Revision of the World Species of *Megaphragma* Timberlake (Hymenoptera: Trichogrammatidae) †

Andrew Polaszek ¹, Lucian Fusu ²*, Gennaro Viggiani ³, Andie Hall ⁴, Paul Hanson ⁵ and Alexey A. Polilov ⁶

1 Department of Life Sciences, Natural History Museum, Cromwell Road, London SW7 5BD, UK; a.polaszek@nhm.ac.uk
2 Research Group in Invertebrate Diversity and Phylogenetics, Faculty of Biology, Alexandru Ioan Cuza University, Bd. Carol I, Nr. 11, 700506 Iasi, Romania
3 Laboratorio de Lotta biologica, Dipartimento di Agraria, Università degli Studi di Napoli “Federico II”, Via Università 100, 80055 Portici, NA, Italy; genviggi@unina.it
4 Core Research Laboratories, Natural History Museum, Cromwell Road, London SW7 5BD, UK; a.hall@nhm.ac.uk
5 Escuela de Biología, Universidad de Costa Rica, San Pedro de Montes de Oca, San Jose 11501-2060, Costa Rica; phanson91@gmail.com
6 Department of Entomology, Faculty of Biology, Lomonosov Moscow State University, 119234 Moscow, Russia; polilov@gmail.com
* Correspondence: lucfusu@hotmail.com
† urn:lsid:zoobank.org:pub:39858D98-8117-407B-ACF2-FBBFE1B231EB.

Simple Summary: Parasitoid wasps of the genus *Megaphragma* are some of the smallest known insects, being as small as some unicellular protozoans. Their life history is not known in great detail, but all species with known biology are parasitoids of thrips eggs (Thysanoptera) and as such, they are potential biological control agents of these pests. At the current state of knowledge of the genus, it is impossible to identify with confidence most of the *Megaphragma* species (original descriptions lack essential details or illustrations; molecular markers are available for very few species; many species are still undescribed while others were described multiple times). We provide the first revision of the genus that includes the formal descriptions and naming of 22 species and a key to all 32 valid species.

Abstract: *Megaphragma* species are important models for basic organismal research, and many are potential biological control agents. We present the first extensive revision of species of the genus *Megaphragma* based on morphological and molecular data. Our revision includes all previously described species, 6 of which are synonymized, and 22 of which are described here as new. We also provide the first key to all species of the genus and reconstruct their phylogeny based on 28S and CO1 molecular markers. The following species are synonymized with *M. longiciliatum* Subba Rao: *M. aligarhensis* Yousf and Shafee syn. nov.; *M. amalphiitanum* Viggiani syn. nov.; *M. decochaetum* Lin syn. nov.; *M. magniciliav Yousf and Shafee syn. nov.; *M. Shimulatam* Hayat syn. nov.; *M. anomalifuniculi* Yuan and Lou syn. nov. is synonymized with *M. polychaetum* Lin. The following species are described as new: *M. antecessor* Polaszek and Fusu sp. nov.; *M. breviciliav Polaszek and Fusu sp. nov.; *M. chienleei* Polaszek and Fusu sp. nov.; *M. cockerilli* Polaszek and Fusu sp. nov.; *M. digitatum* Polaszek and Fusu sp. nov.; *M. fanenitrakely* Polaszek and Fusu sp. nov.; *M. fucicum Polaszek and Fusu sp. nov.; *M. giralti* Viggiani, Fusu, and Polaszek sp. nov.; *M. hansoni* Polaszek, Fusu, and Viggiani sp. nov.; *M. kinihua Polaszek, Fusu, and Viggiani sp. nov.; *M. momookherjeae* Polaszek and Fusu sp. nov.; *M. novickii* Polaszek, Fusu, and Viggiani sp. nov.; *M. noyesi* Polaszek and Fusu sp. nov.; *M. pintoi* Viggiani sp. nov.; *M. polilovi* Polaszek, Fusu, and Viggiani sp. nov.; *M. rivelloi* Viggiani sp. nov.; *M. tamoi* Polaszek, Fusu, and Viggiani sp. nov.; *M. tridens* Fusu, and Polaszek sp. nov.; *M. unmivatam Polaszek and Fusu sp. nov.; *M. vanlenterenii* Polaszek and Fusu sp. nov.; *M. viggianii* Fusu, Polaszek, and Polilov sp. nov.
Keywords: species delimitation; egg parasitoid; Chalcidoidea; integrative taxonomy; molecular phylogeny; DNA barcoding; mini-barcode

1. Introduction

Trichogrammatidae (Hymenoptera: Chalcidoidea) is a family of egg parasitoids that consists of approximately 100 genera and 1000 species [1–3]. The genus *Megaphragma* (tribe Oligositini) currently contains 15 species, all of which are egg parasitoids of Thysanoptera [1]. It includes some of the smallest insects: most species of this genus have a body length of only 0.16–0.3 mm, which is about the same size as a larger unicellular organism such as *Paramecium* [4]. Huber and Noyes [5] provided a review of the body size limit in insects with only three genera of Mymaridae having species smaller than the smallest *Megaphragma*. The genus has been recorded on all continents except Antarctica; though most of the species are confined to the tropics and warmer temperate regions. According to the available data, all species of this genus are egg parasitoids of thrips, but the biology of most species remains unknown. The type of the genus, *M. mymaripenne* Timberlake, was examined by Viggiani [6], who gave details on several previously unused features, in particular on the sculpture present on tergites of the metasoma. The same author described several new species of *Megaphragma* [7,8]. Lin [9] described five new species from China, and Hayat [10] revised the Indian species. The *Megaphragma* of Argentina were studied by Viggiani et al. [11]. Detailed biological data are available for *M. mymaripenne*, *M. polilovi* sp. nov. (under the name *M. mymaripenne*), and *M. longiciliatum* Subba Rao (under the name *M. amalphitanum* Viggiani) [12–14].

Due to their extremely small body size, *Megaphragma* species have become model organisms for studying the miniaturization of insects [15,16] and solving neurobiological problems [17]. The general anatomy and anatomical features associated with miniaturization have been described [18]; the structure of the eye [19], antenna [20,21], and leg structures used for grooming [22], and peculiar features of the genome [23–25] have been studied. Anucleate neurons have been found in three species of *Megaphragma* [18,26] and the unique phenomenon of lysis of the bodies and nuclei of cells at the pupal stage of development has been described [4]. Analysis of the connectome of *Megaphragma* [27,28] and reconstruction of sensory organs at the cellular and subcellular level [28] are currently underway.

In addition to their value for basic research, *Megaphragma* species are potential biological agents for the control of thrips, many of which are important agricultural pests [29,30].

Most *Megaphragma* species descriptions are very brief, and genetic markers are available only for one named species [23,25,31] and three unnamed species [32,33]. Identification keys to species are available only for a few regions and include only selected species. Many specimens cannot therefore be identified. Thus, the lack of a revision makes it extremely difficult to work with these wasps, which are important for basic and applied research.

2. Materials and Methods

2.1. Specimens and Depository Abbreviations

Specimens on slides, mostly type material, were received or deposited in the following institutions: Alexandru Ioan Cuza University of Iași, Romania, Lucian Fusu collection (AICF); Aligarh Muslim University, Aligarh, India (AMU: Mohammad Hayat); Australian National Insect Collection, Canberra, Australia (ANIC: Nicole Fisher); Canadian National Collection of Insects, Ottawa, Canada (CNCI: John Huber); CIRAD/UMR CBGP, Montferrier-sur-Lez, France (CIRAD: Gerard Delvare); Università di Napoli “Federico II”, Dipartimento di Agraria, Collezione di Entomologia, Portici, Italia (DACE: Gennaro Viggiani); Department of Zoology, Plant Protection College, Fujian Agricultural and Forestry University Fuzhou, Fujian, China (FAFU: Naikuan Lin); International Institute of Tropical Agriculture, Cotonou, Benin (IITA: Georg Goergen); Museo de Zoología, Universidad...
de Costa Rica (MZUCR). Natural History Museum of Oman (NHMO); Natural History Museum, London, UK (NHMUK: Natalie Dale-Skey); Musée Royal de l’Afrique Centrale, Tervuren, Belgium (MRAC: Eliane de Coninck); Plant and Food Research New Zealand (formerly DSIR: Jocelyn Berry); University of California, Riverside, USA (UCRC: Serguei Triapitsyn). Additional material was received for identification from several institutions, and a number of recent collections by the authors and Dr John Noyes (NHMUK) contributed substantial material to this revision.

2.2. Morphology

All material was examined on microscope slides for morphological characters using an Olympus BX63 microscope with Nomarski differential interference contrast (DIC) with 40× and 100× objectives. Since the lysis buffer used for DNA extraction (see below) contains proteinase K, there is no need to clear the body with KOH as usually performed before slide mounting. Instead, specimens were extracted from the lysis buffer with an adjustable volume pipette (0.5 to 10 µL) set at 1–2 µL to reduce liquid loss and transferred to distilled water to remove unwanted reagents. Afterward, they were dehydrated using a series of ethanol solutions of increasing concentration and cleared in clove oil as described by Noyes [34]. Afterward, some specimens were mounted laterally in Canada balsam while others were dissected and wings, antennae, head, and body were mounted separately under different coverslips following [34]. However, mounting the abdomen dorsal side up has the disadvantage of making the setae on the sides of the tergites very difficult to see. Where possible, the setae on the disc of the fore wing were counted on the upper and lower surfaces. Body colour was observed on both card-mounted specimens and on slide-mounted specimens in which the generally unremarkable body pigmentation remains preserved. Selected specimens were dried using a critical point drier and examined with an electron microscope as described in Polilov [26].

Morphological terminology (see Figure 1) broadly follows Pinto [2], while terminology of the antennal sensilla follows Diakova et al. [20], albeit with abbreviations that follow the descriptions; e.g., “UST” for “uniporous sensilla trichodea” instead of Diakova et al. [20], who use “TS-UP”.

The following abbreviations are used for morphological terms (see Figure 1b): ASC = aporous sensilla chaetica; C1 = 1st (basal) clavomere; C2 = 2nd (central or apical) clavomere; C3 = 3rd (apical) clavomere; MPS = multiporous placoid sensilla; MT = microtrichia (referred to as “aporous sensilla trichodea, type 1” by Diakova et al. [20]); SB = sensilla basiconica; SS = sensilla styloconica; T1, T2 etc. = metasomal tergite 1, 2 etc.; UST = uniporous sensilla trichodea.

In species with a single discal fore wing seta, its length is important: “short” = shorter than or equal to the distance between the 2 proximal wing fringe setae (i.e., those closest to the seta); long = longer than the distance between the 3 proximal wing fringe setae (see Figure 1c).

A peculiar type of metafemoral spine with a unique shape, structure, and position is present in all species of the ghesquieri-group. Probably non-homologous metafemoral spines are present in other species groups.
Figure 1. Line drawings of *Megaphragma* species: (a) *M. mymaripenne*, female habitus; (b) *Megaphragma* sp., stylized antenna; (c) *Megaphragma* sp. *gesquieri*-group, fore wing.
2.3. Molecular Methods

DNA was extracted using a Qiagen DNeasy Blood and Tissue Kit with modifications as described in Cruaud et al. [35]; specimens were lysed whole for 6–8 h without grinding, then frozen at −80 °C overnight and thawed at room temperature before addition of buffer AL. After about the first 100 extractions the freezing stage was omitted as it appeared not to increase DNA yield significantly.

The primer pair D23F (5′-GAGAGTTCAAGAGTACGTG-3′) [36] and 28Sb also known as D3B (5′-TCGGAAGGAACCAGCTACTA-3′) [37,38] was used to amplify an approximately 850 bp fragment from the 5′ end of the nuclear ribosomal 28S gene spanning the D2–D3 region. In the instances where there was no detectable PCR product, we performed a second PCR using 1 µL of the primary PCR product and the semi-nested primer pair D23F combined with the newly designed reverse primer 28Sbsn (5′-GATGGTTTCATTAGTCTTTCG-3′), which amplified an approximately 800 bp fragment of the 28S rDNA.

The CO1 gene was amplified using the standard primer pair LCO1480 and HCO2198 [39], which amplifies the DNA barcode region for animals [40,41]. In case of failed reactions, we used a pair of internal primers from Fusu and Polaszek [42] that amplify the standard barcode region from two overlapping fragments (mini-barcodes, [43]): a modified LCO1490, named LCO1490M (5′-CAACAAATCATAAAAGATATTGG-3′), pairs with MChaR1 (5′-CCYTITCAAYAAATATCTC-3′), and MChaF1 (5′-CTCTGAATAATAATATAAGATT-3′) pairs with HCO2198.

The PCR conditions were as described in Fusu and Polaszek [42] except the standard barcode region was amplified at 42 °C.

All PCR products were checked by gel electrophoresis in 1% agarose gels, cleaned using AxyPrep PCR clean-up beads as per manufacturer’s instructions, then sequenced bi-directionally using BigDye terminator reaction mix v.3.1 in a 3730xl DNA analyser (Applied Biosystems) at the NHMUK sequencing facility.

The forward and reverse sequences were assembled and corrected using the Staden Package v.1.7.0 [44]. The resulting sequences were aligned in Mega v.7.0.14 [45] with the Clustal W program [46] for the CO1 gene; the 28S gene was aligned with the MAFFT web server [47] using the E-INS-i algorithm, a gap opening penalty of 2, leave gappy regions option activated, and UPGMA as a tree-building method for the guide tree. The CO1 sequences were also translated to amino acids to detect eventual stop codons that indicate NUMTs. The two alignments were first used in single-gene phylogenetic analyses in RAxML-NG v.1.0.0 [48] to detect eventual long branches and misplaced sequences (that might indicate pseudogenes or contaminants) that are to be checked/removed prior to the concatenation of the two datasets. A phylogenetic analysis of the concatenated but unpartitioned dataset using a simple substitution model (K2P) was also conducted in RAxML-NG since over-parameterization of the substitution and partition models might be a problem in a maximum likelihood framework [49], especially when using a comparatively small alignment. For the partitioned analyses, data blocks were delimited in Mesquite v.3.10 [50], CO1 being divided by codon position and 28S was treated as one block. The best partitioning scheme and substitution models were selected using PartitionFinder2 v.2.1.1 [51], with branch lengths proportionally linked and the search option set to all.

Partitioned analyses were run in RAxML-NG [48], which is maximum likelihood (ML) based, and MrBayes v.3.2.7 [52], which is based on Bayesian inference (BI) with the following substitution models as indicated by PartitionFinder2: GTR+G for 28S, HKY+I+G, TIM+I+G, and TIM+G for the 1st, 2nd, and 3rd codon positions of CO1, respectively. For MrBayes, we substituted TIM with GTR, since the former model is not available in this program. In MrBayes two parallel analyses, each with four chains, were run for 10⁷ MCMC generations, with trees and lnLs sampled every 100 generations; all estimated parameters were unlinked among partitions except for branch lengths; convergence of all parameters and estimated sample size values (ESS) above 200 were assessed by examining the trace files in Tracer v.1.7.1 [53]. Support for the maximum likelihood analysis was estimated with rapid bootstrapping (number of replicates determined by the autoMRE criterion [54]).
Bootstrap percentages (BP) over 85% were considered as strong support and BP smaller than 65% as weak. Posterior probabilities (PP) over 0.95 were considered as strong support and those below 0.90 as weak. The trees were imported and modified in FigTree v1.4.4 [55] and Adobe Illustrator.

All sequences were uploaded to GenBank (accession numbers ON555486–ON555643 for 28S and ON557406–ON557518 for CO1). Since a part of the DNA extractions did not yield PCR products, the presence of a DNA code after the label data of a specimen does not necessarily mean that it has an associated DNA sequence. A complete list of specimens with associated DNA sequences and their repository is provided in Appendix A.

2.4. New Species Left Undescribed

We have identified several species that are clearly new based either on their DNA sequences or morphology (or both), but are not described herein for one or more of the following reasons:

- Species known from males only. Within (e.g.) the *ghesquierei*-group, several new species have been identified (at least 7 or 8—see Figure 2), which are known only from males. Since in most cases females are essential for species recognition (e.g., antennal structure, ovipositor length), we have refrained from describing these species here.

- Incomplete specimens. In several instances, new species are indicated by both morphology and DNA sequences, but a crucial morphological character is missing, most often the antennae. These specimens and their sequences have been curated pending the discovery of fresh, complete specimens.

- Poorly-mounted specimens. In a few cases, slide-mounted specimens not represented by DNA sequences appear to be very likely new species. In many cases, the material is simply not in good enough condition for the designation of a holotype to represent the species.

Clearly, there is overlap and gradation between the above categories, and we have used our discretion when deciding whether or not to describe specimens. In all cases, information as to our opinion of species status is included on the specimens.

2.5. A Note on Figures Supplementing the Descriptions

While all new species are fully described, in many cases there are aspects of the morphology that differ so little between species that images of these structures would be superfluous. In these cases, “cf Figure” is used, where the reader is referred to a figure that to all intents and purposes can serve to illustrate the species while actually depicting a different one. This is especially true for many species of the *ghesquierei*-group, where several species are morphologically indistinguishable, and to a lesser extent for *M. mymaripenne*, *M. noyesi* sp. nov., and *M. polilovi* sp. nov. in the *mymaripenne*-group. In every case of extreme morphological similarity, robust molecular data are available to support separate species status. In addition, where possible, illustrations were made from holotypes. Under each photograph, we mention whether it is that of a holotype, neotype, or paratype.

3. Results

3.1. Phylogenetic Analyses

We obtained DNA sequences for a total of 170 *Megaphragma* specimens (158 sequences for 28S and 113 sequences for CO1) (Appendix A). The 28S alignment was 1068 bp in length, while the CO1 alignment was 652 bp, though only shorter sequences (DNA mini-barcodes) were obtained for some species/specimens.
Figure 2. Combined CO1 and 28S sequences analysis of 174 Megaphragma specimens (170 from this study, 4 from GenBank) with species delineated and species-groups indicated: (a) unpartitioned ML analysis (bootstrap values indicated at nodes); (b) partitioned BI analysis (both posterior probabilities and bootstrap values indicated at nodes).
The phylogenetic trees from the single-locus analyses are in general agreement though, for example, the position of *M. antecessor* sp. nov. differs drastically between the two, while some species are present in one data matrix but not the other (Supplementary Figures S2 and S3). They are also in general agreement regarding the clustering of specimens into putative species: all species that are distinct based on CO1 are also distinct based on 28S. An exception is two specimens of *M. digitatum* sp. nov. that are very divergent on CO1, but almost identical on 28S. Both the ML and BI trees from the combined and partitioned dataset show similar topologies, with minor differences; hence, in Figure 2b on the BI tree, both posterior probabilities and bootstrap support were plotted at the nodes. The species that were included in the analysis are split into two major groups: one consisting of mostly species of the mymaripenne-group (species groups are discussed below), the other of species of the ghesquierei-group. Both have high posterior probabilities (0.99 and 1, respectively) but low bootstrap support, indicating strong support based on a low number of characters. Two other small groups are formed by two species each in the antecessor- and polychaetum-groups. The antecessor-group is sister to *M. liui* sp. nov. in both of these trees, while two unnamed species of the polychaetum-group (SAM1 and SAM2) are basal to the mymaripenne-group instead of clustering with *M. giraulti* sp. nov. and *M. cockerilli* sp. nov. (the other two species of the group). The two species of the longiciliatum-group, though forming a monophyletic group with a posterior probability of 1, and a medium bootstrap support of 69%, render the mymaripenne-group paraphyletic.

The two trees based on the combined analysis of both genes have a major difference from the unpartitioned analysis that used a simple substitution model and not the best fit model (Figure 2a); in this latter tree, *M. liui* is recovered in a basal position in the ghesquierei-group, where it belongs based on its morphology. Another major difference between the partitioned analyses and the unpartitioned one is the position of the antecessor-group that is not sister to the ghesquierei-group in the first analyses (Figure 2b) as would be expected by its morphology, while it is retrieved as basal to all other *Megaphragma* in the second tree (Figure 2a).

Even very short DNA sequences are sufficient to place a specimen, though in some cases this is also the explanation for the unstable and likely erroneous position in the phylogenies for some species. For example, HUM9 is correctly placed in the cluster with other *M. noyesi* based on a 296 bp CO1 sequence and the same is true for *M. momookherjeae* sp. nov. retrieved as sister to *M. antecessor* based on a 394 bp CO1 sequence (the morphology of both species places them in the antecessor-group). *Megaphragma antecessor*, *M. liui*, and *M. momookherjeae* that have their positions on the trees drastically altered depending on the analysis (partitioned versus unpartitioned) are represented by short sequences: 519 bp for 28S and 366 for CO1, 344 bp for 28S and 370 for CO1, and 394 bp for CO1, respectively.

3.2. Taxonomy

**Megaphragma** Timberlake, 1924

*Megaphragma* Timberlake, 1924. *Proc. Haw. Entomol. Soc.* 5: 412–414. Type species: *Megaphragma mymaripenne* Timberlake, by original designation.

*Sethosiella* Kryger, 1932. *Bulletin de la Société Royale d’Egypte* 16: 38–39. Type species: *Sethosiella priesneri* Kryger, by original designation. Synonymy by Ghesquière 1939, p. 36.

*Paramegaphragma* Lin, 1992. *Entomotaxonomia* 14(2): 133–135, 138. Type species: *Paramegaphragma stenopterum* Lin, by original designation. Synonymy by Delvare 1993, p. 151.

*Diagnosis.* Female (Figure 1a). Body rather compact, extremely small, length 0.16–0.3 mm. Antenna (Figure 1b) inserted at mid level of the internal orbital line, with short radicle, scape usually elongate, pedicel, anellus, single funicle segment present or absent, clava one -, two -, or three-segmented. Antennal formula: 1 (scape), 1 (pedicel), 1 (anellus), 1 (funicle), 2 (clava); or 1,1,(1),1,1 or 1,1,(1),0,3. The antenna is counted as four- or five-segmented, since the anellus is not counted among the antennomeres. Claval segment.
1 without multiporous placoid sensilla. Mandible with two small teeth. Maxillary palp very small and labial palp vestigial. Eye black unless otherwise stated. Mesosoma rather high, usually shorter than metasoma. Pronotum very short; mid lobe of mesoscutum not much longer than wide, either smooth or with polygonal or striate sculpture; one pair of adnotal setae. Scutellum shorter than mid lobe of mesoscutum, with a pair of setae. Metanotum short; propodeum slightly longer than metanotum, or, in the middle, even longer, with a well-developed central area (disc) that may bear crenulae. Propodeal spiracle placed in an oval groove, and near the internal margin with two very small setae. Fore wing (Figure 1c) extremely narrow compared with other Trichogrammatidae genera, 5.3–10× as long as maximum discal width, with short submarginal vein; costal cell and parastigma not distinct; marginal vein very long, with one short seta at the base and with one or two setae centrally, which when paired may be of similar or very different lengths; stigmal vein very short with one or two setae on the stigma; disc with one or a few setae in one or two rows or glabrous (when there is one seta it is located on the dorsal surface of the wing, when discal setae are more numerous they are located on both dorsal and ventral surfaces of the wing, cf Figure 22d,e). Hind wing without discal fringe on front margin. Legs robust, often with striate sculpture on coxae, also on femora and tibiae. T7 and T8, respectively, without spiracle and cercus.

