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A REVISION OF ANTS OF THE SUBGENUS *POLYRHACHIS* FR. SMITH (HYMENOPTERA : FORMICIDAE : FORMICINAE)

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ABSTRACT. All the 13 nominal taxa of the subgenus *Polyrhachis* are included in this revision. Range, mean, standard deviation, coefficient of variability, coefficient of difference, and the taxonomic distance for 10 morphological measurements and indices are calculated for comparison of different samples. Seven of the eight infraspecific taxa are synonymized, and the other, *mindanaensis*, is raised to specific status. *Montana* from Borneo is described as a new species. A tentative phyletic scheme within this subgenus is proposed.

INTRODUCTION

The genus now known as *Polyrhachis* was first established by Billberg in 1820 under the generic name *Myrma*. The current generic name *Polyrhachis* was introduced by Frederick Smith in 1858. Nineteen subgenera have been recognized in this genus: *Anoplomyrma, Aulacomyrma, Campomyrma, Cephalomyrma, Chariomyrma, Cyrtomyrma, Dolichorhachis, Evelyna, Florencea, Hagiomyrma, Hedomyrma, Johnia, Moleyidris, Myrma, Myrmatopa, Myrmothrinax, Myrmhopla, Polyrhachis*, and *Pseudocyrtomyrma*. The validity of the two generic names and the status of these 19 subgenera have been discussed by Hung (1967). Although the generic name *Myrma* has priority over *Polyrhachis*, it was suggested that the familiar name *Polyrhachis* be retained for this important genus. The replacement of the name *Polyrhachis* by *Myrma* would cause nomenclatorial chaos, not only for the nearly 500 taxa directly involved, but also elsewhere in the classification of the family Formicidae (Hung, 1967). As for the subgenera, only the subgenus *Polyrhachis* (and perhaps also the subgenus *Cyrtomyrma*) is a well-defined group. No clear delimitation can be found among the other subgenera, and they should all be treated as species groups rather than as subgenera (Hung, 1967).

In *Polyrhachis* (*sen. str.*), the following characteristics are known :

1. It has both pro- and mesonotal spines in the worker (this combination is not found in any other group of this genus).

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2. The petiole is columnar, surmounted by two long, hook-shaped spines (this type of petiole is found in *Polyrhachis furcata*, but here the rest of the characters differ widely).
3. A median ocellus is found in the workers of *ypsilon*, *bihamata* and *bellicosa*. *Bellicosa* from the New Guinea area even have two lateral ocelli.
4. In other groups, the petiole of females often looks very much like that of workers both in length and shape. But in this group, it is reduced to about one-third in length, and the spines are tuberculate rather than hook-shaped.

This subgenus is further divided into two species-groups. At present, the following 13 forms are recognized by myrmecologists in this subgenus :

lamellidens-group
lamellidens Fr. Smith, 1874.
craddocki Bingham, 1903.
bihamata-group
bellicosa Fr. Smith, 1858.
var. *crudelis* Emery, 1887.
var. *erosispina* Emery, 1900.
bihamata Drury, 1773.
var. *minor* Karawajew, 1927.
var. *perplexa* Santschi, 1925.
var. *tonsilis* Santschi, 1928.
ypsilon Emery, 1887.
var. *mindanaensis* Emery, 1923.
var. *victoris* Santschi, 1925.
ab. *synacantha* Santschi, 1933.

Although ants of this genus are very common in the Old World, very little taxonomic work, except the description of new forms, has been done. The present revision of this best-defined group of the genus is presented as a step toward revision of the whole genus.

Material and Methods

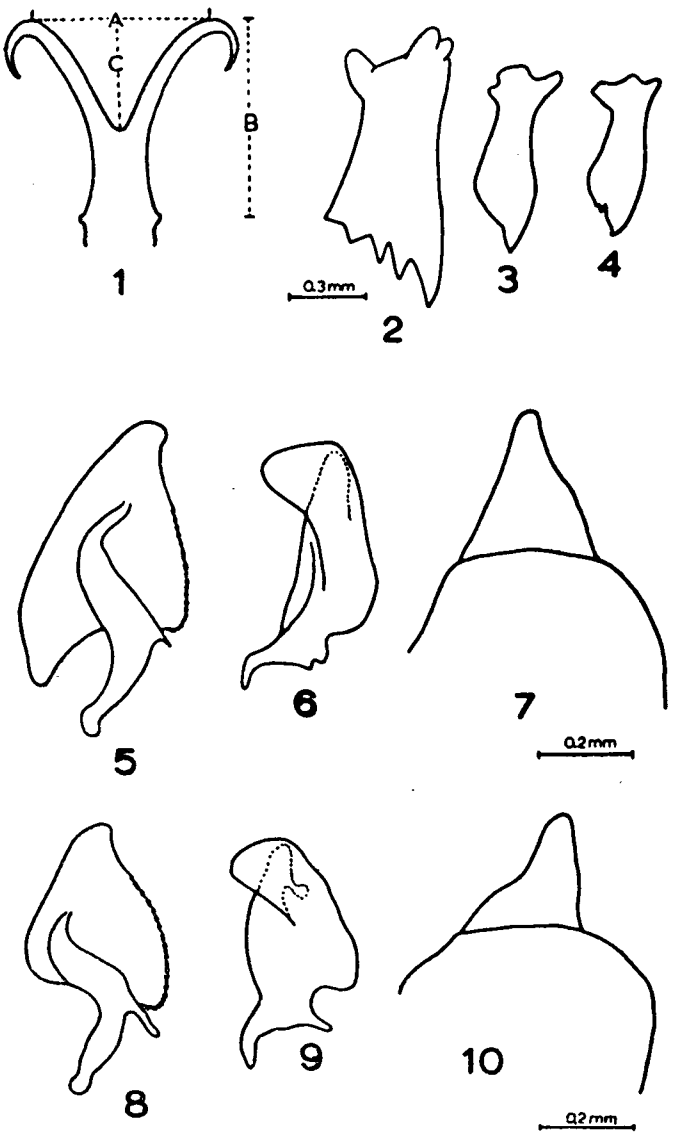
The specimens were kindly provided by the following institutions : Bernice P. Bishop Museum, Honolulu, Hawaii ; British Museum (Natural History), London ; Museo Civico di Storia Naturale, Genoa, Italy ; Museum d'Histoire Naturelle, Geneva, Switzerland ; Naturhistorisches Museum, Basel, Switzerland ; Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts ; Oxford University Museum, Oxford, England ; United States National Museum, Washington, D. C.

Specimens of the worker caste were used in this study because workers are by far the best known and most available of the castes. Several reproductive females of different species were found among the material. Since they were all mounted separately without any associations with workers, it was advisable to ignore them temporarily lest they should cause nomenclatural mistakes. Fortunately, one pin was received containing a male of *Polyrhachis bellicosa* in association with workers. This specimen and another male specimen of *P. lamellidens*, kindly provided by Dr. Keizo Yasumatsu of Kyushu University, Japan, have been used in this study.

Workers were first sorted according to geographic distribution. Material from one area was then compared with material from other areas. The following standard measurements and indices were used for comparison :

1. Head width (HW) : maximum width of the head, measured from gena to gena immediately below the eyes in full face view.
2. Head length (HL) : length of the head, held in perfect full face view, measured from the anteriormost point of the clypeal border to the posteriormost point of the occipital border.
3. Cephalic index (CI) : HW x 100/HL.
4. Scape length (SL) : maximum length of the scape with the basal "neck" excluded.
5. Scape index (SI) : SL x 100/HW.
6. Pronotal width (PW) : maximum width of the pronotum measured at the bases of the pronotal spines.
7. Mesonoto-propodeal length (MPL) : diagonal distance from anterior mesonotal margin to maximum extension of posterolateral propodeal lobe, measured in side view.
8. Metathoracic tibial length (MTL) : the maximum length of the metathoracic tibia.
9. Petiolar spine expansion index (PSEI) : distance between the two tangent points of the hooks as percentage of the height of the hooks (fig. 1, A/C x 100).
10. Petiolar height (PH) : maximum measurable height of petiole, from the tangent point of the hook to the stigma (Fig. 1, B).

All measurements were done by means of a Bausch & Lomb BVB-73 zoom microscope and an ocular micrometer that had been calibrated against a stage micrometer. With a desk calculator the range (R), mean (M), standard deviation (SD) and coefficient of variability (CV=SD x 100/M) of the ten measurements and indices were calculated for all the material from each area. Data from each area were then compared with those from other areas in pairs for each of the ten measurements and indices. The difference is expressed by the coefficient of difference, $CD=(M_b-M_a)/(SD_a+SD_b)$ (Mayr, Linsley and Usinger, 1953). Each measurement or index was considered separately. For



Figs. 1-10. *Polyrhachis* : 1, petiole of *lamellidens* workers ; 2, mandible of *bellicosa* workers ; 3, mandible of *lamellidens* ♂; 4, mandible of *bellicosa* ♂ ; 5, lamina aedeagalis of *bellicosa* ♂; 6, cuspis volsellaris and digitus volsellaris of *bellicosa* ♂ ; 7, outer valve of the *bellicosa* ♂ genitalia ; 8, lamina aedeagalis of *lamellidens* ♂ ; 9, cuspis volsellaris and digitus volsellaris of *lamellidens* ♂ ; 10, outer valve of the *lamellidens* ♂ genitalia.

comparison of the similarity of the material from any two areas, the taxonomic distance of Sokal (1961) was used. It has the following formula :

$$\Delta_{jk}=\left[\sum_{i=1}^{n}(\chi_{ij}-\chi_{ik})^2\right]^{\frac{1}{2}}$$

Only the seven direct measurements were used in the calculation of the taxonomic distance. The three indices were omitted so that all the values used in the calculation have the same unit. All seven measurements were taken into account as a whole.

The Munsell color system was followed in describing the color patterns of these species.

KEY TO THE SPECIES OF ANTS OF THE SUBGENUS *POLYRHACHIS*

BASED ON WORKERS

1. Alitrunk flat dorsally, the sides margined along the whole length 2
   Alitrunk more or less rounded dorsally, the sides not margined along the whole length 3
2. Petiolar spines diverge widely from their base . . . . . **lamellidens**
   Petiolar spines parallel for three-fourths of their length from base . . . . **craddocki**
3. Petiolar spines diverge widely from their base ; if parallel, then petiolar height more than 2.8 mm. 4
   Petiolar spines parallel for a part of their length from base ; if divergent, then petiolar height less than 2.8 mm. 6
4. Pronotal spines stout, black throughout the whole length . . . . . **ypsilon**
   Pronotal spines thin, only the tip is black 5
5. Mesonotal spines widely separated at base ; petiolar height less than 2.2 mm. **montana**
   Mesonotal spines contiguous at base ; petiolar height more than 2.2 mm. **mindanaensis**
6. Propodeal spines distinct and contiguous at base ; if separated and appearing as two ridges with a point at each end, then the gaster is unicolored. . . . . **bellicosa**
   Propodeum with two contiguous ridges, no spines ; gaster bicolored. . . . **bihamata**

1. **Polyrhachis bellicosa** Smith (Figs. 2, 4, 5, 6, 7, 11-15. Tables 1, 2.)

Polyrhachis bellicosa Fr. Smith, 1858, *J. Proc. Linn. Soc. London, Zool.*, 3 : 142, worker. Type locality : Aru. ; Mayr, 1867, *Tijdschr. Ent.*, 10 : 18 ; Bingham, 1903, *Fauna British India, Hymenoptera*, 2 : 387, worker.

Polyrhachis bellicosa var. *crudelis* Emery, 1887, *Ann. Mus. Civ. Stor. Nat. Genova*, (2) 4 : 238, worker. Type locality : Morotai. **New Synonymy.**

Polyrhachis bellicosa var. *erosispina* Emery, 1900, *Ann. Mus. Civ. Stor. Nat. Genova*, (2) 20 : 713, nota, worker. Type locality : Kendari, Celebes ; Karawajew 1927, *Trav. Mus. Zool. Kieff.* 3 : 12, female, fig. 3, nest ; Wilson, 1959, *Ecology*, 40 : 439, 442, ecology. **New Synonymy.**

Distribution : Philippines ; Borneo ; Laos ; Thailand ; Malaya ; Sumatra ; Celebes ; New Guinea ; New Britain ; New Ireland ; Australia.

