Redefinition, Revised Phylogeny, and Relationships of Pseudopsinae (Coleoptera, Staphylinidae)

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ABSTRACT

New evidence is presented to support transfer of the genera *Nanobius, Asemobius,* and *Zalobius* from the Piestinae to Pseudopsinae, currently including only *Pseudopsis.* The subfamily is redescribed, a key to genera given, and the natural history and distribution briefly reviewed. A revised cladistic analysis of the four genera is presented with the conclusion that *Pseudopsis* is the sister group of the remaining genera. The relationships of the subfamily are discussed; a close relationship to the Phloeocharinae rather than to the Oxytelinae is suggested.

INTRODUCTION

The subfamily Pseudopsinae, with the single included genus *Pseudopsis,* has recently been thoroughly revised by Herman (1975). The same author shortly thereafter revised the three piestine genera *Nanobius, Asemobius,* and *Zalobius* (Herman, 1977). In the latter work Herman cited many similarities among these four genera but concluded that the available evidence did not adequately support the hypothesis that the four genera constituted a monophyletic unit; *Nanobius* and its allies were tentatively retained in the Piestinae.

The purpose of the present work is to provide new evidence that, in my view, firmly establishes a close relationship of the four genera and justifies placing them in a single subfamily, Pseudopsinae *sensu novo.* This paper is intended as a supplement to, rather than a replacement for, Herman's revisions (1975, 1977). Thus the treatment is largely limited to making changes in the subfamily description, generic keys, etc. that are required by combining all four genera in one subfamily. A cladistic analysis is presented, combining data from Herman's analyses (1975, 1977) with new data.

MATERIALS AND METHODS

In the course of this study I have examined KOH-cleared, chlorazyl black-stained specimens of the Pseudopsinae with both dissecting and compound microscopes. All species of the subfamily have been examined with the exception of most species of the

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Pseudopsis sulcata complex, which according to Herman (1975) are distinguishable only by details of the aedeagus. Several cleared and partially dissected specimens were critical-point-dried, coated with gold-palladium mixture and examined with a scanning electron microscope.

The cladistic methods used here are essentially those of Herman (1970, 1975, 1977). Other subfamilies of the Staphylinidae and related families such as the Silphidae and Leiodidae have been used as out-groups to determine character polarities.

ACKNOWLEDGMENTS

PSEUDOPSINAE, *SENSU NOVO*

Pseudopsini Ganglbauer, 1895.
Pseudopsinae of authors plus Piestinae: *Nanobius, Asemobius,* and *Zalobius* (see Herman, 1975, 1977 and references therein).

DIAGNOSIS: The structure of the genital segment, with ninth terga dorsally fused in both sexes and with a fine presumed stridulatory file on each side (figs. 1, 2), will distinguish the Pseudopsinae from all other staphylinid subfamilies. The Pseudopsinae are more easily recognizable by a combination of the coarse punctation of the head and pronotum; longitudinal carinae or costae of the pronotum, elytra and sometimes of the head; 11-segmented unclubbed antennae; and either a comb at the apex of the eighth abdominal tergum or a deep incision of the posterior margin of each elytron.

DESCRIPTION: Length 1.8 to 7.0 mm. Body moderately broad, moderately flattened dorsoventrally. Head and pronotum weakly to strongly sculptured with reticulate (large, irregular, subcontiguous) punctures; prono-

tum, elytra, and sometimes head with longitudinal carinae or costae. Vestiture sparse, of simple tapered setae and/or modified scalelike or clubbed setae. Color reddish brown. Body with or without tendency to accumulate mud and debris.

Labrum with anterior margin truncate or sinuate, with exposed epipharyngeal lobes, dorsal surface with long setae. Epipharynx with globosetae near anterior margin. Anteclypeus large and apparently permitting extrusion of labrum. Supra-antennal ridge carinate or not. Epistomal suture present, posteriorly convex, evident externally as ridge or groove. Neck more or less distinct, at least laterally. Antenna slender to relatively stout, 11-segmented, without distinct club. Mandibles prominent, usually asymmetrical, apices acute, each with one to four teeth along mesial margin; molar lobe absent or thin, with microtrichia on mesial surface; prostheca present. Maxilla with lacinia setose and bearing small apical spine; galea with dense brush of setae at apex; and palp four-segmented, fourth segment about as long as or longer than third and wide or narrow. Labium with three-segmented palp; with one to three premental sclerites. Hypopharynx (including ligula) with one to three pairs of apical lobes, the median pair spatulate. Gular sutures separated, divergent anteriorly and posteriorly; submentum and gula not separated by suture. Subocular carina present or absent.

Pronotal lateral margin rounded, serrate, or spinose; dorsal surface broadly elevated. Protergosternal suture present. Procoxal fissure broadly or narrowly open with exposed trochantin, or fissure closed and trochantin concealed. Postprocoxal lobe present. Prohypomeron with or without microporous depression. Procoxae with or without shallow, carina-delimited groove on mesial surface. Prosternal process carinate or spiniform.

