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# Amblyopone

Melanesian Ants of the Genus Amblyopone (Hymenoptera: Formicidae)

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#### Abstract

The known Melanesian ants of genus Amblyopone are reviewed, with a key to species and comprehensive scanning electron micrograph illustrations of each. They are: A. noonadan Taylor (New Britain); A. papuana, sp. nov. (New Guinea); A. celata Mann (eastern Solomon Islands); A. gnoma, sp. nov. (Guadalcanal) and A. australis Erichson (New Guinea, Solomon Islands, New Caledonia, New Hebrides; also widespread in Australia, New Zealand and Tasman Sea islands). The name 'A. australis' is currently applied to a complex of closely related, intractable, biological species.

#### Introduction

This paper supplements Wilson's (1958) review of the Melanesian Amblyoponini, in which two *Amblyopone* species were recognized, *A. celata* Mann and *A. australis* Erichson. An additional species, *A. noonadan*, was described by Taylor (1965), and two further new species, *A. papuana* and *A. gnoma*, are added here.

Most of the material discussed below is from the Australian National Insect Collection. It includes valuable accessions contributed by Dr P. J. M. Greenslade, Rev B. B. Lowery, S. J., Mr D. H. Murphy and Dr P. M. Room, whose cooperation is gratefully acknowledged. Included also are my collections from two field trips to Papua New Guinea. The first of these (August 1962) was financed by the Committee on Evolutionary Biology of Harvard University, and the Bache Fund Committee, American Academy of Arts and Sciences.

Abbreviations for measurements are explained in the description of Amblyopone papuana (p. 828). CI is Cephalic Index (HW  $\times$  100/HL). Measurements are given in millimetres and were made with an eyepiece ruler reading directly to 0.01 mm at  $\times$  100 magnification.

The plates are micrographs prepared by the author with a J.E.O.L. JSM U3 scanning electron microscope. The illustrated specimens have been gold-palladium coated. They include the holotypes of the new species A. papuana and A. gnoma; these each had original coloration conforming with that of their paratypes.

The following abbreviations are used for institutions:

ANIC
BISHOP
B.P. Bishop Museum, Honolulu, Hawaii
BM(NH)
British Museum (Natural History), London
CM
DASF
Department of Agriculture Stock and Fisheries, Port Moresby, Papua New Guinea
Museum d'Histoire Naturelle, Geneva, Switzerland
MCZ
Museum of Comparative Zoology, Harvard University, Cambridge, Mass.

Type specimens of Amblyopone minuta (Forel) (Sumatra), A. besucheti Baroni Urbani (La Digue, Seychelles Is) and A. zwaluwenburgi (Williams) (Oahu, Hawaii) were kindly loaned for study by Dr C. Besuchet (GM) and Mr G. M. Nishida (BISHOP). These specimens, along with types or confidently identified examples of most other species known from South-East Asia, Australia and the Pacific Islands [see list in Brown (1960)], have been checked to certify their status as representatives of species separate from those discussed here.

The Australian species of *Amblyopone* will be reviewed shortly in a companion paper.

## Key to the Melanesian Amblyopone Species (Workers)

- - b Much larger (HW > 0.60 mm), broad-headed (CI > 87) species with 12-jointed antennae
- 2(1). a (Figs 17-20.) Larger species (HW > 1.5 mm); posterior third of frons generally smooth, with scattered punctae, contrasting with striate-rugose anterolateral areas; mandibular teeth in a single rank; anterior clypeal border transverse, with a series of spaced, simple minute denticles; inferior angles of pronotum dentiform. New Guinea to Guadalcanal, New Caledonia, New Hebrides (widespread elsewhere in Australia, New Zealand and Tasman Sea islands)
  A australis Erichson
- 3(2). a (Figs 1-4.) Larger species (HW > 0.96 mm); genal teeth strongly developed, subequal in size to the mandibular apices beyond the first (tiny reclinate) teeth of their masticatory margins; frons coarsely punctuate-rugose, sculptural trend mostly longitudinal but transverse posteriorly; dorsolateral margins of pronotum and propodeum submarginate. New Britain
  A. noonadan Taylor
- 4(3). a (Figs 5-8.) Anterior clypeal border strongly projecting, with teeth arrayed as in Fig. 6; colour dark reddish brown with lighter mandibles, antennae and legs. E. New Guinea ......

# Amblyopone noonadan Taylor

(Figs 1-4)

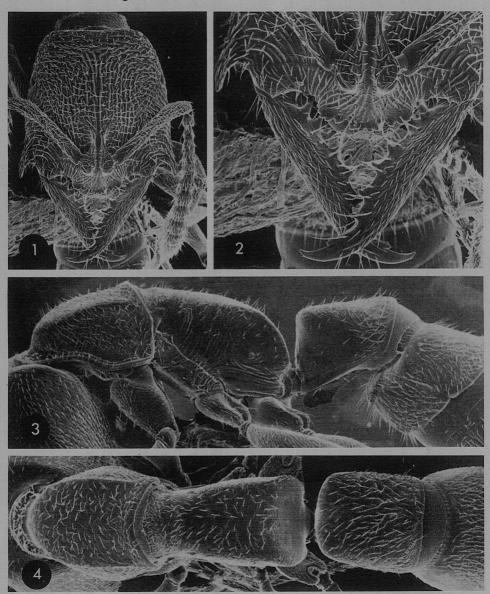
Amblyopone noonadan Taylor, 1965, p. 6, figs 3, 4, worker.

