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COLONIZATION OF THE KRAKATAU ISLANDS BY PSOCOPTERA (INSECTA)

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CONTENTS

Eighty species of Psocoptera, of 15 families, were collected on the four Krakatau islands in 1982–86, about a century after the 1883 eruption of Krakatau. The most abundant species on the Krakataus (in the families Lepidopsocidae, Ectopsocidae and Peripsocidae, which are also three of the four most diverse families on the Krakatau group) are typical early colonizing forms, but several ecologically more specialized taxa are also present, and some are limited to particular kinds of vegetation. Families characteristic of forest habitats, Pseudocaeciliidae, Myopsocidae and Psocidae, are poorly represented on the Krakataus. The faunas of Rakata and Panjang are markedly more diverse than those known for Sertung or Anak Krakatau, and the first pair of islands, the only one of the six possible pairs to consist wholly of mixed secondary forest, show the greatest faunal similarity.

By reference to the presumed source faunas, there is evidence that the most diverse family on the Krakataus, Caeciliidae, (18 species present) is typical of the order as a whole in colonizing ability, whereas the Lepidopsocidae (11), Ectopsocidae (13) and Peripsocidae (11) are relatively good colonizers, and the Pseudocaeciliidae (3), Myopsocidae (2) and Psocidae (4) relatively poor ones. Within the archipelago, the same trends are apparent for the colonization of the young island of Anak Krakatau, which emerged from the sea in 1930. Taking the three other Krakatau islands as the source, the Caeciliidae again show average colonizing ability, and Lepidopsocidae and Ectopsocidae again are relatively good colonizers. The Peripsocidae, however, show up as rather poorer ones in this model. Because species of this family are predominantly bark dwellers their habitat would not be available as early as that for species of the other families, which are found largely on leaf litter and on living leaves.

Progressive development of the psocopteran fauna of the archipelago is discussed in relation to vegetational succession.

1. Introduction

This paper is part of a series (see Thornton & Rosengren (1988) for a general introduction) treating the fauna of the Krakatau Islands, in Sunda Strait, between Java and Sumatra (figure 4), about a century after the destructive eruption of 1883. It provides a review of the known distribution, ecology and relative abundance of the Psocoptera found on the Krakatau Islands, to indicate, for the first time in the Old World tropics, some of the differences between 'relatively mature' and 'relatively pioneer' psocopteran faunas. Comments are made also on the psocopteran fauna of possible source areas for the Krakataus, namely western Java and southwestern Sumatra. Detailed taxonomic papers providing a baseline for future studies on the course of colonization of this order of insects on the island group are published elsewhere (Vaughan *et al.*, 1988*a*, *b*).

Three of the Krakatau islands, Rakata, Panjang and Sertung (figure 1) are believed to be only about 100 years old biologically, in contrast to upland areas of Ujung Kulon, for example, and other areas adjacent to the Sunda Strait which were also sampled during this project and which were much less affected by the 1883 eruption (figure 4). The fourth island, Anak Krakatau, emerged from the sea in 1930, suffered a devastating eruption in 1952, and has been active regularly since then; its biota is no more than about three decades old, and so the island provides a further level of age comparison, within the archipelago, between it and the three older islands (Thornton & Rosengren 1988).

Psocoptera, bark lice, are small, usually winged insects generally associated with vegetation, where they feed by grazing on epiphytic microflora and adventitious organic debris on the surface of leaves and branches. They can occur in considerable numbers, particularly in temperate regions, and are important primary consumers in many food chains (Thornton 1985*a*). Some taxa show marked habitat or host-plant specificity (New 1987) whereas others are much more catholic in incidence, and a range of ecological strategies is found in the order. A few species are widespread and are classic pioneer species: they are found in the aerial plankton (Thornton 1964; Thornton & Harrell 1965), are invariably among the earliest colonizers of vegetation over much of the tropics (see, for example, Simberloff 1976), and have been termed 'tropical waifs' (Mockford 1974). Several such species are parthenogenetic, and tend to be habitat generalists as they occur and feed on many kinds of vegetation. In contrast, other (predominantly sexually reproducing) species may be regarded as specialists as they cannot thrive until particular plant growth forms, associations or taxa are established. Many species are reluctant to fly and aerial dispersal, though frequently recorded, appears to be almost always passive.

In common with many other groups of small and inconspicuous insects, Psocoptera tend not to be collected by non-specialist workers. However, intensive surveys of many parts of the western Pacific during recent years have clearly indicated their value in biogeographical syntheses (Thornton 1985*a*). Many undescribed species occur in collections from tropical regions, but sufficient can now be inferred about the biology of many families and genera to render them useful in studies of community development.

The Psocoptera of Indonesia are not well known, but about 250 species have been described or recorded from the archipelago, 67 of them recently from Bali or Lombok or both (Thornton 1984). Many of the early-described species are difficult to recognize from the descriptions, and several problems of precise nomenclature are not likely to be solved in the near future. Until

now, Psocoptera have been one of the poorest-known insect orders on the Krakatau Islands, whence only two taxa were recorded during the early years of this century. The male of the Javanese *Ptycta schillei* (Enderlein) (Psocidae) was described from a specimen collected on Panjang in May 1908 (Enderlein 1926), and Jacobson (1909) noted an undetermined species from Rakata. This is the nymph of a pale caeciliid (seen, T.R.N.). Dammerman (1948) commented that psocids were also obtained in 1921, but was unsure if the species was identical with one of those earlier recorded. The 1921 specimens have not been traced, but it is virtually certain that a range of species would have been present on Rakata, Panjang and Sertung before that time.

This account is based on material collected on the Krakatau Islands in 1982 (Thornton 1985*b*) and the extensive collections made during the 1984–86 La Trobe University/Bogor Zoological Museum Zoological Expeditions (Thornton & Rosengren 1988). All three authors collected Psocoptera in 1984 and 1985, and T. R. New and I. W. B. Thornton in 1986. The bulked collections, although biased to August and September (towards the end of the 'dry' season) represent the first realistic baseline data on this order for the Krakataus, and collecting sites on the islands are shown in figure 1.

