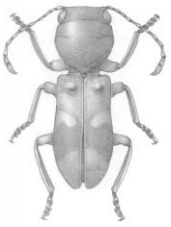


Barriella longicornoides Opitz

WILLIAM F. BARR ENTOMOLOGICAL MUSEUM
TECHNICAL REPORT No. 2

University of Idaho, EPPN Department
875 Perimeter Drive MS 2329
Moscow, ID 83844-2329

University of Idaho

A proposed classification of morphological characters of the prescutum and scutellum for bark beetle genera of Hylesinini and Scolyini (Coleoptera: Curculionidae: Scolytinae)

Malcolm M. Furniss[1] and Luc Leblanc[2]

[1] Principal Research Forest Entomologist and Project Leader, USDA Forest Service, Moscow, ID (Retired).
[2] Curator and Manager of the William F. Barr Entomological Museum.

ABSTRACT

The morphological characters of the prescutum and scutellum of representative species of twenty-three genera of Hylesinini and Scolytini (Coleoptera: Curculionidae: Scolytinae), and two genera of outlier tribes of similar ecological habits, were examined by scanning electron microscopy. Characters involving the prescutum formed three groups: shape, setae, and surface features. Characters of the scutellum involved its shape and attachment to the prescutum. This study uncovered a range of morphological characters, rivaling the traditional antennal characters, useful support to the study of the classification, phylogeny and biology of two tribes of Scolytinae. All taxa studied had a shield-shaped prescutum, except the outlier *Platypus* (Platypodinae: Platypodini). Hylesinini differed significantly from Scolytini in having a greater number of setae with multiple stems and proportionately more genera with a smooth prescutum surface. More stems of the scutellum of Scolytini were tapered than were those of other studied taxa. Comparison of three pairs of sibling species of *Dendroctonus* Erichson indicated that intraspecific morphological characters exhibit differences potentially useful in helping resolve cases of questioned synonymy. The phloeophagous outlier *Pissodes* Germar (Curculionidae: Molytinae) fell within variation present in Hylesinini whereas outlier xylophagous *Platypus* did not resemble any other genus herein.

How to cite this paper: **Furniss, M.M., and L. Leblanc. 2025.** A proposed classification of morphological characters of the prescutum and scutellum for bark beetle genera of Hylesinini and Scolyini (Coleoptera: Curculionidae: Scolytinae). University of Idaho. Barr Entomological Museum. Technical Report 2: 1–20.

INTRODUCTION

Bark and ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) are ecologically significant members of forest communities as decomposers, vectors of disease-causing organisms, and primary tree mortality agents. The genera and species of greatest concern to forest owners and managers are in two tribes: Hylesinini and Scolytini. Hylesinini includes the destructive *Dendroctonus* Erichson. Scolytini includes *Ips* DeGeer and *Scolytus* Geofroy, several species of which are also primary tree killers. For those reasons, and my geographic location and interests at the time, I conducted studies of the external structures involved in vectoring of fungus ascospores such as pits on the elytra of *Ips* (Furniss et al. 1995) (Fig. 4), and a setaceous patch on *Pityoborus* females (Furniss et al. 1987) (Figs. 2–3 herein). The prescutum and scutellum were initially included in that study but discontinued when none was found carrying spores externally. However, much variation was evident in morphological characters of the features of the prescutum and scutellum, which led to classifying them for use in distinguishing genera within tribes of Scolytinae. The prescutum and its associated scutellum form a heavily sclerotized plate on the mesonotum to which the elytra are attached (Fig. 1) (Hopkins 1909).

Traditional taxonomists have relied on morphology to describe and revise species in such genera as *Dendroctonus* Erichson (Hopkins 1909), *Gnathotrichus* Eichhoff (Schedl 1931), *Pityophthorus* Eichhoff (Bright 1981), *Ips (*Hopping 1963), and the inclusive monograph by Wood (1982). More recently, molecular systematics has supplemented morphology, such as in the revision of *Scolytus* by Smith and Cognato (2014).

Morphological features employed in taxonomy of Scolytinae were listed and used in keys by Wood (1986) and for cladistic analysis of Xyleborina by Hulcr et al. (2007). They include characters on the head and its components, especially the antennal club which Wood described as probably the most variable structure found throughout Scolytinae [reiterated by Hopping (1963) regarding *Ips*]. Other listed taxonomic features occur on the remaining body parts, legs and elytra. Wood and other authors have however made little use of the prescutum and scutellum, only noting its general shape and whether it is partially or wholly hidden from view. Three known references contain outline drawings of the prescutum and scutellum of genera of Hylesinini: *Dendroctonus* (Hopkins 1909), *Hyluropinus* (Kaston 1936), and *Gnathotrichus* (Schedl 1931). Schedl's figure of the prescutum of *Ganthotrichus* is erroneous regarding attachment of its scutellum and reference to pits being located on the anterior half of the prescutum (see his Fig. 14). This seems due to his figure being placed with anterior downward. Kaston noted that in *Hyluropinus rufipes* (Eichhoff), the only known species of this genus, the scutellum is indistinctly three to five-lobed on its posterior margin and that the transverse area in the middle third of the prescutum is punctured. This genus is not included in our study. *Dendroctonus valens* Hopkins has a bi-lobed posterior edge of the scutellum; all other species herein lack lobes on the scutellum.

MATERIALS AND METHODS

Scanning Electron Microscopy. Representative specimens of nine genera of Hylesinini (of 20 total genera) and fourteen genera of Scolytini (out of 50), and two outlier genera of similar ecological habits (Table 1) were selected from available series at the W.F. Barr Entomological Museum (WFBM), Moscow, Idaho and the senior author's collections. Elytra of specimens were removed to expose the prescutum before being cleansed in 70% ethanol, air-dried and mounted on metal stubs. Stubs with specimens were sputter-coated 20 m with gold and examined with a Hitachi S570 scanning electron microscope. The prescutum and scutellum of each specimen were photographed with Polaroid Type 55 film. Stubs with voucher specimens relating to this study are deposited in the WFBM.

Taxonomic characters. Characters were defined by visual comparison of the prescutum and associated scutellum. Three groups of character states were defined for the prescutum: 1. Shape (shield); 2. Setae (single stem; multiple stems); 3. Surface (smooth; plate-like, not elevated;

roughened, strongly elevated). Characters of the scutellum were related to its shape (blunt, sides straight or nearly so; blunt or pointed, sides tapered; round or somewhat round, base constricted). Intrageneric variation was also assessed by including three pairs of sibling species of *Dendroctonus*: *D. monticolae* and *D. jeffreyi*; *D. punctatus* and *D. micans*; and *D. valens* and *D. rizophagus* (Figs. 6A–F), the synonymy of which had been in question in the past.

Genus	Prescutum							Scutelllum		
	Shape		Setae		Surface			Shape		
	1	2	1	2	1	2	3	1	2	3
Scolytinae: Hylesinini										
5. *Alniphagus*	x			x		x		x		
6. *Dendroctonus*	x			x	x			x		
7. *Hylastes*	x			x			x			x
8. *Hylesinus*	x			x		x		x		
9. *Hylurgops*	x			x			x			x
10. *Phloeosinus*	x		x			x				x
11. *Polygraphus*	x			x	x					x
12. *Pseudohylesinus*	x			x	x					x
13. *Scierus*	x			x			x			x
Scolytinae: Scolytini										
14. *Conophthorus*	x		x		x					x
15. *Cryphalus*	x			x		x			x	
16. *Crypturgus*	x		-	-			x			x
17. *Dryocoetes*	x		x			x				x
18. *Gnathotrichus*	x		x			x			x	
19. *Ips*	x			x	x			x		
20. *Pityoborus*	x		x			x			x	
21. *Pityogenes*	x		x		x			x		
22. *Pityophthorus*	x		x			x			x	
23. *Procryphalus*	x		x			x			x	
24. *Scolytus*	x			x	x				x	
25. *Trypodendron*	x		x			x			x	
26. *Trypophloeus*	x		-	-		x			x	
27. *Xyleborus*	x		x		x				x	
Mollytinae: Pissodini										
28. *Pissodes*	x			x			x			x
Platypodinae: Platypodini										
29. *Platypus*		x	x			x			x	

Table 1. Morphological character states of the prescutum and scutellum of 23 genera of Hylesinini and Scolytini (Scolytinae), and two outlier tribe genera of similar habit covered under this study. Numbers before genera align with figure numbers. Three pairs of sister species of *Dendroctonus* are treated and illustrated separately.

Prescutum shape
1. Shield-shaped
2. Other than shield-shaped
Prescutum setae
1. Single stem
2. Multipla stems
Prescutum surface
1. Smooth
2. Plate-like, not strongly elevated
3. Roughened, strongly elevated
Scutellum stem
1. Nearly straight
2. Tapered
3. Round or somewhat round; base constricted

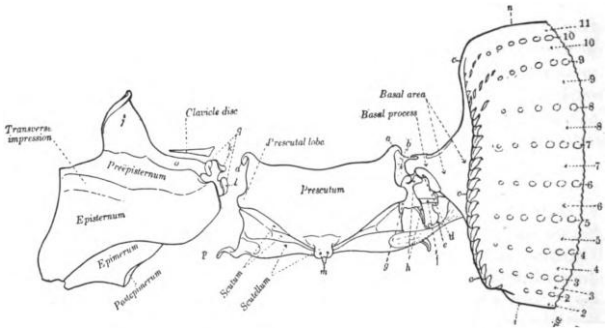


Fig. 1. Prescutum (center, shield-shape) and scutellum (posterior projection m) of *Dendroctonus valens* LeConte (Hylesinini). The elytra attach to it. Among tribes studied herein, the prescutum and scutellum varied in shape, surface and setae. This study illustrates such differences and suggests using them in cladistic study of genera of Scolytinae tribes. Reproduced from Hopkins (1909) (Fig. 19).