Scutellum with apex exposed behind pronotum. Elytra with or without posterior emargination; elytral epipleural ridge present. One or pair of sclerites present anterior to mesosternum but posterior to and not associated with mesothoracic spiracular peritremes (fig. 3). Mesosternum carinate or not.
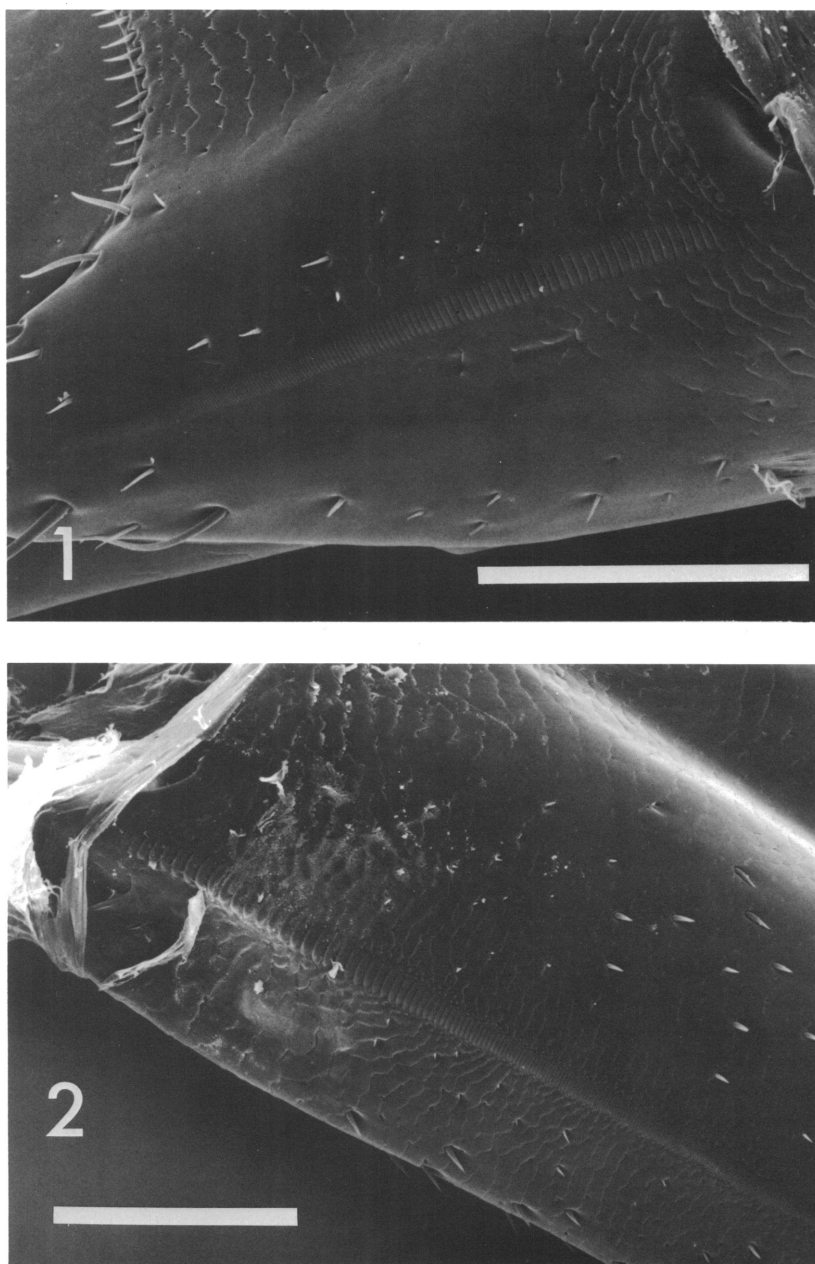
FIGS. 1, 2.   1. *Pseudopsis obtusa,* female, right dorsolateral view of tergum IX. 2. *Nanobius serricollis,* female, left dorsolateral view of tergum IX. Scale line = 0.1 mm.

Mesocoxae contiguous or narrowly separated by meso- and meta-sternal processes. Hind coxae transverse, contiguous.

Tibiae with or without longitudinal rows of spines. Tarsal formula 5-5-5 or (*Pseudopsis minuta* only) 3-3-3. Tarsal empodium bisetose.

Abdominal segments II or III to VII each with one or two pairs of laterosclerites. Terga II (*Pseudopsis*) or III to VII with transverse
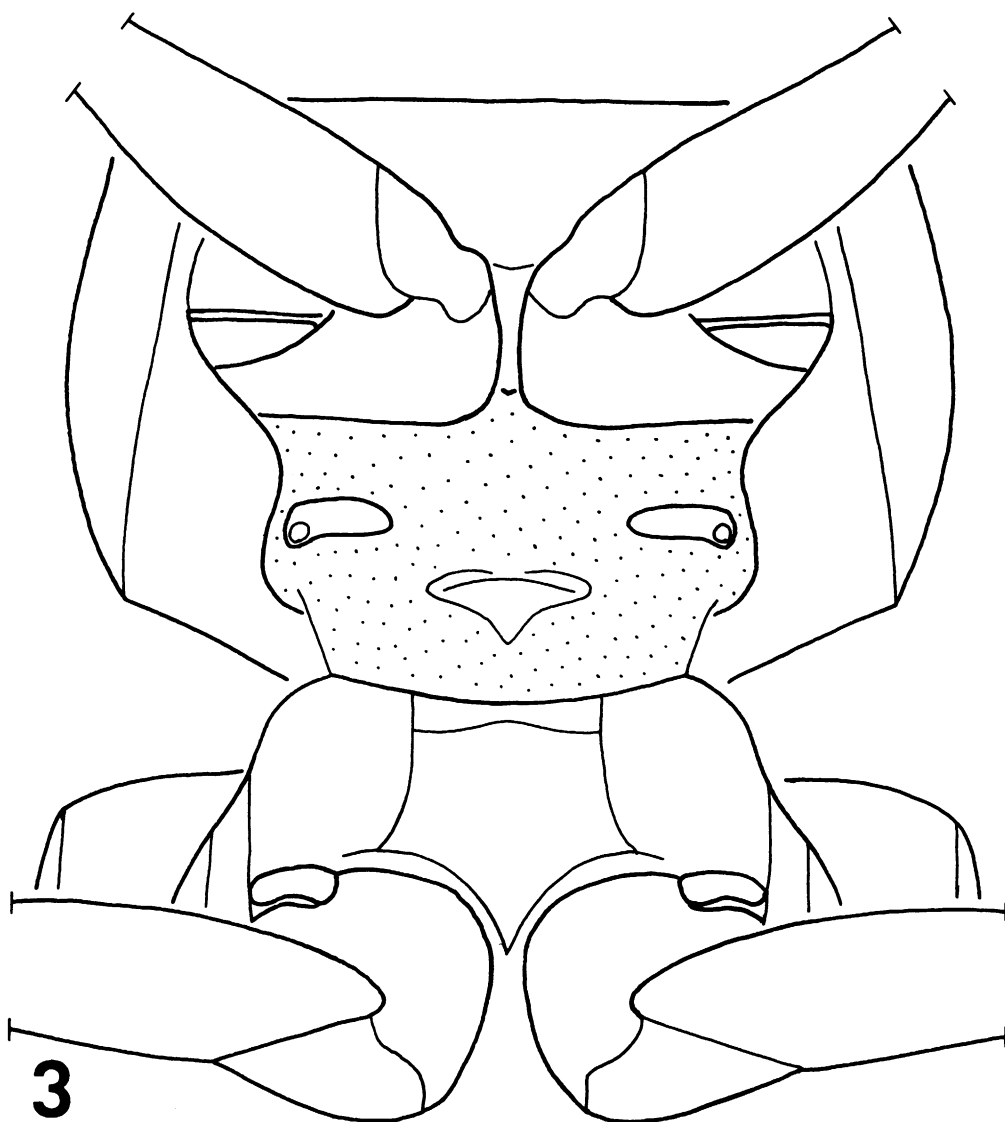
FIG. 3. *Pseudopsis subulata*, pro- and meso-thorax, ventral view.

