

Discovery of Palophaginae (Coleoptera: Megalopodidae) on *Araucaria araucana* in Chile and Argentina

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ABSTRACT

The subfamily Palophaginae (Megalopodidae) proposed in 1990 for two leaf-beetle genera of Australia has since been discovered in South America. Its presence in the Neotropical Region became known to the authors in late 1990 but all efforts to obtain adults in the field and lab had failed until April 1995 when the first adult emerged from rearing. The beetle is described below as *Palophagoides vargasorum* gen. et spec. nov. It is reported from the provinces of Malleco and Cautín in Chile and Neuquén in Argentina. In habitus, size and patterns it is remarkably similar to *Palophagus bunyae* of Queensland and biologically also alike by being associated with the same genus of tree, *Araucaria araucana* (pehuén or monkey-puzzle). Larvae develop in the male strobili (cones); they are already nearly full grown by the time the cones burst open and release the pollen. The mature larva drops to the ground and enters the soil to go through an additional, rather remarkable new instar or prepupal stage (hypermetamorphosis).

Keywords: Megalopodidae Palophaginae; Chile; Argentina; *Araucaria araucana*; male strobili.

INTRODUCTION

It does not often happen that a new and somewhat spectacular group of beetles, shortly after becoming known to science from one particular corner of the globe, is discovered on another, far distant part of it. The group concerned is the subfamily Palophaginae of the family Megalopodidae erected by Kuschel & May (1990) to accommodate rather unusual looking leaf-beetles with a habitus more of cerambycids than of chrysomelids. What is difficult to comprehend is that, although palophagine larvae are abundant in Australia as well as in Chile, adults are hard to come by in the field or through rearing in the laboratory. This is in spite of the special attention which the ancient genus *Araucaria*, their host genus, received for more than 200 years.

Background information on the known adult specimens of Palophaginae

In Australia, the first record of a specimen came from R.E. Turner who obtained it in Kuranda, northern Queensland in 1913, presumably attracted to light. It was named *Cucujopsis setifer* by Crowson (1946), placed in Chrysomelidae Sagrinae, and transferred later to Orsodacninae in the same family (Mann & Crowson 1981). Three further specimens were obtained on one night at light by J.G. Brooks in 1970 at Lamb Range, 18 km SE of Kuranda. Since no *Araucaria* species occur naturally where *C. setifer* has been collected, it is assumed that the hostplant would likely be some *Agathis* species, the only other genus of the family Araucariaceae. The three adult specimens of *Palophagus bunyae* Kuschel so far known were reared from a consignment of bunya-pine (*Araucaria bidwillii*) cones emerging in April and May 1981. The only known specimen of *P. australiensis* Kuschel was obtained two years later at light in northern New South Wales, where solely hoop-pine (*A. cunninghamii*) occurs naturally. Larvae, presumably of *P. australiensis*, were collected from hoop-pine from Cainbale, in the Lamington National Park area, but none developed through to adult.

Rearing methods attempted

Weevils, longhorns and other beetles were obtained in reasonable numbers by beating branches at night and in the day time, by spraying trunks and lower limbs, and by fogging part or whole male and female trees of *Araucaria* species, but no palophagine adult has yet been caught in this way. Mercury vapour lamps and black light have produced some results in Australia but not yet in Chile. Our target was Palophaginae and Nemonychidae, beetle groups that unfold their activities high up in the canopy and rarely fly at low levels to be attracted to light.

Since male cones harbour large numbers of larvae, a project was undertaken to rear all the beetle species developing in them. This was done for several years with excellent results for the Nemonychidae of Australia and Chile. The method employed was indicated in two papers (Kuschel 1989, 1994). Why this method did not work for Palophaginae as well is not obvious. The main rearing was undertaken at the quarantine facilities of the Mt Albert Research Centre in Auckland from consignments of male cones from Australia, Papua New Guinea, New Caledonia, Brazil and Chile. Whenever the consignments had palophagine larvae, it was immediately apparent that these did not travel well because so many arrived dead or dying while those of Nemonychidae were very active and healthy. Still, one of us (BMM) did succeed in breeding through three specimens of *Palophagus bunyae* which had been kept in vials with perlite.

The Chilean palophagine species too proved difficult to rear. After becoming aware in late 1990 that a species of Palophaginae occurred also in Chile, a consignment of male cones of the Chilean *A. araucana* (locally known as pehuén, in the English language as monkey-puzzle) was arranged right away but the larvae did not survive air travel and later handling. During a 1992 trip, a large cage, 150 x 100 cm, was built and set up under a 30-year old planted male araucaria in Frutillar (41°08'S), in southern Chile near the west shores of Lake Llanquihue on well drained soil. Sides and top of the cage were lined with firm fine-meshed plastic netting and the conical roof topped in the centre with a small wooden box holding a preserving jar with its holed-out lid screwed on a lateral opening of the box for easy replacement of jars. Male cones of araucaria from the Conguillío National Park, some 300 km NNE of Frutillar, were spread on top of clean friable soil to cover approximately half of the ground surface. The cage was serviced weekly for a whole year. It produced vast numbers of all the nemonychid and curculionid species but no specimens at all of palophagines although a sample of soil taken a fortnight after installation had a healthy number of larvae and prepupae.

