

Origin of the Polynesian Spiders

Pekka T. LEHTINEN

Zoological Museum, University of Turku
20014 Turku, Finland

Origin of the Polynesian Spiders. - Endemic species comprise ca. 60% of 280 species of Polynesian spiders. The great majority of the East Polynesian endemic species are restricted to mountain-top forests above 800 m, while a part of the West Polynesian endemic species can be found in less spoiled lowland habitats. Contrary to previous opinions, the indigenous spider fauna of Polynesia has not come solely from the west. One-third of the endemic fauna has its closest relatives in South America and/or Hawaii, while only ca. 10 species have their origin in New Zealand or subantarctic areas. The strongest speciation concerns the groups of eastern origin, in Tetragnathidae, Theridiidae, Mysmenidae, Thomisidae, and Salticidae, with most of these comprising the first colonizers several million years ago from South America or Hawaii. In contrast, endemic groups with only 1-2 Polynesian species and apparently no significant speciation within Polynesia seem to have a western origin. Western Polynesia also has a much higher diversity of spider families, as 9 families or new groups are only present in western Polynesia and four families or isolated groups are present only in eastern Polynesia. Moreover, some families and subfamilies are indigenous in the western parts, but only anthropochorous in the eastern parts.

The anthropochorous spider fauna of Polynesia consists mainly of wide-spread species, but many Pacific species have extended their range by anthropochorous dispersal. The spider fauna of Easter Island only consists of anthropochorous species, with many of these having restricted range elsewhere.

The presence of spider genera without any close known relatives in the mountain tops of Polynesia could partly be explained by the island-chain theory. The island chains extending to Polynesia seem to be up to 43 million years old, although none of the recent islands are more than 9 million years in age.

Key-words: Polynesia - origin of species - endemism - eastern species - western species - southern species - cosmopolitan - anthropochorous

INTRODUCTION

This is a short preliminary report of one aspect of "the Polynesia project", a large inventory and revisional program of the terrestrial arthropods of Polynesia, coordinated by myself and largely based on recent field work of the author in 1988–95. Among the zoogeographical issues this report will focus solely on the origin of the Polynesian spider fauna.

This report is based on a parallel taxonomic revision of all families of Polynesian spiders which has been completed for ca. more than half of the families. Nevertheless, all families have been sufficiently investigated to enable a general discussion of different origins. A large body of mainly unpublished material from neighbouring areas (Melanesia, southeast Asia, Australia, New Zealand, Galapagos and Hawaiian islands and South America) has been investigated for classification of the origins of Polynesian spiders.

Several different definitions of Polynesia have been proposed, sometimes including Fiji, Hawaii, and New Zealand. However, here Polynesia will be delimited more strictly, following the practice usual in zoogeographical discussions. This Polynesia (Fig. 1) includes the archipelagoes extending from the Easter Island to the Tonga Islands and in the north from the Line Islands to the Austral Islands.

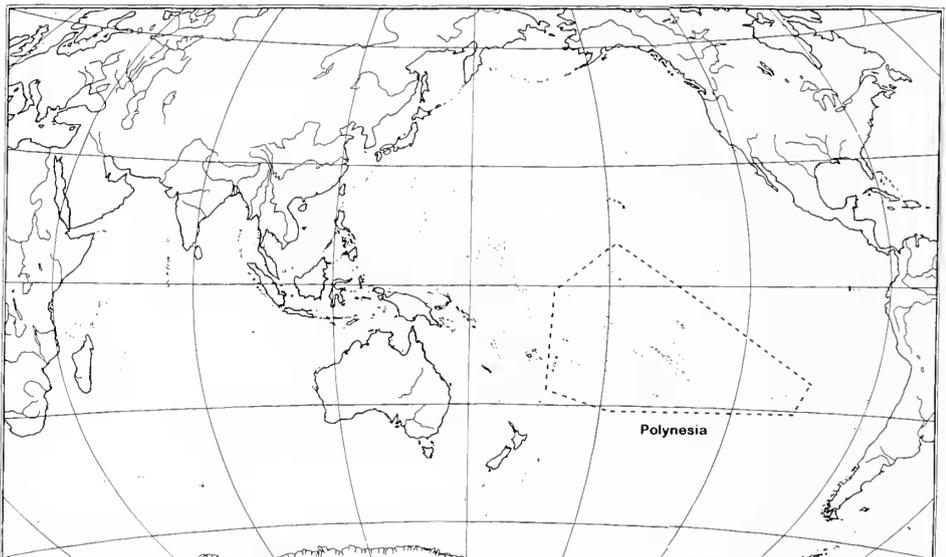


FIG. 1

The Pacific with the delimitation of Polynesia

In the early days of zoogeography Polynesia was simply treated as a subregion of the large Indo-Pacific or Australian regions, though this classification was based solely on the terrestrial vertebrate fauna, which is quite poor in all remote archipelagoes of the Pacific. Although many of the early studies have focused on describing the most frequent Polynesian spiders (KOCH & KEYSERLING 1871–86, KARSCH 1881, RAINBOW 1897, POCKOCK 1898, KULCZYŃSKI 1911, STRAND 1911, 1913, 1915, and ROEWER 1944), none of these authors have speculated on the origins of these spider species due to lack of sufficient information from surrounding areas.

Most discussions on the zoogeography of the Polynesian spiders are derived from taxonomic and faunistic papers published either by BERLAND (1924*a*, 1929, 1939, 1934*a*, 1935*a*, 1938*a,b*, 1942) or by MARPLES (1951, 1955*a,b*, 1957, 1959, 1964). BERLAND (1924*b*, 1930, 1938*a*) discussed also the Polynesian fauna in papers dealing with New Caledonia, New Zealand, and New Hebrides and also published several purely zoogeographical reviews (BERLAND 1928, 1934*b,c*, 1935*b*, 1937). Although both of these authors presented hypotheses concerning the origin of the spider fauna of the Pacific archipelagoes, much of their material was incorrectly assigned at the generic, tribal, or subfamily levels, or was even incorrectly identified. Moreover, much of that material consisted of samples from cultural habitats.