Type-locality. New Britain: Yalom.

This distinctive species requires no further characterization apart from that of key couplets 1b, 2b, and 3a, and the accompanying figures. The median-dorsal posterior pronotal border of the paratype, illustrated in Fig. 3, is somewhat 'peaked'. This is an artifact due to shrinkage of the specimen.

Each mandible carries seven paired or single teeth: (1) The usual very small reclinate, apically directed, subapical tooth. (2-5) A median series of four sets of sharp, acute paired teeth, subequal in size, with the third pair slightly the largest. The elements of each dental pair are similar in size, with the dorsal slightly smaller

than the ventral. (6, 7) Two basal teeth, the first single, a narrow acute cone with blunt apex, its position suggesting homology with the ventral elements of the more apical paired teeth. The second basal tooth is similar to the first and clearly represents the ventral element of a pair, since it has an accompanying minute dorsal tooth at its base (Fig. 2).



Figs 1-4. Amblyopone noonadan, paratype worker (MCZ), standard views. HW 1.04 mm; WL 1.42 mm; petiolar node width 0.57 mm.

The only known workers of A. noonadan are the holotype (CM) and paratype (MCZ), which were collected together on 19 May 1962, 'in and on the ground in newly cleared rainforest', by the Danish Noona Dan Expedition of 1961-62.

Subsequent to my description of this species I have seen three apparently conspecific amblyoponine males, also taken at Yalom by the *Noona Dan* collectors (probably in a Malaise trap) and dated one day earlier, 18 May 1962. These are not males of *Amblyopone australis*, A. gnoma or Myopopone castanea (Fr. Smith), and they do not match an Australian male of Mystrium camillae Emery, a species which might also be present on New Britain. They are considerably larger than would be expected for males of A. papuana or A. celata. I have therefore identified them as A. noonadan. These males have complete wing venation, with the vein  $Rsf \ 2 \cdot 3$  persistent, as in A. celata (Fig. 21). Two specimens are deposited in CM; one in ANIC.

### Relationships

A. noonadan is evidently related to the A. luzonica group of Japan, the Philippines and South-East Asia (Taylor 1965). Its affinities thus apparently do not lie with members of the extensive Australian Amblyopone fauna.

The frontal lobes of this species are more or less intermediate in their degree of proximity when compared with such species as the Japanese A. silvestrii (Wheeler), and A. papuana or A. celata.

The mandibular dentition of A. silvestrii resembles that of A. noonadan (see above), except that, in most specimens, neither basal tooth has an accompanying dorsal element. However, a relatively large worker from Mt Yonaha, Okinawa (23 April 1973, K. Uesu leg.) has a small tooth accompanying the first basal tooth and slightly displaced apically from it. This element is not present in smaller specimens from Honshu, Kyushu or Okinawa (ANIC).

The structure of the Mt Yonaha specimen could be considered morphologically intermediate between that of the other *silvestrii* specimens and that of the European A. impressifrons (Emery). Two workers identified as the latter in the ANIC (Gasturi, Corfu, 20 April 1929, Beier leg.) have five sets of paired teeth and a single, large, more or less triangular, basal tooth. It thus seems likely that in the lineage of A. silvestrii, the fifth (basalmost) set of originally paired teeth has become reduced to a single tooth; that tooth being homologous with the ventral element of an original pair, the dorsal element of which is still represented, though vestigial and displaced, in the Mt Yonaha specimen. The likely course of this reduction could be represented by the morphocline denticated  $\rightarrow$  silvestrii (Mt Yonaha specimen)  $\rightarrow$  silvestrii (other specimens).

In a further related set of features the two North American species A. pallipes (Haldeman) and A. oregonensis (Wheeler) are of special interest. Like demicalization they have five sets of paired median teeth and a single basal tooth. However, the fifth (basalmost) set of paired teeth has associated with it a very small supplementary tooth, forming a triplet. This tooth probably represents the apically displaced dorsal twin of the now single basal tooth. It is very likely homologous with the somewhat vestigial dorsal tooth associated with the second basal tooth of A. gnoma (see above) or A. papuana (see below).

These data imply that, in this lineage of Amblyopone, an original series of six paired teeth has been progressively reduced, by loss of the dorsal elements of the fifth and sixth sets, to the condition seen in most silvestrii workers: namely four sets of paired teeth and two single basal ones. The discussion and figures of Baroni

Urbani (1978), reviewing species of the European group of A. denticulata (Roger) (which includes A. impressifrons), are relevant to this discussion. However, his fig. 2, which illustrates an impressifrons syntype worker, does not seem to conform to the statements of couplet 1 in his key to species (p. 41). The basalmost median



Figs 5-8. Amblyopone papuana, holotype worker, standard views. HW 0.73 mm; WL 1.03 mm; petiolar node width 0.42 mm.

tooth is paired, though its dorsal element is somewhat reduced in size. The ANIC specimens of *impressifrons* agree with the Baroni Urbani figure in their dental configuration, and thus have *five* sets of paired teeth.

Of further interest are several representatives of the Oriental species-group of A. reclinata Mayr present in the ANIC. The apical mandibular structure in these strongly suggests that the reclinate subapical tooth of the above species, and most

others in Amblyopone, is also derived from an original pair of teeth, as the surviving dorsal element.

# Amblyopone papuana, sp. nov.

(Figs 5-8)

Type-locality. New Guinea: Bulolo (7° 13′ S., 146° 35′ E.).

