AUSTRALIAN MUSEUM SCIENTIFIC PUBLICATIONS

Hunt, Glenn S., & Cokendolpher, James C., 1991. Ballarrinae, a new subfamily of harvestmen from the Southern Hemisphere (Arachnida: Opiliones: Neopilionidae). *Records of the Australian Museum* 43(2): 131–169. [22 November 1991].

doi:10.3853/j.0067-1975.43.1991.45

ISSN 0067-1975

Published by the Australian Museum, Sydney

nature culture discover

Australian Museum science is freely accessible online at www.australianmuseum.net.au/publications/6 College Street, Sydney NSW 2010, Australia



Ballarrinae, a New Subfamily of Harvestmen from the Southern Hemisphere (Arachnida, Opiliones, Neopilionidae)

GLENN S. HUNT¹ & JAMES C. COKENDOLPHER²

¹Australian Museum, Division of Invertebrate Zoology, PO Box A285, Sydney South, NSW 2000, Australia

> ²2007 29th Street, Lubbock, Texas 79409, USA

ABSTRACT. The family Neopilionidae (superfamily Phalangioidea) is redescribed along with a redescription of the monotypic type genus Neopilio and the type species N. australis Lawrence. The subfamily Neopilioninae is redefined and contains only N. australis. A new subfamily, Ballarrinae, is erected for Vibone Kauri (southern Africa) and four new genera: Ballarra, Plesioballarra and Arrallaba (southern Australia), and Americovibone (southern South America). Nine new species are described: Ballarra drosera (type species), B. alpina, B. cantrelli, B. clancyi, B. molaris, and B. longipalpus; Plesioballarra crinis (type species by monotypy); Arrallaba spheniscus (type species by monotypy); and Americovibone lanfrancoae (type species by monotypy). The Ballarrinae have highly distinctive pedipalps, characterised by a very long patella, a reflexed tibia and an arcuate tarsus with reduced claw. Australian Ballarrinae possess a distinctive penis carrying a left ventrolateral barbed process and an ovipositor with four spermathecae, rather than two which is the condition in other Ballarrinae and most Phalangioidea. Cladistic analysis is used to explore relationships among Southern Hemisphere non-entapophysate taxa, namely Neopilioninae, Ballarrinae, Megalopsalididae and Enantiobuninae, and their relationship with entapophysate Phalangioidea. Alternate hypotheses concerning relationships are discussed. The significance of characters including pedipalp morphology, distribution of plumose setae and abdominal spiracle structure is also discussed. The Neopilionidae sensu Silhavy (1970) is a paraphyletic group. The Neopilionidae, as defined in this paper, may also prove not to be a monophyletic taxon. Male specimens of Vibone vetusta should help to resolve this question.

HUNT, G.S. & J.C. COKENDOLPHER, 1991. Ballarrinae, a new subfamily of harvestmen from the Southern Hemisphere (Arachnida, Opiliones, Neopilionidae). Records of the Australian Museum 43(2): 131–169.

132

Independently, while researching Australian and South American Opiliones, we found in collections a curious group of phalangioid harvestmen with highly distinctive pedipalps, characterised by having a very long patella, a reflexed tibia and an arcuate tarsus with reduced claw. This pedipalp is very similar to that in the South African species Vibone vetusta which Kauri (1961) described and placed in the family Neopilionidae.

Lawrence (1931) erected a new subfamily, Neopilioninae, within the Phalangiidae for the monotypic Neopilio Lawrence from South Africa. Characters for his new subfamily included: ozopores visible from above; endites of coxa II not directed towards each other at an angle but more or less forming a straight line at right angles to the long axis of the body; first segment of chelicera without a ventral process, cutting teeth subequal in size; pedipalp patella and tibia densely clothed with setae; and claw minute.

South American taxa were added when Mello-Leitao (1933) described Acropiliops ruricola Mello-Leitao and

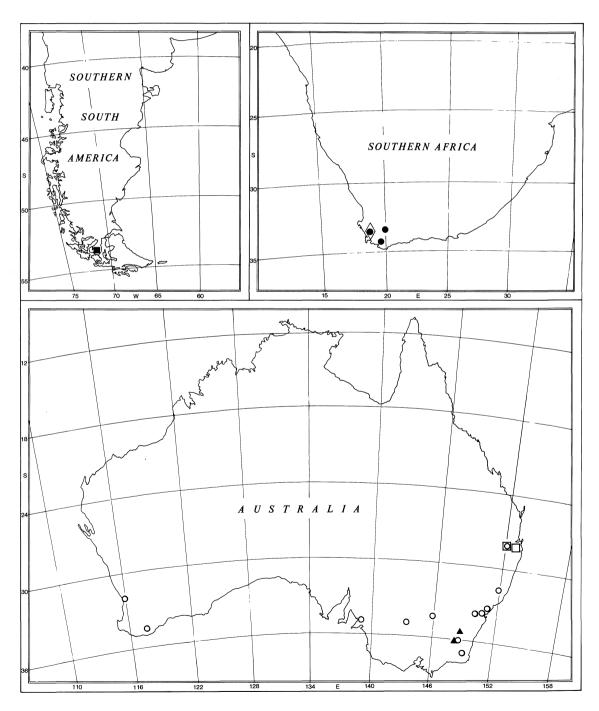


Fig.1. Distribution of family Neopilionidae Lawrence. Open circle = Ballarra; open square = Plesioballarra; closed triangle = Arrallaba; closed circle = Neopilio; open diamond = Vibone; closed square = Americovibone.

synonymised the Enantiobuninae with the Neopilioninae. (The Enantiobuninae is recognised by us as comprising *Thrasychirus* Simon and *Thrasychiroides* Soares & Soares; studies of *A. ruricola* reveal it is misplaced in this group and it will be redescribed elsewhere in the Gagrellidae.)

Kauri (1961) added a further genus from South Africa, *Vibone* Kauri, and elevated the Neopilioninae to family rank. Based on his examination of *N. australis*, he believed the abdominal spiracle of the Neopilionidae differed from other phalangioid taxa in lacking an entapophysis and in being occluded by a grill of closely spaced spines. He found that the spiracle of Megalopsalididae lacked both an entapophysis and a grill. Unfortunately, his observation was based on a study of the Western Australian species *Spinicrus minimus* Kauri which has secondarily lost occluding spines and is not representative of the family (Hunt, in press).

Silhavy (1970) reported his light microscopic survey of selected species from each family level taxon in the Phalangioidea. He concluded that Phalangiidae, Sclerosomatidae and Gagrellidae (= Leiobunidae) all have an entapophysis and lack of grill, although some species possess short spines along the posterior margin of the spiracle. The species he examined from Southern Hemisphere taxa, namely the Neopilionidae, Megalopsalididae and Enantiobuninae, all have a spiracle lacking an entapophysis but possessing a grill. On the basis of this character, he united these taxa in the Neopilionidae and recognised three subfamilies: Neopilioninae (southern Africa), Megalopsalidinae (Australia and New Zealand), and Enantiobuninae (South America).

Our studies, and that of Hunt (in press), suggest that the grill can be derived in different ways and is therefore not a synapomorphy linking Southern Hemisphere taxa. Indeed, grill-like structures are illustrated by Starega (1975) for species in the Ischyropsaloidea and Troguloidea. Lack of an entapophysis is a symplesiomorphy. At our present level of knowledge, the Neopilionidae *sensu* Silhavy (1970) is not defined by a synapomorphy and appears to be a paraphyletic group.

Our present paper explores relationships among these Southern Hemisphere taxa with the aid of cladistic analysis. Taxa with the highly distinctive pedipalp are united in a new subfamily, Ballarrinae, and together with *Neopilio*, are placed in a redescribed Neopilionidae.

Material and Methods

Appendage measurements were done retrolaterally along the dorsal profile, articular membranes excluded. Australian specimens were measured with aid of a camera lucida and Hypad digitiser. Measurements are of the holotype or first listed paratype of the opposite sex unless otherwise stated.

Abbreviations are: BL - body length, CTW - cephalothorax width, CSL - cheliceral second segment

length, PFL – pedipalp femur length, LFL – leg II femur length, LTL – leg II tibia length, PL – penis length, ci – character consistency index, ri – character retention index, M – male, F – female, J – juvenile.

The following abbreviations are used to indicate the location of material examined: AM – Australian Museum, Sydney*, ANIC – Australian National Insect Collection, CSIRO, Canberra, FIS – Forschungsinstitut Senckenberg, Frankfurt am Main, JCC – Personal collection J.C. Cokendolpher, Lubbock, MNHN – Museo Nacional de Historia Natural, Santiago, MOV – Museum of Victoria, Melbourne, QM – Queensland Museum, Brisbane, SAMC – South African Museum, Capetown, UQIC – University of Queensland Insect Collection, St Lucia, WAM – Western Australian Museum, Perth. *AM usually denoted simply by the registration number prefix KS.

Cladistic analyses employed Hennig86 Version 1.5 (Farris, 1988) and involved searching for the shortest tree with extended branch swapping (tree-calculating commands mhennig* and bb*). Rooting was initially by the outgroup but resulted in untenable reversals. Rooting was then by a hypothetical ancestor which was plesiomorphic for all characters. The resulting cladograms (Fig.4) appear much more tenable.

Cladistic Analysis

Discussion of Characters

Principles summarised by Shear & Gruber (1983) have been used to determine polarity: (1) occurrence in outgroups indicates plesiomorphy, (2) less differentiated, more homonomously patterned characters are plesiomorphic, (3) states resembling those of juveniles are plesiomorphic, (4) characters consistently correlated with others known to be apomorphic are also likely to be apomorphic, and (5) correlations between morphological and ecological or distributional characters should be used cautiously. While principle 2 is not commonly used, others working with Opiliones have found it useful (Shear, 1986; Ubick & Briggs, 1989).

Within the Phalangioidea, family level taxa in the Southern Hemisphere, viz Neopilionidae, Megalopsalididae and Enantiobuninae, are all subject to review in evaluating the status of new Australian and South American taxa, namely genera in the Ballarrinae, n. s.fam. Hence, the largely Holarctic entapophysate Phalangioidea was used as an outgroup. The possibility was recognised that this group (consisting of several families) may, in fact, form part of the in-group. For this reason, character states were also polarised by reference to the Caddoidea, the immediate sister group to the Phalangioidea, and the Ischyropsaloidea, the sister group of Phalangioidea + Caddoidea (Martens, 1986).

In the following discussion, numbering of the 20 characters is the same as in Table 1 (see Appendix 1)

and the cladograms (Fig.4). Characters apply to both sexes unless otherwise stated.

Palpal characters. A patella longer than tibia (character 1) is apomorphic by principal 1. This character appears subject to homoplasy. It was used in the initial analysis, deleted, and the analysis rerun.

A tibia reflexed on the patella so that the dorsal angle between them is less than 180° (character 2), together with the lengthening of the patella, is a key synapomorphy of the Ballarrinae which functionally seems to alter the working angle and distance of the tarsus as a raptorial, prey catching organ. A dorsal angle greater than 180° is plesiomorphic by principles 1 & 2.

An arcuate tarsus which is concave dorsad from end to end (character 3) is also synapomorphic for these taxa (excluding Plesioballarra) though curiously the male specimen of Americovibone has a tarsus curved in the opposite sense. The condition in the outgroups where the tarsus is not uniformly curved is plesiomorphic.

A tarsal claw with one or more ventral teeth (character 4) is apomorphic; the plesiomorphic condition of no teeth is present in one of the outgroups (Phalangiinae of the Phalangiidae) and in the Caddoidea, the sister group to the Phalangioidea. A process of secondary reduction of teeth is evident in Pantopsalis undescribed and certain Australian spp. Megalopsalididae. In New Zealand Monoscutinae (Megalopsalididae), only two teeth are present in Monoscutum Forster while they are lacking in Acihasta Forster. It is assumed that the single tooth in the Ballarrinae has been derived through loss.

Loss of the tarsal claw or, if present, reduced and reflexed (character 17) is apomorphic (principle 1). The reflexed nature of the claw may be correlated with its reduction in Neopilio and the Ballarrinae. Character 17 was included in the initial analysis despite being homoplasious as it was a key character for the Neopilioninae sensu Kauri (1961). It was deleted from the data matrix and the analysis rerun.

We support Shear's (1986) view that the presence of plumose setae (character 5) is plesiomorphic. They are widespread in the Phalangioidea, Caddoidea and Ischyropsaloidea (principal 1) and are present in early nymphal instars in at least Ballarra clancyi, n.sp. (principal 3). Absence in the outgroups (and in males of the megalopsalidid Spinicrus) is apomorphic. Individual plumes with bifurcating terminations are regarded as plesiomorphic as they predominate and are also present in the Caddoidea, the sister group of Phalangioidea. Plumes with simple terminations are apomorphic but have been excluded from the final analysis because they appear to arise independently in different taxa (Neopilio, Americovibone, n.sp., and some Enantiobuninae); inclusion creates many additional equally parsimonious trees without clarifying relationships.

Character 6 in the apomorphic state involves restriction of non-plumose sensory setae and non-socketed setae (or loss of the latter) to the distal tip of

the tarsus, together with a correlated distribution of plumose setae along most or all of the tarsus. Functionally, this increases the cover of plumose setae, each of which carries a secretory globule which is thought to assist in food capture. In the plesiomorphic condition (principles 1 & 2), the sensory and non-socketed setae extend along most or all of the tarsus whereas plumose setae are excluded from the distal half. Plesioballarra, n.gen., possesses a larger terminal tuft of sensory setae than in other Ballarrinae and plumose setae are excluded from a larger area, the distal 20% (in a New Zealand megalopsalidid from Broken Hut Cave, Te Kuiti, plumose setae extend well into the distal half, being excluded from the distal 30% of the tarsus - this is considered an independently derived condition; nonsocketed setae occur profusely along the tarsal length).

Excluding *Vibone* where full data are not available, Phalangioidea with the apomorphic palp configuration (*character 2*) are also apomorphic for characters 3, 5 & 6 suggesting there is a functionally related complex. Treating them as separate characters, as has been done in this analysis, will tend to weight the data set. The *Plesioballarra* palp is of interest because the apomorphic state of character 2, while present, is less fully expressed than in related genera and characters 3, 5 & 7 also tend to be more plesiomorphic.

Chelicera. Presence of a ventral process or spur is plesiomorphic by principle 1, its loss is apomorphic (*character 7*). This character appears much subject to homoplasy.

Legs. Presence of pseudoarticulations, often manifested as slight swellings or nodules, in at least the femur of leg II (character 8) is apomorphic. The plesiomorphic condition is present in the 'Phalangiidae' outgroup, Megalopsalididae, Neopilio and some Australian Ballarrinae. The character was included in the initial analysis despite being homoplasious, but was deleted and the analysis rerun.

The presence of teeth on the leg claws of *Americovibone*, n.gen., (*character 18*) is apomorphic by principal 1.

Penis. Sclerotised spines or bristles which are associated with the shaft-glans articulation, tend to have side branches or barbs, and usually arise ventrally are known only in three Southern Hemisphere taxa, namely the Megalopsalididae, Enantiobuninae and Ballarrinae. The tendency of cells adjacent to the articulation to lay down such processes was, in preliminary analyses, regarded by us as a synapomorphy at a lower level of universality than the superfamily, even though the processes have three distinct character states diagnostic of the three taxa: Megalopsalididae possess bristle groups, typically two pairs; Enantiobuninae possess single processes, typically two pairs; Ballarrinae possess a single left lateral process which presumably was primitively paired.

Spines or bristle groups are widespread in other

superfamilies including the Caddoidea and Ischyropsaloidea (Martens, 1986) but in the Phalangioidea these become largely confined to the shaft-glans articulation, or are lost. Hence, in our final analyses, we have regarded the position of these processes as a synapomorphy at the level of the Phalangioidea, that is a plesiomorphy at the family level. Loss of the processes is apomorphic (*character 9*).

The condition in Enantiobuninae most closely resembles that in the Caddoidea and hence is regarded as more plesiomorphic. The bristle groups of the Megalopsalididae (*character 10*) and the single barbed process in the Ballarrinae (*character 11*) are apomorphic.

Nevertheless, the three types of processes associated with the shaft-glans articulation may be interpreted in at least two other ways: as autapomorphies derived from a plesiomorphous naked state, or as autapomorphies derived from a plesiomorphous state of numerous ungrouped spines.

A greatly enlarged barbed process (character 19) is

autapomorphic for Arrallaba, n.gen.

