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Elytral surface structures as indicators of relationships in stag beetles, with special reference to the New Zealand species (Coleoptera: Lucanidae)

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Abstract The elytral vestiture, pits, and surrounding integument in representatives of four lucanid subfamilies have been studied. The vestiture was examined in 35 species and ranged from simple to divided setae and from smooth to ribbed scales. The pits, examined with SEM in 19 species, varied from small dimple-like indentations to large, sharply demarcated depressions with raised floors and an ornately sculptured surface. The elytral ultrastructure is distinctive for genera and for at least one subfamily. Both the vestiture and pits are simplest in the Lampriminae and most complex in the Aesalinae. Differences in the elytral surface structures suggest that the New Zealand aesalines belong in two genera, neither of which is the Australian genus *Ceratognathus*, where they are currently placed.

Keywords Coleoptera; Lucanidae; stag beetles; New Zealand; morphology; elytral surface structures; taxonomy; phylogeny

INTRODUCTION

Gross morphological features of the elytra, such as the size and shape of pits (punctures) and the colour, distribution, and general shape of scales and setae, have been widely used as species characters in Lucanidae (e.g., Holloway 1961; Howden & Lawrence 1974; Endrödy-Younga 1993), but the possibility of using these structures in the higher classification of the family has never been investigated. Following the discovery that the elytral vestiture is generically distinct in *Geodorcus* Holloway, *Dorcus* MacLeay, *Paralissotes* Holloway, and *Lissotes* Westwood (Holloway 1996), I undertook the study on which this paper is based to see whether other lucanid genera could also be recognised by their setae or scales and, if so, whether the elytral vestiture might indicate generic relationships.

Initially, slide-mounted setae and scales from the elytra of 35 species of lucanids were examined and drawn under oil immersion. Scanning electron micrographs were then made of the elytral surface of 19 of these species. In addition to complementing the slide study, the micrographs revealed the previously unknown structure of the pits containing the setae and scales and of the adjacent integumental surface. I was not able to examine representatives of all the lucanid genera. The focus was on the New Zealand lucanids and on exotic species that seemed likely to have relevance to the New Zealand fauna because of subfamily or supposed generic relationships, geographic distribution, or certain morphological features.

MATERIALS, METHODS, AND CONVENTIONS

The project began in 1991 while I was a member of the Insect Systematics Group of DSIR Plant Protection (now part of Landcare Research New Zealand Ltd), Auckland, New Zealand. The specimens are in the New Zealand Arthropod Collection (NZAC), housed at Landcare Research, Auckland. The drawings and micrographs are of surface structures above the declivity on the apical half of the elytron. This part of the body was chosen as the site for examining surface structures because its gross form varies only slightly between species and it is virtually unaffected by sexual dimorphism and allometry. Also, if SEM work is to be done, it is easier and less damaging to the specimen to remove the apex of the elytron than to remove a part of the body such as the

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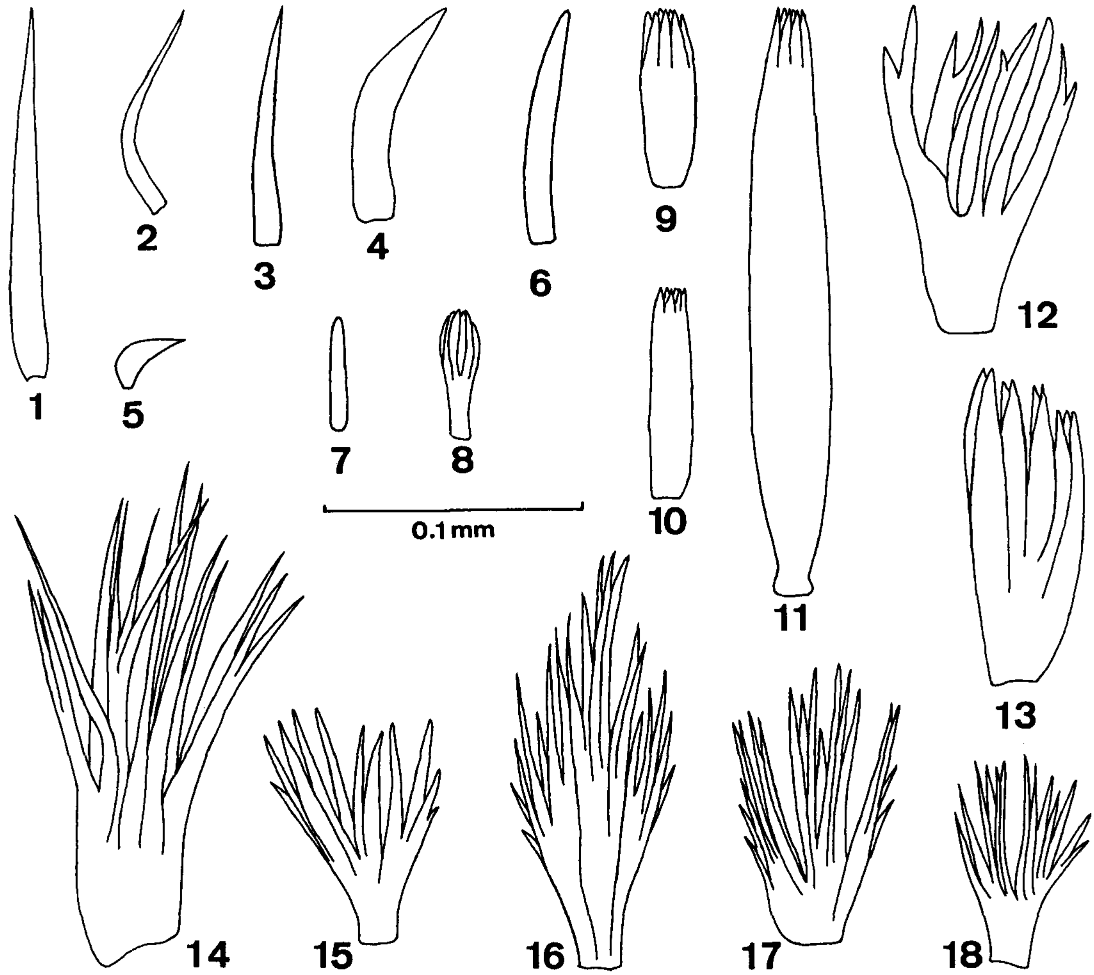

Fig. 1–18 Elytral vestiture of Lucanidae as seen with a compound microscope (1–4, Lampriminae; 5–18, Lucaninae). **1**, *Dendroblax earli*; **2**, *Lamprima adolphinae*; **3**, **4**, *Streptocerus speciosus*; **5**, *Lucanus cervus*; **6**, *Colophon izardi*; **7**, *Lissapterus tetrops*; **8**, *Hoplogonus simsoni*; **9**, *Dorcus brevis*; **10**, *D. parallelipipedus*; **11**, *D. meeki*; **12**, *Apterodorcus bacchus*; **13**, *Serrognathus arfakianus*; **14**, *Geodorcus helmsi*; **15**, *G. novaezealandiae*; **16**, *Aegus gestroi*; **17**, *A. malaccus*; **18**, *A. platyodon*. All figures same scale.

head or pronotum. In the material examined, the types of pits and vestiture on the elytra are the same as those elsewhere on the dorsal surface (as seen with a stereomicroscope) except that they may differ in size, particularly in species exhibiting strong sexual dimorphism and allometry.

Setae and scales to be examined and drawn under oil immersion were removed from dried specimens that were viewed with a stereomicroscope. They were plucked individually from the elytral pits using a fine-tipped pin, transferred from the tip of the pin to a drop of glycerine on a slide, and topped with a coverslip to which slight pressure was then applied. Complex setae and scales which may have parts of their surface stuck together with exudate expand to their full size and shape when subjected to this pressure. The illustrations of slide-mounted setae and scales (Fig. 1–32) were made using a drawing tube.

The micrographs were obtained using a Philips 505 scanning electron microscope and gold-coated pieces of elytra. Elytral samples that look reasonably clean under a stereomicroscope often turn out to be disappointingly dirty when examined with the SEM. As the micrographs in this paper show, elytral details are sharpest in preparations that have been

