



Review of the ant genus *Aenictus* (Hymenoptera: Formicidae) in Australia with notes on *A. ceylonicus* (Mayr)

STEVEN O. SHATTUCK

CSIRO Entomology, P. O. Box 1700, Canberra, A.C.T. 2601, Australia. E-mail: steve.shattuck@csiro.au

Abstract

The Australian members of the ant genus *Aenictus* are revised. Eight species were found to occur in Australia with three described as new (*acerbus* sp. n., *aratus* Forel, *diclops* sp. n., *hilli* Clark, *nesiotis* Wheeler and Chapman, *philiporum* Wilson, *prolixus* sp. n. and *turneri* Forel). *A. hilli* is known only from males and its relationship to the remaining worker-based species is uncertain. Of the seven worker-based species, five are restricted to Australia, one is shared with Papua New Guinea and one is shared with Papua New Guinea and the Philippines. *Aenictus aratus nesiotis* Wheeler and Chapman is removed from synonymy with *A. aratus* and raised to full species, *A. pachycerus impressus* Karavaiev is newly synonymised with *A. aratus* and *A. turneri* is removed from synonymy with *A. ceylonicus* (Mayr). Additionally, the following changes are proposed for non-Australian species: *A. aitkenii* Forel is removed from synonymy with *A. aratus*, *A. aratus asiatica* Forel is removed from synonymy with *A. aratus* and synonymised with *A. aitkenii*, *A. levior* Karavaiev is removed from synonymy with *A. aratus* and raised to full species, *A. orientalis* (Karavaiev) is removed from synonymy with *A. ceylonicus*, *A. papuanus* Donisthorpe is removed from synonymy with *A. ceylonicus* and, together with *A. similis* Donisthorpe, is newly synonymised with *A. orientalis*. A lectotype is designated for *A. impressus* and a neotype for *A. exiguus*.

Key words: Hymenoptera, Formicidae, Aenictinae, *Aenictus*, taxonomy, new species, synonymy, Australia

Introduction

Aenictus occurs throughout Africa and in tropical and subtropical areas from India east through southern China to Taiwan and south to Australia with outlier, temperate-climate species or populations in Japan, Afghanistan, Armenia and south-central Australia (Bolton *et al.*, 2006; Gotwald, 1995; Shattuck, 1999). While widespread, nowhere are they common. All known species are "army ants" and conduct raids using large numbers of workers, primarily attacking other ants, social wasps and termites. While there are reports of these ants preying on other insects and even collecting honeydew from homopterans (Santschi, 1933; Gotwald, 1995), these habits appear to be uncommon. Unfortunately none of the Australian species of *Aenictus* have been studied in detail and only a few overseas species have been examined (for example *A. gracilis* and *A. laeviceps* by Schneirla, 1971) and most of our understanding is based on casual and opportunistic observations.

Foraging raids undertaken by these ants occur both day and night, usually across the ground surface but occasionally also arboreally. During raids, numerous workers attack a single nest or small area, with several workers coordinating their efforts to carry large prey items back to the nest or bivouac. They also have a nomadic life style, alternating between a migratory phase in which nests are temporary bivouacs in sheltered places above the ground and a stationary phase where semi-permanent underground nests are formed. During the nomadic phase bivouacs move regularly, sometimes more than once a day when larvae require large

amounts of food. Individual nests usually contain up to several thousand workers, although nest fragments containing only a few hundred workers are often encountered. Queens are highly specialised and look less like workers than in most ant species. They have greatly enlarged gasters and are termed dichthadiform. New colonies are formed by the division of existing colonies rather than by individual queens as in most ant species.

Aenictus is the only extant genus in the subfamily Aenictinae. It contains 149 valid species and subspecies (Bolton *et al.*, 2006, not counting changes proposed here). The phylogenetic relationship of *Aenictus* to other ants has been investigated by Bolton (1990), Baroni Urbani *et al.* (1992), Brady (2003), Brady and Ward (2005), Brady *et al.* (2006), and Moreau *et al.* (2006). The most recent species-level study of these ants in the Australian region is that of Wilson (1964).

As a result of this study the number of species of *Aenictus* known from Australia has increased from four to eight (with three described as new), one species has moved into synonymy, and two species previously thought to be widely distributed are now known to be limited to much smaller regions. One is known only from males and its relationship to the remaining species is uncertain. Of the seven worker-based species, five are endemic, one is shared with PNG and one with PNG and the Philippines.

Abbreviations of morphological terms

Size and shape characters were quantified and are reported as lengths or indices. Measurements were made with a stereo microscope using a dual-axis stage micrometer wired to digital readouts. The following measurements and indices are reported: CI (cephalic index), HW/HL x 100; HL, maximum head length in full face view, measured from the anterior clypeal margin (excluding the projecting clypeal teeth) to the midpoint of a line drawn across the posterior margin of the head; HW, maximum head width in full face view; ML, mesosomal length measured from the point at which the pronotum meets the cervical shield to the posterior base of the metapleuron, viewed laterally; MTL, maximum length of mid tibia, excluding the proximal part of the articulation which is received into the distal end of the femur; SI (scape index), SL/HW x 100; SL, length of the scape (first antennal segment) excluding the basal constriction and condylar bulb.

Acronyms of museums

AMSA, Australian Museum, Sydney, New South Wales; ANIC, Australian National Insect Collection, Canberra, A. C. T.; BMNH, The Natural History Museum, London, U. K.; MCZC, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U. S. A.; JDMC, Jonathan Majer Collection, Perth, Western Australia; MHNG, Muséum d'Histoire Naturelle, Geneva, Switzerland; MVMA, Museum Victoria, Melbourne, Victoria; NHMB, Naturhistorisches Museum, Basel, Switzerland; OXUM, Oxford University Museum of Natural History, Oxford, U. K.; TERC, Tropical Ecosystems Research Centre, CSIRO, Darwin, Northern Territory.

Overview of Classification

Australian species

acerbus **sp. n.**

aratus Forel

pachycerus impressus Karavaiev (new synonym)

diclops **sp. n.**

hilli Clark (known only from males)

nesiotis Wheeler and Chapman (removed from synonymy with *aratus*, new status as full species)

philiporum Wilson

prolixus **sp. n.**

turneri Forel (removed from synonymy with *ceylonicus*)
deuqueti Crawley
exiguus Clark

Non-Australian species

aitkenii Forel (removed from synonymy with *aratus*)
aratus asiatica Forel (new synonym)
ceylonicus (Mayr)
ceylonicus latro Forel
ceyloncus formosensis Forel
levior Karavaiev (new status as full species)
orientalis (Karavaiev) (removed from synonymy with *ceylonicus*)
papuanus Donisthorpe (removed from synonymy with *ceylonicus*, new synonym of *orientalis*)
similis Donisthorpe (new synonym)

***Aenictus* Shuckard, 1840**

Aenictus Shuckard, 1840: 266.

Typhlatta Smith, 1857: 79 (synonym of *Aenictus* by Forel, 1890: ciii; removed from synonymy as subgenus of *Aenictus* by Wheeler, 1930: 198; synonym of *Aenictus* by Wilson, 1964: 444).

Type species. *Aenictus*: *Aenictus ambiguus* Shuckard, 1860, by original designation. *Typhlatta*: *Typhlatta laeviceps* Smith, by monotypy.

Diagnosis. Workers of *Aenictus* may be separated from other Australian ants by their moderately small size (less than about 4 mm), lack of eyes, long slender bodies and long legs. They are superficially similar to some myrmicines but differ in lacking the frontal lobes and in having the antennal sockets completely visible when viewed from the front (myrmicines have frontal lobes that are expanded towards the sides of the head and partly cover the antennal sockets). Some of the smaller, paler species are also similar to *Leptanilla* workers, but differ in being larger and only ten segments in the antennae rather than 12, and lacking a flexible promesonotal suture.

Males of *Aenictus* can be separated from those of other Australian ants by the exposed antennal sockets and lack of a postpetiole (the gaster is smooth and lacks a constriction between the first and second segments).

