

EPIZOIC SYMBIOSIS: THE PAPUAN WEEVIL GENUS GYMNOPHOLUS (Leptopiinae) SYMBIOTIC WITH CRYPTOGAMIC PLANTS, ORIBATID MITES, ROTIFERS AND NEMATODES¹

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Abstract: The weevil genus *Gymnopholus* is significant because it includes species supporting growth of fungi, algae, lichens and liverworts, which in turn support oribatid mites, rotifers, nematodes, diatoms and other microorganisms. Most of the species supporting the symbiotic association on their backs represent a specialized section of the genus for which a new subgenus is established. They live on leaves of woody plants in moss forest or alpine shrubbery on New Guinea mountains. For fostering the plant growth, the upper surfaces are specially modified, with depressions and grooves, with specialized scales and hairs, and also a sticky secretion is apparently produced. At least 16 species (12 new) of the weevils are involved in this relationship, at least as far as the plants are concerned. Not all harbor the mites. This phenomenon may represent the first reported case of animals living in plants growing on terrestrial insects. For the entire genus, which is limited to New Guinea, 32 new species and 1 new subspecies are described to bring the total to 47, all of which are listed and keyed.

The weevil genus *Gymnopholus* is apparently confined to the mountains of the mainland of New Guinea (fig 1). It includes some of the largest Papuan weevils, and proves extremely interesting from several standpoints, but particularly in regard to symbiotic associations. It has recently been found that a number of species in the genus are hosts to various cryptogamic plants, including fungi, algae, lichens, liverworts and diatoms. These appear to represent the first records of lichens and liverworts on insects and of algae on terrestrial insects². The plants grow primarily on the fused elytra, and often also on the pronotum, rarely on parts of the femora. Living in the plants are oribatid mites (of a

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2. J. L. Gressitt, J. Sedlacek & J. J. H. Szent-Ivany, 1965, *Science* 150: 1833-35. Sir Boris Uvarov has kindly informed me that Ramachandra Rao reported the occurrence of algae on wings of *Schistocerca gregaria* Forsk in India (1940, *Ind. J. Ent.* 2: 93; 1960, *The Desert Locust in India*, p. 334).

new family described in the next paper) as well as rotifers and nematodes. Psocopterans appear to feed on the plants on the weevils. This may also be the first known case of animals living in plants growing on terrestrial insects.

History: Previous studies of this genus are few and limited. K. M. Heller described the genus and its synonym *Aroaphila* from southern Papua in 1901. The weevils were inadequately labelled, or had floated down the Aroa River. Heller named 10 species between 1901 and 1935, largely taken by Germans. Sir Guy Marshall, in 1959 (Bishop Mus. Occ. Pap. 22: 71-81), presented a review of the genus, describing 5 new species, and synonymizing one of Heller's. Evelyn Cheesman, C. A. W. Monckton, J. J. H. Szent-Ivany and I collected the species described by Marshall. He treated 13 species, but overlooked one of Heller's species. Thus 14 species have been recorded heretofore. The total now rises to 47 with the description herewith of 32 new species and 1 new subspecies. Szent-Ivany (1965, Trans. Papua & New Guinea Sci. Soc. 6: 28-31) treated altitudinal distribution of certain species.

Materials: Over 1400 specimens have been studied. Material reported upon here was taken by J. H. Barrett, W. W. Brandt, J. Carlyle, R. S. Carne, H. W. Clissold, Miroslav Erben, E. J. Ford Jr, J. L. Gressitt, Margaret K. Gressitt, D. E. Hardy, R. Hornabrook, B. R. Johnson, Ian Johnson, F. H. A. Kleckham, T. C. Maa, Sir Alan H. Mann, D. K. McAlpine, C. D. Michener, Guy Rosenberg, Josef Sedlacek, Marie Sedlacek, J. H. Sedlacek, Peter Shanahan, J. J. H. Szent-Ivany and J. S. Womersley. Paratypes are to be distributed to California Academy of Sciences (CAS), U. S. National Museum (USNM), British Museum, Nat. Hist. (BMNH), Leiden Museum (LEIDEN), Museum Zoologicum Bogoriensis (BOGOR), Dept. of Agriculture, Stock and Fisheries in Port Moresby (DASF), Australian Museum, Sydney (AM), and Australian National Insect Collection Canberra (ANIC).

The following symbols are used for the four quadrants of New Guinea: NE NG—Northeast New Guinea, SE NG—Southeast New Guinea (Papua), NW NG—Northwest New Guinea, SW NG—Southwest New Guinea (see fig 1). In measurements of the weevils, length is given from front of head with rostrum directed downward and the figure in parentheses is the length including the forward projecting rostrum.

Systematics: *Gymnopholus* belongs to the tribe Eupholini of the subfamily Leptopiinae (Leptopinae, Leptosinae). The subfamily is worldwide, but is primarily represented in tropical and subtropical regions. It includes over 1000 species. The tribe Eupholini is centered in the Papuan Subregion, extending into the Wallacean-Philippine area in the west and into western Polynesia in the east. *Gymnopholus* does not seem entirely homogeneous, but may represent a natural genus. The variety of form among the species is considerable, but in most cases there are intervening links. A new subgenus is described for most of the symbiotic forms and a few others. However, 2 or 3 more subgenera may be required. The available synonym does not apply to any of these. Intra-specific variation is also considerable. It is often difficult to determine if populations from different mountains ranges belong to the same or different species. Obviously populations have diverged to different degrees with different periods of isolation and with different environmental factors. The extent of differentiation in slightly differing localities suggests that speciation is proceeding very actively at present.

Dimorphism is conspicuous in certain species of the typical subgenus. This not only involves sexual dimorphism (very striking in *splendidus* and *gemmifer*), but dimorphism or

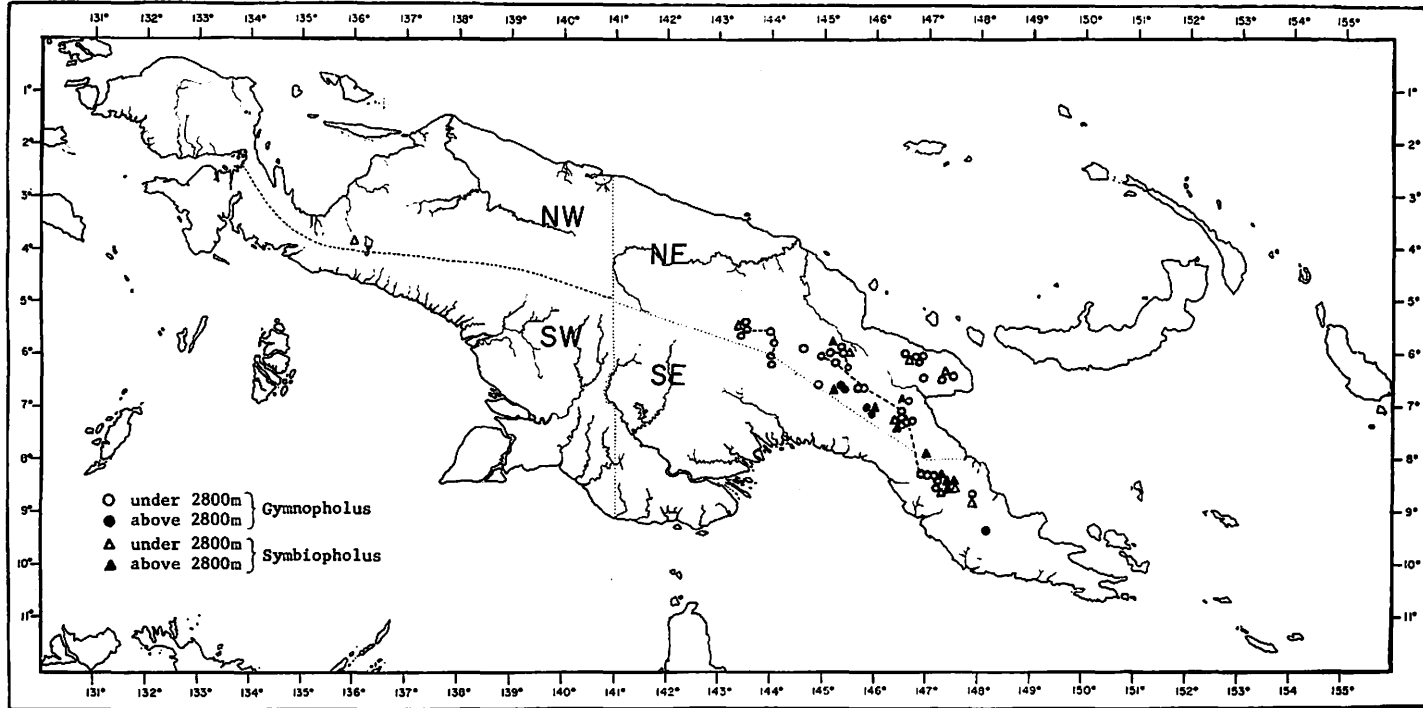


Fig. 1. Map of New Guinea showing occurrence of *Gymnopholus* species, with symbols indicating subgenus and high and medium altitude records. (See discussion of zoogeography in last part of paper.)

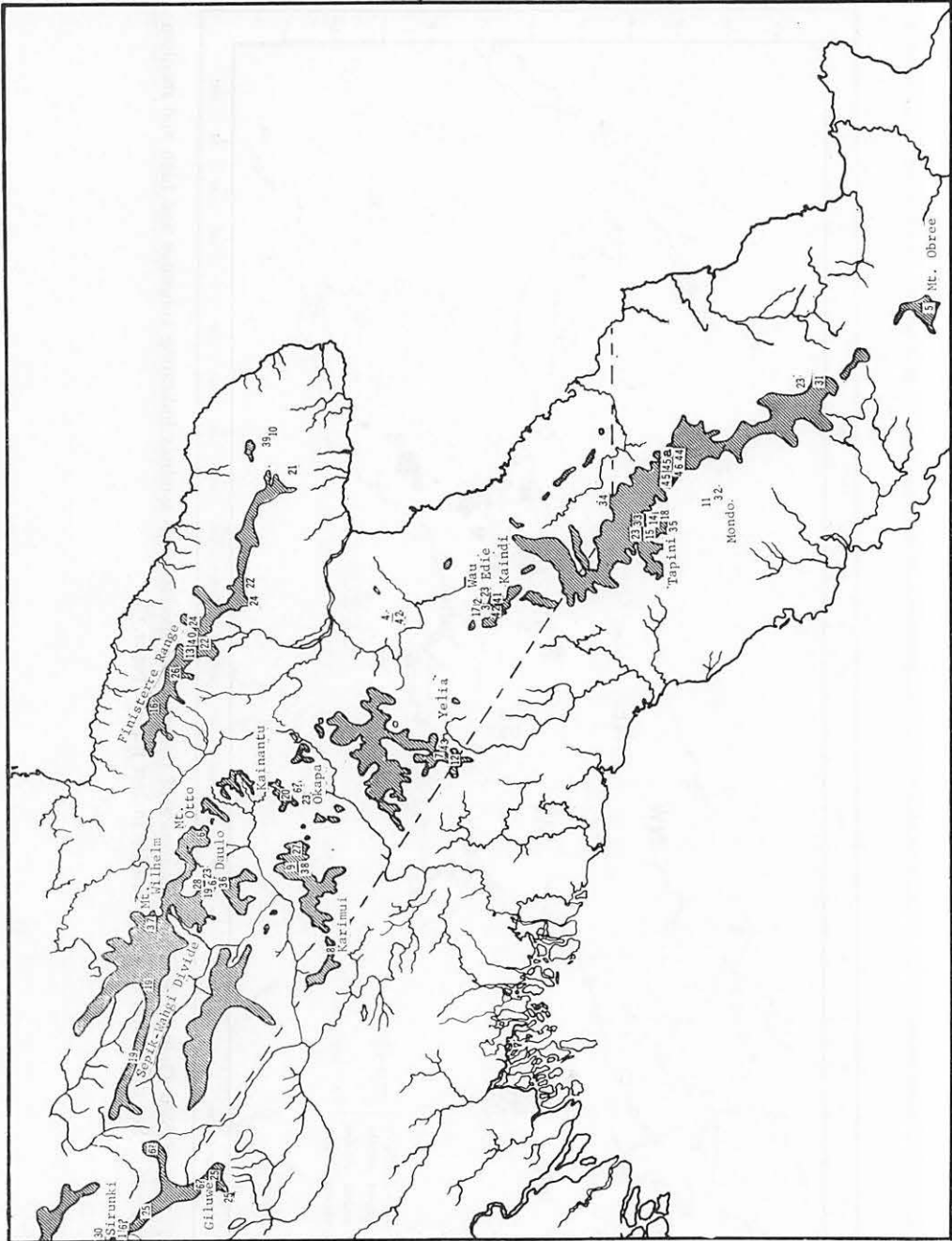


Fig. 2. Map of part of eastern New Guinea showing known occurrence of all but the single westernmost known species. The shaded areas are those above 2400 meters altitude. Numbers are those for the species in the list, key and text. (Map and contour line partly after Brass, 1964, Bull. Am. Mus. Nat. Hist. 127: 152 map insert.) (See latter part of present paper.)

trimorphism among the females (very striking in *marquardti* and *nothofagi*), and also among males (of *nothofagi*). There is very little dimorphism in *Symbiopholus*. Sexual dimorphism in the typical subgenus generally involves the females being much broader than males and being often extensively covered with scales whereas the males are largely glabrous. The differences within a sex involve the presence and absence of depressed areas bearing metallic scales. Where the areas are lacking, the surface has punctures, smooth surface, or minute setae like the rest of the surface, so it is not a question of scales-patches having been rubbed off.

Genus *Gymnopholus* Heller

Gymnopholus Hllr, 1901, Abh. Zool. Mus. Dresden 10 (2) : 8 (type: *G. weiskei* Hllr, monobasic); 1923, Kol. Rundschau 10 : 147.—Marshall, 1959, Bishop Mus. Occ. Pap. 22 (7) : 71.

Aroaphila Hllr, 1901, Abh. Zool. Mus. Dresden 10(2): 9 (type: *A. cyphothorax* Hllr, monobasic); 1913, Archiv Naturgesch. A 79 (1) : 45; 1923, Kol. Rundschau 10 : 147; 1937, Arb. Morph. Tax. Ent. Berlin-Dahlem 4 : 265.

The genus *Aroaphila* was reduced to subgeneric standing by Heller in 1937, and was reduced to a synonym by Marshall in 1959.

Characterized by large size, generally parallel-sided body with long rostrum and strong tubercles on pronotum and elytron.

Arrangement of species: The following arrangement is by tentative species-groups (roman numerals). The first species named in each group gives its name to the group. The attempt is made to arrange the species starting with the most generalized, and proceeding to the most specialized. Actually there is some parallelism in form between the *magister*-group of the typical subgenus and the *audax*-group of *Symbiopholus*, in that both are elongate, and lack pronotal tubercles. The *audax*-group occurs on the western fringe of the known range of the genus, partly at slightly lower altitude than the rest of the members of the subgenus, which almost uniformly support plant growth. There is the possibility that *Symbiopholus* may not be a natural grouping, and that the symbiotic relationship arose at different times in different stages of the ancestral line. However, none appear to be closely related to any of the species-groups of the typical subgenus, except as indicated by the similarity alluded to above between the *magister* and *audax* groups of the respective subgenera. These might represent the link between the two subgenera, and possibly in both cases the most primitive, although *nothofagi* appears to be the most generalized, and closest to the nearest known genera (*Eupholus*, *Rhinoscapa*).

Some additional material is not reported on here. This represents questionable populations appearing to differ to some extent from species which are here described.

A large collection made in the area of Mt Albert Edward by Mr and Mrs Sedlacek in November 1965 was received after the manuscript had been completed. This material represents at least 7 species and descriptions of 3 new species and 1 new subspecies have been added. These have been numbered from 44 to 46, so that the numbers are not entirely in the intended order, although the species are arranged in the intended order in the text and in the following list.

Subgenus *Gymnopholus* s. str.

- I 1. *nothofagi**—2. *urticivorax**
 II 3. *marquardti*—4. *mammifer**—5. *muscosus**—6. *gressitti*—7. *ajax**—8. *splendidus**—
 9. *gemmifer**—10. *carinatus*—11. *angustus*—12. *perspicax**
 III 13. *fulvospretus*—14. *cyphothorax*—15. *marshalli**—16. *suturalis*
 IV 17. *interpres*—18. *brandti**—19. *divaricatus**—20. *glochidionis**—21. *integrirostris*—
 22. *ludificator**
 V 23. *weiskei*—24. *regalis**—25. *sedlaceki**
 VI 26. *magister**—27. *hornabrooki**—28. *szentivanyi**

Subgenus *Symbiopholus*

- VII 29. *audax**—30. *praecox**
 VIII 44. *fallax**
 IX 31. *kokodae*
 X 32. *cheesmanae*—33. *algifer**—34. *symbioticus**—35. *zoarkes**
 XI 36. *reticulatus*—37. *botanicus**—38. *vegetatus**—39. *rugicollis*—40. *fungifer**—41. *lichenifer**—
 45. *h. herbarius**—45a. *h. oribatifer**
 XII 42. *acarifer**—43. *senex**—46. *hepaticus**

KEY TO SPECIES OF *GYMNOPHOLUS*

1. Dorsum dull, generally rough, with some hairs; pronotum generally with reticulations or pits between tubercles, rarely only with small nodes or a weak median groove; elytron generally with depressions, pits or coarse punctures, generally with one or two weak posterior tubercles; dorsum generally with specialized greenish scales and hairs in depressions, and at least in part clothed with lower plants (fungi, algae, lichens, liverworts) in all but newly emerged specimens; almost no sexual dimorphism (*Symbiopholus*) 2
 Dorsum shiny black, at least on ♂ elytron, which only rarely has limited coverage by scales; pronotum smooth, usually glabrous and with a pair of rounded tubercles; elytron largely smooth, largely glabrous, at most with sparse, generally weak punctures; dorsum usually without plant growth; often with considerable sexual dimorphism (*Gymnopholus* s. str.) 20
 2 (1). Scutellum visible, though small; segment 2 of funicle generally longer than 1 and 3 3
 Scutellum invisible; segment 2 of funicle shorter than 1; elytron dull, rugose; length 22 mm 31. *kokodae*
 3 (2). Pronotum lacking a pair of prominent swellings or ridges 4
 Pronotum with a pair of prominent swellings or ridges 5
 4 (3). Pronotum with distinct median groove and scattered shallow punctures; elytron dull but fairly smooth, with scattered weak wrinkles and punctures; elytral apex rounded obtuse; length 2.8 mm 29. *audax**
 Pronotum with weak median groove and scattered small nodes; elytron with

* Described as new.

- obtuse raised lines longitudinally and to some extent transversely, forming shallow irregular depressions, with scattered oblique bristles; elytral apex forming approximately a right angle; length 16-24 mm 30. **praecox***
- 5 (3). Prothorax no wider at side than width at tops of dorsal tubercles; femora rough: vermiculate, strigose or asperate..... 6
 Prothorax generally wider at side than at dorsal tubercles; femora generally smooth, at most weakly rugulose or asperate 10
- 6 (5). Pronotum with rough tubercles (carinate or reticulate), arched in side view ... 7
 Pronotum with smooth rounded tubercles, placed rather far forward, somewhat rectangular in side view; elytron somewhat wrinkled, with shallow depressions 9
- 7 (6). Elytron with gross pits scattered over most of surface; length over 30 mm..... 8
 Elytron with more than second 1/4 lacking deep pits and fairly even; length 30 mm or less..... 46. **hepaticus***
- 8 (7). Pronotum with long, subcarinate tubercles, evenly convex above and at side in cross-section (viewed from fore or aft); elytron with irregularly placed deep depressions; length 27 mm 42. **acarifer***
 Pronotum with rounded rugulose tubercles somewhat flattened above, slightly convex at side; elytron with depressions subregular; length 28 mm 43. **senex***
- 9 (6). Pronotum with a few weak wrinkles between tubercles; elytron fully as broad at middle as at base, with extreme apex barely extending beyond hind tubercle; dorsum with small short green scales with fine, seta-like apices; length 23-32 mm..... 33. **algifer***
 Pronotum coarsely wrinkled between tubercles; elytron widest at base, with extreme apex extending well beyond hind tubercle; dorsum with dense short recumbent setae; length 10-25 mm..... 32. **cheesmanae**
- 10 (5). Pronotal tubercles fairly close, separated by a weak or narrow depression; elytron with somewhat regular reticulation or deep depressions in longitudinal rows..... 12
 Pronotal tubercles widely separated by a broad obtuse or arcuate depression which is often quite deep; elytron with irregular depressions or widely spaced punctures..... 13
- 11 (10). Pronotal tubercles distinct, separated by a space as wide as top of a tubercle..... 11
 Pronotal tubercles nearly merged, separated by a narrow groove; elytron with rows of pits..... 38. **vegetatus***
- 12 (11). Reticulations often sharp on top of pronotal tubercles; elytron with depressions in regular longitudinal rows, and reticulations low and smooth; almost entire surface of elytron very hairy except for upper edges of reticulations; reticulations often white with waxy material..... 37. **botanicus***
 Reticulations generally blunt on pronotal tubercles; elytron with somewhat irregular reticulations, the ridges often high and fairly sharp; surface not conspicuously hairy, the hairs generally in lower parts of depressions 36. **reticulatus**
- 13 (10). Pronotum fairly smooth, somewhat shiny black, not conspicuously rugulose..... 14

- Pronotum strongly rugulose, sometimes pubescent in center 16
- 14 (13). Pronotal tubercles low, smooth, shiny; elytron with very large areas of dense erect hairs..... 15
- Pronotal tubercles high, punctured; elytron with rows of punctures, sparse hairs and small scale patches 44. *fallax**
- 15 (14). Elytron almost entirely pubescent, with frequent lichen growth, sometimes partly ridged longitudinally; pronotum rather closely punctured; length 20-24 mm..... 34. *symbioticus**
- Elytron largely glabrous, somewhat transversely wrinkled on central portion, at most with only 1 or 2 longitudinal ridges; pronotum feebly punctured; length 16-22 mm..... 35. *zoarkes**
- 16 (13). Elytron somewhat rugose, with irregular depressions and sometimes reticulations or areas of dense erect hairs; elytral apex somewhat blunt and subrounded, sometimes obtuse..... 17
- Elytron fairly even, with widely scattered subseriate pits and without reticulations; elytral apex obtuse 39. *rugicollis*
- 17 (16). Elytron with deep pits; pronotum more or less glabrous; elytron at most briefly pubescent 18
- Elytron lacking deep pits, but with dense erect pubescence posteriorly, as well as on pronotum..... 19
- 18 (17). Prothorax vertical at side; depression between pronotal tubercles deep and obtuse or subacute; elytral depressions mostly gradual, without distinct ridges or reticulations 40. *fungifer**
- Prothorax slightly narrowed above at side; depression between pronotal tubercles only moderately deep, somewhat arcuate; elytral depressions fairly deep and abrupt, with distinct ridges or reticulations in part..... 41. *lichenifer**
- 19 (17). Rostrum black, strongly widened anteriorly in central portion, moderately punctured; pronotum with red spine-like setae; elytron fairly smooth 45. *h. herbarius**
- Rostrum tawny orange, stout and subcylindrical in central portion, smooth and weakly punctured; pronotum with tawny spine-like setae; elytron rather uneven, generally with shallow depressions, wrinkles or corrugations 45a. *herbarius oribatifer**
- 20 (1). Pronotum without tubercles 21
- Pronotum with a pair of distinct tubercles, often high but sometimes low..... 24
- 21 (20). Dorsum without pubescent areas, generally very shiny, smooth and in part transversely wrinkled on elytron..... 22
- Dorsum often with greenish yellow to reddish pubescent spots of specialized scales in 2 bands, subbasal and postmedian; if entirely glabrous above, elytron is somewhat seriate-punctate and not transversely wrinkled... 1. *nothofagi**
- 22 (21). Posthumeral ridge not sharp, rounded in cross section; antenna generally pale... 23
- Posthumeral ridge sharp with side vertical; a weaker ridge extending to posterior tubercle; antenna pitchy red..... 28. *szentivanyi**
- 23 (22). Head very finely and closely punctured; pronotum with a single depression anterior to center; elytra fused; ♂ 21-25 mm 26. *magister**
- Head irregularly punctured; pronotum with a pair of depressions anterior to

