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THEMES AND VARIATIONS : BROODPOUCH COTYLEDONS IN AUSTRALIAN ONISCIDEA

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INTRODUCTION

The Oniscidea, commonly known as woodlice, slaters or pillbugs, are a well-recognised part of garden fauna and have a worldwide distribution in all climatic zones with the exception of the polar regions.

Australia has members from 14 (Table 1) of the 34 families currently established (Holdich et al. 1984), thus the group is well-represented here. This is suprising considering that Australia is the driest continent (after Antarctica) on earth with over 2/3 of the area classified as semi arid (Fig. 1), and that the oniscids have often been considered as ill-adapted for terrestrial life.

Until recently, little has been written about the broodpouch cotyledons, outgrowths of the thoracic intersegmental membrane. Vandel (1925) mentions the discovery and naming of the cotyledons by Treviranus in 1816. Verhoeff (1920) mistakenly thought their development was linked to fertilisation, while it is in fact, associated with the presence of eggs in the pouch (Vandel 1925). Finally, their structure was described and it was suggested that their function was to produce broodpouch fluid (Hoese 1984).

No explanation has been given, however, for the variation in numbers and arrangements of cotyledons in different species. It is suggested here that the cotyledon number of a particular species may be a reflection of its taxonomic position and/or its adaptation to aridity, as cotyledons have not been found on marine isopods.

STRUCTURE AND FUNCTION OF COTYLEDONS (Fig. 2)

Cotyledons are finger-like extensions of the ventral intersegmental membrane, and are usually found on pereion segments 2-5, developing after a brooding moult. They have been described as partly hollow and containing haemolymph lacunae, and it has been suggested that they may secrete the broodpouch fluid (Hoese 1984). This fluid is a reflection of the oniscideans ancestral link with marine isopods and their characteristic of laying soft-shelled eggs requiring a fluid medium for development. Akahira (1956) found a mucous mass surrounding the embryos and suggested that the cotyledons may store this. The lengths of the cotyledons vary with the species and the age of the brood.

NUMBER AND ARRANGEMENT OF COTYLEDONS

Cotyledons are not present in all families. They are missing in the 'inferior oniscoids', and are not always found in the more evolved families, and vary in number between species (Vandel 1925). In most Australian specimens examined, cotyledons, if present, are found on segments 2-5, and range in number from four to 28 per animal. In most species, each segment has the same number.

In species with cotyledons, the least number found is four, with one cotyledon placed centrally on each of segments 2-5. This is described as the 'basic' pattern (Fig. 3A). Cotyledons may be found singly (Fig. 3B), or in groups of two or three (Fig. 3C) along the soft ridge of the intersegmental membrane. Those with 12 cotyledons are the next most common, usually having one cotyledon on each side and one placed centrally on each of segments 2-5 (Fig. 3D). Some have groups of three cotyledons placed centrally (Fig. 2). Those with larger numbers all have central and side groups (Fig. 3E) with one exception, a species of Merulaninae, where the six cotyledons per segment lie in a straight line along the intersegmental membrane (Fig. 3F).

EVOLUTIONARY RANKING AND HABITAT

The families found in Australia, including the three introduced ones, are listed in Table 1, and are ranked from primitive to advanced (A.J.A. Green, personal communication). The terms 'primitive' and 'advanced', although often a cause of much dissension, are used here to indicate the increased loss of marine isopod characteristics, and/or the gain of characteristics of adaptive value to increasing terrestriality.

It was stated earlier that in most cases, cotyledons are only found on segments 2-5 and that the number per segment is constant within a species. However, there are exceptions. Four species do not have equal numbers on each of segments 2-5. Armadillidium vulgare (an introduced species) has one cotyledon on segment 2, and three cotyledons on each of segments 3-5, giving a total of ten; a species of Philosciidae has the same arrangement; two species of Australiodillinae have three cotyledons on each of segments 3-5 but only one or two on segment 2. The other exception, an undescribed species possibly belonging to the Trachelipidae, has one cotyledon on segment 1 as well as three on each of segments 2-5.

