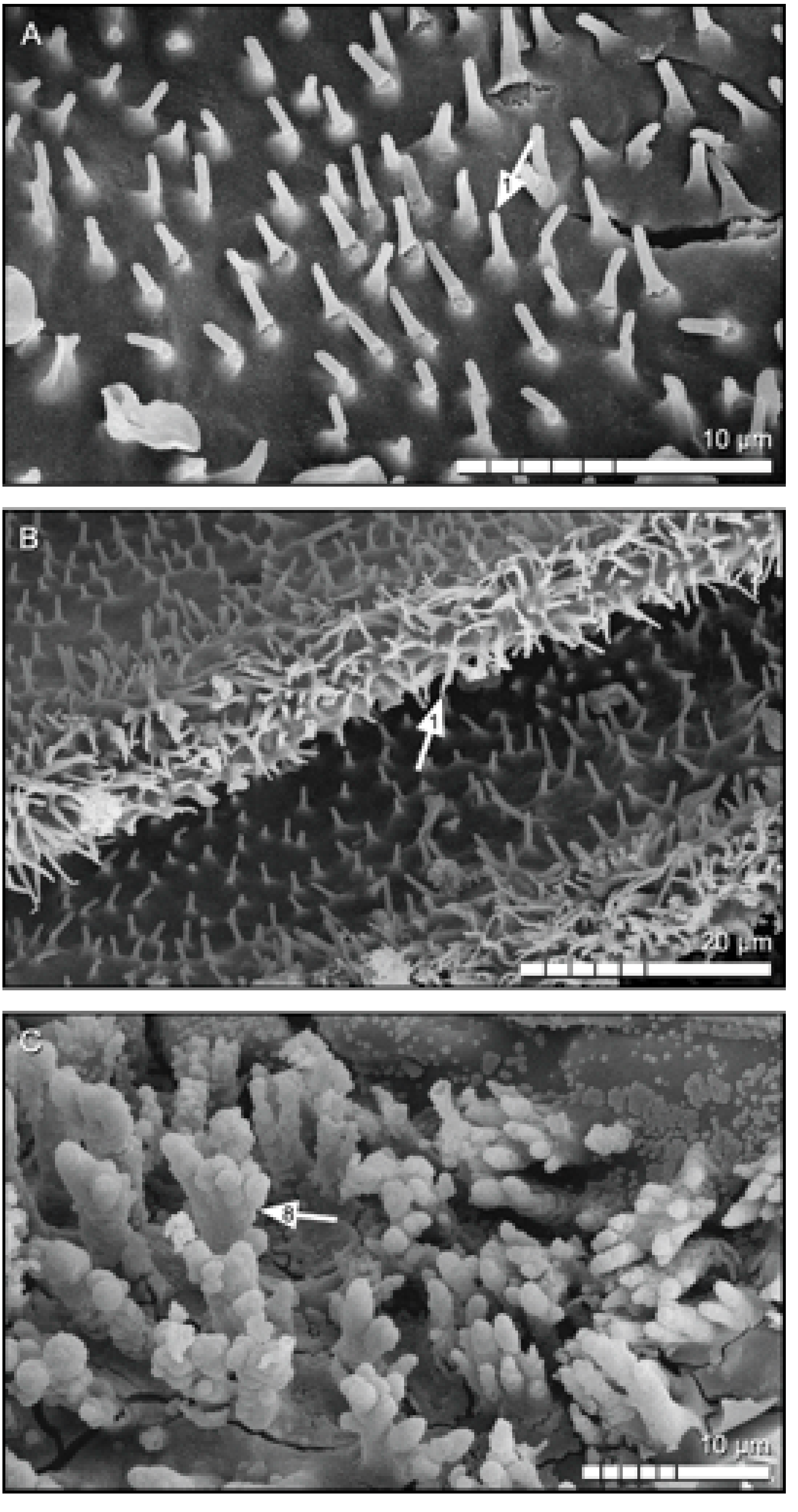

A
1
10 µm
B
1
20 µm
C
3
10 µm

Plate 116. *Timogenes mapuche* Maury, 1975, 1 ♂ (AMNH [LP 4312]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with spines (arrow), posterior view; **C.** movable posterior edge of spiracle with spinelike structures (arrow), sometimes branched, anterior view. Numbers in arrows refer to character states.

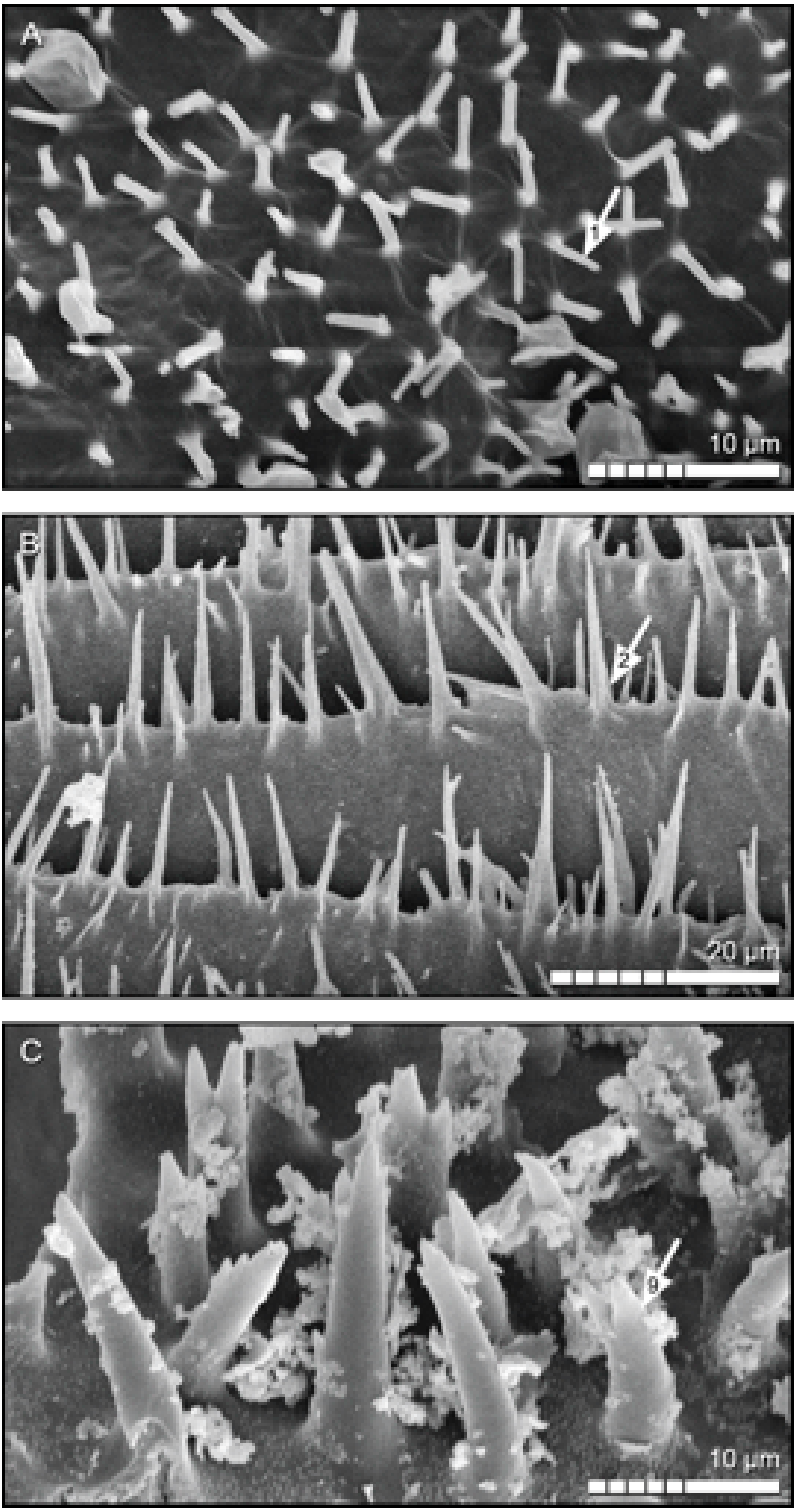

A
10 µm
B
2
20 µm
C
9
10 µm

Plate 117. *Urophonius iheringii* Pocock, 1893, 1 ♀ (AMNH [LP 3457]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with spines (arrow), posterior view; **C.** movable posterior edge of spiracle with branched treelike structures (arrow), anterior view. Numbers in arrows refer to character states.

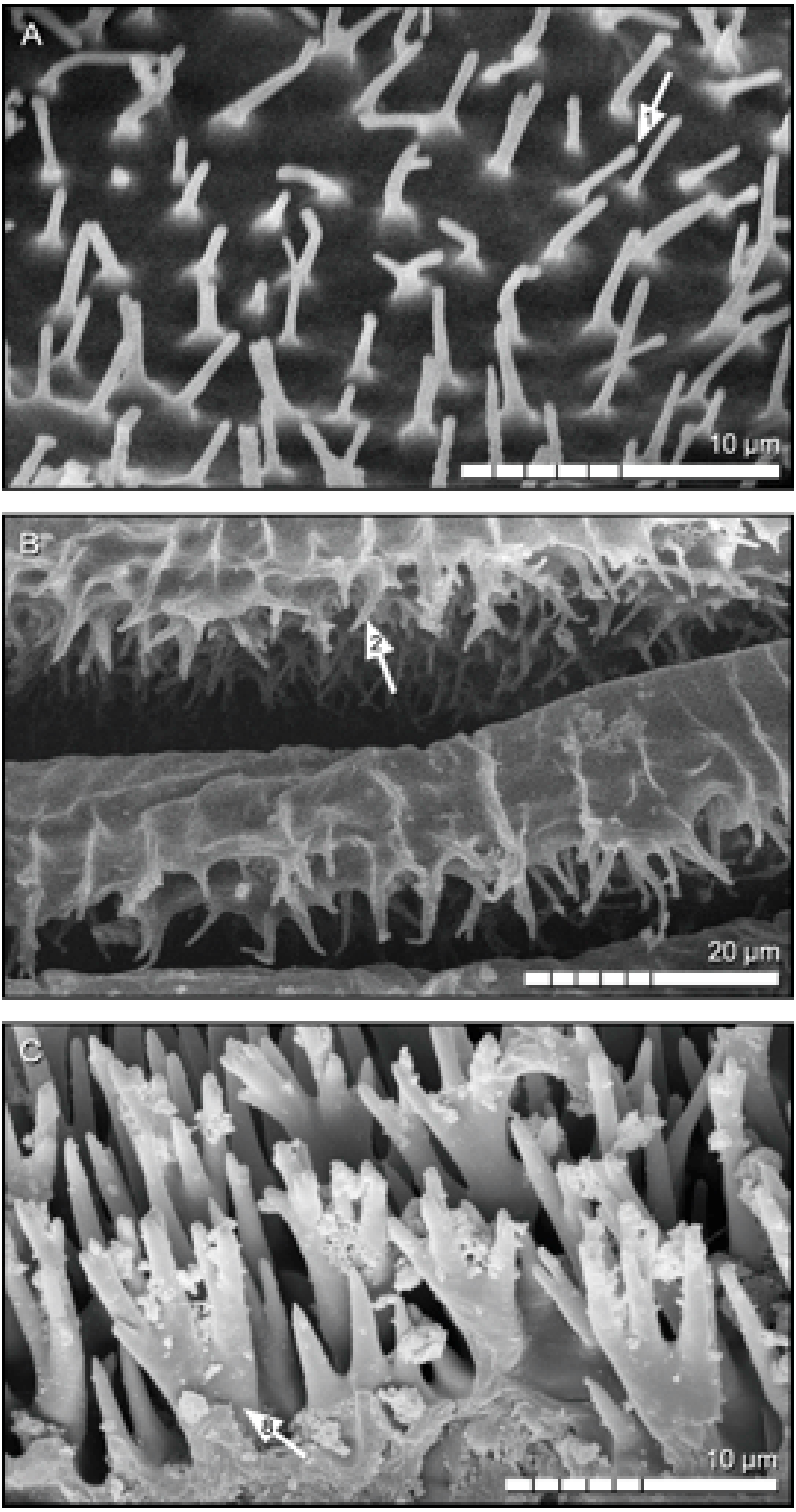

A
10 µm
B
20 µm
C
10 µm

Plate 118. *Urophonius tregualemuensis* Cekalovic, 1981, 1 juv. ♂ (AMNH [LP 5165]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with spines (arrow), posterior view; **C.** movable posterior edge of spiracle with spinelike structures (arrow), sometimes branched, anterior view. Numbers in arrows refer to character states.

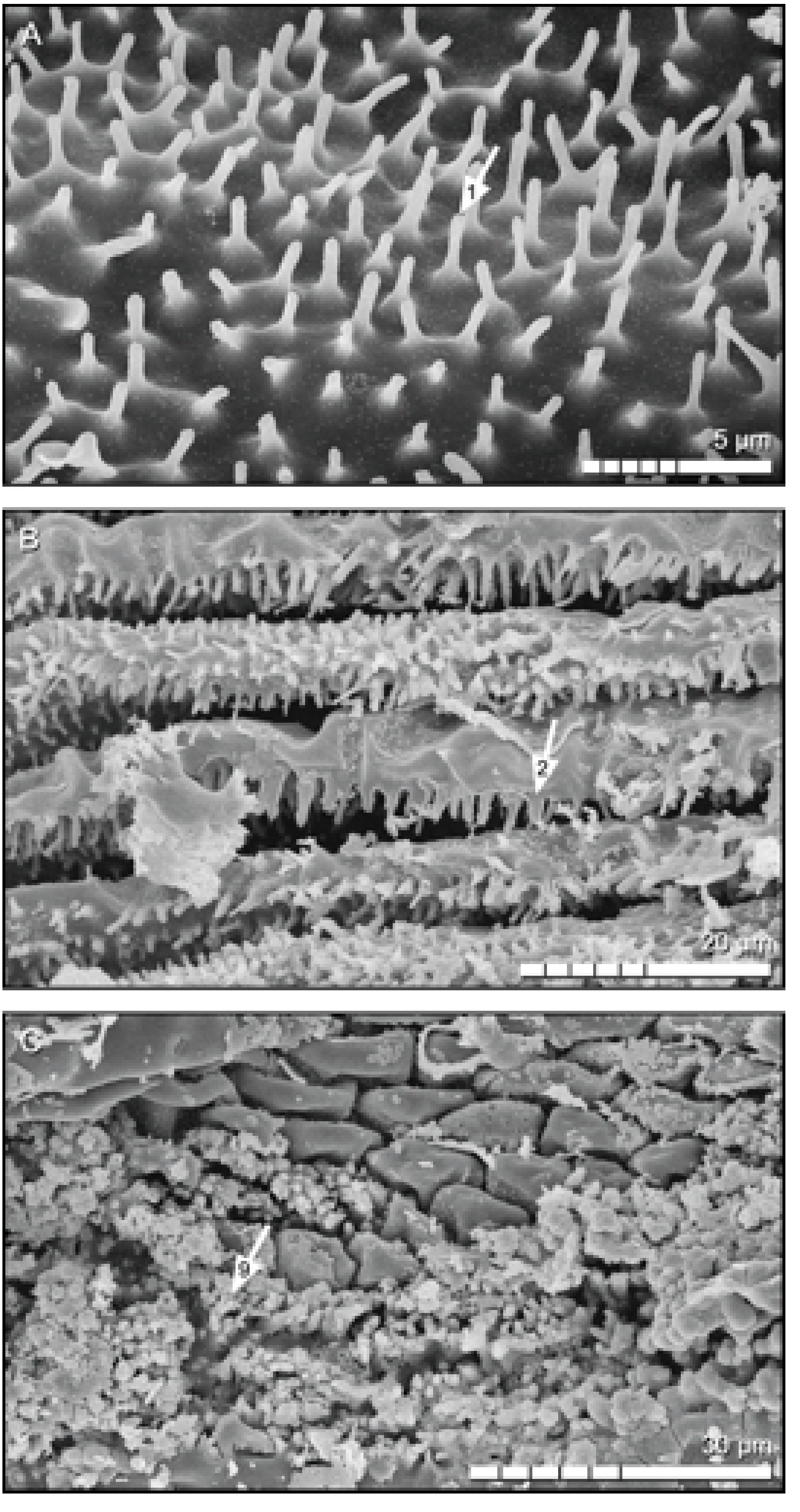

A
1
5 µm
B
2
20 µm
C
3
30 µm

Plate 119. *Vachonia martinezi* Abalos, 1954, 1 juv. ♀ (AMNH [LP 2441]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with spines (arrow), posterior view; **C.** movable posterior edge of spiracle with spinelike structures (arrow), anterior view. Numbers in arrows refer to character states.

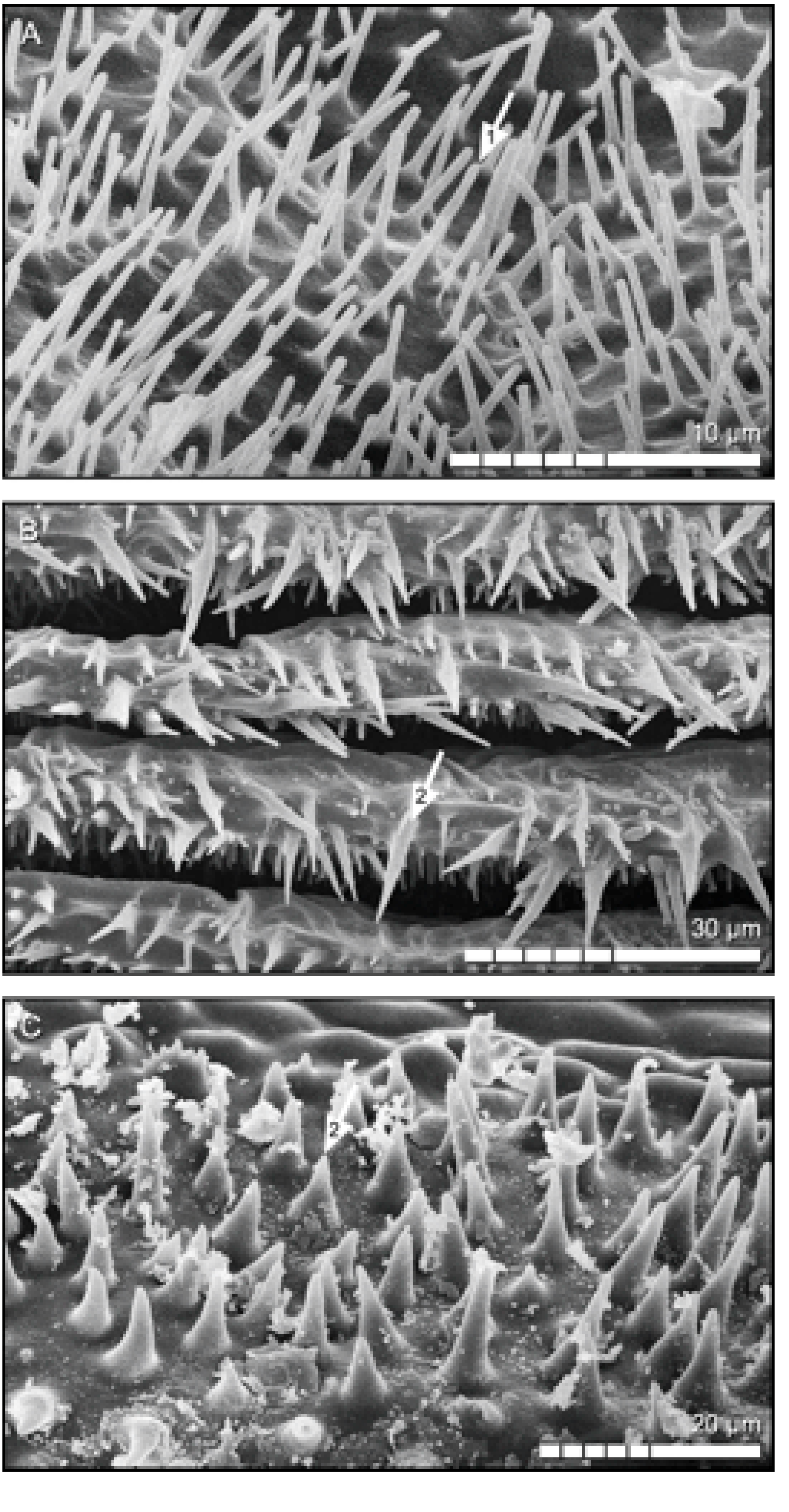

A
1
10 µm
B
2
30 µm
C
2
20 µm

Plate 120. *Urodacus novaehollandiae* Peters, 1861, 1 ♂ (AMNH [LP 1658]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with flattened chisel-like structures (arrow), anterior view. Numbers in arrows refer to character states.

