Taxonomic background of the redlegged earth mite *Halotydeus destructor* (Tucker) (Acarina: Penthaleidae)

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Summary

The early literature on redlegged earth mite *Halotydeus destructor* (Tucker) contains many bibliographic and nomenclatural errors, which hinder study of its taxonomy and biology. Those errors are here corrected. It appears as if the species occurs only in southern Africa, Australia, and New Zealand. Research is required to determine whether it also occurs in Mediterranean Europe, where several related species occur. Research is also required to allow the confident taxonomic recognition of *H. destructor*, so that it may be distinguished from related species in Australia and elsewhere. Possible future biological control strategies cannot be fully exploited until these questions are answered.

Introduction

The redlegged earth mite *Halotydeus destructor* was described taxonomically by Tucker (1925), under the name *Penthaleus destructor*. This bland statement conceals the fact that the species has had an unusually interesting and complicated nomenclatural and bibliographic history. The early literature on the species is full of errors, misunderstandings, and misquotations. These errors confound attempts to determine the native range of the species and its present geographic range, and to consolidate the available information on its biology. It is therefore timely to summarize some of the history of the species, in an attempt to clarify these questions.

The early literature on redlegged earth mite

The redlegged earth mite (RLEM) first appeared in the literature in 1908 under the name earth flea (Jack 1908). Jack gave brief descriptions of its life history and biology, and an account of the damage that the species was causing to vegetables in the Cape Province of South Africa. He did not, however, use any scientific name to describe the species. Banks (1915) referred to the South African earth flea as an unidentified species of *Penthaleus*. Newman (1920) recognized the presence of earth flea in Western Australia, and later (1923, 1924) identified it as *Notophallus bicolor* Froggatt 1921, which had just been described from New South Wales. At the same time Newman (1923) coined the name red legged velvet earth mite for the Western Australian species. Newman then realised that the RLEM of Western Australia was not the same as Froggatt's species from New South Wales, and began referring to the former as *Penthaleus destructor* (Jack) (Newman 1925a, 1925b).

Tucker (1925) described the earth flea taxonomically as *P. destructor*, and gave it the new common name of black sand mite. He also stated that Jack (1908) had not given a description of the earth flea, but had referred to it as *P. destructor*. Tucker is mistaken on both counts – Jack did describe the general appearance of the species, but did not use the name *destructor*, or any other scientific name. Tucker's statements appear to have been based on some manuscript of Jack's that was never published. His error of attributing the name *destructor* to Jack was repeated by subsequent authors (e.g., Womersley 1933, 1941, Newman 1925a, 1925b, Thor and Willmann 1941, Strandtmann and Tilbrook 1968). Newman (1925a, 1925b) compounded the confusion by referring to a publication by "W. E. Jacker", which keyed and described *P. destructor*. This mythical author appears to be a chimera of R. W. Jack and R. W. E. Tucker. The publication referred to is probably Tucker (1925), since Newman quotes it as using the name black sand mite, which had been introduced by Tucker. Jack eventually settled the issue by himself attributing the name *destructor* to Tucker (Jack, 1942).

Swan (1934) performed the very useful service of correcting a number of nomenclatural and historical errors that had been made by previous authors. These included some spelling errors, which should be disregarded – *Halotydaeus, Halodytaeus, Notophalus, bicolour, dicolor*. Newman (1936) then acted to correct his earlier errors, but Swan's efforts appear to have been overlooked by some other authors.

The existence of males

There has been some doubt as to the mode of reproduction of RLEM, and whether or not males exist. Jack (1908) described the male as being smaller than the female, and as having an abdomen that was tapering rather than rounded. Newman (1925a, 1925b) published photographs labelled "adult male", without explanatory text. Neither of these authors offered any evidence that their specimens were in fact males. Womersley (1933) confused the issue when he said that males of RLEM had not been seen, and that Tucker had suggested that *H. destructor* was parthenogenetic. The situation was not helped when the illustration of the male in Newman (1925b and elsewhere) was reproduced in Newman (1936) labelled as a female. Meyer and Ryke (1960) and Meyer (1981) also stated that the males were not known, and attributed to Tucker the view that the species is probably parthenogenetic.

