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Tales of dracula ants: the evolutionary history of the ant subfamily Amblyoponinae (Hymenoptera: Formicidae)

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Abstract. The ants in the subfamily Amblyoponinae are an old, relictual group with an unusual suite of morphological and behavioural features. Adult workers pierce the integument of their larvae to imbibe haemolymph, earning them the vernacular name 'dracula ants'. We investigate the phylogeny of this group with a data set based on 54 ingroup taxa, 23 outgroups and 11 nuclear gene fragments (7.4 kb). We find that the genus *Opamyrma* has been misplaced in this subfamily: it is a member of the leptanilline clade and sister to all other extant Leptanillinae. Transfer of *Opamyrma* to Leptanillinae renders the Amblyoponinae monophyletic. The enigmatic Afrotropical genus *Apomyrma* is sister to all other amblyoponines, and the latter cleave into two distinct and well-supported clades, here termed POA and XMMAS. The POA clade, containing *Prionopelta*, *Onychomyrmex* and *Amblyopone*, is well resolved internally, and its structure supports synonymy of the genus *Concoctio* under *Prionopelta* (**syn.n.**). The XMMAS clade comprises two well-supported groups: (i) a predominantly Neotropical clade, for which we resurrect the genus name *Fulakora* (**stat.r., stat.n.**), with junior synonyms *Paraprionopelta* (**syn.n.**) and *Ericapelta* (**syn.n.**); and (ii) the remaining taxa, or 'core XMMAS', which are manifested in our study as a poorly resolved bush of about a dozen lineages, suggesting rapid radiation at the time of their origin. Most of these XMMAS lineages have been assigned to the catch-all genus *Stigmatomma*, but the more distinctive elements have been treated as separate genera (*Xymmer*, *Mystrium*, *Myopopone* and *Adetomyrma*). Resolution of basal relationships in the core XMMAS clade and reconfiguration of '*Stigmatomma*' to restore monophyly of all named genera will require more extensive genetic data and additional morphological analysis. However, the genus *Bannapone* can be synonymized under *Stigmatomma* (**syn.n.**) because it is embedded within a clade that contains *S. denticulatum*, the type species of *Stigmatomma*. Divergence dating analysis indicates that crown Amblyoponinae arose in the mid-Cretaceous, about 107 Ma (95% highest probability density: 93–121 Ma). The POA and XMMAS clades have estimated crown ages of 47 and 73 Ma, respectively. The initial burst of diversification in the core XMMAS clade occurred in the Late Paleocene/Early Eocene (50–60 Ma). Ancestral range reconstruction suggests that amblyoponines originated in the Afrotropics, and dispersed to the Indo-Malayan region and to the New World. During none of these dispersal events did the ants break out of their cryptobiotic lifestyle.

Introduction

Biological diversity is far from evenly distributed among different kinds of organisms. Evolutionarily successful groups, containing hundreds or thousands of species, often stand in contrast to their depauperate sister lineages (Donoghue & Sanderson, 2015). Biologists have long been intrigued by 'relictual taxa', i.e. groups that are old and yet contain relatively few extant species compared with their relatives (Habel & Assmann, 2010). Typically these relicts retain characteristics considered ancestral in comparison to related clades, and they often live in habitats

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that shield them from competition with their more derived relatives. Study of such organisms can be hampered by their occurrence in cryptic or inaccessible locations (Naskrecki, 2011).

Ants (Hymenoptera: Formicidae) are the most successful and ecologically dominant group of eusocial insects (Hölldobler & Wilson, 1990; Lach *et al.,* 2009), but different clades of ants vary markedly in dominance and diversity and they include a considerable number of taxonomic relicts (Wilson *et al.,* 1956; Rabeling *et al.,* 2008; Yamane *et al.,* 2008; Pie & Feitosa, 2016). The ant subfamily Amblyoponinae falls under this rubric: its species live and forage almost exclusively underground in the soil or undercover in leaf litter and rotten logs, where they hunt specialized prey such as geophilomorph centipedes (Brown, 1960). Occurring in all major biogeographic regions but usually infrequently encountered, amblyoponine ants currently number about 130 described species, apportioned among 13 genera (AntCat, 2016). Although there are additional undescribed (or unidentifiable) amblyoponine specimens in collections, the group is clearly dwarfed in size by other, more prominent ant subfamilies of equivalent (or younger) age, such as Ponerinae, Dorylinae, Formicinae and Myrmicinae (Ward, 2014).

Amblyoponine ants are often considered to be ‘primitive’ in morphology and social behaviour (Haskins, 1970; Traniello, 1982; Masuko, 1986; Ito, 1993; Peeters, 1997; Thorne & Traniello, 2003). The members of this subfamily are typically slow and lumbering in their movements (Wilson, 1958) and do not exhibit some of the more complex forms of communication and social organization seen in other ants. At the same time, they have a number of obviously derived characteristics such as small (or nonexistent) worker eyes, reduction/fusion of sclerites, and a narrow prey spectrum. Other intriguing features of uncertain polarity include the specialized, peg-like setae on the anterior margin of the clypeus (Ward, 1994); the broad attachment of the petiole to the rest of the metasoma (Bolton, 2003); and the habit of adult ants of biting larvae with their mandibles and consuming the exuding haemolymph (Masuko, 1986; Ito & Billen, 1998; Wild, 2005; Ito, 2010). This last behaviour has earned amblyoponines the sobriquet ‘dracula ants’ (Saux *et al.,* 2004), although larval haemolymph feeding is known to occur in a few other ant taxa, including *Leptanilla* and *Proceratium* (Masuko, 1986, 1989).

Despite limited species diversity, the Amblyoponinae show notable phenotypic variation (Fig. 1). Some species in the genus *Mystrium* have bizarre miniature queens smaller in size than the workers and differing markedly in colour (Molet *et al.,* 2009). The genus *Adetomyrma* is characterized by highly modified metasomal morphology in workers, with apparent reversal of tergosternal fusion (Ward, 1994). Ants in the genus *Onychomyrmex* have army ant-like lifestyles, with nomadic colonies and modified wingless queens (Wheeler, 1916; Miyata *et al.,* 2003). The robustly built workers of *Myopopone castanea* paralyse large cerambycid larvae in rotten logs, and apparently transport their larvae to the prey in some instances (Wilson, 1958), although retrieval of food to the nest has also been reported (Ito, 2010).

For most of their taxonomic history, these ants were treated as a tribe, Amblyoponini, within the subfamily Ponerinae (Emery, 1911; Brown, 1954, 1960; Bolton, 1995). The composition of Amblyoponini varied somewhat but was stabilized in a landmark generic revision by Brown (1960). Bolton (2003) noted the heterogeneous nature of the subfamily Ponerinae (as then defined) and, among other actions, he reinstated Amblyoponinae as its own subfamily. This decision has been validated by subsequent molecular phylogenetic studies showing that other taxa are interpolated between these two subfamilies, within a larger assemblage of ants known as the poneroid group (Brady *et al.,* 2006; Moreau *et al.,* 2006; Rabeling *et al.,* 2008; Schmidt, 2013).

The relationships of amblyoponine ants to one another and to other poneroids have not been fully resolved. Inferences based on morphology (Yoshimura & Fisher, 2012) and DNA sequence data (Saux *et al.,* 2004; Brady *et al.,* 2006; Moreau & Bell, 2013) have suggested the existence of two major amblyoponine clades, here termed POA and XMMAS (cf. Yoshimura & Fisher, 2012). But there are two other enigmatic ant genera, currently placed in Amblyoponinae, whose affinities are unclear. *Apomyrma* is an Afrotropical genus, known from one described and several undescribed species, whose peripatetic taxonomic history has seen it assigned to Amblyoponinae, Leptanillinae and its own subfamily, Apomyrminae (Bolton, 2003). *Opamyrma* is a monotypic genus known only from two workers collected in Vietnam; it evinces a curious combination of leptanilline-like and amblyoponine-like features (Yamane *et al.,* 2008). These two taxa, both subterranean and with pale, blind workers, are superficially similar to one another, but whether this is due to close relationship or convergence remains unclear (Ward, 2014).

In this study we investigate the phylogenetic relationships of Amblyoponinae using a comprehensive set of taxa and 11 nuclear gene fragments. We confirm the division of the subfamily into two major clades and we clarify the positions of *Apomyrma* and *Opamyrma*. We also propose several taxonomic changes to bring the classification in line with new phylogenetic findings.

Materials and methods

Taxon sampling and gene sequencing

Our 77-taxon data set consists of 54 amblyoponines, including *Opamyrma hungvuong* and three *Apomyrma* species, as well as 23 outgroups: 19 other ants, and four non-ant aculeate Hymenoptera (Table S1, Supporting Information). Among the latter, two taxa (*Scolia*, *Apterogyna*) were used as ‘outer outgroups’ to root the tree, based on inferred aculeate relationships (Johnson *et al.,* 2013). The sequenced amblyoponines include representatives of all genera, with multiple species of most of them, and 31 species of *Stigmatomma*, a group suspected of being nonmonophyletic (Esteves & Fisher, 2015).

