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Contributions toward a Reclassification of the Formicidae. Part VI. Ponerinae, Tribe Ponerini, Subtribe Odontomachiti. Section A. Introduction, Subtribal Characters. Genus Odontomachus.

William L. Brown, Jr. #264

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William L. Brown, Jr.

Department of Entomology
Cornell University, Ithaca, New York 14853, U.S.A.

(With 27 text-figures and 1 plate)

Table of Contents

Introduction 68
Sources of material 69
Acknowledgements and dedication 69
Tribe Ponerini, Subtribe Odontomachiti 70
  Diagnosis 71
  Bionomics 77
  Distribution 86
  Relationships and origin 88
  Genera 92
  Measurements and indices 95
  Key to genera 96
  Genus *Odontomachus* 96
  Diagnosis 97
  Distribuition 97
  Natural enemies 97
  Revision of species 97
  Species list 100
  Species-groups and phylogeny 107
  Keys to species 111
    New World 111
    Indo-Australian 114
    African 117
    Malagasy 117
  Metric tables 118
Appendix 118

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[1] A contribution from the Cornell University Agricultural Experiment Station, New York State College of Agriculture and Life Sciences, A Statutory College of the State University, Cornell University, Ithaca, New York.

Introduction

Parts I through V of this reclassification (Brown 1952, 1958, 1960, 1965, 1975) have covered Ponerinae tribes Amblyoponini, Platythyreini, Ectatommini, Typhlomyrmecini, Cerapachyini, Cylindromyrmecini, Acanthostichini and Aenictogitini. It was originally planned for Part VI to include Ponerini, the largest tribe of the subfamily, but as work on this part progressed, it became obvious that it would have to be split. Since the large genera *Odontomachus* and *Anochetus* together form a natural taxon within Ponerini, I decided to make this taxon the only subject of Part VI. This part grew, and after a while, considerations of time and money dictated that it in turn be divided into two parts for actual publication.

I offer here section A of Part VI to include an introduction to and general remarks on subtribe Odontomachiti, as well as coverage to the species level of genus *Odontomachus*. The format is like that of Part V, intended to include only the most essential features of a systematic revision. Part VIB, now in an advanced stage of preparation, will include a similar review of *Anochetus* and the list of references for the whole part, and should be published within a year. Regrettably, this means a separation of author-date-page indications in Part VIA from the corresponding full bibliographic references in VIB, but I think this will be only a temporary minor inconvenience to most users, who in any case can find most of these references in the well-known catalogs of Emery (1911), Chapman and Capco (1951), Wheeler (1922) and Kempf (1972).

In its aims and general plan, Part VI is much like Part V (Brown, 1975), especially in that it has been possible to carry out a fair amount of revision at the species level .It should be borne in mind, however, that it is not the main purpose of the reclassification to offer «definitive» revisions of the species in each genus.

As the problems of generic definition were examined, it incidentally proved so convenient to solve many species-level problems in certain genera that it seemed a pity to ignore them, leave them all for a later reviser, and thus waste a significant amount of time, travel and money that had to be applied to the general research in any case.

Any success the species-level revisions and keys for identication may enjoy should be counted as a bonus, even if these sections are the only ones ever consulted by some readers. The whole work at all levels is just another step in the process of arriving at a serviceable classification.

Sources of Material

Depositories of material reviewed in this study are mostly those listed with annotation at the beginning of Part V (Brown 1975). The abbreviations (in parentheses) are standard for Parts V and VI, at least, and the collections are listed in the same order.

Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA (MCZ).
British Museum (Natural History), London, England (BMNH-London).
Museo Civico di Storia Naturale «Giacomo Doria», Genoa, Italy (MCSN-Genoa).
Muséum d'Histoire Naturelle, Geneva, Switzerland (MHN-Geneva).
Museum Nationale d'Histoire Naturelle, Paris, France (MNH-Paris).
Museum für Naturkunde an der Humboldt Universität zu Berlin (MNK-Berlin).
Naturhistorisches Museum, Basel, Switzerland (NM-Basel).
Naturhistorisches Museum, Vienna, Austria (NM-Vienna).
American Museum of Natural History, New York City, USA (AMNH-NY).
Australian National Insect Collection, Canberra, Australia (ANIC-Canberra).
California Academy of Sciences, San Francisco, USA (CAS-San Francisco).
United States National Museum of Natural History, Washington, D. C., USA (USNM-Washington).
Universitetets Zoologiske Museum, Copenhagen, Denmark (UZM-Copenhagen).
Walter W. Kempf Collection, including the ant collections of T. Borgmeier, Brasília, Brasil (WWK).

Added to this list should be the following:

Museu de Zoologia da Universidade de São Paulo, São Paulo, Brasil (MZSP).
Instituut vor Taxonomische Zoölogie (Zoölogisch Museum), Universiteit van Amsterdam, Netherlands (ITZ-Amsterdam).

Acknowledgements and Dedication

The individuals and institutions contributing over the years to the development of this work are mostly the same ones listed in Part V (Brown 1975: 2), plus many more whose names have escaped my records or the recall of the moment. The U.S. National Science Foundation (Grant Nos. 23680, GB-2175, GB-5574, GB-24822, GB-31662) has furnished indispensable support for this and other phases of the reclassification since 1962, and my studies have also been aided by financial backing from Harvard University (Parker Travelling Fellowship, Milton Fund Small Grants, William Morton Wheeler Fund, and other sources) and the John Simon Guggenheim Memorial Foundation for a fellowship year.

Special mention should be made of those individuals who helped importantly with loans, exchanges, gifts of material or notes on types contributing to this revision: Dr. Paul H. Arnaud, Jr. (CAS-San Francisco); Mr. Barry Bolton (BMNH-London); Dr. R. H. Crozier (University of New South Wales); Prof. P. J. Darlington, Jr., the late Mr. P .F. Darlington, and H. E. Evans (MCZ); Ms. Marjorie Favreau (AMNH-NY); Dr. Max Fischer (NM-Vienna); Dott. Delfa Guiglia (MCSN-Genoa); Dr. Peter J. van Helsdingen, Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands; Rev. Fr. W. W. Kempf, O.F.M. (WWK); Dr. E. Königsmann (MNK-Berlin); Dr. Masao Kubota (Odawara, Kanagawa, Japan); Dr. J. F. Lawrence (MCZ); Dr. Jean Lévieux (Université d'Abidjan, Cote d'Ivoire); Dr. P. Oosterbroek (ITZ-Amsterdam), Drs. Stewart Peck and Jarmila Peck (Carleton University, Ottawa, Canada); Dr. Børge Petersen (ZMU-Copenhagen); Dr. Hans Reichardt (MZSP); Dr. E. E. Ross (CAS-San Francisco); Prof. R. Silberglied (MCZ); Dr. David R. Smith (USNM-Washington); Drs. A. Benedict Soans and Joyce Soans (Malabar Christian College, Calicut, India); Prof. E. Tortonese (MCSN-Genoa); Mrs. Janice Scott (MCZ); Prof. E. O. Wilson (MCZ); and Dr. Walter Wittmer (NM-Basel).

I owe special thanks to colleagues abroad who helped in more than ordinary ways to further the success of my collecting trips: Dr. Paulo Vanzolini, Director of the Museu de Zoologia, Universidade de São Paulo; Mr. Graham Guy of the National Museums of Rhodesia, and Charles Jacot-Guillarmod and Laurie Weatherill, of the Albany Museum, Grahamstown, South Africa; Dr. Sampurno Kadarsan, Director, Museum Zoologicum, Bogor, Indonesia; Dr. Jorge Rabinovich, of the Instituto Venezolano de Investigaciones Cientificas, and his students at that time; Prof. Richard B. Root, Department of Entomology, Cornell University, and sometime member of the Departamento de Biologia, Universidad del Valle, Cali, Colombia; Dr. Enrique Ampuero P. and Sr. Victor Hugo Quimí Arce of Instituto Nacional de Investigaciones Agropecuarias, Guayaquil, Ecuador; Drs. A. Benedict Soans and Joyce Soans, of the Malabar Christian College, Calicut, Kerala State, India; and Dr. Lance Woods, Department of Agriculture and Stock, Darwin, Northern Territory, Australia.

This section is dedicated to the memory of Father Thomas Borgmeier, O.F.M., a longtime colleague and friend, whose prodigious entomological labors included many fine studies of ants, among them the classics on the New World army ants and on the fungus-growers of the genus *Atta*. The approach of Father Thomas to his work, to his environment and to the people whose lives touched his was direct and simple, full of good will and innocent enthusiasm. In these troubled times, it is somehow comforting to contemplate a life so well and usefully lived, through pain and joy, as was Thomas Borgmeier's.

Tribe Ponerini, Subtribe Odontomachiti

The tribe Ponerini as constituted in this revision is roughly equivalent to Emery's (1911) Section Euponerinae, including his tribes Ponerini, Leptogenyini and Odontomachini. The tribe Thaumatomyrmecini, with the single genus *Thaumatomyrmex* (revised by Kempf in 1975) is very close to Ponerini, and possibly should be included in the latter tribe. Characters and relationships of the tribe Ponerini will be discussed in Part VII; in Part VI, I am only concerned with the subtribe Odontomachiti, in which I include those Ponerini formerly placed in tribe Odontomachini. I can recognize just two genera in this taxon: *Odontomachus* and *Anochetus*. An abbreviated synonymy of the subtribe follows, plus a characterization and discussion of the subtribe.

Subtribe Odontomachiti[1] (new status)

Odontomachidae Mayr, 1862, Verh. Zool.-Bot. Ges. Wien 12: 708.
Odontomachii Forel, 1893, Ann. Soc. Entomol. Belg. 37: 162, and later authors.
Odontomachinae Ashmead, 1905, Canad. Entomol. 37: 382. — Clark, 1951, Formicidae of Australia 1: 15.
Odontomachini Emery, 1911: 106, and most later authors.

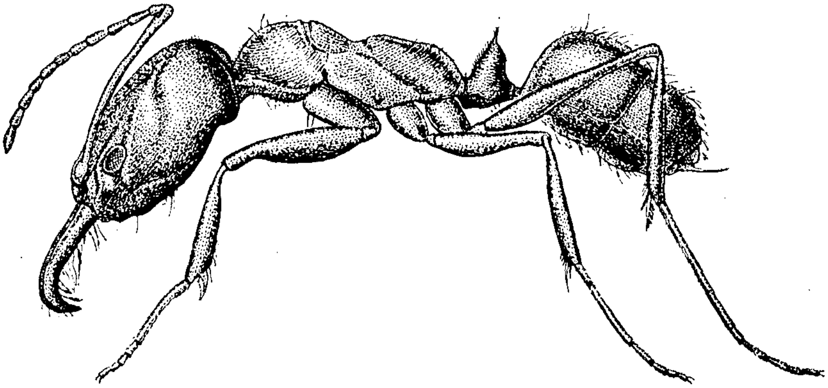

Fig. 1, *Odontomachus simillimus* worker from Papua. (After Wilson and Taylor, 1967)

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[1] I urge that the suffix *-iti* be used for all subtribal names in zoology. The spreading use of *-ina* for this purpose, particularly in Coleoptera, is cause for concern, though many specialists seem to be unaware of the problems it raises. Among objections to *-ina*, an important one is that it is an ambiguously plural ending, and another is that many genera already end in *-ina*, and thus cannot be readily distinguished as to hierarchical level. For further argument, see Brown, 1958, Syst. Zool. 6: 193-194.

Worker: The genera *Odontomachus* and *Anochetus* are among the most distinctive and easily recognized of all ants. The more or less pyriform head, broadened in the anterior third, with the eyes situated at the broadest part on laterally-produced ocular prominences (figs. 2, 10), is combined with elongate, adjacent, subporrect mandibles that lie nearly parallel at full closure, but that open to about 180°, and can be held in the open position when the ant is attacking prey or is threatened by enemies. The mandibles are furnished with long trigger-hairs that are erected and point straight forward in the jaws-open position. These hairs, upon touching something within the swing range, initiate a sudden, convulsive snap of the mandibles against the sensed object, be it insect prey or the skin of a vertebrate intruder. If the object snapped at happens to be steel forceps or a similar smooth, hard instrument, the ant may be flipped backwards several centimeters by the force of the strike slipping off the unyielding surface. Such acrobatics have been observed many times in these genera, as well as in the unrelated trapjawed Dacetini (subfamily Myrmicinae). The mandibles of Dacetini, while superficially somewhat like those of *Odontomachus*, operate on a different plan (Brown and Wilson, 1959). Barth (1960) has shown how they work in *Odontomachus* **[1]**.

Mandibles each with 3 (or 2) teeth in an apical group; ventral, at the apex, is the *apical* tooth; more or less fused to its dorsal side, when present, a smaller *intercalary* tooth; above this, usually a bit proximad on the shaft, is the large, but often worn or broken *subapical* tooth. The mandibular shaft may bear a series of *preapical teeth* or *denticles* along the remaining *masticatory border*, usually decreasing in size basad, or there may be only 1 or 2 *preapical* teeth, or only a *preapical angle*, followed basad by the straight or nearly straight masticatory border, Often the masticatory border has a concave channel running most of its length, separating *dorsal* and *ventral margins*; the *dorsal margin*, when developed, is frequently cultrate, while the *ventral margin* is often at least partly denticulate or crenulate, but these features vary considerably among species, particularly in *Anochetus*, when present at all.

The mandibular bases each consist of a large, complex *condylar head*, extending lateral to and below the level of the shafts, and these condylar heads are fitted into elaborate sockets in the anterior and anterolateral cranium in such a way that the axes of swing are situated rather close together on the anteromedian aspect of the cranium. The clypeus is short, with indefinite posterolateral borders; its median portion is raised, forming a thick, inverted U, the arms of which form a pair of small, rounded lobes, each capping the condylar axis of a mandible. The rounded posterior median part of the clypeus merges into the narrow «frontal triangle», wedged between the posteriorly converging inside margins of the frontal carinae, which meet a little farther back. Lobes of frontal carinae moderately expanded, covering at least part of antennal insertions.

The narrowed posterior part of the cranium consists entirely, in dorsal or lateral view, of the hypertrophied *vertex*, packed with mandibular muscles. The dorsal and lateral surfaces of the cranium are separated from the *occipital face* by a distinct *nuchal carina* (figs. 3, 4), which runs clear around the back of the head and onto the ventral surface, where it is nearly or quite complete at the midline. Presumably, as in other aculeate Hymenoptera, the true occiput is limited to a narrow area bordering the foramen magnum. The cranium is always broader than it is deep dorsoventrally. As seen from dorsal full-face view, the posterior margin is more os less semicircularly excavated, or at least slightly concave, in the middle. The ventral side of the cranium bears a dark *median ventral seam,* marking the position of an internal apophyseal ridge to which muscles are attached; the seam is broadly interrupted a little way anterior to its midlength. Differences in the form of the nuchal carina, ànd in the presence or absence of *posterior apophyseal lines,* are described farther below in the discussion of the genera of Odontomachiti.

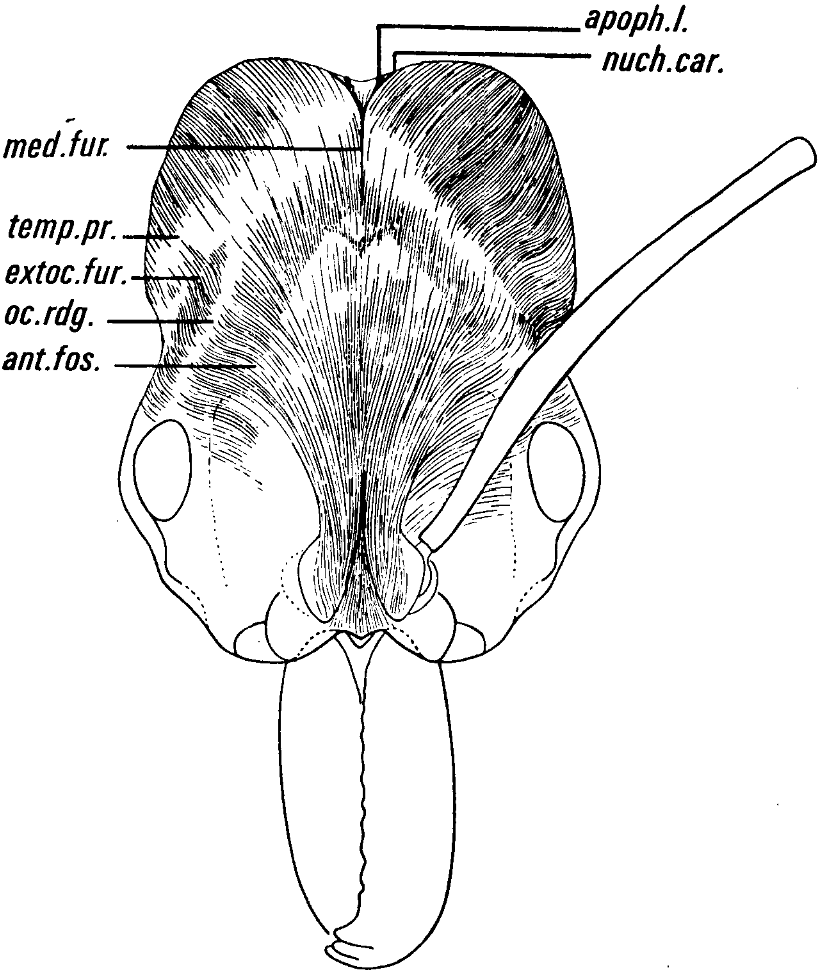

Fig. 2, *Odontomachus erythrocephalus,* head in full-face view, to show nomenclature of cranial topography: *apoph. l.,* left apophyseal line; *nuch. car.,* nuchal carina; *med. fur.,* median furrow; *temp. pr.,* temporal prominence or ridge; *extoc. fur.,* extraocular furrow; *oc. rdg.,* ocular ridge or prominence; *ant. fos.,* antennal fossa. Pilosity and antennal funiculus omitted.

Short *anteroventral apophyseal lines* often parallel the median ventral seam on each side of the buccal opening. The smaller mouthparts are described and figured for *Odontomachus* by Gotwald (1969: 25-26, 33, 112); the main distinctive feature of the tribe is the shape of the labrum, which is longer than in other ponerines, and usually longer than broad, with free margin cleft, and so bilobed. The middorsal surface is usually longitudinally carinate. Maxillary palpi 4-merous in all species surveyed, even the smallest *Anochetus* species, such as *A. myops*, *A. punctaticeps* and *A. mayri.* Labial palpi 4-merous in many, perhaps most, species, but 3-merous in the *haematodus* group of *Odontomachus,* and possibly less than 4-merous in some small *Anochetus,* but a lower limit has not yet been securely established for *Anochetus;* certainly 4-merous labial palpi are common among *Anochetus* species, even when the palpi become very short.

Antennae slender, with long, curved scapes, 12-merous, with prevailingly cylindrical flagellomeres and a tapered apical segment. Compound eyes always present, usually large; reduced to dots in a few *Anochetus* species.

Trunk more or less long and slender, with the dorsal sclerites usually distinguishable, at least in the larger-sized species of both genera. Pronotum separated from mesothorax by a very distinct and probably (always?) flexible suture; metanotum usually distinguishable from mesonotum and propodeum, and metanotal spiracles present, usually distinct, and presumably functional. Propodeum long, with a horizontal (convex, concave, sinuate) dorsal surface, the angle with the declivity broadly rounded in *Odontomachus;* rounded, biangular, or even bidentate in *Anochetus*. Propodeal spiracle small, near the middle of the side, opening elliptical or a short slit.

Legs slender, unremarkable, with slender, usually simple tarsal claws; occasionally a minute vestigial tooth is seen on one or more claws in larger-sized species. Apical tibial spurs 1, 2, 2; in some smaller species 1, 1, 1; medial spur of mesothoracic leg slender, smaller than that of hind leg, and with pectination more reduced.

Petiole varying extremely in shape by genus and species: in *Odontomachus* more or less conical or dome-shaped, always ending in an acute, single-pointed apex; in *Anochetus,* the node can be shaped as in *Odontomachus* or can be conical with rounded apex, columnar with rounded apex, subtruncate, bilaterally dentate, or erect scale-like, with or without emarginate apex. Usually the node shows slight or no development of an anterior peduncle, but a subpetiolar process is present.

Gaster usually more or less compact, tapering rather rapidly caudad, and usually without a «ponerine constriction» between its first (and largest) segment, which is true abdominal segment III, and the second segment (abdominal IV). (Constricted in some *Anochetus*). The first and second segments, although with lateral sutural seams, always seem to have the terga firmly fused to the sterna. Sting long, strong, curved and functional; gonostyli long and slender, slightly broadened apicad.

Sculpture usually consisting of varying areas of striation alternating with smooth and shining surface. In some *Anochetus,* parts of the trunk become rugose, or coarsely costate, and in a few species in both genera, the gastric dorsum is densely punctate, reticulate or striate in place of the usual prevailingly smooth gastric sculpture. Most species in both genera have at least the anterodorsal (frontal) area of the head striate, with the striation spreading fanwise posteriad to varying distances.

Pilosity unremarkable, consisting of long, erect to decumbent fine (occasionally coarse) simple hairs, usually sparsely arranged. Pubescence usually appressed to decumbent, moderately dense to obsolescent.

Colors ranging from dull reddish brown or piceous to dull testaceous (cryptobiotic *Anochetus* species) or bright ferruginous, red-and-black, or red-black-yellow in some of the larger day-foraging aposematic species of *Odontomachus*.

Queen: Like worker, but differing in the characters usual for ponerines; in most species normally alate when virgin. Ocelli present, small, placed near the middle of the dorsum of the head. Head usually relatively broader, mandibles and scapes shorter, petiolar node broader and more compressed axially, than in workers of the same species, and trunk with the usual development of flight sclerites; gaster modestly more voluminous. The overall size difference betwen queen and corresponding workers is usually not very great, making the queen often hard to spot among the circulating workers when a nest is newly opened.

Wing venation in both wings of the complete ponerine pattern, without any trace of 1r in forewing, but Mf2 most often present and uncontracted. Anal lobe of hind wing usually present; may be lost in some of the smaller *Anochetus* species.

Male: Typically euponerine in habitus as well as the definitive characters: mandibles reduced, non-opposable; genital capsule not fully retractile; cerci well developed and conspicuous. In fact, I can find no character or combination of characters in this sex that will unequivocally separate Odontomachiti from Poneriti, or even that will separate males of *Odontomachus* or *Anochetus* from those of a ponerite genus such as *Pachycondyla* s. lat. Even the downcurved pygidial spine is shared by males of the more primitive members of both tribes, as well as some species of *Platythyrea* (Platythyreini).

Odontomachite males are usually told, in my experience, by this generally ponerite habitus and character set, plus the particular shape of the petiolar node, which usually reflects in a more or less muted fashion the shape of the node in the corresponding workers and queens. Thus, the node in *Odontomachus* males is more os less conical, with a narrowly rounded or even pointed apex; in *Anochetus*, the male node varies greatly with the species, so that in *A. mayri*, for example, it is axially compressed and squamiform, with its sharp crest forming two points separated by a deep emargination.

Size varying from 3 or 4 to more than 15 mm total body length, with correspondingly well developed wings. Head broader than long, with half to just about all of the sides of the head occupied by large compound eyes, which usually have weakly emarginate mesal margins in front (dorsal) view, and also weakly emarginate lateral margins as seen from the side. Clypeus small, convex, with convex or nearly straight anterior free margin. Ocelli large, close together, usually situated on an eminence. Mandibles small, narrow, with acute to bluntly rounded apices; at base with a dorsal whitish membranous basin, possibly at least partly the same as Ettershank's (1966) *mandalus*, which may possibly serve to dispense pheromones during mating flights. Distad, a curved dorsal ridge separates the concave outer face from the mainly convex dorsomedial face of the mandible. One or more stout, tapered, porrect setae issue from near the apex of each mandible.

Labrum small, bilobed, with a median cleft, fitting into the space between the mandibles. Maxillary palpi 6-, 5-, or 4-merous, labial palpi 4- or 3-merous, so far as I have been able to count. Some small *Anochetus* may possibly have lower counts, such as 3, 2, but I have not confirmed any counts this low.

Antennae always 13-merous, with short, cylindrical scape and still shorter pedicel; flagellar segments beyond pedicel longer and slender-cylindrical, arranged so that the antennae usually curve circularly up and then downward in dead specimens, as in most ponerine males.

Trunk rather robust, scutum with notauli forming a distinct, impressed Y in some *Anochetus,* an indistinct V in others, and a generally very indistinct or obsolete V in *Odontomachus.*

The unconstricted gaster of most odontomachite workers and queens is usually a feature also of the conspecific males, and we may expect that the gaster of males in such species as *A. inca* has the constriction between the first and second gastric segments wide and deep, as in the worker of that species.

Pygidium produced as a sharp, slender downcurved spine in all known *Odontomachus* males and in some Old World species of *Anochetus;* in other *Anochetus,* the pygidium has the free margin with a median crease and point, or is entire and rounded. Hypopygium linguiform, with parallel sides and rounded or subtruncate apex in *Odontomachus,* but variously formed in *Anochetus:* as a rounded, convex plate; produced as a single setose rod-like piece; produced as paired slender rods; as an emarginate plate, etc.

Genitalia proper much like those of Poneriti, relatively complete and conservative in *Odontomachus,* but modified in various striking ways in the few *Anochetus* species available.

Legs slender; tarsal claws slender, with or without a small submedian tooth. Tibial spurs 1, 2, 2 or 1, 1, 1, paralleling their development in workers and queens of the same species.

Pilosity simple and fine, usually rather sparse; pubescence sparse to dense, usually suberect to decumbent.

Head, petiole and gaster usually smooth or nearly so, though often finely and rather densely punctulate. Trunk usually largely rugulose, rugulose-striate, or densely punctulate in *Odontomachus,* finely and more or less densely punctulate in *Anochetus;* in both genera the pleural areas are smoother and often more shining than dorsal sclerites.

Color ranging from testaceous to black; in *Anochetus,* head sometimes much darker than remainder of body; scutum sometimes with a fuscous pattern consisting of a pair of broad longitudinal bands connected in part by a median element.

Larva (characterization based on that of G. C. and J. Wheeler, 1971: 1213): Body profile like that of *Pachycondyla,* i. e., neck long and slender; head large; abdomen subovoidal, but with the ventral profile nearly straight; anus ventral. Beset with numerous (80-116) tubercles, but none on midventral surface. A typical tubercle consists of a frustum bearing a circle of 4-6 relatively long, slender hairs that are constricted at the point of attachment; seated on this frustum is a spire that bears at its apex a heavy, straight, spinelike hair; integument of spire with short transverse rows of spinules. On the mid-dorsal surface of abdominal segment IV there is usually one or a pair of modified holdfast tubercles in form ranging from almost flush, glabrous areas to low pulley-like, bulbous, or even nearly doorknob-shaped projections, with a sparse fringe of short hairs. Similar structures may be found also on segment V, or may be lacking there; in *O. tyrannicus,* the Wheelers (1952: 652) found that the dorsal holdfast tubercles of segments IV and V were replaced by ordinary seta-tipped tubercles like those on the rest of the body.

Head hairs few and short; mouthparts rather large. Mandibles like those of *Ectatomma* or *Odontoponera:* moderately broad at base, tapering apicad, and weakly to strongly curved, with an acute apical tooth and a medial blade carrying 2 more teeth; on a part of the anterior surface are a few minute spinules in short, transverse rows.

The available information on the morphology and bionomics of odontomachite larvae is summarized by G. C. and J. Wheeler (1952: 642-652, pl. 5, fig. 1-17, pl. 6, fig. 22-29) and added to by them in 1964: 455-456 and 1971: 1212-1213, fig. 25-26.

In view of the present revision some of the old identifications listed by the Wheelers require correction or amplification:

Anochetus sp., [Mt.] Tobang, Borneo, 1300 m, E. Mjöberg, is *A. princeps.*

Odontomachus haematoda specimens listed from Costa Rica and Jamaica and figured in Plate 6, fig. 22-29, are very likely *O. bauri;* the samples from Ceylon that Clausen found parasitized by chalcidoids belonged to *O. simillimus,* and the specimens mentioned by Eidmann and by Emery could have been *haematodus, bauri,* or some other species. «*Odontomachus haematoda clarus*» is *O. clarus;* the species investigated by Haskins and Haskins is *O. brunneus;* the Cuban var. *pallens* is *O. insularis,* and the var. *bruneipes* discussed by Eidmann probably was *O. bauri.* The *O. biolleyi* larvae described by the Wheelers (1952: 651) should be questioned, because the only adults of this species I know to exist in collections are the types. *O. ruficeps coriaria* and *O. cephalotes* of the Wheelers are *O. ruficeps,* and their *O. haematoda insularis* is *O. brunneus.*

The larval characters of the Odontomachiti are in my opinion worth only generic rank within the Ponerini. The tubercle form and the holdfast structures of abdominal segments IV and V are the best characters, but the holdfasts are not universal in the subtribe (*O. tyrannicus* lacks them), and the form of the ordinary tubercles is not really strikingly different from that of some *Pachycondyla (s. lat.)* species, or species currently placed in *Myopias.*

Pupae: Normally enclosed in cocoons; I know of no exceptions. The silk is light to dark brown in color in the finished cocoon. As usual for ponerines, the spinning larvae require some sand or loose dirt as a substrate in order to complete the cocoon normally.

Cryptic characters: No species of odontomachite has yet been studied cytogenetically. The only data on Malpighian tubule number I can offer now is a count of 5 tubules in each of 2 Costa Rican workers of *Anochetus mayri,* a small species that cannot be considered as representative of the whole subtribe. Wheeler and Blum (1973) found a number of alkylpyrazine compounds in *Odontomachus hastatus, O. brunneus* and *O. clarus* that excite alarm behavior in these ants, but repel *Solenopsis invicta.* The pyrazines apparently are produced by the mandibular glands.

Bionomics of Odontomachiti

Habitat. The places where odontomachites live are varied. Where they penetrate into the temperate zone, most species excavate nests in the earth. Occasionally the nest is dug under a covering rock. In the tropics, many nests are also dug in the soil, but in moist forested areas, a common site is the soil beneath a rotting log or other large mass of rotting wood, with extensions of the nest into the log itself. Another frequent nesting site in tropical forest is in the humus and leaf litter at the base of large trees, particularly between buttress roots. *Anochetus* species of medium or small size often nest in small pieces of rotting wood or bark, or even small rotting twigs or seeds and nuts lying in or on the forest litter.

Some species tend to choose more arboreal nest sites. *O. mayi*, as noted by Mann (1911) and by Lenko and myself, is usually found in the Amazon Basin nesting in «ant gardens» — balls of roots and stems of small, specialized plants lodged in or suspended from tree branches; in this case the *Odontomachus* were usually living in company with the smaller dolichoderine ant *Monacis rufescens* [3]. The large and aggressive *O. hastatus* is usually taken in microhabitats off the ground; I have found nests in bromeliads and other epiphytes growing on trees in tropical forest, in the leaf bases of small palms, and in leaf trash gathered in the forks of large trees a meter or more above ground level. In Panama, I found a nest of *O. brunneus* in scanty epiphytic growth on the highest, most exposed dead top branches of a tall forest tree that had been blown down the night before. Old termite nests, both on trees and on the ground, often harbor *Odontomachus* nests, in arid country as well as forest. *Anochetus emarginatus* frequently lives in hollow branches of trees.

Arid-country species, such as *O. bauri* in the Barquisimeto area of Venezuela, *O. clarus* in semidesert Mexico and southwestern U.S., or *A. levaillanti* in South Africa, nest in the soil. Perhaps the most unusual nesting site is that of *O. malignus*, in coral masses on the marine coasts of the Malay Archipelago and Melanesia [22].

Foraging for living animal prey takes place on the soil surface, within the soil-humus-log mold matrix, or on the trunks, branches and foliage of trees and plants wherever these are available. Fragmentary evidence indicates that most epigaeically foraging tropical odontomachites tend to do their foraging at dusk, at night, or during dawn hours. I found *Anochetus africanus* walking on tree trunks only at night in the Ivory Coast, *Odontomachus ruficeps* mainly abroad on trees at dusk and after dark at Mataranka and near Darwin in the Northern Territory of Australia, and *O. bauri* on tree trunks and bushes at night in Panama. *O. malignus* has been found foraging among corals in the intertidal zone at low tide [22].

Some species, particularly those with red heads or other aposematic coloration, apparently forage in the open more during the day. No systematic comparative study has yet been made of foraging hours for different species.

The food of Odontomachiti consists principally of living arthropods caught and killed or incapacitated by the ants. Wheeler (1900: 12) relates vividly how he placed a living house-fly in a nest of *O. clarus* (called by him «*O. haematodes*»):

> «Its movements at once attracted several ants, which began snapping at it like a pack of angry dogs. With each snap a leg or wing was severed and often thrown to a distance of 2 or 3 inches. In less than a minute all the limbs had been shorn from the trunk. The fly was then seized and decapitated».

