PALOPHAGINAE, THEIR SYSTEMATIC POSITION AND BIOLOGY

G. KUSCHEL[1] and B.M. MAY[2]
[1]7 Tropicana Drive, Mt Roskill, Auckland 1004, New Zealand; [2]8/107 Walker Road, Pt Chevalier, Auckland, New Zealand

Abstract

Palophaginae is a subfamily of Megalopodidae proposed as recently as 1990 for two Australian genera. A brief account is now given on the main morphological features of the adult and larva defining the group, on oviposition, hostplant association, feeding, development, frequency, parasitism and predation. Illustrations are presented of adult and larval characters, of stands of an *Araucaria* species, and of male cones that contain the larvae. Adult and larva resemble those of Cerambycinae and Lepturinae, but the adult has antennae that do not flex back against the body and its genitalia are of a completely different type while the larva has an effaced clypeolabral suture and exhibits an extra inactive instar characteristic of a hypermetamorphosis. *Palophagus*, the principal genus of the taxon, has in the adult one of the most complete sets of veins within Chrysomeloidea and Curculionoidea and the larva feeds in the main on pollen of the male cones of *Araucaria* species. The subfamily has since been found also in Chile, again on *Araucaria* male cones. No Palophaginae and no Curculionoidea developing in the male cones seem to become parasitised but adults and nymphs of a species of Anthocoridae do enter the open cones to suck the body juices from nemonychid and curculionid larvae but were not observed on palophagine larvae.

Introduction

It is only five years since the subfamily Palophaginae (Megalopodidae) was proposed by the present authors (1990) for two Australian genera, *Palophagus* Kuschel and *Cucujopsis* Crowson. The rather limited amount of work that could be done on the general morphology of these genera was nonetheless sufficient to show that the taxon did not easily fit into any of the existing higher taxa of the leaf-beetle system. It was found that the new group shared a great number of features with Megalopodinae and that, although both groups differed rather substantially from the bulk of Chrysomeloidea, individually they did not warrant family status.

The association of *Palophagus* with the male cones (strobili) of *Araucaria* species was perceived to be in line with the relict attributes recognized in the adult. It was, consequently, no surprise that the subfamily Palophaginae was discovered, by the senior author, also in South America while the 1990 paper was still in press, and that this South American (more precisely Chilean) species was associated also with the genus *Araucaria* and with male strobili. The Chilean palophagine turned out to be just as elusive as the *Palophagus* species in the adult stage though just as numerous in the larval stage. The fact is that after five years of many attempts to secure adults, none has been obtained in the wild, and that the only one reared through emerged too weak to be able to pump up and extend the wings and elytra properly and died prematurely. Even so,

Chrysomelidae Biology, vol.3: General Studies, pp. 173-185
Edited by P.H.A. Jolivet and M.L. Cox

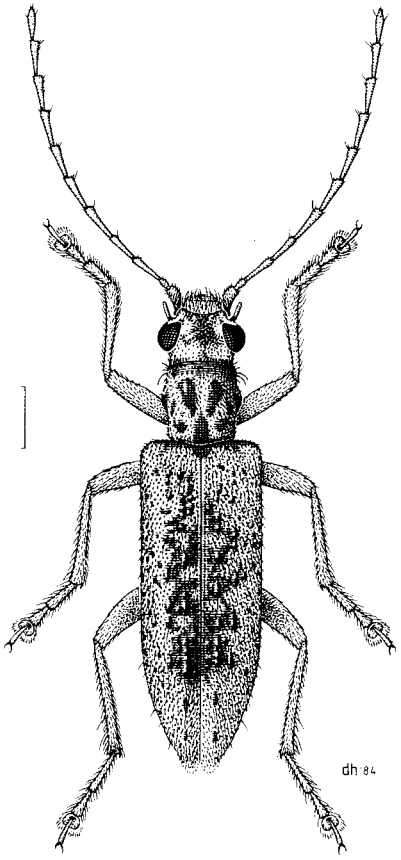


Fig. 1. Palophagus bunyae Kuschel, Bunya Mountains, S. Queensland, Scale = 1 mm.

notwithstanding its partly shrivelled condition, it is good enough for the species to be described, though only on external characters, if nothing better should turn up soon.

Salient attributes of Palophaginae

Adults of Palophaginae have a slender cerambycine or lepturine-like habitus (Fig. 1), a double, highly iridescent mesonotal file for a stridulatory organ – similar to that of Lepturinae – large, coarsely facetted and emarginate eyes, long, forward directed filiform antennae that bent back would extend to about the middle of the elytra, a distinct clypeolabral suture, plurisetose labrum and mandibles, a large, coarsely ridged mola,

