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PAPUA NEW GUINEA AND FIJI, WITH NOTES ON
LARVAL CHARACTERS OF THE OLD WORLD AND
OCEANIAN POLISTINAE (HYMENOPTERA: VESPIDAE)

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**MATURE LARVAE OF SOME POLISTINE WASPS
FROM PAPUA NEW GUINEA AND FIJI, WITH
NOTES ON LARVAL CHARACTERS OF THE
OLD WORLD AND OCEANIAN POLISTINAE
(HYMENOPTERA: VESPIDAE)***

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Abstract

The mature larvae of three *Polistes* and two *Ropalidia* species from Papua New Guinea and Fiji are described. Some larval characters of the Old World and Oceanian Polistinae which seem to be of taxonomic or phylogenetic importance are listed and briefly discussed. RICHARDS' dendrogram of the subfamily Polistinae is critically examined. The position of *Ropalidia* in his phylogenetic tree may be unnatural.

Introduction

It has been demonstrated that the larval characters are useful and important in vespid classification at supraspecific levels and sometimes even at species level (REID, 1942; Sk. YAMANE, 1976). RICHARDS (1978b) presented a key to the subfamilies of the Vespoidea and to the genera of the Polybiini for the mature larvae, and used some larval characters in reconstructing the phylogeny of the subfamily Polistinae. However, the study on the vespid larvae is still very insufficient, especially on the species of the Asian and Oceanian regions. This paper deals with the morphology of mature larva in three *Polistes* and two *Ropalidia* species from Papua New Guinea and Fiji. In this connection some larval characters of the Old World and Oceanian polistine wasps are discussed in relation to their phylogenetic relationships. RICHARDS' (1978b) dendrogram showing the relationships of polistine genera is critically examined.

***Polistes olivaceus* Degeer**

(Fig. 1)

Specimens examined: Some mature larvae, Nov. 27-28, 1977, Voua, Viti Levu Is., Fiji, S. YAMANE leg. (adults determined by Dr. Sôichi YAMANE).

Head. Cranium brownish except for frons and clypeus, deeply emarginate

* Studies on the vespid larvae. III. by Sk. YAMANE.

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posteriorly, with sparse, small punctures and associated very minute setae. Mid-cranial sulcus weak but clearly visible. Frons not separated from the epicranium and clypeus by distinct lines. Antenna relatively large, with 3 to 5 very small sensillae. Temporal band wide but not very long; outer one-third slightly reticulate. Anterior tentorial pit distinct, located on epistomal sulcus and ventral to antenna. Postoccipital sulcus developed; pleurostomal sulcus weak; epistomal sulcus developed but lacking in upper portion. Frons and clypeus defined by their pale colour. Labrum transverse,