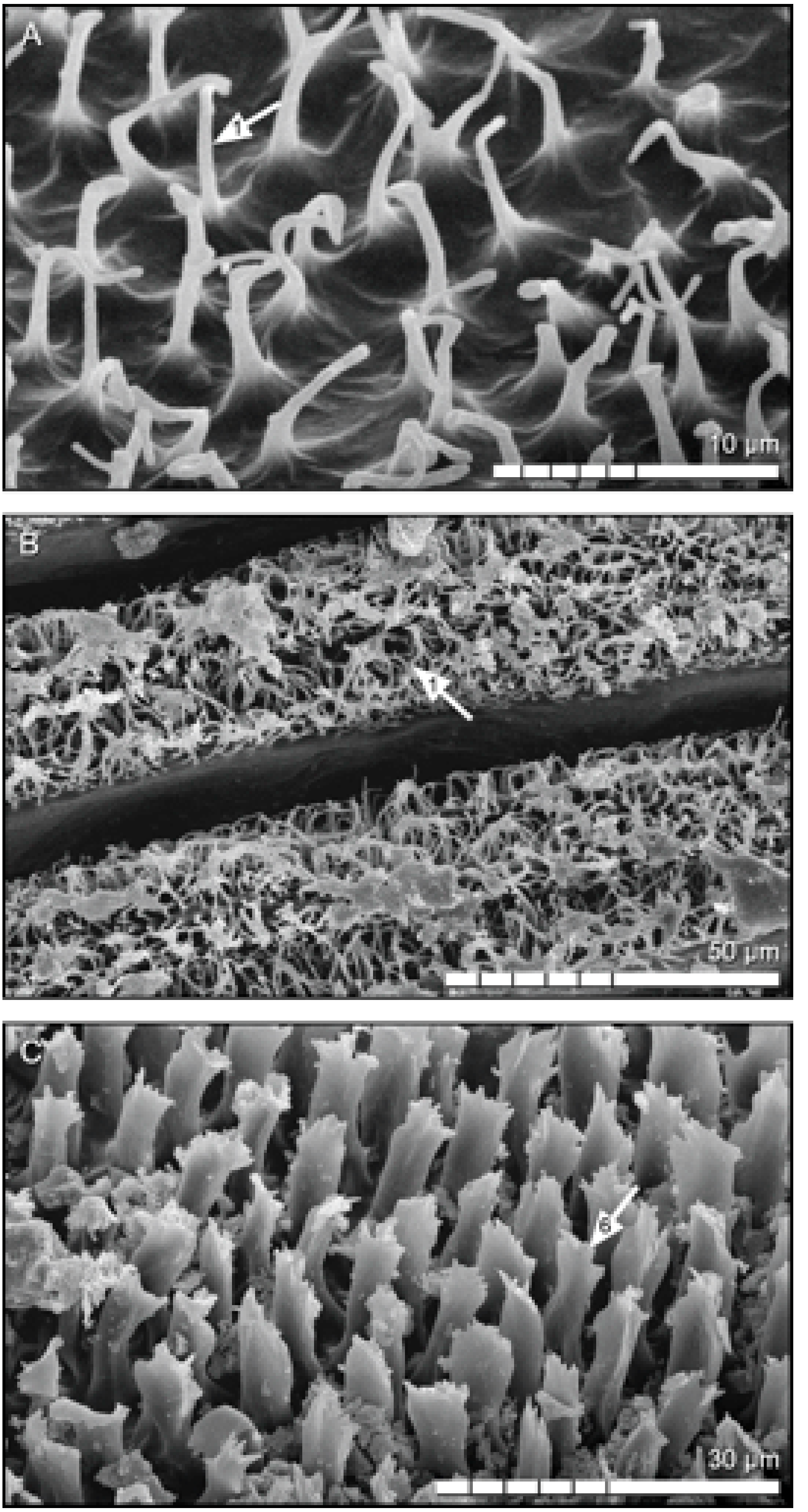

A
10 µm
B
50 µm
C
30 µm

Plate 121. *Urodacus yaschenkoi* (Birula, 1903), 1 ♂ (AMNH [LP 1659]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with flattened structures (arrow), anterior view. Numbers in arrows refer to character states.

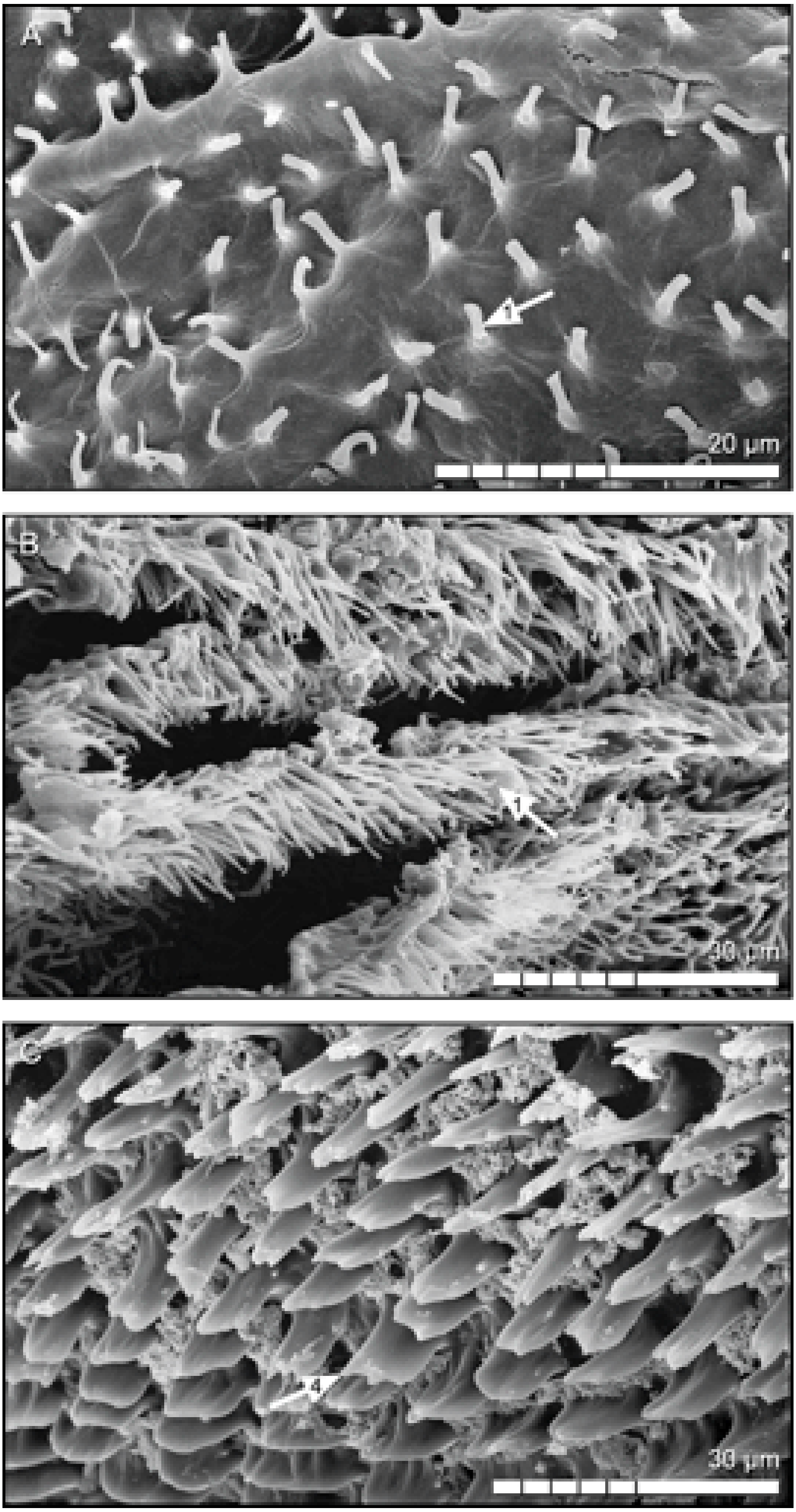

A
1
20 µm
B
1
30 µm
C
4
30 µm

Plate 122. *Heteroscorpion opisthacanthoides* (Kraepelin, 1896), 1 subad. ♂ (AMNH [LP 2706]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with chisel-like structures (arrow), anterior view. Numbers in arrows refer to character states.

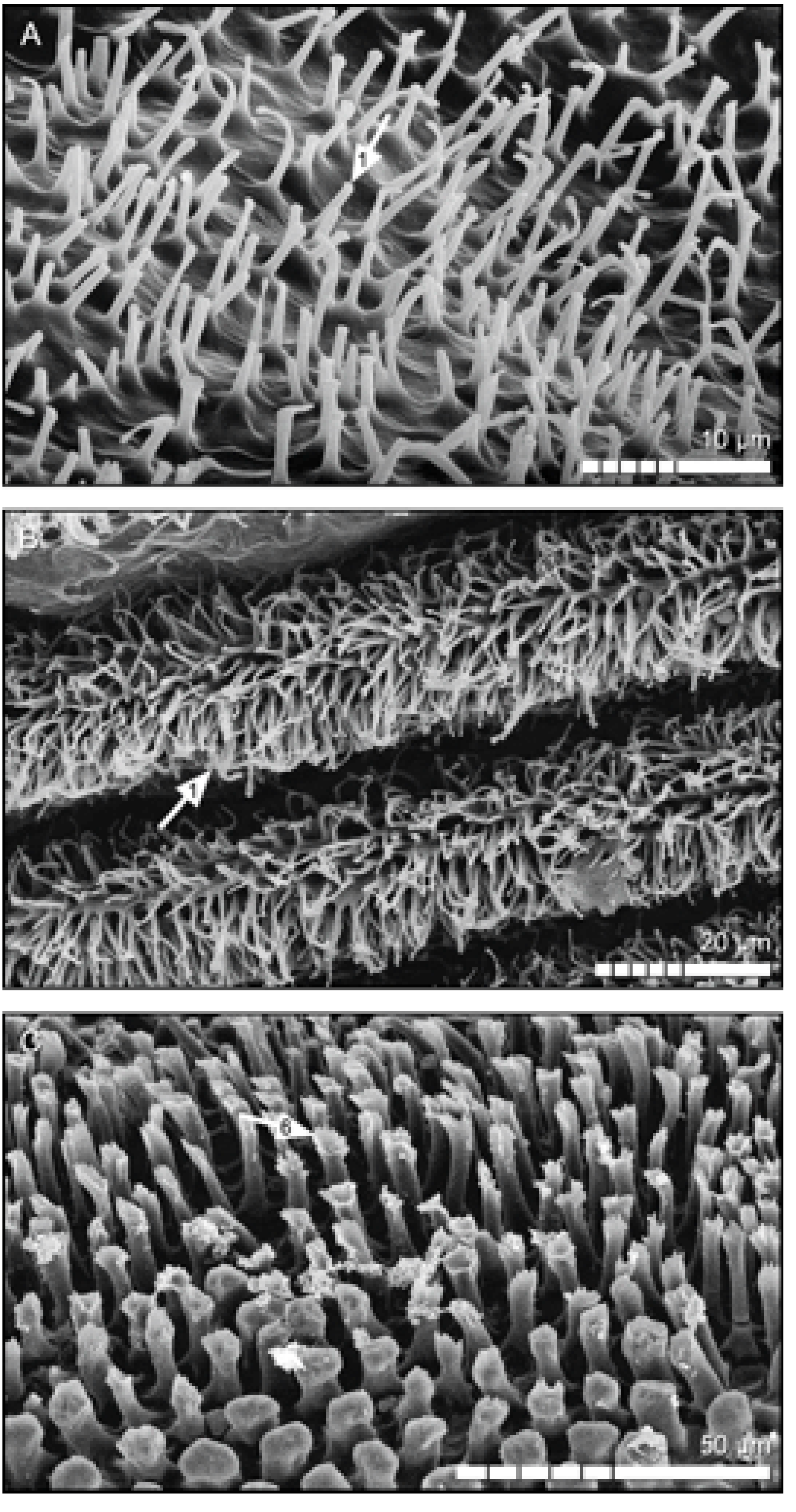

A
10 µm
B
20 µm
C
50 µm

Plate 123. *Hemiscorpius lepturus* Peters, 1861, 1 ♀ (AMNH [LP 4343]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with strong, rigid spines (arrow), posterior view; **C.** movable posterior edge of spiracle with hexagonal tiles (arrow), anterior view. Numbers in arrows refer to character states.

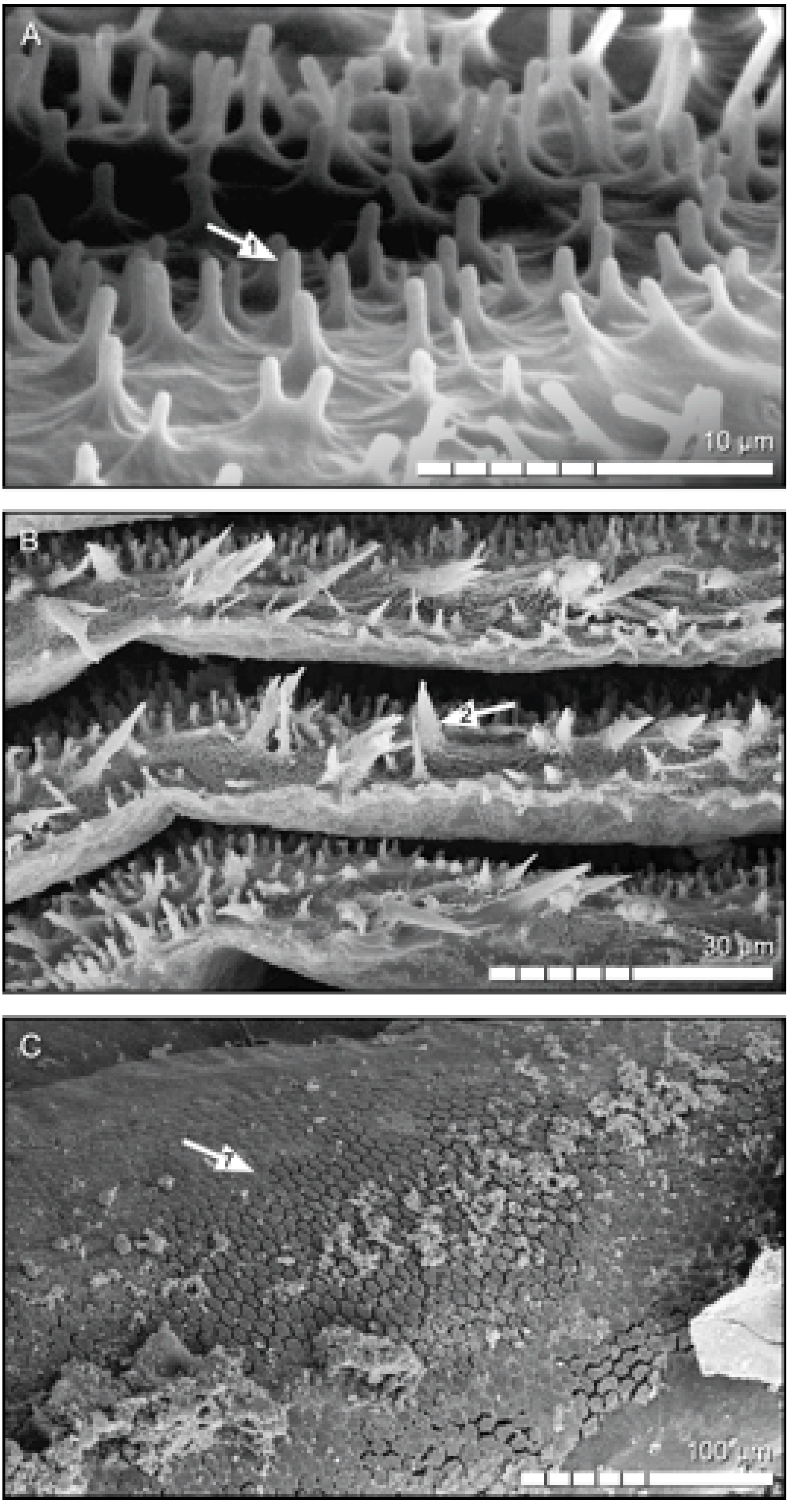

A
10 µm
B
30 µm
C
100 µm

Plate 124. *Cheloctonus anthracinus warreni* Hewitt, 1931, 1 ♀ (MNHN RS 0374): **A.** book lung lamella, smooth dorsal surface, ventral surface with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with columnar structures with hexagonal tiles (arrow), anterior view. Numbers in arrows refer to character states.

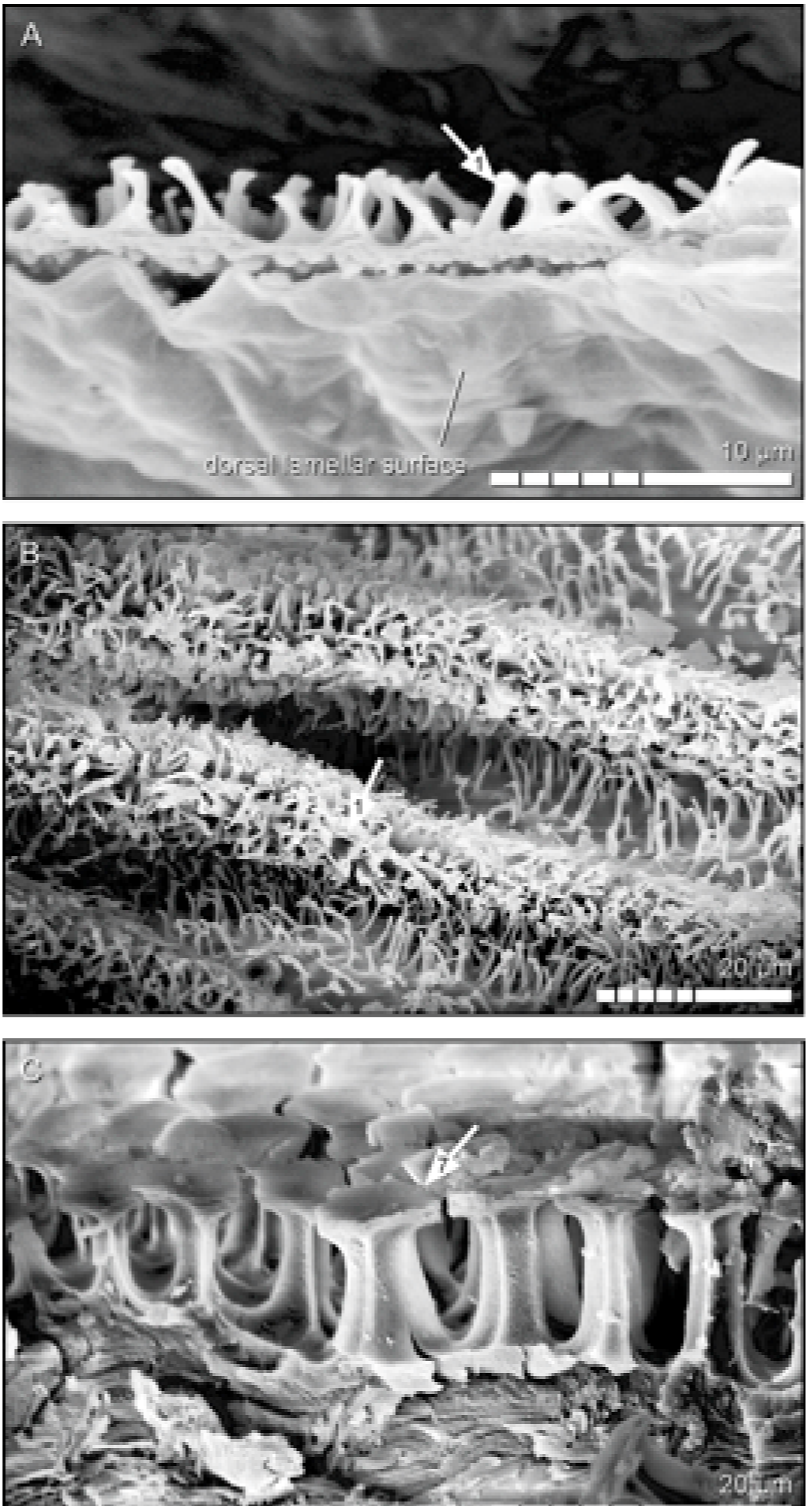

A
dorsal lamellar surface
10 µm
B
20 µm
C

Plate 125. *Cheloctonus jonesii* Pocock, 1892, 1 juv. ♀ (AMNH [LP 1558]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with hexagonal tiles (arrow), anterior view. Numbers in arrows refer to character states.

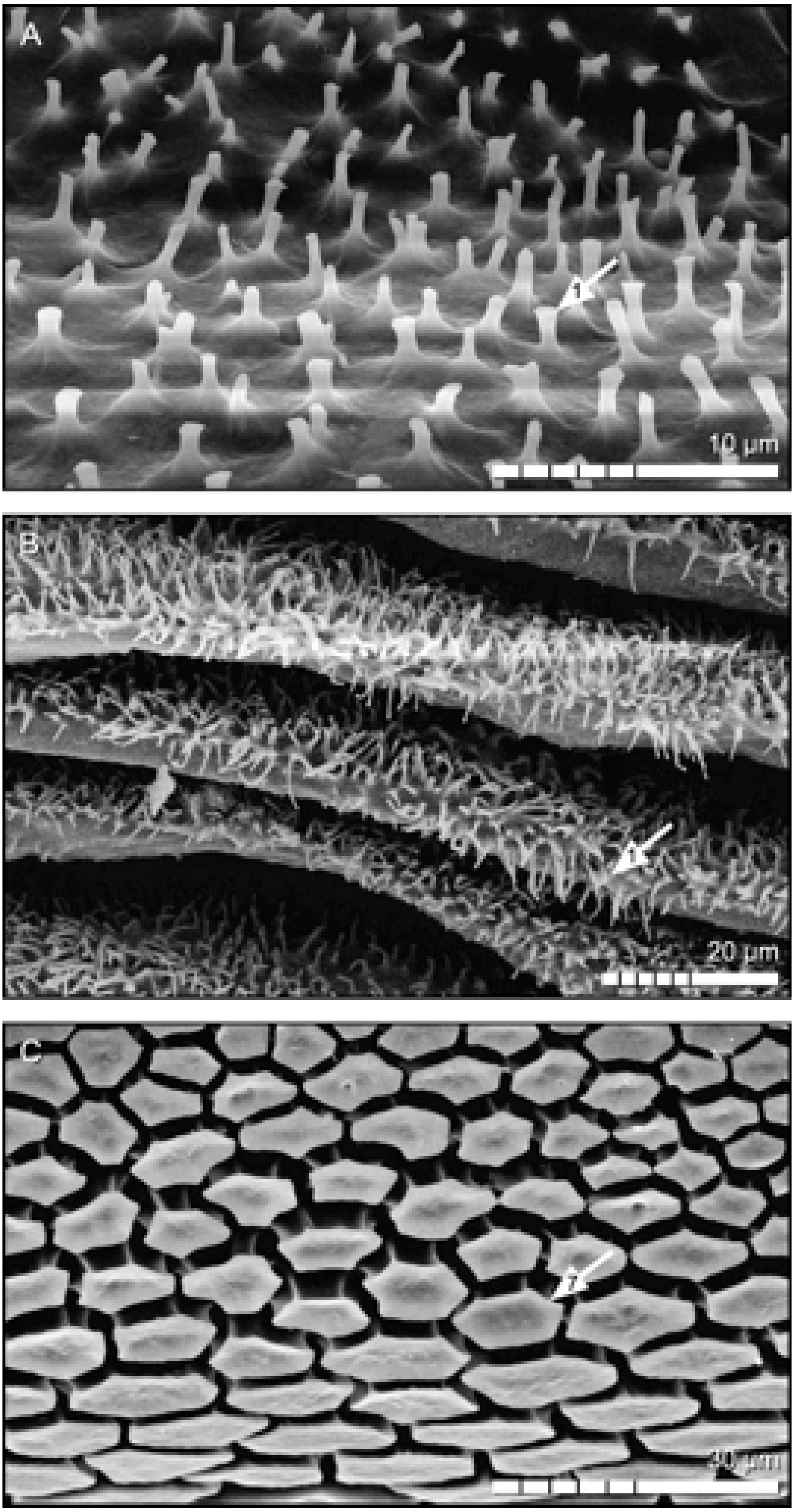

A
10 µm
B
20 µm
C

Plate 126. *Chiromachus ochropus* (C.L. Koch, 1837), 1 juv. ♀ (AMNH [LP 2189]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with hexagonal tiles (arrow), anterior view. Numbers in arrows refer to character states.