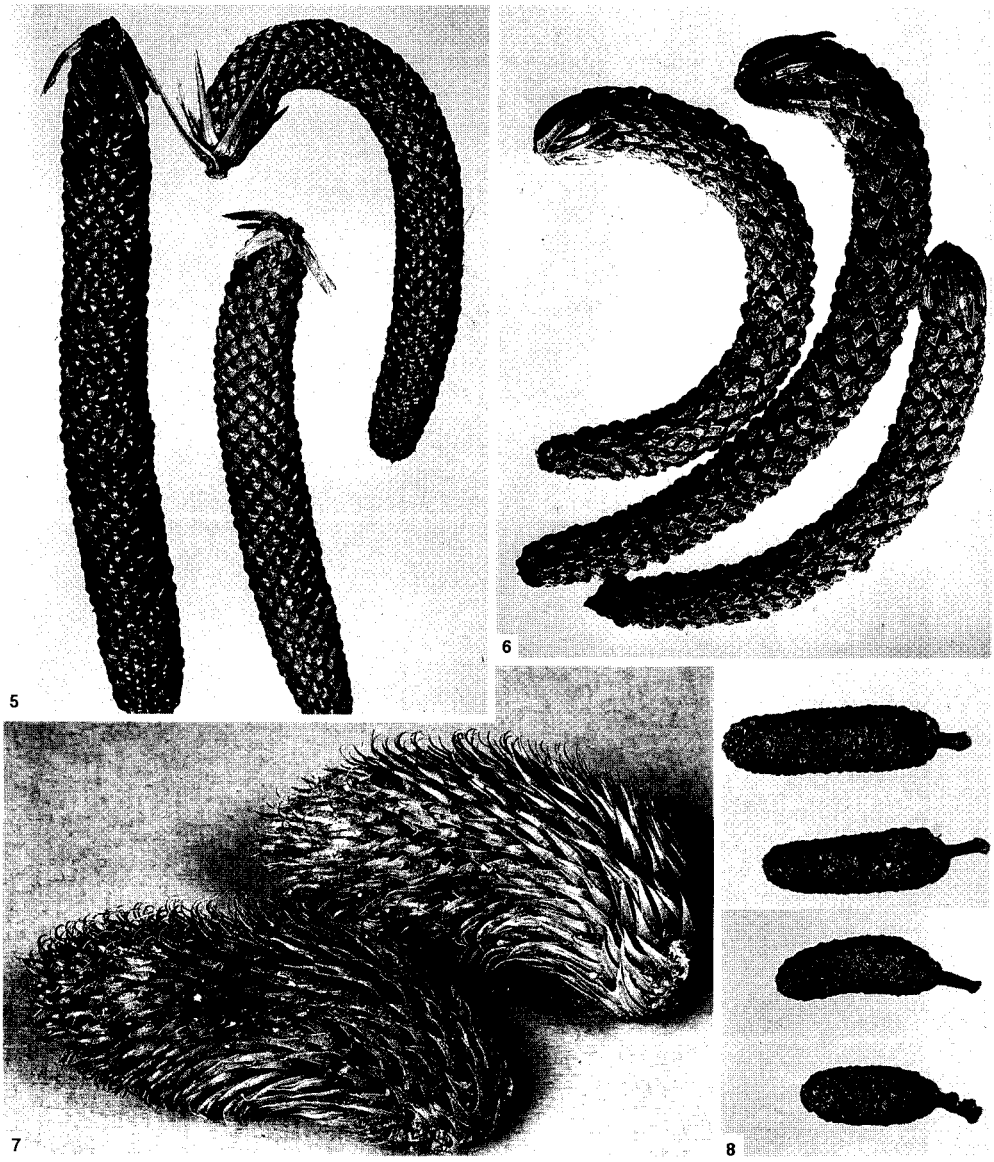
→

Figs 2-4. 2. *Araucaria araucana* on an airfall field of ash and lapilli at 1400 m of altitude, on the ridge at left mingled with *Nothofagus pumilio*, Volcán Lonquimay, Malleco Prov., Chile; 3. a stand of *Araucaria araucana* in undergrowth of *Nothofagus antarctica* behind a bare patch of volcanic airfall at 1050 m of altitude, Parque Nacional Conguillío, Cautín Prov., Chile; 4. *Araucaria araucana* with male cones at the tip of branches to the right, same place as at 3. (Photos by G. Kuschel, Nov/Dec 1994).