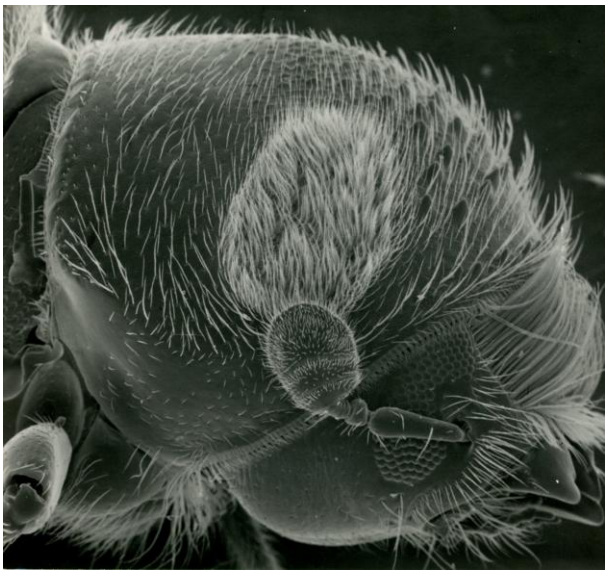


Fig. 2. Right side of prothorax and head of *Pityoborus rubentis* Wood showing the light-colored oval pubescent mycangium possessed by females of this genus. The segmented object in front of it is the antenna. Nutritious yeast spores are raked from the gallery wall and become lodged between the pubescent setae and carried to shaded out branches of a new host tree (see Fig. 3). Reproduced from Furniss et al. (1987). Specimen data: MEXICO, Durango, La Flor; *Pinus lumholtzei*; 24-III-1974; M.M. Furniss.

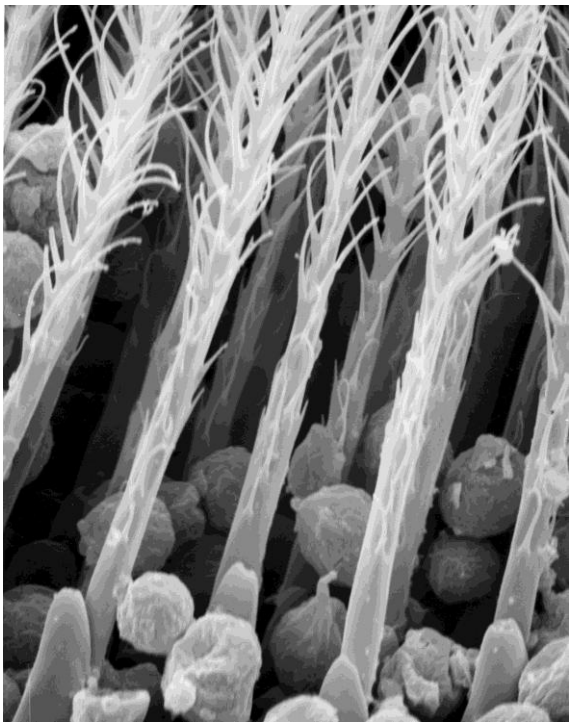


Fig. 3. Magnified section of pubescent patch of *Pityoborus secundus* Blackman showing round yeast spores lodged among overstory of plumose setae.

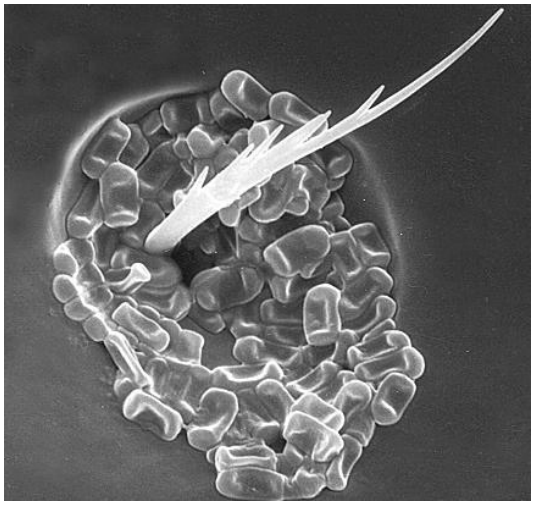


Fig. 4. Ascospores of a pathogenic blue stain fungus, *Ophiostoma pini* and protruding seta of a pit on elytron of the pine engraver bark beetle, *Ips pini* Say. The SEM photos used in the proposed classification were obtained during survey of pit mycangia; however, not found to be present on either prescutum or scutellum. Reproduced from Furniss et al. (1995).

RESULTS

Characters of prescutum and scutellum

Prescutum shape. A shield shape was constant among the studied taxa, except elongate in outlier genus *Platypus* (Platypodini) (Fig. 29) and compressed in *Cryphalus* (Fig. 15).

Prescutum setae. Setae differed between the two tribes, having mainly multiple stems in Hylesinini and single stems in Scolytini. For this classification, multiple stems are grouped. However, with the examination of additional genera, multiple stemmed genera might be divided into three classes: two-stemmed, three-stemmed, and more than three-stemmed. Further, the stems appear to be either smooth or to have projections (barbules?) such as in *Dendroctonus* (Fig. 6) and *Cryphalus* (Fig. 15). However, some stems appear smooth but may have projections obscured by an overlying secreted waxy substance. Thus, this feature is not used. A portion of the anterior end of the prescutum of Hylesinini lacked pits and setae. Scolytini varied regarding this feature, except in *Dryocoetes*, *Gnathotrichus* and *Procryphalus*. Setae were absent from the prescutum of *Phloeosinus*, *Crypturgus* and *Trypophloeus*.

Prescutum surface. The surface of Hylesinini varied evenly between the surface characters, being smooth, plated or rough. Scolytini had proportionately fewer genera with roughened surface and more with plated surface.

Scutellum shape. The shape of the scutellum tended to be rounded in Hylesinini and more variable in Scolytini. Its posterior end is bi-lobed (Fig. 6F) in *Dendroctonus valens*, while lacking lobes in all other species herein. Note, however, that in Hopkins (1909) his drawing (Fig. 1 herein) does not show the lobes of *D. valens* clearly.

Scolytinae: Hylesinini

***Alniphagus* Swaine** (Fig. 5). Prescutum shield-shaped. Setae multi-stemmed, dense with their pits often touching. Surface plate-like, front half without pits or setae. Scutellum blunt with straight sides.

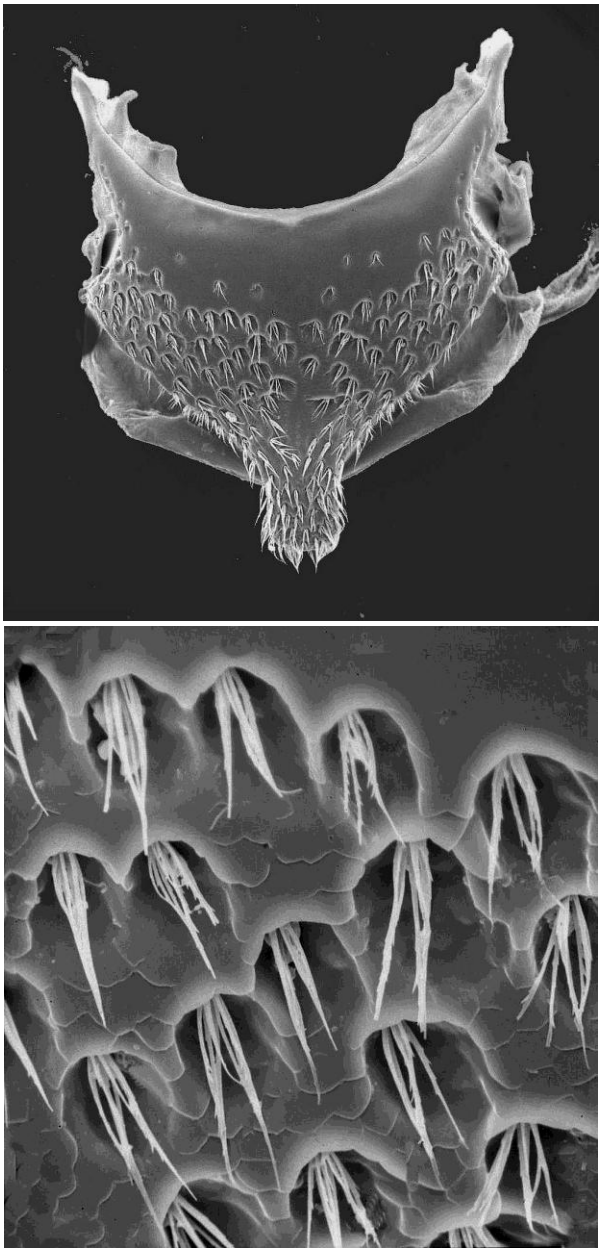


Fig. 5. Prescutum and prescutellar setae of *Alnphagus aspericollis* (LeConte). Prescutum setae. Specimen data: IDAHO, Bonner Co., Fall River Ranger Station; *Alnus* sp.; 29-VII-1967; M.M. Furniss.

Dendroctonus **Erichson** (Figs. 6 A–F). Prescutum shield-shaped. Setae multi-stemmed; typically two and three-branched except four or five-branched on *D. ponderosae* (Fig. 6 D). Surface smooth, pits with setae dense and covering entire prescutum except bare medial space between pits on *D. punctatus* and *D. micans* (Figs. 6 E–F), extending farther on *D. punctatus*. Scutellum sides parallel, blunt end two-lobed on *D. valens* (Fig. 6 B); lobes lacking on *D. rhizophagus* and other sibling pairs and others herein.

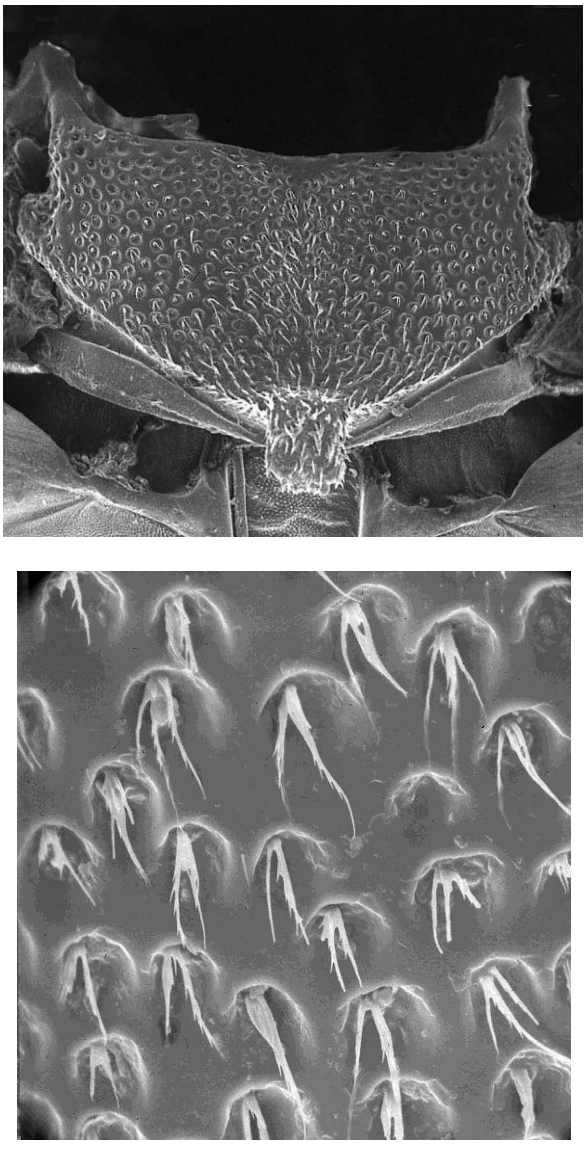


Fig. 6 A. Prescutum and prescutellar setae of *Dendroctonus jeffreyi* Hopkins. Specimen data: CALIFORNIA, Mariposa Co., Yosemite N.P.; *Pinus contorta*; 2-VI- 1918; J.E. Patterson.