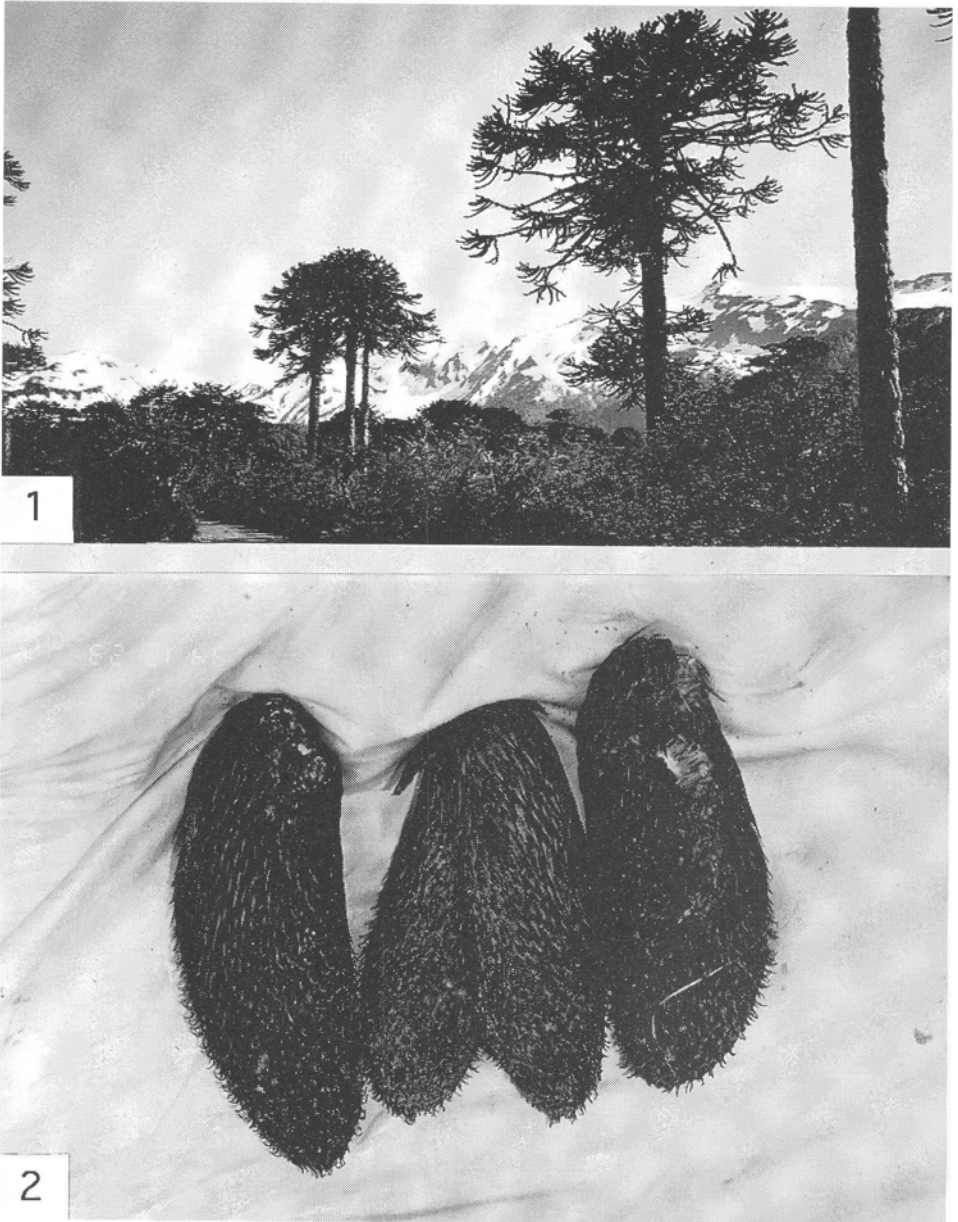
Further rearing trials were undertaken in late 1994. The cage described above was removed from Frutillar to the headquarters of the Parque Nacional Conguillío on the eastern side of Volcán Llaima, which is right inside araucaria forest, to be served by park staff. Besides, four teams took cones from the Volcán Lonquimay skifield to their homes for trying possibly different conditions to breed the leaf-beetle through, two of them finally succeeding but getting only three specimens altogether, none too good for a full study though satisfactory enough for a reasonable description of genus and species.

GK did the fieldwork in 1990/1, 1992/3 and 1994/5 in the araucaria forest of the Chilean Andes and also went over the border to the Argentine side. The new taxa are named and described by GK from adult specimens. Descriptions of larvae are by BMM.