**Male:** As female, but often with postanellar antennomeres shaped differently. Genitalia tubular, very simple and usually small.

**Relationship.** The closest relatives of *Megaphragma* appear to be *Prestwichia* Lubbock and *Sinepalpigramma* Viggiani and Pinto [56]. Unfortunately, sequences for neither of these genera were available for comparison. We have used an *Epoligosita* Girault, two *Oligosita* Walker, and a *Probrachista* Viggiani species as outgroups. These Oligositinae genera are close phylogenetically to *Megaphragma* according to a previous molecular study [33]. Species-group relationships are discussed below.

**Distribution:** Cosmopolitan.

**Hosts and biology.** The known species of *Megaphragma* are all egg parasitoids of Thysanoptera (Supplementary Figure S4) [57–59]. Biological data are available only for a few species, e.g., *M. mymaripenne, M. longiciliatum* (as *M. analphitanum*) [12–14], and are given below where available. It is interesting that at the same locality there may be more than one species of *Megaphragma*, even in Europe. *Megaphragma viggianii* and *M. polilovi* were found in Italy at the same locality and on the same host, while in a single sample from near Barkás Lake in Hungary, there are three species (*M. longiciliatum, M. noyesi,* and the undescribed species represented by the specimen HUM4, close to *M. longiciliatum* but distinct genetically).

**Species groups in *Megaphragma***

On the basis of present knowledge, the following species group are proposed in *Megaphragma*:

- **M. mymaripenne-group:** antenna with a single funicle segment that is longer than wide (this feature also shared by *polychaetum-* and *longiciliatum-* groups); T1 with longitudinal and/or transverse cells, with some denticles laterally within the cells (Figures 17f, 18f and 20b); T2–T4 each with a pair of short setae.

  Included species: *M. funiculatum* Polaszek and Fusu sp. nov., *M. mymaripenne* Timberlake, *M. novickii* Polaszek, Fusu, and Viggiani sp. nov., *M. noyesi* Polaszek and Fusu sp. nov., *M. polilovi* Polaszek, Fusu, and Viggiani sp. nov.

- **M. longiciliatum-group:** same as *mymaripenne-group*, but without cells on T1. According to the phylogenetic analysis, the group appears to be derived from within the *mymaripenne-group* having lost the denticulate cells on T1.

  Included species: *M. longiciliatum* Subba Rao, *M. fanenitrakely* Polaszek and Fusu sp. nov., *M. priesneri* Kryger, *M. viggianii* Polaszek, Fusu, and Polilov sp. nov. The species of the *macrostigmum-group* (*M. caribea* and *M. macrostigmum*) characterized by a four-segmented antenna, might be derived species within this group.
Insects 2022, 13, 561

M. polychaetum-group: antenna with a long, cylindrical, funicle segment; spatulate sensilla at the end of each clava segment, and a robust terminal sensillum on C2, fore wing disc with more than seven setae, often arranged in two rows. Male antenna is particularly distinctive, with an elongate C1, short C2 usually with very long sensilla.

Included species: M. cockerilli Polaszek and Fusu sp. nov., M. giraulti sp. nov., M. polychaetum Lin, M. kinuthiae Polaszek, Fusu, and Viggiani sp. nov. Our molecular analysis also includes two males of this group, representing two undescribed species (vouchers SAM1 and SAM2, NHMUK). They have the antennal structure characteristic for males of the group, but our analyses recover them basal to the mymaripenne- and longiciliatum-groups instead of clustering them with the other two species of the polychaetum-group.

M. ghesquierei-group: antenna without funicle segment and with clava three-segmented, because the funicle is fused with the clava along an oblique suture. Fore wing disc with one seta on the dorsal surface or no setae. Propodeum characteristically produced centrally, almost always with a row of crenulae. Metafemur with a robust spine close to the connection with the tibia. Because of the intergradation in the structure of the antenna between the ghesquierei and other groups, we do not currently consider Paramegaphragma as a valid genus for the species in the ghesquierei- plus stenopterum- groups. It is possible that future analyses, especially including multigene or reduced genome representation data, may lead to the reinstatement of Paramegaphragma Lin as a valid genus. The two species formerly assigned to Paramegaphragma by Lin [9], M. stenopterum and M. macrostigmum, are not closely related and clearly belong to different species-groups (stenopterum-group and macrostigmum-group, respectively), though on morphological grounds stenopterum-group is clearly related to ghesquierei-group or even integral part of it. This is another reason for not recognizing Paramegaphragma.

Included species: M. breviclavum sp. nov., M. chienleei sp. nov., M. deflectum Lin, M. digitatum sp. nov., M. ghesquierei Ghesquière, M. hansoni sp. nov., M. liui sp. nov., M. pintoi Viggiani sp. nov., M. rivelloi sp. nov., M. striatum Viggiani, M. tamoi Polaszek, Fusu, and Viggiani sp. nov., M. tridens Fusu and Polaszek sp. nov., M. vanlentereni Polaszek and Fusu sp. nov.

M. stenopterum-group: same as M. ghesquierei but with clava two-segmented. The antennal structure is very suggestive of the ghesquierei-group, given the similarity between the apparent C1 of the stenopterum-group and that of the ghesquierei-group; i.e., it is actually a funicle completely fused to the clava. In the antecessor-group, the funicle is distinct albeit transverse and anneliform. Pending further evidence, we consider the stenopterum-group as possibly nested within the ghesquierei-group. Megaphragma macrostigmum and M. caribea (macrostigmum-group) were considered by previous authors to belong in a group with M. stenopterum [60], and M. macrostigmum with M. stenopterum were both originally included by Lin [9] in his genus Paramegaphragma. However, the former two species lack any of the obvious apomorphies of the ghesquierei-group except for the apparently lost funicle. Members of the macrostigmum-group are otherwise similar in the structure of the fore wing and sculpture of the mesoscutum to the species in the longiciliatum-, mymaripenne-, and polychaetum- groups and are probably not related to the ghesquierei- and stenopterum-groups. Our molecular analysis did not include M. stenopterum, the only member of this species group.

Included species: M. stenopterum (Lin).

M. antecessor-group: antenna with a transverse funicle segment not much larger than the anellus, and clava one- or two-segmented. Metatibia with a characteristic row of setae (Figures 11d and 21j). The structure of the antenna seems intermediate between that characteristic of the longiciliatum- and mymaripenne- groups and that of the ghesquierei-group. In the latter species group, the antenna is apparently without a funicle, as the funicle is completely fused with the clava by an oblique suture and, hence, the clava appears three-segmented. Our phylogenetic analysis shows that M. antecessor and M. momookherjeeae, while resembling the ghesquierei species group in many features (including fore wing structure and the robust spine on metatibia), appear outside it, and basal to all remaining
Megaphragma except members of ghesquierei-group (partitioned analyses) or the most basal species group of all Megaphragma (unpartitioned analysis).

Included species: M. antecessor Polaszek and Fusu sp. nov., M. momookherjeeae Polaszek and Fusu sp. nov., M. unicalvum Polaszek and Fusu sp. nov.

M. macrostigmum-group: as explained above, M. macrostigmum and M. caribea, while undoubtedly very closely related to each other, appear to have no connection with the ghesquierei-group (our molecular analysis did not include either of these two species). The antenna has the clava two-segmented and no funicle as in the stenopterum-group; the fore wing structure, however, is not similar to the ghesquierei-group but suggestive of the longiciliatum-group, especially M. priesneri; metafemur without the robust spine characteristic for the antecessor-, ghesquierei-, and stenopterum-groups.

Included species: M. caribea Delvare, M. macrostigmum (Lin).

Previously described species

Megaphragma caribea Delvare (Figure 3a–c, Figure 12d–f and Figure 19a–c)

Megaphragma caribea Delvare, 1993. Revue fr. Ent. (n.s.) 15(4): 149–151.

Diagnosis. Female: Antenna four-segmented (excluding anellus), without funicle, clava two-segmented (Figure 3a and Figure 12d); C1 with 16 MT, 2 long UST, 1 SS; C2 with 4 MPS, 2 MT, 1 SB, 1 prominent apical SS (Figure 3a and Figure 12d).

Mid lobe of mesoscutum with large, but shallow polygonal cells (Figures 12e and 19c). Propodeum with central area short. Fore wing 5.5× as long as maximum discal width, marginal vein about twice length of submarginal vein, with two rather long setae (of equal length) present at midpoint of marginal vein (Figure 3c). Metasoma with lines of microspines evident on T2–T6 (cf Figure 19a). Ovipositor 1.7× as long as mesotibia.

Body yellow, with the following slightly darkened: occiput, meso- and meta-coxae, apices of meso- and metafemora. Metasoma with pale brown transverse bands.

Male: Antenna with C1 longer than in female (Figure 19b).

Material examined. Paratypes: GUADELOUPE: Vieux Habitants, 17.XI.1988, coll. J. Etienne, ex eggs Selenothrips rubrocinctus (Giard) on Psidium guajava. Slides n. 8002.4, 8002.6, 8002.9 (2♀, 1♂, NHMUK).

Non-types: COLOMBIA: Cartagena, i.2015, with Heliothrips haemorrhoidalis and Selenothrips rubrocinctus on Terminalia catappa, coll. A.A. Polilov (1♂, AICF).

Species-group placement: M. macrostigmum-group—possibly a subgroup of the M. longiciliatum-group.

Distribution: Colombia, Guadeloupe.

Host: Selenothrips rubrocinctus (Giard).

DNA data: no DNA sequences.

Comments: The species was described in detail by the author. Megaphragma caribea is clearly close to M. macrostigmum (Lin). At present, their discrimination is based on the absence of long UST on the basal clava (C1) of the antenna of the latter species (Figure 6a). Since the original description did not indicate whether the species-group name caribea is a noun or an adjective, following Art. 31.2.2. of ICZN, we treat it as a noun and do not make a gender agreement.

Megaphragma deflectum Lin (Figure 3d–f)

Megaphragma deflectum Lin, 1992. Entomotaxonomia 14(2): 130–131.

Diagnosis. Female: Antenna (Figure 3e) without funicle, clava three-segmented, with C1 and C2 almost fused; C1 with 1 UST; C2 with 1 UST, and ≥4 MT; C3 with ≥2 MPS, 1 MT, and 1 SB.
Figure 3. Line drawings of *Megaphragma* species: (a) *M. caribea*, female antenna (Paratype); (b) *M. caribea*, male antenna (Paratype); (c) *M. caribea*, female fore wing (Paratype); (d) *M. deflectum*, female body dorsal (Holotype); (e) *M. deflectum*, female antenna (Holotype); (f) *M. deflectum*, female fore wing (Holotype); (g) *M. ghesquierei*, male body lateral (Paratype).
Mid lobe of mesoscutum (Figure 3d) with longitudinal striate sculpture extending to scutellum; propodeum (Figure 3d) with central area extended posteriorly, crenulae absent. Fore wing (Figure 3f) 9× as long as maximum width; longest fringe seta 5× as long as maximum discal width. Fore wing disc without setae. Marginal vein with two long subequal setae centrally. Stigmal vein not enlarged, with two sensilla apically. Middle tibia with one large spine basally; metatibia with spine. T1 with elongate cells laterally, 2-3× as long as wide; T2-T4 without setae laterally. Ovipositor 1.7× as long as mesotibia.

Body largely brown, the following paler: legs except coxae and metatibia. Antenna with pedicel pale; scape, C1-C3 darker. Fore wing strongly infuscate basally; stigmal and marginal veins brown; marginal vein very dark centrally.

Male: As female but C3 with fewer MPS and with ASC apically.

Material examined. Holotype ♀ (FAFU). CHINA: Wuyishan, Fujian, 19.x.1987, Wang Jiashe col. Paratype: CHINA: Fuzhou, Fujian, 8.v.1987, N.Q. Lin col. (1♀, FAFU). Non-type: CHINA: Wuyishan, Fujian, 10.x.1987, Wang Jiashe col. (1♂, FAFU).

Species-group placement: M. ghesquierei-group.

Distribution: China.

DNA data: no DNA sequences.

Comments: This species was correctly considered allied to M. ghesquierei Ghesquière mostly due to features of the antenna (Figure 3e), fore wing (Figure 3f), and other characteristics of the body, but M. deflectum can be distinguished easily from that species by the sculpture of the mid lobe of the mesoscutum and the central area of propodeum (Figure 3d). The male “allotype” (paratype) of M. deflectum is actually a male of M. rivelloi sp. nov. (see below).

Megaphragma ghesquierei Ghesquière (Figures 3g and 4a,b)

Megaphragma ghesquierei Ghesquière, 1939. Rev. Zool. Bot. Afr. 33(1): 36–38.

Diagnosis. Female: Antenna without funicle, clava three-segmented, C1 distal margin transverse (cf Figure 3g). C1 with ≥1 MT; C2 with ≥2 MT, ≥2 UST; C3 with ≥2 MPS, 1 MT, and 1 SB.

Mid lobe of mesoscutum anteriorly with reticulate sculpture, remainder with longitudinal striation continuing onto scutellum (cf Figure 3g). Propodeum with a large subtriangular central area. Fore wing 7× as long as maximum width (Figure 4a); the disc pointed distally, without setae. Metasoma with tergites with some short transverse striation centrally, and each with a pair of lateral setae (Figure 4b).

Body dark brown, with the following paler: frons and occiput, scutellum and propodeum, tarsi. Metasoma with tergites and sternites appearing as dark bands (in the slide-mounted types). Fore wing basally strongly infuscate with a dark marginal vein.

Male: Similar to female in all aspects of morphology except genitalia characters.

Material examined. Holotype ♀ (MRAC). D. R. CONGO: Rutshuru, i.1938, ex eggs of Panchaetothrips noxius Priesner on Coffea arabica.

Paratypes: D. R. CONGO: 1♂, on slide with holotype; 3♀ on one slide, with data as holotype except “Neotopotype” in Ghesquière’s writing (MRAC).

Non-type: 1♂, labeled type in the Nowicki collection, no other data (DACE).

Species-group placement: M. ghesquierei-group.

Distribution: D. R. Congo.

Host: Panchaetothrips noxius Priesner

DNA data: no DNA sequences.

Comments: The species is rather easily recognizable by the combination of features of the antenna, mid lobe of mesoscutum, propodeum, fore wing, and metasomal tergites.

The species was intended to be described by Nowicki, but was published by Ghesquière [61] (p. 36) because Nowicki’s manuscript on several African Trichogrammatidae never reached the journal Revue de zoologie et de botanique Africaines in Tervuren where Ghesquière was working. Ghesquière [61] (p.37) gives the date of collection as “XII.1937”, but, as given above, the holotype is labeled: “I.1938”.
Figure 4. Line drawings of *Megaphragma* species: (a) *M. ghesquierei*, female fore wing (Holotype); (b) *M. ghesquierei*, male propodeum and tergites (Paratype); (c) *M. giraulti*, male antenna (Paratype); (d) *M. giraulti*, female antenna (Holotype); (e) *M. giraulti*, male metasoma (Paratype); (f) *M. giraulti*, female lateral meso- and metasoma (Holotype); (g) *M. giraulti*, female antenna, detail (Holotype).
**Megaphragma longiciliatum** Subba Rao (Figure 5e–h and Figure 16e)

*Megaphragma longiciliatum* Subba Rao, 1969. *Proc. R. Ent. Soc. Lond. (B)* 38(7–8): 114.

*Megaphragma aligarhensis* Yousuf and Shafee, 1988. *Indian J. syst. Ent.* 4(2) [1987]: 114.

**Syn. nov.**

*Megaphragma amalpitanum* Viggiani in Viggiani and Bernardo, 1997. *Boll. Zool. Agr. Bach. Ser. II* 29(1): 51–55. **Syn. nov.**

*Megaphragma magniclava* Yousuf and Shafee, 1988. *Indian J. syst. Ent.* 4(2) [1987]: 115–116.

**Syn. nov.**

*Megaphragma decochaetum* Lin, 1992. *Entomotaxonomia* 14(2): 131–132. **Syn. nov.**

*Megaphragma shimalianum* Hayat, 2009. *Oriental Insects* 43: 212–213. **Syn. nov.**

**Diagnosis. Female:** Antenna (Figure 5e and Figure 16e) with clava two-segmented. Funicle with $\geq 2$ MT; C2 with $\geq 6$ MT, 1 UST; C3 with $\geq 3$ MPS, and 1 UST.

Mid lobe of mesoscutum anteriorly with reticulate sculpture. Propodeum with a very short central area. Fore wing 8× as long as wide (Figure 5g). Metasoma (Figure 5h) without subpunctal subpunctal sculpture on tergites, but with some ridges, T2–T4 each with a pair of long setae. Ovipositor 1.1× as long as metositia.

Body brown to dark brown, with the following paler: antenna, legs. Metasoma with tergites and sternites appearing as dark bands (in the slide-mounted types). Fore wing completely hyaline.

**Male:** Similar to female in most characters except genitalia; antennal funicle slightly more elongate than in female, and clava darker than remainder of antenna. C2 without long UST; C3 shorter than in female (Figure 5f).

**Material examined.** Holotype ♀ *M. longiciliatum* (NHMUK). **INDIA:** Bangalore, Avati, ex. *Frankliniella lilivora* Takahashi on *Polyanthes tuberosa*, x.1968, V. P. Rao. Paratypes: 13♂1♂, same data as holotype (NHMUK).

Holotype ♀ *M. aligarhensis* (AMU). **INDIA:** Aligarh, IX.1985, M. Yousuf. Paratypes: CHINA: Fuzhou, Fujian, 30.vi.1987, coll. Lin. Paratypes: CHINA: Fuzhou, Fujian, 30.vi.1987, coll. Lin (1♂, FAFU).

Holotype ♀ *M. decochaetum* (FAFU). **CHINA:** Fuzhou, Fujian, 30.vi.1987, coll. Lin. Paratypes: CHINA: Fuzhou, Fujian, 30.vi.1987, coll. Lin (1♂, FAFU).

Holotype ♀ *M. magniclava* (AMU). **INDIA:** Aligarh, 25.x.1985, M. Yousuf. Paratypes: **INDIA:** Uttar Pradesh, Mainpuri Malau, slide XIV 1, 2, 4, 6.ix.2007, F. R. Khan col. (3♂, 1♂, AMU); Firozabad, Nagla Prabhu, slide IX, 4.ix.2007, F. R. Khan (12♂, AMU).

Non-types: **ARGENTINA:** INTA Oliveros Santa Fe, v.2004, ex *Calothrips phaseoli*, A. M. Molinari col. (2♂ 7♂, DACE, AICF); San Miguel de Tucuman, x–xi.2006, ex *Thysanoptera* eggs on corn, E. Luft col. (2♂, DACE, AICF); Salta Prov., Agus Blancas, Route 19, 22.72° S, 64.40° W, 447 m, 23.iii.2003, swp rainforest along Bolivia border, J. Munro 003-03-24-01 (6♂).

**Material examined.** Holotype ♀ *M. amalpitanum* (DACE). **ITALY:** Vietri sul mare (SA), x.1994, coll. G. Viggiani, ex egg of *Heliothrips haemorrhoidalis* on *Viburnum tinus*. Paratypes: 36♂ 32♂, mostly obtained from the same host collected in the same holotype locality (DACE).