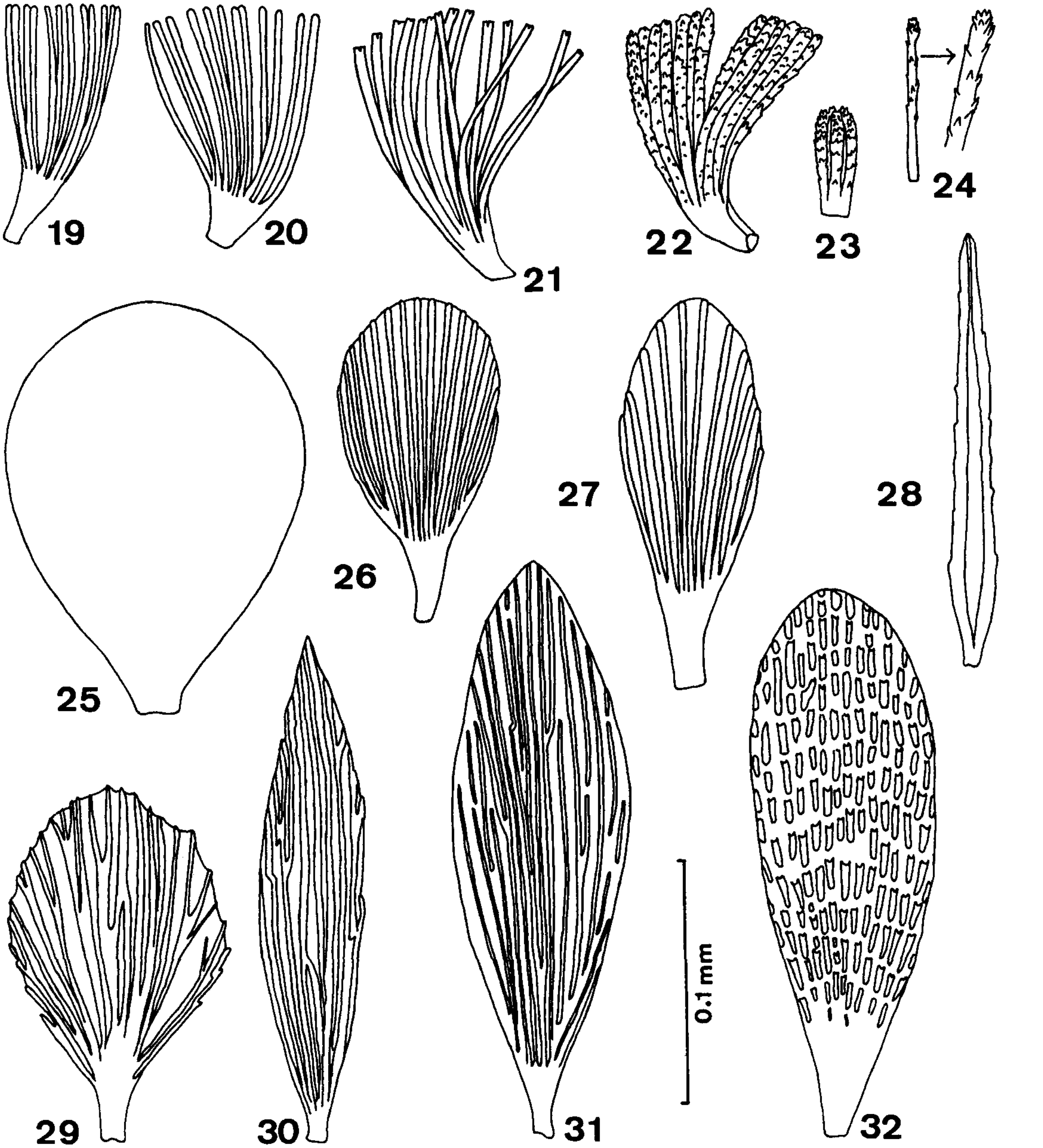

Fig. 19–32 Elytral vestiture of Lucanidae as seen with a compound microscope (19–23, 25–27, Lucaninae; 24, Syndesinae; 28–32, Aesalinae). **19,** *Lissotes menalcas*; **20,** *L. parvus*; **21,** *Sclerostomus cucullatus*; **22,** *Pycnosiphorus caelatus*; **23,** *Ryssonotus nebulosus*; **24,** *Syndesus cornutus*; **25,** *Pholidotus humboldti*; **26,** *Paralissotes oconnori*; **27,** *Paralissotes reticulatus*; **28,** *Nicagus obscurus*; **29,** *Aesalus scarabaeoides*; **30,** *Ceratognathus niger*; **31,** *C. helotoides*; **32,** *C. parrianus*. All figures same scale.

cleaned before being mounted on stubs. Figures 33, 39, 62, 64, 65, 68, and 71–74 are micrographs obtained from elytral pieces that had been cleaned firstly by overnight soaking in a small specimen tube containing water and a few drops of a thick, ammonia-based household cleaner, then, still in this solution, by sonication for about 1 min. This treatment loosens and removes surface debris but does not

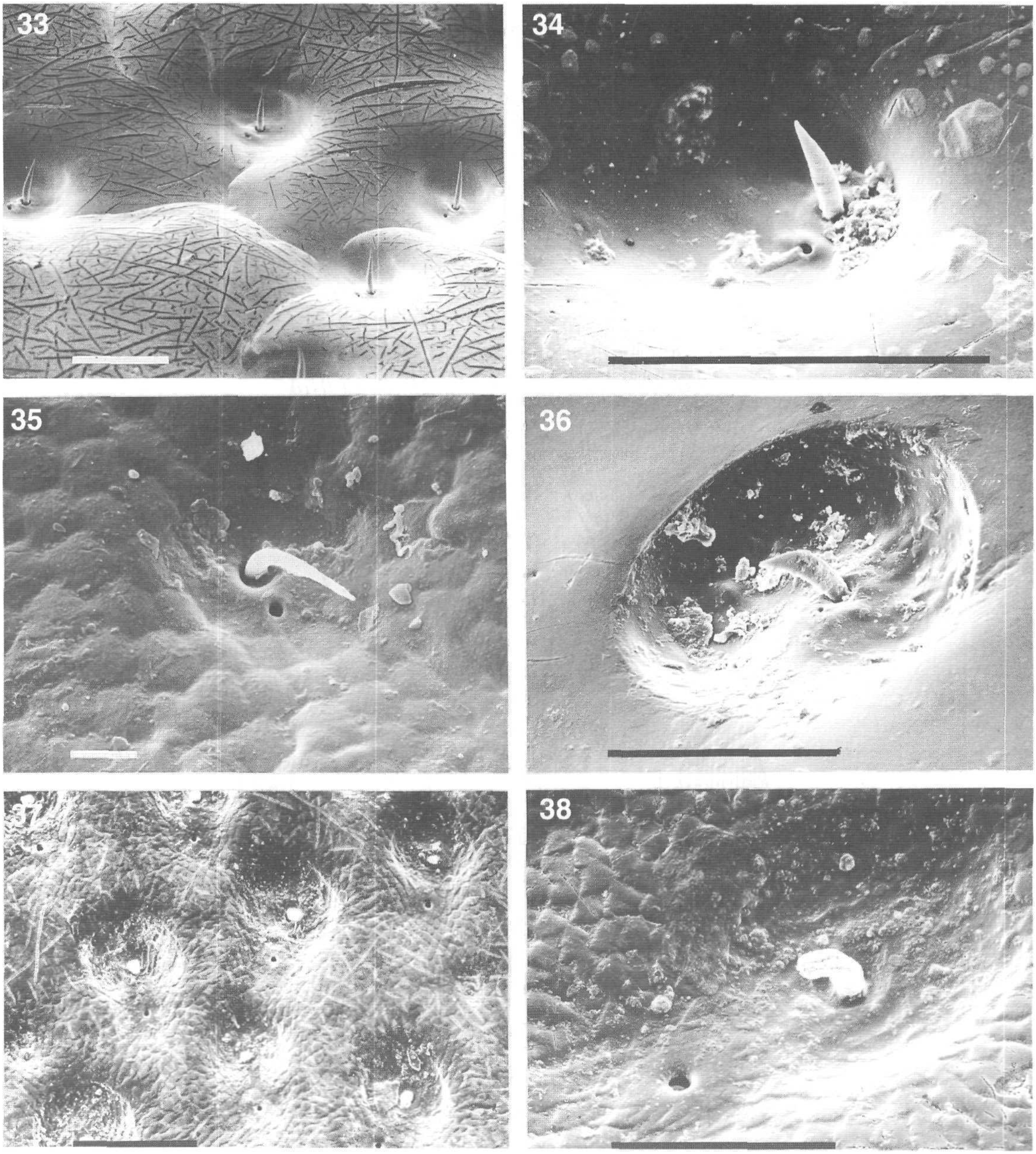

Fig. 33–38 Micrographs of elytral surface structures in Lucanidae (33–36, Lampriminae; 37, 38, Lucaninae). **33, 34**, *Dendroblax earli*: 33, cleaned preparation showing four setae with their associated pores (bar = 0.1 mm); 34, seta and associated pore (bar = 0.1 mm). **35**, *Lamprima aurata*: seta and associated pore (bar = 10 μm). **36**, *Streptocerus speciosus*: scale-like seta and associated pore (bar = 0.1 mm). **37, 38**, *Dorcus parallelipipedus*: 37, several minute setae with their associated pores lying outside the pits (bar = 0.1 mm); 38, seta and associated pore (bar = 0.05 mm).

interfere with the exudate that forms the distinctive patterns on scales, in pits, and on the adjoining integumental surface. Unfortunately, it does not remove the waxy film that sometimes coats the entire elytral surface (Fig. 68). I had previously used ammonia and sonication to clean surface processes in fly larvae and puparia, but did not think of using the same technique to clean lucanid elytra until the SEM work was well advanced. At that stage I was able to make cleaned preparations for only a few of the species.

Altogether 93 micrographs were made, but only 42 of these are shown in this paper. These were chosen for their overall clarity or comprehensive coverage, but in several instances some morphological features show more clearly in the unpublished ones. A complete set of the micrographs, together with label data of the associated specimens, is deposited in the NZAC at Landcare Research and can be viewed by arrangement with the Curator.

Elements of the vestiture that are approximately circular in cross-section are referred to here as setae and those that are either laterally compressed or dorsoventrally flattened are called scales. I am referring to the integumental depression surrounding the socket in which a seta or scale is inserted as a pit rather than a puncture.

The species studied have been assigned to subfamilies following the classification proposed by Holloway (1968) and still in use (D'Hotman & Scholtz 1990; Nel & Scholtz 1990). Throughout the paper, the four subfamilies represented are treated in the order: Lampriminae, Lucaninae, Syndesinae, Aesalinae. In the descriptive section, the genera of each subfamily are dealt with in alphabetical order. This system has not been strictly adhered to on the plates; instead, the figures have been arranged mostly according to similarities in the form of either the vestiture or the pits.