- center; elytra often separated; ♂ 19-21 mm.....27. *hornabrooki**
- 24 (20). Pronotum with disc strongly raised but tubercles nearly fused, with a very weak median depression.....25
 Pronotum with a pair of distinct tubercles, strong or weak, with distinct median depression 26
- 25 (24). Elytral tubercle subacute, oblique on posterior side; antenna without conspicuous pale pubescence 23. *weiskei*
 Elytral tubercle blunt, very stout, transverse on posterior side; antenna with conspicuous silvery pubescence and long flying hairs..... 24. *regalis**
- 26 (24). Pronotum with a relatively small pair of tubercles, occupying less than 1/3 length of prothorax and usually separated by a space about as wide as diameter of one tubercle; dorsum generally with some areas of scales or pubescence in both sexes; elytron with a blunt tubercle.....27
 Pronotum with a pair of strong, high tubercles, lacking a flat area between; and generally sloping to base; dorsum generally glabrous in ♂, sometimes in both sexes..... 31
- 27 (26). Elytron with an oval or subtriangular subbasal area of orange or yellow pubescence or scales 28
 Elytron largely clothed with buff or metallic scales and hairs; body broad (♀)..... 29
- 28 (27). Pronotal tubercles very weak, about size of eyes; elytral patch orange, oval, of narrow scales; elytral tubercle prominent..... 3. *marquardtii* ♂
 Pronotal tubercles larger than eyes; elytral patch of yellow pubescence; elytral tubercle weak 5. *muscosus**
- 29 (27). Pronotal tubercles distinctly raised, larger than eyes; elytron with partly green and partly bronzy clothing.....30
 Pronotal tubercles very weak, about size of eyes; elytron with buff scales, denser on basal depression and posterior 1/2.....3. *marquardtii* ♀
- 30 (29). Elytron with scales largely golden green above, golden orange on apical declivity, with central portion largely smooth and glabrous.....8. *splendidus** ♀
 Elytron with scales largely golden bronzy, partly green, with central portion only in small part glabrous and distinctly grooved longitudinally...9. *gemmifer** ♀
- 31 (26). Elytron with some patches or discal stripes of scales..... 32
 Elytron smooth, glabrous in ♂ or with a straight sutural stripe..... 33
- 32 (31). Elytron with subbasal and lateral orange scale-patches and strong discal tubercle; length 19 mm..... 4. *mammifer**
 Elytron with some distinct, sinuate puncture-rows and weak ridges, a sinuate stripe of green scales in a shallow groove, and a partial similar stripe at side; length 16 mm.....2. *urticivorax**
- 33 (31). Hind femur smooth..... 34
 Hind femur asperate, rugulose or densely pubescent.....45
- 34 (33). Pronotal tubercles tapering and round at top, not overhanging externally; rostrum often grooved above 35
 Pronotal tubercles broad apically, overhanging externally; rostrum rarely grooved above 39
- 35 (34). Pronotal tubercles separated by a deep, subacute cleft; elytron with a blunt,

- nipple-like tubercle; body slender in ♂ 36
 Pronotal tubercles stout, separated by a shallow obtuse depression; elytron with a long acute tubercle; body fairly broad in both sexes 25. **sedlaceki***
- 36 (35). Rostrum grooved medially above 37
 Rostrum not grooved above..... 38
- 37 (36). Pronotal tubercles vertical externally, much broader at base than near apex, and much greater in anterior height than width of anterior collar ... 6. **gressitti**
 Pronotal tubercles slightly projecting externally, not much stouter basally than preapically, hardly taller than anterior collar is wide.....9. **gemmifer*** ♂
- 38 (36). Elytron evenly convex behind raised basal margin; terminal portion of aedeagus nearly as broad as long.....8. **splendidus*** ♂
 Elytron flat on base behind raised margin, strongly raised anterior to middle and subcarinate behind humerus; terminal portion of aedeagus very slender 7. **ajax***
- 39 (34). Scutellum generally longer than broad, usually glabrous or with green pubescence; elytron straight or weakly convex at side..... 40
 Scutellum twice as broad as long, densely clothed with white pubescence; elytron strongly convex at side with tubercle forming a right angle, and with 2 ridges and sutural stripe; length 25 mm 10. **carinatus**
- 40 (39). Depression between pronotal tubercles somewhat rounded; rostrum finely punctured, grooved medially.....41
 Depression between pronotal tubercles subacute or obtuse; rostrum somewhat heavily or closely punctured, flat above 42
- 41 (40). ♂ with small acute elytral tubercle; ♀ with stout blunt elytral tubercle and pale elytral scales 19. **divaricatus***
 ♂ with obtuse obsolete elytral tubercle; ♀ with short angulate elytral tubercle, glabrous..... 18. **brandti***
- 42 (40). Pronotal tubercles somewhat nipple-like, not as a rule evenly sloped behind ... 43
 Pronotal tubercles large, gradually sloping behind to base; rostrum closely and rugosely punctate; elytron narrow with very weak tubercle in ♂ and none in ♀ 22. **ludificator***
- 43 (42). Elytron of ♂ with a minute or obsolete obtuse tubercle; elytron of ♀ with tubercle forming more or less of a right angle, rarely projecting over elytral margin 44
 Elytron of ♂ with a small acute tubercle; elytron of ♀ with a projecting, nipple-like tubercle; rostrum closely impressed with punctures of different sizes, somewhat uneven above 20. **glochidionis***
- 44 (43). Rostrum with sparse large punctures and smaller punctures in between; elytron slender in ♂, with tubercle nearly obsolete; in ♀ somewhat broadened posteriorly, with tubercle distinct and projecting slightly..... 17. **interpres**
 Rostrum with close fine punctures; elytron subparallel, weakly broadened in ♀, with discal tubercle very weak in ♂, relatively weak in ♀...21. **integrirostris**
- 45 (33). Elytron with humeral angle weak, not projecting..... 46
 Elytron with humeral angle strong, projecting laterally 47
- 46 (45). Prothorax with a deep subapical constriction; elytron individually rounded at apex; venter with a broad median stripe of thick pale pubescence to end

- of sternite 2 14. *cyphothorax*
 Prothorax without a deep subapical constriction; elytra jointly rounded or
 acuminate at apex; venter with median stripe of sparse short pubescence;
 length 16-21 mm..... 11. *angustus*
 47 (45). Elytron with a diffuse sutural stripe or no sutural stripe.....48
 Elytron with a distinct sutural stripe in a depressed line and striae with fairly
 close punctures.....16. *suturalis*
 48 (47). Elytra jointly rounded-obtuse apically; femora nearly glabrous; pronotal tuber-
 cles subangulate.....49
 Elytra subtransverse apically; femora densely pubescent; pronotal tubercles
 broad, fairly low and rounded; dorsum very shiny black 12. *perspicax**
 49 (48). Pronotal tubercles subrounded in lateral view, obtuse in longitudinal view ...
 13. *fulvospretus*
 Pronotal tubercles squarish in lateral view, subacute in hind view, with deep
 depression between..... 15. *marshalli**

Subgenus *Gymnopholus* s. str.

Dorsum generally smooth, rarely clothed with metallic scales; very rarely wrinkled or hairy.

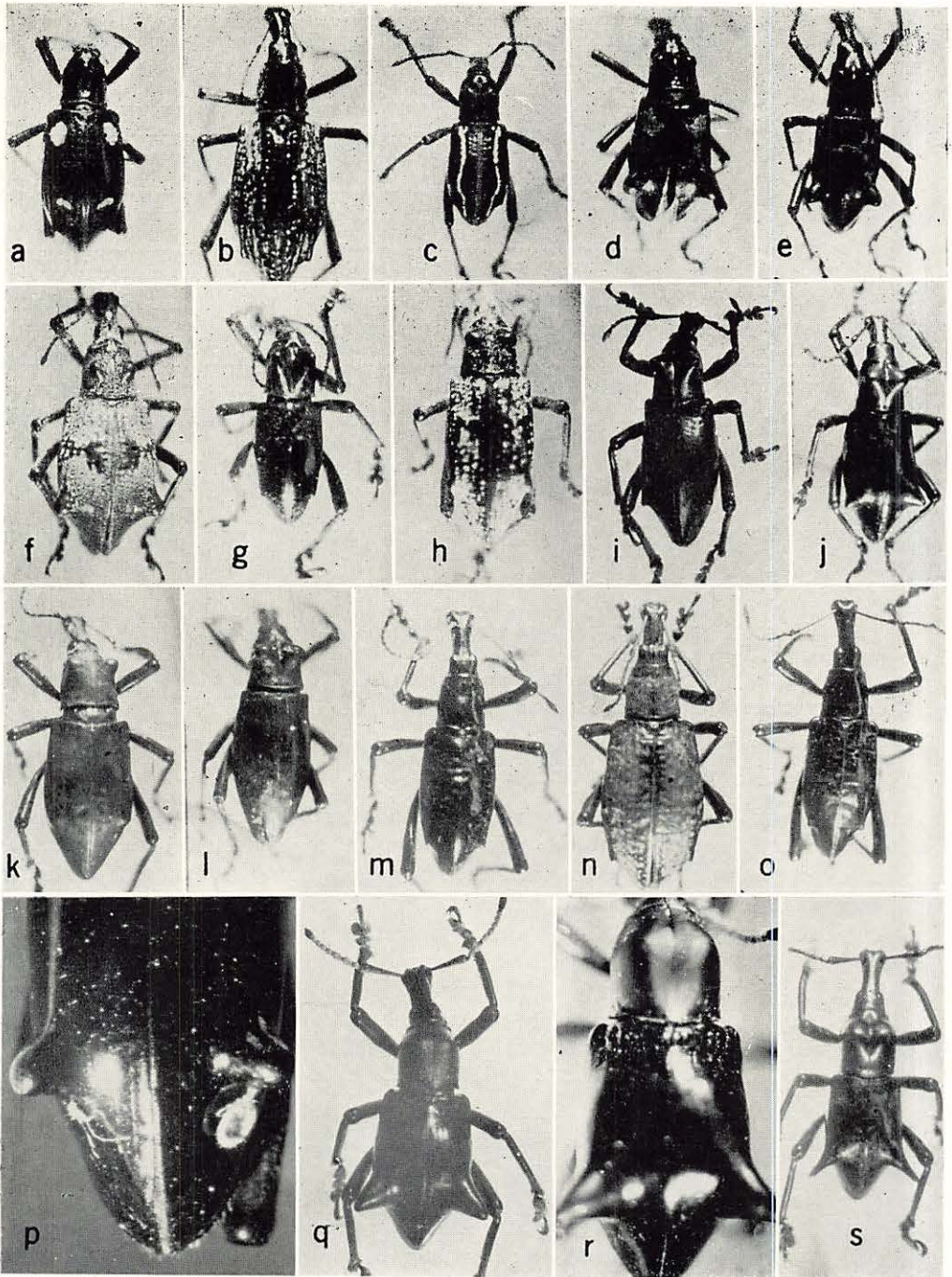
Nothofagi-group

This group is characterized by pronotal swellings almost obsolete and elytral tubercles weak; elytron often with pubescent or scaly areas.

1. *Gymnopholus* (*Gymnopholus*) *nothofagi* Gressitt, n. sp. Figs. 3ab, 5a, 14a.

♂. Shiny black; elytron with a depressed subrounded area of small dense thick golden red scales a short distance from basal margin, a similar, slightly raised oval area below humeral ridge and a shorter transverse patch before posterior tubercle, with a smaller patch external to it on upper portion of side. Dorsum otherwise nearly glabrous, but with finely scattered minute hairs on posterior portion of elytron; ventral surfaces more distinctly clothed with fine sparse pale hairs, mostly golden buff, but in part bluish on thoracic sterna; antenna moderately clothed with oblique hairs and with finer adpressed bluish hairs on funicle; legs moderately clothed with oblique pale hairs and with limited bluish or greenish scale-hairs on coxae and apices of tibiae and on tarsi.

Head 1/2 again as long as prothorax, distinctly narrower at apex of rostrum than at eye, hardly narrowed behind eyes and distinctly narrowed in front of eyes; rostrum parallel-sided in basal 1/3, strongly widened anteriorly, with a distinct median groove above and with a few scattered punctures. *Antenna* extending well beyond base of elytron, slender; scape nearly straight, swollen apically; funicle with segment 2 slightly longer than 1 and 3; club slender, fusiform, acute. *Prothorax* about as broad as long, subparallel-sided, but slightly widened at middle and slightly narrowed at apex and just behind middle; disc fairly even, smooth, finely and sparsely punctured, with a weak depression just anterior to center and another between center and base. *Scutellum* small, longer than



broad. *Elytron* nearly 3.5× as long as broad, with humerus rounded and slightly protruding, basal 1/2 subparallel-sided, then gradually narrowed to oblique apex; disc moderately convex, with subregular rows of moderate punctures and slight wrinkling or secondary punctures; a small distinct tubercle near top of apical declivity; sutural ridge with 2 weak swellings on apical declivity. *Ventral surfaces* fairly smooth, with widely scattered punctures; last sternite fairly flat and more closely punctured. *Legs* fairly slender; femora moderately punctured; hind tarsus with last segment nearly as long as 1+2. Length 17 mm (19.5 including rostrum); breadth 5.6.

♀. Similar to ♂ but broader, with scale patches golden yellow to greenish, and elytral disc smoother but with 3 weak longitudinal ridges. Length 22 (25) mm; breadth 8.8.

Paratypes. This species appears to have two forms in the ♂ and three forms in the ♀. More than half of the ♂♂ lack the pubescent spots on elytron. About half of the ♀♀ are likewise entirely black. A third form of ♀ has scattered metallic green scales along side of prothorax, and covering much of side of elytron and considerable part of outer 1/2 of dorsum of elytron. Sometimes body surface reddish pitchy instead of black. Length 16–28 mm; breadth 5–10 mm.

Holotype ♂ (BISHOP 6812), Lake Sirunki, 2500 m, between Wabag and Laiagam, W. Highlands, NE New Guinea, 16. VI. 1963, J. & M. Sedlacek; allotype ♀ (BISHOP), same data; 23 paratopotypes, same data; 4 paratopotypes, feeding on young foliage of *Nothofagus pulli*, VII. 1962, J. Womersley; 18 paratypes, Kepilam, 2450 m, 11 km SE of Laiagam, 22. VI. 1963, Sedlacek; 3, Laiagam, 2700 m, 19. VI. 1963, Sedlacek; 6, 11 km S of Laiagam, 2500 m, 24. VI. 1963, Sedlacek; 1, 6–12 km W of Wabag, 2020 m, 13. VI. 1963, Sedlacek.

Differs from *marquardti* Hllr in being more ovate, with more convex elytra, weaker posterior tubercle, and smooth pronotum.

A few of the individuals with elytral scale-patches have these covered with a dark red encrustment consisting of fungal growth. Rotifers occur in these fungal mats. This is the only species in the typical subgenus known to have this symbiosis. This species has polymorphism, as does *marquardti*, but though the structural differences are less contrasted, the ♂ has 2 forms and the ♀ has 3 distinct forms.

HOST: *Nothofagus pulli*.

2. *Gymnopholus* (*Gymnopholus*) *urticivorax* Gressitt, n. sp. Figs. 3c, 5d.

♂. Black; femora slightly reddish; elytra slightly tinged with reddish pitchy on central and postmedian portions. Head distinctly clothed with oblique pale hairs, longer anteriorly and shorter posteriorly; antenna moderately clothed with oblique palish hairs, very short on club; prothorax sparsely clothed with minute hairs; elytron largely glabrous but with a thin sutural stripe of minute bluish scales and scattered oblique pale hairs, median portion with a sinuate distinct groove completely filled with dense golden-green scales;

Fig. 3. a, *Gymnopholus nothofagi* n. sp. ♀; b, same; c, *G. urticivorax* n. sp. ♂; d, *G. mammifer* n. sp. ♂; e, *G. ajax* n. sp. ♂; f, *G. gemmifer* n. sp. ♀; g, *G. marshalli* n. sp. ♂; h, *G. interpres* Hllr ♀; i, *G. brandti* n. sp. ♀; j, *G. glochidionis* n. sp. ♀; k, *G. integrirostris* Hllr ♀; l, *G. ludificator* n. sp. ♀; m, *G. magister* n. sp. ♂; n, *G. hornabrooki* n. sp. ♀; o, *G. szentivanyi* ♂; p, *G. gressitti* Mshl ♂ with nymph and full-fed erythraeid mite (*Leptus* sp.) behind left and right elytral tubercles, respectively; q, *G. regalis* n. sp. ♀; r, same; s, *G. sedlaceki* n. sp. ♂.

side with 3 irregular similar marks which are less deeply impressed; apical declivity thinly clothed with blue scales and scattered oblique pale hairs; ventral surfaces with golden-green scales on parts of thoracic sternites and parts of sides of abdominal sternites, remainder moderately clothed with recumbent to slightly raised pale hairs; legs moderately clothed with oblique pale hairs, some blue scales on inner sides of femora and tibiae and on bases of femora.

Head slightly longer than prothorax, parallel-sided in central portion, shallowly grooved on upper portion of rostrum and rather deeply and subreticulately punctured. *Antenna* reaching beyond base of prothorax, moderately slender; scape as long as next 5 segments combined, fairly slender but distinctly swollen at apex; funicle with segment 2 distinctly longer than 1, following distinctly shorter; club slender and fusiform. *Prothorax* distinctly longer than broad, slightly sinuate at side; disc with a moderate tubercle on each side, separated by a distinct groove, area between tubercles obtuse in anterior view, anterior portion of thorax slightly constricted behind anterior margin, deeply depressed on median line not far from apex; surface somewhat irregular, distinctly punctured throughout and with some vertical wrinkles at side. *Scutellum* distinct, with dull pubescence. *Elytron* distinctly longer than head and prothorax combined, subparallel, slightly widened behind middle, narrowed and blunt apically; a rather weak tubercle behind middle, forming continuation of weak ridge on interstice 5, another weak ridge arising from humerus and continuing along interstice 7 to behind middle; other interstices slightly irregular, submedian sinuous depressed stripe largely on interstice 4; punctures irregular, fairly widely spaced, in part quite distinct; interstice 1 with irregular fine punctures; posterior declivity somewhat irregular, suture moderately raised to a short distance before apex. *Ventral surfaces* finely punctured to somewhat vermiculate or rugose. *Legs* asperate punctate to granulose or nodose; hind tarsal segment 1 longer than 3 and shorter than last. Length 15.6 mm (18 including rostrum); breadth 6.

♀. Similar to ♂ but broader; pronotal tubercles a little more widely separated. Length 21 (24) mm; breadth 9.

♂ Paratypes. Pale stripes sometimes nearly white; pronotal tubercles sometimes slightly rounded at top. Length 16-18 (18-21) mm; breadth 6.5-7.2.

Holotype ♂ (BISHOP 6813), Wau, 1400-1500 m, Morobe Distr., NE New Guinea, 20. XII. 1961, J. Sedlacek; allotype ♀ (BISHOP), Mt Missim, nr Wau 1350 m, 16. I. 1962, Sedlacek; 2 paratopotypes, 1300 m, 25. VI. 1961, 20-26. V. 1962, Sedlacek.

Differs from *fulvospretus* Hillr in being smaller, with pronotal swellings much lower, more rounded, and elytron with a nearly complete sinuous groove along middle with close metallic scales, and some short, irregular sublongitudinal similar marks on side.

HOST: *Laportea* sp.

Marquardtii-group

This group is characterized by erect pronotal tubercles and fairly erect nipple-like elytral tubercles. The ♀♀ are often partly clothed with metallic scales.

3. *Gymnopholus* (*Gymnopholus*) *marquardtii* Heller Fig. 5c.

Gymnopholus marquardtii Hillr, 1935, Nova Guinea, Zool. 17 (2): 179, fig. 18 (NE NG: Edie

Creek; DRESDEN).—Mshl, 1959, Bishop Mus. Occ. Pap. 22 (7): 76.

The species has remarkable dimorphism in the ♀. Some are similar to the ♂ except for larger size and greater breadth, but most individuals have a very different appearance, being about twice as wide as ♂♂ and almost entirely covered with buff or reddish brown scales. Elytral tubercle of ♀ stouter than in ♂. Length 16–29 mm.

NE NG: Many specimens from Edie Creek, Mt Kaindi and Bulldog Road, 2100–2500 m, V, VII, VIII, X. 1962–64, J. and J. H. Sedlacek and Shanahan. Two large specimens from near Okapa, XII. 1964, V.1965, Hornabrook, are possibly this species.

4. *Gymnopholus (Gymnopholus) mammifer* Gressitt, n. sp. Figs. 3d, 5d.

♂. Body entirely black; elytron with a subbasal irregular shaped depressed area covered with reddish orange narrow scales, and another similar smaller area external to it on lower part of side; dorsum otherwise glabrous except for a few short reddish hairs on apical declivity, particularly on sutural tubercle; ventral surfaces feebly clothed in part with pale oblique hairs; legs with femora nearly glabrous, tibiae and tarsi well clothed with oblique goldish hairs; antenna sparsely clothed with pale whitish golden hairs.

Head a little longer than prothorax, about as broad at end of rostrum as at eyes; rostrum cylindrical basally, gradually widening to apex, with almost no trace of grooves above and with rather feeble sparse punctures. *Antenna* reaching well beyond humerus, fairly slender; scape moderately thickened at apex; funicle with segment 2 slightly longer than 1 and 3. *Prothorax* slightly broader than long, gradually narrowed from base to apex, a little strongly narrowed at extreme apex; disc with a pair of moderately strong nipple-like tubercles directed somewhat outward and slightly overhanging externally; median groove wide, obtusely arcuate, somewhat more depressed between tubercles and anterior margin. *Scutellum* about as long as broad, somewhat pubescent. *Elytron* about 3× as long as broad; humerus projecting somewhat forward; margin fairly straight at side in basal 1/2, subevenly narrowed posteriorly to obtusely rounded apex; discal tubercle very large, nipple-like; a distinct ridge behind humerus; side subvertical; disc somewhat uneven, depressed subbasally, with some wrinkles along suture and median portion and some slight corrugations at side; suture distinctly raised on apical declivity at two points, second point opposite a moderately large low node near external margin. *Ventral surfaces* moderately shiny, sparsely and feebly punctured. *Legs* moderately slender; hind femur straight, feebly punctured; hind tibia nearly straight, more strongly punctured; last hind tarsal segment as long as 1+2. Length 20.8 mm (24 including rostrum); breadth 9.4.

Holotype ♂ (BISHOP 6814), Mt Shungol, 2400 m, nr Lae, NE New Guinea, XI.1953, Miroslav Erben (ex DASF); paratype ♂, Bome, 1950 m, Goilala, Owen Stanley Range, SE NG, 24.II–7.III.1958, Brandt.

Differs from *marquardti* Hillr in being stout in ♂, with pronotal tubercles much higher and elytron more carinate at side.

5. *Gymnopholus (Gymnopholus) muscosus* Gressitt, n. sp. Figs. 4a, 5e.

♂. Shiny black, with paler, somewhat waxy appearance on tops of tubercles and along sutural portion of elytra. Body practically glabrous above except for a depressed, irregularly shaped patch of dense sulphur yellow pubescence near base of elytron and a similar

oval one at side behind humerus; ventral surfaces with some fine pale pubescence on thoracic sternites; legs with sparse oblique pale hairs; antenna with very few hairs and with very thin pubescence on club.

Head distinctly longer than prothorax, slightly wider at eyes than at end of rostrum and somewhat narrower than at occiput; rostrum somewhat gradually widened from base to near apex, with a fairly distinct median groove for entire length, and a short elliptical groove on upper portion of side, with surface moderately punctured; occiput nearly impunctate. *Antenna* with scape shorter than funicle, somewhat gradually widened to apex; funicle with first 3 segments subequal in length; club subfusiform, slightly constricted at ends of segments, subacute apically. *Prothorax* barely longer than broad, subparallel in basal 3/4, then slightly narrowed anteriorly and distinctly constricted a short distance from apex, the constriction curving posteriorly around bases of tubercles and ending in a depressed area anterior to center; tubercles relatively low, broadly rounded, situated well anterior to middle, rounded externally and depression between them arcuately concave; surface weakly wrinkled in median depression, behind tubercles and on lower portion of outer side. *Scutellum* broader than long. *Elytron* fully 3× as long as broad, with humerus rounded and very slightly projecting, side very slightly widened behind humerus and then gradually narrowed to fairly narrowly rounded apex; a fairly small rounded tubercle at top of apical declivity and a more rounded obtuse one slightly closer to extreme apex than to preceding tubercle; surface moderately smooth, with some incomplete rows of widely spaced punctures and some weak wrinkles along median portion and weaker ones in other areas; a weak ridge extending for a short distance behind humerus and side nearly vertical. *Ventral surfaces* fairly smooth, very weakly punctured. *Legs* moderately slender; femora feebly punctured; hind tibia straight and suddenly expanded at apex; last hind tarsal segment nearly as long as 1+2. Length 20.5 mm (24 including rostrum); breadth 7 mm.

