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A New Genus and Species of Oxytelinae from Australia, With a Description of Its Larva, Systematic Position, and Phylogenetic Relationships (Coleoptera, Staphylinidae)

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ABSTRACT

A distinctive new genus and species of flightless litter-inhabiting staphylinid, *Oxypius peckorum*, is described from extreme southwestern Australia, together with its presumed larva. The systematic position and phylogenetic relationships of the genus are reviewed. *Oxypius* is considered to be most closely related to *Euphantias*, presently placed in the Piestinae. Both genera are here placed in the Oxytelinae close to the genera *Syntomium* and

Deleaster. A revised cladistic analysis is presented for primitive taxa of the Oxytelinae; a need for a revised tribal classification is suggested. A key to separate larvae of the subfamilies Piestinae, Oso-riinae, and Oxytelinae is also given, and existing keys to genera of Oxytelinae are modified to include adults and larvae of *Oxypius* and adults of *Euphantias*.

INTRODUCTION

The genus described below first came to my attention as a larva collected by Dr. John B. Kethley in southwestern Australia in 1976. This larva was obviously a novel larval type, probably of the subfamily Piestinae. However, no adults of that subfamily were known to occur in Western Australia, nor were any adults of allied subfamilies to which the larva might be attributed known from Australia. The mystery was apparently solved when ex-

tensive collections made by Drs. Stewart and Jarmila Peck in southwestern Australia in 1980 produced a dozen collections of adults of a remarkable new genus of staphylinid, in several cases associated with larvae of the unknown type. Subsequent study of the adults has led me to conclude that the genus is most closely related to the controversial genus *Euphantias*, generally placed in the Piestinae. Analysis of adults of both genera

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and of larvae of the new genus suggests, however, that both genera belong in the subfamily Oxytelinae, although some modification of both adult and larval characterizations of that subfamily is required to accept the two genera. Some changes in the cladistic analysis of oxyteline genera worked out by Herman (1970) are also indicated.

The purposes of this paper are to describe the new genus and its larva, to present revised keys allowing for their identification, and to present evidence about phylogenetic relationships of the new genus, including a revised cladistic analysis of certain lineages of the Oxytelinae.

METHODS

A pair of adults were cleared in hot KOH, stained in chlorazyl black, partially dissected and examined under dissecting and compound microscopes as glycerin slides. A second pair was cleared, partially dissected, critical-point dried, coated with gold-palladium mixture and examined with a scanning electron microscope. Two larvae were also cleared, stained in acid fuchsin and examined as mineral oil slides. Drawings were made with the aid of a camera lucida from the slide preparations.

The cladistic methods used here are essentially those of Herman (1970). Out-group comparison is used to determine polarity of character transformations, except as noted in the discussion accompanying the cladistic analysis. The out-groups particularly studied include the staphylinid subfamilies Piestinae, Osoriinae, Pseudopsinae, Phloeocharinae, Omaliinae, and Proteininae and the families Silphidae and Scaphidiidae.

ACKNOWLEDGMENTS

I am grateful to Dr. John F. Lawrence and the CSIRO Division of Entomology, Canberra, for loan of the Pecks' material, and to Dr. John B. Kethley and the Field Museum of Natural History, Chicago, for the loan of Berlese residues containing the original larva. Other material relevant to this study was lent by Dr. Lee H. Herman, Jr., American Museum of Natural History, New York; Dr. David H. Kavanaugh, California Academy

of Sciences, San Francisco; and Dr. Terry L. Erwin, National Museum of Natural History, Washington, D.C., who are also thanked. I am especially indebted to my wife, Margaret K. Thayer, and to Dr. Herman for critically reading and commenting on the manuscript. The SEM photographs were made possible by National Science Foundation grants BMS-7412494 and BMS-7502606, with the assistance of Edward Seling.

OXYPIUS, NEW GENUS

Figures 1-4, 6-30

TYPE SPECIES: *Oxypius peckorum*, new species.

DIAGNOSIS: *Oxypius* may be separated from other staphylinids by a combination of the presence of a glandular reservoir opening on each side of the nearly divided abdominal tergum IX (fig. 6); the fusion of the short abdominal sternum II to sternum III (fig. 4); the presence of a single pair of abdominal laterosclerites per segment (fig. 30); the 5-segmented tarsi (fig. 21); and the strongly trilobed pronotal margins (figs. 1, 22).

DESCRIPTION: Length about 4.5-6.0 mm. Body (fig. 1) elongate, slender, flattened. Head, pronotum, and elytra rugose, irregularly carinate. Dorsum with numerous short, scalelike setae (fig. 24). Much of body normally with fine coating of detritus.

Head with distinct broad neck (fig. 11). Eyes small, prominent. Ocelli absent. Preocular portion of head long, with prominent swelling over base of each antenna. Antenna long, slender, 11-segmented, not clubbed. Epistomal suture present, curved. Labrum (fig. 13) short, weakly emarginate. Epipharynx (figs. 15, 16) complex, with row of globosetae near anterior margin and multifid setae on lateral lobes. Mandibles (fig. 15) not very prominent, apices acute, without subapical teeth; basal molar lobes well developed, well sclerotized, contiguous; prostheca well developed, bearing multifid setae (fig. 17). Lacinia with dense setae, and spines near apex; galea with dense brush of plumose setae at apex; maxillary palp of four segments, the fourth being longest and widest. Hypopharynx (fig. 19) with dense, fine longitudinal combs. Prementum with adoral surface broadly bilobed, bearing single coarse comb

at side and base, fine microtrichia outside this; ventral surface with single large sclerite. Labial palpi free; palps of three segments, the third being longest and widest. Mentum trapezoidal, feebly emarginate anteriorly. Posterior tentorial pits (fig. 12) deeply invaginated, the gular sutures fused anterior to this but abruptly divergent and obsolescent before reaching maxillary foramen; gular sutures separate and divergent from posterior tentorial pits to hind margin of head. Tentorium with heavy posterior and dorsal arms forming vertical pillar between dorsum and venter of head; anterior arms apparently atrophied. Cervical sclerites small, not flattened or platelike.

Pronotum laterally expanded and trilobed, anterior lobe broadly truncate, middle and posterior lobes acute; lateral marginal bead absent. Protergosternal suture absent. Procoxal fissure (figs. 22, 23) nearly closed, trochantin completely concealed. Procoxae not strongly projecting; without mesial groove or ridge articulating with sternum. Procoxal cavities widely open behind. Spiracular peritremes small.

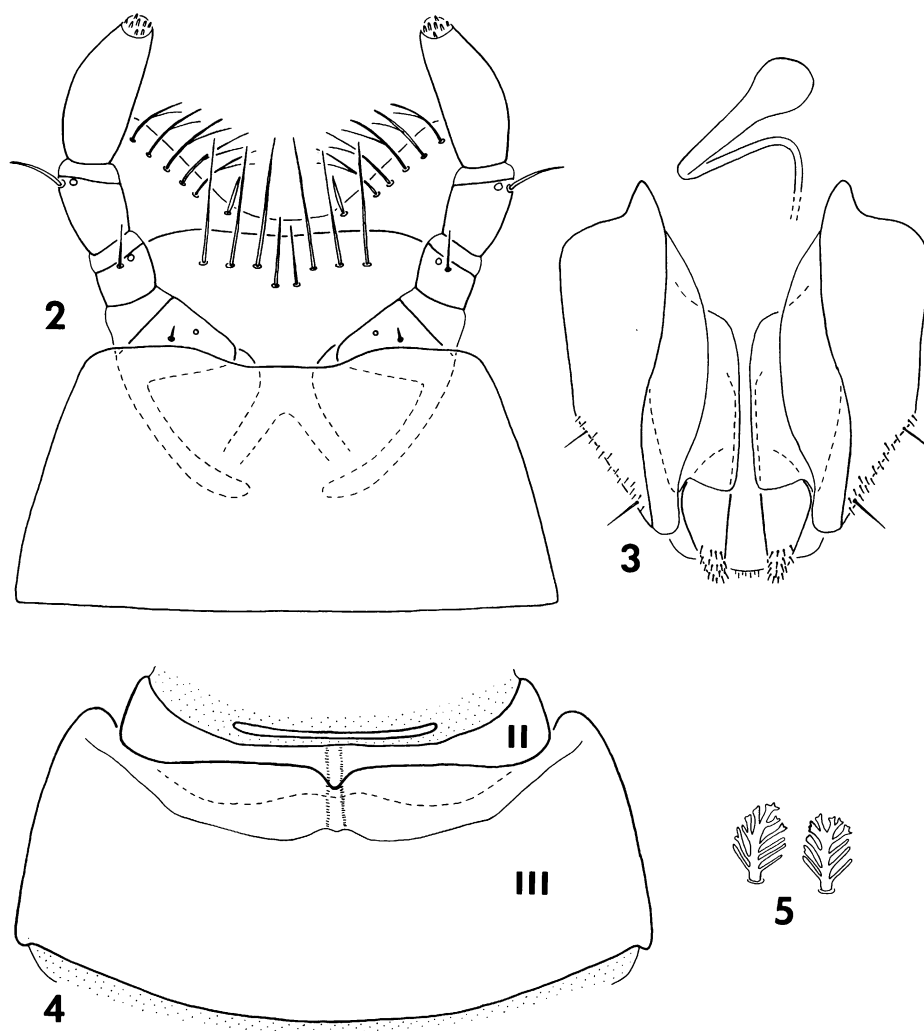
Scutellum (fig. 26) with three rounded impressions on surface, posteriorly glabrous. Elytra (figs. 1, 26) short, basal articulation obsolete; epipleural ridge explanate, abruptly obsolete in apical fifth; epipleural fold abruptly narrowed and obsolete in apical fifth. Elytral-metepimeral and elytral-metapleural interlocking devices virtually absent. Hind wings, including axillary sclerites, absent. Mesosternum (fig. 28) elongate; mesopleurosternal suture present medially as ridge, obsolete anteriorly and posteriorly. Mesepimeral-episternal suture present. Mesocoxae narrowly separated by meso- and meta-sternal processes; mesocoxae globose, trochantin exposed. Metasternum small. Metacoxae small, triangular, hind face oblique. Metendosternite with short narrow stalk, long arms.

Legs fairly long, slender. Tibiae densely setose, without longitudinal ctenidia or rows of spines. Tarsi (fig. 21) 5-segmented. Segments 1-4 short, broad, closely associated, densely setose, without tenent setae; segment 4 broadly lobed below. Fifth segment longer than first four together, with pair of large claws. Empodial setae lacking.



FIG. 1. *Oxypius peckorum*, paratype, uncleaned.