MORPHOLOGY OF ELYTRAL SURFACE STRUCTURES

Subfamily Lampriminae

Dendroblax earli White [New Zealand] (Fig. 1, 33, 34)

Vestiture: Setose, the setae erect, straight, smooth-sided, tapering to a point, and arising centrally in the pits.

Pits: Dimple-like depressions with the sides and floor unsculptured, and with a large pore immediately behind the base of each seta.

Integument adjacent to the pits: Unsculptured. The cause of the surface cracking in Fig. 33 and 34 is unknown.

Lamprima adolphinae (Gestro) [New Guinea] (Fig. 2)

Vestiture: Setose, the setae decumbent, curved, smooth-sided, tapering to a point, and arising centrally in the pits.

Pits and adjacent integument not examined with SEM.

Lamprima aurata (Latreille) [Australia, but a live specimen collected near Puha, north-west of Gisborne, New Zealand, in 1990 is in NZAC] (Fig. 35)

Vestiture: Setose, the setae like those in *L. adolphinae.*

Pits: Dimple-like depressions with polygonally sculptured sides and floor, and with a large pore posteriorly close to the base of each seta.

Integument adjacent to the pits: With sculpturing similar to that of the pits.

Streptocerus speciosus Fairmaire [Chile] (Fig. 3, 4, 36)

Vestiture: Setose-squamose, the elements setose basally but laterally compressed and scale-like distally, suberect, slightly curved, smooth-sided, tapering to a point, and arising centrally in the pits.

Pits: Rather sharp-edged depressions with polygonal sculpturing (obscured by surface film in Fig. 36) on the sides and floor, and with a small pore immediately posterior to the base of each scale-like seta.

Integument adjacent to the pits: With sculpturing as in the pits (visible, vaguely, only on the lower left of Fig. 36).

Subfamily Lucaninae

Aegus gestroi Boileau [Indonesia] (Fig. 16), ***A. malaccus*** Thomson [Indonesia and Malaysia] (Fig. 17), and ***A. platyodon*** Parry [Indonesia] (Fig. 18)

Vestiture: Setose, the setae erect or decumbent, dendritic, with numerous slender, tapering, sharply pointed, smooth-sided branches of varying lengths, and arising centrally in the pits.

Pits and adjacent integument not examined with SEM.

Apterodorcus bacchus (Hope) [Chile] (Fig. 12)

Vestiture: Setose, the setae erect, dendritic, with relatively few broad, tapering, pointed, smooth-sided branches of varying lengths (about 6 main branches, some with forked tips), and arising centrally in the pits.

Pits and adjacent integument not examined with SEM.

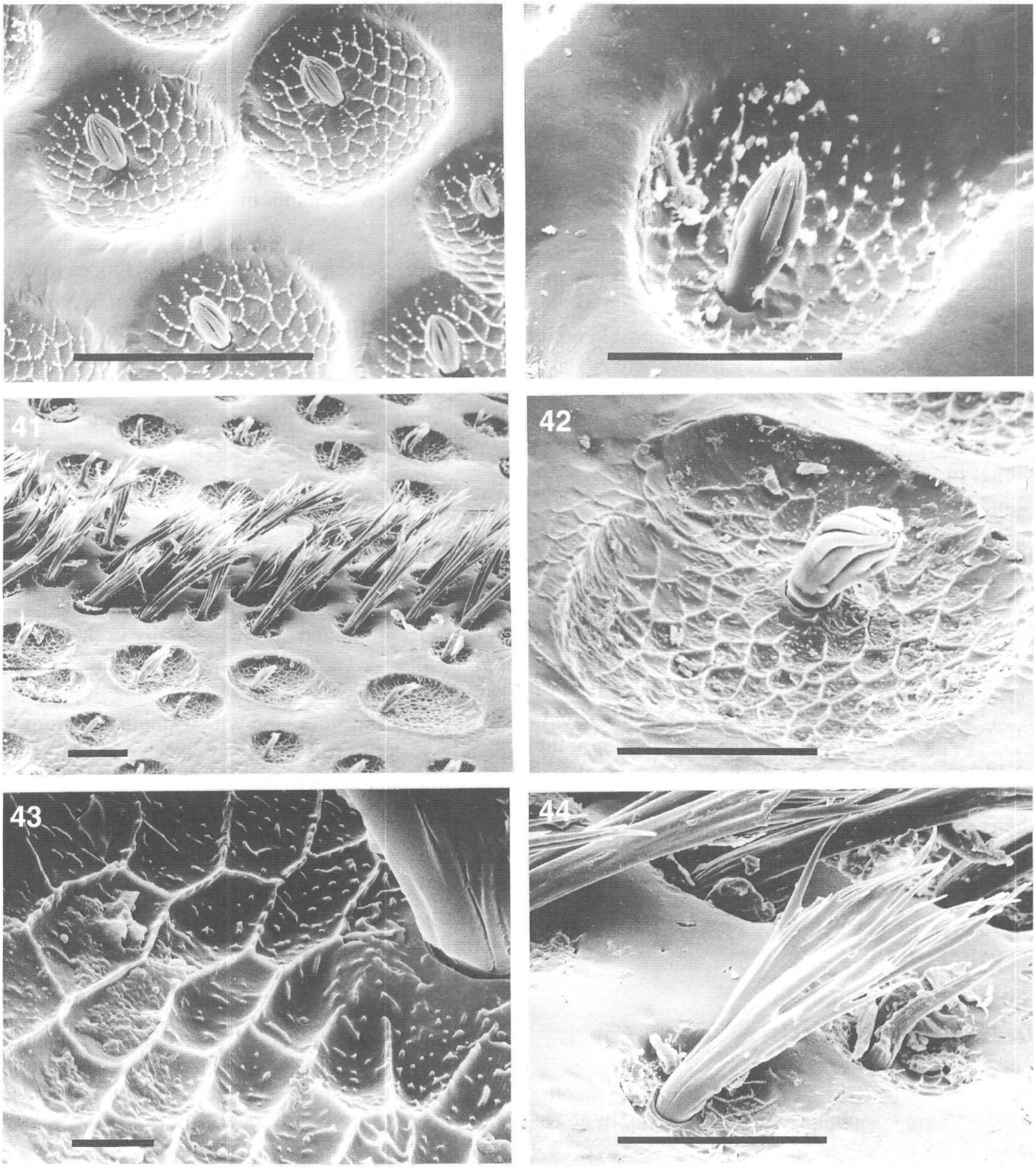

Fig. 39–44 Micrographs of elytral surface structures in Lucanidae (all Lucaninae). **39, 40,** *Geodorcus novaezealandiae*: 39, cleaned preparation of several setae (bar = 0.1 mm); 40, seta and pit showing discrete peaks of exudate in the walls of the polygons (bar = 0.05 mm). **41–44,** *G. helmsi*: 41, alternating tracts of long and short setae (bar = 0.1 mm); 42, short seta, pit, and polygonally sculptured integumental surface (to left of pit) (bar = 0.05 mm); 43, part of the floor of a pit and base of a short seta showing peaks of exudate in the polygon walls (in the upper half of the micrograph) and similar-looking peaks inside the polygons (bar = 10 μm); 44, long setae (bar = 0.1 mm).

Colophon izardi Barnard [South Africa] (Fig. 6)

Vestiture: Setose, the setae erect, slightly curved, smooth-sided, tapering but rather blunt-tipped, and arising centrally in the pits.

Pits and adjacent integument not examined with SEM.

Dorcus brevis Say [North America] (Fig. 9)

Vestiture: Setose, the setae erect, straight or slightly curved, smooth-sided, almost cylindrical, divided at the apex into about 7 short, blunt processes, and arising centrally in the pits.

Pits and adjacent integument not examined with SEM.

Dorcus meeki Boileau [New Guinea] (Fig. 11)

Vestiture: Setose as in *D. brevis* except that the setae are very long.

Pits and adjacent integument not examined with SEM.

Dorcus parallelipipedus (Linnaeus) [Europe] (Fig. 10, 37, 38)

Vestiture: Setose as in *D. brevis*. In Fig. 38, debris or surface film makes the apical processes of the seta look somewhat serrated.

Pits: Dimple-like depressions with polygonal (mainly triangular) sculpturing on the sides and floor.

Integument adjacent to the pits: With sculpturing as in the pits. There is a very large pore close to the posterior margin of each pit (it lies outside the pit).

Geodorcus helmsi (Sharp) [New Zealand] (Fig. 14, 41–44)

Vestiture: Setose, the setae either long or very short, erect to decumbent, dendritic, with numerous tapering, pointed, smooth-sided branches of varying lengths but mainly relatively long, and arising anteriorly in the pit. The long setae (Fig. 14, 41, 44) are close together in narrow longitudinal tracts that alternate with broad tracts of widely spaced short setae (Fig. 41–43). Branches of the individual long setae are stuck together with exudate near the base but are free and divergent apically. The branches of short setae adhere to one another throughout their length and have their tips directed inwards.

Pits: Shallow, saucer-shaped depressions with well-defined margins and polygonally sculptured walls and floor. The pits enclosing the small setae are larger than those enclosing the long setae (Fig. 41). Triangular peaks of exudate which apparently coalesce to form the polygonal sculpturing can be seen in the upper half of Fig. 43, taken near the base of a small seta. Exudate within the polygons is also visible in this micrograph.

Integument adjacent to the pits: With sculpturing as in the pits (mostly obscured by surface film in the SEMs).