An elongate stylus (*character 12*), present in most Ballarrinae, is regarded as apomorphic by principle 1.

The relative lengths of the penis muscle and its tendon show interesting variation tending to fall into two basic character states: long muscle with short tendon, and short muscle and long tendon (Fig.2). The latter is considered apomorphic but the character is not used in the analysis as it appears to have arisen independently in several taxa.

Ovipositor. Although there has been debate as to whether two or four seminal receptacles (*character 13*) is apomorphic for the Phalangioidea (Shear, 1986), we regard two as apomorphic and four as plesiomorphic. Four occur only in the Ballarrinae, in New Zealand Monoscutinae and a possibly related new genus in Australia, and in some *Pantopsalis* spp. (Forster, 1964). In every species examined the dorsal-ventral pair is reduced (Fig.3), extreme reduction occurring in the

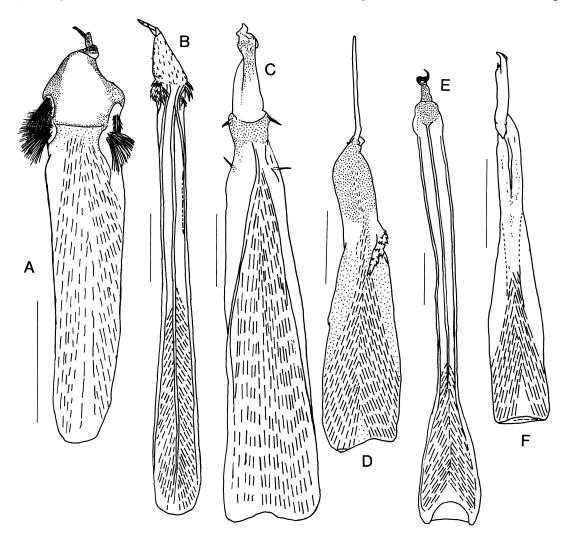


Fig.2. Penis variation in non-entapophysate Phalangioidea. A. Megalopsalidinae (*Spinicrus* sp. ex Sydney); B. Monoscutinae (*Acihasta salebrosa* Forster); C. Enantiobuninae (*Thrasychirus* sp. ex Osorno, Chile); D. Ballarrinae (*Ballarra alpina* n.sp.); E. Neopilioninae (*Neopilio australis* Lawrence); F. Ballarrinae (*Americovibone lanfrancoae* n.sp.). F, dorsal; others ventral. Scale bars 0.1 mm.

monoscutine *Acihasta salebrosa* Forster. In those Megalopsalididae with two receptacles it is the lateral pair that is present. The analyses, however, tend to treat this character as a reversal.

The presence of sensory lobes carrying sensory tufts is plesiomorphic (principal 1). The absence or reduction of the lobes with retention of the sensory tufts is a synapomorphy for the Enantiobuninae (*character 14*).

The presence of only two segments in the ovipositor corpus of *Vibone* (*character* 20) is apomorphic (principal 1). Multiple segments are plesiomorphic.

Spiracle. A spiracle without an entapophysis was regarded by Silhavy (1970) as a key character uniting several taxa into his expanded Neopilionidae. This character is regarded by us as a symplesiomorphy (principles 1 and 2). The apomorphic state of *character* 16 is a spiracle with an entapophysis and attached muscle

which serves to vary the spiracle aperture. It may or may not have grill-like occluding spines. Functionally, the entapophysis with its associated muscle closes the spiracle, presumably limiting water loss and entry by parasites. The grill in non-entapophysate taxa forms a baffle which achieves a similar function, though perhaps less efficiently. (It is not known how the peculiar grill structure of *Caddella africana* (Lawrence) (Kauri, 1961: fig.77G) has been derived and whether it is representative of the Caddoidea).

The spines which form the grill (character 15) can vary considerably but fall into two basic groups (Hunt, in press): those derived by elongation and branching of simple surface micro-ornamentation (plesiomorphic), or those in the Megalopsalidinae which are derived from more specialised 'lace tubercles' (apomorphic by principles 1 and 2). Although unequivocal lace tubercles have not been seen in the three *Pantopsalis* spp.

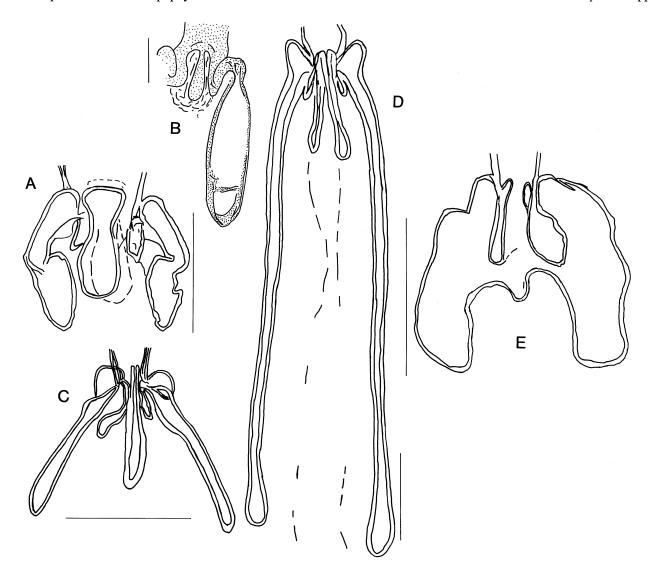


Fig.3. Seminal receptacle variation in Megalopsalididae and Ballarrinae. A,B,E Megalopsalididae. A. ?Monoscutinae (new Australian genus); B. Monoscutinae (*Acihasta salebrosa* Forster); E. Megalopsalidinae (*Spinicrus nigricans* Hickman). C,D Ballarrinae. C. *Arrallaba spheniscus* n.sp.; D. *Ballarra molaris* n.sp. Scale bars: B = 0.2 mm; others = 0.1 mm.

examined, lace-like reticulations occur near or on spine bases resembling a condition in Australian Megalopsalidinae (Hunt, in press). Similar reticulations occur on spines in the enantiobunine *Thrasychirus gulosus* Simon and less clearly in *T. dentichelis* Simon, indicating possible homology with the megalopsalidine spines. This latter condition, however, has been coded as 'unknown' in the analysis because of doubts about homology.

The spines in *Neopilio* and Ballarrinae are very similar but appear to be symplesiomorphic.

Discussion of Relationships

The new subfamily Ballarrinae proved extremely difficult to place within the existing family structure of the Phalangioidea. Several, not necessarily mutually exclusive, hypotheses were evaluated with the help of cladistic analysis. In all analyses, the Ballarrinae were resolved as a monophyletic group, though the possibility of polyphyly is also discussed below.

Hypothesis 1. The Ballarrinae belongs in the Neopilionidae. Analyses 1 and 2 support Kauri's (1961)

view that *Vibone* is close to *Neopilio* (Fig.4A). Hypothesised synapomorphies are a patella longer than tibia (character 1), and a reduced or lost claw (character 17). Other characters that Kauri regarded as significant in defining the Neopilionidae, *viz* orientation of the endite of coxa II and a non-entapophysate spiracle, are regarded as symplesiomorphous, as are the types of spines forming the spiracle grill.

Hypothesis 2. The Ballarrinae, and Megalopsalididae Enantiobuninae monophyletic. This was supported in analysis 3 where the three taxa were united by a synapomorphy in character 4. The relationship with Neopilio + Phalangiidae + Gagrellidae was unresolved because of lack of a synapomorphy. The monophyly of Ballarrinae + Megalopsalididae + Enantiobunidae would be reinforced if our original polarising of character 9 were in error (that is, if the sclerotised processes associated with the shaft-glans articulation are manifestations of a synapomorphy rather than of a symplesiomorphy).

Hypothesis 3. The Ballarrinae is the sister group of the Enantiobuninae. If characters 1, 8 and 17 (suspected homoplasies) are excluded (analysis 3), the

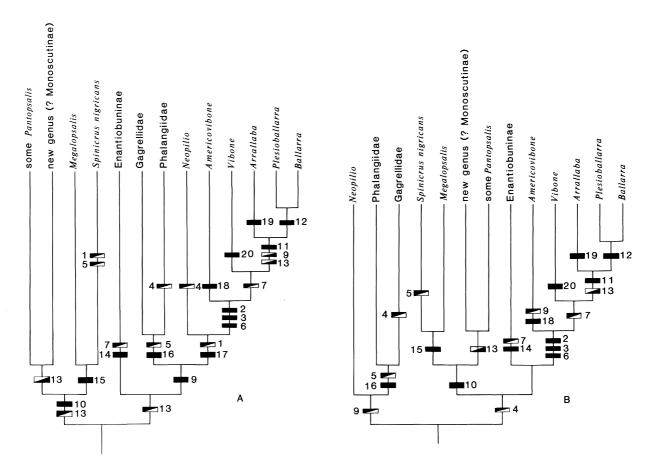


Fig.4. Cladograms of selected phalangioid taxa. A. Analysis 2, one of 8 shortest trees, length 29, ci 65, ri 77; B. Analysis 3, one of 4 shortest trees, length 24, ci 70, ri 79. Solid bar = apomorphy; solid triangle above = homoplasy; solid triangle below = reversal.

Ballarrinae becomes the sister group of the Enantiobuninae (Fig.4B), though there is a lack of a good synapomorphy (they are united only by a possible synapomorphy in character 7, but we have opted for the choice of this character operating at a different level in the cladogram).

However, in the analyses, it was assumed that the plesiomorphic condition of character 10 (paired single sclerotised processes associated with the shaft-glans articulation) occurred in the Enantiobuninae. This character state may be apomorphic with respect to the bristle groups of the Megalopsalididae, and the unpaired single barbed process in Australian Ballarrinae may be derived from it. Certainly, processes in some Enantiobuninae are barbed and not unlike miniature versions of the ballarrine process. Hypothesis 3 would be supported should these processes prove synapomorphous.

Hypothesis 4. The Ballarrinae are the sister group of the Megalopsalididae. Reasons were advanced above for the plesiomorphic status of 4 seminal receptacles (character 13) even though this condition is uncommon in the Phalangioidea. Analysis 3, however, treats them as homoplasic reversals occurring in Australian Ballarrinae and a clade comprising a new genus (?Monoscutinae) and some nominal Pantopsalis spp. The former two taxa 'share' another peculiarity: they have sclerotised processes on only one side of the penis though presumably these were primitively paired. However, the ballarrine penis retains the left ventrolateral barbed process (character 11) whereas the new megalopsalidid retains its right ventrolateral bristles. Nevertheless, the possibility that the ballarrine condition is derived from the other character state through torsion, reduction in number of bristles and enlargement of a single remaining barbed bristle cannot be excluded as these types of developmental processes are involved in penis organogenesis in these groups. Hypothesis 4 would be supported if character 13 proved to be synapomorphous and characters 11 and 20 synapomorphous homologues. Bristles in at least some Megalopsalididae are barbed.

None of the trees in the present analyses showed the Megalopsalididae as the sister group of the Ballarrinae.

Hypothesis 5. The Ballarrinae should be elevated to family rank. On the basis of pedipalp structure, the Ballarrinae appear to be a monophyletic group restricted to Gondwanan continental fragments. Synapomorphies uniting the Ballarrinae with *Neopilio* (characters 1 and 17) are subject to homoplasy within the Phalangioidea and are viewed by us with suspicion. Differences separating the Ballarrinae from the Megalopsalididae or Enantiobuninae seem just as marked as those separating entapophysate family taxa

Hypothesis 6. The Ballarrinae are a

polyphyletic group displaying remarkable convergence in pedipalp structure. The structure of the ballarrine pedipalp could have originated convergently in one or all of the southern continents as a specialised feeding organ. The fact that nothing closely comparable has been found amongst the diversity of Holarctic or tropical Phalangioidea argues against this hypothesis. Differences in penis and ovipositor morphology between Australian and South American species may argue for it.

Conclusion

We consider that sufficient evidence will be gathered to support Hypothesis 5. This evidence will hinge on the discovery of the male of *Vibone vetusta* and comparison of its genitalia with other Ballarrinae and with *Neopilio australis*. Insights should arise if the group is found in New Zealand and radiations exist for study in South America and southern Africa.

At present we are retaining this group in the Neopilionidae (Hypothesis 1) on the grounds of nomenclatural stability.

We also believe that the Enantiobuninae, which some analyses gave as the sister group of the Ballarrinae, should be elevated to family rank on the basis of the highly derived form of the glans, and the loss of sensory lobes from the ovipositor (character 14).

The discovery of further characters may help to resolve family level relationships in the Phalangioidea.

Neopilionidae Lawrence

Phalangiidae: Neopilioninae Lawrence, 1931: 473.–Roewer, 1957: 354.–Ringuelet, 1959: 211.

Neopilionidae: Kauri, 1961: 141-147.—Silhavy, 1970: 171.—Shear, 1975: 68.—Shear, 1982: 110.—Martens, 1978: 55, 229.—Martens, 1986: 304.

Diagnosis. Body less than 3.5 mm long. Openings of ozopores visible from above. Endites of coxae II more or less perpendicular to long axis of body. Lateral abdominal sclerites absent. Corona analis absent or vestigial. Abdominal spiracle lacking an entapophysis, occluded by spines arising predominantly from the anterior margin, lace tubercles or spines with lace-like reticulations absent. Penis with one muscle; glans in more or less same axis as shaft; tufts of bristles or paired spines lacking at shaft-glans articulation but left ventrolateral barbed process may be present. Ovipositor segmented; furca 3-segmented and with sensory lobes; 2 or 4 seminal receptacles. Both pedipalp patella and tarsus longer than tibia; femur through tarsus with plumose setae; tarsal claw small or lacking. Chelicerae usually small. Sexual dimorphism usually slight.

Description. Body small to medium, usually greater than 0.8 and less than 3.5 mm long. Integument usually thin, at the most with minute spines. Eye mound low, rounded, canaliculate, unarmed or with minute spines. Openings of ozopores visible from above. Last 2-4 abdominal tergites faintly defined by grooves; sternites may or may not be clearly defined. Coxae unarmed ventrally except for small setae; endites of coxae II more or less perpendicular to long axis of body. Lateral abdominal sclerites absent. Abdominal spiracle oval, visible or concealed beneath coxae IV, lacking an entapophysis, occluded by spines arising predominantly from its anterior margin, lace tubercles or lace-like reticulations on spines lacking. Leg tibiae with accessory spiracles, often inconspicuous. Penis with one muscle, muscle long (tendon short) or short (tendon long); glans in more or less same axis as shaft; tufts of bristles or paired spines lacking at shaft-glans

articulation but shaft may have left ventrolateral barbed process. Ovipositor segmented; furca usually long and slender, 3-segmented, with sensory lobes; 2 or 4 seminal receptacles. Both pedipalp patella and tarsus longer than tibia, patella often longer than tarsus; femur through tarsus with plumose setae; patella and tibia with or without dense pile of setae; tarsal claw lacking or minute with no ventral teeth, or minute with 1 ventral tooth. Chelicerae small in most species; first segment with or without a ventral spur; jaws with continuous row of teeth of subequal size in most species. Legs long and usually slender; pseudoarticulations often present in all metatarsi, femur II, and tibia II; tarsi each with a simple claw which might have small teeth on each side. Sexual dimorphism slight in most species.

Subordinate taxa. Neopilioninae Lawrence, Ballarrinae n.subfam.

Key to Subfamilies of Neopilionidae

Neopilioninae Lawrence

Neopilioninae Lawrence, 1931: 473.—Roewer, 1957: 354.—Ringuelet, 1959: 211.

Diagnosis. Pedipalp patella and tibia thickened and with dense pile of plumose setae; patella only slightly longer than tibia, angle between them greater than 180°; plumose setae lacking in distal half on tarsus; claw without teeth; leg femora and tibiae without pseudoarticulations.

Description. Integument very thin and soft. Posterior abdominal tergites and sternites faintly defined by grooves; abdominal spiracle usually not concealed beneath coxae IV; spiracle on leg readily visible. Muscle of penis short (tendon long); shaft without left ventrolateral barbed process. Ovipositor with 2 seminal receptacles. Pedipalp patella and tibia thickened and with dense pile of plumose setae; patella only slightly longer than tibia and angle between them greater than 180°; patella shorter than tarsus, plumose setae lacking on distal half of tarsus; claw inserted terminally, reflexed,

without teeth. Chelicerae small, first segment without a ventral spur; jaws each with continuous row of teeth of subequal size. Legs without pseudoarticulations in femora or tibiae, tarsi each with a smooth simple claw. Sexual dimorphism slight, present in pedipalp.