Holotype ♀ *M. decochaetum* (FAFU). **CHINA:** Fuzhou, Fujian, 30.vi.1987, coll. Lin. Paratypes: CHINA: Fuzhou, Fujian, 30.vi.1987, coll. Lin (1♂, FAFU).
28°37′51″ N 77°09′50″ E, 5–7.xi.2003, pan trap, J. Heraty col. (♀ 1, UCRC); Karnataka, W of Mudigere, 850–912 m, 13°07′05″ N 75°30′20″ E, 24.xi.2003, sweep evergreen forest, J. Heraty col. (♂ 1, UCRC). **INDONESIA**: W Java, Gunung Halimun NP, Tea-Forest Junction, 1066 m, 6°41′07″ S 106°31′16″ E, 17.ix.2015, screen-sweep, A. Polaszek col., DNA1147 (♀ 1, NHMUK). **ITALY**: Vietri sul mare, Benincasa, 40°40′ N 44°20′ E, 17.vii.2013, ex Heliothrips haemorrhoidalis on Viburnum tinus, G. Viggiani, DNA: ITM10 (♀ 1, NHMUK). **MALAYSIA**: Sarawak, Mentawai 4°14′ N 114°52′ E, ix.2011, screen-sweep, A. Polaszek col., DNA: SRM1 (♀ 1, NHMUK). **oman**: Hajar Mts, screen-sweep, 20.i.2017 A. Polaszek col., DNA: MO3, MO13, MO20, MO22 (MO13 was destroyed during the DNA extraction) (♀ 1, ♀ 1, NHMO). **PAPUA NEW GUINEA**: Central Province, 15km SE Port Moresby, 1.i.1986, screen-sweep eucalyptus grassland, G. Girdh col. 86-01-01-1 (♀ 1, ANIC). **united arab emirates**: Abu Dhabi Emirate, Al Ain, Al Khabis garden, 24°13.521′N 55°41.955′E, 25–30.iii.2019, yellow pan trap, A. Polaszek, B. Howarth col. (♀ 1, NHMUK). **USA**: Florida, Lake Seminole Park, Seminole, 27°50′–51′ N 82°46′ W 9.vii.2015, sweep, Z. Lahey col., DNA1111, 1112, 1113 (3 specimens, NHMUK, currently misplaced). **Species-group placement**: M. longiciliatum-group. **Distribution**: Argentina, Australia, China, D. R. Congo, France, India, Indonesia (Java), Italy, Malaysia (Borneo, Sarawak), Oman, Papua New Guinea, Portugal [62] (as M. amalphitanum), UAE, and USA. **Hosts**: Caliothrips phaseli (Hood) (Argentina); Frankliniella lilivora Takahashi (India); Heliothrips haemorrhoidalis (Bouché) (Italy). The record from Argentina “ex Thysanoptera eggs on corn” could be from Frankliniella williamsi Hood. **DNA data**: CO1: 8 sequences from 4 countries: D. R. Congo, France, Hungary, Malaysia (Sarawak); 28S: 18 sequences from 8 countries: D. R. Congo, France, Hungary, Indonesia (Java), Italy, Malaysia (Sarawak), Oman, USA. **Comments**: Megaphragma longiciliatum is the most widely distributed Megaphragma species; hence the large number of synonyms. We have examined 150 specimens from 14 countries and have DNA sequences for 18 specimens from 8 very widely distributed countries. We have carefully assessed morphological variation within the specimens examined, and consider that it encompasses the morphological characteristics of the type material of the species synonymized above [7,9,10,63,64]. The holotype of M. longiciliatum is in extremely poor condition. The mountant, presumably gum chloral, has turned black. It is to be hoped that in a few years’ time, the holotype material of the species synonymized above [7,9,10,63,64]. The holotype of M. longiciliatum in is in extremely poor condition. The mountant, presumably gum chloral, has turned black. It is to be hoped that in a few years’ time, the holotype will be destroyed completely, and one of the paratypes, all of which are still in excellent condition, can be designated a neotype. Unfortunately, there is no current provision under the Code to legitimately replace a holotype specimen that has deteriorated irretrievably. **Megaphragma macrostigmum** (Lin) (Figure 6a–d) **Paramegaphragma macrostigmum** Lin, 1992. Entomotaxonomia 14(2): 135–136. **Megaphragma macrostigmum**: Delvare, 1993. Revue fr. Ent. (n.s.) 15(4): 151. **Diagnosis. Female**: Antenna without funicle and clava two-segmented (Figure 6a); C1 with two short MT; C2 with one MPS, one SB, and one UST. Mid lobe of mesoscutum with some large, but shallow polygonal cells. Propodeum with a very short central area. Fore wing 5.3× as long as maximum discal width, with two rather long setae in the middle of marginal vein (Figure 6c); disc with 4–5 setae not in a row. Metasoma with a line of microspines evident on T2–T6 (cf Figure 6d). Ovipositor 2.1× as long as mesotibia. The main features of the antenna and fore wing are illustrated in Figure 6a,c. Body uniformly pale brown, fore wing slightly to moderately infuscate below marginal vein. **Male**: Similar to female in most characters except genitalia; antennal funicle slightly shorter than in female, C1 longer, C2 with long UST (Figure 6b). **Material examined. Holotype ♀ (FAFU). CHINA**: Fuzhou, Fujian, 31.viii.1987, N.Q. Lin col.
Figure 5. Line drawings of Megaphragma species: (a) *M. giraulti*, female fore wing (Holotype); (b) *M. kinuthiae*, female antenna; (c) *M. kinuthiae*, female antenna (detail); (d) *M. kinuthiae*, female fore wing; (e) *M. longiciliatum*, female antenna; (f) *M. longiciliatum*, male antenna; (g) *M. longiciliatum*, female fore wing; (h) *M. longiciliatum*, female dorsal meso-and metasoma.
Paratype: CHINA: Guangzhou, 3.xi.1985 N.Q. Lin col. (1♀, FAFU).
Non-type: CHINA: Guangzhou, 30.x.1985, N.Q. Lin col. (1♂, FAFU).

Species-group placement: M. macrostigmum group—possibly a subgroup of the M. longiciliatum-group.

Distribution: China.

DNA data: no DNA sequences.

Comments: This species is very similar to M. carieba; at present, the only difference from the latter species appears to be the absence of long sensilla on C2.

Megaphragma mymaripenne Timberlake (Figure 1a, Figure 6e–i and Figure 17d)

Megaphragma mymaripenne Timberlake, 1924. Proc. Haw. Entomol. Soc. 5: 414–415.
Megaphragma mymaripenne: Viggiani, 1997. Boll. Lab. Ent. agr. Filippo Silvestri 53: 117–122.

Diagnosis. Female: Antenna (Figure 6h and Figure 17d) with clava two-segmented, funicle with ≥4 MT; C1 trapezoid in lateral view with length 1.5× maximum width or less (longer in dorsal or ventral view), with 2 UST, but without linear sensilla (MPS), ≥9 MT; C2 with ≥3 MPS, 1 MT, 1 SB, and 1 SS (Figure 6i).

Mid lobe of mesoscutum anteriorly with subpolygonal sculpture, but often appearing smooth in slide-mounts. Propodeum with a very short central area. Fore wing (Figure 6e) 9–10× as long as wide, marginal vein with two long setae in the middle, setae on disc more or less regularly in a row of 10–15 setae, and longest fringe seta 5–6× as long as maximum disc width. T1 with sculpture represented by a combination of transverse and longitudinal cells, lateral ones twice as long as wide; sides of some cells with denticles present. The subsequent tergites show rather variable sculpture, differing from the pattern on the first tergum. T2–T4 each with a pair of very short setae.

Body uniformly pale brown, scutellum paler than mesoscutum. Legs pale, wings hyaline. Clava slightly darker than the remainder of the antenna.

Male (hitherto undescribed): same as female but antenna slender, with funicle twice as long as wide and C1 about 1.7× as long as C2. T1 with sculpture not as complete as in the female. Genitalia simple, tubular, 4.5× as long as wide (cf Figure 7f).

Material examined. Holotype ♂ (USNM). USA: Hawaii, Mountain View, i.1920, C.E. Pemberton col.

Paratype: same data and on the same slide with holotype (1♀USNM).

Non-types: ARGENTINA: San Miguel de Tucuman, x–xi.2006, ex Thysanoptera eggs on corn, E. Luft col. (5♀, DACE); ix.2006, from corn, E. Vinla col. (3♂, DACE); Salta Prov., Rosario de la Frontera, 25.83°S 64.88°W, 745 m, 20.iii.2003, sweep forest, J. Munro 003-03-20-01 (1♀, UCRC); La Rioja Prov., Chuquis, 28° 53′ 40″ S 67° 00′ 31″ W, 1575 m, 17.iii.2003, sweep acacia scrub, J. Munro 003-03-17-05 (1♀, UCRC); Salta Prov., Orán, rd to San Andres along Rio Blanca, 23.11° S, 64.52° W, 535 m, 23.iii.2003, sweep scrub and ginger, J. Munro 003-03-23-02 (2♀, UCRC). BRAZIL: Santa Catarina, Nova Teutonia, 17.x.1949, F. Plaumann col. BM 1957-341 (1♀, NHMUK). COSTA RICA: Limón, Hitoy-Cerere Reserve, 9°40′ N 83°02′ W, 100 m, 24–26.ii.2008, J.S. Noyes col. NHM(E)2010-21AQ (1♀, NHMUK). DOMINICAN REPUBLIC: San Cristobal, S. Cristobal Manomatuey, 20 km NW valley, 500 m, 23.iii.1991, L. Masner col. (1♀, UCRC). ECUADOR: 1♀, Galapagos Is., Sta Cruz, Bellavista 2 mi N, 360 m, guava thicket, v–vii.1985, S. and J. Peck col. (CNCI). GUATEMALA: Petén Borg, Domaine Duclos, 28.ii.1989, with Solenothrips rubrocinctus and Heliothrips haemorrhoidalis on Inga ingoides, J. Etienne col. (3♂, NHMUK). ISRAEL: Bet Dagan, ix.1996, ex Heliothrips haemorrhoidalis, M. Wysoki col. (7♀, DACE, AICF). MEXICO: Chiapas, 6.2 miles N Berriozabal, premontane rain forest, 9.viii.1990, 4000′ J.B. Woolley col. (3♀, 2♂, UCRC). USA: California, Orange Co., Irvine, 13.vi.1990, ex Heliothrips haemorrhoidalis on avocado, H.G. Johnson (1♀, NHMUK); California, Orange Co., South Coast Field Station, El Toro, ex Heliothrips haemorrhoidalis on avocado, H.G. Johnson (2♀, 1♂, UCRC); California, Orange Co., 10.ix.1989, ex Heliothrips haemorrhoidalis on avocado N. Hessein col. (1♀, DACE); Virginia, Montgomery Co., 8 km NW Blacksburg, 19–30.vi.1987, MT, rural, 1000 m, BRC HYM. TEAM (1♀, CNCI); California, San Diego Co., Valley Center, Westlilac Rd, Playa Grove, on avocado, H.G. Johnson (7♀, UCRC);
Missouri, Parkville, 39°12′17″ N, 94°40′38″ W, 5.vii.2015, swept, Z. Lahey col., DNA: 1114 (1♀, NHMUK—currently misplaced).

Species-group placement: M. mymaripenne-group.

Distribution: Argentina, Brazil, Chile, Costa Rica, Dominican Republic, Ecuador, Guadeloupe, Israel, Mexico, USA, and Venezuela.

Hosts: Megaphragma mymaripenne is a solitary egg endoparasitoid of several species of Panachetothripinae (Thripidae). The most common host is the widespread Heliothrips haemorrhoidalis. The populations recorded in the USA [12] are represented mainly by females. The population reared in Argentina from maize and identified as M. mymaripenne [11] differs from the known populations of the species: the reared specimens from maize appear to be normally bisexual.

DNA data: 28S: 1 sequence, Missouri (USA).

Comments: This species was described in detail by Timberlake [65], and additional features were given by Viggiani [6]. Megaphragma mymaripenne is extremely difficult to distinguish morphologically from the closely related species M. polilovi, and even from the more distantly related species M. noyesi, with which it has been previously confused. They differ, however, in the length and shape of C1, length of the scape and colour of the radicle, and length of the ovipositor, respectively, as outlined in the key. Without the molecular data, these subtle differences would have been overlooked or treated as intraspecific variability. The correlation between the molecular clades and morphological characters indicates, however, that there are three species involved.

Records from Israel are the only Old-World records for this species; previous records of M. mymaripenne, e.g., from Italy [13,14,66], turned out to be misidentifications of the new species M. polilovi.

Megaphragma polychaetum Lin (Figure 8a–c)

Megaphragma polychaetum Lin, 1992. Entomotaxonomia 14(2): 132–133.

Megaphragma anomalifuniculi Yuan et Lou in Yuan et al., 1997. Journal of Northeast Normal University 4: 62–63. Syn. nov.

Diagnosis. Female: Antenna long and narrow (Figure 8a) with pedicel shorter than the subcylindrical funicle, which has two MT. Clava two-segmented, C1 twice as long as funicle, with two MT and two long UST; C2 with two MPS, two MT, and a terminal basiconic sensillum (SB) slightly shorter than half C2 length.

Mid lobe of mesoscutum with subpolygonal sculpture. Propodeum with a very short central area (Figure 8c). Fore wing (Figure 8b) 8–9× as long as wide, with two short setae in the middle of the marginal vein, and a disc with two distinct rows of 6–8 setae (Figure 8b). Tergites of metasoma without sculpture, but with some short and strong setae. The ovipositor is 1.1× as long as the mesotibia.

Head (including antenna), metasoma, meso-, and metacoxae are very dark. Remainder of body, including legs, pale brown. Fore wing strongly infuscate basally.

Male: Unknown.

Material examined. Paratypes: CHINA: Wuyishan, Fujian, 30.vii.1987, Wang Jiashe col. (3♀, FAFU); 10.vii.1987, 14-051, 14-052 (2♀, FAFU).

Species-group placement: M. polychaetum-group.

Distribution: China.

DNA data: no DNA sequences. DNA sequences are very likely to be close to those of M. cockerilli sp. nov. (see below).

Comments: The type material of M. anomalifuniculi was not available to the authors. According to the illustration given by Yuan and Lou [67], M. anomalifuniculi appears to be similar, if not identical, to M. polychaetum Lin. The features concerning the funicular segment appear to derive from a preparation artifact.
Figure 6. Line drawings of *Megaphragma* species: (a) *M. macrostignum*, female antenna (Paratype); (b) *M. macrostignum*, male antenna (Holotype); (c) *M. macrostignum*, female fore wing (Paratype); (d) *M. macrostignum*, male dorsal metasoma (Holotype); (e) *M. mymaripenne*, female fore wing (Holotype); (f) *M. mymaripenne*, mandible (Holotype); (g) *M. mymaripenne*, maxillary palp (Holotype); (h) *M. mymaripenne*, female antenna (Holotype); (i) *M. mymaripenne*, female antenna (detail of apex) (Holotype).
Figure 7. Line drawings of *Megaphragma* species: (a) *M. nowickii*, female propodeum and T1 (Holotype); (b) *M. nowickii*, male meso- and metasoma (Paratype); (c) *M. nowickii*, female antenna (Holotype); (d) *M. nowickii*, male antenna (Paratype); (e) *M. nowickii*, female fore wing (Holotype); (f) *M. nowickii*, male aedeagus (Paratype).
Figure 8. Line drawings of *Megaphragma* species: (a) *M. polychaetum*, female antenna (Paratype); (b) *M. polychaetum*, female fore wing (Paratype); (c) *M. polychaetum*, female propodeum and metasoma, lateral view (Paratype); (d) *M. priesneri*, female antenna (Neotype); (e) *M. priesneri*, male antenna (non-type); (f) *M. priesneri*, female dorsal meso- and metasoma (Neotype); (g) *M. priesneri*, female fore wing (Neotype).
Megaphragma priesneri (Kryger) (Figure 8d–g and Figure 22e)

Sethosiella priesneri Kryger, 1932. Bulletin de la Société Royale d’Égypte 16: 40.
Megaphragma priesneri: Ghesquière, 1839. Rev. Zool. Bot. Afr. 33(1): 38.

Diagnosis. Female: Antenna (Figure 8d) with pedicel slightly shorter than scape, funicle as long as half pedicel. Clava two-segmented with two long UST on C1 of female; C2 with one MPS and two MT.

Mid lobe of mesoscutum (Figure 8f) anteriorly with subpolygonal sculpture; propodeum with a very short central area. Fore wing (Figure 8g) 7 × as long as wide, with maximum distal width less than 2 × width measured at apex of marginal vein (Figure 8g); maximum fringe seta length 4 × maximum discal width, setae on ventral disc surface short, penultimate one not reaching to the base of the distal (Figure 22e). T1 without sculpture, but with a row of microspines; T2–T4 each with a pair of setae, shorter than their corresponding tergites. Ovipositor 1.1 × mesotibia.

Entire head and body are very dark. Legs and antenna paler. Wings hyaline.

Male: Similar to female in most characters except genitalia. Antenna with funicle and C1 more elongate than in female, without UST on C1; C2 much shorter than in female (Figure 8e).

Material examined. Neotype ♀ (NHMUK), here designated. EGYPT: Tanta, 30.11.30, vine leaves with Retithrips.

Non-types: ISRAEL: Higwe Yisrael, xi.1996, M. Wysoki coll., ex eggs Retithrips syriacus on Vitis vinifera (15 ♀, 3♂, NHMUK, DACE, AICF).

Species-group placement: M. longiciliatum-group.

Distribution: Egypt, Israel.

Host: Retithrips syriacus (Mayet).

DNA data: no DNA sequences.

Comments: Following extensive inquiries over the decades since 1990 in Egypt and Denmark, the holotype (and indeed the remainder of the type series of four specimens) appears to be lost. A specimen with data almost identical to the holotype is in the NHMUK, but has aberrant antennae. Nevertheless, we here designate that specimen as neotype, given that the data are very similar to those of the original type [68] (only the collection date differs by less than a month). Furthermore, all of the remaining morphology accords perfectly with the original description. Unfortunately, extensive efforts to collect fresh specimens in both Egypt and Israel failed.

The neotype designation for M. priesneri (Kryger) satisfies the provisions of Article 75.3 of the International Code of Zoological Nomenclature by: (1) clarifying the taxonomic identity of the species in its accepted modern concept (Article 75.3.1); (2) defining the combination of features of the sculpture of the mesoscutum and T1, propodeal structure and wing proportions as diagnostic for the species (Article 75.3.2); (3) providing data and description sufficient to ensure recognition of the specimen designated (Article 75.3.3); (4) giving reasons (no references available heretofore) for believing that the original type material is lost (Article 75.3.4); (5) selecting a neotype specimen consistent with the original description of the species and that was collected not long (less than 1 month) after the original description (specimen in this case) and, as such, represents the type species (Article 75.3.5); (6) choosing a neotype from the originally cited type locality, Tanta, Egypt (Article 75.3.6); and (7) recording that the neotype is the property of a recognized scientific institution, NHMUK in London (Article 75.3.7).

Megaphragma stenopterum (Lin) (Figure 9e–h)

Paramegaphragma stenopterum Lin, 1992. Entomotaxonomia 14(2): 134–135.
Megaphragma stenopterum: Delvare, 1993. Revue fr. Ent. (n.s.) 15(4): 151.

Diagnosis. Female: Antenna (Figure 9e) without funicle, clava two-segmented, and C2 twice as long as C1. C1 with two MT; C2 with one MPS, two MT, one SB, and one UST.
Figure 9. Line drawings of Megaphragma species: (a) *M. rivelloi*, female antenna (Holotype); (b) *M. rivelloi*, female metasoma (Holotype); (c) *M. rivelloi*, female fore wing (Holotype); (d) *M. rivelloi*, female habitus (Holotype); (e) *M. stenopterum*, female antenna (Paratype); (f) *M. stenopterum*, male antenna (Paratype); (g) *M. stenopterum*, female dorsal meso- and metasoma (Paratype); (h) *M. stenopterum*, female fore wing (Paratype).
Mid lobe of mesoscutum, scutellum, and central area of propodeum longitudinally striate (Figure 9g). Fore wing (Figure 9h) 9× as long as wide, and longest fringe seta 7× as long as maximum discal width, with two long central setae on the marginal vein, one long discal seta; hind margin sinuate. Tergites of metasoma without sculpture or crenulae (Figure 9g).

Body brown, the head darker brown. Fore wing basally strongly infuscate.

**Male**: Almost no discernible differences from female except genitalia characters. Even the antennae are very similar (Figure 9e,f).

**Material examined.** Paratype: **CHINA**: Fuzhou, Fujian, 20.xii.1987, N.Q. Lin col. (1♀, FAFU).

Non-types: **CHINA**: Fuzhou, Fujian, 6.x.1987, N.Q. Lin col. (1♀, FAFU); Fuzhou, Fujian, 20.vi.1987, N.Q. Lin col. (1♂, FAU).

Species-group placement: *M. stenopterum*-group.

**Distribution**: China.

**DNA data**: no DNA sequences.

**Comments**: This species, described in detail by the author, has the unique combination of a single seta on the fore wing and four-segmented antenna without any apparent funicle. A transverse, anelliform funicle is present in *M. uniclavum*, the only other species with a four-segmented antenna and a single seta on the fore wing.

There are differences between the Chinese text and the English text of the original description concerning the collecting dates of the type series. The examined paratype is mentioned in the English part but not in the Chinese part.

*Megaphragma striatum* Viggiani (Figure 10a–d and Figure 21b,c)

*Megaphragma striatum* Viggiani, 1997. **Boll. Lab. Ent. Agr. Filippo Silvestri** 53: 119–120.

**Diagnosis. Female**: Antenna (Figure 10a and Figure 21b) without funicle, clava threesegmented, with C1 having a transverse distal margin. C1 with ≥1 MT; C2 ≥8 MT, and 2 UST; C3 with 2 MPS, ≥2 MT, and 1 SB.

Mid lobe of mesoscutum and scutellum longitudinally striate (Figure 10d). Propodeum with a pronounced subtriangular central area (Figure 21c). Fore wing 8× as long as wide, with one long central seta on the marginal vein, one discal seta, longest fringe seta 4–5× as long as maximum discal width. Metasoma with a row of crenulae on T2 (Figure 21c).

Head and metasoma very dark, mesoscutum brown, the remainder, including legs and antenna, paler. Fore wing infuscate basally.

**Male**: Similar to female in most characters except genitilia.

**Material examined.** Holotype ♂(DACE). **MEXICO**: Chiapas, Ocozocoautla, El Aquacero, 1800–2200′, 8.8.1990, coll. JB Woolley.

Paratypes: 2♀, 2♂, same data as holotype (UCRC).

Non-types: **MEXICO**: Tamaulipas, Alta Cima (nr Goméz Farias), 23°01′ N 99°09′ W, 2.xi.2009, screen-sweep A. Polaszek col., DNA: MXM1 (1♀, NHMUK); 1♀, 1♂, same data as holotype, but not mentioned in the original description (CNCI, UCRC).

Species-group placement: *M. ghesquierei*-group.

**Distribution**: Argentina, Belize, Costa Rica, Mexico.

**DNA data**: CO1: one sequence; 28S: one sequence (both Mexico).
Figure 10. Line drawings of *Megaphragma* species: (a) *M. striatum*, female antenna (Holotype); (b) *M. striatum*, male antenna (Paratype); (c) *M. striatum*, female fore wing (Holotype); (d) *M. striatum*, female dorsal meso- and metasoma (Holotype).
Descriptions of new species

**Megaphragma antecessor** Polaszek and Fusu sp. nov. (Figure 11a–d)

urn:lsid:zoobank.org:act:A68D7B18-ADE4-4EDC-BB04-32A77E063469

**Description. Female:** Head (Figure 11c) with toruli vertical, in contact with each other medially; area below toruli with fine longitudinal sculpture, 1 min seta present laterally on each side. Antenna (Figure 11a) five-segmented (excluding anellus), transverse funicle present; clava two-segmented but these almost completely fused. C1 with $\geq 6$ MT, 3 UST; C2 with 3 MPS and 2 UST; SB not detected but presumably present. Base of C2 with one (apparent) SS.