Wheeler found that *O. clarus* would also eat caterpillars, beetles, and small Hemiptera, as well as sugar, bread, cake, etc.

Ledoux (1952) thought that *Odontomachus* are «strictly entomophagous», based on his observations in West Africa on *O. assiniensis,* but his only reported observations are based on nest-founding queens, which he says will «not touch sugary substances». He finds that the food of *O. assiniensis* «consists above all of termites», although it will also take ather kinds of small insects encountered during its foraging on the soil surface.

O. troglodytes, the African member of the *haematodus* group, to which *O. clarus* also belongs, definitely tends Homoptera. Evans and Leston (1971) show that it attends scale insects *(Stictococcus)* and aphids *(Toxoptera)* on cacao in Ghana, and even builds tents of soil particles over the homopteran colonies. *O. troglodytes* also carries drops of honeydew between its closed mandibles near their tips, a habit recalling that commonly seen in *Paraponera, Ectatomma,* and some large Ponerini, which often carry drops of honeydew or nectar between their partly-open mandibles down from the tree tops to their nests. On the other hand, Evans and Leston found that *O. troglodytes* treats the mealybug *Planococcoides njalensis,* also found on cacao, as prey.

Whether some *Odontomachus* species or groups never feed on sugary substances is a matter for future checking. *Odontomachus* and *Anochetus,* when imbibing liquids, usually do so with their jaws in the locked-open position.

O. assiniensis uses its sting readily to capture termites (up to 8 or 10 mm long, or somewhat less than the length of the ant itself), but smaller insects may be killed by a simple mandibular strike, and carried off without being stung. Queens catch small prey with the mandibles alone, and apparently use their stings only for defense. When the sting is used by workers against termites, the prey is immobilized in a few seconds.

Ledoux found that large flies with a wing removed and given to *O. assiniensis* were finally caught only after repeated attempts, the ant seizing an extremity of the fly's appendages and immediately curling its gaster under in an attempt to sting. The fly often escaped, shaking the ant off by violent motion, but once the ant managed to get its sting between the segments of the fly's abdomen, the struggle quickly ceased. This picture is quite different from that drawn by Wheeler for capture of flies by *O. clarus,* but whether the difference is due to real behavioral dissimilarities between *Odontomachus* species groups can only be settled by further comparative study.

The smaller and more delicate species *Anochetus inermis* has been observed by me in a laboratory nest. The colony came from a piece of rotten wood from the floor of a wet ravine near Bucay in western Ecuador. The colony was fed with small tenebrionid beetle larvae *(Tribolium castaneum),* comparable in size to the *A. inermis* workers, and the latter attacked the prey with their mandibles in the familiar snapping manner, but very cautiously and nervously, with stealthy approach, extremely rapid strike, and instant recoil-retreat. After several attacks of this kind, with intervening periods of waiting, during which the beetle larvae fled, rested, or writhed about in distress, an ant would finally attack with its mandibles and hold them closed on the prey for long enough to deliver a quick sting in the intersegmental membrane. After this, the prey appeared to be paralyzed, or at least subdued, and sooner or later was carried off by the ant to the nest, and eventually placed on an ant larva.

Frequent delays and excursions before the prey are finally immobilized and brought to the ant larvae in the nest may well have the function of allowing time for protective allomones of the prey to dissipate. Many tenebrionid adults, including *Tribolium,* possess potent quinonoid defensive allomones, but the larva is not known to possess quinones in this genus.

Observations by Borgmeier (1920: 37) made in *O. affinis* in southeastern Brasil are contradictory in that he found this ant would feed on honey and sugar solutions, and would regurgitate to the larvae, but it would not feed on termites he offered it. Perhaps the termites in this case were of a kind particularly repellent to the ants. I have observed in both the Old World and New World tropics that some kinds of live or freshly killed termites are shunned by odontomachites and other predaceous Ponerinae, presumably because of protective allomones, even when termites in general were known to be principal foods of the predators concerned.

Population biology. Colombel (1970a, b, 1972) has given us a detailed and extensive study, based on many samples examined in Cameroon, of the population biology of *O. troglodytes* (called by him «*O. haematodes*»). This investigation is the most complete of its kind available for any ponerine ant.

In Cameroon, *O. troglodytes* nests most often in second-growth forest at the bases of dead or diseased trees, under or against logs, or simply in the soil. In some especially favorable districts, Colombel thinks the density of colonies may reach as high as 20 per hectare over wide areas, but he places the mean density at less than 12 per hectare. A secondary habitat is in the heads of palms, especially oil palms *(Elaeis)* where the ants nest in beetle burrows and the axillary spaces at the leaf bases, where soil and humus accumulate. Additionally, some ants live in the soil in treeless areas at the base of hill slopes, etc., in which case the nest rarely extends through a space more than 60 x 60 x 15 = 54,000 cm, or about half a cubic meter. Beyond this, tunnels extend outward up to 3 m, and large colonies may have as many as 20 entrances hidden under leaves, under stones, or in depressions in the soil surface. In such situations, the ants attack earthworms as well as insects.

Of 770 colonies found and sampled, Colombel records only 0.65% as dealate nest-founding queens, though of course these are much harder to discover than are larger colonies. Colonies in the growth stage, with up to about 250 workers, mostly have only a single dealate queen, but colonies with 300 workers are capable of producing their own queens and adding some of them to the nest force, or adopting outside queens, so that nests with populations above 300 eventually arrive at an equilibrium ratio of about 1 queen to every 85 workers.

The great majority of nests found contained more than 300 workers, and in good forest locations, some nests were counted at more than 1,000 (up to nearly 1,300) workers. Colonies are slightly more populous, on the average, during the rainy season than in the dry season, and they are also larger in good forest habitat than are those in nests situated in palms or in soil outside the forest.

The queen lays 1-2 eggs per day during her first year, rising to about 2.5 per day after she is more than a year old (the figures in Colombel's English summary, 1970b: 199, are for eggs per 10 days, and so should be divided by 10). The egg takes about 10 days to hatch, and about 40 more days pass to the eclosion of a worker. The workers hunt effectively only after they are about 4 months old.

The queen's eggs are all capable of development; she lays no special trophic eggs, though some of them — sometimes 1 or 2 out of every 3 laid — are eaten by young larvae. The ovipositon rate of the queen is tied to her nutrition, and therefore to the number of foraging workers she depends upon for her food.

Workers of *O. troglodytes* also lay eggs, and those that develop, being unfertilized, produce only males (after some 54-57 days of development). In queenless colonies, many worker-laid eggs are eaten by workers or young larvae; only 1 in 45 to 1 in 5 male eggs reach adulthood.

Queens inhibit egg-laying in workers when the nest space falls below a critical volume, or when the number of workers per queen drops below about 50. These results suggest pheromonal inhibition by the queen, and experiments with currents of air passed over queens, and with queen extracts, demonstrated that partial control (delay) of worker oviposition was indeed mediated by pheromones originating from the queens.

In nature, *Odontomachus* colonies are often rather dispersed, and I would think that queen control of worker oviposition is probably rarely complete, via pheromonal or any other control route.

Nuptial flight. Ledoux (1952) found that virgin queens of *O. assiniensis* in West Africa leave the nest all through the year, but mostly during the rainy season. Flights do not seem to occur en masse, but by the young queens slipping out one or a few at a time during the evening. They are not as strongly attracted to light as are the males of many species. When a nest is opened containing unmated males, one has to be quick to catch those that have reached full adulthood, because they are quick to escape by flight. Although males of different species of *Odontomachus* and *Anochetus* are commonly taken at light, other species are not. Stewart and Jarmila Peck gave me Malaise trap samples taken in western Ecuador that contained males of several species in both genera, but Malaise traps capture both day- and night-flying insects.

Actual mating has not been observed in nature, so we do not know whether an aerial mating swarm is formed or not. The mandalar basin at the base of the male mandible may well serve to dispense a mating pheromone; this possibility should eventually be open to testing by experiment.

Once having copulated, says Ledoux, the males «are in general killed by the workers», a statement that raises questions. Where are the males when the workers kill them? Have they mated in the nest? Or have they mated outside and returned to their own or a strange nest? Before we accept this statement at face value, I think we need to know some of the details.

Nest founding. The young queens, once fecundated, divest themselves of their wings and dig a short tunnel in the soil, often under a rock or piece of wood, at the end of which is their brood chamber. The entrance is left open, or only partly closed, and the queens issue forth at intervals, often by night, to forage (Haskins and Enzmann 1938: 149; Ledoux, 1952; my own observations on *O. erythrocephalus, O. brunneus* and *O. bauri*). *O. erythrocephalus* queens have twice been observed foraging near midday on a cloudy, rainy day in Colombia. Ledoux found for *O. assiniensis* that the queens first oviposited 3 or 4 days after shedding their wings. The first egg takes 9-10 days to hatch, after which some of the later eggs disappear, perhaps eaten by the queen (thinks Ledoux), but more likely they are fed to the first larva. The eggs are stacked and carried in packets, adhering by a sticky coating to one another.

The first larval stadium lasts about 4 days; the second stadium takes an average of about 5 days. The third instar is a larva of 5-6 mm in length (in *O. assiniensis*), more slender in form than the first two instars. (While most observers agree that ants have either 3 or 4 larval instars, it should be noted that in no single case have the molts all been certainly seen and counted, and until that has been done, I consider that the number of instars is not surely known for any species of ant). After about 4 days in its last (third, according to Ledoux) instar, the larva is covered by the queen with bits of earth, sand or rotten wood, against which it spins its cocoon in about a day.

The time required for pupation is long — more than 20 days (average 24 days according to Ledoux). Meanwhile, other larvae are developing and pupating in their turn, but despite regular and abundant oviposition by the queen (in good conditions) many eggs and larvae disappear beginning at about the third month, so that after 4-5 months, the queen may be accompanied by only 8-10 small (minim) workers. Presumably the workers forage effectively after this early period, which must be a critical time for nest foundation.

Ledoux, noticing that some winged queens when isolated before nuptial flight began to lay eggs, found that these eggs were not cared for, and did not hatch. When he isolated 10-20 queens together with abundant food, he found that a few among them would lose their wings and begin to oviposit. Some females, usually those still with wings, would care for the brood, raising a small proportion of them through larvae to pupation and eclosion of adult males, which were killed, apparently before they could mate with the queens.

All the evidence thus points to arrhenotokous parthenogenesis being the rule in *Odontomachus*. Ledoux' observations with the isolated queen groups are also of interest in their indication of a possible dominance hierarchy among the virgin queens, or «division of labor», as Ledoux terms it.

The experience of Colombel indicates that freshly dealate queens, and even adult workers, may be accepted into colonies other than those in which they were born. Apparently some hostility is shown at first toward aliens, and these may sometimes be killed, but in other cases hostility gives way to acceptance. The loose organization of the nest also suggests that new colonies are sometimes founded by queens with attendant workers at some location toward or beyond the margin of the parent nest. This kind of budding-off of new nests appears to be common among Ponerinae.

Larval development. When Ledoux put a queenless colony of 50-60 *O. assiniensis* workers under observation in an artificial nest, the workers laid eggs and reared a number of adults, all of which turned out to be males. The eggs hatched after 10-11 days and the resultant larvae developed through 4 instars, lasting on the average: I, 5 days; II, 4 days; III, 7 days; IV, 5 days, with the fourth instar reaching a length of 7 mm, and the resultant pupa in its cocoon (9-10 mm) lasting about 25 days, or about 57 days total for the developmental period beginning with oviposition and ending with eclosion. The fourth larval instar, as compared with only 3 in the case of the dwarfed (minim) workers produced by a lone nest-founding queen, is to be noted, but the difficulties in counting larval instars have already been discussed above.

Four larval instars were also reported by Ledoux for worker broods produced from eggs laid by queens taken with workers from a nest in nature; these workers needed only about 48 days to develop from oviposition to eclosure, and the pupal stage took only about 16 days instead of the 24 required of minim pupae. The workers resulting were normal-sized and dark-colored, instead of the dwarfed, light-colored minims of incipient nests. Ledoux here emphasizes the 4- vs. 3-instar larval period as being responsible for the imaginal differences between the two classes of workers, but again it is necessary to issue a warning against the pitfalls of instar-counting of ant broods. In fact, Ledoux gives us only figures for the *means* of body length of the different instars of larvae, which in my experience will usually not allow a reliable separation of size modes in an organism such as an ant larva, which expands, the integument stretching over much of the body, *during* each stadium. The head capsule width is presumably not affected by within-stadium expansion, but Ledoux cites no measurements for this dimension, which in any case is not known to correspond exactly to the sequence of molts. The whole question of instar counts, in my opinion, needs further investigation by more rigorous methods, such as timelapse photography, that will record the actual number of molts for given larvae from hatching to pupation. Meanwhile, we may view Ledoux' account of the origin of differences between minim and «normal» workers as no more than an interesting hypothesis.

Defense. When a nest of any af the larger odontomachite species is breached, some of the workers immediately hide beneath leaves or other objects, while other workers rush about with open jaws, which they snap at foreign objects, or even at leaves and twigs, with an audible tick. On human skin or clothing, a worker will snap her jaws and hold fast to the surface with them, at the same time quickly bringing her gaster around to sting. The sting is long and strong, and to me the effect is shocking and quickly painful. However, at least in the case of *O. bauri,* I did not suffer for long; in a few minutes the pain had subsided, leaving only a slight lingering tenderness. Apparently *O. hastatus* and members of the *tyrannicus* group have more potent stings, but I have not personally experienced them.

Most of the smaller and medium-sized *Anochetus* species feign death when disturbed, crouching flat against the surface, or rolling themselves into a ball and remaining still, often for a minute or more. Only when held do they sting. Their stings can be felt in most cases, but the effect is usually trifling.

Distribution of Odontomachiti

Like most major ponerine taxa, the odontomachites are primarily tropical and subtropical on all continents and large islands, with a few species extending north and south into temperate regions. In northeastern China, *Odontomachus monticola* extends to the end of the North China Plain, to the northwest of Peking, where the winters can be quite cold, and the climate is comparable to that of Kansas. In North America, *Odontomachus clarus* reaches central Texas and southern Arizona, while *O. haematodus* and *Anochetus altisquamis* have their southern limits near Tucumán, in northwestern Argentina. *Anochetus ghilianii,* basically a Moroccan-Algerian species, is found on the north shore of the Strait of Gibraltar, the only point at which odontomachites are known to have been established in Europe. *Anochetus levaillanti* occurs near Grahamstown, South Africa, and it doubtless reaches the coast of the Cape Province; *A. punctaticeps* is already known from south coastal localities. In Australia, *Odontomachus ruficeps* and *Anochetus armstrongi* reach the mallee country in the interior of Victoria, and *O. ruficeps* also is widespread in the interior of southwestern Australia.

Wilson and Taylor (1967) found that *Odontomachus simillimus* is widespread in central Polynesia; *Anochetus graeffei* also reaches Samoa, New Caledonia, etc., and *A. splendidulus* occurs on several islands in Micronesia. Elsewhere, *O. brunneus* was once established on Bermuda (Haskins and Haskins, 1965) and is on Clipperton Island, in the Pacific 670 miles southwest of Mexico (Taylor and Wilson, 1962: 142, as *O. insularis*). *O. clarus* is on Clarion Island, off Mexico, *O. bauri* is in the

Galapagos, and *O. simillimus* is on isolated Christmas Island, in the Indian Ocean south of Java. Undoubtedly, many of the island records represent accidental introductions by man, but the ability of conspicuous, stinging ponerines to spread so far and wide through human commerce or any other means must be regarded as exceptional, and indicative of the general-adaptive nature of the Odontomachiti as a taxon.

Most *Odontomachus* species are found in higher-rainfall areas; *O. bauri* in South America, and *O. clarus* in North America, also extend into semidesert regions; in fact, *O. clarus* is found mainly in such dry areas in Mexico and southwestern U.S. In Australia, *O. ruficeps* also ranges into arid districts in many parts of that country. *Anochetus* has species in habitats ranging from wet to dry, but the real dry-country species are all in the Old World, and even there they are not extreme xerophiles. Judging from the locality records and my own experience, I would say that arid-country *Anochetus* all or mostly are found in xeric scrub, dry open forest or grassland, particularly in microhabitats at least partly in the shade of shrubs or trees.

I conclude from the overall distribution of Odontomachiti that both genera evolved from the tropical forest habitat, and that tropical forest is still their main theater of evolution.

The Odontomachiti completely lack representation in the fossil record. They may well not have been present in the Baltic Amber forests or mid-Tertiary western North America, from which we have extensive ant remains in amber and shales of lacustrine origin, respectively. This could mean that the taxon had not yet evolved, or that it had not yet radiated and spread far from its tropical place of origin, or simply that these ecological zones were not suitable for odontomachites. Absence of Odontomachiti from tropical ant-rich formations, such as the Sicilian, Dominican or Chiapan ambers, all mid-Tertiary in origin, is harder to explain, although relatively large ants such as *Odontomachus* do seem to get caught and preserved in resin drops less frequently than some smaller-sized genera.

We are left without a solid clue to tell whether the odontomachites had their origin in the Old World or the New. *Odontomachus* is only slightly better represented in the Old World than in the New as regards both numbers of species and species-groups, but the New World representation appears unbalanced in that the *haematodus* group includes most of the species there. In *Anochetus*, the Old World complement seems to include more basic stocks and is ecologically more diversified than that of the neotropical region, which probably indicates a longer span of evolution in the Old World. I think we can conclude from the available evidence that the subtribe most likely originated in the Old World wet tropics, that it has gone through a complicated evolution with several waves of dispersal, and that both the evolution and the dispersal may well have been rapid and geologically late.

Relationships and Origin of the Odontomachiti

The odontomachites have for more than a century been considered to be a distinct suprageneric group (Mayr, 1862: 708), and most recent classifications have accorded them tribal rank within the Ponerinae as the Odontomachini. Certainly, their habitus, built around the unique form and function of the snapping mandibles and the head that holds them, renders them instantly recognizable among all ants. Aside from that, and the unispinose or otherwise modified petiolar node, they are rather typical Ponerinae. In fact, it does not take much close consideration of all castes and the larvae and pupae to see that among the tribes of this subfamily, the odontomachites show closest affinities to tribe Ponerini.

Males of *Odontomachus* and *Anochetus* are clearly members of Emery's «Euponerinae», which is to say that they have strongly reduced mandibles that cannot be opposed, genital capsule not [fully] retractile, and subgenital plate (hypopygium) entire (that is, usually not deeply forked or bidentate). Furthermore, the pygidium in *Odontomachus* and a few *Anochetus* is modified into a prominent downcurved spine as in most large and medium-sized males among the genera of Ponerini, and some species of *Platythyrea*. This character state, which I take to be primitive among the stocks represented by *Platythyrea, Odontomachus* and the larger Ponerini, may represent a false sting defensive mechanism, as discussed by Brown (1975). The false sting hypothesis is at least consistent with the loss of the pygidial spine in such small-sized males as those of *Hypoponera* (Ponerini) and many *Anochetus,* in which visual or tactile effects of the spine could scarcely be expected to impress most would-be predators.

The parts of the odontomachite male genital capsule itself are like those of Ponerini in general, and the wing venation of both sexes is «complete», that is, with all of the primitive formicid components (except Ir in the forewing) present; the anal lobe is present on the hind wings of at least the larger *Odontomachus* and *Anochetus* species. In most cases, the tarsal claws are slender and simple, and the tibial apices of the middle and hind pairs of legs each have a larger mesial pectinate and a smaller lateral spur, at least in the large and medium-sized species. These character states are all found also among the genera of Ponerini. The frontal carinae and their lobes are close together in odontomachites, which is not surprising in view of the *Bauplan* of the head, but at least this condition is similar to that seen in Ponerini.

The larvae of odontomachites (G. C. and J. Wheeler, 1952: 642 ff., 1964: 455 ff., 1971: 1212) have clearcut «piligerous tubercles», and are therefore euponerine in the Emery classification. Within the euponerine series of genera, odontomachites can be distinguished as a group (G. C. and J. Wheeler, 1971: 1216) but it seems to me, considering all of the variation among euponerines, that this distinction is hardly to be taken as more than a generic level one.

An adult character state that seems significant to me is the maximally 4-merous condition of both maxillary and labial palpi in workers and queens of both odontomachites and primitive Ponerini. This implies the evolutionary loss of 2 segments of the maxillary palpi, which primitively have 6 segments in ants (and Hymenoptera). In view of the other similarities involved, it seems likely that odontomachites and Ponerini have the 4,4 segmentation of the palpi as a shared primitive condition.

The evidence presented above seems clearly to lead to the conclusion that the odontomachites and Ponerini sprang from a common phyletic stem. Further, since the odontomachites obviously represent a derivative condition with respect to head and mandible form, it follows that they most likely arose from a stock within the Ponerini. (The fossil record tells us nothing about odontomachites, since as far as we know, they are not represented there). The Ponerini, as a tribe consisting predominantly of specialized predators of arthropods, have (not surprisingly) radiated diversely in the form of the main prey-getting structures, the mandibles. I interpret the odontomachite mandible-and-head mechanism as an extreme of this radiation that broke through onto a new general-adaptive plane allowing more efficient capture of many kinds of arthropod prey, and consequently giving rise to a new adaptive radiation.

We know very little about the specificity of *Odontomachus* and *Anochetus* predation, but my own casual observations, made in many countries around the world, as well as on laboratory colonies, suggest that most if not all species take a fairly wide variety of the arthropods available in their respective microhabitats. There are of course bound to be restrictions based on prey size, behavior, and chemical and other defenses, but it should be noted that the quick strike-and-recoil tactics of the odontomachites (with their long mandibles) may represent an optimally safe method of attacking chemically protected or otherwise dangerous prey.

But what of the classification of the odontomachites? If we stress the general-adaptive nature and uniqueness of the worker-queen mandible-head complex, then we most likely should continue to recognize the group as a separate tribe in subfamily Ponerinae. But in their origin and known character systems apart from the prey-getting mechanism, *Odontomachus* and *Anochetus* are rather typical members of Ponerini. It seems to me that a sensible compromise is to include the two genera within tribe Ponerini, but to distinguish them at the subtribal level (subtribe Odontomachiti), at the same time recognizing the equally bizarre *Harpegnathos* as worthy of subtribal rank (Harpegnathiti) alongside the subtribe Poneriti, the last to include the bulk of «typical» genera of tribe Ponerini.

Evolution within the Odontomachiti is a matter of speculation, with few points of relative certainty. It does seem fairly clear that the two genera of the subtribe, *Anochetus* and *Odontomachus*, represent a real phyletic separation in the sense that each taxon is monophyletic, and each represents a separate adaptive radiation. I judge that *Anochetus* represents the primitive stock of the subtribe, and that *Odontomachus* arose from some group of *Anochetus*. This conclusion is supported by the configuration of the head, particularly of the posterior vertex and the apophyseal lines, representing shelf-like internal muscle attachments, developed in *Odontomachus*, but not in *Anochetus*. These apophyseal structures presumably increase the effectiveness of the snap-bite of the mandibles, although there is no direct functional evidence for this assumption. The shelves are unique in *Odontomachus*; that is, they are unknown in other ponerines.

Consistent with this interpretation is the fact that *Anochetus* has radiated more extensively and more radically than *Odontomachus*, implying for one thing that it has had a longer time to do so. *Anochetus* species, e.g., *myops*, *talpa* and *minans*, have the body size, eyes, pigmentation, and tibial spurs all reduced to go with a cryptobiotic adaptive zone, while such species as *emarginatus* retain fair body size, and show large eyes and other specializations for the arboreal or subarboreal lifeway that we know they follow.

We see that *Odontomachus* has attained a larger body size on the average, and tends to occupy the exposed ground-surface and arboreal adaptive zones (foraging fields, and to some extent nest sites) more than it does the hypogaeic and other cryptic ones. Both genera have achieved a wide distribution in the tropics, and both have spread into the temperate zones of the earth to a modest extent north and south, with *Odontomachus* having a slight edge in this respect in most countries. Looked at in one way, we can view *Odontomachus* as a secondary radiation and dispersal of the *Anochetus* stock based on the general-adaptive improvement of mandibular-action mechanics, and perhaps other traits that we do not yet appreciate.

Among the species groups of *Odontomachus* we can hypothesize that the *haematodus* group represents the most recent radiation of the genus. The derivative nature of this group is given away by its loss of a single segment from the labial palpi, lowering the primitive number of palpomeres from 4 to 3. That this loss occurred only once in the genus is suggested by the core similarity of the constituent species in other respects (broad head, short antennae, stout mandibles, shape and sculpture of petiolar node, etc.). The *haematodus* group has most of its species (19) in the New World, but in Africa one of the two species *(troglodytes)* belongs to it, while *O. simillimus*, the most common and widespread member of the genus in the Indo-Pacific area, represents it there. *O. troglodytes* and *O. simillimus* are rather weakly differentiated sibling species close to *O. haematodus* itself and to *O. bauri*, so one is tempted to think of the *haematodus*-group radiation as being South America-based.

The conclusion that there has been a substantial radiation of the *haematodus*-related stock in tropical America is inescapable, but that does not necessarily mean that *troglodytes* and *simillimus* are derived from American ancestors. An alternative hypothesis is that these two species, perhaps together with *O. haematodus*, represent an «apical growing point» of evolution for the genus. In terms of general-adaptive evolution, either *troglodytes* or *simillimus* might even represent the «point of the point». Following this line of reasoning, we could explain the American radiation of the *haematodus* group as successive specializations of an invading pre-*haematodus* stock against relatively weak competitive resistance from already-established older lines represented there today by specialized or geographically localized species such as *O. hastatus*, *O. bradleyi* and *O. mormo*. These 3 species possess 4-merous labial palpi and other characters of body build, sculpture and nodal form that link them more closely to the Old World groups of *tyrannicus*, *saevissimus*, *infandus* and *assiniensis* than to *haematodus*-group members now co-existing with them in South and Central America,

Taken all together, the pattern of occurrence of *Odontomachus* over the earth shows an apparent Darlingtonian (post-drift) succession of evolutionary and distributional waves. The successional series seems most nearly complete today in the Indo-Australian region, where the *tyrannicus* and *saevissimus* groups represent specialized relicts of an early radiation, the *infandus* and *rixosus* groups represent the next wave or waves, and the *ruficeps* group (in Melanesia and Australia) and *assiniensis* (in Africa) represent a still later wave, ancestral in its turn to the *haematodus* group wave. In the New World, *O. mormo* may correspond to the first wave, *O. hastatus* to the same or another early one, and *O. bradleyi* to the Old World *infandus*-group wave.

Discussion of the phylogeny of *Anochetus* species-groups is reserved for the treatment of that genus to be presented in Part VIB of the reclassification.

Odontomachus and *Anochetus,* though obviously closely related, have been separated for more than a century, and during this time, *Stenomyrmex* has been distinguished either as a genus or as a subgenus of *Anochetus.* Emery (1892: 558) raised *Champsomyrmex* for the aberrant species *Odontomachus coquereli,* which fits *Odontomachus* in some characteres and *Anochetus (Stenomyrmex)* in others. Several years ago, after attempting to use the traditional (Emery, 1911: 107-112) diagnostic characters, I decided that all of these groups intergraded broadly, and that they should be included as synonyms within a broadened *Odontomachus* (Brown, 1973: 178 ff.). The MCZ ant collection was rearranged accordingly, and countless specimens were distributed to other collections with determination labels as «*Odontomachus*» replacing the generic name «*Anochetus*» wherever it would previously have been used. But now, at a late stage of manuscript preparation, I suddenly have found a very distinct and unequivocal character that will distinguish *Odontomachus* from *Anochetus* at a glance. By its use, *Champsomyrmex* falls into *Odontomachus* as a synonym, and *Stenomyrmex* into *Anochetus.* But before we discuss this new character, let us review the traditional ones.

It seems clear that species have been placed in either *Odontomachus* or *Anochetus* on three main characters of the workers and queens.

1) Size: larger species are usually *Odontomachus,* smaller ones *Anochetus.* 2) Shape of petiolar node: *Odontomachus* species usually have a more or less conical node with an acute or spiniform summit, while *Anochetus* has a rounded, transverse or bidentate nodal summit. 3) Antennal fossae: *Odontomachus* has distinct fossae, bordered by swellings and confluent on the midline of the vertex (see fig. 2), whereas in *Anochetus,* the fossae are absent, or at least not confluent. Taking the world fauna, most species can be placed in either genus on all three criteria. There remains a residue of species in which these characters occur discordantly. Let us take each criterion in its turn.

1) Size. The species of all groups can be placed on a single size gradient, along which they overlap broadly. *Stenomyrmex* alone includes species such as *horridus,* well down in the *Anochetus* size range, and

others, such as *emarginatus,* that exceed the size of the smallest *Odontomachus* (e. g., *minutus,* small *monticola, brunneus, spissus, simillimus*). Certain *Anochetus* (e. g., *faurei, rothschildi, gladiator*) also enter the *Odontomachus* size range at the small end. In size, *Champsomyrmex coquereli* is in the range of *Odontomachus.*

2) Shape of petiolar node. Although *Odontomachus* species do always have more or less faithful versions of the pointed-conic or uniaculeate node, in some species (e. g., *spissus, biolleyi*) the point is low and blunt. The *Anochetus* species, on the other hand, show very wide variation in nodal shape. In the Indomalayan *princeps* group, species approaching the lower size limits of *Odontomachus* have subconical *(princeps, risii, rugosus)* or even spiniform *(gladiator)* nodal apices. These nodal forms grade into bluntly rounded ones *(levaillanti, orientalis,* etc.), and then an anteroposterior flattening of the nodal summit yields species such as *emarginatus, mayri, punctaticeps* and many others, with chisel-like, emarginate or bidentate apices.

3) Antennal fossae. One of the best arguments against this as a valid generic character is the existence of the Malagasy species *Champsomyrmex coquereli,* which is *Odontomachus* in size and nodal form, but lacks well-developed, confluent fossae. Emery «neutralized» this embarrassing species by assigning it to a monotypic genus. As if this arrangement were not artificial enough, an even more damaging fact can now be entered into the argument. *O. hastatus,* the well-known neotropical species, has large workers which, despite their somewhat *Stenomyrmex*-like habitus, can be classified on all three of the foregoing criteria as bona fide *Odontomachus.* But in the smaller workers of this species, the antennal fossae are absent or ill-defined, and at least are nonconfluent. Thus, in the formal key character, large workers of *hastatus* would run to *Odontomachus,* and small ones to *Anochetus.* The fossae are not really confluent in most *O. panamensis;* in *O. spissus,* they are rudimentary and scarcely form confluent sulci at the midline of the head.

The antennal fossa thus appears to be size-correlated (allometric) through a morphocline of species, but the correlation with size is incomplete and unevenly expressed along this morphocline. In the smaller *Anochetus* species, the approximate position of the missing fossa is often indicated by the posterior edge of a fan of radiating striae on the vertex.

Another character of possible significance is the presence or absence in the male of a downcurved spine on the apex of the pygidium. Some *Anochetus* lack the spine, some *Odontomachus* have it, but for the majority of species, the male remains unknown. In *A. isolatus,* the downcurved spine is well developed; in *A. filicornis* it is present and acute, but short; in *A. madaraszi* it is represented merely by a pointed fold at the pygidial posterior midline.

The evidence we have from the larvae (G. C. and J. Wheeler, e. g., 1971: 1212-1214) also offers little encouragement for splitting *Odontomachus* and *Anochetus* on traditional lines.

Now we come to the new diagnostic character. I was led to discover (or rediscover?) this after rereading the remarks of Mayr (1862: 708 ff.), in which he briefly mentioned as a character diagnostic of worker-queen *Odontomachus* the «tiefe

Furche», fairly obviously referring to a narrow, darkened, suture-like median groove dividing the posterior part of the dorsal surface of the cranium — the region incorrectly called «occiput» in most myrmecological descriptions. He stated that *Stenomyrmex* has a shallow elongate impression in place of this groove, and that it is lacking in *Anochetus*. With a representation of species now much increased over what Mayr knew, we can discount the mere presence of a dorsal groove itself as a generic character, since a morphocline of conditions exists. But in looking at this groove in different species, I noticed something else. The semicircular posterior excision of the head found in all the species of these genera is bordered by a fine carina that passes across the back of the head and down under to its ventral surface, separating the dorsal surface (vertex) of the head from a posterior surface that we can call the «occipital face», while admitting that the true occiput in ants and many other Himenoptera is a problematical region, possibly limited to a narrow rim around the foramen magnum. The carina separating the vertex from the occipital face can be called the «nuchal carina» as a neutral term, derived from vertebrate morphology, of course without any implication of homology.