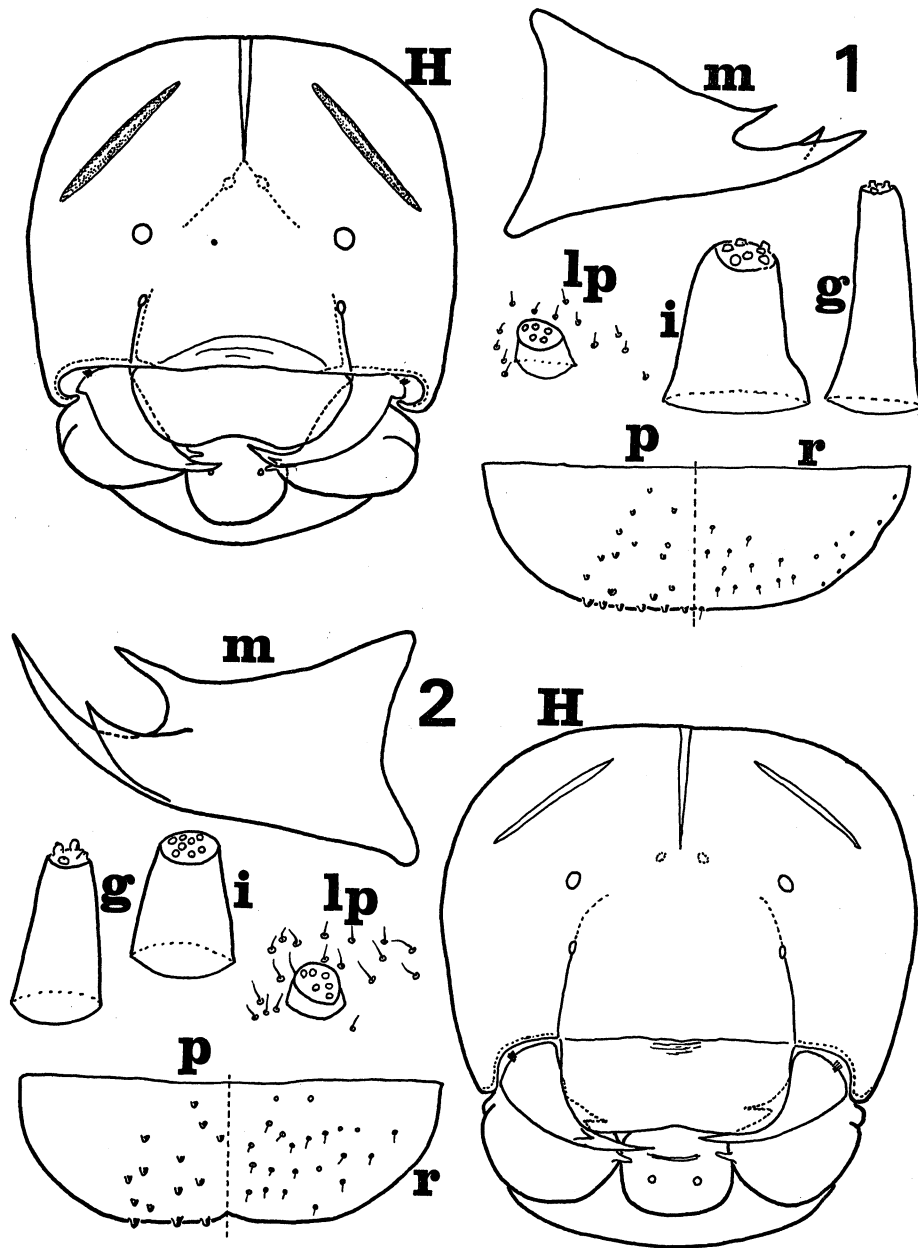


Fig. 1. Larval head of *Polistes (Megapolistes) olivaceus*. H, head in frontal view; m, mandible; r, labrum; p, palate; i, maxillary palp; g, galea; lp, labial palp and setae around it.
 Fig. 2. Larval head of *Polistes (Megapolistes) tepidus malayanus*. (Symbols as in Fig. 1.)

gently emarginate ventrally, with several short setae; palate with small conical sensillae. Mandible wide at base, apically pointed, with a subsidiary tooth near apex and another acute tooth well set back from apex. Maxillary lobe spherical, well developed, with sparse setae; maxillary palp thick, with 7 minute sensillae at top; galea slender than maxillary palp, with 3 sensillae. Prelabium rounded-rectangular, with a pair of palps which have 5 to 6 minute sensillae; around each labial palp more than 10 setae; the remaining part of prelabium with sparse setae or punctures alone. Postlabium also with sparse setae.

Body. Integument with numerous transverse microtubercles, sparse punctures and their associated setae which are very minute. Paired oval areas on the thoracic sternites and pleural lobes well defined. First spiracle largest but less than twice as large as the rest; 2nd spiracle smaller than 3rd; atrium simple.

According to RICHARDS' key (1978a) mandible has only one supplementary tooth, and paired oval areas on meso- and metathoracic pleural lobes are invisible in the material from Seychelles.

Polistes tepidus malayanus Cameron

(Fig. 2)

Specimens examined: Some mature larvae, Dec. 10, 1973 to Jan. 28, 1974, Waitape, Papua New Guinea, T. OKAZAWA leg. (adults determined by Prof. J. VAN DER VECHT).

Quite similar to *P. olivaceus* in general structure. *Head.* Cranium almost entirely brownish, deeply emarginate posteriorly, with distinct punctures (denser than in *P. olivaceus*) and associated short setae; punctation sparser on vertex and gena. Mid-cranial sulcus present but weak. Antenna moderate in size, with 4 minute sensillae. Temporal band wide and relatively short; outer part not distinctly reticulate. Epistomal sulcus lacking in upper portion. Labrum transverse, gently emarginate ventrally, with short setae; palate with conical sensillae but without setae. Mandible wide at base, with two rather long subsidiary teeth well set back from apex. Maxillary palp thick, with about 8 minute sensillae; galea slender, with 4 sensillae. Prelabium rounded-rectangular; labial palp short, with 6 to 7 sensillae, and some 15 short setae around it.