Material examined. New Guinea: Bulolo, Morobe district, holotype worker, 28 paratype workers, paratype dealate female, 15.ix.1970, B. B. Lowery; Kokoda, Northern District, paratype worker, 14.v.1973, P. M. Room.

The Rennell Island record is based on a provisionally identified male in CM (Taylor 1976).

Specimens from the Greenslade accessions are deposited in the ANIC. These records all comprise single worker specimens, except accessions 9919 (three workers, one illustrated in Figs 9-12) and 11,640 (alate female, wing venation illustrated in Fig. 21).

# Additional Description

Worker. General features as in the accompanying figures and key couplets 1b, 2b, 3b and 4b above. Following are the dimensions of the smallest and largest of the available specimens. They are respectively from Dala, Malaita, and Mt Popamanatseu, Guadalcanal (refer above, under A. papuana for explanation of abbreviations): TL c.  $3 \cdot 2$ ,  $4 \cdot 3$ ; HL  $0 \cdot 69$ ,  $0 \cdot 91$ ; HW  $0 \cdot 60$ ,  $0 \cdot 84$ ; SL  $0 \cdot 39$ ,  $0 \cdot 57$ ; ML  $0 \cdot 46$ ,  $0 \cdot 66$ ; PW  $0 \cdot 39$ ,  $0 \cdot 52$ ; WL  $0 \cdot 87$ ,  $1 \cdot 24$ ; dorsal petiolar length  $0 \cdot 30$ ,  $0 \cdot 40$ ; petiolar node width  $0 \cdot 36$ ,  $0 \cdot 48$ ; dorsal postpetiolar length  $0 \cdot 24$ ,  $0 \cdot 32$ ; postpetiolar width  $0 \cdot 44$ ,  $0 \cdot 58$ .

The mandibular dentition includes a minute subapical, four paired median, and two single, acute basal teeth. The anterior basal tooth is sharply pointed and the posterior has its apex narrowly rounded; there are no traces of twin elements to the basal teeth (Fig. 10).

Female. The Mt Austen female (ANIC) is small, compared to the largest worker; she has the following dimensions: TL c. 4·1; HL 0·72; HW 0·62; SL 0·38; ML 0·48; PW 0·51; WL 0·56; dorsal petiolar length 0·33; petiolar node width 0·47; dorsal postpetiolar length 0·32; postpetiolar width 0·58. Fully alate, wing venation as in Fig. 21. General features as in workers, with the usual caste differences.

Despite the wide size range of the workers, and the relatively small size of the female, all specimens studied appear to be conspecific. They show little variation in general features.

This species is abundantly distinct from the other known Melanesian, Oriental and Australian Amblyopone species, and is readily distinguished from the somewhat similar A. papuana. It is notable that the wing venation is complete, with the second and third free abscissae of the radial sector  $(Rsf\ 2\cdot 3)$  persistent, despite the small size of these ants. Other similarly small Australian and New Zealand Amblyopone species, members of the saundersi group, seem generally to have lost this vein, which is incomplete in A. australis and in at least some of the other large Australian species.

to Accelata 1

I have checked A. zwaluwenburgi (Oahu, Hawaii) as a possible junior synonym of A. celata, with negative result (see details below, p. 833).

A. celata is one of a very few ponerine ants reported to lack pupal cocoons (Mann 1919).

# Relationships

The affinities of A. celata seem to be Asian rather than Australian. This species is apparently related to those of the South-East Asian silvestrii group, through A. papuana and A. luzonica. The species in my experience most like A. celata is one of somewhat smaller size, collected in the Gombak Valley, near Kuala Lumpur, W. Malaysia (R. W. Taylor, 13 July 1968) (ANIC). This does not match paratypes of A. minuta (GM), and is evidently undescribed. Small Amblyopone are not easily collected, and there are doubtless some, if not many, species awaiting discovery in the tropical parts of the Indo-Australian area.

# Amblyopone gnoma, sp. nov. (Figs 13-16, 22)

Type-locality. Solomon Islands, Guadalcanal I.: Kukum-Mt Austen Road. Kukum is a research farm near Honiara (9° 28′ S., 159° 52′ E.).

#### Distribution and Material Examined

Known only from Guadalcanal. All specimens were collected by Dr P. J. M. Greenslade and the accession numbers given below are his.

**Solomon Islands: Guadalcanal:** Kukum-Mt Austen Road (Type locality), holotype worker, 10.viii.1966 (acc. 23,445); Mt Austen, alate female, 4.x.1966 (acc. 11,640); dealate female, Mar. 1966 (acc. 21,296); worker, 28.iii.1966 (acc. 22,470); Mt Malukuna, alate female, c. 3000 ft, 9.iv.1966 (acc. 22,662).

Type deposition. Holotype and all female paratypes in ANIC (type No. 7525); worker paratype in MCZ.

#### Worker Diagnosis

Dimensions. (Holotype, paratype; refer above under A. papuana for explanation of abbreviations): TL c. 1.8, 1.9; HL 0.40, 0.43; HW 0.29, 0.32; SL 0.19, 0.21; ML 0.22, 0.24; PW 0.21, 0.22; WL 0.46, 0.51; dorsal petiolar length 0.16, 0.17; petiolar node width 0.18, 0.19; dorsal postpetiolar length 0.15, 0.16; postpetiolar width 0.21, 0.23.