DESCRIPTION OF ADULT

Palophagoides Kuschel gen. nov.

Head (Fig. 3) retractile to near eyes, narrower across eyes than prothorax, rather distinctly constricted behind eyes but only weakly constricted across vertex, lacking median groove. Frons between eyes slightly wider than 1/2 width of head across eyes.



Figs 1, 2: *Araucaria araucana*. 1, scenery with sparsely scattered trees standing in a field of thick layers of recent and old volcanic airfall on the northeastern part of the Parque Nacional Conguillío at 1050 m of altitude, with *Nothofagus antarctica* as the main undergrowth, and the snow covered Sierra Nevada in the background; 2, male cones from Volcán Lonquimay, 1400 m of altitude, in the middle a rare twin-cone. (Photos: G. Kuschel, Dec 1994).

Genae short, equal to 4-5 ommatidia behind mandibles, in male with forward protruding sharp tooth at outer angle of mandibles, in female protruding as rounded lobe. Eyes large, in lateral view nearly as deep (high) as head, strongly convex, with distinct shallow emargination, coarsely faceted, with short interfacetal hairs. Frontoclypeal suture fine;

clypeus flat, nearly twice as broad as long, densely punctate, pubescent. Labrum plurisetose, setae more or less confined to basal area, apical margin with short, fine cilia. Mandibles, maxillae and labium much as in *Palophagus* (Kuschel & May 1990, Figs 2-5), but sensory organ on terminal segment of maxillary palp placed more laterally.

Antennal sockets a little closer to each other than eyes to each other, with area between antenniferous tubercles depressed. Antennae when bent back extending to near middle of elytra in female, extending a little beyond middle in male; segment 1 strongly swollen, with flat inner surface (against eyes), conspicuously curved on outer side, remainder of segments as for *Palophagus*.

Prothorax (Fig.4) transverse, considerably wider than long, strongly rounded on sides, with distinct waist at base; basal rim distinct; sides sharply carinate throughout. Pronotum with 3 pairs of smooth swellings; lateroapical angle with few long setae, basal angle with strong, straight seta arising from rather inconspicuous pit.

Mesonotum with stridulatory organ consisting of two iridescent, very finely ridged files, these separated by fine midline. Scutellum as in *Palophagus*.

Elytra up to 2.4x longer than combined width at shoulders, only moderately wider than prothorax, not striate, densely punctate, lacking scutellar striole and sutural stria, but suture slightly raised at apical third; epipleural carina fine, harp, not extending to apex. Wings very much as in *Palophagus* (Kuschel & May 1990, Fig.8) but with a distinctly shorter jugular vein (j) and without anal cell (c).

Prosternum moderately long, longer in male than female, transversely strigose; notosternal suture obsolescent but enhanced by faint ridge or different pigmentation; flanks below lateral pronotal lobes flat, smooth; fore coxae contiguous, elongate, protruding, closed behind, open laterally to notosternal suture exposing trochantin. Mesosternal process obliquely descending, as wide between coxae as base of antennite 3; middle coxae open laterally to pleurites. Metasternum long, convex; metepisternum strongly widening cephalad, anterior margin strongly oblique; hind coxae narrowly disjunct.

Ventrites free, first four roughly of equal length, last ventrite in male a little shorter than 3 and 4 combined, weakly convex in lateral view, truncate at apex, last ventrite in female as long as 3 and 4 combined, in either sex longitudinally convex but a little more so in female, with moderately deep fovea at apex, apical margin sinuously emarginate (Fig.5) in female. Tergites weakly pigmented, tergite 7 in female as long as last two ventrites, rounded at apex.

Fore and middle tibiae similar in size and shape, weakly incrassate, hind femora conspicuously larger and considerably more swollen, all femora shallowly grooved on lower edge at distal half. Tibiae slender, gradually but rather strongly widening apicad, curved in female, a bit compressed, with rather sharp dorsal edge, coarsely and densely punctate, with long, strong hair in each puncture, distal comb consisting of rather fine setae; all tibiae with two relatively slender spurs. Tarsi moderately robust, depressed, tarsite 1 and 2 widening apicad, tarsite 2 briefly pointed at apical angles, with median lobe, segments 1-3 fully padded underneath; claw segment slender, slightly depressed, with slender simple claws.

Male

Sternite 9 apparently (too teneral to be certain) much as for *Palophagus*. Tegmen half the length of aedeagus, ring entire, not articulated halfway up on sides, main parameral sector at apex in lateral view bevelled at 45° as in *Cucujopsis* (Kuschel & May 1990, Fig.24) but sclerites more similar to those of *Palophagus* (Kuschel & May 1990, Figs 17,19). Aedeagus longer than abdomen, extending into thoracic lumen, slender, depressed, body, measured from base of pedon to apex, 5x longer than wide, apex following direction of body, not upturned, tapering to a point; apodemes nearly 2.5x longer than aedeagal body, apodemal bridge confined to basal 1/4 of apodemes; internal sac extending to end of apodeme; ejaculatory duct pigmented, firm, flagelliform, rather short, only about twice as long as aedeagus with apodemes, not convoluted.