In addition to these papers, even recent work by BERRY & BEATTY (1987) has assumed that the whole Polynesian spider fauna of natural habitats would have originated from the west, Melanesia, southeast Asia or Australia. A part of the fauna was classified as cosmopolitan, but no clearcut distinction was made between anthropochorous and indigenous species by either Berland or Marples.

Scattered new information of the spiders from adjacent Pacific islands has subsequently been presented in many minor papers by various authors (FORSTER 1959, SUMAN 1965, 1967, 1970, GERTSCH 1973, BRIGNOLI 1973, 1976, 1980, LEHTINEN & SAARISTO 1980, LEHTINEN 1981, 1982, OPELL 1983, BEATTY & BERRY 1988*a,b*). The spider fauna of New Zealand has been described in six volumes of a handbook, as well as in several group revisions by Forster and his coworkers. General problems in determining the arachnological biogeography of the Pacific have since been discussed by FORSTER (1975), FORSTER & PLATNICK (1977), LEGENDRE (1978), BERRY & BEATTY (1987), BEATTY *et al.* (1991) and also by myself in several revisional papers and in two preliminary zoogeographical reports (LEHTINEN 1980, 1993). The endemic fauna and speciation processes of some Polynesian endemic groups of spiders in Hawaii have also been recently studied by SUMAN (1970), GILLESPIE (1991, 1992, 1993, 1994), GILLESPIE & CROOM (1992), and GILLESPIE *et al.* (1994), while the results of recent studies of the fauna of the Galapagos Islands has been reported in several papers by a Belgian team (BAERT & MAELFAIT 1986; group revisions). Unpublished material of the present author from the Galapagos and Hawaiian Islands adds important data for the study of Polynesian spiders of South American and Hawaiian origin. BAERT & JOCQUE (1993) compared the zoogeography of spiders in several oceanic islands, but their data from the Marquesas Islands and Easter Island was restricted to the old papers of BERLAND (1924, 1933, 1935*a*) and the

percentages given by them for endemic, cosmopolitan and continental species must now be revised.

Since the syntheses of BERLAND and MARPLES, the spider fauna of all areas surrounding Polynesia have been actively studied by many specialists, including myself. Essential new information, both published and unpublished is now available from Southeastern, Eastern and Southern Asia, Chile, New Zealand, Melanesia, Micronesia, Australia, and the subantarctic islands.

Most of the collecting before the Polynesia-project was done with traditional methods (hand picking, sweep netting, etc.). Different habitats also seem to have been quite unevenly studied, and in many groups the majority of specimens in museums are anthropochorous species from villages or from within their vicinity. Given these limitations, it is not surprising that the general zoogeographical conclusions drawn from such data might be widely erroneous, or at best only partly correct.

The last twenty years of general biogeography have been characterized by a rise in entirely new theoretic approaches based on or parallel to the simultaneous evolution of new hypotheses and findings from geophysics, biological systematics and paleontology, as well as the development of easily applicable computer techniques.

WILSON (1963) concluded that the present geology of the Pacific archipelagoes had resulted from continental drift. The most detailed hypotheses about the history and geological evolution of the Polynesian and Hawaiian seamount-island chains have been presented by MORGAN (1972) and DALRYMPLE *et al.* (1973). They hypothesized that the age of the northwestern parts of these chains is much higher than that of the more recent islands at the southeastern end, and that the Hawaiian chain would be more than 40 million years old and not 1–6 million years as has been generally accepted for the larger islands of the Hawaiian chain (MCDUGALL 1964).

If MORGAN'S (1972) hypothesis of the age and pattern of evolution for the Polynesian island chains were valid, it would also imply that there has been a continuous chain of closely spaced islands both from the northwestern part of the Line Islands through northern French Polynesia and the Gambier Islands to Easter Island as well as another chain from the Marshall and Ellice Islands to the Austral Island chain. However, this geological theory would involve volcanic activity occurring on the ocean bottom, but it would not demonstrate that all parts of such a chain (islands and seamounts) would have ever risen above the surface. Such a view posits a continuum of island chains over a period of 30–50 million years, sufficient for the evolution of very specialized endemic biota, but it would not explain much about the origins of this evolution — except that the oldest islands in the chain are the most northwestern.

Some parts of the oceanic ridges are known to have moved along tranverse fracture zones. Easter Island lies on one of these segments and its present exceptionally long distance from the other islands of the Tuamotu–Gambier islands can be explained by this phenomenon. Unfortunately, most of the endemic arthropod species of the forest soil of Easter Island obviously became extinct in prehistorical time with the destruction of the forests by the Polynesians. Possible remnants of this interesting fauna still await study. Most Easter Island spiders consist of widespread species found around the villages and in the vegetation of open habitats.

It is thus clear that previous conclusions on the origin of Polynesian spiders have been prejudiced due to inadequate collecting in natural habitats, as well as incorrect generic assignment of the majority of species.

POLYNESIAN SPIDER FAUNA

My personal field work for the Polynesia-project has revealed at least 280 species of spiders representing 36 traditional families (44 revised families) in Polynesia, of which ca. 62% are endemic. Nearly 22% of the species are also found in neighbouring parts of Melanesia, Micronesia or South America. Some of these "regional species" have a wider range in the Indo-Pacific region or neighbouring parts of Australia, although they are indigenous to at least some parts of Polynesia. Forty-three species (16%) are mainly synantropic or at least their original dispersal to some Polynesian islands has been aided by man. Part of these are pantropical or even cosmopolitan, but some have obviously come directly from more remote areas (Europe, North America).