We sequenced fragments of 11 nuclear genes: abdominal-A (abdA), elongation factor 1-alpha F2 copy (EF1aF2), long wavelength rhodopsin (LW Rh), arginine kinase (argK), DNA topoisomerase I (Top1), ultrabithorax (Ubx), DNApol-delta (POLD1), NaK ATPase (NaK), Antennapedia (Antp), wingless (wg) and 28S ribosomal DNA (28S). The data matrix has

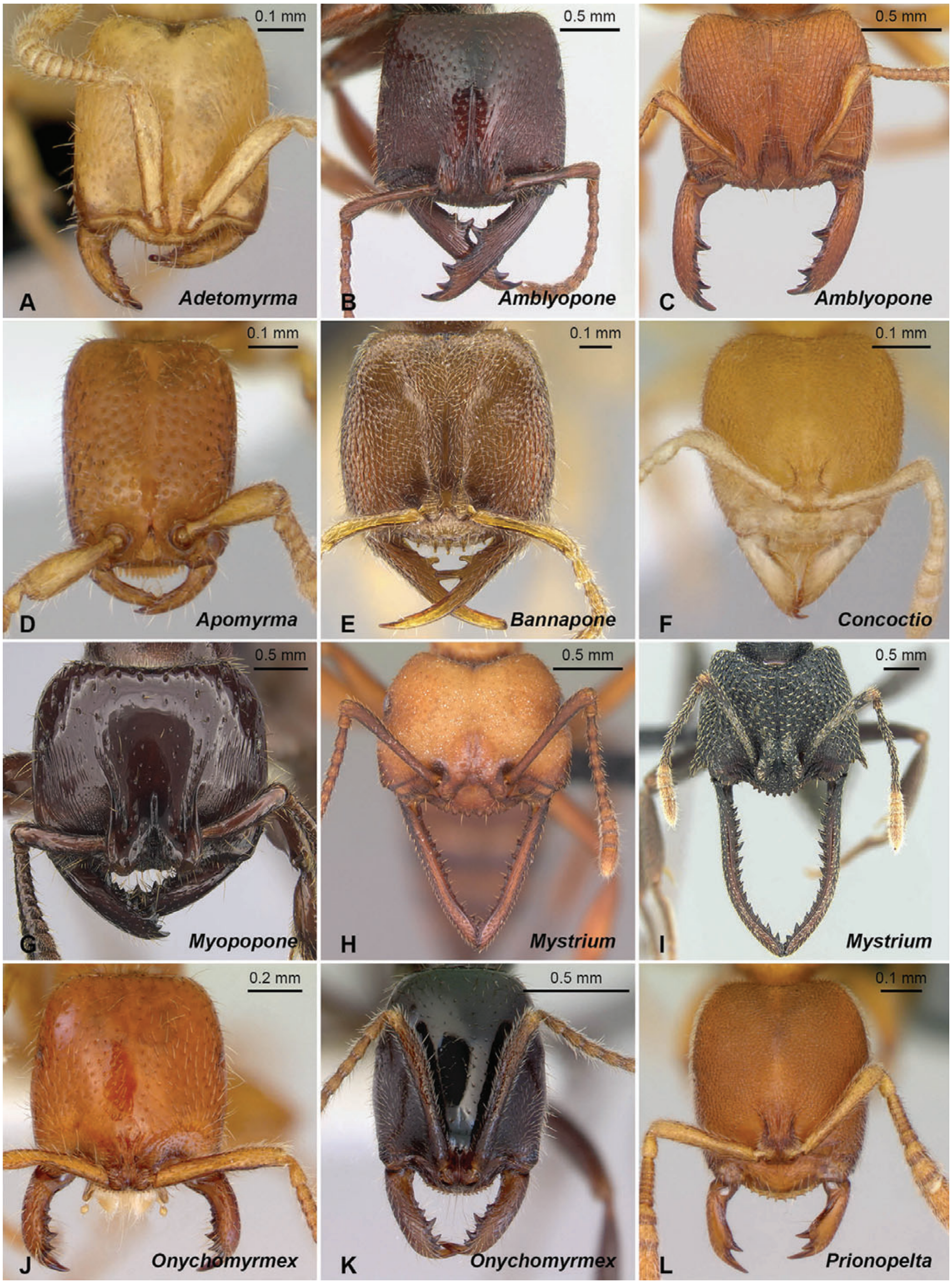

Fig. 1. Morphological diversity in Amblyoponinae. (A–R) Full-face view of worker head; (S–V): lateral view of worker body. (A) *Adetomyrma venatrix* (CASENT0489808); (B) *Amblyopone australis* (CASENT0434465); (C) *Amblyopone longidens* (CASENT0100485); (D) *Apomyrma stygia* (CASENT0000077); (E) *Bannapone scrobiceps* (CASENT0339957); (F) *Concoctio concenta* (CASENT0004306); (G) *Myopopone castanea* (CASENT0260455); (H) *Mystrium mirror* (CASENT0492109); (I) *Mystrium shadow* (CASENT0077648); (J) *Onychomyrmex mjobergi* (CASENT0172295); (K) *Onychomyrmex* AU03 (CASENT0172301); (L) *Prionopelta subtilis* (CASENT0494610); (M) *Stigmatomma rothneyi* (CASENT0914940); (N) *Stigmatomma saundersi* (CASENT0006813); (O) *Stigmatomma zwaluwenburgi* (CASENT0173925); (P) *Stigmatomma mystriops* (CASENT0178868); (Q) *Xymmer* MG04 (CASENT0151732); (R) *Xymmer* MG01 (CASENT0033448); (S) *Amblyopone australis* (CASENT0260444); (T) *Myopopone castanea* (CASENT0260455); (U) *Mystrium janovitzi* (CASENT0006082); (V) *Onychomyrmex doddi* (CASENT0172297). In this study, *S. saundersi* (N) and *S. mystriops* (P) are transferred to the newly resurrected genus *Fulakora* (see text). Images from AntWeb (http://www.antweb.org).

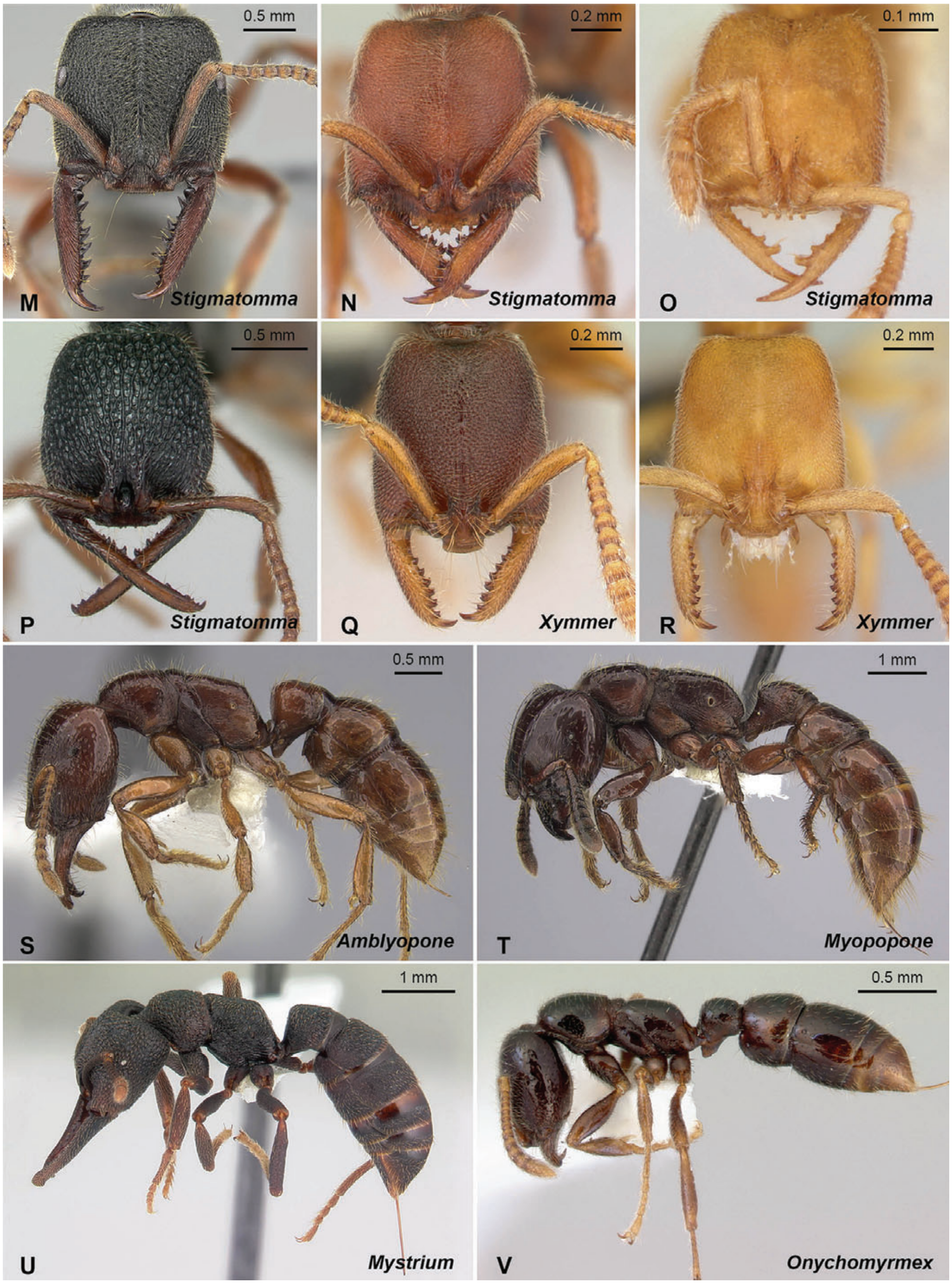

Fig. 1. Continued.

no missing fragments (Table S1, Supporting Information). Of the 847 sequences, 675 were newly generated for this study (GenBank accession numbers KU671399-KU672073).

Methods of DNA extraction, amplification and sequencing are detailed elsewhere (Ward & Downie, 2005; Brady *et al.,* 2006; Ward *et al.,* 2010). For most samples we carried out two rounds of amplification, with the second amplification employing a nested or hemi-nested pair of primers. The primers for three genes new to this study (POLD1, NaK, and Antp) are given in Table S2, Supporting Information. Sequences were assembled with SEQUENCHER v5.2.2 (Gene Codes Corporation, Ann Arbor, MI, U.S.A.), aligned with CLUSTAL X v2.1 (Thompson *et al.,* 1997), and manually edited and concatenated with MACCLADE v4.08 (Maddison & Maddison, 2005). We excluded introns of

Table 1. Partition scheme selected by PARTITIONFINDER.

