

New Zealand harvestmen of the subfamily Megalopsalidinae (Opiliones: Monoscutidae) – the genus *Pantopsalis*

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ABSTRACT: The genus *Pantopsalis* Simon, 1879 and its constituent species are redescribed. A number of species of *Pantopsalis* show polymorphism in the males, with one form possessing long, slender chelicerae, and the other shorter, stouter chelicerae. These forms have been mistaken in the past for separate species. A new species, *Pantopsalis phocator*, is described from Codfish Island. *Megalopsalis luna* Forster, 1944 is transferred to *Pantopsalis*. *Pantopsalis distincta* Forster, 1964, *P. wattsi* Hogg, 1920, and *P. grayi* Hogg, 1920 are transferred to *Megalopsalis* Roewer, 1923. *Pantopsalis nigripalpis nigripalpis* Pocock, 1902, *P. nigripalpis spiculosa* Pocock, 1902, and *P. jenningsi* Pocock, 1903 are synonymised with *P. albipalpis* Pocock, 1902. *Pantopsalis trippi* Pocock, 1903 is synonymised with *P. coronata* Pocock, 1903, and *P. mila* Forster, 1964 is synonymised with *P. johnsi* Forster, 1964. A list of species described to date from New Zealand and Australia in the Megalopsalidinae is given as an appendix.

KEYWORDS: taxonomy, Arachnida, Opiliones, male polymorphism, sexual dimorphism.

Introduction

Harvestmen (Opiliones) are abundant throughout New Zealand, being represented by members of three different suborders: Cyphophthalmi (mite-like harvestmen); Laniatores (short-legged harvestmen); and Eupnoi (long-legged harvestmen; Forster & Forster 1999). The suborder Dyspnoi has not been recorded from New Zealand. The largest species found in New Zealand belong to Eupnoi, in the family Monoscutidae (often referred to as Megalopsalididae), a group comprising two well-distinguished subfamilies, the Monoscutinae (containing the monotypic genera *Monoscutum* Forster, 1948 and *Acihasta* Forster, 1948) and the Megalopsalidinae (Crawford 1992). In New Zealand, the Megalopsalidinae have been placed in two genera, *Pantopsalis* Simon, 1879 and *Megalopsalis* Roewer, 1923 (the latter is also found in Australia). This paper

examines the former genus, which is endemic to New Zealand. The more diverse *Megalopsalis* will be dealt with in another publication. All *Pantopsalis* species described to date are reviewed, and a new species is described.

Species of Monoscutidae are found in native forest the length of the country, from the Three Kings Islands in the north (Forster 1948) to the subantarctic islands in the south (Forster 1964), as well as in Australia (Forster 1949). Despite their wide geographical range and the fact that 37 nominal species are included, the taxonomy of Monoscutidae has been rather neglected, with many species insufficiently described for accurate identification. In addition, the characters used to define genera have been shown to be unreliable (Forster 1964).

The taxa included in the Phalangioidea – the superfamily that includes the Monoscutidae – are notorious for their shortage of useful diagnostic characters (Crawford

1992). Nevertheless, they are an abundant group worldwide, with more than 200 current genera (Crawford 1992), and are probably the most familiar among all the Opiliones. *Phalangium opilio* Linnaeus, 1758 (a species introduced into New Zealand from Europe) was one of the most abundant invertebrate species caught in late summer in pitfall traps in pasture near Nelson in a study conducted from 1970 to 1973 (Martin 1983). Their abundance implies that they are probably significant members of the leaf-litter ecosystem where they occur.

The southern hemisphere members of the Phalangioidea have received far less attention than the northern hemisphere species, as demonstrated by the description of a new subfamily, Ballarrinae, found in Australia, South America, and Africa, as recently as 1991 (Hunt & Cokendolpher 1991). Nevertheless, it seems likely that the Phalangioidea originated in Gondwana, with the northern hemisphere taxa forming a monophyletic subgroup arising from southern hemisphere ancestors (Hunt & Cokendolpher 1991). Therefore, a good understanding of the taxonomy of the Monoscutidae and other southern hemisphere phalangioids is critical to the understanding of the origins of this large and successful group.

Materials and methods

Specimens studied for this paper were obtained from the following institutions: the New Zealand Arthropod Collection, Landcare Research Ltd, Auckland, New Zealand (NZAC); Auckland War Memorial Museum, Auckland, New Zealand (AMNZ); the Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand (MONZ); Canterbury Museum, Christchurch, New Zealand (CMNZ); Otago Museum, Dunedin, New Zealand (OMNZ); and the Natural History Museum, London, England (BMNH). Specimens were stored in 75% ethanol or in picric acid.

External features of specimens were examined under light microscopy. Genitalia were removed from the abdomen by applying pressure to the base of the genital operculum, causing it to open slightly, and using a pin to cut free the sides of the operculum, which was then folded back to reveal the genitalia. The genitalia were removed with a pair of forceps or cut out with a pin, and were examined mounted in alcohol or K-Y brand jelly on a concave slide. Ovipositors were cleared in KOH for at least three hours prior to observation in order to render the seminal

receptacles visible. Drawings and measurements were made with a camera lucida.

Area codes established by Crosby *et al.* (1998) for New Zealand are used. Cephalothorax length and width are given as measurements, because total body length and width are influenced by abdominal deformation or collapse, especially in males (*see* below). Body dimensions and pedipalp measurements are given to the nearest 0.2 mm, while appendage measurements are to the nearest 0.5 mm. Cephalothorax length is measured at the midline, from between the points of attachment of the chelicerae to the centre of the posterior margin. Width is measured at the widest point, between the second and third legs. Measurements of pedipalp patellae are taken from the outer side, and exclude the apophysis if it is present. Measurements of leg tarsi should be regarded as approximate because the tarsi are often coiled, and straightening them is difficult. For species other than *Pantopsalis albipalpis* Pocock, 1902, all available adult specimens were measured; for *P. albipalpis* 11 males (including two broad-chelicerate specimens) and eight females were measured.

The terms 'denticulate' and 'denticle' are used throughout to refer to *any* raised discrete ornamentation, whether pointed or rounded. Many individuals may show both, with intergrading forms between them. The term 'nodule' is occasionally used to imply specifically that the ornamentation is rounded and blunt, but this should be regarded as a variety of denticle, not a different form of ornamentation.

Descriptions of colour refer to preserved specimens. Natural colours may be partially lost in alcohol-preserved material, but the original *pattern* remains, except when colour is totally lost. For example, specimens of *Pantopsalis coronata* Pocock, 1903 do not have the bright articular membranes of *P. phocator* new species (*see* below), but retain the distinctive transverse abdominal stripes.

The abdomens of many preserved specimens are distorted. In heavily sclerotised males the abdomen often collapses entirely and retracts under the cephalothorax. Abdominal characters have therefore not been examined in detail.

Setae on the pedipalps are simple (not branching or plumose) and can be divided into two classes, 'large' and 'small', with a distinct size difference between the two. Large setae can form 'hypersetose areas' (areas with a dense covering of setae), and the distribution of these is taxonomically significant at the genus level.

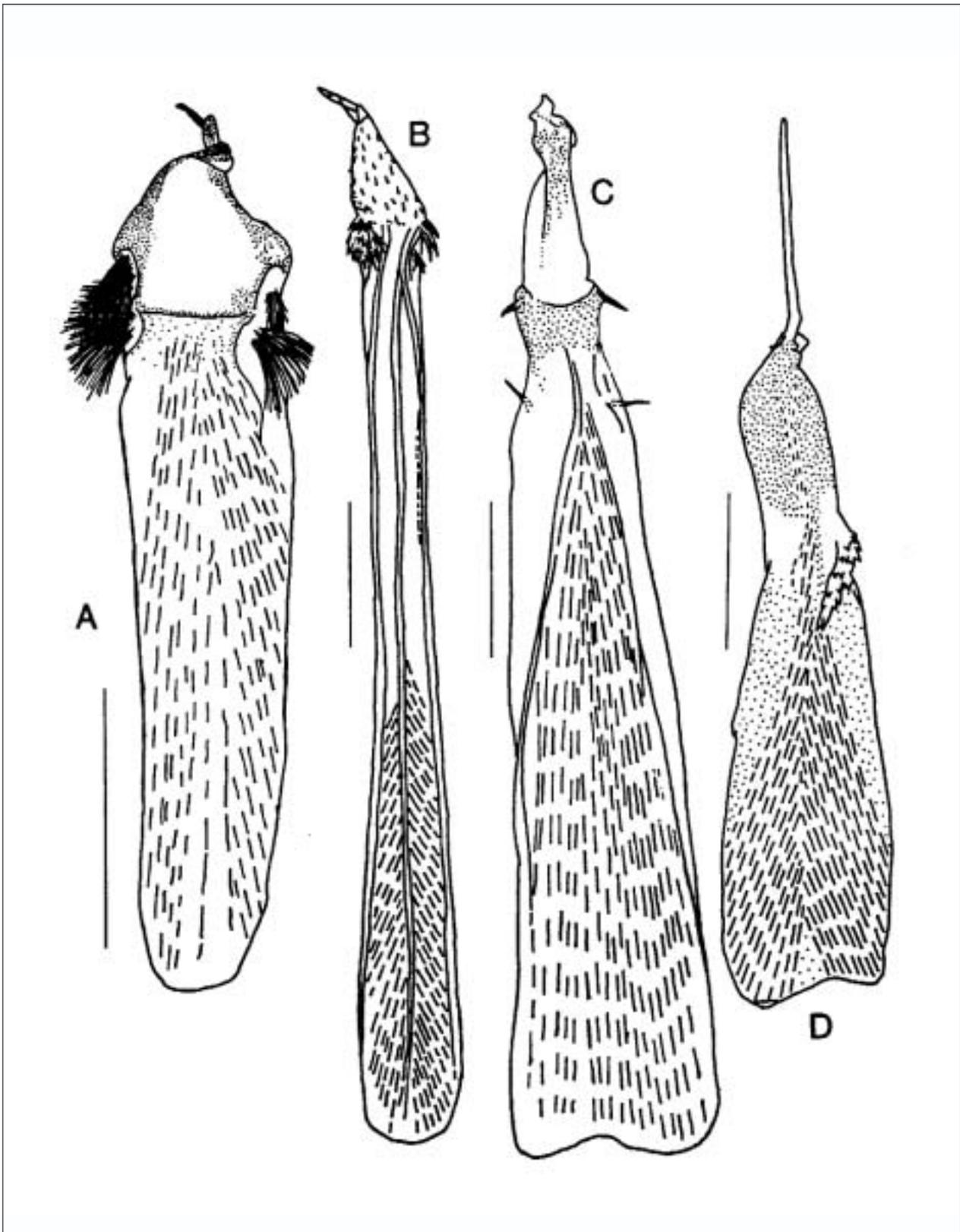


Fig. 1. Penes of southern hemisphere phalangids, showing different bristle patterns: (A) *Spinicrus* sp. (Megalopsalidinae); (B) *Acihasta salebrosa* (Monoscutinae); (C) *Thrasychirus* sp. (Enantiobuninae, Neopilionidae); (D) *Ballarra alpina* (Ballarrinae, Neopilionidae). Scale bars 0.1 mm (from Hunt & Cokendolpher, 1991; used with permission of the publisher).

While numbers of pseudosegments in the legs have been recorded and regarded as significant in the past, they can vary between individuals of the same species and are of doubtful taxonomic value (Hickman 1939). Here, the number of tibial pseudosegments (if they occur) is recorded, but numbers of metatarsal and tarsal pseudosegments are not.

Some species have not been treated in detail, either because specimens were not available (i.e. *Pantopsalis listeri* (White, 1849) and *P. snaresensis* Forster, 1964) or because the species were satisfactorily described in the original paper, such as those from the subantarctic islands described by Forster (1964). In particular, the male holotype of *P. snaresensis* was not located despite a search made by Simon Pollard at the Canterbury Museum, the repository institution given by Forster (1964). Nevertheless, those species have been discussed briefly in the appropriate places in light of the conclusions of this paper.

Taxonomic status of the Monoscutidae

Monoscutidae has previously been referred to as Megalopsalididae. However, Crawford (1992) pointed out that the name Monoscutinae Forster, 1948 has priority over Megalopsalinae [*sic*] Forster, 1949. Megalopsalinae [*sic*] (including *Monoscutum*) was included by Šilhavý (1970) in his extended Neopilionidae, but was raised to family level (and the name corrected to Megalopsalididae) by Martens (1976). Hunt (1990) and Hunt & Cokendolpher (1991) recognised the subfamilies Monoscutinae and Megalopsalidinae as distinct.