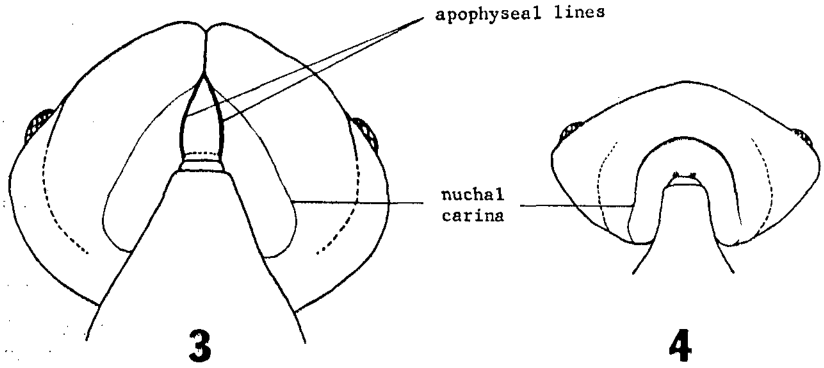

Fig. 3, *Odontomachus infandus* from Cuernos Mts., Negros Oriental, Philippine Is. Fig. 4, *Anochetus gladiator* from Mt. Klabat, NE Celebes. Workers, posterior end of head, to show characters distinguishing the genera.

The nuchal carina in *Anochetus* is evenly and continuously curved across the midline, while in *Odontomachus* it forms a «V» or wedge narrowing dorsad into the middorsal groove.

Furthermore, in *Odontomachus* (but not in *Anochetus*), the occipital face is traversed vertically by a pair of distinct, dark-colored suturelike lines, arising bilaterally in the vicinity of the foramen magnum and curving anterodorsally to converge in the «V» of the nuchal carina, thus adding to its distinctness. The single median dorsal darkened groove of the posterior vertex apparently owes its distinctness to the anterior extension of the fusion of these dark lines. Behind, on the occipital face, the converging lines enclose a triangular or ogival («gothic arch») space that is usually lighter-colored than the adjacent surfaces. The dark lines correspond to internal apophyseal shelves, and so may be called *posterior apophyseal lines*. So far as I have observed in a sample including most of the valid *Odontomachus* and *Anochetus* species, including nearly all of the species intermediate on other generic-diagnostic traits, the character is clearcut. It is illustrated in figs. 3 and 4.

Fortunately, the new character cuts the genera *Odontomachus* and *Anochetus* apart along traditional lines, and using it, the «intermediate» species all fall cleanly one way or the other. The agreement with the conventional generic split is of course compelling evidence for continuing the split, but no reason is apparent for continuing *Champsomyrmex* apart from *Odontomachus*, or *Stenomyrmex* apart from *Anochetus*.

Measurements and Indices

Due to the peculiar form of the head and mandibles in *Odontomachus* and *Anochetus*, and the special importance of size and ratios of head length and width, mandibular length and antennal scape length in species distinction, the conditions of measurement require qualification for these genera.

Head length (HL) is measured «full-face» in the usual way, except that the anterior limit of the head is normally taken as the rounded anterior swellings of the mandibular condyles, which, though not strictly a part of the head proper, nevertheless do complete the outline of the head in front when one or both mandibles are closed (fig. 2).

Head width (HW) in ants is usually taken across the widest part of the head; in the present genera, the head is widest in the anterior quarter or third, across the eyes and ocular prominences. But the most striking allometric differences among the species affect mainly the posterior half of the head (vertex), which in *Odontomachus* and *Anochetus* is slightly to considerably narrower than the width across the eyes. Because the width across the vertex is a more useful character at species level, I have taken HW as the distance between limits of the temporal prominences (fig. 2). In the few difficult cases in which temporal prominences are lacking, HW is taken across that part of the vertex at which the sides are least sharply convergent (most nearly parallel), near or a little behind the midlength of the head. In the case of description of new species, it seems wise to give both the HW across vertex and across eyes as separate data. In figuring the cephalic index (CI) and scape index (SI), I have here used HW across vertex.

Mandible length (ML) is taken on the closed mandibles when the head is viewed in the same plane at which HL is measured, that is, the position in which HL is at a maximum. Since the mandibles are often tilted ventrad from the main axis of the cranium, ML may not be the actual maximum measurable length of the mandibles. Furthermore, ML and HL do not overlap; ML begins basally at the most anterior point(s) of the condylar swellings, which complete the anterior outline of the head as seen from full-face view, as explained above (fig. 2).

Scape length is the maximum measurable length of the scape or chord of the scape, omitting the radicle or basal condylar neck (fig. 2), but including all of the main shaft of the scape and its inner basal acute angle. Scape index (SI) = scape length (SL) × 100/HW.

Key to Genera of Subtribe Odontomachiti (Workers and Queens)

Nuchal carina (separating dorsal from posterior surfaces of head) converging in a V at the midline, and also receiving a pair of prominent, dark posterior apophyseal lines that converge to form the sharp median-dorsal groove of the vertex (figs. 2, 3) .... *Odontomachus*
Nuchal carina forming a broad uninterrupted curve across the postero-dorsal extremity of the head; posterior surface without paired dark apophyseal lines; on vertex, median groove absent or ill-defined and shallow (fig. 4) .... *Anochetus*

Odontomachus

> *Odontomachus* Latreille, 1804, Nouv. Dict. Hist. Natur. 24: 179. Type species *Odontomachus haematoda* = *Formica haematoda* Linnaeus, 1758, monobasic.

≶ *Odontomachus:* F. Smith, 1858: 76; Mayr, 1862: 710; Emery, 1911: 111.

≶ *Formica* Linnaeus, 1758: 579.

> *Pedetes* Bernstein, 1861: 7. Type species *Pedetes macrorhynchus* Bernstein, *nomen nudum* [21], monobasic.

> *Champsomyrmex* Emery, 1892: 558. Type species *Champsomyrmex coquereli* = *Odontomachus coquereli* Roger, 1861, monobasic. New synonymy.

> *Myrtoteras* Matsumura, 1918: 191. Type species *Myrtoteras kuroiwae* Matsumura, 1918, = *Odontomachus monticola,* monobasic.

⋚ *Odontomachus* Brown, 1973: 178, 183, *Anochetus* included in *Odontomachus.*

Worker: With the characters already given for subtribe Odontomachiti. Size medium to large; total length 6 to 20 mm. Head with a deep, narrow, dorsal, median furrow dividing the posterior vertex (fig. 2). Dorsal surface of vertex separated from «occipital face» by a fine, raised nuchal carina (figs. 2, 3) that runs into the median furrow to form a V at the top of the dorsal surface of the cranium. Ocular prominence continued obliquely caudad and mesad to bound roughly a «frontal area» behind; most species have behind this broad, paired extraocular furrows (fig. 2), defined caudad by blunt temporal ridges (lacking in *tyrannicus* and *coquereli* groups). Occipital face with a pair of prominent dark curved apophyseal lines connecting the foramen magnum to the V-shaped dorsal confluence of the nuchal carina with the median furrow. Palpi segmented 4,4, or 4,3.

Trunk slender to robust; mesonotum sometimes bluntly projecting above posterior margin of pronotum, but without a sharp rim or point here. Petiolar node more or less conical, always ending in a single acute apical point. Stridulatory file usually present and well developed on pretergite of second gastric (fourth true abdominal) segment, but lacking in *O. assiniensis.* No constriction of gaster between first and second segments, but second segment sometimes has a saddle-like dorsal depression, especially in *O. infandus.*

Sculpture varying with the species, but at least the «frontal area» of the head, as well as the greater part of the trunk (at least mesonotum and propodeum) regularly striate.

Queen: Like worker, but usually slightly larger, with pterothorax moderately well developed and functional wings; hind wings always with anal lobe. Gaster somewhat larger than in worker. Ergatoid queens rare (normal in *coquereli?*), may easily be confused with mermithized individuals.

Male: Size in the larger end of the odontomachite range (TL 6 to 11 or more mm). Notauli of mesonotum vestigial or absent. Pygidium so far as known always produced as a slender downcurved spine. Hypopygium flat, spatulate or linguiform, with parallel sides and subtruncate to rounded apex; parameres (gonocoxae) subtriangular as seen from the side, with narrowly rounded apices.

Larvae and pupae described above under the subtribe, and the bionomics also summarized there.

Distribution: Throughout the wet tropics and most subtropical areas of Asia, Africa and the New World, with extensions into North and South Temperate Zones and into semidesert areas as outlined under the subtribal treatment above.

Natural enemies. *Odontomachus* is sometimes the victim of mermithid parasitism (see references in Wheeler and Wheeler, 1952: 648), leading to peculiar intermediate adults having an enlarged gaster and head sometimes reduced in size, often with a single median ocellus.

Wheeler and Wheeler also give records of *Odontomachus* as hosts of eucharitid chalcidoid parasitic wasps in the genera *Kapala, Chalcura* and *Schizaspidia*. The planidium larvae of these parasites gain entrance to the ant nest somehow, perhaps phoretically on foraging worker ants, and they apparently feed on ant larvae and pupae.

Mites are frequently seen on the integument of living or preserved odontomachite adults, particularly workers and queens. Mostly these appear to be nymphal uropodids, which may be merely phoretic on the adult ants; very little is known about the ecological role of these mites in the ant nest.

Revision of **Odontomachus** Species

At its inception, somewhere around 1955, this revision of *Odontomachus* began with the classification and roster of species set forth by Emery in the Genera Insectorum (fasc. 118, 1911). The work progressed intermittently at Harvard and Cornell, and the results at various stages drew upon and contributed to faunally-oriented studies by colleagues in close touch, especially E. O. Wilson, for the Melanesian fauna, and W. W. Kempf, for the neotropical fauna. Publications by these authors, particularly Wilson's 1959 Melanesian revision and Kempf's (1972) catalog of the neotropical ants, thus incorporated many interpretations from earlier versions of this revision that we had communicated among ourselves privately. It happened that as my work progressed, new knowledge forced changes in some of what had been committed to print. These changes, on top of an already thoroughly confused series of misidentifications in the old literature, now have the effect of rendering all reviews, catalogs and compilations of *Odontomachus,* particularly those of the New World, obsolete.

It seems a hopeless task to attempt to sort out who meant what species by each of the hundreds of references in the literature, so I urge the users of this review to forget most of the old identifications and records existing in print, especially for *O. haematodus* and its «varieties» and «subspecies». I offer here the opportunity to start afresh from a new base, which has taken into account the types and other classical material as far as possible. Practical testing of this system will of course eventually lead to its next revision.

The present consideration of the Indo-Australian *Odontomachus* fauna must of course take into account E. O. Wilson's (1959) revision of the Melanesian species. This revision was certainly a step in right direction as the first broad treatment of a large segment of the genus on a modern biological-species basis. It cleared away some taxonomic brush by synonymizing no less than 17 names — mostly of varieties and subspecies — and it established the basic taxonomy of at least one *(tyrannicus)* species-group [25]. It would have been convenient merely to base this section on Wilson's review of the fauna concerned for species-level taxonomy, with additions to include the adjacent Oriental and Australian species, but unfortunately his treatment is unsatisfactory in some ways, and basic revision is necessary. In the first place, his limitation of the review to the Melanesian area guaranteed that the taxonomy would be provisional, because in the Indo-Australian area taken as a whole, some species range outside Melanesia. But beyond this problem, which Wilson recognized, his review includes a number of errors, most of which are incorporated in his key to species.

Two names *(politus* and *retrolatior)* of Melanesian forms inadvertently omitted from Wilson's review are synonymized here. In three other instances, he appears to have misjudged earlier descriptions, and in some cases he placed too much faith in the constancy of color and sculptural characters that seem to me to be variable within species. Although he appreciated the fundamental difference between the petiole shape of the *saevissimus* group and the *infandus (papuanus)* group (his fig. 1, here reproduced as my figs. 8 and 9), variation in this character within the groups apparently caused him to mistrust it when he made his key, and to misapply it on occasion. I have no hesitation in using this trait in an early dichotomy in my key (couplet 3), even though verbal description is elusive.

Although I believe the present treatment of the Indo-Australian *Odontomachus* fauna carries the classification closer to the real situation, a number of uncertainties remain. Most of these involve nominal species separated on details of sculpture, color, pilosity, or proportion of head, antennal scapes, etc., all characters known to be variable within species.

For example, *O. papuanus* may well be only a smooth-headed variant of *O. animosus*, paralleling the better-known variation in the Philippine vicariant, *O. infandus*. *O. banksi* could well be only a local morph of *O. infandus*, and *O. latissimus* a broad-headed variant of *O. animosus* (or *O. papuanus*). In fact, all of the members of the *infandus* group (except *O. silvestrii*) might be geographical representatives or morphs of one species.

Despite synonymy of several forms by Wilson and in this review, the *saevissimus* group almost certainly has more names left (5) than there are real species. It seems likely also that *O. ruficeps* should include *O. cephalotes*, and maybe *O. aciculatus* as well. A possibility exists that *O. latidens* is a tropical vicariant of *O. monticola*. At present, the material available, especially from such key areas as West Irian, the Moluccas and Celebes, is simply inadequate as a basis for decisions on these questions. Even allowing for a few undescribed species that may remain undiscovered in the area, I predict that the eventual count of valid species will not be much over 20 for the whole Indo-Australian region. This compares with the 20 species that Wilson recognized just for Melanesia.

I count 150 names of species, subspecies and varieties that have been proposed in, or transferred to *Odontomachus* up to the present, including the 7 species described as new herein. Of this total, one *(macrorhynchus)* is considered a *nomen nudum*, 6 have been transferred to *Anochetus* at one time or another, and 92 names are considered as synonyms of the remaining valid species in *Odontomachus*, which are 51 in number. Of these 51, perhaps 6 are doubtfully distinct *(cephalotes, papuanus, animosus, banksi, opaculus, montanus)*, and it may even be that *monticola* and *latidens* belong to the same species. Thus, only about a third of the 150 names assigned to *Odontomachus* over more than two centuries seem now to represent biological species at the «morpho-species» level of distinction. Though undoubtedly there remain some real species yet to be discovered, both morphospecies and siblings, it is my feeling that the majority of existing *Odontomachus* species has by now been collected, described and named.

The 51 currently recognized species are distributed almost equally between the Old World (28) and the New (23). In the Old World, only 2 species occur in continental Africa, and one of these *(troglodytes)* extends to Madagascar, where an endemic *(coquereli)* also exists. The rest of the Old World complement is Indo-Australian, with the principal concentration of species in Melanesia, and particularly in New Guinea.

Odontomachus Species List

In Part VI, I have followed my practice of Part V (Brown 1975) in listing all of the species (subspecies, varieties) in each of the two genera that were originally described there, and all are included there now. Each name is treated as a species name, regardless of whether it was originally described as a species, subspecies, or variety, because I recognize only the species level as worthy of a formal name in the Linnean system. A whole series of names was originally proposed, and has for a long time been treated, as subspecies or varieties of *O. haematodus*. Where types have been studied, each of these names, considered separately on its merits as representing a probable biological species, has fallen unambiguously into one of two categories: species, and synonyms of species.

It should be emphasized that species in this study are primarily morphospecies in practice, but morphospecies nonetheless considered in the light of the biological species concept. It makes a big difference whether one considers broadly sympatric *haematodus*-group forms occurring widely in Amazonia (e. g., *haematodus, bauri, minutus, brunneus, caelatus, biumbonatus)* as «variants» of one protean species, or as separate species each in its own right. Contrary to the views of writers such as Blackwelder (1967) and Sokal and Crovello (1970), modern evolutionary theory can be used to establish the strong hypothesis that all of these forms represent real species. The very fact of consistent differences occurring over broad regions is evidence in favor of the multispecies hypothesis, considering that population polymorphism is an unlikely alternative in this case.

I do not intend to gainsay the difficulties of the species concept as it applies to finer levels of distinction in this genus. Clearly, it is possible that one or more of the species recognized in this work will eventually be demonstrated to be a complex of sibling species. That remains for gamma-taxonomic investigations of the future. No systematic review should be taken as more than a progress report on the investigation of the taxon under consideration. However, gamma-taxonomic studies are beyond those problems still needing attention at the beta level. For example, the status of nominal species within the *infandus* and *saevissimus* groups mainly appear to call for more material from a wider range of localities.

The species in the *Odontomachus* list that have authors' names enclosed in parentheses were originally described in *Formica* (except *Pedetes macrorhynchus* and *Myrtoteras kuroiwae).*

I have not attempted to indicate «new status» for species here newly raised from subspecific or varietal rank to the status of new species, mainly because a number of them have already been listed at species level by Kempf and other colleagues in catalogs or faunal papers, so that it is hard to be sure about individual cases.

The capital letters placed in parentheses before each specific name indicate the kind of evidence upon which the present generic placement is directly based.

(T) indicates that type material, nidotypes, reliably type-compared material, or similarly authentic specimens have been examined, in most cases by myself; rarely, examination has been made by other myrmecologists.

(P) means that material identified from reasonably good descriptions or other satisfactory evidence has been examined and is thought to be correctly determined.

In cases where the species is not seriously questioned, but no specimens referable to it have been seen, or, if seen, cannot be satisfactorily verified as to identity, no entry has been made before the species name.

(?) signifies that, in my opinion, the species is inadequately described for purposes of distinction and that its taxonomic status is doubtful.

(T) *aciculatus* F. Smith 1833: 119 ☿ W N. Guinea, Misool [2]
= *aeneus* Emery 1911: 534 ☿ n. syn.
= *verticillatus* Stitz 1912: 501 ☿ (syn. Wilson 1959)
(T) *acutidens* Forel = *ruficeps*
(T) *aeneus* Emery = *aciculatus*
(P) *affinis* Guérin 1845: 423 ☿ SE Brasil [3]
(T) *ajax* Forel = *cephalotes*
(P) *allolabis* Kempf 1974: 551 ♀ W Amazon Basin
(P) *angulatus* Mayr 1866: 500 ☿ Fiji Is. [4]
= *politus* Stitz 1925: 116 ☿ n. syn.
(T) *animosus* F. Smith 1861: 102 ☿ W N. Guinea [5]
aruanus Karawajew = *cephalotes*
(T) *assiniensis* Emery 1892: 558 ☿ W, C, & SE Africa [6]
= *fauconneti* Forel 1910: 27 ☿ n. syn.
= *intermedius* Stitz 1911: 378 ☿ n. syn.
= *caffrorum* Santschi 1914: 14 ☿ n. syn.
= *fuscus* Stitz I 1916: 372 ☿ ♀ preocc., n. syn.
= *furvior* Wheeler 1922: 101 ☿ ♀ n. syn.
= *aterrimus* Wheeler 1922: 102 ☿ n. syn.
= *tropicalis* Menozzi 1922: 352 ☿ ♀ ♂ n. syn.
= *flavescens* Bernard 1952: 215 ☿ ♀ n. syn.
= *oblita* Baroni Urbani 1971: 360 (name unnecessarily proposed to replace *fuscus* Stitz I) n. syn.
(T) *aterrimus* Wheeler = *assiniensis*
(T) *banksi* Forel 1910: 121 ☿ S central Luzon [5]
(T) *bauri* Emery 1892: 561 ☿ C. and trop. S. America, Galapagos, W Indies (except Cuba & Bahamas) [7, 17]
? = *unispinosa* (Fabricius) 1793: 539 ☿ *nomen dubium et oblitum,* provisional n. syn.
? = *pubescens* Roger 1861: 25 ☿ *nomen dubium,* provisional n. syn.
? = *microcephalus* Emery 1890: 45 mermithergate, provisional n. syn.
= *paucidens* Emery 1893: 91 ☿ n. syn.
= *sericeus* Provancher 1895: 97 ☿ n. syn.

= *rugisquama* Forel 1908: 35 ☿ n. syn.
= *notata* Mann 1920: 404 ☿ n. syn.
(T) *biolleyi* Forel 1908: 35 ☿ ♀ W coast Costa Rica, mangroves.
(T) *bispinosus* F. Smith to *Anochetus*
(T) *biumbonatus* Brown n. sp. ☿ ♀ Amazon Basin, tropical lowland SE Brasil [8]
(T) *bradleyi* Brown n. sp. ☿ Peru [9]
(T) *breviceps* Crawley = *simillimus*
(T) *bruneipes* Emery = *haematodus*
(P) *brunneus* (Patton) 1894: 618 ☿ SE U.S. to Paraguay & Bolivia, W. Indies [10, 11, 17]
= *ruginodis* Wheeler 1905: 82 ☿ ♀ n. syn.
= *fuscus* Stitz II 1923: 115 ☿ preocc., n. syn.
= *repetita* Baroni Urbani 1971: 361 (name unnecessarily proposed to replace *fuscus* Stitz II) n. syn.
(T) *caelatus* Brown n. sp. ☿ hylean S. America [12]
caffrorum Santschi = *assiniensis*
(T) *cephalotes* F. Smith 1863 ☿ Moluccas, N. Guinea, NE Australia [2]
= *turneri* Forel 1900: 56 ☿ n. syn.
= *ajax* Forel 1910: 10 ☿ n. syn.
= *cruenta* Emery 1911: 251 ☿ ♀ (syn. Wilson 1959)
= *fusca* Emery 1911: 251 ☿ (syn. Wilson 1959)
= *obtusa* Emery 1911: 251 ☿ n. syn.
= *ternatensis* Forel 1911: 252 ☿ (syn. Wilson 1959)
= *yorkensis* Stitz 1911: 356 ☿ n. syn.
= *tamensis* Stitz 1912: 503 ☿ (syn. Wilson 1959)
= *cooktownensis* Forel 1915: 35 ☿ ♂ n. syn.
= *aruanus* Karawajew 1925: 295 ☿ ♂ (syn. Wilson 1959)
= *longitudinalis* Donisthorpe 1940: 108 ☿ (syn. Wilson 1959)
(P) *chelifer* Latreille 1802: 188 ☿ S Mexico to N Argentina
= *leptocephalus* Emery 1890: 45 mermithergate (syn. Emery 1911)
= *theresiae* Forel 1895: 41 ☿ n. syn.
= *emacerata* Santschi 1922: 243 ☿ n. syn.
(T) *clarionensis* Wheeler = *clarus*
(P) *clarus* Roger 1861: 26 ☿ SW U.S., Mexico [10]
= *texana* Buckley 1867: 335 ☿
= *coninodis* Wheeler 1915: 391 ☿ ♀ n. syn.
= *desertorum* Wheeler 1915: 391 ☿ n. syn.
= *clarionensis* Wheeler 1934: 141 ☿ (syn. Taylor and Wilson 1962)
(P) *concentricus* Emery = *papuanus*
(T) *coniferus* Forel = *rixosus*
(T) *coninodis* Wheeler = *clarus*
(T) *cooktownensis* Forel = *cephalotes*
(P) *coquereli* Roger 1861: 30 ☿ Madagascar [13]
= *minor* Emery 1900: 273 ☿ ergatoid ♀
(T) *coriarius* Mayr = *ruficeps*
cornutus Stitz 1933: 67 ☿ W Ecuador [14]
(T) *cruentus* Emery = *cephalotes*
(T) *desertorum* Wheeler = *clarus*
(T) *dulcis* Mann = *minutus*
(T) *emaceratus* Santschi = *chelifer*
(T) *emeryi* Mann = *rufithorax*
(T) *erythrocephalus* Emery 1890: 44 ☿ Costa Rica to W Ecuador [15]
(T) *fauconneti* Forel = *assiniensis*
(T) *flavescens* Bernard = *assiniensis*
(T) *floresensis* Brown n. sp. ☿ Indonesia: Flores I. [5, 16]

(T) *formosae* Forel = *monticola*
(T) *furvior* Wheeler = *assiniensis*
(T) *fuscipennis* Forel = *simillimus*
(T) *fuscus* Emery = *cephalotes*
(T) *fuscus* Stitz I = *assiniensis*
(T) *fuscus* Stitz II = *brunneus*
(P) *ghilianii* (Spinola) to *Anochetus*
(T) *gressitti* Wilson = *rufithorax*
(T) *gulosus* Emery = *testaceus*
haematodus (Linnaeus) 1758: 582 ☿ SE Brasil, NW Argentina, Amazon Basin N to Guyana, W to Andes [17]
= *maxillosus* (DeGeer) 1773: 601 ☿
= *hirsutiusculus* F. Smith 1858: 78 ☿ n. syn.
= *bruneipes* Emery 1893: 91 ☿ n. syn.
= *pallipes* Crawley 1916: 368 ☿ n. syn.
(T) *hainanensis* Stitz = *monticola*
hastatus (Fabricius) 1805: 426 ☿ trop. S. & C. America, forest
= *maxillaris* F. Smith 1858: 77 ☿
(T) *hirsutiusculus* F. Smith = *haematodus*
imperator Emery 1887: 429 ☿ N. Guinea [18]
(T) *infandus* F. Smith 1858: 81 ☿ Philippines [5]
= *philippinus* Emery 1893: 203 ☿ n. syn.
= *striaticeps* Stitz 1923: 117 ☿ n. syn.
(T) *insularis* Guérin 1845: 423 ☿ ♂ Cuba, Bahamas, ? Hispaniola [10]
= *pallens* Wheeler 1905: 82 ☿ ♀ ♂ n. syn.
= *wheeleri* Mann 1920: 405 ☿ n. syn.
(T) *intermedius* Stitz = *assiniensis*
kuroiwae (Matsumura) = *monticola*
(P) *laticeps* Roger 1861: 25 ☿ Mexico, C. America [19]
= *striativentris* Emery 1890: 44 ☿ n. syn.
(T) *latidens* Mayr 1867: 48 ♀ Malaya, Borneo, Sumatra, Java [20]
= *procerus* Emery 1893: 203 ♀ n. syn.
= *sumatranus* Emery 1901: 671 ☿ ♀ n. syn.
(P) *latissimus* Viehmeyer 1914: 31 ☿ NE N. Guinea [5]
leptocephalus Emery = *chelifer*
(T) *linae* Donisthorpe = *saevissimus*
(T) *longi* Forel = *monticola*
(T) *longitudinalis* Donisthorpe = *cephalotes*
macrorhynchus (Bernstein) 1861: 7 ☿ ♀ *nomen nudum* [21]
(T) *magnus* Mayr = *ruficeps*
(T) *major* Forel = *monticola*
(T) *malignus* F. Smith 1859: 144 ☿ Borneo to Solomon Is., reef coral [22]
= *tuberculatus* Roger 1861: 28 ☿ (syn. Wilson 1959)
= *retrolatior* Viehmeyer 1914: 113 ☿ n. syn.
maxillaris F. Smith = *hastatus*
maxillosus (De Geer) = *haematodus*
(T) *mayi* Mann 1912: 39 ☿ Amazon Basin, Guyana [3]
(T) *meinerti* Forel = *minutus*
microcephalus Emery ? = *bauri*
minor Emery = *coquereli*
(T) *minutus* Emery 1894: 146 ☿ S Mexico to S Brasil & Bolivia, SW Colombia [23]
= *meinerti* Forel 1905: 156 ☿ n. syn.
= *dulcis* Mann 1922: 18 ☿ n. syn.
(T) *montanus* Stitz 1923: 116 ☿ N. Guinea [18]

(T) *monticola* Emery 1892: 560 ☿ China, NE India, SE to Viet Nam [20]
= *longi* Forel 1900: 58 ☿ n. syn.
= *punctulatus* Forel 1900: 58 ☿ n. syn.
= *kuroiwae* (Matsumura) 1912: 191 ☿ n. syn.
= *formosae* Forel 1912: 46 ☿ ♀ ♂ (syn. Yasumatsu 1962)
= *major* Forel 1913: 183 ☿ n. syn.
= *pauperculus* Wheeler 1921: 530 ☿ (syn. Yasumatu 1962)
= *hainanensis* Stitz 1923: 115 ☿ n. syn.
= *striata* Menozzi 1929: 329 ☿ n. syn.
(T) *mormo* Brown n. sp. ☿ W. Ecuador [24]
(T) *nietneri* Roger to *Anochetus*
(T) *nigriceps* F. Smith 1861: 103 ☿ N. Guinea, Misool [25]
= *praefectus* Forel 1911: 251 ☿ (syn. Wilson 1959)
(T) *nigrifrons* Donisthorpe = *testaceus*
(T) *notatus* Mann = *bauri*
nubilus Emery = *testaceus*
oblitus Baroni Urbani = *assiniensis*
(T) *obscurior* Forel = *rixosus*
(T) *obscurus* Crawley = *ruficeps*
(T) *obsolescens* Donisthorpe = *tyrannicus*
(T) *obtusus* Emery = *cephalotes*
(T) *opaciventris* Forel 1899: 21 ☿ ♀ S. Mexico to Colombia
(T) *opaculus* Viehmeyer 1912: 6 ☿ N. Guinea [18]
(T) *pallens* Wheeler = *insularis*
(T) *pallidicornis* F. Smith = *simillimus*
(T) *pallipes* Crawley = *haematodus*
(T) *panamensis* Forel 1899: 19 ☿ ♀ ♂ Panama, Costa Rica [3]
(P) *papuanus* Emery 1887: 429 ☿ N. Guinea [5]
= *concentrica* Emery 1897: 557 ☿ (syn. Wilson 1959)
(T) *paucidens* Emery = *bauri*
(T) *pauperculus* Wheeler = *monticola*
(?) *peruanus* Stitz 1933: 68 ♀ *nomen dubium* [26]
(P) *philippinus* Emery = *infandus*
politus Stitz = *angulatus*
praefectus Forel = *nigriceps*
(T) *procerus* Emery = *latidens*
(?) *pubescens* Roger ? = *bauri*
(T) *punctulatus* Forel = *monticola*
repetita Baroni Urbani = *brunneus*
retrolatior Viehmeyer = *malignus*
(T) *rixosus* F. Smith 1857: 64 ☿ SE Asia, Sumatra, Borneo, Java [20, 27]
= *obscurior* Forel 1900: 58 ☿ n. syn.
= *conifera* Forel 1913: 19 ☿ ♀ n. syn.
(T) *rossi* Donisthorpe to *Anochetus*
(T) *rubriceps* Forel = *ruficeps*
(T) *rufescens* Forel = *ruficeps*
(T) *ruficeps* F. Smith 1858: 81 ☿ Australia [2]
(T) = *coriarius* Mayr 1876: 85 ☿ ♂ n. syn.
= *semicircularis* Mayr 1876: 85 ☿ n. syn.
= *magnus* Mayr 1876: 85 ☿ n. syn.
= *sharpei* Forel 1893: 458 ☿ n. syn.
= *acutidens* Forel 1900: 56 ☿ n. syn.
= *rubriceps* Forel 1915: 33 ☿ ♂ n. syn.
= *rufescens* Forel 1915: 34 ☿ n. syn.
= *septentrionalis* Crawley 1915: 30 ☿ n. syn.

= *obscura* Crawley 1922: 437 ☿ n. syn.
(T) *rufithorax* Emery 1911: 534 ☿ N. Guinea to Solomon Is. [18, 28]
= *emeryi* Mann 1919: 303 ☿ ♀ ♂ n. syn.
= *gressitti* Wilson 1959: 488, 492 ☿ n. syn.
rufus Jerdon 1851 to *Anochetus*
(T) *ruginodis* Wheeler = *brunneus*
(T) *rugisquama* Forel = *bauri*
(T) *rugosus* F. Smith to *Anochetus*
(T) *saevissimus* F. Smith 1858: 80 ☿ ?♀ N. Guinea to Moluccas & Solomon Is. [18, 28]
= *tauerni* Stitz 1923 ☿ (syn. Wilson 1959)
= *transversostriatus* Donisthorpe 1932: 53 ☿ (syn. Wilson 1959)
= *linae* Donisthorpe 1940: 107 ☿ ♀ n. syn.
(T) *semicircularis* Mayr = *ruficeps*
(T) *septentrionalis* Crawley = *ruficeps*
(P) *sericeus* Provancher = *bauri*
(T) *sharpei* Forel = *ruficeps*
(T) *silvestrii* Wheeler 1927: 85 ☿ Viet Nam, SE China [29]
= *substriatus* Wheeler 1927: 86 ☿ n. syn.
(T) *simillimus* F. Smith 1858: 80 ♀ S India to Micronesia & C Polynesia [30]
= *pallidicornis* (F. Smith) 1861: 73 ♂ n. syn.
= *fuscipennis* Forel 1913: 19 ☿ ♀ ♂ (syn. Wilson 1959)
= *breviceps* Crawley 1915: 239 ☿ n. syn.
smithii Roger to *Anochetus*
(P) *spissus* Kempf 1962: 17 ☿ Brasil: Mato Grosso
(T) *stanleyi* Wheeler = *troglodytes*
(T) *striaticeps* Stitz = *infandus*
(T) *striativentris* Emery = *laticeps*
(P) *striatus* Menozzi = *monticola*
(T) *substriatus* Wheeler = *silvestrii*
(T) *sumatranus* Emery = *latidens*
(T) *sumbensis* Brown n. sp. ☿ Indonesia: Sumba I. [5, 31]
tamensis Stitz = *cephalotes*
(T) *tauerni* Stitz = *saevissimus*
(T) *ternatensis* Forel = *cephalotes*
(T) *testaceus* Emery 1897: 557 ☿ N. Guinea [25]
= *gulosus* Emery 1902: 160 ☿ (syn. Wilson 1959)
= *nubila* Emery 1911: 250 ☿ (syn. Wilson 1959)
= *nigrifrons* Donisthorpe 1940: 106 ☿ (syn. Wilson 1959)
(P) *texanus* Buckley = *clarus*
(T) *theresiae* Forel = *chelifer*
(T) *transversostriatus* Donisthorpe = *saevissimus*
(T) *troglodytes* Santschi 1914: 58 ☿ tropical Africa, Madagascar [32]
= *stanleyi* Wheeler 1922: 102 ☿ n. syn.
(T) *tropicalis* Menozzi = *assiniensis*
(P) *tuberculatus* Roger = *malignus*
(T) *turneri* Forel = *cephalotes*
(T) *tyrannicus* F. Smith 1859: 455 ☿ N. Guinea & nearby islands, N. Britain [25]
= *obsolescens* Donisthorpe 1940: 106 ♀ ♂
unispinosus (Fabricius) ? = *bauri*
(T) *verticillatus* Stitz = *aciculatus*
(T) *wheeleri* Mann = *insularis*
(P) *yorkensis* Stitz = *cephalotes*
(T) *yucatecus* Brown n. sp. ☿ S Mexico, Guatemala, Belize [33]

Species-groups and Phylogeny

The species of *Odontomachus* can be assigned among 12 more or less arbitrary groups. These groups can be arranged in a series in which the putatively more primitive ones come early, and the more advanced ones fall toward the end. Of course, any given species may exhibit a mixture of primitive and advanced character states, and the judgement about relative primitiveness of a taxon really boils down to a character-by-character assessment and correlations found among the states of the different characters. The main characters considered in a study of phylogeny within *Odontomachus* are the following:

1. Mandibular form and armament (female). It is difficult to separate mandibular characters into separate components. In general, I see the evolutionary progression as moving from long, slender mandibles with 3 slender, acute teeth in the apical trio, and a preapical series of large and sharp teeth diminishing in size basad along the mandibular shaft; toward a shorter, broad kind of mandible with the apical trio of teeth much shorter and thicker, quickly wearing to truncate or rounded, hammer- or bludgeon-like opposable surfaces, while the preapical masticatory border suffers the evolutionary reduction and eventual loss of at least the more distal tooth units as the border is transformed into a crenulate or cultrate shearing edge.