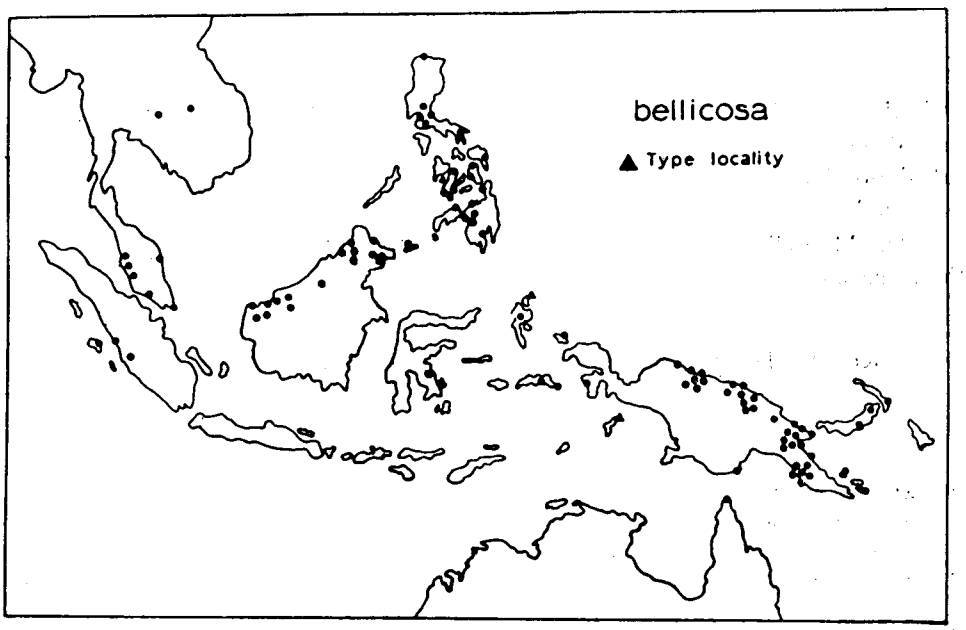


Fig. 11. Distribution of *Polyrhachis bellicosa.*

Holotype : HW 1.80 mm, HL 2.05 mm, CI 88, antennae missing, PW 1.05 mm, MPL 1.95 mm, MTL 3.50 mm, PSEI 110, PH 1.75 mm.

Other Type Material : One syntype worker of *crudelis* measured-HW 1.50 mm, HL 2.00 mm, CI 75, SL 2.75 mm, SI 183, PW 0.98 mm, MPL 2.03 mm, MTL 3.32 mm, PSEI 86, PH 1.75 mm. One syntype worker of *erosispina* measured-HW 1.75 mm, HL 2.13 mm, CI 82, SL 2.63 mm SI 150, PW 0.98 mm, MPL 2.09 mm, MTL 3.32 mm, PSEI 66, PH 2.10 mm.

Worker : HW 1.50-2.18 mm, HL 1.80-2.38 mm, CI 72-95, SL 2.25-3.05 mm, SI 132-183, PW 0.63-1.25 mm, MPL 1.63-2.53 mm, MTL 2.75-4.00 mm, PSEI 44-100, PH 1.55-2.65 mm. Mandibles with 5 teeth sequentially reducing in length, the apical is about twice as long as the basals. Clypeus convex, but not carinated. Head excluding the mandibles, somewhat longer than broad, with slightly rounded sides and rounded occipital border. Three ocelli present. The two lateral ocelli are rather obscure in some specimens. Pronotum marginated. about as long as broad with sides slightly rounded. The marginated ridges of the pronotum do not continue anteriorly into the pronotal spines as in the case of *lammellidens* and *craddocki.* Pronotal spines pointed outward and slightly curved down. Mesonotum rounded with two rather compressed spines raising upwards and curved backward. Metanotal groove replaced by a ridge. Propodeum with basal face more or less flat, but no distinct margins. The

basal face is about one and one-half times as long as the declivity. Petiole columnar bearing a pair of long, hook-shaped spines which in most cases are parallel and even contiguous. Gaster spherical to elliptical with the tergite of the first segment covering almost half of the gaster. Mandibles, clypeus, occipital corners, last three segments of the gaster and sometimes the coxae of front legs and the pleurae with sparse, suberect hairs. Head black. Alitrunk and petiole vary from dark reddish-brown, dusky red to very dusky red. Gaster unicolored black, or bicolored with the first segment lighter in color than the rest of the gaster. Spines mostly with tips black.

Male : Black. Mandibles, clypeus, genae, alitrunk, petiole and coxae with yellowish-brown hairs. Gaster rather shining with hairs along the posterior border of the sternites and the last three tergites. Mandibles with pointed apex and two denticles. Mesonotum convex, alitrunk without any spines. Petiolar spines short and tuberculate. Hind wing with discoidal cell. Genitalia with serrated lamina aedeagalis, both cuspis volsellaris and digitus volsellaris with sensory pegs.

Localities from which specimens have been studied : PHILIPPINES: Dumaguete (J. W. Chapman) ; Horns of Negros, 3600 ft. (J. W. Chapman) ; Tagaya, 470-720 m, Mindanao (H. E. Milliron) ; Tayabas (R. C. McGregor) ; Los Banos (Baker) ; Mt. Makiling (T. C. Maa, O. H. Swezy, F. X. Williams) ; Tawitawi (S. C. Duvag) ; Dansalan (L. Morato, H. E. Milliron) ; Ginoog (A. Reyes) ; Davao (A. Reyes) ; Lambatan (J. W. Chapman) ; Mt. Apo, 5000-6000 ft. (C. F. Clagg) ; Ilocos Norte (C. S. Banks) ; Jolo (A. C. Duyog) ; Mt. Talinas, 1000 m (H. Torrevillas) ;Minalwang, 1050 m, Misamis (H. Torrevillas) ; Los Arcos (C. W. Yoshimoto) ; Biliran I. (R. C. McGregor) ; Mainit (C.M. Yoshimoto) ; Febrica (J. W. Chapman) ; Samar (R. C. McGregor). N. BORNEO : Forest Camp, 19 km N. of Kalabakan (Y. Hirashima) ; Tawau (Ho Kai Him, Y. Hirashima, T. C. Maa) ; Ranau (T. C. Maa) ; Gomantong Caves, Sandakan Residency (T. C. Maa) ; Sapagaya Lumber Camp, Sandakan Bay (J. L. Gressitt) ; Sepilok Forest Res., Sandakan Bay (J. L. Gressitt) ; Liawan (T. C. Maa) ; Tambunan (P. W. Bryant) ; Keningan (T. C. Maa) : Mt. Dulit (E. Mjöberg). SARAWAK : Pangkalan Tebang, Bau Dist. (T. C. Maa) ; Rejang Delta (J. Hewitt) ; Lundu (Anonymous) ; Rambungan (H. Smith) ; Serambu Mt. (H. Smith) ; Mt. Poi (E. Mjöberg). THAILAND : Kao Sabab (Anonymous). LAOS : Ban Van Heue 20 km E. of Phou-kowkuei (J. A. Rondon). MALAYA : Sungei Linam (J. L. Gressitt) ; Kuala Tahan (T. C. Maa) ; Kepong Forest Res., Selangor (T. C. Maa) ; Subang Forest Res., Selangor (T. C. Maa) ; Malacca (Staudinger). SUMATRA : Langkat (N. Dengas) ; Kota Nopan (W. M. Mann). CELEBES : Bantimoerong (W. M. Mann). NEW GUINEA : Bisianumu, E. of Port Moresby, 500 m (J. L. Gressitt, T. C. Maa) ; Bisianumu near Sogeri, workers and one male associated (E. O. Wilson, acc. no. 606) ; Maprik (W. Brandt, J. L. Gressitt); Ifar, Cyclops Mts. 300-600 m (J.L. Gressitt) ; Subitana (W. Brandt); W. Sentani, Cyclops Mts. 150-250 m (T. C. Maa) ; Mt. Misim (Stevens);

TABLE 1.—RANGES, MEANS, STANDARD DEVIATIONS AND COEFFICIENTS OF VARIABILITY OF THE NINE POPULATIONS OF *P. BELLICOSA*

ALL MEASUREMENTS ARE IN MILLIMETRES

Characters	*New Guinea* N=154				*Australia* N=5				*New Britain* N=26				*New Ireland* N=6				*Philippines* N=61			
	R	*M*	*SD*	*CV*	*R*	*M*	*SD*	*CV*	*R*	*M*	*SD*	*CV*	*R*	*M*	*SD*	*CV*	*R*	*M*	*SD*	*CV*
HW	1.60-2.18	1.90	0.14	7.57	1.73-1.80	1.75	0.03	1.51	1.70-2.15	1.93	0.15	7.96	1.70-2.13	1.90	0.19	10.205	1.55-2.00	1.83	0.10	5.60
HL	1.83-2.38	2.15	0.13	5.95	2.00-2.13	2.04	0.06	2.86	2.00-2.38	2.21	0.12	5.51	2.00-2.33	2.15	0.16	7.57	1.80-2.25	2.08	0.12	5.98
CI	82-95	88	2.70	3.07	84-87	85	1.50	1.76	83-92	87	2.82	3.24	85-93	88	2.83	3.21	81-92	88	1.84	2.09
SL	2.25-3.00	2.71	0.16	6.08	2.50-2.63	2.57	0.06	2.55	2.40-3.05	2.76	0.19	6.76	2.50-3.00	2.70	0.21	7.98	2.38-3.00	2.73	0.15	5.50
SI	132-155	142	5.91	4.16	143-150	146	3.28	2.24	138-150	143	3.30	2.31	138-147	142	4.10	2.88	139-164	149	4.84	3.24
PW	0.75-1.20	1.01	0.09	8.79	1.00-1.05	1.01	0.02	2.21	0.93-1.25	1.07	0.31	29.00	0.95-1.18	1.08	0.09	8.43	0.75-1.15	1.00	0.09	9.38
MPL	1.63-2.35	2.05	0.13	6.56	2.00-2.00	2.00	0	0	1.88-2.35	2.10	0.15	7.22	1.95-2.25	2.10	0.14	6.53	1.88-2.50	2.19	0.14	6.26
MTL	2.75-3.88	3.52	0.22	6.15	3.35-3.50	3.40	0.05	1.63	3.00-3.88	3.57	0.21	5.98	3.08-3.93	3.41	0.33	9.71	3.25-4.00	3.69	0.21	5.77
PSEI	44-84	66	8.93	13.54	57-75	65	7.03	10.82	50-78	68	6.97	10.25	60-75	69	5.44	7.88	40-100	59	11.70	19.84
PH	1,55-2.20	1.96	0.13	6.69	2.00-2.00	2.00	0	0	1.93-2.38	2.13	0.13	6.30	2.00-2.25	2.07	0.11	5.46	1.75-2.45	2.18	0.17	7.91