Female

Sternite 8 apparently (also too teneral to be certain) much as in *Palophagus* (Kuschel & May 1990, Fig. 27). Genitalia of sole available specimen poorly developed, hence hemisternites not detectable; spermatheca as in Fig. 6, with rather robust, evenly curved body and long tapering extension, duct and gland inserting at end on opposite sides, gland very fine, nearly filiform, duct wide, of uneven diameter in its course, not pigmented and lacking coils, only about 1.5 mm long, i.e. about 3x the length of spermatheca taken from top of arc to end of extension.

Type species: *Palophagoides vargasorum* sp. nov.

Distribution

Chile: Andes at the Malleco and Cautín provinces, but likely to occur throughout the range of the host tree *Araucaria araucana* to include also part of Biobío province to the North and Valdivia province to the South, as well as the Cordillera Nahuelbuta in the Arauco province, an isolated area of original araucaria stands 100 km to the West of the Andean population. **Argentina:** Neuquén by the border with Chile.

Hostplant

Araucaria araucana (Molina) C. Koch (Araucariaceae), the larva developing in the male strobili (cones).

Remarks

The new genus is strikingly similar to the Australian kin-genus *Palophagus*, differing from the latter by having a broader frons, a strongly incrassate scape, a distinctly transverse, laterally strongly rounded prothorax, a pronotum that is laterally rimmed with a complete sharp carina, a strong long seta on the basal angle of the prothorax, contiguous fore coxae, hind femora that are considerably larger and thicker than the other femora, a laterally non-articulated tegminal ring, a non-convoluted ejaculatory duct that is only about twice the length of the aedeagus, and a wide spermathecal duct that lacks coils and is about 3x longer than the depth of the spermatheca from the top of the arc to the end of the duct/gland extension. The new genus shares with *Cucujopsis* Crowson, the other known palophagine genus from Australia, similar, strongly swollen hind femora, but without a tooth underneath, a strong seta on the hind angles of the prothorax, and angulated tarsi 2, but differs considerably in wing venation, sharp marginal pronotal carina and by having ejaculatory and spermathecal ducts considerably shorter and not coiled.

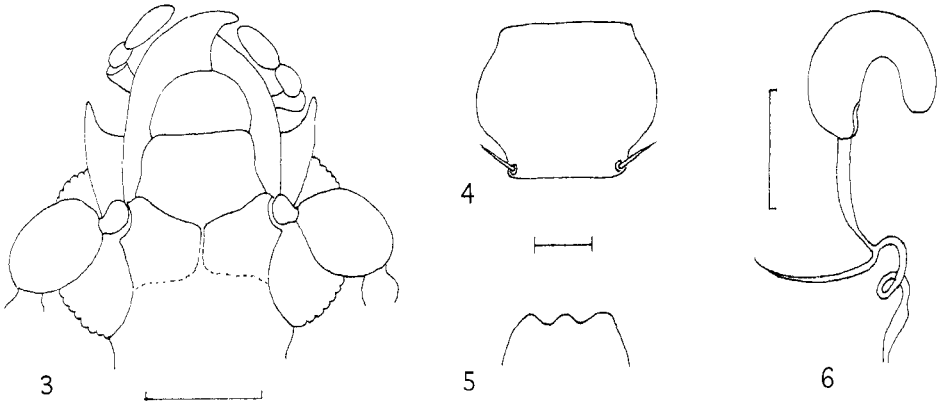
Etymology

From *Palophagus*, a related and similar leaf-beetle genus from Australia, and the Greek *eido* (εἶδω) = to look like, whence the suffix -ides (= English suffix -like), usable for nouns of masculine as well as feminine gender; the gender of the new genus is masculine.

Palophagoides vargasorum Kuschel sp. nov., Figs 3-6

Yellowish brown, with raised bronze areas on head, pronotum and posterior half of elytra, underside and legs a shadow darker. Pubescence fine, inconspicuous, appressed for the most part, hardly any more noticeable at tip of elytra; sensory setae sparse, erect, long, strong, stiff, tapering.

Head not or very superficially impressed across dorsal surface behind eyes. Frons 0.50 - 0.55 width of head across eyes, convex, sparsely, rather uniformly punctate;



Figs 3-6: *Palophagoides vargasorum* adult. 3, head of ♂ showing genal teeth in front of eyes, dorsal; 4, prothorax of ♂; 5, hind margin of ventrite 5 of ♀; 6, spermatheca with gland and part of duct. Scales at 3-5 = 0.5 mm; at 6 = 0.25 mm.

antenniferous tubercles narrowly separate. Antennal segments 3-11 for most part with scattered erect setae, more so on the outer side if bent back.