Key to Species of Australian *Aenictus* based on workers

1. A ridge (parafrontal ridge) present on the front of the head starting between the antennal and mandibular insertions and extending posteriorly; head capsule varying from smooth posteriorly and weakly punctate2
 - Area between antennal and mandibular insertions smooth or at most slightly angular but never ridged (parafrontal ridge absent); head capsule entirely smooth4
2. Pronotum with large smooth areas dorsally and laterally, other areas micro-reticulate *philiporum*
 - Pronotum entirely sculptured with dense micro-reticulations3
3. Scape relatively long (SI > 107) *nesiotis*
 Scape relatively short (SI < 103) *aratus*
4. Head with large pale patches near the posterolateral corners; subpetiolar process generally absent but sometimes present as a slight carina *diclops*

- Head essentially uniform in colour; subpetiolar process large and rectangular5
- 5. Scape relatively long (SI > 89) *prolixus*
Scape relatively short (SI < 91)6
- 6. Body larger (HW > 0.62mm); sculpturing on pronotum extending posteriorly onto the main pronotal body *acerbus*
- Body smaller (HW < 0.62mm); sculpturing on pronotum limited to the anterior sections around the collar, the main body of pronotum smooth *turneri*

***Aenictus acerbus* sp. n.**

(Figs 1–3, 7, 8, 24)

Types. Holotype worker from 9km ENE Mt. Tozer, 12°43'S 143°17'E, Queensland, 5–10 July 1986, J.C.Cardale, ex. pan traps (ANIC, ANIC32-023688). Two paratype workers, same data as holotype (ANIC, ANIC32-023646).

Diagnosis. Head capsule entirely smooth and essentially uniformly coloured; scape relatively short (SI < 91); sculpturing on pronotum extending posteriorly onto the main pronotal body; body larger (HW > 0.62mm). This species is morphologically similar to *A. turneri* but can be separated from it by its larger size and more extensive sculpturing on the pronotum.

Worker Description. Mandible narrow and subtriangular, with a large apical tooth and a smaller subapical tooth followed by 4–6 small teeth and a larger basal tooth; anterior clypeal border varying from weakly convex to weakly concave, located at or slightly posterior to anterior margin of frontal lobes in full face view; parafrenal ridges absent; subpetiolar process a large rectangular to elongate-rectangular projection; head entirely smooth, pronotum with weak, closely spaced punctures dorsally and anteriorly, smooth posterolaterally, remainder of mesosoma finely punctate with weak longitudinal rugae on lateral surfaces; body yellow-red to light red-brown.

Measurements. Worker ($n = 13$) - CI 88–97; HL 0.66–0.73; MTL 0.59–0.67; HW 0.62–0.66; ML 1.07–1.17; SI 81–91; SL 0.53–0.58.

Additional material examined. Australia: Northern Territory: Douglas Daly, CRC Clay Site A5 (Salvarani, A.) (TERC); Douglas Daly, CRC Clay Site A8 (Salvarani, A.) (TERC); PWCNT, Tiwi Island Fauna Survey FR (Woinarski, J.) (TERC); Solar Village Survey, Burnt Slope 3 (Andersen, A.N.) (TERC). Queensland: 9km ENE Mt. Tozer (Cardale, J.C.) (ANIC). Western Australia: Kimberley, CALM Site 4/3 (Weir, T.) (TERC).

Comments. This rare species is known from a limited number of collections in the Kimberley region of Western Australia, northern Northern Territory and on Cape York Peninsula, Queensland. All specimens were collection from pitfall traps or pan traps. It is very similar to *A. turneri* but the differences outlined above under *Diagnosis* seem to hold for all currently available specimens and it is here recognised as a separate taxon.

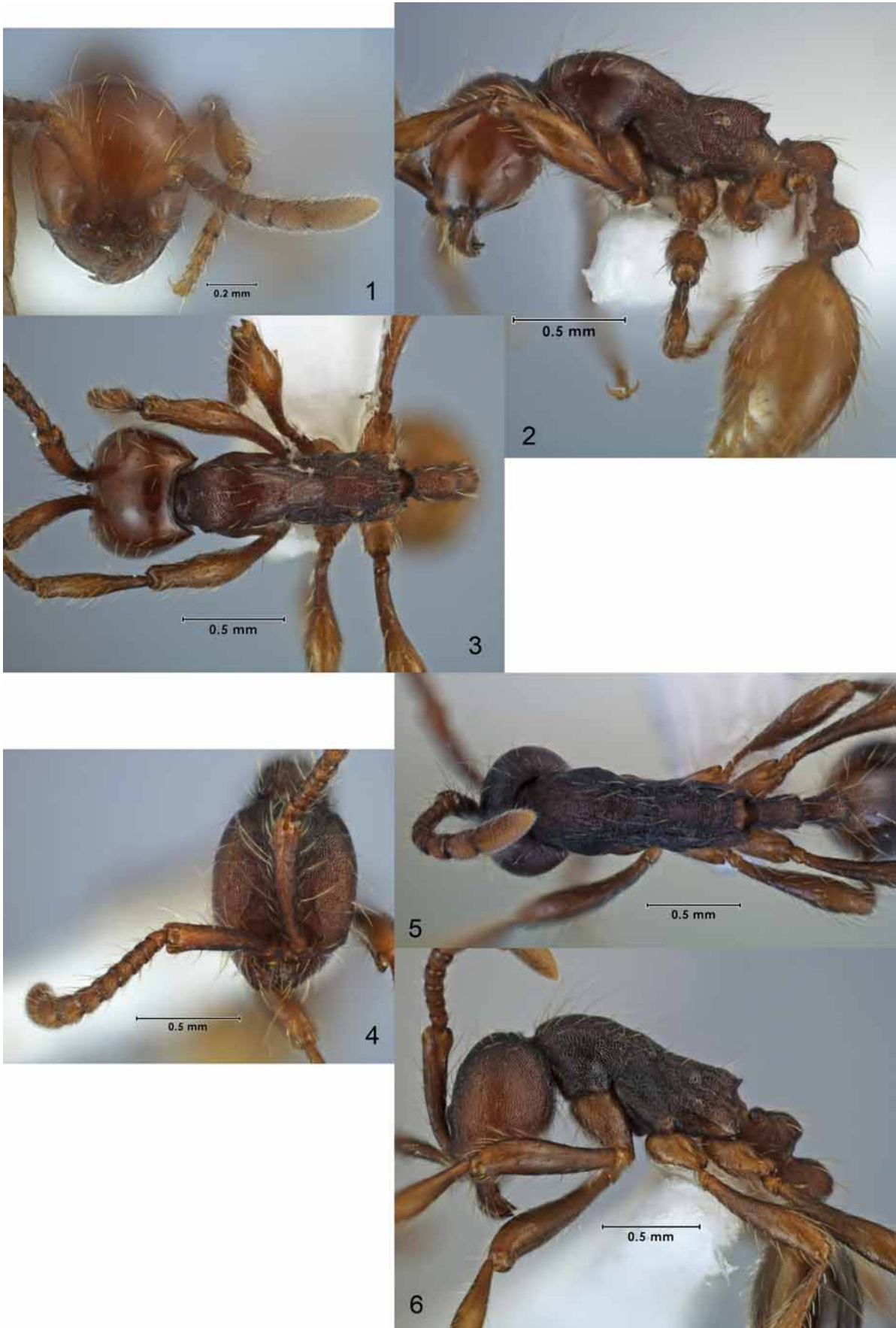
***Aenictus aratus* Forel**

(Figs 4–6, 7, 8, 25)