Geodorcus novaezealandiae (Hope) [New Zealand] (Fig. 15, 39, 40)

Vestiture: Setose, all the setae similar to the short setae in *G. helmsi*. In Fig. 15, the branches of the setae have been spread apart by applying pressure to the coverslip.

Pits: Similar to those containing small setae in *G. helmsi*. Individual peaks of exudate show clearly in the walls of the polygons in Fig. 39 and 40.

Integument adjacent to the pits: With sculpturing as in the pits, but mostly obscured by surface film in the micrographs.

Hoplogonus simsoni Parry [Tasmania] (Fig. 8)

Vestiture: Setose, the setae erect, minute, dendritic, with slender, tapering, smooth-sided branches that could not be separated when pressure was applied to the coverslip, and arising near the centre of the pits.

Pits and adjacent integument not examined with SEM.

Lissapterus tetrops Lea [Australia] (Fig. 7)

Vestiture: Setose, the setae erect, minute, straight, smooth-sided, slightly tapering, rather blunt-tipped, and arising centrally in the pits.

Pits and adjacent integument not examined with SEM.

Lissotes menalcas Westwood [Australia] (Fig. 19, 45, 46)

Vestiture: Setose, the setae decumbent, curved, deeply divided into about 12 smooth-sided, blunt-tipped, cylindrical branches of similar length and diameter, and arising centrally in the pits.

Pits: Shallow, saucer-shaped depressions with polygonally sculptured walls and floor. In the specimen examined with SEM (Fig. 45, 46), the walls of the polygons are made up of minute, discrete beads of exudate that are not coalescent. The polygons contain numerous smaller but similar-looking beads of exudate.

Integument adjacent to the pits: No sculpturing

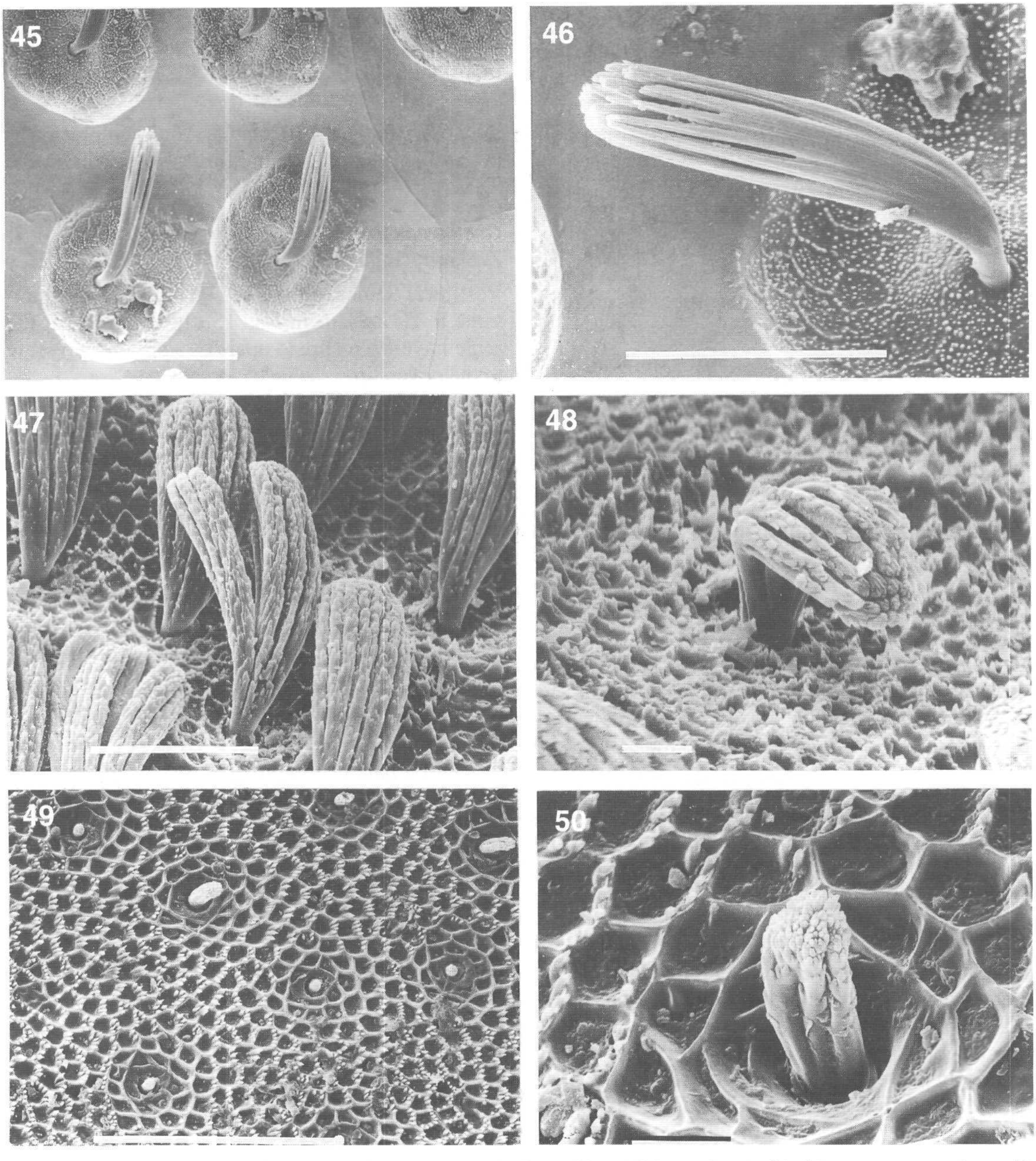

Fig. 45–50 Micrographs of elytral surface structures in Lucanidae (all Lucaninae). **45**, **46**, *Lissotes menalcas*: 45, several divided setae (bar = 0.1 mm); 46, seta and part of a pit showing discrete peaks of exudate in the walls and cavities of the polygons (bar = 0.05 mm). **47**, **48**, *Pycnosiphorus caelatus*: 47, several barbed setae in poorly defined pits (bar = 0.05 mm); 48, barbed seta and polygonal sculpturing with conspicuously peaked walls (bar = 10 μm). **49**, **50**, *Ryssonotus nebulosus*: 49, several barbed setae of varying sizes in very small pits (bar = 0.1 mm); 50, large barbed seta in a pit with smooth-topped polygonal sculpturing that contrasts with peaked sculpturing of the adjacent integument (on left side of the micrograph) (bar = 10 μm).

visible on the micrographs, but surface details seem to be obscured by a continuous coating of exudate.

Lissotes parvus Lea [Tasmania] (Fig. 20)

Vestiture: Setose as in *L. menalcas*.

Pits and adjacent integument not examined with SEM.

Lucanus cervus Linnaeus [Europe] (Fig. 5, 57)

Vestiture: Squamose, the scales minute, decumbent, strongly curved, laterally compressed, smooth-sided, tapering to a point, and arising approximately centrally in the pits.

Pits: Shallow, elongate-oval, rather poorly defined depressions with polygonal (mainly triangular) sculpturing on the sides and floor.

Integument adjacent to the pits: With sculpturing as in the pits.

Paralissotes oconnori (Holloway) [New Zealand] (Fig. 26)

Vestiture: Squamose, the scales suberect, straight, fan-shaped, prominently stalked, with about 15 longitudinal ribs radiating across the lamina from the stalk to the outer margin, and arising centrally in the pits. The lamina between the ribs can be seen only when the scale has been compressed under a coverslip.

Pits and adjacent integument not examined with SEM.

Paralissotes reticulatus (Westwood) [New Zealand] (Fig. 27, 53–56)

Vestiture: Squamose and setose, the scales as in *P. oconnori* except that they are decumbent, curved, and have fewer ribs (about 12). The setae are sparse, erect, minute, deeply divided into about 10 smooth-sided, finger-like processes, and arise in the centre of the pits (Fig. 54, 56).

Pits: Saucer-shaped depressions with well-defined margins and polygonally sculptured walls and floor. Pits containing scales are large but those containing setae are very small.

Integument adjacent to the pits: With sculpturing as in the pits (the sculpturing is partially obscured by exudate in Fig. 54).

Paralissotes triregius (Holloway) [New Zealand] (Fig. 51, 52)

Vestiture: Squamose as in *P. oconnori*. Minute setae of the type seen in *P. reticulatus* are not visible in the micrographs, but if present they could be obscured by exudate (see Fig. 51).

Pits: Similar to those containing scales in *P. reticulatus*. Figure 52 of part of the floor of a pit shows discrete peaks of exudate which have not yet coalesced to form the continuous walls of the polygons.

Integument adjacent to the pits: With sculpturing as in the pits.

Pholidotus humboldti Gyllenhal [Brazil] (Fig. 25)

Vestiture: Squamose, the scales decumbent or suberect, straight, fan-shaped, very short-stalked, with no discernible surface features visible under oil immersion, and arising near the centre of the pits.

Pits and adjacent integument not examined with SEM.

Pycnosiphorus caelatus (Blanchard) [Chile] (Fig. 22, 47, 48)

Vestiture: Setose, the setae suberect, curved, deeply divided into about 12 blunt-tipped, broad, cylindrical branches of similar length and diameter, and arising centrally in the pits.The branches are barbed on their dorsal surface and smooth ventrally.

Pits: Very shallow, poorly defined depressions lined with polygonal sculpturing. The individual polygons are very small and have high walls that are topped by relatively large peaks of exudate.

Integument adjacent to the pits: With sculpturing as in the pits and virtually indistinguishable from these.