Abdominal segments III-VII exceptionally broad, segment III more than $1.5\times$ as wide as segment II and about $1.25\times$ as wide as elytra. Segment III on each side with anterior emargination, involving paratergite and sternite, for reception of elytral epipleural fold (fig. 26). Abdominal tergum I membranous, spiracles small; tergum II lightly sclerotized, without transverse ridge, covered by elytra, spiracles in membrane at edges of tergum; terga III-VIII well sclerotized, exposed, spiracles in edges of terga; terga III-VII each with transverse subbasal ridge. Tergum VII not apically fringed; terga without patches of wing-folding setae. Segments III-VII each apparently with single pair of laterosclerites (figs. 26, 30), each of which has curved basal



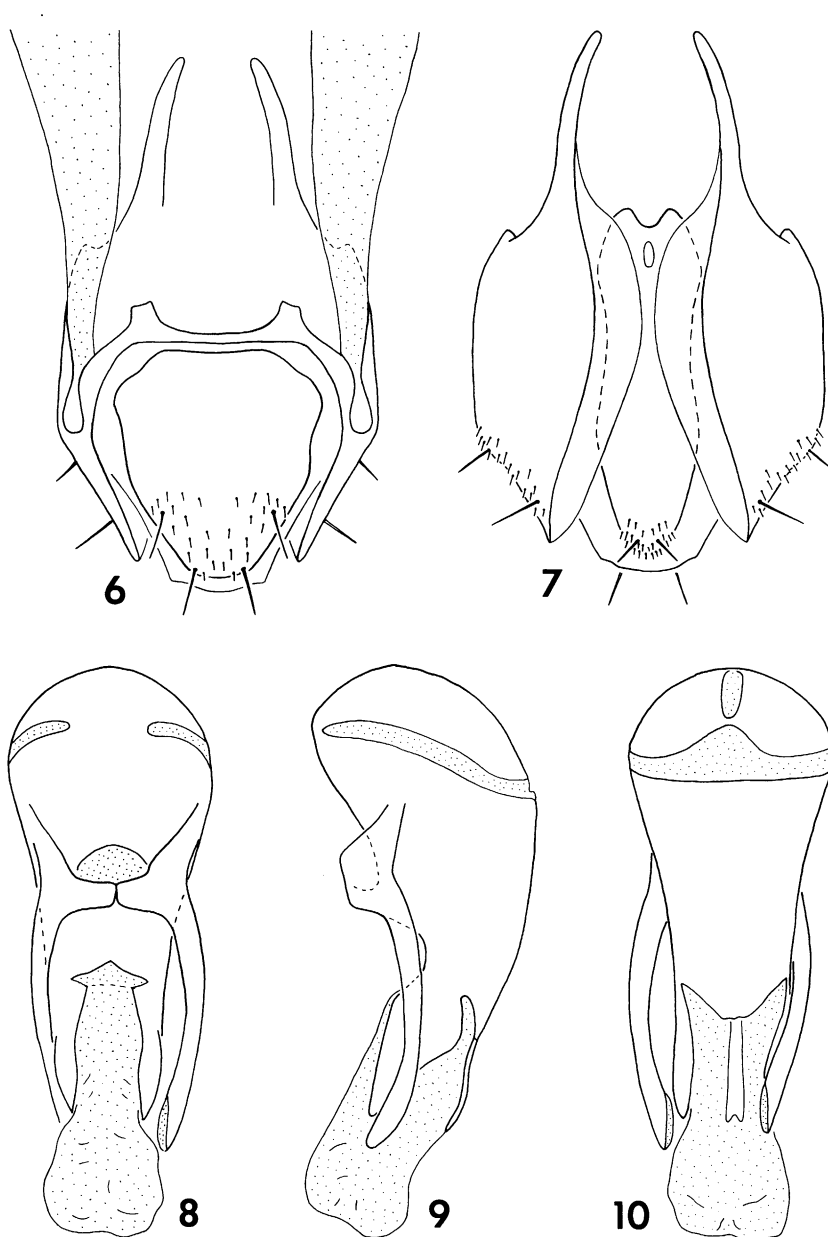
FIGS. 2-5. 2-4, *Oxyptus peckorum*. 2. Labium, ventral view. 3. Female genital segment and spermatheca, ventral view. 4. Abdominal sternites II-III, ventral view. 5. *Euphania insignis*, plumose setae of abdominal tergum V. Not drawn to same scale.

ridge; ridge of laterosclerite of segment III greatly elevated, anteromesial in position, resting against inner side of elytral epipleural fold when abdomen retracted. Thin, lightly sclerotized strip present between laterosclerite and sternite of each segment. Sternite II short, fused to sternite III except at sides; a thin transverse sclerite present anterior to sternite II (fig. 4). Sternites II-III with weakly developed intercoxal processes (figs. 4, 29). Sternites III-VII each with transverse subbasal ridge. Intersegmental membranes be-

tween terga II-VII and sternites III-VII with brick-wall pattern; membranes attached to apex of preceding segment, except at extreme sides of sterna III-VI.

Genital segment (figs. 3, 6, 7) small; tergum IX nearly divided by tergum X medially, the narrow dorsal portion bearing pair of anterior projections; tergum IX on each side with opening of large gland reservoir which extends into segments VII-VIII and is filled with a dark brown fluid.

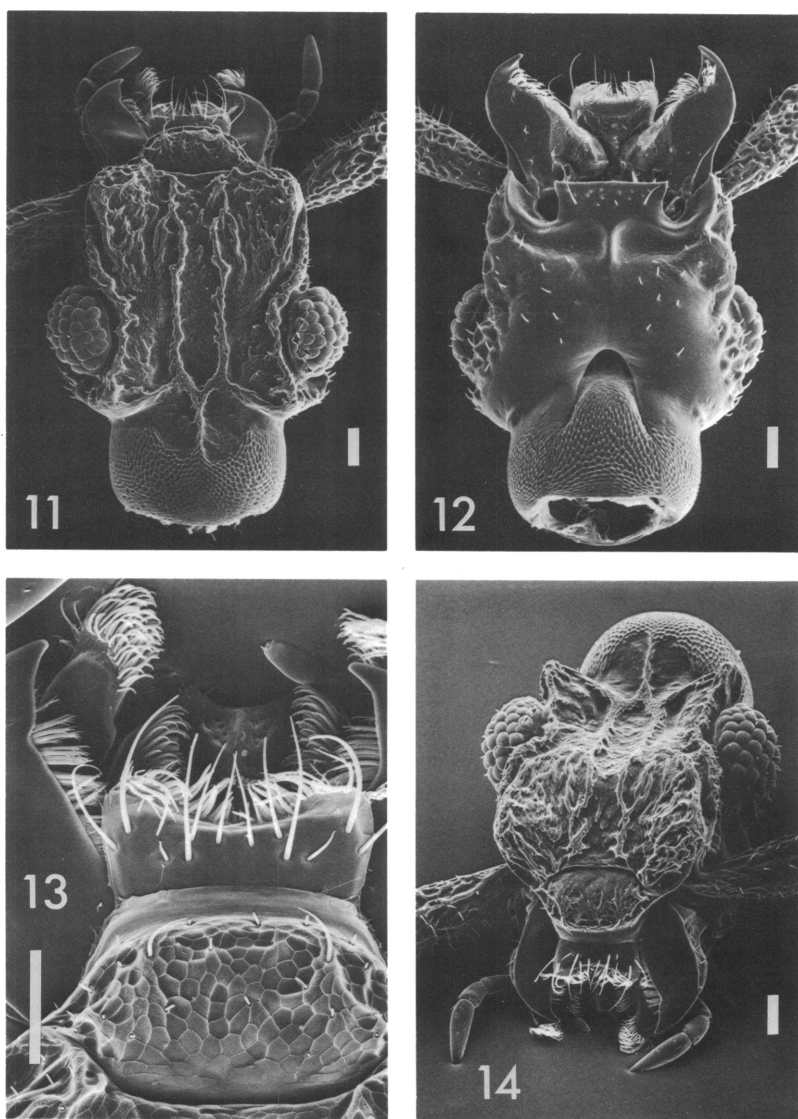
Male. Sternite III with hundreds of small



FIGS. 6–10. *Oxypius peckorum*, male. 6. Genital segment, dorsal view, showing portion of gland reservoirs (stippled). 7. Genital segment, ventral view. 8–10. Aedeagus, dorsal, lateral and ventral views, respectively.

glandular pores scattered over most of surface (fig. 25); pores and internal structures visible with compound microscope at 400 \times . Tergum IX with long anteroventral projections (fig. 7). Sternum IX large, symmetrical. Aedeagus (figs. 8–10) small, short, lying in

repose with dorsal side (bearing parameres) facing left side of beetle; median lobe with large basal pressure plate and with complex, vertically divided apex; parameres long, glabrous but bearing numerous pores; basal piece absent.



FIGS. 11–14. *Oxypius peckorum*. 11. Head, dorsal view. 12. Head, ventral view, maxillary-labial complex removed. 13. Head, anterodorsal view. 14. Head, oblique frontal view. Scale lines = 0.1 mm.

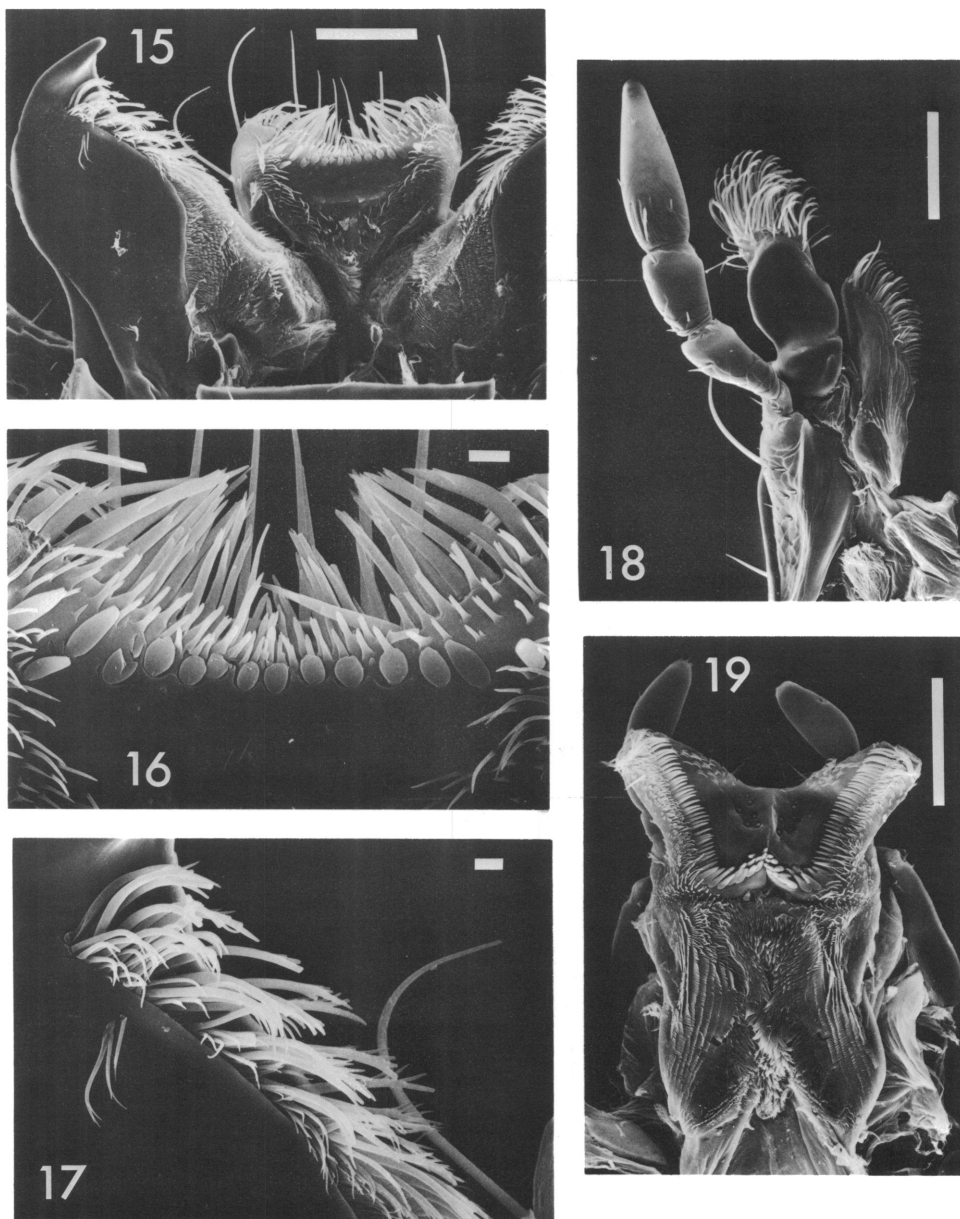
Female. Tergum IX (fig. 3) with very short anteroventral projections. Pair of proximal and distal gonocoxites present, styli absent. Spermatheca a lightly sclerotized simple sac.