Mid lobe of mesoscutum (Figure 11d) with fine longitudinal striation; vertical/ventral anterior mid lobe of mesoscutum with coarse, reticulate sculpture (Figure 11d); propodeum with subtriangular area centrally (Figure 11d) with 3–4 large crenulae; propodeum with hind margin arcuate. Fore wing (Figure 11b) $8.5 \times$ as long as maximum width, maximum distal width is $92 \times$ the maximum basal width; disc with a single short seta, and longest fringe seta $6.5 \times$ maximum discal width. Marginal vein with four setae, the second (from the wing base) robust and blunt; central setae equal in length. Campaniform sensillum present below second seta, a line joining the sensillum to the fourth seta. Stigmal vein with a row of three campaniform sensilla apically. Mesotibia with two large spines basally; metafemur with spine; metatibia with a row of fine, blunt setae extending almost the entire inner length, increasing abruptly in length at the distal tibia (exact length not visible in Figure 11d since setae positioned almost vertically; a similar row of setae is found in *M. momookherjeeae* and *M. uniclavum*, Figure 21j). T1 with smooth area centrally, flanked by two or three longitudinal grooves and a longitudinal cell laterally, extending for the length of the tergum; T1–T4 with very long setae laterally, each longer than its tergum; T2 with a curved row of 6–8 spicules on each side. Ovipositor $1.6 \times$ as long as mesotibia.

Body brown. Occiput and face entirely brown, vertex paler. Antenna pale brown, pedicel paler. Mesosoma with the following brown: mid lobe of mesoscutum centrally, side lobes, axillae, propodeum laterally; remainder of mesosoma pale. Entire metasoma brown, except T1 centrally pale. Fore wing distinctly infuscate basally, below, and including marginal vein.

**Male:** Unknown.

**Material examined.** Holotype ♀ (deposited in NHMUK). COSTA RICA: Puntarenas, Est. Biol. Monteverde, 10°19’ N 83°49’ W, 1540–1890 m, 26.ii.2007, J.S. Noyes BMNH(E) 2010-21, DNA: CRM2.2.

**Species group placement:** *M. antecessor*-group. *Megaphragma antecessor* clusters in different DNA sequence analyses with *M. momookherjeeae* sp. nov. (CO1 and combined analysis, strong support) or as basal to all other *Megaphragma* (28S, weak support). The shapes of the fore wing, propodeum, and to some extent the antenna, are strongly suggestive of the *ghesquieri*-group; presumably unique aspects of both DNA sequences prevent it from clustering with the species in that group.

**Distribution:** Costa Rica

**DNA data:** CO1: one sequence; 28S: one sequence.

**Etymology:** From the Latin *antecessor* (predecessor, precursor), in reference to the basal position of this species in the phylogenetic analyses. Noun in apposition.
Figure 11. Photographs of *Megaphragma* species: (a) *M. antecessor*, female antenna (Holotype); (b) *M. antecessor*, female fore wing (Holotype); (c) *M. antecessor*, female head (Holotype); (d) *M. antecessor*, female dorsal meso- and metasoma (Holotype). Scale bars 20 µm.
**Megaphragma breviclavum** Polaszek and Fusu sp. nov. (Figure 12a–c)

urn:lsid:zoobank.org:act:FF10048F-0F8B-4B17-AF74-6E7C504C2ED4

**Description. Female:** Antenna (Figure 12a) five-segmented (excluding anellus); funicle absent; hence, clava three-segmented, with C1 and C2 almost fused. C1 without UST; C2 with 2 UST, and abundant MT; C3 with 2–3 MPS, SB, and SS.

Mid lobe of mesoscutum (Figure 12b) with longitudinal striate sculpture extending to scutellum; propodeum (Figure 12b) with central area extended posteriorly, crenulae absent. Fore wing (Figure 12c) 7.5 × as long as maximum width; the disc with a single long seta; longest fringe seta 4.5 × as long as maximum discal width. Marginal vein with one long seta centrally, extending to apex of marginal vein. Stigmal vein moderately enlarged, with four sensilla apically. Mesotibiae with one large spine basally; metafemora with spine. T1 with elongate cells laterally, 2–3 × as long as wide; T2–T4 without setae laterally; T5 with long setae laterally. Ovipositor 1.7 × as long as mesotibia.

Body largely brown, the following paler: legs except coxae and metafemur. Antenna with pedicel pale; scape and C1–C3 darker. Fore wing strongly infuscate basally; stigmal and marginal vein brown; marginal vein very dark centrally.

**Male:** C1 and C2 with scattered SS; C2 with 2–3 MT apically; C3 with long apical and ventral UST. Colour and morphology largely as in female.

**Material examined.** Holotype ♀ (deposited in NHMUK). MEXICO: Tamaulipas, Alta Cima (nr Gómez Farias), 23°01′ N 99°09′ W, 2.ii.2009, A. Polaszek col. NHM(E) 2010-21, DNA: MXM2. Paratypes: 1 ♀, 1 ♂ with same data as holotype, DNA: MXM3 and MXM4 (NHMUK).

**Species-group placement:** M. ghesquierei-group.

**Distribution:** Mexico.

**DNA data:** CO1: three sequences; 28S: three sequences.

**Etymology:** A noun in apposition referring to the comparatively short clava.

**Megaphragma chienleei** Polaszek and Fusu sp. nov. (Figure 12g,h and Figure 13a–c)

urn:lsid:zoobank.org:act:0ECA37D4-69CF-412F-B081-5F140B3EBA1D

**Description. Female:** Antenna (Figure 12g) five-segmented (excluding anellus); funicle absent (though anellus extremely large); hence, clava three-segmented, with C1 and C2 strongly overlapping, almost fused; C1 with 1 elongate, apical UST; C2 with ≥10 MT; and C3 with 3 very long UST.

Mid lobe of mesoscutum (cf Figure 13b) smooth with some irregular longitudinal striate sculpture; propodeum (cf Figure 13a) elongate and curved centrally and posteriorly, crenulae present. T1 without elongate cells laterally; T2–T4 with short setae laterally. Ovipositor 2 × as long as mesotibia. Mesotibia with one large spine basally; metafemur with spine. Fore wing (cf Figure 13c) 8 × as long as maximum width, maximum distal width equal to maximum basal width; discal setae absent, longest fringe seta 4.7 × as long as maximum discal width. Marginal vein with two long setae centrally, approximately equal in length. Stigmal vein moderately enlarged, with three sensilla apically.

Head and body uniformly very pale brown. C3 darker than remainder of antenna (Figure 12g). Fore wing basally infuscate (cf Figure 13c).

**Male:** Characteristics as for female (Figure 13a–c) (except antenna and genitalia); although, metasoma darker than in female. Antenna as in Figure 12h, with a much shorter C3 compared to the female.

**Material examined.** Holotype ♂ (deposited in AICF). MALAYSIA: Sabah (Borneo), Danum Valley, 05°01′ N 117°49′ E, 16.ix.2012, fogged tree, T. Cockerill, DNA: SAM12. Paratypes: MALAYSIA: Sabah (Borneo), Maliau Basin Studies Centre, Belian Trail, 04°44′ N 116°58′ E, 20.ix.2012, screen-sweep, A. Polaszek NHM(E) 2010-21, DNA: SAM4 to SAM8 (4♂, 1♀, AICF, NHMUK).

**Species-group placement:** M. ghesquierei-group.

**Distribution:** Malaysia (Borneo, Sabah).

**DNA data:** CO1: four sequences; 28S: six sequences.
Figure 12. Photographs of *Megaphragma* species: (a) *M. breviclavum*, female antenna (Holotype); (b) *M. breviclavum*, female dorsal meso- and metasoma, composite image (Holotype); (c) *M. breviclavum*, female fore wing (Holotype); (d) *M. caribea*, female antenna (flagellum only) (Paratype); (e) *M. caribea*, female dorsal mesosoma (Paratype); (f) *M. caribea*, female fore wing (Paratype); (g) *M. chienleei*, female antenna (Holotype); (h) *M. chienleei*, male antenna (Paratype). Scale bars 20 µm except 50 µm for b, c, and f.
Etymology: Named for pitcher-plant (*Nepenthes*) botanist and wildlife photographer Chien C. Lee (Sarawak, Malaysian Borneo).

*Megaphragma cockerilli* Polaszek and Fusu sp. nov. (Figure 13d–f)

urn:lsid:zoobank.org:act:09B45F53-180F-4204-9AC7-69DE9E352132

Description. Female: Antenna (Figure 13d) five-segmented (excluding anellus); pedicel as long as funicle; funicle 4 × as long as wide; C2 longer than C1. C1 with two prominent dorsal UST, proximal UST almost as long as entire clava; C2 with two MT and an SB, which is only slightly shorter than C2. MPS apparently absent.

Mid lobe of mesoscutum (Figure 13e) entirely with large, coarse reticulation; propodeum with a rhomboid, laterally arcuate central area, its hind margin truncate, with fine crenulae. T1–T4 largely smooth, with scattered denticles and no setae laterally. T5 and T6 with a pair of long setae centrally. Ovipositor 1.1 × as long as mesotibia. Mesotibia without spines basally; metatibia with a row of five spines within the distal inner half; a robust spine towards the apex of the outer surface. Fore wing (Figure 13f) 8.5 × as long as maximum width, maximum distal width 1.4 × maximum basal width; discal setae arranged in 3–4 rows, of 4–6 setae per row, longest fringe seta 5 × as long as the maximum discal width. Marginal vein with two long setae centrally, of equal length. Stigmal vein with two sensilla apically.

Body largely dark brown, mesosoma paler laterally; antenna very dark brown. Fore wing infuscate basally.

Male: Unknown.

Material examined: Holotype ♀ (deposited in AICF): MALAYSIA: Sabah (Borneo), Danum Valley, 05°01′ N 117°49′ E, 16.ix.2012, fogged tree, T. Cockerill, DNA: SAM11.

Species-group placement: *polychaetum*-group. Very close to *M. polychaetum*, differing by the extremely elongate terminal sensillum basiconicum.

Distribution: Malaysia (Borneo, Sabah)

DNA data: CO1: one sequence; 28S: one sequence.

Etymology: Named for our colleague and friend, Dr Tim Cockerill, collector of this species (Falmouth University, UK).

*Megaphragma digitatum* Polaszek and Fusu sp. nov. (Figure 14a–c)

urn:lsid:zoobank.org:act:136D58D7-A1FC-4D46-8F63-A7780E4D0871

Description. Female: Antenna (Figure 14a) five-segmented (excluding anellus); funicle absent; hence, clava three-segmented, with C1 and C2 almost fused; C1 with ≥ 4 MT, without UST; C2 with 2 UST and abundant MT; C3 with 2–3 MPS, SB, and SS.

Mid lobe of mesoscutum (Figure 14b) with longitudinal striate sculpture extending to scutellum; propodeum with central area extending posteriorly, crenulae present; T1 with one elongate cell or groove laterally, 2–3 × as long as wide; T2–T4 without setae laterally. Ovipositor 1.5 × as long as mesotibia. Mesotibia with one large spine basally; metatibia with spine. Fore wing (Figure 14c) 8.5 × as long as maximum width, maximum distal width equal to maximum basal width; the disc with a single long seta, longest fringe seta 5 × as long as maximum discal width. Marginal vein with two setae centrally; proximal seta 5–7 × as long as distal seta, extending to the end of the marginal vein (in Figure 14c, the distal seta is barely visible in the space between the proximal one and the marginal vein). Stigmal vein moderately enlarged, with two sensilla apically.

Body largely brown, the following paler: legs except coxae and metafemora. Antenna with pedicel pale; scape and C1–C3 darker. Fore wing strongly infuscate basally; stigmal and marginal vein brown; marginal vein very dark centrally.

Male: Largely as in female. C1 and C2 with scattered SS; C2 with 2–3 MT apically; C3 with long apical and ventral UST.

Material examined. Holotype ♀ (deposited in NHMUK). COSTA RICA: Puntarenas, Est. Biol. Monteverde, 10°19′ N 83°49′ W, 1540–1890 m, 26.ii.2007, J.S. Noyes BMNH(E) 2010-21, DNA: CRM2.1.
Figure 13. Photographs of *Megaphragma* species: (a) *M. chienleei*, male dorsal meso- and metasoma (Paratype); (b) *M. chienleei*, male dorsal mesosoma (Paratype); (c) *M. chienleei*, male fore wing (Paratype); (d) *M. cockerilli*, female antenna (Holotype); (e) *M. cockerilli*, female dorsal mesosoma (Holotype); (f) *M. cockerilli*, female fore wing (Holotype). Scale bars 20 µm.
Paratypes: **COSTA RICA**: same data as holotype except DNA: CRM2.3, 2.6, 2.9, 2.12 (2♂, 2♀, AICF, MZUCR); Cartago, 12.5 km S Turrialba Rancho Naturalista, 1000 m, 9°50′ N 83°34′ W, 12-14.i.2017, J.S. Noyes BMNH(E) 2017-39, DNA1681 (1♀, NHMUK). **ECUADOR**: Km 26.5 road Dura–Tambo, Estación Experimental Litoral Sur, INIAP, 21.xi.2017, ex Chaetanaphothrips signipennis on Musa paradisiaca, M. Arias col., DNA: ECU3 (3♀, 1♂ AICF, NHMUK, UCRC); same data except DNA: ECU4 (3♀, 2♂ AICF, NHMUK, UCRC); same data but ex Frankliniella parvula, DNA: ECU1 (2♀, NHMUK).

Non-type: same data as holotype (1♀, without wings, NHMUK).

**Species-group placement**: ghesquierei-group.

**Distribution**: Costa Rica, Ecuador.

**Hosts**: Chaetanaphothrips signipennis (Bagnall); Frankliniella parvula Hood.

**DNA data**: CO1: two sequences (Costa Rica); 28S: eight sequences (six Costa Rica, two Ecuador).

**Etymology**: The species name refers to the digitate C3.

----

Megaphragma fanenitrakely Polaszek and Fusu sp. nov. (Figure 14d–f)

urn:lsid:zoobank.org:act:4DE1AD1D-C800-48C7-898B-24353F5355F0

**Description. Female**: Antenna (Figure 14d) five-segmented (excluding anellus), with pedicel slightly longer than funicle (12:8); clava two-segmented, C1 with two UST; one SB at the apex of C1 and C2; apex of C2 (Figure 14d) also with two elongate MPS and a long SB.

Mesoscutum with mid lobe (Figure 14e) entirely with coarse, reticulate sculpture; metanotum and propodeum medially short. Metasoma with a row of microspines on each segment. T1 without cells. Ovipositor 1.1× as long as mesotibia. Mesotibia without spines basally. Metafemur without prominent spine. Fore wing (Figure 14f) 9× as long as wide, maximum distal width 1.5× maximum basal width; the disc with 10 setae is irregularly arranged in 1–2 rows, and the longest fringe seta 6× maximum discal width. Marginal vein with two long setae centrally, of equal length. Stigmal vein moderately enlarged, with three sensilla apically.

Body largely pale brown, mesosoma paler laterally; antenna brown. Wings hyaline.

**Male**: Unknown.

**Material examined. Holotype ♀(deposited in NHMUK). MADAGASCAR**: Nosy Komba, 13°27′45″ S 48°20′18″ E, 460 m, 22.vi.2015, screen-sweep, A. Polaszek col. BMNH(E)2015-122.

Paratypes: **MADAGASCAR**: Nosy Komba, closed canopy forest, 13°27′11″ S 48°20′4″ E, 170 m, 19.vi.2015, yellow pan trap, A. Polaszek col. BMNH(E)2015-122 (2♀, NHMUK).

**Species-group placement**: longiciliatum-group.

**Distribution**: Madagascar.

**DNA data**: no DNA sequences.

**Etymology**: A noun in apposition; “fanenitra kely” = “tiny wasp” (Malagasy).

Megaphragma funiculatum Fusu, Polaszek, and Viggiani sp. nov. (Figure 14g,h and Figure 15a,b)

urn:lsid:zoobank.org:act:B6273DD4-14D8-4C91-9057-489883DA0DDE

**Description. Female**: Antenna (Figure 14g) five-segmented (excluding anellus), pedicel twice as long as funicle, the latter trapezoid, and slightly longer than wide; C1 slightly shorter than C2; C1 with 2 dorsal UST; C2 with ≥3 MPS 1 SB and a short SS.
Figure 14. Photographs of Megaphragma species: (a) *M. digitatum*, female antenna (Holotype); (b) *M. digitatum*, female dorsal mesosoma (Holotype); (c) *M. digitatum*, female fore wing (Holotype); (d) *M. fanenitrakely*, female antenna (Holotype); (e) *M. fanenitrakely*, female mesosoma (Holotype); (f) *M. fanenitrakely*, female fore wing (Holotype); (g) *M. funiculatum*, female antenna (Holotype); (h) *M. funiculatum*, female mesosoma (Holotype). Scale bars 20 µm except 50 µm for c and f.
Mid lobe of mesoscutum smooth, with weakly impressed large subpolygonal sculpture (not visible in paratype which has been strongly macerated). Metanotum and propodeum relatively long centrally, each about half the length of scutellum. Propodeum with short central area, without crenulae. T1 (Figure 15a) sculpture with cells converging centrally, lateral cells 2-3× as long as wide, without denticles (some denticles present on innermost cells). T2–T4 without long setae laterally, each with similar sculpture comprising a central irregular oval cell and elongate lateral cells; those on T3 and T4 divided medially. Ovipositor 1.3× as long as mesotibia. Mesotibia with one large spine basally; metasoma entirely brown, T1 darker than the remainder. Fore wing (Figure 15b) 10× as long as wide, maximum distal width 1.2× maximum basal width; the disc with a single irregular row of five setae; longest fringe seta 5.5× maximum discal width. Marginal vein with two long setae centrally.

Head, including antenna, pale; mesosoma largely pale, anterior half of mesoscutal mid lobe brown; metasoma entirely brown, T1 darker than the remainder. Wings hyaline.

Male: Unknown.

Material examined. Holotype ♀ (deposited in NHMUK). COSTA RICA: Limón, Hitoy-Cerere Reserve, 100 m, 9°40′ N 83°02′ W, 24–26.ii.2008, J.S. Noyes col. NHM(E) 2010-21AQ, DNA: CRM 3.103.

Paratypes: same data as holotype, DNA: CRM 3.46 (1♀, AICF), CRM 3.100 (1♂, MZUCR).

Species-group placement: mymaripenne-group.

Distribution: Costa Rica.

DNA data: 28S: two sequences.

Etymology: Named for the distinctive funicle.

Megaphragma giraulti Viggiani, Fusu, and Polaszek sp. nov. (Figure 4c–g, Figures 5a and 15c)

urn:lsid:zoobank.org:act:9F02CA78-49F3-49D3-A4B8-DC4E3A3033EF

Megaphragma sp.: Huber and Noyes, 2013. J. Hymenopt. Res. 32: 37, Figs 49–51.

Description. Female: Antenna (Figures 4d and 15c) five-segmented (excluding anellus), with pedicel slightly longer than funicle (12:8); clava two-segmented, C1 1.5× as C2, with ≥10 MT and 2 UST; one SB at the apex of C1 and C2, apex of C2 (Figure 4g) also with 2 elongate MPS, a long SB and UST.

Mid lobe of mesoscutum and scutellum without apparent sculpture; metanotum and propodeum medially short. Metasoma with a row of microspines on each segment. T1 without cells (Figure 4f). Ovipositor 1.1× as long as mesotibia. Mesotibia without spines basally. Mesofemur without prominent spine. Fore wing (Figure 5a) 9× as long as wide, maximum distal width 1.5× maximum basal width; disc with 10 setae irregularly arranged in 1–2 rows; fringe with longest seta 6× maximum discal width. Marginal vein with two long setae centrally, of equal length. Stigmal vein moderately enlarged, with three sensilla apically.

Body brown/yellow. Mesosoma largely pale, but mid lobe of mesoscutum brown anteriorly. Scape and pedicel pale, C1–C3 brown. Fore wing slightly infuscate basally.

Male: As female, but antenna (Figure 4c) with C1 approximately 2× C2. Metasoma (Figure 4e) with a row of microspines on each segment.

Material examined. Holotype ♀ (deposited in NHMUK). COSTA RICA: Puntarenas, Est. Biol. Monteverde, 10°19′ N 83°49′ W, 1540–1890 m, 26.ii.2007, J.S. Noyes BMNH(E) 2010-21, DNA: CRM2.4.

Paratypes: COSTA RICA: same data as holotype, DNA: CRM2.5 (1♂, AICF), CRM2.7, 2.8, 2.10, 2.11 (4♀, DACE, MZUCR, NHMUK); Limón, Hitoy-Cerere Reserve, 9°40′ N 83°02′ W, 100 m, 24–26.ii.2008, J.S. Noyes NHM(E) 2010-21AQ, DNA: CRM 3.23/B11, CRM 3.105, B9, E1 (2♂, 2♀, NHMUK); Cartago, 12.5 km S Turrialba, Rancho Naturalista, 1000 m, 9°50′ N 83°34′ W, 12–14.ii.2017, J.S. Noyes BMNH(E) 2017-39, DNA1683 (1♀, NHMUK); Heredia, La Selva Biol. Sta., 10°26′ N 84°01′ W, 75 m, 27–28.ii.2003, J. S. Noyes (1♂, DACE).
Insects 2022, 13, 561

Non-types: **ARGENTINA**: Salta Prov. Orán, road to San Andres along Rio Blanca, 399 m, 23.09° S 63.37° W, 23.iii.2003, J. Munro 003-03-23-02 (1♀, UCRC). **USA**: Northampton, 7 km S Jackson, 23.ix–14.xi.1987, MT, Bald Cypress Swamp, BRC Hym Team (1♀, UCRC).

**Species-group placement**: polychaetum-group. The male antenna is very distinctive in the group, and *M. giraulti* male antenna agrees very well with several other species that definitely belong to the *polychaetum*-group (but without sequence data to back up this assertion).

**Distribution**: Argentina, Costa Rica, USA.

**DNA data**: CO1: four sequences; 28S: eight sequences (all Costa Rica).

**Etymology**: The species is named for A.A. Girault for his pioneering studies on the Trichogrammatidae.

*Megaphragma hansonii* Polaszek, Fusu, and Viggiani sp. nov. (Figure 15d–f)

*urn:lsid:zoobank.org:act:980B8787-BB40-4589-91D4-FB4262F4BA0F*

**Description.** Female: Antenna (Figure 15d) five-segmented (excluding anellus); funicle absent; hence clava three-segmented, with C1 and C2 almost fused; C1 with 1–2 MT; C2 with some MT and 2 UST; C3 with 2–3 MT, 2 MPS, and prominent SB and SS.

