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Biogeography of the Genus *Caleta* FRUHSTORFER (Lepidoptera, Lycaenidae)

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Abstract The genus *Caleta* FRUHSTORFER contains 9 species. Some endemic species occur in Borneo, Sulawesi and the Philippines. Results of the cladistic analysis and distribution patterns of *Caleta* species indicate that Sulawesi has a weak biogeographical association with Borneo, as well as a strong link to Mindanao.

Key words: Lycaenidae; *Caleta*; biogeography; cladistic analysis; Wallacea.

Introduction

The genus *Caleta* FRUHSTORFER, [1922] belongs to Polyommatinae, Lycaenidae, being distributed from India to New Guinea. Males are often encountered while settled on moist forest paths and stream banks. However, females are rarely seen and the host plants of most species are unknown except for a record of *Zizyphus* sp. (Rhamnaceae) as a foodplant of *C. roxus* (GODART) in the Philippines (FUKUDA, 1980) and *Z. oenoplia* on which *C. elna* (HEWITSON) was reared in the Malay Peninsula (ELIOT, 1992).

Biogeographical data on the islands of the Oriental Region have been gathered for the distribution patterns and cladistic analyses of Lepidoptera (e.g. HOLLOWAY, 1990; VANE-WRIGHT, 1991). Lepidoptera, especially butterflies are a very suitable group for biogeographical analysis of the Oriental Region because their distribution data are abundant, including collecting data from thousands of small islands in the region.

The genus *Caleta* seems to be suitable for biogeographical study because it contains some endemic species to Sulawesi, Borneo, Mindanao and New Guinea. In other words, their distribution patterns are well defined with few 'noises'. Biogeographical relationships of areas, especially around Sulawesi, are discussed here on the basis of cladistic analysis of *Caleta* species.

Taxonomy

Caleta is one of the four genera of the *Upolampes* section (HIROWATARI, 1992), being associated with *Upolampes* BETHUNE-BAKER, 1908, *Discolampa* TOXOPEUS, 1929 and *Pistoria* HEMMING, 1964. The *Upolampes* section is characterized by the absence of the brachium and the relatively short phallus in the male genitalia. The monotypic genus *Pistoria* shows close relationship with *Caleta* in the male genitalia, but it has been treated as a distinct genus because of its unique venation and the barrel-shaped phallus (TITE, 1962).

Caleta has not been revised since FRUHSTORFER (1922) established the genus. TOXOPEUS (1929) erected *Pycnophallium* for *roxus* and *elna* without any morphological basis. Subsequently, HEMMING (1964) selected *roxus* as the type species. ELIOT (1973) included *Pycnophallium* in the *Upolampes* section. However, the taxon *Pycnophallium* is untenable because it only represents one of the species groups of *Caleta* judging from the external characters. In fact, *Caleta* is claerly defined by the ventrally well-fused valvae and the name is widely used, but *Pycnophallium* is not adopted by recent workers (D'ABRERA, 1986; SEKI *et al.*, 1991; ELIOT, 1992).

The classification of *Caleta* adopted here is that of HIROWATARI (1992) which mostly accepted the work of TAKANAMI (1989).
The following lists show the species and their distributions.

1. *Caleta decidia* (HEWITSON, [1876]), (Fig. 16)
Lycaena decidia HEWITSON, [1876], Ill. exot., Butts., 5, pl. 1, fig. 4, India.
Distribution: India, Myanmar, Thailand.

2. *Caleta elna* (HEWITSON, [1876]), (Figs. 15, 17B, 19 F–H)
Lycaena elna HEWITSON, [1876], Ill. exot. Butts., 5, pl. 1, fig. 8, Java.
Distribution: India, Myanmar, Thailand, Peninsular Malaya, Sumatra, Java, Borneo, Philippines.

3. *Caleta caleta* (HEWITSON, [1876]) (Figs. 1–2, 17 C, 19 I–J)
Lycaena caleta HEWITSON, [1876], Ill. exot. Butts., 5, pl. 1, fig. 1, Celebes.
Distribution: Sulawesi (Menado, Doluduo, Papayato, Donggala, Palolo, Palopo); Peleng (Peleng).

