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THE PHYLOGENY AND ZOOGEOGRAPHY OF THE ENDEMIC GENERA OF THE HAWAIIAN PTEROMALIDAE (Hymenoptera: Chalcidoidea)[1]

By Carl M. Yoshimoto

B. P. Bishop Museum, Honolulu, Hawaii

Abstract: The Hawaiian Pteromalidae consist of 5 subfamilies and 30 genera, largely of world-wide distribution. Within the subfamily Miscogasterinae, there are 6 endemic genera including 3 new and unique genera which are confined to the Hawaiian Archipelago. A complex of 51 species of the endemic genera exhibits remarkable independent development. The ancestral form of the major evolutionary line is believed to have resembled the present genus *Mesolelaps* Ashmead which gave rise to 4 main lines of specialized groups. A discussion of the phylogenetic characters based on the interrelationship of the propodeum of each group are presented and characters other than the propodeum are supplemented for coherence.

Among the Hawaiian Chalcidoidea, the family Pteromalidae is probably the second most important parasite group and yet the least known because of the difficulty encountered in its classification. The tiny parasitic wasps measure from 0.8 to 3.5 mm in length, are usually metallic green to bluish in color, the head and thorax are densely and reticulately punctate, the tarsi are 5-segmented, and the parapsidal grooves are incomplete. Pteromalids are parasitic on various stages of a great variety of insects; some species are hyperparasites.

This study is an attempt to present the interrelationship between the natural affinities of the endemic genera of the Hawaiian Pteromalidae and their distribution with reference to the phylogenetic development.

The Hawaiian Archipelago extends 2400 kilometers across the Pacific and lies between 178°-154°W. Long. and 18°-28°N. Lat. The Islands are volcanic and are surrounded by great ocean depths. The Archipelago is divided into two main groups—the windward and leeward islands. The highest mountain peak is Mauna Kea, with an altitude of 4135 meters. The island of Kauai is the oldest of the group. The islands are progressively younger to the east with the island of Hawaii the youngest. Wentworth (1927) and Stearns (1946) believed that the main islands evolved during Pliocene or in more recent times and that the windward group is of the Pleistocene period.

The presence of endemic pteromalids in the Hawaiian Islands indicates that these minute parasitic wasps were able at some time to disperse for long distances over ocean bar-

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riers by one of four methods as discussed by Darlington (1938, 1957), Zimmerman (1942, 1948) and Gressitt (1956, 1958, 1961). The empirical data gathered through the Bishop Museum air dispersal program in the Pacific area during the past nine years indicate that small insects with low specific gravity and less compact bodies such as parasitic Hymenoptera are frequently caught in trap nets (Gressitt 1961). Many of the chalcidoids have been collected in nylon nets at sea, some of them as far as 500 kilometers away from the nearest land mass (Yoshimoto & Gressitt 1960, 1961, 1962; Yoshimoto, Gressitt & Mitchell 1962; Harrell & Yoshimoto 1964).

The dispersal route of the endemic ancestral stock of Hawaiian pteromalids is presumed to have been by way of New Guinea-Philippines eastward across the Pacific (Yoshimoto & Ishii 1965). However, it is possible for Neotropical elements to disperse into a westerly air current, then into the upper atmosphere where air currents may carry them across the Pacific, though the distance from Hawaii to the nearest continental land mass may exceed 3200 kilometers over a water barrier.

The first treatment of the Hawaiian Chalcidoidea appeared in *Fauna Hawaiiensis* (1901) by Ashmead listing seven genera and 13 species. Perkins (1910) added three genera and three species to the fauna. In 1924, Timberlake listed 24 introduced species of pteromalids new to the islands and in 1925 erected two new genera for endemic Miscogasterinae. Other investigators since *Fauna Hawaiiensis* have added new records of introduced species in Hawaii.

This present study of pteromalids includes a total of 30 genera and over 60 species of named and undescribed species. The subfamilies are enumerated as follows: Spalangiinae with 1 genus and 6 species; Cerocephalinae with 2 genera and 2 species; Tridyminae with 2 genera and 3 species; Miscogasterinae with 12 genera and over 28 species; and Pteromalinae with 13 genera and 17 species. The endemic pteromalids are in the subfamily Miscogasterinae with a total of 6 genera, 3 of which are new to science, 15 named species and over 34 undescribed species.

Much of the biological data came from O. H. Swezey, who did much rearing of native insects. Other entomologists in Hawaii also contributed to our knowledge of the biology of the local pteromalids.

During recent years I have used a 2-cycle, 1 horse-powered portable gasoline-operated suction machine for collecting chalcids. This mechanical method has proven superior to the conventional insect net in quantity of catch. The number of chalcids collected by this machine is approximately 10 times as much in comparison to sweeping.

The phylogenetic chart of endemic genera of Hawaiian pteromalids (fig. 1) shows that a possible relationship exists in accordance with their natural affinities. The ancestral form gave rise to four main lines containing the specialized groups. There are certain characters common to several related groups. The ancestral stock is assumed to resemble closely the present genus *Mesolelaps* Ashmead, based largely on the large propodeum and second abdominal tergite, and the moderately large thorax.