TABLE 1—Continued

Characters	*Borneo N=89*				*Sumatra N=13*				*Malaya N=12*				*Laos N=14*			
	R	*M*	*SD*	*CV*	*R*	*M*	*SD*	*CV*	*R*	*M*	*SD*	*CV*	*R*	*M*	*SD*	*CV*
HW	1.50-2.00	1.78	0.10	5.62	1.80-1.90	1.85	0.04	2.23	1.70-1.88	1.79	0.05	3.01	1.83-1.93	1.89	0.02	1.17
HL	1.87-2.31	2.05	0.13	6.58	2.08-2.18	2.14	0.03	1.32	2.05-2.25	2.13	0.05	2.44	2.13-2.25	2.20	0.04	1.70
CI	72-95	87	3.06	3.51	84-91	86	1.73	2.01	81-87	84	1.65	1.96	81-88	85	1.92	2.26
SL	2.30-2.85	2.66	0.12	4.69	2.63-2.80	2.72	0.04	1.51	2.58-2.88	2.68	0.09	3.27	2.63-2.83	2.72	0.06	2.11
SI	136-183	150	9.43	6.29	144-153	147	2.86	1.94	144-153	150	3.53	2.35	1.39-1.51	144	2.89	2.01
PW	0.63-1.13	0.95	0.08	8.8	0.95-1.13	1.03	0.05	4.85	0.85-1.05	0.98	0.05	5.29	0.95-1.08	1.00	0.03	3.32
MPL	1.88-2.53	2.21	0.11	5.02	2.25-2.40	2.27	0.05	2.20	2.00-2.38	2.21	0.12	5.26	2.25-2.43	2.33	0.05	2.23
MTL	3.00-3.85	3.48	0.27	7.92	3.50-3.75	3.69	0.30	8.22	3.33-3.80	3.54	0.11	3.12	3.60-3.75	3.68	0.06	1.67
PSEI	50-73	60	6.87	11.45	55-74	63.6	5.82	9.16	57-70	61	3.83	6.27	50-58	53	3.04	5.69
PH	2.07-2.65	2.45	0.14	5.57	2.38-2.55	2.49	0.04	1.65	2.25-2.50	2.38	0.07	3.27	2.50-2.65	2.57	0.04	1.69

Fakfak (T. C. Maa) ; Kokoda-Pitoki (J. L. Gressitt) ; Wum, Upper Jimmi V. 840 m (J. L. Gressitt) ; Kumar, Upper Jimmi V., 1000 m (J. L. Gressitt) ; Wana, Upper Jimmi V., 1500 m (J. L. Gressitt) ; Tsenga, Upper Jimmi V., 1200 m (J. L. Gressitt) ; Oriomo Govt. Sta., Papua (J. L. Gressitt) ; Bulolo, 885-1200 m (E. J. Ford, Jr.) ; Bubia, Markham V., 50 m (J. L. Gressitt) ; Amok, 165 m (T. C. Maa) ; Daradae, 80 km N. of Port Moresby (T. C. Maa) ; Waris, S. of Hollandia, 450-500 m (T. C. Maa) ; Bialowat, Morobe Dist. (Stevens) ; Maffin Bay (E. S. Ross) ; Lae (F. E. Skinner, J. L. Gressitt) ; Wewak (J. L. Gressitt, T. Okada) ; Finschhafen (L. Wagner) ; Nabire, S. Geelvink Bay (H. Holtmann) ; Goodenough Is. (L. Loria) ; Haveri (L. Loria) ; Genjam, 40 km W. of Hollandia (T. C. Maa) ; Otomata Pl'n, 1 m E. of Moresby (J. L. Gressitt) ; Keparra-Sengi nr. Kokoda, 500 m (J. L. Gressitt) ; Sakalang, Salawaket (E. J. Ford, Jr.) ; Hollandia-Kotanica (T. C. Maa) ; Baiyer R., W. Highlands (J. L. Gressitt) ; Kassam 1350 m, 48 km E. of Kainantu (T. C. Maa) ; Suanimbu, 180 m, E. of Maprik (T. C. Maa) ; Normanby Is. (W. W. Brandt) ; Nadzab (E. O. Wilson, acc. 1090) ; Boana, Bunbok V. (E. O. Wilson, acc. 1122) : Bubia, 13 km NW Lae (E. O. Wilson, acc. 1074) ; Lower Busu R., Huon Pen. (E. O. Wilson, acc. 992) ; Sattelberg vic. 660 m, Huon Pen. (E. O. Wilson, acc. 722) ; Zingzingu, 1100 m, Huon Pen. (E. O. Wilson, acc. 767) ; Boingbongen, 900-1000 m, Huon Pen. (E. O. Wilson, acc. 778) ; Gemeheng, 1300 m, Huon Pen. (E. O. Wilson, acc. 782) ; Nganduo. 1000 m, Huon Pen. (E. O. Wilson, acc. 736) ; Joangeng. 1300 m, Huon Pen (E. O. Wilson, acc, 754) ; Valley of Kua R. vic. Zengaru, 800 m, Huon Pen, (E. O. Wilson, acc. 794). NEW BRITAIN : Warongoi V., Gazelle Pen. (J. L. Gressitt) ; Bainings, Gazelle Pen. (J. L. Gressitt) ; Kerawat, Gazelle Pen. (J. L. Gressitt, I. Edwards). NEW IRELAND : Ridge above "Camp Bishop" 15 km up Kait R., 250-750 m (J. L. Gressitt) ; "Camp Bishop" 12 km up Kait R., 240 m (E. J. Ford, Jr.). AUSTRALIA : Cape York (P. F. Darlington).

The type series of *bellicosa*, *crudelis* and *erosispina* were examined. The presence of three ocelli and the similarity in color pattern suggest that they are conspecific. Therefore, *bellicosa*, *crudelis* and *erosispina* are in fact all described from workers of the same species with some minor variations as would be expected from different populations. The question now is whether populations from Celebes, New Guinea, New Britain, New Ireland and Australia (hereafter referred to as the New Guinea area) are significantly different from other populations.

The coefficient of difference (CD) for each of the ten measurements and indices was computed to determine the difference between the New Guinea population and each of the other five populations. Table 2 shows that most of the ten characters have CD values even below the level of conventional subspecific distinctness ; *i.e.*, 75 per cent joint nonoverlap. Only the petiolar height has a CD value far above the level of conventional subspecific difference in all the comparisons, except the Philippine population, which has only 75 to

TABLE 2.—COEFFICIENTS OF DIFFERENCE BETWEEN NEW GUINEA AND OTHER POPULATIONS OF *P. BELLICOSA*

Characters	*New Guinea, N=154 vs Philippines, N=61*		*New Guinea, N=154 vs Borneo, N=89*		*New Guinea, N=154 vs. Sumatra, N=13*		*New Guinea, N=154 vs. Malaya, N=12*		*New Guinea, N=154 vs. Laos, N=14*	
	C.D.	*Joint nonoverlap per cent*	*C.D.*	*Joint nonoverlap per cent*	*C.D.*	*Joint nonoverlap per cent*	*C.D.*	*Joint nonoverlap per cent*	*C.D.*	*Joint nonoverlap per cent*
HW	0.28	<75	0.49	<75	0.27	<75	0.56	<75	0.06	<75
HL	0.28	<75	0.38	<75	0.06	<75	0.11	<75	0.30	<75
CI	0	0	0.17	<75	0.45	<75	0.92	82-84	0.69	<75
SL	0.06	<75	0.17	<75	0.05	<75	0.12	<75	0.04	<75
SI	0.65	<75	0.52	<75	0.57	<75	0.85	80-82	0.23	<75
PW	0.05	<75	0.35	<75	0.14	<75	0.21	<75	0.08	<75
MPL	0.51	<75	0.65	<75	1.19	88-89	0.64	<75	1.50	93-94
MTL	0.39	<75	0.08	<75	0.33	<75	0.06	<75	0.61	<75
PSEI	0.34	<75	0.38	<75	0.13	<75	0.39	<75	1.08	86-86
PH	0.72	75-80	1.83	>96	3.08	>96	2.03	>96	3.49	>96

80 per cent joint nonoverlap. This indicates that by resorting to this character, more than 96 per cent of the New Guinea population can be separated from more than 96 per cent of any of the other populations with the exception of the Philippine population. However, further analysis reveals that this character shows geographical gradation with the New Guinea and the Laos populations at each end (Fig. 12).

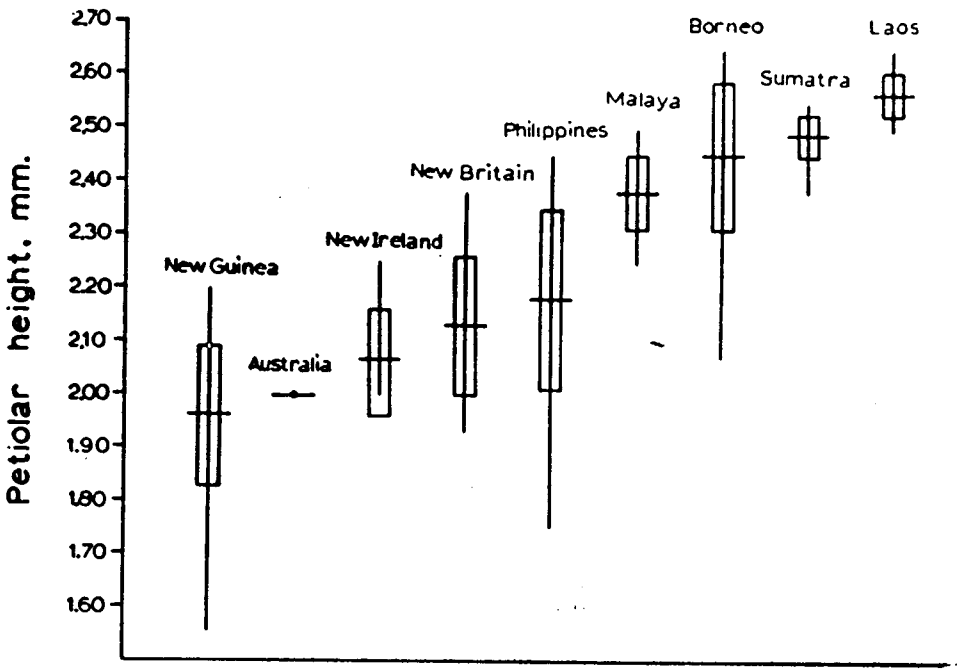


Fig. 12. Variation in the petiolar height of *P. bellicosa* from different localities. The vertical line indicates the total variation of the sample ; the hollow rectangle, one standard deviation on each side of the mean ; and the crossbar, the mean.

Color pattern seems to be a differentiating character between the New Guinea population complex and the other five populations. Workers from the New Guinea area all have a unicolored gaster while those from other areas mostly have a bicolored gaster. Specimens from Celebes have a dark reddish-brown alitrunk and a very dusky red gaster. Material from Australia, New Britain and New Ireland all have a dusky red alitrunk and a black gaster. Although the alitrunk of the workers from New Guinea varies from dusky red to very dusky red, the gaster is still uniformly black. The unicolored gasters are still found among the specimens from Borneo, though the gaster varies from blackish red to very dusky red. But most of the Bornean specimens have a dark reddish-brown first gastric segment with the rest of the gaster very dusky red. As for the alitrunk, it varies from dark reddish-brown, dusky red to very dusky red. Of these three color patterns, only dark reddish-brown is associated with

the bicolored gaster. Material from Laos, Thailand, Malaya and Sumatra have a rather uniform color pattern. They have a dark reddish-brown alitrunk and a dark reddish-brown plus very dusky red bicolored gaster. In Philippine specimens, the gaster is still bicolored, but the color patterns are different. Thus, a worker may have a dusky red alitrunk with a dusky red plus very dusky red gaster, or a dark reddish-brown alitrunk with a dark reddish-brown plus very dusky red gaster, or a moderate reddish-brown alitrunk with a pale reddish-brown plus dark reddish-brown gaster, and finally a pale reddish-brown alitrunk with a pale reddish-brown plus moderate reddish-brown gaster. However, no matter how strikingly the color pattern varies, it is obvious that the color pattern of the New Guinea population has integrated into that of the Borneo population.

Besides color pattern, the presence of three ocelli in the worker is also a distinct feature of the New Guinea population complex. But again, this character is by no means unique. It is true that there is hardly any recognizable ocellus in the specimens from Laos, Thailand, and some from Malaya, Sumatra and Philippines, three very obscure ocelli are still present in most of the specimens from Malaya, Sumatra and Philippines. The Bornean population again links the New Guinea population complex with other populations as far as this character is concerned. Most of the specimens from Borneo have a distinct median ocellus and rather obscure lateral ocelli. Some specimens have three obscure ocelli and there are a few specimens with only the obscure median ocellus.