Monophyly of the Monoscutidae is based on a single character, the presence of paired lateral bristle groups on the penis at the articulation between shaft and glans (Hunt & Cokendolpher 1991). Kauri (1954) illustrated the penis of *Spinicrus minimus* (West Australia) as possessing two lateral rows of bristles, rather than discrete groups. As this was the first illustration of monoscutid genitalia, it requires confirmation – it seems likely that Kauri (1954) failed to recognise the distinction between the bristle groups. Bristles on the penis are found in Caddoidea (the sister taxon of Phalangioidea) and Ischyropsalidoidea (Dyspnoi; Martens 1976), and may be plesiomorphic for the Phalangioidea (Hunt & Cokendolpher 1991). Other groups within Phalangioidea lack bristles, except for

Enantiobuninae, with two pairs of single bristles, and Ballarrinae, with a single barbed left lateral process (see Fig. 1, from Hunt & Cokendolpher 1991). It is possible that the pattern of penile bristles seen in Monoscutidae follows an evolutionary grade, with the pattern in other families being derived from the monoscutid condition. Monophyly of the two subfamilies of Monoscutidae has not been rigorously tested.

Megalopsalidinae contains three genera from Australia and New Zealand: *Megalopsalis*, *Pantopsalis*, and *Spinicrus* Forster, 1949 (Crawford 1992). A fourth genus, *Nodala* Forster, 1949, was assigned to Megalopsalidinae when described, but is now regarded as a junior synonym of *Nelima* Roewer, 1910 in the Sclerosomatidae (Gruber & Hunt 1973). The most distinctive character of the Megalopsalidinae is the enormously enlarged chelicerae of the males. A phylogenetic analysis by Hunt & Cokendolpher (1991) suggested that the Megalopsalidinae was paraphyletic, with *Pantopsalis* closer to Monoscutinae than to the clade formed by *Megalopsalis* and *Spinicrus*. The characters supporting this result were four seminal receptacles in *Pantopsalis* and Monoscutinae (versus two in *Megalopsalis* and *Spinicrus*), and 'lace tubercles' (reticulated tubercles) on the margin of the spiracle in *Megalopsalis* and *Spinicrus*. However, Hunt & Cokendolpher (1991) noted that whether four seminal vesicles are a plesiomorphy or an apomorphy is equivocal. Furthermore, while *Pantopsalis* does not possess lace tubercles, the spines across its spiracle have reticulated bases, and may be homologous with lace tubercles (Hunt 1990). The extreme sexual dimorphism of the Megalopsalidinae was not coded as a character. The analysis of Hunt & Cokendolpher (1991) was not directly centred on Monoscutidae, and its implications for this family require re-examination.

Taxonomic history of *Pantopsalis*

The first megalopsalidine described from New Zealand was named *Phalangium listeri* by White (1849) in a brief description. Simon (1879) redescribed this species as the type species of a new genus, *Pantopsalis*. Colenso (1882) described another species as *Phalangium cheliferooides*. Sørensen (1886) described a new genus and species, *Macropsalis serritarsus*, from Sydney (Australia). Since *Macropsalis* Sørensen was preoccupied by *Macropsalis* Sclater, 1866 (Aves), it was later replaced by *Megalopsalis* Roewer, 1923. Sørensen (1886) distinguished *Macropsalis*

from *Pantopsalis* as it had spines on the eyemound, the abdomen was longer than the cephalothorax, the tibia of the second leg lacked pseudoarticulations, the tibia of the pedipalp was one-and-a-half times longer than the patella (both segments are subequal in *Pantopsalis*), and it possessed a palpal patellar apophysis. Among these characters, spines on the eyemound are found in some *Pantopsalis* species, the abdomen is prone to deformation in preserved specimens, and the number of tibial pseudosegments has been found to vary within species (Hickman 1939). Relative length of palpal tibia and patella has been used as a significant character in other genera (Hunt & Cokendolpher 1991), but it appears to have been ignored in distinguishing *Megalopsalis* and *Pantopsalis* by subsequent authors. Therefore, these genera have so far been distinguished solely by the presence (*Megalopsalis*) or absence (*Pantopsalis*) of a palpal patellar apophysis.

Subsequent *Pantopsalis* species from New Zealand were described by Pocock (1902, 1903) and Hogg (1920). The majority of these early descriptions were based on males only. Pocock (1902) described a female of *P. nigripalpis* Pocock, 1902, but his 'female' was actually a broad-chelicerate male (see 'Polymorphism in Megalopsalidinae' below). After recognising it as a male, Pocock (1903) redescribed that specimen as the type of his new species *Pantopsalis jenningsi*. Hogg (1920) was the first person to describe and identify correctly female Megalopsalidinae, albeit with some uncertainty.

Forster (1949) established the subfamily Megalopsalinae (corrected to Megalopsalididae by Martens, 1976) on the basis of the tarsal claw of the pedipalp being pectinate in Australian *Megalopsalis*, rather than smooth as was part of Roewer's (1923) definition of Phalangüinae. This feature was actually illustrated by Roewer (1911) for *M. serritarsus* but not subsequently commented upon, despite the fact that this character was given high importance by Roewer in his classification of Eupnoi (Roewer 1923). Forster (1949) used the same character as reason for separating the Australian species previously included in *Pantopsalis* as the new genus *Spinicrus*. *Pantopsalis* was therefore restricted to New Zealand. As the Megalopsalidinae was defined by the pectinate palpal claw, *Pantopsalis* was implicitly excluded from it. The intended taxonomic position of *Pantopsalis* was not explained, and Crawford (1992) included it, without comment, in the Megalopsalidinae. Because the presence or absence of ventral teeth on the palpal claw is no longer regarded as a

significant systematic character at the family level (Crawford 1992), and as *Pantopsalis* has the bristle groups on the penis diagnostic of Monoscutidae, the placement of this genus in that family seems reasonable. The sole distinction between *Pantopsalis* and *Spinicrus* is the pectinate palpal claw in the latter. The taxonomic importance of this character is debatable (Crawford 1992), and Suzuki (1973) found that teeth on the palpal claw can wear down with age, which could interfere with their practical use as a reliable character.

Forster (1964) described five new species of *Pantopsalis* from the subantarctic islands of New Zealand. Among these was *P. distincta* (here transferred to *Megalopsalis*), in which the female possesses a palpal patellar apophysis, while the male does not. This cast severe doubt on the distinction between *Pantopsalis* and *Megalopsalis*. While noting this, Forster (1964) did not suggest a solution to the problem.

The current study has identified two forms of palpal patellar apophysis: a large, rounded form found in females of *Pantopsalis* and both sexes of *Megalopsalis grimmetti*; and a small, pointed form found in the remaining New Zealand species of *Megalopsalis*. In *Pantopsalis* and *Megalopsalis grimmetti*, the apophysis is very setose – in males of *Pantopsalis*, a raised hypersetose area corresponds to the apophysis in the female. The hypersetose area on the patellar apophysis of the other *Megalopsalis* species is much smaller, and generally restricted to the outer edge of the apophysis.

Polymorphism in Megalopsalidinae

Species identifications in Megalopsalidinae have been confused by high intra-specific variation. All Megalopsalidinae are sexually dimorphic, while some *Pantopsalis* species also have discrete male polymorphisms.

Dimorphism between males and females is well recognised in Megalopsalidinae, and is arguably the most distinctive character of the subfamily (Forster 1949). Females have small, smooth chelicerae, not as long as the body and usually not rising above the cephalothorax. In contrast, the males have enormous, strongly denticulate chelicerae, at least twice as long as the body and often longer (Forster 1949, 1964; Forster & Forster 1999). Males and females may also differ in their degree of sclerotisation, and in overall colour pattern. Denticulation, if present, is mostly restricted to the males. Often, the only character allowing a connection between males and females is the pattern of setae on the pedipalps. This, too, varies slightly between

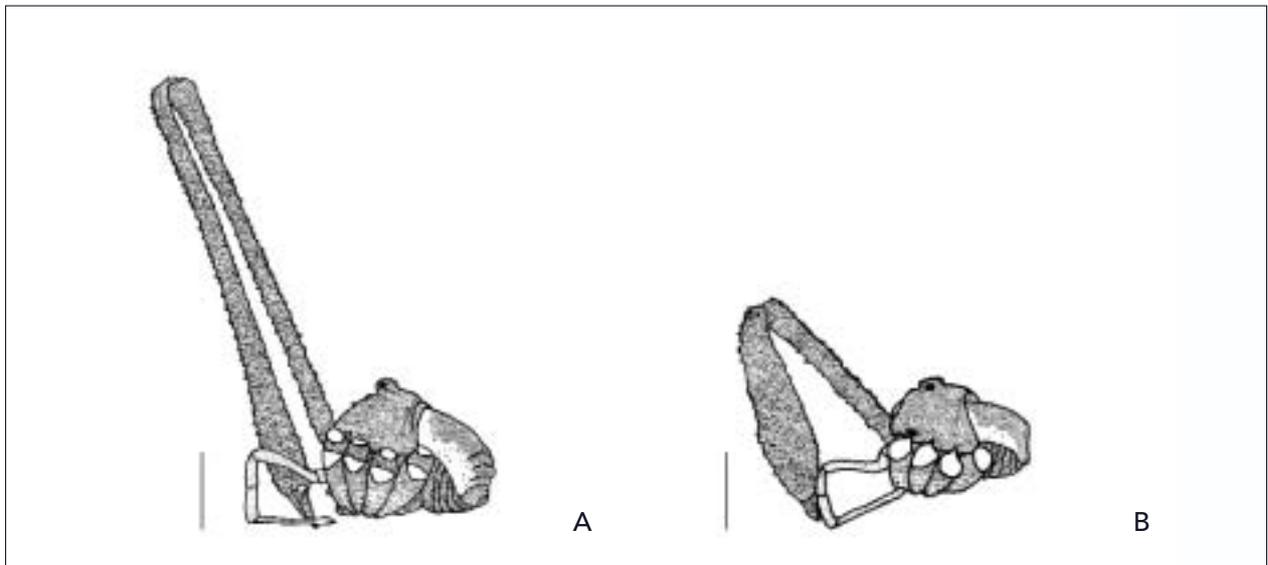


Fig. 2. Lateral view of (A) primary and (B) broad-chelicerate forms of *Pantopsalis phocator*, showing similarity in colour pattern between forms. Scale bars 2 mm.

sexes, with females more setose than males, but the differences are not enough to obscure the similarities.

Male polymorphism or dimorphism is here defined as a pattern of variation found among males of a single species, and is rare in Opiliones. It was first recognised by Forster (1954) in New Zealand Triaenonychidae (Laniatores), and later described for *Pantopsalis mila* Forster, 1964 from Auckland Island (synonymised with *P. johnsi* Forster, 1964; see below). Male polymorphism has also been recorded in Japanese Phalangodidae (Laniatores) by Suzuki (1973) and in Australian Triaenonychidae by Hunt (1981), and may occur in some North American Eupnoi (J. Cokendolpher, personal communication). In all these cases, one male form has fully developed secondary sexual characters, while the other is more similar to the female.

A number of *Pantopsalis* species (*P. albipalpis*, *P. coronata*, *P. johnsi*, and *P. phocator*) show a distinct dimorphism in the shape of the chelicerae between individual males (see Fig. 2), to such an extent that different forms have been described as different species. These species all have very similar penes, and probably form a closely related group. The level of polymorphism recorded in this group of species (referred hereto as the *P. albipalpis* group) has not been described among more distinct *Pantopsalis* species (separated by distinct penes), such as *P. luna* (Forster, 1944) and *P. rennelli* Forster, 1964, but comparable forms have

been described for Opiliones in other families. *P. pococki* Hogg, 1920 is very similar to *P. coronata*, and also probably belongs in the *P. albipalpis* group, but it is only known from the holotype.

The male primary form in the *Pantopsalis albipalpis* group possesses long, slender chelicerae. In the variant form (referred hereto as 'broad-chelicerate'), the chelicerae are much shorter and stouter, and the second segment is more dilated relative to the first segment. In another variant described by Forster (1964), which is referred to as 'effeminate' and known from *P. albipalpis* and *P. johnsi*, the overall colour pattern is lighter and more similar to that of the female or juvenile, and the degree of sclerotisation may be less. Both variants occur in low numbers in the population.

Conspecificity of the two forms is indicated by their complete sympatry and, for the primary and broad-chelicerate forms, by the possession of conspecific characters in colour pattern and appearance. The alternative, that the forms represent very similar sympatric species, would require an unreasonable degree of parallelism – the same colour pattern or cheliceral morphology would have to develop independently in different species inhabiting the same locality. Effeminate males are regarded as conspecific because of the presence of a single form of female per locality. In *Pantopsalis albipalpis*, effeminate and broad-chelicerate males are each known in a proportion of ~1 in 9

(4/37); counting those specimens from Dunedin, Leith, and Opoho only, the frequency is ~ 1 in 7 (4/29) for effeminate males and ~ 1 in 10 (3/29) for broad-chelicerate males. The primary form is also more abundant in other species. In comparison, where male polymorphism is known for species belonging to the Laniatores genus *Nuncia* Loman, 1902, the frequency of effeminate males ranges from ~ 1 in 2 to ~ 1 in 4 (Forster 1954).

