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The biogeography of Gondwanan pseudoscorpions (Arachnida)

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The biogeography of Gondwanan pseudoscorpions (Arachnida). - A review of the pseudoscorpion fauna presumed to have originated in Gondwana prior to the breakup of that supercontinent is presented. Representatives of 12 families are postulated as having Gondwanan origins.

Key-words: Pseudoscorpiones - Arachnida - biogeography - Gondwana.

INTRODUCTION

The biota of the southern continents has been instrumental in the development of biogeographic theories, which was well illustrated by the contentious disputes in the 1960's based upon the theory of continental drift (e.g. DARLINGTON 1965; BRUNDIN 1966). Examples of gondwanan organisms, such as *Nothofagus* and the marsupial mammals, abound in the literature. Amongst the Arachnida, those groups with southern affinities include the spider taxa Migidae (RAVEN 1984, MAIN 1991), Actinopodidae, Hexathelidae (RAVEN 1980), Austrochiloidea (FORSTER *et al.* 1987), Archaeidae and their relatives (FORSTER & PLATNICK 1984) and Orsolobidae (FORSTER & PLATNICK 1985), and the harvestman family Neopilionidae (HUNT & COKENDOLPHER 1991). Numerous others have been documented. While these Gondwanan patterns may be of peripheral interest to many biologists, PLATNICK's (1991) eloquent essay on the invertebrate fauna of the southern temperate zones and their conservation plight highlights a tragic problem of growing magnitude.

Pseudoscorpions are an ancient order of arachnids, with a lengthy, if somewhat fragmentary, fossil record that extends to the Devonian (380 million years before present) (SCHAWALLER *et al.* 1991). Therefore, extremely old biogeographic elements are to be expected amongst at least some clades that have persisted to the Recent. In addition, many pseudoscorpion groups are considered to have extremely low vagility, despite the use of dispersal techniques such as phoresy and rafting by some groups.

This paper attempts to review those pseudoscorpion taxa considered to have originated on the supercontinent Gondwana prior to it's breakup during the Creta-

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ceous, and to highlight several distinct biogeographic patterns recognised amongst the pseudoscorpions of the southern hemisphere.

To qualify as a suspected Gondwanan relict, the known distributions of the taxa considered here were critically examined, and only those taxa, or sister-taxa, that were found on one or more southern continental block were initially included. As pseudoscorpions generally have low powers of dispersal, disjunct continental distributions are normally best explained by continental drift, rather than recent dispersal events by rafting or phoresy.

THE CAST

This list of taxa here postulated to possess Gondwanan distributions is presented in the knowledge that relationships may change, which could alter their potential as Gondwanan representatives (e.g. see *Pycnodithella* and *Cordylochernes*). In addition, some groups which have beeen previously postulated with Gondwanan affinities are reassessed (e.g. Sternophoridae).

The higher classification follows HARVEY (1992) and full taxonomic listings with complete literature citations can be found in HARVEY (1991).

SUBORDER EPIOCHEIRATA

Superfamily **Chthonioidea**
Family Chthoniidae
Subfamily Chthoniinae
Austrochthonius Chamberlin

Numerous species of *Austrochthonius* have been described from South America, New Zealand, Australia and South Africa, where they may be particularly abundant in forest litter. *Austrochthonius* spp., or their purported relatives, have not been found in other portions of Gondwana (e.g. India). A related genus was briefly reported from Madagascar by HEURTAULT (1986).

Pseudochthonius Balzan

Species of this genus have been reported from litter and caves in South America (extending north to Mexico) and central and western Africa. The presence of species on relatively young islands such as the Galapagos (*P. galapagensis* Beier) suggest that dispersal has also occurred more recently.

Sathrochthonius Chamberlin

Species of *Sathrochthonius* have been reported from Australia, New Zealand, New Caledonia and South America, where they are found in leaf litter and caves. The most northerly record is from Venezuela (MUCHMORE 1989).

Pseudotyrannochthoniinae

Members of this unusual subfamily are currently placed in five genera and have been reported from numerous Gondwanan areas, as well as outside of the region.

These include *Pseudotyrannochthonius* (Australia, South America, eastern North America, east Asia), *Afrochthonius* Beier (southern Africa, Madagascar, Sri Lanka), *Allochthonius* Chamberlin (Japan, Korea), *Centrochthonius* Beier (montane regions of Central Asia) and *Selachochthonius* Chamberlin (southern Africa). The generic composition and relationships of this subfamily warrant much further analysis to determine true generic boundaries.

Family Tridenchthoniidae

Anaulacodithella Beier

This genus has been reported from southern Africa, Madagascar, eastern Australia, Lord Howe Island and New Caledonia, where it occurs in leaf litter.