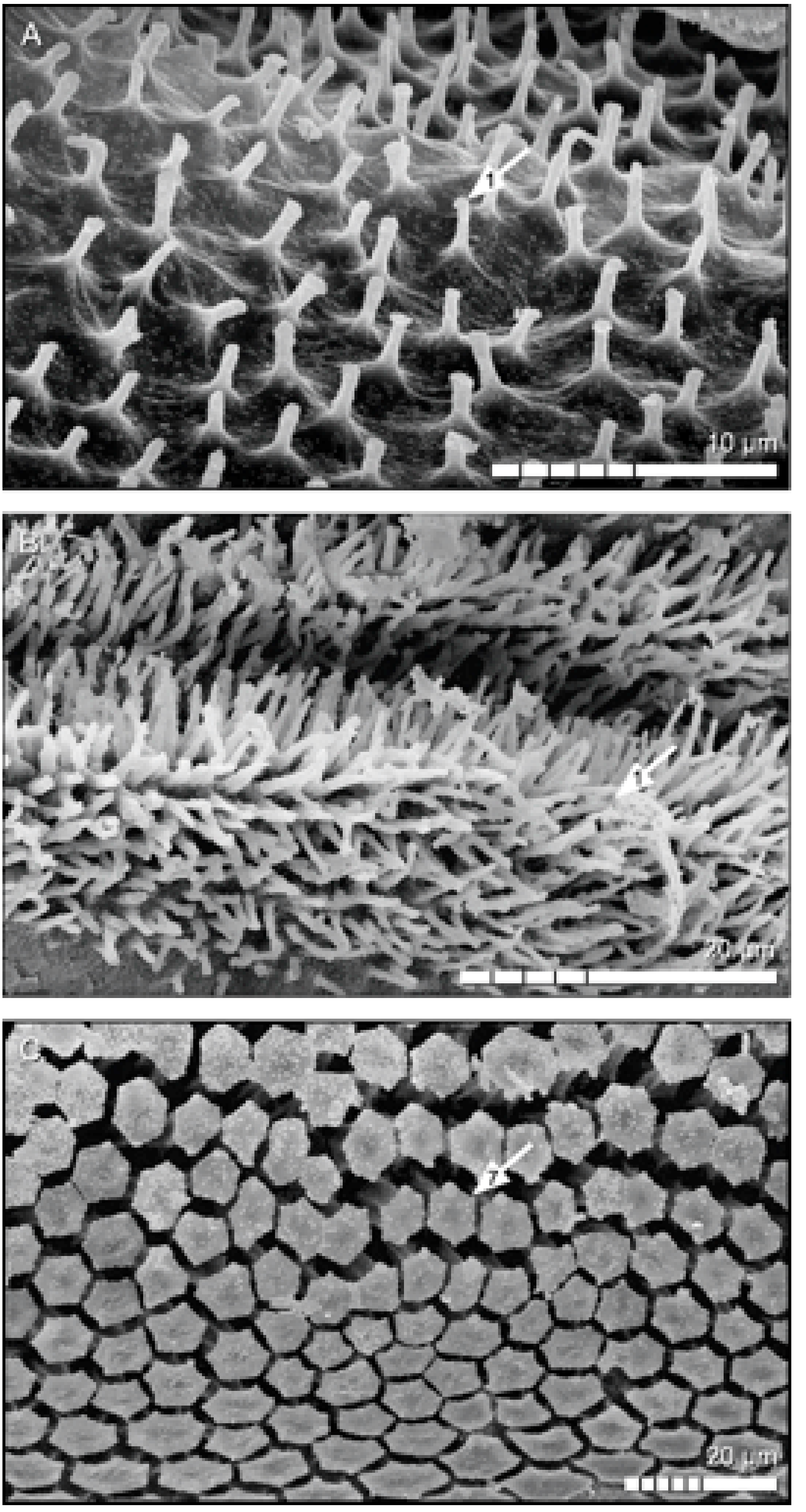

A
10 μm
B
20 μm
C
20 μm

Plate 127. *Hadogenes trichiurus trichiurus* (Gervais, 1843), 1 ♂ (AMNH [LP 3402]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), sometimes branched, viewed from air space; **B.** distal edges of book lung lamellae covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with hexagonal tiles (arrow), anterior view. Numbers in arrows refer to character states.

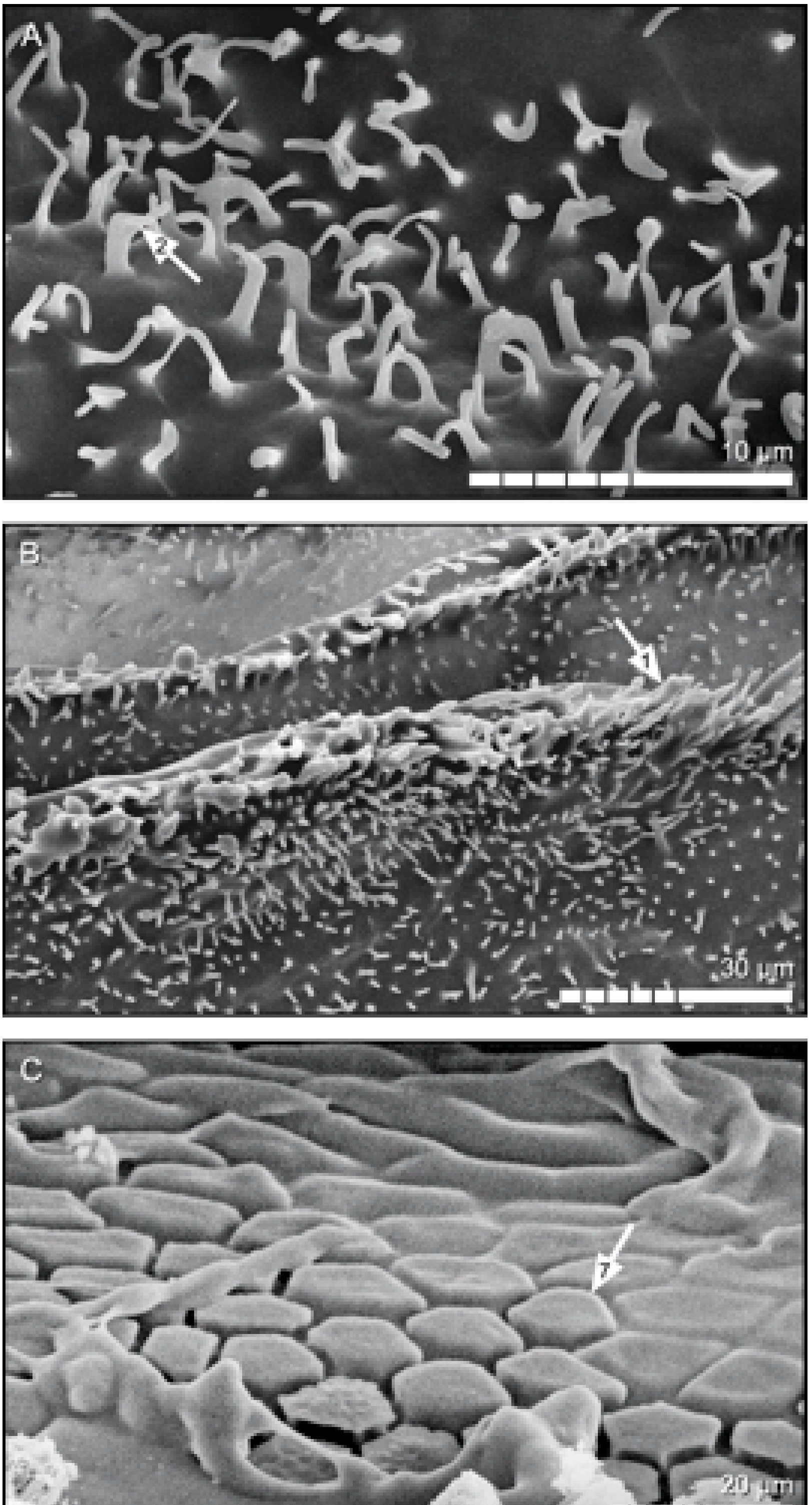

A
10 µm
B
30 µm
C
20 µm

Plate 128. *Hadogenes troglodytes troglodytes* (Peters, 1861), 1 ♂ (AMNH [LP 1315]): **A.** ventral surface of book lung lamella with branched trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae densely covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with hexagonal tiles (arrow), anterior view. Numbers in arrows refer to character states.

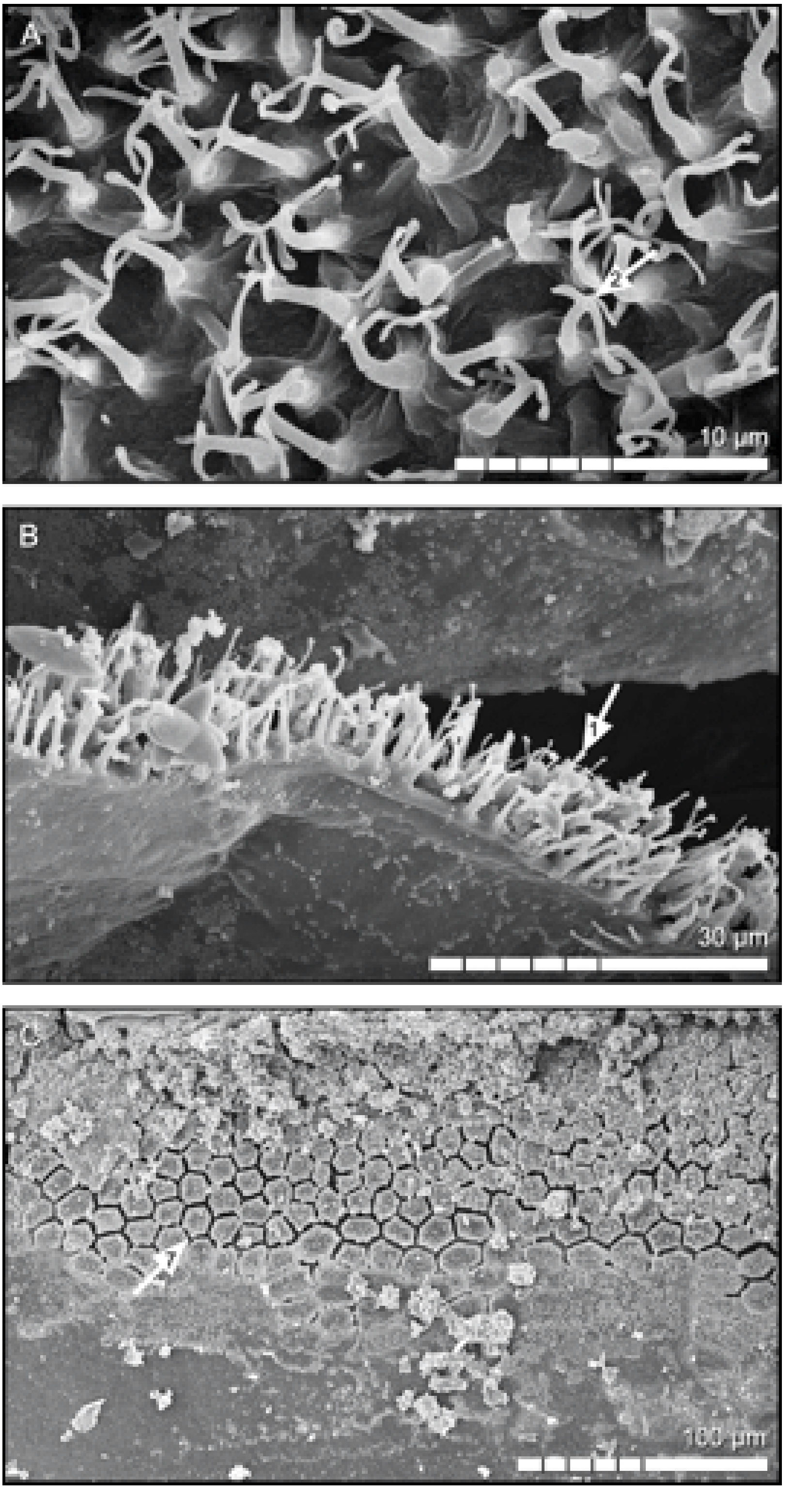

A
2
10 µm
B
1
30 µm
C
1
100 µm

Plate 129. *Hadogenes* sp., 1 ♀ (AMNH [LP 1794]): **A.** ventral surface of book lung lamella with branched trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with hexagonal tiles (arrow), anterior view. Numbers in arrows refer to character states.

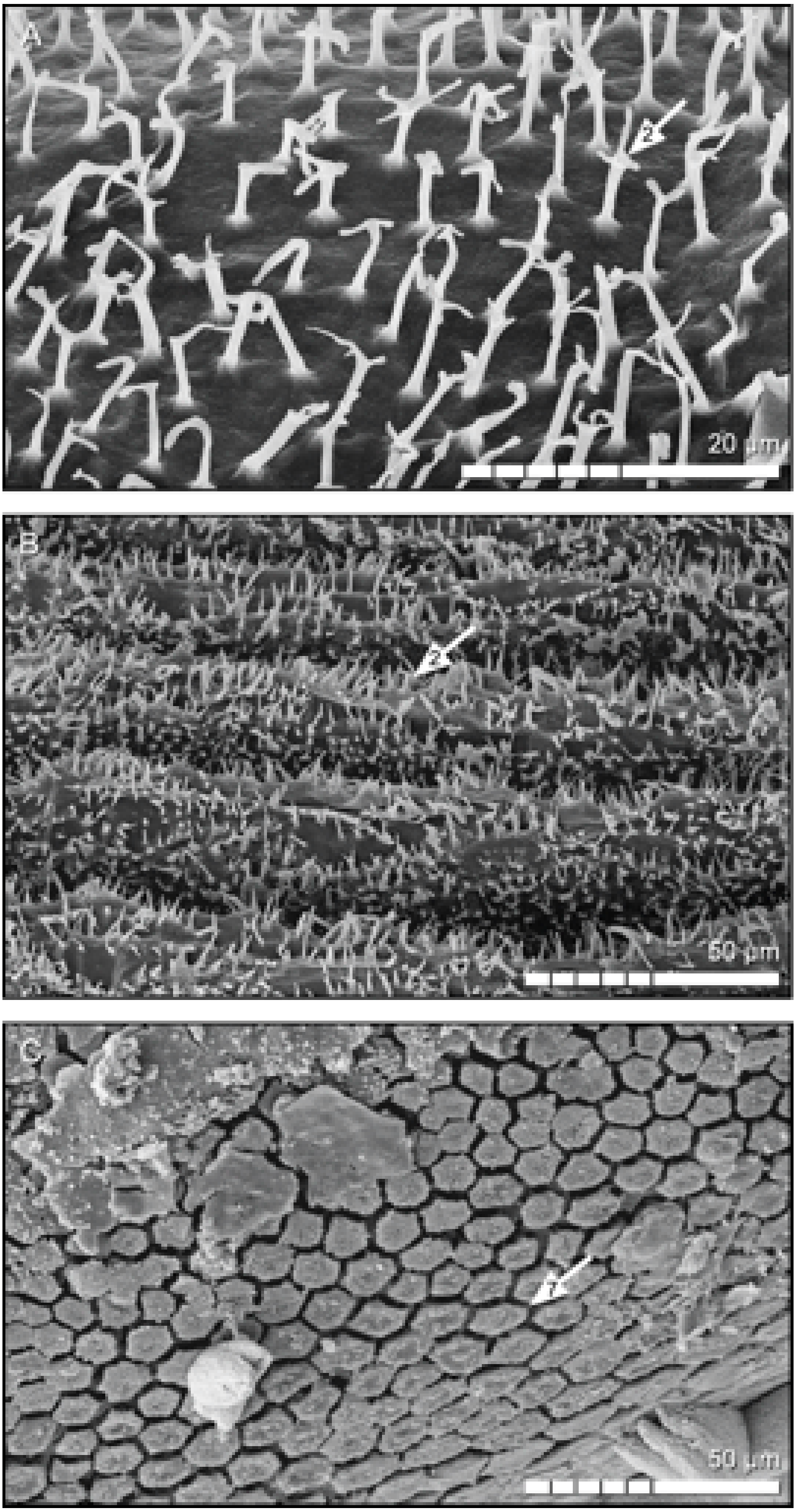

A
20 µm
B
50 µm
C
50 µm

Plate 130. *Iomachus politus* Pocock, 1896, 1 ♂ (AMNH [LP 1514]): **A.** ventral surface of book lung lamella with branched trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with hexagonal tiles (arrow), anterior view. Numbers in arrows refer to character states.

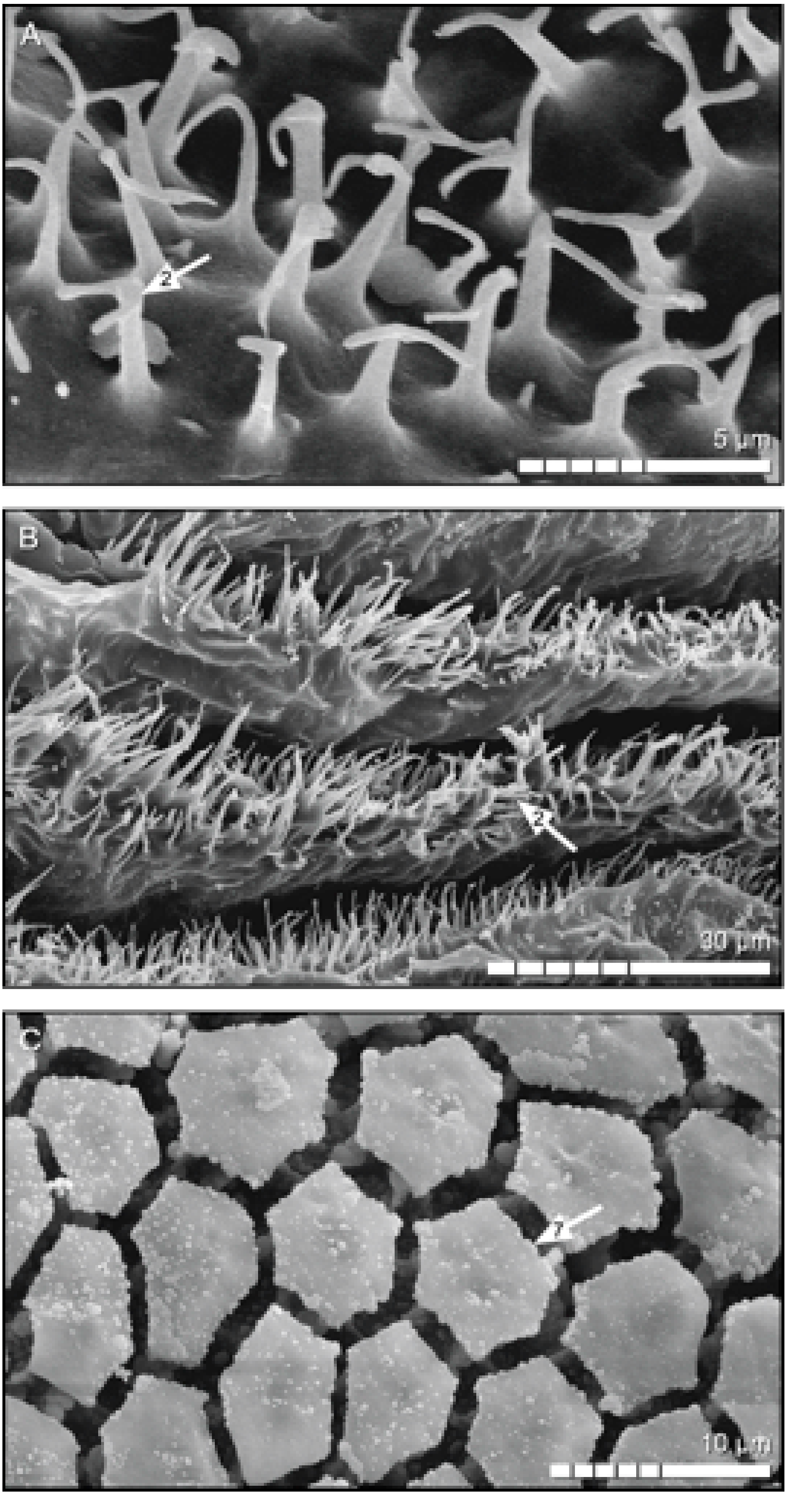

A
5 µm
B
30 µm
C
10 µm

Plate 131. *Liocheles australasiae* (Fabricius, 1775), 1 ♀ (AMNH [LP 1854]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** arcuate distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with hillocklike structures (arrow), anterior view. Numbers in arrows refer to character states.