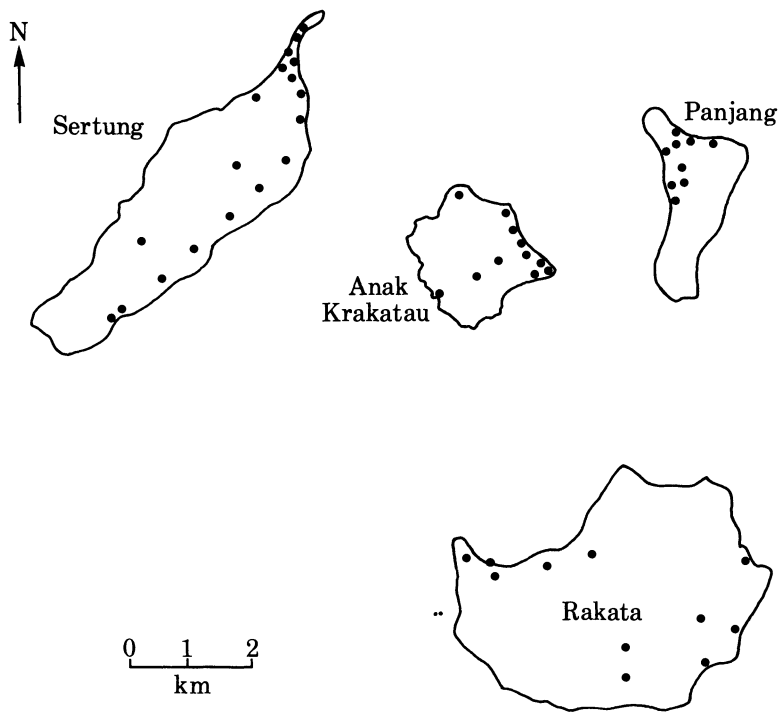

FIGURE 1. The Krakatau Islands, showing sites sampled for Psocoptera.

In 1984, Vaughan visited southwestern Sumatra in April and May and collected around Carita (west Java) in May. Both areas were again visited in late August 1984, and the Ujung Kulon peninsula (figure 4) and nearby island Pulau Peucang were visited for 17 days in 1982 (Thornton) and for about 10 days in 1984 (New, Vaughan). Additional collecting around Carita occurred in 1985 and 1986. Fifty-two species found in Java or Sumatra or both during our work are apparently absent from the Krakataus, and are discussed elsewhere (Vaughan *et al.* 1988*a*), so that this paper deals only with species found on the islands. The other taxa are

enumerated in Appendix 1. New species are here designated by letter codes, which will be referred to in a complete taxonomic account of the fauna (Vaughan *et al.* 1988*b*).

The Krakataus provide a rare opportunity to document diversity of insects associated with vegetation in the tropics against the background of a flora that is almost totally defined, and care was taken to sample from all major vegetation formations and dominant species to assess the taxa associated with particular vegetation types. In contrast to the three older islands, the vegetation spectrum of Anak Krakatau is limited, and the Psocoptera present there are likely to reflect the 'pioneer phase' of colonization. The forests on Java and Sumatra are, in places, considerably more mature than those on the Krakataus. Overall comparison of the fauna of the Krakatau Islands with the 'mainland' Psocoptera, and of Anak Krakatau with the three older islands of the archipelago, may therefore reveal differences between developing and 'mature' psocopteran faunas in Indonesia, and this theme is developed in our discussion.

2. Methods

On all visits psocopterans were collected by beating and sweeping, but some specimens were also obtained from Malaise traps or Winkler extractions from leaf litter.

In 1984, Vaughan attempted to take his samples in a standard fashion from different discrete vegetation types, and these samples were used for initial quantitative appraisal, with the trends there revealed being further investigated on the later expeditions. For quantitative sampling from larger vegetation, one branch on each of ten randomly selected trees at a site, often representing a range of different taxa, was beaten 20 times over a square beating tray (area 0.5 m^2). The specimens from each of the 10 trees were bulked to constitute a sampling unit. Some other vegetation types demanded modifications to this method, to ensure at least reasonable compatibility of foliage density. For palms, three fronds of each of ten trees were beaten, and 30 individual fern fronds constituted a sampling unit. Sweeping of herbaceous vegetation and direct searching of bark and litter were attempted, with no Psocoptera being recovered in 1984, and these methods were thus discontinued, although employed as qualitative techniques on later visits. Quantitative sampling was thus effectively restricted to the lower branches of trees and the understorey, to a height of about 3 m.

Specimens were preserved in 70% alcohol and later sorted, and selected specimens prepared for taxonomic examination by the methods outlined by New (1977).

3. Results

The taxa found

Table 1 summarizes, by a systematic list, the species found on the Krakataus, with the numbers of individuals of each species from each of the four Krakatau islands and an indication of representation of the species found elsewhere in this survey. The following comments amplify the table.

Lepidopsocidae. The three species of *Echmepteryx* Aaron, *Lepidopsocus pretiosus* and *L. marmoratus* are all common and widespread species known from many parts of the western Pacific. *E. madagascariensis* is tropicopolitan. The remaining species are not as well known. *Parasoa haploneura* was described from the Batu Caves (Malaysia), but four species appear to be undescribed. These are mostly represented by few individuals, from only one or two islands,

although several were also collected in other parts of Indonesia. *Nepticulomima lusiae* is known from Fiji and Moorea.

Amphientomidae. A single specimen from a litter sample on Rakata is the only representative of the Amphientomidae known from the islands. It is an undescribed species.

Pachytroctidae. Small numbers of four species of the widely distributed genus *Tapinella* Enderlein were found. Three were described from Bali or Lombok. *T. clypeola* is now known from Sumatra, Java, Lombok and the Krakataus, and is thus very widespread in Indonesia.

Epipsocidae. Two species, both scarce, were found on Rakata. *Epipsocopsis* Badonnel is particularly diverse in the Malaysian region, though few species of the family have been recorded from Indonesia. *E. inornatus* is a Philippines species. The species are typically associated with bark or litter.

Caeciliidae. This was the most diverse family found, with several species being reasonably common on vegetation. The current taxonomic confusion in this family may lead to some revision in the number of species noted here, though several of the described species are known from other parts of Indonesia, as well as elsewhere. Caeciliidae are common in Indonesia, with 56 species being known from other parts of the country. *C. muggenburgi* occurs also in Singapore, the Philippines and Taiwan, and *C. parviareola* Enderlein in New Guinea. Nine of the Krakatau species appear to be new: most are clearly referable to the cosmopolitan genus *Caecilius* Curtis.