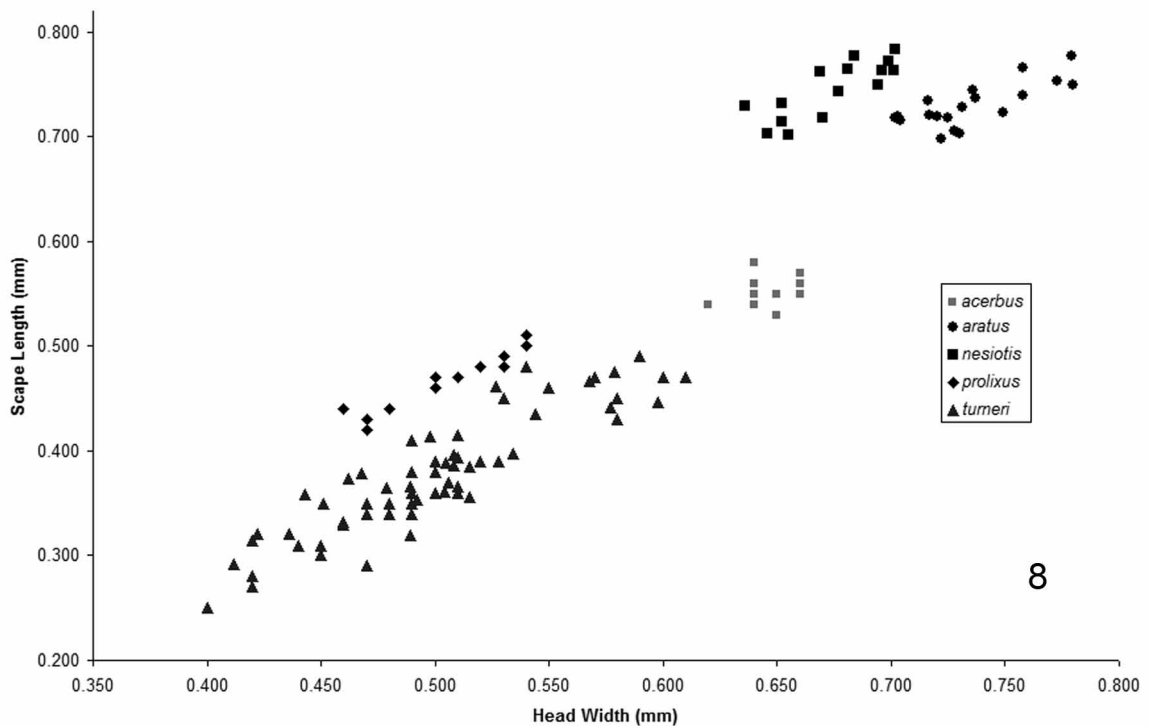
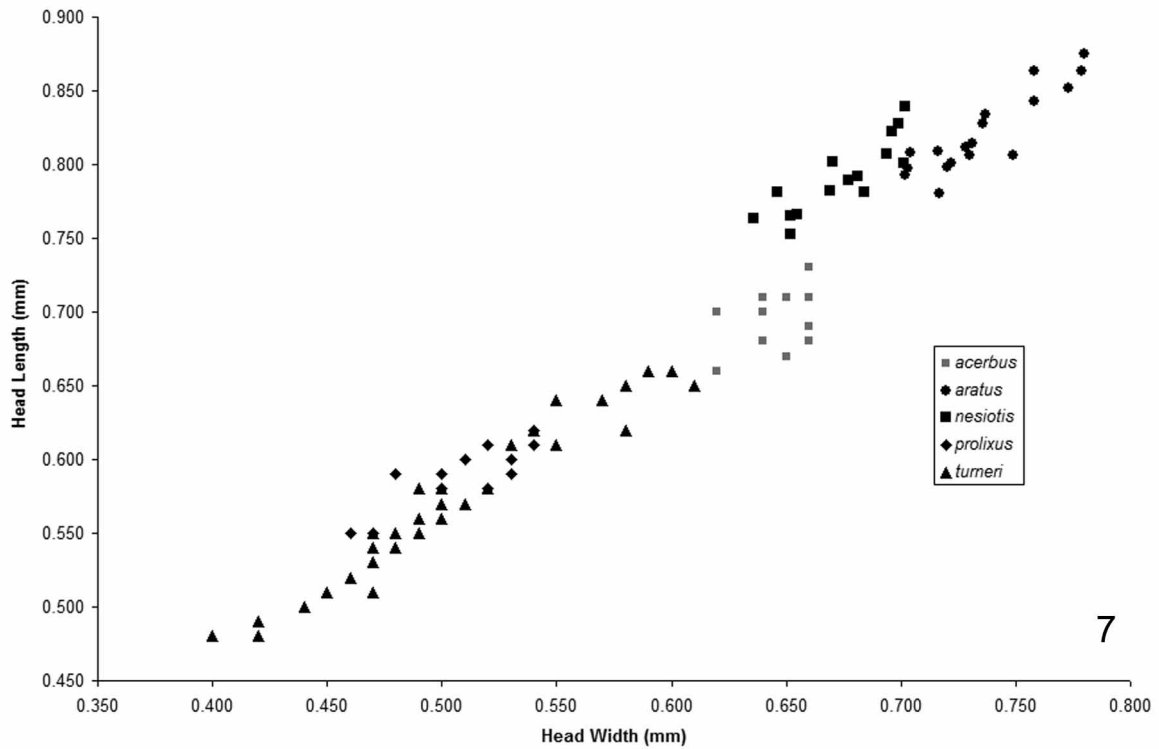
Aenictus aratus Forel, 1900: 74.

Aenictus pachycerus impressus Karavaiev, 1927: 7 (new synonym).

Types. *A. aratus*: Three worker syntypes (MCZC, examined) from Mackay, Queensland. *A. pachycerus impressus*: Lectotype worker from Mackay, Queensland, **here designated** (MHNG).



FIGURES 1–6. *Aenictus acerbus* sp. n. worker. Fig. 1, front of head; Fig. 2, lateral view of body; Fig. 3, dorsal view of body. *Aenictus aratus* Forel worker. Fig. 4, front of head; Fig. 5, dorsal view of body; Fig. 6, lateral view of body.



FIGURES 7–8. Fig. 7, Graph of head length versus head width. Fig. 8, Graph of scape length versus head width.

Diagnosis. Head capsule completely punctate; scape relatively short ($SI < 103$); pronotum entirely sculptured with dense micro-reticulations. This species can be separated from the morphologically similar *A. nesiotis* by the broader head ($CI > 87$ and $HW > 0.70\text{mm}$ compared to $CI < 88$ and $HW < 0.70\text{mm}$) and the relatively shorter scapes ($SI < 103$ compared to $SI > 107$ in *A. nesiotis*).

Worker Description. Mandible triangular with numerous small teeth, those along the medial region of the masticatory margin ill defined; anterior clypeal border broadly convex, extending slightly anterior of frontal lobes; parafrenal ridges well developed, extending posteriorly approximately 1/3 length of head capsule; subpetiolar process broadly convex anteriorly, flat posteriorly; head entirely punctate; mesosoma uniformly punctate, generally with weak, ill-defined longitudinal rugae on dorsum of pronotum and lateral surfaces posterior of pronotum; body brown to black, anterior section of head sometimes lighter, distal antennae and legs always lighter.

Measurements. *Worker* ($n = 18$) - CI 87–93; HL 0.78–0.88; HW 0.70–0.78; MTL 0.67–0.75; ML 1.17–1.29; SI 96–103; SL 0.70–0.78.

Material examined. Australia: *Queensland:* 20km S Sarina Ridge (Lowery,B.B.) (ANIC); 50km NW Townsville (Greenslade,P.J.M.) (ANIC); Henrietta Ck., Palmerston NP (Ward,P.S.) (ANIC); Hinchinbrook Is., Gayundah Ck. (Davies, Thompson & Gallon) (ANIC); Mackay (Turner) (ANIC); *Northern Territory:* Minaelau Creek, Melville Island (Mann,S.) (TERC).

Comments. This species was previously thought to be wide spread and occurring from India eastward into Australia (Wilson, 1964). However, as conceived here this species is restricted to Australia with extra-Australian specimens being referable to *A. aitkenii*, *A. levior* and likely additional as-yet unrecognised species. Detailed examination of this material will be required to resolve the true taxonomic status of these non-Australian ants.

Aenictus pachycerus impressus Karavaiev is here synonymised with *A. aratus*. The nomenclatural history of this name is rather complicated. It was first used by Karavaiev (1926) when describing the variety *levior* (as *Eciton (Aenictus) impressus* var. *levior*). The next year Karavaiev (1927) noted that *A. impressus* had actually never appeared in print and that he had used the name based on a specimen identified and labelled with this name that he had received from Forel. He then contacted Forel who provided notes from his 1893 notebook which listed the name “*Aenictus bengalensis* Mayr rasse *impressus* nov. subsp.”, followed by a short description complete with comparisons to *A. aitkenii* and *A. bengalensis*. The name *impressus* was not mentioned again until Bolton (1995) included it in his catalogue, listing Karavaiev (1927) as the author and noting that the type locality was unknown but was probably India.

During this study two specimens from the Forel Collection (Geneva) were found which were labelled as “*Ae. impressus* For. type” from Mackay, Queensland and collected by Turner, with the label being typical of Forel’s handwriting. These specimens had been more recently labelled as *A. aratus* and were stored with other “*aratus*” specimens, clearly indicating that they were considered to be types of *A. aratus*. This treatment is supported by the original description of *A. aratus* (Forel, 1900) where Mackay is listed as the type locality and Turner as the collector (and where comparisons are made to *A. aitkenii* and *A. bengalensis*).

