

Colonising aliens: caterpillars (Lepidoptera) feeding on *Piper aduncum* and *P. umbellatum* in rainforests of Papua New Guinea

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Abstract. 1. Caterpillar assemblages feeding on two alien plants, *Piper aduncum* and *P. umbellatum*, were studied in lowland rainforest in Papua New Guinea and compared with assemblages from 69 species of native woody hosts, including congeneric *P. macropiper*.

2. Species richness of caterpillars feeding on *P. aduncum* (29 species per 1500 m² of foliage) and *P. umbellatum* (36 species) was higher than the median richness for the 69 native hosts (23 species).

3. The probability that a caterpillar species colonised alien *Piper* increased with its host range from 3% for the species feeding on a single plant family to 92% for the species with host range >10 plant families.

4. The assemblage on *P. aduncum* was dominated by a single species (*Herpetogramma* sp. near *licarsisalis*, Crambidae), which represented 48% of individuals, and also had a high proportion (34%) of rare species, collected as single individuals. This community structure was indistinguishable from that of a typical native host. In contrast, the *P. umbellatum* assemblage was unusual as no species represented >10% of individuals.

5. The aggressive invasion by *P. aduncum* of early successional vegetation is not explained by a competitive advantage due to low herbivore load, as the abundance of caterpillars feeding on it was comparable to that of native pioneer plants.

6. The caterpillar assemblage on *P. aduncum* demonstrated that an assemblage indistinguishable from native assemblages in density, species richness, and dominance structure (but not in host specificity) can originate from the existing species pool in lowland rainforests on a recently established tree species in <50 years.

Key words. Enemy-free space, escape from natural enemies, herbivory, host specificity, invasive alien species, Malesia, niche saturation, non-indigenous, rainforest succession, species diversity.

Introduction

Alien plants invading native vegetation provide a rare opportunity to study herbivorous communities as they are being assembled from the local pool of species with no

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history of contact with their new hosts. Plant introductions can be studied as large-scale manipulative experiments with controls, represented by the alien's herbivore assemblage from its native range (Strong *et al.*, 1977; Zwölfer, 1988; Memmott *et al.*, 2000), or the assemblages on native plants coexisting with the alien in the area of introduction (Strong, 1974b; Leather, 1986). These experiments provide a rare opportunity to study the relative importance of ecological and evolutionary processes in shaping herbivorous assemblages.

At one extreme, a new assemblage indistinguishable in species richness, abundance, and dominance structure from the native assemblages can rapidly form by colonisation from the existing pool of species in a process determined by contemporaneous ecological factors. The other extreme represents a herbivore-free alien plant, which is slowly colonised as a result of evolutionary changes in herbivore species (Strong, 1974b).

One commonly invoked mechanism of invasion by alien plants is escape from natural enemies. Specialist herbivores will be absent from the new region and generalist herbivores are hypothesised to have greater impact on native than introduced plants (Keane & Crawley, 2002).

Studies of alien plants and their herbivores can be particularly rewarding in tropical forest ecosystems, where they can provide an insight in the origin of complex, speciose assemblages. Unfortunately, comparisons between alien and native hosts are rare from the tropics, and often restricted to crops grown in semi-natural situations, such as plantations (Strong, 1974a; Strong *et al.*, 1977; Banerjee, 1981).

Pest species accumulation on tropical plantations of cocoa, tea, and sugarcane reached an asymptote within, at most, a few hundred years, due to rapid recruitment of herbivore species from the native faunas (Strong, 1974a; Strong *et al.*, 1977). Recent data on the relatively low host specificity of leaf-chewing herbivores feeding on rainforest trees (Novotny *et al.*, 2002a,b,c) suggest that colonisation of aliens invading natural rainforest vegetation may also be rapid. Rainforest caterpillars can typically feed on several closely related, congeneric species (Basset & Novotny, 1999; Novotny *et al.*, 2002a,b). This pattern of host specificity suggests that caterpillars from native congeners could rapidly colonise an alien host and form an assemblage similar in composition to the natives. This hypothesis could explain why alien species belonging to exotic genera are more likely to be invasive than are alien species with native congeners (Rejmanek, 1999).

In this study, the origin and structure of caterpillar assemblages colonising two aliens of Neotropical origin, *Piper aduncum* L. and *P. umbellatum* L., in early successional rainforest vegetation in Papua New Guinea is examined. Their species richness, composition, abundance, host specificity, and dominance structure are compared with 69 coexisting assemblages from native woody hosts, representing 45 genera and 23 families, including the native *P. macropiper* Pennant.

Methods

Study plants

Plants were identified by W. Takeuchi and vouchers are deposited in BISH, L, LAE, and US. *Piper aduncum* is found over the entire Neotropical range of the genus *Piper*, from Argentina to Mexico (Burger, 1971). It is recognised as a serious weed in its native range (Lorenzi, 2000), and becomes an aggressive invader where introduced (Meyer, 2000). Whitmore (1991) included *P. aduncum* among the 21 most important woody species invasive in perhumid tropics. The species was introduced to Java in 1860 and is now commonly found throughout Indonesia and Malaysia (Rogers & Hartemink, 2000; Hashimoto *et al.*, 2000). Hartemink (2002) reports on the first known record from New Guinea (near Heldsbach, Morobe Province, September 1935, Clemens 128 at Rijksherbarium Leiden). The first collection in the Papua New Guinea National Herbarium (LAE) is from 1952 (NGF collection number 4719).

The species is now widespread in lowland New Guinea (Henty & Pritchard, 1988); however, the species did not become superabundant in the Madang area until the 1970s, according to local farmers. For instance, its vernacular name in Amben language is *Na Independens* (Independence Tree), to mark its appearance around 1975 when Papua New Guinea attained independence (Petir *et al.*, 1998). As noted by Hartemink (2002), the species is not mentioned in the survey of New Guinean vegetation by Paijmans (1976), perhaps indicating that it had not become widespread in the early 1970s.

Piper aduncum is a small tree. It is by far the most successful woody invader in Papua New Guinea. It invades early stages of rainforest succession, developing in abandoned gardens arising from swidden (slash-and-burn) agriculture, or after natural disturbance, such as in natural forest gaps, landslides and river banks swept by floods. *Piper aduncum* often suppresses native pioneer dominants, such as *Macaranga* species, as it sometimes attains a cover of >75% (Leps *et al.*, 2002). In the young secondary vegetation on abandoned gardens, it was the most common of 171 species, comprising 21% of the basal area (based on 25 quadrats, 400 m² each; J. Leps, unpubl. data).