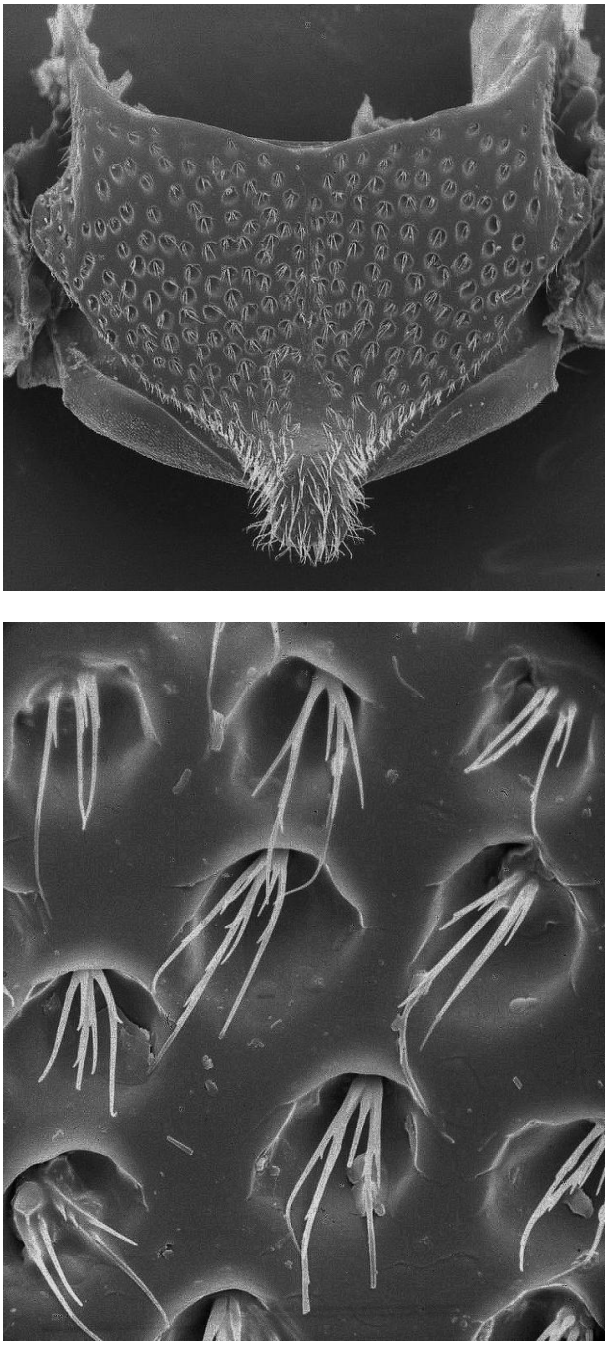
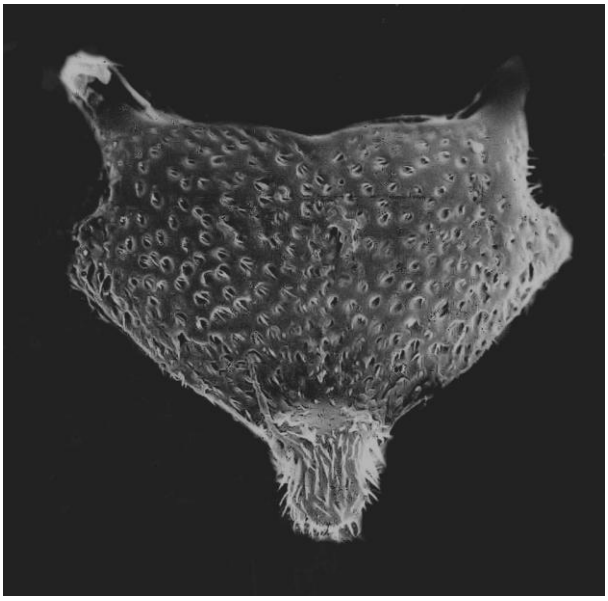


Fig. 6 B. Prescutum and prescutellar setae of *Dendroctonus ponderosae* Hopkins. Specimen data: IDAHO, Kootenai Co., Deception Creek Experimental Forest; *Pinus monticola*; 20-VI-1968; M.M. Furniss.

Fig. 6 C. Prescutum and prescutellar setae of *Dendroctonus punctatus* LeConte, Specimen data: ALASKA, Mile 27 on Haines Road; *Picea glauca*; 12-VI-1961; G. Downing.

Fig. 6 D. Prescutum and prescutellar setae of *Dendroctonus micans* (Kugelann). Specimen data: BELGIUM; *Picea abies*; 1984; J-C. Grégoire.



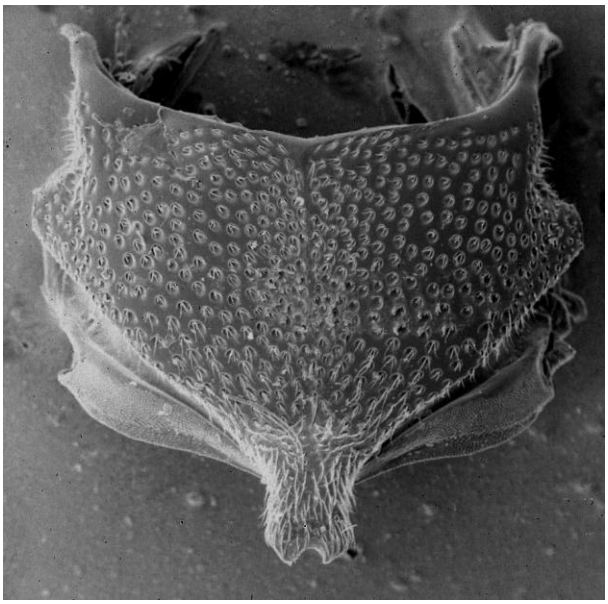


Fig. 6 E. Prescutum and prescutellar setae of *Dendroctonus rhizophagus* Thomas and Bright. Specimen data: MEXICO, Durango, Llano Grande; *Pinus engelmannii*; 30-VII-1978; R. Campos Bolaños.

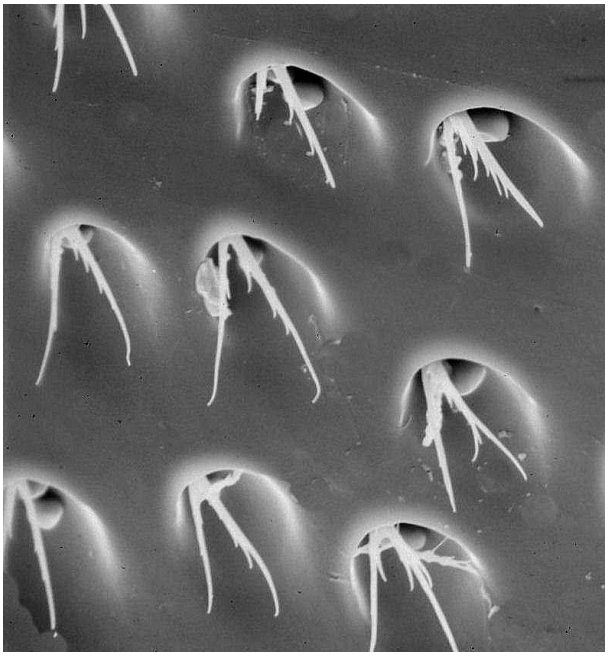


Fig. 6 F. Prescutum and prescutellar setae of *Dendroctonus valens* LeConte. Specimen data: OREGON, Deschutes Co., Middle Sister Mountain; in flight; 4-VII-1968; M.M. Furniss.

Hylastes **Erichson** (Fig. 7). Prescutum shield-shaped. Setae multi-stemmed, moderately dense with pits well spaced. Posterior surface pebble-like, raised; front smooth without pits or setae. Scutellum rounded, base constricted.

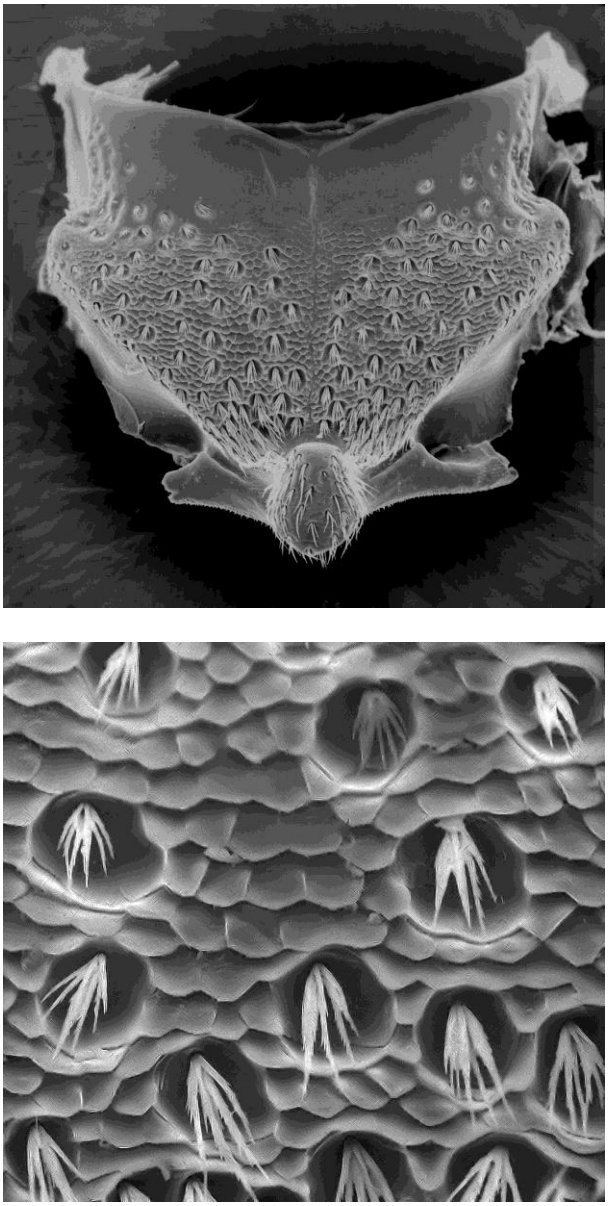


Fig. 7. Prescutum and prescutellar setae of *Hylastes macer* LeConte. Specimen data: IDAHO, Benewah Co., Tensed; In flight; 13-IV-1977; M.M. Furniss

Hylesinus **Fabricius** (Fig. 8). Prescutum shield-shaped. Setae multi-stemmed, dense. Surface lightly plate-like, front one quarter without pits or setae. Scutellum blunt, sides slightly tapered.