Holotype ♂ (BISHOP 6815), Mt Obree, 3075 m, 80 km E of Port Moresby, C. Distr., SE New Guinea (Papua), in rainforest, 22. VII. 1963, G. Rosenberg.

Differs from *marquardtii* Hillr in being longer, with elytron more narrowed posteriorly and much less strongly tuberculate, and with pronotal tubercles stronger and with disc more wrinkled between them.

6. *Gymnopholus* (*Gymnopholus*) *gressitti* Marshall Figs. 4b, 7a.

Gymnopholus gressitti Mshl, 1959, Bishop Mus. Occ. Pap. 22 (7): 77, fig. 4a (Daulo Pass, Asaro-Chimbu Divide, NE NG; BMNH).—Szent-Ivany, 1965, Trans. Papua & New Guinea Sci. Soc. 6: 29.

♂. Slender, parallel-sided, with fairly tall, rounded parallel tubercles on pronotum and prominent nipple-shaped tubercle on elytron; black with often a coppery stripe of V-shaped mark on apical elytral declivity. ♀. Broader, slightly widened in middle, with tubercles similar to those of ♂; entirely black, or with extensive speckling with tan or whitish scales, or with incomplete greenish and bronzy stripes or with 1 or 2 incomplete discal bands of transverse spots of greenish, whitish or coppery edged with greenish scales.

ADDITIONAL MATERIAL. NE NG: Daulo Pass, VI.1955, Gressitt, 4.VII.1957, D. E. Hardy, 2.V.1959, C. D. Michener, 15. V. 1963, Sedlacek; Nenguag, 2200 m, Asaro-Chimbu Divide,

28.VI.1955, Gressitt; 6, Mt Otto, 2200 m, 22-24.VI.1955, Gressitt; 1, Keglsugl, 2500-2720 m, Mt Wilhelm, 1. VII. 1963; 1, 16 km NW of Banz, 1700-2100 m, 28. VI. 1963, Sedlacek; 1, Tambul, 2200 m, NW of Mt Giluwe, 26. V. 1963, Sedlacek; 1, Purosa, 1800-2000 m, nr Okapa, 28. VIII. 1964; 20, Tomba, 2500-2650 m, slope of Mt Hagen, 24. V. 1963, Sedlacek. SE NG: 1, Dimifa, 2200 m, SW of Mt Giluwe, 10.X.1958, Gressitt; 18, Mt Giluwe, 2500-2750 m, 27.V-1.VI.1963, Sedlacek.

7. *Gymnopholus* (*Gymnopholus*) *ajax* Gressitt, n. sp. Figs. 3e, 4c, 5g.

♂. Shiny black; dorsum practically glabrous; venter shiny, with only a very few minute hairs posteriorly; legs with femora glabrous, tibiae with rather few golden oblique hairs and tarsi thinly clothed above.

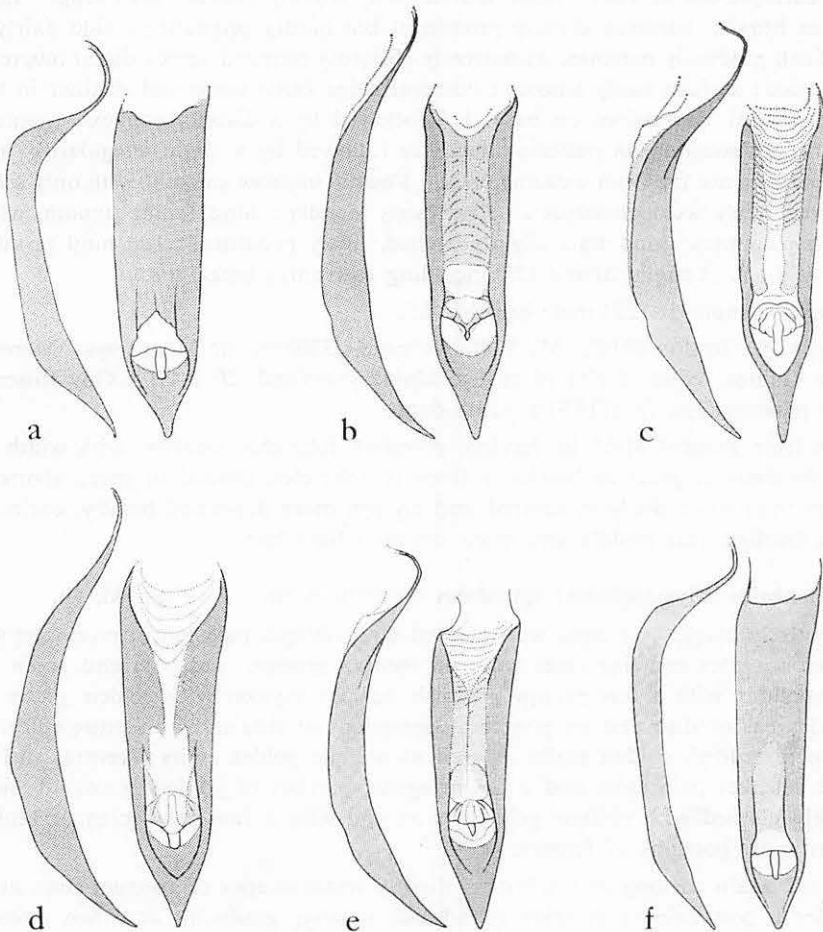


Fig. 4. Aedeagi, side view left, hind (dorsal) view right: a, *Gymnopholus muscosus* n. sp.; b, *G. gressitti* Mshl; c, *G. ajax* n. sp.; d, *G. splendidus* n. sp.; e, *G. gemmifer* n. sp.; f, *G. perspicax* n. sp.

Head 1/3 again as long as prothorax, slightly narrower at apex of rostrum than at eyes, very slightly narrowed behind eyes and then broadened; rostrum subcylindrical in basal 2/5, subevenly broadened apically; upper surface fairly even, without grooves, rather finely, irregularly and indistinctly punctured. *Antenna* reaching well behind humerus; scape nearly straight, somewhat gradually thickened to apex; funicle with segment 2 as long as 1 and slightly longer than 3; club somewhat unevenly fusiform. *Prothorax* about as broad as long, somewhat gradually narrowed from base to apex and slightly constricted between base and middle; disc with a pair of fairly strongly elevated rounded tubercles, more or less vertical externally and rounded-obtuse between; median groove slightly depressed between anterior portions of tubercles; anterior collar not very well defined, slightly swollen on each side of middle; surface fairly smooth and even, with very vague shallow punctures in parts of median depression but for most part apparently punctate; a few very weak vertical corrugations at side. *Scutellum* swollen, slightly broader than long. *Elytron* 3× as long as broad; humerus slightly prominent but hardly projecting; side fairly straight and vertical, gradually narrowed to narrowly obliquely rounded apex; discal tubercle strong, nipple-shaped; surface fairly smooth; humeral ridge fairly sharp and distinct in basal 1/3, a distinct discal depression on basal 1/5 followed by a distinct convexity, sutural ridge with a distinct swelling on posterior declivity followed by a slight irregularity and a low node on surface not far from extreme apex. *Ventral surfaces* smooth, with only a few widely scattered fairly weak punctures. *Legs* fairly slender; hind femur smooth, with only a few weak punctures; hind tibia slightly arched, finely punctured; last hind tarsal segment as long as 1+2. Length 20 mm (24 including rostrum); breadth 8.

Paratype. Length 18 (22) mm; breadth 7.5.

Holotype ♂ (BISHOP 6816), Mt Yelia Volcano, 3300 m, nr Menyamya, Morobe Distr., NE New Guinea, edge of rim of crater, alpine grassland, 20. I. 1963, Guy Rosenberg (ex DASF); paratopotype ♂ (DASF), same data.

Differs from *gressitti* Mshl in having pronotal tubercles weaker, with width of collar anterior to them as great as height of front of tubercles, instead of much shorter, and in having rostrum more finely punctured and elytron more depressed basally, carinate behind humerus, swollen near middle and more stoutly tuberculate.

8. *Gymnopholus (Gymnopholus) splendidus* Gressitt, n. sp. Figs. 4d, 5h.

♀. Entirely black. Antenna well clothed with oblique pale hairs; pronotum with some pale narrow scales and fine erect hairs on median groove, and pale and green scales at side; scutellum with a few narrow greenish scales; elytron with golden green scales on depressed areas of disc and on puncture-depressions at side and with entire apical declivity clothed with reddish golden scales as well as oblique golden hairs; ventral surfaces with scattered suberect pale hairs and a few irregular patches of golden scales at sides; legs moderately clothed with oblique goldish hairs and with a few pale green or bluish brown scales on upper portions of femora.

Head 1/2 again as long as prothorax, slightly wider at apex of rostrum than at eyes and still wider at postoccipt; rostrum cylindrical basally, gradually and then more strongly widened anteriorly, flattish and very weakly depressed medially above with a short groove near base of upper side; surface with moderately sparse fine punctures. *Antenna* reaching to humerus; scape straight, thickened apically; funicle with segment 2 much longer than

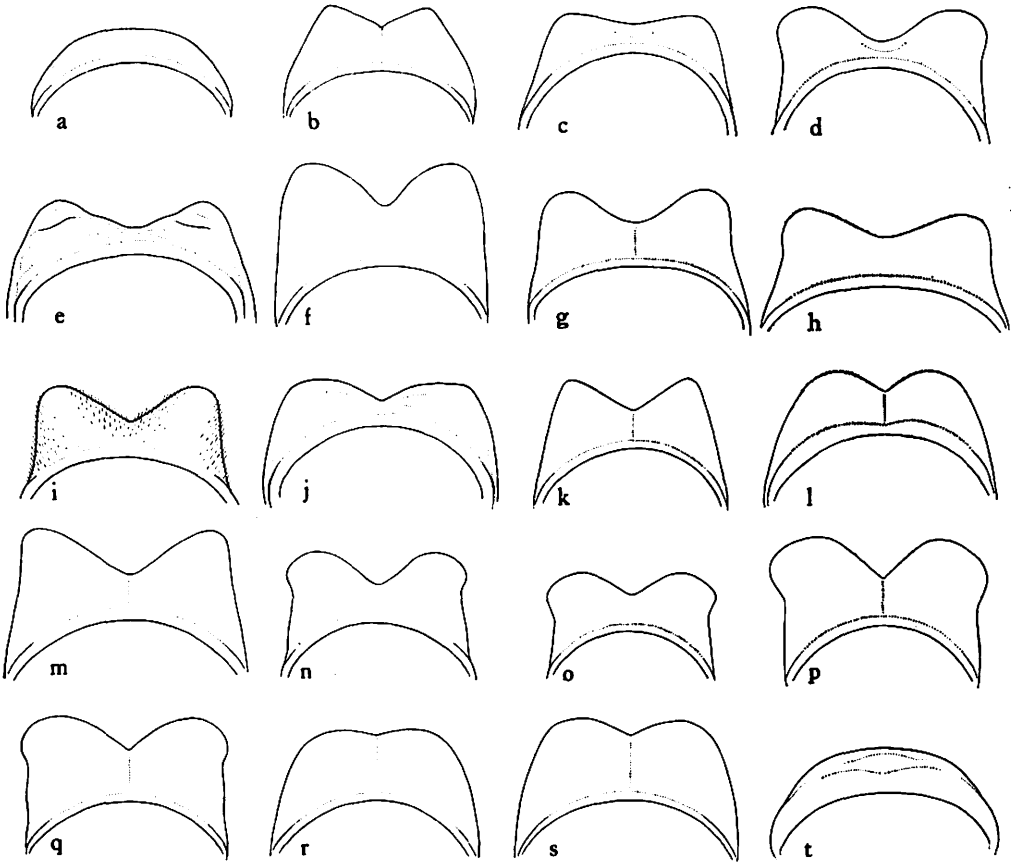


Fig. 5. Dorsal outline of pronotum viewed from behind: a, *Gymnopholus nothofagi* n. sp.; b, *G. urticivorax* n. sp.; c, *G. marquardtii* Hllr; d, *G. mamifer* n. sp.; e, *G. muscosus* n. sp. ♂; f, *G. gressitti* Mshl ♂; g, *G. ajax* n. sp. ♂; h, *G. splendidus* n. sp. ♀; i, *G. gemmifer* n. sp. ♀; j, *G. perspicax* n. sp. ♂; k, *G. fulvospretus* Hllr; l, *G. cyphothorax* Hllr; m, *G. marshalli* n. sp.; n, *G. interpres* Hllr ♂; o, *G. brandti* n. sp. ♂; p, *G. integrirostris* Hllr ♂; q, *G. ludificator* n. sp. ♂; r, *G. weiskei* Hllr ♀; s, *G. sedlaceki* n. sp. ♀; t, *G. magister* n. sp. ♂.

1 or 3; club slender and subfusiform. *Prothorax* slightly broader than long, subparallel-sided in basal 3/4 but slightly broadened at extreme base, distinctly narrowed apically; disc with a pair of strong stout rounded tubercles placed just anterior to middle, subvertical and slightly sinuate externally, broadly obtusely rounded-concave between; a distinct depression between anterior portions of tubercles and a slight depression on each side between tubercle and anterior margin; surface rather finely punctured, otherwise fairly smooth. *Scutellum* slightly broader than long. *Elytron* about 3.5× as long as broad; humerus obtusely rounded, slightly projecting; side fairly straight and vertical, subevenly narrowed to extreme apex at suture; a large stout rounded tubercle on top of apical declivity; suture raised twice on apical declivity with a weak swelling external to second swelling on suture, the external swelling continuing anteriorly as a broad weak ridge

parallel to external margin, becoming weaker on side; surface with distinct rows of depressions at side and on outer part of central portion of disc, with a depressed area coinciding with scale covered area on basal portion, sutural unscaled portion broadened at center and continuing posteriorly as a weak ridge following vestigial second puncture row; a similar weak ridge commencing in basal depression and extending to discal tubercle. *Ventral surfaces* fairly smooth, in part finely and sparsely punctured. *Legs* finely and sparsely punctured, weakly asperate on hind tibiae; last hind tarsal segment longer than 1+2. Length 26 mm (29 including rostrum); breadth 12.7.

Paratype ♀. Metallic scales on dorsum slightly more extensive in coverage, on elytron forming an only slightly interrupted median stripe. Length 25 (28) mm; breadth 11.7.

♂. More slender; black to gray; pronotal and elytral tubercles nipple-like. Length 19.5 (23) mm; breadth 7.5. Paratype, length 16 (19.5) mm; breadth 6.7.

Holotype ♀ (BISHOP 6817), Mt Karimui, NE New Guinea (S of Goroka; adjacent to border to SE NG), mossy forest, 2400 m, 30. XII. 1963, Miroslav Erben; allotype ♂ (BISHOP), same data; ♂ and ♀ paratypes (DASF), same data.

Differs from ♀ *gressitti* Mshl in being stouter, with much of dorsum clothed with metallic golden green and red-gold scales, and with pronotal tubercles lower and elytron more punctured.

9. *Gymnopholus (Gymnopholus) gemmifer* Gressitt, n. sp. Figs. 3f, 4e, 5i.

♀. Body entirely black. Dorsum largely clothed with metallic scales except for tops of tubercles, a large common triangular area on basal 1/2 of elytra and some smaller raised areas across middle of elytron, and humerus; scales not completely covering surfaces but in most cases covering more than 1/2 of space with small bare spaces between scales or between patches of scales; scales pearly pink on head, pale green to coppery on pronotum, green-gold and red-gold on elytral disc and largely pink to orange-gold on apical declivity; ventral surfaces irregularly clothed with pale pinkish scales and a few sparse erect pale hairs; legs unevenly clothed with pinkish and pale green scales and some oblique pale hairs; antenna with pinkish to greenish scales on scape and oblique golden hairs on scape and funicle.

Head 1.6× as long as prothorax, as broad at end of rostrum as at eyes, broader at postocciput; rostrum subcylindrical in basal 2/5, gradually widened anteriorly, flattish and very feebly grooved medially with a short groove on upper side, and surface moderately punctured. *Antenna* just reaching past humerus; scape straight, thickened at apex; funicle with segment 2 slightly longer than 1 and distinctly longer than 3. *Prothorax* slightly broader than long, parallel-sided at middle, somewhat widened to base and narrowed to apex; disc with a pair of moderately strong rounded tubercles with intervening space rounded-obtuse and outer side fairly straight and subvertical; median groove deepened between tubercles and raised anterior marginal strip; surface rather closely punctured. *Scutellum* broader than long. *Elytron* not quite 3× as long as broad; humerus oblique and slightly projecting; side moderately straight and nearly vertical, gradually narrowed to extreme apex; disc slightly depressed before and behind middle, carinate behind humerus and with some rows of depressions on outer part of disc and at side, other areas with very weak depressions or slight longitudinal grooves; tubercle

quite large, strongly raised and rounded at apex; apical declivity with a fairly strongly raised point on suture and a weaker rise below this on suture and another external to it a short distance from apex. *Ventral surfaces* in part finely punctured and slightly irregular. *Legs* long; femora weakly asperate-punctate; hind tibia slightly sinuate, weakly asperate; last hind tarsal segment barely as long as 1+2. Length 24 mm (27.5 including rostrum); breadth 11.5.

♂. Much more slender; lacking metallic scales; elytral tubercle less stout. Length 19.5 (23) mm; breadth 9.2.

Paratypes. ♀ apparently occurring in several forms, some glabrous, some with patches of scales, and one with very short elytral tubercle. Length 19-25 (23-31) mm; breadth 8.2-12.

Holotype ♀ (BISHOP 6818), Mt Michael, 3000-3300 m, S of Goroka, E. Highlands, NE New Guinea, 23.XII.1964, R. Hornabrook; allotopotype ♂ (BISHOP), same data; several paratopotypes (BISHOP, DASF, Hornabrook coll.), same data.

Differs from *gressitti* Mshl in being stouter, with tubercles less erect, and dorsum much more extensively scaled, in ♀ and with elytron less smooth, and somewhat shorter.

10. *Gymnopholus* (*Gymnopholus*) *carinatus* Heller

Gymnopholus (*Aroaphila*) *carinatus* Hllr, 1937, Arb. Morph. Taxon. Ent. Berlin-Dahlem 4 (4): 265, fig. G (Finschhafen; DRESDEN).

This species was omitted from Sir Guy Marshall's paper. Presumably it was collected from the mountains inland from Finschhafen, as I have seen no specimens of the genus definitely taken at sea level, or for that matter from below about 1000 meters altitude. It is only tentatively assigned to this species group.

11. *Gymnopholus* (*Gymnopholus*) *angustus* Marshall Fig. 7b.

Gymnopholus angustus Mshl, 1959, Bishop Mus. Occ. Pap. 22 (7): 80, fig. 5 bc (Papua: Mondo; BMNH).

This species somewhat resembles *gressitti* and *cyphothorax*, but has lower pronotal tubercles. It resembles members of the *interpres*-group. Length 16-21 mm.

SE NG: 4, between Murray Pass and Waitape, 2550-2060 m, 11.XI.1965, J. & M. Sedlacek.

12. *Gymnopholus* (*Gymnopholus*) *perspicax* Gressitt, n. sp. Figs. 4f, 5j.

♂. Shiny black above and below. Dorsum nearly glabrous, a few minute hairs on apical declivity of elytron; antenna with only a few hairs except for pubescence on club; ventral surfaces largely glabrous, some fine hairs on coxae and apical portion of last abdominal sternite; femora with some dense pubescence and short erect hairs on preapical portions and upper part of central portions; tibiae moderately clothed with oblique goldish hairs and a little bluish pubescence at apices; tarsi with sparse pale hairs above and thin bluish pubescence.

Head slightly longer than prothorax, width at eyes slightly greater than at end of rostrum

and slightly less than at occiput; rostrum subparallel-sided in basal $2/5$, strongly widened towards apex; a deep longitudinal groove extending for entire length and as far as posterior margins of eyes, an additional distinct groove on side of upper portion; surface irregularly punctured, somewhat coarsely so at side of rostrum and finely so at apex. *Antenna* with scape distinctly shorter than funicle, widened at apex; funicle with segment 2 distinctly longer than 1 and 3; club fairly stout at middle, subacute apically. *Prothorax* slightly longer than broad, subparallel-sided in basal $3/4$, very slightly expanded at extreme base, narrowed and constricted before apex; disc with a pair of fairly low broadly rounded tubercles situated well anterior to middle, outer side somewhat convex and smooth, depression between tubercles rounded-obtuse, a distinct depression between anterior portions of tubercles and slightly raised anterior collar; surface very smooth, only minutely punctured. *Scutellum* broader than long, truncate apically, finely punctured. *Elytron* $3.5\times$ as long as broad, with humerus obtuse and slightly projecting, sides slightly widened behind humerus then weakly convex at side and gradually narrowed to externally rounded apex; elytral tubercles small, located only about $1/6$ length from apex, followed by a depression and then by a large convex node which is much larger and slightly higher than preceding tubercle; sutural margin somewhat uneven on apical declivity; surface very smooth, with only faint suggestion of weak longitudinal grooves but no punctures; a weak ridge extending a short distance posteriorly from humerus, crossed by some brief corrugations. *Ventral surfaces* smooth, in large part finely punctured. *Legs* long and fairly slender; femora somewhat asperate, somewhat constricted and uneven in pubescent portions; hind tibia nearly straight, suddenly widened at apex; last hind tarsal segment nearly as long as 1+2. Length 22 mm (26 including rostrum); breadth 6.8.

Holotype ♂ (BISHOP 6819), Mt Yelia volcano, nr Menyama, Morobe Distr., NE New Guinea, near edge of rim of crater, 3300 m, alpine grassland, 20.I.1963, Guy Rosenberg.

Differs from *fulvospretus* Hllr in being more elongate, more shiny, with more deeply and narrowly grooved rostrum, more weakly and more rounded-tuberculate pronotal tubercles, and bituberculate elytron.

Fulvospretus-group

This group is characterized by the body being somewhat rounded at side or pronotal tubercles rather weak, and dorsum largely glabrous. It may not be a natural group.

13. *Gymnopholus* (*Gymnopholus*) *fulvospretus* (Heller) Figs. 5k, 6a.

Aroaphila fulvospreta Hllr, 1926, Nova Guinea, Zool. 15 (2): 276, fig. 2 (Mt Bolan, nr Sattelberg, NE NG; DRESDEN).

Gymnopholus fulvospretus Mshl, 1959, Bishop Mus. Occ. Pap. 22(7): 80.

The rather sharply obtuse concavity between the fairly high and rather angulate pronotal tubercles, is fairly characteristic. Most individuals have small blue scales on apical declivity of elytron, and some have a row of white spots along sutural margin or a bluish sutural stripe; elytron distinctly convex at side, and subcarinate.

NE NG: 4, Funiyende, 1200 m, Saidor Subdistr., Finisterre Range, Huon Pen., 24.IX.1958, W. W. Brandt; 11, Matoko, Saidor Subdistr., 29.VIII-24.IX.1958, Brandt; 1, N. side Freyberg Pass, 2550 m, Main Finisterre Range, 1-21.X.1958, Brandt; 1, Zengaren,

1200 m, Huon Peninsula, 28. IV. 1963,
J. Sedlacek.

14. *Gymnopholus* (*Gymnopholus*) *cyphothorax* (Heller) Fig. 5-1.

Aroaphila cyphothorax Hllr, 1901, Abh. Mus. Dresden 10 (2) : 9; 1913, Archiv Naturgesch. A 79(1) : 46 (Aroa R., Papua; DRESDEN).