Tucker's (1925) observation of "several cases of apparent parthenogenesis" could refer to complete female-female parthenogenesis, or to the production of males from unfertilized eggs, a well-known phenomenon in many mite groups. Tucker also stated that copulation had never been observed. This in itself is not surprising, since many mites practise non-copulatory sperm transfer, in which the males deposit a spermatophore which is later picked up by a female. Solomon (1937) described the web-spinning behaviour of *H. destructor*, and noted that there were "small globules of water-like fluid spaced at intervals along the threads". He observed that the specimens spinning web were smaller than adult females, and were probably males. It was suggested at the time that the webbing contains, or is composed of, spermatophores, perhaps with spermatozoa in the fluid droplets (K. R. Norris, in correspondence, 1938). These spermatophores are remarkably different from those typically produced by prostigmatid mites. These are usually erect mushroom-like structures of distinctive shape, produced singly, in which a packet of sperm is supported on a stalk, rather like a golf ball on a tee. The stalk often has attached ramifications and excrescences that are of consistent shape within a species (see for example Krantz 1978, Figure 12). Preliminary observations have shown that the specimens of RLEM that spin web never contain eggs, and have an internal organ resembling an aedeagus, while specimens containing eggs do not spin web and do not have this structure (J. C. Otto, personal communication 1991). Also, the webbing produced by RLEM bears a striking resemblance to that of *Linopodes* sp., in the related family Eupodidae, in which webbing been shown to act as a carrier of spermatophores (Ehrnsberger 1989).

Strandtmann and Tilbrook (1968) distinguished the males and females of *Halotydeus signiensis* by the morphology of the genitalia and the number of genital setae. Baker (1990) also described internal structures, notably the sperm sacs, that allow the recognition of males in other species of Eupodoidea. There appears to be no doubt that males exist in RLEM, but the descriptions that have been published to date are not adequate to allow them to be recognized morphologically.

Geographic distribution of *H. destructor*

Halotydeus destructor was described from Cape Province, South Africa, where it is a widespread and abundant pest. Its biology and behaviour in South Africa have been reviewed by Meyer (1981). The first record of its occurrence in Australia was at Bunbury WA in 1917 (Newman 1925b). Hearsay reports of the time suggested that it came from ship's ballast of South African origin (Johnson 1930). Once in Australia it appears to have spread very quickly, and was recorded in both South Australia and New South Wales in 1930 (Johnson 1930, Anonymous 1930a).

Newman (1925b) observed that *H. destructor* had been found only in South Africa and Western Australia, and inferred that South Africa was its country of origin. This view became established in later literature on the species, from Anonymous (1930b) to Wallace and Mahon (1971). It was later reported as being introduced into New Zealand (Dumbleton, 1947), and as being present in Zimbabwe and Malawi (Jack 1942, Goldsmid 1962). Published maps summarizing these results show its distribution to be southern Africa, Australia, and New Zealand (Anonymous 1958, Anonymous 1960). Macfadyen (1954) recorded one specimen of *H. destructor* from Jan Mayen Island, Greenland (71°N), and suggested that it may have been accidentally introduced there in food supplies. This remarkable record cannot be confirmed, and it is most unlikely that the species is actually established there (Wallace and Mahon 1971).

Womersley (1933) raised the possibility that RLEM had been introduced to South Africa from the Mediterranean climate areas of southern Europe. M.M.H. Wallace made several collecting trips to Europe and north Africa between 1964 and 1969 with the specific objective, among others, of determining whether *H. destructor* occurred there. He collected great numbers of mites and Collembola from pastures and other habitats in southern France, Spain, Morocco, and Italy, but did not find *H. destructor* (Wallace 1966). However, his travels did not include the eastern Mediterranean, on either the African or European shores. Jeppson *et al.* (1975) and Meyer (1981) record *H. destructor* from Cyprus, but this record requires confirmation, since it does not appear in the listings of the mites of Cyprus given by Georghiou (1959, 1977). [*See note added in proof: page 165*]