Prothorax 1.26-1.40x wider than long, distinctly punctate except for smooth, shiny, bronze swellings. Elytra elongate, 2.3-2.4x longer than combined width behind shoulders, 1.3-1.4x wider than prothorax, evenly curved on lateral margin at apex; punctuation similar to that of pronotum, only slightly coarser and deeper.

Male and female characters as at generic description above.

Length 6.5 - 7.0 mm, width 2.0 - 2.5 mm.

Material examined

Three specimens reared from larvae in male strobili of *Araucaria araucana* collected at 1400 m on Vn Lonquimay, Chile, 1 ♀ emerging 3 Apr 1995 at lab (G Kuschel), 2 ♂♂ emerging 12 and 20 Aug 1995 at lab (J.E. Barriga). Holotype male, 6.5 x 2.0 mm, Vn Lonquimay, 1400 m, 12 Aug 1995, J.E. Barriga, at the Museo Nacional de Historia Natural, Santiago, Chile. Paratypes (1 ♂, 1 ♀) at the New Zealand Arthropod Collection, Auckland, New Zealand.

Distribution

Chile: Volcán Lonquimay, Malleco Prov. Larvae (see below) also from Volcán Lonquimay, eastern and western sides of Volcán Llaima, Cautín Prov. from 900 to 1450 m of altitude in the Parque Nacional Conguillío in Chile, and from Neuquén in Argentina.

Hostplant

Araucaria araucana (Araucariaceae), larvae starting development in the male strobili well before these burst open with ripe pollen, remaining in the cones for a few more days till full growth, and feeding all the time principally upon pollen.

Etymology

The species is gratefully named after Javier, Nora, Eduardo, Hernán, Andrés and Verónica Vargas, all at one time or other accompanying and helping the senior author in his pursuit of Nemonychidae and the leaf-beetle species here named *Palophagoides vargasorum* in their honour.

DESCRIPTION OF LARVA

Definition of the genus *Palophagoides* Kuschel**Habitus**

Body cerambycid-like, approximately 4x longer than wide, parallel-sided but with pleural lobes expanded. Head free. Segments distinctly demarcated due to strong musculature. Ambulatory ampullae present on dorsum and venter. Cuticle coarsely spiculate and invested sparsely with setae. Abd IX lacking urogomphi and tergal plate. Legs minute, 3-segmented, lacking claw. Anus terminal with circular opening.

Head and mouthparts

Head transverse, slightly narrower than prothorax, widest behind middle, sides strongly curved; posterodorsal emargination extending to frontal apex (coronal suture absent); 6 ocelli (stemmata) present; frontal suture distinct; endocarinal line present. Mentum unsclerotised. Submentum lightly sclerotised with small pigmented macula anteromedially and narrow basal plate separating it from thoracic sternum. Occipital foramen not divided. Hypopharyngeal bracon absent. Gular sutures not visible. Frontoclypeal suture indistinct. Clypeolabral suture effaced. Labrum transverse, trilobate with median lobe subquadrate. Epipharyngeal lining folded before labral margin and proximally bearing a curved ridge surmounted by a shallow cavity and small pit, and flanked on each side by 4 or 5 pores. Antennae sclerotised, 3-segmented with distal segment small, topped by acute process and accompanied by wide, conical supplementary process. Mandibles with 2 apical teeth and blunt projection on incisor section; molar section bearing double-pronged, upstanding process with both prongs acute. Maxilla 3-segmented; cardo longer than stipes, as long as submentum; palpiger indistinct laterally, mala cylindrical. Labial palps 2-segmented. Ligula non-setose. Premental sclerite present at sides only.

