

TROPICAL RAINFOREST MYGALOMORPH SPIDERS IN THE AUSTRALIAN DESERT: THE IRONY OF AN ADAPTIVE LEGACY

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Abstract

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The semiarid regions of Australia have a high generic diversity of mygalomorph spiders. Several genera are postulated as being "tropical" rainforest genera. Three genera, *Conothele*, *Selenocosmia* and *Cethegus* have been selected for discussion. Persistence of these genera in the arid region is postulated as being due to a combination of natural restriction to relic habitats or those with verisimilitude with rainforest habitats and retention of behavioural attributes which fortuitously fit them to persist. Aspects requiring conservation attention are perceived to be tourism and too frequent fires.

Introduction

The belief in the richness and diversity of life in rainforests, particularly tropical rainforests, forms part of our inherited mythology as reflected in literature and art. No less in biological science, where the diversity of tropical rainforest life provides themes for theory, documentation and estimation: *why* so rich and *how* rich? From the middle of the last century with exploration in the tropics by adventurers and scientists, namely H. W. Bates, Charles Darwin and Alfred Wallace, (and I must mention here the largely overlooked observations of the dominant figure of mid to late nineteenth century spider systematics, Eugene Simon) fascination with this phenomenon has developed into one of the driving themes of evolutionary biology as currently studied — why so rich — what is the mechanism providing this richness and how is it maintained? In the last part of this century, with anxiety about diminution of the biological bank, some biologists have become obsessed with estimating the richness and diversity of life i.e. the array of life at the species level — how many species (Ewing, 1983; Monteith, 1990). The concomitant ideal of documenting this diversity i.e. naming and describing the species and so making a reality of the estimations, is sadly lacking.

In Australia, rainforests (or "closed forests" in some terminologies, e.g., Specht 1981) comprise a small percentage of the landmass. Tropical rainforests are confined to small areas of the northeast coastal region (Specht, 1981, Figure 2; Webb and Tracey, 1981, Figure 1) while wet/dry

seasonal or monsoon rainforest forms small or large pockets in the Kimberley of northern Western Australia (McKenzie, 1991, Figure 3) and the Northern Territory. Dry vine forests in inland and some coastal areas of mid Queensland are also generally included in broad statements about northern or tropical rainforests.

Recently, some zoologists have challenged the "assumption that biodiversity in the tropics is vastly higher than in the temperate zones" (Platnick, 1991) and botanists likewise recognise high diversity outside tropical rainforests. e.g., as in south-western Western Australia (Lamont et al., 1977). In looking at mygalomorph trapdoor spiders it is apparent, and perhaps surprising to those still hungover with the spell generated by the rainforest mythology, that the semiarid regions of Australia are possibly the richest areas at least in terms of generic diversity and behavioural scope. On a broad geographic front, Main (1982) listed 17 of "the 37 or more mygalomorph genera in Australia" as occurring in semiarid and arid regions of Australia. At a smaller scale, a recent study by Main (1996) at Durokoppin in the semiarid Wheatbelt region of Western Australia demonstrated occurrence of at least 25 species in 13 or 14 genera from six families in a small area of less than a square km within a reserve of remnant vegetation of 1030 hectares. It is doubtful whether such taxonomic diversity can be matched in rainforest habitats. Wishart (1993) noted occurrence of eight mygalomorph species in a 95 x 55 m subtropical rainforest remnant at Gerringong in New South Wales. Davies, Gray and other collectors apparently did not find a comparable taxonomic

richness in eastern Australian rainforests during various rainforest surveys, to that found at Durokoppin (see Monteith, and Davies, 1991). Nor did the Bellenden Ker survey in north Queensland produce such a diversity (Monteith and Davies, 1991). Nevertheless it is known from the taxonomic works of Raven (Raven, 1994 and earlier papers), museum collections, my own collection and personal observations that there is indeed a rich mygalomorph fauna in the eastern Australian rainforests including the tropics. Main (1976) also noted 12 species in a short transect across the sclerophyll/rainforest boundary to the *Nothofagus* habitat in Lamington National Park. With later refinements in the taxonomy this number of species and genera would be higher but possibly not as rich as at the Durokoppin site. Surveys in the monsoon rainforests of neither Kakadu (Kikkawa and Monteith, 1980) nor the Kimberley (Main, 1991a) indicated a taxonomic richness to that observed in the semiarid.