Heterolophus Tömösváry

These heavily sclerotised pseudoscorpions are found in eastern Australia, South Africa and South America. The sole Australian species, *H. australicus* Beier, is infrequently collected (Harvey, unpublished data).

Pycnodithella Beier

Only two species of *Pycnodithella*, *P. abyssinica* (Beier) (Ethiopia) and *P. harveyi* Kennedy (eastern Australia) have been described, but they are dubious contenders for a Gondwanan relationship as there may be some doubt as to whether they are actually congeneric.

Superfamily **Feaelloidea**

Family Feaellidae

Feaella Ellingsen

The family Feaellidae has a distinctive distribution centered upon the Indian Ocean. Species of the sole genus *Feaella* have been found in sub-saharan Africa, Madagascar, Seychelles, India, Bangladesh, Sri Lanka and northwestern Australia.

Family Pseudogarypidae

Neopseudogarypus Morris

The sole species of *Neopseudogarypus, scutellatus* Morris, is only known from a single locality in northern Tasmania. Individuals occur on the underside of rocks, especially those that are not fully embedded in the soil (Harvey, unpublished data). The only other living members of the family (*Pseudogarypus*) occur in northern North America (BENEDICT & MALCOLM 1978), although three additional species have been described from Baltic Amber, indicating that they were formerly much more widely distributed.

Although this genus, or any other pseudogarypid, has not yet been found on any other Gondwanan element, the presence of *Neopseudogarypus* in Tasmania is

clearly the result of a vicariant event predating the breakup of Gondwana, and possibly even of Pangea.

SUBORDER IOCHEIRATA

Superfamily **Neobisioidea**

Family Gymnobisiidae

This small family consists of only 4 genera and 11 species. Three genera (*Beierobisium* Vitali-di Castri, *Mirobisium* Beier and *Vachonobisium* Vitali-di Castri) are found in southern South America (including the Falkland Islands), while the remaining genus (*Gymnobisium* Beier) is restricted to southern Africa (VITALI-DI CASTRI & CASTRI 1970).

Family Hyidae

This family was recently relimited by HARVEY (1993) to include only three genera with 9 species from southeast Asia and Sri Lanka (*Hya* Chamberlin), northwestern Australia, India and Madagascar (*Indohya* Beier and *Hyella* Harvey). Although at least one species of *Hya* is widespread in southeast Asia and appears capable of considerable dispersal, it is clear that species of *Indohya* and *Hyella* are much more restricted in distribution, and possess vicariant distributions resulting from continental drift.

Family Syarinidae

Several genera of Syarinidae occur within Gondwanan areas, although most belong to widespread genera (or are closely related to these genera), which indicates that they are capable of widespread dispersal. However, the presence of an undescribed syarinid genus in Tasmania, which appears to represent the sister-group to *Syarinus* Chamberlin, is of considerable interest. Species of *Syarinus* are only known from North America (Canada and U.S.A. as far south as New Mexico) and northern Europe (Austria, Finland, Germany, Norway).

Other syarinid genera, such as *Ideobisium* Balzan, are known from continental blocks in tropical regions (extending as far south as New Zealand), and may qualify for status as a Gondwanan genus. Further work on the relationships and distribution of genera within the Syarinidae are needed to test these hypotheses.

Superfamily **Garypoidea**

Family Garypidae

HARVEY (1992) recently restricted this family to *Garypus* L. Koch and a series of genera centred around *Synsphyronus* Chamberlin. Although the former are widespread in the tropical and subtropical littoral zones, the latter possess a characteristic Gondwanan distribution.

Species of *Anagarypus* Chamberlin have been reported from sea-shore habitats bordering the Indian Ocean, as far east as the Great Barrier Reef, Queensland, Australia. The genus *Synsphyronus* Chamberlin is widespread in Australia and New Zealand, and has been recently collected from New Caledonia (Harvey, unpublished data). The remaining 'synsphyronines' (listed by HARVEY 1992) occur in southern and eastern Africa, as far north as Kenya (*Thaumastogarypus mancus* Mahnert).

Family Geogarypidae

Geogarypus Chamberlin

Geogarypids are generally tropical or temperate pseudoscorpions, with little evidence of Gondwanan affinities. However, the *Geogarypus bucculentus* species-group, characterized by HARVEY (1987), has a strong Gondwanan connection, with species found in Argentina and Chile (*G. pustulatus* Beier), Juan Fernandez Islands (*G. bucculentus* Beier) and southeastern Australia (*G. connatus* Harvey). The presence of a species on Juan Fernandez Islands indicates at least some capacity for dispersal, as the island group are of recent volcanic origin and estimated to be only 4 million years old (see discussion in HARVEY 1987). *Afrogarypus* spp. have been recorded from Africa, Madagascar and Seychelles (M. Judson, pers. comm.).