Mid lobe of mesoscutum (Figure 15e) with longitudinal striate sculpture extending to scutellum; propodeum (Figure 15e) with central area extended posteriorly, crenulae present; T1 with elongate cells laterally, 2–3 × as long as wide; T2–T4 without setae laterally; T5 with long setae laterally. Ovipositor 2 × as long as mesotibia. Mesotibia with one large spine basally; metafemur with spine. Fore wing (Figure 15f) 7 × as long as maximum width, maximum distal width equal to maximum basal width; disc with a single short seta; longest fringe seta 5 × as long as maximum discal width. Marginal vein with one long seta centrally; a minute additional seta next to it. Stigmal vein moderately enlarged, with four sensilla apically.

Body largely brown, the following paler: most of mesosoma except anterior half of mid lobe of mesoscutum, anterior half of T1 and antenna. Fore wing slightly infuscate basally; stigmal and marginal vein pale brown.

**Male**: Largely as in female. C1 and C2 with scattered SS; C2 with 2–3 MT, 1 apically; C3 with long apical and ventral UST.

**Material examined.** Holotype ♀(deposited in NHMUK). **COSTA RICA**: Limón, Hitoy-Cerere Reserve, 9°40′ N 83°02′ W, 100 m, 24–26.i.2008, J.S. Noyes NHM(E) 2010-21AQ, DNA: CRM 3.101 (but no associated DNA sequence).

Paratypes: **COSTA RICA**: same data as holotype except DNA: CRM3.4, 3.17/B5, 3.40/D4, 3.97, 3.99, 3.104 (CRM3.40 lost after DNA extraction) (1♂, 4♂, AIICF, NHMUK); Puntarenas, Est. Biol. La Gamba, 8°42′ N 83°12′ W, 150 m, 13–14.ii.2008, J.S. Noyes BMNH(E) 2010-21AQ, DNA: CRM1.1, 1.2, 1.4, 1.7, 1.12-1.19 (12♂, DACE, MZUCR, NHMUK, UCRC).

**Species-group placement**: ghesquierei-group.

**Distribution**: Costa Rica.

**DNA data**: 28S: seven sequences.

**Etymology**: Named for our colleague and co-author on this paper, Professor Paul Hanson, University of Costa Rica, San José.

*Megaphragma kinuthiae* Polaszek, Fusu, and Viggiani sp. nov. (Figure 5b–d)

*urn:lsid:zoobank.org:act:E6685BED-8C4E-46AB-9E70-9C0F6F6FCF6A*

**Description.** Female: Antenna (Figure 5b) five-segmented (excluding anellus); pedicel as long as funicle; funicle 3 × as long as wide; C1 slightly longer or as long as C2 with two dorsal UST; three elongate MPS extending beyond clava tip.
Figure 15. Photographs of *Megaphragma* species: (a) *M. funiculatum*, female metasoma (Holotype); (b) *M. funiculatum*, female fore wing (Holotype); (c) *M. giraulti*, female antenna (Holotype); (d) *M. hansoni*, female antenna (Holotype); (e) *M. hansoni*, female dorsal meso- and metasoma (Holotype); (f) *M. hansoni*, female fore wing (Holotype). Scale bars 20 µm.
Head with toruli separated by about their own width. Mid lobe of mesoscutum smooth; propodeum with straight hind margin, without crenulae; T1 non-reticulate; T2–T4 with short setae laterally. Mesotibia with two large spines basally; metafemur with spine; metatibia with a row of fine, blunt setae extending almost their entire inner length, increasing abruptly in length distally. Fore wing (Figure 5d) about 9× as long as maximum width, maximum distal width 1.3× maximum basal width; discal setae arranged in two rows, each with 4–5 setae, longest fringe seta 10× as long as maximum discal width. Marginal vein with two long setae centrally. Stigmal vein with two sensilla apically. Ovipositor 1.1× as long as mesotibia.

Body entirely yellow, anterior mesosoma brown, posterior metasoma slightly darker. Wings hyaline.

**Male**: Unknown.

**Material examined.** Holotype ♀ (deposited in NHMUK). **KENYA**: Meru, vi. 1965, ID. No. 2851, CIE 233, BM 196. T. F. Crowe, ex tea leaves.

Paratypes: same data as holotype (6♀, NHMUK). All specimens are on the same slide; the holotype is circled in red.

**Species-group placement**: polychaetum-group. The species appears closest to *M. giraulti* based on morphology.

**Distribution**: Kenya.

**Host**: Not identified, but possibly *Scirtothrips dorsalis* (Hood), a species common on tea in Kenya.

**DNA data**: no DNA sequences.

**Etymology**: Named for our colleague and friend Dr Wanja Kinuthia, National Museums of Kenya, Nairobi.

**Megaphragma liui Polaszek and Fusu sp. nov.** (Figure 16a–d)

urn:lsid:zoobank.org:act:35AD8001-C03B-4711-ADF5-22AFB681F184

**Description. Female**: Antenna (Figure 16a) five-segmented (excluding anellus), C1 and C2 strongly overlapping; C3 elongate, more than half the length of C1 and C2; 1 min UST on C1, two long UST on C2; three elongate MPS extending beyond clava tip.

Head with toruli very close together, separated by about one-third their own width. Mid lobe of mesoscutum (Figure 16b) with fine longitudinal striations, but also with distinct large reticulate cells; propodeum medially with strongly produced hind margin, with two crenulae (Figure 16b). T1 smooth centrally, but with 8–10 elongate cells laterally (Figure 16b); T2–T4 with short setae laterally, lateral cells present. Mesotibia without large spines basally, but a robust spine present at the apex of mesofemur; metafemur with spine; metatibia with a group of fine, sharp setae on inner surface apically. Metacoxa and metafemur (Figure 16c) with distinct longitudinal sculpture ventrally, contrasting with transverse sculpture dorsally. Fore wing (Figure 16d) 7× as long as maximum width, maximum distal width 1× maximum basal width; disc distally pointed, without setae (but one wing with a possible indication of a minute seta); longest fringe seta 4× as long as maximum discal width. Marginal vein with two setae centrally, the proximal one very robust, about 1.5× as long as distal. Stigmal vein with one elongate sensillum apically. Ovipositor 1.9× as long as mesotibia.

Body entirely brown, mesosoma pale posteriorly, T1 with pale areas laterally. C1 very dark, pedicel paler than the remainder of the antenna. Fore wing strongly infuscate basally. Legs dark, tarsi pale.

**Male**: Unknown.

**Material examined.** Holotype ♀ (deposited in UCRC). **BRUNEI**: Temburong Dist., Bukit Patoi trail, 41–290 m, 4°45′21″ N 115°10′30″ E, 4 July 2010, swp dipterocarp forest, J. Mottern M10-065, DNA1656.
Figure 16. Photographs of Megaphragma species: (a) M. liui, female antenna; (b) M. liui, female dorsal meso- and metasoma (Holotype); (c) M. liui, female metacoxa and metafemur (Holotype); (d) M. liui, female fore wing (Holotype); (e) M. longiciliatum, female antenna (Holotype). Scale bars 20 µm except 50 µm for d.
Species-group placement: *ghesquierei*-group. In the concatenated and partitioned analysis, this species is not included in the group (Figure 2b), though in an unpartitioned analysis with a simple substitution model it is one of the most basal species of the *ghesquierei*-group (Figure 2a). It is also retrieved as part of the group in the tree based on the 28S sequences alone, where it is sister to *M. rivelloi* but on a very long branch (Supplementary Figure S3). Hence, morphology, and partly molecular analyses, indicate that our inclusion of the species is correct.

**Distribution:** Brunei.

**DNA data:** CO1: one sequence; 28S: one sequence.

**Etymology:** Named for our colleague and friend Prof. Shu-sheng Liu, Zhejiang University, Hangzhou, China.

**Megaphragma momookherjeeae** Polaszek and Fusu sp. nov. (Figure 17a–c)

urn:lsid:zoobank.org:act:CC6535BA-271C-44CB-9697-CC048ED070E0

**Description. Female:** Antenna (Figure 17a) five-segmented (excluding anellus); transverse funicle present, clava two-segmented; **C1** longer than **C2**; **C1** with ≥ 5 MT, 2 UST, and with fine, longitudinal striation; **C2** with basal SS, 2 UST, and ≥ 4 MPS. Mid lobe of mesoscutum smooth; propodeum without distinct central area. **T1–T4** largely smooth, **T2–T4** with long setae laterally. Ovipositor exserted, exceptionally long for the genus, more than 3× as long as mesotibia (Figure 17b). Mesotibia with a very robust spine basally, 0.4× tibial length; metafemur without spine; metatibia with a row of about 17 spines along almost the entire inner length, and 4 robust spines toward the apex of the outer surface. Fore wing (Figure 17c) 9× as long as maximum width; maximum distal width 1× maximum basal width; disc with a single, minute seta; longest fringe seta 6.5× as long as maximum discal width. Marginal vein apparently with three long setae centrally, of equal length. Stigmal vein with three sensilla apically.

Body largely dark brown; scutellum, propodeum, and lateral mesosoma paler (Figure 17b); antenna pale brown, **C2** darker. Fore wing basally infuscate.

**Male:** Unknown.

**Material examined.** Holotype ♂ (deposited in NHMUK). COSTA RICA: Cartago, 12.5 km S. Turrialba, Rancho Naturalista, 1000 m, 9°50' N 83°34' W, 12–14.ii.2017, J.S. Noyes BMNH(E) 2017-39, DNA1680.

Species-group placement: *M. antecessor*-group. Resembling also the *ghesquierei*-group in some features (e.g., fore wing with one seta), but clearly not clustering with that group in any molecular analyses. It is recovered as sister to *M. antecessor*, and the two clustered together as basal to all species-groups except the *ghesquierei*-group (partitioned analysis), or as the most basal species group of *Megaphragma* (unpartitioned analysis).

**Distribution:** Costa Rica.

**DNA data:** CO1: one sequence.

**Etymology:** Named for Mo Mookherjee, a friend of the first author (AP).

**Megaphragma nowickii** Polaszek, Fusu, and Viggiani sp. nov. (Figures 7a–f and 17e–g)

urn:lsid:zoobank.org:act:126687C2-A7AE-4FC2-810E-11DE6E6D6784

**Description. Female:** Antenna (Figures 7c and 17g) five-segmented (excluding anellus); pedicel twice as long as funicle; funicle twice as long as wide; **C1** slightly shorter or as long as **C2**; **C1** with ≥7 MT; 2 UST; 3 elongate MPS extending beyond clava apex. Mid lobe of mesoscutum smooth, anteriorly with subpolygonal sculpture (cf Figure 7b). Metanotum and propodeum narrow centrally, the latter without an extension or crenulae. **T1** sculpture (Figures 7a and 17f) with cells converging centrally, lateral cells 3× as long as wide, each with 3–5 inward-pointing denticles; **T2–T4** without long setae laterally, all with coarse reticulate sculpture becoming lateral distally. Ovipositor 1.7× as long as mesotibia. Mesotibia with two large spines basally; metafemur with spine; metatibiae with a row of fine, blunt setae extending almost their entire inner length, increasing abruptly in length distally. Fore wing (Figure 7e) 9.5× as long as wide, maximum distal width 1.1× maximum
basal width; disc with a single row of six setae; longest fringe seta 4.5× maximum discal width. Marginal vein with two long setae centrally.

Body entirely brown, metasoma slightly darker posteriorly. Pleural parts of mesosoma and hind legs except for tarsi lighter. Wings hyaline.

**Male**: Largely as in female. Antenna with C1 slightly longer than C2; T1 with an incomplete pattern of cells. Aedeagus as in Figure 7f.

**Material examined**. Holotype ♀(deposited in NHMUK). **D. R. CONGO**: Province Orientale, Yangambi Biosphere Reserve, 15.v.2012, N 0°48.837’ E 24°30.287’, screen sweep, primary forest, A. Polaszek col, BMNH(E) 2012-88, DNA: COM1.16.

**Paratypes**: **D. R. CONGO**: same data as holotype except DNA: COM1.1–1.15, 1.17–1.23, 1.26, 1.27 (2♀, 2♀', AICF, DACE, IITA, NHMUK). **UGANDA**: Mabira Forest, N0°23′22″ E33°00′22″, 1250 m, 1.iii.2015, A. Polaszek, screen sweep, DNA1132/F11 (1♂, NHMUK); Mabira Forest, N0°23′22″ E33°00′22″, 1250 m, 1.iii.2015 A. Polaszek, screen sweep, DNA1116–1118, 1120–1124 (1♂, 7♂', NHMUK).

**Non-types**: **BENIN**: Dept. Zou, Zogbodomey, Massi, 18.xii.1989, ex egg Megalurothrips sjostedti on Pueraria, M. Tamo col. 275 (1♂, 1♀, NHMUK, IITA).

**Species-group placement**: mymaripenne-group.

**Distribution**: Benin, D. R. Congo, Uganda.

**Host**: Megalurothrips sjostedti (Trybom).

**DNA data**: CO1: 25 sequences from D. R. Congo; 28S: 30 sequences from 2 countries: D. R. Congo (21), Uganda (9).

**Etymology**: Named for S. Nowicki for his outstanding contribution to the knowledge of the Trichogrammatidae.

*Megaphragma noyesi* Polaszek and Fusu sp. nov. (Figure 18a)

urn:lsid:zoobank.org:act:63048F49-FCC2-49FF-9E2C-C0552BC1FBF4

**Description. Female**: Antenna (Figure 18a) five-segmented (excluding anellus); pedicel almost twice as long as funicle; funicle slightly longer than wide; C1 shorter than C2; C1 with two dorsal UST; C2 with three elongate MPS extending beyond clava apex.

Mid lobe of mesoscutum and scutellum smooth. Metanotum and propodeum narrow centrally, the latter without an extension or crenulae.

Mesotibia without large spines basally; metafemur without spine; metatibia with a row of robust spines extending along the inner surface of distal half.

Fore wing 9× as long as wide, maximum distal width 1.3× maximum basal width; disc with a single row of six setae, and longest fringe seta 5× maximum discal width. Marginal vein with two long setae centrally, subequal in length (cf Figure 18g). T1 sculpture with cells converging centrally, six lateral cells present, 2–3× as long as wide, each with 1–3 inward-pointing denticles; T2–T4 with lateral cells indicated, with lateral setae not detected (cf Figure 18f). Ovispositor as long as mesotibia. Body largely brown, mesosoma largely pale. T1 very dark brown in contrast to rest of body. Legs pale. Wings hyaline.

**Male**: Largely as in female. Antenna with C1 longer than C2; T1 with an incomplete pattern of cells. Genitalia tubular as in other species, 3× as long as wide.

**Material examined. Holotype ♀(deposited in NHMUK). UK**: England, Surrey, Coulsdon Common, Happy Valley, 51°17′ N 0°07′ W, 168 m, viii.2013, J.S. Noyes BMNH(E) 2013-, DNA: UKM14.

**Paratypes**: **UK**: same data as holotype except DNA: UKM8–13 (UKM9 has DNA sequences but was lost during extraction) (4♀, 1♂', AICF, DACE, NHMUK); East Sussex, Brede High Wood, TQ9432018/19, 30.viii.2019–20.ix.2019, D. Birns col., DNA1612–1619 (1612, 1614 and 1618 have DNA sequences but were lost during extraction) (10♀, 3♂', NHMUK, UCRC).

**HUNGARY**: Örség Nemzeti Park, Barkás Lake, 46°52′ N 16°26′ E, 268 m, 28.vi.2010, J.S. Noyes screen sweeping, BMNH(Ent) 2010-63, DNA: HUM2 (1♀, NHMUK) (HUM3 has DNA sequences but was lost during extraction), HUM5 (1♀, AICF); 4–5 km SW Kőszeg, Meszes Völgy, 47°22′ N 16°31′ E, 431 m, 26.vi.2010, screen sweeping, J.S. Noyes BMNH(Ent) 2010-63, DNA: HUM6 (1♂', AICF); Örség National Park, Lugosi Valley, 46°54′ N 16°27′ E, 231 m, 28.vi.2010, J.S. Noyes, DNA: HUM 8–14, BMNH(Ent) 2010-63 (3♀4♂', NHMUK).
Figure 17. Photographs of *Megaphragma* species: (a) *M. momookherjeae*, female antenna (Holotype); (b) *M. momookherjeae*, female lateral meso-and metasoma (Holotype); (c) *M. momookherjeae*, female fore wing (Holotype); (d) *M. mymaripenne*, female antenna (Holotype); (e) *M. nowickii*, female dorsal meso- and metasoma (Holotype); (f) *M. nowickii*, female dorsal base of metasoma (Holotype); (g) *M. nowickii*, female antenna (Holotype). Scale bars 20 \( \mu m \) except 100 \( \mu m \) for c.
Non-type: CZECH REPUBLIC: Moravia, Vranov, River Dyje, ss riparian forest, 13.viii.1991, L. Masner (1♀, UCRC).

Species-group placement: mymaripenne-group.

Distribution: UK (England); Czech Republic, Hungary.

DNA data: CO1: 21 sequences from 2 countries; 28S: 23 sequences from 2 countries: Hungary, UK.

Etymology: Named for Dr John Noyes of the Natural History Museum, London, for his outstanding contribution to our knowledge of Chalcidoidea. As a chalcid collector, John is unmatched so far, and a major proportion of the material in this study was collected by him.

Megaphragma pintoi Viggiani sp. nov. (Figure 18b–d)

urn:lsid:zoobank.org:act:9C3F4C6B-6290-4DB5-B4E2-6080C11F6C91

Description. Female: Antenna (Figure 18b) five-segmented (excluding anellus); pedicel slightly longer than funicle; funicle 3× as long as wide; C1 slightly longer or as long as C2; C1 with two UST; three MPS extending beyond C2 apex.

Mid lobe of mesoscutum (Figure 18c) smooth, with 5–6 deep striae anteriorly; propodeum with straight hind margin, without crenulae. T1 non-reticulate; T2–T4 with short setae laterally. Ovipositor 1.1× as long as the mesotibia. Metameral without spine but a prominent seta present. Fore wing (Figure 18d) 10× as long as maximum width, and maximum distal width 1.4× maximum basal width; discal setae arranged in 2–3 rows, each with 3–5 setae, longest fringe seta 5.5× as long as maximum discal width. Marginal vein with two long setae centrally. Stigmal vein with two sensilla apically.

Body entirely pale brown (eyes deep purple); legs and antenna pale. Wings hyaline.

Male: Unknown.

Material examined. Holotype ♀ (deposited in PFRNZ). NEW ZEALAND: Auckland, Mt Albert, Science Center, 17.v.1997, ex Heliothrips haemorrhoidalis ex acmena leaves, P. Stevens.

Non-type: COLOMBIA: Supata, 5°04′07″ N 74°16′48″ W, 1800 m, 31.12.2018, sweep, A.A. Polilov col. (1♀, AICF).

Species-group placement: polychaetum-group.

Distribution: Colombia, New Zealand.

DNA data: no DNA sequences.

Etymology: Named for Emeritus Professor John Pinto, formerly of University of California, Riverside, in recognition of his monumental contribution to our understanding of Trichogrammatidae.

Comments: Known so far from only two specimens to date; this species has an apparently extraordinary distribution, being known from Colombia and New Zealand. It seems very likely that it will turn up elsewhere and is probably another cosmopolitan Megaphragma species.

Megaphragma polilovi Polaszek, Fusu, and Viggiani sp. nov. (Figure 18e–g, Figures 19d and 20a,b)

urn:lsid:zoobank.org:act:7A812908-FC9A-4F84-A1C-C922132

Megaphragma mymaripenne: Viggiani and Bernardo, 1998. Boll. Zool. agr. Bach. Ser. II 29: 51–55; Bernardo and Viggiani, 2003. Boll. Lab. Entomol. agr. Filippo Silvestri 58 [2002]: 77–85; Polilov, 2012. Arthropod Struct. Dev. 41(1): 29–34; Makarova et al., 2015. Arthropod Struct. Dev. 44(1): 21–32; Polilov, 2016. At the Size Limit—Effects of Miniaturization in Insects; Polilov, 2017. PLoS ONE 12(5): e0175566; Diakova et al., 2018. PeerJ 6: e6005 (misidentifications).

Description. Female: Antenna (Figures 18e and 20a) five-segmented (excluding anellus); pedicel almost twice as long as funicle; funicle slightly longer than wide, with 3 MT and 1 ASC; C1 shorter than C2; C1 with 17 MT, SS, and 2 UST; C2 with SB, 2 MT, SS, and 4 elongate MPS extending beyond clava apex.
Mid lobe of mesoscutum and scutellum smooth (Figures 18f and 19d). Propodeum with a distinct central area with lateral boundaries in line with those of mesoscutum and scutellum (Figure 19d); two lateral lobes present behind propodeum central area (Figure 19d); propodeum without crenulae. T1 sculpture (Figures 18f and 20b) with cells converging centrally, about six lateral cells, 2× as long as wide, mesal cells each with 2–3 inward-pointing denticles. T2–T4 with 2–3 lateral cells, with short setae laterally. Ovipositor 1.3× as long as mesotibia. Mesotibia with two large spines basally; metafemur without spine; metatibia with a row of fine, blunt setae extending almost its entire inner length, increasing abruptly in length distally. Fore wing (Figure 18g) 9.5× as long as wide, maximum distal width 1.4× maximum basal width; disc with a single row of six setae, longest seta of fringe 5.8× maximum disc width. Marginal vein with two long setae centrally.

Antenna (Figure 18e) with radicle brown, very dark compared to the remainder of the antenna; remainder of body largely brown, mesosoma largely pale, mid lobe of mesoscutum brown anteriorly, an indistinct brown spot on the scutellum. Legs pale. Wings hyaline.

Male: Largely as in female. Antenna with C1 slightly longer than C2; T1 with an incomplete pattern of cells. Genitalia tubular as in other species, 3× as long as wide.

Material examined. Holotype ♀ (deposited in DACE). ITALY: Vietri sul Mare, Benincasa, 40°40′ N 14°44′ E, 17.vii.2013, G. Viggiani ex Heliothrips haemorrhoidalis on Viburnum tinus, DNA: ITM9.

Paratypes: ITALY: same data as holotype, DNA: ITM8, 11, 12, 14 (♀, AICF, DACE, NHMUK).

Species group placement: mymaripenne-group.

Distribution: Italy.

Host: Heliothrips haemorrhoidalis. Males are very rare, and reproduction is normally thelytokous [14] (as M. mymaripenne).

DNA data: CO1: five sequences; 28S: five sequences; all from Italy.

