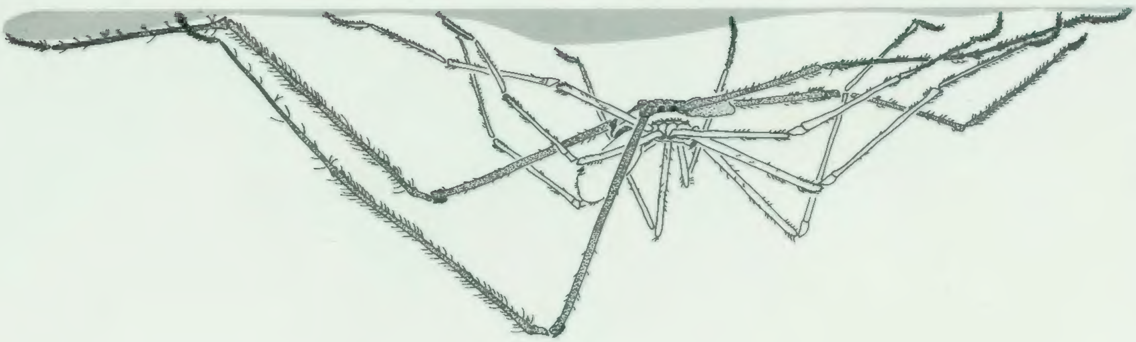
PROCEEDINGS

OF THE

XII INTERNATIONAL CONGRESS OF ARACHNOLOGY



BRISBANE
11 NOVEMBER, 1993

MEMOIRS OF THE
QUEENSLAND MUSEUM

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PART 2

PREFACE

The preparation for this International Congress was superbly managed by two Organising Committees. All members worked very hard and I am very grateful for their cooperation. The Western Australian Museum was the centre of the Scientific and Publications Committee of Dr Mark S. Harvey, Dr Bill F. Humphreys, and Dr Barbara York Main. This group, lead by Mark Harvey, formed a fine team who very capably managed all scientific and publication matters from manuscript submission to acceptance through the Congress program and photographic awards.

The local Organising Committee included Dr Valerie Davies (Secretary), and Ms Tracey Churchill, Ms Jan Green, Ms Judy Grimshaw, Mr Phil Lawless and myself. That group managed diverse aspects of Congress organisation. Mr David Nebauer assisted committee members during the registration process. My preparation was initially assisted by Ms Julie Gallon. In July 1991, Mr Philip Lawless took up the reins from Julie and proved to be a very dedicated and astute lieutenant. Emeritus Professor George Davies assisted the Secretary throughout the entire Congress period.

Delegates from Russia, Kazakhstan, The People's Republic of China, Madagascar, Mexico, Hungary, India, Belgium, North America, Germany, and Namibia were provided with varying degrees of sponsorship by the Queensland Museum Board of Trustees and sponsors. Their travel arrangements, often highly complex and problem-rich, were very capably managed by Ms Joanne Lavelle, then of State of Corporate Travel. Many a Congress delegate will no doubt fondly remember the Committee reception at the International airport. Several appreciated the kind hospitality of Mr Tony Luck, Microrim (Australia), of Camira, in an 'Aussie barbeque' before the Congress.

Organisation of the Post-Congress tour to Cape Tribulation, was greatly facilitated by the much appreciated contributions of Ms Linda Stanley, Ms Esther Cullen, and Cliff and Gail Truelove.

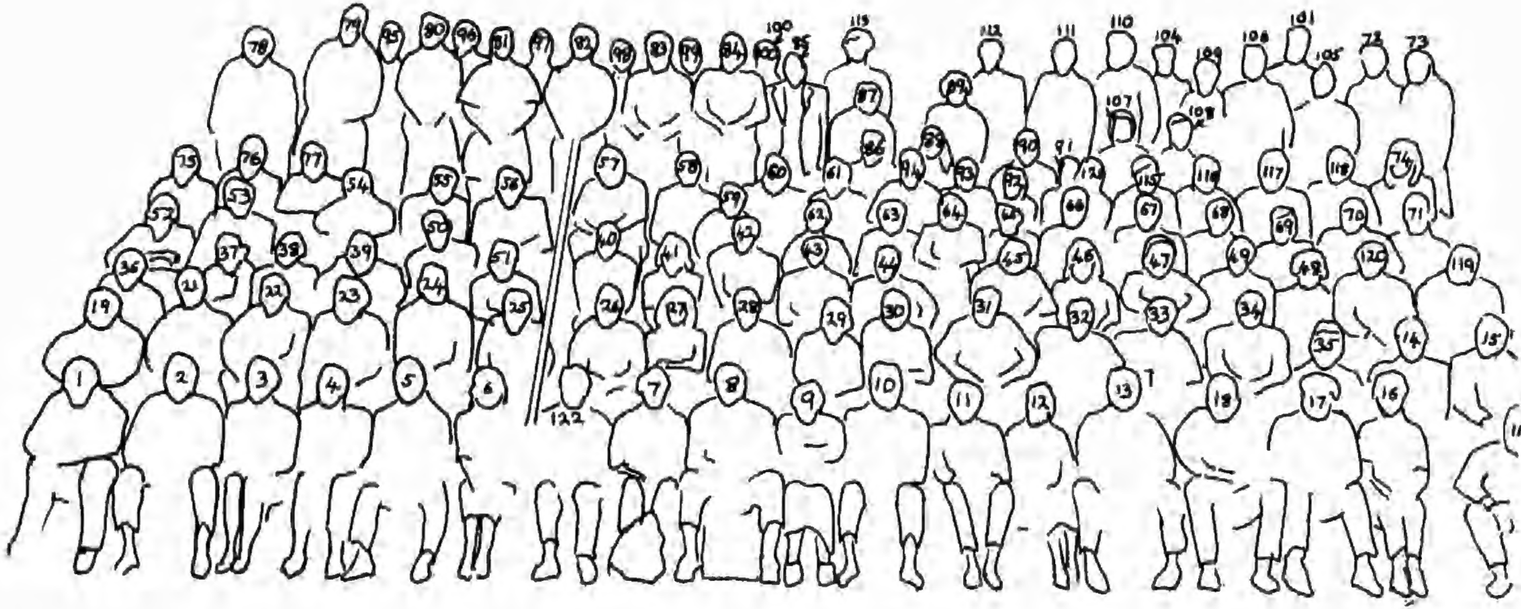
Editorial assistance was provided by Ms Gudrun Sarnes, Philip Lawless and Mr Neale Hall.

The Congress organisers very gratefully acknowledge the financial donations of Australian Geographic Magazine, Western Australian Museum, Amalgamated Pest Control, Australian Museum, Museum of Victoria, South Australian Museum, Commonwealth Bank, University of Queensland–Entomology & Zoology Departments, Griffith University–School of Australian Environmental Sciences, QANTAS Airlines, Australasian Arachnological Society, CSIRO, Division of Entomology, and the British Council. Financial support was also received from International Conference Support (loan) and the Australian Tourist Commission. The Queensland Museum Board of Trustees provided generous support for the Congress and the publication of these proceedings.

Robert J. Raven
Chairman, XIIth International Congress of Arachnology

October 11, 1993

Chairman: Dr Robert Raven.



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PROCEEDINGS OF THE XII INTERNATIONAL CONGRESS OF ARACHNOLOGY

FOSSIL ARACHNIDS–RECENT ADVANCES AND FUTURE PROSPECTS

PAUL A. SELDEN

Selden, P.A. 1993 11 11: Fossil arachnids–recent advances and future prospects. *Memoirs of the Queensland Museum* **33**(2): 389-400. Brisbane. ISSN 0079-8835.

Until 5 years ago, the arachnid fossil record was sparse. It was dominated by a comparative wealth of forms in Carboniferous Coal Measure sediments, and near-modern forms from Palaeogene Baltic amber. Both these relatively well-documented sources and the few reported finds elsewhere in the record suffered from erroneous interpretations. In recent years, new interpretations of existing fossils and a few spectacular new finds have filled in the gaps in the record and changed our knowledge and views of the course of arachnid evolution. Particular examples are: Devonian pseudoscorpions and spiders, book-lungs in Carboniferous scorpions, Triassic mygalomorph spiders, and Jurassic and Cretaceous araneomorph spiders. Phylogenetic systematic analyses of extant arachnids have produced evolutionary scenarios which conflict with the observed fossil record in parts. The newly expanded knowledge of the fossil record allows better tests for the cladograms. Future work on reinterpretation of known Carboniferous and Palaeogene fossils, on rare Mesozoic arachnids, and on arachnids in the earliest known terrestrial ecosystems in the Silurian will add to our knowledge of the fossil record of the arachnids and further enhance testing of phylogenetic hypotheses.□*Aglaspidida, Arachnida, Chelicerata, palaeontology, phylogeny, Pycnogonida.*

Paul A. Selden, Department of Geology, University of Manchester, Manchester M13 9PL, United Kingdom; 10 November, 1992.

For most of this century, one name dominated the literature on fossil arachnids, that of Alexander Petrunkevitch (1875-1964). Petrunkevitch (1955; in Størmer, 1955) summarized the arachnid fossil record to mid-century (Fig. 1) in the 'Treatise on Invertebrate palaeontology' and although he published on amber spiders after 1955, the broad view of the fossil record of chelicerates remained little changed until about a decade ago. Few workers either published on fossil arachnids or disputed Petrunkevitch's assignments during his lifetime. Only recently, during restudy of the fossils, have many errors and misinterpretations in his work come to light.

In the fossil chelicerate record published in the 'Treatise' (Fig. 1), the Merostomata (essentially aquatic chelicerates) are separated from the Arachnida. Second, most of the arachnid side consists of dashed lines converging towards the base of the Cambrian, indicating lack of fossil record and uncertainty of affinities respectively. Third, apart from one dubious palpigrade and some scorpions, there are no other records of Mesozoic (Triassic-Cretaceous) arachnids. Fourth, there is a clear pattern in the temporal distribution of the fossils: a concentration of records in the Upper Carboniferous, and many modern groups also occur in the Palaeogene (early Tertiary). The former records are from the Coal Measures of Europe and North America, for example: Mazon Creek, Illinois; Coseley, England; and Nyrany, Czechoslovakia. The Palaeogene occurrences are mainly from Baltic amber. Although Trigonotarbida and a questionable record of Araneae had been known from the Devonian Rhynie Chert of Scotland since Hirst (1923), they were omitted from the diagram. (In addition, Petrunkevitch knew of undescribed Lebanese amber opilionids and some Cretaceous spiders from Manitoban amber).

Petrunkevitch developed theories on the evolution of arachnids, which resulted in his superordinal classifications of 1945 and 1949. He recognized a number of 'evolutionary trends', such as the movement of the mouth rearwards from the Xiphosura to the arachnids, and the reduction of the metasoma to a tail or pygidium. One of the most important characters used in his classifications is the width of the connection between prosoma and opisthosoma, i.e. reduction of the first abdominal somite to a pedicel. Petrunkevitch (1945) divided the class Arachnida into two subclasses, Latigastra and Caulogastra, on the basis of a broad or a narrow prosoma-opisthosoma connection respectively. Later, Petrunkevitch (1949) added the subclass Soluta to the scheme to include solely his new order Trigonotarbida which he considered exhibit both wide and narrow junctions. Another subclass, the

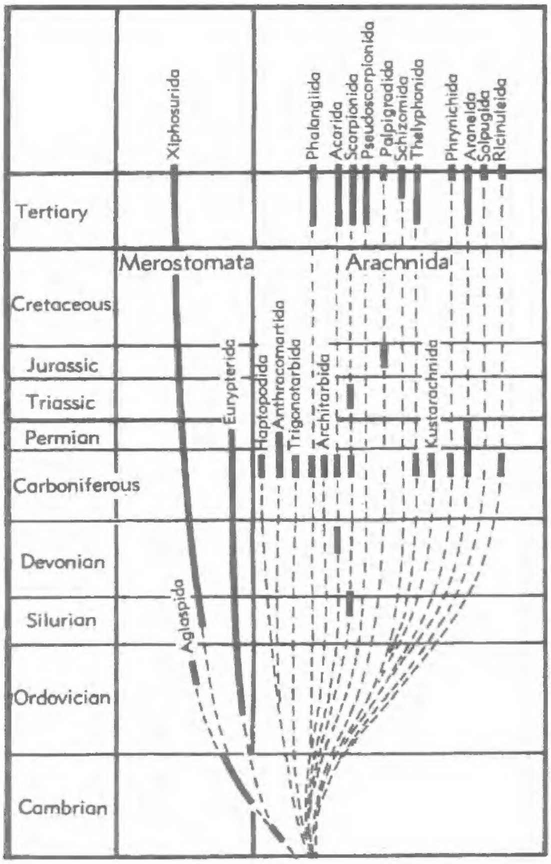


FIG. 1. Stratigraphic ranges of Chelicerata and Aglaspidida and presumed phylogenetic relationships (from Størmer, 1955).

Stethostomata, was created at this time to accommodate the orders Anthracomartida and Haptopoda which supposedly have a broad prosoma-opisthosoma junction and a unique coxosternal region. Petrunkevitch's (1949) classification scheme, used in the 'Treatise', has not stood the test of time. Weygoldt and Paulus (1979) noted its use in some textbooks but pointed out severe deficiencies in the scheme when other characters are taken into account.

Petrunkevitch was a devout proponent of the idea of the 'decoupling' of macroevolution and microevolution. He envisaged major features (those which define higher taxa) originating by mutation or other accelerated evolution, whereas minor morphological differences (those which separate species, for example) could provide only long, slow evolution and rarely produced higher taxa (Petrunkevitch, 1952, 1953). Petrunkevitch (1955) envisaged extinction occurring when irreversible evolutionary trends took groups down blind alleys–useful trends which proved lethal when taken to extreme or when environmental conditions changed. Characters could therefore be described as 'major' or 'minor', depending on the taxonomic rank they diagnose. Provided the 'rank' of a character is not decided *a priori*, there is no problem; however, difficulties arise when character states do not clearly change at taxon boundaries. For example, in a diagnosis of the subclass Soluta Petrunkevitch, 1949 is: 'abdomen composed of 8 to 11 segments' (Petrunkevitch, 1955, p. P107). Petrunkevitch described this variability as the character being in a 'labile' state. So, the subclass Soluta is diagnosed on the *labile condition* of the abdominal segmentation, the presence of *either* a broad *or* a narrow junction between the opisthosoma and prosoma (see above), and the *overall resemblance* of the coxosternal region to that in spiders [my italics]. Petrunkevitch (1955) argued that solutes are not spiders because of the combination of characters in the group, and additionally they showed a single series of marginal plates on the opisthosoma. Obviously, such a group could also be considered a collection of quite different animals placed together through their shared possession of a spider-like coxosternal region.

Restudy of fossil solutes reveals that the problem lies mainly in Petrunkevitch's inability to correctly interpret fossil material. The number of segments in the Soluta is invariably 11 (Shear *et al.*, 1987) but the number Petrunkevitch interpreted in each specimen differed according to its preservation. Thus, where a 2-segmented pygidium was preserved, then 2 additional segments were counted over specimens which did not preserve this organ, and the short first abdominal segment is not always visible in fossils. Similarly, the interpretation of the prosoma-opisthosoma junction depended on how closely these tagmata were conjoined in the fossil.

Petrunkevitch described *Trigonomartus pustulatus*, and noted (1913, p. 104): 'The cephalothorax being much harder, kept more or less its shape, and what appears on it as a median crest was in reality a median groove. The irregular, polygonal depressions were evidently thickened areas of the chitin and formed in life low elevations.' But, two pages before he had diagnosed the new genus thus: 'Carapace triangular with a median crest in the posterior half, covered with irregular polygonal depressions.' Thus he had recognized that the fossils were external moulds but diagnosed the genus as if they were casts. The error perpetuated until 1955 when, in the 'Treatise' (p. P112), the diagnosis became 'Carapace triangular, high, with median crest and a pustulose surface, without eyes. Abdomen with pustulose surface.' Thus, pustules were recognized but the median crest remained, without explanation for the emendation. Furthermore, eyes exist in *Trigonomartus* (Petrunkevitch, 1913, pl. 9, fig. 49, in the same place as in *Aphantomartus* (Pocock 1911, Pl. II, fig. 6). These two genera were synonymized by Selden and Romano (1983). As well as misinterpreting fossils, Petrunkevitch produced some illogical taxonomic arguments. In 1945, he erected the Aphantomartidae for eophrynids with 7 abdominal tergites (i.e. *Aphantomartus areolatus* Pocock, 1911). In 1949, he erected the Trigonomartidae, and, recognizing that *Aphantomartus* had 8 abdominal tergites, not 7, he stated (p. 256): 'This means that the Family Aphantomartidae becomes a synonym of Trigonomartidae, the number of abdominal segments having served as the only character of distinction.' Why not place the contents of the new 'Trigonomartidae' in the existing Aphantomartidae? Aphantomartidae has priority and was redefined by Selden and Romano (1983). Furthermore, illustrations purporting to differentiate *Aphantomartus* and *Trigonomartus* (Petrunkevitch 1955, figs 80, 1 and 3) are unrepresentative and merely emphasise different characters of the same genus. Fig. 80, 3 is not *Aphantomartus areolatus*, as stated in the text, but a copy from Pruvost (1919, fig. 42) of *A. pococki*, with eyes drawn on incorrectly!

Consider also the Phalangiotarbida. Kjellesvig-Waering redescribed this group just before his death in 1979, and the MS was being prepared for posthumous publication (see Kjellesvig-Waering, 1978). In the MS, Kjellesvig-Waering, a renowned taxonomic 'splitter', reduced Petrunkevitch's 10 genera and 13 species to four genera and five species. He stated in the introduction to his MS: 'Seldom, if ever, has a fossil group with such uncomplicated, mostly easily determinable morphological characters, been subjected to such misunderstanding and careless and erroneous work as has the order Phalangiotarbida Haase, 1890. The main reason for this state has been the complete failure of some of the workers in this group to understand fundamental paleontological principles of preservation, for example, molds and casts, external and internal, along with results of compaction and consequent reflection or impression of ventral into dorsal surfaces and vice versa.' Kjellesvig-Waering's conclusions on functional morphology and phylogeny, both in this MS and his other work, are not without dispute, but his long experience with the taxonomy of fossil chelicerates was generally reliable. Kjellesvig-Waering wrote in his MS: 'The question of whether Phalangiotarbida Haase, 1890, or Architarbida Petrunkevitch, 1945 is the proper name for this order of arachnids has not been settled, although it is difficult to understand why any question should have arisen in the first place.' What Petrunkevitch did was to substitute an existing name with one based on better preserved specimens of the order: 'What is more reasonable than to regard the Family Architarbidae as the most characteristic one of the Order and to emphasize this fact by using a proper derivative of the generic name for the Order?' (Petrunkevitch, 1945, p. 11).

The above examples show that much work is needed on fossil arachnids already in collections, in addition to study of the many new fossils awaiting description.

THE FOSSIL RECORD
(Fig. 2)

Arachnid Relatives

The extinct aglaspidids are probably not chelicerates since they bear neither chelicerae nor other features which would ally them with the Chelicerata over any other arthropod group (Briggs *et al.*, 1979). The fossil record does not help to determine the systematic position of the enigmatic pycnogonids. Chelicerae are not a prerequisite for a chelicerate. *Sanctacaris* Briggs and Collins, 1988 from the Middle Cambrian Burgess Shale of British Columbia lacks chelicerae but was included in the phylum because of a combination of characters unique to Chelicerata: six pairs of prosomal appendages, cardiac lobe, prosoma and opisthosoma, and anus at rear of last trunk segment. *Sanctacaris* was described as sister to all other chelicerates, but may not be the oldest chelicerate because a dubious xiphosuran carapace of Lower Cambrian age, *Eolimulus alatus* (Moberg, 1892) was recorded from Öland, Sweden. Xiphosura are the most primitive chelicerates in existence and, though previously allied with the Eurypterida in the Merostomata, most authors place Xiphosura with either the Scorpionida (Bergström, 1979, 1981; Bergström *et al.*, 1980; van der Hammen, 1985, 1986) or as sister to all other chelicerates (except

Sanctacaris) (Grasshoff, 1978; Boudreaux, 1979; Paulus, 1979; Weygoldt and Paulus, 1979; Weygoldt, 1980), thereby rendering Merostomata an unnatural group.

SCORPIONS

Scorpions are the arachnid group with the earliest known ancestors; the most ancient known scorpion is *Dolichophonus loudonensis* (Laurie, 1889) from the Llandovery of the Pentland Hills, near Edinburgh, Scotland. Kjellesvig-Waering (1986) proposed a controversial classification scheme. Stockwell (1989) produced a more acceptable classification scheme of Scorpionida which included fossils, but it has yet to be published formally. A linchpin of Kjellesvig-Waering's classification was the supposed Devonian gilled scorpion described as *Tiphoscorpio hueberi*. Restudy of this material (Selden and Shear, 1992) revealed that it is not a scorpion but an arthropleurid myriapod!

The early Silurian record of scorpions could be interpreted as representing the earliest terrestrial animals since all modern scorpions are terrestrial. However, all Silurian fossil scorpions occur in marine or marginal marine sediments, and morphological features suggest an aquatic mode of life. Petrunkevitch (e.g. 1953) considered all fossil scorpions were terrestrial, but other workers (e.g. Wills, 1947; Stormer, 1970; Rolfe and Beckett, 1984; Kjellesvig-Waering, 1986) argued for an aquatic habitat for Silurian scorpions at least. Evidence for aquatism among fossil scorpions are: gills and digitigrade tarsi, as well as the absence of terrestrial modifications such as coxal apophyses, stigmata, book lungs, trichobothria, highly developed pectines and plantigrade tarsi. There is overlap in the ranges of aquatic and terrestrial scorpions but the first terrestrial forms probably appeared the Devonian (Selden and Jeram, 1989). It is not easy to decide whether a given fossil had an aquatic or terrestrial mode of life; the original environment of the enclosing sediment is commonly the best clue, but a recent find is worthy of especial note: well preserved book lungs in a Carboniferous (Visean) scorpion from East Kirkton, near Edinburgh, Scotland (Jeram, 1990). Few new records of fossil scorpions have turned up in recent years although in the otherwise sparsely recorded Mesozoic, scorpions reported from the Triassic of France (Gall, 1971), and the Cretaceous of Brazil (Campos, 1986) are currently under study.

PSEUDOSCORPIONIDA

Many pseudoscorpions are known from the Tertiary (mainly in ambers, e.g. listed in Schawaller (1982, table 1), and some are known from Cretaceous ambers of Lebanon (Whalley, 1980) and Manitoba (Schawaller, 1991). However, the most important fossil pseudoscorpions are well preserved specimens of *Dracochela deprehendor* (Shear *et al.*, 1989; Schawaller *et al.*, 1991), in the Upper Devonian mudstones of Gilboa, New York. Only protonymph and tritonymph are known which, though modern in many aspects, cannot be assigned with confidence to extant taxa because both diagnostic characters in the fossils and cladistic assessment of extant forms are lacking.

SOLIFUGAE

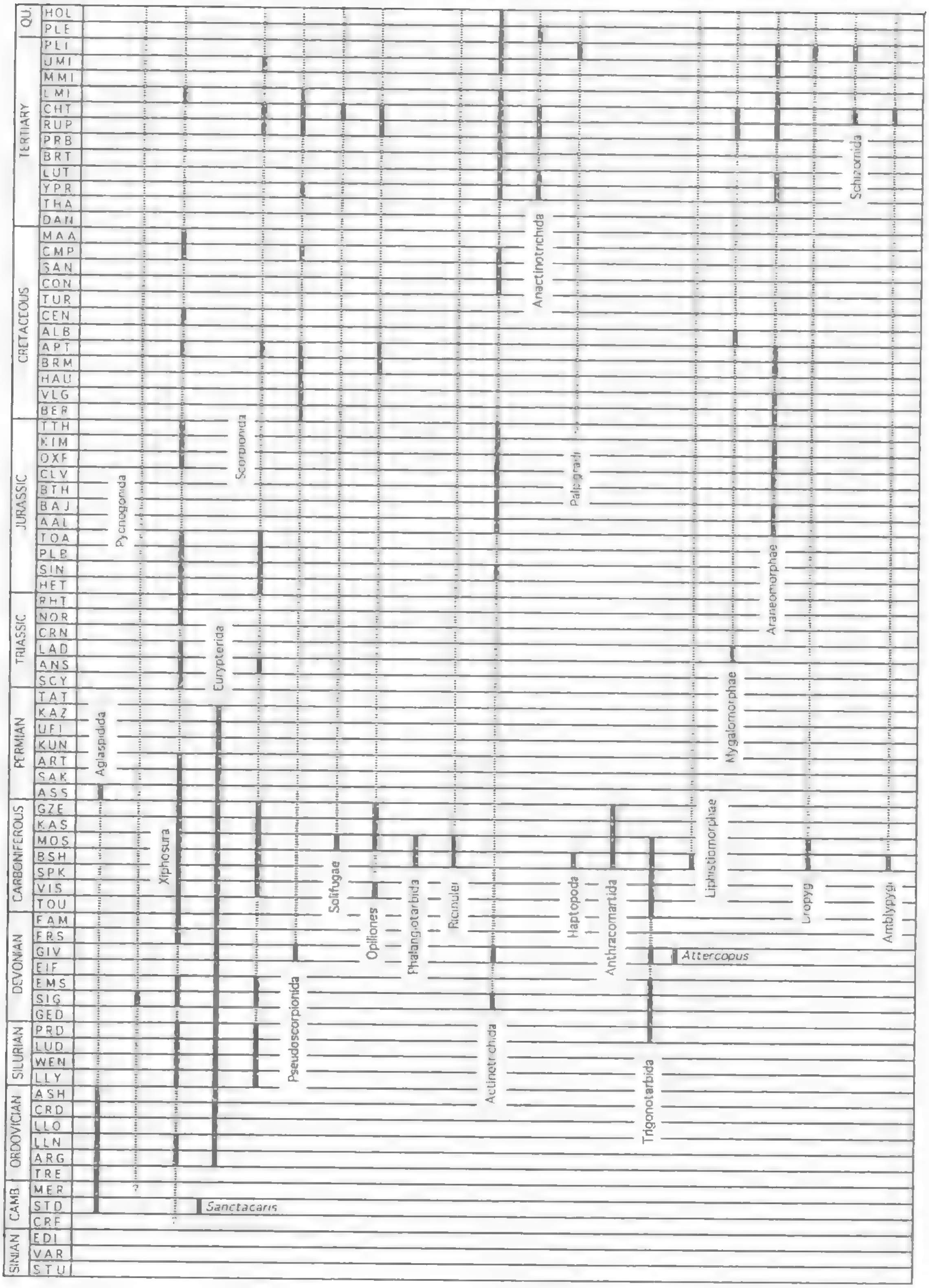
The Carboniferous solifuge, *Protosolpuga carbonaria* Petrunkevitch, 1913, was described as being in a very poor state of preservation. It is impossible to judge the validity of the identification from the published photograph and drawing. The only reliable fossil solifuge is *Happlodontus proterus* Poinar and Santiago-Blay, 1989, from Oligocene Dominican amber.

OPILIONES

Until recently, Opiliones had a fairly typical arachnid fossil record, being known only from Upper Carboniferous strata and Tertiary ambers. In 1985 a specimen was discovered in Lower Carboniferous rocks of East Kirkton, near Edinburgh, Scotland (Wood *et al.*, 1985), and a year later, one was described from the Lower Cretaceous of Koonwarra, Victoria, Australia (Jell and Duncan, 1986). Both of these unnamed specimens are long-legged opilionids but no further identification is possible (pers. obs.).

The order Kustarachnida Petrunkevitch, 1913 is included with the Opiliones, following Beall (1986).

FIG. 2. Current knowledge of the fossil record of Aglaspidida, Pycnogonida and Chelicerata; data in Selden (1993). Solid lines denote actual occurrence in the stage(s) concerned; interrupted lines indicate presumed occurrence in intervening stages. ? denotes doubtful record. Note that taxon ranks are not equivalent; occurrences of important genera *Sanctacaris* (most plesiomorphic chelicerate) and *Attercopus* (oldest and most plesiomorphic spider) are shown separately. Stratigraphic resolution is to stage; abbreviations in second column refer to standard stage names (see e.g. endpapers of Briggs and Crowther, 1990).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Pycnogonida
Xiphosura
Eurypterida
Scorpionida
Pseudoscorpionida
Solifugae
Opiliones
Phalangiotarbida
Ricinulei
Actinotrichida
Anactinotrichida
Palpigradi
Haptopoda
Anthracomartida
Trigonotarbida
Liphistiomorphae
Mygalomorphae
Araneomorphae
Uropygi
Schizomida
Amblypygi
Attercopus
Sanctacaris
?

Phalangiotarbida

The situation of the phalangiotarbids has been described above. This group is only known from the Upper Carboniferous but fossils are widespread in European and North American coalfields.

Ricinulei

Ricinulei are known only from the Upper Carboniferous of Europe and North America, and the New and Old World tropics at the present day (their range extends outside the tropics mainly by cavernicole species). A recent revision of the fossils (Selden, 1992) revealed a greater diversity in the Carboniferous than today, but based on an essentially similar body plan. It appears that the group has remained in warm, humid habitats (equatorial forest litter and caves) throughout its geological history.

Mites

The oldest mites are Actinedida (Prostigmata) from the Lower Devonian Rhynie Chert of Scotland (Hirst, 1923). Other Devonian Actinotrichida are known from Gilboa, New York (Norton *et al.*, 1988, 1989; Kethley *et al.*, 1989). A few Jurassic and Cretaceous Actinotrichida are known (e.g. Bulanova-Zakhavatkina, 1974; Krivolutsky and Ryabinin, 1976; Sivhed and Wallwork, 1978), but the majority of fossil mites are oribatids from Baltic amber (e.g. Koch and Berendt, 1854; Sellnick, 1918, 1931). Anactinotrichida are very poorly represented in the fossil record; there are no fossil Opilioacarida or Holothyrida and only a few, somewhat suspect, records of Ixodida (e.g. Scudder, 1890) and Gamasida (e.g. Hirschmann, 1971). Fossil mites are probably found routinely in palynological preparations but are unreported. With the growth of micropalaeontological techniques in the study of fossil arthropods it is likely that many more fossil mites will be identified.

Palpigradi

The preservation potential of palpigrades is even lower than that of mites. Their small size, thin cuticles and interstitial habitats makes them difficult objects of study when Recent or fossil. *Sternarthron zitteli* Haase, 1890, from the Jurassic lithographic limestone of Solnhofen, Germany, is doubtful; the only good fossil palpigrade is *Palaeokoenenia mordax* Rowland and Sissom, 1980, from the 'Onyx Marble' quarries (Pliocene) of Arizona.

Haptopoda

This monotypic order was established by Pocock (1911) on the basis of the subdivided tarsus of the first leg. Petrunkevitch (1949) cleaned and reexamined the specimens, and redefined the order based on a new interpretation of the abdominal segmentation. The group would repay restudy along with Anthracomartida and Trigonotarbida.

Anthracomartida

Together with Haptopoda, this order forms Petrunkevitch's 1949 subclass Stethostomata. In a discussion of the rationale for separating Stethostomata from Soluta (Shear and Selden, 1986; Shear *et al.*, 1987), it was concluded that the only feature separating anthracomartids from trigonotarbids is two versus one rows of marginal tergal plates on the opisthosoma. Again, this common Upper Carboniferous group needs careful restudy.

Trigonotarbida

Trigonotarbids are the best known extinct arachnid group on account of their excellent preservation in the Devonian Rhynie Chert of Scotland and Gilboa mudstones of New York and are among the first known land animals (Jeram *et al.*, 1990). First described from Upper Carboniferous rocks (Buckland, 1837; Fritsch, 1901; Pocock, 1902, 1903, 1911), Hirst (1923) described the first Devonian specimens (from Rhynie), and Størmer (1970) described forms from the Middle Devonian of Alken-an-der-Mosel, Germany. Trigonotarbida is one of the few arachnids groups found relatively frequently in Palaeozoic terrestrial rocks of from Argentina (Pinto and Hünicken, 1980), Spain (Selden and Romano, 1983), Czechoslovakia (Opluštil, 1985), and Germany (Jux, 1982).

The exquisite preservation of the Rhynie Chert meant that Hirst (1923) could describe minute details of the trigonotarbids from that deposit. Trigonotarbids from Gilboa (Shear *et al.*, 1987) not only confirmed Hirst's observations but also uncovered further morphological features of these interesting animals. Later work has shown that some of the species described as trigonotarbids in 1987 were really spiders or other pulmonate arachnids (Selden *et al.*, 1991), but the systematic position of the Trigonotarbida, sister to all other pulmonates, was strengthened. A trigonotarbid and centipedes, found together with early land plants in Silurian (basal Prídoli) sediments at Ludford Lane, Ludlow, England (Jeram *et al.*, 1990), pushed back the earliest record of land animals by around 16 million years and indicated that trigonotarbids were among the earliest terrestrial animals.

Araneae

Great strides have been made recently in spider systematics (Coddington and Levi, 1991) and concomitantly, new finds of fossil spiders have added to the geological record. The oldest spider is *Attercopus fimbriunguis* Shear, Selden and Rolfe, 1987, from Gilboa; supposed spiders from Rhynie (Hirst, 1923) and Alken-an-der-Mosel (Stormer, 1976) have been disproved (Selden *et al.*, 1991). *Attercopus* is sister to all other spiders; the patella-tibia joint is a rocking joint but in a more plesiomorphic state than other spiders, lacking the 'compression zone Y' of Manton (1977). Autapomorphies of the *Attercopus* clade are: fimbriate paired claws, spinules on the palpal femur, and lack of trichobothria; the latter feature is puzzling.

In spite of descriptions of Devonian and Carboniferous araneomorph spiders (Archaeometidae Petrunkevitch, 1949; Pyritaraneidae Petrunkevitch, 1953), none of those seen by the author could be proved to be a spider at all. Petrunkevitch seemed to concur with Fritsch (1904) and Pocock (1911) in their placement of fossils in the Araneomorphae without question, even if he disagreed with their detailed descriptions. All of these authors seemed to place fossils in Araneomorphae on the basis of their general resemblance to particular groups of araneomorph spiders rather than real characters. For example, Petrunkevitch (1953:107) defined Pyritaraneidae and redefined Arachaeometidae as araneomorph spiders with segmented opisthosomae, differing from each other by their laterigrade and prograde legs respectively. Nowhere is the identification as araneomorphs questioned. Eskov and Zonshtein (1990a) considered segmentation of the opisthosoma in the Pyritaraneidae to be an artifact, but agreed that this family belongs in Araneomorphae. Selden *et al.* (1991) studied *Archaeometa nephilina* Pocock, 1911 in the British Museum (Natural History) and a plaster cast of *A. devonica* Stormer, 1976 from the Senckenberg Museum, concluding that neither species was a spider and that *A. devonica* may not be an arachnid at all. Carboniferous Arthrolycosidae Fritsch, 1904 and Arthromygalidae Petrunkevitch, 1923 in the British Museum (Natural History) can be placed with the mesotheles because of the distinct tergites on their opisthosomae. Eskov and Zonshtein (1990b) argued for a new group of Carboniferous 'labidognathous liphistiomorphs' on the evidence that the fossils lacked chelicerae yet any spider with orthognath chelicerae would have them preserved if the carapace and palps were. This argument presupposes that orthognath chelicerae are always porrect, which they may not be. To argue morphology from preservation (or lack of it!) is a dangerous practice.

Until recently, no mygalomorph spider was known earlier than the Tertiary. Eskov and Zonshtein (1990a) described some mygalomorphs from Siberia and Mongolia, placing them in the modern Mecicobothriidae, Atypidae and Antrodiaetidae. They are exceptionally well preserved, but poorly illustrated and described; in contrast, the line drawings are of high quality. In 1992, with the description of a Triassic mygalomorph, *Rosamygale*, our knowledge of the antiquity of mygalomorphs was more than doubled (Selden and Gall, 1992). This was placed in the extant family Hexathelidae, and suggests a widespread distribution of the family across Pangaea before rifting of the supercontinent. Hexathelids show many plesiomorphic characters among mygalomorphs but nevertheless, mygalomorphs may yet be found in Palaeozoic rocks.

Mesozoic spiders have only recently been discovered. The oldest fossil araneomorph is *Juraraneus rasnitsyni* Eskov, 1984, placed in a new family, Juraraneidae, in the Araneoidea. *Juraraneus*, like the mygalomorphs described by Eskov and Zonshtein (1990a), is well preserved but rather poorly documented for such an important find, so it is difficult to be sure whether the placement is justified. Eskov (1987) has also described Archaeidae from the Jurassic of Kazakhstan from where Filistatidae are currently being described (Eskov, 1990).

Recent finds of Cretaceous araneomorphs have emphasized the diversity of a spider fauna of modern aspect during this period. Unfortunately, some show little morphological detail (Jell and Duncan, 1986), but Selden (1990a) described specimens from the Lower Cretaceous of north-east Spain, beautifully preserved in lithographic limestone. The specimens included a deinopoid and a tetragnathid, so both cribellate and ecribellate orb-web weavers were in existence at this time. In broad terms, by the Tertiary, the spider fauna was almost identical to that of today, and only 3 families are known to have become extinct since the Palaeogene (Eskov, 1990).

Uropygi

Well preserved uropygids are found in Coal Measure rocks in Europe (e.g. Brauckmann and Koch, 1983) and North America. All are placed in the modern Thelyphonidae.

Schizomida

Three species of schizomids are known from the Pliocene 'Onyx Marble' quarries of Arizona and one from the Oligocene of China (Lin *et al.*, 1988).

Amblypygi

Fossil amblypygi are known from the Coal Measures of Europe and North America and from Tertiary ambers (e.g. Schawaller, 1979). Amblypygi may be present in the Devonian of Gilboa: a possible pedipalp tarsus was figured by Shear *et al.* (1984) and *Ecchosis pulchribothrium* Selden and Shear, 1991 may belong in this group (Selden *et al.*, 1991).

ARACHNID PHYLOGENY

Selden (1990b) discussed three recent phylogenetic hypotheses with the evidence of the fossil record (Fig. 3). A cladogram which accurately reflects evolutionary events predicts that successive dichotomies should occur in ascending chronological order, and a complete fossil record should show this. Weygoldt and Paulus's (1979) analysis (Fig. 3c) predicts that palpigrades should occur in strata at least as old as Devonian because the more derived mites and pseudoscorpions occur in beds of that age. In their scheme, Opiliones occupy a derived position. Van der Hammen (1989; fig. 3b) suggested that Opiliones should occur the Cambrian since they are tentatively shown as sister group to Xiphosura + Scorpiones. Shultz (1989, 1990; Fig. 3a) also placed Opiliones in a position which predicts their presence in Silurian times. Since scorpions were aquatic then, so would opilionids have been.

None of the phylogenetic analyses (Fig. 3) incorporated extinct groups. Whilst it is impossible to include ancestors in cladistic analyses, there is no reason why well known extinct groups should not be included, say at the Carboniferous level. Apart from the enigmatic palpigrades and the highly derived Schizomida, for which fossil evidence is lacking, all arachnid orders were in existence by that time.

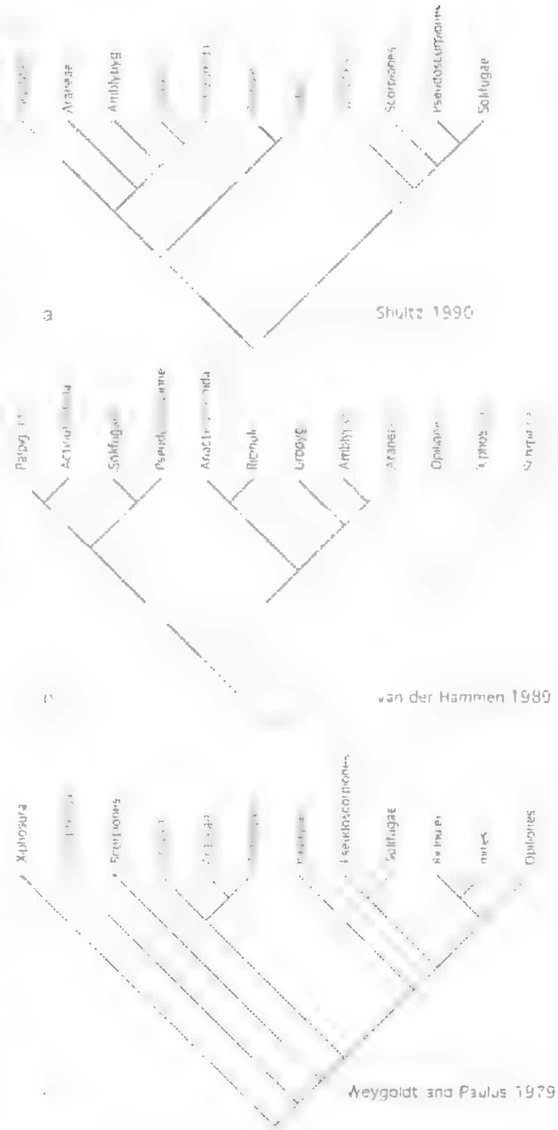

FIG. 3. Cladograms of relationships among the arachnid groups as viewed by a, Shultz (1990); b, van der Hammen (1989); and c, Weygoldt and Paulus (1979). Interrupted lines indicate uncertainty.

FUTURE PROSPECTS

Work in progress includes: palaeophysiology of early terrestrial chelicerates–aquatic and terrestrial adaptations in eurypterids, scorpions, and other Siluro-Devonian arachnids; palaeobiology of the Trigonotarbida; and Cretaceous spiders from Canadian amber and the Santana Formation of Brazil.

Much of Petrunkevitch's work needs revision. A new phalangiotarbid fauna has been collected in recent years from a coal mine tip in Somerset, England (Beall, 1991). Carboniferous Anthracomartida and Haptopoda need to be restudied, particularly in relation to the now extremely well known and possibly related trigonotarbids. The identity of described Amblypygi is in little doubt, but modern descriptions would be helpful. In need of critical examination are: the single fossil solifuge *Protosolpuga* from Mazon Creek, the supposed palpigrade *Sternarthron* from the Jurassic of Germany, and the amber spiders described by Petrunkevitch (e.g. 1942, 1950, 1958). The problem with these spiders is that over the years some of the supposed 'amber' in collections has discoloured, which suggests it may not be truly Palaeogene but rather more recent copal or other resins.

Successful palaeoarachnology requires knowledge of both Recent arachnids and understanding of styles of fossil preservation. Much previous work suffered from erroneous interpretations of one sort or another. Goals for future work are: to understand the origin of the present-day diversity of arachnids and the relationships among the various groups, and the reconstruction of ancient terrestrial ecosystems.

LITERATURE CITED

BEALL, B.S. 1986. Reinterpretation of the Kustarachnida. (Abstract). American Arachnology 34: 4.

1991. The Writhlington phalangiotarbids: their palaeobiological significance. Proceedings of the Geologists Association 102: 161-168.

BERGSTRÖM, J. 1979. Morphology of fossil arthropods as a guide to phylogenetic relationships. Pp. 3-56. In Gupta, A.P. (ed.) 'Arthropod Phylogeny'. (Van Nostrand Reinhold: New York).

1981. Morphology and systematics of early arthropods. Abhandlungen des Naturwissenschaftlichen Verein in Hamburg 23: 7-42.

BERGSTRÖM, J., STÜRMER, W. & WINTER, G. 1980. *Palaeoisopus*, *Palaeopantopus* and *Palaeothea*, pycnogonid arthropods from the Lower Devonian Hunsrück Slate, West Germany. Paläontologische Zeitschrift 54: 7-54.

BOUDREAUX, H.B. 1979. Significance of intersegmental tendon system in arthropod phylogeny and a monophyletic classification of Arthropoda. Pp. 551-86. In Gupta, A.P. (ed.) 'Arthropod Phylogeny'. (Van Nostrand Reinhold: New York).

BRAUCKMANN, C. & KOCH, L. 1983. *Prothelyphonus naufragus* n. sp., ein neuer Geißelscorpion [Arachnida: Thelyphonida: Thelyphonidae] aus dem Namurium (unteres Ober-Karbon) von West-Deutschland. Entomologia Generalis 9: 63-73.

BRIGGS, D.E.G., BRUTON, D.L. & WHITTINGTON, H.B. 1979. Appendages of the arthropod *Aglaspis spinifer* (Upper Cambrian, Wisconsin) and their significance. Palaeontology 22: 167-180.

BRIGGS, D.E.G. & COLLINS, D. 1988. A Middle Cambrian chelicerate from Mount Stephen, British Columbia. Palaeontology 31: 779-98.

BRIGGS, D.E.G. & CROWTHER, P.R. (eds). 1990. 'Palaeobiology: a synthesis'. (Blackwell Scientific Publications: Oxford, London, Edinburgh, Boston, Melbourne).

BUCKLAND, W. 1837. 'The Bridgewater treatises on the power, wisdom and goodness of God as manifested in the creation. Treatise IV. Geology and mineralogy considered with reference to natural theology'. 2nd Edn. (William Pickering: London).

BULANOVA-ZACHVATINA, E.M. 1974. New genera of oribatid mites from the Upper Cretaceous of Taimyr. Paleontologicheskii Zhurnal 2: 141-144.

CAMPOS, D.R.B. 1986. Primeiro registro fóssil de Scorpionoidea na Chapado do Araripe (Cretáceo Inferior), Brasil. Anais da Academia Brasileira de Ciências 58: 135-137.

CODDINGTON, J.A. & LEVI, H.W. 1991. Systematics and evolution of spiders (Araneae). Annual Review of Ecology and Systematics 22: 565-592.

ESKOV, K. 1984. A new fossil spider family from the Jurassic of Transbaikalia (Araneae: Chelicerata). Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1984: 645-653.

1987. A new archaeid spider (Chelicerata: Araneae) from the Jurassic of Kazakhstan, with notes on the so-called "Gondwanan" ranges of recent taxa. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 175: 81-106.

1990. Spider paleontology: present trends and future expectations. Acta Zoologica Fennica 190: 123-127.

ESKOV, K. & ZONSHTEIN, S. 1990a. First Mesozoic mygalomorph spiders from the Lower Cretaceous of Siberia and Mongolia, with notes on the system and evolution of the infraorder Mygalomorphae (Chelicerata: Araneae). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 178: 325-368.

1990b. A new classification for the order Araneida (Arachnida: Chelicerata). Acta Zoologica Fennica 190: 129-137.

FRITSCH, A. 1901. 'Fauna der Gaskohle. IV. Permische Arachniden'. p.56, pls.153-154, text-figs. 359-363.

1904. 'Palaeozoische Arachniden'. (A. Fritsch: Prague). 86pp., 15 pl.

GALL, J.-C. 1971. Faunes et paysages du Grès à Voltzia du nord des Vosges. Essai paléoécologique sur le Buntsandstein supérieur. Mémoires du Service de la Carte Géologique d'Alsace et de Lorraine 34: 1-318.

GRASSHOFF, M. 1978. A model of the evolution of the main chelicerate groups. Symposia of the Zoological Society of London 42: 273-284.

HAASE, E. 1890. Beiträge zur Kenntnis der fossilen Arachniden. Zeitschrift der Deutschen Geologischen Gesellschaft 42: 629-657.

HAMMEN, L. VAN DER 1985. Functional morphology and affinities of extant Chelicerata in evolutionary perspective. Transactions of the Royal Society of Edinburgh: Earth Sciences 76:137-146.

1986. Comparative studies in Chelicerata IV. Apatellata, Arachnida, Scorpionida, Xiphosura. Zoologische Verhandelingen, Leiden 226: 1-52.

1989. 'An introduction to comparative arachnology'. (SPB Academic Publishing: The Hague). x + 576pp.

HIRSCHMANN, W. 1971. A fossil mite of the genus *Dendrolaelaps* (Acarina, Mesostigmata, Digamasellidae) found in amber from Chiapas, Mexico. 69-70. In Petrunkevitch, A. (ed.) Studies of fossiliferous amber arthropods of Chiapas, Mexico. University of California Publications in Entomology: 63, vi + 106pp., 3 pls.

HIRST, S. 1923. On some arachnid remains from the Old Red Sandstone (Rhynie Chert Bed, Aberdeenshire). Annals and Magazine of Natural History (9) 12: 455-474.

JELL, P.A. & DUNCAN, P.M. 1986. Invertebrates, mainly insects, from the freshwater, Lower Cretaceous, Koonwarra Fossil Bed (Korumburra Group), South Gippsland, Victoria. Memoirs of the Association of Australasian Palaeontologists 3: 111-205.

JERAM, A.J. 1990. Book-lungs in a Lower Carboniferous scorpion. Nature 342: 360-361.

JERAM, A.J., SELDEN, P.A. & EDWARDS, D. 1990. Land animals in the Silurian: arachnids and myriapods from Shropshire, England. Science 250: 658-661.

JUX, U. 1982. *Somaspidion hammapheron* n. gen. n. sp.–ein Arachnide aus dem Oberkarbon der subvaristischen Saumsenke NW Deutschlands. Paläontologische Zeitschrift 56: 77-86.

KETHLEY, J.B., NORTON, R.A., BONAMO, P.M. & SHEAR, W.A. 1989. A terrestrial alicorhagiid mite (Acari: Acariformes) from the Devonian of New York. Micropaleontology 35: 367-373.

KJELLESVIG-WAERING, E.N. 1978. The Phalangiotarbida (Arachnida) of Mazon Creek. Geological Society of America, Abstracts with Programs 10: 258-259.

1986. A restudy of the fossil Scorpionida of the world. Palaeontographica Americana 55: 1-287.

KOCH, C.L. & BERENDT, G.C. 1854. 'Die im Bernstein befindlichen Crustaceen, Myriapoden, Arachniden und Apteren der Vorwelt'. (Berlin). 124pp. [Published posthumously with footnotes by A. Menge].

KRIVOLUTSKY, D.A. & RYABININ, N.A. 1976. Oribatid mites in Siberian and Far East amber. Reports of the Academy of Sciences, USSR 230: 945-948. [In Russian].

LAURIE, M. 1889. On a Silurian scorpion and some additional eurypterid remains from the Pentland Hills. Transactions of the Royal Society of Edinburgh 39: 515-590.

LIN QI-BIN, YAO YI-MIN, XIANG WEI-DA & XIA YU-RONG. 1988. An Oligocene micropalaeoentomofauna from Gubei District of Shandong and its ecological environment. Acta Micropalaeontologica Sinica 5: 331-345.

MANTON, S. M. 1977. 'The Arthropoda. Habits, functional morphology, and evolution'. (Clarendon Press, Oxford). xxii + 527 pp.

MOBERG, J.C. 1892. Om en nyupptäckt fauna i block af kambrisk sandsten, insamlade af dr N. O. Holst. Geologiska Föreningens i Stockholm Förhandlingar 14: 103-120.

NORTON, R.A., BONAMO, P.M., GRIERSON, J.D. & SHEAR, W.A. 1988. Oribatid mite fossils from a terrestrial Devonian deposit near Gilboa, New York. Journal of Paleontology 62: 259-269.

1989. Fossil mites from the Devonian of New York State. 271-277. In Channabasavanna, G.P. and Viraktamath, C.A. (eds.) 'Progress in Acarology. Vol. 1. Systematics and Taxonomy of Acari'. (Oxford and IBH Publishing Co. Pvt. Ltd: New Delhi, Bombay, Calcutta).

OPLUŠTIL, S. 1985. New findings of Arachnida from the Bohemian Upper Carboniferous. Vestn. Ustred ust. geol. 60: 35-42.

PAULUS, H.F. 1979. Eye structure and the monophyly of Arthropoda. 299-383. In Gupta, A.P. (ed.) 'Arthropod Phylogeny'. (Van Nostrand Reinhold: New York).

PETRUNKEVITCH, A. 1913. A monograph of the terrestrial Palaeozoic Arachnida of North America. Transactions of the Connecticut Academy of Arts and Sciences 18: 1-137.

1923. On families of spiders. Annals of the New York Academy of Sciences 29: 145-180.

1942. A study of amber spiders. Transactions of the Connecticut Academy of Arts and Sciences 34: 119-464.

1945. Palaeozoic Arachnida of Illinois. An inquiry into their evolutionary trends. Illinois State Museum, Scientific Papers 3(2): 1-72.

1949. A study of Palaeozoic Arachnida. Transactions of the Connecticut Academy of Arts and Sciences 37: 69-315.

1950. Baltic amber spiders in the Museum of Comparative Zoology. Bulletin of the Museum of Comparative Zoology, Harvard University 103: 259-337.

1952. Macroevolution and the fossil record of Arachnida. American Scientist 40: 99-122.

1953. Palaeozoic and Mesozoic Arachnida of

Europe. Geological Society of America, Memoir 53, xi + 1-128 pp.

1955. Arachnida. p.42-162. In Moore, R.C. (ed.) 'Treatise on invertebrate paleontology. Part P. Arthropoda 2', (Geological Society of America and University of Kansas Press: Boulder, Colorado and Lawrence, Kansas). xvii + 181pp.

1958. Amber spiders in European collections. Transactions of the Connecticut Academy of Arts and Sciences 41: 97-400.

PINTO, I.D. & HUNICKEN, M.A. 1980. *Gondwanarachne* a new genus of the order Trigonotarbida (Arachnida) from Argentina. Boletin de la Academia Nacional de Ciencias, Córdoba, Argentina 53: 307-315.

POCOCK, R.I. 1902. *Eophrynus* and allied Carboniferous Arachnida. Part 1. Geological Magazine, decade 4 9: 439-448.

1903. A new Carboniferous arachnid. Geological Magazine, decade 4 10: 247-251.

1911. A monograph of the terrestrial Carboniferous Arachnida of Great Britain. Monograph of the Palaeontographical Society 64: 1-84.

POINAR, G.O. & SANTIAGO-BLAY, J.A. 1989. A fossil solpugid, *Happlodontus proterus*, new genus, new species (Arachnida: Solpugida) from Dominican amber. Journal of the New York Entomological Society 97: 125-132.

PRUVOST, P. 1919. Introduction à l'étude du terrain houiller du Nord et du Pas-de-Calais. La faune continentale du terrain houiller du Nord de la France. Mémoires pour servir à explication de la carte géologique détaillée de la France. (Ministère des Travaux Publics, Paris). 584 pp

ROLFE, W.D.I. & BECKETT, C.M. 1984. Autecology of Silurian Xiphosurida, Scorpionida, and Phyllocarida. In Bassett, M.G. and Lawson, J.D. (eds) 'Autecology of Silurian Organisms'. Special Papers in Palaeontology 32: 27-37.

ROWLAND J.M. & SISSOM, W.D. 1980. Report on a fossil palpigrade from the Tertiary of Arizona, and a review of the morphology and systematics of the order (Arachnida: Palpigradida). Journal of Arachnology 8: 69-86.

SCHAWALLER, W. 1979. Erstnachweis der Ordnung Geißelspinnen in Dominicanischem Bernstein (Stuttgarter Bernsteinsammlung: Arachnida, Amblypygi). Stuttgarter Beiträge zur Naturkunde, Serie B 50: 1-12.

1982. Spinnen der Familien Tetragnathidae, Uloboridae und Dipluridae in Dominicanischem Bernstein und allgemeine Gesichtspunkte (Arachnida, Araneae). Stuttgarter Beiträge zur Naturkunde, Serie B 89: 1-19.

1991. The first Mesozoic pseudoscorpion, from Cretaceous Canadian amber. Palaeontology 34: 971-976.

SCHAWALLER, W., SHEAR, W.A. & BONAMO, P.M. 1991. The first Paleozoic pseudoscorpions (Arachnida, Pseudoscorpionida). American Museum Novitates 3009: 1-17.

SCUDDER, S.H. 1890. Illustrations of the Carboniferous Arachnida of North America, of the orders Anthracomarti and Pedipalpi. Memoirs of the Boston Society of Natural History 4: 443-456, pls 39, 40.

SELDEN, P.A. 1990a. Lower Cretaceous spiders from the Sierra de Montsech, north-east Spain. Palaeontology 33: 257-285.

1990b. The arachnid fossil record. Newsletter of the British Arachnological Society 58: 4-6.

1992. The fossil ricinuleids. Transactions of the Royal Society of Edinburgh: Earth Sciences 83: 595-634.

1993. Aglaspidida, Pycnogonida and Chelicerata. In Benton, M.J. and Whyte, M.A. (eds) 'The fossil record 2', (Chapman and Hall: London, New York, Tokyo, Melbourne, Madras). (in press).

SELDEN, P.A. & GALL, J.-C. 1992. A Triassic mygalomorph spider from the northern Vosges, France. Palaeontology 35: 211-235.

SELDEN, P.A. & JERAM, A.J. 1989. Palaeophysiology of terrestrialisation in the Chelicerata. Transactions of the Royal Society of Edinburgh; Earth Sciences 80: 303-310.

SELDEN, P.A. & ROMANO, M. 1983. First Palaeozoic arachnid from Iberia: *Aphantomartus areolatus* Pocock (Stephanian; Prov. Leon, N.W. Spain), with remarks on aphantomartid taxonomy. Boletino del Instituto Geologia e Mineralogia d'España 94: 106-112.

SELDEN, P.A. & SHEAR, W.A. 1992. A myriapod identity for the Devonian 'scorpion' *Tiphoscorpio hueberi*. Bericht des naturwissenschaftlich-Medizinischen Vereins in Innsbruck, Supplement 10: 35-36.

SELDEN, P.A., SHEAR, W.A. & BONAMO, P.M. 1991. A spider and other arachnids from the Devonian of New York, and reinterpretations of Devonian Araneae. Palaeontology 34: 241-281.

SELLNICK, M. 1918. Die Oribatiden der Bernsteinsammlung der Universität Königsberg. Schriften der Physikalisch-Ökonomischen Gesellschaft zu Königsberg 59: 21-42.

1931. Milben im Bernstein. Bernsteinforschungen 2: 148-180.

SHEAR, W.A., BONAMO, P.M., GRIERSON, J.D., ROLFE, W.D.I., SMITH, E.L. & NORTON, R.A. 1984. Early land animals in North America. Science 224: 492-494.

SHEAR, W.A. & SELDEN, P.A. 1986. Phylogenetic relationships of the Trigonotarbida, an extinct order of arachnids. Actas X Congresos Internacional de Aracnologia, Jaca, España, 1986 1: 393-397.

SHEAR, W.A., SELDEN, P.A., ROLFE, W.D.I., BONAMO, P.M. & GRIERSON, J.D. 1987. New terrestrial arachnids from the Devonian of Gilboa, New York (Arachnida, Trigonotarbida). American Museum Novitates 2901: 1-74.

SHEAR, W.A., SCHAWALLER, W. & BONAMO,

P.M. 1989. Record of Palaeozoic pseudoscorpions. Nature 341: 527-529.

SHULTZ, J.W. 1989. Morphology of locomotor appendages in Arachnida: evolutionary trends and phylogenetic implications. Zoological Journal of the Linnean Society 97: 1-56.

1990. Evolutionary morphology and phylogeny of Arachnida. Cladistics 6: 1-38.

SIVHED, U. & WALLWORK, J.A. 1978. An early Jurassic oribatid mite from southern Sweden. Geologiska Föreningens i Stockholm Förhandlingar 100: 65-70.

STOCKWELL, S.A. 1989. 'Revision of the phylogeny and higher classification of scorpions (Chelicerata)'. Unpublished Ph.D. thesis, University of California, Berkeley.

STØRMER, L. 1955. Merostomata. P4-P41. In Moore, R.C. (ed.) 'Treatise on invertebrate paleontology. Part P. Arthropoda 2'. (Geological Society of America and University of Kansas Press: Boulder, Colorado and Lawrence, Kansas). xvii + 181pp.

1970. Arthropods from the Lower Devonian (Lower Emsian) of Alken-an-der-Mosel, Germany. Part 1. Arachnida. Senckenbergiana Lethaea 51: 335-69.

1976. Arthropods from the Lower Devonian (Lower Emsian) of Alken-an-der-Mosel, Germany. Part 5. Myriapoda and additional forms, with general remarks on fauna and problems regarding invasion of land by arthropods. Senckenbergiana Lethaea 57: 87-183.

WEYGOLDT, P. 1980. Towards a cladistic classification of the Chelicerata. 8th International Congress of Arachnology, Wien, 1980: 331-334.

WEYGOLDT, P. & PAULUS, H.F. 1979. Untersuchungen zur Morphologie, Taxonomie und Phylogenie der Chelicerata. Zeitschrift für Zoologische Systematik und Evolutionsforschung 17: 85-200.

WHALLEY, P.E.S. 1980. Neuroptera (Insecta) in amber from the Lower Cretaceous of Lebanon. Bulletin of the British Museum (Natural History), Geology 33: 157-164.

WILLS, L.J. 1947. A monograph of British Triassic scorpions. Palaeontographical Society Monographs 437, 441: 1-137.

WOOD, S.P., PANCHEN, A.L. & SMITHSON, T.R. 1985. A terrestrial fauna from the Scottish Lower Carboniferous. Nature 314: 355-356.

SCORPIONS AS MODEL VEHICLES TO ADVANCE THEORIES OF POPULATION AND COMMUNITY ECOLOGY: THE ROLE OF SCORPIONS IN DESERT COMMUNITIES

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The diversity (5-16 species) and abundance (0.2-1.0 individuals/m^2) of scorpions suggest that they may be quite ecologically important in desert communities. Ecological importance is considered in terms of population energetics (the quantity of energy and mass flowing through populations) and of regulation of community structure and dynamics (influence on the distribution and abundance of other species). The energetic analysis provided three conclusions: 1) Scorpions monopolise a relatively large share of animal biomass, particularly relative to vertebrates and other arthropods. 2) This relative success is due to a suite of autecological traits (very low metabolism and very high assimilation efficiency leading to low energy requirements; and great tolerances to water stress, heat and starvation) that allows scorpions to prosper under the unpredictable and low food availability conditions that characterise deserts. 3) However, these traits lessen their impact on energetics, prey and competitors. Thus the importance of scorpions relative to homeothermic vertebrates is less than an analysis of density and biomass suggest because scorpions require and process prey in quantities relatively low to their biomass. Nevertheless, as a group, scorpions are probably important conduits of energy flow in deserts.
Research on the interactions among scorpions and between scorpions and spiders strongly suggests that scorpions can play key roles in the structure and dynamics of their communities. Studies in the deserts of California, Baja California and Namibia show that intraguild predation by scorpions is a major force determining the (temporal and spatial) distribution, abundance and age structure of populations of their competitors/prey.□*Araneae, Scorpionida, age structure, distribution, intraguild predation, population and community ecology*.

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Ecology is a rapidly developing area with a great deal of internal argument and disagreement. As in other fields, theory has advanced far more rapidly than empirical work. Consequently, much theory is controversial and in need of empirical evaluation. Scorpions possess a number of characteristics that make them ideal models to test and advance ecological theory. Thus, it is relatively easy to collect rapidly great amounts of data and to manipulate experimentally individuals and entire populations. Research on scorpions has contributed to many areas of population, behavioral and community ecology: e.g., the evolution of life history theory (Polis and Farley, 1980), the evolution and ecology of age-structured populations (Polis, 1984a, 1988; McCormick and Polis, 1986a), the dynamics of cannibalism (Polis, 1980a, 1981, 1984b), the dynamics of intraguild predation (Polis and McCormick, 1986b, 1987; Polis *et al.*, 1989), the evolution and ecology of foraging strategies (Polis, 1980b; Bradley, 1988), patterns and processes in biogeography (Due and Polis, 1986) and the patterns and processes affecting community and food web structure (Bradley, 1983; Polis, 1991a).

In this paper I evaluate the 'ecological importance' of scorpions. Throughout, I indicate how research on scorpions has advanced our general understanding of ecology. Although scorpions occur in almost all non-boreal habitats, I focus on desert scorpions because much evidence suggests that they may be particularly important components of arid ecosystems and are a relatively 'successful' group. They are diverse, some taxa are extraordinarily abundant, and, as a group, they form a large proportion of the biomass of all desert arthropods and easily exceed the biomass of all desert vertebrates. Their success arises partially because they exhibit several physiological and ecological traits that pre-adapt them to the low and unpredictable food levels of deserts.

'Ecological importance' can be expressed in terms of either energetics and nutrient cycling (the quantity of matter and energy flowing through a population or functional group) or regulation of community structure and dynamics (the impact on diversity, distribution and abundance of other populations).

ENERGETICS AND NUTRIENT CYCLING

The importance of desert scorpions on energy and nutrient cycling is a function of the quantity of prey biomass captured. The amount of captured biomass is a function of the density, population biomass, metabolism and efficiency of energy transfer. I now present a very rough approximation of the relative importance of scorpions to the flow of energy and nutrients in desert ecosystems. To approach this question, data were compiled from the literature reporting the diversity, density and biomass of various groups of desert taxa (see Polis, 1990, 1991b; Polis and Yamashita, 1991 for additional details). These data are not without bias and other problems. For example, studies are not usually conducted in areas where the focal taxon is absent or rare; nor are rare species studied as often as common ones. Consequently, the statistics presented here overestimate density and biomass and should be taken as a first approximation of actual parameters. However, the data are instructive and suggest that scorpions could be a major link in the flow of energy through desert communities.

Group	Density (no./ha)	Diversity (no. species)	n
Mammals	43±130	28.5±21.3	14
Birds	0.6±1.1	46.7±27.3	14
Lizards	[illegible]	12±4.6	12
Insects	35,100±54,600	592±796	10
Termites	4,025,000±2,793,000	9.1±15	7
Isopods	241,510±336,850	1.5±0.6	7
Millipedes	1150±214	2.4±2.1	7
Spiders	3220±8800	54.4±26.7	31
Solpugids		9.0±6.7	37
Scorpions	3210±3500	7.1±2.5	58

TABLE 1. Estimated average density and diversity of major taxa of desert macrofauna reported from the literature. Diversity is the mean number of species per taxon from local sites in different deserts. Density statistics were standardized to a per hectare basis. Means are reported with their standard deviations; n = sample size. Note that these statistics should be viewed as very rough approximations rather than absolute values. Note that data on ants were insufficient to include here (see Polis and Yamashita, 1991 for further details).

How do desert scorpions measure against other groups of consumers for these parameters? First, scorpions are relatively speciose in deserts. On the average, 7.1 species co-occur in desert throughout the world (range: 2-16 sympatric species, typically, 5-9 species; Polis, 1990) (see Table 1 for comparison with other desert taxa). Furthermore, populations are often quite dense, averaging>3200 individuals/ha with several species maintaining populations 5000-10,000/ha (e.g., Shorthouse, 1971; Lamoral, 1978; Polis and Farley, 1980; Polis and McCormick, 1986a; Bradley, 1986; Polis, 1990). On the average, scorpions are reportedly more dense than all other macroscopic animal taxa in these deserts except 'insects', termites, and isopods (ants are undoubtedly also more dense) (Table 1). Since scorpions are among the largest of all terrestrial arthropods (adults of most desert species = 0.5-10g; Polis and Farley, 1980), these high densities produce rather large estimates of standing biomass (= density of individual species x mass of individual animal). Each species population of desert scorpion averaged 7.15 kg/ha. Only termites (and probably ants) support a greater population biomass per

Taxon	Population per species	Biomass (kg/ha) per taxon	n
Mammals	1.40	39.9	29
Birds	0.02	0.9	25
Lizards	0.57	6.8	46
'Insects'	0.88	521.2	31
Termites	12.45	113.4	7
Isopods	9.91	12.8	2
Millipedes	1.15	2.8	2
Spiders	0.13	7.1	4
Scorpions	7.15	50.8	17
All vertebrates		47.7	
All arthropods		708.1	
All macrofauna		755.8	

TABLE 2. Estimated population biomass for various taxa taken from literature. Population biomass per species is average wet weight of one species per hectare. This statistic was sometimes reported; however, it was often calculated by multiplying the average mass of an individual times the density. Population biomass per taxa is calculated as the product of population biomass per species and average diversity of that taxon. Note that data on ants were insufficient to include. Additional information is reported in Polis and Yamashita (1991). n refers to the number of species in a particular taxon for which biomass data exist. Note that these statistics are only gross approximations of reality.

species or per taxon (from the ordinal level down) than scorpions (Table 2).

When the biomass of all scorpions living sympatrically in desert areas is calculated (= mass of individual species x average number of sympatric species), scorpions as a group exhibit a greater biomass (= 50.8kg/ha) than all other taxa except termites (=113.4Kg/ha) and the sum of all other insects (=521.2kg/ha; Table 2). Note also that the population biomass of scorpions is higher than any one group of vertebrates (e.g., mammals and lizards average 39.9 and 6.8Kg/ha) or all vertebrates combined (47.7kg/ha). Overall, scorpions form 6.7% of the biomass of all macrofauna species combined, 7.1% of the biomass of all macroarthropods and 106% of the biomass of all vertebrates.

Thus it would appear that they are important conduits for energy transfer in deserts. However, two characteristics lessen their importance. First, they exhibit the highest ecological (production) efficiencies (percent assimilated energy incorporated into new biomass) of all taxa that live in the desert (Table 3). Second, they exhibit metabolisms that are extremely low relative to other poikilotherms and endotherms (Table 4). Although these features are powerful adaptations that allow efficient use of food and partially explain the success of scorpions in deserts, they also function to decrease the amount of energy transferred. Thus a gram of scorpion does not process as much food as a gram of arthropodivorous vertebrate. Overall then, desert scorpions are less important in energy and nutrient cycling than their diversity, abundance and biomass suggest.

How much energy do desert scorpions process? We have two estimates. Polis (1988) calculated that average populations of *Paruroctonus mesaensis* used 9000 grams of prey/ha/year. The Australian *Urodacus yaschenkoi* requires 7900g/ha/year; this translates into 98,400 ants or 31,570 medium sized spiders eaten per hectare per year (Shorthouse, 1971; Marples and Shorthouse, 1982). It is uncertain exactly how such figures for individual scorpions or for the sum of all sympatric species of scorpions compare to those for vertebrates. This is an interesting question to pursue.

Group	P/A%
Insectivorous mammals	0.86
Birds	1.29
Small mammals	1.51
'Other' mammals	3.14
'Homeotherms'	3.1
Fish	9.77
Social insects	10.3
Terrestrial invertebrates*	25.0
Solitary herbivorous insects	38.8
Solitary detritivorous insects	47.0
Solitary carnivorous insects	55.6
Spiders	45-60
Scorpions	68.2

TABLE 3. Ecological (Production Efficiency) of various animal taxa. This efficiency is equal tothe proportion of assimilated energy that is incorporated into new biomass (=Production/Assimilation). Note that the highest efficiencies are found in carnivorous insects, spiders and scorpions. *Terrestrial invertebrates do not include insects or arachnids. (primarily from Humphreys, 1979; see Polis and Yamashita, 1991 for further details).

INFLUENCE ON COMMUNITY STRUCTURE AND DYNAMICS

The second measure of ecological importance is to determine how a taxon influences the dynamics, distribution and abundance of other taxa. In theory, scorpions can influence desert communities in many ways: as predators affecting characteristics of their prey, as prey of other predators and as competitors of other arthropodivores.

One of the basic questions in ecology is: 'What factors determine the distribution and abundance of species?' To approach this question, researchers often focus on groups of similar species that use similar resources; especially those resources the supply of which may be limiting and in demand (e.g., food). Such species groups

Taxon	Metabolic rate (ml/O_2/gm/hr)
Homeotherms (basal rates)	
Mammals	0.07-7.4
shrew	7.4
rodents	1.80
elephant	0.07
Birds	2.3-4.7
Poikilotherms (at 25°C)	
Insects	1.665 ± 1.25
Spiders	0.92 ± 0.92
Scorpions	0.057 ± 0.048

TABLE 4. Metabolic rates of various animal taxa. The data are taken from many sources. The sample size for insects is 82 species; for spiders, 8 species; and for scorpions, 7 species. (see Polis and Yamashita, 1991 for further details).

are called guilds (= a group of species that use resources in a similar way and are thus potential competitors). For example, guilds of desert granivores (birds, ants, rodents) all eat seeds, regardless of specific differences in resource acquisition.

One approach to study guilds is to describe their patterns or structure. By guild structure, we mean the diversity and abundance of species members; spatial and temporal patterns and resource use (i.e., niche characteristics). However, such descriptive studies, although common, are not fully satisfying because they do not directly address the processes that produce the observed patterns.

An alternative approach is to determine if guild members interact, and if so, can such interactions significantly shape guild structure. There are several possible ways that guild members can interact. These range from cooperation and mutualism to competition and even predation. Such predation among guild members is called intraguild predation (Polis and McCormick, 1987; Polis *et al.*, 1989). Intraguild predation is an ubiquitous interaction among many assemblages of potential competitor but has received little formal attention from either theorists or empiricists (Polis *et al.*, 1989).

One major theme of my research with scorpions has been to analyze the characteristics and significance of intraguild predation. Many scorpion prey items (other scorpions, spiders and solpugids) are also potential competitors with scorpions (Polis, 1990; Polis, 1991a, b; Polis and Yamashita, 1991). I present information on three systems; in each, scorpions frequently eat species in the same guild of arthropodivorous predators and such intraguild predation significantly affects the distribution, abundance and population dynamics of these potential competitors. I used scorpions in these studies as models to delineate the characteristics and dynamics of intraguild predation. These studies illustrate how scorpions have proved to be extraordinarily amendable for ecological research: large amounts of data can be collected, interactions (e.g., feedings) observed and quantified relatively easily, and individuals or whole populations manipulated experimentally. For example, in the first study, field data were collected on 130,000 individuals, 2000 feedings and 6000 individual scorpions were manipulated in controlled field experiments.

INTERACTIONS AMONG SCORPIONS IN THE COACHELLA VALLEY

Four species of desert scorpion co-occur in sandy habitats on the floor of the Coachella Valley (Riverside County, California). Three are in the family Vaejovidae (*Paruroctonus mesaensis* Stahnke, *P. luteolus* Gertsch and *Vaejovis confusus* Stahnke); one (*Hadrurus arizonensis* Ewing), the Iuridae (Polis and McCormick, 1986a, 1987). *Paruroctonus mesaensis* form >95% of all individuals and occur at densities in the range of 0.2-0.5 individuals/ha; the other three species are relatively rare. Each species requires 2-5 years to mature and is composed of several distinctly sized year classes. Size changes greatly, e.g., *P. mesaensis* increase 60-80 times in weight from 0.03g (instar 2) to 2.0-2.5g (nongravid adults). The year classes and species overlap to various degrees in use of insect and arachnid prey; average overlap among all species is moderate to high (0.67 [prey size] and 0.43 [prey taxa]). Thus, the scorpions potentially compete for food.

Extensive intraguild predation occurs among the four species; Table 5 presents a matrix of who eats whom. Several factors characterize this intraguild predation: 1) Each species was both an intraguild predator and prey. Such mutual predation occurs simply because the predator scorpion was always larger regardless of the species combination involved (n= 170 scorpion-scorpion predations). Thus scorpions of all species are vulnerable as they grow from small juveniles to full size adults and predatory reversals (mutual predations) are common. For example, young *P. mesaensis* scorpions are eaten by relatively larger adult *P. luteolus* and *Vaejovis confusus*; adult *P. mesaensis* prey on the (now) relatively smaller adults of these species. Thus age/size is a key

	PREY				
PREDATOR	*H.ari*	*P.lut*	*P.mes*	*V.con*	Total
Hadrurus	0.0	6.3	12.5	3.1	21.9
P. luteolus	0.0	33.3	6.7	6.7	46.7
P. mesaensis	0.4	0.5	5.0	8.3	14.2
Vaejovis	0.0	0.0	8.0	4.0	12.0

TABLE 5. Scorpion-scorpion predation in the Coachella Valley. The entries represent the percent of the diet that each species forms as prey for each of the four scorpion species. The diagonal represents intraspecific predation (cannibalism) (from Polis & McCormick, 1987). *H.ari=Hadrurus arizonensis; P.lut = Paruroctonus luteolus; P.mes= Paruroctonus mesaensis; V.con =Vaejovis confusus.*

determinate of intraguild predation: adults are the predators and immature individuals are the prey significantly more frequently than expected by chance. 2) The most common species (*P. mesaensis*) was the predator in 91% of all intraguild predations observed. Its average overlap in prey use (= 0.44) with other scorpion species was second highest. 3) Intraguild predation, at least by *P. mesaensis*, is significantly more frequent when prey availability was low: when <1% of the population was feeding, heterospecifics formed 35% of all diet items. In contrast when the percent feeding was >5%, only 3.2% of all prey were other species of scorpion. 4) Mortality caused by intraguild predation was generally an inverse function of the density of both *P. luteolus* and *V. confusus*; this resulted because much of the surface activity of these two species occurred during (less productive) periods when *P. mesaensis* was absent from the surface. 5) Intraguild predation is important in scorpion population dynamics. When analyzed as percent mortality of small species (here = total number of individuals eaten by *P. mesaensis* divided by the total number ever observed), intraguild predation by *P. mesaensis* killed 8% and 6% of all *P. luteolus* and *V. confusus* ever observed.

Can such high rates of mortality cause the rarity of these species? It is only possible to approach this question using field experiments. Removal of >6000 *P. mesaensis* (=3.2Kg) from 300 (100m^2) quadrats over a 29 month period demonstrated that the rarity of these species is caused substantially by intraguild predation from *P. mesaensis*. 6) Both *P. luteolus* and *V. confusus* (but not *H. arizonensis*) increased significantly (600% and 135%) in removal as compared with 60 control quadrats. It was speculated that the rarity of the largest species (*H. arizonensis*) is a result of a bottleneck in adult recruitment; predation by *P. mesaensis* killed >10% of all newborn *H. arizonensis* observed during the study. 7) The age structure of these smaller species was significantly different in removal areas: first year juveniles were 1.75 to 2.85 more abundant in removals versus controls. This suggest that the numerical response by the rarer species would be even more dramatic if this experiment continued beyond its 29 month period. Note that a plausible alternative hypothesis exists: removal of *P. mesaensis* relaxed exploitation competition and thus allowed the observed increases in density. A robust test failed to detect competition in this system (Polis and McCormick, 1986b, 1987).

Thus, intraguild predation by *P. mesaensis* significantly depressed the abundance of the rarer species. Does intraguild predation likewise affect their distribution? Since predation is apparently a key factor in the population dynamics of these species, natural selection is expected to favor adaptations that reduce the probability that an individual will encounter its predator. Indeed prey often avoid places and times that their predators frequent or where the probability of predation is high (see Polis and McCormick, 1987). Typically, the large predatory entity (e.g., scorpion species and/or age class) occurs in productive periods and microhabitats whereas smaller entities coexist by spatial segregation in a heterogeneous habitat and by temporal displacement.

The temporal and spatial distribution of smaller age classes and species of Coachella Valley scorpions reflect avoidance (in ecological and/or evolutionary time) of larger age classes and species. The overall distribution of *P. luteolus* and *V. confusus* tend to place these species on the surface during times (in winter, late fall) and in places (off sand) characterized by relatively low surface populations of adult *P. mesaensis*. These times and microhabitats support significantly less prey than those used by adult *P. mesaensis*; consequently *P. mesaensis* has a feeding rate (2.95%) significantly greater than all other species combined (1.70%). Further, the minority of *P. luteolus* and *V. confusus* that forage when and where *P. mesaensis* is active suffer a disproportionately greater chance of being eaten by *P. mesaensis*. Intraspecific predation (cannibalism) has produced similar patterns of temporal distribution, feeding and mortality patterns among age classes of *P. mesaensis* (Polis, 1980, 1984a).

Thus, intraguild predation is an important factor limiting the abundance and shaping the distribution of these scorpions. Many other assemblages of desert scorpions exhibit patterns that suggest that scorpion-scorpion predation is a major process shaping distribution and abundance (Polis and McCormick, 1987; Polis, 1990; but see Bradley, 1988).

INTERACTIONS AMONG SCORPIONS, SPIDERS AND SOLPUGIDS IN THE COACHELLA VALLEY

Scorpions also frequently eat competitors other than other scorpions. For example, the diet of the scorpion *P. mesaensis* consisted of 8% spiders and 14% solpugids (Polis and McCormick, 1986b). Does such intraguild predation significantly affect the distribution and abundance of these unrelated taxa? Spiders responded in the above experimental removal of >6000 *P. mesaensis* by doubling in removal quadrats as compared to controls. Surprisingly, neither solpugids nor all insects combined increased significantly (all $p > .05$) in removal plots. These taxa did not increase either because individuals dispersed from removal areas, because the increase of spiders and smaller scorpions compensated for the removal of *P. mesaensis* by eating surplus arthropods, or simply that scorpions exerted little impact on insect populations. The first explanation is likely true for widely foraging solpugids and is possible but unlikely for the more sessile insects. The second explanation is unlikely: the biomass increase of spiders and scorpions represented <10% of the removed *P. mesaensis* biomass. The third explanation, difficult to accept, is nonetheless a real possibility: *P. mesaensis* may take such a small proportion of all insects that its removal does not affect insect density.

INTERACTIONS BETWEEN SCORPIONS AND SPIDERS IN THE NAMIB DESERT

Predation by scorpions on spiders also appears to be a key determinant of spider densities in the Namib Desert (Polis and Seely, unpublished research, 1988, 1989). Both the scorpion *Uroplectes otjimbinguensis* (Karsch) (Buthidae) and the spider *Gandanimeno echinatus* (Purcell) (Eresidae) live under loose bark on larger *Acacia* trees and are the major arboreal predators of insects on such trees. Populations of *G. echinatus* are severely reduced when they co-occur locally on *Acacia erioloba* trees with the scorpion *U. otjimbinguensis*. This system is a model example how predator-prey interactions are complicated greatly by patterns of local distribution. Not all suitable patches (*Acacia* trees) contain the full array of local species capable of existing within the patch. Trees grow along the banks of dry rivers (e.g., the Kuiseb) and become less dense and more sporadic with increasing distance from the river bed. The local abundance of scorpions and spiders on each tree is a function of differential dispersal, extinction and a predator-prey relationship with *U. otjimbinguensis* scorpions eating *G. echinatus* spiders. Although both species are found on river trees, *U. otjimbinguensis* is, with no exceptions, the numerically dominant species (10-50 scorpions/trees) and *G. echinatus* is relatively uncommon (5-20/tree). This occurs because scorpions are effective predators on these spiders.

However, this outcome is more variable on isolated trees further from the river and along smaller washes entering the river. On some trees close to the river, the abundance of scorpions and spiders is similar to that found in the river. However, some trees have no scorpions and great numbers of spiders (50-400/tree); some trees have neither scorpions nor spiders; and some, no scorpions and few (<20) spiders. Overall, trees without scorpions support significantly more spiders (112.3 ± 60.6, $n = 21$) than trees with scorpions (24.5 ± 14.3, $n = 20$) ($p < 0.001$; only experimental trees scored). This variation in abundance and these distributions exist because neither *U. otjimbinguensis* nor *G. echinatus* disperse far from the river, yet spiders disperse further than scorpions. Dense spider populations occur only in more isolated trees where scorpions are absent. In trees quite distant from the river, neither species occur.

Does intraguild predation by *U. otjimbinguensis* scorpions on *G. echinatus* spiders produce such patterns of distribution and abundance? Additions of *Uroplectes* over a one year period to scorpion-free trees ($n = 11$) highly significantly ($p < .001$) reduced *G. echinatus* populations to 42% of that on control trees ($n = 12$). Removal of scorpions from trees ($n = 8$) also produced a highly significant, 2.9 times increase in *G. echinatus* as compared to control trees ($n = 12$) with their full complement of scorpions.

These experiments showed that intraguild predation was concentrated on young spiders and could significantly alter age distributions ($p < .001$ for each of the following comparisons): The smallest size class of spiders on experimental trees represented 49% of the population ($n = 728$ spiders) one year after scorpions were removed compared to only 31% ($n = 221$) on control trees where scorpions remained; similarly, the smallest size class formed 48% of all spiders ($n = 903$) on trees where scorpions were not present compared to 34% ($n = 820$) on those trees to which scorpions were added.

Thus differential dispersal and semi-deterministic biotic interactions combined with differing isolation of patches are major determinants of the distribution, abundance and age structure of these species. In general, historical and stochastic dispersal events in patchy environments are a paramount factor explaining the distribution and abundance of predators and their prey and species of competitors (Polis, 1991b; Polis and

Yamashita, 1991). Such conditions can produce local extinctions or great variance in abundances via deterministic biotic interactions, but promote global coexistence. I suspect that such situations are normal among many species living in the notoriously heterogeneous desert. Many such assemblages occur in patches; differential dispersal, local extinctions and 'hide-and-seek' dynamics are undoubtedly extremely important in determining the exact structure of local assemblages. Unfortunately, little research has focused on these processes. The system with scorpions and spiders on *Acacia* trees is ideally suited to analyze such processes and represent another example of the use of scorpions to advance our comprehension of ecological processes.

INTERACTIONS BETWEEN SCORPIONS AND SPIDERS ON ISLANDS IN THE GULF OF CALIFORNIA

This system shows several of the same general processes as the one on *Acacia* trees in the Namib and illustrates the importance of predator-prey interactions occurring between spatially structured populations. Spider, scorpion and/or lizard populations on small islands (approximately $<1km^2$) are 1-3 orders of magnitude more dense than on larger islands (approximately 1-$1000km^2$) and the mainland; significant negative relationships occur between island size and density for each of these taxa. For example, the scorpion *Centruroides exilicauda* is 2-25 times more abundant on small islands. Three major variables likely explain the great variance in spider abundance: 1) the presence of scorpion predators (often absent from small islands); 2) the dispersal and colonizing ability of spiders relative to scorpions (better colonizers of small islands as compared to scorpions); and 3) differential energy flow from marine to terrestrial systems (much greater to small islands).

This research has been in progress for four years (1989-1992) in the Midrift area of the Gulf on 41 island and 6 mainland sites between Bahia de Los Angeles (Baja California del Norte, Mexico) and Guaymas (Sonora, Mexico) (Polis unpublished). Scorpion and spider abundance were quantified at each site; spiders were counted on >4000 cacti (one sample unit) and $>8000m^2$ of supralittoral shoreline (another sample unit). Insect abundance was estimated at these sites for >1000 trap days.

Small islands ($<1km^2$) exhibit highly significantly greater secondary production of arthropods than larger islands and mainland areas. However, high productivity is not from autochthonous primary production by terrestrial plants. Evidence strongly suggests that allochthonous production from the ocean is the prime source of productivity. Many islands are 'desert islands' with limited primary productivity from terrestrial plants. Several of the most productive small islands support 2-28 plants (individuals, not species) yet 200-1000 spiders can occur on a single cactus!

Small islands are more productive than large islands and mainland areas for two reasons. First, the Perimeter : Area ratio of an island decreases with size (perimeter is a linear function; area, a square function). Thus small islands have relatively more shoreline per unit area of land and consequently, receive relatively more nutrient and energetic input from marine drift (shore wrack–algal and animal detritus). Second, species-area relations are such that small islands lack predators of nesting marine birds; thus small islands support large colonies of pelicans, gulls, petrels and terns.

Marine detritus and material from nesting birds are eaten by many (semi-) terrestrial arthropods. Some arthropods eat dead bird tissue (eggs, chicks, adults) and fish scraps. However, dipteran parasites are dense consumers of nesting birds and form an important conduit of energy from the sea to spiders. Trapping shows that insect abundance is highly significantly ($p<0.001$, all comparisons) greater in both supralittoral zones and around nests than other areas on these islands and on islands with colonies of marine birds compared to those without colonies (also see Due and Polis, 1985). Dietary analysis shows that detritivorous and parasitic arthropods act as conduits of energy from the sea when converted to large populations of terrestrial spiders, scorpions and/or lizards. For example, spiders are 2-5 times more dense on islands with colonies of marine birds versus those without colonies.

Predation is also an extremely important variable determining the abundance of these taxa. On Gulf Midrift islands, spider abundance is significantly lower in the presence of scorpions and lizards (particularly, *Centruroides exilicauda* and *Uta stansburiana*; 1990: $0.19/m^3$ cactus; 1991: $2.5/m^3$) versus their absence ($63.4/m^3$; $28.2/m^3$; both $p<.005$). The importance of scorpions but not lizards on spider abundance is suggested by the analysis of 10 islands near Guaymas in Sonora. Here, spider density is 38 times less

($0.41/m^3$ cactus) on all islands with *C. exilicauda* (n=8) compared to those with lizards ($15.3/m^3$ cactus; n=2).

The final variables in this system are spatial structure and colonization ability. Incidence functions (percent occurrence on islands classified by area) describe the ability of taxa to disperse to and successfully remain on islands of different sizes. The incidence curves suggest that relative ability to colonize small islands roughly can be ranked: Spiders> *Uta* lizards> Scorpions> Nest predators >Songbirds. Colonization would be deterministic if a particular taxon were always present or absent for all islands of a particular size class. In fact, incidence values for smaller island size classes are neither 0 nor 100%, suggesting that presence or absence of a particular taxon is somewhat stochastic. Thus some small islands exhibit high densities of spiders because scorpions are absent whereas other similar sized islands exhibit low densities of spiders because scorpions are present.

An integration of colonizing abilities, productivity and predation is required to understand the distribution and abundance of these taxa. Each factor varies more or less regularly with island size: generally, as size increases, secondary productivity decreases, predation increases and the importance of differential colonizing ability diminishes. Multivariate analysis allows statistical dissection to determine the relative contribution of each of these factors to the observed variance in spider density. This analysis (Table 6) shows that spider density is a significant positive function of prey availability and significantly depressed in the presence of scorpions. Arthropodivorous lizards are a seemingly unimportant factor, explaining almost none of the variance in spider abundance on Midrift islands.

In summary: Productivity sets potential maximal population size. Small islands are much more productive than larger islands because of the relative greater input of marine allochthonous productivity from drift and marine birds. Colonizing ability establishes the insular species combinations; species-area relations show that larger islands are more diverse and support more types of predators. The realized abundance of terrestrial taxa is limited by (intraguild) predation. For example, if scorpion predators are absent, spiders are dense on small, high productivity islands. When scorpions are present, spider density is lower (but still higher than on large islands and the mainland) and the density of scorpions is relatively high. As island size increases, productivity decreases because nest predators are present (thus bird colonies disappear) and allochthonous detrital input decreases as a function of island Perimeter : Area ratio. Eventually, as island size increases (with decreases in productivity and increases in predation), the abundance of spiders, lizards and scorpions decreases until abundance on very large islands approaches that of the mainland. Strong predation from many sources occurs on the relatively low productivity mainland; consequently, populations of spiders, scorpions and lizards are quite low.

1990 data with lizards	df	SS	MS	F	p>F
Regression	4	[illegible]	[illegible]	[illegible]	[illegible]
Error	15	1.42	[illegible]		
Total	19	4.65			
Perimeter: Area				10.3	0.0058
Scorpion presence				4.29	0.0559
Lizard presence				0.32	0.5827
Cactus volume				1.20	0.2902
Total R^2 this model =0.70					
1991 data with lizards	df	SS	MS	F	p>F
Regression	3	3.13	1.04	11.01	0.0004
Error	16	1.51	0.09		
Total	19	4.65			
Perimeter: Area				9.06	0.0083
Scorpion presence				5.80	0.0285
Lizard presence				3.76	0.9687
Total R^2 this model =0.674					

TABLE 6. Multivariate regression of factors that may influence spider abundance on islands in the Gulf of California in 1990 and 1991. The maximum R improvement technique is used; this produces the best model given all the independent variables. Independent variables include lizard presence, scorpion presence, perimeter: area ratio of island, mean cactus volume/island and prey availability/island. The best two variable model includes perimeter: area ratio and scorpion presence. Three variable models are presented with lizards. The effect of lizards is always non-significantly weak, regardless of what higher order model is used.

CONCLUSIONS

This paper presents various types of data to evaluate the 'ecological importance' of scorpions in deserts. Ecological importance was first considered in terms of population energetics (the quantity of energy and mass flowing through scorpion populations) and second, in terms of the regulation of community structure and dynamics (how intraguild predation by scorpions influences the distribution and abundance of their competitors/prey). The energetic analysis provided three conclusions: 1) Scorpions are quite diverse and abundant in deserts. They monopolize a relatively large share of animal biomass in desert communities, particularly relative to vertebrates and other arthropods. 2) Their relative success is due to a suite of autecological traits that are particularly suited to the harsh and variable climatic conditions of deserts. These traits (very low metabolism and very high assimilation efficiency leading to low energy requirements; and great tolerances to water stress, heat and starvation) preadapt them to prosper successfully under the unpredictable and low productivity food availability that characterize deserts. 3) However, these traits (low metabolism and high assimilation efficiencies) lessen their impact on energetics, prey and competitors. Thus the importance of scorpions relative to homeothermic vertebrates is less than an analysis of density and biomass suggest because scorpions require and process prey in quantities relatively low to their biomass. Nevertheless, as a group, scorpions are probably important conduits of energy flow in deserts.

The research on the interactions among scorpions and that between scorpions and spiders strongly suggests that scorpions can play key roles in the structure and dynamics of the communities in which they live. These studies showed that intraguild predation by scorpions was a major force determining the (temporal and spatial) distribution, abundance and age structure of populations of their competitors/prey. However, as an important caveat, these interactions must be viewed in the context of the environment in which they occur. Dispersal ability, spatial structure and productivity are just some of the possible important factors that moderate the predator-prey interaction between scorpions and their intraguild prey.

The role of all ecologists is to integrate these factors to produce a synthetic understanding of the processes and dynamics that structure natural communities. I suggest that scorpions are particularly suited for this task and will continue to be a productive vehicle to advance the theoretical and empirical body of ecology.

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LITERATURE CITED

BRADLEY, R.A. 1983. Complex food webs and manipulative experiments in ecology. Oikos 41: 150-152.

1986. The relationship between population density of *Paruroctonus utahensis* (Scorpionida: Vaejovidae) and characteristics of its habitat. Journal of Arid Environments 11: 165-171.

1988. The influence of weather and biotic factors on the behaviour of the scorpion (*Paruroctonus utahensis*). Journal of Animal Ecology 57: 533-551.

DUE, A.D. & POLIS, G.A. 1985. Biology of the intertidal scorpion, *Vaejovis littoralis*. Journal of Zoology 207: 563-580.

1986. Trends in scorpion diversity along the Baja California peninsula. American Naturalist 128: 460-468.

HUMPHREYS, W.F. 1979. Production and respiration in animal populations. Journal of Animal Ecology 48: 427-454.

LAMORAL, B. 1978. Soil hardness, an important and limiting factor in burrowing scorpions of the genus *Opisthophthalmus* C.L. Koch, 1837 (Scorpionidae, Scorpionida). Symposium of the Zoological Society of London 42: 171-181.

MARPLES, T.G. & SHORTHOUSE, D.J. 1982. An energy and water budget for a population of arid zone scorpion *Urodacus yaschenkoi* (Birula 1903). Australian Journal of Ecology 7: 119-127.

MCCORMICK, S.J. & POLIS, G.A. 1990. Prey, predators and parasites. 294-320. In Polis, G.A. (ed.) 'Biology of Scorpions'. (Stanford University Press: Stanford, California).

POLIS, G.A. 1980a. The significance of cannibalism on the population dynamics and surface activity of a natural population of desert scorpions. Behavioral Ecology and Sociobiology 7: 25-35.

1980b. Seasonal and age specific variation in the surface activity of a population of desert scorpions in relation to environmental factors. Journal of Animal Ecology 49: 1-18

1981. The evolution and dynamics of intraspecific predation. Annual Review of Ecology and Systematics 12: 225-251.

1984a. Age structure component of niche width and intraspecific resource partitioning: can age groups function as ecological species? American Naturalist 123: 541-564.

1984b. Intraspecific predation and "infant killing" among invertebrates. Pp. 87-104. In Hausfater, G. and Hardy, S. (eds). 'Infanticide: Comparative and Evolutionary Perspectives'. (Aldine Publ. Co.: New York).

1988. Exploitation competition and the evolution of interference, cannibalism and intraguild predation in age/size structured populations. 185-202. In Persson, L. and Ebenmann, B. (eds), 'Size Structured Populations: Ecology and Evolution'. (Springer-Verlag: Heidelberg).

1990. Ecology. Pp. 247-293. In Polis, G.A. (ed.), 'Biology of Scorpions'. (Stanford University Press: Stanford).

1991a. Complex trophic interactions in deserts: An empirical critique of food web theory. American Naturalist 138: 123-155.

1991b. Desert communities: an overview of patterns and processes. Pp. 1-26. In, Polis, G.A. (Ed), 'The Ecology of Desert Communities'. (University of Arizona Press: Tucson).

POLIS, G.A. & FARLEY, R.D. 1980. Population biology of a desert scorpion: survivorship, microhabitat, and the evolution of life history strategy. Ecology 61: 620-629.

POLIS, G.A. & MCCORMICK, S.J. 1986a. Patterns of resource use and age structure among species of desert scorpions. Journal of Animal Ecology 55: 59-73.

1986b. Scorpions, spiders and solpugids: predation and competition among distantly related taxa. Oecologia 71:111-116.

1987. Intraguild predation and competition among desert scorpions. Ecology 68: 332-343.

POLIS, G.A., MYERS, C.A. & HOLT, R. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Annual Review of Ecology and Systematics 20: 297-330.

POLIS, G.A. & YAMASHITA, T. 1991. The ecology and importance of predaceous arthropods in desert communities. Pp. 180-222. In Polis, G.A. (ed.), 'The Ecology of Desert Communities'. (University of Arizona Press: Tucson).

SHORTHOUSE, D. 1971. Studies on the biology and energetics of the scorpion, *Urodacus yaschenkoi* (Birula, 1904). (Ph.D. dissertation, Australian National University: Canberra).

INTER-SPECIFIC ASSOCIATIONS INVOLVING SPIDERS: KLEPTOPARASITISM, MIMICRY AND MUTUALISM

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Many spiders have life-styles that involve a relatively close and prolonged association with another species; for example, between a specialist predator and its prey species, or a species may rely on another for either protection from predators or providing a suitable place to live. In asymmetric relationships, where individuals of one species benefit at the expense of the other, each species may act as a selection pressure on the other species. This can result in the evolution of specific adaptations and counter-adaptations that are evident in at least three kinds of inter-specific associations between spiders. These associations, namely kleptoparasitism, mimicry and mutualism are reviewed here. Our understanding of the evolution of these fascinating systems remains limited, despite numerous anecdotal accounts, because only a few studies are experimental. The purpose of this review is two-fold: to illustrate the use of comparative and experimental studies for understanding the evolutionary significance of these inter-specific relationships, and to highlight those gaps in our knowledge that might benefit from this approach.□*Inter-specific associations, spiders, kleptoparasitism, mimicry, mutualism.*

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Individuals of one species can affect individuals of another as a result of competition, predation, parasitism or mutualism. The evolutionary implications of any association between two or more species depends critically on the frequency and nature of the interaction. For example, a species may be the prey of many species of generalist predators. While these predators may represent an important selective pressure favouring anti-predator responses in the prey species, the adaptations of the prey may have little impact on the reproductive success of the predators. In contrast, a predator that preys on only one species can be an important selective force favouring anti-predator adaptations in that species. In turn, the prey species anti-predator adaptations can exert a selective pressure on the predator, favouring improved predatory abilities. Thus, each species acts as a selection pressure on the other, favouring adaptations and counter-adaptations, perhaps leading to characteristics that are increasingly specific to the relationship. However, these improvements need not necessarily change the relative position of each protagonist (Dawkins and Krebs, 1979). The evolution of these specific adaptations and counter-adaptations depends on both the frequency of the interactions and the effects of each protagonist. Host-parasite systems provide a rich seam of examples of such evolutionary processes (e.g. Endler, 1986; Davies *et al.*, 1989; Toft *et al.*, 1991), but there is also some evidence for similar processes in predator-prey systems (e.g. Brodie and Brodie, 1991; Endler, 1991).

INTER-SPECIFIC ASSOCIATIONS IN SPIDERS

Research on the behaviour and ecology of spiders has, with a few notable exceptions, focussed on issues involving single species (e.g. Humphreys, 1988), including foraging behaviour (Reichert and Luczak, 1982; Vollrath, 1987a; Uetz, 1992), habitat choice (e.g. Reichert and Gillespie, 1986), intraspecific competition (e.g. Reichert, 1982), courtship and mating (e.g. Robinson and Robinson, 1982; Elgar, 1992) and social behaviour (Buskirk, 1981; Elgar and Godfray, 1987; Uetz, 1988). Nevertheless, some spiders have relatively specific and prolonged relationships with other species. These relationships often involve predation or avoiding predation, and perhaps a reason why inter-specific interactions involving spiders have been neglected is that spiders are frequently perceived as generalist predators; cursorial or wandering spiders attack any vulnerable prey that they can find, while web-building spiders simply capture any prey that is caught in their web. However, the view that spiders are generalist predators is misleading. Many spiders prey on only a few species using foraging techniques that include building specialised webs; producing chemical compounds that attract prey; utilising the webs or capturing capabilities of other spiders; mimicking prey behaviour; and cooperative foraging (see reviews in Stowe, 1986; Nentwig, 1987). Clearly, the survival and reproductive success of both predator and prey will depend on their predatory and defensive behaviours, and the degree to which the predator depends on the prey as a source of food. Not all associations between spiders and other invertebrates are predator-prey relationships; some species depend on other species for protection from predators, or providing suitable places to live. This review will focus on three inter-specific relationships involving spiders: kleptoparasitism, mimicry and mutualism.

A detailed understanding of the nature of these inter-specific associations will benefit from both experimental and comparative studies. The former can provide insight into both the fitness effects of the association on individuals of each species, and the importance of particular species' traits for maintaining the association. Comparative studies can provide further insight into the selection pressures responsible for the evolution of the association; reveal the implications of these associations for other aspects of the species life-history characteristics; and help formulate ideas that can be subsequently examined experimentally (see Harvey and Pagel, 1992 for review). While emphasising the evolutionary dynamic nature of inter-specific associations, a central theme of this review is to illustrate the use of comparative and experimental studies for understanding these systems, and also to highlight those gaps in our knowledge of arachnid inter-specific associations that might benefit from this evolutionary approach.

KLEPTOPARASITIC ASSOCIATIONS

The webs of spiders are host to numerous insects, including flies, damselflies and wasps (see reviews in Vollrath, 1984, 1987b; Nentwig and Heimer, 1987). Most descriptions of these guests are anecdotal, and consequently the nature of the relationship is poorly understood. The webs of many spiders are also host to numerous other spiders that obtain food from prey caught in the host's web. These spider guests, commonly referred to as kleptoparasites, are represented in at least four families, including the Dictynidae, Mysmenidae, Symphytognathidae and Theridiidae (Table 1). Of these spiders, the genus *Argyrodes* (Theridiidae) is the best documented (see Vollrath, 1984, 1987b).

Evidence of Kleptoparasitism

Argyrodes were originally described as commensals: *Argyrodes* benefit by feeding on the prey items that are caught in the host's web, but the host is not disadvantaged because these prey items do not form part of its diet (e.g. Belt, 1874). However, subsequent behavioural and ecological studies revealed that individual *Argyrodes* remove prey that might otherwise be consumed by the predator. These observations suggest that the relationship between *Argyrodes* and their hosts is more accurately described as kleptoparasitic rather than commensal (see Vollrath, 1984, 1987b).

In fact, kleptoparasitism may also be an inappropriate description. A kleptoparasitic relationship implies that one partner in the symbiosis benefits at the expense of the other, and that the kleptoparasite has certain characteristics that are adaptations to this lifestyle. Studies of several species associations leave little doubt that the latter contention is correct. For example, the symphytognathid *Curimagua bayano* inhabits the webs of a large mygalomorph *Diplura*, either climbing about the funnel web or remaining on the host (Vollrath, 1978). After a *Diplura* has caught, masticated and enveloped a prey item in digestive fluids, the kleptoparasite descends to the prey item and imbibes the liquidized prey. Interestingly, the anatomy of the mouth of *C. bayano* apparently prevents it from being able to capture, hold or masticate its own prey, suggesting that it is an obligate kleptoparasite (Vollrath, 1978).

Several behaviours of *Argyrodes* appear to be adaptations that are specifically related to their kleptoparasitic lifestyle. These spiders can move throughout the web, apparently undetected by the host, and the attempts of the kleptoparasites to obtain prey items may vary according to the behaviour of the host (Vollrath, 1984, 1987b). There are several mechanisms by which kleptoparasitic *Argyrodes* avoid detection or capture by the host: many species drop from the web when challenged by the host, *A. antipodianus* swings away from the web when the host is agitated (Whitehouse, 1986), and *A. ululans* cuts holes in the tangle web of its social spider host *Anelosimus eximius*, forming a tunnel that apparently facilitates escape (Cangialosi, 1991).

Surprisingly, the evidence that the presence of *Argyrodes* has a negative effect on the reproductive success of the host has not been directly assessed. For example, there are no experimental evidence that the growth rate or fecundity of the host is reduced by the presence of *Argyrodes* (or any other genera of kleptoparasites). Instead, the negative impact of *Argyrodes* on its host has been inferred primarily from either the behaviour of the host (e.g. Larcher and Wise, 1985) or from estimates of the energetic costs derived from the loss of prey items obtained by *Argyrodes*. For example, the number of prey items consumed by *Nephila clavipes* is reduced with increasing numbers of *Argyrodes* on the web (Rypstra, 1981), and *A. ululans* removes around 26% of the prey items that are caught in the web of its host *Anelosimus eximius* (Cangialosi, 1990b). Vollrath (1981) examined the potential costs of *Argyrodes* by estimating the energetic requirements of a single kleptoparasite. The daily energy requirements of the 3-4 mg *A. elevatus* is 0.82 J, about 0.5% of the daily requirements of its 975mg (*Nephila clavipes*) host. This proportion increases with larger numbers of kleptoparasites per web; over 40 individuals have been counted on a single *Nephila* web (although the average is 2.2 kleptoparasites per web), suggesting a potentially high energetic cost of this relationship (Vollrath, 1981).

If kleptoparasites exact a cost on host reproductive success, then selection should favour any trait that enables the hosts to reduce that cost. There are several mechanisms by which hosts might reduce the cost of kleptoparasitism: recovering the prey from the kleptoparasite; reducing the kleptoparasites access to the prey; or simply abandoning the web and building another elsewhere. Interestingly, hosts appear to be inefficient at recovering prey (Vollrath, 1979a, b; Rypstra, 1981) although several host species reduce access to their prey by chasing the kleptoparasites (Cangialosi, 1990b) or concealing the prey in retreats (see Cangialosi, 1990b). Larcher and Wise (1985) demonstrated experimentally that hosts are more likely to abandon webs when *Argyrodes* are present than absent. *Nephila clavipes* relocates its web when it is infested with large numbers of kleptoparasites (Rypstra, 1981), although the behaviour of *N. clavipes* may be a response to lower feeding rates, rather than to numbers of kleptoparasites.

Social or communal spiders appear to have fewer defensive options against high kleptoparasite loads, and this cost may be higher if the number of kleptoparasites per web is greater in larger colonies. For example, *Nephila edulis* builds webs in aggregations, and webs in aggregations have higher kleptoparasite loads and infestation rates than those found alone (Elgar, 1989). Re-locating a web away from an aggregation may reduce kleptoparasite load, but the host subsequently does not benefit from the foraging and predator defense advantages of living within an aggregation (e.g. see Uetz, 1988). Moving web sites to reduce kleptoparasite load may not be possible for some social spiders, such as *Anelosimus* that build substantial, permanent webs. Indeed, high kleptoparasite loads are apparently responsible for the demise of some *Anelosimus* colonies (Cangialosi, 1990b) but not others (Vollrath, 1982).

Like their hosts, individual kleptoparasites may also react to variation in prey capture rates. The feeding rates of kleptoparasites are likely to be influenced by both the prey capture rate of the host and the number of other kleptoparasites on the web. Host web capture rates may vary according to both the location and the size of the web. The number of kleptoparasites increases with the web size of several host species (e.g. Elgar, 1989; Cangliosi, 1990a), possibly because larger webs have higher web capture rates that can support more kleptoparasites. Web-building spiders relocate their webs according to prey capture rates (e.g. Gillespie and Caraco, 1987), and *Argyrodes* may behave similarly by moving to different webs (but see Larcher and Wise, 1985). It would be interesting to establish experimentally whether the emigration rate of individual *Argyrodes* increases as a result of lower web capture rates or increased numbers of conspecifics. If the latter, it is possible that the distribution of *Argyrodes* within a population of hosts, particularly those hosts that aggregate, could be predicted by the ideal free distribution (see Milinski and Parker, 1991).

A possible option for kleptoparasites that experience a low feeding rate is to capture and consume the host before moving to the web of another host (e.g. Tanaka, 1984). Some species of *Argyrodes* are either obligate or facultative predators of their hosts (see Table 1). Predatory *Argyrodes* can capture the host through mimicking a prey item (e.g. Whitehouse, 1986) or simply advancing toward the host and attacking it. Such a specialised form of predation is not uncommon in spiders, and has been recorded in several families (e.g. Jackson, 1987; Jackson and Blest, 1982; Jackson and Brassington, 1987; Jarman

TABLE 1: Spiders that are presumed to be kleptoparasites of web-building spiders. Families: Ag, Agelenidae; Am, Amaurobiidae; Ap, Aphantochilidae; Ar, Araneidae; Cl, Clubionidae; Co, Corinnidae; De, Deinopidae; Di, Dipluridae; Er, Eresidae; Gn, Gnaphosidae; Lin, Linyphiidae; Lio, Liocranidae; Ph, Pholcidae; Pro, Prodidomidae; Sa, Salticidae; Td, Theridiidae; Tm, Thomisidae; Ul, Uloboridae; Zo, Zodariidae. Agg, Aggregates; Soc, Social; Sol, Solitary. Web types: O, orb; T, tangle; S, sheet; F, funnel; Sp, space. Body sizes in mm.

Kleptoparasitic taxa	Body size		Host					Guests per web	Assoc*	Source
	♂	♀	Family	Species	Size	Web	Social			
Dictynidae										
Archaeodictyna ulova			Er	*Stegodyphus*		T	Soc		K	Griswold & Meikle-Griswold (1987)
Heteropodidae										
Olios diana			Am	*Badumna candida*		T	Soc	20	K	Jackson (1987)
O. sp. indet.			Am	*Badumna candida*		T	Soc	10	K	Jackson (1987)
O. lamarcki			Er	*Stegodyphus sarasinorum*		T	Soc	10	K	Jackson (1987)
O. obesulus			Er	*Stegodyphus sarasinorum*		T	Soc	8	K	Jackson (1987)
Mysmenidae										
Isela okuncana			Di	*Allothele terretus*		F	Sol		K	Griswold (1985)
Kilifia inquilina			Di	*Thelechoris karschi*		F			K	Coyle *et al.* (1991)
Mysmenopsis archeri			Ph			T			K	Baptisa (1988)
M. capae			Ar	*Cyrtophora*		O			K	Baert (1990)
M. cidrelicola			Di						K	Coyle *et al.* (1991)
M. cienga			Ar	*Cyrtophora*		O			K	Baert (1990)
M. dipluroamigo			Di	*Diplura*		S			K	Vollrath (1978)
M. furtiva	1.5		Di	*Ischnothele xera*		T	Sol	14	K	Coyle *et al.* (1991)
M. gamboa			Di	*Diplura*		S			K	Vollrath (1978)
M. hauscar			Di						K	Coyle *et al.* (1991)
M. ischnamigo			Di	*Diplura*		S			K	Vollrath (1978)
M. monticola			Di	*Ischnothele* sp.		T	Sol	4	K	Coyle & Meigs (1989)
M. pachacutec			Di						K	Coyle *et al.* (1991)
M. palpalis			Di						K	Coyle *et al.* (1991)
M. tibialis			Di						K	Coyle *et al.* (1991)
M. sp. indet.			Di	*Ischnothele reggae*					K	Coyle *et al.* (1991)
Oonopidae										
Oonops pulcher	2.0	1.5	Am	*Amaurobius fenestralis*	8	T			K	Bristowe (1958)
Salticidae										
Simaetha paetula	7.0	7.0	Am	*Badumna candida*		T	Soc		KP	Jackson (1985)
Symphytognathidae										
Curimagua bayano	1.3	1.3	Di	*Diplura* sp.	40	S	Sol		K	Vollrath (1978)
Theridiidae										
*Argyrodes*** *antipodianus*			Ag	*Cambridgea* sp.		F	Sol		KP	Whitehouse (1988a)
A. antipodianus			Ag	*Stiphidion*		F	Sol		KP	Whitehouse (1988a)
A. antipodianus			Am	*Badumna longinquus*		Sp	Sol		KP	Whitehouse (1988a)
A. antipodianus			Ar	*Araneus crassa*		O	Sol		KP	Whitehouse (1988a)
A. antipodianus			Ar	*Eriophora pustulosa*	13	O	Sol		KP	Whitehouse (1988a)
A. antipodianus			Ar	*Cyclosa trilobata*	8	O	Sol		KP	Whitehouse (1988a)
A. antipodianus			Ar	*Leucauge dromedaria*		O	Sol		KP	Whitehouse (1988a)
A. antipodianus			Ph	*Pholcus phalangioides*		Sp	Sol		KP	Whitehouse (1988a)
A. antipodianus			Td	*Achaearanea*		T	Sol		KP	Whitehouse (1988a)
A. antipodianus	3.0	2.5	Ar	*Cyrtophora hirta*	14	O	Sol		K	Elgar *et al.* (1983)
A. antipodianus	3.0	2.5	Ar	*Nephila edulis*	21	O	Agg		K	Elgar (1989)

Kleptoparasitic taxa	Body size		Host					Guests per web	Assoc*	Source
	♂	♀	Family	Species	Size	Web	Social			
A. argyrodes			Ar	*Cyrtophora citricola*		O			K	Vollrath (1984)
A. atopus	2.4	3.4	Ar	*Nephila clavipes*	25	O	Agg	5	K	Vollrath (1987)
A. attenuatus	17.0	9.3	none							Eberhard (1979a)
A. baboquinari	3.7	3.5	Td	*Latrodectus*		T	Sol		K	Exline & Levi (1962)
A. baboquivari	3.7	3.5	Ul	*Philoponella oweni*	6	O	Agg		KP	Smith Trail (1980)
A. cancellatus	3.2	3.8	Ag	*Agelenopsis*		F			K	Exline & Levi (1962)
A. cancellatus	3.2	3.8	Ar	*Argiope aurantia*	22	O			K	Exline & Levi (1962)
A. cancellatus	3.2	3.8	Ar	*Araneus strix*		O			K	Exline & Levi (1962)
A. cancellatus	3.2	3.8	Ar	*Mecynogea lemniscata*		O			K	Exline & Levi (1962)
A. cancellatus	3.2	3.8	Ar	*Metepeira labyrinthea*		O	Sol		K	Exline & Levi (1962)
A. cancellatus	3.2	3.8	Ar	*Nephila clavipes*	25	O	Agg		K	Exline & Levi (1962)
A. cancellatus	3.2	3.8	Ar	*Verrucosa arenta*	9	O			K	Exline & Levi (1962)
A. cancellatus	3.2	3.8	Li	*Frontinella pyramitela*	4	S			K	Exline & Levi (1962)
A. cancellatus	3.2	3.8	Ph	*Pholcus*		space	Sol		K	Exline & Levi (1962)
A. cancellatus	3.2	3.8	Td	*Theridion tepidariorum*	7	T			K	Exline & Levi (1962)
A. caudatus	3.1	3.9	Ar	*Argiope argentata*	16	O	Sol		K	Smith Trail (1980)
A. cochleaforma	2.7	3.7	Ar	*Argiope*		O			K	Exline & Levi (1962)
A. cochleaforma	2.7	3.7	Ar	*Gasteracantha*		O			K	Exline & Levi (1962)
A. colubrinus	25.0		none							Eberhard (1986)
A. cordillera	3.6	3.1	Ar	*Gasteracantha*		O			K	Exline & Levi (1962)
A. cylindratus			Ar	*Araneus ventricosus*		O	Sol		K	Shinkai (1988)
A. dracus	2.3	2.6	Ar	*Nephila clavipes*	25	O	Agg	5	K	Vollrath (1987)
A. elevatus	3.4	4.0	Ar	*Argiope argentata*	16	O		4	K	Vollrath (1979)
A. elevatus	3.4	4.0	Ar	*Gasteracantha*		O			K	Exline & Levi (1962)
A. elevatus	3.4	4.0	Ar	*Nephila clavipes*	25	O	Agg	5	K	Vollrath (1979
A. fictilium	10.0	5.0	Ar	*Araneus*		O			KP	Exline & Levi (1962)
A. fictilium	10.0	5.0	Li	*Frontinella communis*	4	S	Agg		KP	Wise (1982)
A. fictilium	10.0	5.0	Ul	*Philoponella oweni*	6	O	Agg		KP	Smith Trail (1980)
A. fictilium	10.0	5.0	none							Exline & Levi (1962)
A. fissifrons	7.0		Ag	*Agelena limbata*	16	F	Agg	2	KP	Tanaka (1984)
A. fissifrons	7.0		Lin	*Linyphia*		S			KP	Tanaka (1984)
A. fissifrons	7.0		Td	*Theridion japonicum*		T			KP	Tanaka (1984)
A. fissifrons	7.0		Ul	*Philoponella* sp.	3	O	Agg	3	KP	Elgar (pers obs)
A. fissifrons	7.0		Ul	*Uloborus varians*		O			KP	Tanaka (1984)
A. flagellum			none							Eberhard (1986)
A. globosus	2.3	2.3	Ar	*Nephila clavipes*	25	O	Agg		K	Exline & Levi (1962)
A. incisifrons			Ar	*Cyrtophora hirta*	14	O	Sol		K	Elgar *et al.* (1983)

Table 1. *continued*

Table 1. *continued*

Kleptoparasitic taxa	Body size		Host					Guests per web	Assoc*	Source
	♂	♀	Family	Species	Size	Web	Social			
A. incursus	3.8	2.2	Td	*Achaearanea mundula*	6	T	Sol	5	KP	Gray & Anderson (1989)
A. longissimus	24.0	19.0	none							Exline & Levi (1962)
A. miniaceus			Ar	*Nephila maculata*	43	O			K	Robinson & Robinson (1973)
A. nephilae	1.7	2.2	Ar	*Argiope*		O			K	Exline & Levi (1962)
A. nephilae	1.7	2.2	Ar	*Cyrtophora moluccensis*	19	O	Agg		K	Berry (1987)
A. nephilae	1.7	2.2	Ar	*Gasteracantha*		O			K	Exline & Levi (1962)
A. nephilae	1.7	2.2	Ar	*Neoscona*		O			K	Exline & Levi (1962)
A. nephilae	1.7	2.2	Ar	*Nephila*		O			K	Exline & Levi (1962)
A. nephilae	1.7	2.2	Ar	*Nephila maculata*	43	O			K	Robinson & Robinson (1973)
A. pluto	3.9	3.7	Ar	*Argiope aurantia*	22	O			K	Exline & Levi (1962)
A. pluto	3.9	3.7	Ar	*Metepeira labyrinthea*		O	Sol		K	Exline & Levi (1962)
A. pluto	3.9	3.7	Td	*Latrodectus*		T	Sol		K	Exline & Levi (1962)
A. proboscifo	2.6	2.9	Ar	*Gasteracantha*		O			K	Exline & Levi (1962)
A. projiciens	4.0	3.2	Ar	*Metazygia* sp.		O	Sol		KP	Eberhard (1986)
A. sp. A			Ar	*Nephila clavipes*	25	O	Agg	2	K	Rypstra (1981)
A. sp. B			Ar	*Cyrtophora moluccensis*	19	O	Agg		KP	Lubin (1974)
A. sp. C			Ar	*Gasteracantha*		O		23		Vollrath (1981)
A. subdolus	2.6	2.8	Ul	*Philoponella oweni*	6	O	Agg		K	Smith Trail (1980)
A. trigonum	4.2	2.5	Ag	*Agelena limbata*	16	F	Agg		KP	Suter *et al.* (1989)
A. trigonum	4.2	2.5	Ag	*Agelenopsis*		F				Exline & Levi (1962)
A. trigonum	4.2	2.5	Ar	*Mecynogea lemniscata*		O			KP	Wise (1982)
A. trigonum	4.2	2.5	Ar	*Metepeira labyrinthea*		O	Sol		KP	Larcher & Wise (1985)
A. trigonum	4.2	2.5	Lin	*Linyphia marginata*	5	S			KP	Exline & Levi (1962)
A. trigonum	4.2	2.5	Lin	*Neriene radiata*	5	S	Sol		KP	Larcher & Wise (1985)
A. trigonum	4.2	2.5	Td	*Latrodectus*		T	Sol			Exline & Levi (1962)
A. trigonum	4.2	2.5	Td	*Theridion zelotypum*	4	T			KP	Exline & Levi (1962)
A. trigonum	4.2	2.5	Lin	*Frontinella pyramitela*	4	S			KP	Suter *et al.* (1989)
A. ululans	4.0	3.7	Ar	*Nephila clavipes*	25	O	Agg		K	Exline & Levi (1962)
A. ululans	4.0	3.7	Td	*Anelosimus eximius*		T	Soc		K	Cangialosi (1990a)
A. weyrauchi	4.3	3.8	none							Exline & Levi (1962)

* Two categories of relationship ('Assoc') are defined: 'K' is Kleptoparasite only, and 'KP' means that the guest may also capture the host. Some species of *Argyrodes* may be incorrectly categorised as 'Kleptoparasite only because their predatory behaviour has not yet been observed.

** Taxonomy of *Argyrodes* follows Levi and Exline (1962) and thus *Argyrodes*, *Ariamnes* and *Rhomphaea* are not distinguished.

	Body length†		t-statistic
	kleptoparasite only	kleptoparasite and predator	
♀ *Argyrodes*	2.9±0.2 (14)	5.0±1.1 (6)	3.41**
♂ *Argyrodes*	3.2±0.2 (14)	3.7±0.4 (5)	1.21
Dimorphism (♂/♀)	1.11±0.05 (14)	0.82±0.14 (5)	2.58*
Host	21.5±2.6	6.7±0.8 (5)	3.42**

TABLE 2: Differences in kleptoparasite and host body length according to whether the kleptoparasite does or does not also prey on their host.
† values are mean lengths ± SE (sample sizes). Values compared using t-test with pooled variance. Average host body size measures were obtained for *Argyrodes* that have multiple hosts. * $p < 0.05$; ** $p < 0.005$.

and Jackson, 1986; Jackson and Hallas, 1990). A potential cost of this foraging strategy is that the kleptoparasite may become prey to the host. At least one host species has a relatively effective defensive behaviour: when the predatory *Argyrodes* is detected, the host simply cuts the web thereby collapsing it and ensuring that the predator cannot proceed further (e.g. Eberhard, 1979b). Suter *et al.* (1989) report that female *F. pyramitela* can discriminate between conspecific males, prey items and predatory *A. trigonum*, apparently using chemical cues, and respond accordingly.

Comparative Patterns Within *Argyrodes*

What evolutionary sequences are responsible for the diversity of predatory specialisations in *Argyrodes*? Smith Trail (1980) stresses the importance of the kleptoparasites' ability to identify the vibratory signals generated by the host, thus allowing them to stalk and safely capture the host. However, kleptoparasites that also attempt to capture their hosts risk being captured themselves. Consequently they may be more likely to attempt to capture vulnerable hosts, such as those that are smaller (e.g. Smith Trail, 1980; Larcher and Wise, 1985), moulting (e.g. Vollrath, 1984), or even the spiderlings of the host (e.g. Whitehouse, 1986).

If relative body size is important in determining the outcome of attacking the host, then predatory species of *Argyrodes* may be larger than primarily kleptoparasitic species, or the former may tend to specialise on smaller hosts. These predictions are supported by comparative data of body length measures for 20 species of *Argyrodes* (see Table 1). Species of *Argyrodes* were divided into two groups, according to whether they preyed on their hosts: females of *Argyrodes* that are only kleptoparasitic are significantly smaller than those that also prey on their hosts (Table 2). However, males of these two groups of species are not significantly different in body size (Table 2). *Argyrodes* that prey on their hosts also specialise on smaller hosts, compared with the size of the hosts of those species of *Argyrodes* that are only kleptoparasites (Table 2). These comparative data show that, as predicted, the difference in size between *Argyrodes* and its host is greater for those species that are primarily kleptoparasitic compared with those that are also predatory. These comparative data suggest that selection has either favoured larger body size for species that are both kleptoparasitic and prey on their hosts, or it has favoured a further reduction in body size in those species that are primarily kleptoparasitic. The latter argument is consistent with the view that kleptoparasitism is a specialised foraging strategy that evolved from a more general kleptoparasitic and predatory lifestyle (Vollrath, 1984).

The evolutionary sequence leading to the divergence of these two foraging strategies within *Argyrodes* is not known; one may have evolved from the other, or both may have diverged from a common web-building ancestor (see Whitehouse, 1986). Thus, it is not possible, without an accurate phylogeny, to establish whether selection has favoured an increase in body size with the predatory lifestyle, or a decrease in body size is associated with a kleptoparasitic lifestyle. Indeed, the species placed within the single genus *Argyrodes* by Exline and Levi (1962) have been placed by others into three genera: the *Ariamnes*, the *Rhomphaea*, and the *Argyrodes*. In this classification, the *Ariamnes* and *Rhomphaea* groups are primarily host-predators and the *Argyrodes* group are kleptoparasites (Whitehouse, 1987). Thus, the differences described above may be confounded by taxonomic associations (see below). Resolving some of these issues is most likely achieved by experimental manipulation of individuals within a species that shows both kleptoparasitic and predatory behaviour.

An additional pattern revealed by comparative analysis also deserves experimental investigation. The degree of sexual size dimorphism (male length/female length) covaries significantly with the foraging strategies of *Argyrodes*. Males are smaller than females in those species that prey on their host, consistent with patterns of size dimorphism in almost all other spiders (e.g. Elgar *et al.*, 1990; Elgar, 1991, 1992; Vollrath and Parker, 1992). However, males of those species of *Ar-*

Host taxa	Kleptoparasite*	Biology
Agelenidae		
Agelena (2), *Agelenopsis*, *Cambridgea*, *Stiphidion*	*Argyrodes* (4)	KP
Amaurobiidae		
Badumna (2)	*Simaetha*, *Argyrodes*	KK
Amaurobius	*Oonops*	K
Araneidae		
Araneus (5), *Argiope* (4), *Cyclosa*, *Cyrtophora* (2), *Gasteracantha*, *Leucauge*, *Mecynogea*, *Metazygia*, *Metepeira*, *Neoscona*, *Nephila* (3), *Verrucosa*	*Argyrodes* (18)	KP
Cyrtophora	*Mysmenopsis* (2)	KK
Dipluridae		
Allothele	*Isela*	K
Diplura, *Ischnothele*	*Mysmenopsis* (11)	KK
Diplura	*Curimagua*	K
Thelechoris	*Kilifia*	K
Linyphiidae		
Frontinella (2), *Linyphia*, *Neriene*	*Argyrodes* (4)	KP
Pholcidae		
Pholcus	*Argyrodes* (2)	KK
Pholcus'	Mysmenopsis	K
Theridiidae		
Achaearanea, *Theridion* (3), *Anelosimus*, *Latrodectus*	*Argyrodes* (7)	KP
Uloboridae		
Uloborus, *Philoponella*	*Argyrodes* (4)	KP

TABLE 3: Summary of taxonomic distribution of spiders that are host of kleptoparasites (see Table 1 for further details). KP= Kleptoparasites and predators; K=kleptoparasites. * No. species in each genus in parentheses.

gyrodes that are primarily kleptoparasitic are generally larger than their conspecific females (see Table 2). What factors are responsible for this reversal of size dimorphism patterns within this group of spiders? One explanation is that competition between males for access to females may be more intense for kleptoparasitic spiders, and consequently sexual selection has favoured large male size in these species (see also Whitehouse, 1988b).

There is considerable variation in both the number of species that are host to each species of kleptoparasite and the number of kleptoparasite species found on each web-building host species (see also Vollrath, 1984, 1987b). For example, *Argyrodes cancellatus* are found on the webs of at least ten different host species from five families (see Table 3), while the orb-weaver *Nephila clavipes* is host to at least seven species

	Host range		t statistic
	Kleptoparasite only	Kleptoparasite and predator	
No. species*	18	6	
Family	1.6 ± 0.3	2.8 ± 0.7	1.89
Species	2.7 ± 0.7	3.5 ± 1.3	0.57

TABLE 4: Mean host-ranges of *Argyrodes* that are either only primarily kleptoparasitic or they also prey on their host.* refers to *Argyrodes*.

of *Argyrodes*. It is likely that both host-range and parasite-range will expand as more records become available. In contrast, many species appear to be host specific, with one species of kleptoparasite recorded from the web of only one species of host. For example, in certain Peruvian habitats, *Argyrodes ululans* is found only on the webs of the social spider *Anelosimus eximius*, despite considerable effort searching for this kleptoparasite on other potential hosts (Cangialosi, 1990a).

Vollrath (1984) argued that *Argyrodes* can be placed in two general categories; specialists that are host specific but behaviourally versatile, and generalists that invade the webs of many different species but use relatively few techniques to obtain food. Thus, Whitehouse (1988a) considers *Argyrodes antipodianus* a specialist, primarily because its behaviour is versatile, and adults are found primarily on the webs of *Eriophora pustulosa*. Dichotomies like these can be misleading because both host-specificity and behavioural versatility are most likely continuous rather than discrete variables; *A. antipodianus* is found on the webs of several other hosts (Table 1). Furthermore, host-specificity may also vary between populations, depending on the diversity and abundance of potential hosts in different populations. For example, *A. antipodianus* in Whitehouse's (1988a) study may be found primarily on *Eriophora pustulosa* because that is the most common host in her New Zealand population.

The host range of *Argyrodes* may vary according to whether the species is both kleptoparasitic and predatory or whether it is only kleptoparasitic. Purely kleptoparasitic *Argyrodes* may escape host-detection through specialised behaviours, but these behaviours may be effective for relatively few host species. If so, the host ranges of primarily kleptoparasitic *Argyrodes* may be less than for species of *Argyrodes* that are also predatory. The comparative data provide little support for this prediction (Table 4); although the host-range of primarily kleptoparasitic species is less than the range of predatory species, the difference is not statistically significant.

The results of these inter-specific comparative analyses within the genus *Argyrodes* should be interpreted cautiously. These patterns may be confounded by an association between foraging strategy and taxonomic affinity, and thus the differences in body size or host range may be due to other, unknown features that differ between these two groups. This possibility is especially relevant given the ambiguity of the taxonomic arrangement of this genus. Furthermore, some species of *Argyrodes* may be incorrectly assigned to primarily kleptoparasite status simply through lack of observations. Thus, the patterns may change when more data and/or a more accurate phylogeny become available. Nevertheless, the patterns suggest several interesting questions that could be resolved by an experimental approach.

Host Specificity Of Kleptoparasites

Both *Argyrodes* and *Mysmenopsis* belong to web-building families and thus are relatively close phylogenetically (Coddington and Levi, 1991). However, the range and taxonomic affinities of their hosts are substantially different (Table 1). *Argyrodes* have been recorded on the webs of 29 host genera from eight families (Agelenidae, Amaurobiidae, Araneidae, Linyphiidae, Pholcidae, Psechridae, Theridiidae, Uloboridae), and some species have many hosts (see above). In contrast, 11 of the 14 species of *Mysmenopsis* are found on diplurid hosts, with the remaining species found on *Cyrtophora* (Araneidae) and *Pholcus* (Pholcidae). A comparative analysis reveals a significant difference: every species of *Mysmenopsis* has only one host species, while the host range for *Argyrodes* is 2.7 ($\pm$0.7, n=18) species, or 1.6 ($\pm$0.3) host families.

Why is *Mysmenopsis* more host-specific than *Argyrodes*? There are several possible explanations. First, kleptoparasitism may have evolved more recently in *Mysmenopsis* than in *Argyrodes*, and therefore the former kleptoparasite has had less time to expand its host range. Second, the present associations between *Mysmenopsis* and diplurids may have evolved from a common ancestor and subsequently speciated as host/kleptoparasite pairs. Consistent with this is Coyle and Meigs (1989) description of two sister species of kleptoparasites (*Mysmenopsis monticola* and *M. furtiva*) that live on the webs of a pair of undescribed allopatric *Ischnothele* morphs that also appear to be sister species. Third, diplurids may be more sensitive to web invaders than the hosts of *Argyrodes*, and thus the kleptoparasitic behaviours required to avoid detection by one host species are not appropriate for another. In this regard, it is noteworthy that *Argyrodes* are not known to invade diplurid webs, despite the broad taxonomic range of their hosts.

The relatively permanent nature of the host's web is a common characteristic of the hosts of all kleptoparasites (Table 1). Kleptoparasites that live on permanent webs may benefit by spending less time searching for new webs compared with those that are associated with hosts that frequently move their webs. However, it may not be the permanent structure of the web that is important, but rather the tenacity of the web site. For example, the large, nocturnal, Australian orb-weaver *Eriophora transmarina* builds a new web every evening and then destroys it the following dawn. Despite the temporary nature of its web, this spider is also host to many individual *Argyrodes*, probably because it has a high web-site tenacity (M. Herberstein, unpublished data).

MIMICRY BY SPIDERS

Many species of animals, including spiders, resemble other, unrelated species. These resemblances may be visual, chemical, behavioural or acoustic and are usually referred to as mimicry. There are many different types of mimicry, which has precipitated some controversy over its definition (e.g. Endler, 1981; Pasteur, 1982). Two general forms of mimicry are distinguished in this review: defensive mimicry and aggressive mimicry. In the former, the mimetic form is presumed to have evolved because the risk of predation (or parasitism) on the mimic is reduced as a result of its resemblance to the model. The lower mortality occurs because the receiver (the predator) does not usually prey on the model, and fails to distinguish between it and the mimic. Aggressive mimics resemble some feature of their prey species, thereby increasing the chance of capturing the prey model. Both forms of mimicry occur in several families of spiders.

The relationship between mimic, model and receiver is asymmetric; only the mimic benefits and any improvement in the mimic will be favoured rapidly by natural selection. Both the model and the receiver may lose, in defensive mimicry, through increased attack rate and lost

	Spider taxon		Ant Taxa		Source
		Fam	Subfamily	Species	
	Castianeira dubium	Cl	Ponerinae	*Pachycondyla obscuricornis*	Reiskind (1977)
	Mazax pax	Co	Ponerinae	*Ectatomma ruidum*	Reiskind (1970)
	Myrmecium bifasciatum	Co	Formicinae	*Camponotus femoratus*	Oliveira (1988)
	Myrmecium bifasciatum	Co	Myrmicinae	*Megalomyrmex modestus*	Oliveira (1988)
	Myrmecium sp.	Co	Ponerinae	*Pachycondyla unidentata*	Oliveira (1988)
	Myrmecium velutinum	Co	Ponerinae	*Ectatomma lugens*	Oliveira (1988)
	Myrmecotypus cubanus	Co	Formicinae	*Camponotus planatus*	Myers and Salt (1926)
	Myrmecotypus fuliginosus	Co	Formicinae	*Camponotus planatus*	Jackson & Drummond (1974)
	Myrmecotypus rettenmeyeri	Co	Formicinae	*Camponotus sericeiventris*	Reiskind (1977)
	Sphecotypus niger	Co	Ponerinae	*Pachycondyla villosa*	Oliveira (1988)
	Micaria pulicaria	Gn	Myrmicinae	*Acanthomyrmex niger*	Bristowe (1958)
	Micaria sp.	Gn	Myrmicinae	*Aphaenogaster beccarii*	Hingston (1927)
	Micaria scintillans	Gn	Formicinae	*Formica fusca*	Bristowe (1941)
	Phrurolithus festivus	Lio	Formicinae	*Lasias niger*	Bristowe (1941)
	Phrurolithus minimus	Lio	Formicinae	*Formica fusca*	Bristowe (1941)
	Martella furva	Sa	Formicinae	*Camponotus brevis*	Reiskind (1977)
ANT MIMICRY ONLY	*Martella furva*	Sa	Formicinae	*Camponotus fastigatus*	Reiskind (1977)
	Myrmarachne elongata	Sa	Pseudomyrmecinae	*Tetraponera anthracina*	Edmunds (1978)
	Myrmarachne foenisex	Sa	Formicinae	*Oecophylla longinoda*	Edmunds (1978)
	Myrmarachne formicaria	Sa	Formicinae	*Formica rufa*	Bristowe (1941)
	Myrmarachne legon	Sa	Formicinae	*Camponotus acvapimensis*	Edmunds (1978)
	Myrmarachne lupata	Sa	Formicinae	*Polyrhachis*	Jackson (1986)
	Myrmarachne parallela	Sa	Ponerinae	*Pachycondyla carinulata*	Reiskind (1977)
	Myrmarachne parallela	Sa	Ponerinae	*Pachycondyla striatinodis*	Reiskind (1977)
	Myrmarachne plataleoides	Sa	Formicinae	*Oecophylla smaragdina*	Mathew (1954)
	Myrmarachne sp.	Sa	Formicinae	*Polyrhachis simplex*	Hingston (1927)
	Myrmarachne sp.	Sa	Formicinae	*Prenolepis longicornis*	Hingston (1927)
	Myrmarachne sp.	Sa	Myrmicinae	*Pheidole indica*	Hingston (1927)
	Sarinda linda	Sa	Formicinae	*Camponotus planatus*	Jackson & Drummond (1974)
	Synageles occidentalis	Sa	Formicinae	*Myrmica americana*	Cutler (1991)
	Synageles occidentalis	Sa	Formicinae	*Lasius alienus*	Cutler (1991)
	Synageles venator	Sa	Formicinae	*Lasius niger*	Engelhardt (1970)
	Synemosyna sp.	Sa	Pseudomyrmecinae	*Pseudomyrmex mexicanus*	Reiskind (1977)
	Synemosyna americana	Sa	Pseudomyrmecinae	*Pseudomyrmex boopis*	Reiskind (1977)
	Synemosyna aurantiaca	Sa	Pseudomyrmecinae	*Pseudomyrmex*	Oliveira (1988)
	Synemosyna smithi	Sa	Pseudomyrmecinae	*Pseudomyrma elongata*	Myers and Salt (1926)
	Synemosyna smithi	Sa	Pseudomyrmecinae	*Pseudomyrma flavida*	Myers and Salt (1926)
	Zuniga laeta	Sa	Formicinae	*Camponotus femoratus*	Oliveira (1988)
	Zuniga magna	Sa	Ponerinae	*Pachycondyla villosa*	Oliveira (1988)
	Anatea formicaria	Td	Myrmicinae	*Chelaner croceiventre*	Reiskind and Levi (1967)
	Dipoena	Td	Myrmicinae	*Pheidole indica*	Hingston (1927)

TABLE 5 (part). Taxonomic distribution of spiders that mimic ants, including those that also prey on the model. * spiders observed with dead ants. Family abbreviations given in Table 1.

food respectively (see Endler, 1991), and natural selection will favour models that have less resemblance to the mimic (although the strength of this selection will depend on the frequency with which the model is attacked). The degree of resemblance between model and mimic that evolves will depend upon the benefits to the mimic and the costs of mimicry to the model. The costs to the model in aggressive mimicry are more complicated, and depend upon whether the model and the receiver (in this case, the potential prey) is the same individual.

	Spider taxon		Ant Taxa		Source
		Fam	Subfamily	Species	
ANT MIMIC AND PREDATOR	*Castianeira* sp.	Cl	Formicinae	*Camponotus paria*	Hingston (1927)
	Cosmophasis sp. 1	Sa	Formicinae	*Camponotus detritus*	Curtis (1988)
	Cosmophasis sp. 2	Sa	Formicinae	*Camponotus fulvopilosus*	Curtis (1988)
	Myrmarachne sp.	Sa	Formicinae	*Camponotus compressus*	Hingston (1927)
	Tutelina similis	Sa	Formicinae	*Camponotus*	Wing (1983)
	Not identified	Th	Formicinae	*Oecophylla smaragdina*	Cooper et al. (1990)
	Amyciaea albomaculata	Tm	Formicinae	*Oecophylla smaragdina*	Cooper *et al.* (1990)
	Amyciaea forticeps	Tm	Formicinae	*Oecophylla smaragdina*	Hingston (1927); Mathew (1954)
	Bucranium	Tm	Myrmicinae	*Cephalotes (= Cryptocerus)*	Bristowe (1941)
	Aphantochilus rogersi	Ap	Myrmicinae	*Zacryptocerus pusillus*	Oliveira and Sazima (1984)
	Habronestes bradleyi	Zo	Dolichoderinae	*Iridomyrmex purpureus*	R. Allan (pers. comm.)
	Zodarion	Zo	Myrmicinae	*Messor barbarus*	Hingston (1927)

Table 5. continued

Visual Mimicry: Spiders of Ants

Spiders that resemble ants are an especially intriguing form of mimicry that is poorly understood. Many of these spiders not only have an extraordinary physical resemblence with their ant models, but also exhibit particular behaviours that improves the illusion remarkably. Ant-mimics, represented in at least six families of spiders and mimicking the four major subfamilies of ants (Table 5), fall into two categories: those that appear to have little behavioural interaction with the ants and generally avoid contact with them; and those spiders that specialise on capturing and eating their ant models. There are no clear taxonomic affiliations between the species of spider mimics and the species of ant models; ponerine, myrmecine and formicine ants are models for both clubionid, salticid and other spiders. Nevertheless, certain species of ants appear to be models for spiders more frequently than others. For example, seven species of *Camponotus* are models to spider mimics and one species, *C. femoratus*, is a model for two corinnids (*Myrmecium*) and the salticid *Zuniga*; five species of the ponerine genus *Pachycondyla* are models for five different spiders, and the weaver ant *Oecophylla smaragdina* is a model for three species from Australia and India. It is not obvious why spiders mimic these genera of ants more frequently than others.

Some species of spiders mimic more than one species of ant. For example, the clubionid *Castianeira rica* resembles species of both ponerine and myrmicine ants and the different mimetic forms depend upon developmental changes, colour variation in adult females, and sexual dimorphism (Reiskind, 1970). Male *C. rica* resemble *Atta* and *Odontomachus*, while females resemble moderately large ponerines that are within the spiders' colour range. Furthermore, different instars of these spiders mimic ant models of equivalent size: thus the small, black early instars mimic small myrmicine ants, while the older instars resemble medium sized attine ants. Such a close degree of resemblance at different stages in the spiders' development suggests that the selection pressure favouring mimicry is very strong.

Ant mimicry can provide at least three benefits, depending upon whether the spiders prey on their ant models. These benefits include protection from various predators, improved predatory success on the ant prey, and both. Ant-mimics that apparently do not prey on their models are mostly salticids, corinnids and a few gnaphosids (Table 5). Mimics that prey on their models are mostly represented by thomisids and zodarids, although there are also a few records of theridiids, corinnids and salticids (Table 5). The record for the salticid species *Myrmarachne* (Hingston, 1927) is unusual and unlikely to be typical because other species of this large, ant-mimicking genus do not routinely prey on their model ants (e.g. Edmunds, 1978). Only a few genera of salticids are clearly regular ant-predators (e.g. Jackson and van Olphen, 1991, 1992). The theridiid *Dipoena* resembles the de-capitated head of a dead ant which are found in the refuse heap of the ant nest. Hingston (1927) suggests that mimicry in this species is aggressive because it allows the spider to live in the nest of the ants on whom it may prey. However, predation on these ant hosts by *Dipoena* was not observed.

Perhaps the most vexing question concerning defensive ant mimicry by spiders is establishing the identity of the receiver (i.e. the predator or

Spider		Ant		Source
Species	Family	Subfamily	Species	
Deinopis longipes	De	not specified		Robinson & Robinson (1971)
Chrysilla lauta	Sa	not specified		Jackson & van Olphen (1992)
Corythalia canosa	Sa	not specified		Jackson & van Olphen (1991)
Habrocestum pulex	Sa	Formicinae	*Lasius* sp., *Prenolepis* sp.	Cutler (1980)
Habrocestum pulex	Sa	Ponerinae	*Ponera pennsylvanica*	Cutler (1980)
Natta sp.	Sa	not specified		Jackson & van Olphen (1992)
Natta rufopicta	Sa	not specified		Jackson & van Olphen (1992)
Pystira orbiculata	Sa	not specified		Jackson & van Olphen (1991)
Siler semiglaucus	Sa	not specified		Jackson & van Olphen (1992)
Corythalia canosa	Sa	not specified		Edwards *et al.* (1975)
Euryopis californica	Td	Formicinae	*Camponotus*	Porter & Eastmond (1982)
Euryopis coki	Td	Myrmicinae	*Pogonomyrmex*	Porter & Eastmond (1982)
Euryopis funebris	Td	Formicinae	*Camponotus castaneus*	Carico (1978)
Latrodectus hesperus	Td	Myrmicinae	*Pogonomyrmex rugosus*	MacKay (1982)
Latrodectus pallidus	Td	Myrmicinae	*Monomorium semirufus*	MacKay (1982)
Steatoda fulva	Td	Myrmicinae	*Pogonomyrmex badius*	Hölldobler (1971)
Achaearanea sp.	Td	Formicinae	*Oecophylla smaragdina*	Cullen (1991)
Saccodomus formivorous	Tm	Dolichoderinae	*Iridomyrmex*	McKeown (1952)
Strophius nigricans	Tm	Formicinae	*Camponotus crassus*	Oliveira & Sazima (1985)
Zodarion frenatum	Zo	Formicinae	*Cataglyphis bicolor*	Harkness (1976)

TABLE 6: Spiders that specialise on ant prey but are not ant-mimics.Family abbreviations given with Table 1.

parasitoid). Despite widespread reports and descriptions of ant-mimicry by spiders, few studies have addressed this question quantitatively. The visual nature of ant-mimicry suggests that the spiders are gaining protection from visual enemies, including birds (e.g. Belt, 1874; Engelhardt, 1970), wasps (e.g. Edmunds, 1993) and other spiders (e.g. Cutler, 1991). It is unlikely that the visual resemblance to ants provides the spider mimics with protection from either their ant models or other species of ants, because ants perceive the environment primarily by chemical, rather than visual cues (see Hölldobler and Wilson, 1990). Furthermore, many spiders that are either specialist predators of ants (see Table 6) or live in close proximity with ants (Table 7) are not necessarily visual mimics.

Most of the diet of many spiders are other spiders (e.g. Bristowe, 1941, 1958; Reichert and Luczak, 1982; Nentwig, 1987). In contrast, ants are not a common prey item for most spiders, although a few spiders are specialist predators of ants (see Table 6). Thus, ant mimicry may provide some degree of protection from other spiders. Experimental evidence of this possibility is provided by Cutler (1991), who examined whether ant-mimicry in the salticid *Synageles occidentalis*, a mimic of the ant *Myrmica americana*, reduces the risk of predation by two other spiders *Tibellus* (Philodromidae) and *Phidippus* (Salticidae). These spiders do not feed on the ant *M. americana*, but more importantly they were less likely to attempt to capture the mimic *S. occidentalis* than immature *Phidippus* (that are not ant mimics).

Spiders are also prey to a variety of other invertebrates, especially pompilid and sphecid wasps (e.g. Coville, 1987), and acrocerid dipterans (e.g. Schlinger, 1987). These parasitoids are primarily visual hunters and many myrmecophilous arthropods gain protection against these enemies by associating with ants (e.g. Hölldobler and Wilson, 1990). Thus, ant-mimicry may reduce the risk of predation by sphecid and pompilid wasps. Edmunds (1993) provides qualitative data suggesting that ant-mimics *Myrmarachne* are less likely to be taken by the predatory wasp *Pison xanthopus* than might be expected if this wasp was indiscriminate in its choice of prey. Finally, it is interesting to note that no species of lycosid have been reported as ant-mimics (see Table 5), perhaps because these spiders are generally nocturnal foragers and are also seldom victim to sphecid wasps (see Coville, 1987).

Behavioural Mimicry: Courtship Vibrations

Some spiders are renowned for preying exclusively on other spiders. Notable among these

Spider		Ant		Source
Species	Family	Subfamily	Species	
Tetrilus arientinus	Ag	Formicinae	*Formica*	Bristowe (1958)
Eilica puna	Gn	Formicinae	*Camponotus inca*	Noonan (1982)
Acartauchenius scurrilis	Lin	Formicinae	*Tetramorium caespitum*	Bristowe (1958)
Cochlembolus formicarius	Lin	Formicinae	*Formica obscuripes*	Dondale & Redner (1972)
Evansia merens	Lin	Formicinae	*Formica fusca*	Bristowe (1958)
Masoncus	Lin	Formicinae	*Pogonomyrmex*	Porter (1985)
Thyreosthenius biovatus	Lin	Formicinae	*Formica rufa*	Bristowe (1958)
Phrurolithus	Lio	Formicinae	*Crematogaster*	Porter (1985)
Myandra	Pro	not specified		Main (1976)
Cosmosa	Sa	Dolichoderinae	*Tapinoma melanocephalum*	Shepard & Gibson (1972)

TABLE 7: Spiders that have been found within or adjacent to the nests of ants. Family abbreviations given with Table 1.

are the mimetid or pirate spiders that invade the webs and attack the owners of other species of spiders (e.g. Bristowe, 1941). Many of these spiders are aggressive mimics. For example, the mimetid pirate spiders *Mimetus* and *Ero* wait at the periphery of the web of the social spider *Anelosimus studiosus* (Brach, 1977). The mimetids then pluck on the web thereby attracting a host spider that is then captured and eaten. The salticid *Portia* is also well known for its ability to mimic the struggles of prey ensnared in the web of other spiders. The investigating host is then captured by *Portia* (Jackson and Hallas, 1990).

Some species of *Portia* also mimic the male courtship behaviour of their prey species; a behaviour that increases their chances of capturing the unsuspecting female (Jackson and Hallas, 1986). If prey populations suffer high frequencies of this form of mimicry, then *Portia* may act as a selection pressure favouring improved discriminatory abilities in the prey, thereby establishing an an evolutionarily dynamic 'arms race' (*sensu* Dawkins and Krebs, 1979). Evidence of this form of frequency dependent selection is provided by Jackson and Wilcox (1990, 1993), in their study of the predatory-prey relationship between two Australian salticids, *Portia fimbriata* and *Euryattus* sp.

Euryattus females live in a nest comprising a rolled-up leaf, suspended from rock ledges and tree trunks by silk guylines. *Portia fimbriata* is a versatile predator of many salticids and in a Queensland population, it preys on female *Euryattus* sp. using vibratory displays that apparently mimic the courtship behaviour of *Euryattus* males. This behaviour lures *Euryattus* females from their nest, and they are subsequently attacked by *P. fimbriata*. This specialised form of predation by *P. fimbriata* may be responsible for the improved ability of *Euryattus* to recognise and defend itself from *P. fimbriata*, compared with other salticids. For example, *Euryattus* recognises *P. fimbriata* as a potential predator, unlike another prey species *Jacksonoides queenslandica*. Interestingly, this recognition ability is not present in another population of *Euryattus* in which *P. fimbriata* are absent. Experimental trials reveal that *P. fimbriata* attacks and captures these 'naive' spiders more frequently than spiders from the population that is exposed to *P. fimbriata* (Jackson and Wilcox, 1993). It is still not clear whether the two populations of *Euryattus* are conspecifics or represent two different species. The more distantly related the two populations, the less likely that the differences in behaviour are the result of the presence or absence of *P. fimbriata*. Nevertheless, it appears to be a fascinating example of how the foraging behaviour of a predator has apparently acted as a selection pressure influencing the defensive behaviour of its prey.

Chemical Mimicry: Moths and Ants

Spiders produce a variety of chemicals that function to attract conspecifics. Female spiders from many different families produce pheromones that attract members of the opposite sex (e.g. Lopez, 1987; Pollard *et al.*, 1987), and Evans and Main (1993) show experimentally that pheromones may be important for maintaining social cohesion in social spiders. Several taxa of spiders are capable of inter-specific chemical communication, of which the most familiar is the remarkable form of chemical mimicry by bolas spiders (see Stowe, 1986, 1988 for extensive reviews). Bolas spiders, comprising several genera within the Araneidae, do not construct orb-webs but instead swing at their prey a bolas (a droplet of adhesive) attached to the end of a silk thread. Bolas spiders are aggressive mimics and prey exclusively on male moths; the spiders produce a chemical substance that mimics the sex pheromone of its moth prey species (see Eberhard, 1977, 1980; Yeargan, 1988; Stowe, 1986, 1988; Stowe *et al.*, 1987). The exact source of the prey attractant compounds is not known, but is likely to be emitted from the spider (Stowe *et al.*, 1987). The evolution of this specialised foraging technique is particularly intriguing because it involves two phases; the first comprises the production of moth-attracting chemicals (see also Horton, 1979), and the second is the adoption of a specialised use of silk together with the loss of the orb-web. Interestingly, anecdotal observations suggest that the spider swings the bolas in response to vibratory signals generated by the flying moths (Main, 1976).

The mate location mechanism of at least seven families of moths are exploited by bolas spiders, but the range of moth prey species captured by each species of bolas spider varies (Stowe, 1986, 1988; Stowe *et al.*, 1987). Some spiders capture only one species of moth, while *Mastophora cornigera* is capable of capturing at least nineteen moth species (Stowe *et al.*, 1987). There are no obvious taxonomic affinities between the different groups of bolas spider and their moth prey species (Stowe, 1986, 1988). The variation in bolas spider prey-specificity is likely to be related to the bio-geographic distribution of potential moth prey, the chemical compounds produced by the spiders and the chemicals used as moth sex-attractants. Furthermore, some compounds that attract certain species of moth may inhibit attraction of other moths (Stowe *et al.*, 1987).

Since araneid spiders are capable of chemical mimicry of moths, it is not unreasonable to expect that ant-mimicking spiders may be capable of producing chemical compounds that 'appease' ants. Many species of invertebrate myrmecophiles produce chemicals that mimic ant communication chemicals (see Hölldobler and Wilson, 1990). The production of these chemicals can reduce the risk of the ants attacking the myrmecophiles. One group of spiders that are likely to be capable of chemical mimicry are those that live in ant nests (see Table 7). Little is known about these spiders, but some earlier reports may have mistakenly recorded them living in ant nests, rather than adjacent to the nest (see Bristowe, 1941). It is not clear whether these spiders prey on the ant larvae within the ant nest, or simply take advantage of a safe refuge. Whatever the reason, it is unlikely that they could remain in or near ant nests without some chemical protection, because ants rarely tolerate foreign nest intruders. Porter (1985) provided qualitative evidence for the presence of ant recognition pheromones by introducing myrmecophilous spiders *Masoncus* into the nests of different *Pogonomyrmex* ants. *Masoncus* were not attacked if they were re-introduced into their original nests, but the spiders were attacked and killed within minutes if they were placed in the nest of foreign *Pogonomyrmex* or other species of ants. It is not known whether these spiders actively produce the appropriate pheromones, or whether they simply adopt it from the substrate of the nest.

The predatory behaviour of two Australian spiders may also involve chemical mimicry. The Australian basket-web spider *Saccodomus formivorous* (Thomisidae) builds a basket-like web that appears to attract wandering *Iridomyrmex* ants that may venture into the basket web (McKeown, 1952). The spider also taps the ant with its legs, that may further mimic ant communication, and eventually captures the unsuspecting ant. It remains to be seen if *S. formivorous* webs capture only *Iridomyrmex* ants, and whether the ants are actively attracted to the basket-web. The extraordinary predatory relationship between an undescribed theridiid and its weaver ant *Oecophylla smaragdina* prey (see Cooper *et al.*, 1990) may also represent an example of the use of chemical mimicry. This theridiid constructs a web made of several strands of silk suspended between vegetation and additional strands that are anchored to the substrate below. The anchor part is a small white bead of silk that is very attractive to the ants. If the web is complete and an ant bites the silk it is catapulted into the web above, where it is captured by the spider. The bead of silk is often placed near ant 'highways' and can sometimes attract the attention of many individual *O. smaragdina* that all attempt to bite the silk.

MUTUALISTIC ASSOCIATIONS

There are few examples of mutualistic associations between species of spiders or even between spiders and other organisms. This is surprising, given the widespread occurrence of mutualistic associations in other taxa (e.g. Boucher *et al.*, 1982; Smith and Douglas, 1987; Hölldobler and Wilson, 1990), but may reflect the predatory nature of spiders. Tietjen *et al.* (1987) describe an interesting example of a mutualistic association involving the social spiders *Mallos gregalis*. These spiders do not remove the remains of prey from their nest, and this debris becomes a nutrient base for various yeasts. The odour of these yeasts is apparently attractive to various flies, that settle on the prey carcasses and are then captured by the spiders. The association is likely to be mutualistic because the spiders provide food for the yeast and the yeast's presence attracts food for the spider.

The relationship between spiders that live in ants' nests and their ant hosts may also be mutualistic for some species. For example, Shepard and Gibson (1972) found myrmecophilous salticid spiders of the genus *Cotinusa* in 61% of 50 nests of the dolichoderine ant *Tapinoma melanocephalum*. Interestingly, ant nests with *Cotinusa* had more brood per nest, more workers per nest and more brood per worker than those nests without *Cotinusa*. Unfortunately, these differences were not examined statistically, and the greater numbers of ants and brood in the nests with *Cotinusa* may be due to the larger size of the former nests. Nevertheless, Shepard and Gibson (1972) suggest that the spider uses the ant nest as a foundation for the construction of its web, and in return provides the ants with some protection from predators or parasites.

Psechrus and *Philoponella*

Many species of orb-weaving spiders in the genus *Philoponella* (Uloboridae) build their webs within the barrier webs of other araneid, theridiid, agelenid and psechrid spiders (Struhsaker, 1969; Lubin, 1986). These associations were thought to be commensal; *Philoponella* has a place to build a web, but it was assumed that their presence has little effect on the host spider (e.g. Lubin, 1986).

In Madang Province, Papua New Guinea a species of *Philoponella* builds webs between the threads of the tangle web of a large psechrid *Psechrus argentatus*. Not all *Psechrus* webs have *Philoponella*, but as many as 15 males and females can be found on a single host web. Like many small uloborids, *Philoponella* is a communal spider, with several orb-webs sharing support threads. A theridiid *Argyrodes fissifrons* also patrols the barrier web but is never found on the sheet web of the host spider. The number of both *A. fissifrons* and *Philoponella* on a single host web is positively correlated with the size of the host.

The relationship between *P. argentatus* and *Philoponella* appears to be mutualistic (Elgar, unpublished). The growth rate of *P. argentatus* was significantly reduced following experimental removal of both *A. fissifrons* and *Philoponella* from the barrier-web. The lower growth rate during the ten day experimental period may represent a potential reproductive loss of around 30 eggs (estimated from the weights of egg masses). *P. argentatus* probably benefits by increased capture rates as a result of the increased area of tangle web generated by the webs of *Philoponella*, in a way analogous to the webs of some social spiders (see Struhsaker, 1969; Uetz, 1988). The additional webs may increase the probability of arresting insects that then drop into the sheet web, without being caught in the orb-web of *Philoponella*. It seems unlikely that *P. argentatus* benefits from the presence of *A. fissifrons*. In fact, *A. fissifrons* is more likely to have a negative effect on the host because it feeds on prey items caught in the barrier web and also may prey on *Philoponella*: on two occasions, *A. fissifrons* were seen feeding on *Philoponella*, consistent with other reports of the foraging behaviour of this species (see Table 1).