Ryssonotus nebulosus (Kirby) [Australia, but also established in New Zealand] (Fig. 23, 49, 50)

Vestiture: Setose, the setae of varying sizes, erect or suberect, straight, deeply divided into about 6 blunt-tipped, broad, cylindrical, barbed branches of similar length and diameter, and arising centrally in the pits.

Pits: Small, shallow depressions lined with polygonal sculpturing which has a smooth surface.

Integument adjacent to the pits: With sculpturing similar to that in the pits except that the walls are topped with peaks of exudate.

Sclerostomus cucullatus (Blanchard) [Chile] (Fig. 21)

Vestiture: Setose, the setae suberect, curved, deeply divided into about 14 blunt-tipped, broad, cylindrical, smooth-sided branches of similar length and diameter, and arising near the centre of the pits.

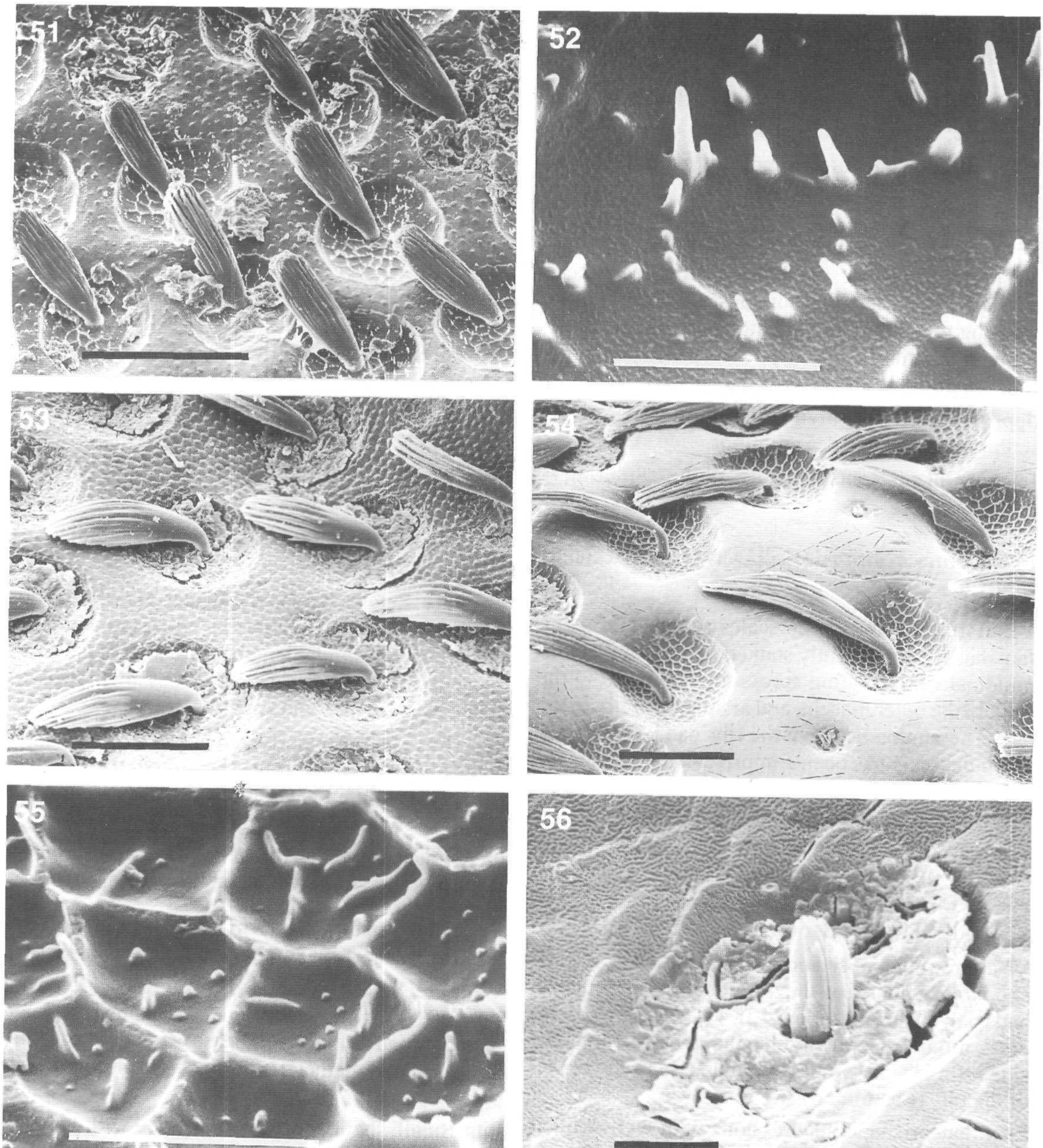

Fig. 51–56 Micrographs of elytral surface structures in Lucanidae (all Lucaninae). **51**, **52**, *Paralissotes triregius*: 51, scales, pits, and adjacent integument with its polygonal sculpturing partly concealed by exudate (bar = 0.1 mm); 52, part of the floor of a pit showing discrete peaks of exudate (bar = 10 μm). **53–56**, *P. reticulatus*: 53, several scales on a section of elytron heavily coated with exudate (bar = 0.1 mm); 54, several scales in large pits and two setae (very small) in small pits (in upper and lower right of micrograph) (bar = 0.1 mm); 55, part of the floor of a pit containing a scale (bar = 10 μm); 56, seta in a small pit filled with exudate (bar = 10 μm).

Pits and adjacent integument not examined with SEM.

Serrognathus arfakianus (Lansbury) [New Guinea] (Fig. 13)

Vestiture: Setose, the setae suberect, straight, deeply incised, with about 10 broad, cylindrical, undivided, smooth-sided, pointed branches, and arising near the centre of the pits. The branches could not be separated when pressure was applied to the coverslip.

Pits and adjacent integument not examined with SEM.

Subfamily Syndesinae

Syndesus cornutus (Fabricius) [Australia, but also established in New Zealand] (Fig. 24, 58–60)

Vestiture: Setose, the setae either long or short, and aligned in alternating longitudinal rows (Fig. 58). Both types are cylindrical and have numerous shallow incisions apically. The long setae are almost straight, barbed except near the base, set in the middle of the anterior wall of their pits, and lie horizontally across the pits (Fig. 24, 59). The short setae are curved, suberect, smooth-sided, and arise near the centre of the pit floor (Fig. 60).

Pits: Large and small approximately circular depressions (in alternating longitudinal rows) with well-defined margins (Fig. 58), the large pits deep and containing long setae, the small pits shallow and containing short setae. The walls and floor of the pits apparently lack sculpture except for a raised ring around the bases of setae inside the small pits (Fig. 60).

Integument adjacent to the pits: Smooth as in the pits.

Subfamily Aesalinae

Aesalus scarabaeoides (Panzer) [Europe] (Fig. 29, 61, 62)

Vestiture: Squamose, the scales either large or small, fan-shaped, prominently stalked, with numerous (at least 10) slightly anastomosing, sometimes forked, longitudinal ribs radiating across the lamina from the stalk to the outer margin (Fig. 29), and arising near the outer margin of the pit floor. In dried scales (Fig. 61, 62), the lamina is not fully extended because of folding between the ribs. The large scales are erect or decumbent and may have a right-angled bend between the stalk and the lamina (Fig. 61). Small scales are erect and have the lamina and stalk in the same plane (Fig. 62).

Pits: Large, shallow, circular or oval depressions with sharply defined margins, almost vertical walls, and a prominently convex floor. The walls and floor are polygonally sculptured.

Integument adjacent to the pits: With sculpturing as in the pits.

Ceratognathus helotoides Thomson [New Zealand] (Fig. 31, 69, 70)

Vestiture: Squamose and setose, the scales decumbent, elongate-oval, sharply pointed, prominently stalked, curved, with numerous (at least 10) slightly anastomosing, entire and fragmented, longitudinal ribs extending across the lamina from the stalk (Fig. 31), and arising off-centre in the pits. The scales are fully extended when dry (Fig. 69, 70). The setae (not shown) are decumbent, thread-like, tapering, about one-third the length of the scales, and arise off-centre in the pits.

Pits: Large, approximately circular, polygonally sculptured, saucer-shaped depressions with sharply defined margins.

Integument adjacent to the pits: With sculpturing as in the pits.

Ceratognathus irroratus (Parry) [New Zealand] (Fig. 67) and ***C. parrianus*** (Westwood) [New Zealand] (Fig. 32, 63–66)

Vestiture: Squamose and setose, the scales decumbent, oval, and not sharply pointed, stalked, rigid, fully extended when dry, and arising near the outer edge of the floor (Fig. 32, 63, 64, 67). The dorsal surface of the scales is covered with a reticulum of fine, predominantly longitudinal ridges separated from each other by conspicuous, deep grooves (Fig. 66). The setae are minute relative to the size of the scales (Fig. 67), erect, cylindrical, and with a shallowly incised apex (Fig. 65).

Pits: Approximately circular, relatively deep depressions with sharply defined margins, almost vertical walls, and a raised, flat-topped floor (Fig. 63–65, 67). The walls and floor are polygonally sculptured.

Integument adjacent to the pits: Extremely finely reticulate (Fig. 65).