It is assumed that prey capture in the more primitive groups is mainly a matter of striking and puncturing the prey with the long, sharp teeth at the ends of the jaws (including the largest, most distal teeth of the preapical series). Thus, the primitive groups may have to depend more in prey with softer integument. We have no useful information on the prey or details of prey capture in the long-toothed groups, but by analogy with the sharp-toothed *Strumigenys* of subfamily Myrmicinae (Brown and Wilson, 1960) one might predict that they will be found to use the sting liberally against prey that have been struck and punctured, and sooner or later held impaled between the tips of the closed jaws (Ledoux, 1952). The longer jaws in the primitive groups may well be adaptive in holding protective allomones released by the prey away from the captor.

In the higher groups of *Odontomachus*, the bludgeon-and-shears jaws can be used against small, soft prey simply to crush them with one or two strikes by the blunt tips, while the shearing action of the sharp preapical masticatory border is effectively used against the appendages of larger or tougher prey by repeated strikes, as long ago witnessed by Wheeler (1900), and many times by myself. This attack by dismemberment would hypothetically require less use of the sting. Unfortunately the differences in mandibular morphology did not impress me with sufficient force until a late stage of this study, and despite numerous opportunities in the field, I am afraid that I have no good behavioral data that bear upon the topic.

Morphological primitiveness of the long-toothed mandible is assumed from the widespread presence of the long-toothed state in the presumed ancestral taxon, *Anochetus,* from the direct application of the reduction rule («Lamarck's Arrow» or «Williston's Rule») to the number and size of teeth on the mandibles, from the correlation of the bludgeon-and-shears type of mandibles at the opposite end of the series with another reduction character, the 3-merous labial palpi, and from the greater morphological diversity and geographical discontinuity of the long-toothed groups.

2. Palpal segmentation (female). The 4, 4 formula is undoubtedly primitive in *Odontomachus,* by both the ancestor-group and reduction rules. The *haematodus* group has 3-merous labial palpi, representing a segment lost by fusion.

3. Sculpture and pilosity-pubescence (female). It is difficult to decide whether in the genus as a whole striation of the entire dorsal surface of the head is a primitive or an advanced character state; this character apparently has suffered some reversals within the genus, as it may have done also independently in *Anochetus.* Extensive striation, or other fine sculpture departing from a smooth surface of the gaster, however, seems to be restricted in *Odontomachus* to the *ruficeps* and *haematodus* groups, which on grounds of the structure of mandibles, head and petiole appear to be closely related. As a correlated state, then, the smooth gaster appears to be primitive. The striate gastric surface (also coarse gastric punctation) appears in *Anochetus,* apparently as a convergent, or at most a parallel, development.

High-density pubescence (particularly of the gastric dorsum), and to some extent abundant longer pilosity, are derivative in *Odontomachus,* and are of course partly correlated with sculptural traits, but intra-group reversals have apparently occurred in both sculptural and pilosity-pubescence states.

4. Development of extraocular furrow and temporal ridge (female). These are of course just different aspects of the same character; without the ridge, there is no furrow defined. The ancestral genus *Anochetus* essentially is in state zero for this character, as are the *tyrannicus* group and *coquereli* in *Odontomachus,* but other *Odontomachus* groups all have the temporal ridge (weak in *O. hastatus*). The development of the character is partly tied to increased widening of the vertex, also an advanced state in *Odontomachus,* but head width varies by its own rules among *Anochetus* species.

5. Polyphenism of workers. There seems to exist a tendency, albeit irregularly expressed, for allometric and absolute size differences to be most marked in some middle-course groups. Thus the *ruficeps* group seems to show greater than usual allometric variation in shape of mandibular teeth, width of vertex and relative length of mandibles and antennae. *O. ruficeps* tends to have a low, broad, truncate or rounded subapical tooth in large workers, while the same tooth is slender and acute in the smallest workers, with intergrades in workers of intermediate sizes. In the *rixosus* group, the subapical tooth is truncate with a concave end in callow workers, but is worn to rounded-truncate in older individuals; smaller-sized workers have this tooth longer and more slender than do large workers.

The neotropical *hastatus, mormo* and *bradleyi* groups each contain only the single species whose names they bear. *O. hastatus* is widespread in tropical America, but the other two species appear to have limited ranges, *O. bradleyi* in the eastern slopes of the Andes in Peru, and *O. mormo* on the western side in Ecuador. All have palpi segmented 4, 4; *hastatus* is most like the Old World *tyrannicus* group, *mormo* like the *infandus* group, *bradleyi* perhaps most like the *rixosus* group.

O. cornutus, from western Ecuador, is also put in its own group until we know more about it.

The *tyrannicus* group consists of the 3 closely related, large Melanesian species *tyrannicus, testaceus* and *nigriceps.* Their lack of a temporal ridge, and therefore of an extraocular furrow, may well be primitive; the larvae (of *tyrannicus,* at least) have standard piligerous tubercles on the dorsal surfaces of abdominal segments IV and V in place of holdfasts.

The *coquereli* group is based on the single Malagasy species of that name, a slender form related to the *tyrannicus* group by head form, but with its own unique sculpture.

The *saevissimus* group, consisting of the 5 large, slender, Melanesian species *saevissimus, opaculus, montanus, imperator,* and *rufithorax,* is similar to the *tyrannicus* group, but the workers and queens have well defined temporal ridges and extraocular furrows; the petiolar node has a peculiar, extremely attenuated form (fig. 8).

The *infandus* group is related to the *tyrannicus* and *saevissimus* groups, and like them, it has palpi segmented 4,4; long, acute, apical, intercalary and subapical mandibular teeth; and a strong preapical series of teeth. But it also shows variable broadening of the vertex and at times some tendency toward the formation of a dome-shaped petiolar node (fig. 9). The species belonging here are still not all satisfactorily defined; they are inhabitants of New Guinea, eastern Indonesia and the Philippines, with one known species in Viet Nam. They are *infandus, papuanus, latissimus, silvestrii, sumbensis, floresensis, banksi, animosus, angulatus* and *malignus*.

The *rixosus* group includes the 3 species *rixosus, latidens* and *monticola* of mainland eastern Asia and the Greater Sunda Islands, a distribution largely complementary to that of the *infandus* group. The *rixosus* group has a truncate or (as worn) low and rounded subapical mandibular tooth, at least in medium-sized and large workers, the head tends to be fairly broad behind, and there is a further tendency towards height reduction and «doming» of the petiolar node. The palpal formula is still 4,4.

The *ruficeps* group includes *ruficeps, cephalotes* and *aciculatus*, from central and western Melanesia and Australia. The first 2 of these, and possibly even all 3, are doubtfully separable as species. The workers are broad-headed, with allometric mandibles; small workers tend to have more slender mandibles with the apical trio of teeth all slender and acute, while large workers have thick mandibles with the apical trio, especially the subapical tooth, short and blunt, or truncate. The head is broad and the petiolar node, while very variable, tends to be thick and often more or less dome-shaped. The gastric dorsum is more or less distinctly striate, coriaceous or otherwise superficially sculptured, at least in part. Palpi segmented 4,4.

The *assiniensis* group includes a single variable species of wet tropical Africa, *O. assiniensis*, which has a broad head and relatively thick mandibles, and a petiolar node more or less like that of the *ruficeps* or *rixosus* groups, with a smooth gastric dorsum. It may be the vicariant of either (or both) of these groups in Africa. Palpi segmented 4,4.

The *haematodus* group includes the large majority (19/23) of New World *Odontomachus* species: *affinis, allolabis, bauri, biolleyi, biumbonatus, brunneus, caelatus, chelifer, clarus, erythrocephalus, haematodus, insularis, laticeps, mayi, minutus, opaciventris, panamensis, spissus, yucatecus*. In the Old World, *simillimus* (Indo-Pacific) and *troglodytes* (Africa-Madagascar) are its only members.

These species are united by the 4,3 palpal formula, checked during this study for all except *panamensis, biolleyi*, and *spissus*, for which suitable material was unavailable. These are so obviously linked to the *haematodus* group by other characters that I have little doubt that the labial palpomere counts conform also.

Within the group we can recognize some indistinct subgroups: *O. affinis, O. mayi* and *O. panamensis* are obviously closely related by their smooth vertex and other characters. The tiny *O. spissus* of northern Mato Grosso also has the vertex smooth, but its short scapes and head shape suggest that it may be a specialized offshoot of something like *O. minutus* or *O. brunneus*. *O. chelifer*, the largest species, is also the most slender (CI 52-61); it may be a relict of the primitive stock of the group in tropical America, but its relatively short, heavy mandibles are like those of its relatives.

If we except *chelifer* and such aberrant narrow-headed members as *allolabis*, we can characterize the *haematodus* group as with broad head (vertex) and short, stout mandibles with relatively short, blunt teeth (at least as worn in larger specimens) in the group of 3 (or 2) at each apex.

The subapical tooth is especially short; in large specimens that are at all worn, this tooth is scarcely or not at all projecting beyond the inner mandibular border. In callow workers, the subapical tooth consists of 2 low, obtuse points with a concavity between them — the whole thing apparently being a reduced homolog of the truncate or hollow-ended subapical tooth as seen in the *rixosus* group. The 2 points are made of thin material, easily worn away, so that the subapical tooth soon becomes, first an angular, then later a rounded, end to the inner mandibular border. The denticles along the inner mandibular (masticatory) borders are at an extreme of reduction for the genus; the apical third or more of this margin varies from edentate (cultrate) to crenulate, with worn, blunt denticles in the middle part, giving way to sharper but finer serration near the base of the mandible. Thus the mandibles, after considerable evolution, have arrived at being a short, heavy pair of shears with blunt, bludgeon-like tips.

The antennae tend to be shorter than in other groups, probably in coadaptation to the shorter mandibles, and this shows up especially in the scapes, which often in larger workers of *haematodus*-group species surpass the posterior border of the head only slightly when they are held straight back; sometimes they even fall short, and in *O. spissus* they always fail to reach the border by a wide margin.

Keys to Species

Note: Before trying the keys, the user should be aware of the special conditions of measurement of this genus, especially for HL and HW (see p. 95). Descriptive statements, especially those concerning gastric sculpture and pubescence, are based on clean, unrubbed specimens; dirty or worn specimens can be misleading. These statements also ignore the normal presence of scattered, coarse piligerous punctures on the gastric dorsum in nearly all of the species.

Queens can often be determined using worker characters, but it should be remembered that queens are usually larger than the corresponding workers, and differ from workers by some allometric characters; e. g., queens often have (proportionately) wider vertex, shorter mandibles and antennal scapes, and antero-posteriorly more compressed petiolar node — the nodal form often being strikingly different in the two castes.

Key to New World Species of Odontomachus — Workers

1. Dorsal surface of head distinctly striate to or nearly to the nuchal carina 2
— Posterior third to half of dorsal surface of head smooth and shining, or nearly so 17

2\. Disc (dorsal surface) of first gastric segment predominantly smooth, punctulate, alutaceous, or reticulate; striation absent, or if present, mixed with other sculpture and distinct only on the posterior half of the disc 3

— Disc of first gastric segment distinctly and evenly striate over its entire surface, at least as seen from dorsal view 15

3\. Mesonotum longitudinally striate (Yucatan Pen. to Vera Cruz and Guatemala) .... *yucatecus* [33]

— Mesonotum prevailingly transversely striate 4

4\. Head more or less bright red (frontal area often infuscate), contrasting with blackish-brown body and yellow legs; size medium (see Table I, fig. 2; Costa Rica to Ecuador W of Andes) .... *erythrocephalus* [15]

— Color combination otherwise; if head is distinctly red, then trunk is red also, or legs are dark 5

5\. Sternum immediately in front of and between metathoracic coxae produced as a slender, acute pair of teeth or spines (fig. 7); disc of first gastric segment densely and finely shagreened and pubescent, usually opaque; body brown, legs yellow to brown (forests of cis-Andean continental S America from Orinoco Delta to Tucumán, Argentina) .... *haematodus* [17]

— Sternum in front of metathoracic coxae with a low transverse ridge, sometimes notched in the middle or bilobed, but not produced as acute, paired teeth (figs. 5, 6; gaster smooth or variously sculptured; color varying, but legs usually dark in samples from continental S America) 6

6\. Disc of first gastric segment as seen from above very finely, densely and regularly punctulate throughout; opaque or nearly so; longest hairs of gastric dorsum 0.6 mm or more in length; large (see Table I) black or dark brown species (Costa Rica to Colombia) .... *opaciventris*

— Disc of first gastric segment otherwise sculptured; shining or, if densely punctulate and opaque, then at least the posterior part becoming longitudinally striate; longest hairs of gastric dorsum < 0.6 mm long 7

7\. Disc of first gastric segment very densely punctulate, opaque, longitudinally striate over a posterior portion of variable extent (Plate 1, D); small species (see Table I), light to dark brown in color (S Mexico to S Brasil and Bolivia, forests) .... *minutus* [23]

— Disc of first gastric segment prevailingly shining, though its surface sometimes alutaceous, shagreened, or even with traces of striation in the posterior portion 8

8\. Head, trunk and petiole nearly or quite concolorous light red or dull yellow; legs yellowish, gaster light brown to blackish 9

— Head, trunk and petiole dark reddish brown or brown to nearly black, legs variable in color, often dark 11

9\. Apex of petiole rather suddenly narrowed to a long, slender spine (Cuba, Bahamas, local on Hispaniola) .... *insularis* [10]

— Petiole conical or subconical in side view; apex acute or even dentate, but not drawn out into a long, slender spine 10

10\. Posterior face of petiole at least feebly concave or sulcate mesad; compound eye usually shorter than maximum W of a mandible (without teeth), rarely slightly longer; sides of head in side view smooth and shining, or, if dull, then the sculpture here not distinctly reticulate-punctulate (Mexico N to S Arizona and C Texas) .... *clarus* [10]

— Posterior face of petiole convex in both directions; compound eye distinctly longer than maximum W of a mandible (without teeth); sides of head, especially the part posterior to extraocular furrow, finely, densely and distinctly reticulate-punctulate and dull (known only from types from Pacific Coast of Costa Rica, possibly in mangroves) .... *biolleyi*

11. Node of petiole with a pair of prominent posterolateral tumosities at about mid-height; apex as seen from side abruptly narrowed to an axially erect, acute tooth (fig. 22); all surfaces of node smooth or nearly so above basal alutaceous part (Plate I, B; Amazon Basin, Guyanas, SE Brasil; forest) .... *biumbonatus* [8]

— Node of petiole without paired posterolateral tumosities; or, if moderate swellings are present, the node is distinctly sculptured with horizontal reticulostriation or costation, or apical spine or tooth inclined caudad from nodal axis (figs. 20-21, 23-27) 12

12. Antennal scape L $>$ 2.15 mm, or if less than that (in minim workers from incipient nests), then the petiolar node is dome-shaped as seen from the side, with distinctly convex outline front and rear up to root of apical spine (fig. 24) 13

— Antennal scape L $<$ 2.15 mm; petiolar node not dome-shaped as seen from the side (figs. 25-27; widespread in American tropics N to U.S.: Georgia; Cuba and Bermuda) .... *brunneus* [11]

13. Anterior face of petiolar node as seen from the side rising steeply from anterior margin, then passing through an obtuse angle into a long section concave in outline to the root of the apical spine (fig. 21); labial palpi 4-merous (E central Peruvian Andes) .... *bradleyi* [9]

— Anterior face of petiolar node otherwise formed (figs. 14, 24, Pl. I, E), either convex, concave or straight from base upward for 1/2 to 2/3 the distance to the root of the apical tooth or spine; labial palpi 3-merous 14

14. Petiolar node as seen from the side dome-shaped, with at least the anterior outline convex from near base to root of apical tooth (fig. 24, Plate 1, E; tropical S and C America, Galapagos, W. Indies except Cuba and Bahamas .... *bauri* [7,17]

— Petiolar node as seen from side gradually tapered dorsad, with basal half to 2/3 of anterior outline concave or straight (fig. 14); grades into form with gaster longitudinally striate above; see couplet 16 (Panama to NE Mexico) .... *laticeps* (part) [19]

15. Striation of gastric dorsum curved-transverse; large, slender species (see metric table; S Mexico to N Argentina; Trinidad; forest) .... *chelifer*

— Striation of gastric dorsum longitudinal 16

16. Mesonotum strongly convex, but broadly sulcate and longitudinally striate on at least the anterior half near midline; appressed pubescence of gastric dorsum nearly obsolete, its individual hairs minute, separated from one another by an average distance of their own length or more (Plate 1, A; fig. 23; Amazon Basin, Guyanas, forest) .... *caelatus* [12]

— Mesonotum gently but evenly convex, transversely striate; reclinate pubescence of gastric dorsum abundant and conspicuous, its individual hairs 2 or more times longer than the average space between them; grades into form with smooth gastric dorsum; see couplet 14 (Panama to NE Mexico) .... *laticeps* (part) [19]

17. Ocular prominences each produced anterolaterally into a stout, acute, oblique, toothlike process (W Ecuador) .... *cornutus* [14]

— Ocular prominences bluntly rounded, as usual 18

18. Antennal scapes very short, not reaching posterior border of head in full-face view; very small species with broad head (see metric table; Mato Grosso) .... *spissus*

— Antennal scapes surpassing posterior border of head viewed full-face 19

19. Antennal scapes at least slightly longer than head (SL > HL); slender species, vertex narrow (CI usually under 55) 20

— Antennal scapes shorter than head (SL < HL); more robust species, vertex broader (CI > 55) 22

20. Apex of mandible with only 2 large teeth (intercalary tooth lacking); size small (HL < 2.3 mm; worker characters deduced from queen; W Amazon Basin) .... *allolabis*

— Apex of mandible with the usual 3 large teeth, including the intercalary tooth; size larger (HL > 2.4 mm) 21

21. Size very large (HL of holotype worker 4.34 mm); head and body virtually hairless except for a few long hairs on posterior half and underside of gaster; petiolar node as in fig. 15; Ecuador: W base of Andes) .... *mormo* [24]

— Size not so large (HL < 3.8 mm); head, trunk, petiole and gaster with abundant fine standing hairs; petiolar node pedunculate anteriorly (fig. 16; S Mexico to Bolivia) .... *hastatus*

22. Mesepisternum with a prominent, narrowly-rounded anteroventral lobe projecting conspicuously on each side when trunk is viewed from above (fig. 11); medium-sized species (see metric table; Amazon Basin, Guyanas; forest) .... *mayi* [3]

— Mesepisternum with at most a low, inconspicuous convexity on its anteroventral margin (fig. 12); size averaging either larger or smaller than *mayi* (see metric table) 23

23. Large species (HL > 2.8 mm; see metric table; SE Brasil) .... *affinis* [3]

— Small species (HL < 2.8 mm; see metric table; Panama, Costa Rica) .... *panamensis* [3]

Key to the Odontomachus Species of the Indo-Australian Region — Workers

1. Head lacking distinct temporal prominences, so that extraocular furrows are undefined posteriad; nuchal carina produced as a distinct flange or collar with a reflexed edge (large, slender species, Melanesia) .... *tyrannicus* group [25] 2

— Head with reasonably well-defined temporal ridges, so that extraocular furrows are demarcated; nuchal carina distinct, but not produced as a flange or collar 3

2. Head, trunk and petiole black or piceous; gaster contrasting brownish-red or brownish-yellow (N. Guinea, N. Britain) .... *tyrannicus*

— Entire head black or piceous; rest of body yellowish-brown (Papua N. Guinea) .... *nigriceps*

— Body, including head, yellowish-brown, though sometimes the head has a dorsocentral part infuscated (Papua N. Guinea) .... *testaceus*

3. Anterior portion of petiolar node drawn out into a low cylindrical or subcylindrical false peduncle occupying 1/3 to 1/2 axial length of petiole; true peduncle reduced to anterior collar; opening of petiolar spiracle remote from anterior base of node and usually well behind apex of subpetiolar process; apical petiolar spine exceptionally

long, gradually tapered from body of node (fig. 8; large, slender forms, Melanesia, possibly W to Celebes) .... *saevissimus* group [18] 4

— Anterior part of petiolar node without a well-defined low, false peduncle, though a brief true peduncle is somentimes present between anterior collar and node; opening of petiolar spiracle close to anterior base of node, and usually almost directly above apex of subpetiolar process; spine of petiolar apex varying in length, but often shorter and less evenly tapered from body of node (figs. 9, 17-19, 1) ... 8

4. Head and gaster dark brown or black; trunk, petiole and legs mostly contrasting yellowish-brown or reddish (N. Guinea to Solomons) .... *rufithorax*

— Head and trunk about the same color; gaster same color or darker 5

5. Head, trunk and legs yellowish-brown to deep reddish-brown; gaster same or darker 6

— Head, trunk, petiole and gaster uniformly dark brown to black (N. Guinea) 7

6. Dorsum of head behind extraocular furrows smooth (Moluccas, and possibly Celebes; N. Guinea to Solomons) .... *saevissimus*

— Posterior dorsum of head almost completely striate and opaque (N. Guinea) .... *montanus*

7. Pronotal disc smooth and shining .... *imperator*

— Pronotal disc finely striate .... *opaculus*

8. Dorsum of first gastric tergum completely striate 9

— Dorsum of first gastric tergum smooth, finely punctate, or alutaceous; partly striate on the posterior half only in some tropical Australian samples 10

9. Striation of first gastric tergum completely gently arched transverse (N. Guinea, may be conspecific with *O. cephalotes*) .... *aciculatus* [2]

— First gastric tergum with some longitudinal striation, if only in a small posteromedian sector (N. Guinea and nearby islands, N and coastal Queensland; grades into, and probably conspecific with, *O. ruficeps*, couplet 11) .... *cephalotes* [2]

10. Posterior vertex bearing small, discrete tumosities on either side of the median dorsal furrow about 1/3 the distance between it and the posterior corners of the head; color uniformly yellowish-orange to orange-brown (N. Borneo to Solomons; marine littoral, associated with reef coral) .... *malignus* [22]

— Vertex lacking such tumosities 11

11. First gastric tergum in part densely and finely coriaceous, alutaceous or longitudinally striate, at least in a strip along the posterior border (Australia, widespread in tropical and in arid inland areas) .... *ruficeps* [2]

— First gastric tergum uniformly smooth and shining, though sometimes with minute, discrete punctures and pubescence distributed over most or all of its dorsal surface 12

12. Subapical tooth of mandible short and broad, < 2 1/2 X as long as wide at midlength, and usually truncate or broadly rounded at apex; in specimens with HL < 3.20, antennal scapes short and vertex broad (SI < 150) 13

— Subapical tooth of mandible longer, usually 2 1/2 or more times as long as wide at midlength, with acute or narrowly rounded apex (apex truncate in most *rixosus*); or else vertex narrower, scapes longer, SI usually over 150 in all sizes of workers 15

13. Dorsum of second gastric segment delicately reticulate (alutaceous) over most of its surface; head always completely striate dorsally; in unrubbed specimens, erect to decumbent longer hairs present on pronotum and widely distributed on first gastric tergum, and reclinate pubescence fairly abundant and conspicuous on gastric dorsum; labial palpi 3-merous (fig. 1; widespread in tropical Indo-Pacific area) .... *simillimus* [30]

— Dorsum of second gastric segment smooth, sometimes opalescent and with a few scattered punctures; vertex smooth or striate; longer hairs only very rarely present on pronotum or posterior part of first gastric tergum, never on anterior of first gastric tergum; pubescence absent or very sparse and inconspicuous on gastric dorsum; labial palpi 4-merous 14

14. Larger species (HL > 3.3 mm); vertex smooth; petiolar node as in fig. 17 (Malaya, Sumatra, Java, Borneo) .... *latidens* [20]

— Smaller species (HL < 3.3 mm); vertex striate in all but the smallest workers from China and Taiwan, but often smooth in other parts of range; petiolar node as in figs. 18 and 19. (NE India, Burma, SE Asia to W and NE China, Taiwan, Ryukyu Is.) .... *monticola* [20]

15. First gastric tergum with a fore-tilted, conspicuously flattened disc, the flattened area usually with a coarse anteromedian pit corresponding to the petiolar spine (Philippine Is.) 16

— First gastric tergum strongly convex in both directions, though a small and shallow anteromedian pit corresponding to the apex of the petiolar spine does occasionally occur 17

16. Large form (temporal HW > 2.0 mm); head light tan or yellowish in color, contrasting with dark brown of body; pubescence well-developed and conspicuous, especially on head and trunk; vertex with reduced striation, partly smooth (S Luzon) .... *banksi* [5]

— Without all of the above character states; temporal HW often < 2.0 mm; head most often reddish-brown, more rarely lighter and contrasting strongly with body; pubescence usually weakly developed; vertex dorsum distinctly striate in samples from Luzon (but may be either smooth or striate in C and S Philippines) ...... *infandus* [5]

17. Preapical tooth of mandible usually truncate, or very blunt; petiolar node conical, with convex surfaces ending abruptly in a short acute apex; vertex mostly smooth, partly striate; pronotum striate (tropical SE Asia, Sumatra, Java, Borneo) .... *rixosus* [27]

— Preapical tooth of mandible pointed, or apex at least narrowly rounded; petiole varying in shape, but petiolar apex usually drawn out into a longer tooth or spine 18

18. First gastric tergum densely sown with fine punctulae separated by smooth interspaces averaging only about 2-3 times the length of a punctular diameter; in unrubbed specimens the punctulae subtend a short, dense pubescence; slender species with long antennae (Viet Nam, SE China) .... *silvestrii* [29]

— First gastric dorsum (when clean) glassy smooth, punctulation and pubescence very sparse or absent 19

19. Pronotum regularly and distinctly striate over all of its dorsal surface; posterior vertex smooth or striate 20

— Pronotum predominantly smooth and shining, or at least the posteromedian part with striation nearly completely effaced, so that the middle here appears smooth and shining in some views, but feebly striate from other views; posterior vertex prevailingly smooth 22

20. Ventrolateral cheeks completely and coarsely striate from eye to mandibular insertion; head dark red, tending to contrast with piceous color of trunk, petiole and gaster; head rather broad (CI > 58) (Flores I.) .... *floresensis* [16]

— Ventrolateral cheeks prevailingly smooth; or at least with a convex smooth area anterior to the eye; head usually about the same color as trunk, petiole and gaster; head usually narrower behind 21

21. Vertex completely and distinctly striate over all the dorsal surface except the extreme posterior slope near nuchal carina, where the sculpture becomes obsolescent (N. Guinea) .... *animosus* [5]

— Vertex behind extraocular furrow prevailingly smooth and shining, with at most a few feeble striae reaching back beyond temporal ridges (fig. 9; N. Guinea, Aru) .... *papuanus* [5]

22. Petiolar node with a short, vertical anterior face abruptly curving into a long, *deeply concave* anterodorsal face that slopes up to the modest apical tooth; slender (CI < 59), shining dark reddish-brown species with reddish-brown legs (Fiji Is.) .... *angulatus* [4]

— Petiolar node with a short, steep anterior face curving into a long, convex or nearly straight (at most feebly concave) anterodorsal face; apical tooth long and slender; CI > 59; legs yellowish, contrasting with brown or black trunk (not in Fiji) 23

23. Pronotal disc with striation effaced only in the middle; head piceous, like trunk (N. Guinea) .... *latissimus* [5]

— Pronotum smooth over nearly all of its surface; head red, contrasting with piceous trunk and gaster (Sumba I.) .... *sumbensis* [31]

Key to the Odontomachus Species of Africa — Workers and Queens

— First gastric tergum with abundant and conspicuous appressed to decumbent pubescence; sides of petiolar node and all of second gastric tergum finely striate or reticulate (widespread in warmer parts of sub-Saharan Africa, NE to Eritrea) .... *troglodytes*

— First gastric segment glassy smooth, without appreciable pubescence, but usually with a few coarse hairs; petiolar node and main (posterior) part of second *gastric tergum prevailingly smooth and* shining (widespread in warmer parts of sub-Saharan Africa) .... *assiniensis*

Key to the Known Odontomachus Species of *Madagascar* — Workers and Queens

— Head narrow behind, without appreciable development of extraocular furrows or temporal ridges; mandibles with long, acute apical and preapical teeth; vertex coarsely transversely striate .... *coquereli*

— Head only slightly narrower across vertex than across eyes, with distinct extraocular furrows and temporal ridges; apical and preapical teeth of mandible short and blunt; vertex finely striate in a longitudinal direction, diverging behind .... *troglodytes*

Table I. Odontomachus of New World -- Metrics of Workers

Species	HL mm	HW mm	ML mm	eye L mm	CI	MI	SI	Specimens localities
mormo	4.14-4.36	2.18-2.36	2.47-2.58	.63-.66	53-54	58-60	187-214	3/3
chelifer	3.20-4.34	1.66-2.64	1.64-2.24	.52-.70	52-61	51-52	156-194	2/2
opaciventris	3.01-3.78	1.92-2.60	1.62-1.94	.42-.55	64-69	51-54	125-148	2/2
caelatus	3.20-3.74	2.23-2.73	1.66-1.92	.47-.55	69-73	51-52	122-136	3/3
biumbonatus	2.78-3.72	1.80-2.50	1.56-1.92	.38-.48	65-68	52-56	118-139	5/4
hastatus	2.81-3.67	1.31-1.86	1.86-2.28	.47-.65	47-51	62-66	224-254	2/2
laticeps	2.72-3.68	1.80-2.68	1.46-1.86	.41-.57	66-73	46-54	120-147	14/8
bradleyi	3.42-3.56	2.09-2.20	1.84-1.92	.49-.52	61-62	53-54	157-164	4/1
affinis	3.01-3.46	1.80-2.15	1.68-1.90	.48-.54	60-62	55-56	152-163	3/2
bauri	2.30-3.12	1.36-2.30	1.18-1.55	.38-.56	59-74	49-54	121-167	12/10
erythrocephalus	2.36-3.00	1.54-2.06	1.26-1.51	.42-.55	65-67	50-53	137-153	2/2
haematodus	2.22-2.98	1.42-2.07	1.13-1.52	.40-.50	64-70	50-52	131-151	4/4
yucatecus	2.38-2.92	1.62-2.04	1.17-1.40	.40-.50	68-70	48-50	115-133	6/4
mayi	2.26-2.80	1.39-1.74	1.22-1.52	.39-.49	58-62	53-55	152-168	3/3
insularis	1.72-2.92	1.23-1.93	0.79-1.47	.25-.47	66-72	46-50	114-141	2/2
clarus	1.82-2.80	1.29-2.01	0.90-1.34	.27-.49	71-74	48-49	117-122	3/3
brunneus	2.00-2.46	1.36-1.75	0.92-1.17	.32-.42	68-74	44-51	114-129	17/9
biolleyi	2.38	1.72	1.29	.50	72	54	140	1
panamensis	2.07-2.32	1.24-1.51	1.12-1.22	.39-.41	60-65	53-54	147-163	4/3
minutus	1.80-2.38	1.17-1.49	0.85-1.27	.27-.35	63-67	47-53	133-154	4/4
spissus	2.20	1.60	0.91	.23	73	41	97	1
allolabis (♀)	1.85	1.05	1.00	---	57	54	202	1

Table II. A Few Odontomachus Species of the Indo-Australian Region -- Metrics of Workers

Species	HL mm	HW mm	ML mm	S L mm	CI	MI	SI	Specimens localities
latidens	3.68-4.27	2.28-2.84	2.02-2.18	3.64-3.83	61-67	51-55	164-134	4/4
rixosus	2.41-3.48	1.40-2.10	1.35-2.00	2.53-3.74	58-65	56-57	181-155	4/4
latissimus (Wamuki)	2.88-3.26	1.74-2.00	1.66-1.66	2.70-3.07	60-61	51-58	154-155	3/1
papuanus (Lae and Huon Pen.)	2.46-3.33	1.24-1.84	1.36-1.82	2.48-3.38	50-55	54-55	184-200	4/3
floresensis	2.54-3.14	1.49-2.07	1.40-1.59	2.57-3.00	59-66	51-55	145-172	5/2
sumbensis	2.27-3.03	1.38-1.93	1.32-1.64	2.18-2.84	61-64	48-58	115-158	3/2
monticola	2.14-3.00	1.52-2.07	1.08-1.72	1.80-2.92	69-71	50-57	118-141	4/3

APPENDIX

This appendix is meant chiefly to include observations on the taxonomy, distribution and biology of particular species and species-groups.