2

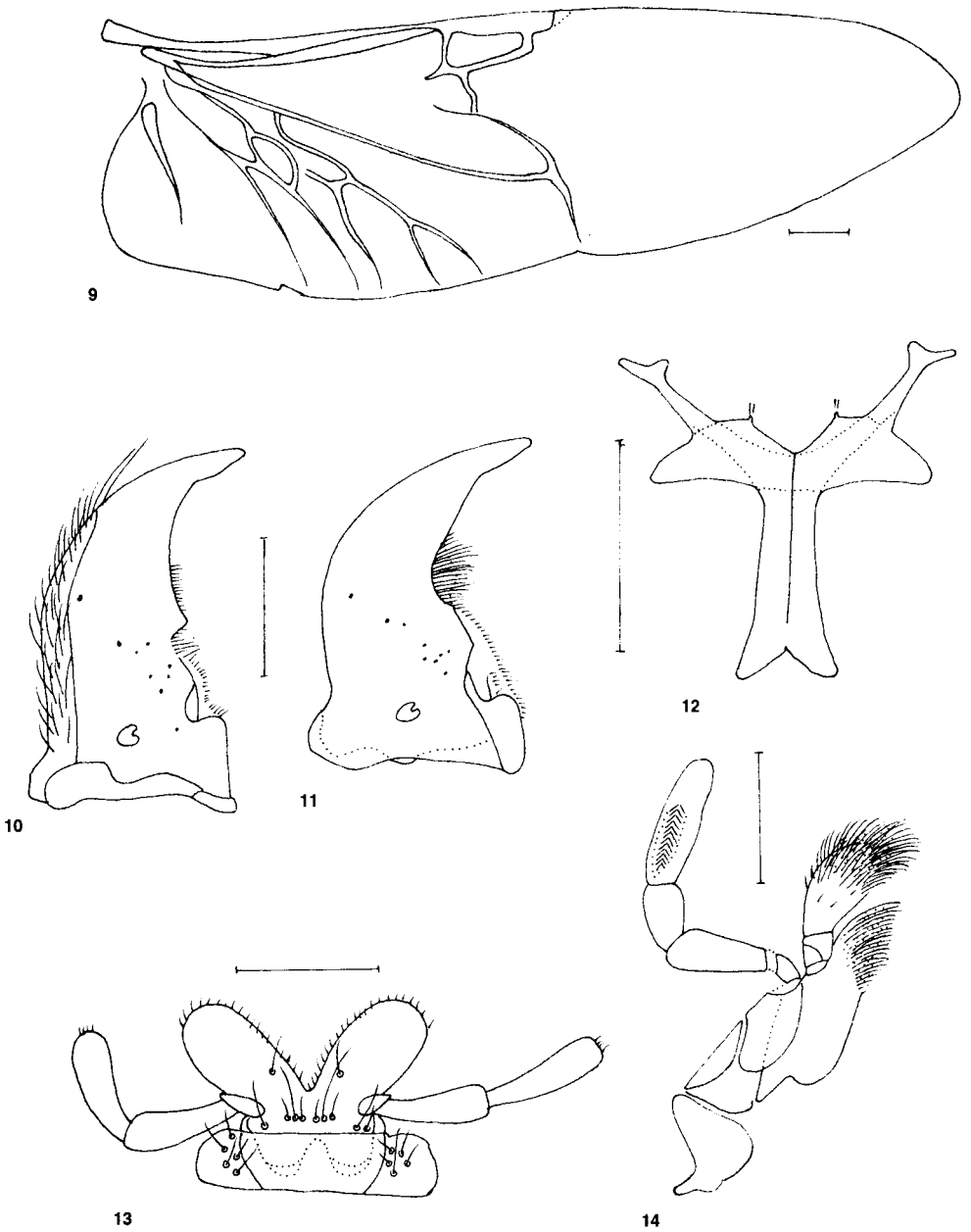
3

4



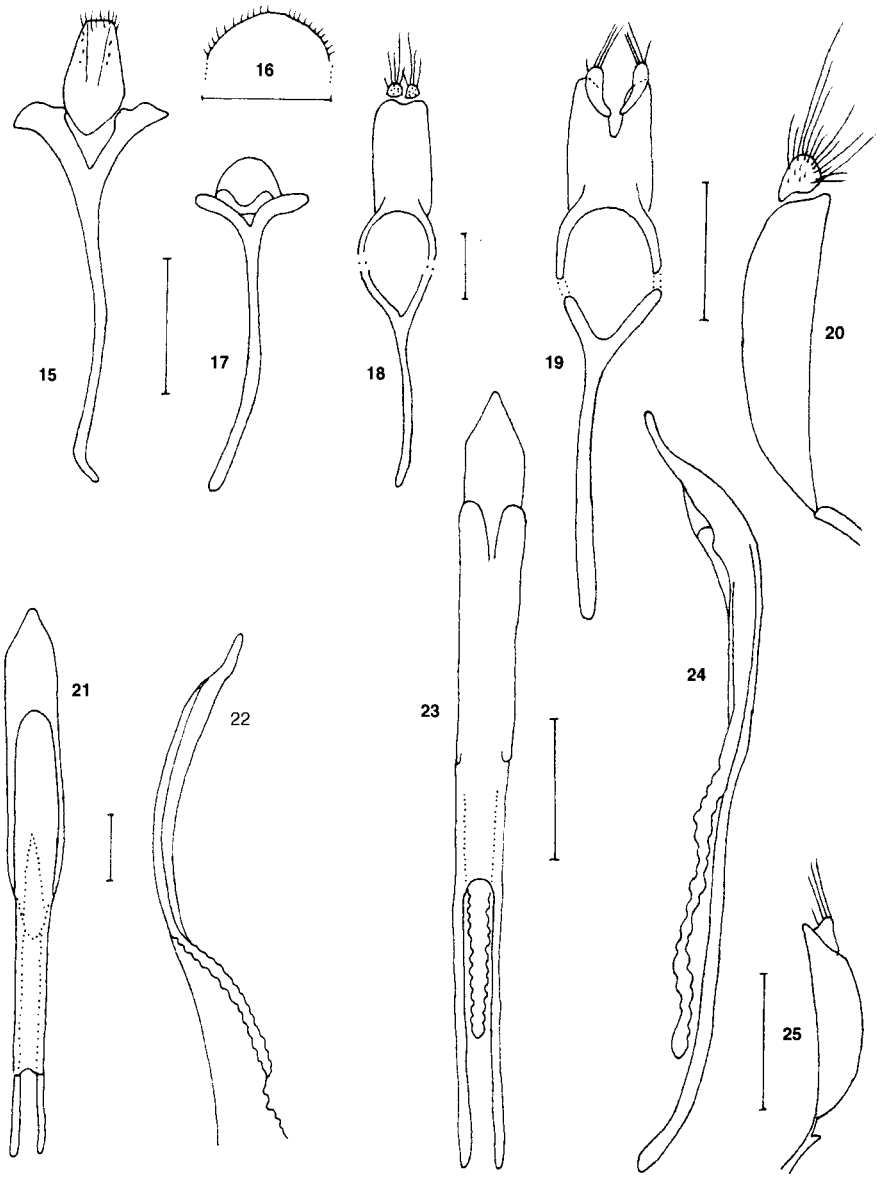
Figs 5-8. Male strobili (cones) of 5. *Araucaria bidwillii*, Bunya Mtns, S. Queensland; 6. *Araucaria cunninghamii*, Cainbable, S. Queensland; 7. *Araucaria araucana*, Volcán Llaima, Chile; 8. *Agathis atropurpurea*, Atherton Tableland, N. Queensland.