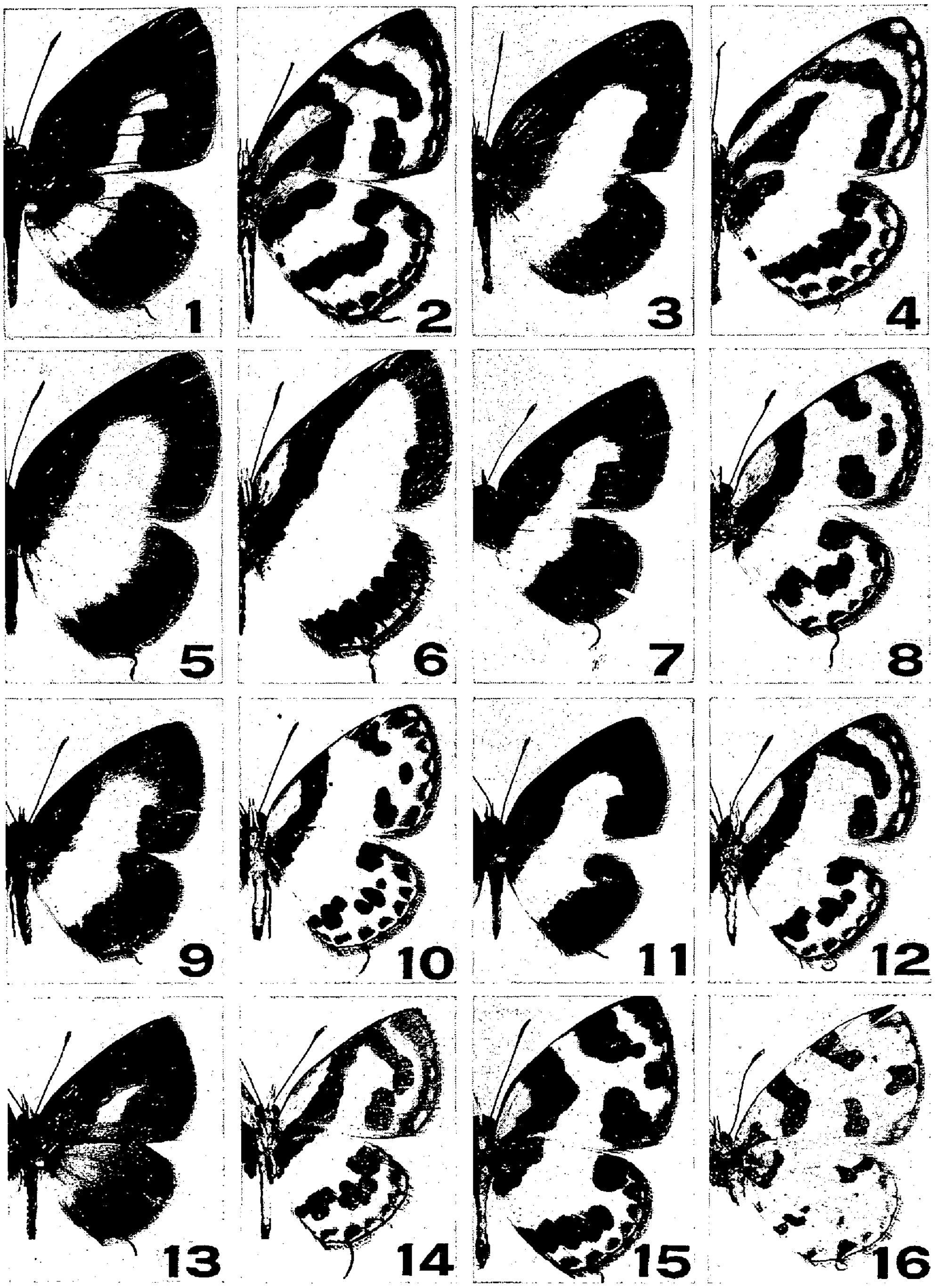
4. *Caleta argola* (HEWITSON, [1876]) (Figs. 3–4, 19 K)
Lycaena argola HEWITSON, [1876], Ill. exot. Butts., 5, pl. 1, fig. 7, Mindanao.
Distribution: Mindanao (Tandag Surigao, Cagayan, Masara Main, Mt. Apo, Davao); Basilan (Maloong); Negros (Mt. Silay).

According to TAKANAMI (pers. comm.), *C. argola* has been collected on Mt. Silay, Negros Island, which appears to be important for biogeographical analysis within the islands of the Philippines.

5. *Caleta roxus* (GODART, [1824]) (Figs. 11–12, 18 A–D)
Polyommatus roxus GODART, [1824], Ency. meth., 9: 659, Kangean, West Java.
Distribution: India, Myanmar, Thailand, Peninsular Malaya, Sumatra, Java, Philippines.

6. *Caleta celebensis* (STAUDINGER, 1889) (Figs. 7–8, 18 I–L)
Castalius roxus var. *celebensis* STAUDINGER, 1899, Dt. ent. Z. [Iris], 2: 96, Sud Celebes.
Distribution: Sulawesi (Menado, Doluduo, Dumoga-Bone National Park, Biromaru, Palolo, Palopo).