No indigenous species of Loxoscelidae, Oecobiidae, Titanocidae, and Zodariidae are found in Polynesia, and the following worldwide families have not succeeded in entering Polynesia: Oxyopidae, Amaurobiidae, Ctenidae, Anapidae, Mimetidae, Trachelidae, and Deinopidae. A palpimanid species was recorded from Kiribati, very close to Polynesia, but it was originally described as *Oonops triangulipes* (Karsch, 1881). Among the well represented families, some dominant worldwide subfamilies are lacking in Polynesia, as Theridiidae: Euryopinae, Zodariidae: Storeninae and Corinnidae: Castianeirinae. In addition to these, no indigenous species of Uloboridae: Uloborinae are present.

Many Gondwanian groups, which are rich in species in neighbouring areas, are also apparently absent in Polynesia, especially Orsolobidae, Stiphidiidae, Psechridae, Micropholcommatidae, Archaeidae, Cycloctenidae, and Stenochilidae.

A large number of the species discussed here belong either to undescribed genera or should be transferred to other genera. No new generic or familial names are used here, though in some cases the most usual binominal combination has been replaced by a previously published, but much less widely used, taxonomically correct combination, marked by an asterisk *. The limitation used for many genera differs widely from those used by Berland, Marples, or other authors dealing with Polynesian fauna. New synonyms are not listed here, while some groups are treated simply by referring to the close relationship between genera. In order to allow interpretation of some details of the results, it has been necessary to publish here a few other taxonomic acts, e.g., the transfer of *Nukuhiva* from Pisauridae to Lycosidae, the transfer of *Chiracanthium* to Micrommatidae Järvi, 1914 and the transfer of *Oonops triangulipes* from Oonopidae to Palpimanidae. The original type designation of the Oonopid genus *Xestaspis* Simon, 1884 (*Oonops loricatus* L. Koch, 1872) is also noted here.

Theridiidae s.lat. includes Hadrotarsidae; Linyphiidae s.lat. also includes Erigonidae, Mynoglenidae and a new group; Oonopidae s.lat. includes all groups of the classical Oonopidae except Orsolobidae; Clubionidae s.lat. includes Micrommatidae, but no other groups of the classical Clubionidae.

TABLE 1

Polynesian spider families

end = N of endemic species; reg = N of regional species; syn = N of synanthropic species;
? = N of sp. of uncertain origin

	N	end	reg	syn	?
Theridiidae s.lat.	49	33	7	8	1
Salticidae	38	19	12	5	2
Tetragnathidae	31	20	8	2	1
Linyphiidae s.lat.	22	12	5	2	3
Oonopidae s.lat.	21	10	6	3	2
Araneidae	17	8	7	2	
Mysmenidae	12	11	1	—	
Pholcidae	9	3	1	4	1
Uloboridae	7	5	1	1	
Thomisidae	7	6	1	—	
Desidae	6	4	2	—	
Clubionidae s.lat.	6	5	—	1	
Scytodidae	5	1	2	2	
Hahniidae	5	5	—	—	
Lycosidae	5	3	2	—	
Gnaphosidae	5	2	—	3	
Ochyroceratidae	4	2	—	1	1
Dictynidae	3	2	—	—	1
Anyphaenidae	3	2	1	—	
Corinnidae	3	1	1	1	
Tetrablemmidae	2	2	—	—	
Heteropodidae	2	1	—	1	
Theridiosomatidae	2	1	1	—	
Symphytognathidae	2	2	—	—	
Loxoscelidae	2	—	—	2	
Oecobiidae	2	—	—	2	
Araneoidae ? family	1	1	—	—	
Barychelidae	1	1	—	—	
Filistatidae	1	1	—	—	
Cryptothelidae	1	1	—	—	
Segestriidae	1	1	—	—	
Dolomedidae	1	1	—	—	
Titanoecidae	1	—	1	—	
Agelenidae	1	—	—	1	
Zodariidae	1	—	—	1	
Nesticidae	1	—	—	1	
[Palpimanidae	1		not included]		
36	280	166	59	43	12
all species % of	280	59.3	21.1	15.4	4.3
? excluded % of	268	61.9	22.0	16.0	—

SPECIATION AND THE ORIGIN OF THE ENDEMIC SPECIES

The endemic species are now strongly concentrated in natural mountain habitats at elevations of over 800 meters in French Polynesia and the highest parts (250 – > 800 m) of the islands in western Polynesia. Among the species-rich families (5 spp. or more), the richest in endemic species are comprised of Hahniidae (100%)

and Mysmenidae (92%), the poorest Scytodidae (20%, but for ssp. 60%), Pholcidae (33%), followed by Araneidae and Oonopidae (47%). No endemic species have been documented on Easter Island. Lowland endemics in eastern Polynesia are restricted to a few intertidal or coastal species (*Parathenna*, *Arangina*, "*Lycosa*"), while several others are present in the more natural habitats of western Polynesia. Two widespread species have invaded the natural habitats of mountain tops by aeronautic dispersal (*Eidmannella pallida* & *Erigone prominens*).

The phylogenetic relationships of the genera of several families are imperfectly known in South America, East and Southeast Asia and Hawaii. For many families, even the limits of the genera have not been established. Therefore, the exact origin could not be confirmed for a part of the Polynesian spider fauna. Two-thirds of these certainly have additional range or closest relatives in Melanesia, southeast Asia or northeastern Australia (western species).