Etymology: Named for our colleague Alexey Polilov, co-author of this paper, for his outstanding contribution to our knowledge of the Trichogrammatidae and miniaturization in insects.

Comments: Found in Italy at the same locality and on the same host as M. viggianii.

Megaphragma rivelloi Viggiani sp. nov. (Figures 9a–d and 21a)

urn:lsid:zoobank.org:act:4436D2E2-590F-4329-A65B-AB562F0E04ED

Megaphragma sp. Viggiani, 2002. Boll. Zool. Agr. Bacch. Ser. II 34: 449–450.

Description. Female: Antenna (Figures 9a and 21a) five-segmented (excluding anellus), pedicel approximately two-thirds the length of C1 and C2; C3 one-quarter shorter than C2; C2 with a single UST; C3 with SB, two MPS, MT, and apical SB.

Mid lobe of mesoscutum and scutellum with longitudinally striate sculpture; propodeum (Figure 9b) with a large subtriangular and crenulated central area. Metasomal tergites without reticulation but with transverse striations, laterally with a row of 2–7 microspines. Ovipositor approximately 1.3× as long as mesotibia. Fore wing (Figure 9c) 6–7× as long as wide; disc without setae; longest fringe seta 4–4.5× as long as the maximum discal width.

Body yellow with brown mostly on mesosoma; fore wing infuscate behind the venation. Male: Largely as in female except for genitalia.

Material examined. Holotype ♀ (deposited in DACE): ITALY: Basilicata, Rivello (PZ), vii.2002, yellow sticky traps in a vineyard.
Figure 18. Photographs of Megaphragma species: (a) M. noyesi, female antenna (Holotype); (b) M. pintoi, female antenna (Holotype); (c) M. pintoi, female mesoscutum (Holotype); (d) M. pintoi, female fore wing (Holotype); (e) M. polilovi, female antenna (Holotype); (f) M. polilovi, female dorsal mesosoma (part) and metasoma (Holotype); (g) M. polilovi, female fore wing (Holotype). Scale bars 20 μm except 50 μm for a, d, and g.
Figure 19. SEM micrographs of Megaphragma species (non-types): (a) *M. caribea*, male habitus; (b) *M. caribea*, male head and antennae; (c) *M. caribea*, male mesoscutum; (d) *M. polilovi*, female dorsal habitus. Scale bars 50 µm for a, 20 µm for b and c, and 100 µm for d.
Figure 20. SEM micrographs of *Megaphragma* species (non-types): (a) *M. polilovi*, female antenna; (b) *M. polilovi*, female metasoma; (c) *M. viggianii*, female habitus; (d) *M. viggianii*, female antenna. Scale bars 20 µm for a, b and d, and 100 µm for c.
Insects 2022, 13, 561

Paratypes: ITALY: same data as holotype (1♀, DACE, NHMUK). INDIA: UP, New Delhi, IARI; 220 m 28°37’51” N, 77°09’50” E, xi.5.2003, pan trap, J. Heraty col. H03-106 (1♂, UCRC). INDONESIA: W Java, Gunung Halimun NP, Tea-Forest Junction, 1066 m, 6°41’07” S 106°31’16” E, screen-sweep, 17.ix.2015; A. Polaszek, DNA1148 (1♀, NHMUK). JAPAN: Tokyo area, ?1984, Takagi col., ex Scirtothrips dorsalis Hood. UK: Surrey, Coulsdon Common, 25.viii.2002, J.S. Noyes, screen sweep (1♂, NHMUK). VIETNAM: Cat Tien NP, sweeping, N11°24’45’’ E107°25’23’’, 25.xi.2016, leg. A.A. Polilov (3♀, 2♂, AICF, UCRC).

Non-type: CHINA: 1♂ misidentified as M. deflectum, Wuyishan, Fujian, 19.x.1987 Wang Jiashe col. (FAU).

Species group placement: ghesquierei-group.

Distribution: China, India, Indonesia, Italy, Japan, UK, Vietnam.

Host: Scirtothrips dorsalis Hood.

DNA data: 28S: 1 sequence (Vietnam).

Etymology: Named for the ancient village of Rivello in Italy, where this extremely widespread species was first discovered. As noted above under M. deflectum, one paratype (male “allotype”) of that species is in fact M. rivelloi.

Megaphragma tamoi Polaszek, Fusu, and Viggiani sp. nov. (Figure 21d,e)

urn:lsid:zoobank.org:act:8F82A348-AFC5-4618-A0C8-416867AC501C

Description. Female: Antenna (Figure 21d) five-segmented (excluding anellus); funicle absent; hence, clava three-segmented, with C1 and C2 almost fused; C1 without UST; C2 with one elongate UST, reaching more than half the length of C3; C3 with MPS, SB, and SS.

Mid lobe of mesoscutum with longitudinal striate sculpture extending to scutellum (cf Figure 14b); propodeum with central area extended posteriorly, crenulae present (cf Figure 15e). T2–T4 without setae laterally. Ovipositor 1.7 × as long as mesotibia. Mesotibia with one large spine basally; metafemur with spine (cf Figure 16c, upper). Fore wing 6 × as long as the maximum width, maximum distal width 1.2 × maximum basal width; disc with a single long seta (Figure 21e), longest fringe seta 3 × maximum discal width. Marginal vein with two setae centrally, equal in length, extending to the end of the marginal vein. Stigmal vein moderately enlarged, with two sensilla apically.

Largely brown, the following paler: legs except coxae and metafemur. Pedicel pale; scape, C1–C3 darker. Fore wing strongly infuscate basally; stigmal and marginal vein brown; marginal vein very dark centrally.

Male: Largely as in female. C1 and C2 with scattered SS; C2 with 2–3 MT apically; C3 with long apical and ventral UST. C3 is darker than preceding segments.

Material examined. Holotype ♀ (deposited NHMUK). BENIN: Agbotagon, 6°49’ N 2°12’ E, 22.iv.1990, M. Tamo 351.

Paratypes: Benin: same data as holotype (8♀, DACE, IITA); Mono Province, 7.x.1988, M. Tamo, D-Vac on cowpea Vigna unguiculata (1♂, NHMUK); Mono Province, 25.ii.1988, M. Tamo, emergence cage Megalurothrips sjostedti on Vigna unguiculata (1♀, IITA); Dept Zou, Zogbodomey, 22.i.1990, ex egg Megalurothrips sjostedti, M. Tamo col. 275, 342 (2♂, IITA); Cotonou, IITA Station, 16.i.1990, ex egg Megalurothrips sjostedti on Pueraria, M. Tamo col. 336 (1♀, NHMUK).

Species group placement: ghesquierei-group.

Distribution: Benin.

Host: Megalurothrips sjostedti.

DNA data: no DNA sequences.

Etymology: Named for our colleague and friend Manu Tamo (IITA, Benin), collector of many Megaphragma specimens.
Figure 21. Photographs of *Megaphragma* species: (a) *M. rivelloi*, female antenna (Holotype); (b) *M. striatum*, female antenna (MXM1 above and Paratype below); (c) *M. striatum*, female metasoma (MXM1); (d) *M. tamoi*, female antenna (Holotype); (e) *M. tamoi*, female fore wing (Holotype); (f) *M. tridens*, female antenna (Holotype); (g) *M. tridens*, male antenna (Paratype); (h) *M. tridens*, female metasoma (Holotype); (i) *M. uniclavum*, female antenna (Holotype); (j) *M. uniclavum*, female metatibia (Holotype); (k) *M. vanlentereni*, female antenna (Holotype); (l) *M. vanlentereni*, female mesosoma (Holotype); (m) *M. vanlentereni*, female fore wing (Holotype). Scale bars 20 μm.
Insects 2022, 13, 561

**Description. Female:** Antenna (Figure 21f) five-segmented (excluding anellus); funicle absent; hence, clava three-segmented, with C1 and C2 almost fused; C1 apparently without UST; C2 with 1 prominent UST, abundant MT, and 1 apical MPS; C3 with MT, 2-3 UST, SB, and SS.

Mid lobe of mesoscutum with longitudinal striate sculpture (cf Figure 14b); propodeum with central area extended posteriorly, crenulae absent (cf Figure 21l). T1 with elongate cells laterally, 2–3× as long as wide (cf Figure 12b); T2–T4 with a short, robust seta near lateral margin; T5 centrally with subparallel striations and with long setae laterally (Figure 21h). Ovipositor 1.7× as long as the mesotibia. Mesotibia with one large spine basally; metatibia with spine. Fore wing 8.5× as long as the maximum width, maximum distal width equal to maximum basal width; disc with a single long seta (cf Figure 12c), longest fringe seta 3.5× as long as maximum discal width. Marginal vein with one long seta centrally, extending to the end of the marginal vein. Stigmal vein moderately enlarged, with four sensilla apically.

Body largely brown, the following paler: legs except coxae and metafemur. Pedicel pale; scape, C1–C3 darker. Fore wing slightly infuscate basally; stigmal and marginal vein brown.

**Material examined.** Holotype ♀ (deposited in NHMUK).

COSTA RICA: Puntarenas, La Gamba Biol. Sta., 150 m, 8°42′N 83°12′W, 13–14.ii.2008, J.S. Noyes BMNH(E) 2010-21AQ, DNA: CRM1.10.

Paratypes: COSTA RICA: same data as holotype, DNA: CRM1.5, 1.8 (1♀, 1♂, AICF, MZUCR); Limón, Hitoy-Cerere Reserve, 9°40′N 83°02′W, 100 m, 24–26.ii.2008, J.S. Noyes NHM(E) 2010-21AQ, DNA: CRM 3.41, 3.102 (1♀1♂, AICF, NHMUK).

**Species-group placement:** ghesquierei-group.

**Distribution:** Costa Rica.

**DNA data:** no DNA sequences.

**Etymology:** From the Latin word *tridens*, in reference to the three apical sensilla on C3, resembling a longer central and two shorter lateral teeth of a trident (from Latin *tri*=three and *dens*=tooth). Noun in apposition.

---

**Description. Female:** Antenna (Figure 21i) four-segmented (excluding anellus); transverse funicle present; clava one-segmented (unique so far for the genus, though antecessor approaches this condition); 2 UST; 3–4 long MPS extending beyond half the clava.

Head with few features discernible due to mounting position, and extensively obscured by eye pigment. Mid lobe of mesoscutum with fine longitudinal striation (cf Figure 14b); vertical/ventral anterior mid lobe of mesoscutum with coarse, reticulate sculpture (cf Figure 3g); propodeum elongate centrally, longitudinally striate with three large crenulae. T2–T4 with very long setae laterally, each longer than its tergum; T3 and T4 with large irregular cells laterally. Mesotibia with two large spines basally; metatibia with spine; metatibia with a row of fine, elongate setae extending almost their entire inner length (Figure 21j). Fore wing 5× as long as maximum width; longest fringe seta 6.7× as long as maximum discal width, maximum distal width versus maximum basal width is unclear; disc (cf Figure 11b) with single short seta. Other details of disc and venation are unclear. Stigmal vein with a row of three sensilla apically. Ovipositor 2× as long as the mesotibia.

Body uniformly pale. Distal metastoma darker. Wings hyaline.

**Material examined.** Holotype ♀ (deposited in NHMUK). COSTA RICA: Heredia, La Selva BS., 10°26′N 84°01′W, 75 m, 28–29.ii.2008, J.S. Noyes BMNH(E) 2010-21 AQ.
Species-group placement: antecessor-group. *Megaphragma uniclavum* is so far unique for the genus having a single claval segment. Despite the very unusual fore-wing structure, it is clearly affiliated with *M. antecessor* (similar mesoscutal sculpture and row of setae on metatibia).

**Distribution:** Costa Rica.

**DNA data:** no DNA sequences.

**Etymology:** This species is so far the only *Megaphragma* known with a single claval segment; hence, the name *uniclavum*. Noun in apposition.

*Megaphragma vanlentereni* Polaszek and Fusu sp. nov. (Figure 21k–m)  
urn:lsid:zoobank.org:act:E76B71C9-D7A7-4005-A7E1-66EC26A146BB

**Description. Female:** Antenna (Figure 21k) five-segmented (excluding anellus); funicle absent; hence, clava three-segmented, with C1 and C2 almost fused; C1 with 2 UST; C3 with three MPS extending beyond apex of clava.

Mid lobe of mesoscutum (Figure 21l) with irregular longitudinal striate sculpture; propodeum (Figure 21l) elongate, curved centrally and posteriorly; crenulae present. T1 without cells; T2–T4 without setae laterally. Ovipositor 1.7× as long as mesotibia. Mesotibia with two large spines basally. Fore wing (Figure 21m) 6.5× as long as maximum width, maximum distal width 1.1× maximum basal width; disc with one short seta, longest fringe seta 4× as long as maximum discal width. Marginal vein with two long setae centrally, of equal length. Stigmal vein moderately enlarged, with three sensilla apically.

Body largely pale with dorsal mesosoma, including propodeum, pale brown. Scape and pedicel pale, C1 and C2 brown, C3 very dark brown in contrast. Fore wing infuscate basally; stigmal and marginal vein distally brown.

**Male:** Unknown.

**Material examined:** Holotype ♀ (deposited in NHMUK). MALAYSIA, Sabah, Maliau Basin Studies Centre, Knowledge Trail, 04°44’ N 116°58’ E, 22.ix.2012, A. Polaszek, screen-sweep, NHM(E) 2010-21, DNA: SAM3.

**Species group placement:** ghèsquierei-group.

**Distribution:** Malaysia (Borneo, Sabah).

**DNA data:** CO1: one sequence; 28S: one sequence (both Malaysia, Sabah).

**Etymology:** Named for our colleague and friend Joop van Lenteren, a pioneer of biocontrol, especially in greenhouses.

*Megaphragma viggianii* Fusu, Polaszek, and Polilov sp. nov. (Figure 20c,d and Figure 22a–d)  
urn:lsid:zoobank.org:act:05F51567-04A0-45D8-91F7-787A041BEB08

Megaphragma amalphitanum: Nedoluzhko et al. 2016. Mitochondrial DNA Part A 27(6): 4526–4527; Polilov, 2016. At the Size Limit—Effects of Miniaturization in Insects; Nedoluzhko et al., 2017. Genom. Data 11: 87–88; Polilov, 2017. *PLoS ONE* 12(5): e0175566; Prokhortchouk et al., 2017. *Mosc. Univ. Biol. Sci. Bull.* 72(1): 30–32; Diakova et al., 2018. *PeerJ* 6: e6005; Sharko et al., 2019. *PLoS ONE* 14(12): e0226485; Polilov et al., 2021. *Sci. Rep.* 11(1): 4717; Boudinot et al., 2020. *J. Zool.* 313(2): 99–113; Diakova and Polilov, 2021. *J. Hymenopt. Res.* 84: 69–73 (misidentifications).

**Description. Female:** Antenna (Figures 20d and 22a) five-segmented (excluding anellus); pedicel 2× as long as funicle; funicle slightly longer than wide; C2 longer than C1; C1 with 1 ASC, 2 MT; C2 with 13 MT, 2 UST; C3 with 2 MPS, 1 SS, and 3 UST extending beyond clava tip.

Mid lobe of mesoscutum (Figure 22b) posteriorly smooth, anteriorly with large, coarse reticulation; propodeum with broad, truncate hind margin; with two widely separated lobes distally and laterally, without crenulae. T1 with a central “V” composed of minute denticles, a row of coarser denticles laterally (Figure 20c), and one elongate cell laterally,
about 2× as long as wide. Metasoma dorsally with rows of denticles laterally on T2 and T3; T2–T4 with moderately long setae laterally. Ovipositor as long as the mesotibia.

Mesotibia without spines basally, a single seta present; metatibia without spine but with three robust setae; metatibia with a row of five or six fine setae extending along half its inner length. Fore wing (Figure 22c) 6× as long as maximum width; maximum distal width 1.5× maximum basal width and more than 2× width measured at the apex of the marginal vein; longest fringe seta 4× as long as the maximum discal width; disc with setae in one or two rows of 4–6 setae, and setae on venal surface long, the penultimate one reaching to the base of the distal (Figure 22d). Marginal vein with two setae centrally, the proximal approximately 2× the length of the distal. Stigmal vein has four sensilla apically.

Head and metasoma dark brown; central/posterior mesoscutal mid lobe and lateral scutellum paler. Remainder of body, including legs, pale. Flagellum darker than remainder; wings hyaline.

Male: Antenna with pedicel almost as long as scape; funicle with two small setae; clava two-segmented; C1 >2× C2; C1 with three setae; C2 with three flagelliform setae; two multiporous plate sensilla and a short terminal process present. Metasoma dorsally with rows of denticles laterally on T1–T3. One individual with funicle apparently fused with C1.

Material examined: Holotype ♀ (deposited in DACE). ITALY: Naples, Massa Lubrense, S. Agata sui Due Golfi, 24.x.2012, 40°36′ N 14°20′ E, 114 m, ex Heliothrips haemorrhoidalis in leaves of Viburnum tinus (G. Viggiani), DNA: ITM1.

Paratypes: ITALY: same data as holotype except DNA: ITM2 (1♂), ITM3 (1♂), ITM4 (1♂), ITM5 (1♂), ITM6 (1♀), ITM7 (1♀) (AICF, NHMUK); same data but without DNA extraction codes (2♀NHMUK); Vietri sul mare, Benincasa, 40°40′ N 44°20′ E, 17.vii.2013, ex Heliothrips haemorrhoidalis on Viburnum tinus (G. Viggiani), DNA: ITM13 (1♀, NHMUK); Liguria, Santa Margherita, iv.2015, A. Polilov, ex Heliothrips haemorrhoidalis on Viburnum tinus, DNA1095, DNA1096 (2♀, NHMUK). GREECE: Koutsoupia, 39.81N 22.80E, 22.viii.2016, Leg. A.A. Polilov, ex Heliothrips haemorrhoidalis on Arbutus sp. (2♀, 1♂, AICF).

Species-group placement: longiciliatum-group.

Distribution: Greece, Italy.

Host: Heliothrips haemorrhoidalis.

DNA data: CO1: eight sequences; 28S: eight sequences.

Etymology: Named for Professor Gennaro Viggiani, specialist of microhymenoptera and biocontrol, and instigator and co-author of this paper.

Comments: Found in Italy at the same locality and on the same host as M. polilovi. According to the CO1 sequence of the mitochondrial genome deposited on GenBank by Nedoluzhko et al. [23], their species is not M. amalphitanum (≡M. longiciliatum) but M. viggianii. Our molecular analysis retrieves the two as sister species. Both have the mid lobe of the mesoscutum reticulate anteriorly, and long lateral setae on T2–T4, though these are longer in the former. In M. longiciliatum T2–T4 have very long setae, at least as long as the tergite (Figure 5h), whereas in M. viggianii T2–T4 have shorter setae, much shorter than the tergite (cf Figure 8f).
Figure 22. Photographs of *Megaphragma* species: (a) *M. viggianii*, female antenna (Holotype); (b) *M. viggianii*, female mesosoma (Holotype); (c) *M. viggianii*, female fore wing (Holotype); (d) *M. viggianii*, female ventral (above) and dorsal (below) wing surface, (Holotype); (e) *M. priessneri*, female ventral (above) and dorsal (below) wing surface (Neotype). Arrows point at the penultimate seta on ventral surface. Scale bars 20 µm.
Key to species of *Megaphragma*

1. Fore wing with a single discal seta (Figures 9h and 10c) or without any discal setae (Figures 3f and 4a) .......................... 2

   * Fore wing with at least one line of 3 or more setae (Figures 3c and 5d) ................................................................. 17

2. Fore wing without discal seta (Figure 3f) .................................................................................................................... 3

   * Fore wing with one discal seta (Figure 9h) .................................................................................................................... 6

3. Mid lobe of mesoscutum entirely with regular longitudinally striate sculpture (Figure 3d) ....................................................... 4

   * Mid lobe of mesoscutum with reticulate sculpture anteriorly (Figure 3g), or with irregular longitudinal sculpture (Figure 13b) .................................................................

4. Female: ovipositor more than 1.5× as long as mesotibia. Male: C3 with terminal sensillum less than 2× length C3 ........................ deflectum

   * Female: ovipositor less than 1.5× as long as mesotibia. Male: C3 with terminal sensillum more than 2× length C3 ........................... rivelloi

5. Mid lobe of mesoscutum with reticulate sculpture anteriorly (Figure 3g) ................................................................. ghesquierei

   * Mid lobe of mesoscutum with irregular longitudinal sculpture (Figure 13b) ................................................................. chienleei

6. Fore wing with discal seta short, ≤distance between 2 proximal wing fringe setae (Figure 11b) ................................................... 7

   * Fore wing with discal seta long, ≥distance between 3 proximal wing fringe setae (Figure 10c) ........................................ 12

7. Female: ovipositor strongly exserted, more than 3× mesotibia (Figure 17b) ................................................................. momookherjeeae

   * Ovipositor slightly or not exserted, less than 2.5× mesotibia ...................................................................................... 8

8. Clava 1-segmented (Figure 21i). Marginal vein with both central setae minute ................................................................. unicalavum

   * Clava 2- or 3-segmented (if 2-segmented, C1 partially fused with C2). Marginal vein with at least one of the central setae elongate .................................................................