Subordinate taxon. Neopilio Lawrence.

Neopilio Lawrence

Neopilio Lawrence, 1931: 473.-Roewer, 1957: 354.-Silhavy, 1970: 174--Kauri, 1961: 143, 190.-Shear, 1982: 110.

Type species. *Neopilio australis* Lawrence, 1931, by monotypy.

Diagnosis and description. As for the subfamily.

Distribution. Known only from the western Cape Province, Republic of South Africa (Fig.1).

Neopilio australis Lawrence Figs 5, 6A-D

Neopilio australis Lawrence, 1931: 473-474, fig.67.— Roewer, 1957: 354.—Kauri, 1961: 141, 143-145, 185, figs 82, 83.—Silhavy, 1970: 171.

Type material. In his description, Lawrence (1931) did not designate a holotype but did refer to 17 specimens from Signal Hill, Cape Town as "Types". This becomes the type series under ICZN Article 72A(b)(vi); 49 other specimens listed are excluded from the type series. In the material examined by us, labels designate two specimens in SAM as "Type No. 1" and "Type No. 2" and 9 specimens in FIS as "Paratypes". LECTOTYPE FEMALE

(here designated). Republic of South Africa: Capetown, Signal Hill (Type locality). Label data: "Type No. 1, Signal Hill, from 150,339", coll. Purcell, no other data, SAM. PARALECTOTYPES (here designated). Signal Hill, label data "Type No. 2, Signal Hill, from 150,339", coll. Purcell, 1F, SAM. Signal Hill, "Paratypes", Roewer coll. -Lfd. No. 2937, 3M, 4F, 2J, FIS. An additional 6 specimens in the type series (not examined) are also Paralectotypes.

Other material examined (all SAM). Republic of South Africa. Signal Hill: 150,339, Purcell, 7/98, 5F, 7J. 144,02 Purcell, 7/96, 1F. 144,07, Purcell, 9/96, 1F. 150,131, Purcell, 8/01, 1F. 150,130, Purcell, 1F. 150,142, R.M. Lightfoot, 4F. 150,393, Purcell, 8/98, 1M, 2F. 150,338, Purcell, 7/98, 2M. 150,392, Lightfoot, 3/96, 2F. Simonstown: 143,98,

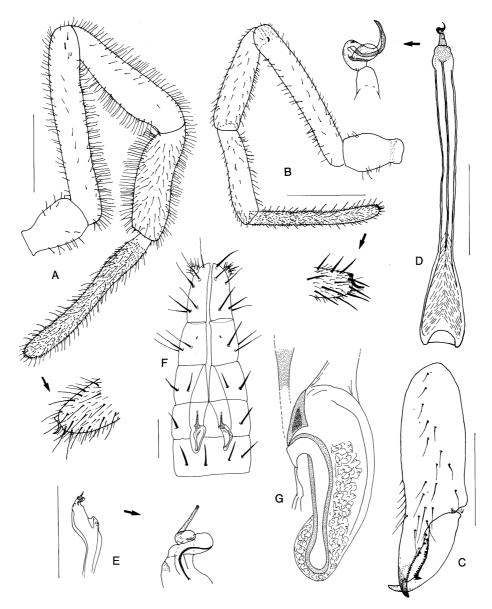


Fig.5. *Neopilio australis* Lawrence. A,B. Pedipalp, male & female; C. Male chelicera; D. Penis, ventral. E. Distal part of penis, lateral; F. Ovipositor, dorsal, distal part; G. Detail of seminal receptacle. Scale bars: F = 0.1 mm; others = 0.5 mm.

Prucell, 9/99, 1M. Touws River: 144,00, Purcell, 9/96, 1F. Newlands, Cape Penninsula: 144,10 Purcell, 8/00, 2M. Hout Bay, Cape Penninsula: 150,391, Lightfoot, 2M, 1F.

Diagnosis. As for the subfamily.

Redescription. Males. *Body*. BL 2.75, maximum width 1.19. Specimens faded; dorsum (at least in females) with faint indication of stripe (Lawrence, 1931: fig.67b), venter pale yellow. Eyes concolorous with body. Anterior margin of cephalothorax smooth, eyemound

low, rounded and smooth or with few minute spicules above. Abdominal tergites with a few minute setae, otherwise smooth; coxae and sternites smooth, the former with a few setae.

Spiracle. Oval, though posterior margin straighter than anterior; surrounded by a raised annulus, particularly posteriorly; partly occluded by grill of closely spaced branching spines arising from the anterior margin; spines long in some specimens, short in others. Integument anterior and posterior to spiracle with numerous rows of micro-ornamentation, sharp close to the spiracle but more distant microtubercles tend to have expanded,

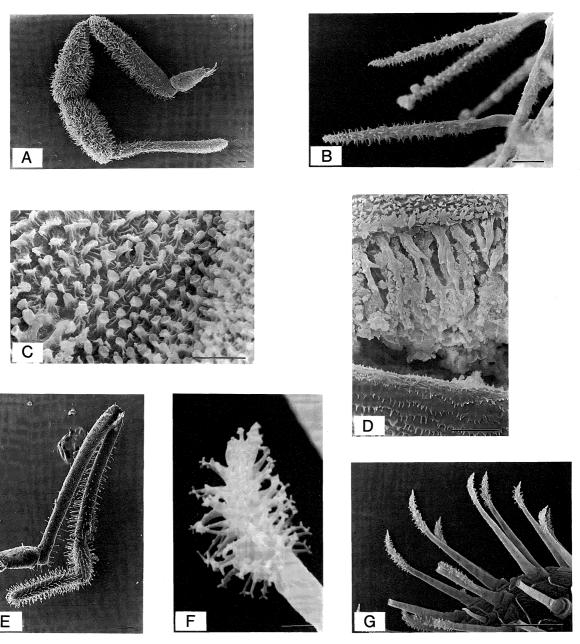


Fig.6. A-D. *Neopilio australis* Lawrence. A. Male pedipalp, retrolateral; B. Plumose setae on pedipalp tibia; C. Microsculpture of ventral abdominal integument; D. Detail of spiracle spines. E-G. *Ballarra drosera* n.sp. E. Pedipalp, retrolateral; F. Plumose seta, distal tip; G. Plumose setae on pedipalp tibia. Scale bars: A,E = $100 \mu m$; B-D = $10 \mu m$; F = $1 \mu m$; G = $20 \mu m$.

concave terminations (may be a shrinkage artifact due to very thin integument).

Chelicerae. Small, entirely smooth, second segment with small equal-sized teeth in single row, those of the immovable jaw bifid or trifid in proximal half, conical in distal half.

Pedipalps. Pale yellow, denticles and claw dark brown. Femur with colourless short setae, more so ventrally; patella, tibia and proximal end of tarsus with brush-like covering; these setae have short plumes along most of their lengths, plumes without terminal bifurcation. Distal half of tarsus with sensory and non-socketed setae, plumose setae lacking; claw inserted terminally, reflexed, minute and without teeth. Lengths (femurtarsus) 1.00, 0.77, 0.69, 0.79. Ratios patella-tibia 1.12, patella to tarsus 0.97.

Legs. Unarmed, femora and tibiae with short setose spines, metatarsi and tarsi with fine minute setae; tarsal formula: 30,57,28-30,33. Measurements (Paralectotype, FIS Lfd 2937):

 Leg
 I
 II
 III
 IV

 Femur
 2.65
 5.09
 2.73
 4.75

 Tibia
 2.50
 4.21
 2.32
 3.17

Penis. Shaft widened basally, glans bent dorsally, rigidly attached to glans; stylus a tightly coiled tube; no bristles or barbed process present near shaft-glans junction.

Description. Females. Similar to male except in the following: body larger; pedipalp longer, patella and tibia more robust and with denser pile of setae; legs shorter. Key measurements: BL 3.75, greatest width 2.05, PFL 1.20, LFL 4.15, LTL 2.95.

Genitalia. Ovipositor not highly sclerotised; with 18 or 19 segments plus 3 elongate furcal segments, slit sensilla 1-1/1-1 on second furcal segment; few setae on terminal 6-9 segments (including furca). Two seminal receptacles consisting of relatively short loops; weakly sclerotised, only distal triangular region darkly pigmented.

Comments. Lawrence (1931) reported secondary sexual characters of the male were absent. Our examination reveals males and juveniles are easily identified from an external examination, as the pedipalps are not as thick as in females.

Kauri (1961: fig.82b) described a juvenile with a double row of teeth on the chelicerae. Among the material at FIS is a juvenile which shows this same pattern - one of the two rows of teeth is on the old cuticle, whereas the second row is visible on the newly forming cuticle. Presumably the specimen Kauri examined had thicker cuticle, because in the juvenile we examined the tips of the shorter cheliceral jaws are also easily observed. Martens' (1978) statement that the

teeth are doubled is presumably based on Kauri's description.

Distribution. Known only from western Cape Province, Republic of South Africa (Fig.1).

Ballarrinae n.subfam.

Diagnosis. Patella and tibia lacking dense pile of setae, dorsal angle between them less than 180°; tarsus with plumose setae along all or virtually all its length, non-socketed setae restricted to area of distal tip or lacking, femur of leg II with pseudoarticulations in some species.

Description. Body small, usually greater than 0.8 and less than 3.5 mm long. Integument usually thin, at the most armed with minute setae. Abdominal spiracle usually concealed beneath coxae IV. Penis shaft usually with strong dorsal keel, muscle usually long (tendon short), left ventrolateral barbed process present or lacking. Ovipositor with 2 or 4 seminal receptacles. Pedipalp patella longer than tibia and usually longer than tarsus, dorsal angle between patella and tibia less than 180°, patella and tibia without dense pile of setae; tarsus usually concave dorsad along its length, plumose setae extend to or almost to distal tip, non-socketed setae restricted to area of distal tip or lacking; tarsal claw lacking, or small, usually inserted ventrodistally, usually with 1 ventral tooth. Chelicerae small in most species; first segment with or without a ventral spur; jaws with continuous row of teeth of subequal size in most species. Legs long and usually slender; pseudoarticulations present in all metatarsi, tibia II, and femur II in some species; tarsi each with a simple claw or a claw with small teeth on each side. Sexual dimorphism slight in most species.

Subordinate taxa. Ballarra n.gen., Plesioballarra n.gen., Arrallaba n.gen., Vibone Kauri, 1961, Americovibone n.gen.

Comments. Ballarra n.gen., has been chosen as the type genus for the new subfamily as it is the best known taxon in the group with six newly described species; other genera are monotypic. Vibone Kauri was described from a single female without the benefit of SEM and this holotype has apparently been lost (L. Cederholm, personal communication). Americovibone n.gen., may prove be representative of a radiation of species in South America. Its characters, including absence of a barbed process on the penis, two spermathecae and the distinctive form of the leg claws may well warrant separate subfamily status when the fauna is better known.

Key to Ballarrinae n.subfam.

1.	First segment of chelicera with ventral process (Fig.23F); leg claws with accessory teeth (Fig.23H,I)
-	- First segment of chelicera without ventral process; leg claws without accessory teeth
2.	Ovipositor with 2 spermathecae (Kauri, 1961: fig.84e)
	- Ovipositor with 4 spermathecae (Fig.3)
3.	Tarsus concave dorsad from end to end; plumose setae extending to distal tip (Fig.6E)
-	- Tarsus not uniformly concave dorsad; plumose setae not extending to distal tip (Fig.21C,D)
4.	Dorsum with heavily pigmented mesial stripe (Fig.22B); stylus of penis short and twisted, barbed process longer than glans (Fig.22E,F)
	- Mesial stripe, if present, silvery; stylus long and gently curved, barbed process shorter than glans (Fig.8C,D)

Ballarra n.gen.

Type species. Ballarra drosera n.sp by original designation.

Diagnosis. Dorsum lacks prominent heavily pigmented mesial stripe; pedipalp tarsus concave dorsad and subequal to or shorter than patella, plumes usually restricted to brush at setal tip; stylus usually sub-equal to or longer than glans, barbed process much shorter than glans.

Description. Body usually small and soft, unarmed except for scattered small setae; eyemound rounded, unarmed, interocular groove usually shallow or only present posteriorly; dorsum often with mesial silvery patches which may coalesce into an irregular stripe; spiracle with either flattened spines or spines essentially round in cross-section, spines on anterior wall generally more strongly developed, spines virtually lacking in *B. alpina*; chelicerae in both sexes of similar size except for *B. molaris* where greatly enlarged in males; patella subequal to or longer than tarsus, tarsus

curved distad, plumose setae extend to tarsal tip, sensory setae few and restricted to extreme tarsal tip, non-socketed setae present distoventrally and/or terminally, not forming a complete subdistal ring, or non-socketed setae absent, claw tiny, reflexed and inserted ventrodistally, or absent; metatarsi and tibia II in all species and femur II in some species with pseudoarticulations; leg tarsi with 15 or more articles; penis with stylus usually subequal to or longer than glans, barbed process much shorter than glans, barbs few or numerous; ovipositorcorpus of more than 2 segments, lateral seminal receptacles penetrate 4-10 segments, dorsal and ventral penetrate 2-3 segments; furca with 3 segments, second with 1-1:1-1 slit sensilla.

Etymology. Aboriginal word for spear barbs, alluding to the barbed process on the penis which is characteristic of Australian species in the subfamily. Feminine in gender.

Distribution. Eastern mainland Australia from southern Queensland to northern Victoria, and Western Australia.

Key to Ballarra n.gen.

1.	Leg II femur with pseudoarticulations (often difficult to see in faded specimens)
	Leg II femur without pseudoarticulations
2.	Leg II femur with greater than 5 pseudoarticulations; pedipalp claw lacking
-	Leg II femur with less than 5 pseudoarticulations; pedipalp claw minute
3.	Barbed process on penis bent perpendicular to long axis of penis (usually visible through integument) (Figs 11-12)
	Barbed process on penis sub-parallel to long axis of
	penis (usually visible through integument) (Fig.7)4
4.	Sclerotised rim of spiracle usually clearly seen against pale abdomen using stereomicroscope; under SEM anterior rim essentially lacking spines
	Sclerotised rim of spiracle usually not easily seen, under
	SEM anterior rim with a few flattened spines
5.	Pedipalp long (femur sub-equal to body length), coxa without denticulate process near the mouth
	Pedipalp shorter (femur less than 75% body length), coxa with large denticulate process near the mouth (Fig.16C)

Ballarra drosera n.sp.

Figs 6E-G, 7-9

Type material. HOLOTYPE: AM KS Budthingeroo Creek, Boyd Plateau, Kanangra-Boyd National Park, via Jenolan Caves, NSW, 33°54'S 150°02'E, near pluviometer, under log, Eucalyptus fastigata - E. dalrympleana - E. viminalis forest, G.S. Hunt, 7 Aug. 1987; 1M. PARATYPES: AM KS 19435, same data; 1F. AM KS 19436, same data; 1M. AM KS 19437, same locality, 17 Mar. 1988; 2F. AM KS 19438, same locality, G.S. Hunt, T. Grant & C. Bradley, 11 June 1972; 4M,2F. JCC, same data, 2M,2F. AM KS 19439, same locality, G.S. Hunt, 15 Aug. 1972; 1F. AM KS 19440, same locality, 22 July 1972; 1F. AM KS 19441, same locality, 1 July 1972; 2M. AM KS 19442, Blood Filly Creek, Boyd Plateau, Kanangra-Boyd National Park, NSW, 33°53'S 150°04'E, in grass, E. fastigata - E. viminalis forest, M.R. Gray, G.S. Hunt, J. McDougal, 27 Mar. 1976; 1F. AM KS 21666, Jenolan Caves, NSW, 33°49'S 150°02'E, Playing Fields area, E. viminalis forest, pit-trap, G.S. Hunt, 15 June - 27

July 1989; 1M. AM KS 19443, Lithgow, NSW, hillside in valley in north-east corner of town, under log, *Eucalyptus* forest, 33°29'S 150°10'E, G.S. Hunt, 2 July 1972; 1F.