Several Polynesian spider genera have no known close relatives. Two new Polynesian groups of Araneoidea s.lat. seem to originate from southeast Asia, while the enigmatic Marquesan genus *Uapon* is quite isolated.

The majority of species with eastern origin live in the mountainous islands of French Polynesia, while the species with southern origin are only exceptionally (*Parosimoni*) confined to Rapa Island and many of these are found even in the Marquesas Islands.

1. Eastern species

One-third could be termed "eastern species", with 16% having South American affinities and an additional 12–13% most probably originating from South America via the Hawaiian or Galapagos islands. The largest group of South American origin consists of the theriid tribe Anelosimini (*Cylognatha* & some undescribed genera) with ca. 10 endemic species, all anyphaenids, and most ochyroceratids (*Cernteocera* & unplaced species). Three groups with strong Polynesian speciation also have parallel speciation in the Hawaiian islands: *Mecaphesa* (Thomisidae) (LEHTINEN 1993), Hawaiian "*Tetragnatha*" (GILLESPIE 1991, 1992, 1993, 1994) and the Hawaiian Salticid group related to *Bianor*.

The Oonopid species of the Pacific region are poorly known, but at least *Triaeris lepus*, "*Oonopinus*" *kilikus*, and "*Scaphiella*" *ula* (SUMAN 1965) are present both in Hawaii and Polynesia and seem to have their relatives in the Neotropical region. The only endemic scytodid species of Polynesia has all its relatives in Central America, Galapagos Islands, and Eastern Micronesia, with the mysmenid genus *Tamasesia* probably having also a similar range. The two corticolous Polynesian gnaphosid species have not yet been assigned to genera, but their affinities (*Sergiohus* and *Herpyllus*) suggest an eastern origin.

Many pantropical anthropochorous species (e.g. *Physocyclus globosus*, "*Scytodes*" *fusca*, and "*S.*" *longipes*, and *Ostearius melanopygius*) are of South American origin, and at least *Frigga crocota*, *Dendryphantes mordax*, **Tarapaca concinna*, and *Loxosceles laeta* have spread directly from there to Polynesia.

Three families, Anyphaenidae (endemic *Australaena* & an unidentified South American species), Segestriidae (unplaced "*Ariadna*" without males), and Mynoglenidae (all undescribed spp.), as well as the enigmatic *Uapon maculata* have not been found in western Polynesia. Representatives of "*Ariadna*" s.lat. are present in Melanesia and the Philippines, though the Polynesian species seem to be more closely related to Neotropical groups of this unrevised group.

2. Southern species

The eleven indigenous southern species (< 5%) have their closest relatives in New Zealand or in the subantarctic islands. Most of them belong to Linyphiidae s.lat. (*Paro*, *Maorineta*, four undescribed Mynoglenidae), but the coastal dictynid genus *Arangiina* from New Zealand also has Polynesian species. A new theriid genus from Polynesian mountain tops is related to *Armitigera* from the islands outside New Zealand. Five originally European and North American species among the anthopchorously spread species have probably dispersed to Eastern Polynesia (mainly Easter Island) through southern South America or New Zealand.

Most species shared by Polynesia and Australia are either widespread or synanthropic in either of these regions (*Gea heptagon*, *Eriophora transmarina*).

3. Pacific species

Two coastal groups of spiders with numerous endemic species are found in the Pacific. The genus *Paratheuma* (alternatively listed in Desidae and Dictynidae) resides in intertidal habitats and has extended its range into Japan (YAGINUMA 1990), the Caribbean region and the coast of Mexico (BEATTY & BERRY 1988a,b). The unrevised lycosid genus, including "*Lycosa tongatabuensis*" and several related species is found in open coastal habitats and also has a Pacific range, although not found in Central America. The mountain-top lycosid species *Nukuhiva adamsoni* is a more distant relative of this group, despite its originally being described (BERLAND 1933) and always catalogued as Pisauridae.

Non-coastal Pacific groups are represented by the deviating Uloborid genus Tangaroa, sometimes classified as a subfamily (LEHTINEN 1967). Endemic species of this genus have been reported in New Caledonia and Micronesia, but none have been found in the westernmost parts of the Pacific. Another, but still unnamed group, consists of several local endemics of Scytodidae ranging from Kalimantan to Micronesia, Polynesia, and the Galapagos islands. The Galapagos species has consistently been misidentified as "*Scytodes*" *hebraica*, but the holotype of the latter belongs to a strictly Neotropic, unnamed genus.

**Xestaspis loricata* (Oonopidae) is widespread in the archipelagoes of the central Pacific, and *Lucetia distincta* from Cuba is congeneric; *Xestaspis* is at least a valid subgenus of *Gauasomorpha*. Another genus of Oonopidae s.lat., a new genus related to *Orchestina* is only known from different parts of Polynesia, but may be more widespread.

Some large worldwide genera have undergone speciation within the Pacific, leading to species groups restricted to the Pacific region: Tetragnathidae: *Glenognatha* ("Hivaoa"), Araneidae: *Neoscona* (*maculatipes*-group), Theridiidae: *Argyrodes* (*unimaculatus*-group) and *Ariamnes*. The Pacific species of *Glenognatha* constitute the largest assemblage of Pacific endemic spiders. The species, originally assigned to *Hivaoa* and *Dyschiriognatha*, constitute a group of ca. 20 endemic species, but most *Hivaoa* spp. (BERLAND 1933, 1942) are not closely related to the type species of *Hivaoa*. *Hivaoa* was synonymized with *Glenognatha* by LEVI (1980), and a worldwide revision of its subgenera and species groups have not yet been completed.