Ceratognathus niger Westwood [Tasmania] (Fig. 30, 71–74)

Vestiture: Squamose and setose, the scales decumbent to suberect, elongate-oval with a sharply pointed tip, stalked, fully extended when dry (Fig. 30, 71), and inserted in the centre of the pit. The dorsal surface of the lamina has about 12 slightly anastomosing, longitudinal ridges extending from

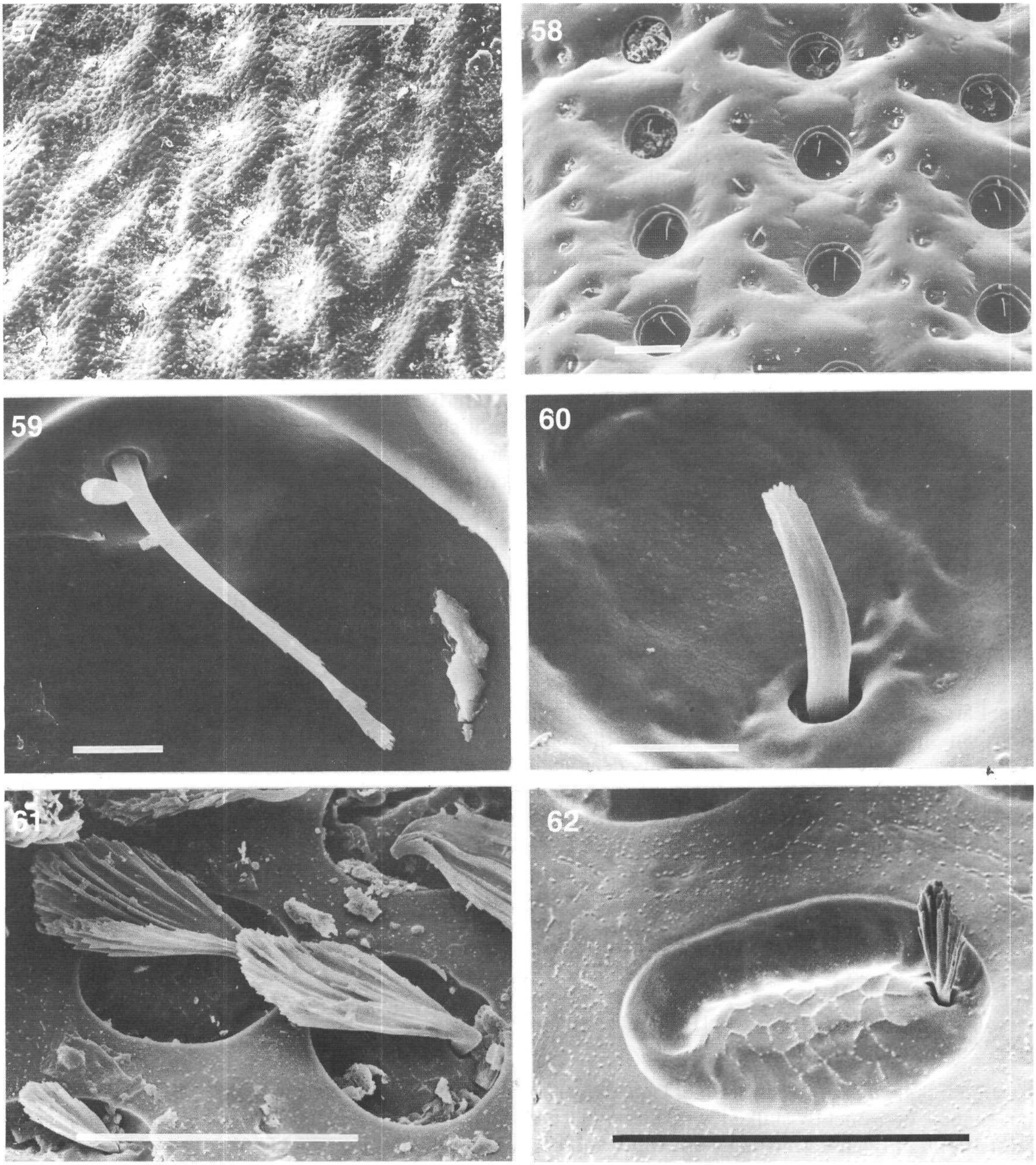

Fig. 57–62 Micrographs of elytral surface structures in Lucanidae (57, Lucaninae; 58–60, Syndesinae; 61, 62, Aesalinae). **57**, *Lucanus cervus*: scales (appearing as minute white triangles, most easily seen in right third of micrograph) in poorly defined, elongate-oval pits (bar = 0.1 mm). **58–60**, *Syndesus cornutus*: 58, alternating rows of large and small pits containing slender setae (bar = 0.1 mm); 59, long barbed seta in anterior wall of large pit (bar = 10 μm); 60, small seta inserted in the centre of a small pit (bar = 10 μm). **61, 62**, *Aesalus scarabaeoides*: 61, three large scales and one small scale (partly obscured at lower left) (bar = 0.1 mm); 62, cleaned preparation of a small scale inserted near the outer margin of the convex, sculptured pit floor, and showing polygonal sculpturing of the adjacent integument (bar = 0.1 mm).

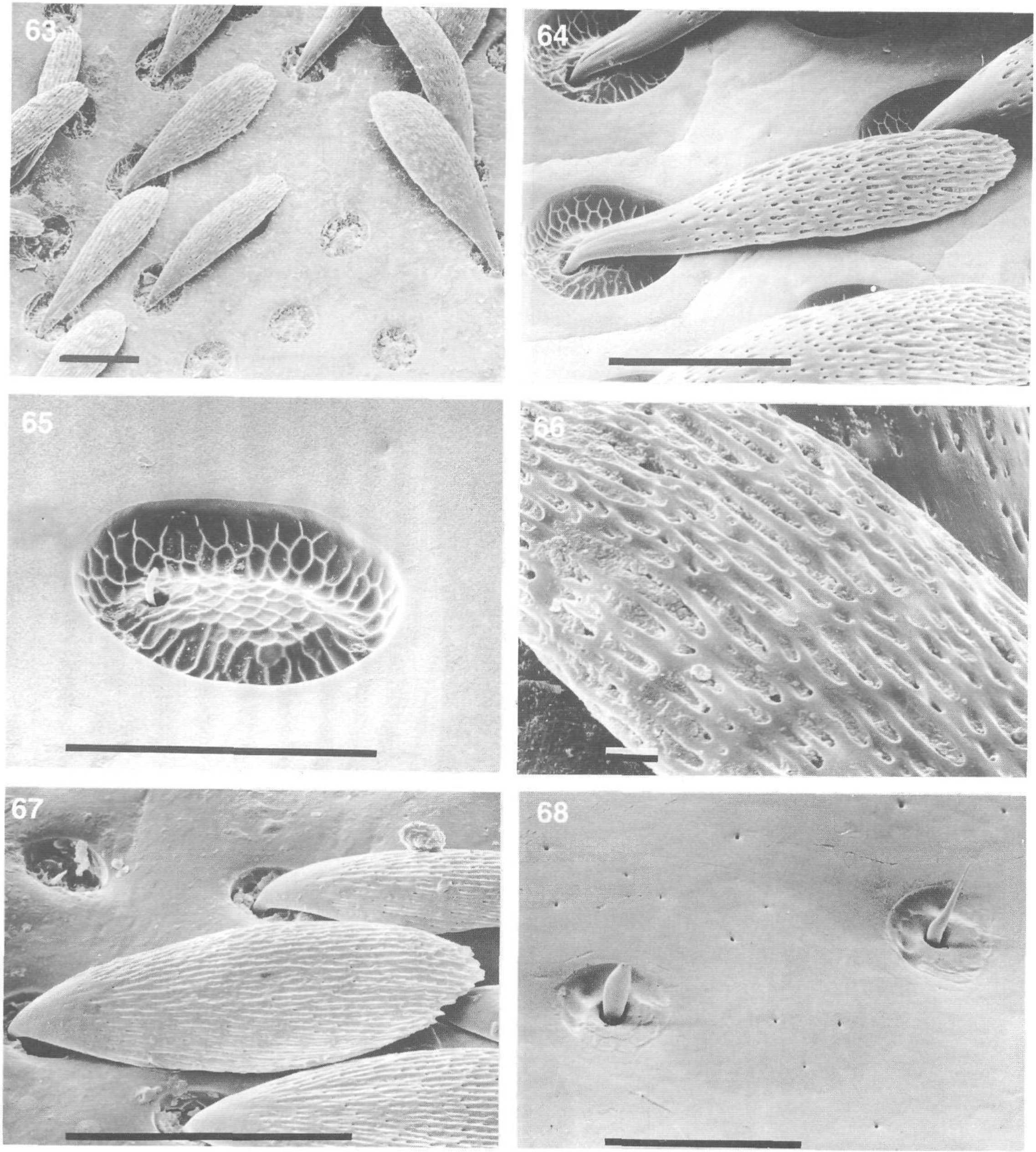

Fig. 63–68 Micrographs of elytral surface structures in Lucanidae (all Aesalinae). **63–66**, *Ceratognathus parrianus*: 63, large scales and minute setae (four in lower right of the micrograph) in pits filled with with detritus or exudate (bar = 0.1 mm); 64, cleaned preparation showing scales inserted near the walls in sculptured pits (bar = 0.1 mm); 65, cleaned preparation of a seta in a pit that has a convex but flat-topped floor, and also showing the finely reticulate surface of the adjacent integument (bar = 0.1 mm); 66, part of the dorsal surface of a scale showing anastomosing ribs (bar = 10 μm). **67**, *C. irroratus*: three scales and a minute seta (top left) all inserted near the walls of their pits (bar = 0.1 mm). **68**, *C. passaliformis*: cleaned preparation of a narrow scale (on the right, with an elongate tip) and a broad seta (on the left, with a divided tip) slightly off-centre in polygonally sculptured pits, and also showing faint polygonal sculpturing on the adjacent integument (bar = 0.05 mm).