Stenopsocidae. Three species were found on the Krakataus, and others have earlier been recorded from Indonesia. The two species of *Stenopsocus* Hagen may be new, but *Taeniostigma elongatum* is very widely distributed in the Oriental Region.

Amphipsocidae. One species of *Amphipsocus* McLachlan was found on the three older islands of the Krakatau group, and at Carita on the west coast of Java. The family is not diverse in Indonesia, whence only three other species of *Amphipsocus* are known.

Ectopsocidae. The 13 species of *Ectopsocus* McLachlan include several undescribed species and others that are widespread. The most abundant species, *E. titschacki*, is known from many parts of the world, including Africa and South America. *E. cinctus* occurs in India, Malaysia, Vietnam, Hong Kong and Australia, as well as Bali and Lombok; it was found during our work also on Sumatra and at Ujung Kulon.

Peripsocidae. The 11 species of *Peripsocus* Hagen were relatively rare, though several were found on more than one island. About seven species were hitherto known from Indonesia. Some, such as *P. reicherti*, are widespread species, but others are clearly new.

Pseudocaeciliidae. One of the three species appears to be new. The unusual *Phallocaecilius hirsutus* occurred on the older Krakatau islands and Java: the species is otherwise known from Hong Kong. *Pseudocaecilius citricola* is a tropicopolitan species.

Archipsocidae. Two of the three species found occur also on Bali, but their relationship with the two Indonesian species recorded by Soehardjan (1958) is not yet clear. No large populations of these colonial Psocoptera were found on the Krakataus.

Philotarsidae. Representatives of two widely distributed genera, *Haplophallus* Thornton and *Aaroniella* Mockford, were found. *H. orientalis* is a widely distributed Oriental species and the others are new species.

Hemipsocidae. Two widespread species of *Hemipsocus* Selys-Longchamps were found, neither commonly. The systematics of this genus in the Orient is confused.

Psocidae. Small numbers of three species were found on vegetation, though one was

TABLE 1. PSOCOPTERA FOUND ON THE KRAKATAU ISLANDS, 1982–1986

	number of individuals on				
	Rakata	Sertung	Panjang	Anak Krakatau	found elsewhere in this survey
Lepidopsocidae					
Echmepteryx lunulata Thornton, Lee & Chui	78	49	44	33	Java, Sumatra
E. madagascariensis (Kolbe)	2	—	33	—	Java, Sumatra
E. pallida Smithers	144	176	462	20	Java, Sumatra
Lepidopsocus 'F'	3	—	2	—	Java
L. 'H'	2	—	—	—	—
L. marmoratus (Banks)	1	10	3	—	Sumatra
L. pretiosus (Banks)	41	21	40	82	Java, Sumatra
Nepticulomima lusiae Thornton	1	—	1	—	Java
N. 'B'	1	—	—	15	—
Parasoa haploneura Thornton	—	—	2	—	—
Soa 'AB'	1	—	1	1	—
Amphientomidae					
Seopsis 'LA'	1	—	—	—	—
Pachytroctidae					
Tapinella baliensis Thornton	4	—	9	—	Java
T. spinosa Thornton	—	—	—	1	—
T. clypeola Thornton	1	—	—	—	Java, Sumatra
T. sp.	—	—	1	—	—
Epipsocidae					
Epipsocopsis 'UK'	1	—	—	—	Java
E. inornatus Banks	3	—	—	—	—
Caeciliidae					
Caecilius baliensis Thornton	—	—	1	—	—
C. casarum Badonnel	1	—	—	2	Java
C. laleus Thornton	3	1	11	—	Java
C. muggenburgi Enderlein	20	2	9	—	Java
C. parviareola Enderlein	27	1	18	9	Java
C. soehardjani Smithers	—	—	—	1	Java
C. traceus Thornton	8	—	6	1	—
C. velectus Thornton	—	—	1	—	—
C. 'C'	4	—	—	—	—
C. 'F'	1	1	7	47	Java, Sumatra
C. 'K'	—	—	4	11	Java
C. 'W'	15	—	—	—	—
C. 'Y'	—	—	2	—	—
C. '40'	3	—	—	—	—
C. 'ED'	—	—	1	—	—
C. bifasciatus? New & Thornton	1	—	—	—	Java
Fuelleborniella '26'	—	1	1	—	Java
Paracaecilius '22D'	1	—	—	—	—
Stenopsocidae					
Stenopsocus 'A'	1	—	1	—	—
S. '170'	1	—	—	—	—
Taeniostigma elongatum (Hagen)	5	1	—	—	—
Amphipsocidae					
Amphipsocus 'A'	1	1	3	—	Java

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

TABLE 1. (*Cont.*)

	number of individuals on				
	Rakata	Sertung	Panjang	Anak Krakatau	found elsewhere in this survey
Ectopsocidae					
Ectopsocus baliosus Thornton & Wong	3	—	1	5	Java
E. cinctus Thornton	11	27	11	7	Java, Sumatra
E. coccophilus Ball	19	6	6	1	Java
E. hypandrus Thornton	6	—	—	—	Java
E. maindroni Badonnel	—	6	—	—	Java
E. ornatus Thornton	—	—	1	—	Java
E. paraplesius Thornton & Wong	2	—	—	—	—
E. salpinx Thornton & Wong	7	9	2	—	Sumatra
E. titschacki Jentsch	46	26	15	6	Java, Sumatra
E. 'A'	1	—	—	—	Java
E. 'B'	1	1	4	1	Sumatra
E. 'J'	21	1	18	2	—
E. '220'	—	2	—	—	—
Peripsocidae					
Peripsocus bifidus Thornton	2	—	—	2	—
P. brachyura Thornton & Wong	—	1	—	—	—
P. circinus Thornton & Wong	—	1	—	—	—
P. reicherti Enderlein	3	1	—	—	Java
P. similis Enderlein	—	2	—	1	—
P. variatus Soehardjan & Hamann	2	—	3	—	Java
P. 'C'	4	5	9	2	Java
P. 'D'	1	—	2	—	—
P. 'E'	3	—	4	—	Java
P. 'H' (= I, I?)	3	—	3	—	—
P. 'AE'	—	—	1	—	—
Pseudocaeciliidae					
Lobocaecilius 'G'	2	—	6	—	Java, Sumatra
Phallocaecilius hirsutus (Thornton)	20	5	2	—	Java
Pseudocaecilius citricola (Ashmead)	1	—	3	—	Java
Archipsocidae					
Archipsocopsis fernandi Pearman	8	3	13	3	Java, Sumatra
Archipsocus 'E'	—	—	1	—	—
A. sanurensis Thornton	—	—	1	—	Java
Philotarsidae					
Aaroniella 'B'	1	—	—	—	—
Haplophallus orientalis Thornton	—	4	—	7	—
H. 'C'	5	—	4	1	—
Hemipsocidae					
Hemipsocus africanus Enderlein	6	—	—	—	Java
H. luridus Enderlein	2	—	4	—	Java
Psocidae					
Psocidus 'C'	—	—	—	13	—
Ptycta 'K'	—	—	1	—	Java
Ptycta 'C'	1	—	—	31	—
Myopsocidae					
Lophopterygella camelina Enderlein	—	—	1	—	—
L. 'D'	1	—	—	—	—