The two male forms reported in species of Triaenonychidae differ in the degree of development of the secondary sexual characters, with one form being more similar to the female (Forster 1954, Hunt 1981). Suzuki (1973) reported Phalangodidae showing a similar dimorphism, with one male form having enlarged chelicerae and the other having them the same size as in the female. While described as effeminate forms, these variants are not necessarily equivalent to the effeminate forms in *Pantopsalis*, which aside from colour pattern and sclerotisation show full development of male secondary sexual characters. The developmental

causes of variant forms in *Pantopsalis* are unknown. While Forster (1954) suggested a purely genetic origin for polymorphism in harvestmen, Hunt (1981) found that the development of effeminate males in Triaenonychidae was caused by nymphs overwintering at instar 4 or earlier, while nymphs that matured to normal males overwintered at instar 5. Variant forms may therefore be environmentally induced. If the causes of polymorphism are hereditary, their low frequencies in the population suggest they exist at a competitive disadvantage in *Pantopsalis*.

Comparable polymorphisms are known from a number of animal species (Gross 1996, Roff 1996), such as stag beetles and acarid mites (Radwan 1993, Radwan & Bogacz 2000). Often, the polymorphism persists because lesser development of secondary sexual characters allows benefits such as greater longevity (Radwan & Bogacz 2000), faster development time, or greater fecundity (Roff 1996). One of these factors may be behind the polymorphism in *Pantopsalis*.

Systematics

Pantopsalis Simon, 1879

TYPE SPECIES: *Phalangium listeri* White, 1849 (by monotypy).

DESCRIPTION: Body rounded. Carapace sclerotised; usually more or less denticulate in male, smooth in female. Eyes black. Ozopores visible from above. Posterior margin of cephalothorax raised in ridge, separated by distinct groove from last segment. Free tergite of male cephalothorax sclerotised. Punctures scattered laterally on dorsum of abdomen. Venter of abdomen and coxae smooth. Male usually dark except in *P. snaresensis*, *P. rennelli*, and effeminate male forms of other species; female lighter with light-coloured dorsal median stripe. Chelicerae of male enormously enlarged; both segments heavily denticulate. Chelicerae of female not enlarged; denticles present or absent dorsally on first segment, absent elsewhere. Labrum triangular in profile; smooth. Femur of pedipalp smooth; patella and tibia subequal in length; patella of female with rounded apophysis; hypersetose areas towards distal end of inner dorsal side of patella and tibia in both sexes, covering apophysis and often lighter in colour than remainder of pedipalp in female; tarsal claw smooth (except in *P. rennelli*). Legs round in cross-section. Spine on dorsal distal margin of coxa of legs I to III. Femora of all legs denticulate in males, femora of legs of females smooth. Other leg

segments of both sexes smooth, except for dorsal distally projecting spines at distal end of patella, and paired ventral spines on pseudoarticulations of metatarsus and tarsus. Articulation between metatarsus and tarsus lacks paired ventral spines. Penis with two short pairs of bristle groups at junction between shaft and glans. Ovipositor with four looped seminal vesicles. Chitinous grate over spiracle (Hunt 1990); no entapophysis.

COMMENTS: *Pantopsalis* may be distinguished from *Megalopsalis* by the features shown in Fig. 3. The differing forms of the palpal patellar apophysis have already been described above in 'Taxonomic history of *Pantopsalis*'. *Pantopsalis* females may be distinguished from *Megalopsalis grimmetti* by the subequal length of the patella and tibia of the pedipalp – in *M. grimmetti*, the tibia is approximately twice the length of the patella (excluding the apophysis). In *Pantopsalis*, the outer edge of the movable finger of the male chelicera is smoothly convex, while in *Megalopsalis* the fingers are extended, with a distinct concavity towards the end. Finally, the bristle groups on the penis are much shorter in *Pantopsalis* than they are in *Megalopsalis*.

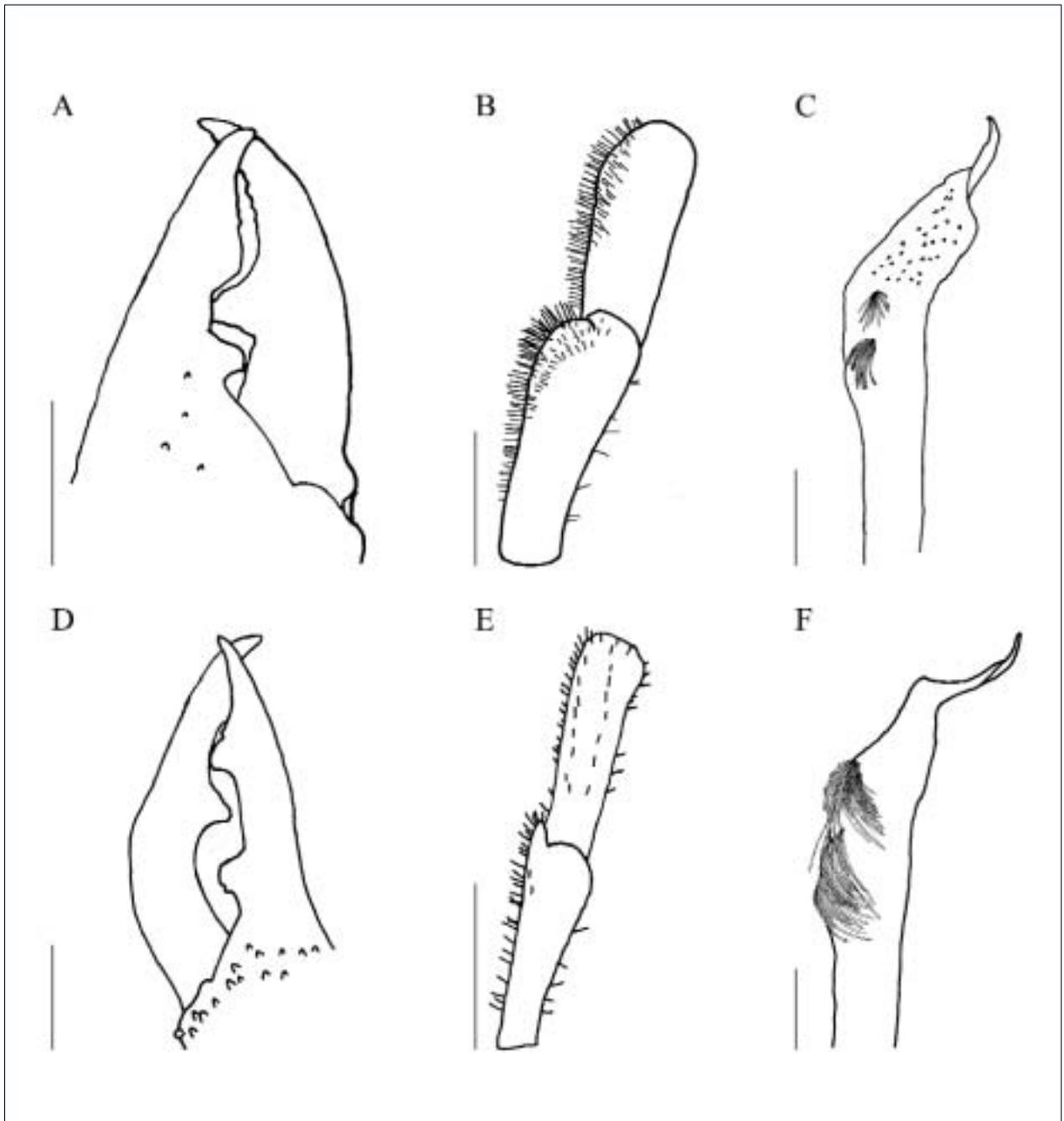


Fig. 3. Comparison between distinguishing features of genera: (A–C) *Pantopsalis*; (D–F) *Megalopsalis*.

- (A) Fingers of male chelicera of *P. phocator*;
- (B) dorsal view of patella and tibia of female pedipalp and
- (C) lateral view of penis of *P. albipalpis*.
- (D) Fingers of male chelicera,
- (E) dorsal view of patella and tibia, and
- (F) lateral view of penis of *M. chiltoni*.

Note outwardly convex form of chelicera in *Pantopsalis* vs. more extended form in *Megalopsalis*; denser setation on pedipalp of *Pantopsalis*; and longer bristle groups on penis of *Megalopsalis*. Scale bar for (A) 0.5 mm, (B) and (E) 1 mm, (C) and (F) 0.2 mm, (D) 2 mm.

Pantopsalis distincta Forster, 1964, *P. grayi* Hogg, 1920, and *P. watti* Hogg, 1920 possess the characters of *Megalopsalis*, and should therefore be transferred to that genus. Thus, *Pantopsalis* is restricted here to a much more homogeneous group.

Distinguishing the species of this genus is problematic. Few species are separated by differences in genitalia, and the differentiation of other species requires further study. The numbers of denticles, punctures, and other ornamentations in males vary significantly within single

localities, and are of little use as diagnostic characters at species level. Perhaps a population genetics study may prove useful for delimiting species in this group, where intra-specific exceeds inter-specific variation.

Females are very similar, and may not be identifiable to species. Effeminate males share female colour patterns (see 'Polymorphism in Megalopsalidinae'), and are also not likely to be identifiable to species. Characters of effeminate males are described under the heading 'Variation' for each species for which they are known.

***Pantopsalis listeri* (White, 1849)**

Phalangium listeri White, 1849: 6 (according to Sørensen 1886); White 1850 (reprint): 52. **Type(s)**: presumed lost.

Pantopsalis listeri (White, 1849): Simon 1879: 73; Sørensen 1886: 56; Roewer 1911: 102, Pl. 1, Fig. 9, 1912: 274, Pl. 4, Fig. 7, 1923: 863.

COMMENTS: White's (1849) original description of *P. listeri* was extremely brief, and inadequate for species identification. Simon's (1879) redescription was more detailed but, as Simon did not indicate if he was using White's original material, there is a possibility that Simon's (1879) redescription may refer to another species. No type depositary was given, and while other types of White's were deposited at BMNH (S. Pollard, personal communication), *P. listeri* could not be located there (J. Beccaloni,

personal communication). The type locality was given only as 'New Zealand' by White (1849), and 'South Island' by Simon (1879). In the absence of type specimens, it is not possible to know what *Pantopsalis listeri* is, an unfortunate situation considering that this is the type species of the genus. Fortunately, Simon's (1879) redescription is enough to be confident that *P. listeri* is at least congeneric with other species placed in *Pantopsalis*.

***Pantopsalis albipalpis* Pocock, 1902 (Figs 4 and 5)**

Pantopsalis albipalpis Pocock, 1902: 399.

Pantopsalis albipalpis Pocock: Roewer 1911: 102, 1912: 275, 1923: 864.

Pantopsalis nigripalpis nigripalpis Pocock, 1902: 399. **New synonym.**

Pantopsalis nigripalpis nigripalpis Pocock: Roewer 1911: 102, 1912: 275, 1923: 864.

Pantopsalis nigripalpis spiculosa Pocock, 1902: 399. **New synonym.**

Pantopsalis nigripalpis spinulosa Pocock (*lapsus calami*): Roewer 1912: 275, 1923: 864.

Pantopsalis jenningsi Pocock, 1903: 437. **New synonym.**

Pantopsalis jenningsi Pocock: Roewer 1911: 102, 1912: 276, 1923: 865.

Holotype of *P. albipalpis* (♂ in BMNH): BMNH [printed] 1890.6.23 [hand] \ *Pantopsalis albipalpis* [hand] \ Pocock [hand], [off-white label] Maungatua \ 90.6.23 [hand], [off-white label] *Pantopsalis albipalpis* Poc T. [hand].

Lectotype of *P. nigripalpis nigripalpis* (♂ in BMNH): BMNH [printed] 1892.12.27 [hand] \ *Pantopsalis nigripalpis* [hand] \ Pocock [hand] \ Loc. [printed] New Zealand [hand], [off-white label] Dunedin 92.12.27.1 [hand], [off-white label] *Pantopsalis nigripalpis*, Poc \ Type [hand], [pale yellow label] *Pantopsalis nigripalpis* Poc \ 'Type' \ Maungatua 1892-12-27 \ NEW ZEALAND \ LECTOTYPE [printed]. Designated below.