Piper umbellatum is also of a Neotropical origin, introduced to and now widely distributed in Asia (Jaramillo & Manos, 2001). The oldest collections in Bogor Herbarium are from 1896 (Java) and 1908 (Philippines). The time of arrival to New Guinea is not known. The oldest New Guinea specimen was collected in 1933 during the Archbold Expedition (Brass collection number 3796) during some of the first intensive botanical exploration of the island. The alien status in Asia and Africa of this widely distributed species was disputed (Verdcourt, 1996; Yongqian *et al.*, 1999), but recent molecular analysis demonstrated its Neotropical origin (Jaramillo & Manos, 2001). *Piper umbellatum* is a large herb or sub-shrub which grows in open secondary vegetation. It is usually not very

common and unlike *P. aduncum* it does not suppress the local vegetation.

The South Pacific islands include approximately 40 native species of *Piper* (Jaramillo & Manos, 2001). All native *Piper* in the study area are climbers so, unfortunately, it was not possible to compare alien and native *Piper* of similar growth form. The most common species, *Piper macropiper*, was selected for the study. Unlike the two alien species, it grows both in secondary and primary forests. *Piper macropiper* is widespread in Southeast Asia and Malesia (Chew, 1972).

Insect sampling

The study was situated in lowland evergreen rainforests (>150 species of woody plants per hectare; Laidlaw *et al.*, in press) in Madang Province, Papua New Guinea. The average annual rainfall in this area is 3558 mm, with a moderate dry season from July to September; and mean air temperature is 26.5 °C (McAlpine *et al.*, 1983). Fieldwork was concentrated in primary and secondary forests near Baitabag, Ohu, and Mis Villages (145°41–48'E, 5°08–14'S, ≈0–200 m).

All externally feeding caterpillars (Lepidoptera), including leaf rollers and leaf tiers, were collected by hand from the foliage of *P. aduncum*, *P. umbellatum*, and *P. macropiper*. All species were sampled continuously for a period of 13 months, from October 2000 to November 2001. Sampling amounted to 3300 m² of foliage area examined for *P. aduncum*, 2500 m² for *P. umbellatum*, and 2300 m² for *P. macropiper*. Sampling was performed mostly by parataxonomists (Basset *et al.*, 2000).

In the laboratory, each caterpillar was provided with fresh leaves of the plant species it was collected from and reared to an adult whenever possible. Only the specimens that fed were considered in the analyses. Caterpillars and adults were assigned to morphospecies and the latter were verified by specialist taxonomists and identified as far as possible. The morphospecies thus correspond to species, except that some of them have not been formally described and named. Taxonomic methods and classification used are detailed in Holloway *et al.* (2001). Vouchers are deposited in the Smithsonian Institution (Washington) and the National Agricultural Research Institute (Port Moresby).

The taxonomic circumscription of this target group of herbivores was suitable for ecological analysis as caterpillars represented >95% of species, individuals, and biomass of all holometabolous larvae feeding externally on the foliage (Novotny *et al.*, 2002a).

Data analysis

Caterpillar data from the two alien species of *Piper* were compared with analogous data on caterpillar assemblages feeding on 69 native species of woody plants from 45 genera

and 23 families (listed in Novotny *et al.*, 2002a). This selection included 15 *Ficus* species and one *Artocarpus* species (Moraceae), six *Macaranga* species and nine species representing other Euphorbiaceae genera, four *Psychotria* species and 12 species representing other Rubiaceae genera, three *Syzygium* species (Myrtaceae), *Piper macropiper*, and 18 species representing other families from the major lineages of flowering plants. Further, species from various parts of the successional gradient were represented. Their successional preferences were measured as the biomass (basal area) maximum along the successional gradient created by swidden agriculture, from abandoned gardens to young secondary, old secondary, and primary forests (see Leps *et al.*, 2001 for details). Species with optima in the first two stages were denoted as pioneers in this study.

Caterpillars were collected from the same study sites, using identical sampling protocols as in the present study (Novotny *et al.*, 2002a,c). Each plant species was sampled for a 12-month period during 1995–2002. The resulting data included 35 025 caterpillars from 531 species, providing a solid basis for comparison. The data on caterpillar assemblages were obtained by sampling 1500 m² of foliage per plant species. For comparative analyses, *Piper* data were reduced to this sample size by random removal of some samples.

Host specificity was quantified as the variance of the species' distribution among 23 hosts, each from a different family. Lloyd's index $L = 1 + (S_x^2 - \bar{X})/\bar{X}^2$, where S_x^2 and \bar{X} are variance and mean of the sample, was used as this index and is considered to be the best way of standardising variance with respect to the mean (Leps, 1993). Only species represented by at least 10 individuals were used for this analysis, in order to reduce dependence of L on species abundance. The L value is minimal for an equitable distribution among hosts (i.e. indiscriminate polyphagy) and increases with unevenness among hosts (i.e. host specificity). Each caterpillar assemblage was characterised by the average L calculated for all species feeding on a particular host. All parameters characterising caterpillar assemblages are reported as median (1st–3rd quartile).

Similarity between assemblages from different hosts was characterised by the percentual similarity index, $PS = 100 \sum \min(a_i, b_i)$, where a_i and b_i are dominance values of species i in samples from hosts a and b , defined as the number of individuals of species i divided by the total number of individuals in a sample. The index ranges from 0 (no common species) to 100 (dominance values of all species are identical). Each caterpillar assemblage was characterised by an average PS calculated from 22 comparisons with assemblages from different plant families. Assemblages from hosts with congeneric species included into the study (*Ficus*, *Macaranga*, *Psychotria*, and *Syzygium*) were also characterised by average PS calculated from all available comparisons (1–14, depending on the host genus) with assemblages from the same genus. PS was used because it is insensitive to rare species, which are very difficult to sample in tropical insect communities (Novotny & Basset, 2000).

Similarity relationships between assemblages were also explored by detrended correspondence analysis using $\log(N+1)$ transformed abundance data, down-weighting of rare species, and detrending by segments options in Canoco software (ter Braak & Smilauer, 2003).