Main (1991b) noted 25 genera of the "forty or so" named mygalomorph genera as occurring in "rainforests". However, this number included genera occurring in southern or temperate rainforest while the present discussion is concerned only with those found in tropical rainforests (although of course some of those genera may occur in temperate rainforests as well). The present study notes 26 genera occurring in tropical rainforests (Table 1). Most of these occur also in tall, open forest (mesophytic or sclerophyll forest) but a few are confined to tropical rainforest, e.g., *Masteria* and *Sason*. A few others (e.g., *Kiama*, *Australothele*, *Carral*, *Migas* and *Plesiothele*) are also confined to rainforest but including southern rainforests and *Nothofagus*.

The theme of this paper concerns those genera which are regarded as being primarily "tropical rainforest genera" but which also extend into semiarid regions. In that such genera are adapted to humid or seasonally humid forest situations it may appear anomalous that some species occur in semiarid/arid regions. I shall now attempt to show that it is the very nature of the spiders' adaptations to tropical rainforest habitats which ironically enables them to live in the desert region. Furthermore I argue (contrary to some of my earlier interpretations) that the spiders, rather than having invaded the desert, have been stranded there following the retreat of their original tropical rainforest landscapes.

Taxonomic diversity of Australian Mygalomorphae

There are ten families of Mygalomorphae currently recognized from Australia (Raven, 1985a). Recent taxonomic revisions have brought the number of mygalomorph genera of mainland Australia and offshore islands and Tasmania to 43 according to Main (1985a) and with those recorded or described since then (Main, 1985b, 1985c, 1986, 1991c; Raven, 1986, 1988, 1994; Churchill and Raven, 1992) plus some reinstated, and one found not to occur in Australia (Raven, 1994), there are now 57 named genera considered valid while there are still several recognised but unnamed genera (pers. obs.).

Tropical rainforest and desert — terminology and distribution

Before discussing the occurrence of rainforest genera in the "desert" some definition of the boundaries of the two habitat regions in the present context is necessary. I use the term rainforest to mean predominantly closed "wet" forest but also to include seasonal i.e. monsoon forest as in the Kimberley and Northern Territory and vine thickets as in Queensland. Thus "tropical rainforest" as used here equates roughly to "closed forest" of Specht (1981, Fig.2).

Northern "open forest woodland" of Specht (1981, Fig. 4) actually embraces many patches of rainforest as documented in McKenzie et al (1991) and patches and gallery forest in the Northern Territory. Thus tropical rainforest in small or large areas is mostly found within the rainfall isohyets of 750mm per annum and above (see Nix, 1981, Figure 10).

"Desert" and semiarid/arid is loosely defined here to encompass that huge interior of Australia with less than 500 mm rainfall per annum, receding to less than 250 mm and 150 mm (see Nix, 1981, Figure 10). The southern boundary accepted in the present context is not as restrictive as that defined as the 250 mm isohyet by Williams and Calaby (1985) and followed by Morton et al (1995, Figure 3.1). However, there are many refugia associated with topographic features throughout the whole of the low rainfall areas of Australia — refugia which can be regarded as harbouring biotic leftovers of an earlier "wetter" climatic regime. Striking examples are found in the valleys of the Central Australian mountains, the gorges of the Hamersley Ranges in Western Australia and around low

hills and granite outcroppings on the subdued landscapes of the Western Australian Plateau and Eyre Peninsula in South Australia. Morton et al. (1995) list 74 refugia in the semiarid and arid region.

Even outside these obvious refugial areas, within the "desert" there are numerous microhabitats which present, in microcosm, habitats that have verisimilitude with tropical rainforests. These persistent, small and large, scattered and isolated refugia preserve certain taxa which by their overall distribution suggest a tropical rainforest origin. However, it is not just that such taxa may have been left *in situ* as the continent has become dryer and wet forest habitats have shrunk. There are also behavioural and life history factors peculiar to the relic genera which favour their persistence.

Furthermore the weather patterns, as well as the vegetation cover and topography of rainforest and "desert" refuges play a big part in maintaining the genera in their peripheral range. Northern rainforest and open forests and woodland regions are dominated by summer rain (Nix, 1981, see Figure 1); the semiarid and desert, south of the tropics by winter rain.