7. *Caleta manovus* (FRUHSTORFER, 1918) (Figs. 9–10, 18 E–H)
Castalius roxus manovus FRUHSTORFER, 1918, Tijdschr. Ent., 61: 34, Nord Borneo, Kina Balu.
Distribution: North Borneo (Mamut, Poring, Ranau, Keningau).



Figs. 1–16. Adults of *Caleta* spp. —— 1, 2, *C. caleta* (Hewitson), ♂, Palolo, Sulawesi; 3, 4, *C. argola* (Hewitson), ♂, S. Davao, Mindanao; 5, 6, *C. mindarus* (C. & R. Felder), ♂, Nabire, Irian Jaya; 7, 8, *C. celebensis* (Staudinger), ♂, N. Sulawesi; 9, 10, *C. manovus* (Fruhstorfer), ♂, Poring, N. Borneo; 11, 12, *C. roxus* (Godart), ♂, Cameron Highland, Malaysia; 13, 14, *C. rhode* (Hopffer), ♂, Bantimurung, S. Sulawesi; 15, *C. elna* (Hewitson), ♂, Bali; 16, *C. decidia* (Hewitson), ♀, Sri Lanka. 2, 4, 6, 8, 10, 12, 14, 15, 16: Undersides of the wings.

8. *Caleta rhode* (HOPFFER, 1871) (Figs. 13–14, 19 A–D)
   Lycaena rhode HOPFFER, 1871, Stett. ent. Ztg., 35: 27, Celebes.
   Distribution: Sulawesi, Lesser Sundas.
9. *Caleta mindarus* (C. & R. FELDER, [1865]) (Figs. 5–6, 19 E)
   Lycaena mindarus C. & R. FELDER, [1865], Reise Novara, (2): 286, pl. 33, figs. 13, 14, New Guinea.
   Distribution: New Guinea.

Morphological Characters and Cladistic Analysis

For cladistic analysis, 15 characters were selected (Table 1). The data matrix was analysed by the WAGNER Algorithm method and the shortest tree was estimated. Rooting of the cladogram and character polarities were determined by selecting the genus *Upolampes* as an outgroup (Table 2). The characters are described below with brief discussions on their polarities.

Head. As in all other members of the Polyommatinae, general structure of the head is constant and condition of the eyes provides little information (HIROWATARI, 1992). The labial palpus is 3-segmented, the second segment usually longest in the Polyommatinae. The relative length of the segments varies, but in *caleta* and *argola*, the third segment is apparently longer (more than 1.2 times as long as the first segment) than in other species of the genus (less than 0.8 times as long as the first). This is considered to be an apomorphic condition (character 3).

Wing venation. The bases of veins 10 (R_1) and 11 (Sc) are separate in *Upolampes* (Fig. 17 A) and in *decidia*, connate in *elna* (Fig. 17 B), and stalked in the other species (Fig. 17 C). The last condition is considered apomorphic (character 2). In *Pistoria*, the bases of veins 10 and 11 are stalked and veins 11 and 12

Table 1. Characters and their transformations.

1. Ventral portion of valvae: separate (0)→fused (1)
2. Forewing veins 10 (R_2) and 11 (R_1): separate or connate (0)→stalked (1).
3. Third segment of labial pulpus: short ($<0.8\times$first segment) (0)→long ($>1.2\times$first segment) (1).
4. Socius: rounded (0)→pointed (1)
5. *roxus*-type valval process: absent (0)→present (1)
6. Inner process of socius: absent (0)→present (1)
7. *mindarus*-type valval process: absent (0)→present (1)
8. Long bristles of valva: absent (0)→present (1)
9. Ventral dent of suprazonal sheath; absent (0)→present (1)
10. Process of sacculus: short (0)→long (1)
11. Serrate keel on dorsal surface of suprazonal sheath: absent (0)→present (1)
12. Phallus: short and cylindrical (0)→large, expanded at anterior portion (1)
13. Valval process: short (not beyond socius) (0)→long (beyond socius) (1)
14. Gnathos: absent (0)→present (1)
15. Valva: not expanded (0)→expanded laterally (1)

0: plesiomorphic; 1: apomorphic

Table 2. Character state matrix for *Caleta* spp.

Species	Characters*														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1. *decidia*	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0
2. *elna*	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0
3. *caleta*	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
4. *argola*	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
5. *roxus*	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0
6. *manovus*	1	1	0	0	1	1	0	0	0	0	0	0	1	0	0
7. *celebensis*	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0
8. *rhode*	1	1	0	0	0	1	1	0	0	0	0	0	0	1	0
9. *mindarus*	1	1	0	0	0	0	1	0	0	0	0	0	0	0	1
10. outgroup**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

* See text and Table 1.