SOME CONCLUSIONS AND PROSPECTS

The relationship between kleptoparasitic *Argyrodes* and their hosts has been extensively examined, yet the effects of the association on the fitness components of either *Argyrodes* or its host are presently unquantified. Consequently, it may be inappropriate to call these species kleptoparasites because (a) they may not take prey that the host would otherwise feed on and (b) their hosts may not suffer a fitness cost. Of course, many other well documented host-parasite systems similarly fail to quantify the fitness effects of the presumed parasite (see Toft *et al.*, 1991). Nevertheless, circumstantial evidence that the presence of *Argyrodes* has influenced the biology of at least a few host species suggests that kleptoparasitism is an evolutionarily dynamic relationship. Comparative analyses reveal interesting differences in the biology of kleptoparasites that do, or do not, also prey on their host. However, there are no obvious explanations for the evolution of this behaviour.

There are interesting parallels between chemical mimicry by the bolas spider and vibratory mimicry by the salticid *Portia*; both are examples of aggressive mimicry in which the mimic exploits the mate-attracting mechanism of the model. They also illustrate the broad spectrum of sensory mechanisms that are exploited and the range of phylogenetic similarity between model and mimic. The models are clearly disadvantaged by the mimics, and selection is likely to favour mechanisms that allow the victims to distinguish between their conspecific mates and the spider predators. There is some evidence of this selection for *Euryattus*, the model of *Portia*, but there are no data on the impact of bolas spiders on their model moth populations (but see Yeargan, 1988), nor is it known whether the ability of male moths to discriminate between conspecific female pheromones and bolas spider mimics has changed. One difference between these two mimicry systems is that the victims of *Portia* are female, but the victims of bolas spiders are male. This difference may have implications for the relative strength of selection in these types of aggressive mimicry, and the degree to which the model and mimic have undergone an evolutionary arms race.

Defensive mimicry of ants by spiders is taxonomically widespread but has received little experimental attention, compared with studies of other invertebrate taxa (e.g. McIver, 1987). In almost all cases the receiver is not identified and the fitness cost to the ants, as a result of defensive mimicry by these spiders, has not been quantified. Nevertheless, the degree of visual mimicry in many spiders suggests that there has been strong selection for this form of protection against predators. The inter-specific variation in the degree of resemblance between spider mimics and their ant models suggests an evolutionary process reflecting differences in the discriminatory abilities of the receivers. These differences may also reflect the frequency with which the spiders and ants co-occur, and the kind of substrate on which both are found. Finally, ant mimicry by spiders that also prey on their models begs the question of whether specialisation on ant prey followed ant mimicry, or vice-versa.

Mutualisms involving spiders have received little attention, compared with other inter-specific associations. There are several explanations: the Araneae may be characterised by an absence of mutualisms; these mutualisms simply have not been detected; or non-mutualistic associations may even have been incorrectly inferred. For example, the impetus of my study of *Psechrus*, *Philoponella* and *Argyrodes* was to reveal the fitness costs to the host of what appeared to be a kleptoparasitic relationship. The correct nature of the relationship between the species was only revealed experimentally, and this is likely to be true of many other inter-specific associations described in this review. But irrespective of the true nature of these relationships, inter-specific associations involving spiders provide a rich seam of biological systems that pose a variety of fascinating questions.

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LITERATURE CITED

BAERT, L. 1990. Mysmenidae (Araneae) from Peru. Bulletin de Institute Royal Scientifique de Nationale Belgique 60: 5-18.

BAPTISA, R. 1988. On *Mysmenopsis* (Mysmenidae) a kleptoparasite of Pholcidae. American Arachnology 38: 4.

BELT, T. 1874. 'The Naturalist in Nicaragua'. (John Murray: London).

BERRY, J.W. 1987. Notes on the life history and behavior of the communal spider *Cyrtophora moluccensis* (Doleschall) (Araneae, Araneidae) in Yap, Caroline Islands. Journal of Arachnology 15: 309-319.

BOUCHER, D.H., JAMES, S. and KEELER, K.H. 1982. The ecology of mutualism. Annual Review of Ecology and Systematics 13: 315-347.

BRACH, V. 1977. *Anelosimus studiosus* (Araneae: Theridiidae) and the evolution of quasisociality in theridiid spiders. Evolution 31: 154-161

BRISTOWE, W.S. 1941. 'The Comity of Spiders'. Volume 2. (Ray Society: London).

1958. 'The World of Spiders'. (Collins: London.)

BRODIE, E.D., III & BRODIE, E.D. 1991. Evolutionary response of predators to dangerous prey: reduction of toxicity of newts and resistance of garter snakes in island populations. Evolution 45: 221-224.

BUSKIRK, R.E. 1981. Sociality in the Arachnida. Pp. 281-367. In: H.R. Hermann (ed.). 'Social Insects'. Volume II. (Academic Press: New York).

CANGIALOSI, K.R. 1990a. Life cycle and behaviour of the kleptoparasitic spider, *Argyrodes ululans* (Araneae, Theridiidae). Journal of Arachnology 18: 347-358.

1990b. Social spider defense against kleptoparasites. Behavioral Ecology and Sociobiology 27: 49-54.

1991. Attack strategies of a spider kleptoparasite: effects of prey availability and host colony size. Animal Behaviour 41: 639-647.

CARICO, J.E. 1978. Predator behaviour in *Euryopis funebris* (Hentz) (Araneae: Theridiidae) and the evolutionary significance of web reduction. Symposium of the Zoological Society of London 42: 51-58.

CODDINGTON, J.A. & LEVI, H.W. 1991. Systematics and the evolution of spiders (Araneae). Annual Review of Ecology and Systematics 22: 565-592.

COOPER, D., WILLIAMSON, A. & WILLIAMSON, C. 1990. Deadly deception. Geo 12(1): 87-95.

COVILLE, R.E. 1987. Spider-hunting sphecid wasps. Pp. 309-318. In: W. Nentwig (ed.). 'Ecophysiology of Spiders'. (Springer-Verlag: Heidelberg).

COYLE, F.A. & MEIGS, T.E. 1989. Two new species of kleptoparasite *Mysmenopsis* (Araneae, Mysmenidae) from Jamaica. Journal of Arachnology 17: 59-70.

COYLE, F.A., O'SHIELDS, T.C. & PERLMUTTER, D.G. 1991. Observations on the behaviour of the kleptoparasitic spider *Mysmenopsis furtiva*. Journal of Arachnology 19: 62-66.

CULLEN, E. 1991. Observations on an ant-eating theridiid spider. Australasian Arachnology 42: 3-6.

CURTIS, B.A. 1988. Do ant-mimicking *Cosmophasis* prey on their *Camponotus* models? Cimbebasia 10: 67-70.

CUTLER, B. 1980. Ant predation by *Habrocestum pulex* (Hentz) (Araneae: Salticidae). Zoologischer Anzeiger, Jena 204: 97-101.

1991. Reduced predation on the antlike jumping spider *Synageles occidentalis* (Araneae: Salticidae). Journal of Insect Behavior 4: 401-407.

DAVIES, N.B., BOURKE, A.F.G. & BROOKE, M. DE L. 1989. Cuckoos and parasitic ants: interspecific brood parasitism as an evolutionary arms race. Trends in Ecology and Evolution 4: 274-278.

DAWKINS, R. & KREBS, J.R. 1979. Arms races between and within species. Proceedings of the Royal Society of London B 205: 489-511.

DONDALE, C.D. & REDNER, J.H. 1972. A synonym proposed in *Perimones*, a synonym rejected in *Walckenaera*, and a new species described in *Cochlembolus* (Araneida: Erigonidae). Canadian Entomologist 104: 1643-1647.

EBERHARD, W.G. 1977. Aggressive chemical mimicry by a bolas spider. Science 198: 1173-1175.

1979a. *Argyrodes attenuatus* (Theridiidae): a web that is not a snare. Psyche 86: 407-413.

1979b. Predatory behaviour of an assassin spider, *Chorizopes* sp. (Araneidae), and the defensive behaviour of its prey. Journal of the Bombay Natural History Society 79: 522-524.

1980. The natural history and behavior of the bolas spider *Mastophora dizzydeani* sp. n. (Araneae). Psyche 87: 143-169.

1986. Web building behavior of anapid, symphytognathid and mysmenid spiders (Araneae). Journal of Arachnology 14: 339-356.

EDMUNDS, M. 1978. On the association between *Myrmarachne* spp. (Salticidae) and ants. Bulletin of the British Arachnological Society 4: 149-160.

1993. Does mimicry of ants reduce predation by wasps on salticid spiders? Memoirs of the Queensland Museum 33: 507-512.

EDWARDS, G.B., CARROLL, J.F., WHITCOMB, W.H. 1975. *Stoides aurata* (Araneae: Salticidae), a spider predator of ants. Florida Entomologist 57: 337-346.

ELGAR, M.A. 1989. Kleptoparasitism: a cost of aggregating for an orb-weaving spider. Animal Behaviour 37: 1052-1054.

1991. Sexual cannibalism, size dimorphism and courtship behavior in orb-weaving spiders (Araneae). Evolution 45: 444-448.

1992. Sexual cannibalism in spiders and other invertebrates. Pp. 129-156. In: M.A. Elgar and B.J. Crespi (eds). 'Cannibalism: ecology and evolution among diverse taxa'. (Oxford University Press: Oxford).

ELGAR, M.A. & GODFRAY, H.C.J. 1987. Sociality and sex ratios in spiders. Trends in Ecology and Evolution 2: 6-7.

ELGAR, M.A., GHAFFER, N. & READ, A. 1990. Sexual dimorphism in leg length among orb-weaving spiders: a possible role for sexual cannibalism. Journal of Zoology, London 222: 455-470.

ELGAR, M.A., POPE, B. & WILLIAMSON, I. 1983. Observations on the spatial distribution and natural history of *Cyrtophora hirta* (L. Koch) (Araneae: Araneidae). Bulletin of the British Arachnological Society 6: 83-87.

ENDLER, J.A. 1981. An overview of the relationships between mimicry and crypsis. Biological Journal of the Linnean Society 16: 25-31.

1986. 'Natural Selection in the Wild'. (Princeton University Press: Princeton).

1991. Interactions between predators and prey. Pp. 169-196. In: J.R. Krebs and N.B. Davies (eds). 'Behavioural Ecology: an Evolutionary Approach'. (Blackwells: Oxford).

ENGELHARDT, W. 1970. Gestalt und Lebensweise der Ameisenspinne *Synageles venator* (Lucas). Zugleich ein Beitrag zur Ameisenmimikryforschung. Zoologischer Anzeiger 185: 317-334.

EVANS, T.A. & MAIN, B.Y. 1993. Attraction between social crab spiders: silk pheromones in *Diaea socialis*. Behavioral Ecology 4: 99-105.

EXLINE, H. & LEVI, H.W. 1962. American spiders of the genus *Argyrodes* (Araneae, Theridiidae). Bulletin of the Museum of Comparative Zoology 127: 75-204.

GILLESPIE, R.G. & CARACO, T. 1987. Risk sensitive foraging strategies of two spider populations. Ecology 68: 887- 899.

GRAY, M.R. & ANDERSON, G.J. 1989. A new Australian species of *Argyrodes* Simon (Araneoidea: Theridiidae) which preys on its host. Proceedings of the Linnean Society of New South Wales 111: 25-30.

GRISWOLD, C.E. 1985. *Isela okuncana*, a new genus and species of kleptoparasitic spider from southern Africa (Araneae: Mysmenidae). Annals of the Natal Museum 27: 207-217.

GRISWOLD, C.E. & MEIKLE-GRISWOLD, T. 1987. *Archaeodictyna ulova*, new species (Araneae: Dictynidae), a remarkable kleptoparasite of group-living eresid spiders (*Stegodyphus* spp., Araneae: Eresidae). American Museum Novitates 2897: 1-11.

HARKNESS, R.D. 1976. Further observations on the relation between an ant *Cataglyphis bicolor* (F.) (Hym., Formicidae), and a spider, *Zodarium frenatum* (Simon) (Araneae: Zodariidae). Entomologists Monthly Magazine 112: 111-121.

HARVEY, P.H. & PAGEL, M.D. 1992. 'The Comparative Method in Evolutionary Biology'. (Oxford University Press: Oxford).

HINGSTON, R.W.G. 1927. Field observations on spider mimics. Proceedings of the Zoological Society, London 1927: 841- 858.

HÖLLDOBLER, B. 1971. *Steatoda fulva* (Theridiidae), a spider that feeds on harvester ants. Psyche 77: 202-208.

HÖLLDOBLER, B. & WILSON, E.O. 1991. 'The Ants'. (Harvard University Press: Cambridge). 732pp.

HORTON, C.C. 1979. Apparent attraction of moths by webs of araneid spiders. Journal of Arachnology 7: 8.

HUMPHREYS, W.F. 1988. The ecology of spiders with special reference to Australia. Pp. 1-22, In: A.D. Austin and N.W. Heather (eds), 'Australian Arachnology'. (Australian Entomological Society Miscellaneous Publication No. 5: Brisbane).

JACKSON, J.F. & DRUMMOND, B.A., III. 1974. A batesian ant- mimicry complex from the Mountain Pine Ridge of British Honduras, with an example of transformational mimicry. American Midland Naturalist 91: 248-251.

JACKSON, R.R. 1985. The biology of *Simaetha paetula* and *S. thoracica*, web-building jumping spiders (Araneae: Salticidae) from Queensland: co-habitation with social spiders, utilization of silk, predatory behaviour and intra-specific interactions. Journal of Zoology, London (B) 1: 175-210.

1986. The biology of ant-like jumping spiders (Araneae, Salticidae): prey and predatory behaviour of *Myrmarachne* with particular attention to *M. lupata* from Queensland. Zoological Journal of the Linnean Society 88: 179-190.

1987. The biology of *Olios* spp., huntsman spiders (Araneae, Sparassidae) from Queensland and Sri Lanka: predatory behaviour and cohabitation with social spiders. Bulletin of the British Arachnological Society 7: 133-136.

JACKSON, R.R. & BLEST, A.D. 1982. The biology of *Portia fimbriata*, a web-building jumping spider (Araneae: Salticidae) from Queensland: utilization of webs and predatory versatility. Journal of Zoology, London 196: 255-293.

JACKSON, R.R. & BRASSINGTON, R.J. 1987. The biology of *Pholcus phalangioides* (Araneae, Pholcidae): predatory versatility, araneophagy and aggressive mimicry. Journal of Zoology, London 211: 227-238.

JACKSON, R.R. & HALLAS, S.E.A. 1986. Comparative biology of *Portia africana*, *P. albimana*, *P. fimbriata*, *P. labiata*, and *P. schultzi*, araneophagic, web-building jumping spiders (Araneae: Salticidae): utilisation of webs, predatory versatility, and intraspecific interactions. New Zealand Journal of Zoology 13: 423-489.

1990. Evolutionary origins of displays used in aggressive mimicry by *Portia*, a web-invading araneophagic jumping spider (Araneae: Salticidae). New Zealand Journal of Zoology 17: 7-23.

JACKSON, R.R. & VAN OLPHEN, A. 1991. Prey-capture techniques and prey preferences of *Corythalia canosa* and *Pystira orbiculata*, ant-eating jumping spiders (Araneae, Salticidae). Journal of Zoology, London 223: 577-591.

1992. Prey-capture techniques and prey preferences of *Chrysilla*, *Natta* and *Siler*, ant-eating jumping spiders (Araneae, Salticidae) from Kenya and Sri Lanka. Journal of Zoology, London 227: 163-170.

JACKSON, R.R. & WILCOX, R.S. 1990. Aggressive mimicry, prey-specific predatory behaviour and predator recognition in the predator-prey interactions of *Portia fimbriata* and *Euryattus* sp., jumping spiders from Queensland. Behavioral Ecology and Sociobiology 26: 111-119.

1993. Evidence of predator-prey co-adaptation of *Portia fimbriata* and *Euryattus* sp., jumping spiders from Queensland. Memoirs of the Queensland Museum 33: 557-560.

JARMAN, E.A.R. & JACKSON, R.R. 1986. The biology of *Taieria erebus* (Araneae, Gnaphosidae), an araneophagic spider from New Zealand: silk utilisation and predatory versatility. New Zealand Journal of Zoology 13: 521-541.

LARCHER, S.F. & WISE, D.H. 1985. Experimental studies of the interaction between a web-invading spider and two host species. Journal of Arachnology 13: 43-59.

LOPEZ, A. 1987. Glandular aspects of sexual biology. Pp. 121-132. In, W. Nentwig (ed.), 'Ecophysiology of Spiders'. (Springer-Verlag: Heidelberg).

LUBIN, Y.D. 1974. Adaptive advantages and the evolution of colony formation in *Cyrtophora* (Araneae:

Araneidae). Zoological Journal of the Linnean Society 54: 321-339

1986. Web building and prey capture in the Uloboridae. Pp. 132-171. In: W. Shear (ed.). 'Spiders: Webs, Behavior and Evolution'. (Stanford University Press: Stanford.)

MACKAY, W.P. 1982. The effect of predation of Western widow spiders (Araneae: Theridiidae) on harvester ants (Hymenoptera: Formicidae). Oecologia (Berlin) 53: 406-411.

MAIN, B.Y. 1976. 'Australian Spiders'. (Collins: Sydney).

MATHEW, A.P. 1954. Observations on the habits of two spider mimics of the red ant, *Oecophylla smaragdina* (Fabr.). Journal of the Bombay Natural History Society 52: 249-263.

MCIVER, J. 1987. On the myrmecomorph *Coquilletia insignis* Uhler (Hemiptera: Miridae): arthropod predators as operators in an ant-mimetic system. Zoological Journal of the Linnean Society 90: 133-144.

MCKEOWN, K.C. 1952. 'Australian Spiders: their lives and habits'. (Angus and Robertson: Sydney).

MILINSKI, M. & PARKER, G.A. 1991. Competition for resources. Pp. 137-168. In: Krebs, J.R. and Davies, N.B. (eds). 'Behavioural Ecology: an evolutionary approach'. (Blackwells: Oxford).

MYERS, J.G. & SALT, G. 1926. The phenomenon of myrmecoidy, with new examples from Cuba. Transactions of the Entomological Society of London 1926: 427-435.

NENTWIG, W. 1987. The prey of spiders. Pp. 249-263. In: W. Nentwig (ed.), 'Ecophysiology of Spiders'. (Springer-Verlag: Heidelberg).

NENTWIG, W. & HEIMER, S. 1987. Ecological aspects of spider webs. Pp. 211-225. In: W. Nentwig (ed.). 'Ecophysiology of Spiders'. (Springer-Verlag: Heidelberg).

NOONAN, G.R. 1982. Notes on interactions between the spider *Eilica puno* (Gnaphosidae) and the ant *Camponotus inca* in the Peruvian Andes. Biotropica 14: 145-148.

OLIVEIRA, P.S. 1988. Ant-mimicry in some Brazilian salticid and clubionid spiders (Araneae: Salticidae, Clubionidae). Biological Journal of the Linnean Society 33: 1-15.

OLIVEIRA, P.S. & SAZIMA, I. 1984. The adaptive bases of ant-mimicry in a Neotropical aphantochilid spider (Araneae: Aphantochilidae). Biological Journal of the Linnean Society 22: 145-155.

PASTEUR, G. 1982. A classificatory review of mimicry systems. Annual Review of Ecology and Systematics 13: 169-199.

POLLARD, S.D., MACNAB, A.M. & JACKSON, J.J. 1987. Communication with chemicals: pheromones and spiders. Pp. 133-141. In: W. Nentwig (ed.). 'Ecophysiology of Spiders'. (Springer-Verlag: Heidelberg).

PORTER, S.D. 1985. *Masoncus* spider: a miniature predator of collembola in harvester-ant colonies. Psyche 92: 145-151.

PORTER, S.D. & EASTMOND, D.A. 1982. *Euryopis coki* (Theridiidae), a spider that preys on *Pogonomyrmex* ants. Journal of Arachnology 10: 275-277.

REICHERT, S. E. 1982. Spider interaction strategies: communication vs. coercion. Pp. 281-315. In: P.N. Witt and J.S. Rovner (eds). 'Spider Communication: Mechanisms and Ecological Significance'. (Princeton University Press: Princeton).

REICHERT, S.E. & GILLESPIE, R.G. 1986. Habitat choice and utilization in web-building spiders. Pp 23-48. In: W. Shear (ed.). 'Spiders: Webs, Behavior and Evolution'. (Stanford University Press: Stanford).

REICHERT, S.E. & LUCZAK, J. 1982. Spider foraging: behavioral responses to prey. Pp. 353-385. In: P.N. Witt and J.S. Rovner (eds). 'Spider Communication: Mechanisms and Ecological Significance'. (Princeton University Press: Princeton).

REISKIND, J. 1970. Multiple mimetic forms in an ant-mimicking clubionid spider. Science 169: 587-588.

1977. Ant-mimicry in Panamanian clubionid and salticid spiders (Araneae: Clubionidae, Salticidae). Biotropica 9: 1-8.

REISKIND, J. & LEVI, H.W. 1967. *Anatea*, an ant-mimicking theridiid spider from New Caledonia (Araneae: Theridiidae). Psyche 74: 20-23.

ROBINSON, M.H. & ROBINSON, B. 1971. The predatory behavior of the ogre-faced spider *Dinopis longipes* F. Cambridge (Araneae: Dinopidae). American Midland Naturalist 85: 85-96.

1973. Ecology and behavior of the giant wood spider *Nephila maculata* (Fabricius) in New Guinea. Smithsonian Contributions to Zoology 149: 1-76.

1982. Courtship and mating behavior in spiders. Annual Review of Entomology 27: 1-20.

RYPSTRA, A.L. 1981. The effects of kleptoparasitism on prey consumption and web relocation in a Peruvian population of the spider *Nephila clavipes*. Oikos 37: 179-182.

SCHLINGER, E.I. 1987. The biology of Acroceridae (Diptera): true endoparasitoids of spiders. Pp. 319-327. In: W. Nentwig (ed.). 'Ecophysiology of Spiders'. (Springer-Verlag: Heidelberg).

SHEPARD, M. & GIBSON, F. 1972. Spider-ant symbiosis: *Cotinusa* spp. (Araneidae: Salticidae) and *Tapinoma melanocephalum* (Hymenoptera: Formicidae). Canadian Entomologist 104: 1951-1954.

SHINKAI, A. 1988. A note on the web silk theft by *Argyrodes cylindratus* (Thorell) (Araneae: Theridiidae). Acta Arachnologica 36: 115-119.

SMITH, D.D. & DOUGLAS, A.E. 1987. 'The Biology of Symbiosis' (Edward Arnold: London).

SMITH TRAIL, D. 1980. Predation by *Argyrodes* (Theridiidae) on solitary and communal spiders. Psyche 87: 349-355.

1981. Energetic considerations of a spider parasite-spider host system. Revue Arachnologique 3: 37-44.

1982. Colony foundation in a social spider. Zeitschrift für Tierpsychologie 60: 313-324.

1984. Kleptobiotic interactions in invertebrates. Pp. 61-94 In: C.J. Barnard (ed.). 'Producers and Scroungers: Strategies of Exploitation and Parasitism'. (Chapman and Hall: Beckenham).

1987a. Growth, foraging and reproductive success. Pp. 357-370. In: W. Nentwig (ed.). 'Ecophysiology of Spiders'. (Springer-Verlag: Heidelberg).

1987b. Kleptobiosis in spiders. Pp. 274-286. In: W. Nentwig (ed.). 'Ecophysiology of Spiders'. (Springer-Verlag: Heidelberg).

STOWE, M. K. 1986. Prey specialization in the Araneidae. Pp. 101-131. In, W. Shear (ed.). 'Spiders: Webs, Behavior and Evolution'. (Stanford University Press: Stanford).

1988. Chemical mimicry. Pp. 513-587. In: K.C. Spencer (ed.). 'Chemical Mediation of Coevolution'. (Academic Press: New York).

STOWE, M.K., TUMLINSON, J.H. & HEATH, R.R. 1987. Chemical mimicry: bolas spiders which attract male moth prey emit components of prey sex pheromone blends. Science 236: 964-967.

STRUHSAKER, T.T. 1969. Notes on the spiders *Uloborus mundior* (Chamberlin and Ivie) and *Nephila clavipes* (Linnaeus) in Panama. American Midland Naturalist 82: 61-63.

SUTER, R.B., SHANE, C.M. & HIRSCHEIMER, A.J. 1989. Spider vs. spider: *Frontinella pyramitela* detects *Argyrodes trigonum* via cuticular chemicals. Journal of Arachnology 17: 237-241.

TANAKA, K. 1984. Rate of predation by a kleptoparasitic spider, *Argyrodes fissifrons*, upon a large host spider, *Agelena limbata*. Journal of Arachnology 12: 363-367.

TIETJEN, W.J., AYYAGARI, L.R. & UETZ, G.W. 1987. Symbiosis between social spiders and yeast: their role in prey attraction. Psyche 94: 151-158.

TOFT, C.A., AESCHLIMANN, A. & BOLIS, L. 1991. 'Parasite-Host Associations: Coexistence or Conflict?' (Oxford University Press: Oxford).

UETZ, G.W. 1988. Group foraging in colonial web-building spiders: evidence for risk sensitivity. Behavioral Ecology and Sociobiology 22: 265-270.

1992. Foraging strategies of spiders. Trends in Ecology and Evolution 7: 155-159.

VOLLRATH, F. 1978. A close relationship between two spiders: *Curimagua bayano* synecious on a *Diplura* species. Psyche 85: 347-353.

1979a. Behaviour of the kleptoparasitic spider *Argyrodes elevatus* (Araneae, Theridiidae). Animal Behaviour 27: 515-521.

1979b. Vibrations: their signal function for a spider kleptoparasite. Science 205: 1149-1151.

VOLLRATH, F. & PARKER, G.A. 1992. Sexual dimorphism and distorted sex ratios in spiders. Nature 360: 156-159.

WHITEHOUSE, M.E.A. 1986. The foraging behaviours of *Argyrodes antipodiana* (Theridiidae), a kleptoparasite spider from New Zealand. New Zealand Journal of Zoology 13: 151-168.

1987. "Spider eat spider": the predatory behaviour of *Rhomphaea* sp. from New Zealand. Journal of Arachnology 15: 355-362.

1988a. Factors influencing specificity and choice of host in *Argyrodes antipodiana* (Araneae, Theridiidae). Journal of Arachnology 16: 349-355.

1988b. To mate or fight? Male-male competition and alternative mating strategies in *Argyrodes antipodiana* (Theridiidae, Araneae). Behavioural Process 23: 163-172.

WING, K. 1983. *Tutelina similis* (Araneae: Salticidae): an ant mimic that feeds on ants. Journal of the Kansas Entomological Society 56: 55-58.

WISE, D.H. 1982. Predation by a commensal spider, *Argyrodes trigonum*, upon its host: an experimental study. Journal of Arachnology 10: 111-116.

YEARGAN, K.V. 1988. Ecology of a bolas spider, *Mastophora hutchinsoni*: phenology, hunting tactics, and evidence for aggressive chemical mimicry. Oecologia 74: 524-530.

VERTICAL DISTRIBUTION AND ABUNDANCE OF PSEUDOSCORPIONS (ARACHNIDA) IN THE SOIL OF TWO DIFFERENT NEOTROPICAL PRIMARY FORESTS DURING THE DRY AND RAINY SEASONS

JOACHIM ADIS AND VOLKER MAHNERT

Adis, J. and Mahnert, V. 1993 11 11: Vertical distribution and abundance of pseudoscorpions (Arachnida) in the soil of two different neotropical primary forests during the dry and rainy seasons. *Memoirs of the Queensland Museum* **33**(2): 431-440. Brisbane. ISSN 0079-8835.

Pseudoscorpions were extracted from 0-14cm soil depth in two dryland (upland) forests near Manaus, Brazil. In a primary forest on yellow latosol, about 1700 specimens per m^2 were obtained during the dry season and 1135 during the rainy season. They accounted for 10-15% of all arthropods extracted, excluding Acari and Collembola. In a primary forest on white sand soil (campinarana), about 530 specimens per m^2 were obtained during the dry season and 480 during the rainy season. They accounted for only 3-4% of all arthropods extracted, again excluding Acari and Collembola. Significant but different correlations were found in both forest types between the abundance of pseudoscorpions and changing moisture, temperature and pH conditions in relation to soil depth and season. Neither during the dry season nor during the rainy season was the abundance of pseudoscorpions in mineral subsoils higher in response to the changing soil moisture content in organic layers. This was reported for arthropods from forests in the seasonal tropics where periods without precipitation occur. Results are discussed at the species level. They are compared with published data on the vertical distribution and abundance of pseudoscorpion species from the yellow latosol of a secondary dryland forest (dry season and rainy season) from the same region.

In zwei Festlandwäldern in der Umgebung von Manaus wurden Pseudoskorpione aus 0-14cm Bodentiefe extrahiert. In einem Primärwald auf gelbem Latosolboden wurden während der Trockenzeit 1700 und während der Regenzeit 1135 Individuen pro m^2 nachgewiesen. Sie repräsentierten 10-15% aller extrahierten Arthropoden, Acari und Collembola ausgenommen. In einem Primärwald auf Weißsandboden (campinarana) wurden während der Trockenzeit 530 und während der Regenzeit 480 Individuen pro m^2 nachgewiesen. Sie repräsentierten nur 3-4% aller extrahierten Arthropoden, Acari und Collembolen wiederum ausgenommen. Signifikante aber unterschiedliche Korrelationen ergaben sich in beiden Waldtypen zwischen der Abundanz der Pseudoskorpione und der sich ändernden Feuchte, der Temperatur und dem pH in Bezug auf Bodentiefe und Jahreszeit. Weder während der Trockenzeit, noch während der Regenzeit, war die Abundanz der Pseudoskorpione im mineralischen Unterboden als Folge auf die sich ändernde Feuchte im organischen Oberboden höher. Dies wurde für Arthropoden in Wäldern der saisonalen Tropen, die Trockenperioden durchlaufen, nachgewiesen. Die Ergebnisse werden auf Artniveau diskutiert. Sie werden mit publizierten Daten über die Vertikalverteilung und Abundanz von Pseudoskorpionarten aus einem Sekundärwald auf gelbem Latosolboden im gleichen Gebiet verglichen. □*Pseudoscorpiones, abundance, seasonality, vertical distribution, Neotropics.*

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In those wet but markedly seasonal tropics where periods without precipitation occur, terrestrial arthropods are reported to migrate to mineral subsoils in the dry season as a response to changing humidity in organic layers (Beck, 1964; Bullock, 1967; Goffinet, 1976; Lawrence, 1953; Levings and Windsor, 1984; Liebermann and Dock, 1982; Merino and Serafino, 1978; Petersen and Luxton, 1982; Rybalov, 1990; Strickland, 1947; Willis, 1976 and others). Central Amazonian dryland (= non-flooded upland) forests experience a rainy season (December-May; average monthly rainfall 211-300mm) and a 'dry' (= drier) season (June November; average monthly rainfall 42-162mm). Annual precipitation is 2105mm (based on 75 years of records from the meteorological station at Manaus, cf. Ribeiro and Adis, 1984). About 75% of the rainfall (1500mm) is recorded during the rainy season. This had no observable difference in vertical distribution of terrestrial arthropods in primary forests on yellow latosol

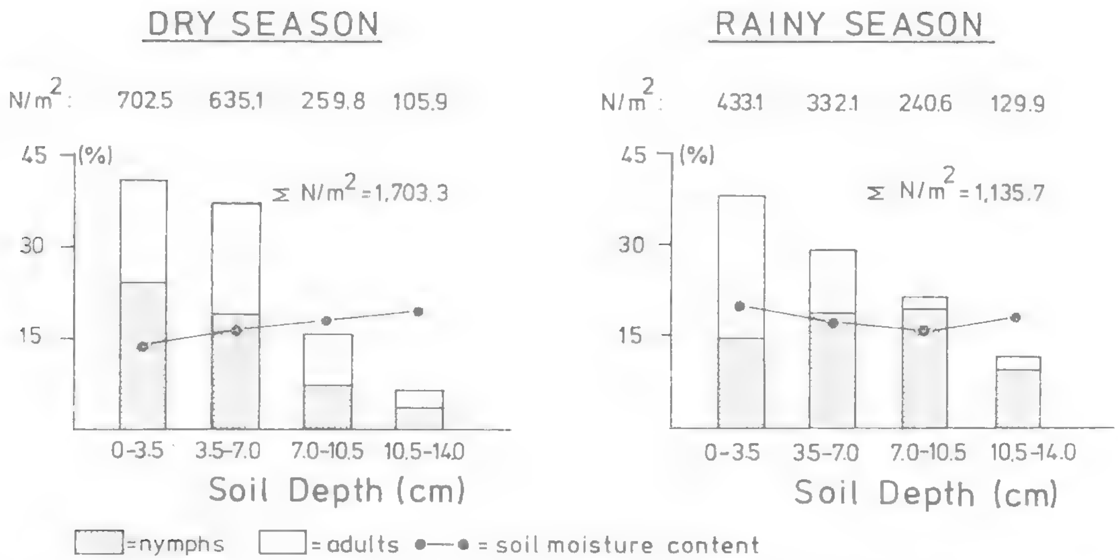

FIG. 1. Distribution of pseudoscorpions in soil and soil moisture content (both in %). Samples taken every 3.5cm to depth of 14cm in dry season and in rainy season in primary dryland forest on yellow latosol near Manaus, Brazil. Total catch each season = 100%. Abundance for each soil layer (N/m^2) and for total catch/ season (ΣN/m^2).

and on white sand soil (Adis *et al.*, 1989a, b, unpublished data; Morais, 1985). However, results were based mainly on data for orders. Evaluation of sampling data at the species level is now possible for pseudoscorpions, since identification has been completed by the second author.

STUDY AREAS

Primary Forest on Yellow Latosol

Sampling was carried out during the rainy (March) and dry seasons (October) of 1987 in a dryland terra firme forest at the Ducke Forest Reserve (= Reserva Florestal A. Ducke, 2°55'S, 59°59'W) of the National Institute for Amazonian Research (INPA, Manaus), situated on the Manaus-Itacoatiara highway (AM-010; cf. Penny and Arias, 1982). The area sampled was classified as high terra firme forest (Takeuchi, 1961; cf. Brinkmann, 1971) with several species of large, broad-trunked trees (with or without buttresses). The trees reached 44m in height (average height: 22m) and formed a closed canopy. Approximately 235 species, representing 43 families of trees, were recorded in the study area. Most frequent were Leguminosae, Rosaceae, Lauraceae, Sapotaceae and Lecitidaceae. The forest had a patchy understorey and a scanty herb layer. Guillaumet (1987), Lechthaler (1956), Prance (1990), Prance *et al.* (1976) and Rodrigues (1967) provide detailed botanical descriptions of the forest. Microclimatic data are given by Decico *et al.* (1977), Marques *et al.* (1981) and Ribeiro and Nova (1979). The soils near the Ducke Forest Reserve were described by Falesi and Silva (1969) as deep, yellow latosols, strongly weathered, excessively to very strongly acidic, of heavy texture in all profiles (A-C: 0-110cm) and with clay content of the B horizon varying from 50-70%. In the study area, where entomological long-term investigations have previously been undertaken (Adis and Schubart, 1984; Morais, 1985; Penny and Arias, 1982), the soil carried a 1-3cm thick humus layer (A_o), interspersed with fine roots and a thin leaf litter, covering most of the surface. For further details on the study area see Penny and Arias, 1982.

During the 1987 rainy season, 322mm of rain were recorded in March (data from the meteorological station at Ducke Forest Reserve, provided by M. de N.G. Ribeiro at INPA, Manaus). On the day of sampling (March 20, 1987) soil moisture content (= weight difference between wet and dried soil samples in%) was 20.0% at 0-3.5cm (= humus layer), 17.5% at 3.5-7cm, 15.5% at 7-10.5cm and 17.7% at 10.5-14cm soil depth, respectively (= mineral subsoil) (Fig. 1). Soil temperature at 10 a.m. decreased from 25.2°C in the top 3.5cm to 24.5°C at a soil

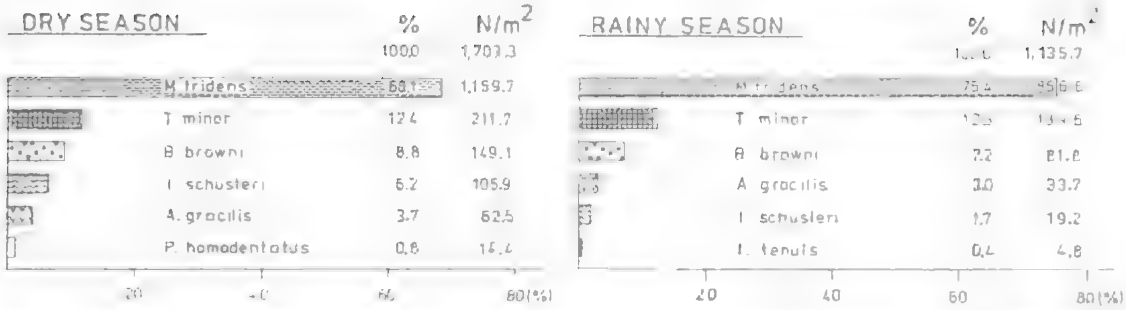

FIG. 2. Dominance (%) and abundance (N/m²) of species of pseudoscorpions extracted from 1m² of soil (0-14cm depth) during dry season (October 1987) and rainy season (March 1987) in primary dryland forest on yellow latosol near Manaus, Brazil. Total catch of each season = 100%. (See text for further explanation).

depth of 14cm. The soil pH increased from 3.3 in the top 3.5cm to 3.8 in the lower layers (3.5.-14cm). During the 1987 dry season, 139mm of rain were recorded in October (data from the meteorological station at Ducke Forest Reserve). On the day of sampling (October 14, 1987) soil moisture content increased from 13.6% in the top 3.5cm to 19.1% at a soil depth of 14cm (Fig. 1) and the soil pH increased from 3.3 to 3.8. Soil temperature at 11 a.m. varied slightly (24.6-24.7°C) from the surface to 14cm.

Primary Forest on White Sand Soil

Sampling was carried out during the rainy season (March) and the dry season (August) of 1988 in a dryland campinarana forest of the Biological Reserve INPA/SUFRAMA (approx. 2°30'S, 60°10'W), at km 45 (formerly km 62) on the Manaus Boa Vista highway (BR-174). Campinarana (= caatinga arbórea) was classified as a low, relatively light forest on white sand soil with thin-stemmed trees 10-20m high, with occasional large, broad-trunked individuals, with or without buttresses, a patchy understorey and no herb layer (Guillaumet, 1987; Anderson, 1981; Lisbôa, 1975). Data on geomorphology and soil genesis are found in Chauvel *et al.* (1987). Floral inventories have been given by Lisbôa (1975), Braga (1979), Anderson *et al.* (1975), Anderson (1981) and Guillaumet (1987), while the microclimatic data were provided by Ribeiro and Santos (1975). In the study area, the white sand soil carried a humus layer that was 10-11cm thick (A_0), penetrated by a matting of roots and a thin, surface-covering leaf litter.

During the 1988 rainy season, 293mm of rain were recorded in February and 280mm in March (data from the meteorological station of EMBRAPA/UEPAE, km 54). On the day of sampling (March 18, 1988) soil moisture content (= weight difference between wet and dried soil samples in %) increased from 20.1% in the top 3.5cm to 26.2% at 10.5cm depth (= humus layer) and dropped to 9.9% at 10.5-14cm (= white sand soil) (Fig. 4). Soil temperature at 11 a.m. decreased from 24.7°C in the top 3.5cm to 24.5°C at a soil depth of 14cm. The pH of the soil was 3.2 (0-3.5cm), 3.3 (3.5-7cm), 3.6 (7-10.5cm) and 3.7 (10.5-14cm), respectively. During the 1988 dry season, 77mm of rainfall were recorded in August (data from the meteorological station of EMBRAPA/UEPAE, km 54). On the day of sampling (August 05, 1988) soil moisture content decreased from 21.9% in the top 3.5cm to 9.5% at 10.5cm depth (= humus layer) and to 9.3% at 10.5-14cm (= white sand soil; Fig. 4). Soil temperature at 3 p.m. decreased from 27.1°C in the top 3.5cm to 25.5°C at a soil depth of 14cm. The pH of the soil was 3.6 (0-3.5cm), 3.5 (3.5-7cm), 3.5 (7-10.5cm) and 3.6 (10.5-14cm), respectively. The relative light intensity on the forest floor was about 2.1% (210 lx; comparative value in the open air at 3 p.m., 10.000 lx (overcast sky); cf. Brinkmann, 1970, 1971).

METHODOLOGY

In both study areas, six soil samples were taken along a transect at random intervals with a split corer (a steel cylinder with lateral hinges; diameter 21cm, length 33cm) which was driven into the soil with a mallet. Each sample was taken to a depth of 14cm and was then divided into four subsamples of 3.5cm each. Animals were extracted from subsamples following a modified method of Kempson (Adis, 1987). All pseudoscorpions were separated by species [adults (males and females), nymphal instars] and their

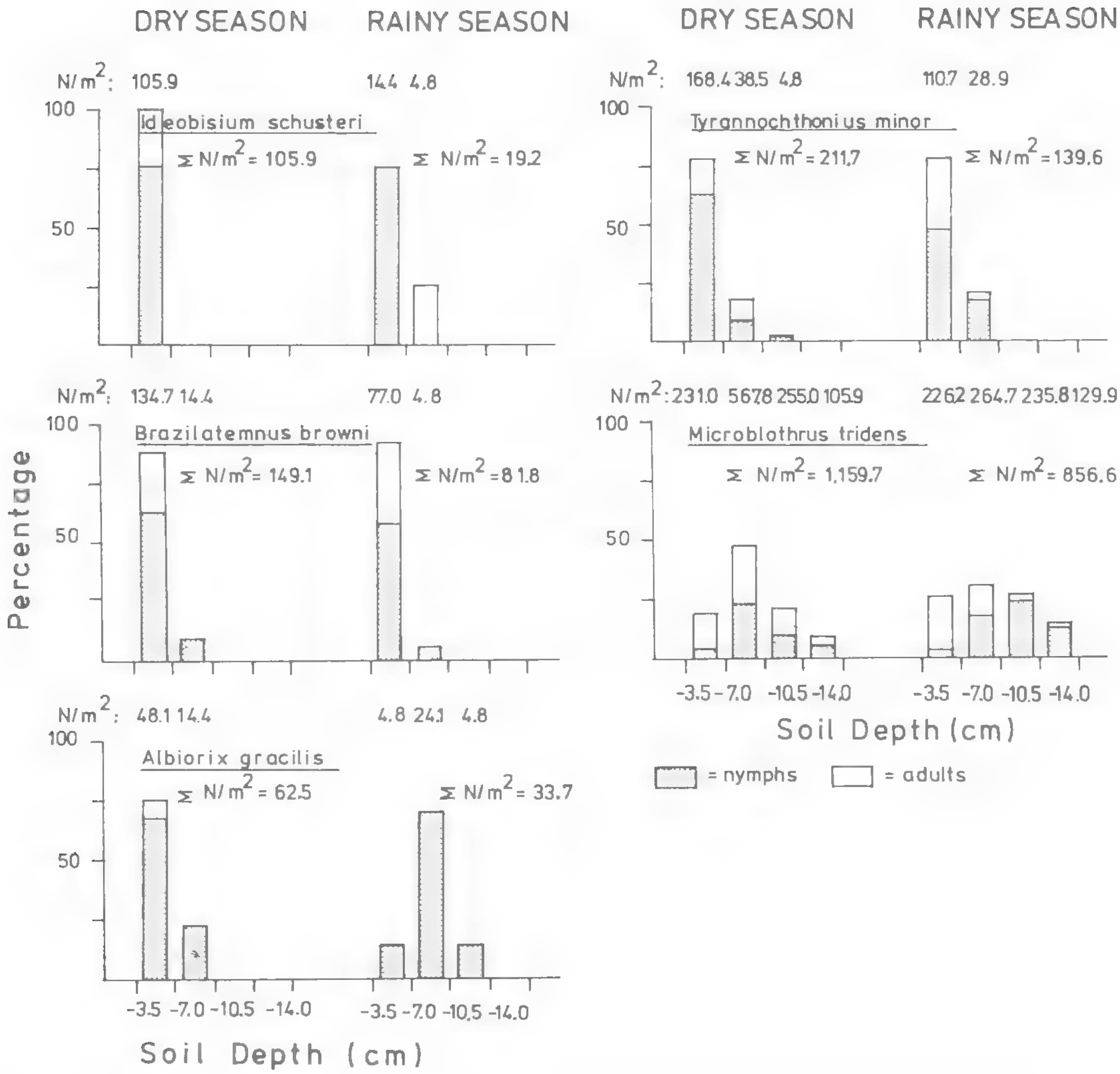

FIG. 3. Vertical distribution of five species of pseudoscorpions in soil (%). Samples taken every 3.5cm to depth of 14cm during dry season and rainy season in primary dryland forest on yellow latosol near Manaus, Brazil. Total catch each season = 100%. Abundance for each layer (N/m^2) and total catch per season (Σ N/m^2).

abundance was calculated for 1 m^2. Vertical distribution of adults and nymphs in relation to changing conditions of soil moisture content, temperature and pH was statistically evaluated with the linear correlation test (Cavalli-Sforza, 1972), using the original field data.

RESULTS

Primary Forest on Yellow Latosol

Pseudoscorpions accounted for 10-15% of all arthropods extracted from 1m^2 soil of 14cm depth (10,000-12,000 ind./m^2, Acari and Collembola disregarded) in the study area (Adis *et al.*, unpublished data). During the dry season, about 41% of all 1,700 ($\pm$71) pseudoscorpions were collected from the top 3.5.cm, 37% from below the humus layer (3.5-7cm) and 22% at 7-14cm depth. About 54% of all specimens collected represented juvenile stages (Fig. 1: nymphs). Decreasing abundance of pseudoscorpions at greater soil depths was significantly correlated with increasing soil moisture content (adults and nymphs: $P<0.01$, $r = -0.998$, nymphs only: $P<0.05$, $r = -0.956$; $n = 4$). During the rainy season, vertical distribution was similar (Fig. 1):

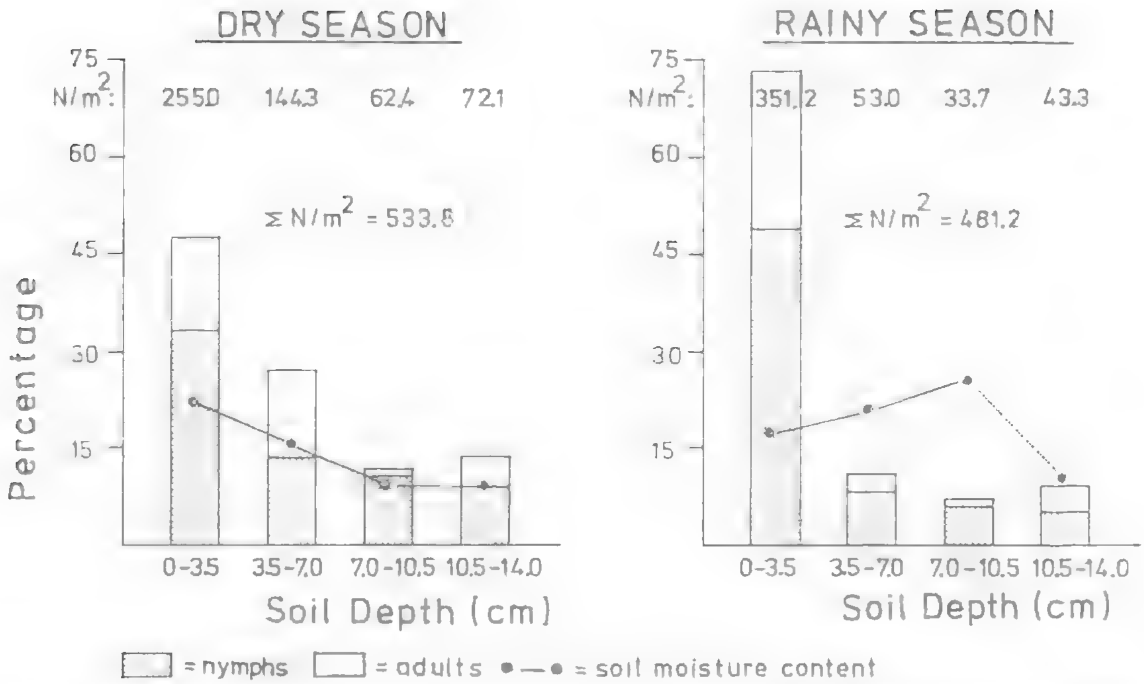

FIG. 4. Distribution of pseudoscorpions in soil and soil moisture content (both in %). Samples taken every 3.5cm to depth of 14cm during dry season and rainy season in primary dryland forest on white sand soil near Manaus, Brazil. Total catch each season = 100%. Abundance for each soil layer (N/m^2) and total catch / season (ΣN/m^2)

38% of the 1,100 ($\pm$46) pseudoscorpions were recovered from the top 3.5 cm, 29% from 3.5-7cm and 33% from 7-14cm soil depth. About 61% of the total catch were nymphs. Decreasing abundance of pseudoscorpions at greater soil depths was significantly correlated with decreasing soil temperature (adults and nymphs: $P<0.01$, $r = +0.993$, nymphs only: $P<0.05$, $r= +0.956$; $n = 4$).

Six species of pseudoscorpions were collected in both seasons (Fig. 2). All were previously reported from soils of Amazonian dryland forests (Mahnert and Adis, 1985). Syarinidae were most abundant, with *Microblothrus tridens* Mahnert (dry season: 1160$\pm$55 ind./m^2, rainy season: 860$\pm$24 ind./m^2), *Ideobisium schusteri* Mahnert and *Ideoblothrus tenuis* Mahnert accounting for 74-78% of the total catch (Fig. 2). Chthoniidae was the next most abundant family, with *Tyrannochthonius (T.) minor* Mahnert (= *Lagynochthonius minor* (Mahnert)); dry season: 212$\pm$17.4 ind./m^2, rainy season: 140$\pm$14 ind./m^2) and (dry season only) *Pseudochthonius homodentatus* Chamberlin representing 12-13% of the total catch. Less abundant (>10%) were Miratemnidae (*Brazilatemnus browni* Muchmore[1]; dry season: 149$\pm$20 ind./m^2, rainy season: 82$\pm$13 ind./m^2) and Ideoroncidae (*Albiorix gracilis* Mahnert). Few differences in dominance were found for species captured during both seasons, however their abundance varied (Fig. 2).

Except for *A. gracilis*, vertical distribution of pseudoscorpions in the soil differed between species but not within species when comparing different seasons (Fig. 3). *I. schusteri* and *B. browni* were only found at 0-7cm soil depth, with abundances being greatest in the top 3.5cm. This is also true for *T. minor* which lived, like *A. gracilis*, to a soil depth of 10.5cm. However, occurrence was restricted to the upper 7cm in *T. minor* during the rainy season and in *A. gracilis* during the dry season (Fig. 3). *I. tenuis* was found only at a soil depth of 3.5-7cm (= below the humus layer) during both seasons, whereas *M. tridens* occurred in all soil layers (0-14cm). During the dry season, significant correlation was observed between decreasing abundance of *T. minor* and greater soil depths (Fig. 3) and the

[1] At this locality, *B. browni* is apparently smaller. It may have adapted to its environment, thus representing an eco-species.

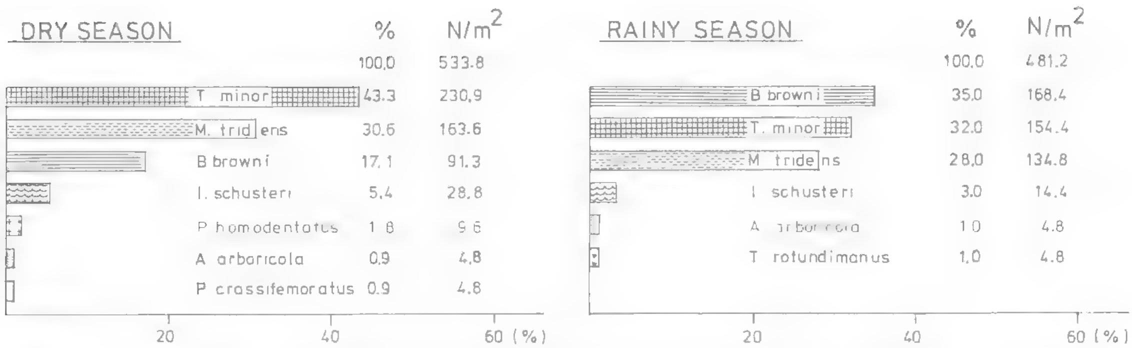

FIG. 5. Dominance (%) and abundance (N/m^2) of species of pseudo scorpions extracted from 1m^2 soil (0-14cm depth) during dry (August 1988) and rainy (March 1988) seasons in primary dryland forest on white sand soil near Manaus, Brazil. Total catch of each season = 100%. (See text for further explanation).

increased soil moisture content ($P<0.05$; adults and nymphs: $r = -0.959$, adults only: $r = -0.968$; $P<0.10$; $r = -0.936$ for nymphs only; $n=4$, respectively). Similar results were recorded from *A. gracilis* ($P<0.05$; adults and nymphs: $r = -0.969$, nymphs only: $r = +0.974$; $n = 4$). During the rainy season, decreasing abundance of *T. minor* and *B. browni* (Fig. 3) was significantly correlated with increasing pH values at greater soil depths (*T. minor*: $P<0.05$, $r = -0.970$ for adults and nymphs, $r = -0.951$ for nymphs only and $P<0.01$, $r = -0.994$ for adults only; *B. browni*: $P<0.01$, $r = -0.998$ for adults and nymphs and $r = -0.995$ for nymphs only; $n = 4$, respectively). In *M. tridens*, the increasing abundance of nymphs at greater soil depths was significantly correlated with decreasing soil moisture content ($P<0.05$, $r = -0.977$; $n = 4$). The decrease in abundance of adults, however, was significantly correlated with the decrease of the soil temperature at greater soil depths ($P<0.05$, $r = +0.962$; $n = 4$). This was also observed for nymphs of *T. minor* ($P<0.05$, $r = +0.951$; $n = 4$). Neoteny and potential parthenogenesis were confirmed for *M. tridens*, with sexually mature tritonymphs (= males) being absent (cf. Adis and Mahnert, 1990a; Mahnert, 1985).

Primary Forest on White Sand Soil

Pseudoscorpions accounted for 3-4% of all arthropods extracted from 1m^2 soil of 14cm depth (14,000-15,000 ind./m^2, Acari and Collembola disregarded) in the study area (Adis *et al.*, 1989a, b). During the dry season, about 48% of the total 530 ($\pm$22) pseudoscorpions were collected from the top 3.5cm, 27% from 3.5-7cm, 12% from 7-10.5cm (= humus layer) and 13% from the white sand soil layer (10.5-14cm). About 66% of all specimens collected represented juvenile stages (Fig. 4: nymphs). Decreasing abundance of pseudoscorpions at greater soil depths was significantly correlated with decreasing soil moisture content ($P<0.05$; adults and nymphs: $r = +0.965$, adults only: $r = +0.952$; $n=4$) and decreasing soil temperature ($P<0.05$; adults and nymphs: $r = +0.967$; $n=4$). During the rainy season, vertical distribution was similar but more pronounced (Fig. 4): 73% of the 480 ($\pm$27) pseudoscorpions were taken from the top 3.5cm, 11% from 3.5-7cm, 7% from 7-10.5cm and 9% from the white sand soil layer (10.5-14cm). About 68% of the total catch were nymphs. No significant correlation was found between the vertical distribution of pseudoscorpions and changing conditions of soil moisture content, soil temperature and pH.

Seven species of pseudoscorpions were obtained during the dry and six species during the rainy season (Fig. 5). All were previously reported from soils of Amazonian dryland forests (Mahnert and Adis, 1985). Chthoniidae were most abundant, with *Tyrannochthonius (T.) minor* Mahnert (dry season: 231$\pm$13 ind./m^2, rainy season: 154$\pm$15 ind./m^2), *T. (T.) rotundimanus* Mahnert and *Pseudochthonius homodentatus* Chamberlin accounting for 33-45% of the total catch (Fig. 5). Syarinidae was the next most abundant family with *Microblothrus tridens* Mahnert (dry season: 164$\pm$10 ind./m^2, rainy season: 135$\pm$8 ind./m^2) and *Ideobisium schusteri* Mahnert (dry season: 29$\pm$3 ind./m^2, rainy season 14$\pm$4 ind./m^2) accounting for 31-36% of the total catch. The Miratemnidae were represented by *Brazilatemnus browni* Muchmore (17-35%; dry season: 91$\pm$6 ind./m^2, rainy season: 168$\pm$16 ind./m^2). Less abundant ($\leq$ 1%)

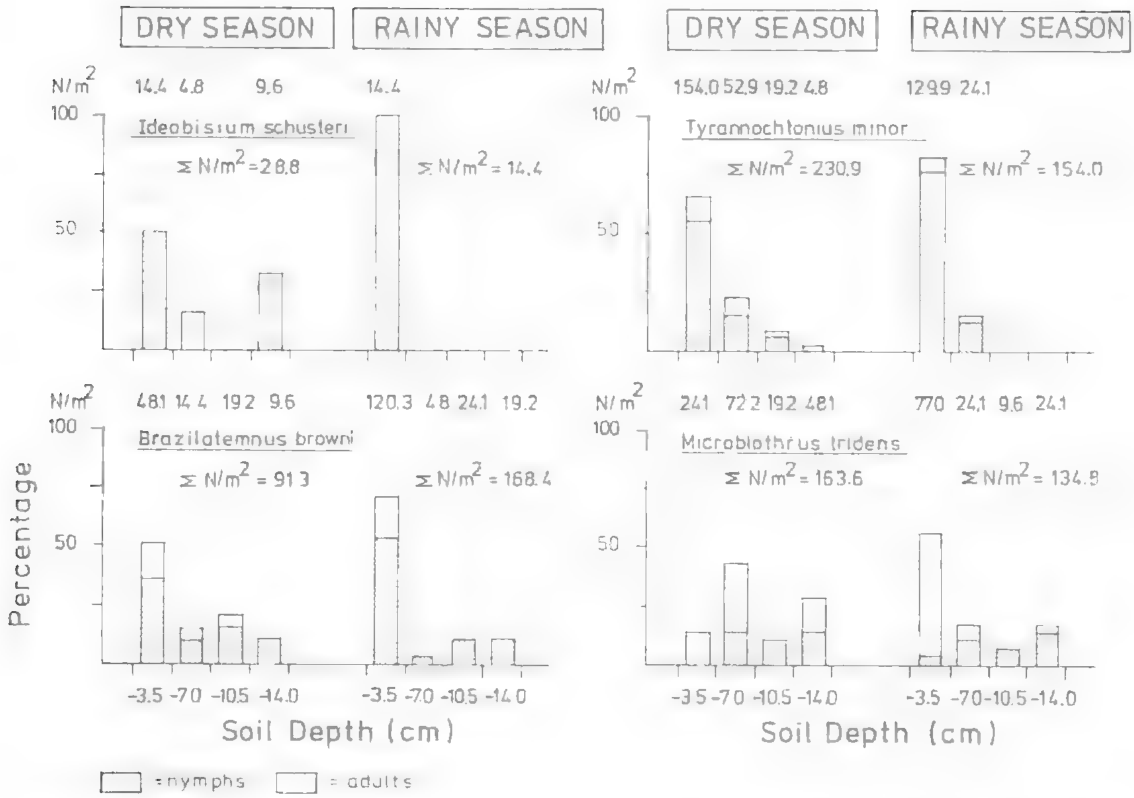

FIG. 6. Vertical distribution of four species of pseudoscorpions in soil (%). Samples taken every 3.5cm to depth of 14cm during dry and rainy seasons in primary dryland forest on white sand soil near Manaus, Brazil. Total catch of each season = 100%. Abundance given for each soil layer (N/m^2) and for total catch per season ($\Sigma N/m^2$).

were Ideoroncidae (*Albiorix gracilis* Mahnert) and Chernetidae (*Pseudopilanus crassifemoratus* Mahnert). The same four species (*T. minor*, *B. browni*, *M. tridens* and *I. schusteri*) were the most abundant in both seasons, however, their dominance in the total catch per season varied (Fig. 5). In two species, vertical distribution differed with the seasons. During the rainy season, *T. minor* and *I. schusteri* were found only from 0-7cm and in the top 3.5cm of soil, respectively. Both species were found throughout the 0-14cm soil sample during the dry season (Fig. 6). Their abundance was greatest in the top 3.5cm, independent of seasons. This is also true for *B. browni* which, together with *M. tridens*, occurred throughout the 0-14cm soil sample during the dry season as well as the rainy season. Adults of *M. tridens* were somewhat more abundant in the top 7cm, whereas no adults of *I. schusteri* were collected, probably due to low catch numbers. *A. arboricola* was restricted to the top 3.5cm. During the dry season, significant correlation between abundance and soil conditions was observed in *T. minor*: its abundance decreased at greater soil depths as the soil moisture content ($P<0.05$, $r = +0.979$ only for adults; $P<0.10$, $r = +0.935$ for adults and nymphs, $r = +0.900$ for nymphs only; $n = 4$, respectively) and the soil temperature decreased ($P<0.05$, $r = +0.967$ for adults and nymphs, $r = +0.972$ for adults; $P<0.10$, $r = +0.939$ for nymphs only; $n = 4$, respectively). No significant correlation was found during the rainy season between the vertical distribution of species and the abiotic factors investigated. In *M. tridens* sexually mature tritonymphs (= males) were absent, which confirms neoteny and potential parthenogenesis in this species (cf. 4.1.).

DISCUSSION

In Central Amazonia the abundance of pseudoscorpions in primary and secondary dryland forests on yellow latosol accounted (independently of seasons) for 3-5% of all arthropods extracted from $1m^2$ soil of 14cm depth and for 10-15% when Acari and Collembola were excluded (cf. Adis *et al.*, 1987a, b, unpublished data). In the primary forest on white sand soil, their abundance was only 0.7-0.9% and 3-4%, respectively, due to large numbers of Pauropoda and Diplura (cf. Adis *et al.*, 1989a, b). About two-thirds of all pseudoscorpions recovered from the soil of the primary and secondary forest on yellow latosol (61-67% of the total catch) and about three-quarters of the primary white sand forest (75-84%) inhabited the top 7cm. No species were found to occur exclusively in the lower, mineral subsoil (e.g. in 10.5-14cm soil depth). Two species (*T. minor*, *B. browni*) were more abundant in the upper, organic layer in the three forests which were investigated (Figs 3, 6; fig. 3 in Adis and Mahnert, 1990a). *M. tridens*, *T. minor* and *B. browni* were the most abundant species, representing 89-95% of the total catch in the primary forests on yellow latosol and on white sand soil. They represented 58-74% of the total catch in the secondary forest on yellow latosol, where *I. tenuis* and *A. gracilis* were frequent as well (22-33% of the total catch; cf. Adis and Mahnert, 1990a). The similar spectrum of pseudoscorpion species in forests on yellow latosol and on white sand soil and especially the lack of endemic species in the latter forest type, confirm the geological results of Chauvel *et al.* (1987). They reported that the white sand area investigated represents the final stage of podzolisation, i.e. the transformation of clayey latosols to white sandy podzols by (long-term) weathering and leaching processes. If the white sand area were a large dried-up old riverbed, species composition would be different from the yellow latosol area (cf. Adis and Mahnert, 1990b).

Neither during the dry nor the rainy season was the abundance of pseudoscorpions in mineral subsoils higher in response to the changing moisture content in organic layers. This phenomenon has been reported in arthropods in the seasonally-dry tropical forests, where periods without precipitation occur [cf. climate diagrams for Central America (Walter and Lieth, 1960-67) and for Manaus (Worbes, 1986)]. Higher or lower abundance of (at least some) species at a distinct soil depth seems to be related to different abiotic factors. For example, the decreasing abundance of *T. minor* with soil depth during the dry season was correlated with soil moisture content in two forest types: negatively with increasing moisture content values in the primary forest on yellow latosol and positively with decreasing soil moisture in the primary forest on white sand soil (cf. 4.1, 4.2.). In addition, decreasing abundance with depth was also related to somewhat lower temperatures recorded from the lower levels of soil in the white sand forest. During the rainy season, no correlation was found between species abundance and soil moisture content in these two forest types. However, in the forest on yellow latosol there was positive correlation between decreased abundance of nymphs and lower soil temperatures and negative correlation between decreased abundance of nymphs, nymphs and adults ($P<0.05$) and increased soil pH. At greater soil depths there was an even higher statistical probability ($P<0.01$) of negative correlation between decreased abundance of adults and increased pH. Correlation between abundance and soil moisture content has not yet been reported for *T. minor* from the secondary forest on yellow latosol (Adis and Mahnert, 1990a). The more homogeneous occurrence of *M. tridens* in 0-14cm soil depth (Figs 3, 6; fig. 3 in Adis and Mahnert, 1990a) was correlated with soil moisture content as well: there was positive correlation between decreasing numbers of nymphs and soil moisture in the primary forest on yellow latosol during the rainy season and, correspondingly, negative correlation between increasing abundance of nymphs and decreasing soil moisture content at greater soil depths in the secondary forest on yellow latosol (cf. Adis and Mahnert, 1990a). In adults, however, there was a positive correlation between decreased abundance and soil moisture content (secondary forest) and between decreased abundance and lower temperatures at greater soil depths (primary forest).

These data all suggest that factors other than soil moisture content (abiotic and/or biotic ones) may as well cause the different distribution of pseudoscorpion species in the soil. A significant correlation, for example, was found between the abundance of pseudoscorpions and Collembola in the secondary forest on yellow latosol ($P<0.05$; dry season: $r = +0.969$, rainy season: $r = +0.989$; $n = 4$) and in the primary forest on white sand soil (dry season: $P<0.01$, $r = +0.991$, rainy season: $P<0.05$, $r = +0.967$; $n = 4$). This relationship has to be investigated in more detail, as springtails represent a potential food source for pseudoscorpions (cf. Jones, 1975; Ressl and Beier, 1958; Weygoldt, 1969). Thus, complementary studies should be carried out on reproduction patterns, food availability and trophic structure over a one-year period (cf. Adis *et al.*, 1988). Data also show that the number of samples taken per soil layer (n= 6) was sufficient for a species dominance of 5% of the total catch, as standard deviation did not exceed 20%. Results indicate that terricole pseudoscorpions of primary dryland forests on white sand soil and of secondary dryland forests on yellow latosol represent the terricole species spectrum of a primary dryland forest on yellow latosol, which has been altered either by geomorphological/geochemical processes or human impact (cf. Morais, 1985; Rodrigues, 1986). Habitat preference in pseudoscorpions and the many habitat types existing in Amazonia are considered to be major reasons for the high species diversity found in neotropical pseudoscorpions (cf. Adis and Mahnert, 1985, 1990b).

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LITERATURE CITED

ADIS, J. 1987. Extraction of arthropods from neotropical soils with a modified Kempson apparatus. Journal of Tropical Ecology 3: 131-138.

ADIS, J. & MAHNERT, V. 1985. On the natural history and ecology of Pseudoscorpiones (Arachnida) from an Amazonian blackwater inundation forest. Amazoniana 9: 297-314.

1990a. Vertical distribution and abundance of Pseudoscorpiones (Arachnida) in the soil of a Neotropical secondary forest during the dry season and rainy season. Acta Zoologica Fennica 190: 11-16.

1990b. On the species composition of Pseudoscorpiones from Amazonian dryland and inundation forests in Brazil. Revue suisse de Zoologie 97: 49-53.

ADIS, J. & SCHUBART, H.O.R. 1984. Ecological research on arthropods in Central Amazonian forest ecosystems with recommendations for study procedures. 111-144. In J.H. Cooley and F.B. Golley (eds) 'Trends in ecological research for the 1980s.' (NATO Conference Series, Series I: Ecology, Plenum Press: New York, London).

ADIS, J., MORAIS, J.W.DE & RIBEIRO, E.F. 1987a. Vertical distribution and abundance of arthropods in the soil of a Neotropical secondary forest during the dry season. Tropical Ecology 28: 174-181.

ADIS, J., MORAIS, J.W.DE & MESQUITA, H.G.DE 1987b. Vertical distribution and abundance of arthropods in the soil of a Neotropical secondary forest during the rainy season. Studies on Neotropical Fauna and Environment 22: 189-197.

ADIS, J., MAHNERT, V., MORAIS, J.W.DE & RODRIGUES, J.M.G. 1988. Adaptation of an Amazonian pseudoscorpion (Arachnida) from dryland forests to inundation forests. Ecology 69: 287-291.

ADIS, J., MORAIS, J.W.DE, RIBEIRO, E.F. & RIBEIRO, J.C. 1989a. Vertical distribution and abundance of arthropods from white sand soil of a Neotropical campinarana forest during the rainy season. Studies on Neotropical Fauna and Environment 24: 193-200.

ADIS, J., RIBEIRO, E.F., MORAIS, J.W.DE & CAVALCANTE, E.T.S. 1989b. Vertical distribution and abundance of arthropods from white sand soil of a Neotropical campinarana forest during the dry season. Studies on Neotropical Fauna and Environment 24: 201-211.

ANDERSON, A.B. 1981. White-sand vegetation of Brazilian Amazonia. Biotropica 13: 199-210.

ANDERSON, A.B., PRANCE, G.T. & ALBUQUERQUE, B.W.P.DE 1975. Estudos sobre a vegetação das Campinas Amazônicas -III. A vegetação lenhosa da Campina da Reserva Biológica INPA SUFRAMA (Manaus-Caracaraí, km 62). Acta Amazonica 5: 225-246.

BECK, L. 1964. Tropische Bodenfauna im Wechsel von Regen-und Trockenzeit. Natur und Museum 94: 63-71

BRINKMANN, W.L.F. 1970. Relative light intensity measurements in a secondary forest (capoeira) near Manaus, Amazonia, Brazil. Boletim do INPA (Manaus, Brazil), Pesquisas Florestais 17: 1-6.

1971. Light environment in tropical rain forest of Central Amazonia. Acta Amazonica 1: 37-49.

BULLOCK, J.A. 1967. The Arthropoda of tropical soils and leaf litter. Tropical Ecology 8: 74-87.

BRAGA, P.I.S. 1979. Subdivisão fitogeográfica, tipos de vegetação, conservação e inventário florístico da floresta amazônica. Acta Amazonica 9 (Suplement): 53-80.

CAVALLI-SFORZA, L. 1972. 'Grundzüge biologisch-medizinischer Statistik.' (G. Fischer: Stuttgart).

CHAUVEL, A., LUCAS, Y. & BOULET, R. 1987. The dynamics of the Amazonian terra-firme forest: On the genesis of the soil mantle of the region of Manaus, Central Amazônia, Brazil. Experientia 43: 234-241.

DECICO, A., SANTOS, H.M., RIBEIRO, M.DE N.G. & SALATI, E. 1977. Estudos climatológicos da Reserva Florestal Ducke, Manaus, AM. I. Geotemperaturas. Acta Amazonica 7: 485-494.

FALESI, I. & SILVA, B.N.R.DA 1969. Os solos da área Manaus-Itacoatiara. Série Estudados e Ensaios no.

1. Secretaria de Produção do Amazonas. (IPEAN: Belém, Brasil).
GOFFINET, G. 1976. Ecologie édaphique des milieux naturels du Haut-Shaba (Zaïre). I. Charactéristiques, écotopiques et synécologie comparée des zoocénoses intercaliques. Revue d'Écologie et de Biologie du Sol 12: 691-722.
GUILLAUMET, J.-L. 1987. The dynamics of the Amazonian terra-firme forest: Some structural and floristic aspects of the forest. Experientia 43: 241-251.
JONES, P.E. 1975. Notes on the predators and prey of British pseudoscorpions. Bulletin of the British Arachnological Society 3: 104-105.
LAWRENCE, R.F. 1953. 'The biology of the cryptic fauna of forests with special references to the indigenous forests of South Africa.' (Cape Town).
LECHTHALER, R. 1956. 'Inventário das árvores de um hectare de terra firme da zona "Reserva Florestal Ducke" município de Manaus.' (Amazônia (Botânica) no. 3, INPA: Manaus, Brazil).
LEVINGS, S.C. & WINDSOR, D.M. 1984. Litter moisture content as a determinant of litter arthropod distribution and abundance during the dry season on Barro Colorado Island, Panama. Biotropica 16: 125-131.
LIEBERMANN, S. & DOCK, C.F. 1982. Analysis of the leaf litter arthropod fauna of a lowland tropical evergreen forest site (La Selva, Costa Rica). Revista de Biologia Tropical 30: 27-34.
LISBõA, P.L. 1975. Estudos sobre a vegetação das Campinas Amazônicas. II. Observações gerais e revisão bibliográfica sobre as campinas amazônicas de areia branca. Acta Amazonica 5: 211-223.
MAHNERT, V. 1985. Weitere Pseudoskorpione (Arachnida) aus dem zentralen Amazonasgebiet (Brasilien). Amazoniana 9: 215-241.
MAHNERT, V. & ADIS, J. 1985. On the occurrence and habitat of Pseudoscorpiones (Arachnida) from Amazonian forests of Brazil. Studies on Neotropical Fauna and Environment 20: 211-215.
MARQUES, A.DE O.F., RIBEIRO, M.DE N.G., SANTOS, H.M.DOS & SANTOS, J.M.DOS 1981. Estudos climatológicos da Reserva Florestal Ducke, Manaus-AM. IV. Precipitação. Acta Amazonica 11: 759-768.
MERINO, J.F. & SERAFINO, A. 1978. Variaciones mensuales en la densidad de microartrópodos edáficos en un cafetal de Costa Rica. Revista de Biologia Tropical 26: 291-301.
MORAIS, J.W. DE 1985. 'Abundância e distribuição vertical de Arthropoda do solo numa floresta primária não inundada.' (M.Sc. Thesis INPA: Manaus, Brazil).
PENNY, N.D. & ARIAS, J.R. 1982. 'Insects of an Amazon forest.' (Columbia University Press: New York).
PETERSEN, H. & LUXTON, M. 1982.. A comparative analysis of soil fauna populations and their role in decomposition processes. Oikos 39: 288-387.
PRANCE, G.T. 1990. The floristic composition of the forests of Central Amazonian Brazil. 60-71. In Gentry, A.H. (ed.) 'Four neotropical rain forests.' (Yale University Press: New Haven).
PRANCE, G.T., RODRIGUES, W.A. & SILVA, M.F.DA 1976. Inventário florestal de um hectare de mata de terra firme km 30 da Estrada Manaus-Itacoatiara. Acta Amazonica 6: 9-35.
RESSL, F. & BEIER, M. 1958. Zur Ökologie und Phänologie der heimischen Pseudoskorpione. Zoologische Jahrbücher. Abteilung für Systematik, Oekologie und Geographie der Tiere 86: 1-26.
RIBEIRO, M.DE N.G. & ADIS. J. 1984. Local rainfall variability–a potential bias for bioecological studies in the Central Amazon. Acta Amazonica 14: 159-174.
RIBEIRO, M.DE N.G. & NOVA, N.A.V. 1979. Estudos climatológicos da Reserva Florestal Ducke, Manaus, AM. III. Evaporatranspiração. Acta Amazonica 9: 305-309.
RIBEIRO, M.DE N.G. & SANTOS, A.DOS 1975. Observaçoes micro climáticas no ecossistema Campina Amazônica. Acta Amazonica 5: 183-189.
RODRIGUES, J.M.G. 1986. 'Abundância e distribuição vertical de Arthropoda do solo, em capoeira de terra firme.' (M.Sc. Thesis, INPA: Manaus, Brazil). 80 p.
RODRIGUES, W.A. 1967. Inventário florestal piloto ao longo da estrada Manaus-Itacoatiara: Dados preliminares. Atas do Simpósio sobre Biota Amazônica 7: 257-267.
RYBALOV, L.B. 1990. Comparative characteristics of soil macro fauna of some tropical savannah communities in Equatorial Africa: preliminary results. Tropical Zoology 3: 1-11.
STRICKLAND, A.H. 1947. The soil fauna of two contrasted plots of land in Trinidad, British West Indies. Journal of Animal Ecology 16: 1-10.
TAKEUCHI, M. 1961. The structure of the Amazonian vegetation. II. Tropical rain forest. Journal of the Faculty of Science. University of Tokyo. Section 3: Botany 8: 1-26.
WALTER, H. & LIETH, H. 1960-67. 'Klimadiagramm-Weltatlas.' (G. Fischer: Jena).
WEYGOLDT, P. 1969. 'The biology of pseudoscorpions.' (Harvard University Press: Cambridge, Massachusetts).
WILLIS, E.O. 1976. Seasonal changes in the invertebrate litter fauna on Barro Colorado Island, Panama. Revista Brasileira de Biologia 36: 643-657.
WORBES, M. 1986. Lebensbedingungen und Holzwachstum in zentral amazonischen Überschwemmungswäldern. Scripta Geobotanica 17: 1-112.

NEST ASSOCIATES OF *CLUBIONA ROBUSTA* L. KOCH (ARANEAE: CLUBIONIDAE) IN AUSTRALIA

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Austin, A.D. 1993 11 11: Nest associates of *Clubiona robusta* L. Koch (Araneae: Clubionidae) in Australia. *Memoirs of the Queensland Museum* 33(2): 441-446. Brisbane. ISSN 0079-8835.

The nests of *Clubiona robusta*, whether or not they contain a resident female spider, are usually inhabited by other invertebrates, here termed nest associates. The abundance and diversity of nest associates for *C. robusta* are described from sampled nests. Associates recorded were: other spiders, Acarina, Mollusca and insects of the orders Collembola, Coleoptera, Heteroptera, Hymenoptera, Lepidoptera, Neuroptera, Psocoptera and Thysanoptera. The presence of a resident female was a factor which affects the abundance and diversity of associates. Biological notes on each group of nest associates are given. Results for *C. robusta* are compared with data on other spiders in the same habitat, and other categories of nest associates used in other studies.□*Araneae, Clubionidae, parasitoid, predator, eggs, spider nest.*

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Most vagabond spiders build a silken retreat in which they moult, mate, lay eggs and protect themselves and their eggs from predators and extreme environmental conditions (Jackson, 1979; Jackson and Griswold, 1979; Pollard and Jackson, 1982; Austin, 1984a, 1988; Wolf, 1990). Different species construct a great variety of retreats which vary in size, structural complexity and the location in which they are placed. For *Clubiona robusta* L. Koch, a moderate-sized clubionid (body length about 15 mm) which inhabits the corticating (shedding) bark of eucalypt trees in south-eastern Australia, two types of retreats have been recognized: flimsy, thin, silk-walled moulting chambers constructed by juveniles, and thicker walled nests constructed by mature females for egg laying (Austin, 1984a).

Whatever the structure of spider retreats, they often attract an array of other invertebrates (termed 'nest associates') which utilize them in a variety of ways (Auten, 1925; Jackson and Griswold, 1979; Griswold, 1986). This aspect of spider retreats has been examined only rarely. A study of the nest associates of the salticid *Phidippus johnsoni* Peckham and Peckham in the U.S.A. by Jackson and Griswold (1979) is the only known detailed work. Jackson and Griswold (1979) divided nest associates into eight categories, following the three described by Auten (1925), based on their biological relationship with the resident spider, its eggs or the nest itself (see Table 1). Most of these biological categories have also been recognized for two eresid species in South Africa (Griswold, 1986).

During a study of the biology of *C. robusta* in South Australia (Austin, 1984a, 1988), incidental observations showed that 1) most nests contained at least some associates, 2) associates inhabited both vacant and occupied nests, and 3) the size range of associates appeared to differ between vacant and occupied nests. This study then sets out to detail the diversity and abundance of nest associates found in *C. robusta* nests, and the factors that might determine their number and size.

MATERIALS AND METHODS

Nests of *C. robusta* were collected from under the bark of eucalypt trees with large plates of corticating bark at their bases (i.e. *Eucalyptus camaldulensis, E. cladocalyx, E. leucoxylon* and *E. viminalis*) in the Mylor area of the Adelaide Hills, South Australia (see Austin, 1984a). Nests were collected at random in the summer (December-February) over three years (1979-1981). Nests constructed only in that summer were included in samples. The whiter, fresher colour of the silk was used to distinguish them from nests built in previous seasons. Samples included vacant nests, nests containing a resident spider, and nests containing a resident spider and egg-mass or hatched juveniles. In the field, after bark plates were removed from trees, nests were gently teased away and placed in screw-top plastic vials (40 mm dia.). A large white dish prevented accidental loss of any associates or resident spiders. In the laboratory, when nest associates were en-

Category	Description
1a	Endoparasitoids of spiders that seek out and/or emerge from their hosts inside nests
1b	Ectoparasites and ectoparasitoids of spiders that seek out and/or emerge from their hosts inside nests
2	Endoparasitoids of eggs in nests
3a	Predators of eggs in nests (including 'ectoparasitoids')
3b	Predators of spiders in nests
4	Scavengers feeding on dead spiders or other material in nests
5	Predatory spiders that adopt nests as a predatory device
6	Spiders that adopt the nests of other spiders as a refuge or substitute for constructing their own nests
7	Organisms (other than spiders) that adopt nests as a refuge or pupation site
8	Accidental inhabitants
9	Conspecific males

TABLE 1. Categories of nest associates, modified after Jackson and Griswold (1979) (see text for further information).

countered, details of the nest were recorded along with any relevant biological information for the associate, and they were then preserved in 70% alcohol for identification. Parasitized spider eggs and the larvae and pupae of mantispids, pompilids, Diptera and Lepidoptera were left to emerge prior to preservation. As in Jackson and Griswold (1979), nest associates only within the nest, within the silk matrix of the nest wall, or under the nest were collected, not those completely outside or near the nest. To compare differences in the diversity, size and abundance of associates between vacant nests and those occupied by a resident female, 30 nests of each type were collected at random in the field during January 1980 and examined.

Voucher specimens of each nest associate were lodged in the Department of Crop Protection insect collection, Waite Campus, University of Adelaide, South Australia.

RESULTS

Over 400 nests sampled during the summers of 1979 to 1981, yielded over 40 species of nest associates including Acarina, Araneae, Collembola, Coleoptera, Diptera, Heteroptera, Hymenoptera, Lepidoptera, Neuroptera, Psocoptera, Thysanoptera and Mollusca (Table 2). The biological association of each associate with *C. robusta* (categories listed in Table 1), whether determined by direct observation or only assumed, is also given for each species in Table 2. The exact category of individual associates could be assigned only for those species whose biology was observed directly (e.g., parasitoids or predators of eggs or adult *C. robusta*–?*Ogcodes* sp., *Ceratobaeus masneri* Austin), or for those species whose biology was well enough known to rule out all categories except one (e.g., Lepidoptera pupating in nests or Hymenoptera which specifically parasitize other spiders). For other associates, multiple categories are listed to indicate the range of biological associations that might exist. For many species it was impossible to determine whether nests were being used as a specific refuge or the species was there by accident (categories 7/8). For others, their association with *C. robusta* appeared to vary. Gnaphosid and segestriid spiders were observed in the field preying on subadult *C. robusta* (category 3b, see below), as well as constructing their own nests inside those of the host spider (category 6).

Nest associates seemed to occur both in vacant nests and those occupied by a female spider, there appearing to be fewer and smaller associates in the latter. To test these hypotheses, i.e. that occupied nests had fewer and smaller associates, the fauna from 30 occupied nests and 30 vacant nests were compared (Table 3). Of the 40 recognized taxa that were collected during the 1979-81 survey, 28 were found in the 60 sampled nests, with Diptera and Neuroptera being the ordinal taxa not recorded. The 30 occupied nests had substantially fewer nest associates (total 147) compared with vacant nests (227) (see Table 3). Using a Wilcoxin test (Zar, 1984) occupied nests contained significantly fewer associates per nest than vacant nests ($Z = 2.36$, $P < 0.02$), and significantly fewer associates larger than 2.5 mm in length ($Z = -4.38$, $P < 0.0001$). The two major groups of associates that seemed to differ most notably between vacant and occupied nests were other species of spiders and Coleoptera, which were both mostly represented by individuals much greater than 2.5 mm long. This specific size was chosen to test for differences in size of nest associates because previous work on *C. robusta* has shown that this is about the minimum size for potential prey that females spiders can physically handle (Austin, 1988). Hence, one suggested cause for fewer large associates in occupied nests is that they would be killed or driven away by the resident spider.

Biology of Nest Associates

Assigning nest associates to one or more biological categories first required that those used by Jackson and Griswold (1979) be modified. In particular, endo- and ectoparasitoids have been

Taxonomy of nest associate	Associate Category	C. robusta		
		I	II	III
Acarina: Mesostigmata				
Phytoseiidae *Seiulus* sp.	4/7/8	+	5	2
Acarina: Prostigmata				
Bdellidae *Bdellodes harpax* (Atyeo)	4/7/8	+	2	2
Cyta latirostris (Hermann)	4/7/8	+	1	1
Anystidae genus & sp. indet.	4/7/8	+	6	7
?Eupalopsellidae genus & sp. indet	4/7/8	+	1	2
Erythraeidae genus & sp. indet	4/7/8	+	3	2
Araneae				
Clubionidae *Clubiona cycladata* Simon	3a/6/8	+	3	2
C.robusta L.Koch ♂	9	+	8	2
Clubiona spp. juveniles*	6/8	+	16	11
Gnaphosidae *Intruda* sp.	3a/3b/6/8	+	2	0
Hahniidae *Scotospilus* sp.	3a/6/8	+	0	0
Lamponidae *Lampona* sp.	3a/3b/6 /8	+	1	0
Salticidae *Myrmarachne* sp.	3a/6/8	+	3	0
Servaea sp.	3a/6/8	+	1	0
Segestriidae *Ariadna* sp.	3a/3b/6 /8	+	2	0
Collembola				
Entomobryidae *Drepanura* sp. 1 & 2*	4/7/8	+	11	7
Neanuridae *Setanodosa* sp.	4/7/8	+	5	3
Coleoptera				
Coccinellidae *Scymus parallelus* Blackburn	4/7/8	+	5	2
Dermestidae *Anthrenus* sp.	4/7/8	+	2	1
Trogoderma antipodum Blackburn	4/7/8	+	1	0
Tenebrionidae genus & spp. indet.*	4/7/8	+	11	6
Diptera				
Acroceridae ? *Ogcodes* sp.	1a	+	0	0
Chloropidae *Pseudogaurax* sp.	3a	+	0	0
Heteroptera				
Reduviidae *Empicoris rubromaculatus* (Blackburn)	3a/7/8	+	4	2
Pentatomidae *Nezara viridula* L.	7/8	+	0	0
Poecilometis sp.	7/8	+	0	0
Hymenoptera				
Eulophidae *Tetrastichus* sp.	3a	+	0	0
Formicidae *Iridomyrmex* sp.	3a	+	3	0
Scelionidae *Ceratobaeus clubionus* Austin	7/8	+	2	2
C. lamponae (Hickman)	7/8	+	0	0
C. masneri Austin	2	+	4	7
Gryon sp.	7/8	-	1	0
Trissolcus sp.	7/8	-	0	1
Pompilidae *Epipompilus* sp.	3a	+	0	0
Lepidoptera				
Limacodidae *Doratifera* sp. (pupa)	7	-	1	0
genus & spp. indet. (larvae)*	7/8	+	0	0
Neuroptera				
Mantispidae *Austromantispa* sp.	1b/3a	+	0	0
genus & sp. indet. (larva)	1b/3a	+	0	0
Psocoptera				
Lepidopsocidae genus & spp. indet.*	4/7/8	+	2	5
Liposcelidae *Liposcelis* sp.	4/7/8	+	6	8
Thysanoptera Thripidae genus & spp. indet.*	4/7/8	+	6	7
Mollusca: Gastropoda Helicidae *Cochlicella ventrosa* (Ferussac)	4/7/8	+	1	0

TABLE 2. Nest associates in nests of *Clubiona robusta* and category of associate to which they belong (see Table 1 and text). I = associates found at least once (+) in occupied or vacant nests over three-year period (1979-81); II = no. of nests in which each associate occurred in sample of 30 vacant nests (Jan 1980); III = no. of nests in which each associate occurred in sample of 30 nests occupied by ♀ spiders (Jan 1980); * = nest associate represented by more than one species.

distinguished (categories 1a and 1b), and predators of spiders and their eggs divided into separate categories (3a and 3b). The term 'parasitoid' (Askew, 1971) is used for species that kill their host (e.g., scelionid egg parasitoids), and 'parasite' for species that feed from but normally do not kill their host (e.g., mantispid larvae feeding on adult spiders, see below). 'Ectoparasitoids' of eggs, a term used by some authors, are not distinguished from egg predators (Austin, 1985; LaSalle, 1990). Also, a new category has been added; that of conspecific males (category 9, see below).

Notes on the biology of nest associates were made both in the field and on nests and associates kept for short periods in the laboratory, during the three-year survey of nests.

Scavengers, refuge seekers and accidental inhabitants. Most nest associates belong to one of these categories (25/40 taxa), but without detailed biological studies on individual species, it was impossible to determine in which specific category they belonged. The major groups are Acarina, Collembola, Coleoptera, Pentatomidae (Heteroptera), Lepidoptera, Psocoptera (New, 1974), Thysanoptera and Mollusca. In addition, three parasitic wasps can be categorized as either refuge seekers or accidental inhabitants; *Ceratobaeus clubionus* Austin, an egg parasitoid of other clubionid spiders (not *C. robusta* -Austin, 1984b), *Ceratobaeus lamponae* (Hickman), an egg parasitoid of *Lampona* spp. (Hickman, 1967a), and *Trissolcus* sp. and *Gryon* sp., egg

Statistics	Nest resident	
	no ♀	resident ♀
No. of nests sampled	30	30
Total no. of associates	227	147
Mean no. of associates/nest	7.63	4.90
Total no. of associates >2.5mm	72	13
% of associates>2.5 mm	31.7	8.9
Mean no. of associates/nest>2.5mm	2.33	0.47

TABLE 3. No. of nest associates for vacant nests and nests occupied by resident ♀ spider.

parasitoids of pentatomid bug eggs (Masner, 1976).

Other spiders that use C. robusta nests. More than 50% of vacated nests were occupied by other spiders, including conspecifics, many of which had constructed moulting retreats or their own nests inside that of *C. robusta* (category 6). Sixteen of 30 vacant nests contained juvenile *Clubiona* which, in most cases, could not be identified to species. Some of these may have come from previously hatched eggmasses in the same nest. However, 11 of 30 occupied nests also contained *Clubiona* juveniles, 8 of which contained gravid female *C. robusta* and no previously hatched eggmasses, indicating that these juveniles had migrated from other nests. Ten out of 60 nests sampled in January 1980 contained conspecific adult males, two cohabitating with mature females and eight found in older, vacated nests. Other spiders were encountered more rarely in the survey and only in vacant nests. All species, except for the hahniid *Scotospilus* sp. and the segestriid *Ariadna* sp., at least once constructed retreats or nests inside nests of *C. robusta*.

Parasitoids and parasites of adult C. robusta. Only on two occasions were such organisms recorded. One acrocerid fly (?*Ogcodes* sp.) was reared from a female *C. robusta* (category 1a) (Schlinger, 1987) and a single mantispid larva (possibly *Austromantispa* sp.) was found attached to the pedicel of a gravid female inside a nest (category 1b). Some mantispids are now known to act as ectoparasites of female spiders as small larvae and then as predators of the eggs as larger larvae (Redborg, 1982; Redborg and Macleod, 1983).

Predators of adult C. robusta. The only potential predators of adult *C. robusta* collected during the study were other large spiders, but no such predation was noted (category 3b). Four cases of predation on subadult *C. robusta* outside of retreats were recorded, two each by *Intruda* sp. and *Ariadna* sp. Also, no spider were noted using *C. robusta* nests as a predatory device (category 5, see Jackson, 1976; Jackson and Griswold, 1979).

Parasitoids and predators of C. robusta eggs. An endoparasitic wasp, *Ce. masneri*, was the most commonly noted species (category 2) and was associated with vacant nests, occupied nests without eggmasses, and occupied nests with eggmasses. This wasp caused the highest level of egg mortality (22-25%, Austin, 1984b, 1988) of all species found feeding on eggs. Four species thought to be specific predators ('ectoparasites' of other authors) were seen feeding on *C. robusta* eggmasses only rarely (category 3a). These included a chloropid fly, *Pseudogaurax* sp., on three occasions (Austin, 1985), a eulophid wasp, *Tetrastichus* sp. (LaSalle, 1990), a pompilid wasp, *Epipompilus* sp. (Pollard, 1982), each on one occasion, and a mantispid, *Austromantispa* sp., on two occasions. The only generalist predator of eggs recorded was the ant *Iridomyrmex* sp. which was observed feeding on eggmasses and hatched eggs several times, but only in vacant nests (Austin, 1988). Other possible predators of eggs include a reduviid, *Empicoris rubromaculatus* Blackburn, and other spiders.

Nest Associates of Other Spiders on Eucalypt Bark

During the 1979-81 survey, while collecting nests of *C. robusta*, nests of three relatively common spiders were also collected and their nest associates examined. Observations on these three species are presented here. Other species were either too rarely encountered to report on here or were not found associated with their nests.

Servaea sp. (Salticidae). This same species (or one very similar) was figured as *Plexippus validus* Urquhart by Hickman (1967b), who described some aspects of its biology in Tasmania. The spider constructs a flattened, circular nest (30-40 mm dia.) of dense, white silk, similar in appearance and density to cotton wool. Twenty-five nests were collected: 20 occupied by female spiders, and 10 contained eggmasses or hatched juveniles. Only six associates were identified from these nests: *Austromantispa* sp. 2 (two nests), *Ogcodes* sp. (one nest), *Pseudogaurax* sp. 2 (seven nests), *Iridomyrmex* sp. (one nest), *Anthrenus* sp. (one nest) and an unidentified carabid beetle (one nest). *Iridomyrmex* sp. was feeding on eggs inside a vacant nest. The *Austromantispa* sp., *Ogcodes* sp. and *Pseudogaurax* sp. in these nests were different from those in *C. robusta* nests. Mites, Collembola and

Psocoptera were seen in some nests but were not extracted and identified. No scelionid wasps were reared from eggmasses.

Breda jovialis (L. Koch) (Salticidae). This easily recognized salticid builds a disc-shaped nest (about 30 mm dia.) with two prominent tubular entrances opposite each other (Hickman, 1967b). The surface of the nest is hardened and parchment-like, but the inside is lined with dense, flocculent, white silk. Seventeen nests were collected: six had resident, gravid females, and five had females with eggmasses. Only two associates were identified, and both were feeding on eggs. These were *Idris* sp. (Scelionidae) and *Pseudogaurax* sp. Another scelionid is known to parasitize *B. jovialis* eggs elsewhere in Australia (Hickman, 1967a; Austin, 1981), but this species was not found in South Australia. As for *Servaea* sp., mites, Collembola and Psocoptera were seen in a few nests but were not extracted and identified.

Ariadna sp. (Segestriidae). This species builds a flattened oval or tubular nest with walls of similar construction and silk density to that of *B. jovialis*. Only nine nests were collected, all contained resident females, and four contained eggmasses. The only nest associates recorded were the larvae of a hymenopteran egg predator in one nest. These failed to develop and thus could not be identified. No mites, Collembola and Psocoptera were seen in the nests of this species.

DISCUSSION

The number of species of nest associates collected from *C. robusta* nests and the major taxa represented were similar to that found in nests of a salticid, *P. johnsoni* (Jackson and Griswold, 1979). However, *C. robusta* differed in that many more contained associates: of the 60 sampled nests 55 (92%) contained at least one associate, whereas only 1.2 % of *P. johnsoni* nests were occupied by associates. No nests of *P. johnsoni* occupied by a resident female spider contained associates, whereas most occupied *C. robusta* nests did (87%). *P. johnsoni* nests also differed in that a much greater proportion of recorded associates were spiders (66%), whereas for *C. robusta*, even excluding Acarina and Collembola, only 26% of associates were spiders. The reason for these differences is unclear, but is probably due to differences between the habitats of the two spiders and the size and nature of potential invertebrate faunas that exist at the two locations. Certainly, the bark of eucalypt trees examined in this study harbour a large and diverse invertebrate fauna that acts as a reservoir for *C. robusta* nests. Also, the apparent high and consistent abundance of this fauna means that there is probably a much greater chance of nests being inhabited, compared with the places *P. johnsoni* constructs nests, i.e., under rocks, pieces of wood, and in hollow reeds (Jackson, 1979).

Occupied nests of *C. robusta* have smaller nest associates compared with vacant nests presumably because resident spiders are known to kill and feed on intruders larger than 2.5mm. Also, females are known to guard their eggmasses and kill even distasteful intruders in nests (Austin, 1988). However, the aggressiveness of resident spiders does not explain why there are fewer small associates (<2.5 mm) in occupied nests (see Table 2). One possible reason for this is that the activity of female spiders in building, repairing and tidying nests, disturbs many small invertebrates and they move away.

The notes on nest associates of other spiders given here pose some questions. Generally the nests of the three species examined have structurally more complex nests than does *C. robusta*, and this is associated with them having far fewer nest associates. In the light of this association, further research on nest associates could profitably examine the structure of nests as a factor regulating the number and types of nest associates, as could differences in the behaviour of resident spiders inside their nests.

Finally, the biological categories proposed by Jackson and Griswold (1979) for the nest associates of *P. johnsoni* were directly applicable to the associates recorded here for *C. robusta* and the other three spiders examined and, thus, probably can be applied to the associates of any nest-building vagabond spider. We have modified their scheme in two points: 1) to distinguish between endo- and ectoparasitoids, because these two types of parasitoids have basically different biologies (Austin, 1985; LaSalle, 1990), and 2) to include conspecific males as a new category, which were found in both occupied and vacant nests.

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LITERATURE CITED

ASKEW, R.R. 1971. 'Parasitic Insects'. (Heinemann: London). 316pp.

AUSTIN, A.D. 1981. *Hickmanella*, a new genus of Scelionidae from Australia (Hymenoptera: Proctotrupoidea). Journal of the Australian Entomological Society 20: 303-308.

1984a. Life history of *Clubiona robusta* L. Koch and related species (Araneae, Clubionidae) in South Australia. Journal of Arachnology 12: 87-104.

1984b. The fecundity, development and host relationships of *Ceratobaeus* spp. (Hymenoptera: Scelionidae), parasites of spider eggs. Ecological Entomology 9: 125-138.

1985. The function of spider egg sacs in relation to parasitoids and predators, with special reference to the Australian fauna. Journal of Natural History 19: 359-376.

1988. Guarding behaviour, eggmass shape and the eggsac in *Clubiona robusta* L. Koch (Araneae: Clubionidae). Pp.87-95. In A.D. Austin and N.W. Heather (eds). 'Australian Arachnology'. (The Australian Entomological Society: Brisbane).

AUTEN, M. 1925. Insects associated with spider nests. Annals of the Entomological Society of America 18: 240-250.

GRISWOLD, T.M. 1986. Nest associates of two species of group-living Eresidae in South Africa. Actas X Congress Internationale Arachnologie Jaca/Espana 1: 275.

HICKMAN, V.V. 1967a. New Scelionidae (Hymenoptera) which lay their eggs in those of spiders. Journal of the Entomological Society of Australia (N.S.W.) 4: 15-39.

1967b. 'Some Common Spiders of Tasmania'. (Tasmanian Museum and Art Gallery: Hobart). 112pp.

JACKSON, R.R. 1976. Predation as a selection factor in the mating strategy of the jumping spider *Phidippus johnsoni* (Salticidae, Araneae). Psyche 83: 243-255.

1979. Nests of *Phidippus johnsoni* (Araneae, Salticidae): characteristics, pattern of occupation, and function. Journal of Arachnology 7: 47-58.

JACKSON, R.R. & GRISWOLD, C.E. 1979. Nest associates of *Phidippus johnsoni* (Araneae, Salticidae). Journal of Arachnology 7: 59-67.

LASALLE, J. 1990. Tetrastichinae (Hymenoptera: Eulophidae) associated with spider egg sacs. Journal of Natural History 24: 1377-1389.

MASNER, L. 1976. Revisionary notes and keys to world genera of Scelionidae (Hymenoptera: Proctotrupoidea). Memoirs of the Entomological Society of Canada 97: 1-87.

NEW, T.R. 1974. Psocoptera from nests of the colonial spider *Ixeuticus candidus* (Koch) (Dictynidae) in Western Victoria. Australian Entomological Magazine 2: 2-6.

POLLARD, S.D. 1982. *Epipompilus insularis* (Hymenoptera: Pompilidae), a parasitoid of hunting spiders. New Zealand Journal of Zoology 9: 37-40.

POLLARD, S.D. & JACKSON, R.R. 1982. The biology of *Clubiona cambridgei* (Aranea, Clubionidae): intraspecific interactions. New Zealand Journal of Ecology 5: 44-50.

REDBORG, K.E. 1982. Interference by the mantispid *Mantispa uhleri* with the development of the spider *Lycosa rabida*. Ecological Entomology 7: 187-196.

REDBORG, K.E. & MACLEOD, E.G. 1983. *Climaciella brunnea* (Neuroptera: Mantispidae): a mantispid that obligately boards spiders. Journal of Natural History 17: 63-73.

SCHLINGER, E.I. 1987. The biology of Acroceridae (Diptera): true endoparasitoids of spiders. 319-327. In W. Nentwig (ed.). 'Ecophysiology of Spiders'. (Springer-Verlag: Berlin).

WOLF, A. 1990. The silken nests of the clubionid spider *Cheiracanthium pennyi* and *Cheiracanthium punctorium* (Araneae, Clubionidae). Acta Zoologica Fennica 190: 397-404.

ZAR, J.H. 1984. 'Biostatistical Analysis'. (Prentice-Hall: New Jersey). 718pp.

A TENTATIVE ANALYSIS OF THE SPIDER FAUNA OF SOME TROPICAL OCEANIC ISLANDS

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The spider fauna of oceanic islands in the Pacific (Galápagos, Juan Fernandez, Easter Island, Marquesas, Hawaii), the Atlantic (Saint Helena) and the Indian Ocean (Comoros, Seychelles) is analysed. Family composition, size frequency distribution, species/area relationship, the origin of the faunas and their qualitative compositions are discussed. The colonization of the islands by spiders appears to be greatly influenced by the accessibility of the island, its habitat diversity and the speciation capacity of particular groups. Most of the fauna is composed of species transported by man. Thorough analysis of island faunas is still hampered by the lack of complete published data sets.
Les faunes aranéologiques des îles océaniques situées dans le Pacifique (Galápagos, Juan Fernandez, Marquises, Hawaii) l'Atlantique (Sainte-Hélène) et l'Océan Indien (Comores, Seychelles) sont analysées. Leur composition au niveau de la famille, la distribution des fréquences de taille, leur origine et leur composition qualitative sont discutées. La colonisation des îles par les araignées semble être fortement influencée par l'accessibilité de ces îles, leur diversité en habitats et la capacité de spéciation de certains groupes. Une grande partie des faunes est composée d'espèces apportées par l'homme. Une analyse complète des îles océaniques est encore impossible à cause du manque de données complètes publiées. □*Araneae, island zoogeography.*

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Most studies of island spiders have been confined to the description and enumeration of species. A general explanation of the composition of the araneological fauna of islands has not been tried. The availability of many almost complete species lists of remote oceanic and granitic islands allows us to analyse these spider faunas and try to understand their compositions. Only a few data-sets (those of Galápagos and Saint Helena) are nearly complete and most others are likely to grow considerably. For several islands the species lists included many unidentified species submitted for study to us or present in other collections (e.g. Cocos: Natural History Museum of Los Angeles County). Nevertheless we have tried to find patterns in the composition of the tropical island spider faunas.

MATERIAL AND METHODS

Apart from the spiders of the Galápagos and the Comoros, all data used are from the literature (Table 1). Hence, in the analysis of the size distribution, we had to use the total length, which is a less reliable measure than carapace width or the size of another sclerotised body part.

To compare the family composition, the number of species in each family was expressed as a percentage of the total number of species. The Renkonen-index was used to calculate the percentage of similarity.

RESULTS AND DISCUSSION

Family Similarity

Because the islands are in different zoogeographical provinces, a comparison of their faunas on the species level is not informative.

Similarity on family level was surprisingly high between the Galápagos, the Hawaiian Archipelago (Pacific) and Saint Helena (Atlantic), reaching ca 70% (Fig. 1). A second group (ca 60% similarity) consists of the Seychelles and Cocos Islands. These distinct vegetation belts, as on the main islands of the first group, seems important and induces a similar family composition. These islands were initially covered entirely by forest. The southern pacific Easter Island and Juan Fernandez, now covered by a gramineous, so called pampa-vegetation, have little similarity in family constitution.

Body Length Frequency Distribution

In tropical continental habitats, e.g. savanna

Island/archipelago	Area (km^2)	Highest elevation (m)	Distance to nearest continent (km)	Age (my)	Literature Consulted
Cocos I. (CO)	46.6	849	500 (Costa Rica)		Hogue and Miller (1981)
St Helena I.(SH)	120	705	1800 (Africa)	14.3	Benoit (1977)
Easter I. (PA)	165.8	530	3760 (Chile)	2.5	Skottsberg (1920), Berland (1924)
Juan Fernandez I. (JF)	178	1500	660 (Chile)	10	Skottsberg (1954)
Seychelles Arch. (SE)	273	914	932 (Madagascar)	65	Benoit (1978a, b), Saaristo (1978)
Marquesas Arch. (MA)	1274	1200	6000 (Peru)		Berland (1935, 1939)
Galápagos Arch. (GA)	7882	1707	960 (Ecuador)	9	Jackson (1985), Baert *et al.* (1989a, b)
Hawaii Arch. (HA)	16504	4206	4000 (Mexico)	70	Suman (1964, 1965), Gertsch (1973)
Comores Arch.	2237	2300	300 (Madagascar)	1	Jocqué (1985)

TABLE 1. Summary data (age is approximate) of islands and archipelagos considered.

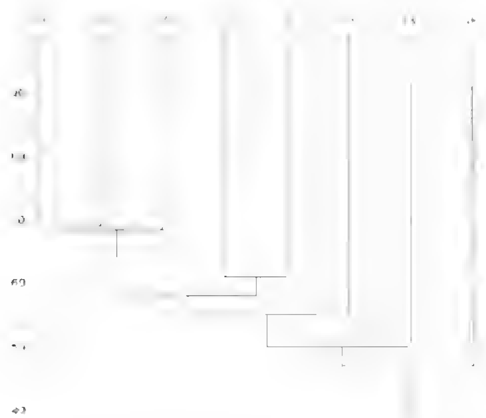

FIG. 1. Dendrogram of the similarities between the islands/archipelagos on family level.

and secondary forest in Ivory coast (Jocqué, 1980), middle-size spiders in the class of 4-6mm dominate (Fig. 2). However, data for Ivory Coast are based entirely on pitfall trap samples. That may bias the size frequency distribution towards higher or lower averages. On the other hand, the collections from islands are clearly biased towards larger spiders. Earlier collectors are more likely to have taken conspicuous large webspiders than small soil dwelling spiders. As for the other analyses it is probably too early to detect relevant differences in size distributions on different islands as compared to the situation on the continent.

Only spiders from Galápagos, Cocos Island and the Seychelles seem on average smaller than those from the collections made with pitfall traps in West Africa (Table 2). As only the difference GA-RCI is significant ($\chi^2 = 23.84$; $P< 0.02$) it seems that the discrepancies are further meaningless. However, complete data from the islands and fully comparable data from the continent might reveal more differences in average size of island and continental spiders. We expect selection to favour small spiders during the colonisation process. Thus, many more small spider species are likely to be present on islands than on the continent. Smaller spiders live in higher densities than bigger ones and the possibility that they reach an island is statistically higher than for larger spiders. Moreover, smaller spiders are usually better aeronauts although young stages of larger spiders have often been observed to balloon as well. The chance that a raft–rafting being an important mean of colonisation–contains a 'propagule' is also likely to be higher for smaller spiders than for larger ones.

However, the possibility for survival of spiders that reach an island is probably better for larger than for smaller ones but the enormous differences in specific ecophysiological characters make it difficult to generalise.

The Seychelles are granitic continental fragments and must have had a well-balanced fauna when they separated from the mainland. Hence, they should have elements of a continental spider fauna. Apparently this is not so. Some unusually large soil-dwelling spiders do exist on the island (see below), but the smallest size class seem more important on that archipelago, just as on the others. The Seychelles are a group of small islands with the largest not exceeding 15km^2. When ocean levels were higher these islands must have been tiny and the chance for extinction very high. Larger spiders occur in smaller populations. Thus, they are more liable to become extinct hence the otherwise unexpected dominance

TABLE 2. Mean body length (mm), number of species and standard deviation (RCI = Ivory Coast).

	SH	SE	PA	CO	GA	JF	MA	HA	RCI
$\bar{x}$	6.75	5.57	6.45	4.79	5.52	7.63	6.40	6.82	5.82
n	95	125	22	29	136	31	41	122	134
SD	4.47	4.62	3.47	4.20	[illegible]	5.58	3.35	[illegible]	3.91

of smaller spiders on the Seychelles. The spider fauna of Seychelles is probably too little known because the two main expeditions (Benoit 1978, Saaristo 1978) were in the dry season.

Frequency distribution histograms for the smaller Pacific islands (Easter, Juan Fernandez and Cocos) and for the Marquesas archipelago, show very irregular shapes. The distribution seems to have several peaks.

There may be several reasons for this:

1 the fragmentary knowledge of their spider fauna. Few spider species are listed for these islands in the literature. Occasional samples, made by other zoologists during brief visits to Easter Island, yielded important new records of spider species. That is apparently true of our knowledge of the spider fauna of most tropical islands.

2 Cocos and Easter Island are still too young or are so isolated (Easter Island in the centre of the South Pacific Gyre; Juan Fernandez amidst the northerly directed Humboldt Current) that they are difficult to colonise and an equilibrium in their spider communities has not yet been reached.

3 due to their limited size and low habitat diversity these islands cannot support more species and do indeed have several size distribution peaks.

Relation between Island Area and Species Density

Tropical African oceanic islands are far richer in species and their species/area relationship is much higher (0.48-0.81) than for tropical Pacific oceanic islands (Table 3). The very small Cocos Island lying the closest to a continental landmass is exceptional in this respect (0.60). Tropical Pacific archipelagos (0.01-0.04) and the southern pacific islands (0.14-0.18) have relatively low species/area relationships. It is not clear why the African off-shore islands are so much richer than the others. The source areas may be richer but that must be proven by thorough studies of the continental spider faunas. Many more species may have been introduced on the African islands. This is probably true for Saint Helena that has an unusual large proportion (44%) of introduced spiders, mainly from temperate regions. It is doubtful whether that is a sufficient explanation.

There is a relationship between altitude (highest elevation) of the island and the number of species present (Fig. 3.1: $r = 0.677$, $p > 0.01$) and between area of the island and the number of species present (Fig. 3.2: $r = 0.716$, $p > 0.001$). In both cases there is a significant correlation.

Origin of Faunas

As the distance from an island from the mainland increases, its component of continental species decreases.

Very striking is the much lower percentage of continental species on the African islands as compared to those of the Pacific. The same is true for the southern Pacific islands Juan Fernandez and Easter Island. This could be explained by their isolated position. Juan Fernandez lies in the middle of the northerly directed Humboldt Current, whereas Easter Island is situated a long distance from the continent in the centre of the South Pacific Gyre, making the arrival by rafting rather unlikely.

The presence on the Galápagos islands of northern, central (with Antillean elements), as well as southern American elements, could be explained by their special situation astride the equator. The archipelago lies in such a position that it is reached by the warm Niño Current in the rainy season and by the cold Humboldt Current in the dry season. The Californian Current of the Northern Hemisphere runs southwards along the North American coast and reaches the Panama Basin where it is warmed up and turns towards the Galápagos as the Niño Current. The southern Humboldt Current runs northwards along the south American coast and turns westward near the equator towards the Galápagos. Rafts can easily be transported from the north as well as from the south. A floating raft takes about two to four weeks to reach the islands from the South American mainland (Schatz, 1991).

Furthermore, there was a broad connection between the Caribbean region and the eastern Pacific area from 48 my until 3.5 -3 my ago (Woodring, 1959; Jones and Hasson, 1965) with a sea current running from the Atlantic to the Pacific (Petuch,1982). The Panama isthmus was plugged some 3 my ago by the Caribbean Plate which was shoved in between the north and south American plates. At that time the Galápagos islands had already emerged from the sea. It is acceptable that many fauna elements of the Caribbean reached the Galápagos at that time. Nearly 82% of the known spider species of Cocos Island are continental species.

The Marquesas have more species of Pacific origin. This can be expected because of the position of this archipelago at the margin of the Polynesian province (NE end of the south

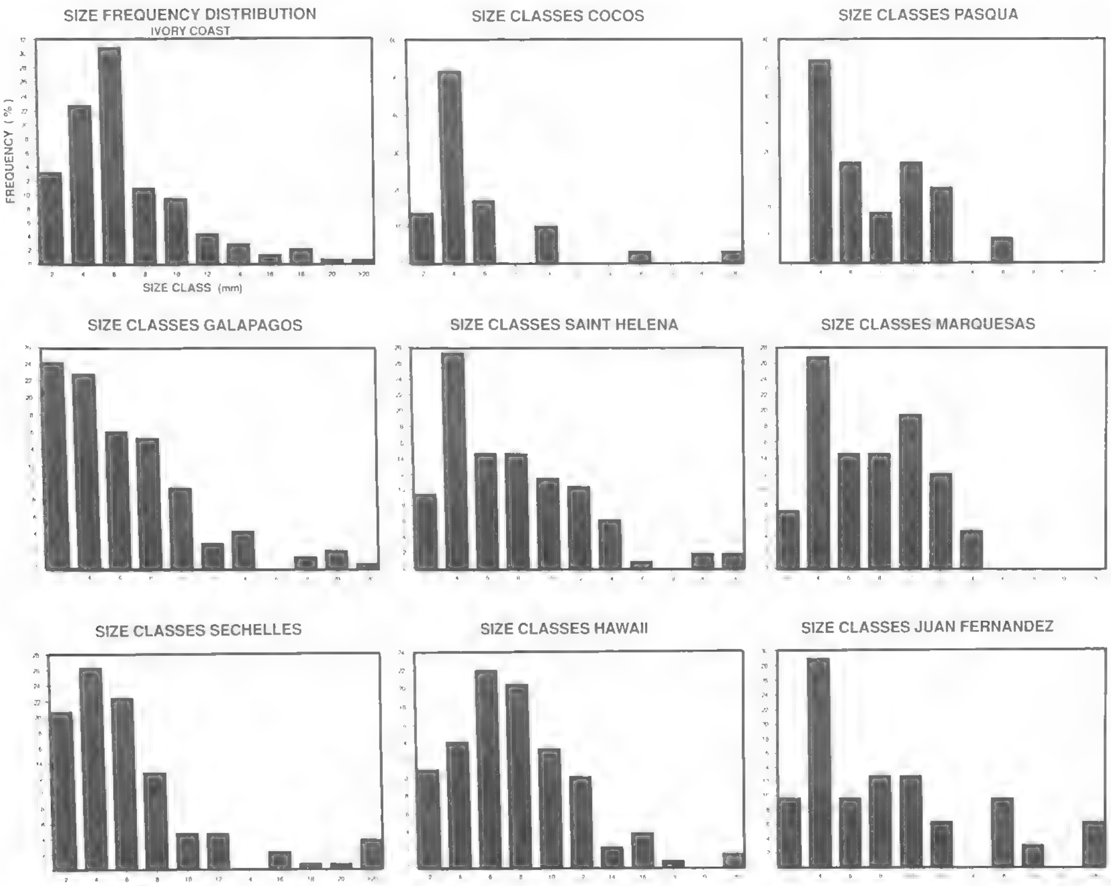

FIG. 2. Frequency distribution histograms of total body length (over 2mm size classes) for each island or archipelago.

equatorial archipelagos chain). In contrast, Hawaii and Galápagos have only a low percentage of Polynesian species as the distances between them and the Polynesian archipelagos are too extensive.

The term 'endemic' must be used now with great care because the continental faunas are far from being well known. This is especially so for the neotropical spider fauna. Many regions have been sampled only superficially or not at all. Few families have been thoroughly revised and new studies will be needed once the 'black holes' have been filled. For instance, the figures in table 2 for Galápagos are based upon 70% of the total of the recognised species. Hence, 46 species have yet to be identified. At this stage in our knowledge one is never sure that the species one describes from an oceanic island really has a dispersion restricted

Island/Archipelago	S	S/area	Continental distribution	Pacific origin	Cosmopolitan species	Endemic
Cocos I. (CO)	30	0.63	82% (A)			18%
Galápagos Arch. (GA)	146	0.02	32% (A)	4%	9%	60%
Hawaii Arch. (HA)	168	0.01	11% (A)	5%	19%	64%
Marquesas Arch. (MA)	48	0.04		31%	20%	50%
Juan Fernandez I. (JF)	32	0.18	17% (A)		17%	70%
Easter I. (PA)	23	0.14	22% (AU)		66%	12%
Seychelles Arch. (SE)	131	0.48	9% (E)		18%	65%
St Helena I. (SH)	98	0.81	7% (E)	44%	45%	

TABLE 3. The spider fauna of islands and archipelagos. Percentage of species with distribution 1° continental (A=American; E=African; Au=Australian), 2° cosmopolitan and 3° species known only from island or 'Endemic'. Values based only on described species.

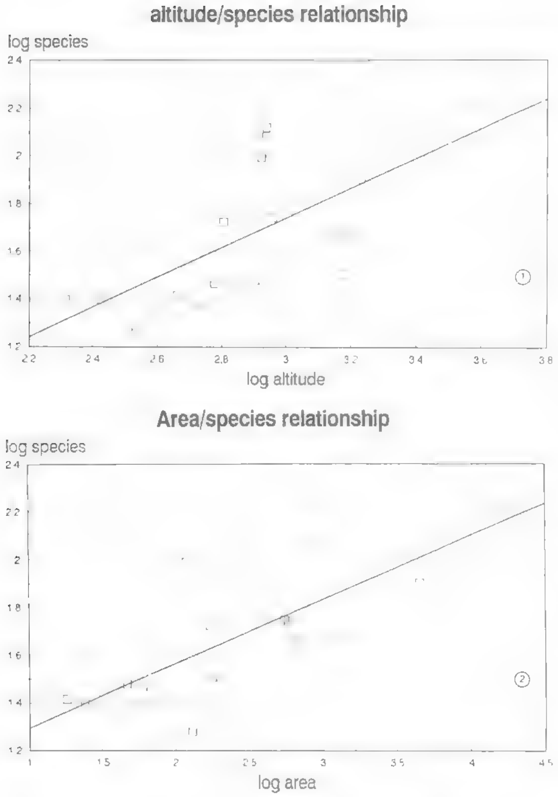

FIG. 3. 1, 2. Relationship between no. of spider species (N) and: 1, altitude (highest elevation) of island or archipelago (logN = -0.6224 log alt.(m)); 2., island/archipelago area (logN = 0.2686 log area + 1.0269).

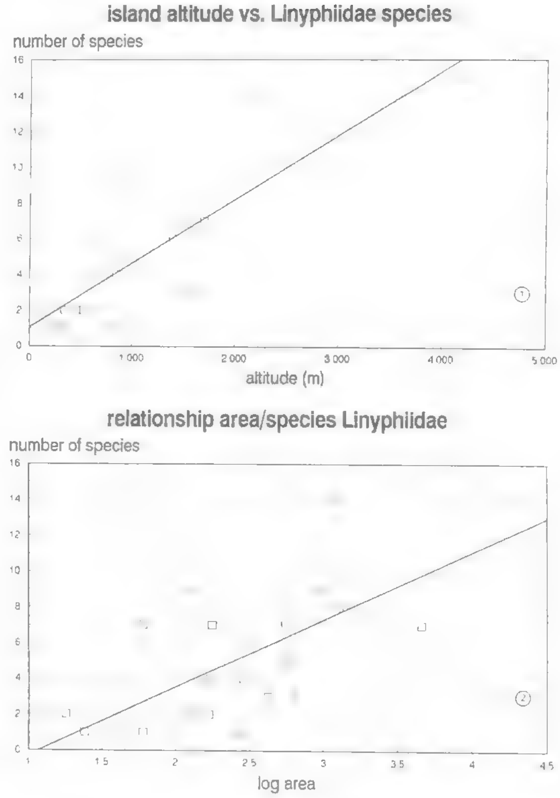

FIG. 4.1, 2. Relationship between no. of linyphiid species (L): 1, and altitude (L = 0.0035 alt(m) + 1.0544; 2., and island/archipelago area (L = 3.7886 log area - 4.0344) (separate islands in archipelagos). (S = no. species).

to that island for it may not yet have been found on the continent. We may therefore seriously question whether we can validly use the proportion of endemics for the analysis of an island fauna. However, we consider that the percentage of endemics we now recognise reflects the rough proportion of real endemics that will eventually be shown to exist.

Cocos Island seems to have few (18%) 'endemic' species. It lies relatively close to the continent. Once the distance to the continent exceeds 900km, we find an 'endemic' proportion in between 50 and 65%. The high percentage of 'endemics' on Hawaii (64%) is probably due to its old age and thus the long period of isolation of the archipelago. The high percentage for the Galápagos islands (60%) may perhaps be due to the fragmentary knowledge of the South American spider fauna (the main reason why one third of the Galápagos spider fauna is not yet identified).

The high percentage (70%) of 'endemics' on Juan Fernandez is very striking. Though close to the mainland, it is a rather isolated island (Humboldt Current) with an environment rendered harsh by the very special climatological conditions.

The proportion of cosmopolitan species on the islands varies between 0 and 20%, with two striking exceptions: Saint Helena with ca 44% and Easter Island with 60% (this figure is based on only 10 species). Most of these species are introduced and restricted to human settlements. This shows the great impact man has had on the spider fauna of Saint Helena.

All the islands considered here do have human settlements, native on Hawaii, Easter Island and Marquesas, but immigrated in historical times on the others. Human settlements invariably result in deforestation for arable land and subsequent introduction of ubiquitous species. Most often this is detrimental to the original fauna. Even more damage can be done with the introduction of domesticated animals (cattle, dogs, cats, rodents, etc.) and cultivated plants. Accidental introductions can also have serious consequences as for instance the Little Fire Ant (*Wasmannia auropunctata*) on Galápagos. This species haunts large areas, devastating nearly all living animal organisms.

QUALITATIVE ANALYSIS

Qualitative analysis of the distribution of particular groups on islands is perhaps more revealing than quantitative analyses which are still hampered by the incompleteness of many data sets.

Spiders that do not balloon do not seem well adapted to colonise oceanic islands. Good examples are seen in the Zodariidae. Only four species, if we include *Cryptothele*, are present on the islands considered. On the Seychelles we find the endemic *Cryptothele alluaudi* Simon; the Comoros have *Asceua radiosa* Jocqué on Grande Comore and *Diores seiugatus* Jocqué on Mohéli (Jocqué, 1986). *Zodarion trispinosum* Suman is known from Hawaii. The presence of a *Zodarion* on Hawaii, completely outside its main distribution is puzzling, but is probably explained by an introduction as is the presence of *Z. fulvonigrum* (Simon) in North America. The Mygalomorphae are found only on two of these archipelagos. Six species in three families (Benoit, 1978) occur on the Seychelles. Five of these are endemic, the sixth species, *Idioctis intertidalis* (Legendre and Benoit), is also found on Madagascar and Grande Comore, where it occurs together with the endemic *Moggridgea nesiota* Griswold. The presence of these spiders, all but one apparently true endemics, on the Seychelles is explained by its granitic nature, which implies that they have had a fauna from the moment they were separated from the continent. The Comoros are probably more easily colonised than other islands, possibly by rafting, as that archipelago is close to its source area, Madagascar, for which the spider fauna is unfortunately poorly known.

Linyphiidae can be considered excellent colonisers mainly because many frequently balloon. However, linyphiids appear to be able to occupy few habitats. Jocqué (1984, 1985) explained that interference competition in tropical lowland with ants is apparently too important to allow the presence of many linyphiid species. As ants are less common at higher altitude many more linyphiid species tend to be present in highland than at low elevations (e.g. Scharff, 1992). (Since ant diversity and density are linked to climatic conditions, the impression may exist that they are the determining factor.) The presence of an important number of Linyphiidae on high islands was already illustrated for the Comoros (Jocqué, 1985). This is particularly true for islands. There is a significant correlation between the altitude of island and the number of species of Linyphiidae present (Fig. 4.1: $r = 0.780$, $p < 0.001$) and between area of the island and the number of linyphiid species present (Fig. 4.2: $r = 0.688$, $p < 0.001$). There is a third aspect relevant to the colonisation of islands: parapatric speciation on the spot. The Lycosidae are a good example. Wolf spiders might be expected to be good colonisers. Their juvenile stages are active ballooners, and transport by rafting is also a likely means of dispersal if only because lycosids are very common on banks of rivers and in marshes from where rafts are supposed to be derived. However, the number of insular species is quite low compared to the high number of species in continental tropical areas. (Galápagos: 6 species; Hawaii: 11; Cocos: 1; Juan Fernandez: 2; Saint Helena: 7; Seychelles: 2; Comorós: 3). Moreover, almost all species from islands in this study have no continental distribution and must be considered endemics of each island. Only *Bristowiella seychellensis* (Bristowe) is known from both Seychelles and Comorós. Their apparently high speciation rate may be related to this. Of special note, some species at high altitudes on some islands are apparently derived from species at low altitudes. A well documented case is that of *Bristowiella* on the Comoros where two closely related species have clearly differentiated habitats: *Bristowiella seychellensis* living in short grassy vegetation from sea level to about 1500m and *Bristowiella kartalensis* Alderweireldt living in recent lava flows with sparse vegetation from about 600m upwards (Alderweireldt, 1988). Another interesting case is that of the Hawaiian cave dwelling lycosids which have strongly reduced eyes or none and which clearly speciated on the islands themselves (Gertsch, 1973).

On Galápagos, a group of six species apparently derived from the most common one ('Lyc 3'). It occurs over the whole archipelago and occurs mainly in coastal salt marshes. Another species ('Lyc 5') occurs only on the low island Española. The four other species are confined to the high pampa zones of the volcanoes Sierra Negra and Cerro Azul ('Lyc 1') on Isabella, on San Cristóbal ('Lyc 2'), on Santa Cruz ('Lyc 4') and the Alcedo volcano on Isabella ('Lyc 6'). The revision of this remarkable species-group is in preparation.

A fourth example of such segregated parapatric populations is found on Juan Fernandez where 2 *Lycosa* species are found, one living along the coast, the other living in the higher pampa zone.

These statements reveal three important factors influencing the composition of island faunas. In the first place, there is the accessibility of the island, mainly its distance to a source area. In the second place, the diversity of the island's habitats is important. Particular spiders such as mygalomorphs and zodariids are only present on those islands that are easily reached or already had a fauna when they became isolated. Other families, although good colonisers, appear to be restricted by the ecological conditions of the island they can reach. Speciation appears to be the third factor which may be important in the colonisation of habitats that can hardly be reached by the normal ways of dispersal. The effect of niche pressure (Jocqué, 1982) is likely to be an important mechanism in this respect.

CONCLUSION

The faunal composition we now find on many islands is far from being natural. At the same time we know little about the arthropod fauna of most oceanic islands. This makes the analysis and comparison of the faunas very hard. The influence of speciation processes is probably largely overlooked in connection with the compensation of extinction.

LITERATURE CITED

ALDERWEIRELDT, M. 1988. On the genus *Bristowiella*, with the description of *B. kartalensis* n. sp. from the Comoro Islands (Araneae, Lycosidae). Bulletin of the British Arachnological Society 7: 269-272.

BAERT, L., MAELFAIT, J.-P. & DESENDER, K. 1989a. Results of the Belgian 1986 -expedition: Araneae, and provisional checklist of the spiders of the Galápagos archipelago. Bulletin van het Koninklijk Belgisch Instituut voor Natuurwetenschappen 58: 29-54.

1989b. Results of the Belgian 1988-expedition to the Galápagos islands: Araneae. Bulletin van het Koninklijk Belgisch Instituut voor Natuurwetenschappen 59: 5-22.

BENOIT, P. 1977. Araneae. Introduction. In 'La Faune terrestre de l'ile de Sainte-Hélène. Quatrième partie'. Annalen van het Koninklijk Museum voor Midden-Afrika, Zoologische Wetenschappen 220: 12-188.

1978a. Contributions à l'étude de la faune terrestre des îles granitiques de l'archipel des Séchelles. Introduction. Revue de Zoologie Africaine 92: 390-404.

1978b. Contributions à l'étude de la faune terrestre des îles granitiques de l'archipel des Séchelles. Araneae Orthognatha. Revue de Zoologie Africaine 92: 405-420.

BERLAND, L. 1924. Araignées de l'île de Pâques et des îles Juan Fernandez. In 'The Natural History of Juan Fernandez and Easter Island'. Vol. III, Zoology: 419-437.

1935. Araignées des îles Marquises. In 'Marquesan Insects-II'. Bernice P. Bishop Museum Bulletin 114: 39-70.

1939. Nouvelles araignées marquisiennes. In 'Marquesan Insects-III'. Bernice P. Bishop Museum Bulletin 142: 35-63.

GERTSCH, W. 1973. The cavernicolous fauna of Hawaiian lava tubes. 3. Araneae (Spiders). Pacific Insects 15: 163-180.

HOGUE, C. & MILLER, S. 1981. Entomofauna of Cocos Island, Costa Rica. Atoll Research Bulletin 250: 29pp.

JACKSON, M. 1985. 'Galápagos, a natural history guide'. (The University of Galgary Press).

JOCQUÉ, R. 1980. 'Verspreidings-, aktiviteits- en groeipatronen bij spinnen (Araneida), met speciale aandacht voor de arachnofauna van de Kalmthoutse heide'. (Doctoraatsverhandeling Rijksuniversiteit Gent). 181 pp.

1982. Niche pressure and the optimum exploitation hypothesis. Biologisch Jaarboek Dodonaea 50: 168-181.

1984. Considérations concernant l'abondance relative des araignées errantes et des araignées à toile vivant au niveau du sol. Revue Arachnologique 5: 193-204.

1985. Linyphiidae (Araneae) from the Comoro Islands. Revue de Zoologie Africaine 99: 197-230.

1986. Ant-eating spiders from the Comoros (Araneae, Zodariidae). Revue de Zoologie Africaine 100: 307-312.

JONES, D.S. & HASSON, P.F. 1965. History and development of the marine invertebrate faunas separated by the central american isthmus. Pp. 325-356. In Stehli F.G. and Webb S.D. (eds). 'The Great American Biotic Interchange'.

MACARTHUR R.H. & WILSON, E.O. 1967. 'The theory of island biogeography'. (Princeton University Press: new Jersey). 198pp.

PETUCH, E.J. 1982. Paraprovincialism: remnants of paleoprovincal bounderies in recent marine molluscan provinces. Proceedings of the Biological Society of Washington 95: 774-780.

SAARISTO, M. 1978. Spiders (Arachnida, Araneae) from the Seychelle Islands, with notes on taxonomy. Annales Zoologici Fennici 15: 99-126.

SCHARFF, N. 1992. The Linyphiid fauna of Eastern Africa (Araneae, Linyphiidae). Distribution, patterns, diversity and endemism. Biological Journal of the Linnean Society 45: 117-154.

SCHATZ, H. 1991. Arrival and establishment of Acari

on oceanic islands. Pp. 613-618. In Dusbábek F. and Bukva, V. (eds). 'Modern Acarology'. Vol. 2. (Academia, Prague and SPB Academic Publishing: The Hague).
SKOTTSBERG, C. 1920. Notes on a visit to Easter Island. Pp. 2-20. In 'The Natural History of Juan Fernandez and Easter Island'. Vol. 1.
1954. A geographical sketch of the Juan Fernandez Islands. Pp. 89-192. In 'The Natural History of Juan Fernandez and Easter Island'. Vol. 1.
SUMAN, T. 1964. Spiders of the Hawaiian Islands: Catalog and Bibliography. Pacific Insects 6: 665-687.
1965. Spiders of the Family Oonopidae in Hawaii. Pacific Insects 7: 225-242.
WOODRING, W.P. 1959. Geology and paleontology of canal Zone and adjoining parts of Panama. Description of Tertiary mollusks (Gastropoda: Vermetidae to Thaididae). United States Geological Survey Professional Paper 306: 147-240.

THE REPRODUCTIVE ECOLOGY OF *EUSCORPIUS FLAVICAUDIS* IN ENGLAND

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The reproductive ecology of the scorpion *Euscorpius flavicaudis* was studied both in the field in England (at a colony dating back 120 yrs), and under semi-natural conditions in the laboratory. Before the mating season males become vagrant to search for females. On encountering a pregnant female or one with young, in her 'burrow', the male may mate-guard her until her period of maternal care ends and she becomes receptive to him. Large males have a higher mating success than small males. Two instars of adult males exist in this population of scorpions: large 7th instars and small 6th instars, and the reasons for this apparently paradoxical situation are explored. □*Euscorpius, mate-guarding, mating, life-history.*

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Evolutionary and behavioural ecology are relatively young disciplines; and have to date concentrated on using the more 'familiar' animals as subjects: birds, mammals and insects. These disciplines have largely passed arachnids by. Increasingly, however, we are beginning to realise the utility of arachnids as model animals in helping to elucidate general evolutionary principles.

Although there has been considerable increase in behavioural ecological interest in spiders in recent years, scorpions have been largely ignored. This is perhaps because they are difficult animals with which to work – long-lived, inactive, elusive and nocturnal. This paper outlines some of the main findings of a study of scorpion reproductive ecology. It is unfortunately incomplete; posing more questions than it solves; but, I hope that it illustrates the fact that, as in so many areas of their biology, scorpions are idiosyncratic, fascinating and more complex than they may first appear. This study combines the power of controlled laboratory experiments and the ease of laboratory observations with the reality of what is observed in the field; and, by so doing, for the first time the events surrounding the courtship of a scorpion are explored and placed in an ecological context.

THE STUDY ANIMAL

Euscorpius flavicaudis (de Geer), common throughout southern Europe (Birula, 1917), also occurs in England, most probably as a result of introductions. This species is a successful colonising species (Fage, 1928; Wanless, 1977; Lourenco & Vachon, 1981) and is often found associated with buildings (Wanless, 1977). Colonies have been reported from several locations in England, but only one, at Sheerness Docks, Kent (51°26'N, 0°45'E) has lasted many years and is of considerable size. The first record of scorpions at Sheerness is a label on a specimen of *Euscorpius flavicaudis* in the Natural History Museum, London: 'Taken in Sheerness Dockyard, 1870, J.J. Walker' (P.D. Hillyard, *in lit.*).

METHODS

Field Observations

At Sheerness Docks, most present buildings and the perimeter wall date from 1823 (Benton, 1992a). Scorpions are common in areas little frequented by people; and are especially common living in the perimeter wall. This old wall is about 4m high and 66cm thick. It shows the effects of time, with the mortar between the bricks crumbling away, creating 'cracks' which the scorpions readily inhabit. My study area was a 104m length of perimeter wall (bounding ornamental and vegetable gardens). The field study was conducted from January 1988 to July 1989, during which 92 visits were made to Sheerness Docks (totaling 500 hours of observations). Scorpions were observed using a portable ultra-violet light. Benton (1992a) details field methods.

Laboratory Observations

To allow more complete observations and experimentation a laboratory colony of *Euscorpius* was set up, modelled on the habitat at Sheerness. This consisted of a plywood wall (2.44m x 5.79m), covered in sandpaper, with 144 slots (2.5

x 5.1cm) cut into the face. Into these slots were fitted artificial 'cracks' 12 cm long. These were open to the wall and closed at the far end. A layer of soil was placed at the base of the wall. This soil was periodically damped to mimic rain; and each week woodlice (the scorpion's natural food) were released onto it. This colony was kept under a natural photoperiod, and as near natural temperature and humidity as possible. Observations and experiments were conducted at night, when the wall was illuminated by lamps fitted with deep-red filters (invisible to scorpions: Machan, 1968). Unless being used in an experiment, the scorpions (collected at Sheerness) were allowed to move freely around the wall. Benton (1991a) details colony setup.

EXPERIMENTAL METHODS

In this study of male contest behaviour for females during the mating season, 11 males were used. On the artificial wall 40 x 40cm enclosures were made around a single crack. A female carrying young was placed in this crack, and later an experimental male was added. Thirty minutes after this male had encountered and entered the crack a second male was added. After encountering the crack the second male would attempt to enter. The males would then meet, assess each other and fight. This procedure was then immediately repeated. The two replicates constituted a 'contest' (and in all cases the results were unambiguous, and identical for each replicate). In total 110 contests were conducted (with each male as 'owner' against every other male as intruder). Contest order was randomly selected. Other methods are detailed in Benton (1992b), and scorpion mensuration in Benton (1991b).

RESULTS

BACKGROUND

Like most scorpions, *E. flavicaudis* is nocturnal. During the day and over the winter, they are not visible as they have retreated to the back of their cracks in the wall. At night, depending on the season, most scorpions evident are at the entrance to their cracks where they remain immobile, with their claws outstretched and open. The most common prey items are isopods (*Porcellio scaber*) (64%) and then conspecifics (12%) (Benton, 1992a).

SEASONS

Scorpion activity at Sheerness is highly seasonal. Over the winter very few (if any) can be seen. The numbers build up during the spring and peak in late summer (Benton, 1992a) before decreasing again to winter levels. As these scorpions live for several years (Benton, 1991b) this pattern reflects varying patterns of behaviour, rather than gross mortality and natality. For most of the year, most scorpions seen are in their crack (for November to June only $8 \pm 11\%$ of all scorpions observed are out of their cracks). However, in summer, on average, $24 \pm 9\%$ of scorpions observed were on the wall surface. Adult males make up most surface-active animals: 3-4x more males are seen on the wall surface than adult females over the summer (Figs 1a, b).

The number of females giving birth or with young peaks when female activity on the wall surface (Fig. 1a) is least. Females with young remain deep within their cracks, and were never observed to venture onto the wall surface. Indeed, females in the last stages of pregnancy also appeared to show a marked reduction in activity.

Most matings at Sheerness (Fig. 1b) are just after the number of females with young peaks (Fig. 1a). Known females with young were found to be unreceptive to males until 2 ± 1.2 days (n=12) after the juveniles had moulted and climbed off her dorsum (Benton, 1992b).

About 3 weeks after male surface-activity begins, the number of matings observed peaks (Fig. 1b). Only at this time can males and females be found together in the same crack. These periods of cohabitation averaged 10 ± 9.9 nights (range 1-30; n=19; data from field). Cohabiting occurred only prior to mating, and whilst the female was either carrying young, or in late pregnancy (Benton, 1992b). Males were associated sometimes with females living in shallow cracks (n=3); in which case the males spent the day in a deep crack nearby and 'commuted' to the female's crack to spend the night sitting at the entrance. The identity of the male mating with a specific female was known for 15 cases of cohabitation: in 14 the male had been recently cohabiting (P<0.005) with that female. Females of this species do not appear to assess males, and will mate with any male present when they become receptive (Benton, 1992b). If a male's encounter rate with females is low, and a female's receptivity is predictable, then a male encountering a soon-to-be receptive female may do better waiting for her to become receptive, rather than leaving her and risking trying to find a female nearer receptivity (Grafen and Ridley, 1983); and this seems to be the case with these scorpions (Benton, 1992b). This behaviour can also benefit

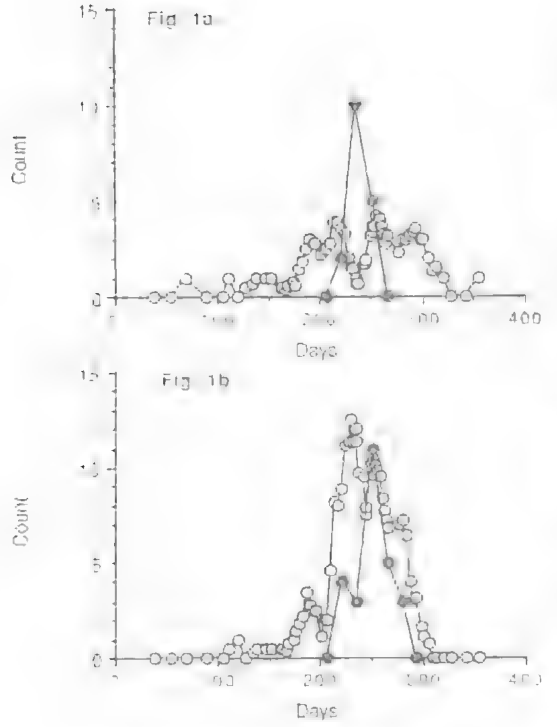

FIG. 1. Reproductive season of *Euscorpius flavicaudis* in England, 1988. (a) Seasonality of adult female surface-activity and no. of births. Female surface-activity is smoothed over two weeks: nightly count shown as average of preceeding and following week's counts. No. of births (for each half-month) estimated from no. of females giving maternal care, and date at which this ended. (b) Seasonality of adult male surface-activity (smoothed over two-weeks), and half-monthly count of no. of matings (observed no. of matings plus no. of spermatophores found). Data originally, in part, in Benton 1992b.

the females for two reasons. Firstly, it ensures that they are mated. Secondly, a major advantage of maternal care in scorpions is to prevent predation of the juveniles (Benton, 1991a), so having a male at the front of the crack prevents entrance by other scorpions which may aid this role.

In all cases of cohabitation, the male stations himself near the entrance, with the female behind him. Males attempting to enter the crack encounter the currently cohabiting males, and each tries to grasp the other's claws. Within a very few seconds one male retreats and flees from the crack. Males therefore fight for 'possession' of a crack occupied by a female in the period before she becomes receptive.

To investigate male mate-guarding contests 110 contests were staged between 11 males (each male as 'owner' against each of the others as 'intruder'). The proportion of contests won correlated very strongly with measures of scorpions size, and most strongly with pedipalpal claw length (r_s=0.97, $P<0.001$). This is to be expected as *E. flavicaudis* uses its claws as its main offensive weapon. In 80% of contests, the larger-clawed male won; when the smaller-clawed male won (20%), it was the 'owner' in most (91%) contests. Both relative claw-size and ownership status had highly significant effects on contest outcome (two-way ANOVA, size: F=68.5; df 1,36; $P<0.0001$; status: F=42.7; df 1,36; $P<0.0001$): large-clawed males usually won contests, but if contestants were closely matched in size then ownership status decided the outcome (giving an advantage equivalent to about 11% longer claws).

Size and Sexual Advantage

In the laboratory, males differed in reproductive success: some males mated twice, some once and some not at all. Larger males mated more often than small males (Fig. 2). This size advantage is for two reasons. Firstly, as described above, larger males are better competitors for female-occupied cracks. Secondly, about 40% of matings are not preceded by mate-guarding. These fall into three broad categories: non-pregnant females at the start of summer, females not found by males before their maternal care has ended and (most rarely) females who have mated already (this is possible as a spermatocleutrum is not secreted in this species). Large males obtain more matings from all three categories than small males. This is because, for each category of mating, females are initially unwilling to court. When a female is mate-guarded prior to her receptivity, she encounters the male frequently, and upon becoming receptive begins courting without aggression. Conversely, when a male encounters a non-pregnant female, or one without young he immediately attempts to court. The male grabs (or attempts to grab) the female's claws and stings her (Benton, 1990). Indeed, the start of a courtship (without mate-guarding) is indistinguishable from a cannibalistic attack. Large males are better at mating with these unwilling females as, unusually for scorpions, large males can be larger than females. In this species, and others (Polis, 1980), size (especially claw-size) is a good predictor of the outcome of cannibalistic contests. At the start of courtship, males

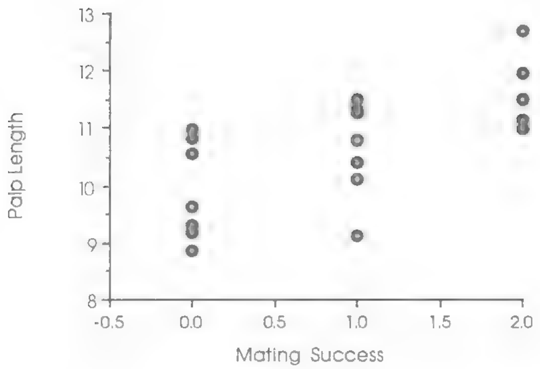

FIG. 2. Relationship between size (claw-length) and mating success in laboratory males free on wall surface (mean ± SD). Difference between groups is significant (Kruskal-Wallis, H=11.4, P=0.003).

sting females, and larger males can eat adult females (and often do: 10 cases observed in the laboratory), therefore, large males essentially give females the choice of being cannibalised or accepting courtship. Small males obtain fewer matings as they have a smaller (or nonexistant) size-advantage over females (Fig. 3) and therefore are more likely to flee from those females who are not immediately willing to court.

Size Dimorphism

Sexually mature adult males are recognised by the secondary sexual characteristic of a notch in the pedipalpal fingers (Fig. 3). Adult males can differ markedly in size, and this is especially noticeable when one considers claw size, which increases allometrically with body size, such that larger males have disproportionately larger claws (Fig. 3). The frequency distribution of adult male claw sizes at Sheerness was dimorphic (Fig. 4). This dimorphism also occurs with other measures of size, such as prosoma length (Benton, 1991b). This dimorphism probaly arises because there are two instars of adult male in the population at Sheerness: 6th and 7th (see also Benton, 1991b).

DISCUSSION

Two points are noteworthy. Firstly, the reproductive ecology of *Euscorpius flavicaudis* is much more complex than previously imagined. Naively placing pairs of scorpions together in a laboratory situation to watch the courtship would present a very misleading picture because the most significant behaviours occur before actual courtship. Precopulatory mate-guarding has not been reported in scorpions, but is known to occur in some spiders (e.g. Vollrath, 1980; Watson, 1990) and occurs widely across the animal kingdom (Ridley, 1983). For precopulatory mate-guarding to evolve, males must gain an advantage by staying with a female prior to her becoming receptive rather than searching for a receptive female. Two criteria may determine this situation: firstly, if a male can predict when a female is going to become receptive, and, secondly if receptive females are difficult to find. The former may occur if females become receptive following a moult (e.g. Watson, 1990), or as in the case of these scorpions, after maternal care. The latter criterion may result from female receptivity being very limited in time (e.g., in *Gammarus* female receptivity is limited to a brief period between moulting and the hardening of the amphipod's exoskeleton: Grafen and Ridley, 1983), low population densities (and so low encounter rates) or because of high male mortality

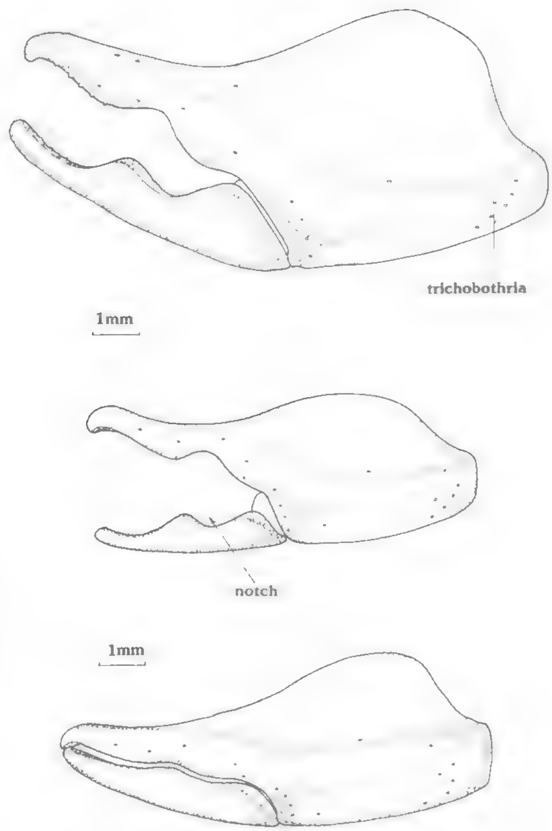

FIG. 3. Claws of two adult ♂♂ (a, b) and one adult ♀ (c) same scale. Note secondary sexual characteristic: notch in fingers.

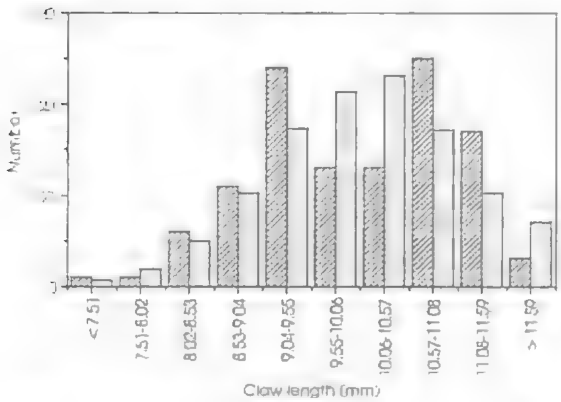

FIG. 4. Distribution of claw-sizes in adult ♂♂ is significantly non-normal. Filled bars are observed distribution; stippled bars are expected normal distribution given mean and standard deviation of data. (χ^2=21.1, P<0.005).

during mate-searching (Vollrath, 1980). The period of female receptivity is reduced where the paternity of a male is ensured by being the first male to mate with a female (so called first-male sperm priority), which may be common in arachnids (e.g. Vollrath, 1980; Watson, 1990). A virgin female is far more valuable to a male than one which is already mated. Thus, *Euscorpius flavicaudis*, first-male sperm-priority and low population densities, coupled with the female's receptivity being predictable, may make it more profitable for a male encountering a female engaged in maternal care to mate-guard her rather than risk searching for another female nearer receptivity.

Secondly, there seems to be a paradox. Adult males exist as two instars in the population. This itself is not a novel finding (see Francke and Jones, 1982). It is surprising that any males mature at the smaller instar since the smaller males seem to be at such a disadvantage in obtaining mates. Natural selection would quickly eliminate any tendency to mature at a disadvantageous size.

The paradox suggests two explanations. First, large males may have an advantage only in a mating season. As large males have more instars, they probably take longer to mature. Although males mate more in the short-term, the younger they mature presumably the more seasons in which to find mates. Perhaps there is a mixed evolutionarily stable strategy (ESS) such that the short-term gains enjoyed by 'large males' are offset by the losses due to having one less season in which to mate, so that, on average, the lifetime reproductive success of 'large' and 'small' males is equal. This ESS could be maintained by frequency dependent selection (Benton, 1992b): large males do relatively better when rare (as they suffer little competition) so their frequency is increased in the population by natural selection. However, when large males are common their gains are reduced, because of increased competition between them, to a point where they are offset by the cost of delaying maturity. Hence, an evolutionary equilibrium is reached between the genes controlling maturation at the 6th and 7th instars.

Secondly, an alternative explanation for this paradox is that there may be phenotypic plasticity in the maturation stage. A gene that can produce a variety of phenotypes depending on the environment is said to exhibit phenotypic plasticity (Lessels, 1991). The 'optimal' time at which to mature may depend on factors such as food availability, and thus growth rate (Stearns and Koella, 1986). For example, if food is plentiful, and an individual is large for its cohort it may be best to mature early. Conversely, if an individual is small for its cohort then it may be better to delay maturity until more food is encountered. This seems to be the case in many spiders (e.g., Deevey, 1947; Vollrath, 1980). This subject will be discussed further elsewhere (Benton, in preparation).

LITERATURE CITED

BENTON, T.G. 1990. 'The behaviour and ecology of scorpions.' (Unpublished Ph.D. thesis, University of Cambridge.)

1991a. Reproduction and parental care in the scorpion, *Euscorpius flavicaudis*. Behaviour 117: 20-28.

1991b. The life history of *Euscorpius flavicaudis* (Scorpiones, Chaetidae). Journal of Arachnology 19: 105-110.

1992a. Determinants of male mating success in a scorpion. Animal Behaviour 43: 125-135

1992b. The ecology of *Euscorpius flavicaudis* in England. Journal of Zoology, London 226: 351-368.

BIRULA, A.A.B. 1917. 'Scorpions: Fauna of Russia and adjacent countries; Arachnoidea, Volume 1: Scorpiones.' (Petrograd: translated from the Russian by the Israeli Programme of Scientific Translation, Jerusalem, 1965).

DEEVEY, G.B. 1949. The developmental history of *Latrodectus mactans* (Fabr.) at different rates of feeding. American Midland Naturalist 42: 189-219.

GRAFEN, A. & RIDLEY, M. 1983. A model of mate guarding. Journal of Theoretical Biology 102: 549-567.

FAGE, L. 1928. Remarques sur la dispersion en France et l'acclimation en France de l' "*Euscorpius flavicaudis*" (De Geer). Association Francais pour l'avancement des sciences, La Rochelle 1928: 650-652.

FRANCKE, O.F. & JONES, S.K. 1982. The life history of *Centruroides gracilis* (Latreille). Journal of Arachnology 9: 223-239.

LOURENCO, W.R. & VACHON, M. 1981. Complements à la description d'*Acanthrothraustes brasiliensis* (Mello-Leitão, 1931) (=*Teuthraustes brasiliensis* Mello-Leitão, 1931), synonyme d'-*Euscorpius flavicaudis* (Geer, 1778) (Scorpiones, Chactidae). Journal of Arachnology 9: 223-228.

LESSELS, C.M. 1991. The evolution of life histories. Pp. 32-68. In Krebs, J.R. and Davies, N.B. (eds.) 'Behavioural Ecology: an evolutionary approach'. 3rd Edition. (Blackwell Scientific Publications: Oxford).

MACHAN, L. 1968. Spectral sensitivity of scorpion eyes and the possible role of shielding pigment effect. Journal of Experimental Biology 49: 95-105.

POLIS, G.A. 1980. The significance of cannibalism on the demography and activity in a natural population of desert scorpions. Behavioural Ecology and Sociobiology 7: 25-35.

RIDLEY, M. 1983. 'The explanation of organic diversity.' (Clarendon Press: Oxford).

STEARNS, S.C. & KOELLA, J.C. 1986. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. Evolution 40: 893-913.

VOLLRATH, F. 1980. Male body size and fitness in the web-building spider *Nephila clavipes*. Zeitschrift für Tierspsychologie 53: 61-78.

WANLESS, F.R. 1977. On the occurrence of the scorpion *Euscorpius flavicaudis* (DeGeer) at Sheerness Port, Isle of Sheepey, Kent. Bulletin of the British Arachnological Society 4: 74-76.

WATSON, P. J. 1990. Female-enhanced male competition determines the first male and principle sire in the spider *Linyphia litigiosa*. Behavioural Ecology and Sociobiology 26: 77-90.

COMPARATIVE POSTEMBRYONIC DEVELOPMENT OF ARACHNIDS

ALAIN CANARD AND ROLAND STOCKMANN

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A common model is used to describe the growth of various arachnid groups. In these predators there is retardation of development of the first instars, along with greater maternal care for the clutch and even, as far as some groups are concerned, in a viviparous development. Mites, which have very diversified biologies, have developments which have evolved in many different ways.
Les développements des différents groupes d'arachnides sont décrits en suivant une trame commune. Il apparaît ainsi une évolution des groupes de prédateurs qui se traduit par une augmentation du retard de développement des premiers stades, en liaison avec des soins à la ponte croissants, avec même pour certains groupes des développements vivipares. Les Acariens, de biologies très diverses, ont en conséquence des développements qui ont évolué dans des voies très différentes.□*Development, arachnids, growth.*

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Analysis of developmental types used in arachnids is very great diverse in the terms used to describe these phenomena. This diversity tends to partially hide some similar points in the developmental process. Authors often use terminology and analyse specific to a single group or species, instead of referring to general concepts relating to all arthropods.

This study compares the developmental processes using the same terms, and we will only use specialised terms if it is absolutely necessary. All developments cannot be discussed in detail here; definitions and more precise descriptions can be found in Canard and Stockmann (1992).

METHODS

Our study is based mainly on literature, enriched with our observations on arachnid growth, particularly on spiders and scorpions.

First, we will evoke the main concepts and definitions used and will then define the different scales of development for each taxon. Taxa which are exclusively predatory are here represented by to the increasing level of care devoted to the clutch. Mites, which have diverse biologies, will be studied separately later.

RESULTS

Concepts and Definitions

POSTEMBRYONIC DEVELOPMENT, HATCHING AND BIRTH

The development, defined as initially embryonic, starts with the first divisions of the egg and continues with the formation of tissues. After hatching or birth, the development is qualified as postembryonic. The postembryonic organism is then covered with an external integument and develops outside of the egg membrane or the female's genital tract. Various organs appear and develop, some will not be functional until late developmental stages (e.g. genital organs). Externally, the development is shown by changes in the cuticle. Reiteration of this concept may seem pointless, but the study of arachnids requires some explanations about hatching and birth.

Hatching, i.e. the opening and release from the egg's membrane, can be a long process. It may take a few days for some spiders, and sometimes some moults can be observed between the beginning of the opening of the egg's membranes and their complete liberation. Hence, the postembryonic period does start with the opening of the egg's membranes. This does not make it necessary to look for a phenomenon before hatching as, for example, Legendre (1958) and Vachon (1958b) did as they chose the 'inversion' to define the beginning of the postembryonic period. Moreover, this proposition has one drawback: it makes the postembryonic development begin at a time when the organism is not covered by a tegument.

Birth appears as a well and easily defined phenomenon, without ambiguity. However, in pseudoscorpions, the organism leaves the female's genital tract and moves into a ventral

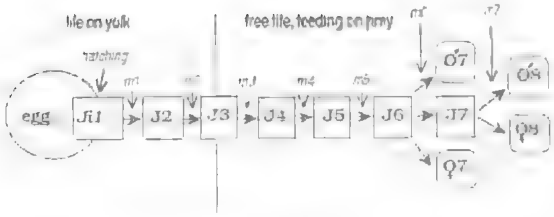

FIG. 1. Stages of postembryonic development of an opilionid, *Liobunum rotundum* (Phalangidae, Palpatores) (after Gueutal, 1943 and Naisse, 1959). (m = moult, **Ji** = incompleted juvenile, J = juvenile).

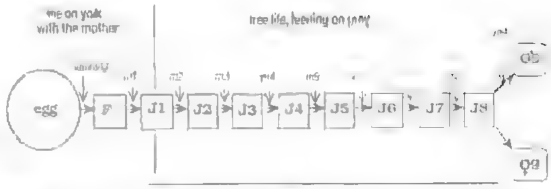

FIG. 2. Postembryonic development scheme of a solpugid, *Eremobates durangonus* (after Muma, 1966).

brood pouch, which is like an external extension of the female's genital tract. Once in the pouch, development continues and the organism still receives nutritive fluid from the mother. Therefore, the start of the postembryonic development of pseudoscorpions should be when they leave the pouch, rather than when they leave the female's genital tract, as others have stated.

INSTARS AND STASES

The instar is the organism between two moults. Generally, among arthropods, the external form does not significantly change between these two stages, except for the short periods of pre- and post-exuviation. However, among some mites, the external morphology and biology are modified while the cuticle remains. Hence, Henking (1882) distinguished two forms, called instars ('stade'), one active and the other motionless. Although this use of the term 'instar' was followed only by a few authors to describe the development of few mites, another acarologist (Grandjean, 1938), considered that the term was too indefinite and proposed the term 'stase'. The definition of stase changed later, but this term is the basis for an evolutionary concept (Grandjean, 1954; André and Jocqué, 1986; André, 1989).

We use 'instar' here in its usual definition, which means an organism between two moults (for endocrinal considerations, see Canard and Stockmann, 1992). To keep the general definition, we will discuss the concept of stase later. When the animal presents separate biologies linked with two different aspects during the same instar, we call them 'forms' and give them two different names.