Other material examined. AM KS 19431, Bondi State Forest, south-south-east of Bombala, NSW, 37°08'S 149°09'E, "woodlot 1" of 1980 Australian Museum ecological study, under logs in shallow grassy valley, G.S. Hunt, 6 Apr. 1988; 1M,1F. AM KS 19432, same data; 3M,3F. AM KS 11345, same locality, woodlot 1, Australian Museum ecological study, litter berlesate, 27 Sept. 1980; 1M,2F. AM KS 11984, same data, 4 July 1980; 1F. AM KS 19447, Mount Wog Wog, 17km south-east of Bombala, NSW, 37°04'S 149°28'E, CSIRO survey, C.R. Margules, July 1987; 6M,4F. AM KS 19448, same data, Oct. 1987; 1F,1J.

Diagnosis. Bars of pigment on abdomen penetrated by mesial silvery patch; spiracle occluded by a few flattened spines rather than numerous elongate spines rounded in cross-section; pedipalp tarsus with non-socketed setae distoventrally and terminally, claw with

ventral tooth; barbed process not strongly bent across axis of penis shaft, barbs greater than 10 and less than 20.

Description. Males (Boyd Plateau population). *Body.* BL 1.14, CTW 0.83-0.96 (mean 0.90, n = 8). Dorsal pattern (recently collected specimen) as figured, mesial bars of dark brown pigmentation reflecting segmentation, each penetrated by a mesial silvery patch fully enclosed by the pigment; dorsum with irregular silvery stripe placed more laterally. Venter very light brown, abdomen darker laterally and posteriorly; intersternite sutures silvery. Anterior margin not deeply indented. Eyemound mostly black, low, up to 0.7 its length from anterior margin, slightly steeper anteriorly than posteriorly, unarmed; interocular groove shallow. Coxobuccal region as figured; endites, labrum and labium not heavily sclerotised.

Spiracle. Length 0.030, width 0.012. Spines on anterior wall broad and flat, some with multiple terminations; posterior wall relatively unarmed. Rows of microornamentation anterior to spiracle poorly developed; posterior micro-ornamentation well developed but irregular, replaced more posteriorly by rows of linguoform-globular papillae.

Chelicerae. Brown, gracile. Teeth as in Figure 8G, subequal. CSL 0.57-0.67 (0.62).

Pedipalps. Very dark brown, slender. Plumose setae as figured. Non-socketed setae on tarsus placed distoventrally; tarsal claw tiny, with ventral tooth. PFL 0.89-1.00 (0.95), ratio patella-tibia 2.22-2.44 (2.27), patella to tarsus 1.19-1.32 (1.23). Femur-tarsus lengths (of holotype): 1.04, 0.69, 0.26, 0.58.

Legs. Femora brown but darker subdistally, femur IV with dark sub-proximal band; patellae, metatarsi and tarsi almost black; metatarsi with prominent distal silvery band. Femur II with 2-3 pseudoarticulations. Tarsi not minutely divided into articles, only 3 articles very short. Tarsal formula: 16, 27-31, 13-18, 16-18. Measurements:

Leg	I	II	III	IV
Femur	1.40	3.55	1.23	2.64
Tibia	1.13	3.50	1.02	1.64

Genitalia. PL 0.96; ratio shaft:glans:stylus 0.51:0.22: 0.26. Barbed process slender, axis sub-equal to shaft axis; barbs moderately numerous (15-16, n=2), terminal barb elongate. Basilateral flanges of stylus as figured, basiventral flanges almost absent.

Description. Females. Similar to male except in the following: body larger, CTW 0.89-1.15 (1.07, n = 7);

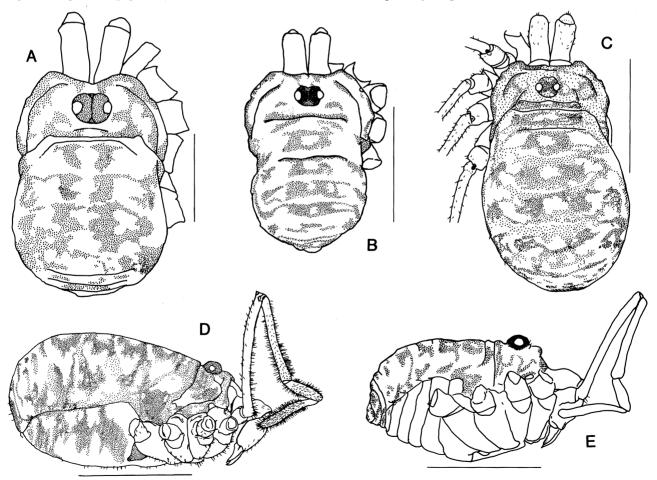


Fig.7. Ballarra drosera n.sp. A. Body of paratype male ex Bondi State Forest, dorsal; B,E. Male ex Boyd Plateau, dorsal & lateral; C,D. Female ex Boyd Plateau, dorsal & lateral. Scale bars 0.5 mm.

chelicera and pedipalp relatively longer, legs relatively shorter. Tarsal formula: 15-17,24-33,15-16,15-19. Key measurements: BL 1.42, CTW 0.90, CSL 0.72, PFL 1.19, LFL 3.15, LTL 3.02.

Genitalia. Ovipositor as figured; lateral spermathecae penetrate 7 segments; dorsal and ventral spermathecae

penetrating 3 segments.

Variation. The Bondi State Forest population differs from the Boyd Plateau population in the following: bars of pigment on abdomen more disrupted laterally and mesially by silvery-gold areas, mesial

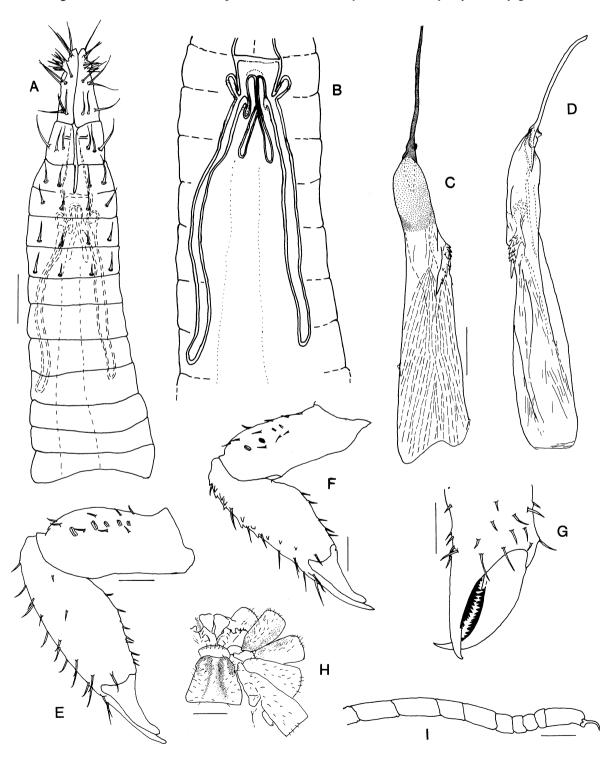


Fig.8. Ballarra drosera n.sp. A. Ovipositor; B. Detail of seminal receptacles; C,D. Penis, ventral & lateral. E,G. Female chelicera, retrolateral & dorsal, F. Male chelicera, retrolateral; H. Coxal and buccal region, female. I. End of tarsus of leg 1, retrolateral. Scale bars 0.1 mm.

silvery-gold patches tend to coalesce to form a stripe; integument anterior to spiracle with narrow zone of micro-ornamentation, posterior to spiracle micro-ornamentation sharper and more clearly defined; penis

with barbed process slightly more robust and with terminal barb shorter, basiventral flanges of stylus moderately well developed. The Mount Wog Wog population resembles that of Bondi State Forest except

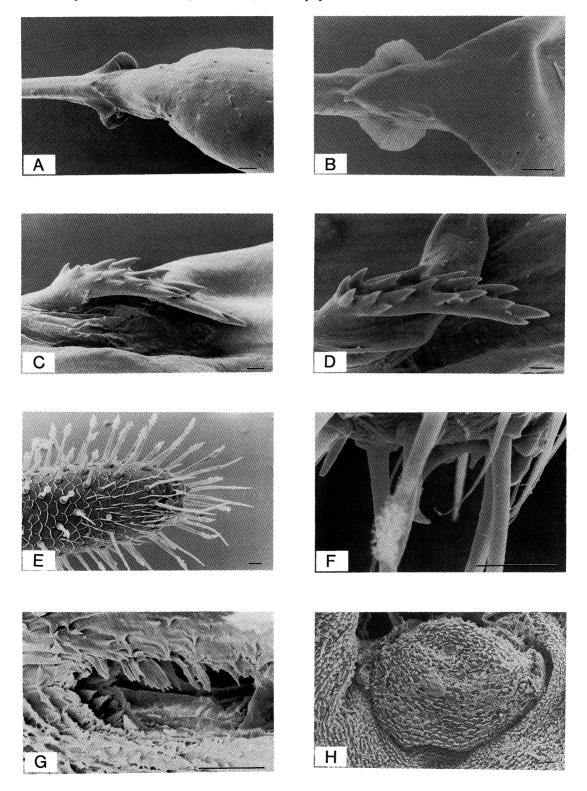


Fig.9. Ballarra drosera n.sp. A-D. Detail of penis, ventral: A,C. Base of stylus & barbed process ex Boyd Plateau; B,D. ex Bondi State Forest; E. Tip of pedipalp tarsus, retroventral; F. Detail of pedipalp claw, lateral; G. Detail of spiracle spines. H. Anal operculum and vestige of corona analis, male. Scale bars 10 µm.

that many individuals have attenuated pedipalps.

Comments. Ballarra drosera is most closely related to B. alpina n.sp.; somewhat less so to B. cantrelli, n.sp., and B. clancyi, n.sp. Differences shown by the southern populations (Bondi State Forest and Mount Wog Wog) may warrant separate species status but a decision should await further study including that of intervening populations.

Since going to press, specimens of a new species from the Adelaide region, South Australia, have been found in the South Australian Museum's collection. This species is close to *B. drosera*.

Etymology. The specific epithet refers to the dewlike secretory droplets on the pedipalp setae, in life reminiscent of sticky hairs on the carnivorous plant *Drosera*.

Natural history. Adults have been collected from March-August (Boyd Plateau) and April-October (southern populations). Under logs; tends to occur near the boundary between the saturated and dry parts of the

log (Hunt, 1979).

Distribution. New South Wales: western Blue Mountains from Boyd Plateau to Lithgow, and Monaro region in the south-east of the State.

Ballarra alpina n.sp.

Figs 10, 11A-D

Type material. HOLOTYPE: AM KS 19136, Smiggin Holes, Kosciusko National Park, NSW, 36°24'S 148°26'E, snow gum (Eucalyptus pauciflora) woodland near quarry, 1700 m, under logs & in litter, G.S. Hunt & M.M. Zabka, 5 Apr. 1988; 1M. PARATYPES: AM KS19137, same data; 1F. AM KS19138, same data; 2M, 1F

Additional material examined. AM KS19139, Mount Kosciusko area, Kosciusko National Park, NSW, open snow gum woodland, 1800 m, K. Green, 1987; 4M,1F,3J (specimens damaged).

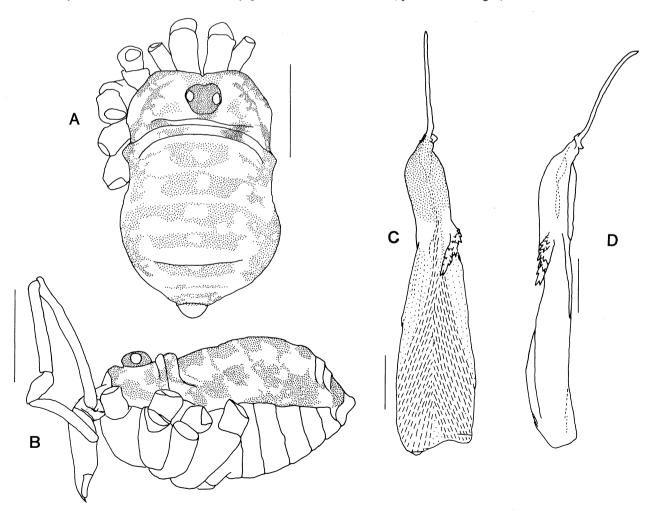


Fig.10. Ballarra alpina n.sp. A,B. Body, dorsal & lateral of male; C,D. Penis, ventral & lateral. Scale bars: A,B = 0.5 mm; C,D = 0.1 mm.

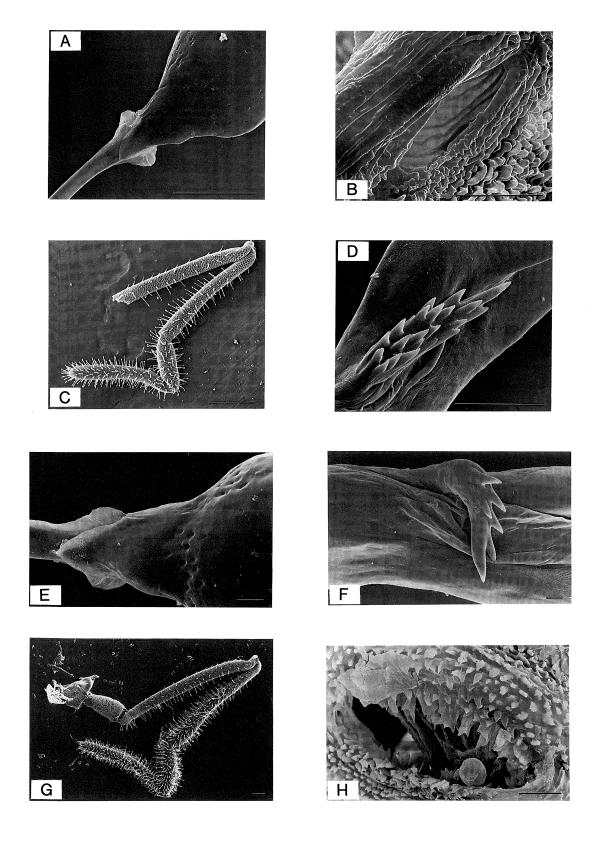


Fig.11. Ballarra spp. A-D. B. alpina n.sp.; E-H. B. cantrelli n.sp. A,E. Base of stylus, ventral; D,F. Barbed process, ventral; C,G. Pedipalp, retrolateral; D,H. Spiracle. Scale bars: A,B = 50 μ m; C = 200 μ m; D = 20 μ m; F,H = 10 μ m; G = 100 μ m.

Diagnosis. Similar to *B. drosera* but spiracle easily seen against paler abdomen and almost without occluding spines, and barbs on penis barbed process more numerous.

Description. Males. Body. BL 1.43, CTW 0.83. Dorsal pattern as figured, similar to B. drosera except that mesial silvery patches slightly smaller and some not completely enclosed anteriorly by pigment. Otherwise similar to B. drosera except that eyemound closer to anterior margin, eye set high on eyemound, interocular groove moderately deep.

Spiracle. Length 0.041, width 0.009. Clearly visible against pale abdomen. Spines on anterior and posterior wall almost completely lacking; integument anterior to spiracle essentially smooth, micro-ornamentation poorly developed immediately posterior to spiracle but followed by very broad linguoform grading posteriorly to narrow linguoform papillae.

Chelicerae. Form similar to B. drosera. CSL 0.62.

Pedipalps. Form and setal disposition similar to *B. drosera*. Lengths (femur-tarsus) 0.83, 0.55, 0.25, 0.47. Ratios patella to tibia 2.20, patella to tarsus 1.17.

Legs. Form similar to *B. drosera*; femora through metatarsi with prominent distal silvery patch; tarsal formula: 15, 25-26,15,17. Measurements:

Leg I II III IV Femur 1.24 2.94 1.29 2.18 Tibia 0.98 2.98 0.94 1.43

Genitalia. PL 0.58; ratio shaft:glans:stylus 0.53:0.20:0.27. Barbed process about 20° to shaft axis, terminal barb shorter and barbs more numerous (22) than *B. drosera*; basiventral flange of stylus more strongly developed.

Description. Females. Sexual dimorphism slight, similar to *B. drosera*. Tarsal formula: 14,26,13,16. Key measurements: BL 2.27, CTW 1.09, CSL 0.70, PFL 0.95, LFL 2.36, LTL 2.46.

Genitalia. Lateral receptacles penetrate 8 ovipositor segments; dorsal and ventral 3.

Comments. Ballarra alpina is very close to the Bondi State Forest population of B. drosera but differs markedly in spination of spiracle. The limited collecting data suggest there may be genetic isolation from B. drosera due to asynchronous life histories, adults of B. alpina being active in warmer months, B. drosera in cooler months.

Etymology. The specific epithet refers to the high altitude of the type locality in the "Australian Alps".