Results

The number of caterpillar species feeding on *P. aduncum* (32 species) and *P. macropiper* (13 species) is not total, as neither species accumulation curve reached an asymptote (Fig. 1). In contrast, the species accumulation curve for *P. umbellatum* levelled off at 45 species, indicating that the samples were representative. Both alien species of *Piper* had relatively high species richness (29 species per 1500 m² of foliage on *P. aduncum* and 36 species on *P. umbellatum*) in comparison with native assemblages, which had a median of 23 (15–33) species per 1500 m² of foliage. In contrast, *P. macropiper* assemblage was species-poor (10 species).

The composition of Lepidoptera species on the three *Piper* species (Table 1) was dominated by the tribes Boarmiini (Geometridae: Ennominae) and Archipini (Tortricidae: Tortricinae), which are mostly polyphagous. There were a few species of other subfamilies of Geometridae (Geometrinae, Larentiinae, and Sterrhinae), as well as one species of Olethreutinae (Tortricidae). Lymantriidae and Psychidae were well represented, also likely to be polyphagous. Fewer species of Crambidae (Pyraustinae) and Noctuidae (Acontiinae, Catocalinae, Eriopinae, Hadeninae, Plusiinae), and one species each of Arctiidae (Arctiinae), Gelechiidae, Immidae, Lecithoceridae, Limacodidae, and Nymphalidae (Charaxinae) were recorded. Pyraloidea (including Crambidae) and Noctuoidea were dramatically under-represented relative to the total number of

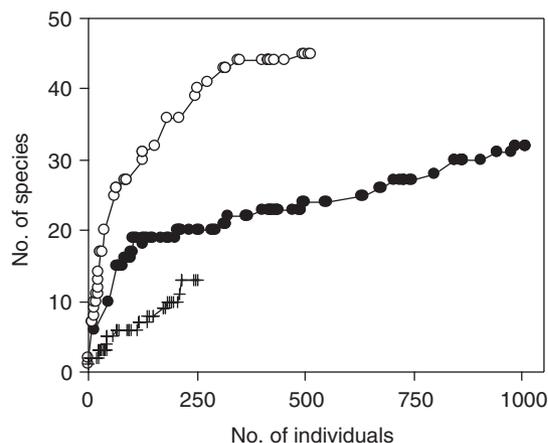


Fig. 1. Species-accumulation curves for caterpillars feeding on *Piper aduncum* (●), *P. umbellatum* (○), and *P. macropiper* (+). Individual samples are amalgamated in the sequence as they were collected from 26 October 2000 to 8 November 2001.

species of the various families known to occur in the Madang area.

The density of caterpillars on *P. aduncum*, 592 caterpillars per 1500 m² of foliage, was high in comparison with the median density of 431 (305–732) caterpillars on the native hosts. It was also close to median density of 656 (463–1060) caterpillars for pioneer species. The density on *P. umbellatum* (265 caterpillars) and *P. macropiper* (197 caterpillars) was comparably low. *Piper umbellatum* had a higher species richness than predicted from the caterpillar density of native assemblages, while the species richness on *P. aduncum* was close to that expected for native species (Fig. 2). The *P. macropiper* assemblage was markedly impoverished.

The *P. aduncum* assemblage was dominated by *Herpetogramma* species near *licarsisalis* (Walker) (Crambidae, Pyraustinae) (Fig. 3), which represented 48% of all individuals (Table 1). In contrast, 11 species (34%) were collected as single individuals (singletons). This dominance structure was statistically indistinguishable from that typical for native assemblages, which were characterised by median dominance of the most common species, 48 (34–70)%, and the median percentage of singletons, 44 (36–50)% (Fig. 4). In contrast, the dominance structure of the other two *Piper* assemblages was highly unusual. The *P. umbellatum* assemblage was dominated by two equally common *Adoxophyes* species (Tortricidae), each of them representing only 9% of the assemblage. This was the lowest dominance amongst all 71 assemblages studied. The *P. macropiper* assemblage represented an opposite extreme as a single species (*Craspedosis ovalis* Warren, Geometridae; Fig. 3) represented 93% of the entire assemblage, the third highest dominance found among the assemblages studied (Table 1).

Among the 59 caterpillar species that colonised one or both alien *Piper* species, eight species were not found on any native plant species among the 69 species sampled and with no hosts reported in Robinson *et al.* (2003). The species with unknown host range on native vegetation represented 13% of species and 50% of individuals on *P. aduncum* and 11% of species and 8% of individuals on *P. umbellatum* (Fig. 5). Notably, 488 individuals of *Herpetogramma* near *licarsisalis* were collected on *P. aduncum* but not on any of the 70 other plants studied (Table 1).

Forty-four other species were feeding on native hosts other than Piperaceae, and 11 of them were also feeding on native *P. macropiper*; two remaining species were not found on native hosts in this study but were reported from numerous host families in the literature (Robinson *et al.*, 2003). No native *Piper* specialists, feeding on *P. macropiper* but not on other native host families, colonised alien *Piper* species. In particular, 233 individuals of *Craspedosis ovalis* were collected on *P. macropiper* but none were found on alien *Piper* species.

Caterpillars colonising alien *Piper* species were often generalists feeding on several native families (Table 1). While only 3% from the local pool of species feeding on a single native plant family also colonised alien *Piper* species, virtually all (92%) generalist species feeding on >10 families did so (Fig. 6). The average host specificity of caterpillar

Table 1. Composition of caterpillar assemblages from *Piper aduncum* (Pa), *P. umbellatum* (Pu), and *P. macropiper* (Pm). Fam – the number of host families other than Piperaceae recorded at the study sites; FamR – the number of host families worldwide recorded by Robinson *et al.* (2003), the numbers including Piperaceae are marked by an asterisk. Note that the sampling effort was not identical among the hosts.