BROODPOUCHES IN GENERAL

There are other broodpouch characteristics that should be mentioned here. All the volvational or 'rolling' families, with one exception, have an extension to the pouch area (Fig. 4A, B) formed by the posterior invagination of the sternal epithelium of the sixth and seventh segments. Mead (1963) describing Helleria brevicornis Ebner, calls this an 'internal sac'. This recess is not present in the two Australian species of

Actaeciidae, but has been found in a species of Philosciidae, a non-roller. The other characteristic, again only present in rollers, is the dorsal displacement of eggs and embryos (Fig. 4C). This is possibly an adaptation to allow the animal to roll up. In non-rollers, the pouch extends ventrally to contain the enlarging brood (Fig. 4D), and this could hinder the rolling action (Barnard 1932).

DISCUSSION

When the two proposals linking cotyledon number to taxonomic position and habitat humidity are considered, a clear correlation appears (Table 1). Those with none or few cotyledons are mostly species from the more primitive families, the members of which are generally confined to supralittoral or reliably moist habitats. Those with the most cotyledons are species of the Armadillidae, the most advanced family which includes almost half of the described Australian oniscids, in particular the arid zone species.

Animals living in arid habitats could have a problem with loss of broodpouch fluid due to dehydration. This might be overcome in two ways. First, the cotyledons could secrete more fluid or second, the number of cotyledons could be increased. Species from six of the eight Australian subfamilies of Armadillidae can be found in the arid, semi-desert areas, and these species have the most cotyledons.

A question now arises regarding the species with no cotyledons. Where does their broodpouch fluid come from? The answer is possibly from the external water conducting system of the type present in species from moist environments, and from secretion by the female from the ventral integument (Hoese 1984).

Two of the three families lacking cotyledons are supralittoral and are generally considered primitive. These are the Tylidae and the Ligiidae. The Styloniscidae, although not halophilic, are also considered to be primitive and are usually found in very moist leaf litter where there are free water droplets. The other supralittoral, primitive family, the Scyphacidae, provides an anomaly. Four species of Alloniscus, one of the three genera of Scyphacidae, have been found with 12 cotyledons. This seems a large number for a primitive family (aquatic species do not have any cotyledons) and for one from a consistently humid habitat. Possibly their behaviour, when compared with that of other beach species, necessitates this large number of cotyledons. No breeding specimens from the other two genera have yet been found for comparison.

The Actaeciidae, although supralittoral, are considered an advanced family. As yet, no breeding specimens have been collected. However, many females examined have two unusual characteristics. First, they do not have a recess under segments 6 and 7 in common with all other rollers and second, where oostegites are present, they do not enclose the pouch area and can only be described as ´stunted´. It may be that they have a pre egg-laying moult and that the full oostegites will develop at the next moult when the eggs are laid. If this is so, this sequence has not been noted for any other oniscid. Possibly they have what has been called a ´basket-like pouch´ (Hoese 1984), typical of marine isopods. In which case, why are they ranked so high?

Haloniscus searlei is an anomaly in any terms. It is found in inland salt lakes yet is classified as an oniscid, a terrestrial isopod. It is considered to be secondarily aquatic (Chilton 1920), and it may be that adaptation to extreme aridity on land enabled it to survive the equally dehydrating effect of high salinity. It has an upper salinity tolerance of 159 parts per thousand (Bayley & Williams 1966). The function of the 12 cotyledons in this species has yet to be determined. It could be different from those in non-aquatic environments.

Four species of Trachelipidae have been collected from arid areas. All have only four cotyledons but were found in ant nests where the humidity is relatively high and constant, so lessening the problems of dehydration of the broodpouch fluid.

The second family found consistently in arid areas is the Armadillidae, the most advanced family. The largest numbers of cotyledons are found in armadillid species.

It is the exceptions to the emerging patterns relating cotyledon numbers to humidity and evolutionary ranking, that are of particular interest. Further study of these species continues, particularly the situations where species from different families and with much variation in cotyledon numbers, share the same habitat. The problem of evaluating the differences in microhabitats within a common macrohabitat will be studied, and the interactions in terms of time and space between different species within a common habitat will be examined to determine if differences in behaviour also relate to differences in cotyledon number.