Natural history. Dr Ken Green's ecological study in Kosciusko National Park (Green, 1988) involved pitfall trapping in all seasons 1983 to 1986. Several immatures and some adults were sorted from a single February sample at Smiggin Holes. It is not known if adults hibernate, or whether the species overwinters in the egg or juvenile stage.

Distribution. Subalpine areas in Kosciusko National Park, New SouthWales.

Ballarra cantrelli n.sp.

Figs 11E-G, 12

Type material. Holotype: QM \$15523, Bald Mountain area, via Emu Vale, Qld, 28°14'S 125°25'E, 1000-1300 m, B.K. Cantrell, 17-22 May 1969; 1M. PARATYPES: QM \$15524, same data; 1F. UQ, same data, 1F. UQ, same data; 10M,9F. AM KS 21420, same locality, B.K. Cantrell, 27-31 Jan. 1972; 1M. AM KS 19433, same locality, T. Weir, Feb. 1970; 1F. AM KS5678, Lorne State Forest, via Lorne, NSW, 31°34'S 152°36'E, site 86(5), pitfall trap, D. Milledge, 1 Sept. - 19 Dec. 1979; 1M. AM KS 16064, same site, 29 Oct. - 10 Dec. 1978; 1M,1F. AM KS 15995, same location, site 86(4), 29 Oct. - 10 Dec. 1978; 1F. AM KS 1813, same location, site 87(2), 27 Aug. - 24 Sept. 1978; 1M.

Diagnosis. Abdomen without clearly defined mesial silvery patches penetrating bars of pigment; eyes set high and posteriorly on eyemound; pedipalp claw without ventral tooth; barbed process bent perpendicular to penis shaft, 4-6 barbs; stylus extremely long.

Description. Males. Body. BL 1.52, CTW 0.78. Dorsal pattern as figured; abdomen with heavy dark brown pigmentation mediodorsally interrupted by thin transverse silvery stripes/patches and flanked laterally by longitudinal silvery zone; cephalothorax predominantly pale. Sternites strongly pigmented except at sutures. Anterior margin not strongly indented. Eyemound black, low, unarmed; eyes large, set high and posteriorly on eyemound; interocular groove shallow. Endites, labium and labrum not heavily sclerotised.

Spiracle. Length 0.050, width 0.020. Spines on anterior wall broad and flattened, usually terminally bi- or multifurcate; posterior wall with smaller and fewer spines. Narrow zone of strong micro-ornamentation anterior to spiracle; posteriorly rows of lamellate micro-ornamentation succeeded by closely spaced papillae not as globular as in *B. drosera*.

Chelicerae. Gracile; teeth delicate and nearly equal in size. CSL 0.64.

Pedipalps. Tarsus with non-socketed setae distoventrally and at tip; claw tiny, without ventral tooth. Lengths (femur-tarsus) 0.82, 0.64, 0.27, 0.51; ratios patella to tibia 2.37, patella to tarsus 1.25.

Legs. Slender. Femur II with 3 pseudoarticulations, only 3-5 very short articles distally on tarsi. Tarsal formula: 15,31,15,17. Measurements:

 Leg
 I
 II
 III
 IV

 Femur
 1.37
 3.24
 1.24
 2.23

 Tibia
 1.01
 3.00
 1.00
 1.60

Genitalia. PL 0.65; stylus very long, ratio shaft:glans:stylus 0.46:0.22:0.32. Barbed process perpendicular to shaft axis; only 4-6 barbs. Basal flanges as figured; basiventral flange well developed.

Description. Females. Similar to male except in the following: body larger, appendages relatively shorter. Tarsal formula: 15,26,13,16. Key measurements: BL 1.68, CTW 1.03, CSL 0.60, PFL 0.76, LFL 2.48, LTL 2.27.

Genitalia. Ovipositor as figured; lateral receptacles penetrate 8-9 segments; ventral and dorsal 3 segments.

Comments. This species is closely allied to B. drosera

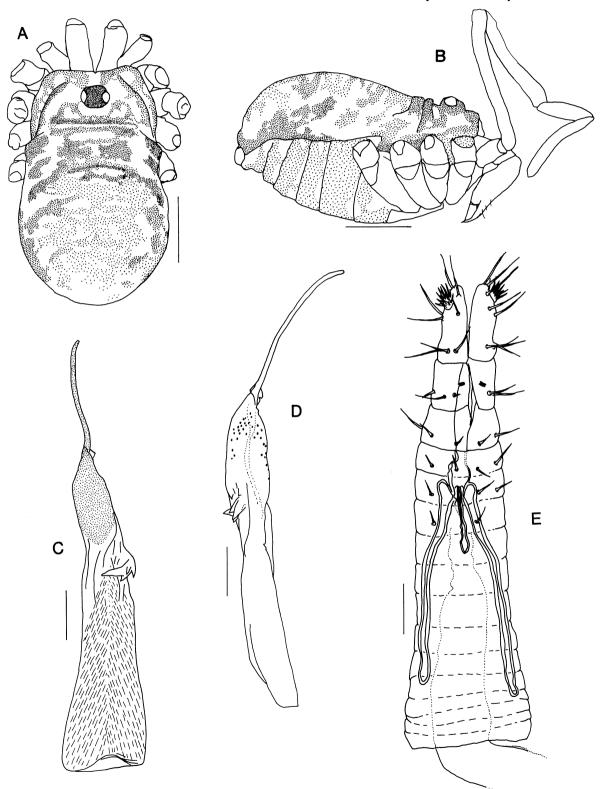


Fig.12. Ballarra cantrelli n.sp. A,B. Body of female, dorsal & lateral; C,D. Penis, ventral & lateral, E. Ovipositor, ventral. Scale bars: A,B = 0.5 mm; C-E = 0.1 mm.

despite the striking apomorphy of the penis barbed process.

Etymology. The specific epithet acknowledges the contribution of Dr Bryan Cantrell to Opiliones research and for collecting most of the specimens of this new species.

Distribution. Coastal ranges of eastern Australia from Taree area of New South Wales to Emu Vale area of southern Queensland though apparently not occurring on the Lamington Plateau.

Ballarra clancyi n.sp. Figs 13, 14, 15A-E

Type material. HOLOTYPE: AM KS19122, Lane

Cove, Sydney, bushland north side of Epping Road next to Stringy Bark Creek, NSW, 34°47'S 151°08'E, under log, G.S. Hunt, 16 July 1988; 1M. PARATYPES: AM KS 19123, same data, 19 Sept. 1987; 1F. AM KS19124, same data; 1M. AM KS19125; same locality, berlesate NSW Dept of Agriculture Argentine Ant Survey, M.J. Fletcher & G.P. Fitt, 17 June 1987; 1M,3J. AM KS19128, same data, 23 June 1983; 1F,3J. AM KS 19126, Wyong, NSW, 33°17'S 151°26'E, crack in garden path, J. Clancy, 13 Aug. 1987; 1F. AM KS 19127, same locality, in kitchen, J. Clancy, 18 Aug. 1987; 1F.

Additional immature material examined. AM KS 19129-35, numerous immatures, type locality.

Diagnosis. Abdomen dorsum extensively pigmented but with many small silvery patches; eyemound set less than 0.5 its length from strongly indented anterior margin; pedipalp tarsus curved strongly dorsad, lacking

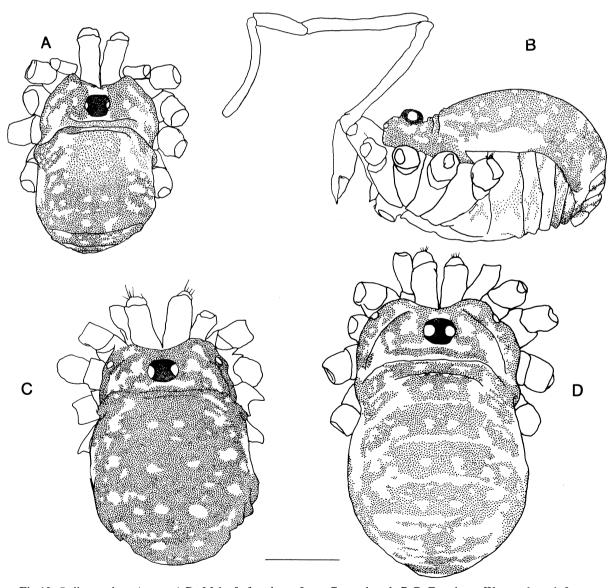


Fig.13. Ballarra clancyi n.sp. A,D. Male & female ex Lane Cove, dorsal; B,C. Female ex Wyong, lateral & dorsal. Scale bar 0.5 mm.

non-socketed setae and claw; barbed process of penis broad distally, greater than 30 barbs; femur of leg II with 7-9 conspicuous pseudoarticulations.

Description. Males. Body. BL 1.45, CTW 0.86. Dorsal colour pattern (freshly killed specimen) as figured; abdomen largely dark purplish-brown penetrated by silvery spots and patches, bars of pigment across each segment tending to have a pair of mesial silvery spots. Venter paler. Anterior margin strongly indented above chelicerae. Eyemound black, relatively large, unarmed, set only about 0.4 its length behind anterior margin; eyes large; interocular groove shallow. Endites, labium and labrum not heavily sclerotised.

Spiracle. Length 0.062, width 0.015. Spines on anterior wall more numerous and rounded in cross-section than

B. drosera, usually with 1 or 2 terminations; spines on posterior wall numerous but very short. Integument anterior to spiracle folded but virtually without microornamentation; posterior to spiracle with rows of sharp micro-ornamentation; more posteriorly microornamentation tends to be bluntly conical and less globular than in B. drosera.

Chelicerae. Gracile; denticles on dorsal surface strong; teeth subequal; CSL 0.80.

Pedipalps. Very dark brown. Long and slender. Tarsus very strongly curved dorsad; non-socketed setae and claw lacking. Many of the setal plumes appear to be trifid. Lengths (femur-tarsus) 1.05, 0.82, 0.39, 0.69. Ratios patella to tibia 2.10, patella to tarsus 1.19.

Legs. Dark brown. Femur II with 7-9 pseudoarticulations. Tarsus II distally with numerous

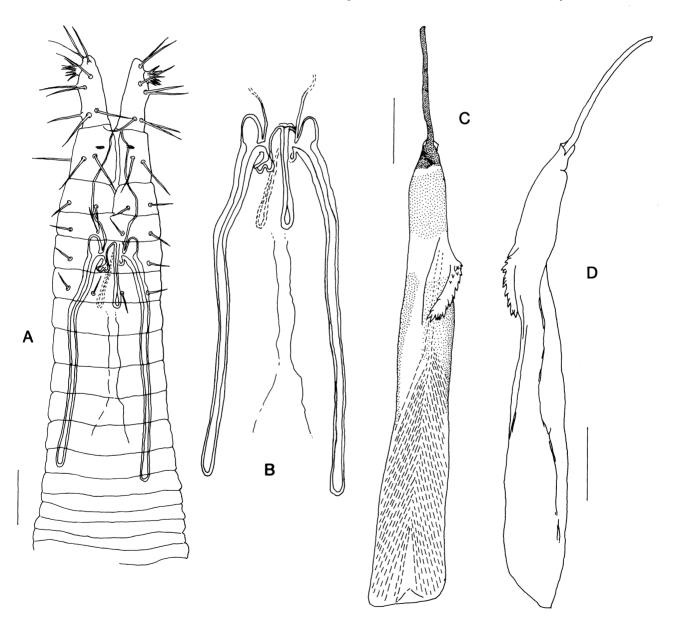


Fig.14. Ballarra clancyi n.sp. A. Ovipositor, ventral; B. Detail of seminal receptacles; C,D. Penis, ventral & lateral. Scale bars 0.1 mm.

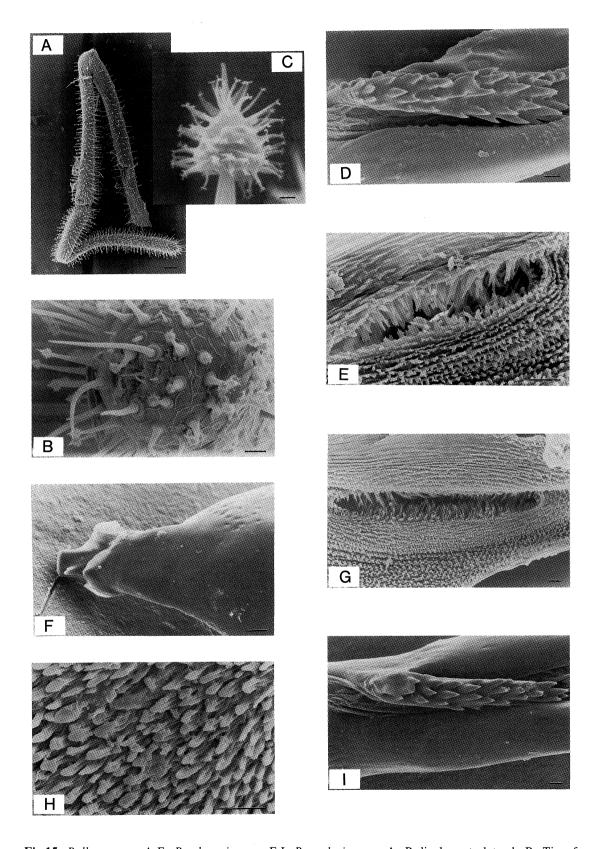


Fig.15. Ballarra spp. A-E. B. clancyi n.sp.; F-I. B. molaris n.sp. A. Pedipalp, retrolateral; B. Tip of tarsus, end view; C. Detail of plume brush on plumose seta; D,I Barbed process of penis, ventral; E,G. Spiracle. F. Base of stylus (stylus broken), ventral; H. Microsculpture of integument posterior to spiracle. Scale bars: $A = 100 \mu m$; $C = 1 \mu m$; others $10 \mu m$.

short articles; other tarsi distally with 3 short articles. Tarsal formula: 20,50,17,19. Measurements:

Leg	I	II	III	IV
Femur	2.13	4.82	2.04	
Tibia	1.64	4.66	1.58	_

Genitalia. PL 0.85; ratio shaft:glans:stylus 0.61:0.17:0.22. Barbed process wide distally, axis at about 25° to shaft axis; barbs very numerous (35).

Description. Females. Similar to male except in the following: dorsal pigmentation of Paratypes KS 19123 and KS 19126 with abdomen more broken by transverse silvery stripes though KS 19127 similar to male. Body larger, pedipalp and legs shorter. Tarsal formula: 17,44,17,18. Key measurements: BL 2.42, CTW 1.10, CSL 0.84, PFL 1.37, LFL 3.88, LTL 3.69.

Genitalia. Ovipositor as figured; lateral receptacles penetrate 9-10 segments; ventral and dorsal 3 segments.

Variation. Colour pattern varies between Wyong and Lane Cove individuals (Fig.13) but larger samples are needed to determine whether this is intra- or interpopulational variation.

Comments. This species, like *B. molaris*, has the most apomorphic pedipalp in the genus in terms of the combination of curvature of the tarsus, loss of claw and non-socketed setae and restriction of plumes to a brush at the setal tip.

Etymology. The specific epithet acknowledges the collecting work of Mr John Clancy which drew our attention to the existence of this species in the Sydney region.

Natural history. Numerous juveniles were present in berlesates taken in autumn-early winter 1983. Adults have been collected in winter-spring.

Distribution. Sydney region, New South Wales.

Ballarra molaris n.sp.

Figs 15F-I, 16, 17

Type material. HOLOTYPE: MOV K0904, Liparoo State Forest, west of Wemen, 7.9 km north-west of junction of Mid-Victorian Highway & Annuello Road, Vic, 34°46'S 142°33'E, LCC Mallee Survey, site 17, young-medium River Red Gum (*Eucalyptus camaldulensis*) near Murray River, a few large trees, grass understorey, drift fence pitfall trap, A.L. Yen, Sept. 1986; 1M. PARATYPES: MOV K0906, same data; 1F. AM KS 19140, same data; 1M,1F. MOV K0907-14, same data; 7M,1F. MOV K0905, Liparoo State Forest, 9.7 km north-west of junction of Mid-Victorian Highway & Annuello Road, Vic, 34°45'S 142°32'E, LCC Mallee Survey, site 20, on bank of Murray River, River Red Gum with sparse grass and herb

understorey, altitude 60 m, drift fence pitfall trap, A.L. Yen, Sept. 1986; 1M. PARATYPE: ANIC, Beelbangera, NSW, 34°15'S 146°06'E, F.J. Gay, 8 July 1969; 1M.