However, as well as winter rain which may be very irregular, the whole of the vast inland also experiences some summer rain associated with isolated thunderstorms and cyclones or monsoonal rains which occasionally extend well south of the tropics. These unpredictable rain events now profoundly affect the persistence of "tropical" elements of the mygalomorph fauna in desert regions.

Tropical rainforest genera — distribution and characteristics

It is now pertinent to state that of the 57 currently accepted mygalomorph genera in Australia, 37 occur in rainforests and of these 26 occur in tropical rainforests (Table 1). Of the latter, many genera also occur in open forest and some have species in drier habitats ranging from woodland to heath and desert. The following seven genera are found *only* in rainforests: *Kiama*, *Australothele*, *Carrai*, *Masteria*, *Plesiothele*, *Migas* and *Sason*. Of these, *Masteria* and *Sason* are restricted to northern i.e. tropical rainforest. Data on rainforest and other relevant habitat distributions to arrive at the information summarised in Table 1 is derived from Main (1985a) where bibliographic sources are given e.g. taxonomic literature associated with species descriptions and later publications (mainly

taxonomic papers but some natural history works) of Churchill and Raven (1992), Gray (1987, 1992), Main (1985b, 1985c, 1986, 1991a, 1991c, 1995, 1996), Raven (1984a, 1984b, 1985b, 1986, 1993, 1994) and to some extent from data with museum collections and finally from my own observations and field records.

I have selected for the present discussion the three genera *Conothele* (Ctenizidae), *Selenocosmia* (Theraphosidae) and *Cethegus* (Dipluridae) which have in common a distribution right across the north i.e. throughout the tropics and primarily in rainforest and which extends widely through other southern habitats within the general "desert" region but they are excluded from the extreme southwest and southeast of the continent. This distribution suggests a tropical origin and possibly a relatively recent entry into Australia, especially for *Conothele* and *Selenocosmia* both of which also occur to the north of Australia, a hypothesis already espoused by Main (1981, 1982). *Cethegus* in having partly and perhaps primarily a tropical and subtropical rainforest distribution (Main, 1960; Raven, 1984c) can similarly be regarded as being a recent denizen of the semiarid. *Aname* (Nemesiidae) and *Missulena* (Actinopodidae) occur widely throughout the continent including the tropical north. *Aname* also occurs in Tasmania from where however *Missulena* is absent. The distribution of *Idiommata* (Barychelidae) may parallel that of the three selected genera and some of its behavioural attributes may similarly account for its broad habitat inclusion. The genus is currently under review by Raven (1994). The remaining genera have more restricted ranges (Table 1).

All those genera occurring in rainforest appear to be dependent on a moist, shaded habitat and species of the three genera also occurring in "desert" areas selected for discussion are restricted to more or less permanently moist habitats as I will show below.

Behavioural and life style characteristics of rainforest "deserticoles"

Most genera which exhibit strong adaptations to desert living are regarded as old, autochthonous Australian genera (Main, 1981). The three "rainforest" genera under discussion persist in the desert firstly by avoiding the desert environment (they are situated in refugia however miniscule), and secondly by retaining a suite of behavioural and life style attributes appropriate to their original rainforest habitat and which

now predispose or fortuitously fit them to survive in generalized arid areas. (In view of the controversy surrounding such terms as pre-adaptation and related contrivances, I am reluctant to add to the confusion by using similar words like "a predisposition" but nevertheless dare to coin the term "fortuitous adaptation"!).

Main (1982) summarised the desert adaptations of mygalomorphs to include morphologi-

cal features which reduce water loss and various combinations of behavioural characteristics such as (1) avoidance of environmental conditions through fossorial habits (2) sedentary life style e.g. burrow site fidelity (3) specialised foraging strategies and seasonal feeding by non-aestivating segments of the population (4) coincidence of reproductive behaviour and dispersion of juveniles with rainy periods (however erratic) (5) extreme longevity of females (6)

Table 1. The 26 genera which occur in tropical rainforest and the extent of their distribution i.e. to include southern areas and whether absent from the southwest and southeast corners of Australia. * = 14 genera which extend into "desert" (arid/semiarid). P = present; sw, southwest, se, south east.