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

well-represented in Malaise-trap catches on Anak Krakatau. *Ptycta schillei*, recorded from Panjang in 1908, was not found in our surveys.

Myopsocidae. Single specimens of two species of *Lophopterygella* Enderlein were collected, including *L. camelina*, originally described from Java.

Incidence on different vegetation types

The vegetational associations of the Krakatau Psocoptera, based on Vaughan's 1984 collections, are summarized in table 2. In all, 10 vegetation types were distinguished in the survey, some not occurring on the islands but included here for comparison of sampling on Java and Sumatra.

Table 2. Representation of Psocoptera on different vegetation types on the Krakataus, Java and Sumatra in 1984

	vegetation type[a]									
family	A	B	C	D	E	F	G	H	I	J
Lepidopsocidae	331	36	115	19	17	27	171	1	—	44
Pachytroctidae	3	10	—	—	3	—	—	—	—	—
Epipsocidae	1	1	—	1	13	—	—	—	—	—
Caeciliidae	67	1	13	9	1	—	12	8	2	1
Amphipsocidae	7	—	—	—	—	—	—	1	—	—
Ectopsocidae	111	21	69	—	—	38	13	—	2	2
Peripsocidae	14	2	5	1	—	—	6	9	—	—
Hemipsocidae	141	12	2	—	12	—	—	—	—	—
Pseudocaeciliidae	13	5	5	4	15	1	1	2	1	—
Archipsocidae	165	1	—	—	3	1	2	2	—	—
Philotarsidae	6	—	—	1	—	—	—	—	—	—
Psocidae	3	—	—	—	—	—	—	—	—	2
Myopsocidae	3	—	—	—	—	—	—	24	—	—
total sample units	43	6	13	4	6	5	4	3	2	4
presence on Krakataus	yes	yes	yes	yes	no	yes	no	no	yes	yes

[a] A, inland trees and understorey; B, dead vegetation; C, coastal trees and shrubs; D, ferns; E, palms; F, herbaceous plants; G, narrow-leaved trees; H, bamboo; I, *Schefflera* forest; J, *Casuarina equisetifolia*.

(*a*) 'General inland trees and understorey' was the most intensively examined environment, and includes a wide range of plant taxa. All psocopteran families were present but the most abundant, Lepidopsocidae, far outnumbered others. Ectopsocidae and Caeciliidae were also particularly well represented. Archipsocidae included two colonies, comprising 85 individuals of *Archipsocus fernandi* and 34 of *A. sanurensis* at Carita, and 139 Hemipsocidae were captured in a single colony in southern Sumatra.

(*b*) 'Dead vegetation'. This resource is patchy in incidence, and was sampled opportunistically where it was available. Lepidopsocidae was the most abundant family present, followed by Ectopsocidae, Hemipsocidae and Pachytroctidae.

(*c*) 'Coastal trees and shrubs' included only plants facing directly on to a beach. The fauna was dominated, again, by Lepidopsocidae and Ectopsocidae. Several species of each family tended to coexist in this habitat: all species of *Ectopsocus* from Rakata, for example, occurred on coastal vegetation.

(*d*) 'Ferns'. No species was restricted to ferns. Six families were present but Ectopsocidae was a notable absence as many Ectopsocidae have been found on pteridophytes elsewhere.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

(*e*) 'Palms'. Not sampled on the Krakataus. At Carita, no Psocoptera were found on living palm foliage. In contrast, dead palm fronds were a favoured habitat, with Hemipsocidae, Epipsocidae and Pseudocaeciliidae reaching their greatest mean number per sampling unit on this vegetation. Lepidopsocidae was the most abundant family.

(*f*) 'Herbaceous plants' were sampled separately as 'coastal' and 'inland' habitats. Ectopsocidae reached their greatest density on coastal herbaceous plants, and Ectopsocidae and Lepidopsocidae were the only families on inland herbs.

(*g*) 'Narrow-leaved trees'. Not sampled on the Krakataus. At Carita, this vegetation yielded the highest mean number per sampling unit (Lepidopsocidae) for any taxon–vegetation combination in this sampling series (table 2). Levels of Ectopsocidae, Peripsocidae and Caeciliidae were also high.

(*h*) 'Bamboo'. Sampled only at Carita. A myopsocid was the most abundant species, and was not found elsewhere. Peripsocidae and Caeciliidae were also relatively common.

(*i*) 'Schefflera forest'. Very few psocids were taken in this wet forest found on the upper levels of Rakata. They included representatives of Caeciliidae, Pseudocaeciliidae and Ectopsocidae.

(*j*) '*Casuarina equisetifolia*'. Lepidopsocidae was the most abundant family in samples from *Casuarina* on Sertung, Anak Krakatau and at Belimbing (coast of Sumatra). No psocopterans were collected from the exposed casuarinas on the steep northern cliff of Rakata.

4. Discussion

The psocopteran fauna of the Krakatau islands is undoubtedly rich, and many of the species are likely to have been present for a considerable period. About 28 species of the total of 80 now found on the islands are, at present, known only from the Krakataus, but most of the others occur in other parts of Indonesia and (in some cases) considerably further afield. It is highly unlikely that members of the former category are limited to the Krakataus, and a major difficulty of discussing many aspects of the Oriental Psocoptera is the cautious interpretation necessitated by generally inadequate specialist collecting in the area. Biogeographical interpretation must, therefore, be extremely tentative, as the faunas of Java and Sumatra are still poorly known. However, in contrast to many other groups of insects, the fauna can be documented at the species level and some constructive inferences on the ecology of the various taxa can be made.