Succession of Instars

We limit our study to a morpho-biological description of the successive instars. These instars can follow each other in phase (Vachon, 1953) in which all instars are of same kind. These different types are defined in Table 1.

DIFFERENT DEVELOPMENTAL ROUTES

Opilionids

The eggs are laid isolated from each other and then abandoned. The emergent animal depends on its yolk reserves. It looks like a juvenile harvestman but morphologically differs from following instars by the unpigmented integument and lack of some characteristics, such as unformed chelicerae, unsegmented tarsus, absence of median eyes, etc. Therefore it is an incomplete juvenile: Ji_1 (term taken from Holm, 1940 concerning spiders) (= 'larve' according to Juberthie, 1965). It also has temporary organs (one or two egg teeth located on dorsum of cephalothorax).

After the first moult, the animal differs from the imago only by its size and by sexual characteristics. It is a juvenile, the second of the juvenile phase: J_2 (= 'nymphe' according to Juberthie, 1965). Although active, it still lives on its yolk reserves. After one moult, the juvenile opilionids (J_3) scatter and then feed on prey they catch. Usually, 6-7 juvenile instars occur before it becomes an imago, more rarely there are 5 to 8. The number of moults may vary from with individuals of a species, and according to the developmental conditions; this number is generally the same for both sexes.

On becoming a breeding instar (imagos) the opilionid cease moulting (adults), although some may live for be 5-6 years (Juberthie, 1965).

Solifugids

The female isolates herself in burrow but does give care to her eggs.

The animal which hatches is incomplete, motionless and lives on its yolk reserves. It is unpigmented, has no eyes and no racquet organs. Two types may be distinguished. The first is in the Galeodidae (Vachon, 1958a; Junqua, 1966). It does not look like the imago and keeps the aspect it had while under the constraint of the membranes of the egg; it is a foetal instar: **F** (= 'larve' of Vachon, 1958a or Junqua, 1966, = 'post-embryo' of Muma, 1966). The second type is present in some Solpugidae (Lawrence, 1947)

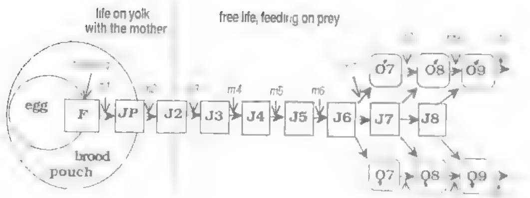

FIG. 3. Scheme of the different stages of the postembryonic development of an amblypygid, *Tarantula marginemaculata* (after Weygoldt, 1970).

and some Karschiidae (Thaler, 1982). It looks like the imagos (juvenile), but lacks some structures and has temporary organs like thorny continuations of the legs. It is an incomplete juvenile: **Ji_1** (= 'primärlarve' of Thaler, 1982).

A further moult results in an animal which has all the adult organs, except those linked with reproduction. This juvenile is, according to the species, the first or the second of the phase (= 'nymphe' of Vachon, 1958a; Junqua, 1966; Muma, 1966). It remains with the female until its integument is hard enough, then it disperses and lives on its own, feeding itself on prey it catches. The number of instars before reaching the status of imago varies according to the individuals. The imagos have a short life expectancy comprising only one instar (adult).

Amblypygids

The female carries the eggs under its abdomen in a brood pouch generated by the genital tract during egg-laying. The incubation period of the clutch may last 3 months (Weygoldt, 1970). Hatching takes place in the brood pouch.

The organism released from the egg's membranes has a foetal aspect with the prosoma bent towards the abdomen and its appendages tight along the body. It is very incomplete (appendages incompletely segmented, absence of setae and of sensory organs, etc.), motionless and lives on its yolk. It is a foetal instar: **F** (= 'deutembryo' of Weygoldt 1970).

After one moult, the animals leave the brood pouch and attach themselves under the females's abdomen. They still live on their yolk, can move, and look like imagos (juvenile), but some structures are lacking and the internal organisation is incomplete (digestive tract, circulatory system, etc.). It is an incomplete juvenile instar which has particular organs on the legs, a dorsal continuation at the distal end of the tibiae (Weygoldt, 1970) and, in some families, an adhesive organ at the tip of the tarsus. It lives on the mother and is

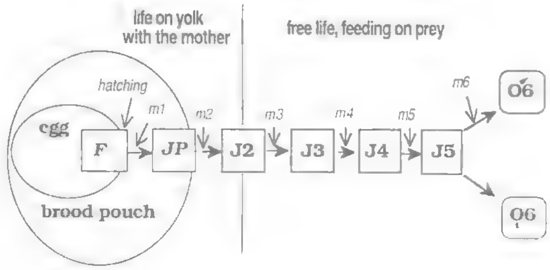

FIG. 4. Scheme of the different stages of the postembryonic development of *Typopeltis stimpsonii* (Thelyphonidae) (after Yoshikura, 1965).

adapted to this life, so with reference to Scorpions, we call it the pullus: **JP** (= 'embryon' of Pereyaslawzewa 1901, and 'praenymphe' of Weygoldt 1970).

The pullus moult while on the mother and then leaves her. Through this moult it acquires all the characteristics of the adult (except the reproductive organs). It is a juvenile instar: **J_2**. After a short gregarious period, the juveniles scatter and live on their own, feeding themselves. The number of juvenile instars may vary between individuals (Weygoldt, 1970) and, after one year, they become an imago.

The imagos of both sexes go on moulting and, under good conditions, the females keep growing after this moult. Therefore, there are no 'adults'.

Uropygids

The female isolates herself in a burrow, and lays her eggs in a newly secreted transparent ventral sac.

Hatching occurs in the brood pouch. It corresponds to a quasi-simultaneous release of the egg's membranes and of the integument of an instar similar to the foetal instar of the Amblypygids: **F** (= 'primärlarve' of Kästner, 1949 and 'prelarva' of Yoshikura, 1965). This instar, which was already formed in the egg, has a very short postembryonic life.

The animal released after hatching and after the first moult, can move and climb upon the mother's back. In general morphology, it looks like the adult (juvenile phase), but lacks some organs (median and lateral eyes are not yet visible, flagellum unsegmented, etc.). It has particular organs linked with its life on the mother, including pad-like organs at the tip of the legs, instead of claws. It is a pullus: **JP** (= 'sekondärlarve' of Kästner, 1949; 'larva' of Yoshikura, 1965). After a 'diapause', there is a moult which releases a juvenile instar: **J_2** (=

Forms	Characteristics			Symbols
Non-breeding	different morphology from imagos	motionless instars which do not feed themselves	embryonal aspect unsegmented appendages	foetal instar
			segmented appendages	nymph
		active instar		larva
	same morphology as imagos	several organs which do not function	no temporary organs	incomplete juvenile
			temporary organs linked to life on mother	pullus
		only non-functional genital organs		juvenile
Breeding (= imagos)		with moulting		imago

TABLE 1. Characteristics of different kinds of instars.

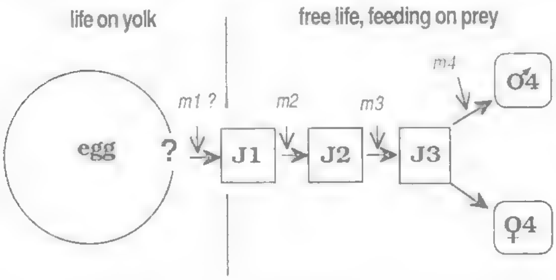

FIG. 5. Scheme of postembryonic development of *Prokoenenia wheeleri* (after Rucker, 1903).

'pullus' of Kästner, 1949; = 'protonymph' of Yoshikura, 1965). They are still gregarious but move around the burrow and begin to feed themselves. After one winter spent together, they then moult and scatter. Subsequent moults usually occur annually, but may be less frequent (Yoshikura, 1965).

Imagos do not seem to moult (adults). Their size of each species does not vary much.

Palpigradids

The sexual biology of palpigradids is almost unknown. Moreover, nobody has ever succeeded in breeding palpigradids. Therefore, knowledge about their postembryonic development is based on observations of natural populations. Under these conditions three immature instars have been determined for many species (Condé, 1984).

The three instars of *Prokoenenia wheeleri* correspond to juvenile instars (Rucker, 1903). Their morphology evolves in a quantitative manner (number of bristles, articulations of the flagellum, evolution of genital parts, etc.).

Spiders

The degree of maternal care given to the clutch varies between species. Some spiders abandon their cocoon (e.g. araneids). Others carry it in their chelicerae or attached to their spinnerets.

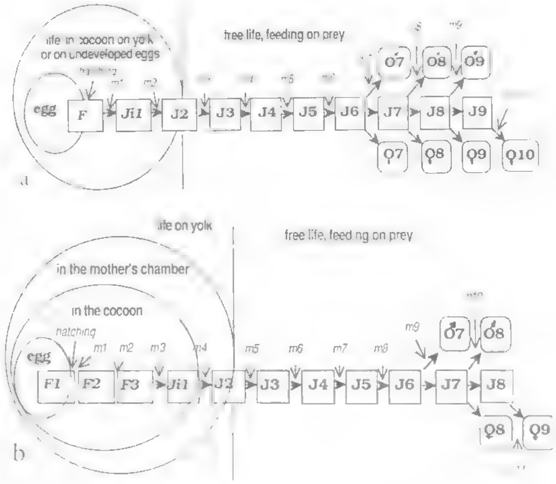

FIG. 6. Postembryonic development in two spider species that (a) abandons its clutch (*Larinioides cornutus*) (after Ysnel, 1992), and (b) cares for young (*Philaeus chrysops*) (after Bonnet, 1933; Canard, 1984).

Others keep their clutch with them in their silk chamber (e.g. salticids).

Hatching occurs in the cocoon and it sometimes takes a few hours before the first instar is released. This instar is generally foetal: **F** (= 'prélarve' of Vachon, 1958b, = 'pullus' of Canard, 1984). Among some orthognathids it remains intrachorional and is therefore not postembryonic. Its very thin cuticle bursts during hatching when the egg membranes open. Among several species which give care to the clutch, there is a series of 2 or 3 instars of this kind: **F**$_1$, **F**$_2$, **F**$_3$ (Canard, 1987). As they cannot move, they stay in the cocoon.

The following instars are mobile and look like a spider (juvenile) but the first one or two still lack some adult characteristics: they are incomplete juvenile (**Ji**) (= 'larves' and 'prénymphes' of Vachon, 1958b). In some cases, the first instar of

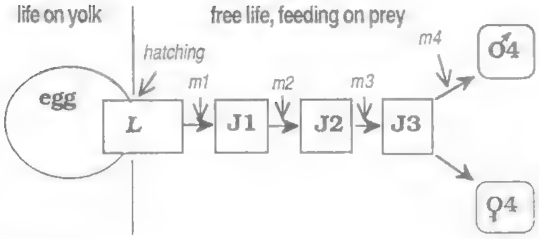

FIG. 7. Scheme of postembryonic development stages of ricinuleid *Crytocellus palaezi* (after Pittard and Mitchell, 1972).

this phase is very incomplete, but in some others, some characters can only be shown absent using an SEM. These first incomplete juvenile instars live on their yolk, but some also feed on undeveloped eggs, which they can pierce with a cheliceral blade. Dispersal takes place after the moult which releases a juvenile equipped with all its organs (J). Juveniles then live on prey they catch (= 'nymphes'; Vachon, 1958b). The total number of juvenile instars may vary within a species. Males often become an imago in fewer instars than females.

Female orthognathids and filistatids can still moult. In labidognathids, imagos do not moult any more (adults). In nature, all male spiders die without moulting.

Ricinuleids

Hatching releases an active individual, which catches prey but which has only three pairs of legs and therefore does not present the general arachnid characteristics. It differs from the imago, and is a larva: **L**. The three instars that follow resemble the imago, and possess 4 pairs of legs; however, they lack genitalic structures. They are juveniles instars: $\mathbf{J_1}$, $\mathbf{J_2}$, $\mathbf{J_3}$ (= 'nymphes' of Pittard and Mitchell, 1972). There is only one imaginal instar (adult).

Pseudoscorpions

The eggs are laid in a brood pouch where they feed upon maternal nutrients with the aid of the embryonic membrane. Growth of the embryos bursts the chorion and the external side of the brood pouch to which they remain attached by the buccal region. Their form is not differentiated. Within a few seconds, the mother injects a nutritive fluid which trebles their volume (= 'larves gonflées' of Vachon, 1938; 'deutembryons' of Weygoldt, 1969). Organogenesis continues and a moult occurs which releases an animal which emerges by an anterior cephalothoracic tooth.

The released instar looks like the imago, but retains some non-evolved characteristics (sensorial system, silk glands, digestive tract, etc.). It is an incomplete juvenile: $\mathbf{Ji_1}$ (= 'larve II' and 'protonymphe' of Vachon, 1938; 'protonymph' of Weygoldt, 1969). Some species apparently retain a foetal aspect (Judson, 1990). The first free instar sometimes remains and moults in the chamber constructed by the female (Weygoldt, 1969). The animal lives alone after this moult. The number of following juvenile instars is fixed to two: $\mathbf{J_2}$ (= 'deutonymphe'), $\mathbf{J_3}$ (= 'tritonymphe'). Each instar can be identified through its trichobothriotaxy (Vachon, 1938). Imagos do not moult any more.

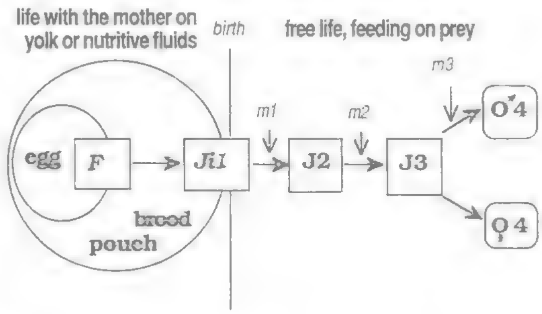

FIG. 8. Postembryonic development of a pseudoscorpion, *Chelifer cancroides* (after Vachon, 1938).

Scorpions

Eggs hatch in the female's genital tract (viviparous species) or soonafter laying (ovoviviparous species).

Newly born scorpions climb onto the mother's back and remain there, living on yolk reserves. They resemble an adult (juvenile) but is incomplete (without trichobothria, unpigmented integument, without specific bristles, etc.). It has temporary organs linked to life on the mother's back, such as legs without claws but bearing adhesive organs at their tip. This incomplete juvenile is a pullus: **JP** (= 'larve' of Vachon, 1940).

After one moult on the mother's back, the juveniles periodically move to the ground, where they begin hunting and eating for the first time. They disperse afterwards and live alone. The second instar is a complete one ($\mathbf{J_2}$). The number of juvenile instars may vary according to sex. Mostly there are 6 to 7 instars, but it may vary from 5 (*Orthochirus*) to 10 (*Diplocentrus*) (Polis, 1990). Imagos do not seem to moult, but it may be possible (Stockmann, 1968).

Mites

The Acari have many more developmental

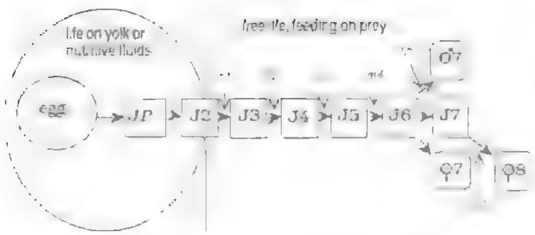

FIG. 9. Postembryonic development stages of a scorpion, *Euscorpius italicus* (after Angermann, 1957).

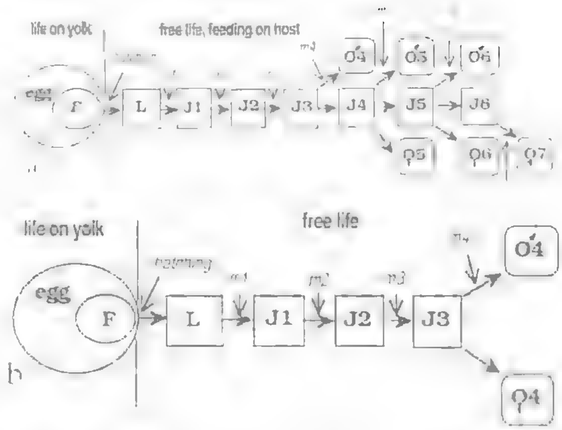

FIG. 10. Succession of stages in postembrional development of mites. (a) Argasidae, *Ornithodoros maritimus* (after Guiguen, 1990); (b) Oribatidae (*Carabodes wilmanni*) (after Bellido, 1983).

types than other arachnids. The eggs are often abandoned. There is a first instar which has a foetal aspect, but it remains intrachorionic, except in some cases (Coineau, 1977). This instar can be compared with foetal instars of other arachnids (F), but it is not postembryonic.

The first free instar is obviously different from the imago because it usually has only 3 pairs of legs. It moves and can feed itself. It is a larva: L.

The following instars are eight-legged and only differ from the imagos by some quantitative or sexual characteristics: they are juveniles (J) (= 'nymphes'). The number of instars is often fixed for a species, at 1 or 2, more often a maximum of 3, but up to 4-5 in the Argasidae.

After these immature instars imagos appear, which do not moult anymore (adults) (= 'prosopon' of Reuter, 1909).

In the thrombidiids, there are periods of inactivity between larval and juvenile stages and between juvenile and adult stages. At such times, the animal is covered by the original cuticle, but secretes a new tegument under it, which becomes the tegument of the next instar. In many other cases, motionless instars can be distinguished, sometimes comparable to real nymphs or to specific survival-forms, which allow for dispersal.

DISCUSSION AND CONCLUSIONS

Terminology and Concepts

Most terms used in other arthropods can also be used in arachnids. We have used only the original terms of pullus, foetal instars and incomplete juvenile.

The foetal instar, although it has been defined for arachnids (Canard, 1987), is not specific to this group. It is evident in some insects and myriapods (= 'prolarves', 'prélarves', 'pseudo-foetus', etc.).

The incomplete juvenile instars belong to the juvenile phase of which they form a part (J_1 followed by J_2). One can recognize the systematic group of the imago, therefore they are not larvae, but genital organs and furthermore some other structures are lacking. This 'incomplete' situation is not always easy to observe morphologically. However, biological information is useful, because these instars are nearly always unable to live on their own.

The pullus (Pavlovsky, 1924) is an incomplete juvenile instar with special adaptations to life on the mother, such as pad-like organs on the tip of the legs.

The presence of two morpho-biological forms during the same instar among mites is rare amongst the arthropods (except Diptera), but it does not raise any problems of description and does not require any fundamental vocabulary changes; it simply requires more accurate definitions.

Chronological and Morpho-biological Descriptions

In the development of a systematic group of arachnids, except in ricinuleids, pseudoscorpions and perhaps palpigradids, there is no fixed number of instars. Therefore it would be unwise to base a study on few species and to fix the chronology, because some still unknown developments may modify the established system. Theoretical systems of this kind were proposed by Reuter (1909) for mites and by Vachon (1958b) for spiders. Thus, the constant presence of three post-larval juvenile instars (=nymph) in mites stated by Reuter and often followed (protonymphe, deutonymphe, tritonymphe) does not conform to most species, in which there are less than 3 juvenile instars and even less to those with 4 to 6 instars (e.g. *Ornithodoros maritimus*).

Developmental analyses based on a fixed number of instars (chronological) establishes common points between instars of different species, in order to envisage evolutionary pathways. But these common points will always remain hypothetical, and moreover, these pathways can be elucidated without this system. Therefore we do not wish to use a method with no decisive advantages and, because of its fixed character, limited development descriptions, because species which do not suit the established system are excluded. In mites, for example, the number of instars is considered fixed to one larval, three juvenile instars and the adult. However, in many species one or more juvenile instars are missing and sometimes there are more than three juvenile instars. For mites there is, depending on the species, a variable number of instars.

Evolutionary Pathways

Immature instars of arthropods are adapted to special lifestyles or environments and sometimes differ from those of imagos. Often these adaptations influence the morphology so deeply that it is difficult to distinguish the imago from the immature forms (larva). Such differences are less marked among the arachnids (larvae absent except in mites and ricinuleids).

A good correlate probably exists between the increased level of care by the mother to its clutch and the increased number of incomplete instars at the start of the development.

Moreover, the biology and morphology of early instars can be observed and explained as adaptations to life in the cocoon or with the mother, e.g., the temporary organs such as distal, pedal pad-like organs of pullus (attaching to the mother) or the cheliceral blade of some incomplete juvenile spiders (feeding on undeveloped eggs). The viviparous cases do depend on the same kind of evolutionary processes.

The evolution of many arachnids has probably been characterized by growing care of the clutch correlated with the increasingly and later development of the first instars. Thus, the instars are both incomplete and regressed, because these adjectives depend on the point of view considered: ontogenetic or evolutionary. This corresponds to the 'deux temps' of Grandjean (1954) and, to a certain extent, to the 'state approach' and the 'stase approach' of André (1989).

Mites present great diversity in their biology and, unlike other arachnids, are not all predators. Therefore, they have followed different evolutionary pathways and sometimes metamorphosis takes place, with larvae and nymphs (similar in these cases to those of holometabolic insects) or with 'survival' instars which enable them to disperse.

This evolution of clutch or juvenile care by the mother does not indicate phylogenetic relations in the different orders, because it is a general phenomenon within the animal world and can appear independently in different groups.

LITERATURE CITED

ANDRÉ, H.M. 1989. The concept of stase. Pp. 3-14. In: H.M. André and J.C. Lions (eds). 'L'ontogénèse et le Concept de Stase chez les Arthropodes'. AGAR: Wavre.

ANDRÉ, H.M. & JOCQUÉ, R. 1986. The definition of stases in spiders and other arachnids. Mémoires de la Société Royale Belge d'Entomologie 33: 1-14.

ANGERMANN, H. 1957. Uber verhalten, Spermophorenbildung und Sinnesphysiologie von *Euscorpius italicus* Hbst. und Verwandten Arten (Scorpiones, Chactidae). Zeitschrift für Tierpsychologie 14: 276-302.

BELLIDO, A. 1983. Etude morphologique et écologique de *Carabodes willmanni* Bernini, 1975 (Acari, Oribatei) dans une formation pionnière de la lande armoricaine. Thèse 3ème cycle Rennes I. 79 pp.

BONNET, P. 1933. Le cycle vital de *Philaeus chrysops* Poda (Aranéide, Salticide). Archives de Zoologie Expérimentale 75: 129-144.

CANARD, A. 1984. Contribution à la connaissance du développement, de l'écologie et de l'écophysiologie des Aranéides de landes armoricaines. Thèse Doct. Etat, Rennes: 389 pp., annexe: 152pp.

1987. Analyse nouvelle du développement postembryonnaire des araignées. Revue Arachnologique 7: 91-128.

CANARD, A. & STOCKMANN, R. 1992. Données comparées sur le développement postembryonnaire des arachnides. Bulletin de la Société Scientifique de Bretagne 61 n° h.s. 1, 1990: 19-50.

COINEAU, Y. 1977. La première prélarve ellatostatique connue chez les Acariens. Acarologia 19: 46-54.

CONDÉ, B. 1984. Les palpigrades: quelques aspects morpho- biologiques. Revue Arachnologique 5: 133-143.

GRANDJEAN, F. 1938. Sur l'ontogénie des Acariens. Comptes-rendus de l'Académie des Sciences. Paris 206: 146-150

1954. Les deux sortes de temps et l'évolution. Bulletin biologique de la France et la Belgique 88: 413-433.

GUEUTAL, J. 1943. Du développement postembryonnaire de *Phalangium opilio* L. Bulletin de la Société Zoologique de France 57: 98- 100.

GUIGUEN, C. 1990. Cycle et écologie d'*Ornithodoros (Alectorobius) maritimus* Vermeil et Marguet (Acarina: Argasidae) parasite d'Oiseaux de mer. Bulletin de la Société française de Parasitologie, Supplément 1: 316.

HENKING, H. 1882. Beiträge zur Anatomie, Entwicklungsgechichte und Biologie von *Trombidium fuliginosum* Herm. Zeitschrift für wissenschaftliche Zoologie 37: 553-663.

HOLM, A. 1940. Studien über die Entwicklung und die Entwicklungsbiologie der Spinnen. Zoologiske Biddrag Uppsala 19: 1-214.

JUBERTHIE, C. 1965. Données sur l'écologie, le développement et la reproduction des Opilions. Revue d'Ecologie et de Biologie du Sol 2:377-397.

JUDSON, M.L.I. 1990. The remarkable protonymph of *Pseudochthonius* (Chelonethi, Chthoniidae). Bulletin de la Société Européenne d'Arachnologie, n° h.s. 1: 159-165.

JUNQUA, C. 1966. Recherches biologiques et histophysiologiques sur un Solifuge saharien. Thèse Doct. Etat Paris. 124 p.

KÄSTNER, A. 1949. Zur Entwicklungsgechichte von Prosoma *Thelyphonus caudatus* L. (Pedipalpi). 2. Teil. Die Entwicklung der Mundwerkzeuge, Beinhüften und Sterna. Zoologische Jahrbücher, Anatomie und Ontogenie 70: 169-197.

LAWRENCE, R.F. 1947. Some observations on the eggs and newly hatched embryos of *Solpuga hostilis* White (Arachnida). Proceedings of the Zoological Society of London 117: 429-434.

LEGENDRE, R. 1958. Contribution à l'étude du développement embryonnaire des Araignées. Bulletin de la Société Zoologique de France 83: 60-75.

MILLOT, J. 1949. Ordre des Amblypyges. 563-588. In: P.P. Grasse (ed.). 'Traité de Zoologie'. Vol 6. Masson: Paris.

MUMA, M.H. 1966. The life cycle of *Eremobates durangenus* (Arachnida: Solpugida). Florida Entomologist 49: 233-242.

NAISSE, J. 1959. Neurosécrétion et glandes endocrines chez les Opilions. Archives de Biologie 70: 217-264.

PAVLOVSKY, E.N. 1924. Studies on the organization and development of scorpios. Quarterly Journal of Microscopical Science, London 68: 615-640.

PEREYASLAWZEWA, S. 1901. Développement embryonnaire des Phrynes. Annales des Sciences Naturelles, Zoologie. 8ème serie, 13: 117-304.

PITTARD, K. & MITCHELL, R.W. 1972. Comparative morphology of the life stages of *Cryptocellus palaezi* (Arachnida, Ricinulei). Graduate Studies Texas Tech University 1: 1-77.

POLIS, G. 1990. 'Biology of Scorpions'. (Stanford University Press: Stanford).

REUTER, E. 1909. Zur Morphologie und Ontogenie der Acariden. Acta Societatis Scientarum Fennicae 36(4): 1-288.

RUCKER, A. 1903. Further observations on *Koenenia*. Zoologische Jahrbücher, Systematik (Ökologie), Geographie und Biologie 18: 401-434.

STOCKMANN, R. 1979. Développement postembryonnaire et cycle d'intermus chez un Scorpion Buthidae: *Buthotus minax occidentalis* (Vachon et Stockmann). Bulletin du Muséum National d'Histoire Naturelle de Paris, 4ème série 1: 405- 420.

THALER, K., 1982. Die Primärlarve der Walzenspinnen *Gyllipus* cf. *cypriotica* Lawrence (Arachnida, Solifugae, Karschiidae). Mitteilungen der Schweizerischen Entomologischen Gesellschaft 55: 93-95.

VACHON, M. 1938. Recherches anatomiques et biologiques sur la reproduction et le développement des Pseudoscorpions. Thèse Doct. Etat, Paris: 1-207; Annales des Sciences Naturelles, Zoologie, série 11: 1-207.

1940. Sur la systématique des scorpions. Mémoires du Muséum National d'Histoire Naturelle de Paris 2: 241-260.

1958a. La larve de *Galeodes arabs* C.L. K. (Arachnide, Solifuge). Comptes Rendus de l'Académie des Sciences, Paris 246: 477- 480.

1958b. Contribution à l'étude du développement post-embryonnaire des Araignées. 1ère note: généralités et nomenclature des stades. Bulletin de la Société Zoologique de France 82, 1957 (1958): 337-354.

WEYGOLDT, P. 1969. 'The Biology of Pseudoscorpions'. (Harvard University Press: Cambridge, Mass.).

1970. Lebenzyklus und postembryonische Entwicklung der Geisselspinne *Tarantula marginemaculata* C.L. Koch (Chelicerata, Amblypygi) im Laboratorium. Zeitschrift für Morphologie der Tiere 67: 58-85.

1975. Untersuchungen zur Embryologie und Morphologie der Geisselspinne *Tarantula marginemaculata* C.L. Koch (Arachnida, Amblypygi, Tarantulidae). Zoomorphologie 82: 137-199.

YOSHIKURA, M. 1965. Postembryonic development of a whip scorpion, *Typopeltis stimpsonii* (Wood). Kumamoto Journal of Science, Series B Biology 7: 21-50.

1975. Comparative embryology and phylogeny of Arachnida. Kumamoto Journal of Science, Series B Biology 12: 71-142.

YSNEL, F.1992. Impact trophique et valeur bioindicatrice d'une population d'Araignées: Exemple d'une espèce à toile géométrique *Larinioides cornutus* (Araneidae). Thèse Université Rennes I. 217 pp.

COURTSHIP, MATING AND POST-OVIPOSITION BEHAVIOUR OF *HYPOCHILUS POCOCKI* PLATNICK (ARANEAE, HYPOCHILIDAE)

K. M. CATLEY

Catley, K.M. 1993 11 11: Courtship, mating and post-oviposition behaviour of *Hypochilus pococki* Platnick (Araneae, Hypochilidae). *Memoirs of the Queensland Museum* 33 (2): 469-474. Brisbane. ISSN 0079-8835.

Courtship and mating in *Hypochilus pococki* Platnick is described for the first time for any member of the superfamily Hypochiloidea. Five phases of male behaviour are recognised; pre-courtship, non-contact courtship, contact courtship, copulation and post-copulatory behaviour. Chemotactic stimulation seems to be the prime releaser of male courtship behaviour which involves web-tugging, mutual leg-stroking and female guarding. Post-oviposition behaviour is described and the role of a previously undescribed sheet web, constructed by females after oviposition as well as early instar spiderlings, is discussed in terms of its phylogenetic implications.□*Hypochilus, courtship, phylogenetics, sexual selection, web construction.*

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The significance of undertaking ethological studies of spiders in the family Hypochilidae stems from the phylogenetic position of the family as a relic taxon at the base of the Infraorder Araneomorphae (Platnick, 1977; Forster *et al.*, 1987). Diagnosis of behavioural units that are used in such processes as web construction (Coddington, 1986) and courtship (Platnick, 1971; Helversen, 1976; Coyle and O'Shields, 1990) may prove useful in future phylogenetic analysis. This paper describes the courtship and mating behaviour of *Hypochilus pococki* in the laboratory and attempts to recognise potentially informative behavioural sequences. Egg sac construction is also described and attention drawn to a previously undescribed silk construct, a 'veil web' built by post egg-laying females as well as early instar spiderlings. Apart from one incomplete observation by Fergusson (1972) of mating in *Hypochilus thorelli* Hoffman (=*Hypochilus pococki*), this is the first detailed description of reproductive behaviour for any member of the superfamily Hypochiloidea.

The genus *Hypochilus* comprises five species confined to the Southern Appalachian highlands of eastern North America, two species from central and northern California and one from central Colorado. Two additional species, one from New Mexico and the other from the San Bernardino Mountains of southern California will soon be described (Catley in prep.). These haplogyne cribellate spiders build characteristic 'lampshade' webs on rock surfaces often close to running water. All species appear to be allopatric and exhibit an interesting pattern of disjunct endemism (Catley, 1991; Huff and Coyle, 1992). Males moult to maturity later than females, typically appearing in early August. They move extensively (presumably in search of females) and do not associate with penultimate females, suggesting that there is no first male sperm precedence (Eberhard *et al.* in press).

MATERIALS AND METHODS

Despite extensive day and night observation during 1990 and 1991, no courtship or mating behaviour was observed in the field. *Hypochilus* can be very difficult to maintain in the laboratory; they are affected adversely by changes in humidity and only occasionally can they be persuaded to construct a web, making feeding problematical. Following several unsuccessful attempts to establish a mature female in the laboratory, a single specimen collected in July 1990 from Wolf Creek watershed, Cullowhee, Jackson County NC, established a web in a 50x30cm glass tank. The tank was furnished with a sloping wooden framework (45°angle) covered with sandpaper to simulate an overhanging rock ledge. The floor was covered with vermiculite to a depth of 5cm and was kept very moist.

After the female attacked and killed the first male introduced into the arena, she was allowed to feed for a period of one week. The second male was introduced on August 28 1990 and a total of 7 hours 47 mins of male/female encounters were filmed using a Panasonic WV-D5000 video re-

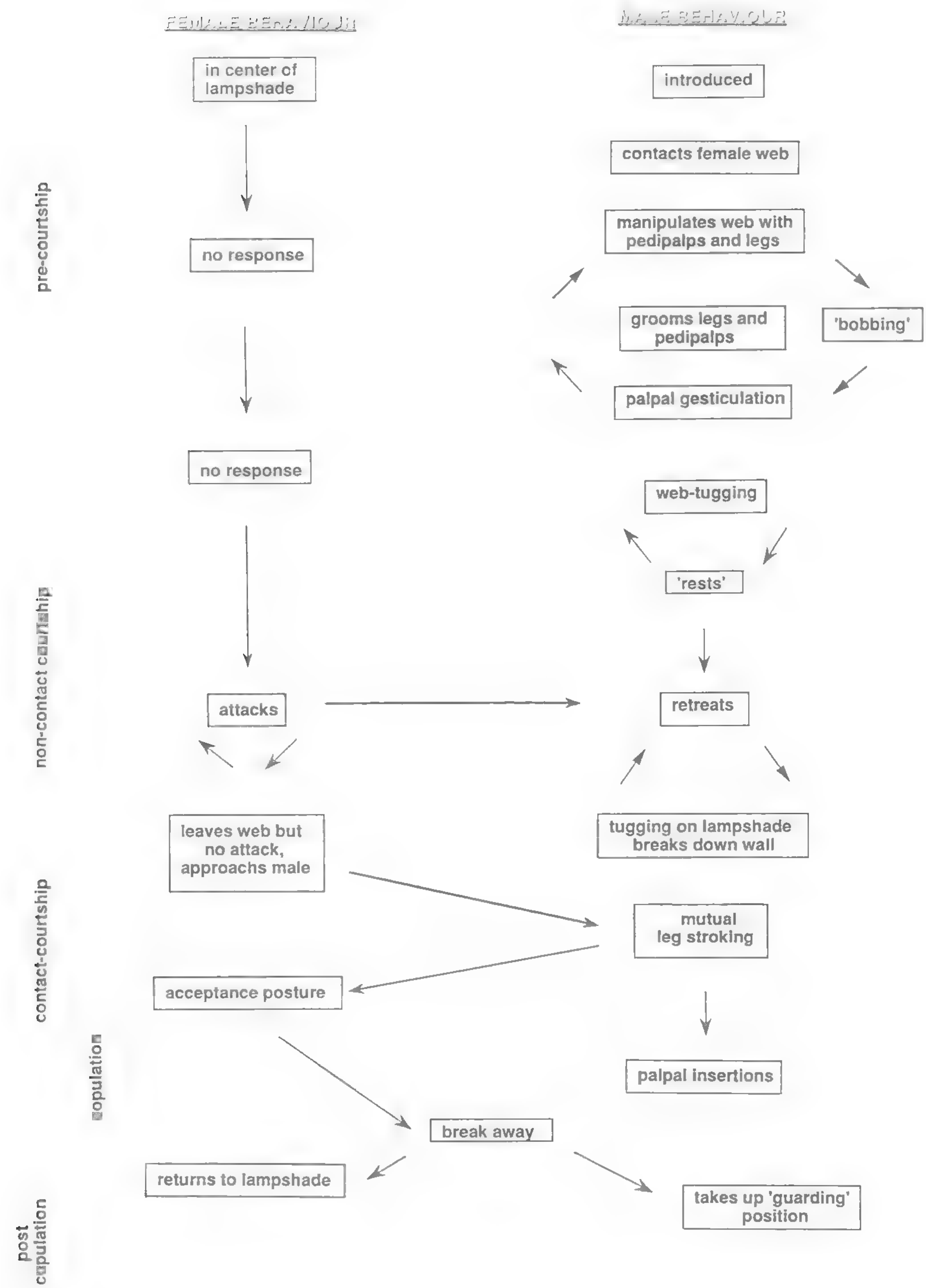

FIG. 1. Sequence of courtship and mating behaviour in *Hypochilus pococki* formulated from encounters in the laboratory involving two males and a single female (see text for explanation).

corder fitted with a Micro-Nikkor 55mm close-up lens. Sessions were annotated by verbal comments recorded through the audio channel of the video camera. Data analysis was achieved using slow motion and freeze frame functions of a VCR.

RESULTS

The description of courtship and mating presented here is a composite derived from laboratory observations of only two males and a single female and therefore may not be representative.

Male courtship behaviour can be divided into five distinct phases: pre-courtship, non-contact courtship, contact courtship, copulation and post-copulation (Fig. 1). The following behavioural units were diagnosed.

Male Behavioural Units

PRE-COURTSHIP

Leg and pedipalpal grooming. Within a few minutes of a male being introduced into the arena, the legs and pedipalps were used to manipulate female silk. A web constructed by the same female but which had been abandoned for several weeks elicited the same response. Rubbing the tarsi and metatarsi of legs 1, 2 and 3 together, as well as drawing them and the pedipalps between the open chelicerae (and presumably the endites) occurred immediately after the first and subsequent encounters with the female web. The pedipalps were rubbed vigorously across the silk for extensive periods, this was followed either by drawing them through the mouthparts, as described above, or by rapid pedipalpal gesticulations.

Bobbing. Flexing of the legs resulted in the whole body moving up and down relative to the substrate. Bobbing is often interspersed between sessions of leg and pedipalp grooming.

NON-CONTACT COURTSHIP

Web-tugging. The male pulled on the cribellate lampshade web of the female with his first pair of legs. Such actions, repeated in bouts lasting 3-7 seconds interspersed with periods of inactivity lasting from 5 secs. to several mins., can result in the side wall of the lampshade being partially destroyed.

CONTACT COURTSHIP

Leg-stroking. The female eventually left the web as a result of male tugging and approached the male, waving her front pair of legs. The male held his ground (unlike previous female approaches which appeared aggressive and from which the male quickly withdrew). A long session of mutual leg-stroking followed, involving mainly legs one and two. The male maintained a constant, very rapid stroking of the female's legs (mainly metatarsi and tibiae) and body as she appeared to become progressively more cataleptic, and eventually assumed the acceptance posture. This stroking session lasted for 3 mins. 12 secs–more than twice the period of copulation itself.

COPULATION

Palpal insertions. Following mutual leg-stroking the female oriented her abdomen at 45° to the substrate and adopted a semi-cataleptic acceptance posture. The male faced the female and advanced, with pedipalps fully extended, to a position where his dorsal cephalothorax was adjacent to the female's sternum (Fig. 2). It was not entirely clear whether or not the male tapped on the female's genital area with his palps prior to insertion as described for some araneids (Robinson and Robinson, 1980). Such apparent tapping may simply be attempts to locate the opening to the bursa copulatrix.

The palps were inserted alternately, the right followed by the left, each insertion lasted 3-10 seconds with the whole insertion sequence lasting 1 min. 22 secs. To achieve insertion from this position requires that the palpal organ be twisted through 90° at the same time as the pedipalp is straightened. The copulatory phase ended abruptly when the female broke away from the male, who was immediately pursued some distance from the web. At no time during courtship or mating was the male observed to lay down silk.

POST-COPULATION

'Guarding' posture. After copulation, the male, after a brief period of palpal grooming, took up a characteristic position close to the female, often touching her. His legs were extended parallel to the substrate, with the first three pair directed anteriorly, and the fourth pair directed posteriorly. The first pair of legs were held in such a position such that the femora were at 30° to the longitudinal axis of the prosoma, while the remaining podites tended to converge distally over the female. This seems to be a characteristic position seen often in the field. It was maintained

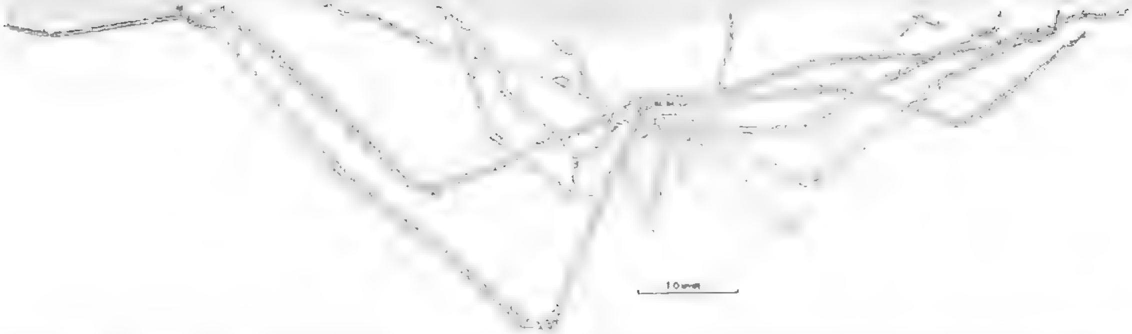

FIG. 2. Mating position of *Hypochilus pococki* (for the sake of clarity not all male appendages are illustrated).

for 2.5 hours after which the female attacked and badly injured the male.

Female Behavioural Units

NON-CONTACT

Attack. The female failed for long periods to show any response to the male's web-tugging but did eventually respond by rushing out of the lampshade and pursuing him. Three attacks appeared in earnest, with the male withdrawing rapidly. The fourth response was instigated more slowly (with reduced speed and vigour); this change in 'intent' appeared to be sensed by the male, who did not retreat. This encounter led directly to contact courtship and copulation (Fig. 2).

CONTACT COURTSHIP

Leg stroking. See male behaviour.

COPULATION

Acceptance posture. A semi-cataleptic position with the abdomen held at 45° to the substrate (Fig. 2) occurring after contact courtship (extensive leg stroking) with the male.

POST-COPULATION

Egg laying ethology. Twenty days after copulation, the female laid eggs and constructed an egg-sac. First a saucer-shaped disc of pink silk was laid down onto which the eggs were deposited. This was then closed up to form a flattened sphere. The pink colour of the silk has been corroborated by several observations in the field, however, when the egg-sac is ready to be covered in cryptic material its colour is off-white. A second egg-sac was produced on October 4, followed by a much smaller egg-sac on October 17, and the final egg-sac was constructed on November 6. Each was suspended from the framelines of the web while particles were incorporated in the outer layer of the egg-sac. This involved the spider descending to the substrate and carrying pieces of vermiculite back to the web in her chelicerae (in the field egg cases are covered with particles of moss or lichen (Fergusson, 1972; pers. obs.).

Two egg-sacs were 'screened in' by a particular type of sheet web not previously described for *Hypochilus*. Observations from the field show that a similar 'veil web' is also constructed by early instar spiderlings (Catley, 1991). The silk is of very different appearance from either framework or cribellate silk and appears as a dense, finely woven sheet. Its purpose, either as a vertical 'veil' in front of egg-sacs (typically those suspended in a fissure in the rock), or as a barrier underneath which a number of very early instar spiderlings build their regular prey catching lampshade webs, may be protective.

DISCUSSION

The function of courtship in spiders may be most simply expressed as: alerting the female to the presence of the male, the possible suppression of female predatory behaviour and stimulation of the female to accept copulation. Variations on this basic theme have been voiced by several authors including Bristowe (1958), Crane (1949) and Platnick (1971); most expand the concept to include elements of species specific recognition, advertisement of sexual availability and the functioning of a releaser system. Other components which may also be important are male behavioural elements designed to ensure his post-copulation survival.

Accounts of courtship and mating in other more primitive spider taxa are scant, but include information on the Mesothelae: Liphistiidae, *Heptathela* (Haupt, 1977); Mygalomorphae: Nemesiidae (Buchli, 1962); Atypidae (Clark, 1969); Dipluridae (Coyle and O'Shields, 1990). Whereas behavioural observations for spiders in the Araneoclada are available from Bristowe (1941, 1958) various families, Crane (1949) for salticids, and Robinson and Robinson (1978, 1980) for araneids, this account of courtship and mating in *Hypochilus* is the first to be published for any lower (non-Araneoclada) araneomorph spider.

The courtship and mating repertoire of *Hypochilus* is relatively underived and given the families' phylogenetic position the behavioural units which comprise it may be hypothesised to represent the plesiomorphic condition of araneomorph reproductive behaviour in general. Given a larger data base within the Araneomorphae, comparison of behavioural characters will allow correct polarity decisions to be made and the resulting data set, combining both morphological and ethological characters, should provide a more stringent test of phylogeny.

Leg and pedipalpal grooming behaviours performed by the male upon contact with the female web may be indicative of the occurrence of female pheromone on the web. Such pre-contact encounters were necessary to release web-tugging behaviour in these observations (n=4) and is consistent with Platnick's (1971) hypothesis that chemotactic stimuli are prime releases of male courtship behaviour in haplogyne spiders. It has been suggested that the longer anterior legs of male *Hypochilus* confer superior mobility when locating females (Fergusson, 1972; Eberhard *et al.* in press). However, such pronounced sexual dimorphism may have had its origin in courtship behaviour. The extreme length of the first legs, by maximising the distance between male and female during web-tugging, should increase the male's chance of surviving female attacks. Such interactions may also provide an opportunity for sexual selection by female choice to occur (Eberhard, 1985), the female testing male 'fitness' by repeated attacks.

Contact courtship was initiated when the female eventually left the lampshade and approached the male. Such behaviour may not however be typical. Fergusson (1972) reported that in the one encounter he observed the male scrambled into the lampshade with the female. The long period of mutual leg-stroking may play a role in placating the female, resulting in her adopting the acceptance posture. It may well be homologous with the 'leg fencing' behaviour seen in some diplurid spiders (Coyle and O'Shields, 1990).

Copulation was achieved in the mating position (Fig. 2; position 1 of Kaston, 1981). Alternate palpal insertions, as observed in *Hypochilus*, should be considered plesiomorphic when encountered in other araneomorph spiders (using *Hypochilus* as an outgroup) and as apomorphic when palps are inserted simultaneously. Simultaneous palpal insertion has been documented in the following families, Dysderidae, Segestriidae, Oonopidae, Scytodidae and Pholcidae (Bristowe, 1958) but appears not, as Bristowe concluded, to be plesiomorphic for the Araneoclada. Simultaneous insertion may well prove to be a synapomorphy for the higher haplogynes, Dysderoidea plus 'Scytodids' (Coddington and Levi, 1991).

The post-copulatory position taken up by the male is believed to represent a guarding posture. *Hypochilus pococki* males have been shown conclusively not to associate with penultimate females (Eberhard *et al.* in press). Hence, that the numerous occasions when males were found in this position in the field, suggest that they represent in fact, post-mating situations, and that the male was most likely guarding the female and thus his chance of paternity.

The implications of the 'veil' web produced by the female following egg-sac construction require further comment. *Hypochilus* egg-sacs are superbly cryptic and most are not concealed by such a 'veil' web (Shear, 1969; Fergusson, 1972; Catley, 1991). The behaviour of some females in concealing egg-sacs might have primitively represented a selective advantage from vertebrate or hymenopteran predation.

Accepting the cladistic hypothesis of Forster *et al.* (1987) on the relationships of the Hypochiloidea and Austrochiloidea, data on sheet web construction in these taxa suggests that the lampshade web of *Hypochilus* is autapomorphic. *Ectatosticta davidi* (Simon), the sister taxon of *Hypochilus*, constructs a sheet web (Li and Zhu, 1984) as do all known members of Austrochilidae (Forster *et al.*, 1987). Ontogenetic evidence, based on the observation that very early instar spiderlings also construct a sheet web (Catley, 1991), also supports this hypothesis and lends some weight to the suggestion that the plesiomorphic web construct of araneomorph spiders was the sheet web.

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LITERATURE CITED

BRISTOWE, W.S. 1941. The Comity of Spiders. vol. II. (Ray Society: London).

1958. The World of Spiders. (Collins: London).

BUCHLI, H. 1962. Note préliminaire sur l'accouplement des araignées mygalomorphes *Nemesia caementaria*, *Nemesia dubia* et *Pachylomerus piceus*. Vie et Milieu 13: 167-178.

CATLEY, K.M. 1991. The phylogenetic relationships of the species of the lampshade spider genus *Hypochilus* (Araneae, Hypochilidae). (Unpublished Masters thesis, Western Carolina University).

CLARK, D. J. 1969. Notes on the biology of *Atypus affinis* Eichwald. Bulletin of the British Arachnological Society 1: 36-39.

CODDINGTON, J. A. 1986. The monophyletic origin of the orb-web. Pp. 319-363. In Shear, W. A. (ed). 'Spiders. Webs, behavior, and evolution'. (Stanford University Press: Stanford, California).

CODDINGTON, J. A. & LEVI, H.W. 1991. Systematics and evolution of spiders (Araneae). Annual Review of Ecology and Systematics 22: 565-92.

COYLE, F. A. & O'SHIELDS, T. C. 1990. Courtship and mating behavior of *Thelechoris karschi* (Araneae, Dipluridae), an African funnel web spider. Journal of Arachnology 18: 281-296.

CRANE, J. 1949. Comparative biology of salticid spiders at Rancho Grande, Venezuela. Part IV. An analysis of display. Zoologica 34: 159-214.

EBERHARD, W. G. 1985. Sexual selection and animal genitalia. (Harvard University Press:Cambridge).

EBERHARD, W. G., GUZMAN-GOMEZ, S. & CATLEY, K. M. (in press). Correlation between spermathecal morphology and mating systems in spiders. Biological Journal of the Linnean Society.

FERGUSSON, I. C. 1972. Natural history of the spider *Hypochilus thorelli* Marx (Hypochilidae). Psyche 79: 179-199.

FORSTER, R.R., PLATNICK, N.I. & GRAY, M.R. 1987. A review of the spider superfamilies *Hypochiloidea* and *Austochiloidea* (Araneae, Araneomorphae). Bulletin of the American Museum of Natural History 185: 1-116.

HAUPT, J. 1977 Preliminary report on the mating behaviour of the primitive spider *Heptathela kimurai* (Kishida) (Araneae, Liphistiomorphae). Zeitschrift für Naturforschung 32: 312-314.

HELVERSEN, O. VON 1976. Gedanken zur Evolution der Paarungsstellung bei den Spinnen (Arachnida, Araneae). Entomologica Germanica 3: 13-28.

HUFF, R. P. & COYLE, F. A. 1992. Systematics of *Hypochilus sheari* and *Hypochilus coylei*, two southern Appalachian lampshade spiders (Araneae, Hypochilidae). Journal of Arachnology 20: 40-46.

KASTON, B.J. 1981. Spiders of Connecticut. State Geological and Natural History Survey of Connecticut. Department of Environmental Protection. Bulletin 70.

LI, ZHONSHAN & ZHU, CHAUNDIAN, 1984. *Ectatosticta davidi* (Simon, 1888) of China (Araneae: Hypochilidae). Journal of the Bethune Medical University 10(5): 510 (in Chinese).

PLATNICK, N. I. 1971. The evolution of courtship behaviour in spiders. Bulletin of the British Arachnological Society 2(3): 40-47.

1977. The hypochiloid spiders: a cladistic analysis with notes on the Atypoidea (Arachnida, Araneae). American Museum Novitates 2627: 1-23.

ROBINSON, M.H. & ROBINSON, B. 1978. The evolution of courtship systems in tropical araneid spiders. Symposia of the Zoological Society of London 42: 17-29.

1980. Comparative studies of the courtship and mating behavior of tropical araneid spiders. Pacific Insects Monograph 36: 1-218

SHEAR, W. A. 1969. Observations on the predatory behavior of the spider *Hypochilus gertschi* Hoffman (Hypochilidae). Psyche 76: 407-417.

EFFECTS OF SAMPLING METHOD ON COMPOSITION OF A TASMANIAN COASTAL HEATHLAND SPIDER ASSEMBLAGE

TRACEY B. CHURCHILL

Churchill, T.B. 1993 11 11: Effects of sampling method on composition of a Tasmanian coastal heathland spider assemblage. *Memoirs of the Queensland Museum* 33(2:): 475-481. Brisbane. ISSN 0079-8835.

The composition of a spider community in coastal heathlands of north-east Tasmania was derived from a 16 month survey using pitfall traps, sweep net and visual search sampling methods incorporated into a replicated, standardised sampling program. This interpretation of composition is shown to rely on the relative efficiency of the three collecting methods to sample the taxa present. Since mature spiders are required to confirm species identity, the differential selection of age and sex classes by the methods is illustrated. Whilst pitfall traps catch a greater number of taxa (at all taxonomic levels) and adult spiders, certain taxa are not or barely represented by this widely used technique. The subjective nature of the visual search method allows for the potential to target mature spiders. Limits of the sampling methods are emphasised in response to a growing dependence on survey data for the assessment of biodiversity.□*Araneae, methodology, biodiversity, heathland, invertebrates, community.*

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Surveys of spider communities in Australia have primarily been motivated by specific taxonomic interests in this relatively unknown faunal group. Whilst this has lead to invaluable improvements in taxonomy, such collections are increasingly being utilised to extract data for the making of critical conservation management decisions. It is therefore necessary that further consideration be given to the factors that can affect the interpretation of survey results.

The primary factor that limits the comparability of data from different locations or times is the method used to sample spiders. Different methods can preferentially sample certain microhabitats and/or particular taxa (Merrett and Snazell, 1983). For example, the commonly used pitfall trap selects ground active species (Duffey, 1974; Merrett and Snazell, 1983; Lowrie, 1985) and the use of this method alone can produce species lists that under-represent more sedentary or foliage inhabiting members of the community.

The effectiveness of different sampling techniques can be influenced by behavioural differences between not only taxa, but also age or sex classes of a given species. For example, males of many species are more readily captured by pitfall traps than females due to their active search for a mate (Merrett, 1967, 1968), which may represent ground activity in an otherwise foliage dwelling taxa. Since mature specimens are usually required to identify species or genera, the ability to catch adults will effect the accuracy of a species list.

By adopting a suite of collecting techniques to target spiders both on the ground and in vegetation, the chances of sampling all taxa present are increased and thus data more useful for community studies are collected (Uetz and Unzicker, 1976). Accordingly, a combination of pitfall trap, sweep net and visual search methods was selected for a 16 month survey of spiders in the north-east coastal corner of Tasmania. The area is largely developed as sheep and cattle grazing properties, although to the seaward side of the remaining coastal *Eucalyptus* and *Casuarina* forests is often a margin of heathland dominated by members of the Proteaceae, Casuarinaceae, Epacridaceae, Papilionoideae and Xanthorrhoeaceae. An increasing impact of recreational and residential development threatens the remaining heathland (Kirkpatrick, 1977). In this paper, the composition of spiders in the heathland community is inferred by the list of spider taxa collected over the survey period. The relative efficiency of the three sampling methods in capturing dominant taxa is then compared to illustrate how the choice of method can influence the final interpretation of community composition or species richness.

MATERIALS AND METHODS

Spiders were collected using pitfall traps, sweep net and by visual searching, each of which was standardised for effort and replicated. At monthly intervals from October 1986 to January 1988, sampling was carried out during a one week field trip. Two replicate 90m^2 sites were selected at each of two study areas, Waterhouse Point and Eddystone Point. Within each site there were nine 18m^2 plots placed 18m apart in three rows of three. This allowed for three replicate plots per sampling method, allocated initially at random. For the relevant plot the following sampling routine was employed: a) Nine pitfall traps were set 4.5m apart in a 3 x 3 matrix using 9cm diameter traps; b) one sweep sample of 50 sweeps was taken using a 28cm diameter net in a 12 x 3 m area and c) visual searching for 30 minutes was made over a 3 x 3m area. Spiders were preserved in 70% alcohol, identified to species where possible, and lodged with the Queen Victoria Museum, Launceston, Tasmania.

The three sampling methods were considered to be complementary in their selection of taxa occupying different strata. Pitfall traps sample spiders mobile on the ground, in contrast to sweep netting which targets spiders in the foliage. Visual searching can reveal spiders in any microhabitat, but a bias was shown towards those secured within web retreats, as such groups may not be amenable to capture by the previous two methods.

RESULTS AND DISCUSSION

Composition

A total of 8,625 spiders were collected using all three methods over 16 months, and these spiders comprised 130 species of the Araneomorphae in 97 genera and 34 families (see Table 1). Names could not be allocated to 26% of genera and 92% of species, indicating further that many Australian groups need taxonomic revision (Davies, 1985; Raven, 1988). The most diverse families in terms of the number of species were the Salticidae (14 spp.) and Gnaphosidae (11), followed by the Theridiidae (9), Zodariidae (9), Thomisidae (8) and Araneidae (8). The four most abundant species were, in decreasing order Diaea sp. (5.8%), *Badumna vandiemani* (5.3%), *Odo* sp. (4.3%), *Hestimodema* sp. (4.1%).

The number of spiders falling into pitfall traps depends on their activity (Mitchell, 1963;

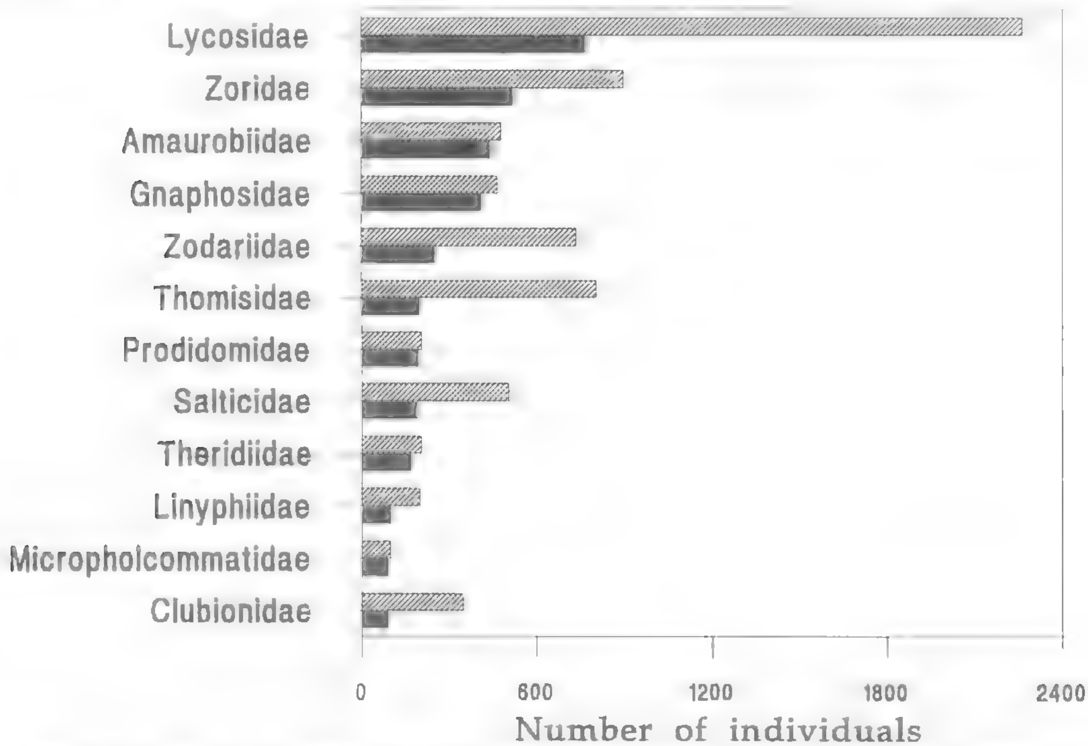


FIG. 1. Number of individuals (shaded bars) and adults (black bars) for the twelve dominant spider families.

Amaurobiidae

Genus A sp.1 *
Genus A sp.2 *
Genus B sp.
Genus C sp.
Genus D sp.

Amphinectidae

Amphinecta milvinus (Simon, 1903)
Mamoea sp.

Araneidae

Cyclosa sp.
Eriophora biapicata (Koch, 1871)
Gasteracantha minax Thorell, 1859
Genus E sp.
Genus F sp.
Genus G sp.
Genus H sp.
Genus I sp.

Clubionidae

Cheiracanthium sp.
Clubiona sp. 1
Clubiona sp. 2
Clubiona sp. 3
Genus J sp.

Corinnidae

Asadipus sp.
Castianeira sp.
Supunna sp.

Cyatholipidae

Hanea sp
Matilda sp.

Desidae

Austmusia sp.
Badumna vandiemani Gray, 1983 *
Forsterina sp.
Tuakana sp.

Dictynidae

Callevophthalmus sp.1
Callevophthalmus sp.2

Gnaphosidae

Anzacia sp.1 *
Anzacia sp.2 *
Eilica sp. *
Megamyrmaekion sp.
Micaria sp.
Trachycosmus sp. *
Zelotes sp.1
Zelotes sp.2
Zelotes sp.3
Genus K sp.
Genus L sp.

Hadrotarsidae

Hadrotarsus sp.1
Hadrotarsus sp.2
Genus M sp.

Hahniidae

Neoaviola sp.

Heteropodidae

Neosparassus sp.

Linyphiidae

Laetesia sp.1 *
Laetesia sp.2
Laetesia sp.3
Laetesia sp.4
Genus N sp.
Genus O sp.

Lycosidae

Artoria sp.1 *
Artoria sp.2 *
Artoria sp.3
Artoria sp.4 *
Artoria spp.
Lycosa funesta (Koch, 1849)
Lycosa speciosa (Koch, 1879)
Lycosa sp.

Micropholcommatidae

Micropholcomma sp.1
Micropholcomma sp.2
Textricella sp.1
Textricella sp.2 *
Textricella sp.3

Mimetidae

Australomimetus sp.

Miturgidae

Miturga sp.1
Miturga sp.2
Uliodon velox (Hickman, 1930)
Uliodon sp.

Mysmenidae

Genus P sp.

Nicodamidae

Nicodamus melanozanthus (Urquhart, 1893)

Oecobiidae

Oecobius annulipes Lucas, 1846

Oonopidae

Orchestina sp.
Genus Q sp.

Oxyopidae

Genus R sp.

Pararchaeidae

Pararchaea sp.

Pisauridae

Dolomedes sp.

Prodidomidae

Molycria sp. *

Salticidae

Lycidas sp.
Maratus sp. *
Opisthoncus sp.
Pseudosynagelides sp.
Servaea sp.
Genus S sp.1
Genus S sp.2
Genus S sp.3
Genus S sp.4
Genus T sp.
Genus U sp.
Genus V sp.
Genus W sp.
Genus X sp.

Stiphidiidae

Biaimi sp.
Corasoides australis Butler, 1929
Stiphidion facetum Simon, 1902

Tetragnathidae

Deliochus sp.
Phonognatha sp.
Tetragnatha sp.

Theridiidae

Achaearanea sp.
Dipoena sp.
Episinus sp.
Euryopis sp.
Phoroncidia trituberculata (Hickman, 1951)
Steatoda sp.1
Steatoda sp.2
Steatoda livens (Simon, 1895)
Theridion sp. *

Thomisidae

Cymbacha sp. *.
Diaea sp. *
Sidymella sp.1
Sidymella sp.2
Sidymella sp.3
Sidymella sp.4
Sidymella longipes (Koch, 1874)
Stephanopis sp.

Toxopidae

Laestrygones setosa Hickman, 1969

Trochanteriidae

Corimaethes sp.

Zodariidae

Asteron sp. *
Asteron "reticulatum"
"Australatica" sp.
Habronestes sp.1
Habronestes sp.2
Habronestes "bradleyi"
Neostorena sp.1
Neostorena sp.2
Nostera sp.

Zoridae

Argoctenus sp.
Hestimodema sp. *
Odo sp. *
Thasyraea sp.

TABLE 1. List of spiders collected from Tasmanian coastal heathlands. Asterisk indicates the 20 most abundant species.

Greenslade, 1964; Uetz and Unzicker, 1976; Merrett, 1983) and not necessarily on actual abundance in the community (Merrett, 1967; Merrett and Snazell, 1983). Individuals active on foliage presumably experience a higher probability of being knocked into a sweep net and for the visual search method the chance of noticing spiders would be increased by their activity (Curtis, 1980). Therefore it is stressed that references to abundance in this paper relate to numbers caught and not population size.

With respect to the number of individuals, the collections were dominated by the Lycosidae (26% of the total), Zoridae (10%), Thomisidae (9%) and Zodariidae (9%) (Fig. 1). The families Salticidae, Amaurobiidae, Desidae and Gnaphosidae then account for the next 22%. With the exception of the zodariids and zorids, these families are amongst the largest in Australia (Raven, 1988). The Araneidae, which are otherwise the most abundant Australian spider family (Raven, 1988), comprised only a minor component of this collection (1.4%).

The dominance hierarchy (Fig. 1) is determined by the number of adults in each family. However, as it is not standardised as to whether the whole data set (including immatures) or only the adult data are used to describe patterns of family dominance in a given community, a comparison is made to both (Fig. 1). The interpretation of relative abundance of families is affected by which category is used. Given that only adult data are useful for comparisons at the generic or species level, adult data seem the better choice for assessments of biodiversity.

Effects of Sampling Method on Composition

Pitfall traps collected the most individuals (6212), followed by visual searching (1900) and sweep netting (513). However, as the sampling effort of pitfall traps far exceeds that of sweep netting and visual searching, comparisons of taxa between methods are made relative to the total of each method.

Due to a reliance on acquiring mature spiders from surveys to confirm species and generic level identifications, Fig. 2 presents the differential distribution of age and sex classes for each sampling method. Pitfall traps clearly caught the greatest percentage of males (35%) and visual searching, the least (3%). Females are also collected more by pitfall traps, although the difference between methods is not as distinct. Accordingly, the percentage of immature spiders increases from pitfall traps (46%), through sweep

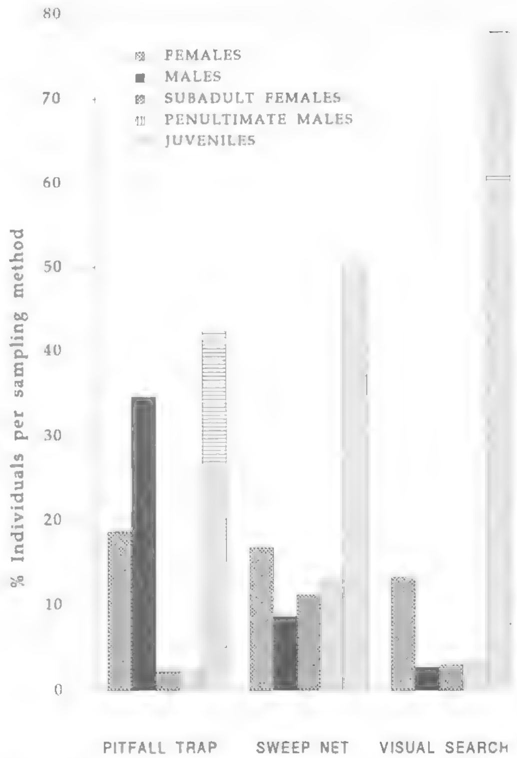


FIG. 2. Percentage of individuals in each sampling method for the different age and sex classes.

net (75%) to visual search (84%) methods. From these results pitfall traps seem to be the most efficient at selecting mature spiders from the coastal heathland community.

The total number of families, genera, and species can be compared to that collected by each sampling method (Table 2). At each taxonomic level, pitfall traps sample the most taxa (between 87-94% of the total), followed by visual searching (41-66%) and sweep netting (25-41%). It is relevant to point out that the results presented here were derived over a 16 month survey period. The likelihood of recording certain taxa using a given sampling method for typically shorter survey periods depends on the relative ease with which they are collected by that method (it also depends on the temporal abundance of taxa, to be discussed elsewhere). The percentage of adult

	Total	Pitfall	Sweep	Visual
Family	34	32	14	23
Genus	97	84	30	45
Species	130	113	33	53

TABLE 2. The number of taxa in total, and for each sampling method at three taxonomic levels.

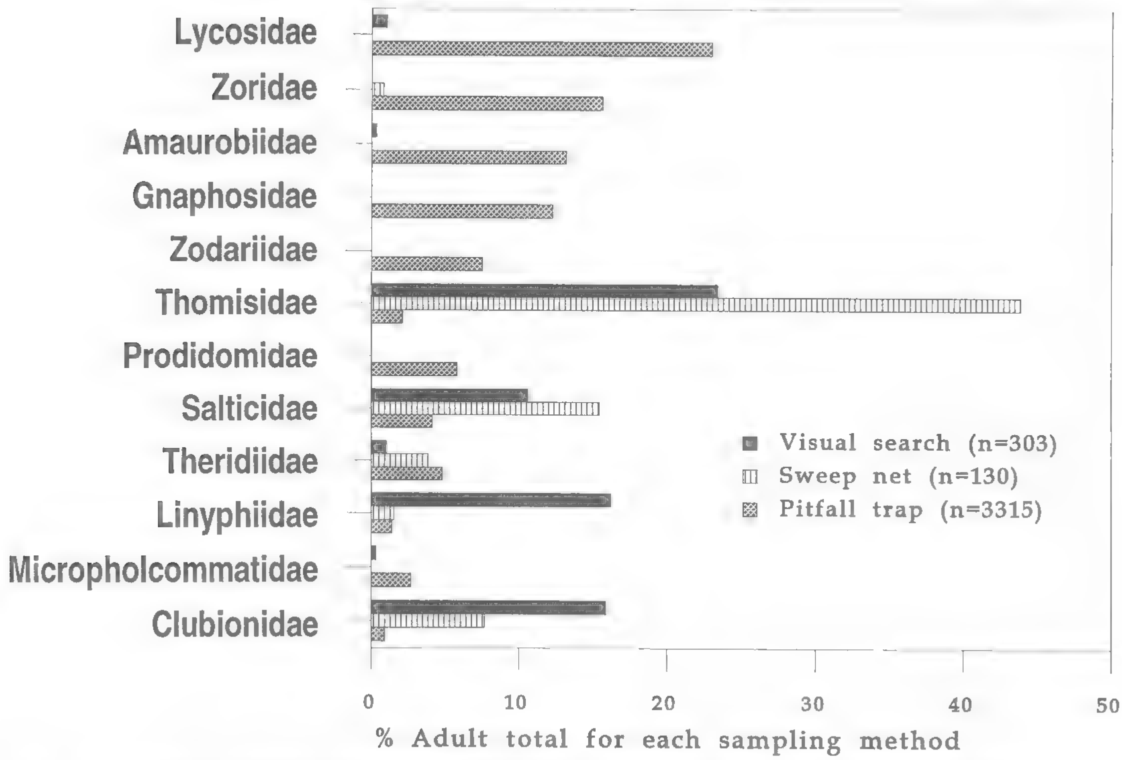


FIG. 3. Percentage of the adult spider total for each sampling method for the 12 dominant spider families.

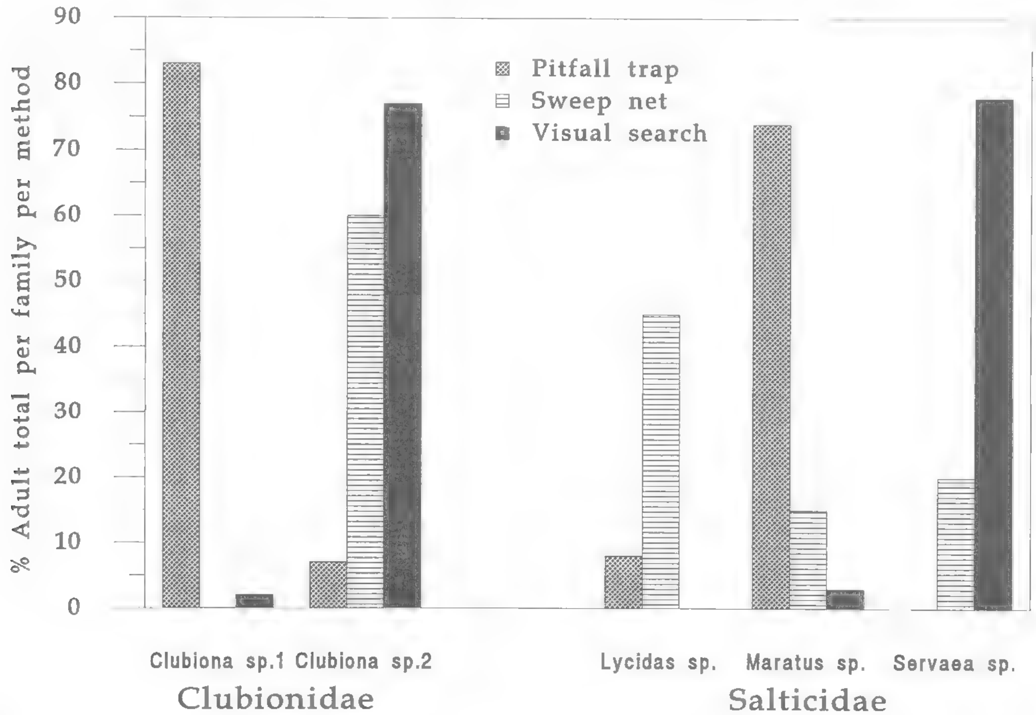


FIG. 4. Percentage of the adult spider total for each sampling method of Clubionidae and Salticidae.

spiders sampled by each method varies over the 12 dominant families (Fig. 3). Ground dwelling spiders such as gnaphosids or zodariids are exclusively caught by pitfall traps. Despite lycosids and zorids being sampled by all methods, there is a reduced chance that they would be represented by sweep net and visual searching over a shorter survey period. If only pitfall traps were used, the probability of representing the families Thomisidae or Salticidae is markedly reduced. Linyphiids, due to their habit of building low webs under the foliage are primarily amenable to capture by visual searching. Consequently, the results show that there is a greater probability of representing some families over others according to the method used.

The number of species in each family are distributed differently across sampling methods (Table 3). Whilst the ground dwelling spiders such as the gnaphosids and zorids have all their species falling into pitfall traps, other families have a pattern of species distribution across methods quite different to the distribution of individuals. For example, thomisids may be best sampled using sweep netting and visual searching (Fig. 3). Yet, these methods inadequately sample all the thomisid species collected (Table 3). The contrast is explained by the two most abundant thomisids, *Diaea* sp. and *Cymbacha* sp. being collected mostly by sweep net and visual search methods. Further examples include all clubionid species being sampled by all three methods (compared to a very unequal distribution of individuals) and a greater number of salticid species being sampled by pitfall traps (compared to this method catching the least number of salticids).

The number of individuals of the dominant species of clubionids and salticids illustrates that the differential selection of taxa by sampling method also operates at the species level (Fig. 4). Within the Clubionidae, despite the two species being collected by all three methods, *Clubiona* sp. 1 was almost exclusively sampled by pitfall traps, whereas *Clubiona* sp.2 was more often taken by a sweep net or visual searching. Similarly, the three dominant salticid species were preferentially sampled by the three different methods. Hence, if one sampling method was favoured over any other, especially for a shorter survey period, many species would be omitted from the final species list.

Family	Total	Pitfall trap	Sweep net	Visual
Amaurobiidae	5	5	0	1
Clubionidae	5	3	3	3
Gnaphosidae	11	11	0	0
Linyphiidae	6	6	1	6
Lycosidae	7	7	0	0
Micropholcommatidae	5	5	0	1
Prodidomidae	1	1	0	0
Salticidae	14	9	7	6
Theridiidae	9	6	2	3
Thomisidae	8	8	2	3
Zodariidae	9	9	0	0

TABLE 3. Number of species in total and for the three sampling methods for 12 dominant families.

IMPLICATIONS FOR THE FUTURE SURVEY OF SPIDER COMMUNITIES

There is currently no spider sampling technique that is unbiased. The success of any method is usually related to certain aspects of spider behaviour and therefore generally represents an incomplete range of taxa. Whilst this may be readily acknowledged by arachnologists, the limitations of a given method is not always clarified in the interpretation of community composition. This is particularly important when non-arachnologists utilise the information as representative of the whole community.

Despite the use of three sampling methods in this survey, the species list is not unbiased. In this study, sweep net and visual search methods were carried out during the day and may therefore not select nocturnally active taxa. Visual searching included looking at the ground, but effective sampling of leaf litter was not undertaken, and this micro-habitat can harbour distinctive families (Raven, 1988). The visual search method is also subjective in terms of where the search focus is directed. Attention was paid in this survey to sample spiders in positions (particularly in nests) that were not as vulnerable to the other two collecting methods. Where the objective of the survey is to estimate taxonomic composition of the spider fauna, the efficiency of both the visual search and sweep net methods could be improved by avoiding the collection of distinctly immature spiders.

Also, the equipment design can effect the number of individuals and taxa caught (eg., for pitfall traps see Luff, 1975 and Curtis, 1980). Temporal factors can further influence which taxa are susceptible to capture by a given method and as discussed by Abraham (1983), this can be related to seasonal migration of spiders between vegetative strata. To enhance the comparability of survey data, there is therefore a need to standardise methodology, equipment design, sampling effort and timing. Yen and Butcher (1992) also make this plea in respect of terrestrial invertebrate surveys for the ultimate goal of conservation. Methodological limitations need to be taken into account during the final interpretation of taxonomic lists for a more useful assessment of the fauna. These aspects are stressed in the light of a rapidly growing reliance on such data sets for conservation and management in Australia, and the need to critically assess invertebrate survey methods for estimating the loss of biodiversity worldwide (Coddington *et al.*, 1991).

ACKNOWLEDGEMENTS

A survey of spiders of the north-east coastal heathland was supported by the Plomley Foundation at the Queen Victoria Museum, Launceston, Tasmania, who also funded curation of half of the spider collection. Specimens were identified and the curation completed with resources kindly provided by the Arachnology section, Queensland Museum (Brisbane) and with taxonomic advice from Mark Harvey (Nicodamidae), Rudy Jocqué (Zodariidae), Rolly Mackay (Lycosidae), Robert Raven (all other taxa) and Marek Zabka (Salticidae). Completion of the project has been possible through an Australian Postgraduate Research Award at Griffith University, Brisbane.

LITERATURE CITED

ABRAHAM.J. 1983. Spatial and temporal patterns in a sagebrush steppe spider community (Arachnida, Araneae). Journal of Arachnology 11: 31-50.

CODDINGTON, J.A., GRISWOLD, C.E., DAVILA, D.S., PENARANDA, E. & LARCHER, S.F. 1991. Designing and testing sampling protocols to estimate biodiversity in tropical ecosystems. Pp. 44-60. In Dudley, E.C. (ed.) 'The unity of evolutionary biology: proceedings of the fourth international congress of systematic and evolutionary biology'. (Dioscorides Press: Portland, Oregon).

CURTIS, D. 1980. Pitfalls in spider community studies (Arachnida, Araneae). Journal of Arachnology 8: 271-280.

DAVIES, V. TODD 1985. Araneomorphae (in part). Pp. 49-125. In Walton, D.W. (ed.) 'Zoological Catalogue of Australia. 3. Arachnida'. (Australian Government Printing Service: Canberra).

DUFFEY, E. 1974. Comparative sampling methods for grassland spiders. Bulletin of the British Arachnological Society 3: 34-37.

GREENSLADE, P.J.M. 1964. Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). Journal of Animal Ecology 33: 301-310.

KIRKPATRICK, J.B. 1977. 'The Disappearing Heath'. (Tasmanian Conservation Trust Incorporated).

LOWRIE, D.C. 1985. Preliminary survey of wandering spiders of a mixed coniferous forest. Journal of Arachnology 13: 97- 110.

LUFF, M.L. 1975. Some features influencing the efficiency of pitfall traps. Oecologia 19: 345-357

MERRETT, P. 1967. The phenology of spiders on heathland in Dorset: I. Families Atypidae, Dysderidae, Gnaphosidae, Clubionidae, Thomisidae and Salticidae. Journal of Animal Ecology 36: 363-374.

1968. The phenology of spiders on heathland in Dorset: I. Families Lycosidae, Pisauridae, Agelenidae, Mimetidae, Theridiidae, Tetragnathidae, Argiopidae. Journal of Zoology (London) 156: 239-256

1983. Spiders collected by pitfall trapping and vacuum sampling in four stands of Dorset heathland representing different growth phases of heather. Bulletin of the British Arachnological Society 6: 14-22

MERRETT, P. & SNAZELL, R. 1983. A comparison of pitfall trapping and vacuum sampling for assessing spider faunas on heathland at Ashdown Forest, south-east England. Bulletin of the British Arachnological Society 6: 1-13.

MITCHELL, B. 1963. Ecology of two carabid beetles, *Bembidion lampros* (Herbst) and *Trechus quadristriatus* (Schrank) II.Studies on populations of adults in the field with special reference to the technique of pitfall trapping. Journal of Animal Ecology 32: 377-392.

RAVEN, R.J. 1988. The current status of Australian spider systematics. Pp. 37-48. In, Austin, A.D. and Heather, N.W. (eds) 'Australian arachnology'. The Australian Entomological Society Miscellaneous Publication No. 5.

UETZ, G. E. & UNZICKER, J.D. 1976. Pitfall trapping in ecological studies of wandering spiders. Journal of Arachnology 3: 101-111.

YEN, A.L. & BUTCHER, R.J. 1992. Practical conservation of non-marine invertebrates. Search 23: 103-105.

A NEW SPIDER GENUS (ARANEAE: AMAUROBIOIDEA) FROM RAINFORESTS OF QUEENSLAND, AUSTRALIA

VALERIE TODD DAVIES

Davies, V. Todd. 1993 11 11: A new spider genus (Araneae: Amaurobioidea) from rainforests of Queensland, Australia. *Memoirs of the Queensland Museum* **33**(2): 483-489. Brisbane. ISSN 0079-8835.

Malala gen.nov. is described and its relationships discussed; descriptions of two new species, *Malala lubinae* sp.nov. and *Malala gallonae* sp.nov. are given, including their spigot morphology. *Malala* is considered *incertae sedis* within the Amaurobioidea (*sensu* Lehtinen).□*Araneae, Amaurobioidea, new taxa, spigot morphology.*

Valerie Todd Davies, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; 28 October, 1992.

Many amaurobioid spiders in Australia no longer spin a web; they are usually vagrants either in litter or foliage and typically the forelegs have strong ventral spination. Two species of a tree-frequenting genus are described here.

ABBREVIATIONS. Measurements: cephalothorax length (CL) and width (CW), abdomen length (AL) and width (AW). Eyes: anterior median (AME), anterior lateral (ALE), posterior median (PME), posterior lateral (PLE), anterior row (AR), posterior row (PR). Spinnerets: anterior (ALS), median (PMS), posterior (PLS). Collectors: R.J. Raven (RJR), N. Hall (NH), V.E. Davies (VED). *On figures*: **ac** aciniform spigot; **als**, anterior spinneret; **at**, anal tubercle; **c**, conductor; **cp**, protuberance on ♂ chelicera; **cy**, cylindrical spigot; **e**, embolus; **fb**, frontal bristle on ♂ chelicera; **fs**, frontal spur on ♂ chelicera; **Map**, major ampullate spigot; **map**, minor ampullate spigot; **ms**, median sclerite; **n**, nubbin; **pi**, piriform spigot; **pls**, posterior spinneret; **tf**, tegular flange; **to**, tarsal organ. All specimens are lodged in the Queensland Museum.

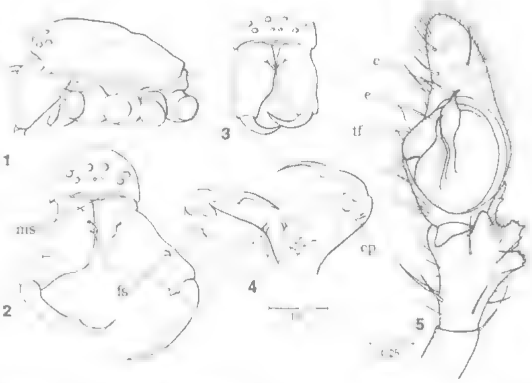
Malala gen. nov.

TYPE SPECIES

Malala lubinae, sp. nov.

DIAGNOSIS

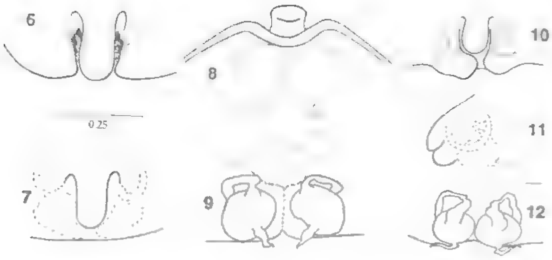
Three-clawed, pale clubionine-like with long spinose legs. Eyes in almost straight rows; AME much smaller than other eyes. Narrow median sclerite above chelicerae. Chelicera with one or two long frontal bristles proximally; pointed frontal spur distally in ♂. ♂ palp without median apophysis; elaborate tibial apophysis with dorso-retrolateral element.



FIGS 1-5. *Malala lubinae*. 1, 3, ♀. 1, cephalothorax (lateral), 3, eyes and chelicerae (frontal), 2, 4, 5, ♂. 2, eyes and chelicerae (frontal), 4, chelicerae (ventral), 5, palp (ventral).

DESCRIPTION

Straw-coloured ecribellate spiders with little or no pattern on abdomen. Carapace rounded dorsally, gradually declining in height behind fovea (Fig. 1). Anterior row of eyes straight, posterior row slightly recurved from above, procurved from front. Canoe-shaped tapetum in indirect eyes. Clypeus x 2 AME; narrow median sclerite above chelicerae (Figs 2,3). Sternum longer than wide, broadly truncate anteriorly, pointed posteriorly. Labium about as wide as long, a little more than half the length of the endite. Four-5 retromarginal cheliceral teeth; proximal ridge leading to 3-5 promarginal teeth, 2 small medial teeth between first and second marginals. Without long retrolateral filamentous setae at base of fang. Legs long (1243), trochanters unnotched. Coxae I longer than IV. Without plumose (ciliate) hairs on body or legs. Numerous strong ventral spines on tibiae and metatarsi I and



FIGS 6-12. *Malala* spp. epigyna. 6-9, *M. lubinae*, ventral, ventral (cleared), posterior, dorsal. 10-12, *M. gallonae*, ventral, lateral, dorsal.

II; metatarsi long, without preening combs; tarsi short. Trichobothria in a single row on metatarsi and tarsi. Bothria grooved, collariform (Fig. 14); tarsal organ with pear-shaped opening (Fig. 13). Superior claws 7-8 teeth, inferior claw 2 teeth; 2 pairs of fringed accessory claw setae present; ♀ palpal claw 2-3 teeth. Colulus. Spinnerets: ALS much larger than PLS; one major ampullate (gland) spigot and nubbin on ALS. Epigynum small with scape-like median structure; anterior gonopores. Male palp with spiniform embolus, membraneous conductor. Tibial apophysis with 3 processes; the anterior process branched or unbranched, the posterior ones 'toothed' and facing each other. Respiratory system with 4 tracheal tubes in abdomen; broad inner tubes branching and rebranching; slender outer tubes simple.

Etymology

The generic name is derived from 'malal' an aboriginal word for spider.

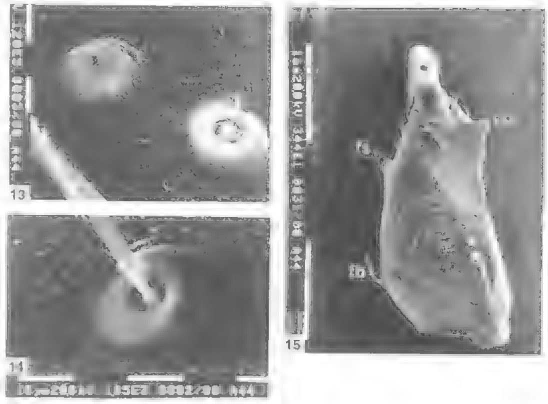
Malala lubinae sp. nov.
(Figs 1-9, 13-17, 20-27)

Material Examined

TYPES. Lamington National Park, southeastern Queensland. Holotype: ♀, Nagarigoon, 8.iv.1976, VED, NH, S20349. Paratypes: Nagarigoon, 1 ♂, 8.iv.1976, VED, NH, S20350; 4 ♀, 2 j, S20351; Binna Burra, 1 ♂, 1 ♀, 27-30.iii.1976, RJR, VED, S20352; 5 ♀, 11-12.ii.1981, Y. Lubin, RJR, VED, S20353; 1 ♀ with spiderlings in sealed leaf, S20354; Mt Hobwee, 1 ♀, 3-8.iv.1976, RJR, VED, S20355; O'-Reillys, 1 ♂, 15-16.xi.77, VED, E. Dahms, S20356.

Description

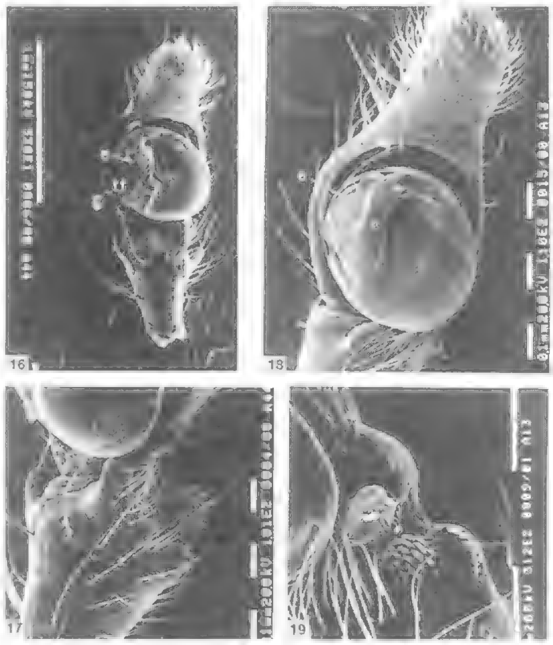
Female: CL 3.6, CW 2.6, AL 3.8, AW 2.5. Ratio of AME:ALE:PME:PLE is 4:10:9:10; width of AR is 21, PR is 25. Sternum longer than



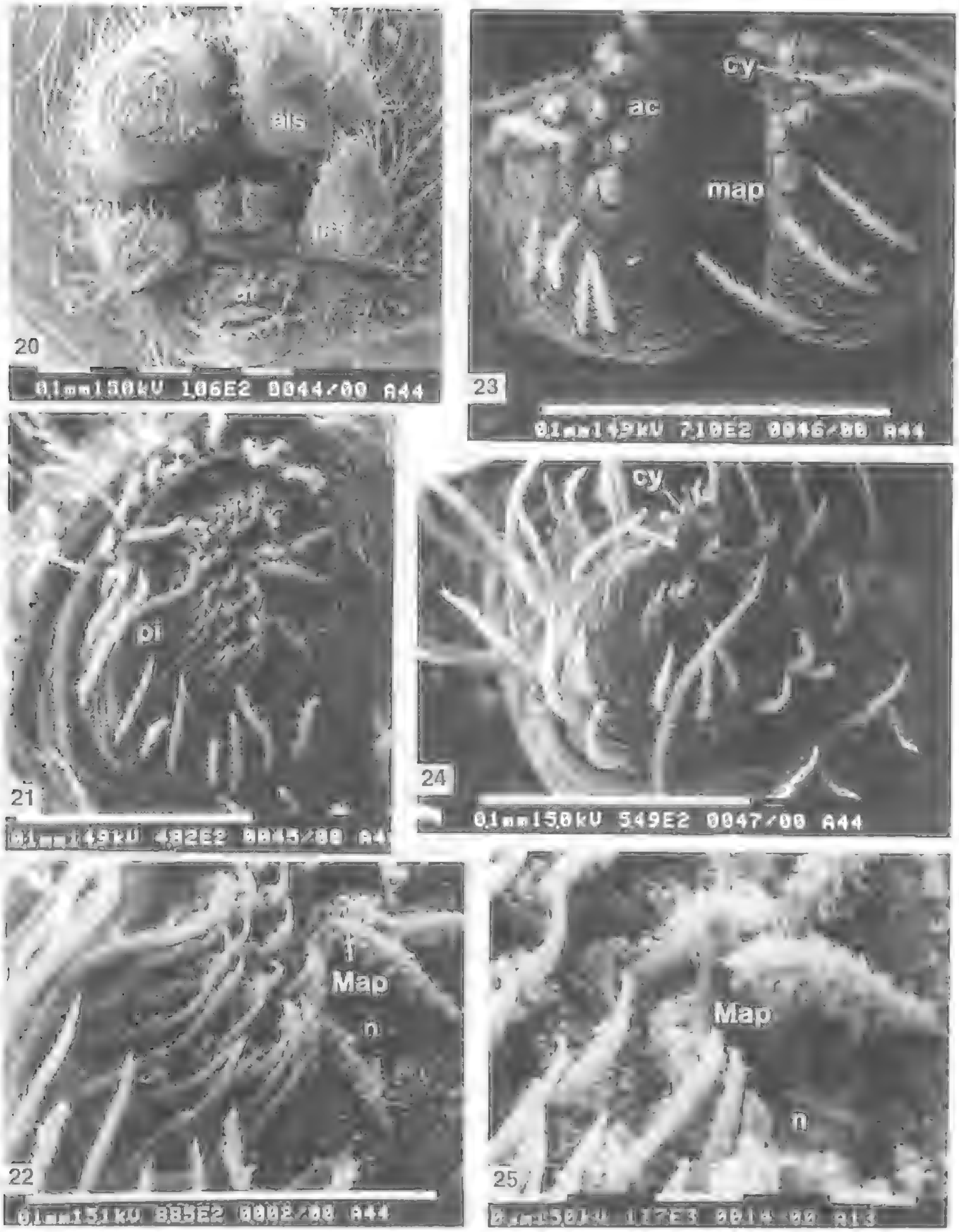
FIGS 13-15. *Malala lubinae*. 13, tarsal organ and bothrium, 14, trichobothrial base, 15, ♂, chelicera (prolateroventral).

wide 1:0.8; endite 1:0.6. Chelicera with 5 retromarginal teeth and 5 promarginal; second proximal tooth largest. Chelicera with 2 stout frontal bristles; low retrolateral swelling near base of fang; fang with slight ventral projection. Length of coxae I:IV is 1:0.6. Leg measurements are given in Table I.

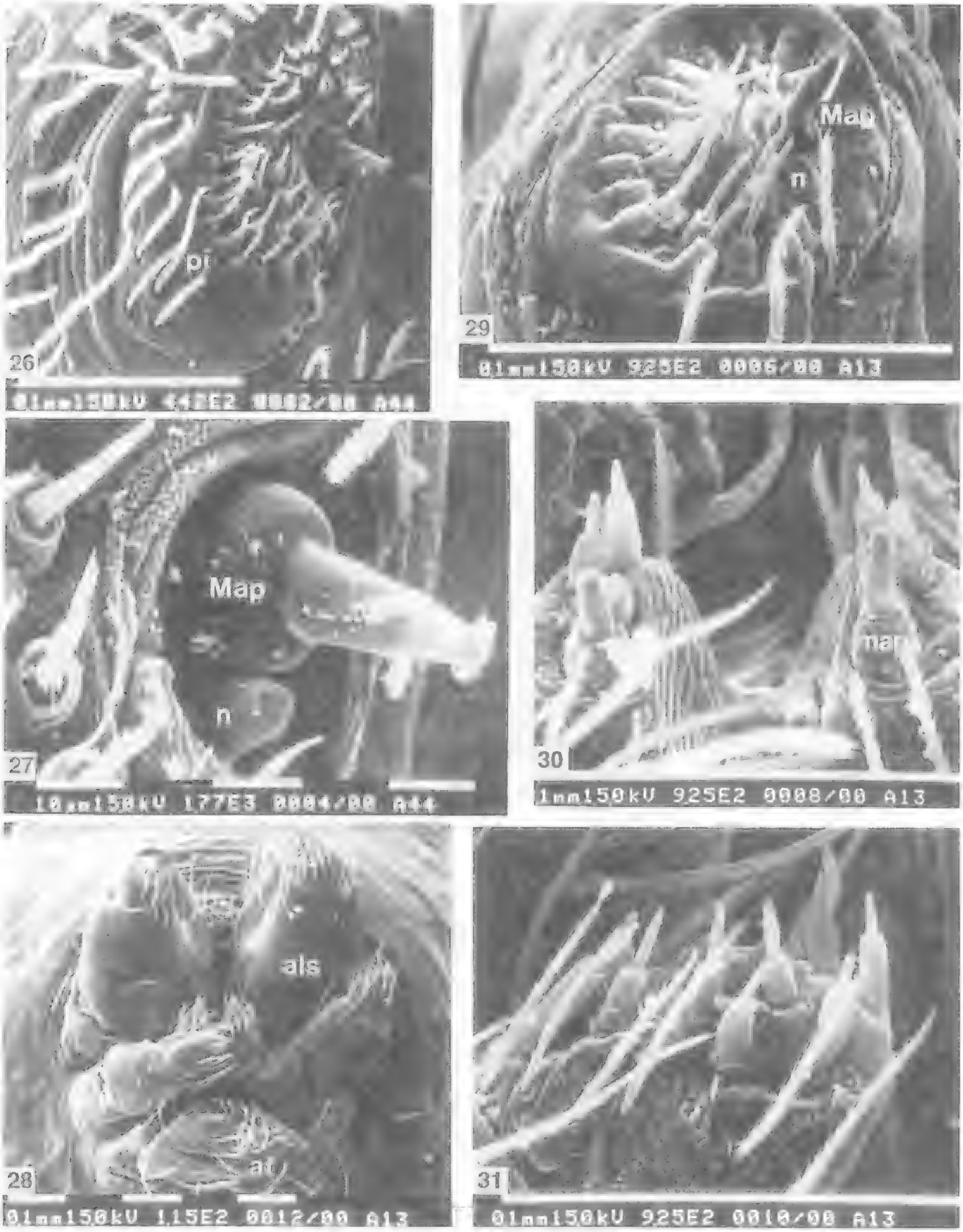
Notation of spines. Femora: palpi, D0-1-1; I, D1-1-1, PO-0-2, RO-0-2; II, D1-1-1, PO-1-2, R0-1-1; III, D0-1-1, PO-2-1, RO-1-1; IV, D1-1-1, PO-0-1, R0-0-1. Patellae: palpi, D0-0-1; Tibiae:



FIGS 16-19. ♂ palps. 16, 17, *M. lubinae*. 16, left palp, 17, tibial apophysis. 18, 19, *M. gallonae*. 18, left palp, 19, tibial apophysis.



FIGS 20-25. ♀ *M. lubinae* spinnerets. 20, spinneret group. 21, 22, 25, right ALS. 23, PMS. 24, right PLS



FIGS 26-31. *Malala* spp. spinnerets. 26, 27, penultimate ♀ *M. lubinae*. 26, right ALS, 27, major ampullate spigot and nubbin on ALS. 28-31 ♂ *M. gallonae*. 28, spinneret group, 29, right ALS, 30, PMS, 31, left PLS.

palpi, D1-0-1, P1-1-0; I, P2-1-1, V7-6-2, R1-1-1; II, P2-1-1, V5-5-1, R1-2-0. III, P2-1-0, V2-1-2, R2-1-0; IV p1-1-1, V1-1-2, R1-1-1. Metatarsi: I, P2-2-1, V4-3-1, R1-1-1; II P2-1-1, V4-2-3, R1-1-2; III, D2-2-2, P1-0-1, V2-2-1, R1-0-1; IV, D2-2-2, P1-0-1, V2-2-1, R0-1-1. Tarsi: palpi, P2-1-0, V0-0-2. Palpal tarsi swollen distally. Dorsal abdomen with slight foliate pattern. Epigynum very small (Figs 6-9).

Spinnerets: ALS much larger than PLS (Fig. 20). ALS with one large major ampullate spigot (Map), a nubbin (n) and about 30 piriform (pi) spigots arranged in 2 groups (Figs 21, 22, 25). The major ampullate spigot and nubbin are shown more clearly in a penultimate female (Figs 26, 27). PMS (Fig. 23) with large minor ampullate spigot (map), 3 aciniform gland spigots (ac) and one cylindrical gland spigot (cy). PLS (Fig. 24) with one large cylindrical spigot and 10 aciniform spigots.

Other females varied in size: CL 2.9-3.9, CW 2.3-2.9, AL 3.5-4.4, AW 2.3-2.8.

Male: CL 3.1, CW 2.3, AL 3.3, AW 2.0. Ratio of AME:ALE:PME:PLE is 5:9:8:9. Chelicerae divergent; 2 stout setae (fb) crossing over frontally with lesser one above; pointed spur (fs) distal to these. Four teeth on retromargin of chelicera, 4 on promargin; conical protuberance (cp) near base of fang; fang long with marked ventral projection (Figs 2,4,15). Length of coxae I:IV is 1:0.7. Leg measurements are given in Table 1.

Notation of spines: Femora: palpi, D0-1-1; I, D1-1-1, P0-0-2, R0-1-1, II, D1-1-1, P0-2-1, R0-1-2; III, D0-1-1, P0-1-1, R0-1-1; IV, D1-1-1, P0-0-1, R0-0-1. Patellae: palpi, D0-0-1. Tibiae: I, P2-1-1, V7-4-1, R1-1-1; II, P2-1-1, V6-4-1, R1-1-1; III, P2-1-0, V2-1-2, R1-1-1; IV, P2-0-1, V1-1-2, R1-1-1. Metatarsi: I, P2-1-1, V4-2-2, R1-1-1; II, P2-1-1, V3-3-2, R1-1-1; III, D0-1-1, P2-0-1, V3-2-2, R1-1-1; IV, D0-1-1, P1-1-1, V2-2-2, R1-1-1.

♂ palp (Figs 5,15): tegulum extended to form anterior prolateral flange; embolus, arising ventrally on tegulum, tapers to a point; conductor membraneous with pointed sclerotized tip; cymbial tip shorter than length of tegulum. Tibia with 3 retrolateral processes, the anterior one branched.

Variation in size: CL 3.1-3.3, CW 2.4-2.5, AL 3.6-3.8, AW 2.1-2.2.

Biology

The spiders were collected from branches or foliage of trees in the rainforest. The egg sac was placed with the spider in a sealed portion of the prickly leaf blade of *Calamus muelleri*, the lawyer vine.

Malala gallonae sp. nov.
(Figs 10-12, 18, 19, 28-31)

Material Examined

TYPES. Holotype: ♀, Bellenden Ker Range, 1054 m, 17.x-24.xi.1981, Earthwatch/ Queensland Museum Expedition, S20357. Paratypes. Same data as holotype; 1 ♂, S20358, 1 ♀, S20359; 1 ♀, S20360. 1 ♂, same locality, 25-31.x.1981, S20361. 1 ♂, Malaan State Forest, 20-4.iv.1978, RJR, VED, S20362. Upper Boulder Creek, 11km NW Tully, 850-1000m, 1 ♀, 17-18.xi.1984, J. Gallon, VED, S20363; 1 ♀, S20364; 1 ♂, 6.xii.89, G.B. Monteith, S20365. All in northeastern Queensland.

Female: CL 2.7, CW 2.0, AL 3.2, AW 1.9. Ratio of AME:ALE:PME:PLE is 4:8:9:8. Chelicerae with single stout elongate frontal bristles crossing each other. Four retromarginal, 3-4 promarginal teeth on chelicerae. Fang with slight ventral projection. Length of coxae I:IV is 1:0.8. Leg measurements are given in Table 1.

Notation of spines: Femora: palpi, D0-0-1; I, D1-1-1, P0-2-1, R2-1-2; II, D1-1-1, P0-2-1, R1-2-1; III, D0-1-1, P0-2-1, R0-2-1; IV, D1-1-1, P0-0-1, R0-0-1. Patellae: palpi, D0-0-1. Tibiae: palpi, D1-0-1, P2-1-0; I, P2-1-1, V6-5-1, R2-1-1; II, P2-1-1, V5-5-1, R2-1-1; III, P2-1-0, V0-2-0, R1-2-0; IV P1-1-0, V0-1-0, R1-1-0. Metatarsi: I, P2-1-1, V4-2-3, R1-1-2; II, P2-1-1, V4-2-2, R2-0-1; III, D2-2-2, P1-0-1, V2-2-1, R1-0-1; IV D2-2-2, P1-1-1, V2-2-1, R0-0-1. Epigynum (Figs 10-12).

Variation in size: CL 2.6-2.8, CW 2.0-2.1, AL 3.0-3.4, AW 1.8-2.5.

Male: CL 2.4, CW 1.8, AL 2.9, AW 1.4. Ratio of AME:ALE:PME:PLE is 4:8:9:8. Chelicerae slightly divergent; single enlarged setae crossing over frontally, pointed spur distally; without protuberance near base of fang. Three retromarginal, 4 promarginal teeth. Leg measurements are given in Table 1. Notation of spines is similar to ♂ *M. lubinae*.

♂ palp (Figs 18,19): tegulum without prolateral flange, embolus arising prolaterally. Cymbium tip a little shorter than length of tegulum. Tibia with 3 retrolateral processes, the anterior one with 2 branches.

Spinnerets: ALS (Fig. 29) have a large major ampullate spigot, a nubbin and about 20 piriform spigots. PMS (Fig. 30) have a large minor ampul-

TABLE 1. Leg measurements (mm) of *Malala* spp. *Bowed.

Leg	Fe	Pa	Ti	Me	Ta	Total
M. lubinae						
♀ palp	1.5	0.5	0.9	-	1.3	4.2
I	3.5	1.2	3.9	3.1	0.9	12.6
II	2.7	1.2	3.0	2.6	0.8	10.3
III	2.0	1.0	1.6	2.0	0.7	7.3
IV	2.6	1.0	2.3	2.9	0.9	9.7
♂ palp	1.5*	0.5	0.7	-	1.2	3.9
I	3.2	1.2	3.7	3.1	1.0	12.2
II	2.5	1.0	2.8	2.5	0.9	9.7
III	1.9	0.8	1.2	1.8	0.7	6.4
IV	2.3	0.9	2.1	2.5	0.8	8.6
M. gallonae						
♀ palp	1.1	0.5	0.7	-	1.0	3.3
I	3.1	1.0	3.6	3.1	0.9	11.7
II	2.6	1.0	2.9	2.6	0.8	9.9
III	1.8	0.8	1.5	1.9	0.6	6.6
IV	2.3	0.8	2.0	2.5	0.8	8.4
♂ palp	1.1	0.4	0.5	-	1.2	3.2
I	2.9	1.0	3.9	3.1	0.9	11.8
II	2.5	0.9	2.7	2.5	0.8	9.4
III	1.8	0.7	1.3	1.8	0.6	6.2
IV	2.0	0.7	1.8	2.3	0.7	7.5

late spigot and 3 aciniform spigots. PLS (Fig. 31) have 10 aciniform spigots.

Variation in size: CL 2.0-2.8, CW 2.0.

DISCUSSION

Malala, a 3-clawed ecribellate, has a single row of tarsal trichobothria of increasing length distally and a single row of metatarsal trichobothria. The ♂ palp has a complex tibial apophysis and no median apophysis. The ♂ chelicerae diverge distally and have a pointed frontal spur distally. The median tracheal trunks are branched. The anterior lateral spinnerets have one major ampullate gland spigot and a nubbin. From these and other characters *Malala* clearly belongs in the amaurobioid/dictynoid complex of families. In his world revision of cribellates, Lehtinen (1967) recognised one major superfamily Amaurobioidea with 6 families. Describing New Zealand spiders, Forster (1970) and Forster and Wilton (1973) defined two groups, Dictynoidea and Amaurobioidea, based on the branching or non-branching respectively of the median tracheal trunks. However, Gray (1983) found that *Forsterina*, an acknowledged close relative of *Badumna* (classified by Forster and Wilton in Desidae: Dictynoidea) has simple median trunks thus invalidating the branching as a synapomorphy for the dictynoids. Gray's evidence suggests that the branching may be important only at the generic level in the same way as the extension of the trunks into the cephalothorax is regarded. In their recent paper on the higher systematics of Araneae, Coddington and Levi (1991) state that 'these superfamilies are among the largest cladistic problems at the family level' and that the difficulty of definition 'partly stems from heterogeneity within families'. I would add that the few Australian genera on which some of these families are based compared with the large number yet to be described, also contributes to this difficulty.

Most Australian rainforest cribellates which range in size from small to very large have a nondescript but recognisable abdominal pattern (see Lehtinen, 1967: 435), a divided cribellar field, a single row of tarsal trichobothria increasing in length distally and a row of metatarsal trichobothria. The ♂ palp has a complex tibial apophysis and a median apophysis is usually present. I am persuaded to return to Lehtinen's classification and regard these Australian spiders as belonging in the Amaurobioidea.

Only one dictynid, *Callevophthalmus* is described from Australia. It is found in grassland and open forest and not, so far as I know, in rainforest. It is a small spider with a distinct abdominal pattern and an entire cribellar field. It has no tarsal trichobothria and a single metatarsal trichobothrium. The ♂ palp has a small tibial apophysis, a large T-shaped conductor extending beyond the edge of the cymbium retrolaterally and has no median apophysis. The ♂ chelicerae are indented prolaterally and have a proximal frontal process; these modifications do not appear to be homologous with those of *Malala*. *Callevophthalmus* is similar to *Arangina* from New Zealand and to *Dictyna*.

This is the first description of spigot morphology in an ecribellate amaurobioid. In general, cursorial spiders use silk only as a drag-line, and for the construction of the cocoon in the ♀. Thus, it is expected they will have fewer kinds of spigots than the web-spinning (cribellate) amaurobioids. *Malala* has 3 aciniform spigots on the PMS and 10 on the PLS. The typical small aciniform spigots which provide silk for swathing prey (Kovoor, 1987) are not present in *Malala*. The lack of these in contrast to their abundance in cribellate amaurobioids and dictynoids (Coddington, 1990b) is probably associated with

Malala's nomadic existence. The presence of one major ampullate gland spigot (Map) and a nubbin on the ALS is found in dictynoids (notably in *Dictyna*) and in the Orbiculariae (Coddington, 1990a) as well as in some other taxa (Platnick *et al.*, 1991). The nubbin (presumably a remnant of a second major ampullate spigot) may be homoplasious in *Malala*.

The fringed accessory claw setae present in *Malala* are probably an adaptation to tree- or foliage-dwelling and are similar to those found in some New Zealand spiders (Forster, 1970; figs 28-31) from a similar habitat. They are unlike the serrate setae which are involved in handling silk in araneoids. The presence of a narrow median sclerite above the chelicerae in *Malala* may be apomorphic. Marples (1962) mentions that a triangular sclerite is present in *Matachia* but not in *Paramatachia*.

At present I am unable to place *Malala* in a family and consider it *incertae sedis* within the Amaurobioidea (*sensu* Lehtinen).

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LITERATURE CITED

CODDINGTON, J.A. 1990a. Ontogeny and homology in the male palpus of orb-weaving spiders and their relatives, with comments on phylogeny (Araneoclada: Araneoidea, Deinopoidea). Smithsonian Contributions to Zoology 496: 1-52.

1990b. Cladistics and spider classification: araneomorph phylogeny and the monophyly of orbweavers (Araneae: Araneomorphae: Orbiculariae). Acta Zoologica Fennica 190: 75-87.

CODDINGTON, J.A. & LEVI, H.W. 1991. Systematics and evolution of spiders (Araneae). Annual Review of Ecology and Systematics 22: 565-592.

FORSTER, R.R. 1970. The spiders of New Zealand. Part III. Otago Museum Bulletin 3: 1-184.

FORSTER, R.R. & WILTON, C.L. 1973. The spiders of New Zealand. Part IV. Otago Museum Bulletin 4: 1-309.

GRAY, M.R. 1983. The taxonomy of the semi-communal spiders commonly referred to the species, *Ixeuticus candidus* (L. Koch) with notes on the genera *Phryganoporus*, *Ixeuticus* and *Badumna* (Araneae, Amaurobioidea). Proceedings of the Linnean Society of New South Wales 106: 247-261.

KOVOOR, J. 1987. Comparative structure and histochemistry of silk-producing organs in arachnids. Pp 160-186. In, Nentwig, W. ed. 'Ecophysiology of Arachnids'. (Springer-Verlag:Berlin).

LEHTINEN, P.T. 1967. Classification of the cribellate spiders and some allied families, with notes on the evolution of the suborder Araneomorpha. Annales Zoologici Fennici 4: 199-468.

MARPLES, B.J. 1962. The Matachiinae, a group of cribellate spiders. Journal of the Linnean Society of London 44: 701-720.

PLATNICK, N.I., CODDINGTON, J.A., FORSTER, R.R. & GRISWOLD, C.E. 1991. Spinneret morphology and the phylogeny of haplogyne spiders (Araneae, Araneomorphae). American Museum Novitates 3016: 1-73.

AN INVENTORY OF THE SPIDERS IN TWO PRIMARY TROPICAL FORESTS IN SABAH, NORTH BORNEO

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Deeleman-Reinhold, C.L. 1993 11 11: An inventory of the spiders in two primary tropical forests in Sabah, North Borneo. *Memoirs of the Queensland Museum* 33(2): 491-495. Brisbane. ISSN 0079-8835.

Collecting trips were made to a primary rainforest area at 1500-1900m altitude (Mt Kinabalu National Park) and a primary lowland rainforest (Danum Valley Field Centre) in Sabah, North Borneo. For comparison, a strongly degraded secondary forest in the town Kota Kinabalu was also sampled. All the material, with the exception of the mygalomorphs and salticids, has been identified and compared with collections from Sarawak, Kalimantan and Sumatra. 254 species were distinguished in approximately 120 genera, 35 could be identified as known species, seven of which were clearly synanthropic, the rest are undescribed. 207 species were found in one locality only: 85% of the species from Kinabalu, 70% of the species of Danum and 50% of the species from the town park. Widespread species were found mainly in the Araneidae, Pholcidae, Oonopidae, Clubionidae and Salticidae. A list of the genera and species is given. □*Biodiversity, rainforest, Asia, Araneae.*

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Tropical rainforests, covering only 6% of the Earth's surface, are believed to harbour more than half of all terrestrial animal species, of which less than 10% are described at present (Stork and Gaston, 1990). Inventorying the spider fauna of rainforests in south-east Asia has given spider taxonomy a new turn, especially so after the introduction of a new sampling method that targets canopy arthropods.

Most rainforests in Asia have now been destroyed or degraded, but the number of undescribed species is still overwhelming. The rapid destruction of our rainforests is an incentive to securing as much data as possible as ... 'an extensive program of inventorying aimed at estimating diversity of species ... is essential for a fuller understanding of the role of biodiversity in ecosystem function' (Coddington *et al.*, 1992).

Records of spiders from Borneo are extremely poor. With more than 30,000 species of spiders described so far, only about 160 named spider species have been described or recorded for the whole of Borneo; 65 of these are salticids. Only 96 spider species were reported from Borneo before World War I. Wanless and Hillyard (1984) present a list of species collected during the arachnological survey of Gunung Mulu National Park, Sarawak; 360 species were collected in all families, 38 of which were identified with known species, another 14 with reserve; 20 identified species are salticids. From Sabah, a mere 20 spider species are known, all published since 1979 (Deeleman-Reinhold, 1980, 1987; Lehtinen, 1979, 1981, 1982; Levi, 1982, 1983; Okuma, 1988; Platnick and Murphy, 1984; Wanless, 1987).

In a privately undertaken program of inventorying spiders of primary and secondary forests in south-east Asia, during the last 14 years I have been engaged, with the help of other, partly autochthonous collectors, in surveying the spider fauna of south-east Asia, mainly Indonesia, Malaysia, Thailand, Sri Lanka and the Philippines. As part of this initiative, I made three collecting trips to Sabah in the north-eastern part of Borneo.

METHODS

In June 1979, July 1980 and April-May 1991, I collected spiders in the primary rainforest of Mount Kinabalu National Park at altitudes of 1500-1900m. In May 1991, 2 days were spent collecting at an altitude of 500m (Poring Hot Springs). In May 1991, spiders were collected in lowland primary forest around the Danum Valley Field Centre in eastern Sabah. For comparison, some time was also spent collecting in the town park in Kota Kinabalu.

The spiders were collected by hand picking, sweeping, litter sieving and pitfall trapping on the ground. All araneomorph spiders, with the exception of the Saltieidae have been identified (Tables 1-3). The collected spiders were compared with most specimens of the above mentioned south-east Asia collection. Identification was done as

Oonopidae
Dysderina sp. (1)
Gamasomorpha sp. (2), Sabah
sp. (2)
Ischnothyreus sp. (4)
Opopaea ? (1)
Orchestina sp. (1)
sp. (1), Sabah, only below 600m
Plectopilus sp. (1)
Xyphinus lemniscatus Deeleman
sp. (1). *
Undescribed genus (1), also lower in secondary forest
Tetrablemmidae
Ablemma
Borneomma
Sabahya
circumspectans Deeleman, also lower in secondary forest
roberti Deeleman
kinabaluana Deeleman
bispinosa Deeleman
sp. (1)*
Ochyroceratidae
Psiloderces sp. (1)
Speocera sp. (1)
Undescribed genus (1)
Scytodidae
Scytodes pallida Doleschall, widespread*
Pholcidae
Uthina sp. (1), Sabah
sp. (1)*
Spermophora sp. (1), Sabah
miser Bristowe, widespread*
Belisana sp. (1)
Undescribed genus (1)
Heteropodidae
Heteropoda sp. (1)
sp. (1)canopy walk*
Thelcticopis sp. (1)
Olios sp. (1)*
Undescribed genus (1), in grass
Undescribed genus (1), canopy walk*
Ctenidae
Ctenus sp. (1)
Clubionidae s.l.
Clubioninae
Cheiracanthium sp. (1)
Clubiona sp. (4)
sp. (1) canopy walk*
sp. (1)widespread
Phrurolithinae
Otacilia sp. (1), also at 500m
Sesieutes sp. (1), Sabah
sp. (1)
Teutamus sp. (1)
Orthobula sp. (1), Sabah
Corinninae
New genus (1)
Gnaphosidae
Jacaena sp. (1), on the lawn
Palpimanidae
Bougrius sp. (1)
Zodariidae
Asceua sp. (1)
sp. (1)*
Mallinella sp. (3)
Undescribed genus? (2)
Thomisidae
Borboropactus sp. (1)
Lycopus sp. (1), also at 500m
Misumenops sp. (1), canopy walk*
Pagida sp. (1)
Phrynarachne sp. (1)
Oxyopidae
Oxyopes sp. (1), canopy walk*
Pisauridae
Polybaea sp. (1)
Lycosidae
Pardosa sp. (1)
Undescribed genus (1)
Hippasinae (1)
Hahniidae
Alistra sp. (1)
Hahnia (2)
Hersiliidae
Hersilia sp. (1)
Theridiidae
Achaearanea mundula (L. Koch), widespread
tepidariorum (C.L. Koch), worldwide
sp. (1)
spp. (3)*
Anelosimus sp. (1), canopy walk*
Argyrodes xiphias Thorell, widespread
Rhomphaea sp. (1)
Chrysso sp. (1)
Coleosoma sp. (2), Sabah
Coscinida sp. (1)
sp. (1)*
Dipoena sp. (5)
sp. (1)*
Episinus sp. (2)
Janula sp. (1), Sabah
Meotipa sp. (1)*
Phoroncidia sp. (2), Sabah
sp. (1)*
Theridion sp. (4)
spp. (3)*, 1 on canopy walk
Undescribed genus (2)
sp. (1), also at 500m
Undescribed genus (1)
Mimetidae
Mimetus sp. (3)
Theridiosomatidae
Plato sp. (1)
Theridiosoma sp. (1)
Mysmenidae
Undescribed genus (1)
Tetragnathidae
Leucauge celebesiana Walckenaer, widespread
spp. (2), Sabah
Glenognatha sp. (1)
Mesida sp. (4)
Undescribed genus I (2)
Undescribed genus II (2), also at 500m
Undescribed genus III, (1), also at 500m
Araneidae
Araneus sp. (1)
Argiope reinwardtii Doleschall, widespread
aemula (Walckenaer), widespread
Cyclosa bifida Doleschall, widespread
Cyrtophora sp. (1)
? *Eriophora* sp. (1)
Gasteracantha sp. (1)*
Milonia brevipes Thorell, widespread
Neoscona nautica L. Koch, world tropics
Undescribed genus (1)
Linyphiidae
Neriene beccarii Thorell, widespread
Kuala sp. (1)
Parameioneta sp. (1)
Nasoona sp. (3)
sp. (1)*
Undescribed genus II (1)
Undescribed genus III (1)
Undescribed genus IV (1)
Undescribed genus V (2)
Uloboridae
Philoponella sp. (1)
Uloborus lugubris Thorell, widespread*
Psechridae
Psechrus kinabalu Levi

Table 1. Spiders from Mount Kinabalu, 1500-1900m (Headquarters and Power Station) and 500m (Poring Hot Springs), primary rainforest, 18 collecting days in April-May, June and July. Family order is 'phylogenetic'. List gives no. of undescribed species in parentheses and notes on species.*= only at 500m.

much as possible with the aid of modern revisions but, where these do not exist, I had to rely on the keys in Simon (1892-1903) and the Latin descriptions (without illustrations) of Thorell (1877-1899) and Simon. Many nineteenth century types deposited in Genova, Paris and London were studied. Only species of which adults were collected are considered here.

RESULTS

From the three main prospected localities in Sabah, a total of 254 species from most spiders families (for practical reasons the mygalomorphs and the salticids were excluded) could be distinguished. Of these, 35 species could be identified as described species, seven of which are clearly synanthropic.

On Mt Kinabalu (1500-1900m), 135 species were collected in 18 days (41 species represented by one specimen only); 25 species were collected in two collecting days at Poring Hot Springs, lower down on the mountain slope at 500-600m; four of these were shared with the 1500-1900m site (see Table 1). For six of the 19 described and named species this is the type locality (Deeleman-Reinhold, 1980, 1987; Levi, 1982). 132 species (85%) were collected only in Kinabalu; 24 species were also found elsewhere.

Oonopidae
Dysderina sp. (1)
Gamasomorpha sp. (2), Sabah
Ischnothyreus peltifer (Simon), world tropics
sp. (5)
Opopaea ? sp. (1), Sabah
Orchestina sp. (1)
Plectopilus sp. (1), Sabah
Xyphinus sp. (1)
Tetrablemmidae
Ablemma sp. (1)
Ochyroceratidae
Merizocera sp. (1)
Speocera sp. (1)
Pholcidae
Calapnita phasmoides Deeleman, Borneo
Smeringopus pallidus (Blackwall), world tropics
Pholcus sp. (2) (1) in logged area
Spermophora sp. (1), Sabah
Belisana sp. (1)
Heteropodidae
Heteropoda sp. (1)
sp. (1), in logged area
Olios sp. (1)
Ctenidae
Ctenus sp. (1)
Gnaphosidae
Micythus sp. (1)widespread
Clubionidae s.l.
Clubioninae
Cheiracanthium sp. (1)
Clubiona sp. (3)
Castianeirinae
Aetius sp. (1)
Phrurolithinae
Sesieutes sp. (1), Sabah
Corinninae
Undescribed genus (1)
Palpimanidae
Boagrius sp. (1)
Zodariidae
Malinella sp. (2)
Thomisiidae
Borbonopactus sp. (1)
Loxobates sp. (1), in logged area
Pagida sp. (1), in logged area
Peritraeus sp. (1)
Synema sp. (1)
Talaus sp. (1), in logged area
Tmarus sp. (2), in logged area
Pisauridae
Polybaea sp. (1)
Oxyopidae
Oxyopes lineatipes C.L. Koch, widespread
sp. (1)
Tapponia superba Thorell, widespread
Lycosidae
Hippasa
Wadicosa birmanica (Thorell), widespread, in logged area;
Pardosa pusiola (Thorell), widespread
Hahniidae
Alistra sp. (1)
Hersiliidae
Hersilia sp. (1)
Theridiidae
Achaearanea sp. (1)
Argyrodes sp. (1)
Cephalobares sp. (1)
Chrysso sp. (1)
Coleosoma sp. (1), Sabah
Coscinida sp. (1)
Dipoena sp. (2)
Episinus sp. (1)
Janula sp. (1), Sabah
Theridion sp. (4)
Undescribed genus (1)
Mimetidae
Mimetus sp. (1)
Mysmenidae
Undescribed genus (1)
Anapidae
Pseudanapis paroculus Simon, widespread
Leucauge sp. (1), Sabah
sp. (1)
Glenognatha sp. (1)
Araneidae
Caerostris sp. (1)
Cyclosa bifida Doleschall, widespread
mulmeinensis (Thorell), widespread
Gasteracantha sp. (1)
Gea subarmata Thorell, widespread
Larinia phthisica L. Koch, widespread
Milonia trifasciata Thorell, widespread
Neoscona nautica L. Koch, world tropics
sp. (1)
Poltys sp. (1)
Undescribed genus I (1)
Undescribed genus II (1)
Linyphiidae
Undescribed genus (1)
Uloboridae
Philoponella sp. (2)

Table 2. Spiders from Danum Valley Field Centre, primary lowland forest, 8 collecting days in May; some species, mostly Thomisidae, in freshly logged area. Family order is 'phylogenetic'. List gives no. of undescribed species in parentheses and notes on species.

Compared to the lowland catches, a predominance of Linyphiidae was found.

In primary lowland forests around Danum Valley Field Centre in East Sabah, 90 species were collected in 9 days (Table 2); 14 species have been previously described. Of these, 67 species (70%) were only found at Danum, and 23 were also found elsewhere. In a freshly logged area, thomisids were particularly diversified.

In the secondary forest of Signal Hill in the township of Kota Kinabalu, 16 species were collected, 7 of which could be identified to species. Eight species were found also elsewhere, and 8 species (50%) were collected only on that site.

DISCUSSION

The main conclusion is that in tropical forests, spider species known from only one locality are enormously preponderant even though all distribution types from cosmotropical to very restricted ranges were encountered.

In a total of 254 species from the three localities (Tables 1-3), 207 were collected at one locality only, 92 of which were 'singletons'. Is this due to the lack of data only, or is a high percentage of endemic species real? This phenomenon occurs much more frequently in some families than in others. Quite often, in adjacent localities a sister species is found. In a long-term inventory of a 1-2 km^2 area on the northern side of the Sibolangit range, on Gunung Leuser in Sumatra (Deeleman-Reinhold, unpublished data), spiders were collected once a week for two years. A similar study was conducted on the other side of the ridge. Less than half of the species were found on both sides of the range! Therefore, endemism in spiders seems characteristic of primary rainforests, even though the real extent of distribution ranges will only be revealed after long and extensive sampling. For example, recent studies on south-east Asian Linyphiidae (Millidge and Russell-Smith, 1992) report 27 species, 26 of which new, described in 11 new and four known genera; all new species were recorded from only one locality (see also Scharff, 1992).

Also, widely distributed species were often found in human-made habitats. In such habitats most species described in the last century were found. In the course of identifying large south-

Oonopidae	*Psilochorus* sp. (1)widespread	sp. (1)
Ischnothyreus peltifer (Simon), world tropics	**Ctenidae**	**Tetragnathidae**
sp. (1)	*Ctenus* sp. (1)	*Leucauge* sp. (1)
Plectoptilus sp. (1)	**Clubionidae** s.l.	**Araneidae**
Ochyroceratidae	*Oedignatha scrobiculata* Simon, widespread	*Neoscona punctigera* Doleschall, widespread
Psiloderces sp. (1)	**Palpimanidae**	**Uloboridae**
Theotima minutissima (Petrunkevitch), world tropics	*Boagrius* sp. (1)	*Uloborus humeralis* Hasselt, widespread
Pholcidae	**Theridiidae**	
Uthina luzonica Simon, widespread	*Janula* sp. (1)	
	Theridion tenuissima Thorell, widespread	

Table 3. Spiders from town-park Signal Hill, Kota Kinabalu (2 collecting days). Family order is 'phylogenetic'. List gives no. of undescribed species in parentheses and notes on species.

east Asian collections it appeared that the majority of the species described prior to the early 20th century occur in habitats created by humans rather than in the rainforests. Thus, the spider fauna of the latter is still almost unknown.

A high degree of endemism seems to occur in certain families; other families which include a relatively high number of widely distributed species are Araneidae, Gnaphosidae, Oonopidae, Pholcidae and Salticidae. Occasionally, one or two species in a family are able to disperse considerably, whereas their relatives have remained limited to a restricted area. Among the best dispersers are some of the smallest known litter-dwelling spiders, with a body length of less than 1mm, which independently seem to have developed methods to overcome the vicissitudes of ballooning, e.g. the tiny armoured anapid *Pseudanapis paroculus* Simon is distributed over much of tropical south-east Asia both in primary and secondary forests. The small ochyroceratid *Theotima minutissima* (Petrunkevitch) and the oonopid spider *Ischnothyreus peltifer* (Simon) are distributed over the palaeo- and neotropics, where they live side by side with local congeners. Also larger spiders have been found to be widely distributed in humid forest, such as some *Cyclosa*, *Argiope*, *Acusilas*, *Neoscona* and *Gasteracantha* species, but also the delicate, almost transparent pholcid *Calapnita vermiformis* Simon.

The number of small-range species in both primary and secondary evergreen forests seems to be enormously higher than we are used to in temperate climates. Very few wide-spread species seem to occur naturally on Mount Kinabalu; more were found in lowland forest.

It is premature to estimate the total number of species present. Richest in species probably is the family Salticidae. Also numerous in species are the Theridiidae, Oonopidae, Araneidae, Clubionidae s.l. and Tetragnathidae in that order (see also Wanless and Hillyard, 1984 for Gunung Mulu).

Some genera have been particularly speciose in primary forest. In *Ischnothyreus* I found 11 species in Sabah (10 undescribed); in *Theridion* 11; in *Dipoena* 8; and in *Clubiona* 8 (all undescribed).

One final remark on diversity. Among the strongly represented families, diversity in the following families appears to be higher than average: Pholcidae, Clubionidae *s. lat.*, Tetragnathidae, Araneidae, Linyphiidae.

This study indicates that, when replacing primary forest by secondary plantations, the loss of species diversity of spiders is enormous.

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LITERATURE CITED

CODDINGTON, J., HAMMOND, P., OLIVIERI, S., ROBERTSON, J., SOKOLOV, V., STORK, N. & TAYLOR, E. 1991. Monitoring and inventorying biodiversity from genes to ecosystems. Pp. 83-117. In, Solbrig, O. (ed.), 'From genes to ecosystems: a research agenda for biodiversity.' (IUBS: Paris).

DEELEMAN-REINHOLD, C.L. 1980. Contribution to the knowledge of the southeast Asian spiders of the families Pacullidae and Tetrablemmidae. Zoologische Mededelingen 56: 65-82.

1987. Revision of the genus *Xyphinus* Simon (Araneae: Oonopidae). Acta Arachnologica 35: 41-56.

LEHTINEN, P.T. 1979. Spiders of the Oriental-Australian region I. Lycosidae: Venoniinae and Zoicinae. Annales Zoologici Fennici 16: 1-22.

1980. Spiders of the Oriental-Australian region III. Tetrablemmidae, with a world revision. Acta Zoologica Fennica 162: 1-151.

1982. Spiders of the Oriental-Australian region IV. Stenochilidae. Annales Zoologici Fennici 19: 115-128.

LEVI, H.W. 1982. The spider genera *Psechrus* and *Fecenia* (Araneae: Psechridae). Pacific Insects 24: 114-138.

1983. The orb-weaver genera *Argiope*, *Gea* and *Neogea* from the western Pacific region (Araneae: Araneidae, Argiopinae). Bulletin of the Museum of Comparative Zoology, Harvard 150: 247-338.

MILLIDGE, A.F. & RUSSELL-SMITH, A. 1992. Linyphiidae from rainforests of Southeast Asia. (Araneae). Journal of Natural History 26: 1367-1404.

OKUMA, C. 1988. Five new species of *Tetragnatha* from Asia (Araneae: Tetragnathidae. Esakia 26: 71-77.

PLATNICK, N.I. & MURPHY, J.A. 1984. A revision of the spider genera *Trachyzelotes* and *Urozelotes* (Araneae, Gnaphosidae). American Museum Novitates 2792: 1-30.

SCHARFF, N. 1992. The linyphiid fauna of eastern Africa (Araneae: Linyphiidae) - distribution patterns, diversity and endemism. Biological Journal of the Linnean Society 45: 117-154.

SIMON, E. 1892-1895. 'Histoire Naturelle des Araignées' vol. 1. 2nd edition. (Encyclopédie Roret: Paris).

1897-1903. 'Histoire Naturelle des Araignées' vol. 2. 2nd edition. (Encyclopédie Roret: Paris).

STORK, N. &GASTON, K. 1990. Counting species one by one. New Scientist ,11 August 1990: 43-47.

THORELL, T. 1877. Studi sui Ragni Malesi e Papuani I. Annali del Museo Civico di Storia Naturale Giacomo Doria, Genova 10: 341-634.

1878. Studi sui Ragni Malesi e Papuani II. Annali del Museo Civico di Storia Naturale Giacomo Doria, Genova 13: 1-317.

1881. Studi sui Ragni Malesi e Papuani III. Annali del Museo Civico di Storia Naturale Giacomo Doria, Genova 17: vii-xxvii, 1-720.

1890a. Studi sui Ragni Malesi e Papuani IV, 1. Annali del Museo Civico di Storia Naturale Giacomo Doria, Genova (2) 8: 1-419.

1890b. Diagnoses Aranearum aliquot novarum in Indo-Malesia inventarum. Annali del Museo Civico di Storia Naturale Giacomo Doria, Genova 30: 132-172.

1892. Studi sui Ragni Malesi e Papuani IV, 2. Annali del Museo Civico di Storia Naturale Giacomo Doria, Genova 31: 1-490.

WANLESS, F.R. 1987. Notes on spiders of the family Salticidae 1. The genera *Spartaeus*, *Mintonia* and *Taraxella*. Bulletin of the British Museum of Natural History (Zoology) 52: 107-137.

WANLESS, F.R. & HILLYARD, P.D. 1984. Arachnological notes from Gunung Mulu National Park with a list of the spiders recorded from Borneo and a preliminary list of the harvestmen of the Park. Sarawak Museum Journal 51 (ns) 30: 53-64.

A REVIEW OF FACTORS INFLUENCING THE DISTRIBUTION OF SPIDERS WITH SPECIAL REFERENCE TO BRITAIN

ERIC DUFFEY

Duffey, E. 1993 11 11: A review of factors influencing the distribution of spiders with special reference to Britain. *Memoirs of the Queensland Museum* 33(2): 497-502. Brisbane. ISSN 0079-8835.

Available data on factors influencing spider distribution are synthesized using mainly British and other European information. The importance of landscape history is stressed, in fragmenting ancient natural habitats and creating new ones. It is postulated that this has reduced the number of specialists and allowed a range expansion of pioneer and euryoecious species. A tentative classification of life strategies is proposed. Habitat diversity and microspatial distribution are discussed with examples. □*Spiders, habitat preferences, geographic distribution, life strategies.*

Eric Duffey, Cergne House, Wadenhoe, Peterborough, PE8 5ST, United Kingdom; 3 November, 1992.

Many attempts have been made to categorise the habitats of spiders according to their preferences for dampness, dryness, shade, light, warm or cool temperatures. In addition, increasing knowledge derived from extensive collections made during the last 50 years in Britain and the rest of Europe have made it possible to draw distribution maps (Locket *et al.*, 1974; Ransy and Baert, 1985, 1987a, 1987b; Janssen and Baert, 1987; Ransy *et al.*, 1990; Alderweireldt and Maelfait, 1990; Canard, 1990), even though their incompleteness is acknowledged. The distribution of some species shows a clear influence of latitude and longitude, with north-south or east-west trends, or an association with major habitat formations. This paper discusses some factors which influence spider distribution, such as landscape history and geographic range, habitat preferences, adaptation to man-made biotopes and small-scale environmental differences, with the object of categorising the occurrence of species according to life strategy.

Islands of modest size such as Britain are poorer in species than adjacent continental areas. For example, the spider fauna of Belgium, a near neighbour, which is only 1/8th the size of Britain and has 75km of coastline compared with Britain's 19 000 km, and a lower landscape diversity, has almost as many recorded species (600) (Keckenbosch *et al.*, 1977) as Britain's 622 (Roberts, 1985-87).

Habitat labels based only on local information may be unsatisfactory, since (in Britain and the rest of Europe) we know that (a) some widespread species are found in different habitats according to where they occur in their geographic range; (b) within a restricted area some species are found only, or mainly, in 2 very different habitats, for example sand-dunes and marshes; (c) some species are so widespread that they are difficult to characterise in terms of habitat preferences; (d) species confined to only one specialised habitat are generally few in number and often rare. Examples are presented in this paper.

Nomenclature follows Roberts (1985-87) for spiders and Anon. (1964-80) for plants.

LANDSCAPE HISTORY AND PATTERN OF SPIDER DISTRIBUTION

Britain was largely forested before human settlement but forests are now much modified scattered remnants. This extensive environmental change will have favoured some species and disadvantaged others. For example, when the surviving rare species associated with major formations in Britain are listed (Table 1) most are recorded for coastal systems which–apart from the more limited mountain tops–are the least modified components of the present-day landscape. Species which are regarded as 'characteristic' of major habitat formations (Ratcliffe, 1977) (Table 2) may also be identified. The high numbers recorded for grassland, dry heaths and coasts probably reflect a great expansion of range by open-ground species after forest clearance.

The extent of habitat modification and disturbance is difficult to quantify because the type and intensity of change varies from place to place. In the case of wetlands, however, there is a common factor in that alteration to the water table has a greater impact on the fauna than other uses made

TABLE 1. Numbers of British spider species in the IUCN categories Endangered, Vulnerable and Rare, assigned to major habitats (compiled by P. Merrett in Bratton, 1991).

Coast- dune, shingle, saltmarsh, cliff	24
Dry lowland heaths	14
Fens-mesotrophic to eutrophic	12
Deciduous woodlands in lowlands	10
Caledonian (ancient) pine forest, Scotland	5
Grasslands-acidipholous to calcicolus	7
Wet heath/bog—oligotrophic	7
Open moorland, uplands and mountains	4

of these areas by man. In 1969 11 fens in East Anglia were surveyed by a group of arachnologists hand-collecting for a total of 10 hours per site. Each hourly collection was kept separate. The similarity between the faunas of the 11 fens in terms of abundance of each species present was assessed using Mountford's Index of Similarity (Mountford, 1962). Three groupings were derived, of which 2 were more similar than either was to the third group. The 8 fens in groups 1 and 2 had survived with little change to their water regimes at that time, while the third group had suffered falling water tables and hence vegetation changes (Duffey, 1974). The mean numbers of species for groups 1 and 2 were 53.2 and 50.0, respectively, and 34.6 species for group 3. Most of the rarer and more specialised fen species (*Marpissa radiata* (Grube, 1859); *Hygrolycosa rubrofasciata* (Ohlert, 1865); *Neon valentulus* Falconer, 1912; *Carorita paludosus* Duffey, 1971; *Centromerus incultus* Falconer, 1915; *Maso gallicus* Simon, 1894) were recorded in groups 1 and 2.

HABITAT VERSATILITY IN SPIDERS

The ability of many spiders to live successfully in a range of different environments has been little studied. The best known examples are pioneer species that are good aeronauts and the first to colonise newly created habitats. Meijer (1977) discusses this for Dutch polders, and Duffey (1978) for croplands and grasslands. Not all aeronauts behave in this way. *Erigone arctica* (White, 1852) and *E. longipalpis* (Sundevall, 1830) are often abundant on coastal driftlines and saltmarshes but are rare inland. The former is found on mountainsides in Sweden (the late A. Holm, pers. comm.) and both have been recorded on inland saline areas as well as in sewage works.

TABLE 2. Numbers of British spider species assessed as characteristic of various major habitats (compiled by P. Merrett in Ratcliffe, 1977)

Grasslands	74
Dry lowland heaths	63
Coastal formations	53
Deciduous woodlands	34
Fens	31
Wet heath/bog	21
Open moorland	17
Caledonian pine forest	14

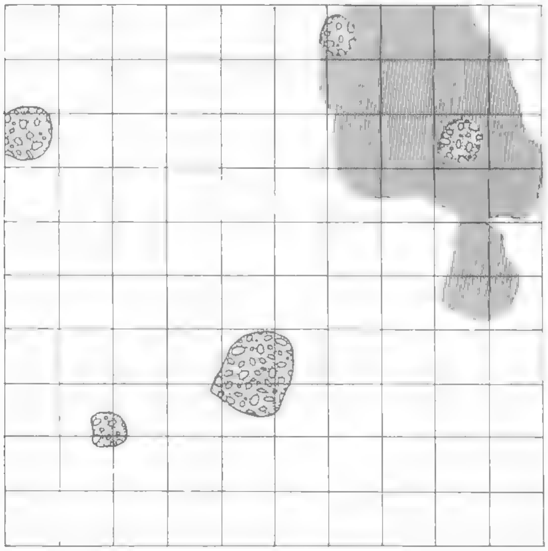
This provides evidence that they disperse over long distances but survive in only a few places.

Agricultural land has been colonised by species whose natural habitats are sand-dunes and stony open ground, for example *Troxochrus scabriculus* (Westring, 1851) and *Milleriana inerrans* (O.P.-Cambridge, 1884). *Porrhomma convexum* (Westring, 1861) is also frequent on cultivated land but elsewhere occurs in caves, mines, culverts (Locket and Millidge, 1953), and under stones by stream and lake shores (K. Thaler, pers. comm. and Duffey, unpublished).

The stone-filled filter beds of sewage works attract another cave species, *Lessertia dentichelis* (Simon, 1884), together with *Leptorhoptrum robustum* (Westring, 1851), whose natural habitat is freshwater marshes and wet meadows, and also *E. longipalpis* and *P. convexum*. The environment of filter-beds is completely artificial and uniform with stable temperature and high humidity, forming a 'super habitat' in which few species occur but in much higher numbers than found in nature.

The ability of some species to live successfully in two contrasting habitats was first noted by Bristowe (1939) and described as 'diplostenoecism' by Duffey (1974) and 'doppeltes ökologisches Vorkommen' by Schaefer and Tischler (1983). The best-known examples are those species found on coastal dunes and also in marshes–*Synageles venator* (Lucas, 1836), *Tibellus maritimus* (Menge, 1875), *Clubiona juvenis* Simon, 1878, *Hypomma bituberculatum* (Wider, 1834) and *Thanatus striatus* C.L. Koch, 1845. The last is also found in dry grasslands. *Sitticus rupicola* (C.L. Koch, 1837) is widespread on stony mountainsides in central Europe (Prószynski, 1978) but in England occurs only on coastal shingle banks.

Competitive relationships may also influence choice of habitat and hence distribution. *Zelotes electus* (C.L. Koch, 1834) is the characteristic species of this genus on coastal sand-dunes in



FIGS 1A-C. Distribution of spiders on 2.5x2.5m plot divided into 25x25cm quadrats on a Danish heathland.
1A. Vegetation map: Blank space, heather; lined shading, grass tussocks; cobbled, mosses, lichens and small stones.

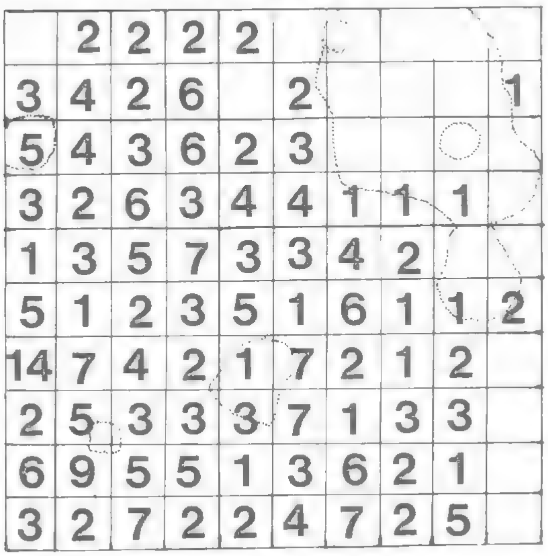


FIG. 1B. *Trichopterna cito*. A small web-spinning linyphiid almost confined to open ground with short, sparse vegetation; not a known active aeronaut nor a pioneer (Table 3) but a Narrow Specialist. Spread of heather eliminates it.

Britain whereas *Z. pusillus* (C.L. Koch, 1833) is associated with inland heaths, dry grasslands and open, stony ground. However, *Z. electus* was found (Anon., 1979) to extend only as far north as south-east Scotland and at higher latitudes was replaced on the coastal dunes by *Z. pusillus*.

All these species can adapt to different environmental conditions and emphasise the need to study habitat selection throughout the whole geographic range of a species before its distribution status can be understood.

EFFECTS OF HABITAT FRAGMENTATION

Several distribution maps in Locket *et al.* (1974) show widely scattered records for certain species which may indicate a decline from a former continuous distribution.

Lepthyphantes midas Simon, 1884 is an ancient forest specialist and is associated with loose bark and dead timber or birds' nests made of twigs. It is only known from 4 scattered sites in Britain where ancient forest survives. Similarly, wetlands have suffered serious losses, including the Fen Basin, East Anglia, which was progressively drained from Roman times and lost the remaining large areas of marsh in the mid-19th century. The local lycosid *Hygrolycosa rubrofasciata* (Ohlert, 1865) survives in the two remaining fenland areas and also in numerous small fen relicts around the

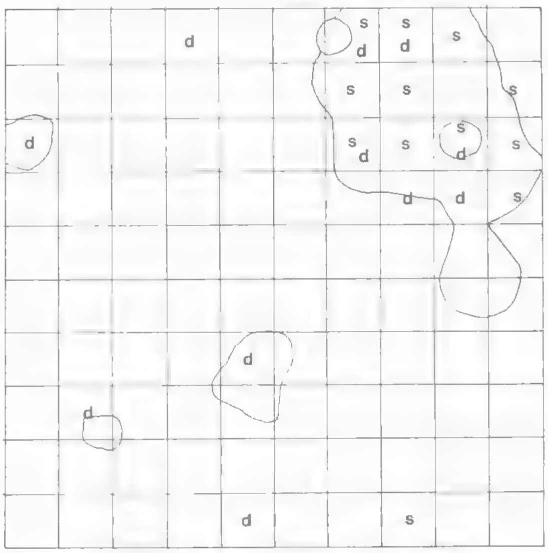


FIG. 1C. Other species preferred cover of heather plant or grass tussocks, e.g. *Scotina gracilipes* (Blackwall, 1859) (s) and *Dipoena prona* (Menge, 1868) (d). Each record refers to a catch of 1-5 individuals.

TABLE 3. Classification of life strategies and adaptability to environmental diversity based on British spiders.

PIONEER SPECIES	Active aeronauts which disperse freely, exploiting newly created open ground where competition is low. Widely distributed in temporary or changing habitats such as agricultural cropland, gardens, urban areas, leys and other types of disturbed ground or vegetation.
GENERALISTS	Common species with a capacity to adapt to a wide range of semi-natural habitats and permanent artefacts in the man-made environment. May be difficult to assign to a particular habitat.
BROAD SPECIALISTS	A. Widespread, euryoecious, or 'characteristic' species (Table 2) associated with major habitats such as deciduous woodland, marshes, heaths or ancient grassland, but may be found in many different variants of the chosen major formations.
	B. Diplostenoecious species, mostly widespread and associated with 2 different habitats but usually more common in one than the other. Occasionally much more abundant in man- made habitats than in the natural environment. This grouping grades into species successful in 3 or more different environments.
NARROW SPECIALISTS	Stenoecious species which seem confined to clearly defined habitat. Includes rare species in low numbers and others which may be locally abundant, although confined to a restricted area because the habitat is scarce.

margins of the Fen Basin. Are these relicts of a former more extensive distribution?

Lowland heathland has also suffered severe losses, having been reduced to many small fragments by agricultural reclamation with a consequent loss of biodiversity (Webb, 1990). *Eresus niger* (Petagna, 1787) was formerly more widespread in heaths in southern England but is now known from only one locality where the population is small.

In contrast, some species are able to live in a range of different habitats, and thus overcome the problem of fragmentation. If this characteristic is also combined with active aeronautic dispersal, the chances of finding isolated suitable environments will be further enhanced. For example, *Pardosa palustris* (L., 1758) is the most active aeronaut of the common lycosids found in Britain and northern Europe (Richter, 1970). Few have been recorded in a wide variety of habitats, including marshes, grasslands, heathlands, and agricultural crops, but occasionally is found to be dominant, as in moist hay meadows in river valleys and on some sand-dunes. In a survey of dune systems in Scotland (Anon., 1979) it was the most abundant lycosid, although it was not recorded on all the dune areas which were studied. It seems that the active aeronautic behaviour of *P. palustris* enables it to move about freely and its ability to exploit many different habitats gives it a high ranking as an opportunist. Kessler (1973) also showed that *P. palustris* is able to produce more eggs per unit of body size under field conditions than 7 other *Pardosa* species. This may be an advantage when colonising new areas.

Adaptability to environmental diversity varies from species to species, so that a gradient exists from those which are very widespread (usually many species) to those which appear to be confined to a specialised habitat (relatively few species). The different components of this gradient are outlined in Table 3, and modified from Duffey (1975a).

HABITAT DIVERSITY AND MICROSPATIAL DISTRIBUTION

The structure of the vegetation, the litter layer and physical features of the environment have a strong influence on spider distribution and species composition (Duffey, 1962, 1968, 1974; Edwards *et al.*, 1975; Uetz, 1991). There is evidence that all species, however widespread, are influenced in some way by habitat structure. This was shown by comparing the fauna in different quadrats of a simple vegetation type on a Danish heathland (Duffey, 1974). Fig. 1 shows the differences in species and numbers of spiders between 100 25x25cm quadrats in a block measuring 250x250cm. The vegetation consisted of a heather plant (*Calluna vulgaris* (L.) Hull, 1808) in one corner of the block, and a few scattered grass tussocks of *Deschampsia flexuosa* ((L.) Trin., 1836), while most of the area was covered with mosses, lichens and small stones. The species in Fig. 1 occurred in clearly defined microhabitats. *Trichopterna cito* (O.P.-Cambridge, 1872), which was widespread in the open ground of moss and lichen, avoided the heather, and was also absent from 4 quadrats on the right-hand side of the sampling area which had been trampled. Similar results are reported by Jocqué (1973), who studied the fauna of different types of woodland litter layers in Belgium. On a heathland ranging from dry to wet areas, Snazell (1982) sampled the spider fauna by pitfall trapping at 154 random points over 12 months. By Principal Components Analysis on the 45 most numerous species he was able to show a wide gradation from specialised to broad habitat preferences, which conform well with the categories in Table 2.

In an experiment in tall grassland in England, faunal changes were recorded in grass litter modified by trampling. Samples of grass litter enclosed in nylon-mesh bags (20x20x8cm) received 3 different treading treatments (5 treads/month, 10 treads/month and an undisturbed control series) (Duffey, 1975b). There were 25 replicates in each case. After 12 months the volume of the litter in the controls had fallen by 50 % due to natural decay, but those having had 10 treads/month had fallen by 81 %. Of the 10 most frequent species, 5 were eliminated by the treading after 12 months, and the total numbers of all species fell by 84 %. Of the 5 remaining species, 3 showed little response to the treading, their numbers falling only marginally. The higher level of treading in this experiment was very light compared with that on a public footpath in a popular area, but the effect on the litter fauna was quite dramatic.

CONCLUSIONS

The modification of the European landscape through many centuries has been the greatest influence determining the distribution of spider species. Natural and near-natural habitats are now rare, as are the specialist species associated with them. Today many species have adapted to man-made environments, whether permanent or temporary, and those preferring open-ground conditions have greatly expanded their range. A gradation of life strategies (or adaptability) from pioneer species to narrow specialists is proposed. Superimposed on these factors are the influences of major climatic zones and the microspatial variations in the abiotic environment. All these features should be considered when defining the distribution and habitat characteristics of a species, drawing on evidence from the whole geographic range.

ACKNOWLEDGEMENTS

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LITERATURE CITED

ANON. 1964-80. 'Flora Europaea'. 5 vols. (Cambridge University Press, Cambridge).

1979. 'The invertebrate fauna of dune and Machair sites in Scotland, Vol.I'. (Project 469 Report to Nature Conservancy Council: Peterborough).

ALDERWEIRELDT, M. & MAELFAIT, J.-P. 1990. 'Catalogus van de Spinnen van Belgie, Deel VII, Lycosidae'. (Studiedocumenten No. 61, Koninklijk Belgisch Instituut voor Natuurwetenschappen: Brussel).

BRATTON, J.H. (ed.) 1991. Arachnida. 121-219. In 'British red data books. 3. Invertebrates other than insects'. (Nature Conservancy Council: Peterborough).

BRISTOWE, W.S. 1939. 'The comity of spiders, Vol. 1'. (Ray Society: London).

CANARD, A. (ed.) 1990. Araignées et scorpions de l'ouest de la France: catalogue et cartographie provisoire des espèces. Bulletin de la Société Scientifique de Bretagne 61(1): 1-302.

DUFFEY, E. 1962. A population study of spiders in limestone grassland: description of study area, sampling methods and population characteristics. Journal of Animal Ecology 31: 571-599.

1968. An ecological analysis of the spider fauna of sand dunes. Journal of Animal Ecology 37: 641-674.

1974. 'Nature reserves and wildlife' (Heinemann Educational Books: London).

1975a. Habitat selection by spiders in man-made environments. Proceedings of the 6th International Arachnological Congress, Amsterdam, 1974: 53-67.

1975b. The effects of human trampling on the fauna of grassland litter. Biological Conservation 7: 255-274.

1978. Ecological strategies in spiders, including some characteristics of species in pioneer and mature habitats. Symposia of the Zoological Society of London 42: 109-123.

DUFFEY, E. & GREEN, M.B. 1975. A linyphiid spider biting workers on a sewage-treatment plant. Bulletin of British Arachnological Society 3: 130-131.

EDWARDS, C.A., BUTLER, C.G. & LOFTY, J.R. 1975. The invertebrate fauna of the Parks Grass plots, II. Surface fauna. Report Rothamsted Experimental Station, 1975(2): 63-89.

JANSSEN, M. & BAERT, L. 1987. 'Catalogus van de Spinnen van Belgie, Deel IV, Salticidae'. (Studiedocumenten No. 43, Koninklijk Belgisch Instituut voor Natuurwetenschappen: Brussel).

JOCQUÉ, R. 1973. Spider fauna of adjacent woodland areas with different humus types. Biologisches Jahrbuch Dodonaea 41: 153-178.

KEKENBOSCH, J., BOSMANS, R. & BAERT, L. 1977. 'Liste des araignées de la faune de Belgique'. (Institut Royal des Sciences Naturelles de Belgique: Bruxelles).

KESSLER, A. 1973. A comparative study of the production of eggs in eight *Pardosa* species in the field (Araneidae, Lycosidae). Tijdschrift voor Entomologie 116: 23-41.

LOCKET, G.H. & MILLIDGE, A.F. 1953. 'British spiders'. 2 vols. (Ray Society: London).

LOCKET, G.H., MILLIDGE, A.F. & MERRETT, P. 1974. 'British spiders, Vol. III', (Ray Society: London).

MEIJER, J. 1977. The immigration of spiders (Araneidae) into a new polder. Ecological Entomology 2: 81-90.

MOUNTFORD, M.D. 1962. An index of similarity and its application to classificatory problems. Pp. 43-50. In Murphy, P.W. (ed.). 'Progress in soil zoology'. (Butterworths: London).

PROSZYNSKI, J. 1978. Distributional patterns of the Palaearctic Salticidae (Araneae). 335-43. In Murphy, P.W. (ed.) 'Symposia of the Zoological Society of London No. 42, Arachnology'.

RANSY, M. & BAERT, L. 1985. 'Catalogus van de Spinnen van Belgie, Deel II. De Cribellatae'. (Studiedocumenten No. 25, Koninklijk Belgisch Instituut voor Natuurwetenschappen: Brussel).

1987a. Catalogue des araignées de Belgique, Pt 3. Les Araneidae. Documents de Travail No. 36. (Institut Royal des Sciences Naturelles de Belgique: Bruxelles).

1987b. Catalogue des araignées de Belgique, Pt 5. Anyphaenidae, Argyronetidae, Atypidae, Dysderidae, Mimetidae, Nesticidae, Oonopidae, Oxyopidae, Pholcidae, Pisauridae, Scytodidae, Segestriidae, Eusparassidae, Zodariidae, Zoridae. Documents de Travail No. 46 (Institut Royal des Sciences Naturelles de Belgique: Bruxelles).

RANSY, M., KEKENBOSCH, J. & BAERT, L. 1990. Catalogue des araignées de Belgique, Pt 6. Clubionidae et Liocranidae. Documents de Travail No. 57. (Institut Royal des Sciences Naturelles de Belgiques: Bruxelles).

RATCLIFFE, D. A. (ed.). 1977. Spiders. Pp. 95-101. In 'A nature conservation review, Vol. I'. (Cambridge University Press: Cambridge).

RICHTER, C.J.J. 1970. Aerial dispersal in relation to habitat in eight wolf spider species (*Pardosa*, Araneae, Lycosidae). Oecologia, Berlin 5: 200-214.

ROBERTS, M. J. 1985-87. 'The spiders of Great Britain and Ireland'. 3 vols. (Harley Books: Colchester).

SCHAEFER, M. & TISCHLER, W. 1983. 'Wörterbücher der Biologie; Oekologie'. (Gustav Fischer: Jena).

SNAZELL, R. 1982. Habitat preferences of some spiders on heathland in southern England. Bulletin of the British Arachnological Society 5: 352-360.

UETZ, G.W. 1991. Habitat structure and spider foraging. Pp. 325-348. In Bell, S.S., McCoy, E. D. and Mushinsky, H.R. (eds). 'Habitat structure, the physical arrangement of objects in space'. (Chapman and Hall: London).

VAN WINGERDEN, W. 1977. 'Population dynamics of *Erigone arctica* (White) (Araneae, Linyphiidae)'. Doctoral thesis, Free University of Amsterdam.

WEBB, N. R. 1990. Changes on the heathlands of Dorset, England between 1978 and 1987. Biological Conservation 51: 273-286.

THE DEVELOPMENT OF THE ASYMMETRICAL WEB OF *NEPHILENGYS CRUENTATA* (FABRICIUS)

JANET EDMUNDS

Edmunds, J. 1993 11 11: The development of the asymmetrical web of *Nephilengys cruentata* (Fabricius). *Memoirs of the Queensland Museum* 33(2): 503-506. Brisbane. ISSN 0079-8835.

In the field, young *Nephilengys cruentata* (Fabricius) remain on the barrier threads of their mother's web for about ten days, before moulting. Some do not initially disperse far, and may even remain on the barrier threads to build their first web. These first webs are complete orbs. As the spiderlings grow the hub of the web is spun approximately three quarters of the way up the web; later there are no spirals above the hub. At this stage some spiders join the hub to the barrier, forming a 'tent' under which the spider rests. The true retreat, of a tube that is closed at the end away from the hub, develops gradually as the spiders grow further.□*Nephilengys, web development, evolution of webs.*

Janet Edmunds, Mill House, Mill Lane, Goosnargh, Preston PR3 2JX, United Kingdom; 12 November, 1992.

Nephilengys cruentata (Fabricius) is common throughout tropical Africa. In Ghana it lives in savanna and forest edge areas. Under natural conditions it attaches its web to trees, but it has frequently adapted to attaching it to dwellings. It was very common at Legon in such situations. The adult female is large but the male is much smaller. The webs of larger spiders are usually a roughly triangular partial orb. The hub is at the upper apex, where there is a cylindrical retreat, closed at the end away from the hub. There is an extensive barrier above and behind the viscid web; the main attachment between the two is at the hub. The hub and retreat are often in the angle between a wall and the ceiling or overhang. This paper presents data on the shape of the web of *N. cruentata* from the earliest instars to adults.