Tropical Rainforest	Widespread	East/Aust only	Absent se/sw
Actinopodidae			
* <i>Missulena</i>	+	—	P
Ctenizidae			
* <i>Conothele</i>	+	—	—
Dipluridae			
* <i>Cethegus</i>	+	—	—
<i>Namirea</i>	—	+	—
<i>Masteria</i>	—	+ne Qld	—
Hexathelidae			
* <i>Hadronyche</i>	—	+& Eyre P	P se
Idiopidae			
* <i>Arbanitis</i>	+	—	P
<i>Cataxia</i>	—	+Qld only	—
<i>Homogona</i>	—	+	P se
Migidae			
<i>Migas</i>	—	+	P se
Nemesiidae			
* <i>Aname</i>	+	—	P
* <i>Chenistonia</i>	+	—	P
* <i>Kwonkan</i>	+w half Aust	—	Psw
<i>Xamiatus</i>	—	+	—
<i>Namea</i>	—	+	—
*? <i>Yilgarnia</i>	+w half Aust	—	—
Theraphosidae			
* <i>Selenocosmia</i>	+	—	—
Barychelidae			
* <i>Idiommata</i>	+	—	Psw
* <i>Synothele</i>	+WA/SA	—	Psw
<i>Trittame</i>	—	+ne	—
<i>Sason</i>	—	+ne	—
<i>Zophorame</i>	—	+ne	—
* <i>Mandjelia</i>	+	—	—
* <i>Ozycrypta</i>	—	+ne/cent	—
<i>Tungari</i>	—	+ne	—
<i>Moruga</i>	+n/trop	—	—

capacity to fast for long periods (7) iteroparous reproduction and (8) limited dispersal capacity in most species.

At the same time these attributes were given as explaining the restricted geographic ranges of many such species which "are tied to particular habitat types categorized by soil/vegetation attributes". Conversely it was pointed out that *Conothele* has a wide geographic range "assisted by its aerial dispersal" and that "the large, aggressive and relatively mobile *Selenocosmia stirlingi* has been able to colonize unstable habitats of the interior".

It is these contrary attributes, plus additional ones but all reminiscent of their rainforest heritage, of *Conothele* and *Selenocosmia* and shared by *Cethegus*, which I wish to emphasise here as being the "fortuitous adaptations" enabling them to live in the desert region. In other words they live *in* the desert but are not *of* the desert.

In considering the "fortuitous adaptations" of *Conothele*, *Selenocosmia* and *Cethegus* the salient ones are probably associated with the following factors:

1. Persistence in relic microhabitats within the arid region;
2. Adoption of microhabitats with verisimilitude with rainforest habitats;
3. Burrow/nest structure;
4. Dispersion method of juveniles;
5. Mobility i.e. capacity to relocate nest/burrow site;
6. Foraging behaviour; and
7. Reproductive behaviour and phenology.

I will now discuss each of the genera in turn to show the relevance of these factors to persistence of the respective taxa as deserticoles.

Conothele

The genus has a wide distribution from Burma, various island groups through New Guinea and Australia (Roewer, 1942; Main, 1981; Raven, 1985). It occurs generally in rainforest and open forest in humid, tropical regions. Nests are usually in the ground but some rainforest species are arboreal and make small cocoon-like tubes with trap doors in bark, thus avoiding inundation in very wet habitats (Main, 1993). Spiders are moderate sized, with a smooth shiny cuticle, very spiny anterior legs and apart from courting males and dispersing juveniles spiders never leave the nest.

(1) In semiarid and arid regions in Australia spiders occur in shaded cliff faces of mountain valleys as in the Hamersley Ranges and other

similar sites in Western Australia and various mountain blocks ("ranges") in Central Australia. Although rocky, these sites due to their geological structure encourage seepage into soil interstices. This dampness combined with shade albeit of shrubs and tussocks provides a habitat that mimics in microcosm an earlier rainforest habitat, of which indeed such sites are relics.

(2) Elsewhere in open country of the dry interior the spiders are found in association with rock tumbles around low hills, and in clay and alluvial soils in small depressions of drainage lines. Thus they occur in either relic microhabitats (valleys of mountain ranges which also retain ancient flora such as *Livistona*) or in habitats with verisimilitude.