| Species | Family | Pa | Pu | Pm | Fam | FamR |
|---|----------------|-----|----|----|-----|------|
| <i>Herpetogramma</i> sp. nr. <i>licarsisalis</i> (Walker) | Crambidae | 488 | 0 | 0 | 0 | 0 |
| <i>Adoxophyes thoracica</i> Diakonoff | Tortricidae | 103 | 44 | 1 | 13 | 0 |
| <i>Adoxophyes tripselia</i> (Lower) | Tortricidae | 81 | 38 | 2 | 12 | 0 |
| <i>Adoxophyes nebrodes</i> Meyrick ¹ | Tortricidae | 66 | 30 | 0 | 11 | 0 |
| <i>Adoxophyes</i> sp. | Tortricidae | 35 | 44 | 0 | 11 | 0 |
| <i>Homona mermerodes</i> Meyrick | Tortricidae | 32 | 30 | 0 | 11 | 3 |
| <i>Adoxophyes</i> sp. <i>templana</i> complex | Tortricidae | 27 | 20 | 1 | 15 | 0 |
| <i>Adoxophyes</i> n. sp. | Tortricidae | 26 | 17 | 0 | 15 | 0 |
| Unidentified sp. PSYC005 [no adult reared] | Psychidae | 23 | 16 | 0 | 17 | 0 |
| <i>Adoxophyes fasciculana</i> (Walker) | Tortricidae | 21 | 12 | 0 | 14 | 28 |
| <i>Amblychia angeronaria</i> Guenee | Geometridae | 21 | 3 | 0 | 0 | 0 |
| Unidentified sp. PSYC021 [no adult reared] | Psychidae | 20 | 13 | 0 | 3 | 0 |
| <i>Spodoptera litura</i> (Fabricius) | Noctuidae | 14 | 12 | 0 | 0 | 74 |
| Unidentified sp. PSYC022 [no adult reared] | Psychidae | 10 | 2 | 2 | 2 | 0 |
| <i>Cleora repetita</i> Butler | Geometridae | 8 | 9 | 1 | 6 | 7 |
| <i>Dysgnathia nigropunctata</i> (Bethune-Baker) | Tortricidae | 6 | 7 | 0 | 2 | 0 |
| <i>Eucyclodes absona</i> (Warren) | Geometridae | 6 | 0 | 0 | 2 | 0 |
| <i>Homona trachyptera</i> Diakonoff | Tortricidae | 5 | 2 | 0 | 7 | 6 |
| <i>Homona</i> nr. but not <i>salacanis</i> (Meyrick) | Tortricidae | 4 | 2 | 0 | 8 | 2 |
| <i>Ophiorrhada deceptor</i> Diakonoff | Tortricidae | 3 | 0 | 0 | 1 | 0 |
| <i>Eumeta variegata</i> (Snellen) | Psychidae | 2 | 11 | 0 | 10 | 29* |
| <i>Scythropiodes</i> sp. nr. <i>perissa</i> (Diakonoff) | Lecithoceridae | 1 | 38 | 6 | 5 | 0 |
| <i>Moca congrualis</i> (Walsingham) | Immidae | 1 | 16 | 0 | 13 | 0 |
| <i>Scopula castissima</i> Warren | Geometridae | 1 | 10 | 0 | 1 | 0 |
| <i>Isotenes</i> sp. nr. but not <i>miserrana</i> (Walker) | Tortricidae | 1 | 5 | 1 | 2 | 0 |
| Unidentified sp. PSYC023 [no adult reared] | Psychidae | 1 | 1 | 2 | 1 | 0 |
| Unidentified sp. CRAM074 [no adult reared] | Crambidae | 1 | 0 | 1 | 1 | 0 |
| Unidentified sp. GEOM107 | Noctuidae | 1 | 0 | 0 | 0 | 0 |
| <i>Arctornis</i> sp. nr. <i>intacta</i> Walker | Lymantriidae | 1 | 0 | 0 | 3 | 0 |
| <i>Olene</i> sp. | Lymantriidae | 1 | 0 | 0 | 4 | 0 |

Table 1. Continued.

| Species | Fam | Pa | Pu | Pm | Fam | FamR |
|--|--------------|------|------|------|-----|------|
| <i>Chrysodeixis dinawa</i> (Bethune-Baker) | Noctuidae | 1 | 0 | 0 | 0 | 0 |
| Unidentified sp. TORT031 [no adult reared] | Tortricidae | 1 | 0 | 0 | 1 | 0 |
| <i>Spilosoma niceta</i> Stoll | Arctiidae | 0 | 41 | 0 | 4 | 0 |
| Unidentified sp. GEOM127 [no adult reared] | Geometridae | 0 | 32 | 0 | 0 | 0 |
| <i>Hyposidra talaca</i> Walker | Geometridae | 0 | 28 | 0 | 11 | 30 |
| <i>Ectropis bhurmitra</i> (Walker) | Geometridae | 0 | 6 | 0 | 12 | 30* |
| Unidentified sp. LYMA009 [no adult reared] | Lymantriidae | 0 | 4 | 0 | 4 | 0 |
| <i>Hyposidra</i> sp. probably <i>talaca</i> Walker | Geometridae | 0 | 3 | 0 | 4 | 0 |
| Unidentified sp. TORT055 | Gelechiidae | 0 | 3 | 0 | 1 | 0 |
| <i>Nacoleia</i> sp. nr. <i>obliquialis</i> Hampson | Crambidae | 0 | 2 | 0 | 0 | 0 |
| <i>Eois</i> sp. | Geometridae | 0 | 2 | 0 | 1 | 0 |
| Unidentified sp. LYMA057 [no adult reared] | Lymantriidae | 0 | 2 | 0 | 0 | 0 |
| <i>Adoxophyes</i> sp. TORT155 | Tortricidae | 0 | 2 | 0 | 1 | 0 |
| <i>Macrothyma sanguinolenta</i> (Diakonoff) | Tortricidae | 0 | 2 | 0 | 1 | 0 |
| <i>Thalassodes</i> (s.l.) <i>albifusa</i> (Warren) | Geometridae | 0 | 1 | 2 | 2 | 0 |
| <i>Homodes tomolybda</i> Meyrick | Thyrididae | 0 | 1 | 1 | 6 | 1 |
| <i>Idiophantis</i> probably n. sp. | Gelechiidae | 0 | 1 | 0 | 0 | 0 |
| <i>Eucyclodes albilauta</i> (Warren) | Geometridae | 0 | 1 | 0 | 1 | 0 |
| <i>Paradr-omula xylinoipa</i> Meyrick | Geometridae | 0 | 1 | 0 | 4 | 0 |
| Unidentified sp. LIMA008 [no adult reared] | Limacodidae | 0 | 1 | 0 | 9 | 0 |
| Nygmini sp. LYMA033 | Lymantriidae | 0 | 1 | 0 | 1 | 0 |
| Unidentified sp. LYMA055 [no adult reared] | Lymantriidae | 0 | 1 | 0 | 2 | 0 |
| <i>Tiracola plagiata</i> (Walker) complex | Noctuidae | 0 | 1 | 0 | 0 | 31* |
| <i>Polyura pyrrhus</i> (L.) | Nymphalidae | 0 | 1 | 0 | 1 | 1 |
| <i>Craspedosis ovalis</i> Warren | Geometridae | 0 | 0 | 233 | 0 | 0 |
| Unidentified sp. NOCT072 [no adult reared] | Hesperiidae | 0 | 0 | 1 | 1 | 0 |
| Individuals total | | 1012 | 518 | 254 | | |
| Species total | | 32 | 45 | 13 | | |
| Foliage area sampled (m ²) | | 3300 | 2500 | 2300 | | |

*Matches Diakonoff's figure of female *A. nebrodes* (Diakonoff, 1952), but the association with males is not clear.