Another character to be noted is the propodeal spines. In New Guinea, New Britain, New Ireland, Celebes, and Australian specimens, the two spines appear as two ridges with a point at each end and they are separated. Material from Loas, Thailand, Malaya, Sumatra and Philippines have two sharp propodeal spines contiguous at the base forming a V. These two types of propodeal spines are again found among the specimens from Borneo

In summary, specimens from the New Guinea area tend to have a darker color and a unicolored gaster. In addition, they have three ocelli, a shorter petiole spine, and two separated ridgy propodeal spines. Specimens from other populations tend to have a lighter color and a bicolored gaster. The petiolar spines are longer and the propodeal spines are sharp and contiguous at the base. There is also a tendency towards loss of the ocellus in these populations.

All of these geographical variations are clinal. There is an increase in mean petiolar height from the insular populations to the continental populations. But the decrease in color intensity and the increase in the obscurity of the ocellus are from the New Guinea area to the Philippines. In other words, these three characters are not in exact geographical concordance with any of the others, and yet these are the most distinct geographical variations that have been observed so far. Therefore, none of the populations can be considered discrete taxonomic entities.

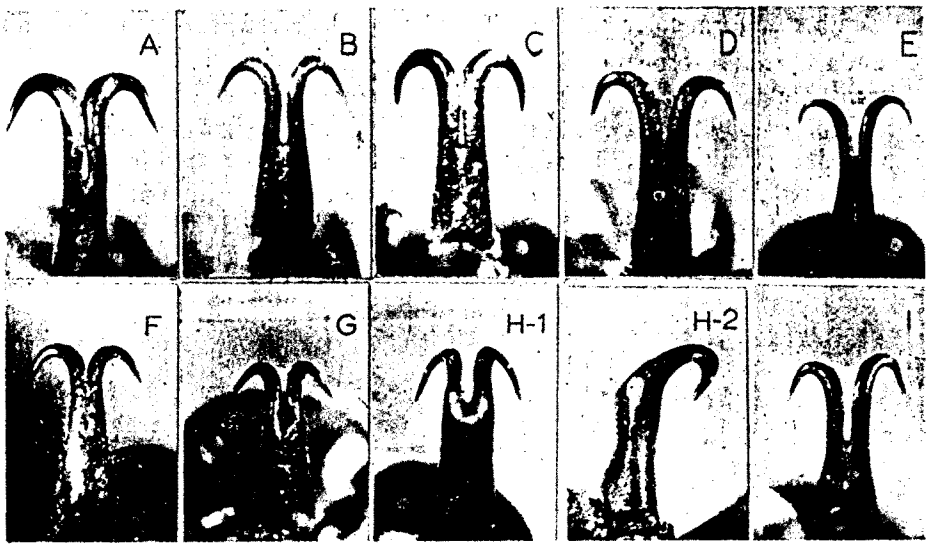


Fig. 13 Variation in the shape of the petiole in *P. bellicosa*. A, from worker outside of the New Guinea area. B-I, from workers from New Guinea area except E also from Philippines.

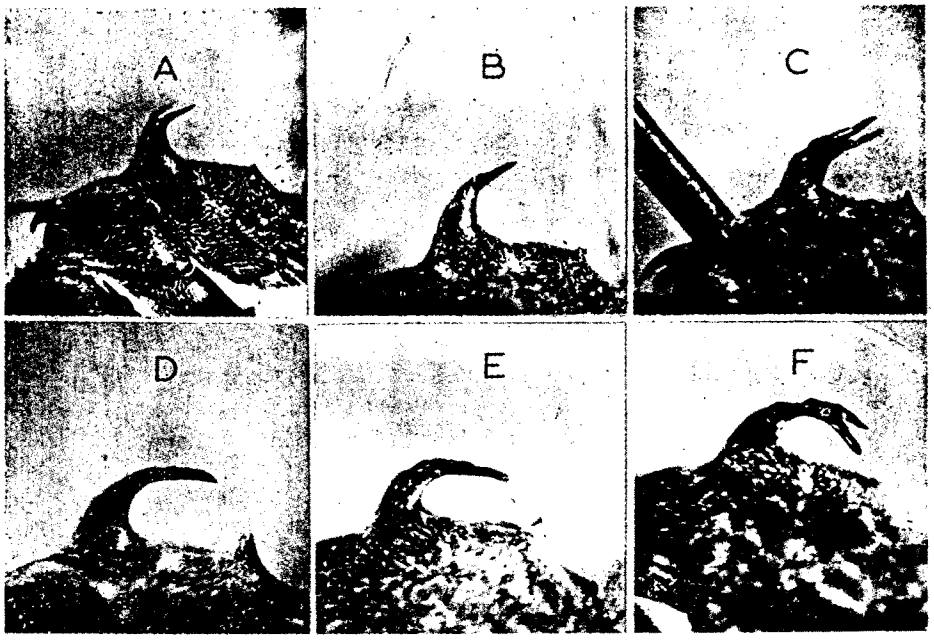


Fig. 14. Variation in the shape of the mesonotal spine in *P. bellicosa*. A, from worker outside of the New Guinea area. B-F, from workers in the New Guinea area.

Like many other *Polyrhachis* ants, the shape of the petiole in this group also shows striking variation (Fig. 13). However, this is a chaotic variation without any stable type to be followed. The only generalization that can be made is that specimens from the New Guinea area have shorter, separated hooks while those from other populations have long, contiguous hooks. Another chaotic variation is the mesonotal spines. In general, the New Guinea population complex has lanceolate mesonotal spines sometimes with gnawed edges (Fig. 14, B-F) while the other populations have rather pyramidal spines (Fig. 14, A)

For comparison of the similarity between any of two populations, the taxonomic distance was calculated. The result is shown in fig. 15. Based upon this

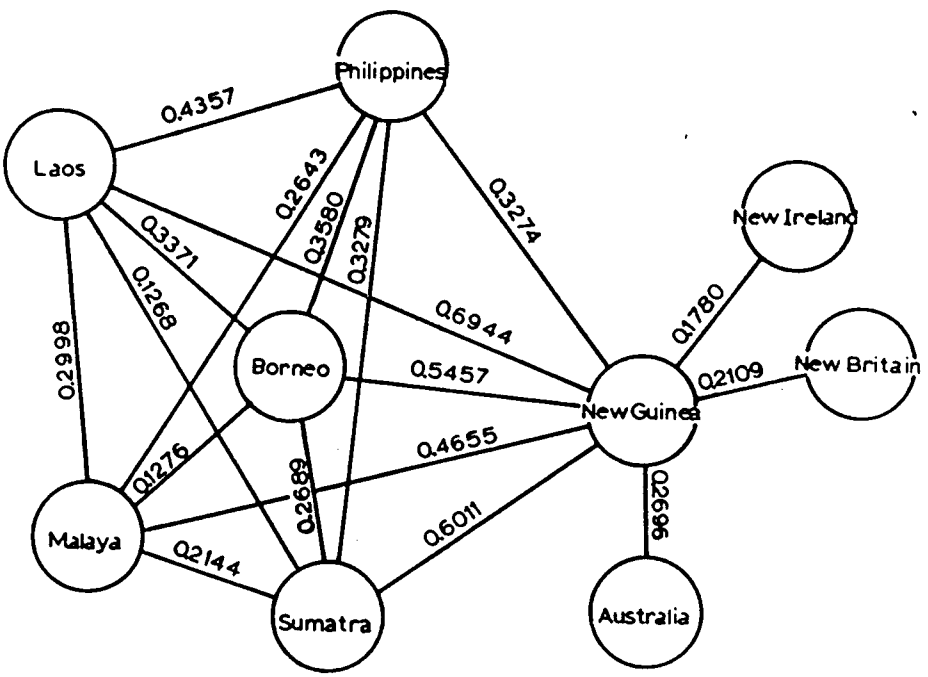


Fig. 15. Taxonomic distances between different populations of *P. bellicosa.*

value, the New Guinea population is more similar to the Philippine population than to the Borneo population. However, other characters such as color pattern and the presence of one or three ocelli suggest a reverse course of resemblance.

In many evolutionary lines there is an increase in size (Mayr and Vaurie, 1948), and for macroscopic meristic characters in general, a phylogenetic change in number much more frequently results in decrease than in an increase (Brown, 1965). Since the New Guinea population has the shortest petiole and three ocelli, it is very likely that the other populations were all derived from New Guinea. This assumption is further supported by the fact that the New Guinea

population also shows a very high variability for most of the quantitative characters studied (of. the CV values in table 1) and a high variation in both the mesonotal and petiolar spines (of. Figs. 13 and 14). It was probably this high variability which made it possible for the New Guinea population to colonize marginal islands.

Biology : In New Guinea, *bellicosa* nests are found mostly in herbaceous and shrubby ground vegetation ; the workers commonly forage on the ground (Wilson, 1959). A nest was also found between fallen leaves in a dry forest in Amboina (Karawajew, 1927).

2. Polyrhachis bihamata (Drury) (Figs. 16-22. Tables 3, 5-7.)

Formica bihamata Drury, 1773, *Illustr. Nat. Hist.*, **2** : 73, pl. 38, figs. 7-8, worker. Type locality : Drury gave "Island of Johanna near Madagascar," evidently in error ; Fr. Smith, 1857, *J. Proc. Linn. Soc. Zool.*, **2** : 58, fig. 19, worker ; Fr. Smith, 1860, *J. Proc. Linn. Soc. Zool. Suppl.*, **5** : 97, worker ; Mayr, 1867, *Tijdschr. Ent.*, **10** : 18, worker ; Mayr, 1872, *Ann. Mus. Civ. Stor. Nat. Genova*, **2** : 9, female ; Emery, 1887, *Ann. Mus. Civ. Stor. Nat. Genova*, (2) **4** : 238, worker ; Forel, 1891. *Grandidier Hist. Physic. Nat. Polit. Madagascar*, **20** : 78, worker, female ; Bingham, 1903, *Fauna British India, Hymenoptera*, **2** : 386, fig. 125, worker, nest; Donisthorpe, 1942, *Ann. Mag. Nat. Hist.* (11) **9** : 70, male.

Polyrhachis bihamata var. *perplexa* Santschi, 1925, *Bull. Soc. Vaud. Sci. Nat.*, **56** : 92, worker. Type locality : Muong Pek, Laos. **New Synonymy.**

Polyrhachis bihamata var. *minor* Karawajew, 1927, *Trav. Mus. Zool. Kieff.*, **3** : 12, worker. Type locality : Buitenzorg, Java. **New Synonymy.**

Polyrhachis bihamata var. *tonsilis* Santschi, 1928, *Tijdschr. Ent.*, **71** : 133, worker. Type locality : Sibolangit, Sumatra. **New Synonymy.**

Distribution : Lower Burma ; Tenasserim, extending into the Malay Peninsula, Sumatra, Borneo, Java and Moluccas. Fr. Smith (1858) cited this species from India, but it has never been reported from that area by any other author.

Syntypes : Four workers of *perplexa* measured-HW 2.30-2.45 mm, HL 2.63-2.75 mm, CI 87-89, SL 3.35-3.58 mm, SI 138-146, PW 1.25-1.37 mm, MPL 4.50-4.88 mm, PSEI 67-71, PH 3.00-3.18 mm. Two workers of *tonsilis* measured-HW 2.15-2.25 mm, HL 2.50 mm, CI 86-90, SL 3.13-3.15 mm, SI 139-146, PW 1.05-1.13 mm, MPL 2.50 mm, MTL (missing), PSEI 67-68, PH 2.75-2.90 mm.