Superfamily **Olpioidea**

Family Menthidae

The disjunct distribution of the Menthidae (see VITALI-DI CASTRI 1969; HARVEY & MUCHMORE 1990) raises questions over its biogeographic origins, and there is a possibility that the family has a Gondwanan origin. However, more collections are needed to test this hypothesis, and the family has been excluded from Table 1.

Family **Olpiidae**

Subfamily Olpiinae

Austrohorus Beier and *Horus* Chamberlin

These genera were cited by MAIN (1981) as an example of a Gondwanan group, based upon BEIER's (1966) assertion that the two genera are sister-groups. Although this is probable, a more thorough review of the Olpiinae will be needed to test BEIER's hypothesis.

Superfamily **Sternophoroidea**

Family Sternophoridae

The generic composition of the Sternophoridae was relimited by HARVEY (1985) to three genera (*Afrosternophorus* Beier, *Garyops* Banks and *Idiogaryops* Hoff), and it was suggested that the group may have had its origins in Gondwana.

However, HARVEY (1985) cited several problems with that hypothesis (e.g. lack of South American records), and a Gondwanan origin now appears unlikely, hence the family has not been included in Table 1.

TABLE 1

Synopsis of Gondwanan pseudoscorpions.

	Australia	New Guinea	New Zealand	New Caledonia	South America	Africa	Madagascar	Seychelles	India/ Sri Lanka	Comments
CHTHONIDAE										
Austrochthonius	+	–	+	–	+	–	–	–	–	
Sathrochthonius	+	–	+	+	+	–	–	–	–	
Pseudochthonius	–	–	–	–	+	+	–	–	–	
Pseudo-tyrannochthoniinae	+	–	–	–	+	+	–	–	–	Other members in central and east Asia, North America
TRIDENCHTHONIDAE										
Anaulacodithella	+	–	–	+	–	+	+	–	–	
Heterolophus	+	–	–	–	+	+	–	–	–	
Pycnodithella	+	–	–	–	–	+	–	–	–	
FEAELLIDAE										
Feaella	+	–	–	–	–	+	+	+	+	
PSEUDOGARYPIDAE										
Neopseudogarypus	+	–	–	–	–	–	–	–	–	Sister-group in northern hemisphere
GYMNOBISIIDAE										
Gymnobisium	–	–	–	–	–	+	–	–	–	
All other genera	–	–	–	–	+	–	–	–	–	
HYIDAE										
Indohya	+	–	–	–	–	–	+	–	+	
SYARINIDAE										
Undescribed genus	+	–	–	–	–	–	–	–	–	Sister-group in northern hemisphere.
GARYPIDAE										
Anagarypus	+	–	–	–	–	+	–	–	+	Littoral zone
Synsphyronus	+	–	+	+	–	–	–	–	–	
Other 'synsphyronines'	–	–	–	–	–	+	+	–	+	
GEOGARYPIDAE										
Geogarypus bucculentus species-group	+	–	–	–	+	–	–	–	–	
Afrogarypus	–	–	–	–	–	+	+	+	–	
CHELIFERIDAE										
Philomaoriinae *(Philomaoria)*	–	–	+	+	–	–	–	–	–	Also Lord Howe Is.
Protochelifer	+	–	+	–	–	–	–	–	–	
CHERNETIDAE										
Goniochernetinae	+	–	–	–	–	+	–	–	–	
Americhernes	+	–	–	–	+	–	–	–	–	Also some Pacific Islands
Condylochernes	+	–	–	–	+	+?	–	–	–	
WITHIIDAE										
Nesowithius	–	–	–	–	–	+	+	+	–	

Superfamily **Cheliferoidea**

Family Cheliferidae

Protochelifer Beier

Species of *Protochelifer* have been reported from Australia and New Zealand, where they are mostly confined to temperate leaf litter or under three bark. Two species appear to be obligate cavernicoles.

Family Chernetidae

Subfamily Chernetinae

Myrmochernes Tullgren, *Xenochernes* Feio and *Marachernes* Harvey

This group was recently recognised by HARVEY (1994) and accorded tribal status (Myrmochernetini), at least until further phylogenetic work has been completed on the 'chernetines', an extremely large group of chernetids which are currently lacking synapomorphies. *Myrmochernes* (South Africa) and *Xenochernes* (Brazil) were clearly shown to be sister-groups, although the position of *Marachernes* (southern Australia) was considered more tenuous.