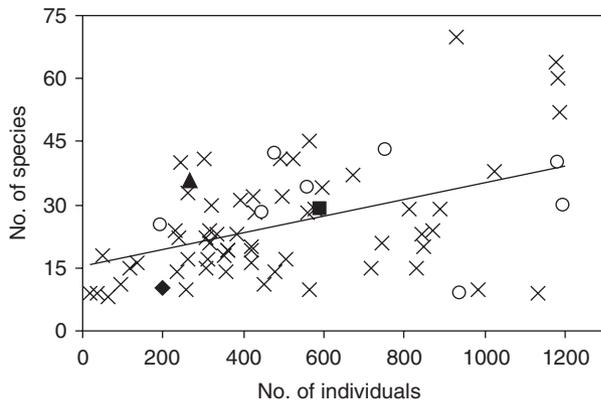


Fig. 2. Number of caterpillar specimens and species collected from 1500 m² of foliage from *Piper aduncum* (■), *P. umbellatum* (▲), *P. macropiper* (◆), and other native hosts (○ – pioneer species, × – others). A linear regression was fitted for all native hosts.

species in the assemblages on *P. aduncum* ($L = 8.4$) and *P. umbellatum* ($L = 6.4$) was therefore lower than the median value for native hosts $L = 15.5$ (11.1–19.6), as well as the value for *P. macropiper* ($L = 16.5$).

The high proportion of generalists in caterpillar assemblages on the alien *Piper* species resulted in their higher average similarity with assemblages feeding on native plants from different families ($PS = 5$ for *P. aduncum* and 8 for *P. umbellatum*) than the median value for assemblages from the native allofamilial hosts $PS = 1$ (0.5–2). The role of generalist species was also demonstrated by detrended correspondence analysis of *Piper* species and 22 plants representing different families (Fig. 7), as the two alien species were not outliers with respect to native species in the ordination space defined by first two axes. Further, they were not grouped with other assemblages feeding on basal angiosperms (APG II, 2003), which are the hosts most closely related to *Piper* in the samples.

Likewise, the assemblages on *P. aduncum* and *P. umbellatum* were similar to one another ($PS = 43$) as both hosts were colonised from the same pool of predominately generalist species. In contrast, the complete absence of native *Piper* specialists among caterpillars colonising *P. aduncum* and *P. umbellatum* resulted in their low similarity with *P. macropiper* ($PS = 2$ and 5 respectively). This was a markedly lower similarity than the median $PS = 38$ (32–43) for assemblages from native congeneric hosts.

Discussion

Despite their recent origin, the caterpillar assemblages feeding on the two alien *Piper* species have attained species richness comparable to that of native hosts. In particular, the assemblage from *P. aduncum*, which has originated during the past 50 years in the study area, has species richness, density, and dominance structure indistinguishable from assemblages feeding on native hosts. This result supports

the observation that herbivore assemblages may arise rapidly on novel hosts (Strong, 1974a,b; Strong *et al.*, 1977; Kennedy & Southwood, 1984); however, it should be noted that the externally feeding herbivores studied here are more likely to rapidly colonise alien hosts than endophages (Strong *et al.*, 1984). Certain specialised guilds, such as those exploiting flowers or seeds, may be even completely absent in recently colonised areas (Zwölfer, 1988; Memmott *et al.*, 2000) and introduced plants may suffer lower levels of damage even from generalist herbivores (Wolfe, 2002).

The abundance of herbivores and the damage they inflict on their *Piper* (and other) hosts are largely independent of the species richness of their assemblages (Marquis, 1991; Basset & Höft, 1994). The impact of herbivores on alien species is often low, relative to their native congeners, at least in the temperate zone where data are available (Keane & Crawley, 2002). Caterpillars tend to be the most important leaf-chewing herbivores on tropical vegetation in terms of biomass and plant damage (Barone, 1998; Novotny *et al.*, 2002a) and their abundance on *P. aduncum* was similar to that on other native species, including pioneers from the habitats which are invaded by *P. aduncum*. The absence of a difference between native and alien trees in the abundance of caterpillars was found also in Britain (Yela & Lawton, 1997).

In an earlier study at Wau, Papua New Guinea, *Piper plagiophyllum* K. Sch. & Laut., a native tree common in montane rainforests, hosted only 10 caterpillar species (Basset, 1996; Basset *et al.*, 1996). Of the 10 species, only three were reared to adults (Basset *et al.*, 1996: 176): *Craspedosis aurigulta* Warren (originally misidentified as *Milionia* sp.) (Geometridae: Ennominae), *Ectropis bhumitra* Walker (a widespread polyphagous pest) (Geometridae: Ennominae), and *Isotenes* sp. (but not the same as the Madang species) (Tortricidae: Tortricinae). Thus, the fauna at Wau shows general similarities to that of *Piper* at Madang.

There are few other studies focusing on *Piper*-feeding Lepidoptera for comparison. In Costa Rica, the assemblage is dominated by the geometrid subfamily Larentiinae, rather than the Ennominae that dominate in Papua New Guinea (Marquis, 1991). Studies of the related *Macropiper excelsum* (Forst. f.) Miq. in New Zealand (Hodge *et al.*, 1998) show the dominant herbivore is *Cleora scriptaria* (Walker) in the Ennominae (Boarmiini).

There are no published host records for the genus *Craspedosis* (e.g. Robinson *et al.*, 2003 and G. Robinson, pers. comm.), but with the recognition of one species on *Piper* at Madang, and another at Wau, it is possible that *Craspedosis* is a *Piper* specialist.