The widespread orb-web spider *Neoscona theis* provides a good example of a pacific lowland or middle altitude species of a worldwide species group. Although it is found along the coasts of the Asian mainland, everywhere else in inland Asia this genus is represented by other species, while a close relative *Neoscona morcli* lives in the remaining tropical coasts and archipelagoes of Africa and the Caribbean.

"*Leucauge*" *gramulata* is another instance of an orb-weaver with similar range. However, there are no close relatives in the Neotropical region, and this large Old World genus still lacks a valid name.

4. Western species

A large majority of Polynesian endemic species can be classified as western species, although there are no large species groups. In addition to the species discussed here, many species of unknown origin most probably have their closest relatives in Melanesia or southeast Asia.

First, it must be emphasized that six spider families with a wide range to the west of Polynesia are restricted to western Polynesia (Tonga & Samoa Islands, etc.): Tetrablemmidae (*Fallablenma* & *Tetrablemma*), Symphytognathidae (*Patu*), Theridiosomatidae (*Andasta* & "*Theridiosoma*"), Cryptothelidae (*Cryptothele*), Dolomedidae ("*Dolomedes*"), Barychelidae (*Idiactis*), as well as some well-defined subdivisions of families as Tetragnathidae: Nephilinae (*Nephila*), Corinnidae: Oedignathinae (*Oedignatha*) and a group of Araneoidea s.lat. ("*Bathyphantes*" *paradoxus*) probably representing an undescribed family. In many cases, the Polynesian species is the easternmost one in a large Indo-Pacific or Old World genera (*Tetrablemma*, *Cryptothele*, *Oedignatha*).

Some genera with considerable speciation in Melanesia have extended their range into western Polynesia: *Artoria* (Lycosidae), *Daramuhmia* (Uloboridae), *Ulesanis* and a new genus (Theridiidae), *Hirtia* and a new genus (Clubionidae) and *Bigois* (Hahniidae). The delimitation of many Melanesian Salticid genera is still unstable, though the Polynesian "genera" *Flacillula*, *Ravalu*, *Tatari*, and "*Pseudomaevia*" sensu BERLAND, 1942 are synonymous or closely related to more widespread, mainly Melanesian genera.

Numerous endemic species of quite uncertain origin have been recorded. Many of these are not discussed here, but some examples are offered to highlight the

deficiencies in our present knowledge. The type species of the deviating minute soil theridiid *Tekellina* has been reported from the Caribbean region, though a rather widespread undescribed species has been found in western Polynesia and another undescribed species in India. An oonopid species is certainly found from two well-studied archipelagoes, the Seychelles and the Easter Island. The common western Polynesian dictynnid of the vegetation layer, *Banaidja bifasciata*, and the predominant erigonid genus of the Marquesan mountain tops, *Uahnka*, have no known relatives. A minute slow-moving spider with unique feeding habits and gnathocoxal structure from Samoa may represent a new family in Araneoidea s.lat.

BAERT & JOCQUE (1993) used the term "continental species" for a part of spider species of oceanic islands. They claimed that 22% of Easter Island species would be continental (Australian). However, there are no indigenous species left in Easter Island and no continental indigenous species in eastern Polynesia. Synanthropic species cannot be classified continental. The species of western Polynesia extending their range into continental Asia or Australia are all found in disturbed habitats and therefore more or less anthropochorous (e.g., "*Argyrodes*" *nigra*, *Ulesanis sextuberculata*, *Nephila phmipipes*, *Tylorida striata*, *Andasta semiargentea*, *Tetragnatha demissa*) or belong to different subspecies (both *Dictis* spp).

ORIGIN OF THE NON-ENDEMIC INDIGENOUS SPECIES

This category includes numerous inaccuracies, as many groups have not been properly revised outside Polynesia. The whole picture is also confused by the fact that many "indigenous" species are not actually indigenous to all islands within their range but have been randomly aided by human activities.

Most species of this group consists of web spinning spiders of Araneoidea s.lat. They are widespread in the Southeast Asian archipelagoes, and many of these also live in the coastal areas of the Asian mainland: Araneidae: *Gea heptagon*, *Cyrtophora moluccensis*, *Anepsion rhomboides*, Tetragnathidae: *Tetragnatha demissa*, *T. macilenta*, *T. laqueata*, *T. protensa*, "*Leucauge*" *granulata*, *Tylorida striata*, *Nephila phmipipes*, Theridiidae: "*Argyrodes*" *nigra*, Mysmenidae: *Mysmenella illectrix*, Theridiosomatidae: *Andasta semiargentea*, Linyphiidae: *Nesioneta pacificana*, Erigonidae: *Erigone bifirca*.

Spiders of other groups are represented by salticids (*Thorelliola ensifera*, *Athamas whitmaei*, **Zenodorus microphthalmus*, *Bavia aericeps*, **Ascyrtus opulentus*, pholcids ("*Pholcus*" *ancoralis*, *Holocnemius piritarsis*) and some Oonopids (*Opopaea santeri*, *O. lena*, "*Dysderina*" *insnlona*) and scytodids (*Dictis tardigrada*, *D. striatipes*), as well as the only Pacific titanocid *Pandava laminata*.

For many species, the known range is restricted to Melanesia and Polynesia only, as in *Efate albobicincta*, "*Flacillula*" *minuta*, and *Cytaea piscula* (Salticidae), "*Diaea*" *praetexta* (Thomisidae), *Chiracanthium mordax* (Clubionidae s.lat.), and the coastal lycosid, most often referred to as "*Lycosa tongatabnensis*".

ORIGIN OF THE ANTHROPOCHOROUS SPECIES

Many Polynesian anthropochorous species were absent from samples of BERLAND and MARPLES and some species were not classified as anthropochorous or were incorrectly identified. A few species which are usually classified as synanthropic also live in Polynesia as far as the most natural mountain tops (*Eidmannella pallida*). It has certainly spread to many uninhabited areas through aerial dispersal and thus is not always anthropochorous. Other widespread species with partly anthropochorous, partly aerial dispersal are the Linyphiids *Microbathyphantes palmaris* and *Nesioneta pacificana*.