Other species of *Halotydeus*

The genus *Halotydeus* was erected by Berlese (1891) to accommodate one species, *H. hydrodromus* (Berlese and Trouessart 1889), which was described from rocks on the beach in France and Italy. Berlese (1891) illustrated the species and described it as black with red legs and a medio-dorsal red spot. This red spot resembles that of *Penthaleus major* (Dugès 1834), but Berlese explicitly states that *H. hydrodromus* has its anus terminal, while the anus is dorsally placed in *Penthaleus*. *H. hydrodromus* was subsequently found to be abundant on beach rocks at low tide in Ireland (Halbert 1920). *H. hydrodromus* variety *albolineatus* Halbert 1915 was described from rocks on a beach in Ireland, and is distinguished by a white dorsal stripe. *H. hydrodromus albolineatus* also occurs in the littoral zone on the western Mediterranean coast of France (Schuster 1958). *Halotydeus mollis* Luxton 1986 was collected on a mangrove beach in Hong Kong, *H. signiensis* Strandtmann and Tilbrook 1968 is found in moss on Signy Island (South Orkney Islands), and Talker *et al.* (1981) recorded an unidentified species of *Halotydeus* from the intertidal zone in the Philippines.

The situation surrounding *Halotydeus egregius* is confused. Berlese (1891) described *Penthaleus egregius* from several localities in Italy (Venice, Tuscany, Naples, Sicily). Berlese then (1903) transferred *P. egregius* to a new genus *Chromotydaeus* Berlese 1903, on the grounds that its anus was ventral, and not dorsal as it is in *Penthaleus*. This is puzzling, since Berlese (1891) clearly illustrates *P. egregius* with a terminal anus, which would place it in *Halotydeus* (see for example the key of Strandtmann 1981). Womersley (1941) suggested that *P. egregius* was actually a species of *Halotydeus*, and recorded it from Western Australia. Baker (1946) also considered that *H. egregius* belonged in the genus *Halotydeus*, and recorded it from orchard soil in Texas. Berlese (1891) and Thor and Willmann (1941) report that *H. egregius* is usually found on bare dry soil in the summer, and is uncommon in wet habitats. The Australian records given by Womersley (1941) do not appear to be consistent with this observation, all having been collected between April and November, or "in winter". Also, field notes of the time (by K.R. Norris) show that most of these specimens were collected in moss, and not in pasture. They were referred to in these notes not as *H. egregius*, but by an unpublished name that suggests that their legs are longer than those of *H. destructor*. It is unlikely that Womersley's record of *H. egregius* from Australia actually refers to *H. destructor*, since the colour difference between these two species seems to be distinct, at least in living specimens. The body of *H. destructor* has always been described as entirely black, while the red dorsal spot of *H. egregius* was described by Berlese, and has been observed in Australian specimens (Womersley 1941). It is possible that Womersley's specimens of "*H. egregius*" are neither *egregius* nor *destructor*, but belong to another species of unknown identity. The status of this record should be critically re-assessed on the basis of freshly collected specimens. Schuster (1958) rightly pointed out that the red pigments in these species are lost when the mites are preserved in alcohol or mounted on slides, so old museum specimens may be difficult to identify.

It should also be noted that *H. destructor* varies in colour. Womersley (1933) noted the existence of specimens with a brown dorsal surface sharply demarcated from the black ventral surface. It has subsequently been shown that these specimens are those infected with a parasitic fungus (Petch 1940). Tucker (1925) noted some specimens in South Africa that he described as "greyish or yellow mottled" in colour, which may represent cases of the same fungal infection.

Family-level relationships

Some authors have stated that *H. destructor* is related to a group of predators (e.g., Tucker 1925). This impression was created by the use of a classification that placed *Halotydeus* in a broadly conceived family Eupodidae, which included groups of predatory mites that are now placed elsewhere. However, most modern taxonomists consider that *Halotydeus* belongs to the separate family Penthaleidae within the superfamily Eupodoidea (for example Krantz 1978, Strandtmann 1981, Kethley 1982). In this classification the genera have been divided among five smaller families, which more closely reflect the biology of their constituent species.

