

Onychophora of New Zealand; past, present and future

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ABSTRACT

The phylum Onychophora has long been regarded as an important group in evolutionary biology due to its phylogenetic position, ancient history, and Gondwanan distribution. Only recently, however, has the extent of species diversity in Australia been realised. This paper reviews those recent findings and the implications they have for studies of the New Zealand onychophoran fauna.

Keywords: Onychophora, phylogenetics, New Zealand, conservation, species identification.

INTRODUCTION

Phylogenetic position

The Onychophora (velvet worms) are often considered to be missing links or living fossils and are most commonly referred to as 'peripatus' after the first genus described (Guilding 1826). Since their discovery, their phylogenetic position has been the subject of considerable debate. Initially they were thought to be an "aberrant mollusc" (Guilding 1826); however, Moseley (1874) reported many characters held in common with arthropods. The lack of a hard exoskeleton and jointed appendages are the most notable differences, and form the basis on which the Onychophora have long been considered transitional between arthropods and annelids. The recent application of molecular information has not yet helped to clarify this position: 12S rRNA sequence data (Ballard *et al.* 1992) suggest that the Onychophora are to be included in the arthropods as a sister group to the myriapods. In contrast Wheeler *et al.* (1993) produced a synthesis of both morphological and molecular characters (18S rRNA) which reaffirmed monophyly of the arthropods, and the Onychophora appear clearly as a sister group.

History

The antiquity of these organisms is well documented, relying on an informative fossil record. The earliest fossils which resemble present day onychophorans in terms of their lobopodial body organisation are the marine species *Xenusion anerswaldae* Pomeckj from the Early Cambrian Baltic (Krumbiegel *et al.* 1980), *Aysheaia pendunculata* Walcott from the Middle Cambrian Burgess Shale of British Columbia (Whittington 1978), and *A. prolata* Robison from the Middle Cambrian Wheeler Formation of Utah (Robison 1985). It is not clear whether fossils such as from the Late Carboniferous Mazon Creek beds of Illinois (Thompson & Jones 1980) and a similar unnamed form from the Late Carboniferous Montceau-Mines in central France (Heyler & Poplin 1988) were of marine or terrestrial origin because they have been found in the presence of both terrestrial and marine flora and fauna. However, the present-day distribution of Onychophora on land masses of Gondwanan origin suggests that terrestrialisation may have occurred only on Gondwana.

The phylum Onychophora is divided into two families: the Peripatidae (found in the Antilles, Mexico, Central America, northern South America, equatorial West Africa, and Southeast Asia) and the Peripatopsidae (found in Chile, South Africa, Australia, and New Zealand). The presence of both families in Africa suggests that divergence took place before the break up of Gondwana, again highlighting the antiquity of these organisms.

Biology

Today, the Onychophora are restricted to moist microhabitats such as within and under rotting logs, under stones, and within leaf litter, owing to their inability to control

water loss. They are nocturnal predators which trap their prey using a sticky substance expelled from a pair of modified limbs, the oral papillae, located on either side of the head. They then use saliva to partially break down their meal before ingestion (Newlands & Ruhberg 1978; Read & Hughes 1987). Observations of predatory behaviour in the wild are very limited.

Reproductive strategies in this group are incredibly diverse, including oviparity, ovoviviparity, viviparity with yolk-free eggs, and placental viviparity (Dendy 1902; Anderson & Manton 1972). Parthenogenesis has also been documented (Read 1988). Males most commonly produce spermatophores, which they transfer to the female (Storch & Ruhberg 1977). Recent discoveries of previously undescribed Australian onychophorans in which the males possess head structures that appear to be involved in sperm transfer (Tait & Briscoe 1989; 1990), have considerably advanced our current knowledge. Most aspects of onychophoran reproductive behaviour such as when and how often fertilisation occurs, are little known.

NEW ZEALAND ONYCHOPHORA

In New Zealand five species in two genera are currently recognised. The genera are separated on the basis of reproductive strategy, *Peripatooides* being viviparous and *Ooperipatellus* oviparous.

Additional distinctive features of *Peripatooides* are the lack of crural glands and their external openings (found at the base of legs in males), and the lateral position of the anal gland openings on the pygidium. These features distinguish *Peripatooides* from all genera currently described from Australia. The lack of crural glands is shared with two other genera, *Metaperipatus* Clark from Chile, and *Paraperipatus* Willey from New Guinea. *Peripatooides novaezealandiae* Hutton is the most common and abundant species of its genus, is found widespread throughout New Zealand. It is characterised by possessing 15 pairs of legs, 3 and 4 spinous pads on the underside of the legs, and 3 (rarely 4) distal papillae on the feet. *P. suteri* Dendy has been reported only from Stratford (Dendy, 1894), Mt Taranaki (Lake Rotokare) (Ruhberg 1985) and Whakapapa (Tait & Briscoe, 1995). This species possesses 16 pairs of legs, 4 (rarely 3) spinous pads and 4 (rarely 3) distal foot papillae. *P. indigo* Ruhberg apparently also has a restricted distribution, having been reported from only two sites in the north-west Nelson region. Its most distinctive feature is the possession of 5 distal foot papillae, while having 15 pairs of legs in common with *P. novaezealandiae* and 4 (rarely 3) spinous pads in common with *P. suteri*.