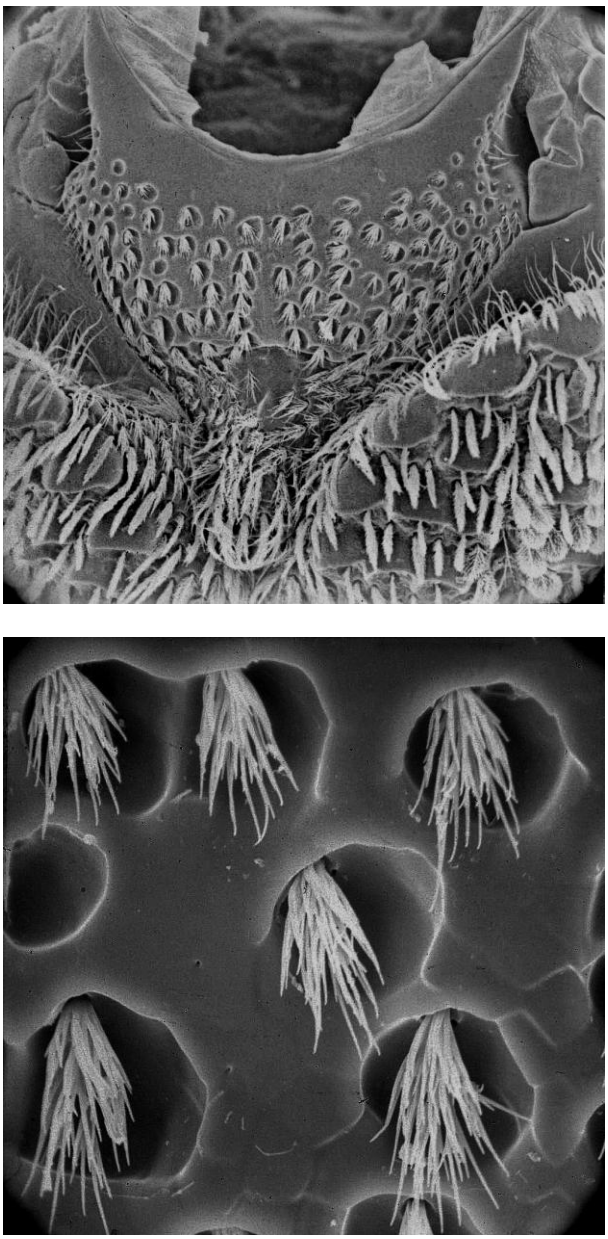


Fig. 8. Prescutum and prescutellar setae of *Hylesinus californicus* (Swaine). Specimen data: CALIFORNIA, Siskiyou Co., Hilt; Ash; 18-IV-1933; Paul Rice.

Hylurgops **LeConte** (Fig. 9). Prescutum shield-shaped. Setae multi-stemmed, moderately dense with pits well spaced. Posterior surface pebble-like, raised; front smooth without pits or setae. Scutellum rounded, base constricted.

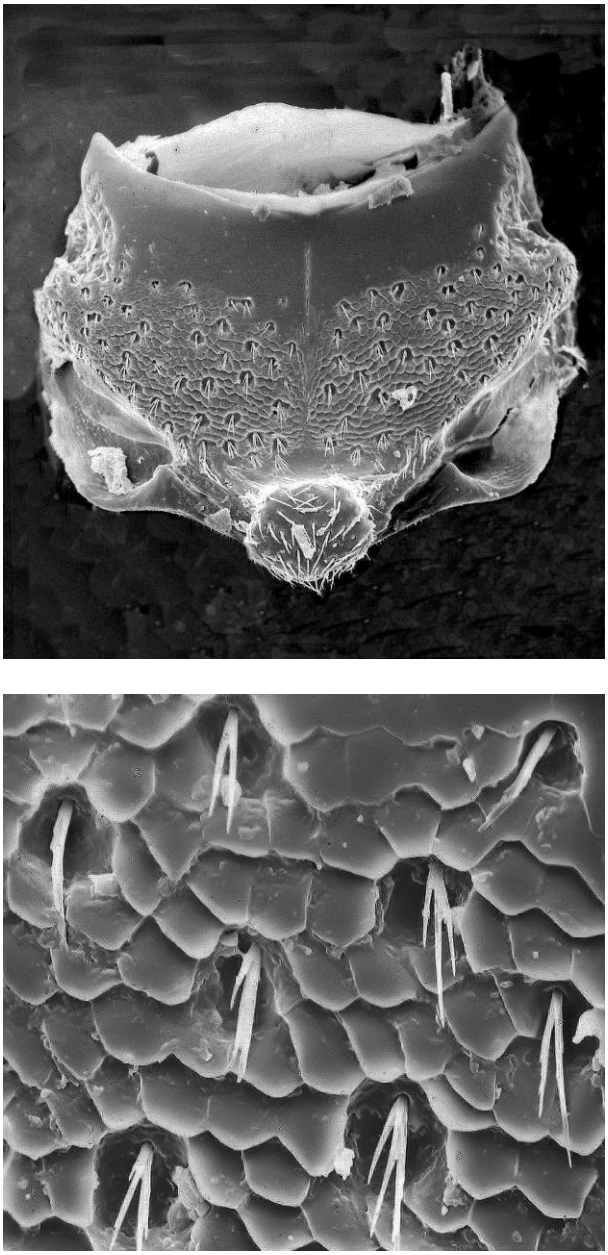


Fig. 9. Prescutum and prescutellar setae of *Hylurgops* (=*Pachysquamus*) *subcostulatus subcostulatus* (Mannerheim). Specimen data: IDAHO, Benewah Co., Tensed; in flight; 13-IV-1977; M.M. Furniss.

Phloeosinus **Chapuis** (Fig. 10). Prescutum shield-shaped, somewhat compressed. Setae absent except sparse, short projections on posterior surface. Anterior surface divided into network of cells, not raised. Scutellum abnormal, truncated round, base constricted.

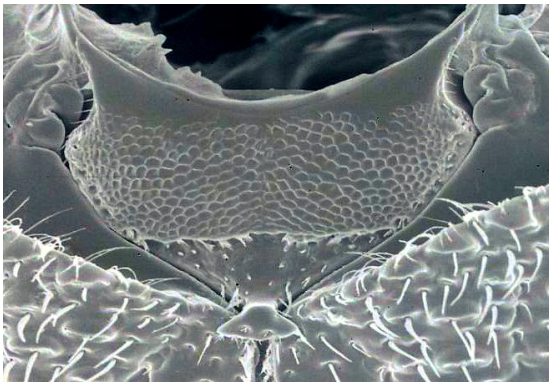


Fig. 10. Prescutum of *Phloeosinus pini* Swaine. Specimen data: IDAHO, Fremont Co., Henrys Lake; *Picea glauca x engelmanii*; 21-VII-1984; M.M. Furniss.

Polygraphus **Erichson** (Fig. 11). Prescutum shield-shaped. Setae multi-stemmed, dense with their pits often touching. Surface smooth, covered with pits except antero-laterally. Scutellum rounded, base constricted.

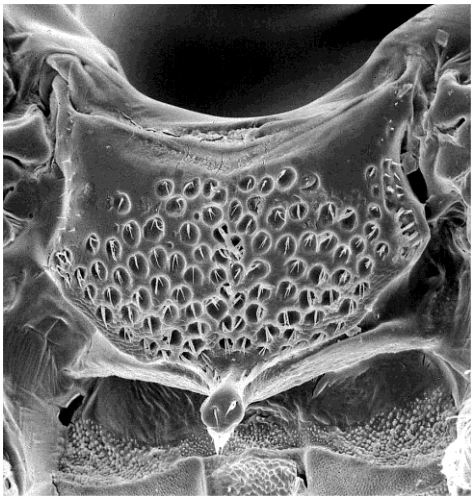


Fig. 11. Prescutum of *Polygraphus rufipennis* (Kirby). Specimen data: IDAHO, Idaho Co., Magruder Ranger Station; *Picea engelmanni*; 1-IX-1956; M.M. Furniss.

Pseudohylesinus **Swaine** (Fig. 12). Prescutum shield-shaped. Setae multi-stemmed, moderately dense with pits well-spaced. Surface smooth, pits and setae confined to posterior half. Scutellum rounded, base constricted.

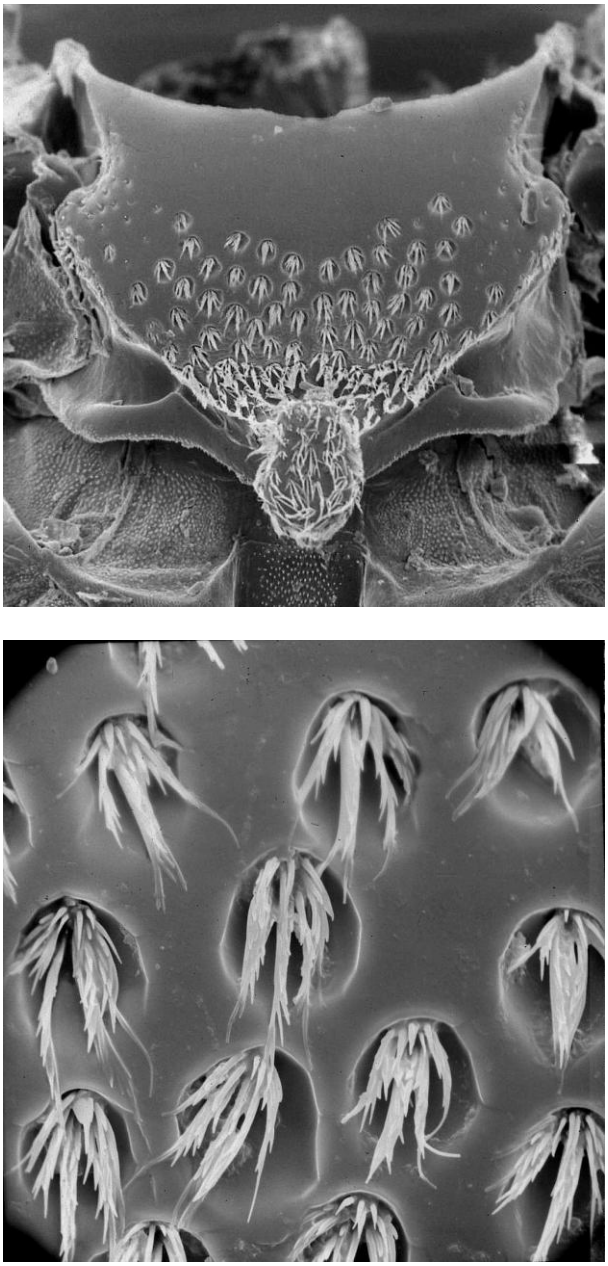


Fig. 12. Prescutum and prescutellar setae of *Pseudohylesinus granulatus* (LeConte). Specimen data: IDAHO, Latah Co., Big Sand Cr.; flight trap; 9-VI-1969; M.M. Furniss.