General features as in Figs 13-16. Distinguished from all other known Amblyopone species by the combination of minute size, 10-jointed antennae and double ranked mandibular teeth. The dentition (Fig. 14) includes a tiny reclinate subapical tooth, followed by a median series of four sets of paired teeth of about equal size, with the first pair slightly the smallest, the third largest. The elements of each dental pair are progressively less closely associated through the series until the fourth, in which the dorsal element, which is also reduced in size, is displaced apically by about one-third the distance separating the third and fourth ventral teeth. There are in addition two small, erect, unpaired acute basal teeth, the first slightly lower and more sharply pointed than the second (Fig. 14). There are no traces of eyes. Colour pale yellowish brown, the mandibles, antennae and legs a shade lighter.

to A. celata p.830 To Apapuara,

Type deposition. Holotype and most paratypes, including female, in ANIC (type No. 7524); paratypes in BISHOP, BM (NH), CM, DASF, GM, MCZ.

## Worker Diagnosis

Dimensions. (Holotype, selected smallest Bulolo paratype, selected largest Bulolo paratype, Kokoda paratype): aggregate total length (TL) c. 4·2, 3·9, 4·5, 3·7 (this measurement is greatly affected here by relative contraction of the gastral segments); midline head length, including clypeal denticles (HL) 0·81, 0·78, 0·86, 0·73; head width, immediately behind genal teeth (HW) 0·73, 0·69, 0·76, 0·64; maximum chord length of scape (SL) 0·51, 0·49, 0·54, 0·45; outer length of mandible (ML) 0·62, 0·58, 0·63, 0·53; pronotum width (PW) 0·46, 0·43, 0·50, 0·41; Weber's length of mesosoma (WL) 1·03, 0·99, 1·11, 0·93; midline length of petiolar dorsum 0·40, 0·36, 0·42, 0·35; petiolar node width 0·42, 0·39, 0·45, 0·36; midline length of postpetiolar dorsum 0·32, 0·29, 0·33, 0·27; postpetiolar width 0·50, 0·47, 0·55, 0·44. Palpal formula (holotype dissected) maxillary 3: labial 2.

Specimens of this species should be easily identifiable. Diagnostic characters as in key couplets 1b, 2b, 3b, and 4a above; general features as in Figs 5-8.

The mandibular dentition includes a minute reclinate subapical tooth, separated by a relatively long diastema from the first of four sets of paired median teeth. These are followed by two basal teeth, each clearly representing the ventral element of an original pair, since the dorsal elements of each are present. That of the first is a small, somewhat vestigial tooth situated about halfway between its twin and the basalmost set of paired teeth. It clearly aligns with the dorsal elements of the paired series, while its twin is ventrally serial. The second basal tooth has its apparent dorsal twin present as a rounded cusp on its dorsal surface (Fig. 6).

## Female Diagnosis

The female paratype resembles the workers in all the usual features. Her mesosomal structure is complete, indicating the normal presence of wings; compound eyes and ocelli are well developed. The specimen has the following dimensions: HL 0.82; HW 0.73; SL 0.51; ML 0.62; PW 0.51; WL 1.13; dorsal petiolar length 0.39; petiolar node width 0.44; dorsal postpetiolar length 0.35; postpetiolar width 0.55.

#### Relationships

A. papuana provides a plausible link between A. celata and the Asian silvestrii group species A. silvestrii and A. luzonica (Wheeler & Chapman). Its affinities appear to be with South-East Asian rather than Australian species of Amblyopone. Types or type-compared specimens of all species of the A. saundersi group have been examined in confirming the separate status of A. papuana.

# Amblyopone celata Mann (Figs 9-12, 21)

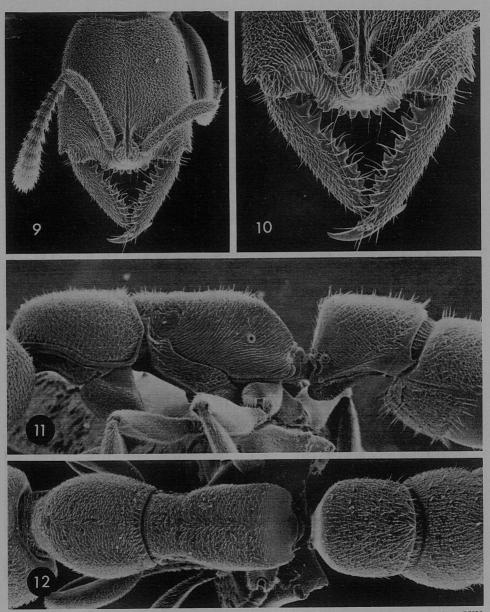
#### Synonymy

See Wilson (1958, p. 143). Mann (1919) placed *celata* in *Stigmatomma* subgenus *Fulakora*, now synonymized under *Amblyopone* (Brown 1960).

# Distribution and Material Examined

Known only from the Solomon Is., with most previously published records stemming from the original 1916 collections of W. M. Mann (WMM). All of the follow-

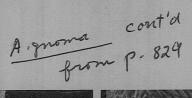
ing records not credited to others were gathered by Dr P. J. M. Greenslade; the accession numbers are his.