Body. Integument with numerous microtubercles; thoracic sternites 1-3 and 1st abdominal sternite with many medium-sized setae; 1st to 3rd thoracic tergites, 1st abdominal tergite and 2nd abdominal sternite with shorter setae; other segments with very short setae or punctures alone. First spiracle largest but much less than twice as large as the rest; 2nd spiracle slightly smaller than 3rd.

This species is easily distinguished from *P. olivaceus* in the following points: subsidiary teeth of mandible subequal in size, both well set back from apex; and thoracic segments and 1st abdominal segment with many distinct setae (bristles). This first character has also been observed in the Japanese *Polistes jadwigae jadwigae* D.T. and

the Taiwanese *P. rothneyi gressitti* VECHT, and may be seen in most of the *Megapolistes* species.

Polistes (Polistella) sp.

(Fig. 3)

Specimens examined: Some mature larvae, Jan. 11, 1974, Yabobo near Madang, Papua New Guinea, T. OKAZAWA leg. (adults determined by Prof. J. VAN DER VECHT).

Head. Cranium extensively brownish between the temporal bands including antennal regions and outside the epistoma, emarginate posteriorly, with numerous long hairs (vertex, gena and clypeus which are pale coloured lack them); punctures large. Mid-cranial sulcus present in upper half, narrow. Frons not separated from the epicranium and clypeus. Antenna small, with 5 to 6 minute sensillae. Temporal band wide and relatively short; outer half to two-thirds reticulate. Postoccipital sulcus developed; pleurostomal sulcus weak; epistomal sulcus lacking in upper portion. Labrum pale coloured, strongly transverse, with fine setae and several conical sensillae near ventral margin; palate with a few inconspicuous punctures. Mandible slender, tapering, with two subsidiary teeth well set back from apex (one large and the other small). Maxillary lobe developed, with medium-sized setae; maxillary palp and galea relatively long, subequal in size; each with 3 to 4 minute sensillae. Prelabium subcircular, slightly longer than wide (in Fig. 3H the prelabium appears to be improperly wider than long); labial palp moderate in height, with 4 minute sensillae, with more than 10 setae around it. Postlabium with sparse punctation.

Body. Integument with numerous minute tubercles which are transverse and not pointed apically as in *Ropalidia*, with sparse punctation. First abdominal sternite with many long hairs which are never seen in the subgenus *Megapolistes*. Paired oval

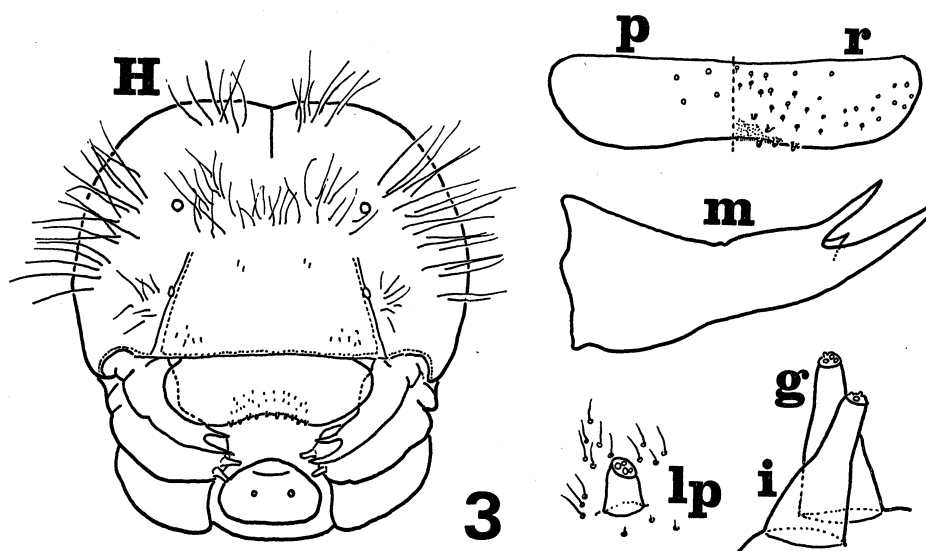


Fig. 3. Larval head of *Polistes (Polistella) sp.* (Symbols as in Fig. 1.)

areas on thoracic sternites and pleural lobes well defined in at least mounted and stained specimens. First spiracle largest, but less than twice as large as the rest; 2nd spiracle second largest; the rest distinctly smaller than 1st and 2nd.