The reasons for a notably low species richness of caterpillars on the native *P. macropiper* can only be speculated. It is a herbaceous climber with locally low biomass, unlike all other plants studied; however, *P. plagiophyllum*, a native tree common in montane rainforests, was also species-poor (Basset, 1996; Basset *et al.*, 1996). It is therefore possible that *Piper* has a species-poor caterpillar fauna in New Guinea, possibly also elsewhere.

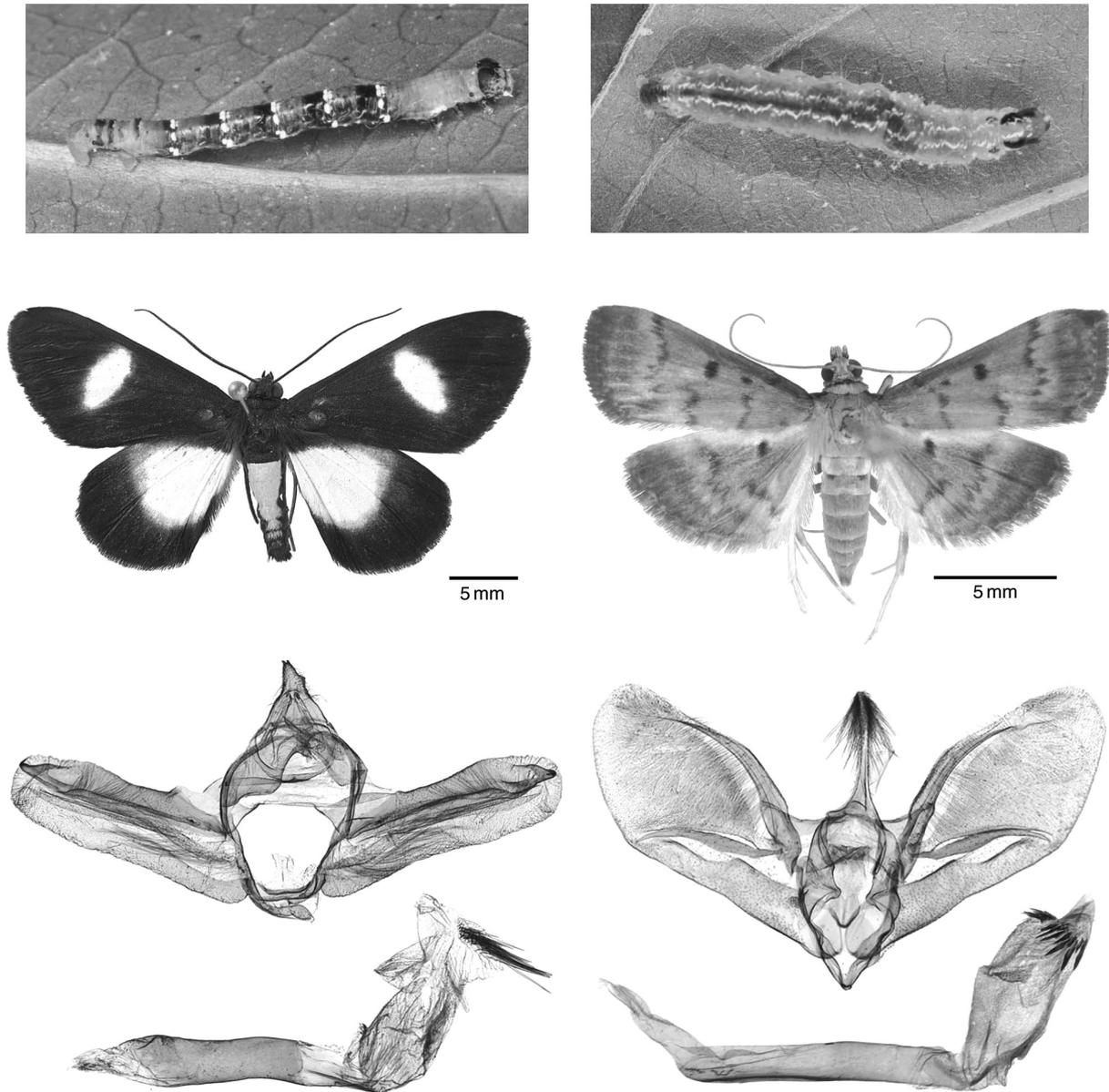


Fig. 3. Larva, adult, and male genitalia of *Herpetogramma* sp. near *licarsialis* (Walker) from *Piper aduncum* (right) and *Craspedosis ovalis* Warren from *Piper macropiper* (left).

Unsurprisingly, polyphagous species tend to be better colonisers of alien plants than specialists (Strong *et al.*, 1984; Zwölfer, 1988; Fraser & Lawton, 1994). This was true in this study, as generalists were more likely to colonise alien *Piper* species than species feeding on one or several native families. Low host specificity on alien *Piper* hosts can be transient as herbivore assemblages on novel plants can rapidly develop towards higher specialisation (Andow & Imura, 1994).

It is notable that virtually all widely polyphagous species were able to colonise alien *Piper*, which lends support to the suggestion by Lawton and Strong (1981)

that *species exhaustion* is a better description of the process of rapid colonisation of alien plants by herbivores than *species saturation*. *Piper aduncum* has diverse secondary metabolites (Orjala *et al.*, 1994), that none the less failed to stop generalists from colonising it. In contrast, many generalist species feeding on the two alien species of *Piper* were not found on *P. macropiper*. It is not clear whether they cannot feed on it, or use it so rarely that they are difficult to find. Note that the sampling of the caterpillar assemblage from *P. macropiper* was incomplete, as indicated by the non-asymptotic species accumulation curve.

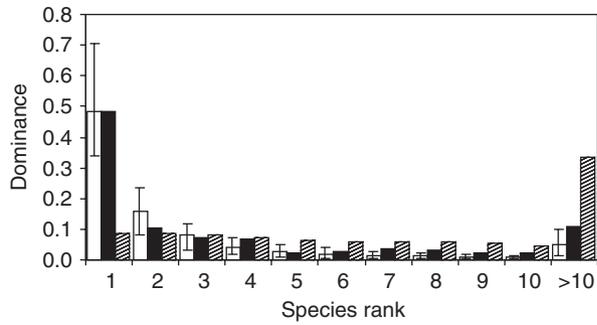


Fig. 4. Dominance in caterpillar assemblages from native hosts, *Piper aduncum* and *P. umbellatum*. The proportion of individuals is represented by the 1st, 2nd, ..., 10th most abundant species in an assemblage, and by all remaining species combined (rank >10) is reported for 69 native assemblages (medians with 1st and 3rd quartiles; empty bars), *Piper aduncum* (solid bars), and *P. umbellatum* (hatched bars). Dominance distribution in *P. umbellatum* is significantly different from native species, while the distribution in *P. aduncum* is not (Kolmogorov–Smirnov tests, $P=0.05$).