ETYMOLOGY: A combination of *Oxy*, from Oxytelinae, and *pi*, from Piestinae, with the masculine ending *us*. The name alludes to the oxyteline affinities and piestine resemblances of adults and larvae of the new genus.

DISCUSSION: Evidence for the subfamily

placement and cladistic relationships of *Oxypius* is presented in separate sections below.

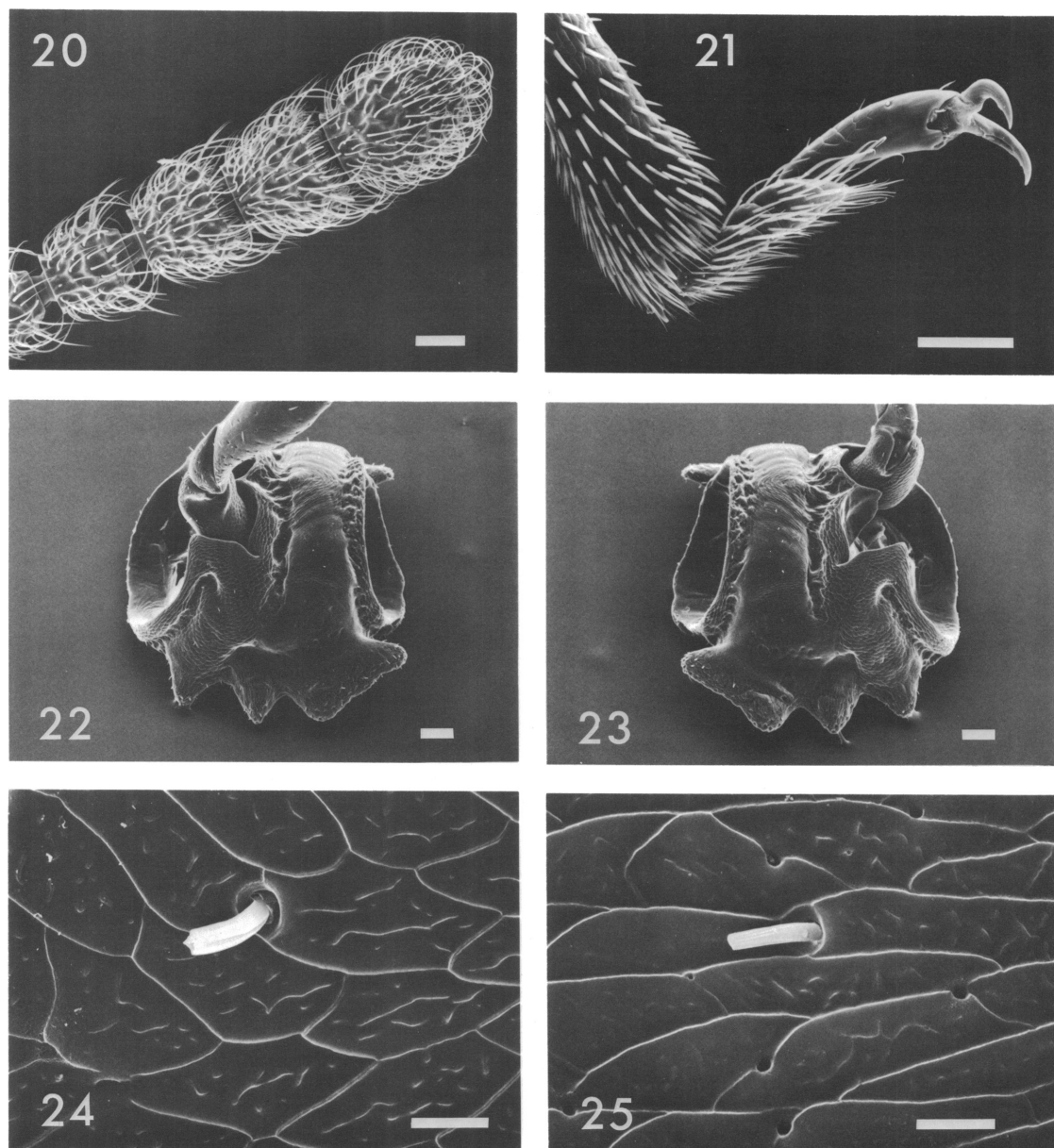
In Herman's (1970) key to the genera of the Oxytelinae of the world, *Oxypius* will run readily to couplet 9 and probably to couplet 10 and to the genus *Syntomium*. Couplets 9 and 10 of the key may be replaced by the following couplets to include *Oxypius* as well as the genus *Euphantias*, here transferred to the Oxytelinae (see below):



FIGS. 15–19. *Oxypius peckorum*. 15. Mandibles and epipharynx, ventral view. 16. Epipharynx, ventral view. 17. Detail of mesial edge of right mandible, ventral view. 18. Left maxilla, dorsal view. 19. Hypopharynx and labium, dorsal view. Scale lines = 0.1 mm. or (16, 17) 0.01 mm.

- 9(8). Abdominal segments III to VI apparently with two laterosclerites per segment (Herman, 1970, fig. 71); gular sutures confluent except at base (Herman, 1970, fig. 10) 10
Abdominal segments III to VI with four

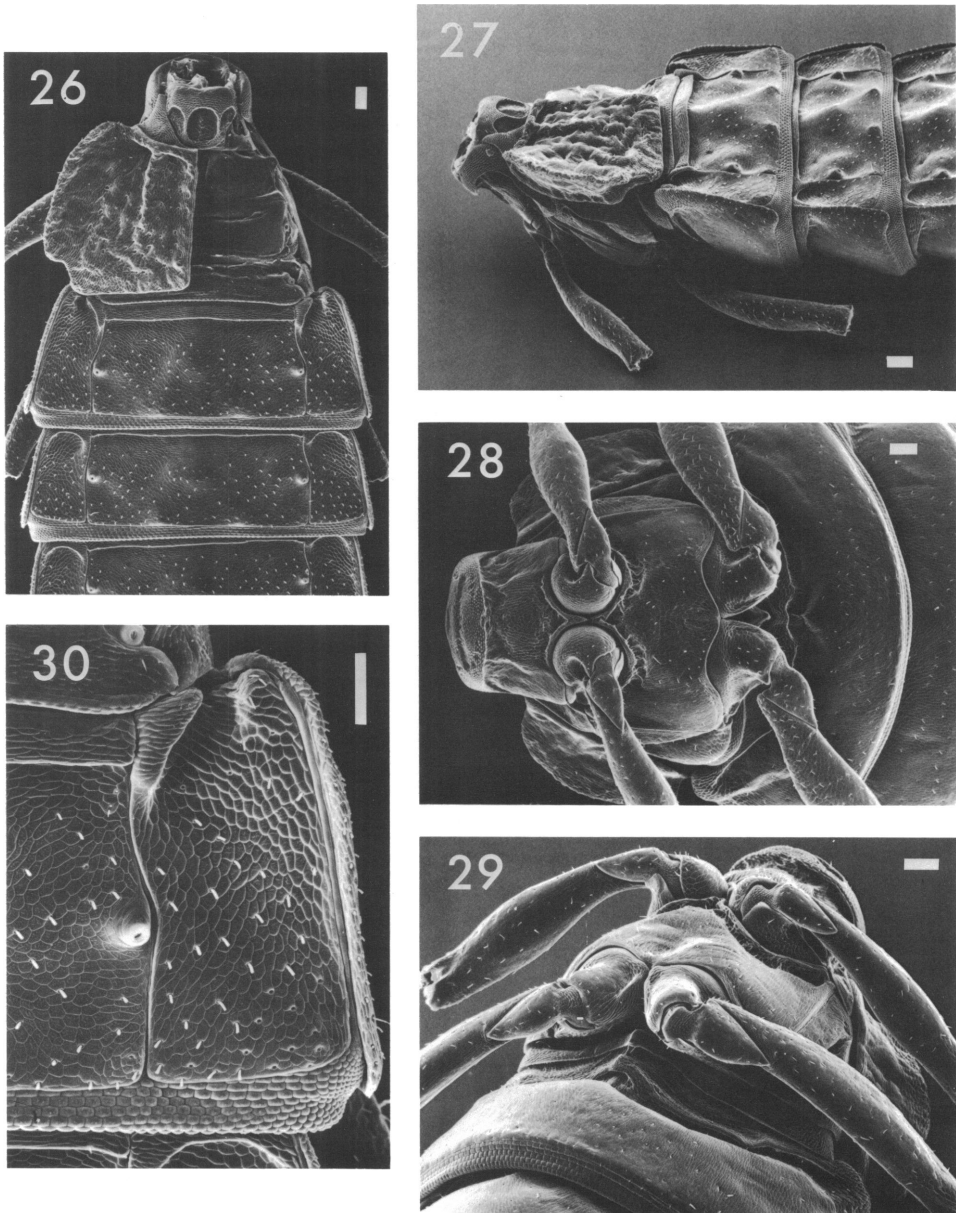
- laterosclerites per segment (Herman, 1970, fig. 68); gular sutures confluent or separate 10b
10(9). Tarsal formula 5-5-5; dorsum without plumose setae but may have truncate setae 10a



FIGS. 20–25. *Oxypius peckorum*. 20. Antenna, apex. 21. Protarsus, male, oblique ventral view. 22. Prothorax, left ventrolateral view. 23. Prothorax, right ventrolateral view, right coxa removed. 24. Abdominal tergum III, detail. 25. Abdominal sternite III, male, detail. Scale lines = 0.1 mm. or (24, 25) 0.01 mm.

Tarsal formula 3-3-3; dorsum densely
covered with plumose setae (fig. 5)
..... *Euphanias*
10a(10). Lateral margin of pronotum not trilobed;

head, pronotum and elytra not coarsely
sculptured and irregularly carinate;
Holarctic *Syntomium* (part)
Lateral margin of pronotum strongly tri-



FIGS. 26–30. *Oxypterus peckorum*. 26. Pterothorax-abdomen, right elytron removed, dorsal view. 27. Same, left dorsolateral view. 28. Pterothorax-abdomen, ventral view. 29. Same, oblique posteroventral view. 30. Abdominal segment III, right side, dorsal view. Scale lines = 0.1 mm.

lobed (fig. 22); head, pronotum and elytra coarsely sculptured and irregularly carinate (fig. 1); Australian
 *Oxypterus*
 10b(9). Tarsal formula 4-4-4; basal three tarsal

articles compressed and closely associated (Herman, 1970, fig. 48); gular sutures confluent except at base (Herman, 1970, fig. 10); Neotropical
 *Crassodemus*

Tarsal formula 5-5-5; tarsal articles distinct (Herman, 1970, fig. 52); gular sutures narrowly separated along entire length (Herman, 1970, fig. 7); Holarctic *Manda*

***Oxypius peckorum*, new species**

Figures 1-4, 6-30

HOLOTYPE: Male. AUSTRALIA: WESTERN AUSTRALIA: Walpole N.P., "Tingle Tree," June 18-27, 1980, S. & J. Peck, SBP 63, berlesate fungi and litter. Deposited in Australian National Insect Collection, Canberra.