METHODS

Spiders of all ages were observed living on the verandahs of a private dwelling and of the Zoology Department at Legon, but it was not possible to follow individual spiders in the field or captivity. Web size and length of the first leg of each spider were measured, although the relation between spider size and instars was not determined. The vertical asymmetry, lateral asymmetry and shape (circularity) of the web were determined from the ratios of vertical radii, horizontal radii and the two diameters respectively, all measured to the nearest 5mm; N for all figs is given in Table 1.

RESULTS

The cocoon is laid close to the web, often on a wall or ceiling. When the spiderlings emerge, they remain close to where they have emerged in a tight bunch on the barrier web for about ten days, spinning extra irregular threads. After the first post emergence moult, they disperse, but many remain close to the mother's web, some even building their first catching web in the threads of the barrier web.

When the spiders are grouped into different size classes based on leg 1 length, the extent of the web below the hub increases with each succes-

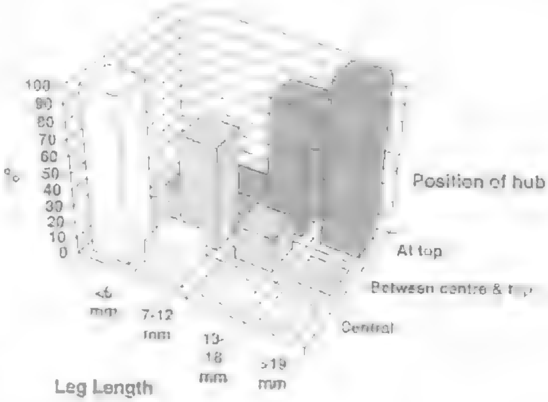

FIG. 1. Changes in vertical asymmetry in webs of *N. cruentata* with different leg lengths. At top: ratio of upper to lower radius = 0; Between centre and top: ratio of upper to lower radius >0 <1; Central: ratio of upper to lower radius = 1 .

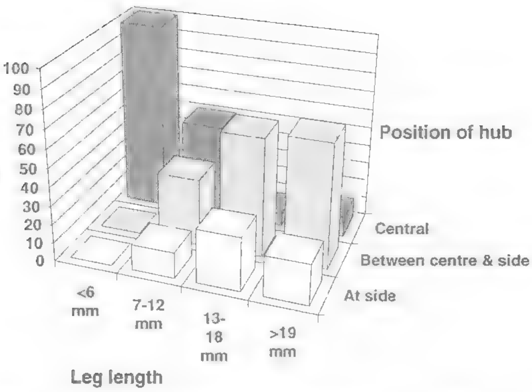

FIG. 2. Changes in lateral asymmetry in webs of *N. cruentata* with different leg lengths. At side: ratio of two horizontal radii = 0; Between centre and side: ratio of two horizontal radii >0 <1; Central: ratio of two horizontal radii = 1.

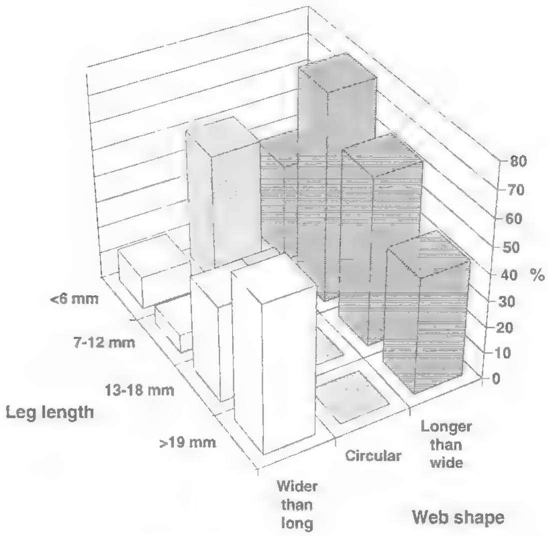

FIG. 3. Changes in shape in webs of *N. cruentata* with different leg lengths. Longer than wide: vertical diameter > horizontal diameter; Central: vertical diameter = horizontal diameter; Wider than long: vertical diameter < horizontal diameter.

sive class, while that above the hub increases slightly before decreasing to zero (Table 1).

The vertical asymmetry increases with size (Fig. 1): spiders with leg 1 <6mm spin complete orbs. As they grow, less web is spun above the hub, so that the hub is then about three quarters of the way up the web. Larger spiders, with leg 1 >19mm have no web above the hub. Because of the difficulty in following individual spiders, the time span over which these web changes occurred is not known.

Early webs are symmetrical laterally (Fig. 2), but webs of larger spiders show greater variation and may be markedly asymmetrical laterally; at the extreme the hub is completely to one side. Some early webs are also circular or nearly so (Fig. 3), however very few webs of spiders with leg 1 > 6mm have the vertical and horizontal diameters of the same size.

During these changes in the proportions of the viscid web, the barrier increases (Fig. 4). The very first webs have no barrier or just a few threads, which are attached to the orb at only a few points. But over some days more threads are added, until the barrier is a fairly dense cone shaped tangle behind the orb, and more firmly fixed to the web. Small pellets of detritus, similar in size and shape to the spiderling and of the same pale grey colour, usually occur in the barrier (Edmunds and Edmunds, 1986). These may deflect attacks of potential predators.

The development of the retreat increases with the size of the spider (Fig. 5). Spiders with the hub

TABLE 1. Body size and web dimensions (in mm) in different size classes (based on leg 1 length) of *Nephilengys cruentata*.

Leg 1 length	<6	7-12	12-18	>19
Body size	<3.5	3.5-7.0	7.0-9.0	>9.0
N	8	14	14	9
Hub-web top:mean	38.1	47.1	19.2	0
range	25-50	0-80	0-100	0
Hub-web bottom: mean	38.1	109.3	180.0	478.9
range	25-50	45-170	140-260	200-700
Web Width: mean	73.8	117.9	177.4	431.1
range	70-90	80-180	80-290	240-850

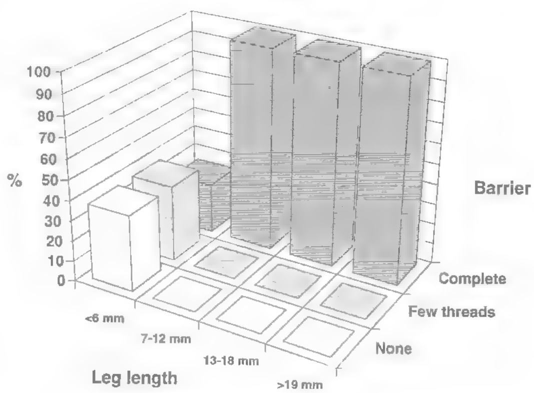

FIG. 4. Development of barrier in webs of *N. cruentata* with different leg lengths.

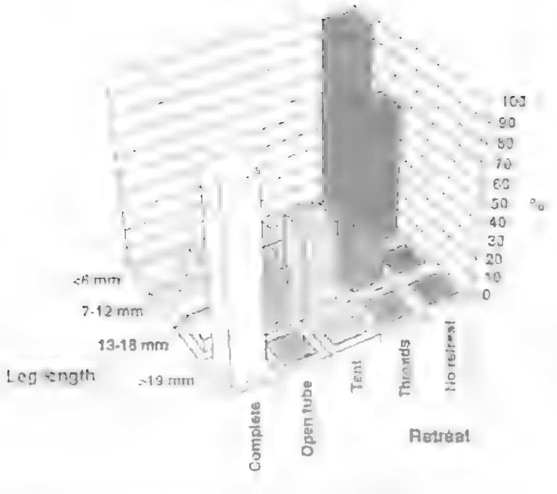

FIG. 5. Development of retreat in webs of *N. cruentata* with different leg lengths.

at the centre or part of the way up the web rest at the web hub and there is no retreat. When the hub is built at or very close to the apex, the first stages of a retreat are formed as a denser group of threads within the barrier close to the hub. As more threads are added, this becomes a roof-like tent between the hub and the barrier, or sometimes an open ended tube. Spiders with leg 1 >19mm normally had a closed tubular retreat, like an adult.

Early webs are very fine, and it is not easy to see the details of the individual threads. However, a complete web appears to be spun in one operation, unlike larger webs which are spun in two or more sections on different days. The temporary spiral does not appear to be left up, though more detailed observations would be needed to confirm this. Larger spiders leave the temporary spiral in the finished web.

DISCUSSION

The webs of most adult female Nephilinae are not typical orbs. Most *Nephila* species build incomplete orbs, with the hub near the top (Robinson and Robinson, 1973, figs 2, 20; pers. obs.). However, unlike *Nephilengys*, there are threads above the hub, including in some instances a few sticky spirals. In *Nephila plumipes* large, probably mature, females were seen in Brisbane, Australia, that had several sticky radii above the hub. However, in at least some individuals, these appeared to have been laid as pendulum turns, rather than complete spirals (pers. obs.). *Nephila* does not build a retreat and the spider rests at the hub. Like *Nephilengys*, there are barrier webs, though on both sides, and often above the orb. These are supportive and probably also defensive (Robinson and Robinson, 1973). *Herennia ornatissima* (Doleschall) constructs a very long web, with almost parallel sides (Robinson and Lubin, 1979). The spider sits in a cup-shaped depression of dense silk that forms the hub. It is towards the top of the web, though there are several sticky spirals above it. The spider has no barrier web, but as it builds very close to tree trunks, it would be difficult to find a place to build one.

Larger juvenile Nephilinae build webs like the adults, and a few observations have been published on the very early webs. The first webs of *Nephila clavipes* (Linnaeus) are circular (Comstock, 1948; Levi and Levi, 1968). Brown and Christenson (1983) give measurements of the webs of *N. clavipes* spiderlings between 2 and 9mm body length. The webs show an increase in vertical asymmetry as they grow. However, unlike *Nephilengys cruentata*, even the instars that spin the first catching webs had the hub approximately two thirds of the way up the web. Both species seem to spin the hub at the top of the web when they reach a similar size. Webs with spirals above the hub are spun by juvenile *Nephila maculata* (Fabricius) (Robinson and Robinson, 1973, figs 5, 6), and possibly by *Nephila senegalensis* (Walckenaer) (Clausen, 1987). The webs of juvenile *Herennia ornatissima* (Robinson and Lubin, 1979) are also more like a complete orb.

The fact that the earliest webs of at least some species of Nephilinae are complete orbs indicates that the orb is a primitive characteristic in them, and that the incomplete orbs of the larger spiders are derived. There are other spiders which have a highly modified orb-web, but build a more complete orb as a juvenile. Spiders of the genus *Scoloderus* build extremely elongated inverted ladder webs, with the hub towards the base. The juveniles of *Scoloderus tuberculifer* O.P.-Cambridge have webs that are far less distorted (Eberhard, 1975). However, even the smallest *S. cordata* (Taczanowski) have elongated ladders (Stowe, 1978). In *Araneus atrihastulus* from New Zealand, which builds a web that is elongated both above and below the hub, some of the proportions of juvenile webs are less extreme (Forster and Forster, 1985). It would be interesting to find the very early webs of other spiders with atypical webs, such as that of the spider that built the ladder web observed by Robinson and

Robinson (1972) in New Guinea, now identified as close to *Tylorida* (Eberhard, 1990b). Other aspects of web construction and use may be more derived in adults than in juveniles, such as the angle of the spring line and resting position of the spider in *Epeirotypus* sp. from Costa Rica (Eberhard, 1986). However, in the west African *Pararaneus cyrtoscapus* (Pocock), the conical horizontal webs of juveniles are more derived than the planar vertical of adult females (Edmunds, 1978).

If it is confirmed that young *Nephilengys cruentata* build webs in one piece and destroy temporary spirals, then the adult behaviour of leaving the temporary spirals in place is presumably also a secondary modification. There are other characteristics of the webs of Nephilinae that are derived. Despite their size, the webs of adults have a finer mesh compared to some other orb weavers (personal observation). Eberhard (1982, 1990a) concludes that some characteristics of the web building behaviour of *Nephila clavipes*, such as the unique method of laying the sticky spiral, are an adaptation to spinning a tightly meshed web, even though other aspects (e.g. frame construction) are primitive. Levi (1986), Eberhard (1990a) and Coddington (1990) classify the Nephilinae with the Metinae and tetragnathids, rather than with *Araneus* and its relatives. The derived nature of the partial orb of the larger Nephilinae would be consistent with this classification.

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LITERATURE CITED

BROWN, S.G. & CHRISTENSON T.E. 1983. The relationships between web parameters and spiderling predatory behavior in the orb-weaver *Nephila clavipes*. Zeitschrift für Tierpsychologie 63: 241-250.

CLAUSEN, I.H.S. 1987. On the biology and behaviour of *Nephila senegalensis senegalensis* (Walckenaer, 1837). Bulletin of the British Arachnological Society 7: 147-150.

CODDINGTON, J.A. 1990. Ontogeny and homology in the male palpus of orb- weaving spiders and their relatives, with comments on phylogeny (Araneoclada: Araneoidea, Deinopoidea). Smithsonian Contributions to Zoology 496: 1-52.

COMSTOCK, J.H. 1948. 'The spider book'. Revised and edited by W.J. Gertsch (Comstock Publishing: Ithaca).

EBERHARD, W.G. 1975. The 'inverted ladder' orb web of *Scoloderus* sp. and the intermediate orb of *Eustala* (?) sp. (Araneae: Araneidae). Journal of Natural History 9: 93-106.

1982. Behavioral characters for the higher classification of orb-weaving spiders. Evolution 36: 1067-1095.

1986. Ontogenetic changes in the web of *Epeirotypus* sp. (Araneae, Theridiosomatidae). Journal of Arachnology 14: 125-128.

1990a. Early stages of orb construction by *Philoponella vicina*, *Leucauge mariana*, and *Nephila clavipes* (Araneae, Uloboridae and Tetragnathidae), and their phylogenetic implications. Journal of Arachnology 18: 205-234.

1990b. Function and phylogeny of spiders webs. Annual Review of Ecology and Systematics 21: 341-372.

EDMUNDS, J. 1978. The web of *Paraneus* [*sic*] *cyrtoscapus* (Pocock 1899) (Araneae: Araneidae) in Ghana. Bulletin of the British Arachnological Society 4: 191-196.

EDMUNDS, J. & EDMUNDS, M. 1986. The defensive mechanisms of orb weavers (Araneae: Araneidae) in Ghana, West Africa. Pp. 73-89. In Eberhard, W.G., Lubin, Y.D. and Robinson, M.H. (eds). Proceedings of the Ninth International Congress of Arachnology, Panama (Smithsonian Institution: Washington D.C.).

FORSTER, L.M. & FORSTER, R.R. 1985. A derivative of the orb web and its evolutionary significance. New Zealand Journal of Zoology 12: 455-465.

LEVI, H.W. 1986. The neotropical orb-weaver genera *Chrysometa* and *Homalometa* (Araneae: Tetragnathidae). Bulletin of the Museum of Comparative Zoology 151: 91-215.

LEVI, H.W. & LEVI, L.R. 1968. 'A guide to spiders and their kin'. (Golden Press: New York). 160pp.

ROBINSON, M.H. & LUBIN, Y.D. 1979. Specialists and generalists: the ecology and behavior of some web-building spiders from Papua New Guinea. Pacific Insects 21: 97-132.

ROBINSON, M.H. & ROBINSON, B. 1972. The structure, possible function and origin of the remarkable ladder-web built by a New Guinea orb-web spider (Araneae: Araneidae). Journal of Natural History 6: 687-694.

1973. Ecology and behavior of the giant wood spider *Nephila maculata* (Fabricius) in New Guinea. Smithsonian Contributions to Zoology 149: 1-76.

STOWE, M.K. 1978. Observations of two nocturnal orbweavers that build specialized webs: *Scoloderus cordatus* and *Wixia ectypa* (Araneae: Araneidae). Journal of Arachnology 6: 141-146.

DOES MIMICRY OF ANTS REDUCE PREDATION BY WASPS ON SALTICID SPIDERS?

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A common predator of spiders at Legon, Ghana, is the wasp *Pison xanthopus*, 96% of whose prey were salticids. The data from cells built by 31 wasps containing over 800 spiders are used to examine whether mimicry of ants gives protection against *Pison*. Comparison of salticids in wasp cells with those found on nearby vegetation shows that fewer ant mimics (*Myrmarachne* spp.) are taken than one would expect if wasps were capturing salticids in proportion to their occurrence, but also that some individual wasps specialize in capturing *Myrmarachne*. Implications for the searching image hypothesis are discussed. □*Batesian mimicry, ant-mimicry, Salticidae, predation, search image, Pison, Myrmarachne.*

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Ant mimicry has evolved in several spider families, e.g. Salticidae, Clubionidae, Thomisidae, Aphantochilidae and Theridiidae (Hingston, 1927; Mathew, 1954; Reiskind and Levi, 1967; Reiskind, 1977; Edmunds, 1974, 1978; Wanless, 1978; Oliveira and Sazima, 1984, 1985; Oliveira, 1988). Some of the most precise morphological and behavioural resemblances to ants occur in the salticid genus *Myrmarachne* which is widespread in both the Old and New Worlds, especially in the tropics (Wanless, 1978). At Legon, Ghana, three species of *Myrmarachne* are common, each one closely resembling one species of ant when it is full grown but a different ant species when it is immature (Edmunds, 1978). This mimicry could have two advantages for the spider:

1. It could deceive the ants and so enable the spider to creep up and prey on them. This is aggressive mimicry as may possibly occur in the thomisid *Amyciaea forticeps* (Mathew, 1954), and is well documented for the aphantochilid *Aphantochilus rogersi* (Oliveira and Sazima, 1984);

2. It could deceive a predator into mistaking it for an ant which that particular predator does not eat. This is batesian mimicry.

Myrmarachne do not normally attack ants, so there is no support for aggressive mimicry (Edmunds, 1978; Wanless, 1978). Indeed whenever an ant comes near they use their acute eyesight and quick reactions to avoid contact. This suggests a danger of being killed if caught by the ants (Edmunds, 1978; Wanless, 1978). Direct evidence supporting batesian mimicry is sparse. Edmunds (1974, 1978) argued that because few insectivorous birds prey on ants, the ant mimics associated with them would also escape predation. He further attempted to show that ant-mimicking spiders are less often taken by the wasp *Pison xanthopus* than are other salticids, but there were rather little data available at that time. More recently, the American ant mimic *Synageles occidentalis* was found being preyed on much less than are non-mimicking salticids by the philodromid *Tibellus oblongus*, and the large salticid *Phidippus clarus* ignored or avoided *Synageles* and ants in exactly the same way, while continuing to attack non-mimicking salticids (Cutler, 1991)

More data on the prey of *Pison xanthopus* are given here to test the theory that ant mimicry gives protection against spider-hunting wasps.

MATERIAL

Mud cells of *Pison xanthopus* were collected from window frames at the University of Ghana, Legon, Ghana between 1969 and 1973. Individual wasps build from 1-6 cells in a row. Each cell is stocked with 5-10 paralysed salticid spiders and an egg is laid on one of these. The spiders were preserved in alcohol and identified, usually to genus or species. They were also classed as either good ant mimics (*Myrmarachne*), poor ant mimics (*Cosmophasis* sp.) or non-mimics (other genera). Most of the spiders are now in the collection of the Natural History Museum, London. Identification of the spiders was confirmed by F.R. Wanless, and the wasp was determined by the late Professor O.W. Richards.

Spider	Habitat: Leaf litter	Short grass	Long grass	Shrubs	Tree trunks	In wasp cells
Good ant mimics						
Myrmarachne foenisex Simon				+	+	+
Myrmarachne elongata Szombathy			+	+		+
Myrmarachne legon Wanless				+		+
Myrmarachne uvira Wanless				+		
Poor ant mimics						
Cosmophasis sp.		+	+	+	+	+
Non-mimics						
Thyene sp			+	+	+	+
Hyllus sp			+			
Stenaelurillus sp			+		+	
Rhene sp					+	+
Cyllobelus rufopictus Simon	+					
Hasarius adansoni (Audouin)		+				
Schenkelia modesta Lessert					+	
Menemerus sp					+	+
Pseudicius sp					+	+
Other non-mimicking salticids		+	+			+

TABLE 1. Salticid spiders in five habitats at Legon, May-July 1973.

RATIONALE

If ant mimicry deceives wasps so that they do not capture ant-mimicking spiders as often as non-mimics, then the proportion of ant mimics to non-mimics should be lower in wasp cells than in the natural environment. If wasps are not deceived then the proportion of ant mimics should be the same. The test of this hypothesis is to compare the incidence of ant mimics in wasp cells with those found in the field.

WHERE DOES *PISON* HUNT?

First, the wasp's hunting range must be established so that a random sample of salticids can be collected from the same place. *Pison* is small, difficult to follow in flight, and was observed hunting on only a few occasions. Each time it was running and making short flights over leaves of shrubs. It was never observed on the ground or in grass, but as I spent more time examining shrubs than any other habitat, this is not conclusive. I therefore collected salticids from several different habitats at Legon. If the species of spider taken by wasps correspond with those found in one particular habitat then the wasps are probably hunting in that habitat.

The habitats are: leaf litter; short, regularly cut grass; long grass and herbage; 1-3m high shrubs; and tree trunks. The spectrum of spiders in wasp cells is most similar to those found in shrubs and trees (Table 1). The canopy was not sampled but probably has a similar fauna. However, it is unlikely that the wasps were hunting in short grass, leaf litter or long grass.

RESULTS

Spiders in Wasp Cells and on Shrubs

Some variation in the numbers of spiders caught by each wasp (Table 2) is due to the different numbers of cells completed by the wasps when collected. Cells with full grown larvae or pupae were ignored since the spiders in them were reduced to carapace cuticles, but cells with eggs or young larvae contained spiders that were intact and so are included. The spiders caught by each wasp came from 2-9 cells, e.g. on 3 Feb 1973, the first cell contained a pupa, the second a full grown larva, and the third had nine spiders but no egg. The wasp presumably was killed before fully provisioning this cell.

Of 872 spiders found, 837 were salticids (Table 2); 160 were 'good' ant mimics (i.e. *Myrmarachne* spp.), judged by the human eye, and a further 15 can be classed as poor (behavioural) ant mimics (i.e. *Cosmophasis* spp.). In 1973, every shrub in Zoology (twice) and in Botany (once) was searched (see Edmunds, 1978). All salticids found were scored as either a good mimic, a poor mimic or a non-mimic. The differences between types are highly significant ($\chi^2_{(2)} = 49.04$, $p<0.001$; Fig. 1). *Pison* clearly take significantly fewer good ant mimics than they do poor mimics or non-mimics compared with their incidences in the environment.

However, wasps searching by running quickly over vegetation are unlikely to find spiders resting in their retreats beneath or between leaves. So perhaps the comparison should be made between the numbers of spiders in wasp cells and the numbers foraging on leaves (excluding those in retreats). These figures are also given in the upper part of Fig. 1 (the black bars only): 61.9% of spiders on shrubs were good mimics compared with 19.1% in wasp cells. This too is highly significant, again indicating that wasps take many fewer good mimics than poor or non-mimics ($\chi^2_{(2)} = 64.15$, $p<0.001$). The proportion of poor

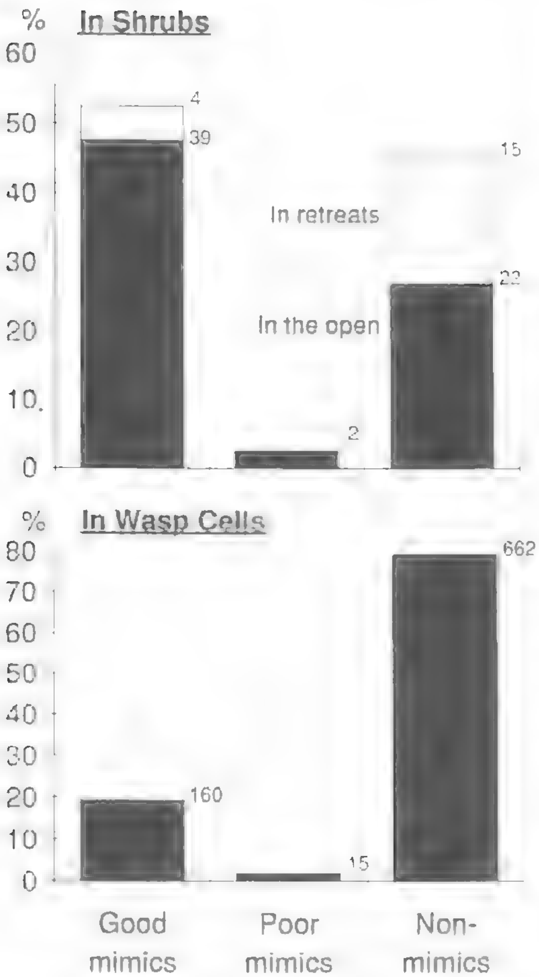

FIG. 1. Comparison of good, poor and non-ant mimicking salticids on shrubs and in cells of *Pison xanthopus*.

mimics taken by wasps is not significantly different from that of the non-mimics, so in the analysis that follows the poor (behavioural) mimic *Cosmophasis* is treated as a non-mimic.

Spatial or Seasonal Variation

These comparisons are of spiders on shrubs in February and May 1973 with spiders in wasp cells collected over 3.5 years. The relative numbers of *Myrmarachne* and of other salticids vary throughout the year and over different parts of the University campus, and this may account for the differences in proportions of spider prey taken by wasps. Evidence against this possibility is (1) that there was no significant difference in the relative numbers of *Myrmarachne* and of other salticids collected on shrubs in February and in May 1973 (Edmunds, 1978); (2) that the three wasp cells (taken 22 Jan- 3 Feb 1973) from close to where the shrubs were surveyed had between them eight *Myrmarachne* and 54 other salticids compared with 24 *Myrmarachne* and 26 other salticids on the shrubs on Feb 2; this difference is highly significant ($\chi^2_1 = 15.0$, $p < 0.001$); and (3) that the data (Table 2) show no clear evidence of spiders occurring at particular sites or in certain seasons. So, while there may be some variation in spider species at different times and places at Legon, such variation is unlikely to account for the very different numbers of salticids taken by wasps assuming that they take different species in proportion to their frequency in the population.

No Wasps Near Dangerous Ants

Most *Myrmarachne* taken by *Pison* were black and identified as *M. legon* and *M. elongata* (Wanless, 1978) but some immature specimens could not be identified. Only one specimen of the very common *M. foenisex*, in a total of 160 *Myrmarachne*, was taken. It was a juvenile whose body was red-brown and black (Edmunds, 1978, Fig. 1), quite unlike *Oecophylla*, but very similar to the smaller ant *Crematogaster castanea* which only lives close to *Oecophylla* (Edmunds, 1978). *M. foenisex* closely associates with the aggressive red weaver ant *Oecophylla longinoda*, of similar colour. Adult *M. foenisex* are probably too large for *Pison* to attack, but since it captures many young black *Myrmarachne* one might expect it to take young *M. foenisex* as well. Young *M. legon* are quite similar to young *M. foenisex*, but they do not associate with *Oecophylla* nor with *C. castanea*. Many young *M. legon* but very few *M. foenisex* were taken by *Pison*. Hence, *Pison* probably avoids hunting on plants overrun by *Oecophylla*.

If *Pison* does not hunt on plants with *Oecophylla*, then salticids found with these ants need to be omitted from the comparison of ant mimics and non-mimics on shrubs and in wasp cells (Table 3). Of salticids on shrubs, 49% are good ant mimics compared with 19% in wasp cells. This difference is highly significant, and remains so if spiders in retreats are excluded ($p < 0.001$).

Wasps clearly take fewer *Myrmarachne* than one would predict if they caught them in proportion to their occurrence in the environment. This is therefore good evidence for the defensive value of ant mimicry against predation by *Pison*.

		Mimics		Non-ant mimicking spiders												
Date	Place	My	Co	Ps	Rh	Te	Me	Vi	So	Th	Sa	Mo	Fi	Os	Of	All
28.9.69	Zool				26											26
29.9.69	Zool	2		8	1											11
13.1.71	Bot.	6		29	1											36
11.2.71	Bot	34	1		1	6				2	2					46
12.3.71	Hill	4		44		1	1				1	2				53
11.4.71	Zool.	1		29										1		31
19.4.71	Maths			32			1							1		34
5.2.72	ISSER	15	11	2												28
15.2.72	Zool.			22					1				3			26
15.2.72	Zool.	10	2	4					2							18
15.3.72	Zool														33[1]	33
27.3.72	Zool	1		24	1											26
14.4.72	ISSER			36					1							37
16.5.72	Zool			20	1											21
22.5.72	Zool.			28	1			1					1			31
22.5.72	ISSER			24					1							25
- 7.72	ISSER			28									2			30
6.7.72	ISSER	25														25
1.11.72	Hill	5		36		1		2					1			45
8.11.72	Zool.	15		16						1						32
13.11.72	Zool.	8		17	19									1		45
15.11.72	Zool	18	1													19
18.1.73	Hill			26											1[2]	27
22.1.73	Bot	6		25		1		8					2		1[3]	43
24.1.73	Bot.	1				9										10
3.2.73	Bot.	1		5			1			2						9
13.2.73	Agric						11									11
21.2.73	Hill	5		6												11
23.3.73	Hill	1		33		1	1									36
27.5.73	ISSER	2		25					1							28
28.5.73	Agric.			19												19
	Total	160	15	538	51	19	15	11	6	5	3	2	9	3	35	872

TABLE 2. Spiders in cells of *Pison xanthopus* at Legon, Ghana, 1969-1973. Key to Places at University of Ghana, Legon: Faculty of Agriculture, Agric.; Depart. of Botany, Bot.; Institute of Statistical, Social and Economic Research, ISSER; 36 Legon Hill, Hill; Depart. of Mathematics, Maths; Depart. of Zoology, Zool. [1] - 17 Thomisidae, 6 Theridiidae, 5 Clubionidae, 2 Oxyopidae, 1 Araneidae, 1 Selenopidae, 1 Philodromidae. [2] - Oxyopidae. [3] - Gnaphosidae. Taxon head is abbreviated in order: My, *Myrmarachne* sp.; Co, *Cosmophasis* sp.; Ps, *Pseudicius* sp.; Rh, *Rhene* sp.; Te, *Telamonia* sp.; Me, *Menemerus* sp.; Vi, *Viciria* sp.; So, *Sonoita lightfooti;* Th, *Thyene* sp.; Sa, *Saitis* sp.; Mo, *Mogrus* sp.; Fi, Fissident sp.; Os, other Salticidae; Of, other spider families.

wasps who between them took only eight *Myrmarachne* out of 73 spiders (11%), while it failed to protect them from the fourth wasp which took 34 *Myrmarachne* out of 46 prey (74%). Overall, 25 individual wasps took only 38 *Myrmarachne* out of 693 spiders (5.5%), indicating that they had been deceived by the mimicry. The other seven wasps took 122 *Myrmarachne* out of 179 spiders (68.2%) indicating that they had overcome the defence of mimicry to the extent that they preyed almost exclusively on ant mimics (a wasp on 6 July 1972 took 25 *Myrmarachne* and no other spiders, while in the other six wasps *Myrmarachne* taken were never less than 45%).

For the poor ant mimic, *Cosmophasis*, the 15 spiders taken by wasps (Table 2) represent 1.7% of all salticids taken, or 2.1% excluding *Myrmarachne*. This is less than their relative frequency on shrubs (2.4% of all spiders or 5.1% excluding *Myrmarachne*), but the differences are not significant. However, one wasp (on 5.2.72) caught 11 *Cosmophasis* while all other wasps very rarely took them. Therefore, even poor mimicry of ants appears to give some protection against most wasps, but occasionally a wasp will specialize on this species, just as other wasps do with *Myrmarachne*.

Do Individual Wasps Hunt Specific Prey?

All wasps do not take a similar spectrum of spiders, but each individual preys on one or two species of spider (Table 2). Thus the first wasp in the table preyed on *Rhene* sp., the second and third on *Pseudicius* sp. and the fourth on black species of *Myrmarachne*. Ant mimicry was obviously of defensive value against the first three

Hunting by the Searching Image Method

The term searching image was used to describe the way in which tits (Paridae) collect caterpillars for their young: each bird tends to bring insects

TABLE 3. Percentages of *Myrmarachne* (Myrm) and other salticids on shrubs at Legon, and in cells of *Pison xanthopus*. Figures in brackets are numbers and percentages found in open (i.e. not in retreats).

Source of spiders	N	Myrm	Others	$\chi^2_{(1)}$
Shrubs-all data	82 (63)	52.4 (61.9)	47.6 (38.1)	46.3 (59.8)
Wasp cells	837	19.1	80.9	
Shrubs-omitting *M. foeniser* & all spiders with ants *Oecophylla* & *Crematogaster castanea*	53(41)	49.1 (58.5)	50.9 (41.5)	25.5 (34.6)
Wasp cells	836	19.0	81.0	

of predominantly a single species for several days and then to abruptly switch to another species (Tinbergen, 1960). Tinbergen hypothesized that the birds recognised caterpillars by particular characters which they 'assimilated in a kind of learning process' and that in their search for prey they looked for these particular characters. Later authors have used the words 'searching image' and 'search image' interchangeably, but its definition has been refined following Croze (1970), Dawkins (1971), Krebs (1973), Lawrence and Allen (1983) and Guilford and Dawkins (1987). It is now generally understood to mean a perceptual change in a predator that temporarily increases its ability to detect particular cryptic prey which it has recently encountered. Searching image needs to be distinguised from various other types of preference that predators may show for particular prey (Krebs, 1973; Lawrence and Allen, 1983), so it is probable that the behaviour observed by Tinbergen which he called hunting by means of a 'specific searching image' would today not be considered a proven example of searching image behaviour.

Individual *Pison xanthopus* clearly concentrate on one or a few species of prey; is this because it hunts using a searching image or by some other method? In a recent critique of the search image concept Guilford and Dawkins (1987, 1988a,b) argue that all studies purporting to demonstrate searching images can actually be explained better in terms of variation in search rate. They make two predictions which can distinguish between the two hypotheses. First, the search rate hypothesis predicts that mimetic prey should take longer to find than non-mimics, so wasps that have learned to find them will slow down their search rate. The searching image hypothesis makes no such prediction. Second, the searching image hypothesis predicts that because of perceptual specialization, wasps concentrating on one type of prey will ignore others. The search rate hypothesis makes no prediction about concentration on one prey interfering with finding other prey. These observations do not explicitly test either prediction, but I consider that *Pison* is not hunting by adjusting its search rate because different wasps concentrate on different prey implying that capture of several prey of one species interferes with capture of other species. The two wasps at ISSER on 5th and 6th of July 1972 took very different prey. If they had been hunting simply with different search rates then the first wasp should have taken some *Myrmarachne* while the second should have taken some *Pseudicius*. This total concentration on one species of prey is not easy to explain on the search rate hypothesis.

If *Pison* is not capturing prey by adjusting its search rate, there are at least three other hunting methods that might result in the concentration on particular species of prey shown in Table 2:-

1. Wasps might have some sort of preference for one prey rather than another. This is unlikely if the preference is based on taste because the wasps sting but do not eat the prey.

2. Wasps could be searching in different places:-

a. Individual wasps might search in different microhabitats. If each species of spider lives in a slightly different microhabitat on the shrubs then individual wasps could catch different species of spider. Evidence in favour of this is the wasp on 18 Mar 1972 which concentrated on thomisid and other non-salticid spiders. Because it initially caught some of these spiders it is reasonable to suppose that it learned to hunt in particular areas or in a particular way such that it continued to catch these spiders instead of salticids.

b. Wasps might search in one area before going on to another. If spiders are clumped instead of being randomly spaced, then individual wasps hunting in the same general area could capture different species of spider. I often found two or three spiders of one species on a shrub so the distribution is clumped rather than random. However, there is no exclusion of one species by another, and the clumping may simply be of recently mated pairs or of parents with young that have failed to disperse. This impression has not been quantified, but I consider it unlikely that it could explain the extreme specialization on one species (Table 2).

3. The wasps may have a perceptual searching image as implied by Croze (1970). Wasps of other genera can learn the configuration of landmarks near their burrows (see Tinbergen,

1958), and this presumably involves some perceptual memory not unlike that in ourselves when we search for something with a particular image in our mind.

It is unclear which of the above methods of prey capture or if another method (e.g., Krebs, 1973) is involved. But certainly some such behaviour occurs both in *Pison* and in other wasps, e.g. the sphecid *Chalybion fuscipenne* (J. Edmunds, 1990).

CONCLUSIONS

Clearly, ant-mimicking spiders are common, more so than non-mimics in some habitats. Ant mimicry may give protection against wasps such as *Sceliphron* which prey on spiders of various families (Edmunds, 1974; J. Edmunds, 1990). The results confirm the suggestion from a preliminary, less rigorous study (Edmunds, 1974), that ant mimicry is of protective value against the specialist predator *Pison xanthopus*. The evidence that behavioural ant mimicry protects *Cosmophasis* against *Pison* is not conclusive; it may be protective against other wasps or against birds. Wanless (1978) and Curtis (1988) have evidence that spiders of this genus prey on ants, so this mimicry could also be aggressive rather than defensive in function.

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LITERATURE CITED

CROZE, H. 1970. Searching image in carrion crows. Zeitschrift für Tierpsychologie, Supplement 5: 1-85.

CURTIS, B.A. 1988. Do ant-mimicking *Cosmophasis* prey on their *Camponotus* models? Cimbebasia (Windhoek) 10: 67-70.

CUTLER, B. 1991. Reduced predation on the antlike jumping spider *Synageles occidentalis* (Araneae: Salticidae). Journal of Insect Behavior 4: 401-407.

DAWKINS, M. 1971. Perceptual changes in chicks: another look at the 'search image' concept. Animal Behaviour 19: 566-574.

EDMUNDS, J. 1990. Wasp predation on orb web spiders (Araneidae) in Ghana. Acta Zoologica Fennica 190: 117-122.

EDMUNDS, M. 1974. 'Defence in animals: a survey of anti-predator defences'. (Longman: London). 357 pp.

1978. On the association between *Myrmarachne* spp. (Salticidae) and ants. Bulletin of the British Arachnological Society 4: 149-160.

GUILFORD, T. & DAWKINS, M.S. 1987. Search images not proven: a reappraisal of recent evidence. Animal Behaviour 35: 1838-1845.

1988a. Search image versus search rate: a reply to Lawrence. Animal Behaviour 37: 160-162.

1988b. Search image versus search rate: two different ways to enhance prey capture. Animal Behaviour 37: 163-165.

HINGSTON, R.W.G. 1927. Field observations on spider mimics. Proceedings of the Zoological Society of London 56: 841-858.

KREBS J.R. 1973. Behavioural aspects of predation. Pp. 73-111. In Bateson, P.P.G. and Klopfer, P.H. (eds) 'Perspectives in ethology. Vol. 1'. (Plenum Press: London).

LAWRENCE, E.S. & ALLEN, J.A. 1983. On the term 'search image'. Oikos 40: 313-314.

MATHEW, A.P. 1954. Observations on the habits of two spider mimics of the red ant, *Oecophylla smaragdina* (Fabr.). Journal of the Bombay Natural History Society 52: 249-263.

OLIVEIRA, P.S. 1988. Ant-mimicry in some Brazilian salticid and clubionid spiders (Araneae: Salticidae, Clubionidae). Biological Journal of the Linnean Society 33: 1-15.

OLIVEIRA, P.S. & SAZIMA I., 1984. The adaptive bases of ant-mimicry in a neotropical aphantochilid spider (Araneae: Aphantochilidae). Biological Journal of the Linnean Society 22: 145-155.

1985. Ant-hunting behaviour in spiders with emphasis on *Strophius nigricans* (Thomisidae). Bulletin of the British Arachnological Society 6: 309-312.

REISKIND, J. 1977. Ant-mimicry in Panamanian clubionid and salticid spiders (Araneae: Clubionidae, Salticidae). Biotropica 9: 1-8.

REISKIND, J. & LEVI, H.W. 1967. *Anatea*, an ant-mimicking theridiid spider from New Caledonia (Araneae: Theridiidae). Psyche 74: 20-23.

TINBERGEN, L. 1960. The natural control of insects in pine woods. I. Factors influencing the intensity of predation by songbirds. Archives Néerlandaises de Zoologie 13: 265-343.

TINBERGEN, N. 1958. 'Curious naturalists'. (Country Life: London). 280 pp.

WANLESS, F.R. 1978. A revision of the spider genera *Belippo* and *Myrmarachne* (Araneae: Salticidae) in the Ethiopian region. Bulletin of the British Museum (Natural History) (Zoology) 33: 1-139.

ABUNDANCE AND STRUCTURE OF FOSSORIAL SPIDER POPULATIONS

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Fairweather, P.G. 1993 11 11: Abundance and structure of fossorial spider populations. *Memoirs of the Queensland Museum* 33(2): 513-518. Brisbane. ISSN 0079-8835.

Preliminary findings from an ecological study of large fossorial spiders, especially mygalomorphs, made in two locations in eastern New South Wales are given. The abundance of burrowing spiders was assessed in eight habitats: dry sclerophyll forests on sandstone and shale substrata, wet sclerophyll forests on sandstone, pastures, suburban gardens, pine windbreaks along roadside verges, coastal cliffs, and coastal swamps. The spiders included several species of Lycosidae, two Idiopidae and one Hexathelidae. Each species was restricted in its range of habitats and dominated the burrowing spider assemblage in only one or two habitats. The population structure of burrow sizes is described and compared for dense populations.□*Araneae, Idiopidae, Hexathelidae, Lycosidae, ecology, burrowing, sampling, distributions, habitats, size frequencies.*

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The field ecology of burrowing spiders in Australia has rarely used quantitative methods (but see Humphreys, 1988). Nor were field experimental manipulations used to test specific hypotheses, as in other branches of ecology (Underwood, 1990). These first quantitative observations of the abundance, size structure and habitat associations of large burrowing spiders from two locations near Sydney are part of environmental studies of funnelweb and trapdoor spiders.

The abundance, distribution and ecological interactions of fossorial spiders have been studied overseas in detail (see e.g. Buchli, 1969; Laing, 1978; McQueen, 1983; Conley, 1985; Fernandez-Montraveta *et al.*, 1991; Miller & Miller, 1991). The general biology, systematics and evolution of Australian mygalomorph spiders have been studied (see Main, 1976; Raven, 1988). The few quantitative ecological studies from Australia focussed on arid habitats (e.g. Main, 1987; Kotzman, 1990), upland sites (e.g. Humphreys, 1976), or used pitfall trapping (e.g. Curry *et al.*, 1985). In contrast, this study was on the warm temperate coast of eastern Australia.

METHODS

Study Sites and Habitat Types

Two locations near Sydney, New South Wales, and situated on Hawkesbury sandstone substratum, were sampled. Galston (33°41'S, 150°21'E) is a semi-rural village that has become suburban since 1972 and retains pockets of bush. Study habitats were located at 170-210m altitude. Patonga (33°30'S, 151°15'E) is a coastal village on the Hawkesbury River estuary and surrounded by Brisbane Waters National Park (Benson & Fallding, 1981). Study habitats were located at 5-80m altitude. At each location, all sites were within 2km of each other. I sampled six habitats in each location, although only three were present in both locations (Table 1).

Sampling and Analysis of Data

The sampling, October 1991-March 1992, was non-destructive. Quadrats (0.25 m^2) were randomly placed and then searched for individual spiders, burrows and trapdoors. All rocks, logs and litter in each quadrat were overturned and searched. I counted spiders, burrows or webs of each species in each quadrat. I sampled 10 quadrats in each of two sites in each habitat at each location (n=240 quadrats in all). The paired sites were replicate patches of habitat at the same elevation, as similar as possible, at least 100m apart and 100-1000m^2 in area. Site boundaries were located randomly on habitat maps before sampling. Spatial variability in each habitat was assessed by comparing spider densities in each pair of sites.

This design allowed a three-factor hierarchical ANOVA to examine the partitioning of spider abundance (as density=no. per quadrat) among the fully nested factors of Location, Habitat within Locations and Site within Habitat (Sokal and Rohlf, 1981). ANOVAs were done after assumptions were checked using Cochran's test for heterogeneity of variances. Means and standard errors of spider densities were calculated for each habitat and site. All statistical and graphical analyses were performed with SYSTAT Version 5 software (Wilkinson, 1990).

Location	Habitat type	Trees	Shrubs	Ground layer	Litter	Common spider	Less common spiders
Galston	Wet sclerophyl forest (WSF)	dense	dense	dense, rocks	dense, moist	*Atrax*	wolf
	Dry sclerophyll forest (DSF)	sparse	dense	little, rocks	dense, dry	none	*M. rapax*, wolf
	Garden lawns (GL)	none	few	grass	none	none	*M. rapax*, wolf
	Shale turpentine forest (STF)	dense	few	grass, logs	sparse, moist	*Atrax*	wolf, *M. rapax*
	Pine road verge (PRV)	pines	few	some grass	deep, dry	*M. gracilis*	wolf *M. rapax*
	Pasture	none	none	grass	little	none	none
Patonga	Wet sclerophyll forest (WSF)	dense	dense	dense, rocks	dense, moist	none	wolf, *M. rapax*, *Atrax*
	Dry sclerophyll forest (DSF)	sparse	sparse	little, rocks	dense, dry	none	wolf
	Sea cliffs (SC)	few	few	some roots, rocks	sparse, moist	*M. gracilis*	wolf, *M. rapax*
	She-oak swamp (SS)	sparse	none	some	dense, moist	*M. rapax*	none
	Garden lawns (GL)	none	few	grass	little	none	*M. rapax*, wolf
	Sports ground	none	none	grass	none	none	none

KEY TO HABITATS

DSF: characteristic open woodland (Benson & Fallding 1981; Benson & Howell 1990) in exposed positions on Hawkesbury sandstone plateaux, dominated by *Angophora costata*, *Eucalyptus haemastoma*, *E. gummifera* and *E. sparsiflora*; understorey of sclerophyllous shrubs of Fabaceae, Proteaceae and Myrtaceae; litter layer dense but dry; sandy soil; many ant nests and sandstone outcrops.

WSF: in moist gullies and other sheltered locations; many of the same tree species in the canopy, also *E. piperita* and *E. eximia*; compared with DSF; shrubs and creepers more mesophyllic and denser, with pockets of smaller trees–*Pittosporum undulatum*, *Tristaniopsis laurina* and *Ceratopetalum apetalum*; litter layer dense, moist, compacted; ant nests fewer; soil with more humus but about the same amount of rocky outcrops.

GL: cultivated exotic grasses regularly mown to <4 cm high, and probably also treated with fertilisers, herbicides and pesticides; little bare ground and almost no litter.

PRV: pine trees (*Pinus radiata*) along road verges, rarely mown and graded; deep litter of pine needles; soil with humus-rich, dry layer above hard clay-loam; understorey some *Acacia* and *Pittosporum* shrubs, & grasses.

STF: open forest in Fagan Park on ridgetop Wianamatta shale (Benson & Howell 1990), dominated by turpentine, *Syncarpia glomulifera*; other trees included *E. punctata*, *E. paniculata*, *E. acmenioides*, *E. resinifera*, *E. globoidea* and *A. floribunda*; shrub layer mainly of young trees; ground cover of grasses, logs and sparse litter.

SS: estuarine swamp dominated by she-oaks, *Casuarina glauca*; ground layer of *Juncus kraussi*, she-oak needles and saltmarsh succulents; lowest areas inundated by highest tides, but areas around sandstone outcrops higher and drier. Bushfire burnt this habitat and dry sclerophyll forest early 1991.

SC: sea cliffs immediately above rock platforms in the estuary; vertical walls of loamy soil covered with sparse leaf litter, mosses; some creepers and grasses common around roots of trees and shrubs on cliff edge. The least extensive habitat in area; 10 m or less high along seashore.

At Galston, the last habitat was pasture grazed by horse and cattle. Grass height, 6-40 cm; grasses probably fertilised infrequently; patches of bare soil rare.

At Patonga, a lawn and bare ground area around a sporting ground was the last habitat, very similar to the pasture at Galston except grass mown regularly to <4 cm high.

TABLE 1. Habitat characteristics, with spiders and occurrence of rocks, logs or tree roots. Common spiders = density > 1 per m^2. Abbreviations used in text are also given for each habitat.

Species were identified by burrow characteristics and observations of spiders seen at the burrow entrances either at night or during late afternoons on overcast days. Initially, I excavated at least 30 burrows of each type to obtain specimens for more thorough identification, and to investigate burrow structures and food remains. I measured maximum diameter of all burrows in quadrats (and outside them at some sites to increase sample sizes to >30). I tested for differences among size frequency distributions of burrow diameters using Kolmogorov-Smirnov (KS) 2-sample tests.

Sampling was repeated in late summer (Feb.-March) in some habitats to assess temporal variation between, before, and after the breeding season (roughly mid-sampling). In particular, abandoned burrows (with signs of decay and unoccupied) were noted. Burrows under rocks and logs were counted in some habitats because funnelwebs seemed restricted to such locations (e.g. short burrows in unconsolidated soils).

RESULTS

SPIDER SPECIES

Six species in three families are here grouped into four ecological types. *Misgolas gracilis*

(Rainbow & Pulleine, 1918) is a large idiopid that builds deep, oblique burrows with a trapdoor among leaf litter in friable soils. The lids varied from flimsy and merely silk-covered with a thin layer of dirt to quite robust plugs for older spiders; this may be related also to the amount of litter present. In moist areas, the lid often grew moss and liverworts. *M. gracilis* was found only in SC and PRV habitats (Table 1).

Misgolas rapax Karsch, 1878 is also large with a burrow like *M. gracilis* but without a trapdoor. Often litter and vegetation around the burrow entrance were incorporated into the flared opening. Their burrows were more vertical than those of *M. gracilis*. The idiopids were identified using Main (1985), Mascord (1970, 1980). *M. rapax* was found in eight habitats but abundantly only in SS (Table 1).

Atrax robustus Cambridge, 1877 is the Sydney funnelweb spider (Hexathelidae). Several similar species are known from areas near the study locations, but all spiders collected were identified as *A. robustus* using Gray (1988), Scott (1980), Main (1985), Mascord (1970, 1980) (some smaller spiders were minimally confamilial). Most spiders were found under rocks and logs where characteristic silk tubes led to shallow burrows made in mostly unconsolidated soils and humus. Thus, all spiders were examined in the field but collections were limited to avoid depletion of the populations and for safety. *Atrax* was found in only two habitats but was a dominant in both (Table 1).

Wolf spiders (Lycosidae) built narrow, vertical burrows without lids and with much flimsier silk linings than did *M. rapax*. They were identified using McKay (1985) and references therein. The species excavated were *Lycosa godeffroyi* L. Koch, 1865, *L. leuckartii* (Thorell, 1870) and *Pardosa serrata* (L. Koch, 1877), the latter with characteristic palisades around the burrow. Other species but not excavated include *L. furcillata* L. Koch, 1867, *L. pictiventris* L. Koch, 1877, and *L. palabunda* L. Koch, 1877. Due to this uncertainty over the exact identity of the occupants of some burrows, I lumped data on all lycosid burrows into 'wolf spiders'. I found these in nine habitats but most commonly in WSF (at Patonga only) and PRV (Table 1).

ABUNDANCES

No spiders or burrows were found in quadrats sampled in the pastures or sports ground (Table 1, Fig. 1), although lycosids had been seen there. Neither habitat will be discussed further. Very sparse populations (of only lycosids and *M. rapax*) were found in open habitats–DSF and GL.

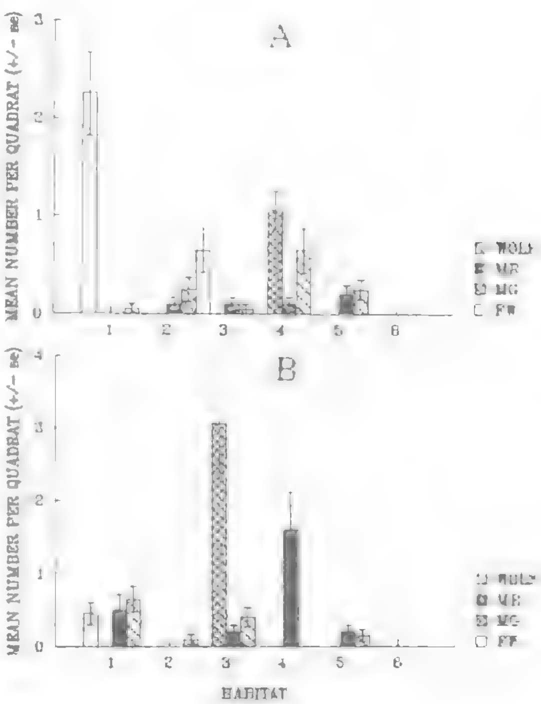

FIG. 1. Abundance (no. per $0.25m^2$) of each species group versus habitat. A, at Galston, habitats are: 1=WSF, 2=DSF, 3=STF, 4=PRV, 5=GL, 6=pasture; B, at Patonga, habitats are: 1=WSF, 2=DSF, 3=SC, 4=SS, 5=GL, 6=sport ground. MR=*M. rapax*, MG=*M. gracilis*, FW= *Atrax* and WOLF=lycosids. Means and standard errors calculated from n = 20 quadrats in each habitat (i.e. sites were pooled).

The abundance in the five occupied habitats at each location showed differences between habitats and species groups. An ANOVA of total spider density among locations/habitats/ sites (Table 2) showed no significant difference between the locations but large differences among the habitats within locations. At Galston, highest spider densities were found in PRV and WSF habitats, fewer in STF and very few in GL and DSF habitats. At Patonga, SC had the greatest densities, followed by WSF and SS habitats, and very few in the GL and DSF habitats.

Habitats with dense spider populations in either location were dominated by a particular species. At Galston, *Atrax* was the most common spider in the WSF and STF habitats but was not found in other habitats. At Patonga, *Atrax* was found only in the WSF habitat. *M. rapax* occurred in four habitats at Patonga and Galston, but

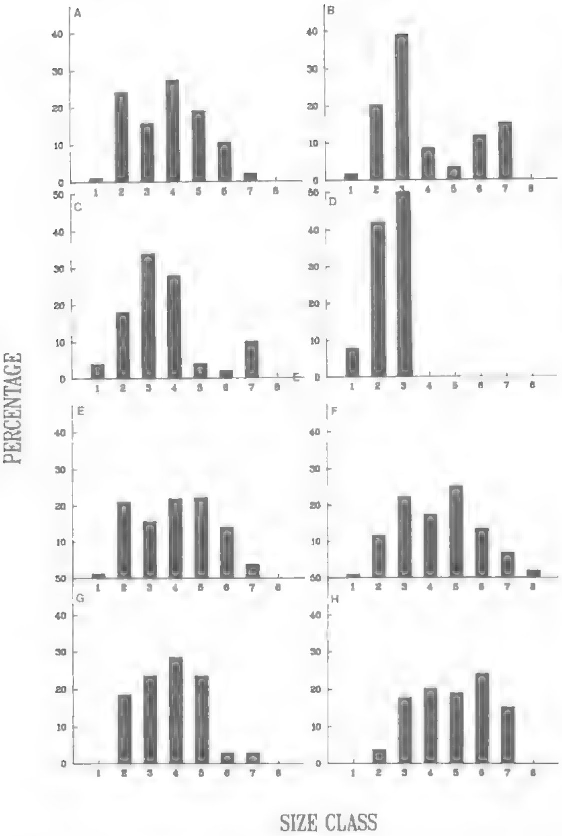

FIG. 2. Representative size frequency distributions of burrow diameter for dense populations of each species. Diameters grouped into eight equal size classes (to show large range with reasonable numbers in each): 1 =0-4.9mm; 2 =5-9.9; 3 =10-14.9; 4 =15-19.9; 5 = 20-24.9; 6 = 25-29.9; 7 = 30-34.9; and 8 ⩾ 35mm across the burrow entrance. A) *Atrax* from WSF, Galston, $n = 95$; B) *Atrax* from STF, Galston, $n = 59$; C) *Atrax* from WSF, Patonga, $n = 50$; D) lycosids from PRV, Galston, $n = 38$; E) *M. gracilis* from SC, Patonga, $n = 189$; F) *M. gracilis* from PRV, Galston, $n = 83$; G) *M. rapax* from SS, Patonga, $n = 102$; H) *M. rapax* from GL, Galston, $n = 79$.

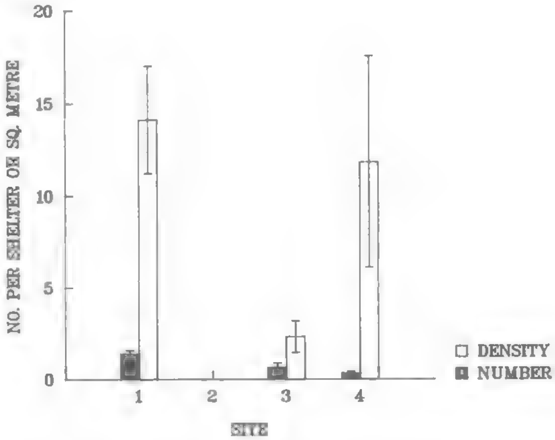

FIG. 3. Abundance of *Atrax* under rocks and logs in some habitats, expressed as no. per rock or log, and density (no. per m^2 of rock or log microhabitat). Area of each rock and log estimated from product of two, perpendicular linear dimensions in contact with the ground. Sites (sample sizes) were: 1=WSF at Galston (n = 43 rocks); 2=DSF at Galston (n=27 rocks); 3=STF at Galston (n =20 logs); and 4=WSF at Patonga (n=18 rocks).

dominated only in the SS habitat. *M. gracilis*, in contrast, was found in only one habitat in each location, but dominated the spider assemblage in both. In the SC habitat at Patonga, this species had the greatest mean density found in this sampling (>12 m^{-2}). Lycosids were found in five habitats at Galston and four at Patonga but they were never dominant. No species group was either positively or negatively correlated with any other in these samples (for all r, $P > 0.05$, $n = 200$).

The patchiness of mean spider abundance in any habitat was examined by the Sites within Habitat factor in the nested ANOVA (see Sokal and Rohlf, 1981). For total spider density and *M. rapax* alone, the two sites sampled within each habitat differed significantly (Table 2) . Because the sites were chosen randomly from the total habitat, this result indicates medium-scale variability in abundance of total spiders and *M. rapax* (i.e. at scales of about 100m).

Size Frequencies

Sample sizes of burrow diameter of sufficient number could be obtained only in habitats with dense populations. The burrow size structure (Fig. 2) of these populations showed differences (by KS tests) among species that were consistent across habitats. Very small burrows (< 5mm) were not found for *M. rapax* and only commonly for lycosids. *Atrax* showed bimodality in two habitats with the modes occurring at sizes corresponding to pre-reproductive juveniles and mature females (Fairweather, unpublished data). The other species had more unimodal burrow diameter frequency distributions. Lycosid burrows were much narrower on average than the mygalomorphs (Fig. 2). *M. gracilis* had the largest burrows overall.

Temporal Variation

Sampling before and after the breeding season showed few changes. The proportion of burrows of *M. gracilis* in the PRV habitat (Galston) that were abandoned and decaying increased from 4.6% (n= 64) in December to 9.6% (n = 60) in March. These abandoned burrows did not, however, differ in size from the occupied ones (P> 0.05 by KS tests), suggesting no size selectivity in either mortality or abandonment by breeding males. The proportion of *Atrax* that were juvenile (i.e. <15mm and with no enlarged pedipalps on males) increased from November to February from 12% (n = 67) to 44% (n = 84) across all three occupied habitats.

MICROHABITATS

Within each habitat, burrows were found more frequently in particular situations. For example, *M. rapax* in the SS habitat (Patonga) were only found in areas around rock outcrops and none in the lower, inundated part of the swamp. *M. gracilis* was most abundant in moist, mossy patches in SC habitat (Patonga) and in areas covered with litter rather than bare ground in the PRV habitat (Galston). All *Atrax* webs encountered were seen under or against either rocks or logs, although thorough searches were also made amongst litter and in grass clumps. This prompted sampling centred on rocks or logs in three habitats at Galston and one at Patonga (Fig. 3). The abundance of *Atrax* under rocks and logs differed with habitats. None were found in DSF, despite abundant rocks. Counts of webs per rock or log were similar in the three occupied habitats. When expressed on a per area basis (i.e. m^2 of rock or log), the densities were much greater and differed among these habitats (Fig. 3).

DISCUSSION

This study suggests several hypotheses.

1. These species rarely encounter each other in nature, suggesting little competition occurs among them. I located each species group in more than one habitat, but they tended to dominate different ones. *Atrax* were favoured by apparently more moist conditions under shelter; although exfoliated rocks were abundant in the drier DSF habitat, no *Atrax* were found beneath them. *M. gracilis* was found in relatively exposed positions (sea cliff and road verge) with the most compact soil, whereas *M. rapax* dominated more open habitats (in terms of the litter and ground layers). Lycosids were the most widespread group, which may reflect that data of several species were lumped. Characterisation of habitats regarding soil, litter and vegetation conditions is needed.

2. Specific habitat characteristics favour different species. As well as the above habitat segregation, microhabitat preferences were also shown by several groups, most strikingly for *Atrax*, which was found in moist areas under shelter. Predictive relationships of abundance with environmental variables (e.g. soil nutrients, organic matter, compaction and moisture; litter amount, moisture and temperature; size and depth of shelter) may be established. Experiments on the effects of shelter, litter and moisture conditions on the abundance of these spiders are needed.

Factor	df	F-ratios				
		All spiders	*Atrax*	*M. gracilis*	*M rapax*	Wolf
Location	1	0.19	1.21	0.38	1.93	0.003
Habitat	8	3.34*	73.43*	8.93	0.88	[illegible]*
Site	10	[illegible]	0.25	[illegible]	9.54*	0.31

TABLE 2. Three-factor, hierarchical ANOVA of density (number per quadrat) of total spiders and each species group analysed separately. *=Significance at P <0.05 level; df, degrees of freedom; df for residual, 180, and for total, 199. Total N=200 0.25 m2 quadrats; only five habitats used here.

3. Fossorial spiders respond adversely to many human impacts on their environments. This has implications for the interaction of these spiders with people and their activities. Few or no fossorial spiders were resident in habitats that lacked a litter layer or were regularly mown, watered, treated with chemicals or graded. The spiders can burrow in such open habitats (Fairweather pers. obs.), so perhaps the conditions may not be attractive to prey. There is some longer term evidence of declines in two of these populations associated with increasing urbanisation, direct disturbance, bushfire and vegetative change (Fairweather unpub. data).

4. Dense populations have been established for several years, at least. Size frequency distributions of burrows revealed juveniles in each dense population, therefore recruitment had occurred and no population was relict. Several very large burrows were present in the populations of the three mygalomorphs, probably indicating matriarchs (*sensu* Main, 1987). The abundance and size structure did not alter from October to March, which implies short-term stability for these long-lived spiders. Behaviour consistent with breeding behaviour over summer was seen for the mygalomorphs. Lycosids with egg sacs were seen only in spring and autumn.

5. Predation by some populations may strongly influence the assemblages of their prey. *M gracilis* and *Atrax* were quite dense in particular microhabitats, with some very large spiders; this and their predatory habits suggest that their role as predators in the ground-layer ecosystem would be worth further study.

In conclusion, large fossorial spiders are not evenly distributed across a variety of habitats, and each habitat is dominated in numerical terms by one or few species. Although the study was done in two contrasting locations, the generality of these results awaits scrutiny with further data as does the cause of any of the patterns described for the first time here.

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LITERATURE CITED

BENSON, D. & HOWELL, J. 1990. 'Taken for granted: the bushland of Sydney and its suburbs'. (Kangaroo Press: Sydney).

BENSON, J.S. & FALLDING, H. 1981. Vegetation survey of Brisbane Water National Park and environs. Cunninghamia 1: 79-113.

BUCHLI, H.H.R. 1969. Hunting behavior in the Ctenizidae. American Zoologist 9: 175-193.

CONLEY, M.R. 1985. Predation versus resource limitation in survival of adult burrowing wolf spiders (Araneae: Lycosidae). Oecologia 67: 71-75.

CURRY, S.J., HUMPHREYS, W.F., KOCH, L.E. & MAIN, B.Y. 1985. Changes in arachnid communities resulting from forestry practices in karri forest, south-west Western Australia. Australian Forest Research 15: 469-480.

FERNANDEZ-MONTRAVETA, C., LAHOZ-BELTRA, R. & ORTEGA, J. 1991. Spatial distribution of *Lycosa tarentula fasciiventris* (Araneae, Lycosidae) in a population from central Spain. Journal of Arachnology 19: 73-79.

GRAY, M.R. 1988. Aspects of the systematics of the Australian funnel web spiders (Araneae: Hexathelidae: Atracinae) based upon morphological and electrophoretic data. Pp. 113-125. In Austin, A.D. and Heather, N.W. (eds) 'Australian Arachnology'. (Australian Entomological Society Miscellaneous Publication No. 5: Brisbane).

HUMPHREYS, W.F. 1976. The population dynamics of an Australian wolf spider, *Geolycosa godeffroyi* (L. Koch 1865) (Araneae: Lycosidae). Journal of Animal Ecology 45: 59-80.

1988. The ecology of spiders with special reference to Australia. Pp. 1-22. In: Austin, A.D. and Heather, N.W. (eds). 'Australian Arachnology'. (Australian Entomological Society Miscellaneous Publication No. 5: Brisbane).

KOTZMAN, M. 1990. Annual activity patterns of the Australian tarantula *Selenocosmia stirlingi* (Araneae, Theraphosidae) in an arid area. Journal of Arachnology 18: 123-130.

LAING, D.J. 1978. Studies on populations of the tunnel web spider *Porrothele antipodiana*. Tuatara 23: 67-81.

MAIN, B.Y. 1976. 'Spiders'. (Collins: Sydney).

1985. Arachnida: Mygalomorphae. Pp. 1-48. In Walton, D.W. (ed.) 'Zoological Catalogue of Australia Vol. 3'. (Australian Government Publishing Service: Canberra).

1987. Persistence of invertebrates in small areas: case studies of trapdoor spiders in Western Australia. Pp. 29-39. In Saunders, D.A., Arnold, G.W., Burbridge A.A. and Hopkins, A.J.M. (eds) 'Nature conservation: the role of remnants of native vegetation'. (Surrey Beatty & Sons: Sydney).

MASCORD, R. 1970. 'Australian spiders in colour'. (Reed: Sydney).

1980. 'Spiders of Australia: a field guide'. (Reed: Sydney).

MCKAY, R.J. 1985. Arachnida: Araneomorphae: Lycosidae. Pp. 73-88. In Walton, D.W. (ed.) 'Zoological Catalogue of Australia Vol. 3'. (Australian Government Publishing Service: Canberra).

MCQUEEN, D.J. 1983. Mortality patterns for a population of burrowing wolf spiders, *Geolycosa domifex* (Hancock), living in southern Ontario. Canadian Journal of Zoology 61: 2758-2767.

MILLER, P.R. & MILLER, G.L. 1991. Dispersal and survivorship in a population of *Geolycosa turricola* (Araneae, Lycosidae). Journal of Arachnology 19: 49-54.

RAVEN, R.J. 1988. The current status of Australian spider systematics. Pp. 37-47 In Austin, A.D. and Heather, N.W. (eds) 'Australian Arachnology'. (Australian Entomological Society Miscellaneous Publication No. 5: Brisbane).

SCOTT, G. 1980. 'The funnelweb' (Darling Downs Institute: Toowoomba).

SOKAL, R.R. & ROHLF, F.J. 1981. 'Biometry'. (Freeman: New York).

UNDERWOOD, A.J. 1990. Experiments in ecology and management: their logics, functions and interpretations. Australian Journal of Ecology 15: 365-389.

WILKINSON, L. 1990. 'SYSTAT: the system for statistics'. (SYSTAT: Evanston).

BIOGEOGRAPHIC PATTERN OF PHYLOGENY IN A CLADE OF ENDEMIC HAWAIIAN SPIDERS (ARANEAE, TETRAGNATHIDAE)

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The biota of the Hawaiian archipelago offers an ideal system with which to study the dynamics behind the evolutionary process, both because the islands harbour many speciose lineages, and because they are arranged within a chronological time frame. Over the past 5 years I have begun to uncover an unexplored radiation of one of Hawaii's most abundant and conspicuous invertebrate groups: the spider genus *Tetragnatha*. The current study focuses on a small clade within the lineage, in which all the component species have abandoned web-building, instead foraging as cursorial predators. I examine 2 primary questions: 1. What has been the relative importance of strict geographic isolation (populations on different volcanoes) versus divergence between contiguous habitats (populations on the same volcano) in the evolution of this clade? 2. Does the phylogeny indicate a pattern of ecological and distributional change which could suggest that ecological rather than sexual shifts may underlie species formation? I generated a phylogeny based on morphological characters, and compared this phylogeny to the biogeographic pattern of the Hawaiian Islands. The results suggest that, for this clade of cursorial species, speciation requires strict geographic isolation, and ecological (more than sexual) shifts appear to play a role in initiating divergence. Considering the islands as a series of evolutionary snapshots, I would also speculate that speciation is commencing on the youngest island (Hawaii), and developing on the adjacent older island of Maui. □*Tetragnatha, phylogeny, Hawaii, speciation, allopatry.*

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Species represent one of the basic units of evolution, yet the processes by which they are formed remain poorly understood (Mayr, 1963). Studies of the Hawaiian biota have lent considerable insight into the mechanisms underlying speciation. These studies are highlighted by the Hawaiian *Drosophila*, in which sexual selection through female choice appears to play an integral role in inducing species formation among small populations colonizing geographically isolated islands (Carson, 1968; Carson and Kaneshiro, 1976; Kaneshiro, 1988). One may ask whether it is possible to generalize from these studies that adjustments in the sexual environment are largely responsible for driving species radiations. Other studies outside the Hawaiian Islands have found that ecological changes in isolation are more important in driving species proliferation (Mayr, 1963; Grant, 1986). When a species is released from interaction with related species, by whatever means, it may broaden its habitat use and exhibit much more variation among individuals (Lack, 1971; McCune, 1990). The argument is that if such a reproductively isolated incipient species were reunited with its parent, selection could act on the ecological variability to minimize the resources jointly used by both species, leading to further ecological divergence (Mayr, 1963; Grant, 1986).

The Hawaiian archipelago (Fig. 1) provides a natural laboratory for studies of speciation (Simon, 1987). First, the extreme isolation of the islands has allowed repeated and explosive diversification of species in a large number of lineages including honeycreepers (Berger, 1981; Freed et al., 1987), land snails (Cooke *et al.*, 1960), crickets (Otte, 1989) and drosophilid flies (Kaneshiro and Boake, 1987). Further, the islands are a series of volcanoes arranged within an identifiable chronological time frame; the currently high islands range from Kauai, the oldest and most eroded, to Hawaii, the youngest, highest and largest, with 5 separate volcanoes.

This study uses a lineage of spiders to examine speciation patterns within the context of the Hawaiian archipelago. The spiders belong to the long-jawed orb-weaving genus *Tetragnatha*, which comprises a large number of endemic species in the Hawaiian Islands (Gillespie, 1991, 1992). Outside the archipelago, *Tetragnatha* are among the most widespread and conspicuous spiders worldwide, yet collectively they are also

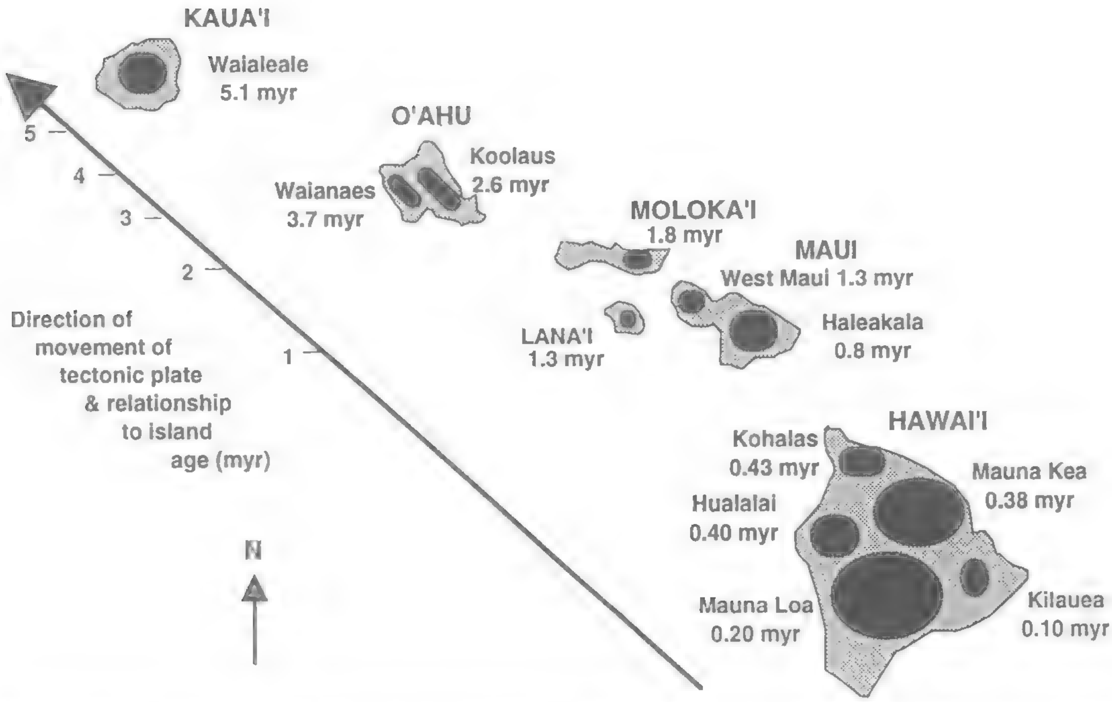

FIG. 1. Major land masses of the Hawaiian archipelago, indicating approximate age, and direction of movement of tectonic plate.

one of the most homogeneous, both in morphology (elongate bodies and long legs) and ecology (orb web generally built over or near water) (Wiehle, 1963; Levi, 1981; Gillespie, 1986, 1987). Hawaiian species of *Tetragnatha* represent a paradox, exhibiting considerable morphological and ecological diversity. Until 1992, the sole reference to endemic Hawaiian representatives of the genus was based on descriptions of a single species by Karsch (1880) and 8 species by Simon (1900, redescribed by Okuma, 1988). I have now described an additional 16 species (Gillespie, 1991, 1992), and have collected more than 60 new taxa that span a broad spectrum of colours, shapes, sizes, ecological affinities, and behaviours. In terms of courtship behaviour, however, Hawaiian representatives of the genus display the simple cheliceral locking mechanism characteristic of the genus (Levi, 1981; Gillespie, pers. obs.).

Here I examine a small clade (the 'spiny-leg' clade) within the radiation of Hawaiian *Tetragnatha*. Representatives of this clade are characterized by a cursorial habit, and do not build webs (Gillespie, 1991). Further, in common with other representatives of the genus (Levi, 1981), but in striking contrast to the *Drosophila* radiation, these spiders display minimal courtship behaviour. Because explanations for species formation in the Hawaiian *Drosophila* rely heavily on the elaborate courtship behaviour of the group, the absence of such behaviour in the Hawaiian *Tetragnatha* suggests that alternative explanations might be required to account for species proliferation. The questions I address in this study are: 1. What has been the relative importance of strict geographic isolation (taxa diverge on different volcanoes) versus divergence between contiguous habitats (taxa diverge on the same volcano) in the evolution of the spiny-leg clade of Hawaiian *Tetragnatha*? I generated a phylogeny for the clade based on morphological characters, and then compared the phylogeny to the biogeographic pattern and history of the islands. 2. Does the phylogeny indicate a pattern of ecological and distributional change which could suggest that ecological rather than sexual shifts may underlie species formation?

METHODS

Collection and Ecological Measurements

Spiders were collected by visual night searching at various times of the year between 1987 and 1991 in wet, mesic and dry native forest in all of the currently high Hawaiian Islands (Kauai, Oahu, Molokai, Lanai, Maui and Hawaii; Fig. 1). Habitats from which spiders were taken were scored as wet (>450cm average annual rainfall), mesic (250-450cm) or dry (<250 cm). Elevation was categorized as low (<1000 m), medium-low (1000-1700m), medium-high (1700-2000m) and high (>2000m). Microhabitat associations were determined by categorizing the specific site from which an individual was collected (roots, fern fronds, against bark, etc.) (Gillespie, 1987).

Phylogenetic Analysis

I used a cladistic approach (Hennig, 1966) based on morphological characters to determine relationships among the spiny-leg clade of Hawaiian *Tetragnatha*. I scored a total of 30 characters relating to cheliceral armature (upper and lower tooth rows), leg spination, and colour of the cephalothorax and abdomen (Table 1). In addition, I scored characters from the detailed structure of the male palp using a Hitachi S-800 scanning electron microscope. I used a Hawaiian web-building species of *Tetragnatha*, *T. stelarobusta* Gillespie as an outgroup in the analysis because molecular data indicate that this species belongs to a closely related sister clade of the spiny-leg species (H.B. Croom, pers. comm.).

Characters were analyzed as unordered states (i.e., any character state permitted to transform directly into any other state) using Fitch (Fitch, 1971) and Wagner (Farris, 1970) parsimony in PAUP (Swofford, 1990) under the accelerated transformation method of optimization. Character states were polarized as primitive or derived by outgroup comparison (Maddison *et al.*, 1984), and characters were scaled for equal character weighting regardless of the number of states. A branch-and-bound search was conducted to find the shortest tree. The data were then reanalyzed by successive approximations, weighting characters according to their rescaled consistency index (Farris, 1969, 1989).

Relationship between Species Phylogeny and Island Biogeography

To test the importance of strict geographic isolation in initiating divergence, and the extent to which regular ecological and distributional changes have accompanied species formation, I compared the resulting phylogeny to the biogeographic locations of the component taxa within the Hawaiian archipelago.

RESULTS

Collection and Ecological Measurements

Representatives of the spiny-leg clade of Hawaiian *Tetragnatha* occur on each of the high islands. All are restricted to wet forest except for *T. brevignatha* Gillespie, *T. restricta* Simon and *T. quasimodo* Gillespie, which occur in wet, mesic, and sometimes dry, forest. The ranges over which the different species were found is listed in table 2. Microhabitat associations were loose, although the bright green species (*T. tantalus* Gillespie, *T. polychromata* Gillespie, *T. brevignatha*, *T. macracantha* Gillespie, *T. waikamoi* Gillespie and *T. kauaiensis*) were collected almost entirely from leaves, whereas the darker coloured *T. kamakou* Gillespie, *T. perreirai* Gillespie, *T. pilosa* Gillespie, *T. quasimodo* and *T. restricta* were collected from brown or red-brown substrates.

Phylogenetic Analysis

When characters were scaled for equal weighting regardless of number of states and unordered, a total of 7 most parsimonious trees were generated (consistency index 0.517, retention index 0.509). Subsequent weighting by successive approximations had little effect on the tree topology, and gave a single tree of unweighted length 76 (consistency index 0.725, retention index 0.765). Fig. 2 shows the tree with explanations of the characters defining each node. The characters defining species are marked as bars.

Relationship between Species Phylogeny and Island Biogeography

As can be seen from this phylogeny based on morphological characters (Fig. 2), the most closely related species are never found on the same island. The only regular pattern of ecological and distributional change through the Hawaiian Islands is the broadening habitat usage on the younger islands. In particular, taxa on the oldest islands (Kauai and Oahu) are all endemic to single volcanoes, while on the youngest island, Hawaii, there are no species endemic to the island, despite its much larger size (5 volcanoes). In addition, taxa on the youngest island occupy a much broader range of habitat types: *T. brevignatha*, for example, is found at all elevations and in dry, mesic and wet forest on Hawaii Island, whereas representatives of this species on East Maui occur only in mesic forest at middle elevations. Distributions of representatives of the clade on East Maui show some anomalies. In particular,

		stel	kau	pil	mac	pol	tant	wak	brev	perr	kam	rest	quas
1	♀ first tooth: tiny/moderate size/as large as others	1	1	1	1	1	1	2	1	1	1	1	0
2	♂ first tooth: absent /bump/finger	2	2	2	0	1	1	2	0	2	2	2	2
3	♂ 'sl' (first tooth down margin): bent up/straight/bent down	1	1	1	1	1	0	1	0	1	1	1	2
4	♂ 'sl' close to 'T' (second tooth down margin)?	0	0	0	0	0	0	0	0	0	1	1	1
5	♂ apical tooth (lower chelicera) present?	1	1	0	0	0	1	1	0	1	0	0	0
6	No. large teeth on lower margin ♂ chelicera: 1/ 2	0	1	0	1	1	1	1	0	1	1	0	1
7	♂ lower tooth row: short/ long	1	1	0	1	1	1	1	0	0	1	0	1
8	♂ teeth 3 and 4 on lower margin much smaller than rest?	1	1	1	0	1	1	1	1	0	1	1	1
9	♂ teeth 5 onwards larger than 3 and 4?	1	1	1	0	1	1	1	1	1	1	1	1
10	♂ first two teeth well separated?	1	0	1	1	1	1	0	0	0	0	0	0
11	Curl on terminal projection, conductor: none/ slight/ complete	0	1	1	1	0	2	2	1	1	1	2	0
12	Terminal projection of conductor points: straight/ backward/ forward	0	2	2	2	0	2	2	2	2	2	2	1
13	Cap of conductor tip: shallow/ deep	0	0	1	1	0	0	0	0	1	1	1	0
14	Cap ridge of conductor tip: lateral/ medial	0	0	0	0	0	1	1	0	1	0	0	0
15	Backward projection of conductor tip: above/ at same level/ below cap	0	0	0	1	1	0	0	0	1	1	1	1
16	Spur of conductor tip: indistinct/ prominant	0	1	1	1	1	1	1	1	1	1	1	1
17	Spur of conductor tip: angled up/ straight out/ hooked down	1	2	0	2	1	1	1	0	1	2	0	0
18	Floor and spur base of conductor tip: at same level/ separated	0	0	0	1	1	0	0	0	1	1	1	1
19	Separation of conductor cap and pleats: large/ small	1	0	0	0	0	0	0	0	0	0	0	0
20	Cap of conductor: wide/ medium/ high	0	0	0	2	0	0	0	0	1	2	2	0
21	Cap of conductor: rounded/ pointed right/ flat	0	0	2	0	0	1	1	2	0	0	0	2
22	Tip of conductor twists to show underside?	0	1	1	1	1	1	1	1	1	1	1	1
23	Venter color: translucent/ dark	1	0	1	0	0	0	0	0	1	1	1	1
24	Venter pattern: plain/ median bar/ paired spots.	1	1	2	1	1	1	1	0	0	0	1	1
25	Sternum color: translucent/ opaque	1	0	1	0	0	0	0	0	1	0	1	1
26	Orb webs built?	0	1	1	1	1	1	1	1	1	1	1	1
27	Tip of ♂ conductor projection: blunt/ pointed	0	0	0	0	1	1	1	1	1	1	1	1
28	Seminal receptacles: no swelling/swelling angled down/ angled up	0	2	0	2	0	2	2	2	1	1	2	2
29	Dorsum color: brown/ variable/ green	0	1	0	2	2	2	2	2	0	0	0	0
30	Tibial spines (lateral,medial, dorsal): 332/ 442/ 552	0	1	2	2	1	2	1	2	0	0	0	1

TABLE 1. Characters used for generating phylogeny. stel = *T. stelarobusta*; kau = *T. kauaiensis*; pil = *T. pilosa*; mac = *T. macracantha*; pol = *T. polychromata*; tant = *T. tantalus*; wak = *T. waikamoi*; brev = *T. brevignatha*; perr = *T. perreirai*; kam = *T. kamakou*; rest = *T. restricta*; quas = *T. quasimodo*.

there are three bright green species, one endemic to this volcano (*T. macracantha*), one shared with West Maui (*T. waikamoi*) and *T. brevignatha* shared with Hawaii Island. The East Maui species exhibit parapatric ranges, with only very narrow zones of overlap, and are more closely related to species on other islands rather than to each other.

DISCUSSION

Differentiation between species of the spiny-leg clade of Hawaiian *Tetragnatha* appears never to have occurred on the same mountain mass: in no situation are two sister species found on the same volcano, or even on the same island. This phylogeny based on morphological characters therefore strongly suggests that strict geographic isolation (between islands only) is necessary for the initiation of species formation. Such isolation appears also to underlie speciation events in the Hawaiian *Drosophila* (Carson and Templeton, 1984). The phylogeny of the Hawaiian spiny-leg *Tetragnatha* also indicates that species colonize in a generally southerly direction, with the most ancestral taxa occupying the oldest island, Kauai. In addition, colonization of the most recent island (Hawaii) may be associated with ecological release: populations of each of the three species that have colonized Hawaii Island, *T. quasimodo*, *T. restricta* and *T. brevignatha*, occupy a broad

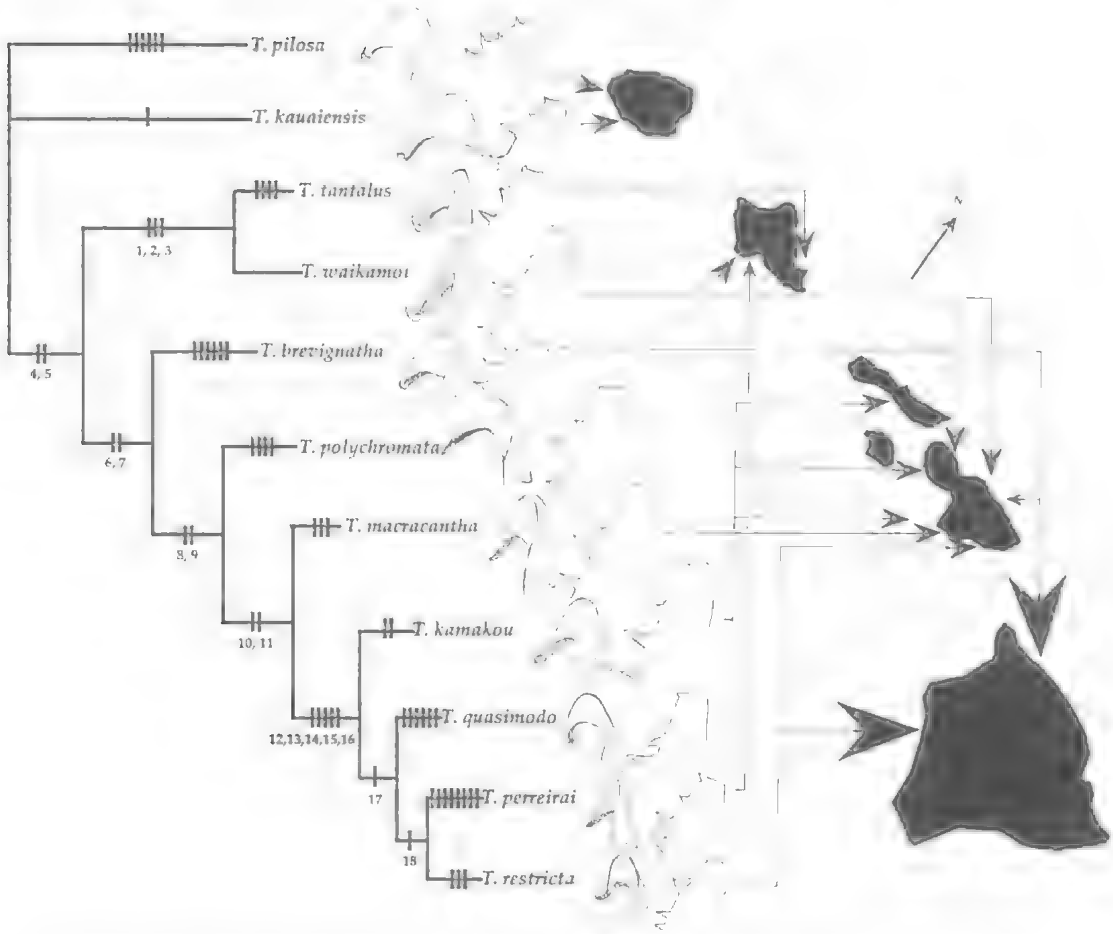

FIG. 2. Phylogeny of the Hawaiian spiny-leg *Tetragnatha* based on morphological characters. Explanations are given for characters defining each node; characters defining species are marked as bars. Sketches of the tip of the male conductor (left) and the upper surface of the apical portion of the male chelicera (right) are included for ease of comparison. Arrows point to the location of a species in the archipelago, with the size of an arrow tip being approximately proportional to the size of the distribution of a given species. Character changes defining each node are as follows. **1**, Conductor terminal projection: short->long. **2**, Conductor cap ridge: lateral->medial. **3**, Conductor cap: rounded->pointed. **4**, Conductor cap tip: blunt->pointed. **5**, Colour: brown/variable->green. **6**, First upper cheliceral tooth lost. **7**, First lower cheliceral tooth lost. **8**, First 2 lower margin cheliceral teeth-> well separated. **9**, Conductor backward projection at level-> below cap. **10**, Conductor cap: low->high. **11**, Backward projection conductor spur->angled down. **12**, Venter: pale->dark. **13**, Abdomen colour: green->brown. **14**, First dorsal cheliceral tooth->finger. **15**, Cheliceral 'sl' tooth-> closer to 'T'. **16**, First 2 lower cheliceral teeth-> closer. **17**, Conductor backward projection hooked up-> angled down. **18**, Lower tooth row long-> short.

range of habitat types. In particular, *T. brevignatha* is found in almost every habitat type on Hawaii Island, whereas representatives of the species on East Maui are confined to a narrow band of mesic forest at middle elevation.

There are some distinct differences between the pattern of phylogeny I have generated here for the Hawaiian *Tetragnatha* and patterns suggested for the Hawaiian *Drosophila*. The Hawaiian *Drosophila* generally demonstrate single volcano endemism, one species having its closest relatives on an adjacent volcano. In contrast, the phylogeny I have generated for the spiny-leg species of Hawaiian *Tetragnatha* suggests a non-uniform and disjunct pattern. Possible explanations for the *Tetragnatha* pattern may best be

ISLAND	HAWAII											MAUI						MO	LA	OAHU			KA
VOLCANO	Mauna Loa							M. Kea		Kh	Hu	W	Haleakala					Ka	La	Wainaes		Ko	Wai
	S	W	W	E	E	Saddle		E	E				N	N	E	E	W						
Elevation	1-2	0-1	1-2	0-1	1-2	0-1	1-2	0-1	1-2	1-2	1-2	1-2	0-1	1-2	0-1	1-2	1-2	1-2	1-2	0-1	1-2	0-1	1-2
tantalus																						X	
polychromata																				X	X		
brevignatha		X	X		X		X	X	X	X	X			X									
macracantha													X		X	X							
waikamoi												X		X	X	X							
kauiensis																							X
kamakou												X		X		X							
perreirai																					X		
pilosa																							X
quasimodo	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X		X	X	X			

TABLE 2. *Tetragnatha* species collected at different sites (islands, volcanoes and elevations, x 100m) through the Hawaiian Islands. Islands: MO= Molokai; LA= Lanai; KA= Kaui. Volcanoes: M. Kea= Mauna Kea;Kh= Kohala; Hu = Hualalai; W= W. Maui; Ka= Kamakou; La= Lanaihale; Ko= Koolaus; Wai = Waialeale.

considered by viewing the Hawaiian archipelago as a series of evolutionary snapshots, with speciation starting on Hawaii Island and developing on East Maui. The three species on the recently formed Hawaii Island are likely to be relatively recent colonists that have expanded their range and habitat use. Such ecological release subsequent to colonization is considered an important step in initiating species divergence in Galapagos finches (Grant, 1986). However, the widespread species on Hawaii Island are remarkably homogeneous, and none are endemic to the island. It may be that Hawaii Island is too young for speciation to have occurred in the spiny-leg Hawaiian *Tetragnatha*. The situation suggests that considerable movement of individuals occurs within the island, and gene flow between islands has been sufficient to prevent speciation during the period of existence of Hawaii Island.

The adjacent older volcano of East Maui was once part of the island complex, 'Maui Nui' (comprising Molokai, Lanai, East and West Maui). This island was likely first invaded by *T. tantalus*. Males may be better colonists than females (Bishop, 1990), but spiderlings would also arrive, and eventually give rise to a population that would expand its range on that island. However, colonists would continue to arrive on Maui Nui, and, at least initially, the original colonists would not be reproductively isolated from the secondary colonists of the same species. It is also possible that, if the secondary colonists included closely related heterospecifics, hybridization might occur, as newly forming taxa tend to have poorly developed sexual discrimination (Kaneshiro, 1976, 1983; Carson *et al.*, 1989). Indeed, it is possible that both *T. macracantha* and *T. brevignatha* arose through hybridization, which may play an important element in the formation of species in general (Endler, 1989).

As sexual discrimination and ecological adaptation develop, invaders would presumably lose their ability to colonize an occupied land mass. The pattern of distribution of representatives of the spiny-leg clade on older islands suggests that closely related taxa cannot maintain coexistence on the same land mass unless they have undergone sufficient ecological divergence. The situation on East Maui may therefore represent an unstable state: ultimately, a single species will take over the land mass, as a result of introgression or competitive displacement.

The mechanism I have proposed for speciation among representatives of the spiny-leg Hawaiian *Tetragnatha* remains speculative. However, the repeated ecological release of newly forming taxa strongly suggests that ecological changes have played some role in initiating species divergence, as does the finding that two populations (Maui versus Hawaii) of an apparently diverging species (*T. brevignatha*) differ only in terms of their habitat occupation. I suggest that, unlike the Hawaiian *Drosophila* in which sexual selection has been heavily implicated in the speciation process (Kaneshiro, 1983; Kaneshiro and Giddings, 1987), ecological factors (range expansion, reinvasion, competition) may be more important among the spiny-leg species of Hawaiian *Tetragnatha*.

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LITERATURE CITED

BERGER, A.J. 1981. 'Hawaiian Birdlife'. (University of Hawaii Press: Honolulu).

BISHOP, L. 1990. Meteorological aspects of spider ballooning. Environmental Entomology 19: 1381-1387.

CARSON, H.L. 1968. The population flush and its genetic consequences. Pp. 123-137. In Lewontin, R.C. (ed). 'Population Biology and Evolution'. (Syracuse University Press: Syracuse, New York).

CARSON, H.L. & KANESHIRO, K.Y. 1976. *Drosophila* of Hawaii: Systematics and ecological genetics. Annual Review of Ecology and Systematics. 7: 311-346.

CARSON, H.L. & TEMPLETON, A.R. 1984. Genetic revolutions in relation to speciation phenomena: The founding of new populations. Annual Review of Ecology and Systematics 15: 97-131.

CARSON, H.L., KANESHIRO, K.Y. & VAL, F.C. 1989. Natural hybridization between the sympatric Hawaiian species *Drosophila silvestris* and *Drosophila heteroneura*. Evolution 43: 190-203.

COOKE, C., MONTAGUE, J. & KONDO, Y. 1960. Revision of Tornatellinidae and Achatinellidae (Gastropoda, Pulmonata). B.P. Bishop Museum Bulletin 221: 1-303.

ENDLER, J.A. 1989. Conceptual and other problems in speciation. Pp. 625-648. In Otte, D. and Endler, J.A. (eds). 'Speciation and its Consequences'. (Sinauer Associates: Sunderland, Massachusetts).

FARRIS, J.S. 1969. A successive approximations approach to character weighting. Systematic Zoology 18: 374-385.

1970. Methods for computing Wagner trees. Systematic Zoology 19: 21-34.

1989. The retention index and the rescaled consistency index. Cladistics 5: 417-419.

FITCH, W.M. 1971. Toward defining the course of evolution: minimal change for a specific tree topology. Systematic Zoology 20: 406-416.

FREED, L.A., CONANT, S. & FLEISCHER, R.C. 1987. Evolutionary ecology and radiation of Hawaiian passerine birds. Trends in Evolutionary Biology 2: 196-203.

GILLESPIE, R.G. 1986. 'Between population comparison of resource acquisition in the long jawed orb weaving spider *Tetragnatha elongata*'. Ph.D Dissertation. (University of Tennessee: Knoxville: Tennessee).

1987. The mechanism of habitat selection in the long jawed orb weaving spider *Tetragnatha elongata* (Araneae, Tetragnathidae). Journal of Arachnology 15: 81-90.

1991. Hawaiian spiders of the genus *Tetragnatha*: I. Spiny Leg Clade. Journal of Arachnology 19: 174-209.

1992. Hawaiian spiders of the genus *Tetragnatha* II. Species from natural areas of windward East Maui. Journal of Arachnology 20: 1-17.

GRANT, P.R. 1986. 'Ecology and Evolution of Darwin's Finches'. (Princeton University Press: Princeton, New Jersey).

HENNIG, W. 1966. 'Phylogenetic Systematics'. (University of Illinois Press: Urbana, Illinois).

KANESHIRO, K.Y. 1976. Ethological isolation and phylogeny in the planitibia subgroup of Hawaiian *Drosophila*. Evolution 30: 740-745.

KANESHIRO, K.Y. 1983. Sexual selection and direction of evolution in the biosystematics of the Hawaiian Drosophilidae. Annual Review of Entomology 28: 161-178.

1988. Speciation in the Hawaiian *Drosophila*. Bioscience 38: 258-263.

KANESHIRO, K.Y. & BOAKE, C.R.B. 1987. Sexual selection and speciation: issues raised by Hawaiian drosophilids. Trends in Ecology and Evolution 2: 207-211.

KANESHIRO, K.Y. & GIDDINGS, L.V. 1987. The significance of asymmetrical sexual isolation and the formation of new species. Evolutionary Biology 21: 29-43.

KARSCH, F. 1880. Sitzungs-Berichte der Gesellschaft Naturforschender freunde zu Berlin. Jahrgang. Sitzung vom 18: 76-84.

LACK, D. 1971. 'Ecological Isolation in Birds'. (Harvard University Press: Cambridge, Massachusetts).

LEVI, H.W. 1981. The American orb-weaver genus *Dolichognatha* and *Tetragnatha* north of Mexico (Araneae: Araneidae, Tetragnathinae). Bulletin of the Museum of Comparative Zoology Harvard 149: 271-318.

MADDISON, W.P., DONAGHUE, M.J. & MADDISON, D.R. 1984. Outgroup analysis and parsimony. Systematic Zoology 33: 83-103.

MAYR, E. 1963. 'Animal Species and Evolution'. (Harvard University Press: Cambridge, Massachusetts).

MCCUNE, A.R. 1990. Evolutionary novelty and atavism in the *Semionotus* complex: relaxed selection during colonization of an expanding lake. Evolution 44: 71-85.

OKUMA, C. 1988. Redescriptions of the Hawaiian spiders of *Tetragnatha* described by Simon (Araneae, Tetragnathidae). Journal of the Faculty of Agriculture Kyushu University 33: 77-86.

OTTE, D. 1989. Speciation in Hawaiian crickets. Pp. 482-586. In Otte, D. and Endler, J.A. (eds). 'Speciation and its Consequences'. (Sinauer Associates: Sunderland, Massachusetts).

SIMON, C. 1987. Hawaiian evolutionary biology: an introduction. Trends in Ecology and Evolution 2: 175-178.

SIMON, E. 1900. Arachnida. Fauna Hawaiiensis 2: 443-519, pls. 15-19.

SWOFFORD, D.L. 1990. PAUP 3.0s. Phylogenetic analysis using parsimony, version 3.0. (Illinois Natural History Survey: Champaign, Illinois).

WIEHLE, H. 1963. Tetragnathidae. Tierwelt Deutschlands 49: 1-76.

A NEW SPECIES OF KARSCHIIDAE (SOLIFUGAE, ARACHNIDA) FROM KAZAKHSTAN

ALEXANDER V. GROMOV

Gromov, A.V. 1993 11 11: A new species of Karschiidae (Solifugae, Arachnida) from Kazakhstan. *Memoirs of the Queensland Museum* 33(2): 527-528. Brisbane. ISSN 0079-8835.

The new solpugid species *Karschia mangistauensis* of the family Karschiidae is described from material collected in south-western Kazakhstan. The relationship of the new species is given, as well as the list of solpugids currently known from Kazakhstan.
En se basant sur le matériel récolté au Sud-Ouest du Kazakhstan on décrit une nouvelle espéce de solifuge *Karschia mangistauensis* de la famille Karschiidae. On donne les affinités de la nouvelle espéce aussi que la liste des solifuges connues à présent au Kazakhstan.☐*Solpugids, Karschiidae, Karschia, Kazakhstan.*

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The solpugid fauna of Kazakhstan is poorly known. Only 13 species were recorded from the region by Birula (1938): these are *Karschia zarudnyi* Birula, *Eusimonia turkestana* Kraeplin, *Anoplogylippus dsungaricus* Roewer, *A. rickmersi* (Kraeplin), *Hemigylippus lamelliger* Birula, *Galeodes araneoides* Pallas, *G. turkestanus* Kraepelin, *G. caspius* Birula, *G. fuscus* Birula, *G. pallasi* Birula, *Paragaleodes heliophilus* Heymons, *P. pallidus* Birula and *Daesia rossica* Birula.

The present paper concentrates on material collected from Mangyshlak and Ustyurt Plateaus (south-western Kazakhstan). Solpugids were preserved and studied in 70% alcohol using a binocular microscope MBS-1. Their determination was done according to Walter (1889), Birula (1938) and Roewer (1932-1934, 1941).

MORPHOLOGY AND BIOLOGY
Family KARSCHIIDAE

Karschia mangistauensis sp. nov.
(Figs 1-10; table 1)

Material Examined

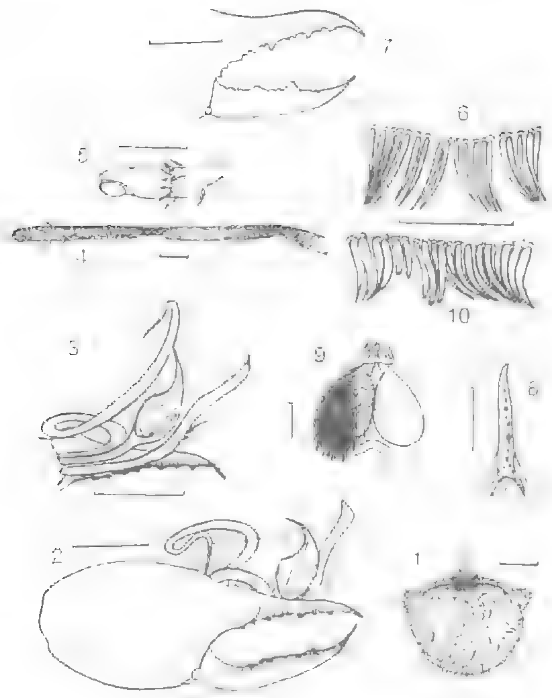
TYPES. Holotype ♂, Zhylandy Cape, Yeraliev District, Mangyshlak Plateau, Mangistau Area, South-Western Kazakhstan, (43°06'N, 51°39'E), 2 May 1991, A.V. Gromov. Paratypes: South-Western Kazakhstan: Mangistau Area: Mangyshlak Plateau: 2 ♂, 2 ♀, same data, except 2-4 May 1991, K.U. Balmukanov, A.V. Gromov, K.B. Dzhankurazov; 1 ♂, Aktau City [Shevchenko], (43°11'N, 51°39'E), 28 April 1991, K.U. Balmukanov; Ustyurt Plateau: 1 ♂, Kugusem Well, 68.5 km E of Akkuduk Village, Yeraliev District, (43°10'N, 54°53'E), 2-5 May 1990, S.I. Ibraev; 1 ♀, Sulykkyzylsai Well, 69.5 km NE of Akkuduk Village, Mangistau District, (43°28'N, 54°43'E), 12 May 1991, E.E. Kopdykbaev. Holotype and 1 ♀ paratype preserved in Zoological Institute, St Petersburg [Leningrad], the remaining material in the author's collection.

Diagnosis

The new species is closely related to *Karschia cornifera* Walter, 1889 from Turkmenistan, from which it differs by the colouration, by the shape of upper modified mesolateral seta near the base of cheliceral fingers, by the number of teeth on the fixed finger and by the spinulation of pedipalps.

Description

Male (holotype). Total length 21 mm. Body colouration light yellow-brown, with greyish head and thorax and grey-yellow abdomen with darker tergites. Chelicerae yellow, distally including brownish-black teeth. Pedipalps (Fig. 4): proximal part of femur yellow, distal part of femur and the remaining segments greyish. Legs yellow. Ocular tubercle (Fig. 1) dark, with numerous hairs, sparse short setae and 2 long setae. Near the base of the cheliceral fingers there is a mesal row of long setae: the upper two are strongly modified and thickened (Figs 2, 3). Armature of pedipalps (Fig. 5): protarsus (basitarsus, metatarsus auct.) with 9 promesolateral spines, tarsus with 1 mesobasal spine. Third abdominal segment with 46 broad ctenidia, fourth one with 19 ctenidia (Fig. 6).



FIGS 1-10. *Karschia mangistauensis*, sp. nov. 1-6, male; 7-10, female. 1, propeltidium, dorsal view. 2, right chelicera, ectal view. 3, modified setae near base of fingers, and flagellum on left cheliceral fixed finger, mesal view. 4, 5 right pedipalp, mesoventral view; coloration (4); spinulation (5). 6, ctenidia on fourth sternite of abdomen, ventral view. 7, right chelicera, ectal view. 8, right cheliceral fixed finger, ventral view. 9, genital opercula, ventral view. 10, ctenidia on fourth sternite of abdomen, ventral view. Scale line = 1 mm.

Body length of paratypes 17-21 mm, number of promesolateral spines 6-10, mesobasal spine of tarsus sometimes absent, fourth abdominal segment with 17 or 19 ctenidia.

Female paratype. Body colouration lighter than in male, with darker pedipalps. Distal part of femur IV light brown. The head behind ocular tubercle with slight longitudinal light brown line. Ocular tubercle as in male, occupying less than 1/3 of clypeus width. Fixed fingers are straight from above, their length no more than the width of chelicerae. Armature of chelicerae as in Figs 7, 8. Genitalia (Fig. 9) with pale rosy ectolateral setae. Fourth abdominal segment with 19 pale rosy ctenidia which are thicker than in male (Fig. 10).

	Length
Chelicerae	4.4, 1.6 wide
Propeltidium	2.4, 3.5 wide
Pedipalp: total (with coxa)	18.2
tibia	4.9
basitarsus	3.8
Leg I (with coxa)	14.1
Leg II (with coxa)	12.4
Leg III (with coxa)	16.6
Leg IV (with coxa)	25.3

TABLE 1. Measurements (in mm) of *Karschia mangistauensis*, sp. nov.

Biology

Night solpugid in clayey desert under stones during day.

ACKNOWLEDGEMENTS

I am grateful to Messrs K.U. Balmukanov and K.B. Dzhankurazov (Kazakh State University, Alma-Ata) for their assistance in capturing of the new species, Mr S.I. Ibraev and Mr E.E. Kopdykbaev (Institute of Zoology, Kazakhstan Academy of Sciences, Alma-Ata) for their material kindly presented to me, and to Dr A.A. Zyuzin (Institute of Zoology, Kazakhstan Academy of Sciences, Alma-Ata) for translation of manuscript. I am also indebted to Dr Ch. K. Tarabaev (Institute of Zoology of Kazakhstan Academy of Sciences, Alma-Ata) who presented my paper at the XII International Congress of Arachnology (Brisbane, Australia).

LITERATURE CITED

BIRULA, A.A. [BIALYNITSKIJ-BIRULA], 1938. Solifugae. In: Fauna of the USSR, Arachnida, vol. 1(3). (Academy of Sciences of the USSR: Moscow-Leningrad. (in Russian)

ROEWER, C.F. 1932-1934. Solifugae, Palpigradi. In: Dr H. G. Bronn's Klassen und Ordnungen des Tierreichs, Teil 5, Abteilung 4, Buch 4, 723 pp. Bremen.

1941. Solifugen 1934-1940. Veröffentlichungen aus dem Deutschen Kolonial- und Übersee-Museum in Bremen 3(2): 97-192.

WALTER, A. 1889. Transkaspische Galeodiden. In: Wissenschaftliche Ergebnisse der im Jahre 1886 in Transkaspien 1 (Zoologische Abtheilung). Lieferung 6: 103-117.

A NEW SPECIES OF *AMAUROBIOIDES* O.P.-CAMBRIDGE (ANYPHAENIDAE: ARANEAE) FROM SOUTH AUSTRALIA

D.B. HIRST

Hirst, D.B. 1993 11 11: A new species of *Amaurobioides* O.P.-Cambridge (Anyphaenidae: Araneae) from South Australia. *Memoirs of the Queensland Museum* **33**(2): 529-532. Brisbane. ISSN 0079-8835.

The littoral spider *Amaurobioides isolatus* sp. nov. is described from South Australia and is the first new species of the genus from the Australian mainland. The male palp of *A. litoralis* Hickman is re-illustrated. Biogeography is discussed. ☐*Araneae, Anyphaenidae, Amaurobioides, new species.*

David B. Hirst, South Australian Museum, North Terrace, Adelaide, South Australia 5000, Australia; 6 November, 1992.

The genus *Amaurobioides* O. Pickard-Cambridge, 1883 occurs in New Zealand (Cambridge, 1883), Campbell Island (Hogg, 1909), South Africa (Hewitt, 1917) and was reported from Tasmania (Hickman, 1949) and Chile (Forster, 1970). Forster (1975) included the south-east coast of Australia in the distribution of the genus but that was not cited by Main (1981) or Davies (1986). The specimen(s) to which Forster (1975) referred were deposited in the Australian Museum, Sydney (AM) but were not labelled as *Amaurobioides* (unpublished data) and have not been found (pers. comm., M. Gray). No further material has been reported from mainland Australia. Once *Amaurobioides* was found on the rocky shoreline of the eastern side of Gulf St Vincent in South Australia , deliberate searching in similar habitats on Eyre Peninsula, Fleurieu Peninsula and Kangaroo Island showed the species was widespread.

Types of *A. litoralis* Hickman, 1949 (syntype series of 1 ♂ and 3 ♀♀ from Tasmania) deposited in AM, were examined. Hickman made no special type designations but the male seen (AM KS6410) is labelled 'Holotype'. Hence, the label designation is invalid (Art. 73iii). The series also includes two females of an undescribed species (Forster, 1970). Forster, when noting that this type material comprised two sympatric species, stated that the larger form was *A. litoralis* while the smaller form was undescribed.

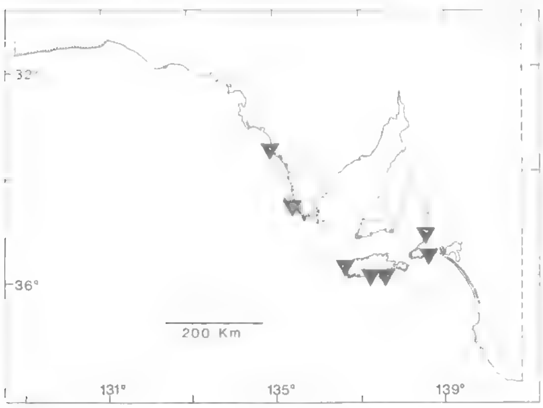


FIG. 1. Southern portion of South Australia showing the distribution of *Amaurobioides isolatus*. Shaded coastline may include suitable habitats.

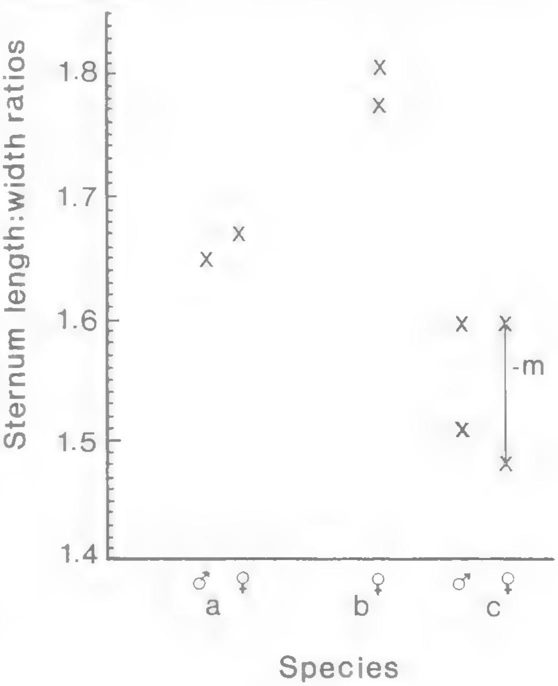


FIG. 2. Comparison of sternum length: width ratios: a, b, *A. litoralis*: small form (a); large form (b); c, *A. isolatus*. m, mean.

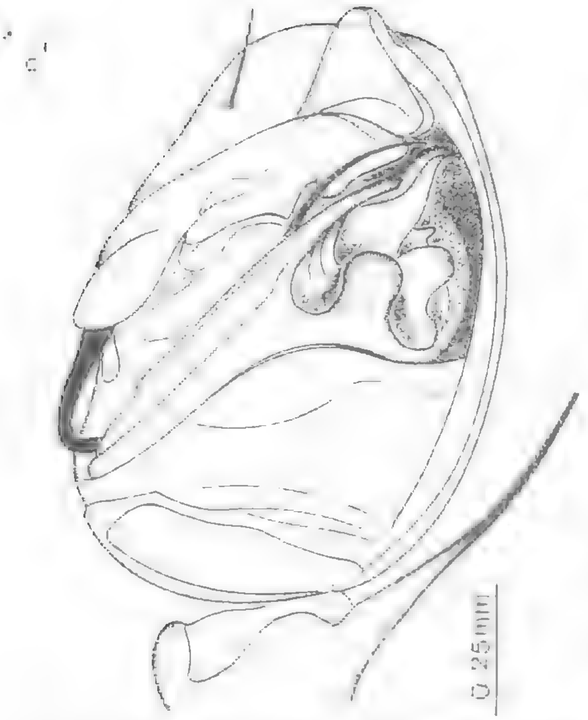


FIG. 3. *A. litoralis*. Tibial apophysis and cymbium of syntype ♂ AM KS6410, ventral.

The ♂ is similar in size to the sole smaller ♀ of the type series, and not to the two larger ♀♀ as suggested by Forster (also captions for figures of the two forms appear to be transposed as the larger specimen figured is called the small form). This is supported by comparisons of the sternum length:width ratio (Fig. 2). Ratios: ♂, 1.65 and smaller type ♀ 1.67; larger ♀♀, 1.77, 1.81; ♀ *A. isolatus* 1.48-1.60 (n=14, mean =1.56) and 2 ♂♂, 1.51, 1.60. Although based only on Australian material seen, the conspecific ♂ of the larger and undescribed form would probably attain a ratio in excess of 1.70.

The ♂ palp of *A. litoralis* is re-illustrated here; the ♀ epigynum was adequately illustrated in Forster (1970, figs 487, 488).

METHODS AND MATERIALS

Hairs are omitted from illustrations. ♀ genitalia were dissected then cleared in lactic acid. All measurements are in millimetres. *Abbreviations*: CL, carapace length; CW, carapace width; AL; abdomen length; AW, abdomen width, MOQ, median ocular quadrangle; aw, anterior width; pw, posterior width; L or l, length, W, width; K.I., Kangaroo Island; DH, D. Hirst.

Amaurobioides isolatus sp. nov.
(Figs 1, 2, 4-9, Table 1)

Material Examined

TYPES. Holotype ♂, Blanche Point, 35°15'S, 138°28'E, 1.iii.1986, DH, N1992206. Paratypes: allotype ♀, same data as above, N1992207; ♀ (with spiderlings), Elliston, 33°39'S, 134°53'E, 31.iii.1987, DH, D. Lee, N1992218; ♀, juv., same data, N1992216-7; ♀, 5 penult. ♂, 2 penult. ♀, same data as holotype but 25.i.1986, N1992208-15; penult. ♀, Petrel Cove, 35°36'S, 138°36E, 1.ii.1991, DH, N1992219; ♀, 4 juv., Point Avoid, 34°41'S, 135°19'E, 31.iii.1987, DH, D. Lee, N1992221; ♀ (with spiderlings), juv., same data, N1992220; 2 ♀, juv., Point Ellen, K.I., 36°00'S, 137°11'E, 10.xi.1987, DH, N1992222-3; ♀ (with eggsac), Point Tinline, K.I., 35°59'S, 137°37'E, 11.xi.1987, DH, N1992224; ♂♀, Port Willunga, 35°16'S, 138°28'E, in retreats 0.5m above base of large rock on beach, 14.vi.1992, DH, N1992234-5; 4 ♀, juv., West Bay, K.I., 35°54'S, 136°32'E, 6.xi.1987, D, N1992225-9. All in South Australia and deposited in South Australian Museum.

Diagnosis

The ♂ of *A. isolatus* is recognised by the shape of the primary conductor. *A. isolatus* further differs from the two Tasmanian species in having the sternum relatively broader while the ♀ epigynum is smaller and less sclerotised. The ♂ has spination of tibia I identical to the ♀, a feature shared with *A. maritimus* O.P.-Cambridge, from which it is separated by the genitalia.

Description

MALE. CL 3.79, CW 2.56. AL 4.48, AW 2.41.

Colour in alcohol: Carapace yellow-brown, yellow posterior to fovea and laterally to above anterior legs, caput dark orange-brown, clypeus and lateral edge of face brown. Chelicerae red-brown, darker distally. Maxillae and labium orange-brown, anterior margins cream. Sternum cream, margins orange. Legs cream-yellow, anterior metatarsi and tarsi darker, coxae cream. Palp cream, cymbium brown. Abdomen cream with dark red-brown pattern dorsally and laterally, typical for genus. Venter darker around spiracle and posteriorly to spinnerets, dark area extending anteriorly from spiracle in two narrow lines almost to epigastric furrow.

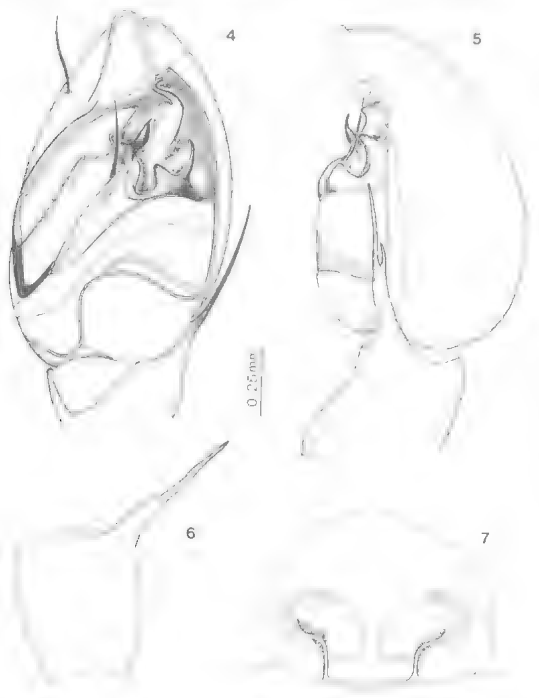
Carapace elongate, longer than broad in ratio 19:13, short imperfect longitudinal fovea [presumably straight in normal specimens]. Striae barely evident, adpressed setae black, upright setae on caput between fovea and ocular region. Eye group occupies less than half width of caput. AME 0.10, ALE 0.17, PME = PLE 0.18.

	Leg 1	Leg 2	Leg 3	Leg 4	Palp
Fe	3.32(2.67)	3.30(2.61)	2.71(2.46)	2.98(2.51)	1.50(1.40)
Pa	1.53(1.59)	1.56(1.48)	1.33(1.39)	1.47(1.50)	0.59(0.65)
Ti	3.40(2.50)	3.23(2.43)	2.24(1.82)	2.74(2.32)	0.65(0.66)
Me	3.19(2.34)	2.99(2.25)	2.40(1.96)	2.59(2.15)	- (-)
Ta	1.67(1.42)	1.42(1.29)	1.02(0.95)	0.97(0.95)	1.26(1.24)
Total	13.11(10.52)	12.50(10.06)	9.70 (8.58)	10.75 (9.43)	4.00 (3.95)

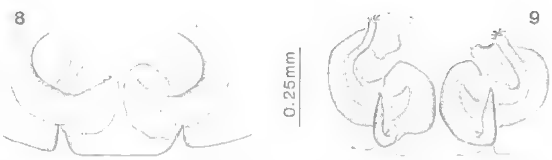
TABLE 1. Leg lengths of *Amaurobioides isolatus*. Values are for holotype ♂ (allotype ♀).

Interspaces: AME-AME 0.05, AME-ALE 0.04, PME-PME 0.11, PME-PLE 0.12, AME-PME 0.14, ALE-PLE 0.08. MOQ; aw: pw: l = 0.26: 0.47: 0.39. Width of clypeus to AME 0.10. Chelicerae with three teeth on both margins. Sternum: L 2.12, W 1.40. Legs. (Table 1) Scopula sparse, particularly on posterior pairs. Leg spination; no spines on patellae or tarsi. Ventral tibiae and metatarsi spines usually paired, occasionally single. Leg I, fe d3 p1, ti v6, me v3. Leg II, fe d3 p1, ti p1 v6, me v4. Leg III, fe d3 p1 r1, ti p1 r1 v5 (v6 on right), me p3 r3 v6. Leg IV, fe d3 p1 r1, ti r1 v3, me p2 r2 v5. Palp, fe d3 p1, pa with one stout bristle dorsally at distal end, ti many long stout bristles, cymbium with three short weak spines prolaterally.

Palp. Tibia with left apophysis having short



FIGS 4-7. *A. isolatus*. 4-5, Left tibial apophysis and cymbium of holotype ♂, 4, ventral, 5, retrolateral; 6, right tibia and apophysis; 7, epigynum of allotype ♀.



FIGS 8-9. *A. isolatus*. 8-9, cleared vulva of paratype ♀ N1992208, 8, ventral, 9, dorsal.

dorsal median secondary prong (Fig. 5), right apophysis lacking accessory prong (Fig. 6), possibly normal state.

FEMALE (as ♂ except as follows).CL 4.21, CW 2.89. AL 6.97, AW 4.16.

Eyes. AME 0.11, ALE 0.20, PME 0.19, PLE 0.20. Interspaces; AME -AME 0.08, AME-ALE 0.06, PME-PME 0.12, PME-PLE 0.14, AME-PME 0.17, ALE-PLE 0.10. MOQ; aw: pw: l = 0.29: 0.50: 0.46. Width of clypeus to AME 0.06. Sternum: L 2.30, W 1.48. Legs. (Table 1)

Epigynum. Fossa broad, anterior margins vaguely defined by what appears to be subcuticular sclerotisation of vulva (Fig. 7). Vulva of paratype N1992208 shown in Figs 8, 9 [allotype not dissected].

Variation

CL of paratype ♂, 3.48; the tibial apophysis of both palps lack accessory prongs and the fovea is straight. CL of paratype ♀; 3.22-4.74, mean 4.35 (n=13).

Etymology

The specific epithet, *isolatus*, reflects the isolated nature of the species distribution.

NATURAL HISTORY

Habits are similar in other *Amaurobioides*. Silk retreats are assumed to be permanent although many spiders collected or observed at Blanche Point in February were wandering over the rocks at night. Several penultimate ♂♂♀♀ were collected in this way and kept alive for some time, one ♂ eventually maturing 3 months later. Most insects placed with the spiders, including moths and terrestrial isopods, were not fed upon. Small flies (mostly *Drosophila*) were more readily accepted (Forster, 1970: 167). Littoral isopods were not tried as a food source (Hickman, 1949). Since then a specimen of *A. isolatus* at Blanche Point lunged at and grasped a small littoral isopod half its size with its anterior legs, hesitated and then released the isopod, retreating to its position at the entrance to the nest. Small flies, often seen resting in sheltered areas at night along the coast, are another likely food source. Females with spiderlings (26 and 42) in the retreat were found in mid-autumn at both Point Avoid and Elliston while spiderlings and an eggsac were found in separate retreats in November on Kangaroo Island.

BIOGEOGRAPHY

Most areas sampled were within the splash zone on rock faces sheltered from the full velocity of the sea, but retreats were seen in an exposed and treacherous area at Cape du Couedic, Kangaroo Island. Known populations are separated by unsuitable or sandy coastline of varying lengths (Fig. 1). *Amaurobioides* may have dispersed across the intervening ocean by parachuting on silk lines or drifting on flotsam to settle and inhabit their present littoral environments. Forster (1970) considered that claim to be overstated as a number of distinct forms, some sympatric, were present in New Zealand. Platnick (1976) reinforced that in the Laroniinae.

Since Australia's separation and subsequent drift from the other continents of Gondwanaland, the South Australian coastline has been altered by changes in sea level during the last ice-age. The rocky cliffs of Blanche Point and southern coast of Kangaroo Island which now provide a habitat for *Amaurobioides* were formed during the last ice-age over Tertiary deposits and have since been uplifted and weathered (Daily *et al*., 1979). One population in D'Estrees Bay, Kangaroo Island, consisted of only a few individuals on a small isolated rock outcrop backed by a low sandstone ledge. Similarly, near Port Willunga and 2km south of Blanche Point, individuals exist on a few older limestone rocks remaining on the wide sandy beach which are reached by the normal high tide. Although backed by cliffs, no spiders were found on these. Cliffs also abut the sea in areas north of Blanche Point to Marino Rocks but as yet *Amaurobioides* has not been found. *Amaurobioides* is unlikely to be found from Victor Harbour on the Fleurieu Peninsula to at least Robe in the south-east of South Australia. Extensive sand dunes which now form the Coorong and much of the coast to the south are part of that area built up during inundation by the sea in the Miocene and the Pleistocene, and the few rocky outcrops now present have remained isolated since.

In summary, *Amaurobioides* is one of the few true Gondwanan spider genera left in South Australia presumably because continual changes to the coast have occurred gradually. Littoral spiders have moved with it through dispersal and colonising adjacent new areas of rocky terrain or re-establishing itself into old areas within a suitable distance from the receding or insurgent sea. The sympatry of species of *Amaurobioides* in New Zealand and Tasmania probably occurred by migration over land following uplift or weathering of unsuitable coastline between two separated species and exposing a continuous rocky habitat, rather than by dispersal on silk lines.

ACKNOWLEDGEMENTS

I am grateful to Dr M. Gray (AM) for the loan of types of the Tasmanian *Amaurobioides* and to Mr L.N. Nicolson for commenting on an early draft of the manuscript.

LITERATURE CITED

CAMBRIDGE, O.P.- 1883. On some new genera and species of spiders. Proceedings of the Zoological Society of London 1883: 352-365.

DAILY, B., MILNES, A.R, TWIDALE, C.R., BOURNE, J.A. 1979. Geology and geomorphology. In 'Natural History of Kangaroo Island'. (Royal Society of South Australia: Adelaide).

DAVIES, V.T. 1986. 'Australian spiders, Araneae. Collection, preservation and identification'. (Queensland Museum Booklet No. 14. Brisbane).

FORSTER, R.R. 1970. The spiders of New Zealand. Part III. Otago Museum Bulletin No. 3: 1-184.

1975. The spiders and harvestmen. In Kuschel, G. (ed.) 'Monographiae biologicae: biogeography and ecology of New Zealand'. (W. Junk: Netherlands).

HEWITT, J. 1917. Descriptions of new South African Arachnida. Annals of the Natal Museum 3: 687-711.

HICKMAN, V.V. 1949. Tasmanian littoral spiders with notes on their respiratory systems, habits and taxonomy. Papers and proceedings of the Royal Society of Tasmania 1948: 31-43.

HOGG, H.R. 1909. Spiders and Opiliones from the Subantarctic Islands of New Zealand. The Subantarctic Islands of New Zealand 1, Wellington 1909, 155-181.

MAIN, B.Y. 1981. Australian spiders: diversity, distribution and ecology. In Keast, A. (ed.) 'Ecological Biogeography of Australia' Vol. 2. (W. Junk, Netherlands).

PLATNICK, N.I. 1976. Drifting spiders or continents?: vicariance biogeography of the spider subfamily Laroniinae. Systematic Zoology 25: 101-109.

IMPLICATIONS OF THE PHYLOGENY OF PIMOIDAE FOR THE SYSTEMATICS OF LINYPHIID SPIDERS (ARANEAE, ARANEOIDEA, LINYPHIIDAE)

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The araneoid family Pimoidae (new rank) is hypothesized to be the sister group of Linyphiidae. *Louisfagea* Brignoli is a junior synonym of *Pimoa* Chamberlin and Ivie (new synonymy). The characters that support the monophyly of Pimoidae and of Linyphiidae plus Pimoidae are discussed. Explicit outgroup comparison to the closest relatives of linyphiids (i.e., pimoids) allows studies of character evolution and character polarization within linyphiids and the assessment of previous phylogenetic hypotheses for the family. Preliminary data on the implications of pimoid phylogeny for linyphiid systematics are evaluated, based mainly on morphological characters. Linyphiid monophyly is discussed.

La familia araneoide Pimoidae (nuevo rango) es, hipotéticamente, el grupo hermano de Linyphiidae. El género *Louisfagea* Brignoli se considera sinónimo de *Pimoa* Chamberlin and Ivie (nueva sinonimia). Se discuten los caracteres que apoyan la monofilia de Pimoidae y de Linyphiidae más Pimoidae. La utilización explícita del criterio de comparación con el grupo externo de los linífidos (es decir, los pimóidos) permite estudiar la evolución y polarización de caracteres en linífidos, así como la evaluación de anteriores hipótesis filogenéticas sobre esta familia. Se evalúan los datos preliminares, basados en caracteres morfológicos principalmente, sobre las implicaciones de la filogenia de los pimóidos para la sistemática de los linífidos. También se discute la monofilia de Linyphiidae. □*Pimoidae, Linyphiidae, Pimoa, cladistics, phylogeny, monophyly, homology.*

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Linyphiids are one of the dominant spider groups in the Holarctic region. Despite their overwhelming diversity and involved taxonomic history the phylogenetic structure of the family and their relationship to other araneoids are very poorly understood. In this paper I present some preliminary data on the systematics of pimoids, confirming their sister-group relationship to linyphiids, and on the cladistic structure of a small sample of linyphiid genera. A revision and numerical cladistic analysis of the pimoids and the sample of linyphiid taxa (Hormiga, in press), together with detailed character information, will be published elsewhere shortly. The study of the phylogeny of the pimoids requires the inclusion of at least a sample of linyphiids (their putative sister-group) in order to assess character state polarities by means of outgroup comparison. It is in such a context that the present study should be considered, since the small sample of genera used here can by no means account for the whole range of linyphiid diversity. However, quantitative cladistic analysis of the data presented here enables for some testable hypotheses on linyphiid systematics and character evolution, by explicitly stating phylogenetic relationships in terms of synapomorphies rather than by the more speculative approaches that have commonly been used in traditional linyphiid higher systematics. This approach enables us to evaluate comparative morphological data (or any other kind of biological data) in a cladistic context. Hypotheses on phylogeny and character homology hypotheses are indistinguishable because 'every hypothesis of homology is a hypothesis of monophyletic grouping' (Patterson, 1982). Finally, the present study allows for a preliminary test of the phylogeny of the linyphiid subfamilies proposed by Wunderlich (1986).

MATERIALS AND METHODS

Taxa

Nine linyphiid, five pimoid, and two non-linyphiid araneoid genera that are possible outgroups of the pimoid-linyphiid complex are used in this study. The linyphiid taxa selected represent the subfamilies and tribes used by Wunderlich (1986) in his phylogenetic scheme for Linyphiidae (given here in parentheses): *Linyphia triangularis* (Clerck) and *Microlinyphia dana* (Chamberlin and Ivie)(Linyphiinae, Linyphiini); *Bolyphantes luteolus* (Blackwall) and *Lepthyphantes tenuis* (Blackwall)(Linyphiinae, Micronetini); *Erigone psychrophila* Thorell and *Walckenaeria directa* (O.P.-Cambridge) (Erigoninae); *Haplinis diloris* (Urquhart) and *Novafroneta vulgaris* Blest (Mynogleninae); and *Stemonyphantes blauveltae* Gertsch (Stemonyphantinae). The pimoids (which contain 21 species, including 11 new species (Hormiga, in press) are represented here by five species: *Pimoa* (=*Louisfagea*) *rupicola* (Simon), *P.* (=*Louisfagea*) *crispa* (Fage), *P. altioculata* (Keyserling), *P. breviata* Chamberlin and Ivie, and *P. curvata* Chamberlin and Ivie. *Tetragnatha versicolor* Walckenaer and *Zygiella x-notata* (Clerck) are used as outgroups of the pimoid-linyphiid clade. The affinities of *Zygiella* are problematic: the genus is currently placed in Tetragnathidae, although not long ago it was thought to belong in Araneidae. Recent analyses of Araneoidea relationships by Coddington and Scharff suggest that *Zygiella* is either sister to Araneidae or Araneinae, i.e. it is the most basal taxon within araneids or basal within the araneine clade (Scharff and Coddington, pers. comm.).

Taxonomic note: I have used taxonomic decisions that will be soon discussed in greater detail elsewhere. The Pimoinae Wunderlich are raised to familial status (Pimoidae, NEW RANK) and are therefore removed from the Linyphiidae. Treating pimoids as a linyphiid subfamily produces a great change in the diagnosis of Linyphiidae, since it is largely based in male genitalic characters which are absent in the Pimoidae (e.g., intersegmental paracymbium, loss of the araneoid conductor, loss of the araneoid median apophysis, presence of a radix and a column, etc.). Once it is established that pimoids and linyphiids are sister-groups, the assignment of ranks is arbitrary. The exclusion of pimoids renders Linyphiidae more homogeneous and easier to diagnose. *Louisfagea* Brignoli, as presently defined, is polyphyletic (Hormiga, in press). The removal of *crispa* would leave the remaining species of *Louisfagea* as a paraphyletic genus. *Louisfagea* is regarded here as a junior synonym of *Pimoa* Chamberlin and Ivie (NEW SYNONYMY). Throughout this paper the taxon name Linyphiidae (linyphiids) does not include the pimoids.

Characters

The data set contains 47 characters (Table 1): 33 male and female genitalic characters, 5 spinneret spigot characters, 7 other morphological somatic characters, and 2 behavioral characters. The data consist mostly of original observations, but a few characters have been extracted from the literature. Although this data set integrates information from several character systems, it especially focuses on male palp and spinneret spigot morphology. The methods of study and of homology assessment of spinneret spigot morphology follow those of Coddington (1989). The work on linyphiid morphology (including the descriptive studies on male palp, spinneret spigot, and tracheal system morphology) will also be published elsewhere.

Analysis

The data set was analyzed using the computer program for phylogenetic analysis Hennig86 ver. 1.5 (Farris, 1988). Multistate characters were treated as non-additive (unordered).

RESULTS

Characters

Character distributions are summarized in Table 1. The desmitracheate tracheal system (*sensu* Millidge, 1984; character 35) is a synapomorphy of the erigonine clade. I have not been able to confirm some of the tracheal morphologies described by Millidge (1986). I have examined the tracheal system of several erigonine genera (*Erigone aletris* Crosby and Bishop, *E. psychrophila*, *Gonatium rubens* (Blackwall), *Grammonota angusta* Dondale, and *Hypselistes florens* (O.P.-Cambridge)) and have not found evidence of the median tracheae open-

TABLE 1. Rows represent characters and columns taxa. The first state is 'state 0', the second is 'state 1', etc. '?' represents missing data and '—' non-applicable states. The last two columns give the consistency index (CI) and the weight (W) assigned to the character in the successive character weighting analysis (see text). Taxon numbers: 0 = *Tetragnatha versicolor*, 1 = *Zygiella x-notata*, 2 = *Linyphia triangularis*, 3 = *Microlinyphia dana*, 4 = *Bolyphantes luteolus*, 5 = *Lepthyphantes tenuis*, 6 = *Erigone psychrophila*, 7 = *Walckenaeria directa*, 8 = *Haplinis diloris*, 9 = *Novafroneta vulgaris*, 10 = *Stemonyphantes blauveltae*. The remaining taxa are species of *Pimoa*: 11 = *rupicola*, 12 = *crispa*, 13 = *altioculata*, 14 = *breviata*, 15 = *curvata*. Characters: 1-30, male genitalia; 31-33, female genitalia; 34-40, somatic morphology; 41-45, spinneret spigot morphology; 46, 47, behaviour.

		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	CI	W
1	Cymbium morphology: without dorsoectal denticulated process (DDP); with DDP	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1.00	10
2	DDP denticles: numerous (20); few (<20)	—	—	—	—	—	—	—	—	—	—	—	0	0	1	1	1	1.00	10
3	Pimoid cymbial sclerite (PCS): absent; present	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1.00	10
4	PCS -cymbium connection: sclerotized, rigid; membranous, flexible	—	—	—	—	—	—	—	—	—	—	—	0	1	1	1	1	1.00	10
5	PCS membranous ridge: absent; present	—	—	—	—	—	—	—	—	—	—	—	1	0	0	0	0	1.00	10
6	PCS shape: U; elongated anteroposteriorly; reversed J	—	—	—	—	—	—	—	—	—	—	—	0	2	1	1	1	1.00	10
7	Paracymbium attachment:integral; intersegmental	1	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0.50	4
8	Paracymbium morphology: straight; large-pointed apex; U or J; linguiform-fused to PCS; triangular; short-procurved; *St* type	0	1	3	3	3	3	3	3	3	3	2	4	6	5	5	5	1.00	10
9	Paracymbium apophyses: present; absent	0	0	1	1	0	0	1	1	1	1	1	1	1	1	1	1	0.50	3
10	Petiole:otherwise; fused to subtegulum	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1.00	10
11	Tegular suture: conspicuous; subtle or absent	—	—	—	—	—	—	—	—	—	—	—	0	0	1	1	1	1.00	10
12	Mynoglenine tegular apophysis: absent; present	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1.00	10
13	Suprategulum: absent; fused; articulated	0	0	1	1	1	1	1	1	0	0	2	0	0	0	0	0	1.00	10
14	Median apophysis: present; absent	1	0	1	1	1	1	1	1	1	1	1	0	0	0	1	1	0.33	3
15	Conductor: present; absent	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	1.00	10
16	Conductor form: small and undivided; large and bilobate	0	0	—	—	—	—	—	—	—	—	—	0	0	0	1	1	1.00	10
17	Embolus length: long and filiform; short	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0.50	2
18	Embolic membrane: absent; present	—	0	1	0	1	1	1	1	1	1	0	—	—	—	—	—	0.50	2
19	Pimoid embolic process (PEP): absent; present	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1.00	10
20	PEP conformation: undivided; divided	—	—	—	—	—	—	—	—	—	—	—	1	0	0	0	0	1.00	10
21	PEP base: narrow; wide and lamelliform	—	—	—	—	—	—	—	—	—	—	—	0	0	1	1	1	1.00	10
22	Radix: absent; present	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0.50	4
23	Column (distal haematodocha): absent; present	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0.50	4
24	Fickert's gland: absent; present	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1.00	10
25	Terminal apophysis: absent; present	—	0	1	1	1	1	1	0	0	0	0	—	—	—	—	—	0.50	3
26	Lamella characteristica: absent; present	—	0	1	1	1	1	0	0	0	0	0	—	—	—	—	—	1.00	10
27	♂ pedipalpal tibial apophysis: absent; dorsal, rounded; retrolateral; ventral	0	0	0	0	0	0	2	2	0	0	3	1	1	1	1	1	1.00	10
28	♂ pedipalp tibial spines: not clustered; distal row	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1.00	10
29	Prolateral trichobothria in male palpal tibia: two; one	0	0	1	1	1	1	1	1	0	1	1	0	0	0	0	0	0.50	4
30	Retrolateral trichobothria in ♂ palpal tibia: 2; 4; 3;>4	1	0	2	0	0	0	0	0	2	0	0	2	2	2	2	2	0.50	3
31	Epigynum form protrudes: less than its width; more	—	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1.00	10
32	Dorsal plate of epigynum, projections: absent; present	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1.00	10
33	Atrium: absent; present	—	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0.50	2
34	Mynoglenine cephalic sulci: absent; present	0	0	0	0	0	0	?	0	1	1	0	0	0	0	0	0	1.00	10
35	Tracheal system: haplotracheate; desmitracheate	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1.00	10
36	Ectal chelicerae of ♂: smooth; with stridulatory striae	0	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	0.33	1
37	Retrolateral teeth ♀ chelicera: 3; >3; 2	0	0	1	1	1	1	1	0	1	1	?	2	0	?	2	2	0.50	5
38	♀ pedipalpal tarsal claw: present; absent	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0.50	2
39	Leg autospasy: otherwise; at patella-tibia	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1.00	10
40	Trichobothrium metatarsus IV: present; absent	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0.50	3
41	PMS: with anterior aciniform brush; without	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1.00	10
42	Aciniform spigots in ♀ PMS: > 1; 1; absent	0	0	0	0	0	0	0	0	0	0	2	2	1	2	2	2	0.66	10
43	PLS mesal cylindrical spigot base: same size; enlarged	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1.00	10
44	PLS aciniform field: random spigots; elongated field	1	0	1	1	1	1	1	1	1	1	1	—	—	—	—	—	1.00	10
45	Aciniform spigots in ♀ PLS: >1; 1; absent	0	0	0	0	0	0	0	0	0	0	2	1	1	2	2	2	0.66	10
46	♂ spins sperm web while: above sperm web; below it	?	?	0	0	?	0	1	?	1	?	?	?	?	?	?	?	1.00	10
47	♂ position during ejaculation: above sperm web; below	?	?	0	0	?	0	1	?	1	?	?	?	?	?	?	?	1.00	10

ing directly to separate spiracles, as Millidge reported. The mentioned erigonines posses a tracheal atrium (*contra* Millidge, 1986:57), which, using an aqueous solution of chlorazol black, stains similarly to the rest of the tracheal system. The spiracle is most visible at both ends, where it is wider and rounded, although there is a slit connecting both ends. Such ends are not a closed circle (i.e., they are not separate spiracles), as Millidge's illustrations seem to suggest (e.g. his figure 5), since they are open at its inner part to the interconnecting slit. *Stemonyphantes blauveltae* and *Allomengea pinnata* (Emerton) have tracheal atria opening through a single spiracle, contrary to Millidge's assertion that in both genera the atrium opens via two spiracles. Atria opening via a single spiracle were also found in *Drapetisca alteranda* Chamberlin, *Centromerus sylvaticus* (Blackwall), *Lepthyphantes flavipes* (Blackwall), *L. tenuis* (Blackwall), and *L. intricatus* (Emerton). These latter genera were also reported by Millidge (the first one only implicitly) to have the atrium opening via two spiracles. In the two latter species the slit is very similar to the one reported here for the erigonines, with markedly wider round ends (this fact might have caused them to be taken as having two spiracles).

The spinneret spigot morphology characters (41-45) support the monophyly of the pimoids and of the pimoid-linyphiid clade (Hormiga, in press). Linyphiid and pimoid spigot morphology is consistent with the araneoid groundplan (Coddington, 1990b; Peters and Kovoor, 1991; Hormiga, in press). The pimoid-linyphiid clade lacks the PMS aciniform brush found in primitive orbicularians (character 41), but so do many tetragnathids and the theridiids. Pimoids and linyphiids share the position of the mesal cylindrical spigot on the periphery of the PLS, but this is not exclusive to the pimoid-linyphiid clade: it is also found in *Zygiella x-notata* (pers. observ.) and in some other tetragnathids (Coddington, pers. comm.; Platnick *et al.*, 1990). An enlargement of the base of the peripheral cylindrical spigot of the PLS (character 43) is characteristic of pimoids and linyphiids. Pimoids have drastically reduced the PMS and PLS aciniform fields (characters 42 and 45): they either have one or none aciniform spigots on each spinneret. *Stemonyphantes* has also lost, presumably in parallel, the aciniform spigots in both the PMS and the PLS.

The use of the mating sequence and the transfer of sperm (characters 46-47) as taxonomic characters in linyphiids was studied by van Helsdingen (1965, 1969, 1983). Blest and Pomeroy (1978) studied the sexual behavior of *Haplinis diloris*. I have used data from van Helsdingen's observations as valid for the different species of *Lepthyphantes* and *Microlinyphia* in my data, under the assumption that there is no variation for the characters under study at the intrageneric level. For *Erigone psychrophila*, I have also used data from other species in the same genus, namely *E. dentipalpis* and *E. longipalpis* (Gerhardt (1927, 1923) cited in van Helsdingen (1983)). The male position during the construction of the sperm web (fork and web) and during ejaculation is below the sperm web in erigonines and mynoglenines, and above (only the web, the fork is constructed from below) in Linyphiini and Micronetini.

Analysis

The data (Table 1) were analyzed using the implicit enumeration option of Hennig86, which found four equally parsimonious cladograms with a length of 81 steps and consistency and retention indices of 0.74 and 0.81 respectively. These four topologies differ in the interrelationships of pimoids and in the position of *Stemonyphantes*, which in one of the four cladograms is sister to the pimoids. This latter topology is the result of the parallel loss of the aciniform fields in pimoids and linyphiids. Deactivating the characters that account for the number of aciniform spigots in the PMS and PLS (42 and 45, respectively) and using the implicit enumeration option three cladograms are obtained. These three cladograms are the same as those obtained with the 'active' characters, with the exclusion of the topology that clusters *Stemonyphantes* with pimoids. Successive character weighting (Farris, 1969; Carpenter, 1988) was used, as implemented by Hennig86, to choose a cladogram from the set of four equally parsimonious cladograms. A single iteration produced one cladogram (Fig. 1), which corresponds to one of the original set of four. This result is stable in a second iteration. Because this cladogram is based on the most consistent characters it is preferred as a hypothesis for explaining the relationships of this sample of taxa. The cladistic analysis of this selection of pimoid taxa produces results (i.e. tree topologies) fully congruent with those obtained in Hormiga (in press), in which a total of 20 pimoid species were analyzed together with the same sample of linyphiids and the two outgroup genera.

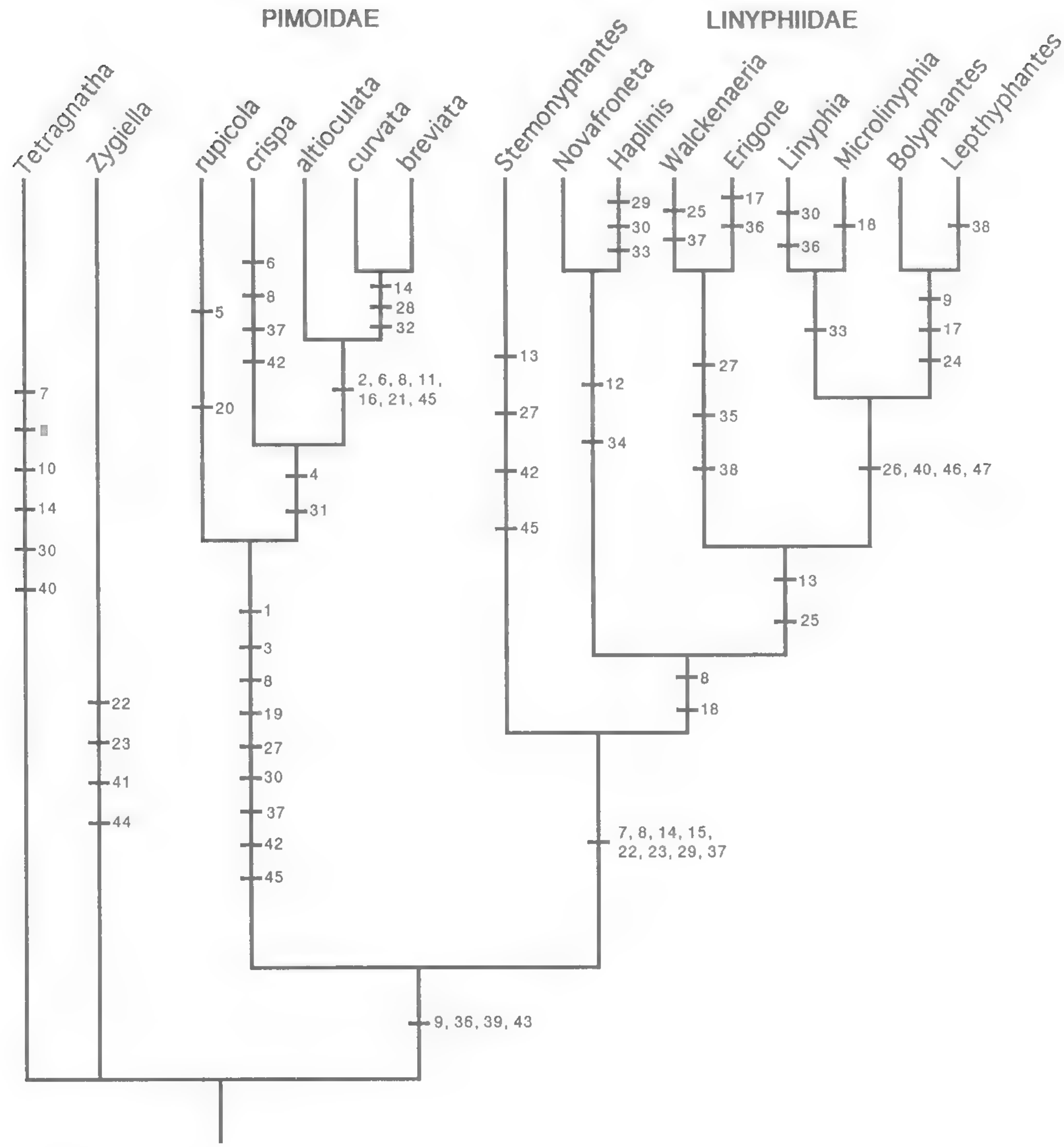

FIG. 1. Preferred minimum length cladogram for the taxa and characters in Table 1 (three equally parsimonious alternative topologies exist; see text). The cladogram length is 81 steps; the consistency and retention indices are 74 and 81, respectively.

DISCUSSION

Monophyly of the Pimoid-Linyphiid Clade

Pimoids and linyphiids emerge as a monophyletic assemblage, unambiguously supported by the presence of cheliceral stridulatory striae, patellar autospasy, and the enlargement of the peripheral cylindrical spigot base in the PLS. Paracymbial apophyses are secondarily absent (i.e. lost) in the pimoid-linyphiid clade, although they are regained in the Micronetini. All these characters (except the patellar autospasy) exhibit some degree of homoplasy.

Millidge (1988) rejected the inclusion of Linyphiidae in Araneoidea, and instead related them to Agelenidae (*s. lat.*), Amphinectidae, and other taxa currently placed in Amaurobioidea and Dictynoidea. His hypothesis on the exclusion of linyphiids from Araneoidea has been elegantly rebutted by Coddington (1990b), who stated that linyphiids exhibit 9 out of the 10 synapomorphies that support the monophyly of Araneoidea. Pimoids share the same 9 araneoid synapomorphies. Peters and Kovoor (1991) studied the structure, histochemistry, and function of the spinning apparatus of *Linyphia triangularis* and concluded that the data did not provide any indication of close relationship between Linyphiidae and Agelenidae. Certainly Millidge's hypothesis lacks character support. The available data clearly argue in favor of the inclusion of the pimoid-linyphiid clade in Araneoidea. Furthermore, Millidge's idiosyncratic method of phylogenetic inference is flawed because, among other things, it seems to suggest the use of symplesiomorphies (by 'reversing' the outgroup comparison method) to establish family relationships (p. 254). It is well known that grouping by plesiomorphic character states produces paraphyletic groups (Hennig, 1966) and therefore should be avoided.

A major problem in araneoid phylogeny is the placement of the theridiid and the linyphiid-pimoid lineages, in which the orb web architecture has been lost (Coddington and Levi, 1991). Cyatholipidae have been suggested as another possible sister group of linyphiids (Coddington, 1990a). While the sheet web might support this hypothesis, the evidence provided by the morphological data is, at the moment, inconclusive.

Monophyly of Pimoids

Pimoid monophyly is supported by nine synapomorphies, six of them from male palpal morphology and two from spigot morphology. It is interesting to note that none of the pimoid-linyphiid synapomorphies refer to palpal morphology, which is quite different in these two lineages and might reflect a very old time of divergence and/or a rapid rate of character change for the male genitalia. The highly derived spigot morphology of pimoids is unique among araneoids. With the exception of *Stemonyphantes* no other araneoids have been reported to loose all the aciniform gland spigots.

Monophyly, Character Analysis, and Cladistic Structure of Linyphiids

Linyphiid monophyly is supported by eight synapomorphies. Seven of these eight characters (i.e. all except character 8) are homoplasious. With the increasing number of studies that use quantitative cladistic methods it is becoming clear that homoplasy is quite common (Coddington and Levi, 1991). Coddington (1990b) noted that many of the most useful characters for the inference of araneomorph phylogeny were homoplasious. Griswold (in press), in his study of the Lycosoidea, arrived at a similar conclusion for female genitalic characters. Linyphiids are not an exception, and this fact will not surprise most linyphiid taxonomists. For example, intersegmental paracymbia (character 7), similar to the linyphiid type, are also found in *Tetragnatha* and *Pachygnatha* (Levi, 1981:274, 286). Millidge (1988:258) considers the two latter cases as integral paracymbia, different from the linyphiid type, in which case the homoplasy would be removed from this character. But regardless of possible instances of homoplasy, the intersegmental paracymbium is a putative synapomorphy for linyphiids. Coding the paracymbial morphology (character 8) is not an easy task. I have taken a conservative approach by coding it with a high number of character states (seven), in part due to the high morphological diversity of this structure. The coding used produced no extra length (the character's consistency index is 1), but by itself it provides little grouping information (only two states occur in more than one taxon). The states are thus 'ordered' by the tree topology generated by all characters (the final optimization of the character on the cladogram was done by hand, because several equally parsimonious optimizations exist). Blest (1979) and Wunderlich (1986) consider that mynoglenines and erigonines share the same type of paracymbium ('simple paracymbium'). Van Helsdingen (1986:122) argued against this view by pointing out that many linyphiine genera also have the so-called 'simple' paracymbium. Although in some cases erigonines and mynoglenines seem to have morphologically 'simpler' paracymbia (short proximal and distal branches, sometimes J-shaped, without apophyses) than some of the linyphiini and micronetini, I cannot see a clear-cut distinction between these two states. I have coded all the linyphiids (except *Stemonyphantes*) as having the same overall paracymbium morphology (with a proximal and a distal branch of varying length and being more or less J or U-shaped). The paracymbium type found in *Stemonyphantes* is considered by Millidge (1988) as an intermediate form between the integral and intersegmental types. This latter type of paracymbium is inferred to be the primitive state for linyphiids. This state is subsequently transformed into the paracymbium morphology found in the rest of linyphiids. Coding mynoglenines and erigonines as sharing the same unique character state (i.e., the 'simple' paracymbium), as Blest and Wunderlich have suggested, produces no changes in the cladogram topology.

The presence of a median apophysis and a conductor on the tegulum is regarded as plesiomorphic for araneoids (Coddington, 1990a). Pimoids have a conductor and a median apophysis (Hormiga, in press). The absence in linyphiids of a true (i.e. tegular) conductor and a median apophysis (Coddington, 1990a) are regarded as synapomorphies for linyphiids (characters 15 and 14, respectively). Two potential synapomorphies of linyphiids, the radix and the column, are waiting for resolution of the outgroup of the pimoid-linyphiid clade in order to be tested. The linyphiid radix (character 22) might be homologous to the araneid radix, and therefore plesiomorphic for linyphiids, if araneids are the sister group of pimoid-linyphiids (Coddington, 1990a). The same happens with the linyphiid column or stalk (*sensu* Saaristo, 1971; character 23) that connects the radix to the tegulum/suprategulum. The column could be homologous to the distal haematodocha if araneids are sister to the pimoid-linyphiid clade (Coddington, 1990a). If that is not the case, the homology of the linyphiid radix and column with its presumed equivalents in Araneidae might be refuted, and these characters would function as synapomorphies of linyphiids (this latter alternative is the one mapped on Figure 1). Linyphiids seem to have reduced the number of prolateral trichobothria in the male palpal tibia (character 29) from two (pimoids and outgroups in the data set) to one. However this putative synapomorphy of linyphiids might loose generality (i.e. might be refuted) in a data set with a larger sample of taxa. The same might happen to the number of retrolateral teeth on the female chelicera (character 37), which is four or more in all but one of the linyphiid taxa in the data set, and acts as putative synapomorphy for linyphiids.

The linyphiid suprategulum (character 13) is a projection of the tegulum that bears the column and through which the sperm duct passes (Saaristo (1971, 1975); Millidge (1977); Coddington (1990a)). However, the suprategulum might not be homologous across all linyphiids. The tegular projection that Blest (1979, figs 596-602) and Blest and Pomeroy (1978, figs 2, 4) call the 'suprategulum' in New Zealand mynoglenines does not bear the column (which in some cases is far from it, e.g. *Pseudafroneta*, in Blest's figure 597) and has no sperm duct going through it. I have interpreted the mynoglenines as lacking a suprategulum (*sensu* Saaristo) and coded its tegular apophysis as a structure synapomorphic for mynoglenines and not homologous to the suprategulum ('mynoglenine tegular apophysis', character 12). However, the tegular apophysis of *Haplinis* seems to be functionally analogous to the suprategulum in some linyphiids (van Helsdingen (1965, 1969); Blest and Pomeroy (1978)) in engaging the socket of the epigynal scape, but data on the functioning of the genitalia across taxa are still very scarce. The suprategulum of *Stemonyphantes* is articulated to the tegulum by means of a membranous connection (van Helsdingen, 1968:124; pers. observ.) and is different from the rest of linyphiid suprategula which are fused to the tegulum (character 13). The cladogram in Figure 1 suggests the possibility of independent origins for these two types of suprategula, and therefore questions its homology (secondary absence of the suprategulum in the mynoglenines -versus independent gains-requires one additional step).

The linyphiid embolic membrane (van Helsdingen, 1969) is not homologous to the araneoid conductor because of their different position (but see Coddington, 1990a:16). The embolic membrane (character 18) is a putative synapomorphy for all linyphiids, with the exclusion of the basal genus *Stemonyphantes*. The 'embolic membrane' *Microlinyphia* is not an outgrowth of the column, as in most linyphiids (van Helsdingen, 1986:123), but a structure 'arising from (the) membranous connection of radix, base of embolus, and dorsal side of lamella' (van Helsdingen, 1970:6). I have interpreted it as not homologous to the column-positioned embolic membranes, but the nature of this membrane remains dubious. The alternative, i.e. coding it as an embolic membrane shifted to a radical position in *Microlinyphia*, produces no change in the cladogram topology.

The terminal apophysis (character 25) is a synapomorphy for erigonines plus linyphiines, but its interpretation offers several problems. The first is its homology with its homonym in araneids (Saaristo 1971, 1975; Coddington, 1990a). Such homology is dependent, among other things, on a sister-group relationship between araneids and linyphiids (plus pimoids), but even so the homology is not obvious. *Zygiella x-notata* (which is considered here as an araneid) lacks anything similar to a terminal apophysis, pimoids lack the radix (therefore, we do not know if they ever had such apophysis), and basal linyphiids (i.e. *Stemonyphantes* and the mynoglenines) have simple radices and no terminal apophysis. The cladogram in Fig. 1 suggests independent origins (i.e. non homology) for the terminal apophysis in araneids and linyphiids. If the embolic division of *Stemonyphantes* is interpreted as simple (and not simplified) it also suggests that complex embolic divisions in araneids and in linyphiids arose independently. This latter interpretation would question the monophyly of araneids plus linyphiids (e.g. Coddington, 1990a:14). Second, and at a less inclusive level, not all erigonines and linyphiines have a terminal apophysis. Evaluation of the homology of these apophyses requires a more detailed cladistic structure for the family (i.e. more taxa and more characters). Another radical sclerite, the lamella characteristica (character 26), is a putative synapomorphy for the linyphiines. Further support for the monophyly of Micronetini plus Linyphiini is given by the loss of metatarsus IV trichobothrium (character 40) and the position of the male during the construction of the sperm web and during ejaculation (characters 46 and 47). The phylogenetic information provided by the latter two characters should be regarded as provisional, because of the high number of missing entries for these characters in the matrix. According to Blest and Pomeroy (1978) *Haplinis* is unique among linyphiids in having an expansion of the palp prior to its locking to the female genitalia, while in the remaining linyphiids for which this trait is known the male first locks its palp to the epigynum and then expands the haematodocha. However, in a recent study on African linyphiids Scharff (1990:62) described a similar expansion prior to locking for *Neriene kibonotensis* (Tullgren). More data on the distribution of this character are needed in order to establish it as a mynoglenine synapomorphy.