***Ropalidia marginata jucunda* Cameron**

(Fig. 4)

Specimens examined: Some mature larvae, Dec. 27, 1973, Kundiwa, Papua New Guinea, T. OKAZAWA leg. (adults determined by Prof. J. VAN DER VECHT).

Head. Cranium brown (lower margin of clypeus paler), nearly circular, evenly emarginate posteriorly, with many strong setae. Mid-cranial sulcus quite weak. Frons not separated from the epicranium and clypeus which is strongly transverse, ventrally emarginate and laterally defined by epistomal sulcus. Antenna relatively large, with 2 to 4 quite small sensillae. Temporal band rather long, not reticulate. Postoccipital and hypostomal sulci developed; pleurostomal sulcus weak; epistomal sulcus lacking in upper portion. Labrum pale in colour, transverse, slightly emarginate ventrally, with several rather large conical sensillae near ventral margin; palate without setae or conical sensillae. Mandible slender, sharply pointed apically, with a subsidiary acute tooth near apex. Maxillary lobe not very developed, with a distinct, sclerotized ring at base, apically with microscopic denticles, without distinct setae; maxillary palp with 4 sensillae, two of which are situated on the produced half of the palp; galea divided into two lobes, each lobe with one minute sensilla. Prelabium subcircular; labial palp similar to maxillary palp in shape, with 4 minute sensillae; a pair of setae with raised socket are behind labial palps and just below the lower salivary lip; lower half of prelabium with small punctures. Postlabium moderately developed, not concave below, with several medium-sized setae and small punctures.

Body. Integument with microscopic denticles all over the body segments; those on 2nd and 3rd thoracic sternites large, quite dense and very often connected into rows. Integument also with small punctures which are much sparser than the microscopic denticles; each puncture with a short seta. First thoracic sternite with some strong, rather long setae. Paired oval areas on thoracic sternites and pleural lobes distinct in at least stained specimens. First spiracle more than twice as large as 2nd in diameter; atrium bare.

***Ropalidia turneri* Richards**

(Fig. 5)

Specimens examined: Some mature larvae, Dec. 23, 1973, Wau, Papua New Guinea, T. OKAZAWA leg. (adults determined by Prof. J. VAN DER VECHT).

Head. Cranium brown (gena and lower margin of clypeus paler), with very minute sparse punctures, without setae. Mid-cranial sulcus weak. Frons not separated from the epicranium and clypeus. Antenna moderate in size, with 3 to 4 minute sensillae.