Assembling this information, what seems to have happened is that Forel (around 1893) determined that he had a new taxon which he intended to name *impressus* and labelled the specimens using this name. However, when preparing the 1900 description he changed the name to *A. aratus* but neglected to update the specimen labels. He then sent a pin from this series to Karavaiev, who used the name on the specimen (*impressus*) when establishing *A. levior* (Karavaiev, 1926) not realising that this name was unpublished. Karavaiev (1927) then made matters worse by providing enough information for the name to be considered available by Bolton (1995). To confuse things further Forel’s (1893 notes and 1900) comparisons with the Indian species *A. aitkenii* and *A. bengalensis* implied that this is an Indian species. In fact, it would appear that both of these names, *A. aratus* and *A. impressus*, are based on the same type series from Mackay, Queensland. Using this assumption, a single specimen housed in Geneva is here selected as the lectotype for both names, relegating *A. impressus* as a junior objective synonym of *A. aratus*.

The published literature for this species is limited. Wilson (1964) discussed the biology and taxonomy of this and related species (under the single name “*A. aratus*”) and Disney and Kistner (1991) discuss parasitism by phorid flies.

***Aenictus diclops* sp. n.**

(Figs 9–11, 26)

Types. Holotype worker from Telegraph Line Crossing, Jardine River, Cape York, Queensland, 15–17 June 1969, G.Monteith (ANIC, ANIC32-023689). 29 paratype workers, same data as holotype (ANIC, MCZC, QMBA, ANIC32-015742, ANIC32-015768, ANIC32-015774, ANIC32-029319, ANIC32-032139).

Diagnosis. “Eye spots” present on posterolateral corners of head; subpetiolar process generally absent but sometimes present as a slight carina. This is the only known Australian species of the genus with “eye spots” (pale pigmentation on the dorsolateral region of the head capsule).

Worker Description. Mandible subtriangular, with a large apical tooth, a smaller subapical tooth and a series of 4-ca.10 ill-defined crenulations; anterior clypeal border convex, extending anterior of anterior surfaces of frontal lobes in full face view; parafrontal ridges absent (although a sharp angle is present immediately posterior of the lateral clypeal margin); subpetiolar process absent or at most a thin carina; head entirely smooth, posterior pronotum smooth, anterior pronotum and entire mesonotum with weak, fine punctations, mesopleuron with longitudinal rugae, propodeum similar to mesonotum but sculpturing less well developed, especially anteriorly; body yellow-red with “*Typhlatta*” spots (pale yellow patches) on posterolateral corners of head.

Measurements. Worker ($n = 9$) - CI 83–88; HL 0.85–0.95; HW 0.74–0.83; MTL 0.78–0.97; ML 1.39–1.59; SI 95–103; SL 0.71–0.83.

Additional material examined. Australia: Queensland: 9km ENE Mt. Tozer (Cardale, J.C.) (ANIC).

Comments. This is one of the rarest species of Australian *Aenictus*, being known from only two collections on northern Cape York Peninsula. Its closest relatives, species formerly placed in the subgenus *Typhlatta*, are found from India east to the Philippines and south to Papua New Guinea. This species is similar to the PNG species *A. huonicus* but differs in having more extensive sculpturing on the mesosoma and petiole.

***Aenictus hilli* Clark**

Aenictus hilli Clark, 1928: 38.

Types. Holotype male from Malanda, Queensland (ANIC, examined).

Comments. *A. hilli* was described by Clark (1928) from a single male collected at Malanda, Queensland. There are numerous males in ANIC which are morphologically similar to the type of *A. hilli*. Unfortunately none are associated with workers. In addition, the remaining described Australian species are all worker-based and without associated males. This makes it impossible to positively associate *A. hilli* with any of these other species. Distribution patterns give little clue as to the association either as *Aenictus aratus*, *A. nesiotis*, *A. prolixus* and *A. turneri* all occur in the general area of the type locality of *A. hilli*. Thus there is currently insufficient information to associate *A. hilli*, or any of these other males, with any of the worker-based species. As a result *A. hilli* is here treated as a valid species and these additional males tentatively associated with it until such time that worker-associated males or fresh material suitable for molecular analysis can be secured.

Material examined (all unassociated males). **Australia: Northern Territory:** 34 mi. NW of Dorisvale HS (Mendum, M.) (ANIC); 39 km E of Alice Springs (Cardale, J.C.) (ANIC); 4 mi. W of Coolibah H.S. (Mendum, M.) (ANIC); 48 mi. SW of Daly River (Mendum, M.) (ANIC); 5mi. ENE Victoria River Downs (Kelsey, L.P.) (ANIC); Daly River Mission (Hutchinson, J.F.) (ANIC); Katherine (Kelsey, L.P.) (ANIC); Todd River, 9 km N by E of Alice Springs (Cardale, J.C.) (ANIC); **Queensland:** Bamaga (Sedlacek, J.) (ANIC); Lockerbie, Cape York (Sedlacek, J.) (ANIC); Malanda (Hill, G.F.) (ANIC); West Claudie River, Iron Range (Monteith, G.B. & Cook, D.) (ANIC); **Western Australia:** Carson Escarpment (Common, I.F.B. & Upton, M.S.) (ANIC); Drysdale River (Common, I.F.B. & Upton, M.S.) (ANIC).



FIGURES 9–14. *Aenictus diclops* sp. n. worker. Fig. 9, front of head; Fig. 10, dorsal view of body; Fig. 11, lateral view of body. *Aenictus nesiotis*. worker. Fig. 12, front of head; Fig. 13, dorsal view of body; Fig. 14, lateral view of body.



FIGURES 15–20. *Aenictus philiporum* Wilson worker. Fig. 15, front of head; Fig. 16, dorsal view of body; Fig. 17, lateral view of body. *Aenictus prolixus* sp. n. worker. Fig. 18, front of head; Fig. 19, dorsal view of body; Fig. 20, lateral view of body.



FIGURES 21–23. *Aenictus turneri* Forel worker. Fig. 21, front of head; Fig. 22, dorsal view of body; Fig. 23, lateral view of body.

***Aenictus nesiotis* Wheeler and Chapman, n. stat.**

(Figs 7, 8, 12–14, 27)