and a large, deeply bilobed ligula and large palpi (Figs. 10-14). The elytra are irregularly punctate lacking a scutellar striole and a sutural stria, and have a fine, low epipleural carina and long, robust sensory setae. The wing venation of *Palophagus* is as shown in Fig. 9, it is at least as complete as that of any cerambycid or chrysomelid. Fore coxae conical, fore-coxal cavities closed behind but partly open laterally, mid-coxal ones open right through to the mesosternal pleurite, all ventrites free, with



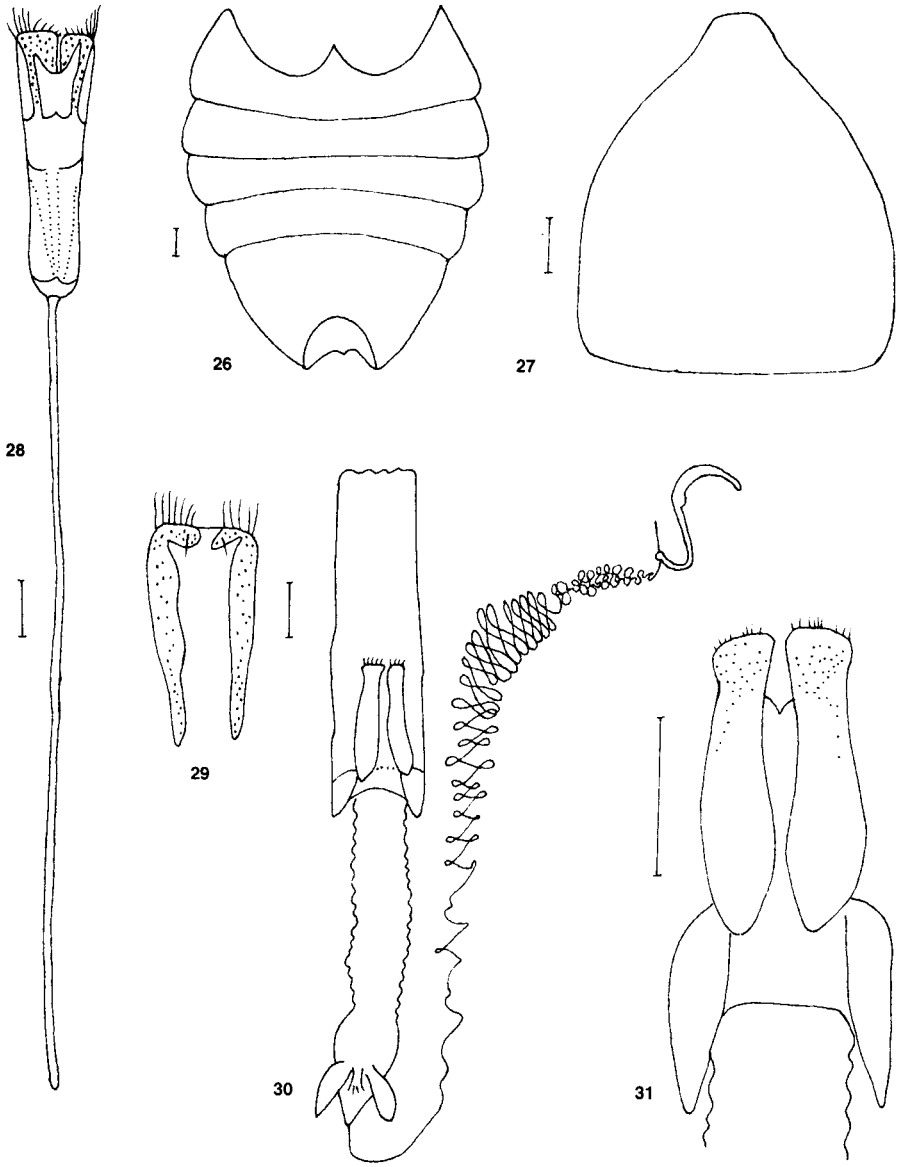
Figs 9-14. Palophagus bunyae: 9. hind wing; 10. left mandible, dorsal; 11. right mandible, ventral; 13. labium, ventral; 14. left maxilla, dorsal. *Cucujopsis setifer*: 12. metendosternite. Scales = 0.5 mm. (Kuschel and May, 1990).

straight transverse sutures; femora lacking carinae and crenulated ridges; all tibiae with 2 distinct spurs; tarsite 2 with an apical median lobe projecting on to tarsite 3, claw segment slender, with very small, finely setose empodium and thin, simple and divaricate claws. Male and female genitalia similar to those illustrated at Figs. 15-31.