Scierus **LeConte** (Fig. 13). Prescutum shield-shaped. Setae multi-stemmed, sparse. Posterior surface pebble-like, raised; front smooth without pits and setae. Scutellum rounded, base constricted.

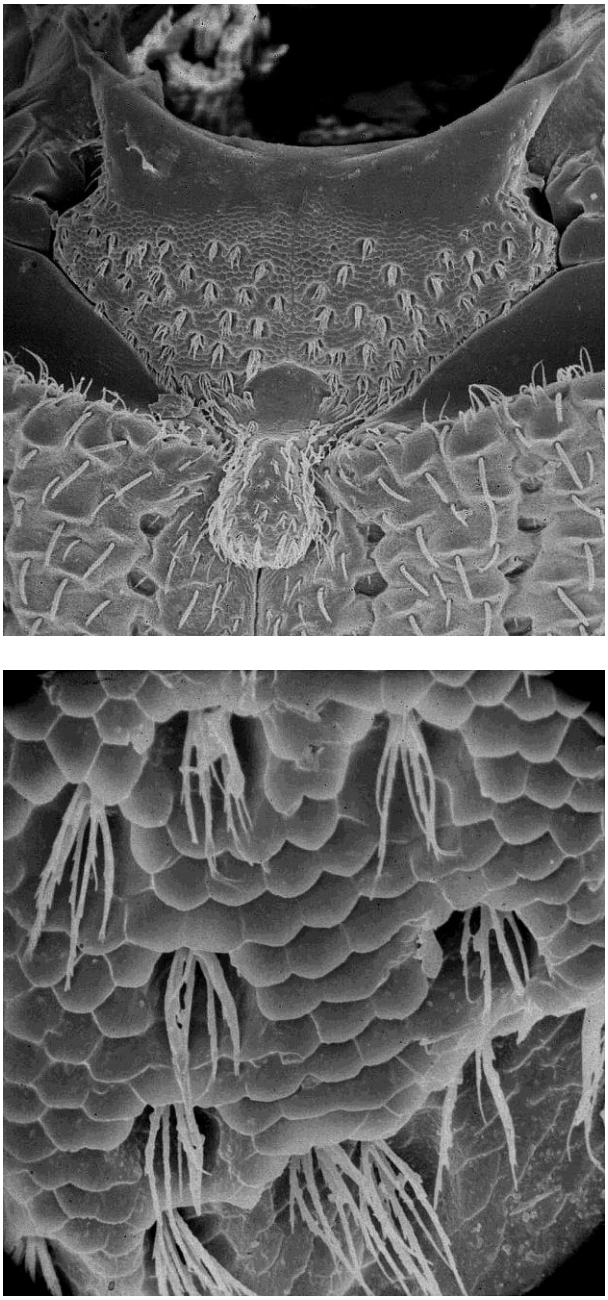


Fig. 13. Prescutum and prescutellar setae of *Scierus annectens* LeConte. Specimen data: IDAHO, Valley Co., McCall; flight trap; 23-VI-1972; R.D. Oakes.

Scolytinae: Scolytini

***Conophthorus* Hopkins** (Fig. 14). Prescutum shield-shaped. Setae single-stalked, their pits sparse, absent in small areas antero-laterally and posteriorly. Surface smooth. Scutellum rounded, base constricted.

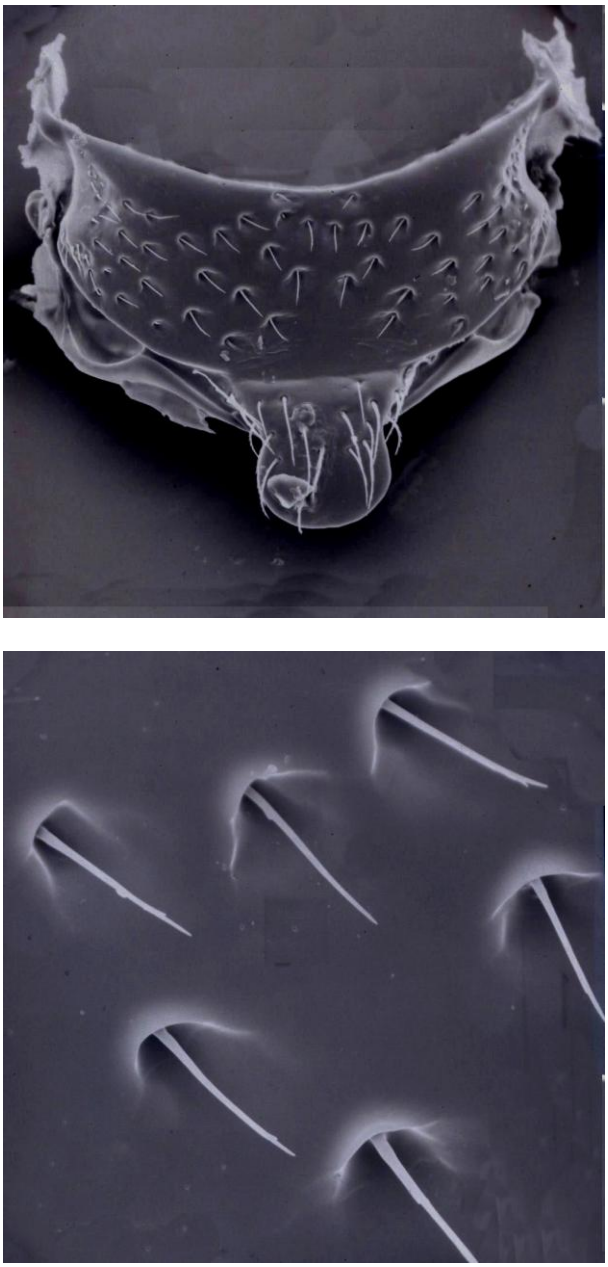


Fig. 14. Prescutum and prescutellar setae of *Conophthorus cembroides* Wood. Specimen data: MEXICO, Chihuahua, Sierra Catalina Mountains; pinyon pine; 23-IV-1981; M.M. Furniss.

***Cryphalus* Erichson** (Fig. 15). Prescutum shield-shaped, somewhat compressed. Setae multi-stemmed, moderately dense. Surface plate-like. Scutellum sharply tapered to a point**.**

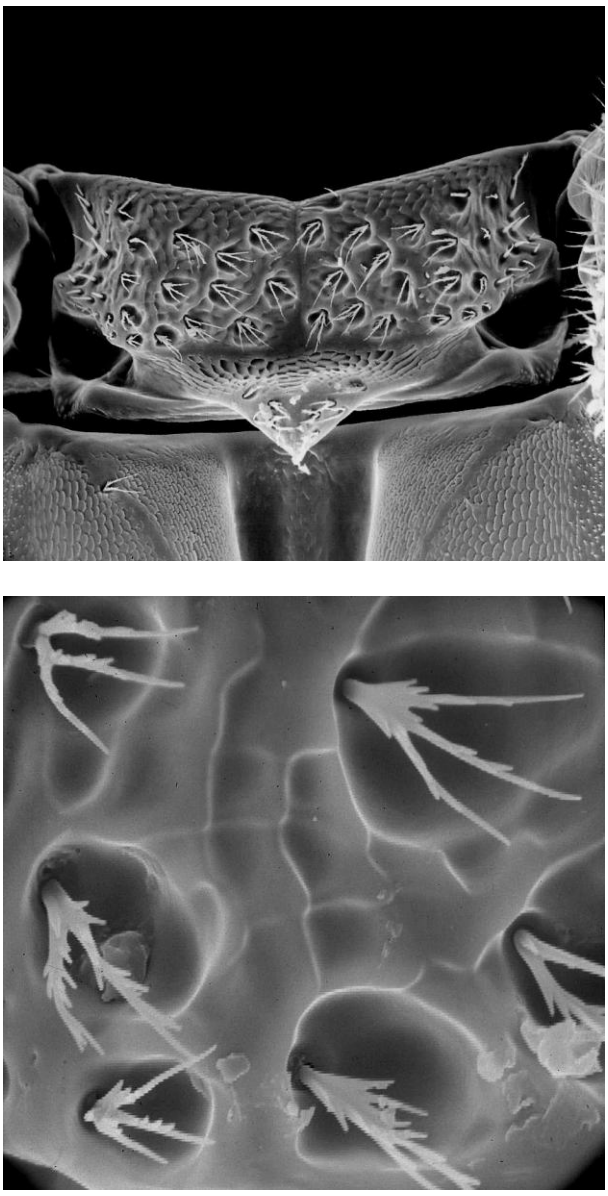


Fig. 15. Prescutum and prescutellar setae of *Cryphalus ruficollis* Hopkins. Specimen data: IDAHO, Latah Co., Little Baldy Mountain; *Abies grandis*; 29-VI-1967; M.M. Furniss.

***Crypturgus* Erichson** (Fig. 16). Prescutum shield-shaped. Setae absent. Surface pebbly, strongly raised. Scutellum half round.