Cordylochernes Beier

Species of *Cordylochernes* have been reported from South America (as far north as Mexico), northwestern Australia and South Africa. However, the apparent Gondwanan origin for the genus should be treated very cautiously, as the sole South African species, *C. octenoctus* (Balzan), was probably mislabelled (VACHON 1942), and the sole Australian species, *C. dingo* Harvey, may be misplaced (HARVEY 1990).

Heterochernes Beier

BEIER (1976) stated that the monotypic New Zealand genus *Heterochernes* was related to *Dinocheirus* Chamberlin, which at that time was known only from the Americas (it has since been reported from Europe - see references in HARVEY 1991). This relationship has not been tested by examination of the female spermathecae, and I am unwilling to ascribe a Gondwanan relationship to *Heterochernes* until this has been carried out.

Reischekia Beier

This genus is known only from three species with disjunct distributions (*R. coracoides* Beier and *R. exigua* Beier from New Zealand and *R. papuana* Beier from Irian Jaya), and I have not found any further species in Australia or other Gondwanan regions. However, local extinctions may have occurred over a previously wider distribution, and the genus may qualify as an ancient lineage dating back to the breakup of Gondwana.

Subfamily Goniochernetinae

Four genera are currently thought to constitute the Goniochernetinae (*Calymmachernes* Beier, *Conicochernes* Beier, *Goniochernes* Beier and *Metagoniochernes*

Vachon), although HARVEY (1995) has tentatively questioned the supposed monophyly of the subfamily. *Calymmachernes* and *Conicochernes* occur in Australia, *Goniochernes* in central and western Africa, and *Metagoniochernes* in central Africa, Madagascar and Japan.

Family Withiidae

Nesowithius Beier

This genus has been reported from Africa and the Seychelles (see references in HARVEY 1991), and was reported from Madagascar by HEURTAULT (1986). Despite the possibility that at least one species can be distributed anthropogenically (MAHNERT 1988), this genus seems a logical candidate for inclusion as a Gondwanan element.

RECURRING PATTERNS

The most familiar patterns concerning the Gondwanan pseudoscorpion fauna is the presence of groups with 'traditional' gondwanan distributions encompassing South America, Australia, New Zealand, South Africa, and occasionally Madagascar and New Caledonia, with their complete absence from other regions. These include *Austrochthonius*, *Sathrochthonius* and *Heterolophus*.

Some groups are less widely distributed and are currently thought to be restricted to only two or three Gondwanan fragments. Examples include:

- South America and Africa: Gymnobisiidae and *Pseudochthonius*.
- Africa and Madagascar: *Afrogarypus* and *Nesowithius*.
- Africa and Australia *Pycnodithella* and Goniochernetinae.
- South America and Australia: *Geogarypus bucculentus* species-group and *Americhernes* (also extending into North America and found on some Pacific islands).
- Australia and New Zealand: *Protochelifer*.
- New Zealand and New Caledonia: *Philomaoria*.

HARVEY (1996) discussed the unusual distributions of several groups occurring around the rim of the Indian Ocean (western Australia, India, southern Africa and Madagascar), but which are generally lacking from eastern Australia, New Zealand and South America. These include the Feaellidae, Indohyinae (Hyidae) and the 'synsphyronines' (Garypidae), as well as several other arthropod groups such as *Moggridgea* (Araneae: Migidae) (MAIN 1991), *Archaeochlus* (Diptera: Chironomidae) (CRANSTON *et al.* 1987) and the Opilioacarida (Acari) (HARVEY 1996). These seem to signify a significantly different Gondwanan element.

Three other pseudoscorpion groups may represent Pangeal remnants, highlighting extremely ancient divergence dates. These include the Pseudogarypidae (Tasmania and North America, with Baltic Amber fossils) and the clade *Syarinus* (North America, Europe) + undescribed genus (Tasmania). To date, these groups have only been found in one Gondwanan region (Tasmania) but they may have either become extinct other southern continents or have not yet collected in these regions. Other pseudoscorpion groups may possess modern distributions that are the result of

Pangeal origins (e.g. Pseudotyrannochthoniinae), but do not appear to be as clearcut as the two highlighted here.

It is apparent from this brief summary that many pseudoscorpion taxa possess modern distributions that qualify them as candidates for old Gondwanan relicts that evolved prior to the breakup of Gondwana during the Cretaceous. However, the pseudoscorpion fauna of the southern temperate regions is still poorly known, even at the generic level, and much further work is needed to fully understand these fascinating regional faunas and their interrelationships.

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