9. Marginal vein with 2 central setae, the distal one minute, less than 0.2× as long as the proximal seta (Figure 15f) ................ hansi

   * Marginal vein with 2 central setae, either subequal in length (Figure 11b), or the distal one about 0.5× as long as the proximal seta (Figure 16d) ................................................................. 10

10. Funicle present, transverse (Figure 11a); clava 2-segmented ................................................................. antecessor

   * Funicle absent; clava 3-segmented ................................................................................................................................. 11

11. Mid lobe of mesoscutum entirely with evident regular longitudinally striate sculpture while reticulate cells hardly visible (Figure 21l) ................................................................. vanlentereni

   * Mid lobe of mesoscutum entirely with fine regular longitudinally striate sculpture, surface divided into obvious reticulate cells (Figure 16b) ................................................................. liui

12. Marginal vein with one central seta (Figure 12c) ................................................................................................................... 13

   * Marginal vein with two central setae ................................................................................................................................. 15

13. T2–T4 of metasoma each with a robust seta near lateral margin; T5 centrally with subparallel striations (Figure 21h). Male: C3 elongate, length more than 3× basal width, with very long sensilla (Figure 21g) ......................................................... tridens

   * T2–T4 of metasoma without a seta near lateral margin; T5 centrally with reticulate sculpture (Figures 12b and 21c). Male: C3 elongate or short, with less prominent sensilla (Figure 10b) ......................................................... 14

14. T2–T5 each with rows of prominent denticles laterally; T3 and T4 centrally with reticulate sculpture (Figure 21c). Female: C3 long (Figure 21b). Male: C3 long, length more than 2× basal width (Figure 10b) ................................................................. striatum

   * T2–T5 with denticles reduced to faint protrusions, especially on T3 and T4; T3 and T4 centrally with sculpture consisting of faint striae (Figure 12b). Female: C3 short (Figure 12a). Male: C3 short, length less than 2× basal width ........................................ brevicalavum

15. Clava 2-segmented ......................................................................................................................................................... stenopterum

   * Clava 3-segmented ......................................................................................................................................................... 16
16 Marginal vein proximal central seta 2–3× length of distal central seta (Figure 21e) ....................................................... tamoii
  * Marginal vein proximal central seta about 7× longer than distal seta (Figure 14c) .......................................................... digitatum
17 Antenna 4-segmented (excluding anellus) ....................................................................................................................... 18
  * Antenna 5-segmented (excluding anellus) ....................................................................................................................... 19
18 Female: C1 with 2 very short UST, much shorter than C1 (Figure 6a). Male: C1 2× as long as maximum width … macrostigmum
  * Female: C1 with 2 long UST, each as long as C1 (Figure 3a). Male: C1 3× as long as maximum width … caribea
19 T1 with characteristic sculpture consisting of distinct cells with denticulate margins (Figures 1a, 17f and 18f) ................. 20
  * T1 various, but not as above; elonagte cells may be present on sides of T1 (Figures 12b and 16b) .......................... 24
20 Female: T2 sculpture with many closed cells (Figure 17f); ovipositor 1.7× mesotibia .................................................. nowickii
  * Female: T2 sculpture without closed cells (occasionally a single cell in noyesi); ovipositor 1.3× mesotibia or shorter … 21
21 Mid lobe of mesoscutum reticulate with comparatively large cells (Figure 14h) .................................................... funiculatum
  * Mid lobe of mesoscutum smooth, or appearing longitudinally striate ................................................................. 22
22 Female: C1 trapezoid in lateral view, length 1.5× maximum width or less. Male: funicle trapezoid, slightly longer than wide …
  * Female: C1 parallel sided and elongate, 2× as long as wide or more. Male: funicle elongate, approximately 2× as long as wide
    (male unknown in M. polilovi) ........................................................................................................................................... 23
23 Scape 4× maximum width; radicle concolorous with scape, both pale (Figure 18a); ovipositor length 1× mesotibia … noyesi
  * Scape 6× maximum width; radicle darker compared to scape (Figure 18e); ovipositor length 1.3× mesotibia … polilovi
24 Mid lobe of mesoscutum coarsely reticulate over most of its surface (Figures 13e and 14e) ............................. 25
  * Mid lobe of mesoscutum reticulate only anteriorly (Figure 3g), or sculpture different (smooth Figure 4f, striate Figure 3d) ... 27
25 Fore wing with base hyaline (not infuscate; Figure 14f) .................................................................................. fanenitrakely
  * Fore wing with base infuscate (Figure 13f) ............................................................................................................ 26
26 C2 with apical SB only slightly shorter than C2 (Figure 13d) (male unknown) .................................................... cockerelli
  * C2 with apical SB less than 1/2 length of C2 (Figure 8a) ........................................................................ polychaetum
27 T2–T4 with very long setae laterally (Figure 5b), at least as long as the tergite ......................................................... 28
  * T2–T4 with short setae laterally (Figure 8f), much shorter than the tergite ........................................................... 29
28 T1 with long lateral setae. Female: funicle with long, robust UST (Figure 15c) ........................................................... giraultii
  * T1 without long lateral setae (Figure 5h). Female: funicle without long, robust ventral UST (Figures 5e and 16e) … longiciliatum
29 Mid lobe of mesoscutum reticulate anteriorly (Figures 8f and 22b) ............................................................. 30
  * Mid lobe of mesoscutum with different sculpture (Figure 18c), or smooth .......................................................... 31
30 Fore wing with maximum distal width <2× width measured at apex of marginal vein (Figure 8g); setae on ventral fore wing disc
  short, penultimate one not reaching to the base of the distal (Figure 22e) ............................................................. priessneri
  * Fore wing with maximum distal width >2× width measured at apex of marginal vein (Figure 22c); setae on ventral fore wing disc
    long, penultimate one reaching to the base of the distal (Figure 22d) ............................................................... viggiani
31 Mid lobe of mesoscutum smooth. Female: proximal UST attached close to the mid point of C1, shorter than C1 (Figure 5b) …
  * Mid lobe of mesoscutum with anterior striae (Figure 18c). Female: proximal UST attached close to the base of C1, longer than C1
    (Figure 18b) .................................................................................................................................................. pintoi
4. Discussion

The present study is the culmination of more than 10 years of intensive collecting and examination of several thousand *Megaphragma* specimens from all over the world, including type material of all but one of the previously described species. Without the molecular dimension, our conclusions would have been very different. For example, the separation of *M. noyesi* and *M. polilovi* from *M. mymaripenne* would not have been possible, and these species have been confused in the past. Within the *ghesquierei*-group, morphological differences between species that are very distinct based on DNA, are completely undetectable in many cases. Some of this is no doubt due to the limitations of light microscopy, even when using techniques such as Nomarski differential interference contrast (DIC), coupled with focus stacking. Morphological evolution at species level is apparent for several structures, most notably the antenna, but also the setae and spines on the middle and hind legs, the fore wing, the structure of the propodeum, and that of metasomal terga showing variation in microsculpture and chaetotaxy (of diagnostic value). Species can be relatively easily grouped based on features of these morphological characters, and the *ghesquierei*-group, in particular, can be defined based on features of three characters: fusion of the funicle with the clava, development of the central propodeum, and metafemoral spine. The *mymaripenne*-group is less easily defined, with the loss of the otherwise characteristic sculpture of *T1* having occurred in the *longiciliatum* subgroup. The shape of the fore wing, and its discal and marginal ciliation appear to be critical in reflecting species evolution in this genus. Future studies should carefully assess the setation of the upper and underside of the fore wing, something that is very difficult once the specimen has been slide-mounted. No doubt future studies, including more scanning electron microscope imaging, will reveal additional patterns of morphological variation in the genus.

Perhaps the most surprising discovery of this study is the extraordinary distribution of some species. *Megaphragma longiciliatum*, under our new and broader definition, is found from Southeast Asia to Northwest Europe, as well as in North America, the Congo, and the Middle East. In this respect, as well as in terms of their physical size, the *Megaphragma* species parallel some Protozoa. The phrase “everything is everywhere, but the environment selects” [69], originally applied to Protozoa, certainly seems to apply to several *Megaphragma* species. Previous theories attempting to explain ubiquitous distributions of particular species of organisms have attributed this to their large population sizes, rather than to any inherent properties of such groups [70]. This argument appears to be so entirely back to front (i.e., “some species are cosmopolitan because they have huge populations”) that it can be easily dismissed. It is precisely the inherent property of minuteness, among other attributes discussed below, that is the main reason for these species having cosmopolitan distributions. Minuteness is directly related to dispersive ability, which can be largely passive for minute organisms; although, *Megaphragma* are known to be good at directional flight [28]. Our study, despite being very patchy in terms of the sample sizes of most species, suggests a mixed pattern of dispersal and distribution, with ubiquitous species as well as apparently endemic ones, as shown previously for about 200 Protozoa species [71]. Minuteness also directly affects the relationship between the species and its immediate microhabitat. We can assume that for an organism whose adults are around one-quarter of a millimeter, and whose developmental stages are entirely within a closed environment (the thrips egg), the macroecological factors of climate and temperature are less important, at least for some species. Hence, e.g., *M. rivelloi* appears to be as suited to the humid rainforests of SE Asia as it is to the much drier countryside of Southern England, and the same must be true for other species. Humidity, and especially avoidance of desiccation, are critical for the survival of minute terrestrial organisms, and *Megaphragma* species are known to have very thin cuticle [18] (see also Supplementary Figure S1). Even if air masses could transport minute hymenopterans quickly across the globe, desiccation would be a major impediment [72]. However, given that for most of their adult life *Megaphragma* species are likely to be in close proximity to living plant tissue, and hence access to moisture, it is probable that these immediate microclimatic conditions override...
the macroecological conditions already mentioned, and hence some of the remarkable latitudinal distributions of, e.g., *M. longiciliatum, M. pintoi*, and *M. rivelloi*. As well as both direct and passive colonization of new geographical areas, human movement of plant material containing thrips eggs, and *Megaphragma* life stages is inevitable, and has certainly contributed to a large extent to the cosmopolitan distribution of some species. Adaptation to, and dependence on, microhabitat conditions, especially humidity, have undoubtedly also contributed to their human-mediated distribution through the movement of plant material. Another explanation for species of egg parasitoids having extremely wide distributions has been their assumed defencelessness, and the relative uniformity of their hosts [73]. Whilst the former appears to be generally true, the latter clearly is not. Parasitoids that parasitize eggs are in some cases able to additionally parasitize Lepidoptera larvae, braconid cocoons, and even act as hyperparasitoids of other egg parasitoids. This extreme range of hosts has been reliably documented in *Centrodora darwini* (Girault) [74]. Other egg parasitoids appear to be extremely specific in which species they will either attack and/or develop successfully on, and this is particularly true of many species in the hyperdiverse genus *Telenomus* (e.g., [75]). Thus, a huge range of levels of host species specificity exists across egg parasitoids. In several taxa, eggs are entirely free of any parasitoids (aphids, whiteflies, and scale insects), while their (relatively) close relatives (leafhoppers and their relatives) are very heavily parasitized [76]. Clearly, the ability to evade or resist being parasitized at the egg stage is highly heterogeneous across the insects. In the case of *Megaphragma*, it is difficult to tell how host specific they are; in the few cases where there are rearing records from more than one host, they belong to different genera of the same family. Most likely as in other groups of parasitoid wasps, members of *Megaphragma* are a mix of generalists and specialist species [77].

As stated above, in several lineages *Megaphragma* has diversified to produce numerous cryptic species, many of which appear indistinguishable morphologically, at least using the techniques employed in this study. All future studies of these and similar organisms must rely to an extent on DNA data, and it may be that species will be described solely on differences in DNA where these differences can be demonstrated to be reasonably accurate proxies for biological species distinctions.

**Supplementary Materials:** The following supporting information can be downloaded at: [https://www.mdpi.com/article/10.3390/insects13060561/s1](https://www.mdpi.com/article/10.3390/insects13060561/s1), Figure S1: Confocal laser micrograph of *M. longiciliatum* (female from Oman). Blue areas are the least sclerotized and yellow the most strongly sclerotized (Photo A. P.); Figure S2: Phylogenetic tree of CO1 in *Megaphragma*, unpartitioned analysis in RAxML-NG; Figure S3. Phylogenetic tree of 28S in *Megaphragma*, unpartitioned analysis in RAxML-NG; Figure S4: a *Heliothrips haemorrhoidalis*, the host of *Megaphragma* sp., b eggs of *Heliothrips haemorrhoidalis* with exit hole of *Megaphragma* sp., c pupa of *Megaphragma* sp. in egg of *Heliothrips haemorrhoidalis* (Photo G. Viggiani).

**Author Contributions:** Conceptualization, A.P., L.F. and G.V.; methodology, A.P., L.F., A.H. and A.A.P.; validation, A.P. and L.F.; formal analysis, A.P. and L.F.; investigation, A.P., L.F., G.V., A.H., P.H. and A.A.P.; resources, A.P., A.A.P., P.H. and G.V.; data curation, A.P. and L.F.; writing—original draft preparation, A.P., L.F., G.V. and A.A.P.; writing—review and editing, A.P., L.F., G.V., A.H., P.H. and A.A.P.; visualization, A.P., L.F., G.V. and A.A.P.; project administration, A.P., P.H. and G.V.; funding acquisition, A.P., G.V. and A.A.P. All authors have read and agreed to the published version of the manuscript.

**Funding:** This research was funded by the UK Royal Society under International Joint Project with grant number JP100330/2010 awarded to A.P. and G.V.; A.A.P. gratefully acknowledges financial support from the Russian Foundation for Basic Research (project no. 20-04-00642).

**Institutional Review Board Statement:** Not applicable.

**Informed Consent Statement:** Not applicable.
Data Availability Statement: All sequences were deposited in GenBank. Voucher specimens are deposited in the collections listed under Specimens and depository abbreviations. All data and materials will be publicly available.

Acknowledgments: Claire Griffin at the NHM sequencing facility carried out all Sanger sequencing. Kiara van der Kroon-Polaszek enhanced many of the line drawings, all of which were originally drawn by Gennaro Viggiani. John Huber (Canadian National Collection of Insects, Arachnids and Nematodes, Agriculture and Agri-Food Canada), Zachary Lahey (Department of Evolution, Ecology, and Organismal Biology, The Ohio State University), and an anonymous reviewer are acknowledged for their constructive suggestions that greatly improved the manuscript.

Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Details of the specimens used for the molecular analyses are provided in Table A1.

Table A1. Voucher specimens, their repository, and accession numbers for the 28S and CO1 sequences.

| Nr | Voucher | Species          | Country  | Type | Repository | 28S bp + gaps | Accession nr | 28S bp | CO1 bp | Accession nr |
|----|---------|------------------|----------|------|-----------|--------------|--------------|--------|--------|--------------|
| 1  | COM1 1  | M. novickii      | D. R. Congo | Paratype | DACE | 1095 (212 indels) | ON555486 295 | ON557406 |
| 2  | COM1 2  | M. novickii      | D. R. Congo | Paratype | DACE | 1095 (211 indels) | ON555494 652 | ON557417 |
| 3  | COM1 3  | M. novickii      | D. R. Congo | Paratype | DACE | 1095 (211 indels) | ON555502 652 | ON557426 |
| 4  | COM1 4  | M. novickii      | D. R. Congo | Paratype | DACE | 1000 (211 indels) | ON555503 652 | ON557427 |
| 5  | COM1 5  | M. novickii      | D. R. Congo | Paratype | DACE | 1092 (211 indels) | ON555504 652 | ON557428 |
| 6  | COM1 6  | M. novickii      | D. R. Congo | Paratype | DACE | 1085 (211 indels) | ON555505 652 | ON557429 |
| 7  | COM1 7  | M. novickii      | D. R. Congo | Paratype | NHMUK | - - | 592 | ON557430 |
| 8  | COM1 8  | M. novickii      | D. R. Congo | Paratype | NHMUK | 1087 (212 indels) | ON555506 652 | ON557431 |
| 9  | COM1 9  | M. novickii      | D. R. Congo | Paratype | NHMUK | 1095 (211 indels) | ON555507 366 | ON557432 |
| 10 | COM1 10 | M. novickii      | D. R. Congo | Paratype | NHMUK | 1087 (211 indels) | ON555487 652 | ON557407 |
| 11 | COM1 11 | M. novickii      | D. R. Congo | Paratype | NHMUK | 414 (121 indels) | ON555488 652 | ON557408 |
| 12 | COM1 12 | M. novickii      | D. R. Congo | Paratype | AICF | 1093 (212 indels) | ON555489 652 | ON557409 |
| 13 | COM1 13 | M. novickii      | D. R. Congo | Paratype | DACE | 1048 (212 indels) | ON555490 652 | ON557410 |
| 14 | COM1 14 | M. novickii      | D. R. Congo | Paratype | DACE | 1049 (209 indels) | ON555491 652 | ON557411 |
| 15 | COM1 15 | M. novickii      | D. R. Congo | Paratype | DACE | - - | 652 | ON557412 |
| 16 | COM1 16 | M. novickii      | D. R. Congo | Holotype | NHMUK | 1106 (211 indels) | ON555492 652 | ON557413 |
| 17 | COM1 17 | M. novickii      | D. R. Congo | Paratype | DACE | - - | 652 | ON557414 |
| 18 | COM1 18 | M. novickii      | D. R. Congo | Paratype | DACE | 1106 (211 indels) | ON555493 652 | ON557415 |
| 19 | COM1 19 | M. novickii      | D. R. Congo | Paratype | DACE | - - | 652 | ON557416 |
| 20 | COM1 20 | M. novickii      | D. R. Congo | Paratype | DACE | 1106 (212 indels) | ON555495 652 | ON557418 |
| 21 | COM1 21 | M. novickii      | D. R. Congo | Paratype | AICF | 1106 (212 indels) | ON555496 652 | ON557419 |
| 22 | COM1 22 | M. novickii      | D. R. Congo | Paratype | IITA | 1106 (208 indels) | ON555497 652 | ON557420 |
| 23 | COM1 23 | M. novickii      | D. R. Congo | Paratype | IITA | 1106 (209 indels) | ON555498 522 | ON557421 |
| 24 | COM1 24 | Megaphragma sp. | D. R. Congo | Paratype | NA | - - | 369 | ON557422 |
| 25 | COM1 25 | Megaphragma sp. | D. R. Congo | Paratype | NA | 684 (245 indels) | ON555499 369 | ON557423 |
| 26 | COM1 26 | M. novickii      | D. R. Congo | Paratype | IITA | 1106 (212 indels) | ON555500 652 | ON557424 |
| 27 | COM1 27 | M. novickii      | D. R. Congo | Paratype | IITA | 1106 (211 indels) | ON555501 652 | ON557425 |
| 28 | COM2 1  | M. longiciliatum | D. R. Congo | Paratype | AICF | 918 (206 indels) | ON555508 652 | ON557433 |
| 29 | COM2 2  | Megaphragma sp. | D. R. Congo | Paratype | NHMUK | 1045 (239 indels) | ON555509 391 | ON557434 |
| Nr | Voucher | Species         | Country       | Type Status | Repository | 28S bp + gaps | Accession nr | CO1 bp | Accession nr |
|----|---------|----------------|---------------|-------------|------------|---------------|--------------|--------|--------------|
| 30 | COM2 3  | *M. longiciliatum* | D. R. Congo   | NA          | NHMUK      | 896 (206 indels) | ON555510    | -      | -            |
| 31 | COM2 4  | Megaphragma sp.  | D. R. Congo   | NA          | NHMUK      | 680 (124 indels) | ON555511    | 652    | ON557435     |
| 32 | CRM1 4  | *M. hansoni*     | Costa Rica    | Paratype    | NHMUK      | 534 (117 indels) | ON555513    | -      | -            |
| 33 | CRM1 16 | *M. hansoni*     | Costa Rica    | Paratype    | NHMUK      | 1106 (255 indels) | ON555512    | -      | -            |
| 34 | CRM2 1  | *M. digitatum*   | Costa Rica    | Holotype    | NHMUK      | 1062 (264 indels) | ON555514    | -      | -            |
| 35 | CRM2 2  | *M. antecessor*  | Costa Rica    | Holotype    | NHMUK      | 647 (123 indels) | ON555518    | 366    | ON557437     |
| 36 | CRM2 3  | *M. digitatum*   | Costa Rica    | Paratype    | MZUCR      | 1106 (265 indels) | ON555519    | 652    | ON557438     |
| 37 | CRM2 4  | *M. giraulti*    | Costa Rica    | Holotype    | NHMUK      | 679 (158 indels) | ON555520    | -      | -            |
| 38 | CRM2 5  | *M. giraulti*    | Costa Rica    | Paratype    | AICF       | 689 (159 indels) | ON555521    | 291    | ON557439     |
| 39 | CRM2 6  | *M. digitatum*   | Costa Rica    | Paratype    | MZUCR      | 1036 (264 indels) | ON555522    | -      | -            |
| 40 | CRM2 7  | *M. giraulti*    | Costa Rica    | Paratype    | DACE       | 1048 (269 indels) | ON555523    | 291    | ON557440     |
| 41 | CRM2 8  | *M. giraulti*    | Costa Rica    | Paratype    | MZUCR      | 679 (151 indels) | ON555524    | -      | -            |
| 42 | CRM2 9  | *M. digitatum*   | Costa Rica    | Paratype    | MZUCR      | 679 (151 indels) | ON555525    | -      | -            |
| 43 | CRM2 10 | *M. giraulti*    | Costa Rica    | Paratype    | NHMUK      | 646 (158 indels) | ON555515    | 296    | ON557436     |
| 44 | CRM2 11 | *M. giraulti*    | Costa Rica    | Paratype    | MZUCR      | 490 (156 indels) | ON555516    | -      | -            |
| 45 | CRM2 12 | *M. digitatum*   | Costa Rica    | Paratype    | AICF       | 646 (151 indels) | ON555517    | -      | -            |
| 46 | CRM3 4  | *M. hansoni*     | Costa Rica    | Paratype    | NHMUK      | 938 (250 indels) | ON555530    | -      | -            |
| 47 | CRM3 17 | *M. hansoni*     | Costa Rica    | Paratype    | NHMUK      | 1106 (255 indels) | ON555528    | -      | -            |
| 48 | CRM3 23 | *M. giraulti*    | Costa Rica    | Paratype    | NHMUK      | 1043 (269 indels) | ON555529    | -      | -            |
| 49 | CRM3 40 | *M. hansoni*     | Costa Rica    | NA          | lost       | 691 (374 indels) | ON555531    | -      | -            |
| 50 | CRM3 46 | *M. funiculatum* | Costa Rica    | Paratype    | AICF       | 1101 (233 indels) | ON555532    | -      | -            |
| 51 | CRM3 97 | *M. hansoni*     | Costa Rica    | Paratype    | NHMUK      | 473 (137 indels) | ON555533    | -      | -            |
| 52 | CRM3 103 | *M. funiculatum* | Costa Rica    | Holotype    | NHMUK      | 761 (210 indels) | ON555526    | -      | -            |
| 53 | CRM3 104 | *M. hansoni*     | Costa Rica    | Paratype    | NHMUK      | 1025 (255 indels) | ON555527    | -      | -            |
| 54 | DNA ECU1 | *M. digitatum*   | Ecuador       | Paratype    | NHMUK      | 679 (152 indels) | ON555534    | -      | -            |
| 55 | DNA ECU4 | *M. digitatum*   | Ecuador       | Paratype    | AICF       | 849 (321 indels) | ON555535    | -      | -            |
| 56 | DNA980  | Megaphragma sp.  | D. R. Congo   | NA          | NHMUK      | 1106 (261 indels) | ON555584    | -      | -            |
| 57 | DNA1111 | *M. longiciliatum* | USA          | NA          | NHMUK      | 1013 (225 indels) | ON555536    | -      | -            |
| 58 | DNA1112 | *M. longiciliatum* | USA          | NA          | NHMUK      | 1030 (225 indels) | ON555537    | -      | -            |
| 59 | DNA1113 | *M. longiciliatum* | USA          | NA          | NHMUK      | 912 (266 indels) | ON555538    | -      | -            |
| 60 | DNA1114 | *M. mymaripenne* | USA          | NA          | NHMUK      | 1056 (228 indels) | ON555539    | -      | -            |
| 61 | DNA1116 | *M. novickii*    | Uganda        | Paratype    | NHMUK      | 1085 (211 indels) | ON555540    | -      | -            |
| 62 | DNA1117 | *M. novickii*    | Uganda        | Paratype    | NHMUK      | 1085 (211 indels) | ON555541    | -      | -            |
| 63 | DNA1118 | *M. novickii*    | Uganda        | Paratype    | NHMUK      | 1085 (212 indels) | ON555542    | -      | -            |
| 64 | DNA1119 | Megaphragma sp.  | Uganda        | NA          | NHMUK      | 1031 (238 indels) | ON555543    | -      | -            |
| 65 | DNA1120 | *M. novickii*    | Uganda        | Paratype    | NHMUK      | 473 (93 indels)  | ON555544    | -      | -            |
| 66 | DNA1121 | *M. novickii*    | Uganda        | Paratype    | NHMUK      | 806 (181 indels) | ON555545    | -      | -            |
| 67 | DNA1122 | *M. novickii*    | Uganda        | Paratype    | NHMUK      | 1052 (211 indels) | ON555546    | -      | -            |
| 68 | DNA1123 | *M. novickii*    | Uganda        | Paratype    | NHMUK      | 1085 (211 indels) | ON555547    | -      | -            |
| 69 | DNA1124 | *M. novickii*    | Uganda        | Paratype    | NHMUK      | 1085 (212 indels) | ON555548    | -      | -            |
| 70 | DNA1132 | *M. novickii*    | Uganda        | Paratype    | NHMUK      | 1085 (209 indels) | ON555549    | -      | -            |
| 71 | DNA1147 | *M. longiciliatum*| Indonesia    | NA          | NHMUK      | 1097 (202 indels) | ON555550    | -      | -            |
| 72 | DNA1612 | *M. noyesi*      | UK            | NA          | lost       | 1067 (213 indels) | ON555551    | -      | -            |
| 73 | DNA1613 | *M. noyesi*      | UK            | Paratype    | NHMUK      | 1106 (213 indels) | ON555552    | 607    | ON557441     |
Table A1. Cont.