A. European — Mediterranean species have spread mainly to Easter Island, but some of them have succeeded in becoming also established on tropical islands. Some species (*Stearodea grossa*) have obviously invaded Easter Island from South America, while the route for other species of this category remains unclear (Linyphiidae: *Leptyphantes tenuis*, Pholcidae: *Pholcus phalangioides*, Oecobiidae: *Thalamia navus*, Loxoscelidae: *Loxosceles rufipes*, Gnaphosidae: *Trachyzelotes kulczynskii* and *Urozelotes rusticus*, Tetragnathidae: *Tetragnatha nitens*, and Ageleidae: *Tegenaria domestica*). The species comprising this category are mostly recent immigrants that have spread to Polynesia after the appearance of Europeans.

B. North American species. "*Coleosoma*" *adamsoni* (Theridiidae) seems to originate from the New World, most probably from North America, where several related species have been recorded. It is also present in a variety of natural habitats in Polynesia. *Zodarion trispinosum* has come to Hawaii and Polynesia from North America, but it may be an unrevised species of Palaearctic origin (cf. BAERT & JOCQUE 1993). In addition, two North American salticids are found on Easter Island.

C. Neotropical species. *Creugas cetratus* and *Meriola arcifera* (Corinnidae) as well as an unidentified species of Anyphaenidae, and *Selkirkiella* sp. (Theridiidae), *Tarapaca concinna* (Oecobiidae), and *Loxosceles laeta* (Loxoscelidae) certainly represent the anthropochorous fauna originating from South America. *Frigga crocuta* (Salticidae) has mostly spread anthropochorously, although it is also permanent inhabitant of lower mountain habitats.

D. Indo-Pacific species. In contrast to the species indigenous to parts of Polynesia, these species are characterized by a distinctly discontinuous Polynesian range, such as *Gasteracantha mammosa* and *Gea heptagon* (Araneidae) and *Odontodrassus javanus* (Gnaphosidae). The latter species has widely penetrated into natural habitats on the uninhabited Henderson Island (BENTON & LEHTINEN 1995). Some indigenous western Polynesian–Melanesian species have spread only anthropochorously to the eastern parts of Polynesia: *Cyrtophora moluccensis* (Araneidae) and "*Pritha*" *bakeri* (Filistatidae). *Chiracanthium mordax* ("Clubionidae") and *Pandava laminata* (Titanocidae) may belong to either of these categories. *Eriophora transmarina* is also widespread in Australia, but its total range is obscure. Species of the genera *Erigone* and *Eperigone* are frequent aeronauts, and as such their exact colonization history is difficult to trace.

E. Species of the Old World tropics. *Neoscona vigilans* (Araneidae), **Parasteatoda mundula* (Theridiidae), *Microbathypantes palmarius* (Linyphiidae) and *Opopaea punctata* (Oonopidae) are widespread in the Old World tropics, but seem to reach their eastern limit in Polynesia.

F. Pantropical species are mostly ancient introductions and their actual routes to Polynesia cannot be traced. Some of them are known to have their origin in the Neotropical region (Ochyroceratidae: **Theotima minutissima*, Oonopidae: *Heteroopsis spinimanus*, Erigonidae: *Ostearius melanopygius*, Scytodidae: "*Scytodes*" *fusca*, "*S.*" *longipes*). Other pantropical species include: Uloboridae: *Zosis geniculatus*, Theridiidae: *Nesticodes rufipes*, **Parasteatoda tepidaria*, *Coleosoma floridana*, Salticidae: *Menemerus bivittatus*, *Hasarius adansonii*, *Plexippus paykulli*, Heteropodidae: *Heteropoda venatoria*, Pholcidae: *Smeringopus elongatus*, *Artema mauriciana*, *Phlysocyclus globosus*. *Latrodectus geometricus* (Theridiidae) is very widespread in the Southern hemisphere, but has arrived in Easter Island from Chile.

It is interesting to note that two strictly synanthropic Pholcid species, *Artema mauriciana* and *Phlysocyclus globosus* have strongly declined since the Second World War. Their indoor habitats have probably been conquered by *Nesticodes rufipes*, *Zosis geniculatus*, and even the indigenous "*Pholcus*" *ancoralis*.

ACKNOWLEDGMENTS

The editor and two referees made useful comments to the text of the lecture. Mr Ken Pennington kindly made the linguistic check.

REFERENCES

- BAERT, L. & JOCQUE, R. 1993: A tentative analysis of the spider fauna of some tropical oceanic islands. Proceedings of the XII International Congress of Arachnology, Brisbane. *Memoirs of the Queensland Museum* 33(2): 447–454.
- BAERT, L. & MAELFAIT, J.-P. 1986: Spider communities of the Galapagos Islands (Ecuador). *Actas X Congreso Internacional de Aracnologia* I: 183–188.
- BEATTY, J.A. & BERRY, J.W. 1988a: The spider genus *Paratheuma* Bryant (Araneae, Desidae). *Journal of Arachnology* 16: 47–54.
- BEATTY, J.A. & BERRY, J.W. 1988b: 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.
- BENTON, T. & LEHTINEN, P.T. 1995: Biodiversity and origin of the non-flying terrestrial arthropods of Henderson Island. In T. BENTON & T. SPENCER (ed.) *The Pitcairn Islands: biogeography, ecology and prehistory*. *Journal of the Linnean Society of London* 56: 261–272.
- BERLAND, L. 1924a: Araignées de l'île de Pâques et des îles Juan Fernandez. *The Natural History of Juan Fernandez and Easter Island* 3(3): 419–437.
- BERLAND, L. 1924b: Araignées de la Nouvelle Calédonie et des îles Loyalty. In: F. SARASIN & J. ROUX: *Nova Caledonia, Zoologie* 3(2): 159–255.