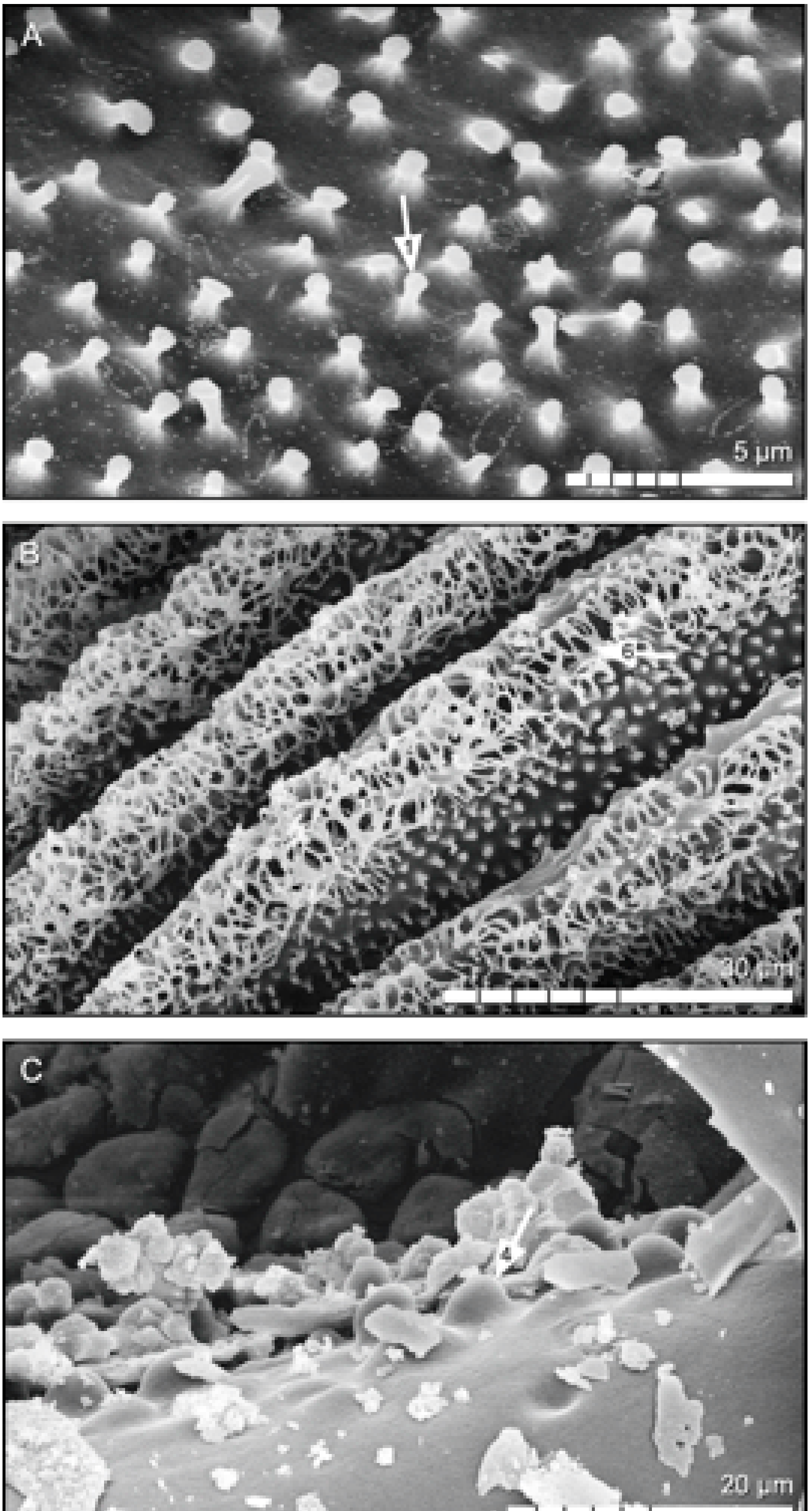

A
5 µm
B
C
20 µm

Plate 132. *Liocheles australasiae* (Fabricius, 1775), 1 ♀ (AMNH [LP 4764]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** arcuate distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with chisel-like structures (arrow), anterior view. Numbers in arrows refer to character states.

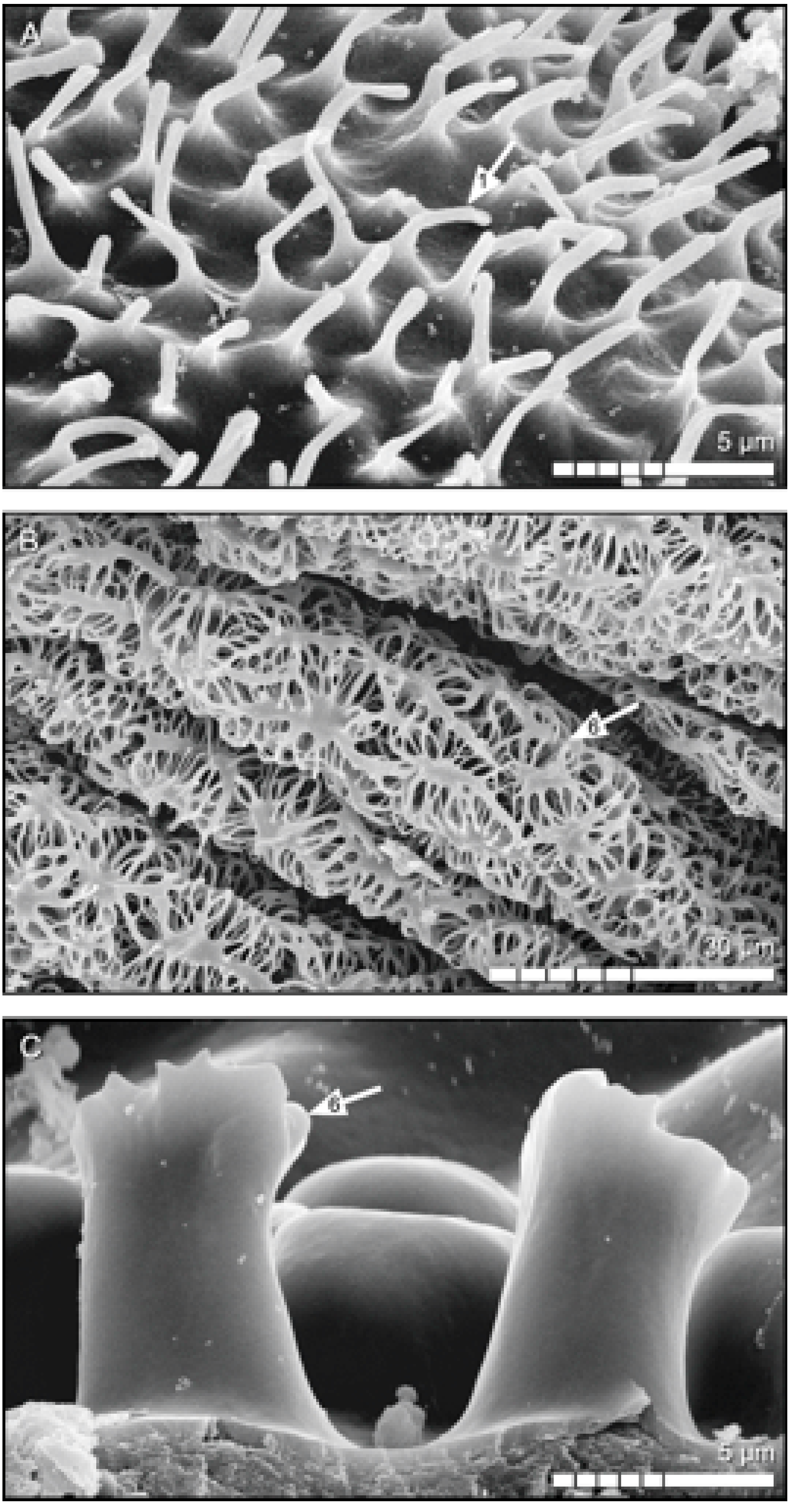

A
5 µm
B
30 µm
C
5 µm

Plate 133. *Liocheles waigiensis* (Gervais, 1843), 1 ♀ (AMNH [LP 1502]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** arcuate distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with flattened to chisel-like structures (arrow), anterior view. Numbers in arrows refer to character states.

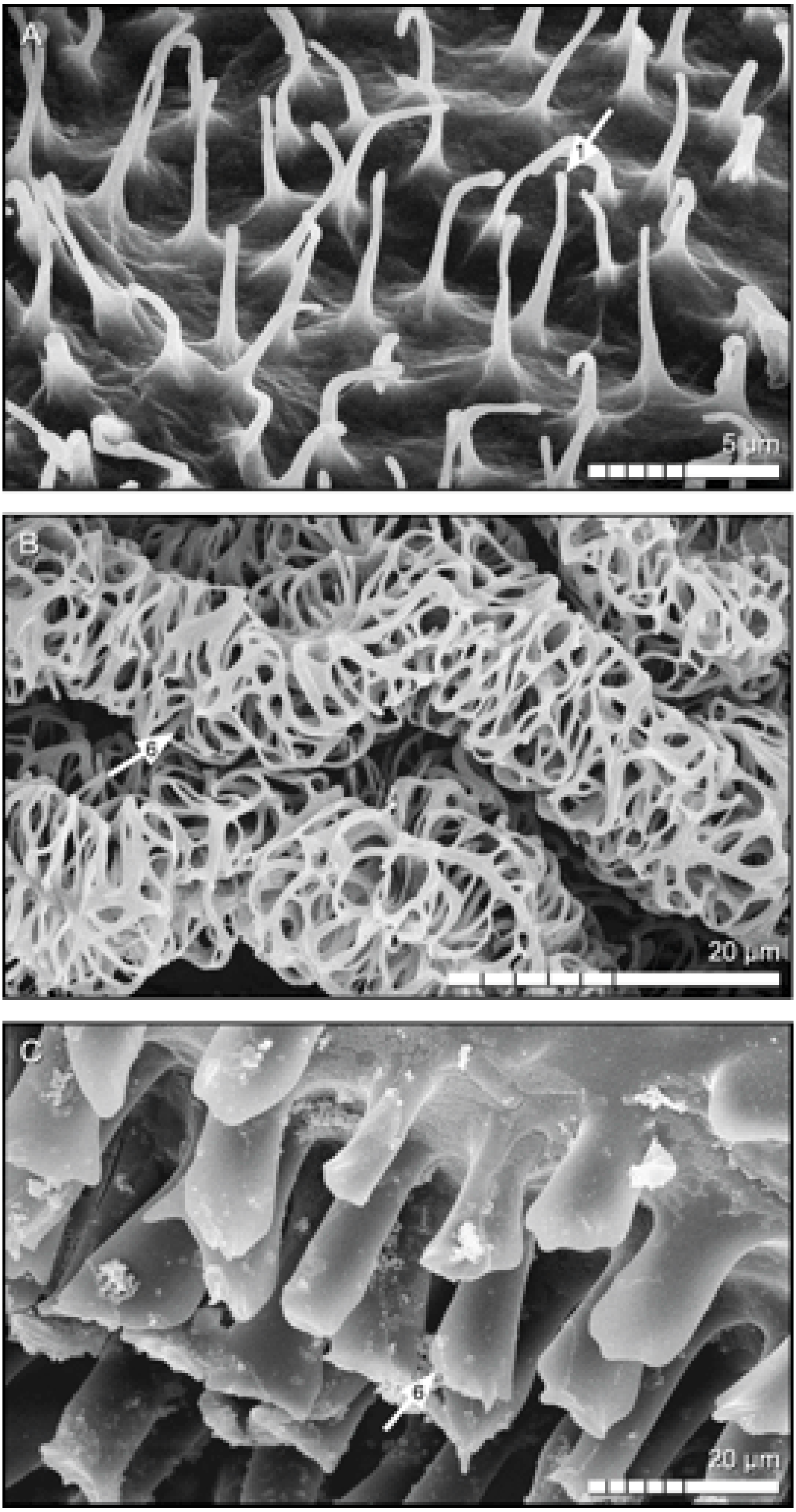

A
1
5 µm
B
6
20 µm
C
6
20 µm

Plate 134. *Liocheles waigiensis* (Gervais, 1843), 1 ♀ (MNHN RS 8350): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** arcuate distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with chisel-like structures (arrow), anterior view. Numbers in arrows refer to character states.

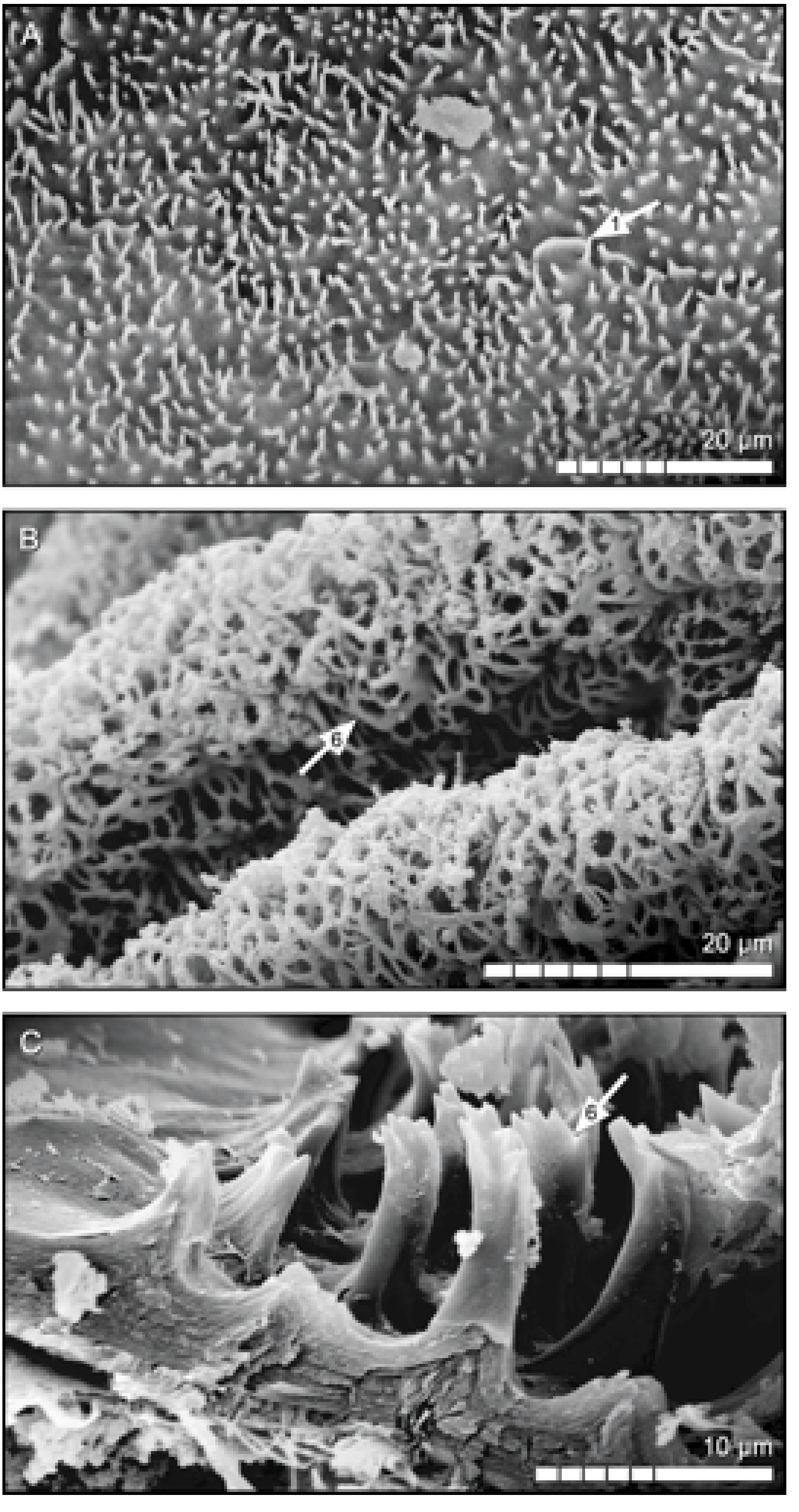

A
1
20 µm
B
6
20 µm
C
6
10 µm

Plate 135. *Opisthacanthus elatus* (Gervais, 1844), 1 ♀ (AMNH [LP 1837]): **A.** ventral surface of book lung lamella with branched trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with hexagonal tiles (arrow), anterior view. Numbers in arrows refer to character states.

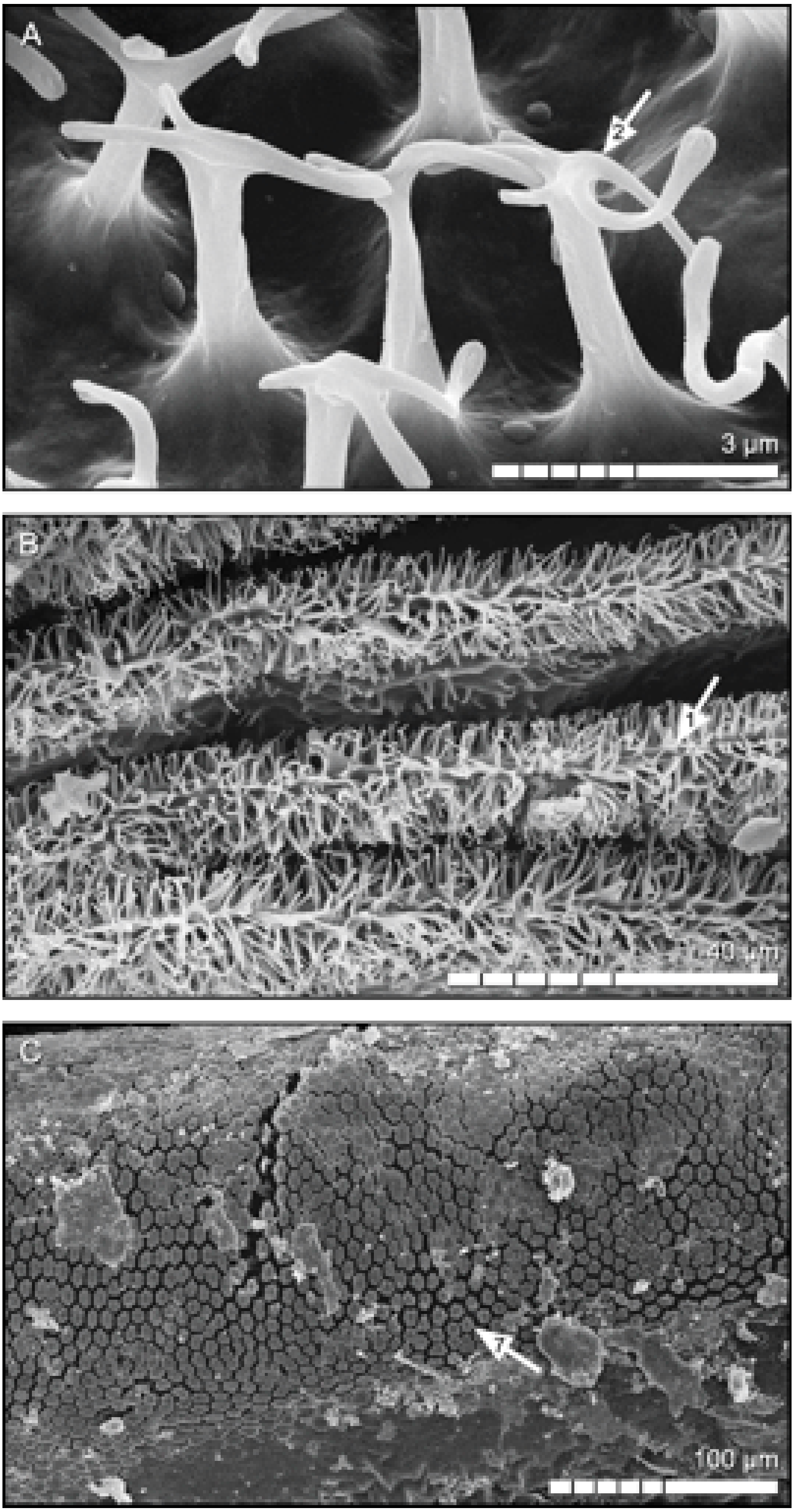

A
3 µm
B
40 µm
C
100 µm

Plate 136. *Opisthacanthus madagascariensis* Kraepelin, 1894, 1 ♀ (AMNH [LP 2799]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with hexagonal tiles (arrow), anterior view. Numbers in arrows refer to character states.