PARATYPES: 47 specimens, all collected by S. & J. Peck, except as noted. AUSTRALIA: WESTERN AUSTRALIA: same data as holotype (six males, three females). Walpole N.P., "Tingle Tree," July 4, 1980, SBP 81, berlesate casuarina log litter (one male). Walpole N.P., Collier Rd., June 19, 1980, SBP 67, berlesate litter at base of tingle tree (two males, one female). Walpole N.P., Zig Zag Rd., June 20-27, 1980, SBP 70B, berlesate rotted log litter and fungi (two males, one female). Walpole N.P., Hilltop Rd., June 21, 1980, SBP 75, berlesate karri and tingle tree litter (five males, two females). 12 mi. N of Walpole, ca. 250 m., Oct. 24, 1969, R. W. Taylor, marri forest, ANIC berlesate No. 148, leafmold (one female). Quininup, 29 km. SSE Manjimup, July 13-16, 1980, SBP 112, berlesate karri forest litter (one male). 54 km. SE of Manjimup, June 22-26, 1980, SBP 77B, berlesate jarrah forest litter (one male). Pemberton, Brockman N.P., July 9, 1980, SBP 103, berlesate karri litter with fungi (five males, one female); Oct. 26, 1969, R. W. Taylor, karri forest, ANIC berlesate No. 151, leafmold (one female). Pemberton, The Cascades, July 7, 1980, SBP 96, berlesate fungi and jarrah litter (two males, two females). Pemberton, The Cascades, July 7, 1980, SBP 97, logs and leaf litter (two females). Pemberton, Warren N.P., July 12, 1980, SBP 106, berlesate karri litter and moss (five females). Pemberton, Warren N.P., July 5, 1980, SBP 86, berlesate karri litter with fungi (two males, one female). Deposited in Australian National Insect Collection, Canberra; Museum of Comparative Zoology, Cambridge; American Museum of Natural History, New York; Field Museum of Natural History, Chicago; Canadian National

Collection, Ottawa; British Museum (Natural History), London; and my own collection.

DIAGNOSIS: *Oxypius peckorum*, the only species presently included in *Oxypius*, may be recognized by the characters given in the generic diagnosis.

DESCRIPTION: Length 4.5 to 6.0 mm. Color reddish brown, usually appearing grayish brown because of adhering detritus. Body shaped as in figure 1, moderately flattened. Body surfaces with reticulate microsculpture and microrugosities (fig. 24), not strongly shining. Body surfaces with numerous, but not dense, minute scalelike setae (figs. 24, 25). Head and pronotum irregularly and intermittently carinate; elytra with scattered very coarse punctures, each elytron with a poorly developed longitudinal carina about one-third from suture on anterior half.

Head length (excluding mouthparts) about 1.4× head width (across eyes). Head with most strongly developed carina running from supra-antennal lobe, past mesial margin of eyes and ending in obtuse post-ocular prominence; deep groove present between this carina and eye. Eyes prominent, coarsely faceted, each with about 30-35 facets. Antenna about 3× as long as head width; all segments elongate and roughly sculptured; segments 1-4 with few scattered long setae only; segments 5-11 also with increasingly numerous intermediate length setae; segments 9-10 with apical periarticular band of digitiform sensilla (fig. 20), which are also present on apical half of last segment. Labrum as in figure 13. Mandibles as in figure 15. Maxilla as in figure 18; segment 4 of palp with about four prone digitiform sensilla externally at base. Labium as in figure 2. Gular sutures and venter of head as in figure 12.

Pronotal length about 0.82× maximum width, which is at posterior corner of anterior notal lobe. Pronotal width about 1.4× head width. Anterior notal lobe shelf-like with acute anterior and square posterior corners; middle and posterior notal lobes acute.

Elytral length (along suture) about 0.47× combined elytral width, and about 0.45× pronotal length. Combined elytral width about 1.20× pronotal width and 0.82× greatest abdominal width. Elytra not fused but poorly articulated at base. Pterothoracic sterna as in figure 28; mesosternal length at midline about 1.1× metasternal length.

Abdomen longer than combined length of head and thorax; maximum width about 1.2× combined elytral width. Terga III–VI each with rounded callus at middle, and pair of paramedian calluses along posterior edge (fig. 27). Spiracles on segments III–VII elevated.

Male. Genital segment and aedeagus as in figures 6–10.

Female. Ovipositor as in figure 3. Spermatheca as in figure 3.

Gut. Gut with long loop which is half as long as abdomen. Gut contents include fungal hyphae, a few spores, and a large quantity of decayed plant material.

DISTRIBUTION AND HABITAT: *Oxypius peckorum* is known only from a 100-km. long area of extreme southwestern Australia, roughly between the towns of Walpole, Manjimup, and Pemberton. This is an area of tall, wet sclerophyll forest dominated by species of *Eucalyptus*, especially karri (*E. diversicolor*) and jarrah (*E. marginata*). Most collections of *Oxypius* were made by Berlese funnel extraction of forest leaf litter, often including fungi or portions of rotting logs. Collections from debris under bark made at the same localities did not contain *Oxypius*, nor did forest litter collections made at the same season in drier wooded areas outside the above region. Wet sclerophyll forests similar to those in which *Oxypius* has been found occur in eastern Australia, but extensive sampling of forest litter in those areas has not produced anything resembling *Oxypius*. At present, then, it appears that *Oxypius peckorum* is restricted to forest litter in the small zone of wet sclerophyll forest in extreme southwestern Australia.

ETYMOLOGY: Named in honor of its main collectors, Drs. Stewart B. Peck and Jarmila Kukalova-Peck of Carleton University, Ottawa, whose tireless worldwide collecting efforts have produced so many interesting new staphylinoids and other organisms.

MATERIAL EXAMINED: 48 specimens, listed above as type material.

LARVA OF *OXYPIUS PECKORUM*

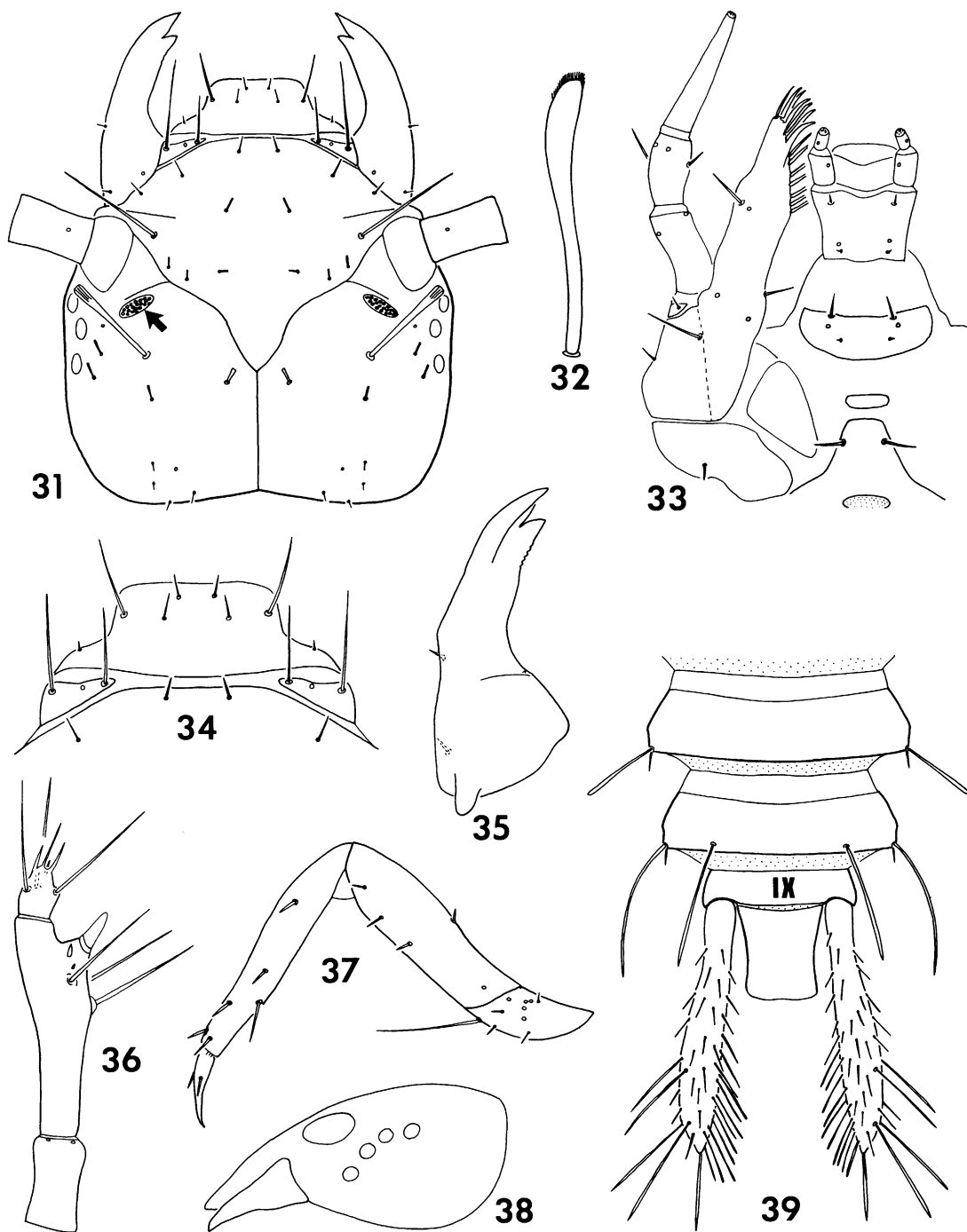
Figures 31–39

DIAGNOSIS: *Oxypius* larvae may be distinguished from all known staphylinid and other Coleoptera larvae by possession of the fol-

lowing characters in combination: head with four ocelli in a curved line (fig. 38); mandibles as in figure 35, symmetrical; labium as in figure 33, ligula transverse, truncate; “frayed” setae present (fig. 32); and long, clubbed, one-segmented urogomphi (fig. 39).

DESCRIPTION: Length of mature larva about 5 or 6 mm. Head width 0.60 mm. Antennal length 0.50 mm. Maximum width (metanotum and intermediate abdominal terga) 0.83 mm. Form elongate, parallel-sided, moderately flattened. Color of dorsum brown; of venter and appendages light brown, of prementum and abdominal segment X dark brown. Body surfaces, especially dorsum, with microsculpture consisting of fine asperities and curved ridges bearing fine teeth. Vestiture complex, on dorsum consisting primarily of a few long and numerous short specialized or “frayed” setae (fig. 32); elsewhere mainly scattered simple setae.