(A note regarding the names of Australian species is necessary. Many of the species collected are previously unrecorded and undescribed. I have found ten species novelle this year including two from a family and two from a genus both new to Australia. At least six other species may also be new, but the early type descriptions are often vague, and the illustrations, if present, are inadequate for positive identification. For the purposes of this study, classification to generic level is acceptable, therefore no species names, with the exceptions of Armadillidium vulgare and Haloniscus searlei have been used.)

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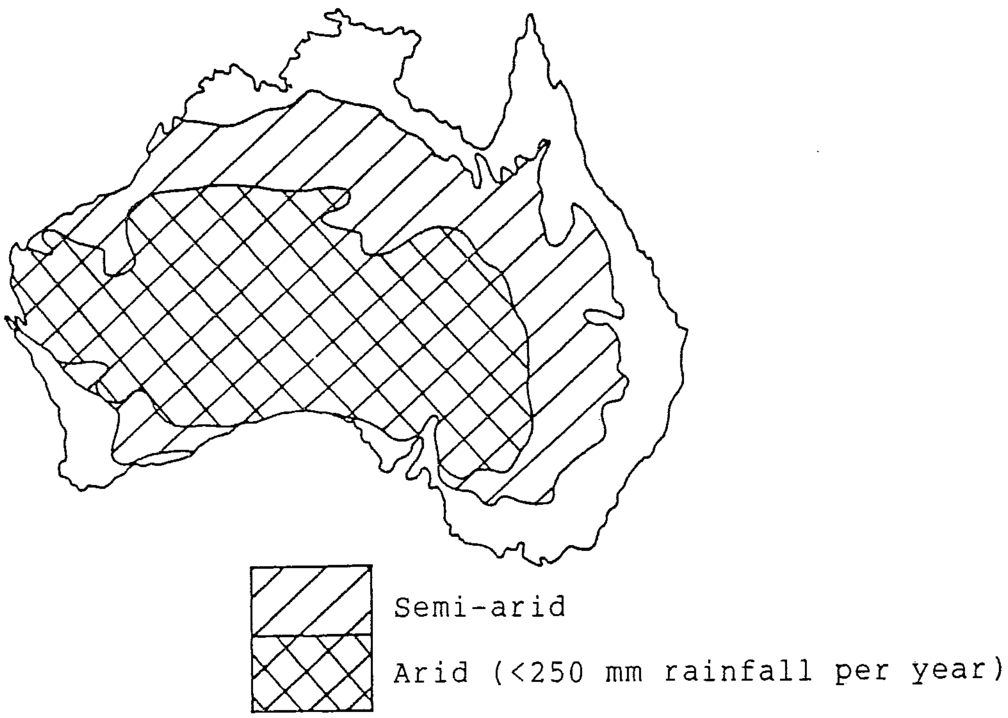


Fig. 1 : Arid areas of Australia (after Davey 1983).