Diagnosis. Relatively large; male chelicerae large with greatly enlarged tooth on each finger; pedipalp coxa with incrassate denticulate process prolaterally, pedipalp tarsus without claw; leg tarsi finely subdivided into numerous short articles; spines on posterior wall of spiracle better developed than anterior; stylus and glans subequal in length, stylus with sharp tooth distal to basoventral flange.

Description. Males. Body. BL 2.62, CTW 1.95. Dorsal pattern (recently collected specimen) as figured; abdomen with mesial bars of pigment broken by silvery patches and flanked by semicontinuous silvery zone with heavily pigmented patches more laterally; eyemound surrounded by pale zone. Sternites predominantly silvery in some individuals, heavily pigmented in others. Some individuals very melanic. Cephalothorax high and much more rigid than abdomen; anterior margin not strongly indented. Eyemound low and placed about its length behind anterior margin; interocular groove absent except posteriorly. Coxobuccal region of Beelbangera specimen as figured: endites of pedipalp and coxa I, labium and labrum heavily sclerotised; pedipalp coxa prolaterally with incrassate, heavily denticulate process; these features less well developed in some Victorian specimens.

Spiracle. Very long, length 0.160, width 0.020. Spines on anterior wall not as strongly developed as those on posterior wall; spines long, multiply terminated, not markedly flattened. Spiracle flanked anteriorly and posteriorly by multiple closely spaced rows of sharp micro-ornamentation, replaced well posterior to spiracle by very densely packed linguoform-globular papillae.

Chelicerae. Massive, though allometrically smaller in smaller males. Second segment dark brown with black areas; each finger with 1 very large tooth and many small teeth. CSL 2.08.

Pedipalps. Tarsus markedly curved dorsad; claw and non-socketed setae apparently lacking. Lengths (femurtarsus) 1.70, 1.44, 0.58, 0.94; ratios patella to tibia 2.48, patella to tarsus 1.53.

Legs. Femora stout except for leg II. Femora dark brown; patellae and tibiae lighter but often dark laterally; metatarsi light; tarsi dark brown-black. Femora lack pseudoarticulations. Tarsi very finely divided with numerous short articles. Tarsal formula: 19,47,17,19. Measurements:

Leg	I	II	\mathbf{III}	IV			
Femur	1.51	3.30	1.58	2.29			
Tibia	1.27	3.41	1.25	1.74			

Genitalia. PL 1.02; ratio shaft:glans:stylus 0.64:0.17:0.18.

Basilateral flanges asymmetrical, right flange pointed; basiventral flange well developed with small sharp peg distal to it. Barbed process with numerous barbs (29); proximal barbs covered by flap of integument (possibly an artifact).

Description. Females. Similar to male except in the following: body longer; chelicerae small with teeth more even in size. Tarsal formula: 15,42,17,17. Key measurements: BL 3.27, CTW 1.51, CSL 1.09, PFL 1.54, LFL 4.12, LTL 4.09.

Genitalia. Ovipositor as figured; lateral spermathecae penetrate 8-9 segments; ventral and dorsal penetrate 3.

Comments. This species is placed in *Ballarra* on the basis of synapomorphies of the pedipalp, setal plumes and the long stylus and lateral seminal receptacles. A new

genus may need to be erected should this highly distinctive species be representative of a radiation of species, for example, along the river systems of inland Australia.

Etymology. The specific epithet refers to the denticulate process on each pedipalp coxa which may be used like millstones or nutcrackers to break hard-bodied prey.

Natural history. This species, which occurs in semiarid Australia (between 250 and 500 mm rainfall), has been collected between July and August. It is not known whether adults aestivate or whether another life history strategy is employed.

Distribution. River Red Gum forest, Murray and

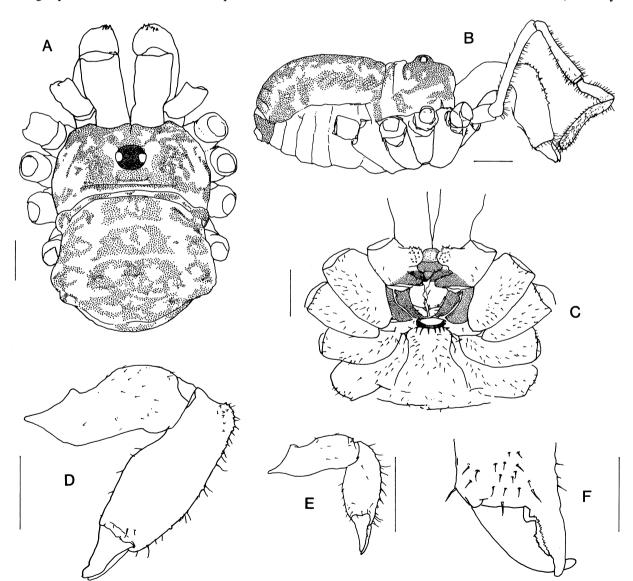


Fig.16. Ballarra molaris n.sp. A,B. Body, dorsal and lateral; C. Coxal and buccal region, ventral; D,F. Male chelicera, lateral & dorsal view of chelae; E. Female chelicera, lateral. B, ex Beelbangera; others ex Liparoo State Forest. Scale bars: A-C = 0.5 mm; D-F = 0.1 mm.

Murrumbidgee Rivers, semiarid zone, Victoria and New South Wales.

Ballarra longipalpus n.sp.

Figs 18, 19A-D

Type material. HOLOTYPE: WAM 87/1270, 6 km at 15° from Mullaloo Beach, WA, 31°47'S 115°44'E, A. Chapman & R. How, 3-17 Sept. 1978; 1M. PARATYPES: WAM 88/748-9 Reabold Hill, Perth, WA, 31°57'S 115°46'E, pitfall traps (RH6), J.D. Majer, 28 Aug. 1976; 2M. WAM 88/750, same data; 1F. WAM 88/751, same data; 1F.

Additional material examined. WAM 88/738-47,

Reabold Hill, WA, pitfall traps (RH5), J.D. Majer, 30 June 1976; WAM, 90/1352-3, Perth, Kings Park, WA, ex tree traps, S.J. Curry, 31 July 1978; WAM 88/737, Dwellingup, WA, 32°43'S 116°04'E, Plavins Plots, pitfall traps, S.J. Curry, 28 June 1979; J. WAM 88/132, same locality, S.J. Curry, 29 July 1977; J. WAM 55/5001-2, Gosnells, WA, 32°05'S 116°00'E; 1M,1F (damaged). WAM 87/1271, 1301, Porongorups, WA, 34°42'S 117°53'E, Eucalyptus diversicolor Karri-Acacia understorey, J.A. Springett, 13 Apr. 1971; WAM, 90/1222, 5 km north-east of Mount Lesueur, 30°10'S 115°15'E, pit-trap, J. Gaull & Party, 13 July 1990, F.

Diagnosis. Pedipalp extremely long and thin; pedipalp tarsus curved distad, non-socketed setae very few and at extreme tip of tarsus, claw lacking; seminal receptacles penetrate 4 ovipositor segments.

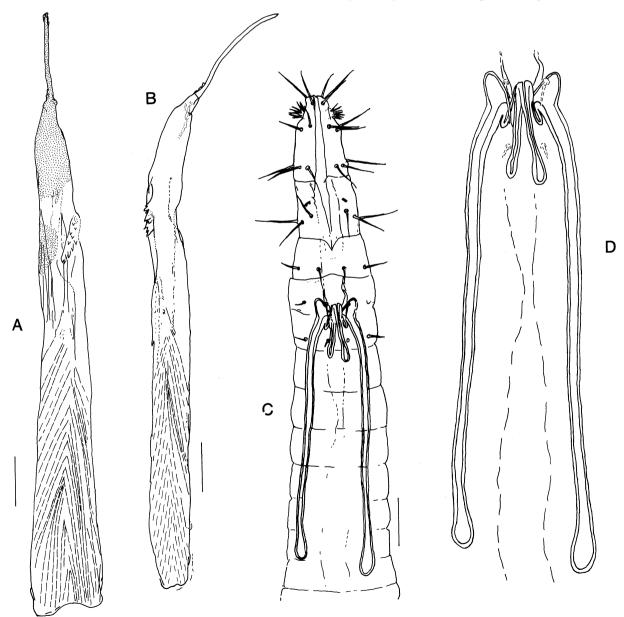


Fig.17. Ballarra molaris n.sp. A,B. Penis ex Beelbangera, ventral & lateral; C. Ovipositor ex Liparoo State Forest; D. Detail of seminal receptacles. Scale bars 0.1 mm.

Description. Males. Body. BL 1.26, CW 0.82. Dorsal pattern on abdomen similar to B. drosera with dark brown segmental bars broken by a mesial silvery patch. Eyemound large, unarmed, interocular groove moderately deep; eyes large, situated high on eyemound and directed up at angle of about 30°. Venter mostly pale.

Spiracle. Length 0.070, width 0.010. Spines on anterior wall much more numerous and rounder in cross-section than in *B. drosera*; greater tendency for spines to develop on posterior wall. Integument anterior to spiracle with a very narrow zone of sharp microornamentation, posterior to spiracle with numerous closely spaced rows of sharp micro-ornamentation replaced more posteriorly by linguoform microornamentation.

Chelicerae. Second segment dorsally with setae but without small denticles; teeth subequal. CSL 0.68.

Pedipalps. Very attenuated. Tarsus long, curved dorsad; plumose setae extend to extreme tip, sensory setae and non-socketed setae very few and at extreme tip; claw lacking. Lengths (femur-tarsus) 1.33, 1.02, 0.35, 0.75; ratio patella to tibia 2.91, patella to tarsus 1.36.

Legs. Dark brown. Femora lack pseudoarticulations. Tarsi distally with several short articles. Tarsal formula:

30.28.54.-. Measurements:

Leg	I	Π	III	IV
Femur	1.48	3.19	1.60	2.64
Tibia	1.30	3.05	1.27	1.91

Genitalia. PL 0.086; ratio shaft:glans:stylus 0.59:0.26: 0.15; glans long and thin, distally reflexed dorsad. Barbed process oriented at about 25° to shaft axis; barbs moderately numerous (21); basilateral flanges broad, basiventral flanges strong.

Description. Females. Similar to male except in the following: appendages relatively longer. Tarsal formula: 26,27,-,28. Key measurements: BL distorted, CTW 0.78, CSL 0.80, PFL 1.75, leg II missing.

Genitalia. Lateral seminal receptacles penetrate 4 ovipositor segments, dorsal and ventral 2 segments.

Variation. Body of Reabold Hill specimens more extensively pigmented.

Comments. This species does not fit easily into *Ballarra* because of the more plesiomorphic condition of: stylus and seminal receptacle length, plume brush on

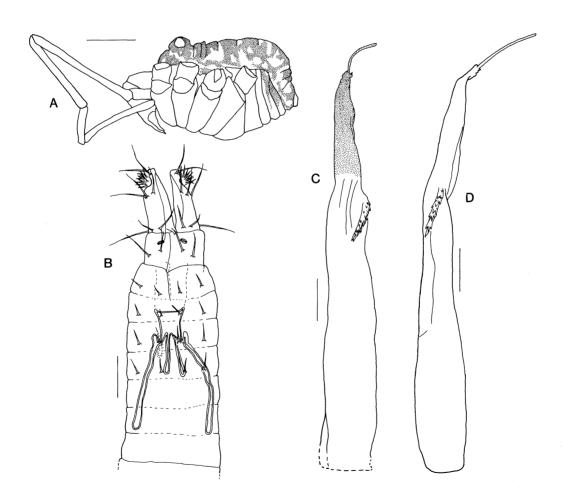


Fig.18. Ballarra longipalpus n.sp. A. Body of male, lateral; B. Ovipositor, ventral (distal part); C,D. Penis, ventral & lateral. B-D ex Reybold Hill. Scale bars: A = 0.5 mm; others 0.1 mm.

each seta, and lack of pseudosegmentation in femur II. It differs from *Plesioballarra*, however, in the form of the pedipalp, and from *Arrallaba* in the form of the

penis. We have avoided creating a monotypic genus for this species; it is placed in *Ballarra* rather than *Plesioballarra* because of the seemingly plesiomorphous

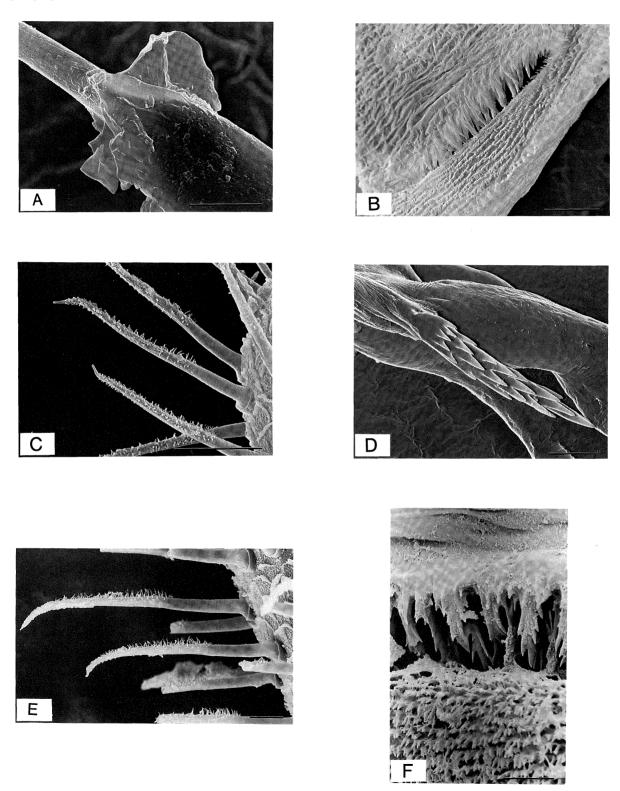


Fig.19. Ballarrinae. A-D. Ballarra longipalpus n.sp., ex Reabold Hill; E,F. Arrallaba spheniscus n.sp. A. Base of stylus, ventral (right side damaged); B. Spiracle; C,E. Plumose setae on pedipalp; D. Barbed process of penis, ventral; F. Detail of spiracle spines. Scale bars: A,D,E = $10 \mu m$; B,C,F = $20 \mu m$.

nature of most similarities with the latter genus and because of the weight we attach to similarities in pedipalp structure. The juveniles collected in the Porongorups National Park are tentatively assigned to *B. longipalpus*.

Etymology. The specific epithet refers to the extremely long pedipalps.

Natural history. Collections from April-July contain immatures, those in August and September adults.

Distribution. Perth region, and possibly the Porongorups Range near Albany, Western Australia.

Plesioballarra n.gen.

Type species. Plesioballarra crinis n.sp., by original designation.

Diagnosis. Dorsum lacking prominent heavily pigmented mesial stripe, pedipalp tibia about 0.66 patella length, tarsus not concave dorsad, longer than patella, plumose setae not extending to distal tip but replaced subdistally by prominent zone of sensory and nonsocketed setae, plumes extend down most of setal length; stylus about 0.5 glans, barbed process much shorter than glans.

Description. Body small, integument soft; eyemound large, interocular groove prominent; plumose setae on pedipalp with plumes along most of setal length; pedipalp patella longer than tibia but shorter than tarsus, tibia about 0.5 patella length; tarsus not curved dorsad, plumose setae not extending to tip of tarsus, non-socketed setae forming a complete subdistal ring, claw easily seen at X12 magnification; all femora lack pseudoarticulations, latter present in tibia II and metatarsi; stylus of penis shorter than glans, basilateral flanges very broad, basiventral flanges well developed; barbed process much shorter than glans; lateral seminal receptacles penetrate 6 ovipositor segments, dorsal and ventral 2 segments, 1:1-1:1 slit sensilla on second furcal segment.

Etymology. This genus has several seeming plesiomorphies associated with the pedipalp (cladistic analysis resolves them as reversals). Gender is feminine.

Distribution. Border ranges of eastern New South Wales to Queensland.

Plesioballarra crinis n.sp.