Head (fig. 31) elongate, flattened. Four pigmented ocelli on each side, in a curved line (fig. 38). Ecdysial lines end in antennal foramen. Glandular area present behind antennal foramen (fig. 31). Antenna as in figure 36; posterior face of first segment and of basal articulating membrane with numerous asperities; first segment glabrous, second and third segments each with three macrosetae, second segment with one large and two small sensory appendages, third segment with four small setiform sensory appendages near apex. Frons on each side with suture connecting anterior tentorial pit and dorsal mandibular articulation. Labrum as in figure 34, with three sclerotized areas; without internal apodemes. Epipharynx with numerous microtrichia, especially along sides. Mandibles (fig. 35) symmetrical, each with: single large subapical tooth, irregularly serrate proximal to this tooth; small rounded basal lobe bearing a single minute tooth; and two small setae on external surface. Maxilla (fig. 33) with transverse cardo; with lightly sclerotized maxillary articulating area; with elongate stipes separated by narrow band of membrane from very elongate mala. Mala not divided at apex, with numerous articulated and a few non-articulated spines along mesial edge, with a few setae or sensilla at apex but no plumose setae. Maxillary palp of three segments, not counting incomplete basal “palpifer”; first segment longer than second,



FIGS. 31-39. *Oxypius peckorum*, mature larva. 31. Head, dorsal view, showing glandular area (arrow). 32. Specialized macroseta of abdominal tergum VI. 33. Maxillary-labial complex, ventral view. 34. Labrum, dorsal view. 35. Right mandible, ventral view. 36. Right antenna, ventral view. 37. Right proleg, anterior view. 38. Head, schematic, left lateral view showing arrangement of four ocelli. 39. Abdominal apex, dorsal view. Not drawn to same scale.

apical segment with single prone digitiform sensilla at external side of base. Hypopharynx with two or three lateral rows of fine mesally-directed microtrichia, apically with scattered short rows or single microtrichia. Labium (fig. 33) consisting of prementum, mentum, and two submental sclerites, the posterior submental sclerite fused posteriorly to head capsule. Ligula transverse, apically truncate, separated by membranous suture from ventral premental sclerite. Labial palps of two segments; palpigers fused to form ventral premental sclerite. Head ventrally without definite sutures; with lateral ridge extending posteriorly from ventral mandibular articulation and delimiting maxillary foramen; with deep pit at point of attachment of posterior arms of tentorium. Tentorial bridge attached to posterior arms of tentorium just above ventral surface of head. Cervicosternum consisting of single triangular sclerite.

Thoracic and first eight abdominal segments consisting of single tergum and sternum each, except abdominal sternum I with large median and pair of small lateral sclerites. Segments IX–X without sutures between tergum and sternum. Thoracic and first abdominal terga with midlongitudinal ecdysial line. Thoracic terga II–III, abdominal terga and sterna I–IX each with thickened brown band along anterior margin; same terga, except abdominal IX, with transverse ridge about one-third behind anterior margin. Mesothoracic spiracle in projecting membranous lobe; abdominal spiracles in edges of terga I–VIII; all spiracles annular. Legs (fig. 37) long, slender, similar to one another.

Ninth abdominal segment (fig. 39) small, about half as long and two-thirds as wide as eighth segment. Urogomphus long, one-segmented, widest about one-fourth from apex; about twice as long as tenth abdominal segment and as long as segments VII–IX taken together. Tenth abdominal segment elongate, cylindrical; eversible membranous anal lobes with no distinct teeth visible at 400 \times .

Gut. Gut with long loop, about half as long as abdomen. Gut contents include fungal hyphae, decayed plant material, and pieces of arthropod cuticle (possibly Acarina).

LARVAL INSTARS: Two size classes of larvae have been collected, which from their size are presumed to represent the final (III?) and

penultimate (II?) instars. Measurements are: instar II, head width 0.43–0.47 mm. (mean 0.45 mm.), total length about 4 mm.; instar III, head width 0.57–0.60 mm. (mean 0.58 mm.), total length about 6 mm.

MATERIAL EXAMINED: Seven larvae. AUSTRALIA: WESTERN AUSTRALIA: Walpole N.P., "Tingle Tree," June 18–27, 1980, S. & J. Peck, SBP 63, berlesate fungi and litter (one larva III, with 10 adults). Walpole Nat. Pk., 8 km. NE Walpole, "Giant Tingle Area," Dec. 19, 1976, Leg. J. Kethley, FM(HD) #76-513, Ber. #147, mixed *Eucalyptus* litter (one larva III). Quininup, 29 km. SSE Manjimup, July 13–16, 1980, S. & J. Peck, SBP 112, berlesate karri forest litter (two larvae II, with one adult). 54 km. SE of Manjimup, June 22–26, 1980, S. & J. Peck, SBP 77B, berlesate jarrah forest litter (one larva II, with one adult). 35 km. WSW of Manjimup, July 14–17, 1980, S. & J. Peck, SBP 115, berlesate jarrah forest litter (one larva III). Pemberton, The Cascades, July 7, 1980, S. & J. Peck, SBP 97, logs and leaf litter (one larva II, with two adults). Deposited in Australian National Insect Collection, Canberra; Museum of Comparative Zoology, Cambridge; Field Museum of Natural History, Chicago; and my own collection.

DISCUSSION: The larvae here described as those of *Oxypius peckorum* have not been reared to establish their identity. The larvae are attributed to this species for the following reasons: 1. All six larval collections are from the same region, forest type, and microhabitat (forest litter) as those in which adults are found, and four of the larval collections included one or more adults. 2. The three larger larvae are of suitable size to be final instar larvae of the adults. 3. The characteristics of the larvae would lead to their being placed as either the Oxytelinae, Piestinae, or Osoriinae (see, e.g., Kasule, 1966). No Piestinae have been found in Western Australia, and the only Oxytelinae (other than *Oxypius*) and Osoriinae known to occur there and large enough to be attributed to the larger larval instar belong to widespread genera, some species of whose larvae are known to me. As will become apparent in the cladistic analysis below, both these larvae and *Oxypius* adults have characteristics that lead independently to their being placed as isolated, primitive

members of the Oxytelinae, a position occupied by no other larvae or adults known to occur in Western Australia.

In Kasule's (1966) key to subfamilies of larvae of the Staphylinidae, *Oxypius* larvae will run to couplet 6 and probably to the Oxytelinae, but they differ from the characterization of the Oxytelinae in having four rather than three or fewer ocelli. The discovery of *Oxypius* larvae, as well as larvae of other genera of the Oxytelinae, Piestinae, and Osoriinae unknown to Kasule at the time his key was written, requires some modification in keys dealing with these three subfamilies. The following new key is based on personal examination of larvae of one or more species of each genus listed, and may be substituted for couplets 6 and 7 of Kasule's (1966) subfamily key.

KEY TO KNOWN LARVAE OF THE PIESTINAE, OSORIINAE, AND OXYTELINAE

1. Six ocelli on each side of head; ligula bi- or quadrilobed (Piestinae, part) 2
Four or fewer ocelli (or none) on each side of head; ligula truncate or broadly rounded at apex 3
- 2(1). Ligula elongate, bilobed at apex; antenna longer than head width, basal segment setose Trigonurini (*Trigonurus*)
Ligula transverse, quadrilobed at apex; antenna less than half as long as head width, basal segment glabrous Apateticini (*Nodynus*)
- 3(1). Left and right mandibles approximately symmetrical, with same number (usually one or two) of large subapical teeth; first segment of maxillary palp as long as or longer than second segment, or urogomphi falciform; abdominal spiracles usually in edges of terga or in pleural sclerites; tentorial bridge attached to posterior arms of tentorium, or apparently absent; urogomphus one-segmented; ocelli 4, 3, 1, 0 ... Oxytelinae (*Oxypius*, *Syntomium*, *Homalotrichus*, *Bledius*, *Teropalpus*, *Ochtheophilus*, *Carpelimus*, *Sartallus*, *Platystethus*, *Oxytelus*, *Anotylus*)
Left and right mandibles with dissimilar dentition, or with scooplike or molar-like lobes near apex; first segment of maxillary palp shorter than second; abdominal spi-

- racles in membrane beside terga; tentorial bridge attached to ventral surface of head, or if attached to posterior arms of tentorium (Osoriini) then mandibles with subapical molar-like lobes; urogomphus one- or two-segmented, not falciform 4
- 4(3). Head with two large sclerites (mentum, submentum) between prementum and posterior tentorial pits; ocelli 4, 1 Piestinae: Piestini (*Siagonium*, *Piestoneus*, *Piestus*, *Hypotelus*)
Head with a single large sclerite (fused mentum and submentum) between prementum and posterior tentorial pits; ocelli 4, 3, 2, 1, 0 Osoriinae (*Eleusis*, *Renardia*, *Zeoleusis*, *Lispinus*, *Nacaeus*, *Thoracophorus*, *Glyptoma*, *Clavilispinus*, *Leptochirus*, *Priochirus*, *Holotrochus*, *Osorius*)

Note: The attribution of six ocelli to *Lispinus* larvae and five ocelli to *Siagonium* and *Leptochirus* larvae by Paulian (1941) has not been confirmed by later observations. Larvae of several species of each genus examined by me have four ocelli on each side.

The four ocelli of *Oxypius* larvae will prevent the genus from running through keys to genera of oxyteline larvae such as those in Kasule (1968) and Topp (1978). The following couplet may be added to the beginning of either cited key to include *Oxypius*:

0. Dorsum of body with numerous long and short specialized or "frayed" setae; urogomphi long, clubbed *Oxypius*
Dorsum of body with simple tapered setae only; urogomphi shorter, tapered to acute tip 1

Note: The attribution of three ocelli to *Syntomium* larvae by many authors including Kasule (1968) and Topp (*op. cit.*) is probably in error; examined larvae of *Syntomium confragosum* have on each side of the head three dorsal ocelli plus an isolated antero-ventral ocellus that could easily be overlooked. Couplet 1 of both cited keys should therefore be modified to give four, rather than three, ocelli for *Syntomium*.

SYSTEMATIC POSITION (ADULT)

During my attempt to determine the relationship of *Oxypius* to other Staphylinidae,

it became apparent that *Oxypius* shared more characteristics with the genus *Euphanias* than with any other genus known to me. Because *Euphanias* is poorly known, a brief review of the history of the genus is given.

The genus *Euphanias* Fairmaire and Laboulbène, 1856 (= *Pholidus* Mulsant and Rey, 1856, preoccupied) has long been controversial. Since its description various authors have placed the genus in or near what would now be called the subfamilies Oxytelinae (e.g., Kraatz, 1857; Fauvel, 1871), the Phloeocharinae (e.g., Jacquelin du Val, 1857), or the Piestinae (e.g., Ganglbauer, 1895 and most subsequent authors), or the genus has been placed in its own subfamily (Rey, 1880; Portevin, 1929). The genus was not included in Herman's (1970) generic revision of the Oxytelinae. *Euphanias* currently contains five rare species (four apparently known only from original type material): *boiteli* Normand (Tunisia); *ganglbaueri* Bernhauer (Santa Catarina, Brazil); *insignis* Mulsant and Rey (Mediterranean region); *pliginskii* Bernhauer (Crimea); and *pusanovi* Blinsein (southern Ukraine, USSR). At least the type species, *insignis*, is known to inhabit plant debris and decomposing algae on the banks of brackish and salt water bodies (Fauvel, 1871; Rey, 1880). The genus has not been critically studied in nearly a century, has never been adequately described or illustrated, and the species are in need of revision, but such tasks are beyond the scope of the present work. The characterization of the genus adopted here and used as the basis for the cladistic analysis of figure 41 is taken from two females of the type species, *E. insignis*; one of these specimens was cleared and partially dissected.