- BERLAND, L. 1928: Remarques sur la répartition et les affinités des Araignées du Pacifique. *Proceedings of the Pan-Pacific Science Congress* 3, Tokyo (1): 1044–1054.
- BERLAND, L. 1929: Araignées (Araneida). *Insects of Samoa and other Samoan terrestrial Arthropoda* 8: (2): 35–78.
- BERLAND, L. 1930: Les Araignées des îles avoisinant la Nouvelle Zélande et les relations entre l'Australie et l'Amérique du Sud. *Comptes Rendus des séances de la Société de biogéographie* 1930(60): 90–94.
- BERLAND, L. 1933: Araignées des îles Marquises. Pacific Entomological Survey Publication 7(3). *Bernice P. Bishop Museum Bulletin* 114: 39–70.
- BERLAND, L. 1934a: Araignées de Polynésie. *Annales de la Société entomologique de France* 103: 321–336.
- BERLAND, L. 1934b: Les Araignées de Tahiti. Pacific Entomological Survey Publication 6(21). *Bernice P. Bishop Museum Bulletin* 113: 97–107.
- BERLAND, L. 1934c: Les Araignées du Pacifique. Contribution à l'étude du peuplement zoologique et botanique des îles du Pacifique. *Publications de la Société biogéographique* 4: 155–180.
- BERLAND, L. 1935a: Nouvelles Araignées marquisiennes. *Bernice P. Bishop Museum Bulletin* 142 (*Pacific Entomological Survey Publication* 8(4)): 31–63.
- BERLAND, L. 1935b: Les Araignées des îles Marquises et la Biogéographie. *Comptes Rendus des séances de la Société Biogéographique* 100: 27–28.
- BERLAND, L. 1937: Comment les Araignées ont peuplé le Pacifique. *Bulletin de la Société océanique* 1(2): 77–80.
- BERLAND, L. 1938a: Araignées des Nouvelles Hébrides. *Annales de la Société entomologique de France* 107(2): 121–190.
- BERLAND, L. 1938b: Liste des Araignées recueillis à Maupiti (îles de la Société) par M. Ropiteau. *Bulletin de la Société des études océaniques* 6(2): 47–48.
- BERLAND, L. 1942: Polynesian spiders. *Occasional Papers of the Bernice P. Bishop Museum* 17: 1–24.
- BERRY, J. & BEATTY, J. 1987: Biogeography of Pacific Island spiders: a progress report. *American Arachnology* 36: 3.
- BRIGNOLI, P.M. 1973: Ragni della Melanesia I. Un nuovo *Tetrablemma* di Guadalcanal (Isole Salomone). *Memorie della Società entomologica italiana* 52: 79–88.
- BRIGNOLI, P.M. 1976: Spiders from melanesia II. A new *Apiacera* from the Bismarck Islands. *Stenstrupia* 4: 23–26.
- BRIGNOLI, P.M. 1980: On a few Mysmenidae from the Oriental and Australian regions. *Revue suisse de Zoologie* 87: 183–192.
- DALRYMPLE, G.P., SILVER, E.A. & JACKSON, E.D. 1973: Origin of the Hawaiian Islands. — *In*: SKINNER, B.J. (ed.) *Earth's history, structure, and materials. Readings from American Scientist*: 112–126.
- FORSTER, R.R. 1959: The spiders of the family Symphytognathidae. *Transactions of the Royal Society of New Zealand* 86: 269–329.
- FORTSER, R.R. 1975: The spiders and harvestmen. *Biogeography and ecology of New Zealand*: 493–506. *W. Junk, Den Haag*.
- FORSTER, R.R. & PLATNICK, N.I. 1977: A review of the spider family Symphytognathidae. *American Museum Novitates* 2619: 1–29.
- GERTSCH, W.J. 1973: The cavernicolous fauna of Hawaiian lava tubes. 3. Aranea. *Pacific Insects* 15: 163–180.
- GILLESPIE, R.G. 1991: Hawaiian spiders of the genus *Tetragnatha*. I. Spiny Leg Clade. *Journal of Arachnology* 19: 229–230.
- GILLESPIE, R.G. 1992: Hawaiian spiders of the genus *Tetragnatha*. II. Species from natural areas of windward East Maui. *Journal of Arachnology* 20: 1–17.