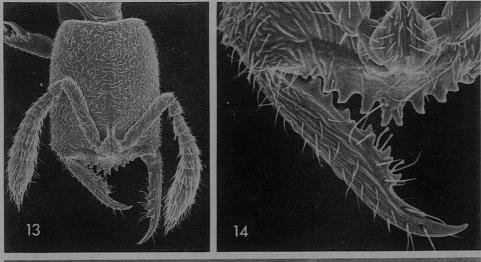


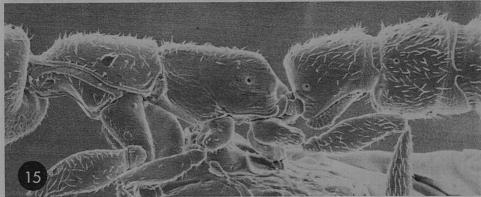
Figs 9-12. Amblyopone celata, worker, standard views, Mt Austen, Guadalcanal (ANIC). HW 0.75 mm; WL 1.12 mm; petiolar node width 0.45 mm.

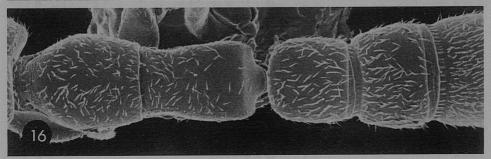
Santa Ysabel: Fulakora (type locality), WMM. San Jorge: Sept. 1965, P. N. Lawrence, BM(NH). New Georgia: Munda, Feb. 1966 (acc. 22,347). Guadalcanal: Kukum-Mt Austen Rd, 1966; Mt Austen, Nov. 1963 (acc. 9919), 14.x.1964 (acc. 11,640); Mt Popamanatseu, 5000 ft, Oct. 1965 (acc. 20,476). Nggela (= Florida): Soso, Dec. 1965 (acc. 20,955); Tulagai, WMM. Malaita: Auki, WMM; Dala, Feb. 1965 (acc. 16,584). San Cristoval: Wai-ai, WMM. Rennell: Hutuna, Mar. 1963, T. Wolff.

I have studied worker specimens from most of the WMM accessions (MCZ).









Figs 13-16. Amblyopone gnoma, holotype worker, standard views. HW 0.29 mm; WL 0.46 mm; petiolar node width 0.18 mm.

#### Female Diagnosis

Dimensions. (Smallest paratype (acc. 22,662), largest paratype (acc. 11,640): TL c.  $2 \cdot 0$ ,  $2 \cdot 2$ ; HL  $0 \cdot 43$ ,  $0 \cdot 45$ ; HW  $0 \cdot 32$ ,  $0 \cdot 34$ ; SL  $0 \cdot 22$ ,  $0 \cdot 23$ ; ML  $0 \cdot 25$ ,  $0 \cdot 27$ ; PW  $0 \cdot 25$ ,  $0 \cdot 26$ ; WL  $0 \cdot 60$ ,  $0 \cdot 61$ ; dorsal petiolar length  $0 \cdot 19$ ,  $0 \cdot 20$ ; petiolar node width  $0 \cdot 20$ ,  $0 \cdot 21$ ; dorsal postpetiolar length  $0 \cdot 16$ ,  $0 \cdot 17$ ; postpetiolar width  $0 \cdot 26$ ,  $0 \cdot 27$ .

General features consistent with those of workers. Antennae bilaterally 10-jointed. Compound eyes, well developed, 0.07-0.09 mm in diameter, with about

35-40 minute, distinct facets. Ocelli relatively quite large, about 0.02 mm in diameter. Palpal formula (2 specimens, 1 dissected), Maxillary 3 : Labial 2. All specimens have complete mesosomal structure, and are, or were, clearly fully alate. Wing venation (Fig. 22) more reduced than in any other known amblyoponine ant (or ponerine, except Probolomyrmex). Forewing with distinct stigma and closed 'costal', 'median', 'submedian' and 'radial' cells, enclosed by the usual veins, which are easily identified by comparison with a 'complete' wing like that of A. celata (Fig. 21). Hindwing with a single weak vein, presumably representing R + Sc. Colour as in workers.

## Relationships

I have closely checked four other species in considering the possible identity of A. gnoma: (1) The Sumatran A. minuta (Forel [two syntype workers from GM collection examined; presumably those discussed by Brown (1960 p. 196)]. As Brown's redescription implies, this species is quite different from A. gnoma. The specimens have the following dimensions: HL 0.58; HW 0.49, 0.50; SL 0.30, 0.31; ML 0.41; PW 0.31, 0.32; WL 0.75 (smallest specimen only measured); dorsal petiolar length 0.28; petiolar node width 0.30; dorsal postpetiolar length 0.23, 0.24; postpetiolar width 0.36, 0.37. The antennae are 12-jointed. (2) The Hawaiian A. zwaluwenburgi (Williams) (headless and damaged holotype worker examined, BISHOP). This specimen also could not be conspecific with the A. gnoma type. Its dimensions are: PW 0.25; WL 0.50; dorsal petiolar length 0.16; petiolar node width 0.22. (3) The neotropical A. degenerata of Borgmeier (1957), of which I have seen no specimens. This species, which is known from Brazil and Surinam (Kempf 1961), is very similar to A. gnoma in size and general features. Its antennae, however, are seven-jointed, and the mandibular teeth single-ranked. These matters have been confirmed separately by Professor W. L. Brown, jr, and the late Fr W. W. Kempf, using specimens in the MCZ and Borgmeier-Kempf collections (personal communications). This species is therefore adequately distinct from A. gnoma. (4) A. besucheti Baroni Urbani, recently described from La Digue I., Seychelles Is (Baroni Urbani 1978). This species is clearly close to A. gnoma; indeed, the two could well be cognate in their genus.