Ooperipatellus was originally erected to contain all oviparous onychophorans having 14 pairs of legs (Dendy 1902). Two species have been described in New Zealand. *O. insignis* Dendy possesses the characteristic 14 pairs of legs, and is widely distributed in the alpine regions of the South Island, with only five records from the North Island to date. It is also the only species in common with Australia, where it is found in Victoria and Tasmania; indeed it was first described as *Peripatus insignis* by Dendy (1890) from Mt Macedon, Victoria. In New Zealand, this species was initially described from Lake Te Anau, under the name *P. viridimaculatus* (Dendy 1900a). Subsequent examination of New Zealand and Australian material did not reveal any morphological feature to distinguish between them, and they were synonymised in the genus *Ooperipatellus* (Dendy 1900b, 1902). More recently, a second species with only 13 pairs of legs was described as *O. nanus* by Ruhberg (1985); it is known only from the Takitimu Mountains in Southland.

RECENT DISCOVERIES

In Australia a previously unknown species, *Cephalofovea tomahmontis*, was identified recently (Ruhberg *et al.* 1988), in part on the basis of its molecular distinctiveness as determined using allozyme electrophoresis. A very important morphological character was also discovered, male head structures which appear to be involved in mating (Tait &

Briscoe 1990). These structures can occur as modified dermal papillae or as highly complex pits with sclerotised spines. These discoveries precipitated a further extensive revision of the Australian onychophoran fauna (Reid, 1996 in press) where previously only eight species contained within six genera were described (Ruhberg 1985). Further application of molecular techniques has resulted in the recognition of more than 70 previously undescribed species (Tait *et al.* 1990; Briscoe & Tait 1995), approximately doubling the world's known onychophoran fauna. Chromosome data show that extensive karyotypic evolution has occurred in the viviparous Peripatopsidae of eastern Australia (Rowell *et al.* 1995). Groupings of taxa based on chromosomal data were also found to be consistent with groupings inferred from morphological data. Recent molecular work using DNA sequence data supported this Australian radiation, and provided further evidence to suggest that this radiation is indeed ancient (Gleeson *et al.* in prep.).

Why then have previous morphological revisions been unable to uncover so many new species? There has been a history of considerable debate and discussion surrounding the taxonomy of Onychophora (Tait *et al.* 1990; Ruhberg 1992). In general, the difficulties encountered when determining species status are mostly attributable to a lack of non-conflicting morphological characters, as this group is extremely conservative. Other contributing difficulties include sympatry involving two or more species, and the recent discovery that many species have extremely restricted distributions (Tait & Briscoe 1990), such that previous sampling strategies were perhaps inadequate.

Given such a species explosion in Australia, New Zealand must surely have the potential to harbour a proportional number of new species. A preliminary isozyme electrophoresis survey undertaken by Tait & Briscoe (1995) uncovered five distinct groups of viviparous New Zealand onychophorans which differed by more than 50% of the presumptive loci scored. Morphological examination suggests that a new genus exists in the Leith Valley and Caversham regions of Dunedin. A subset of DNA sequence data from an extensive survey which has recently begun, also supports these findings (D.M. Gleeson, unpublished data). There are reports of bright green onychophorans (Harris 1991), and many other morphological anomalies identified from material in the New Zealand Arthropod Collection await formal description. Clearly a revision of the New Zealand fauna is required.

CONSERVATION

Onychophora have been classified in the IUCN Invertebrate Red Data Book as 'vulnerable' (Wells *et al.* 1983). This is mostly due to the susceptibility of their habitat, often sensitive rainforest environments, to disturbance. Accounts of habitat disturbances which have led to the elimination of onychophorans at particular sites are given by Wells *et al.* (1983). These include the apparent extinction of the South African *Typhloperipatus williamsoni* Kemp by forest fire. Furthermore, it appears that many species exist as small localised populations in habitats which currently have no conservation status or legal protection. The Leith Valley and Caversham populations of an apparent new genus, are good examples in New Zealand.

Recently, the Onychophora in general have been suggested as warranting priority for conservation (New 1995) owing primarily to their status as living fossils. Due to their predatory nature they also have potential as indicator species in the assessment of biodiversity. However, a more thorough account of their patterns of distribution, preferred habitats, and associated fauna are needed if they are to be of any such use. This need for information has recently been highlighted in regard to the preservation of Birch Island in the lower Clutha River, Otago, which is threatened with inundation for the purposes of a hydro-electric scheme. Closer investigation of the invertebrate fauna on this island has revealed what is apparently a previously unknown species of onychophoran (N. Tait, personal communication). Further investigation is then obviously required to determine the range of this species. Owing to their vulnerability to over-collecting, it is most important that future research on our Onychophora be as non-destructive as possible and carefully monitored.

CONCLUSION

The Onychophora are truly intriguing and unique organisms. If we are to conserve this distinctive element of our fauna it is imperative that onychophoran diversity be documented in the near future, before further undescribed species are threatened with extinction. A molecular approach which requires only minimal material and can utilise previously collected specimens is currently being pursued at Manaaki Whenua - Landcare Research. This approach is designed to uncover monophyletic groupings which have been missed in previous revisions, and which warrant formal description. It will also allow evolutionary relationships to be determined between such groupings and, in parallel with Australian research, document the origins of the New Zealand onychophoran fauna.

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