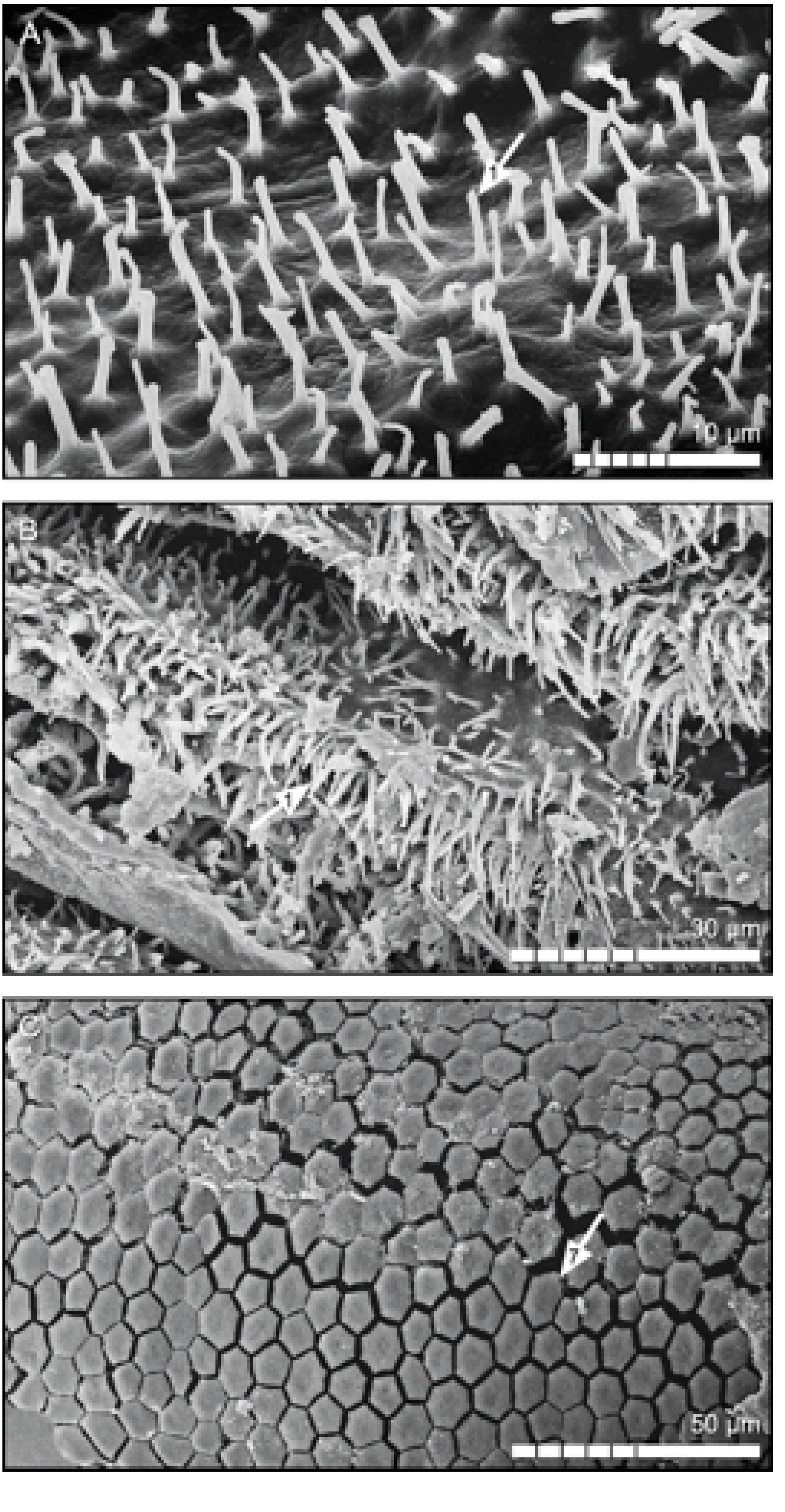

A
10 µm
B
30 µm
C
50 µm

Plate 137. *Opisthacanthus validus* Thorell, 1876, 1 juv. ♀ (AMNH [LP 3379]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), rarely branched, viewed from air space; **B.** distal edges of book lung lamellae covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with hexagonal tiles (arrow), transition to atrial wall, anterior view. Numbers in arrows refer to character states.

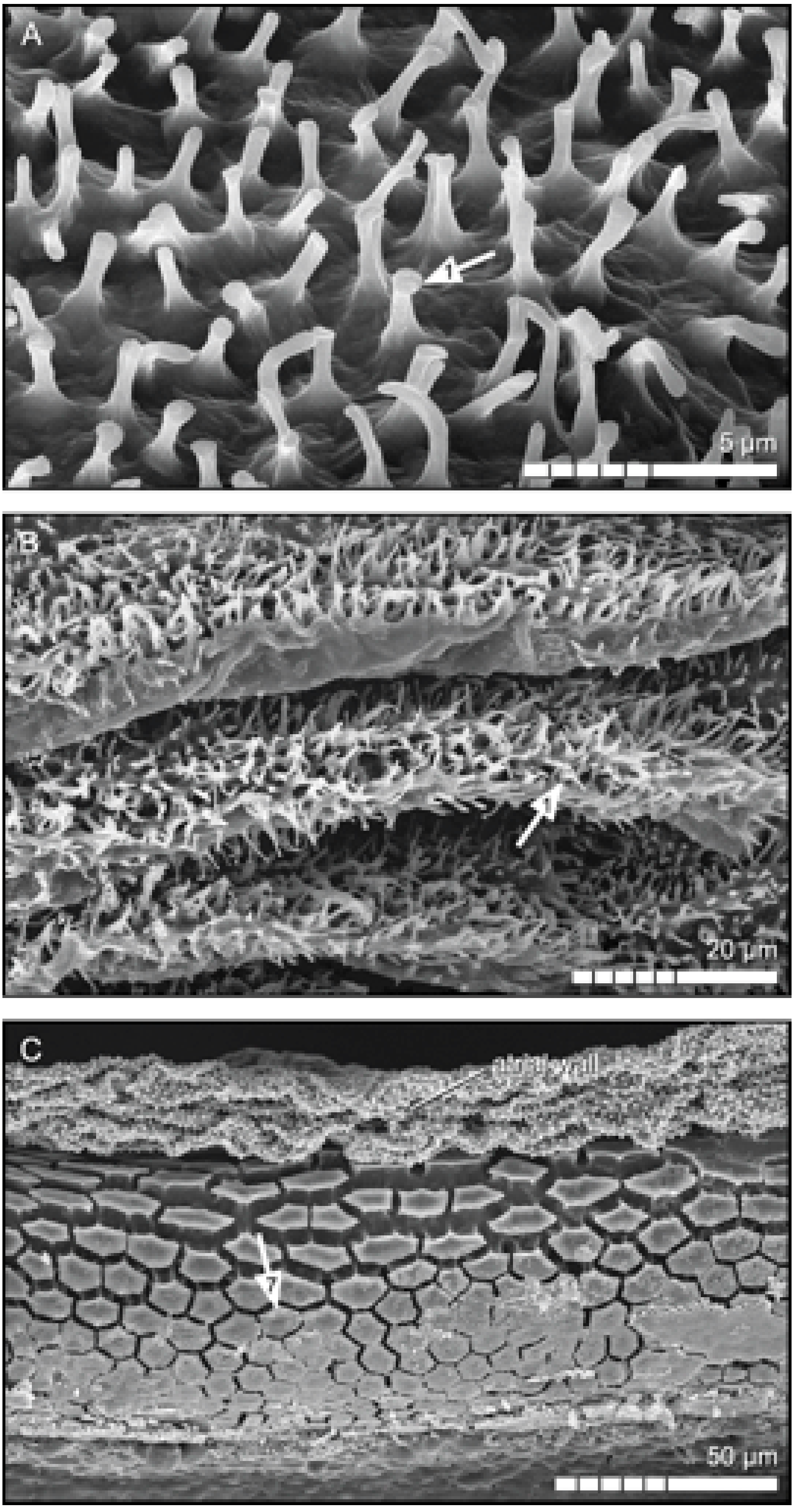

A
5 µm
B
20 µm
C
50 µm

Plate 138. *Palaeocheloctonus pauliani* Lourenço, 1996, 1 ex. (MNHN RS 3970): **A.** ventral surface of book lung lamella with branched (arrow) and simple trabeculae, viewed from air space; **B.** distal edges of book lung lamellae covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with hexagonal tiles (arrow), anterior view. Numbers in arrows refer to character states.

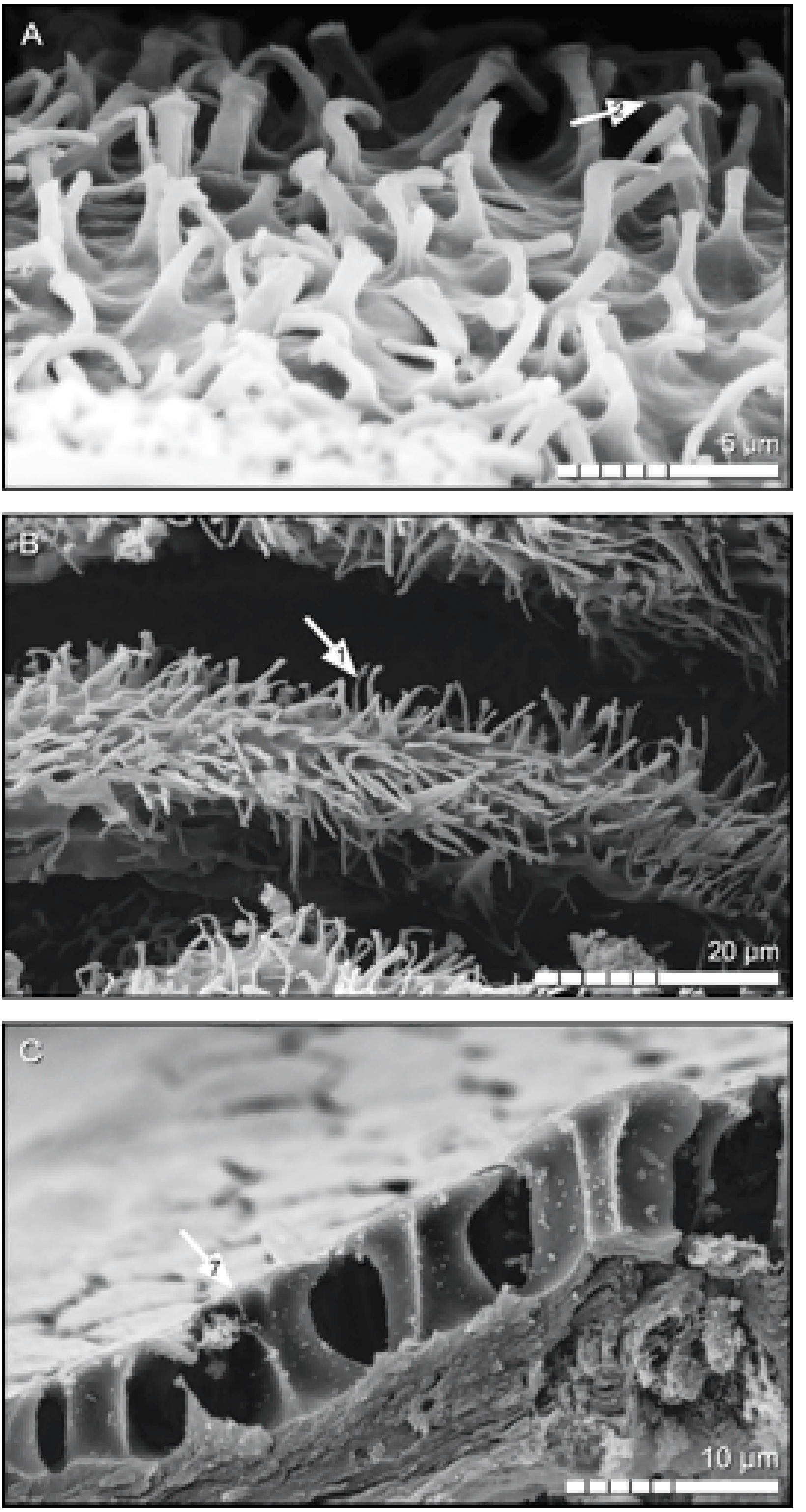

A
6 µm
B
1
20 µm
C
7
10 µm

Plate 139. *Bioculus comondae* Stahnke, 1968, 1 juv. ♀ (AMNH [LP 4738]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** arcuate distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with hexagonal tiles (arrow), anterior view. Numbers in arrows refer to character states.

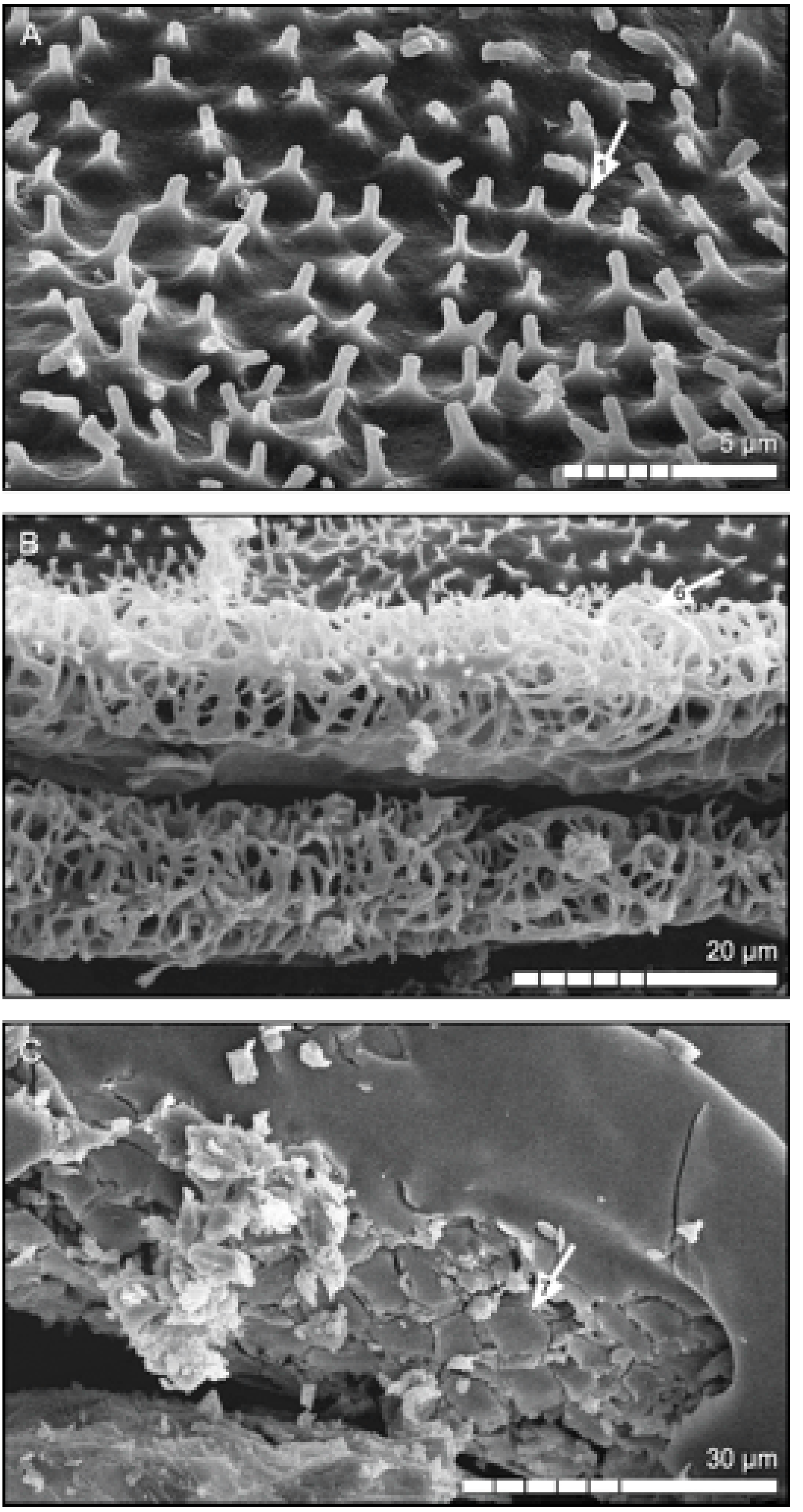

A
5 µm
B
20 µm
C
30 µm

Plate 140. *Cazierius gundlachii* (Karsch, 1880), 1 ♂ (AMNH [LP 1779]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** arcuate distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with hexagonal tiles (arrow), anterior view. Numbers in arrows refer to character states.

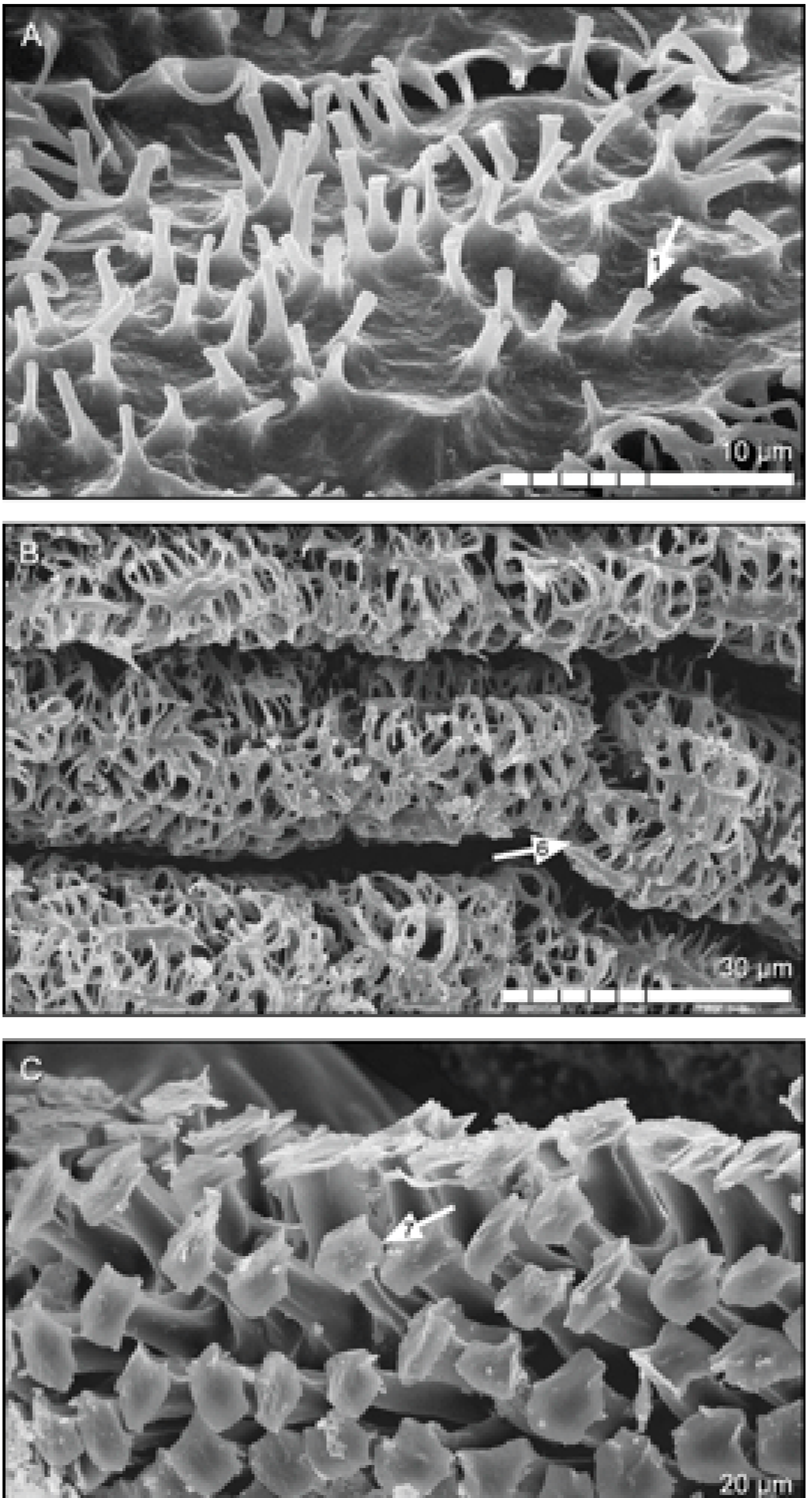

A
1
10 µm
B
6
30 µm
C
7
20 µm

Plate 141. *Didymocentrus lesueurii* (Gervais, 1844), 1 ♀ (AMNH [LP 3638]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** arcuate distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with hexagonal tiles (arrow), anterior view. Numbers in arrows refer to character states.