Worker : HW 1.88-2.50 mm, HL 2.25-2.75 mm, CI 75-97, SL 3.00-3.50 mm, SI 133-170, PW 1.05-1.40 mm, MPL 2.38-3.15 mm, MTL 4.00-4.75 mm, PSEI 64-115. PH 2.50-3.13 mm. Alitrunk more or less rounded. Pronotum somewhat flat above but without traces of margins. Pronotal spines pointed outwards and bent backwards. Mesonotum with two pyramidal spines contiguous at base, rising upwards and bent backwards. Metanotal groove replaced by a ridge. Propodeum with two contiguous ridges. Basal face inclined, about

twice as long as the declivity. Petiole columnar bearing a pair of long, somewhat flattened hook-shaped spines which in most cases are parallel or even

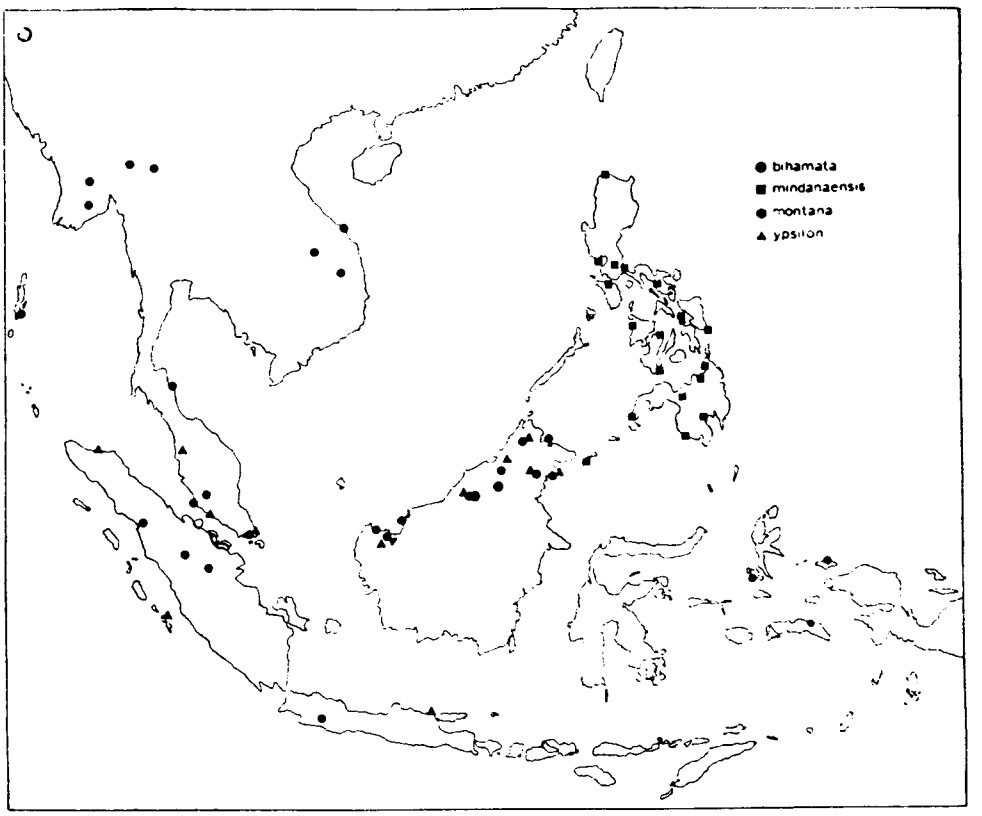


Fig. 16. Distribution of *P. bihamata, mindanaensis, montana* and *ypsilon*.

contiguous. Body sparsely covered with suberect hairs. Head black. Alitrunk, petiole, gaster and legs moderate reddish-brown or grayish-red, but the tip of the gaster is always darker in color.

Localities from which specimens have been studied: VIETNAM : Pleiku (R. E. Leech) ; Karyu Danar (N. R. Spencer). LAOS : Muong Pek (V. de Salvaza) ; Nuong Ya (R. E. Wheeler). THAILAND : Chiengmai (T. C. Maa, D. C. and E. B. Thurman) ; Doi Suthep (D. and E. Thurman) ; Nakhon Si Thammarat (H. Smith) ; Pahtoop Mts. (T. D. A. Cockerell). BURMA (G. B. King). MALAYA : Selangor (T. C. Maa) ; Kuala Tahan (Anonymous). ANDAMAN ISLANDS : Bijajag (B. B. Osmaston). SUMATRA : Sibolangit (J. B. Corporaal) ; Pematang (J. Mathews, W. M. Mann) ; Bangkinang (W. M. Mann), Lampeham (G. Fair-child). BORNEO : Tawau (T. C. Maa) ; Tanau, 500 m (T. C. Maa) ; Kalabakan (T. C. Maa) ; Sapagaya Lumber Camp, Sandakan

TABLE 3.—RANGES, MEANS, STANDARD DEVIATIONS, AND COEFFICIENTS OF VARIABILITY OF *P. BIHAMATA* FROM DIFFERENT LOCALITIES

ALL MEASUREMENTS ARE IN MILLIMETRES

Characters	*Borneo* N=32				*Sumatra* N=12				*Malaya* N=10				*Thailand* N=15			
	R	*M*	*SD*	*CV*	*R*	*M*	*SD*	*CV*	*R*	*M*	*SD*	*CV*	*R*	*M*	*SD*	*CV*
HW	2.00-2.50	2.27	0.12	5.29	1.88-2.46	2.21	0.16	7.24	2.18-2.40	2.32	0.07	3.02	2.08-2.45	2.32	0.10	4.44
HL	2.38-2.75	2.58	0.09	3.49	2.25-2.75	2.54	0.13	5.12	2.50-2.70	2.61	0.06	2.29	2.38-2.75	2.62	0.11	4.39
CI	84-92	88	2.40	2.73	75-97	87	5.97	6.86	87-91	88	1.21	1.37	87-92	88	1.46	16.53
SL	3.00-3.50	3.26	0·13	3.99	3.05-3.41	3.24	0.13	4.01	3.25-3.50	3.37	0.09	2.67	2.88-3.50	3.29	0.14	4.41
SI	133-154	143	6.20	4.33	135-170	147	10.38	7.06	141-149	145	3.27	2.25	138-149	141	3.23	2.28
PW	1.08-1.38	1.24	0.07	5.64	1.05-1.30	1.20	0.07	5.83	1.13-1.40	1.23	0.08	6.50	1.00-1.35	1.22	0.09	7.38
MPL	2.58-3.15	2.82	0.14	4.96	2.38-2.88	2.70	0.18	6.67	2.50-2.88	2.77	0.11	3.97	2.50-3.00	2.78	0.13	4.68
MTL	4.00-4.75	4.41	0.18	4.08	4.13-4.65	4.44	0.15	3.38	4.18-4.68	4.51	0.15	3.32	3.90-4.68	4.46	0.21	4.71
PSEI	64-115	86	10.02	11.65	64-92	77	9.36	12.15	57-89	66	10.11	15.31	60-92	77	8.65	11.23
PH	2.63-3.13	2.86	0.13	4.54	2.50-3.08	2.84	0.18	6.34	2.75-3.05	2.92	0.12	4.11	2.63-3.20	2.89	0.19	6.57

Bay (J. L. Gressitt) ; Kaingaran (P. W. Bryant) ; Rajang Delta (T. C. Maa) ; Serambu Mt., Kuching (H. Smith) ; Lundu (T. C. Maa, N. W. Smith) ; Base of Mt. Dulit (E. Mjöberg).

Like *bellicosa*, there is an increase in mean values of most of the measurements from the insular to the continental populations, although it is not as distinct as in *bellicosa* (cf. Table 3). I was not able to gain access to any type or material of either *bihamata* or *minor*, but I have studied syntypes of *perplexa* and *tonsilis*. The measurements of these two type series are all within the limits of the *bihamata* workers studied. As Santschi (1928) stated, the variety *tonsilis* is a transition between *bihamata* and *bellicosa*. But the over-all characters are much more like *bihamata* as shown in the syntype workers. The minor variations in size, color and pubescence are not significant enough for me to recognize it as a taxonomic entity. As to *perplexa*, even Santschi himself confused this variety with the typical *bihamata* and admitted that intermediates are not wanting (Santschi, 1925). The brief description of the other variety *minor* does not give us sufficient information about its taxonomic features. However, if the major differences are the smaller size and the somewhat reddish color of this variety (Karawajew, 1927), it is quite obvious that the single worker upon which Karawajew described this form is only an individual variant of the Java population of *bihamata*. Further, the name *minor* is preoccupied by Forel, 1886.

A single male labelled "Dukhun, ex coll. Sykes." was described as *Polyrhachis bihamata* by Donisthorpe (1942). Since no worker specimen is associated with this male, it may be questioned whether it is really *bihamata*.

Biology : In East India, one *bihamata* nest of silky yellowish-brown material was found close to the ground in the center of a clump of bamboos (Bingham, 1903).

3. **Polyrhachis ypsilon** Emery (Figs. 16-22. Tables 4-7)

Polyrhachis ypsilon Emery, 1887, *Ann. Mus. Civ. Stor. Nat. Genova*, (2) 4 : 239, worker. Type locality : Singapore ; Bingham, 1903, *Fauna British India, Hymenoptera*, 2 : 387, fig. 126, worker.

Polyrhachis ypsilon var. *victoris* Santschi, 1925, *Bull. Soc. Vaud. Sci. Nat.*, 56 : 93, worker. Type locality : Labuang Bilik, Sumatra. **New Synonymy.**

Polyrhachis ypsilon ab. *synacantha* Santschi, 1933, *Bull. Mus. R. Hist. Nat. Belge*, 9 : 2, worker. Type locality : Kp. Makoendjoeng, Borneo. **New Synonymy.**

Distribution : The Malay Peninsula, Sumatra, Java, and Borneo. Forel (1893) also received this species from Ceylon.

Lectotype (herein designated from a syntype in the collection of Museo Civico di Storia Naturale). HW 2.62 mm, HL 3.00 mm, CI 87, SL 3.90 mm, SI 149, PW 1.60 mm, MPL 3.07 mm, MTL 5.40 mm, PSEI 150, PH 3.17 mm. Clypeus convex, slightly carinated. Median ocellus present, no lateral ocelli. Alitrunk rounded. Pronotum somewhat flat on top, but no traces of margins present. Pronotal spines very stout, pointing outwards and slightly backwards, black throughout

the whole length. Mesonotal spines less pyramidal than in *bihamata*, rising upwards and bent backwards, parallel when viewed from top. Metanotal groove present. Propodeum with two contiguous ridges between basal face and the declivity. The basal face is about twice as long as the declivity. The face of the declivity flat and slightly margined along the sides. Mesonotal spines only the distal half black. Petiole columnar, with two long, hook-shaped spines diverging widely from their base, with left hook slightly longer than right hook. Body densely covered with hairs. Antennae and legs black. Alitrunk dark reddish-brown. Gaster reddish-black.

Other Type Material : One paralectotype worker of *ypsilon* measured-HW 2.63 mm, HL 3.00 mm, CI 88, SL 3.75 mm, SI 142, PW 1.50 mm, MPL 3.25 mm, MTL 5.07 mm, PSEI 140, PH 3.45 mm. Three syntype workers of *victoris* measured-HW 2.58-2.63 mm, HL 2.88-3.00 mm, CI 88-90, SL 3.65-3.75 mm. SI 140-145, PW 1.45-1.50 mm, MPL 3.15-3.25 mm, MTL 4.85-5.00 mm, PSEI 80-107, PH 3.50-3.55 mm.

Worker : HW 2.13-2.88 mm, HL 2.50-3.14 mm, CI 80-105, SL 3.00-4.00 mm, SI 121-154, PW 1.20-1.81 mm, MPL 2.80-3.63 mm, MTL 4.25-5.56 mm, PSEI 67-180, PH 2.50-3.75 mm.

Localities from which specimens have been studied : BORNEO : Forest camp, 19 km N. of Kalabakan (Y. Hirashima) ; Tawau (Y. Hirashima, T. C. Maa, Ho Kai Him) ; Pajan (E. Mjöberg) ; Tambunan (P. W. Bryant) ; Forest Camp 9.8 km SW of Tenom (Y. Hirashima) ; Ranau, 500 m (T. C. Maa) ; Kuching (H. Smith) ; Sadong (H. Smith) ; Base of Mt. Dulit (E. Mjöberg). SUMATRA : Labuang Bilik (V. Surbek) ; Wai Lima, Lampongs (Karny) ; Bireuen (W. M. Mann). MALAYA : Perak (R. Martin) ; Malacca (Shandinger).