I have examined the holotype and two worker paratypes of A. besucheti (GM), and attribute to that species a worker and a dealate female deposited in the ANIC, and labelled: Singapore: University of Singapore campus, worker, June 1964, Imperata grassland soil; Bukit Timah National Park, dealate female, 4.x.1965, degraded coastal hill forest on granite (Murphy berlesate No. 124). These were collected by D. H. Murphy. The worker conforms to the besucheti original description, and closely matches the types of that species; there can be little doubt that the female is conspecific.

These specimens have the following *Dimensions* (worker, female; abbreviations as above): TL c. 1·8, 1·9; HL 0·40, 0·39; HW 0·29, 0·29; SL 0·20, 0·20; ML 0·23, 0·22; PW 0·20, 0·24; WL 0·45, 0·51; dorsal petiolar length 0·16, 0·15; petiolar node width 0·18, 0·18; dorsal postpetiolar length 0·14, 0·13; postpetiolar width 0·21, 0·22. Note that SI (abbreviated as ISC) was expressed as SL  $\times$  100/HL by Baroni Urbani in the original description. It is given, more conventionally, as SL  $\times$  100/HW in this paper.

All available specimens of A. besucheti and A. gnoma have been considered in preparing the following list of characters by which gnoma differs from besucheti (compare figs 15 and 16 of Baroni Urbani (1978) with Figs 13-16):

(1) Mandibular dentition. Workers of both species consistently have four sets of paired mandibular teeth; however, in *gnoma* the dorsal element of the fourth (basal) set is displaced apically from its partner. Queens of *gnoma* resemble their workers, but the Singapore *besucheti* queen has only three sets of paired teeth, the fourth set being represented by a single (ventral) tooth.

- (2) Clypeal dentition. The median clypeal tooth is single in all *besucheti* specimens, but represented by a pair of median teeth in *gnoma* specimens.
- (3) Palpal formula. Two gnoma females have Maxillary 3: Labial 2, as reported above. Baroni Urbani found Maxillary 1: Labial 2 in the worker of besucheti. The palpi are obscured in the gnoma worker paratypes, precluding a count of their segments.
- (4) The Singapore queen has 11-jointed antennae; those of *gnoma* females are 10-jointed, as in the workers.
- (5) The ocelli of *gnoma* females are larger and more distinct than those of the *besucheti* female.

These differences are consistent in the available material. If they remain so as more specimens come to hand my separation of these species will be supported. It seems certain that besucheti and gnoma are closely related, perhaps representing south-eastern Asian and Melanesian siblings. The Seychelles population of besucheti could be derived from a human introduced propagule of south-eastern Asian origin. These ants could be very easily transported in small amounts of soil attached to plants, root crops etc.

Amblyopone gnoma is one of several known very small members of its genus. Despite its aberrant wing venation, reduced number of antennomeres, relatively slender stature, short antennae and legs, and the lack of eyes in the worker, A. gnoma is not as structurally reduced as are some other small Amblyopone species. A. degenerata has only seven antennomeres, though the second segment of the funiculus shows feeble traces of sutures, suggesting that it is comprised of three original segments (Borgmeier 1957; Kempf, personal communication). In addition, unlike gnoma, degenerata has mandibular dentition consisting of a single rank of teeth. In this regard A. tropicalis Brown (Barro Colorado I., Panama) is neatly intermediate between degenerata and more conservative Neogean species. Its mandibular teeth are partly double-ranked, but the dorsal rank consists of short spurs, each 'representing a vestigial twin of a pair' (Brown 1962). Elsewhere among Amblyopone species reduction of the mandibular dentition to a single row has occurred mainly among some of the larger Australian species (Brown 1960). Funicular segment counts of lower than 11 have been reported only for the two species discussed above.

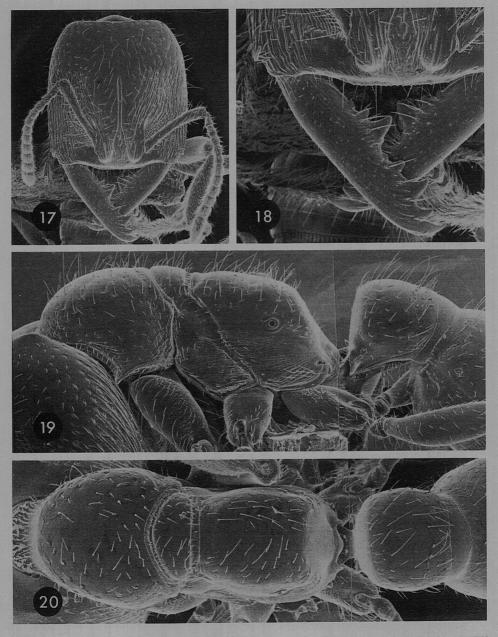
The wing venation of *gnoma* females (Fig. 22) is relatively very reduced. Elsewhere in *Amblyopone* reduction of venational elements consists almost exclusively in the complete or partial deletion of vein  $Rsf\ 2\cdot 3$  (see Fig. 21). Details of wing venation are not known for *A. degenerata*.

A further minute and undescribed Amblyopone, from north Queensland rain forests, is represented in the ANIC. This species is almost as small as A. gnoma; it has 12-jointed antennae, and single-ranked mandibular dentition. A. smithi Brown (type locality near Mt Lofty, S.A.) is almost as small, but has both the antennal segmentation and mandibular dentition unreduced (Brown 1960).