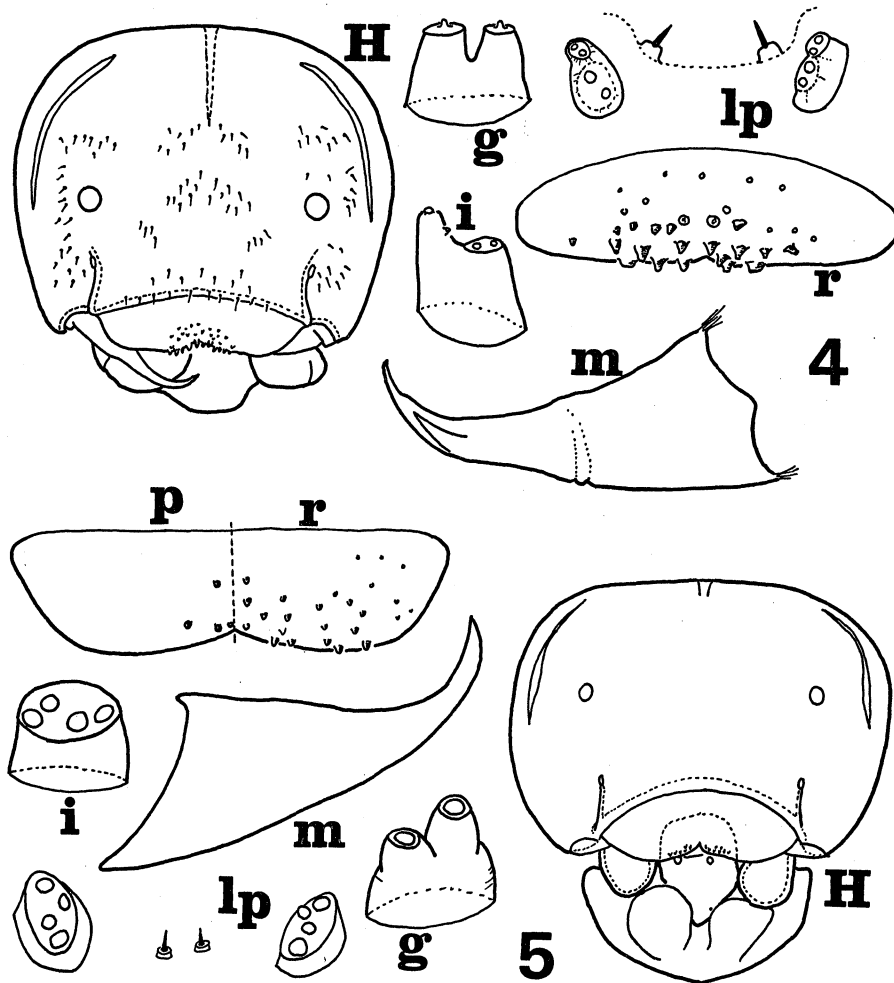


Fig. 4. Larval head of *Ropalidia (Icariola) marginata jucunda*. (Symbols as in Fig. 1.)

Fig. 5. Larval head of *Ropalidia (Icariola) turneri*. The whole head (H) is viewed slightly from below so that the clypeus appears to be improperly emarginate ventrally. (Symbols as in Fig. 1.)

Temporal band wide and long; outer half reticulate. Postoccipital and hypostomal sulci developed; pleurostomal sulcus weak; epistomal sulcus lacking in upper portion. Labrum pale in colour, transverse, gently emarginate ventrally, with many conical sensillae; palate with a few conical sensillae, without punctures or setae. Mandible slender, monodentate, without subsidiary tooth at all. Maxillary lobe not very developed, with a sclerotized basal ring, without setae; maxillary palp thick and short, with 4 minute sensillae; galea divided into two lobes, each with a sensilla. Prelabium wide above, much narrowed below; labial palp short, with 4 sensillae; paired setae with raised sockets and very close to each other. Postlabium not concave below.

Body. Integument with numerous microscopic denticles; 2 to 4 such denticles often arranged in a row on the thoracic and 1st and 2nd abdominal segments.

Integument also with sparse minute punctures and setae. First abdominal sternite sclerotized, with many strong setae; 3rd thoracic sternite sparsely with such setae posteriorly. First spiracle largest, more than twice as large as the rest.

In Queensland, the mature larvae of this species are noted to have strong setae (bristles) on all the thoracic sternites and none on the 1st abdominal sternite (RICHARDS, 1978a).

Some Important Larval Characters

Up to now only 32 species in 5 genera (*Polistes*, *Ropalidia*, *Belonogaster*, *Polybioides* and *Parapolybia*) of Old World and Oceanian Polistinae have been studied for the larval morphology (RICHARDS, 1978a, b; S. & Sk. YAMANE, 1979; KOJIMA in preparation). They include *Belonogaster junceus* F., *Polybioides tabidus* F., *Parapolybia varia* F. and *P. indica indica* SAUSS. which have been examined in the course of this study. No species of the genus *Sulcopolistes*, the subgenera *Stenopolistes*, *Nygmopolistes* and *Gyrostoma* of the genus *Polistes*, and the subgenera *Ropalidia* and *Paraicaria* of the genus *Ropalidia* has been studied (for the subdivisions of the genera *Polistes* and *Ropalidia*, see RICHARDS, 1973, 1978a). Thus, species and subgenera so far studied are quite restricted in number and so general conclusions can hardly be reached, but it may be useful to enumerate and discuss some larval characters which seem to be of taxonomic or phylogenetic importance. Here we follow RICHARDS' division of the Polistinae into three tribes: Polistini (two genera), Ropalidiini (one genus), and Polybiini (three genera in Old World; 23 New World genera are excluded from discussion).

1. *Setae on the upper surface of maxillary lobe.* Punctures and more or less distinct associated setae are observed on the upper surface of maxillary lobe in all the genera except for *Ropalidia*. Since many eumenids and vespines also have such setae (GRANDI, 1935; REID, 1942), the lack of them in *Ropalidia* may be a derived condition.

2. *Basal ring of maxillary lobe.* *Ropalidia* species have the maxillary lobe with a sclerotized basal ring. This character may be peculiar to this genus and a derived one.