- GILLESPIE, R.G. 1993: Biogeographic pattern of phylogeny in a clade of endemic Hawaiian spiders (Araneae, Tetragnathidae). *Proceedings of the XII International Congress of Arachnology, Brisbane. Memoirs of the Queensland Museum* 33(2): 519–526.
- GILLESPIE, R.G. 1994: Hawaiian spiders of the genus *Tetragnatha*. III. *T. acuta* clade. *Journal of Arachnology* 22: 161–168.
- GILLESPIE, R.G., CROOM, H.B. 1992: Patterns and process in speciation: a comparative approach using a hawaiian spider radiation. *American Journal of Botany* 79: 127.
- GILLESPIE, R.G., CROOM, H.B. & PALUMBI, S.R. 1994: Multiple origins of a spider radiation in Hawaii. *Proceedings of the National Academy of Sciences* 91: 2290–2294.
- KARSCH, F. 1881: Arachniden und Myriopoden Mikronesiens. *Berliner entomologische Zeitschrift* 25: 15–16.
- KULCZY(SKI, W. 1911: Araneae et Arachnoidea Arthrogastra. In: Botanische und zoologische Ergebnisse einer wissenschaftlichen Forschungsreise nach den Samoainseln, dem Neuguinea-Archipel und den Solomon inseln von März bis Dezember 1905 von Dr Karl Rechinger. III Teil N:o 4. *Denkschriften der Akademie der Wissenschaften, Wien* 85: 389–411 pl XVI.
- KOCH, L. & KEYSERLING, E. 1871–1886: *Die Arachniden Australiens, nach der Natur beschrieben und abgebildet*. Nürnberg, 1489 pp. & 123 Pls.
- LEGENDRE, R. 1978: Réflexions sur le peuplement actuel des arachnides du globe. *103e Congrès national de la Société des savants, Nancy* 3: 45–55.
- LEHTINEN, P.T. 1980: Arachnological zoogeography of the Indo-Pacific region. *Verhandlungen, 8. Internationaler Arachnologen-Kongress, Wien* 1980: 499–504.
- LEHTINEN, P.T. 1981: Spiders of the Oriental–Australian region III. Tetrablemmidae, with a world revision. *Acta Zoologica Fennica* 162: 1–151.
- LEHTINEN, P.T. 1982: Spiders of the Oriental–Australian region IV. Stenochilidae. *Annales Zoologici Fennici* 19: 115–128.
- LEHTINEN, P.T. 1993: Polynesian Thomisidae — a meeting of Old and New World groups. *Proceedings of the XII International Congress of Arachnology, Brisbane. Memoirs of the Queensland Museum* 33(2): 585–591.
- LEHTINEN, P.T. & SAARISTO, M.I. 1980: Spiders of the Oriental–Australian region II. Nesticidae. *Annales Zoologici Fennici* 17: 47–66.
- LEVI, H.W. 1980: The orb-weaver genus *Mecynogea*, the subfamily Metinae and the genera *Pachygnatha*, *Glenognatha* and *Azilia* of the subfamily Tetragnathinae north of Mexico (Araneae: Araneidae). *Bulletin of the Museum of Comparative Zoology* 149: 1–75.
- MARPLES, B.J. 1951: Pacific symphytognathid spiders. *Pacific Science* 5: 47–51.
- MARPLES, B.J. 1955a: Spiders from Western Samoa. *Journal of the Linnean Society of London (Zoology)* 42: 453–504.
- MARPLES, B.J. 1955b: Spiders from some Pacific Islands. *Pacific Science* 9: 69–76.
- MARPLES, B.J. 1956: Spiders in Samoa and the southwest Pacific. *Proceedings of the 8th. Pacific Science Congress III A*: 1573–1574.
- MARPLES, B.J. 1957: Spiders from some Pacific Islands. *Pacific Science* 11: 386–395.
- MARPLES, B.J. 1959: Spiders from some Pacific Islands, III. The Kingdom of Tonga. *Pacific Science* 13: 362–367.
- MARPLES, B.J. 1960: Spiders from some Pacific islands, part IV. The Cook Islands and Niue. *Pacific Science* 14: 382–388.
- MARPLES, B.J. 1964: Spiders from some Pacific Islands. Part 5. *Pacific Science* 18: 399–410.
- MORGAN, W.J. 1972: Deep mantle convection plumes and plate motion. *Bulletin of the American Association of Petrology and Geology* 56: 203–213.
- OPELL, B.D. 1983: A review of the genus *Tangaroa* (Araneae, Uloboridae). *Journal of Arachnology* 11: 287–295.

- POCOCK, R.I. 1898: List of the Arachnida and "Myriopoda" obtained in Funafuti by Prof. W.J. Sollas and Mr. Stanley Gardiner, and in Rotuma by Mr. Stanley Gardiner. *Annals and Magazine of Natural History* (7) 1: 321-329.
- RAINBOW, W.J. 1897: The Arachnidan fauna of Funafuti. The Atoll of Funafuti. Part 2. *Memoirs of the Australian Museum* 3: 105-124.
- ROEWER, C.F. 1944: Einige Araneen von Prof. Dr Sixten Bocks Pazifik-Expedition 1917-1918). *Meddelanden från Göteborgs Musei, Zoologiska Avdelning* 104: 1-10.
- STRAND, E. 1911: Vorläufige Diagnosen neuer Spinnen, insbesondere aus der Südsee, des Senckenbergischen Museums. *Archiv für Naturgeschichte* 77: 202-207.
- STRAND, E. 1913: Neue indoaustralische und polynesische Spinnen des Senckenbergischen Museums. *Archiv für Naturgeschichte* 79 A: 147-162.
- STRAND, E. 1915: Indoaustralische papuanische und polynesische Spinnen des Senckenbergischen Museums, gesammelt von Dr E. Wolf, Dr J. Elbert u. a. in Wissenschaftliche Ergebnisse der Hanseatischen Südsee-Expedition 1909. *Abhandlungen von der Senckenbergischen Naturforschenden Gesellschaft* 36: 181-284, Pl. XIII-XIX.
- SUMAN, T.W. 1965: Spiders of the family Oonopidae in Hawaii. *Pacific Insects* 7: 225-242.
- SUMAN, T.W. 1967: Spiders (Prodidomidae, Zodariidae, and Symphytognathidae) in Hawaii. *Pacific Insects* 9: 21-27.
- SUMAN, T.W. 1970: Spiders of the family Thomisidae in Hawaii. *Pacific Insects* 12: 773-864.
- WILSON, J.T. 1963: Continental Drift. (reprint in Continents Adrift 6). *Scientific American* 1970: 41-56.
- YAGINUMA, T. 1990: A spider genus *Litisedes* Oi is synonymized with *Paratheuma* Bryant. *Nanki Seibutu* 32: 1-6.