The species–discovery curve for the archipelago (figure 2) suggests that 42 days of collecting resulting in about 1400 adults has been sufficient to encounter a high proportion of the species present, and the curves for Rakata, Panjang, and Anak Krakatau, although based on lower numbers of specimens (459, 508 and 216 respectively), also tend to flatten towards the end of our surveys. That for Sertung, from which 230 specimens were collected, shows little or no such trend, and we believe this island has been undersampled.

The most abundant Krakatau species were, in descending order of commonness, *Echmepteryx pallida* (782 individuals), *E. lunulata* (204), *Lepidopsocus pretiosus* (184), *Ectopsocus titschacki* (93) and *Caecilius parviareola* (67), all of which occurred on all four islands. The first three, lepidopsocids, are likely to be parthenogenetic, as no males were collected, and this strategy may aid rapid colonization. These were also abundant in Java and Sumatra. Only five further species (four of *Ectopsocus*, one of *Archipsocopsis*) were found on all islands, and most were relatively uncommon.

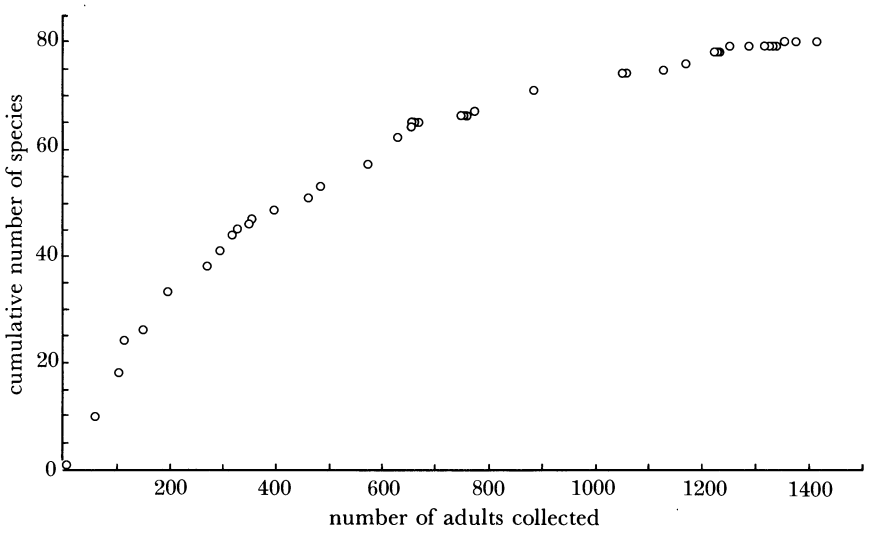

FIGURE 2. Species discovery curve for Psocoptera on the Krakatau archipelago, 1982–86.

In the Psocidae, no Cerastipsocini were found, and the taxa present belong to the presumably more vagile groups of the family. The absence of Liposcelidae, although most are wingless, is likely to reflect lack of direct searching in subcortical habitats. Pachytroctidae may show alary polymorphism, but only fully winged adults were found. Likewise, brachypterous individuals of Lepidopsocidae (except *Parasoa*), Caeciliidae and Ectopsocidae were not observed. No apterous adult Psocoptera were found on the islands, other than for a few Archipsocidae, in which this feature reflects polymorphism as colonies develop.

The vegetation survey yielded results that were generally expected. Lepidopsocidae was the most abundant family on nearly all vegetation types, and several species were very widespread, a finding entirely in keeping with our collecting in other parts of the western Pacific. Ectopsocidae were second only to Lepidopsocidae in overall abundance, but were ecologically rather more restricted. They were especially common on herbaceous plants and coastal trees and shrubs. Caeciliidae occurred in smaller numbers, and some species were also widely distributed on different kinds of living vegetation. Many of the Pseudocaeciliidae were associated with dead foliage and coastal vegetation, and most other families were more restricted in habitat. An unusual association was the incidence of *Haplophallus* 'C', representing an otherwise almost wholly arboreal genus, on ferns at 250 m on Rakata. If the data in table 2 are assessed on a 'numbers per sample' basis, Lepidopsocidae are unusually diverse on narrow-leaved trees.

The index of diversity (α) for the archipelago is 16.7 ± 1.0, which is between those for Psocoptera of tropical forests in Trinidad (11.8–14.8 (Evans 1977)) and Panama (19.6 (Broadhead 1983)) collected by methods similar to those used here. The species–abundance curve fits the log series satisfactorily, validating the use of this index. These values contrast with values for Psocoptera in Europe (1.3 (Broadhead 1958)) and temperate southeastern Australia (3.2 (New 1975)), the latter being based on suction trap catches. Since α depends on the range of habitat sampled (sampling should ideally be random) these comparisons should be treated with caution. The differences between tropical and temperate diversities, however, are large and consistent.

Not unexpectedly, Rakata, by far the highest (777 m) and largest (12.5 km^2) island, which has the most diverse flora, yielded more species (57) than any other, although the fauna of Panjang (145 m, 2.7 km^2) is also diverse (48 species). Rakata has a high index of diversity ($\alpha = 15.9 \pm 1.2$), that of Panjang being somewhat lower (11.3 ± 1.0). The fauna of Sertung (182 m, 7.9 km^2) is anomalous in having the same number of species (27) and being very similar in spectrum to that of the young island Anak Krakatau (196 m, *ca.* 2.3 km^2 but only *ca.* 17 hectares† vegetated). Indices of diversity for both islands are relatively low, 6.7 ± 0.9 for Sertung and 7.1 ± 1.0 for Anak Krakatau. The anomaly is probably partly due to the biased sampling of Sertung's range of habitats (see below), which would result in an underestimate of α, although the undersampling noted above would tend to overestimate it.