Erigonine monophyly is supported by the retrolateral tibial apophysis of the male palp, the loss of the female palpal claw, and the desmitracheate tracheal system (*sensu* Millidge, 1984). In the present dataset the epigynal atrium (character 33) is the only synapomorphy supporting the monophyly of Linyphiini. An epigynal atrium is also present in the mynoglenine genus *Haplinis* (Blest, 1979:100) but absent in *Novafroneta* (Millidge 1984:241). The cladogram suggests independent origins for these two atria; its homology is therefore questionable (similar epigynal atria are also present in other linyphiids, not included here, that are not closely related to the Linyphiini; Millidge, 1984; van Helsdingen, *in litt.*). Three synapomorphies support the monophyly of Micronetini: the paracymbial apophyses, a short embolus (it also occurs in *Erigone*), and the presence of Fickert's gland in the radix.

The nature of the clypeal glands is another interesting problem in linyphiid evolution. Whether the mynoglenine sub-ocular sulci are or are not homologous to the male erigonine post-ocular sulci is a matter of debate. Mynoglenine sub-ocular sulci are found both in males and females (they are very similar in both sexes; juveniles also have functional sulci, at least in the species of *Haplinis* studied by Blest and Taylor, 1977), they do not play any active role during the courtship (at least in the species studied by Blest and Pomeroy, 1978), and they probably elaborate defensive secretions (Blest and Taylor, 1977; but this latter hypothesis has not been empirically tested, although the unique ultrastructure of the clypeal secretory cells is consistent with the synthesis of a toxic product). On the other hand, erigonine post-ocular sulci (as well as the cephalic elevations) are found (mostly) in adult males. These erigonine sulci usually have pores associated with glands that are cytologically different from those of the mynoglenine sulci (Blest and Taylor, 1977; Schaible *et al.*, 1986; Schaible and Gack, 1987), and they play an active mechanical role during the courtship (they are gripped by the female cheliceral fangs). Nevertheless, these erigonine glands are not always associated with cephalic specializations. Mynoglenine and erigonine ocular sulci can be interpreted as homologous structures within the same transformation series or as two independent developments. The available evidence is not easily interpreted in either way. The mynoglenine and erigonine sulci differ in their position, in the cytological structure of their associated glands, and in their behavioral role. It seems that the available data argue against the homology hypothesis, since they fail to meet the classical homology criteria of position and detailed similarity. Congruence with other character systems offers a powerful test of the homology hypothesis of the sulci. Blest (1979:165) argued that the most economical hypothesis (i.e. parsimonious) 'would suggest that the sulci of the mynoglenine type gave rise directly to the kind found in Erigoninae'. Mapping his hypothesis on his cladogram (*op. cit.*, p. 172, which in parenthical notation can be summarized as: Mynogleninae (Linyphiinae, Erigoninae)) requires the gain of the mynoglenine type of sulci in the common ancestor of all linyphiids, profound modifications (morphological, cytological, and behavioral) of the sulci to achieve the erigonine type of sulci (either in the ancestral erigonines or at the level of the linyphiine-erigonine ancestor) and finally the loss of the sulci (and its accompanying glands and behavior) in the linyphiines. The alternative hypothesis (i.e. non homology of mynoglenine and erigonine sulci) maps on the mentioned cladogram as two independent gains of the two types of sulci. The evolution in parallel of the erigonine and mynoglenine sulci would then account for their differences. Although the latter hypothesis is more parsimonious (in both Blest's and my cladogram) this question cannot be truly tested until more data (taxa, particularly those with any type of sulci and/or glands, and information on the glands) are included in the data set. This is due to the effect that mynoglenine and erigonine cladogram topologies might have on the optimization of the character(s) on the linyphiid cladogram. Only then we will be able to asses alternative hypotheses on the evolution of these cephalothoracic specializations.

The linyphiid tracheal system needs to be studied in detail and re-evaluated. New morphological descriptions are needed, since at least some of the available comparative data are inaccurate (see above). Millidge's (1986, figure 12) scheme for the evolution of the tracheal system in linyphiids is therefore not valid, because it is partially based on inaccurate data.

The most parsimonious hypothesis to explain the data presented in this study is the cladogram depicted in Figure 1, which suggests (as well as the three equally parsimonious alternatives that exist) relationships different from those proposed by Wunderlich (1986:106). The mynoglenines are considered here to be relatively basal linyphiids, while Wunderlich suggested them as sister to the erigonines. Both hypotheses agree on considering the pimoids and *Stemonyphantes* as the most basal clades, and on the monophyly of the Micronetini plus the Linyphiini. To use either of these two phylogenies as a classification would be premature. Wunderlich did not explicitly list the synapomorphies that define the monophyletic groups in his cladogram, synapomorphies are mixed up with diagnostic characters (some of which are not synapomorphic), and there is no mention of the genera included in each monophyletic group, even in a schematic manner. My study should be considered only a preliminary sketch of linyphiid relationships. Clearly, a much larger sample of taxa is needed before the main monophyletic groups can be established. The addition of new taxa and new characters might affect the cladogram topology presented here. As we have seen, non-homoplasious characters for wide ranges of taxa are more the exception than the rule, and different character systems often delimit conflicting monophyletic groups. When large numbers of taxa and characters are studied quantitative studies are imperative. Cladistic studies provide explicit and testable hypotheses of relationship and are recognized as the most reliable method for retrieving the phylogenetic pattern that underlies organic diversity. Not until this approach is adopted will advances in linyphiid higher classification become a reality.

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LITERATURE CITED

BLEST, A.D. 1979. Linyphiidae-Mynogleninae. Pp. 95-173. In R.R. Forster and A.D. Blest. The spiders of New Zealand, part V. Otago Museum Bulletin 5: 1-173.

BLEST A.D. & POMEROY, G. 1978. The sexual behaviour and genital mechanics of three species of *Mynoglenes* (Araneae: Linyphiidae). Journal of Zoology (London) 185: 319-340.

BLEST A.D. & TAYLOR, H.H. 1977. The clypeal glands of *Mynoglenes* Simon and some other linyphiid spiders. Journal of Zoology (London) 183: 473-493.

CARPENTER, J.M. 1988 Choosing among multiple equally parsimonious cladograms. Cladistics 4: 291-296.

CODDINGTON, J.A. 1989. Spinneret silk spigot morphology: evidence for the monophyly of orbweaving spiders, Cyrtophorinae (Araneidae), and the group Theridiidae plus Nesticidae. Journal of Arachnology 17: 71-95.

1990a. Ontogeny and homology in the male palpus of orb-weaving spiders and their relatives, with comments on phylogeny (Araneoclada: Araneoidea, Deinopoidea). Smithsonian Contributions to Zoology 496: 1-52.

1990b. Cladistics and spider classification:

Araneomorph phylogeny and the monophyly of orbweavers (Araneae: Aranemorphae; Orbiculariae). Acta Zoologica Fennica 190: 75-87.

CODDINGTON, J.A. & LEVI, H.W. 1991. Systematics and evolution of spiders (Araneae). Annual Review of Ecology and Systematics 22: 565-592.

FARRIS, J.S. 1969. A successive approximations approach to character weighting. Systematic Zoology 18: 374-385.

1988. Hennig86, version 1.5. (Computer program distributed by its author, 41 Admiral Street, Port Jefferson Station, NY 11776).

GRISWOLD, C.E. (in press). Investigations into the phylogeny of lycosoid spiders and their kin (Arachnida, Araneae, Lycosoidea). Smithsonian Contributions to Zoology.

HENNIG, W. 1966. 'Phylogenetic Systematics'. (University of Illinois Press: Urbana). 263pp.

HORMIGA, G. In press. A revision and cladistic analysis of the spider family Pimoidae (New Rank, Araneoidea, Araneae). Smithsonian Contributions to Zoology

LEVI, H.W. 1981. The American orb-weaver genera *Dolichognatha* and *Tetragnatha* north of Mexico (Araneae: Araneida, Tetragnathinae). Bulletin of the Museum of Comparative Zoology 149: 271-318.

MILLIDGE, A.F. 1977. The conformation of the male palpal organs of Linyphiid spiders and its application to the taxonomic and phylogenetic analysis of the family (Araneae: Linyphiidae). Bulletin of the British Arachnological Society 4: 1-60.

1984. The taxonomy of the Linyphiidae, based chiefly on the epigynal and tracheal characters (Araneae: Linyphiidae). Bulletin of the British Arachnological Society 6: 229- 267.

1986. A revision of the tracheal structures of the Linyphiidae (Araneae). Bulletin of the British Arachnological Society 7: 57-61.

1988. The relatives of the Linyphiidae: phylogenetic problems at the family level (Araneae). Bulletin of the British Arachnological Society 7:253-268.

PATTERSON, C. 1982. Morphological characters and homology. Pp. 21-74. In Joysey, K.A. and Friday, A.E. (eds) 'Problems of Phylogenetic Reconstruction'. (Systematics Association Special Volume No. 21, Academic Press: London and New York).

PETERS, H.M. & KOVOOR, J. 1991. The silk-producing system of *Linyphia triangularis* (Araneae, Linyphiidae) and some comparisons with Araneidae. Structure, histochemistry and function. Zoomorphology 111: 1-17.

PLATNICK, N.I., CODDINGTON, J.A., FORSTER, R.R. & GRISWOLD, C.E. 1991. Spinneret morphology and the phylogeny of haplogyne spiders (Araneae, Araneomorphae). American Museum Novitates 3016: 1-73.

SAARISTO, M.I. 1971. Revision of the genus *Maro* O.P.-Cambridge (Araneae, Linyphiidae). Annales Zoologici Fennici 8: 463- 482.

1975. On the evolution of the secondary genital organs of Lepthyphantinae (Araneae, Linyphiidae). Proceedings of the 6th International Arachnological Congress (Amsterdam, 1974): 21-25.

SCHAIBLE, U. & GACK, C. 1987. Zur Morphologie, Histologie und biologischen Bedeutung der Kopfstrukturen einiger Arten der Gattung *Diplocephalus* (Araneida, Linyphiidae, Erigoninae). Verhandlungen des Naturwissensschaftlichen Vereins in Hamburg 29: 171-180.

SCHAIBLE, U., GACK, C. & PAULUS, H.F. 1986. Zur Morphologie, Histologie und biologischen Bedeutung der Kopfstrukturen männlicher Zwergspinnen (Linyphiidae: Erigoninae). Zoologische Jahrbücher (Systematik) 113(3): 389-408.

SCHARFF, N. 1990. Spiders of the family Linyphiidae from the Uzungwa mountains, Tanzania (Araneae). Entomologica Scandinavica, Supplement No. 36: 1-95.

VAN HELSDINGEN, P.J. 1965. Sexual behaviour of *Lepthyphantes leprosus* (Ohlert) (Araneidae: Linyphiidae), with notes on the function of the genital organs. Zoologische Mededelingen (Leiden) 41: 15-42.

1968. Comparative notes on the species of the holarctic genus *Stemonyphantes* Menge (Araneida, Linyphiidae). Zoologische Mededelingen (Leiden) 43(10): 117-139 .

1969. A reclassification of the species of *Linyphia* Latreille, based on the functioning of the genitalia (Araneida, Linyphiidae) I. Zoologische Verhandelingen (Leiden) 105: 1-303

1970. A reclassification of the species of *Linyphia* Latreille, based on the functioning of the genitalia (Araneida, Linyphiidae) II. Zoologische Verhandelingen (Leiden) 111: 1-86.

1983. Mating sequence and transfer of sperm as a taxonomic character in Linyphiidae (Arachnida: Araneae). Verhandlungen des Naturwissensschaftlichen Vereins in Hamburg 26: 227-240.

1986. World distribution of Linyphiidae. Pp. 121-126. In Eberhard W.G., Lubin Y.D., Robinson B.C. (eds) 'Proceedings of the Ninth International Congress of Arachnology, Panama, 1983'. (Smithsonian Institution Press: Washington, D.C.).

WUNDERLICH, J. 1986. 'Spinnenfauna gestern und heute'. (Erich Bauer Verlag bei Quelle and Meyer: Wiesbaden).

CRITERIA FOR IDENTIFYING THERMAL BEHAVIOUR IN SPIDERS: A LOW TECHNOLOGY APPROACH

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The widespread occurrence of thermal behaviour in diurnally active web spiders is either largely ignored or not recognised. Thus it obfuscates some explanations of the function of the stabilimentum on spiders webs. Thermal behaviours of four spiders (*Nephila edulis, N. maculata, Gasteracantha minax* and *Neogea* sp.) are examined using technology which is often inappropriate for field studies. Many thermal behaviours are recognised as well as behaviours which facilitate thermal behaviour. The thermal correlates of these behaviours are established. Some observational criteria are derived, which require only simple equipment, by which thermal behaviours may be recognised in the field and distinguished from other behavioural patterns.□*Araneae, orb-weavers, thermal behaviour, thermoregulation, stabilimentum.*

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Many orb-web spiders remain active at the web hub during the day, where they can continue to feed, mate, and defend their web site from the same and other species, as well as produce or respond to attractant signals (acoustic, tactile, visual or chemical). The seasonal and diurnal duration of this activity can be extended by adopting behaviours that warm the spider (Robinson and Robinson, 1974, 1978; Biere and Uetz, 1981) when it would otherwise be too cold or else that prevent it from overheating (Lubin and Henschel, 1990; Humphreys, 1978, 1987a, 1991, 1992).

I consider below mainly behaviours that prevent overheating. In essence, in hot weather the spider postures so as to align the long axis of its body with the sun's rays and in this position it tracks the sun's apparent movement during the day. Such behaviour is not exclusive to spiders of open country nor in tropical climates but is found also in both temperate and tropical forest spiders (Biere and Uetz, 1981; Humphreys, 1991, 1992 and unpublished). The standard interpretation of this thermal behaviour relies on a simple physical model; posturing minimises the projected surface area (silhouette) exposed to the sun's radiation and so reduces the heat load (Fig. 1), lowering equilibrium body temperature (Willmer and Unwin, 1981: but see Humphreys, 1986) or, in an anti-predator hypothesis, minimising the silhouette against the brightest background, else the body area most brightly illuminated.

Recent observations have shed some light on this seemingly simple process and revealed a sequence of behaviours serving to reduce progressively the heat loading, behaviours that are themselves mostly graded (Humphreys, 1992). These include stilting, drooping, orientation, front leg raising, abdomen pointing, posturing, front leg rotation and web abandonment. Associated behaviours include silk laying and agitation (Humphreys, 1992 and unpublished). In addition, the use of a disc stabilimentum as a sun shade, suggested by Robinson and Robinson (1973: 283), is an effective thermal behaviour in *Neogea* sp. (Humphreys, 1992). Such behaviours not only maintain the animal within its heat tolerance range, but also serve to maintain the body temperature (T_b) within a narrow range (presumably some optimum temperature) for extended periods of time (Humphreys, 1974, 1978, 1991). As body temperature has wide implications in physiological, behavioural, ecological and evolutionary contexts (Willmer, 1991), it is important to recognise thermal behaviour in spiders in order to allow different types of explanations for their behaviours.

That the thermal behaviour of spiders is not being recognised or is not being reported in the literature can be drawn from work on stabilimenta on spiders' webs. While stabilimenta have many different forms, they are mostly thought to provide mechanical support (Robinson and Robinson, 1973), to function as anti-predator devices (Eberhard, 1973, Edmunds and Edmunds, 1986; Lubin, 1986), to attract prey (Ewer, 1972; Craig and Bernard, 1990) or to collect water (Olive, 1980; see also Ewer, 1972; Robinson and Robinson, 1973: 283). *Neogea* sp. in

Papua New Guinea uses a disc stabilimentum as a parasol, which, together with a sequence of other behaviours, each themselves graded, reduces its heat loading (Humphreys, 1992). The demonstration that stabilimenta may be used in a thermoregulatory role raises questions concerning many observations which have been interpreted as supporting the anti-predator role of stabilimenta.

Some observations and deductions have resulted in an anti-predator function being ascribed to the stabilimentum. However, in the absence of other information, these observations are equally open to interpretation in terms of thermoregulatory hypotheses (see Humphreys, 1992). For example -1. Only spiders that remain at the hub of the web during the day produce stabilimenta (Eberhard, 1973). 2. Spiders with stabilimenta may shuttle from one side of the web to the other (*ibid.*). 3. The legs assume an 'aligned posture' by day but not by night (*ibid.*). 4. The amount of silk used is directly related to openness of the habitat (Marson, 1947).

Eberhard (1973) found that *Uloborus diversus* Marx used more silk in its stabilimentum on light than on dark nights (see also 4. above). The trend for larger stabilimentum at brighter sites camouflaged those spiders most susceptible to attack. However, without pertinent behavioural data, it is not possible to refute the hypothesis that the open sites are more exposed to direct sunlight and thus that the stabilimenta are used to protect the spider from ultra violet light (but see Craig and Bernard, 1990) or to reduce its heat load.

Posturing by spiders that remain by day at the web hub is rarely mentioned in the literature on stabilimenta and defense mechanisms. For example, although Edmunds and Edmunds (1986: 83) found that species of *Argiope*, *Nephila*, *Leucauge*, *Cyrtophora* and the Gasteracanthinae remain at the hub of the web during the day, they made no mention of posturing. In the Australasian region species in all these genera readily posture and track the sun (Humphreys, 1991, 1992; W.F. Humphreys, unpublished).

Clearly, thermoregulation hypotheses need more consideration in field studies of diurnally active spiders. More recently this has occurred (Henschel *et al.*, 1992; Humphreys, 1991, 1992; Lubin and Henschel, 1990; Ward and Henschel, 1992) but such studies often require expensive equipment to examine the thermal behaviour. Such equipment may be inappropriate to a field biologist primarily interested in observation and manipulation to examine behavioural or sociobiological problems. There needs to be some observational criteria using only low technology by which thermal behaviour may be recognised and distinguished from other behavioural patterns.

The examination of thermoregulation in orb-weaving spiders is problematical as most methods used on vagrant spiders (thermal preferendum apparatus, thermocouple implantation, temperature transmitters) are not appropriate. The most promising apparatus for such studies is the use of remote infrared telemetry (Suter, 1981; Humphreys, 1991, 1992), although model spiders may be effectively used to determine T_e (Riechert and Tracy, 1975; Henschel *et al.*, 1992).

Can criteria be established which would enable workers, using cheap and readily available equipment, to establish that spiders are behaving in a manner consistent with thermoregulation and to identify the thermal conditions under which they initiate such behaviour?

METHODS

Observations on *Nephila edulis* (Labillardière) were made both on Rottnest Island and in Perth, on *Gasteracantha minax* Thorell in the southwest, of Western Australia, and on *Nephila maculata* (Fabricius) in mangrove at Port Benoa, Bali, Indonesia.

Spider temperatures were recorded from 1100 -1500 hours using an infra-red thermometer, described elsewhere (Humphreys, 1991, 1992). The temperature was recorded of undisturbed spiders resting above and below the hub of the web, both in the shade and in the sun. It was recorded at intervals and as soon as possible (<3s) after a change in behaviour. Spider behaviour changed according to the incident light; this varied because the site was sometimes shaded by trees or by clouds. To induce more behavioural sequences the spider was sometimes shaded artificially and the direction and strength of the incident sunlight adjusted using a mirror. A plane mirror was used to alter the apparent position of the incident radiation at about the same intensity as the natural sunlight and a concave mirror was used to alter the apparent position of the incident radiation and at an intensity continuously variable from greater to less than the intensity of the direct sunlight. In the field, control of intensity was crude in the wind owing to movement of the web, and hence the spider; control of the intensity

Behaviour	Mean	s.d.	n	Range
Repose in shade	32.6 a	2.10	12	29.0-35.1
Repose in partial sun	32.4 ab	1.59	19	29.2-34.3
Repose in sun	35.0 b	1.66	47	31.6-38.1

TABLE 1. Mean temperature (T_b °C) of *N. edulis* in Repose position on Rottnest Island, Western Australia. T_b of spiders in Repose differs according to energy intensities of their location (shaded, partly shaded, sunlight: ANOVA - $F_{S\ 2,75} = 19.895$, $P<0.001$). Common letters include means not differing significantly (Fisher's PLSD at $\alpha = 0.05$).

of radiant energy is therefore relative and greater or less than the natural incident radiation.

The following temperatures are mentioned: T_a = of ambient shaded air; T_b = of the spider's body which by default is the abdomen (T_{ab}), otherwise the thorax (T_{th}). The environmental temperature (T_e) which is used as a shorthand for the effective heat load on the spider taking account of all energy gains and losses. Means are followed in parentheses by the standard deviation of the mean, and sample size.

Definitions required for this discussion are given below (see also Humphreys, 1991, 1992).

Abandon web: the spider leaves the web, often after a sequence of very agitated movements, and moves to the shade provided by the objects to which the main anchor lines of the web are attached.

Abdomen pointing: the abdomen alone is orientated to the sun as a prelude to full posturing. This behaviour is strongly represented in some species (Humphreys, 1992).

Agitation and body lift: the spider appears agitated and circles its body around the web's hub and in the process the body is raised away from the web. The latter is sometimes seen on its own and they are included here under the same behaviour. This body lift is not comparable to stilting (Humphreys, 1992).

Drooping: the spider hangs limply from the back legs with apparent loss of hydrostatic pressure; the appearance is like that adopted by a spider immediately after moulting while the new cuticle is hardening.

Fabian position (Humphreys, 1991): the spider aligns its long axis parallel to the direction of incident sunlight with the prosoma facing away from the sun. This position may be achieved by orientation and/or posturing. When the incident sunlight is parallel to the web plane then the Fabian position may be the same as the Repose position (Humphreys, 1991). Continued adoption of the Fabian position results in the long axis of the spider tracking the sun during the day.

Front legs raised: legs I and II are raised off the web and aligned parallel to the incident radiation; this occurs as a graded sequence with the first pair being raised before the second pair.

Orientation: the angle of the saggital plane of the spider is rotated to lie parallel to the solar azimuth while the long axis of the body stays in the plane of the web.

Part orientation: the spider is not in the Repose position and has partly orientated its saggital plane between the Repose position and the orientated position.

Posturing: change in the angle between the web plane and the anterior-posterior axis of the spider.

Repose position: spiders occupy the lower or upper surface of the hub with the prosoma pointing downwards; the anterior-posterior axis of the spider is parallel to the plane of the web.

Rotate front legs: following front legs raising the legs are rotated forwards such that they are stretched out in front of the spider and lie in the shade of its body when it is fully postured; this may occur as a graded sequence with the first pair being rotated before the second pair.

Silk laying: adjusts the web stuctrure near the hub apparently to aid leg placement the better to posture and orientate to achieve the full Fabian position. This facilitates subsequent thermoregulatory behaviour but is not itself thermoregulatory.

Start to posture: when the spider changes the angle between its anterior-posterior axis and the plane of the web such that its long axis is parallel to the incident radiation.

Stilting: describes the 'standing on tiptoe' behaviour of scorpions used to prevent overheating (Alexander and Ewer, 1958); here it describes similar behaviour in spiders (Humphreys, 1992).

EVIDENCE

Statements otherwise unsupported are based on my unpublished observations.

Repose Position And Thermoregulation

Spiders adopt the repose position if T_e is below some critical level and they do so whether they are in shade or sun, hence, direct sunlight alone does not cause spiders to posture. However, T_b in sun is higher than in shade (Table 1). For example, during cool weather (low T_a) in the sun and during hot weather in the shade all individuals are in the Repose position on their webs if not otherwise engaged in activities such as mating, web building, etc.

When T_e is not sufficient to cause posturing in *G. minax* the proportion of spiders in the Repose position during daylight does not differ between sunlit (36/38) and shaded (32/33) sites ($\chi^2_1 = 0.016$, P=0.90).

The mean T_b temperature of *N. edulis* in the Repose position was directly related to the intensity of the incident radiation such that spiders in the sun were hotter than partly or fully shaded spiders (Table 1).

Spiders on non-horizontal webs almost invariably rest on the underside of the web with the prosoma pointing down. However, spiders resting in positions other than the Repose position should not be taken as proof of thermoregulatory behaviour because some species, such as *Verrucosa* and *Cyclosa*, reputedly adopt a head up stance (Foelix, 1982: 139), as does *G. minax* at night and *Argyrodes antipodianus* O.P. Cambridge, generally.

Orientation and Posturing: Evidence for Thermoregulatory Function

In hot weather, spiders orient or posture on the web to attain the Fabian position and then track the sun's apparent movement. They do this irrespective of web orientation. Heat and sunlight are needed to obtain these behaviours. On very hot days, spiders may leave the web altogether and seek shade. Large spiders assume Fabian posture earlier than small ones possibly because under given environmental conditions large spiders reach higher body temperatures. However, small spiders may have lower threshold T_b's.

In hot weather an individual spider in the sun will use reorientation and/or posturing to align the anterior-posterior axis of its body parallel to the direction of incident sunlight with the prosoma facing away from the sun and thus achieve the Fabian position (Robinson and Robinson, 1974, 1978; Humphreys, 1991, 1992). The spider will adjust this position during the day and track the apparent movement of the sun (Humphreys, 1991).

In hot weather all individuals in the sun orientate in the same direction irrespective of the orientation of their webs; namely they all assume the Fabian position by posturing and/or reorientation (Humphreys, 1991).

Heat alone does not cause the thermal behaviour because in hot weather under heavily overcast conditions spiders do not assume the Fabian position. However, if intermittent direct sunlight strikes the spider it assumes the Fabian position intermittently.

On very hot days spiders may assume the Fabian position in the morning and afternoon but leave the web to seek shade during the middle of the day. Such activity patterns have been reported for many heliothermal spiders (Humphreys, 1978, 1987a, 1987b) and other taxa (e.g. reptiles: Heatwole, 1970).

N. edulis abandons the web at 44.8°C (±0.50, 3) and moves into shade. In Perth, Western Australia, when the shaded air temperature was extreme (46.2°C) many *N. edulis* failed to seek cooler places and fell dead from their shaded webs through heat stress (G.A. Harold, pers. comm., 1991).

Large spiders assume the Fabian position earlier in the day than do small spiders (e.g., *N. maculata*)– this is consistent with the thermoregulation hypothesis because larger bodies have a higher temperature excess (Willmer and Unwin, 1981). However, the threshold temperatures for given behaviours could be size related and lower in small than in large spiders. This is consistent with the seeming generality that the tolerance zones of animals are related to the temperatures experienced. For example, very small *N. edulis* start to posture at 36.0°C (±2.39, 4), significantly cooler, by an average of 4.4°C ($F_{s1,25}$ =13.279, p=0.002), than adult spiders undergoing the same behaviour (40.4°C ±2.16, 27).

Orientation and Posturing in Response to Manipulation

Experiments with redirected and intensified sunlight can be conducted to influence the behaviour of spiders to assist in determining whether the behaviour is thermoregulatory without having to measure body temperature. The results are consistent for several species including *Arachnura higginsi*, *N. edulis*, *N. maculata*, *G. minax* and *Neogea* sp.

In cool sunny weather when the spiders are in the Repose position, additional heating (by concentrating redirected sunlight using a concave mirror), results in the spider orientating–and/or posturing if necessary–to assume the Fabian position. The redirected sunlight does not alone alter the behaviour of the spider (sunlight redirected at natural intensity using a plane mirror). Hence, posturing is dependent on the intensity of the heat applied.

In hot weather a spider which has assumed the Fabian position will resume the Repose position if clouds obscure the sun or it is artificially shaded even if lower than the natural insolation is reflected onto it by means of a concave mirror.

Spiders in the Fabian position in the sun will, if artificially shaded, assume a new Fabian position

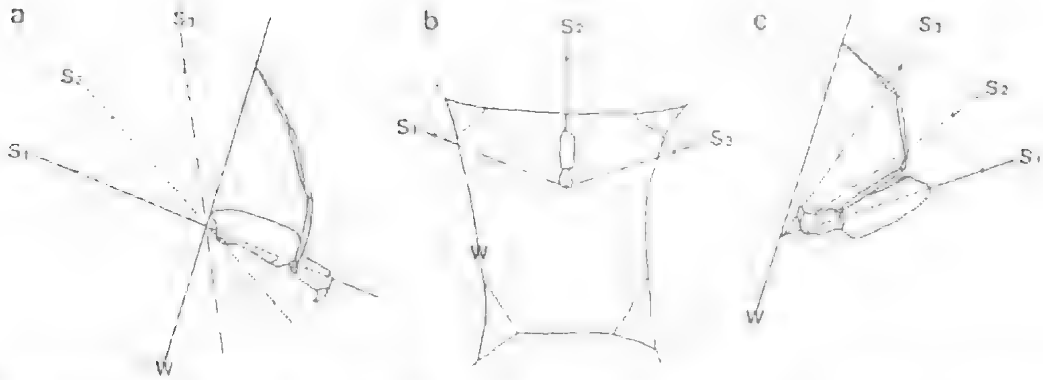

FIG. 1 Thermoregulatory postures adopted by golden web spider, *N. clavipes*. Lines projecting from three successive positions of sun (*S1*, *S2*, *S3*) indicate corresponding orientations of long axis of spider's body. Lateral views (a,c) and plan view (b) of web show posture assumed in response to ventral (through the web) insolation; b lateral insolation; c dorsal insolation (redrawn from Robinson and Robinson, 1974).

if the direction of the sun is artificially changed by means of a mirror.

In hot weather when the spiders are in the Repose position in the shade, redirection of unconcentrated sunlight, by means of a plane mirror or a concave mirror, results in the spider orientating and/or posturing if necessary to assume the Fabian position.

In hot weather, when the spiders are in a Fabian position, adding reflected sunlight from a plane mirror results in the spider orientating with respect to the mean angular direction of the two sources of incident radiation (when angle <90°). A spider posturing between two heat sources will turn towards the one increased in intensity and *vice versa*. Hence, the Fabian position moves towards the incident radiation of the mirror if the heat reflected from the mirror is increased and towards incident radiation of the sun if the heat reflected from the mirror is decreased.

If redirected light comes from above the horizontal plane of the web spiders rapidly change their Fabian position; if redirected light comes from below the horizontal plane of the web, a naturally impossible position, spiders appear confused and change position frequently and some species never achieve the Fabian position (e.g. *N. maculata*).

Cascading Behaviours

Many thermally related behaviours that have been categorised are themselves graded so that they each develop progressively rather than switch from one state to another.

For example as *Neogea* sp. warms in the sun, it exhibits a progression of distinct behaviours, each of which is graded and which are associated with increasing temperature of the abdomen (Humphreys, 1992). When a spider in the Repose position on the disc stabilimentum is heated by the sun it initially 'stilts', as has been described for scorpions. The spider gradually raises its body away from the disc surface until it has full downward extension of all legs and seems to be standing on 'tiptoe', thus removing the body of the spider as far as possible from the disc's surface.

On further heating, *Neogea* sp. progressively orientates its body and then gradually postures, starting with the abdomen. It rotates the tip of the abdomen towards the incident radiation and this minimises the projected surface area of the abdomen exposed to the sun. As the posturing develops the prosoma also is aligned with the abdomen so that the entire spider is orientated prosoma from the sun with minimal silhouette area exposed. Eventually the legs themselves are rotated forwards until they are parallel to the long axis of the spider in which position they are in the shadow of the abdomen, as is the prosoma; this is the full Fabian Position from which the spider tracks the sun (Humphreys, 1991, 1992). By these means the spiders potentially can obtain very fine control of their silhouette area and hence on their temperature.

In *N. edulis* many behaviours were recognisable as similar to those observed in other spiders (e.g. orientation, posturing, agitation: Humphreys, 1991, 1992), whereas others have not previously been reported or recognised (e.g. drooping). Some behaviours recognised may be components of the same behavioural sequence. For example, Agitation, in which the spider circles around the hub, involves the body being raised slightly from the web, a behaviour sometimes seen on its own. Both behaviours are included here under the same category. Thermally there appears little difference between three categories recognised here as different behaviours (agitation and body lift, front legs raised, and start to posture). Work conducted under more controlled conditions in the laboratory may separate thermally these behaviours or allow their pooling using more rigorous criteria.

Eleven behavioural categories are recognised in *N. edulis*, ranging from Repose to web abandonment which occur between T_b of 33.9 and 44.8°C (Table 2). The spider temperature associated with many of these behaviours is significantly different from others. Some of these behaviours reduce the projected body surface area exposed to the sun and thus, under the predictions of the physical model, should result in lower equilibrium body temperature, all else being equal (e.g. orientation, posturing, leg raising, leg rotation and web abandonment). Other behaviours may not be thermoregulatory but are associated with the onset of the next behaviour in the graded series (e.g. agitation and body lift) or facilitate a subsequent stage (e.g. silk laying to enable correct leg placement for full posturing).

As in *Neogea* sp. (Humphreys, 1992), some behaviours themselves form a graded series which should proffer gradually increased thermoregulatory effects. Both front leg raising and front leg rotation occur initially in the front legs followed by the second pair of legs. In addition contralateral legs are not necessarily lifted or rotated at the same time.

Behaviour	Mean	s.d.	n	Range
Repose - see Table 1	—	—	—	
Part orientation	33.9	0.57	6	33.1-34.7
Drooping	36.5	1.57	8	35.4-38.8
Orientation	38.7a	2.30	9	34.2-40.3
Agitation and body lift	38.7a	2.09	21	35.2-43.5
Front legs raised	38.9a	2.84	11	35.0-43.3
Start to posture	40.4b	2.16	27	34.8-43.6
Silk laying	41.1bc	1.34	6	39.3-42.6
Rotate front legs	42.4cd	0.99	10	41.2-44.3
Abandon web	44.8d	0.50	3	44.3-45.3

TABLE 2. Mean temperature (T_b °C) of *N. edulis* on Rottnest Island, Western Australia, associated with different behaviours (ANOVA - $F_{s\ 8,93} = 15.233$, $P<0.001$). Common letters include means not differing significantly (Fisher's PLSD at $\alpha = 0.05$).

DISCUSSION

Two classes of observation refute the hypothesis that posturing serves an anti-predator role as stated in the introduction.

Firstly, if the Fabian position reduce the silhouette area against the brightest part of the sky as an anti-predator defense (i.e. to make them less visible) then they should posture to the sun under clear conditions irrespective of the intensity of the sunlight; they do not. Furthermore, under conditions of patchy heavy clouds (cumulus and cumulo-status) against a clear sky, the spiders should assume a Fabian position with respect to the brightest sector of the sky; they do not.

Secondly, many thermally related behaviours are themselves graded so that they are exhibited progressively as the spider warms. This provides the strongest evidence for the thermoregulation hypothesis because partial stilting, posturing or orientation (Humphreys, 1992) makes no sense under alternative hypotheses but is entirely consistent with, and predicted from, the thermoregulation hypothesis.

The body temperature of a spider is a complex function of many intrinsic factors (size, morphology, attitude, physiology, reflectance, etc.) as well as factors extrinsic to the individual (e.g. wind speed, turbulence, air temperature, incident radiation and its spectral characteristics; Monteith and Unsworth, 1990). It is because T_b is a complex function of intrinsic and extrinsic factors that makes T_a a poor predictor of thermal behaviour. Hence, the observation that a spider may not always assume the Fabian position (or other presumptive thermoregulatory behaviour) at the same T_a does not imply that the behaviour has no thermoregulatory significance. For example, *Lycosa godeffroyi* Koch in Canberra began basking at much lower T_a in winter (4°C) than in summer (17°C) and reached 35°C on clear winter days at T_a of 11°C (Humphreys, 1974, 1978); the latter shows the dominant role of boundary layer effects for such surface dwelling spiders. Although orb-weaving spiders are often high above the ground, such boundary layers may assume more importance in those orb weaving spiders that incorporate a surface in their web (e.g. *Neogea* sp. and leaf curling species; Humphreys, 1992).

These many classes of observation support the hypothesis that the posturing and/or reorientation that spiders undergo in intense sunlight is of thermoregulatory significance. Many are not alone adequate to support unequivocally the thermoregulation hypothesis (e.g. Table 3: 4, 6 , 9), some, in combination with others, support the

Condition at spider	Manipulation	Behavioural response and thermal consequences
1[a] Cool weather in shade	Nil	Repose; $T_b=T_a$
2[a] Cool weather in sun	Nil	Repose; $T_b>T_a$
3[a] Cool weather in sun	=*S*	Repose; $T_b>T_a$
4[a] Cool weather in sun	>*S*	Orientate and/or posture; $T_s>T_c$
5[a] Hot weather in shade	Nil	Repose; $T_b=T_a$
6[a] Hot weather in shade	= *s* or >*s*	Fabian
7[a] Hot weather in sun	Nil	Orientate and/or postureX tracks sun; minimise T_b
8 Hot weather in sun	<<*S*	Repose
9 Hot weather in sun	=*S* or >*S*	Fabian
10 Very hot day in shade	Nil	Repose; *in extremis* may suffer heat death without posturing
11 Very hot day in sun	Nil	Seeks shade
12 Population in hot sun	Varied web orientation	All spiders orientate in same direction; minimise T_b
13 Population in hot sun	Large & small spiders	Large spiders posture earlier in day than small
14 Hot weather in sun	=*S* perpendicular to sun	Spider postures mid-way between two incident heat sources
15* Grade n-1 behaviour	>*S*	Grade n behaviour; behavioural cascade culminating in Fabian
16 Hot weather in sun	=*S* below horizontal	Apparent confusion in some species;> T_b
17 Cool weather in shade	=*s*	Posture to > exposure to heat source; $T_b>T_a$

TABLE 3. Summary of characteristics of thermoregulatory behaviour in orb-weaving spiders. *Definitions*: Spiders assume Fabian position in hot but not in cold weather. S denotes sunlight redirected onto the spider at about intensity of natural sunlight using a plane mirror (=*S*) or at greater or less than natural intensity using a concave mirror (>*S* or < *S*). The spider is simultaneously artificially shaded (*s*) or not (*S*). Numbers with * are considered alone, and numbers followed by common letters are considered together, to support strongly the thermoregulation hypothesis.

hypothesis (e.g. 1-7), while others support no other hypothesis (e.g. 15).

While the emphasis here has been on behaviours that reduce the heat load, spiders should use behaviours to warm them in order to enhance the time they are at optimal temperatures. This is the case in burrow dwelling lycosids (Humphreys, 1974, 1978, 1987a, 1987b) as well as in orb web spiders which may seasonally orientate their webs to maximise the projected surface area to warm more or faster (Carrell, 1978; Tolbert, 1979).

While there is an indication of size related effects in thermoregulatory behaviour in *Nephila* spp., as may be expected theoretically using a simple physical model, no such size effect was observed in *Stegodyphus lineatus* Latreille (Henschel *et al*., 1992).

While the thermal behaviour of spiders is much more sophisticated than has been accepted, the presumed advantages of such fine tuning are not understood. None the less, the recognition of such behaviour is an important aspect of field studies and the means to do so are required, especially for smaller spiders which are intractable subjects for direct recording of temperature in the field. However, the sensible use of this schema should allow easy appraisal of the overt body positions of spiders in the field as to their likely thermoregulatory significance and it should assist in disentangling thermoregulatory from other behaviours.

A thermoregulator with the battery of finely graded behaviours seen here should, under ideal conditions, be able to maintain a near constant body temperature under a wide range of environmental conditions. In practice their temperatures fluctuate markedly with every air movement, at least partly owing to their small thermal capacity. If the spiders are innately incapable, owing to their small mass, of precise thermoregulation, why have they developed such a wide range of sophisticated behaviours which should permit precise thermoregulation?

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LITERATURE CITED

ALEXANDER, A.J. & EWER, D.W. 1958. Temperature adaptive behaviour in the scorpion, *Opisthophthalmus latimanus* Koch. Journal of Experimental Biology 35: 349-359.

BIERE, J.M. & UETZ, G.W. 1981. Web orientation in the spider *Micrathena gracilis* (Araneae: Araneidae). Ecology 62: 336-344.

CARREL, J.E. 1978. Behavioural thermoregulation during winter in an orb-weaving spider. Symposium of the Zoological Society of London 42: 41-50.

CRAIG, C.L. & BERNARD, G. D. 1990. Insect attraction to ultraviolet-reflecting spider webs and web decorations. Ecology 71: 616-623.

EBERHARD, W.G. 1973. Stabilimenta on the webs of *Uloborus diversus* (Araneae: Uloboridae) and other spiders. Journal of Zoology, London 171: 367-384.

EDMUNDS, J. & EDMUNDS, M. 1986. The defensive mechanisms of orb weavers (Araneae: Araneidae) in Ghana, West Africa. Pp. 73-89. In Eberhard, W.G., Lubin, Y.D. and Robinson, B.C. (Eds). Proceedings of the Ninth International Congress of Arachnology, Panama, 1983. (Smithsonian Institution Press: Washington, D.C.).

EWER, R.F. 1972. The devices in the web of the West African spider *Argiope flavipalpis*. Journal of Natural History 6: 159-167.

FOELIX, R.F. 1982. Biology of Spiders. (Harvard University Press: Cambridge, Massachusetts).

HEATWOLE, H. 1970. Thermal ecology of the Desert Dragon *Amphibolurus inermis*. Ecological Monographs 40: 425-457.

HENSCHEL, J.R., WARD, D. & LUBIN, Y. 1992. The importance of thermal factors for nest-site selection, web construction and behaviour of *Stegodyphus lineatus* (Araneae: Eresidae) in the Negev Desert. Journal of thermal Biology 17: 97-106.

HUMPHREYS, W.F. 1974. Behavioural thermoregulation in a wolf spider. Nature, London 251: 502-503.

1978. The thermal biology of *Geolycosa godeffroyi* and other burrow inhabiting Lycosidae (Araneae) in Australia. Oecologia, Berlin 31: 319-347.

1986. Heat shunting in spiders. Pp. 41-46. In Congresso Internacionale Arachnologia, vol. I. (Ed. J.A. Barrientos). Jaca, Spain.

1987a. The thermal biology of the wolf spider *Lycosa tarentula* (Araneae: Lycosidae) in northern Greece. Bulletin of the British Arachnological Society 7: 117-122.

1987b. Behavioural temperature regulation. Pp. 56-65. In, Nentwig, W (ed). 'Ecophysiology of Spiders'. (Springer-Verlag: Berlin.)

1991. Thermal behaviour of a small spider (Araneae: Araneidae: Araneinae) on spinifex in Western Australia. Behavioural Ecology and Sociobiology 28: 47-54.

1992. Stabilimenta as parasols: shade construction by *Neogea* sp. (Araneae: Araneidae, Argiopinae) and its thermal behaviour. Bulletin of the British Arachnological Society 9: 47-52

LUBIN, Y.D. 1986. Web building and prey capture in Uloboridae. Pp. 132-171. In Shear, W.A. (Ed). Spiders: webs, behavior, and evolution. (Stanford University Press: Stanford, California).

LUBIN, Y.D. & HENSCHEL, J.R. 1990. Foraging at the thermal limit: burrowing spider (*Seothyra*, Eresidae) in the Namib Desert dunes. Oecologia 84: 461-467.

MARSON, J. 1947. Some observations on the ecological variation and development of the cruciate zig-zag camouflage device of *Argiope pulchella* (Thor.). Proceedings of the Zoological Society of London 117: 219-227.

MONTEITH, J.L. & UNSWORTH, M.H. 1990. Principles of environmental physics. (Edward Arnold: London).

OLIVE, C.W. 1980. Foraging specializations in orb-weaving spiders. Ecology 61: 1133-1144.

RIECHERT, S.E. & TRACY, C.R. 1975. Thermal balance and prey availability : Bases for a model relating web-site characteristics to spider reproductive success. Ecology 56: 265-284.

ROBINSON, M.H. & ROBINSON, B. 1973. The stabilimenta of *Nephila clavipes* and the origin of stabilimentum-building in Araneids. Psyche 80: 277-288.

1974. Adaptive complexity: the thermoregulatory postures of the golden-web spider *Nephila clavipes* at low altitudes. American Midland Naturalist 92: 386-396.

1978. Thermoregulation in orb-weaving spiders: new descriptions of thermoregulatory postures and experiments on the effects of coloration. Zoological Journal of the Linnean Society, London 64: 87-102.

SUTER, R.B. 1981. Behavioural thermoregulation: solar orientation in *Frontinella communis* (Linyphiidae), a 6-mg spider. Behavioural Ecology and Sociobiology 8: 77-81.

TOLBERT, W.W. 1979. Thermal stress of the orb-weaving spider *Argiope trifasciata* (Araneae). Oikos 32: 386-392.

WARD, D. & HENSCHEL, J.R. 1992. Experimental evidence that a desert parasitoid keeps its host cool. Ethology 92:135-142.

WILLMER, P. 1991. Thermal biology and mate acquisition in ectotherms. Trends in Ecology and Evolution 6: 396-399.

WILLMER, P.G. & UNWIN, D.M. 1981. Field analyses of insect heat budgets: reflectance, size and heating rates. Oecologia 50: 250-255.

HYPERTROPHY OF MALE GENITALIA IN SOUTH AMERICAN AND AUSTRALIAN TRIAENONYCHIDAE (ARACHNIDA: OPILIONES: LANIATORES)

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Hunt, G.S. and Maury, E.A. 1993 11 11: Hypertrophy of male genitalia in South American and Australian Triaenonychidae (Arachnida: Opiliones: Laniatores). *Memoirs of the Queensland Museum* 33(2): 551-556. Brisbane. ISSN 0079-8835.

Hypertrophy of male genitalic elements, particularly the stylus, is described and discussed. A stylus is regarded as hypertrophied if stylus length is sub-equal to or longer than truncus length. Greatest hypertrophy occurs in the Australian species *Cluniella distincta* Forster (stylus x4.5 truncus) and a new genus, new species from South America (x2.5 truncus). Other species discussed are *Araucanobunus juberthiei* Muñoz-Cuevas from South America, and *C. minuta* Forster, *Rhynchobunus arrogans* Hickman, *Tasmanobunus parvus* Hickman, *Tasmanonuncia* sp., *Allobunus distinctus* Hickman and *Thelbunus mirabilis* Hickman from Australia. To accommodate an elongate stylus, the truncus is often shortened, and the genital operculum and sternum modified so that the genital orifice is located more anteriad. Hypertrophy of the stylus may be associated with the hypertrophy or reduction of other terminal elements. In *Cluniella* spp, and the two South American species penetration of the stylus occurs along a very long vagina; the spermathecae are situated at the base of the ovipositor. Hypertrophy may have evolved as a consequence of sexual selection. □*Opiliones, Triaenonychidae, male genitalia, hypertrophy, morphology, sexual selection.*

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The triaenonychid penis comprises a basal truncus supporting an apical complex which includes the stylus and associated plates, processes and setae. In the primitive condition, three sets of plates are present (Fig. 1A): the dorsolateral plates which are embryologically derived from the truncus and the dorsal plate and ventral plate embryologically related to the stylus (Martens, 1986). Both the dorsal and ventral plates were apparently primitively paired but are now fused, at least basally. The ventral plate carries setae. Certain taxa have undergone loss or reduction of plates (Martens, 1986; Hunt and Hickman, 1993). A few taxa have undergone extreme hypertrophy in the length of the stylus with one or more of the associated plates frequently showing correlated hypertrophy, or reduction, depending on the taxon.

HYPERTROPHIED STRUCTURES

CLUNIELLA SPP.

The most extreme hypertrophy of the stylus known for the family occurs in *Cluniella distincta* Forster, 1955 of SE Queensland and NE New South Wales (Fig. 2A). The stylus is x4.5 truncus length. There is correlated morphological change in the female where spermathecae occur basally in the ovipositor (Fig. 5C), unlike the usual condition where the spermathecae occur sub-apically. Therefore, the long stylus probably penetrates almost the whole length of the ovipositor to reach the spermathecae. The dorsolateral plates of the penis are elongate, gradually tapering to x2 ventral plate length (Fig. 2B). The dorsal plate is either lacking or intimately fused with the stylus; the latter is suggested by the subterminal lateral processes on the stylus which may be homologous to terminations of the dorsal plate (see *Thelbunus mirabilis* below, Fig. 5A). The ventral plate is reduced in size, and the number of inferior setae is reduced from three to two pairs.

The extreme stylus is accommodated within the body by shortening of the truncus, and by elongation of the genital operculum and posterior invagination of the sternum which together shift the genital opening anteriad. The sternum margins tend to follow the genital operculum (Fig. 5E; cf. female genitosternal region, Fig. 5F) but when the operculum is lifted the shape resembles that in Fig. 5H.

Cluniella minuta Forster, 1955, which overlaps in distribution with *C. distincta*, has undergone less radical elongation of the stylus (Figs 2C-D). Nevertheless, the stylus is x1.4 truncus length. The spermathecae are also basal despite the

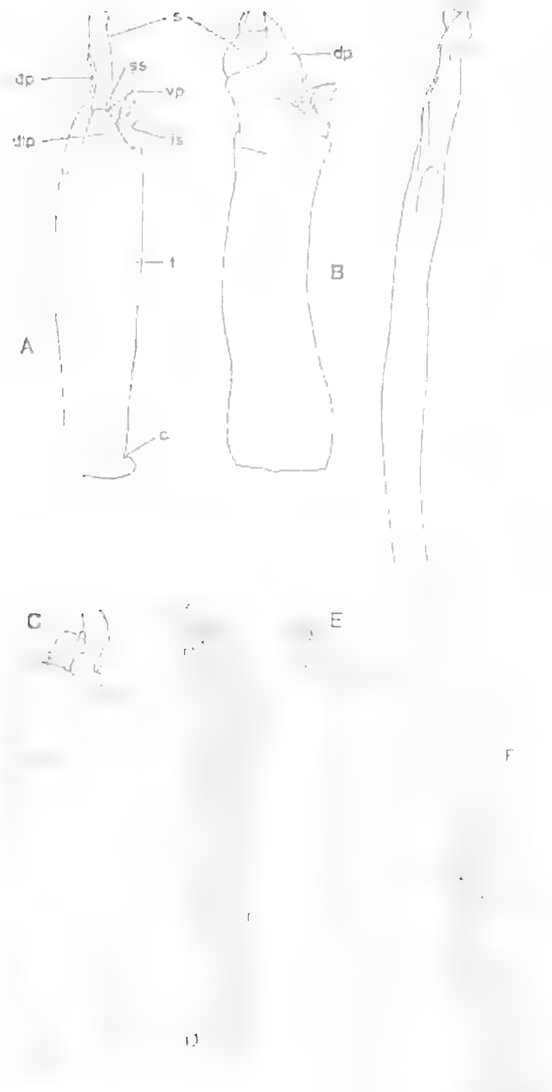


FIG. 1. Variation in ♂ genitalia of some Australian Triaenonychidae. A: *Hickmanoxyomma cavaticum*; B: *Glyptobunus signatus*; C: *Tasmanonyx montanus* D: *Dipristes serripus* (muscle shown); E: *Lomanella raniceps*; F: *Cluniella distincta* (muscle shown); c = constriction for membrane attachment; dlp =dorsolateral plate; dp = dorsal plate; is = inferior seta; s =stylus; ss =superior seta; t =truncus; vp =ventral plate.

shorter stylus. The dorsolateral plates are elongated to a similar extent to *C. distincta* while the ventral plate, though reduced, bears 3 pairs of inferior setae. The truncus is less shortened, the genital operculum is not elongate and the sternum is long and narrow. In both species, the constriction in the truncus where penis sheath membranes attach is basal.

The differences between the two species are not due to infraspecific variation, such as male dimorphism reported in some Australian genera (Hunt, 1985). Characters distinguishing *C. minuta* include a very long calcaneus compared with astragalus in leg I.

Araucanobunus juberthiei Muñoz-Cuevas, and New Genus, New Species (Maury, in prep.)

A. juberthiei from southern South America shows moderate hypertrophy of the stylus with stylus length about 1.3 truncus length (Figs 3A-B). An undescribed species referrable to a new genus (Maury, in prep.), but apparently with close genitalic affinities to *A. juberthiei*, has undergone greater hypertrophy with stylus length x2.5 truncus length (Fig. 3C). The dorsolateral plates are present in both species, but the dorsal plate is apparently lost (or intimately united with the stylus). The truncus in the undescribed species is greatly shortened, in *A. juberthiei* much less so.

Both species have an elongate genital operculum and a short, subtriangular sternum (for example, see Figs 5G-I). When closed, the genital operculum virtually obliterates the sternum.

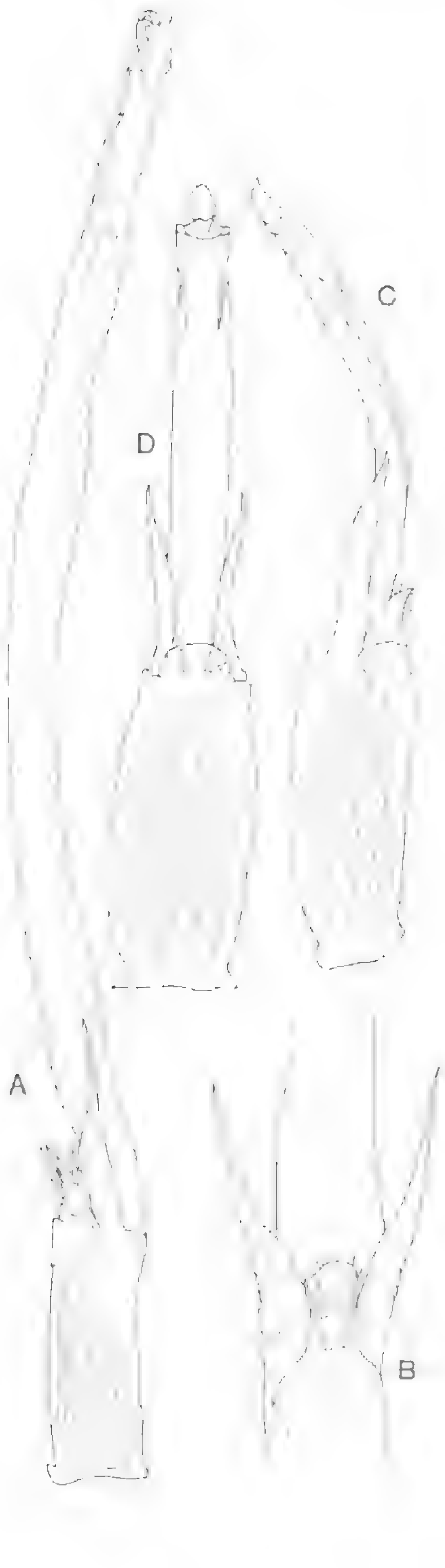
Unlike the condition in *Cluniella*, the constriction is situated mid-way along the truncus in both species (Figs 3A-D). As in *Cluniella*, the spermathecae are situated at the base of the ovipositor at the end of a long vagina (Fig. 5D: *A. juberthiei*). There appear to be no significant infraspecific variations in size or shape of the genitalia in these species.

Rhynchobunus arrogans Hickman

This species, from NE Tasmania, also has a prominent constriction at about mid-way along the truncus (Fig. 4A). *R. arrogans* belongs to a lineage distinguished by loss of the dorsolateral plates. The dorsal plate envelopes the stylus basally and terminates ventral to it. *R. arrogans* is very close to, if not congeneric with, *Glyptobunus signatus* Roewer (Hunt, in prep.). The stylus is x1.3 truncus length. The spermathecae are subterminal. The ventral plate is reduced but still carries the normal complement of setae for this lineage (Figs 4A-B). *R. arrogans* has an elongate genital operculum but lacks a triangular sternum.

Tasmanobunus parvus Hickman

This species is closely allied to, or possibly congeneric with, *R. arrogans* and *G. signatus* as



it lacks dorsolateral plates, its stylus carries a subdistal dorsal barb, and the dorsal plate terminates ventral to the stylus (Figs 4C-D). The stylus is subequal in length to the truncus and the dorsal plate has undergone complementary elongation. The constriction around the truncus is more subdued and situated somewhat more basally.

TASMANONUNCIA N.SP.

This species belongs to the same general lineage as *R. arrogans* in that it lacks dorsolateral plates (Hunt, in prep.). However, the stylus carries a subdistal dorsal tuft of hairs instead of a single barb (Figs 4E-F). Stylus length is subequal to truncus length and, as with *Tasmanobunus parvus*, the dorsal plate is greatly elongate.

ALLOBUNUS DISTINCTUS HICKMAN

A. distinctus, from NW Tasmania, has a prominent constriction mid-way along the truncus. The stylus is modestly elongate, being subequal in length to the truncus. The ventral plate, however, is hypertrophied, uniting with other sclerotisations to form an elongate cylinder around the proximal half of the stylus (Figs 4G-H). The male of *A. distinctus* has a triangular sternum and a moderately elongate genital operculum.

THELBUNUS MIRABILIS HICKMAN

Unlike the *Rhynchobunus* lineage, this NE Tasmanian species belongs to a lineage with well developed dorsolateral plates. The stylus is hypertrophied but the problem of space is partly solved by the stylus being twice folded back on itself (Fig. 5A). The dorsal plate is also elongate and closely integrated with the stylus, bifurcating into two lobes just below the stylus tip. The ventral plate setae are greatly hypertrophied and differentiated into different forms (Fig. 5B). This species also has a short triangular sternum (though not unlike the female) and an elongate genital operculum (Figs 5J-K).

Thelbunus n.sp. has a less elaborate stylus and its sternum less modified and genital operculum less elongate (sternum illustrated in Fig. 6).

OTHER OPILIONES

Hypertrophy of the stylus has also been recorded in the neopilionid *Ballarra* spp (suborder Palpatores) from Australia (Hunt and Coken-

FIG. 2. Hypertrophied ♂ genitalia of *Cluniella* spp. A, B: *C. distincta*, A = lateral, B = ventral view of ventral and dorsolateral plates. C, D: *C. minuta*, lateral and ventral.

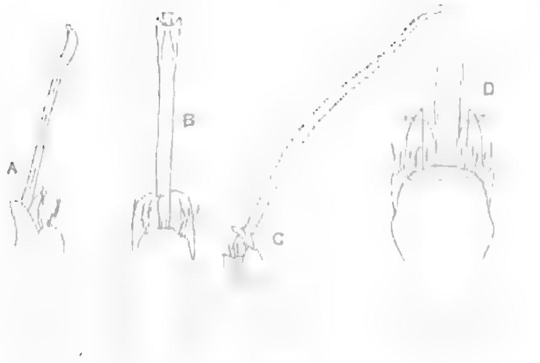


FIG. 3. Hypertrophied ♂ genitalia of South American Triaenonychidae. A, B: *Araucanobunus juberthiei*, lateral and ventral. C, D: New genus, new species (Maury, in prep.), lateral, ventral (part).

dolpher, 1991). Unlike the situation in *Cluniella* spp. and the South American species, the spermathecae are greatly elongate, opening into a short vagina but ending basally in the ovipositor. The long stylus is presumably inserted down the elongate spermatheca, not an elongate vagina as occurs in *Cluniella*.

Other taxa exhibit elongation of the truncus, e.g., many species of the triaenonychid genus *Lomanella* (Hunt and Hickman, 1993).

DISCUSSION

An elongate stylus is frequently, but not invariably, associated with an elongation of the genital operculum and a shortening and broadening of the sternum which together serve to elongate the cavity in which the penis lies (also, shortening of the truncus may compensate for the elongate stylus).

These changes in genitosternal architecture seem to have arisen independently in several distantly related gerera. Within the one genus, both normal and hypertrophy-related genitosternal architecture can occur. For example, *Cluniella minuta* has evolved a moderately elongate stylus while retaining a 'normal' long, narrow sternum and rounded genital operculum. *C. distincta* has undergone much greater elongation of the stylus with consequent changes in the sternum and genital operculum.

It seems more probable that the situation in *C. minuta* is more 'primitive', while the syndrome of extreme characters in *C. distincta* represents a more derived condition. Thus, in the *Cluniella* lineage, space limitations of an elongate stylus

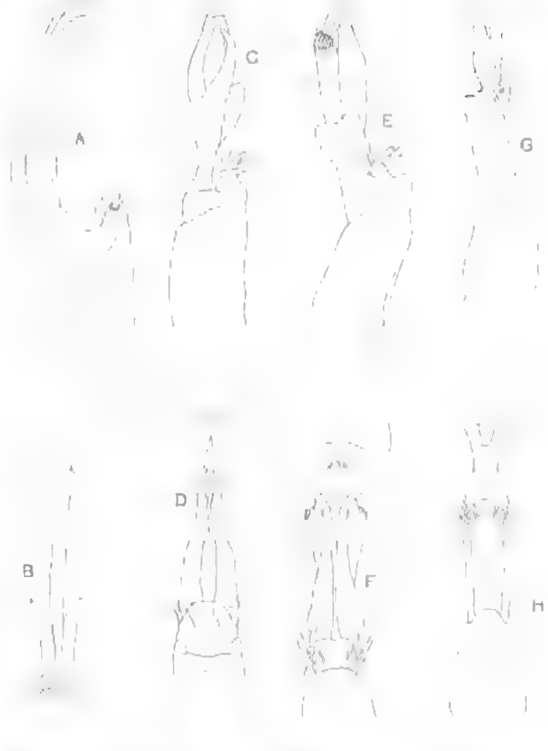


FIG. 4. Hypertrophied ♂ genitalia in Tasmanian Triaenonychidae. A, B: *Rhynchobunus arrogans*, lateral and ventral. C, D: *Tasmanobunus parvus*, lateral and ventral. E, F: *Tasmanonuncia* n.sp. (Hunt, in prep.), lateral and ventral. G, H: *Allobunus distinctus*, lateral and ventral.

seem initially accommodated by shortening of the truncus (*C. minuta* condition). Changes to the genital operculum and sternum evolved later.

Cluniella spp. and the two South American species described above show close correspondence in many features associated with stylus hypertrophy: great elongation of stylus, modification of sternum and genital operculum, shortening of truncus, and spermathecae situated basally in the ovipositor at the end of a very long vagina.

The question is whether these features indicate a close phylogenetic relationship or whether they are examples of convergence. The latter is supported because:

1. Modifications to genitosternal architecture appear to have arisen independently within the *Cluniella* lineage, evolving from the 'normal' condition as occurs in *C. minuta*.

2. Attachment of penis sheaths is basal in *Cluniella* and mesial in South American species.

3. The penes of the South American species

FIG. 5. Hypertrophy of genitalia in *Thelbunus mirabilis* and modified structures associated with genitalic hypertrophy in various Triaenonychidae. A, B: *T. mirabilis*, lateral and detail of lateral showing hypertrophy and modification of ventral plate setae. C,D: Ovipositor in *Cluniella distincta* and *Araucanobunus juberthiei* respectively showing basal seminal receptacles. E, F: Genitosternal region of *C. distincta*, ♂ and ♀ respectively. G, I: Genitosternal region of South American new genus, new species (Maury, in prep.), ♂ and ♀ respectively; H = shape of sternum in ♂ after genital operculum removed. J, K: genitosternal region of *T. mirabilis*, ♂ and ♀ respectively; go = genital operculum; sp = spermatheca; st = sternum; v = vagina (not delineated in *C. distincta*).

show closer affinity with the South American genus *Triaenonychoides* (see Maury, 1987)) rather than with Australian genera.

4. Apart from the basal spermathecae and long vagina, the ovipositor of the South American species appears to be of the typical triaenonychid form. The ovipositor of both *Cluniella* spp. is highly derived in having a very membranous tip, in lacking well developed sensory lobes, and in carrying vestigial setae. In some specimens examined the membranous tip was inflated and had 'ballooned' out the genital orifice. This morphology suggests that the female may assist penetration by inflating the ovipositor so that it partly engulfs the stylus. Thus, assuming that the male *C. minuta* has not undergone a reversal in genitosternal architecture, the derived ovipositor seems to have evolved before shortening of the male sternum and elongation of the genital operculum.

Thus, the genomes of *Cluniella* and the two South American taxa have the capacity to allow quite remarkable convergence in a syndrome of characters. The overall effect appears the same, but the details differ.

Why have such vastly elongate styluses evolved, particularly to the extreme shown by *C. distincta*? Sexual selection by female choice is favoured by Eberhard (1985) as the most generally applicable explanation for 'extravagant' genitalia. Eberhard proposes that 'male genitalia function as 'internal courtship', devices to increase the likelihood that females will actually use a given male's sperm to fertilize her eggs rather than those of another male'. In the case of *Cluniella* and the South American species, it is postulated that males with the largest styluses have greater success than males with smaller styluses and hence contribute more of their genes to the next generation. The genitalia may stimulate the female prior to or during copulation and so activate the appropriate responses, or it might provide the right mechanical and sensory 'fit' during copulation. The basal spermathecae in the ovipositor of *Cluniella* spp. and the two South American species (and the long stylus matching the long spermathecae in *Ballarra* spp.) suggest that the correct mechanical fit may at least be part of the answer.

A search for congeners and an analysis of inter- and intraspecific variation, as well as behavioural studies, may yield further data to resolve these questions.

ACKNOWLEDGEMENTS

The first author was assisted by an Australian Biological Resources Study grant. Drs Michael Gray (Australian Museum) and A. Roig-Alsina (Museo Argentino de Ciencias Naturales), and Mr James Cokendolpher (Lubbock, Texas), commented on the manuscript. Mr Roger Springthorpe did the illustrations and Ms Sue Lindsay the SEMs.

LITERATURE CITED

EBERHARD, W.G. 1985. 'Sexual Selection and

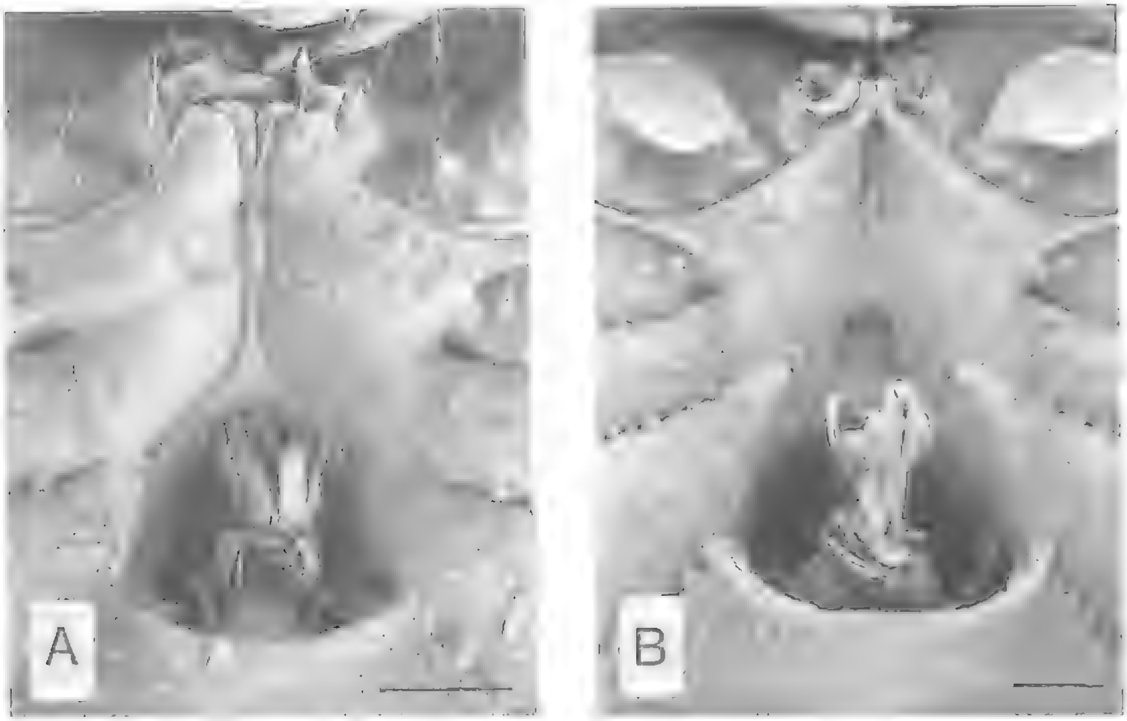


FIG. 6. Genitosternal region in *Thelbunus* spp. and variation in sternum; A = sp. nov.; B = *T. mirabilis*. Genital operculum lifted; note recess in sternum where folded stylus fits. Scale bars= 500μm.

Animal Genitalia'. (Harvard University Press: Cambridge, Mass). 244pp.

HUNT, G.S. 1985. Taxonomy and distribution of *Equitius* in eastern Australia (Opiliones: Laniatores: Triaenonychidae). Records of the Australian Museum 36: 107-125.

HUNT, G.S. & COKENDOLPHER, J.C. 1991. Ballarrinae, a new subfamily of harvestmen from the Southern Hemisphere (Arachnida, Opiliones, Neopilionidae). Records of the Australian Museum 43: 131-169.

HUNT, G.S. & HICKMAN, J.L. 1993. A revision of the genus *Lomanella* Pocock and its implications for family level classification in the Travunioidea (Arachnida: Opiliones: Triaenonychidae). Records of the Australian Museum 45:81-119.

MARTENS, J. 1986. Die Grossgliederung der Opiliones und die Evolution der Ordnung (Arachnida). Actas X Congreso Internacional de Aracnologia, Jaca, España 1: 289-310.

MAURY, E.A. 1987. Triaenonychidae Sudamericanos. IV. El genero *Triaenonychoides* H. Soares 1968 (Opiliones, Laniatores). Boletin de la Sociedad de Biología de Concepción, Chile 58: 95-106.

MUÑOZ-CUEVAS, A. 1973. Descripcion de *Araucanobunus juberthiei* gen. et sp. nov. de Triaenobunini de Chile (Arachnida, Opiliones, Triaenonychidae). Physis, Buenos Aires, Secc. C 32(84): 173-179.

PREDATOR-PREY CO-EVOLUTION OF *PORTIA FIMBRIATA* AND *EURYATTUS* SP., JUMPING SPIDERS FROM QUEENSLAND

ROBERT R. JACKSON AND R. STIMSON WILCOX

Jackson, R.R. and Wilcox, R.S. 1993 11 11: Predator-prey co-evolution of *Portia fimbriata* and *Euryattus* sp., jumping spiders from Queensland. *Memoirs of the Queensland Museum* 33(2): 557-560. Brisbane. ISSN 0079-8835.

Portia is a salticid that preys on other spiders and *Euryattus* sp. is a salticid that nests inside suspended rolled-up leaves. *Portia* and *Euryattus* are sympatric at a site near Cairns but not known to be sympatric at other sites studied. *Portia* from the Cairns site practices a unique prey-specific predatory behaviour against *Euryattus*, and *Euryattus* from this site is efficient at detecting and defending itself against *Portia*. *Euryattus*, but not *Portia*, is present at a site near Davies Creek which, although only ca 15km from the Cairns site, is more xeric and at a higher elevation. Three types of tests were carried out to compare *Portia*'s efficiency at catching adult allopatric versus sympatric *Euryattus* (Test 1), allopatric *Euryattus* juveniles versus juveniles of another salticid species on which *Portia* is known to prey (Test 2) and allopatric versus sympatric *Euryattus* juveniles (Test 3). In these tests, *Portia* behaved similarly toward allopatric (Davies Creek) and sympatric (Cairns) *Euryattus*, except that it attacked and killed allopatric more often than sympatric *Euryattus*. Allopatric *Euryattus*, in contrast to Cairns *Euryattus*, appeared not to recognize an approaching *Portia* as a predator.□*Portia fimbriata, Euryattus, Jacksonoides, co-evolution, allopatry, sympatry.*

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Portia is a genus of specialized jumping spiders (Salticidae) that prey on other spiders (Jackson and Hallas, 1986). *Portia* is a detritus mimic and has a unique, slow, choppy style of locomotion that seems to preserve its crypsis. There are seven described species of *Portia*, distributed in the tropics of Africa, Asia, and Australasia (Wanless, 1978). A population of *Portia fimbriata* (Doleschall) in Queensland uses specialized behaviour to catch other species of salticids (Jackson and Blest, 1982). This population of *P. fimbriata* also uses a prey-specific predatory behaviour against females of a particular sympatric salticid, *Euryattus* sp. (Jackson and Wilcox, 1990).

Euryattus females suspend a dead, rolled-up leaf by strong guylines from rock ledges and tree trunks, then use the leaf as a nest (Jackson, 1985). *Portia* has never been observed to attempt to catch *Euryattus* by going inside the rolled-up leaf. However, in Queensland, *P. fimbriata* uses vibratory displays to lure *Euryattus* females from their nests (Jackson and Wilcox, 1990). These displays apparently mimic courtship displays of *Euryattus* males (Wilcox and Jackson, unpubl. data). Other species of *Portia* and populations of *P. fimbriata* in areas from which *Euryattus* is absent do not perform these displays (Jackson and Wilcox, 1990).

Queensland *P. fimbriata* will wait for hours at a time for *Euryattus* to come out of its nest (Jackson and Wilcox, 1990). Often, *Euryattus* actively defends itself by leaping at *Portia* and driving it away (Jackson and Wilcox, 1990). This is unusual behaviour for a salticid. From thousands of observations of interactions between *P. fimbriata* and many different species of salticids (Jackson and Hallas, 1986), it is evident that *Euryattus* is more efficient than other salticids at recognizing and defending itself against an approaching *Portia*. Also, in laboratory tests (Jackson and Wilcox, 1990), *Euryattus* readily recognized an approaching *Portia* as a potential predator, whereas *Jacksonoides queenslandica*, another salticid on which *P. fimbriata* feeds (Jackson and Blest, 1982), did not recognize *P. fimbriata*. This suggests an evolutionary 'arms race' (sensu Dawkins and Krebs, 1979) between *Euryattus* and *P. fimbriata*. Frequent predation by *P. fimbriata* on *Euryattus* may have favoured special abilities in *Euryattus* to recognize and defend itself against *P. fimbriata*. This, in turn, may have resulted in the evolution of refinements of *P. fimbriata*'s predatory behaviour. To test this hypothesis, we must compare the behaviour of *Euryattus* in populations with and without *Portia*. Recently, such an opportunity arose when *Euryattus* were found in an area in which *Portia* was not known.

MATERIALS AND METHODS

Cages, maintenance, terminology, basic testing procedures and analysis are given in Jackson and Wilcox (1990). Laboratory cultures of sympatric *Euryattus*, *J. queenslandica* and *P. fimbriata* were established, using spiders collected from rainforest near Cairns at about sea level (see Jackson, 1985; Jackson and Hallas, 1986). A laboratory culture of allopatric *Euryattus* was established from spiders collected in an *Acacia-Eucalyptus* woodland beside Davies Creek, near Davies Creek National Park in the Atherton Tableland (about 15km from the study site near Cairns and at c. 500m elevation). *Portia* has never been recorded from this and other Atherton Tableland habitats (Wanless, 1978; Jackson, unpubl. data). Unless noted otherwise, all spiders tested were reared in the laboratory from eggs of field-collected spiders. No individual spiders were used in more than one test. In this paper, we refer to *Euryattus* from Cairns and Davies Creek as 'sympatric *Euryattus*' and 'allopatric *Euryattus*', respectively. There were no evident differences related to general behaviour between these two populations of *Euryattus*. In particular, similar leaves were suspended by females for nests and males courted with similar vibratory displays.

The systematics of the genus *Euryattus* remains uncertain. Whether the two populations of *Euryattus* we studied are one or two different species is not now known. Voucher specimens were deposited at the Florida Collection of Arthropods (Gainesville) and the Queensland Museum.

We conducted three tests. In Test 1, *Portia* was given access to an adult allopatric *Euryattus* female in her nest. In Test 2, on alternate days, *Portia* was given access to a juvenile (2-3mm in body length) allopatric *Euryattus* and a juvenile (2-3mm) *J. queenslandica* in a bare cage (i.e., no nest or other objects present). In Test 3, on alternate days, *Portia* had access to a juvenile (2-3mm) of an allopatric and a juvenile of a sympatric *Euryattus* in a bare cage. To begin each type of test, *Portia* was placed into a cage containing the other spider shortly after lights came on in the laboratory (0800 hours). Spiders were observed continuously until predation occurred or until 4h had elapsed. Each test was either identical or at least similar to tests carried out previously (Jackson and Wilcox, 1990).

Data from Test 1 using allopatric *Euryattus* adults were compared to data from the identical type of tests using sympatric *Euryattus* adults in an earlier study (Jackson and Wilcox, 1990) to see whether *Portia*'s capture efficiency against allopatric *Euryattus* adults was greater than against sympatric *Euryattus* adults. Test 2 using allopatric *Euryattus* juveniles was compared to type 2 tests in Jackson and Wilcox (1990) using sympatric *Euryattus* juveniles and *J. queenslandica* juveniles. We already know that *Portia* captures *J. queenslandica* juveniles more efficiently than it captures sympatric *Euryattus* juveniles (Jackson and Wilcox, 1990). Here we examine whether *Portia*'s capture efficiencies against these two salticids vary when *Euryattus* is allopatric. Test 3 enabled us to compare *Portia*'s efficiency at capturing allopatric and sympatric *Euryattus* juveniles.

Adult body length is c.8mm for both *J. queenslandica* and *P. fimbriata* and for both populations of *Euryattus*. Jackson and Wilcox (1990) used three size classes, defined by the ratio of prey to predator body volume, when testing *P. fimbriata* with juvenile salticids: small (0.1-0.25), medium (0.5-1), and large (1.5-2). Only two of these (medium and large) were used here.

McNemar tests for significance of changes were used for statistical analyses of the results from Tests 2 and 3, these tests being designed as paired comparisons (Sokal and Rohlf, 1981): each individual *Portia* was used in one test with one salticid and another test with the other salticid 48 h earlier or later (decided randomly). Yates' corrections were applied to the McNemar tests, and the Bonferroni adjustment (see Rice, 1989) was made to significance levels whenever single data sets were used in multiple comparisons.

RESULTS

TEST 1: *EURYATTUS* ADULT IN NEST

P. fimbriata behaved similarly toward allopatric (herein) and sympatric (Jackson and Wilcox, 1990) *Euryattus*, except that it attacked and killed allopatric *Euryattus* more frequently than sympatric *Euryattus* (Fig. 1, test of independence, $P<0.01$). Allopatric *Euryattus* appeared less prone than sympatric *Euryattus* to recognize *P. fimbriata* as a predator: 85% of the *P. fimbriata* got onto the leaf with allopatric *Euryattus*, but only 43% got onto the leaf with sympatric *Euryattus*; 23% of sympatric *Euryattus*, but only 4% of allopatric *Euryattus*, drove *P. fimbriata* away (Fig. 1).

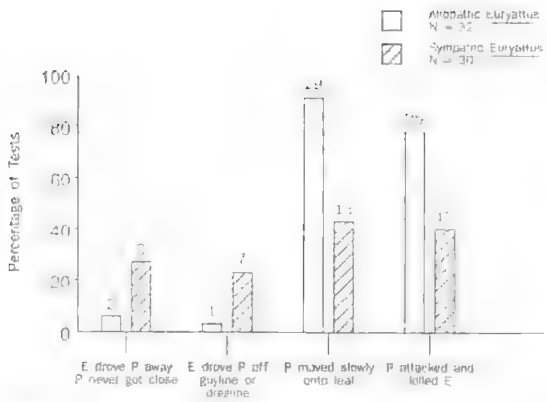

FIG. 1. *P. fimbriata* (P) tested with adult allopatric (Davies Creek) and sympatric (Crystal Cascades) *Euryattus* females (E) in suspended, rolled-up leaves. Data for sympatric *Euryattus* from Jackson and Wilcox (1990). Close: on leaf or guyline connected to leaf, or dropping on dragline toward leaf. For each outcome of test, number given above bar and percentage is read from axis.

TEST 2: JUVENILE *EURYATTUS* AND *JACKSONOIDES QUEENSLANDICA*

There was no evidence that *Portia* captured or stalked *J. queenslandica* more frequently than allopatric *Euryattus* (Figs 2, 3, McNemar tests, NS). Allopatric *Euryattus* did not appear to recognize *Portia* as a predator any more readily than did *J. queenslandica*.

TEST 3: CAIRNS AND DAVIES CREEK *EURYATTUS* JUVENILES

There was no evidence that *Portia* stalked sympatric *Euryattus* any more frequently than allopatric *Euryattus*, but *Portia* caught allopatric

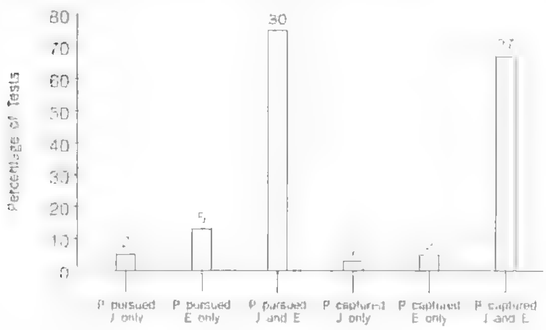

FIG. 2. Responses of *P. fimbriata* (P) to medium size (see text) allopatric *Euryattus* (E) and sympatric *J. queenslandica* (J). 40 paired tests: each *Portia* tested with one *Euryattus* and, on an alternate day, with one *Jacksonoides* (see text). Data for 'P pursued neither J nor E' and 'P captured neither J nor E' not displayed.

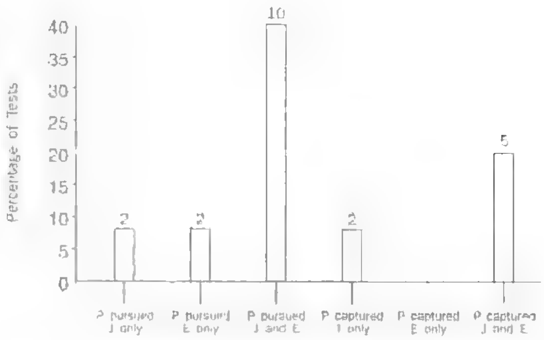

FIG. 3. Responses of *P. fimbriata* (P) tested with large (see text) allopatric *Euryattus* (E) and sympatric *J. queenslandica* (J). 25 paired tests: each *Portia* tested with one *Euryattus* and, on an alternate day, with one *Jacksonoides* (see text). Data for 'P pursued neither J nor E' and 'P captured neither J nor E' not displayed.

Euryattus more often that it caught sympatric *Euryattus* (Figs 4, 5).

DISCUSSION

Only one population of *Portia fimbriata* from Cairns studied (Jackson and Wilcox, 1990) is sympatric with *Euryattus*. *Euryattus* suspends a rolled-up leaf for a nest, and this is the only salticid sympatric with the Cairns *Portia*, or with any other *Portia* studied, known to do this. Only the Cairns *Portia* is known to use a prey-specific predatory behaviour against *Euryattus*. The sympatric (Jackson and Wilcox, 1990), but not the allopatric, *Euryattus* appears readily to recognize and defend itself against *Portia*. In fact, the al-

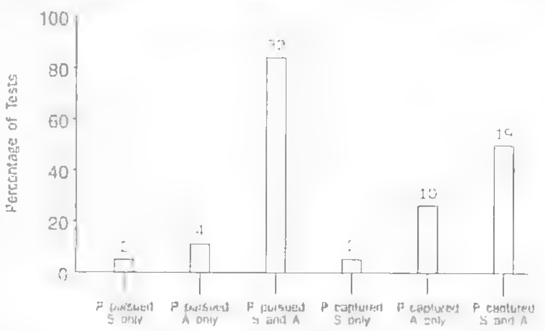

FIG. 4. Responses of *P. fimbriata* (P) to medium size (see text) sympatric (S) and allopatric (A) *Euryattus* sp. juveniles. 38 paired tests: each *Portia* tested with one sympatric and, on an alternate day, with one allopatric *Euryattus* (see text). Data for 'P pursued neither S nor A' and 'P captured neither S nor A' not displayed.

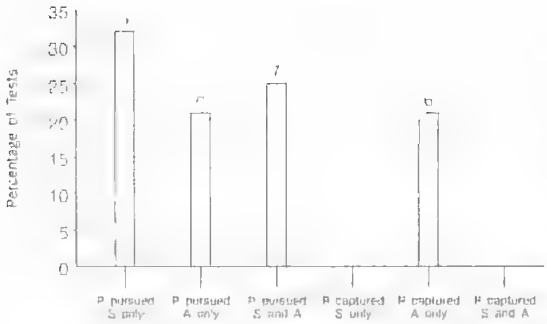

FIG. 5. Responses of *P. fimbriata* (P) to large (see text) sympatric (S) and allopatric (A) *Euryattus* sp. juveniles. 28 paired tests: each *Portia* tested with one sympatric and, on an alternate day, with one allopatric *Euryattus* (see text). Data for 'P pursued neither S nor A' and 'P captured neither S nor A' not displayed.

lopatric *Euryattus* appears to be no better than *J. queenslandica* at escaping predation by *Portia* , whereas *Portia* captured *J. queenslandica* more efficiently than it captured the sympatric *Euryattus* (Jackson and Wilcox, 1990). The ability of the Cairns *Euryattus* appears to be a predator-specific antipredator behaviour.

Population differences were evident despite there being no known prior experience of the predator by the prey or the prey by the predator under laboratory rearing conditions in this and the earlier (Jackson and Wilcox, 1990) study. These findings suggest that, in the Cairns area, *Portia* and *Euryattus* appear to have acted as selective agents on the evolution of each other's behaviour.

ACKNOWLEDGEMENTS

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LITERATURE CITED

DAWKINS, R. & KREBS, J.R. 1979. Arms races between and within species. Proceedings of the Royal Society, London B 205: 489-511.

JACKSON, R.R. 1985. The biology of *Euryattus* sp. indet., a web-building jumping spider (Araneae, Salticidae) from Queensland: utilization of silk, predatory behaviour and intraspecific interactions. Journal of Zoology, London (B) 1: 145-173.

JACKSON, R.R. & BLEST, A.D. 1982. The biology of *Portia fimbriata*, a web-building jumping spider (Araneae, Salticidae) from Queensland: utilization of webs and predatory versatility. Journal of Zoology, London 196: 255-293.

JACKSON, R.R. & HALLAS, S.E.A. 1986. Comparative biology of *Portia africana*, *P. albimana*, *P. fimbriata*, *P. labiata*, and *P. schultzi*, araneophagic, web-building jumping spiders (Araneae, Salticidae): utilisation of webs, predatory versatility, and intraspecific interactions. New Zealand Journal of Zoology 13: 423-489.

JACKSON, R.R. & WILCOX, R.S. 1990. Aggressive mimicry, prey-specific predatory behaviour and predator-recognition in the predator-prey interactions of *Portia fimbriata* and *Euryattus* sp., jumping spiders from Queensland. Behavioral Ecology and Sociobiology 26: 111-119.

RICE, W.R. 1989. Analyzing tables of statistical tests. Evolution 43: 223-225.

SOKAL, R.R. & ROHLF, F.J. 1981. 'Biometry'. (Freeman: San Francisco).

WANLESS, R.F. 1978. A revision of the spider genus *Portia* (Araneae: Salticidae). Bulletin of the British Museum (Natural History) Zoology 34: 83-124.

"WE'LL MEET AGAIN", AN EXPRESSION REMARKABLY APPLICABLE TO THE HISTORICAL BIOGEOGRAPHY OF AUSTRALIAN ZODARIIDAE (ARANEAE)

R. JOCQUÉ

Jocqué, R. 1993 11 11: "We'll meet again", an expression remarkably applicable to the historical biogeography of Australian Zodariidae (Araneae). *Memoirs of the Queensland Museum* 33: 561-564. Brisbane. ISSN 0079-8835.

The largest subfamily of the Zodariidae, the Zodariinae, contains 31 genera and has endemic representatives on all tropical continents. The sequence in this clade first indicates that the Australian zodariid fauna is the result of a combination of vicariance and dispersal events. Only three zodariid genera are not endemic to Australia. It is argued that two of these, *Mallinella* and *Asceua*, have reached Australia by dispersal over forest-covered areas. It is remarkable that the endemic Australian genera in the Zodariinae are more closely related to the African ones than are the Neotropical genera which is in contrast with the current ideas on chronology in plate tectonics. A possible explanation might be found in the past and present distribution of forests. The appearance of this type of vegetation on the Cretaceous-Tertiary boundary, might also be invoked to explain bipolar distributions in Africa.

La plus importante des sous-familles des Zodariidae, les Zodariinae, contient 31 genres, dont des endémiques sur chaque continent tropical. La séquence dans ce grand clade indique d'abord que la composition de la faune australienne serait le résultat d'une combinaison de vicariance et de dispersion. Seuls trois genres trouvés en Australie n'y sont pas endémiques. On avance l'argument selon lequel deux d'entre eux ont réussi à atteindre l'Australie par dispersion à travers des aires couvertes de forêts. Il est remarquable que les genres endémiques australiens soient plus proches des genres africains que de ceux d' Amérique du Sud ce qui contredit les idées courantes concernant la chronologie de la dérive des plaques. Une explication possible pourrait se trouver dans la distribution passée et actuelle des forêts équatoriales. La génèse de ce type de végétation, à la fin du Crétacé, pourrait également expliquer la distribution bipolaire de certaines vieilles lignées d'invertébrés. ☐*Africa, Gondwanaland, distribution, vicariance.*

Rudy Jocqué, Koninklijk Museum voor Midden-Afrika, B-3080 Tervuren, Belgium; 13 October, 1992.

The Zodariidae are a medium-size pantropical family of mainly nocturnal, ground-living spiders. Except for the members of the subfamily Storenomorphinae they are virtually all burrowers to some degree. Some simply dive into sand (*Psammoduon*) or hide in litter (*Asceua, Mallinella*) whereas others make a complex retreat consisting of a burrow with a trapdoor (*Psammorygma, Neostorena*) or an igloo-like construction of pebbles or grains of sand (*Diores, Zodarion*). This sedentary lifestyle and the fact that zodariids do not balloon explains why most species have small distribution ranges. It also makes them an ideal subject for zoogeographical studies, moreover since a cladistic analysis of the family is available (Jocqué, 1991).

THE AUSTRALIAN ZODARIIDAE

Most Australian zodariids, estimated at several hundred species, belong to genera endemic to the Australian continent. There is no trace of any representatives of these genera on any other continent (Table 1).

Genus	Distribution	Habitat
Asceua	Palaeotropics & Australia	circumforest
Asteron	Australia	steppe -woodland
Cyrioctea	southern Gondwana	dunes
Habronestes	Australia	steppe -woodland
Ishania	South and Central America	circumforest
Mallinella	Palaeotropics & Australia	tropical forest
Neostorena	Australia	steppe -woodland
Storena	Australia	steppe -woodland
Storosa	Australia	steppe -woodland
Tenedos	South and Central America	steppe -circumforest

TABLE 1. Distribution and habitat of some zodariid genera.

Three genera have representatives elsewhere and in fact have the centre of their distribution outside Australia. The first one is *Cyrioctea*, the only genus in the Cyriocteninae, found exclusively in sandy habitats such as arid dunes and sand deserts. It has a typical Gondwanan distribution

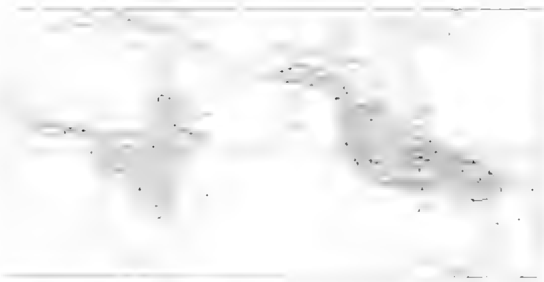

FIG. 1. Approximate distribution of *Mallinella*.

with representatives in South Africa, Chile and Australia (*Cyrioctea raveni* Platnick and Griffin). Both the other genera, *Mallinella* and *Asceua*, have an enormous distribution which appears to be linked with old world forests. One species of each has reached the northern tip of Australia.

The Australian zodariid fauna is thus apparently composed of three different stocks: a strictly endemic one, a southern Gondwanan one and a third element that could be quoted as old world forest fauna. To understand this composition we have to go back to an era before the breakup of Gondwanaland.

The Zodariidae indeed have a basic Gondwanan distribution with the more plesiomorphic taxa represented in Africa, Australia and South America. These are the Cyrioctcinae, the Lachesaninae and the more plesiomorphic members of the Zodariinae. The latter taxon is now known to include what has been described as the subfamily Storeninae (Jocqué, 1991, 1992). Thirty-one out of 47 genera now belong in the Zodariinae. However, the more apomorphic members of the subfamily (Femoral Gland Clade or FGC), having several synapomorphies (femoral gland, lack of chilum, flattened incised hairs, fused chelicerae) are present only in Africa (including part of the Palaearctic) and tropical Asia. The same applies to the Storenomorphinae and the Cydrelinae which are restricted to tropical Africa and tropical Asia.

When Africa got finally separated from other major landmasses, slightly more than 100 mybp, these three groups were apparently not yet in existence. The bulk of the zodariid fauna outside that continent is therefore supposed to be derived of the plesiomorphic taxa present at the time of the split-off. However, from the above it is clear that India (and part of South East Asia ?) carried a much more modern assemblage of Zodariidae when it moved towards its present position. Indeed, there is no evidence that at least purely tropical forest organisms (e.g., *Mallinella*) originating in Africa, have been able to reach India via a northern itinerary. No forest connection has ever existed via the mediterranean and the Arabian peninsula. This paradox is discussed below.

Virtually all Zodariidae are restricted to habitats lying in a climatic zone with a marked dry season. In the Neotropics only a few species (in *Ishania* and *Tenedos*) seem to have adapted to moist forest and no zodariids have so far been found in Amazonia. In Australia no true forest-inhabiting species belonging to endemic genera appear to be present, although some species in the genera *Neostorena*, *Asteron*, *Storosa* and *Habronestes*, occur in dense woodland. But the most common and widely distributed forest inhabiting genus is doubtlessly *Mallinella*. This genus has an enormous distribution (Fig. 1): it occurs in virtually all African forests from Senegal in the west to the Chimanimani Mts. (Zimbabwe) (Jocqué, unpublished data) in the south and Kenya and Ethiopia in the east, but is remarkably absent from the South African forests which emphasizes its inability to cross unforested zones. It is present in montane rainforest in India and Nepal and occurs in virtually all dense forests in the Far East, as far as New Guinea. One species has reached the northeastern tip of Australia. This is apparently a very recent event as that species, *Mallinella zebra* Thorell, occurs on both New Guinea and Australia. Considering the fractionating of this genus in the rest of its distribution range and the fact that no speciation has occurred in this case, there is little doubt that the arrival occurred during the Pleistocene ice-ages, during which there was a land-bridge linking New-Guinea and Australia (Keast, 1983). A well documented case of a less recent Asian invader is that of *Tamopsis* (Hersiliidae) which is supposed to have arrived in northern Australia during the Miocene (Baehr, 1988). This relatively early arrival has resulted in clockwise colonization of almost the entire circumference of the Australian continent and the appearance of many strongly related species.

A second recent zodariid arrival is that of an undescribed species of *Asceua* (Jocqué, in preparation) which can be characterized as a circum-forest genus. Its ecological status is fairly similar to those genera mentioned above, which occasionally occur in dense woodland or even rainforest in the case of the South American *Ishania* and *Tenedos*. The distribution of *Asceua* (Fig. 2) is even larger than that of *Mallinella* and

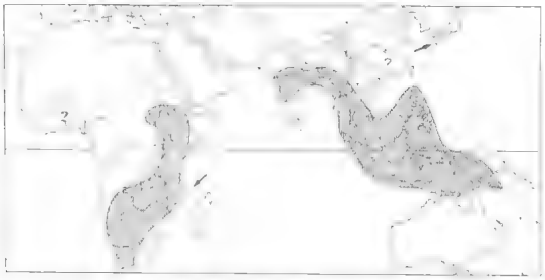

FIG. 2. Approximate distribution of *Asceua*.

the patterns overlap only partially. Although several Asian species are known to occur in rainforest (Bosmans and Hillyard, 1990; P. Schweninger pers. comm. 1989; C. Deeleman-Reinhold, pers. comm. 1988; J. Murphy, pers. com. 1988) no representatives are found in African lowland rainforest. On the other hand it is present in rather dry areas in southern Africa. Considering its very restricted distribution area in Australia, it is supposed to have arrived there at the same time as *Mallinella*.

Two closely related lines of zodariines which had been separated for about a hundred million years thus met again.

Assuming that *Mallinella* was initially better adapted to rainforest conditions, it would be interesting to study if the arrival of *Mallinella zebra* has induced a shift in the rest of the zodariid fauna in the area it now occupies, and whether it is still expanding.

GENERAL DISTRIBUTION OF THE ZODARIINAE

The monophyletic assemblage of the Zodariinae is largely composed of genera which are endemic to particular continents (Jocqué 1991, fig. 41). Remarkably, the African genera are apparently more closely related to the Australian Zodariinae than to those in South America. The five Neotropical genera are indeed near the root of the zodariine branch whereas the Australian ones are situated in between the Afrotropical and the Palaeotropical ones (the latter group has an apparently recent outflow into the Palaearctic). The reduced area-cladogram resulting from these relationships is given in Fig. 3. This statement is at least puzzling: it is in contrast with the timing of major plate tectonic events that caused the breakup of Gondwanaland, as deduced from geological data and corroborated by many biogeographical data (e.g. Nelson and Platnick, 1980). However, not only is there much controversy about the original position of many plates, the timing and the mechanics of the movement are also subject to a debate. The expansion theory of Carey (1975) and Shields (1979, 1983) positions several plates in different places than does the classical theory (Norton and Sclater, 1979; Owen, 1983). According to the latest data (Veevers *et al.*, 1991; Scotese *et al.*, 1988; Powell *et al.*, 1988) it appears that India split off from Gondwanaland together with the southern continents Australia and Antarctica. How then can one explain the fact that India and Sri Lanka share many apomorphic monophyletic taxa with Africa (e.g., *Hermippus*, Storenomorphinae, Cydrelinae, members of the FGC)? Briggs (1987) thinks that India, on its course to Asia, became again attached to north-east Africa by the end of the Cretaceous, a remarkable hypothesis that might explain the apparent faunal anomaly. It would certainly explain how forest dwelling spiders like *Mallinella* and *Asceua* have reached Asia.

The main question that is raised by the zodariid cladogram is why the Australian taxa are more strongly related to the African than to the South American ones.

A possible explanation is that the few typical forest inhabiting zodariid genera did only evolve after the main continents had broken away from Africa. Broad-leaved forests arose at least during the Cretaceous but became dominant in equatorial conditions on the Cretaceous-Tertiary boundary (Wolfe, 1987; Wolfe and Upchurch, 1986, 1987). It is strange that in the context of African biogeography no mention has been made of the dramatic shift that has been brought about by the appearance of broad-leaved evergreen forest. The conditions at ground level in this kind of forest and the former conifer forests were probably as different as they are for instance in present-day rainforest and miombo in Africa. The faunas of these vegetation types are equally very different. Dense miombo woodland and submontane evergreen forest within each other's sight on the Nyika Plateau in Malawi, contain completely different litter-layer spider faunas with hardly any genus overlap in the spider families that have been studied (Zodariidae, Linyphiidae, Lycosidae, Tetragnathidae; Jocqué, unpublished data).

The present day bipolar distribution of many ancient African taxa of ground-dwelling invertebrates might therefore be explained in the light of the evolution of broad-leaved rain forest

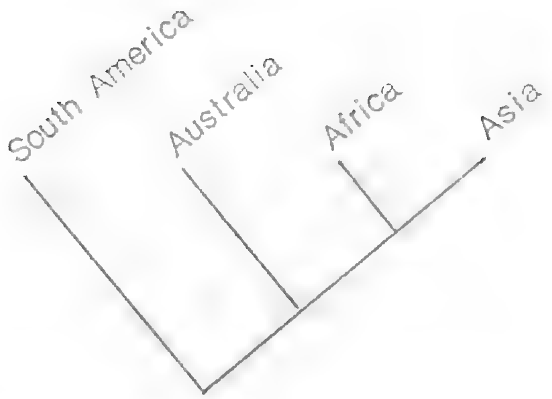

FIG. 3. Area cladogram of tropical continents as based on the clade of the Zodarinae.

during the Cretaceous. This novel type of vegetation with a very new structure and hence ecological conditions, split most existing taxocoenoses that had to adapt to the new forest conditions. In the Zodariidae only very few genera succeeded in doing so. In Africa only *Mallinella* really developed into a specialised forest spider genus.

The remote relationship of South American and African Zodariidae may well be the result of similar events at the time of the breakup of Gondwanaland favouring the dispersion of particular genera, hampering that of others.

LITERATURE CITED

BAEHR, B. & BAEHR, M. 1988. Zur Systematik, Phylogenie und Zoogeographie der *Tamopsis arnhemensis-circumvidens-tropica* Gruppe (Araneae, Hersiliidae) aus Australien. XI. Europaisches Arachnologisches Colloquium, TUB-Dokumentation Kongresse und Tagungen 38: 238-249.

BOSMANS, R. & HILLYARD, P. 1990. Spiders of the family Zodariidae from Sulawesi, Indonesia (Arachnida; Araneae: Zodariidae). Bulletin of the British Arachnological Society 8: 147-160.

BRIGGS, J. 1987. 'Biogeography and plate tectonics'. (Elsevier: Amsterdam-New York).

CAREY, W. 1975. The expanding earth: an essay review. Earth Sciences Review 11: 105-143.

JOCQUÉ, R. 1991. A generic revision of the spider family Zodariidae (Araneae). Bulletin of the American Museum of Natural History 201: 1-160.

1992. A new species and the first males of *Suffasia* with a redelimitation of the subfamilies of the Zodariidae (Araneae). Revue Suisse de Zoologie 99: 3-9.

KEAST, J. 1983. In the steps of Alfred Russel Wallace: Biogeography of the Asian-Australian interchange zone. Pp. 367-407. In Sims, R., Price, J. & Whalley, P. (eds). 'The emergence of the biosphere.' (Academic Press: London and New York).

NELSON, G. & PLATNICK, N.I. 1980. A vicariance approach to historical biogeography. Bioscience 30: 339-343

NORTON, I.O. & SCLATER, J.G. 1979. A model for the evolution shield of the Indian Ocean and the breakup of Gondwanaland. Journal of Geophysical Research 84: 6803-6830.

OWEN, H.G. 1983. 'Atlas of continental displacement, 200 million years to the present.' (Cambridge University Press: Cambridge).

POWELL, C.McA., ROOTS, S.R. & VEEVERS J.J. 1988. Pre-breakup continental extension in East Gondwanaland the early opening of the eastern Indian Ocean. Tectonophysics 155: 261-283.

SCOTESE, C.R., GAHAGAN, L.M. & LARSON, R. 1988. Plate tectonic reconstructions of the Cretaceous and Cenozoic oceanic basins. Tectonophysics 155: 27-48.

SHIELDS, O. 1979. Evidence for initial opening of the Pacific Ocean in the Jurassic. Palaeogeography, Palaeoclimatology, Palaeoecology 26: 181-220.

1983. Trans-Pacific biotic links that suggest earth expansion. Pp. 199-205. In S.W. Carey (ed). 'The expanding earth, a symposium.' (University of Tasmania: Hobart).

VEEVERS, J.J., POWELL, C.Mca.. & ROOTS, S.R. 1991. Review of seafloor spreading around Australia. I. Synthesis of the patterns of spreading. Australian Journal of Earth Sciences 38: 373-389.

WOLFE, J. 1985. Late Cretaceous-Cenozoic History of deciduousness and the terminal Cretaceous event. Palaeobiology 13: 215-226.

WOLFE, J. & UPCHURCH, G. 1986. Vegetation, climatic and floral changes across the Cretaceous-Tertiary boundary. Nature 324: 148-152.

1987. North American nonmarine climates and vegetation during the late Cretaceous. Palaeogeography, Palaeoclimatology, Palaeoecology 61: 33-77.

BASIC ARCHITECTURE OF THE OVARY IN THE GOLDEN SILK SPIDER, *NEPHILA CLAVATA*

AKIO KONDO, EIKO CHAKI AND MITSUHIRO FUKUDA

Kondo, A., Chaki, E. and Fukuda, M. 1993 11 11: Basic architecture of the ovary in the golden silk spider, *Nephila clavata*. *Memoirs of the Queensland Museum* 33 (2): 565-570. Brisbane. ISSN 0079-8835.

In gravid females of the golden silk spider, *Nephila clavata* L. Koch, the ovaries are composed of flat cisternae. To clarify whether the cisternal structure is primarily or secondarily formed by pressure from mature eggs, ovary development was examined from early subadults to mature spiders. Serial paraffin sections of the early subadults definitely show that a pair of longitudinal furrows, presumptive lumina of the ovaries, lined with loose cell layers, penetrate perpendicularly into the ovarian tissue. So the basic architecture of the ovary in *N. clavata* is primarily flat cisterna.
Im Falle von reifen Weibchen von *Nephila clavata* setzen sich die Ovarien aus flachen Beuteln zusammen. Um herauszufinden, ob diese strukturelle Fläche angeboren ist oder durch den Druck der reifen Eiern gebildet wird, wurde die Entwicklung der Ovarien vom frühen Subadult bis zum reifen Adult untersucht. In den seriellen Paraffinstückchen vom frühen Subadult zeigte sich, daβ ein Paar longitudinale Furchen, die mit zerstreuten Zellenschichten verstärkt wurden, d.h. die präsumptive Lumen, perpendiklar in die Ovariumgewebe gehen. Daraus kann man schlieβen, daβ die Grundarchitektur von diesen Ovarien angeboren aus flachen Beuteln besteht. □*Spider, Nephila, ovary, histology.*

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The golden silk spider, *Nephila clavata* L. Koch, is able to deposit egg masses twice (Kondo, 1988; Shimojana, 1971). Prior to the first oviposition, gravid females possess complicated ovaries whose lumina are expanded among mature eggs. After the second oviposition, the ovarian lumen of exhausted females is not closed and contains immature oocytes and yolk granule debris. In both cases, the basic architecture of the ovary is not clearly identified. In vigorous females immediately after first oviposition, the lumen of the ovary is completely closed and the ovarian epithelium protrudes many young oocytes into the body cavity. In this case the ovarian tubes elongate dorsally and ventrally to form flat cisternae, as if the lumina have been squeezed between mature eggs, already ovulated at the first oviposition, side by side (Kondo and Chaki, 1991).

Generally, however, the spiders have a pair of tubular ovaries or ring-like ovaries. The present study tries to clarify whether the cisternal architecture of the ovary of *N. clavata* is primarily or secondarily formed by pressure from mature eggs.

MATERIALS AND METHODS

Four female subadult and two adult *Nephila clavata* were collected in Funabashi, Central Japan, from late August to early September.

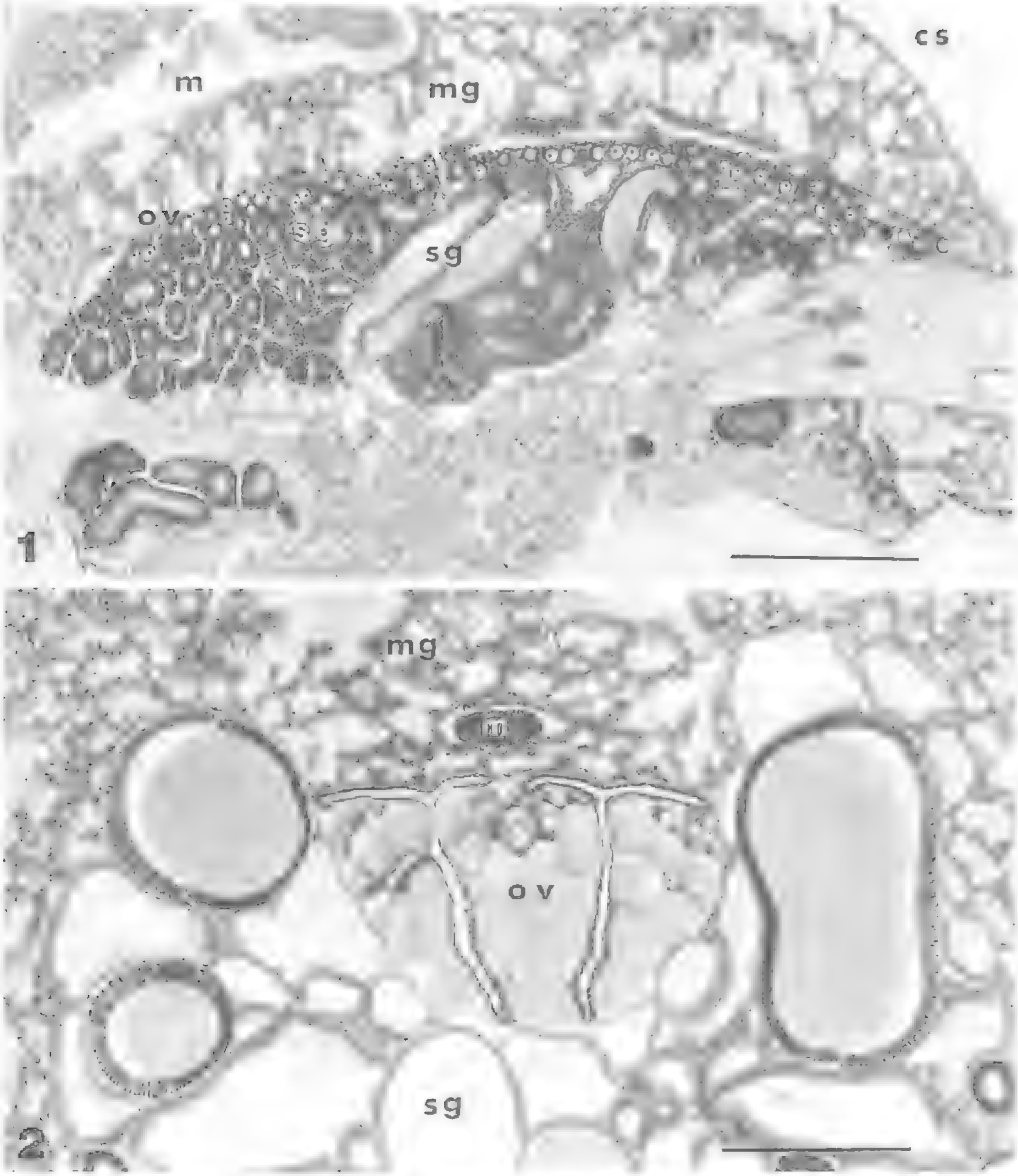
After removal of the cuticle, the entire body or the opisthosoma was fixed in FAA (formalin 5, ethanol 15, glacial acetic acid 1) for 5-21 hours, dehydrated in graded strength of ethanol, embedded in paraffin and sectioned at 6-10μm. Before sectioning, a cut surface of the sample containing mature eggs was treated with distilled water (Kondo, 1969). Serial paraffin sections were stained with Mayer's acid-haemalaum and eosin.

RESULTS

SUBADULTS

A pair of ovaries was situated behind the book lung extending to the cloacal sac and surrounded by the midgut glands dorsally and by silk glands laterally and ventrally (Figs 1, 2). Although the ovarian tissue was divided in two at the anterior and posterior ends, the left and right ovaries were not separated from each other and formed single rod-shaped tissue for the most part.

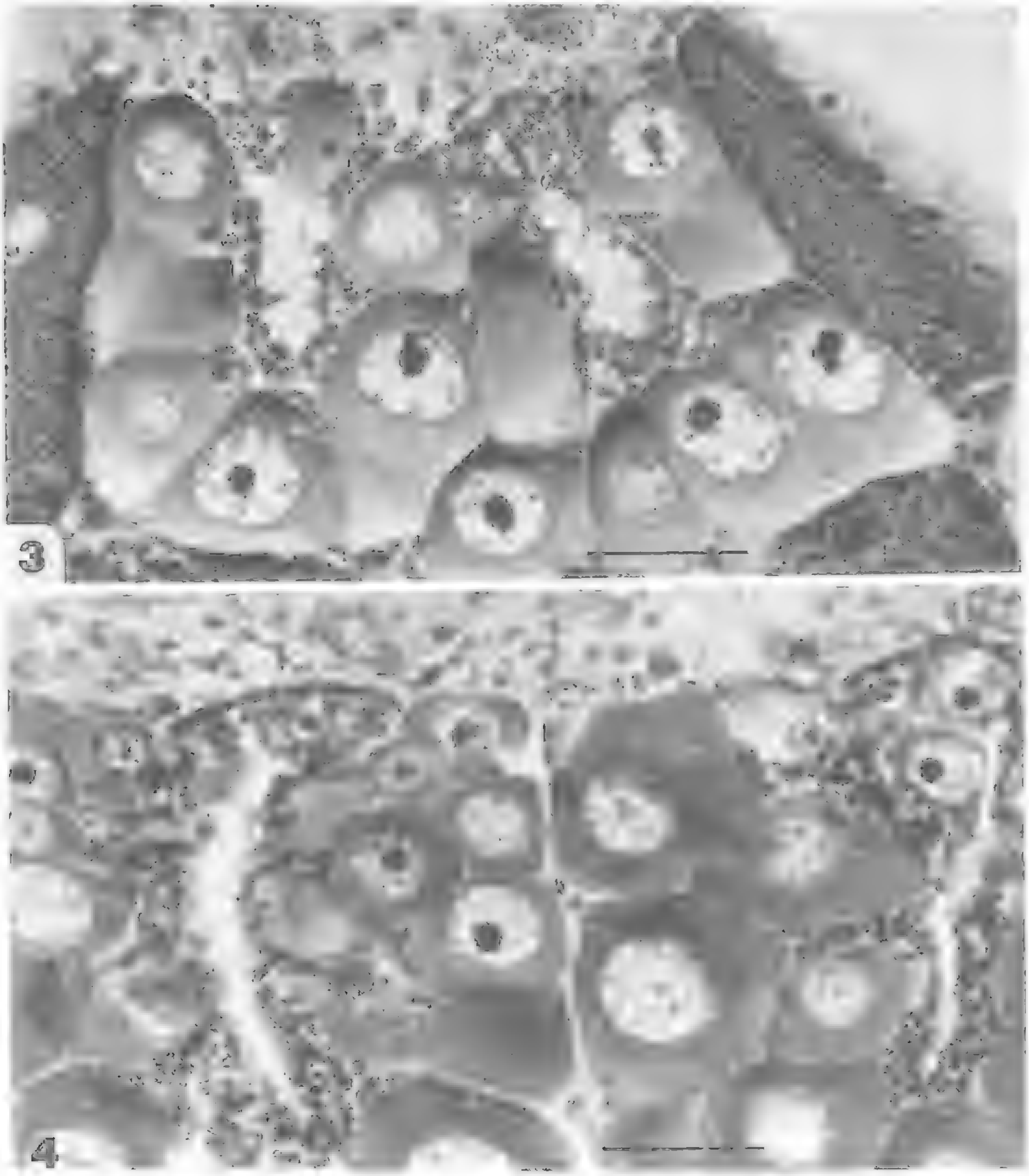
Maximum width and thickness of the ovarian tissue were 250μm and 150μm in a small subadult with cephalothorax 1.6 mm wide, 2.6 mm long, and 500μm and 220μm in a large subadult



FIGS 1, 2. 1. Longitudinal section of a large subadult.cs: cloacal sac, m: midgut, mg: midgut gland, ov: ovary, sg: silk gland. 2. Transversal section of a female immediately after final moulting. m: midgut, mg: midgut gland, ov:ovary, sg: silk gland. Scales: 0.5 mm.

whose cephalothorax was 2.8 mm and 4.2 mm respectively.

In transverse sections the ovarian tissue was trapezoidal. In a small subadult, two furrows lined with a loose cell layer penetrated from the upper side of the trapezoid into the ovarian tissue (Fig. 3). The loose cell layer may be the ovarian wall or the ovarian epithelium. Then the furrows seemed to be surrounded by a single layer of the oocytes. Most oocytes, whose cytoplasm was strongly basophilic, were cuboidal or polygonal and 40-50μm in diameter.

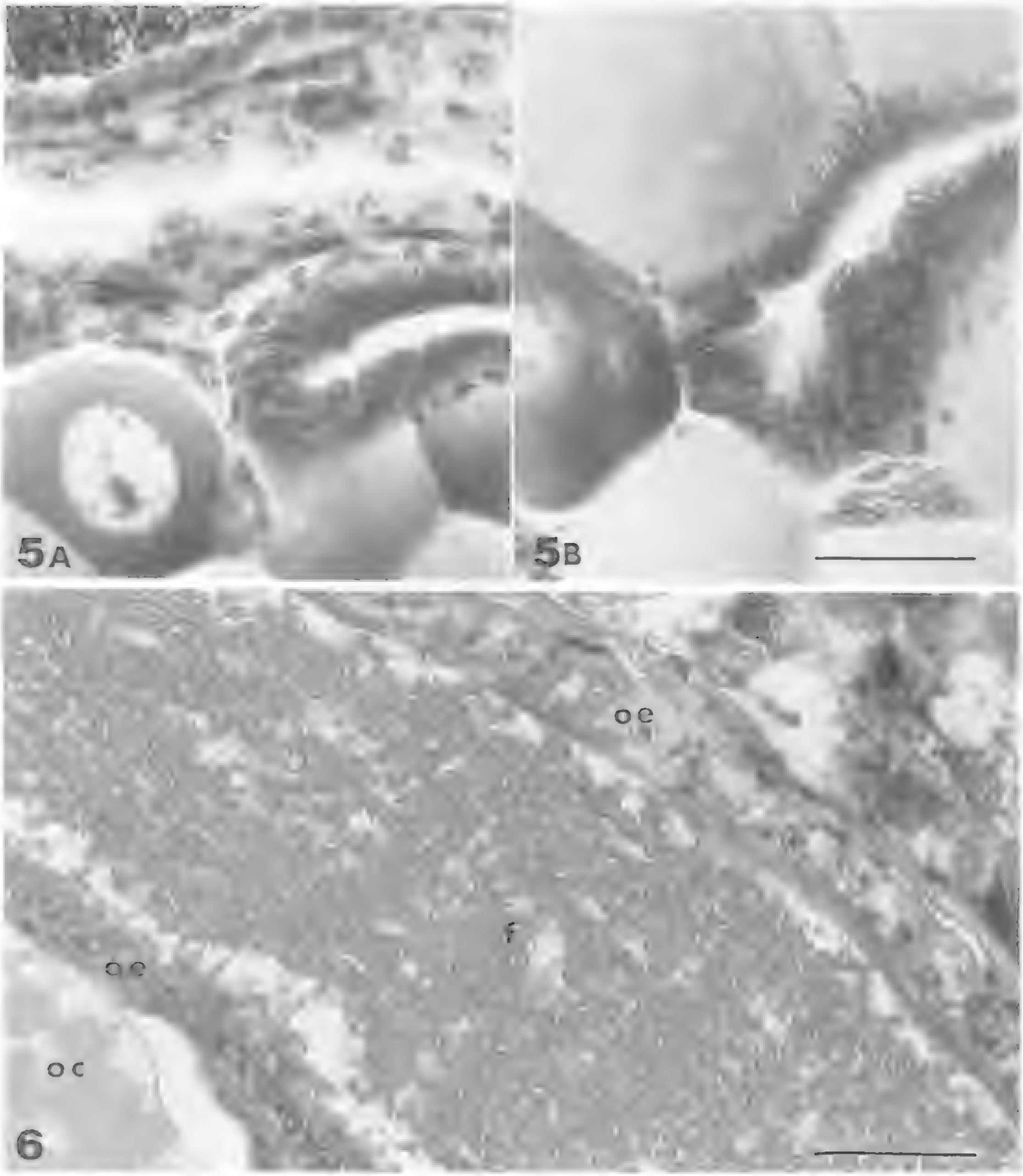


FIGS 3, 4. Transverse section of ovarian tissue in small subadult (3) and in large subadult (4). Scales. 50μm

The spherical germinal vesicle was 25-35μm in diameter and contained an extremely basophilic and slightly eosinophilic nucleolus. Yolk granules had not formed. The vitelline body or Balbiani's yolk nucleus was not observed.

Each oocyte was connected with the ovarian wall through a short egg stalk or the funiculus. The cells constituting the ovarian wall were more or less columnar and had ellipsoidal nuclei in the basal part and vacuolated protoplasm in the distal part facing the presumptive lumen of the ovary.

In the large subadult, profiles of the oocytes closely resembled the oocytes in the small subadult, though they increased slightly in number



FIGS 5, 6. 5. Transverse section of ovary in female immediately after final moulting. A. Median dorsal part of ovary. B. Distal part of F-shaped lumen of ovary. 6. Lumen of ovary filled with eosinophilic fine granules in a gravid female. f: eosinophilic fine granules, oc: oocyte, oe: ovarian epithelium. Scales: 50µm.

and volume (Fig. 4). A prominent feature was the appearance of narrow lumina in the ovaries, while vacuolate cells in the ovarian wall remained in depth at both the anterior and posterior ends of the ovarian tissue.

ADULTS

In an adult presumably immediately after its final moult, the width of the entire ovaries was approximately 1.0 mm and the lumen of the ovary was F- or T-shaped, branching laterally (Fig. 2). The left and right ovarian epithelia were not fused, but connected with the oviducts. Total number of oocytes counted in one female was 1,390 including the small oocytes. No oocytes were observed above the dorsal side of the horizontally developing lumina.

Oocytes reached a diameter of 170µm. Germinal vesicles were 40-60µm in diameter. The nucleolus was collapsed and dispersed into nucleoplasm. Cytoplasm of the oocyte was less basophilic (Fig. 2). The eosinophilic yolk granules were neither formed nor accumulated. The ovarian wall seemed to be a simple columnar or pseudostratified epithelium composed of slender, compactly arranged and extremely basophilic cells. Flat cells were lined up between the ovarian epithelium and the oocytes (Fig. 5).

In a gravid female whose ovaries reached 4.0 mm in width, the ovary contained many developing oocytes 380-460µm in diameter, and few immature oocytes. The developing oocytes were filled with eosinophilic yolk granules and had a germinal vesicle 50-60µm in diameter. The lumen of the ovary branches among the developing oocytes. The lumen of the ovary contained eosinophilic fine granules which were presumably a kind of cement substance used to hold the egg mass after oviposition (Fig. 6).

DISCUSSION

The formation of the ovary in *Nephila clavata* was examined from the early subadult stage. The small subadult employed was possibly a nymph of the 6th or 7th instar prior to the penultimate moult. In any case, at an early stage, the longitudinal ovarian walls arise as loose cell layers penetrating from the dorsal side of the ovarian tissue perpendicularly into the mass of the oocytes. The epithelial cells are vacuolated in their distal part and form a lumen which is I-shaped in transverse section. Then, the ovarian epithelium constructs flat rather than cylindrical cisternae.

By the final moult the lumina have been formed in the vacuolated portion of the ovarian epithelium. Immediately after the final moulting, while the oocytes increase in number and volume, a few branches of the lumen arise, mostly in the posterior half of the ovary, forming F- or T-shaped profiles in transverse sections. Simultaneously the oocytes grow and become less basophilic, perhaps due to a cytoplasmic increase. The loose cell layer in the small subadult transforms gradually into columnar epithelium composed of slender, compact and strongly basophilic cells by the final moult. Since the oocytes are connected with this epithelium through egg stalks, it seems to be the ovarian epithelium in the strict sense, though flat cells are aligned along the outside of this epithelium.

Subsequently the oocytes begin vitellogenesis and accumulate eosinophilic yolk granules in their cytoplasm. The lumina of the ovaries continues to branch amongst the oocytes and on the surface of the mass of the oocytes, and they are filled with eosinophilic fine granules which correspond to fine granules attaching to the surface of the chorion of the lycosid egg (Kondo, 1969), the spheres on the chorion (Humphreys, 1983, 1987) or cement substance of the egg mass (Kondo and Chaki, 1991).

In *N. clavata*, the ovarian epithelia of the left and right ovaries are not directly connected with each other, though in archaeid spiders they are connected through a bridge in the posterior portion of the ovaries to form a H-shaped organ (Traciuc and Legendre, 1970). Interstitial tissue, however, does not exist between the left and right ovaries, so the ovaries of *N. clavata* form a single rod-shaped organ. This rod-shaped structure was confirmed not only from both transverse and horizontal sections but also by dissection of the opisthosoma.

In conclusion, in *N. clavata* the basic architecture of the ovary is primarily composed of flat cisterna.

LITERATURE CITED

HUMPHREYS, W.F. 1983. The surface of spiders' eggs. Journal of Zoology, London 200: 303-316.

1987. The accoutrements of spiders' eggs (Araneae), with an exploration of their functional importance. Zoological Journal of the Linnean Society, London 89: 171-201.

KONDO, A. 1969. The fine structures of the early spider embryo. The Science Report of the Tokyo Kyoiku Daigaku, Section B No. 207: 47-67, pls 1-8.

1988. Effects of incubation temperature on the embryonic development and the oviposition in the silk spider, *Nephila clavata* L. Koch. Proceedings of Arthropodan Embryological Society of Japan No. 23: 21-22.

KONDO, A. & CHAKI, E. 1991. Histological studies on the ovaries of the golden silk spider, *Nephila clavata* L. Koch, before and after oviposition. Proceedings of Arthropodan Embryological Society of Japan No. 26: 9-10.

SHIMOJANA, M. 1971. Studies on the genus *Nephila* in Okinawa Island. (1) Studies on the life cycle of *Nephila clavata*. Biological Magazine Okinawa 7: 1-18 (In Japanese).

TRACIUC, E. & LEGENDRE, M.R. 1970. Données anatomiques sur l'appareil genital femelle des Archaeidae (Araneides). Comptes Rendus Hebdomadaires des Séances de l'Academie des Sciences, Série D, Sciences Naturelles 270: 1918-1921.

NEW PREY RECORDS FOR SPIDER HUNTING WASPS (HYMENOPTERA: POMPILIDAE) FROM THE NETHERLANDS

P. KOOMEN AND T.M.J. PEETERS

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In the southern Netherlands, 56 spider prey were collected, and identified, together with their pompilid predators. Those data are compared with data from the literature for northwestern Europe. *Anoplius* spp. seem to prey mainly upon ground dwelling spiders. A strong preference for the wolf spider *Trochosa terricola* was found for *Anoplius viaticus*, in agreement with data from Bristowe (1948). *Episyron rufipes* and *Caliadurgus fasciatellus* attack only orbweb building spiders. Data for *Auplopus carbonarius* and *Dipogon subintermedius* suggest that these species prefer to hunt on vertical planes like tree-trunks. *Arachnospila rufa*, *Pompilus cinereus*, and *Priocnemis* spp. appear to be non-selective.
Dans le sud des Pays-Bas, 56 araignées, proies de Pompilides, on été récoltées avec leurs prédateurs et identifiées. Les données acquises ont été comparées avec les celles de la littérature concernant les observations réalisées aux Pays-Bas et dans les pays voisins. *Anoplius* spp. montre une nette prédilection pour les araignées terricoles. Conformément aux données de Bristowe (1948), *Anoplius viaticus* préfère de loin *Trochosa terricola*. *Episyron rufipes* et *Caliadurgus fasciatellus* s'attaquent seulement aux araignées qui construisent des toiles orbiculaires. Les observations sur *Auplopus carbonarius* et *Dipogon subintermedius* suggèrent que ces espèces chassent de préférence sur des plans verticaux comme des vieux murs ou des troncs d'arbres. *Arachnospila rufa*, *Pompilus cinereus* et les *Priocnemis* spp. semblent être des espèces non sélectives. ☐*Araneae, predation, Pompilidae, selectivity, The Netherlands.*

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Female Pompilidae attack and paralyse spiders with their sting. Each captured spider is the food of a larva that hatches from an egg laid on the spider. Before oviposition, most European pompilids transport their prey to burrows excavated in the soil, or to pre-existing cavities, e.g., behind bark or between stones (Gauld & Bolton, 1988). Knowledge of pompilid prey is limited for obvious reasons: most hymenopterists are interested only in pompilids and not so much in their prey. Arachnologists tend to accept prey of Pompilidae gratefully, but without identifying their predators. As a consequence, data on prey hardly exist, are out of date and/or are unreliable because of changed taxonomic views, or do not go beyond generic level (e.g., Day, 1988; Oehlke and Wolf, 1987). However, collectively, all published data suggest some prey specialization, but it is not clear if this is due simply to opportunistic behaviour of pompilids, catching only (or mainly) the most abundant prey. A way to gather more knowledge concerning possible preferences of pompilids, is to catch pompilid predators *with* their prey, and to accurately identify them both. Autecological information on the spiders may give a clue as to whether pompilid species only catch what they can, or prefer, for some reason, some species of prey over others. This paper reports on the first results of such a study which began in 1987.

METHODS AND MATERIALS

Pompilids were studied at several locations, mainly in the southern Netherlands, near of Tilburg. Unless stated otherwise, the second author located pompilids by eye and intercepted prey-transporting females using glass tubes and an insect-net. Prey were collected and preserved in alcohol. Predators were collected only if identification in the field was not possible. Wasps were identified with the aid of Wolf (1972), Day (1988) and Oehlke and Wolf (1987). Identification of spiders was based mainly on Roberts (1985ab, 1987). Not all spiders could be identified to species level, because some were juvenile, thus lacking the genital organs necessary for a proper identification. Autecological data on spiders are derived from Jones (1983) and Maurer and Hänggi (1990). All spiders and wasps collected will be lodged in the National Museum of Natural History, Leiden, The Netherlands.

RESULTS

In total, 56 pompilid prey were collected. Data are summarized below. For each specimen the specific date and collecting site are given because both may have influenced hunting behaviour of the wasps. When more than one prey record is available for a single pompilid species, common characteristics of the prey are given that may point to a preference of the actual wasp.

POMPILINAE:

Anoplius concinnus (Dahlbom): *Pardosa* sp. (1 juv., Thorn, 13.x.1990); *Trochosa ruricola* (Degeer) (1♂, Thorn, 13.x.1990). Both are wolf spiders, Lycosidae. They were excavated from a, supposedly, single burrow between pebbles in a gravelpit, after a female *A. concinnus* had been observed showing nest building activity.

Anoplius infuscatus (Vander Linden): Lycosidae (1 juv., Moergestel, 30.iv.1988); *Alopecosa accentuata* (Latreille) (1 juv. Nieuw-Bergen, 6.ix.1991). Both are wolf spiders.

Anoplius viaticus (Linnaeus): *Agroeca brunnea* (Blackwall) (1♀, Beegden, 12.v.1991); *Trochosa terricola* Thorell (1♀ excavated, Alphen en Riel, 5.v.1989; 1♀+1♂, do., 3.v.1988; 1♀, 15.iv.1989, Apeldoorn; 7♀, Beegden, 12.v.1991; 1♀, Hilvarenbeek, 1.v.1988; 3♀+1♂, Berkel-Enschot, 5.v.1989; 1♀, Drunen, 9.v.1989; 1♀, Loon op Zand, 12.iv.1991; 1♀ excavated, Moergestel, 24.iv.1989; 2♀, do., 27.iv.1989; 2♀, do., Moergestel; 2♀, do., 5.v.1989; 1♀, do., 29.v.1989; 1♀, do., 23.vi.1989; 10♀+1♂, do., 29.iii.1990); *Pardosa monticola* (Clerck) (1♀, Beegden, 18.v.1989). All three species are ground dwelling spiders.

Arachnospila rufa (Haupt): *Alopecosa fabrilis* (Clerck) (1♂, Nieuw-Bergen, 1.ix.1991).

Auplopus carbonarius (Scopoli): *Haplodrassus* sp. (1 juv. found in a beehive in one of a group of barrel-shaped cells typical of *A. carbonarius* (Grandi, 1961: 75; Wahis, 1949: 99), Baarle-Nassau, 1991); *Clubiona brevipes* Blackwall (1♀, Udenhout, 11.viii.1990). Both are nocturnal hunters often hiding in silk retreats during the day.

Episyron rufipes (Linnaeus): *Larinioides cornutus* (Clerck) (1♀, Helvoirt, 16.viii.1991); *Nuctenea umbratica* (Clerck) (1 juv., Moergestel, 26.vi.1990). Both are orbweb building spiders.

Pompilus cinereus (Fabricius): Lycosidae (1 juv., Moergestel, 4.viii.1987).

PEPSINAE:

Caliadurgus fasciatellus (Spinola): *Agelenatea redii* (Scopoli) (1 juv., Moergestel, 4.x.1989).

Dipogon subintermedius (Magretti): *Segestria senoculata* (Linnaeus) (1♀ found in a cavity in an old pollard-willow (*Salix alba*), Tilburg, 23.vii.1991).

Priocnemis fennica Haupt: *Clubiona terrestris* Westring (1♀, Hilvarenbeek, 29.ix.1990).

Priocnemis minuta (Vander Linden): Gnaphosidae (1 juv., Moergestel, 17.viii.1988).

Priocnemis susterai Haupt: *Drassodes cupreus* (Blackwall) (1♀, Boxtel, 21.v.1988).

DISCUSSION

The new observations can be compared to data from the literature on pompilids in The Netherlands (Benno, 1969; Bouwman, 1915ab, 1916; Chrysanthus, 1947; Lefeber and Van Ooijen, 1988; Thijsse, 1907; Walrecht, 1936) and nearby countries (Bristowe, 1948; Day, 1981, 1988; Oehlke and Wolf, 1987; Wahis, 1948, 1955, 1962; Wolf, 1971). A summary with references included is given in Table 1. Comments for each pompilid species follow hereafter.

Anoplius concinnus was found with wolf spiders (Lycosidae) as prey. This is in agreement with the literature, where several genera of Lycosidae are mentioned.

Both in The Netherlands and in other countries, a preference for wolf spiders has been recorded for *Anoplius infuscatus*. Beside these, Thomisidae and Agelenidae are mentioned. Most members of these families are 'sit-and-wait' predators, but there are some exceptions, for instance *Thanatus* species and the males of *Textrix* species. So, the available data may point to a preference for ground dwelling spiders.

Anoplius viaticus appeared to prey almost exclusively on the wolf spider *Trochosa terricola* (Lycosidae). These observations are neither restricted to one locality, nor to a short period. Only in two of 41 cases (5%), *A. viaticus* caught other species: *Pardosa monticola* (Lycosidae) and *Agroeca brunnea* (Clubionidae). This suggests that *A. viaticus* did not simply catch the most abundant wandering spider, but rather searched actively for *T. terricola*. In literature on The Netherlands, the *Lycosa* sp. mentioned by Thijsse (1907) might refer to almost any modern lycosid genus. From data on prey elsewhere, the list given by Bristowe (1948) matches our data very well: he found in only seven of 47 cases (15%) prey that were not *Trochosa terricola*. However, other papers indicate several families and genera. Some are hunters by day like Lycosidae, while others are nocturnal hunters (*Drassodes*) or inhabitants of sheet webs (*Agelena*). Common attributes of the recorded spider genera are their medium to large size (5-13 mm) and the strata they occupy: on or near ground level. Most also prefer rather dry and/or sandy places as does *A. viaticus* (*Thanatus*, *Aelurillus*, *Pardosa monticola*, *Trochosa terricola*), but this is not true for

Predator	Prey
Anoplius concinnus	**Lycosidae** (D2): *Arctosa* (O&W), *Pardosa* sp. (K&P, L&VO, O&V), *Trochosa ruricola* (K&P)
Anoplius infuscatus	**Thomisidae** (D2): *Thanatus* (O&W). **Lycosidae** (D2, K&P): *Alopecosa accentuata* (K&P), *Arctosa* (O&W), *Pardosa* (O&W), *Pirata* (O&W), *Tricca* (O&W), *Trochosa* (L&VO, O&W), *Xerolycosa* (O&W). **Agelenidae** (D2): *Textrix* (O&W).
Anoplius viaticus	**Gnaphosidae** (D2): *Drassodes* (O&W). **Clubionidae:** *Agroeca brunnea* (K&P). **Thomisidae** (D2): *Thanatus* (O&W). **Salticidae** (D2): *Aelurillus* (O&W). **Lycosidae** (D2, T): *Alopecosa* (O&W; sub *Tarentula*), *A. accentuata* (B: sub *Tarentula a.*), *A. aculeata* (W3), *A. pulverulenta* (B, W2: sub *Tarentula carinata*), *Arctosa* (O&W), *A. perita* (B), *Pardosa* (O&W), *P. hortensis* (W2), *P. monticola* (B, K&P). *Trochosa* (O&W). *T. terricola* (B, K&P, W3). **Pisauridae**: *Pisaura mirabilis* (O&W, W2). **Agelenidae** (D2): *Agelena* (O&W).
Arachnospila rufa	**Gnaphosidae** (D2): *Drassodes* (O&W), *Gnaphosa* (O&W). **Clubionidae** (D2): *Cheiracanthium* (O&W). **Salticidae** (D2): *Aelurillus* (O&W). **Lycosidae** (D2): *Alopecosa* (O&W: sub *Tarentula*), *A. fabrilis* (P&K), *Trochosa* (O&W).
Auplopus carbonarius	**Zoropsidae**: *Zoropsis* (Wo). **Segestriidae** (D2): *Segestria* (Wo). **Gnaphosidae** (D2): *Aphantaulax* (Wo), *Haplodrassus* sp. (K&P). **Clubionidae** (D2): *Cheiracanthium* (Wo), *Clubiona* (Wo), *C. brevipes* (K&P). **Anyphaenidae** (D2). **Thomisidae** (D2): *Philodromus* (Wo). **Salticidae** (D2): *Dendryphantes* (Wo), *Evarcha* (Wo), *Sitticus* (Wo). **Lycosidae** (D2): *Lycosa* (Wo). *Trochosa* (Wo). **Agelenidae** (D2): *Agelena* (Wo). **Tetragnathidae**: *Meta* (Wa).
Episyron rufipes	**Lycosidae** (D2: only some cases). **Tetragnathidae**: *Meta* (D2). **Araneidae**: *Agelenatea redii* (B: sub *Araneus r.*), *Araneus* (D2, O&W), *A. diadematus* (B), *Argiope* (O&W), *Gibbaranea gibbosa* (L&VO; sub *Araneus gibbosus*), *Larinioides cornutus* (B: sub *A. foliata*, K&P), *Nuctenea umbratica* (K&P).
Pompilus cinereus	**Atypidae**: *Atypus* sp. (C). **Zoropsidae**: *Zoropsis* (O&W). **Gnaphosidae** (D1): *Pterotricha* (O&W). **Clubionidae** (D1). *Cheiracanthium* (O&W). **Zoridae** (D1): *Zora* (O&W). **Thomisidae** (D1): *Xysticus* (O&W). **Salticidae**: *Aelurillus* (O&W), *Ballus* (C: not sure). **Lycosidae** (B1, C, D1, K&P): *Alopecosa* (O&W: sub *Tarentula*), *Arctosa* (O&W), *A. perita* (B, B1, D1, D2, L&VO), *Pardosa* (O&W), *Pirata* (O&W). *Trochosa* (O&W). *Xerolycosa* (D1, D2). **Pisauridae** (D1): *Dolomedes* (O&W). **Araneidae**: *Araneus* (O&W).
Caliadurgus fasciatellus	**Tetragnathidae**: *Meta* (D2, O&W), *M. segmentata* (L&VO). **Araneidae**: *Agelenatea redii* (K&P) *Araneus* (D2, O&W), *A. alsine* (B2), *A. diadematus* (Be, B2, W1), *A. quadratus* (W1).
Dipogon subintermedius	**Segestriidae**: *Segestria* (O&W), *S. senoculata* (D2, K&P). **Salticidae**: *Salticus* (O&W).
Priocnemis fennica	**Clubionidae**: *Clubiona terrestris* (K&P). **Lycosidae**: *Pardosa pullata* (D2)
Priocnemis minuta	**Gnaphosidae** (K&P).
Priocnemis susterai	**Gnaphosidae**: *Drassodes* (O&W), *D. cupreus* (K&P).

TABLE 1. Summary of the prey records in the literature for the pompilid species for which this study gives new data. References are abbreviated: B = Bristowe, 1948; Be = Benno, 1969; B1 = Bouwman, 1915b; B2 = Bouwman, 1916; C = Chrysanthus, 1947; D1 = Day, 1981; D2 = Day, 1988; K&P = Koomen & Peeters, this study; L&VO = Lefeber and Van Ooijen, 1988; O&W = Oehlke and Wolf, 1987; T = Thijsse, 1907; Wa = Walrecht, 1936; Wo = Wolf, 1971; W1 = Wahis, 1948; W2 = Wahis, 1955; W3 = Wahis, 1962.

Agroeca brunnea, an inhabitant of wet places. So, although our observations and Bristowe (1948) suggest a strong preference for only one species of Lycosidae, data from other countries show a much broader spectrum of prey. This may point to a preference for *Trochosa terricola*, that is abandoned when the latter species is not available.

Arachnospila rufa is not selective: spiders with various sizes, and from several habitats and strata have been recorded. Our observations support these data.

For *Auplopus carbonarius*, the observations that Segestriidae, *Clubiona brevipes*, Anyphaenidae, and *Dendryphantes* were prey items may point to a preference for spiders that walk along, or hide in crevices in, vertical planes, e.g. walls or tree-trunks. Species with (at least occasionally) similar habits are found in most of the other families and genera recorded (*Zoropsis*, *Aphantaulax*, *Haplodrassus*, *Philodromus*, *Evarcha*, *Sitticus*, *Agelena*, *Meta*), but without species identifications, the hypothesis that *A. carbonarius* is mainly a vertical hunter cannot be supported or falsified. Several authors note that *A. carbonarius* has a habit of amputating the legs of its preys (e.g., Grandi, 1961: fig. 48; Oehlke and Wolf, 1987). This did not occur in the two cases we noted. Both the *Haplodrassus* and the *Clubiona* prey still had all of their legs.

Episyron rufipes was found to prey upon two araneid spiders. Using data from other countries (see Table 1) it can be deduced that *E. rufipes* specializes on orbweb building spiders.

For *Pompilus cinereus* many different prey are known, including burrowing spiders (*Atypus*), orbweb building spiders (*Araneus*), and xerophylic (*Arctosa perita*, *Aelurillus*) and hygrophylic species (*Dolomedes*). This suggests no specificity at all. To date, only one juvenile wolf spider can be added.

Caliadurgus fasciatellus is a second pompilid species that is obviously specialized in capturing orbweb building spiders. The *Araneus redii* prey fits well within these data (Table 1).

The recorded prey of *Dipogon subintermedius* are in conformity with its observed hunting places: tree-trunks and piles of fences. *Segestria senoculata* is known to build its retreat in these places, and jumping spiders from the genus *Salticus* may also be found there.

For the three species of *Priocnemis*, viz., *P. fennica*, *P. minuta*, and *P. susterai*, reliable data from the literature are few, because formerly these species were not distinguished as separate taxa. Prey recorded so far do not suggest any high degree of selectivity.

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LITERATURE CITED

BENNO, P. 1969. Aantekeningen bij enige Nederlandse wegwespen (Hymenoptera, Pompilidae). Entomologische Berichten, Amsterdam 29: 72-76.

BOUWMAN, B.E. 1915a. De wegwespen en hun parasiet. (*Pompilus* en *Ceropales*). De Levende Natuur 20(1):226-229.

1915b. De wegwespen en hun parasiet. (*Pompilus* en *Ceropales*). De Levende Natuur 20(13): 241-246.

BRISTOWE, W.S. 1948. Notes on the habits and prey of twenty species of British hunting wasps. Proceedings of the Linnean Society of London 160: 12-37.

CHRYSANTHUS, P. 1947. Spinnen en Hymenoptera Aculeata. Tijdschrift voor Entomologie 88: 482-488.

DAY, M.C. 1981. A revision of *Pompilus* Fabricius (Hymenoptera: Pompilidae), with further nomenclatural and biological considerations. Bulletin of the British Museum (Natural History), Entomology 42(1): 1-42.

1988. Spider wasps. Hymenoptera Pompilidae. Handbook for the Identification of British Insects 6(4): 1-60.

GAULD, I. & BOLTON, B. (eds.) 1988. The Hymenoptera. (British Museum (Natural History): Oxford University Press). 332pp.

GRANDI, G. 1961. Studi di un entomologo sugli Imenotteri superiori. Bolletino dell'Istituto di Entomologia dell'Università di Bologna 25: 1-659.

JONES, D. 1983. 'A guide to spiders of Britain and Northern Europe.' (Hamlyn: London).

LEFEBER, V. & VAN OOIJEN, P. 1988. Verspreidingsatlas van de Nederlandse Spinnendoders (Hymenoptera: Pompilidae). Nederlandse Faunistische Mededelingen, Leiden 4: 1-56.

MAURER, R. & HÄNGGI, K. 1990. Katalog der Schweizerischen Spinnen. Documenta Faunistica Helvetiae 12: 1-33 + 189pp.

OEHLKE, J. & WOLF, H. 1987. Beiträge zur Insekten-Fauna der DDR: Hymenoptera-Pompilidae. Beiträge zur Entomologie, Berlin 37(2): 279-390.

ROBERTS, M.J. 1985a. 'The spiders of Great Britain and Ireland 1: Atypidae to Theridiosomatidae.' (Harley Books: Colchester).

1985b. The spiders of Great Britain and Ireland 3: Colour Plates-Atypidae to Linyphiidae. (Harley Books: Colchester).

1987. 'The spiders of Great Britain and Ireland 2: Linyphiidae and checklist.' (Harley Books: Colchester).

THIJSSE, J.P. 1907. De wegwesp (*Pompilus viaticus*). De Levende Natuur 12(4): 66-68.

WAHIS, R. 1948. Nidification de *Calicurgus hyalinatus* F. (Hyménoptère Pompilidae). L'-Entomologiste 4: 210-213.

1955. Contribution à l'étude des Hyménoptères Pompilidae. 1. Les *Priocnemis* belges voisins du *Priocnemis perturbator* Harris (*fuscus* auct.). Bulletin et annales de la Société Royale d'-Entomologie de Belgique 91(3/4): 92-108.

1962. Les Pompilides belges de la collection Adolphe Crevecoeur (Hymenoptera: Pompilidae). Bulletin et annales de la Société Royale d'-Entomologie de Belgique 98(19): 324-338.

1986. Catalogue systématique et codage des Hyménoptères Pompilides de la Région Ouest-Européenne. Notes fauniques de Gembloux 12: 3-91.

WALRECHT, B.J.J.R. 1936. De levensloop van *Pseudagenia carbonaria* Scop. De Levende Natuur 41(5): 148-153.

WOLF, H. 1971. Prodromus insectorum Bohemoslavakiae 10: Hymenoptera Pompiloidea. Acta faunistica entomologica Musei Nationalis Pragae 14(3): 1-76.

1972. Hymenoptera -Pompilidae. Insecta Helvetica, Fauna 5: 1-176.

GROUND-LIVING SPIDERS (ARANEAE) ONE YEAR AFTER FIRE IN THREE SUBARCTIC FOREST TYPES, QUÉBEC (CANADA)

SEPPO KOPONEN

Koponen, S. 1993 11 11: Ground-living spiders (Araneae) one year after fire in three subarctic forest types, Québec (Canada). *Memoirs of the Queensland Museum* 33(2): 575-578. Brisbane. ISSN 0079-8835.

The ground-living spider fauna was studied one year after fire using pitfall traps in three forest types of subarctic Québec, July-August 1990. About 30 species, of the total 47 found at burned sites, were regarded as pioneer or colonizer species. Spiders captured commonly at burned sites included e.g. *Gnaphosa microps* Holm, *G. muscorum* (L. Koch), *Pardosa hyperborea* (Thorell), *P. uintana* Gertsch, *Trochosa terricola* Thorell, *Alopecosa aculeata* (Clerck), *Diplocentria bidentata* (Emerton), and *Sisis rotundus* (Emerton). Some species were found only or predominantly at unburned sites; e.g. *Pardosa moesta* Banks and *Lepthyphantes complicatus* (Emerton).

En juillet-août 1990, une année après des incendies, la faune des araignées habitant sur le sol des trois types de fôret du Québec subarctique a été étudiée en utilisant des pièges-fosses. Environ 30 espèces, d'un total de 47 trouvées dans les sites brûlés, ont été considerées comme des espèces pionnières ou colonisatrices. Les araignées capturées généralement dans les sites brûlés comprennent par exemple *Gnaphosa microps* Holm, *G. muscorum* (L. Koch), *Pardosa hyperborea* (Thorell), *P. uintana* Gertsch, *Trochosa terricola* Thorell, *Alopecosa aculeata* (Clerck), *Diplocentria bidentata* (Emerton), et *Sisis rotundatus* (Emerton). Quelques espèces ont été trouvées seulement ou principalement dans les sites non brûlés, par exemple, *Pardosa moesta* Banks et *Lepthyphantes complicatus* (Emerton). □*Araneae, forest fire, subarctic, Canada.*

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Fire history, effect of fire on forest vegetation, and postfire succession of plant cover have been studied in detail in northern Québec (e.g. Payette *et al.*, 1989). By contrast, very little is known about the effects of fire on spiders in northern forests of North America. In central Alaska, Beckwith and Werner (1979) suggested that the decrease of many arthropod populations after fire can be attributed to increasing spider populations and predation by spiders. Data from temperate forests of North America are also markedly scant (e.g. Pearse, 1943; Buffington, 1967). Pearse (1943) listed about 35 species of spiders from burned pine forests in North Carolina; however, individual numbers were low.

In forests of northern Europe, postfire spider faunas and their succession have been studied both after natural fires and prescribed burning (e.g. Huhta, 1971; Schaefer, 1980; Hauge and Kvamme, 1983; Koponen, 1988, 1989). Data from subarctic forests of Europe are available only from northern Finland (Huhta, 1971; Koponen, 1988, 1989).

This paper deals with the effects of fire on ground-living spiders at the beginning of faunal succession in three forest types in the subarctic zone of Québec, Canada. Forest fires occurred in midsummer 1989; samples were collected in 1990 during the first postfire summer.

MATERIALS AND METHODS

The study areas were situated 1) at Lac Ekomiak (53°23'N, 77°30'W), south of La Grande/Radisson and 2) at Kuujjuarapik (Poste-de-la-Baleine; 55°17'N, 77°48'W) on the eastern coast of Hudson Bay (Fig. 1). Both study areas were near the northern limits of the boreal forest.

1. At Lac Ekomiak, large areas of forest (thousands of sq. km) were burned in midsummer 1989. The study sites situated near the border of this extensive fire area were in dry and mesic forest. The main tree species were *Pinus banksiana* Lamb. and *Picea mariana* (Mill.) B.S.B. at dry sites; *Picea mariana* and *Larix laricina* (Du Roi) K. Koch at mesic sites. The ground layer of the dry sites was characterized by *Cladonia* and *Pleurozium*; that of the mesic sites by *Sphagnum* and *Pleurozium*. The fire had been very intensive and had killed all trees and destroyed field and ground layer vegetation totally. The trapping

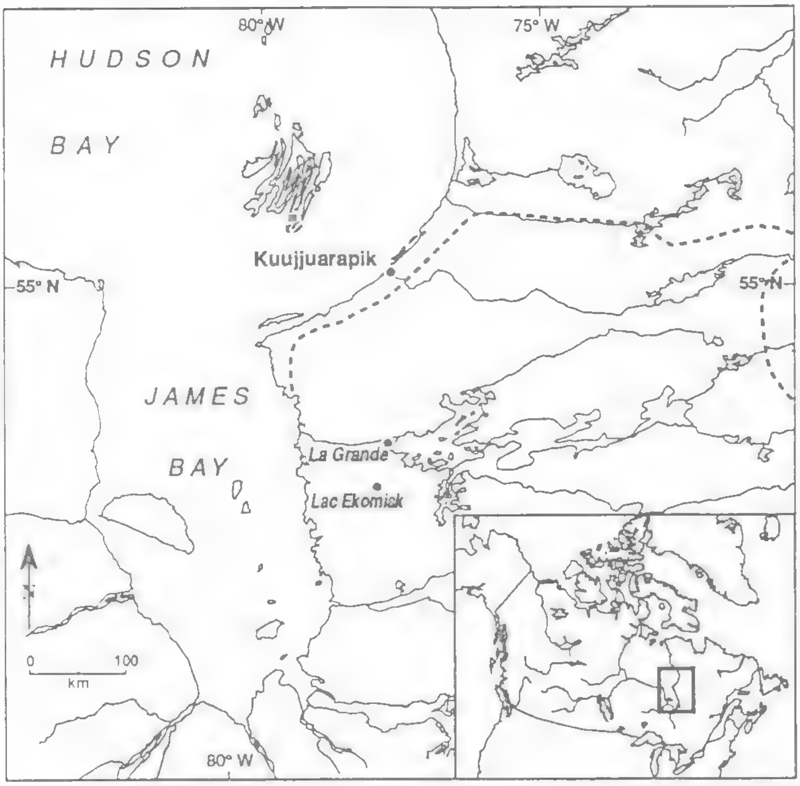

FIG. 1 (left). Postfire study sites at Lac Ekomiak and Kuujjuarapik, Québec. Broken line indicates the northern limit of the continuous (subarctic) forest.

TABLE 1 (right). Total number of individuals in major spider families, total number of species, diversity (H) and evenness (E) for pitfall trap material at Lac Ekomiak and Kuujjuarapik, Québec. LDB = Lac Ekomiak dry burned, LDC = Lac Ekomiak dry unburned, LMB = Lac Ekomiak mesic burned, LMC = Lac Ekomiak mesic unburned, KB = Kuujjuarapik burned, KC = Kuujjuarapik unburned site

	LDB	LDC	LMB	LMC	KB	KC
Lycosidae, inds.	59	16	45	32	104	28
Linyphiidae, inds.	44	35	34	22	110	172
Gnaphosidae, inds.	6	8	6	3	11	3
Others, inds.	6	5	6	14	3	0
Total, inds.	115	64	91	71	228	203
Species richness	24	13	15	18	31	20
Shannon H	3.98	3.27	3.50	3.52	3.62	3.31
Evenness E	0.87	0.88	0.90	0.84	0.73	0.77

period was 24 July-20 August 1990; traps were not changed during the period.

2. At Kuujjuarapik, a small area (about 50 x 15m) of *Picea glauca* (Moench) Voss forest was burned in July 1989. The site is in an isolated, small-sized woodland near forestline. Ground layer was dominated by *Pleurozium* and *Empetrum*. The field and ground layer vegetation was destroyed but the intensity of fire had been less than at Lac Ekomiak. The trapping period was 14 July-19 August 1990. The traps were changed once (1 August).

Ten traps were placed at each site (dry burned, dry unburned, mesic burned and mesic unburned) at Lac Ekomiak and five traps at each site (burned and unburned) at Kuujjuarapik. Pitfall traps were plastic cups (diameter 6.5cm, height 7cm) with ethylene glycol (2.5cm) as a preservation liquid. They were provided with covers (12 x 12cm) against rainfall and litter, and there was 2-3cm space between the cover and the ground. Traps were placed in a line at each site, average distance between the traps being 2m.

The indices used are Shannon-Wiener index of diversity:

$$H = -\sum_{i=1}^{s}(p_i)(log_2\, p_i)$$

and evenness: E = H/logS (S = number of species, p_i = proportion of total sample belonging to the *i*th species). The spider material is deposited in the Zoological Museum, University of Turku, Finland.

	Species	n	%BS	site 'preference'
DRY SITE	*Alopecosa aculeata*	6	100.0	only at burned
	Pardosa hyperborea	15	93.3	strongly to burned
	Diplocentria bidentata	10	90.0	strongly to burned
	Trochosa terricola	16	75.0	to burned
	Pardosa spp.*	31	58.1	equally occurring
	Gnaphosa spp.	8	50.0	equally occurring
	Agyneta olivacea	7	42.9	equally occurring
	*Hilaira herniosa***	13	15.4	to control
MESIC SITE	*Pardosa hyperborea*	10	90.0	strongly to burned
	Diplocentria bidentata	6	83.3	to burned
	Gnaphosa microps	9	66.7	slightly to burned
	Pardosa spp.*	42	64.7	slightly to burned
	Ozyptila gertschi	13	46.2	equally occurring
	*Hilaira herniosa***	7	14.3	to control
	Pardosa maesta	15	0.0	only at control

TABLE 2. Common spiders (≥ 6) trapped at burned and unburned (control) sites, at Lac Ekomiak, Québec. n = total number of individuals trapped, both sites combined; %BS = percentage individuals caught at burned site. * = *Pardosa uintana*, *P. mackenziana* and *P. xerampelina*; ** = adults of *H. herniosa* and juvenile *Hilaira* specimens.

Species	n	% BS	'preference'
Pardosa hyperborea	16	100.0	only at burned site
Pocadicnemis americana	6	100.0	only at burned site
Arctosa alpigena	9	77.8	to burned site
Pardosa uintana	100	74.0	to burned site
Gnaphosa muscorum	10	70.0	slightly to burned site
Sisis rotundus	10	60.0	equally occurring
Sisicottus montanus	22	59.1	equally occurring
Agyneta allosubtilis	19	15.8	to control site
Latithorax obtusus	13	15.4	to control site
Lepthyphantes alpinus	7	14.3	to control site
*Hilaira herniosa**	66	13.6	to control site
Lepthyphantes complicatus	19	5.3	strongly to control site

TABLE 3. Common spiders (≥ 6) trapped at burned and unburned (control) sites at Kuujjuarapik, Québec. n = total no. of individuals trapped, both sites combined; % BS = percentage individuals caught at burned site; * = adults of *H. herniosa* and juvenile *Hilaira* specimens.

RESULTS

A total of 772 spiders was collected from 6 study sites (3 burned, 3 unburned) in northern Québec during July-August, 1990. Individuals of two families, Linyphiidae and Lycosidae, clearly dominated all collections; individuals of Gnaphosidae ranked third among trap captures (Table 1).

Both at Lac Ekomiak and at Kuujjuarapik, trap captures were higher at burned sites than at unburned sites. This was mainly due to the great numbers of Lycosidae caught at open burned sites. The figures for the two most abundant families were (Lac Ekomiak and Kuujjuarapik combined): Lycosidae 208 at burned and 76 at unburned sites, Linyphiidae 188 and 229 respectively. In general, at the burned sites, the diversity (H) was higher or equal compared to the unburned controls (Table 1).

Altogether 56 species were caught, 37 species were trapped at Lac Ekomiak and 34 at Kuujjuarapik. Number of species from burned sites was 47; from unburned sites 37; 28 species were common to both burned and unburned sites. Linyphiidae (Erigoninae and Linyphiinae), Lycosidae, and Gnaphosidae were numerically dominant in species number, with 31 (24 and 7), 9 and 6 respectively.

Species that actively colonized the burned sites included, among the lycosids, *Pardosa hyperborea* (Thorell) in both study areas and *Alopecosa aculeata* (Clerck) at Lac Ekomiak (Tables 2, 3). The species group of *Pardosa uintana* Gertsch, *P. mackenziana* (Keyserling) and *P. xerampelina* (Keyserling), including many juveniles, as well as *Arctosa alpigena* (Doleschal) at Kuujjuarapik, and *Trochosa terricola* Thorell at Lac Ekomiak, also were more abundant at burned than unburned sites.

The gnaphosids caught, *Gnaphosa microps* Holm and *G. muscorum* (L.Koch), were slightly more abundant at burned than unburned sites. Of the linyphiids (Erigoninae), *Diplocentria bidentata* (Emerton) and *Pocadicnemis americana* Millidge apparently 'preferred' burnt areas (Tables 2, 3).