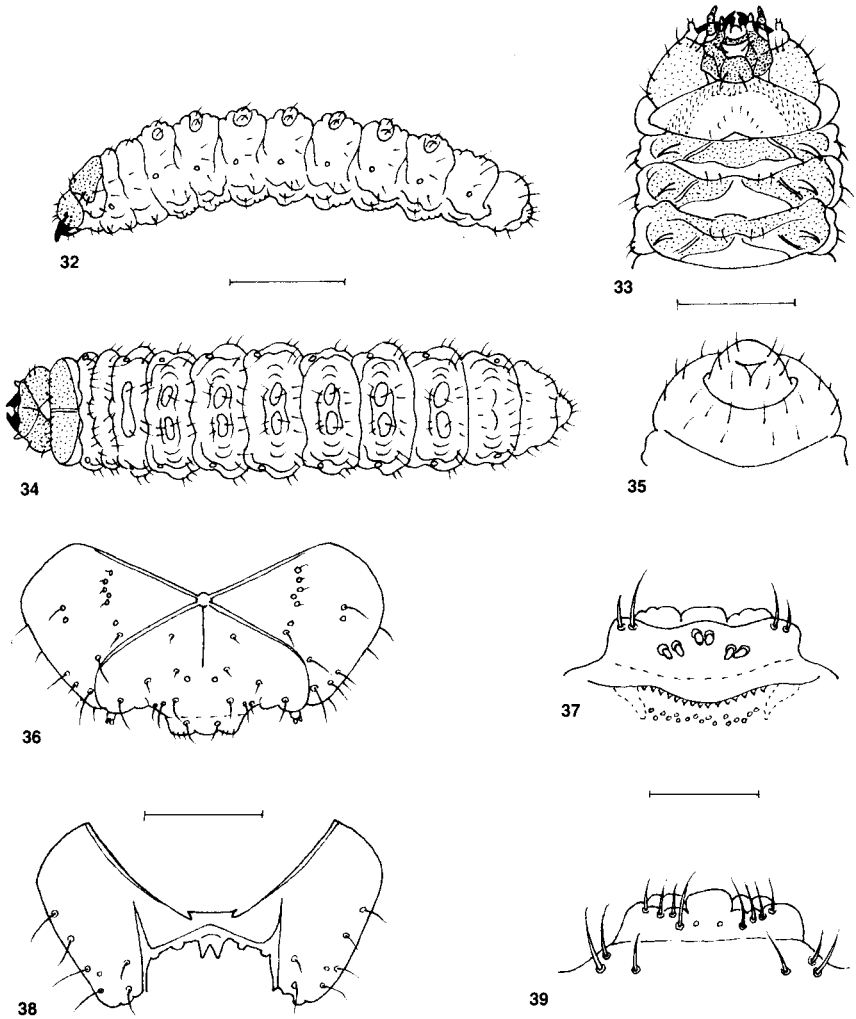
Figs 15-25. Palophagus bunyae, male: 15. sternite 9, ventral; 16. tergite 9, dorsal; 18. tegmen, dorsal; 20. parameral part of tegmen, lateral; 21,22. aedeagus, dorsal and lateral. *Cucujopsis setifer*: 17. sternite 9, ventral; 19. tegmen, dorsal; 23,24. aedeagus, dorsal and lateral; 25. parameral part of tegmen, lateral. Scales = 0.3 mm. (Kuschel and May, 1990).

Larvae of Palophaginae are dull yellow with a leathery cuticle and, after the manner of cerambycid larvae, have ambulatory ampullae dorsally and ventrally on each segment of the body which is straight-sided, depressed and approximately 4.5 times longer than wide. The ninth segment is unsclerotised and lacks urogomphi. The anal cleavage is Y-shaped. The cuticle does not carry the sclerotised tubercles of Chrysomelinae,



Figs 26-31. Palophagus bunyae, female: 26. abdomen; 27. tergite 7, dorsal; 28. sternite 8, ventral; 29. tergite 8, dorsal; 30. genitalia, with genital pocket, ventral; 31. hemisternites, ventral. Scales = 0.2 mm. (Kuschel and May, 1990).