** The genus *Upolampes* is selected as an outgroup.

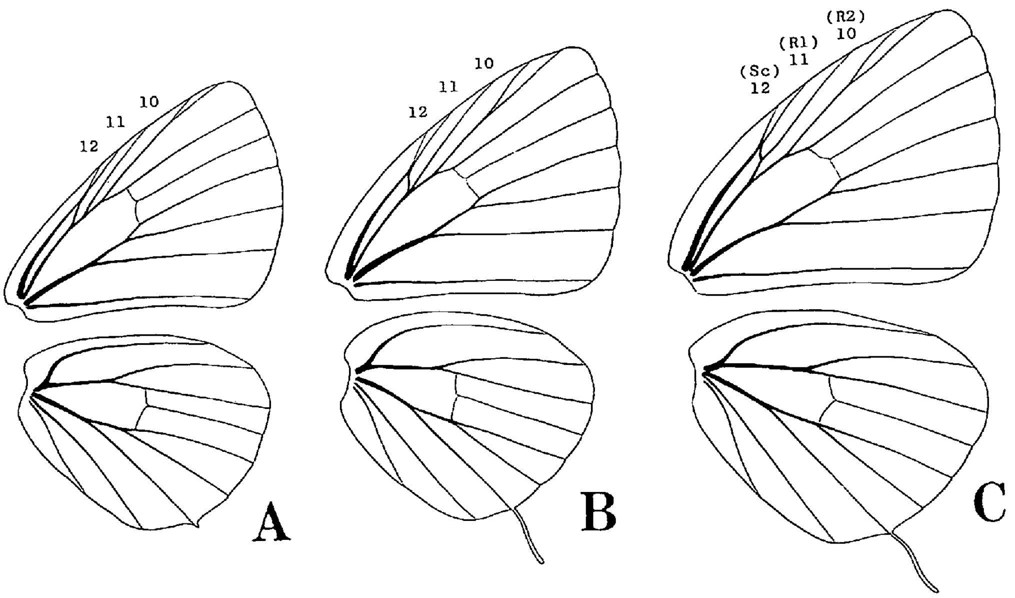


Fig. 17. Wing venations of the *Upolampes* section. —— A, *Upolampes evena* (HEWITSON), ♂, New Guinea; B, *Caleta elna* (HEWITSON), ♂, N. Borneo; C, *C. caleta* (HEWITSON), ♂, Sulawesi.

are anastomosed to the costa. This might represent a terminal condition of the transformation series of the veins of this group. If so, it is possible that *Pistoria nigropuncutata* BETHUNE-BAKER, 1908 shares a common ancestor with some *Caleta* species other than *decidia* and *elna*. Further study of this New Guinean species may partly affect the result of the present study, but no influence is expected on such biogeographical links as Sulawesi–Mindanao, and Sulawesi–Borneo disscussed below.

Male genitalia. The gnathos is usually absent in the tribe Polyommatini, but is exceptionally present in *rhode* (character 14, Fig. 19 B). The brachium is present in the most groups of the Lycaenidae, but absence of the brachium is one of the important characters of the *Upolampes* section. However, in *manovus*, *celebensis* and *rhode*, an inwardly-directed process, which is obviously different from the normal lycaenid brachium, is present on the inner lamina of the socius (character 6, Figs. 18 E–F; 18 I–J; 19 A–B). It has presumably been secondarily derived after a complete reduction of the brachium. The socius is usually semicircular and posterior margin is rounded in most lycaenid species, but in *caleta* and *argola*, it is triangular and pointed posteroventrally and this is apparently a synapomorphic condition (character 4, Fig. 19 I, K). The phallus is usually small and short, but in *roxus* it is large and expanded at the anterior portion (character 12, Fig. 18 C–D). In *elna*, a unique sclerite comprising a serrate keel is present on the dorsal surface of the suprazonal sheath (character 11, Fig. 19 G–H), and in *decidia* the ventral end of the suprazonal sheath is strongly sclerotized and grooved (character 9). The valvae are well fused with each other ventrally in all *Caleta* species, and this is a synapomorphic condition of the genus (character 1). In *mindarus*, the lateral wall of valva is well expanded (character 15). *Caleta* has two forms of valval process: a) *roxus*-type (*roxus*, *manovus*, *celebensis*) (character 5, Fig. 18 A, E, I) being posteroventrally-directed and upwardly gently curved (it is elongated beyond socius in *manovus*) (character 13); b) *mindarus*-type (*rhode*, *mindarus*) (character 7, Fig. 19, A, E) being posteriorly-directed and almost straight in lateral view. As TAKANAMI (1989) noted, the valval process of individuals of *rhode* from Flores is obviously shorter than that from Sulawesi. The valval process of individuals from Timor is much shorter than that from Flores. Similarly, a geographical cline is discernible in the length of the valval process in *mindarus*. It is shorter in Irian Jaya specimens than in those specimens from Papua New Guinea. More sophisticated analysis of the geographic variation of these taxa may provide useful information on the biogeography of the islands of the Lesser Sundas and New Guinea.