Many species were represented by less than 6 individuals captured, and consequently not included in the Tables 2, 3. Several were found only at burned sites. This group included: *Gnaphosa parvula* Banks, *Zelotes fratris* Chamberlin, *Pardosa furcifera* (Thorell), *Neon nelli* Peckham and Peckham, *Sisicus apertus* (Holm), *Ceraticelus atriceps* (O.P.-Cambridge), *Horcotes quadricristatus* (Emerton), *Sciastes truncatus* (Emerton), *Tunagyna debilis* (Banks), *Walckenaeria atrotibialis* O.P.-Cambridge, *W. castanea* (Emerton), *W. directa* (O.P.-Cambridge) and *W. tricornis* (Emerton).

Several species seemed to lack habitat specificity and were equally found in marked numbers at both burned and unburned sites. Such species included the linyphiids, *Sisis rotundus*

(Emerton), *Sisicottus montanus* (Emerton) and *Agyneta olivacea* (Emerton); and the thomisid *Ozyptila gertschi* Kurata. These generalist species must be regarded as colonizer species because of their common occurrence at burned sites. Although only in a few cases (*Pardosa hyperborea* and *P. uintana*) 'preferences' to burned areas were statistically significant, about 30 of the 47 species caught at burned sites can be regarded as potential colonizers in the subarctic postfire forests investigated.

Species that clearly avoided burned sites were the linyphiids *Lepthyphantes complicatus* (Emerton), *L. alpinus* (Emerton), *Hilaira herniosa* (Thorell), *Latithorax obtusus* (Emerton), and *Agyneta allosubtilis* Loksa. Of the lycosids, *Pardosa moesta* Banks was found only at the unburned mesic forest at Lac Ekomiak.

DISCUSSION

The burned areas at Lac Ekomiak and at Kuujjuarapik greatly differed both in the intensity of fire and in the size of area burned. At Kuujjuarapik, spiders easily colonized the burned site from surrounding nearby natural areas. By contrast, at Lac Ekomiak, species colonizing the burned sites came from long distances (i.e., several hundred metres), especially at the dry burned site. The possible survival of spiders in the burnt area during the fire is open to discussion (cf. McKay, 1979: 246); however, at the dry burned site its seems to be improbable due to the intensity of the fire.

The spider community trapped at burned sites one year after fire was rich; the diversity (H) was not lower than at unburned sites. Similar results were found in subarctic Finland during the first postfire summer (Koponen, 1988). This contrasts with some earlier studies (Schaefer, 1980; Metz and Dindal, 1980). However, also Schaefer (1980) observed high diversity values already two years after fire in pine forests of Germany.

Some of the species that colonized burned sites in northern Québec are considered pioneer species in other northern areas, e.g. *Diplocentria bidentata* in burned areas of northern Finland (Koponen, 1988).

ACKNOWLEDGEMENTS

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LITERATURE CITED

BECKWITH, R.C. & WERNER, R.A. 1979. Effects of fire on arthropod distribution. Pp. 53-55. In Viereck, L.A. and Dyrness, C.T. (eds) 'Ecological effects of the Wickersham Dome fire near Fairbanks, Alaska'. (USDA, Forest Service, General Techn. Rep., PNW-90).

BUFFINGTON, J.D. 1967. Soil arthropod populations of the New Jersey Pine Barrens as affected by fire. Annals of the Entomological Society of America 60: 530-535.

HAUGE, E. & KVAMME, T. 1983. Spiders from forest-fire areas in southeast Norway. Fauna Norvegica, Ser. B, 30: 39-45.

HUHTA, V. 1971. Succession in the spider communities of the forest floor after clear-cutting and prescribed burning. Annales Zoologici Fennici 8: 483-542.

KOPONEN, S. 1988. Effect of fire on spider fauna in subarctic birch forest, northern Finland. Technische Universität Berlin, Dokumentation Kongresse und Tagungen 38: 148-153.

1989. Effect of fire on ground layer invertebrate fauna in birch forest in the Kevo Strict Nature Reserve, Finnish Lapland. Folia Forestalia 736: 75-80.

MCKAY, R.J. 1979. The wolf spiders of Australia (Araneae: Lycosidae): 12. Descriptions of some Western Australian species. Memoirs of the Queensland Museum 19: 341-275.

METZ, L.J. & DINDAL, D.L. 1980. Effects of fire on soil fauna in North America. Pp. 450-459. In Dindal, D.L. (ed.) 'Soil Biology in Related to Land Use Practices'. Proceedings of the 7th International Colloquium of Soil Zoology, Syracuse.

PAYETTE, S., MORNEAU, C., SIROIS, L. & DESPONTS, M. 1989. Recent fire history of the northern Québec biomes. Ecology 70: 656-673.

PEARSE, A.S. 1943. Effects of burning-over and raking-off litter on certain soil animals in Duke Forest. American Midland Naturalist 29: 406-424.

SCHAEFER, M. 1980. Effects of an extensive fire on the fauna of spiders and harvestmen (Araneida and Opilionida) in pine forests. Proceedings of the 8th International Congress of Arachnology, Vienna: 103-108.

DIVERGENT TRANSFORMATION OF CHELICERAE AND ORIGINAL ARRANGEMENT OF EYES IN SPIDERS (ARACHNIDA, ARANEAE)

OTTO KRAUS AND MARGARETE KRAUS

Kraus, O. and Kraus, M. 1993 11 11: Divergent transformation of chelicerae and original arrangement of eyes in spiders (Arachnida, Araneae). *Memoirs of the Queensland Museum* **33**(2): 579-584. Brisbane. ISSN 0079-8835.

In various higher taxa of the Araneae (e.g., Mesothelae, Migidae, Hypochilidae), the chelicerae and their fangs show an intermediate position between those commonly called orthognathy and labidognathy. This stage is considered to form part of the ground pattern of spiders; accordingly, it is called plagiognathy (new term). It is concluded that plagiognathy gave rise to orthognathy and labidognathy as divergent adaptational developments. In most instances, plagiognathy is correlated with the maintenance of the original (plesiomorphous) arrangement of the lateral eyes (= ALE + PLE + PME) in triads or semi-triads. The previous assumption that orthognathy and the arrangement of eight eyes in two subparallel rows are characters that were already present in ancestral spiders is refuted.

Bei verschiedenen höheren Taxa der Araneae (z.B. Mesothelae, Migidae, Hypochilidae) weisen die Cheliceren sowie deren Klauen eine intermediäre Position zwischen Orthognathie und Labidognathie im üblichen Sinne auf. Diese Anordnung wird als Teil des Grundmusters der Echten Spinnen angesehen und hierfür die neue Bezeichnung Plagiognathie eingeführt. Von diesem primären plagiognathen Zustand werden sowohl die Orthognathie als auch die Labidognathie als divergente Entwicklungen mit unterschiedlichem Anpassungswert abgeleitet. In den meisten Fällen ist Plagiognathie korreliert mit dem Erhalt der ursprünglichen (plesiomorphen) Anordnung der Seitenaugen (VSA + HSA + HMA) in Form von Triaden oder Semi-Triaden. Die bisherige Annahme ist nicht länger aufrecht zu erhalten, wonach Orthognathie und die Anordnung von 8 Augen in zwei Querreihen als Komponenten des Grundmusters der Spinnen angesehen worden waren. □*Araneae, plagiognathy, orthognathy, labidognathy, lateral eyes, triads.*

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It is generally believed that the chelicerae in spiders can be arranged in either of two different ways, described by the terms orthognathy and labidognathy. Orthognathy is commonly thought to represent the primitive (plesiomorphic) character stage (Foelix, 1982: 3; Platnick and Gertsch, 1976: 13). At first glance, this view seems to be supported by the fact that a strictly orthognathous arrangement of these mouthparts is also present in the outgroup of the Araneae, i.e., in the Amblypygi. Hence, the idea that orthognathy is a plesiomorphic feature seems to be the most parsimonious explanation. Accordingly, labidognathy is regarded as a derived (apomorphic) feature. Kaestner (e.g., 1952, 1953a, b) presented arguments supporting the assumption that labidognathous, i.e., cooperating chelicerae had various functional advantages. He produced a model (Fig. 1) illustrating the transformation of a 'primitive' orthognathous arrangement into the labidognathous position. However, it is difficult to imagine how this could have happened gradually, and Kaestner did not explain why orthognathy had been maintained in a considerable number of higher taxa.

Simon (1892: 64, 82) pointed out that the Liphistiidae and Migidae had arrangements of the chelicerae that did not fit very well into the generally accepted orthognathy/labidognathy scheme. Later authors ignored such 'deviations', however, and continued to base the distinction of two major subtaxa of spiders–Mygalomorphae (=Orthognatha) and Araneomorphae (=Labidognatha) on different positions of the chelicerae. Kaestner alone remarked on the intermediate arrangement of these mouthparts in Actinopodidae and in *Hypochilus*, but apparently he too continued to adhere to the typological orthognathy/labidognathy concept. One main aspect of his study was therefore to classify the chelicerae in *Hypochilus* as orthognathous *or* labidognathous.

In this paper, we will present relevant facts, most of them already known for decades, and discuss conclusions allowed by alternative concepts.

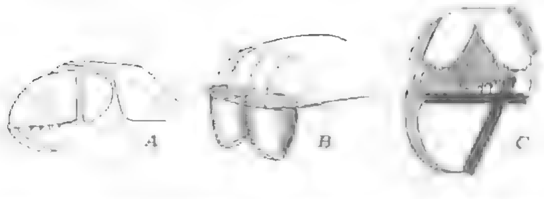

FIG. 1. Transformation of chelicerae as supposed by Kaestner. A, orthognathy, left chelicera omitted, front of prosoma nearly vertical. B, labidognathy, dotted lines and arrows indicate how front of prosoma (with chelicerae) shifted from original vertical to a horizontal position (rotation of basal segments of chelicerae not indicated). C, suggested economy of relatively small cooperating labidognathous chelicerae compared with a single orthognathous chelicera (hatched); both seize objects of same size.–(From Kaestner, 1953b).

This approach leads directly into a critical discussion of another generally accepted dogma in arachnology—that the eight eyes present in the ground pattern in spiders were originally arranged in two more or less parallel rows. In the nearest outgroups (Amblypygi, Uropygi), however, the arrangement of these eight eyes is quite different: the lateral eyes form triads on both sides of the prosoma. Such triads also occur in certain spiders. We therefore also plan to adopt a somewhat unconventional approach, discussing the question as to whether the presence of such triads in various subtaxa of the Araneae could be a persisting plesiomorphic character expression.

RESULTS AND INTERPRETATIONS

CHELICERAE

FACTS.

Orthognathy is commonly regarded as plesiomorphic. However, precisely those spiders that have the greatest number of plesiomorphies in common (Platnick and Gertsch, 1976) do not show an orthognathous position of their chelicerae: in the Liphistiidae (Figs 2a-b) the basal segment (paturon) of these mouthparts is relatively short, inflated and obliquely positioned. Further, the longer axis of this basal segment is orientated obliquely downwards, and not horizontally and paraxially as in 'true' Orthognatha (Figs 2c-d). The corresponding position of the fangs is also oblique, and anything but paraxial, in contrast to the position of the fangs in *Atypus*, for example (see Simon, 1892: 64).

The same situation as in *Liphistius* is also found in various subtaxa of the Mygalomorphae. In 1892, Simon (: 82) described similar arrangements in the Migidae, referring to 'chélicères très courtes, convexes à la base, mais ensuite brusquement inclinées, presque verticalement ...' (see Fig. 2e). Kaestner (1952: 118) studied *Sason robustum* (O. P.-Cambridge, 1883) as a representative of the Barychelidae and characterized the chelicerae as short and subvertically inclined. In the same paper, Kaestner demonstrated that obliquely arranged chelicerae were also present in the Actinopodidae (Fig. 2f); he described the situation in *Missulena occatoria* (Walckenaer, 1805) and concluded: 'I cannot see any biological reason for such conditions. But as torsions of this kind play an important role in the origin of labidognathy, it is interesting to see that they [the torsions] may also occur in the Orthognatha' (transl. from German).

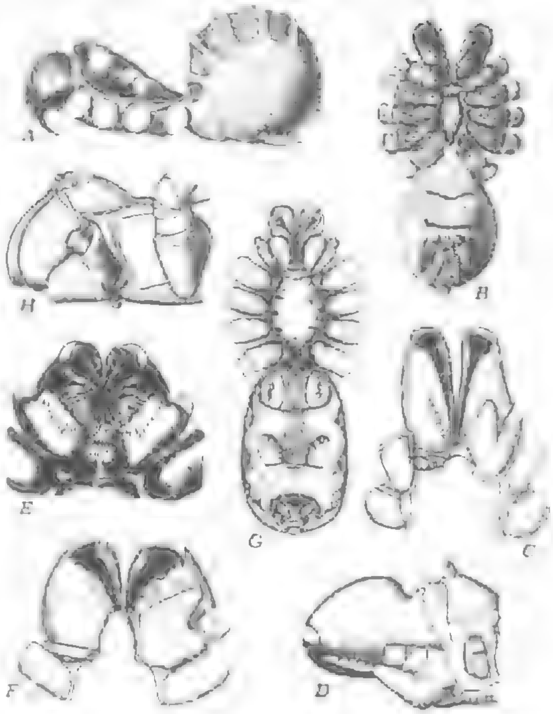

FIG. 2. Position of chelicerae and fangs, lateral and ventral views. A-B, Mesothelae: *Liphistius* sp. C-D, Atypidae: *Atypus affinis*. E, Migidae: *Migas quintus*. F, Actinopodidae: *Missulena occatoria*. G, Hypochilidae: *Hypochilus gertschi*. H, *H. thorelli*.–(A-B from Millot, 1949; C-D, F, H from Kaestner, 1952; E from Wilton, 1968).

It is worth mentioning that the chelicerae even of the oldest known spider, *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987) (Middle Devonian), had short basal segments and also fangs (Selden *et al.*, 1991, e.g., plate 1, figs 6-8).

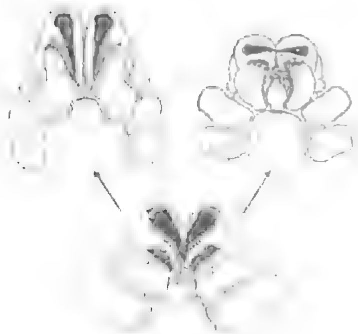

FIG. 3. Orthognathy (left) and labidognathy (right) as apomorphic character states derived from plagiognathy (bottom).

Unfortunately, their original position is unknown.

Chelicerae with an oblique position are also found in a taxon that unquestionably belongs to the Araneomorphae (= Labidognatha *auct.*): the Hypochilidae (Figs 2g-h). Again, it was Kaestner (1952: 132) who studied details. He concluded that the mouthparts in *Hypochilus* were of the orthognathous type in construction and expressed the view (Kaestner, 1952: 114) that 'the majority of important characters present in *Hypochilus* is in accordance with the Orthognatha, whereas the number of features present in Labidognatha only is very low. For this reason, I must remove the genus from the suborder Labidognatha and either place it in the Orthognatha or set it up in a suborder of its own' (transl. from German).

INTERPRETATION

Kaestner maintained that labidognathy was an advanced character state, which had developed from an orthognathous ground pattern by gradual transformation (Kaestner, 1953a: 60; Fig. 1). He felt that *Hypochilus* (and the Hypochilidae) should be regarded as transitory stages and explained the oblique position also present in the Barychelidae and Actinopodidae as a parallel development. Furthermore, he regarded the 'semi-orthognathous' chelicerae in *Dysdera* (Dysderidae) as intermediate. Kaestner thought, then, that various transitory stages still existed, forming a 'phylogenetic link' between the two extreme character states.

We reject this judgement based on typology, and postulate that an oblique position of the chelicerae, including the fangs, really represents the plesiomorphic situation (Fig. 3). As a new term is needed, we would like to suggest 'plagiognathy' to designate this original position of the chelicerae. Accordingly, the plagiognathous position present in the ground pattern of the Araneae has been secondarily transformed in two different directions, both apomorphic character states: orthognathy and labidognathy (Fig. 3). We see various arguments in support of this hypothesis:

a) It explains why orthognathy is not encountered in the Mesothelae (*Liphistius*, *Heptathela*).

b) The absence of orthognathy in representatives of several mygalomorph families is explained.

c) The fact that the Hypochilidae are not labidognathous is explained by the simple assumption that the original plagiognathy has been maintained in this group of the Araneomorphae. Nonetheless, in all other Araneomorphae (this means in the Neocribellatae, the sister taxon to the Hypochilidae) labidognathy has been achieved and is regarded as an apomorphy of this taxon. This conclusion is not invalidated by the fact that superficially orthognathous arrangements originated secondarily in a few sexually dimorphic araneomorph taxa (e.g., in males of the salticid genus *Myrmarachne*).

d) Kaestner's typological and entirely theoretical model suggesting how a supposed transition from orthognathy to labidognathy could come about (Fig. 1) is replaced by a new concept (Fig. 3). This postulates divergent and gradual evolutionary change of the ground pattern, that is to say, of plagiognathy.

e) Kaestner's complicated assumption that obliquely arranged chelicerae originated in parallel both in the Mygalomorphae and the Araneomorphae is replaced by a simple, comprehensive hypothesis.

The only remaining conflict seems to be that reflected in the strictly orthognathous position of the chelicerae in the most closely related outgroups of the Araneae (Amblypygi, Uropygi). If our 'plagiognathy hypothesis' is correct, it must be assumed that orthognathy in the Araneae is a different and thus independent secondary development within the mygalomorph spiders. There is no question but that this contradiction needs some further examination.

Preliminary investigations have already suggested that orthognathy in Amblypygi may be different from orthognathy in spiders: the basal segment in amblypygid chelicerae has a long, stout apodeme at its proximal dorsolateral border, which reaches deeply into the broad, flat prosoma. This peculiarity is lacking in plagiognathous and also in orthognathous chelicerae of spiders. We expect that more detailed studies on the functional morphology, including the musculature, will demonstrate that orthognathy in uropygids and amblypygids differs from orthognathy in spiders. This would support our view and could perhaps constitute point f) in the list of positive arguments above.

EYES

Surprisingly, plagiognathous spiders (for example Mesothelae, Migidae, Hypochilidae) share a special arrangement of the eyes (Figs 4g, e, c): anterior lateral, posterior lateral and posterior median eyes are grouped closely together. This prompts the following remarks on the question as to how the eyes were grouped in the ground pattern of the Araneae.

As designations widely used in taxonomic descriptions (AME, ALE, PME, PLE) disregard the origin of these 'ocelli', some notes on the homolgy of the eyes of spiders may be appropriate to ensure that we understand each other: the anterior median eyes (AME) will be called 'median eyes' by us, as they are homologous with the median eyes of other arthropods (for example those in Xiphosura, 'ocelli' in insects, and the three components of crustacean nauplius eyes). All other eyes, three on each side, will be called 'lateral eyes' (ALE + PLE + PME), as they are homologous with the paired original compound eyes in arthropods, for example, in xiphosurans.

FACTS

It is commonly believed that an arrangement in two transverse rows of eight eyes is plesiomorphic. Only two weak aspects support this view, however: (a) there is no reason at all to doubt that the presence of eight eyes forms part of the araneid ground pattern, and (b) their arrangement in two rows is widely observed both in the Mygalomorphae (for example the Actinopodidae; see Simon, 1892: 79, figs 81-83) and in the Araneomorpha (for example Araneidae, Eusparassidae, Thomisidae).

On the other hand, lateral eyes more or less distinctly grouped in triads occur in various groups of spiders. Mesothelae, Migidae and Hypochilidae have already been mentioned. Almost perfect triads occur in Pholcidae (Fig. 4f). The same is true of Amblypygi (Fig. 4b) and Uropygi, the direct outgroups to spiders!

The arrangement of the eyes in the extinct Trigonotarbida deserves special attention. According to Selden *et al.* (1991: 254), they form the sister group of all other pulmonate taxa (= Araneae + Amblypygi + Uropygi + Schizomida). Devonian trigonotarbids had the usual two median eyes, and the lateral eyes were represented by up to 9 (12 ?) lenses (Fig. 4a). Three of these were major lenses, while the others were minor lenses arranged in the interspace between the major ones (Shear *et al.*, 1987). This kind of transformation of the original compound eyes clearly indicates that a triad of major lateral eyes is a feature of the ground pattern of the pulmonates as a whole; accordingly, the loss of the minor lateral eyes could be regarded as an autapomorphy of all other pulmonates, including spiders. This secondary reduction of the minor lateral eyes may explain why most triads are not perfectly closed, not even in amblypygids (Fig. 4b).

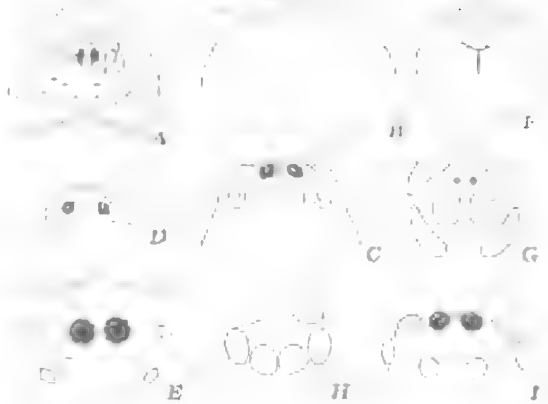

FIG. 4. Position of median (black) and lateral eyes in Trigonotarbida, Amblypygi and Araneae. A, Trigonotarbida: *Gilboarachne griersoni*, reconstruction of prosoma (from Shear *et al.*, 1987). – B, Amblypygi: *Damon* sp, C, Hypochilidae: *Hypochilus gertschi*. D, Atypidae: *Atypus affinis*. E, Migidae: *Poecilomigas* sp. F, Pholcidae: *Pholcus circularis*. G, Mesothelae: *Liphistius* sp. H, Dysderidae: *Dysdera* sp. I, Agelenidae: *Agelena* sp. (Not to scale).

The peculiarity 'lateral eyes in triads' is commonly used as a character in spider identification keys, but as far as we can tell, its potential bearing on phylogeny has never been discussed. Could it be that triads of lateral eyes are part of the ground pattern in the Araneae?

A survey of how the lateral eyes are positioned in representatives of higher taxa of spiders shows that almost perfectly 'closed' triads (as in pholcids) are rare. In most instances, the three lateral eyes on each side are somewhat dissociated. In addition to the Mesothelae and Migidae already mentioned, we should also like to draw attention to the Atypidae (Fig. 4d) and to the illustrations in Raven's comprehensive study of the Mygalomorphae (1985). In many cases the posterior lateral and the posterior median eyes are closely connected, with some distance between them and the anterior laterals. *Hypochilus* shows slightly dissociated triads (Fig. 4c). The Dysderidae (Fig. 4e) and Oonopidae are six-eyed spiders, having the median eyes completely reduced. In dysderids, the lateral eyes are closely grouped together, resembling the arrangement of the laterals in the Mesothelae. In many groups within the Araneomorphae, diads are present instead of triads. They are formed by the ALE + PLE, with the PME separated. This arrangement can be found in Austrochilidae and especially in most Theridiidae and Linyphiidae, for example. Diads also occur in groups characterized by a secondary loss of the PME, such as Scytodidae.

INTERPRETATION

The assumption that eight eyes arranged in two transverse rows were already present in the ground pattern of the Araneae is not supported by any concrete fact; nor would this at all correspond with the situation in the nearest outgroups. It would mean that triads and triad-like arrangements of the lateral eyes in spiders were classifiable as parallel developments (homoplasies). This is unlikely. In accordance with the position of the eyes in the Amblypygi and Uropygi, we expect that the laterals were primarily grouped as triads (ALE + PLE + PME). This hypothesis is supported by five arguments:

a) Triads of major lateral eyes (lenses) already existed in Devonian Trigonotarbida; hence, triads apparently form part of the ground pattern of all pulmonates among arachnids.

b) The postulated configuration is in good agreement with the arrangement of the eyes in the direct outgroups.

c) Triads and semi-triads present in various groups of the Mygalomorphae and also of the Araneomorphae must no longer be explained by assumed parallel origin.

d) Various types of somewhat dissociated lateral eyes can be explained by a secondary separation of the ALE or of the PME from the others, which frequently remain in contact with each other.

e) Simon's 'oculi laterales utrinque contigui' (e.g., 1894: 517), that is to say, the occurrence of diads can be explained as part of the original triad.

To some extent, the question remains open, as to how it is possible to distinguish between eye positions that can be regarded as more or less modified triads and other positions, with secondarily approximated ALE and PLE.

PERSPECTIVES

Apparently, plagiognathy is part of the ground pattern of the Araneae. Developments in the directions of orthognathy and labidognathy can easily be explained as divergent evolutionary changes (Fig. 3). The question therefore arises of how these might be correlated with functional aspects. As an impetus for further discussion, we propose the following working hypotheses:

a) In the Mygalomorphae, orthognathy may be correlated with the capture of prey on the ground. Under such conditions, the two parallel fangs of the chelicerae can easily penetrate the victim on a substrate like two stabs of a dagger. It seems remarkable that a semi-orthognathous position of the chelicerae has originated secondarily in the Dysderidae: they kill woodlice on the substrate.[1]

b) In the Araneomorphae, the origin of labidognathy may be correlated with the evolution of capture webs (sheet, frame, orb webs etc.). These could make it more efficient to bite the prey with two opposing chelicerae or fangs, whereas plagiognathous and, even more, orthognathous chelicerae might not penetrate but rather push away the victim: there is no longer any substrate 'supporting' prey animals.

c) Plagiognathy and the maintenance of lateral triads or semi-triads of eyes apparently form part of the ground pattern of spiders; these features are confined to more 'primitive' groups. The presence and the various types of transformation of these two characters should be integrated into current concepts on the phylogeny of the Araneae (see, for example, Raven, 1985; Coddington, 1990). At present, our view of features of an araneid ground pattern and succeeding evolutionary changes seems to be somewhat at odds with various published cladograms; they hence could be partially wrong. We feel that this conflict may be due to the possibility that characters assumed to be synapomorphies in various cladograms (see,

[1] But see Kaestner (1953a: 62). He believed that the position of the chelicerae in *Dysdera* was a 'phylogenetic link' between orthognathy and labidognathy. Unfortunately, he was not aware that the first postembryonic stages were nearly labidognathous, with relatively shorter basal segments and only slightly oblique fangs (pers. observ.). In *Dysdera*, the final semi-orthognathous position was gradually acquired in later instars.

e.g., Platnick and Shadab, 1976, fig. 1; Raven, 1985, fig. 1) may well turn out to be symplesiomorphies; e.g., Raven's characters 35 (eyes spread widely across the prosoma; same as Platnick and Shadab's character 1) and 36 (male pedipalps: conductor of bulb present; see Kraus, 1978, figs 12, 14-16).

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LITERATURE CITED

CODDINGTON, J.A. 1990. Ontogeny and homology in the male palpus of orb-weaving spiders and their relatives, with comments on phylogeny (Araneoclada: Araneoidea, Deinopoidea). Smithsonian Contributions to Zoology 496: 1-52.

FOELIX, R.F. 1982. 'Biology of spiders'. (Harvard University Press: Cambridge and London). 306pp.

KAESTNER, A. 1952. Die Mundwerkzeuge der Spinnen, ihr Bau, ihre Funktion und ihre Bedeutung für das System. 1. Teil: Orthognatha; Palaeocribellata. Zoologische Jahrbücher (Anatomie) 72(1): 101-146.

1953a. Die Mundwerkzeuge der Spinnen, ihr Bau, ihre Funktion und ihre Bedeutung für das System. 2. Teil: Herleitung und biologische Bedeutung der Labidognathie. Zoologische Jahrbücher (Anatomie) 73(1): 47-68.

1953b. Die Mundwerkzeuge der Spinnen, ihr Bau, ihre Funktion und ihre Bedeutung für das System. 3. Teil: Die Cheliceren der Labidognatha (Dipneumones). Mitteilungen aus dem Zoologischen Museum in Berlin 29(1): 3-54.

KRAUS, O. 1978. *Liphistius* and the evolution of spider genitalia. Symposia of the Zoological Society of London 42: 235-254.

MILLOT, J. 1949. Ordre des Aranéides (Araneae). Pp. 589-743. In Grassé, P.P. (ed.), Traité de Zoologie. Anatomie, Systématique, Biologie. (Masson: Paris).

PLATNICK, N.I. & GERTSCH, W.J. 1976. The suborders of spiders: A cladistic analysis. American Museum Novitates 2607: 1-15.

PLATNICK, N.I. & SHADAB, M.U. 1976. A revision of the mygalomorph spider genus *Neocteniza* (Araneae, Actinopodidae). American Museum Novitates 2603: 1-19.

RAVEN, R.J. 1985. The spider infraorder Mygalomorphae (Araneae): cladistics and systematics. Bulletin of the American Museum of Natural History 182(1): 1-180.

SELDEN, P.A., SHEAR, W.A. & BONAMO, P.M. 1991. A spider and other arachnids from the Devonian of New York, and reinterpretations of Devonian Araneae. Palaeontology 34(2): 241-281.

SHEAR, W.A., SELDEN, P.A., ROLFE, W.D.I., BONAMO, P.M. & GRIERSON, J.D. 1987. New terrestrial arachnids from the Devonian of Gilboa, New York (Arachnida, Trigonotarbida). American Museum Novitates 2901: 1-74.

SIMON, E. 1892-1895. 'Histoire naturelle des Araignées. Vol. 1'. (Librairie encyclopédique de Roret: Paris). 1084pp.

WILTON, C.L. 1968. Migidae. In Forster, R.R. 'The spiders of New Zealand, vol. II'. Otago Museum Bulletin 2: 73-126.

POLYNESIAN THOMISIDAE - A MEETING OF OLD AND NEW WORLD GROUPS

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The Polynesian thomisid fauna is postulated as consisting of an Hawaiian-east Polynesian New World group, living mainly in isolated populations in the mountains and of representatives of two western lowland groups originating from Australia and Southeast Asia. The former group has apparently speciated into numerous endemic species, while the latter groups are represented by a single, widespread species and a rare Tongan species, respectively. The ranges of the eastern and western groups do not overlap. The species of New World origin have been described or previously attributed to *Misumena*, *Misumenops*, or *Synaema*. All such species are included here in *Mecaphesa* Simon, 1900 with the type species from Hawaii. *Misumenops* F.O. Pickard-Cambridge, 1900 has the type species from Eastern Brazil and has no close relatives in Polynesia or in the Old World. A widespread Old World group is also recognized here and tentatively included in *Massuria* which appear to be related to the New Guinean *Loxoporetes*. *Diaea* as currently recognized is polyphyletic and the species occurring in west Polynesia (*Diaea praetexta* (L. Koch, 1865)) is postulated to belong to a group requiring a new generic delimitation and name. *Hedana subtilis* L. Koch, 1874, also of Asian origin is here regarded as having affinity with *Tharrhalea*. The poorly described thomisid species of the isolated, southernmost island group of Polynesia, Rapa Island has not been studied. □*Araneae, Thomisidae, Polynesia, biogeography.*

Pekka T. Lehtinen, Zoological Museum, University of Turku, 20500 Turku, Finland; 11 March, 1993.

Many zoogeographical discussions, including spiders, are flawed because of poor taxonomy. The zoogeography of the Polynesian spider fauna has been discussed by Berland (1927, 1928, 1929, 1930, 1933, 1934a, b, c, 1935a, b, 1937, 1938a, b, 1942, 1947), but his discussions were based on unrevised taxa. His conclusions were often affected by misidentifications and unevenness of data available. Most spiders for these papers consisted of assorted samples made by non-specialists and many were synanthropic species found near villages.

I have been working towards a zoogeographical synthesis of the Polynesian spider fauna for ten years. Extensive personal field work in mountain tops, but also in the disturbed zone has been the most important method in the elimination of anthropochorous dispersal and distinctly synanthropic species from all speculations on the origin of the fauna of natural habitats.

The taxonomic revision of all families present seems to be necessary for any valid zoogeographical conclusions. As the first step I have carried out a 'generic' revision of Polynesian families which allows the placing of most Polynesian species groups of spiders into named or still unnamed groups of supraspecific taxa instead of zoogeographically useless concepts such as the 'worldwide' *Misumenops*, *Theridion*, *Hahnia*, or *Leucauge*. Some recent papers on Polynesian spiders have been published (e.g. Marples, 1955a, b, 1957, 1959, 1960, 1964; Berry and Beatty, 1987; Beatty and Berry, 1988; Beatty *et al.*, 1991). I have previously discussed some aspects of the spider zoogeography of the Pacific region (Lehtinen, 1980). Polynesian thomisids have also been described by Strand (1913).

The evolution of Polynesian Thomisidae has resulted in the most striking example of local speciation of spiders in Polynesia. The Thomisidae discussed comprise only the subfamily Thomisinae in the sense of Suman (1970) and various other authors. The Philodromidae are not a sister group of Thomisidae, but rather of the Heteropodidae.

The geological history of the Polynesian archipelagoes is now well known (Wilson, 1963; Duncan and McDougall, 1974; Dalrymple *et al.*, 1975). An ancient continent of Pacifica has been proposed (with differing placement and size) marginally affecting to the historical zoogeography of Polynesia (e.g. Nur and Ben-Avraham, 1977; Craw, 1983). Most geophysicists agree that the Polynesian islands are not parts of ancient land masses broken by processes of the plate tectonics, but rather chains of current islands and seamounts representing former islands (Dalrymple *et al.*, 1975).

The origin of the Polynesian fauna therefore can be explained only by long distance dispersal from different directions (Gressitt and Yoshimoto, 1963) and partly by intrapolynesian speciation processes within the island chains (cf. also Carson, 1984; Fosberg, 1991). The use of the basic principles of the vicariance biogeography (Nelson and Platnick, 1981) will be essential for explaining the origin of groups of biota with complex patterns in their recent ranges. Craw's (1978) variant of panbiogeography, later named spanning-tree biogeography by Platnick and Nelson (1988) is a useful method for comparisons of area including also permanently oceanic island groups and it can be recommended for the analysis of many other groups of spiders. When patterns of distribution are very simple and anthropochorous dispersal in historical time has not thoroughly obscured the original patterns (cf. Stoddart, 1968), conclusions can be made with Craw's method such as have actually long been used by zoogeographers (e.g. Gressitt, 1961) before the concept of 'the most parsimonious area relationship' was defined and named.

In spite of the current taxonomic confusion of the Thomisidae on a global scale some generalisations on the zoogeography of the family are possible in the Pacific area. This paper presents the suggested relationships and zoogeography of the Thomisidae of Polynesia according to rich new material and results of my unpublished revisional work.

TAXONOMIC REMARKS

The nominate subfamily of Thomisidae should be called Thomisinae, although the name Misumeninae has been widely used, also, e.g. recently by Dippenaar-Schoeman (1983). Two groups of greenish or yellowish species without abdominal modifications are easily recognizable, one with conspicuous modifications in the ocular area (*Thomisus*-group), the other without such modifications (*Misumena*-group). The limitation of thomisine groups has been vague. Simon (1895) originally listed *Misumena*, *Heriaeus*, and *Diaea* in different tribes, while at the other extreme, the *Misumena*-group of Dippenaar-Schoeman (1983) includes not only *Thomisus*, but also *Runcinia*.

No phylogeny of thomisine groups is known and detailed discussion is beyond the scope of this study. However, the *Misumena*-group has apparently retained many plesiomorphic characters. Some groups with striking individual adaptive modifications (e.g. *Heriaeus* and *Runcinia*) may be closely related to this group.

There are most probably many other endemic species of Thomisinae in the mountains of French Polynesia, but a revision is excluded here.

The definition and delimitation of thomisine genera has been based traditionally on a few adaptive characters, including number, length, and type of setae on the carapace (Simon, 1895; Mello-Leitão, 1929; Schick, 1965; Tikader, 1980; Dondale and Redner, 1978; Levy 1985; Ono, 1988), but little attention has been paid to general patterns of the genital organs and type of sexual dimorphism. In contrast to conventions in the taxonomy of other spider groups, the naming of individual setae of the thomisid carapace has been used by some recent specialists (Schick, 1965; Dippenaar-Schoeman, 1983). This terminology is widespread in acarine taxonomy.

Some genera have been very obscurely defined and therefore all catalogues list them as being very widespread and species rich, e.g. *Misumena*, *Misumenops*, *Diaea*, and *Synaema*. All these generic names appear in thomisids described or listed from Polynesia. Even a superficial comparison of the descriptions or type material from many species of these genera (L. Koch, 1874; Kulczynski, 1911; Chrysanthus, 1964; Tikader, 1980) reveals that they are typical 'waste-basket' groups, where most species are not closely related to the respective type species.

The phylogenetic classification of the west Polynesian '*Diaea*' and the east Polynesian '*Misumenops*' has been time-consuming, as all basic taxonomic work on Indo-Pacific and Neotropical Thomisidae was done before modern taxonomic principles and methods became established. Most structural characters used as generic criteria in Thomisidae seem to be minor convergently evolved adaptations. The type species of all three large widespread genera in question, *Misumenops*, *Diaea*, and *Misumena*, are atypical or 'peripheral' species, not closely related to the Pacific species. Actually the placing of many tropical species in these three genera have been repeatedly changed, depending mainly on emphasis laid on single adaptive characters, e.g. type and pattern of setae on carapace, pattern of leg spines, eye pattern, etc.

The setation of the carapace is variable in the Polynesian groups of Thomisidae. Nevertheless, in *Mecaphesa*, sympatric species may be best identified by differences in length and density of

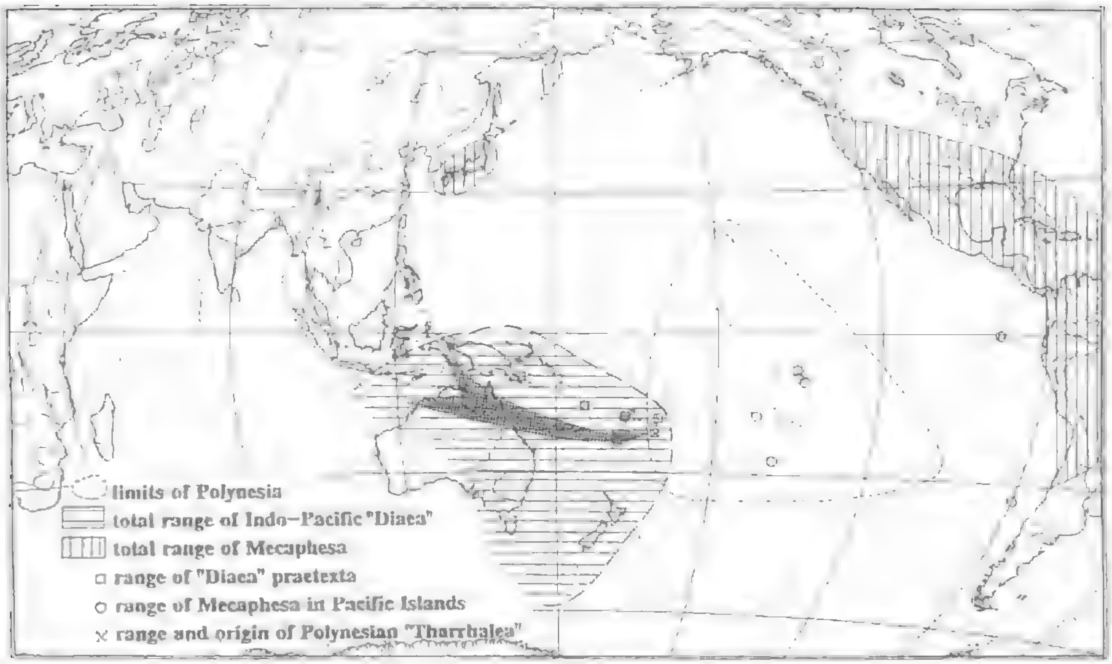

FIG. 1. Geographic ranges and source of Polynesian thomisid groups.

the carapace setae. The shape of the carapace is variable in *Mecaphesa*, while the shape of the abdomen is variable in both '*Diaea*' and *Mecaphesa*, even within one population.

The colour pattern is variable also, although the 'usual' colouration for most species provides a reasonable guide to identification, if large populations are available.

POLYNESIAN THOMISIDS OF NEW WORLD ORIGIN

Most east Polynesian thomisids have been long included in *Misumenops* F.O. Pickard-Cambridge, 1900 (Berland, 1933, 1934b, 1942; Suman, 1970), although Roewer (1954) transferred all Hawaiian species to *Misumenoides* F.O. Pickard-Cambridge, 1900.

Many Hawaiian and North American species of *Misumenops* sensu Schick (1965) were originally described in *Misumena* or *Diaea*, and Neotropical species also in *Metadiaea* Mello-Leitão, 1929.

The adaptive radiation of Hawaiian Thomisidae indicates that essential changes in the shape of the carapace are possible without other than minor changes in the male palpal structure. The Hawaiian thomisid species were listed by Simon (1900) in *Misumena* (6 spp.), *Diaea* (2 spp.), *Synaema* (4 spp.), and *Mecaphesa* (2 spp.), but by Suman (1970) in *Misumenops* (14 spp), *Synaema* (1) and *Mecaphesa* (3 spp.). I have checked the type material of all Hawaiian thomisids preserved in the Bishop Museum and, in my opinion, both male and female genitalia of *Synaema naevigerum* Simon, 1900 are much closer to the genitalia of all Hawaiian '*Misumenops*' than those of the type of *Synaema*, *S. globosum* (Fabricius, 1775) from Europe. The relative width of the ocular area is certainly a parallelism in true *Synaema* and the Hawaiian '*Synaema*'. The blunt setae of *Mecaphesa* s. str. have been independently modified, and the three species constitute a sister group of the Hawaiian '*Misumenops*' and '*Synaema*' together. The genital organs of both sexes are again more or less similar and not at all related to *Oxyptila* or *Heriaeus*, as claimed by Simon (1900). Suman (1970) was not familiar with the Palaearctic thomisids and had no opinion on this matter, but he published useful drawings of the genitalia of all Hawaiian thomisids. This group of '*Misumenops*' is also present in Japan, as *Misumenops kumadai* Ono, 1985 and in western North America at least 13 species (*celer*-group), listed by Schick (1965) in *Misumenops (Misumenops)*. *Misumenops inclusus* Banks, 1902 from Galapagos Islands and *M. sjoestedti* Berland, 1924 from Juan Fernandez Islands are

SE Asian/Australian origins (western lowlands)	Neotropical origins (eastern highlands)	Uncertain origin (Rapa)
'*Diaea*' *praetexta* belongs to probably new group *Hedana subtilis* belongs to *Tharrhalea*	Species previously attributed to *Misumena*, *Misumenops* and *Synaema*	'*Misumenops*' *rapaensis*

TABLE 1. Hypothesis of generic placement and zoogeographic origins of species groups of Thomisidae represented in Polynesia.

additional members of this genus in the Pacific region.

The generic name *Misumenops* is here reserved for the group of Neotropical species that are unambiguously related to *M. maculissparsa* (Keyserling, 1891), a species with a well developed tutacular process in cymbium and a complex of tibial apophyses that is widely different from any Pacific species. *M. pallens* (Keyserling, 1880) and *M. pallida* (Keyserling, 1880) were recently revised by Rinaldi (1983) without comparison to the type species. These widespread Neotropical species are not close to *M. maculissparsa*, but they may remain in the same genus. On the other hand, the concept of *Mecaphesa* is here widened to also include most Polynesian, some other Pacific and many north American '*Misumenops*', the more plesiomorphic branch of this genus. '*Misumenops*' *rapaensis* Berland (Berland, 1934) from the isolated Rapa Island with a terrestrial fauna of peculiar affinities probably belongs elsewhere.

The widespread Holarctic *M. tricuspidatus* (Fabricius, 1775) is removed from this genus, but its final generic placement must wait for a more complete revision of Thomisinae: Misumenini. The structure of the male tibial apophysis, including the microstructure of its tip, is different from all other thomisids known to me. *M. japonicus* (Bösenberg and Strand, 1906) is a relative or even a member of *Diaea*, while the *asperatus* group of *Misumenops* (Schick, 1965) may belong to *Metadiaea* and the *coloradensis* group represents a distinct genus, not close to *Mecaphesa* or *Misumenops*.

The synonymic history of *Metadiaea* is confusing, too, as the authors discussing this problem (Toledo Piza, 1937; Caporiacco, 1954; Rinaldi, 1983) have based their opinions on the data from speices other than the type species, *M. fidelis* Mello-Leitão, 1929 from Minas Gerais, Brazil. I agree with Rinaldi (1983) in transferring the other species to *Misumenops pallida*-group, but not the type of the genus, and *Metadiaea* remains a valid American genus probably including also North American species.

There is a widespread Southeast Asian-New Guinean group with short scutate male abdomen and with genital organs of both sexes close to *Runcinia*. Their male tibial apophysis is similar to *Mecaphesa*, including the characteristic ribbed tip. The New Guinean *Loxoporetes* known only by the female is probably related to, or even congeneric with this group, of which most species have been described as *Misumena*. This group will probably be named *Massuria* Thorell, 1887 and it might be a plesiomorphic sister group of the widespread and widely sympatric *Runcinia*.

POLYNESIAN THOMISIDS OF OLD WORLD OR AUSTRALIAN ORIGIN

The greenish thomisids from Samoa and Tonga islands have been described as different species (L. Koch, 1874; Rainbow, 1902: New Hebrides; Strand, 1913), all referred to *Diaea*. A critical survey of several large populations reveals that there is only one widespread species, '*D.*' *praetexta* (L. Koch, 1865) with large infrapopulational variation in the colour pattern, but quite small variation in the structure of the genital organs. In contrast to east Polynesian and Hawaiian thomisids this species lives in the vegetation of lowlands and is also common in Fiji and Vanuatu.

At least *D. sticta* and *D. limbata* (Kulczynski, 1911) within the widespread and common Melanesian *Diaea* spp. as well as the east Australian *D. multopunctata* L. Koch, 1874 and *D. prasina* L. Koch, 1876 are congeneric with *D. praetexta*. This group of Australian-Polynesian '*Diaea*' deserves generic status, but until some 'old' thomisine genera from the Indo-Pacific area have been revised the erection of a new genus would be hasty. The type species of *Diaea*, *Araneus dorsatus* Fabricius, 1775, probably together with some other Palaearctic species has male and female genital organs resembling *Heriaeus* (Loerbroks, 1983). The deviating non-genitalic characters of *Heriaeus* are adaptations to life in the desert.

Hedana subtilis L. Koch, 1874 was described from one male and a juvenile from Tonga, western Polynesia. Most probably it is not congeneric with the Australian type species *H. gracilis* L. Koch, 1874 and several other species from Southeast Asia to New Zealand. It has not been compared with the type of *Tharrhalea* from N. Australia, but it seems, at least, to belong to the same tribe as *T. maculata* from New Guinea. *H. pallida* Koch, 1876, described from juvenile specimens from Tonga most probably is a synonym of *H. subtilis* or even '*D.*' *praetexta*. In addition to these two very old records there is also a recent record of a subadult female from Tonga. *Hedana* and *Tharrhalea* have been catalogued in Stephanopinae (Simon, 1895; Roewer, 1954; Bonnet, 1957), but '*H.*' *subtilis* belongs to Thomisinae.

I have seen relatives of *H. subtilis* (? *Tharrhalea*) in New Guinea and southeast Asia and the range of this unnamed group is more or less similar, but possibly extending farther northwards, when compared to that of the '*Diaea*' *praetexta*-group.

ZOOGEOGRAPHICAL CONCLUSIONS

The Polynesian thomisid fauna has apparently arrived from two opposite directions, South America and Melanesia. These two elements are not known to be mixed in any part of Polynesia (map in Fig. 1).

New World element (*Mecaphesa*) probably first arrived in Hawaii, where an explosive speciation has taken place, resulting in 17 known species (Suman, 1970: in three genera), most having a small range up in the mountains. Galapagos Islands (1 or several spp.) and Juan Fernandez Islands constitute another possible source of immigration for the East Polynesian *Mecaphesa* spp. They have further evolved to at least six, but probably more local endemics. There are also sympatric montane species, at least in the Marquesas Islands, but most probably also in Tahiti. The majority of East Polynesian species live on mountain tops, but a few species have occassionally been recorded also in lowland.

The Oriental-New Guinean genus of the *Misumena*-group, here tentatively called *Massuria* has not been found in the intervening Melanesian archipelagoes and must be excluded from possible sources of origin of the east Polynesian *Mecaphesa*, although both groups belong to Misumenini, a group probably older than any mid-Pacific archipelagoes.

There are no known thomisids in the Central Polynesian islands (Cook Islands, Tokelau Islands, Niue, etc.) (Marples, 1955b, 1957, 1960, 1964) or in the low coral islands north of Samoa (Rainbow, 1897; Roewer, 1944). In spite of additional collecting both in the lowland as well as in the mountains of Rarotonga by myself, no *Mecaphesa* spp. have been observed. The absence of *Dinea praetexta* in disturbed lowland habitats of Rarotonga seems to show that anthropochorous dispersal of this species is not very effective, although its frequency in the more western archipelagoes can be partly explained by this type of short distance dispersal.

The Australian Thomisidae appear to have arrived through Melanesia, where Fiji and Vanuatu share the same common lowland species, '*Diaea*' *praetexta* and several closely related species are present in New Guinea and Eastern Australia. The other west Polynesian thomisid species, '*Tharrhalea*' *subtilis* belongs to a group that has a wider range including southeast Asia. In spite of intensive field work in Samoa and Tonga during 1991-92, there are still no montane thomisids known in the western archipelagoes of Polynesia.

There are some other Polynesian spiders of Neotropical origin (Anyphaenidae, some Theridiidae, etc.), but most spider families represented in Polynesia are of Melanesian, southeast Asian or New Zealand origin.

ACKNOWLEDGEMENTS

This study is part of a long range programme on Indo-Pacific spiders, including field and museum work during the last 20 years. This work has only been possible through the generous cooperation of numerous persons, who could not be listed separately here. Useful comments were also presented by two referees and an editor. The map was kindly drawn by Ms. Maija Mustonen, and the original English text was checked by Mrs Alice Moore.

LITERATURE CITED

BEATTY, J.A. & BERRY, J.W. 1988. Four new species of *Paratheuma* (Araneae, Desidae) from the Pacific. Journal of Arachnology 16: 339-347.

BEATTY, J.A., BERRY, J.W., & MILLIDGE, A.F. 1991. The Linyphiid spiders of Micronesia and Polynesia with notes on distribution and habitats. Bulletin of the British Arachnological Society 8: 265-274.

BERLAND, L. 1924. Araignées de l'ile de Pâques et des îles Juan Fernandez. The Natural History of Juan Fernandez and Easter Island 3: 419-437.

1927. Note sur les Araignées recueillies aux îles Marquises par le R.P. Siméon Delmas. Bulletin du Muséum National d'Histoire Naturelle, Paris 38: 366-368.

1928. Remarques sur la répartition et les affinités des Araignées du Pacifique. Proceedings of the Pan-Pacific Science Congress, 3, Tokyo (1): 1044-1054.

1929. Araignées (Araneida). Insects of Samoa and other Samoan terrestrial Arthropoda, vol. 8: 35-78.

1930. Les Araignées des îles avoisinant la Nouvelle Zélande et les relations entre l'Australie et l'-Amerique du Sud. Compte Rendu de Séances, Société de Biogeographie, Paris 1930(60): 90-94.

1933. Araignées des îles Marquises. Bulletin of the Bernice P. Bishop Museum 114 (Pacific Entomological Survey Publication 7): 39-70.

1934a. Les Araignées du Pacifique. Contribution à l'étude du peuplement zoologique et botanique des îles du Pacifique. Publ. Soc. Biogéographie 4: 155-180.

1934b. Les Araignées de Tahiti. Bulletin of the Bernice P. Bishop Museum 113 (Pacific Entomological Survey Publication 6(21)): 97-107.

1934c. Araignées de Polynésie. Annales de la Société Entomologique de France 103: 321-336.

1935a. Nouvelles Araignées marquisiennes. Bulletin of the Bernice P. Bishop Museum 142 (Pacific Entomological Survey Publication 8(4)): 31-63.

1935b. Les Araignées des îles Marquises et la Biogéographie. Compte Rendu de Séances, Société de Biogeographie, Paris 100: 27-28.

1937. Comment les Araignées ont peuplé le Pacifique. Bulletin de la Société Océanographique 1: 77-80.

1938a. Araignées des Nouvelles Hébrides. Annales de la Société Entomologique de France 107: 121-190.

1938b. Liste des Araignées recueillis à Maupiti (îles de la Societe) par M. Ropiteau. Bulletin de la Société étude Océanographique 6: 47-48.

1942. Polynesian spiders. Occasional Papers of the Bernice P. Bishop Museum 17: 1-24.

1947. Araignées. XVI. in Croisière du Bougainville aux îles australes françaises. Mémoires du Muséum National d'Histoire Naturelle, Paris 20: 53-54.

BERRY, J. & BEATTY, J. 1987. Biogeography of Pacific Island spiders: a progress report. American Arachnology 36: 3.

BONNET, P. 1957. Bibliographia Araneorum 2(3): 1927-3026. (Les Artisans de L'Imprimerie Douladoure: Toulouse).

BÖSENBERG, H. & STRAND, E. 1906. Japanische Spinnen. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft in Frankfurt a. Main 30: 93-422.

CAPORIACCO, L. DI, 1954. Araignées de la Guyane Française du Museum d'Histoire Naturelle de Paris. Commentationes Pontificiae Academia Scientiarum 16: 45-193.

CARSON, H.L. 1984. Speciation and the Founder Effect on a New Oceanic Island. PP. 45-54. In, Radovsky, F.J., Raven, P.H. and Sohmer, S.H. (eds), Biogeography of the Tropical Pacific.

CHRYSANTHUS, FR. 1964. Spiders from South New Guinea VI. Nova Guinea, Zoology 28: 87-104.

CRAW, R. 1978. Two biogeographical frameworks: Implications for the biogeography of New Zealand. A review. Tuatara 23: 81-114.

1983. Panbiogeography and vicariance cladistics: Are they truly different? Syst. Zool. 32: 431-437.

DALRYMPLE, G.P., SILVER, E.A. & JACKSON, E.D. 1975. Origin of the Hawaiian Islands. In: Skinner, B.J. (ed.), Earth's history, structure, and materials. Readings from American Scientist: 112-126.

DIPPENAAR-SCHOEMAN, A.S. 1983. The spider genera *Misumena*, *Misumenops*, *Runcinia* and *Thomisus* (Araneae, Thomisidae) of southern Africa. Entomology Memoirs of the Department of Agriculture, Republic of South Africa 55: 1-66.

DONDALE, C.D. & REDNER, J.H. 1978. The crab spiders of Canada and Alaska. Araneae: Philodromidae and Thomisidae. The Insects and Arachnids of Canada 5: 255 pp. (Supply and Services Canada: Hull).

DUNCAN, R.A. & MCDOUGALL, I. 1974. Migration of volcanism with time in the Marquesas Islands, French Polynesia. Earth and Planetary Science Letters 21: 414- 420.

FOSBERG, F.R. 1991. Pacific Oceanic Island Biodiversity in a geohistoric perspective. Proceedings of the XVII Pacific Science Congress, Honolulu: 71-73.

GRESSITT, J.L. 1961. Problems in the zoogeography of Pacific and Antarctic Insects. Pacific Insects Monograph 2: 1-94.

GRESSITT, J.L. & YOSHIMOTO, C.M. 1963. Dispersal of animals in the Pacific. Pp. 283-293. In, Gressitt, J.L. (ed.), Pacific Basin Biogeography.

KOCH, L. & KEYSERLING, E. 1871-1886. Die Arachniden Australiens, nach der Natur beschrieben und abgebildet. 1489 pp. (Bauer and Raspe: Nürnberg). (Thomisidae 1874: 492-610 and 1876: 742-824).

KULCZYNSKI, W. 1911. Spinnen aus Süd-Neu-Guinea. Nova Guinea 9 (Zoology 2): 109-148.

LEHTINEN, P.T. 1980. Arachnological zoogeography of the Indo-Pacific Region. Verhandlungen des 8. Internationalen Arachnologen-Kongreß, Wien, 1980: 499- 504.

LEVY, G. 1985. Araneae: Thomisidae. Fauna Palaestina, Arachnida, vol. II: 1-115. (Israel Academy of Sciences and Humanities: Jerusalem).

LOERBROKS, A. 1983. Revision der Krabbenspinnengattung *Heriaeus* Simon (Arachnida: Araneae: Thomisidae). Verhandlungen des Naturhistorischen Museum in Hamburg (N.F.) 26: 85-139.

MARPLES, B.J. 1955a. Spiders from Western Samoa. Journal of the Linnean Society of London, Zoology 42: 453-504

1955b. Spiders from some Pacific Islands. Pacific Science 9: 69-76.
1957. Spiders from some Pacific Islands II. Pacific Science 11: 386-395.
1959. Spiders from South Pacific Islands III. The Kingdom of Tonga. Pacific Science 13: 362-367.
1960. Spiders from some Pacific islands, part IV. The Cook Islands and Niue. Pacific Science 14: 382-388.
1964. Spiders from some Pacific Islands V. Pacific Science 18: 399-410.
MELLO-LEITÃO, C.F. DE 1929. Aphantochilidas e Thomisidas do Brasil. Archivos do Museu Nacional, Rio de Janeiro 31: 9-358.
NELSON, G. & PLATNICK, N.I. 1981. Systematics and biogeography: cladistics and vicariance. (Columbia University Press: New York).
NUR, A. & BEN-AVRAHAM, Z. 1977. Lost Pacifica Continent. Nature 270: 41-43.
ONO, H. 1988. A revisional study of the spider family Thomisidae (Arachnida, Araneae) of Japan. (National Science Museum: Tokyo).
PLATNICK, N.I. & NELSON, G. 1988. Spanning-tree biogeography: shortcut, detour, or dead-end? Systematic Zoology 37: 410-419.
RAINBOW, W.J. 1897. The Arachnidan fauna of Funafuti. Memoirs of the Australian Museum 3: 105-125.
1902. Arachnida from the South Seas. Proceedings of the Linnean Society of New South Wales 26: 521-532.
RINALDI, I.M.P. 1983. Contribuiçao ao estudo das Misumeninae do Brasil (Araneae, Thomisidae). Revista Brasileira de Entomologia 27: 147-153.
ROEWER, C.F. 1944. Einige Araneen von Prof. Dr. Sixten Bocks Pazifik-Expedition 1917-1918. Meddelanden från Göteborgs Museum Zoologiska Avdelning 104: 1-10.
ROEWER, C.F. 1954. Katalog der Araneae von 1758 bis 1954, vol. IIA. (Institut Royal des Sciences Naturelles de Belgique: Bruxelles).
SCHICK, R.X. 1965. The crab spiders of California (Araneae, Thomisidae). Bulletin of the American Museum of Natural History 129: 1-180.
SIMON, E. 1895. Histoire Naturelle des Araignées, vol. 1(4): 761-1084. (Librairie Encyclopédique de Roret: Paris).
1900. Arachnida. Pp. 443-519. In, Sharp, D. (ed.), Fauna Hawaiiensis, or the Zoology of the Sandwich Isles, vol. 2. (Cambridge University Press: Cambridge).
STODDART, D.R. 1968. Isolated island communities. Science Journal 4: 32-38.
STRAND, E. 1913. Neue indoaustralische und polynesische Spinnen des Senckenbergischen Museums. Archiv für Naturgeschichte 1913 A 6: 113-123.
SUMAN, T.W. 1970. Spiders of the family Thomisidae in Hawaii. Pacific Insects 12: 773- 864.
TIKADER, B.K. 1980. Thomisidae (crab-spiders). The Fauna of India, Araneae, vol. 1, part 1: 1-247.
TOLEDO PIZA, S. 1937. Novos Thomisidos do Brazil. Folia de Clinic. Biologia, São Paulo 9: 179-183.
WILSON, J. TUZO, 1963. Continental drift. Scientific American 208: 86-100.

SCORPION DISTRIBUTION IN A DUNE AND SWALE MALLEE ENVIRONMENT

N.A. LOCKET

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A system of stable and vegetated dunes, separated by occasionally flooded swales, contains populations of six scorpion taxa. *Urodacus yaschenkoi* (Birula) digs deep burrows in the soft soil of the dunes, but the shallower burrows of *U. armatus* Pocock are concentrated at their base, extending onto the swale for ca. 50m. *Lychas jonesae* Glauert, *L. variatus* (Thorell) and *Isometroides angusticaudis* Keyserling occur on the swale but not the dunes. *Cercophonius kershawi* Glauert has occasionally been found in litter beneath mallee trees on the dunes. Soil hardness may account for *U. yaschenkoi* occurring only on the dunes. *Isometroides*, a spider predator, occurs where spider burrows are found. Predation by the larger *Urodacus* may account for the buthids not extending onto the dunes.□ *Scorpions, Australia, ecology, habitat.*

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An area of scrub near Berri in the South Australian Riverland consists of a series of stable dunes bearing mallee trees and shrubs interspersed with flat grassy swales, which show signs of occasional flooding. This locality contains a population of *Urodacus yaschenkoi*. Blacklighting on and between the dunes showed that five other scorpion taxa are present in the area but not uniformly distributed. Observations are now presented on these populations and their distribution across the dune- swale system.

Two of the taxa found do not accord with the descriptions given by Koch (1977). One, a *Lychas*, corresponds to Glauert's (1925) unillustrated description of *L. jonesae*, apparently from a single specimen collected near Kalgoorlie, Western Australia. Koch (1977), who examined the holotype, included *L. jonesae* in *L. marmoreus* but did not give reasons for doing so. The present specimens resemble *L. alexandrinus*, widely distributed in arid Australia (Koch, 1977, map 4), but differ significantly from it and from *L. marmoreus*. They agree closely, except in colouration, with the (markedly faded) type of *L. jonesae*. An illustrated redescription of *L. jonesae* is in preparation, and the present specimens referred to that species meanwhile.

The other belongs to the genus *Isometroides*, which Main (1956) suggested was monospecific, all specimens being referable to *I. vescus*, a view supported by Koch (1977). The Berri specimens agree better with the descriptions of Keyserling (1885), Kraepelin (1916) and Glauert (1925, 1963) of *I. angusticaudis*, and are certainly not typical of *I. vescus*. An account of the genus *Isometroides* is in preparation, and the present specimens referred to *I. angusticaudis* in anticipation of that work.

Many factors influence the distribution of scorpions, including latitude and climate, type of terrain and soil hardness. Biotic factors such as intra-guild competition and predation are also important (Polis, 1990). The latitude of the study site, ca 34°, is within the range of maximum scorpion diversity, given by Polis (1990) as 23-38°. Within this belt up to ca 10 species may occur sympatrically in the northern hemisphere, though most locales have only 3-7. Diversity is greatest in desert regions, with 24 of the 28 communities of six or more being in subtropical deserts, where terrain may range from loose sand to hard packed stony ground. Soil hardness was closely related to species distribution in *Opisthophthalmus* by Lamoral (1978). Bradley (1986) showed that populations of the burrowing *Paruroctonus utahensis* were denser on soft soils than hard, and that its burrowing was impaired by the hardening of the soil due to rain. Vegetation patterns correlated both with soil type and scorpion population, but areas with different scorpion densities contained similar biomass of potential prey. Bradley also demonstrated the destruction caused by flooding to a population of *P. utahensis*.

Polis (1990) shows that biotic factors may well affect the composition and balance of a population. He gives strong evidence on the important influence of scorpions on the community in which they live, by competition through predation on other invertebrates or cannibalism of smaller scorpion species, and of smaller conspecific instars. Individual scorpions of different species but similar size may well compete direct-

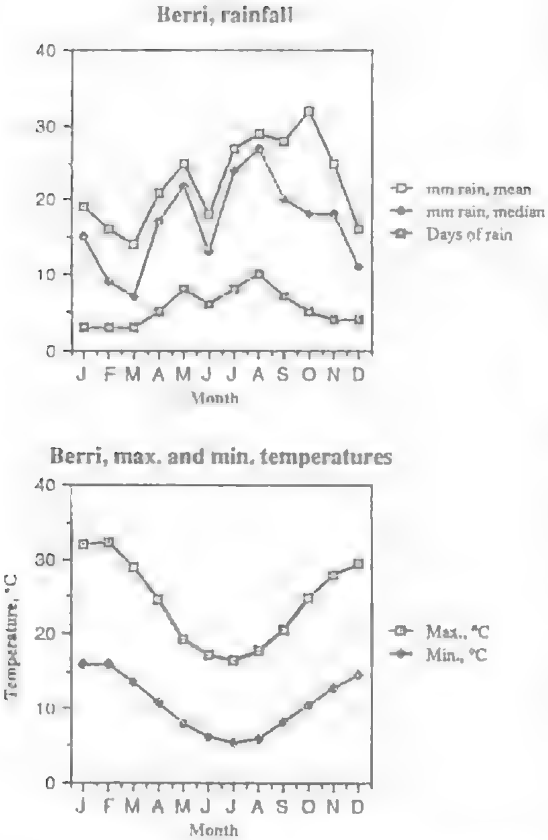

FIG. 1. Temperature and rainfall, Berri (nine year average).

ly for food, since most are generalist predators, perhaps leading to one species becoming dominant. Different sized scorpions may take different groups of prey, based on size, though the young of a large species may compete directly with adults of a smaller when the individuals are of comparable size.

METHODS

The site is about 8 km NNE. of Berri, 140°38'E, 34°13'S, in the South Australian Riverland. The climate at Berri is warm and dry (Fig. 1). A transect 10m wide was laid out from dune to dune across a swale, some 300m. The nature of the soil was noted, and trees and shrubs more than a few cm high plotted to the nearest 1m.

Single-, or on one occasion two-day, visits were made to the study site on fourteen occasions, on moonless nights when possible, between March 1989 and May 1992. On each visit the parts of the transect containing the characteristic burrows of *Urodacus yaschenkoi* were noted. On one occasion in summer all the burrows within the transect were marked with numbered tags. Burrow identification was confirmed and specimens obtained by trapping burrows away from the transect. The traps were plastic vending machine cups, ca 200cc capacity, dug into place at the burrow mouth, the burrow opening directly at the lip of the cup. The traps were visited at least 1h after sunset, when scorpions had emerged from the burrows and fallen into the cup.

Date	*U.yasch.*	*U.armat.*	*I.angust.*	I.variatus	*L.jonesae*
16 Sep 89	0	0	4	0	0
24 Mar 90	4	3	4	0	1
15 Sep 90	0	1	2	0	3
20 Oct 90	0	0	10	0	7
10 Nov 90	0	0	5	0	27
15 Dec 90	0	0	11	2	21
15 Jan 91	0	0	11	0	16
16 Mar 91	0	11	0	0	18
5 Oct 91	14	14	2	2	1
2 Nov 91	0	0	5	0	1
7-8 Dec 91	9	6	5	1	70
2 Feb 92	1	1	1	0	41
29 Feb 92	6	11	11	1	59
2 May 92	0	2	6	1	
TOTAL	34	52	78	6	265

TABLE 1. Catches of scorpions, blacklighting only.

Smaller burrows, without the curved entrance of *U. yaschenkoi*, were identified as those of *U. armatus* by digging out the scorpion. On three occasions *U. armatus* was identified by blacklight at a burrow mouth which was then marked and examined next day.

Blacklighting was carried out, away from the transect but within the dune-swale system, on each visit by two persons, working parallel to each other and approximately 100m apart. Blacklighting, commencing at various times after sunset, on some occasions as soon as it became dark enough and on others up to 1.5h after sunset, was continued for ca 2h.

Urodacus yaschenkoi and *U. armatus* could be distinguished in the field by blacklight. *Isometroides*, except very small individuals, was distinguishable from the *Lychas* species, but the two *Lychas* could not be told apart until the catch was examined indoors. This took place on return from the field, when notes on weather, capture sites and behaviour were written. Detailed plots of specimen location were not made, but it was possible to assign the taxa to dune, dune base or

FIG. 2. View of transect across swale, looking north from southern dune. 1, sandy soil at base of dune. 2, low bank beside old track. 3, track. 4, swale. 5, far dune. See also Figs 3 and 4.

swale. Identifications were confirmed on return to the laboratory.

RESULTS

The transect, running N-S, extends 300m from the top of one dune, ca 6m high, across the flat swale, to the top of the next dune (Fig. 2). The dunes bear scattered mallee trees, *Eucalyptus oleosa* and *E. brachycalyx*, numerous bushes of native hop, *Dodonaea* sp., and clumps of *Spinifex*. The swales are lightly covered with grass and other low plants, with sparse bushes of native hop and of *Cassia nemophila* var. *platypoda* (Fig. 3).

Catch data are summarised in Table 1 and distributions in Fig. 4. *Urodacus yaschenkoi* burrows occur on the dunes, mainly in the open but a few under light cover. In January 1991, 80 burrows were located and marked within the transect, but by October, 56 tags either were not related to a visible burrow or had been disturbed by animals. Of the three *U. armatus* burrows marked while blacklighting, two had been closed by next day, and would have been missed apart from the marker. No further attempts were made to trace the fate of individual burrows. Individual *U. yaschenkoi*, usually adult males, were found by blacklighting in December-February, mainly on the dunes but including one ca. 50m onto the swale. *U. yaschenkoi* were also observed at their burrow mouths by blacklight in summer.

Urodacus armatus burrows were occasionally found on the dunes, but most were at the dune base and for up to 50m onto the swale. *U. armatus*, mostly immature, found by blacklight had a similar distribution , with occasional examples up to ca 100m onto the swale. Immature individuals have sometimes been found clinging to low vegetation within a few cm of the ground. *U. armatus*, recognisable by blacklight from *U. yaschenkoi* by their squat pedipalps, have been seen at the burrow mouth between October and February

Three species of buthid, *Lychas jonesae*, *L. variatus* and *Isometroides angusticaudis* have been found, only on the swale, by blacklighting. *L. jonesae*, commonest overall, though on occasions outnumbered by *I. angusticaudis*, occurs all across the swale, but often near low vegetation near the dune base. Some have been found clinging to stems within a few cm of the ground.

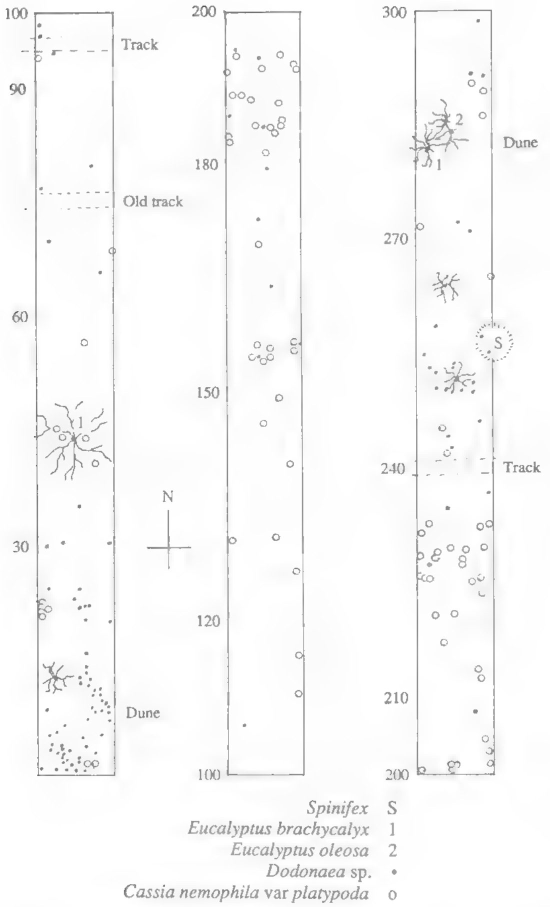

FIG. 3. Plot, to scale, of distribution of major plants across transect. Distances in metres.

mostly head down, but none have been found high in bushes.

Lychas variatus has been taken occasionally, never more than two and frequently none, in an evening. Insufficient have been found to comment on their distribution on the swale.

Isometroides angusticaudis has mostly been found on the surface by blacklight, among low grass rather than taller vegetation and extending up to but not above the dune base. A few have been dug by day from the burrows of lycosid spiders, abundant on the swale but not the dunes.

One *Cercophonius kershawi* (identified from Acosta (1990)) was found in May 1992 by kicking over leaf litter beneath mallee trees while blacklighting. (Two juvenile *Lychas variatus* were caught in the same way on dunes within 1 km of the transect in June 1987).

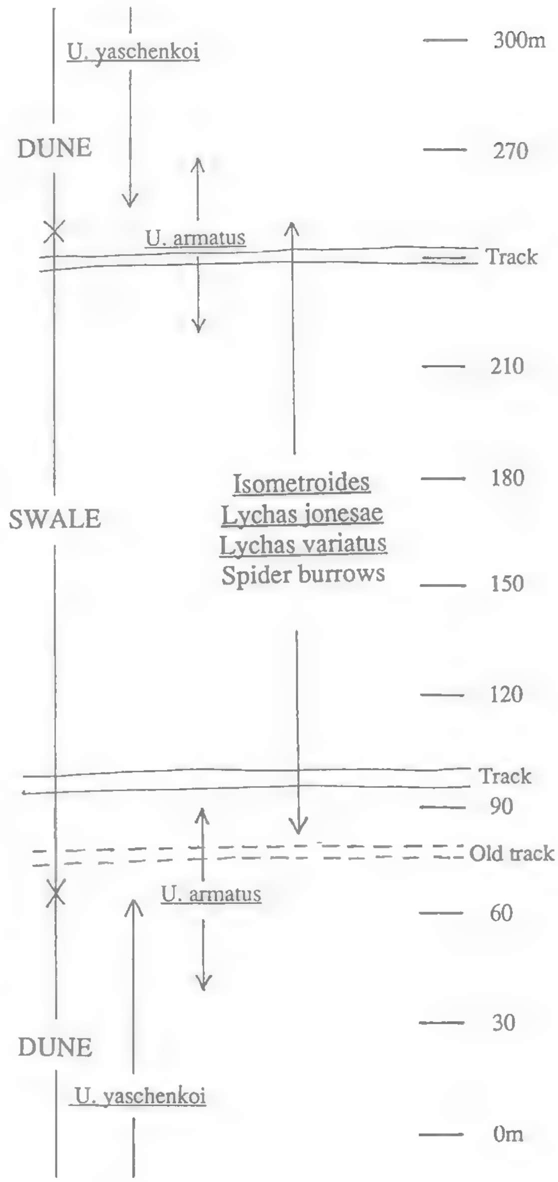

FIG. 4. Distribution of scorpions across dune and swale system. *Urodacus yaschenkoi* occurs on the dunes, *U. armatus* at their bases and the three buthids on the swale.

DISCUSSION

Many labels in collections state a locality, without details of microhabitat. The population disparity now described from localities a few meters apart suggests that it may be helpful to define localities more precisely.

Lamoral (1978), studying two burrowing

species of *Opisthophthalmus*, found clear separation of two otherwise sympatric species, strongly correlated with soil hardness, a factor probably also important in *Urodacus*. Koch (1978) found the depth and tortuosity of *Urodacus* burrows within a species greater with aridity. There is also a species difference: *U. yaschenkoi* and *U. hoplurus* dig deeper and more spiral burrows than *U. armatus*. Koch (1981) noted that *Urodacus* scorpions show little correlation with soil type, but more with softness and the chance of reaching water by burrowing. Shorthouse (1971), Shorthouse and Marples (1980) and Koch (1978) have described the spiral burrows up to 1m deep of *U. yaschenkoi* in loose sandy soil. The dune soil at Berri is of this type. Most burrows of *U. armatus*, seldom more than 30cm deep, are in the firmer soil at the dune base and swale, though some occur up the dunes, in what appears otherwise to be *U. yaschenkoi* territory.

Koch (1981) considered three Australian zones, a moist temperate southern, semi-arid to desert central and humid tropical northern, associating various scorpions with these zones: *Urodacus yaschenkoi* and *U. armatus* he regarded as mainly central forms. He found scorpion distribution not correlated with vegetation type, single species occurring in a wide range of habitats. He suggested that range-determining factors include temperature, precipitation and biotic factors, e.g. competitive exclusion. He also examined morphological characters, suggesting that large size, longer metasomal segments and spines, more granulation, and higher pectine tooth counts are aridity-linked in *Urodacus*, while large size, light colouration, more granulation, higher pectine tooth counts and a less prominent subaculear tooth are aridity- linked traits associated in *Lychas*. He regarded *Isometroides* as showing the culmination of these buthid traits. Of the sympatric species at Berri, both *Urodacus* are pale and smooth, their pectine counts largely overlap, but *U. yaschenkoi* is large and *U. armatus* small. *L. variatus* and *I. angusticaudis* are both pale but mottled though *L. jonesae* is small and dark, with subaculear tooth intermediate between the other two buthids.

The swale, where *Isometroides* has been collected by blacklight, contains numerous lycosid spider burrows, up to 30cm deep in hard soil. *Isometroides* was recognised by Main (1956) as a spider predator and collected by her from their burrows. Four have been so collected in the present study, but no concerted digging has been done.

The habit of clinging to vegetation close to the ground, also observed in immature *U. armatus* by G.T. Smith (personal communication), may enable scorpions to avoid wandering predators. Some scorpions, e.g. *Centruroides exilicauda* in America, are frequently found in bushes well off the ground, but such climbing has not been seen in the present case.

The total catches of buthids suggest that *Lychas jonesae* is dominant on the swale, though on occasions more *Isometroides* have been caught. *L. variatus* is much less common than either. *Isometroides* is known to be a specialist burrowing spider predator. Probably the *Lychas* species are less specialised, though little is known of their diet; one instance of *L. jonesae* eating an immature *U. armatus* was the only act of predation observed. Insufficient is known of the habits of the two *Lychas* to indicate why the smaller should be commoner.

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LITERATURE CITED

ACOSTA, L.E. 1990. El genero *Cercophonius* Peters, 1861 (Scorpiones, Bothriuridae). Boletin de la Sociedad de Biología de Concepción (Chile) 61: 7-27.

BRADLEY, R.A. 1986. The relationship between population density of *Paruroctonus utahensis* (Scorpionida: Vaejovidae) and characteristics of its habitat. Journal of Arid Environments 11: 165-172

GLAUERT, L. 1925. Australian Scorpionidea. Part 1. Proceedings of the Royal Society of Western Australia 11: 89-118.

1963. Check list of Western Australian scorpions. Western Australian Naturalist 8: 181-185.

KEYSERLING, E. 1885. Part 32. Pp. 1-48. In Koch, L. and Keyserling, E. 'Die Arachniden Australiens nach der Natur bescrieben and abgebildet'. (Bauer & Raspe: Nürnberg).

KOCH, L.E. 1977. The taxonomy, geographical distribution and evolutionary radiation of Australo-Papuan scorpions. Records of the Western Australian Museum 5: 81-367.

1978. A comparative study of the structure, function and adaptation to different habitats of burrows in the scorpion genus *Urodacus* (Scorpionida, Scorpionidae). Records of the Western Australian Museum 6: 119-146.

1981. The scorpions of Australia: aspects of their ecology and zoogeography. Pp. 875-884. In Keast, A. (ed.), 'Ecological biogeography of Australia'. (Junk: The Hague).

KRAEPELIN, K. 1916. Results of Dr E. Mjöberg's Swedish scientific expeditions to Australia 1910-1913. 4. Scolopendriden und Skorpione. Arkiv für Zoologi 10: 1-43.

LAMORAL, B.H. 1978. Soil hardness, an important and limiting factor in burrowing scorpions of the genus *Opisthophthalmus* C.L. Koch 1837 (Scorpionidae, Scorpionida). Symposia of the Zoological Society of London 42: 171-181.

MAIN, B.Y. 1956. Taxonomy and biology of the genus *Isometroides* Keyserling (Scorpionida). Australian Journal of Zoology 4: 158-164.

POLIS, G.A. 1990. Ecology. Pp. 247-293. In Polis, G.A. (ed.), 'The biology of scorpions.' (Stanford University Press: Stanford).

SHORTHOUSE, D.J. 1971. 'Studies on the biology and energetics of the scorpion *Urodacus yaschenkoi*.' (Unpublished Ph.D. Thesis, Australian National University: Canberra).

SHORTHOUSE, D.J. & MARPLES, T.G. 1980. Observations on the burrow and associated behaviour of the arid zone scorpion *Urodacus yaschenkoi* Birula. Australian Journal of Zoology 28: 581-590.

FROM FLOOD AVOIDANCE TO FORAGING: ADAPTIVE SHIFTS IN TRAPDOOR SPIDER BEHAVIOUR

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Fossorial habits protect many mygalomorph spiders from both biotic and environmental factors. However burrows in some habitats are vulnerable to sheet flooding. Spiders in diverse habitats counter the hazard of flooding in various ways. A comparative account of adaptive specialisations, particularly of burrows, in flood avoidance is presented. Such primary modifications sometimes lead to new foraging opportunities. Examples are given of modified foraging as a consequence of burrow adaptations. The origins of such constructions are hypothesised in relation to changing climatic regimes and modified habitats. The idiopid genera *Homogona* Rainbow and *Neohomogona* Main are restored from synonymy. □*Mygalomorphae, Trapdoor spiders, burrows, flood avoidance, foraging, Australia.*

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Most mygalomorph spiders are terrestrial and either make burrows, silk tubes or webs or combine a web with a burrow. A few are arboreal and either make tubes in the bark of trees or have webs in crevices or under bark; their nests are generally not associated with foliage. Of the 15 currently recognised families of Mygalomorphae (Raven, 1985), 10 occur in Australia and of these, seven have at least some representatives with trapdoors. A burrow provides protection from the physical environment, from weather conditions and from predators and parasites; it provides a brood chamber for eggs and spiderlings. A burrow is also a lair from which a spider perceives and ambushes or intercepts prey; thus it provides a foraging base. All these functions have been commented on many times in the literature over the last century, the earliest comprehensive study possibly being that of Moggridge (1873, 1874).

In its simplest form a burrow has an 'open' entrance from which a spider makes short sorties in pursuit of prey. In extreme habitats, the entrance may be sealed with silk or soil for added protection during certain times of the year, for example during summer drought or winter snow falls. Folding collars and finally hinged doors give maximum security and protection. The protective advantage of a door has been shown to be offset by the hinge-line inhibiting the foraging area of a spider but nevertheless many door builders have overcome this disadvantage by various modifications to the burrow (Coyle, 1981; Main, 1986).

This paper discusses the adaptive behavioural responses associated with nest structure and site, of Australian mygalomorph spiders, to the hazard of flooding and shows that these primary adaptations have sometimes secondarily created new foraging opportunities for spiders. In particular the previously unreported nest of an undescribed species of *Aname* which exhibits both 'primary' and 'secondary' responses in its flood-avoidance tactics is described also.

FLOOD AVOIDANCE BEHAVIOUR

In certain terrestrial habitats, burrows and silk tubes and webs face the physical hazard of flooding. Generally the complexity of habitats in rainforest and mesophyll forest provides some sort of buffer against flooding; there is greater capacity for absorption of rainfall in the vegetation and litter of a forest floor than there is for example in desert or semi-arid country where sheet flooding on bare ground is a common phenomenon. Even so some rainforest situations are subject to water logging and flooding associated with torrential downpours. Likewise where rain is markedly seasonal as in monsoon rainforests the alternation of wet and dry conditions means that some habitats experience sudden saturation or inundation. Main (1976, 1982b) and Cloudsley-Thompson (1982, 1983) discussed some of the burrow modifications of mygalomorphs which prevent flooding. Avoidance of flooding is different to behaviours whereby spiders withstand immersion by enclosing the body in a bubble of air.

In summary, in avoiding flooding of nest sites, mygalomorph spiders have adapted behaviourally in several ways:

(1) By moving the nest site–behaviour prior to, during or after the event.

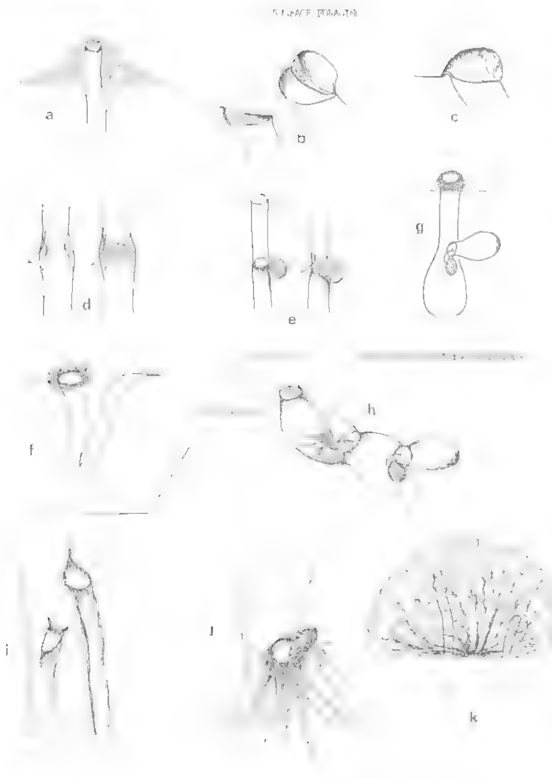

FIG. 1. Flood avoidance specialisations of mygalomorph burrows: (a) soil and pebble levee of *Kwonkan wonganensis*; (b) bath plug door (Idiopidae); (c) dome or 'cap' of an *Aganippe* species (Idiopidae); (d) 'sock' of *Anidiops* (Idiopidae); (e) 'pebble' and collar closure of burrow of *Stanwellia nebulosa* (Nemesiidae); (f) side shaft and escape 'hatch' of burrow of *Aname diversicolor* (Nemesiidae); (g) side shaft with door in nest of *Idiommata* sp. (Barychelidae); (h) profile of nest of a *Teyl* sp. (Nemesiidae) with entrance atrium and subterranean doors (and sideshaft); (i) aerial tube of *Misgolas robertsi* (Idiopidae) supported on tree trunk; (j) extended tube with trapdoor of *Aganippe castellum* (Idiopidae) supported against stem of shrub; (k) silk and soil tube of 'turret-building' *Aname* sp. (Nemesiidae) in foliage of shrub.

(2) By permanently reinforcing the nest e.g. burrow (and/or opening) against inundation–prevention.

(3) By modifying the nest structure so that part of it is safeguarded against inundation–prevention.

(4) By modifying the nest so that it is (in part) sited beyond the reach of intermittent flooding–prevention.

(5) By adopting an arboreal instead of terrestrial habitat.

Examples of these adaptations will now be given.

(1) Mygalomorphs elsewhere have been recorded as moving nest sites prior to inundation. The Amazonian web-weaving diplurid *Ischnothele guianensis* makes webs on tree trunks in the rainforest which is seasonally inundated. Spiders move their web sites higher up the trunks as the water level rises (Hofer, 1991). The Australian diplurid genus *Cethegus* (curtain web spiders), which makes copious webs sometimes associated with a burrow retreat, amongst stones, or against logs or shrub stems, is widespread across tropical Australia, the interior and southwestern Western Australia (Main, 1960, 1991a and unpublished; Raven, 1984). A study on a species at Durokoppin in the Western Australian wheatbelt showed that the spiders move their web sites after rain damage (Main, unpublished). Another species which occurs amongst the rocks of water courses in the Kimberley rainforest patches (Main, 1991a) presumably moves web sites during the 'wet' when the habitat is inundated. Although dependent on a web for prey capture these spiders are remarkably agile on the ground, and thus could readily decamp if flooded out of their nest sites, following which a web could be readily reconstructed (unlike some architecturally complex burrows of other mygalomorph families).

(2) Even 'open' burrows, if lined with silk frequently have collapsible or folding collars which can prevent flooding, for example as in many nemesiids and some *Misgolas* species, e.g. *M. pulchellus* (Rainbow & Pulleine) (pers. obs.). Collars are sometimes strengthened with litter or by a surrounding pile of soil or silk-bound pebbles (Fig. 1a) e.g. the levees of some nemesiids including *Kwonkan wonganensis* (Main) (originally described as *Dekana* (Main, 1977, plate 15)) (see also Main (1981, plate 1, fig. d) with reference to the levee of a 'diplurine' burrow). The ctenizid *Conothele*, the actinopodid *Missulena* and some barychelids have secure doors and parchment or canvas-like, silk linings which are more-or-less impermeable. Most idiopid species construct well defined burrows and all except some species of *Homogona*[1], *Neohomogona*[1] and *Misgolas* have a trapdoor. Many idiopid species which have adapted to flood-prone habitats, ranging from rainforest to desert

[1]The idiopid genera *Homogona* Rainbow and *Neohomogona* Main were synonymised with *Cataxia* Rainbow by Raven (1985). They are here formally restored from synonymy and diagnosed in Main (1985).

and particularly in bare ground or sloping creek banks, frequently have permanently reinforced burrows including thick plaster walls coated with dense silk, and thick, close fitting bath-plug like doors or tightly fitting caps (Figs 1b, c). Such secure nests also provide protection against predators, parasites and adverse physical conditions, including dessication.

(3) Some species of Idiopidae, Nemesiidae, Barychelidae and Hexathelidae safeguard particular areas of their burrows against inundation. Such safeguards include (a) special blocks in the lumen or (b) sideshafts with 'escape' hatches or (c) one or more sidechambers with 'internal' trapdoors. Examples of the above are:

(a) Some species which have either an open entrance (e.g., *Misgolas* spp.) or a flimsy door (e.g., *Anidiops*) have a collapsible collar ('sock', see Main, 1957, 1976, plate 9 and 1985, figs 209, 210) consisting of a detachable section of the silk lining which can be pulled downwards by the spider thus blocking the burrow (Fig. 1d). Water seeping down the walls or flowing into the burrow is deflected by the infolded 'neck' of the sock and soaks into the surrounding soil leaving the lower section of the silk lined burrow unflooded. A similar structure in *Stanwellia nebulosa* (Rainbow & Pulleine) (Fig. 1e) is further reinforced by an attached, artificial pebble which seals the lower silk lined part of the burrow (Rainbow & Pulleine, 1918, pl. 20; Main, 1964, 1972 figs 22a, b, 1976). Although these devices are generally considered a protection against predators (see Main, 1956a regarding *Anidiops* (=*Gaius*) their original function was probably prevention against flooding (see Main, 1976 regarding *Stanwellia*).

(b) Nests of some species have silk sideshafts with 'escape' hatches at the surface (see Fig. 1f) which probably enable the spiders to escape flooding as well as intrusive predators. Examples are the burrows of 'wishbone' spiders of the genus *Aname* (Main, 1982a, fig. 1; 1976, pl. 10) and *Misgolas ornata* (Rainbow) (Main, 1985: 33).

(c) Sideshafts with 'internal' trapdoors are constructed by several undescribed species of *Teyl* (Nemesiidae) (earlier attributed to *Ixamatus*, see Main (1976, pp. 86-88, fig. 21)), by *Hadronyche* (Hexathelidae) (see Main, 1964:40, fig. j; 1976, fig. 18c; Gray, 1984, fig. 31 (described as *Atrax*)), *Idiommata* (Barychelidae) (Main, 1976, fig. 19d; Raven & Churchill, 1991: 35) and *Missulena* (Actinopodidae) (Main, 1956b). While the sideshafts of all species studied are known to function as brood chambers and also sometimes as protection from predators it is probable that the original function was that they offset flooding of the main shaft of the burrow (see Fig. 1g). Considering the habitat of *Teyl* species this is unequivocal.

(4) Burrows of some species are continued as tubes above the ground or litter surface and may be strengthened into free standing palisades (by the attachment of leaves, twigs and debris) which deflect sheet flooding in bare ground or prevent immersion in water-soaked litter. Examples include the tubes of *Homogona cunicularius* Main (Main, 1983, fig. 15), *Misgolas hirsutus* (Rainbow & Pulleine) (pers. obs.) and *Neohomogona stirlingi* and *N. bolganupensis* Main (Main, 1985, fig. 219). Tubes that extend a considerable distance above the substrate are attached to rocks, tree buttresses, exposed roots e.g. *Misgolas robertsi* (Main and Mascord) and related species (Main and Mascord, 1974, pl. 1a, b; Mascord, 1970 pl. 2 fig. 4), logs e.g. *Cataxia maculata* Rainbow (Main, 1969, figs 30, 31) or stems of shrubs e.g. *Aganippe castellum* Main (Main, 1986, figs 2, 4i; 1987, fig. 6). The first examples have open tubes, sometimes with flanged, collapsible collars but *A. castellum* has a trapdoor (Figs 1i, j). All are effective in flood avoidance by having the entrance above the 'flood level' following a deluge.

The previously undescribed but remarkable burrow/tube of an undescribed species of *Aname* extends as a turret-like tube amongst supporting foliage of shrubs. The genus *Aname* which is widespread but endemic in Australia and Tasmania, occurs in varied habitats, is taxonomically diverse and includes many undescribed species.

The turret-building species occurs in semi-arid country in southeastern Western Australia and Eyre Peninsula in South Australia. Nests have been observed in mallee/spinifex associations (*Eucalyptus*/*Triodia*) (Figs 2a, b, c) but also in mulga and amongst chenopod shrubs in seasonally swampy habitats. The spiders make shallow burrows lined with silk which extend as tubes into the foliage of supporting tussocks or shrubs and open either within the foliage or above the canopy (Fig. 1k). The outside of the tube is heavily but irregularly coated with soil. During and after rain, sheet flooding occurs in such sites, and particularly in the sandy loam of mallee/spinifex associations, water flows in a slurry around the spinifex hummocks. Burrows appear to be deepened (and/or remade) after rain and the sodden spoil dumped on the lip of the tube and outside the

Siting of burrow opening		PRIMARY ADAPTATION		SECONDARY ADAPTATION
		Flood avoidance through modified burrow structures	Unmodified foraging	Specialised foraging in response to 'new' opportunities
FOSSORIAL	Ground	—open* burrows: collars& folding collars & levees	surface	
		—closed* burrows: reinforced walls & doors	surface	
	Subterranean	— sub-surcae closures of lumen (open or closed burrow)	surface	
		—supernumerary chambers with doors		subsurface (pitfall captures)
	Elevated	extension of open tubes against vertical support		arboreal and semi-aerial
		—extension of closed burrow (with door) against plant stem		arboreal
		extension of open tube into foliage		foliage canopy
CORTICOLOUS		— open or closed tubes in bark		arboreal

TABLE 1. Siting of mygalomorph burrows primarily modified in flood avoidance and those secondarily resulting in specialised foraging methods. * open = without door; closed = with trapdoor.

entrance. Thus the turret is heightened progressively while much of the paste-like spoil pours down the outside wall, solidifying into a kind of stucco as it does so. Tubes up to 25cm have been observed within the supporting scaffolding of spinifex hummocks. The sometimes bulky structures belie the relatively small size of the artificers (up to 4.5mm carapace length). Occasionally free-standing tubes (but small and only up to 10cm high), away from shrubs, are found (see Main, 1982b, fig. 2). Most unsupported tubes may collapse (at ground level) and be destroyed during flooding while at least the aerial section of those amongst the tussocks remain relatively intact.

(5) Mygalomorphs which have their nests sited completely on the trunks of trees are found only in very wet forests. Their nests in such situations appear well protected against inundation. Australian examples include theraphosids which make silk retreats under bark in north Queensland (pers. observation), the nemesiid, *Chenistonia villosa* Rainbow and Pulleine which makes defined silk tubes in crevices of *Casuarina* bark in the karri forest of southwest Western Australia (pers. observation), species of the ctenizid, *Conothele*, in tropical Queensland (Main, 1976) illustrated in McKeown (1963), the barychelid *Sason* in north Queensland (Raven, 1986) and migids e.g. *Moggridgea tingle* Main (Main, 1991b). *C. villosa* and *M. tingle* both make nests in the ground also, in sites not vulnerable to water logging. This is probably a secondary habitat adopted in response to gradual drying of the climate and environment where the bark of trees would be subject to dessication.

NEW FORAGING OPPORTUNITIES

Foraging 'techniques' of mygalomorphs are closely associated with burrow structure. Burrows of some species are constructed with special adjuncts that enhance foraging, such as silk trip threads or attached twiglines. Main (1957, 1982b, 1987) described some combinations of burrow structure, morphology and foraging behaviour in relation to the habitats occupied and noted the relative efficiency of the various foraging strategies.

In modifying behaviour and burrow structure in flood avoidance, some species have as a consequence been exposed to 'new' foraging opportunities. Table 1 summarises the categories of 'primary' burrow modifications and sitings associated with flood avoidance and any 'secondary' changes of foraging behaviour. Reinforcement to burrows and doors which do not involve alteration of siting of the entrance, do not generally result in modification of foraging method. However, any modifications which alter the siting of burrow entrances away from the surface of the ground do result in specialised (predatory) foraging behaviour.

A striking example of a subterranean entrance is that constructed by a group of *Teyl* species. Although most species of *Teyl* have open burrows, a few build doors in flood avoidance. Several species have surface doors in bare open ground but the foraging method is similar to that of species with open holes (Main, 1986). Several species which occur in deep litter in seasonally flood-prone, braided creeks and the flats around salt lakes in southern Western Australia have evolved a further specialisation. An open 'false entrance' leads into a cup-like pouch or atrium which has on its inner wall a trapdoor (entrance

FIG. 2. *Aname* sp. Habitat and turrets (a) mallee/spinifex shrubland on sandy loam soil west of Balladonia, Western Australia; (b) spinifex shrubs with 'turrets'; (c) turret in spinifex, note open entrance.

proper) which leads into the main shaft of the burrow; a second trapdoor leads from the main shaft into a blind sideshaft (Fig. 1h). These doors provide a double safety valve in the event of flooding (Main, 1976). The false entrance/atrium functions like a pit-fall trap which 'catches' crawling insects that are then seized by the spider as it straddles the open door inside (Fig. 1h) (Main, 1982b fig. 7d). The pit-trap also provides a clear foraging area for the subterranean entrance-proper, unencumbered by the litter which would otherwise impede the plug-like door. Notable examples of elevated nests (supported against tree trunks), the primary adaptation of which has been flood avoidance but which has secondarily resulted in arboreal foraging, are those of *Misgolas robertsi* (see Mascord, 1970 p.12; Main 1976, plate B5) and *Aganippe castellum* (Main, 1986, 1987 p. 34 and fig. 6).

Spiders, the nests of which are sited on the trunks of trees but which have no contact with the ground and are thus corticolous, similarly have adopted an arboreal foraging behaviour. *Conothele* (possibly *Conothele arboricola* Pocock), *Sason* and *Chenistonia villosa* and *Moggridgea tingle* are thus all arboreal foragers although the latter two are recognised as being facultative in their behaviour. Even *Idioctis* species which extend their tubes above the tide level (or are sealed against tidal rise), sometimes against mangrove stems (Abraham, 1924), are probably in effect arboreal foragers.

However, until recently there was no known example of an Australian mygalomorph which fed in the foliage or canopy of vegetation. Therefore, the turret-building species of *Aname* is of interest. The tubes open either in gaps amongst the foliage or above the canopy of tussocks and shrubs. The spiders presumably do not venture far, if at all, away from the entrance (and are unlikely to crawl down the outside of the tube to the ground) and thus are dependent on insects creeping amongst and on the foliage and flying insects as they alight. This would mean that they are a truly foliage or canopy forager as distinct from arboreal spiders which forage on the trunks of trees and shrubs.

BURROW MODIFICATIONS AS A RESPONSE TO HISTORICAL ENVIRONMENTAL CHANGES

The arboreal tubes and most corticolous nests in mesophytic and rainforest habitats have evolved *in situ* in continuously humid habitats (but where some sites may experience extreme flooding). In contrast, of those flood-adapted nests which occur now in semi-arid and arid habitats most have evolved (*in situ*) from mesophytic denizens but as a result of a general drying of the habitat associated with climatic aridification. Paradoxically while probably making simple tubes and burrows in a "primitive", uniformly wet habitat the spiders have been exposed to the the hazard of sheet flooding as a result of periodic deluges associated with a dryer, but seasonal climate. Nevertheless, clearly a few such species do belong to taxonomic groups which already had burrows and doors well adapted to sudden deluges in rainforest and mesophytic habitats, e.g., species of *Arbanitis*.

Much of the semi-arid woodland, shrubland and saltbush steppe of southern Australia enjoyed a consistently wet climate and supported mesophytic forest and rainforest interspersed with swampland during the early Tertiary (Cookson, 1973; Cookson & Pike, 1953, 1954; Truswell, 1990). With progressive drying of the climate and development of a markedly seasonal weather pattern the vegetation was altered, leaving some relictual, moist microhabitats in juxtaposition with other seasonally alternating wet/dry microhabitats some of which now experience periodic, sudden inundation.

Certain species of trapdoor spiders whose taxonomic relatives in rainforest and mesophytic habitats lack specialised burrow structures have responded to seasonal sheet flooding in arid habitats by modifying burrow structures in flood avoidance. Notable types of burrow modification in the western part of the continent, which are hypothesised as having evolved in direct response to (geologically) historical changes in the environment are the burrows of *Aganippe castellum*, *Teyl* species with both surface and subterranean doors and the aerial tubes of the *Aname* species. Main (1986) discussed the probable origin of the semi-arboreal nest of *A. castellum*, its anti-flooding function and adoption of a 'new' foraging behaviour. This dual adaptation probably evolved during the late Miocene/Pliocene in response to fluctuating wet/dry seasons and fragmentation of the landscape into a mosaic of wet and dry microhabitats. It also has been postulated earlier (Main, 1976) that the single surface door of some *Teyl* species evolved in response to climatic/habitat changes towards a seasonal weather regime and more open habitat. The turret nest of the *Aname* species has probably, similarly developed contemporaneously, in response to the drying of the climate, in different geographic habitats but which also occur in areas subjected to some seasonal, torrential or at least very heavy rain which causes flash flooding.

LITERATURE CITED

ABRAHAM, H.C. 1924. Some mygalomorph spiders from the Malay Peninsula. Proceedings of the Zoological Society, London 1924: 1091-1124.

CLOUDSLEY-THOMPSON, J.L. 1982. Desert adaptations in spiders. Scientific Reviews on Arid Zone Research 1: 1-14.

1983. Desert adaptations in spiders. Journal of Arid Environments 6: 307-317.

COOKSON, I.C. 1953. The identification of the sporomorph *Phyllocladidites* with *Dacrydium* and its distribution in southern Tertiary deposits. Australian Journal of Botany 1: 64-70.

COOKSON, I.C. & PIKE, K.M. 1953. The Tertiary occurrence and distribution of *Podocarpus* (Section *Dacrycarpus*) in Australia and Tasmania. Australian Journal of Botany 1: 71-82.

1954. The fossil occurrence of *Phyllocladus* and two other Podocarpaceous types in Australia. Australian Journal of Botany 2: 60-88.

COYLE, F.A. 1981. The role of silk in prey capture by non-araneomorph spiders. American Arachnology 24: 6.

GRAY, M.R. 1984. The taxonomy of the *Atrax adelaidensis* species-group (Macrothelinae: Mygalomorphae) with notes on burrowing behaviour. Records of the South Australian Museum 18: 441-452.

HOFER, H. 1990. The spider community (Araneae) of a Central Amazonian blackwater inundation forest (igapo). Acta Zoologica Fennica 190: 173-179.

MAIN, B.Y. 1956a. Taxonomy and biology of the genus *Isometroides* Keyserling (Scorpionida). Australian Journal of Zoology 4: 158-164.

1956b. Observations on the burrow and natural history of the trap-door spider *Missulena* (Ctenizidae). Western Australian Naturalist 5: 73-80.

1957. Biology of aganippine trapdoor spiders (Mygalomorphae: Ctenizidae). Australian Journal of Zoology 5: 402-473.

1960. The genus *Cethegus* Thorell (Mygalomorphae: Macrothelinae). Journal of the Royal Society of Western Australia 43: 30-34.

1964. 'Spiders of Australia.' (Jacaranda: Brisbane).

1969. The trap-door spider genus *Cataxia* Rainbow (Mygalomorphae: Ctenizidae)-taxonomy and natural history. Journal of the Australian Entomological Society 9: 15-21.

1972. The mygalomorph spider genus *Stanwellia* Rainbow & Pulleine (Dipluridae) and its relationship to *Aname* Koch and certain other diplurine genera. Journal of the Royal Society of Western Australia 5: 100-114.

1976. 'Spiders.' (Collins: Sydney).

1977. Spiders. Pp. 100-107. In Kenneally, K. (ed.) 'The natural history of the Wongan Hills'. Handbook 11. (Western Australian Naturalist's Club: Perth).

1981. Australian spiders: diversity, distribution and ecology. Pp. 807-852. In Keast, A. (ed.) 'Ecological biogeography of Australia.' (Junk: The Hague).

1982a. Notes on the revised taxonomic position of the Black Wishbone spider *Dekana diversicolor* Hogg (Mygalomorphae: Dipluridae). Journal of the Royal Society of Western Australia 65: 25-29.

1982b. Adaptations to arid habitats by mygalomorph spiders. Pp. 273-283. In Barker, W.R. and Greenslade, P.J.M. (eds) 'Evolution of the flora and fauna of arid Australia'. (Peacock Publications: Frewville).

1983. Systematics of the trapdoor spider genus *Homogona* Rainbow (Mygalomorphae: Ctenizidae: Homogoninae). Journal of the Australian Entomological Society 22: 81-92.

1985. Further studies on the systematics of ctenizid trapdoor spiders: a review of the Australian genera (Araneae: Mygalomorphae: Ctenizidae). Australian Journal of Zoology, Supplementary Series 108: 1-84.

1986. Trapdoors of Australian mygalomorph spiders: protection or predation? Pp. 95-102. In Barrientos, J.A. (ed.) 'Actas X Congreso Internacional de Aracnologia 1.' (Jaca).

1987. Persistence of invertebrates in small areas: case studies of trapdoor spiders in Western Australia. Pp. 29-39. In Saunders, D.A., Arnold, G.W., Burbidge A.A. and Hopkins, A.J.M. (eds) 'Nature conservation: the role of remnants of native vegetation.' (Surrey Beatty: Chipping North).

1991a. Kimberley spiders: rainforest strongholds. Pp. 271-293. In McKenzie, N.L., Johnston, R.B. and Kendrick, P.G. (eds) 'Kimberley rainforests', (Surrey Beatty: Chipping North).

1991b. Occurrence of the trapdoor spider genus *Moggridgea* in Australia with descriptions of two new species (Araneae: Mygalomorphae: Migidae). Journal of Natural History 25: 383-397.

MAIN, B.Y. & MASCORD, R. 1974. Description and natural history of a "tube-building" species of *Dyarcyops* from New South Wales and Queensland (Mygalomorphae: Ctenizidae). Journal of the Entomological Society of Australia 8: 15-21.

MASCORD, R. 1970. 'Australian spiders in colour.' (A.H. and A.W. Reed: Sydney).

MCKEOWN, K. 1963. 'Australian spiders.' (Angus and Robertson: Sydney).

MOGGRIDGE, J.T. 1873. 'Harvesting ants and trap-door spiders.' (Reeve: London).

1874. 'Supplement to harvesting ants and trap-door spiders.' (Reeve: London).

RAINBOW, W.J. & PULLEINE, R.H. 1918. Australian trap-door spiders. Records of the Australian Museum 12: 81-169.

RAVEN, R.J. 1984. Systematics of the Australian Curtain-web spiders (Ischnothelinae: Dipluridae:

Chelicerata). Australian Journal of Zoology, Supplementary Series 93: 1-102.
1985. The spider infraorder Mygalomorphae (Araneae): cladistics and systematics). Bulletin of the American Museum of Natural History 182: 1-180.
1986. A revision of the spider genus *Sason* Simon (Sasoninae, Barychelidae, Mygalomorphae) and its historical biogeography. Journal of Arachnology 14: 47-70.
RAVEN, R.J. & CHURCHILL, T.B. 1991. A revision of the mygalomorph spider genus *Encyocrypta* Simon in New Caledonia (Araneae Barychelidae). In Chazeau, J. & Tillier, S. (eds). 'Zoologia Neocaledonica 2.' Memoires du Museum National d'Histoire Naturelle, Paris (A) 149: 31-86.
TRUSWELL, E. 1990. A curious and diverse flora. Pp. 25-31. In Neville, S. (ed.) 'The Australian environment, taking stock looking ahead.' (Australian Conservation Foundation: Canberra).

INTRASPECIFIC PREDATION IN *CLUBIONA CORTICALIS* (ARANEAE: CLUBIONIDAE)

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Marc, P. 1993 11 11: Intraspecific predation in *Clubiona corticalis* (Araneae: Clubionidae) *Memoirs of the Queensland Museum* 33(2): 607-614. Brisbane. ISSN 0079-8835.

Clubiona corticalis is supposed to be a useful biological control agent of lepidopteran larvae (e.g. Tortricidae) in orchards. Thus, the levels of its intraspecific predation especially when bred in captivity must be determined. Predation is a risk at mating and dispersal. Cannibalism during mating, studied at 13°C, 20°C and 27°C and without prey in cages, remains low (1.5%) during the first 24 hours at all temperatures. After 24 hours cannibalism increased and was significantly higher at 27°C than at 13°C after one week. Males were 72% of the victims. Males can mate twice with different without increasing the risk of cannibalism. The spiders were studied for 12 days after dispersal. Until Day 3, no intraspecific predation occured, whatever the availability of prey for juveniles. Intraspecific predation is very much reduced by the availability of sufficient prey, and a female given prey did not feed on its own progeny. *Clubiona corticalis* pourrait être utilisée en verger pour lutter contre des larves de lépidoptères (Tortricidae). Il était donc important de connaître les niveaux de prédation intraspécifique chez cette espèce, lorsqu'elle est élevée en captivité. Il est montré qu'il y a des risques de prédation à deux moments du développement: l'accouplement et la dispersion. Le cannibalisme durant l'accouplement, étudié à 13°C, 20°C et 27°C sans proie dans les enceintes, reste faible à toutes les températures (1.5%) pendant les premières 24 heures. Après 24 heures, le cannibalisme augmente. Il est significativement plus fort à 27°C qu'à 13°C après une semaine. Les mâles sont les victimes dans 72% des cas et peuvent s'accoupler deux fois avec des femelles différentes sans augmenter les risques de cannibalisme. Les jeunes araignées sont étudiées pendant douze jours après la dispersion. Quelle que soit la disponibilité en proies, aucun cas de prédation intraspécifique n'intervient jusqu'au troisième jour. Ensuite, la disponibilité en proies dimunue de façon très significative le niveau de canabalisme. A noter qu'une femelle disposant de proies, n'exerce aucune prédation sur sa progéniture.□*Biology, Europe, laboratory, Araneae, France, breeding, auxiliary, intraspecific predation, Clubiona corticalis, dispersal, mating.*

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Clubionids are wandering, nocturnal spiders (Marc, 1990a), and certain species are efficient in caterpillar control in orchards (Mansour *et al.*, 1980; Marc and Canard, 1989). The study of the arachnofauna in apple orchards led us to take an active interest in whether *Clubiona corticalis* (Walckenaer) can be used in biological control of pest caterpillars. In the laboratory, all instars of *C. corticalis* can consume large quantities of lepidopteran larvae, especially tortricids, harmful to orchards (Marc, unpublished data). However, the efficacy of using *C. corticalis* in biological control remains uncertain. Spiders are generally envisaged as having high rates of intraspecific and interspecific predation (Bristowe, 1958; Greenstone, 1978). If this is true for *C. corticalis*, then its effectiveness in biological control would be reduced, i.e., an increase in spider densities in the field would increase cannibalism. Thus, data on rates of cannibalism in *C. corticalis* are needed.

In *Anyphaena accentuata* (Walckenaer), *Philodromus cespitum* (Walckenaer) and *Diaea dorsata* (Fabricius) (the most abundant non-web spinning spiders in apple orchards), intraspecific and interspecific recognition minimizes cannibalism (Marc, 1992). Whether this is true of *C. corticalis* is not known. *C. corticalis* occurs in very high densities on pines (Marc, 1990b) where they build silk nests under bark for refuge during the day (Marc, 1990a). Partially flaking bark are favoured shelters on which concentrations of 6-12 nests can be found in 10-15cm^2 (often the clustered nests are stuck together). Furthermore, nests of other clubionids, *Clubiona brevipes* Blackwall, *C. leucaspis* Simon and *Ceto laticeps* (Canestrini), often adjoin those of *C. corticalis*. These aggregations suggest low intraspecific and interspecific predation in nature. However, laboratory bred spiders for use as auxiliaries may present special problems. In captivity, intraspecific predation at critical moments of develop-

ment may be artificially high because contact between individuals is more frequent. Mating and dispersal are likely to be critical periods (Fig. 1). This work determines levels of cannibalism in *C. corticalis* when bred in captivity.

MATERIALS AND METHODS

Subadult spiders (one instar before maturity) were collected in winter, in a forest under the bark of *Pinus sylvestris*. Removed from the field in Ependorff micro-tubes, they were separated into males (recognisable at this instar by a bulging palpal tarsus) and females. Each individual was then placed in Petri dishes (9 cm in diameter and 1.5 cm high) for breeding. Damp cotton wool kept humidity high in cages. Individuals were fed with two flies (*Lucilia*, Diptera) three times per week. Unless otherwise specified all procedures and observations where carried out in the laboratory. All enclosures are here referred to as 'cages'.

Cannibalism during Mating

In each of 135 Petri dishes, one male was placed with a virgin female, and no food was added for the week of the experiment. Breeding cages were kept at 13°C, 20°C and 27°C under long photoperiod (L-D=16-8), and were observed several times a day. Males and females used for mating had all moulted to adults at least two weeks before.

Cannibalism After Dispersal

Dispersal, in this species, is when the juveniles at instar 2 leave the female's breeding-nest. Cannibalism, from dispersal (when the first juvenile leaves the breeding-nest) for 12 days was observed on eight egg masses from mating carried out. The egg masses were inside the female's cages (25ml Petri dishes). These observations were carried out at 20°C and in a L:D photoperiod of 16:8. Two groups of 4 egg masses each were set up:

- no prey for the juveniles. In two cages the female had been separated from her progeny.
- *Drosophila* provided for juveniles. The female was taken out of one dish.

Lucilia were given to the females left in the cages every day from the second day after the dispersal of the first of the juveniles. The caged spiders were observed 2-3 times a day for 12 days and the status–alive, death by cannibalism, or death by other causes, or still inside the nest–recorded.

RESULTS AND DISCUSSION

Cannibalism during Mating

In the final moult the reproductive organs are completely formed. Trophic, and locomotory activities and very different behaviour in two sexes of the *C. corticalis* species also appear (Marc, 1992). In the field, males become adults about 10 days before females (Marc, unpublished data). Males then seek females, inside whose nests mating takes place. Because of this asynchrony of maturity, males frequently mate with females soon after the latter moult and at which time females do not feed; they remain in their nest without feeding for 1-2 days after moulting (Marc, 1990a). These two days appear, therefore, to be an especially favourable time for the male to mate because, during this time, the female is only slightly aggressive. Males may also build a nest adjoining those of the subadult females and thus fertilise them soon after the final moult. This was also observed by Austin (1984) in *C. robusta* L. Koch and by Wolf (1990) in *Cheiracanthium pennyi* Cambridge and *Cheiracanthium punctorium* (Villers). The mating of many other species takes place just after the final moult of females. Jackson (1980a) reported that 161 species use tactics of cohabitation (the male stays with the immature female to mate with her after she has undergone her adult moult).

Here, successful mating could be obtained several weeks after the final moult of both sexes. The male approaches the female by tapping on her nest. Copulation, which takes place inside the female's nest, lasts for about 3 hours. The male, mounted on the female's back and facing the same direction, forms an angle of about 45° to her. From this position, he applies each palp consecutively into her epigyne. One male can fertilize the eggs of at least 3-4 females. Mating can also take place outside the female's nest without cannibalism. On the other hand, in other species, intraspecific interactions outside the nest were more 'lethal' (Jackson, 1988a; Jackson and Macnab, 1989).

Intraspecific predation was observed in 13% of the cases for all matings (Fig. 2). The most favourable conditions to reduce the risks of cannibalism during mating would have been to place the males in the female's cages just after the female's moulted, or, at least, in the presence of prey. Yet, here, males were brought to females which had moulted at least 15 days before. Furthermore, no food was provided. Because, to be practicable for production of auxiliary popula-

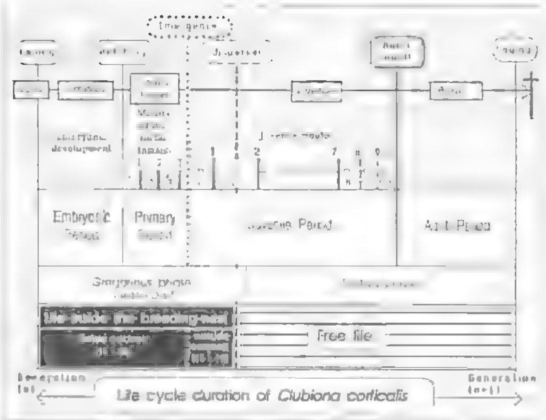

FIG. 1. Life cycle of *Clubiona corticalis*. Terminology in Canard (1987). *In.1*, *in.2* and *in.3* indicate the foetal instars, and in.1 to in.10 the juvenile ones (last juvenile instars, 9 and 10, not present in every individual). Numbers in parentheses indicate duration in days. * (2-3) refer to Time spent by juveniles close to breeding-nest just after dispersal.

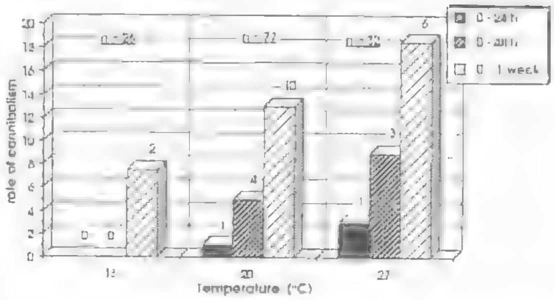

FIG. 2. Intraspecific predation rate during mating experiment on *C. corticalis* without prey at 13, 20 and 27°C. Symbols indicate the period of predation; n = no. of pairs tested; values on histogram bars =no. cases recorded.

tions for biological control, the time needed for care during laboratory breeding must be minimal. Synchronized mating was more practicable. Likewise, the absence of prey in the mating cages simplifies the work. Cannibalism observed after one week (13%) was very much higher than that in the field.

Predation before 24 hours, whatever the temperature, were rare (1.5%) (Fig. 2), but thereafter increased with time and after one week the rate of cannibalism was significantly lower (p) at a lower temperature (7.5% at 13°C and 18.5% at 27°C).

The spider's activity is probably related to the temperature. Indeed, locomotory activity increases with temperature and greatly increases the probability of interindividual encounters and, therefore, the risks of aggressiveness, especially in the absence of prey.

Cannibalism in 24 hours was rare, whatever the temperature, even though the trophic needs of females, especifically after adult moulting, must be high considering ovule production. This can be explained simply by the smaller need for food after only one day of fasting, when this time is sufficient to guarantee mating. Indeed, the pairing time was quite short. Within 5 hours of the individuals being brought together, 75% of the matings had begun, and mating itself lasted 3 hours. We observed, however, that one male could mate several times with the same female which lengthens the interaction, but it seems that this has no effect on the number of egg masses or on the descendants produced by the female. At 13°C no intraspecific predation occurred before 48 hours, and the females were fertilized normally and laid fertile eggs in the same way as at 20°C and 27°C.

In all pairs where intraspecific predation occurred once in the week after the start of the experiment, males are more often (72%) the victim. We did not observe a relation between weight and the individuals eaten, and sometimes smaller individuals ate larger ones. There is no significant sexual dimorphism in *C. corticalis*.

In contrast, even though size is not important, males do move more than females (Marc, 1990a). Conceivably, this weakens males relative to similar sized females. Furthermore, males who have smaller trophic needs and mate several times with different females display less aggressiveness towards their partners. This may partly explain why males were more often the victims of cannibalism.

A male can mate once or twice without significantly increasing the rate of cannibalism after one week (9% for one mating and 14% for two matings; $p>0.05$). However, after two further matings (3 or 4), intraspecific predation increases significantly to 33% ($p<0.05$) if compared to a male which mated only once. However, the male is not always the victim.

In *C. reichlini* Schenkel, males and females can mate several times without cannibalism (Hengmei and Hongquan, 1987). Equally, in interactions of *C. cambridgei* L. Koch, no cannibalism occurred between virgin males and females during the 38 interactions studied (Pollard and Jackson, 1982). Generally, species of *Clubiona* do not seem to be very aggressive

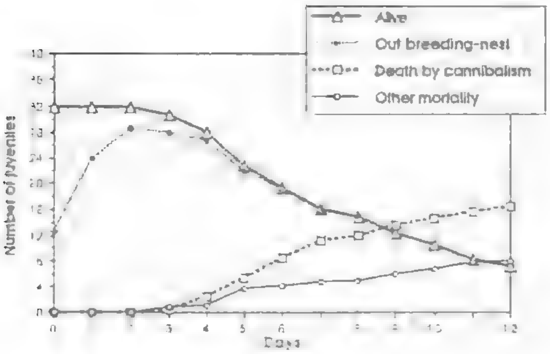

FIG. 3. Survival of juveniles (2nd instar) of *C. corticalis* during 12 days after dispersal, without prey.

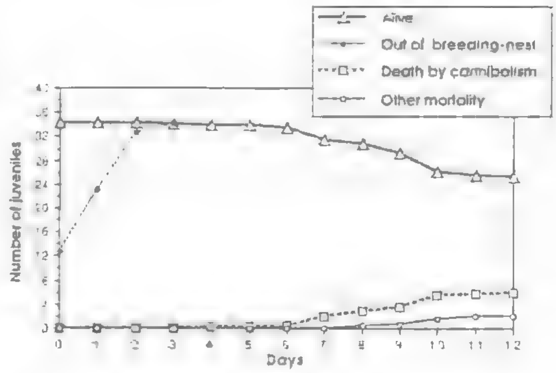

FIG. 4. Survival of juveniles (2nd instar) of *C. corticalis* in the presence of prey.

toward each other during mating. Apparently, to eliminate cannibalism in *C. corticalis,* males and females should be brought together at about 13°C and individuals should be kept paired for about 24 hours. Furthermore, the presence of prey at 13°C should make the cohabitation of males and females perfectly feasible for several days without intraspecific predation occurring. Such conditions during mating should minimize the manpower needed and lower production costs.

Cannibalism After Dispersal

Juveniles leave the breeding-nest, built by the female, after 1-4 days. Then, they remain grouped around the nest for about 2-3 days before dispersal. This gregarious phase lasts 17-20 days at 20°C (15-17 days in the breeding-nest and 2-3 days around the nest) (Fig. 1). It is only from the juvenile instar 2 (as defined by Canard, 1987), that juveniles begin to hunt. Until leaving the breeding-nest juveniles use on their vitelline reserves and, some attack the undeveloped eggs in the nest. Indeed, weight differences between juveniles leaving the breeding-nest indicate the existence of trophic activity in some individuals, as there are no significant weight differences known to occur between eggs in the same batch in the spider (Lecaillon, 1905). Furthermore, this trophic activity does not seem linked to the female feeding her juveniles by regurgitation or the consumption by the juveniles of a trophic egg-mass as, for example, in *Amaurobius* (Amaurobiidae) (Tahiri *et al.*, 1989). At this point, mortality is the highest in many species (Austin, 1984). It may be even more delicate in a captive breeding situation as the juveniles, in large numbers in the cages, would devour each other.

The dispersal of the juveniles given prey can spread over 4 days (Fig. 3). There was no significant difference between the cages with a female and those with one removed ($p>0.05$). Thus, females did not attack their own progeny after dispersal for at least the first 12 days and on the condition that prey was available. Cannibalism between the juveniles first began 3-4 days after the first dispersal and coincided with the expression of the first agonistic behaviour observed. Next, the number of juveniles decreased until there are about 10 individuals per cage towards the eleventh day.

When the juveniles were fed *Drosophila* (Fig. 4), the female's influence on this period of her progeny's development was similar. On the other hand, intraspecific predation was almost non-existant in the first 6 days and continued to be minimal afterwards, being about 5% after 10 days. There is a highly significant difference between the two groups after the 12 days of study ($p<0.001$). Thus, with prey in the breeding cage, cannibalism decreased and was almost eliminated. Rypstra (1983), likewise, found in several spider species that intra-individual tolerance increased and cannibalism decreased when maintained at extremely high prey levels. Also, Krafft *et al.* (1986) were able to prolong the juvenile social period by giving juveniles abundant food. Austin (1984) recorded a high mortality in the breeding of *C. robusta*, cannibalism being one of the two major causes of mortality. On the other hand, in nature, spiders, which are potential prey of the highest density in the environment, only represented only 3% of prey actually consumed (Austin, 1984). Austin suggested that the highest mortality occurs at the dispersal instar.

The rest of the development presents fewer

Fam	Genus or species	Authority
Club	*Supunna picta*	Jackson & Poulsen (1990)
Gnap	*Taieria erebus*	Jarman & Jackson (1985)
Liny	*Oedothorax insecticeps*	Kiritani *et al.* (1972)
Lyco	*Lycosa pseudoannulata*	Kiritani *et al.* (1972)
	Pardosa lugubris	Edgar (1969)
	P. purbeckensis	Schaefer (1974)
	P. ramulosa	Yeargan (1975)
	Pirata piraticus	Schaefer (1974)
Mime	*Ero aphana**, *E. furcata**	Gerhardt (1924), Bristowe (1941), Czajka (1963), Canard (1984)
	*Mimetus maculosus**, *M.* sp.*	Jackson & Whitehouse (1986)
Oxyo	*Peucetia viridans*	Turner (1979)
Phol	*Holocnemus pluchei*	Blanke (1972)
	*Pholcus phalangioides**	Jackson & Brassington (1987), Jackson & Rowe (1987)
Salt	*Brettus adonis*°*, *B. cingulatus*°*	Jackson & Hallas (1986a)
	Cocalus gibbosus	Jackson (1990b)
	Cobanus mandibularis	Jackson (1989)
	Cyrba algerina°*	Jackson & Hallas (1986a)
	C. ocellata°*	Jackson (1990c)
	Euryattus sp.	Jackson (1985a)
	Gelotia sp.°*	Jackson (1990d)
	Jacksonoides queenslandica°	Jackson (1988a)
	Phaeacius malayensis, *P.* sp.	Jackson & Hallas (1986a), Jackson (1990a)
	Plexippus paykulli	Jackson & Macnab (1989)
	Phidippus johnsoni	Jackson (1977)
	Portia°*	Jackson & Hallas (1990)
	Portia fimbriata°*	Jackson (1982a, 1986b), Jackson & Blest (1982), Jackson & Hallas (1986b), Jackson & Wilcox (1990)
	P. africana°*, *P. albimana*°*	Jackson & Hallas (1986b)
	P. labiata°*, *P. shultzi*°*	Jackson & Hallas (1986b)
	Simaetha paetula	Jackson (1985b)
	Tauala lepidus	Jackson (1988b)
Scyt	*Scytodes longipes*	Nentwig (1985)
Ther	*Achaearanea camura*	Jackson (1988b)
	Achaearanea tepidiorum	Rypstra (1986)
	Rhomphaea	Enders (1974)

TABLE 1: Literature review of araneophagic spiders: species principally or strongly araneophagic. *, 'aggressive mimicry' = to perform a variety of vibratory behaviour in which the prey-spider responded as it normally would to its own prey. °, oophagy.

problems of cannibalism. Six groups of juveniles were bred together with 5 per Petri dish from instar 2-6 and no cannibalism was noted. Furthermore, the periodic absence of prey during a few days (3-5) in the cages did not result in intraspecific predation, but behaviour of escape and avoidance was observed. Similar observations had been made on sub-adults and adult females bred at 25-30 individuals per cage (30×20×20 cm) over 2 months.

Therefore, in breeding *C. corticalis*, the provision of *Drosophila* to juveniles at the dispersal stage should be sufficient to eliminate intraspecific predation. Then, 5 days after dispersal when all juveniles are out of the breeding-nest and no cannibalism has occured, the division of these juveniles at instar 2 with about 5 per Petri dish, should prevent cannibalism later.

Family	Genus or species	Authority
Anyphaenidae	*Anyphaena accentuata*	Marc (1992)
Heteropodidae	*Olios diana*[k], *O. lamarcki*[k], *O. obesulus* *O.* sp.	Jackson (1987)
Hexathelidae	*Porrhothele antipodiana*	Jackson & Pollard (1990)
Philodromidae	*Philodromus cespitum*	Marc (1992)
Salticidae	*Holoplatys* sp.	Jackson & Harding(1982)
	Myrmarachne lupata	Jackson (1982b)
Thomisidae	*Diaea dorsata*	Marc (1992)

TABLE 2: Literature review of araneophagic spiders: species which are little or not araneophagic. [k], species kleptoparasitic which are not araneophagic.

CONCLUSIONS

Intraspecific predation in *C. corticalis* during two especially susceptible periods of development (mating and dispersal) involves limited risks of cannibalism which can be eliminated. Mating must be at 13°C. Males in the enclosures with females must be limited to 24 hours, and dispersing juveniles must have sufficient prey. Cannibalism should not, therefore, be an obstacle to the mass breeding of this species for biological control.

Rates of intraspecific and interspecific predation have often been considered very high in spiders. The main enemies of spiders are often other spiders (Bristowe, 1941; Foelix, 1982). Certain species partially practice araneophagy (e.g. *Pardosa lugubris* (Walck-enaer), *Lycosa annulata* Thorell), and a few make it their speciality (e.g. *Mimetus*, *Ero*, *Portia*) (Table 1). In fact, the species most studied for cannibalism are araneophagic in nature. In contrast, in other species, araneophagy appears to be almost non-existant (Table 2) even without prey (e.g. *Anyphaena accentuata*, *C. corticalis*, *Diaea dor-*

sata, *Philodromus cespitum*) and it is absent in social spiders such as *Mallos gregalis* (Simon) (Jackson, 1979, 1980). Behaviour of a few spider species cannot be applied to all. The degree of araneophagy of a species must be based on only that one. Therefore, the levels of intraspecific and interspecific predation amongst the more abundant species in agrosystems in which a spider is a possible biological control agent must be studied. A simple method has been finalised for spiders which do not spin a web (Marc, 1992).

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LITERATURE CITED

AUSTIN, A.D. 1984. Life history of *Clubiona robusta* L. Koch and related species (Araneae, Clubionidae) in South Australia. Journal of Arachnology 12: 87-104.

BLANKE, R. 1972. Untersuchungen zur Ökophysiologie und Ökethologie von *Cyrtophora citricola* Forskal (Araneae, Araneidae) in Andalusien. Forma Function 5: 125-206.

BRISTOWE, W.S. 1941. 'The Comity of Spiders'. Vol. 2. (Ray Society: London).

1958. The Clubionoidea - Gnaphosidae, Clubionidae and Anyphaenidae. Pp. 116-132. In, 'The World of Spiders'. Ed. Collins (revised 1971).

CANARD, A. 1984. Contribution à la connaissance du développement, de l'écologie, et de l'écophysiologie des Aranéides de landes armoricaines. (Thèse de Doctorat Etat, Rennes, 389pp + annexe).

1987. Analyse nouvelle du développement postembryonnaire des araignées. Revue Arachnologique 7: 91-128.

CZAJKA, M. 1963. Unknown facts of the biology of the spider *Ero furcata* (Villers) (Mimetidae, Araneae). Polskie Pismo Entomologiczne 33: 229-231.

ENDERS, F. 1974. Vertical stratification in orb-web spiders (Araneidae: Araneae) and a consideration of other methods of coexistence. Ecology 55: 317-328.

EDGAR, W.D. 1969. Preys and predators of the wolf spider *Lycosa lugubris*. Journal of Zoology (London) 159: 405-411.

FOELIX, R.F. 1982. 'The Biology of Spiders'.(Harvard University Press: Cambridge, Mass).

GERHARDT, U. 1924. Weitere studien über die biologie der spinnen. Archiv für Naturgeschichte 90: 85-192.

GREENSTONE, M.H. 1978. The numerical response to prey availability of *Pardosa ramulosa* (McCook) (Araneae: Lycosidae) and its relationship to the role of spiders in the balance of nature. Symposium of the Zoological Society of London 42: 183-193.

HENGMEI, Y. & HONGQUAN, W.B. 1987. A study on the biology of the spider *Clubiona reichlini*. Acta Zoologica Sinica 33: 255-261.

JACKSON, R.R. 1977. Prey of the jumping spider *Phidippus johnsoni* (Araneae: Salticidae). Journal of Arachnology 5: 145-149.

1979. Comparative studies of *Dictyna* and *Mallos* (Araneae, Dictynidae). II. The relationship between courtship, mating, aggression and cannibalism in species with differing types of social organization. Revue Arachnologique 2: 103-132.

1980. Comparative studies of *Dictyna* and *Mallos*: V. Tolerance and resistance to starvation. Psyche 87: 211-220.

1982a. The biology of *Portia*, a web-building jumping spider (Araneae, Salticidae) from Queensland: intraspecific interactions. Journal of Zoology (London) 196: 295-305.

1982b. The biology of ant-like jumping spiders: intraspecific interactions of *Myrmarachne lupata* (Araneae, Salticidae). Zoological Journal of the Linnean Society 76: 293-219.

1985a. The biology of *Euryattus* sp. indet., a web-building jumping spider (Araneae, Salticidae) from Queensland: utilization of silk, predatory behaviour and intraspecific interactions. Journal of Zoology (London) 1: 145-173.

1985b. The biology of *Simaetha paetula* and *S. thoracica*, web-building jumping spiders (Araneae, Salticidae) from Queensland: cohabitation with social spiders, utilization of silk, predatory behaviour and intraspecific interaction. Journal of Zoology (London) 1: 175-210.

1986a. Cohabitation of males and juvenile females: a prevalent mating tactic of spiders. Journal of Natural History 20: 1193-1210.

1986b. Web building, predatory versatility, and the evolution of the Salticidae. Pp. 232-267. In, Shear, W.A. (ed.), 'Spiders: Webs, Behavior, and Evolution'. (Stanford University Press: Stanford)

1987. The biology of *Olios* spp., huntsman spiders (Araneae, Sparassidae) from Queensland and Sri Lanka: predatory behaviour and cohabitation with social spiders. Bulletin of the British Arachnological Society 7: 133-136.

1988a. The biology of *Jacksonoides queenslandica*, a jumping spider (Araneae: Salticidae) from Queensland: intraspecific interactions, web-invasion, predators, and prey. New Zealand Journal of Zoology 15: 1-37.

1988b. The biology of *Tauala lepidus*, a jumping spider (Araneae: Salticidae) from Queensland: display and predatory behaviour. New Zealand Journal of Zoology 15: 347- 364.

1989. The biology of *Cobanus mandibularis*, a jumping spider (Araneae: Salticidae) from Costa Rica: intraspecific interactions, predatory behaviour, and silk utilisation. New Zealand Journal of Zoology 16: 383-392.

1990a. Ambush predatory behaviour of *Phaeacius malayensis* and *Phaeacius* sp. indet., spartaeine jumping spiders (Araneae: Salticidae) from tropical Asia. New Zealand Journal of Zoology 17: 491-498.

1990b. Predatory and nesting behaviour of *Cocalus gibbosus*, a spartaeine jumping spider (Araneae: Salticidae) from Queensland. New Zealand Journal of Zoology 17: 483-490.

1990c. Predatory versatility and intraspecific interactions of *Cyrba algerina* and *Cyrba ocellata*, web-invading spartaeine jumping spiders (Araneae: Salticidae). New Zealand Journal of Zoology 17: 157-168.

1990d. Predatory and silk utilisation behaviour of *Gelotia* sp. indet. (Araneae: Salticidae: Spartaeinae), a web-invading aggressive mimic from Sri Lanka. New Zealand Journal of Zoology 17: 475-482.

JACKSON, R.R. & BLEST, A.D. 1982. The biology of *Portia fimbriata*, a web-building jumping spider (Araneae, Salticidae) from Queensland: utilization of webs and predatory versatility. Journal of Zoology (London) 196: 255-293.

JACKSON, R.R. & BRASSINGTON, R.J. 1987. The biology of *Pholcus phalangioides* (Araneae, Pholcidae): predatory versatility, araneophagy and aggressive mimicry. Journal of Zoology (London) 211: 227-238.

JACKSON, R.R. & HALLAS, S.E.A. 1986a. Predatory versatility and intraspecific interactions of spartaeine jumping spiders (Araneae: Salticidae): *Brettus adonis*, *B. cingulatus*, *Cyrba algerina*, and *Phaeacius* sp. indet. New Zealand Journal of Zoology 13: 491-520.

1986b. Comparative biology of *Portia africana*, *P. albimana*, *P. fimbriata*, *P. labiata*, and *P. shultzi*, araneophagic, web-building jumping spiders (Araneae: Salticidae): utilisation of webs, predatory versatility, and intraspecific interactions. New Zealand Journal of Zoology 13: 423-489.

1990. Evolutionary origins of displays used in aggressive mimicry by *Portia*, a web-invading araneophagic jumping spider (Araneae: Salticidae). New Zealand Journal of Zoology 17: 7-23.

JACKSON, R.R. & HARDING, D.P. 1982. Intraspecific interactions of *Holoplatys* sp. indet., a New Zealand jumping spider (Araneae: Salticidae). New Zealand Journal of Zoology 9: 487-510.

JACKSON, R.R. & MACNAB, A.M. 1989. Display, mating, and predatory behaviour of the jumping spider *Plexippus paykullii* (Araneae: Salticidae). New Zealand Journal of Zoology 16: 151-168.

JACKSON, R.R. & POLLARD, S.D. 1990. Intraspecific interactions and the function of courtship in mygalomorph spiders: a study of *Porrhothele antipodiana* (Araneae: Hexathelidae). New Zealand Journal of Zoology 17: 499-526.

JACKSON, R.R. & POULSEN, B.A. 1990. Predatory versatility and intraspecific interactions of *Supunna picta* (Araneae: Clubionidae). New Zealand Journal of Zoology 17: 169-184.

JACKSON, R.R. & ROWE, R.J. 1987. Web-invasion and araneophagy by New Zealand and Australian pholcid spiders. New Zealand Journal of Zoology 14: 139-140.

JACKSON, R.R. & WHITEHOUSE, M.E.A. 1986. The biology of New Zealand and Queensland pirate spiders (Araneae, Mimetidae): aggressive mimicry, araneophagy and prey specialization. Journal of Zoology (London) (A), 210: 279-303.

JACKSON, R.R. & WILCOX, R.S. 1990. Aggressive mimicry, prey-specific predatory behaviour and predator-recognition in predator-prey interactions of *Portia fimbriata* and *Euryattus* sp., jumping spiders from Queensland. Behaviour Ecology and Sociobiology 26: 111-119.

JARMAN, E.A.R. & JACKSON, R.R. 1985. The biology of *Taieria erebus* (Araneae, Gnaphosidae) an araneophagic spider from New Zealand: silk utilization and predatory versatility. New Zealand Journal of Zoology 13: 521-541.

KIRITANI, K., KAWAHARA, S., SASABA, T. & NAKASUJI, F. 1972. Quantitative evaluation of predation by spiders on the green rice leafhopper, *Nephotettix cinticeps* Uhler, by a sight-count method. Researches on Population Ecology, Kyoto University 13: 187-200.

KRAFFT, B., HOREL, A. & JULITA, J.M. 1986. Influence of food supply on the duration of the gregarious phase of a maternal-social spider, *Coelotes terrestris* (Araneae, Agelenidae). Journal of Arachnology 14: 219-226.

LECAILLON, A. 1905. Nouvelles recherches sur la biologie et la psychologie des *Chiracanthion*. Bulletin de l'Association Philomatique d'Alsace et de Lorraine 7: 224-252.

MANSOUR, F., ROSEN, D., SHULOV, A. & PLAUT, H.N. 1980. Evaluation of spiders as biological control agents of *Spodoptera littoralis* larvae on apple in Israël. Acta Oecologica, Oecologia Applicata 1: 225-232.

MARC, P. 1990a. Nycthemal activity rhythm of adult *Clubiona corticalis* (Walckenaer, 1802) (Arachnida, Clubionidae). Acta Zoologica Fennica 190: 279-285.

1990b. Données sur le peuplement d'Aranéides des troncs de pins. C.R. XII Coll. Européen d'Arachnologie, Paris (1): 255- 260.

1992. Intraspecific and interspecific interactions between spiders from apple orchards. Comptes Rendu XIII Coll. Européen d'Ararachnologie, Neuchâtel (Suisse).

MARC, P. & CANARD, A. 1989. Les essais d'utilisation des Araignées en lutte biologique.

Bulletin de la Société Scientifique de Bretagne 14: 149-172.
NENTWIG, W. 1985. Feeding ecology of the tropical spitting spider *Scytodes longipes* (Araneae, Scytodidae). Oecologia (Berlin) 65: 284-288.
1986. The prey of spiders. Pp. 249-264. In, W. Nentwig (ed.), 'Ecophysiology of Spiders'. (Springer-Verlag: Berlin).
POLLARD, S.D. & JACKSON, R.R. 1982. The biology of *Clubiona cambridgei* (Araneae: Clubionidae): intraspecific interactions. New Zealand Journal of Ecology 5: 44-50.
RYPSTRA, A.L. 1983. The importance of food and space in limiting web-spider densities; a test using field enclosures. Oecologia (Berlin) 59: 312-316.
1986. High prey abundance and a reduction in cannibalism: the first step to sociality in spiders (Arachnida). Journal of Arachnology 14: 193-200.
SCHAEFER, M. 1974. Experimentelle Untersuchungen zur Bedeutung der interspezifischen Konkurrenz bei 3 Wolfspinnen-Arten (Araneae: Lycosidae) einer Salzweise. Zoologische Jahrbücher, Systematik (Ökologie), Geographie und Biologie 101: 213-235.
TAHIRI, A., HOREL, A. & KRAFFT, B. 1989. Etude préliminaire sur les interactions mère-jeunes et jeunes-jeunes chez deux espèces d'*Amaurobius* (Araneae, Amaurobiidae). Revue Arachnologique 8: 115-128.
TURNER, M. 1979. Diet and feeding phenology of the green lynx spider, *Peucetia viridans* (Araneae: Oxyopidae). Journal of Arachnology 7: 149-154.
WOLF, A. 1990. The silken nest of the clubionid spiders *Cheiracanthium pennyi* and *Cheiracanthium punctorium* (Araneae, Clubionidae). Acta Zoologica Fennica 190: 397-404.
YEARGAN, K.V. 1975. Prey and periodicity of *Pardosa ramulosa* (McCook) in alfafa. Environmental Entomology 4: 137-141.

COMPARATIVE MORPHOLOGY OF THE SEXUALLY DIMORPHIC ORB-WEAVING SPIDER *ARGIOPE BRUENNICHI* (ARANEAE: ARANEIDAE)

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Müller, M.C. and Westheide, W. 1993 11 11: Comparative morphology of the sexually dimorphic orb-weaving spider *Argiope bruennichi* (Araneae: Araneidae). *Memoirs of the Queensland Museum* **33**(2): 615-620. Brisbane. ISSN 0079-8835.

Although the web building spigots of the glandulae aggregatae and the glandulae flagelliformes are not functional in mature males, adult *Argiope bruennichi* and *A. lobata* males are able to build webs. The structure of these webs is described. The aciniform spigots on the intermediate spinnerets of *A. bruennichi* males have degenerated to a great extent. Culture experiments with *A. bruennichi* enabled us to follow differences in the development of female and male morphology. The presence of the tubuliform spigots in the sixth instar suggests one possible evolutionary hypothesis concerning sexual dimorphism in spiders.
Nach der Reifehäutung sind die aggregaten und flagelliformen Spulen–welche als Triade die Fangfäden sezernieren–auf den hinteren Spinnwarzen der Männchen nur rudimentär ausgebildet. Trotz dieser Reduktion spannen adulte *Argiope bruennichi* und *A. lobata* Männchen Radnetze, deren Struktur beschrieben wird. Auf den mittleren Spinnwarzen subadulter und adulter *A. bruennichi* Männchen ist ein hoher Prozentsatz der aciniformen Spulen unvollständig ausgebildet. Durch Aufzucht der Wespenspinne war es möglich, morphologische geschlechtsspezifische Unterschiede in der Postembryonalentwicklung festzustellen. Das frühe Auftreten der tubuliformen Spulen im weiblichen Spinnapparat kann als Argument für eine Hypothese zur Evolution des Sexualdimorphismus interpretiert werden. □ *Development, sexual size dimorphism, spinning apparatus, male orb-webs, tubuliform spigot.*

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Sexual dimorphism varies across taxa, but the question of whether highly dimorphic species occur as a result of selection for large female or small male size remains controversial.

Gerhardt (1924) observed that both carnivorous feeding habits and cannibalism endanger male spiders before, during and after copulation (Elgar and Nash, 1988). Darwin (1890) and Bristowe (1929) suggested that their small size protects the males from the females which do not recognize males of reduced size as prey. In contrast, Gerhardt (1924) and Vollrath (1980) argue that 'the females have evolved to be larger, allowing greater egg production' (Vollrath, 1980: 165).

Morphological investigations of sexual size dimorphism are rare; for example Sekiguchi (1955a, b) compared the spinning apparatus in male and female spiders. The present investigation examines whether or not there are morphological data that could be used to assess these different ideas, by analysing the spinning apparatus in different instars of *Argiope bruennichi*.

MATERIALS AND METHODS

Adult males and females of *Argiope bruennichi* (Scopoli, 1772) were collected from Dabas (Hungary), and subadult males and cocoons from Wittenberg-Lutherstadt (Germany).

Specimens of *A. bruennichi* were raised individually from the third instar. Some individuals from each instar were fixed in Carnoy's fluid immediately after moulting. The lengths and widths of the prosoma were measured. For SEM studies the spinning apparatus was removed and the spinnerets were dehydrated in ethanol and critical point dried with carbon dioxide. After sputtering with gold, they were analysed with a Cambridge Stereoscan 250. For light microscopy the spinnerets were separated into smaller pieces and embedded in Swann-fluid.

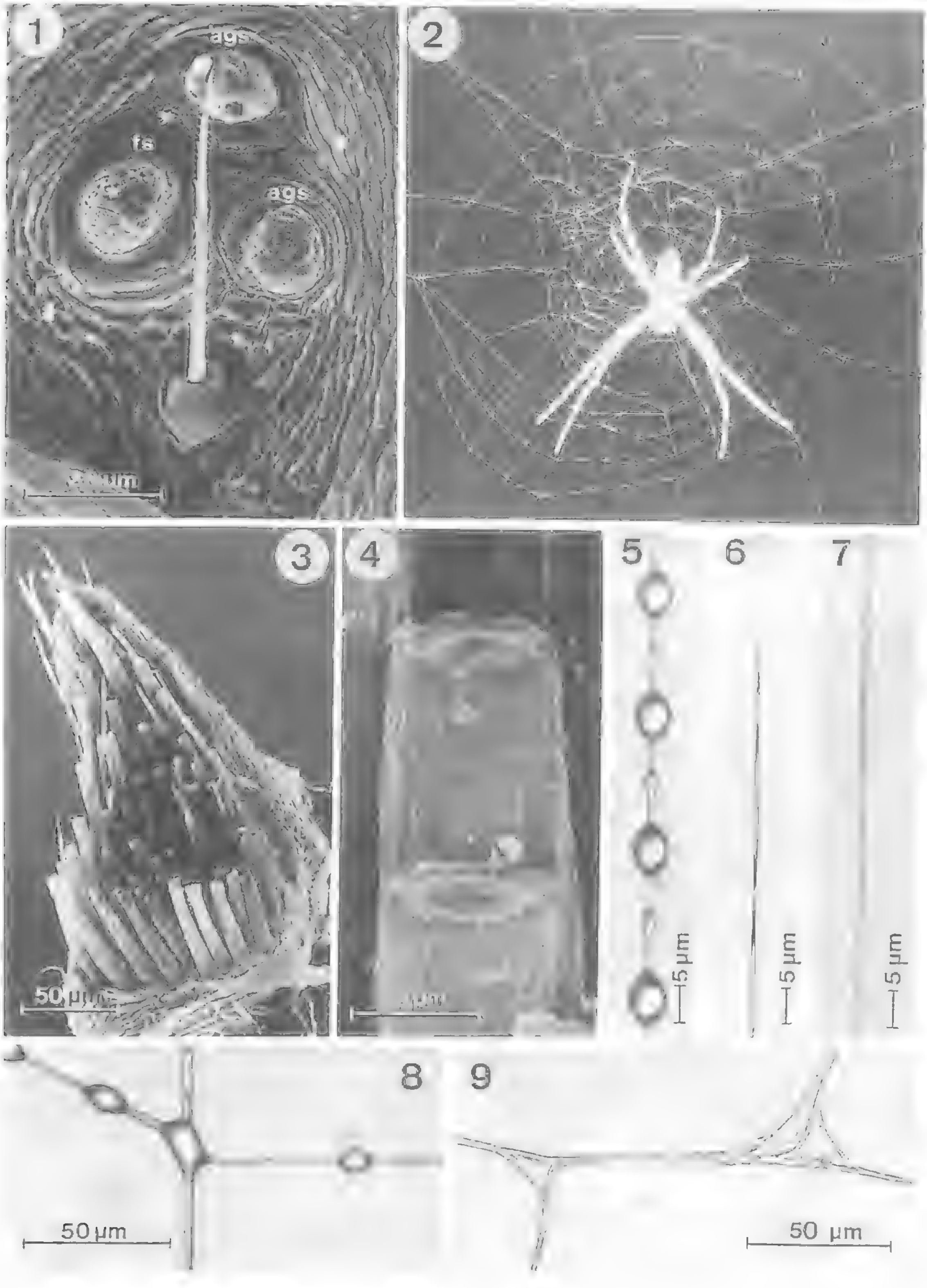
Subadult males of *A. bruennichi* were kept in plexiglass frames from the penultimate stadium until they died.

Early instars were fed with greenflies (Aphidina) and *Drosophila melanogaster* while older stages were provided with various insects captured in the field.

RESULTS

ADULT *ARGIOPE* MALES CAN SPIN WEBS

The posterior spinnerets of adult males are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equipped only with rudimentary projections of the triad spigots (Fig. 1). These aggregate and flagelliform spigots–which usually furnish the capture threads–obviously do not function. Nevertheless, adult males of *A. bruennichi* and *A. lobata* spun rudimentary orb-webs (Fig. 2). These webs were destroyed every day during our study and the spiders renewed them almost daily. Subadult males spun normal orb-webs with the typical stabilimentum until the last moult. Webs spun after the terminal moult were smaller than subadult webs. They showed an irregular structure; but radia and a spiral were present. This spiral consisted of a few turns with remarkably increasing space outwards thus showing a closer resemblance to the auxiliary spiral than to the capture spiral. No droplets adhered to the spiral threads when the spiders were sprayed with water using an atomiser. They seemed to be thinner than capture threads and were not sticky. Prey thrown into the webs did not adhere to the spiral threads. A microscopical investigation revealed that their structure also strongly resembled auxiliary threads (Figs 5-7). The auxiliary nature of the web was confirmed by comparing the connection points of different types of threads with the radia (Figs 8-9).

Intermediate Spinnerets of Adult Males

The number of piriform and aciniform spigots for each sex were counted under the light microscope. There were fewer bases than apical parts of the aciniform spigots in the intermediate spinnerets of males. SEM examinations showed that a surprisingly high number of apical parts were degenerated (Figs 3-4). Only 19.2% (6 individuals) of the aciniform spigots on the intermediate spinnerets were fully developed. This degeneration was less in subadult males.

Postembryonic Development of Body Size

The shape of the opisthosoma changed during the development of *A. bruennichi*. The spherical form changed into an elongated one, reaching the proportion of adult spiders at the sixth instar. This pattern is clearly shown by the length/width-quotient of the opisthosoma in each instar (see Table 1). The development of both prosoma and opisthosoma was nearly uniform for all individuals until the sixth instar, although the intervals between the moults varied (instar III to IV: 17-73 days; instar IV to V: 11-52 days). Following the sixth instar (when subadult males could be first determined) the sexes developed differently (Fig. 15). This pattern of development of sexual dimorphism is less apparent in the prosoma.

	II	III	IV	V	VI	VII	VIII	♂	♀
	1.3	1.4	1.4	1.6	1.9	1.8	2.0	1.9	1.9
S.D.	0.09	0.08	0.04	0.09	-	-	-	0.14	0.56

TABLE 1. *Argiope bruennichi.* Length/width-quotients and standard deviation of the opisthosoma for different instars (II-VIII) and adults (n = 62).

Postembryonic Development of the Spinning Apparatus

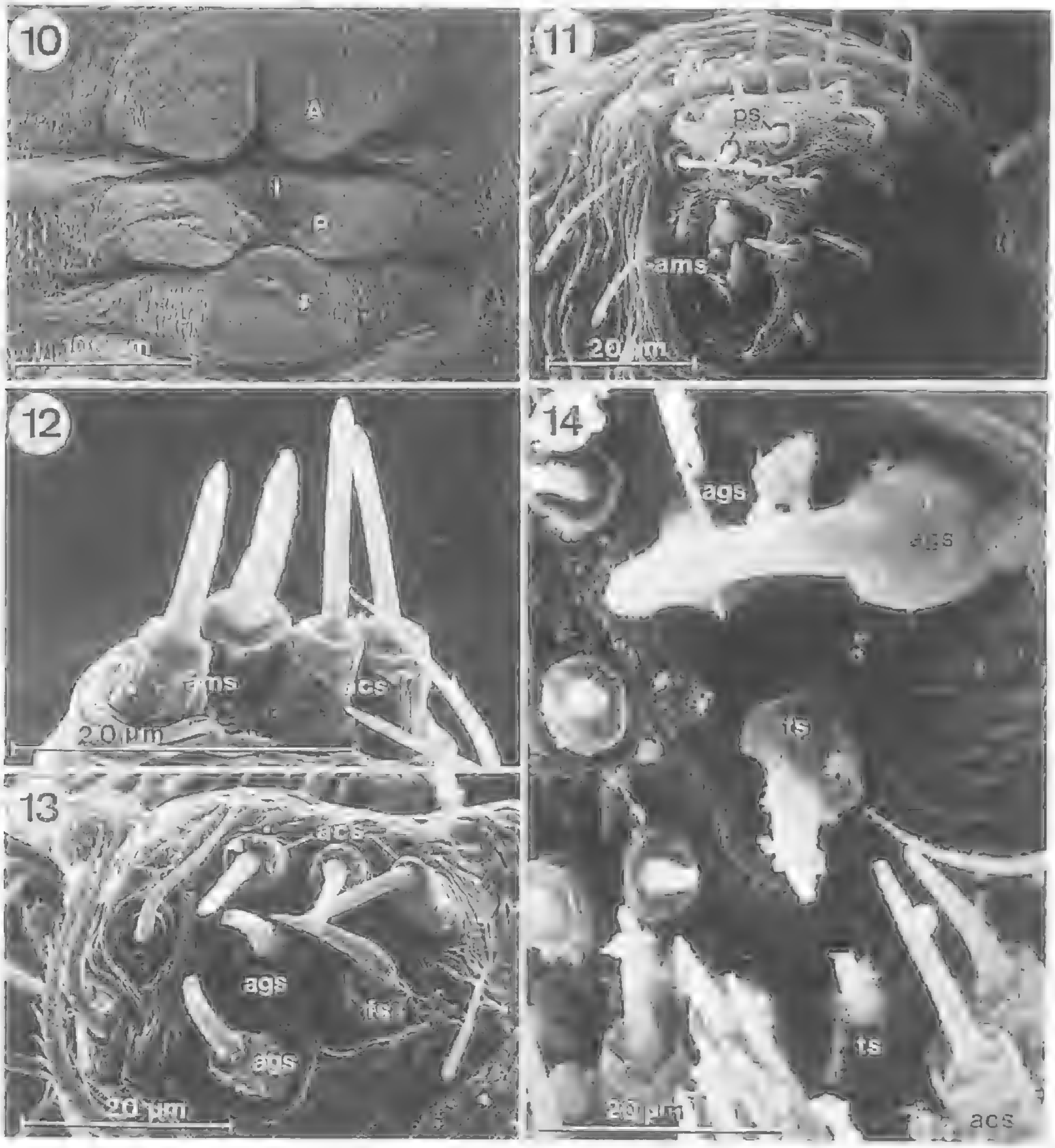
The development of the spinnerets was documented by counting the piriform and aciniform spigots. None of these fusules was found in the second instar (Fig. 10). Six piriform (anterior spinnerets), two aciniform (intermediate spinnerets) and three aciniform spigots (posterior spinnerets) were counted for third instar individuals (Figs 11-13). The development of the spigot number was uniform until the sixth instar. From that stadium on, the sexes developed differently as shown for the aciniform spigots on the posterior spinnerets (Fig. 16). Although the anterior and intermediate spinnerets develop in the same way (Fig. 16), the differentiation of the sexes is less obvious.

Tubuliform spigots were also first observed in the sixth instar of female spiderlings (Fig. 14).

DISCUSSION

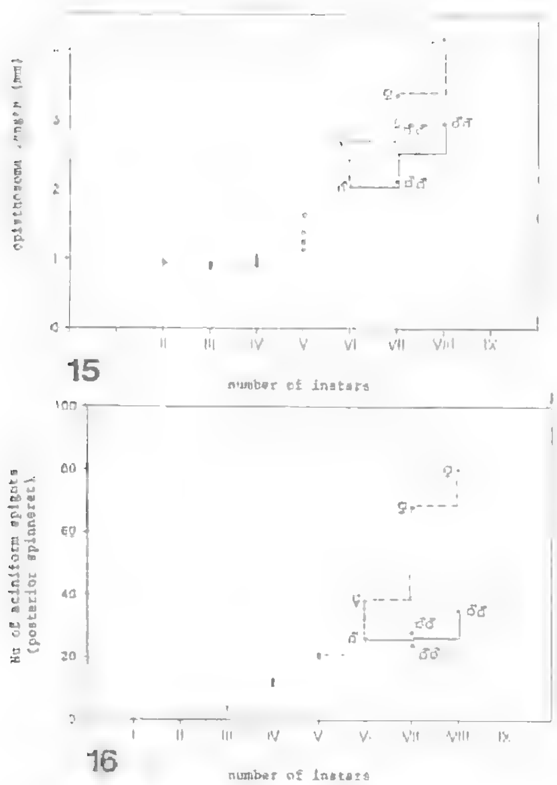
The degeneration of the triad spigots on male posterior spinnerets during the terminal moult was first described by Sekiguchi (1955b) and subsequently documented for other species. These morphological reductions in males were explained by changes in their behaviour: adult males cease spinning webs and instead search for females. Emerton (1878) and McCook (1890) mentioned that small webs were spun by *Argiope aurantia* males, but no information about the structure of these webs was provided. This study shows that *A. bruennichi* and *A. lobata* males are capable of spinning webs. The spiral threads of

FIGS. 1-9. 1. Triad spigots at posterior spinneret of adult male. Apical parts of aggregate (ags) and flagelliform (fs) spigots missing, bases vestigal. 2. Orb-web of adult *Argiope bruennichi* male. 3. Intermediate spinneret of adult male. Many apical parts of aciniform spigots missing. 4. Detail of 3. 5-9. Different structures of male webs. 5: Capture thread (subadult male); 6: Auxilliary thread (subadult male); 7: Spiral thread (adult male); 8: Junction of a capture thread with a radia; 9: Junction of a spiral thread with a radia.