3. *Well-developed maxillary lobe.* In *Polistes* maxillary lobe is markedly developed. In some species of *Ropalidia* they are somewhat swollen, but less conspicuous than in *Polistes*. The other genera have those of normal size and shape. The much developed maxillary lobe in *Polistes* might have evolved along with their specialized feeding habits (Sk. YAMANE, 1976) and may be a derived character.

4. *Apically bilobed galea.* Apically bilobed galea is seen in most examined species of *Ropalidia*, *Parapolybia* and *Polybioides*, and each lobe typically has only one minute sensilla (one of the two lobes rarely has two sensillae in *Parapolybia*). On the other hand, in *Polistes* the galea is usually unilobed, with 3 or 4 sensillae; in the subgenus *Polistes* it is weakly bilobed but the larger lobe bears 2 or 3 sensillae. Also in *Belonogaster junceus* the galea is not bifid but with only two sensillae. The bilobed galea may not be an apomorphic character for some Old World genera, but reduction in the number of sensillae on the apex of galea may have some phylogenetic importance.

In some *Ropalidia* species the maxillary palp is also somewhat specialized (Fig. 4).

5. *The number of sensillae on labial palp.* This character is not very stable and varies even within a given species. However, it should be noted that the number of sensillae is quite stable (four) in at least *Ropalidia* species examined by S. & Sk. YAMANE (1979) and KOJIMA (in preparation), and in this study. In *Belonogaster*, *Polybioides* and *Parapolybia* the number ranges from 2 to 4, usually 3 or 4. On the other hand, *Polistes* species, except those belonging to the subgenus *Polistes*, have 5 or more sensillae (max. 7) on the labial palp. In the subgenus *Polistes*, however, 3 or 4 sensillae are normally seen. Although the stability in the number of sensillae in *Ropalidia* is notable, the taxonomic value of this character is still unclear.

6. *Trilobed labrum.* Though the vespidae larval labrum is usually weakly bilobed, the present study has revealed that the labrum of *Belonogaster junceus* is clearly trilobed (see also Richards' 1978b key, but species are not stated). As any species with such a labrum has not been found in the other vespidae genera, the trilobed labrum in *Belonogaster* is well considered to be a derived character.

7. *Raised socket of the paired setae behind labial palps.* S & Sk. YAMANE (1979) first described this condition in two Nepalese *Ropalidia* species belonging to the subgenus *Icariola*. KOJIMA (in preparation) confirmed it in three species of another subgenus, *Icarielia*, from the Philippines. The two species (*Icariola*) examined in this study also have the raised socket (Figs. 4, 5, lp). RICHARDS (1978a, b) does not mention this character, but it is highly possible that in most of the *Ropalidia* species it is observed. The present study shows that this character is also present in *Belonogaster junceus*. In the other Polybiini genera *Polybioides* and *Parapolybia* the paired setae are arising from the socket which is not distinctly raised but is more clearly defined than in *Polistes*. This character was not referred to in REID (1942) for the New World Polybiini.

8. *Paired oval areas on thoracic sternites and pleural lobes.* The paired oval areas have been noted to indicate the position of wing or leg buds underneath the larval skin (REID, 1942), and this view is followed in Sk. YAMANE (1976). RICHARDS (1978b) laid stress on this character when trying to separate the *Polistes-Ropalidia* complex from the Polybiini. According to him the mature larvae of the former often have well-defined paired oval areas on the thoracic sternites and pleural lobes, while those of the latter always lack such structures. This observation has perhaps influenced his dendrogram showing the relationships of the polistine genera. By examining the mature larvae of some Old World Polybiini during the course of this study we could easily find these structures in all of them (in at least stained specimens). Therefore, RICHARDS' distinction of the *Polistes-Ropalidia* complex from the Polybiini clearly becomes void when the Old World species are taken into account.

9. *Large first spiracle.* In polistine larvae the first spiracle is more or less larger than the rest. In *Polistes* it is almost as large as or only slightly larger than the rest. However, in the tribe Ropalidiini and Old World species of Polybiini it is much larger

than or often more than twice as large as the rest. Such a condition is among the New World Polybiini seen only in *Mischocyttarus*. Since *Mischocyttarus* does not exhibit a close affinity with *Ropalidia* or Old World Polybiini in any other character, this condition might have evolved independently in both the groups, and may be considered to be a derived character.