Euphanias and *Oxypius* share numerous characters which, in the context of staphylinids as a whole, are in a derived condition in these two genera. Some of these derived character states are unique to *Oxypius* and *Euphanias*, most notably the exceptionally broad abdomen which is abruptly widened at the third segment, with correlated modifications to accommodate the elytra. An explicit list of synapomorphies for the two genera may be found by reference to figure 41 and table 1 and is not repeated here. The two genera will henceforth be considered sister

taxa, and the question of subfamily placement addressed.

Oxypius and *Euphanias* lack the following apomorphic characters that are considered to be diagnostic for higher taxa to which the genera might be (or have been, in the case of *Euphanias*) attributed: characteristic glandular openings of abdominal sternum VIII (Omaliinae, Proteininae, Neophoninae); longitudinal row of wing-folding spicules (Phloeocharinae); strongly developed groove on mesial surface of procoxae for reception of prosternal process (Piestinae, most Osoriinae); absence of abdominal laterosclerites (Osoriinae); abdominal terga and sterna fused (most Osoriinae); stridulatory file on each side of ninth abdominal tergum (Pseudopsinae, including *Nanobius*, *Asemobius*, and *Zalobius*); and absence of intercoxal process of abdominal sterna II and III (Oxytelinae, many other taxa of Staphylinidae).

Oxypius and *Euphanias* each have the outlets of a pair of glandular reservoirs opening on the ninth abdominal tergum (fig. 6), a character considered unique to the subfamilies Oxytelinae (Herman, 1970) and Pseudopsinae (Herman, 1975). The structure of the ninth abdominal tergum in these two subfamilies differs considerably (Newton, 1982), raising doubts about the homology of the glands and the position of their openings. In the Oxytelinae (and in *Oxypius* and *Euphanias*) the ninth tergum is nearly or quite divided dorsally by the tenth tergum, a derived condition. In the Pseudopsinae the ninth tergum is broadly continuous dorsally, whereas each side of the tergum bears a stridulatory file unique in the family. *Oxypius* and *Euphanias* share the presence of scalelike setae with most genera of Pseudopsinae, but such setae are also found in other staphylinids such as *Eupiestus* (Piestinae). *Oxypius*, but not *Euphanias*, shares similarities in habitus, sculpturing and detritus accumulation with some genera of the Pseudopsinae, but again these characters appear elsewhere in the Staphylinidae and have apparently been developed independently within several subfamilies.

In addition to possessing a configuration of the ninth abdominal tergum and glandular openings identical with those of the genera of Oxytelinae, *Oxypius* and *Euphanias* have

the general characteristics of Oxytelinae given by Herman (1970) with one exception: the presence of an intercoxal carina on abdominal sterna II and III in *Oxyptius* (fig. 4) and *Euphantias* and its absence in Oxytelinae. Such a carina is found, usually in more highly developed form, in at least some members of all other subfamilies considered above and in allied families; it is, however, lost in many groups of the Staphylinidae including some members of the Pseudopsinae (*Pseudopsis*) and the Osoriinae (Eleusini). I consider the presence of the carina in *Oxyptius* and *Euphantias* to be insufficient reason to exclude the genera from the Oxytelinae when other characters such as ninth tergal glands are taken into consideration, and therefore place both genera in the Oxytelinae. As will be seen below, *Euphantias* and *Oxyptius* share many characters with certain genera of Oxytelinae.

CLADISTIC ANALYSIS (ADULT)

Were it not for Herman's (1970) comprehensive generic revision and cladistic analysis of the Oxytelinae, any attempt to precisely relate *Oxyptius* and *Euphantias* to the other genera of the subfamily would be beyond the scope of the present work. The existence of such an analysis not only permits but indeed stimulates refinement and revision as new taxa or new data become available.

The revision of portions of Herman's cladistic analysis attempted here is based in large part on the data presented in Herman (1970). In addition to determining character states for the added taxa *Oxyptius* and *Euphantias*, however, I have critically examined at least one species of all genera shown on the cladograms (figs. 40, 41) as well as members of the following genera: *Manda*, *Plan-eustomus*, *Aploderus*, *Bledius*, *Blediotrogus*, *Teropalpus*, *Ochtheophilus*, *Carpelimus*, *Scitotrogus*, *Sartallus*, *Parosus*, and *Oxytelus*. A large number of new characters, required primarily by the addition of *Oxyptius* and *Euphantias*, have been added. The changes required by the addition of the two genera and the new characters are few. When combined with a revised interpretation of one of the characters used by Herman, however, the need for a fundamental restructuring of the

basal branching pattern of the Oxytelinae becomes apparent.

Tentatively, at least, I accept Herman's decisions on the polarity of character transformations for all but one of the 51 characters employed in his analysis (Herman, 1970, table 1). The exception is Herman's character 34, in which a weakly sclerotized or reduced second abdominal sternite is considered derived relative to a well-developed second sternite. A related character, the presence of a long articulating membrane connecting the second and third sternites, is correlated exactly with the presence of a well-developed second sternite; this character was not used by Herman. In all non-oxyteline Staphylinidae known to me, with a minor exception noted below, the second sternite is fused to the third sternite, and is usually less than half as long as, and more lightly sclerotized than, the third sternite. Within the Oxytelinae, the genera *Syntomium*, *Oxyptius*, and *Euphantias* have the reduced, fused second sternite characteristic of other staphylinid subfamilies. *Deleaster* and the "*Coprophilus* group" (*Coprophilus*, *Coprostygnus*, and *Homalotrichus*) have a reduced second sternite with a very short immobile membranous connection to the third sternite. All remaining genera of the Oxytelinae have a well-developed second sternite articulated to the third by a long connecting membrane. I regard the well-developed, articulated second sternite as a highly and uniquely (within the Oxytelinae) derived condition.

A similar development is found elsewhere in the Staphylinidae only in the tribe Eleusini of Osoriinae. Of the three genera placed in the tribe, *Eleusis* and *Renardia* have a second sternite of the "*Deleaster*" type with immobile membranous suture between sternites II and III, whereas *Zeoleusis* has a long connecting membrane between sternites II and III. Both the second sternite and the connecting membrane of *Zeoleusis* are shorter than in those Oxytelinae with a well-developed, articulated second sternite. Since no other characters suggest a direct relationship of the Eleusini to Oxytelinae, and several characters of adults and larvae are at least consistent with placement of the Eleusini in Osoriinae, I regard the similarities in devel-

opment of the second sternite as independently derived in the two taxa.

Herman (1970) did not give reasons for his choice of polarity in the development of the second sternite, which ran counter to his own criterion of out-group comparison. The unlikelihood of creating a membranous connection between fused sclerites is widely assumed. In the present case, a well-developed and articulated second abdominal segment is probably correlated with increased abdominal motility: it contributes to elongation of the abdomen and to a less restricted thoraco-abdominal joint. Many other staphylinids have independently developed a motile abdomen without adopting this particular stratagem, however.

Table 1 presents the plesiomorphic and apomorphic states of the characters to be used in this analysis. Figure 40 is a condensed representation of the branching sequence of Herman's (1970) figure 1 on which the relevant characters from my table 1 are superimposed. These characters include those used in Herman's analysis of the same taxa (with reversed interpretation and repositioning of character 43) plus some additional characters. Some of Herman's characters are not shown on his figure 1 at all places in which they should appear. For example, only three characters (10, 17, 19) are shown in derived condition for the Oxytelini, but at least three others (11, 20, 38) should have been indicated. Note too that the derived condition of character 17 is readily derivable from either condition of character 16 and that character 16 may therefore be indicated as a synapomorphy uniting all Oxytelinae, rather than the Coprophilini alone as Herman assumed. (Some additional minor changes involving missing or misplaced characters have been made.)

Two changes in the branching sequence of figure 40 are required if the most parsimonious arrangement of taxa is desired. The placement of *Syntomium* requires four character reversals, including those involving loss of an articulated second sternite, as well as independent derivation of characters 30 and 31 in *Syntomium* and *Deleaster*. If *Syntomium* is moved to the *Deleaster* branch and characters 11, 20, 30, and 31 are considered

synapomorphic for the two genera, the net result is the elimination of three of the character reversals (38, 43, 45) and two independent derivations (30, 31) with the addition of only one independent derivation (10). (See fig. 41.)

A much more significant change is also suggested. The placement of the Oxytelini as the sister group of all other Oxytelinae has little justification. Such placement requires the independent derivation of the well-developed, articulated second sternite (43, 45) in the Oxytelini and in a portion of the Coprophilini, as well as the independent derivation of four additional characters (10, 11, 20, 38) in the two tribes. If the Oxytelini is moved to the position vacated by *Syntomium*, an independent derivation of all six cited characters is eliminated and no new independent derivations or reversals are required.

The net result of the above changes is the branching sequence shown in figure 41. In this cladogram *Oxypius* and *Euphantias* with their attendant characters have been added in the most parsimonious arrangement. This results in the two genera being sister groups with some 13 shared derived characters. Together *Oxypius* and *Euphantias* are most closely related to *Syntomium* with which they share four synapomorphies. These three genera in turn share an additional four synapomorphies with *Deleaster*. If Herman's interpretation of character 38 is correct, then the *Deleaster-Euphantias* clade is the sister group of all remaining Oxytelinae. Because the relationships among the three genera of the "*Coprophilus* group" cannot be unambiguously resolved with the characters used by Herman (1970) and because my reversal of character 43 removes the only synapomorphy given for the group, the genera are shown as part of a polytomy in figure 41.

Alternative arrangements and alternative interpretations of some characters used in the analysis were tried but resulted in decreased parsimony. For example, if the presence of an intercoxal carina (42) is considered to be a primitive condition in *Oxypius* and *Euphantias* rather than a secondary derivation as assumed, and if the branching pattern of figure 41 is retained, then the carina must have been lost at least three times (in *De-*

TABLE 1
Relative Plesiomorphy and Apomorphy of Characters Used for a Cladistic Analysis of Oxytelinae^a