Blocks	Partition	Model
AA_pos1, DP_pos2, UB_pos1	p1	HKY + I + G
AA_pos2, UB_pos2	p2	GTR + I + G
AA_pos3	p3	HKY + I + G
F2_pos3	p4	K80 + I + G
F2_pos1, NK_pos1, TP_pos1	p5	GTR + I + G
AK_pos2, F2_pos2	p6	GTR + I + G
AK_pos3, LR_pos3, NK_pos3	p7	GTR + I + G
LR_pos1	p8	SYM + I + G
LR_pos2	p9	GTR + I + G
AK_pos1, DP_pos1	p10	SYM + I + G
TP_pos3	p11	K80 + I + G
TP_pos2	p12	HKY + I + G
AP_pos3, UB_pos3	p13	K80 + I + G
DP_pos3	p14	HKY + I + G
NK_pos2	p15	K80 + I
AP_pos1	p16	GTR + I + G
AP_pos2	p17	GTR + I + G
Wg_pos3	p18	GTR + I + G
28S, Wg_pos1, Wg_pos2	p19	GTR + I + G

Codes for each gene are as follows: AA, abdominal-A; F2, elongation factor 1-alpha F2 copy; LR, long-wavelength rhodopsin; AK, arginine kinase; TP, DNA topoisomerase 1; UB, ultrabithorax; DP, DNApol-delta; NK, NaK ATPase; AP, Antennapedia; Wg, wingless; and 28S, 28S ribosomal DNA.

LW Rh (544 bp in the alignment) and ArgK (1422 bp), as well as hypervariable regions of 28S (157 bp) and autapomorphic indels in the exons of abdA (3 bp), Antp (66 bp) and Wg (18 bp). After these exclusions the data matrix comprised 7426 bp, of which 3523 sites were variable and 2945 were parsimony-informative. This matrix has been deposited in TreeBase (S18847).

Data analysis: partitioning

We partitioned the sequence data into 31 blocks, corresponding to 28S and the three codon positions of each of the ten protein-coding genes. We then ran PARTITIONFINDER v1.1.1 (Lanfear *et al.,* 2012) to choose among partition schemes and models, with models = mrbayes, model_selection = bic, and search = greedy. This resulted in the 19-partition scheme and models indicated in Table 1.

Phylogenetic analyses

For phylogenetic inference under maximum likelihood (ML) we used GARLI 2.0 (Zwickl, 2006), as implemented on the CIPRES Science Gateway V. 3.3 (http://www.phylo.org/portal2), and employed the 19-partition scheme selected by PARTITIONFINDER. Departures from GARLI default settings were as follows: genthreshfortopoterm was set to 200 000, as opposed to the default of 20 000; and modweight was set to 0.01, i.e. 0.0005 × (#partitions + 1), as opposed to the default of 0.05. Forty search replicates were undertaken in the search for the ML tree. A bootstrap analysis was also conducted using 100 bootstrap replicates and genthreshfortopoterm set to 100 000.

Bayesian analysis was carried out with MRBAYES 3.2.3 (Ronquist *et al.,* 2012), as implemented on CIPRES, using the same 19-partition scheme. We set brlenspr to unconstrained:exponential (100), corresponding to a mean length prior of 0.01 (as opposed to the MRBAYES default of 0.1), which better matches the shorter branch lengths in this data set (see also Ward *et al.,* 2010). We ran MRBAYES for 40 million generations, with nchains = 4, nruns = 2, sample freq = 1000, and the default 25% burn-in. Indications that stationarity had been achieved included: (i) standard deviation of split frequencies values of ~0.01 or less; (ii) potential scale reduction factor values of 1.000 for all parameters; (iii) minimum effective sample size (ESS) values > 2000; and (iv) similar harmonic mean likelihoods between the two runs.

We also ran a second MRBAYES analysis, similar to the above, except that rather than assigning a fixed substitution model to each partition we sampled across model space (lset nst = mixed) for each partition. This yielded results almost identical to the first analysis, with respect to tree topology and node support, so we present the results of the first (fixed model) analysis only.

Divergence dating

We conducted divergence dating with BEAST 2.3.0 (Bouckaert *et al.,* 2014) on a data matrix from which outgroups had been excluded. Because of concerns that partitioned analyses can result in spurious precision of divergence time estimates (Dos Reis *et al.,* 2014; Zhu *et al.,* 2015), we treated this as a single partition to which we applied the GTR + G model. We chose an uncorrelated lognormal relaxed-clock model with a Yule birth process. Three fossil-calibrated nodes were assigned lognormal priors on age (Table 2), while the root node (Amblyoponinae) was assigned a diffuse normal prior with a mean of 90 Ma and a 95% highest probability density (hpd) of 70–110 Ma, to capture the range of prior estimates appearing in the literature (Brady *et al.,* 2006; Moreau & Bell, 2013; Schmidt, 2013). Based on the results of previous ML and Bayesian analyses *Apomyrma* was constrained to be sister to all other amblyoponines. We ran BEAST for 50 million generations, sampling every 5000 generations. Examination of log files with TRACER v1.6 (Rambaut *et al.,* 2014) indicated that stationarity had been achieved by five million generations (all ESS values > 700), so we employed a burn-in of 10%.

Biogeographic inference

We investigated range evolution in amblyoponine ants with the dispersal–extinction–cladogenesis model of LAGRANGE v20130526 (Ree & Smith, 2008). We coded each terminal taxon according to its occurrence in six major biogeographic areas: Neotropical (T), Nearctic (N), Palearctic (P), Afrotropical (E), Indomalayan (O), and Australasian regions (A) (Cox, 2001). The input for this analysis was the ultrametric tree generated by BEAST, with branch lengths in units of time (Ma), and a matrix of distribution ranges of the terminal taxa (Table S3, Supporting

Table 2. Prior age distributions applied to three fossil-calibrated nodes for BEAST dating analysis.

Taxon (stem-group)	Offset	Median	95% quantile	Log (mean)	Log (SD)	Comments
Stigmatomma denticulatum group	42	55	80	2.57	0.65	*Stigmatomma groehni*, in Baltic amber, said to be member of *S. denticulatum* group (Dlussky, 2009)
Stigmatomma mystriops group	15	40	60	3.22	0.36	Undescribed species from Dominican amber, similar to *S. mystriops* (AntWeb CASENT0906275)
Prionopelta	15	40	60	3.22	0.36	Undescribed *Prionopelta* species from Dominican amber (Wilson, 1988)

Information). The adjacency matrix and dispersal rates (over two time periods: 0–50 and 50–110 Ma) were the same as those used in Ward *et al.* (2015), and the maximum ancestral range size was set to three areas.

Results

Phylogenetic relationships

Maximum likelihood and Bayesian analyses yielded similar tree topologies, with comparable branch support (Fig. 2). The Amblyponinae are part of a poneroid clade that is sister to the formicoids. Leptanillinae and *Martialis* fall outside these two groups. One of the more striking findings concerns the placement of *Opamyrma*. It is recovered as sister to Leptanillinae and the clade comprising these two taxa has very strong support: Bayesian posterior probability (PP) of 1.00 and ML bootstrap support (MLBS) of 100%. The (Leptanillinae + *Opamyrma*) clade is well separated from the Amblyoponinae, with the latter being more closely related to other poneroids and even to the formicoid clade than to leptanillines (Fig. 2). With *Opamyrma* removed, the Amblyoponinae are monophyletic (PP = 1.00, MLBS = 92%), with *Apomyrma* (PP = 1.00; MLBS = 100%) sister to the remaining taxa (PP = 1.00, MLBS = 65%). These remaining taxa are further divided into two distinct clades, POA and XMMAS, each with maximum support (PP = 1.00, MLBS = 100%).

The POA clade comprises *Prionopelta*, *Concoctio*, *Onychomyrmex* and *Amblyopone*. The last two genera, both confined to the Australian biogeographic region, are recovered as sister taxa (PP = 1.00, MLBS = 94% for the combined clade). *Concoctio*, a monotypic African genus, appears to be nested within, or at least closely related to, the tropicopolitan genus *Prionopelta*. This result motivates synonymy of *Concoctio* under *Prionopelta* (see later).

Most amblyoponine diversity resides within the XMMAS clade, containing species assigned to the genera *Xymmer*, *Myopopone*, *Mystrium*, *Adetomyrma* and *Stigmatomma*, as well as *Bannapone* and *Paraprionopelta*. Most of these are monophyletic (PP 1.00, MLBS 100%) or monotypic, but the genus *Stigmatomma*, as currently defined, is highly artificial. It essentially encompasses all of the less derived members of XMMAS. The type species, *S. denticulatum*, is part of a well-supported group (PP = 1.00, MLBS = 100%) of Palearctic and Southeast Asian species that includes *Bannapone*. The XMMAS clade as a whole is divided into two very well-supported groups (PP = 1.00, MLBS = 100%): (i) a predominantly Neotropical clade, for which we resurrect the genus name *Fulakora* (see later); and (ii) all remaining taxa, here referred to as 'core XMMAS'. In contrast to the other parts of the amblyoponine phylogeny, the base of core XMMAS is very poorly resolved, manifested as a bush-like radiation of a dozen lineages – seven well-supported clades (PP = 1.00, MLBS = 100%) and five isolated species. This limits our ability to reconfigure the genus-level classification of the subfamily.

Nevertheless, the XMMAS clade does include a number of well-supported subgroups with distinct biogeographic affinities. *Fulakora* appears to be largely restricted to the Neotropics, with a few species in New Zealand, eastern Australia, New Guinea and the Solomon Islands. Within core XMMAS there are subgroups of species occurring in the Afrotropics (*Adetomyrma*), Southeast Asia (*Myopopone*) or both (*Mystrium*, *Xymmer*).

Divergence dates and biogeographic history

The chronogram resulting from the BEAST analysis (Fig. 3) suggests that the subfamily Amblyoponinae is indeed an old clade, with a crown-group origin in the mid-Cretaceous, about 107 Ma (95% hpd, 93–121 Ma). Discounting the *Apomyrma* lineage, the remaining amblyoponines have an estimated crown age of 101 Ma (95% hpd, 88–115 Ma). The two sister groups, the XMMAS clade and the POA clade, have estimated crown origins of 73 Ma (95% hpd, 64–83 Ma) and 47 Ma (95% hpd, 38–57 Ma), respectively, indicating more extensive pruning of early lineages in the latter. Initial diversification of the 'core XMMAS' clade took place 50–60 Ma, in the late Paleocene/early Eocene.