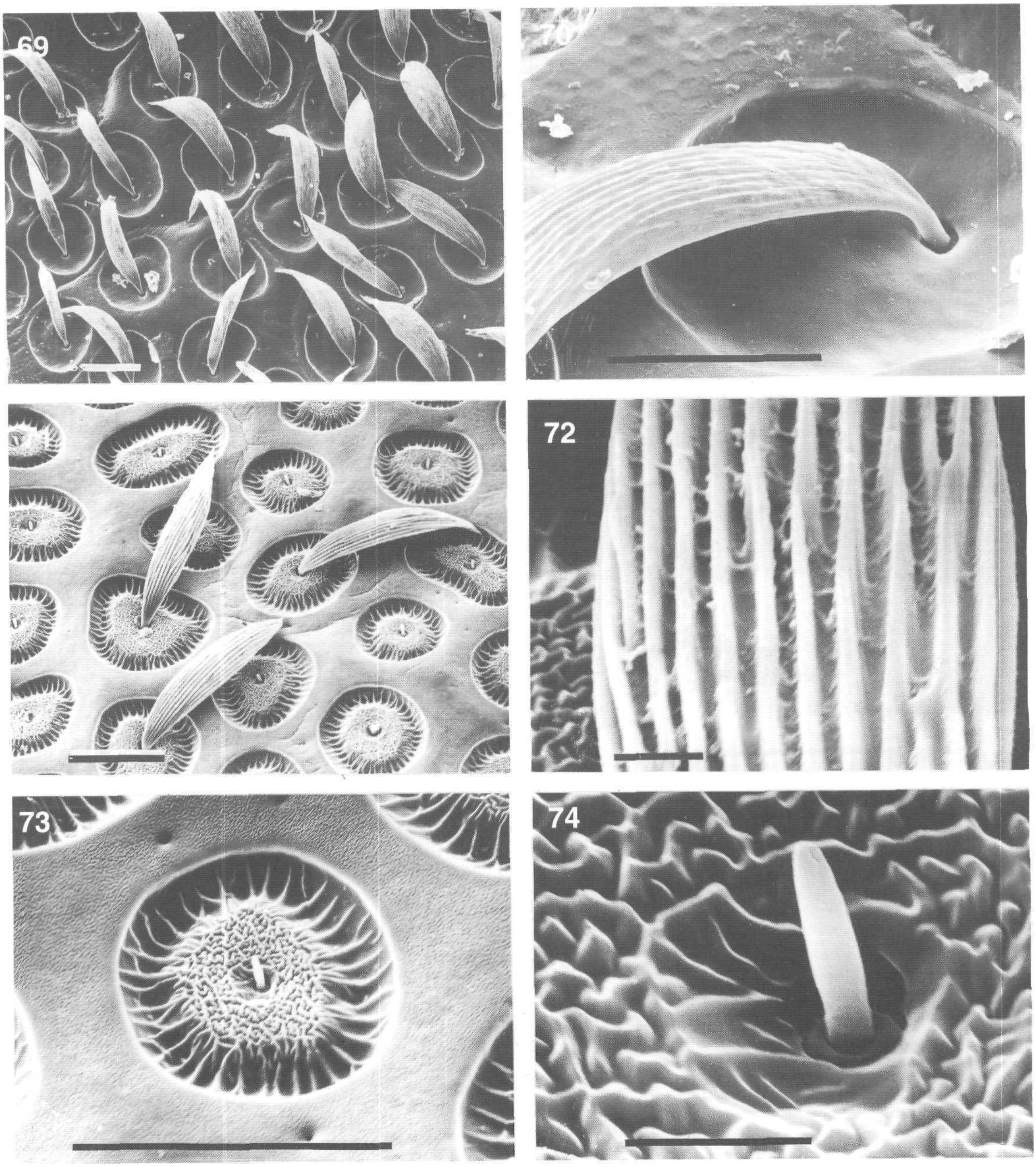

Fig. 69–74 Micrographs of elytral surface structures in Lucanidae (all Aesalinae). **69, 70**, *Ceratognathus helotoides*: 69, numerous scales on a piece of elytron heavily coated with exudate (bar = 0.1 mm); 70, scale off-centre in a polygonally sculptured pit (the sculpturing faint, but discernible to right of bar line) and sculptured surface of integument outside the pit (bar = 0.05 mm). **71–74**, *C. niger* (all cleaned preparations): 71, three scales and numerous setae all arising centrally in the pits (bar = 0.1 mm); 72, dorsal surface of part of a scale showing slightly anastomosing longitudinal ribs (bar = 10 μm); 73, seta in the centre of a pit with a raised, flat-topped floor and ribbed walls, and finely reticulate integument surrounding the pit (bar = 0.1 mm); 74, enlargement of the seta in Fig. 73 showing its incised apex, the socket surrounding its base, and part of the crumpled, corrugated floor of the pit (bar = 10 μm).

the stalk to the margin (Fig. 30, 72). The setae are minute relative to the size of the scales (Fig. 71), erect, cylindrical, with a shallow incision at the apex, and are set in the centre of the pit (Fig. 73, 74).

Pits: Approximately circular, somewhat saucer-shaped depressions with well-defined margins, concave walls, and a raised but flat-topped floor, the walls vertically ribbed with a few of the ribs forked, the floor with crumpled corrugations (Fig. 73, 74).

Integument adjacent to the pits: Extremely finely reticulate (Fig. 65).

Ceratognathus passaliformis Holloway [New Zealand] (Fig. 68)

Vestiture: Squamose and setose, the scales minute, suberect, hemispherical in cross-section, short and broad basally, and somewhat flagellate apically, the setae minute, cylindrical, notched apically, the scales and setae inserted slightly off-centre in the pits.

Pits: Shallow, circular, slightly concave depressions with well-defined margins and polygonal sculpturing on the walls and floor.

Integument adjacent to the pits: With sculpturing as in the pits (the polygons barely visible in Fig. 68).

Nicagus obscurus LeConte [North America] (Fig. 28)

Vestiture: Squamose, the scales suberect, long, narrow, short-stalked, and inserted near the anterior margin of the pit. The lamina of the scale is bordered laterally by a pair of ribs which extend from the stalk almost to the apex.

Pits and adjacent integument not examined with SEM.

DISCUSSION

Of the three elytral structures examined, the vestiture, consisting of setae and scales, has the greatest number of character states. Setae may be undivided (entire) or divided, have smooth or barbed surfaces, be tapering or parallel-sided, and have sharp or blunt tips. Undivided setae may be short or long, and equal or unequal in length.

Scales are stalked or sessile, erect to decumbent, fan-shaped, elongate-oval, or almost parallel-sided, and their apices are rounded or pointed. They may lack surface features or have longitudinal ribs that are either discrete or anastomosing. In their dry (?normal) state, scales may be fully extended and rigid or folded longitudinally so that parts of the lamina are concealed. There are three insertion positions for setae and scales in the pits—centrally or anteriorly in the pit floor, or centrally in the anterior wall.

Pits may be dimple-like depressions or sharp-edged, shallow or deep cavities. Their floor may be concave or raised, and if raised either convex or flat-topped. Sharply demarcated pits may have concave walls or their walls may be almost vertical. The pit surface may be the same as that of the adjoining integument or differently sculptured. The pit floor is either devoid of pores or contains a single large pore.

The integument adjacent to the pits may be polygonally or triangularly sculptured, very finely reticulate, or lack surface sculpturing. In some preparations the sculpturing is almost obscured by a coating of exudate (e.g., Fig. 39, 42) which probably reaches the surface through minute pores that are scattered over the integument (e.g., Fig. 68, 73). In one species there is an exceptionally large integumental pore close to the posterior margin of each pit (Fig. 37, 38). The polygonal sculpturing of both the pits and the surrounding integument is not associated with any pores and appears to be formed from substances that solidify after diffusing through cell walls (e.g., Fig. 40, 46, 52, 62).

Features of the elytral ultrastructure in the four subfamilies are summarised below.

Subfamily Lampriminae

This small subfamily comprising about four genera and fewer than 20 species is confined to Australia, New Guinea, New Zealand, Norfolk and Lord Howe Islands, and Chile. The elytral surface structure, examined in representatives of three genera that are widely separated geographically, is the simplest that was seen. The pits are shallow integumental indentations containing a simple seta which is inserted near the centre of the pit floor and has a conspicuous pore close to its base. The surface structure of the pits is the same as that of the surrounding integument. The combination of a pit, a simple seta, and an associated pore is the basic secretory unit on the integument of insects. The straight, erect, radially symmetrical setae of *Dendroblax* (Fig. 33) are completely unmodified. *Lamprima* (Fig. 35) and *Streptocerus* (Fig. 36) have curved setae, and those of *Streptocerus* are flattened and scale-like apically. Whether the unsculptured elytral surface in *Dendroblax* represents an unmodified condition is unclear. In *L. aurata* and *S. speciosus*, the elytra are sculptured. Lampriminae is the only subfamily that can, at present, be defined by its elytral pits and vestiture.

Subfamily Lucaninae

Lucaninae is the largest lucanid subfamily. It has more than 90 genera, over 1000 species, and is distributed worldwide. Elytral samples representing seven genera were examined with the scanning electron microscope, and setae and scales from species belonging to a further eight genera were examined and drawn under oil immersion.