10. *Setae on body integument.* More or less long, distinct setae (or bristles) are often observed on the body surface in *Ropalidia* and *Polistes*. However, their position varies among species or groups, so the taxonomic value of these setae remains doubtful at present.

11. *Connected microscopic denticles on body integument.* Generally the body integument is extensively covered with numerous minute structures which are apically rounded (like tubercles) in *Megapolistes* and *Polistella* of the genus *Polistes*, while they are apically pointed (like denticles) in *Polistes* s. str., *Ropalidia* and the three Polybiini genera. This character is without doubt useful in classifying genera or subgenera, but its phylogenetic value is unclear.

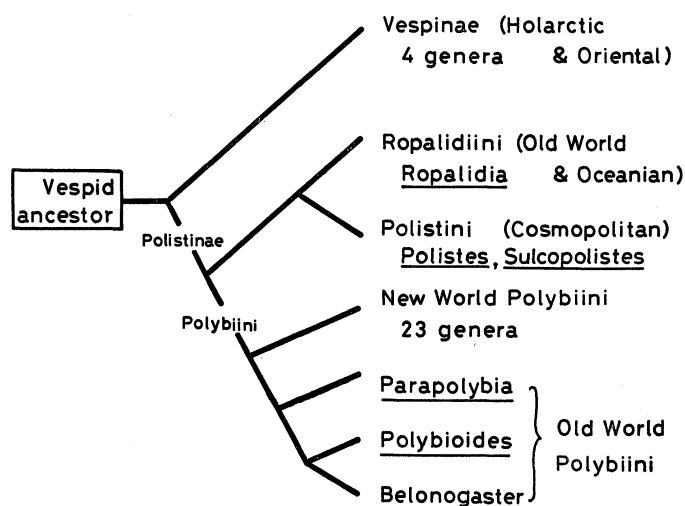


Fig. 6. Dendrogram showing relationships of the polistine genera, reproduced from RICHARDS (1978b). It is modified in shape, but the branching pattern is strictly retained. The New World genera other than *Polistes* are lumped together under "New World Polybiini".

Ropalidia species have denticles of which a few to several tend to be connected into rows especially on the thoracic segments (see S. & Sk. YAMANE, 1979, fig. 2J, K; KOJIMA, in preparation, figs. 43, 44), though RICHARDS (1978a) does not mention this character for Australian species. The present study has revealed that, though less conspicuous than in *Ropalidia*, this condition also occurs in *Belonogaster junceus*.

In presenting his dendrogram showing the relationships of the polistine genera of the world RICHARDS (1978b) considers the Polistini-Ropalidiini complex to be a monophyletic group, placing the Polybiini on the other branch (Fig. 6). Although

he has used many characters of various sorts, i.e., adult, larval, nest architectural and behavioural, his reconstruction of phylogeny seems not to have hard basis. He does not specify any derived (apomorphous) character for the Polistini-Ropalidiini complex. The main larval character which seemed to associate *Polistes* with *Ropalidia* (visible paired oval areas on the thorax) has been invalidated by the present study as discussed above. We have failed to find derived larval or adult characters supporting RICHARDS' view*.

Instead we have found two important larval characters (7 and 11 in the above list), which seem to indicate derived condition, associating *Ropalidia* with *Belonogaster*. This association is also supported by some adult characters shared by both the genera such as the lack of pronotal fovea, of scrobal furrow on mesepisternum and of dorsal groove on mesepisternum. However, the monophyly of these genera cannot be demonstrated by these findings alone. In fact other adult characters suggest a closer relationship of *Belonogaster* to *Polybioides* than to *Ropalidia* (the numbers of joints of antenna, and of maxillary and labial palps; cf. VECHT, 1966).

Another approach opposing RICHARDS' view has been made by JEANNE (1980) who has emphasized a distinctive behavioural character, the meconium-extracting by the adult, which is peculiar to the Ropalidiini-Old World Polybiini complex. Thus he argues that the Old World polistine genera other than *Polistes* and *Sulcopolistes* form a natural group because such an intricate behaviour is not likely to have evolved among them by convergence or parallelism. Although at present there is no available adult or larval character supporting JEANNE's assumption, efforts along this line will be rewarding.

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* In Polistini and Ropalidiini the muscle slit of propodeum (propodeal orifice) tends to be narrow and dorsally acute, and this condition may be apomorphous. Though there are intermediates and exceptions particularly on the part of *Ropalidia*, this character may have some phylogenetic importance as suggested by RICHARDS (1978b).

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