Low overlap between herbivore assemblages from the native and alien *Piper* species was rather unexpected, as it contrasted with large overlaps typical among caterpillar faunas among native congeneric hosts, as well as results from temperate studies on congeneric alien and native plants (e.g. Sampson, 1994; Burki & Nentwig, 1997). One possible factor is the different growth form of the native and alien species. All native *Piper* species in the study area were climbers, which may have influenced the composition of their herbivore assemblages. *Piper macropiper* was also the only climber among the 69 native

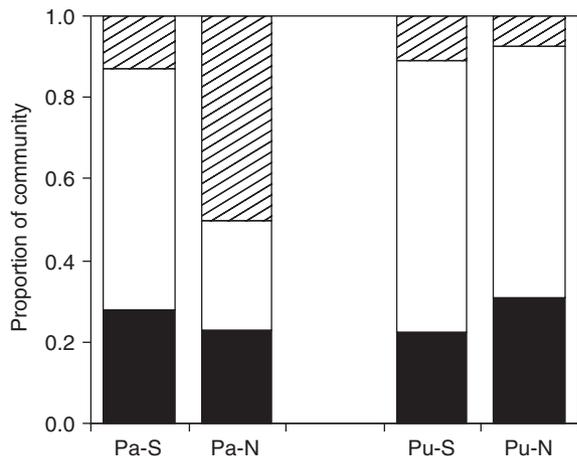


Fig. 5. Native hosts of caterpillar species colonising invasive species of *Piper*. The proportion of species (S) and individuals (N) in the assemblages from *Piper aduncum* (Pa) and *P. umbellatum* (Pu), which were also found on *P. macropiper* and plants from other families (black), only plants from other families (white), or which were not found on any native plants (hatched). Note that no species feeding on alien *Piper* hosts also fed only on the native *P. macropiper*.

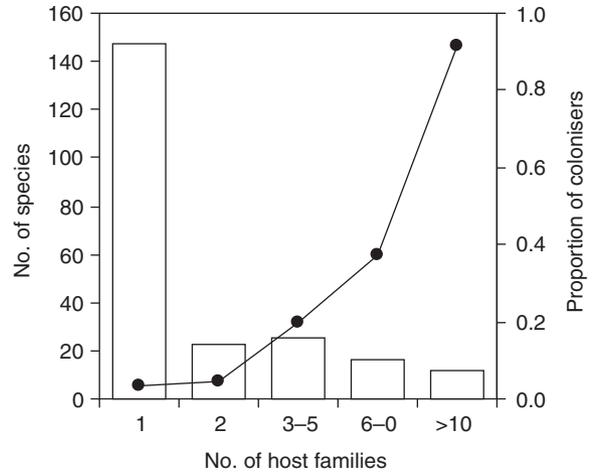


Fig. 6. Relationship between host specificity and probability of colonising alien *Piper* species. The number of caterpillar species feeding on 1, 2, 3–5, 6–10, and >10 native plant families (bars) and the proportion of these species feeding also on one or both alien species of *Piper* (line) is reported for all species collected from native vegetation as ≥ 10 individuals.

plants studied, and its caterpillar assemblage was unusual in several respects, particularly by its low abundance, low species richness, and high dominance by a single species. This proposition requires further research, but growth form has been identified as an important influence

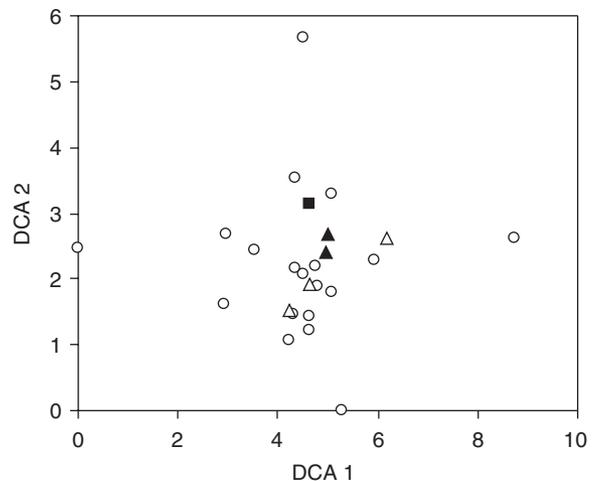


Fig. 7. Detrended correspondence analysis (DCA) of caterpillar assemblages from alien *Piper aduncum* and *P. umbellatum* (\blacktriangle), native *P. macropiper* (\blacksquare) and other native hosts, each from a different family (basal angiosperms – \triangle , other lineages – \circ). Basal angiosperms (from left to right): *Kibara* cf. *coriacea* (Monimiaceae), *Eupomatia laurina* (Eupomatiaceae), *Myristica* cf. *sepicana* (Myristicaceae); outliers (with DCA 1, DCA 2 coordinates): *Mantilloa* cf. *plurijuga* (Caesalpiniaceae) (0, 2.5), *Ficus wassa* (Moraceae) (8.7, 2.6), *Premna obtusifolia* (Verbenaceae) (5.3, 0), and *Psychotria micralabastra* (Rubiaceae) (4.5, 5.7); other species listed in Novotny et al. (2002a).

on herbivore assemblages (Ward *et al.*, 1995; Ødegaard, 2000).

The alien and native species were also phylogenetically rather distant within the genus *Piper* (Jaramillo & Manos, 2001) and may not share the same secondary metabolites, which are very diverse in *Piper* (Parmar *et al.*, 1997). This may restrict host plant ranges of herbivores to only certain species. For instance, none of the 19 species of Geometridae studied on 45 species of *Piper* at a Neotropical site fed on more than seven species (Marquis, 1991).