Age estimates for individual genera are mostly in the range 15–20 Ma, bracketed by *Xymmer* (29 Ma; 95% hpd, 23–36 Ma) and *Adetomyrma* (10 Ma; 95% hpd, 6–14 Ma). The newly resurrected *Fulakora* is older, at 52 Ma (95% hpd, 43–62 Ma), while the remaining, paraphyletic assemblage of *Stigmatomma* species dates to 59 Ma (95% hpd, 53–66 Ma).

Ancestral range inferences suggest that the Paleotropics have been the predominant arena for amblyoponine diversification (Fig. 3), with an origin in the Afrotropical region. *Apomyrma*

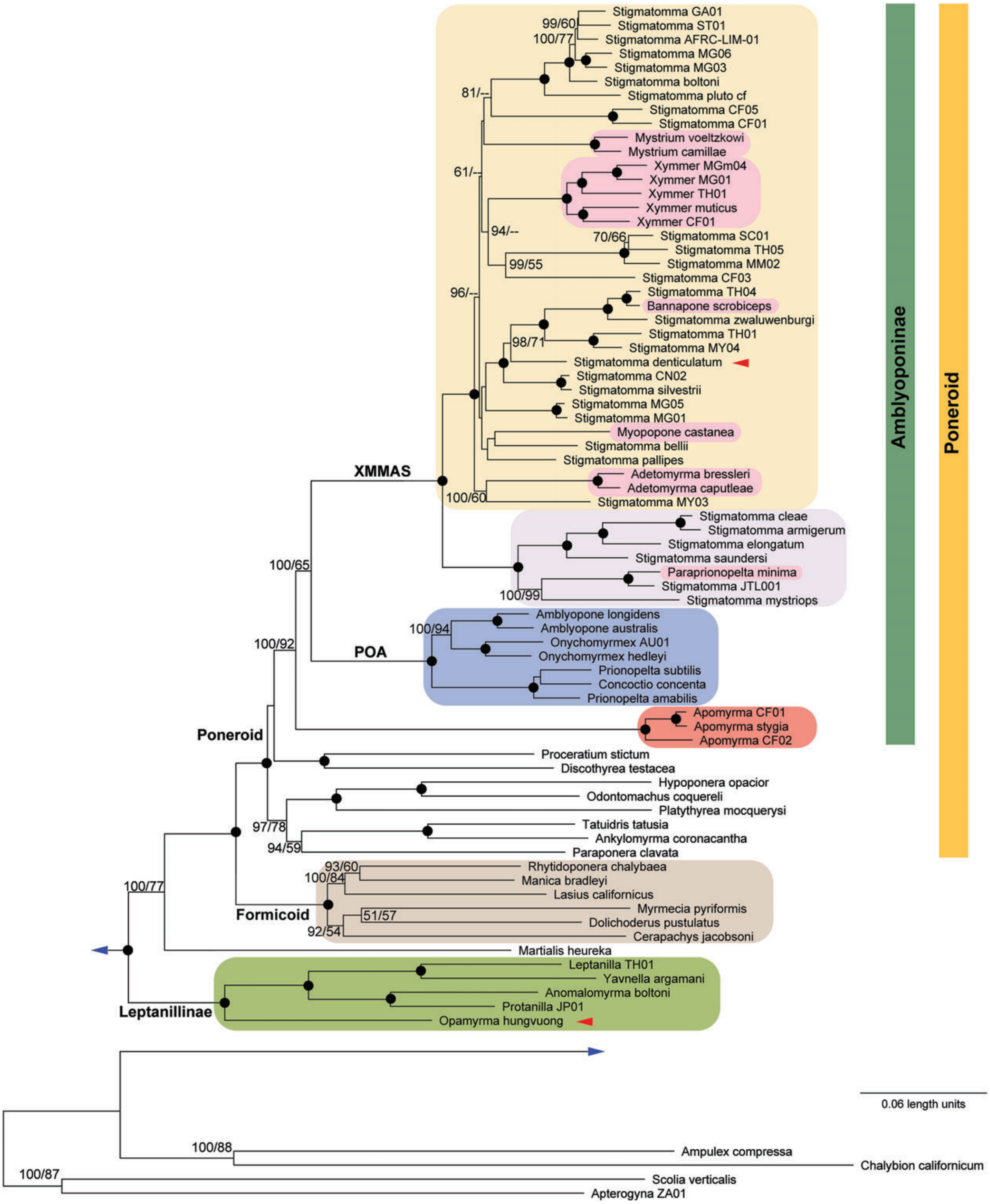

Fig. 2. Phylogeny of the ant subfamily Amblyoponinae and related taxa, based on 11 nuclear genes. This is the maximum likelihood (ML) tree found by GARLI (−ln L 113531.8202), with node support derived from separate Bayesian and ML bootstrap analyses. Support values >50 are indicated at each node as Bayesian posterior probability (PP) × 100, followed by ML bootstrap percentage (MLBS). Black dots signify support values of 100/100. Two taxa of particular interest are highlighted with red arrows: *Stigmatomma denticulatum*, the type species of *Stigmatomma*; and *Opamyrma hungvuong*, a species whose phylogenetic placement has been unclear. 'POA' and 'XMMAS' signify two major clades of Amblyoponinae. The subclade highlighted in grey, which is sister to all other XMMAS, corresponds to the genus *Fulakora*, newly resurrected in this study (see text). 'Poneroid' and 'Formicoid' refer to two major groups of ants, here both recovered as monophyletic.

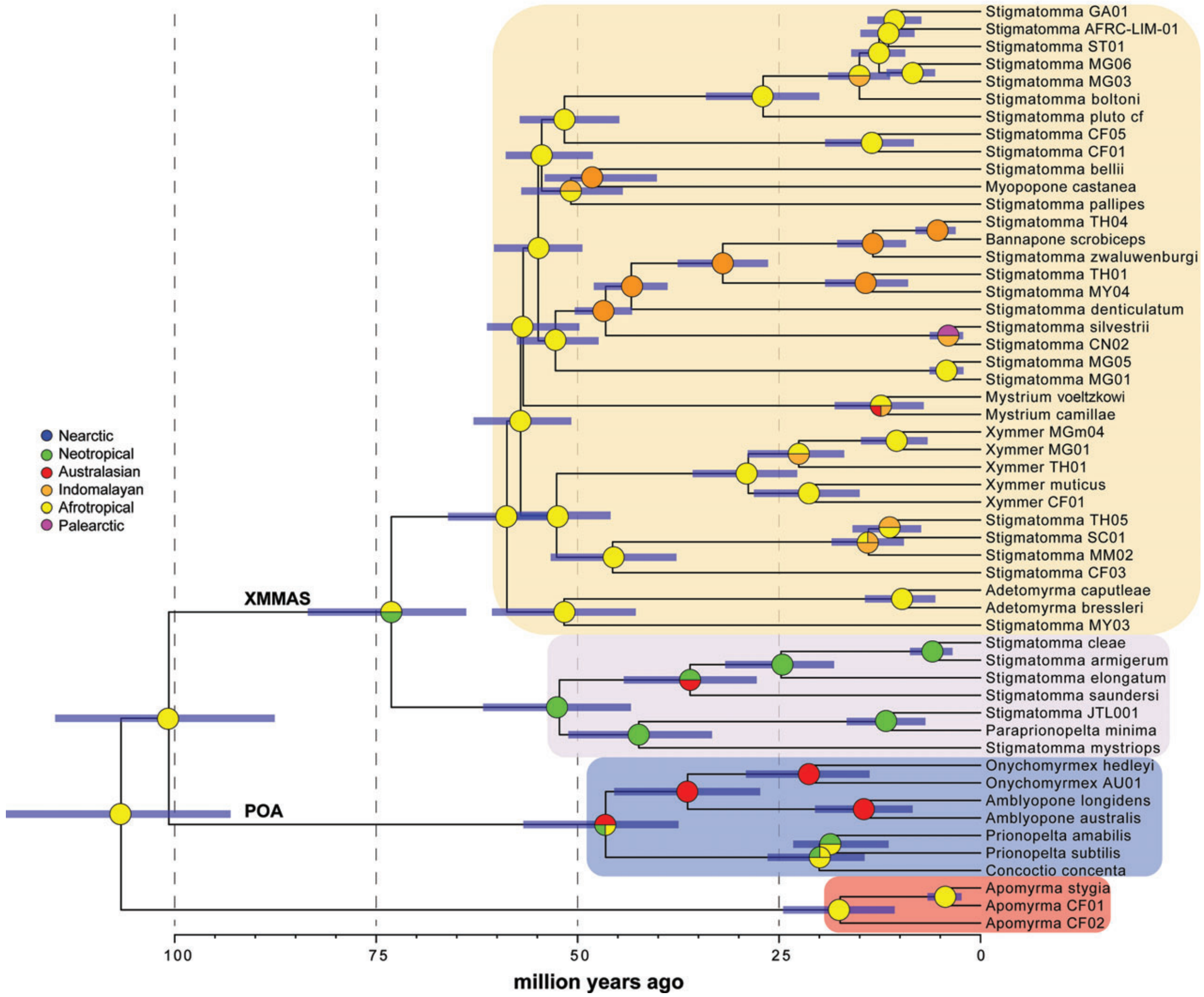

Fig. 3. Chronogram and biogeographic history of the Amblyoponinae based on BEAST2 and LAGRANGE analyses. Horizontal blue bars depict the 95% highest probability density of age estimates. Biogeographical analysis employed a dispersal–extinction–cladogenesis model, and six regions. The ancestral range inheritance scenario with the highest relative probability is indicated for the two descending branches of each node; the lower half of the sphere refers to the lower descending branch; the upper half to the upper descending branch. Most (75%) of the relative probabilities are greater than 0.60, but for some deeper nodes the most probable scenario has weak support and there are alternative scenarios of only slightly lower relative probability. Table S4, Supporting Information, provides a more detailed account of range inheritance scenarios for the major lineages of Amblyoponinae.

has remained confined to the African continent but the other amblyoponines dispersed (at a slow rate) to Indomalaya, the Palearctic, and the Neotropics. Such reconstructions have high probability for most branches, but there remains greater uncertainty in deeper parts of the tree (Table S4, Supporting Information).