subbasal ridge; terga with or without baso-lateral ridges or basal, longitudinal carinae; terga without wing-folding setae or spicules; tergum VIII with apical cuticular comb or median process, or with apex rounded. Spiracles placed in edges of terga II (*Pseudopsis*) or III to VIII. Sternum I represented by strap-like sclerite, medially divided or not. Sternite II short and fused to sternite III. Sternites II and III with or without median longitudinal carina; sternites III to VII with (*Pseudopsis*)

or without transverse subbasal ridge. Abdominal intersegmental membranes with or without pattern; attached to apex or anterior to apex of preceding segment.

Tergum IX of both sexes consisting of single large sclerite with fine file on each side (figs. 1, 2), the ridges of the file becoming more closely spaced posteriorly. Anterior, dorsolateral margins of tergum IX with sinuation or shallow emargination which, in *Pseudopsis* at least, marks the opening of a

large glandular reservoir. Tergum X ovoid or triangular, placed in large apical emargination of tergum IX.

Male. Aedeagus symmetrical or asymmetrical, with or without parameres, with or without basal piece. Aedeagus in repose with parameres facing dorsal surface of beetle.

Female. Coxites circular to oval in cross-section and free, or flattened and fused to one another. Styli present and small, or absent. Intergonopodal sclerite present or absent.

TAXA INCLUDED: The subfamily as redefined here includes four genera:

Asemobius Horn (one species, *A. caelatus* Horn, from western North America)

Nanobius Herman (one species, *N. serricollis* (LeConte), from western North America)

Pseudopsis Newman (30 species as listed by Herman (1975) from the Holarctic and Neotropical regions and New Zealand)

Zalobius LeConte (two species as listed by Herman (1977) from western North America)

KEY TO GENERA OF THE PSEUDOPSINAE

1. Last segment of maxillary palp less than a third as wide as penultimate segment; procoxal fissure widely open, trochantin well exposed; abdominal terga with basolateral ridges, tergum VIII with comb on posterior margin; abdominal sterna II and III without intercoxal carina .. *Pseudopsis*
   Last segment of maxillary palp subequal in width to penultimate segment; procoxal fissure narrowly open or closed, trochantin barely or not visible; abdominal terga without basolateral ridges, tergum VIII without comb on posterior margin; abdominal sterna II and III with midlongitudinal intercoxal carina 2

2(1). Antenna densely pubescent from seventh segment to apex; procoxal fissure closed, trochantin concealed; mesocoxae separated by meso- and meta-sternal processes; head with dorsal basal carinae .... *Nanobius*
   Antenna densely pubescent from eighth segment to apex; procoxal fissure narrowly open, trochantin not concealed; mesocoxae contiguous; head without dorsal basal carinae 3

3(2). Subocular carina present; lateral margin of pronotum coarsely serrate; abdominal terga without longitudinal basal carinae .... *Asemobius*
   Subocular carina absent; lateral margin of pronotum spinose; abdominal terga III to VI each with one basal midlongitudinal carina .... *Zalobius*

NATURAL HISTORY

All species, as far as known, occupy cool temperate montane forested regions (Herman, 1975, 1977). *Pseudopsis* and *Nanobius* species are most commonly found in moist forest floor litter; some *Pseudopsis* species have also been associated with dung, fungi, or mammal nests in the same areas. *Zalobius* and, from the single known record, *Asemobius* species are found in wet moss or flood debris along small mountain streams.

No direct feeding observations have been made on pseudopsines. *Nanobius* gut contents indicate predation on other animals (Herman, 1977). Cleared specimens of all examined species lack the masses of fungal hyphae, spores, algae, or decomposing organic detritus in the gut that characterize fungivorous, algophagous or saprophagous staphylinid species such as those of the subfamilies Piestinae, Osoriinae, and Oxytelinae (personal observ.). These characteristics and the structure of the mouthparts, especially the mandibles and hypopharynx, suggest that pseudopsine adults are carnivorous as are other staphylinids with similar mouthparts and known feeding habits (e.g., the phloeocharine *Charhyphus picipennis*, based on personal observ.).