Gymnopholus cyphothorax: Marshall, 1959, Bishop Mus. Occ. Pap. 22(7) : 80.—Szent-Ivany, 1965, Trans. Papua & New Guinea Sci. Soc. 6: 31 (Goilala).

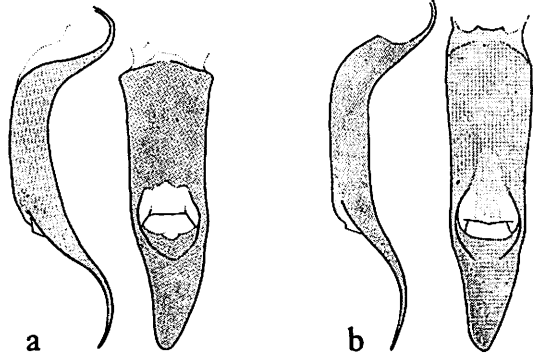


Fig. 6. Aedeagi, side view left, hind (dorsal) view right: a, *G. fulvospretus* Hllr; b, *G. marshalli* n. sp.

This species is characterized by the strongly rounded pronotal tubercles, with a fairly deep cleft between. Length 18–26 (21–29) mm.

SE NG: Goilala Subdistr., Owen Stanley Mts: 14, Loloipa, 1500 m, 25.XI.1957–30.I.1958, W. W. Brandt; 9, Bome, 1950 m, 16–31.III.1958; 6, Tapini, 1100 m, 16–25.XI.1957, Brandt; 5, Tororo, 1560 m, 21–24. II. 1958, Brandt: 1, along road between Eremolavava and Kolo-lavava, 2100 m, 14.VI.1962, Szent-Ivany.

15. *Gymnopholus* (*Gymnopholus*) *marshalli* Gressitt, n. sp. Figs. 3g, 5m, 6b.

♂. Black, slightly shiny above and below. Body largely subglabrous above but with scutellum densely clothed with white pubescence and with sparse short oblique hairs on apical declivity and small dark blue scales along lower and outer portions of apical declivity and outer side of elytron; pronotum with a few very short sparse hairs and a very few narrow blue scales at posterior portion. Ventral surfaces moderately clothed with oblique goldish hairs and scattered areas of narrow blue scales; legs moderately clothed with oblique tawny hairs and some blue scale, mainly on tarsi.

Head distinctly longer than prothorax, wider at eyes than at end of rostrum but narrower than at occiput; rostrum subparallel-sided in basal 2/5, then strongly widened, broadly and shallowly grooved above with a less distinct groove on upper side, and surface with irregular punctures, partly fairly deep and close. *Antenna* with scape somewhat gradually thickened and then more swollen at apex; funicle with segment 2 distinctly longer than 1 and 3; club somewhat unevenly fusiform and blunt at apex. *Prothorax* slightly longer than broad, weakly rounded at side, narrowed some distance from base and slightly broadened to basal margin; anterior portion gradually narrowed and very slightly constricted at side a short distance from apex; disc with a pair of very high tubercles which are straight at side, oblique internally and slightly rounded at apices; groove between tubercles distinct and subangulate, a fairly deep rounded depression between anterior portions of tubercles a short distance from apex; surface in large part finely and rather sparsely punctured, a little more heavily so on anterior collar, which is fairly distinct. *Scutellum* distinctly broader than long. *Elytron* a little more than 3× as long as broad, with humerus slightly swollen but hardly projecting, side slightly widened behind base and gradually narrowed toward

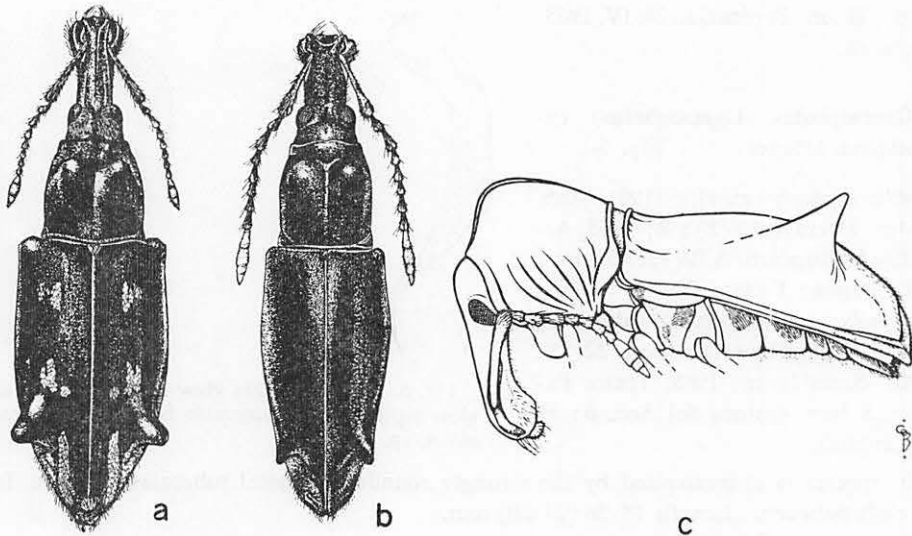


Fig. 7. a, *Gymnopholus gressitti* Mshl ♀; b, *G. angustus* Mshl ♀; c, *G. weiskei* Hllr ♂, lateral outline (after Marshall, 1959, Bishop Mus. Occ. Pap. 22: 78, 80).

the obliquely rounded apex; an obtuse tubercle on side of upper part of apical declivity; suture with 2 swellings on apical declivity; surface with fairly regular rows of small punctures and with a short incomplete ridge behind humerus. *Ventral surfaces* with moderately large scattered punctures and with dense fine punctures also on last sternite; abdominal sternites 4 and 5 not very strongly raised apically. *Legs* moderately slender; femora asperate; tibiae more finely asperate; last hind tarsal segment longer than 1+2. Length 21 mm (23.5 including rostrum); breadth 6.8.

Paratypes. Length 19–25 (21.5–27.5) mm; breadth 7–7.5.

Holotype ♂ (BISHOP 6820), Bome, 1950 m, Goilala area, Owen Stanley Mts, SE New Guinea, 1–15.IV.1958, W. W. Brandt; 2 paratopotypes, same data except 16–30.IV and 24. II to 7. III. 1958.

Differs from *fulvospretus* Hllr in having the pronotal tubercles much higher, vertical externally and sharply oblique internally, making them subacute in hind view and more angulate in side view. Named for the late Sir Guy A. K. Marshall, who contributed so much to the knowledge of Papuan and other weevils.

16. *Gymnopholus (Gymnopholus) suturalis* (Heller)

Aroaphila suturalis Hllr, 1910, Wien. Ent. Ztg. 29: 181 (NE NG: Kani Mts.; DRESDEN); 1913, Archiv Naturgesch. A 79 (1): 46.

Gymnopholus suturalis: Marshall, 1959, Bishop Mus. Occ. Pap. 22 (7): 79.

Characterized by a sutural stripe of white scales. Possibly the type locality is Mt Kant in the Finisterre Range.

Interpres-group

This group is characterized by the pronotal tubercles extending outward and overhanging the sides; elytral tubercles often weak or obsolete.

17. *Gymnopholus* (*Gymnopholus*) *interpres* Heller Figs. 3h, 5n, 8a.

Gymnopholus (*Aroaphila*) *interpres* Hllr, 1935, Nova Guinea, Zool. 17(2): 180 (Edie Creek; DRESDEN).—Marshall, 1959, Bishop Mus. Occ. Pap. 22 (7): 76.

This species is distinct from *intergrirostris*, with rostrum somewhat grooved medially, pronotum impunctate and more overhanging at side, and with elytron somewhat less smooth, more striate in ♀, and with a more distinct postmedian tooth in ♀. Length 16–27 mm (based on larger series than of *intergrirostris*).

NE NG: 5, Edie Creek, 2100 m, nr Wau, 5–10. X. 1961, J. & J. H. Sedlacek; 3, above Wau, 1700 m, 28.XII.1961, Sedlacek; 11, Mt Kaindi, 2300 m, above Edie Creek; 6. X. 1962, 14. X. 1964, 17–19. VIII. 1965, Sedlacek; 15, Bulldog Rd, 2200–2500 m, 19–29 km S of Wau, 28. V. 1962, Sedlacek.

18. *Gymnopholus* (*Gymnopholus*) *brandti* Gressitt, n. sp. Figs. 3i, 5o, 8b.

♂. Shiny black, slightly frosted. Head hairy anteriorly; antenna with moderately long oblique hairs on scape and funicle; elytron somewhat pubescent near apex; ventral surfaces sparsely pubescent beneath; legs moderately hairy.

Head slightly longer than prothorax; rostrum gradually narrowed anteriorly, rather closely punctured, slightly depressed medially; occiput with a slight depression well behind eyes. *Antenna* reaching slightly beyond base of prothorax; scape nearly as long as next 5 segments; segment 4 distinctly longer than 5; club slender, fusiform. *Prothorax* as long as broad, gradually narrowed anteriorly; disc with a prominent tubercle on each side which overhangs externally; surface finely punctured above and anteriorly. *Scutellum* small, narrow. *Elytron* more than 3× as long as prothorax, slightly widened behind base, narrowed and subacute apically; tubercle distinct, broad and blunt; a prominent tubercle on posterior declivity, with suture weakly convex from base to tubercle; apical declivity subvertical; disc with very fine striae with weak punctures; some irregular depressions along lateral margin. *Ventral surfaces* smooth or sparsely punctured. *Legs* long and fairly slender; tibiae strongly punctured; hind tarsal segment 1 distinctly longer than 3. Length 15 mm (17.5 including rostrum); breadth 4.8.

♀. Stout, widest behind middle with distinct but short blunt tubercle on elytron; elytral disc with fine striae with minute punctures; some fine green hair-like scales on anterior portion of pronotum and on scutellum. Length 22.5 (25) mm; breadth 8.

Paratypes: Length 16–25 (18.5–28) mm; breadth 5–8.6.

Holotype ♂ (BISHOP 6821), Bome, 1950 m, Goilala Distr., Owen Stanley Mts, Papua, 1–15.IV.1958, W. W. Brandt; allotype ♀ (BISHOP), same data; 28 paratypes (BISHOP, CAS, USNM, BMNH, ANIC, DASF), 24.II–15.IV.

Differs from *intergrirostris* Hllr in being relatively shorter, with elytron more wrinkled and with tubercle more distinct, particularly in ♀, and elytral suture convex and sloping to posterior tubercle instead of horizontal as far as tubercle.

19. *Gymnopholus (Gymnopholus) divaricatus* Gressitt, n. sp. Fig. 8c.

♂. Somewhat shiny black. Body nearly glabrous, a few pale hairs and a very few greenish scales along posterior portion of outer margin of elytron, very sparse minute pale hairs on posterior portion of abdomen, sparse fine hairs on femora, and longer oblique goldish hairs on tarsi and distal portions of tibiae; antenna with a few oblique hairs on undersides of scape, sparse hairs on funicle and close brownish pubescence on club.

Head a little longer than prothorax, wider at eyes than near end of rostrum and widest at occiput; rostrum subparallel-sided in basal 1/3, then gradually, then strongly widened anteriorly, with apical portion rounded at side; dorsal surface grooved on occiput, with a small deep pore between eyes, and slightly depressed medially on rostrum which is some-

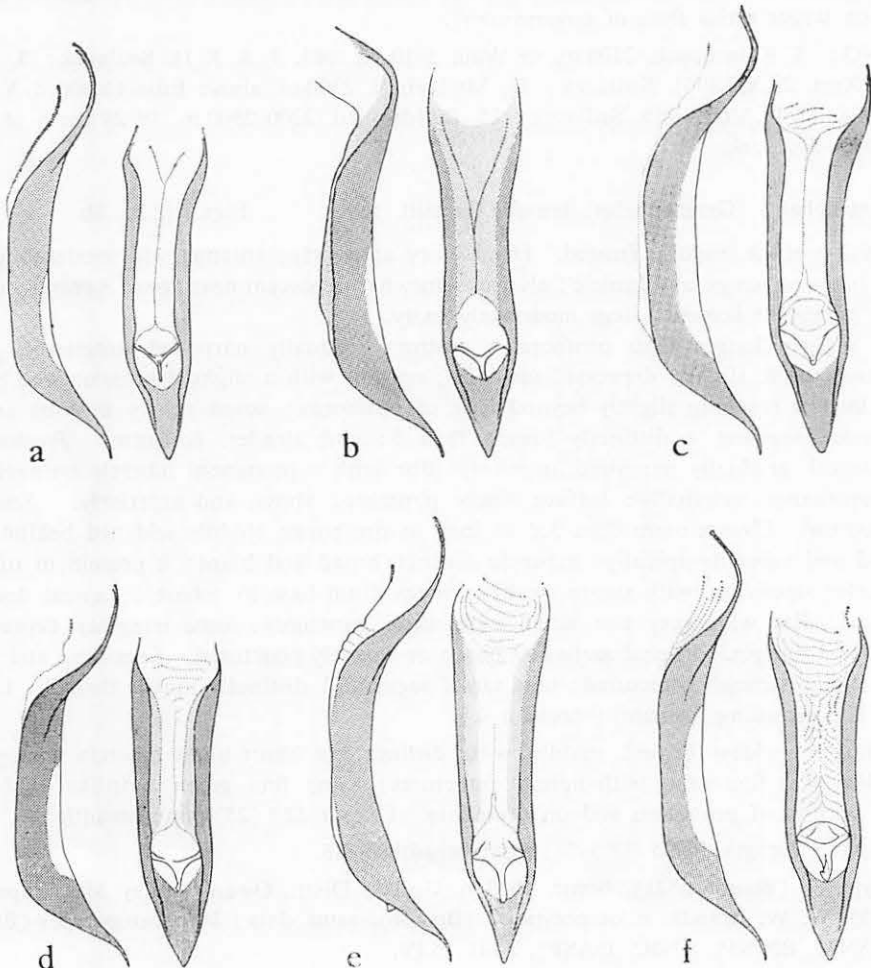


Fig. 8. Aedeagi side view left, hind (dorsal) view right: a, *G. interpres* Hllr; b, *G. brandti* n. sp.; c, *G. divaricatus* n. sp.; d, *G. glochidionis* n. sp.; e, *G. integrirostris* Hllr; f, *G. ludificator* n. sp.

what closely punctured, and with a short groove on upper portion of side. *Antenna* reaching to humerus; scape nearly reaching to hind margin of eye, strongly swollen apically and distinctly punctured; funicle with segment 2 barely longer than 1 and 3; club slender and fusiform. *Prothorax* as long as breadth at base, somewhat gradually narrowed from base to near apex and then slightly constricted a short distance from apex; disc with a pair of strongly swollen tubercles somewhat anterior to center, tubercles projecting outward at side and slightly overhanging the nearly vertical smooth side; surface fairly smooth, without distinct punctures. *Scutellum* small, longer than broad. *Elytron* slender, very slightly widened behind humerus, and gradually narrowed almost to apex; surface fairly smooth, with incomplete rows of feeble punctures, a small subacute tubercle some distance from apex, and suture with 2 swellings on apical declivity. *Ventral surfaces* fairly smooth, with fine punctures becoming larger and closer towards apex of abdomen. *Legs* slender, femora fairly smooth with weak punctures; hind tibia nearly straight; hind tarsus with segment 1 shorter than 2+3 and shorter than last. Length 21.5 (25 including rostrum); breadth 6.7.

♀. Dorsum with finely scattered pale buff to pearly scales, sparse or lacking on central portion of elytron, denser on each side of humeral ridge and on apical declivity; pronotal tubercles smaller than in ♂ but projecting more laterally and with concavity between more obtuse; elytral tubercle stronger, blunt. Length 21 (25) mm; breadth 9.5.

Paratypes (♂♂). Length 16-18 (19-21) mm; breadth 5.7-5.8.

Holotype ♂ (BISHOP 6822), Tumbul Pass, 1800 m, Sepik-Wahgi Divide, N of Banz, 21. VII.1955, Gressitt; allotype ♀ (BISHOP), Daulo Pass, 2500 m, Chimbu-Asaro Divide, 12. VI. 1955, Gressitt; 6♂ paratypes: Daulo Pass, 12. VI. 1955, Gressitt and 15. V. 1963, Sedlacek; Ahl Valley, 1750 m, above Nondugl, Wahgi Vall., 8. VII. 1955, Gressitt; Kofena Area, nr Daulo Pass, VI.1955, Szent-Ivany.

Differs from *gressitti* Mshl in being smaller, with pronotal tubercles produced outwards at sides and elytral tubercles much smaller in ♂. Differs from *glochidionis* in having pronotal tubercles more produced outward, aedeagus more evenly tapered apically, etc. and ♀ largely scaly. The allotype was identified as *integrivostris* by Marshall.

20. *Gymnopholus* (*Gymnopholus*) *glochidionis* Gressitt, n. sp. Figs. 3j, 8d.

♂. Rather shiny black; not quite so shiny on venter and legs. Dorsum nearly glabrous, a few short hairs on rostrum and a very few brownish hairs and a few greenish scales along posterior parts of sutural and outer elytral margins; antenna moderately clothed with oblique pitchy reddish hairs; legs with a few short hairs on femora and some metallic green scale-hairs along part of basal 1/2 of upper portion of hind femur; tibia moderately clothed with oblique reddish buff hairs; tarsi with oblique pale hairs and adpressed green scale-hairs.

Head barely longer than prothorax; nearly as broad at end of rostrum as at eyes, hardly narrowed behind eyes; rostrum slightly narrowed a short distance from base then gradually widened and then suddenly widened, somewhat closely punctured above with two sizes of punctures, fairly flat on upper surface and hardly grooved medially but with a short deep groove on upper part of side. *Antenna* reaching to humerus; scape distinctly thickened apically, moderately punctured; funicle with segment 2 distinctly longer than 1

and 3; club evenly fusiform, subacute. *Prothorax* slightly longer than broad, subparallel in basal 1/2, gradually narrowed apically and slightly constricted a short distance from apex, slightly broadened at extreme base; disc with a pair of strong tubercles which are convex above and slightly projecting and overhanging at side; surface smooth, with only very minute punctures. *Scutellum* small, slightly longer than broad. *Elytron* slender, fully 4× as long as broad; humerus rounded, not projecting; side slightly widened anterior to middle and then gradually narrowed towards oblique and slightly obtuse side of apex; discal tubercle distinct, short and subacute; surface smooth but finely striate with minute or obsolete punctures and suture with a distinct swelling on apical declivity and another swelling near extreme apex. *Ventral surfaces* fairly smooth, partly punctured on abdomen. *Legs* fairly slender; hind femur moderately punctured, not distinctly asperate; hind tibia distinctly punctured, slightly arched; hind tarsus with last segment as long as 1+2. Length 20.8 mm (24 including rostrum); breadth 6.8.

♀. Pronotal tubercles slightly more projecting externally, cavity between them rounded-obtuse; elytral tubercle stronger, forming a subequilateral triangle in dorsal view; tubercle on suture rather prominent; scales along apical margin somewhat coppery. Length 22.5 (26) mm; breadth 9.7.

Paratypes. Elytral tubercles sometimes quite acute and sometimes bluntly rounded. Length 17-26 (19-28) mm; breadth 4.8-11.8.

Holotype ♂ (BISHOP 6823), Purosa, 2020 m, nr Okapa, S of Kainantu, E. Highlands, NE New Guinea, 28.VIII.1964, J. & M. Sedlacek; allotype ♀ (BISHOP), same data; 6 paratypes, same data; 1 paratype, 24-26 km SE of Okapa, 1800-1900 m, 25.VIII.1964, Sedlacek; 12 paratypes, Okapa, I, V, X. 1965, R. Hornabrook; 15 paratypes, Ilafo, 2300 m, N of Okapa, defoliating *Glochidion*, 7.I.1965, J. J. H. Szent-Ivany & Gressitt; 2, Mt ridge nr junction of Lamari & Azana rivers, 2700 m, Okapa area, 18.IV.1962, Sir Alan H. Mann. Some specimens from Dauilo Pass, 12.VI.1955, Gressitt, 15.V.1963, Sedlacek, Kofena, VI.1955, Szent-Ivany and Ahl Valley, Nondugl, 8.VII.1955, Gressitt, are not designated paratypes.

Differs from *integrivostris*, *interpres*, *divaricatus* and *ludificator* in having ♂ distinctly toothed on elytron and ♀ with a projecting tubercle instead of a tooth at end of broadened part of side, or untoothed side.

21. *Gymnopholus* (*Gymnopholus*) *integrivostris* (Heller) Figs. 3k, 5p, 8e.

Aroaphila integrivostris Hllr, 1913, Archiv Naturgesch. A 79 (1): 43 (Sattelberg; DRESDEN); 1926, Nova Guinea, Zool. 15 (2): 276, fig 1.

Gymnopholus integrivostris: Marshall, 1959, Bishop Mus. Occ. Pap. 22 (7): 76.

This species is characterized by very high, outwardly directed pronotal tubercles, elytron slender and almost toothless in ♂ and broad postmedially with an obtuse tooth in ♀, and with rostrum without a median groove. Length 15.5-28 mm.

NE NG: 7, Tobo to Zengaren, 1000-1500 m, Huon Peninsula, 25.IV.1963, J. Sedlacek; 6, Zengaren, 1200 m, 28.IV.1963; 3, Laleng, 1300-2000 m, 23.IV.1963, J. Sedlacek. Part of the material identified as of this species by Marshall is here placed under *ludificator* n. sp.

22. *Gymnopholus* (*Gymnopholus*) *ludificator* Gressitt, n. sp. Figs. 3l, 5q, 8t.

♂. Entirely black. Dorsum largely glabrous, a very few oblique golden to reddish

hairs on apical declivity and along outer part of posterior 1/6 of elytron; ventral surfaces with only a few scattered oblique pale hairs near apex of abdomen; legs poorly clothed with hairs on femora, more regularly clothed on tibiae and tarsi; antenna with scattered oblique reddish yellow hairs.

Head a little longer than prothorax, barely wider at eyes than at apex of rostrum; rostrum slightly widened in basal 1/2, suddenly widened preapically, its upper surface fairly flat and unevenly punctured, and 2 incomplete ridges on upper part of side. *Antenna* with scape straight, slender, strongly widened apically; funicle with segment 2 longer than 3, subequal to 1; club fairly slender and subfusiform. *Prothorax* slightly longer than broad, fairly straight at side, gradually narrowed from base to near apex with a slightly constricted collar at apex; disc with a pair of very strongly swollen tubercles, distinctly overhanging externally above vertical sides; median groove deep, approximately forming a right angle at middle and more deeply depressed before reaching anterior margin; surface fairly smooth, with faint small punctures. *Scutellum* longer than broad. *Elytron* 3.5× as long as broad; humerus not projecting; side very slightly widened for a short distance behind humerus and then gradually narrowed to obliquely obtuse apex; discal tubercle obsolete; suture with a fairly prominent common tubercle on apical declivity and another swelling near apex beside a low swelling which continues anteriorly for a short distance parallel to external margin; surface with faint regular rows of small punctures on almost entire surface, most of punctures about 1/3 as large as interspaces. *Ventral surfaces* fairly shiny, with very few punctures. *Legs* slender; hind femur minutely punctured; hind tibia straight and more strongly punctured; last hind tarsal segment longer than 1+2. Length 18.5 mm (22.5 including rostrum); breadth 5.5.

♀. Similar to ♂ but with elytron distinctly broadened in middle; also without discal tubercle; elytral surface with punctures rather fine; surface in part finely wrinkled. Length 23 (28) mm; breadth 7.8.

Paratypes. Sometimes a vestigial obtuse elytral tubercle in ♂. Length 20-21 (24-25) mm; breadth 5.8-8.0.

Holotype ♂ (BISHOP 6824), Sepalakembang, 1920 m, Salawaket Mts, Huon Peninsula, NE New Guinea, 11-14.IX.1956, E. J. Ford, Jr.; allotype ♀ (BISHOP), 11.IX.1956, Ford; 2♂ paratopotypes, 11, 15.IX.1956; 1 paratype ♀, Baidoang, 1800 m, Salawaket Range, 15.IX.1956, Ford; 1 paratype ♂, Funiyende, 1200 m, Saidor Subdistr., Finisterre Range, 24-30.IX.1958, W. W. Brandt.

Differs from *integrifrons* Hllr in having pronotal tubercles less diverging and overhanging in ♂, and elytron toothless or nearly so at side and evenly convex in ♀. Differs from *interpres* Hllr in lacking teeth on elytron in both sexes.