Holotype of *P. nigripalpis spiculosa* (♂ in BMNH): BMNH [printed] 1891.2.28 [hand] \ *Pantopsalis nigripalpis* [hand] \ *spinulosa* [sic] Poc. [hand], [off-white label] 91.2.28 \ Jennings [hand], [off-white label] *Pantopsalis nigripalpis*, Poc \ subsp. *spiculosa*, Poc [hand], [pale yellow label] BMNH 1891-2-28 \ *Pantopsalis nigripalpis spiculosa* Poc [printed].

Holotype of *P. jenningsi* (♂ in BMNH): BMNH [printed] BM1890.6.23 [hand] \ *Pantopsalis jenningsi* Pocock [hand] \ 1903 [hand], [off-white label] Maungatua \ 90.6.23 [hand], [off-white label] *Pantopsalis jenningsi*, Poc Type [hand].

OTHER MATERIAL EXAMINED: DN. 1 ♂, Dunedin, 2 Feb. 1958, in garden (OMNZ); 1 ♀, same, 10 Oct. 1958 (OMNZ); 10,

same, 10 Feb. 1959, in garden (OMNZ); 1 ♂, same, Jan. 1960 (OMNZ); 1 ♂, same, 20 Dec. 1978 (OMNZ); 2 ♂, same, 10 Jan. 1983, in garden (OMNZ); 1 ♂, 1 ♀, Leith, 20 Jan. 1976 (OMNZ); 1 ♀, Leith Saddle, Dunedin, 19 May 1967, pitfall (OMNZ); 1 ♂, same, 30 Sep. 1973 (OMNZ); 1 ♀, same, Dec. 1975 (OMNZ); 1 ♂, 1 ♀, same, Dunedin, 19–29 Dec. 1975, malaise trap (NZAC); 4 ♂, 2 ♀, same, grid ref. (NZMS18) 417-281, Jan. 1976 (OMNZ); 1 ♂, same, 4–14 Feb. 1976, malaise trap (NZAC); 1 ♂, 2 ♀, same, 26 Feb.–6 Mar. 1976, malaise trap (NZAC); 1 ♂, same, 8–30 May 1976, malaise trap (NZAC); 1 ♀, same, 10 Aug.–3 Sep. 1976, malaise trap (NZAC); 1 ♂, same, 11 Feb. 1978, litter (OMNZ); 1 ♂, same, Jan. 1982 (OMNZ); 1 ♀, same, 22 Jan. 1966 (OMNZ); 1 ♂, 2 ♀, 4 juv., same, 27 Dec. 1966 (OMNZ); 4 ♀, same, 12 Jan. 1978 (OMNZ); 2 ♂, same, Dunedin, 27 Dec. 1985 (OMNZ); 1 ♂, Lower Clutha, Tuapeka West, 60–120 m, 21 Dec. 1985–18 Jan. 1986, pit trap in *Nothofagus* forest (NZAC); 1 ♂, Opoho [Ohoho], 22 Feb. 1943, in raspberries (MONZ); 2 ♂, 2 ♀, Opoho Bush, Dunedin, Jan. 1946 (MONZ); 3 ♀, Sullivan's Dam, Dunedin, 1600' [490 m], 16 Feb. 1943, in leaf mould (MONZ); 1 ♂, same, 1200' [370 m], 20 Feb. 1943, from among base of flax (MONZ); 2 ♂, 1 ♀, Tomahawk, 14 Mar. 1943, at base of cutty grass plants at edge of swamp (MONZ); 1 ♂, Upper Waitati Valley Rd, 7 Mar. 1997, swept by rocky stream (AMNZ).

MALE: Cephalothorax length 1.8 ± 0.4 mm, width 3.0 ± 0.8 mm, medium brown, with or without mottling. Dorsum of abdomen dark to purple-brown. Paler medial stripe down dorsum in some specimens, varying from barely noticeable to distinctly reddish to nearly white. Medial stripe extending laterally on fourth segment, forming either triangular shape or lateral 'arms'. Black spots present along segmental boundaries on abdomen in some specimens, lighter brown punctures scattered along lateral margins. Venter of abdomen concolorous with dorsum, white spots and/or streaks present in some specimens; coxae of legs slightly darker, chocolate-brown. Small denticles scattered over carapace, especially in front of and around eyemound. Density and number of denticles variable. Eyemound concolorous with carapace, denticulate. Chelicerae medium brown. Denticles sometimes lighter than background colour of chelicerae. Length of segment I of chelicera 10.0 ± 2.5 mm and segment II 12.5 ± 2.5 mm in primary form, segment I 5.0 mm and segment II 7.0 ± 0.5 mm in broad-chelicerate form. Pedipalps vary from dark brown to light golden-brown, end of tarsus white; dorsal pair of denticles sometimes present at distal end of femur, sometimes few scattered very small denticles on main body of femur. Femur of pedipalp 1.8 ± 0.4 mm, patella 0.8–1.0 mm, tibia 0.8–1.0 mm, tarsus 2.0 ± 0.4 mm. Legs dark brown. Leg measurements as in Table 1. Tibia II with four to six pseudosegments; tibia IV not divided into pseudosegments.

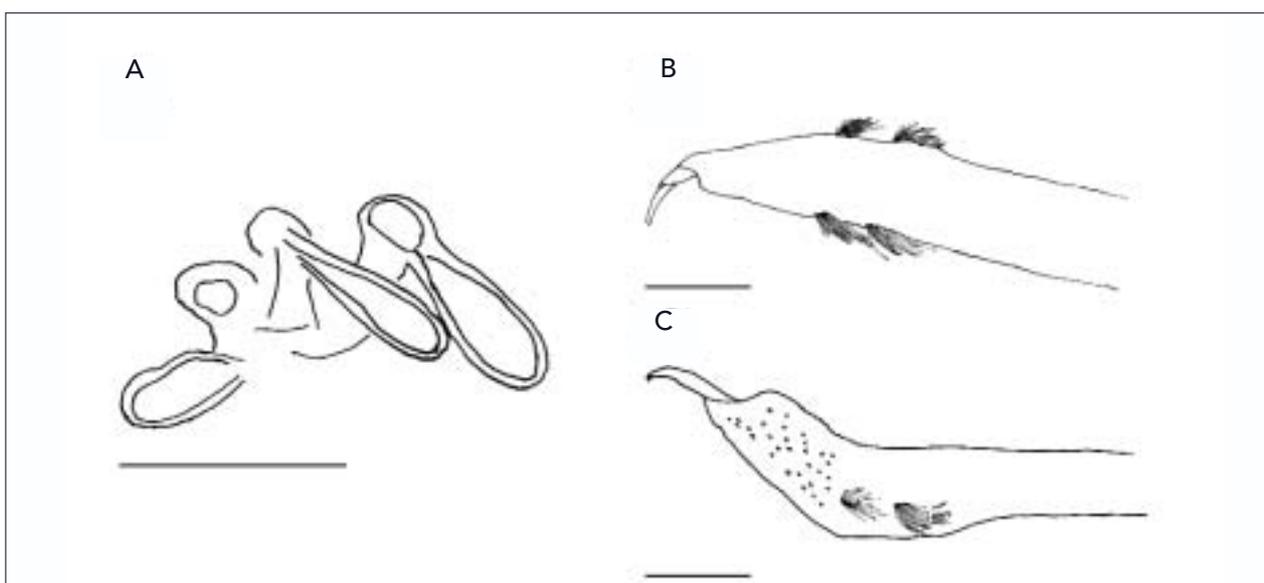
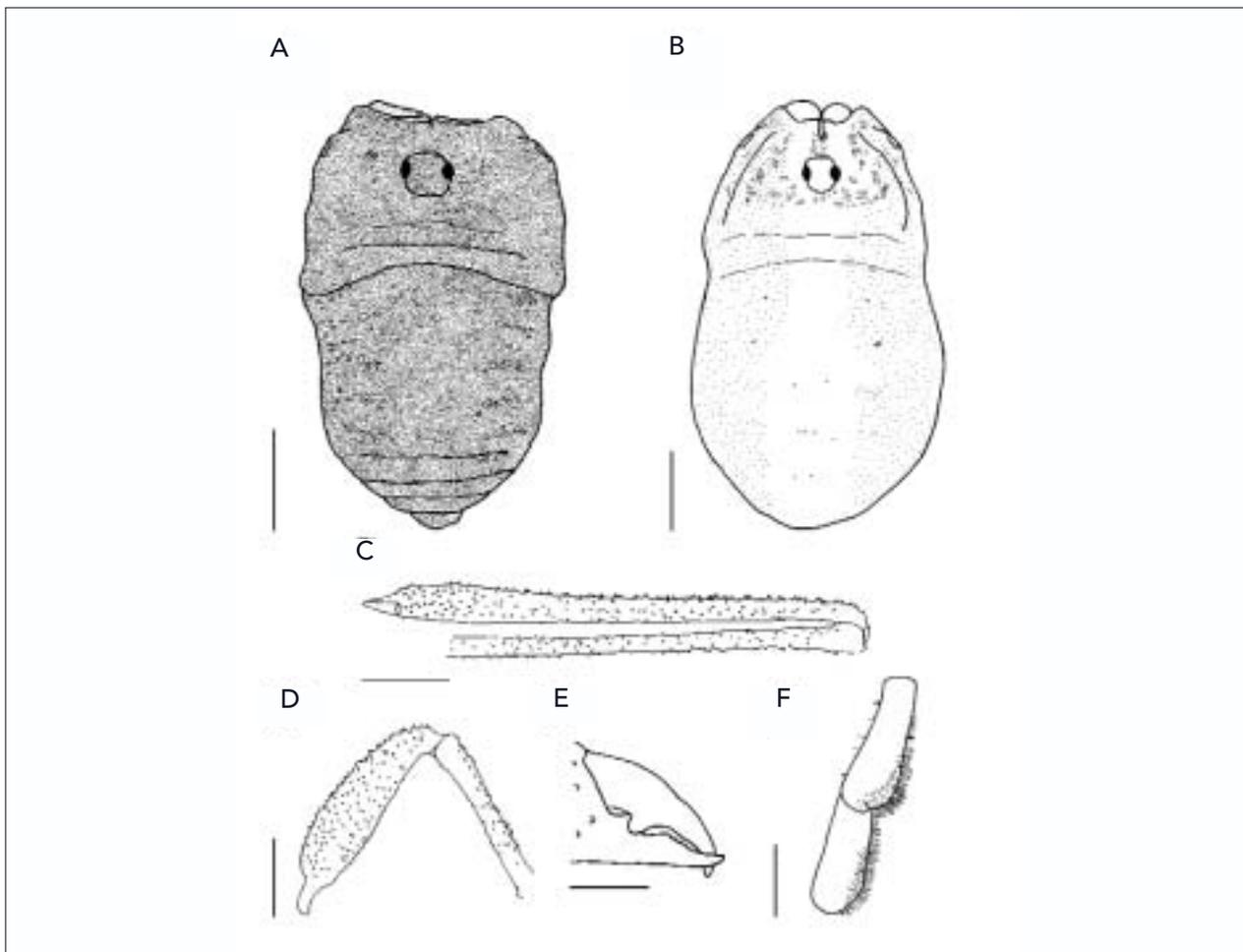
JUVENILE MALE: Specimens identified as juvenile males have an appearance that resembles a female (described below), with a smooth carapace and legs, and a pink medial stripe with white 'arms'. They also possess palpal apophyses as in the female. However, the chelicerae are longer than in females, and extend slightly higher than the

top of the eyemound. Immature specimens are recognised by the fused front of the genital operculum.

VARIATION: This species appears to be quite variable, and a few extreme exceptions are mentioned here. One individual examined from Leith Saddle has an eyemound that is noticeably lighter (golden-brown) than the surrounding carapace (medium brown). Another from Lower Clutha has transverse rows of light circular patches along the segmental boundaries on the venter of the abdomen, and a denticle on the underside of the labrum. The basic colour of the pedipalps appears to be dark brown except for the white tips of the tarsi. In some specimens, the pedipalps are much lighter, from golden-brown to almost white. Denticulation of the femur, if present, is very moderate. The paired denticles at the distal end of the femur are found in the majority of specimens. The medial stripe on the abdomen is often more prominent in lighter specimens, but the correlation is not strict and the exact shape of the medial stripe may vary. Only in the darkest specimens is the medial stripe completely indistinguishable, though such individuals (which include the holotype of *Pantopsalis nigripalpis*) may have lost some of their colour as a result of preservation. One specimen examined from Leith Saddle has indistinct silvery transverse stripes on the lateral margins of segments I to III, similar to *P. coronata*.

Three specimens are significantly lighter than the remaining specimens. One from Leith Saddle has white spots around the posterior margin of the carapace. The medial stripe is indistinct, except for the 'arms', which are white. The lateral punctures on the dorsum of the abdomen are distinguished by white haloes. The coxae of the legs are medium brown distally and golden-brown proximally.