Immature stages and life histories are unknown for all Pseudopsinae. Although other workers and I have made numerous collections of adults of all genera except *Asemobius* and have simultaneously searched for larvae, none that could be attributed to the pseudopsine genera have yet been found.

BIOGEOGRAPHY

Herman (1975) has analyzed the distribution of the widespread genus *Pseudopsis*. He concluded, from the number and diversity of species and from his proposed cladistic history of the genus, that *Pseudopsis* origi-

nated in the New World, possibly in western North America, with subsequent dispersal by some taxa to Eurasia and to South America and New Zealand. The addition of the three genera *Nanobius, Asemobius,* and *Zalobius* to the Pseudopsinae as the sister group of *Pseudopsis* reinforces Herman's proposal of a North American origin of the subfamily since these three genera are confined to western North America.

CLADISTIC ANALYSIS

Herman has provided separate cladistic analyses of the species of *Pseudopsis* (Herman, 1975) and of *Nanobius, Asemobius* and *Zalobius* (Herman, 1977). The hypothesis here that these four genera together form a monophyletic unit requires a new cladistic analysis to determine the synapomorphies shared by all four genera and to determine the cladistic relationships among the genera. Characters and character polarities are adopted from Herman (1975, 1977) with a few changes noted below, and a number of new characters are added (see table 1). The most parsimonious branching sequence of the four genera (based on these characters) is given in figure 4.

This cladistic analysis suggests that all four genera share at least 12 synapomorphies. Of these, the single most significant one is the newly discovered file located on each side of the ninth tergum in all species of Pseudopsinae (character 43; figs. 1, 2). This file has been found in no other staphylinids. Virtually all other synapomorphies shown for the four pseudopsine genera in figure 4 are known to occur elsewhere in the Staphylinidae, although many are uncommon and some, such as character 33, are probably not homologous with apparently similar character transformations found elsewhere. In combination with the unique file, I think these synapomorphies provide strong support for the monophyly of the Pseudopsinae as defined here.

The relationships of the genera of the Pseudopsinae shown in figure 4 represent the most parsimonious arrangement possible using the characters and character polarities of table 1. Alternative branching patterns would result

in an increased number of independently derived apomorphic character states among the four genera and would, I believe, represent less probable cladistic histories of the genera.

A number of characters used in the analysis that are problematic or of special interest will be discussed individually. The numbers in parentheses refer to character transformations of table 1.

Modified setae (4) vary in structure and in placement, and were subdivided by Herman (1975, 1977) into clubbed and scalelike setae. It is not clear whether these setal types are derivable from one another or whether scalelike setae in *Pseudopsis* and *Zalobius* are homologous or not; for these reasons, modified setae of either type are here lumped and treated as a single synapomorphy.

A longitudinally carinate or costate head (6) occurs in *Nanobius* and in some *Pseudopsis* species. The configuration of costae or carinae differs in the two genera and has probably been independently derived.

A transverse nuchal impression (8) is found in all genera except *Asemobius* which is here assumed to have lost it. Herman (1977) chose the opposite polarity, which would require an independent derivation of the nuchal impression in the other three genera.

The hypopharynx (21) of most other staphylinids is broadly bilobed. A hypopharynx very similar to that of *Pseudopsis* and *Asemobius* (21A) is found in some Phloeocharinae (*sensu lato*) and is here considered to be independently derived or, possibly, synapomorphic for these two subfamilies.

A mesial procoxal groove (32) of the type found in some Pseudopsinae occurs in some genera of many staphylinid subfamilies, as noted by Herman (1977). The polarity of this character transformation is thus open to doubt.

Sclerites in the connecting membrane between pro- and meso-sterna (33) occur in several staphylinid subfamilies and in the Silphidae-Silphinae. The location of these sclerites immediately anterior to the mesosternum and posterior to, and not associated with, the mesothoracic spiracular sclerites is apparently found only in the Pseudopsinae, in Apateticini of Piestinae and in the Silphi-

TABLE 1
Relative Plesiomorphy and Apomorphy of Characters Used for Cladistic Analysis of Pseudopsinae[a]

Plesiomorphic (P)	Apomorphic (A)
1. Pronotum and elytra without carinae or costae	Pronotum and elytra longitudinally carinate or costate
2. Punctation of head and pronotum punctiform	Punctation of head and pronotum reticulate
3. Dorsum of head, pronotum and elytra clean, without accumulations of mud and debris	Dorsum of head, pronotum, and elytra with accumulations of mud and debris
4. Setae unmodified	Some body setae modified
5. Setae large, visible with dissecting microscope	Setae small, visible only with compound microscope at *ca.* 400×
6. Head not longitudinally carinate or costate	Head longitudinally carinate or costate
*7. Neck absent	Neck present as lateral constriction and dorsal transverse impression
8. Neck distinguished dorsally by transverse impression	Neck not distinguished dorsally
*9. Antenna densely pubescent from fourth, fifth, or sixth segment to apex	Antenna densely pubescent from seventh segment to apex
10. (=9A)	Antenna densely pubescent from eighth segment to apex
11. Subocular carina absent	Subocular carina present
12. Epistomal suture evident externally as groove	Epistomal suture evident externally as ridge
13. Labrum without peglike setae on anterior margin	Labrum with row of peglike setae on anterior margin
14. Epipharynx without globosetae	Epipharynx with globosetae present, forming median patch
15. (=14A)	Epipharyngeal globosetae present, forming transverse row on anterior edge
*16. Mandibles without subapical teeth	Mandibles with one or more large subapical teeth on mesial edge
*17. Mandibles without serrate edges	Right mandible with dorsal, subapical serrate edge
*18. Mandibles with large molar lobes bearing mesial grinding surfaces	Mandibles with thin molar lobes bearing mesial microtrichia
*19. (=18A)	Mandibles without interacting molar lobes
*20. Maxillary palp with fourth segment subequal in width to third	Maxillary palp with fourth segment less than a third as wide as third segment
*21. Hypopharynx broadly bilobed at apex	Hypopharynx with two pairs of lobes, the median pair spatulate and subcontiguous at base, the lateral pair acute
*22. (=21A)	Hypopharynx with six lobes, both lateral pairs acute
*23. (=21A)	Hypopharynx with median pair of lobes largely fused to lateral pair
*24. Labium with palpigers free	Labium with palpigers completely fused to one another
25. Mentum not carinate	Mentum with midlongitudinal carina
26. Gula not carinate	Gula carinate