In *decidia*, long bristles, which are longer than the height of the ring, are present on the ventral area of the valva (character 8). The presence of an elongated process of the sacculus is unique to *elna* (character 10).

Female genitalia. From the limited amount of material available, it appears that the general structure of the genitalia (*i.e.*, shape of the corpus bursae, attachment point of the ductus seminalis, etc.) is constant in the *Upolampes* section. The shape of the genital plate appears useful for phylogenetic analysis, but sufficient material was not available for the present study.

Discussion

For a more precise understanding of areas of endemism, collecting localities of four species available to the author are plotted in Fig. 20. The area cladogram in

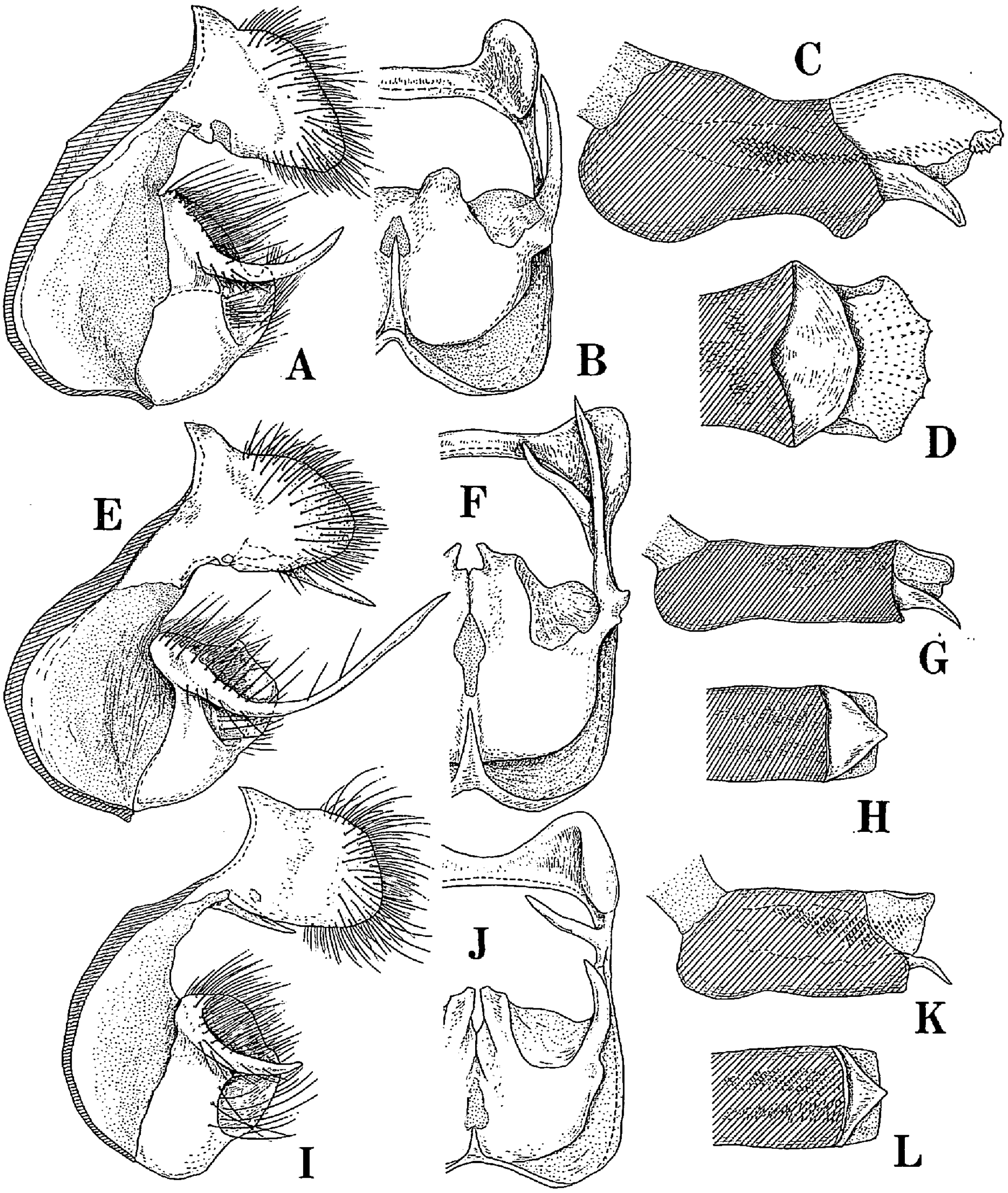


Fig. 18. Male genitalia of *Caleta roxus* (Godart), W. Malaysia (A–D), *C. manovus* (Fruhstorfer), N. Borneo (E–H) and *C. celebensis* (Staudinger), N. Sulawesi (I–L). —— A, E, I, Whole genitalia except phallus in lateral view; B, F, J, ditto, ventro-posterior view; C, G, K, phalli in lateral view; D, H, L, ditto, ventral view.

Fig. 21 was constructed from the cladistic analysis of *Caleta* species and their distributions. *Caleta caleta* and *argola* are confined to Sulawesi and Mindanao, respectively, and these two species were inferred as sister species. The two taxa are sometimes regarded as being conspecific (Fruhstorfer, 1918, 1922; D'Abrera,