Two specimens examined from Leith Valley and Dunedin represent the effeminate form, and have a tan



Above top: Fig. 4. *Pantopsalis albipalpis*. Dorsal view of (A) male and (B) female, scale bars 1 mm; lateral view of (C) primary-form and (B) broad male chelicera, scale bars 2 mm; (E) fingers of male chelicera, scale bar 0.5 mm; (F) dorsal view of patella and tibia of female pedipalp, showing apophysis and hypersetose areas, scale bar 1 mm.

Above lower: Fig. 5. *Pantopsalis albipalpis*. (A) Seminal receptacles; (B) ventral and (C) lateral view of penis; scale bars 0.2 mm.

Table 1 Leg measurements of *Pantopsalis albipalpis* males (in mm).

Leg	I	II	III	IV
Femur	6.5 ± 1.0	11.0 ± 2.0	5.5 ± 1.0	7.5 ± 1.5
Patella	1.0–1.5	1.5–2.0	1.0–1.5	1.5
Tibia	4.5 ± 1.0	9.5 ± 2.5	4.5 ± 0.5	6.0 ± 1.5
Metatarsus	6.0 ± 1.0	5.0 ± 0.5	5.5 ± 1.0	7.5 ± 1.5
Tarsus	11.0 ± 2.0	29.5 ± 7.0	11.0 ± 1.5	15.0 ± 3.5

Table 2 Leg measurements of *Pantopsalis albipalpis* females (in mm).

Leg	I	II	III	IV
Femur	4.0 ± 1.0	7.5 ± 1.5	4.0 ± 1.0	6.5 ± 1.0
Patella	1.0–1.5	1.5	1.0–1.5	1.5
Tibia	3.5 ± 0.5	8.0 ± 1.5	3.5 ± 0.5	5.5 ± 1.0
Metatarsus	3.5 ± 1.0*	3.5 ± 0.5	4.0 ± 1.5	6.0 ± 1.5
Tarsus	8.5 ± 1.0	22.5 ± 3.0**	8.5 ± 1.5	12.5 ± 2.0

* A single specimen had a metatarsus I measuring 6.0 mm long on one side only.

** A single specimen had a tarsus II measuring 16.0 mm long on one side only.

(very light whitish-brown) background colour, a white stripe extending from either side of the eyemound to the anterior margin of the carapace, and a silvery-white eyemound. The anterior corners of the carapace are medium brown. The posterior portion of the cephalothorax in one specimen is white with black stripes and streaks. The dorsum of the abdomen is mostly black and white (salt-and-pepper), with a white medial stripe and tan lateral punctures. There is a large irregular tan patch front of centre, but this is probably due to loss of colour. The coxae, pedipalps, and chelicerae are white, with irregular brown patches on the coxae. The dorsum of the abdomen of the other specimen is mottled tan with a white medial stripe. The coxae and chelicerae are tan and the pedipalps are white.

FEMALE (ADULT AND JUVENILE): Adult cephalothorax length 1.8 ± 0.4 mm, width 2.4 ± 0.2 mm. White medial stripe, tinged pink and flecked with white, down entire carapace and dorsum of abdomen. Two brighter 'arms' on stripe on third segment of abdomen. Carapace on either side of

medial stripe has tan and silver patches; last segment of cephalothorax and dorsum of abdomen on either side of medial stripe mottled tan or brown. White patch flecked with black on either side of dorsum of abdomen extending onto edge of venter, obscuring boundary between abdomen and venter. Punctures same colour as background but surrounded by haloes of contrasting colour. Eyemound silver-white, darker in middle line, no black setae. Venter of abdomen mottled grey-brown or black and white. Coxae reticulate white on tan. First segment of chelicerae reticulated white on tan dorsally, flecked with blackish-brown ventrally; medial dorsal row of denticles. Second segment reticulated white on tan, giving way to white distally; medial dorsal denticles on proximal half smooth distally. Length of segment I of chelicera 1.0–1.5 mm, segment II 2.5 ± 0.5 mm. Pedipalps mottled mauve and tan. Pedipalp measurements as for male. Legs mottled mauve and tan; femora smooth. Leg measurements as in Table 2. Tibia II with four to six pseudosegments; tibia IV not divided into pseudosegments.

COMMENTS: *Pantopsalis albipalpis* is distinguishable from *P. luna* and *P. rennelli* by differences in the penes (stylus ventral as opposed to dorsal in *P. luna*, glans with a length of 0.27 mm as opposed to 0.19 mm in *P. rennelli*), and from *P. coronata*, *P. pococki*, and *P. phocator* by the absence of the distinct striped colour patterns present in those species.

Three taxa have been synonymised with *Pantopsalis albipalpis* in this paper. The holotype of *P. albipalpis* is a uniform tan colour, and was described as such by Pocock (1902). However, this colour is an artefact of preservation. *Pantopsalis nigripalpis nigripalpis*, described in the same paper, represents another specimen of the same species that has retained its natural colour. The synonymy of these species was confirmed by examining *in situ* the genitalia of the holotype of *P. albipalpis*. The distal end of the penis matches those of specimens from the Dunedin area that fit the description of *P. nigripalpis nigripalpis*. The name *P. albipalpis* has page priority.

The vial containing the type of *Pantopsalis nigripalpis nigripalpis* included two specimens, one of which is a frac-

tion of the size of the other, and probably represents a different species. Pocock's (1902) original description applies to the larger specimen, and it is unlikely that the smaller specimen was considered. Therefore, the larger specimen is here designated as the lectotype of *Pantopsalis nigripalpis nigripalpis*, while the second specimen is separated as *Megalopsalidinae* sp. indet.

Pantopsalis nigripalpis spiculosa was distinguished from *P. nigripalpis nigripalpis* on the basis of greater denticulation on the carapace. However, variation in degree of denticulation is common in *P. albipalpis*, and the difference is not great enough to justify recognition of a separate taxon.

The type specimen of *Pantopsalis jenningsi* was originally identified by Pocock (1902) as possibly being the female of *P. nigripalpis*, but was described later as a new species by Pocock (1903) when he recognised it as a male. In fact, it represents the broad-chelicerate form of *P. albipalpis*, while the types of *P. albipalpis* and *P. nigripalpis* represent the primary form.

Pantopsalis cheliferooides (Colenso, 1882)

Phalangium (Phrynus) cheliferooides Colenso, 1882: 166.

Phalangium cheliferooides Colenso: Forster 1944: 184.

Pantopsalis cheliferooides (Colenso, 1882): Vink in Nicholls *et al.* 2000: 46.

Holotype ♂ in CMNZ (specimen is in a vial, which is itself placed inside a jar – date when jar label was written is unknown):

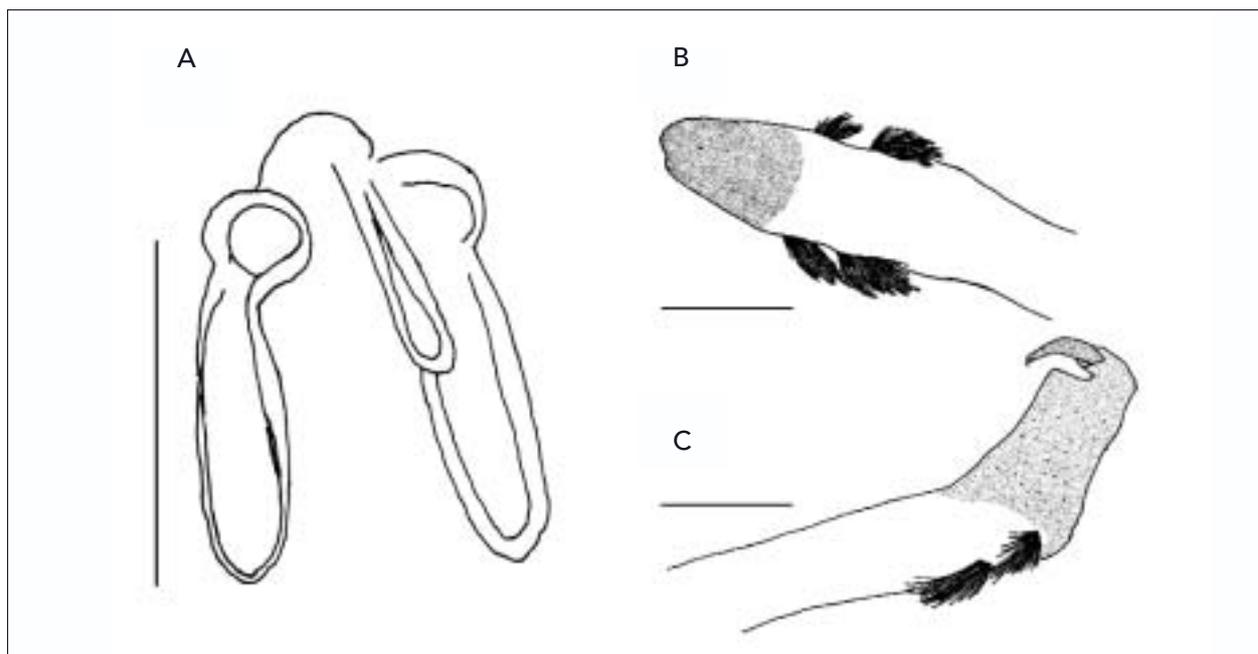
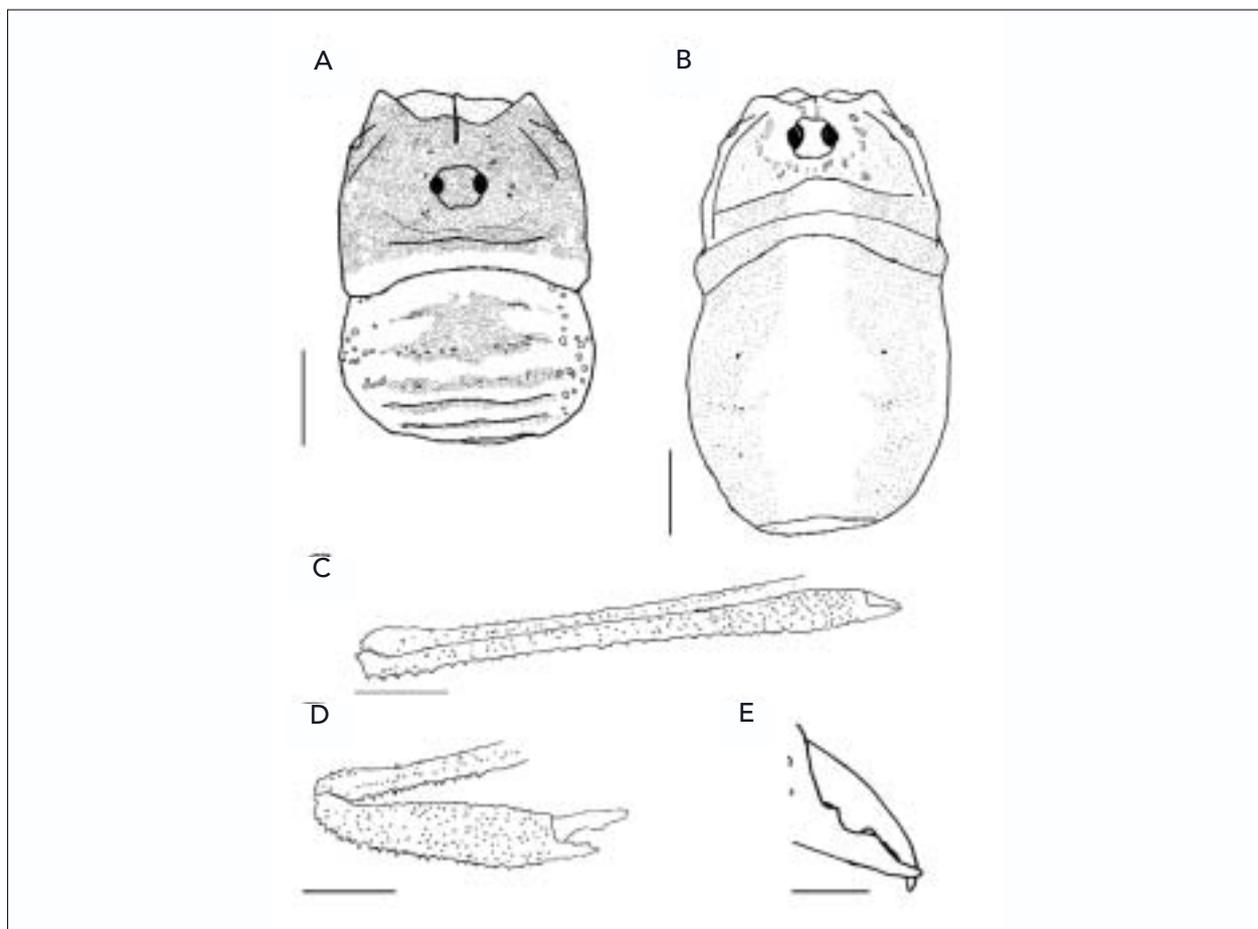
Phrynus \ cheliferooides \ Colenso, Type [hand, label in vial]; Holotype. \ *Phrynus cheliferooides* \ (Colenso), 1883. \ *Phalangium (Phrynus) cheliferooides* Colenso, \ Loc. Seventy-mile Bush, \ Colenso, W., Trans. N.Z. Inst., vol. 15, p. 166, 1883 [printed, label in jar].