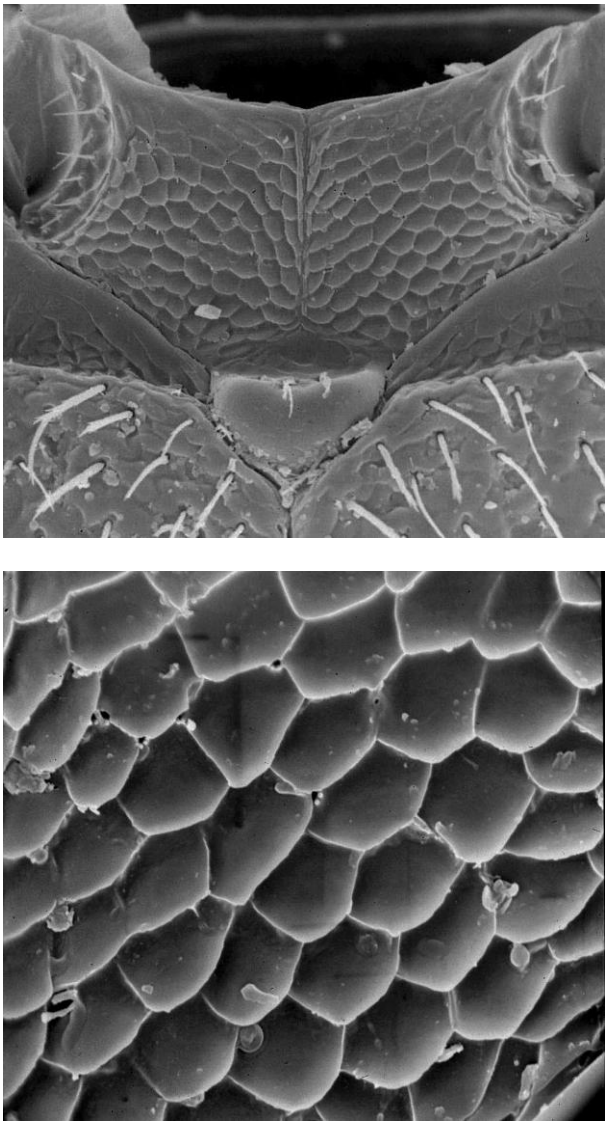


Fig. 16. Prescutum and prescutellar details of *Crypturgus borealis* Swaine. Specimen data: UTAH, Dixie National Forest, Pine Lake; *Abies lasiocarpa*; 11-V-1981; M.M. Furniss.

***Dryocoetes* Eichhoff** (Fig. 17). Prescutum shield-shaped. Setae single-stalked, their pits sparse and confined to posterior half. Surface plate-like. Scutellum round, constricted at base.

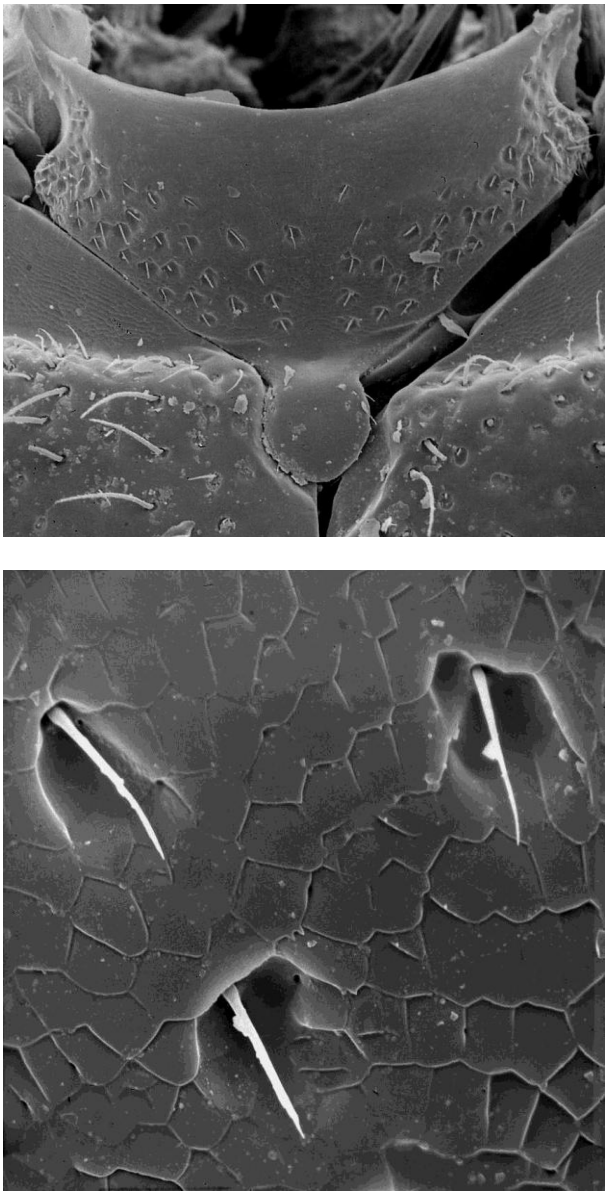


Fig. 17. Prescutum and prescutellar setae of *Dryocoetes confusus* Swaine. Specimen data: UTAH, Dixie National Forest, Pine Lake; *Abies lasiocarpa*; 11-V-1981; M.M. Furniss.

Gnathotrichus **Eichhoff** (Fig. 18). Prescutum shield-shaped**.** Setae sparse, single-stalked, their pits located in two lateral groups on posterior. Surface plate-like. Scutellum half round, broad at base.

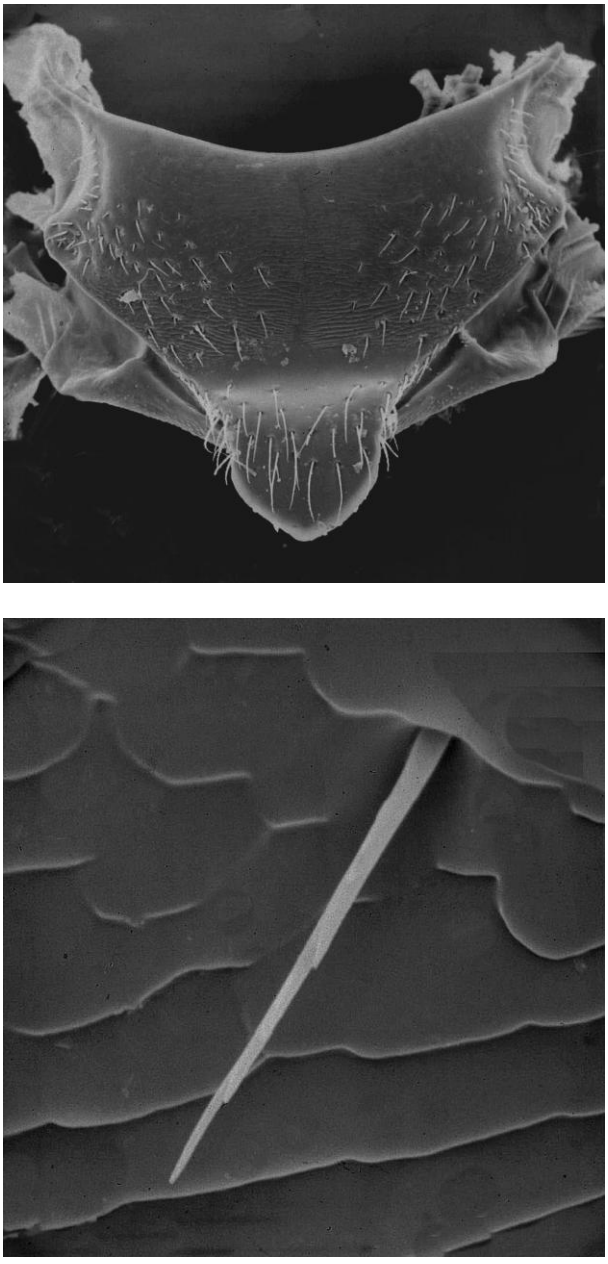


Fig. 18. Prescutum and prescutellar seta of *Gnathotrichus retusus* (LeConte). Specimen data: IDAHO, Kootenai Co., Deception Creek Experimental Forest; flight trap; 19-VI-1968; M. M. Furniss.

Ips **De Geer** (Fig. 19). Prescutum shield-shaped**.** Setae varying from one to two-stalked with their pits dense, sometimes touching. Surface smooth. Scutellum extended, tapered.

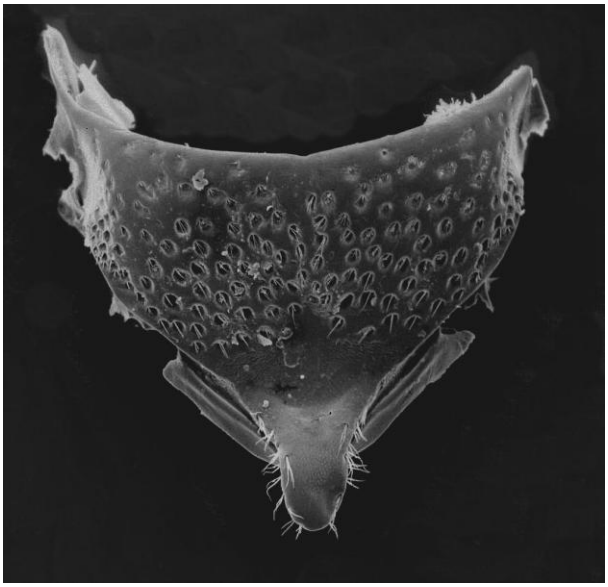


Fig. 19. Prescutum of *Ips emarginatus* (LeConte). Specimen data: IDAHO, Benewah Co., Plummer; pheromone trap; 26-IV-1977; M.M. Furniss.

Pityoborus **Blackman** (Fig. 20). Prescutum shield-shaped. Setae single-stalked, their pits very sparse. Surface plate-like. Scutellum rounded, slightly constricted at base.