(3) The burrow of *Conothele* in most sites is relatively shallow, and lined with a stocking-like tube of tough silk that adheres to a plaster wall and with a tightly-fitting, cap-like silk/soil door. The base of the burrow unless in the process of being deepened is usually fully lined. Thus the burrow acts like a sealed flask — preventing flooding during immersion in wet tropical sites. Secondly this secure tube in flood prone areas in the otherwise dry inland similarly protects the spiders and conversely ameliorates environmental desiccating conditions.

(4) Juveniles disperse aerially (although it is assumed not over great distances) which assists dissemination in rugged terrain or habitats with patchy shrubbery or rocky sites. The method is advantageous in steep sided, rocky gorges as well as open woodland with discontinuous favourable microhabitats.

(5) In unstable creek banks, as in the rainforest (such as in the Kimberley and many northern Australian sites) and steep slopes in open forest e.g., north Queensland and New Guinea, if the burrows are washed over by sheet flooding or even partly dislodged the spiders are securely cocooned because of the sealed stocking structure of the nest and the spiders can relocate or reestablish after being buffeted by sudden crosive conditions.

(6) Spiders are typical sit-and-wait predators and do not fully emerge from the burrow when capturing prey. This possibly limits them to high-prey habitats. However the habitats they occupy would also appear to favour invertebrate density. Spiders do not store rejectamenta in the basally sealed burrow but eject it at the surface (personal observations) which again implies a certain transitoriness unlike the extreme sedentary nature of most arid adapted species which

arc more vulnerable to sudden disturbance of habitat (and habitually store rejectamenta).

(7) Little is known about the reproductive behaviour of the genus other than that wandering of males and juvenile dispersion is linked with rainy periods (at whatever season).

"*Selenocosmia*"

The genus occurs from India to New Guinea and Australia (Roewer, 1942). However the family representatives of Theraphosidae in Australia require taxonomic revision and the generic category "*Selenocosmia*" is loosely applied in the present context. Schmidt (1995) transferred the Australian species of *Selenocosmia* to *Phlogius* in which genus early species were originally placed. The spiders are very large and hairy with long legs. Spiders make very deep burrows.

(1), (2) and (3) While it is difficult to identify "desert" sites of a relictual nature, most habitats (throughout the inland in various States) certainly have verisimilitude in that they are lowlying, wet or seasonally wet, in relatively unstable situations and may be flooded during the rainy season. Because the spiders are already adjusted to inundation of burrows (e.g. in seasonal "swamps" or "bogs" in the Kimberley) inundation in flood prone, arid flats is not inimical. It is possible that the very deep burrows maintain air pockets. Also the furriness of the spiders' bodies encourages formation of an enclosing air bubble thus spiders may be immersed without drowning. The earliest records of the habitat of the "barking" or "whistling" spider, *Selenocosmia stirlingi* is in the classic account of the spider in *The Report of The Horn Expedition* (Spencer, 1896) where the spiders are noted as occurring in "grassy flats amongst low hills". These would be the swales between the ranges and sand dunes, low lying areas subject to sheet flooding and temporary boggy conditions following intermittent rain. They in this way resemble seasonal wet/dry depressions where other species occur in the Kimberley and north Queensland (pers. obs.)

(4) Little is known about juvenile dispersion other than that it is assumed spiderlings scatter freely on the ground (Kotzman, 1986).

(5) Spiders appear to be readily mobile and there is some evidence (Kotzman, 1986 and pers. obs.) that spiders move sites at least in arid habitats.

(6) Spiders may lay an entrapping mesh of web

around the burrow entrance. In addition they emerge to hunt or actively chase prey.

(7) Spiders are mostly summer breeding, which in the monsoon forests at least ties in with the "wet". In the arid region spiders are more opportunistic, males taking advantage of irregular summer rains to wander. Longevity of females enables individual spiders to forego breeding during drought years while persisting as a population (a common strategy of arid adapted mygalomorphs (Main, 1976, 1978)).