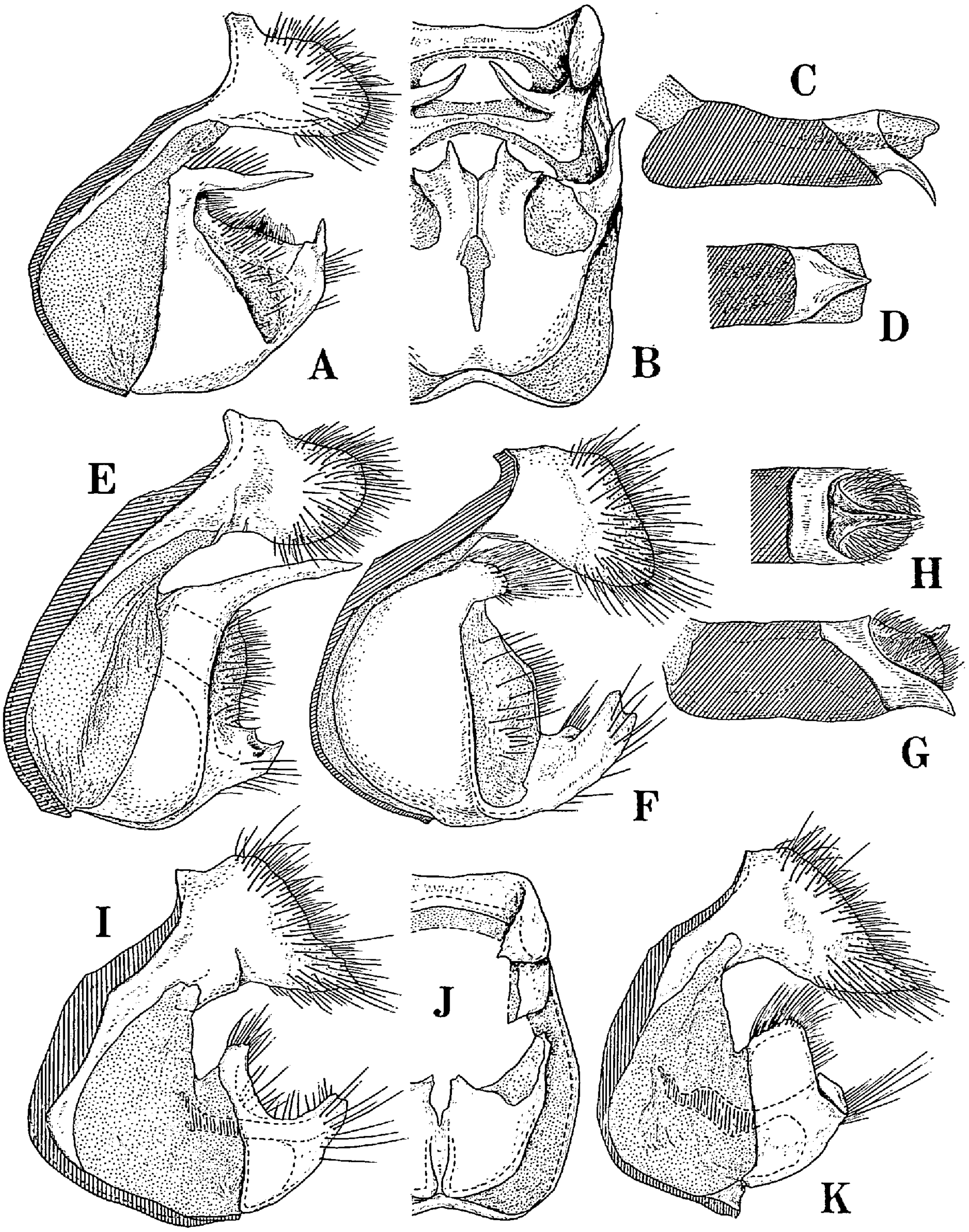


Fig. 19. Male genitalia of *Caleta rhode* (HOPFFER), S. Sulawesi (A–D), *C. mindarus* (C. & R. FELDER), Irian Jaya (E), *C. elna* (HEWITSON), Malaysia (F–H), *C. caleta* (HEWITSON), N. Sulawesi (I, J) and *C. argola* (HEWITSON), Mindanao (K). —— A, E, F, I, K, Whole genitalia except phallus in lateral view; B, J, ditto, ventroposterior view; C, G, phalli in lateral view; D, ditto, ventral view; H, ditto, dorsal view.

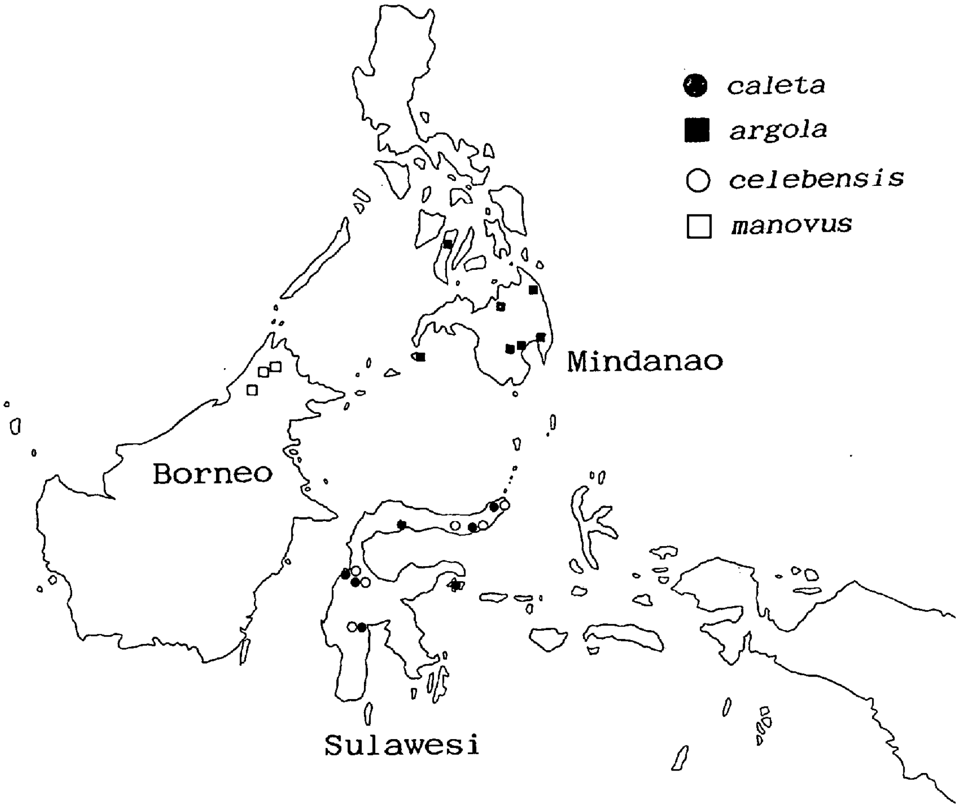


Fig. 20. Collecting localities of four endemic species of *Caleta*.