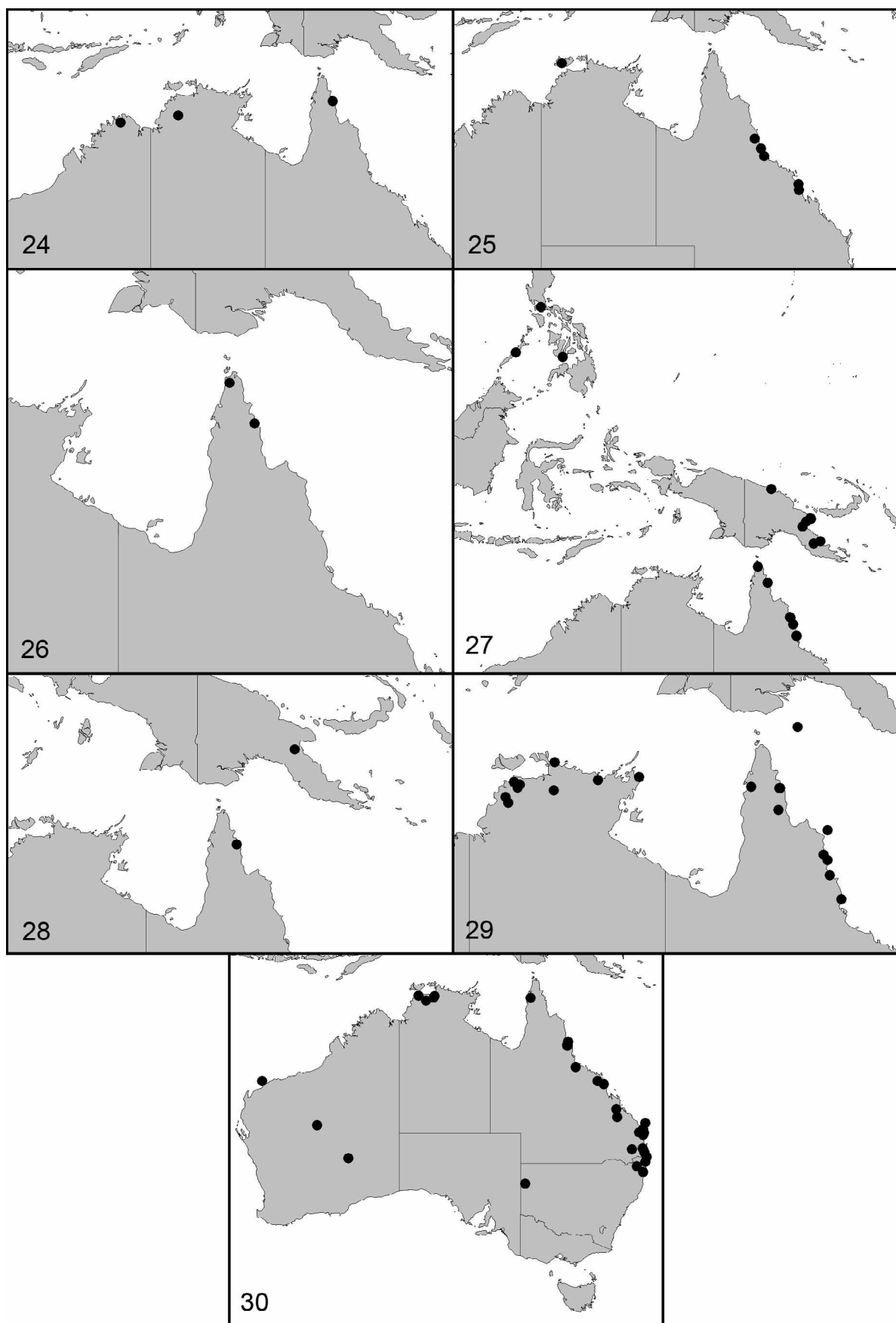
Aenictus (Aenictus) aratus subsp. *nesiotis* Wheeler, W.M. & Chapman, in Wheeler, 1930: 208.

Types. One syntype worker from Los Banos and 39 syntype workers from Dumaguete, Philippine Islands (MCZC, examined).

Diagnosis. Head capsule completely punctate; pronotum entirely sculptured with dense micro-reticulations. This species is most similar to *A. aratus*, but differs in the narrower head (CI < 88 and HW < 0.70mm compared to CI > 87 and HW > 0.70mm in *A. aratus*) and the longer scapes (SI > 107 compared to < 103 in *A. aratus*).

Worker Description. Mandible triangular with numerous small teeth, those along the medial region of the masticatory margin ill defined; anterior clypeal border broadly convex, extending slightly anterior of frontal lobes; parafrontal ridges well developed, extending posteriorly approximately 1/3 length of head capsule; subpetiolar process broadly convex anteriorly, flat posteriorly; head entirely punctate; mesosoma uniformly punctate, generally with weak, ill-defined longitudinal rugae on dorsum of pronotum and lateral surfaces posterior of pronotum; body brown to black, anterior section of head sometimes lighter, distal antennae and legs always lighter.

Measurements. Worker ($n = 15$) - CI 82–88; HL 0.75–0.84; HW 0.64–0.70; MTL 0.67–0.79; ML 1.11–1.24; SI 107–115; SL 0.70–0.78.



FIGURES 24–30. Distribution of material examined during this study. Fig. 24, *A. acerbus*; Fig. 25, *A. aratus*; Fig. 26, *A. diclops*; Fig. 27, *A. nesiotis*; Fig. 28, *A. philiporum*; Fig. 29, *A. proluxus*; Fig. 30, *A. turneri*.

Material examined. Australia: *Queensland:* 20km N Cairns (Lowery,B.B.) (ANIC); 4.5km NNW Cape Tribulation (Wild,A.L.) (ANIC); 40 m. from Laceys Cr. (Taylor,R.W. & Feehan,J.E.) (ANIC); Cape Tribulation (Kistner,D.H., Kistner,A.C., Nutting,W.L. & Nutting,R.D.) (ANIC); Emmagen Ck., 5.0 km N of Cape Tribulation (Monteith,G.B., Yeates & Thompson) (ANIC); Noah Creek, Cape Tribulation (Moneith,G.B.) (ANIC); S2 Mission Beach (Cermak,M.) (ANIC). **Papua New Guinea:** *East Sepik:* Yawasora nr. Wewak (Taylor,R.W.) (ANIC); *Morobe:* Bulolo (Lowery,B.B.) (ANIC); Ebabaang, Mongi Watershed, Huon Pen. (Wilson,E.O.) (MCZC); Kua River, Laulaunung (Wilson,E.O.) (MCZC); nr. Lae (Taylor,R.W.) (ANIC); *Northern:* 3.2km N of Kokoda;(Lowery,B.B.) (ANIC); Buna (Room,P.M.) (ANIC); Kokoda Trail nr. Kokoda;(Lowery,B.B.) (ANIC). **Philippine Islands:** Los Banos (Williams,F.X.) (MCZC); Dumaguete (Chapman,J.W.; Schneira,T.C.) (ANIC, MCZC); Iwahig Penal Colony (Lowery,B.B.) (ANIC).

Comments. This is the widest spread Australian species of *Aenictus* with populations occurring in the Philippines and Papua New Guinea. The non-Australian material placed here shows only minor differences from Australian populations, none of which suggest separate species are involved. These differences include a slightly broader anterior petiolar face and less distinct sculpturing in Philippines specimens (especially those from Palawan) compared to most PNG/Australian specimens. However, both of these characters show considerable variation with essentially all morphologies found in both regions. Because of this all specimens are considered to belong to a single wide-ranging species. The larva described by Wheeler and Wheeler (1984) under the name *A. aratus* originated from the Philippines and had previously been identified as "*A. a. nesiotus* var. *fraterculus*" (an unavailable infrasubspecific name associated with *A. aratus* by Wilson, 1964). It is likely this larva belongs to *A. nesiotus* rather than *A. aratus* as *A. aratus* is not known to occur in the Philippines.

Aenictus philiporum Wilson

(Figs 15–17, 28)

Aenictus philiporum Wilson, 1964: 473, fig. 74.

Types. Holotype worker and 5 paratype workers from Iron Range, Queensland (MCZC, examined).

Diagnosis. Head capsule smooth posteriorly and weakly punctate between the frontal carinae and above the mandibular insertions; pronotum with large smooth areas dorsally and laterally, other areas micro-reticulate.

Worker Description. Mandible broad, triangular, with 6–9 widely spaced short teeth; anterior clypeal border broadly convex, even with or slightly posterior to anterior margin of frontal lobes; parafrenal ridges present; subpetiolar process weakly developed, broadly rounded anteriorly, flat posteriorly; head smooth laterally, remainder weakly to moderately punctate; posterior section of pronotum and entire mesonotum completely smooth to very weakly reticulate; anterior of pronotum, mesopleuron and entire propodeum weakly punctate; body red-brown, head, antennae and legs lighter yellow-red.

Measurements. *Worker* ($n = 10$) - CI 88–94; HL 0.66–0.71; HW 0.59–0.67; MTL 0.47–0.57; ML 0.96–1.06; SI 83–89; SL 0.52–0.59.

Material examined. Australia: *Queensland:* Claudie River, Iron Range (Monteith,G.) (ANIC). **Papua New Guinea:** *Morobe:* Bulolo (Lowery,B.B.) (ANIC).

Comments. This rare species has been collected only a limited number of times on Cape York Peninsula, Queensland and in eastern Papua New Guinea. Nothing is known concerning its biology.

***Aenictus prolixus* sp. n.**

(Figs 7, 8, 18–20, 29)

Types. Holotype worker from Baroalba Gorge, 12°50'S 132°52'E, 18 Nov. 1972, R.W.Taylor & J.E.Feehan, Acc. N. 72.1076, rainforest, under stone (ANIC, ANIC32-002810). 18 paratype workers, same data as holotype (ANIC, MCZC, QMBA, ANIC32-015781).

Diagnosis. Head capsule entirely smooth and essentially uniformly coloured; scape relatively long (SI > 89); subpetiolar process large and rectangular. This species is most similar to *A. acerbus* and *A. turneri* but can be separated from these by the longer scapes.