FIGS 10-14. Developmental stages of spinning apparatus. 10: Second instar; anterior (A), intermediate (I) and posterior spinnerets (P) are undeveloped; 11-13: Third instar; 11: Anterior spinneret with six piriform (ps) and two ampullate (ams) spigots; 12: Intermediate spinneret with two aciniform (acs) and two ampullate (ams) spigots; 13: Posterior spinneret with three aciniform spigots (acs) and the triad (consisting of two aggregate (ags) and one flagelliform (fs) spigots; 14: Detail of posterior spinneret of ♀spiderling at sixth instar. Tubuliform spigot (ts) is clearly to differentiate from aciniform spigots (acs). Note arrangement of triad: aggregate (ags) and flagelliform (fs) spigots stay apart from each other, typical for subadults.

these webs resemble auxiliary threads, and therefore are not furnished by the triad glands which still exist immediately after the last moult (see Sekiguchi, 1955b). The auxiliary thread type was recognized because the threads were not covered with glue droplets. However, it is possible that these threads are not auxillaries: Vollrath and Edmonds (1989) found that the glue is soluble in



FIGS 15-16. Postembryonic development of *Argiope bruennichi*: 15: Opisthosoma length; 16: Number of aciniform spigots at posterior spinneret.

water and Peters and Kovoor (1991) argue that the glue does not necessarily fall into droplets.

It is not clear why adult males produce these rudimentary webs, but their poor design suggests that it is unlikely that they function to catch prey. That adult males rejected food offered with tweezers can support this assumption.

The females in spider genera that exhibit extreme size dimorphism are usually hemisessile. Thus courtship and mating is achieved by male mobility. Male mobility is achieved by using bridging lines and ballooning (Peters, 1990). McCook (1890) described these balloon lines as consisting of quite a number of threads that remain separated from one another, which suggests that they are furnished by the aciniform spigots. The degeneration of these aciniform spigots on the intermediate spinnerets of adult *Argiope bruennichi* males may occur because the remaining spigots are sufficient to produce the balloon lines. Alternatively, these threads may originate from other spigots. If the aciniform spigots of the posterior spinnerets furnish the balloon lines, then their degeneration on the intermediate spinnerets would not disadvantage the males. Since adult males do not depend on the additional function of the aciniform threads (in terms of prey wrapping) their degeneration may be interpreted as a morphological adaptation to an altered style of life.

These results suggest that the development of sexual dimorphism takes place in the sixth instar.

Townley *et al.* (1991) reported tubuliform spigots in *Araneus cavaticus* in the fourth instar, which is equivalent to the sixth instar of *Argiope*. Townley *et al.* (1991) suggested that the tubuliform spigots are present that early in order to 'stake out sites for the functioning spigots of mature females, because the tubuliform glands are poorly developed and do not serve any function at that time'. This explanation seems unlikely because the spinnerets are reorganized and the number of fusules increases with each moult.

In contrast, we consider the existence of the tubuliform spigots already at the sixth instar in female spiderlings to be an indication for the hypothesis that phylogenetically earlier females reached maturity at this developmental stage.

In females the tubuliform spigots may indicate the penultimate stadium as do the swollen palpi in males. While the males become mature, females undergo another series of moults (3-4) to reach maturity. During their phylogenetic history, the females in the subadult stage–more exactly in the penultimate stadium–undergo a prolongation of their development resulting in a larger body size, directly correlated with higher egg production. Therefore, sexual size dimorphism may have evolved to produce larger females, a hypothesis as especially presented by Gerhardt (1924) and Vollrath (1980).

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LITERATURE CITED

BRISTOWE, W.S. 1929. The mating habits of spiders, with special reference to the problems surrounding sex dimorphism. Proceedings of the Zoological Society of London 21: 309-358.

DARWIN, C. 1890. 'Die Abstammung des Menschen und die geschlechtliche Zuchtwahl'. (Bd. 1, E. Schweitzerbart'sche Verlagsbuchhandlung, Stuttgart).

EMERTON, J.H. 1878. 'The structure and habits of spiders'. (Salem).

ELGAR, M.A. & NASH, D.R. 1988. Sexual cannibalism in the garden spider *Araneus diadematus*. Animal Behaviour 36: 1511-7.

GERHARDT, U. 1924. Neue Studien zur Sexualbiologie und zur Bedeutung des sexuellen Größendimorphismus der Spinnen. Zeitschrift für Morphologie und Ökologie der Tiere 1: 507-538.

MCCOOK, H.C. 1890. 'American spiders and their spinning work'. vol. 2. (Philadelphia).

PETERS, H.M. 1989. On the structure and glandular origin of bridging lines used by spiders for moving to distant places. Acta Zoologica Fennica 190: 309-314.

PETERS, H.M. & KOVOOR, J. 1991. The silk-producing system of *Linyphia triangularis* (Araneae, Linyphiidae) and some comparisons with Araneidae. Zoomorphology 111: 1-17.

SEKIGUCHI, K. 1955a. Differences in the spinning organs between male and female spiders. Science Reports of the Tokyo Kyoiku Daigaku University, Section Zoology 8: 23-32.

1955b. The spinning organs in sub-adult geometric spiders and their changes accompanying the last moulting. Science Reports of the Tokyo Kyoiku Daigaku University, Section Zoology 8: 33-40.

TOWNLEY, M.A., HORNER, N.V., CHERIM, N.A., TUGMON, C.R., TILLINGHAST, E.K. 1991. Selected aspects of spinning apparatus development in *Araneus cavaticus* (Araneae, Araneidae). Journal of Morphology 208: 175-192.

VOLLRATH, F. 1980. Why are some spider males small? A discussion including observations on *Nephila clavipes*. 8. Internationaler Arachnologen Kongreß, Wien, 165-169.

VOLLRATH, F. & EDMONDS, D.T. 1989. Modulation of the mechanical properties of spider silk by coating with water. Nature 340: 305-7.

A METHOD TO DEVELOP AN 'INDICATOR VALUE' SYSTEM FOR SPIDERS USING CANONICAL CORRESPONDENCE ANALYSIS (CCA)

RALPH PLATEN

Platen, R. 1993 11 11: A method to develop an 'indicator value' system for spiders using Canonical Correspondence Analysis (CCA). *Memoirs of the Queensland Museum* 33(2): 621-627. Brisbane. ISSN 0079-8835.

Multivariate Canonical Correspondence Analysis (CCA) is used to derive 'indicator values' for spiders, similar to those used for plants. The data set consists of activity abundance values of spiders, sampled by pitfall trapping in various habitat types (mires, woods, dry grassland) in the Berlin area. Light exposure, soil moisture and temperature were also measured at the sites. Species scores are plotted as a function of environmental factors within an ordination diagram. The method used to determine the indicator value from this ordination diagram is presented. The system of indicator values is regarded as a suitable method to evaluate sites and areas easily. Advantages and limitations are discussed.

Mit Hilfe der multivariaten statistischen Methode Kanonische Korrespondenz Analyse (CCA) werden Zeigerwerte für Webspinnen, ähnlich denen für Pflanzen ermittelt. Die Entwicklung dieses Zeigerwertsystems und dessen Anwendung wird im Prinzip beschrieben. Der verwendete Datensatz besteht aus Aktivitätsabundanzwerten von Spinnen, die mit Bodenfallen in unterschiedlichen Biotoptypen (Mooren, Wäldern und Trockenrasen) im Gebiet von Berlin gefangen wurden. Die an den Standorten gemessenen abiotischen Faktoren Licht, Temperatur und Bodenfeuchte werden mit in die CCA einbezogen. An Hand von Beispielen wird der Weg erläutert, Zeigerwerte aus Ordinationsdiagrammen zu ermitteln. Mit Hilfe einiger Arten werden Anwendungsbereich und Beschränkungen des Zeigerwertsystems aufgezeigt und diskutiert. Das Zeigerwertsystem wird als eine brauchbare Methode betrachtet, um Standorte und Untersuchungsgebiete relativ leicht mit Hilfe der Spinnen zu bewerten. □ *Araneae, indicator value, multivariate analysis.*

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Ecosystems change under anthropogenic influences faster than their structures and functions can be analysed. It is therefore difficult to make well-founded comments about their ability to withstand external pressure, or about possibilities for their protection or renaturalisation. The complex ecological questions this deficit poses will require field work involving as many environmental factors and groups of organisms as possible.

GOALS

A first step is the description of the ecological behaviour of species in the field. A further step is to derive evaluations for the sites, biotopes or areas of study from the ecological behaviour of the species. For example when establishing whether an area should be protected, for purposes of planning and biotope-management as well as when studying the changes at the sites under anthropogenic influence, an efficient evaluation system which beyond that is easy to handle will be necessary.

A number of evaluation systems have recently been developed, e.g. for soil organisms by Wodarz *et al.* (1992), for epigaeic predatory arthropods (spiders and ground beetles) by Haenggi (1987) and Platen (1989, 1992), for spiders by Martin (1991) and for ground beetles by Mossakowski and Paje (1985). Some of these evaluation systems describe the ecological behaviour of the species in the field very precisely (Martin, 1991), or allow a differentiated evaluation of sitse or areas of study (Mossakowski and Paje, 1985; Haenggi, 1987; Platen, 1989). Some evaluation systems, however, have the disadvantage that lengthy calculations are necessary for synoptic evaluation for different sites or areas (Wodarz *et al.*, 1992; Haenggi, 1987). In other cases parameters are used in the calculations which are not stable for time and/or locality, such as a low local abundance of a species, or the numbers of individuals of a species caught in a year (Mossakowski and Paje, 1985). The evaluation systems mentioned can also only be applied locally where, as a result of intensive field work, the ecological behaviour of species along abiotic gradients is known.

A much simpler method would be the application of an indicator value system similar to that for plants of Ellenberg *et al.* (1991). It would then no longer be necessary to redetermine and re-evaluate the ecological behaviour of a species for each local investigation, since this would already be contained in the key values. Nor would the evaluation involve complicated calculations.

My aim has been to develop just such an indicator value system for spiders.

MATERIAL AND METHODS

DATA

The data consisted of the activity abundances of spider species. These were determined using ground traps in the Berlin area for open and wooded sites in moors, in various types of forest and for heathland and semi-dry and dry meadows. The investigation period was a full year in each case. Activity abundance is defined by Heydemann (1953) as the number of individuals, which has been trespassed a borderline (which is represented by the diameter of the pitfall trap) within a certain period of time. Parallel to the trap catches the following abiotic factors were also measured:

The soil water content (measured as the percentage by volume of water in the upper soil layer), the light exposure using the method described by Friend (1961), and the effective temperature after Pallmannn *et al.* (1940). The sites are described in detail in Platen (1989).

GENERAL

The activity abundance of the spider species and the measurements of the abiotic factors are analysed using Canonical Correspondence Analysis (CCA; Jongman *et al.*, 1987), using the program CANOCO Version 3.10 (Braak, 1988, 1991). The results of this analysis are displayed as ordination diagrams using CANODRAW (Smilauer, 1990).

Before running CCA the spider data had been masked according to dominance in a formal way: species which did not have an activity abundance of at least 1% at a site were removed from the data set. This meant that of the original 281 spider species only 111 remained for the further analysis.

Furthermore a transformation of the raw data was carried out. Instead of the abundance values their square roots were used.

RESULTS

ORDINATION DIAGRAMS

The CCA results with abiotic factors light exposure and temperature, as well as soil water content, are shown graphically (Figs 1, 2). The horizontal axis corresponds to the first CCA axis and the vertical to the second CCA axis. The 111 species of spider are represented by an 'x', together with an abbreviation of the name as far as possible. Using CANOPLOT it was also possible to determine the coordinates and the name of a species which could not be presented unambiguously in the diagram.

Initially the axes of the site factors light exposure and soil water content are extended beyond the origin (Fig. 1). The factor along the 'environmental axes' increases in the direction of the arrow. The origin marks the mean value for the entire data set. Species whose position lies between the arrowhead of an environmental axis and the origin have a larger weighted mean. Where the origin is between the arrowhead and the position of the species, its weighted mean is smaller than the overall mean. For interpretation a perpendicular is projected for each species in turn onto the environmental axis according to their sequence (cf. Jongman *et al.*, 1987). *Xysticus ninnii* and *Thanatus arenarius* occupy the brightest sites, and *Pardosa agrestis* and *Baryphyma pratense* the warmest sites (Fig. 1). Species at extremes of the axes represent limits of the area for a two-factor system, and thus form the start and end points of the indicator value scale. The distance between these points is measured and divided into five equal parts. The species are then noted for each class with the appropriate indicator value.

The determination of indicator values for three factors requires at least two ordination diagrams. Initially an indicator value is assigned for all three individual factors, then for all combinations of two factors. The result always remained the same. For the representation of all three factors in an ordination diagram the class of a species can, however, change, in some cases considerably, since the relative spatial distances of the species in three-factor constellations cannot be represented in a two-dimensional coordinate system without distortion. For the determination of indicator values from the data of individual environmental variables the solution (Figs 1, 2) is an optimum.

Moisture is strongly negative correlated with the 1st CCA-Axis (Inter-set correlation: -0.919)

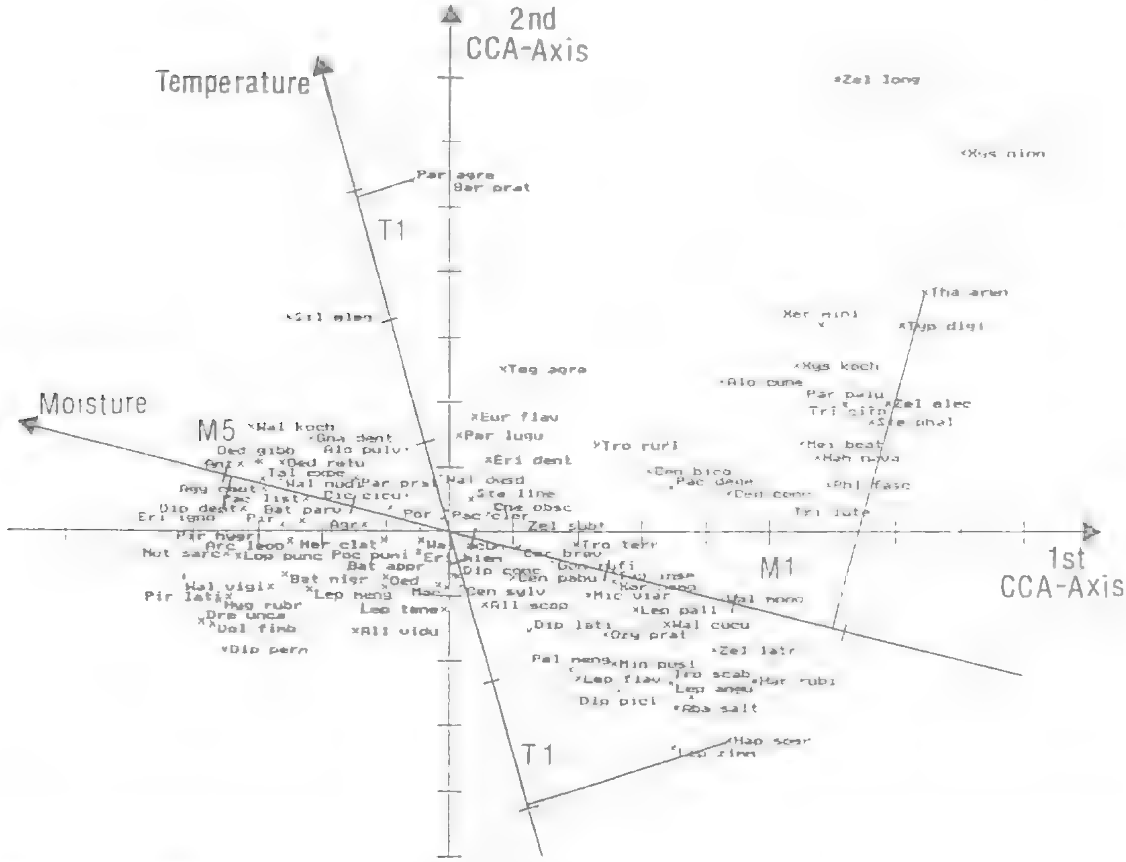

FIG. 1. CCA ordination diagram with 111 spider species represented by an 'x' and environmental variables moisture and temperature represented by arrows. The part of the arrows to derive indicator values are devided into five parts (M1-M5 and T1-T5 respectively). For further explanation see text.

(Fig. 1) which means that the horizontal species distribution is best explained by light and less by temperature (Inter-set correlation with 1st CCA-Axis: 0.26, with 2nd CCA-Axis: 0.538). Hence, the vertical species distribution is best explained along the 2nd CCA-Axis.

The Inter-set correlation between light and 1st CCA-Axis is 0.955 which means that the data set again is best explained by this abiotic factor. Temperature is strongly correlated with 2nd CCA-Axis (Inter-set correlation with 1st CCA-Axis: 0.0367, with 2nd CCA-Axis: 0.6177).

Indicator Values (Table 1)

The last two columns contain details of the ecological type and habitat type in which the species predominantly occurs in the Berlin area (after Platen *et al.*, 1991). The data are intended only to demonstrate the principle of this method. In view of the limited data set the indicator values cannot claim to be comprehensive or generally valid. Some examples will show the similarities and differences between the indicator values and other methods of determining ecological behaviour.

The distribution of *Xysticus ninnii* is centered exclusively on dry meadows. F1, L5, and T4 reflect this ecological behaviour well.

Diplocephalus permixtus: Occurring mostly in wet alder forest-habitats characterised by high soil water content, low light exposure and low temperatures. This is expressed with adequate precision by the indicator values F5, L1 and T2.

Diplocephalus picinus: F2, L1 and T1 characterise its habitat preferences, namely shadowy sites with low pH in dry mixed forests.

Pardosa agrestis: In this case the indicator value does not reflect the ecological behaviour, as a result of the inadequacy of the data set. The species occurs mostly on arable farmland and

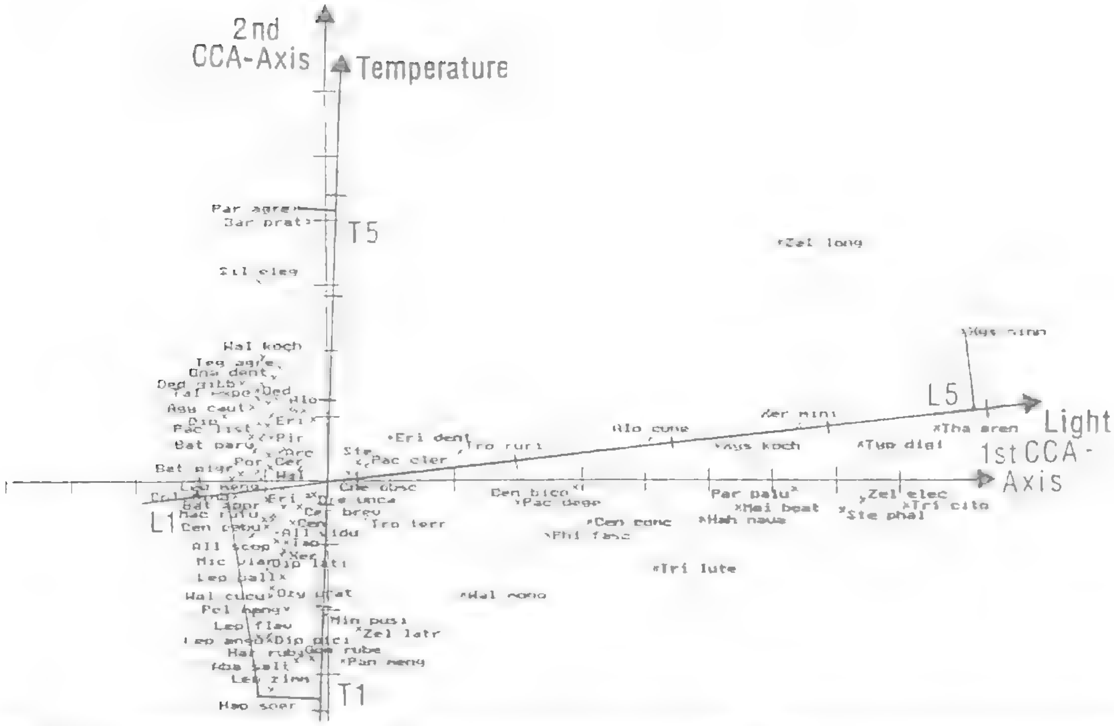

FIG. 2. CCA ordination diagram with 111 spider species represented by an 'x' and environmental variables light and temperature represented by arrows. The part of the arrows to derive indicator values are divided into five parts (L1-L5 and T1-T5 respectively). For further explanation see text.

other open, rather dry habitat types (Platen *et al.*, 1991). While T5 describes the behaviour in terms of temperature, the indicated soil water content (F5) is too high and the light exposure too low (L1). This is because in the data set it only occurred on one site (a former moor which was still wet in comparison to the sites on mineral soils), so that as an outsider it had an extreme position in the ordination diagram. The data set did not include arable farmland sites.

Comments

This method is a relatively easy one to determine indicator values for spiders and other soil arthropods (cf. Platen, 1992).

Indicator values have the advantage that with only a few values the ecological behaviour of a species can be characterised. Mean indicator values can be calculated, and in the absence of the measurements or vegetation surveys they allow a rough quantitative assessment of environmental variables for a investigation site, habitat type or an area of study. The use of indicator values obviates the need for complicated calculations for the evaluation of sites, as required by some evaluation systems (Mossakowski and Paje, 1985; Haenggi, 1987; Platen, 1989).

Some reservations concerning the applications of indicator values are necessary. As already emphasised by Ellenberg *et al.* (1991), indicator values describe the ecological behaviour of species in a multiple system of biotic and abiotic factors, from which those chosen in this paper are regarded as the key abiotic factors for the spiders. They do not, however, describe their physiological optima.

Indicator values for animals underlie more restrictions as those for plants because animals are mobile and often change their habitat for overwintering (Schaefer, 1976). Therefore in the strict sense they are valid only for Adults which does not change their habitat within their period of maturity. As juvenile animals were not included in the data set this holds true for this investigation.

Indicator values should never be used in the same way as measurements. They are ordinal, and are not suited for use in statistical (including multivariate) methods requiring higher scale data.

The indicator values determined above are always valid only for the data set used. Since they were limited to only a few types of biotope the results above can only be regarded as being a first approximation. The results of the analysis are greatly dependent on the type and number of habitats types and of the frequency with which various species occur there. The combination of a wet, light site (F5, L5) is not represented by an indicator value, although it is relevant for a number of species (*Drepanotylus uncatus*, *Antistea elegans*) (Table 1). However, since almost 2/3 of the 30 sites investigated were wet, and most species occurred with almost the same frequency in wet habitats, these species grouped close to the origin. Species which occur frequently, but only at one or two dry sites with very high light exposure are far from the origin, so that there is a higher differentiation of the axis over the bright range.

A generally valid indicator value system would need to analyse all known spider species of Germany or Central Europe for all existing types of biotope (abiotic factor combinations) in one data set, from which the indicator values could then be derived. The scale could then be expanded, or other environmental factors, such as the biotope structure, could be included. A problem would be the large number of measurements required.

A further problem is that the CCA only depicts species correctly in the ordination diagram if they have an unimodal response curve along a factor gradient (Jongman *et al.*, 1987). By plotting the frequencies of species at all habitat types sorted according to the levels of a factor, it is possible to determine bi-modal, multi-modal or continuous responses. The coordinates of all the habitats where the species occurs with high frequency can be entered in the ordination diagram, making it possible to recognise a corresponding range of occurrence on the environmental axis. For this species, as is the case with some plant species, an indifferent response to this factor for the species or to give a range of the indicator value (cf. Ellenberg *et al.*, 1991) may be possible.

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LITERATURE CITED

BRAAK, C.J.F. TER 1988. CANOCO - a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical correspondence analysis, principal components analysis and redundancy analysis (Version 2.1)]. Technical report LWA 88-02, Groep Landbouwwiskunde, Wageningen

1990. Update notes. CANOCO Version 3.10. Manuscript, Agricultural Mathematics Group, Wageningen.

ELLENBERG, H., WEBER, H.E., DÜLL, R., WIRTH, V., WERNER, W. & PAULISSEN, D. 1991. Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobotanica XVIII: 1-248.

FRIEND, D.T.C. 1961. A simple method of measuring integrated light values in the field. Ecology 42: 577-580.

HÄNGGI, A. 1987. Die Spinnenfauna der Feuchtgebiete des Großen Mooses, Kt. Bern. 2. Die Beurteilung des Naturschutzwertes naturnaher Standorte anhand der Spinnenfauna. Mitteilungen der Naturforschenden Gesellschaft in Bern N.F. 44: 157-185.

HEYDEMANN, B. 1953. Agrarökologische Problematik, dargetan an Untersuchungen über die Tierwelt der Bodenoberfläche der Kulturfelder. (Thesis, Kiel). 433 pp.

JONGMAN, R.H.G., BRAAK, C.J.F. TER & TONGEREN, O.F.R. (eds.), 1987. 'Data analysis in community and landscape ecology.' (Pudoc Books: Wageningen).

MARTIN, D. 1991. Zur Autökologie der Spinnen (Arachnida: Araneae) I. Charakteristik der Habitatausstattung und Präferenzverhalten epigäischer Spinnenarten. Arachnologia Mitteilungen 1: 5-26.

MOSSAKOWSKI, D. & PAJE, F. 1985. Ein Bewertungsverfahren von Raumeinheiten an Hand der Carabidenbestände. Verhandlungen, Gesellschaft Ökologie in Bremen 1983 13: 747-750.

PALLMANN, H., EICHENBERGER, E. & HASELER, A. 1940. Eine Methode der Temperaturmessung bei ökologischen oder bodenkundlichen Untersuchungen. Berichte, Schweizerische Botanische Gesellschaft 50: 337-362.

PLATEN, R. 1989. Struktur der Spinnen- und Laufkäferfauna (Arach.: Araneida, Col.: Carabidae) anthropogen beeinflußter Moorstandorte in Berlin (West); taxonomische, räumliche und zeitliche Aspekte. (Thesis: Technische Universität Berlin) 470 pp.

PLATEN, R., MORITZ, M. & BROEN, B.v. 1991. Liste der Webspinnen- und Weberknechtarten (Arach.: Araneida, Opilionida) des Berliner Raumes und ihre Auswertung für Naturschutzzwecke (Rote Liste). Pp. 243-275. In A. Auhagen, R. Platen and H. Sukopp (eds). 'Rote Listen der gefährdeten Pflanzen und Tiere in Berlin'. (Landschaftsentw.: Umweltforsch, S6).

PLATEN, R. 1992. Die Entwicklung eines Zeigerwertsystems für Laufkäfer (Col.: Carabidae) mit Hilfe einer "Canonical Correspondence Analysis"

(CCA). Verhandlungen der Gesellschaft für Ökologie 21: 321-326.

SCHAEFER, M. 1976. Experimentelle Untersuchungen zum Jahreszyklus und zur Überwinterung von Spinnen (Araneida). Zoologische Jahrbücher, Systematik (Ökologie), Geographie und Biologie 103: 127-289.

SMILAUER, P. 1990. CANODRAW. A companion program to CANOCO for publication-quality graphical output. (Ithaca).

WODARZ, E., AESCHT, E. & FOISSNER, W. 1992. Der Bodenbiologische Index (BI) - ein quantitatives Maß für die Bodenqualität. Verhandlungen der Gesellschaft für Ökologie 21: (in press).

TABLE 1. Indicator values for soil water content (F), light (L), temperature (T) of 111 common spider species of varying types of habitat. ET=Ecological type: h = hygrophilic, (h) = weakly hygrophilic, x=xerophilic, (x)=weakly xerophilic, eu= euryoecious open-space dwellers, w=forest type, (w) = also in open spaces, hw=sparse forest species, (h)w=inhabits mesophilic deciduous forests, (x)w=inhabits forest on acid soil, h(w)=depending on type of preferred habitat: inhabits unwooded wet habitats or sparse forest. - = no preferred habitats. Family (C): Ag, Agelenidae; Dy, Dysderidae; Gn, Gnaphosidae: Ha, Hahniidae; Li, Linyphiidae; Lc, Liocranidae; Ly, Lycosidae; Ph, Philodromidae; Pi, Pisauridae; Sa, Salticidae; Te, Tetragnathidae; Tr, Theridiidae; Tm, Thomisidae; Zo, Zoridae.

SPECIES	F	L	T	ET	C
Wet Forests					
Pachygnatha listeri Sundevall	5	1	3	hw	Te
Bathyphantes approximatus (O.P.C.)	4	1	3	h(w)	Li
B. nigrinus (Westring)	5	1	3	hw	Li
Diplocephalus permixtus (O.P.C.)	5	1	2	h(w)	Li
Diplostyla concolor (Wider)	4	1	2	(h)(w)	Li
Gonatium rubellum (Blackwall)	3	1	2	hw	Li
Porrhomma pygmaeum (Blackwall)	4	1	3	h(w)	Li
Walckenaeria atrotibialis (O.P.C.)	4	1	2	(w)	Li
Pirata hygrophilus (Thorell)	5	1	3	h(w)	Ly
Deciduous forests					
Centromerus sylvaticus (Blackwall)	4	1	2	(h)w	Li
Ceratinella brevis (Wider)	3	1	2	(h) w	Li
Diplocephalus latifrons (O.P.C.)	3	1	2	(h)w	Li
Gongylidium rufipes (Sundevall)	3	1	2	(h)(w)	Li
Lepthyphantes pallidus (O.P.C.)	2	1	2	(h)(w)	Li
L. tenebricola (Wider)	4	1	2	(h)w	Li
L. zimmermanni Bertkau	2	1	1	(h)w	Li
Microneta viaria (Blackwall)	3	1	2	(h) w	Li
Neriene clathrata (Sundevall)	4	1	3	(h) w	Li
Pardosa lugubris (Walckenaer)	4	1	3	(h) w	Ly
Dry mixed forests					
Harpactea rubicunda (C.L. Koch)	1	1	1	(x)w	Dy
Abacoproeces saltuum (L. Koch)	2	1	1	(x)w	Li
Centromerita concinna (Thorell)	2	3	2	(x)(w)	Li
Centromerus pabulator (O.P.C.)	3	1	2	(x)(w)	Li
Diplocephalus picinus (Blackwall)	2	1	1	(x)w	Li
Gonatium rubens (Blackwall)	2	1	1	(x)w	Li
Lepthyphantes angulipalpis (Westring)	2	1	1	(x)w	Li
Lepthyphantes flavipes (Blackwall)	2	1	1	(x)w	Li
Macrargus rufus (Wider)	4	1	2	(x)w	Li
Minyriolus pusillus (Wider)	2	1	1	(x)w	Li
Panamomops mengei Simon	1	1	1	(x)w	Li
Tapinocyba insecta (L. Koch)	2	1	2	(x)w	Li
Walckenaeria acuminata Blackwall	4	1	3	(x)w	Li
W. cucullata (C.L. Koch)	2	1	2	(x)w	Li
W. dysderoides (Wider)	4	1	3	(x)w	Li
W. monoceros (Wider)	2	2	2	(x)w	Li
Euryopis flavomaculata (C.L. Koch)	4	1	4	(x)(w)	Tr
Trochosa terricola Thorell	3	2	2	(x)(w)	Ly
Xerolycosa nemoralis (Westring)	2	1	2	(x)(w)	Ly
Cicurina cicur (Fabricius)	4	1	3	(x)(w)	Ag
Agroeca brunnea (Blackwall)	4	1	3	(w)	Lc
Haplodrassus soerenseni (Strand)	1	1	1	(x) w	Gn
Zelotes subterraneus (C.L. Koch)	3	1	3	(x)(w)	Gn
Ozyptila praticola (C.L. Koch)	2	1	2	(x) w	Tm
Waterside sites					
Gnathonarium dentatum (Wider)	5	1	4	h	Li
Moors					
Agyneta cauta (O.P.C.)	5	1	3	h(w)	Li
Diplocephalus dentatus Tullgren	5	1	3	h(w)	Li
Drepanotylus uncatus (O.P.C.)	5	1	3	h	Li
Erigonella ignobilis (O.P.C.)	5	1	3	h	Li
Lepthyphantes mengei Kulczynski	5	1	3	h(w)	Li
Lophomma punctatum (Blackwall)	5	1	3	h	Li
Notioscopus sarcinatus (O.P.C.)	5	1	3	h	Li
Oedothorax gibbosus (Blackwall)	5	1	4	h	Li
Silometopus elegans (O.P.C.)	5	1	5	h	Li
Tallusia experta (O.P.C.)	5	1	4	(h)	Li
Walckenaeria alticeps Blackwall	5	1	4	h(w)	Li
W. kochi (O.P.C.)	5	1	4	h	Li
W. nudipalpis (Westring)	5	1	4	h	Li
W. vigilax (Blackwall)	5	1	3	h	Li
Arctosa leopardus (Sundevall)	5	1	3	h	Ly
Hygrolycosa rubrofasciata (Ohlert)	5	1	3	h	Ly
Pardosa pullata (Clerck)	5	1	3	h	Ly
P. latitans (Blackwall)	5	1	3	h	Ly
P. piraticus (Clerck)	5	1	3	h	Ly
P. piscatorius (Clerck)	5	1	3	h	Ly
P. tenuitarsis Simon	5	1	4	h	Ly
Trochosa spinipalpis (F.O.P.C.)	5	1	3	h(w)	Ly

TABLE 1. *continued*

SPECIES	F	L	T	ET	C
Dolomedes fimbriatus (Clerck)	5	1	3	h	Pi
Antistea elegans (Blackwall)	5	1	4	h	Ha
Reeds					
Baryphyma pratense (Blackwall)	5	1	5	h	Li
Wet Meadows					
Allomengea scopigera (Grube)	3	1	2	h	Li
A. vidua (L. Koch)	4	1	2	h	Li
Ceratinella brevipes (Westring)	4	1	3	h	Li
Erigonella hiemalis (Blackwall)	4	1	3	(h)(w)	Li
Oedothorax fuscus (Blackwall)	4	1	2	eu	Li
O. retusus (Westring)	5	1	4	eu	Li
Pelecopsis mengei (Simon)*	3	1	1	h	Li
Pardosa palustris (Linné)	1	4	3	eu	Ly
P. prativaga (L. Koch)	4	1	3	eu	Ly
Cough-grass sites					
Centromerita bicolor (Blackwall)	2	3	3	(x)(w)	Li
Ruderal sites					
Bathyphantes parvulus (Westring)	5	1	3	eu	Li
Pocadicnemis pumila (Blackwall)	4	1	3	eu	Li
Stemonyphantes lineatus (Linné)	4	2	3	(x)	Li
Trochosa ruricola (De Geer)	3	2	3	eu	Ly
Arable fields					
Bathyphantes gracilis (Blackwall)	4	1	3	eu	Li
Erigone atra (Blackwall)	3	2	3	eu	Li
E. dentipalpis (Wider)	4	2	3	eu	Li
Pardosa agrestis (Westring)	5	1	5	(x)	Ly
Tegenaria agrestis (Walckenaer)	4	1	4	(x)	Ag
Heathland					
Tricca lutetiana (Simon)	1	3	2	(x)	Ly
Zelotes latreillei (Simon)	2	1	1	(x)	Gn
Dry grassland					
Pachygnatha degeeri Sundevall	2	2	3	eu	Te
Meioneta beata (O.P.C.)	1	4	3	x	Li
Trichopterna cito (O.P.C.)	1	5	3	x	Li
Troxochrus scabriculus (Westring)	2	1	1	x	Li
Typhochrestus digitatus (O.P.C.)	1	5	3	x	Li
Steatoda phalerata (Panzer)	1	5	3	x	Tr
Alopecosa cuneata (Clerck)	2	3	3	x	Ly
A. pulverulenta (Clerck)	4	1	3	eu	Ly
Xerolycosa miniata (C.L. Koch)	1	4	4	x	Ly
Hahnia nava (Blackwall)	1	4	3	x	Ha
Agroeca proxima (O.P.C.)	4	1	3	(x)	Lc
Zelotes electus (C.L. Koch)	1	5	3	x	Gn
Z. longipes (L. Koch)	2	4	5	x	Gn
Thanatus arenarius L. Koch	1	5	4	x	Ph
Xysticus kochi Thorell	1	4	3	x	Tm
X. ninnii Thorell	1	5	4	x	Tm
Aelurillus v-insignitus (Clerck)	1	5	4	x	Sa
Phlegra fasciata (Hahn)	1	3	2	x	Sa
No obvious habitat preferences					
Cnephalocotes obscurus (Blackwall)	3	1	3	eu	Li
Zora spinimana (Sundevall)	4	1	3	eu	Zo

THE SPIDERS OF THE HIGH-ALTITUDE MEADOWS OF MONT NIMBA (WEST AFRICA): A PRELIMINARY REPORT

C. ROLLARD

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Spiders are abundant in the high-altitude meadows of the Nimba mountains, in Guinea. Collections have been carried out in this ecosystem where grass ground cover is dominant: this preliminary study at the family level concerns specimens collected in March 1991. It already gives some data on the localisation of the spiders. More than 20 families are represented along the mountain tops. A provisional list of these spiders has been drawn up. Most specimens were Araneidae, Gnaphosidae, Hersiliidae, or Salticidae. Their distribution in the herbaceous stratum as well as along an altitude gradient between 800-1700m is being analysed.

Les araignées sont abondantes dans les prairies de haute altitude des Monts Nimba, en Guinée. Des récoltes ont été effectuées dans cet écosystème où la couverture herbacée est dominante. Cette étude préliminaire au niveau des familles concerne les spécimens collectés en mars 1991. Elle apporte déjà quelques éléments sur la localisation des araignées. Plus de 20 familles sont représentées sur ces sommets et une liste provisoire en a été établie. La plupart de ces araignées sont des Araneidae, des Gnaphosidae, des Hersiliidae ou des Salticidae. Leur distribution est analysée dans la strate herbacée ansi que selon un gradient altitudinal entre 800 et 1700m. □*Spiders, biogeography, Africa, montane.*

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The Mont Nimba biosphere reserve, located in West Africa, is the subject of a multidisciplinary study as part of a UNESCO pilot project. These mountains have been classified as an Integral Natural Reserve since 1944. Over the past 50 years, many more animals have been collected during several scientific expeditions directed by Professor Maxime Lamotte (Lamotte, 1943). Many papers have been published on the Nimba mountain range. However works on the spider fauna are non- existent. Hence the organization of the spider populations are still little known. Especially in this tropical region, no work deals with the ecology of spiders except for the research initiatives in the Ivory Coast, in the savanna of Lamto (Lamotte, 1943, 1967; Blandin, 1974; Blandin and Célérier, 1981).

With this subject of research in mind, another field trip was made to Guinea in March 1991. The new collection of spiders made there compliments those of Mr Lamotte and his associates. This abundant material is in the process of being classified. An attempt is being made to describe the structure and function of the spider community in this tropical ecosystem.

The programme focuses on the spiders of the high-altitude meadow, relatively less-frequently collected than those of the savanna or the head of ravines (Lamotte, 1958). This environment is characterized by the strong contrast between the dry and rainy seasons. It presents a characteristic fauna with several endemic species.

In this paper, preliminary data dealing with the localisation of the different families of spiders collected in March 1991 are presented. The overall study will lead to a more detailed inventory of the spiders along the mountain ridges, as well as a better knowledge of their distribution with altitude and the relative abundance of the different species.

ENVIRONMENT AND CLIMATE

Mont Nimba is situated in High Guinea, near the borders of Liberia and the Ivory Coast (Fig. 1). It extends from SW to NE for about 30 km into guinean territory. All the crests stand over 1000m. The mountainside is steep and notched by valleys with sheer slopes. No trees or shrubs are present on the crests. Only some small trees of the inferior savanna grow at lower altitude on the slopes (Schnell, 1966). Above 900-1000m, the forest is confined particularly to the ravines. The mountain range is covered by herbaceous plants with a grassland structure. The term of montane or sub-montane has been given to this

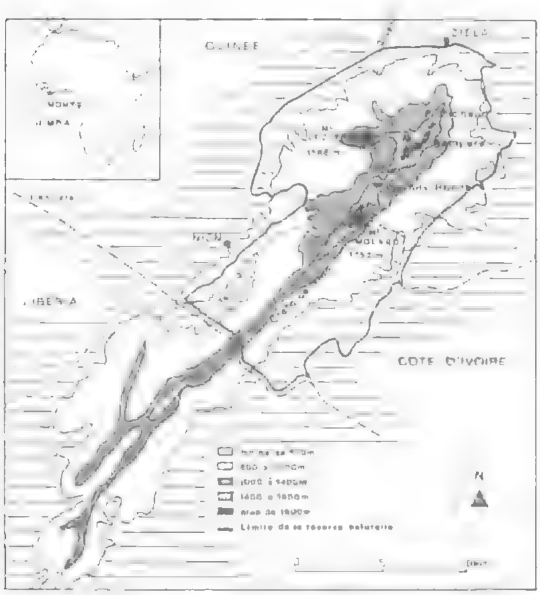

FIG. 1. Map of Mont Nimba, West Africa. Situation of the various sample zones along the Mont Nimba crest.

crest vegetation (Schnell, 1987). In this type of meadow, located in the guinean part of Nimba, the low (about 20-30cm or less) graminaceous species *Loudetia kagerensis* is abundant and constant. This grass forms a predominant group associated with other tall or short species, varying from site to site.

Mont Nimba receives abundant rainfall and a dry season not exceeding three and a half months. Generally, high-altitude meadows are often covered in fog during the rainy season, from May to November. Precipitation is fine and stable. During the other periods of the year, clouds scale the slopes and progressively cover the crest. Thus the humidity, which is closely bound to the degree of precipitation and nebulosity, varies with altitude and also along the crest. For example, the crest of Nion, spreading upwards to Mont R. Molard in the NE, is wetter than either Mont P. Richaud or the region of Sempéré (Leclerc *et al.*, 1955). Nevertheless, seasonal variations do exist. In the meadow, this factor does not seem to be very important to the ecological cycle of the fauna.

The spiders listed here were collected in March 1991, during the transition period just before the rainy season. Sudden storms or regular strong precipitations occur in the late afternoon from April onwards.

FIG. 2. Total no. spiders taken during March 1991.

METHODS

Up until now, the high-altitude meadows of Mont Nimba have rarely been sampled. The present study lasted 20 days (8-27 March) with only 14 days of sampling. The first phase consisted in obtaining an overall idea of the spider communities over the whole crest. The collecting program was prepared as follows: 4 days in Sempéré, Grands Rochers; 4 days on the Nion crest, 2 days in Grands Rochers, R. Mollard; 3 days on Mont Leclerc and 1 day in Ziela, P. Richaud.

No strictly quantitative sampling methods were used. Several gathering squares (1m x 1m) were made but the results are insufficient. In addition, these quadrats have not been well materialized because the transport of materials was not easy. Only the sizes were marked by various elements found on the ground. Furthermore, this type of analysis is rare in these environments. Some information on the vertical distribution of the spiders was obtained by the use of beating and ground sweeping methods. A few specimens found on the high sections of the grass were captured, but this is certainly not a representative

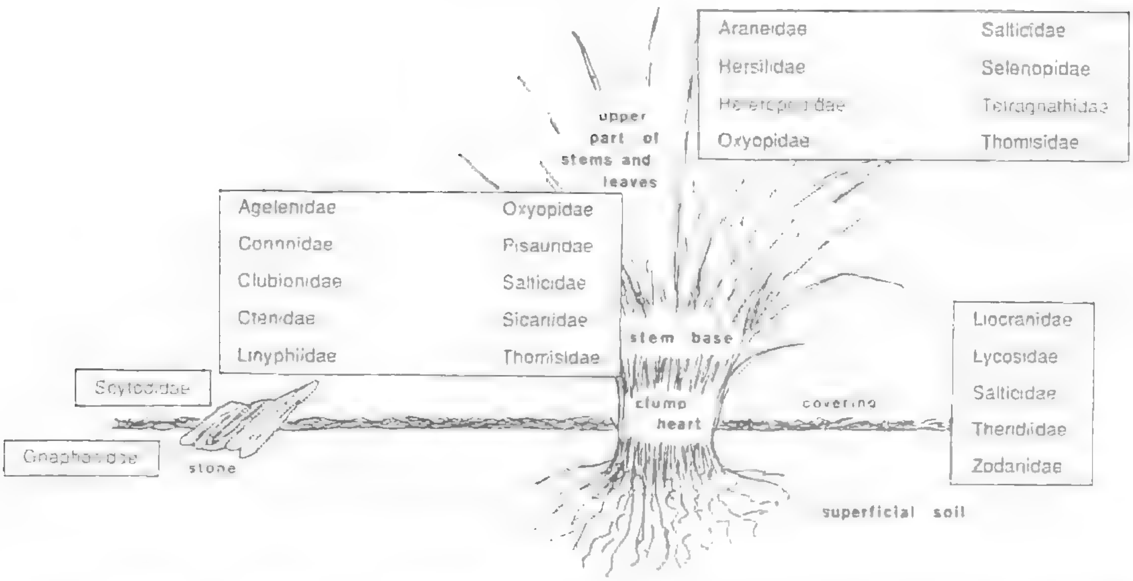

FIG. 3. Distribution of families in epigean environment.

sample of the spider fauna of the herbaceous stratum.

So, in the low herbaceous stratum, samples were made by visual searching in vegetation and under stones, using forceps and pooters. Collecting was only carried out during the daytime and was therefore not exhaustive. The time spent on Mont Nimba was rather short: the researchers stopped collecting at the end of an hour at each site.

A mean of 40 individuals was collected per day, by one to three collectors depending on the days and the availability of the expedition members.

RESULTS

Families Identified

For each sample, the spiders were sorted and enumerated by family. Young and adult spiders were counted together. Immature spiders represent about 54% of all specimens found.

Mygalomorphs were collected, but not in great numbers: 0.5% (2/435). For the moment, the inventory of this suborder has not been established at the family level. Similarly, about 9% (39/435) of the collection is still at the level of indeterminate araneomorph. Therefore, we are only able to present results of the determinate araneomorph families, which correspond to 394 specimens. The names used follow Brignoli (1983) and Platnick (1989).

At least 21 families have been recorded along this crest, of the roughly 100 families known worldwide (Table 1). This relatively high number provides a good idea of the diversity of this environment. The high-altitude meadow-like plateau savanna characterized by the grass species *Loudetia*, is usually considered to be one of the poorest habitats. However, this type of environment clearly possesses an important variety of spiders.

Furthermore, the relative frequencies of these spiders gives another indication of their diversity (Fig. 2). The physionomy of the araneological community is characterized by the predominance of Araneidae which represent around 21% of determined spider families. Four other families were common: Gnaphosidae (57/394), Hersiliidae (59/394), Salticidae (46/394) and Thomisidae (35/394). We note that these spiders are generally large and therefore easier to find. The same observation can be applied to other families which are more easily collected, especially for a certain size. However, the fewer Clubionidae, Lycosidae, Oxyopidae, Pisauridae, Selenopidae and Tetragnathidae in the collections could indicate that they are less abundant in the meadow during this period of the year. The specimens belonging to most other families are generally small and consequently poorly collected. In addition, Liocranidae and Zodariidae are active and move quickly on the soil, so they frequently evaded capture.

Vertical Structure of the Spider Community

The quality of a sampling must take into con-

Agelenidae	Hersiliidae	Scytodidae
Araneidae	Linyphiidae	Selenopidae
Clubionidae	Liocranidae	Sicariidae
Corinnidae	Lycosidae	Tetragnathidae
Ctenidae	Oxyopidae	Theridiidae
Heteropodidae	Pisauridae	Thomisidae
Gnaphosidae	Salticidae	Zodariidae

TABLE 1. List of spider families on Mont Nimba

sideration the biology and the size of the spiders. All families are represented, in spite of the small number of specimens. Around two-thirds of these families frequent the herbaceous stratum and most are diurnal (Fig. 3).

On the upper part of the stems and leaves of plants, the spider community is composed of eight families of which the Araneidae, Tetragnathidae, Hersiliidae and Thomisidae are the most common. The former two build their webs about 20 cm above the soil. Of all Araneidae, Oxyopidae and Salticidae, 25, 2 and 1 specimens respectively were collected by beating and sweeping of the ground. Ten families are present at the base of the stems or in the center of the clumps, Clubionidae being the most abundant. The clubionids are nocturnal hunters and easily found in nests among the vegetation. Five families occur in the superficial soil layer. The Lycosidae constitute most of the collections. Gnaphosidae are mostly nocturnal hunters found in nests among stones. Scytodidae are also found nocturnally active around stones.

Thus, each level of this epigean environment seems to possess its own spider community, characterized by its family composition. Nevertheless, some of them such as the Salticidae, Thomisidae and Oxyopidae are present at all levels of the vegetation and the soil surface. Only analysis at the species level will permit the clarification of the distribution of the spiders in each stratum.

Altitudinal Distribution

The spiders were collected along the crest, mainly situated above an altitude of 1200m. The results are presented by altitudinal classes of 200m, principally because of the small numbers of spiders, and the various sampling zones are indicated in Fig. 1.

An overall view indicates that some families appear to be better represented at the highest altitudes, from 1200m to around 1700m (Table 2). The numbers of Gnaphosidae and Clubionidae regularly increase. Most other families did not

ALTITUDE (m)	800–1000	1000–1200	1200–1400	1400–1600	1600–18[illegible]
Oxyopidae					9
Theridiidae					1
[illegible]				2	
Sicariidae				2	
Selenopidae				1	
Ctenidae				1	
[illegible]				1	
Agelenidae			4		
Corinnidae			5		
Tetragnathidae			16		
Gnaphosidae			5	17	35
Clubionidae			3	5	10
Zodariidae		2		[illegible]	
Araneidae	4		11	11	56
Salticidae	4	1	6	9	24
Hersiliidae	1		32	21	13
Thomisidae	3	2	9	13	6
Lycosidae	2	8	8	5	3
[illegible]	1				1
Heteropodidae	3	1			
Pisauridae	1	1			
TOTAL NUMBER OF SPECIMENS	25	15	102	87	155
NUMBER OF FAMILIES	8	6	10	13	10

TABLE 2. Altitudinal distribution of spider families in meadow of Mont Nimba.

provide many specimens, with the exception of Tetragnathidae. These spiders are perhaps rare or difficult to observe, but it is all the more interesting to note that their distribution is limited to a certain altitude. In the same way, Eusparassidae and Pisauridae are found only up to 1200m, in low vegetation. The lack of data, between 1000 and 1200m altitude, for the Araneidae and Hersiliidae is probably due to sampling problems. Spiders of these families as well as the Salticidae, Thomisidae and Lycosidae, are certainly present at the different altitudes, and it is likely that the same is the case for the Zodariidae. The family diversity seems to increase slightly with altitude.

The collections made on slopes from 800m upwards concentrated particularly on Mont Leclerc (Table 3). Here too, we note the diversity of the spider fauna, with 14 families present of the 21 listed for Mont Nimba. The same families are found at the highest altitudes. Only Zodariidae and Clubionidae are not encountered below 1400m. Salticidae, Hersiliidae, Thomisidae and Lycosidae can be found from 800 to 1600m.

We also compared the spider families found at three points along the crest: P. Richaud, Grands Rochers and Nion crest, between 1200 to 1600-

ALTITUDE (m)

	800–1000	1000–1200	1200–1400	1400–1600
Sicariidae				1
Ctenidae				1
Liocranidae				1
Clubionidae				4
Zodariidae				7
Gnaphosidae			2	14
Araneidae	4		3	3
Salticidae	4	1	2	3
Hersiliidae	6			12
Thomisidae	3		3	11
Lycosidae	2	4	1	3
Heteropodidae	2	1		
Pisauridae	3	1		
Scytodidae	1			
TOTAL NUMBER OF SPECIMENS	25	7	11	60
NUMBER OF FAMILIES	8	4	5	11

TABLE 3. Altitudinal distribution of spider families on Mont Leclerc.

1700m altitude (Table 4). Seven families are present on the Nion crest, clearly a lower diversity than on P. Richaud with eleven families. Six families were observed at all three places. Only Tetragnathidae were found south of the crest. This place seems to be more humid than the others at different periods of the year. The spiders found there are generally hygrophilous species.

For the moment, we cannot provide definitive results on the ecological requirements of the families present only on P. Richaud and Grands Rochers. However, more precise information, at the species level will, hopefully, be available in the future.

COMMENTS

Spiders occupy an important place among the invertebrate fauna of Mont Nimba. They are represented by about twenty families which is a relatively large number for this type of highland meadow. This study is only a first approach; the diversity of the spider community according to stratum and altitudinal level will certainly prove to be rewarding, both quantitatively and qualitatively, with the determination of species. Publication of the final results will probably be delayed because of taxonomic difficulties.

Nevertheless, this study already gives some results at the family level. Prudence in the interpretation of these results is necessary, because the families do not always form homogenous ecological units. The sampling methods used must also be taken into consideration. In the tables and figures, we see that the distributions found are dependent on the collecting effort. In this study we used mostly visual-hunting, with no collecting at night. So we only have a partial sample of the spider families, mainly representing those with diurnal activities. As yet, pitfall traps have not been used to intercept nocturnal spiders. Nevertheless, an estimation of the spiders present along the Mont Nimba crest and their spatial distribution has been made.

We observe several components of this spider

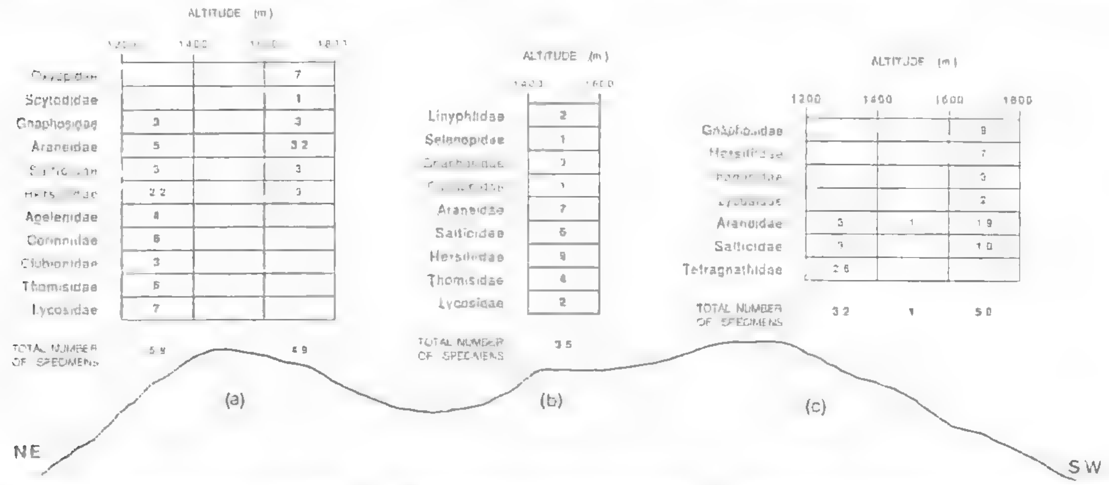

TABLE 4. Altitudinal distribution of spider families along Nimba crest, from SW to NE: (a) Pierré Richaud; (b) Grands Rochers; (c) Nion crest before Richard-Molard.

community, not forgetting the movements of wandering spiders. There are groups on the soil surface principally characterized by Lycosidae and Salticidae; three other families, Liocranidae, Zodariidae and Theridiidae exist in smaller numbers. Groups in the lower part of the vegetation includes ten families, the most with few representatives; Clubionidae, Thomisidae and Salticidae exist in great numbers. A last group exist of the upper part of the herbaceous stratum where Araneidae, Hersiliidae and Tetragnathidae are found in a great numbers; the five other families are less well represented.

The comparison between the northern and southern parts of the crest indicates a possible tendency of one family (Tetragnathidae) to prefer greater humidity. The altitudinal distribution shows that some families, such as Araneidae, Salticidae, Hersiliidae, Thomisidae and Lycosidae, are present from 800 to 1752m. On the contrary, other families are preferentially localised at the highest or lowest altitudes. The spider families found between the altitudes 800 and 1000m, can be considered as being roughly comparable with those present in typical savanna with *Loudetia*. In this environment, there are a great number of spider families (Gillon and Gillon, 1974). More data will be required to confirm these tendencies, as well as their presence on the slopes according to a greater altitudinal gradient and along the whole of the Mont Nimba crest. In addition, some comparisons among sites, including absence of families, might be artefacts, due to relative rareness of representatives.

The study of all spiders collected during the previous expeditions directed by Prof. Lamotte will certainly provide supplementary elements to the various points mentioned in this paper. It will be necessary to characterize, with more precision, the araneological fauna of Mont Nimba. Blandin and Célérier (1981) already noted the misreading of this fauna in West Africa. In addition the well-collected environments are essentially savanna rather than high-altitude meadow.

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LITERATURE CITED

BLANDIN, P. 1974. Les peuplements d'Araignées de la savane de Lamto. Bulletin de liaison des Chercheurs de Lamto 3: 107-135.

BLANDIN, P. & CELERIER M.L. 1981. Les Araignées des savanes de Lamto (Côte d'Ivoire). Publication Laboratoire de Zoologie, Ecole Normale Supérieure, 21, 2 fasc., 586 pp.

BRIGNOLI, P. 1983. 'A catalogue of the Araneae described between 1940 and 1981'. (Manchester University Press: Manchester).

GILLON, D. & GILLON, Y. 1974. Comparaison du peuplement d'invertébrés de deux milieux herbacés ouest-africains: Sahel et savane préforestière. La Terre et la Vie, 28: 429-474.

LAMOTTE, M. 1943. Premier aperçu sur la faune du Nimba. Faculté des Sciences Universitaires, Paris, n.845.

1958. Le cycle écologique de la savane d'altitude du Mont Nimba (Guinée). Annales de la Société Royale de Zoologie de Belgique 89: 119-150.

1967. Recherches écologiques dans la savane de Lamto (Côte d'Ivoire) : présentation du milieu et du programme de travail. La Terre et la Vie 21: 197-215.

LECLERC, J.C., RICHARD-MOLARD, J., LAMOTTE, M., ROUGERIE, G. & PORTERES, R. 1955. La chaîne du Nimba. Essai géographique. Mémoire de l'I.F.A.N., 43, 270 pp.

PLATNICK, N.I. 1989. 'Advances in Spider Taxonomy 1981-1987'. (Manchester University Press: Manchester).

SCHNELL, R. 1966. Guinée. Acta Phytogeographica Suecica 54: 69-72.

1987. Les formations herbeuses montagnardes des monts Nimba (Ouest africain). Bulletin du Museum National d'histoire naturelle, Paris, 4, sér. 9(2): 137-151.

VISUALLY MEDIATED RESPONSES IN THE LYCOSID SPIDER *RABIDOSA RABIDA*: THE ROLES OF DIFFERENT PAIRS OF EYES

J.S. ROVNER

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Video images of conspecifics were presented to *Rabidosa rabida* (Walckenaer) (Araneae: Lycosidae) to study the roles of different pairs of eyes in a wolf spider. Four groups of spiders had one pair of eyes occluded, and four had all but one pair occluded. Various control groups were also tested. The PLE were essential for sizeable orientation turns of up to about 160°. The PME served for rapid, long distance approaches toward the stimulus; they also initiated orientation turns of up to about 50°. If close to the stimulus, the ALE initiated small turns of up to about 20° and mediated small approaches. The AME did not mediate any responses. Courtship could be triggered in males via the PLE or the PME. In females, only the PME mediated receptive display responses to temporally patterned leg I movements seen in anterior or lateral views of a courting male. ☐*Araneae, Lycosidae, eyes, vision, communication.*

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Very little behavioural research has been carried out on vision in lycosid spiders, compared to the extensive studies on salticid spiders (reviewed in Forster, 1985). In lycosid spiders, occlusion of the eyes has been used to test for differences in the roles of the main vs. secondary eyes (Homann, 1931) as well as the anterior vs. posterior eyes (Acosta *et al.*, 1982); however, the results of both of these studies were confounded by the lack of controls for vibratory stimuli. The only successful behavioural investigation of the role of particular eyes in lycosids (Magni *et al.*, 1964) demonstrated the importance of the AME in astronomical orientation and was accomplished by covering all but a single pair of eyes in each group tested. Occlusion of only one pair of eyes at a time has proven useful in several behavioural studies of salticid vision (e.g., Forster, 1979).

In the present study of the lycosid spider *Rabidosa rabida* (Walckenaer), I used both methods of occlusion to examine the roles of different pairs of eyes in detecting visual stimuli and mediating appropriate responses. By using video images as stimuli (Clark and Uetz, 1990), I eliminated the possibility that vibrations or chemicals from conspecifics could confound the results.

METHODS AND MATERIALS

Penultimate *Rabidosa rabida* (formerly *Lycosa rabida*) were collected in late June (1990 and 1991) in Athens County, Ohio, USA. The methods of maintenance and the laboratory conditions during testing have been described previously (Rovner, 1989). Spiders were not used in testing until 1 week after the final moult. Tests were conducted between 1000 and 2200 hours.

For each test the spider's home cage, with its resident within, was placed with its narrow front side facing a small television set (black and white Magnavox BH-3907; screen = 9.2cm wide, 6.6cm high), which received a playback signal from a Sony recorder (SL-HFR70). The clear front side of the plastic cage (the other sides were opaque) was 7cm wide and was located 3cm from the screen. I removed the cage cover and, if necessary, gently positioned the spider with an artist brush to insure that the screen would be within the visual field of the spider's useable eyes. (I used separate brushes for males and females). Then, a glass cover (one for each sex) was placed on top of the cage. A front-silvered mirror fixed at 45° to the floor was 0.5m above the cage. A video camera (JVC GX-8NU) was aimed at both the mirror and an adjacent, second, identical television set receiving the same signal from the playback recorder as the first set. This yielded (on a second, identical recorder) a kind of split-screen recording. On the left was a dorsal view of the spider, which facilitated the measurement of turning angles (accurate to the nearest 5°) and speeds of locomotion. On the right was a view of the video image concurrently being presented to the spider. Thus, the relationship of the video stimulus to the spider's response could later be analyzed.

Subjects used for video presentations were recorded against a plain, pale background and illuminated evenly by a 32-W, circular fluorescent bulb 0.5m above the arena. The camera was located at a distance yielding a screen image the size of the actual subject (average body lengths: female=18mm; male=12mm). The 15-min video playback for females was a pheromone-stimulated, courting male; his occasional position changes provided nearly equal proportions of anterior and lateral views of his display (total number of courtship bouts = 51). The 10-min video playback for males was a lateral view of a female walking to and fro in an elongate glass arena (passes across the screen =15 leftward and 15 rightward). Some preliminary tests made use of prey images provided by a 10-min video of three crickets (*Acheta domesticus*, 10mm body length) walking to and fro.

To cover the eyes of spiders, I painted them with two coats of water-based enamel (Top Color Hobbylack, Pelikan AG). That this insured complete occlusion had been established previously (Rovner, 1989). Spiders were tested one or more days later.

I ran two preliminary tests to see if painting or its related procedures lowered responsiveness. All the eyes of five females were covered with two separately applied coats of clear paint. Five other females were briefly anaesthetised (carbon dioxide) and then restrained for 6 hr, thereby duplicating the procedure used when painting the eyes. However, at the two times that paint would have been applied (0 hr and +3 hr), I used water instead. The next day, when exposed to video images of crickets, the clear-painted spiders were less responsive than were the water-brushed spiders. The latter seemed as responsive as untreated spiders.

There were three control groups, each with 10 females and 10 males; these 60 individuals were given two trials apiece. One group consisted of untreated spiders exposed to the conspecific video playback, to determine how readily fully sighted spiders respond. A second group, also untreated, was exposed to a 10-min video of an empty arena, to determine if that alone had a stimulating effect. (Light from the screen = about 800 lux; incident light from above = about 350 lux.). The third group consisted of fully blinded spiders exposed to the conspecific playback, to see if such spiders would perform behaviours (orientation, rapid approach, or display) that I assumed would only occur in this study as visual responses.

There were eight experimental groups, each having 10 spiders of each sex. In four experimental groups a single pair of eyes was occluded; in four others, all but one pair was occluded. Since one of the untreated control spiders had failed to respond to video playback within two trials and since the preliminary tests had indicated that painting the eyes can reduce responsiveness, I gave unresponsive experimental spiders additional opportunities to respond, up to a limit of five trials. One or more days separated consecutive trials undergone by any individual spider.

RESULTS

During testing of control groups, all of the untreated females and all but one of the untreated males showed 'orientation' and/or 'long-range approach.' Most (16/20) did so in the first trial. 'Orientation' involved a single, rapid pivot that resulted in the spider facing the image. This pivot had a mean speed (SD) of $121 \pm 51.7°/s$ ($N = 12$), about eight times faster than turns that occurred during wandering, $16 \pm 12.4°/s$ ($N = 11$). A 'long-range approach' covered a distance of up to 10cm, the maximum being limited by cage depth (12.5cm). The speed of an approach, 5.9 ± 3.32 cm/s ($N = 22$), was about ten times faster than walking during wandering, 0.6 ± 0.31cm/s ($N = 36$). (The above speeds are not the maxima attained, since I included the acceleration and deceleration phases in each bout of locomotion.) No orientation or approach responses occurred in the empty arena or fully blind controls.

Results of the eye occlusion experiments are summarized in Table 1. Spiders with any one of the four pairs of eyes occluded were still capable of orientation; those with occluded PME did not show approach. When all but one pair of eyes was occluded, the only group failing to show orientation was the one limited to use of the AME; and the only group that still showed long-range approach was the one with useable PME. When close to the cage front, a few spiders having only useable ALE did perform a near-field approach response, edging forward less than one body length. For all the responding experimental groups, the mean number of trials ($\pm$SD) needed to obtain either an orientation or a long-range approach to the image was 1.2 ± 0.53 ($N = 63$) for females and 2.4 ± 1.24 ($N = 55$) for males (Mann-Whitney *U*-test, $Z = -6.545$, $P < 0.0001$).

Spiders with useable PLE showed orientation

Condition	Orientation		Long range approach		Display	
	♀	♂	♀	♂	♀	♂
Untreated	6	6	8	7	3	5
Empty arena	0	0	0	0	0	0
Fully blind	0	0	0	0	0	0
No PLEs	6	7	10	4	5	3
No PMEs	10	6	0	0	0	4
No ALEs	10	7	9	5	4	3
No AMEs	10	6	9	6	4	3
Only PLEs	10	7	0	0	0	5
Only PMEs	9	6	10	5	5	2
Only ALEs	3	1	0	0	0	0
Only AMEs	0	0	0	0	0	0

TABLE 1. Number of ♀ and ♂ spiders responding to video playback. $N = 10$ spiders/sex/condition. Each spider was allowed more than one trial to respond: controls, up to two trials; experimentals, up to five trials. Only ♂♂ that also performed orientation or approach are included under 'Display'.

turns of up to about 160°. Those with only the PME useable performed orientation turns of up to about 50°. If near the stimulus, those with only the ALE useable showed orientation turns of up to about 20°.

During playback of male courtship, only those females with non-occluded PME performed leg-waving receptive displays (Table 1). This brief display occurred 3.0 ± 1.9s ($N = 30$) after the abrupt termination of the male's courtship bout. The receptive display was sometimes performed unimpeded, this being the case in females which had not yet reached the front of the cage. However, it was usually constrained, since most females quickly approached the cage front and rested their anterior legs against the wall. Still, the timing of their response remained precise. Females showed this display while seeing anterior or lateral views of the courting male.

Up to 6/10 of the males tested in each condition performed courtship display, which occurred in every group. It even occurred in two males during the empty arena playback and in three of the fully blinded males, such data reflecting a previously noted readiness of *R. rabida* to sometimes court in response to subnormal stimuli (Rovner, 1968). Perhaps these non-visually stimulated courtships were triggered by mechanical cues resulting from my moving the cage to the testing site or from my positioning the spider with a brush (to duplicate the procedure used on experimental spiders). For this reason, only courtships occurring during trials in which orientation or approach also occurred were scored as visually initiated displays. (This may have prevented some visually stimulated males that were facing the stimulus at the outset from being included in the courtship total for some experimental groups.) Only males with useable PLE or PME showed courtship accompanied by orientation, and only males with non-occluded PME showed courtship accompanied by approach (Table 1).

DISCUSSION

Data presented here indicate that *R. rabida*'s posterior eyes play major roles in mediating responses to important visual stimuli, as was earlier predicted for lycosids on anatomical grounds (Homann, 1931; Land, 1981). The PLE serve the same function that they do in salticid spiders, that of detecting stimuli in an extensive visual field and initiating the largest orientation turns. They cannot mediate approach behaviour. On the other hand, the PME are essential for mediating rapid, long-range approaches to stimuli. They can also initiate orientation turns of up to 50°.

As to the anterior eyes, at close range the ALE can play small roles in orientation and approach. This contradicts Land's (1981) suggestion that only the large posterior eyes are involved in prey capture. As predicted for lycosids by Land (*ibid.*), the AME of *R. rabida* play no role by themselves in mediating turns or approaches toward a target. Whether they serve for other than polarized light detection (Magni *et al.*, 1964) remains to be explored.

The present findings on the anterior eyes of *R. rabida* may not apply to all lycosids. For example, unlike *R. rabida*, in *Arctosa variana* the AME are larger than the ALE (*ibid.*). Also, local tiering is found in the retinae of the AME of *Geolycosa godeffroyi* but not in the type genus *Lycosa* (Blest and O'Carroll, 1989). Furthermore, the finding of high nocturnal sensitivity in the anterior eyes of *Lycosa tarentula* (Carricaburu *et. al.*, 1990) suggests that an understanding of the capabilities of the anterior eyes of lycosids will require examining different species under various illumination conditions. Finally, I must point out that I did not test for any possible collaboration between different pairs of eyes. Collaborative visual mechanisms were revealed in salticid spiders by ipsilateral blinding (Forster, 1979).

As in the salticids (Forster, 1985), orientation and approach are the initial behavioural responses of lycosid spiders to moving images, whether prey or mating partners. Thus, the performance of such behaviours does not specify the spider's motivational state. However, the fact that twice as many trials were needed to obtain these behaviours in males as in females suggests that such initial responses relate primarily to predation, i.e., that adult females, on average being hungrier than males, are more responsive to visual stimulation. A subsequent occurrence of display behaviour indicates a switch to sexual motivation.

For display to occur in females the PME have to be useable, and they are sufficient by themselves for mediating this response. The fact that lateral as well as anterior views of the courting male elicited responses suggests that the cue is movement of the male's black leg I: it extends forward in a pumping-like motion of increasing frequency and then abruptly flexes back. Unlike salticid face-to-face courtship, in which the perceived form of the male may be as important for the female as his behaviour (*ibid.*), female *R. rabida* need not view the male's anterior. Apparently, detection of a temporal pattern of movement suffices for recognition.

As to visually-triggered courtship display, male *R. rabida* differ from male salticids, which require one particular pair of eyes, the AME (*ibid.*). Stimulation of either pair of a male *R. rabida*'s posterior eyes suffices for triggering courtship. If the PLE are involved, orientation precedes display. If the PME are involved, approach can precede display, although it need not do so.

Given that the movement-detecting PLE are sufficient for courtship onset in *R. rabida*, an adequate stimulus in this species may be any object of an appropriate size, speed, and perhaps movement pattern entering the extensive visual field of the PLE. Since the other three pairs of lycosid eyes are also assumed to be movement detectors (Land, 1981), there may be no need to require their involvement in additional visual analysis before initiating courtship. However, this may not be true for all lycosids. In particular, female *Pardosa laura* have been hypothesized to use form vision for species discrimination (Suwa, 1984). If male *P. laura* likewise do so, eyes other than the PLE would be have to be used for such form analysis in order to inititate courtship.

LITERATURE CITED

ACOSTA, J., ORTEGA, J. & RODRIGUEZ-SANABRA, F. 1982. Vision and predatory behaviour in *Lycosa fasciiventris*. 6th European Neuroscience Congress, Malaga, Spain: 21-22.

BLEST, A.D. & O'CARROLL, D. 1989. The evolution of the tiered principal retinae of jumping spiders (Araneae: Salticidae). Pp. 155-170. In R.N. Singh and N.J. Strausfeld (eds). 'Neurobiology of sensory systems'. (Plenum Press: New York).

CARRICABURU, P., MUÑOZ-CUEVAS, A. & ORTEGA-ESCOBAR, J. 1990. Electroretinography and circadian rhythm in *Lycosa tarentula* (Araneae, Lycosidae). Acta Zoologica Fennica 190: 63-67.

CLARK, D.L. & UETZ, G.W. 1990. Video image recognition by the jumping spider *Maevia inclemens* (Araneae: Salticidae). Animal Behaviour 40: 884-890.

FORSTER, L.M. 1979. Visual mechanisms of hunting behaviour in *Trite planiceps*, a jumping spider (Araneae: Salticidae). New Zealand Journal of Zoology 6: 79-93.

1985. Target discrimination in jumping spiders (Araneae:Salticidae). Pp. 249-274. In F.G. Barth (ed). 'Neurobiology of arachnids'. (Springer-Verlag: New York).

HOMANN, H. 1931. Beiträge zur Physiologie der Spinnenaugen. III. Das Sehvermögen der Lycosiden. Zeitschrift für Vergleichende Physiologie 14: 40-67.

LAND, M.F. 1981. Optics and vision in invertebrates. Pp. 471-592. In H. Autrum (ed). 'Comparative physiology and evolution of vision in invertebrates. Handbook of sensory physiology VII/6B'. (Springer-Verlag: New York).

MAGNI, F., PAPI, F., SAVELY, H.E. & TONGIORGI, P. 1964. Research on the structure and physiology of the eyes of a lycosid spider. II. The role of different pairs of eyes in astronomical orientation. Archives Italiennes de Biologie 102: 123-136.

ROVNER, J.S. 1968. An analysis of display in the lycosid spider *Lycosa rabida* Walckenaer. Animal Behaviour 16: 358-369.

1989. Wolf spiders lack mirror-image responsiveness seen in jumping spiders. Animal Behaviour 38: 526-533.

SUWA, M. 1984. Courtship behavior of three new forms in the wolf spider *Pardosa laura* complex. Journal of Ethology 2: 99-107.

THE SPATIAL DYNAMICS OF LINYPHIID SPIDERS IN WINTER WHEAT

K.D. SUNDERLAND AND C.J. TOPPING[†]

Sunderland, K.D. and Topping, C.J. 1993 11 11: The spatial dynamics of linyphiid spiders in winter wheat. *Memoirs of the Queensland Museum* 33 (2): 639-644. Brisbane. ISSN 0079-8835.

The density of linyphiid spiders was monitored accurately throughout the growing season in a field of winter wheat in southeast England in 1990 and 1991. Numbers increased until harvest in 1991, but declined before harvest in 1990, possibly due to drought conditions. The pattern of natality in 1991 closely mirrored the pattern of change in density, suggesting that reproduction, rather than immigration, was the predominant factor underlying the increase in density. Aerial activity, as measured by deposition traps and a rotary trap in the field, and a suction trap at the edge of the field, increased progressively during the growing season. Results from a short-term field caging technique, used to measure net migration rates, indicated that there was little immigration before July (thereafter high sampling variance, caused by aggregation in weedy patches, precluded meaningful analysis).□*Araneae, Linyphiidae, spatial dynamics, winter wheat, density, natality, migration.*

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There are few studies of the population dynamics of predators. For example, Stiling (1988), in an examination of the incidence of density-dependence in invertebrate populations, quotes 62 population dynamics studies; of these 60 relate to phytophages, 2 to parasitoids and none to predators. There are also few population dynamics studies of migratory species, because of the methodological problems involved in quantifying migration. The present study, of the population dynamics of linyphiid spiders (the species concerned are all migratory predators), was undertaken to collect some basic data in this neglected area, and also because these species are known to be valuable predators of crop pests (Sunderland *et al.*, 1986). This paper summarises the main trends for total linyphiids; consideration will be given to individual linyphiid species in later publications.

METHODS AND MATERIALS

Total spider density was measured throughout most of the growing season of 1990 in a 17ha field of winter wheat (c.v. Pastiche) in southeast England. In 1991, density, natality and migration were measured in a 3ha field of winter wheat (c.v. Riband), 24km from the 1990 study field. The fields were treated with agrochemical applications, following normal farm practice; insecticides were not required in either year.

DENSITY SAMPLING

Twenty-five $144m^2$ squares were marked out inside a 60 x 60m area (adjacent to one edge of the field in 1990 and 30m from the nearest edge in 1991). Fifteen density samples were taken at each sampling interval (approximately weekly) following a Latin Square design. The sample unit consisted of a randomly-selected $0.5m^2$ area of ground delimited by a metal ring and sampled using a vacuum insect net (D-vac). Vegetation and the top 1cm of ground, within the $0.5m^2$ sampled by D-vac, were then immediately hand-searched for spiders. The suction catch was kept at 10°C and returned to the laboratory for live-sorting. Therefore spiders were collected from $7.5m^2$ of habitat (crop, ground surface and immediate sub-surface) on each occasion (Topping and Sunderland, 1992). The D-vac collected only about 50% of the total number of spiders present in a sample unit, the other 50% were uncovered by hand-searching (see also Sunderland *et al.*, 1987).

NATALITY

Adult female linyphiids were collected from the field, adjacent to the 60 x 60m area, at weekly intervals and incarcerated individually in 9cm diameter plastic Petri dishes lined with moist filter paper. The dishes were returned immediately to a ventilated box in the study field and examined at weekly intervals. Mean daily temperatures in the Petri dishes did not diverge from field temperatures (measured on the ground surface, under weed cover) by more than 1°C (warmer in spring, cooler in summer). The dishes were inspected at weekly intervals and the following statistics recorded (i) proportion of spiders producing eggsacs in the first week of incarceration, (ii) time (days) to emergence of spiderlings, (iii) number of spiderlings emerging, and (iv) number of undeveloped eggs (by dissection of the eggsac). These results were used, in conjunction with information on the density of adult females, to calculate daily natality rates for each species and then combined to give a composite spider natality curve.

Net Migration Rate

Migration to and from small areas of the crop was suppressed by the use of ten stainless steel spider-proof cages. The cages were circular, $0.5m^2$ by 1m tall, and made of mesh with 3 x 2.5 perforations mm^{-2} (too small to allow passage of first instar linyphiid spiders). The bases of the cages were sealed with sufficient compacted soil to prevent entry or exit of any spiders. Total spider density inside the cages was assessed as above. Because the cages were moved to a new location within the Latin Square each week, there was assumed to be insufficient time for the processes of natality and mortality to be significantly affected by the changed microclimate inside the cages; therefore differences in the change in density from one week to the next between caged and uncaged parts of the crop were considered to be a measure of net migration.

Aerial Density of Spiders

A 46cm Propeller Suction Trap (Taylor, 1955), with an air throughput of $70m^3$ min^{-1} and a sampling height of 142cm above the ground surface, located at the edge of the study field, was emptied daily. In addition, a rotary insect net was used to collect spiders within the field, 25cm above the top of the crop canopy. The 10m long rotor arm travelled at 6.3m sec^{-1} and the 56 x 25cm net at the end of the rotor arm (which was designed to sample air isokinetically, (Taylor, 1962)) processed $53.8m^3$ min^{-1} and was also emptied daily. To measure rates of input of spiders into the field, a set of seven deposition traps were deployed at 15m intervals between the rotor and the 60 x 60m area. Each trap consisted of a 10cm deep, $1m^2$, fibreglass tray, filled with water and ethylene glycol (20:1) plus 1% detergent, fitting inside a $1.6m^2$ metal tray containing the same fluid. The outer tray acted as a barrier to prevent spiders walking from the crop into the inner tray, which therefore received only aerial immigrants. As the crop grew, the deposition traps were progressively raised on wooden supports to maintain the level of the fluid surface constantly at *ca.* 5cm above the top of the crop canopy. The traps were emptied at approximately weekly intervals.

Nomenclature follows Roberts (1987).

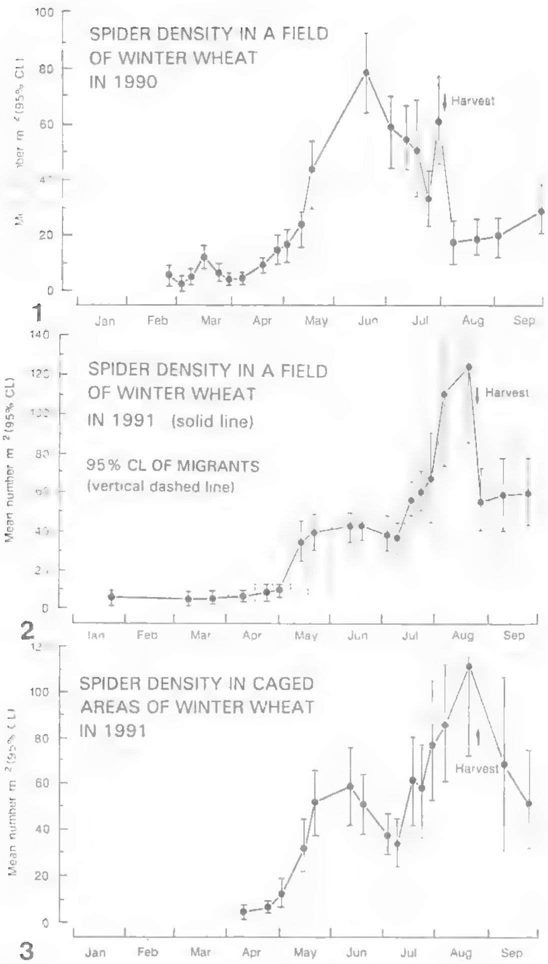
RESULTS

The study was based on data from more than 39,000 individuals belonging to 53 species. 12 species were dominant (Table 1). All species belong to the family Linyphiidae, with the exception of the tetragnathid *Pachygnatha degeeri*. *Lepthyphantes tenuis* was the most abundant species in 1991 and the second most abundant in 1990. Species composition was similar in the two years, the only notable differences being that *Meioneta rurestris* was relatively more abundant in 1990, the reverse being true for *Oedothorax* spp. Here, all spiders are treated as a group.

In 1990, density of total spiders increased in spring to reach a peak of $78m^{-2}$ on 18 June and thereafter declined, apart from a short-lasting peak (made up entirely of immature spiders) just before harvest (Fig. 1). The pattern was different in 1991 (Fig. 2); spider density built up in two steps (the first in May/June, the second in August) to reach a peak of $123m^{-2}$ just before harvest. Mean air temperatures in June and July were slightly higher in 1990 (15.1°C) than 1991 (14.9°C), but rainfall was considerably lower (68mm in 1990 cf 191mm in 1991). The semi-drought conditions in the summer of 1990 may have had a deleterious effect on spider survival.

Species	1990	1991
Meioneta rurestris (C.L. Koch)	32.5	5.4
Lepthyphantes tenuis (Blackwall)	27.8	31.3
Erigone atra (Blackwall)	9.8	13.3
Milleriana inerrans (O. P.-Cambridge)	5.2	0.4
Erigone promiscua (O. P.-Cambridge)	5.0	6.3
Erigone dentipalpis (Wider)	4.2	5.0
Pachygnatha degeeri Sundevall	2.0	0.2
Bathyphantes gracilis (Blackwall)	2.7	8.6
Oedothorax fuscus (Blackwall)	2.4	12.0
Oedothorax retusus (Westring)	2.1	3.9
Panamomops sulcifrons (Wider)	1.0	0.1
Oedothorax apicatus (Blackwall)	0.3	6.9
Others*	5.0	6.6

TABLE 1. Species composition of adult spiders in density samples in 1990 (n=1562) and 1991 (n=1457).



FIGS. 1-3. Total spider density in a field of winter wheat: 1990 (Fig. 1); 1991 (solid line) and 95% CL of number of migrants m^{-2} (vertical dashed lines) (Fig. 2); in caged areas, 1991 (Fig. 3).

Density in the caged areas of the crop in 1991 followed a similar pattern to that in uncaged areas (Fig. 3). 95% confidence limits increased during July and August (Figs 2, 3) due to aggregation of spiders in weedy patches of the crop (significantly more spiders in weedy than bare areas; paired t-test, $n = 5$ dates, $p = 0.05$).

The pattern of change in density with respect to time is examined, below, in relation to natality and migration for 1991.

Natality rates were *c.* $4m^{-2}$ day^{-1} in the spring, briefly 10-$15m^{-2}$ day^{-1} in late July, then $8m^{-2}$ day^{-1} in August. The pattern of daily natality was similar to the patterns for immature spider density (Fig. 4) and total spider density (Fig. 2); this is

Date	M	95% CL
9 April	2.1	(-1.2- 5.4)
23 April	2.2	(-2.3- 6.7)
1 May	-2.0	(-8.7- 4.7)
14 May	2.7	(-11.8-17.2)
21 May	-12.8	(-29.5- 3.9)
11 June	-16.5	(-33.9- 0.9)
18 June	-8.0	(-23.1- 7.1)
3 July	0.7	(-13.2-14.6)
9 July	2.9	(-10.4-16.2)
17 July	-5.1	(-26.7-16.5)
23 July	1.8	(-20.5-24.1)
29 July	-9.5	(-43.8-24.8)
5 August	24.2	(-19.9-68.3)
19 August	12.7	(-41.4-66.8)
9 September	-10.0	(-52.7-32.7)
24 September	7.1	(-19.6-33.8)

TABLE 2. Indices of net aerial migration, M (95% CL), in 1991.

circumstantial evidence that reproduction (as opposed to immigration) is the predominant process driving increase in density of spiders in the field. Data on migration can be examined in the light of this hypothesis. Aerial activity of spiders, as measured by catches in the 1.4m suction trap at the edge of the field, tended to increase steadily from March to August, and this was followed by a much larger increase in September (Fig. 5). A similar pattern of aerial activity was evident inside the field, as indicated by the catch in deposition traps and in the rotary trap (Fig. 6). To assess whether there had been a a net gain or loss of spiders from the field over a particular period, the density of spiders inside caged areas was compared with the density outside,to give an index of net migration (M);

$$M = (F2-F1)-(C2-F1) = F2-C2$$

where F1 and F2 are densities in the uncaged part of the field in weeks 1 and 2 respectively, and C2 is the density in the caged part of the field in week 2. (F2-F1 represents change in numbers due to natality, mortality and migration, whereas C2-F1 represents change in numbers due to natality and mortality alone, because migration was suppressed by caging). The standard error of M is calculated as the square root of [SE $F2^2$ + SE $C2^2$]; the 95% CL's on M are therefore large because they are compounded of two standard errors. Values of M are shown in Table 2. Positive values indicate immigration and negative values indicate emigration. However, all 95% CL's span the range from negative to positive and therefore no significant net migration can be demonstrated.

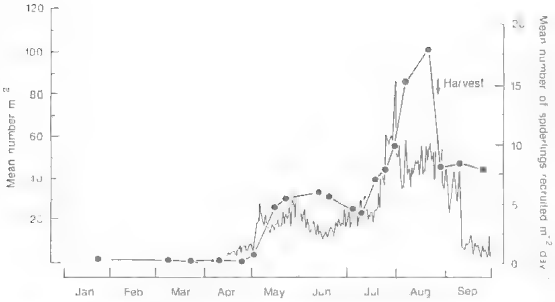
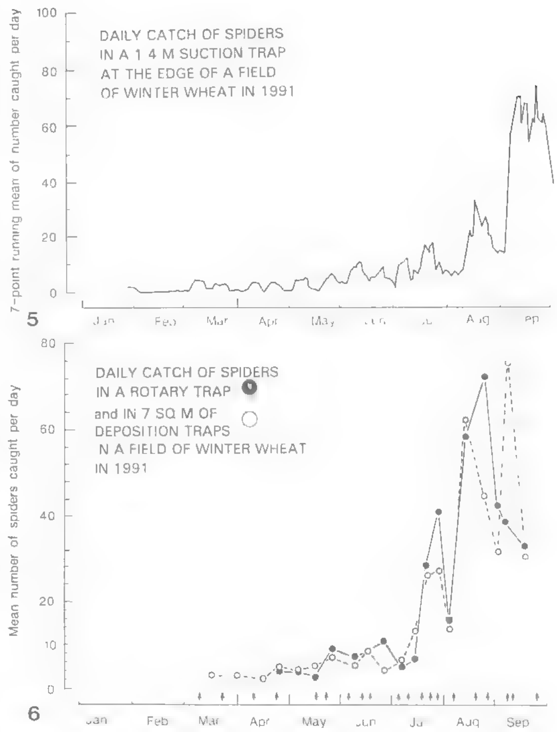


FIG. 4. Total immature spider density (●) and total spider natality (continuous line) in a field of winter wheat in 1991.

These 95% CL's are plotted on the curve of total spider density (Fig. 2); the extent of the dotted line above and below the density curve shows the amount of immigration and emigration, respectively, that could have occurred between any two dates. The following conclusions can be drawn; (i) any migration that may have occurred in April was small (i.e. on a similar scale to density sampling variance), (ii) if immigration occurred in May and June it must also have been on a small scale, but there could have been a large emigration, and (iii) in July, August and September 95% CL's were very large (due to spider aggregation, see above), with no obvious bias in favour of either immigration or emigration.



FIGS. 5, 6. Daily catch of total spiders in winter wheat field in 1991. 5. In 1.4m suction trap at edge of field; 6. In rotary trap (●) and in 7m^2 of deposition traps .

DISCUSSION

There appear to be no previous quantitative arachnological studies in which the seasonal patterns of natality and migration are compared with the seasonal pattern of density using consistent units. Examples of other arachnological studies involving density or natality estimation are given below. The majority of investigations where density has been measured are for grassland; peak densities of lycosid and linyphiid spiders vary greatly according to location (Table 3). Densities are often lower in graminaceous crops (Table 3). The peak spider density of 123m^{-2} in the present study is comparable with, if somewhat greater than, densities recorded in cereals by other authors (Table 3). In common with the present investigation, nearly all the studies in Table 3 reported large confidence limits due to aggrega-

Species	Family	Habitat	Density	Author(s)
Geolycosa godeffroyi (L.Koch)	Lycosidae	pasture	1	Humphreys, 1976
Trochosa terricola Thorell	Lycosidae	grass heath	70	Workman, 1978
Pardosa palustris (Linnaeus)	Lycosidae	alpine meadow	9	Steigen, 1975
Oedothorax fuscus (Blackwall)	Linyphiidae	pasture	155	De Keer and Maelfait, 1987
Erigone atra (Blackwall)	Linyphiidae	pasture	318	De Keer and Maelfait, 1988
Erigone arctica (White)	Linyphiidae	dune grass	330	van Wingerden, 1977
Total spiders		*Festuca* grass	840	Duffey, 1962
Total spiders		rye grass	43	Alderwiereldt, 1987
Total spiders		maize	49	Alderwiereldt, 1987
Oedothorax and *Erigone*	Linyphiidae	winter wheat	53	Nyffeler and Benz, 1988
Total linyphiids		winter wheat	60	Fraser, 1982
Total spiders		winter wheat	75	Sunderland 1987

TABLE 3. Maximum density estimates (number m^{-2}) in a range of arachnological studies.

tion of spiders. There seem to be no previous publications describing the seasonal pattern of spider natality, but a few authors (eg Steigen, 1975; Workman, 1978) have recorded natality at specific times of year. Schaefer (1978) estimated the egg density of the linyphiid *Floronia bucculenta* in grassland during the spring to be 98-151m^{-2} depending on location. The maximum spring natality of the linyphiid *Erigone arctica* in coastal grassland was claimed to be 2584m^{-2} (van Wingerden, 1977), which is considerably greater than the total natality (8 dominant linyphiids) of 789m^{-2} between March and October in the present study; this difference may underly the relative sparseness of spiders in crops compared with natural grassland (Table 3). Although the intensity of aeronautic activity has been measured using sticky traps (Duffey, 1956, van Wingerden, 1977, Greenstone *et al.*, 1985), window traps (Meijer, 1976; De Keer and Maelfait, 1987, 1988) and suction traps (Dean and Sterling, 1985; Sunderland, 1987, 1991), there appear to be no previous attempts to directly quantify the impact of migration on population density. The use of short-term field cages in the present study provided useful estimates of the upper limits to migration (except when sampling variance became very large) and it is expected that this technique will yield better results when data are analysed for individual species. In addition, when the rotary trap has been calibrated, it should be possible to estimate rates of aerial immigration and emigration from a comparison of deposition and rotor catches.

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LITERATURE CITED

ALDERWEIRELDT, M. 1987. Density fluctuations of spiders on maize and Italian ryegrass fields. Mededelingen van de Fakulteit Landbouwwetenschappen Rijksuniversiteit Gent 52: 273-282.

DEAN, D.A. & STERLING, W.L. 1985. Size and phenology of ballooning spiders at two locations in eastern Texas. Journal of Arachnology 13: 111-120.

DE KEER, R. & MAELFAIT, J.P. 1987. Life history of *Oedothorax fuscus* (Blackwall, 1834) (Araneae, Linyphiidae) in a heavily grazed pasture. Revue d'Ecologie et de Biologie du Sol 24: 171-185.

1988. Observations on the life cycle of *Erigone atra* (Araneae, Erigoninae) in a heavily grazed pasture. Pedobiologia 32: 201-212.

DUFFEY, E. 1956. Aerial dispersal in a known spider population. Journal of Animal Ecology 25: 85-111.

1962. A population study of spiders in limestone grassland. Journal of Animal Ecology 31: 571-599.

FRASER, A.M. 1982. 'The role of spiders in determining cereal aphid numbers'. Thesis (University of East Anglia) 121p.

GREENSTONE, M.H., MORGAN, C.E. & HULTSCH, A.L. 1985. Spider ballooning: development and evaluation of field trapping methods (Araneae). Journal of Arachnology 13: 337-345.

HUMPHREYS, W.F. 1976. The population dynamics of an Australian wolf spider, *Geolycosa godeffroyi* (L. Koch 1865) (Araneae: Lycosidae). Journal of Animal Ecology 45 : 59-80.

MEIJER, J. 1976. The immigration of spiders (Araneida) into a new polder. Ecological Entomology 2: 81-90.

NYFFELER, M. & BENZ, G. 1988. Prey and predatory importance of micryphantid spiders in winter wheat fields and hay meadows. Journal of Applied Entomology 105: 190-197.

ROBERTS, M.J. 1987. 'The spiders of Great Britain and Ireland, Vol. 2,'(Harley Books: Colchester, England)

SCHAEFER, M. 1978. Some experiments on the regulation of population density in the spider *Floronia bucculenta* (Araneida: Linyphiidae). Symposia of the Zoological Society of London 42: 203-210.

STEIGEN, A.L. 1975. Energetics in a population of *Pardosa palustris* (L.)(Araneae, Lycosidae) on Hardangervidda. Pp. 129-144. In F. Wielgolski (ed). 'Fennoscandian tundra ecosystems Part 2'. (Springer: Berlin).

STILING, P. 1988. Density-dependent processes and key factors in insect populations. Journal of Animal Ecology 57: 581-593.

SUNDERLAND, K.D. 1987. Spiders and cereal aphids in Europe. Bulletin SROP/WPRS 1987/X/1: 82-102.

1991. The ecology of spiders in cereals. Proceedings of the 6th International Symposium on Pests and Diseases of Small Grain Cereals and Maize. Board of Plant Protection, Halle/Saale, Germany 1:269-280.

SUNDERLAND, K.D., FRASER, A.M. & DIXON, A.F.G. 1986. Field and laboratory studies on money spiders (Linyphiidae) as predators of cereal aphids. Journal of Applied Ecology 23: 433-447.

SUNDERLAND, K.D., HAWKES, C., STEVENSON T., MCBRIDE, L.E., SMART, L.E., SOPP, P.I., POWELL, W., CHAMBERS, R.J. & CARTER, O.C.R. 1987. Accurate estimation of invertebrate density in cereals. Bulletin SROP/WPRS 1987/X/1: 71-81.

TAYLOR, L.R. 1955. The standardization of air-flow in insect suction traps. Annals of Applied Biology 43: 390-408.

1962. The absolute efficiency of insect suction traps. Annals of Applied Biology 50: 405-421.

TOPPING, C.J. & SUNDERLAND, K.D. 1992. Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat. Journal of Applied Ecology 29: 485-491.

WINGERDEN, W.K.R.E. VAN 1977. 'Population dynamics of *Erigone arctica* (White) (Araneae, Linyphiidae)'. (Thesis, Free University: Amsterdam). 147pp.

WORKMAN, C. 1978. Life cycle and population dynamics of *Trochosa terricola* Thorell (Araneae: Lycosidae) in a Norfolk grass heath. Ecological Entomology 3: 329-340.

MORPHOLOGY OF THE EMBRYOS AT GERM DISK STAGE IN *ACHAEARANEA JAPONICA* (THERIDIIDAE) AND *NEOSCONA NAUTICA* (ARANEIDAE)

HIROHUMI SUZUKI AND AKIO KONDO

Suzuki, H. and Kondo, A. 1993 11 11: Morphology of the embryos at germ disk stage in *Achaearanea japonica* (Theridiidae) and *Neoscona nautica* (Araneidae). *Memoirs of the Queensland Museum* 33(2): 645-649. Brisbane. ISSN 0079-8835.

Embryos at the germ disk stage were investigated by electron microscopy in *Achaearanea japonica* (Theridiidae) and *Neoscona nautica* (Araneidae). In both spiders, the germ disk was composed of spherical cells, which had almost no large yolk granules. In the inner part of the embryo, several large yolk granules were packed by cell membrane with various organelles and glycogen granules similarly to lycosid spiders. In *Achaearanea japonica* there were very flat cells which possessed several large yolk granules in the surface region where the germ disk was not formed. In *Neoscona nautica* cells were not observed in that region at all, so the packages of large yolk granules were exposed directly to perivitelline space. The araneid type can be distinguished from the agelenid and theridiid type.
Die Embryonen von *Achaearanea japonica* (Theridiidae) und *Neoscona nautica* (Araneidae) im Stadium der Keimscheibe wurden mittels des Elektronenmikroskops untersucht. Die Keimscheiben der beiden Spinnen bestanden aus sphärischen Zellen, die große Dotterkörnchen nur selten hatten. In dem inneren Teil von dem Embryo wurden manche großen Dotterkörnchen mit verschiedenen Organellen und Glykogenkörnchen von der Zellmembran gepackt, wie im Falle von den lycosiden Spinnen. Im Falle von *Achaearanea japonica* gab es sehr flache Zellen, die manche großen Dotterkörnchen hatten, in dem oberflächlichen Bezirk, wo die Keimscheibe nicht gebildet wurde. Im Falle von *Neoscona nautica* wurden die Zellen in dem Bezirk schließlich nicht beobacht, also waren die Packe von großen Dotterkörnchen direkt in der Perivitellinhöhle entblößt. Der araneide Typus soll sich von dem ageleniden Typus und dem theridiiden Typus unterscheiden. ☐*Spider, Achaearanea, Neoscona, embryo, germ disk, morphology.*

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Three types of germ disk formation are known in the embryos of spiders. In the most common type known in Agelenidae, the germ disk is formed on a hemisphere of the egg as the result of transformation of squamous blastoderm cells in this region into spherical cells. Egg surface of the other hemisphere is covered with squamous cells (Holm, 1952). In the second type known in Theridiidae, the most blastoderm cells converge

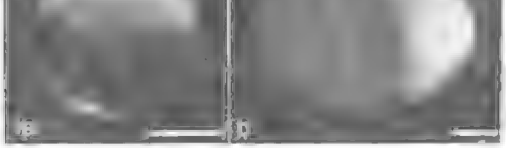
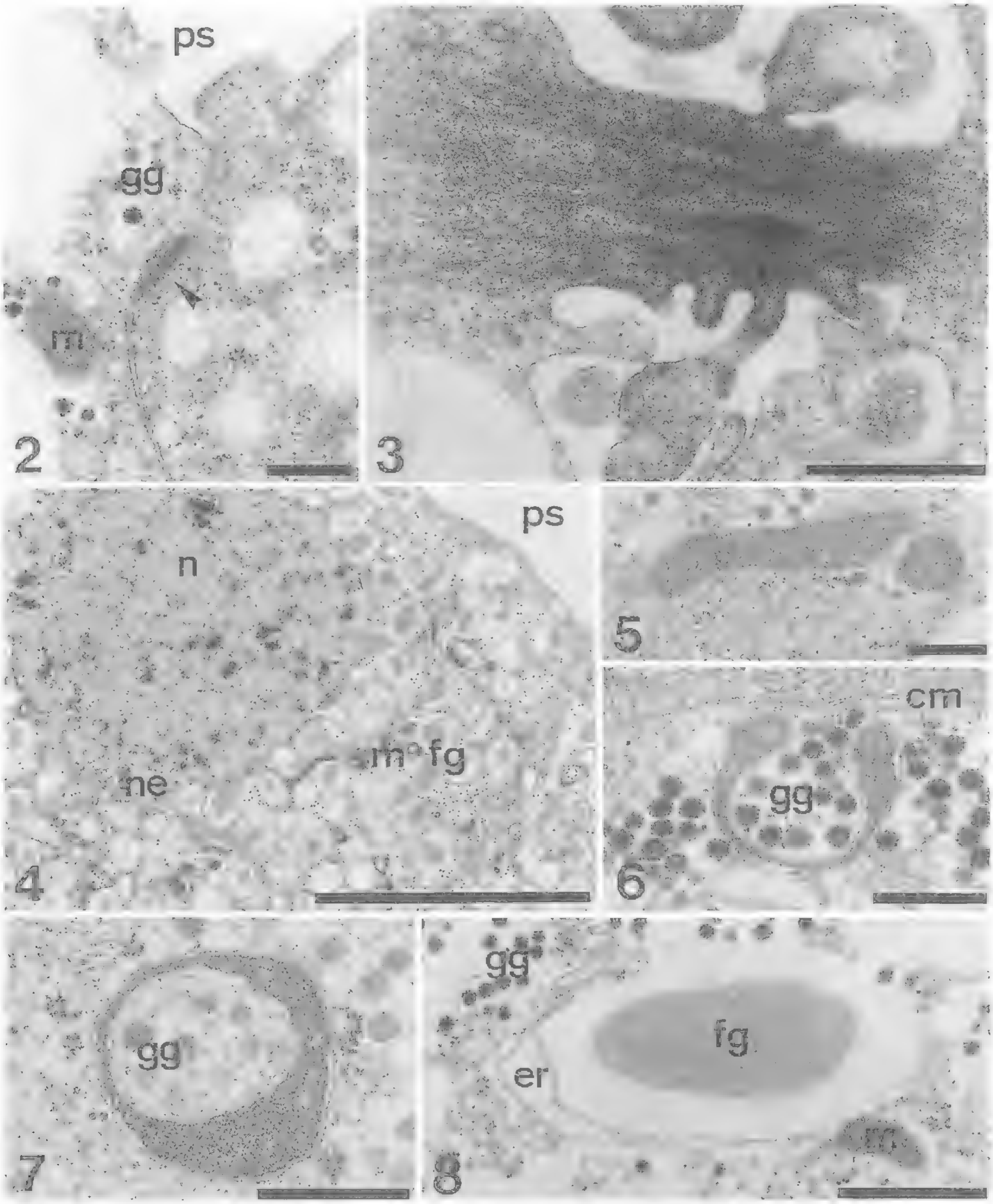


FIG. 1. The embryo at germ disk stage in *Achaearanea japonica* (a) and *Neoscona nautica* (b). In *A. japonica*, a few cells are found on region where germ disk is not formed. In *N. nautica*, exposed yolk mass is found on that region. Scale=0.2mm.

on the germ disk region and few cells remain on the other hemisphere (Montgomery, 1909). In the third type found in many Araneidae, a rip appears in the blastoderm, so the yolk mass is exposed (Sekiguchi, 1957). Then all blastoderm cells take part in germ disk formation, and any cells are not observed in the region where the germ disk is not formed. A comparative study of the spider embryos at germ disk stage was carried out under light microscope (Kondo and Yamamoto, 1975). The study of germ disk formation under electron microscope was executed in lycosid spiders, whose germ disk formation is the agelenid type (Kondo, 1969, 1970). We had to examine whether remaining cells connect each other or not in theridiid type and whether extreme thin cells exist or not at the superficial region where the germ disk is not formed in araneid type. In present study, electron microscopic investigation of the embryos at germ disk stage was carried out in *Achaearanea japonica* and *Neoscona nautica*.



FIGS. 2-8. 2. *A. japonica*. Peripheral region of two germ disk cells. (0.5μm.) Arrowhead: Desmosome-like structure, 3. A mid-body. Many microtubules. (1μm.) 4. A germ disk cell. Main components of cytoplasm are fatty granules (fg) with medium electron dense matrix, and no large yolk granules. (10μm.) n: nucleus, ne: nuclear envelope. 5. Mitochondria have high electron dense matrix and the cristae are found faintly. (0.5μm.) 6. Cup-shaped mitochondrion. (0.5μm). cm: cell membrane. 7. Ring-shaped mitochondrion. (0.5μm.) 8. Fatty granule (fg) lacking complete limiting membrane, but partly enclosed by smooth-surfaced endoplasmic reticulum (er). (1μm.) gg: glycogen granules, m: mitochondria, ps: perivitelline space. Scales in parentheses.

MATERIALS AND METHODS

Achaearanea japonica (Bösenberg and Strand) (Theridiidae) and *Neoscona nautica* (L. Koch) (Araneidae) were used here. In *A. japonica*, the eggs collected in August were used. In *N. nautica*, the eggs laid in glass tubes at laboratory were used. The observation of the live eggs was carried out in liquid paraffin, where the opaque chorion became transparent. The eggs were fixed for 3 hours at 4°C in 2% paraformaldehyde and 2.5% glutaraldehyde solution in 0.1M phosphate buffer, pH 7.4, containing 0.2M sucrose. Through fixation, the eggs were cut in half with a tungsten needle. After rinsing more than one hour with the same buffer containing 0.2M sucrose, the samples were postfixed for one hour at 4°C in 2% osmic acid in 0.1M phosphate buffer, pH 7.4, without sucrose. After rinsing with the same buffer without sucrose, samples were dehydrated in ethanol series, transferred to propylene oxide, and embedded in Quetol-812. Ultrathin sections were cut on a ultra-microtome, LKB-4800, stained with uranyl acetate and lead citrate, and examined under Hitachi HU-12A electron microscope. Thick sections were prepared simultaneously, and stained with methylene blue for light microscopy.

RESULTS

Achaearanea japonica

The eggs were spherical and 0.5mm in diameter. Typical theridiid type germ disk formation was observed (Fig. 1a). At 25°C, the eggs took 24 hours to the germ disk stage after oviposition.

The germ disk was formed as a single layer composed of spherical cells, but the cells piled up in its central region. The diameter of germ disk cells was about 30μm, and that of nuclei was about 15μm. Desmosome-like structures were observed between germ disk cells at the superficial region (Fig. 2), but interdigitations were not observed. Mid-bodies were observed rarely (Fig. 3). Narrow cytoplasmic bridge connected cells adjacent to each other, and contained many microtubules.

The main components of cytoplasm were fatty granules, 1-3μm in diameter, with a matrix of a medium electron density (Figs 4, 8). The limiting membrane was often obscure. The germ disk cell had almost no large yolk granules. Fine yolk granules, less than 5μm in diameter, were observed.

Mitochondria had a high electron dense matrix, and the cristae were found faintly (Fig. 5). Many figures of mitochondria showed oval or curved bars, and several showed cups (Fig. 6) or rings (Fig. 7).

Smooth-surfaced endoplasmic reticula were often found enclosing fatty granules (Fig. 8). Rough-surfaced endoplasmic reticula were not observed.

Typical Golgi bodies were rare. Vesicles were generally observed in the cytoplasm. The glycogen granules, 0.1μm in diameter, were very high electron dense, and scattered.

The superficial region where the germ disk was not formed was occupied by remaining flat cells. These cells were about 100μm in length, about 25μm in thickness at the central part, but often less than 1μm near the peripheral one (Fig. 9). The diameter of nuclei was about 13μm. Desmosome-like structures were observed between remaining cells (Fig. 9).

Several large yolk granules occurred in these remaining cells. The largest yolk granule was 20μm in diameter. Vesicles were sometimes arranged along the large yolk granules (Fig. 10).

The interior of the embryo was filled with yolk packages composed of several large yolk granules, various organelles and glycogen granules, and enclosed by cell membrane (Fig. 11).

Neoscona nautica

Ellipsoidal eggs of *N. nautica* had longer axis measuring 1.2mm and shorter axis measuring 1mm. At 23°C, 45 hours were needed from oviposition to establish the germ disk (Fig. 1b).

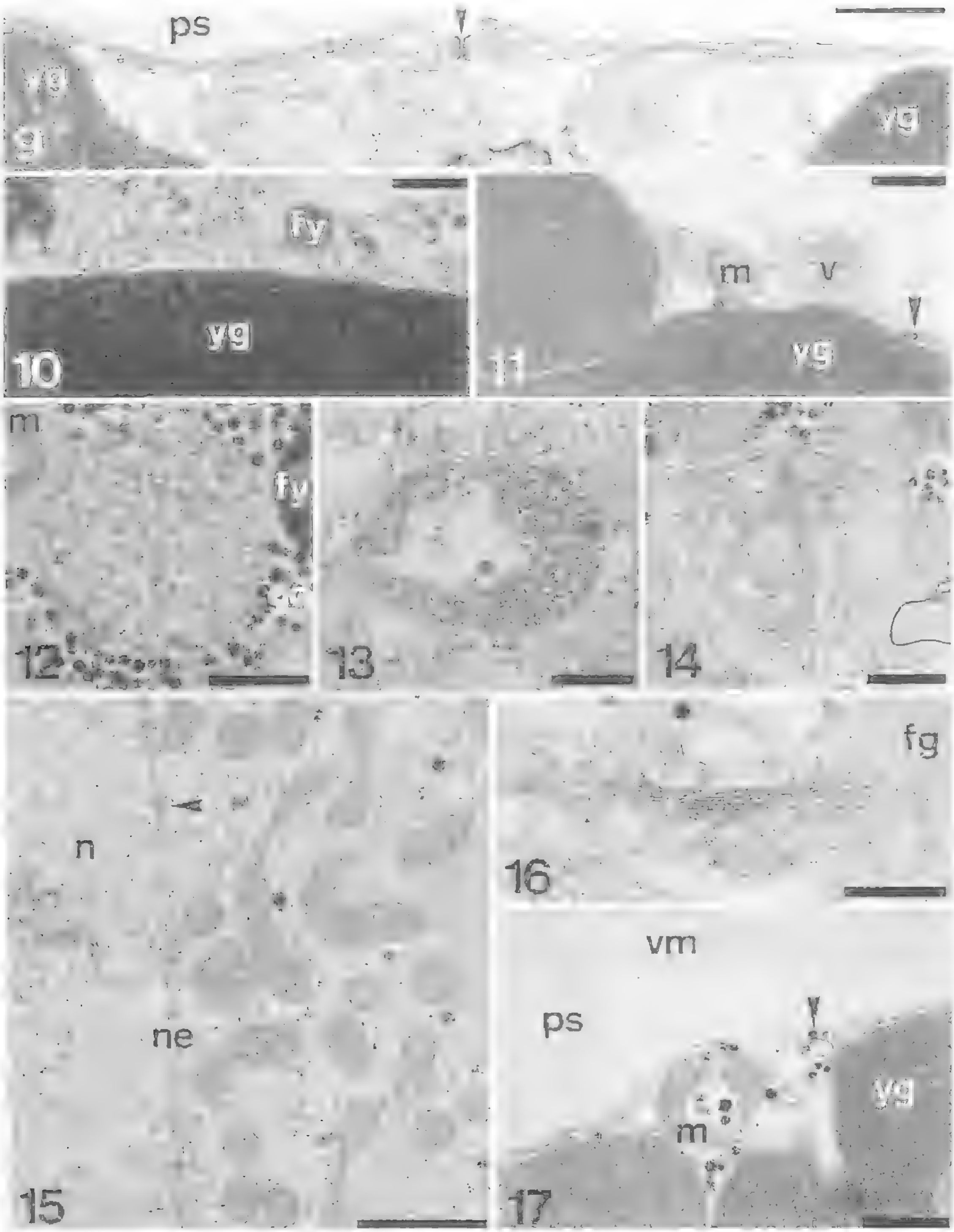
The germ disk was a single layer of spherical cells, but the cells piled up in its central region. The cell diameters were about 45μm, and those of nuclei were about 20μm. Between these cells, there were desmosome-like structures but no interdigitations.

Various types of lysosome-like bodies were observed (Figs 12-14). Mitochondria often crowded around the nucleus (Fig. 15). Several Golgi bodies were observed (Fig. 16). Other components of cytoplasm were similar to those of *A. japonica*.

No blastoderm cells were observed in the surface region where the germ disk was not formed (Fig. 17).

DISCUSSION

In this study, some cup- or ring-shaped



mitochondria were observed. These types of mitochondria were not reported in the embryos of lycosid spiders (Kondo, 1969, 1970), but they were figured in embryo of *A. tepidariorum* (Suzuki and Kondo, 1991). In *N. nautica*, many mitochondria were found surrounding the

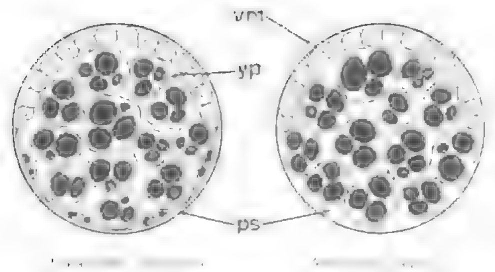


FIG. 18. Schematic figures of embryos at germ disk stage in *A. japonica* (left) and *N. nautica* (right). In both spiders, the germ disk is composed of spherical cells, which have almost no large yolk granules. The interior of the embryos is filled with yolk packages (yp). In *A. japonica*, there are very flat cells which possess several large yolk granules in the surface region where the germ disk is not formed. In *N. nautica*, any cells are not found in that region, so the yolk packages are exposed directly to perivitelline space (ps). vm: vitelline membrane.

nucleus. This phenomenon was reported in lycosid spiders (Kondo, 1969). In *N. nautica*, many lysosome-like bodies, described also in lycosid spiders (Kondo, 1969), were observed, however histochemical studies are needed for final identification.

In both spiders, *A. japonica* and *N. nautica*, interdigitations were not observed, but they were reported in germ disk region of lycosid spiders (Kondo, 1970).

In the inner part of the embryo in both spiders, several large yolk granules were packed by cell membrane with various organelles and glycogen granules. These structures were described as yolk spheres in lycosid spiders (Kondo, 1969). Since nucleus was not observed in them, these packages of large yolk granules were distinguished from yolk cells. In this investigation, detailed observation of yolk cells was not carried out.

The embryo at germ disk stage in *A. japonica* had very flat cells with several large yolk granules (Fig. 18). Distinct differences of cytoplasm were not observed between spherical germ disk cells and flat remaining cells. As in *A. tepidariorum* (Suzuki and Kondo, 1991), except for the large yolk granules and extreme flat shape in the remaining cells, the fine structure of embryo at germ disk stage in *A. japonica* was similar to that in lycosid spiders belonging to agelenid type.

In *N. nautica*, the yolk packages were exposed directly to the perivitelline space (Fig. 18).

LITERATURE CITED

HOLM, Å. 1952. Experimentelle Untersuchungen über die Entwicklung und Entwicklungsphysiologie des Spinnenembryos. Zoologiska Bidrag från Uppsala 29: 293-424.

KONDO, A. 1969. The fine structure of the early spider embryo. The Science Reports of the Tokyo Kyoiku Daigaku, Section B 207: 47-67.

1970. Morphological study on the spider's embryonic cells at germ disk stage. Japanese Journal of Developmental Biology 24: 20-21. (in Japanese)

KONDO, A. & YAMAMOTO, N. 1975. Comparative morphology on the early spider embryos. Atypus 63: 13. (in Japanese)

MONTGOMERY, T. H. 1909. The development of *Theridium*, an Aranead, up to the stage of reversion. Journal of Morphology 20: 297-352.

SEKIGUCHI, K. 1957. Reduplication in spider eggs produced by centrifugation. The Science Reports of the Tokyo Kyoiku Daigaku Section B 8: 227-280.

SUZUKI, H. & KONDO, A. 1991. Fine structure of the germ disk in the theridiid spider, *Achaearanea tepidariorum* (C. Koch). Proceedings of Arthropodan Embryological Society of Japan 26: 11-12.

FIG. 9-17. 9-11. *A. japonica* 9. Extreme flat shape in peripheral part of remaining cells. A desmosome-like structure (Arrowhead) is found between cells. (1μm). 10. A large yolk granule included in remaining cell. Arranging vesicles along yolk granule (0.5μm). 11. Peripheral part of yolk package in inner part of embryo. Large yolk granules, a ring-shaped mitochondrion (m), vesicles (v), and glycogen granules (arrowhead) are packed by cell membrane. (1μm).
12-17. *N. nautica* 12. A lysosome-like body including amorphous matrix. A ring-shaped mitochondrion (m) is found. (1μm) 13. A lysosome-like body including many small vesicles (1μm). 14. A lysosome-like body including several double membranes or myelin-like structure. (1μm) 15. Mitochondria around nucleus (n) showing nuclear pore (arrowhead) and nuclear envelope (ne)(1μm). 16. A Golgi body. (0.5μm). 17. Superficial region where germ disk is not formed. A yolk package composed of large yolk granules (yg), a cup-shaped mitochondrion (m), glycogen granules (arrowhead), and vesicles are exposed directly to perivitelline space (ps). (1μm) Abbreviations: fg: fatty granule, fy: fine yolk granule, gg: glycogen granules, ps: perivitelline space, yg: yolk granule, vm: vitelline membrane. Scale line in parentheses.

AN EXPERIMENT ON COLONIZATION OF KARAKURT (*LATRODECTUS TREDECIMGUTTATUS*, BLACK WIDOW SPIDER) ON ISLAND TERRITORIES IN KAZAKHSTAN

CHINGIS K. TARABAEV

Tarabaev, C.K. 1993 11 11: An experiment on colonization of karakurt (*Latrodectus tredecimguttatus*, Black Widow spider) on island territories in Kazakhstan. *Memoirs of the Queensland Museum* **33**(2): 651-652. Brisbane. ISSN 0079-8835.

To create an artificial, controllable population of *Latrodectus tredecimguttatus* (karakurt) with the aim of collecting venom, an experiment on mass colonisation of southern population spiders on an island territory was carried out. Retardation of the overwintering stage under laboratory conditions ensured the availability of large numbers of karakurt for colonisation and eliminated its uncontrollable reproduction in neighbouring territories.

Pour créer une population artificiele bien contrôlée des *Latrodectus tredecimguttatus* (karakurt) dans le but d'obtenir du venin on a mis une expérience de la dissémination des Araignées de la population méridionale sur le territoire insulairs. Le delai du stade hivernant dans les conditions de laboratoire assure la stabilisation du nombre de masse de karakurt pour leur colonisation et élimine leur reproduction non-contrôlée sur les territoires adjacents. □*Colonisation, karakurt, egg sacs, Latrodectus.*

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In Kazakhstan, mass annual collections of venom-producing arachnids are carried out to obtain their venom for medicinal and other purposes. Black widow spiders ('karakurt', *Latrodectus tredecimguttatus* (Rossi)) are caught in the greatest numbers. At the same time, their abundance varies from year to year: quite often periods occur during which one can hardly find a single specimen (see Marikovskij, 1956; Levi, 1983; Tarabajev, 1990). A bite from a karakurt is an appreciable danger. Hence, during periods of great abundance, it must be controlled. In connection with this problem, we carried out an experiment on karakurt colonisation on an island with the aim of creating an abundant and controllable artificial population.

MATERIALS AND METHODS

The experiment was performed on the small island 'Malyj' (1.4km^2) in Alakol' Lake (46°08'N, 81°52'E) near the northern border of the known karakurt distribution: the 2nd instar spiderlings emerging from egg sacs are often affected here by the late frosts which occur in April-May (Tarabajev, 1990). In contrast, the development of spiders is critically restricted by the shortened warm season: if the postembryos within the egg sacs have no time to develop into the overwintering 1st instar spiderlings, they die during winter (Marikovskij, 1956). This phenomenon stipulated the possibility of creating a numerous, yet controllable karakurt population. To do so we retarded the development of spiderlings and then released the 2nd instars over the island. As a result, the spiderlings avoid the disastrous late frosts but the postembryos of the new generation in their egg sacs would not have time to develop into overwintering 1st instar spiderlings. This phenomenon is therefore the necessary condition for the possibility of creating a controllable karakurt population, as well as for elimination of uncontrollable mass reproduction of spiders on the neighbouring territories. For the intensification of degree-days deficit effect, the spiderlings from 500 egg sacs of *Latrodectus tredecimguttatus* collected in Uzbekistan (southern population from Dzhizak Steppe) were used in our experiment. Before the colonisation we made a census of the native population of karakurt on the island.

During winter, egg sacs of southern population spiders with overwintering first instar spiderlings were kept in the laboratory (temperature 0-5°C). In the second half of May these were placed into a gauze-covered 20 litre vessel at room temperature (18-22°C), for their reactivation from winter diapause. After moulting in their egg sacs, many spiderlings emerged; then the vessel which contained them was placed in a refrigerator (4-5°C) until June.

Before mass colonisation, a census of the natural karakurt population on 'Malyj' Island was carried out by the visual investigation of the whole island territory fit for the settling by the southern population spiders of karakurt (ca. 8500 m^2).

RESULTS

While making a census of the native karakurt population on 'Malyj' Island before mass colonisation on 12 June 1988, we found one nest from the previous year with two empty egg sacs, and two more old nests. Six living karakurt specimens of 4-5th instar were also found. By late August there were 3726 nests from the southern population, or one specimen per 2-3m^2. Three females of the native karakurt population were also found: they differed by their larger size (no females were measured). In 28 nests of southern population spiders there was only one egg sac per nest: no egg sacs were found in the rest, while in three nests of native population spiders there were two egg sacs in each. Dissection of egg sacs confirmed our views. In four egg sacs of the native karakurt population there were postembryos, in two there were first instar spiderlings, while only eggs were found in 20 egg sacs of the southern population.

Of 100 nests examined in May 1989, 74 nests were without egg sacs–some nests were ruined; 26 nests each had one egg sac, all eggs were dead. These results confirmed that due to the artificially retarded development of southern population spiders in the northern conditions of Alakol' Lake the eggs had died within the egg sacs as they had insufficient time to develop to the overwintering first instar spiderlings (the average Alakol' area temperature in September is no more than 10-15°C).

We therefore propose the following scheme for the creation of many controllable artificial black widow populations for the purpose of obtaining venom.

In August-September, mass collection of females must be carried out. These females are kept in collection boxes for 2-3 weeks until they lay their egg sacs in these boxes. (This phenomenon was first noticed by us when studying the technique of mass collecting from the field). Females are subsequently used for obtaining venom while egg sacs are kept at room temperature until the 1st instar spiderlings emerge (overwintering stage). After that the egg sacs must be kept in a refrigerator at 0-5°C until the following season.

After the reactivation of spiderlings in spring, they are released over the island, which they recolonised effectively. Every August-September, mass collection of females is carried out, and the cycle is renewed.

Thus, the indubitable advantage of our method is the elimination of uncontrollable mass reproduction of karakurt and the absence of any necessity of special egg sacs collecting for colonisation.

LITERATURE CITED

LEVI, H.W. 1983. On the value of genitalic structures and coloration in separating species of widow spiders (*Latrodectus* sp.) (Arachnida: Araneae: Theridiidae). Verhandlungen des Naturwissenschaftlichen Vereins zu Hamburg (NF) 26: 195-200.

MARIKOVSKIJ, P.I. 1956. [Tarantula and karakurt: morphology, biology, toxicity]. (Kirghiz SSR Academy of Sciences Publishers: Frunze.). [in Russian]

TARABAJEV, CH. 1990. Winter frosts and late frosts as the reason of karakurt (Black Widow Spider, *Latrodectus tredecimguttatus*) depression in Kazakhstan. Bulletin de la Societe Europeenne d'Arachnologie (Comptes Rendus du XII^{eme} Colloque Europeen d'Arachnologie, Paris (France), 2-4 juillet 1990), No. hors serie 1: 346-348.

DISTRIBUTION OF *LATRODECTUS* (THERIDIIDAE), *ERESUS* AND *STEGODYPHUS* (ERESIDAE) IN KAZAKHSTAN AND CENTRAL ASIA

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Tarabaev, C.K., Zyuzin, A.A. and Fyodorov, A.A. 1993 11 11: Distribution of *Latrodectus* (Theridiidae), *Eresus* and *Stegodyphus* (Eresidae) in Kazakhstan and Central Asia. *Memoirs of the Queensland Museum* 33(2): 653-657. Brisbane. ISSN 0079-8835.

The distributions of three *Latrodectus* species (*L. tredecimguttatus*, *L. dahli* and *L. pallidus*), and of three eresid species (*Eresus niger*, *E. tristis* and *Stegodyphus lineatus*) within the Kazakhstan-Central Asian region are analysed based on the literature and on original data. *Latrodectus tredecimguttatus* presumably occupies almost the entire Kazakhstan territory, while two other widow species are local and more southern: both of them are first recorded here within Kazakhstan. Preliminary morphological and mating analyses show that both '*Latrodectus tredecimguttatus*' and '*Eresus niger*' within the territory of Kazakhstan and Central Asia are composite species: the first consists of at least one species different from the European *L. tredecimguttatus*, and the second consists of at least three separate species. On a analysé la distribution de trois espèces du genre *Latrodectus* (*L. tredecimguttatus*, *L. dahli* et *L. pallidus*) et de trois espèces de la famille Eresidae (*Eresus niger*, *E. tristis* et *Stegodyphus lineatus*) dans la région du Kazakhstan et de l'Asie centrale d'après le données littéraires et originales. L'aire d'habitation de *Latrodectus tredecimguttatus* comprend, hypothétiquement, presque tout le territorie du Kazakhstan, tandis que deux autres espèces sont locales et plus méridionales: l'une et l'autre sont mentionnées ici pour la première fois pour Kazakhstan. L'analyse morphologique préalable et les expériences d'accouplement montrent que *Latrodectus tredecimguttatus* aussi bien que *Eresus niger* au Kazakhstan et à l'Asie Centrale sont des espèces collectives: dont la première se compose, au moins, d'une espèce différente de *L. tredecimguttatus* d'Europe et l'autre se compose, au moins, des trois espèces séparées.□*Latrodectus, Eresus, Stegodyphus, distribution.*

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The genus *Latrodectus* (Theridiidae) and the family Eresidae have not been studied very much in Central Asia. Before 1950 only one *Latrodectus* species was known from the former territory of the U.S.S.R.–*L. tredecimguttatus* (Rossi), or 'karakurt'. Two years later, Spassky (1952) first reported *L. pallidus* O. Pickard-Cambridge from the western, desert regions of the Turanian zoogeographic province [=Turkmenistan territory]. Later Charitonov (1954) described the new subspecies *L. pallidus pavlovskii* from Turkmenistan (the so-called 'white karakurt'). Twenty years later Tystshenko and Ergashev (1974) found in Uzbekistan another black widow species, *L. dahli* Levi. Amongst the Eresidae, three species have previously been recorded: *Eresus niger* (Petagna), *E. tristis* Kroneberg and *Stegodyphus lineatus* (Latreille).

This paper deals with new collections and data relating to the two groups and species distributions. Also, we suggest that previous broad species concepts, especially within *L. tredecimguttatus* and *E. niger*, must be revised.

MATERIALS AND METHODS

This work is based on material collected mainly by us in Kazakhstan and Central Asia. Our specimens were compared with those from Europe and North Africa. Spiders were examined in 70% alcohol using binocular microscopes MBS-1 and MBS-10. Preliminary experiments on mating between European *L. tredecimguttatus* and Widows from Kazakhstan were also carried out.

Abbreviations: BIN, Biological Institute, Novosibirsk, Russia; IZA, Institute of Zoology, Alma-Ata; MCZ, Museum of Comparative Zoology, Cambridge, Massachusetts, USA; MNHN, Muséum National d'Histoire Naturelle, Paris, France; ZISP, Zoological Institute, St. Petersburg; ZMMU, Zoological Museum of the Moscow University.

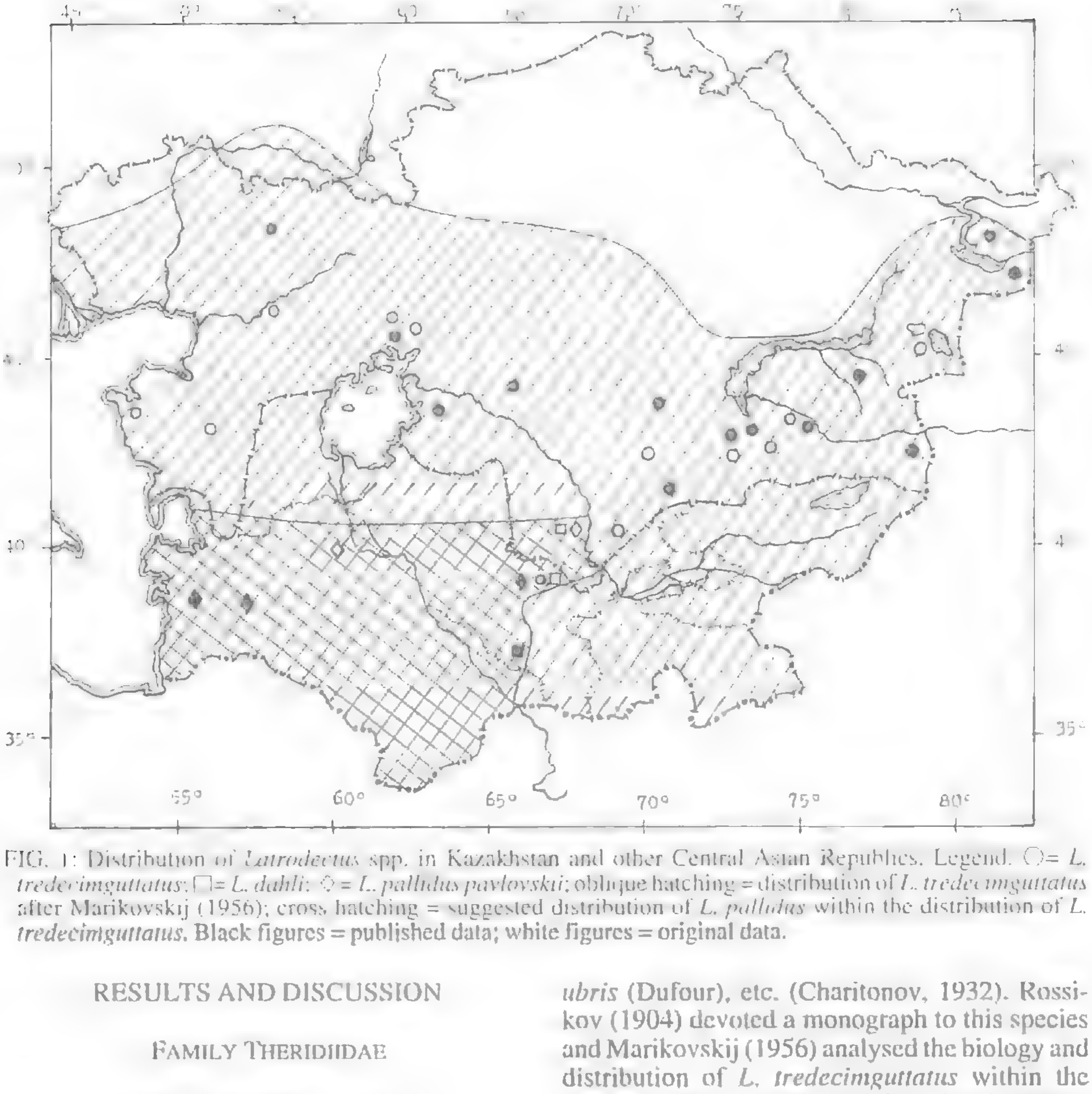

FIG. 1: Distribution of *Latrodectus* spp. in Kazakhstan and other Central Asian Republics. Legend. ○= *L. tredecimguttatus*; □= *L. dahli*; ◇ = *L. pallidus pavlovskii*; oblique hatching = distribution of *L. tredecimguttatus* after Marikovskij (1956); cross hatching = suggested distribution of *L. pallidus* within the distribution of *L. tredecimguttatus*. Black figures = published data; white figures = original data.

RESULTS AND DISCUSSION

FAMILY THERIDIIDAE

Latrodectus Walckenaer

REMARKS

The northern border of the widow spiders' distribution within the former USSR seems to pass near 52°N (Fig. 1).

Latrodectus tredecimguttatus (Rossi) 'Karakurt'

REMARKS

Within the former USSR this species has been known under the names *L. conglobatus* C.L. Koch, *L. erebus* Savigny and Audouin, *L. lugubris* Motchoulsky, *L. tredecimguttatus* var. *lugubris* (Dufour), etc. (Charitonov, 1932). Rossikov (1904) devoted a monograph to this species and Marikovskij (1956) analysed the biology and distribution of *L. tredecimguttatus* within the former USSR. According to this author, karakurts are found over almost all of Kazakhstan (Fig. 1). However, existing difficulties in the systematics of *Latrodectus* species (see Levi, 1983), as a rule, result in too wide an interpretation of their distribution. When investigating *Latrodectus* species, we found that adult females of *L. tredecimguttatus* from Italy had a light spotted abdomen while Kazakhstan specimens were completely black. Dr G. Schmidt (pers. comm.) considers the karakurt from Kazakhstan to be the species *Latrodectus lugubris* (Dufour) described from Egypt. Preliminary experiments on mating carried out in 1991 together with Mr D. Weickmann-Zwoerner (Germany) showed that

Kazakhstan specimens could not cross with European *L. tredecimguttatus* (two males from Kazakhstan were used).

At present the distribution of *L. tredecimguttatus* as delimited by Marikovskij (1956) must be revised, as we now suppose the traditional '*L. tredecimguttatus*' in Kazakhstan to be a separate species.

Material Examined

Italy: 3 ♀, Lazio, near Priverno, 16 May 1962, fields and stones, H. Levi (MCZ). Kazakhstan and Central Asia: many males and females from different localities (IZA).

Latrodectus dahli Levi

Remarks

This very localised species among the Central Asian republics occurs in Uzbekistan only (Tystshenko & Ergashev, 1974; Ergashev, 1990); in Kazakhstan, it was found by us first in the Kyzylkum Desert (two females, det. Dr Y.M. Marusik)(Fig. 1). We have compared our specimens with the female paratype of *L. dahli* from Iran and found their resemblance in the hairiness of the abdomen's dorsum (long slender spines and rather long setae between them: see also Tystshenko and Ergashev, 1974, fig. 3). Nevertheless, the epigynal opening in all our specimens is 4 times as wide as long, while in the female paratype it is only 3.4 times as wide as long; slight differences are also in the vulvae (cf. Levi, 1959, figs 11, 12; Tystshenko and Ergashev, 1974, figs 4, 5). As the male of *L. dahli* from the type locality is up to now undescribed, we cannot be sure that our specimens belong to real *L. dahli*.

Material Examined

Iran: 1 paratype ♀, Bushire, Persian Gulf (MCZ). Uzbekistan: 1 ♂, 1 ♀, Kashkadarja Area, Karshi Steppe, N.E. Ergashev. Kazakhstan: 2 ♀, South Kazakhstan Area, Kyzylkum Desert, 77.5k NW of Chardara Vill., 5-6 Jun 1989, Tarabaev, Fyodorov, Zyuzin (IZA).

Latrodectus pallidus pavlovskii Charitonov (Fig. 1)

Remarks

Within Kazakhstan, it was found by us first in the Kyzylkum desert, which is probably its northernmost limit. To clarify the taxonomic position of *L. pallidus pavlovskii*, thorough comparison of our spiders with the type material or topotypes of *L. pallidus* is necessary.

Material Examined

Turkmenistan: 1♀, Tashauz Area, Shakhsenem, under *Artemisia*, 9 Oct 1983, O.S. Soyunov. Uzbekistan: 4 ♀, Dzhizak Area, 'Kyzylkum' state farm, 16 Jul 1982, N.E. Ergashev. Kazakhstan: 1♀, South Kazakhstan Area, Kyzylkum Desert near Tabakbulak Vill., 24 Aug 1991, A.A. Zyuzin, B.M. Gubin (1 ♂, 2 ♀ of Tabakbulak population in laboratory) (IZA).

Family Eresidae

Eresus Walckenaer

Eresus niger (Petagna)

Remarks

Published and original data on the distribution of this species within the Sibero-Kazakhstan-Central Asian region, in the European part of Russia (see Charitonov, 1932) and in Europe (see Bonnet, 1956) show that the northern limit of its area seems to pass near 56°N: thus, *E. niger* is theoretically distributed over the whole Kazakhstan and the Central Asian region. Preliminary analysis of material we have at our disposal show that at least three separate species of the '*Eresus niger*' complex occur in Kazakhstan (Fig. 2). The acute deficit of specimens of both sexes taken from the same place is the main obstacle to a detailed taxonomic study.

According to Merrett and Millidge (1992), the correct name for the species *Eresus niger* (Petagna) is *Eresus cinnaberinus* (Olivier) (see also Lehtinen, 1967, p. 233).

Material Examined

France: 2 ♂, 2 ♀ 2 juv., Col du Ceris, 15 Sep 1908; Banyuls, 31 May 1909 (MNHN, No. AR 838). Spain: 3 ♂, 4 ♀, La Granja, Jun 1908 (MNHN, No. AR 837). Mongolia: 1 ♂, 'Potanin, Schenkel det. 1946' (MNHN, No. AR 852). Hungary: 1 ♂, Csákberény, Vertes, 20 Sep 1991, V.V. Dubatolov, V.G. Mordkovitch. Russia: 3 ♂, Bashkir Reserve, Bashart, I.V. Stebaev; 1 ♂, Novosibirsk Area, 13k W of Karasuk Vill., 7 Sep 1989; 5 ♂, ibidem, 27k SE of Zdvinsk Vill., Malyje Chany Lake, 10 Sep 1989, V.P. Pekin. Turkmenistan: 1 ♂, Kopetdag Reserve, 15 May 1988, Karpenko; 2 ♂, 25 Aug 1988, ibidem, 15k W of Firyuza Vill., Mount Dushak, 2100 m; 1 ♂,

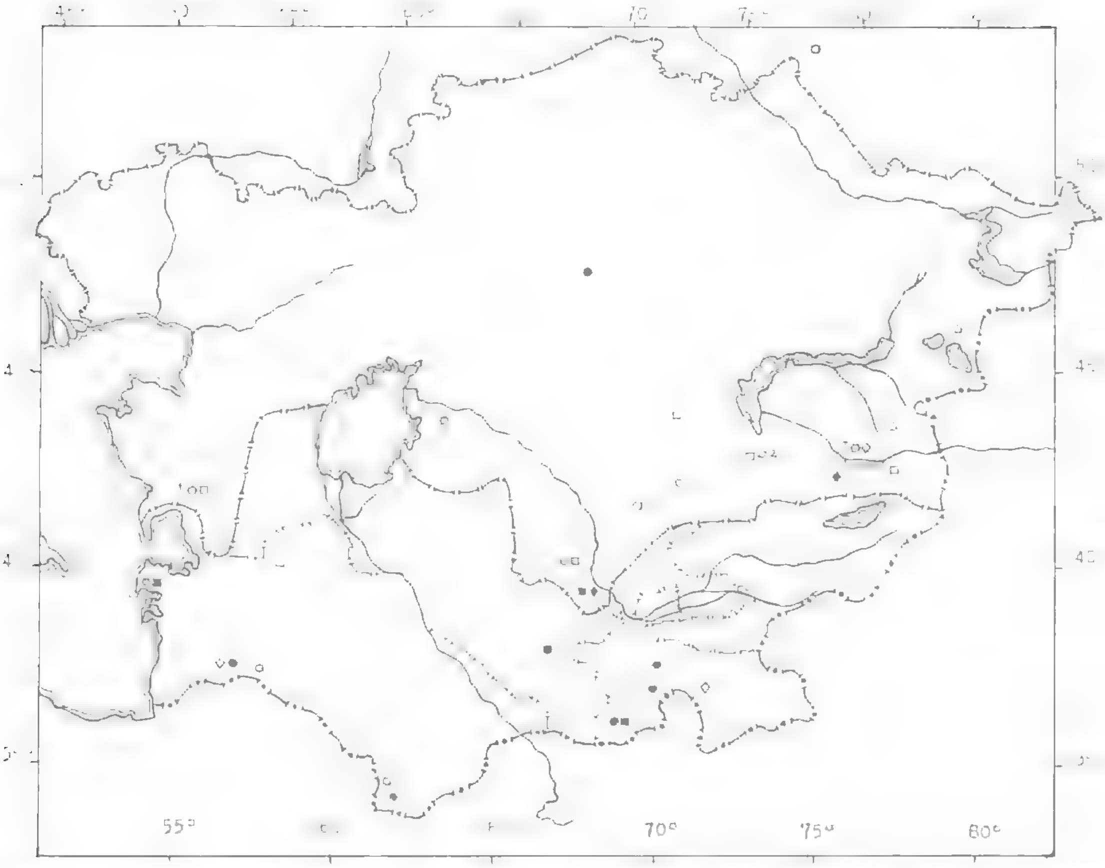

FIG. 2: Distribution of eresid spiders in Kazakhstan and other Central Asian Republics. Legend: ○= '*Eresus niger*' complex: 1, 2, 3, = *E.* sp. 1, 2, 3 (see text); ◇=E. tristis; □= *Stegodyphus lineatus*. Black figures = published data; white figures = original data.

ibidem, Firyuza Vill., 3 Apr 1991, V.V. Dubatolov, V.K. Zinchenko; 1 ♂, Kugitang Range, 5k SE of Bazar Depe Vill., 13-19 May 1991, V.V. Dubatolov (all BIN). Kazakhstan: numerous ♂♂♀♀ from different parts of Kazakhstan (see Fig. 2) (IZA).

Eresus tristis Kroneberg

Remarks

According to published data, this species was previously found only in southern and South-Eastern Kazakhstan (Kroneberg, 1875; Spassky and Shnitnikov, 1937); beyond the borders of the former USSR, *E. tristis* was found only in China by G.N. Potanin's expedition: see Simon (1895), 'la riv. Sotschshan au N. de la chaîne du Tjan-Shan'. [Charitonov (1932) wrongly placed this site within the former USSR territory].

Males of *E. tristis* can be readily separated from those of *E. niger* by the black colour of their abdomen and legs (as in *E. niger* females), sometimes with white markings. Despite this very distinctive feature, *E. tristis* was recently synonymised with *E. niger* based on the similarity of their genitalia (see Nenilin and Pestova, 1986). However, our preliminary data showed sufficient differences of *E. tristis* from all of our 'red' males in the fine structure of the male palp; at the same time, black males from different parts of Kazakhstan and Central Asia have very similar palp structure. The main taxonomic problem is that the female of this species is up to now unknown.

Material Examined

Kazakhstan: 1 ♂ holotype, South Kazakhstan Area, 'Syrdarja, the end of April', A.P. Fedtschenko's Turkestan Scientific Expedition by the Natural History Amateurs' Society (ZMMU No. Ta 1104); 1 ♂, Alma-Ata Area, 5k NE of Kapchagaj City, A.A. Fyodorov (IZA).

Turkemistan: 3 ♂, Western Kopetdag Ridge, near Kara-Kala Vill., 7 Feb 1979, I. Morozova (ZISP). Tadzhikistan: 1 ♂, 'turn to Chashma, 9.V.1986, Itka' (BIN).

Stegodyphus Simon

Stegodyphus lineatus (Latreille) (=*Eresus arenarius* Kroneberg)

REMARKS

This species was previously known from Turkmenistan, Uzbekistan and Southern Kazakhstan. We have found it considerably northwards and eastwards (Fig. 2).

MATERIAL EXAMINED

Many males and females from: Spain; Italy (Sicily); Algeria; Tunisia (Kairouan) (MNHN No. AR 785, 786); different parts of Kazakhstan and Central Asian republics (see Fig. 2) (IZA).

ACKNOWLEDGEMENTS

For placing the necessary material at our disposal and for assistance in experiments we are grateful to: Prof. H.W. Levi (Cambridge, Massachusetts, USA), Drs D.V. Logunov, V.V. Dubatolov (Novosibirsk), K.G. Mikhailov (Moscow), V.I. Ovtsharenko (St. Petersburg) (all Russia), Ch. Rollard (Paris, France), and Mr D. Weickmann-Zwoerner (Weissenburg, Germany).

LITERATURE CITED

BONNET, P. 1956. 'Bibliographia Araneorum', vol. 2(2): 919-1026. (Douladoure: Toulouse).

CHARITONOV, D.E. 1932. Katalog der Russischen Spinnen. Annuaire du Musée Zoologique, Leningrad 32 (Beilage): 1-206.

1954. [The new representative of the genus *Latrodectus* from Turkmenia (*Latrodectus pallidus* O.P. Cambr. subsp. *pavlovskii* n.)]. Zoologicheskij Zhurnal 33: 480-485. [in Russian]

ERGASHEV, N.E. 1990. ['Ecology of the venomous spiders in Uzbekistan']. ('Fan' Publishers: Tashkent). [in Russian]

KRONEBERG, A. 1875. Araneae. In: Fedtschenko, A.P., 'Reise in Turkestan, Zoologischer Theil', vol. 2: 1-58. Moscow.

LEHTINEN, P.T. 1967. Classification of the cribellate spiders and some allied families, with notes on the evolution of the suborder Araneomorpha. Annales Zoologici Fennici 4: 199-430.

LEVI, H.W. 1959. The spider genus *Latrodectus* (Araneae, Theridiidae). Transactions of the American Microscopical Society 28: 7-43.

1983. On the value of genitalic structures and coloration in separating species of widow spiders (*Latrodectus* sp.) (Arachnida: Araneae: Theridiidae). Verhandlungen des Naturwissenschaftliches Vereins zu Hamburg, (NF) 26: 195-200.

MARIKOVSKIJ, P.I. 1956. ['Tarantula and karakurt: morphology, biology, toxicity']. (Kirghiz SSR Academy of Sciences Publishers: Frunze). [in Russian]

MERRETT, P. & MILLIDGE, A.F. 1992. Amendments to the check list of British spiders. Bulletin of the British Arachnological Society 9: 4-9.

NENILIN, A.B. & PESTOVA, M.V. 1986. [The spiders of the family Eresidae in the USSR fauna]. Zoologicheskij Zhurnal 65: 1734-1736. [in Russian]

ROSSIKOV, K.N. 1904. [The venomous spider karakurt]. Agricultural monograph. Trudy Byuro po Entomologii 5 (2): 1-232. St. Petersburg. [in Russian]

SIMON, E. 1895. Arachnides recueillis par Mr G. Potanine en Chine et en Mongolie (1876-1879). Bulletin de l'Académie Impériale des Sciences de St. Petersburg, (5) 2 (4): 331-345.

SPASSKY, S.A. 1952. [The spiders of the Turanian zoogeographic province]. Entomologicheskoje Obozrenije 32: 192-205. [in Russian]

SPASSKY, S.A. & SHNITNIKOV, V.N. 1937. [Materials on the spider fauna of Kazakhstan]. Trudy Kazakhstanskogo Filiala AN SSSR 2: 265-300. [in Russian]

TYSTSHENKO, V.P. & ERGASHEV, N. 1974. [*Latrodectus dahli* Levi (Aranei, Theridiidae), a species of venomous spiders new in the USSR fauna]. Entomologicheskoje Obozrenije 53: 933-937. [in Russian].

GEOGRAPHIC VARIATION OF THE NUMBER OF B-CHROMOSOMES IN *METAGAGRELLA TENUIPES* (OPILIONES, PHALANGIIDAE, GAGRELLINAE)

N. TSURUSAKI

Tsurusaki, N. 1993 11 11: Geographic variation of the number of B-chromosomes in *Metagagrella tenuipes* (Opiliones, Phalangiidae, Gagrellinae). *Memoirs of the Queensland Museum* 33(2): 659-665. Brisbane. ISSN 0079-8835.

Chromosomes of *Metagagrella tenuipes* (L. Koch) (Arachnida, Opiliones, Phalangiidae, Gagrellinae) were surveyed in 8 populations in Japan. Almost every individual examined had one or more (highest number per cell was 19) supernumerary or B-chromosomes, in addition to the basic set of chromosomes (2n=18). These B-chromosomes are heterochromatic, and during meiosis they appear to behave as univalents. The number of B-chromosomes varied both among and within populations. The number also fluctuated to some extent among cells from the same individual, suggesting nondisjunction at mitotic anaphases. No correlation could be elucidated between the number of B-chromosomes and external morphologies or habitat type. The number of B-chromosomes may affect growth rate, and in turn reduce the synchrony of breeding within a population.

Die Chromosomen von *Metagagrella tenuipes* (L. Koch) (Arachnida, Opiliones, Phalangiidae, Gagrellinae) wurden in 8 japanischen Populationen untersucht. Fast jedes überprüfte Individuum wies eines oder mehrere (die höchste Anzahl pro Zelle war 19) überzählige oder B-Chromosomen zusätzlich zum Standardchromosomensatz (2n = 18) auf. Diese B-Chromosomen sind heterochromatisch und scheinen sich während der Meiose als Univalente zu verhalten. Die Zahl der B-Chromosomen variiert sowohl zwischen als auch innerhalb von Populationen. Sie schwankt in gewissem Ausmaß auch zwischen Zellen aus ein und demselben Individuum, was auf Non-Disjunction bei mitotischen Anaphasen schließen läßt. Zwischen der Anzahl der B-Chromosomen und der äußeren Morphologie oder Habitattypen konnten keine Korrelationen gefunden werden. Es besteht die Möglichkeit, daß die Zahl der B-Chromosomen die Wachstumsrate beeinflussen und in der Folge die Synchronie der Fortpflanzung innerhalb einer Population reduzieren kann.□*Opiliones, Metagagrella tenuipes, Japan, B-chromosomes, geographic variation.*

Nobuo Tsurusaki, Department of Biology, Faculty of Education, Tottori University, Tottori 680, Japan; 29 October, 1992.

The harvestman *Metagagrella tenuipes* (L. Koch) is widespread throughout Japan but with a peculiar habitat and distribution pattern. In southern Japan, this opilionid is typically coastal. However, in northern Japan, it also occurs inland and prefers open habitats, e.g. parks and gardens, that are affected by moderate human disturbance.

During a chromosomal survey of this species, the number of chromosomes varied both within and among populations, with a range of 2n=18 to 36. Moreover, the number of chromosomes varied somewhat from one cell to another in almost all individuals. Close examination of mitotic and meiotic chromosomes revealed that the karyotype of this species is usually composed of 2n=18 standard chromosomes and one or more supernumerary or B-chromosomes, and that the latter cause the overall chromosome number to vary. Here, I will describe the karyotype, nature of the B-chromosomes, and pattern of geographic variation in the B-chromosome number.

MATERIALS AND METHODS

The specimens used for chromosome examination are listed (Table 1, Fig. 1). Cytological data were obtained from air-dried preparations of testes or ovaries of field-collected adults and penultimates. The technique used is described in Tsurusaki (1985) and Tsurusaki and Cokendolpher (1990). In some cells, patterns similar to C-bands were observed despite the fact that these cells had received no special treatment. In many individuals the number of B-chromosomes varied from cell to cell. In such cases, the chromosome number of each is represented by a modal number.

For two populations (Nakajima and Maruyama), lengths of femur I of the specimens used in the chromosome preparation were measured with an eyepiece graticule.

Detailed collection data on the specimens examined are listed in the appendix.

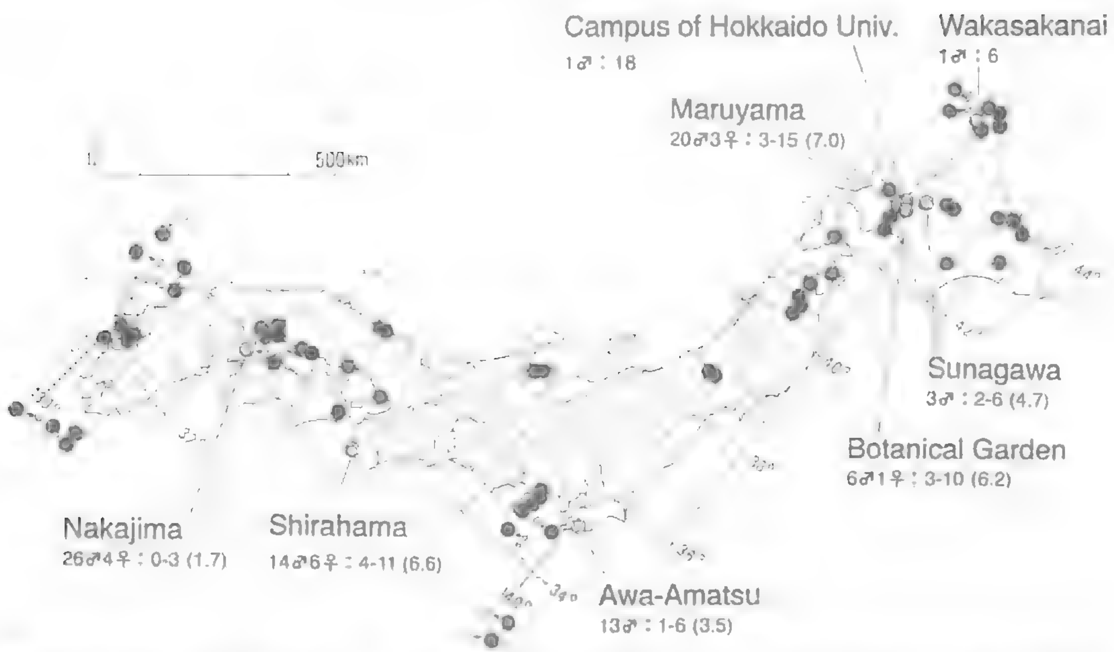

FIG. 1. Map of populations of *M. tenuipes*, Japan, used here (double open circles) with records compiled from literature (e.g. Suzuki, 1973; Suzuki and Tsurusaki, 1983) and data in the appendix (solid circles). No. of samples and range of B-chromosome number in each study population are shown, with means in parentheses.

RESULTS

Karyotypes and Nature of B-Chromosomes

The chromosome number of this species varied enormously among and within populations. From comparisons of the karyotypes of individuals with the lowest chromosome number, 2n=18, to those from others with 2n=19 and greater, and from analyses of both meiotic chromosomes and unintentionally obtained C-banded chromosomal spreads, the chromosome number of the standard karyotype, which consists of so-called A-chromosomes alone, was determined to be 2n=18 for both males and females (Figs 2-3).

1. Standard karyotype (Fig. 3)

Autosomes consist of 8 pairs of medium-sized metacentrics (Nos. 4 and 5), submetacentrics (Nos. 1, 3, 7, 8), and subtelocentrics (Nos. 2 and 6). The X chromosome, the largest, is subtelocentric, while Y is submetacentric and similar in size to chromosome No. 1. In C-banded mitotic metaphases, centromeric regions of the A-chromosomes were positively stained (Figs 4-5). No prominent differences were found among the

TABLE 1. B-chromosome numbers in 8 populations of *Metagagrella tenuipes*. NOTES: [1] S = seashore habitats, I = inland habitats e.g. parks, fields; [2] Range, mean and mode not for all cells counted but for values represented by mode of each individual; [3] Calculated only for samples with >5 individuals; [4] One or more were juveniles.

Locality and habitat type in parentheses[1]	Date	Specimens examined	Number of B-chromosomes[2]				
			min.	max.	mean	mode	SD[3]
Wakasakanai (S)	9-IX-1985	1 ♂[4]	6	6	6	6	-
Sunagawa (I)	8 & 15-X-1986	3 ♂	2	6	4.7	6	-
Campus of Hokkaido Univ. (I)	18-IX-1981	1 ♂	18	18	18	18	
Botanical Garden, Sapporo 1982 (I)	5-IX-198	5 ♂, 1 ♀	4	10	6.2	4	2.40
as above, 1986 (I)	8-VIII & 9-IX-1986	8 ♂, 2 ♀	3	9	6.2	5, 7, 8	1.93
Maruyama, Sapporo (I)	5-IX-1986	20 ♂, 3 ♀	3	15	7.0	6	2.75
Awa-Amatsu (S)	27-VIII-1984	13 ♂	1	6	3.5	4	1.39
Shirahama (S)	29-VII-1983	14 ♂, 6 ♀[4]	4	11	6.6	6	1.60
Nakajima (S)	26-VIII-1986	26 ♂, 4 ♀	0	3	1.7	1, 2	1.02

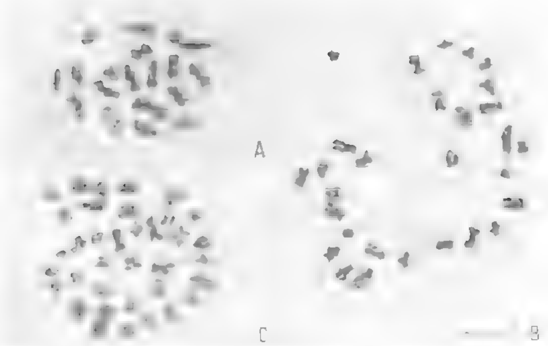

FIG. 2. Representative chromosome complements at spermatogonial mitotic metaphase of male *Metagagrella tenuipes*. A, Nakajima, 2n=18 (18A's); B, Maruyama, 2n=28 (18A's + 10B's); C, campus of Hokkaido Univ., 2n=37 (18A's + 19B's). Scale = 5μm.

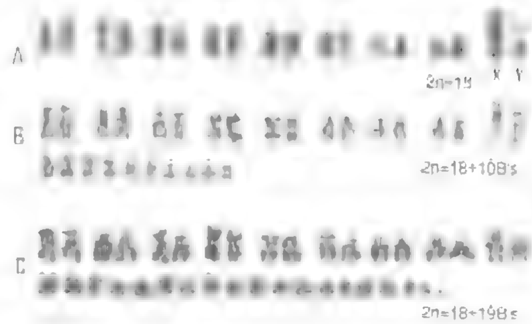

FIG. 3. Karyotypes of male *Metagagrella tenuipes* based on the photographs in Fig. 2. A, Nakajima; B, Maruyama; C, campus of Hokkaido Univ. B-chromosomes are arranged on the second row in B and C. Scale = 5μm.

standard karyotypes of individuals from various populations.

2. B-chromosomes

In addition to a set of standard chromosomes described above, almost all chromosomal spreads contained at least one B-chromosome. These were meta- or submetacentric, equal to or smaller than the shortest pairs (No. 8) of the A-complement (Fig. 3). In C-banded chromosome spreads, the B's were heteropycnotic, darkly staining along their total lengths (Figs 4-5). During meiosis, the B's remained univalent (Fig. 4-5) even when the cell carried 2 or more. The number of B's varied considerably from one cell to the other within a single individual, possibly due to nondisjunction at anaphase during mitosis.

Numeric variation in B's among individuals within populations was also evident (Fig. 6). No significant differences were found in the number of B's between the sexes from any population (Mann-Whitney U-tests for each of four populations where both sexes were sampled, P=0.48-0.96).

Geographic Variation in Number of B's

The number of B-chromosomes varied significantly among populations (single classification ANOVA: F=34.6; d.f.=7; P<0.001) (Figs 1 and 6, Table 1). The lowest and the highest population means of the number of B's were 1.7 for Nakajima (n=30) and 18 for the campus of Hokkaido University (n=1), respectively, and the means of the other populations lay between the two extremes, range = 3.5-7. However, no significant correlations could be detected between the number of B's and characteristics such as latitude (Spearmann's coefficient of rank correlation, r_s=0.19, n=8, P>0.05) and habitat types (seashore or inland: Mann-Whitney U-test, P>0.05).