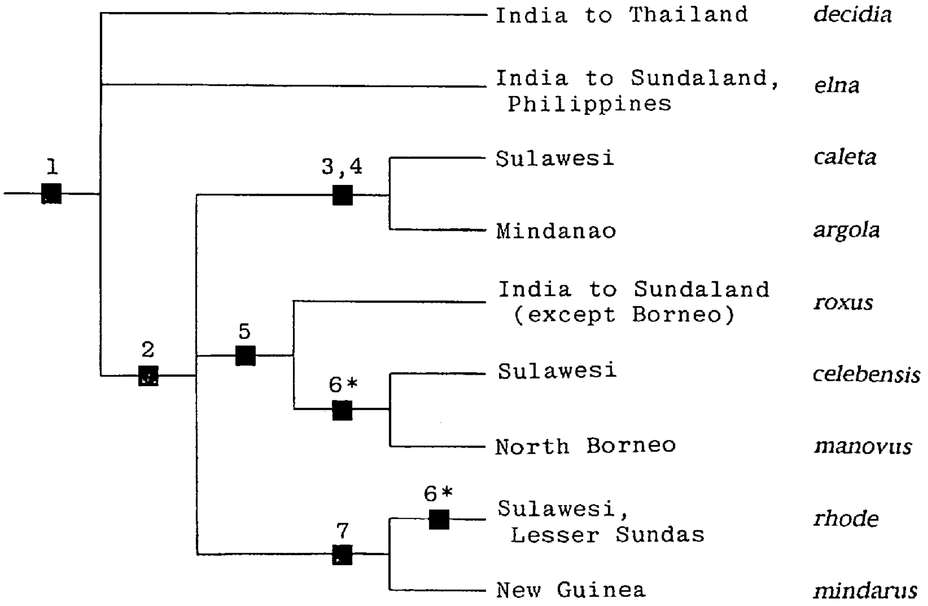


Fig. 21. Area cladogram for the genus *Caleta*.
* Character 6 is present independently in *celebensis*+*manovus* and in *rhode*.

1986) regardless of their external differences. In fact, their genital structure shows a close relationship between these two taxa and their monophyly is obvious. As a result, it is apparent that Sulawesi shares biogeographical associations with Mindanao.

In the Lepidoptera, a Sulawesi-Mindanao (or Philippines) link has been pointed out by many authors. For example, de JONG (1983, 1990) pointed out a Sulawesi-Philippine link from the phylogenetic relationships and unique distribution patterns of *Matapa* (Hesperiidae). HOLLOWAY (1987) indicated a Sulawesi-Philippine relationship from cladistic analyses and distribution patterns of *Besida* and subgenus *Erconholda* of *Phalera* (Notodontidae). HEPPNER (1989) figured the collecting data of *Ischnuridia virginella* (Tineidae), which is restricted to Sulawesi and Mindanao. CHIBA (1988, 1989) indicated the Sulawesi-Philippine link from the distributions of *Choaspes platini* and *Acerbas duris* complex (Hesperiidae). According to VANE-WRIGHT (1991), Sulawesi shows a 'strongest single link' to Mindanao than to any other 'surrounding regions', having a total of 12 butterfly species present only on Sulawesi and Mindanao.

It is possible to consider that these distribution patterns resulted from the same geological event. However, the geotectonic origins of this region are complex and disparate. In fact, the Malay Archipelago moth genera treated by HOLLOWAY (1990) provide several patterns of area cladograms. According to AUDLEY-CHARLES (1987), islands of South-east Asia formed part of eastern Gondwanaland. VANE-WRIGHT (1990) noted that 'A sequence of exchanges of these derived species, notably from the Philippines to Sulawesi, and from Sulawesi to the Moluccas, appears to have occurred. This has given some cohesion to the butterfly fauna of Wallacea, . . .' Inferred from *Caleta*, the Sulawesi-Philippine component seems to have been isolated for long term from surrounding islands, producing unique sister species: *caleta*+*argola*.

On the other hand, *celebensis* from Sulawesi, and *manovus* from North Borneo are inferred as sister species. However, their monophyly is weak because the inferred synapomorphy, occurrence of the inner process of the socius in these two species, is also present in *rhode*. If another less parsimonious tree containing monophyletic entities *manovus*+*celebensis*+*rhode* is proposed based on the hypothesis that the presence of the process is a synapomorphy of these taxa, interpretation of some biogeographical relationships should be altered. For example, Lesser Sundas-New Guinea relationship shown by the monophyly of *rhode* and *mindarus* would have to be rejected. A component of the distributions of *manovus*+*celebensis*+*rhode* is Borneo+Sulawesi+Lesser Sundas. This implies that there still remains Sulawesi-Borneo relationship. As VANE-WRIGHT (1991) noted, Sulawesi has only a weak relationship with Borneo. However, this does appear to exist based on the data given here.

It is possible to theorize an existence of the component of Sulawesi and Borneo. In fact, MICHAUX (1991) suggested that Mindanao, parts of Borneo, and western

Sulawesi 'form a single tectonic unit'. Some authors, such as KATILI (1978), suggested that Sulawesi and Borneo collided in the late Pliocene. KATILI postulated that the Makassar Strait evolved by the separation of Borneo and Sulawesi during the Quaternary. These hypotheses are not generally accepted (VANE-WRIGHT, 1991), but warrant further investigation. Although YATA (1989, 1990) attributed Sulawesi-Borneo relationship of the *tilaha* group of *Eurema* (Pieridae) to the result of a dispersal, this might reflect a relatively younger geological connection of Sulawesi and Borneo.

Area of endemism (HUMPHRIES & PARENTI, 1986) can be perceived not only from the occurrence of a species in a region, but also by the presence of a monophyletic group of organisms occupying the region. This analysis of *Caleta* has provided one of the important 'signals' for biogeographical analysis of Wallacea.

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