Figs 20-21

Type material. HOLOTYPE: QM 15521, Bald

Mountain area, via Emu Vale, Qld, 28°14'S 152°25'E, T. Weir, Feb. 1970; 1M. PARATYPES: QM 15522, 1150-1300m, B.K. Cantrell, 27-31 Jan. 1972; 1F. QM, same data; 1M,8F. UQ, T. Weir, Feb. 1970; 1M. UQ, 1000-1500m, B.K. Cantrell, 17-22 May 1969; 1F. AM KS 20144, same data; 1M. AM KS20143, T. Weir, Feb. 1970; 2M,1J. UQ, 1000-1300 m, B.K. Cantrell, 22-27 Jan. 1971; 1M. UQ, B.K. Cantrell, 26-30 Jan. 1973; 1M,2F. Lamington National Park, 28°15'S 153°10'E: QM, B.K. Cantrell, 4 Jan. 1968; 1M,2F. UQ, same data; 1M. ANIC, Wiangaree State Forest, NSW, 28°22'S 153°05'E, 1050 m, T. Weir & A. Calder, 10-12 Feb. 1983; 1F.

Other immature material examined. Mount Bithongabel, Lamington National Park, Qld, 28°15'S 153°09'E: QM, stick brushing berlesate no. 203, rainforest, G.B. Monteith, 8 Oct. 1979; 1J. QM, sweeping, V.E. Davies & R. Raven, 16 Nov. 1977; 1J.

Diagnosis. Interocular groove deep. Pedipalp tarsal claw prominent; plumose setae not extending to tip of tarsus but replaced by subdistal band of non-socketed setae and terminal tuft of sensory setae; plumes extend along most of setal length. Leg tarsi distally with numerous short articles. Penis stylus much shorter than glans; basal flanges pointed distad; barbed process at 45° to shaft axis.

Description. Males. *Body.* BL 2.23, CTW 1.21. Dorsal colour pattern (old specimen in alcohol) as figured, dark brown with yellow-brown and silvery patches; large silver-gold saddle-like patch posterior to metapeltidium; anterior to eyemound pale. Eyemound large, deeply canaliculate, with a few dorsal spicules, pale except for eye pigment. Eyes large, directed up at about 30° to horizontal. Venter pale but abdomen pigmented at margins.

Spiracle. Length 0.13, width 0.04. Spines on anterior wall extremely dense, attenuated, with multiple terminations; those on posterior wall dense but less developed. Spiracle ringed by broad zone of closely spaced rows of sharp micro-ornamentation, more posteriorly with rows of widely spaced linguoform-globular papillae.

Chelicerae. Basal segment dorsally with large pale patch. CSL 0.73.

Pedipalps. Stout. Large pale band about half way along femur, patella and tarsus. Dorsal angle between patella and tibia only slightly less than 180°. Tarsus not curved dorsad. Plumes extend along most of setal length. Plumose setae on tarsus replaced subterminally by zone of non-socketed setae and terminally by tuft of socketed and non-socketed setae. Claw prominent compared with other Neopilionidae. Lengths (femur-tarsus) 1.30, 0.78, 0.52, 0.93; ratios patella to tibia 1.50, patella to tarsus 0.84

Legs. Pale band about half way along femora and tibiae; articulations and pseudoarticulations pale. Femur II without, tibia II with pseudoarticulations; tarsal articulations often swollen; tarsi strongly prehensile with numerous short articles. Tarsal formula: 29,52,32,33.

Measurements:

 Leg
 I
 II
 III
 IV

 Femur
 2.53
 5.25
 2.41
 3.77

 Tibia
 1.99
 4.84
 1.88
 2.69

Genitalia. PL 1.24; stylus relatively short, glans elongate, ratio shaft:glans:stylus 0.64:0.23:0.13. Barbed process oriented at about 45° to penis axis; barbs numerous (26 and 28, n = 2). Basilateral flanges of stylus strongly

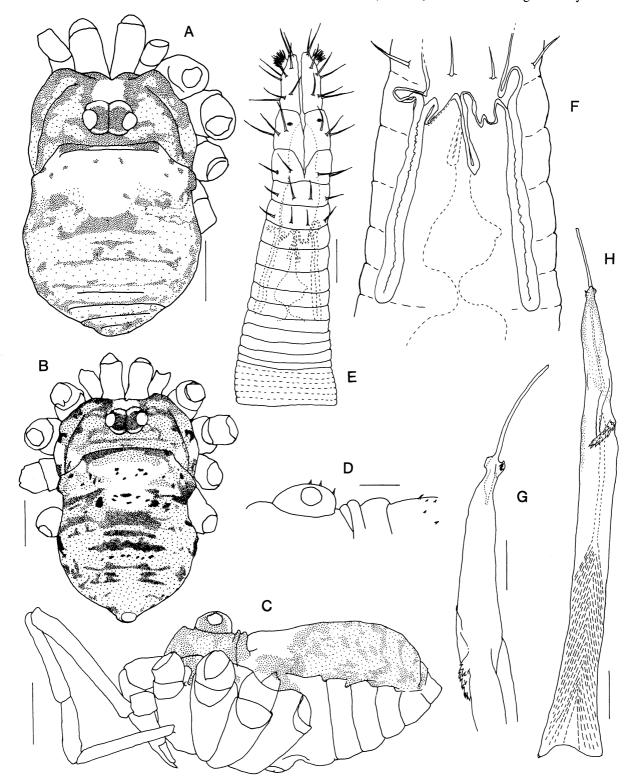


Fig.20. Plesioballarra crinis n.sp. A,C. Body of male ex Bald Mountain, dorsal & lateral; B. Body of male ex Lamington Plateau, dorsal; D. Detail of eyemound, lateral; E. Ovipositor, dorsal; F. Detail of seminal receptacles; G,H. Penis, lateral & ventral. Scale bars: A-D = 0.5 mm; E-H = 0.1 mm.

pointed; basiventral flanges strongly developed.

Description. Females. Similar to males except in the following: body slightly larger, pedipalp and legs

shorter. Key measurements: BL 2.43, CTW 1.40, CSL 0.83, PFL 1.08, LFL 3.33, LTL 3.42 Tarsal formula: 30,55,31,31.

Genitalia. Lateral spermathecae penetrate 6 ovipositor

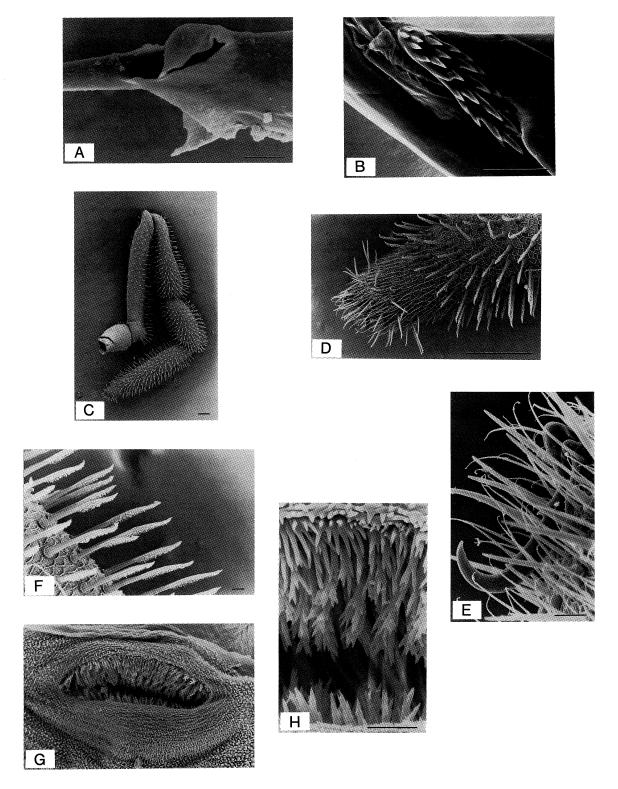


Fig.21. Plesioballarra crinis n.sp. A. Base of stylus, ventrolateral; B. Barbed process of penis, ventral; C. Pediplap, retrolateral; D. Detail of pedipalp tarsal tip; E. Detail of pedipalp tarsal claw; F. Plumose setae on pedipalp; G. Spiracle; H. Detail of spiracle spines. Scale bars: A,E-H = $10 \mu m$; C,D = $100 \mu m$.

segments, dorsal and ventral 2 segments.

Comments. The structure of the pedipalp distinguishes this species from all other Ballarrinae. *Plesioballarra crinis* resembles the Western Australian *B. longipalpus* n.sp., in the prominent interocular groove, the absence of pseudosegmentation in the femur of leg II, the relatively short stylus with prominent basal flanges, the relatively short seminal receptacles and the form of the plumose setae.

Etymology. The specific epithet is a Latin noun meaning 'tuft of hair' and refers to the remnant tuft-like cluster of sensory setae at the tip of the pedipalp tarsus.

Natural history. Juveniles have been collected in spring-summer, adults January to May.

Distribution. Border Ranges of south-eastern Queensland and north-eastern New South Wales.

Arrallaba n.gen.

Type species. Arrallaba spheniscus n.sp., by original designation.

Diagnosis. Abdomen with prominent virtually continuous heavily pigmented mediodorsal stripe; pedipalp tibia less than 0.5 patella length, tarsus concave dorsad and shorter than patella, plumes extend along most of setal length; stylus of penis extremely short and twisted, barbed process longer than glans, flattened.

Description. Body large for Ballarrinae, elongate; integument soft; abdomen dorsally with prominent virtually continuous median stripe; plumose setae on pedipalp with plumes along most of setal length; pedipalp patella longer than tibia and tarsus, tibia less than 0.5 patella; tarsus curved distad, plumose setae extend to tip of tarsus, sensory and non-socketed setae confined to extreme tip, latter not forming a subdistal ring, claw absent; leg femora without pseudoarticulations, latter in tibia II and metatarsi; stylus of penis extremely short, coiled; barbed process greatly enlarged, longer than glans, flattened; lateral spermathecae penetrating 3 ovipositor segments, dorsal and ventral penetrating 2 (perhaps 3) segments; sexual dimorphism slight.

Etymology. A latinised backward spelling of the new genus *Ballarra* emphasising the opposite state of many characters. Gender is feminine.

Distribution. "Australian Alps" region of south-east mainland Australia.

Arrallaba spheniscus n.sp.

Figs 19E-F, 22

Type material. HOLOTYPE: ANIC, 1km north of

Mount Gingera, Brindabella Range, ACT, 35°35'S 148°46'E, stop 18, in gutter trap, D.C.F. Rentz & J. Balderson, 21 Feb. - 10 May 1979; 1F. PARATYPES: ANIC, same data; 1F. AM KS 19121, same data; 1F. ANIC, South Ramshead, Kosciusko National Park, NSW, 36°28'S 148°20'E, altitude 1750 m, pit trap, K. Green, summer-autumn 1982-1983; 1F. ANIC, same data, 1M.

Diagnosis. See generic diagnosis.

Description. Females. Body. Elongate, BL 4.07, CTW 1.66. Dorsal pattern as figured, pigmented areas maroon-brown; prominent median stripe, wider at metapeltidium and broken only posteriorly by thin intersegmental lighter patches; median stripe accentuated by flanking pale stripe; dorsum heavily pigmented laterally. Sternites heavily pigmented except at sutures. Anterior margin strongly indented above chelicerae. Eyemound black, situated about 0.7 its length behind anterior margin, moderately large and armed with a few small spicules; interocular groove shallow.

Spiracle. Elongate, length 0.130, width 0.020. Spines on anterior wall complex, somewhat flattened in section, with multiple terminations; enlarged spines on posterior wall absent. Integument anterior to spiracle smooth; posterior to spiracle with closely spaced rows of sharp micro-ornamentation.

Chelicerae. Elongate and slender. Each finger with moderately enlarged proximal tooth and row of small subequal teeth. CSL 1.36.

Pedipalps. Relatively shorter than in *Ballarra*. Tarsus short, curved dorsad but not strongly; non-socketed setae in small terminal group; claw lacking. Lengths (femur-tarsus) 1.46, 1.24, 0,50, 0.89; ratios patella to tibia 2.48, patella to tarsus 1.39.

Legs. Relatively short and stout. Distal half of tarsi finely divided into many short articles, strongly prehensile. Tarsal formula: 25,46,24,29. Measurements:

Leg	I	II	III	IV
Femur	1.78	2.76	1.99	2.49
Tibia	1.54	2.64	1.56	2.19

Genitalia. Terminal portion of ovipositor as figured; lateral spermathecae penetrate 3 segments, dorsal and ventral penetrate 2 (perhaps 3) segments.

Description. Male (badly damaged). Similar to female except in the following: second segment of chelicera slightly more robust; pedipalp tarsus relatively shorter; legs relatively longer. Tarsal formula: 25,43,28, 31. Measurements: body distorted, CSL 1.34, pedipalp lengths (femur-tarsus) 1.20, 1.02, 0.40, 0.85, ratios patella to tibia 2.55, patella to tarsus 1.20.

Leg	I	II	\mathbf{III}	IV
Femur	2.12	3.76	2.02	3.11
Tibia	1.79	3.43	1.83	2.86

Genitalia. PL 0.847; shaft relatively long and very broad, glans relatively short and very narrow, stylus extremely short and tightly curved, ratio shaft:glans: stylus 0.78:0.20:0.03; barbed process greatly enlarged,

164

longer than glans, flattened in section, curved distally across midventral line of shaft; barbs mostly on margin of process closest to mid-line of shaft.

Comments. The structure of the penis distinguishes this species from all other Ballarrinae. The species resembles *B. clancyi* and *B. molaris* in loss of nonsocketed setae and tarsal claw from the pedipalp, and also the relatively short legs and finely divided tarsus of the latter.

Etymology. The specific epithet refers to the shape and positioning of the barbed process which calls

to mind a penguin's wing; Spheniscus being the type genus of the penguin family.

Natural history. Despite a seasonal pitfall trapping project in the Mount Kosciusko region which extended over two years and a gutter trapping project in the Brindabella Ranges, the few individuals were trapped only in summer-autumn (Dr Ken Green, personal communication).

Distribution. "Australian Alps" of south-eastern mainland Australia, from Brindabella Range to Mount Kosciusko area.

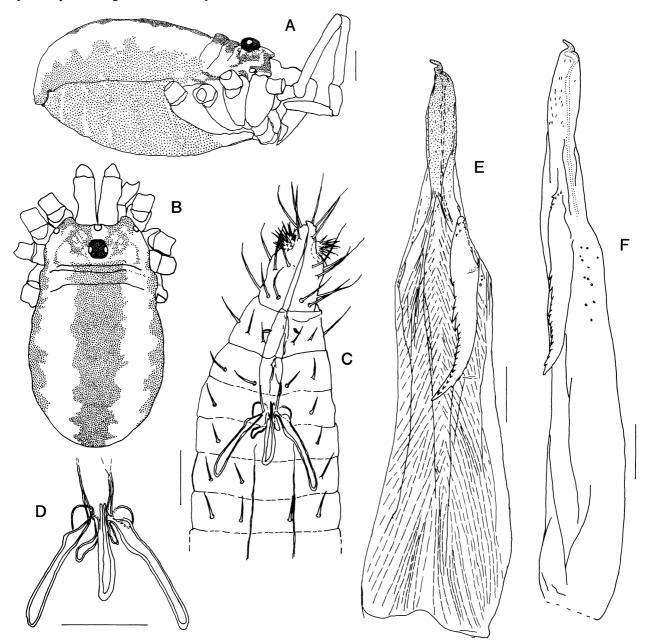


Fig.22. Arrallaba spheniscus n.sp. A,B. Body of female, lateral & dorsal. C. Ovipositor, dorsal (distal part); D. Detail of seminal receptacles; E,F. Penis, ventral & lateral. Scale bars: A,B = 0.5 mm; others 0.1 mm.

Vibone Kauri, 1961

Vibone Kauri, 1961: 143.–Silhavy, 1970: 171, 174.– Lawrence, 1981: 17.–Shear, 1982: 110.–Martens, 1978: 229.

Type species. Vibone vetusta Kauri, 1961, by original designation.

Diagnosis. As far as can be determined from Kauri's drawings and excellent description of the female holotype of *V. vetusta*, *Vibone* is similar to *Ballarra* females except in having an ovipositor corpus with only 2 segments, 2 seminal receptacles, a tibia greater than 0.5 length of patella and more pronounced pseudo-articulatory nodules on all leg femora.

The seminal receptacles are in the superior part of the internal vagina, each consisting of an elongated loop.

As in some other Ballarrinae, the palpal claw is lacking.

Description. See Kauri (1961). The only specimen, the female holotype, has apparently been lost.

Natural history. The only known specimen, a mature female, was collected on 18 December at 730 m elevation from moist ground litter in a humid valley with abundant undisturbed native vegetation (trees and bushes).

Distribution. Known only from the type locality, Table Mountain, Republic of South Africa (Fig.1).