Weiskei-group

This group is characterized by a very large pronotal swelling of nearly fused tubercles, and a very large elytral tubercle.

23. *Gymnopholus (Gymnopholus) weiskei* Heller Figs. 5r, 7c.

Gymnopholus weiskei Hllr, 1901, Abh. Mus. Dresden 10 (2): 8, fig. 1 (Papua: Aroa River; DRESDEN).—Marshall, 1959, Bishop Mus. Occ. Pap. 22 (7): 78, fig. 4bc.—Szent-Ivany,

1965, Trans. Papua & New Guinea Sci. Soc. 6: 30.

Gymnopholus forticornis Heller, 1935, Nova Guinea, Zool. 17(2): 179 (Edie Creek; DRESDEN).

This species appears to be the most abundant and widespread of the genus, besides being the type species. However, it may consist of several species or subspecies. It is extremely variable, and rather variable in any given population. It is characterized in particular by the very large elytral tubercle. Length 18-35 mm.

About 300 specimens. NE NG: Bulolo, Wau, Edie Creek, Mt Kaindi, Bulldog Road, Aiyura, Kainantu, Kamilo Council area, Okapa, Purosa, Kumangkera, Daulo Pass, Chimbu Valley. SE NG: Tapini, Eromolavava-Kololavava, Chirima River. Taken by Szent-Ivany, Gressitt, Sedlacek, Brandt, Hornabrook, Barrett. The altitude range of this species is 1000-2700 meters.

HOSTS: *Tephrosia candida*, *Melia azedarach*, *Pipturus argenteus*, *Trema amboinensis*.

24. *Gymnopholus* (*Gymnopholus*) *regalis* Gressitt, n. sp. Fig. 3q-r.

♂. Shiny black; slightly shiny frosted black on pronotum; antenna with funicle and inner side of scape densely clothed with silvery adpressed hairs as well as long oblique silvery hairs; prothorax pubescent on posterior edge; scutellum with a few minute pale hairs; elytron with a few pale hairs at extreme apex and along posterior half of outer margin; ventral surfaces with a few small patches of thorny hair-scales along lateral portions and a few scattered erect hairs along median portion; legs with femora partly glabrous; tibiae and tarsi fairly well clothed with oblique golden hairs.

Head distinctly longer than prothorax, wider at end of rostrum than at eyes, not narrowed behind eyes; rostrum subparallel-sided in basal 2/5, strongly widened anteriorly, with a shallow median groove above and a fairly long groove on upper part of side; surface rather finely and sparsely punctured. *Antenna* just exceeding humerus, stout; scape gradually thickened to apex; funicle with segment 2 barely longer than 1 and 3, much longer than 4 and following; club moderately swollen in center, subacute apically. *Prothorax* slightly longer than broad, subparallel in basal 3/5, slightly widened at extreme apex, distinctly widened anteriorly and slightly constricted at sides a short distance from apex; disc very strongly swollen, with tubercles fused, with a very weak depression and fine median depressed line between; anterior portion sloping subregularly to anterior margin with just a slight concavity behind anterior margin and posteriorly somewhat evenly convex to posterior margin; surface smooth and even, appearing somewhat frosted with microscopic punctures on small flat discs; some weak vertical corrugations below middle of side. *Scutellum* small, longer than broad. *Elytron* nearly 4× as long as breadth at middle with discal tubercle very strong and subacute, extending well beyond lateral margin; surface quite smooth, depressed postbasally and with some very weak incomplete longitudinal depressions and a few rows of obsolete punctures at side; extreme apex slightly roughened and punctured. *Ventral surfaces* with irregular weak punctures. *Legs* long; hind femur feebly punctured; hind tibia more strongly punctured; last hind tarsal segment as long as 1+2. Length 24.5 mm (29.5 including rostrum); breadth 11.8 at tubercles.

♀. Similar to ♂ but broader; elytral tubercles slightly stouter. Length 28 (32) mm; breadth 14.2.

Paratypes. Length 26-28 (31-35) mm; breadth 11.5-15.5.

Holotype ♂ (BISHOP 6825), Matoko, 2000 m, Saidor Subdistr., Finisterre Mts, Huon Pen., NE New Guinea, 29.VIII-5.IX.1958, W. W. Brandt; allotopotype ♀ (BISHOP), same data; 8 paratopotypes, same data; 1 paratype, Sepalakembang, 1920 m, Salawaket Mts, Huon Pen., 15.IX.1956, E. J. Ford, Jr.

Differs from *weiskei* Hillr in having antennal funicle densely clothed with long silvery gray hairs, pronotum broader at top, vertical at side, elytron smoother with tooth more slender (less equilaterally triangular) but less acute and more sinuate on upper side, and in being larger in average size.

25. *Gymnopholus* (*Gymnopholus*) *sedlaceki* Gressitt, n. sp. Fig. 3s.

♂. Shiny black. Dorsum glabrous except for some oblique golden buff hairs along suture on apical declivity and a few hairs in depressions along posterior portion of external margin of elytron; antenna with moderately long sparse hairs on funicle; some patches of golden buff pubescence along lateral margin of abdomen and thinner similar pubescence on each side of middle of metasternum and still thinner pubescence on underside of abdomen; tibiae with golden bristles apically; tarsi moderately clothed with golden buff hairs.

Head slightly longer than prothorax, rather finely and not very closely punctured; rostrum strongly widened apically, broader preapically than width at eyes; dorsal surface with feeble incomplete groove preapically; a slight depression between eyes. *Antenna* reaching beyond base of prothorax; scape nearly as long as funicle; segments 2 and 3 subequal in length; 5-8 shorter; club fusiform. *Prothorax* slightly longer than broad, feebly convex and vertically corrugated at side; disc with a strong even swelling on each side, swelling separated by a distinct depression; a short anterior collar; posterior portion of disc sloping evenly to basal margin except for a narrow groove close to margin. *Scutellum* minute, depressed. *Elytron* more than twice as long as prothorax, somewhat wider, subparallel-sided anteriorly; disc raised on basal margin, depressed behind basal margin and with a very strong slender acute tooth somewhat behind middle; sutural ridge wrinkled and strongly raised behind tubercle; some shallow depressions along lateral margin and some smaller ones on apical declivity. *Ventral surfaces* smooth and shiny on glabrous areas, feebly punctured. *Legs* long and slender, weakly punctured except on tarsi and apices of tibiae; hind tarsal segment 1 barely longer than 3. Length 25 mm (28 including rostrum); breadth at shoulders 5.8; breadth at elytral tubercles 11.

♀. Less shiny black; rostrum finely grooved medially; antenna less hairy; elytron nearly glabrous. Length 26 (29) mm; breadth at humerus 8.2; breadth at elytral tubercles 12.4.

Paratypes: Length 20-28 (23-31) mm; breadth at tubercles 10-15.

Holotype ♂ (BISHOP 6826), Tomba, 2450 m, 38 km W of Mt Hagen, W. Highlands, NE New Guinea, 21-24.V.1963, J. Sedlacek; allotopotype ♀ (BISHOP), same data; 18 paratopotypes (BISHOP, CAS, USNM, BMNH, ANIC, DASF), same data; 2, 11 km S of Mt Hagen town, 2200 m, 21.V.1963, Sedlacek; 9, Koibuga, 1500 m, 5.VII.1963, H. Clissold; 3, Mt Giluwe, 2200 m, 5.VI.1963, Sedlacek; 1, Karimui, 1000 m, NE NG, malaise trap, 4.VI.1961, J. L. & M. K. Gressitt; 2, Aiyurop, 1530 m, nr Mendi, S. Highlands, Papua, 7.X.1958, Gressitt.

Differs from *weiskei* Hllr in being narrower, with a distinct depression between pronotal swellings, with somewhat of an anterior collar on prothorax, with elytral tubercle more slender and more acute, and with patches of pale pubescence lacking on side of metasternum.

Magister-Group

This group is characterized by nearly non-tuberculate pronotum, slender body and dorsum very shiny in ♂, somewhat rough in ♀.

26. *Gymnopholus* (*Gymnopholus*) *magister* Gressitt, n. sp. Figs. 3m, 5t.

Very shiny black; antenna reddish castaneous with club pitchy; femora and tibiae slightly tinged with reddish; tarsus largely pitchy red. Body largely glabrous; head with a few erect pale hairs anteriorly; scutellum slightly pubescent; antenna thinly clothed with oblique pale hairs; elytron with a very few hairs at apex; legs thinly clothed with sparse pale hairs; ventral surfaces with very sparse erect pale hairs, becoming slightly dense only at extreme apex of last sternite.

Head distinctly longer than prothorax, rather smooth but with minute punctures, sparser at side; upper surface hardly grooved, with a short narrow depression between anterior portions of eyes and with a shallow anterior groove starting between antennal insertions. *Antenna* extending to base of elytron, slender; scape nearly as long as funicle, slender, straight and slightly swollen at apex; funicle with segment 2 distinctly longer than 1 which is longer than remainder; club slender, fusiform and acute. *Prothorax* slightly longer than broad, subcylindrical, slightly narrowed anteriorly; surface smooth and only slightly irregular, finely and irregularly punctured, without dorsal swellings but with a slight depression on median line anterior to center and with a slight constriction at each side near apex. *Scutellum* small, subtriangular. *Elytron* much longer than head and prothorax combined, subparallel, slightly widened just anterior to middle, with a fairly weak tubercle at side 1/3 length from apex; apical portion narrowed and conjointly rounded; apical declivity only slightly irregular; surface smooth and shiny, slightly wrinkled along suture, with very sparse and irregular punctures, mostly minute but with a few moderate-sized punctures; lateral declivity with some wrinkles and vertical depressions. *Ventral surfaces* very smooth and almost impunctate at side, sparsely and finely punctured medially. *Legs* long and slender; hind femur fairly straight, minutely punctured; hind tarsal segment 1 longer than 3 and shorter than last. Length 21 mm (24 including rostrum); breadth 6.6.

Paratypes. Length 24-26 (27-29) mm; breadth 7.5-8.6.

Holotype ♂ (BISHOP 6827), nr Freyberg Pass, N. side, 2550 m, Main Finisterre Range, NE New Guinea, 1-21. X. 1958, W. W. Brandt; 6 paratopotypes (BISHOP, CAS, BMNH, ANIC), same data. 1 paratype, Daulo Pass, 2400 m, Asaro-Chimbu Divide, NE New Guinea, 15. VI. 1955, Gressitt. A ♀ from the type locality is so large (38 mm) that it is not designated allotype.

Differs from *weiskei* Hllr in being much more slender, more shiny, without pronotal tubercles and with very weak elytral tubercles.

27. *Gymnopholus* (*Gymnopholus*) *hornabrooki* Gressitt, n. sp. Fig. 3n.

♂. Shiny black; antenna bright orange ochraceous with most of club pitchy brown.

Dorsum practically glabrous; antenna with rather few oblique pale hairs and thin pubescence on club; ventral surfaces with rather sparse short hairs, mostly on median portions of sternites; legs with limited oblique hairs under sides of tibiae and upper surfaces of tarsi.

Head nearly 1/2 again as long as prothorax, about as broad at apex of rostrum as at eyes, broader posteriorly; rostrum slightly narrowed for a distance from base, then gradually and then suddenly widened, upper surface flat but not grooved, a slight depression between anterior portions of eyes, surface rather finely and irregularly punctured, occiput more closely punctured. *Antenna* reaching to well behind humerus; scape nearly as long as funicle, straight, thickened at apex; segment 2 of funicle longer than 1 and much longer than 3 and each of following; club moderately slender, fusiform. *Prothorax* as long as broad, subparallel in basal 3/4, very slightly widened at base and rather slightly narrowed anteriorly; disc without tubercles, a pair of slight depressions anterior to center and a weaker depression just behind center; surface rather finely punctured, with two sizes of punctures, the finer ones quite dense on each side of central portion, thus giving pronotum a slightly less shiny appearance than elytron. *Scutellum* swollen, about as long as broad. *Elytron* nearly 4× as long as broad; humerus rounded and slightly protruding; side very slightly widened a short distance behind humerus, weakly convex in central portion of side and gradually narrowed to slightly rounded apex; a fairly weak tubercle near upper portion of apical declivity; surface fairly smooth with very few punctures and with only a slightly incomplete median depression and a fairly short posthumeral ridge. *Ventral surfaces* rather smooth, with widely scattered punctures on sternites. *Legs* fairly long and slender; femora rather smooth and feebly punctured; hind tibia slightly sinuate; last hind tarsal segment nearly as long as 1+2. Length 21.5 (26.5 including rostrum); breadth 8.

♀. Body somewhat stouter; dorsum in large part minutely punctulate, more deeply and regularly so on pronotum; posterior portion of elytron with minute hairs. Length 25 (29) mm; breadth 10.4.

Paratypes. Length 22-25 (25-28) mm; 6.3-7.0.

Holotype ♂ (BISHOP 6825), Mt Michael, 3300-3600 m, S of Goroka, NE New Guinea, 23.XII.1964, R. Hornabrook; allotype ♀ (BISHOP), 3 paratypes (Hornabrook coll., BMNH, DASF), same data.

Differs from *magister* n. sp. in being smaller, a little less shiny, with head irregularly punctured, antenna paler, pronotum with 2 small depressions anteriorly, and elytron less wrinkled. Named for Dr R. Hornabrook, medical researcher studying the kuru disease, who collected this and other fine species in the Okapa and Mt Michael areas.

28. *Gymnopholus* (*Gymnopholus*) *szentivanyi* Gressitt, n. sp. Fig. 30.

♂. Shiny black; antenna dull pitchy red on scape, blackish on apex of scape, reddish brown on funicle and pitchy brown on antennal club. Body glabrous above, with very sparse short pale hairs beneath; femora nearly bare; tibiae with oblique pale hairs beneath; tarsi moderately clothed with oblique golden hairs above.

Head more than 1/2 again as long as prothorax, as broad at apex of rostrum as at eyes, slightly narrowed behind eyes and then broadened; rostrum cylindrical in basal 1/3, subevenly widened to apex, rather sparsely and weakly punctured above, a slight depression between anterior portions of eyes; occiput only a little more closely punctured than upper

surface of rostrum, which lacks distinct grooves above. *Antenna* $1/2$ as long as body, slender; scape nearly as long as funicle, nearly straight, strongly thickened apically; segment 2 of funicle distinctly longer than 1 and 3; club fairly slender, irregularly subfusiform. *Prothorax* not quite as long as breadth at base, slightly narrowed between middle and base, gradually narrowed anteriorly; disc fairly even, without tubercles, a weak depression just anterior to center; surface with fairly sparse weak punctures. *Scutellum* slightly longer than broad. *Elytron* $4\times$ as long as broad; humerus rounded and fairly prominent, followed by a distinct posthumeral ridge to behind middle; side vertical, weakly convex, narrowed to obliquely rounded apex; a rather weak tubercle at top of apical declivity, preceded by a ridge commencing at about end of basal $1/3$; surface somewhat transversely wrinkled, otherwise quite smooth and very weakly punctured. *Ventral surfaces* smooth, sparsely and weakly punctured. *Legs* long and slender; femora smooth, minutely punctured; hind tibia nearly straight, moderately punctured apically; first hind tarsal segment not quite as long as 1+2. Length 22.5 mm (27 including rostrum); breadth 7.5.

Paratypes. Length 18-20 (22-24) mm; breadth 6.5-7.0.

Holotype ♂ (BISHOP 6829), N of Daulo Pass (Asaro-Chimbu Divide), 2500 m, in moss forest, E. Highlands, NE New Guinea, 15.VI.1955, Gressitt; 2 paratopotypes (BISHOP, DASF), same data except 12.VI.1955, J. J. H. Szent-Ivany.

Differs from *magister* n. sp. in being slightly smaller, with posthumeral ridge sharp and side of elytron vertical, discal ridge of elytron much more distinct, antenna duller, and dorsum lacking minute punctures in addition to usual fine punctures on head and pronotum. Named for Dr J. J. H. Szent-Ivany, of Dept. Agriculture, Port Moresby, who collected several of the interesting new species described in this paper, and interested others in finding additional species.

Subgenus *Symbiopholus* n. subgen.

This subgenus is characterized by special modifications of the dorsal surfaces to encourage the establishment, growth and protection of cryptogamic plants. The modifications include depressions, pits and grooves between rugae. The dorsum is at least rough, and to some extent with specially modified hairs or scales. A secretion appears to serve for the encouragement of plant growth. Dorsal surface in general rough, more or less clothed with modified hairs and scales; pronotum generally rugose-vermiculate, sometimes hairy or rarely smooth; elytron with 1 or 2 weak postmedian tubercles.

Type species: *Gymnopholus reticulatus* Marshall, 1959.

Audax-group

This group is characterized by pronotum nearly flat and dorsum rather rough but without strong pits or depressions.

29. *Gymnopholus* (*Symbiopholus*) *audax* Gressitt, n. sp. Figs. 9ab, 11a.

♀. Black, slightly shining; antenna slightly reddish pitchy. Body in part clothed with sparse oblique hairs, mostly on depressed basal portion of elytron, around subapical elytral tubercle, and on legs and ventral surfaces; very few hairs on head and hair sparse on antenna.

Head slightly longer than prothorax, gradually widened from a short distance anterior to eyes; rostrum distinctly grooved medially and with scattered punctures. *Antenna* reaching well beyond base of prothorax; scape long and slender, not quite straight and slightly swollen apically; pedicel with segment 2 slightly longer than 1 and 3, following shorter; club slender, slightly blunt, closely pubescent. *Prothorax* distinctly longer than broad, subcylindrical, slightly narrowed anteriorly to end of basal 1/5, slightly collared anteriorly; surface somewhat irregular with scattered shallow punctures and a shallow median groove, slightly deeper at end of anterior 1/4. *Scutellum* broader than long, convex. *Elytron*



Fig. 9. a, *Gymnopholus audax* n. sp. ♂; b, same, anterior portion; c, *G. praecox* n. sp. ♂; d, same, anterior portion; e, *G. symbioticus* n. sp. ♀; f, *G. zoarkes* n. sp. ♀; g, *G. reticulatus* Mshl ♂; h, same, ♀; i, *G. vegetatus* n. sp. ♀; j, *G. fungifer* n. sp. ♂, dorsum almost entirely covered with fungal/algal growth; k, same, with young lichen on pronotum; l, *G. acarifer* n. sp. ♀; m, *G. senex* n. sp. ♀.

irregular, raised on basal margin, widened a short distance behind base and again anterior to middle, then gradually narrowed and rounded-truncate apically; disc somewhat uneven, depressed and slightly wrinkled at base, raised parallel to suture in postbasal and central portions, raised at suture and top of apical declivity and with a very weak tubercle on each side of apical declivity with some wrinkles or punctures in depressed areas around tubercle; remainder of surface with weak wrinkles or very weak and sparse punctures. *Ventral surfaces* moderately smooth, with a few widely scattered punctures, becoming more dense and with slight pubescence at apex of last sternite. *Legs* fairly stout; femora slightly asperate to coarsely granulose. Length 25 mm (28.6 including rostrum); breadth 8.7.

Holotype ♀ (BISHOP 6830), Itouda (Itoda), 1550 m, Kamo Valley, nr Wissel Lakes, NW New Guinea, 13.VIII.1955, Gressitt.

Differs from *cyphothorax* Hllr in being more elongate, nearly lacking pronotal tubercles and with elytral tubercle much farther posteriorly.

30. *Gymnopholus* (*Symbiopholus*) *praecox* Gressitt, n. sp. Figs. 9cd, 11b.

♂. Black, somewhat dull to slightly satiny, somewhat shiny on abdomen and femora. Body thinly clothed with oblique silvery golden hairs, very short and sparse on upper surface of head and on pronotum, slightly longer and partly in longitudinal rows on elytron.

Head distinctly longer than prothorax, nearly as broad at end of rostrum as at eyes which are fairly prominent; rostrum parallel-sided in basal 2/5, then gradually and then more suddenly widened, upper surface fairly flat, with sparse punctures and a weak groove on each side. *Antenna* reaching beyond base of elytron, fairly slender; scape slender and arched, slightly thickened at apex; funicle with 2nd segment longer than 1st and 3rd, and following segments swollen apically; club fusiform and acute. *Prothorax* barely longer than broad, subparallel in basal 1/4, then slightly widened to somewhat anterior to middle, then rounded and narrowed with a very slight constriction a short distance from apex; surface slightly irregular, with a shallow irregular median depression and most of disc with low rounded asperate punctures, much smoother at side. *Scutellum* small, barely longer than broad. *Elytron* somewhat more than 3× as long as broad, with humerus weak and rounded, hardly extending beyond base of prothorax, gradually widened to slightly before middle and then gradually narrowed toward apex which is oblique and narrowed to a blunt point; disc somewhat convex in central portion with 3 weak longitudinal raised lines, the innermost starting from base and remainder of surface with subregular rows of shallow depressions partly with a small puncture each; some of punctures on basal portion slightly asperate. *Ventral surfaces* moderately punctured, more coarsely so on last abdominal sternite. *Legs* not very long or stout; hind femur not nearly reaching apex of elytron, slightly swollen, with flat asperities; hind tibia nearly straight, thickened at apex and subasperate; hind tarsus with last segment as long as 1+2. Length 17 mm (19.5 to end of rostrum); breadth 6.4.

♀. Somewhat stouter; pronotum less grooved in basal 2/3; elytron with ridges more strongly raised at middle. Length 21 mm (24 including rostrum); breadth 8.7.

Paratypes. Length 16-21 (19-24) mm; breadth 5-8.

Holotype ♂ (BISHOP 6831), Lake Sirunki, 2550 m, W. Highlands, NE New Guinea, 17. VI.1963, J. & M. Sedlacek; allotype ♀ (BISHOP), same data; 24 paratypes, same

data; 11 paratypes, Kepilam, 2540 m, 21.VI.1963, Sedlacek.

Differs from *reticulatus* Mshl in being smaller, less parallel-sided, with pronotum much less swollen and more even, and elytron not reticulate and much more even. Because of its weak humerus and relatively smooth dorsum, this might represent another genus, but it is related to *audax* and other species described here which seem to bridge the gap. This species has some slight suggestions of fungal growth on the dorsum.

Fallax-group

This group is characterized by fairly smooth, rather strongly raised pronotal tubercles, rather short, convex and somewhat even elytron, with seriate punctures, sparse suberect setae and small patches of scales. This group may represent another subgenus, or at least a link between the two present ones, as it has strong sexual dimorphism like parts of the typical subgenus.

44. *Gymnopholus* (*Symbiopholus*) *fallax* Gressitt, n. sp. Figs. 11n, 15ab.

♂. Black, with parts of coxae, ventral surfaces and undersides of femora reddish to pitchy. Body somewhat uniformly clothed with oblique pale hairs, weaker on pronotum and longer on head and abdomen; scutellum pubescent; elytron with occasional small patches of pale scales in small depressions; antenna and legs with fairly long oblique hairs. Legs with adpressed green scale-hairs.

Rostrum subparallel-sided in central portion, not very strongly widened anteriorly, distinctly grooved medially and on each side of upper surface, rather strongly punctured. *Antenna* with scape strongly thickened apically, reaching to just beyond middle of eye; funicle fairly slender, segment 2 much longer than 1 and 3; club slender and elliptical. *Prothorax* 3/4 as long as rostrum, slightly broader than long, moderately smooth and rather weakly punctured; tubercles fairly high, tapering and rounded at apex, much less widely separated than sides. *Scutellum* small, transverse. *Elytron* relatively short and stout, convex, subacute apically; surface somewhat evenly convex but rough and with rows of weak punctures, with small nodes and wrinkles; posterior tubercle quite weak and blunt; suture distinctly raised near top of apical declivity. *Ventral surfaces* moderately even, entirely punctured. *Legs* moderately slender; hind femur with small nodes and punctures; hind tibia nearly straight, slightly asperate; hind tarsal segment 1 shorter than 2+3 and much shorter than last. Length 20 mm (24 including rostrum); breadth 9.

♀. Similar in structure to ♂ but larger; body largely clothed with small subrounded greenish to golden scales. Length 24 (28.5) mm; breadth 11.2.

♂ Paratypes. Length 12-21 (15-24) mm; breadth 7-9.