Taxonomic changes

The new phylogeny presented here provides the basis for several taxonomic changes. We are conservative in these actions, proposing only modifications that are supported by results with strong statistical support in the tree (Fig. 2). For all generic and species names cited, the author, year, and original citation can be found in AntCat (2016). Taxonomic changes are given in tabular format in Table S5, Supporting Information.

Opamyrma is here transferred from Amblyoponinae to the subfamily Leptanillinae. Its position as sister to other Leptanillinae was recovered in all analytical treatments, with maximum support. In the original description of this genus (Yamane *et al.,* 2008), the authors noted similarities to Leptanillinae (shape of clypeus, configuration of metapleural gland orifice, and hypertrophied pygidium) and expressed some uncertainty about its placement in Amblyoponinae. Those reservations now appear to have been fully justified. The definition of subfamily Leptanillinae is hereby expanded to include *Opamyrma*, whose workers have a single-segmented waist (the petiole), in contrast to other Leptanillinae whose workers have a two-segmented waist composed of the petiole (A2) and postpetiole (A3).

Opamyrma (Leptanillinae) is separable from *Apomyrma* (Amblyoponinae), which also has a one-segmented nodiform waist, by the placement of the helcium. In *Apomyrma*, the helicium is attached low down on the anterior face of the first gastral segment (A3), while in *Opamyrma* the helcium is attached at mid-height, as in other Leptanillinae.

Based on its placement within *Prionopelta* in the ML tree (Fig. 2), the genus *Concoctio* is synonymized (**syn.n.**) under *Prionopelta*, and its sole species, *concenta*, is transferred to the latter genus (**comb.n.**).

Fulakora **stat.r., stat.n.** is resurrected from synonymy under *Stigmatomma* and elevated to genus (it was previously a subgenus) to contain the species in the predominantly Neotropical clade that is sister to all other XMMAS taxa (see earlier). There are only two XMMAS lineages in the New World, and they have complementary distributions: *Stigmatomma pallipes* and two related species in North America, and *Fulakora* in Central and South America. *Fulakora* is also present in Australia and adjacent islands, where it overlaps marginally with other XMMAS species. *Paraprionopelta* and *Ericapelta*, both described from Argentina, are newly synonymized (**syn.n.**) under *Fulakora.*

Fulakora can be distinguished from *Stigmatomma* as follows. In workers of New World *Stigmatomma* (i.e. *S. pallipes* and relatives), the frontal lobes and antennal sockets are widely separated by a broadly rounded or triangular section of clypeus, and the teeth along the mid-length of the mandible are fused at the base. In contrast, in New World *Fulakora* workers, the frontal lobes are usually fused or separated by a very narrow extension of the clypeus. If the frontal lobes are widely separated (e.g. *F. mystriops*), then the inner surface of the mandible has two separate rows of teeth. In Australasian *Fulakora*, the frontal lobes are fused, the anterior subpetiolar process (keel) has a distinct fenestra, and the mesonotum is generally separated from the propodeum by a metanotal groove. In Australasian *Stigmatomma*, the subpetiolar process lacks a fenestra and the mesonotum is not separated from the propodeum by a metanotal groove.

The following are new combinations (except where noted otherwise) in *Fulakora*: *agostii*, *armigera*, *bierigi* (**comb.r.**), *celata* (**comb.r.**), *chilensis* (**comb.r.**), *cleae*, *degenerata*, *egregia*, *elongata* (**comb.r.**) (including synonyms *elongata barretoi*, *elongata minor*, *elongata paranensis*), *exigua*, *falcata*, *gnoma*, *gracilis* (**comb.r.**), *heraldoi*, *lucida* (**comb.r.**), *lurilabes*, *minima*, *monrosi*, *mystriops*, *orizabana* (including synonym *tropicalis*), *papuana*, *punctulata* (**comb.r.**), *saundersi* (**comb.r.**), *smithi*, and *wilsoni*. All transfers are from *Stigmatomma*, except *minima*, which is transferred from the newly synonymized *Paraprionopelta*. The revived combinations refer to previous combinations with *Fulakora* as a subgenus.

During examination of Australasian *Stigmatomma* species, two species were found to belong to the POA clade. *Stigmatomma ferrugineum* (including synonym *mandibularis*) is reassigned to *Amblyopone* (**comb.r.**) based on the shape of clypeus, mandibular dentition and frontal lobes. *Stigmatomma glauerti* is transferred to the genus *Onychomyrmex* (**comb.n.**) based on the presence in the male of two apical mandibular teeth and in the worker of proximal frontal lobes and an elongate apical tooth on the mandible. As a consequence, the erstwhile monotypic genus *Lithomyrmex* (of which *glauerti* is the type species), which was previously a junior synonym of *Stigmatomma*, becomes a junior synonym (**syn.n.**) of *Onychomyrmex*.

Bannapone is newly synonymized (**syn.n.**) under *Stigmatomma*, on the basis that it is embedded within the clade that contains the type species of that genus, namely *S. denticulatum*. We cannot fully resolve the '*Stigmatomma* problem' here, but no matter how the genus is ultimately redefined, it will almost certainly have to encompass *Bannapone* to avoid paraphyly of *Stigmatomma* (Fig. 2). Thus, although *Bannapone* has distinctive dentition (Eguchi *et al.,* 2015), it is properly interpreted as a specialized subset of taxa, nested within *Stigmatomma* (sensu stricto). This new synonymy results in the following transfers to *Stigmatomma*, all revived combinations unless otherwise noted: *caliginosum*, *crypticum* (**comb.n.**), *fulvidum*, *mulanae* (**comb.n.**), *pertinax*, *scrobiceps* (**comb.n.**), and *zwaluwenburgi*.

Discussion

Phylogenetic analyses based on 54 ingroup taxa and 11 nuclear genes reveal the principal divergence events within Amblyoponinae. *Opamyrma* is definitively excluded from the subfamily; the genus *Apomyrma* is sister to all other amblyoponines; and the latter split into the distinct and well-supported POA and XMMAS clades. Crown Amblyoponinae arose in the mid-Cretaceous, about 107 Ma, while the POA and XMMAS clades have estimated origins 47 and 73 Ma, respectively. The XMMAS clade comprises two well-supported groups: a predominantly Neotropical clade (*Fulakora*) and a poorly resolved bush of about a dozen lineages (core XMMAS). Diversification of the clades within this bush took place 50–60 Ma, in the late Paleocene/early Eocene. Morphologically distinctive elements in core XMMAS have been treated as separate genera (*Xymmer*, *Mystrium*, *Myopopone* and *Adetomyrma*), but many of the less divergent species have been placed in the catch-all paraphyletic genus, *Stigmatomma*. Our data are insufficient to allow resolution of basal relationships in core XMMAS and this also prevents full-scale reconfiguration of '*Stigmatomma*' to ensure monophyly of all recognized genera in the subfamily. This will require more comprehensive taxon and gene sampling, as well as additional morphological analyses.

Phylogenomic data offer the promise of better resolution of the more intractable parts of the ant tree-of-life (Blaimer *et al.,* 2015). This includes the 'core XMMAS' radiation in the amblyoponine tree, and the sequence of branching events separating Amblyoponinae from other poneroids. Our ML tree recovers Proceratiinae as the sister group of Amblyoponinae, but without convincing support (Fig. 2). These poneroid divergences are old (mid-Cretaceous) and subtended by short branches; they may prove to be challenging to resolve, even with genome-scale data.

Ancestral range reconstruction indicates that amblyoponines originated in the Afrotropics, and dispersed to the Indomalayan, Australasian and Neotropical regions (Fig. 3). For some of the more prominent, species-rich ant subfamilies, such as Formicinae and Myrmicinae, a New World origin is considered more likely (Moreau & Bell, 2013; Blaimer *et al.,* 2015; Ward *et al.,* 2015), although the subfamily Dolichoderinae appears to have arisen in the Paleotropics (Ward *et al.,* 2010). All such groups of dominant ants dispersed widely, however, and radiated extensively in other continental areas. This occurred throughout the Tertiary, accompanied by major innovations in nesting behavior, feeding biology and social organization. In contrast, there is no evidence that at any time in their long evolutionary history amblyoponines broke out of their cryptobiotic lifestyle, even during the period of rapid divergence of the 'core XMMAS' lineages 50–60 Ma. Retention of subterranean habits may have buffered these ants from above-ground drivers of extinction, especially competition with more aggressive ant clades. For the last 100 million years, it would seem, 'dracula ants' have stayed under the radar screen, nesting in cryptic locations, hunting specialized prey, and feeding on the haemolymph of their food-digesting larvae. Because of their elusive habits, many details of the biology and taxonomy of amblyoponines remain to be elucidated.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/syen.12186

Table S1. List of taxa sampled, voucher specimen codes, and GenBank accession numbers.

Table S2. Primers of three genes, DNApol-delta (POLD1), NaK ATPase (NaK) and Antennapedia (Antp), newly designed and employed in this study.

Table S3. Taxon distribution matrix, based on six biogeographic areas: Neotropical (T), Nearctic (N), Palearctic (P), Afrotropical (E), Indomalayan (O) and Australasian (A) regions.

Table S4. Range inheritance inferences for major clades of Amblyoponinae, based on LAGRANGE analysis.

Table S5. Summary of taxonomic changes in Amblyoponinae.

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Supporting Information

Table S1. List of taxa sequenced, with specimen codes (unique voucher numbers) and GenBank accession numbers. For collection details of each voucher specimen see AntWeb (www.antweb.org).