MALE: Cephalothorax length 2.0 mm, width 3.0 mm. Carapace (especially in front of eyemound) and eyemound heavily and irregularly denticulate. Cephalothorax and abdomen black. Chelicerae slender, primary form; length of segment I 10.0 mm, segment II 11.5 mm. Pedipalp white, red-pink at base and blackish at tip. Femur of pedipalp 1.8 mm, patella 1.0 mm, tibia 1.0 mm, tarsus 2.6 mm. Leg I only still attached; femur 8.0 mm, patella 1.5 mm, tibia 5.5 mm, metatarsus 7.0 mm, tarsus 13.0 mm. Colours taken directly from Colenso (1882), as holotype has faded to dull grey-brown.

COMMENTS: *Pantopsalis cheliferooides* cannot yet be distinguished from other species of *Pantopsalis*, and should be regarded as a *nomen dubium*. However, it is geographically isolated from other members of the genus, and examination of further specimens from the type locality may allow its identity to be properly established. The female is unknown.

William Colenso was one of the great polymaths of the nineteenth century – missionary, linguist, naturalist, and even, when circumstances required it, bookbinder (Hooker, in the introduction to Colenso 1845). Though primarily a botanist, Colenso also dabbled in entomology. Colenso was uncertain as to whether he was describing a harvestman, whip scorpion, or pseudoscorpion. Therefore, he chose a name that incorporated all three, describing it simultaneously in the genus *Phalangium* (harvestmen), and subgenus *Phrynus* (whip scorpions), while giving it the specific name *cheliferooides* ('resembling *Chelifer*', a pseudoscorpion). The genera used by Colenso correspond to groups recognised as orders today.

Forster (1944) and Marples (1944) both referred to *Phalangium cheliferooides* as probably being either a *Megalopsalis* or *Pantopsalis*, but did not comment further. Vink (in Nicholls *et al.* 2000) transferred *Phalangium cheliferooides* to *Pantopsalis*.



Above top: Fig. 6. *Pantopsalis coronata*. Dorsal view of (A) male and (B) female, scale bars 1 mm; lateral view of (C) primary-form and (D) broad male chelicera, scale bars 2 mm; (E) dentition of male chelicera, scale bar 0.5 mm.

Above lower: Fig. 7. *Pantopsalis coronata*. (A) Seminal receptacles; (B) ventral and (C) lateral view of penis; scale bars 0.2 mm.

Table 3 Leg measurements of *Pantopsalis coronata* males (in mm).

Leg	I	II	III	IV
Femur	6.0 ± 2.0	10.5 ± 1.0	5.5 ± 0.5	8.0 ± 1.0
Patella	1.0–1.5	1.5	1.0–1.5	1.0–1.5
Tibia	5.0	9.5 ± 0.5	4.0–4.5	6.0–6.5
Metatarsus	5.5 ± 0.5	5.0 ± 0.5	5.0–5.5	8.0 ± 1.0
Tarsus	10.0 ± 1.5	26.0 ± 1.0	11.0–11.5	15.0 ± 1.5

Table 4 Leg measurements of *Pantopsalis coronata* females (in mm).

Leg	I	II	III	IV
Femur	3.5–4.5	8.0–8.5	4.0	6.0–6.5
Patella	1.0	1.0–1.5	1.0	1.0–1.5
Tibia	3.5–4.0	7.5–8.0	3.0–3.5	5.0–5.5
Metatarsus	2.5–4.0	2.5–3.5	2.5–4.5	6.5
Tarsus	7.0–8.0	21.0	7.5–8.5	12.0–12.5

***Pantopsalis coronata* Pocock, 1903 (Figs 6 and 7)**

Pantopsalis coronata Pocock, 1903: 436.

Pantopsalis coronata Pocock: Roewer 1911: 102, 1912: 277, 1923: 865.

Pantopsalis trippi Pocock, 1903: 437. **New synonym.**

Pantopsalis trippi Pocock: Hogg 1909: 278, Fig. 4 (*see* ‘Comments’ below); Roewer 1911: 102, 1912: 276, 1923: 865.

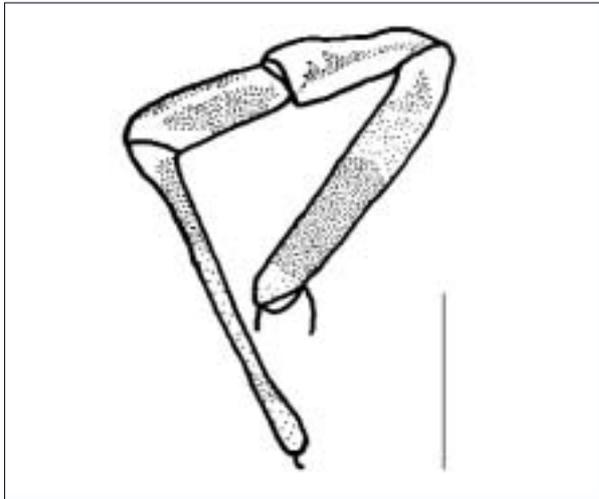
Holotype of *P. coronata* (♂ in BMNH): BMNH [printed] 1903.3.12.1 [hand] \ *Pantopsalis coronata* [hand] \ Pocock 1903 [hand] \ Loc. [printed] New Zealand [hand], [off-white label] 03.3.12.1 \ Timaru, Canterbury, N. Zealand [hand], [off-white label] *Pantopsalis coronata*, Poc. Type [printed].

Holotype of *P. trippi* (♂ in BMNH): BMNH [printed] 1903.3.12.2 [hand] \ *Pantopsalis trippi* Pocock [hand] \ 1903 [hand] \ Loc. [printed] New Zealand [hand], [off-white label] 03.3.12.2 \ Timaru, Canterbury, N. Zealand [hand], [off-white label] *Pantopsalis trippi*, Poc. Type [hand].

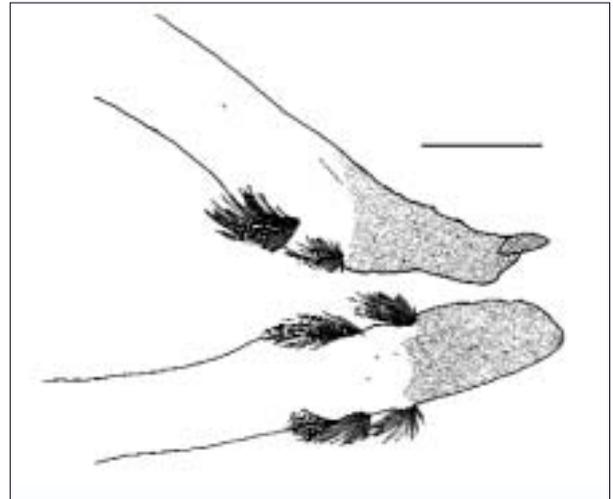
OTHER MATERIAL EXAMINED: SC. 3 ♂, 3 ♀, Peel Forest, 9 Feb. 1946, from ferns (MONZ).

MALE: Cephalothorax length 1.6 ± 0.4 mm, width 2.6 ± 0.6 mm. Cephalothorax (including eyemound) medium brown, except for transverse orange-red (Pocock 1903) band across last segment and first segment of dorsum of abdomen (faded to yellow in holotype). Some brown on anterior and posterior margins of first segment of abdomen. Second and third segments of abdomen have silver transverse stripes, medially interrupted with brown; fourth, fifth, and sixth segments have brown anterior and

silver posterior stripes. Orange punctures scattered along lateral margins of abdomen, extending into brown transverse stripes. Eyemound mostly smooth, with few minute denticles on posterior side. Few scattered nodules on carapace, especially on eyemound. Venter of abdomen orange-tan, but for dark brown genital operculum and dark brown depressions on first segment. Coxae of legs dark brown with lighter reticulations. Chelicerae medium brown. Length of segment I of chelicera 9.5 ± 3.5 mm and segment II



Left: Fig. 8. *Pantopsalis halli*, outer lateral view of female pedipalp (setae not shown), scale bar 1 mm.



Right: Fig. 9. *Pantopsalis luna*, (A) lateral and (B) ventral view of penis, scale bar 0.2 mm.

10.5 ± 3.5 mm in primary form; segment I 5.0 mm and segment II 6.5 mm in broad-chelicerate form. Pedipalps medium brown, with tan tip to tarsus. Femur of pedipalp 1.6 ± 0.2 mm, patella 0.8 ± 0.2 mm, tibia 0.8 ± 0.2 mm, tarsus 2.0 ± 0.2 mm. Legs dark brown to tibia, metatarsus lighter brown, tarsus tan. Leg measurements as in Table 3. Tibia II with four or five pseudosegments; tibia IV not divided into pseudosegments.

VARIATION: Pocock's (1903) statement that the orange-red band across the abdomen and cephalothorax is missing in the holotype of *Pantopsalis trippi* is inaccurate, as a faded yellow band is present. However, that band is not as extensive (covering only the posterior half of the last cephalothoracic segment) and distinct as in the holotype. In the Peel Forest specimens, the transverse stripe across the boundary between cephalothorax and abdomen is white with a pinkish tinge rather than yellow, except in the single broad-chelicerate male, where it is a dark pinkish colour.

FEMALE: Cephalothorax length 1.6–1.8 mm, width 2.8 mm. Carapace has U-shaped white patch around and in front of eyemound, bordered by horseshoe shape of irregular medium brown patches. Two parallel medium brown stripes from eyemound to anterior margin of carapace; rest of carapace silver. Final segment of cephalothorax and dorsum of abdomen mostly tan, with a broad white medial stripe to end of abdomen. Two white 'arms' to stripe on third segment. Irregular black spots along segmental boundaries on abdomen. Lateral margins of dorsum of body white, with scattered tan punctures. Eyemound

white, smooth. Venter of abdomen and coxae mottled tan and white. Chelicerae mottled tan and white. First segment dorsally denticulate. Length of segment I of chelicera 1.0 mm, segment II 2.5 mm. Pedipalps white. Pedipalp measurements as for male. Legs mottled brown and tan. Leg measurements as in Table 4. Tibia II with four pseudosegments; tibia IV not divided into pseudosegments.

COMMENTS: This species can be distinguished from *Pantopsalis albipalpis* by the reduced denticulation on the carapace and the transverse orange-red and silver stripes on the abdomen. It can be distinguished from *P. phocator* by the absence of white articular membranes in the male, and the presence of the transverse silver stripes. *Pantopsalis pococki* differs in the sharper, more extensive denticulation on the carapace.

The holotypes of *Pantopsalis coronata* and *P. trippi* are very similar except for the chelicerae, but still represent one species, with *P. coronata* being the broad-chelicerate form and *P. trippi* the primary form. The difference in colour between the Timaru and the Peel Forest specimens may be due to loss of natural colour. Unfortunately, no specimens other than the two types were available from their respective type localities and a more detailed comparison cannot be made.

Hogg (1909) attributed a specimen from Stewart Island to *Pantopsalis trippi*, but this record requires confirmation as the chelicera shown in his figure suggests his specimen may belong to a species of *Megalopsalis*.

Pantopsalis halli Hogg, 1920 (Fig. 8)

Pantopsalis halli Hogg, 1920: 34, Pl. 1, Fig. 4.

Lectotype (♀ in BMNH): 1924.III.1.1243 K7 \ *Pantopsalis halli* Hogg ♀ cotype \ Mt Algidus, Rakaia Gorge, N.Z. \ J. Hall Hogg Coll. [hand]; Mt Algidus, Rakaia Gorge N.Z. J. Hall \ [illegible] 13 \ *Pantopsalis Halli* sp nov Type. [hand]; LECTOTYPE \ *Pantopsalis halli* Hogg, 1920 \ Det. C. Taylor 2002. Designated below.

OTHER MATERIAL EXAMINED: MC. 1 ♀, Mt Algidus, 11 Feb. 1946 (MONZ).