The vestiture in individual species consists of either setae or scales or a combination of both. Of the lucanines examined, *Colophon* (Fig. 6) and *Lissapterus* (Fig. 7) have the simplest setae. They are undivided, smooth-sided, and have a rather blunt tip. The setae are shallowly incised at the apex in *Dorcus* (Fig. 9–11) and more deeply incised in *Hoplogonus* (Fig. 8). *Aegus*, *Apterodorcus*, *Geodorcus*, and *Serrognathus* (Fig. 12–18) have dendritic setae with smooth, tapered branches. Deeply incised setae with parallel-sided, smooth, blunt-tipped branches of equal length are present in *Lissotes* and *Sclerostomus* (Fig. 19–21). *Pycnosiphorus* and *Ryssonotus* (Fig. 22, 23) have setae similar to these except that the branches are barbed. In three genera, scales form the major or sole type of vestiture: *Lucanus* (Fig. 5) has minute, laterally compressed, triangular scales, and *Pholidotus* (Fig. 25) and *Paralissotes* (Fig. 26, 27) both have large, dorsoventrally flattened, somewhat fan-shaped scales. Those in *Pholidotus* apparently lack any surface features, but the scales of *Paralissotes* have discrete longitudinal ridges extending across the lamina. The lamina between the ridges is visible only when the scales are compressed under a coverslip. The vestiture of *Paralissotes* also includes minute, deeply incised setae (Fig. 54, 56). In the material examined the setae and scales all arise near the centre of the pits and have no closely associated pores.

Pits of the lucanines examined with the SEM all have a concave floor and surface sculpturing similar to that of the adjacent integument. The pit margin is sharply defined in *Dorcus* (Fig. 37, 38), *Geodorcus* (Fig. 39–42), *Lissotes* (Fig. 46, 47), and *Paralissotes* (Fig. 51, 54) but poorly defined in *Lucanus* (Fig. 57), *Pycnosiphorus* (Fig. 47), and *Ryssonotus* (Fig. 49).

The integument adjacent to the pits is visibly sculptured in all of the genera examined with SEM except *Lissotes*, where the surface detail is apparently obscured by exudate. In *Dorcus* and *Lucanus*, the sculpturing is triangular and rather scale-like, but in the other genera it is polygonal and consists of coalescent peaks of exudate. *D. parallelipipedus*, the only *Dorcus* species examined with SEM, is special in having a large integumental pore near the posterior margin of each pit. Whether this pore is present throughout the genus has yet to be determined.

Subfamily Syndesinae

Syndesinae comprise four genera (Holloway 1968) and about 25 species, and are distributed almost worldwide. *Syndesus cornutus*, an Australian species that has become established in New Zealand, is the only syndesine that was examined. Its vestiture consists of two types of setae, either long and barbed or short and smooth, in alternating longitudinal rows. Both types have barbed apices. The long setae arise anteriorly in the wall of very large pits (Fig. 59), and the short setae arise centrally on the floor of small pits (Fig. 60). The pits and surrounding integumental surface are unsculptured.

Subfamily Aesalinae

Aesalinae are distributed worldwide and comprise about 35 described species, which are currently placed in four genera: *Aesalus* Fabricius, *Ceratognathus* Westwood, *Lucanobium* Howden & Lawrence, and *Nicagus* Leconte. A full study was made of elytral surface structures in *Aesalus scarabaeoides* and *Ceratognathus niger*, type species of their respective genera, and of several New Zealand species included in *Ceratognathus*. The elytral vestiture of *Nicagus obscurus*, the type species of its genus, was drawn under oil immersion and its pits were examined with a stereomicroscope.

The vestiture in all the species examined consists mainly or entirely of longitudinally ribbed scales. In the inquiline New Zealand lucanid *C. passaliformis* the scales are minute, lack a distinct lamina, and appear to consist of only a single rib (Fig. 68). The scales of *N. obscurus* and *N. japonicus* Nagel (the latter examined only with a stereomicroscope) are large, elongate, almost parallel-sided, and have a pair of ribs that are joined together proximally then extend along the entire length of the lateral margins (Fig. 28). The scales of *A. scarabaeoides* (Fig. 61), *A. asiaticus* Lewis, and *A. imanishii* Inahara & Ratti (the two last-named species examined only with a stereomicroscope) are fan-shaped and have numerous ribs, some of which are forked and anastomosing. On dried specimens the scales are longitudinally folded, incompletely expanded, and somewhat frilly. At low magnifications, even with SEM, they could be mistaken for dendritic setae because the lamina is almost invisible between the conspicuous ribs, hence the need to make slide preparations of the vestiture.

The other aesalines that were examined have scales that are rigid, somewhat oval, and fully expanded when dry. In *C. niger* (Fig. 71) and *C. helotoides* (Fig. 70), some of the ribs are forked but most are undivided. In *C. parrianus* (Fig. 66) and *C. irroratus* (Fig. 67), adjacent ribs are connected throughout their length by short transverse branches. The vestiture of *C. niger* and the New Zealand *Ceratognathus* species includes minute setae which have an entire tip in *C. helotoides* but are shallowly incised in the other species (Fig. 65, 68, 74). No setae were seen in *Nicagus* or *Aesalus*. The minute, erect structures in some of the pits of *A. scarabaeoides* are scales (Fig. 62). In *C. parrianus*, *C. irroratus*, and the *Aesalus* species I examined, the elements of the vestiture are inserted anteriorly in the pits (Fig. 62, 65), but in the remaining species their insertion is either central or very slightly off-centre (Fig. 68, 69, 71).

The pits are sharply demarcated in all the species examined. In *C. passaliformis* and *C. helotoides* they have a concave floor and sculpturing similar to that of the adjoining integument. In the remaining species, including those examined only with a stereomicroscope (*A. asiaticus*, *A. imanishii*, *N. obscurus*, and *N. japonicus*), the pit floor is raised (Fig. 62, 65, 73) and the pit sculpturing seen in the micrographs is either the same as that on the adjoining integument (Fig. 62) or completely different from it (Fig. 65, 73).

The integument adjacent to the pits is polygonally sculptured in *A. scarabaeoides*, *C. passaliformis*, and *C. helotoides* but very finely reticulate in *C. irroratus*, *C. parrianus*, and *C. niger*.

Since 1960 all the New Zealand aesalines have been placed in *Ceratognathus* (Benesh 1960; Holloway 1961), but the form of their elytral surface structure suggests that they neither belong in this genus nor are a monophyletic group: *C. parrianus*, *C. irroratus*, and allied species constitute a different genus from *C. helotoides*, *C. passaliformis*, and their relatives. Obviously, genera cannot be established on elytral structures alone, but it seems certain from the comparative work I am currently doing on the New Zealand and Australian aesalines that confirming generic characters will be found elsewhere on the body and in the genitalia.

Howden & Lawrence (1974) and Lawrence & Newton (1995) consider the Aesalinae to include only *Aesalus* and *Lucanobium*. They place *Nicagus* and the Australian and New Zealand species of *Ceratognathus* in the Nicaginae, mainly because of differences in the form of the prosternal process (lobed anteriorly and touching the metasternum posteriorly in Aesalinae, neither lobed nor touching the metasternum in Nicaginae), the first two abdominal sternites (fused in Aesalinae, free in Nicaginae), and the antennal club (weakly lamellate and apparently not dimorphic in Aesalinae, strongly lamellate and dimorphic in Nicaginae). According to Howden & Lawrence (1974), the Aesalinae also differ from Nicaginae in having an ocular canthus, but they have confused the canthus with the preocular process, a triangular projection which may extend across the eye but which does not intrude into it (Holloway 1969).

Nothing in the elytral ultrastructure of *C. niger*, *C. irroratus*, and *C. parrianus* suggests that these species belong in any subfamily other than Aesalinae. In common with *Aesalus*, they have large pits with a raised floor and scales with longitudinal, anastomosing ribs. As well, in *A. scarabaeoides*, *C. irroratus*, and *C. parrianus*, the pits are polygonally sculptured and the scales are inserted anteriorly in the pit floor. The elytra of *Nicagus* were not examined with SEM, but by using a stereomicroscope I was able to see that some of the elytral pits in *N. obscurus* and *N. japonicus* have a raised floor, and that the vestiture in both species consists of narrow scales with longitudinal marginal ribs. A raised floor represents a derived state in the pits of Lucanidae. Whether it is a more widespread feature of stag beetles than is currently suggested is not known, but for the present it seems appropriate to unite in Aesalinae the genera *Aesalus* and *Nicagus*, the Australian *Ceratognathus* species, and the New Zealand species currently in *Ceratognathus* that have a raised pit floor. Details of the pits of *Lucanobium* are not available. The subfamily affiliation of *C. helotoides*, *C. passaliformis*, and related species that do not have a raised floor in their elytral pits has yet to be determined.

Although the number of species examined in this project is small, there is sufficient evidence to show that the form of the vestiture and pits on the elytra of lucanids is constant in genera and throughout the subfamily Lampriminae. Present indications are that the Aesalinae may be definable by their complex pit structure. The discovery of a distinctive lamprimine elytral ultrastructure may shed new light on the taxonomic position of the Baltic amber lucanid *Paleognathus succini* Waga, which has been grouped with genera in both Lampriminae and Lucaninae (Holloway 1960). With the use of just a stereomicroscope, it should be possible to see enough elytral detail to determine whether this fossil is a lamprimine. A great deal more SEM work needs to be done on the elytral structures in species assigned to the subfamily Lucaninae. To date, genital and other commonly used characters have not been able to provide a satisfactory grouping of its genera. I am hopeful that the form of the elytral surface structures will help to clarify relationships throughout the Lucanidae.

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