# Amblyopone australis Erichson (Figs 17-20)

Synonymy

The Melanesian synonymy of this widespread putative species is summarized by Wilson (1958, p. 142), and the more extensive synonymy of names based on



Figs 17-20. Amblyopone australis, worker, standard views, Tapini, Papua New Guinea (ANIC). HW 2·24 mm; WL 2·64 mm; petiolar node width 0·77 mm.

material from Australia, New Zealand, and the Tasman Sea islands by Brown (1960, p. 167). In all, 12 names, previously assigned specific, subspecific or infrasubspecific status, have been considered by these authors as junior synonyms of australis. The resulting simplified nomenclature is more practical than that of Wheeler (1927). However, we cannot assume with confidence that the Amblyopone australis of this nomenclature refers to a single biological species. Several lines of evidence involving karyology (Imai et al. 1977), and definite or likely sympatric associations between consistent 'forms' of the 'species' in Australia, and between 'australis' and its sibling A. leae Wheeler on Lord Howe I., suggest that we are in fact dealing here with a complex of closely similar biological species. Unfortunately it is not possible at present to delimit, characterize or enumerate the component species in this complex, and when this is accomplished some of the names presently held in synonymy will doubtless need to be reinstated. In the meantime application of the name australis, as suggested by Brown and Wilson, provides our best, if not only, reasonable nomenclatorial action, though only so long as this name is understood to indicate an area of clear taxonomic doubt. We certainly are not able to assume that this nomenclatorial species is coextensive in its definition with a biological species, as is usually implied by the use of specific names.

The exclusively Melanesian names included as synonyms of australis by Wilson are: laevidens Emery (levidens of authors), previously listed from New Guinea and the Solomons, and nana Emery, previously reported from New Caledonia and the New Hebrides.

This species needs no characterization apart from that provided by the accompanying key (couplets 1b, 2a) and Figs 17-20.

#### Distribution

Eastern and south-western mainland Australia, Tasmania, Lord Howe I., Norfolk I., New Zealand (North Island), New Caledonia, New Hebrides (Tanna), New Guinea and Solomon Is (Kolombangara, Guadalcanal, Malaita).

Melanesian records. Unless otherwise indicated the New Guinea records listed here were gathered by the author, and those from the Solomon Islands by Dr P. J. M. Greenslade. The accession numbers are Greenslade's. This material is deposited in the ANIC.

New Guinea: Eastern Highlands District: Aiyura 1900 m, 2000 m, June 1962. Morobe District: Finisterre Range, Gusap River Valley, I record between 3000 and 6000 ft, Nov. 1965, R. Pullen; Mt Kaindi, c. 2300 m, 15.vi.1972; Bulolo River Valley, 6 km NE. of Wau, 1100 m, June 1962; Wau, near Bishop Museum Field Station, 1200 m, June 1962; Kunai Creek Valley, 1300 m, June 1962; Joangeng, 1500 m (Wilson 1958); Ebabaang, 1400 m (Wilson 1958). Central District: Tapini, 1100–1200 m, Aug. 1962. Northern District: 8 km S. of Kokoda, 800 m, 1.vi.72.

**Solomon Islands: Kolombangara:** Kuzi, 4000 ft, Aug. 1966. **Guadalcanal:** Mt Jonapau, 2600 ft (accs 18,048, 18,194), 3500 ft (acc. 18,118), May 1965; Mt Popamanatseu, 4500 ft (accs 20,187, 20,266), 5000 ft. (acc. 18,811), 5500 ft (acc. 20,227), Oct. 1965. **Malaita:** Interior near Fourafi, 1916 (Mann 1919).

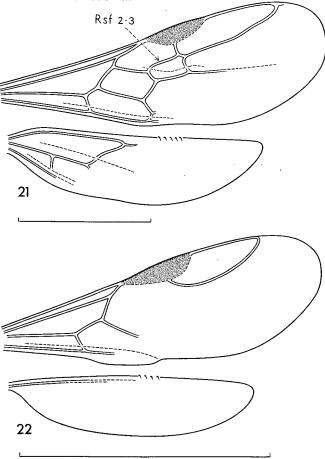
New Caledonia: Mt Panie, 500 m; Mt Canala, 700 m (Emery 1914).

New Hebrides: Tanna (Wilson 1958).

#### Bionomics

My New Guinea collections are all from closed mid-montane or montane rain forest, mostly from rotting wood. The Greenslade accessions were gathered from

rotting wood in montane forest. Note that all of these collections are from high elevations, most of them certainly above 800 m. Such records seem to be characteristic in the tropical parts of the range of this remarkably widespread species, as indicated also by the Wilson records from New Guinea and Tanna (Wilson 1959), and Emery's from New Caledonia.



Figs 21 and 22. Amblyopone, female wing venation: 21, A. celata, Mt Austen, Guadalcanal; 22, A. gnoma, Mt Austen, Guadalcanal. Scale lines, 1 mm.

A similar high-elevation distribution pattern evidently occurs further south between latitudes 16° 30′ and 18° 30′, in tropical north Queensland, in the main base-of-peninsula' rain forests of the Mossman-Tully area. I have surveyed this area extensively and have taken A. australis frequently, but only at elevations above 330 m. The species has never been encountered at a number of well worked sites at lower elevations in this area. The depressed lower elevational limit, compared with that in New Guinea, could be explained as a result of latitudinal shift. Further north on Cape York Peninsula australis has been collected at Upper Lankelly Creek in the McIlwraith Range, near Coen, in rain forest of the 'mid-peninsula' system (G. B. Monteith, 10-11 June 1971) (ANIC).