Worker Description. Mandible triangular, with a large apical tooth and a smaller subapical tooth followed by 6–7 (rarely 5) small teeth and a larger basal tooth; anterior clypeal border weakly convex to weakly concave, located at or anterior to anterior margins of frontal lobes in full face view; parafrontal ridges absent; subpetiolar process a large rectangular project, an elongate flange sometimes present on the posterior corner; head entirely smooth, pronotum weakly reticulate on collar, smooth posteriorly and laterally, mesonotum smooth, mesopleuron and propodeum finely punctate with longitudinal rugae laterally; body yellow-red, mesosoma slightly darker.

Measurements. Worker ($n = 13$) - CI 81–90; HL 0.55–0.62; HW 0.46–0.54; MTL 0.43–0.57; ML 0.84–0.98; SI 89–96; SL 0.42–0.51.

Additional material examined: Australia: *Northern Territory:* Baroalba Gorge (Taylor,R.W. & Feehan,J.E.) (ANIC); Fauna Survey Central Arnhem Land, P41, Djabidy Djabidy (Mann,S.) (TERC); Fauna Survey Darwin Region, P48, Tjenya Falls (Mann,S.) (TERC); Fogg Dam (Reichel,H.) (TERC); Gove (Majer,J.D.) (ANIC); Holmes Jungle, Darwin Region (Andersen,A.N.; Reichel,H.) (TERC); Howard Springs Res. (Hoffmann,B.) (TERC); Mary River Study, Mt. Daly (Armstrong,M.) (TERC); Murgarella (Tiedeman,S.C.) (ANIC); Surprise Ck. Falls, Litchfield Park (Hoffmann,B.) (TERC); *Queensland:* 3km ENE Mt. Tozer (Cardale,J.C.) (ANIC); 4.5km NNW Cape Tribulation (Ward,P.S.; Wild,A.L.) (ANIC); Horne Creek, 23km N Coen (Ward,P.S.) (ANIC); Iron Range (Jenkins,R.) (ANIC); Kuranda, Black Mt. Road (Taylor,R.W. & Feehan,J.) (ANIC); Lizard Island (Hoffmann,B.; Shepherd,U.) (TERC); Moses Ck., 4 km N by E Mt. Finnigan (Cardale,J.C.) (ANIC); S3 Mission Beach (Cermak,M.) (ANIC); Torres Strait, Murray Is. (Heatwole,H.) (ANIC); Weipa, MRRP Study Site N26 (Andersen,A.N.) (TERC).

Comments. This common species is found in northern Northern Territory and northern Queensland. It is most similar to *A. acerbus* and *A. turneri* but can be separated as outlined above under *Diagnosis*. It is probable that at least some of the males here associated with *A. hilli* may actually belong to this species.

***Aenictus turneri* Forel, rev. stat.**

(Figs 7, 8, 21–23, 30)

Aenictus turneri Forel, 1900: 75 (junior synonym of *A. ceylonicus* by Wilson, 1964: 452; revised status as valid species).

Aenictus deueti Crawley, 1923: 177 (junior synonym of *A. turneri* by Brown, 1952: 123).

Aenictus exiguus Clark, 1934: 21 (junior synonym of *A. turneri* by Brown, 1958: 5; junior synonym of *A. ceylonicus* by Wilson, 1964: 452; removed from synonym with *A. ceylonicus*, junior synonym of *A. turneri*).

Types. *Aenictus turneri*: Worker syntypes from Mackay [approx. 21°09'S 149°11'E], Queensland (GMNH, ANIC, examined). *Aenictus deueti*: Worker syntypes from Lismore [approx. 28°49'S 153°16'E], New South Wales (4 in AMSA; 3 in ANIC (Naumann *et al.* 1994) (examined); 7 in MVMA; 5 in MCZC; additional specimens probably in OXUM). *Aenictus exiguus*: Neotype worker from Lake Eacham National Park, 17°18'S 145°37'E, Queensland, 25–27.ix.1972, R. W. Taylor, rainforest, ground strays (ANIC32-023690, non-types from same nest series, ANIC32-015780) (here designated).

Diagnosis. Head capsule entirely smooth and essentially uniformly coloured; scape relatively short (SI < 91); subpetiolar process large and rectangular. This species can be separated from the otherwise similar *A. prolixus* by the shorter scape, and from *A. acerbus* by its smaller size and largely smooth pronotum.

Worker Description. Mandible narrow to narrowly subtriangular (depending on number of denticles), with a large apical tooth, a smaller subapical tooth, 0–6 denticles and 1–2 basal teeth (always two basal teeth if denticles are absent); anterior clypeal border flat to convex, posterior of anterior surfaces of frontal lobes in full face view; parafrontal ridges absent; subpetiolar process subrectangular, sometimes with a posterior flange; head and pronotum entirely smooth (except the pronotal collar, which is punctate), mesopleuron and entire propodeum with weak, ill defined punctations under weak longitudinal rugae; body uniform yellow, mesosoma, petiole and postpetiole slightly darker.

Measurements. *Worker* ($n = 37$) - CI 83–94; HL 0.48–0.66; HW 0.40–0.61; MTL 0.29–0.59; ML 0.64–1.00; SI 61–89; SL 0.25–0.49.

Material examined. Australia: *New South Wales:* Fowlers Gap Stn, 110km N Broken Hill (Davison, E.A.) (ANIC); Glenugie State Forest, 15mi. S Grafton (Lowery, B.B.) (ANIC); Lismore (collector unknown; Duequet, C.F.) (ANIC); Mt. Nullum, Murwillumbah (Lowery, B.B.) (ANIC); Murwillumbah (Lowery, B.B.) (ANIC); Whiporie, 55km S Casino (York, A.) (ANIC); *Northern Territory:* Annaburroo, CRC Clay Site B15 (Salvarani, A.) (TERC); CSIRO Labs, Darwin (Salvarani, A.) (TERC); Kakadu Nat. Park, Kapalga (Andersen, A.N.) (TERC); Kakadu Nat. Park, Munmarlary (Andersen, A.N.) (TERC); Kapalga, Kakadu Natl. Pk (Andersen, A.N.) (ANIC); Kidman Sprs., CRC Clay Site B4 (Salvarani, A.) (TERC); OSS Study Site D6b, Ranger Lease (Andersen, A.N.) (TERC); OSS Study Site N4, Ranger Lease (Andersen, A.N.) (TERC); Wildman Rsv., High Gamba (Ryan, B.) (TERC); *Queensland:* 5 km NbyE of Mt. Morgan (Taylor, R.W. & Weir, T.A.) (ANIC); Adams Credition State Forest, Clarke Range, Mackay (collector unknown) (TERC); Atherton Tableland, Yungaburra Region, Donaghys Corridor (Cutter, A. & King, J.) (TERC); Backshall Farm, Malanda (Cutter, A.D.) (ANIC); Bauple, State Forest 958 (House, A.P.N. & Vanderwoude, C.) (TERC); Callide Ck. Mine, Biloela, Site 10 (Smith, A.) (TERC); Cedar Creek, Tamborine Mt. (Brown, W.L.) (ANIC); Cooloola (Plowman, K.) (ANIC); Cooloola Natl. Pk., Noosa R. (Greenslade, P.J.M.) (ANIC); Cooloola, Chalambar (Greenslade, P.J.M.) (ANIC); Crystal Cascades (collector unknown) (TERC); Lake Eacham National Park (Taylor, R.W.) (ANIC); Fraser Island, Bsh101 (Collier, P.) (TERC); Fraser Island, CTF21 (Collier, P.) (TERC); Mackay (collector unknown) (ANIC); Malanda, Backshall Farm 1989 Planting (Cutter, A.D.) (TERC); Prince Henry Drive, Toowoomba (Weatherill, L.) (ANIC); Suburban Brisbane (Vanderwoude, C.) (TERC); Townsville Field Training Area/Tabletop M2 RIPA (Woinarski, J.) (TERC); Weipa, MRRP Study Site Pinus B (Andersen, A.N.) (TERC); *Western Australia:* 146.8km SSE Newman (van Leeuwen, S. & Bromilow, R.N.) (JDMC); Barrow Island (Callan, S. & Edwards, K.) (JDMC); Mulga, NE Goldfields (Pringle, H.J.R.) (TERC).