Holotype ♀ (BISHOP 6832), Iongai, 1800-2000 m, nr Mt Albert Edward, Owen Stanley Mts, Papua, 8.XI.1965, J. & M. Sedlacek; allotype ♀ (BISHOP), same data; 16 paratypes (BISHOP, CAS, USNM, BMNH, ANIC, DASF), same data.

Differs from other species in the combination of ♀ elytron scaly but with very weak tubercle, and pronotum with fairly strong tubercles, and elytron with evenly scattered hairs, a few small patches of scales, and rows of weak punctures; not close to any other known species.

Kokodae-group

This group is characterized by scutellum being hidden by elytra, and elytra being grooved.

31. *Gymnopholus* (*Symbiopholus*) *kokodae* Marshall Fig. 10a.

Gymnopholus kokodae Mshl, 1959, Bishop Mus. Occ. Pap. 22 (7) : 73, fig. 2a (Kokoda, SE NG : BMNH).

Pronotal tubercles low, fairly smooth; scutellum invisible; elytron grooved and somewhat wrinkled. Length 22 mm. No additional material.

Cheesmanae-group

This group is characterized by fairly smooth dorsum with extensive pubescence on elytra and often on pronotum also.

32. *Gymnopholus* (*Symbiopholus*) *cheesmanae* Marshall Figs. 10b, 11c, 14b.

Gymnopholus cheesmanae Mshl, 1959, Bishop Mus. Occ. Pap. 22 (7) : 78, figs. 1a, 5a (Mt Tafa, Papua; BMNH).

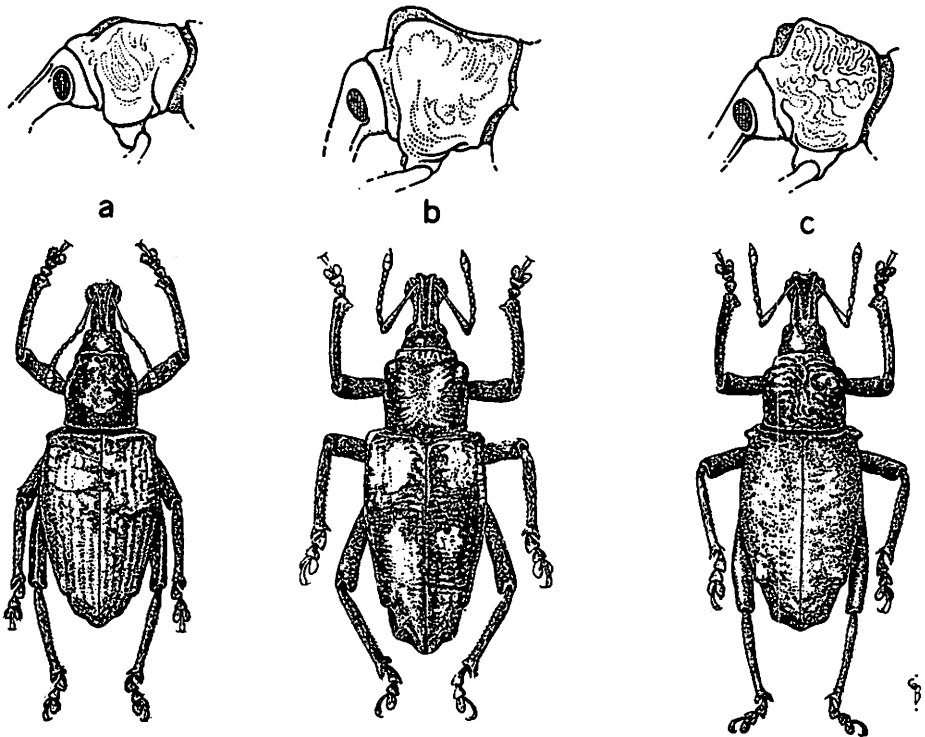


Fig. 10. Oblique-side view of prothorax, above, and dorsal view, below: a, *Gymnopholus kokodae* Mshl; b, *G. cheesmanae* Mshl; c, *G. rugicollis* Hllr (after Marshall, 1959, Bishop Mus. Occ. Pap. 22: 72, 74, 80).

This species is strongly narrowed posteriorly, and very hairy above. It supports primarily algal and fungal growth, which support rotifers, at least. Length 12–28 mm.

SE NG: 25, Murray Pass to Woitape, 2750–2550 m, nr Mt Albert Edward, 11. XI. 1965, J. & M. Sedlacek.

33. *Gymnopholus* (*Symbiopholus*) *algifer* Gressitt, n. sp. Figs. 11d, 12ei, 13bef, 14c.

♂. Black, pitchy brown on posterior part of head, anterior border and parts of sides of prothorax, extreme base and lateral margin of elytron and posterior portion of abdomen. Dorsum, and side of prothorax, largely clothed with green or bluish green scales which taper to form a short bristle apically; some of scales feather-like with several branches; antenna and legs with oblique pale hairs.

Head longer than prothorax; rostrum gradually narrowed anteriorly, nearly twice as broad anteriorly as just before eyes, strongly grooved medially and with a lesser groove on upper side; frons depressed and finely punctured. *Antenna* nearly reaching to base of prothorax; scape punctured and strongly thickened apically, reaching to eye; funicle with segment 2 much longer than 1, which is somewhat longer than 3; club fusiform with segment 1 much longer than 4, finely pubescent. *Prothorax* longer than broad, subparallel but slightly wider anterior to middle and narrowed apically; disc with a very large longitudinal tubercle on each side, slightly overhanging externally and gradually sloping internally; depression fairly even and rounded at bottom but with a few weak wrinkles at side; depression fairly broad and nearly flat anteriorly; surface finely and rather closely punctured; side somewhat coarsely and obliquely wrinkled. *Scutellum* minute. *Elytron* long, subparallel, slightly narrowed posteriorly, with apex roughly rounded and with a weak tubercle just before and above apex and another stronger tubercle higher and farther forward at side; surface irregular, with depressions, partly in longitudinal rows on most of surface, with a weakly raised line on central portion and continuing to posterior tubercle, a short distance from suture; raised areas largely punctured; an irregular ridge extending backward from humerus to just before middle; side fairly smooth but slightly irregular and finely punctured. *Ventral surfaces* fairly smooth with punctures on posterior portions of some abdominal sternites; metasternum extremely short, slightly shorter than a coxa between mid and hind coxae. *Legs* long and fairly straight, subrugulose- to asperate-punctate. Length 30 mm; breadth 9.5.

♀. Largely similar in structure but with some irregular depressions on basal portion of pronotum, wrinkles largely horizontal on side of pronotum, elytron with humeral ridge depressed just behind humerus and then raised and continued to behind middle, and posterior elytral tubercle much weaker than anterior tubercle. Length 33 mm (35.5 including rostrum); breadth 12.6.

Paratypes: Pronotal depression fairly smooth to somewhat obliquely wrinkled just behind middle; elytron black with green scales in depressed areas, but generally appearing dirty gray-brown to ashy gray because of fungal growth on back, and also on pronotal depression or even on outer side of pronotal swelling. Length 21–32 (23–35) mm; breadth 7.5–12.5.

Holotype ♂ (BISHOP 6833), Bome, 1950 m, Gailala Subdistr., Owen Stanley Mts, Papua, 16–31.III.1958, W. W. Brandt; allotype ♀ (BISHOP), same data; 33 paratypes, same

data or 24.II to 15.IV, Brandt: 2, Eremolavava Farm, 2100 m, 1.IX.1963, on second growth in forest clearing, J. J. H. Szent-Ivany; 1, along road between Eremolavava and Kolo-lavava, Goilala Subdistr., 2000 m, 14.VI.1962, Szent-Ivany. (See Szent-Ivany, 1965, Trans. Papua & New Guinea Sci. Soc. 6: 31). 4, Murray Pass to Woitape, 2550-2050 m, 11.XI. 1965, J. & M. Sedlacek.

Differs from *cheesmanae* Mshl in being larger, with scape more suddenly swollen apically, head not constricted behind eyes, pronotum not vermiculate between tubercles and elytron with longitudinal rows of depressions, but without transverse wrinkles or grooves.

34. *Gymnopholus (Symbiopholus) symbioticus* Gressitt, n. sp. Figs. 9e, 11e.

♂. Black, in part shiny, in part dull; head, pronotum and scutellum more or less glabrous; elytron densely clothed with hairs on upper surface which are generally matted with a secretion and with dense fungal or other growth; side of elytron glabrous; ventral surfaces with a very few scattered goldish hairs; legs with femora sparsely clothed and tibiae and tarsi more heavily clothed with oblique pale golden hairs.

Head a little longer than prothorax, nearly as broad at apex of rostrum as at eyes, hardly narrowed behind eyes; rostrum narrowed a short distance from base and then strongly widened anteriorly, flattish and very weakly depressed along median line and without any groove on upper side; surface finely and sparsely punctured. *Antenna* not quite reaching humerus; scape distinctly shorter than funicle, stout apically; funicle with segment 2 about as long as 1 and much longer than 3; club unevenly thickened in middle, strongly tapered but blunt apically. *Prothorax* slightly broader than long, subparallel but slightly uneven in basal 1/2, strongly narrowed and slightly collared apically; disc with a rounded obtuse tubercle on each side slightly anterior to middle and with a weakly obtuse depression between, and slightly deeper between anterior portions of tubercles; surface fairly smooth, finely and sparsely punctured; a few weak vertical corrugations on lower part of side. *Scutellum* convex, slightly broader than long. *Elytron* about 3× as long as broad; humerus slightly swollen but hardly projecting; side very weakly convex, gradually narrowed to rounded and obliquely truncate apex; discal tubercle fairly weak and blunt, followed by a depression and then a large swollen area which is larger than tubercle, as well as a somewhat swollen suture on apical declivity; surface fairly smooth at side, uneven above with vague longitudinal grooves or rows of punctures more or less hidden by dense hairs which are generally matted and covered with vegetation. *Ventral surfaces* with only a few scattered fine punctures. *Legs* with hind femur fairly smooth, moderately punctured; hind tibia slightly arched, sparsely punctured; last hind tarsal segment slightly longer than 1+2. Length 19 mm (23 including rostrum); breadth 7.

♀. Slightly stouter; elytral tubercle a little more distinct, elytral disc with some irregular transverse ridges. Length 24 (27) mm; breadth 9.3.

Paratypes. Length 19-24 (22-27) mm; breadth 6.8-9.3.

Holotype ♂ (BISHOP 6834), Mt Strong, 3500 m, alpine grassland, defoliating *Rhododendron commonae*, 30.VIII.1963, J. J. H. Szent-Ivany; allotype ♀ (BISHOP), same data; 53 paratypes, same data; 2 paratypes, 14.XI.1963, F. H. A. Kleckham; 4 paratypes, 30.VIII.1963, I. Johnson & J. Carlyle; 2 paratypes, VII.1962, M. Erben.

Differs from *kokodae* Mshl in having a distinct scutellum, in being more oblong, with

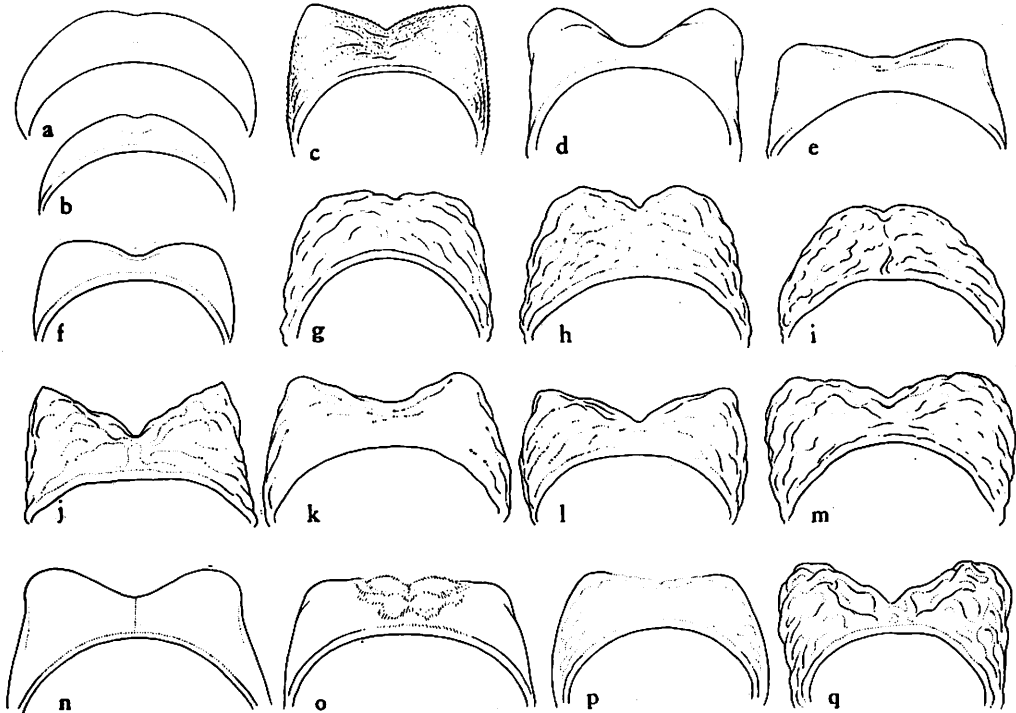


Fig. 11. Dorsal outline of pronotum viewed from behind: a, *Gymnopholus audax* n. sp.; b, *G. praecox* n. sp.; c, *G. cheesmanae* Mshl ♂; d, *G. algifer* n. sp.; e, *G. symbioticus* n. sp.; f, *G. zoarkes* n. sp.; g, *G. reticulatus* n. sp.; h, *G. botanicus* n. sp.; i, *G. vegetatus* n. sp.; j, *G. fungifer* n. sp.; k, *G. lichenifer* n. sp.; l, *G. acarifer* n. sp.; m, *G. senex* n. sp.; n, *G. fallax* n. sp.; o, *G. h. herbarius* n. sp.; p, *G. h. oribatifer* n. subsp.; q, *G. hepaticus* n. sp.

distinct reddish brown hairs on elytron and in having pronotum smoother and less rugose and elytron less seriatly grooved longitudinally, with more frequent transverse wrinkles.

This species has a high percent of individuals densely covered on elytra with fungal growth, and with about 1 in 10 specimens with extensive lichen growth (*Parmelia* sp.) covering more than half of elytral surface. The pronotum is rarely vegetated. (See Szent-Ivany, 1965, Trans. Papua & New Guinea Sci. Soc. 6: 30).

35. *Gymnopholus* (*Symbiopholus*) *zoarkes* Gressitt, n. sp. Figs. 9f, 11f.

♂. Fairly shiny black; elytron with some sparse short pubescence near base and posteriorly; femora red except at apices; legs rather weakly clothed with goldish pubescence; antenna with a few silvery golden hairs on funicle and thin pubescence on club; ventral surfaces with only a few sparse hairs along median portion and near apex.

Head slightly longer than prothorax, nearly as broad at apex of rostrum as at eyes, hardly narrowed behind eyes; rostrum slightly narrowed to a short distance from eyes, then gradually and then more strongly widened anteriorly, distinctly grooved above and with a lesser groove on upper part of side; surface finely and sparsely punctured. *Antenna* not

reaching to humerus; scape gradually thickened apically, moderately punctured; funicle with segment 2 barely longer than 1 and distinctly longer than 3; club fairly short and stout, subacute apically. *Prothorax* slightly broader than long, subparallel in basal 1/2, slightly constricted near base and widened at extreme base, rounded and narrowed anteriorly and slightly constricted at side a short distance from apex; disc with a low rounded swelling on each side anterior to center, and a rounded concavity between ridges, deepest near anterior portions of tubercles and disappearing before apex; surface finely and irregularly punctured. *Scutellum* about as long as broad. *Elytron* 3.5× as long as broad; humerus very slightly swollen, hardly projecting; side slightly broadened, subevenly convex and gradually narrowed to rounded-obtuse apex; discal tubercle rather weak and blunt, followed by a shallow depression and then a fairly large smooth raised area close to suture which is somewhat raised; surface with incomplete rows of weak punctures and a few uneven transverse wrinkles; side moderately smooth, slightly wrinkled and punctured. *Ventral surfaces* smooth, with very few punctures. *Legs* moderately stout; hind femur fairly smooth and weakly asperate-punctate; last hind tarsal segment as long as 1+2. Length 16.8 mm (19.6 including rostrum); breadth 5.9.

♀. Slightly stouter; elytron strongly carinate behind humerus, vertical at side; humerus partly reddish; disc with a depressed pubescent subbasal area continuing intermittently to behind middle; antenna with very few oblique hairs; abdominal sternites 1 and 2 strongly convex. Length 22.5 (26.4) mm; breadth 9.0.

Paratypes. Elytron sometimes more extensively pubescent. Length 16.5-18 (18-25) mm; breadth 5.5-8.5.

Holotype ♂ (BISHOP 6835), Murray Pass, W. slope, 2750-2800 m, Papua, on tree fern, 4. XI.1965, J. & M. Sedlacek; allotype ♀ (BISHOP), same data; 23 paratypes (BISHOP, USNM, CAS, BMNH), same data, 1, Murray Pass, W. slope, 2700-2900 m, 5-6. XI; 6 paratypes (AM, ANIC, DASF), Sidibamu, 3300 m, nr Waitape, C. Distr., Papua, 14. X. 1963, D. K. McAlpine.

Differs from *kokodae* Mshl in being smaller, with distinct scutellum, more shiny black dorsum and more transversely wrinkled elytra.

This species has more limited fungal growth than does *symbioticus*, corresponding with the smoother, less pubescent dorsum.

Reticulatus-group

This group is characterized by the pronotum more or less vermiculate, or at least rugose. The elytra have various pits or depressed areas.

36. *Gymnopholus* (*Symbiopholus*) *reticulatus* Marshall Figs. 9g, 11g, 12j.

Gymnopholus reticulatus Mshl, 1959, Bishop Mus. Occ. Pap. 22 (7): 75, fig. 3 (Daulo Pass, Asaro-Chimbu Divide, NE NG: BMNH).—Szent-Ivany, 1965, Trans. Papua & New Guinea Sci. Soc. 6: 29.

This species supports mainly fungal and algal growth in the pits on elytra and grooves between rugae on pronotum. Lichen growth is rather rare, but limited growth of *Physcia* sp. occurs in the pronotal depression of one specimen from Daulo Pass (June 1955, Gres-

sitt), and some unidentified lichen on elytra of a specimen from Kofena (June 1955, Szent-Ivany). Length 20-32 mm.

NE NG: This species was described from 18 specimens from Daulo Pass, 11 of them from Bishop Mus. Additional material: 9, Daulo Pass, 2400 m, 15.V.1963, J. Sedlacek; 1, Daulo Pass, 2500 m, 2.V.1959, C. D. Michener; 3, Nenguag, 2500 m, Asaro-Chimbu Divide, 29.VI.1955, Gressitt; 1, Marafunka, 2400 m, E. Highlands, 13.VII.1962, J. H. Barrett.

37. *Gymnopholus* (*Symbiopholus*) *botanicus* Gressitt, n. sp. Figs. 11h, 13d.

♂. Black; raised reticulations on elytral disc often covered with a white waxy material, or obscured by plant growth, or black; pronotum with depressed areas and lower portions moderately clothed with fairly long pale hairs which are oblique and often curved; scutellum similarly clothed; elytron with sides of depressions on disc similarly clothed; ventral surfaces largely glabrous, a few pale hairs along median portion and on extreme apex of abdomen; legs thinly clothed on femora, moderately clothed on tibiae and tarsi with oblique golden buff hairs.

Head slightly longer than prothorax, as broad at end of rostrum as at eyes, very slightly narrowed behind eyes; rostrum subcylindrical in basal 2/5, not grooved above and with a very fine raised median line, but with a distinct groove on upper part of side; surface finely and closely punctured. *Antenna* barely reaching to humerus; scape distinctly thickened apically, with a few large punctures; funicle with segment 2 distinctly longer than 1 and 3. *Prothorax* distinctly longer than broad, subparallel-sided in basal 1/2, very slightly widened at extreme base, subevenly narrowed anteriorly with a moderately constricted apical collar; disc with a pair of high irregular tubercles, with a distinct obtuse depression between them; median groove irregular, somewhat deeply depressed anterior to tubercles; surface very strongly and coarsely vermiculate except on much of apical collar. *Scutellum* about as long as broad. *Elytron* about 4× as long as broad; humerus slightly rounded but hardly projecting; sides slightly widened behind humerus and then gradually narrowed to obtusely rounded apex; discal tubercle quite small, followed by a depression and then a large obtusely rounded raised area near apex; disc with subregular longitudinal rows of depressions which have flat glabrous bottoms forming narrow ellipses or oblongs, intervening areas subreticulate-vermiculate, with some fairly distinct partial transverse ridges more strongly raised than longitudinal or oblique ridges; side with partial rows of shallow punctures. *Ventral surfaces* fairly shiny, largely impunctate. *Legs* long; hind femur fairly smooth, finely punctured; hind tibia straight, more closely punctured; last hind tarsal segment as long as 1+2. Length 21 mm (24 including rostrum); breadth 6.8.

♀. Stouter; elytral tubercle a little larger and followed by a deeper depression. Length 26 (30) mm; breadth 9.7.

Paratypes. Dorsal reticulate pattern varying from white to tawny to black, depending on presence of waxy layer or vegetation. Length 19.5-28 (23-31) mm; breadth 6.0-9.3.

Holotype ♂ (BISHOP 6836), Mt Wilhelm, 2600-3000 m, NE New Guinea, 2. VII. 1963, J. Sedlacek; allotype ♀ (BISHOP), same data; 78 paratopotypes, same data or 2800-2900 m, 6.VII.1963; 1 paratopotype, 2830 m, mossy forest, XI.1962, M. Erben; 13 paratypes, Lake Sirunki, 2800-2900 m, 15. VI. 1963, Sedlacek.

Differs from *reticulatus* Mshl in often having a tan coloration with whitish reticulation,

and less often gray and black, in having reticulations on pronotal tubercles sharp and coarser, and with a broader and more truncate emargination between pronotal tubercles, with more regular and more hairy elytral depressions and with less sharp and less strongly raised reticulations.

This species is not as heavily affected by plant growth as *reticulatus*. However, in addition to fungi, algae and lichens, this species also occasionally supports liverworts.

38. *Gymnopholus* (*Symbiopholus*) *vegetatus* Gressitt, n. sp. Figs. 9i, 11i.

♀. Black, to a considerable extent clothed above with a layer of white waxy material apparently secreted by derm and serving to help support extensive fungal growth; this secretion on raised reticulations giving the impression of a white vermiculate pattern on elytron; femora in part reddish pitchy. Upper surfaces of prothorax and elytron in part clothed with fairly thick hairs in depressed areas; rest of body subglabrous except for oblique silvery golden hairs on antenna, tibiae and tarsi.

Head at eyes slightly narrower than postoccipt and barely broader than at end of rostrum; rostrum slightly narrowed anterior to base and somewhat gradually broadened to apex, its upper surface fairly smooth, without any distinct groove and with very weak punctures. *Antenna* reaching to base of elytron; scape straight, gradually thickened to rounded apex, nearly as long as funicle; segment 2 of latter longer than 1 and 3; club slender, acute apically. *Prothorax* as broad as long, subparallel in basal 3/5, gradually narrowed to apex; disc swollen, with a pair of irregular tubercles which are nearly merged into a single central swelling, with only a narrow groove between; surface coarsely vermiculate, with partly vertical corrugations at side; tops of tubercles slightly vermiculate. *Scutellum* minute. *Elytron* slightly broadened to about middle, somewhat gradually narrowed posteriorly with extreme apex obtuse but slightly produced at sutural angle; a moderate tubercle near top of apical declivity and a weaker swelling slightly closer to extreme apex than to former, and close to a slight swelling on suture just above extreme apex; surface with fairly irregular longitudinal series of deep depressions, transverse and longitudinal ridges between these depressions forming subregular reticulations. *Ventral surfaces* largely smooth; abdominal sternites 3 and 4 strongly raised apically; last flat and very weakly punctured. *Legs* long; femora slender, weakly punctured; hind tibia nearly straight, slender, suddenly thickened apically; hind tarsal segment 1 much shorter than last. Length 28.5 mm (32 including rostrum); breadth 11.8.

Holotype ♀ (BISHOP 6837), Mt Michael, 3160 m, Eastern Highlands, NE New Guinea, 23.XII.1964, R. Hornabrook.