Thorax and abdomen

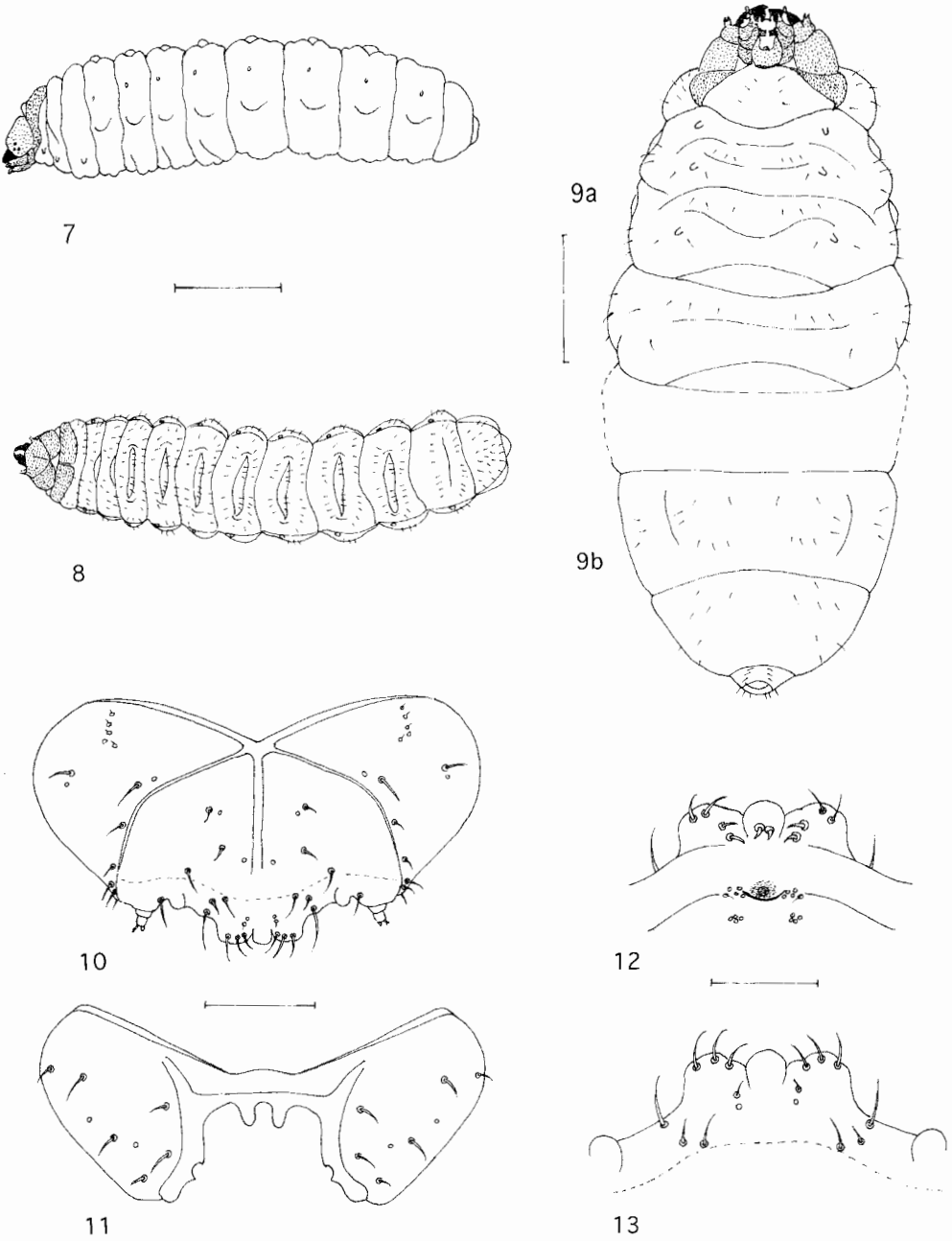
Pronotal shield pigmented, with narrow median line. Prosternum with triangular eusternal area defined by converging setae. Abdomen with ambulatory ampullae distinct dorsally and ventrally on Abd II to Abd VII; more or less obsolete on Abd I and Abd VIII; dorsopleural lobes well defined. Spiracles subcircular with short, contiguous, annulated airtubes, aligned obliquely dorsad. Legs represented by 3-segmented papilla without claw. Anus terminal with circular opening. Alimentary canal having unarmed proventriculus; mycetomes absent around cardiac valve; anterior ventriculus 0.6 length of body; posterior section bent Z-wise, not coiled; gastric caeca absent; Malpighian tubules arranged 3+3; cryptonephridium symmetrical.