The major differences in diversity, between Rakata and Panjang on the one hand and Sertung and Anak Krakatau on the other, reflect the differential occurrence of relatively few families. In particular, Lepidopsocidae and Caeciliidae (table 1) are considerably more diverse on Rakata and Panjang and Peripsocidae and Pseudocaeciliidae somewhat so. Ectopsocidae were relatively uniform in richness on all islands, and other families were represented by very few species. Caeciliidae (18 species) was the most diverse of the 15 families represented on the island group, followed by Ectopsocidae (13), Peripsocidae and Lepidopsocidae (both 11). At the family level, the islands fall into the same two pairs, with Anak Krakatau and Sertung each having only about half the families present on either Panjang or Rakata. However, the more diverse families noted above occur on all the islands, and together constitute a very high proportion of our collections. Sorensen's quotient of similarity, *QS*, between the different islands for total Psocopteran faunas and for the most diverse families is given in table 3 with

Table 3. Similarity of psocopteran faunas of island pairs of the Krakataus

(Quotients of similarity are given for total Psocoptera and for the four most diverse families. Sorensen's *QS* is calculated as $2J/(A+B)$, where J is the number of joint (shared) species and A and B are the numbers of species on each island. A modification of this (in parentheses) is *QS* multiplied by the number of species in the smaller fauna divided by the number of species in the larger fauna, to compensate for differences in faunal size. Islands denoted by initials.)

island pair	total	Lepidopsocidae	Caeciliidae	Ectopsocidae	Peripsocidae
R/AK	0.48 (0.23)	0.67 (0.33)	0.47 (0.26)	0.75 (0.45)	0.40 (0.17)
R/S	0.45 (0.21)	0.57 (0.23)	0.50 (0.23)	0.67 (0.53)	0.33 (0.24)
R/P	0.65 (0.55)	0.84 (0.76)	0.45 (0.45)	0.78 (0.62)	0.77 (0.66)
AK/S	0.52 (0.52)	0.67 (0.53)	0.36 (0.30)	0.71 (0.54)	0.50 (0.30)
AK/P	0.48 (0.27)	0.57 (0.32)	0.47 (0.26)	0.71 (0.54)	0.22 (0.13)
P/S	0.51 (0.29)	0.62 (0.27)	0.63 (0.28)	0.75 (0.75)	0.18 (0.15)
average similarity between all pairs	0.52 (0.35)	0.66 (0.41)	0.48 (0.30)	0.73 (0.57)	0.40 (0.27)

a modification to correct for differences in faunal size. Faunal overlap between islands is indicated in figure 3. Both *QS* values are consistently high for inter-island comparisons of Ectopsocidae, probably reflecting the ubiquity of ephemeral habitats, such as dead foliage, frequented by many of the more widespread species of this family.

The high level of similarity between the psocopteran faunas of the youthful Anak Krakatau

† 1 hectare = 10^4 m^2.

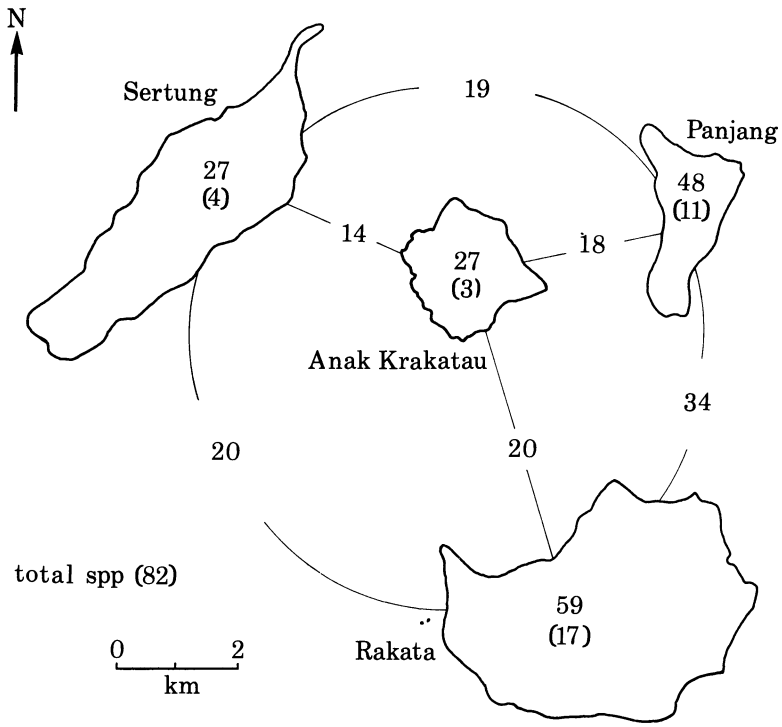

FIGURE 3. Numbers of Psocoptera on each island of the Krakataus, and in common between island pairs. Figures in parentheses are numbers of species found only on each island.

and the biologically older Sertung, and the low similarity quotients, particularly the modified value, between Sertung and its companion islands Rakata and Panjang, all three of which are of the same biological age, are at first sight anomalous. Both Anak Krakatau and Sertung have a paucity of species and the high similarity index for these islands may reflect undersampling of Sertung. It may also be due to a collecting bias on Sertung towards the early successional vegetation of the spit. This northern peninsula is a young, dynamic feature no more than three decades old (Thornton & Rosengren 1988) and has a vegetation cover quite different from the older, main part of the island, and similar to that on Anak Krakatau (*Casuarina* woodland and grassland). We sampled the spit and the ecotone between this and the 'island proper', as well as the southern region of the island, which, like Panjang and Rakata, is clothed in mixed secondary forest. Sertung was certainly badly affected by eruptions of Anak Krakatau in the early 1950s (Thornton & Rosengren 1988), but Panjang may have been affected to a similar extent. The greater *QS* for Anak Krakatau and Sertung compared with that for Anak Krakatau and either Panjang or Rakata may in part be a reflection of the fact that of the three older islands, Sertung alone is a temporal 'amalgam' with its younger region, the spit, bearing vegetation at an early stage of colonization, like that of Anak Krakatau. This would also explain the consistently high similarities between the faunas of Rakata and Panjang in table 3; this pair is the only one of the six possible pairs of islands that lacks the early vegetational phases and involves only mixed secondary forest.

Overlap between our collections on the islands and our recent collections in adjacent putative source areas is shown in figure 4. Carita and Sumatra, in particular, were undersampled in the 1980s but the collections are sufficient to indicate the relative 'taxonomic balance' in these areas at the time of our sampling.