Plesiomorphic	Apomorphic
*1. Head, pronotum and elytra smooth or with rounded elevations	Head, pronotum and elytra roughly sculptured with irregular, incomplete longitudinal carinae (fig. 1)
*2. Body surfaces clean	Body surfaces, especially dorsum, with accumulation of mud and fine debris
*3. Body without specialized, scalelike setae	Body, especially dorsum, with numerous scalelike setae (figs. 24, 25)
*4. Scalelike setae sparse, not plumose (fig. 24)	Scalelike setae plumose, densely covering dorsum (fig. 5)
*5. Stridulatory system absent	With presumed stridulatory system consisting of enlarged ridged area near inner base of metatibia and curved row of teeth at each side of abdominal sternite III
*6. Head not constricted to form neck	Head constricted to form distinct, broad neck (fig. 11)
*7. Frons with slightly elevated supraantennal swelling or ridge	Frons with large rounded supra-antennal lobe (fig. 14)
8. Epistomal suture present	Epistomal suture absent
*9. Mandibles without subapical teeth (fig. 15)	Mandibles each with two subapical teeth
10. Fourth segment of maxillary palp stout and elongate (fig. 18)	Fourth segment of maxillary palp subulate
11. Gular sutures completely separate	Gular sutures confluent medially (fig. 12)
*12. Posterior tentorial attachment not or slightly invaginated	Posterior tentorial attachment deeply invaginated (fig. 12)
13. Pronotal lateral marginal bead present	Pronotal lateral marginal bead absent
*14. Pronotal lateral margin not explanate	Pronotal lateral margin broadly, obtusely explanate (fig. 22)
*15. Pronotal lateral margin not multilobed	Pronotal lateral margin trilobed (fig. 22)
16. Protergosternal suture evident as groove	Protergosternal suture evident as ridge
17. Protergosternal suture present	Protergosternal suture absent (fig. 22)
18. Procoxal fissure open, trochantin exposed	Procoxal fissure nearly or quite closed, trochantin concealed (fig. 22)
19. Procoxal fissure present	Procoxal fissure absent
20. Elytra striate	Elytra not striate
*21. Elytra not costate	Elytra each with three obtuse costae
*22. Elytral epipleural ridge present as fine carina, attaining elytral apex	Elytral epipleural ridge present as obtusely explanate lateral ridge, absent from apical fifth (fig. 26)
*23. Elytral epipleural fold complete, attaining elytral apex	Elytral epipleural fold abruptly narrowed and obsolete in apical fifth (fig. 27)
*24. Hind wings present, functional; elytra freely articulated at base; elytral-metepimeral and elytral-metanotal locking devices present, functional	Hind wings completely absent; elytra partially fused to mesonotum at base; elytral-metepimeral and elytral-metanotal locking devices obsolete or absent
25. Mesocoxae separated by elongate mesosternal process	Mesosternal process reduced and mesocoxae contiguous
26. Mesocoxae separated by elongate mesosternal process	Mesocoxae separated by mesosternal and metasternal processes (fig. 28)
27. Tibial longitudinal spinous row present	Tibial longitudinal spinous row absent (fig. 21)
28. Metatibial longitudinal ctenidium present	Metatibial longitudinal ctenidium absent
29. Tarsi 5-5-5 segmented	Tarsi 3-3-3 segmented
*30. Tarsal empodium bisetose	Tarsal empodium glabrous (fig. 21)

TABLE 1—(Continued)

Plesiomorphic	Apomorphic
*31. Abdominal segment III at most $\frac{9}{10}$ as wide as elytra taken together	Abdominal segment subequal in width to elytra taken together
*32. Abdominal segment III subequal in width to elytra taken together	Abdominal segment III a fifth wider than elytra taken together (fig. 1)
*33. Abdominal segment II about $\frac{4}{5}$ as wide as segment III	Abdominal segment II less than $\frac{2}{3}$ as wide as segment III (fig. 4)
*34. Abdominal segment III without modification for accommodation of closed elytra	Abdominal segment III with anterior margin notched for reception of elytra (fig. 26)
*35. Intersegmental membranes between abdominal segments III–VII with “brick wall” pattern (fig. 30)	Intersegmental membranes of abdomen without pattern
*36. Intersegmental membranes between abdominal segments III–VII attached to apex of preceding segment (fig. 29)	Intersegmental membranes of abdomen attached to inner surface of preceding segment anterior to apex of segment
*37. Abdominal wing-folding setae or spicules present on one or more terga	Abdominal wing-folding setae or spicules absent
38. Abdomen with one pair of laterosclerites per segment III–VII (fig. 26)	Abdomen with two pairs of laterosclerites per segment III–VII
*39. Abdominal paratergite III without elevated process	Abdominal paratergite III with elevated process that rests against inner apex of elytral epipleural fold (fig. 30)
40. Abdominal tergum VII with spinulate or fimbriate apex	Abdominal tergum VII with smooth apex
*41. Abdominal tergum IX without openings of glandular reservoirs	Abdominal tergum IX with openings of pair of large glandular reservoirs (fig. 6)
*42. Abdominal sternites II and III with mid-longitudinal intercoxal elevation or carina (fig. 4)	Abdominal sternites II and III without intercoxal elevation or carina
*43. Abdominal sternite II, at narrowest point, about a fourth or less as long as sternite III (fig. 4)	Abdominal sternite II half or more as long as sternite III
*44. Abdominal sternite II solidly fused to sternite III (fig. 4)	Abdominal sternites II and III separated by thin membranous suture which does not allow relative movement of the sternites
*45. Abdominal sternites II and III separated by thin membranous suture	Abdominal sternites II and III separated by connecting membrane that is half or more as long as sternite II
*46. Ovipositor with distinct apical stylus	Ovipositor without stylus (fig. 3)

^a Those marked with an asterisk (*) were not used by Herman (1970). Adult characters only.

leaster, in *Syntomium*, and in all remaining Oxytelinae). Alternatively, if the loss of the carina is considered uniquely derived, and *Oxypius* plus *Euphantias* become the sister group of all other Oxytelinae, the eight characters shared with *Syntomium* and four with *Deleaster* would become independently derived. The polarity of some of these characters could be reversed to solve this problem (e.g., characters 11, 20, 30, and 31 could be

reversed and shown as derived conditions for the “*Coprophilus* group” and remaining Oxytelinae), but such reversals could not be supported by out-group comparison as can the selected character polarities.

I believe the cladistic relationships shown in figure 41 represent the best estimate that can be made at present with available characters. In particular, I regard the monophyly of the *Deleaster-Euphantias* clade as highly

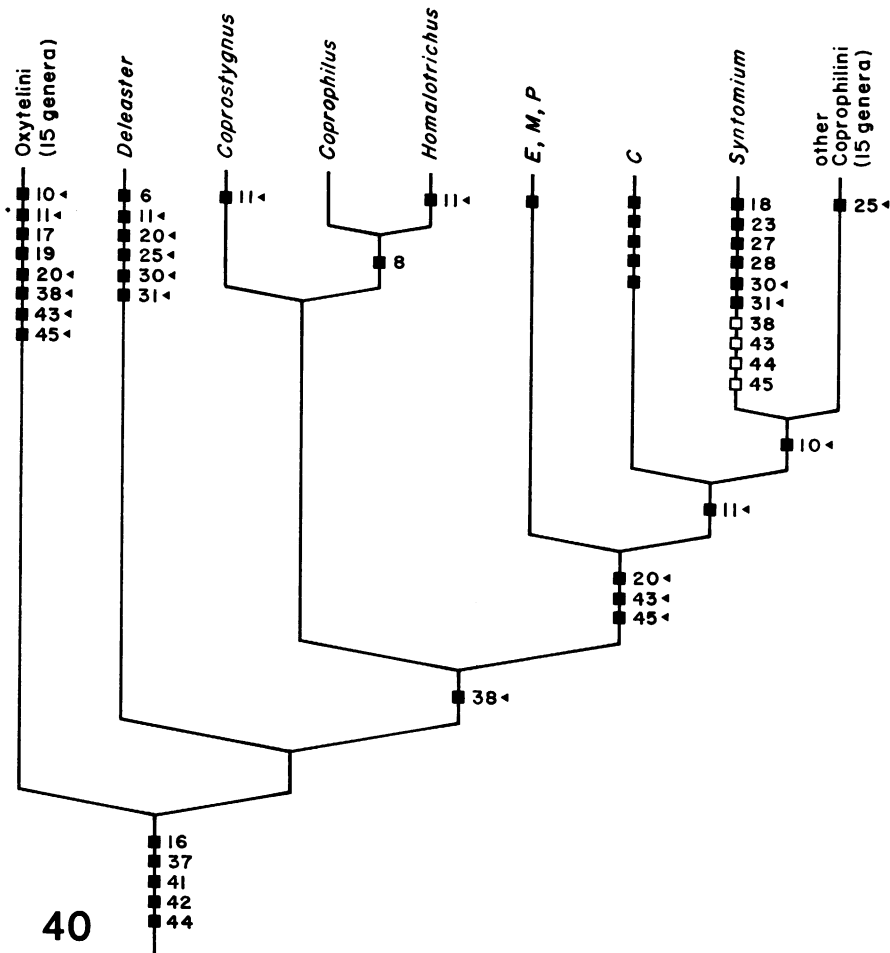


FIG. 40. Cladistic analysis of the two tribes and of some genera of Oxytelinae, condensed from Herman (1970, fig. 1). Numbers refer to character transformations listed in table 1. A solid square indicates a transformation from plesiomorphic to apomorphic state; an open square indicates a reverse transformation. A triangle following a number indicates a character transformation that occurs more than once on this cladogram. For identity of unnamed genera see Herman (1970, fig. 1).

probable and the indicated relationships among the four included genera as firmly established. Further work is clearly needed to confirm Herman's (1970) assumption of monophyly of the "Coprophilus group" (see fig. 41), and to establish whether the *Deleaster-Euphantias* clade (as assumed here based on the adult evidence of character 38) or the "Coprophilus group" (as some larval evidence cited below would suggest) is the sister group of all remaining Oxytelinae. I regard the clade including all the Oxytelinae other

than the *Deleaster-Euphantias* clade and the "Coprophilus group" as well established by the unique development of the large, articulated second abdominal sternite (43, 45). Basal cleavages within this clade, however, are at present founded on only a few characters that are known to have become independently derived on two or more occasions within Oxytelinae, and further analysis may well suggest the need for changes. Both of the surviving synapomorphies (17, 19) for the tribe Oxytelini are multiply derived within

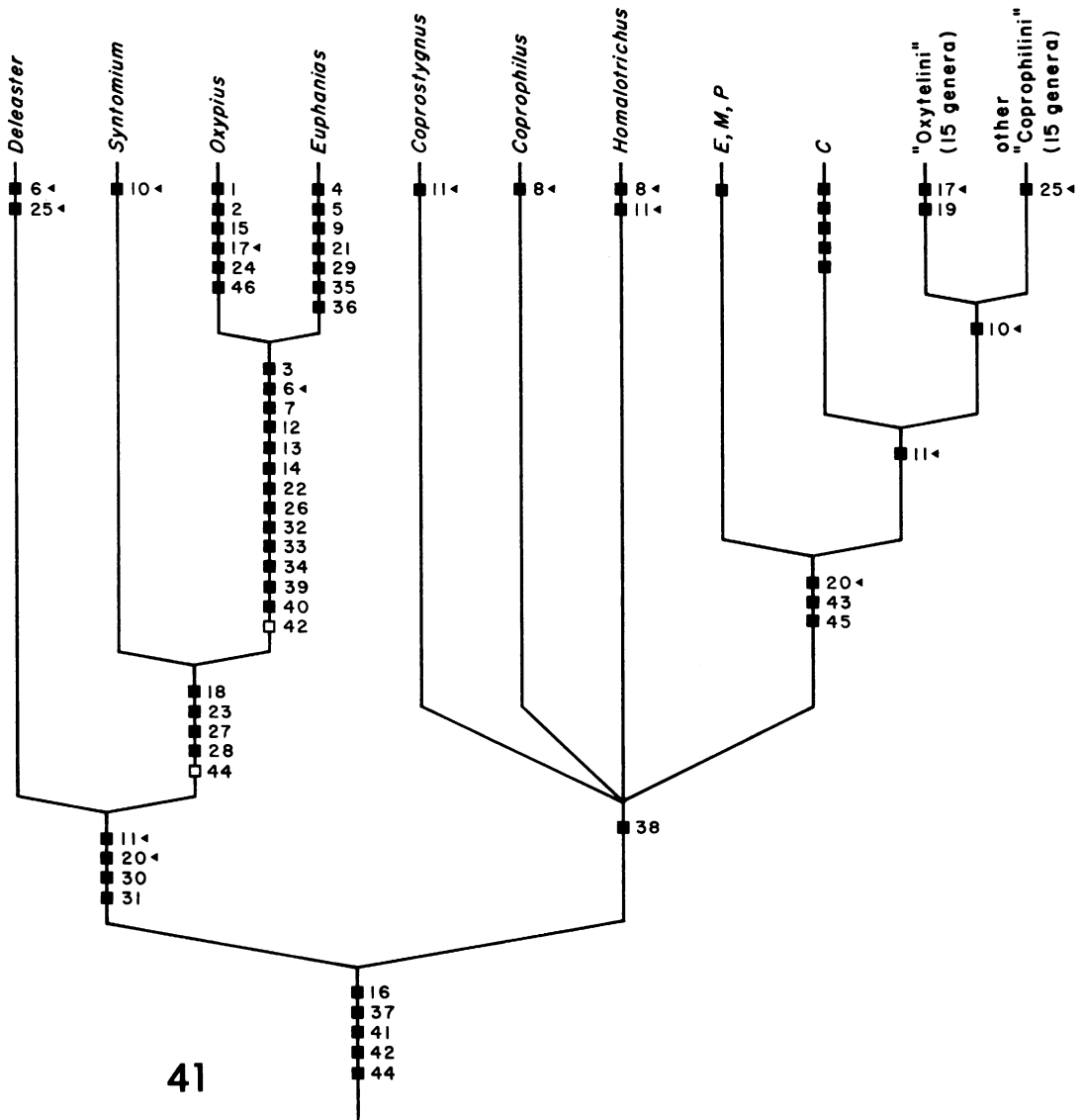


FIG. 41. Cladistic analysis of some genera of Oxytelinae, modified from figure 40 by the addition of *Oxyptus* and *Euphanias* and by other changes explained in the text. Numbers refer to character transformations listed in table 1. For other explanation see figure 40.

the "other Coprophilini" of figure 41, and some changes may be necessary within both groups.