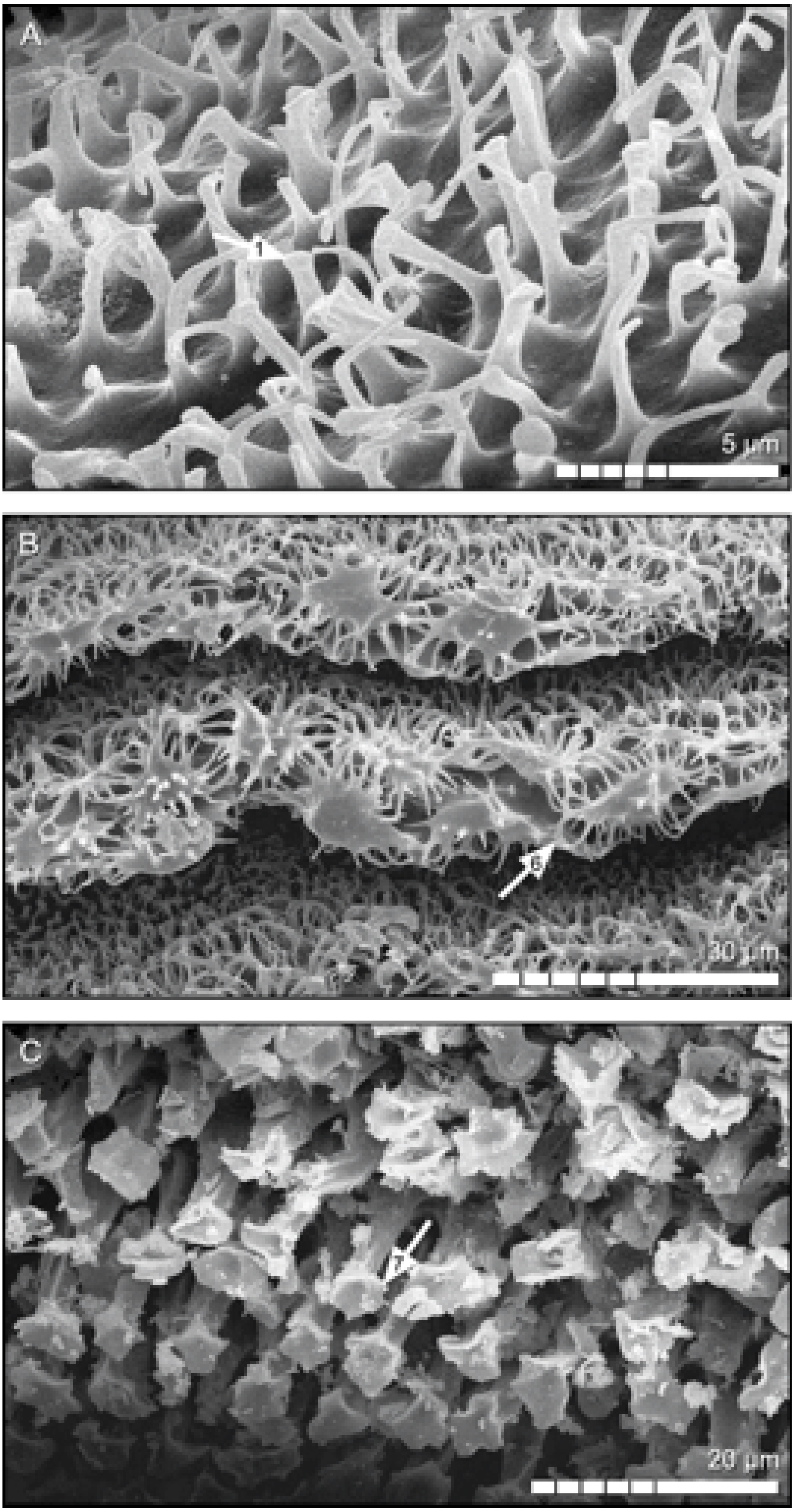

A
1
5 µm
B
6
30 µm
C
7
20 µm

Plate 142. *Diplocentrus mexicanus mexicanus* Peters, 1861, 1 ♀ (AMNH [LP 2055]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** arcuate distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with hexagonal tiles (arrow), anterior view. Numbers in arrows refer to character states.

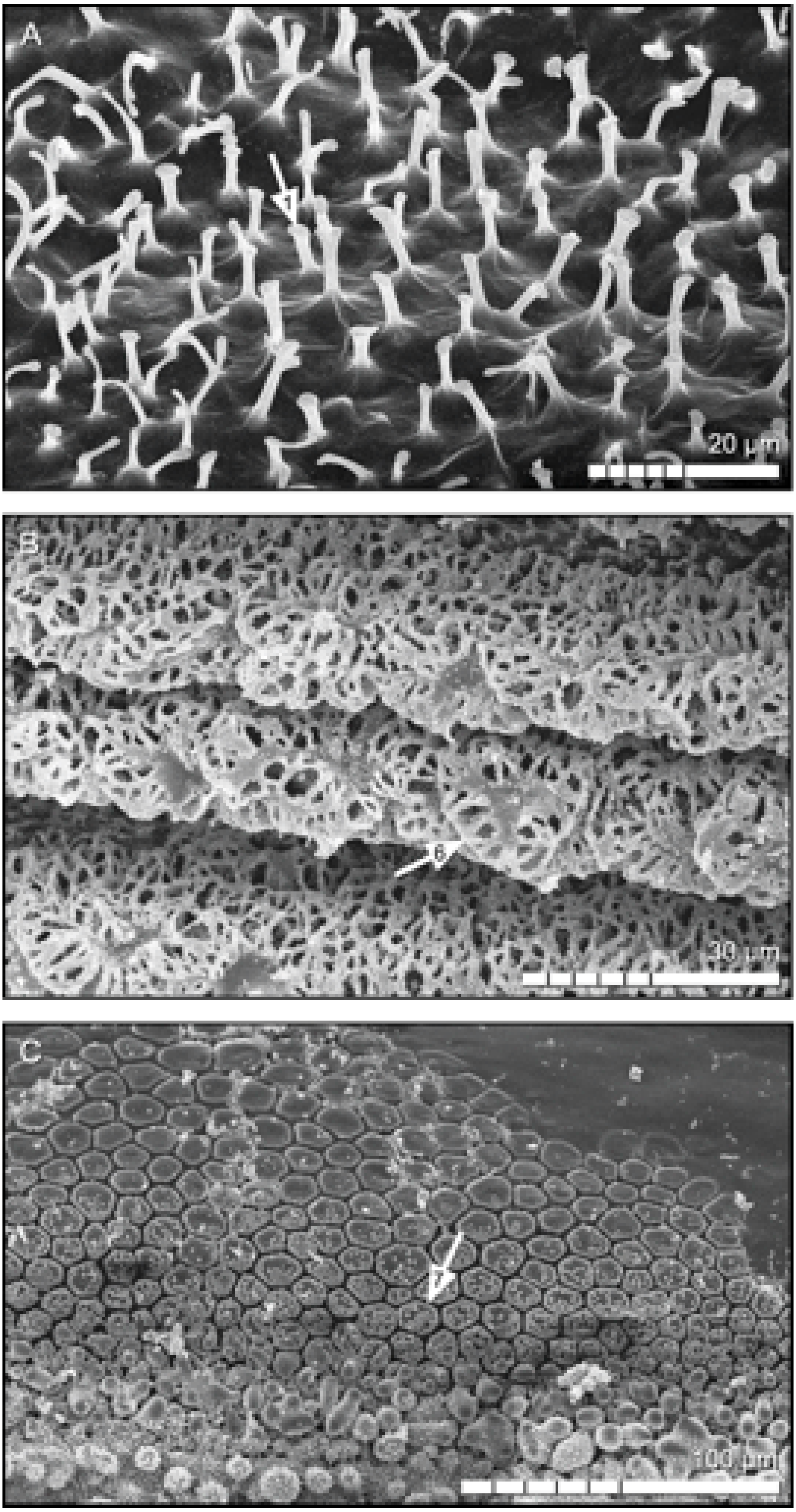

A
20 µm
B
30 µm
C
100 µm

Plate 143. *Heteronebo granti* Pocock, 1899, 1 juv. ♀ (AMNH [LP 1634]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** arcuate distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with hexagonal tiles (arrow), anterior view. Numbers in arrows refer to character states.

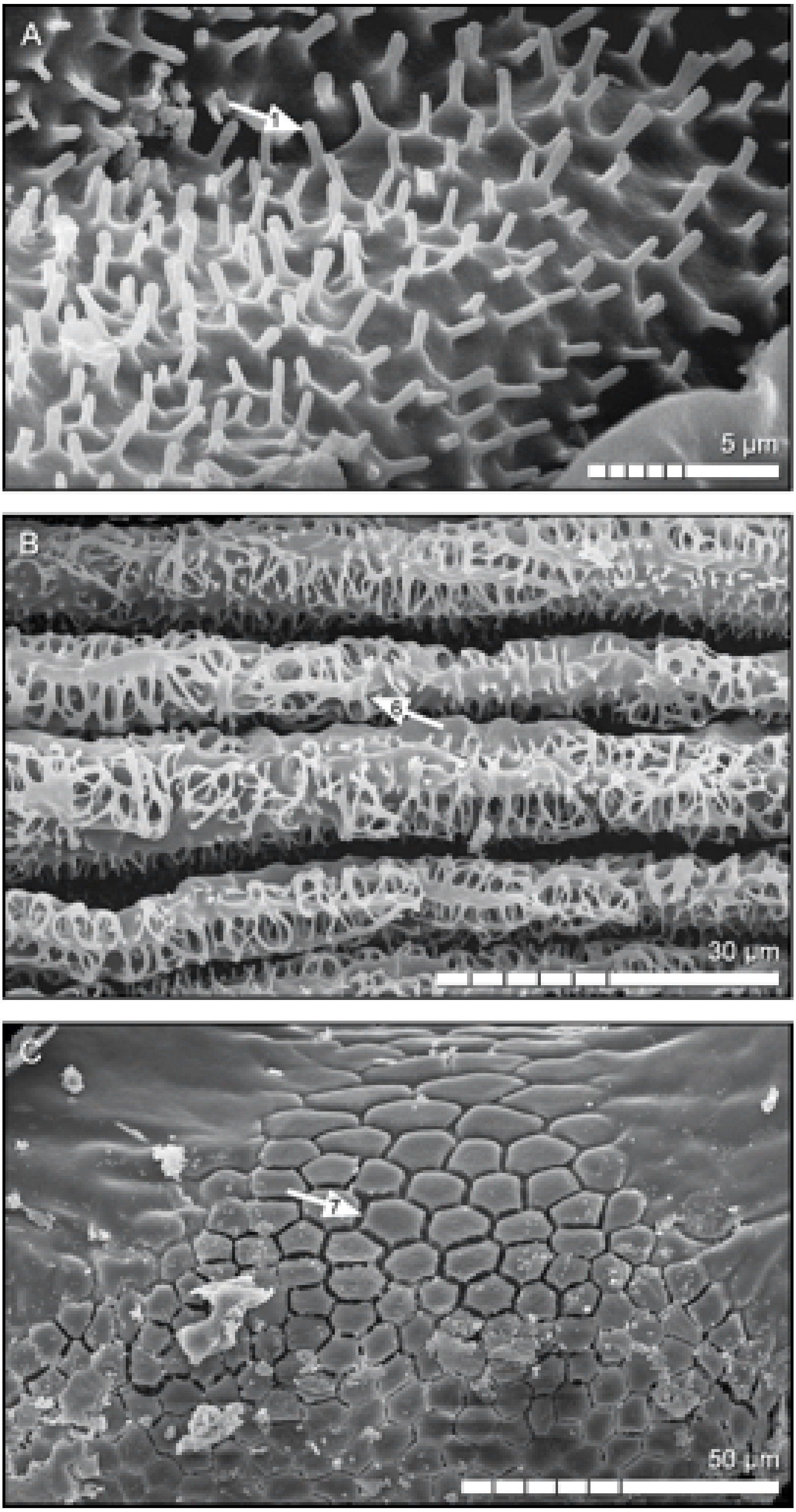

A
1
5 µm
B
6
30 µm
C
7
50 µm

Plate 144. *Nebo hierichonticus* (Simon, 1872), 1 juv. ♂ (AMNH [LP 1561]): **A.** ventral surface of book lung lamella with simple trabeculae (arrow), viewed from air space; **B.** arcuate distal edges of book lung lamellae (arrow), posterior view; **C.** movable posterior edge of spiracle with hexagonal tiles (arrow), anterior view. Numbers in arrows refer to character states.

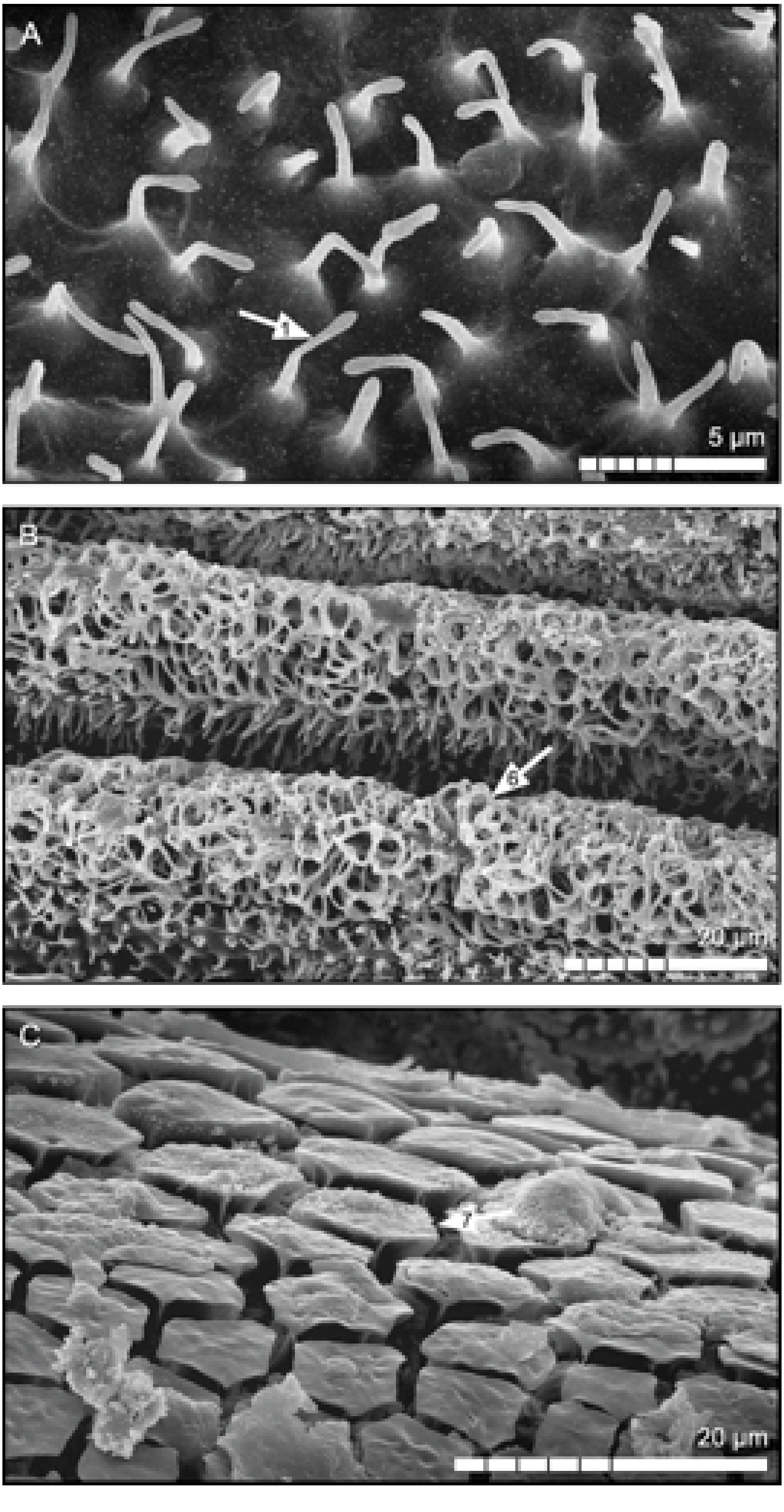

A
5 µm
B
20 µm
C
20 µm

Plate 145. *Heterometrus fulvipes* (C. L. Koch, 1837), 1 ♀ (AMNH [LP 4324]): **A.** ventral surface of book lung lamella with branched trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with hexagonal tiles (arrow), anterior view. Numbers in arrows refer to character states.

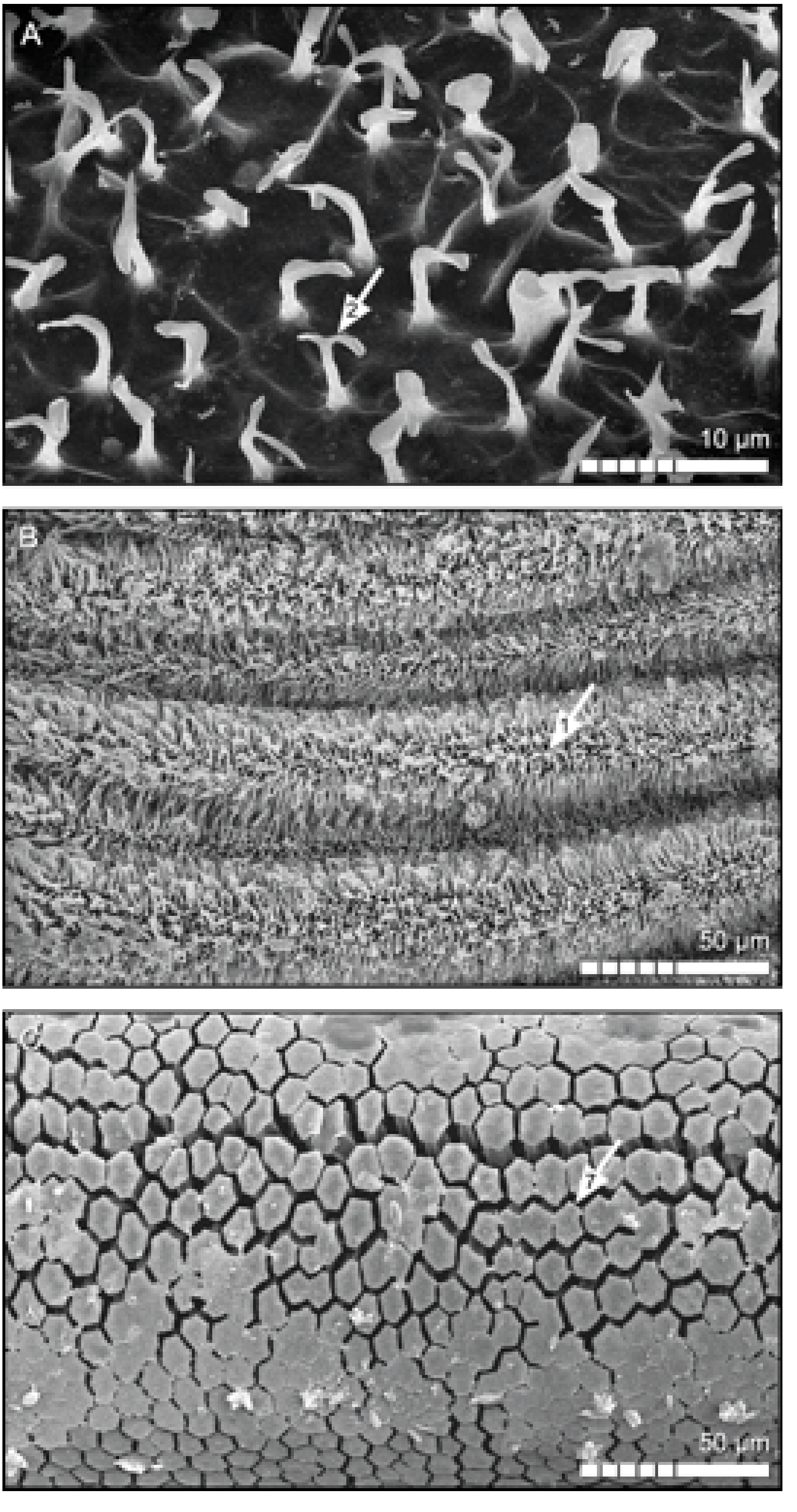

A
10 µm
B
50 µm
C
50 µm

Plate 146. *Heterometrus spinifer* (Ehrenberg, 1828), 1 ♂ (AMNH [LP 1604]): **A.** ventral surface of book lung lamella with branched trabeculae (arrow), viewed from air space; **B.** distal edge of book lung lamella covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with hexagonal tiles (arrow), anterior view. Numbers in arrows refer to character states.

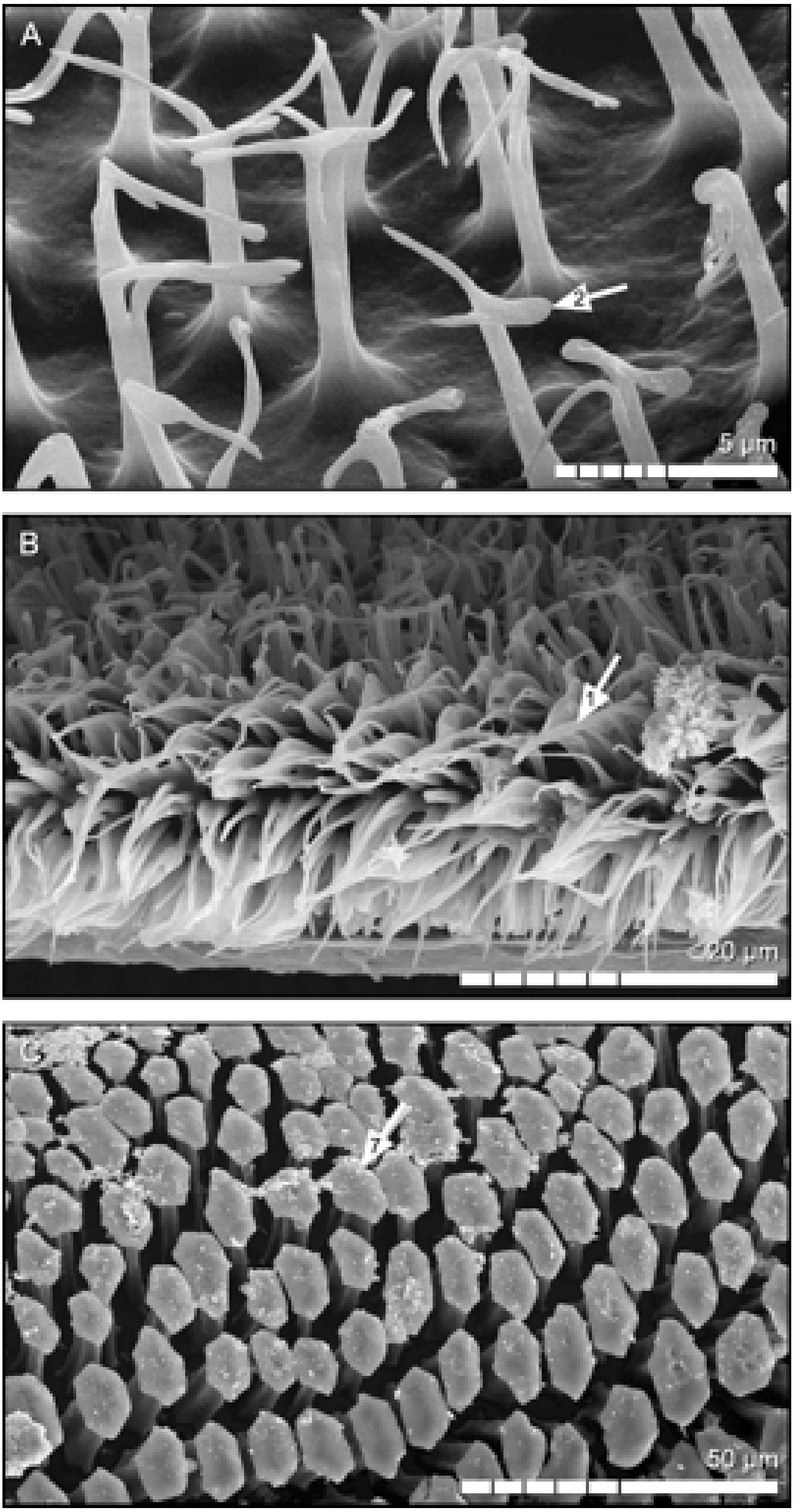

A
2
5 µm
B
1
20 µm
C
7
50 µm

Plate 147. *Heterometrus swammerdami* Simon, 1872, 1 ♂ (AMNH [LP 1607]): **A.** ventral surface of book lung lamella with branched trabeculae (arrow), viewed from air space; **B.** distal edge of book lung lamella covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with hexagonal tiles (arrow), anterior view. Numbers in arrows refer to character states.