Wilson (1959), Brown (1960) and Taylor (1972) have separately commented on the northern biogeography of this ant. We agree that A. australis is probably an Australia-based species which has moved northwards into New Guinea. The data reviewed above suggest that, in Melanesia and northern Australia, australis has very strong predilection for relatively cool forests at high elevations, and that it might have moved into Melanesia from temperate Australia through the available montane 'islands' of suitable habitat in north Queensland. The ability of this species to use stepping-stone islands in trans-oceanic dispersal is well evidenced by its distribution in archipelagic eastern Melanesia, and in the islands east of Australia. This ability might have aided its northern dispersal.

Very few Australia-based ants inhabiting rain forest seem to have dispersed northwards into montane New Guinea. Other species or superspecies with known distribution patterns suggestive of such dispersal include Rhytidoponera purpurea (Emery), the Cryptopone crassicornis (Emery) complex [including crassicornis and the probably synonymous C. rotundiceps (Emery) of New Caledonia and northeastern Australia (= Ponera mjobergi (Forel)], the Chelaner rubriceps (Mayr) species-group (including C. edentatus (Emery) in New Guinea) and the Prolasius formicoides (Forel) species-group, which is represented at high elevations in northern Australia and New Guinea.

Both Wilson (1958) and Brown (1960) have noted the apparent complementarity of distribution in New Guinea between A. australis and its 'closest ecological equivalent', the widespread South-East Asia-based amblyoponine, Myopopone castanea (Fr. Smith). This last species is a predominantly lowland insect found mostly at altitudes below 500 m, though I have taken it in sympatric association with A. australis at 800 m near Kokoda (see records listed above under A. australis). Wilson and Brown have implied that this complementarity is due mainly to competitive displacement of one of these species by the other at appropriate elevations. I believe the observed situation can best be explained as a resultant of the separate biogeographic histories of these ants. Myopopone castanea probably originated in tropical South-East Asia as a species essentially adapted to life in low-elevation, fully 'tropical' rain forests. Like many such species in New Guinea its range seems to be severely limited by the climatic effects correlated with increasing elevation. Amblyopone australis, on the other hand, has its distribution, in New Guinea and Cape York Peninsula, centred on cool, higher-elevation rain forests. It is evidently unable to tolerate the climatic conditions of more indubitably tropical forests at lower altitudes. This, I suggest, is in accord with its apparent status as a primarily Australian faunal element adapted to cool temperate habitats. It is notable that australis populations are best developed in the southern part of Australia, and that the species is capable even of tolerating winter snow cover in the Australian Alps, Tasmania and New Zealand (personal observations). In Australia, north of about latitude 22°S. at least, its distribution is restricted to scattered cool temperate areas of montane forest, occurring as 'islands' in a 'sea' of less suitable habitats. The New Guinea Highlands and the mountains of eastern Melanesia are simply outliers of this cool montane 'archipelago' to which A. australis has dispersed. I suggest then that these two organisms might have been 'programmed' for distributional complementarity long before their separate dispersal histories brought them together on New Guinea.

The range of *Myopopone castanea* extends into Cape York Peninsula, where it is known south only to Iron Range (at c. 12° 45′ S.); all records are from rain forests at low elevations (ANIC).

These two species thus exemplify several of the distributional patterns characteristic of the biogeography of insects on Cape York Peninsula, as outlined by Taylor (1972).

#### References

Baroni Urbani, C. (1978). Contributo alla conoscenza del genere Amblyopone Erichson (Hymenoptera: Formicidae). Bull. Soc. Entomol. Suisse 51, 39-51.

Borgmeier, T. (1957). Myrmecologische Studien, I. An. Acad. Brasil. Ciênc. 29, 103-28.

Brown, W. L., Jr (1960). Contributions towards a reclassification of the Formicidae. III. Tribe Amblyoponini. Bull. Mus. Comp. Zool. Harv. Coll. 122, 145-230.

Brown, W. L., Jr (1962). A new ant of the genus Amblyopone from Panama. Psyche J. Entomol. 69, 73-6.

Imai, H. T., Crozier, R. H., and Taylor, R. W. (1977). Karyotype evolution in Australian ants. Chromosoma (Berl.) 59, 341-93.

Kempf, W. W. (1961). A survey of the ants of the soil fauna in Surinam. Stud. Entomol. 4, 481-524. Mann, W. M. (1919). The ants of the British Solomon Islands. Bull. Mus. Comp. Zool. Harv. Coll. 63, 273-391.

Taylor, R. W. (1965). New Melanesian ants of the genera Simopone and Amblyopone of zoogeographic significance. Breviora 221, 1-11.

Taylor, R. W. (1972). Biogeography of insects of New Guinea and Cape York Peninsula. In 'Bridge and Barrier: The Natural and Cultural History of Torres Strait'. (Ed. D. Walker.) pp. 213–30. (Australian National University Publication: Canberra.)

**Taylor, R. W.** (1976). The ants of Rennell and Bellona islands. Nat. Hist. Rennell I., Br. Solomon Is. Vol. 7, pp. 73-90.

Wheeler, W. M. (1927). Ants of the genus Amblyopone Erichson. Proc. Am. Acad. Arts Sci. 62, 1-29.

Wilson, E. O. (1958). Studies on the ant fauna of Melanesia. I. The tribe Leptogenyini. II. The tribes Amblyoponini and Platythyreini. *Bull. Mus. Comp. Zool. Harv. Coll.* 118, 101-53.

Wilson, E. O. (1959). Adaptive shift and dispersal in a tropical ant fauna. Evolution 13, 122-44.

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