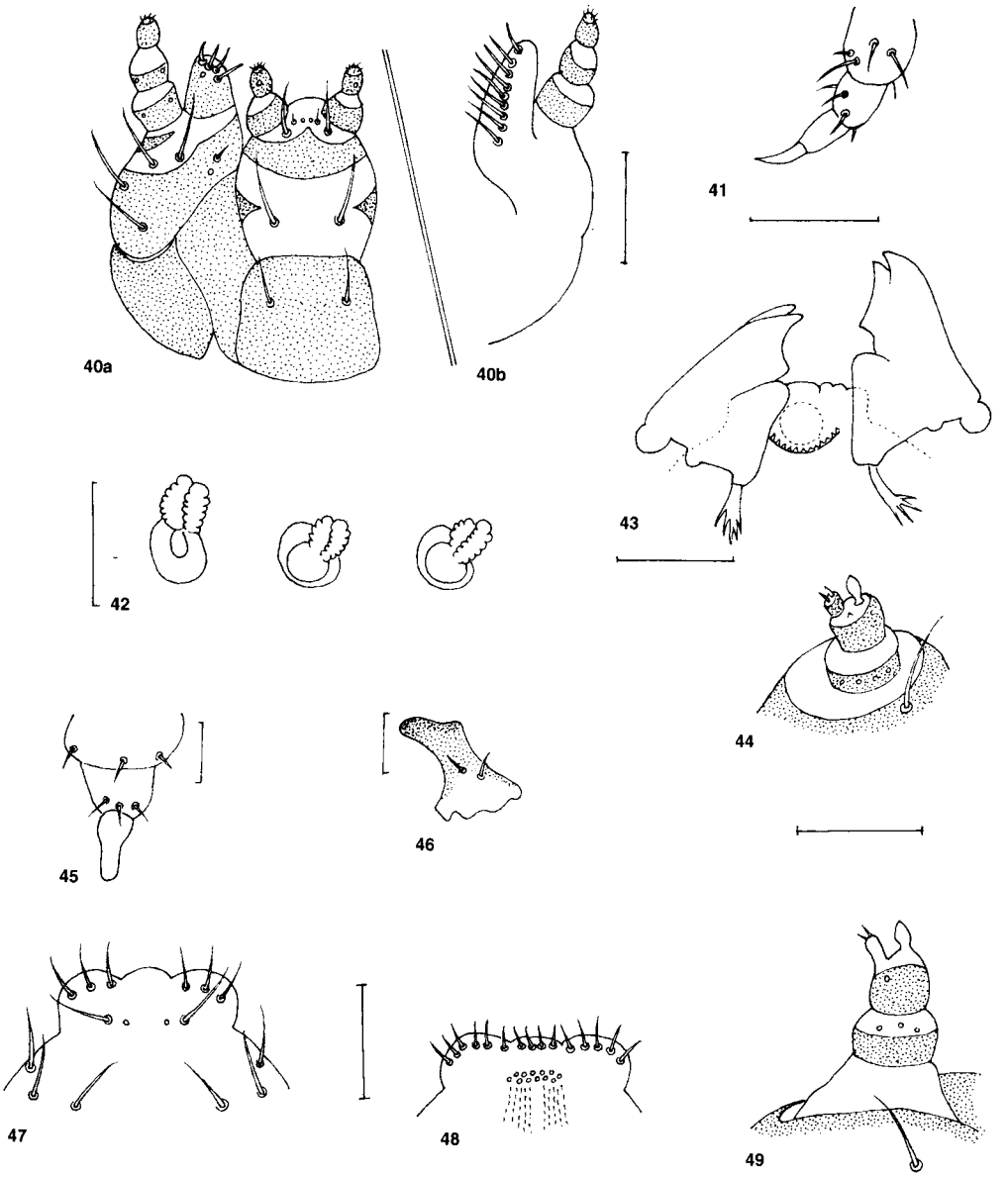
Galerucinae and Alticinae and the setal pattern, in formal descriptions, fits the nomenclature used for Curculionidae. 3-segmented, clawed legs are present on each of the thoracic segments. The head is transverse with strongly rounded sides and the postero-dorsal emargination extends to the frontal apex as in Lepturinae. The antennae, set within a retractable membrane, are 3-segmented with two apical supplementary processes. They are very similar to those of *Leptura sanguinolenta* Linnaeus. There are 6



Figs 32-39. Palophagus bunyae, larva: 32. habitus, lateral; 33. head and thorax, ventral; 34. habitus, dorsal; 35. Abd IX and Abd X, ventral, showing anal cleavage; 36. head, dorsal; 37. epipharyngeal lining; 38. head, ventral; 39. clypeolabrum and part of frons. Scales = 2.0 mm for 32,34, 1,0 mm for 33,35,38; 0.25 mm for 37,39. (Kuschel and May, 1990).

stemmata, the frontal suture is distinct and an endocarinal line is present. The clypeolabral suture is vestigial and the frontoclypeal suture effaced as in the primitive weevil family Nemonychidae, another group feeding almost exclusively on pollen. The mandibles, in addition to two apical teeth on the incisor section, bears a large upstanding molar process. The epipharyngeal lining, which is folded behind the labral margin, bears 6 peg-like setae and a curved line of denticles. The 3-segmented maxillary palps are set on a palpiger bearing a lateral sclerite and a cylindrical mala. Labial palpi are 2-segmented and the ligula is non-setose above a premental sclerite. The mentum and submentum are divided by a distinct suture.