Differs from *reticulatus* Mshl in being larger, with elytral reticulations more regular and with pronotal tubercles much closer together and nearly fused into a single tubercle.

Fig. 12. a, *Gymnopholus fungifer* n. sp. ♀, with fungi and lichen *Parmelia* sp.; b, *G. lichenifer* n. sp. ♂, with lichen *Parmelia* (*P.*) *reticulata* Tayl.; c, same with dorsum covered with fungal/algae growth and with young lichen, *Parmelia* sp.; d, same enlarged, with some oribatid mites showing as shiny dots behind lichen; e, *G. algifer* n. sp. with fungal/algae growth and young lichen; f, *G. lichenifer* ♂, with lichen *Parmelia* (*P.*) *crenata* Kurok. (sect. *Hypotrachyna*); g, same, ♀, with lichen *Anaptychia* sp.; h, same, ♂, with dorsum covered with fungal/algae growth; i, *G. algifer*, base of left elytron of same individual as in e, showing oribatid mites among fungi; j, *G. reticulatus* Mshl with young lichen, *Physcia* sp., on center of pronotum growing on fungus garden.



The type has extensive fungal growth on pronotum and elytra. Much of the dorsal pubescence is hidden by the growth. On the pronotum it is somewhat difficult to distinguish between ridges and fungal growth.

39. *Gymnopholus* (*Symbiopholus*) *rugicollis* (Heller) Fig. 10c.

Aroaphila rugicollis Hillr, 1913, Archiv Naturg. A 79 (1): 44, fig. 6 (Sattelberg, NE NG: DRESDEN).

Gymnopholus rugicollis: Marshall, 1959, Bishop Mus. Occ. Pap. 22 (7): 75, figs. 1b, 2b.

Pronotal tubercles steep anteriorly, rugose; humeri prominent; elytra with isolated small pits. Length 18-34 mm.

40. *Gymnopholus* (*Symbiopholus*) *fungifer* Gressitt, n. sp. Figs. 9jk, 11j, 12a, 14d.

♂. Black, shiny beneath and dull above, only moderately shiny on head. Body sparingly clothed above with somewhat tufted scales, mostly in depressions and on posterior portions of elytron; head and antenna with only a few oblique hairs, ventral surfaces largely glabrous, some pubescence at end of abdomen; legs with femora very sparingly pubescent but with denser hairs on tarsi and apices of tibiae.

Head distinctly longer than prothorax; rostrum parallel-sided only on basal portion and gradually widened to apex which is much broader than base, upper surface very shallowly depressed medially and with a shallow depressed area on each side of basal portion; surface of rostrum weakly punctured; occiput still more finely punctured. *Antenna* reaching to about base of elytron; scape somewhat suddenly and weakly swollen apically; funicle with segment 2 longer than 1 and 1.5× as long as 3; club fairly short, fusiform. *Prothorax* barely longer than broad, somewhat parallel-sided in basal 3/5, then somewhat gradually narrowed, slightly collared at apex with apical portion somewhat declivitous above; disc strongly raised on each side with tubercles which are slightly convex exteriorly and obliquely declivitous interiorly with median depression somewhat irregular, and fairly narrow and deep at bottom; surface coarsely and irregularly vermiculate; tops of tubercles almost carinate. *Scutellum* minute. *Elytron* long, slightly protuberant at side of humerus, then slightly narrowed and slightly broadened anterior to middle, gradually narrowed posteriorly and somewhat bluntly and obtusely rounded at apex; a weak tubercle just before and above apex, preceded by a depression and then another fairly weak tubercle about 1/4 elytral length from apex; surface with irregular depressions of varying depths, deepest just behind base and on posterior portion. *Ventral surfaces* largely glabrous and shiny, with sparse and weak punctures, denser on last abdominal sternite; metasternum shorter than mid or hind coxa; abdominal sternites 3 and 4 very short and swollen, to form transverse ridges. *Legs* long and slender; femora finely and sparsely punctured; hind tibia nearly straight; tarsi broad. Length 20.5 mm (24 including rostrum); breadth 7.4.

♀. Prothoracic tubercles more distinctly carinate; elytral depressions weaker on post-median portion; scales metallic golden green, small and rounded; tarsi somewhat reddish, with metallic scales of various tinges of blue and green, with a few at apices of tibiae. Length 24 (28) mm; breadth 9.3.

Paratypes: Considerable variation in structure but prothorax always very strongly raised

and subcarinate at each side and strongly vermiculate. Extensive fungal growth in depressions of pronotum and elytron often presenting a splotched gray-brown to pale buffy-brown appearance, sometimes with patches of paler lichen growth. Length 20-30 (23.5-35) mm; breadth 6.8-12.

Holotype (BISHOP 6838), nr Freyberg Pass, N. side, 1550 m, Main Finisterre Range, Huon Peninsula, NE New Guinea, 1-21. X. 1958, W. W. Brandt; allotype ♀ (BISHOP), same data; 21 paratopotypes (BISHOP, CAS, USNM, BMNH, ANIC, DASF, DRESDEN), same data; 1 paratype, Funyende, 1200 m, Saidor, Finisterre Range, 24-30.IX.1958, Brandt.

Differs from *reticulatus* Mshl in being somewhat stouter, with pronotal rugosities stronger, sharper and less dense, and elytral depressions less regular, with deeper depressions near base and weaker ones in center; easily recognized by the very wide, generally obtuse or rounded-obtuse concavity between pronotal tubercles and the carinate, externally almost vertical tubercles.

This species supports extensive fungal growth. Lichen growth, *Parmelia* sp. occurs on 2 specimens.

41. *Gymnopholus* (*Symbiopholus*) *lichenifer* Gressitt, n. sp. Figs. 11k, 12b-d, f-h, 13ac, 14e.

♂. Black; bases of femora pitchy reddish brown. Depressions on dorsum clothed with minute subrounded metallic golden-green scales generally with sides of depressions bearing minute reddish brown branched hairs which appear to bear a reddish sticky secretion; antenna and anterior end of head with oblique pale hairs; pubescence on antennal club silvery gray; legs with sparse oblique pale hairs, becoming longer and denser on apices of tibiae.

Head considerably longer than prothorax; rostrum slightly narrowed anteriorly in central portion and strongly widened at anterior end, with a narrow median dorsal groove and a shorter groove on each side; occiput finely punctured. *Antenna* reaching nearly to base of prothorax; scape somewhat gradually thickened to apex and sparsely punctured; funicle longer than scape, with segment 2 longer than 1 and 3 and apical segments barely longer than broad; club fusiform, subacute. *Prothorax* hardly longer than broad, slightly widened in middle and gradually narrowed to apex which is weakly collared; disc with a large tubercle on each side somewhat anterior to middle, somewhat rounded above, compressed at side, with intervening space rather shallowly rounded-concave; surface with irregular depressions and raised vermiculate ridges or subrounded callosities; outer side on tubercle with some large depressions and with subvertical wrinkles on lower part of side. *Scutellum* minute. *Elytron* fairly long, subparallel in basal 1/2, then gradually narrowed and obtusely rounded apically; humerus very slightly projecting; apex with a blunt tubercle on apical declivity preceded by a depression and then a small subacute tubercle near top of declivity; surface with irregular depressions, fairly deep on basal portion and on much of upper surface, with some irregular vermiculation or reticulation between, and much weaker, smaller and arranged in longitudinal rows, at side. *Ventral surfaces* rather shiny black; metasternum shorter than mid or hind coxa; abdominal sternites 3 and 4 quite short and convex; last sternite convex and slightly punctured. *Legs* long and slender; femora weakly punctured; hind tibia slightly arched, irregularly punctured; tarsi broad bearing a few bluish scales; claws very weakly divergent. Length 19 mm (23 including rostrum); breadth 7.4.

♀. Pronotum smoother, with depressions larger and more flat. Elytral depressions less

numerous, particularly at side, and in part shallower; last abdominal sternite depressed and fairly flat, not distinctly punctured. Length 26 (31) mm; breadth 10.4.

Paratypes: Pronotal tubercles quite variable, often quite low, but almost always with

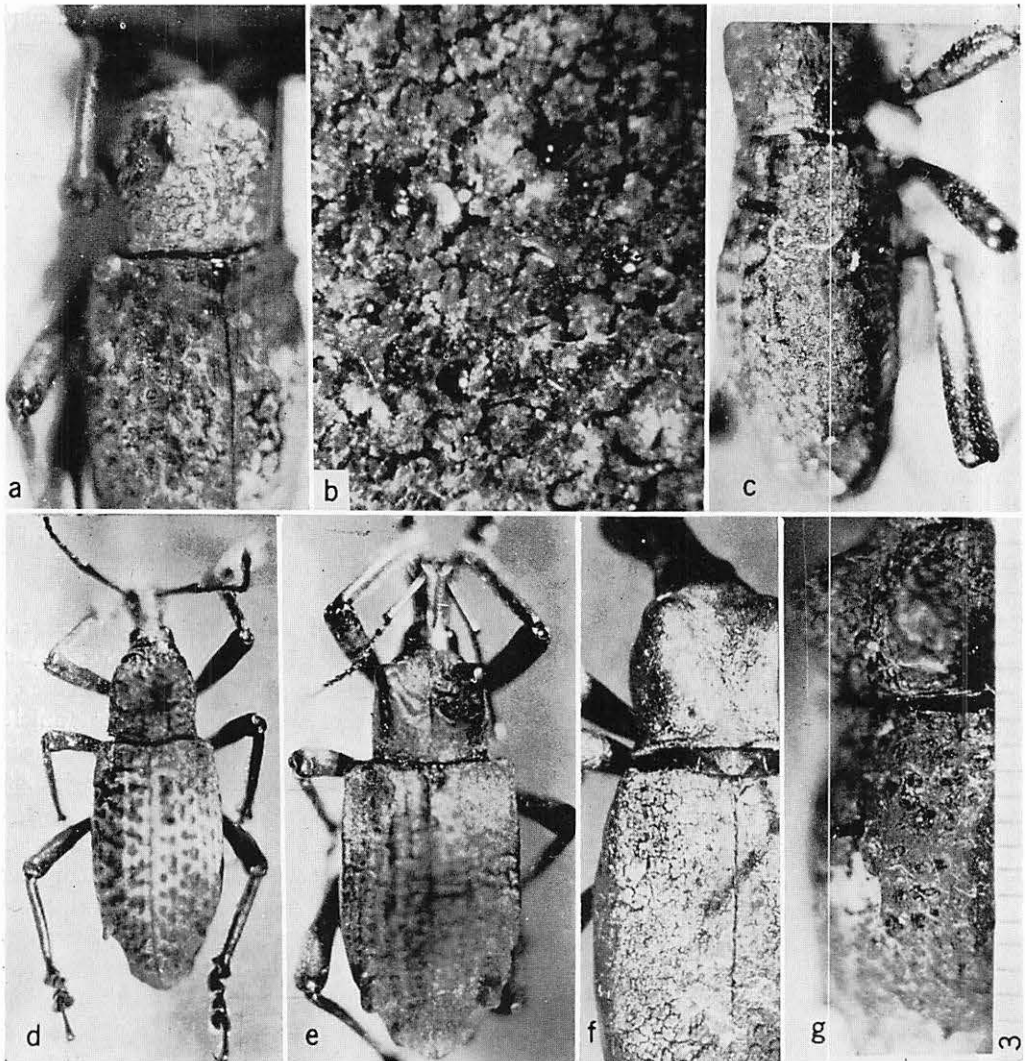


Fig. 13. a, *Gymnopholus lichenifer* n. sp. ♀ with dense covering of fungal growth, with some fruiting areas, on pronotum, and oribatid mites largely hidden in cells in fungal/algal growth in pits on basal 1/2 of left elytron; b, portion of elytron of *G. algifer* n. sp. with dense growth of fungi and blue-green algae, showing several partly to largely hidden oribatid mites and a small round (orange) fungal fruiting body in center beside incipient growth of lichen (white); c, *G. lichenifer* with fairly extensive fungal/algal growth with several psocopterans and their exuviae adhering; d, *G. botanicus* n. sp. ♀, with moderate fungal/algal growth; e, *G. algifer*, fairly fresh individual with early fungal/algal growth; f, same, with heavy covering of fungal/algal growth; g, *G. acarifer* with 3-4 oribatid mites among fungal/algal growth in each pit on basal 1/2 of right elytron.

some vermiculations or depressions on both sides; elytral depressions less conspicuously variable than pronotum. Length 19.29 (22-33) mm; breadth 7.5-10.8.

Holotype ♂ (BISHOP 6839), Bulldog Road, 2500 m, 19-29 km S of Wau, NE New Guinea, 31.V.1962, J. Sedlacek; allotopotype ♀ (BISHOP), same data; 9 paratopotypes, same data; 36 paratypes (BISHOP, CAS, USNM, BMNH, ANIC, DASF, DRESDEN), Mt Kaindi, 2300 m, above Edie Creek, 16 km S of Wau, I.1963, 1.VII.1965, Sedlacek, 1.I.1965, Gressitt; 4 paratypes, Bulldog Road, 2350 m, 32 km S of Wau, 30.V.1962, Sedlacek; 7 paratypes, Edie Creek, 2200 m, 16 km S of Wau, IX.1961, II.1962, VIII.1963, Sedlacek; 10 paratypes, behind Wau, 1700 m, I.1963, VII.1956, Sedlacek.

Differs from *reticulatus* Mshl in being stouter, less narrowed behind, with prothorax more vertical anteriorly, with tubercles much more separated, broadly concave between them and subvertical externally, and elytron with less regular reticulations and depressions and a more distinct tubercle on lower part of apical declivity.

This species supports the most prolific fungal and lichen growth observed. The former often covers entire pronotum and elytra, and the latter sometimes the entire elytra. Dr M. E. Hale estimates that this lichen growth may have required from three to five years to develop. Lichens found on this species include *Parmelia* (*Parmelia*: *Hypotrachyma*) *crenata* Kurokawa, *P.* (*P.*: *Reticulata*) *reticulata* Taylor, *P.* sp. and *Anaptychia* sp.

45. *Gymnopholus* (*Symbiopholus*) *herbarius herbarius* Gressitt, n. sp. Figs 11o, 15c-g.

♂. Black, slightly dull above and shiny beneath. Pronotum with dense erect white hair in median depression and sparse stout red setae which are shorter than pale hairs; elytron with both whitish hairs and stout red setae, sparse and limited on base and dense and covering most of apical 1/3 of upper portion, intervening space with very fine sparse pubescence; legs and antenna with sparse oblique pale hairs; ventral surfaces subglabrous.

Head distinctly longer than prothorax; rostrum hardly grooved above, finely punctured, strongly widened apically. *Antenna* with scape stout apically; funicle with segment 2 barely longer than 1 and somewhat longer than 3; club moderately stout. *Prothorax* barely longer than broad, slightly convex and ridged on lower part of side; disc weakly punctured, partly rugose between the moderately rounded tubercles which are less widely separated than middle of sides. *Scutellum* small. *Elytron* narrow, subparallel, narrowed and rounded apically; surface fairly even, with series of very weak depressions, and with 2 weak tubercles apically besides swelling on suture on apical declivity. *Ventral surfaces* shiny, feebly punctured. *Legs* fairly slender, moderately wrinkled or punctured; hind tibia straight; hind tarsal segment 1 hardly longer than 2 or 3, much shorter than last. Length 21 mm (25 including rostrum); breadth 6.8.

♀. Body stouter, rounded-obtuse apically. Length 24.5 (29) mm; breadth 9.

♂ Paratypes. Length 16.5-27 (20-31) mm; breadth 5.4-10.6.

Holotype ♂ (BISHOP 6840), W. slopes, Murray Pass, 2700-2900 m, nr Mt Albert Edward, SE NG, 5-6. XI. 1965, J. & M. Sedlacek; allotopotype ♀ (BISHOP), same data; over 100 paratopotypes, same data; 100 additional paratypes, between Waitape and Murray Pass, 2450-2800 m, 4.XI, Mt Albert Edward, 2800-3200 m, some on *Rhododendron*, 6. XI. 1965, J. & M. Sedlacek.

Differs from *cheesmanae* Mshl in being stouter and less narrowed posteriorly, with pronotal

tubercles less strongly raised and less widely separated than sides of prothorax. Fungal and lichen growth is quite common on this species.

45a. *Gymnopholus (Symbiopholus) herbarius oribatifer* Gressitt, n. subsp. Fig 11p, 15h.

♂. Black, dull above, shiny beneath; rostrum yellowish orange except at apex. Pronotum and posterior portion of elytron possibly pubescent, but heavily encrusted with fungal growth; stout erect setae tawny instead of red; elytron with distinct depressions; tubercles very weak. Length 19 mm (23 including rostrum); breadth 6.

♀. Similarly colored; stouter; elytral tubercle fairly strong. Length 26 (31) mm; breadth 11.

Paratypes. Length 17-27 (20-32) mm; breadth 5.8-11.

Holotype ♂ (BISHOP 6841), Iongai to Murray Pass, E slopes Wharton Range, Owen Stanley Mts, SE NG, 2300-3000 m, 7, 10.XI.1965, J. & M. Sedlacek; allotype ♀ (BISHOP), same data; 35 paratypes, same data.

Differs from the typical form, which is found on the opposite side of the same range, in being rougher above, with pitted and reticulate elytron; and in having rostrum stouter, more cylindrical in central portion, orange instead of black, and smoother and more finely punctured. This subspecies is heavily vegetated, particularly with fungi (all specimens collected), and supports a high population of the oribatid mite. Almost no mites were found on the larger series of the typical form.

Acarifer-group

This group is characterized by a very large body, broad prothorax with tubercles large, widely separated and projecting farther out than middle of side of prothorax, vermiculate pronotum, and strongly foveate elytron.

42. *Gymnopholus (Symbiopholus) acarifer* Gressitt, n. sp. Figs. 9l, 11-l, 13g.

♀. Black, dull on dorsum and shiny on venter. Body largely glabrous, a very few hairs on apex of abdomen and on coxae; legs with very sparse pale hairs, longer and denser on tarsi and apices of tibiae; head and antenna with rather few hairs.

Head distinctly longer than prothorax; rostrum subparallel-sided in basal portion, then gradually and then very strongly narrowed to apex, medially grooved above, with a wide groove on each side in basal portion; occiput finely and somewhat closely punctured. *Antenna* reaching to base of elytron; scale reaching nearly to posterior margin of eye, moderately swollen apically; funicle with segment 2 slightly longer than 1 and distinctly longer than 3, last 1.5× as long as broad; club fusiform, blunt apically. *Prothorax* distinctly broader than long, widest just behind middle, narrowed and briefly collared apically; tubercles very widely separated, slightly convex both externally and internally, briefly ridged longitudinally at summit; surface coarsely vermiculate, with irregular depressions. *Scutellum* minute. *Elytron* stout, subparallel basally and gradually narrowed and bluntly rounded apically; humerus projecting slightly upward and outward; apical declivity produced on suture just before apex and with a weak obtuse tubercle a short distance from apex and preceded by a depression and then a smaller but more acute tubercle just before apical declivity; disc with irregular deep depressions, some separated by narrow ridges

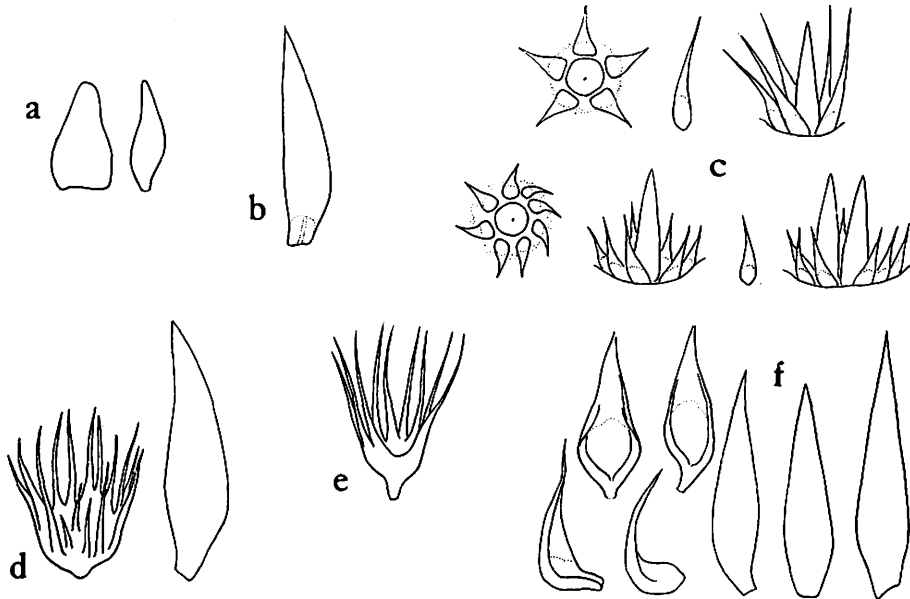


Fig. 14. Samples of minute specialized scales on elytra of *Gymnopholus* spp., all magnified about $\times 100$: a, *Gymnopholus* (s. str.) *nothofagi* n. sp., stout tubercle-like scale, length about 0.1 mm, top and side views; b, *G. (Symbiopholus) cheesmanae* Mshl; c, several samples from *G. (S.) algifer* n. sp. - those in whorls are situated in a single puncture; top views, at left, show stout nature of erect central spike; d, *G. (S.) fungifer* n. sp.; e, *G. (S.) hepaticus* n. sp.; f, *G. (S.) lichenifer* n. sp.

and others by fairly wide raised smoothish areas, depressions sometimes in groups separated by partial ridges or low ridges, bottoms of concavities often somewhat flattened; side of elytron fairly even, with very few depressions. *Ventral surfaces* smooth and glossy, with a few sparse punctures at sides; metasternum very short between mid and hind coxae. *Legs* long; femora slightly sinuate and somewhat wrinkled, with feeble punctures; hind tibia nearly straight, with large bristle-bearing punctures distally; tarsi with bristles but without distinct scales. Length 28.5 mm (32.5 including rostrum); breadth 9.8.

Paratypes: Length 24-29 (28-34) mm; breadth 10-10.6.

Holotype ♀ (BISHOP 6842), Mt Kaindi, 2300 m, 16 km SW of Wau, 8-9.VI.1962, J. Sedlacek; 2 paratypes, Bulldog Road, 2850 m, 32 km S of Wau, 29-30.V.1962, Sedlacek. 3 specimens (ex DASF), close to this species, but not designated paratypes: 2, Mt Shungol, 2200 m, nr Lae, XI.1963, Miroslav Erben; 1, Mt Amingwina, 3300 m, nr Wau, alpine grassland, 18-25.IX.1963, Guy Rosenberg.

Differs from *reticulatus* Mshl in being much stouter, with pronotal tubercles much more widely separated and with elytra bearing very deep, irregularly placed concavities, instead of regular seriate cavities and reticulations.

This species bears growth of fungi, lichens, liverworts and perhaps also algae. One of the paratypes bears about 60 oribatid mites among the fungi growing in the elytral cavities, with a few mites on the pronotum.

43. *Gymnopholus* (*Symbiopholus*) *senex* Gressitt, n. sp. Figs. 9m, 11m.

♀. Black; parts of antenna and tarsi slightly pitchy. Body practically glabrous; only a few very short hairs on antenna, parts of thoracic sternites and inner sides of tibiae; hairs on tarsi and apices of tibiae very short.