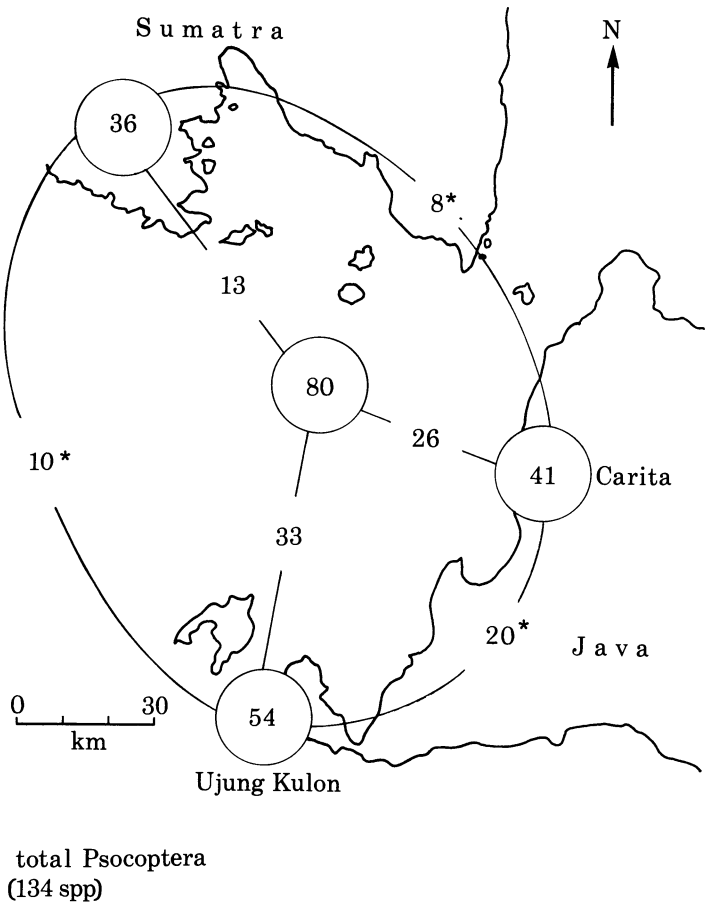

FIGURE 4. Numbers of species of Psocoptera of the Krakataus shared with Sumatra, Carita and Ujung Kulon, and shared between the latter areas. The asterisked figures represent only the species occurring on the Krakataus which are shared between peripheral areas of the Sunda Strait.

In table 4, the faunal spectrum of the Krakataus is compared with that for the fauna of the rest of Indonesia as determined from a summary of earlier Indonesian records (Soehardjan 1958; Soehardjan & Hamman 1959; and other publications up to 1983). Also included is the faunal spectrum of the islands of Bali and Lombok (Thornton 1984), as representing a fauna of about the same size as that on the Krakataus and sampled by similar short-term surveys, using collecting methods closely comparable to those employed on the Krakataus.

Inspection of table 4 shows that whereas the Bali–Lombok fauna has a family spectrum very close to that of Indonesia (minus the Krakataus), the proportions of several families on the Krakataus depart markedly from those in the 'source' area. Lepidopsocidae, Ectopsocidae and Peripsocidae appear to be over-represented on the Krakatau Islands in relation to other parts of Indonesia, but the proportion of Caeciliidae, the most diverse family on the Krakataus, is no different from that in the rest of the country. Species of the three former families are known to be early colonizers of disturbed habitats (see below). The Pseudocaeciliidae, Psocidae and to a lesser degree the Myopsocidae, are relatively under-represented on the Krakataus.

Other than for greater representation of Lepidopsocidae, which are not diverse in the Caribbean area, this faunal spectrum shows substantial parallels with the colonization by

Table 4. Relative taxonomic balance of Krakatau Psocoptera compared with other parts of Indonesia

	number of species (% of total)		
family	Krakataus	Bali–Lombok	all Indonesia (including Bali–Lombok, excluding Krakataus)
Lepidopsocidae	11 (13.8)	5 (6.7)	20 (7.8)
Pachytroctidae	4 (5.0)	3 (4.0)	8 (3.1)
Amphientomidae	1 (1.3)	2 (2.7)	5 (2.0)
Epipsocidae	2 (2.5)	1 (1.3	6 (2.3)
Caeciliidae	18 (22.5)	15 (20.0)	56 (21.9)
Stenopsocidae	3 (3.8)	4 (5.3)	10 (3.9)
Amphipsocidae	1 (1.3)	3 (4.0)	5 (2.0)
Ectopsocidae	13 (16.3)	8 (10.7)	23 (9.0)
Peripsocidae	11 (13.8)	4 (5.3)	13 (5.1)
Pseudocaeciliidae	3 (3.8)	8 (10.7)	27 (10.5)
Archipsocidae	3 (3.8)	2 (2.7)	4 (1.6)
Philotarsidae	3 (3.8)	1 (1.3)	10 (3.9)
Hemipsocidae	2 (2.5)	2 (2.7)	5 (2.0)
Psocidae	3 (3.8)	13 (17.3)	43 (16.8)
Myopsocidae	2 (2.5)	3 (4.0)	13 (5.1)
Psyllipsocidae	0	0	1 (0.4)
Trogiidae	0	0	1 (0.4)
Liposcelidae	0	0	1 (0.4)
Calopsocidae	0	0	4 (1.6)
Psilopsocidae	0	0	1 (0.4)
total Psocoptera	80	74	256

Psocoptera of mangrove islets off Florida after defaunation experiments (Simberloff 1976). One species of *Ectopsocus* occurred there after only 21 days and, of 24 species colonizing within two years, four were *Ectopsocus*, four *Peripsocus* and one a lepidopsocid. Lepidopsocidae, *Ectopsocus*, and *Hemipsocus* tend to be associated with early successional vegetation and dead foliage, and the common Krakatau species are very widespread, at least in the Old World tropics. They are typical early colonizers of secondary vegetation in many parts of the Pacific, and can rapidly build up large populations. Likewise, some Caeciliidae are particularly associated with grasses and similar low vegetation. In contrast, such families as Amphientomidae, Psocidae and Myopsocidae (the two latter being bark dwellers and fungal feeders) tend to occur predominantly in arboreal situations, often closed forest habitats, which are relatively poorly represented on the Krakataus. Thus the paucity of these families there is not unexpected, and the finding of a single amphientomid in litter may reflect an unusual habitat association for this family.

It would be possible to quantify relative success in colonizing the Krakataus by families of the Indonesian psocopteran fauna by measuring the extent to which the proportion of each family in the Krakataus' fauna departs from its proportion in the source fauna. Those families with large, positive departures from source proportions could be termed good colonizers, relative to those with large, negative departures, poor colonizers. However, departure from the source proportion by one family will affect the departure in others because we are dealing with proportions of a total fauna. Such family indices, although indicative of relative success, would not be entirely independent of one another.