DISCUSSION

Characteristics of the B-Chromosomes

According to Jones and Rees (1982), B-chromosomes have been reported in over 1000 species of plants and more than 260 species of animals. In Arachnida, however, only three species of Acari have been shown to have B's: *Aponomma fimbriatum* and two species of *Haemaphysalis* (Oliver and Bremner, 1968; Oliver *et al.*, 1974).

The B-chromosomes in *Metagagrella tenuipes* have the following characteristics that are typical for B's recorded in various other organisms (White, 1973; Jones and Rees, 1982; Werren *et al.*, 1988; Shaw and Hewitt, 1990; Jones, 1991): (1) they are smaller than most members of the A-complement; (2) they appear to be comprised of a large amount of constitutive heterochromatin; (3) they remain univalent during meiosis; (4) the number of B's varies from one cell to another even within an individual, indicating they display nondisjunction at anaphases of spermatogonial mitoses.

However, the frequency and the number of B's were rather unusual. In this species, every population sampled contained B's and the frequency within a population was up to 87% in Nakajima and 100% in the other 7 populations. The number of B's retained per individual of this species was also extraordinarily high; the population means had a range from 3.5 to 7 in 6 out of 8 populations

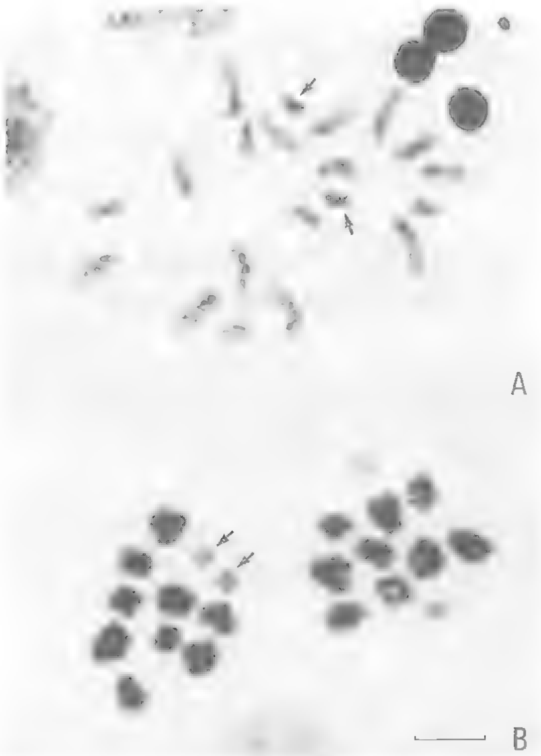

FIG. 4. C-banded mitotic metaphase (A) and meiotic metaphase I (B) in ♂ *M. tenuipes* from Sunagawa, with 2 B-chromosomes (arrowed). Scale = 5μm.

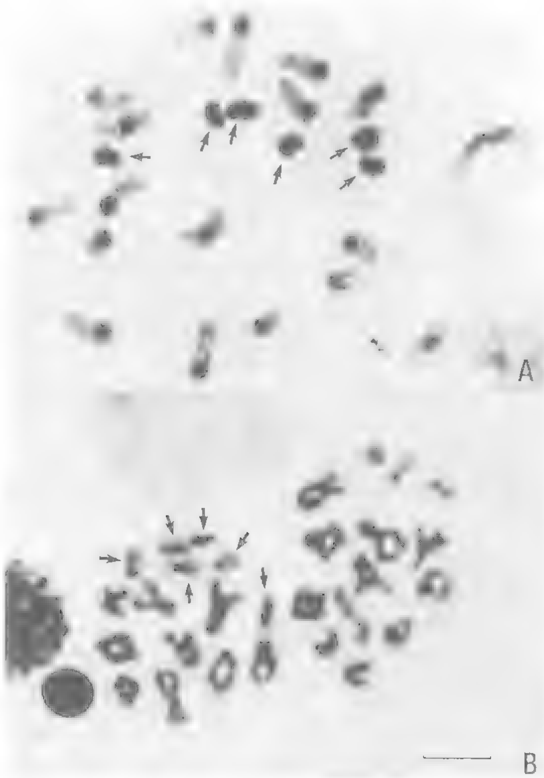

FIG. 5. C-banded mitotic metaphase (A) and diakinesis - metaphase I (B) in ♂ *M. tenuipes* from Maruyama, with 6 B-chromosomes (arrowed). Note: 9 bivalents formed by 9 pairs of A-complement of chromosomes. Scale = 5μm.

(Table 1). The higher end was found in the single male sampled from the campus of Hokkaido University, whose modal number of 18 B's was exhibited by 30 cells and the maximum number of 19 in 3 cells (Figs 2-3). These are among the highest numbers of B's in animal species so far recorded, close to the number 'about 20' in *Xylota nemorum* (Diptera: Syrphidae) (Boyes and Van Brink, 1967).

Effect of B's on Phenotype

Metagagrella tenuipes shows marked variation both among and within populations in external morphology, such as body size, leg lengths, degree of development of a spine on the dorsal scutum, number of noduli on the legs, and coloration of the body (Suzuki, 1973; Suzuki and Tsurusaki, 1983). However, no correlation was found between these characters and the number of B-chromosomes (Fig. 7). These facts are consistent with the observation that the B's are C-band positive. If these B's are indeed genetically inactive, numerical variation of B's would lead to no effect on the phenotype of their owner.

Although few studies have demonstrated any exophenotypic effect due to B's, some show a relationship between the number of B-chromosomes and the rate of development (Hewitt and East, 1978; Harvey and Hewitt, 1979). Thus, there is a possibility that the presence of B-chromosomes retards the cell cycle due to the additional DNA or its organization which is possibly different from A-chromosomes. In turn, these effects may influence the growth and development of the whole organism (Jones and Rees, 1982). Such influences might be related to an unusual feature of the life history of this species, namely, high variability among individuals in the time to reach maturity. The duration of coexistence of juveniles and adults of this species at Maruyama is estimated to be about three weeks, whereas it is less than 1-2 weeks in other species of opilionids having no B-chromosomes, such as *Oligolophus aspersus*, *Leiobunum japonicum*, and two species of *Nelima* from the same locality (Tsurusaki,

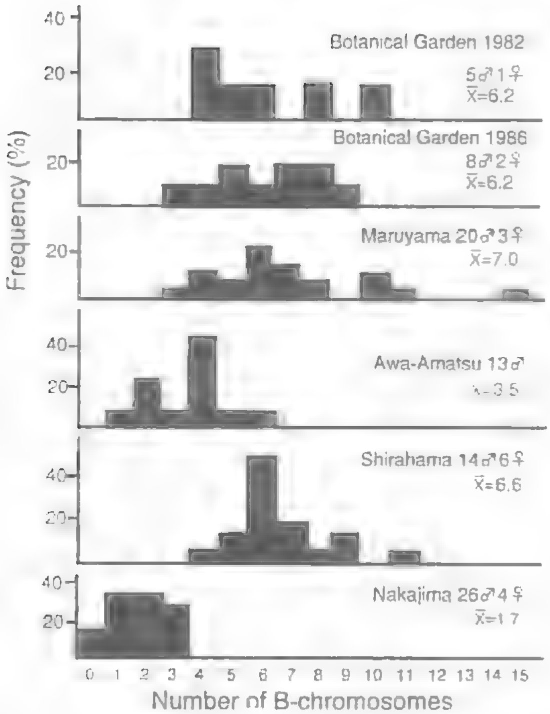

FIG. 6. Frequency distribution of B-chromosome numbers in 6 samples from 5 populations. The other 3 populations (Wakasakanai, Sunagawa, and campus of Hokkaido Univ.) omitted due to paucity of specimens surveyed.

unpublished data based on weekly field-collections made in 1979). The same phenomenon is also inferred from field-data from various localities all over Japan. This versatility in the timing of final molting of this species might be ascribed to the numerical variation of B-chromosomes. Further study is needed.

Geographic Variation in Number of B's

The fact that the B's are found in every population over a wide geographic range of this species indicates that they are of rather ancient origin. Marked morphological variation among the B-chromosomes also attests to their long evolutionary history. However, it is also possible that they might be produced *de novo* from the A-complement by recurring mutation.

Although B's appear widespread across the species range, the number of B's considerably varied among populations, with a fairly wide range from 1.7 at Nakajima to 18 on the campus of Hokkaido University. In each population, the number of B's may be stable for at least several years; there was no significant difference in their

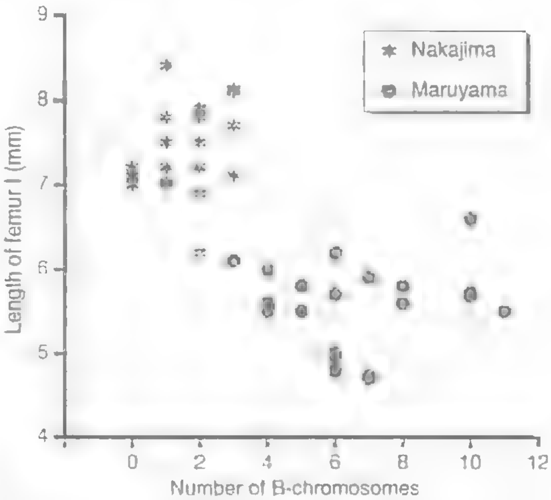

FIG. 7. Relation of length of femur I to number of B-chromosomes in 2 populations (Nakajima and Maruyama) of *M. tenuipes*. No significant correlation between 2 variables in each population [$r = 0.305$ ($P>0.1$) for Nakajima; $r = 0.065$ ($P>0.1$) for Maruyama], although both characters show prominent differences between two populations. Two variables may be negatively correlated (although spuriously) between populations. Leg lengths decrease with increase in latitude (Tsurusaki, unpubl.) but the number of B's does not.

frequencies in the Botanical Garden at Sapporo which were sampled in 1982 and 1986 (Fig. 6). If B-chromosomes were inherited in a non-Mendelian manner, and were neutral in phenotypic expression, the frequency of B's would not be stable. For example, it might be expected that the crossing of a male with 3 B's and a female with 3 B's would produce some offspring with 4 or more B's. However, no individuals with more than 3 B's are found in Nakajima population. This indicates that some selection pressure limits the number of B's that one individual can retain in a particular population. It is still uncertain what factors determine the population mean and the range of the number of B's. However, this species may be useful in studying various aspects of B's and 'selfish' DNA, including the controversial issues on the level of selection discussed by Werren *et al.*, (1988) and Shaw and Hewitt (1990).

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LITERATURE CITED

BOYES, J.W. & VAN BRINK, J.M. 1967. Chromosomes of Syrphidae III. Karyotypes of some species in the tribes Milesiini and Myolepini. Chromosoma 22: 417-455.

HARVEY, A.W. & HEWITT, G.M. 1979. B-chromosomes slow development in a grasshopper. Heredity 42: 397-401.

HEWITT, G.M. & EAST, T.M. 1978. Effects of B chromosomes on development in grasshopper embryos. Heredity 41: 347-356.

JONES, R.N. 1991. B-chromosome drive. American Naturalist 137: 430-442.

JONES, R.N. & REES, H. 1982. 'B Chromosomes'. (Academic Press: London).

OLIVER, J.H. & BREMNER, K.C. 1968. Cytogenetics of ticks. III. Chromosomes and sex determination in some Australian ticks (Ixodoidea). Annals of the Entomological Society of America 61: 837-844.

OLIVER, J.H., TANAKA, K. & SAWADA, M. 1974. Cytogenetics of ticks (Acari: Ixodidae) 14. Chromosomes of nine species of Asian Haemaphysalines. Chromosoma 45: 445-456.

SHAW, M.W. & HEWITT, G.M. 1990. B-chromosomes, selfish DNA and theoretical models: where next? 197-223. In Futuyma, D.J. and Antonovics, J. (eds). 'Oxford Surveys in Evolutionary Biology, Vol. 7'. (Oxford University Press: New York).

SUZUKI, S. 1973. Opiliones from the South-west Islands, Japan. Journal of Science of the Hiroshima University, Ser. B, Div. 1 (Zoology) 24: 205-279.

SUZUKI, S. & TSURUSAKI, N. 1983. Opilionid fauna of Hokkaido and its adjacent areas. Journal of the Faculty of Science, Hokkaido University, Ser. VI, Zoology 23: 195-243.

TSURUSAKI, N. 1985. Taxonomic revision of the *Leiobunum curvipalpe*-group (Arachnida, Opiliones, Phalangiidae). I. *hikocola*-, *hiasai*-, *kohyai*-, and *platypenis*-subgroups. Journal of the Faculty of Science, Hokkaido University, Ser. VI, Zoology 24: 1-42.

TSURUSAKI, N. & COKENDOLPHER, J.C. 1990. Chromosomes of sixteen species of harvestmen (Arachnida, Opiliones, Caddidae and Phalangiidae). Journal of Arachnology 18: 151-166.

WERREN, J.H., NUR, U., & WU, C.-J. 1988. Selfish genetic elements. Trends in Ecology and Evolution 3: 297-302.

WHITE, M.J.D. 1973. 'Animal Cytology and Evolution, 3rd ed.'. (Cambridge University Press: Cambridge).

APPENDIX New material of *M. tenuipes* used in Fig. 1. Data in order: locality, altitude if available and needed, no. individuals, no. specimens dissected in parentheses if needed (Value may not be as in Table 1, since no countable chromosomal spreads were obtained for some specimens), date collected, collector (NT = N. Tsurusaki; YN=Y. Nishikawa).

HOKKAIDO: I. Rebun, Kabukai, Kabukai Elementary School, 10m, 1 juv., 11-VIII-1990, YN. I. Rishiri, Oshidomari, ca. 20m, 1 ♂, 8-VIII-1985, Y. Kuwahara; Oshidomari, 5m, 1 ♀, 2 juv., 7-9-VIII-1990, S. Ueno, M. Sato, YN, Fujino, 10m, 1 juv., 7-VIII-1985, NT. Wakkanai: Soya Point, 1m, 2 ♂, 3 ♀, 1 juv., 2-IX-1988, NT; Wakkanai Port, 2m, 4 ♀, 5 juv., 7-VIII-1985, S. Ishimaru, NT. Esashi-gun, Hamatonbetsu-chô, Beniya-Genseikaen, 2 ♂, 1 ♀, 8 juv., 14-15-VIII-1990, YN, S. Ueno. Teshio-gun, Toyotomi-chô, Wakasakanai, on coastal sand dune: 1 juv. (1 juv.), 9-VIII-1985, NT; 1 ♂, 1 ♀, 1-IX-1988, NT, T. Tanabe. Toyotomi-chô, Toyotomi Spa, 2 ♂, 1 ♀, 1 juv., 12-13-VIII-1990, YN. Monbetsu-gun, Engaru-chô, Engaru JR Station, 2 juv., 30-VI-1985, NT. Kamikawa-gun, Tôma-chô, Tôma Cave, outside cave, 4 ♀, 29-30-VIII-1985, N. Yoshida. Sunagawa, On a bank of R. Penke-Utashinai, 1 ♂ (1 ♂), 8-X-1986; 2 ♂ (2 ♂), 15-X-1986, NT. Sapporo: campus of Hokkaido Univ., 1 ♂, 1 ♀, 18-IX-1981, NT; Botanical Garden of Hokkaido Univ.: 9 ♂, 9 ♀ (5 ♂, 1 ♀), 5-IX-1982, NT; 13 ♂, 16 ♀, 5-IX-1984; 7 juv. (7 juv.), 8-VIII-1986; 3 ♂ (3 ♂), 9-IX-1986, NT. Sapporo, Maruyama, 23 ♂, 19 ♀ (20 ♂, 3 ♀), 5-IX-1986, NT. Tomakomai, Tomakomai Experiment Forest of Hokkaido Univ., 1 ♂, 3 ♀, 19-IX-1980, NT. YAMAGATA PREF.: Obanazawa-shi, Obanazawa, 1 ♂, 1 ♀, 4 juv., 29-VIII-1983, A. Otaka; 6 ♂, 1 ♀, 4-X-1984, A. Otaka; Obanazawa-shi, along Route 347, 2 ♀, 9-X-1988, T. Tanabe. CHIBA PREF.: Awa-gun, Amatsu-Kominato-chô, Awa-Amatsu, Saneiri coast: 1 ♂, 1 ♀, 2 juv., 21-V-1983; 1 ♂, 18-IX-1983, K. Ishii; 2 ♂, 1 ♀, 18-XII-1983, K. Ishii. Awa-Amatsu, Saneiri, Matsugabana, under growth of maritime fern, *Cyrtomium falcatum*, 1-2m, 23 ♂, 21 ♀ (16 ♂), 27-VIII-1984, NT. TOKYO PREF.: I. Hachijo, Mine, 2 ♂, 2 ♀, 17-18-XI-1983, H. Okada. TOYAMA PREF.: Toyama-shi: Yokogoshi, 1 ♀, 20-X-1978; 1 juv., 18-V-1990, N. Nunomura; Hamakurosaki, *Pinus thunbergi* forest, 1 juv., 2-V-1979; 3 ♂, 1 ♀, 6-VIII-1980, N. Nunomura. WAKAYAMA PREF.: Nishimuro-gun, Shirahama-chô, Shirahama, Seto Marine Biological Lab., 1 ♂, 3 ♀, 10-VII-1983, S. Otsuka; 29 ♂, 41 ♀, 43 juv. (16 ♂, 1 ♀, 9 juv.), 29-VII-1983, NT. TOTTORI PREF.: Iwami-gun, Iwami-chô, Uradome coast, Kamogaiso, 4 ♂, 3 ♀, 7-IX-1988, NT, R. G. Holmberg; Ketaka-gun, Ketaka-chô, Yatsukami, Anedomari coast, 1 ♂, 3 ♀, 5-IX-1987, NT. OKAYAMA PREF.: Oku-gun, Ushimado-chô, Ushimado Marine Biological Station of Okayama Univ., Benten-iwa, 1 ♂, 4 ♀, 10-VIII-1983, T. Sato. HIROSHIMA PREF.: I. Nômi-jima, Irukanohana: 12 juv., 13-VI-1976; 1 ♂, 4-VII-1977, NT. EHIME PREF.: Onsen-gun, Nakajima-chô, I. Nakajima, Okushi: 3 ♀, 6-7-VIII-1971; 1 ♀, 13-VIII-1974, NT; Okushi, Seno-hana, 51 ♂, 69 ♀ (30 ♂, 6 ♀), 26-VIII-1986, NT. I. Nakajima: Himegahama, 1 ♀, 13-VIII-1974, NT, I. Takashima off Himegahama, 3 ♂, 3 ♀, 6-VIII-1971, NT. Matsuyama, Mt. Fukumi, Fukumiji, 860m, 2 juv., 6-IX-1970, NT. NAGASAKI PREF.: Iki-gun, Ishida-chô, Kukishoku, 4 ♂, 5 ♀, 2 juv., 20-VI-1990, M. Yamashita. KUMAMOTO PREF.: Ushibuka-shi, I. Tojima, 2 juv., M. Yoshikura; Amakusa-gun, Itsuwa-chô, Oniike, 3 ♂, 1 ♀, 2 juv., 8-VII-1958, M. Yoshikura; Matsushima-chô, Aitsu, 4 ♂, 1 ♀, 10-VIII-1957 M. Yoshikura; Matsushima-chô, I. Maejima, 2 ♂, 4 ♀, 20-VII-1963, M. Yoshikura. KAGOSHIMA PREF.: I. Yakushima, Shiratani-Unsui-kyô to Mt. Miyanoura-dake, 1 ♀, 2-5-VIII-1983, H. Okada. I. Tanegashima: Hamada, 1 juv., 11-VII-1983, Sk. Yamane; Makigawa, 3 juv., 3-5-V-1984, Sk. Yamane. Kumage-gun, Kamiyaku-chô, I. Kuchinoerabu-jima, 1 ♂, 27-IX-1984, Collector unknown.

MATING BEHAVIOUR AND FEMALE SPERM STORAGE IN *PHOLCUS PHALANGIOIDES* (FUESSLIN) (ARANEAE)

G. UHL

Uhl, G. 1993 11 11: Mating behaviour and female sperm storage in *Pholcus phalangioides* (Fuesslin) (Araneae). *Memoirs of the Queensland Museum* 33(2): 667-674. Brisbane. ISSN 0079-8835.

Females of *Pholcus phalangioides* do not possess receptacula seminis but store transferred spermatozoa in their genital cavity. The spermatozoa are embedded in glandular secretion that is discharged from two accessory glands situated in the posterior wall of the genital cavity. The gland cells belong to a complex type of class 3 cells according to the classification of Noirot and Quennedy (1974, 1991). With the sperm mass of a single copulation the females are able to fertilize several batches of eggs, although the sperm might be easily washed out with the passage of the first batch of eggs (Forster, 1980). Nevertheless, females allow repeated copulations. The first copulation usually took over an hour but subsequent copulations lasted only a few minutes, no matter whether the female mated with the same or with a different male. Copulations after egg-laying tended to be long. Male spiders might achieve reproductive advantage in copulating with any female they meet and females might have an interest in filling up their storage capacities.

Pholcus phalangioides Weibchen besitzen keine Receptacula seminis im üblichen Sinne, sondern speichern die während einer Kopulation übertragenen Spermien im Hohlraum des Uterus externus. Die Spermien werden dort in ein Sekret eingelagert, welches von zwei akzessorischen Drüsen produziert wird. Diese Drüsen befinden sich in der posterioren Wand des Uterus externus. Die Drüsenzellen sind nach einem Klassifikationssystem, das für epidermale Drüsenzellen von Insekten erstellt wurde (Noirot and Quennedy, 1974, 1991), einem komplizierten Typ der Klasse 3 zuzuordnen. Mit den Spermien, die während einer einzigen Kopulation übertragen wurden, können die Weibchen mehrere Eigelege befruchten (Uhl, in press a), entgegen der Annahme, die Spermien könnten während der ersten Eiablage leicht ausgewaschen werden (Forster, 1980). Die Weibchen lassen dennoch mehrere Kopulationen zu, wobei die erste Kopulation gewöhnlich über eine Stunde dauert, jede weitere Kopulation schon nach wenigen Minuten abgebrochen wird, unabhängig davon ob es sich um das selbe oder um ein neues Männchen handelt. Nach einer Eiablage lassen die Weibchen wieder lange Kopulationen zu. Für die Männchen mag es von Vorteil sein sich mit jedem Weibchen zu paaren dem sie begegen, und Weibchen könnten ein Interesse daran haben ihre Speicherkapazität voll auszuschöpfen. ☐*Araneae, Pholcidae, Pholcus phalangioides, sperm storage, glands, secretion, ultrastructure, repeated matings, copulation duration.*

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Most female spiders store sperm within storage structures that are spatially separated from the genital cavity. Some 'primitive' spider families such as Diguetidae, Liphistiidae, Archaeidae and Pholcidae retain the sperm mass within the genital cavity itself (Forster, 1980). Forster assumed that the bursal storage mode has little survival value as the sperm mass gets flushed out with the passage of the eggs and therefore, storing the spermatozoa in spatially separated storage structures would eliminate the need for repeated insemination. Despite the bursal storage mode, female *Pholcus phalangioides* (Fuesslin) are able to fertizile numerous batches of eggs with the sperm of a single insemination (Uhl, in press a). However, the females probably do not rely on the amount and fertility of the spermatozoa transferred during a single copulation. This would be risky as the spermatozoa might be defective or insufficient. I expect the females to fill up their storage capacity by means of repeated matings at least after egg-laying when few clumps of spermatozoa remain in the genital cavity after oviposition. However, if the female does not have the opportunity to copulate repeatedly, the stored spermatozoa can be sufficient for fertilizing following egg batches successfully. This study will also give a brief morphological account on the bursal storage mode in *P. phalangioides* and will present histological and ultrastructural findings on the glandular tissue that exudes its product into

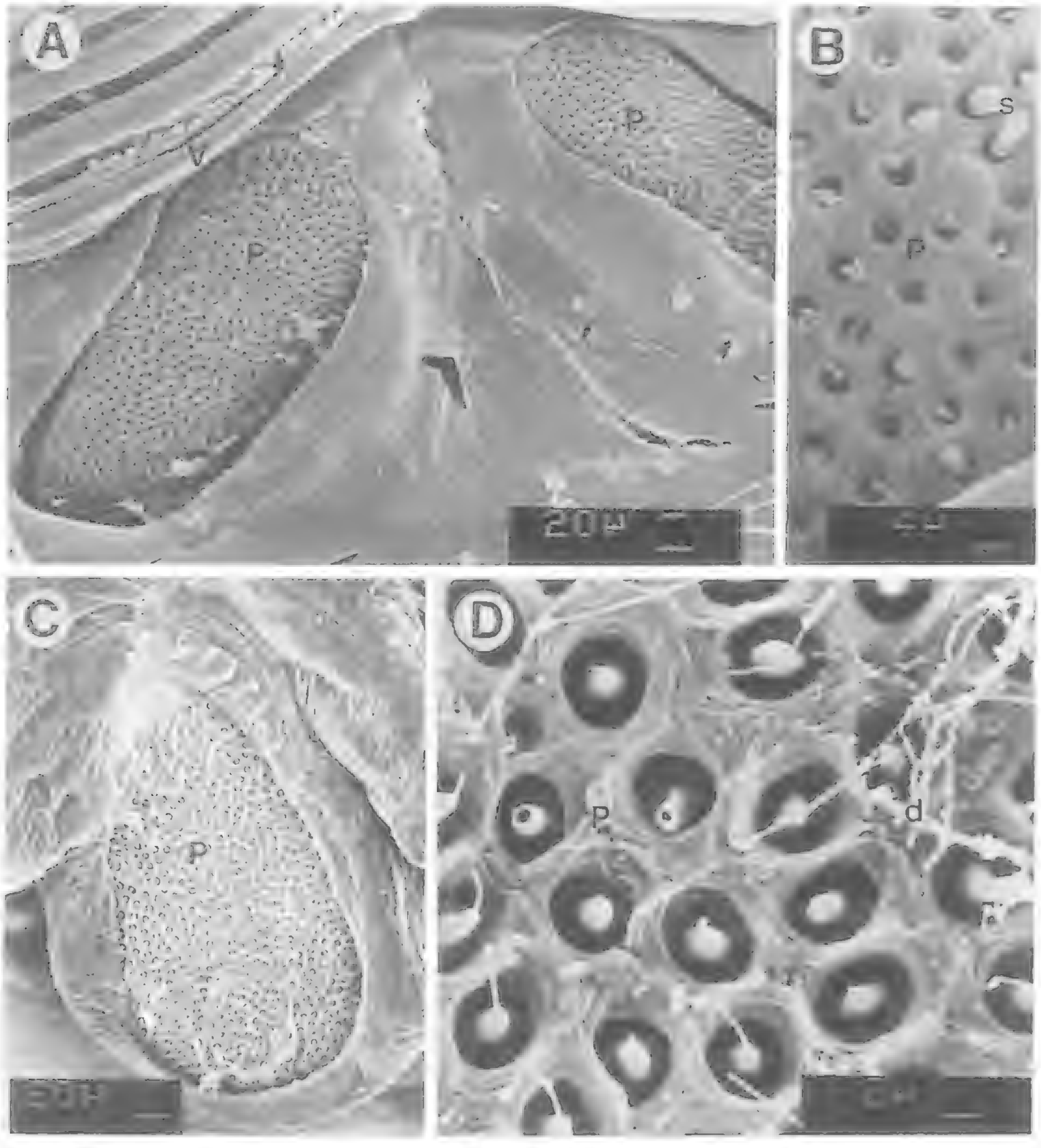


FIG. 1. Dorsal wall of genital cavity of *P. phalangioides*. A, Pore plates viewed from genital cavity; B, Pores that exude secretion, C, One pore plate from its dorsal side, glandular tissue removed; D, cuticular ductules of accessory glands.

the genital cavity for sperm storage. For more detailed information see Uhl (in press b, c).

MATERIAL AND METHODS

Juvenile *Pholcus phalangioides* were reared individually in the lab. To investigate mating behaviour the spiders were kept in couples in plastic boxes (16.5x9x6.5cm) and their behaviour was recorded day and night on video tape.

Five different experimental set-ups were used in order to answer the indicated questions:

1. Duration of copulation: Virgin females were offered unexperienced males.

2. Copulation duration with sperm-depleted males: Virgin females were offered recently experienced males (1/2 hour after termination of copulation).

3. Repeated matings with same partner: Previously virgin females were kept with previously unexperienced males for up to 20 days.

4. Repeated matings with changing partner: 1/2 hour after their first copulation females were offered unexperienced males.

In order to check the influence of box-size on mating behaviour 4 experiments were carried out using 2.5 times bigger boxes (18x12x11.5cm).

5. Duration of copulation after egg-laying: Post-oviposition females that had mated once were allowed to copulate again with unexperienced males.

For SEM studies adult females were anaesthetized, dissected and fixed in 70% ethanol or Bouin. In order to investigate the sclerotized parts of the female genital tract, the female genitalia were put in 5% NaOH solution until the soft parts were dissolved. Some genitalia were opened or cut with a sharp razorblade to locate the sperm mass in the genital cavity. They were dehydrated in ethanol, CP-dried, sputter coated with gold and examined in a Zeiss Semco Nanolab 7.

For light- and electron microscropy the spiders were anaesthetized and dissected in glutaraldehyde. After fixation in 2% osmium tetroxide/-glutaraldehyde, they were post-fixed in osmic acid (modified after Franke *et al.*, 1969), dehydrated in graded series of alcohol followed by propylene oxide and embedded in Epon. The semithin sections (0.7-1 μm) were cut with glass knives on a Reichert OmU3 and stained with toluidin. Ultrathin sections were cut with glass knives and diamond knife. They were stained with uranyl acetate, counterstained with lead citrate and examined in a Zeiss EM9 electron microscope.

RESULTS

Mating Behaviour

1. Virgin females copulated with unexperienced males over an hour ($\bar{x}$=64.5 minutes; sd=26.6; shortest duration: 16 min, longest duration: 122 min; n=42). This supports findings of Reagan and Reagan (1989) who investigated 104 pairs (mean copulation duration: 72.3 min; sd=43.3; shortest: 10 min, longest: 304 min).

2. Five males that had mated with virgin females (long copulation I) were brought half an hour after copulation to another virgin female. All copulations were long ($\bar{x}$: 56.8 minutes). The males probably refill their copulatory organs prior to the second copulation. The filling was observed in only one case by chance and was not detectable on the video recording.

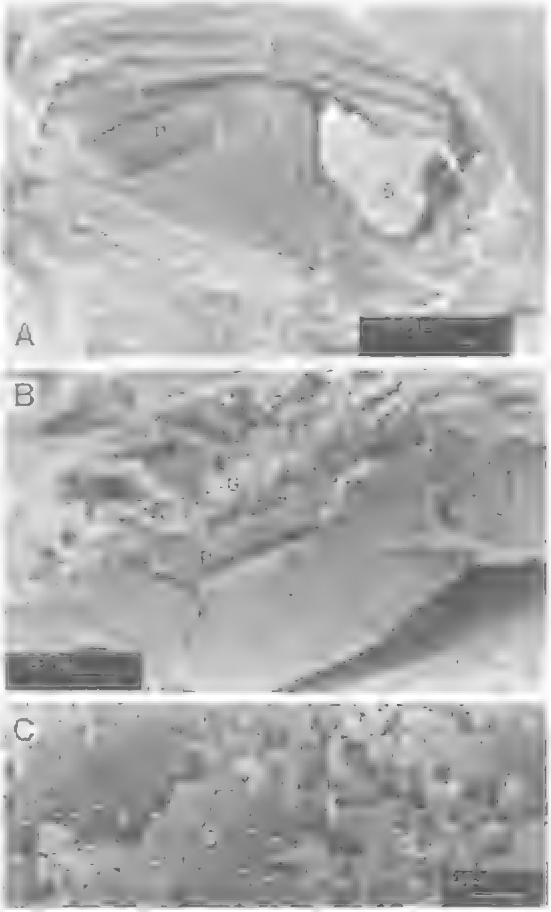


FIG. 2. A, Genital plate flipped back, dorsal wall of genital cavity revealed. Two pore plates, one concealed by secretory 'plug'; B, secretory 'plug' in genital cavity cut sagittally; C, Sperm mass in female secretion in female genital tract.

3. Unexperienced males and females were kept in pairs up to 20 days. Six females out of 12 allowed copulation from time to time: one female copulated twice, four females copulated 3 times, one female copulated five times. The second and the following copulations were always very short, they took only 2 to 5 minutes. Copulation duration tended to decrease in successive matings.

4. Unexperienced males were brought to females that had already mated once (long copulation I). In 9 of 14 cases the females allowed

Experimental set-up	n	Copulation duration (min.)
1. Virgin ♀ with unexperienced ♂	42	64.5 (16-122; 26.6)
2. Virgin ♀ with recently experienced ♂	5	56.8 (37-75; 13.9)
3. Second copulation with same ♂	6*	3.6 (2-5; 1.02)
4. Second copulation with unexperienced ♂	9*	2,6 (1,5-5; 1,0)
5. Post-oviposition ♀ with unexperienced ♂	7	59.6 (21-103; 31.4)

TABLE 1. Mating behaviour in *P. phalangioides* as a function of female reproductive history. *Only cases of copulation given. Range and standard deviation in parentheses.

further copulation. Again, second copulations lasted only a few minutes (1.5-5 min). Control experiments using bigger boxes showed that 3 females out of 4 allowed repeated matings (4.5; 2; 1 + 1 min).

5. Seven females that had mated once (long copulation 1) and were kept separately afterwards, had access to males after oviposition. Copulation duration was long.

Copulation duration seems to depend on the reproductive history of the females (Table 1).

The Genital Cavity

The dorsal (posterior) wall of the genital cavity is characterized by two oval pore plates (Fig. 1A). The pore plates converge in direction of the ridges and grooves that make up the heavily sclerotized valve which separates the genital cavity from the oviducts. Both plates are perforated by pores of 3-5μm in diameter (Fig. 1B). The pores are in contact with gland cells that exhude their glandular secretions into the cavity (Fig. 1B).

The tissue-free pore plates reveal the canal zones of the glandular tissue when looked at from their dorsal side (Fig. 1C). Situated in cavities, cone-shaped hollow structures are apparent (Fig. 1D). These are the distal regions of the canals that open into the uterus externus as the pores of the pore plate. Proximally the canals change into thin ductules that exhibit a rough surface after 6-10μm (Fig. 1D).

Sperm Storage

The accessory glands discharge their products through the pores of the pore plates into the genital cavity and form two portions of secretory 'plugs'. (Fig. 2A). During copulation, the male transfers sperm mass into the female secretion (Fig. 2B). The spermatozoa are surrounded by individual secretory envelopes, they are coiled and inactive (Fig. 2C).

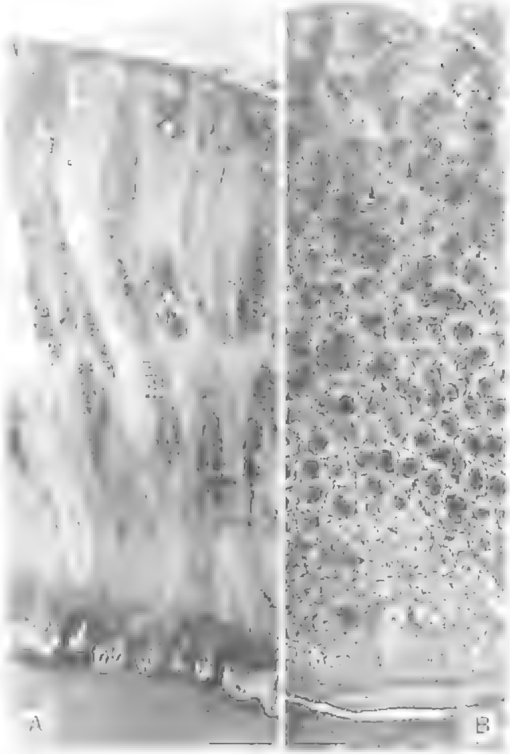


FIG. 3. Semithin section of accessory glands. A, Longitudinal section. Arrows mark nuclei of different cell types. Ba: basal lamina, E2: outer envelope cell, G: gland cell, m: microvilli, P: pore plate, s: secretion of the gland cells, S: secretion in genital cavity; B, Transverse section. Arrows and stars mark nuclei of different cell types. Scale lines: 20μm.

The Accessory Glands

The glandular tissue is composed of highly elongated cells (Fig. 3). Different cell types form the gland with various nuclei at different levels (Fig. 3A). The gland consists of lightly stained cells whose nuclei lie close to the basal lamina, and densely stained cells with more distal nuclei. Nuclei of other cell types lie mainly in the centre.

Secretory vesicles are apparent in the densely stained cells (the gland cells G). Accumulations of such vesicles are found in the apical second third of the glandular tissue. Each accumulation forms two portions of tightly packed secretory globules that discharge their contents into a common reservoir which is homogeneously coloured (Fig. 3A, B).

Bordering on the gland's orifices is a zone of greyish coloration that is formed by the light coloured cells (outer envelope cells E2).

Histology and ultrastructure show that the glandular tissue includes many similar units, each provided with a cuticular ductule that leads to the pore plate (Fig. 3A). Each unit comprises two gland cells and two envelope cells. The two gland cells (G1, 2) join each other to form a common reservoir (Fig. 4, 5B). They are rich in granular endoplasmic reticulum (Fig. 5A), mitochondria and dense secretory vesicles and exhibit numerous golgi complexes in the supranuclear region. The vesicles vary in size (up to 1.5μm in diameter) and get more numerous in the distal cell region. They are enclosed in a close-fitting membrane which is obscured by the matching density of the mature granula. The inner envelope cell (E1) surrounds and partially separates the two gland cells (Fig. 5B, C, D) and forms the proximal part of the ductule (Fig. 4C). The outer envelope cell (E2) surrounds all of the previously mentioned cells. Its cytoplasm is poor in organelles (Fig. 5A, B, D). It produces the distal part of the ductule and forms numerous microvilli that gather round the ductule and the orifice (Fig.5E) and represent the greyish zone visible in the semithin section of Fig. 3A.

The gland cells and the outer envelope cell form a so-called basal labyrinth adjacent to the basal lamina (Figs 4, 5A). The glandular units are separated from each other by elongated epithelial cells.

DISCUSSION

The glandular units of the accessory glands in *P. phalangioides* belong to class 3 cells (Noirot and Quennedy, 1974, 1991). According to that classification, a gland cell is associated with a cuticular ductule that has been secreted by a 'canal' cell. In *P. phalangioides* however, there are two gland cells that are always connected by a common microvilli region, one inner and one outer envelope cell that form a double ensheathing of the gland cells. Moreover, both envelope cells take part in producing the canal that leads to the pore plate. Therefore, the glands studied here belong to a complicated type of class 3 cells.

There is some information on gland structures in female spider genitalia. The glands of the receptaculum seminis of Telemidae belong to class 1 type of gland cells (Lopez and Juberthie-Jupeau, 1983), and in some Theraphosidae De Carlo (1973) stated a class 1 composition. However, the light microscope study of Kovoor (1981) indi-

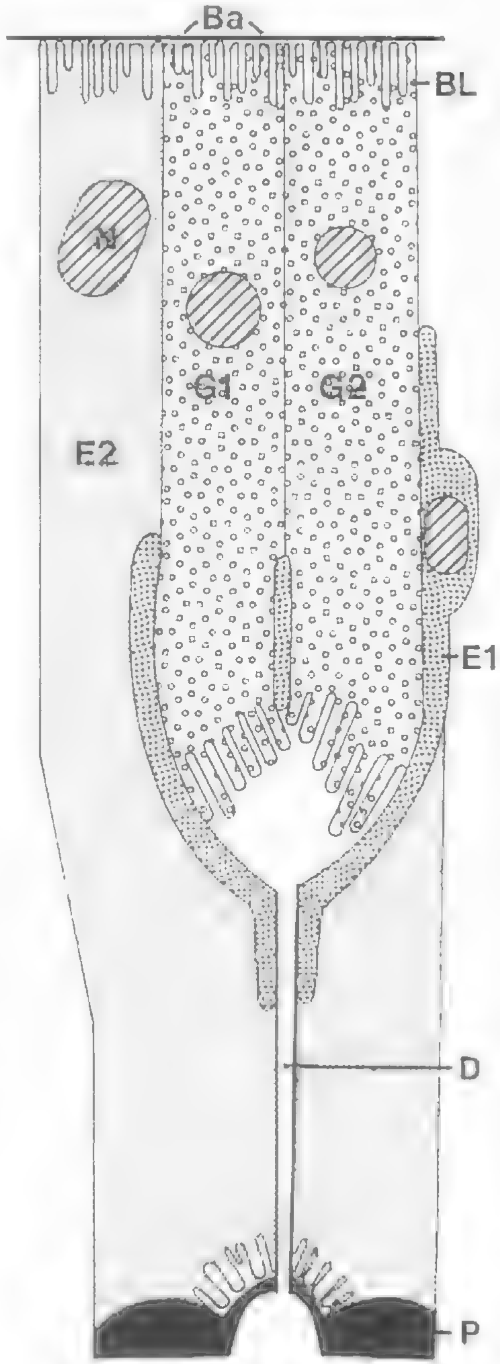
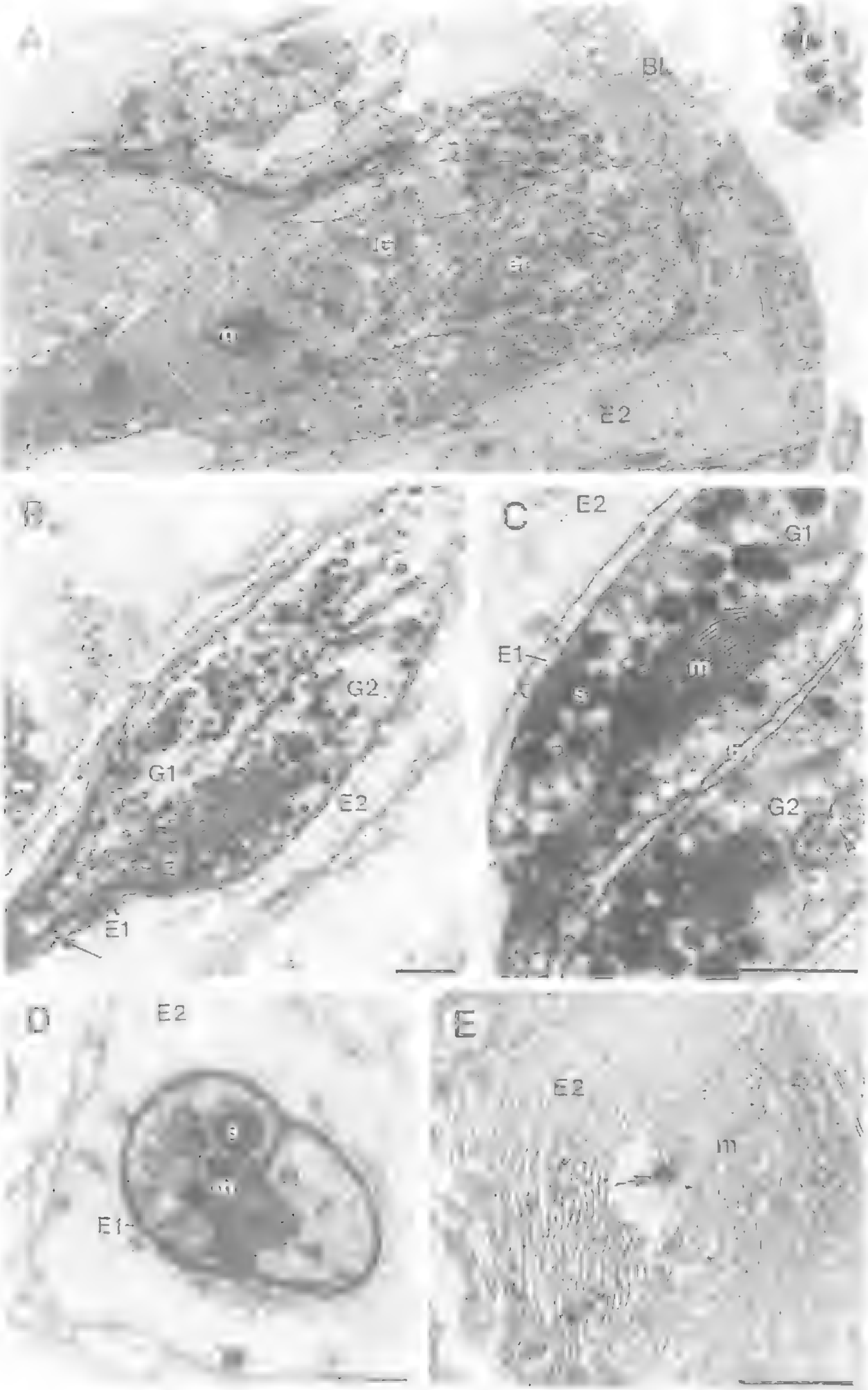


FIG. 4. Schematic reconstruction of one glandular unit of accessory glands. Ba: basal lamina, BL: basal labyrinth, D: ductule, E1: inner envelope cell, E2: outer envelope cell, G1, 2: gland cells, N: nucleus, P: pore plate.


A
BL
E2
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cates that a more complex gland composition as in *P. phalangioides* might not be exceptional.

The glandular units of *P. phalangioides* could function as a two-component-system, as the outer envelope cell shows conspicuous microvilli that surround the orifices of the ductules. This indicates secretory activity although the outer envelope cell contains no stainable secretory droplets or granules. Their product could have got lost during fixation or, the cells produce and release their product only on demand. Not all the secretory activities of cells are accompanied by microscopically detectable accumulation of the product in the cytoplasm. Apart from that, the outer envelope cell exhibits a basal labyrinth. It contributes to enhance the exchange of molecules between the haemolymph and the cells (Berridge and Oschmann, 1972) and characterizes active cells that take up or transfer material from or to the haemolymph.

The glandular secretions might serve various functions such as nutrition of the sperm (Coyle *et al.*, 1983; De Carlo, 1973; Engelhardt, 1910; Forster, 1980), pheromone production (Kovoor, 1981) or sperm displacement from the spermathecae into the genital cavity during oviposition (Forster *et al.*, 1987; Lopez, 1987; Lopez and Juberthie-Jupeau, 1983). Brignoli (1976) and Lopez and Juberthie-Jupeau (1983) considered activation of sperm prior to fertilization. The glandular tissue might be responsible for triggering activation via a secretory product that gets released exclusively before oviposition. Further, the females might achieve advantages from resorbing the sperm mass out of the genital cavity.

I consider the secretion in the female genital tract of *P. phalangioides* serves primarily as a depot for the sperm that guarantees successful storage as the onset of the female receptivity corresponds with the time needed to fill the genital cavity with glandular secretion (Uhl, in press a). Concerning any other possible functions, specific investigations are still lacking.

The bursal storage mode is considered a 'primitive' mode with little survival value as the spermatozoa are liable to be washed out during oviposition (Forster, 1980). Nevertheless, females of *P. phalangioides* succeed in producing several fertile batches of eggs after a single mating (Uhl, in press a).

Although females do not depend on repeated insemination, they allow further copulations. These always last only a few minutes in constrast to the first copulation that lasts over an hour and there is no apparent difference in copulation duration between second copulations with the same or with a different male. If new males are able to replace sperm of a previous male, longer copulations would be expected. Such short copulations may suggest that males are able to assess female virginity or reproductive history during insertion of their palpal structures and then decide on further investment of time and energy.

It has yet to be investigated whether successive copulations result in a transfer of spermatozoa at all, which will also give information on sperm precedence. Provided they transfer sperm and fertilise at least some eggs, it would be advantageous for males to mate with any female they meet. The females, on the other hand, can be expected to fill their storage structure with as many spermatozoa as possible to achieve the highest possible reproductive success. Depending on the amount of sperm already accumulated in the genital cavity females might allow further copulations and hence, decide on copulation duration. Indeed, there is some evidence that the female terminates copulation.

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FIG. 5. Ultrathin sections of accessory glands. A) Longitudinal section. Nuclear region of gland cells. B, Longitudinal section. Two gland cells join to form common microvilli region, surrounded by two envelope cells forming first part of canal (arrow). C) Longitudinal section. Microvilli region. Arrow shows cleaving bacterium D) Transversal section. Beginning of ductule. Gland cells joined, enveloped twice. E) Microvilli region of outer envelope cell close to pore plate. Small ductule (arrow). BL: basal labyrinth. E1. Inner envelope cell, E2, outer envelope cell, er: endoplasmatic reticulum, G1: gland cell 1, G2: gland cell 2, n: nucleus. m: microvilli. s: secretory droplets. All scale lines, 2μm.

LITERATURE CITED

BERRIDGE, M.J. & OSCHMAN, J.L. 1972. 'Transporting epithelia'. (Academic Press, New York, London).

BRIGNOLI, P.M. 1976. Ragni d'Italia XXIV. Note sulla morfologia dei genitali interni dei Segestriidae e cenni sulle specie italiane (Araneae). Fragmenta Entomologica 12: 19-62.

COYLE, F.A., HARRISON, F.W., MCGIMSEY, W.C. & PALMER, J.M. 1983. Observation on the structure and function of spermathecae in haplogyne spiders. Transactions of the American Microscopical Society 102: 272-280.

DE CARLO, J.M. 1973. Anatomia microscopica de las espermatecas de los generos *Grammostola* y *Acanthoscurria*. Physis Seccion C. Buenos Aires 32(85): 329-342.

ENGELHARDT, V. 1910. Beiträge zur Kenntnis der weiblichen Copulationsorgane einiger Spinnen. Zeitschrift für wissenschaftliche Zoologie 96: 32-117.

FORSTER, R.R. 1980. Evolution of the tarsal organ, the respiratory system and the female genitalia in spiders. Verhandlungen des 8.Internationalen Arachnologen Kongreß, Wien 1980: 269-283.

FORSTER, R.R., PLATNICK, N.I. & GRAY, M.R. 1987. A review of the spider superfamilies Hypochilidae and Austrochilidae (Araneae, Araneomorphae). Bulletin of the American Museum of Natural History 185: 1-116.

FRANKE, W.W., KRIEN, S. & BROWN, R.M. 1969. Simultaneous glutaraldehyde-osmium tetroxide fixation with postosmication, an improved fixation procedure for electron micoscropy of plant and animal cells. Histochemistry 19: 162-164.

KOVOOR, J. 1981. Une source probable de pheromone sexuelles: les glandes tégumentaires de la région génitale des femelles d'araignées. Atti della Società Toscana di Scienze Naturali, Memoire Serie B, Supplemento 88: 1-15.

LOPEZ, A. 1987. Glandular aspects of sexual biology. Pp. 121-131. In Nentwig, W. (ed.). 'Ecophysiology of spiders'. (Springer: Berlin, Heidelberg, New York).

LOPEZ, A. & JUBERTHIE-JUPEAU, L. 1983. Structure et ultrastructure de la spermathèque chez *Telema tenella* Simon (Araneae, Telemidae). Mémoires Biospéologiques 10: 413-419.

NOIROT, C. & QUENNEDY, A. 1974. Fine structure of insect epidermal glands. Annual Review of Entomology 19: 61-80.

1991. Glands, gland cells, glandular units: some comments on terminology and classification. Annales de la Societé Entomologique de France (N.S.) 27: 123-128.

REAGAN, N.L. & REAGAN, A.P. 1989. Mating and egg production in *Pholcus phalangioides*. American Arachnological Society, Newsletter 40.

UHL, G. (in press a). Sperm storage and repeated egg production in female *Pholcus phalangioides* (Fuesslin) (Araneae). Bulletin de la Societé Neuchâteloise des Sciences Naturelles. Actes de la XIIIème Colloque Européen d'Arachnologie, Neuchâtel 2.-6. Sept. 1991.

(in press b). Genital morphology and sperm storage in *Pholcus phalangioides* (Fuesslin) (Araneae). Acta Zoologica, Stockholm 74.

(in press c). Ultrastructure of the accessory glands in female genitalia of *Pholcus phalangioides* (Fuesslin) (Araneae Arachnida). Acta Zoologica, Stockholm 74.

THE BIOLOGY OF SPIDERS AND PHENOLOGY OF WANDERING MALES IN A FOREST REMNANT (ARANEAE: MYGALOMORPHAE)

GRAHAM F.C. WISHART

Wishart, G.F.C. 1993 11 11: The biology of spiders and phenology of wandering males in a forest remnant (Araneae: Mygalomorphae). *Memoirs of the Queensland Museum* 33(2): 675-680. Brisbane. ISSN 0079-8835.

Eight syntopic mygalomorph species, four of one genus, are recognised as inhabitants of a small remnant forest. Over six years 1,207 mature males were trapped and collected from a nearby home swimming pool and the wandering times of mature males of the species are compared. The population density within the forest is estimated. It is suggested the high number is because of an 'edge effect' supported by a reduction in predator numbers, an 'island effect' and that mygalomorphs have low dispersion powers, long life cycle and sedentary life style.□*Mygalomorphae, Hadronyche, Misgolas, Stanwellia, community, forest, remnant, phenology, population, syntopic, wandering.*

Graham F.C. Wishart, 'Scalloway', Willowvale, Gerringong, New South Wales 2534, Australia; 23 November, 1992.

Phenological studies of spiders commonly consider the distribution and abundance of species in relation to habitat variation or disturbance (Peck and Whitcomb, 1978; Koch and Majer, 1980). Studies of male spider wandering patterns are less common and are usually associated with taxonomic revisions of particular groups (Coyle, 1971; Raven, 1984). Main (1982) synthesised male wandering data for her studies of arid zone spiders.

This paper presents male wandering patterns over a six year period for six species of syntopic

FIG. 1. Aerial view, easterly aspect, from study site towards Gerringong township.

FIG. 2. Aerial view, south-westerly aspect, of study site. Pool length is 10m.

forest mygalomorphs and also discusses possible ecological effects which could account for the viability of the spider population. The long term data gathering was enabled by the serendipitous location of an in-ground swimming pool acting as a large pit-fall trap close to remnant forest.

STUDY AREA

The study site is on the property 'Scalloway' (34°44'11"S, 150°47'23"E) (Figs. 1, 2), near Gerringong, N.S.W., and is a remnant piece of marginal Complex Notophyll Vine Forest (Bywater, 1978) at an altitude of 110m. It is a fragment (ca 95m x 55m) of the original 'Illawarra Scrub', varying forest types which occupied much of the coastal strip east of the escarpment in South Eastern Australia between the towns of Stanwell Park in the North and Bomaderry on the Shoalhaven River in the south, a distance of 75km. Land clearing removed over 80% of this original vegetation (Fuller and Mills, 1985) and took place mainly between 1850 and 1910, the remnants being restricted to land unsuitable for grazing because of steep gradients and rock outcrops.

The forest overstory includes the trees *Syncarpia glomulifera* and *Alphitonia excelsa* and several vine species forming a discontinuous canopy at a height of about 12m. The understory consists mainly of the small tree *Commersonia fraseri* and the exotic woody scrambling shrub *Lantana camara*. *L. camara* intrudes within the forest but is dense and extensive around the forest edge (not allowed for in the forest dimensions) preventing the entry of cattle.

The site is on the edge of a ridge and slopes rapidly downwards to the north east. The soil is of volcanic origin. The surface soil is thin and spread over a basalt bedrock. Large but moveable rocks are prolific. Leaf litter is ca 5cm deep.

METHODS

Wandering mygalomorph spiders trapped in a 10m long swimming pool 15m from the forest edge were collected daily from 1 July 1985 to 30 June 1991. Variables possibly affecting the numbers of spiders trapped, such as domestic lighting, maintenance of grounds and ability of different species to wander further or more quickly than others, were not taken into account. For three years from 28 August 1986 to 25 October 1989 the burrows within a plot $1.5m^2$ were examined weekly.

RESULTS

Community Composition

Mature males of eight species of mygalomorph spiders were collected from the pool, viz.: *Misgolas hubbardi* Wishart, 1992 (Idiopidae), *M. dereki* Wishart, 1992, *M. kirstiae* Wishart, 1992, *M. robertsi* (Main and Mascord, 1974), *Hadronyche* sp. (Illawarra group) and *Atrax* sp.

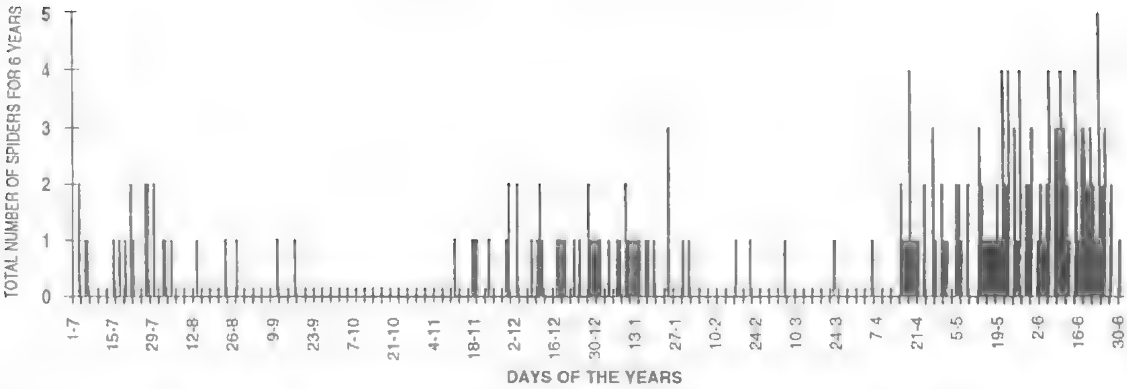


FIG. 3. Total number of *Misgolas hubbardi* captured on same days of years for six years from 1.7.85 to 30.6.91.

(Hexathelidae), *Stanwellia hoggi* (Rainbow, 1914) (Nemesiidae), and *Kiama lachrymoides* Main and Mascord, 1971 (Cyrtaucheniidae). The *Hadronyche* sp. is that referred to as *Hadronyche* sp. 20 by Gray (1987). The *Atrax* sp. is smaller but similar morphologically to *A. robustus* Cambridge, 1877. It differs also in that males wander from October to December whilst those of *A. robustus* wander mainly in January (Gray, 1986). They are considered here to be different species.

Population Density

Because much of the surface area of the forest floor is covered by large rocks and occupied by trees the 1.5 m^2 plot cannot be representative of the whole forest area. However, an extrapolation (based on the assumption that the ratio of the number of burrows occupied by all mature female spider species to the number of burrows occupied by *M. hubbardi* is equivalent to the ratio of the number of captured mature male spiders of all species to the number of captured mature male spiders of *M. hubbardi*) indicates there should be 41 mature female mygalomorphs per m^2 in the 1.5m^2 plot.

In the 1.5m^2 plot the maximum number of burrows counted at one time was 55. These included open burrows, those known to exist but temporarily sealed and very small open burrows of which most failed to persist. There were 27 burrows larger than 8 mm in diameter of which 10 were each occupied by a mature female *M. hubbardi*. Due to physical limitations in accurate-

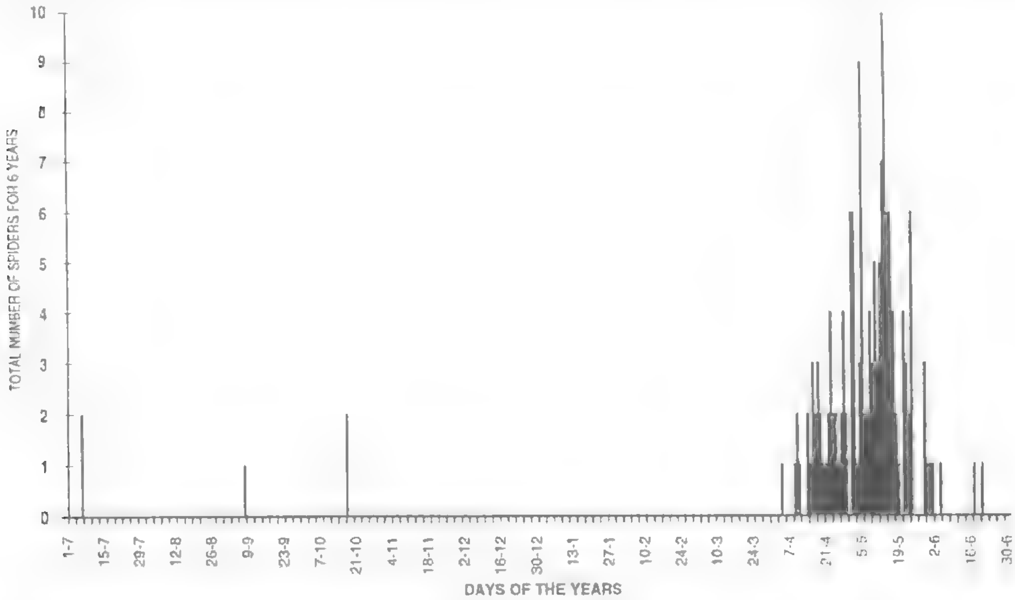


FIG. 4. Total number of *Misgolas dereki* captured on same days of years for six years from 1.7.85 to 30.6.91.

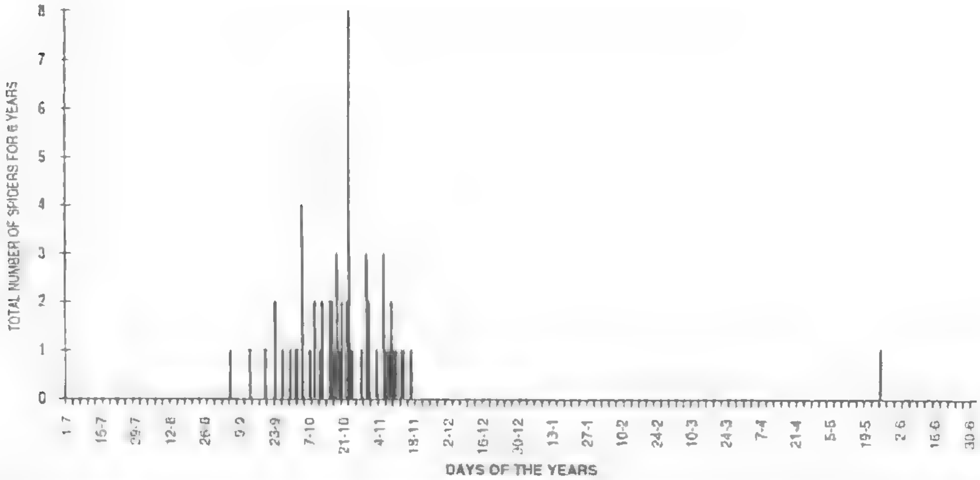


FIG. 5. Total number of *Misgolas kirstiae* captured on same days of years for six years from 1.7.85 to 30.6.91.

ly counting small burrows and recognizing the presence of the burrows of *M. kirstiae* and *Hadronyche* sp. the total count must fall short of the actual mygalomorph population.

PHENOLOGY OF WANDERING MALES (Table 1)

Wandering mature males of *M. hubbardi* were found almost throughout each year (Fig. 3). The extensive wandering period of *M. robertsi* is interrupted during January and February when the frequency of capture is reduced (Fig. 6). The wandering period for *S. hoggi* is also long, extending over six months (Fig. 8). As is customary to expect of male mygalomorphs, the wanderings of *M. dereki* (Fig. 4), *M. kirstiae* (Fig. 5) and *H.* sp. (Fig. 7) are restricted to short and more precise annual periods. The collections of *Atrax* sp. and *K. lachrymoides* were too small for deductions to be conclusive.

During the six year period, 11 female *S. hoggi* were also trapped in the pool during the months from March to October.

Species	Total trapped	Peak active periods	% in peak periods	No. trapped per day
Misgolas hubbardi	197	April-July	58	0·3
		Nov.-Jan.	20	0·2
Misgolas dereki	153	Apr.-June	98	0·7
Misgolas kirstiae	61	Sept.-Nov.	98	0·7
Misgolas robertsi	158	Nov.-May	96	0·4
Hadronyche	606	March-May	96	0·29
Stanwellia hoggi	26	May-Nov	100	0·1
Atrax sp	5	Oct.-Nov	100	0·2
Kiama lachrymoides	1	Nov		
Total	1207			

TABLE 1. Summary of numbers and timing of male spiders trapped in pool from 1 July 1985 to 30 June 1991.

DISCUSSION

No previous reports have been found of either eight species of mygalomorph spiders or four species of one genus (*Misgolas*) of spiders existing elsewhere syntopically or sympatrically.

The high proportion of mature female *S. hoggi* collected is surprising, 11 females to 26 males, and 10 of the 11 were taken at times coincidental with the male wandering period. The number reflects the long-legged, male-like morphology of the female adapting it to roam. Further, that only one male *K. lachrymoides* was collected may indicate the inability of the male of this species to wander a long distance a reflection in this case of the male's short-legged female-like morphology. The usual sexual dimorphism of mature burrowing mygalomorph spiders (female bulky, stout legged; male less bulky, long legged) is contradicted in these two species.

Some possible reasons for the dense mygalomorph spider population are offered. First, predators of mygalomorph spiders may have become extinct in the area following human settlement. For example, the bandicoot (*Perameles nasuta* Geoffroy, 1804), reputed to be a mygalomorph spider predator (Main, 1976; Preston-Mafham, 1984) and once very common in Willowvale, has been rarely seen by the author and not at all for 15 years. Here then, possibly, is

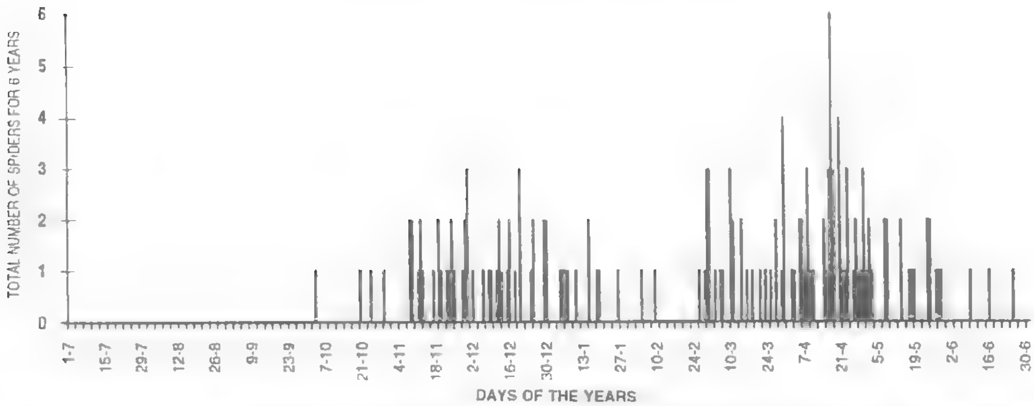


FIG. 6. Total number of *Misgolas robertsi* captured on same days of years for six years from 1.7.85 to 30.6.91

a paradox where habitat destruction and the introduction of feral animal pests, may increase, not decrease, mygalomorph spider numbers by decreasing spider predators.

Second, the concentration may result from an 'Island Effect' where it is found that the population of an individual species can be far greater than expected when the species is insulated within a small ecological system (separate pers. comms, M.Gray and R.Raven). Also Main (1987) proposed that mygalomorphs are admirably fitted to persist in small isolated areas because of their low dispersion powers, long life cycle and sedentary life style.

Finally, in a larger (ca. 300 ha) forest with complete canopy and separated from the 'Scalloway' site by *ca.* 400m of pasture land there is a paucity of mygalomorph spider burrows and few insects suitable for prey. Burrows are more common near the forest edge, and so too is insect life with grasshoppers, moths and crickets prolific. Because the 'Scalloway' forest remnant is small it is in effect a forest edge throughout with an abundance of suitable prey. Laurence (1991) states, 'In the tropics, forests near edges exhibit striking changes in microclimate, vegetation structure and composition, disturbance regimes, and invasions of species from adjacent habitats. Thus, in fragmented systems, species that tolerate edge conditions are often favoured'. I suggest that this is the explanation for the presence of this dense mygalomorph population.

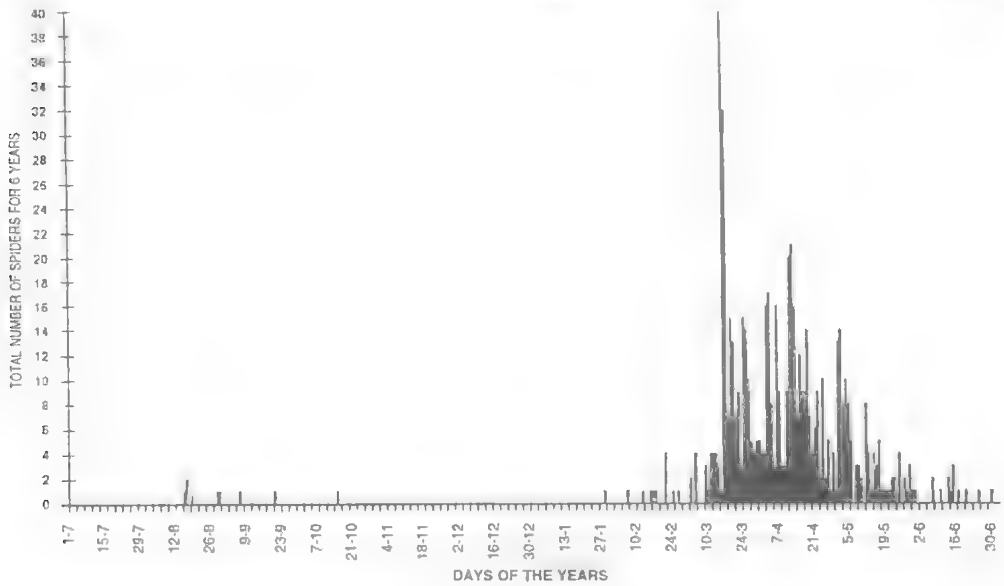


FIG. 7. Total number of *Hadronyche* sp. captured on same days of years for six years from 1.7.85 to 30.6.91.

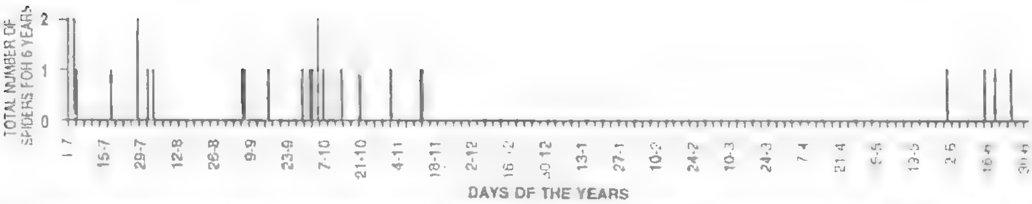


FIG. 8. Total number of *Stanwellia hoggi* captured on same days of years for six years from 1.7.85 to 30.6.91.

ACKNOWLEDGEMENTS

My thanks to the Australian Museum and Dr Michael Gray for the provision of facilities and advice; Mr Paul Askew for field assistance; Mr Harry Mitchell for aerial photographs; Mr George Browning for helpful criticism; and Dr Robert Raven of the Queensland Museum for computing suggestions and encouragement. Especially do I thank my neighbour, Dr Peter Linklater, for the execution of statistical work and the preparation of the graphs and Dr Bill Humphreys of the Western Australian Museum for comments on the data and guidance. I am grateful to the CSIRO Science and Industry Endowment Fund for its support.

LITERATURE CITED

BYWATER, J. 1978. Distribution and ecology of rainforest vegetation and fauna in the Illawarra. (Thesis, University of Wollongong).

CAMBRIDGE, O.P.- 1877. On some new genera and species of Araneidea. Annals and Magazine of Natural History (4) 19: 26-39.

COYLE, F.A. 1971. Systematics and natural history of the mygalomorph spider genus *Antrodiaetus* and related genera (Araneae: Antrodiaetidae). Bulletin of the Museum of Comparative Zoology 141: 269-402.

FULLER, L. & MILLS, K. 1985. Native trees of central Illawarra. (Weston and Co.: Kiama).

GRAY, M.R. 1986. A systematic study of the funnel web spiders (Mygalomorphae: Hexathelidae: Atracinae). (Unpublished Ph.D. Thesis. Macquarie University).

1987. Distribution of the funnel web spiders. Pp. 312-321. In Covacevich, J., Pearn, J. & Davie, P. (eds). 'Toxic plants and animals'. (Queensland Museum: South Brisbane).

KOCH, L.E. & MAJER, J.D. 1980. A phenological investigation of various invertebrates in forest and woodland areas in the south-west of Western Australia. Journal of the Royal Society of Western Australia 63: 21-28.

LAURENCE, W.F. 1991. Ecological correlates of extinction proneness in Australian tropical rain forest mammals. Conservation Biology (5) 1: 79-89.

MAIN, B.Y. 1976. 'Spiders'. (Collins: Sydney).

1982. Adaptations to arid habitats by mygalomorph spiders. Pp. 273-283. In Barker, W.R. *et al.* (eds). 'Evolutions of the flora and fauna of arid Australia'. (Peacock Publications: Frewville).

1987. Persistence of invertebrates in small areas: case studies of Trapdoor spiders in Western Australia. Pp. 29-39. In Saunders, D. *et al.* (eds). 'Nature conservation: the role of remnants of native vegetation.' (Surrey Beatty and Sons: Sydney).

MAIN, B.Y. & MASCORD, R.M. 1971. A new genus of diplurid spider (Araneae: Mygalomorphae) from New South Wales. Journal of the Australian Entomological Society 6: 24-30.

1974. Description and natural history of a "tube-building" species of *Dyarcyops* from New South Wales and Queensland (Mygalomorphae: Ctenizidae). Journal of the Australian Entomological Society 8: 15-21.

PECK, W.B. & WHITCOMB, W.H. 1978. The phenology and populations of ground surface, cursorial spiders in a forest and a pasture in the south central United States. In Merrett, P. (ed.). 'Arachnology'. Symposia of the Zoological Society of London 42: 131-137.

PRESTON-MAFHAM, R. & K. 1984. 'Spiders of the world.' (Blandford Press: Dorset).

RAINBOW, W.J. 1914. Studies in Australian Araneidae. Records of the Australian Museum 10: 187-270.

RAVEN, R.J. 1984. A new diplurid genus from eastern Australia and a related *Aname* species (Diplurinae: Dipluridae: Araneae). Australian Journal of Zoology, Supplementary Series 96: 1-51.

WISHART, G.F.C. 1992. New species of the trapdoor spider genus *Misgolas* Karsch (Mygalomorphae: Idiopidae) with a review of the tube-building species. Records of the Australian Museum 44:263-278.

THE MACARONESIAN CAVE-DWELLING SPIDER FAUNA (ARACHNIDA: ARANEAE)

JÖRG WUNDERLICH

Wunderlich, J. 1993 11 11 : The Macaronesian cave-dwelling spider fauna. *Memoirs of the Queensland Museum* 33(2): 681-686. Brisbane. ISSN 0079-8835.

The composition of the cave-dwelling spider fauna of the Macaronesian Islands–Madeira, the Azores and the Canary Islands–is compared with the endemic epigean spider fauna of these archipelagos. The grades of adaptations in the cave-dwelling spiders are compiled, and the following questions are discussed: from which geographic regions did the stem species come? What can be said about the evolution of the species? How old are the cave-dwelling spider species?

Die Fauna der Höhlenspinnen der Makaronesischen Inseln - Madeira, Azoren und Kanarische Inseln- wird mit der endemischen epigäischen Fauna dieser Archipele verglichen. Der Grad der Anpassung an das Höhlenleben wird untersucht und verglichen; die folgenden Fragen werden diskutiert: Wo liegt der Ursprung der Stammarten? Was kann über die Evolution und das Alter der höhlen-bewohnenden Arten gesagt werden?□*Araneae, troglobites, Canarian and Macaronesian Islands, Island biology, biogeography, evolution.*

Jörg Wunderlich, Hindenburgstr. 94, D-75334 Straubenhardt 3, Germany; 7 December, 1992.

Some island groups in the northern Atlantic–the Canary Islands, the Azores, the Archipelago of Madeira, the small Ilhas Selvagens and by most authors (but not by me) the Cape Verde Islands–are called Macaronesian Islands (Fig. 1). The Macaronesian Islands are mainly of volcanic origin, only the Eastern Islands (Fuerteventura, Lanzarote) are partly of continental origin and have been probably connected with Africa some million years ago.

The first troglophilic and troglobitic Macaronesian spiders were described in 1985 from Tenerife. Now cave-dwellers are known from Madeira (1 species), from the Azores (1 species) and from the Canary Islands (at least 17 endemic species, see Wunderlich, 1991), by far most species are known from Tenerife: at least 11 species = 10% of the endemics (and perhaps there are hundreds of mostly undescribed insect species of different orders).

Especially on the Canary Islands there are many caves. The best studied system of caves on Tenerife - cueva del Viento, cueva Reventon - is more than 16km long; the length of all Macaronesian caves is perhaps more than 100km, and only a few have been examined intensively.

MACARONESIAN CAVE-DWELLING SPIDERS

Nearly all cave-dwelling spiders are endemics of one island or even only one cave (Table 1):

Three species of those listed (Table 1) are not restricted to a single island:

1. *Meta bourneti* Simon, 1929 (Tetragnathidae) is a west-palearctic species introduced to a cave on Tenerife (Canary Islands);
2. *Agraecina canariensis* Wunderlich, 1991 (Liocranidae) is known from caves on Gran Canaria and Tenerife (Canary Islands);
3. *Rugathodes pico* (Merrett and Ashmole, 1989) (Theridiidae) is known from caves on Pico and Fajal (Azores).

Here I deal with five questions: 1. What is the composition of the Macaronesian fauna of troglophilic and troglobitic spiders and what are the differences to the epigean fauna? 2. Which species are extremely well adapted as cave-dwellers? 3. From which geographic regions did the stem species come? 4. What can be said about the evolution of the species? 5. How old are the cave-dwelling spider species?

Cave-Dwelling and Epigean Spiders

The most diverse spider families are shown in Figs 2-3. In the Canarian troglophilic and troglobitic cave-dwellers (Fig. 2): Dysderidae (at least 35%), Linyphiidae (25%) and Pholcidae (25%), the sum of these 3 families is 85%. (No Oecobiidae).

In the epigean endemic species (Fig. 3) the composition is quite different: Dysderidae 16%, Linyphiidae 15%, Pholcidae 13%, the sum of these 3 families is 44%, only half compared with the cave-dwellers. In the families Dysderidae

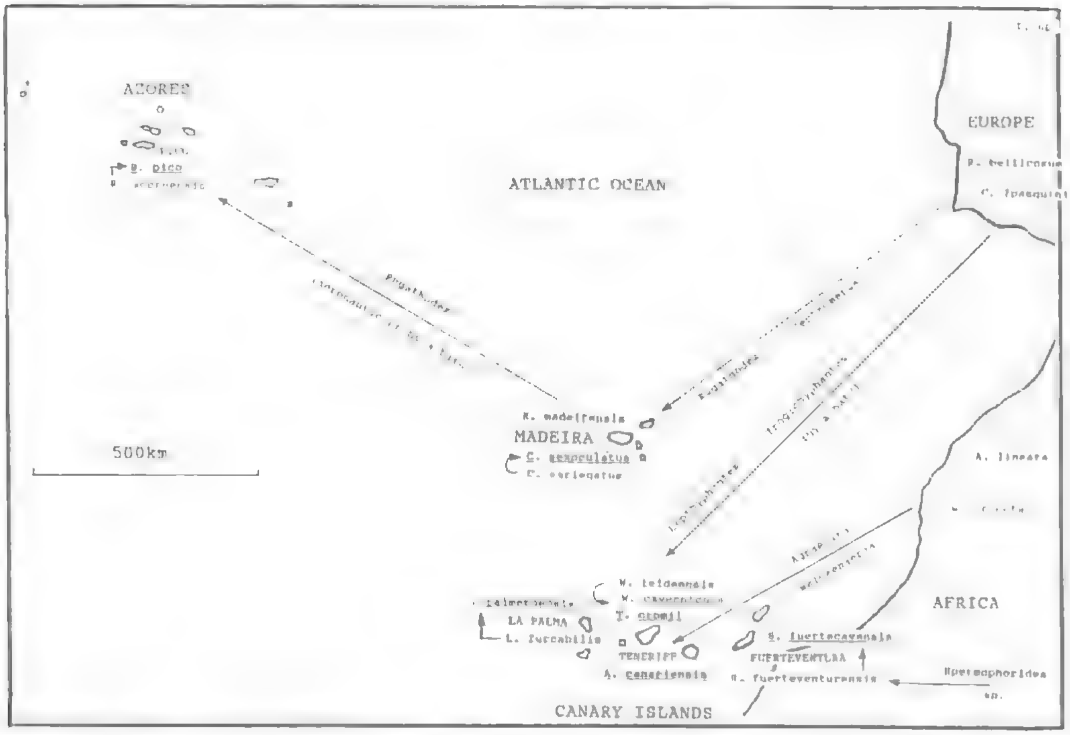


FIG. 1. The Macaronesian Archipelagos. Some Macaronesian cave-dwelling spiders (underlined) and their European and Macaronesian relatives.

(only *Dysdera*) and Pholcidae (*Pholcus* and *Spermophorides*) *all* epigean genera have evolved cave-dwelling species; in the Linyphiidae only members of 5 from 21 genera with endemic species have evolved cave-dwellers (= 25%). *Dysdera* is the genus richest in species in caves and out of caves on the Canarian and Macaronesian Islands. Oecobiidae probably do not find their prey -ants- in the caves.

Highly Adapted Cave-dwellers?

Different grades of adaptation to cave life in the Macaronesian spiders is evident in three structures (Table 1): the size of the eye lenses, the body pigmentation and length and slenderness of legs.

Some true cave spiders of *Dysdera* have reduced eyes, but neither depigmentation nor long and slender legs. I do not know the explanation. Thus, perhaps the eye reduction is the best indicator regarding the grade of adaptation to cave life in spiders. For discussion below I choose the following five spider species.

1. *Meta bourneti* (Tetragnathidae, Tenerife) is restricted to deeper parts of caves, but the eyes are not reduced, the body is only slightly depigmented, and the legs are nearly of normal length. This species has been introduced from Europe or North Africa.

2. Not strongly adapted is *Agraecina canariensis*, but very variable in the depigmentation and in eye reduction (grades 1-3, Figs 4- 5). The variation is intrapopular. This seemingly troglophilic subterranean species is not restricted to caves.

3. In four Canarian species of *Spermophorides*, the eyes are more or less reduced (Figs 8-11); the eyes of an epigean *Spermophorides* sp. from Tenerife are normal (Fig. 12). Cave-dwelling *Spermophorides* spp. are not strongly related. The known species occur on four different islands. So the eye reduction must have been evolved independently four times.

4. *Rugathodes pico* is restricted to caves. The spiders are strongly depigmented, they have strongly reduced eyes and the legs are long and slender (grades 3-4, Fig. 6a; cf. Fig. 6b the related epigean *R. acoreensis*).

5. In *Troglohyphantes oromii* (Ribera and Blasco, 1986) (Linyphiidae, Tenerife), the eyes are tiny or completely absent (Fig. 13), body and legs

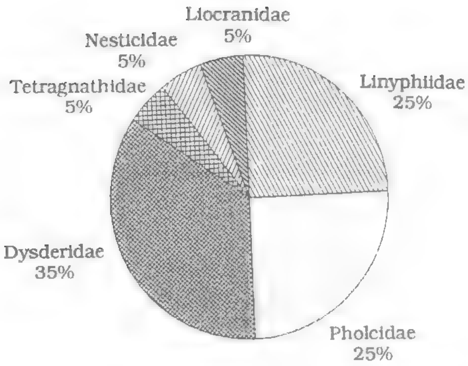


FIG. 2. Composition of Canarian families of troglophilic and troglobitic spiders based on 18 species.

are completely depigmented, the legs are very long and slender (all grades between 3 and 4). The adaptations in *Canarionesticus quadridentatus* (Nesticidae, Tenerife) and in ?*Metopobactrus cavernicola* (Linyphiidae, Tenerife) are similar. These species show the strongest adaptations to cave life.

Species	Di	R.E.	Dep	Leg	T
Meta bourneti	Wpal,T	0	≤1	≤1	<2
Agraecina canariensis	CI (GC,T)	0-3	0-3	1	1-7
Dysdera labradaensis	CI (T)	2	0	0	2
D. ratonensis	CI (LP)	2	0	0	2
Lepthyphantes palmeroensis	CI (LP)	1	1	1	3
D. chioensis	CI (T)	3	0	1	4
D. ambulotenta	CI (T)	3-4	0	0	3-4
Pholcus baldiosensis	CI (T)	2	3	0	5
Spermophorides flava	CI (GC)	2	3	1	6
S. reventoni	CI (T)	1-2	1	2	≤5
D. esquiveli	CI (T)	?3-4	1	1?	≥5
S. fuerteventurensis	CI (F)	2	3	≤1	≤6
Walckenaeria cavernicola	CI (T)	1-2	1-2	3	6
S. justoi	CI (EH)	2-3	3	3	≤9
D. unguimmanis	CI (T)	4	2-3	≤4	~10
Centromerus sexoculatus	M	3	4	2-3	≤10
Rugathodes pico	AZ	3	3	3-4	≤10
?*Metopobactrus cavernicola*	CI (T)	3-4	3	3-4	~10
Troglohyphantes oromii	CI (T)	3-4	4	3-4	~11
Canarionesticus quadridentatus	CI (T)	4	3	4	11

TABLE 1. The Macaronesian troglophilic (at least the first two and perhaps the first five species) and troglobitic spider species and the grades of their adaptations from 0 (normal structures as in epigean taxa) to 4 (= eyeless or almost so/ completely depigmented/ very long legs, the species listed below); AZ = Azores, CI = Canary Islands, EH = El Hierro, F = Fuerteventura, GC = Gran Canaria, LP = La Palma, M = Madeira, T = Tenerife, Wpal = West Palearctic). Di, distribution; R.E., reduced eyes, Dep, depigmentation; Leg, long & slender legs; T, Total.

Origin of the Stem Species

Macaronesian cave-dwelling neoendemic spiders and their European relatives. The hypothetical origin of all species is the West-Mediterranean area, most came from Europe (Fig. 1), e.g. species of *Rugathodes* to the Azores - Madeira seems to be a 'stepping stone', *Centromerus* to Madeira. *Troglohyphantes* came perhaps from Spain to Tenerife, but the sister species is unknown. *Walckenaeria* came from North Africa to Tenerife, *Agraecina* came from Europe or North Africa to Tenerife (and Gran Canaria).

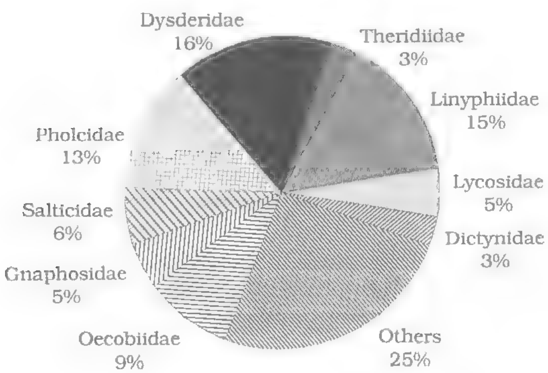
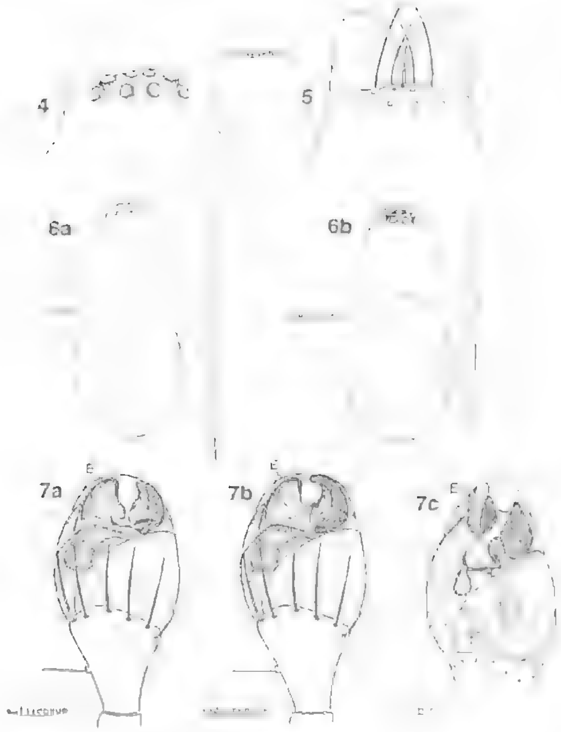


FIG. 3. Composition of Canarian families of *epigean* spiders based on more than 400 species.

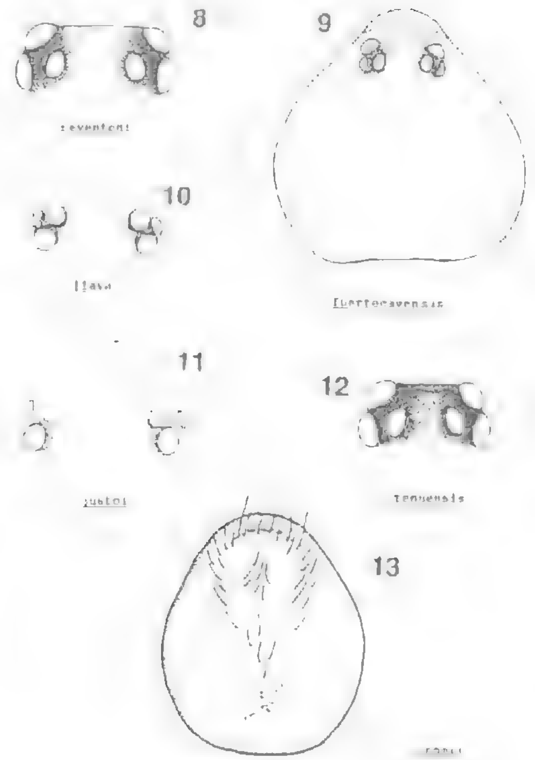
The occurrence of cave-dwelling species of the different genera on *Tenerife* - e.g. *Walckenaeria*, *Troglohyphantes* and *Agraecina* - are remarkable (Fig. 1). The highest Macaronesian mountain, the 3718m high Teide on Tenerife, seems to be a 'catcher' of aeronautic (ballooning) spiders which came from the Western Mediterranean area. This finding is supported by the relationships of the endemic spider fauna of the Teide and the Cañadas, an area surrounding this high mountain (cf. Wunderlich, 1991: 104-107).

Evolution of Macaronesian Cave-dwelling Spiders

In some spiders, e.g. *Canarionesticus quadridentatus* and *Troglohyphantes oromii*, no related epigean species is known, and almost nothing can be concluded about their evolution.



FIGS 4-7. 4-5. Variable eye reduction in subterranean Canarian *Agraecina canariensis* Wunderlich, 1991 (Liocranidae). 6, 7. *Rugathodes*. 6, ♂ body with eyes and right tibia I from the Azores: 6a, of the cave-dwelling *R. pico*; 6b, of the epigean *R. acoreensis*. 7. Right male pedipalps ventral: 7a, *R. bellicosum* (Simon, 1873), Europe; 7b, *R. madeirensis* Wunderlich, 1987, Madeira; 7c, *R. pico* (cavernicolous) and *R. acoreensis* (epigean), Azores. These species show no differences. (E = embolus).



FIGS 8-11. Eye reduction in Canarian cave-dwellers spiders: 8, *Spermophorides reventoni* Wunderlich, 1991; Fig. 9, *S. fuertecavensis*; 10, *S. flava* Wunderlich, 1991; 11, *S. justoi* Wunderlich, 1991. 12. Eyes of the epigean *S. tenoensis* Wunderlich, 1991, Tenerife. 13. Sometimes completely eyeless prosoma of cave-dwelling *Troglohyphantes oromii*, Tenerife.

(Several species are not well studied, e.g. *Dysdera* species, or only one sex is known). In this connection *Troglohyphantes oromii* is of special interest because nearly all species of this genus are troglophilic or troglobitic cave-dwellers as well as the species from Tenerife. I can imagine that there has never existed an epigean stem species on Tenerife and that the ancestors, perhaps as a cocoon, has been transported by a bat directly from a European cave to a cave on Tenerife. Several species or subspecies of bats fly from Europe via Madeira to the Canary Islands (Dr. Biscoito, Mus. Munic. Funchal, Madeira, pers. comm.). This hypothesis would explain why there is no epigean *Troglohyphantes* spp. on Tenerife or another Canary or Macaronesian Island. Otherwise I do not want to exclude the possibility that this species is a paleoendemic relict (Peck, 1990: 372-373).

Based on the very similar genital organ, in *Rugathodes pico* and *acoreensis* they are identical, I found some strongly related spider species (Table 3). In the cave-dwelling *R. pico* (Table 1 and discussed above), the adaptations to cave life and the differences in some non-genital structures compared with epigean species are very distinct: the eye reduction, the depigmentation and the prolongation of the legs, Fig. 6a; compare Fig. 6b of the epigean species, which is also known from the Azores. Otherwise the genital structures in the two Azorean species show *no* differences in both sexes (Fig. 7c), but there are distinct differences to *madeirensis* from Madeira (Fig. 7b) and *bellicosum* from Europe (Fig. 7a). So I do believe that *R. pico* and *R. acoreensis* are true sibling

Introduced species	Paleaoendemic species	Neoendemics
Meta bourneti	*Canarionesticus quadridentatus* (Nesticidae, Tenerife). No known relative.	The epigean sibling or sister species/stem species is known, usually from same island. To this group belong most Macaronesian cave spiders, see below (genesis/evolution), Dysderidae, Pholcidae, Linyphiidae, Theridiidae and Liocranidae.

TABLE 2. Historical groups of Macaronesian cave-dwelling spiders. Position of *Troglohyphantes oromii* in list is uncertain; it has no known epigean relative. See below: possible transport by a bat.

species (or even subspecies?) and that *R. acoreensis* also is the stem species of *R. pico*.

In *Spermophorides*, differences in genital and non-genital structures are distinct in both sexes, and perhaps they are not sister species. The remaining species in this list are known only from females.

Martin *et al.* (1989) assume that some Canarian troglobites can be considered as relict species which evolved after changes in the climate 'since there have been alternating wet and dry periods ...causing important changes in the fragile insular ecosystem on the surface.' (See below: *Rugathodes*). Furthermore the yearly seasonal changes–hot and dry summers, cooler and more humid winters especially on the Eastern Canary Islands–did perhaps initiate vertical movement of some species into the ground in the summer and also autecological changes for instance in *Centromerus fuerteventurensis* Wunderlich, 1991 (Linyphiidae). In this species, which is not a cave-dweller, the eyes are reduced as well as in species of *Scotargus* (Linyphiidae) and *Altella* (Dictynidae) of other Canarian islands (Wunderlich, 1991).

Borges and Oromí (1991) do prefer the 'adaptive shifting theory' of Howarth (1973). 'This theory does not invoke isolation during climatic (or volcanic?) changes but instead proposes that the partly adapted ancestors shifted into newly developed niches.' In my opinion this theory can well explain the genesis of some Macaronesian cave-dwelling spider species including the ones listed above (see Peck, 1990: 366-368). Especially there exists large caves and lava tubes on the Canary Islands, and there are many ecological niches.

From the Macaronesian Islands and its spiders I know three kinds of preadaptations which support the 'adaptive shifting theory':

1. A lot of Canarian species are known as hypogean spiders and were caught using special traps in the ground in the so-called 'mesocavernous shallow stratum' (Wunderlich, 1991: 11). From this stratum and from accidental captures under stones I know Canarian species of *Dysdera*, *Spermophorides*, *Lepthyphantes*, *Walckenaeria*, *Altella*, *Zimirina* and others. These spiders have moderately reduced eyes and are more or less depigmented, they seem to be troglophilous and not macrocavernicolous, but microcavernicolous or myrmecophilous. *Agraecina canariensis* is a species of this stratum but it also penetrates caves. (A closely related species has been newly discovered in a Romanian cave).

2. Another preadaptation is offered in the conditions in the laurisilva (the relict laurel forest): high humidity and low changes in temperature. For example I found the laurisilva species *Troglonata madeirensis* Wunderlich, 1987 (Anapidae s.l.) in the wet and light part near the entrance of a cave on Madeira (Sao Vincente). I collected ♂ ♀ of *Lepthyphantes mauli* Wunderlich, 1991 (Linyphiidae) in the same part of this cave; this species probably also came from the wet forest near the cave.

3. The third kind of biotopes that lead to troglobitic conditions are under stones and under leaves on trees at places with a high humidity near stretches of water. At such places, under stones as well as under leaves on trees, I found on the Azores *R. acoreensis*, the epigean sibling/stem species of the cave-dwelling *R. pico*. Under a stone over flowing water on Tenerife I found partly depigmented spiders of *Walckenaeria alba*.

Age of Macaronesian Cave-dwelling Spider Species

The age of the Macaronesian caves remains unknown. The youngest Macaronesian Islands, the Western Azorean and the Western Canarian Islands, are only very few (1-2?) million years old. Two spider species, *Pholcus roquensis* and *Walckenaeria cavernicola*, are cave-dwellers at the Cañadas on Tenerife. The greatest age of these species could be the same as the age of this part of Tenerife, at least 200 000 (up to 2 million) years.

Rugathodes pico is known only from caves of the Azorean islands Pico (a young island) and Fajal. After Ashmole (in litt. 1991) these Azorean

Cave-dwelling species	Epigean relatives	Island	Family
Spermophorides fuertecavensis	*S. ?fuerteventurensis*	Fuerteventura (Canary Is.)	Pholcidae
Centromerus sexoculatus, and sp. nov.	*C. variegatus*	Madeira	Linyphiidae
Lepthyphantes palmeroensis	*L. furcabilis*	La Palma (Canary Is.)	Linyphiidae
Walckenaeria cavernicola	*W. teideensis*	Tenerife (Canary Is.)	Linyphiidae
Rugathodes pico	*R. acoreensisi*	Pico and Fajal (Azores)	Theridiidae

TABLE 3. Macaronesian cave-dwelling troglophilic or troglobitic spiders and their nearest epigean relatives, possible stem/ sister/sibling species from same island.

Islands had perhaps a land bridge during the last glaciation. So this species probably evolved from its closely related epigean stem species, near or identical with *R. acoreensis*, perhaps not later than 10 000 years ago (= 10 000 generations). From genital structures, in both sexes there are no differences, speciation should have happened, geologically, not long ago, that means at the end of the last glaciation. But this idea is very vague; perhaps the speciation happened much later, and *R. pico* was transported by bats from one island to the other only very few thousand years ago (Wunderlich, 1991: 200-201). Wunderlich (1991) gives further details of these cave-dwelling spiders and their taxonomy.

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LITERATURE CITED

BORGES, P. & OROMI, P. 1991. Cave-dwelling ground beetles of the Azores (Col., Carabidae). Mémoires de Biospéologie 18: 185-191.

HOWARTH, F.G. 1973. The cavernicolous fauna of Hawaiian lava tubes. 1. Introduction. Pacific Insects 15: 139-151.

MARTIN, J.L. *et al.* 1989. Sur les relations entre le troglobies et les espèces epigées des Iles Canaries. Mémoires de Biospéologie 16: 25-34.

PECK, S.B. 1990. Eyeless arthropods of the Galapagos Islands, Ecuador: composition and origin of the cryptozoic fauna of a young, tropical, oceanic archipelago. Biotropica 22: 366-381.

WUNDERLICH, J. 1991. Die Spinnen-Fauna der Makaronesischen Inseln. Taxonomie, Ökologie, Biogeographie und Evolution. The spider fauna of the Macaronesian Islands. Taxonomy, Ecology, Biogeography and Evolution. Beitraege Araneologie, vol. 1, 619 pp.

RELATIONSHIP BETWEEN FOOD INTAKE AND SPIDER SIZE IN TEMPERATE ZONES: EXPERIMENTAL MODEL FOR AN ORB-WEAVING SPIDER

FRÉDÉRIC YSNEL

Ysnel, F. 1993 11 11: Relationship between food intake and spider size in temperate zones: experimental model for an orb-weaving spider. *Memoirs of the Queensland Museum* 33(2): 687-692. Brisbane. ISSN 0079-8835.

A method is presented that allows calculation of the energy intake by an orb-weaving spider, *Larinioides cornutus* (Araneae: Araneidae) under natural conditions throughout the spider's life. A laboratory study provides several relationships between individual energetic consumption and size of spiders depending on the thermal conditions of their environment. I observe a preferred temperature (21°C) at which spiders have the biggest consumption. A model (pseudo-cubic spline) is constructed for the calculation of energy intake by each juvenile instar. Energy requirements of the adult population are estimated from the repor-duction rate observed in the field. The energy requirements under natural conditions and the total weight of prey consumed by the population in the course of its biological cycle can be inferred. In the mesophilous heathland investigated, the total fresh weight of prey consumed by the population during the life cycle is 18.2 $kg.ha^{-1}$.

Cette étude vise à relier les taux de survie, de croissance et de reproduction d une espèce Orbitèle *Larinioides cornutus* (Araneae: Araneidae), au nombre de proies consommées en milieu naturel au cours du cycle biologique. Cette analyse est déduite d une approche bioénergétique. Au laboratoire, les consommations énergétiques et la croissance des araignées sont testées en fonction de l environnement thermique. Ces expériences mettent en évidence la présence d un optimum thermique d ingestion qui modifie la croissance et la consommation des individus. Un modèle d ajustement (spline pseudo-cubique) liant la température, la taille des araignées et la température ambiante est proposé pour estimer l énergie ingérée en phase juvénile. L énergie ingérée en phase adulte est estimée en comparant les paramètres taux de reproduction -consommation calculés en élevage, au taux de reproduction observés en milieu naturel. Les besoins énergétiques sont ensuite convertis en quantité de proies capturées. Sur la lande mésophile étudiée, la population capture en poids frais, 18.2 kg de proies par hectare au cours du cycle biologique.□*Population energetics, Araneae, Araneidae, Larinioides cornutus.*

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Among the many studies already carried out about the trophic spectrum of the araneids (Nentwig, 1987), some suggest that the population of spiders–wandering spiders or non-migrant spiders–can utilize a significant proportion of the secondary productivity of natural areas (Kajak, 1967; Robinson and Robinson 1970; van Hook, 1971; Blandin and Celerier, 1981; Nyffeler, 1982). Moreover, some studies emphasize that the growth increment (Vollrath, 1988), the rate of reproduction (Riechert, 1974; Wise, 1979) or the density of individuals (Kajak, 1977) observed in the populations can fluctuate with the number of prey caught. Thus, the characteristics of population dynamics of spiders partly depend on the quantity of prey captured; they can give data about the secondary productivity and consequently about the biological resources of natural biotopes.

However, no study has been done in temperate climates to link the characteristics of population dynamics of spiders with the quantity or the quality of trophic resources. My work on *Larinioides cornutus* (Clerk, 1758) (Araneae: Araneidae) (Ysnel, 1989) describes demographic evolution and reproduction rate of a population in a mesophilous heathland in western France (Ysnel, in press). Besides this, laboratory studies showed a thermal dependance between spider size and food intake (Ysnel, 1990). This study attempts to combine previous results to estimate the number of prey captured by a natural population of spiders during its development.

MATERIALS AND METHODS

This study is based on the calculation of the energy intake during the postembryonic develop-

Instar	13°C		16.5°C		21°C		26°C	
	n	C ±SD	n	C ±SD	n	C ±SD	n	C ±SD
J2	-	-	7	19.03 (5.03)	8	18.75 (6.38	7	12.70 (3.3)
J3	-	-	7	44.60 (11.25)	8	50.54 (24.39)	7	28.74 (13.97)
J4	-		9	116.70 (26.9)	14	83.88 (37.86)	12	74.90 (37.8)
J5	2	165	9	241.62 (71.75)	13	134.00 (32.5)	9	181.66 (111.9)
J6	-	-	7	471.95 (190.12)	12	333.90 (86.27)	9	595 (196.56)
J7	6	1438.4 (393)	7	999.14 (317.15)	12	647.70 (166.65)	3	668.39 (22.55)
J8		-		-	4	1120.69 (456)	1	2581.5
J9			-		1	1029.6	-	

TABLE 1: Average values of consumption (C, joules) during each juvenile instar. (n = number of individuals tested, SD = standard deviation).

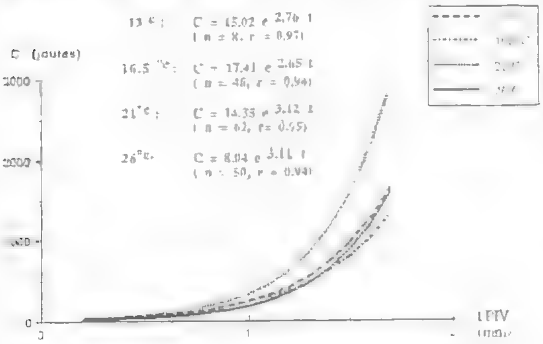

FIG. 1. Theoretical relationship between spider size and consumption in intermoult periods (n = no. of measurements, r = correlation coefficient).

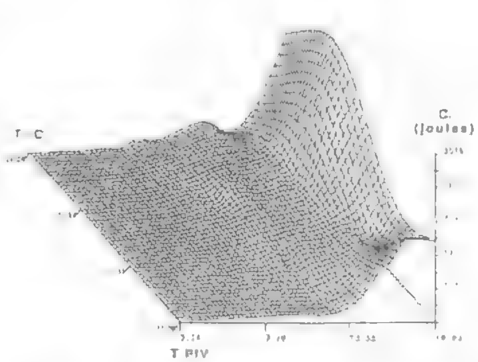

FIG. 2. Pseudo-cubic spline showing relationship between spider size (T PIV), consumption in intermoult period (C) and air temperature (T°C).

ment of *L. cornutus*. To estimate energy requirements during juvenile development, I refer to results on the individual energy consumption of spiders at different temperatures (Ysnel, 1990); thus, only the main references of the experimental conditions are described. Young spiders from cocoons reared in the laboratory were divided into three groups by temperatures-16.5°C, 21°C and 26°C. (These values are a little lower than those in my previous work; they agree with more accurate values using an electronic thermograph). Spiders required a varied diet for survival therefore they were reared to maturity using three prey species: the first instars were fed with adult *Drosophila melanogaster* and the last instars were fed with calliphorid flies (*Calliphora vomitaria* and *Lucilia sericata*). Three times a week, all spiders received a fixed number of prey according to their age. Juvenile spiders were kept under a light regime of LD 12:12. Furthermore, 8 spiders collected in the field at stages 4 and 6 and were reared in the laboratory at 13°C. For these spiders, the energy consumption was studied after the first moult in captivity.

As adults, only females feed (adult males no longer build webs). In nature, females can mate in autumn but egg-laying occurs only under long days from May to August. During this period, females lay, on average, only one egg-sac and disappear soon after laying (Ysnel, in press). Therefore, energy consumption is estimated in

Instar	13°C		16.5°C		21°C		26°C		
		T ± SD	n	T ± SD	n	T ± SD	n	T ± SD	K.W.
J2		-	7	0.27 ± 0.033	8	0.28 ± 0.024	7	0.27 ± 0.026	P<0.7
J3			7	0.40 ± 0.043	9	0.37 ± 0.018	8	0.37 ± 0.032	P<0.2
J4		-	6	0.56 ± 0.07	12	0.47 ± 0.05	9	0.58 ± 0.09	P<0.05
J5	2	0.87	9	0.91 ± 0.142	13	0.64 ± 0.08	10	0.86 ± 0.13	P<0.08
J6	-	-	6	1.24 ± 0.186	10	0.92 ± 0.105	9	1.42 ± 0.27	P<0.08
J7	6	1.68 ± 0.1	7	1.63 ± 0.237	11	1.21 ± 0.143	3	1.34 ± 0.04	P<0.04
J8	-	-	-	-	4	1.49 ± 0.11	1	1.89	
J9	-	-	-	-	1	1.66		-	

TABLE 2. Average lengths of tibia IV (T, mm) and comparison of values for 16.5°C, 21°C and 26°C. (n = no. of measurements, SD = standard deviation K.W. = Kruskall- Wallis test).

13°C				16.5°C				21°C			
T	N1	C	C/egg	T	N1	C	C/egg	T	N1	C	C/egg
2.25	115	1083.15	9.41	2.15	82	772.85	9.425	2.13	78	797.1	10.2
2.32	131	1215.20	9.27	2.40	95	679.20	7.14	2.10	87	719.3	8.26
2.50	144	1333.00	9.25	2.28	96	700.40	7.30	2.40	140	1338.9	9.50
2.02	108	948.70	8.77	2.13	50	569.13	11.38	1.87	40	600.71	2.01
2.03	105	-		2.10	75	-		1.80	50	644.31	2.90
2.47	128	-		2.24	65	-		2.02	57	723.81	0.05
2.45	138	-						1.98	58	871.8	15.03
2.43	126	-	-								

TABLE 3. Consumption of ♀and no. of eggs /cocoons at 3 temperatures. (T = length of tibia 4 ; N1 = no. eggs/first egg-sac; C=energy intake by / in joules; C/egg =energy intake for pro-duction of 1 egg).

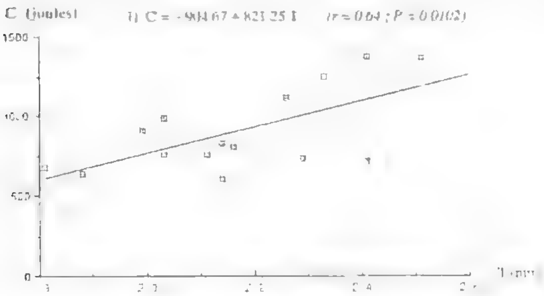

FIG. 3. Relationship between size of females (T) and energy (C) required to elaborate first egg-sac.

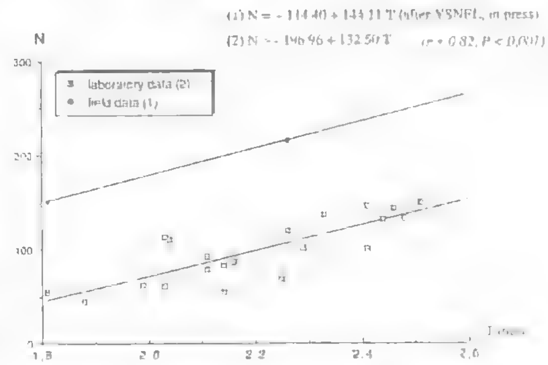

FIG. 4. Relationship between no.of eggs (N) produced in first cocoon and size (T) of females.

adults based on the energy intake needed to produce one cocoon. With this aim, 22 over-wintering fecund females were collected and reared in the laboratory under long days (LD = 16 : 8) and different temperature conditions (13°C, 16.5°C, and 21°C). After the females oviposited, we determined the relationship between the energy intake, the female size (length of tibia IV) and the number of eggs per cocoon.

For each juvenile instar and the adult, the energy intake was determined by the difference between the energy in the whole captured prey and that in the food remains. Calorific determinations for all prey and food remains were made using a Parr bomb calorimeter (Ysnel, 1990).

From the phenology of different instars in nature, the developments of the species have been worked out (Ysnel, in press). Spiderlings emerging from egg sacs laid from late spring to early summer become adult before winter and form a first cohort of individuals (cohort C1). Spiderlings which appear later (end of summer) form a second cohort in the population (cohort C2); they are still immature in winter and become adults early next summer. In analysing the demographic evolution of the population (from 20 m^2 sample areas) during the life cycle, the number of surviving spiders per instar was counted for the two cohorts (Ysnel, 1992). For each juvenile instar, the energy consumption was inferred from the average size of spiders (length of tibia IV) and the thermal environment in the field. Daily meteorological data were classified in four temperature classes (T< 16°C; 16.5°C <T< 18°C; 18.5°C < T < 22°C; T > 22°C) and the average value of each class calculated. The energy ingested is determined from the relative proportion of each phase of temperature during one intermoult period. The average value of the caloric

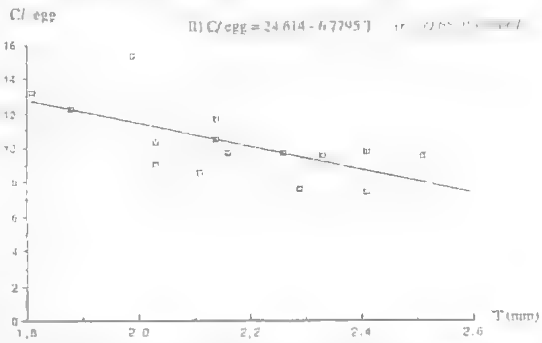

FIG. 5. Relationship between energy required to produce one egg (C/egg/Joules) and size of ♀ (T).

Method 1				Method 2				
Size	TNEL	C(J) (lab.)	TNEF	C (J) (field)	Size	TNEF	C/egg (J)	C (J) Field
2	68.4	737.83	173.8	1874.8	2	173.8	11.05	1921.4
2.3	107.8	934.2	217.0	1981.6	2.3	217.0	9.02	1957.8
2.6	147.5	1230.6	260.9	2176.4	2.6	260.9	8.30	2165.1

TABLE 4. Comparison of consumption (C, joules) of adult ♀ from method; 1, 2 Theoretical no. of eggs (laboratory, TNEL), in (field, TNEF).

equivalent of insects captured in the field is 22.6 J/mg dry weight (Ysnel, 1992). Cummins and Wuyscheck (1971) found that the dry weight of most insects is equivalent to 20-30% of the wet weight. To transform dry weight (x) into wet weight (Y), I used the conversion factor calculated for calliphorid flies (Y = x/0.262; Ysnel, 1990).

RESULTS AND DISCUSSION

Individual Consumption, Spider Size and Thermal Conditions of Juveniles

The number of instars needed to reach maturity varied with the growth conditions. In Araneidae, the first free-living instar is called J2 (Canard, 1987). From 5 to 8 immature instars may variously precede adulthood. Average consumptions per instar are calculated for four temperatures (Table 1). Average consumption also varies with instar and growth conditions. In each group, an overall connection between the instar of development of a spider and the energy intake of that instar cannot be deduced because individual variation is considerable. However, for all individuals, whatever the instar, there is a good correlation between individual consumption and spider size the intermoult (Table 2). For each temperature with all instars merged, we can fit all the observed values to four exponential graphs corresponding to four different equations (Fig. 1). The four curves show that the individual consumption varies with temperature. For the tested temperature range, and spiders of similar size, I observed a 'preferred temperature of consumption' (21°C) at which the energy intake at the intermoult is maximal (Ysnel, 1990).

Near the thermal preferendum, spiders have the highest consumption but the growth increment is paradoxically the smallest. From instars J4 onwards, individuals kept at 21°C are significantly smaller in size than individuals kept at 16.5°C and 26°C (Kruskall-Wallis test, Table 2). Using the energy budget equation of Petrusewicz and MacFadyen (1970), the energy dissipated as heat (respiration) could be increasing (while the energy retained as growth is decreasing) and the spiders must be more active at 21°C. In contrast, when the temperature deviates from the thermal preferendum, the energy allowed for the activity of spiders must be less important (probably because spiders progressively fall into quiescence or aestivation) and the energy retained as growth increases.

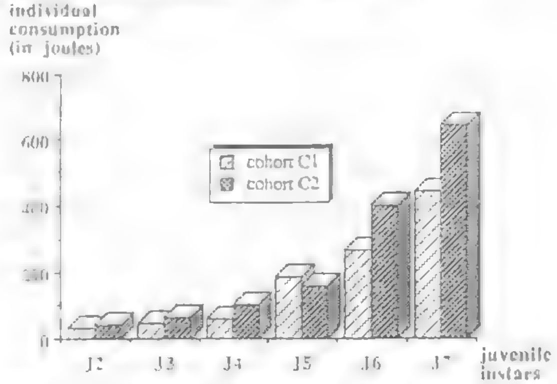

FIG. 6. Estimated individual consumption per instar under field conditions.

One can estimate the energetic requirements of spiders C (ρ)(x, y), by interpolating the pooled data to a single regression model linking spider size and air temperature during the intermoult, to the individual energy consumption. The method, based on the 'homogeneous spline functions with several variables' (Duchon, 1980) allows us to

	Cohort C1				Cohort C2				Population		
Instar	Size	C ind.	n	C1	Size	C ind.	n	C2	N/m^2	C	kg/ha
J2	0.260	30.5	247	7523	0.26	44	159	6996	20.3	14254	1.22
J3	0.363	45.8	127	5817	0.40	63.38	92	5831	11	11648	0.98
J4	0.558	60.9	102	6212	0.57	101.8	29	2952	6.6	9164	0.77
J5	0.831	187.7	86.5	16240	0.78	158	28	4424	5.7	20664	1.74
J6	1.140	264.8	71	18801	1.14	400.54	27	10815	4.9	29216	2.50
J7	1.330	442.3	18	7961	1.36	641.8	7	4493	1.25	12454	1.05

TABLE 5. Estimated mean energy consumption per juvenile instar in field conditions of individuals (C.ind.), all Cohorts 1 (C1) & 2 (C2), & of total population (C); n =abundance of different instars; N/m^2= spider density; kg/ha =mean total weight (kg/ha) of food consumed/instar).(Ysnel, 1992).

	size ± SD	N	C/egg	E/Fn	C	
Cohort C1	1.845 ± 0.18	169	11.43	1931.7	24	46361
Cohort C2	1.91 ± 0.13	164	11.66	1912.2	37	70751

TABLE 6. Estimated mean energy consumption of adults (N = estimated no. of eggs/cocoon; E/egg = energy intake to produce one egg; E/F = energy intake by ♀; n: = no. ♀♀ per cohort; C = total consumption of ♀♀/cohort).

adjust significantly the whole experimental values to a pseudo-cubic spline (Fig. 2) by means of the following formula :

$$C(\rho)(x,y)=\sum_{i=1}^{n} \lambda i\,(\rho)((x-xi)^2+(y-yi)^2)^{\frac{3}{2}}+\alpha 1x+\alpha 2y+\beta$$

where ρ is the tension parameter ($\rho = 5$), x = spider size at intermoult, y = air temperature. αi, $\alpha 1$, $\alpha 2$ and β are calculated by the solution of a linear system.

This model estimates the energy requirements during an intermoult period of any juvenile instar, under these experimental conditions.

Energy Consumption during Adult Phase

The individual consumption of all females (Table 3) is plotted against spider size (Fig. 3); the regression line can be used as a calibration curve to estimate the consumption of females independent of thermal environment. The number of eggs per cocoon also showed a significant linear relationship (Fig. 4) with female size.

However, the number of eggs in cocoons in the laboratory (line 2) and those in nature (line 1) clearly indicate that breeding females produce fewer eggs in the laboratory. Two hypotheses can be advanced to explain this result:

- the food consumption of breeding females in the laboratory is lower than that of females in nature; consequently fewer eggs are produced in the laboratory.

- for females of the same size, the number of eggs produced in nature is favoured by a varied diet.

The ratio 'energy consumption/number of eggs produced' gives an index (C/egg) of the energy required to produce one egg (Table 3). The values of 'C/egg' are dependant on female size (Fig. 5). Two methods are now used to study the energy consumption of females:

- method 1: For females of a given size, the regression equation I (Fig. 3) allows the calculation of the energy consumption to produce a given number of eggs. When females produce more eggs (as in nature), we estimate the energy consumption using a simple rule of 3.

- method 2: In nature, we can estimate the number of eggs produced by females using the regression equation I (Fig. 4). The energy consumption is then calculated by referring to the values of 'C/egg' given for the females of the same size (Fig. 5, regression equation II).

Theoretical values of the consumption of females derived by the two methods are similar (Table 4). Hence, the energy required to produce one egg is not influenced by the feeding regime of spiders. The number of eggs per cocoons is dependant on female size and on the quantity of food intake. We use the ratio C/egg to estimate the energy requirements of the adult population in the field.

Energy Requirements in Nature

For individuals of the same juvenile instars, the consumption varies with time of year of the spiders appear (Table 5). Individuals of cohort C2 have, in most instars, an higher consumption than those of cohort C1 although the average size in the two cohorts is similar (Fig. 6). Hence, the spiders of cohort C2 live closer to the thermal preferendum than those of cohort C1.

According to the caloric equivalent of the prey caught in natural areas (22.6 J/mg dry weight), we can estimate the food consumption of the orb-weaving population. In the mesophilous heathland investigated, the total fresh weight of prey consumed by the population in its biological cycle is 0.036 kg/20 m^2 which amounts to 18.2 kg/ha. The amount of food ingested varies with the instar. The high mortality rate (Table 5) reduces total consumption in the first three juvenile instars. In later instars, although the spider density decreases, food intake by the population increased owing to a concommitant increase in individual consumption. The quantity of prey caught by adult females is higher than for the whole juvenile population (Table 6, Fig. 7).

CONCLUSIONS

The species responds to variation of the trophic conditions in both body size and the number of eggs produced. These two biological parameters constitute indices of reference to estimate the quantity of prey caught by the population during the biological cycle. Compared with the results of others (Table 7), the food intake by the population of *Larinioides cornutus* represents from 8.2-36.4% of the total food consumption of the spider communities of different ecosystems. In other respects, the food ingested in the biotope studied

Biotope	Prey killing rate (kg/ha/year)	Country
Reed belt of lake	5-12	Austria
Grassland	52	U.S.A.
Grassland	>150	Switzerland
Grassland	120	Poland
Forest	100	Germany
Spartina swamp	215	U.S.A.

TABLE 7. Prey killing rate by spider communities of vegetation of different ecosystems (after Nyffeler, 1982).

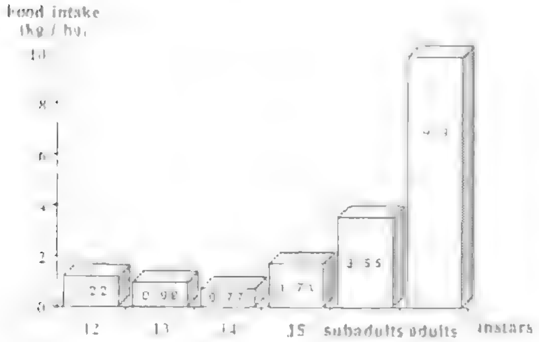

FIG. 7. Food intake by population in biological cycle.

is five times as important as the food ingested by the population studied by Kajak (1967) in a Polish grassland. This is the only analysis of the characteristics of population dynamics of an orb-weaving spider in a temperate region and emphasizes the importance of the secondary productivity.

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LITERATURE CITED

BLANDIN, P. & CELERIER, M.L. 1981. Les Araignées des savanes de Lamto (Côte d'Ivoire). Organisation des peuplements, bilans energétiques, place dans l'écosystème. Publs Lab. Zool. E.N.S. Paris 21 (2 fasc.): 1-586.

CANARD, A. 1987. Analyse nouvelle du développement postembryonnaire des Araignées. Revue Arachnologique 7: 91-128.

CUMMINS, K.W. & WUYSCHECK, J.C. 1971. Caloric equivalents for investigations in ecological energetics. Mitt. Internat. Verein. Limnol. (18): 158 pp.

DUCHON, J. 1980. 'Fonction splines homogènes à plusieurs variables.' (Thèse de Doctorat d'Etat, Université Supérieure de Mathématiques Générales, Institut National de Paris Grignon.)

KAJAK, A. 1967. Productivity of some populations of web spiders. Pp. 807-820. In K. Petrusewicz (ed.). 'Secondary Productivity of Terrestrial Ecosystems.' (Warsawa).

1977. Analysis of consumption by spiders under laboratory and field conditions. Ekol. Pol. 26: 409-427.

NENTWIG, W. 1987. The prey of spiders. Pp. 249-263. In W. Nentwig (ed). 'Ecophysiology of Spiders.' (Springer: Heidelberg).

NYFFELER, M. 1982. Field studies on the ecological role of spiders as insect predators in agrosystems. (D.Sc. Thesis, Swiss Fed. Inst. Technol., Zurich, Aku-Photodruck).

PETRUSEWICZ, K. & MACFADYEN, A. 1970. Productivity of terrestrial animals. IBP Handbook 13 (Blackwell Scientific Publications: Oxford).

RIECHERT, S.E. 1974. Thoughts on the ecological signifance of the spiders. Bioscience 24: 352-356.

ROBINSON, M.H. & ROBINSON, B. 1970. Prey caught by a sample population of the spider *Argiope argentata* (Araneae: Araneidae) in Panama: a year's census data. Zoological Journal of the Linnean Society 49: 345-358.

VAN HOOK, R.I. 1971. Energy nutrient dynamics of spider and orthopteran poulations in a grassland ecosystem. Ecological Monographs 41: 271-285.

VOLLRATH, F. 1988. Spider growth as an indicator of habitat quality. Bulletin of the British Arachnological Society 7: 217-219.

WISE, D.H. 1979. The effect of an experimental increase in prey abundance upon the reproductive rates of two orb weaving spider species (Araneae: Araneidae). Oecologia, Berlin 41: 289-300.

YSNEL, F. 1989. Caractérisation des stades de développement de *Larinioides cornutus* (Araneae, Argiopidae) par la trichobothriotaxie. C.R. XI^{ème} Europaïsches Arachnologisches Colloquium. Tub-Dokumentation Kongresse und Tagungen Berlin 38: 72-78.

1990. Energy consumption of the orb-weaving spider *Larinioides cornutus* (Araneae, Araneidae) during the postembryonic development under different temperature conditions. XI International Congress of Arachnology, Turku, Finland. Acta Zoologica Fennica 190: 409-414.

1992. Impact trophique et valeur bioindicatrice d'une population d'Araignées: exemple d'une espèce à toile géométrique *Larinioides cornutus* (Araneidae). (Thèse de Doctorat d'Université, Université de Rennes I, France). 217 pp.

(in press). Data points for a study of population dynamics of an orb-weaving spider (*Larinioides cornutus*, Araneae, Araneidae). Actes du XIII^{ème} Colloque Européen d'Arachnologie, Neuchâtel, Suisse, 1991.

STUDIES ON THE WOLF SPIDERS (ARANEAE: LYCOSIDAE). I. A NEW GENUS AND SPECIES FROM KAZAKHSTAN, WITH COMMENTS ON THE LYCOSINAE

ALEXEY A. ZYUZIN

Zyuzin, A.A. 1993 11 11: Studies on the wolf spiders (Araneae: Lycosidae). I. A new genus and new species from Kazakhstan, with comments on the Lycosinae. *Memoirs of the Queensland Museum* 33(2): 693-700. Brisbane. ISSN 0079-8835.

A new genus *Oculicosa* (Araneae: Lycosidae; Lycosinae) is established and a new species *Oculicosa supermirabilis*, sp. nov. is described from South-western Kazakhstan. Relationships of the new species are analysed. The role of some morphological features of burrowing lycosids is specified. Tegular (median) apophysis in all members of the subfamily Lycosinae is declared to serve as the functional conductor of the embolus: the mechanism of its action is analysed. The role of some structures and the use of corresponding names is specified, the comparison of the main subfamilies is given. The structure of the tribe Trochosini Zyuzin, 1990 is revised: this tribe is divided into two subtribes including non-burrowing and burrowing forms.

On établit un genre nouveau *Oculicosa* (Araneae: Lycosidae: Lycosinae) et décrit une espèce nouvelle *Oculicosa supermirabilis* sp. n. du Sud-Ouest du Kazakhstan. Les affinités de l'espèce nouvelle sont analysées. On précise le rôle des quelques indices morphologiques des Lycosidés creusants. On a déterminé que l' apophyse tegulaire (median) chez tous les membres de la sous-famille Lycosinae sert de conducteur fonctionnel d'embolus: le mécanisme de sont action est analysé. On précise le rôle de quelques structures et l'usage des noms correspondants, la comparaison des principales sous-familles est donnée. On fait une révision de la structure de la tribu Trochosini Zyuzin, 1990: cette tribu se divise en deux sous-tribus insérant des formes non-creusantes et creusantes. □*Lycosidae, Oculicosa, conductor.*

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Burrowing spiders of the family Lycosidae within Kazakhstan are poorly known. Records exist only for *Allohogna singoriensis* (Laxmann, 1770), *Lycosa nordmanni* (Thorell, 1875) (= *L. narbonensis* auct., non Latreille, 1806), and *L. alticeps* (Kroneberg, 1875) (see Charitonov, 1932; Dubinin, 1946). However, of those, only the distribution in Kazakhstan of *A. singoriensis* has been well studied (see Marikovskij, 1956). The only large non-burrowing lycosid reported from Kazakhstan is *Hogna radiata* (Latreille) (see Schmidt, 1895: Aral Sea and Mangyshlak Plateau). That report is very doubtful, as the author studied juvenile specimens only.

MATERIAL AND METHODS

Spider material I collected in 1989 in Karynzharyk sands, South-western Kazakhstan, are used here. Specimens were captured at night with the use of a miner's head torch: spider's eyes reflect torch light at the distance of 20-25m and even more. Spiders were examined in 70% alcohol using binocular microscopes. To understand the relative position of different parts of the male and female genital apparatus during copulation, dissected tegular apophyses of males were attached to female epigynes (Fig. 5). Eye measurements are given in eyepiece micrometer units (x32). Genitalia and their parts for scanning electron microscopy were preserved in ethanol, air-dried, mounted on stubs, gold-coated and examined in a JEOL JSM-T200 at 15kv.

Abbreviations: ALE, anterior lateral eyes; AME, anterior median eyes; ARE, anterior row of eyes; AZ, private collection of the author; L, leg; LC, carapace length; P, palp; PLE, posterior lateral eyes; PME, posterior median eyes; TA, tegular apophysis; WC, carapace width; ZMMU, Zoological Museum of the Moscow University.

MORPHOLOGY AND DISCUSSION

Oculicosa gen. nov.

TYPE SPECIES

Oculicosa supermirabilis sp. nov.

DIAGNOSIS

Medium size (body length 12-20mm). Cephalothorax: head strongly elevated, thorax in both sexes behind ALE is evidently descending

	PME	PLE	AME	ALE
PME	-	0.93 0.98	0.33-0.36	0.23 0.24
PLE	1.02-1.07		0.34-0.38	0.23-0.24
AME	2.80-3.00	2.67-2.93	-	0.63-0.71
ALE	4.20 4.42	4.10-4.30	1.40-1.58	

TABLE 1. Relative size of eyes in *Oculicosa supermirabilis*, sp. nov. (2♂, 2♀)

towards abdomen (Fig. 1), lateral sides of head are almost vertical. Carapace is relatively narrow, ratio LC/WC is 1.44-1.50. PME and PLE are very large, height of ocular field is 0.39-0.42 of LC (Fig. 2). ARE recurved, AME larger than ALE (Fig. 3). Row 1 is 1.64-1.70 times shorter than row 2; row 3 is 1.19-1.23 times wider than row 2. Clypeus narrow, its height less than 1 diameter of AME. Retromargin of cheliceral fang furrow with 2 large equal teeth. Ti + Mt I and II with 2 ventral pairs of spines except apical ones. Base of embolus in lateroapical position, TA is transverse lamella with narrow stout process by its base, directed ventrad, and with sclerotized edge situated distally (Figs 6-8). TA on its inner (dorsal) side with deep narrow transverse sinuous channel opened at the distal end of sclerotized edge. Epigyne has narrow anterior part and widened posterior (genital) parts where transverse genital part of septum is situated (Fig. 4).

Distribution

South-Western Kazakhstan.

Oculicosa supermirabilis sp. n.
(Figs 1-4, 6-8)

Material Examined

TYPES. Holotype ♂, South-Western Kazakhstan, Mangistau Area, Yeraliev District, 37 km S of Akkuduk Vill., Karynzharyk sands (42°38'N, 54°03'E), clay soil, S.I. Ibraev and A.A. Zyuzin (ZMMU), 14-15 May 1989. Paratypes: 7 ♂, 3 ♀, same data; 1 ♂, 3 ♀, same data, except 15-16 May 1989 (1 ♀ paratype in ZMMU, remainder in AZ).

FIGS 1-4. *Oculicosa supermirabilis*, sp. nov.: 1, female carapace, lateral view. 2, ditto, dorsal view. 3, ditto, frontal view. 4, epigyne. 5, position of tegular apophysis on epigyne in *Alopecosa cuneata* (Clerck) during copulation. Abbreviations: ap, anterior pocket of epigyne; ch, channel of tegular apophysis; ch. op., channel opening; eg, epigynal groove; gen.op, genital opening of epigyne; gps, genital part of septum; sp, septal pedicle; vs, ventral spur('hook') of tegular apophysis evident through cuticle.

Description

Female. Carapace brown or light brown. Lateral bands wide, continuous, forming wide light 'cheeks' at the sides of head. Median band represented by yellowish rhomboidal spot lying

Female (carapace length = 7.0mm)								Male (carapace length = 7.05 mm)						
Leg	Femur	Patella	Tibia	Met.	Tarsus	Total	T/CL	Femur	Patella	Tibia	Met.	Tarsus	Total	T/CL
1	5.20	2.40	3.70	3.40	1.50	16.50	2.36	6.20	2.70	5.15	5.50	2.50	22.05	3.13
2	5.00	2.15	3.35	3.35	1.80	15.65	2.24	6.10	2.60	4.80	5.60	2.60	21.70	3.08
3	4.60	2.00	3.20	4.00	1.80	15.60	2.23	6.00	2.35	4.60	6.70	2.70	22.35	3.17
4	5.80	2.30	4.30	5.70	2.25	20.35	2.91	7.30	2.50	5.80	8.50	3.25	27.35	3.88
P	2.70	1.50	1.60	-	2.00	7.80	1.12	3.20	1.50	1.60	-	2.10	8.40	1.19

TABLE 2. *Oculicosa supermirabilis*, sp. nov., length of leg and palp segments in millimetres. T/CL, total leg length/ carapace length; met., metatarsus.

above median furrow (Fig. 2); sometimes this spot is triangular with its base near PLE. Ocular field yellowish-brown, with dark spots around eyes. Carapace evidently descending behind PLE and is supplied with dense fur-like whitish hairs at its edge. Legs: coxae covered dorsally with dense whitish long hairs. Remaining segments uniform yellowish; their length given in Table 2. Leg spination: femora I and II with 2 promesolateral spines; tibiae I and II with 2-2 ventral spines and 2 small apical ones, 1-1 mesolateral, no ectolateral spines; tibiae III and IV with 1-1 dorsal; metatarsi I and II with 2-2 ventral + 4 apical, 1-1 mesolateral, no ectolateral spines; tarsi I-IV dorsally with 2 submedian long setae. Palp: all segments uniform yellowish, but tarsus distally a little darker, tarsal claw long, slightly curved, with 4 very small teeth. Abdomen: sides with dispersed dark points; dorsal pattern consists of brownish lanceolate stripe with dark margins, series of light spots lying below, and whitish spots of different size around. This pattern is covered with dense whitish pubescence. Ventral side above epigastrum dark, with dense dark hairs and bristles, sparse dark hairs are also on spinnerets and at stigmal area, the remainder uniform whitish, but sometimes there are 2 closely situated, almost parallel longitudinal dark lines. Coxae ventrally yellowish-brown, sternum yellowish with some dark hairs on sides, labium and maxillae yellow-brown. Chelicerae reddish-brown, basal segment is covered with long dense whitish-grey hairs and bristles in front. Retromargin of cheliceral fang furrow with 2 teeth, promargin with 3. Body length 15.0-20.2 mm, LC 6.5-8.0 mm. Epigyne: Fig. 4.

Male. Body covered with white hairs. Pattern of both carapace and abdomen as in female, but carapace covered with many whitish-grey adpressed hairs. Ocular field with long and dense whitish hairs. Carapace edged with a narrow stripe of long dense fur-like whitish (silvery) hairs directed anteriad; many short, adpressed silvery hairs also at sides of head and form 'cheeks'. Legs: colouration as in female, coxae dorsally with long and dense silvery hairs. Length of legs as in Table 2. Leg spination: femora I and II as in female; tibiae I-IV with 1-1 dorsal spines, sometimes only prodorsal remains, laterally on each side 1-1, ventrally 2-2 + 2 apical; metatarsi I and II with 1-1 lateral on each side, ventrally 2-2 + 5 apical; tarsi I and II dorsally with 2 submedian long setae. Palp: segments yellow, cymbium distally brownish; all segments covered with white hairs: femur with sparse hairs, patella with many short and adpressed hairs, tibia and cymbium (except its distal part) with long and dense hairs. Dentation of cheliceral furrow as in female. Body length 12.0-13.8 mm, LC 6.3-7.3 mm. Palpus: Figs 6, 7.

FIGS 6-8. *Oculicosa supermirabilis*, sp. nov.: 6, male palpus, ventral view. 7, ditto, lateral view. 8, male tegular apophysis with synembolus, apical view. Abbreviations: ch. op., channel opening of tegular apophysis; dep, tegular depression; pl, palea; pr, stout process of tegular apophysis; sed, sclerotized edge of tegular apophysis; sem, synembolus.

Ecology

All adults were collected in clayey parts of Karynzharyk sands.

Discussion

Oculicosa supermirabilis is closely related to some species of *Lycosa* s. lat., namely *Lycosa alticeps* (Kroneberg, 1875) and *L. medica* (Pocock, 1889), but differs from them by the

	Lycosinae	Evippinae	Pardosinae	Wadicosinae[1]	Venoninae[2]	Piratinae
1	a2-a3	a2	a2	a2	usually a1	a1-a2
2	b1; seldom b3 [3]	b1	b1	b1	b1-b2	b1; seldom b2 [4]
3	usually c1, seldom c2 & c3	c3	c3	c1	c1	c1, seldom c2 [5]
4	d1, seldom d3	d2	d2	d2	d2	d1-d3
5	e2	e3	e1	e2	e1	e3
6	f1	f1	f1, f2	f1	f1	f3
7	g1	g1	g1	g2	g1	g1
8	h1	h1	h1	h2	h2-h3	h1
9	i2, seldom i3	i3	i1	i4	?	i5
10	j1	j2 [6], j6 and j2 [7]	j3	j4	j5	j6
11	k1; k5, usually k2; seldom k7 [3]	k2	k1, usually k2	k3	k4	k5-k6; seldom k4

CHARACTERS

1. Size: a1, small; a2, medium; a3, large-very large
2. Carapace, cephalic area: b1, high; b2, narrow; b3, protruding basally with anterior row of eyes
3. Carapace, posterior ocular trapezium: c1, trapezoidal; c2, wide trapezoidal; c3, +/-quadrangular
4. Carapace, size of anterior eyes: d1, variable; d2, small; d3, comparatively large
5. Male palp, origin of embolus: e1, mesolateral; e2, lateroapical; e3, distal (apical)
6. Male palp, shape of embolus: f1, long curved spine; f2, enlarged at tip; f3, short, combined with conductor
7. Male palp, tegulum: g1, no sclerotized processes; g2, with 1-2 stout well sclerotized processes
8. Male palp, tegular (median) apophysis: h1, thick, well sclerotized; h2, weakly sclerotized (membranous); h3, absent
9. Male palp, bed of tip of resting embolus: i1, small tegular depression; i2, enlarged tegular depression; i3, deep dorsal channel of TA; i4, tegular depression on upper tegular process; i5, deep ascending tegular groove
10. Male palp, character of conductor: j1, deep dorsal transverse channel of TA; j2, deep dorsal longitudinal channel of TA; j3, thick well-sclerotized basal part of palea concealed by tegulum; j4, opened (free) transverse sclerotized lateral process of the basal part of palea; j5, opened large apical; j6, combined with embolus (single complex)
11. Epigyne: k1, variable; k2, median inverted T-shaped plate; k3, entire plate with 2 parallel oblong grooves above; k4, simple entire plate; k5, simple hairy plate; k6, hairy plate with lateral sclerites; k7, posteriorly protruding hairy plate

TABLE 3. Comparison of lycosid subfamilies. Notes: [1] *Wadicosa*; [2] after Lehtinen & Hippa, 1979; [3] *Hippasa*; [4] *Aulonia*; [5] *Hygrolycosa*; [6] *Xerolycosa*; [7] *Evippa*.

shape of epigyne and tegular apophysis, by the profile of carapace (cf. Kroneberg, 1875, pl. IV, fig. 28; Pocock, 1889, pl. XIII, fig. 1), as well as by relatively larger PME and PLE, presence of only 2 teeth at the retromargin of chelicerae (in *L. alticeps* and *L. medica* 3), colouration of the ventral side of abdomen and smaller body length.

The descending carapace in both sexes of *Oculicosa supermirabilis*, fur-like hairs at the edges of carapace, and the long and dense whitish hairs on the dorsal side of coxae indicate a burrowing way of life (see also Zyuzin and Zarko, 1989; Zyuzin, 1990), although I could not find the burrows of this species. Our investigations showed that carapace pubescence together with dense hairs on the coxae considerably diminish the friction between the coxae and the edges of carapace; in the much more active males these features are more pronounced and supplemented with many dorsal adpressed whitish-grey hairs on the carapace thus facilitating their movements in burrows. The role of carapace descent is as follows. The comparatively long femora III and IV press against the carapace when moving in narrow burrows: the length of femur IV is slightly longer than the carapace slope. Long-legged males of burrowing lycosids very often have a low flattened carapace (as well as females of the genus *Lycosa* s. str., e.g. *Lycosa tarantula* and *L. nordmanni*: see Zyuzin, 1990): this compensates for the lack of descent, facilitates the folding of very long femora and improves the mobility of these spiders. I suggest that the strongly descending carapace not only in females but also in males (as in *Oculicosa*), together with comparatively narrow carapace, indicates the burrowing way of life from the early juvenile stages up to their imaginal moult: therefore, the distribution of such species is probably very restricted. On the contrary, in *Lycosa nordmanni* and *Allohogna singoriensis* with their flattened carapace in males, mature females seem to be more or less burrowing, while the juveniles, especially early stages, are active. This feature undoubtedly facilitates aerial dispersion of juveniles: as a result, both of these species are widely distributed.

PALPAL MORPHOLOGY

Further discussion concerns the terms 'conductor' and 'terminal apophysis', as their interpretation by different authors is sometimes rather contradictory.

Conductor

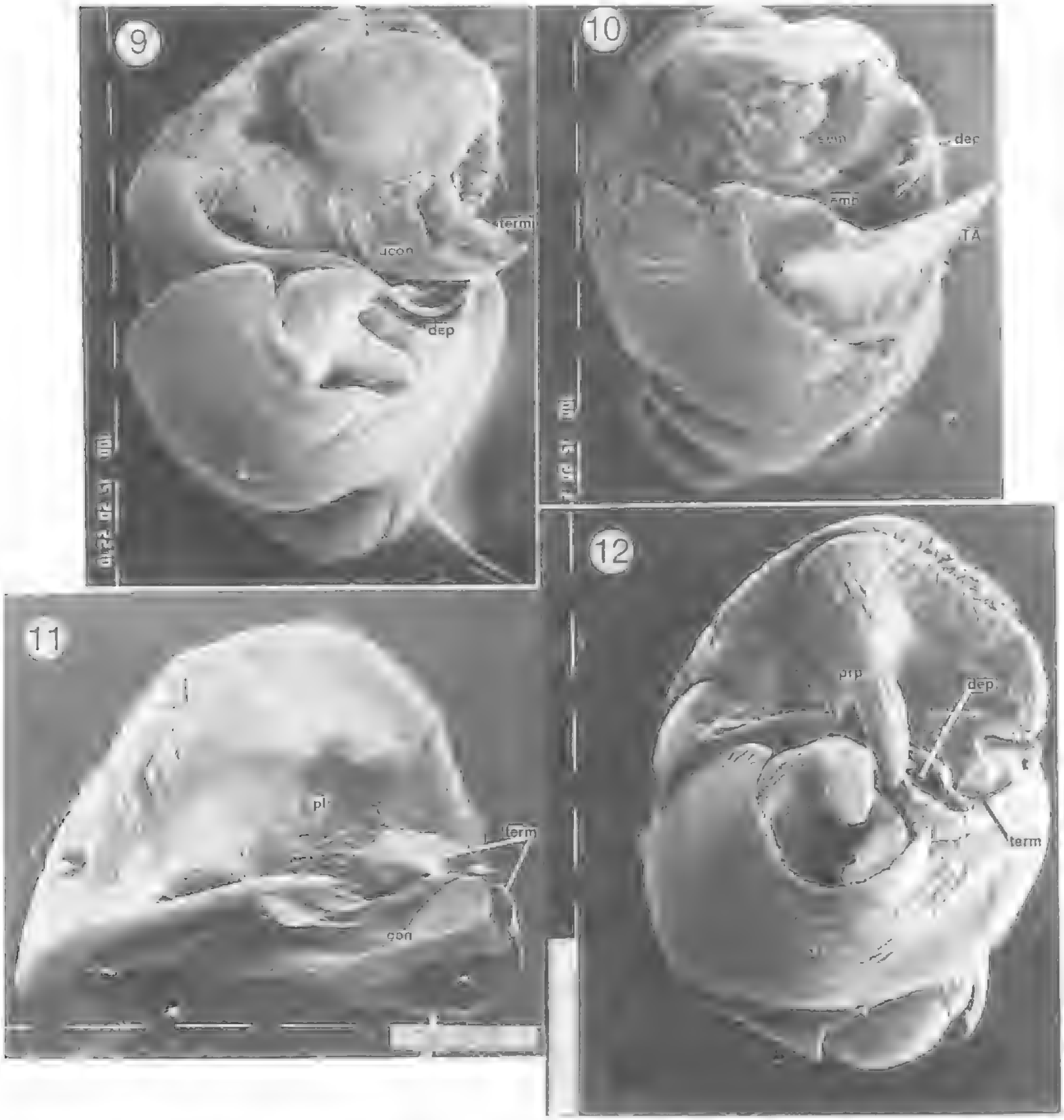
The tip of the resting embolus in both Pardosinae (at least in *Pardosa* and *Acantholycosa*) and Lycosinae lies in the oblong depression of the tegulum: in Pardosinae this depression is rather small and spoonlike (Figs 9, 12), while in Lycosinae it is enlarged, sometimes strongly, and usually forms the tegular lobe (Fig. 10; Dondale, 1986, figs 12, 13). In an unexpanded palp of Pardosinae the depression of the tegulum fully separates the embolus from the true (functional) conductor which is the transverse well-sclerotized groove situated near the base of the terminal part (shield, palea) of the genital bulb and almost fully concealed by the tegulum (Figs 9, 12). In members of Lycosinae, the enlarged depression of the tegulum is regarded as the conductor of the embolus (see Dondale and Redner, 1979; Dondale, 1986), though this bed for the resting embolus does not fit to assist the exact movement of the embolus tip to the female copulatory opening. Lehtinen and Hippa (1979) write: 'We are aware that "conductor" is not a very suitable name for the outer part of the Lycosid embolic division, because it is not always a functional conductor'. Our investigations have shown that the deep transverse channel on the inner (dorsal) surface of tegular apophysis opened at its narrow distal end and diagnostic for all members of the subfamily Lycosinae (Dondale, 1986) is intended for the embolus and undoubtedly directs its tip to the copulatory opening: thus, the TA of Lycosinae serves as the functional conductor. The mechanism of operation of such a conductor during copulation is shown in *Alopecosa cuneata* (Clerck) (Fig. 5), while the hooked ventral spur of the TA comes into contact (forms a hook-up) with the anterior pockets of the epigyne, the ventral rib of the 'hook' enters the longitudinal epigynal groove, so that the channel opening lying at the distal end of TA comes into proximity with the copulatory opening of the epigyne.

Above the embolus and behind the TA in many species of Lycosinae is situated a narrow, sharpened laminar process (see Figs 6-8) usually slightly grooved on its ventral side: the proposed name for this laminar process of palea in Lycosinae is 'synembolus', as it always accompanies the embolus and has the same direction. I suppose that the embolus during copulation enters the TA channel together with the laminar synembolus which directs the embolus to the channel and probably locks the last as a stopper, fully excluding the deviation of the embolus. Thus, the synembolus plays the role of auxiliary conductor. In species of the *Alopecosa pulverulenta* group the synembolus is fused with the base of the palea, so that only an ectal tooth remains at its external side: in this case all the base of the palea goes to the wide 'antechamber' before the channel.

Dondale (1986) correctly regards the subfamily name Hippasinae to be a junior synonym of the Lycosinae. In representatives of the genus *Hippasa* TA also serves as the functional conductor: despite the lack of an atrium in some *Hippasa* species (e.g. *Hippasa deserticola* Simon, and *H. cinerea* Simon) and the agelenid habit of the spiders, I regard them, as well as allied genera, to represent the tribe Hippasini Simon, stat. nov. in the subfamily Lycosinae (see Table 3).

Besides the Lycosinae, the conductor is represented by the tegular apophysis in two other subfamilies: Evippinae (type: *Evippa* Simon) and Allocosinae (type: *Allocosa* Banks).

1. Evippinae. Members of this subfamily have a hooked longitudinal TA which somewhat resembles the transverse trochosoid 'hook' of Lycosinae. As in the species of Lycosinae, the members of Evippinae have a distinct channel on the inner (dorsal) side of TA and a pedicled septum widened posteriad (Zyuzin, 1985, figs 15, 16, 20-22). But, despite these similarities, the genera *Evippa* and *Xerolycosa* have a number of features which allow them to be regarded as members of the separate subfamily. Thus, the channel on the dorsal side of TA in Evippinae is longitudinal (in all Lycosinae it is transverse); the whole embolus is situated in a deep depression and forms a very characteristic recurved flat loop; the base of embolus always has an apical position; the palea is strongly reduced; and the epigynal grooves are very shallow and lie at the level of the septal pedicle. Besides, in *Evippa* spp. the synembolus is transformed into a narrow functional conductor which is constantly situated in a channel of TA and projected beyond the TA limits: in this case TA serves as an auxiliary conductor. In *Xerolycosa* spp. the functional conductor is represented by TA: the embolus constantly lies in a channel (see Zyuzin, 1985); the



FIGS 9-12. Scanning electron micrographs: 9, 10, 12, genital bulbs dissected from cymbia; 11, palea with embolus and conductor dissected from genital bulb). 9, *Pardosa sodalis* Holm. 10, *Hogna radiata* (Latreille). 11, *Pardosa chionophila* L. Koch. 12, *Pardosa turkestanica* (Roewer). Abbreviations: con, conductor; dep, tegular depression; emb, embolus; pl, palea; prp, process of palea; sem, synembolus; TA, tegular apophysis; term, terminal apophysis; ucon, upper branch of conductor. Scale bar=0.1mm.

synembolus is strongly reduced and fused with the semi-transparent extension of the embolus.

2. Allocosinae. In *Allocosa* spp. TA is double-branched, the channel is situated on the dorsal side of the narrow basal branch and holds the tip of the resting embolus; and the atrium of the epigyne is lost (see Dondale and Redner, 1983; Dondale, 1986). Besides, the basal part of the pardosoid palea probably serves as an auxiliary conductor directing the embolus into the channel of TA in the expanded palpus.

In the genus *Pirata* and allied genera (*Piratula, Aulonia, Hygrolycosa*) the functional conductor is combined with a short thin embolus in a common sickle-shaped complex resting in a deep and narrow ascending tegular groove. The distal position of the well sclerotized conductor in representatives of the subfamily Venoniinae (*Venonia* and allied genera: see Lehtinen and Hippa, 1979) does not allow us to include *Pirata* in the subfamily Venoniinae, as Dondale (1986) did. *Pirata* and allied genera probably deserve to be included in the separate subfamily Piratinae (type: *Pirata* Sundevall, 1832) (see Table 3).

Terminal Apophysis

Very often the palea in Pardosinae (at least in *Pardosa* and *Acantholycosa*) above the embolic division is supplied with a stout, very sclerotized process: many authors (e.g. Holm, 1947; Tongiorgi, 1966; Kronestedt, 1975) designate this process as the terminal apophysis. Dondale (1986) writes '... the terminal apophysis ... is believed to assist the finding and penetration of the copulatory opening by the embolus tip'. It is therefore obvious that, to play this very important role, the terminal apophysis must be situated immediately above the end of the conductor (Figs 9, 11; Kronestedt, 1975, fig. 3); sometimes the dentiform terminal apophysis is situated directly at the outer part of the conductor (see Dondale and Redner, 1984, figs 21, 25, 26). At the same time, there are many cases when the much larger paleal process is situated far above the conductor, i.e. so that it cannot assist the exact penetration of the embolus tip into the female copulatory opening (Fig. 12); however, such a process is also wrongly designated as the terminal apophysis (see Lowrie and Dondale, 1981, fig. 10; Dondale and Redner, 1984, fig. 5; Dondale, 1986, fig. 7). Tongiorgi (1966, fig. 1) correctly designates the true terminal apophysis and the laminar process: the destination of such a process is otherwise, e.g. to protect the resting embolus, or to make an engagement during copulation.

An incorrect designation of terminal apophysis is also used by Buchar (1976, figs 7, 8): in his fig. 8 it is a mere tubercle of the palea, while in fig. 7 (*Pardosa thaleri*) this author confuses it with the narrow laminar conductor sharpened at the tip and characteristic for the *Pardosa bifasciata* group. The similar conductor shape, also designated as the terminal apophysis, is in the species '*Pardosa*' *oncka* Lawrence (see Kronestedt, 1987, fig. 4C).

In some works the synembolus of Lycosinae is also called the terminal apophysis (see Dondale and Redner, 1979, 1990; Dondale, 1986). But, as the synembolus only directs the embolus to the channel of TA (see above), the role of the true terminal apophysis is fulfilled by the ventral process(es) of TA fixing the last on the female epigyne. The designation of the ectal tooth of palea in the *Alopecosa pulverulenta* group as the terminal apophysis (see Kronestedt, 1990) is also incorrect: actually this tooth is the synembolus (see above).

Formerly (see Zyuzin, 1990), I restricted the Lycosini to burrowing lycosids only, and erected the new tribe Trochosini for non-burrowing genera of Lycosinae. Herein the structure of both these tribes is revised: thus, I include in Trochosini only those genera that are characterized by the very peculiar TA which has a transverse lamella with a ventrally directed trochosoid 'hook', or spur, and the epigynal septum with a distinct narrow pedicle, widened posteriad, very often in the shape of an inverted 'T'; epigynal grooves on either side of septal pedicle are rather deep and distinct. Both non-burrowing and burrowing lycosids are included in this very large tribe, undoubtedly having a common origin; in accordance with this view the tribe Trochosini is divided into two subtribes: Trochosina Zyuzin, stat. nov. (including the non-burrowing genera *Trochosa*, *Alopecosa* s. str., *Hogna* s. str., *Schizocosa*), and Geolycosina, subtrib. nov. (including the burrowing genera *Arctosa* s. str., *Geolycosa*, *Allohogna* with a very characteristic carapace profiles: see Zyuzin, 1990, fig. 1). There are many species throughout the world, including African ones, which also belong to the Trochosini: the generic and subtribal position of these remain obscure due to the artificial system of Roewer (1959-1960).

As shown in Fig. 5, the length of the epigynal groove and septal pedicle in species of Trochosini is correlated with the length of the ventral spur of TA.

As to the tribe Lycosini, I place here only the members of *Lycosa* s. str. with their very peculiar genitalia, and some allied species referred to *'Allocosa'*, *'Hogna'* and probably *Metatrochosina* (Roewer, 1959-1960, figs 124, 126, 129, 219, 304-305, 517).

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LITERATURE CITED

BUCHAR, J. 1976. Über einige Lycosiden (Araneae) aus Nepal. Khumbu Himal 5: 201-227.

CHARITONOV, D.E. 1932. Katalog der Russischen Spinnen. Beilage zum Annuaire du Musée Zoologique, Leningrad, 32. 206pp.

DONDALE, C.D. 1986. The subfamilies of wolf spiders (Araneae: Lycosidae). Actas del X Congreso Aracnológico, Jaca, España, vol. 1: 327-332.

DONDALE, C.D & REDNER, J.H. 1979. Revision of the wolf spider genus *Alopecosa* Simon in North America (Araneae: Lycosidae). Canadian Entomologist 111: 1033-1055.

1983. The wolf spider genus *Allocosa* in North and Central America (Araneae: Lycosidae). Canadian Entomologist 115: 933-964.

1984. Revision of the *milvina* group of the wolf spider genus *Pardosa* (Araneae: Lycosidae). Psyche 91: 67-117.

1990. The wolf spiders, nurseryweb spiders, and lynx spiders of Canada and Alaska (Araneae: Lycosidae, Pisauridae, and Oxyopidae). The Insects and Arachnids of Canada 17. 383 pp. (Agriculture Canada: Ottawa).

DUBININ, V.B. 1946. [Inhabitants of mammal holes in South-Khazakhstan Area and their significance for man]. Izvestija Akademii Nauk Kazakhskoj S.S.R., Parasitological Series 4: 93-102. [in Russian]

HOLM, Å. 1947. Egentliga Spindlar. Araneae. Fam. 8-10, Oxyopidae, Lycosidae och Pisauridae. Svensk Spindelfauna vol. 3, 48 pp.

KRONEBERG, A. 1875. Araneae. In: Fedtschenko, A.P. Reise in Turkestan, Zoologischer Theil 2: 1-58.

KRONESTEDT, T. 1975. Studies on species of Holarctic *Pardosa* groups (Araneae, Lycosidae). I. Redescription of *Pardosa albomaculata* Emerton and description of two new species from North America, with comments on some taxonomic characters. Zoologica Scripta 4: 217-228.

1987. On some African and Oriental wolf spiders (Araneae, Lycosidae): redescription of *Pardosa oncka* Lawrence from Africa, with notes on its generic position. Journal of Natural History 21: 967-976.

1990. Separation of two species standing as *Alopecosa aculeata* (Clerck) by morphological, behavioural and ecological characters, with remarks on related species in the *pulverulenta* group (Araneae, Lycosidae). Zoologica Scripta 19: 203-225.

LEHTINEN, P.T. & HIPPA, H. 1979. Spiders of the Oriental-Australian region. I. Lycosidae: Venoniinae and Zoicinae. Annales Zoologici Fennici 16: 1-22.

LOWRIE, D.C. & DONDALE, C.D. 1981. A revision of the *nigra* group of the genus *Pardosa* in North America (Araneae, Lycosidae). Bulletin of the American Museum of Natural History 170: 125-139.

MARIKOVSKIJ, P.I. 1956. [Tarantula and karakurt. Morphology, biology, toxicity]. (Academy of Sciences of Kirghiz S.S.R.: Frunze). 281 pp. [in Russian]

POCOCK, R.I. 1889. Arachnida, Chilopoda and Crustacea. In: Aitchison, J.E.T. The Zoology of the Afghan Delimitation Commission. Transactions of the Linnean Society of London (2) 5, Zoology: 110-121.

ROEWER, C.F. 1959-1960. Araneae Lycosaeformia II (Lycosidae). Exploration du Parc National de l' Upemba. Mission G.F. De Witte, fascicule 55. Institut des Parcs Nationaux du Congo Belge. 1040 pp. (Bruxelles).

SCHMIDT, P. 1895. Beitrag zur Kenntniss der Laufspinnen (Araneae Citigradae Thor.) Russlands. Zoologische Jahrbücher, Abteilung für Systematik 8: 439-484.

TONGIORGI, P. 1966. Italian wolf spiders of the genus *Pardosa* (Araneae: Lycosidae). Bulletin of the Museum of Comparative Zoology 134: 275-334.

ZYUZIN, A.A. 1985. [Generic and subfamilial criteria in the systematics of the spiders family Lycosidae (Aranei), with the description of a new genus and two new subfamilies]. Proceedings of the Zoological Institute, Leningrad 139: 40-51. [in Russian]

1990. Studies on burrowing spiders of the family Lycosidae (Araneae). I. Preliminary data on structural and functional features. Acta Zoologica Fennica 190: 419-422.

ZYUZIN, A.A. & ZARKO, M.V. 1989. The structural and functional features of digging spiders of the family Lycosidae (Araneae). In: XI International Congress of Arachnology, Turku, Finland, 7-12 August, 1989. Abstracts. Reports from the Department of Biology, University of Turku 19: 116.

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