[1] Barth (1960) offers an explanation of how the snap-jaw apparatus works in *Odontomachus affinis*. Observations on living and dead workers and queens of additional species in *Odontomachus* and *Anochetus* suggest that the mechanism is similar in all odontomachites, but the matter has not been carefully investigated in any of these additional forms.

In *O. affinis* each mandible terminates at its base in a massive condylar head, which is basically a cylinder lying largely lateral to the main mandibular shaft. The axis af this cylinder runs roughly dorsoventrad with respect to the main axis of the cranium, so that the mandible is restricted in action to swinging out hinge-like away from the midline and back. The condylar head has prominences and hollows along its perimeter, and these correspond to hollows and processes on the anterior margin of the cranium. Fitting together in the jaws-open position, these hollows and projections on the condyle and cranium lock the jaws into this position when the shafts are opened widely enough, and considerable adductive force must be applied to loose the condyle from the locked position, hollows then overriding projections with a snap, so that the opposite mandibles swing inward until they collide on the midline.

The adductive force is supplied not only by powerful adductor muscles deployed longitudinally in the massive cranium, but also by a sclerotized, spoon-shaped or J-shaped part of the adductor tendon inserted on the mandibular condyle. As the mandibles are opened by the abductor muscles, each spoon-shaped piece is deformed as a powerful spring, and the energy stored in its elastic bending is released in instantaneous adductive action once the locking mechanism for the jaws-open position is overcome.

Some details of the locking and release of the mandible from the jaws-open position are still not absolutely clear to me from Barth's account, but the main essentials of the lock-and-spring mechanism are plausibly presented. Such spring-snap arrangements are common in insects in many instances where very rapid movement is required — often at rates beyond the capability of muscles acting directly. The action of the wings in many insects, for example, involves more complex cases of this kind of mechanism. I am indebted to Thomas Eisner for help in understanding the Barth explanation and a discussion of snap mechanisms in general.

The use of the mandibles in prey-getting and defense by odontomachite workers and queens in life has been observed many times (e. g., Wheeler, 1900), but one aspect of their attacks on prey arthropods has perhaps not been sufficiently emphasized. My own observations on cultured and wild workers of *Odontomachus brunneus* from Florida, *O. simillimus* in southern India, and *Anochetus inermis* in Ecuador, all show that these species are usually cautious and hesitant in their attacks on potential prey. Many approaches to insects supplied are tentative, and are not carried through in snap attacks, though the ants' mandibles are carried open to about 180° in readiness for a snap. Often at first snaps fall short of actually touching the prey insect, and when they later strike home, the ant immediately recoils in retreat, even when to a human observer the prey appears to be tender and vulnerable, without appreciable structural defenses.

Developments during the past 20 years have taught us the importance of chemical defense systems in arthropods (reviewed by Eisner 1970). These systems often appear to be directed particularly against ants as effective, abundant and near-ubiquitous predators. Many observations of predatory ponerine ants (mostly unpublished) that I myself have made over the years convince me of the vital importance to the ants of counter-adaptations to the prey's chemical defenses. Body-wiping behavior, glassy integument, and long tongs-like mandibles are all examples of counter-adaptations to noxious liquid defense allomones exuded or sprayed by prey.

I take the sudden strike-and-recoil behavior of odontomachites to be an alternative means of handling «hot» prey. The mandibular strike can do sudden, severe damage to the prey, and the rapid retreat of the ant helps it to avoid the ensuing release of protective allomones, many of which are emitted only after sufficiently severe trauma to the victim.

Defensive substances on or around the prey are usually soon dissipated, diluted or absorbed by the environmental background, eventually leaving the ant free to move in for the kill and removal to the nest. Defensive substances, incidentally, may have provided the ultimate evolutionary stimulus for the commonly-observed, seemingly dilatory behavior of predatory ants in delaying the return of prey to the nest, and its presentation to the larvae. This behavior, often so maddening to the observer, may well function to rid the prey of concentrations of the allomones potentially harmful to the larvae.

[2] In 1959, Wilson revised the Melanesian component of the *O. cephalotes* complex and synonymized under *cephalotes* six varieties that had been attached either to it or to *O. ruficeps*. While he was making this study, he incidentally rough-sorted the considerable amount of material in this complex from continental Australia deposited in the MCZ. At that time it seemed to us that two species were represented among the Australian samples. One of these species, corresponding to *O. ruficeps,* has the first gastric segment shining, smooth or superficially aluta-

ceous, passing into opaque or subopaque shagreening along the posterior segmental margin. This form is very variable in size, color, and shape of petiole, and tends to have especially fine striate sculpture on the dorsum of the head, at least in western and central Australian specimens. It ranges widely in the Northern Territory of Australia, and extends far southward into Western Australia, South Australia, Victoria and New South Wales in the drier interior parts of these states. In Queensland, it occurs mainly inland, with scattered records north to the Cairns area. Northwestern samples tend to be more reddish in color, particularly the head, while southern samples are more often concolorous piceous.

The other species corresponds to *O. cephalotes,* which, as Wilson showed, is widespread in New Guinea. Like *ruficeps,* it is very variable in body size, color, shape of petiolar node, and sculpture. In Australia, this form is known only from Queensland: several localities along Cape York Peninsula; Cairns-Kuranda-Atherton Tableland region at the base of the peninsula, and south along the coast to the vicinity of Bowen, at least. *O. cephalotes* is recognized by the opaque striate discal sculpture of the first gastric segment, longitudinal behind, and usually arching across the anterior part of the disc. The individual striae of this sculpture are finely pitted, and the intervening costulae are sometimes broken into granular segments, which largely accounts for their matt appearance. Samples with such broken sculpture are relatively rare, and are known only from northern Queensland at the base of Cape York Peninsula (e. g., var. *ajax*).

Since the preliminary sort, some more relevant material has become available from northern Queensland, and this includes a few specimens that appear to be intermediate between *ruficeps* and *cephalotes* in the critical matter of sculpture of gastric segment I. Such specimens generally have the rear of the segment more or less distinctly longitudinally striate for varying distances, giving way in the middle of the disc to coriaceous (alutaceous) or smooth and shining sculpture, e.g., Kuranda (W. M. Wheeler), north of Mareeba (P. F. Darlington), 10-15 miles east of Mt. Garnet (Darlington).

From these facts alone, I was led to suppose that *ruficeps* and *cephalotes* might be conspecific, with the *cephalotes* pattern of gastric sculpture occupying New Guinea, the Moluccas and Cape York southward along the coast of northern Queensland, and the *ruficeps* pattern representing the species in much of the rest of Australia. Sculptural intergrades were then found in the «right places», in northern Queensland, mostly where high-rainfall coastal areas were giving way to the drier interior. The trouble is that only a few intergradient specimens are known, and we need more of them to be sure of their nature and the details of their geographical distribution.

The picture is complicated by the fact that the available material from the northern third of the Northern Territory of Australia can be separated into two types on the basis of gastric sculpture. In the first type, the first gastric segment is smooth or nearly so to near the posterior border, where a band of more or less distinct shagreening usually intervenes. This type includes some very large workers (HW often > 2.30 mm), usually with the petiolar node slanted caudad and tapering gradually into an apical spine, although series with smaller workers exist.

The second type has the first gastric segment smooth or coriaceous, and more or less shining in the front and middle parts, and longitudinally striate in the posterior part. The most completely (and opaquely) sculptured sample is one from Johnston River, Melville Island (W. Bateman). The «second type» tends to be smaller and to be associated with a shorter, more abruptly tapered node, with stronger striation around the front and sides. The two types have been collected sympatrically, but not from the same nests, in the vicinity of Darwin and at Katherine, Northern Territory (W. L. Brown).

The form of the second type suggests possible intergradation, as one goes northward (toward Melanesia) in the Northern Territory, between *ruficeps* and *cephalotes,* but the lack of intergrades between the two types in the Northern Territory samples we have so far is a problem that can only be settled by more material, particularly nest series, of this complex.

The best I can do with the present resources is to reconfirm the very close (possibly conspecific) relationship between *ruficeps* and *cephalotes,* to list their obvious synonyms, and to indicate a problem within the nominal *ruficeps* of the upper Northern Territory.

There remain two special remarks to be made. First, the dentitional characters emphasized by Crawley (1922) in his analysis of this complex are scarcely to be rated as very important, considering the great variation in apical tooth size and shape in all the larger *Odontomachus* species, due especially to allometry and wear. Second, *O. sharpei* was based on a single individual, obviously a pathological worker of *O. ruficeps* with a swollen, misshapen gaster, in part yellowish in color and apparently the result of an internal parasite.

Outside of Australia, other problems exist concerning the relationship of *O. cephalotes* with the two nominal species, *O. aciculatus* and *O. aeneus.* All three forms in New Guinea have striate gastric sculpture, with the last two, both from the western part of the great island (West Irian), being striate in a transverse direction. The New Guinea *cephalotes* populations have exceedingly variable gastric striation. Examples are available with the entire first segment longitudinally striate, while in most samples, some anterior part of the first segment is transversely striate, with various degrees of arching over a posterior zone or posteromedian pocket of longitudinal striation. In some samples, transverse striation occupies at least 70% of the length of the first segment.

Thus we are faced with a situation in which samples with only small parts of the first gastric segment longitudinally striate are nevertheless placed in *O. cephalotes* together with specimens in which the whole segment is longitudinally striate, while examples with all-transverse striation are put into *O. aciculatus* or *O. aeneus.* It seems to me at least doubtful that the difference between «completely transverse» and «0-70% transverse» really by itself marks a species difference.

O. aeneus has been separated from *O. aciculatus* on the basis of its metallic integumental reflections, stressed by Emery. I have now studied the *aeneus type* (ZMA-Amsterdam), and compared it with West Irian samples, including specimens almost certainly part of the type series of *O. aciculatus* in the British Museum, as well as variants that would otherwise be classed as *O. cephalotes* on sculptural details. Metallic surface reflections and iridescence of varying kinds and degress are of course commonplace in *Odontomachus,* including the complex under discussion, and they are subject to considerable intrinsic variation, as well as modification by grease or dirt on the integumental surfaces of different samples. The *aeneus* holotype (Wendesi, W. Irian) does have weak bronzy and violaceous reflections on head and trunk, but these are also found in *aciculatus*. In the *aeneus* type, the striation of the upper vertex is feeble, and extends only partway down the sides. Emery apparently never saw *aciculatus* types, and Wilson, who left *aeneus* as a distinct species, seems never to have examined *aeneus* types.

I believe that comparison now shows that *O. aeneus* and *O. aciculatus* are conspecific, and formal synonymy is indicated. The synonymy of *O. aciculatus* with *O. cephalotes* (and eventually with *O. ruficeps*) is regarded as a possibility for future investigation. Further samples of this complex are needed, particularly whole nest series from West Irian, in order better to judge the variability of the gastric sculpture and metallescence traits.

[3] *O. affinis, O. mayi* and *O. panamensis* form a tight subgroup within the *haematodus* group. Although the 3 species are very similar, *affinis* averages larger in size (Table I) and is darker (reddish-brown) in color, and, as Kempf has pointed out, it lacks the strongly salient anteroventral lobes of the mesepisternum that are characteristic of *O. mayi* (fig. 11). *O. affinis* and *O. mayi* differ more strikingly in distribution and habits. *O. affinis* is restricted to wet subtropical forests in SE Brasil (Espirito Santo to Santa Catarina). In São Paulo State, at least, it occurs in and under rotten logs in plateau forest; I did not find it in the warmer lowland forest along the coast.

O. mayi is a medium-sized species, in life a bright ferruginous in color, which fades somewhat in preserved specimens. In our travels in the Amazon in 1962, Karol Lenko and I found this species 3 times in the Manaus and Benjamin Constant areas, each time in forests in mixed «ant-garden» nests with the similarly-colored but much smaller dolichoderine *Monacis rufescens,* the same ant with which Mann first found it in the Amazon Basin. In 1971, however, my wife and I took an unmixed colony of *O. mayi* in a bromeliad growing on a tree in «caatinga» forest on white sand 61 km north of Manaus on the road then being constructed northward to Caracaraí («Estrada Rio Branco»).

This species is known from Amapá Territory and also from the Guyanas; a winged queen in MNHN-Paris bears the label «Haut Carsevenne» [French Guyana] and was collected by Geay.

The still smaller form *O. panamensis* (fig. 12) lacks the protruding lobes of the lower mesepisternum, but dried specimens are similar to *O. mayi* in color. The nesting habits of *O. panamensis,* so far collected only in forest in Panama and Costa Rica, remain unknown. Until we have more information about this species, doubts will remain about its distinctness from *O. mayi.*

[4] I did not record any examination of the type of *O. politus* during a hasty visit to the Museum für Naturkunde in East

Berlin, but Stitz' description leaves no doubt that he had before him a specimen of *O. angulatus*. Only two *Odontomachus* are known from Fiji: *angulatus* and *simillimus,* and they cannot be confused. I found *O. angulatus* foraging by day in the shade of heavy native forest at two points on the Nausori Highlands in southwestern Viti Levu during May 1972.

[5] The *infandus* group connects the *saevissimus* and *tyrannicus* groups on the one hand to the *rixosus* and *ruficeps* groups on the other. The species vary from slender, with rather narrow vertex, to moderately stout; the petiole is very variable within and between species, but it always has a long and slender apical spine inclined caudad (fig. 9). The anterior outline from side view varies from obtusely angulate (where the low, steep, anterior face meets a concave or straight anterodorsal face), or the anterior and anterodorsal faces may merge more or less gradually to form a single convex outline.

The populations in the Philippines, referred to as *O. infandus* and *O. banksi,* have the first gastric tergum obliquely flattened, and usually with a coarse, irregular median dimple, apparently impressed by the petiolar spine during pupation. Otherwise, they correspond very well to the meager samples of *O. papuanus* and *O. animosus* we have from New Guinea. I am provisionally considering this difference as one of species rank (see key, couplet 15), though I have doubts about it.

One problem arises with specimens recorded as from Celebes. Although I failed to collect any members of the group during a hurried 3-week trip in northeastern, southwestern and southeastern Celebes, there is a specimen in MCZ labeled «Celebes, Forel Coll.», and a specimen exists in MNK-Berlin labeled as from «Togian Inseln, (Meyer)» in the Gulf of Tomini. Unfortunately, the MCZ specimen lacks the petiole and gaster, and I do not know the shape of the first gastric tergum in any other Celebes samples. Also, I know of no samples of *Odontomachus* from the northern Moluccas, though the *infandus* group may well occur there. Without further information, then, the boundary between *infandus* and *papuanus-animosus* cannot be drawn except in a very rough way. Apart from the New Guinea-Philippines axis of distribution, the new species *O. floresensis* [16] and *O. sumbensis* [31] represent the *infandus* group in the Lesser Sundas, and *O. silvestrii* may be taken as a somewhat more aberrant vicariant in Viet Nam. *O. floresensis* is relatively slightly differentiated from *infandus*-group members, but *O.*

sumbensis is more strongly so, perhaps reflecting its greater isolation below the Sunda Chain.

Since we have no collections from neighboring islands in the Lesser Sunda chain, it is impossible to say how far either of these forms extends beyond the ranges as known at present. My guess is that *O. sumbensis* (the most distinct form) may be restricted to Sumba, while it is more likely that *O. floresensis* extends westward to Komodo (and Sumbawa?) and eastward toward Alor. These last islands, however, remain to be collected; it is surprising how poorly they are known for insects, and particularly for ants. *O. sumbensis* and *O. floresensis* appear to be isolated members of the *infandus* group, most closely related to *O. latissimus* by their relatively broad heads.

The Philippine sample available is a very large one (more than 400 specimens), mainly assembled by the late Dr. James W. Chapman. Unfortunately, this basically fine representation is afflicted with some problems. In the first place, we have no indication whether some of the series, apparently collected at one place and at one time, mainly in the Cuernos Mts., near Dumaguete, Negros Oriental, represent single nests or collections of strays from several nests. It seems that both mixed and single-next series occur in this lot, but we can rarely be sure which is which. There are also some label uncertainties in Chapman's material. For example, a printed label reading «Dumaguete» with Chapman as collector, may be noted in scribbled pencil in the reverse side as from a locality in Mindanao, with the collector as Domingo Empeso, Chapman's collaborator. Obviously, the Chapman localities must be accepted only with reservations. Furthermore, many of Chapman's samples suffer from poor preparation and from mold acquired mostly during the war years, when the collection was for a time in rustic storage while the Chapmans were interned in prison camp. Many series were cleaned and remounted for this study with considerable difficulty and some loss of specimens.

At first sight, the Philippine samples seemed to sort out nicely into 3 species, corresponding to *O. infandus* (head completely striate above, primarily in Luzon, but also sparingly southward), *O. banksi* (a large form with conspicuously lighter-colored head, shining and only vestigially striate over the vertex, localized in south central Luzon), and *O. papuanus philippinus* (a large, reddish-brown form with vertex largely smooth and shining, predominant in the central and southern Philippines).

Even making allowances for the possibly mixed nature of some of Chapman's series, certain of the Dumaguete-area samples appear to be intergradient in the crucial character of striation of the vertex. Furthermore, the striation of the pronotum, characteristically longitudinally-whorled in Luzon *infandus* series, but often transverse farther south, is inconstant and often discordant with head sculpture in the Dumaguete samples. Further signs of intermediacy may be seen in samples from northern Mindanao: Anakan Lumber Co., Ginoog, Misamis (A. Reyes); Lanao (D. Empeso); Masawan, Zamboanga del Norte, 4400 [ft?] (D. Empeso).

O. banksi could also be a part of this intergradation, since samples with light-colored head, but striate vertex, come from Samar I. (McGregor et al.), and Bohol I. (A. Alcala) «from leaf bases of coconuts». The Bohol series has the striation of the vertex somewhat weak, shining and partly effaced behind, but the pubescence is only weakly developed. Collections of «typical» *O. banksi* are restricted to a small part of Luzon south and east of Laguna de Bay, in Laguna and the adjacent part of Quezon provinces, and both *banksi* and «typical» *infandus* bear labels from Lucban in Quezon Province. Only careful collecting in south central Luzon will resolve the relationship between these two forms. They could be morphs of one variable species, or else locally-displacing species of a character-displacement pair.

We may summarize the Philippine situation by indicating the conspecificity of *philippinus* and *infandus*. Stitz' race *striaticeps* is of course the «typical» form of *infandus*, and *O. banksi* is left provisionally as a distinct species.

From northeastern New Guinea, we have a reasonably uniform set of collections made by E. O. Wilson, referable to *O. papuanus;* these samples all have the upper vertex smooth and shining, but in a few specimens, weak traces of striation extend back beyond the extraocular furrows onto the temples. In the type of *O. animosus* and in 2 specimens (BMNH-London and MCZ) from Madew, St. Joseph R., 2000-3000 ft., N. Guinea, (A. Wollaston) the vertex is almost completely striate, becoming indistinct on the posterior downslope of the head, just before the nuchal carina. Although I am inclined to regard *papuanus* and *animosus* as sculptural variants of one species, there is not enough material available, nor are there clear enough signs of intergradation, to serve as a basis for formal synonymy.

In his original description of *O. latissimus,* Viehmeyer (1913) writes, «Pronotum mit konzentrischen, hinten sehr s[e]ichten, geschlossenen, ovalen Bogenlinien; die Mitte derselben glänzend glatt». Wilson (1959: 486), in the first lug of his couplet 7, leading to couplet 10 and *latissimus,* wrote: «Most of the pronotum, including all of its dorsal surface exclusive of the anterior «neck», completely lacking striae, its surface either shagreened or smooth and shining». Wilson saw no *latissimus* types, and it seems that he misjudged Viehmeyer's words insofar as the pronotal sculpture is concerned.

In 3 workers from Wamuki, 800 m, Huon Peninsula, NE New Guinea, referred by Wilson (1959: 497) to *O. papuanus,* the heads are broad behind (see Table II) and the striation is almost completely effaced and the surface definitely shining in the posterior center of the pronotal disc.

The type of *O. latissimus* came from Sattelberg, also on the Huon Peninsula, and Viehmeyer's sketch of the head agrees well with the Wamuki specimens. Also, the profile of the long anterodorsal face of the petiolar node is almost perfectly straight (very feebly concave) in the Wamuki workers, matching well with the original description. Although *O. latissimus* could be a morph or local variant of *O. papuanus,* as Wilson evidently regarded the Wamuki sample, I am inclined to treat it as a separate species on the scanty evidence available.

[6] Gathered in *O. assiniensis* are a number of variants, mostly color forms, that do not seem to me to deserve formal taxonomic status. The type of *assiniensis* (MCSN-Genoa) is a larger worker with light red head, the reddish extending back somewhat into the brown trunk. The type locality is «Assinie», Côte d'Ivoire, a coastal village and area near the Côte d'Ivoire-Ghana border on the coast. The red head and yellow legs are characteristic of forest zone specimens from Ghana, according to B. Bolton (in. litt.), and the type of subspecies *flavescens,* from the Nimba Mountains of Côte d'Ivoire (MNHN-Paris) belongs to this same form.

Samples from both forest and drier areas, on the coast as well as inland in West Africa, have the head brown or dark brown like the rest of the body, but often retain the yellow legs. In Zaire, variants with part or all of the trunk pale brown in color, contrasting with dark brown head and gaster, correspond to the types of subsp. *fauconneti* and var. *furvior.* More uniform dark brown specimens, usually with brown legs, come from the Zaire-Sudan border region, Zaire and elsewhere in central Africa; these correspond to the types of *intermedius, fuscus,* and *aterrimus*. The syntypes of *intermedius* (MNK-Berlin) have the pronotum with striation whorled, arched or transverse. The type of var. *tropicalis,* from Principe I. in the Gulf of Guinea is also a large, dark form. The variety *caffrorum* also seems to fit into this spectrum of variation, although the type was not carefully studied. An undescribed variant collected by W. H. Gotwald and by I. Lieberburg in the forest near Makokou in Gabon is large in size, brown in color, and has the node and a large area at the base of the gaster, as well as the legs, reddish-yellow.

The species can be confused only with *O. troglodytes,* but *assiniensis* averages larger in size, has more shining integument, obsolescent pubescence and pilosity, and a higher, more compressed petiolar node. Also, as Barry Bolton (in. litt.) first noticed, *O. assiniensis* has 4-merous labial palpi, while *O. troglodytes* has them 3-merous.

[7] *O. bauri* is a very widespread and variable species that usually has been lumped with «*O. haematodes*». Of many sculptural variants, we can sort out one major trend toward coarser sculpture, particularly in the striation of the petiolar node (Plate 1, E), in samples from moist forest in continental South and Central America, while samples from the llanos and semidesert areas of Venezuela, Colombia and adjacent areas tend to have finer sculpture, with the petiolar node being delicately striate or striate-reticulate. The continental wet forest populations also tend in many cases to be larger, darker, more robust, and to have a thicker, more dome-shaped petiolar node in the worker.

O. bauri extends southward through Colombia and Ecuador on both sides of the Andes, and on the Pacific side it probably reaches south as far as real lowland or foothills forest does — possibly into Peru. In western Colombia and Ecuador, it is the dominant species of the genus, and is not accompanied here by *O. haematodus,* but only locally by *O. erythrocephalus* among closely related species (*haematodus* group; the much smaller and more cryptic *O. minutus* occurs on the Pacific side in wet forest, and *O. brunneus* may extend here also, but these are probably not serious competitors). Even on Barro Colorado Island in the Canal Zone, *O. bauri* is the most commonly collected, and probably dominant, species of the genus, though 5 or 6 congeners co-occur there. The Galapagos populations, which furnished the type of *bauri,* probably arose from Ecuadorean propagules, perhaps transported the islands accidentally by man.

The llanos populations extend through the Orinoco Delta (where they previously were mistakenly regarded by me as intergrades between *bauri* and *haematodus*) and Trinidad (the *O. sericeus* of Provancher), from that island extending into the Antilles as far as Hispaniola and Jamaica, but not Cuba or the Bahamas. *Formica unispinosa* Fabricius, described from Guadeloupe and long regarded as a synonym of *O. haematodus,* may be the same as *bauri.* Since at least *O. brunneus* also is widespread in the Lesser Antilles, the identity of *unispinosus* remains in some doubt, and it seems best to regard it as a *nomen oblitum,* which it is under the Code.

Roger's variety *pubescens* of *O. haematodus* in the old sense, from La Guaira, Venezuela, is possibly another early name for *bauri,* here rejected for similar reasons. A vigorous search for type material of var. *pubescens* in MNK-Berlin and elsewhere in European museums has proven fruitless, and the name is best placed in the *oblitum* category.

The West Indian *bauri* are even more variable than the mainland populations, and they tend to be smaller and with less dome-shaped petiolar nodes; the legs are often partly or entirely reddish or yellow in color.

The Hispaniolan form, which my wife and I collected widely in the Dominican Republic, especially in the pine-covered mountains of the southwestern and central parts of the country, and which is widespread in Haiti (MCZ), approaches black in color, but has the coxae and part of the femora contrasting brownish orange. In the Samaná Peninsula and some drier parts of the island, the color is lighter, especially the brown trunk, and the legs tend to be all yellow. The form from Hispaniola corresponds to Emery's var. *paucidens.* A dark brown, slender variant with yellowish legs, superficially very like the typical *O. haematodus,* inhabits Jamaica and Mona Island. From Puerto Rico the samples available vary somewhat («var. *notatus*») but are basically brown, usually with the trunk — or at least the propodeum — and the petiole lighter and more reddish. The legs are yellowish to dull orange, at least over the coxae and basal half of femora. Many of the lighter specimens are in old museum lots, whereas the series we took in the Dominican Republic in 1975 are all blackish, mostly with blue iridescent reflections on the mesopleura, and have the orange leg bases rather brightly contrasting, indicating that fading may be important in older preserved specimens of Antillean samples.

South of the llanos, *O. bauri* is widespread in the Amazon Basin and the lower eastern foothills of the Andes up to at least 1000 m in Peru. It reaches the mouth of the Amazon near Belém, in the east, and extends southward through the forests of northern Mato Grosso and beyond into more open country. In most of Amazonia, it is less common than *O. haematodus*. The southern limits of *O. bauri* are not well known, due to its previous confusion with other species, but it has been collected at several localities in western São Paulo State by Karol Lenko, including Ilha Solteira in the Rio Paraná. The MCZ has a sample taken at Buriti, near Cuiabá in central Mato Grosso (R. Duffield leg.), and an alate queen from Quincemil (750 m) in SE Peru. I regard it as certain that *O. bauri* extends well into Bolivia, but I have seen no specimens from that country yet. It also is found in dry northeastern Brasil, in Ceara and Paraíba.

Although *bauri* is common in Panama and around the Golfo Dulce in SW Costa Rica, it is less common in northern Costa Rica. I took an alate queen near Guapiles, in northern Limon Province, so the species may well reach into the Nicaraguan lowlands, but I have seen no specimens of *bauri* from Nicaragua or countries to the north, where *O. laticeps* prevails.

[8] **Odontomachus biumbonatus** new species
(Fig. 22, Plate 1, B)

Worker, holotype: TL 13.6, HL 3.66, HW (across vertex) 2.50, HW (across ocular prominences) 2.76, ML 1.90, scape L 2.96, eye L 0.48, WL 3.76 mm; CI 68, MI 52, SI 118.

Paratypes (smallest worker, Rio Tarumã, Amazonas): TL 10.3, HL 2.78, HW (vertex) 1.80, HW (ocular prominences) 2.08, ML 1.56, scape L 2.50, eye L 0.38, WL 3.00 mm; CI 65, MI 56, SI 139.

Holotype and 4 worker paratypes from 4 localities, including those with largest and smallest heads: TL 10.3-13.6, HL 2.78-3.72, HW (vertex) 1.80-2.50, ML 1.56-1.92, WL 3.00-3.76, SL 2.50-3.00 mm; CI 65-68, MI 52-56, SI 118-139, ex 36 paratypes from 9 localities.

Description of worker, composite: Head and mandibles massive, form as in *O. laticeps*, vertex notably wider than trunk and gaster. Callows with finely serrate inner (ventral) mandibular borders and three stout sharp-edged teeth at apex, the basalmost of these of these subrectangular and with 1-2 smaller supplementary points on proximal edge. Older specimens (most foraging workers) with the apical teeth more or less worn down to rounded stumps. Palpi segmented 4, 3. Striation of head complete on dorsum, moderately fine (6-7 striae per 0.1 mm sample square on middle of left half of vertex), extending nearly halfway down sides, shining. Antennal fossae and sides of head smooth and shining, usually bluish-opalescent. Mandibles nearly smooth above, shining, with a few coarse punctures. Outer borders of mandibles, like antennae, densely punctate, weakly shining, with dense appressed to decumbent pubescence. Scapes slightly surpassing posterior margins of head when held back. Cervical cavity and underside of head smooth and shining.

Trunk robust; metanotum developed as a depressed transverse band, separated from mesonotum by a narrow depression with short longitudinal rugae. Propodeum weakly convex in profile over anterior half, followed by a shallow concavity of variable extent. Anterior propodeal convexity usually weakly longitudinally sulcate as seen from above. Declivity short and moderately convex.

Pronotum finely striate in very varied patterns: whorled, longitudinal, oblique, or transverse, but normally with at least some transverse striation forming a posterior band; mesonotum and propodeum transversely striate, the striae coarser on propodeal declivity. Mesopleura smooth and shining, except for anterior and posteroventral ends, which have variable striation; smooth part oten bluish opalescent.

Head in center of vertex with a pair of long, anteriorly inclined hairs (L 0.04-0.05 mm), and sometimes in front of these a few shorter decumbent to suberect hairs. Long oblique hairs also present on undersides of mandibles, anterior underside of head (a few very short, delicate erect hairs here also), and coxae, trochanters and basal half of undersides of femora. Pronotum with a group of 4-10 coarse, curved erect hairs, mostly 0.05-0.06 mm. long.

Pubescence on head moderately abundant but spaced, decumbent to appressed, crossing the striation in most places, and therefore easily seen at a magnification of 20x. On trunk, pubescence inconspicuous, more restricted, dilute, mostly directed caudad and appressed. Legs shining, finely punctulate and with dense, short decumbent pubescence, except posterior (mesial) surfaces of femora, which are smooth and shining.

Petiolar node shape as in fig. 22; the characteristic abruptly rooted apical spine is slender, acute and nearly erect, i.e., on or near the major axis of the node, and may even be tilted slightly cephalad. Posterior face of node vertically sulcate; sulcus flanked near mid-height by a pair of low swellings, best seen in oblique posterolateral view, from which the species takes its name. Node shining, smooth or nearly so on all surfaces above the alutaceous basal part, with scattered punctures; fine decumbent pubescence directed upward on anterior face and sides.

First gastric tergum glassy smooth, often with bluish reflections, with scattered coarse punctures from which arise numerous tapered, fine, yellowish hairs, subdecumbent to suberect, about 0.15 to 0.55 (mostly 0.3-0.4 mm.) long. Pubescence long (0.12-0.15 mm.) and fine, appressed to decumbent, conspicuous but not crowded, the separated hairs only rarely touching one another (Plate 1, B). Remaining segments of gaster also shining, with a partly feeble alutaceous sculpture varying to smooth and shining, with punctures. In some samples, especially from Pará and Amazonian Peru, even the disc and posterior part of the first gastric tergum may have a very faint microreticulum visible in good light at magnifications of about 40x or more, but this does not interfere with the shininess of the integument of this segment. All segments of gaster, both above and below, with numerous hairs and sparse pubescence like the first tergum.