TABLE 1—(*Continued*)

Plesiomorphic (P)	Apomorphic (A)
27. Pronotum without deep pits	Pronotum with deep pits near anterior and posterior margins
28. Prohypomeron unmodified	Prohypomeron with microporous depression
*29. Procoxal fissure widely open, trochantin well exposed	Procoxal fissure narrowly open, trochantin barely exposed
*30. (=29A)	Procoxal fissure closed for most of its length, trochantin concealed
*31. Prosternal process cariniform	Prosternal process spiniform
32. Procoxa without carina-delimited mesial groove	Procoxa with shallow, carina-delimited mesial groove
*33. Antemesosternal sclerites absent	One or pair of antemesosternal sclerites present (fig. 3)
*34. Mesosternum not carinate	Mesosternum midlongitudinally carinate
*35. Mesocoxae narrowly separated by mesosternal or meso- and metasternal processes	Mesocoxae contiguous
36. Elytron with posterior margin entire	Elytron with lateral portion of posterior margin deeply incised
37. Abdominal terga without basolateral ridges	Abdominal terga with basolateral ridges
38. Abdominal terga without longitudinal carinae	Abdominal terga each with partial median longitudinal carina
39. (=38P)	Abdominal terga each with several partial longitudinal carinae
40. Abdominal tergum VIII with unmodified posterior margin	Abdominal tergum VIII with comb on posterior margin
41. (=40P)	Abdominal tergum VIII with posterior margin biemarginate
42. Abdominal tergum IX without openings of large gland reservoirs	Abdominal tergum IX with openings of pair of large gland reservoirs anteriorly at dorsolateral margin
*43. Abdominal tergum IX without "stridulatory" file	Abdominal tergum IX with fine "stridulatory" file on each side (figs. 1, 2)
*44. Some of abdominal terga with patches of wing-folding setae or spicules	Abdominal terga without wing-folding setae or spicules
*45. Abdominal segments III–VI with a single pair of laterosclerites per segment	Abdominal segments III–VI with two pairs of laterosclerites per segment
*46. Abdominal intersegmental membranes between segments III–VII attached to apex of preceding segment	Abdominal intersegmental membranes attached to inner surface of preceding segment anterior to its apex
*47. Abdominal intersegmental membranes of segments III–VII with pattern of minute sclerites	Abdominal intersegmental membranes without pattern
*48. Abdominal sternites II and III with midlongitudinal intercoxal carina	Abdominal sternites II and III not midlongitudinally carinate
49. Tergum IX of male with lateral portion compressed and triangular in lateral view, not reaching beyond apex of tergum X	Tergum IX of male with lateral portion cylindrical and produced well beyond apex of tergum X

TABLE 1—(*Continued*)

Plesiomorphic (P)	Apomorphic (A)
50. Aedeagus with U-shaped basal piece	Aedeagus without basal piece
*51. Tergum IX of female divided dorsally by tergum X	Tergum IX of female broadly fused dorsally anterior to tergum X
52. Female with intergonopodal sclerite	Female without intergonopodal sclerite
53. Coxites separate	Coxites fused basally
54. Coxites cylindrical or slightly flattened	Coxites broadly flattened
55. Stylus elongate	Stylus reduced, knoblike
56. Stylus present	Stylus absent

[a] Those marked with an asterisk (*) were not used by Herman (1975, 1977).

dae-Silphinae. Tentatively, I am assuming that these sclerites have been independently derived in the three taxa cited, and that these sclerites are not homologous with the more anterior sclerites associated with mesothoracic spiracular sclerites in the Tachyporini and other Staphylinidae.

The presence of openings of large gland reservoirs in the ninth tergum (42) of *Pseudopsis* is unusual and is apparently found elsewhere only in the subfamily Oxytelinae (Herman, 1970). This character was considered synapomorphic for the two taxa by Herman (1975). It should be mentioned, however, that the openings in *Pseudopsis* are at the anterior edge of tergum IX, whereas in the Oxytelinae the openings are in the terga or in a deep invagination of the anterior margin of the terga. Furthermore, the configuration of the ninth and tenth terga is quite different in the Oxytelinae (ninth terga separated dorsally by tenth tergum and "stridulatory" files absent) and in *Pseudopsis* (ninth terga broadly fused dorsally anterior to tenth tergum, and "stridulatory" file present on each side). The configuration of ninth and tenth terga is identical in *Pseudopsis* and in the other three genera of Pseudopsinae which apparently lack the glandular reservoirs. These genera do, however, have an inflection in the anterior margin of the ninth tergum similar in placement and appearance to the point at which each gland reservoir of *Pseudopsis* opens. The gland reservoirs of some species of *Pseudopsis* are quite difficult to detect (Herman, *in litt.,* and personal observ.)

and it is perhaps possible that such reservoirs exist in the other genera of Pseudopsinae but are not detectable without analysis of better preserved specimens. It is also possible that gland reservoirs have been lost in the other pseudopsine genera. Based on the evidence available at present, I conclude that the gland openings are probably independently derived in *Pseudopsis* and in the Oxytelinae.