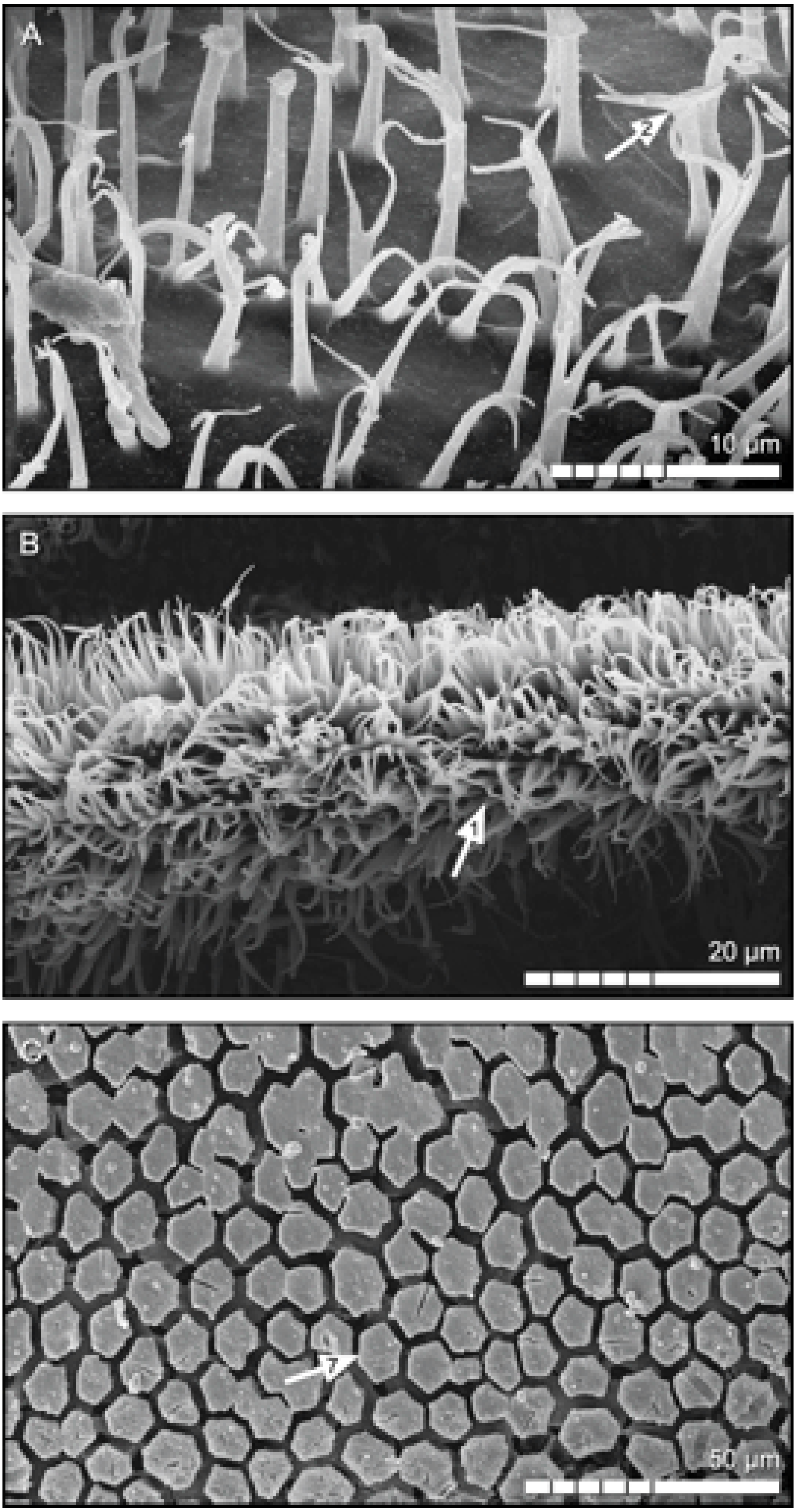

A
10 µm
B
20 µm
C
50 µm

Plate 148. *Opistophthalmus boehmi* (Kraepelin, 1896), 1 ♀ (AMNH [LP 1827]): **A.** ventral surface of book lung lamella with branched trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with spines (arrow), posterior view; **C.** movable posterior edge of spiracle with hexagonal tiles (arrow), anterior view. Numbers in arrows refer to character states.

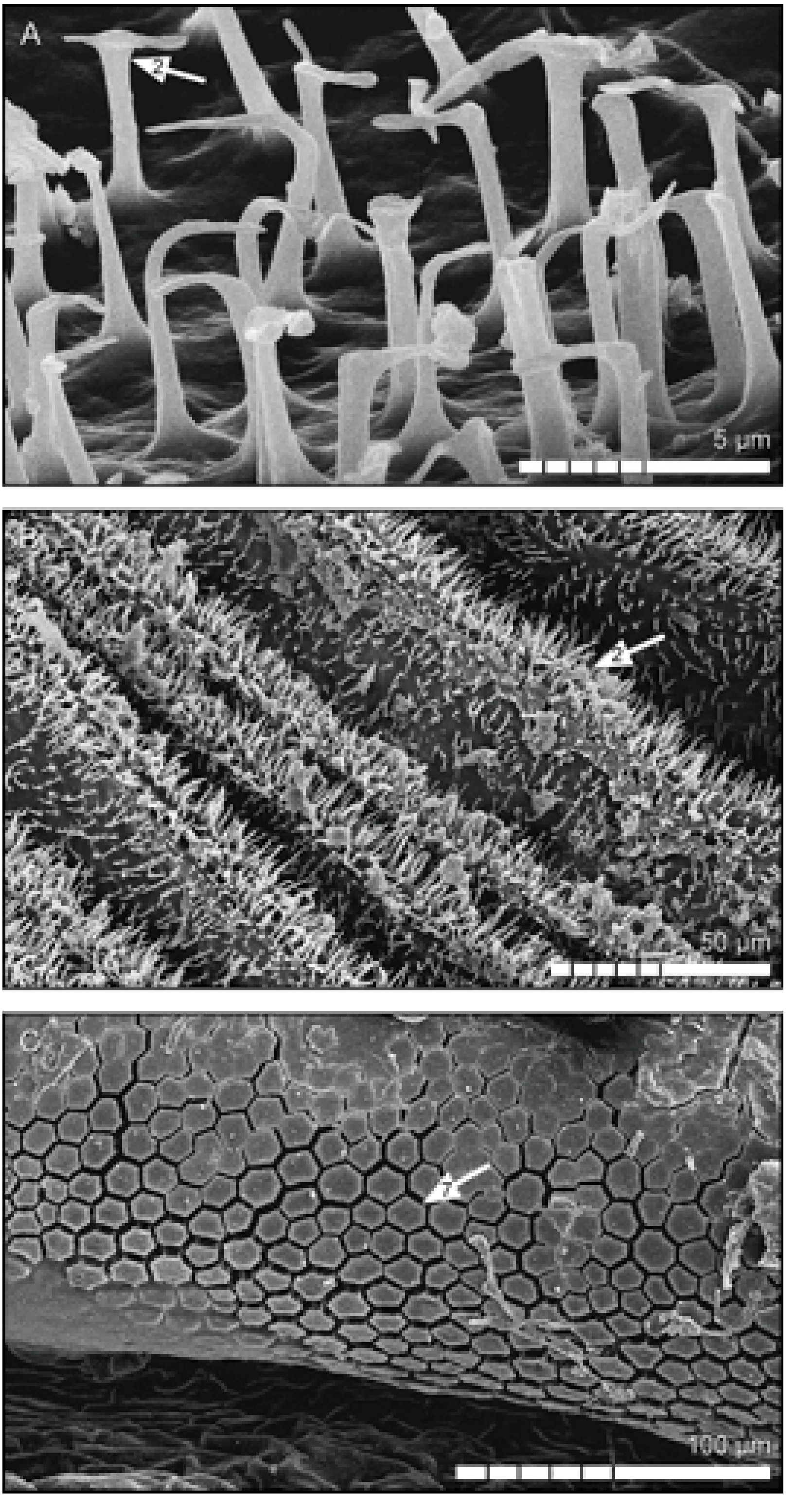

A
5 µm
B
50 µm
C
100 µm

Plate 149. *Opistophthalmus capensis* (Herbst, 1800), 1 ♀ (AMNH [AH 1266]): **A.** ventral surface of book lung lamella with branched trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with hexagonal tiles (arrow), anterior view. Numbers in arrows refer to character states.

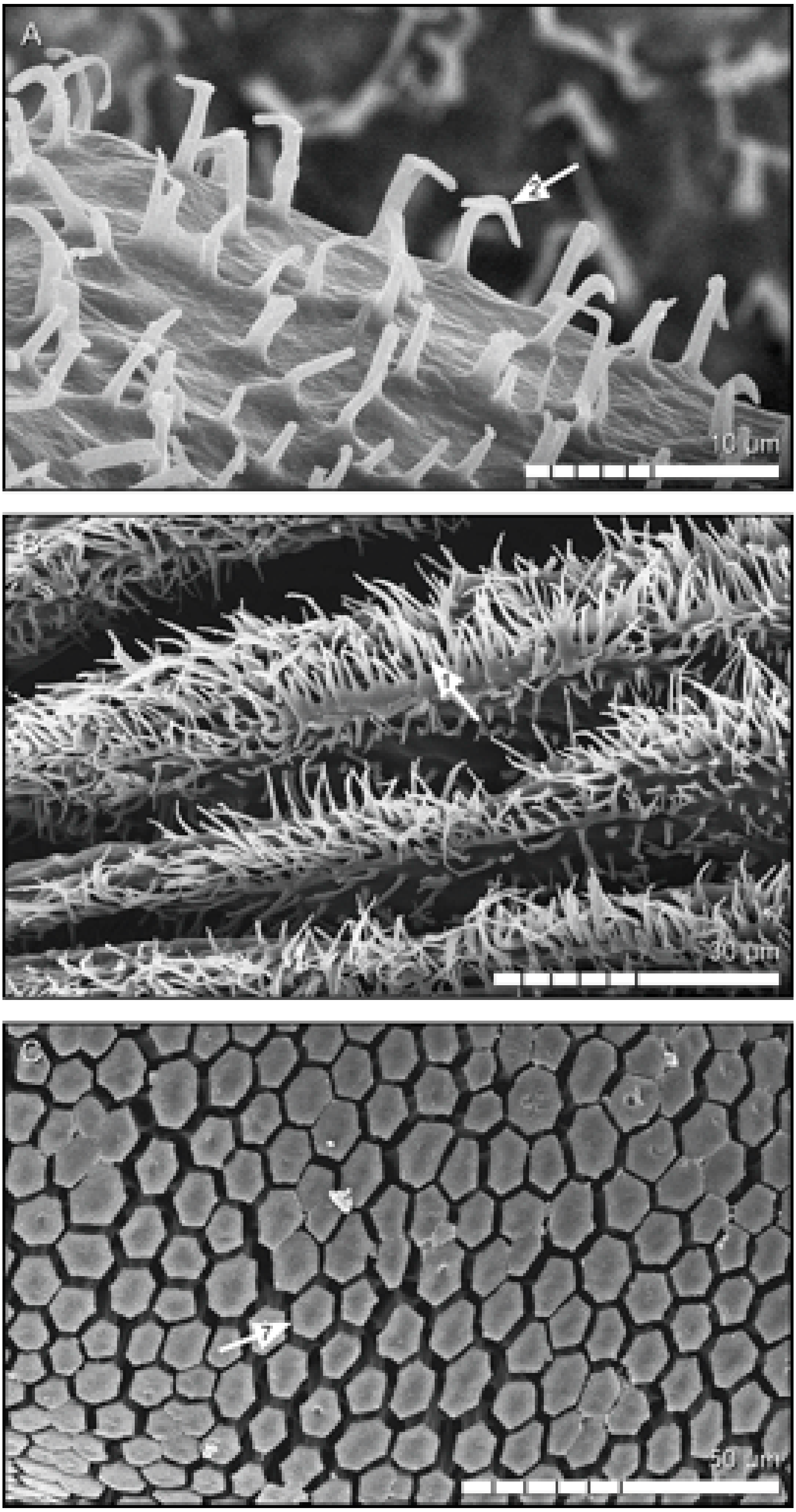

A
10 µm
30 µm
C
50 µm

Plate 150. *Opistophthalmus glabrifrons* Peters, 1861, 1 ♀ (AMNH [LP 1074]): **A.** ventral surface of book lung lamella with branched trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with hexagonal tiles (arrow), anterior view. Numbers in arrows refer to character states.

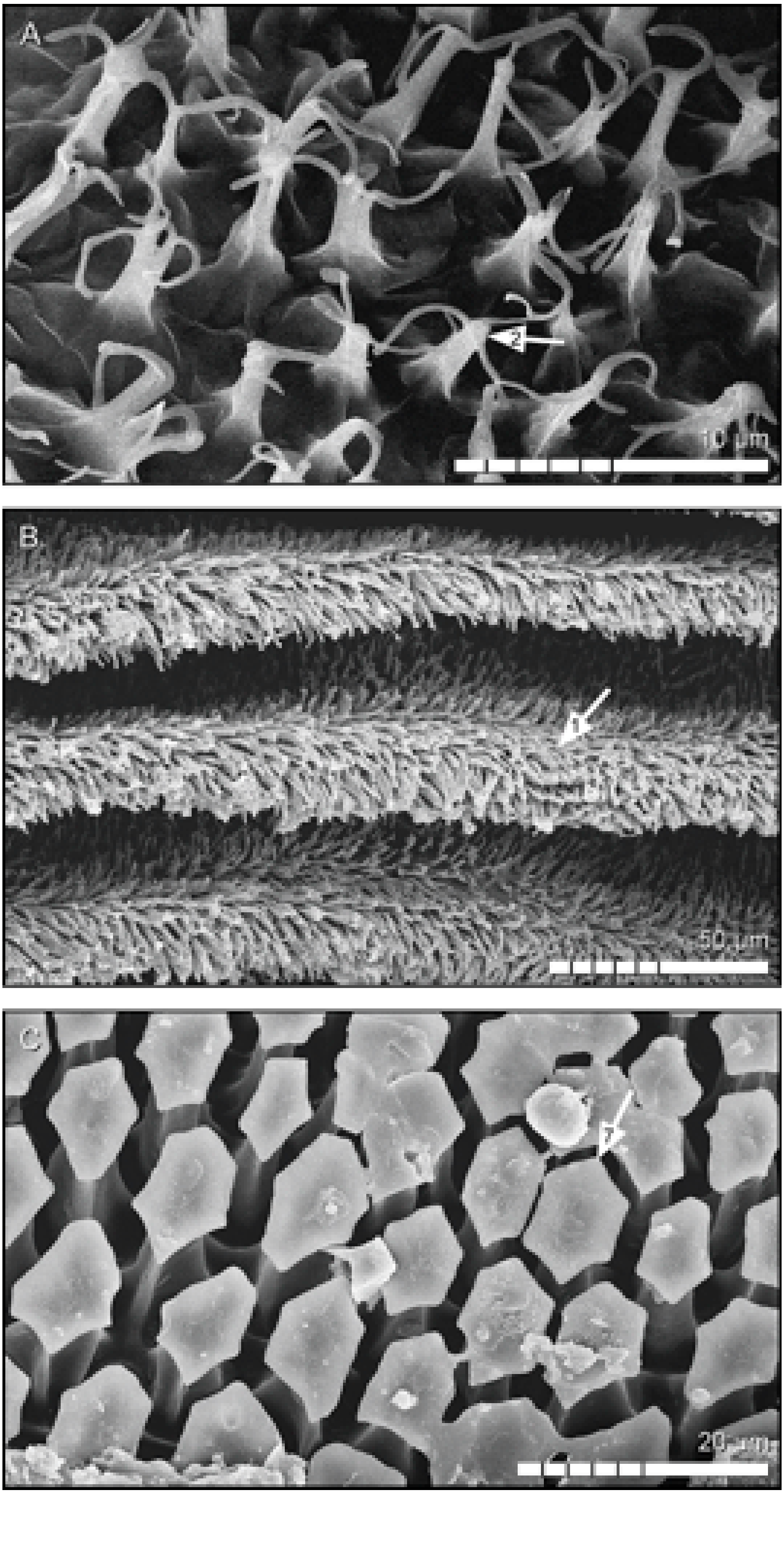
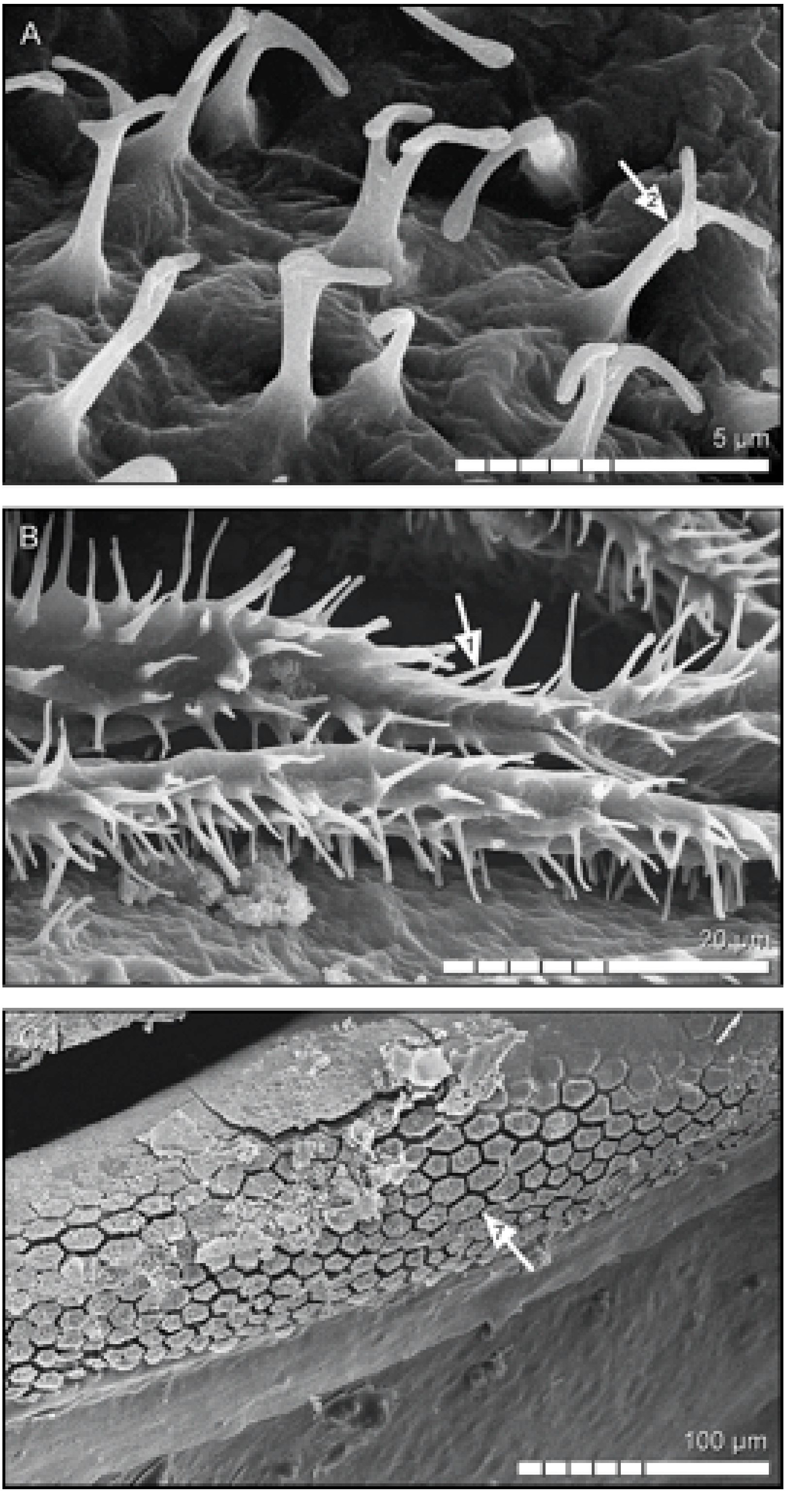

A
10 µm
B
50 µm
C
20 µm

Plate 151. *Opistophthalmus holmi* (Lawrence, 1969), 1 ♀ (AMNH [LP 1082]): **A.** ventral surface of book lung lamella with branched trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with hexagonal tiles (arrow), anterior view. Numbers in arrows refer to character states.