Comments. This is the most common, widespread and southern-most species of *Aenictus* found in Australia. It occurs in a range of habitats from dry sclerophyll through *Banksia* shrublands and into rainforests. As with other species nests are in soil generally under rocks and logs on the ground. The queen has been collected only once, by B. B. Lowery, together with workers from Murwillumbah, NSW, in September, 1962. It is likely that at least some of the males here associated with *A. hilli* actually belong to this species.

Morphologically, the subpetiolar process is always subrectangular but shows considerable variation, even within single nest series. The anterior face is always angular and the posterior face a gentle to strong convexity, but the posterior angle often has a projecting flange that varies from short to long. This flange is visually striking and gives the appearance of a greater amount of variation that is actually present based on the underlying process. When the flange is present the posterior face tends to be more strongly convex while in cases where the flange is absent the posterior face is more weakly convex. Even though widespread, the outlying populations are similar to others. For example the Fowlers Gap specimens (from western New South Wales) are similar to those from Lismore (some 1100km to the east) in the shape of subpetiolar process and in having reduced sculpturing compared to others. There would appear to be minimal geographic differentiation within

this species.

Aenictus turneri is similar to the Indonesian and Papua New Guinean species *A. orientalis* but differs in having the humeral angles of the pronotum rounded rather than weakly angular and in being essentially uniform in colour (the head and legs are noticeably lighter than the mesosoma in *A. orientalis*).

A number of distinct species from the Philippines have been associated with *A. turneri* (when all were considered conspecific with *A. ceylonicus*). Most of the Philippine species differ from *A. turneri* in having thin, weakly convex subpetiolar processes. However, one species (based on specimens from 18km E Naga City and Camp, Dumaguete, both in MCZC) has a projecting rectangular subpetiolar process similar to that found in *A. turneri*. This material differs from Australian specimens in having shorter legs (especially tibiae), a more block-like postpetiolar node (although there is some variation in Australian material) and a darker, more reddish and less yellowish mesosoma; it is here treated as belonging to a separate species. These Philippine specimens are very similar to the types of *A. ceylonicus* var. *latro* Forel, which is currently a junior synonym of *A. ceylonicus*.

Aenictus exiguus was last considered in detail by Brown (1958). Unfortunately he apparently did not have access to the type specimen, a holotype worker from Cairns district, Queensland, reported as being in the South Australian Museum. A search during this study failed to find this specimen and it is assumed to have been lost. The only clue to the identity of this species is Clark's (1934) illustration. In this figure the scape is short, as in *A. turneri* rather than long, as found in *A. prolixus*. Based on this it is assumed that Clark's *exiguus* is conspecific with *A. turneri*. To secure this treatment a neotype is designated, this specimen being considered conspecific with *A. turneri*.

Non-Australian Species

Aenictus aitkenii Forel, rev. stat.

Aenictus aitkenii Forel, 1901: 475 (junior synonym of *A. aratus* by Wilson, 1964: 446; revised status as valid species).
Aenictus aratus var. *asiatica* Forel, 1911: 453 (junior synonym of *aratus* by Wilson, 1964: 446; removed from synonymy with *A. aratus*, new synonym of *A. aitkenii*).

Types. *Aenictus aitkenii*: Worker syntypes from Kanara, Thana and Travancore, India (not examined). *Aenictus aratus* var. *asiatica*: Worker syntype from Sri Lanka (not examined).

Comments. This species is similar to *A. aratus* (with which it has been treated as a junior synonym) and *A. nesiotis* but differs in having a broader head (CI > 87 versus CI < 88 in *nesiotis*), and broader and more bulbous petiole and postpetiole (both are narrower in *aratus* and *nesiotis*). The scape is also relatively longer than in the others (SI > 115 versus SI < 115). It is similar to *levior* in the shape of the head but differs in having longer scapes. This species is so far known only from India and Sri Lanka.

Aenictus ceylonicus (Mayr)

Typhlatta ceylonica Mayr, 1866: 505 (combination in *Aenictus* by Dalla Torre, 1893: 7).
Aenictus ceylonicus var. *latro* Forel, 1901: 477 (junior synonym of *A. ceylonicus* by Wilson, 1964: 452).
Aenictus ceylonicus var. *formosensis* Forel, 1913: 188 (junior synonym of *A. ceylonicus* by Wilson, 1964: 452).

Types. *Typhlatta ceylonica*: Worker syntypes from Sri Lanka (NHMW, not examined). *Aenictus ceylonicus* var. *latro*: Three worker syntypes from Poona, India (MCZC, examined). *Aenictus ceylonicus* var. *formosensis*: Worker syntypes from Taiwan (not examined).

Comments. As previously conceived (Wilson, 1964: 452) this species extended from India and Sri Lanka

eastward to Taiwan and south to Australia and contained eight junior synonyms (*formosensis* Forel, *latro* Forel, *orientalis* Karavaiev, *papuanus* Donisthorpe, *similis* Donisthorpe, and *turneri* Forel (with its junior synonyms *deuqueti* Crawley and *exiguus* Clark)). When discussing the specimens placed in *ceylonicus* Wilson (1964) recognised at least some of the variation noted in this study (for example, see Wilson's figs. 37–44), but interpreted this variation as intraspecific. For example he mentioned that the subpetiolar process varies considerably in its development, but did not appreciate that this variation occurs in discrete states and shows a strong geographic pattern suggesting that a series of species are involved. A careful re-examination of these characters, combined with considerably more material, has resulted in significantly different conclusions being drawn compared to Wilson (1964).

An examination of currently available material has found that the old “*ceylonicus*” contains a large number of species, including *A. ceylonicus* (strict sense), *A. acerbus*, *A. orientalis*, *A. papuanus*, *A. prolixus* and *A. turneri*. To determine the identity of *A. ceylonicus* itself will require considerable work and is beyond the scope of the present study. However, there are a wealth of morphological characters which allow the development of robust species hypotheses as has been demonstrated above for the Australian fauna. Having said that, morphological differences among species are often subtle and require considerable attention to detail to decipher. The following notes are provided as a starting point for a full revision of these ants.

Most of the Indian specimens share the configuration of the subpetiolar process, which forms a rounded anterior lobe followed by a posterior flat to concave extension ending at the junction with the postpetiole. Others have an elongate rectangular subpetiolar process, including the types of *A. latro*. Specimens with both of these morphologies can be found throughout Asia including in Taiwan, the Philippines, Vietnam and Indonesia. But while material from Vietnam has a rectangular subpetiolar process it has the dorsal surface of the mesosoma smooth and lacking any indication of the metanotal groove (most other species have at least a weak angle at the metanotal groove). Thus while the shape of the subpetiolar process is important it must be used in conjunction with other characters when determining species boundaries.

While the work undertaken here is preliminary, it clearly shows that the situation surrounding this species, and close relatives, is much more complex than that recognised by earlier workers. As a first step in clarifying this situation the names *A. orientalis* and *A. turneri* are treated as valid species, *A. papuanus* and *A. similis* are transferred to synonymy with *A. orientalis* while *A. formosensis* and *A. latro* are retained as junior synonyms of *A. ceylonicus*. However this should be treated as preliminary until all relevant material can be studied in detail.

***Aenictus levior* (Karavaiev), n. stat.**

Eciton (*Aenictus*) *impressus* var. *levior* Karavaiev, 1926: 425 (junior synonym of *A. aratus*: Wilson, 1964: 446; new status as full species).

Types. Worker syntypes from Buru Island, Indonesia (not examined).

Comments. *Aenictus* material from Indonesia is uncommon in collections and drawing conclusions on the species involved is difficult. However, it would appear that *levior* is a valid species and not a junior synonym of *aratus* as suggested earlier. Morphologically this species has a head shape similar to *aitkenii* (relatively broad) but the scape is shorter. However, this analysis is based on limited material and should be considered tentative until additional specimens become available. Material referable to this species has been examined from Sumatra, Indonesia, peninsular Malaysia and Sarawak, Malaysia.

***Aenictus orientalis* (Karavaiev), n. stat.**

Eciton (*Aenictus*) *ceylonicus* subsp. *orientalis* Karavaiev, 1926: 423 (junior synonym of *A. ceylonicus* by Wilson, 1964: 452; new status as valid species).

Aenictus papuanus Donisthorpe, 1941: 129 (junior synonym of *A. ceylonicus* by Wilson, 1964: 452; removed from synonymy with *A. ceylonicus*, new synonym of *A. orientalis*).