Body color in mature workers dark reddish-brown to piceous, often appearing black or nearly so to the naked eye. Mandibles, antennae and legs usually a little lighter, castaneous.

Queen, alate (4 specimens: 1 from Kartabo, Guyana; 1 from Icoaraci, Pará, Brasil, colony series B-22, with workers; 2 from Quincemil, SE Peru): TL 14.2-15.1, HL 3.40-3.60, HW (vertex) 2.40-2.46, ML 1.86-1.94, scape L 2.92-3.06, WL 4.10-4.40, forewing L 8.4-9.0 mm.; CI 68-71, MI 54-55.

With the usual differences from the worker. Pronotum transversely, scutum longitudinally striate; scutellum nearly smooth to obscurely longitudinally striate, shining. Wings tinged with brown.

Holotype [MZSP] and 12 paratype workers [MZSP, MCZ] from Limoncocha and vicinity, Prov. Napo, 00°24'S, 76°36'W, ECUADOR, H. R. Hermann No. 386 and strays, also strays by P. L. Kazan. Other paratypes: PERU: Dept. Huanuco, Tingo Maria vic., nest no. R-9, W. L. Brown and W. Sherbrooke. Monson Valley, near Tingo Maria, E. I. Schlinger and E. S. Ross. Dept. Cuzco, Quincemil, 700 m, Sept. 1962, 2 winged queens at light, L. Peña. BRASIL: Pará: Icoaraci, near Belém, 31 Aug. 1962, W. L. Brown, nest no. B-21 with winged queen in rotten wood. Pirelli Rubber Plantation, Iriboca, nest no. B-274, P. F. Darlington. Utinga, near Belém, no. B-116, P. F. Darlington. Canindé, Rio Gurupá, B. Malkin. Amazonas: Ponta Negra, near Manaus, W. L. Brown, no. M-156. High falls on Rio Tarumã near Manaus, W. L. Brown, no. M-103. Guaporé: Madeira-Mamoré Railroad Camp 41, about 306 km SW of Porto Velho (W. M. Mann). São Paulo: Caraguatatuba, Reserva Florestal, 40 m (K. Lenko). GUYANA: Kartabo, winged queen, 31 Aug. 1920, W. M. Wheeler.

This species, formerly misidentified as *O. laticeps* in some collections, is marked by large size, broad head and mandibles, shining, sparsely pubescent gaster, and above all, by the shape of its petiole (fig. 22). It is very widespread in the Amazon Basin, and so far as known, nests mainly in rotten wood. It is probably widespread also in lowland tropical forests in southeastern Brasil.

[9] **Odontomachus bradleyi** new species

Worker, holotype: TL 14.8, HL 3.56, HW (across vertex) 2.20, HW (across ocular prominences) 2.53, ML 1.92, scape L 3.46, eye L 0.52, WL 4.14 mm; CI 62, MI 54, SI 157.

Paratypes, 4 workers from type locality: TL 14.1-14.8, HL 3.42-3.54, HW 2.09-2.17, ML 1.84-1.88, scape L 3.40-3.44, eye L 0.49-0.51, WL 4.00-4.10 mm; CI 61-62, MI 53-54, SI 159-164.

Description of worker, composite: A large, brown species near the upper size range of *O. laticeps, O. biumbonatus* and *O. caelatus,* but with relatively narrower head, particular form of petiolar node, and with labial palpi 4-merous as well as maxillary palpi.

Mandibles massive, as in the 3 species just mentioned; dorsal subapical tooth worn roud-ended, or ground down to its base in old specimens; truncate or with an emarginate apex in younger ones. Head nearly parallel-sided behind ocular prominences, sides feebly converging caudad, posterior margin biconvex, concave in the middle. Antennal fossae confluent; extraocular furrows and temporal ridges developed.

Trunk robust; mesonotum strongly convex, especially anteriorly, sloping downward behind to mesometanotal suture, which is broad and with more or less distinct longitudinal ribs. Metanotum short, transverse, usually bounded in front by a cross-carina; outline of surface variable, sloping upward caudad. Propodeum slightly convex in lateral-view outline, with a shallow but distinct saddle centered just behind midlength. Mesepisternum with a distinctly defined margin along its whole dorsal length.

Petiole (of holotype 0.80 mm long) anterior face steep and convex for about the first 0.1 mm above anterior collar, then concave (for about 0.3 mm) to beginning of slender apical spine, into which the node tapers gradually above. Apical spine straight, or very feebly curved posteriad, its axis inclined slightly posteriad. Posterior outline of node generally concave from posterior collar to apical spine, but with a feebly convex middle section (fig. 21); posterior face of node mostly flat, with a faint impression about halfway up.

Striation of head and trunk moderately coarse (5 striae per 0.1 mm sample square in middle of left half of vertex), on sides of head extending laterad only to level of eye, and beyond this smooth and shining, with only scattered fine puctures and some faint bluish iridescence. A similar but narrow smooth zone extends across the back of each lobe of the vertex along the nuchal carina, but these smooth zones do not quite reach the midline at the V. Pronotum longitudinally striate mesad, but concentrically around the disc, so that cervix and anterior face of pronotum are transversely striate, and its sides are obliquely striate fanwise. Mesonotum, metanotum and propodeum striate transversely as seen from above. Petiolar node indistinctly striate around front, sides and basal strip of rear face, the striae on the sides horizontal above, but sloping downward caudad below mid-height. Apex and spine of node, also lowest part of sides, and most of posterior face, nearly or quite smooth and shining. Mesepisternum finely vertically striate over anterior quarter or third, and with a few coarse vertical striae in posterior corner, otherwise smooth and shining. Propodeal spiracle small, subelliptical to reniform, not much longer than broad.

First gastric tergum smooth and shining, with a few coarse piligerous punctures and spaced fine ones associated with the pubescence. Second gastric tergum alutaceous (finely reticulate) and with coarse but ill-defined punctures, the latter especially numerous anteriad; surface moderately shining. Third and fourth gastric terga partly alutaceous and with some coarse punctures; fifth (last exposed) tergum mostly smooth and shining, with fine spaced punctures.

Pilosity only moderately well developed; standing hairs on dorsal surface mostly 0.3-0.4 mm long, gradually tapered to apex: the usual pair on the center of cephalic dorsum, 2-6 or so on pronotal disc, 35-50 or so inclined caudad on gastric dorsum, some smaller ones on ventral surfaces of mandibles and gaster, and a few on coxae.

Pubescence fine and short, but fairly abundant and visible even at magnifications as low as 10 X; mostly appressed and decumbent, sparse on mandibles, more abundant on antennal scapes and legs, where some of the individual tiny hairs are erect or suberect. Dorsum of head and trunk with hairs of pubescence generally running across the striation, rather than along with it. Anterior upper face of petiolar node with fine decumbent pubescence; on gastric tergum I fine, appressed, individual pubescence hairs averaging about twice as long as average distance between them; pubescence longer and danser on terga II-IV. On underside of gaster, pubescence is appressed to suberect.

Color medium reddish brown, gaster darker brown above; smooth areas of sides of head, mesepisterna, and gastric dorsum with a more or less distinct bluish iridescence; mandibles dark brownish; legs sordid yellow to castaneous.

Queen and male unknown.

The type series consists of 4 workers from Huacapistana, Dept. Junin, Peru, 3 June 1920 (J. C. Bradley), and a single additional worker with the same data, but «1-2 June 1920». The series of 3 June also has «# 535», but I have been unable to find an entry corresponding to this number in Prof. Bradley's notes in the Cornell Lot Book. The lot number for the collection is 569, covering the Cornell University Expedition. Huacapistana is on the Rio Tarma, a tributary of the Rio Chanchamayo, on the trail or road between Tarma (elev. about 3050 m) and San Ramón, at the confluence of R. Tarma and R. Chanchamayo (elev. about 825 m). The elevation of Huacapistana is given by Prof. Bradley in the Lot Book as «5000 ft.» (1524 m), which is doubtless a rough approximation.

O. bradleyi is an interesting species. Though in its habitus it is a thoroughly ordinary neotropical *Odontomachus,* the 4-merous labial palpi indicate that it can not even belong to the *O. haematodus* group. It will be interesting to see how restricted its geographical distribution actually is; right now, it is known only from the type locality.

[10] The taxonomy of the two *Odontomachus* species known to have ranges extending into the United States has been confused by all authors since before the turn of the century. Central to the confusion has been the long-standing misidentification of Guérin's *O. insularis.* This species, as determined from the type worker, here designated as lectotype, in Paris (MNHN), and confirmed by the original description, is the reddish form with yellowish appendages and dark (piceous or black) gaster, common and widespread in Cuba and the Bahamas. So far as I have been able to determine from actual specimens, the true *insularis* does not occur on the continent of North America or in the Florida Keys, although it would not be surprising to find it somewhere in Florida. The varieties *pallens* and *wheeleri* are just the ordinary *insularis,* judging from their types. In var. *wheeleri,* the dorsum of the propodeum and the petiole are perhaps more yellowish than usual, but this condition is approached by occasional workers in other nest series. Wheeler described *pallens,* apparently, while thinking the dark Cuban species, here referred to as *O. brunneus,* was *insularis.*

O. insularis has cephalic striation so fine that Guérin could not see it when he wrote the original description, and it has a sericeous look at lower magnifications. The male is black or piceous in color, with a brown gaster, and the worker has palpal segmentation 4, 3. In addition to the many records of *insularis* from Cuba (type locality) and the Bahamas, I have seen a single worker labeled as from Diquini, Haiti (W. M. Mann).

Odontomachus clarus is a very closely related species replacing *insularis* on the continent, where it ranges from Central Texas and southern Arizona southward in Mexico at least to Mexico City and the state of Guerrero, apparently mainly in arid and semiarid areas on the Mexican Plateau and in the cordilleras. Although it is more variable in size and color, *clarus* is like *insularis,* and it also shares with *insularis* the dark-colored male and 4, 3 palpal segmentation. In fact, the only reliable worker character I can find to separate the two is the different development of the acute apex of the petiolar node. In *insularis,* the node narrows fairly abruptly (in side view) to a long, thin, backcurved spine, which may occupy a quarter or more of the total height of the node. In *O. clarus,* the node as seen from the side tapers rapidly to a much shorter spine, which often is not really a spine at all, but simply a sharp conical apex. The shortest and most stumpy nodes tend to occur in small, pale yellowish-brown individuals from the northern limits of the species in Central Texas, and especially in the mountains of southeastern Arizona (Huachuca, Chiricahua and Santa Rita Mountains at altitudes of 1000-1500 m., for examples). The mountain samples have been considered as a separate subspecies *coninodis,* but I see no need to give a formal name to these depauperate ecotypes or ecophenotypes occurring at the upland range boundary of a variable species. Samples from nearby Tucson, taken at lower altitudes in the desert (types of subsp. *desertorum*) are large, richly colored, and similar to samples of *O. clarus* from much farther south in Mexico; I do not hesitate to call them conspecific without making further distinction. A transect of collections taken from the Sonoran desert flats up into the mauntains should establish clines connecting the lowland and upland forms. Until this transect is properly established, there will of course remain some doubt as to whether the upland form might be a local species. The subspecies *clarionensis* is based on a worker from Clarion Island, far out in the Pacific of Mexico. This worker proves to be a rather typical specimen of *O. clarus,* as already indicated by Taylor and Wilson (1961) without comment.

So far, we have established that one of the two *Odontomachus* entering the United States is the mainly Mexican species *O. clarus* in Texas, New Mexico and Arizona. The other species is southeastern in the U. S., occurring in Florida, southern Georgia and southern Alabama. It was originally described as *Atta brunnea* by Patton in 1894, and this name has languished in the synonymy of *O. haematodus* for most of the years since then (Emery, 1911). From the description and the type locality (Thomasville, Georgia) there is no doubt about what biological species Patton's name fits; it is an *Odontomachus,* and only one *Odontomachus* occurs in the area. This is a dark brown species with a very deep red, very finely striate head, usually appearing blackish to the naked eye. It is common around hammocks, swamps, and pine, turkey oak and palmetto flats throughout much of Florida and the neighboring counties of Georgia, and it is the form to which the name *Odontomachus haematodus insularis* has been most commonly applied in the U. S. (e. g., Creighton, 1950: 56). It has also been called *O. haematodus* var. *hirsutiusculus* by various authors, and is so labeled in certain European and other collections, but the real *hirsutiusculus* is actually a synonym of the typical *haematodus* [17].

About 1960, I discovered that the Floridian-Georgian form was probably conspecific with what W. M. Wheeler had described in 1905 as *O. haematodes insularis* var. *ruginodis* from Bahaman and Cuban specimens. The name was partly inappropriate, because the U. S. and some other samples lack the transverse striation of the back of the petiolar node that attracted Wheeler's attention in the types. Despite this variation, it then seemed to me that the name *ruginodis* applied to a species found over a vast area ranging from Georgia south through the West Indies, Mexico and South America to Paraguay and Bolivia (although in the Amazon Basin, this species has been confused with *O. haematodus*) [17].

Following this discovery, and before any consideration of the name *brunneus* came into the picture, I discussed my findings with E. O. Wilson and other colleagues, and the combination *Odontomachus ruginodis* was used for the first time in print by Wilson (1964) in his paper on the ants of the Florida Keys. Although several colleagues know about the change, the binomial combination has probably not appeared in print more than 2 or 3 times, and the latest supplement to the Catalog of the Hymenoptera of Noth America (Krombein *et al.,* 1967: 348) still refers to the U. S. form as «*haematoda insularis*». The name «var. *ruginodis*», placed with *O. haematoda* or *O. haematoda insularis,* was used after 1905 a few times by W.

M. Wheeler in lists of species of different West Indian Islands, and once by M. R. Smith (1937) in a list of the ants of Puerto Rico. European workers meanwhile used «*hirsutiuscula*» for this species as found in South America, while to my knowledge, *ruginodis* in any combination was not used for any North American sample before 1964. Thus, the great preponderance of mentions of this species in the literature have employed names that were incorrectly applied to it, and its nomenclature can scarcely be called «stable».

Since *ruginodis* was originally published as a variety of a subspecies in a quadrinomial combination, there is doubt about its availability as a species-group name until its publication as a binomial combination in 1964. To further complicate the problem, the name *O. h.* var. *fuscus* was applied by Stitz to this same species, although the name *fuscus* was already preoccupied twice, once by Stitz himself. Baroni Urbani supplied a replacement name, var. *repetita,* for Stitz' second *fuscus.* Another consideration is the fact that the *ruginodis* types and some other West Indian samples have the transversely striate rear face of the petiolar node, while North American populations lack distinct striation here. Thus, devotees of the trinomen might wish to recognize two subspecies on this basis, at which time the U. S. and some other populations would need a subspecies name or names.

With all of these doubts and complications, it seems to me the best course is to return to a point of relative certainty and adopt the name *brunneus* for the North American populations and, if one accepts my interpretation, for the whole species. This action does not violate the spirit of the new «statute of limitations» rule (replacing the controversial article 23b of the Code) adopted by the 17th International Congress of Zoology at Monaco in 1972 (Bull. Zool. Nomencl. 29: 177; 1972), since in my opinion it will give a stable, legitimate name to a species that has never had one since 1894.

We may capsulize the foregoing discussion in terms of summary synonymy:

O. insularis Guérin (Bahamas, Cuba, Haiti)
= var. *pallens* Wheeler
= var. *wheeleri* Mann
O. clarus Roger (Mexico, S. W. U. S., Clarion I.)
= *haematodus desertorum* Wheeler
= *haematodus coninodis* Wheeler
= *haematodus clarionensis* Wheeler

O. brunneus (Patton) (S. E. U. S. to Bolivia and Paraguay, West Indies)
= *haematodus insularis* of authors, not Guérin
= *haematodus hirsutiusculus* of authors, not F. Smith
= *haematodus insularis* var. *ruginodis* Wheeler
= *haematodus* var. *fuscus* Stitz (preoccupied)
= *haematodus* var. *repetita* Baroni Urbani (nom. pro *fuscus* Stitz)

[11] *O. brunneus* is a variable species, but the samples placed here all have the common characters of modest size, broad head, short mandibles, short antennal scapes (surpassing posterior border of head by no more than length of first funicular segment), very fine cephalic striation (striae in 0.1 mm square in middle of left side of vertex 10-14; in samples from hylean South America, usually 7-9), longitudinal striation of pronotal disc with concentric peripheral striation, transverse striation of mesonotum, and densely pubescent gastric dorsum. The head is most often brownish red in color, lighter than the piceous or brown of the rest of the body, but many exceptions occur; hylean samples are usually uniformly piceous or blackish, with brown or yellowish legs, like the *O. haematodus* that they apparently mimic in this area [17].

Gastric sculpture is typically smooth and shining, with abundant fine, spaced punctures, but again hylean samples are different, being finely reticulate or alutaceous and subopaque in addition to the punctulation and pubescence, apparently in imitation of *O. haematodus*.

The petiole most often is shaped as figs. 25-27, but samples from southern Mexico and the Lesser Antilles often have a shorter, thicker, more dome-shaped node with short apical spine. Finally, in hylean South America, the node is often shaped more as in *O. haematodus* (fig. 20), with an attenuated apical spine. The sculpture of the node varies considerably from place to place, being almost perfectly smooth front and rear in most samples from the continental U. S. (Florida, Georgia, Alabama), but horizontally striate on the sides, across the posterior face, or both (most tropical mainland and West Indian samples); the striation on the sides may be very fine (Minas Gerais, Pará), and the rear face of the node is sometimes merely finely reticulate in South America. The posterior face of the node is usually rather broadly sulcate vertically, and the sides of the sulcus sometimes form raised margins.

In view of the complex of characters found in hylean South America in forest areas where *O. haematodus* is common and probably dominant, the possibility of independent species status has been considered for these populations. However, such status seems contraindicated. In the first place, no «typical» *O. brunneus* have been found in this vast area in forest habitat occupied by *O. haematodus,* and we know of no single locatities where both «typical» and «mimic» forms of *O. brunneus* have been found together. *O. brunneus* occurs from the coastal plain of southeastern U. S., Bermuda, Clipperton Island, the Bahamas, all major and most minor islands of the West Indies (except Trinidad?), Mexico, and Central America, in more or less typical form, and at least enters northern Colombia (Rio Frio, Magdalena, P. J. Darlington leg.). We next find the typical form in southern Mato Grosso, Paraguay and Bolivia. It is difficult to imagine that the species is completely absent from the vast intervening area of Amazonia and the Guyanas. Finally, we have at least some samples with mixtures of «typical» and «mimic» characters from Mato Grosso: Xingu (Alvarenga and Werner) and Barra do Tapirapé (B. Malkin), just where one vould expect to find them. Another intergradient sample is a reddish-brown series with «typical» petiole (fig. 27), but with lightly alutaceous gastric dorsum, from 6 km east of Mariana, Minas Gerais, Brasil, about 1000 m, on steep mountainside at the edge of a *Cecropia* stand in sandy soil, nest under a rock (W. L. Brown).

O. brunneus occurs sympatrically with several other species, most notably *O. bauri,* over much of the West Indies, Panama, Costa Rica, Colombia and the Amazon Basin, and also, significantly, with its sibling species, *O. yucatecus;* we even have a worker of *brunneus* from 10 km east of Campeche, Mexico (E. O. Wilson # 146), which is the type locality for O. *yucatecus* [33].

O. brunneus seems able to co-exist with other forms partly by tolerating the more extreme marginal habitats. Thus, in addition to its northern and southern geographically marginal occurrences in North America, and in the Pantanal of Paraguay, etc., it tends to exist in places within the tropics where other *Odontomachus* species are sparse or absent, e. g., swamp forest, epiphytes on bare or exposed branches of trees in the forest canopy, savanna, palm groves, and the like.

[12] **Odontomachus caelatus** new species

(Fig. 23, Plate 1, A)

Worker, holotype: TL 12.0, HL 3.20, HW (across vertex) 2.24, HW (across ocular prominences) 2.48, ML 1.66, scape L 2.94, eye L 0.47, WL 3.64 mm; CI 70, MI 52, SI 131.

Paratypes (smallest worker of 43, Great Batavia Island, Cuyuni R., Guyana; largest, Dept. Junin, Peru) TL 12.5-14.4, HL 3.24-3.76, HW (across vertex) 2.23-2.73, HW (across ocular prominences) 2.49-2.87, ML 1.70-1.92, scape L 3.04-3.33, eye L 0.48-0.55, WL 3.54-4.22; CI 69-73, MI 51-52, SI 122-136.

Description of worker, composite: A large, robust species, reddish brown to dark brown in color, usually appearing black to the naked eye, with broad vertex and massive mandibles, resembling in a general way the large workers of *O. bauri*, *O. laticeps* and *O. biumbonatus*, and like them with palpi segmented 4,3. Diagnostic characters are mainly those of sculpture, pilosity-pubescence, and form of mesonotum and petiolar node.

(1) Dorsum of head and body very regularly and moderately finely striate (about 7 striae per 0.1 mm sample square on middle of left half of vertex), the striation extending far down the sides of the head, into the extraocular furrows and laterad of the eyes, and covering most of the temples. The furrows of the striation are microsculptured at the bottom, and their intervening ridges are only moderately shining, so that the general surface is moderately shining. Pronotal striation prevailingly longitudinal, becoming curved and generally trending concentrically around the edges of the disc. *Mesonotum longitudinally striate in the middle*, at least anteriorly; longitudinal-arched, or even steeply arched on the sides, so that the posterior mesonotal striae are obliquely diverging caudad, or in some cases, even transverse. Metanotal striation variable; longitudinal, oblique or transverse. Anterior tip of propodeum longitudinally, or else transversely striate like the rest of the propodeal dorsum. Petiolar node finely horizontally or obliquely striate around the front and sides on the lower 2/3 or so, the striation becoming indistinct and erratic higher up; apical spine nearly or quite smooth. Disc of first gastric segment evenly longitudinally striate, the furrows more or less distinctly septate or punctate, the striation becoming more broken and opaque on the sides of the tergum. Second segment also longitudinally striate, the furrows here more distinctly punctate. Third and fourth terga variably striate, fifth tergum nearly smooth, shining, with fine reticulate-striate or alutaceous sculpture on the sides.

Mesepisternum usually completely striate, though the middle posterior part tends to have the striation weaker and more shining.

(2) Pilosity and pubescence reduced, except for a median pair of coarse suberect hairs at the usual position in the middle of the cranial dorsum, a few (1-9) coarse curved hairs on the pronotal disc, 0-4 on mesonotum, and *30-50 thick but pointed hairs, mostly 0.4-0.6 mm long*, on dorsal surface of gaster; others 0.3-0.4 mm long on ventral surface. A few very fine, short hairs exist on the clypeus. Pubescence obsolescent, appressed to subappressed, detectable only in certain lights on the gastric dorsum, where on the first tergum the individual tiny hairs are spaced apart at an average distance about the same as, or more than, their average length (Plate 1, B); usually a little more abundant and closer together on the second tergum, but here still dilute. Appressed, fine, sparse pubescence on femoral apices, and becoming somewhat denser on tibiae, tarsi and antennae; abseut or extremely inconspicuous on head, trunk and petiolar node.

(3) Mesonotum more strongly convex than usual in the genus, especially anteriad, but also more or less distinctly longitudinally sulcate in the middle.

(4) Transverse ridge between metasternal coxae at most forming a pair of low, blunt lobes with a hollow between.

(5) Petiole distinctive in form (fig. 23); above the short, weakly convex basal part, a long sloping section of the side-view profile of the node is nearly straight; profile of posterior face gently convex just above mid-height; apical spine slender, laterally compressed, usually slightly to distinctly back-tilted from the main axis of the node. Rear face of node weakly impressed near the middle.

(6) Color reddish brown (possibly faded) to blackish brown; appendages, especially antennal funiculi, sometimes a bit lighter and more reddish than rest of body. Bluish opalescence sometimes present on mandibles, antennal fossae, sides of head, etc., but less marked than in some other species.

Queen unknown.

Male (a single example from the holotype nest series): TL 8.4, HL 1.24, HW (including eyes) 1.60, eye L 0.75, WL 3.48, forewing L 5.8 mm. Color dark brown; head and trunk almost black.

Mandibles about 0.22 mm long (insertion to apex); apices irregularly rounded; a diagonal carina runs from the outer margin near base to mesal margin near apex; mesal to this carina, nearly the basal half of the dorsal surface is whitish in color, concave, and probably semimembranous; this area may represent a holding and evaporating basin of mandibular gland pheromones. Maxillary palpi 5-merous, the apical segment very long and slender, and apparently consisting of 2 segments fused; labial palpi each 3-merous. Clypeus strongly convex.

Mesonotum finely longitudinally striate, subopaque; notauli (true parapsidal sutures) obsolete; scutum with a strong median longitudinal seam, carinate in front and groove-like behind; scutellum convex, with a median sulcus. Metanotum narrow, transversely striate, with a strong, raised, sharply rounded median carina. Propodeum with indistinct striation in front, diverging in a broad V behind, becoming transverse on the declivitous area. Petiole and gastric dorsum finely roughened, only feebly shining.

Erect hairs delicate, sparse, chiefly on mandibles, mesonotum and gaster. Body and appendages generally with a rather dense, short, brown appressed to suberect pubescence.

Distinguished from the males of *O. haematodus* and *O. bauri* by its larger size and uniformly dark color.

Holotype worker (MZSP) and accompanying workers and a male from the same nest are from the Reserva Ducke, Municipio of Manaus,

Plate 1. Scanning electron micrographs showing details of sculpture, pilosity and pubescence in workers of neotropical *Odontomachus*. A, *O. caelatus* paratype from Limoncocha, Ecuador, disc of first gastric tergum X 54. B, *O. biumbonatus* paratype from Limoncocha, Ecuador, disc of first gastric tergum X 54. C, *O. haematodus*, center of disc of first gastric tergum X 108. D, *O. minutus* from Piraçununga, S. Paulo, Brasil, center of disc of first gastric tergum X 108. E, *O. bauri*, side view of petiole and adjacent structures of a large specimen from Panama X 42.

Amazonas State, Brasil, W. L. and D. E. Brown, No. V-6, 9 June 1972, in rotten wood in rain forest.

Paratypes (43 workers) are from widely separated localities in the Amazon-Guyana basins, all in rain forest: BRASIL: Terr. Amapá: Serra do Navio (K. Lenko). Amazonas: Igarapé Marianil, on Rio Branco (Caracaraí) Road, 20-24 km NE of Manaus (W. L. Brown, 22 Aug 1962, No. M-7). Pará: Pirelli Rubber Plantation, Iriboca (P. F. Darlington, 21 Aug 1962, No. B-279. Near mouth of R. Curuá, 30 April 1963 (F. G. Werner). PERU: Dept. Loreto, W. F. Walsh, Jr., Aug. 1939. ECUADOR: Prov. Napo, Limoncocha (P. L. Kazan). GUYANA: Great Batavia Island, Cuyuni River (W. M. Wheeler, 4 Aug. 1920, Nos. 371, 374). Kartabo (Wheeler, 16 July 1920, No. 701).. Dunoon (F. M. Gaige, 12 Aug. 1914, No. 340).

Paratypes deposited in MZSP, MCZ, CU, and WWK. All of the collections from Brasil, Ecuador, and Guyana are known to have been collected in the forest, and probably this species always lives in the wet forest. Nests collected by me were taken in rotten wood or under leaves in the soil at the base of a large tree.

The worker of this species is distinguished above all by its large size and the clear longitudinal striation of the gastric dorsum and part or all of the mesonotum. The swollen, sulcate mesonotum and the petiolar form are also distinctive. Probably it ranges widely in the Amazon Basin and the Guyanan forests.

[13] *Odontomachus coquereli* is a slender, reddish brown, primitive species, aberrant in its own right, in general habitus and shape of petiole most similar to the neotropical *O. hastatus* (fig. 16), and also related to the *tyrannicus* and *saevissimus* groups. The head is remarkable for its vertex with weak median furrow, and lack of extraocular furrows and temporal ridges. Even the antennal fossae are obsolete near the midline of the head. The teeth of the apical trio are all acute, and the preapical series is strongly developed, with the 3 teeth nearest the apex long and acute, but diminishing in size basad. The coarsely transversely rugose-striate surface of the vertex is also distinctive. This species has every appearance of being a long-isolated relict of an ancient world fauna of *Odontomachus*.

The variety *minor*, later raised to subspecies rank by Emery (1911: 111), seems only to be a smaller-sized variant of *O. coquereli;* the distinguishing characters mentioned are especially variable in this genus. The structure of the back of the head is typical of *Odontomachus*, and there is no good reason to continue separation of *Champsomyrmex* as a monotypic genus.

The records of the species so far all come from the northeastern quarter of Madagascar. For a bibliography and records, see Weeler 1922: 1013.

[14] *O. cornutus,* the most aberrant of all *Odontomachus* species, was briefly but reasonably well described by Stitz, who also gave a small and rather diagrammatic drawing of head and mandibles, without antennae. This is all we know of the species, because the unique type was destroyed with the collections of the Hamburg Museum during the fire bombings of World War II.

Stitz' drawing shows a rather broad head (CI near 67), vertex with almost parallel sides, slightly constricted near midlength, just at the extraocular forrow. The ocular prominences are each produced obliquely forward and outward as a stout, acute tooth (ocular prominences bluntly rounded in all other known Odontomachiti). Although the size is very large (TL about 16.5 mm, HL about 4.3 mm, based on Stitz' measurements as extrapolated to his drawing), the eyes are relatively small — EL somewhere near 0.36 mm as judged from the drawing. As drawn, the mandibles seem too slender and weak for such a large species; MI is estimated at about 51 or 52.

The integument is described as «brown» in color, and «strongly shining. Head surface smooth, with seta-bearing punctures...» The frontal area bears fanlike striation. The disc of the pronotum is transversely striate, its sides with striation curved so that they appear longitudinally striate, as does the posteromedian border of the pronotum also. Mesonotum and propodeum strongly transversely striate. Petiolar node smooth and shining front and rear, except for setal punctures. «All parts of the body except the upper mandibular surfaces with scattered, generally long, yellowish brown hairs, longest in the upper surface of the head, underside of mandibles, and on the gaster».

Stitz cited Bucay, Ecuador as the locality of collection. This locality is east of Guayaquil at the western base of the Andes in Guayas Province. In 1973 I spent most of one day searching a forest ravine near Bucay, and found there the type of *O. mormo* n. sp., described herein [24], but failed to collect *O. cornutus.* Another day in forest patches above Cochancay, farther south along the Andes in Cañar Province, also failed to turn up *O. cornutus,* so at this time, no known specimens of the species exist in collections. Of course, we know nothing of its biology, and until more specimens are secured we shall not even be sure what species group it belongs to.

[15] *O. erythrocephalus* (fig. 2) is a lowland forest species ranging, so far as known, from NE Costa Rica to NW Ecuador

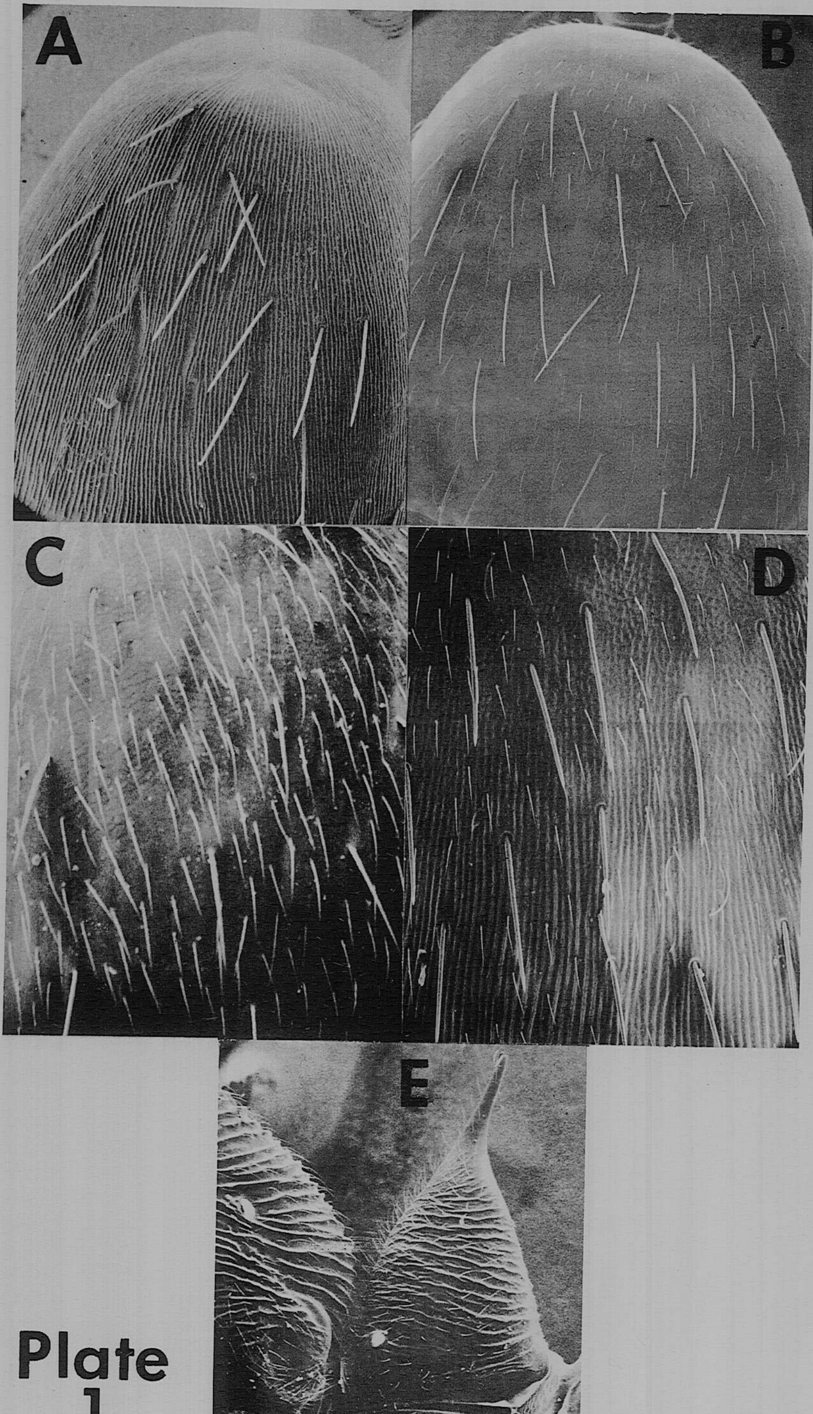

Plate 1

on the western side of the Andes. It seems to be a more diurnal-foraging species than other *Odontomachus* within its range. I have found 2 nests under rotting logs on Barro Colorado Island in the Panama Canal Zone. At Anchicayá, Dept. Valle, Colombia, I found a dealate queen foraging on an overgrown roadside bank on a wet and misty day at noon.