The variety *victoris*, which Santschi deseribed from Sumatra, is merely a geographical variant with a slight change in color. I cannot locate the type of *synacantha*, which was also described by Santschi from Borneo. Judging from the original description, the single specimen he used to describe this form is just an individual variant of the Borneo population. Three of my specimens from Borneo fit his description. The petiolar spines are all parallel for some distance. However, there are not any other significant deviations from the syntype worker of *ypsilon* and other specimens.

4. Polyrhachis mindanaensis (Emery), new status (Figs. 16-22. Tables 4-6)

Polyrhachis ypsilon var. *mindanaensis* Emery, 1923, *Ent. Mitt.*, **12** : 62, worker. Type locality : Zamboanga, Philippines.

Distribution : Philippines.

Lectotype : (Herein designated from a syntype in the collection of Museo Civico di Storia Naturale). HW 2.25 mm, HL 2.62 mm, CI 86, SL 3.40 mm, SI 151, PW 1.25 mm, MPL 2.67 mm, MTL 4.57 mm, PSEI 151, PH 2.50 mm.

TABLE 4.—RANGES, MEANS, STANDARD DEVIATIONS, AND COEFFICIENTS OF VARIABILITY OF *P. MONTANA*, *MINDANAENSIS*, AND *YPSILON*

ALL MEASUREMENTS ARE IN MILLIMETRES

Characters	*P. montana* N=22				*P. mindanaensis* N=100				*P. ypsilon* fr. Borneo N=62				*P. ypsilon* fr. Sumatra N=15			
	R	*M*	*SD*	*CV*	*R*	*M*	*SD*	*CV*	*R*	*M*	*SD*	*CV*	*R*	*M*	*SD*	*CV*
HW	2.07-2.30	2.17	0.06	2.76	2.15-2.65	2.42	0.12	4.96	2.13-2.88	2.57	0.17	6.61	2.25-2.75	2.46	0.16	6·50
HL	2.30-2.50	2.40	0.05	2.08	2.50-2.90	2.71	0.10	3.69	2.50-3.14	2.87	0.16	5.57	2.63-3.00	2.79	0.14	5.02
CI	88-93	90	1.39	1.54	83-96	89	2.35	2.64	85-105	90	2.98	3.31	80-93	88	2.97	3.37
SL	2.75-3.05	2.96	0.26	8.78	3.00-3.83	3.50	0.16	4.57	3.00-4.00	3.62	0.20	5.52	3.25-3.75	3.51	0.17	4.84
SI	132-141	136	2.51	1.84	133-158	144	4.19	2.91	121-150	140	4.60	3.28	136-154	143	4.55	3.18
PW	1.05-1.25	1.15	0.06	5.22	1.00-1.50	1.27	0.09	7.08	1.25-1.81	1.52	0.14	9.21	1.20-1.75	1.37	0.20	1.46
MPL	2.50-2.75	2.59	0.26	10.04	2.50-3.25	2.87	0.13	4.53	2.80-3.63	3.29	0.21	6.38	2.80-3.33	3.04	0.19	6.25
MTL	3.88-4.25	4.12	0.31	7.52	4.13-5.32	4.75	0.24	5.05	4.25-5.56	4.97	0.27	5.43	4.50-5.25	4.79	0.24	5.01
PSEI	155-288	190	15.44	81.26	57-167	115	17.39	15.12	67-180	129	23	17.83	80-170	130	26.22	20.17
PH	1.88-2.13	2.01	0.08	3.98	2.25-3.10	2.66	0.16	6.01	2.80-3.75	3.31	0.23	6·95	2.50-3.55	2.99	0.35	11.86

Median ocellus present, no lateral ocelli. Pronotum somewhat flat but without traceable margins. Pronotal spines stouter than in *bihamata*, only black at tip. Mesonotum with two spines pyramidal in shape, closer together than in *ypsilon*, but not as in *bihamata*. Metanotal groove present. Propodeum with horizontal ridge between basal face and the declivity but without traceable margines along the sides.

Paralectotype : One worker measured-HW 2.38 mm, HL 2.75 mm, CI 86, SL 3.60 mm, SI 151, PW 1.40 mm, MPL 3.00 mm, MTL 4.72 mm, PSEI 143, PH 2.35 mm.

Worker : HW 2.15-2.65 mm, HL 2.50-2.90 mm, CI 83-96, SL 3.00-3.83 mm, SI 133-158, PW 1.00-1.50 mm, MPL 2.50-3.25 mm, MTL 4.13-5.32 mm, PSEI 57-167, PH 2.25-3.10 mm.

Localities from which specimens have been studied : PHILIPPINES : Limay, Luzon, (G. Boettcher, R. C. McGregor) ; Ginoog, Misamis (A. Reyes) ; Lucban, Luzon (R. C. McGregor) ; Mt. Iriga, 500-600 m, Camarines Sur, Luzon (H. M. Torrevillas) ; Calicoan I. (F. F. Bibby) ; Sacret Mt., Lanao (J. W. Chapman) ; Lake Mainit, Mindanao (C. M. Yoshimoto) ; Minalwang, Misamia (H. Torrevillas) ; Milbuk, Mindanao (H. E. Milliron) ; Boleto Pass, Luzon (R. C. McGregor) ; Zamboanga, Mindanao (H. E. Milliron, L. W. Quate, B. P. Clark) ; Fabrica, Negros (H. W. Chapman) ; Flores, Panay (R. C. McGregor) ; Culasi, Panay, (R. C. McGregor) ; Laguna, Luzon (R. C. McGregor) ; Baco, Mindoro (P. deMesa) ; Los Banos (F. X. Williams, Baker, U. B. Uichanco) ; Dansalan, Lanao (Henry Lopez) ; Mt. Apo, Mindanao (C. F. Clagg) ; Bongao Is., Sulu Arch. (H. E. Milliron) ; Mt. Makiling, Luzon (F. X. Williams, O. H. Swezey, Baker) ; Dumaguete, Negros (J. W. Chapman) ; Biliran Is. (R. C. McGregor).

This was first described as a variety of *ypsilon*, probably because it also has widely divergent petiolar spines. However, further study shows that it has combined characters of *bihamata* and *ypsilon*. The following is an analysis of these characters :

bihamata elements—

1. Smaller body size.
2. Less hairy.
3. Pronotal spines only black at tip and curved backwards.
4. Mesonotal spines contiguous at base.

ypsilon elements—

1. Pronotal spines relatively stout.
2. Antennae and legs longer.
3. Petiolar spines widely diverged.

Because of these mixed characters, specimens from the Philippines are sometimes called *bihamata* by one author and *ypsilon* by another. However, neither *bihamata* nor *ypsilon* possesses these combined characters. Possibly this is *bihamata* showing "character release" after sympatry and displacement elsewhere with *ypsilon*. But at present I do not have enough data to substantiate this. The color pattern, pronotal spines, and the body size strongly suggest that this is closer to *bihamata* than to *ypsilon*.

5. Polyrhachis montana Hung, sp. nov (Figs. 16-22. Tables 4-5)

Distribution : BORNEO. Type locality : Mt. Murud. The type series was collected by E. Mjöberg at Mt. Murud and Mt. Dulit. No data was given.

Holotype : HW 2.20 mm, HL 2.43 mm, CI 90, SL 3.00 mm, SI 141, PW 1.13 mm, MPL 2.60 mm, MTL 4.13 mm, PSEI 200, PH 1.90 mm. Mandibles with 5 teeth sequentially reducing in length, the apical is about twice as long as the basals. Clypeus convex, slightly carinated. Head, excluding the mandibles, somewhat longer than broad, slightly rounded. Median ocellus present. No lateral ocelli. Alitrunk more or less rounded. Pronotum slightly marginated with two spines rather stout at base pointing outwards and curved with the tips slightly pointing backwards. Mesonotum with two widely separated pyramidal spines raising upwards, outwards and bending backwards at an angle greater than 90 degrees. Metanotal groove obscure. Propodeum with the basal face about three times as long as the declivity. Declivity with one inclined ridge on each side forming an isosceles triangle with the top angle and the bottom leg notched. No distinct ridge between the basal face and the declivity. Petiole columnar, but rather flattened, bearing two long hook-shaped spines diverging widely from their bases. Gaster slightly elliptical with the tergite of the first segment covering about two-fifths of the gaster. Body densely covered with light brown suberect hairs. Antennae and head very dusky red. Mandibles dusky red. Alitrunk and petiole moderate reddish-brown. Pronotal, mesonotal and petiolar spines black at tip. Legs dark reddish-brown. Gaster dark reddish-brown with the first segment slightly lighter.

Paratypes : 7 workers from Mt. Murud measured-HW 2.08-2.25 mm, HL 2.33-2.50 mm, CI 89-92, SL 2.75-3.05 mm, SI 132-141, PW 1.05-1.25 mm, MPL 2.50-2.75 mm, MTL 4.00-4.25 mm, PSEI 175-200, PH 1.88-2.13 mm. 14 workers from Mt. Dulit SL 2.88-3.15 mm, SI 133-139, PW 1.05-1.25 mm, MPL 2.50-2.75 mm, MTL 3.88-4.37 mm, PSEI 160-200, PH 1.95-2.25 mm.

Type Deposition : Holotype and paratype in MCZ ; paratypes in the U. S. National Museum and Bishop Museum.

The unique character of this new species is its low petiole, which has more than 96 per cent joint nonoverlap with any of the species compared (cf. Table 5). It also has a relatively high per cent of nonoverlap with other species in most of

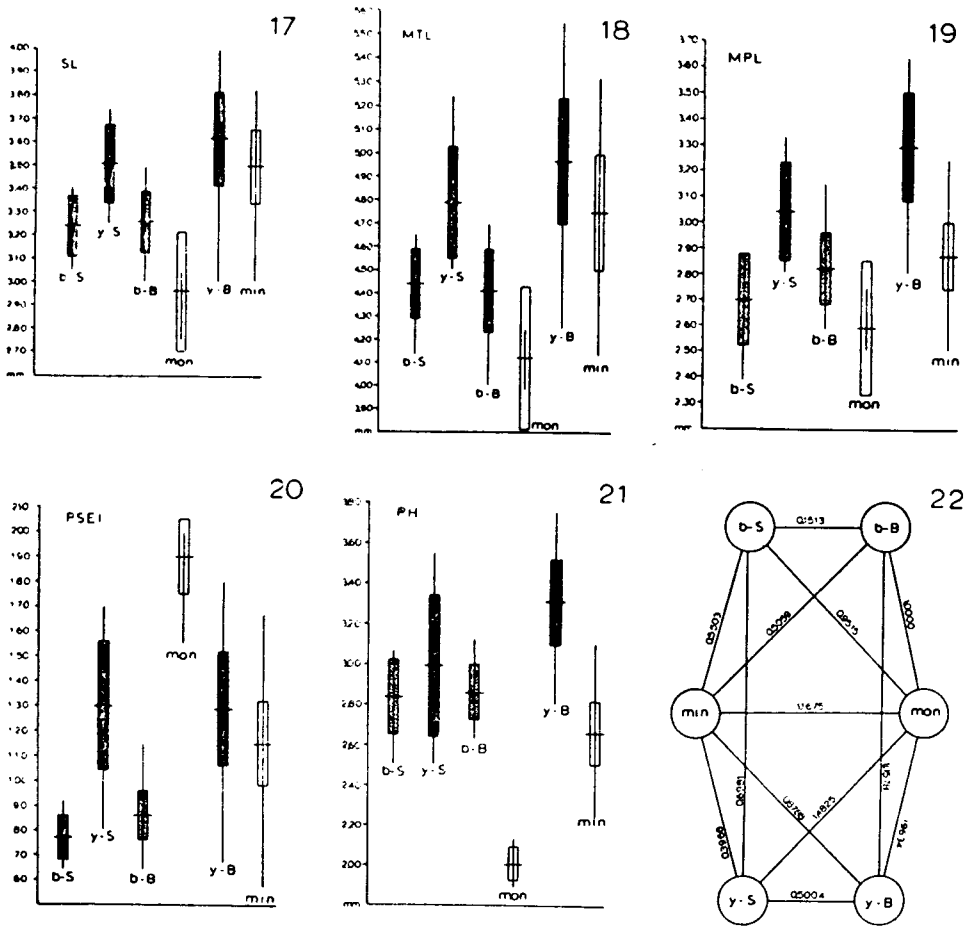


Fig. 17. Variation in the scape length of *P. bihamata*, *ypsilon*, *montana* and *mindanaensis*. b-S *bihamata* from Sumatra ; b-B *bihamata* from Borneo ; y-S *ypsilon* from Sumatra ; y-B *ypsilon* from Borneo ; mon *montana* ; min *mindanaensis*. The vertical line indicates the total variation of the sample ; the rectangle, one standard deviation on each side of the mean ; and the crossbar, the mean.