Americovibone n.gen.

Type species. Americovibone lanfrancoae n.sp., by original designation.

Diagnosis. Chelicera with ventral spur on the basal segment; pseudosegments present in the palpal segments of the female and at least leg femora and tibiae II-IV of both sexes; pedipalp patella longer than tibia or tarsus, palpal claw absent; leg claws with lateral teeth on each side; penis lacking barbed process, ovipositor with 2 spermathecae.

Description. Minute harvestmen with relatively long legs. Eye mound and body unarmed, smooth. Chelicerae with spur on basal segment. Female pedipalp with pseudosegments in femur and patella; pedipalp patella longer than tibia and tarsus, tarsus concave dorsad along its length in female and curved in opposite sense in male, tarsal claw and non-socketed setae absent, plumose setae extend to the tarsal tip, plumes not clearly bifurcate. Leg femora and tibiae with pseudosegments, claws with lateral branches on each side. Penis without bristle groups or processes.

Ovipositor corpus of more than 2 segments, 2 spermathecae.

Etymology. The generic name is a contraction of "American *Vibone*" and is feminine in gender.

Distribution. Known only from southern Chile (Fig.1).

Americovibone lanfrancoae n.sp.

Figs 23-24

Type material. Chile, Peninsula de Brunswick, Magallanes: HOLOTYPE: MNHN, Reserva Nacional Magallanes, 8 km west of Punta Arenas, J. Peterson C., 24 Feb.-23 Mar. 1978, Trampa Barber no. 13-2nd Trampeo; 1M. PARATYPE: AM KS20142, same data, Trampa Barber no. 11-1st Trampeo; 1F.

Description. Male. Body. BL 0.86, CTW 0.64. Dorsum light brown on lateral edges of cephalothorax and abdomen, with remainder of cephalothorax brown and eye mound dark brown; abdomen with three indistinct transverse bands of dark brown, middle band broken in centre (pattern unclear as abdomen is shrivelled); venter light tan to yellowish. Integument thin, smooth except for legs which are subimbricate to rugose in appearance. Few minute setae on coxae and sternites. Eyemound smooth, unarmed, wider than long, removed from edge of cephalothorax by less than mound length, not canaliculate. Anterior edge of cephalothorax impressed in front of eyemound. Spiracles undetected (due to small size and dark pigmentation).

Chelicerae. Brown with black denticles on jaws, basal portion of first segment whitish. Relatively short and slender; basal segment with retrolateral row of 4 or 5 slit sensilla; unarmed except for few minute setae and mesal series of bi- and tri-pointed scales; ventral spur on basal segment; CSL 0.44.

Pedipalps. Brown, bases of femur and trochanter whitish. Femur with distodorsal slit sensillum. Femur, tibiae, patellae, and tarsus with plumose setae of subequal size, tarsus with greatest density; plumes restricted to the setal tip; integument smooth, lacking pseudosegments. Lengths (femur-tarsus) 1.35, 0.95, 0.47, 0.68; ratios patella to tibia 2.02, patella to tarsus 1.40. Palp not examined with SEM.

Legs. Brown, white ring on last article of metatarsus, base of femur whitish. Long and slender; femora I-IV with numerous pseudosegments (-,13,6,7-9), distal two especially noticeable and enlarged as nodules; tibiae through tarsi also with pseudosegments. Tarsal formula: -,-,30,30-34. Measurements:

 Leg
 I
 II
 III
 IV

 Femur
 2.88
 1.77
 2.51

 Tibia
 1.54
 2.40

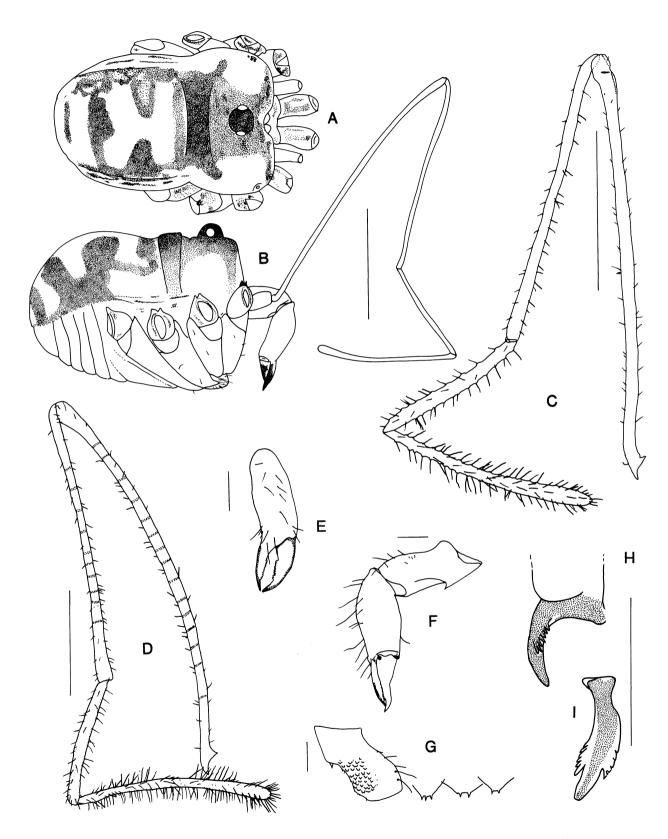


Fig.23. Americovibone lanfrancoae n.sp. A,B Body of male, dorsal & lateral (slightly reconstructed from distorted specimen); C,D. Pedipalp, male & female; E. Male chelicera, second segment, dorsal; F. Male chelicera, retrolateral; G. Basal segment, prolateral with detail of bi- and tri-pointed scales; H,I. Tarsal claw of leg I, lateral & dorsal. Scale bars: A-D = 0.5 mm; others 0.1 mm.

Genitalia. Glans shorter and more slender than in Ballarra, stylus with a contorted loop arising on the dorsolateral end; shaft compressed dorsoventrally on lateral sides.

Description. Female. Similar to the male except in the following; pedipalp tarsus concave dorsad, more setose; plumes extend down most of setal length; pedipalp femur and patella with pseudosegments, 16:17, 10:11 respectively.

SEM of the female palp. Plumose setae extend to distal tip of tarsus; plumes extend along most of setal length, not obviously bifurcate; sensory setae very few, restricted to tarsal tip; non-socketed setae and claw lacking.

Measurements. Body distorted, CSL 0.46, pedipalp lengths femur-tarsus 1.97, 1.37, 0.63, 0.98, ratio patella to tibia 2.17, patella to tarsus 1.40. Legs missing.

Ovipositor. With 3-segmented furca, plus 8 rings; slit sensilla of furca are replaced by small ridges on

each side; paired seminal receptacles within third and fourth rings from furca; setae present on furca and distal 7 rings; seminal receptacles each consisting of 1 short single loop with 2 lateral extensions.

Comments. The spicules (pointed scales) on the chelicerae are present on both sexes. It is possible they are used in sound production. The spicules resemble those found on some members of the Schizomida, which are also found on both sexes and have been questionably proposed as stridulatory structures (Cokendolpher, 1988).

The curious difference between the male and female in the form of the pedipalp tarsus and setal plumes suggests the possibility of two sympatric species. A larger series is required to determine this.

Natural history. Both known specimens were collected in Barber traps set in evergreen coige forest (*Nothofagus betuloides*) at 250 m with a 50° slope and a floor of 5-7 cm of dead leaves. A detailed account of this forest is provided by Dollenz A. (1982).

Distribution. Known only from the Peninsula de Brunswick, Patagonia, Chile (Fig.1).

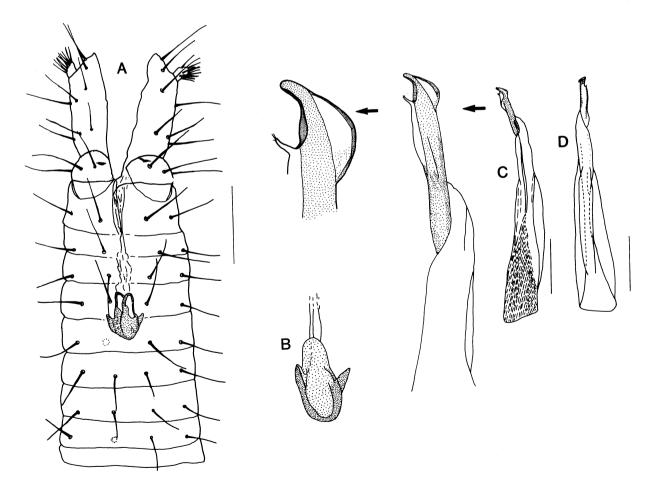


Fig.24. Americovibone lanfrancoae n.sp. A. Ovipositor, dorsal; B. Detail of seminal receptacle; C. Penis, lateral, with detail of glans and stylus; D. Penis, ventral. Scale bars 0.1 mm.

ACKNOWLEDGMENTS. The first author was supported by an Australian Biological Resources Study grant and the second author in part by the Department of Biological Sciences and The Museum, Texas Tech University, Lubbock.

We are grateful to Dra. Dolly Lanfranco-Leverton, Instituto de la Patagonia, Punta Arenas, Chile, for providing specimens of Americovibone lanfrancoae together with habitat data, and Thrasychirus spp. We thank Dr H. Robertson of the South African Museum, Capetown, who loaned type material of Neopilio and Dr Manfred Grasshoff, Forschungsinstitut Senckenberg, Frankfurt, West Germany, for specimens of Neopilio and Thrasychirus. Dr R.R. Forster (Otago Museum, Dunedin, New Zealand) and Dr R.G. Ordish and Dr John Yaldwyn (National Museum of New Zealand, Wellington) sent specimens of Acihasta and Monoscutum for the second author to study. Dr Robert Raven and Dr Valerie Davies (Queensland Museum, Brisbane), Ms Margaret Schneider, (University of Queensland, Entomology Department Collection, St Lucia), Dr Bruce Halliday (CSIRO Australian National Insect Collection, Canberra), Dr Chris Margules (CSIRO Division of Wildlife & Ecology, Canberra), Dr Ken Green (Australian and New Zealand Antarctic Research Expeditions, Hobart), Dr Alan Yen (Museum of Victoria, Melbourne), Dr Mark Harvey (Western Australian Museum, Perth) and Dr Murray Fletcher (NSW Department of Agriculture, Sydney) provided much of the Australian Ballarrinae material. Dr Lennart Cederholm, Zoology Museum, University of Lund, Norway, instituted an extensive search for the type of Vibone vetusta.

We thank Dr Michael Gray (Australian Museum) and Dr William A. Shear (Hampden-Sydney College, Virginia) for commenting on the manuscript. Thanks are also extended to Ms Sue Doyle (Macquarie University, Sydney) and Ms Judy Thompson and Mr Geoff Avern (Australian Museum) for help with SEM, and Mr Martyn Robinson and Mr Roger Springthorpe, Sydney, for help with illustrations.

References

- Cokendolpher, J.C., 1988. Review of the Schizomidae (Arachnida, Schizomida) of Japan and Taiwan. Bulletin of the National Science Museum, Tokyo, Series A, 14(4): 159–171.
- Dollenz A., O., 1982. Fitosociologia de la Reserva Nacional Magallanes. I. Estudio delarea Cerro Mirador-Rio de las Minas. Annales del Instituto de la Patagonia, Punta Arenas 13: 171–181.
- Farris, J.S., 1988. Hennig86. Version 1.5. New York.
- Forster, R.R., 1964. The Araneae and Opiliones of the Sub-Antarctic Islands of New Zealand. Pacific Insects Monograph 7: 58–115.
- Green, K., 1988. A Study of Antechinus swainsoni and Antechinus stewarti and their Prey in the Snowy Mountains. PhD Thesis, Zoology Department,

- Australian National University, Canberra.
- Hunt, G.S., 1979. Male Dimorphism and Geographic Variation in the Genus *Equitius* Simon (Arachnida, Opiliones). PhD thesis, School of Zoology, University of New South Wales.
- Hunt, G.S., (in press). Taxonomic value of spiracle microstructure in the Megalopsalididae (Opiliones, Phalangioidea). Acta Zoologica Fennica.
- Kauri, H., 1961. Opiliones. South African Animal Life. Results of the Lund University Expedition in 1950-1951. 8: 9–197.
- Lawrence, R.F., 1931. The harvest-spiders (Opiliones) of South Africa. Annals of the South African Museum 29: 341–508.
- Martens, J., 1978. Spinnentiere, Arachnida. Weberknechte, Opiliones. Die Tierwelt Deutschlands, Gustav Fischer, Jena, Teil 64, 464 pp.
- Martens, J., 1986. Die grossgliederung der Opiliones und die evolution der ordnung (Arachnida). Actas X Congreso Internacional de Aracnologia, Jaca, Espana 1: 289–310.
- Mello-Leitao, C.F., 1933. Quatro novos Palpatores neotropicos. Annales da Academia Brasileira Sciencias 5(3): 99-103.
- Ringuelet, R.A., 1959. Los Aracnidos argentinos del Orden Opiliones. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ciencias Zoologicas 5(2): 127–439.
- Roewer, C.F., 1957. Uber Oligolophinae, Caddoinae,
 Sclerosomatinae, Leiobuninae, Neopilioninae und
 Leptobuninae (Phalangiidae, Opiliones Palpatores).
 (Weitere Weberknechte XX). Senckenbergiana Biologica 38(5/6): 323-358.
- Shear, W.A., 1975. The opilionid family Caddidae in North America, with notes on species from other regions (Opiliones, Palpatores, Caddoidea). Journal of Arachnology 2: 65-88.
- Shear, W.A., 1982. Opiliones. Pp.104–110. In S.P. Parker (ed.). Synopsis and Classification of Living Organisms, Vol.2. McGraw-Hill Book Company, New York, 1232 pp.
- Shear, W.A., 1986. A cladistic analysis of the opilionid superfamily Ischyropsaloidea, with descriptions of the new family Ceratolasmatidae, the new genus *Acuclavella* and four new species. American Museum Novitates 2844: 1–29.
- Shear, W.A. & J. Gruber, 1983. The opilionid subfamily Ortholasmatinae (Opiliones, Troguloidea, Nemastomatidae). American Museum Novitates 2757: 1-65.
- Starega, W., 1975. Opiliones Kosarze (Arachnoidea). Fauna Polski, Polska Akademia Nauk, Instytut Zoologii, Warszawa, Tom 5, 196 pp.
- Silhavy, V., 1970. Nouvelles Recherches sur la Famille des Neopilionidae Lawrence. Bulletin du Museum national d'Histoire naturelle, 2e Serie, 41(1): 171–175.
- Ubick, D. & T.S. Briggs, 1989. The harvestmen of the family Phalangodidae. 1. The new genus *Calicina*, with notes on *Sitalcina* (Opiliones: Laniatores). Proceedings of the California Academy of Sciences 46(4): 95–136.

Accepted 18 July, 1990

APPENDIX 1

Table 1. Full character matrix used in cladistic analysis of selected Phalangioidea (0 = plesiomorphic, 1 = apomorphic, ? = unknown or not relevant).

Characters	1	2	3	4	5					10					15	i				20
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phalangiidae	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	?	0
Gagrellidae	0	0	0	1	1	0	0	1	1	0	0	0	1	0	0	1	0	0	?	0
Megalopsalis	0	0	0	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0	?	0
Some Pantopsalis spp.	0	0	0	1	?	0	0	0	0	1	0	0	0	0	?	0	0	0	?	0
N.gen. (?Monoscutinae)	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	?	0
Spinicrus nigricans	1	0	0	1	1	0	0	0	0	1	0	0	1	0	1	0	0	0	?	0
Enantiobuninae	0	0	0	1	0	0	1	1	0	0	0	0	1	1	?	0	0	0	?	0
Neopilio	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	?	0
Americovibone	1	1	1	?	0	1	0	1	1	0	0	0	1	0	?	?	1	1	?	0
Plesioballarra	1	1	0	1	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0
Arrallaba	1	1	1	?	0	1	1	0	0	0	1	0	0	0	0	0	1	0	1	0
Ballarra	1	1	1	1	0	1	1	1	0	0	1	1	0	0	0	0	1	0	0	0
Vibone	1	1	1	?	?	?	1	1	?	?	?	?	1	0	?	?	1	0	?	1

The following protocol was followed:

Analysis 1. Full data set of 20 characters

Analysis 2. Character 8 deleted (Fig.4A)

Analysis 3. Characters 1, 8 and 17 deleted (Fig. 4B).