The usually bright reddish head (often infuscate in the mid-frontal region) in contrast with the blackish body and yellow legs, is diagnostic for this species. This color combination, probably aposematic, is seen also in the Old World in such unrelated forms as *O. assiniensis* (typical West Arican variant) and *O. floresensis* n. sp. from Indonesia.

A male taken from «log debris and thatch» with workers and alate queens from near El Valle, Cocle Prov., Panama (H. S. Dybas) has HW (including eyes) 1.33, WL 3.02 mm, with robust trunk; petiolar node acute at apex. Color: trunk dark brown; scutum with an obscure fuscous pattern; posterior half of trunk piceous, approaching black, as is also the petiolar node. Vertex dark brown, face yellowish brown; antennae, legs and gaster castaneous. Mandibles with irregularly acute apices, each with the usual strong apical seta. Palpi segmented 4,3, though on one side, the long apical segment shows a sharp constriction near midlength.

[16] **Odontomachus floresensis** new species

Worker, holotype: TL 12.7, HL 3.00, HW (across vertex) 1.90, HW (across ocular prominences) 2.25, ML 1.56, scape L 2.84, eye L 0.50, WL 3.96 mm; CI 63, MI 52, SI 149.

Paratypes, 12 workers from type locality (Nangagete) and 3 from Wodeng, Flores; only 3 were measured in detail, including the largest and smallest specimens, and the metrics are given combined with those of the holotype in Table II.

Description of worker, composite: A relatively broad-headed member of the *infandus* group with cephalic dorsum and pronotum distinctly striate completely or nearly completely; head and mandibles deep red; trunk, petiole and gaster piceous to black (pronotum and gastric apex more or less suffused with reddish); legs and antennal funiculi yellow; antennal scapes castaneous. Petiolar node with a very short, inconspicuous peduncle; rising from this, the anterior face of the node is gently convex in outline for a variable distance, and above that, weakly concave to the root of the spine, and sometimes all the way to the tip of the spine. The spine itself is back-tilted, long and very slender, taking up about 1/3 the height of the node as measured from the lateral suture of the petiole, and is straight or gently curved caudad. Posterior face of node steeply sloping, side-view outline sinuate, concave at root of spine, convex at upper part of node, and feebly concave beneath the convexity. The convex upper face is obscurely sulcate on the midline. Similarly shaped nodes are seen in occasional specimens of *O. papuanus*, but in *papuanus* and *infandus*, the concavity of the upper anterior face of the node is usually much more profound. In *O. floresensis*, the spine is more abruptly narrowed at its base than in related forms, except *sumbensis;* in *sumbensis*, the node is thicker anteroposteriorly, and the spine is shorter than in *floresensis*. In view of the great variability of nodal shape in the *infandus* group, the value of these characteres is debatable.

The striation of the head in *O. floresensis* is moderately coarse (about 5 striae in a square of 0.1 mm in the middle of the left side dorsal surface of the vertex) and extends back to a narrow smooth strip just before the nuchal carina, and down the sides of the head to a level below the eyes; also the cheeks are striate between eye and mandibular insertion. Some specimens, including the holotype, show a tendency to have the striation effaced in a narrow strip along each side of the median furrow on the upper vertex, and the surface here may be nearly or quite smooth, with a few scattered punctures.

Pronotal striation fine, transverse, often forming a flattened transverse whorl on the front part of the disc. Mesonotum low, its anterior edge not so sharply projecting above pronotal posterior margin as in *O. sumbensis*, and the mesonotal surface more convex from front to rear. Metanotum usually not markedly impressed, often convex, though separated from the propodeum by a distinct suture. Propodeal dorsum distinctly but very shallowly concave near midlength. Mesonotum and metanotum finely, propodeum more coarsely, transversely striate. Coxae, node and gaster smooth and shining. Legs shining, but minutely and densely punctulate and finely pubescent. Mandibles minutely roughened and punctate above, subopaque. Antennal scapes minutely and densely punctulate, pubescent, only weakly shining. Mesopleura finely vertically striate anteriorly and near upper margin; smooth with blue opalescent reflections and scattered punctures over posteromedian part. Pubescence on head, mandibles and gaster appressed, very sparse and fine, visible only in certain lights; better developed (but still not conspicuous) and decumbent on underside of head, on trunk and front and sides of petiolar node. Erect hairs on body very sparse: the usual middorsal cranial pair; 2-3 pairs of short hairs on the underside of the head near the mouth, plus the usual coarse sense hairs on the mandibles; usually 1-6 long, curved erect hairs on pronotal disc; zero to a few fine hairs on anterior coxal surfaces; zero to 3-4 fine erect hairs on posterior of first gastric tergum, and scattered, long fine hairs on underside and apical segments of gaster and on undersides of coxae, bases of femora, etc.

The first gastric tergum is strongly convex in both directions, not at all flattened, and the second tergum has the usual shallow transverse impression. Labial palpi 4-merous, but rather short and stout. Antennal scapes surpassing posterior border of head by more than the length of the pedicel (funicular segment I); proportions of funicular segments as described for *O. sumbensis*.

Holotype (MCZ) and 12 paratypes (MCZ, BMNH-London, and elsewhere) from Nangagete, about 60 km east of Maumere on the north coast of Flores Island, Indonesia, July 1972 (W. L. Brown), and 3 workers from Wodeng, about 31 km east of Maumere, also near the north coast of Flores, on another day in July 1972 (Brown). Both localities are in the lowlands along the main road along the north shore of Flores. At Nangagete, the ants were taken foraging near midday in scrubby second growth forest, and nesting under a log in the shade. At Wodeng, the ants were foraging by day on the floor of a shady remnant of tropical evergreen forest growing on a hillside seepage area. In life, the red head and yellow legs are bright and contrast with the blackish color of the rest of the body; the pattern is probably aposematic. The color pattern is the best means of distinguishing *O. animosus*, a similar form of the *infandus* group. *O. sumbensis* is similar, but has the vertex and pronotal disc smooth, and the petiolar node and spine lower. As stated elsewhere, all of these forms could possibly be geographical representatives of *animosus* or another species in the *infandus* group, but I am following the hypothesis that the insular forms, at least, are member species of a superspecies.

[17] The *Odontomachus* of the *haematodus* group are found primarily in the New World tropics, where they are represented by a number of species so closely related, and at the same time so variable, that they have defied analysis for more than a century. Mostly, these species have been considered to belong to a single protean species, *O. haematodus*, with or without distinction as subspecies or varieties. Applying the modern biological species concept, I found it fairly easy ten to twenty years ago to distinguish a number of the forms as good species. Furthermore, the identity of the Linnean species *O. haematodus* was established from the color details, «pedes flavi... Corpus nigrum» and the circumstances of collection (by Linnaeus' studant Rolander during his brief sojourn in Paramaribo) explicit and implicit in the original description. This species proved to be the most commonly collected wet tropical forest species in Brasil and neighboring cisandean countries south of the Llanos. But serious problems remained. Another large, dark-colored, coarsely striate species was found to occur in Central America, transandean South America, and sporadically throughout forested parts of Brasil, here often sympatrically with *O. haematodus*. This species corresponds to the types of Emery's *O. bauri* from the Galapagos, and Forel's *O. haematodus* var. *rugisquama* from Costa Rica. Unfortunately, a few samples that appeared to be intergradient between the «typical» *haematodus* and *bauri* were found in southeastern Venezuela, near the boundary between the Llanos and the Guyanan forest, as well as farther north in Venezuela, and some apparent intergrades even turned up within the Amazonian forests in northern Brasil and elsewhere.

Samples from Trinidad, the Lesser Antilles, Puerto Rico and Hispaniola also were found to be intermediate between *haematodus* and *bauri* in sculpture and color. I was unable to explain this situation to myself without assuming widespread hybridization at some sympatric localities, but not at others, and this interpretation did not satisfy me. Pressure of other problems forced me to set this one aside for deeper study at a later date.

A solution to the main problem here came in stages from an unexpected quarter. Prof. Carl W. Rettenmeyer and his student at the time, Peter L. Kazan, were studying the biology of *Eciton rapax* at Limoncocha in Amazonian Ecuador during the late 1960's and early 1970's. This army ant gains a significant amount of its prey by raiding the nests of ponerine ants, among them various species of *Odontomachus*. Thus Limoncocha collections came to contain an array of sympatrically-occurring *Odontomachus* species in good sample sizes. The sorting of these forms was done by Kazan and by Ms. Lois Morales, then Dr. Rettenmeyer's technical assistant, and samples were eventually submitted to me for determination. I recognized among them all of the forms I had accumulated from Amazonia during my own travels there, and from other collections, and these included not only such species as *haematodus, bauri, minutus, caelatus* n. sp., and *biumbonatus* n. sp., but also some small-sized forms similar in some ways to *haematodus,* but with important features of *O. brunneus.* Although these large sympatric samples helped to clear up the situation, it remained for Lois Morales' discovery of a key character to fix the species limits of *O. haematodus* against similar species. She found that one population at Limoncocha consistently combined typically *haematodus* characters (medium-sized slender body, long antennal scapes, yellow legs, particular form of petiole — as in fig. 20 — and shagreened, pubescent gastric dorsum) with the development of paired, slender, acute sternal spines from the transverse ridge just in front of the metathoracic coxae. This character is readily seen (in clean specimens already point-mounted) upon the removal of one of the hind legs with its coxa, and can often be viewed in unencumbered intact specimens from obliquely in front, or even from behind. The sternal spines are attenuated and lie very closely together, and are often unequal in length (fig. 7). Examination of numerous samples from tropical America and elsewhere in the world show that *haematodus* has the longest, most acute metasternal teeth; these are not quite as long in samples from Argentina (Raco, Tucumán) as those from farther north, but the difference between these and other neotropical species is still distinct. Among the species related to *O. haematodus,* only the species here identified as *O. troglodytes,* from sub-Saharan Africa, has metasternal spines about as long as those of *haematodus* itself [32].

Other species of the *haematodus* complex in the New World have the metasternal ridge merely convexly raised (fig. 5), or, in species such as *O. bauri,* bicuspid with a notch in the middle (fig. 6); the cusps becoming more than low, blunt projections only in some *O. yucatecus* [33].

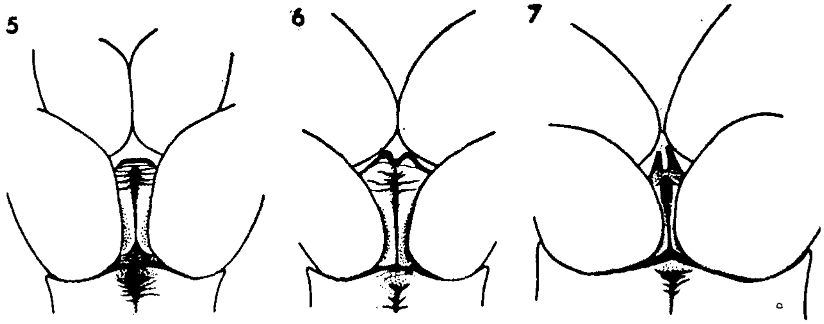

Fig. 5, *O. brunneus.* Fig. 6, *O. bauri.* Fig. 7, *O. haematodus.* Workers, all from Limoncocha, Napo, Ecuador, ventral aspect of posterior trunk viewed from underneath and looking rearward, with last two pairs of coxae, to show form of "metasternal" process.

The discovery of the metasternal character enabled us to re-evaluate the supposed intergrades between *O. haematodus* and *O. bauri.* It turned out that a few of these intergrades were only *O. haematodus* with legs darker (more brownish) than usual. But the rest lacked the slender, produced metasternal teeth, and these last samples also proved to differ from *O. haematodus* in other ways.

Analysis of this «intermediate» residue revealed that it consisted of 2 different species: first, a larger one resembling *bauri,* but with a tendency to have much finer sculpture, particularly on the petiolar node. Some variants of this species also showed various grades of finely reticulate sculpture on the gastric dorusum. In fact, this larger form intergrades completely with «more typical» *bauri,* and I have assigned it to *bauri,* thus considering it to represent only a part of the considerable variation of that species, which will be discussed separately [7].

The second species hiding in the «intermediate» residue was a smaller one with short scapes, fine cephalic sculpture, and a rather narrow petiolar node as seen from the side. In the Limoncocha samples, Kazan and Morales had already distinguished this species, and I had tentatively recognized it as a variant of what I now call *brunneus*. With the metasternal character as a discriminant key, it soon became clear that the smaller «intermediate» component was in fact the hylean population of *O. brunneus*, which over most of the range of *O. haematodus* tended to converge toward the latter in a probable Müllerian mimicry relationship.

Thus was explained another puzzle: the apparent absence of *O. brunneus* from a vast area of territory between Panama in the north and Mato Grosso (where it had long been known) in the south. In 1960, I had found *O. brunneus* nesting only in exposed situations on the upper forest canopy on Barro Colorado Island in the Canal Zone, and had wondered if *O. brunneus* might not be leap-frogging competing *Odontomachus* species in the Hylea by existing there only in this and other marginal habitats. There might still be some reality corresponding to this speculation, but at least we now know that *brunneus* occurs widely over most of South America; some records based on specimens I have examined are listed under that species [11].

In summary, *O. haematodus* is a distinct species occurring only in continental South America in the cis-Andean tropical forests. *O. bauri* and *O. brunneus* are much more wide-ranging and variable species that blanket the range of *O. haematodus*, and may tend to mimic it to some extent in sympatry. *O. haematodus* can be distinguished by its acutely produced, paired metasternal teeth, supplemented by metric characters (see Table I), as well as those of color, sculpture, pilosity and pubescence.

Because of the long-prevailing confusion in the taxonomy of the *haematodus* complex, locality records taken uncritically from publications or museum labels are not to be trusted. I have personally confirmed about 90 separate collections of *O. haematodus* from about 70 localities. Except for 3 specimens in MCZ labeled «Lima, Peru, Soukup Coll.», which I regard as a probable locality error, all localities are in continental South America east of the Andean Divide and south of the Llanos. *O. haematodus* is a forest ant that prefers low elevations. It is widespread and common in the rain forest of the Guyana region, and reaches the Orinoco Delta (N. A. Weber leg.). Throughout the Amazonian forests it is the most frequently collected *Odontomachus* species. In the northwestern part of this region, its limits are unknown, but it is common in eastern Ecuador at Limoncocha (H. Hermann, P. Kazan leg.), in the neighborhood of Benjamin Constant, Brasil, and Leticia, Colombia (W. L. Brown leg.), and I suppose that it reaches the northeastern Amazonian forest limits in east central Colombia. It is rare or absent in the higher and drier parts of central Brasil, but is common again in the forests of lowland southeastern Brasil, extending south along the coast at least to São Paulo state at Caraguatatuba (K. Lenko, W. L. Brown leg.), and possibly farther; on the wet uplands of São Paulo behind the coast, *O. affinis* replaces *O. haematodus.* Records from Misiones and Corrientes provinces in northern Argentina may apply to this or another species, but *O. haematodus* samples are available from Raco, near Tucumán in NW Argentina (N. Kusnezov). A specimen labeled «Yungas, Bolivia» is in MCZ; *haematodus* reaches into the eastern foothills of the Andes at Tingo Maria (W. L. Brown), Satipo, Dept. Junin (W. F. Walsh), and elsewhere in Peru. Two workers labeled «Paltaybamba, 5000 ft.», (Yale Peruvian Expedition, 1911) are in MCZ.

[18] After Wilson's (1959) revision and the present treatment of the *saevissimus* group, we are left with *rufithorax (= emeryi, = gressitti),* which is discussed separately [28], and the 4 species *montanus, opaculus, saevissimus* and *imperator,* which are all color-sculptural variants of the same basic body plan. Except for *saevissimus,* for which I have fairly good representation ranging locally through New Guinea, New Britain and New Ireland, as well as Ceram and Amboina in the Moluccas and Guadalcanal Island: Gold Ridge (E. S. Brown), Sutakiki R., 2000 ft (P. Greenslade), these forms are all known from only one or two collections each on the New Guinea mainland.

Interestingly, *O. rufithorax,* which also seems to be very local on the New Guinea mainland, has been collected widely in the Solomon Islands (Isabel, Florida, Bougainville), but not on Guadalcanal, so far as I know, by Brown, Greenslade or other accomplished collectors who have resided on the island. This pattern of mutual exclusion on individual islands of the Solomons group, if it is found to hold after further study, would be good additional evidence that *rufithorax* and *saevissimus* are acting as biological species.

The two dark brown or blackish forms *imperator* and *opaculus* could well be sculptural variants of one species, and *montanus* could likewise be a more extensively striate *saevissimus.* If color varies much, synonymy could well cross the line between *saevissimus* and *imperator.* Without more material of this complex

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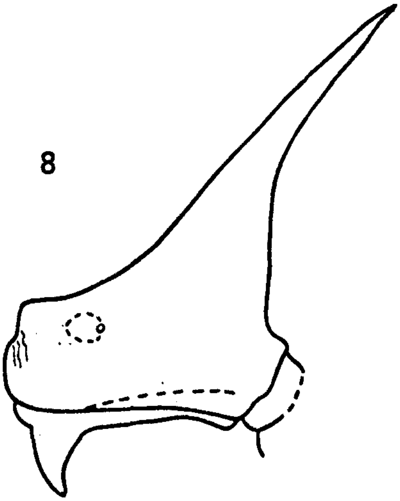

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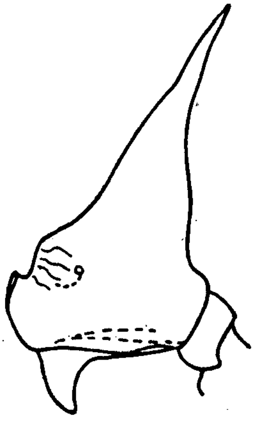

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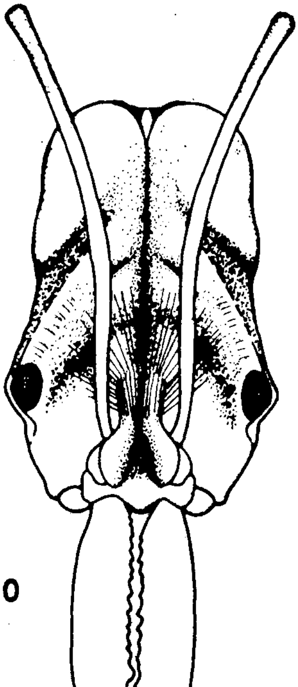

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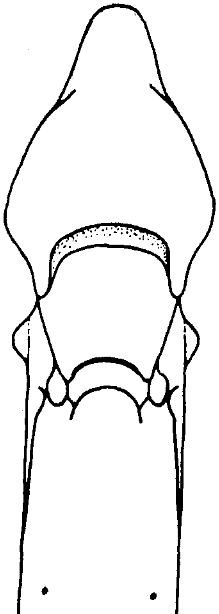

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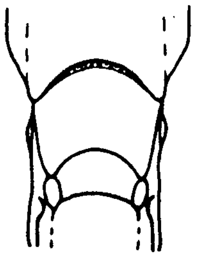


Fig. 8, *O. imperator*, and Fig. 9, *O. papuanus*. Side views of petioles and adjacent structures of syntype workers in MCSN-Genoa, after Wilson, 1959. Fig. 10, *O. mormo*, head of holotype worker in fullface view, pilosity omitted. Fig. 11, *O. mayi* worker from 61 km. N Manaus, Amazonas, dorsal view of trunk to show metapleural lobes. Fig. 12, *O. panamensis*, worker from type series, Bugaba, Panama, dorsal view of middle part of trunk to show reduced metapleural lobes.

from the mainland of New Guinea, there is not much more to be said about these 4 species except that their limits and variation remain unclear.

[19] *O. laticeps* is a most interesting species inhabiting Central America and Mexico, where it is found mostly in forested areas. Records assigned to it from South America actually belong for the most part to the new species *O. biumbonatus* [8].

O. laticeps comes in two extreme forms, one of which has head, trunk, petiole and appendages dull, light red in color, while the gaster is usually brownish or blackish, with strong bluish reflections, and the first two gastric terga are completely, distinctly, finely and opaquely longitudinally striate over their discal surfaces; this form corresponds to the type of *O. striativentris*. Most such samples come from the lowland forests on the Atlantic side of Costa Rica. The other extreme is a form with dark reddish brown to piceous forebody and black gaster, the first two terga smooth and shining discad, with scattered fine punctures. This form ranges from upland Costa Rica (and doubtless the mountains of Panama) north in tropical Mexico to southern Tamaulipas; Roger's type of «var. *latidens*» (of *haematodus*), from Cordoba, Veracruz, can be assigned here with confidence.

The two extreme forms are connected by a series of samples from localities spread from Panama to southern Mexico, showing different combinations and degrees of development of the color and sculptural characters. Here are a few examples:

Barro Colorado Island, Panama Canal Zone (R. W. and W. Taylor); a series of workers found foraging in one restricted area in the forest has the gastric dorsum smooth and shining, but with diffuse fine longitudinal striation on posterior half of first tergum. In color, this sample is dark brown, with dark reddish brown trunk, black gaster and light castaneous legs.

Costa Rica, Osa Peninsula: 5 km west of Rincon de Osa, 50 m (J. Wagner and J. Kethley), a very dark worker, almost black, with dark brown legs, first 2 gastric terga finely but distinctly striate throughout.

Central Meseta of Costa Rica: San José, Cartago, and Agua Caliente (W. M. Wheeler): these samples, while predominantly of the dark, smooth extreme, contain scattered workers having faint, fine striation in the middle of the first tergum, mostly near its posterior border. The elevation of the Meseta is over 1000 m.

Eastern Mexico: Tamaulipas, Gomez Farias (400-600 m) vicinity, and Rancho del Cielo (1070 m), tall cloud forest (W. L. Brown); Veracruz, various localities (E. O. Wilson, W. L. Brown); dark smooth form; occasional specimens in several samples are like the upland Costa Rican examples, dark in color and with faint traces of longitudinal striation at the rear of the first tergum. A dealate queen from 3 km south of Huatusco, near the road to Fortin de las Flores (Brown) is nearly black, but has most of the disc of tergum I patchily covered with fine longitudinal striation, though it is still rather strongly shining.

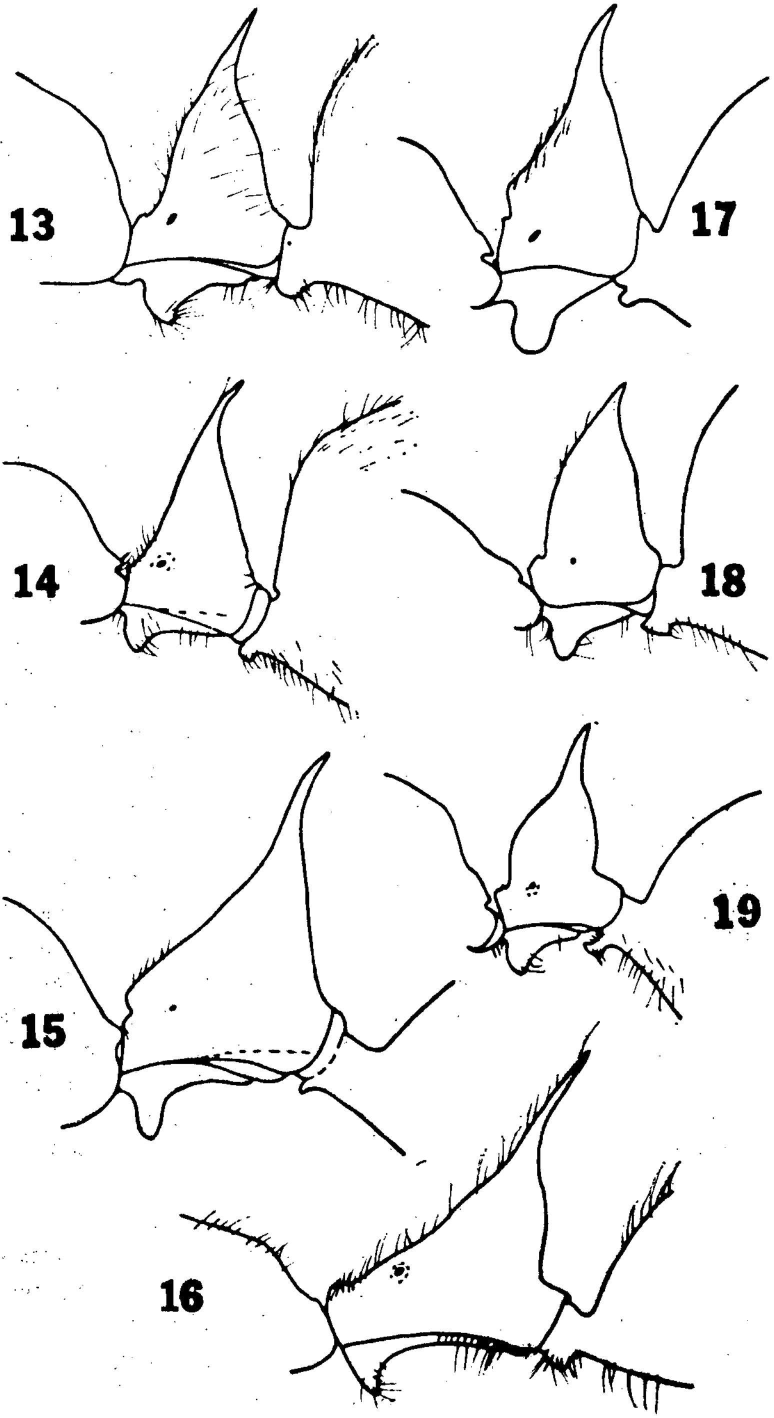
Western and southern Mexico: Guerrero, Highway 95, about 55 miles north of Acapulco (W. H. Gotwald), in pine woods, one worker, reddish brown with slightly infuscate gastric dorsum, first 2 terga finely and densely longitudinally striate discad, sericeous-opaque, nearly as strongly as in Costa Rican lowland samples.

A specimen from Pueblo Nuevo, near Tezonapa, Veracruz (E. O. Wilson) is of the dark form with smooth tergum I, and a worker from 10 km east of the city of Campeche (E. O. Wilson) is dark and smooth, with only faint posterior traces of striation on tergum I. These last two localities are also those for part of the type series of *O. yucatecus* n. sp. [33].

Guatemala: Los Amates (Kellerman), a dark worker with very faint traces of striation on the rear of tergum I. Mocá (W. M. Wheeler), 6 rather dark workers with densely striate tergum I, but in one of these, the striation is effaced and the surface smooth and shining on the anterior half of the first tergum. Retalhuleu (Stoll), 3 dark brown workers with tergum I striate over posterior half to 2/3 of disc, but the striae only moderately strong, and the surface more or less shining. Cave 4 miles south of Flores (D. McKenzie), 4 workers, dark reddish-brown with dark brown gaster, distinctly striate and sericeous opaque over first 2 tergal discs. Trece Aguas, Alta Verapaz (E. A. Schwarz) 2 workers, dark reddish brown, gaster black, first 2 terga distinctly striate over whole discs.

San Salvador: 2-4 km south of Quezaltepeque on north slope of Volcan S. Salvador, shady ravine in coffee plantation (W. L. Brown), 4 workers of the dark, smooth form, feeble traces of striation on posterior part of first tergum.

Belize: Augustine Mt., Pine Ridge (C. C. Porter), 1 dark reddish brown worker with dark brown gaster, first tergum shining but with feeble longitudinal striation in middle and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posterior parts, passing marginally iinto fine shagreening anteriad; tergum II shagreened.

The above samples taken together seem to indicate that we are dealing with a single variable species that tends to have a dark form with smooth gastric dorsum in upland situations, and a light reddish to dark form with striate gaster in wet lowlands, though exceptions occur in both directions.

[20] The common Chinese species of *Odontomachus* is *O. monticola,* though W. M. Wheeler consistently called it «*O. haematoda*» in his papers on the ants of China. *O. monticola* occurs throughout eastern China, reaching to well beyond Peking on the North China Plain. In the West, in Szechuan, I collected it in farm compounds in the rice fields at Hsuang Liu, near Chengtu, and even above 1000 m in the mountains (Chao Kung Shan) of the Tibetan Scarp just west of Kuan Hsien. I did not find it in southern Shensi, despite extensive collecting around Han Chung, Pao Ch'eng and Sian. It has been taken on Hainan Island («var. *hainanensis*»), Taiwan («var. *formosae*») and Okinawa («*kuroiwae*»); and variants *longi* and *punctulatus* have been described from Assam. The type locality of *monticola* is «Indo China», but in addition to the syntypes, I have seen only 2 workers from Lo Choh Tong in that country. *O. monticola* does not seem to penetrate farther south into the tropical parts of southeastern Asia, where the similar species *O. rixosus* and *O. latidens* apparently replace it.

The most conspicuous variation within *O. monticola* involves the sculpture of the posterior third or more of the head, the vertex («occiput» in most literature), which in full-sized Chinese workers — those above about 2.50 mm head length (HL) — is largely or entirely distinctly striate on its dorsal surface. The pronotal disc is also distinctly transversely striate in most Chinese specimens. But the type of subspecies *pauperculus,* a small worker (HL 2.14 mm) from Mokanshan, Chekiang, has the vertex and pronotal disc smooth and shining. A very similar specimen was taken by me at Chao Kung Shan, in the mountains west of Kuan Hsien, Szechuan Province (HL 2.21 mm). At

Figs. 13-19, workers of *Odontomachus* species, petiole and adjacent structures in side view. Fig. 13, *O. opaciventris* from the Rio Toro Amarillo, near Guapiles, Limon Prov., Costa Rica. Fig. 14, *O. laticeps* from lowland rain forest at La Selva Field Station, Heredia Prov., Costa Rica. Fig. 15, *O. mormo,* holotype. Fig. 16, *O. hastatus* from the Rio Toro Amarillo, Limon Prov., Costa Rica. Fig. 17, *O. latidens* from Mt. Dulit, N Borneo. Fig. 18, *O. monticola* from Chao Kung Shan, near Kuan Hsien, Szech'uan, China. Fig. 19, *O. monticola* from Wo Fu Ssu, near Peking, China.

both Mokanshan and Chao Kung Shan, *O. monticola* is a common ant, and it seems unlikely to me that *pauperculus* can represent a distinct sympatric species. Rather, it appears to be only the nanitic worker of *monticola,* in this case one that shows an allometric decline of the striate sculpture. This hypothesis is supported by the HW/HL plot, on which *O. monticola* and *O. pauperculus* share a common regression axis.