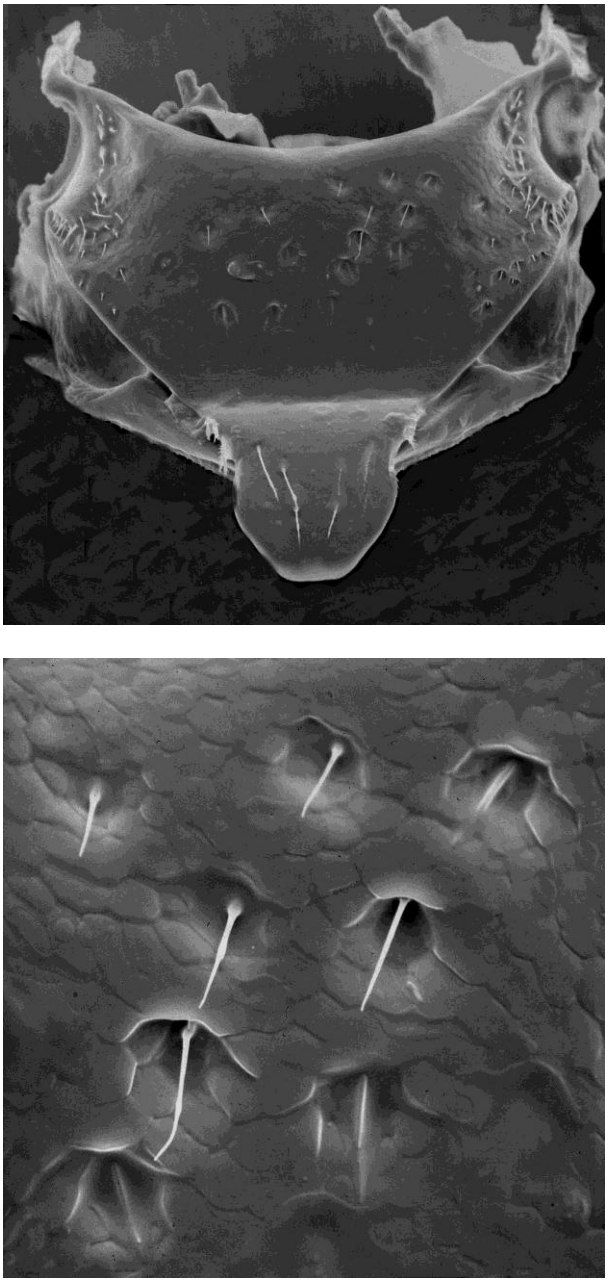


Fig. 20. Prescutum and prescutellar setae of *Pityoborus secundus* Blackman. Specimen data: MEXICO, Durango, La Flor; *Pinus lumholtzei*; 24-III-1974, M.M. Furniss.

Pityogenes **Bedel** (Fig. 21). Prescutum shield-shaped, somewhat compressed**.** Setae single-stalked, rather sparse and evenly distributed. Surface basically smooth. Scutellum elongate, tapered.

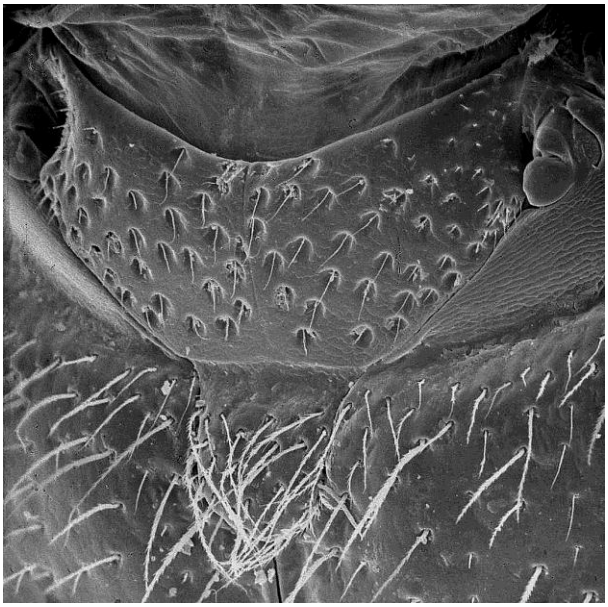


Fig. 21. Prescutum of *Pityogenes carinulatus* LeConte. Specimen data: IDAHO, Kootenai Co., Athol; in flight; 22-VII-1976; M.M. Furniss.

Pityophthorus **Eichhoff** (Fig. 22). Prescutum shield-shaped**.** Setae single-stalked, moderately dense, absent at posterior. Surface smooth to lightly imprinted. Scutellum tapered.

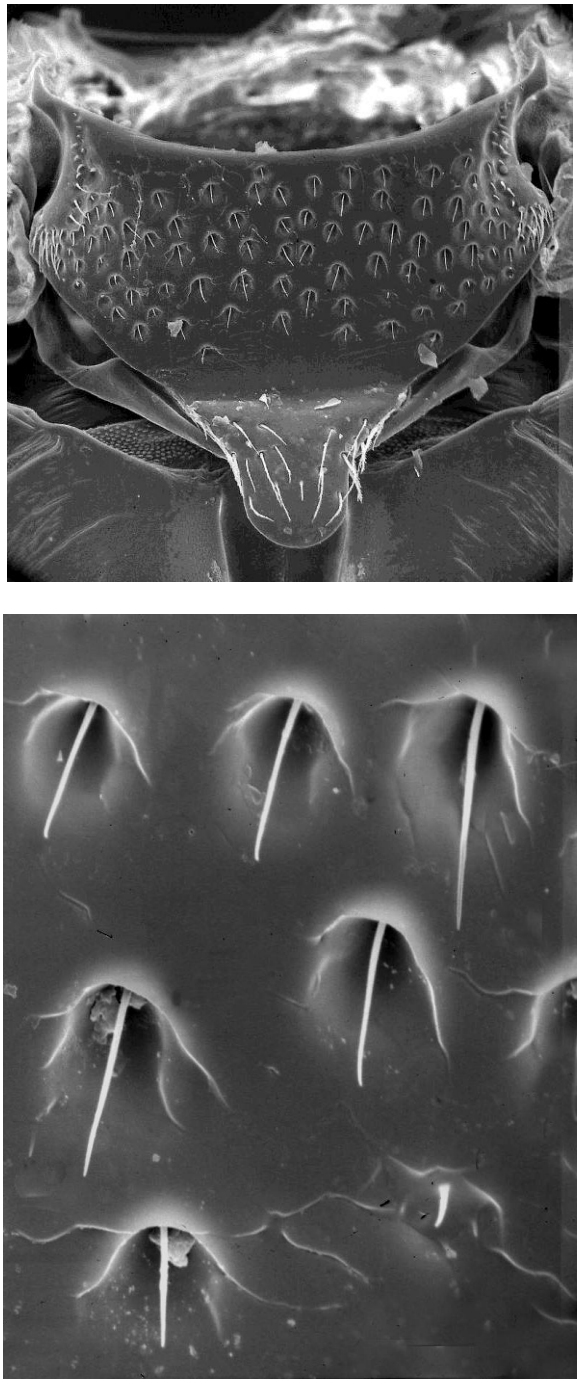


Fig. 22. Prescutum and prescutellar setae of *Pityophthorus crassus* Blackman. Specimen data: MEXICO, Coahilla, Mesa de las Tablas; *Pinus strombiformis*; 2-V-1981; M.M. Furniss.

Procryphalus **Hopkins** (Fig. 23). Prescutum shield-shaped. Setae single-stalked, sparse, absent on anterior half. Surface lightly imprinted. Scutellum rounded, base broad.

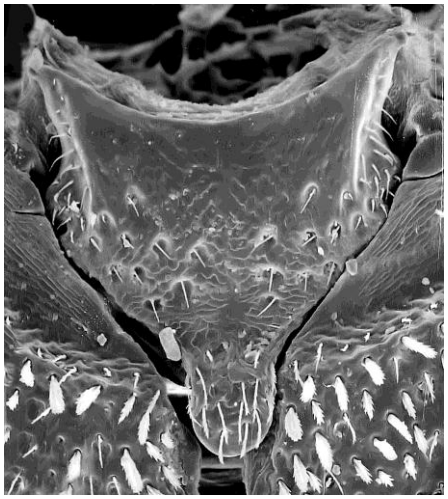


Fig. 23. Prescutum of *Procryphalus mucronatus* (LeConte). Specimen data: IDAHO, Boundary Co., Spread Creek; *Populus tremuloides*; 9-VI-1986; M.M. Furniss.

Scolytus **Geoffroy** (Fig. 24). Prescutum shield-shaped**.** Setae multi-stalked, their pits varying in density from sparse in center to dense laterally. Surface smooth. Scutellum strongly tapered to a dull point, base broad.

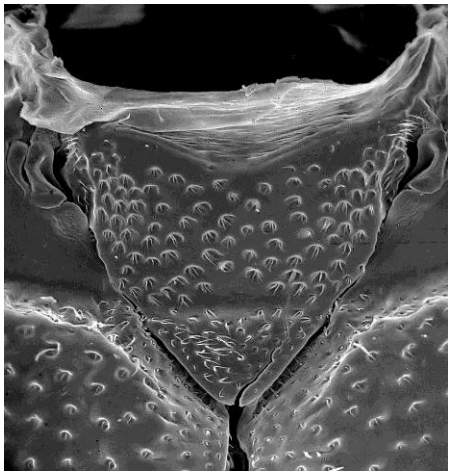


Fig. 24. Prescutum of *Scolytus monticolae* Swaine. Specimen data: IDAHO, Latah Co., Moscow Mountain; *Pseudotsuga menziesii*; 24-X-1967; M.M. Furniss.

***Trypodendron* Stephens** (Figs. 25 A–B). Prescutum shield-shaped. Setae single-stalked, sparse, becoming dense on lateral posterior. Surface lightly imprinted plate-like. Scutellum elongate, tapered to rounded end.

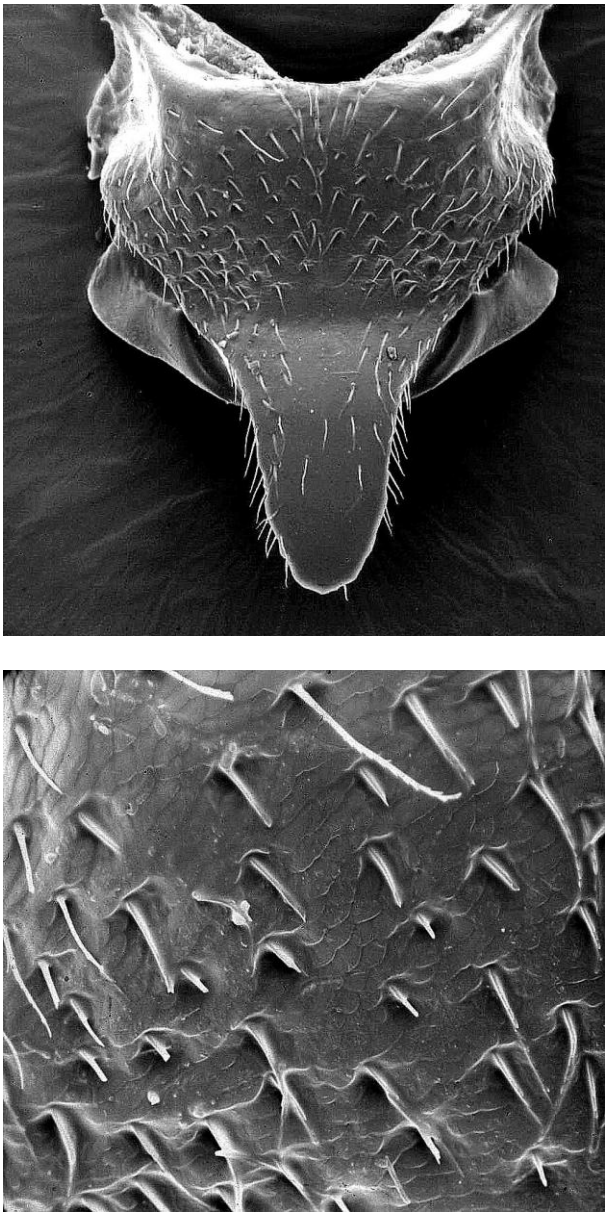


Fig. 25. Prescutum and prescutellar setae of *Trypodendron lineatum* (Olivier). Specimen data: IDAHO, Kootenai Co., Deception Creek Experimental Forest; In flight; 18-VI-1968; M.M. Furniss.