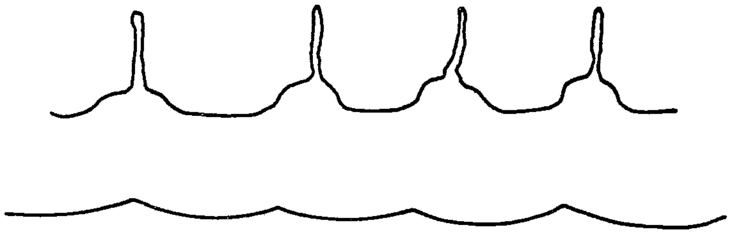
Table 1. Australian Oniscidea

INFRAORDER	SECTION	SUPERFAMILY	FAMILY	HABITAT	COTYLEDON TOTAL	COTYLEDON PER SEGMENT	RECESS	ROLLER
Tylomorpha			Tylidae	Beach	0	0 0 0 0 0	✓	✓
Ligiamorpha	Diplocheta		Ligiidae	Beach	0	0 0 0 0 0	X	X
	Sinocheta		Styloniscidae	Moist	0	0 0 0 0 0	X	X
	Crinocheta	Oniscoidea	Scyphacidae	Beach	12	0 3 3 3 3	X	X
			Oniscidae	Terrestrial	4	0 1 1 1 1	X	X
			Haloniscus searlei	Salt Lake	12	0 3 3 3 3	X	X
			Philosciidae sp.1	Terrestrial	4	0 1 1 1 1	X	X
			sp.2		8	0 2 2 2 2	✓	X
			sp.3		10	0 1 3 3 3	X	X
			Halophilosciidae	Beach	———	———	———	X
			Bathytropidae	Beach	———	———	———	X
			Platyarthridae	Terrestrial	———	———	———	X
		Porcellion-oidea	Porcellionidae	Terrestrial	4	0 1 1 1 1	X	X
			Trachelipidae	Arid/ants	4	0 1 1 1 1	X	X
				Terrestrial	13	1 3 3 3 3	X	X
			Armadillidiidae	Terrestrial	10	0 1 3 3 3	✓	✓
			Actaeciidae	Beach	———	———	X	✓
			Armadillidae	Arid/ Terrestrial				
		(Subfamily)	Australiodillinae	3 spp.	10	0 1 3 3 3	✓	F
					11	0 2 3 3 3	✓	F
					12	0 3 3 3 3	✓	F
			Aust/Cubarinae	2 spp.	28	0 7 7 7 7	✓	F
			Cubarinae	5 spp.	24	0 6 6 6 6	✓	✓
			Merulaninae	3 spp.	24	0 6 6 6 6	✓	✓
			Armadillinae	1 sp.	24	0 6 6 6 6	✓	✓
			Acanthodillinae	2 spp.	———	———	✓	✓
			Lobodillinae	———	———	———	✓	✓
			Buddelundiinae	6 spp.	16	0 4 4 4 4	✓	✓
					20	0 5 5 5 5	✓	✓
					———	———	✓	✓
			Akermaninae	———	———	———	———	X

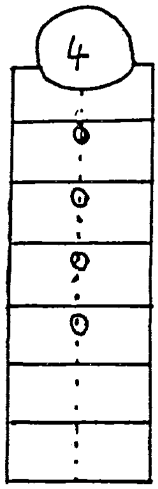
——— = no specimens or cotyledon information

F = folds, incomplete roller

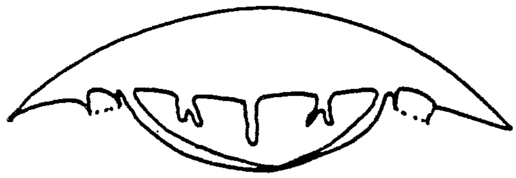
Fig. 2 : Scanning electron micrograph of broodpouch cotyledons on a species of Alloniscus (oostegites removed). Each of segments 2-5 have three cotyledons arranged in a central group. Scale bar = 1 mm.



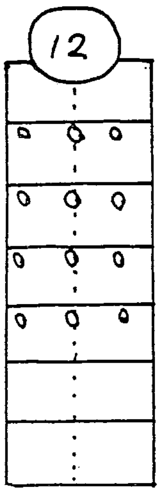
(B) L.S. through mid-line



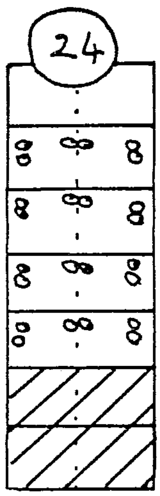
(A) Basic pattern



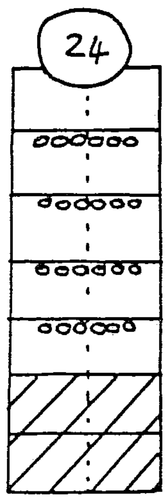
(C) T.S. through intersegmental membrane



(D)