Taxon	Voucher	28S	Wg	Abd-A	LW Rh	EF1aF2	ArgK	Top1	Ubx	POLD1	NaK	Antp
Adetomyrma bressleri	CASENT0007350	KU671399	KU671552	KU672023	KU671501	KU671450	KU671603	KU671666	KU671729	KU671869	KU671946	KU671792
Adetomyrma caputleae	CASENT0491481	EF012956	EF013664	EF013084	EF013536	EF013375	KU671604	KU671667	KU671730	KU671870	KU671947	KU671793
Amblyopone australis	CASENT0106229	KJ860056	KJ861944	KJ861331	KJ861515	KJ859868	KJ861141	KJ861752	KJ860481	KU671871	KU671948	KU671794
Amblyopone longidens	CASENT0100485	KU671400	KU671553	KU672024	KU671502	KU671451	KU671605	KU671668	KU671731	KU671872	KU671949	KU671795
Apomyrma CF01	CASENT0086291	KU671401	KU671554	KU672025	KU671503	KU671452	KU671606	KU671669	KU671732	KU671873	KU671950	KU671796
Apomyrma CF02	CASENT0086073	KU671402	KU671555	KU672026	KU671504	KU671453	KU671607	KU671670	KU671733	KU671874	KU671951	KU671797
Apomyrma stygia	CASENT0007017	EF012967	EF013675	EF013095	EF013547	EF013390	KU671608	KU671671	KU671734	KU671875	KU671952	KU671798
Bannapone scrobiceps	CASENT0339957	KU671403	KU671556	KU672027	KU671505	KU671454	KU671609	KU671672	KU671735	KU671876	KU671953	KU671799
Concoctio concenta	CASENT0004306	EF012983	EF013691	EF013111	EF013563	EF013410	KU671610	KU671673	KU671736	KU671877	KU671954	KU671800
Myopopone castanea	CASENT0106147	KU671404	KU671557	KU672028	KU671506	KU671455	KU671611	KU671674	KU671737	KU671878	KU671955	KU671801
Mystrium camillae	CASENT0172778	KU671405	KU671558	KU672029	KU671507	KU671456	KU671612	KU671675	KU671738	KU671879	KU671956	KU671802
Mystrium voeltzkowi	CASENT0076622	EF013022	EF013730	EF013150	EF013602	EF013463	KU671613	KU671676	KU671739	KU671880	KU671957	KU671803
Onychomyrmex AU01	CASENT0106176	KU671406	KU671559	KU672030	KU671508	KU671457	KU671614	KU671677	KU671740	KU671881	KU671958	KU671804
Onychomyrmex hedleyi	CASENT0106018	EF013029	EF013737	EF013157	EF013609	EF013472	KU671615	KU671678	KU671741	KU671882	KU671959	KU671805
Opamyrma hungvuong	CASENT0178347	KU671407	KU671560	KU672031	KU671509	KU671458	KU671616	KU671679	KU671742	KU671883	KU671960	KU671806
Paraprionopelta minima	CASENT0628950	KU671408	KU671561	KU672032	KU671510	KU671459	KU671617	KU671680	KU671743	KU671884	KU671961	KU671807
Prionopelta amabilis	CASENT0052775	KU671409	KU671562	KU672033	KU671511	KU671460	KU671618	KU671681	KU671744	KU671885	KU671962	KU671808
Prionopelta subtilis	CASENT0494610	EF013048	EF013756	EF013176	EF013628	EF013493	KU671619	KU671682	KU671745	KU671886	KU671963	KU671809
Stigmatomma AFRC_LIM_01	CASENT0280597	KU671410	KU671563	KU672034	KU671512	KU671461	KU671620	KU671683	KU671746	KU671887	KU671964	KU671810
Stigmatomma armigerum	CASENT0179452	KU671411	KU671564	KU672035	KU671513	KU671462	KU671621	KU671684	KU671747	KU671888	KU671965	KU671811
Stigmatomma bellii	CASENT0179569	KU671412	KU671565	KU672036	KU671514	KU671463	KU671622	KU671685	KU671748	KU671889	KU671966	KU671812
Stigmatomma boltoni	CASENT0179570	KU671413	KU671566	KU672037	KU671515	KU671464	KU671623	KU671686	KU671749	KU671890	KU671967	KU671813
Stigmatomma CF01	CASENT0408409	KU671414	KU671567	KU672038	KU671516	KU671465	KU671624	KU671687	KU671750	KU671891	KU671968	KU671814
Stigmatomma CF03	CASENT0406733	KU671415	KU671568	KU672039	KU671517	KU671466	KU671625	KU671688	KU671751	KU671892	KU671969	KU671815
Stigmatomma CF05	CASENT0088635	KU671416	KU671569	KU672040	KU671518	KU671467	KU671626	KU671689	KU671752	KU671893	KU671970	KU671816
Stigmatomma cleae	CASENT0101452	KU671417	KU671570	KU672041	KU671519	KU671468	KU671627	KU671690	KU671753	KU671894	KU671971	KU671817
Stigmatomma CN02	CASENT0064288	KU671418	KU671571	KU672042	KU671520	KU671469	KU671628	KU671691	KU671754	KU671895	KU671972	KU671818
Stigmatomma denticulatum	CASENT0906827	KU671419	KU671572	KU672043	KU671521	KU671470	KU671629	KU671692	KU671755	KU671896	KU671973	KU671819
Stigmatomma elongatum	CASENT0100517	KU671420	KU671573	KU672044	KU671522	KU671471	KU671630	KU671693	KU671756	KU671897	KU671974	KU671820
Stigmatomma GA01	CASENT0011479	KU671421	KU671574	KU672045	KU671523	KU671472	KU671631	KU671694	KU671757	KU671898	KU671975	KU671821
Stigmatomma JTL001	INB0003698567	KU671422	KU671575	KU672046	KU671524	KU671473	KU671632	KU671695	KU671758	KU671899	KU671976	KU671822
Stigmatomma MG01	CASENT0135098	KU671423	KU671576	KU672047	KU671525	KU671474	KU671633	KU671696	KU671759	KU671900	KU671977	KU671823
Stigmatomma MG03	CASENT0034580	KU671424	KU671577	KU672048	KU671526	KU671475	KU671634	KU671697	KU671760	KU671901	KU671978	KU671824
Stigmatomma MG05	CASENT0042894	KU671425	KU671578	KU672049	KU671527	KU671476	KU671635	KU671698	KU671761	KU671902	KU671979	KU671825
Stigmatomma MG06	CASENT0068192	KU671426	KU671579	KU672050	KU671528	KU671477	KU671636	KU671699	KU671762	KU671903	KU671980	KU671826
Stigmatomma MM02	CASENT0097917	KU671427	KU671580	KU672051	KU671529	KU671478	KU671637	KU671700	KU671763	KU671904	KU671981	KU671827
Stigmatomma MY03	CASENT0179446	KU671428	KU671581	KU672052	KU671530	KU671479	KU671638	KU671701	KU671764	KU671905	KU671982	KU671828
Stigmatomma MY04	CASENT0235146	KU671429	KU671582	KU672053	KU671531	KU671480	KU671639	KU671702	KU671765	KU671906	KU671983	KU671829

Stigmatomma mystriops	INB0003690672	KU671430	KU671583	KU672054	KU671532	KU671481	KU671640	KU671703	KU671766	KU671907	KU671984	KU671830
Stigmatomma pallipes	CASENT0106070	AY703554	AY703621	AY703688	AY703755	EF013381	KJ523366	KJ523716	KJ523633	KU671908	KU671985	KU671831
Stigmatomma pluto_cf	CASENT0217030	KU671431	KU671584	KU672055	KU671533	KU671482	KU671641	KU671704	KU671767	KU671909	KU671986	KU671832
Stigmatomma saundersi	CASENT0006813	KU671432	KU671585	KU672056	KU671534	KU671483	KU671642	KU671705	KU671768	KU671910	KU671987	KU671833
Stigmatomma SC01	CASENT0159676	KU671433	KU671586	KU672057	KU671535	KU671484	KU671643	KU671706	KU671769	KU671911	KU671988	KU671834
Stigmatomma silvestrii	CASENT0000049	KU671434	KU671587	KU672058	KU671536	KU671485	KU671644	KU671707	KU671770	KU671912	KU671989	KU671835
Stigmatomma ST01	CASENT0095448	KU671435	KU671588	KU672059	KU671537	KU671486	KU671645	KU671708	KU671771	KU671913	KU671990	KU671836
Stigmatomma TH01	CASENT0119829	KU671436	KU671589	KU672060	KU671538	KU671487	KU671646	KU671709	KU671772	KU671914	KU671991	KU671837
Stigmatomma TH04	CASENT0128891	KU671437	KU671590	KU672061	KU671539	KU671488	KU671647	KU671710	KU671773	KU671915	KU671992	KU671838
Stigmatomma TH05	CASENT0131234	KU671438	KU671591	KU672062	KU671540	KU671489	KU671648	KU671711	KU671774	KU671916	KU671993	KU671839
Stigmatomma zwaluwenburgi	CASENT0187702	KU671439	KU671592	KU672063	KU671541	KU671490	KU671649	KU671712	KU671775	KU671917	KU671994	KU671840
Xymmer CF01	CASENT0087255	KU671440	KU671593	KU672064	KU671542	KU671491	KU671650	KU671713	KU671776	KU671918	KU671995	KU671841
Xymmer MG01	CASENT0494854	KU671441	KU671594	KU672065	KU671543	KU671492	KU671651	KU671714	KU671777	KU671919	KU671996	KU671842
Xymmer MGm04	CASENT0079533	KU671442	KU671595	KU672066	KU671544	KU671493	KU671652	KU671715	KU671778	KU671920	KU671997	KU671843
Xymmer muticus	CASENT0006827	EF012960	EF013668	EF013088	EF013540	EF013380	KU671653	KU671716	KU671779	KU671921	KU671998	KU671844
Xymmer TH01	CASENT0119328	KU671443	KU671596	KU672067	KU671545	KU671494	KU671654	KU671717	KU671780	KU671922	KU671999	KU671845
Ampulex compressa	CASENT0217334	KU671444	KU671597	KU672068	KU671546	KU671495	KU671655	KU671718	KU671781	KU671923	KU672000	KU671846
Ankylomyrma coronacantha	CASENT0406734	KJ860057	KJ861945	KJ861332	KJ861516	KJ859869	KJ861142	KJ861753	KJ860482	KU671924	KU672001	KU671847
Anomalomyrma boltoni	CASENT0217032	KU671445	KU671598	KU672069	KU671547	KU671496	KU671656	KU671719	KU671782	KU671925	KU672002	KU671848
Apterogyna ZA01	CASENT0106304	KJ860058	KJ861946	KJ861333	KJ861517	KJ859870	KJ861143	KJ861754	KJ860483	KU671926	KU672003	KU671849
Cerapachys jacobsoni	CASENT0106233	KJ523194	KJ523510	KJ523841	KJ523731	KJ523786	KJ523310	KJ523655	KJ523572	KU671927	KU672004	KU671850
Chalybion californicum	CASENT0106103	EF012981	EF013689	EF013109	EF013561	EF013407	KU671657	KU671720	KU671783	KU671928	KU672005	KU671851
Discothyrea testacea	CASENT0270725	KU671446	KU671599	KU672070	KU671548	KU671497	KU671658	KU671721	KU671784	KU671929	KU672006	KU671852
Dolichoderus pustulatus	CASENT0106164	FJ939792	FJ940028	FJ939824	FJ939995	FJ939963	FJ939859	KJ523685	KJ523602	KU671930	KU672007	KU671853
Hypoponera opacior	CASENT0106093	AY703555	AY703622	AY703689	AY703756	EF013428	KU671659	KU671722	KU671785	KU671931	KU672008	KU671854
Lasius californicus	CASENT0106045	EF012998	EF013706	EF013126	EF013578	EF013430	KJ523346	KJ523692	KJ523609	KU671932	KU672009	KU671855
Leptanilla TH01	CASENT0119792	KU671447	KU671600	KU672071	KU671549	KU671498	KU671660	KU671723	KU671786	KU671933	KU672010	KU671856
Manica bradleyi	CASENT0106022	EF013006	EF013714	EF013134	EF013586	EF013443	FJ939877	KJ523698	KJ523615	KU671934	KU672011	KU671857
Martialis heureka	CASENT0106181	KU671448	KU671601	KU672072	KU671550	KU671499	KU671661	KU671724	KU671787	KU671935	KU672012	KU671858
Myrmecia pyriformis	CASENT0106088	AY703567	AY703634	AY703701	AY703768	EF013454	FJ939878	KJ523699	KJ523616	KU671936	KU672013	KU671859
Odontomachus coquereli	CASENT0499525	EF013026	EF013734	EF013154	EF013606	EF013469	KU671662	KU671725	KU671788	KU671937	KU672014	KU671860
Paraponera clavata	CASENT0106092	AY703556	AY703623	AY703690	AY703757	EF013477	KJ523355	KJ523704	KJ523621	KU671938	KU672015	KU671861
Platythyrea mocquerysi	CASENT0106094	AY867453	AY867422	AY867469	AY867484	EF013484	KJ861145	KJ861756	KJ860485	KU671939	KU672016	KU671862
Proceratium stictum	CASENT0106095	AY703557	AY703624	AY703691	AY703758	EF013497	KJ861146	KJ861757	KJ860486	KU671940	KU672017	KU671863
Protanilla JP01	CASENT0007002	EF013053	EF013761	EF013181	EF013633	EF013499	KU671663	KU671726	KU671789	KU671941	KU672018	KU671864
Rhytidoponera chalybaea	CASENT0106000	EF013058	EF013766	EF013186	EF013638	EF013505	FJ939885	KJ523705	KJ523622	KU671942	KU672019	KU671865
Scolia verticalis	CASENT0106107	EF013060	EF013768	EF013188	EF013640	EF013507	KU671664	KU671727	KU671790	KU671943	KU672020	KU671866
Tatuidris tatusia	CASENT0423526	EF013067	EF013775	EF013195	EF013647	EF013516	KJ861147	KJ861758	KJ860487	KU671944	KU672021	KU671867
Yavnella argamani	CASENT0235253	KU671449	KU671602	KU672073	KU671551	KU671500	KU671665	KU671728	KU671791	KU671945	KU672022	KU671868