Perhaps the ancestral stock which resembles the genus *Mesolelaps* was once commonly found on all of the Hawaiian Islands, but since the coming of man, immigrant animals and plants and loss of native forest in lowlands, the endemic biota today has been pushed to the highlands. The range of the ancestral stock may have been from littoral areas

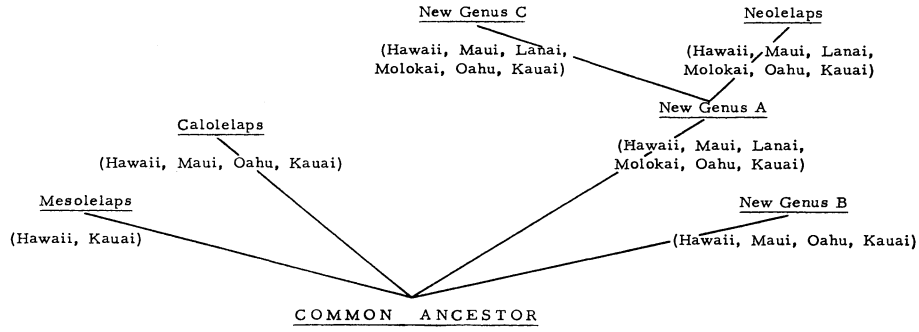

Fig. 1. Phylogeny of endemic Hawaiian genera of Pteromalidae.

to 1200 meters in elevation.

In spite of intensive fieldwork in the Hawaiian Islands in recent years, only 20 specimens of *Mesolelaps* were collected on the island of Hawaii; from the island of Kauai, despite its being the oldest island, only a single specimen has been collected. Because of insufficient data on the male genitalia, cyto-genetics, biologies and immature stages, I am unable to discuss them here. However, future findings on these subjects may present some interesting evidences to the problem of phylogeny.

From the ancestral stock evolved six genera, *Calolelaps* Timberlake (=*Stictolelaps* Timberlake), *Neolelaps* Ashmead, a new genus A (=*Toxeuma* of Ashmead, not of Walker), based on *Toxeuma hawaiiensis* Ashm.; a new genus B (*=*Astichus* of Ashmead, not of Forester) based on *Astichus cyanea* Ashm.; a new genus C based on a new species; and *Mesolelaps* Ashmead, which features the reduction of the second abdominal tergite, antennae, petiole, median carina and lateral areas of the propodeum and to some extent body size. It is probable that there were several introductions of the ancestral type in Hawaii. Evidence indicates that under optimum ecological conditions, profuse speciation evolved in the endemic genera as shown in new genus A, *Neolelaps* and *Calolelaps*.

Mesolelaps possesses a weak median carina and netted lateral carinae of the propodeum, moderately large hind coxa, petiole thick, 2× as long as broad and antennae with thickened funicle segments.

In *Calolelaps*, the median carina of the propodeum is reduced and becomes somewhat indistinct, the surface has a thimble-like punctation and is somewhat rugose, and antennal funicle segments are fluted with a distinct club at apex.

The lateral and the median carinae of the propodeum in the new genus A are thickened and their lateral areas smooth and highly polished. The funicles segments of the antennae are reduced in length, while the club is thicker in width. The male antennae of the funicle segments are reduced, and they appear filiform rather than the usual fluted to thickened segments.

The propodeum of *Neolelaps* is somewhat elongate with the apex of the neck region sub-

* Ashmead (1901) misidentified *Astichus cyanea* and placed it with the family Eulophidae. It was later keyed to tribe Tridymini, subfamily Tridyminae, (Yoshimoto 1965). However, under careful reexamination this species should be placed with the Miscogasterinae because of its petiolate abdomen.