Aenictus similis Donisthorpe, 1948: 131 (junior synonym of *A. ceylonicus* by Wilson, 1964: 452; removed from synonymy with *A. ceylonicus*, new synonym of *A. orientalis*).

Types. *Eciton* (*Aenictus*) *ceylonicus* subsp. *orientalis*: Three worker syntypes from Wammar, Aru Island, Indonesia (ANIC, examined). *Aenictus papuanus*: Two worker syntypes from Malufu, Wharton Range, Papua New Guinea (MCZC, examined). *Aenictus similis*: Fourteen worker syntypes from Maffin Bay, Irian Jaya, Indonesia (2 in MCZC, examined).

Comments. In this species the pronotal humeral angles are well developed, causing the anterodorsal surface of the pronotum to be nearly vertical, in dorsal view the area between the humeral angles is weakly convex to weakly concave. This is in contrast to the otherwise similar *A. prolixus* and *A. turneri* where the humeral angles are weakly developed and the anterodorsal section of the pronotum is gradually sloping, the area between the humeral angles being moderately convex. In addition, *A. orientalis* can be separated from *A. prolixus* by the shorter scapes (SI 65–82 vs. 89–96) and from *A. turneri* by the yellow head and legs which contrast with the yellow-red mesosoma (the body is essentially uniform in colour in *A. turneri*). This species is known from eastern Indonesia and New Guinea.

Acknowledgements

I would like to thank Alan Andersen, Barry Bolton, Stefan Cover, and Roy Snelling for making material in their care freely available, Natalie Barnett for preparing the illustrations, and Natalie Barnett and Robyn Meier for capturing specimen information. Discussions of Asian species of *Aenictus* with Katsuyuki Eguchi were especially helpful. The editorial comments of Alan Andersen, Roy Snelling and an anonymous reviewer are most welcome.

References

- Baroni Urbani, C., Bolton, B. & Ward, P.S. (1992) The internal phylogeny of ants (Hymenoptera: Formicidae). *Systematic Entomology*, 17, 301–329.
- Bolton, B. (1990) Army ants reassessed: the phylogeny and classification of the doryline section (Hymenoptera, Formicidae). *Journal of Natural History*, 24, 1339–1364.
- Bolton, B. (1995) *A new general catalogue of the ants of the world*. Harvard University Press, Cambridge, Massachusetts, 504 pp.
- Bolton, B., Alpert, G., Ward, P.S. & Naskrecki, P. (2006) *Bolton's Catalogue of Ants of the World: 1758–2005*. Harvard University Press, Cambridge, Massachusetts (CD-ROM).
- Brady, S.G. (2003) Evolution of the army ant syndrome: the origin and long-term evolutionary stasis of a complex of behavioral and reproductive adaptations. *Proceedings of the National Academy of Sciences (USA)*, 100, 6575–6579.
- Brady, S.G. & Ward, P.S. (2005) Morphological phylogeny of army ants and other dorylomorphs (Hymenoptera: Formicidae). *Systematic Entomology*, 30, 593–618.
- Brady, S.G., Schultz, T.R., Fisher, B.L. & Ward, P.S. (2006) Evaluating alternative hypotheses for the early evolution and diversification of ants. *Proceedings of the National Academy of Sciences (USA)*, 28, 18172–18177.
- Brown, W.L., Jr. (1952) New synonymy in the army ant genus *Aenictus* Shuckard. *Psyche*, 58, 123.
- Brown, W.L., Jr. (1958) The army ant *Aenictus exiguus* Clark a synonym. *Psyche*, 64, 5.
- Clark, J. (1928) Australian Formicidae. *Journal of the Royal Society of Western Australia*, 14, 29–41.
- Clark, J. (1934) New Australian ants. *Memoirs of the National Museum, Victoria*, 8, 21–47.

- Crawley, W.C. (1923) Myrmecological notes. New Australian Formicidae. *Entomologist's Record and Journal of Variation*, 35, 177–179.
- Dalla Torre, C.G. de. (1893) *Catalogus Hymenopterorum*, hucusque descriptorum systematicus et synonymicus, 7, 289 pp. Lipsiae.
- Disney, R.H.L. & Kistner, D.H. (1991) A new genus of Australasian/Oriental Phoridae associated with driver ants (Diptera; Hymenoptera, Formicidae). *Sociobiology*, 18, 269–281.
- Donisthorpe, H. (1941) Descriptions of new species of ants from New Guinea. *Annals and Magazine of Natural History*, (11) 7, 129–144.
- Donisthorpe, H. (1948) A fourth instalment of the Ross Collection of ants from New Guinea. *Annals and Magazine of Natural History*, (12) 1, 131–143.
- Forel, A. (1890) *Aenictus-Typhlatta* découverte de M. Wroughton. Nouveaux genres de formicides. *Annales de la Société Entomologique de Belgique. Comptes-rendus*, 34, cii–cxiv.
- Forel, A. (1900) Ponerinae et Dorylinae d'Australie. Récoltés par MM. Turner, Froggatt, Nugent, Chase, Rothney, J.-J. Walker, etc. *Annales de la Société Entomologique de Belgique*, 44, 54–77.
- Forel, A. (1901) Les formicides de l'Empire des Indes et de Ceylan. Part 8. Sous famille Dorylinae. *Journal of the Bombay Natural History Society*, 13, 462–477.
- Forel, A. (1911) Sur le genre *Metapone* n. g. nouveau groupe des Formicides et sur quelques autres formes nouvelles. *Revue Suisse de Zoologie*, 19, 445–459.
- Forel, A. (1913) Fourmis de Tasmanie et d'Australie récoltées par MM. Lae, Froggatt etc. *Bulletin de la Société Vaudoise des Sciences Naturelles*, (5) 49, 173–195.
- Gotwald, W.H. (1995) *Army ants: the biology of social predation*. Cornell University Press, Ithaca and London, 320 pp.
- Karavaiev, V. (1926) Ameisen aus dem Indo-Australischen Gebiet. *Treubia*, 8, 413–445.
- Karavaiev, V. (1927) Ameisen aus dem Indo-Australischen Gebiet. III. *Zbirnyk Prats' Zoolohichnoho Muzeju*, 3, 3–52.
- Mayr, G. (1866) Myrmecologische Beiträge. *Sitzungsberichte der k. Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe*, 53, 484–517.
- Moreau, C.S., Bell, C.D., Vila, R., Archibald, S.B. & Pierce, N.E. (2006) Phylogeny of the ants: Diversification in the age of angiosperms. *Science*, 312, 101–104.
- Naumann, I.D., Cardale, J.C., Taylor, R.W. & MacDonald, J. (1994) Type specimens of Australian Hymenoptera (Insecta) transferred from the Macleay Museum, University of Sydney, to the Australian National Insect Collection, Canberra. *Proceedings of the Linnaean Society of New South Wales*, 114, 69–72.
- Santschi, F. (1933) Contribution à l'étude des fourmis de l'Afrique tropicale. *Bulletin et Annales de la Société Entomologique de Belgique*, 73, 95–108.
- Shattuck, S.O. (1999) Australian Ants: Their biology and identification. *Monographs in Invertebrate Taxonomy*, 3, 1–226.
- Shuckard, W.E. (1840) Monograph of the Dorylidae, a family of these Hymenoptera Heterogyna. *Annals and Magazine of Natural History*, (1)5, 258–271.
- Smith, F. (1857) Catalogue of the hymenopterous insects collected at Sarawak, Borneo; Mount Ophir, Malacca; and at Singapore, by A. R. Wallace. *Journal of the Proceedings of the Linnaean Society of London, Zoology*, 2, 42–88.
- Schneirla, T.C. (1971) *Army ants. A study in social organization*. W. H. Freeman & Co., San Francisco, 349 pp.
- Wheeler, G.C. & Wheeler, J. (1964) The ant larvae of the subfamily Dorylinae: supplement. *Proceedings of the Entomological Society of Washington*, 66, 129–137.
- Wheeler, G.C. & Wheeler, J. (1984) The larvae of the army ants: a revision. *Journal of the Kansas Entomological Society*, 57, 263–275.
- Wheeler, W. M. (1930) Philippine ants of the genus *Aenictus* with descriptions of the females of two species. *Journal of the New York Entomological Society*, 38, 193–212.
- Wilson, E.O. (1964) The true army ants of the Indo-Australian area. *Pacific Insects*, 6, 427–483.