Some additional characters whose evolutionary polarity is uncertain may provide further support for the relationships of the genera of the *Deleaster-Euphanias* clade hypothesized in figure 41. The following

characters unite the indicated taxa and are not, or are only rarely, found in other Oxytelinae: *Oxyptus* and *Euphanias* lack a transverse subbasal ridge of abdominal tergum II; have a straplike transverse sclerite anterior to abdominal sternum II (rather than a pair of sclerites as in *Syntomium*, *Deleaster*, the "Coprophilus group" and some other Oxy-

telinae, or no sclerite as in remaining Oxytelinae); and have eyes with few unusually large facets. *Oxypius*, *Euphantias*, and *Syntomium* have three somewhat similar impressed areas on the scutellum, but there is much variation in scutellar impressions within Oxytelinae; a trilobed impression similar to that of *Oxypius* is found in *Anotylus* and allied genera of higher Oxytelini, for example (Herman, 1970). *Deleaster*, *Syntomium*, and *Oxypius* (*Euphantias* unknown) have two unusual male characters in common: abdominal sternite III bears large numbers of minute glandular pores, and the aedeagus has a large basal pressure plate.

The cladistic analysis of figure 41 suggests that two divergent evolutionary trends in abdominal motility have occurred within the Oxytelinae. The ancestral oxyteline is assumed to have lost the abdominal intercoxal carinae found in most primitive staphylinids, and to have developed a membranous but non-motile joint between the second and third abdominal sterna. These initial steps in reducing the integrity of the thoraco-abdominal joint and "stretching" the basal abdominal segments are found among existing oxytelines in *Deleaster* and in the genera of the "*Coprophilus* group." In all "higher" Oxytelinae abdominal motility is greatly enhanced by elongation of the second sternite and the development of a long membranous connection between it and the third sternite. The presence of two pairs of laterosclerites per segment rather than one in "higher" oxytelines as well as in the "*Coprophilus* group" is probably also correlated with an increase in abdominal motility (Newton, to be published elsewhere). In the *Deleaster-Euphantias* clade, in contrast, a strong reverse trend has apparently occurred. The development of a broadened abdomen that is closely coadapted to the thorax has resulted in a shortened second abdominal sternite fused to the third and in a secondary development of sternal intercoxal processes. The result is the reduced thoraco-abdominal motility characteristic of most primitive staphylinids.

The conclusion that the *Deleaster-Euphantias* clade is the most primitive group of Oxytelinae is supported indirectly by non-cladistic data. The four genera are all cold-adapted, and show relict distribution patterns

both within and between genera that encompass the northern and southern cool temperate regions. The genera are morphologically and, from the meager available information, biologically isolated from one another, suggesting antiquity of phylogenetic origin. *Oxypius peckorum*, in particular, has morphological characteristics indicating a long history of flightlessness, has an apparently very restricted range of about 100 km., has been collected as adults only in winter, and is many thousands of kilometers from species of the other genera in the Holarctic and Neotropical regions. Cold adaptation and similar relict distribution patterns also characterize the three genera of the "*Coprophilus* group," but these genera show far less morphological divergence among themselves. Nearly all the remaining genera of the Oxytelinae inhabit the warm temperate and tropical regions of the world, show less morphological divergence from one another and have less disjunct distribution patterns.

SYSTEMATIC POSITION AND CLADISTIC ANALYSIS (LARVA)

As mentioned above in the discussion following the description of *Oxypius peckorum* larvae, these larvae will key out to the vicinity of the subfamilies Piestinae, Osoriinae, and Oxytelinae in standard keys such as those of Kasule (1966) and Topp (1978). *Oxypius* larvae share at least three probably derived characters with known larvae of those three subfamilies: 1. Ligula transverse, broadly truncate. 2. Cervicosternum triangular, consisting of a single sclerite. 3. Saprophagous or omnivorous feeding habits.

Among the three subfamilies, *Oxypius* larvae have four derived characters found in all or nearly all known larvae of Oxytelinae: 1. Maxillary palp with first segment longer than second. 2. Palpigers of prementum fused to form a single sclerite. 3. Abdominal spiracles placed in the terga rather than in membrane just outside of the terga. 4. Urogomphi one-segmented. (Characters 2 and 4 also occur in larvae of some Piestini and many Osoriinae.)

Oxypius larvae lack the following derived characters found in larvae of Piestinae and Osoriinae: 1. Mandibles with strongly asymmetrical dentition or more complex armature

(Piestini, Osoriinae). 2. Mentum and submentum fused (Osoriinae). 3. Tentorial bridge attached to head capsule, rather than to posterior arms of tentorium (Piestini, Osoriinae except Osoriini). 4. Long, setose antenna, and densely setose patches on meso- and metasternum (Trigonurini). 5. Ligula quadrilobed (Apateticini).

Characteristics of *Oxypius* larvae thus are most consistent with placement of the genus in the subfamily Oxytelinae. Of over 40 genera included in this subfamily, species of fewer than a dozen genera have been adequately described and/or available to me as larvae. Under these circumstances a detailed cladistic analysis would be premature. In lieu of such an analysis, I will briefly review the distribution and cladistic implications of several characters that may prove useful in future studies on oxyteline larvae.

The following apomorphic character states are found in the indicated genera of Oxytelinae:

1. Ocelli three (*Bledius*, *Teropalpus*, *Carpelimus*, *Ochtheophilus*, *Sartallus*), one (*Platystethus*, *Oxytelus*, *Anotylus*), or absent (*Coprophilus*, *Homalotrichus*).
2. Mandible with two subapical teeth, one dorsal and one ventral (all genera except *Oxypius* and *Bledius*, with a single dorsal tooth, and *Syntomium*, with two dorsal teeth).
3. Plumose or multifid setae present at apex of mala (*Syntomium*, *Bledius*, *Teropalpus*, *Carpelimus*, *Sartallus*).
4. First segment of maxillary palp longer than second segment (all genera except *Coprophilus*, *Homalotrichus*).
5. Labial palpi fused to one another (all genera except *Coprophilus*, *Homalotrichus*).
6. Ventral sclerites of prementum and ligula fused (*Syntomium*, *Carpelimus*, *Platystethus*, some *Oxytelus*).
7. Mentum and submentum more or less fused (*Platystethus*, *Oxytelus*, *Anotylus*).
8. Tentorial bridge apparently absent (actually present but extremely slender, threadlike) (*Platystethus*, *Oxytelus*, *Anotylus*).
9. Abdomen with pleural sclerites (*Homalotrichus*, *Bledius*; *Coprophilus* unknown).
10. Abdomen with spiracles in pleural sclerites (*Bledius*).
11. Body broad, onisciform (*Syntomium*).
12. Urogomphi strongly falcate (*Coprophilus*, *Homalotrichus*).
13. Urogomphi long, clubbed (*Oxypius*).

14. Ninth abdominal segment unusually small relative to eighth segment (*Oxypius*).
15. Numerous "frayed" setae present (*Oxypius*).

Note: The characterization of *Coprophilus* is based on Pototskaya (1967); all other genera have been examined.

Of the 15 apomorphies listed above, only two (nos. 4 and 5) are shared by *Oxypius* and one or more other oxyteline genera. In both of these cases, the synapomorphy is found in all oxyteline genera except *Homalotrichus* and probably *Coprophilus*, which have the plesiomorphic conditions of first maxillary palpal segment shorter than second and free labial palpi. However, *Oxypius* and *Syntomium* larvae have four ocelli on each side of the head, which is plesiomorphic relative to the three or fewer ocelli of all other oxyteline genera (no. 1). *Oxypius* and *Bledius* larvae have a probably plesiomorphic mandibular dentition (no. 2) relative to the two subapical mandibular teeth of all other oxyteline larvae. Larval evidence thus does not conclusively relate *Oxypius* to any other genus or group of genera of the Oxytelinae, although it does suggest that the genus is a relatively primitive member of the subfamily.

Three characters (nos. 13, 14, and 15) are tentatively considered autapomorphic for *Oxypius* larvae. Frayed setae (no. 15) are not found in other examined oxyteline larvae but do occur in some Piestinae (e.g., *Trigonurus*, *Nodynus*) and in some other staphylinid subfamilies, and their presence could possibly be a plesiomorphic condition. Larvae of *Euphania*, the sister genus of *Oxypius* based on adult structure (see above), are unknown. If the hypothesized sister-group relationship of *Oxypius* and *Euphania* is correct, then one or more of the autapomorphies (nos. 13, 14, and 15) known for *Oxypius* larvae may actually be synapomorphic for *Oxypius* and *Euphania*.

CONCLUSIONS

Although the subfamily placement of *Oxypius peckorum* is not intuitively obvious, cladistic analyses of both adult and larval characteristics lead to a similar conclusion: that the genus is a primitive member of the subfamily Oxytelinae. Inadequate knowledge of oxyteline larvae hampers further analysis

based on larval structure, but adult characters permit a precise placement of *Oxypius* relative to other oxyteline genera (fig. 41). The geographical and morphological isolation of *Oxypius* suggests great antiquity of the genus.

The phylogenetic conclusions represented by figure 41 indicate that Herman's (1970) tribal division of the Oxytelinae cannot be maintained without change. His tribe Coprophilini (see fig. 40) has no definite synapomorphies to justify its recognition as a monophyletic taxon. The placement of the Oxytelini as a relatively derived subgroup of the Coprophilini as advocated here (fig. 41) makes the Coprophilini paraphyletic. The problem might be solved in several ways, from dividing the subfamily into six or more tribes to completely eliminating tribal categories within the subfamily.

At present I believe there are too many uncertainties in the cladistic analysis of figure 41 (discussed above at the conclusion of that analysis) to justify any formal tribal reorganization until specialists on the Oxytelinae can evaluate and corroborate the conclusions presented here.

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