***Trypophloeus* Fairmaire** (Fig. 26). Prescutum shield-shaped. Setae absent. Surface plate-like. Scutellum short, base broad, tip round**.**

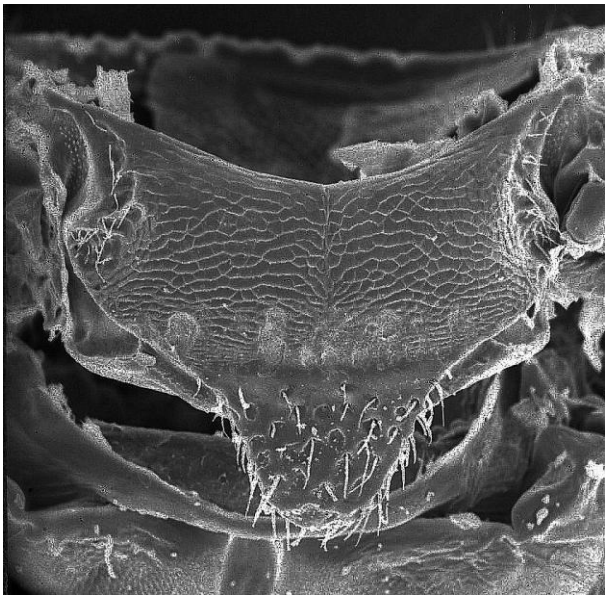


Fig. 26. Prescutum of *Trypophloeus populi* Hopkins. Specimen data: WASHINGTON, Whitman Co., Kamiak Butte; *Populus tremuloides*; 18-VI-1994; M.M. Furniss.

***Xyleborus* Eichhoff** (Fig. 27). Prescutum shield-shaped (distorted by angle of view on figure). Setae single-stalked, their pits moderately dense. Surface lightly imprinted. Scutellum tapered, tip round.

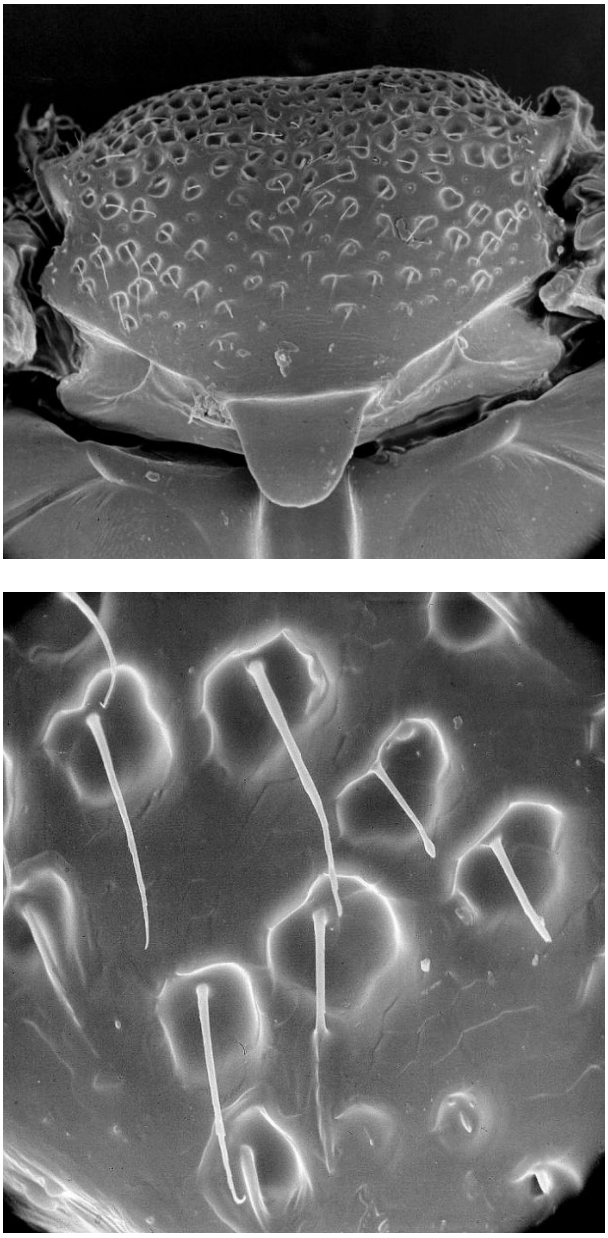


Fig. 27. Prescutum and prescutellar setae of *Xyleborus dispar* (Fabricius). Specimen data: IDAHO, Adams Co., Council; *Ulmus parvifolia*; 6-IV-1987; Chad Gibson.

Molytinae: Pissodini

***Pissodes* Gernar** (Fig. 28). Prescutum shield-shaped, anterior two thirds smooth. Setae absent. Posterior surface with dense rows of raised pebble-like texture and setae with multiple stalks. Scutellum round, separated from prescutum during preparation of specimen on photograph.

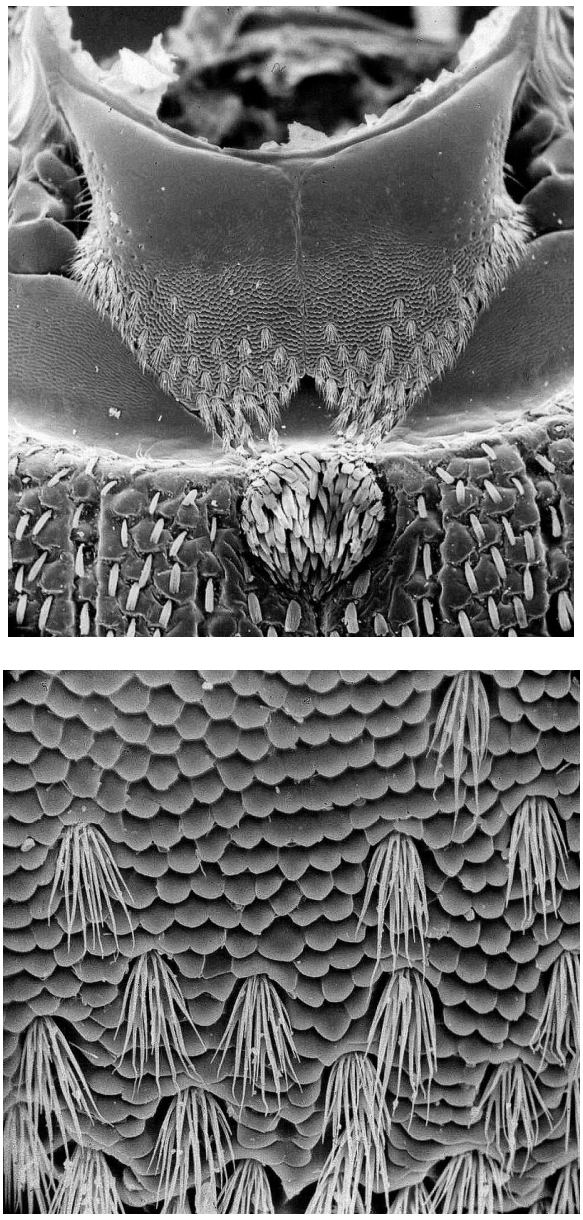


Fig. 28. Prescutum and prescutellar setae of *Pissodes fasciatus* LeConte (Molytinae: Molynini). Specimen data: IDAHO, Valley Co., Krassel Ranger Station; *Pseudotsuga menziesii*; 7-V-1957; M.M. Furniss.

Platypodinae: Plapypodini

Platypus **Herbert** (Fig. 29). Prescutum elongated, median groove running its length. Scutellum Y-shaped, elongate, tapered, setae short, single stalked, sparse. Surface lightly wrinkled.

Fig. 29. Prescutum of *Platypus pini* Hopkins (Platypodinae: Platypodini). Specimen data: ARIZONA, Coconino Co., Flagstaff; *Pinus ponderosa*; 9-V-1981; M.M. Furniss.

DISCUSSION

Why the morphology of the prescutum and scutellum of bark beetles has received little attention by taxonomists is speculative. Early taxonomists may have found that the antennae morphology, coupled with other external features were readily viewed and sufficient for describing their species. Otherwise, the elytra must be removed to examine features of the prescutum and scutellum, as was done in this study, to uncover these additional morphological character details. Also, SEM technology did not exist in early times and may still not be readily available to many investigators. Adding to this neglect is that a specimen needs to be permanently cemented to a metal stub and gold-coated; a destructive practice not appropriate for a primary type specimen or a very rare species.

This study shows a wide range of characters rivaling those traditionally provided by the antennae. Inclusion of additional genera may uncover further distinctive character states, such as features of setae, and comparisons of characters of beetles associated with different hosts (e.g., conifers and angiosperms), phloem or xylem habitat, and geographic distribution (as influenced by climate).

Comparison of three pairs of sibling species of *Dendroctonus* indicates a rather high stability of morphological characters used in this study; whereas the comparison of inter-generic characters reveals remarkable diversity. Even so, intra-generic differences are apparent in the pairs. An example is the two-lobed scutellum of *D. valens*, separating it from *D. rizophagous*, with which it had been synonymized.

Morphology of prescutum and scutellum of outlier *Pissodes* fitted within that of the genera of Hylesinini of this study, suggesting possible character similarity driven by ecology. *Platypus*, of xylophagous habit, resembled no other genus studied. including several of the same habit, and appears to be more distant from them.

ACKNOWLEDGMENTS

Christine Davitt (now deceased), Electron Microscopy Center, Washington State University, Pullman, assisted with the SEM work. Roger A. Beaver, Chiang Mai, Thailand, provided taxonomic information related to this study and reviewed the manuscript. The manuscript was also reviewed by Sandra J. Kegley, Forest Entomologist, USDA Forest Service, Cœur d'Alène, Idaho, and Anthony I. Cognato, Holistic Insect Systematics Laboratory, Michigan State University, East Lansing.

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