The fine file (43) at each side of abdominal tergum IX was overlooked by Herman (1975, 1977), but is found in all examined pseudopsine species. A careful search among other staphylinids has produced no comparable structure. The file resembles known stridulatory files, except for the great change in spacing between individual ridges from the widely spaced anterior ridges to the extremely close and fine posterior ridges (see figs. 1, 2). The file is in such a position that it would rub against the apex of the inflexed sides of tergum VIII as the ninth segment is in- or evaginated. An alternative function of the file, suggested by the close proximity of the gland opening of *Pseudopsis* (42) to the anterior end of the file, is that the file might somehow aid in the dispersal or application of the gland secretion. Since the file is as well developed in the other pseudopsine genera (which apparently lack glands) as in *Pseudopsis,* this possible function seems unlikely. Those workers with access to living material of this unfortunately rare and spottily distributed subfamily should attempt to determine the functional significance of both the files and glands.

Pseudopsis   Nanobius   Asemobius   Zalobius

Pseudopsis:
4 ◄
6 ◄
11 ◄
17
20
24 ◄
32 ◄
35 ◄
37
40
42
48
50 ◄
52 ◄
53
54
56 ◄

Nanobius:
4 ◄
5
6 ◄
22
26 ◄
27
30
39
41
45 ◄
50 ◄
52 ◄

Asemobius:
8
11 ◄
47

Zalobius:
4 ◄
13
15
19
23
24 ◄
25
26 ◄
38
45 ◄
49
56 ◄

(Asemobius + Zalobius node):
10
12
35 ◄
46

(middle node):
3
9
28
29
31
32 ◄
34
36

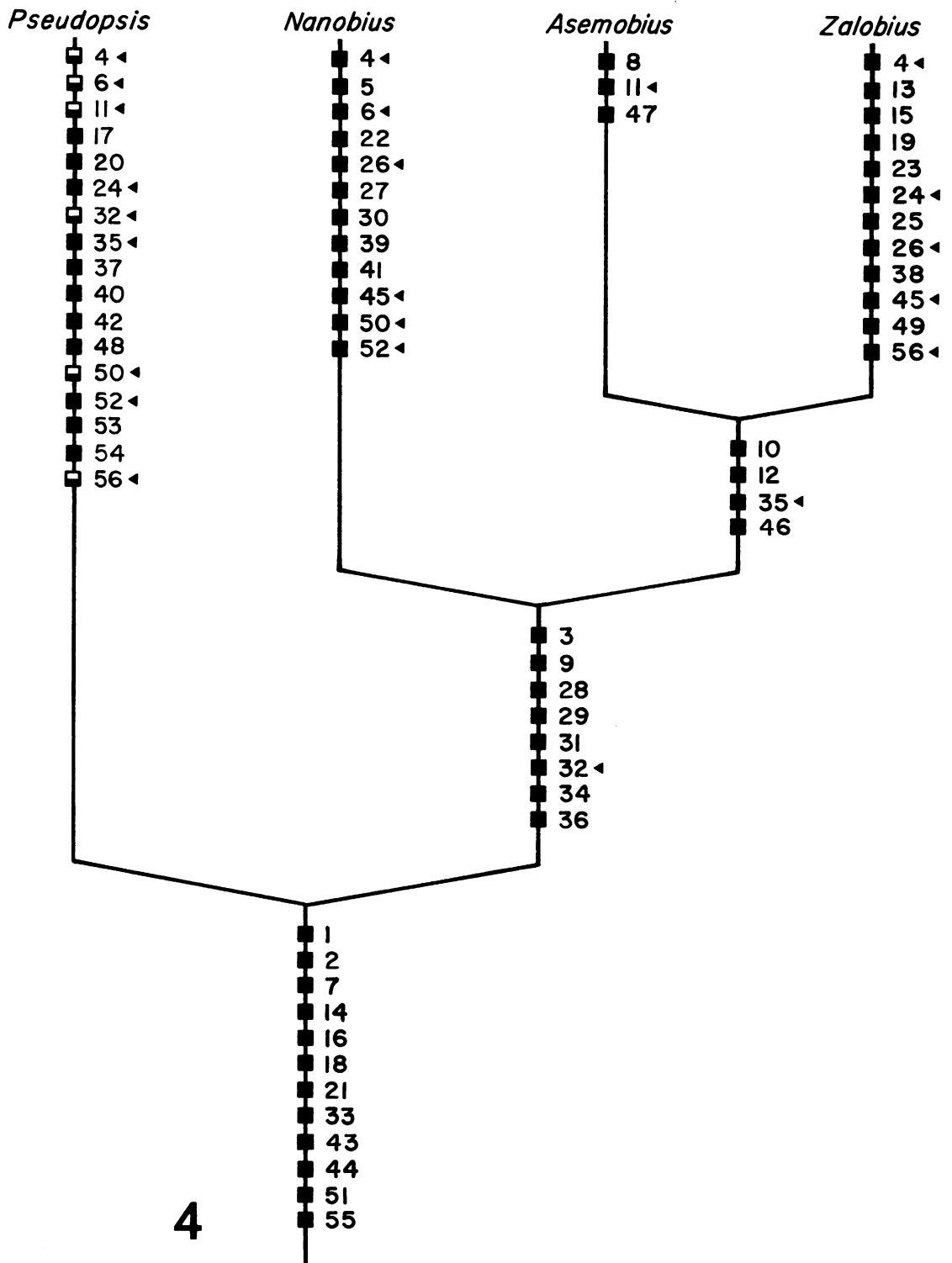(base node):
1
2
7
14
16
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43
44
51
55

4

FIG. 4. Cladistic analysis of the genera of Pseudopsinae. Numbers refer to character transformations listed in table 1. Half-filled squares indicate that only some species of the genus show the apomorphic condition of that character. A triangle following a number indicates a character transformation that occurs independently on this cladogram.