Remark

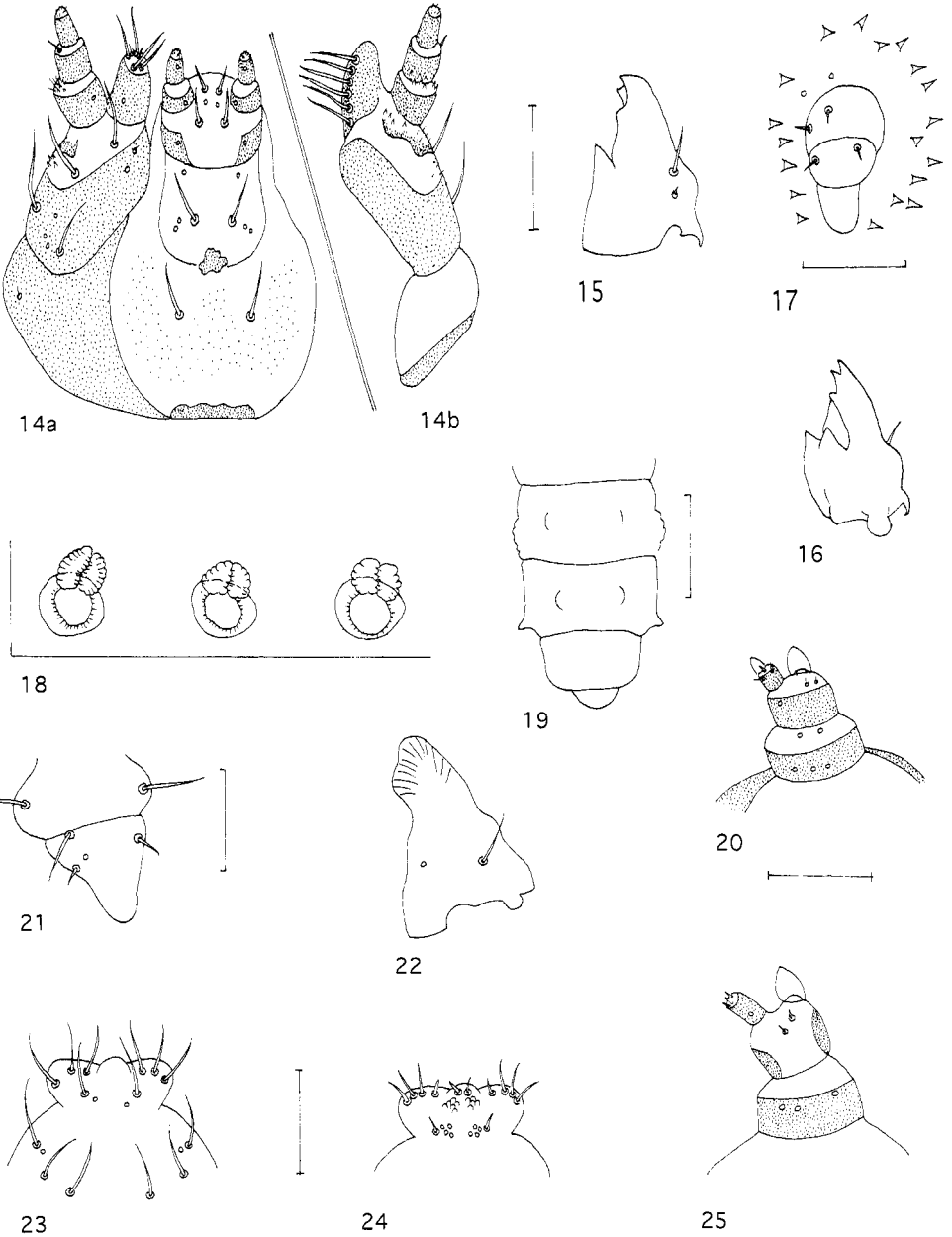
An earlier instar (8.5 x 1.5 mm) has a pointed tubercle on Abd VIII, caudad of the dorsopleural lobe (Fig 19).

Description of the species *Palophagoides vargasorum* Kuschel, Figs 7-25**Material examined**

Chile: Cautín Province: Parque Nacional Conguillío, eastern side of Vn Llaima, 1000 m, 12 Dec 1990, 18 larvae; same area at 1050 m, 14 Dec 1990, 5 larvae; western side of Vn Llaima, Parque Los Paraguas, 1400 m, 14 Dec 1990, 1 larva; same area at 1450 m, 12 Feb 1993, 1 prepupa in soil beneath tree. Malleco Province: Vn Lonquimay, 1400 m, 99 larvae from 9 cones collected on 23 Dec 1994 having vacated them between 28 Dec 1994 and 4 Jan 1995 and transformed into prepupae soon after. **Argentina:** Carirriñe in Neuquén Territory, 1070 m, 6 Jan 1991, 2 larvae retrieved from soil under the host tree, which moulted to prepupae on 26 Jan 1991. All material obtained from male cones of *Araucaria araucana* by G. Kuschel.



Figs 7-13: *Palophagoides vargasorum* larva. 7, habitus, lateral (setae omitted); 8, habitus, dorsal; 9, habitus, ventral (9a, head, thorax and Abd I; 9b, Abd VIII, Abd IX and Abd X, showing anal opening); 10, head, dorsal; 11, head, ventral; 12, epipharyngeal lining; 13, labrum-clypeus. Scales at 7, 8 = 2.0 mm; at 9-11 = 1.0 mm; at 12, 13 = 0.25 mm.



Figs 14-25: *Palophagoides vargasorum* larva (14-20) and prepupa (21-25). Larva: 14, maxilla and labium (14a, ventral; 14b, maxilla, dorsal); 15, mandible, outer; 16, mandible, inner; 17, leg and surrounding cuticle; 18, spiracles, showing alignment; 19, early instar, terminal segments, dorsal; 20, antenna. Prepupa: 21, leg; 22, mandible; 23, labrum-clypeus; 24, epipharyngeal lining; 25, antenna. Scales at 19 = 1.0 mm; at 14-16, 22 = 0.25 mm; at 18, 20, 23-25 = 0.125 mm; at 17, 21 = 0.036 mm.

several grains on their way through. Although most of the larvae had finished feeding, the gut contents of two less advanced specimens showed pollen grains which were split, by the point of a molar prong perhaps, rather than crushed. Many grains in the gut were entire and would presumably pass out undigested. The method of pollen crushing may be compared with that in Nemonychidae where the grains are retained by a concave hypopharyngeal sclerome to be split by a diagonal ridge, usually crenate or toothed, on the mola of each mandible (May 1994).