Table S2. Primers of three genes, DNApol-delta (POLD1), NaK ATPase (NaK), and Antennapedia (Antp), newly designed and employed in this study. Principal primers are in bold font; others were used for amplifying shorter, overlapping fragments of DNA. Coordinates are based on the indicated GenBank sequences. Three reverse primers (suffixed “ER”) start within introns and cannot be precisely referenced. Primer exon sequence is divided into respective codons.

Gene	Primer	Sequence (5' - 3')	Coordinates	GenBank # for coordinates
POLD1	**DP4159F**	GTM GCR AAY ATG ATG AAY ACY TG	4159-4181	NC_007075 (Apis mellifera)
POLD1	DP4184F	TG CAR ATA YTG CTY ATY GAR AG GT	4184-4207	NC_007075 (Apis mellifera)
POLD1	DP4184F2	TG SAA AAR TTR CTY ATY GAY AG GT	4184-4207	NC_007075 (Apis mellifera)
POLD1	DP4284F	CAYAG R AAY CCA MAY KCY GC	4284-4303	NC_007075 (Apis mellifera)
POLD1	**DP4299F**	GCY GCB RTV GAT TAY GCY AAR CA	4299-4321	NC_007075 (Apis mellifera)
POLD1	DP4299F2	GAY GCK ATK RAT TAY GCA AAR CA	4299-4321	NC_007075 (Apis mellifera)
POLD1	DP4528F	AG AAA GSW GAG GAW CCY ATM TAY GT	4528-4552	NC_007075 (Apis mellifera)
POLD1	DP4555F	TG SAR AAY AGY ATY CCR ATH GAY AC	4555-4579	NC_007075 (Apis mellifera)
POLD1	DP4569F	CCT ATT GAY ACD AMW TAY TAT TTA GAA AAY C	4569-4599	NC_007075 (Apis mellifera)
POLD1	DP4575F	GAY ACR AMY TAY TAY YTR GAR AAT CA	4575-4600	NC_007075 (Apis mellifera)
POLD1	DP4587F	TAT YTR GAR AAT CAA YTR GCR AAA CC	4587-4612	NC_007075 (Apis mellifera)
POLD1	DP4620F	CGY ATH TTY GAR CCV ATY CTY GGB GA	4620-4645	NC_007075 (Apis mellifera)
POLD1	DP4429R	GC YAR YTC RAC RTG YGC YTG YTT YGC	4429-4404	NC_007075 (Apis mellifera)
POLD1	DP4645R	TC RCC RAG RAT DGG YTC RAA DAT RCG	4645-4620	NC_007075 (Apis mellifera)
POLD1	DP4693R	GW CYT YGT RCG YGT RTG RTC DCC	4693-4671	NC_007075 (Apis mellifera)
POLD1	DP4912R	C YTG RCA YCT YTG RCA YTC BGT CCA	4912-4887	NC_007075 (Apis mellifera)
POLD1	**DP4927R**	TC YTG RTG RAG RCT BCC YTG RCA	4927-4905	NC_007075 (Apis mellifera)
POLD1	**DP4944R**	AC TT RGA RCA DAT AAC TTC YTG RTG	4944-4920	NC_007075 (Apis mellifera)
POLD1	DP4944R2	AC TT WGT GCA TAA WAC TTC YTG RTG	4944-4920	NC_007075 (Apis mellifera)
NaK	**NK642F**	ATY ATG GAR TCR TTC AAG AAY ATG GTR CC	642-670	AF044974 (Dros. melanogaster)
NaK	NK717F	GCS GAR GAY YTG GTR YTV GGS GAC GT	717-742	AF044974 (Dros. melanogaster)
NaK	NK718F	CG GAG GAY CTY GTS YTS GGC GAY GT	718-742	AF044974 (Dros. melanogaster)
NaK	NK735F	GGC GAY GTC GTC GAD GTK AAR TTC GG	735-760	AF044974 (Dros. melanogaster)
NaK	**NK750F**	GTK AAR TTC GGY GAY CGK ATM CCG GC	750-775	AF044974 (Dros. melanogaster)
NaK	NK958F	GC GAT CAR ACR GTG ATG GGM AGG ATY GC	958-985	AF044974 (Dros. melanogaster)
NaK	NK1002F	CTK GAY ACM GGH GAR ACR CCG ATC GC	1002-1027	AF044974 (Dros. melanogaster)
NaK	NK1020F	CCG ATC GCY AAR GAR ATH CAY CAY TT	1020-1045	AF044974 (Dros. melanogaster)
NaK	NK1284F	TCG ACY ATY TGY TCG GAY AAR ACB GG	1284-1309	AF044974 (Dros. melanogaster)
NaK	NK1513F	TK AAC GGY GAY GCB TCY GAR GCY GC	1513-1537	AF044974 (Dros. melanogaster)
NaK	NK1084R	AC RCC GAG RAA BAC RGC RAC RCC RGT	1084-1059	AF044974 (Dros. melanogaster)
NaK	NK1126R	AG CCA RTG RTA ACC CAR RAT RAA RGC	1126-1101	AF044974 (Dros. melanogaster)
NaK	NK1351R	AA CCA CAT RTG CGC MAC YGT CAT DCG	1351-1326	AF044974 (Dros. melanogaster)
NaK	NK1372R	GC RTC GAT RAT CTG ATT GTC GAA CCA CAT	1372-1344	AF044974 (Dros. melanogaster)
NaK	NK1588R	TT CCK RAT RCC CAT RAC RTC RCC CA	1588-1564	AF044974 (Dros. melanogaster)
NaK	**NK1757ER**	AC CTT YTC YTT GCC RCC RAT RAA DAT RGT	~1757-1731	AF044974 (Dros. melanogaster)
NaK	**NK1757ER2**	CSYAC CTT YTC YTT GCC RCC RAT	~1757-1740	AF044974 (Dros. melanogaster)
NaK	NK1798R	TA MGC GTT RTT GAA YGC YTC YTT CAT YTC	1798-1770	AF044974 (Dros. melanogaster)
NaK	NK1963R	GC CCK RGG YGG RTC RAT CAT AGA CAT	1963-1938	AF044974 (Dros. melanogaster)

NaK	NK2011R	C CAT GAT GAC CTT RAT GCC GGC KGA ACG	2011-1992	AF044974 (Dros. melanogaster)
Antp	**AP113F**	GTAGC ATG AGT TCG TAY TTY GC	113-134	NM_001011571 (Apis mellifera)
Antp	**AP127F**	CG TAY TTY GCG AAT TCG TAY ATC CC	127-149	NM_001011571 (Apis mellifera)
Antp	AP346F	TAY CCR AGG TTT CCB CCR TAY AAY CG	346F-371	NM_001011571 (Apis mellifera)
Antp	AP556F	GCK GTC GAT CAY CAR GGH AGC GT	556-578	NM_001011571 (Apis mellifera)
Antp	AP419R	CC RTG YTC YTG YTG RTG YTG RTA RTA	419-394	NM_001011571 (Apis mellifera)
Antp	AP610R	C RAC SAG RGG YGG RCT RTC BGG	610-589	NM_001011571 (Apis mellifera)
Antp	AP644R	TG YTG RCT RTG CAT RTG RTG CAT	644-619	NM_001011571 (Apis mellifera)
Antp	**AP914R**	CT YCT CAT CCA MGG RTA YAA HGG	914-892	NM_001011571 (Apis mellifera)
Antp	**AP922ER**	TYACC RAA YTG ACT YCT CAT CCA	~922-904	NM_001011571 (Apis mellifera)

Table S3. Taxon distribution matrix, based on the following six biogeographic regions: T, Neotropical; N, Nearctic; P, Palearctic; E, Afrotropical; O, Indomalayan; and A, Australasian. Species were assigned to the region(s) in which they are believed to be indigenous. The Malagasy species, *Prionopelta subtilis*, was coded as Afrotropical and Indomalayan because related species occur in Indomalaya, and the genus *Prionopelta* would otherwise have its presence in that region unrecorded.