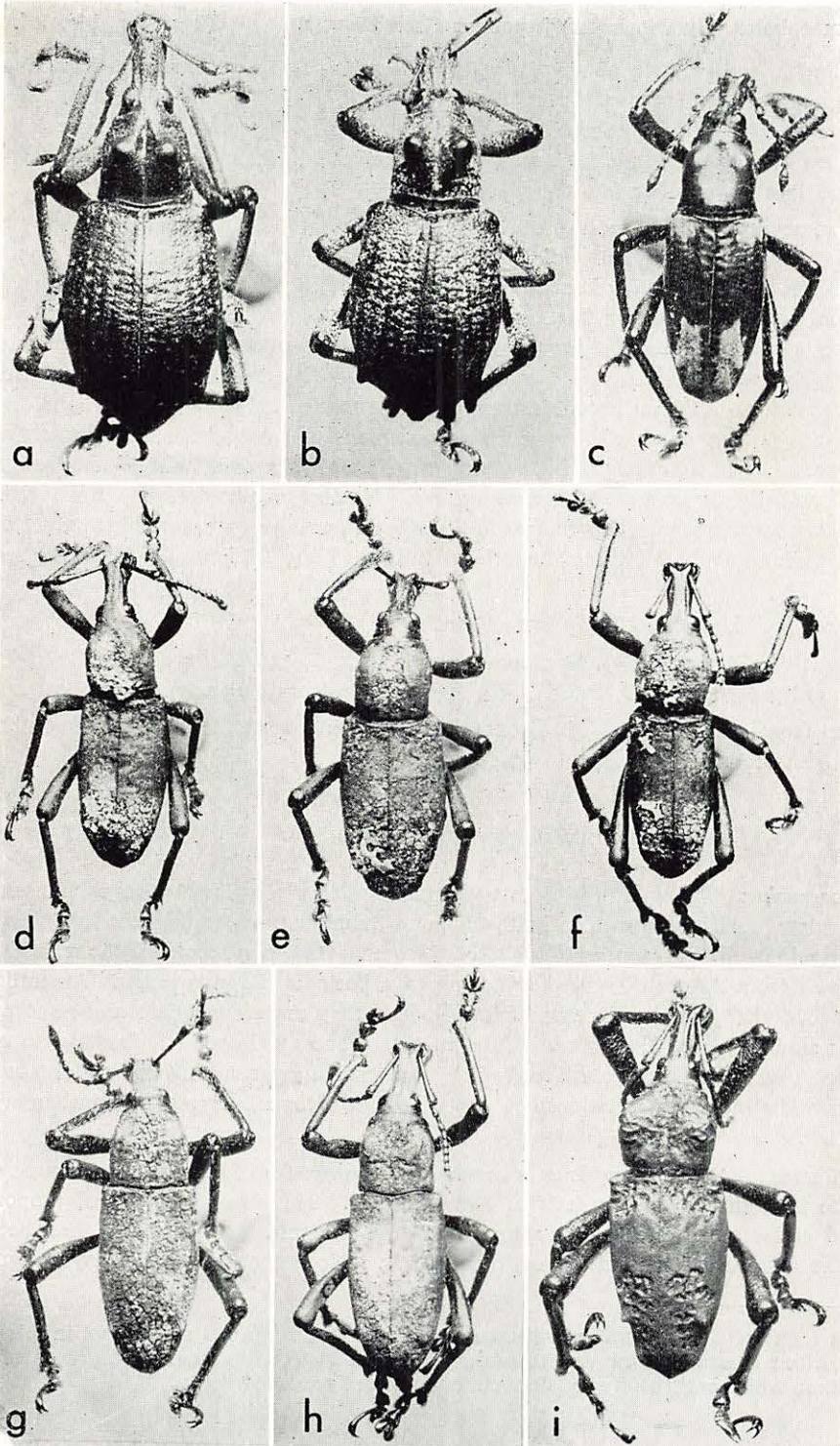
Head at eyes slightly narrower than at end of rostrum and distinctly narrower than at postocciput; rostrum narrowest near base, somewhat gradually broadened apically, grooved medially and on each side of upper surface, with rather vague and sparse punctures. *Antenna* reaching to base of elytron; scape slender, nearly straight, somewhat suddenly thickened apically, nearly as long as funicle; first 2 segments of funicle subequal; club somewhat unevenly fusiform. *Prothorax* slightly broader than long, subparallel, but uneven, in basal 1/2, then somewhat arcuately narrowed anteriorly and slightly constricted before apex; disc with a very large tubercle on each side which is somewhat vertical externally and weakly convex above, forming an irregularly rounded apex and a somewhat obtuse depression between; surface irregularly vermiculate, particularly on upper portion and outer side of tubercle. *Scutellum* small, broader than long. *Elytron* stout, distinctly wider than prothorax, subparallel in basal 2/5, then somewhat gradually narrowed and obtusely rounded apically forming a common obtusely rounded apex; side vertical, a fairly distinct ridge extending backward from the slightly tuberculate humerus, a blunt tubercle at top of apical declivity and a somewhat larger more rounded tubercle between former and apex, and 2 swellings on apical sutural ridge; upper surface with large deep pits, partly arranged in 3 double rows separated by incomplete ridges. *Ventral surfaces* fairly smooth, very sparsely punctured, with abdominal sternites 3 and 4 very short and strongly raised. *Legs* fairly stout; femora transversely wrinkled and hind femur thickest at apex; hind tibia slightly arched, in part weakly asperate; tarsi broad, bare above, last segment longer than 1 and 2 combined. Length 28.5 mm (34 including rostrum); breadth 10.6.

Holotype ♀ (BISHOP 6843), Mt Yelia volcano, nr Menyama (Meniama), edge of rim of crater, 3300 m, alpine grassland, 20.I.1963, Guy Rosenberg.

Differs from *acarifer* n. sp. in being much more glabrous, in having pronotum more rounded and less ridged on outer edge of tubercle and more shallowly grooved medially, and in having elytron with more regular and more independent pits, with suggestions of longitudinal rows and with 2 discal ridges besides posthumeral ridge, and with subapical tubercles more pronounced.

The type specimen has moderately extensive fungal growth in the elytral pits. It appears to be a very old specimen, and may have lost hairs on body and appendages normally present on its relatives. The habitat of this species may be too sunny to permit extensive fungal and lichen growth, or its habits may provide too much abrasion.

Fig. 15. *Gymnopholus* (*Symbiopholus*) spp: a, *G. fallax* n. sp. ♂; b, same, ♀; c, *G. h. herbarius* n. sp. ♂, fresh adult without plants, showing areas of long fine pubescence and spike-like setae in central pronotal depression, humeral areas and posterior elytral areas; d-f, same, ♂♂, with fungal-algal-lichen growth started in the same pubescent areas shown in c; g, same ♂, with entire dorsum of pronotum and elytra covered with continuous fungus garden, with some incipient lichen growth; h, *G. h. oribarifer* n. subsp. ♂, dorsum largely covered with fungal-algal growth, partly lichenized; i, *G. hepaticus* n. sp. ♀, fairly fresh adult bearing very early growth of fungi, algae, lichens and liverworts in elytral depressions and pronotal concavity.



46. *Gymnopholus* (*Symbiopholus*) *hepaticus* Gressitt, n. sp. Figs. 11q, 14e, 15i.

♂. Black, largely dull above and shiny beneath. Depressed areas of pronotum with minute green and golden metallic compound scales and with a few short erect stout red setae; scutellum with pale pubescence; depressed areas of elytron with some scales similar to those on pronotum; smoother areas with sparse minute hairs; venter subglabrous; antenna and legs with rather few oblique pale hairs.

Head somewhat longer than prothorax; rostrum parallel-sided basally, very strongly widened anteriorly, grooved medially above and on upper part of side, finely punctured. *Antenna* with scape gradually broadened apically, reaching to hind margin of eye; funicle fairly stout, segment 2 longer than 1 and 3; club fairly stout. *Prothorax* distinctly broader than long, wider at sides of tubercles than at middle of side of prothorax; tubercles very large, widely separated, coarsely vermiculate, with median depression irregular. *Scutellum* small, transverse. *Elytron* broad, narrowed and rounded-obtuse apically; humerus tuberculate; disc with a number of very deep depressions at base and with a larger area of deep depressions in apical 1/2, intervening area relatively even with a few shallow depressions and slightly granulose-punctate surface. *Venter* smooth, minutely punctured. *Legs* somewhat stout, corrugated on femora and toothed internally on tibiae, hind tarsal segment 1 nearly as long as 2+3 but much shorter than last. Length 25 mm (30 including rostrum); breadth 9.2.

♂ Paratype. Length 26 (30.5) mm; breadth 9.

Holotype ♂ (BISHOP 6844), W slopes Murray Pass, 2700-2900 m, nr Mt Albert Edward, Owen Stanley Mts, SE NG, 5-6.XI.1965, J. & M. Sedlacek. Paratype, same data.

Differs from *acarifer* in having pronotal tubercles more rounded in lateral outline and elytron with second 1/4 lacking deep foveae.

ZOOGEOGRAPHY-EVOLUTION

Zoogeography: This genus appears to be purely Papuan in the zoogeographic sense. Its known close relatives are also in the Papuan Subregion, extending out to Sulawesi and the Philippines on the west and to Fiji on the east. Only two species of the tribe Eupholini are known from Australia, and they belong to a basically Papuan genus. Australia has a number of other genera of the subfamily, but they are all endemic and none are very close or similar to the Eupholini. Thus in this group the Papuan fauna has no close tie with the Australian fauna, with only 2 known exchanges resulting from Pleistocene connection. The apparent relationships are with the Oriental Region rather than with the Australian.

The distribution of *Gymnopholus* is somewhat puzzling, for of over 1400 specimens studied, only one is from the western half of New Guinea³. This is entirely out of proportion to the field collecting time spent in appropriate environments. No material has been seen from the Bismark Archipelago or Solomon Is. No authentic records are known to me

3. As a result of a misunderstanding it was concluded that there was no material in this genus at the Leiden Museum. However, there do prove to be specimens from the Third Archbold Expedition, which will modify the distributional picture presented here.

Table 1. Altitudinal range of known *Gymnopholus* species*

Altitude range in meters	Subgenus <i>Gymnopholus</i> s. str.					Subgenus <i>Symbiopholus</i>		
	Species-groups: I, III	II	IV	V	VI	VII-X	XI	XII
1000-1500	urticivorax fulvospretus (suturalis)*	(carinatus)*		weiskei				
1500-2000	fulvospretus cyphothorax marshalli	angustus	integristrostris ludificator	weiskei		audax** fallax** (kokodae) cheesmanae algifer		
2000-2500	nothofagi fulvospretus	marquardtii gressitti splendidus	interpres brandti divaricatus glochidionis	weiskei regalis sedlaceki	magister szentivanyi	algifer cheesmanae	(rugicollis) fungifer lichenifer	acarifer
2500-3000	nothofagi	mammifer mucosus gressitti		weiskei sedlaceki		praecox** zoarkes	reticulatus botanicus h. herbarius h. oribatifer	acarifer hepaticus
3000-3500		ajax gemmifer perspicax			hornabrooki	symbioticus zoarkes	vegetatus h. herbarius	acarifer senex

* Species in parentheses are of somewhat questionable altitudinal origin.

** Lacking symbiotic growth.

from below 1000 meters in altitude. It appears as if this genus is very actively evolving, and that isolation of populations at or near the tops of various mountains in this geologically rather young area is producing many new races or species. The two species with the widest apparent distribution, *weiskei* and *gressitti*, appear to be highly variable and to be segregating into subspecies or separate species.

On the first map (fig 1) the known distribution of the entire genus is presented, with symbols segregating the species of the 2 subgenera, and of the higher altitude and medium altitude species. A very wide gap is seen between the known occurrences of the westernmost species and the next westernmost. Essentially, the great majority of known species are from the Western Highlands, Eastern Highlands, Madang and Morobe districts of North-east New Guinea and the Central District of Papua (Southeast New Guinea). The principal mountain ranges involved are the Bismark Range, associated ranges to its southwest and southeast, the Finisterre and Saruwaged ranges on the Huon Peninsula, the Owen Stanley Mts in the southeast, and a few isolated mountains or smaller ranges.

On the second map (fig 2) the part of eastern New Guinea is shown which covers the ranges of all the known species other than the single western species. The 2400 meter contour line shows that most of the species occur at nearly this altitude, or higher. The numbers are those used for the species in the list, key and text. Table 1 lists the species by altitude ranges, under groupings of species-groups. From this table it is seen that one species, *weiskei*, has a very great vertical range, but that most species are restricted in altitudinal occurrence. Also, certain species groups have a fairly limited vertical range, as IV (*interpres*-group), from 1500 to 2500 meters. Further, *Symbiopholus* average from higher altitudes than *Gymnopholus* s. str. In many cases only one species of a species-group occurs on a single mountain or range, but in a few instances two species of a species-group occur in almost the same locality and altitude-range. This is shown in Table 2, which demonstrates the high correlation of number of species to number of species-groups on most mountains. For instance, at Daulo Pass there are five species of five species-groups, and in the Finisterres (more than one mountain), six species of five species-groups are known. This suggests that when populations become isolated on various mountains, most of the species-groups had already evolved, and occurred in the different areas. Then they would have further differentiated, resulting in different species of each species-group on different mountains. It may be seen that where one or more species are in common (shown by brackets on left, Table 2), the areas are joined by the 2400 meter contour line (fig 2).

Evolution: Evolution in *Gymnopholus* provides some interesting material for consideration. Probably the smooth forms (typical subgenus) are the more ancestral, even though their relatives, *Eupholus* and *Rhinoscapha*, are largely covered with scales. The smooth species are the ones occurring lower in altitude, on the average, and are in part more generalized, although some bear strong elytral tubercles and high pronotal swellings, and some also have marked sexual dimorphism. The development of trimorphism within one sex (as in *nothofagi*) is again puzzling, particularly since that species is felt to be the most generalized in the genus. That species is also interesting because it is the only member of the typical subgenus known to support plant growth. It has very specially modified scales which are very stout and almost pyriform (fig 14a). Some of the specialized scales on species of *Symbiopholus* are complex, resembling blossoms (fig 14c), or are otherwise unusual. Some species have very fine long hairs surrounding stout spike-like setae, in areas

Table 2. Numbers of species in different mountain ranges, approximately west to east. (brackets at left indicate one or more species in common, excluding *weiskei*)

Mountain or area	Altitude of coll'n	Species	Species-groups	Subgenera	
				<i>Gymnoph.</i>	<i>Symbioph.</i>
Wissel Lakes	1550	1	1		×
{ Lake Sirunki	2500	3	3	×	×
{ Mt Hagen	2500	1	1	×	
{ Mt Giluwe	2200	1	1	×	
Mt Wilhelm	2800	1	1		×
{ Sepik-Wahgi Div.	2000	1	1	×	
{ Daulo Pass	2500+	5	5	×	×
{ Mt Otto	2200	2	2	×	×
Mt Karimui	2500	1	1	×	
Mt Michael	3000+	3	3	×	×
Okapa-Purosa	2000±	3	3	×	
Mt Yelia	3300	3	2	×	×
{ Finisterre	13-2500	6	5	×	×
{ Saruwaged	14-2500	5	4	×	×
Mt Shungol	2750	2	2	×	×
Eddie-Kaindi-Bulldog	12-3000	6	5	×	×
Mt Strong	3500	1	1		×
Goilala area	13-2500	5	5	×	×
{ Mt Albert Edward	20-3200	6	4	×	×
{ Mt Tafa-Mondo	1600±	2	2	×	×
Kokoda area	1000+	2	2	×	×
Mt Obree	3010	1	1	×	

commonly matted with vegetation.

Flight loss is general in the genus, but may not be of very ancient derivation, as most individuals have wings of about 1/2 to 2/3 normal size, and the elytra are often rather weakly fused. In all species the metathorax is of greatly reduced size, indicating degeneration of wing muscles. Very likely the loss of flight would have been a prerequisite to the evolution of the symbiotic relationships, as the flight of a heavy beetle would probably be too disturbing to the plants and associated biota, particularly through rubbing the elytral surfaces on landing in vegetation. Flight loss also undoubtedly has had a great deal to do with the development of the local speciation in the genus resulting in differing populations on the different mountains or ranges. Because of the fairly pronounced altitudinal limitations of most species, there is little chance of gene-flow between populations which have become adapted to moss forest above the altitudes of connecting ranges.

Explanation of the evolution of the symbiotic relationships involved in the species of *Symbiopholus* requires speculation. Each species has some special modifications related to the encouragement of the plant growth. This involves depressions, pits, etc, on pronotal and elytral surfaces, specially modified scales or hairs, and a sticky secretion.

The development of different forms within a species, and particularly within one sex of one species might be the result of selection for different genes with different favorable effects, or some genetic throwbacks. It appears that the different forms occur in the same populations, rather than representing divergence with geographical isolation.

Presumably the presence of plant growth on the backs of the weevils serves the function of protective resemblance of plants, and thus protection from natural enemies, resulting in natural selection for reproduction of individuals favoring the plant growth. This could account for a general evolutionary trend towards increase in the development of the structural modifications, and the secretion, thus favoring plant growth.

Members of a few species (*reticulatus*-group) often have the non-pubescent derm of the dorsum apparently covered with a white waxy layer of unknown function. This is sufficiently developed to give the beetle a pale pattern. Sometimes this appears to represent pigmentation of the derm, and sometimes a waxy layer, or both. Possibly this might serve as camouflage, as it is often difficult to distinguish from fungal growth. It might be a useful adaptation derived as a byproduct of the evolution of a secretion to foster plant growth, which in itself serves the function of protective resemblance.

Host relationships: These weevils feed on the leaves of woody plants growing in moss forest, or at the upper forest edge and in the alpine shrubbery zone. Members of the typical subgenus feed on *Nothofagus*, *Laportea*, *Melia*, *Trema*, *Pipturus*, *Tephrosia*, *Glochidion* and other trees. Some of the more common species, like *weiskei*, feed on several genera of hosts. Species of *Symbiopholus* feed on *Rhododendron* and other woody genera.

SYMBIOSIS

Of the approximately 1400 specimens at hand of this genus, about 850 belong to the subgenus *Symbiopholus*, and about 675 show some development of plant growth on their backs. The species involving symbiosis live on woody plants in fairly high altitude moss forest on various mountains. They thus occur in a very damp environment, with high humidity all of the year, and considerable shade from rain clouds and fog. Temperatures are moderate, in general probably ranging from 12° to 33°C.

The dorsal surface of the weevil is often entirely clothed with a blanket of fungal growth, mixed with algae. More rarely a part, or even all, of the elytral surface is covered with lichen growth (fig 12b). Liverworts are generally scarce on *Gymnopholus*, but may be extensive in growth on elytra of some large cryptorrhynchine weevils living in the same environments.

The fungus gardens vary in depth, but are sometimes a millimeter deep on fairly level surfaces. They may be deeper where the grooves or depressions are deeper. In general there appears to be a mixture of blue-green algae with fungi of several groups. In addition, there are algae of another type, which almost resemble young moss growth, though generally sparse. About 3% of the individuals of the symbiotic species have conspicuous lichen growth, but another 5 to 6% have early growth, and still more have incipient growth. Since lichens grow slowly, it is obvious that these weevils must be long-lived. An age as great as 5 years has been suggested to account for lichen growth covering the entire elytra.

The relationship with the plants appears to represent true mutualistic symbiosis. The plants apparently derive a suitable substrate which perhaps offers some protection from enemies, and the weevils derive a coat giving them a protective resemblance to plant growth on parts of trees, or at least camouflage. The weevils appear to be specially modified to encourage the establishment and growth of the plants.

There are perhaps 12 families of plants involved in the association. These include the

following, which represent only partial and provisional determinations.

Fungi

- Fungi Imperfecti: Phyllostictales: ?Leptostromataceae (dark-walled fructification)
 " " " : ?Nectrioidaceae (yellow pycnidium)
 Ascomycetes: Helotiales: ?Helotiaceae (pale yellow discomycete)
 " " : Helotiaceae (minute discomycete with dark ascocarp)
 " : Hemisphaeriales: ?Micropeltaceae (superficial, flattened, dark-walled ascocarp having a central opening)

Algae⁴

- Cyanophycophyta
 Cyanophyceae: several types
 Trentepohliaceae: (to be verified)
 Other families

Lichens

- Physciaceae: *Physcia* sp. (on *G. reticulatus*)
Anaptychia sp. (on *G. lichenifer*)
 Parmeliaceae: *Parmelia* (*Parmelia*: *Hypotrachyna*) *crenata* Kurokawa (on *G. lichenifer*)
Parmelia (*Parmelia*: *Reticulata*) *reticulata* Taylor (on *G. lichenifer*)
Parmelia spp. (on *G. spp.*)

Liverworts

- Jungermanniales: Metzgeriineae: Metzgeriaceae: *Metzgeria* sp.
 " : Jungermannineae: Lejeuniaceae

Fungi have been found growing on 14 species of *Gymnopholus* (13 *Symbiopholus*, and also on *nothofagi* in the typical subgenus). Algae grow on most or all of the same species. Lichens has been observed on 10 species in the genus and liverworts on 4 species.

The plants appear to thrive on some smooth areas on the beetles backs, but more particularly in pits, grooves and depressions and on areas covered with specialized scales or setae (see figs 12-14). Since these scales and setae differ from those of weevil relatives lacking the symbiotic arrangement, it seems very likely that the scale modifications have been influenced by the symbiosis, in an evolutionary sense. The sticky secretion is found particularly on the elytra, and the elytra are more often vegetated than the prothorax. It appears that the secretion serves the purpose of nourishing and providing a substrate for the plants. It may be exuded from orifices on each side of the mesonotum.

Living more or less within the fungal growth with intermixed algae are numerous oribatid mites representing a new family (see following paper by Aoki). The mites are generally burrowing within the plant growth, and often seem to have formed cells in which they feed. Being only about 0.2 mm long when mature, the mites are often completely hidden under the surface of the plant growth. As many as 75 mites have been on the back of a weevil, without removing plant growth to detect those that might be completely hidden (see fig 13). The mites are also fairly abundant under lichen growth on the weevils. Since all stages of the mite occur in the same niche, it seems obvious that the mite spends

4. Additional algae identified while article was in press are: Chroococcales: Chroococcaceae; and Nostocales: Nostocaceae, Oscillatoriaceae (or Scytonemataceae).

its whole life history on the backs of the weevils. The mites clearly feed on the fungal growth, and may feed on algae and lichens also. Undoubtedly the mites spread from weevil to weevil during mating of the latter, and perhaps also by crawling on the plants from one weevil to another. It seems probable that the mites may transfer the plant spores from one weevil to another in moving about. However air-borne spores may also be trapped in the sticky secretion on the backs of the weevils. This secretion seems to serve as a nutritive substrate on which the plants may commence their growth. The lichens demonstrate vegetative reproduction, which simplifies the process of dispersal.

Apparently the oribatid mites on the different species of weevils all belong to a single species. This suggests that the environment on the different beetles is fairly uniform from the standpoint of the mites, and that the isolation of the populations on different mountain ranges has had on appreciable effect on the evolution of the mites. It is not yet known whether these mites occur in the same types of plants on more normal substrates, or whether they occur only on the weevils. The groups of plants represented on the weevils are mostly of wide occurrence. Many of the lichens live normally on bark and many of the fungi occur as a rule on leaves. One of the lichens identified is of cosmopolitan occurrence, and another was known previously from Japan, Philippines and Borneo.

The mites occur scattered through and within the fungus gardens, but often concentrate in deeper pits. There may often be 3 or 4 together in a large puncture (fig 13g). Mites have been found on about 110 weevils of 5 species from the Owen Stanley Mts and from mountains in the Morobe District. Their apparent absence from the appropriate niche on *G. fungifer* in the Finisterre Mts is interesting, and likewise from the hairy-sided, flat-bottomed pits on *vegetatus*, *botanicus* and *reticulatus*, which look so appropriate for the mites.

Various structures of the weevils appear to help protect the plants and prevent their being rubbed off the hosts' backs. The various pits, concavities, tubercles and stiff setae help serve this purpose. There is little evidence that the male weevils do significant damage to the plants in the process of copulation.

Also living within the plant growth, primarily in fungal growth, on the weevils' backs are rotifers and nematodes. These are of small size, the rotifers measuring about 40 μ and the nematodes about 150 μ in length. The former are red and the latter colorless. These probably perform a saprophytic function, though they might feed upon the living plants. They are generally present on the same weevils which bear the oribatid mites, and may feed primarily in the areas where the mites have partially destroyed the plants. However, rotifers occur on *nothofagi* and *cheesmanae* which appear to lack the mites. Diatoms, and probably other microorganisms, also occur in this microenvironment.

Dead psocopterans and their exuviae adhering to the bodies of some of the weevils suggest that the bark lice were feeding on the plant growth on the weevils. Presumably the bark lice would feed particularly on algae, but perhaps also on fungi.

Parasitism: These weevils are rather commonly parasitized by mites of the family Erythraeidae, genus *Leptus*. These mites generally feed on the undersides of the weevils, and on the legs and antennae, but sometimes on the dorsum. On occasion mites attach behind the elytral tubercles in the typical subgenus (see fig 3p). A few other types of mites, including uropodines, occur sporadically on the weevils, but their ecological roles are not clearly understood.