Many subfamilies of staphylinids have members with either one or two pairs of laterosclerites per segment (45). I have followed Herman (1970) in assuming that one pair is plesiomorphic, because it is prevalent among primitive staphylinids and allied families and is most readily derivable from the condition (no laterosclerites) found in other staphylinoid families such as the Silphidae and Leiodidae. Although coded as derived for *Zalobius,* only two segments have two pairs of laterosclerites while the remainder have one pair.

Abdominal intersegmental membranes between segments III and VIII (46) are usually attached at the apex of each preceding segment in Coleoptera and in many Staphylinidae, but are attached preapically in many staphylinid subfamilies. The same membranes in staphylinids usually have a distinct pattern of minute sclerites (47); this pattern is reduced or absent in many subfamilies and genera, especially those in which the attachment is preapical.

The U-shaped sclerite (50) surrounding the basal orifice of the aedeagus was assumed by Herman (1975, 1977) to be independently derived wherever it occurs. A similar sclerite occurs in the same position in many staphylinids (e.g., some Omaliinae, Proteininae, and Paederinae as well as some Pseudopsinae) and in members of other staphylinoid families such as the Silphidae, Leiodidae, and Ptiliidae. I know of no reason not to consider this sclerite as a homologue of the basal piece of other Coleoptera, which has been reduced in all the Staphylinoidea and lost in many taxa of this superfamily. Thus I have reversed Herman's polarity of this character change.

In most primitive Staphylinidae, in closely allied families such as the Silphidae and Leiodidae, and in most other Coleoptera the sclerites of abdominal segments IX and X are strongly sexually dimorphic. In females, these sclerites form the ovipositor (Tanner, 1927). Tergum IX of females is usually represented by a pair of sclerites (paraprocts) that are separated by tergum X (proctiger). The dorsal fusion of these sclerites to form a single tergum IX anterior to tergum X (51) results in a configuration similar to that of males, which in most Coleoptera have a single tergum IX anterior to tergum X. Such a

convergence in dorsal appearance of male and female terminalia is not uncommon in the Staphylinidae and has occurred in a few other families such as the Hydraenidae and Ptiliidae.

An intergonopodal sclerite (52) of the ovipositor is found in many staphylinids as noted by Herman (1977), and in many other Coleoptera (Tanner, 1927). I consider such sclerites homologous and so reverse Herman's polarity assignment.

It should be noted that in spite of the addition of numerous new characters and in spite of a few reversals of character polarities selected by Herman (1977), the branching sequence among the genera *Nanobius, Asemobius,* and *Zalobius* in figure 4 is the same as that in Herman's most-parsimonious cladogram (Herman, 1977, fig. 2) of the same genera. The cladistic analysis of the species or species groups of *Pseudopsis* given by Herman (1975) would be virtually unaffected by the changes or additions made here. One exception would be the addition of an autapotypic trait (tarsal formula 3-3-3 rather than 5-5-5) to the *Pseudopsis minuta* branch; this tarsal reduction was overlooked by Herman (1975).

SUBFAMILY POSITION

Herman presented analyses of possible subfamily relationships for *Pseudopsis* (1975) and for the three genera *Nanobius, Asemobius,* and *Zalobius* (1977). He concluded that *Pseudopsis* was the sister group of all the Oxytelinae, based exclusively on the presence and position of exit of a pair of abdominal gland reservoirs. Similarities to other subfamilies, especially the Phloeocharinae and Piestinae, were noted. A more detailed analysis of characters shared by *Nanobius, Asemobius,* and *Zalobius* with various other staphylinid taxa was given. These three genera were found to share more derived characters (carinate body, epipharyngeal globosetae, dorsally fused ninth tergum) with *Pseudopsis* than with any other staphylinids. However, these synapomorphies are absent in the Oxytelinae, which share with *Pseudopsis* the glandular openings in the ninth tergum. Herman concluded that this contradiction prevented a satisfactory resolution of

relationships of these taxa; he tentatively retained *Pseudopsis* as sole representative of the Pseudopsinae and Pseudopsinae as the sister group of the Oxytelinae, while retaining *Nanobius, Asemobius,* and *Zalobius* in the subfamily Piestinae even though no synapomorphies that would justify such placement had been found.

In the present work I have pointed out, in the cladistic analysis of figure 4, a number of additional synapomorphies shared by *Pseudopsis, Nanobius, Asemobius,* and *Zalobius.* Most important among these is the presumed stridulatory file on each side of abdominal tergum IX (figs. 1, 2), unique in the Staphylinidae. In my view these synapomorphies in combination firmly establish that the four genera together form a monophyletic unit, here called the Pseudopsinae (*sensu novo*).

It follows that either the ninth tergal glandular openings of *Pseudopsis* and the Oxytelinae are a convergent development, or that the glandular openings have had a wider distribution in the past and have been lost in *Nanobius, Asemobius,* and *Zalobius,* and possibly in other taxa. If the glands have been lost in *Nanobius, Asemobius,* and *Zalobius,* or if they are present in those genera but not detected with available material, then a sister-group relationship of the Pseudopsinae (*sensu novo*) and Oxytelinae would still be possible.