A
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B
20 µm
100 µm

Plate 152. *Pandinus cavimanus* (Pocock, 1888), 1 ♀ (AMNH [LP 3259]): **A.** ventral surface of book lung lamella with branched trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with hexagonal tiles (arrow), anterior view. Numbers in arrows refer to character states.

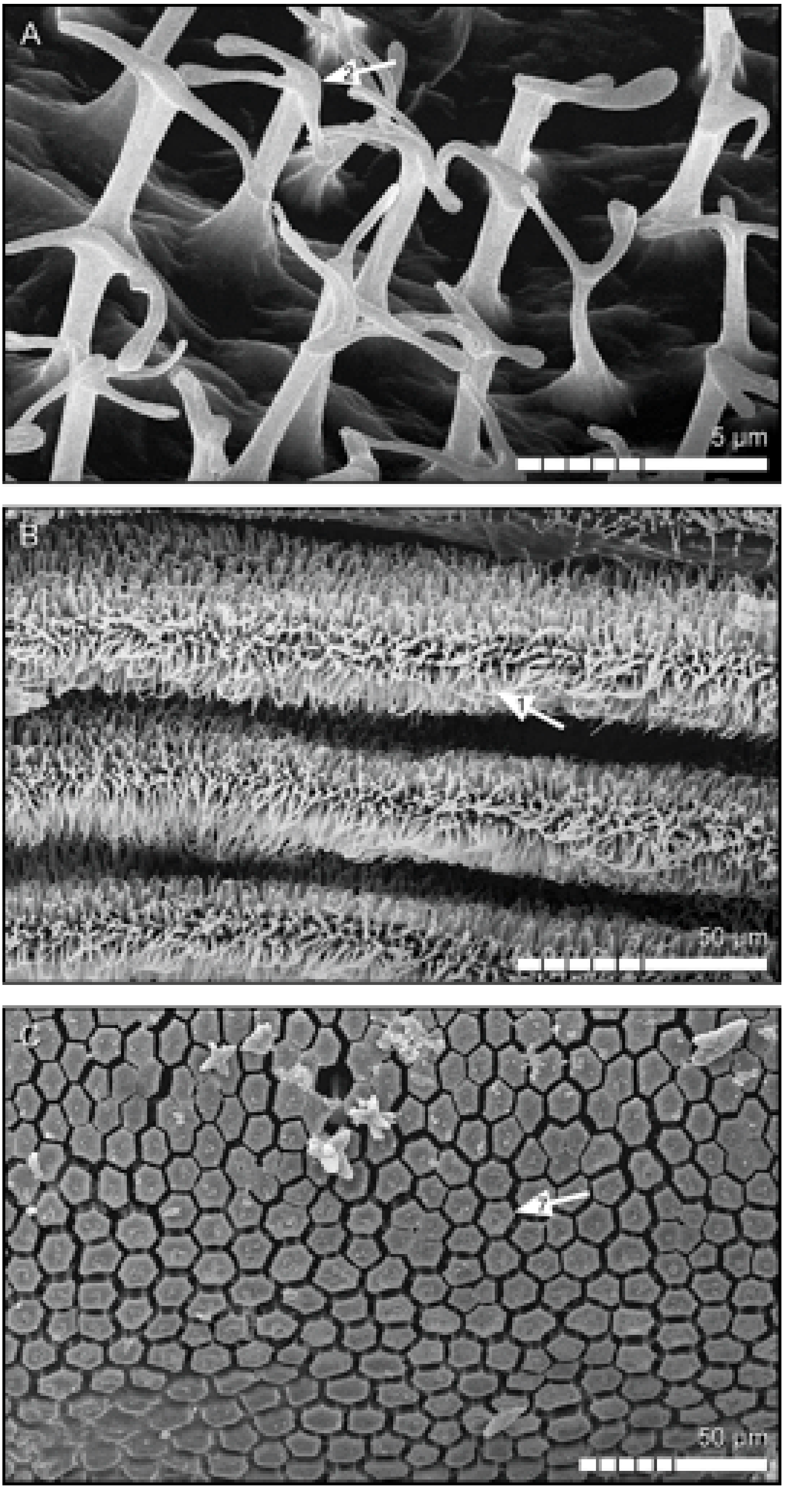

A
5 µm
B
50 µm
C
50 µm

Plate 153. *Pandinus imperator* (C.L. Koch, 1841), 1 ♀ (AMNH [LP 4836]): **A.** ventral surface of book lung lamella with branched trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with hexagonal tiles (arrow), anterior view. Numbers in arrows refer to character states.

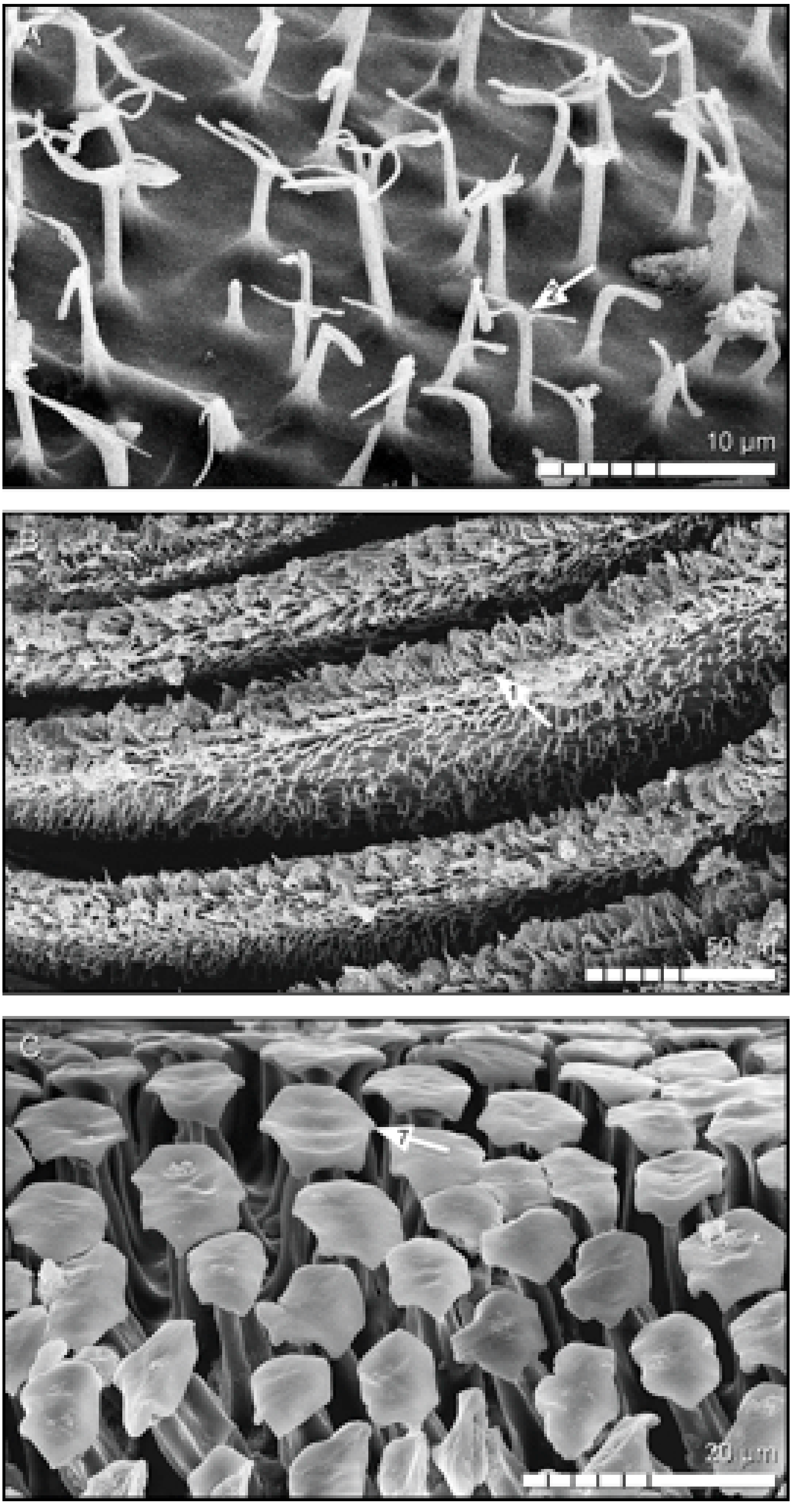

10 µm
C
20 µm

Plate 154. *Scorpio maurus fuliginosus* (Pallary, 1928), 1 ♂ (AMNH [LP 1930]): **A.** ventral surface of book lung lamella with branched trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with hexagonal tiles (arrow), anterior view. Numbers in arrows refer to character states.

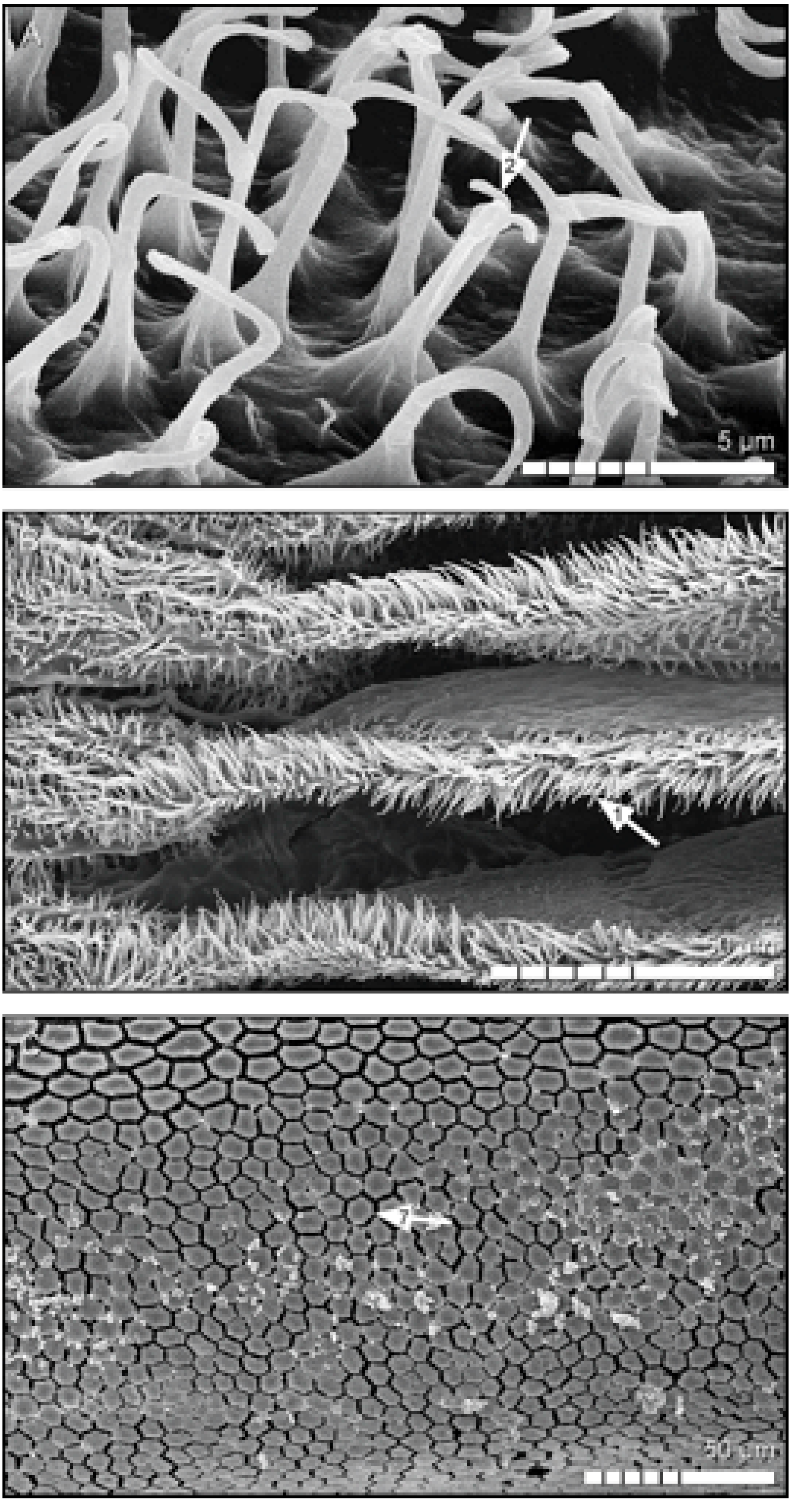

A
5 µm
50 µm

Plate 155. *Scorpio maurus fuscus* (Ehrenberg, 1829), 1 ♂ (AMNH [LP 1556]): **A.** ventral surface of book lung lamella with branched trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with bristles (arrow), posterior view; **C.** movable posterior edge of spiracle with hexagonal tiles (arrow), anterior view. Numbers in arrows refer to character states.

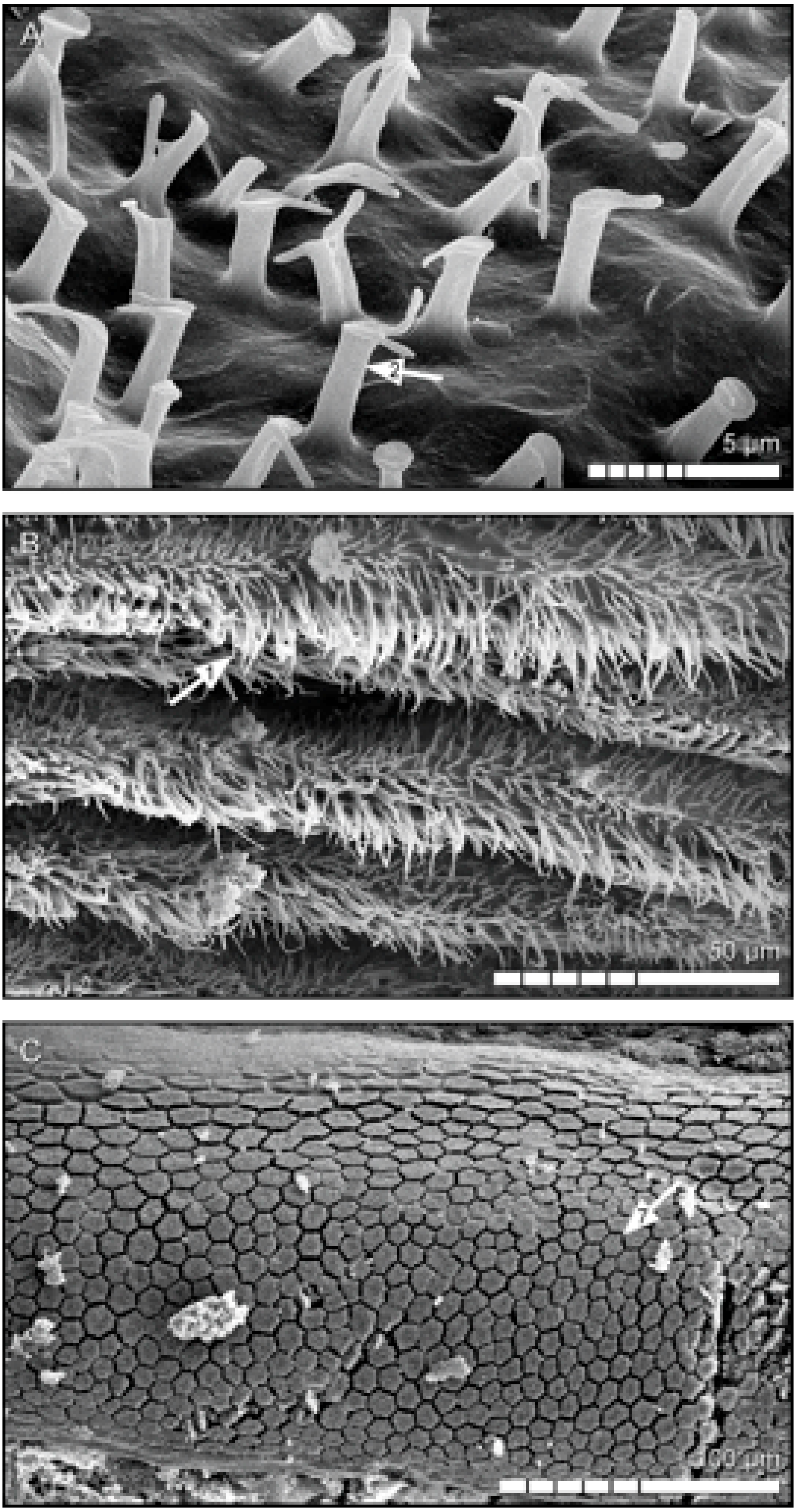
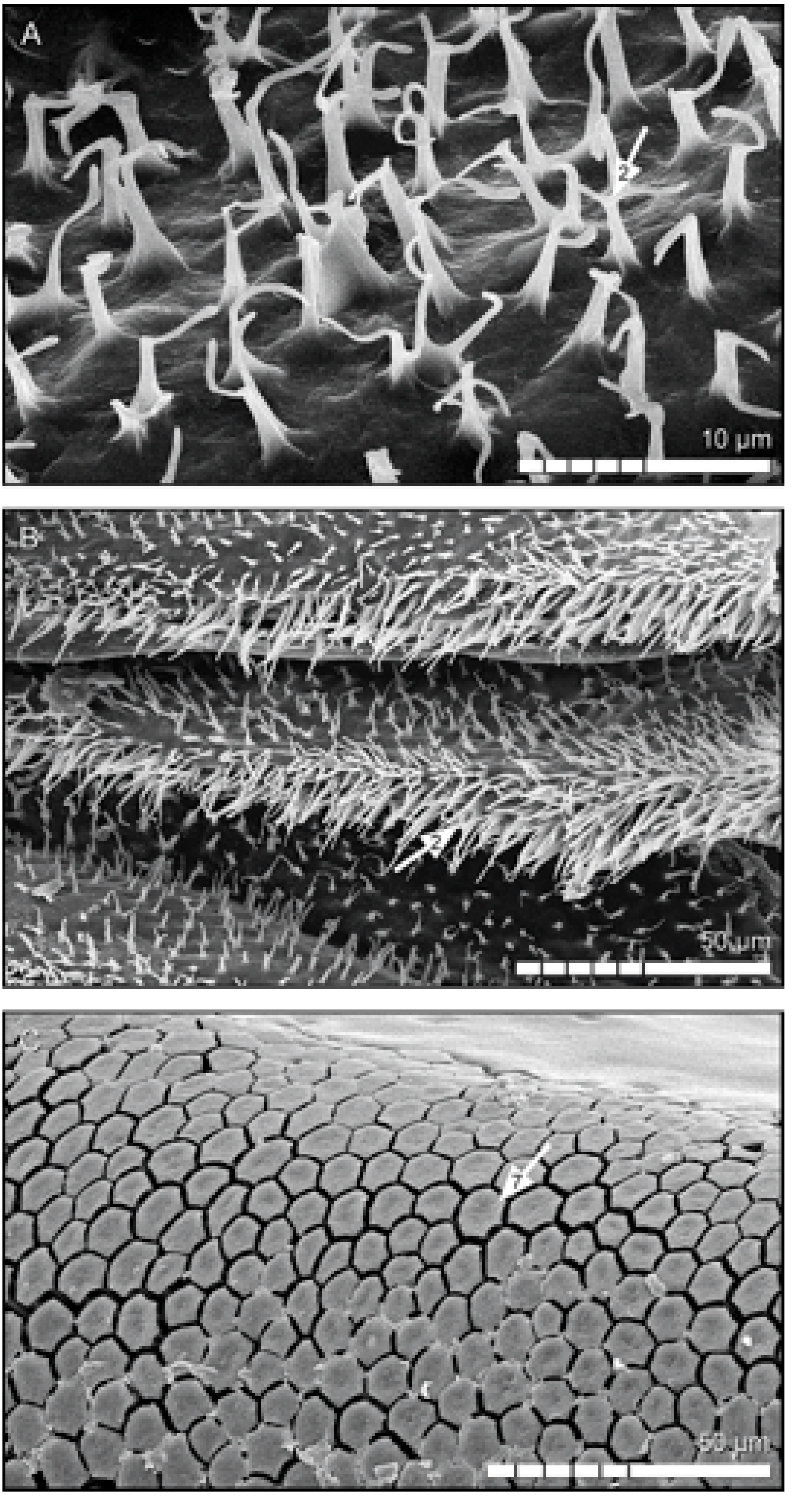

A
5 µm
B
50 µm
C

Plate 156. *Scorpio maurus palmatus* (Ehrenberg, 1828), 1 ♀ (AMNH [LP 1532]): **A.** ventral surface of book lung lamella with branched trabeculae (arrow), viewed from air space; **B.** distal edges of book lung lamellae covered with spines (arrow), posterior view; **C.** movable posterior edge of spiracle with hexagonal tiles (arrow), anterior view. Numbers in arrows refer to character states.


A
2
10 µm
B
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50 µm
C
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50 µm