The family Rhagidiidae are all predatory, and have strong chelicerae with opposable digits for biting prey. They occur in soil, leaf litter, moss, under bark, and in caves. The family Strandtmanniidae comprises only two species, both of which occur in leaf litter. Their feeding habits are unknown, but they have robust raptorial chelicerae that strongly suggest predation. The Eupodidae, Penthalodidae, and Penthaleidae have modified chelicerae with weak opposable digits, and almost all appear to be plant feeders. The Eupodidae are found in damp soil, humus, and moss, and have a worldwide distribution. Some species are fungivorous in commercial mushroom houses, others have been recorded feeding on algae, but most have not been studied biologically. The Penthalodidae are all highly ornamented, and occur in moss, algae, and leaf litter. The species whose biology has been studied are thought to feed on algae, fungi, and lichens.

The family Penthaleidae is a small one, comprising only *Halotydeus* Berlese 1891, *Penthaleus* Koch 1836, *Linopenthaleus* Willmann 1951, and *Linopenthaloides*

Strandtmann 1981. Womersley (1941) and Baker (1946) included the genera *Stereotydeus* and *Penthalodes* in the family Penthaleidae, but these are now considered to be better placed in the separate family Penthalodidae. *Linopenthaleus* comprises one species collected in grass and under rocks in the Austrian alps, and *Linopenthaloides* comprises one species from a cave in New Zealand. Only two species of Penthaleidae have been studied biologically, *H. destructor* and *P. major*, and even these are not clearly defined taxonomically. Many other names have been used in the genus *Penthaleus*, as reviewed by Thor and Willmann (1941), but most of these are not taxonomically recognizable, and their biology is completely unknown. It is not known whether any of these are economically important pests, but it is possible that some literature records of *P. major* actually belong to different species.

Conclusions

Despite its economic importance, and despite the fact that it has been studied continuously for over 80 years, *Halotydeus destructor* still conceals many mysteries. Past research has not established its native range with any certainty, and has not produced clear published evidence of its mode of reproduction. There has never been a comprehensive set of detailed taxonomic illustrations that allow it to be recognized with complete confidence, so some records of *H. destructor*, whether based on field observations or preserved specimens, could refer to other species. While this taxonomic uncertainty remains, accurately directed biological control strategies will not be possible. A program of careful taxonomic research on the Eupodoidea that is currently under way should make considerable progress towards solving these problems (Baker 1990), but more comparative material is required from many areas.

H. destructor belongs to a cosmopolitan genus of plant-feeding mites that appears to have its greatest diversity in littoral habitats. The native range of *H. destructor* appears to be in southern Africa, except for the possibility that it occurs in Mediterranean Europe. This possibility should be re-examined, in a collecting expedition during the European winter. Collecting should concentrate on broad-leaved weeds and leguminous pastures on light sandy soils, and should give priority to Cyprus and the eastern Mediterranean. If RLEM can be found in Europe, that area is likely to also contain natural enemies that are potential candidates for biological control.

Collecting for RLEM should include beach and tidal mudflat habitats, to provide comparative material of the species known to occur in the littoral environment. It will be necessary to distinguish *H. destructor* from other species of *Halotydeus*, notably *H. egregius*, *H. hydrodromus*, and *H. hydrodromus* variety *albolineatus*. Conventional morphological characters should be sought, to allow these species to be separated. During collecting, it is important that the collector make detailed descriptions, illustrations, and preferably colour photographs, of living and freshly-killed specimens, to record their colours. The collector should also develop methods of long-term preservation of specimens that allow their vital colours to be retained. It would also be useful to obtain fresh comparative material of the species of *Halotydeus* that are known to occur in southeast Asia and North America.

Research is also required to determine how male RLEM can be recognized morphologically, and whether fertilization is necessary for completion of the life cycle. If fertilization is required for development, it will be necessary for males and females to recognize each other, or for females to recognize spermatophores. This recognition is likely to involve pheromones, and may offer opportunities for specific methods of pest control by mating disruption. If, on the other hand, RLEM can reproduce by parthenogenesis, its populations could consist of a series of clones, strains, or varieties. The existence of these infraspecific forms will complicate its biological control, especially if host-specific natural enemies are to be used against it.

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Note added in proof:

The Cyprus record of *H. destructor* is now known to be an error (L.R. Jeppson, personal communication). RLEM has not been recorded from Europe.

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