In the pupa, the cuticle is glabrous with red-brown, moderately long, finely tapering setae, mounted on small tubercles. The eyes are large and prominent. The elongate an-



Figs 40-49. Palophagus bunyae: (40-44) larva: 40. maxilla and labium (a. ventral; b. maxilla, dorsal); 41. leg; 42. spiracles of thorax, Abd V and Abd VIII; 43. mandibles and epipharyngeal row of denticles, showing relative size and position of a pollen grain; 44. antenna. (45-49) prepupa: 45. leg; 46. mandible; 47. labrum-clypeus; 48. epipharyngeal lining; 49. antenna. Scales = 0.25 mm for 40,43,46,47,48; 0.125 mm for 41,42,44,49; 0.062 mm for 45. (Kuschel and May, 1990).

tennae are inserted below the eyes, curve backwards behind the fore and middle femora, then ventrad to meet the fore tarsi. The ninth segment is terminated by paired setose bosses but urogomphi (pseudocerci) are absent. The secondary pterotheca (wings) are as long as the primary ones (elytra).

Geographical distribution

Queensland and northern New South Wales in Australia, the provinces of Malleco and Cautín in Chile.

Biological notes

Hostplant

It is known that the *Palophagus* species and the still unnamed, closely related, Chilean genus are associated with *Araucaria*, a genus of conifers that was already present in early Jurassic times. The larvae of these palophagines develop in the sporophylls (scales) of the male strobili (cones). Those of *Palophagus* feed on the horny parts of the sporophylls and on unripe and ripe pollen alongside nemonychid larvae such as *Notomacer* Kuschel. The only four specimens of *Cucujopsis setifer* Crowson known to have been collected were secured at or near Kuranda, N of Cairns in northern Queensland where no *Araucaria* but some *Agathis* species occur. Although the *Agathis* male cone samples collected on the Atherton Tableland, SW of Cairns, were in excellent condition, no palophagine larvae were observed or reared from them. Still, it is assumed that *Agathis* is the most likely host genus for the *Cucujopsis* species.

Oviposition

Because the adult has a broad mouth and its hemisternites are blunt and short, not more than 0.5 mm long in the largest species, and because vaginal pouches are present and presumed to secrete a sticky substance, it is assumed that the eggs are placed on or near the male strobili. The question of when these eggs are laid, whether it is shortly before the male cones shed the pollen or at some other time, remains unanswered. No adults seem to be present shortly before or after the cones open up and the larvae of at least the Chilean species are nearly full grown by the time the strobili burst open, therefore it is conceivable that oviposition takes place much earlier, possibly shortly after the adults have emerged in autumn, when the young cones are already quite evident.

Feeding

No feeding of adults was observed in the field or the laboratory. Owing to the features of the mouthparts, which appear to be admirably adapted for feeding on pollen, and that no pollen of *Araucaria* or *Agathis* would be expected to be available at the time of emergence in autumn, the adult is probably able to feed on pollen other than that of the larval hostplant as most Cerambycinae and Lepturinae do. The authors have noted in their 1990 paper that '*Palophagus* larvae when first seen were in mature strobili, in the central pith, chewing the stalks of the spent sporophylls. When younger cones were examined, the larvae, never more than one at a time, were found to be feeding on pollen in company with an abundance of nemonychid larvae.' The proventriculus of the larva is unarmed, yet nearly all of the pollen grains found in the ventriculus itself were either split open or fragmented. It therefore seems likely that the mandibles are used as tools for grinding, helped perhaps by the curved line of denticles on the epipharynx which could hold the pollen grains for long enough to provide a crushing surface. Mann and Crowson (1981) noted that a definite molar part is lacking in all other known larvae of

Chrysomelidae, even though present in some adults. In such cases, its presence was apparently correlated to the habit of pollen feeding.

Development

Because all the cones sent from Australia for our programme had been picked up from the ground and had already been open for some hours or days, the impression then gained was that the palophagine larvae developed about as quickly as those of most Nemonychidae in hardly more than about 10 days. Later it was discovered that the larvae of the Chilean palophagine were almost fully grown by the time the cones burst open and that these did not leave immediately but in the following 3 to 8 days. It is now apparent that palophagine larvae require a much longer time for their full development than most nemonychids that share the cones with them. Some notes from the field book on the Chilean species are reproduced here:

23 Dec 94: 10 unopened cones, 13-15 cm long by 6 cm thick, were plucked from a tree at 1400 m of altitude by the main ski lodge of Volcán Lonquimay, Malleco Prov., Chile.

25 Dec 94: one cone commenced opening up and shedding pollen. It was immediately dissected. A not overly cautious examination revealed the presence of larvae of the following three beetle groups: (1) Palophaginae: 6 large, nearly full grown larvae, plus one larva of a smaller stage, all inside the microsporangia (pollen sacs); (2) Nemonychidae: 2 very small larvae, 1 in a gallery of the central pith (cone axis), the other in a pollen sac; (3) Curculionidae: 12 moderately large larvae of *Araucarietius viridans* Kuschel, the largest of the three derelomine species developing in the male cones, all in the pithy cone axis.