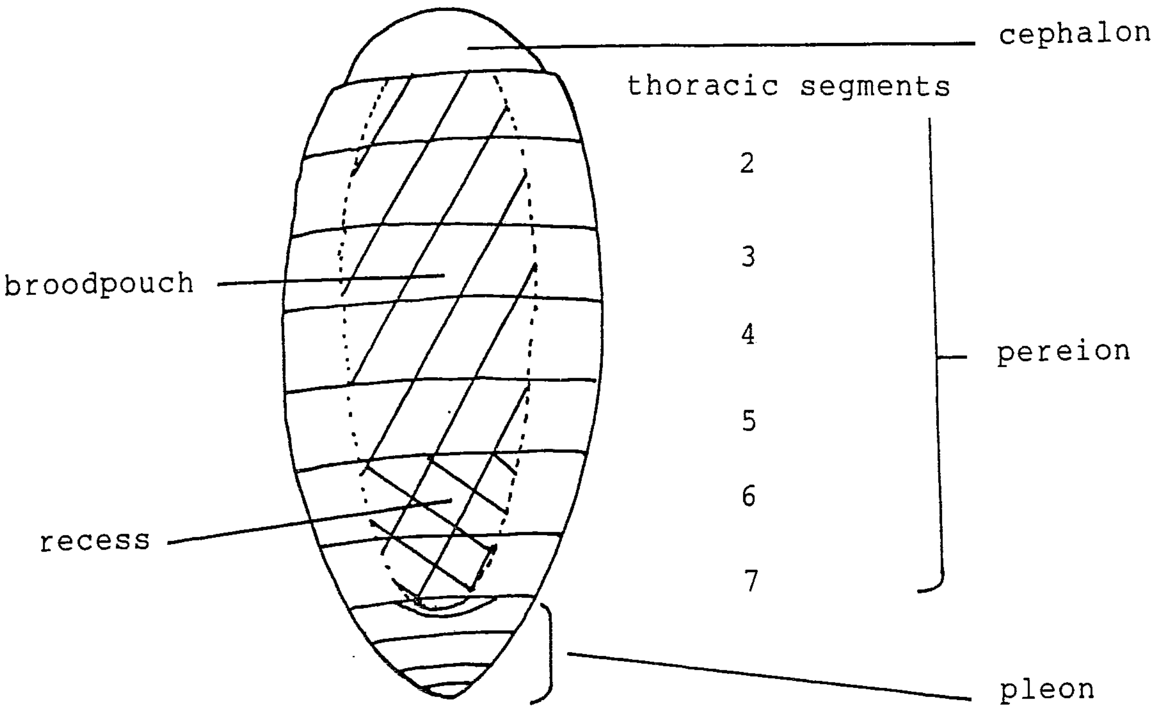
(E)



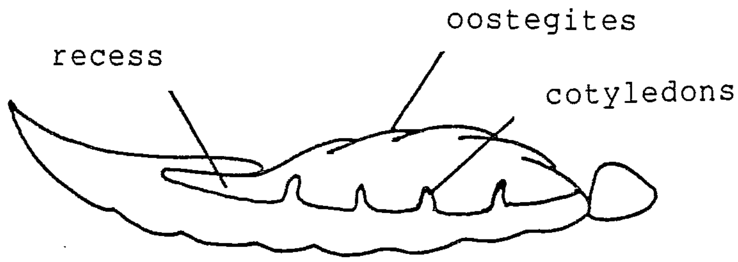
(F)

//// = Recess

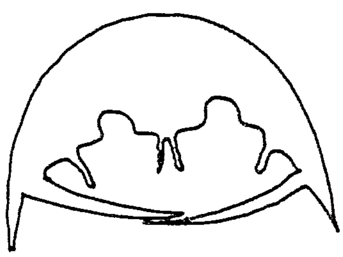
Fig. 3 : Patterns and structure of broodpouch cotyledons in terrestrial isopods.



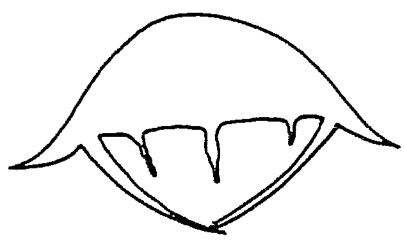
(A) Schematic ventral view of a 'roller'



(B) L.S. through mid-line of a 'roller'



(C) T.S. through broodpouch of a 'roller'



(D) T.S. through broodpouch of a 'non-roller'

Fig. 4 : Broodpouch structure in 'rollers' and 'non-rollers'.