Table 2: Comparison with larva of *Palophagus bunyae* Kuschel of Australia.

<i>Palophagoides</i>	<i>Palophagus</i>
Legs lacking tarsal claw.	Tarsal claw present.
Dorsal ampullae bearing 3 setae each side.	Dorsal ampullae bearing 1 seta each side.
Anal opening O-shaped.	Anal opening Y-shaped.
Premental sclerite visible at sides only.	Premental sclerite entire.
Mandible with molar process 2-pronged.	Mandible with molar process simple.
Epipharyngeal lining with median curved ridge simple, surmounted by circular pit.	Epipharyngeal lining with median curved ridge serrate, not surmounted by pit.
Maxillary mala with 6 dorsal setae.	Maxillary mala with 9 dorsal setae.
Submentum with small anteromedian macula and separated from prosternum by narrow basal plate, otherwise sclerotised lightly.	Submentum fully sclerotised, lacking macula, contiguous with prosternum.

BIOLOGY

The genera *Palophagus* and *Palophagoides* are definitely associated with *Araucaria* species in Australia and Chile while the host of *Cucujopsis* remains unknown although believed to be *Agathis*. The diet of adults is presumed to be pollen judging by the features of the mouthparts. The larvae live and develop to full maturity in the male strobili (cones) and then vacate them to go through a quite differently looking prepupal instar in the soil. A sample for observation and rearing was taken at the skifield of Volcán Lonquimay in Chile at 1400 m of altitude on 23 December 1994. Ten unopened cones were set aside for close observation. These cones were 13-15 cm long and 6 cm wide and burst open almost simultaneously within 24 hours of the first one doing so. One was immediately dissected for close examination. It had six large, more or less full grown larvae and a smaller larva of Palophaginae without exception inside microsporangia (pollen sacs), two very small larvae of Nemonychidae, one in a pollen sac, the other in a gallery in the central pith (cone axis), and 12 moderately large larvae of Curculionidae, all these in the fleshy cone axis. The cones when collected were rock-hard and extensively coated with dry resin. They did not show any lesions that may have hinted at oviposition sites or points of entry of larvae.

Three days after the cones had opened up and were releasing pollen, nine larvae were crawling freely on the tray, a further 23 two days later, another 34 larvae the day after, and the last three larvae left the cones eight days after the first larvae had appeared. The nine cones under observation produced altogether 99 larvae of *Palophagoides*, 70 of *Mecomacer* (Nemonychidae) and 121 of *Araucarietius* (Curculionidae), an average of 32.2 larvae per cone. More biological information on Palophaginae is published elsewhere (Kuschel & May 1996).

Larvae of *Palophagoides* are quite mobile. They may crawl for several metres on the ground before entering the soil. If they enter normal, easily draining soil they usually go no deeper than about 20 cm, but they seem to go much deeper down if volcanic airfall of ash and lapilli covers the ground. This impression was gained by digging more than 50 cm deep in the forest under male trees without finding a single palophagine larva. As the volcanic airfall is loose and light even rather soft-bodied beetles, as Palophaginae and Nemonychidae are, should encounter little resistance on their way up from the pupation chambers.

A diapause of one or two years is well documented for Nemonychidae in Australia and Chile (Kuschel 1994; May 1994). Present indications are that some specimens of *Palophagoides* might defer development also, at least for one year, because prepupae of the batch of larvae collected in late December 1994 remain alive and apparently in good health a year and two months later at the time of writing.

Araucaria araucana displays pollen-shedding cones from mid-November to mid-January at the latest. One of the reared adult *Palophagoides* emerged in early April and the other two in August, thus taking between 5 and 7 months to finish development since leaving the cones. In Australia, *A. bidwillii* 'flowers' from mid-September to mid-October and *A. cunninghamii* for a much longer period in spring through to summer. The three specimens of *Palophagus bunyae* bred from cones collected in late September and early October emerged in April and May. The climatic conditions are considerably milder on the Bunya Mountains than in the Cordillera of the Andes where snow may cover the ground of the araucaria forest completely for four or more months of the year, usually from the end of May to well into October. As all five nemonychid species that share the cones of *A. araucana* with *Palophagoides* emerge to hibernate in the forest canopy before the ground gets thickly covered in snow during May or early June, it may be assumed that *Palophagoides* would do likewise.

The question of precisely when and how oviposition might take place remains unanswered. Eggs are laid either in the cones before these burst open or in the cones once open. The nemonychid genus *Rhynchitomacerinus* and the curculionid genus *Eisingius* seem to lay the eggs into open cones, whilst *Palophagoides*, *Mecomacer* (Nemonychidae) and *Araucarietius* (Curculionidae) species on unopen cones. The precise time when the latter group of beetles oviposit is unknown, which, judging by the advanced stage of development the larvae are found at the moment the strobili burst open, it could be months rather than weeks before this hour.

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