In the hills of Assam and Burma and in the Ryukyus, the tendency for striation of vertex and pronotum to be effaced affects not only the small-sized workers, though many of these are smaller than most in China, but also those of workers with HL in the neighborhood of 2.50 or greater. Workers from 3 separate Okinawan collections (F. G. Werner, C. T. Parsons) with HL 2.14-2.57 mm have vertex smooth and pronotum nearly so. The type of var. *longi* (Assam) is on the small side, and has both vertex and pronotal striation largely effaced, whereas subsp. *punctulatus,* also from Assam, is larger and has the vertex smooth but the pronotum striate, like the Indo-Chinese specimens, including the *monticola* types. Forel's statement about the more distinct division of the «occiput» and the deeper median furrow thereof in *punctulatus* is difficult for me to appreciate when comparison is made using *monticola* syntypes in his collection; this and the puncture character he cites are trifling at best. Menozzi's *O. latidens striata,* judging from the description, is just the common Chinese mainland form of *monticola,* resembling other specimens in MCZ from Hong Kong, its type locality. Syntypes of the varieties *formosae* and *major* in the Forel Collection and MNK-Berlin are only smaller and larger variants, respectively, of the Taiwanese population of *O. monticola.* The variety *hainanensis* (MNK-Berlin) is like the mainland *monticola.*

The tendency of southern and eastern populations of *monticola* to lose the striation of the vertex and pronotum is interesting because this trend — at least the smooth or nearly smooth vertex — is a more constant characteristic of the two southern neighbors, *O. rixosus* and *O. latidens,* which are so closely similar to each other and to *O. monticola* that it is not even now completely clear to me that all three are really separate species. The possibility must be considered that *latidens,* and perhaps even *rixosus,* are the tropical representatives of the Chinese *monticola.*

Although I feel that the evidence favors treating the three as separate species, we will not be sure of this relationship until we have adequate nest series of these forms from the presumed region of sympatry or parapatry in southeastern Asia — perhaps in Thailand and Cambodia, from which no samples are available to me. *O. latidens* is known from queens from Java, Sumatra and Malaya, and workers from Sumatra and Borneo. The collections all appear to represent solitary specimens, though at least one worker was found mounted on the same pin as 2 workers of *O. rixosus* from Mt. Penrissen, N. Borneo (E. Mjöberg).

The three species are compared in Table II for the important metric characters and ratios of head, mandibles and scape.

[21] *Pedetes macrorhynchus* was proposed as a name in a letter from Java by Bernstein (1861) published in Vienna. From the brief and vague reference, it seems likely that the subject was some Javanese *Odontomachus,* perhaps *rixosus* or *simillimus,* but there is no real description sufficient to recognize any species.

[22] *O. malignus* is an unusual species that deserves further study. Wilson (1959) summarized its wide range (Borneo to Santa Cruz Islands) and emphasized its marine littoral habitat, its apparent attachment to coral, and the fact that it can be found foraging far out in the intertidal zone at low lide. By a startling coincidence, I was pondering this matter as I studied the available material of *O. malignus* on the very day that I received, without advance notice, a parcel containing 4 workers of this species and a covering letter from my friend, Dr. J. E. Lloyd, of the University of Florida.

The workers, which are a very dark orange-brown, darker than the other material of the species now available, were taken by Dr. Lloyd on an old, raised coral reef at the edge of the sea at Alexishafen, near Madang, Papua New Guinea, while he was studying a *Luciola* firefly (Coleoptera: Lampyridae) that frequents the same habitat. In his paper on the lampyrid, Lloyd (1973) sets the scene: «The surf of the Bismarck Sea pounds these ragged, pocked revetments; portions of them are inundated at high tide, seas wash over them, and salt spray rains upon them... adjacent vegetation... a woody shrub *Pemphis acidula,* Lythraceae, which is found throughout tropical Asia and the insular Pacific... sprawled over the landward edge of the reef at one of the sites».

In a subsequent letter, Dr. Lloyd describes the nest entrance, a crack in the coral, surrounded by coffee-colored tailings, including coral fragments, mined by the ants. It is probable that Lloyd's colony was not under water at normal high tide, but the possibility exists that this or other nests of *O. malignus* do suffer submersion from time to time. If so, one imagines that they might exist in air pockets in the coral that have passages entering only from below. The omaniid bug *Corallocoris marksae* is cited by Woodward (1958) as regularly sheltering at high tide in such places under periodically submerged coral rocks along the Great Barrier Reef off Queensland, and emerging to feed on the exposed reef when the tide goes out. But whether or not *O. malignus* nests are ever covered by sea water, the existence of the ant in this habitat raises some fascinating questions. If it forages regularly in the intertidal zone, how does it time its excursions from and back to the nest? What is its food? Does it possess physiological protection against salt water? This is an autecological problem that might well make a wonderful doctoral thesis.

In addition to the new New Guinea record, I have found specimens in J. W. Chapman's collection [MCZ] from Tawitawi (A. C. Duyog) and Sitanki, Jolo Island (A. Herre) in the Sulu Archipelago of the southern Philippines. A male placed with this species in MCZ comes from Teuhungano, Rennell Island (J. D. Bradley, 14 October 1953). It is light brownish-yellow and has the petiolar node rounded above.

[23] *O. minutus* is a modest-sized species with opaque striatopunctate gastric dorsum (Plate 1, D). It is very widely distributed and common in forested parts of Central and South America. The color varies from dull ferruginous to dark brown, and the lighter-colored forms are most common in Central America; the types of Mann's *dulcis* are light specimens. A *meinerti* type (ZM-Copenhagen) examined through the kindness of Dr. Børge Petersen is clearly just a Venezuelan specimen of *minutus*. *O. minutus* is collected commonly in leaf litter samples, especially those run through Berlese funnels or other extraction systems, and it seems to be a more cryptic species than most of those related to *O. haematodus*. On Barro Colorado Island in the Panama Canal Zone, I took two nests in the forest under rotten logs, and in central Brasil I found the species common in the litter of gallery forests in the cerrado areas (near Brasilia) and in Mato Grosso. The most northern known record is from Pueblo Nuevo, near Tezonapa, Veracruz, Mexico (E. O. Wilson).

It reaches Paraguay and Santa Catarina State, Brasil, in the south (Kempf, 1972: 172).

[24] **Odontomachus mormo** new species

(Figs. 10, 15)

Worker, holotype: TL 18.8, HL 4.34, HW (across vertex) 2.30, HW (across ocular prominences) 2.80, ML 2.58, scape L 4.66, eye L 0.61, WL 5.78 mm; CI 53, MI 59, SI 203.

A very large species related to *O. hastatus*, but differing in the following characters:

(1) Head broader and with sides of vertex nearly parallel, only feebly converging posteriad behind temporal ridges; posterior angles broadly rounded, but more sharply so than in *hastatus*. Posterior border biconvex, with a median concavity bounded by the V of the nuchal carina. Carina distinct, but not raised into a narrow collar as it is in *hastatus*. Extraocular furrows and temporal ridges more distinct than in *hastatus*; antennal fossae deep and confluent at the deep median furrow, which runs forward nearly to the midlength of the head. Striation of frontal region coarse, spreading fanwise only to the posterior limits of the antennal fossae.

(2) Mandibles more robust than in *hastatus* (maximum W, without teeth, about 0.6 mm in the *mormo* holotype, 0.5 mm in the largest *hastatus* workers available), outer borders gently but distinctly convex in outline seen full-face. Large dorsal subapical tooth broad, hardly more than twice as long as broad, with bluntly rounded (subtruncate) apex; in unworn *hastatus*, this tooth is much more slender and has an acute, or at least conical apex. Teeth on inner margin of blade low, blunt, decreasing in size basad, 10-11 in number, followed at base by 3-6 minute serrations.

(3) Striation of pronotum and mesonotum fine and distinct, transverse on the discs, not effaced in holotype (center of posterior pronotal disc usually smooth and shining in *hastatus*).

(4) Entire trunk relatively more robust (less attenuated) in *mormo* than in *hastatus*; as seen from the side, mesonotal and metanotal outlines both feebly convex, meeting at the deep suture to form a distinct, broadly open V (in *hastatus*, mesonotum concave, forming a shallow saddle with metanotum; suture between them scarcely interrupting the concave outline of the saddle).

(5) Petiole of a special shape (fig. 15), not distinctly subpedunculate in front as in *hastatus*, but the anterior face gently concave in about its upper 2/3, below root of apical spine. Node smooth and shining.

(6) Most of body entirely without erect hairs. One pair of long inclined hairs near the middle of the cephalic dorsum, close to the posterior edge of the frontal striated area. A few other short, fine, inconspicuous hairs here and there on anterior part of head, especially on free clypeal margin, under-mouthparts, and a few on anterior half of ventral surface of head, on anterior and ventral surfaces of coxae, on flexor edges of femora, on distal flexor surfaces of tibiae, undersides

of petiole and gaster, and dorsal surface of first gastric tergum near its posterior margin. Longer fine hairs (0.4-0.6 mm long) on the 4 segments of gastric apex, and some longer oblique hairs ranged along the undersides of the inner mandibular borders. *O. hastatus* has abundant fine erect pilosity over most of the body.

Pubescence distinct only on scapes, tibiae and tarsi, where it is short, fine, and appressed to obliquely erect. Dilute appressed pubescence on mandibular shafts. On trunk, petiole, and especially on the smooth and shining gastric dorsum, pubescence is extremely fine and dilute, so that the gaster, at least, seems free of it except at high magnifications in certain lights, when widely separated, very fine, appressed hairs are sometimes visible.

(7) Mesepisternal margin distinct its whole length above (often obliterated in front of metathoracic spiracle in *hastatus*); metasternal surface vertically striate over about anterior quarter, otherwise smooth, with satiny blue lustre.

(8) Head, mandibles, trunk, petiole, and tibiae dark reddish brown; gaster, mandibular apices and tarsi piceous; coxae and femora dull yellow, the femora infuscated apicad. The smooth parts of the body, especially sides of head, mesepisterna, and node, with bluish iridescence.

Additional metric data: petiole L 1.21, petiole height above spiracle 1.30, without ventral process 1.70, including ventral process 2.01, left hind femur L 4.62, left hind tibia L (without basal condyle) 3.70 mm.

Holotype [MCZ] a unique taken in wet forest in a ravine leading up into the first (westernmost) foothills of the Andes just east of the highway, about 3 km SW of Bucay, Prov. Guayas, Ecuador, by W. L. Brown, July 1973. The worker was found walking slowly on the ground in shade near midday; seen alive, it was at first thought to be a large specimen of *O. chelifer*.

Paratype workers: Two specimens were received belatedly, when this manuscript was nearly finished. They were both collected in 1975 in Prov. Pichincha, Ecuador, by Stewart and Jarmila Peck. The first worker, slightly larger than the holotype, comes from 3 km east of Tandapi, 1300 m, in wet ravine (B-303). The second is a partial specimen, consisting only of head and pronotum with appendages, from Tinalandia, 16 km southeast of Santo Domingo de los Colorados, 680 m, in litter berlesate. This last specimen is a little smaller than the holotype, and has the palpi extended and segments countable at 4,4. The measurements of these samples are the extreme values entered in Table I.

Queen and male unknown.

This species is the largest *Odontomachus* in the New World, equalling and slightly exceeding the largest workers of *O. chelifer* available for study. The records are all from Ecuador west of the Andes. It will be interesting to see how far north and south the range of this species extends.

[25] Wilson (1959) reduced the *tyrannicus* group by synonymy from 8 species, subspecies and varieties to just 3 species: *tyrannicus, testaceus* and *nigriceps*. The small additional amount of material made available since 1959 does nothing to bring

Wilson's treatment into question, and it is accepted here. The group, as far as known, is restricted to New Guinea, New Britain and nearby islands of West Irian.

[26] Stitz described *peruanus* as a variety of *O. haematodus,* but there is no reason to believe that he knew what the real *haematodus* was. It seems likely to me that his «Stammform» of *haematodus* was what I here call *O. bauri,* or else a combination of *bauri* and the true *haematodus.* The type of *peruanus,* destroyed in the wartime fire-bombing of Hamburg, was a queen from «Canchamayo», Peru, possibly referring to the Rio Chanchamayo.

According to the brief description, the type was «Etwas robuster als die Stammform». Stitz goes on to say that, while the Stammform has the entire propodeal dorsum transversely striate, in *peruana* only the posterior part of the propodeal dorsum is like this. The anterior part, beginning at the suture with the metanotum, has fanwise, posteriorly diverging striation that recurves on the sides and is finer than the striation of the posterior part.

It may eventually be possible to match this sketchy description with the queen of a known or unknown species from the western Amazon Basin or the eastern slopes of the Andes, but for the time being it does not compare well with the available queens of any of the larger *haematodus*-group species from South America, including *haematodus, bauri, biumbonatus,* and *caelatus.* Since I have no good idea of what the name represents, it is listed here as *dubium* and excluded from the key and discussions, with the hope that it will eventually find its way onto the List of Officially Rejected Names.

[27] *O. rixosus* is the common species in the forests of tropical southeastern Asia, Sumatra, Java and Borneo. Forel felt that some samples from Burma and Thailand, var. *obscurior,* were smaller and darker than those from Sumatra and Singapore, but the differences are slight and inconstant. Javanese samples are often rather small and dark. The variety *conifera* is another slight variant in nodal form from Java, not worth nomenclatorial distinction. I did not find *O. rixosus* on Celebes, and it is absent from the extensive Chapman Collection of material from Mindanao and those Philippine islands to the north of Mindanao.

[28] Through the kindness of Dr. P. Oosterbroek (ITZ-Amsterdam), I have been able to examine 3 syntypes of Emery's *O. imperator* subsp. *rufithorax*: a worker from Timena, New Guinea (now West Irian), and 2 from Tawarin in the same country The Timena example bears Emery's determination label, and is here designated as lectotype of *O. rufithorax.* These specimens are in my opinion conspecific with the species later described by Mann as *O. emeryi* and Wilson as *O. gressitti.* In Wilson's (1959: 486) key, *rufithorax,* at couplet 11, follows from the first lug of couplet 7: «Most of the pronotum, including all of its dorsal surface exclusive of the anterior 'neck' completely lacking striae, its surface either shagreened or smooth and shining». Emery's description of *rufithorax,* however, reads, «le corselet et le petiole sont striés fortement en travers», which agrees perfectly with his types before me.

The *rufithorax* types have the extraocular furrows striate, the striae extending slightly onto the temporal ridges. The head and gaster are dark brown, and the trunk and petiole are dull, fairly light reddish, with legs a trifle lighter. In the type series of *O. emeryi,* all from the Solomons, the sample from Fulakora (Ysabel) has the extraocular furrows distinctly and usually completely striate, but in the sample from Maliali (Florida) the striae vary from indistinct to obsolete in this furrow. In large and small workers and an alate queen from Kokure, 690 m, southern Bougainville (E. J. Ford, Jr., 1956), the extraocular furrows are completely smooth and shining. Mann cited differences between his *emeryi* and *rufithorax* in the depth of the red of the trunk, and in the sculpture of the head, but since Mann never saw Emery's types, at least the sculptural differences were never specified. Actually, the differences in depth o fcolor between Mann's types and the *rufithorax* types are relatively slight, the more distinctly darkened mesonotum against a lighter general truncal color being the most noticeable trait in most Solomons samples. But this is a variable character, and even the *rufithorax* types have the mesonotum faintly darker than adjoining parts of the trunk.

Wilson described *O. gressitti* from 2 specimens: the holotype, from Nondugl, 1750 m, Ahl Valley, NE New Guinea; and a paratype from 1100 m on Guadalcanal. The paratype (MCZ) is a small specimen of *O. saevissimus* as here conceived. The holotype is said by Wilson to «most closely» resemble *O. papuanus.* He writes that, «It bears a superficial resemblance to *linae* Donisthorpe but differs markedly from that species in its smaller size, distinctive coloration, and *papuanus*-type petiolar node». In his photograph (Wilson 1959: fig. 4, no. 8), however, the node of the holotype of *gressitti* is clearly of the *saevissimus-imperator* form by Wilson's own criteria, except that the spine is not slightly decurved, as it is in most *saevissimus*-complex specimens. This is a very variable character, and the variation appears to be partly allometric. In any case, Wilson's description of the *O. gressitti* holotype agrees well with a slightly larger (but still small, HL 3.60 mm) worker, one of those from Kokure, Bougainville, just cited above.

In the fairly extensive material now available, *rufithorax* and *saevissimus* seem to be distinguishable over a wide range from western New Guinea through the Solomons, and though the distinction is mainly one of color, I see no reason to treat them as other than good species on the present evidence.

[29] The MCZ has 3 syntype workers of *O. silvestrii* (Dong Mo, Indochina) and 5 of its var. *substriatus* (Tocco, Indochina); both series were collected in 1925 by F. Silvestri. The *substriatus* types are badly leached and partly collapsed, as though they had been in caustic or acid, and the differences cited by Wheeler disappear when this condition is considered. This is a slender species with prominent teeth along the inner mandibular borders; it is smaller than *infandus,* and has a peculiar thickset petiolar node that is rather suddenly narrowed above into the apical tooth. The densely and finely punctate gastric dorsum, with correspondingly dense pubescence, is characteristic.

[30] *O. simillimus,* known through most of the literature as «*O. haematodes*», was revised by Wilson (1959: 499-500), and its Pacific distribution is outlined in Wilson and Taylor (1967: 31-32). There remain to be added the junior synonyms *Ponera pallidicornis* (based on a male specimen from Makassar, Celebes; type in BMNH-London, examined) and *O. haematodus* var. *breviceps* (based on a worker from Christmas Island in the Indian Ocean south of Java; type in BMNH-London, examined).

O. simillimus workers (fig. 1) and queens have mostly rather fine, glossy dorsal striation on head and trunk, and they are closely related to *O. haematodus* and *O. troglodytes,* but unlike these two species, *simillimus* has the metasternal process low and rounded, much as in fig. 5.

The male is dark, with castaneous to blackish trunk, sometimes showing a faint fuscous scutal pattern when the trunk is brown; head and gaster varying shades of brown or yellowish brown; legs light to dark brown. Wings of queen, and sometimes of male, usually rather dark.

Outside the range as usually stated, *O. simillimus* is found in the SW part of the Indian Peninsula, especially in the Western Ghats in Kerala State (A. B. Soans and W. L. Brown, several localities).

[31] **Odontomachus sumbensis** new species

Worker, holotype: TL 12.8, HL 3.03, HW (across vertex) 1.93, HW (across ocular prominences) 2.22, ML 1.64, scape L 2.84, eye L 0.51, WL 4.10 mm; CI 64, MI 48, SI 115.

Paratypes, 7 workers from type locality (Mao Marru) and 1 from Kananggar, Sumba; only 2 were measured in detail, and the measurements are given combined with those of the holotype, which was the largest of all the specimens in the type series, in Table II.

Description of warker, composite: A relatively broad-headed member of the *infandus* group (palpal formula 4,4) with apical, intercalary and subapical teeth of mandibles normally acute, the subapical tooth long-conical, and a strong preapical series of 7-10 teeth on the inner margin; of these preapical teeth, the first and second counting away from apex toward base are large, triangular, the second usually largest (in one specimen, a denticle exists between these two teeth), and from there decreasing in size to the base of the mandible. Antennal scapes when held straight back surpassing the posterior border by an amount about equal to the length of the pedicel (first funicular segment), or by a little more in the smallest specimen. Second funicular segment much longer than pedicel and subequal to third; beyond the third, segments decreasing slightly in length toward apex; apical segment only slightly longer than second.

Trunk rather slender; pronotum with a fairly long, tapered anterior cervical portion and a gently convex, sloping anterior face. Mesonotum as seen from the side tilting upward cephalad, with a narrowly rounded anterior edge projecting upward rather sharply above posterior margin of pronotum. Mesonotal profile almost straight (feebly convex) but seen from above it is convex from side to side. Metanotum distinct, impressed slightly but distinctly below level of propodeal dorsum. Side-view profile of propodeal dorsum long, straight to very feebly concave.

Petiole broad and as seen in side view, thick from front to rear, with a very brief anterior peduncle; anterior face forming one long, sloping convexity from peduncle to root of apical spine, where the profile changes to a very slight concavity from root to apex of the fairly long, sharp, posteriorly inclined spine. Posterior profile of node bisinuate; concave at root of spine, convex at a posterior, slightly swollen portion of the upper posterior nodal face, and below this nearly vertical, or even slightly concave to near base. Seen from the rear, the swollen upper rear face of the node is feebly sulcate vertically on the midline. Thus the lateral outline of the petiole is much like that of *O. biumbonatus* (fig. 22), but with the apical spine back-tilted instead of erect. Gaster high, strongly vaulted above, the first tergum not flattened or impressed, but strongly convex in both directions; tergum II with a well developed stridulatory file on the acrotergite, behind this a feeble transverse impression, after which the tergum is broadly convex in both directions.

Sculpture of the usual striate type on the head and trunk, but the striation effaced and replaced on the vertex and sides of head, and posterior half of disc of pronotum, by a smooth or nearly smooth, shining surface. Striation weak behind ocular ridges, distinct in extraocular furrows, but not extending back beyond temporal ridges, nor below level of eyes on sides of head. Cheeks from in front of eyes to mandibular insertions nearly or quite smooth. Cervix and front half of pronotal disc finely transversely striate, striae becoming weaker caudad, and finally effaced completely or nearly completely on posterior disc, where in some lights on some specimens, feeble traces of transverse striation can still be seen on an essentially smooth and shining convex surface. Rest of trunk transversely striate, vertically striate on sides, except middle and most of posterior part of mesopleura, which are smooth and shining. The above smooth areas mostly bear scattered punctures. Petiolar node and all normally exposed surfaces of gaster glassy-smooth and shining.

Pilosity, and especially pubescence, in generally weakly developed (some specimens rubbed). The usual long middorsal cephalic pair, 3-6 fine, erect hairs on underside of head near buccal opening, 0-6 fine, erect hairs in pronotum, 1-5 short, erect hairs near posterior border of gastric tergum I, and a rather sparse complement of long, fine hairs on underside of gaster and on dorsum of second and apical gastric segments. Pubescence appressed to subappressed, fine, nearly obsolete, except on legs; especially reduced and sparse on node and gaster, where almost invisible in most lights.

Head ferruginous red; trunk, petiole and gaster piceous (perhaps nearer black in life or in fresh specimens; types probably somewhat faded), pronotum more or less suffused with reddish; legs yellow; antennae light reddish brown; funiculi yellowish brown.

Queen and male unknown.

Holotype (MCZ) and 7 paratypes (MCZ, BMNH-London) from *Mao Marru*, 450 *m*, Sumba Island, Indonesia; and a single paratype (MCZ) from Kananggar, 700 m, Sumba, all collections by K. Dammerman, May 1925. This species is related to *O. latissimus* from New Guinea and to *O. floresensis* from the nearby island of Flores. As befits its relatively isolated source island, situated below the main Sunda chain, *O. sumbensis* is the most distinct member of its subgroup. The coloration, with red head, blackish body and yellow legs, is much like that of *floresensis*, but the reduced sculpture is quite different. The shape of the petiolar node is also different, being thicker and more convex (more dome-like), with the apical spine shorter in *sumbensis* than in *floresensis*, and the preapical series of mandibular teeth are somewhat larger in *sumbensis*. For a metric and proportional comparison, see Table II.

After all is said and done, both this species and *floresensis* could well be only extreme insular variants of *O. papuanus* or one of the other *infandus* group species. This group needs much more study on New Guinea.

[32] *O. troglodytes* is the *haematodus* group representative in Africa. It is very close to *O. haematodus*, even to having a similarly acutely produced metasternal process (fig. 7), but it has brown legs instead of the yellow legs most common in

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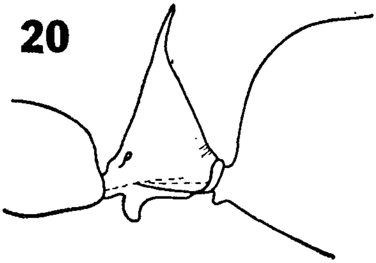

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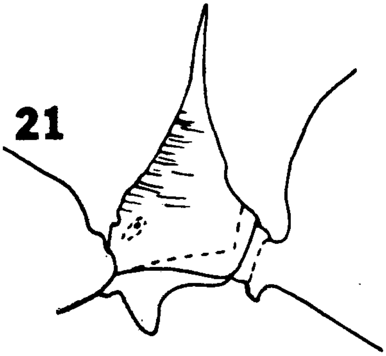

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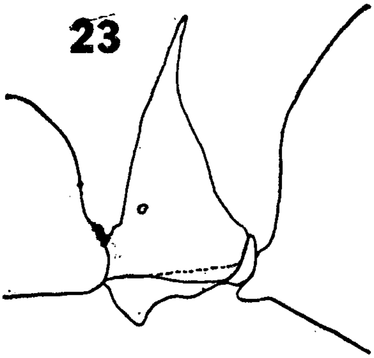

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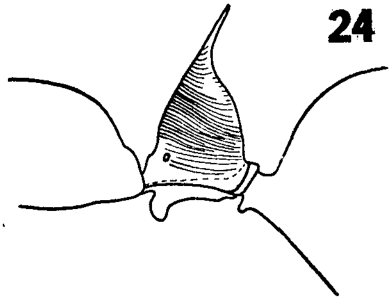

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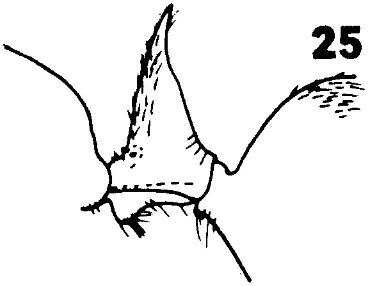

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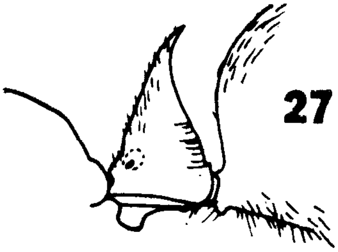

haematodus. Also, the antennal scapes are shorter, when held straight back usually surpassing the posterior border of the head by less than the length of the first funicular segment (by more than the length of the first funicular segment in most *haematodus*), and the sides of the petiolar node are usually more coarsely striate and more opaque in *troglodytes* than in *haematodus*. Still, occasional specimens can be found that would be difficult to place to either species without knowing the provenience.

The males of *troglodytes* are prevailingly brownish yellow or yellowish brown, with trunk, as usual, darkest.

O. troglodytes is widespread and often common in Africa in second-growth forest, open woodland and the more moist types of savanna. It ranges from the southern Sudan, Eritrea and West Africa south to Natal, and I found it in the spray-soaked forest alongside Victoria Falls in Rhodesia. The lectotype, in NM-Basel, is from the caves at Shimoni, south of Mombasa in southernmost Kenya. Types of *O. haematoda* var. *stanleyi* were compared directly with the lectotype, and only slight differences exist, like those seen in many other series of this species, usually reported in the literature as «*O. haematodes*». For further synonymy and records (only African and Malagasy references and records apply to true *O. troglodytes*), see Wheeler 1922b: 793 ff. and 1922c: 1013-1014.

In the review of Bionomics of Odontomachiti, in earlier pages of this part, the extensive findings of Colombel (1970a, 1970b, 1972) and Evans and Leston 1971) for «*O. haematodus*» actually apply to *O. troglodytes*.

[33] **Odontomachus yucatecus** new species

Worker, holotype: TL 10.1, HL 2.74, HW (across vertex) 1.91, HW (across ocular prominences) 2.09, ML 1.32, scape L 2.40, eye L 0.47, WL 3.08 mm; CI 70, MI 48, SI 115. (For metrics of paratypes, see Table I).

Description of worker, composite: Very similar to North and Central American *O. brunneus* in habitus; color; form and proportions of head, mandibles, and antennae; sculpture (except mesonotum and petiole), and

Figs. 20-27, workers of neotropical *Odontomachus* species, petioles and adjacent structures in side view. Fig. 20, *O. haematodus* from Kartabo, Guyana. Fig. 21, *O. bradleyi* paratype. Fig. 22, *O. biumbonatus* paratype from Rio Tarumã, N of Manaus, Amazonas. Fig. 23, *O. caelatus*, paratype from Limoncocha, Napo Prov., Ecuador. Fig. 24, *O. bauri*, small specimen from Barro Colorado I., Panama Canal Zone. Fig. 25, *O. brunneus* from Spring Creek, Decatur Country, Georgia, USA. Fig. 26, *O. brunneus* from Limoncocha, Napo Prov., Ecuador. Fig. 27, *O. brunneus* from Mun. Mariana, Minas Gerais, Brasil.

in the abundant subappressed pubescence and erect pilosity, but body size averages larger, mesonotum longitudinally (instead of transversely) striate, petiolar node slightly different in shape and distinctly and regularly horizontally striate on sides and posterior face up to root of apical spine.

Some of the more important characters shared by *brunneus* and *yucatecus* are discussed under *brunneus* [11], since that species had never been adequately characterized. The distinctive features of *O. yucatecus* are the following:

(1) Sculpture. The dorsum of the head is very finely striate, as in *brunneus;* a 0.1 mm sample square in the middle of the left side of the vertex contains about 8-9 striae, and the surface here appears sericeous at moderate magnifications. Pronotum prevailingly longitudinally striate, as in *brunneus,* with the striae bowed outward on the sides. Mesonotum longitudinally striate, the striae punctulate and sometimes weakly diverging anteriad. The costulae are also minutely pitted and in part sometimes slightly wavy, so that the mesonotal sculpture is more opaque than that of pronotum. The longitudinal striation varies in different samples, sometimes extending back across metanotum and even onto the anterior part of the propodeum, where the striae may form a U-shaped pattern, open anteriad.

Sides and rear of petiolar node with very distinct and regular horizontal striation, approaching in coarseness the nodal striation of forest samples of *O. bauri.* Across the anterior face of the node, the striation is more or less reduced to fine reticulo-striation mesad, and this surface is shining at the very midline in some samples.

The first and second gastric segments are prevailingly smooth and shining between the numerous fine punctures that give rise to the subappressed pubescence.

(2) The petiolar node shape is intermediate between that of the «average» *O. brunneus* and the «average» forest *O. bauri* in anteroposterior thickness, but it differs from the usual condition of both in having the apical spine rather abruptly back-tilted, with an obtuse but distinct angle in side view marking the juncture of the anterior face with the spine proper. The outline of the main anterior sloping face of the node itself is almost perfectly straight, varying from very slightly convex to feebly concave over variable distances, as in «average» *O. haematodus* (fig. 20), but the abrupt back-tilting of the apical spine together with this conformation, and with the gently convex outline of the posterior face, is characteristic of *O. yucatecus.* Viewed from above and to the rear, the posterior nodal face appears flat to feebly sulcate in the middle. The apical spine is smooth, laterally compressed and more or less blade-like, tapered toward its apex, and has a straight to weakly concave anterior edge as seen from the side.

(3) Pubescence and pilosity much like that of *O. brunneus,* but the erect hairs tending to be even more numerous and larger: 8-16 hairs on vertex and frontal strip and carinae, 10-16 on pronotum, and many on both upper and lower surfaces of gaster; also some on underside of mandibles, head, and pronotum, and anterior faces of fore coxae. In this strong vestiture, *O. yucatecus* resembles *O. laticeps.*

(4) The color of most *O. yucatecus* samples is basically dark reddish brown, with the gaster and dorsal surfaces tending to be a little darker, and the legs, antennae and bases of mandibles castaneous brown. The

Belize specimen is piceous to ,very nearly black, with black gaster and dark brown legs; only the antennal funiculi are medium brown. All specimens have tinges of opalescent blue, particularly on the smoother parts of the body, such as the side of the head, smooth central part of mesopleura, and sides and dorsum of first gastric segment.

(5) The metasternal ridge in two workers examined has a pair of distinct toothlike structures separated by a narrow, deep median groove, but the teeth are much shorter and less acute than in *O. haematodus*. Other specimens show a metasternal ridge much like that in some *O. bauri* workers (fig. 6).

Queen and male still unknown.

Holotype (MCZ) and 4 paratype workers from Mexico: Campeche: 10 km east of Compeche (E. O. Wilson, No. 132) strays. Other paratypes from Mexico: Yucatan: Near mouth of second cave on San Roque Road, Oxkutzcab (A. S. Pearse) 1 worker. Vera Cruz: Pueblo Nuevo, near Tezonapa, degraded tropical evergreen forest (E. O. Wilson, No. 250, 2 workers). Guatemala: Antigua, 1 worker, and Escuintla, 1 worker, both by W. M. Wheeler. Belize: Belmopan, second growth *Cecropia*-palm forest litter berlesate (S. and J. Peck) 1 worker. Paratypes in MCZ, WWK.

This is a modest-sized species, in habitus intermediate between *O. brunneus* and *O. bauri,* but its longitudinally striate mesonotum will distinguish it at once from these two species, as well as from the larger-sized, partly sympatric *O. laticeps.*

So far as the few available records indicate, *O. yucatecus* seems to be widely distributed in the Yucatan Peninsula and neighboring Guatemala and Belize, as well as the lowlands of Veracruz. We should expect it to be found in the Isthmus of Tehuantepec and in Honduras.

Notes supplied by Wilson indicate that the type collection made near Campeche came from leaf litter in thorn forest.

«To be followed by Part VI B, including Genus *Anochetus,* Bibliography and Index of Scientific Names».