Fig. 18. Variation in the metathoracic tibial length of *P. bihamata*, *ypsilon*, *montana*, and *mindanaensis*. Abbreviations and explanation as in fig. 17.

Fig. 19. Variation in the mesonoto-propodeal length in *P. bihamata*, *ypsilon*, *montana*, and *mindanaensis*. Abbreviations and explanation as in fig. 17.

Fig. 20. Variation in the petiolar spine expansion index in *P. bihamata*, *ypsilon*, *montana*, and *mindanaensis*. Abbreviations and explanation as in fig. 17.

Fig. 21. Variation in the petiolar height in *P. bihamata*, *ypsilon*, *montana*, and *mindanaensis*. Abbreviations and explanation as in fig. 17.

Fig. 22. Inter and intra-specific taxonomic distances of *P. bihamata*, *ypsilon*, and *mindanaensis*. Abbreviations as in fig. 17.

TABLE 5.—COEFFICIENTS OF DIFFERENCE BETWEEN *MONTANA* AND OTHER SPECIES

Characters	*montana vs. ypsilon* (Borneo)		*montana vs. bihamata* (Borneo)		*montana vs. ypsilon* (Sumatra)		*montana vs. bihamata* (Sumatra)		*montana vs. mindanaensis*	
	C.D.	*Joint nonoverlap per cent*	*C.D.*	*Joint nonoverlap per cent*	*C.D.*	*Joint nonoverlap per cent*	*C.D.*	*Joint nonoverlap per cent*	*C.D.*	*Joint nonoverlap per cent*
HW	1.74	95-96	0.55	<75	1.32	90-91	0.18	<75	1.39	91-92
HL	2.24	>96	1.28	90	2.05	>96	0.78	75-80	2.07	>96
CI	0	0	0.53	<75	0.46	<75	0.41	<75	0.27	<75
SL	1.43	92-93	0.77	$75\text{-}8_0$	1.28	90	0.72	75-80	1.28	90
SI	0.01	<75≅0	0.80	75-80	0.99	82-84	0.01	≅0	1.19	88-89
PW	1.85	>96	0.69	75-80	0.85	75-80	0.38	<75	0.80	75-80
MPL	1.49	93-94	0.57	<75	1.00	84-85	0.25	<75	0.72	75-80
MTL	1·46	92-93	0.59	<75	1.22	88-89	0.69	75-80	1.14	87-88
PSEI	1.51	95-94	4.08	>96	1.44	92-93	4.56	>95	2.28	>96
PH	4.19	>96	4.05	>69	2.28	>96	3-19	>96	2.71	>96

TABLE 6.—COEFFICIENTS OF DIFFERENCE BETWEEN *MINDANAENSIS* AND OTHER SPECIES

Characters	*mindanaensis vs. bihamata* (Borneo)		*mindanaensis vs. bihamata* (Sumatra)		*mindanaensis vs. ypsilon* (Borneo)		*mindanaensis vs. ypsilon* (Sumatra)	
	C.D.	*Joint nonoverlap per cent*	*C.D.*	*Joint nonoverlap per cent*	*C.D.*	*Joint nonoverlap per cent*	*C D.*	*Joint nonoverlap per cent*
HW	0.62	<75	0.75	75-80	0.52	<75	0 14	<75
HL	0.68	<75	0.74	75-80	0.61	<75	0.33	<75
CI	0.21	<75	0.24	<75	0.19	<75	0.19	<75
SL	0.83	75-80	0.90	80-82	0.33	<75	0.30	<75
SI	0.10	<75	0.20	<75	0·45	<75	0·11	<75
PW	0·19	<75	0.44	<75	1·09	86-87	0·34	<75
MPL	0.18	<75	0.55	<75	1·23	89	0·53	<75
MTL	0·81	75-80	0.79	75-80	0·43	<75	0·08	<75
PSEI	1.06	85-86	1.42	92-93	0·35	<75	0·34	<75
PH	0·69	75-80	0.53	<75	1·67	95-96	0·65	<75

TABLE 7.—COEFFICIENTS OF DIFFERENCE BETWEEN *BIHAMATA* AND *YPSILON* AND EACH SPECIES FROM DIFFERENT LOCALITIES

Characters	*bihamata* (Sumatra) *vs.* *bihamata* (Borneo)		*bihamata* (Sumatra) *vs.* *ypsilon* (Sumatra)		*ypsilon* (Borneo) *vs.* *ypsilon* (Sumatra)		*ypsilon* (Borneo) *vs.* *bihamata* (Borneo)	
	C.D.	*Joint nonoverlap per cent*	*C.D.*	*Joint nonoverlap per cent*	*C.D.*	*Joint nonoverlap per cent*	*C.D.*	*Joint nonoverlap per cent*
HW	0.21	<75	0.78	75-80	0.33	<75	1.03	84-85
HL	0.18	<75	0.92	82-84	0.27	<75	1.16	87-88
CI	0.12	<75	0.11	<75	0.34	<75	0.37	<75
SL	0.08	<75≅0	0.90	80-82	0.30	<75	1.09	86-87
SI	0.24	<75	0.27	<75	0.43	<75	0.28	<75
PW	0.28	<75	0.63	<75	0.44	<75	1.33	90-91
MPL	0.37	<75	0.92	82-84	0.62	<75	1.34	91
MTL	0.09	<75≅0	0.90	80-82	0.35	<75	1.24	89-90
PSEI	0.46	<75	1.49	92-93	0.02	<75≅0	1.30	90-91
PH	0.06	<75≅0	0.28	<75	0.55	<75	1.25	89-90

the measurements and indices (cf. Figs. 17-21, Table 5). Its propodeum also has a longer basal face, which is about three times as long as the declivity. The declivity has one ridge on each side forming an isosceles triangle with the top angle and the bottom leg notched. The mesonotal spines are lower in profile and farther apart than any other species. The taxonomic distances between this and other species from different localities are also highly significant (cf. Fig. 22). The distance between *montana* and *bihamata* or *ypsilon* from Borneo and Sumatra are greater than the distance between *bihamata* and *ypsilon* when they are sympatric either in Borneo or Sumatra. All this evidence suggests that *montana* is a distinct species.

Biology : So far known only from Mt. Murud and Mt. Dulit.

6. Polyrhachis lamellidens Smith (Figs. 1, 3, 8-10, 23. Table 8.)

Polyrhachis lamellidens Fr. Smith, 1874, *Trans. Ent. Soc. London*, p. 403, worker. Type locality : Hiogo, Japan ; Mayr, 1878, *Verh. Zool.-Bot. Ges. Wien*, 28 : 652, worker ; Wheeler, 1906, *Bull. Amer. Mus. Nat. Hist.*, 22 : 327, fig. 2, worker ; Fukano, 1908, *Konch. Sek. Gifu, 12 : 271*, figure, worker, nest ; Yano, 1911, *Dobutsu-gaku Zashi,*

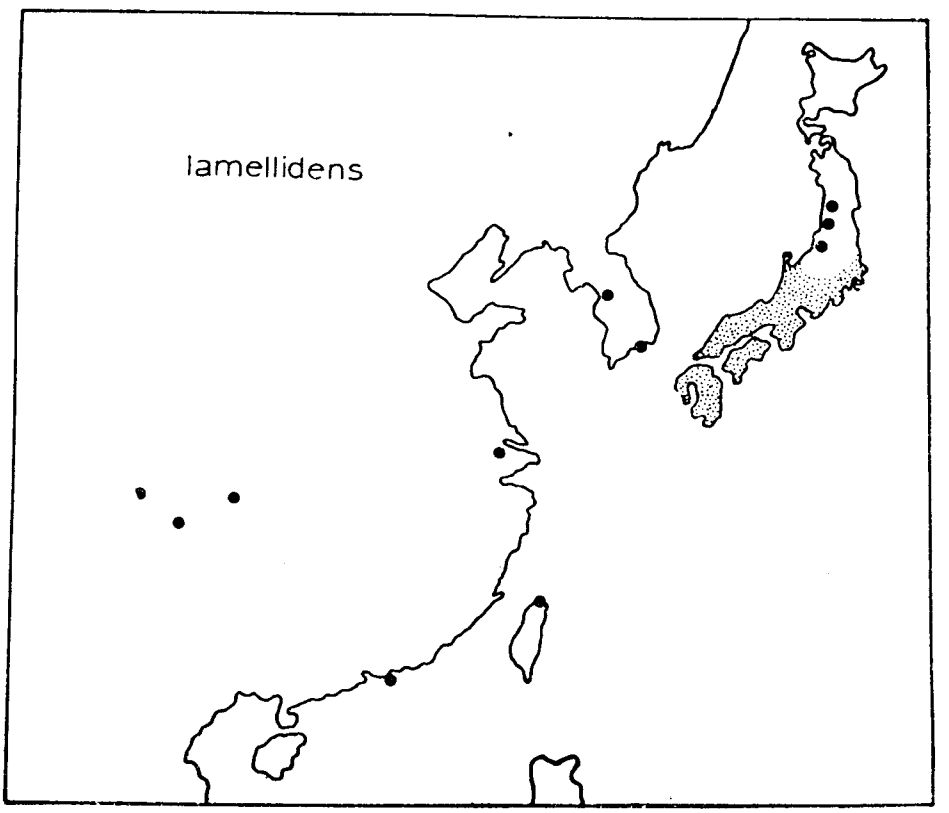


Fig. 23. Distribution of *P. lamellidens*.

23 ; 250, worker. female, male, larva, nest, flight ; Teranishi 1929, *Dobutsu-gaku Zashi*, 41 : 242, habits. distribution ; Donisthorpe, 1937, *Ann. Mag. Nat Hist.*, 19 : 627, female; Wheeler and Wheeler, 1953, *Ann. Ent. Soc. America*, 46 : 210, larva ; Okamoto 1957, *Gensi*, 5 : 42 habits ; Kohriba, 1963, *Kontyu*, 31 : 200, parasitic life.

Distribution : Japan, Korea, Mainland China, Formosa and Hong Kong.

Holotype (BM Type Hym. 11-262, worker) : HW 2.00 mm, HL 2.15 mm, CI 93, SL 2·62 mm, SI 131, PW 1·37 mm, MPL 2.00 mm, MTL 3.00 mm, PSEI 163, PH 1.87 mm.

Worker : HW 1.70-2.08 mm, HL 1.88-2.25 mm, CI 84-94, SL 2.15-2.63 mm SI 122-134, PW 1.10-1.50, mm, MPL 1.80-2.15 mm, MTL 2.65-3.08 mm, PSEI 140-233, PH 1.65-2.13 mm. Clypeus convex, with a sharp central longitudinal carina. No ocellus. Alitrunk margined with prominent ridges which are sharply interrupted at the pronounced promesonotal suture and the metanotal groove. Pronotum about as broad as long, its lateral ridge continued anteriorly on each side into a long spine, which is directed outward and forward and slightly curved downward at its tip. The spine is about as long as the pronotum. Mesonotum broader than long, bearing at the middle of each side a short rapidly tapering spine curved upward, outward and inclined backward. Propodeum about one-seventh longer than broad with ridge along the side extending posteriorly into a short, blunt spine which is about half the length of the propodeum. The ridge also continues down along the side of the declivity. Petiole columnar, anterior face convex, bearing a pair of long, somewhat flattened, hook-shaped spines, which diverge laterally and are inclined over the basal segment of the gaster. Gaster spherical with the tergite of the first segment covering almost half of the gaster. Mandibles, clypeus, occiput and legs with sparse, suberect hairs. Pubescence very sparse on the head and gaster, more abuudant on the pleurae and base of the gaster. Head very dusky red and finely shagreened. Alitrunk and petiole dark reddish-brown and punctate-rugulose. Gaster very dusky red and very shiny.