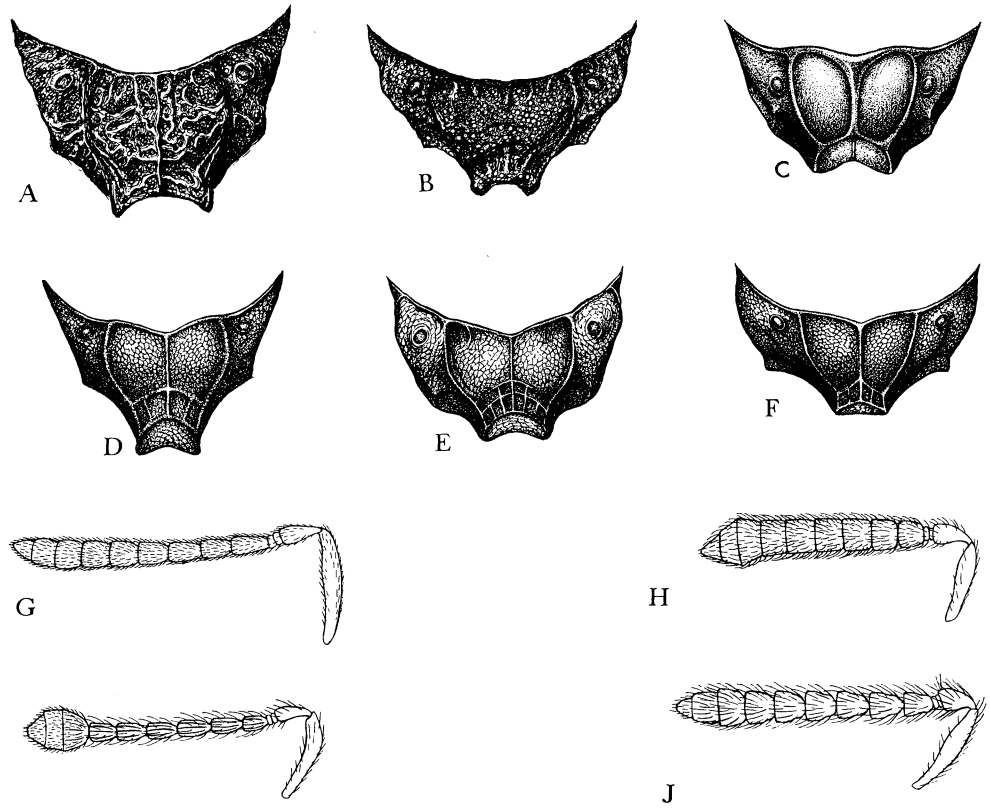

Fig. 2. Propodeum: A, *Mesolelaps*; B, *Calolelaps*; C, new genus A; D, *Neolelaps*; E, new genus C; F, new genus B. Antennae: G, *Neolelaps*; H, *Calolelaps*; I, *Neolelaps*; J, new genus C.

cylindrical; the surface is finely reticulate. The funicle segments of the female are fluted and the antennal club is distinct; the male antenna is filiform and resembles that of new genus A. About half of the species possess either a fuliginous spot or band below the stigmal vein or a second spot or band near the apical margin of the forewing. The remainder of the species are without any markings on the forewing.

The mesonotum and the scutellum are flattened and appear broad dorsally in new genus C. The propodeum is broadened at its sides; the median carina is thin, and the apex resembles that of *Neolelaps* but is slightly broader. The male antenna is filiform, resembling that of *Neolelaps*.

In new genus B, the characters resemble several genera. The antenna is similar to that of *Neolelaps*. On the other hand, the thorax is slightly flattened dorsally and resembles that of new genus C. The propodeum is related to that of new genus A. However, the flattened vertex of the head, the projection-like structure located on both sides of the lateral margins of the compound eyes and the maculate forewings completely differentiate this group from the others.

The monotypic offshoot of *Mesolelaps* is extremely rare in collections with only 35 speci-

mens having been collected, largely from one locality on the island of Hawaii and one lone specimen from Kauai. *Calolelaps*, allied to *Mesolelaps* with 5 species and possibly 2 undescribed species, is also rare, each species represented by a single isolated record except for 2 species which are commonly found on Oahu and Kauai. New genus B, a small unique group from the highlands and probably related to new genus A is considered to be independently derived from the same ancestral stock. In recent fieldwork, approximately 2,000 specimens of Chalcidoidea were collected during 11-16 September 1965, at Kokee, Kauai and only a single specimen of new genus B was found in the collection. New genus A the most divergent member of the group as compared from other genera gave rise to a greater variety of species including 6 known and several undescribed species. Members of this group are represented in all of the windward islands. *Neolelaps*, an offshoot of new genus A (Zimmerman 1948) gave rise to 2 species and possibly over 3 undescribed species. And another offshoot from the new genus A line, new genus C with a single species is abundant and widely known from all of the windward islands. The three genera, new genus A, *Neolelaps* and new genus C are more closely related to each other than *Calolelaps* to new genus A.

There are definitely 3 other forms which I have not put into genera because of few specimens at hand; beside these forms, there are several intermediate forms relating to the six known genera.

In the study of Micronesian Pteromalidae, I found no relationship with the Hawaiian forms, though there is a possibility of uncovering a related genus in Palau or the Bonin Islands.

It is interesting to note that there are no records of endemic pteromalids from Niihau, Kaula or the leeward islands. This brings to mind three main points: 1, the absence of pteromalids is due to inadequate collecting; 2, though pteromalids were present at one time on the islands, they have completely disappeared in recent times due to extinction

Table 1. Distributional list of endemic Hawaiian Pteromalidae.

	Number of species										
	Hawaii	Maui	Lanai	Molokai	Oahu	Kauai	Niihau	Nehoa	Laysan	Midway	Kure
Miscogasterinae											
Mesolelaps (2 species)	1	–	–	–	1	1	–	–	–	–	–
Calolelaps (6 species)	1	1	–	–	1	3	–	–	–	–	–
Neolelaps (24 species)	12	14	6	8	14	19	–	–	–	–	–
New Genus A (13 species)	9	6	3	4	7	6	–	–	–	–	–
New Genus B (5 species)	2	2	–	2	2	3	–	–	–	–	–
New Genus C (1 species)	1	1	–	1	1	1	–	–	–	–	–

of their hosts; 3, as Usinger pointed out (1942), the number of species decreases progresively from large to small islands with the number steadily decreasing toward the extreme leeward end of the chain, except for Oahu (because of more collectors there).

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