FEMALE: Cephalothorax length 2.0 mm, width 3.0 mm. Carapace mottled white and light brown, broad white stripe on either side of eyemound to anterior margin of carapace. Eyemound white with black margin around each eye. Dorsum of abdomen with white medial stripe, broadening to triangular shape at third segment, rest of dorsum of abdomen brown with white spots scattered on lateral margins. Venter of abdomen mottled brown and white. Coxae mostly white, mottled with dark brown. First segment of chelicera denticulate dorsally, reticulate white on tan dorsally, mottled dark brown and white ventrally; second segment has proximal part reticulate white on brown dorsally, dark brown ventrally; distal part tan. Length of segment I of chelicera 1.0 mm, segment II 2.0 mm. Femur of pedipalp striped dark brown and tan, spotted with white; tibia and patella striped dark brown and white longitudinally; patellar and tibial hypersertose patches tan; tarsus striped dark brown and tan. Femur of pedipalp 1.8 mm, patella 1.0 mm, tibia 1.0 mm, tarsus 2.2 mm. Legs striped dark brown and tan, liberally spotted with

white. Leg measurements as in Table 5. Tibia II has four to six pseudosegments; tibia IV is not divided into pseudosegments.

COMMENTS: The lectotype of this species is poorly preserved, and the greater part of the description given above is based on the specimen collected in 1946. The male of this species is unknown, and so the status of this species is uncertain.

Hogg (1920) assigned four other specimens to this species, three males and a female. While it was not made explicit which specimen of the original five was to be the holotype, the word ‘cotype’ on the label of the specimen examined here suggests that all five were syntypes. As the other four specimens (not examined) were apparently ‘much shrivelled and without label’ (Hogg 1920), their collection locality and conspecificity with the specimen examined here is uncertain. To prevent any possibility of confusion, the labelled specimen is here designated as lectotype.

Pantopsalis johnsi Forster, 1964

Pantopsalis johnsi Forster, 1964: 107, Figs 150–1, 159–60, 166–8.

Pantopsalis mila Forster, 1964: 109, Figs 147–9, 155–6, 163–5. **New synonym.**

Holotype of *P. mila* (♂ in MONZ): Terror Cove, Port Ross \ Auckland Islands \ New Zealand \ 10 Jan. 1963 – K.A.J. Wise \ On rata trunk with \ cockroaches. [hand]; *Pantopsalis mila* \ Forster, 1964 \ HOLOTYPE ♂ [hand].

OTHER MATERIAL EXAMINED: AU. 4 ♂, 4 ♀, Auckland I., Laurie Harbour, Terror Cove, 1 Mar. 1981, insect spray (NZAC).

COMMENTS: In his original description, Forster (1964) commented on the fact that two closely related species were living together in the same locality on the subantarctic Auckland Island. In fact, these two ‘species’ are not distinct; *Pantopsalis johnsi* is the broad-chelicerate and *P. mila* is the primary form of a single species. *Pantopsalis johnsi* has page priority. Unfortunately, the holotype of *P. johnsi*, while listed as being deposited in the Canterbury Museum in the original paper, was not mentioned in a recent list of types held by that museum (Nicholls *et al.* 2000) and could not be located there (S. Pollard, personal communication).

Forster (1964) claimed the species were distinguished by genital form, as well as by the chelicerae. However, the

differences in male genitalia are related to the fact that the penis of *Pantopsalis mila* is illustrated in ventral view, while that of *P. johnsi* is shown in lateral view. Differences in the receptacula seminis of the females are probably due to preparation. Differences in the female colour pattern were recorded, but the female of *P. mila* was noted to be immature.

Forster also described an effeminate form of *Pantopsalis mila*. While not as effeminate as that found in *P. albipalpis*, it provides additional evidence that such polymorphism is widespread in the genus.

No features have been described that would allow *Pantopsalis johnsi* to be distinguished from *P. albipalpis*.

Table 5 Leg measurements of *Pantopsalis halli* females (in mm).

Leg	I	II	III	IV
Femur	4.0	7.0	3.5	5.5
Patella	1.0	1.5	1.0–1.5	1.0
Tibia	3.5	6.5	3.0–3.5	4.5
Metatarsus	3.0 ± 0.5	2.5*	3.0–3.5	4.5–5.0
Tarsus	7.5	18.0 ± 2.5	7.5–8.0	11.5 ± 1.0

* The 1946 specimen had a metatarsus that was 5.0 mm long on one side only.

Table 6 Leg measurements of *Pantopsalis luna* males (in mm).

Leg	I	II	III	IV
Femur	8.5–9.0	14.0 ± 1.0	7.0 ± 0.5	9.5–10.0
Patella	1.0–1.5	2.0	1.5	1.5
Tibia	6.0 ± 1.0	13.5 ± 1.0	5.0 ± 0.5	7.5 ± 0.5
Metatarsus	7.0 ± 0.5	5.0–5.5	6.0–6.5	9.5 ± 0.5
Tarsus	14.5 ± 1.0	?	15.5 ± 1.5	21.0 ± 1.5

Table 7 Leg measurements of *Pantopsalis phocator* males (in mm).

Leg	I	II	III	IV
Femur	6.5 ± 1.0	9.5 ± 1.5	5.5 ± 0.5	7.5 ± 1.5
Patella	1.5	1.5–2.0	1.0–1.5	1.5
Tibia	5.0 ± 1.0	8.5 ± 1.5	4.5 ± 0.5	6.5 ± 1.0
Metatarsus	5.5 ± 1.0	4.0	5.5 ± 1.0	8.0 ± 1.5
Tarsus	10.5 ± 2.0	26.5 ± 4.0	11.0 ± 1.0	14.5 ± 2.0

However, in light of the wide separation of the known geographical ranges of these two species, and with other species (e.g. *P. phocator*) being found in intervening locali-

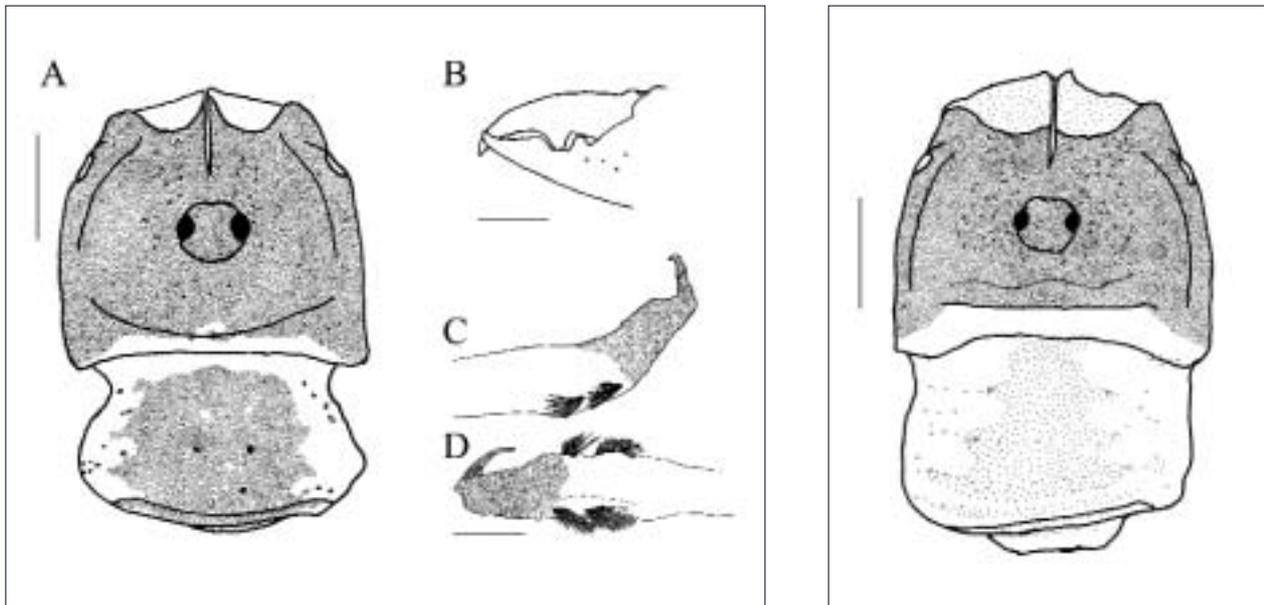
ties, it would be premature to synonymise *P. albipalpis* and *P. johnsi* until more specimens from the type locality of *P. johnsi* have been examined.

***Pantopsalis luna* (Forster, 1944) new combination (Fig. 9)**

Megalopsalis luna Forster, 1944: 190, Pl. 66, Figs 1–3.

Holotype ♀ in MONZ: Waiho Gorge \ A. Castle \ Type Specimen \ *Megalopsalis* \ *luna* 2/18 [hand, off-white label].

OTHER MATERIAL EXAMINED: **WD.** 3 ♂, Waiho Gorge, Sth Westland, 21 Jul. 1927; 2 ♀, Waino [*sic*] Gorge, 12 Jul. 1943 (MONZ).



Left: Fig. 10. *Pantopsalis phocator*. (A) Dorsal view of male, scale bar 1 mm; (B) fingers of male chelicera, scale bar 0.5 mm; (C) lateral and (D) ventral view of penis, scale bar 0.2 mm.

Right: Fig. 11. *Pantopsalis pococki*, dorsal view of male. Scale bar 1 mm.

MALE: Cephalothorax length 2.4–2.6 mm, width 3.6 mm. Cephalothorax (including eyemound) yellow-brown, lightly denticulate in front of eyemound. Eyemound smooth. Coxae of legs yellow-brown. Chelicerae yellow-brown, with second segment orange-brown distally. Segment I of chelicera 12.5 ± 1.0 mm, segment II 14.0 ± 0.5 mm. Pedipalps white with yellow base to femur. Femur of pedipalp 2.0–2.2 mm, patella 1.2 mm, tibia 1.2 mm, tarsus 2.6–2.8 mm. Legs yellow-brown. Leg measurements as in Table 6. Tibia II with six pseudosegments; tibia IV not divided into pseudosegments.

COMMENTS: Forster's (1944) description of this species was based on the female only, and this is the first description of the male. The overall colour as described here is lighter

than *Pantopsalis albipalpis*, but this may be an artefact of preservation. The species can, however, be distinguished by the form of the male genitalia, which in *P. luna* has the stylus placed dorsally on the glans rather than ventrally as in all other species for which the genitalia have been examined. The glans also forms a more obtuse angle with the shaft (150–160 degrees, in contrast to 130–140 degrees in *P. albipalpis*). The available specimens of *P. luna* are also larger than those of *P. albipalpis*; however, this character should be treated with caution as a distinguishing feature until the range of size variation is known. The female holotype appears darker than *P. albipalpis* females, but this too may be an artefact.

***Pantopsalis phocator* new species (Figs 2 and 10)**

Holotype ♂ in NZAC: NEW ZEALAND, SI Stewart I. \ Codfish I. Sealers Bay \ 4 Dec. 1981, B.A. Holloway \ supralittoral plants [printed]; HOLOTYPE \ *Pantopsalis phocator* \ Det. C. Taylor 2002.

Paratypes: SI. 1 ♂, Codfish I., Sealers Bay, 4 Dec. 1981, supralittoral plants (NZAC); 1 ♂, same, 12 Dec. 1966 (NZAC).
ETYMOLOGY: From Latin *phoca* (seal), to indicate a sealer, in reference to the type locality.

MALE: Cephalothorax length 2.2 ± 0.2 mm, width 3.0 ± 0.2 mm, medium brown except for bright white transverse stripe across last segment with pinkish tinge medially, also covering first segment of dorsum of abdomen. Scattered

denticles, especially in front of eyemound. Articular membrane between carapace and chelicerae bright white. Dorsum of abdomen except first segment mostly dark brown, lighter medially with few white or black spots.

Table 8 Leg measurements of *Pantopsalis pococki* males (in mm).

Leg	I	II	III	IV
Femur	6.0	11.0	5.5	8.0
Patella	1.0	1.5	1.0	1.0
Tibia	4.5	?	4.0	?
Metatarsus	6.0	?	5.5	?
Tarsus	10.5	?	10.5	?

Lateral margins of dorsum except first segment silver, with dark brown punctures scattered throughout silver. Final segment of dorsum white. Eyemound concolorous with carapace, smooth except for few small denticles posteriorly. Venter of abdomen dull lilac-brown. Coxae medium brown, lighter in patches. Chelicerae medium brown. Articular membrane between first and second segments bright white. Length of segment I of chelicera 11.5 ± 1.0 mm and segment II 14.0 ± 1.0 mm in primary form; segment I 5.0 mm and segment II 6.0 mm in secondary form. Pedipalps pink, except white tip to tarsus. Femur of pedipalp 1.6–1.8 mm, patella 1.0 mm, tibia 0.8–1.0 mm, tarsus 2.0 ± 0.2 mm. Legs brown, except tan tarsi. Leg measurements as in Table 7. Tibia II has five to seven pseudosegments; tibia IV may or may not be divided into two pseudosegments.