Male : Black and hairy with yellowish-brown hairs all over the body except the legs. Mandibles with pointed apex, masticatory border unarmed. Mesonotum convex, alitrunk without any spines. Petiolar spines short and tuberculate. Hind wing without discoidal cell. Genitalia with serrated lamina aedeagalis and pegged cuspis volsellaris and digitus volsellaris.

Localities from which specimens have been studied : JAPAN : Tachikawa (L. Gressitt) ; Tokyo (L. Gressitt) ; Kanagawa (H. Sauter) ; Odawara (H. Imai). KOREA keiki-do, Keijo-fu (T. J. Jo). MAINLAND CHINA : Chungking (D. C. Graham) ; Suifu (D. C. Graham) ; Yachow (D. C. Graham) ; Mokanshan (N. G. Gee) ; Soochow (N. G. Gee). FORMOSA : Shinten (R. Takahashi).

Specimens from Japan, Western China and Central China have been measured. No significant variation was observed among them (cf. Table 8).

TABLE 8.—RANGES, MEANS, STANDARD DEVIATIONS AND COEFEICIENTS OF VARIABILITY OF *P. LAMELLIDENS* FROM DIFFERENT LOCALITIES

ALL MEASUREMENTS ARE IN MILLIMETRES

Characters	*Japan N=17*				*Eastern China N=16*				*Central China N=11*			
	R	*M*	*SD*	*CV*	*R*	*M*	*SD*	*CV*	*R*	*M*	*SD*	*CV*
HW	1.75-2.05	1.88	0.02	1.06	1.70-2.08	1.87	0.11	5.83	1·70-1·95	1.83	0.08	4.48
HL	1.95-2.25	2.11	0.09	4.59	1.90-2.13	2.07	0.10	4.88	1·88-2·10	2.03	0.09	4.63
CI	84-92	89	2.08	2.33	87-94	90	2.06	2.29	86-94	90	3.11	3.46
SL	2.25-2.58	2.41	0.12	5.03	2.25-2.63	2.39	2.10	4.31	2·15-2·50	2.35	0.10	4.42
SI	122-134	128	3.62	2.83	123-138	127	3.97	3.13	122-136	128	3.28	2.57
PW	1.12-1.50	1.23	0.10	8.21	1.00-1.37	1.21	0.11	9.50	1.10-1·30	1.19	0.07	5.71
MPL	1.88-2.13	1.97	0.09	4.47	1.80-2.15	1.98	0.09	4.54	1·80-2·13	1.98	0.10	4.95
MTL	2.65-3.05	2.87	0.12	4.32	2.70-3.25	2.90	0.16	5.48	2·65-3·00	2.86	0.13	4.58
PSEI	141-200	166	16.80	10.12	140-186	171	17.78	10.39	150-233	177	21.34	12.06
PH	1.65-2.00	1.83	0.10	5.63	1.75-2.08	1.91	0.14	7.12	1.68-2.00	1·81	0.11	6.08

Biology : Nests of *lamellidens* are usually found in rotten logs (Yano, 1911), but occasionally underground (Brown, pers. commun.). Yano (1911) also observed one colony to temporarily occupy a nest of *Camponotus herculeanus japonicus* in the ground while moving into a new nest in a bamboo fence. Kohriba (1963) put one female into the observation cage with 12 workers of *Camponotus herculeanus japonicus* after her nuptial flight. She was later accepted and her broods were tended by the host workers. The flight season is from late October to early November although male and female alates were also found in late July (Yano, 1911). The chromosome numbers are n=21, 2n=42 (Imai, pers. commun.).

7. Polyrhachis craddocki Bingham

Polyrhachis craddockii Bingham 1903, *Fauna British India, Hymenoptera*, 2 : 403, worker. Type locality : Upper Burma, the trans-Salween Shan States.

Distribution : Upper Burma, known only from type locality.

Holotype (BM Type Hym. 11-663) : HW 1.55 mm, HL 1.75 mm, CI 88, SL 1.90 mm, SI 122, PW 1.00 mm, MPL 1.60 mm, MTL 2.25 mm, PSEI 44, PH 1.80 mm.

Paratypes : HW 1.65-1.72 mm, HL 1.87-1.92 mm. CI 87-92, SL 2.07-2.15 mm, SI 124-130, PW 1.15-1.37 mm, MPL 1.80-2.00 mm, MTL 2.50-2.65 mm, PSEI 45-53, PH 2.10-2.17 mm.

As Bingham (1903) pointed out, this species is close to *lamellidens*, but differs in the shape of its petiolar spines, which are close together and parallel for three-fourths of their length rather than widely divergent from their base as they are in *lamellidens*.

Conclusion

The definitions of the species now most widely accepted are variants or equivalents of those of Mayr (1942, 1963). However, there are several classes of difficulties one may encounter when trying to apply this biological species concept to concrete situations (Simpson, 1961). One of them is that the definition depends on a criterion, interbreeding, that usually is not and sometimes cannot be observed. This is the most serious problem for museum workers who, in many cases, can only study the preserved specimens with brief data provided by the collector. My present study on this totally Old World group of ants encountered the same difficulty. Fortunately, abundant material from various parts of the range of most species has enabled me to undertake a rather intensive morphological analysis both quantitatively and qualitatively.

Most of the eight infraspecific forms in this subgenus were based on certain minor morphological differences, such as slight variations in size and color; several of them were even described from single specimens. An analysis of large

series of specimens soon reveal that these variations are mostly individual and of no taxonomic signficance. The only exception is *mindanaensis* which turns out to be a unique taxonomic entity occupying the Philippines.

Recently, this variety has been treated as a subspecies by one of my colleagues in spite of the controversy on the subspecies concept raised by Wilson and Brown (1953). As already pointed out in previous section, *mindanaensis* could very well be *bihamata* showing "character release" after sympatry and displacement elsewhere with *ypsilon*.

The phenomenon of character displacement (Brown and Wilson, 1956) was also noted in *bihamata* and *ypsilon* which overlap geographically. As shown in both fig. 22 and table 7, the difference between *bihamata* and *ypsilon* is greater in Borneo than in Sumatra. This may be due to the fact that they are found sympatrically in many cases in Borneo and allopatrically in Sumatra (cf. Fig. 16). The difference between these species are accentuated in the zone of sympatry and weakened when they are allopatric.

In the previous section on *bellicosa*, it was assumed that the New Guinea population is the parental population of this species. This assumption is based on the theories that in the course of evolution there is often an increase in size (Mayr and Vaurie, 1948) and a decrease for macroscopic meristic characters (Brown, 1965), and the parental population is usually more variable in characters. The same argument also holds true at the interspecific level.

Polyrhachis bellicosa is apparently the most primitive species. Workers from most of its range possess three distinct ocelli and are the smallest in size. In addition, the mandibles of the male have two denticles. Starting with this species, the following morphological tendencies are noted :

1. Reduction in the number of ocelli.
2. Loss of denticles in the mandibles of the male.
3. Separation of the mesonotal spines at base.
4. Expansion of the petiolar spines.
5. Increase in size.
6. Reduction in the variability of the characters.

As shown in fig. 24, in the course of evolution, there was probably a split of the prototypic *bellicosa* into two groups. One group led to *lamellidens* and *craddocki*, which have the alitrunk margined along the whole length of the sides. The mandibles of the male *lamellidens* do not have any denticles. Since this is the only group in which the workers do not have an ocellus, and it has the northernmost distribution in the genus, it is probably the most advanced group in this subgenus. The other group leads to *bihamata*, *montana*, *mindanaensis*, and *ypsilon*. The alitrunk in these four species is more or less rounded and the median ocellus is present. Morphologically, *bihamata* is closer to *bellicosa* than any of the other three species. Although larger in size than *montana*, the worker of *bihamata* has one pair of mesonotal spines contiguous at

base and the petiolar spines are parallel. *Montana* occupies a rather specialized niche. So far it is found only on the mountain or the mountain range, although

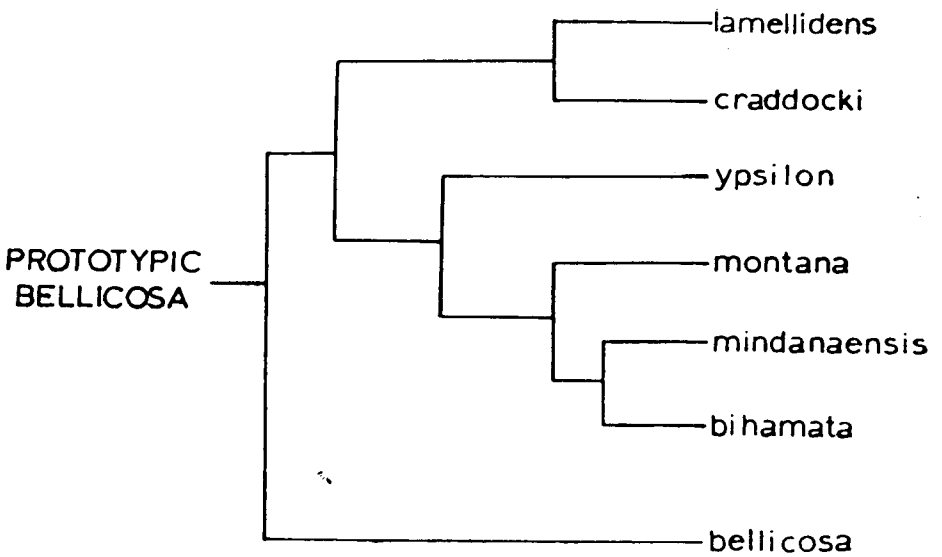


Fig. 24. Tentative phyletic scheme within the subgenus *Polyrhachis*. The prototypic *bellicosa* presumably originated from New Guinea.

both *bihamata* and *ypsilon* were found at the base of these mountains. It is very close to *bihamata* except that the mesonotal spines are widely separated at the base and the petiolar spines are widely divergent. *Ypsilon* is the largest in size in four species along this line of evolution. *Mindanaensis* has mixed characters of both *bihamata* and *ypsilon*, but is very different from *montana*.

The previous discussion is based mainly on the morphological characters and is not intended to show the actual phylogenetic relationship of these species. Our present knowledge on the biology of this group of ants is very scanty. Much more work has to be done before a more satisfactory speculation on the phylogeny of this group can be made.

SUMMARY

The subgenus *Polyrhachis* is the best defined group in the genus *Polyrhachis*, which is confined to the Old World. Eight infraspecific taxa have been described in this subgenus. Their taxonomic statuses are discussed.

Large series of material from various parts of the range of each species were used for biometric analysis in this study. Range, mean, standard deviation, and coefficient of variability for ten morphological measurements and indices of each sample were calculated. The coefficient of difference and the taxonomic

distance of every two samples in pair were also computed. In addition, shape, number, and color of different structures were also used in this study.

The following infraspecific taxa are synonymized : *crudelis* and *erosispina* under *bellicosa* ; *minor*, *perplexa*, and *tonsilis* under *bihamata* ; *synacantha* and *victoris* under *ypsilon*. The variety *mindanaensis* of the species *ypsilon* is raised to specific status. One new species, namely *montana*, is described from Borneo. A tentative phyletic scheme within this subgenus is also proposed. It is assumed that *bellicosa* is the most primitive species and the prototypic *bellicosa* presumably originated from New Guinea.

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LITERATURE CITED

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