Caterpillar assemblages feeding on native trees are typically dominated by a single or few species while at once having numerous rare species (singletons). The dominant species are typically specialists, but it remains unclear what factors determine their identity and the extent of their dominance (Novotny & Basset, 2000; Novotny *et al.*, 2002c). The assemblage from *P. aduncum* conformed to this pattern. Its most common caterpillar species recruited from Crambidae, similar to the dominants of 18 out of the 69 native hosts studied (Novotny *et al.*, 2002c). On the native vegetation, Crambidae species are mostly specialised to a single plant genus, but able to feed on numerous congeneric hosts (Novotny *et al.*, 2002c). This pattern of host specificity would suggest one or, more likely, several *Piper* species as native hosts for *Herpetogramma* sp. near *licarsisalis*, the dominant on *P. aduncum*. In contrast to this expectation, the dominant species was not feeding on *P. macropiper*, and did not colonise the alien congener, *P. umbellatum*. The identification of *Herpetogramma* sp. near *licarsisalis* (Walker) (morphospecies CRAM066) is problematic. *Herpetogramma licarsisalis* was 'described from Sarawak but [is] widespread in tropical and subtropical Asia and in the islands of the western Pacific' although introduced to Hawaii (Munroe, 1989: 203) and southern Europe (Goater & Knill-Jones, 1999); however, this is a species complex that needs revision and existing synonymy of taxonomic names under *licarsisalis* cannot be trusted (see Shaffer & Munroe, 1989 for a parallel case). It may include a mixture of widely ranging and localised species. The study species here is very close to *licarsisalis* as figured by Clarke (1971:76), Yamana (1960: plate XLV), and Barrion and Litsinger (1987), but differs slightly in male genitalia and wing coloration (Fig. 3). It is also very similar to *Herpetogramma simillima* (Hampson), described from Fergusson Island, New Guinea. It did not match any of the Neotropical *Herpetogramma* species represented in the Smithsonian Institution or Natural History Museum (London). *Herpetogramma licarsisalis* of Barrion and Litsinger (1987) is considered oligophagous on grasses and sedges, although they offered few broad-leaved plants in feeding trials. It is believed that the material represents a native species in the *licarsisalis* complex, although it cannot be conclusively proven that this is not an immigrant pest species possibly introduced to New Guinea along with its host.

Non-asymptotic accumulation of species with increasing sample size and numerous singleton species were other features of *P. aduncum* assemblage shared with those on native hosts. Singletons can be either polyphagous species that are

rare on a marginal host plant, or genuinely rare specialists adapted to survival on their host at low densities (Novotny & Basset, 2000). The identical dominance patterns in native hosts and *P. aduncum*, where there has been insufficient time for adaptation by herbivores to the host, lend support to the former hypothesis.

In conclusion, the results suggest that a species-rich assemblage of caterpillars resembling indigenous assemblages in dominance structure (but not in species composition) can rapidly originate from the existing species pool in lowland rainforests, even on a recently established tree species. Some of the key characteristics of the novel assemblages, such as the predominance of generalist species and the large number of singleton species, can be explained using knowledge of the native herbivore assemblages. Other features of these assemblages, however, such as the low overlap with the native *Piper* species and a strong dominance of the *P. aduncum* assemblage by a single caterpillar species, which is neither a wide generalist nor a *Piper* specialist, remains puzzling. The dominance structure of the caterpillar assemblage on *P. aduncum* is identical with that on the native vegetation, but the reasons for this particular assemblage structure remain unexplained.

Whitmore (1991) commented that 'Why introduced [woody] pioneers rarely supplant native ones [in perhumid tropics] despite possession of all the useful attributes is to me a deep mystery.' *Piper aduncum*, however, does supplant native pioneers, and the reasons for its success remain unclear (Leps *et al.*, 2002). At any rate, it cannot be attributed to reduced herbivory, at least not that caused by caterpillars, as the abundance of caterpillars on *P. aduncum* is comparable to that on native pioneers.

The study of convergence between the structure of the novel assemblages recently formed on *P. aduncum* and *P. umbellatum* in New Guinea with those from the hosts' native geographical range could provide additional information on the importance of local species pools in determining assemblage structure and perhaps also shed light on some of the problems discussed above. Unfortunately, the only study of Neotropical caterpillars feeding on these two hosts (Marquis, 1991) was limited to Geometridae on *P. aduncum* and did not find any species feeding on this host. There are only two Lepidoptera species reported from *P. aduncum* in Robinson *et al.* (2003). Janzen and Hallwachs (2003) report 24 species from Costa Rica, mostly from HesperIIDae (nine species), Noctuidae (five species) and Nymphalidae (four species). These results indicate a very different taxonomic structure of caterpillar assemblages from that in New Guinea, although it should be noted that HesperIIDae were collected with higher sampling effort than other families so that their prominence was probably a sampling artefact. Lee Dyer (pers. comm.) reports an *Eois* sp. (Geometridae) feeding on *P. aduncum* in La Selva (Costa Rica).

The study of herbivorous assemblages on alien plants is still seen primarily as a practical exercise of finding suitable agents for biological control, while its potential to advance understanding of the assembly rules for biological

communities is largely ignored. Records of caterpillars feeding on *P. aduncum* in various habitats at different latitudes and altitudes across its native range, as well as various continental and island areas invaded by this species, could serve as a model for the ecology of biological invasions as was the analogous data set from *Pteridium aquilinum* for community ecology (Lawton *et al.*, 1993).

Acknowledgements

We thank parataxonomists J. Auga, W. Boen, M. Damag, S. Hiuk, B. Isua, R. Kutil, M. Manumbor, M. Mogia, K. Molem, and E. Tamtiai for assistance. Numerous collectors, acknowledged elsewhere, assisted with insect collections. Bishop Museum (Honolulu), Natural History Museum (London), as well as the Bogor and Lae herbaria, provided critical facilities for taxonomic work. W. Takeuchi and K. Fiedler provided valuable comments on the manuscript. Numerous colleagues provided taxonomic help, particularly W. Takeuchi, K.V.N. Maes, D.R. Davis, J.D. Holloway, J. Brown, M. Horak, G. Robinson, K. Sattler, M. Shaffer, M.A. Solis, K. Tuck, and M. Vaswani. The project was funded by U.S. National Science Foundation (DEB-94-07297, 96-28840, 97-07928, and 02-11591), Czech Academy of Sciences (A6007106, Z 5007907), Czech Ministry of Education (ES 041), Czech Grant Agency (206/99/1115), Darwin Initiative for the Survival of Species, Otto Kinne Foundation, and National Geographic Society (5398-94).

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Accepted 12 May 2003