VARIATION: Specimens vary in the degree of development of the transverse white stripe, which may cover only the posterior margin of the final segment of the cephalothorax, and may be interrupted medially. The specimen

***Pantopsalis pococki* Hogg, 1920 (Fig. 11)**

Pantopsalis pococki Hogg, 1920: 34, Pl. 1, Figs 3a and 3b.

Holotype ♂ in BMNH: 1924.III.1.1241. K4 \ *Pantopsalis pococki* Hogg TYPE \ Mt Dick, N.Z. \ J. Hall Hogg Coll. [hand]; Mt Dick N.Z. J. Hall, 1914 K4 \ *Pantopsalis Pococki* sp nov \ Type \ Jim [hand].

MALE: Cephalothorax length 2.4 mm, width 3.0 mm. Cephalothorax (including eyemound) medium brown, except for final segment yellow, heavily denticulate. Eyemound lightly denticulate. Dorsum of abdomen tan medially, yellow laterally, medium brown spots along segmental boundaries. Fourth to seventh segments of abdomen have tan anterior margins, yellow transverse stripes on posterior margins. Lateral margin of dorsum of abdomen dull brown with scattered orange-tan punctures. Venter of abdomen

collected in 1966 is completely tan due to loss of colour, except for the white transverse stripe and the white articular membranes in front of the carapace.

COMMENTS: The female of this species is unknown. Female *Pantopsalis* specimens, as well as an effeminate male, are known from different localities on Codfish Island (specimens in MONZ), but they have not been collected from the type locality of *P. phocator*. Therefore, they cannot definitely be assigned to this species.

Pantopsalis phocator is very similar to *P. coronata*, but it can be distinguished from it and from *P. albipalpis* by the bright white articular membranes, which together with the transverse stripe are resistant to colour loss. Note, however, that the pinkish tinge in part of the transverse stripe may represent the natural colour, which has otherwise been bleached white. Also, *Pantopsalis phocator* has more denticulation on the carapace than *P. coronata*, and the grey abdominal areas are restricted to the lateral sides, not extending medially in transverse stripes.

dull yellow-brown. Coxae medium brown, proximally reticulate. Chelicerae slender; primary form; orange-brown, darker distally than proximally. Segment I of chelicera 9.5 mm, segment II 11.5 mm. Femur of pedipalp yellow, rest of pedipalp white. Femur of pedipalp 1.6 mm, patella 0.8 mm, tibia 0.8 mm, tarsus 2.0 mm. Legs medium brown, except for tan tarsus. Leg measurements as in Table 8.

COMMENTS: The female of this species is unknown. *Pantopsalis pococki* is very similar to *P. coronata*, and the

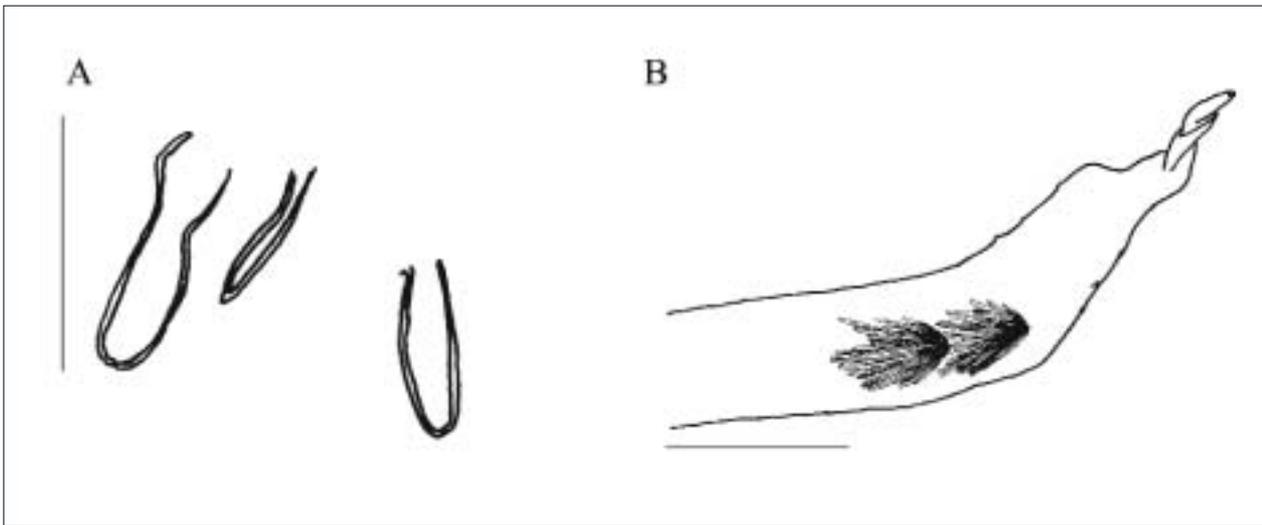


Fig. 12. *Pantopsalis rennelli*. (A) Seminal receptacles; (B) lateral view of penis; scale bars 0.2 mm.

colour differences described between them may be the result of preservation, as the overall pattern is the same. The original description by Hogg (1920) gives the colour of the abdomen as dark brown medially and yellow-grey to grey laterally. The only notable difference between the two species is the degree of denticulation on the carapace. While the degree of denticulation can vary between

individuals of the same species – as in the case of the new synonyms *P. nigripalpis nigripalpis* and *P. nigripalpis spiculosa* (see above) – I believe that *P. pococki* and *P. coronata* are probably distinct species. *Pantopsalis coronata* has very few denticles on the carapace, and they are small and rounded. In contrast, *Pantopsalis pococki* is one of the most heavily denticulate species of the genus.

***Pantopsalis rennelli* Forster, 1964 (Fig. 12)**

Pantopsalis rennelli Forster, 1964: 112, Figs 174–80.

Holotype ♂ in MONZ: Venus Cove \ Campbell Island \ New Zealand \ 2 Feb. 1963 – Rennell \ Ex tussock – 0–2 m [hand]; *Pantopsalis rennelli* \ Forster, 1964 \ HOLOTYPE ♂ [hand].

OTHER MATERIAL EXAMINED: CA. 3 ♀, Campbell I., 26 Feb. 1981, HWM – supralittoral, beating *Hebe* and *Coprosma*; 1 ♂, 2 ♀, 2 juv., Campbell I., Beeman, 18 Feb. 1981, insect spray, *Poa* and *Dracophyllum* on bank; 1 ♂, Campbell I., Beeman Camp, 17 Feb. 1981, under wood in *Dracophyllum* scrub; 7 ♀, Campbell I., Beeman Cove Flats, Feb. 1981, beating; 1 ♂, 6 ♀, Campbell I., Camp Cove, 22 Feb. 1981, beating *Acaena* and *Bulbinella*; 3 ♀, same, 23 Feb. 1981, beating; 5 ♂, 2 ♀, 3 juv., same, 27 Feb. 1981, insect spray and beating; 1 ♀, same, Feb. 1981, ex *Dracophyllum*; 2 ♂, 9 ♀, Garden Cove, Feb. 1981, on *Dracophyllum*; 1 ♀, Campbell I., Mt Honey W. 25 m, 17 Feb. 1981, insect spray *Coprosma* rock face; 1 ♀, Campbell I., Northwest Bay, Hut, 24 Feb. 1981, beating *Dracophyllum*; 1 ♂, Campbell I., Northwest Harbour, 24 Feb. 1981, beating *Dracophyllum* in hut area; 1 ♀, 1 juv., Campbell I., Tucker Cove Flats, 18 Feb. 1981, beating (all previous specimens in NZAC); 1 ♀, Venus Cove, Campbell Island, 2 Feb. 1963, ex tussock – 0–2 m (allotype in MONZ).

COMMENTS: *Pantopsalis rennelli* species is a typical member of the genus, and it was the only monoscutid species found in a large collection from Campbell Island. The single pair of seminal receptacles illustrated by Forster (1964) for this species was not observed in any female of this or other species of *Pantopsalis* examined, which instead had four

seminal receptacles. However, as Forster did not appear to have retained the genitalia he removed, the original dissected specimen could not be re-examined for this study.

The male of *Pantopsalis rennelli* can be distinguished from other males of *Pantopsalis* by its small size, light colour, lack of denticles on the carapace, and the small

size of the penis. The glans of *P. rennelli* has a length of 0.19 mm and depth of 0.13 mm, in contrast to a length of 0.27 mm and depth of 0.15 mm in *P. albipalpis*.

Conclusions and questions

The genus *Pantopsalis* is easily distinguished from *Megalopsalis*, the only other genus of Megalopsalidinae in New Zealand. However, the separation of the species of *Pantopsalis* is a more difficult task. Genitalia, while usually significant in arthropod taxonomy and Opiliones taxonomy in particular (e.g. Tsurusaki 1985, Ubick & Briggs 2002), are quite homogeneous among the species of *Pantopsalis*. A similar situation is found with the North American genus *Dalquestia* Cokendolpher, 1984 (Cokendolpher & Sissom 2000). Both of these genera contain mostly allopatric species, perhaps reducing the selective pressure for genital variation if this is, as commonly thought (Jocqué 2002), a factor in establishing mate suitability.

Most of the differences between species of *Pantopsalis* seem at first glance to be fairly minor, and certainly pale in comparison with the quite significant differences between forms of the same species. The male polymorphism found in this genus is probably the most interesting feature described in this paper. Male polymorphism is widely known among Opiliones and often occurs in groups that are not closely related. Is male polymorphism more widely distributed in Opiliones than currently realised? This is entirely possible considering the lack of knowledge of most members of the order. Has male polymorphism developed (and perhaps been lost) repeatedly? If so, what are the factors that have given rise to this condition? Many more questions about all aspects of the biology of *Pantopsalis* still remain unanswered.

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Appendix: checklist of the Megalopsalidinae

Since the establishment of Megalopsalidinae by Forster (1949), no complete checklist has appeared of its constituent species, and the opportunity is taken to present one here. Initial combinations are given for species whose generic name has changed since their original description. The genus *Pantopsalis* is restricted to New Zealand, and *Spinicrus* to Australia. The majority of species of *Megalopsalis* are found in New Zealand, except the Australian *M. serritarsus* and *M. hoggi*.

Family Monoscutidae Forster, 1948

Subfamily Megalopsalidinae Forster, 1949

Genus *Megalopsalis* Roewer, 1923

[= *Macropsalis* Sörensen, 1886 *non* Sclater, 1866]

M. serritarsus (Sörensen, 1886) (type species)

[= *Macropsalis serritarsus*]

M. chiltoni chiltoni (Hogg, 1909)

[= *Macropsalis chiltoni*]

M. chiltoni nigra Forster, 1944

M. distincta (Forster, 1964) **new combination**

[= *Pantopsalis distincta*]

M. fabulosa (Phillipps & Grimmett, 1932)

[= *Macropsalis fabulosa*]

M. grayi (Hogg, 1920) **new combination**

[= *Pantopsalis grayi*]

M. grimmetti Forster, 1944

M. hoggi (Pocock, 1902) [= *Macropsalis hoggi*]

M. inconstans Forster, 1944

M. marplei Forster, 1944

M. triascuta Forster, 1944

M. tumida Forster, 1944

M. turneri Marples, 1944

M. watti (Hogg, 1920) **new combination**

[= *Pantopsalis watti*]

Genus *Pantopsalis* Simon, 1879

P. listeri (White, 1849) (type species) (*nomen dubium*)

[= *Phalangium listeri*]

P. albipalpis Pocock, 1902

P. cheliferooides (Colenso, 1882) (*nomen dubium*)

[= *Phalangium (Phrynus) cheliferooides*]

P. coronata Pocock, 1903

P. balli Hogg, 1920

P. johnsi Forster, 1964

P. luna (Forster, 1944) [= *Megalopsalis luna*]

P. phocator Taylor, 2004

P. pococki Hogg, 1920

P. rennelli Forster, 1964

P. snaresensis Forster, 1964

Genus *Spinicrus* Forster, 1949

S. camelus Forster, 1949

S. continentale (Roewer, 1923) [= *Pantopsalis continentalis*]

S. minimum Kauri, 1954 [gender corrected from *S. minimus* – W. Starega, personal communication 2004]

S. nigricans Hickman, 1957

S. porongorupense Kauri, 1954 [gender corrected from *S. porogorupensis* – W. Starega, personal communication 2004]

S. stewarti Forster, 1949

S. tasmanicus (Hogg, 1909) [= *Pantopsalis tasmanica*]

S. thrypticus Hickman, 1957

Not Megalopsalidinae (see Gruber & Hunt, 1973)

Nodala Forster, 1949 [junior synonym of *Nelima* Roewer, 1910]

Nelima dunni Forster, 1947 (type species of *Nodala*) [junior synonym of *Nelima doriae* (Canestrini, 1871)]