Cethegus

Commonly called "curtain web spiders", these spiders have long spinnerets (associated with their profuse web building). They are moderately sized, hairy, with relatively long legs which tend to turn backwards at the tips. Although they are web weavers, they are remarkably agile on the ground and can move very quickly. In rainforests the spiders make diffuse silk tubes amongst rocks, in logs or on irregular cliff faces. In monsoon forest they frequently occur in the rocky river beds. These are inundated during the "wet" when the spiders are possibly washed out or enclosed in their flocculent silk and temporarily submerged. There is no data to suggest that spiders leave their burrows and climb trees or vegetation *prior* to the onset of inundation as occurs with some South American *Ischnothelines* (Hofer, 1990) but this is another possibility. However, their taxonomic affinity with this group suggests also a behavioural flexibility which may include a predisposition to transient web siting.

(1) Like *Conothele*, *Cethegus* often occurs in rocky cliff faces which determine seepage of moisture to the surface or in cracks in "relict" habitats in gorges and valleys in the arid region.

(2) and (3) A notable behaviour in open, semi-arid habitats is that spiders site the burrow and curtain web against a supporting butt of a shrub or small tree which secondarily provides the benefit of harvesting water into the burrow which ramifies the soil amongst the roots. Water harvesting by trees and shrubs in arid areas is a well known phenomenon (Slatyer, 1965; Nulsen et al., 1986).

(4) Juveniles are aurally dispersed (Main, 1995 and unpublished records).

(5) Spiders appear to relocate nest sites in unstable rainforest habitats (inferred behaviour) (Main, 1993) and certainly relocate (due to rain damaged webs and burrows) after rain in semi-arid habitats. The relocation of numerous nests

has been documented at Durokoppin (Main, 1993, pers. obs., unpublished records).

(6) Spiders ensnare prey in their webs and take a variety of crawling and flying insects and other arthropods. The web probably ensnares a higher prey take than that available to typical sit-and-wait trapdoor spiders.

(7) As with other genera reproductive behaviour and dispersion is opportunistic depending on seasonal or irregular rain. However there is some evidence (pers. records) that males develop more rapidly than most mygalomorph species. Precocious development, as argued by Main (1991) would mean lower mortality due to shortened exposure to environmental hazards and thereby increased surety of reproduction in unstable, flood prone (tropical) and climatically unpredictable (arid) habitats.

Discussion

The three tropical rainforest genera *Conothele*, *Cethegus* and *Selenocosmia* have been shown from the taxonomic literature, museum collections and personal observations and collections to be also widely distributed throughout Australia, including the low rainfall areas but exclusive of the mesophytic southwest and south east forests and southern coastal regions. Evidence from natural history observations and distribution records substantiates the hypothesis that these genera survive in the broad semiarid to desert region, not by having evolved specific adaptations to the desert but by retaining adaptations which primarily fitted them to the instability of wet (even if only seasonally wet) tropical habitats.

At the same time the spiders do not appear to have expanded their habitat range but rather to have become restricted to relic rainforest habitats or to "newer" microhabitats which exhibit verisimilitude, at least seasonally, with wet tropical habitats. Even where *Cethegus* occurs in the dry, open "desert" country of the Western Australian Goldfields, which appears to have little resemblance to tropical rainforest, there are reminders of an earlier, wetter scenario in the scattered presence of the kurrajong trees, *Brachychiton gregorii*. Cycads and the *Livistona* palms persist in gorges of the Central Australian Ranges and the latter in some isolated gorges in northwestern Australia (Humphreys et al., 1990). Nor do these spiders demonstrate specific behavioural specialisations comparable to those of the endemic, autochthonous genera. Thus it seems that the apparent rainforest

"deserticoles", by virtue of retaining their rainforest life style and repertoire of adaptations (transmuted as "fortuitous adaptations") are masquerading as "deserticoles".

In the light of this the implications for conservation management are obvious. Especial care needs to be directed to preserving intact relic sites in gorges and less easily identifiable sites with "verisimilitude". In that rainforest habitats are generally not fire prone, relic habitats within the arid zone need to be protected to prevent an edge erosion by fires. With the present infiltration of tourism (see also Morton et al., 1995) that is oriented to once off, casual, sight seeing visitations, the increasing danger of disturbance simply by people pressure to many biologically resilient but physically brittle sites is inevitable. And this is quite apart from the inimical effects of too frequent fires upsetting the habitats and faunal populations.

The spiders *cannot* be the only potential victims — but they are surely the silent advocates for a whole suite of invertebrates.

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