Evidence other than the presence and position of ninth tergal gland openings that would support a sister-group relationship of the Pseudopsinae and Oxytelinae is very scarce. Of the 12 synapomorphies of the Pseudopsinae shown in figure 4, only two (nos. 44 and probably 55) also characterize all the Oxytelinae. These two apomorphies are known to have been independently derived in many other staphylinid subfamilies and are perhaps the weakest of all detected synapomorphies of the Pseudopsinae. In contrast, the Oxytelinae share a number of less common synapomorphies with the subfamilies Piestinae and Osoriinae: divided ninth terga in both sexes; similar mouthparts including numerous multifid or plumose setae of the labrum, mandibular prostheca and galea; and saprophagous adult (and larval) feeding habits with resultant masses of decomposed plant material, fungi, etc. in the gut. The sister group of the Oxytelinae is probably best sought among a portion or all of the Piestinae and Osoriinae. Since the Piestinae and Osoriinae have no trace of ninth tergal glands, I would conclude that ninth tergal glands have been independently evolved in the Oxytelinae and in some or all the Pseudopsinae.

Some characteristics of many Pseudopsinae such as pronotal and elytral carinae, scalelike setae and detritus accumulation occur in a variety of staphylinids as noted by Herman (1977), and I agree with Herman that such occurrences have probably arisen independently in or within the subfamilies in which they are found. All of these characteristics are found in a newly discovered genus from Australia which is described and discussed in detail elsewhere (Newton, 1982). The piestine genus *Euphanias* also has elytral carinae and scalelike setae and has occasionally been considered to be allied to *Pseudopsis* (e.g., by Mulsant and Rey, 1856). Evidence that both *Euphanias* and the new Australian genus belong in the Oxytelinae and are closely related to *Syntomium* is presented elsewhere (Newton, *op. cit.*), and the similarities to the Pseudopsinae are considered to be a result of convergence.

If the Pseudopsinae are excluded from the group of subfamilies including the Piestinae, Oxytelinae, and Osoriinae, then where does the subfamily belong in relation to other staphylinids? Herman (1975) pointed out the near identity of the hypopharynx in *Pseudopsis* and in some Phloeocharinae, and the presence of globosetae in *Rimulincola* which is usually placed in the Phloeocharinae. Unfortunately, this small subfamily of fewer than a dozen genera is poorly known. Neither the subfamily as a whole nor many of the included genera have been adequately characterized, and the limits of the subfamily are unstable with some included genera (*Rimulincola, Olisthaerus, Giulianium*) probably belonging elsewhere. Any detailed consideration of the relationship of the Pseudopsinae to Phloeocharinae is, therefore, beyond the scope of the present work.

Immature stages have not yet been described for any member of the Pseudopsinae. [According to comments of P. M. Hammond (*in litt.*), larvae of *Pseudopsis* were reared by

W. O. Steel and are in the British Museum (Natural History), but these cannot now be located.] Discovery (or rediscovery) of the larva of any pseudopsine should provide a test of the alternative hypotheses of subfamily relationships just discussed. If Herman's (1975) hypothesis that *Pseudopsis* is the sister group of the Oxytelinae is correct, and/or if the placement of *Nanobius, Asemobius,* and *Zalobius* in the Piestinae is correct, then we would expect pseudopsine larvae to possess several synapomorphies shared by larvae of the Piestinae, Oxytelinae and Osoriinae. These include saprophagous feeding habits, a transverse truncate ligula (except the piestine genus *Trigonurus*), bifid, multifid, or more highly modified mandibular apices, and a cervicosternum of a single sclerite (see Newton, 1982). In contrast, if pseudopsine larvae are predatory as suggested by adult evidence plus the usual correlation of adult and larval feeding habits in Staphylinidae, then the larval mouthparts would be expected to resemble those of relatively generalized predatory staphylinid larvae such as occur in the Phloeocharinae and Omaliinae. We might then find an acute mandible with serrate inner edge and at most a single subapical tooth, a digitiform ligula, and perhaps a three-segmented cervicosternum as is usual among staphylinid larvae.

At present I tentatively leave the Pseudopsinae as a subfamily of uncertain position within the Staphylinidae, and suggest that the sister group of the subfamily be sought among the Phloeocharinae or allied subfamilies (see Hammond, 1975) rather than among the Piestinae, Oxytelinae, and Osoriinae.

LITERATURE CITED

Ganglbauer, Ludwig
 1895. Die Käfer von Mitteleuropa. Band II. Familienreihe Staphylinoidea. 1. Theil: Staphylinidae, Pselaphidae. Vienna, 880 pp.
Hammond, Peter
 1975. The phylogeny of a remarkable new genus and species of gymnusine staphylinid (Coleoptera) from the Auckland Islands. Jour. Ent. (B), vol. 44, no. 2, pp. 153–173.
Herman, Lee H., Jr.
 1970. Phylogeny and reclassification of the genera of the rove-beetle subfamily Oxytelinae of the world (Coleoptera, Staphylinidae). Bull. Amer. Mus. Nat. Hist., vol. 142, pp. 343–454.
 1975. Revision and phylogeny of the monogeneric subfamily Pseudopsinae for the world (Staphylinidae, Coleoptera). *Ibid.,* vol. 155, pp. 241–318.
 1977. Revision and phylogeny of *Zalobius, Asemobius* and *Nanobius,* new genus (Coleoptera, Staphylinidae, Piestinae). *Ibid.,* vol. 159, pp. 45–86.
Mulsant, E., and Claudius Rey
 1856. Description d'un coléoptère inédit constituant un genre nouveau voisin du G. Pseudopsis (famille des brachélytres). Ann. Soc. Linn. Lyon, ser. 2, vol. 3, pp. 7–11.
Newton, Alfred F., Jr.
 1982. New genus and species of Oxytelinae from Australia, with description of its larva, systematic position and phylogenetic relationships (Coleoptera, Staphylinidae). Amer. Mus. Novitates no. 2744, pp. 1–24.
Tanner, Vasco
 1927. A preliminary study of the genitalia of female Coleoptera. Trans. Amer. Ent. Soc., vol. 53, pp. 5–50, pls. 2–15.