28 Dec 94: 9 larvae left the remaining 9 cones;

29 Dec 94: not checked on this day;

30 Dec 94: 23 additional larvae had vacated the 9 cones;

31 Dec 94: 34 further larvae had emerged;

1 Jan 95: 20 extra larvae came out;

2 Jan 95: 6 more larvae were out;

3 Jan 95: 4 larvae appeared on this day;

4 Jan 95: the last 3 larvae had left the 9 cones.

In short, a total of 99 palophagine larvae had vacated the 9 cones submitted for observation, an average of 11 larvae per cone. The same 9 cones had produced 70 *Mecomacer* larvae, probably of 4 different species, three of these about the same size as the palophagine, having left the cones from 5 to 14 days after the last palophagine larva had done so, an average of 7.8 larvae per cone; there were also 121 larvae of *Araucarietius viridans* which had abandoned the cones from 30 December to 9 January, which makes an average of a little over 13 specimens per cone. A total of 290 larvae, ranging in length from 4 to 9 mm, have come out from 9 cones, each cone containing on average 32.2 specimens. Considering that approximately three male trees occur per hectare (roughly 95% of trees of *Araucaria araucana* are monoecious) and that each tree bears at least 500 cones, one hectare should easily produce anything between 15000 and 30000 adult palophagine specimens in Chile annually. And yet, the species has eluded capture in the more than 200 years of effort made by man to cover the fauna of this particular tree since J.I.Molina described it in 1782 as *Pinus araucana*.

Although intensive rearing from male cones of *Araucaria* and *Agathis* had been carried out by the authors for well over a decade, no larvae of any other Coleoptera or other insect orders were ever noticed feeding on pollen.

When fully fed, the larvae crawled away from the cones, by this time on the ground. They were able to move easily on their venter, unlike cerambycid larvae which roll around helplessly when deprived of their tunnel walls. In the substrate, *Palophagus* and the Chilean species undergo a partial hypermetamorphosis. A cell is formed wherein the larva moults to an inactive prepupal stage and certain morphological changes occur. The head is no longer pigmented except for the mandibular tips and articulation points which are blackish; the antennae and palps are pale brown. The mouthparts have become non-functional and therefore simplified. Thus the epipharyngeal lining is no longer folded behind the labral margin and the curved row of denticles has disappeared. The mandibles are immovable with the incisor teeth obsolete and the molar absent. The intersegmental areas of the palps and antennae are swollen. The claws on the legs have become fused with the terminal segment. The spiracles are closed and airtubes vestigial. This phenomenon was observed in the laboratory when larvae, placed separately in glass vials containing fine perlite, made their cells in full view.

In *Palophagus*, after 5-6 months, a further moult to the pupal stage occurred. The final ecdysis to adult took place after another 30-50 days. Head capsule measurements showed that two larval instars in addition to the prepupal instar, were present in September, but the total number of instars could not be determined.

Parasitism and predation

Here it may be noted also that all the groups developing in the male cones seem to be entirely free from parasites (parasitoids) at least in the larval and pupal stages but are not entirely free from predators. As mentioned earlier, there is one anthocorid species in Chile which is common in open cones and attacks avidly the nemonychid and curculionid larvae.

Impact of the larvae on the cones

It may appear at a first glance that if so many adults and larvae are living inside the cones at the expense of cone tissue and pollen, production of pollen would be enormously impaired. However the cones are large and the pollen sacs massive in relation to the whole sporophyll, thus the quantity of pollen that remains unaffected is very substantial. Each cone that bursts open releases a veritable cloud of pale yellow pollen. 'Flowering' cones seem to be a special delicacy to parrakeets which forage on the tree crowns in pairs or small flocks. All the numerous fresh cones that are invariably found on the ground of a Chilean araucaria tree are there because of rather frequent visits by the 'austral parrakeet', known in the country by the name of 'cachaña' (*Enicognathus ferrugineus* [Müller]), which in the process of tearing the cones apart, does manage to rip many off the tips of branches. On Araucaria trees, the cones on the upper branches are well out of reach to man in normal situations. Climbing of trees is difficult, virtually impossible when dealing with the Chilean species, which in the English language is known as 'monkey puzzle' (although no monkeys occur in the native country), a name presumably given because of branches and upper trunk being studded with dense, very hard and prickly leaves. Thanks to the birds dropping the cones to the ground, the rich life inside the cones has been revealed. In this way, it was a fairly easy task to discover whether something like a palophagine species occurred also in South America.

Acknowledgments

We wish to express our thanks to D.W. Helmore, Landcare Research, for providing the habitus drawing of *Palophagus bunyae* reproduced in the paper.

References

Kuschel G. and B.M. May, 1990. Palophaginae, a new subfamily for leaf-beetles feeding as adult and larva on araucarian pollen in Australia (Coleoptera:Megalopodidae). Invertebrate Taxonomy 3: 697-719.

Mann, J.S. and R.A. Crowson, 1981. The systematic position of *Orsodacne* Latr. and *Syneta* Lac. (Coleoptera:Chrysomelidae), in relation to characters of larvae, internal anatomy and tarsal vestiture. Journal of Natural History 15: 722-749.

(other references in the first paper cited above).