Colonization success may also be assessed simply by the proportion of a family's source

species that occur on the archipelago, and this would be mathematically independent of the measure for other families. Thus colonization ratio, CR, $= K/S$ where K is the number of species occurring both on the Krakataus and in the source area, and S the total number of species occurring in the source area. However, because collecting on the Krakataus has been more intensive than general collecting in Indonesia in past years (except the Bali and Lombok collections), some species known from the Krakataus have not yet been found elsewhere in the country although they very probably occur there. Such species would not be counted in calculating the colonization ratio, which would thus be an underestimate. Moreover, the lower the colonization ratio calculated in this way, the greater would be the underestimation.

In an attempt to avoid this underestimation we have made the assumption that species found only on the Krakataus are in fact present elsewhere in the source area but have been missed. Colonization ratio has been calculated, for each of the Indonesian families, as $CR' = (K+K')/(S+K')$, where K' is the number of species found only on the Krakataus.

A relative colonization ratio (RCR) measures the CR' for each family against the CR' for the Psocoptera as a whole, $RCR = CR'_{\text{family}}/CR'_{\text{Psocoptera}}$. Thus a family with RCR greater than one has a greater proportion of its source species (known and assumed) on the Krakataus than the average for Psocoptera, a family with an RCR of one is typical of the Psocoptera as a whole in colonizing ability, and one with RCR less than one, with less than the average proportion of source species on the Krakataus, may be regarded as a relatively poor colonizer.

Lepidopsocidae, Ectopsocidae and Peripsocidae have large values for RCR, Pseudocaeciliidae, Psocidae and Myopsocidae small ones, and the ratio for Caeciliidae is one (table 5).

TABLE 5. RELATIVE COLONIZING ABILITY OF MAJOR PSOCOPTERAN FAMILIES (a) TO THE KRAKATAU ISLANDS FROM THE REST OF INDONESIA AND (b) TO ANAK KRAKATAU FROM THE OTHER KRAKATAU ISLANDS

(Figures are relative colonization ratios, RCR (see text).)

	about 100 years		about 30 years	
family	Indonesia	a	Krakataus	b Anak Krakatau
Lepidopsocidae		1.6		1.3
Caeciliidae		1.0		1.0
Ectopsocidae		1.7		1.4
Peripsocidae		2.0		0.8
Pseudocaeciliidae		0.4		0.0
Psocidae		0.3		3.0
Myopsocidae		0.5		0.0

Within the archipelago, whereas the psocopteran fauna of Rakata undoubtedly reflects a relatively 'mature' species complement associated with diverse vegetation, that of Anak Krakatau can – conversely – be regarded as a relatively 'pioneer' fauna. The latter island is vegetated over only some 17 hectares of its about 2.3 km^2 area, and the predominant vegetation is *Casuarina* woodland (12 hectares covered with trees), with some grassland (5 hectares). Our sampling of this small area was sufficiently intensive to ensure that few resident species would have been overlooked: only 2 of the 27 species we found were discovered among the last 32% of individuals collected. Water traps and Malaise traps located well away from vegetation on Anak Krakatau (Thornton *et al.* 1988) yielded material of several species, but

most were also captured on vegetation. Few species were present in large numbers, but *Caecilius* 'F' appeared to be both common and largely restricted to *Imperata* grasses, and almost all species occurred on other islands of the group. The Anak Krakatau species are an ecologically broad subset of the Psocoptera on the archipelago (only 2 of its 27 species are not found on the other islands), and include very few relatively specialist taxa. The relatively high incidence of Psocidae in our Malaise trap samples on Anak Krakatau and their very low incidence on vegetation on the island suggest that aerial dispersal is the most important mode of colonization. There are thus clear indications that the Psocoptera of Anak Krakatau reflect an earlier phase of colonization than do those of the other islands, Rakata and Panjang in particular.

Values of *RCR* calculated for the major Krakatau families with Anak Krakatau as the 'target' island and the other Krakatau islands as the source are given in table 5. The Krakataus:Anak Krakatau model is largely independent of the Indonesia:Krakataus model considered above, so that comparison of the two models is informative. Immigrants from the mainland could have become established directly on Anak Krakatau, of course, without the intermediary of the other islands of the Krakatau group. Considering the very small area of vegetation on Anak Krakatau (17 hectares in 1984) compared with that on the other islands (2300 hectares) we have discounted this in our Krakataus:Anak Krakatau model, and have assumed that Anak Krakatau's immigrant species have all arrived from the other Krakatau islands. For the Krakataus:Anak Krakatau model the indices for Lepidopsocidae and Ectopsocidae are again large and similar to those for the Indonesia:Krakataus model, and the index for Caeciliidae is again one. The value of *RCR* for Peripsocidae is lower than it is in the Indonesia:Krakatau model, suggesting that this family is not predominant among very early colonizers. Species of Lepidopsocidae and Ectopsocidae inhabit litter and dead leaves, and are *r*-strategy species that exploit a shifting patchwork of ephemeral habitats; caeciliid species occur predominantly on grasses and living foliage. Many species of Peripsocidae are fungus-feeding inhabitants of twigs and bark, a habitat that would be available at a later stage of the vegetational succession than would those of the other three families. Only three species of Psocidae occur on the Krakataus and all occur on Anak Krakatau, accounting for the high *RCR* for this family.

Finally, the wide spectrum of species found on Sumatra or Java or both during our work, but which were not found on the Krakataus (Appendix 1), indicates that there is potential for considerable further increase in species diversity on the islands. Several species known from both sides of the Sunda Strait appear still to be absent from the Krakataus. The overlap figures from our collections (figure 4) show that colonization potential exists even in the families best represented on the islands, which are generally also the most diverse families in these source areas.

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PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Appendix 1. Summary of Psocoptera found in coastal areas of Sumatra and Java but not found on the Krakatau Islands, 1984–86

	west Java			
family	Carita	Ujung Kulon	southern Sumatra	total
Lepidopsocidae	—	2	3	5
Pachytroctidae	1	3	1	4
Epipsocidae	1	—	1	1
Caeciliidae	2	3	5	9
Ectopsocidae	—	—	3	3
Peripsocidae	2	1	1	4
Pseudocaeciliidae	3	4	4	9
Philotarsidae	2	1	—	2
Hemipsocidae	2	—	1	3
Psocidae	1	3	—	4
Myopsocidae	2	3	2	7
Trogiidae	—	1	—	1
totals	16	21	21	52

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