	T	N	P	E	O	A
Adetomyrma_bressleri	0	0	0	1	0	0
Adetomyrma_caputleae	0	0	0	1	0	0
Amblyopone_australis	0	0	0	0	0	1
Amblyopone_longidens	0	0	0	0	0	1
Apomyrma_CF01	0	0	0	1	0	0
Apomyrma_CF02	0	0	0	1	0	0
Apomyrma_stygia	0	0	0	1	0	0
Bannapone_scrobiceps	0	0	0	0	1	0
Concoctio_concenta	0	0	0	1	0	0
Myopopone_castanea	0	0	0	0	1	1
Mystrium_camillae	0	0	0	0	1	1
Mystrium_voeltzkowi	0	0	0	1	0	0
Onychomyrmex_AU01	0	0	0	0	0	1
Onychomyrmex_hedleyi	0	0	0	0	0	1
Paraprionopelta_minima	1	0	0	0	0	0
Prionopelta_amabilis	1	0	0	0	0	0
Prionopelta_subtilis	0	0	0	1	1	0
Stigmatomma_AFRC_LIM_01	0	0	0	1	0	0
Stigmatomma_armigerum	1	0	0	0	0	0
Stigmatomma_bellii	0	0	0	0	1	0
Stigmatomma_boltoni	0	0	0	0	1	0
Stigmatomma_CF01	0	0	0	1	0	0
Stigmatomma_CF03	0	0	0	1	0	0
Stigmatomma_CF05	0	0	0	1	0	0
Stigmatomma_cleae	1	0	0	0	0	0
Stigmatomma_CN02	0	0	0	0	1	0
Stigmatomma_denticulatum	0	0	1	0	0	0
Stigmatomma_elongatum	1	0	0	0	0	0
Stigmatomma_GA01	0	0	0	1	0	0
Stigmatomma_JTL001	1	0	0	0	0	0
Stigmatomma_MG01	0	0	0	1	0	0
Stigmatomma_MG03	0	0	0	1	0	0
Stigmatomma_MG05	0	0	0	1	0	0
Stigmatomma_MG06	0	0	0	1	0	0
Stigmatomma_MM02	0	0	0	0	1	0
Stigmatomma_MY03	0	0	0	0	1	0
Stigmatomma_MY04	0	0	0	0	1	0
Stigmatomma_mystriops	1	0	0	0	0	0
Stigmatomma_pallipes	0	1	0	0	0	0
Stigmatomma_pluto_cf	0	0	0	1	0	0
Stigmatomma_saundersi	0	0	0	0	0	1

Stigmatomma_SC01	0	0	0	1	0	0
Stigmatomma_silvestrii	0	0	1	0	0	0
Stigmatomma_ST01	0	0	0	1	0	0
Stigmatomma_TH01	0	0	0	0	1	0
Stigmatomma_TH04	0	0	0	0	1	0
Stigmatomma_TH05	0	0	0	0	1	0
Stigmatomma_zwaluwenburgi	0	0	0	0	1	1
Xymmer_CF01	0	0	0	1	0	0
Xymmer_MG01	0	0	0	1	0	0
Xymmer_MGm04	0	0	0	1	0	0
Xymmer_muticus	0	0	0	1	0	0
Xymmer_TH01	0	0	0	0	1	0

Table S4. Range inheritance inferences for major clades of Amblyoponinae, based on LAGRANGE analysis. The range inheritance scenario is expressed as [left|right], where “left” and “right” are the ranges inherited by the descendant upper branch and the descendant lower branch, respectively, of each clade depicted in Fig. 3. Only splits (scenarios) with relative probability > 0.05 are given. The ancestral ranges are abbreviated as follows: T, Neotropical; N, Nearctic; P, Palearctic; E, Afrotropical; O, Indomalayan; and A, Australasian.

Clade	**Range**	**lnL**	**Relative probability**
Amblyoponinae	[E|E]	-96.78	0.2455
	[TE|E]	-97.52	0.117
	[TEA|E]	-97.58	0.1105
	[EA|E]	-97.75	0.09348
	[TEO|E]	-98.32	0.05297
Apomyrma	[E|E]	-95.42	0.9627
all except *Apomyrma*	[E|E]	-96.63	0.285
	[T|T]	-98.22	0.05834
POA clade	[A|TE]	-95.93	0.5752
	[A|E]	-97.34	0.1404
	[A|EO]	-97.94	0.07718
	[A|TEA]	-98.04	0.06997
XMMAS clade	[E|T]	-96.56	0.3082
	[E|TA]	-97.09	0.1813
	[EO|T]	-97.65	0.1033
	[E|E]	-97.84	0.08565
	[E|A]	-98.07	0.06789
Ericapelta	[T|T]	-96.19	0.4422
	[T|TA]	-96.26	0.4131
	[T|TEA]	-98.19	0.06035
“core XMMAS”	[E|E]	-95.79	0.6648
	[EO|E]	-97.38	0.1353

Table S5. Summary of proposed taxonomic changes in Amblyoponinae.

(1) *Concoctio*, junior synonym of *Prionopelta*

Prionopelta Mayr, 1866
= *Concoctio* Brown, 1974 **syn.n.**

Species transferred from *Concoctio* to *Prionopelta*:
concenta (Brown, 1974) **comb.n.**

(2) *Fulakora* resurrected from synonymy and elevated to genus

Fulakora Mann, 1919 **stat.r., stat.n.**
=*Ericapelta* Kusnezov, 1955 **syn.n.**
=*Paraprionopelta* Kusnezov, 1955 **syn.n.**

Species transferred from *Paraprionopelta* (*minima*) and *Stigmatomma* (others) to *Fulakora*:
agostii (Lacau & Delabie, 2002) **comb.n.**
armigera (Mayr, 1887) **comb.n.**
bierigi (Santschi, 1930) **comb.r.**
celata (Mann, 1919) **comb.r.**
chilensis (Mayr, 1887) **comb.r.**
cleae (Lacau & Delabie, 2002) **comb.n.**
degenerata (Borgmeier, 1957) **comb.n.**
egregia (Kusnezov, 1955) **comb.n.**
elongata (Santschi, 1912) **comb.r.**
=*elongata barretoi* (Bruch, 1921)
=*elongata minor* (Santschi, 1922)
=*elongata paranensis* (Santschi, 1925)
exigua (Clark, 1928) **comb.n.**
falcata (Lattke, 1991) **comb.n.**
gnoma (Taylor, 1979) **comb.n.**
gracilis (Clark, 1934) **comb.r.**
heraldoi (Lacau & Delabie, 2002) **comb.n.**
lucida (Clark, 1934) **comb.r.**
lurilabes (Lattke, 1991) **comb.n.**
minima (Kusnezov, 1955) **comb.n.**
monrosi (Brown, 1960) **comb.n.**
mystriops (Brown, 1960) **comb.n.**
orizabana (Brown, 1960) **comb.n.**
=*tropicalis* (Brown, 1962)
papuana (Taylor, 1979) **comb.n.**
punctulata (Clark, 1934) **comb.r.**
saundersi (Forel, 1892) **comb.r.**
smithi (Brown, 1960) **comb.n.**
wilsoni (Clark, 1928) **comb.n.**

Note: revived combinations listed above refer to previous combinations with *Fulakora* as a subgenus; they are new combinations at the rank of genus.

(3) *Bannapone*, junior synonym of *Stigmatomma*

Stigmatomma Roger, 1859
  = *Bannapone* Xu, 2000 **syn.n.**

Species transferred from *Bannapone* to *Stigmatomma*:
caliginosum (Onoyama, 1999) **comb.r.**
crypticum (Eguchi, Bui, Yamane & Terayama, 2015) **comb.n.**
fulvidum (Terayama, 1987) **comb.r.**
mulanae (Xu, 2000) **comb.n.**
pertinax (Baroni Urbani, 1978) **comb.r.**
scrobiceps (Guénard, Blanchard, Liu, Yang & Economo, 2013) **comb.n.**
zwaluwenburgi Williams, 1946 **comb.r.**

(4) *Lithomyrmex*, junior synonym of *Onychomyrmex*

Onychomyrmex Emery, 1895
  = *Lithomyrmex* Clark, 1928 **syn.n.**

Species transferred from *Stigmatomma* to *Onychomyrmex*:
glauerti (Clark, 1928) **comb.n.**

(5) Species transferred from *Stigmatomma* to *Amblyopone*

Amblyopone Erichson, 1842
ferruginea F. Smith, 1858 **comb.r.**

(6) *Opamyrma* excluded from Amblyoponinae

Opamyrma (with sole species *Opamyrma hungvuong*) is excluded from Amblyoponinae and placed in subfamily Leptanillinae, unassigned to tribe.