| Nr  | Voucher   | Species              | Country | Type Status | Repository | 28S bp + gaps | Accession nr | CO1 bp | Accession nr |
|-----|-----------|----------------------|---------|-------------|------------|----------------|--------------|--------|--------------|
| 74  | DNA1614   | M. noyesi            | UK      | NA          | lost       | 1106 (213 indels) | ON555553    | -      | -            |
| 75  | DNA1615   | M. noyesi            | UK      | Paratype    | NHMUK      | 908 (189 indels) | ON555554    | 607    | ON557442     |
| 76  | DNA1616   | M. noyesi            | UK      | Paratype    | NHMUK      | 1106 (213 indels) | ON555555    | 607    | ON557443     |
| 77  | DNA1617   | M. noyesi            | UK      | Paratype    | UCRC       | 1106 (213 indels) | ON555556    | -      | -            |
| 78  | DNA1618   | M. noyesi            | UK      | NA          | lost       | 1106 (213 indels) | ON555557    | -      | -            |
| 79  | DNA1619   | M. noyesi            | UK      | Paratype    | UCRC       | 1106 (213 indels) | ON555558    | 607    | ON557444     |
| 80  | DNA1626   | Megaphragma sp.      | Brunei  | NA          | NHMUK      | 1067 (271 indels) | ON555559    | -      | -            |
| 81  | DNA1628   | Megaphragma sp.      | Singapore | NA       | NHMUK      | 1096 (266 indels) | ON555560    | 394    | ON557445     |
| 82  | DNA1630   | Megaphragma sp.      | Singapore | NA       | NHMUK      | -              | -            | 394    | ON557446     |
| 83  | DNA1632   | Megaphragma sp.      | Singapore | NA       | NHMUK      | -              | -            | 394    | ON557447     |
| 84  | DNA1638   | Megaphragma sp.      | Brunei  | NA          | NHMUK      | 1071 (265 indels) | ON555561    | -      | -            |
| 85  | DNA1640   | Megaphragma sp.      | Singapore | NA       | NHMUK      | 1046 (156 indels) | ON555562    | 394    | ON557448     |
| 86  | DNA1641   | Megaphragma sp.      | Singapore | NA       | NHMUK      | 1106 (269 indels) | ON555563    | 394    | ON557449     |
| 87  | DNA1642   | Megaphragma sp.      | Brunei  | NA          | NHMUK      | 1106 (269 indels) | ON555564    | 394    | ON557450     |
| 88  | DNA1643   | Megaphragma sp.      | Brunei  | NA          | NHMUK      | 975 (264 indels) | ON555565    | 394    | ON557451     |
| 89  | DNA1644   | Megaphragma sp.      | Brunei  | NA          | NHMUK      | 1106 (271 indels) | ON555566    | 394    | ON557452     |
| 90  | DNA1645   | Megaphragma sp.      | Brunei  | NA          | NHMUK      | 1042 (268 indels) | ON555567    | 394    | ON557453     |
| 91  | DNA1650   | Megaphragma sp.      | Brunei  | NA          | NHMUK      | 1072 (270 indels) | ON555568    | -      | -            |
| 92  | DNA1651   | Megaphragma sp.      | Brunei  | NA          | NHMUK      | 1048 (222 indels) | ON555569    | 394    | ON557454     |
| 93  | DNA1652   | Megaphragma sp.      | Brunei  | NA          | NHMUK      | 1106 (267 indels) | ON555570    | 394    | ON557455     |
| 94  | DNA1655   | Megaphragma sp.      | Brunei  | NA          | NHMUK      | 1000 (270 indels) | ON555571    | 394    | ON557456     |
| 95  | DNA1656   | M. liui              | Brunei  | Holotype    | UCRC       | 900 (556 indels) | ON555572    | 370    | ON557457     |
| 96  | DNA1659   | Megaphragma sp.      | Brunei  | NA          | NHMUK      | 1038 (270 indels) | ON555573    | -      | -            |
| 97  | DNA1661   | Megaphragma sp.      | Brunei  | NA          | NHMUK      | 1106 (266 indels) | ON555574    | -      | -            |
| 98  | DNA1665   | Megaphragma sp.      | Singapore | NA       | NHMUK      | 1106 (266 indels) | ON555575    | 394    | ON557458     |
| 99  | DNA1668   | Megaphragma sp.      | Brunei  | NA          | NHMUK      | 1106 (267 indels) | ON555576    | 394    | ON557459     |
| 100 | DNA1674   | Megaphragma sp.      | Brunei  | NA          | NHMUK      | 1106 (265 indels) | ON555577    | -      | -            |
| 101 | DNA1678   | Megaphragma sp.      | Singapore | NA       | NHMUK      | 1095 (266 indels) | ON555578    | 394    | ON557460     |
| 102 | DNA1679   | Megaphragma sp.      | Brunei  | NA          | NHMUK      | 1106 (218 indels) | ON555579    | -      | -            |
| 103 | DNA1680   | M. momookherjeae     | Costa Rica | Holotype | NHMUK      | -              | -            | 394    | ON557461     |
| 104 | DNA1681   | M. digitatum         | Costa Rica | Paratype | NHMUK      | 1106 (265 indels) | ON555580    | 367    | ON557462     |
| 105 | DNA1682   | Megaphragma sp.      | Costa Rica | NA       | NHMUK      | 932 (257 indels) | ON555581    | -      | -            |
| 106 | DNA1683   | M. giraufli          | Costa Rica | Paratype | NHMUK      | 1055 (270 indels) | ON555582    | 394    | ON557463     |
| 107 | DNA1686   | Megaphragma sp.      | Vietnam  | NA          | NHMUK      | -              | -            | 652    | ON557464     |
| 108 | DNA1687   | M. rivelloi          | Vietnam  | Paratype    | AICF       | 1106 (259 indels) | ON555583    | -      | -            |
| 109 | DNAMO03   | M. longiciliatum     | Oman     | NA          | NHMO       | 420 (102 indels) | ON555588    | -      | -            |
| 110 | DNAMO013  | M. longiciliatum     | Oman     | NA          | NHMO       | 1106 (224 indels) | ON555585    | -      | -            |
| 111 | DNAMO20   | M. longiciliatum     | Oman     | NA          | NHMO       | 1106 (224 indels) | ON555586    | -      | -            |
| 112 | DNAMO22   | M. longiciliatum     | Oman     | NA          | NHMO       | 1106 (224 indels) | ON555587    | -      | -            |
| 113 | FRM2      | M. longiciliatum     | France   | NA          | NHMUK      | 1106 (213 indels) | ON555589    | 652    | ON557465     |
| 114 | FRM3      | M. longiciliatum     | France   | NA          | NHMUK      | 1106 (213 indels) | ON555590    | 652    | ON557466     |
| 115 | FRM4      | M. longiciliatum     | France   | NA          | AICF       | 1106 (213 indels) | ON555591    | 652    | ON557467     |
| 116 | FRM5      | M. longiciliatum     | France   | NA          | NHMUK      | 1106 (213 indels) | ON555592    | 652    | ON557468     |
| 117 | FRM6      | M. longiciliatum     | France   | NA          | NHMUK      | 1106 (213 indels) | ON555593    | 652    | ON557469     |
## Table A1. Cont.

| Nr | Voucher | Species                  | Country  | Type          | Status | Repository           | 28S             | CO1              |
|----|---------|--------------------------|----------|---------------|--------|----------------------|-----------------|------------------|
|    |         |                          |          |               |        |                      | bp + gaps  | Accession nr | bp   | Accession nr |
| 118| HUM1    | *M. longiciliatum*       | Hungary  | NA            | NHMUK  | 679 (122 indels)      | 652           | ON555740       |
| 119| HUM2    | *M. noyesi*              | Hungary  | Paratype      | NHMUK  | 1060 (213 indels)     | 650           | ON557476       |
| 120| HUM3    | *M. noyesi*              | Hungary  | NA            | lost   | 1061 (213 indels)     | 652           | ON557477       |
| 121| HUM4    | Megaphragma sp.          | Hungary  | NA            | NHMUK  | 1010 (216 indels)     | 652           | ON557478       |
| 122| HUM5    | *M. noyesi*              | Hungary  | Paratype      | AICF   | -                     | -             | -               |
| 123| HUM6    | *M. noyesi*              | Hungary  | Paratype      | NHMUK  | 641 (152 indels)      | 652           | ON557481       |
| 124| HUM7    | *M. noyesi*              | Hungary  | Paratype      | NHMUK  | 679 (125 indels)      | 652           | ON557482       |
| 125| HUM8    | *M. noyesi*              | Hungary  | Paratype      | NHMUK  | 649 (125 indels)      | 652           | ON557472       |
| 126| HUM9    | *M. noyesi*              | Hungary  | Paratype      | NHMUK  | 1040 (213 indels)     | 295           | ON557473       |
| 127| HUM10   | *M. noyesi*              | Hungary  | Paratype      | AICF   | -                     | -             | -               |
| 128| HUM11   | *M. noyesi*              | Hungary  | Holotype      | AICF   | -                     | 296           | ON557483       |
| 129| HUM12   | *M. noyesi*              | Hungary  | Paratype      | NHMUK  | -                     | -             | 574             | ON557474       |
| 130| ITM1    | *M. viggianii*           | Italy    | Holotype      | DACE   | 1106 (219 indels)     | 652           | ON557483       |
| 131| ITM2    | *M. viggianii*           | Italy    | Paratype      | NHMUK  | 1106 (219 indels)     | 652           | ON557488       |
| 132| ITM3    | *M. viggianii*           | Italy    | Paratype      | NHMUK  | 934 (217 indels)      | 631           | ON557489       |
| 133| ITM4    | *M. viggianii*           | Italy    | Paratype      | NHMUK  | 1106 (219 indels)     | 652           | ON557490       |
| 134| ITM5    | *M. viggianii*           | Italy    | Paratype      | AICF   | 1050 (219 indels)     | 652           | ON557491       |
| 135| ITM6    | *M. viggianii*           | Italy    | Paratype      | AICF   | 1106 (219 indels)     | 652           | ON557492       |
| 136| ITM7    | *M. viggianii*           | Italy    | Paratype      | NHMUK  | 1047 (219 indels)     | 652           | ON557493       |
| 137| ITM8    | *M. polilovi*            | Italy    | Paratype      | DACE   | 1080 (208 indels)     | 641           | ON557494       |
| 138| ITM9    | *M. polilovi*            | Italy    | Holotype      | DACE   | 1088 (208 indels)     | 641           | ON557495       |
| 139| ITM10   | *M. longiciliatum*       | Italy    | NA            | NHMUK  | 1081 (213 indels)     | 652           | -               | -               |
| 140| ITM11   | *M. polilovi*            | Italy    | Paratype      | AICF   | 1080 (208 indels)     | 641           | ON557484       |
| 141| ITM12   | *M. polilovi*            | Italy    | Paratype      | NHMUK  | 1081 (208 indels)     | 652           | ON557485       |
| 142| ITM13   | *M. viggianii*           | Italy    | Paratype      | NHMUK  | 1081 (219 indels)     | 652           | ON557486       |
| 143| ITM14   | *M. polilovi*            | Italy    | Paratype      | NHMUK  | 1080 (208 indels)     | 641           | ON557487       |
| 144| MXM1    | *M. striatum*            | Mexico   | NA            | NHMUK  | 995 (297 indels)      | 652           | ON557496       |
| 145| MXM2    | *M. breviclavum*         | Mexico   | Holotype      | NHMUK  | 1010 (298 indels)     | 652           | ON557497       |
| 146| MXM3    | *M. breviclavum*         | Mexico   | Paratype      | NHMUK  | 878 (514 indels)      | 652           | ON557498       |
| 147| MXM4    | *M. breviclavum*         | Mexico   | Paratype      | NHMUK  | 1000 (298 indels)     | 652           | ON557499       |
| 148| SAM1    | Megaphragna sp.          | Malaysia | NA            | NHMUK  | 1106 (269 indels)     | 296           | ON557500       |
| 149| SAM2    | Megaphragna sp.          | Malaysia | NA            | NHMUK  | 1065 (248 indels)     | 356           | ON557503       |
| 150| SAM3    | *M. vanlentereni*        | Malaysia | Holotype      | NHMUK  | 1017 (263 indels)     | 652           | ON557504       |
| 151| SAM4    | *M. chienleei*           | Malaysia | Paratype      | NHMUK  | 1106 (268 indels)     | 652           | -               | -               |
| 152| SAM5    | *M. chienleei*           | Malaysia | Paratype      | NHMUK  | 1106 (268 indels)     | 652           | ON557505       |
| 153| SAM6    | *M. chienleei*           | Malaysia | Paratype      | AICF   | 1106 (268 indels)     | 652           | ON557506       |
| 154| SAM7    | *M. chienleei*           | Malaysia | Paratype      | NHMUK  | 1106 (268 indels)     | 652           | ON557507       |
| 155| SAM8    | *M. chienleei*           | Malaysia | Paratype      | NHMUK  | 1106 (268 indels)     | 652           | ON557508       |
| 156| SAM9    | Megaphragna sp.          | Malaysia | NA            | NHMUK  | 1106 (271 indels)     | 652           | ON557509       |
| 157| SAM10   | Megaphragna sp.          | Malaysia | NA            | NHMUK  | 1080 (225 indels)     | 641           | ON557501       |
| 158| SAM11   | *M. cockerilli*          | Malaysia | Holotype      | AICF   | 1073 (222 indels)     | 460           | ON557502       |
| 159| SAM12   | *M. chienleei*           | Malaysia | Holotype      | AICF   | 1074 (268 indels)     | 652           | -               | -               |
Table A1. Cont.

| Nr  | Voucher | Species         | Country   | Type     | Status | Repository     | bp + gaps | Accession nr | bp          | Accession nr |
|-----|---------|-----------------|-----------|----------|--------|----------------|-----------|--------------|-------------|--------------|
| 161 | SRM1    | *M. longiciliatum* | Malaysia  | NA       | NMHUK  | 513 (287 indels) | ON555634  | 652          | ON557510    |
| 162 | SRM2    | *Megaphragma* sp. | Malaysia  | NA       | NMHUK  | 1044 (248 indels) | ON555635  | 624          | ON557511    |
| 163 | SRM3    | *Megaphragma* sp. | Malaysia  | NA       | NMHUK  | 679 (124 indels)  | ON555636  | 601          | ON557512    |
| 164 | UKM8    | *M. noyesii*     | UK        | Paratype | lost   | 647 (125 indels)  | ON555642  | -            | -           |
| 165 | UKM9    | *M. noyesii*     | UK        | Paratype | AICF   | 1106 (213 indels) | ON555643  | 652          | ON557518    |
| 166 | UKM10   | *M. noyesii*     | UK        | Paratype | NMHUK  | 1106 (213 indels) | ON555637  | 652          | ON557513    |
| 167 | UKM11   | *M. noyesii*     | UK        | Paratype | NMHUK  | 1106 (213 indels) | ON555638  | 652          | ON557514    |
| 168 | UKM12   | *M. noyesii*     | UK        | Paratype | DACE   | 1106 (213 indels) | ON555639  | 652          | ON557515    |
| 169 | UKM13   | *M. noyesii*     | UK        | Paratype | NMHUK  | 1106 (213 indels) | ON555640  | 652          | ON557516    |
| 170 | UKM14   | *M. noyesii*     | UK        | Holotype | NMHUK  | 1047 (213 indels) | ON555641  | 652          | ON557517    |
| 171 |         | “*M. amalphitanum*” |          |          |        | -              | -         | 652          | KT373787    |
| 172 | D1224   | *Megaphragma* sp. | GenBank   | NA       |        | 1048 (230 indels) | AY623543  | -            | -           |
| 173 | D1229   | *Megaphragma* sp. | GenBank   | NA       |        | 1106 (260 indels) | AY623544  | -            | -           |
| 174 | D1243   | *Megaphragma* sp. | GenBank   | NA       |        | 1106 (240 indels) | AY623545  | -            | -           |
| 175 | O19     | *Oligosita* sp.  | GenBank   | NA       |        | 659 (195 indels)  | MG285509  | 603          | MG004913    |
| 176 | D1219   | *Epopolisita* sp.| GenBank   | NA       |        | 1106 (301 indels) | AY623546  | -            | -           |
| 177 | D0760   | *Oligosita sanguinea* | GenBank  | NA       |        | 1106 (291 indels) | AY623551  | -            | -           |
| 178 | D0886   | *Probrachista* sp.| GenBank   | NA       |        | 1106 (288 indels) | AY623553  | -            | -           |

References
1. Noyes, J.S. Universal Chalcidoidea Database. Available online: https://www.nhm.ac.uk/our-science/data/chalcidoids/database/ (accessed on 15 October 2021).
2. Pinto, J.D. A review of the New World genera of Trichogrammatidae. J. Hymenopt. Res. 2006, 15, 38–163.
3. Viggiani, G.; Dipartimento di Agraria, Laboratorio di Lotta Biologica, Università degli Studi di Napoli “Federico II”, Portici, Italy. 2021; Unpublished data.
4. Polilov, A.A. The smallest insects evolve anucleate neurons. Arthropod Struct. Dev. 2012, 41, 29–34. [CrossRef] [PubMed]
5. Huber, J.; Noyes, J. A new genus and species of fairyfly, Tinkerella nana (Hymenoptera, Mymaridae), with comments on its sister genus Kikiki, and discussion on small size limits in arthropods. J. Hymenopt. Res. 2013, 32, 17–44. [CrossRef]
6. Viggiani, G. Notes on the type of Megaphragma Timberlake (Hymenoptera: Trichogrammatidae). Boll. Lab. Ent. Agr. Filippo Silvestri 1997, 53, 117–122.
7. Viggiani, G.; Bernardo, U. Two species of Megaphragma (Hymenoptera Trichogrammatidae), egg-parasitoids of Heliothrips haemorrhoidalis Boučé (Thysanoptera) in southern Italy, with description of a new species. Boll. Zool. Agr. Bach. Ser. II 1997, 29, 51–55.
8. Viggiani, G. A species of Megaphragma (Hymenoptera: Chalcidoidea: Trichogrammatidae), one of the smallest known insects, new for Italy. Boll. Zool. Agr. Bach. Ser. II 2002, 34, 449–452.
9. Lin, N.Q. Descriptions of five new species of Megaphragma and Paramegaphragma gen. nov. (Hymenoptera: Trichogrammatidae) from China. Entomotaxonomia 1992, 14, 129–138.
10. Hayat, M. Records and descriptions of Trichogrammatidae from India (Hymenoptera: Chalcidoidea). Orient. Insects 2009, 43, 201–227. [CrossRef]
11. Viggiani, G.; Luft Albarracin, E.; Virla, E. The species of Megaphragma Timberlake (Hymenoptera: Trichogrammatidae) from Argentina. Zootaxa 2009, 2308, 65–68. [CrossRef]
12. Hessein, N.A.; McMurtry, J.A. Observations on Megaphragma mymaripenne Timberlake (Hymenoptera: Trichogrammatidae), an egg parasite of Heliothrips haemorrhoidalis (Boučé) (Thysanoptera: Thripidae). Pan-Pac. Entomol. 1988, 64, 250–254.
13. Viggiani, G.; Bernardo, U. Distribuzione e attività di ooparassitoidi di Heliothrips haemorrhoidalis Boučé (Thysanoptera) su piante della macchia mediterranea. Phytophaga 1998, 8, 13–20.
14. Bernardo, U.; Viggiani, G. Biological data on Megaphragma analphitanum Viggiani and Megaphragma mymaripenne Timberlake (Hymenoptera: Trichogrammatidae), egg-parasitoid of H. haemorrhoidalis (Boučé) (Thysanoptera: Thripidae) in southern Italy. Boll. Lab. Ent. Agr. Filippo Silvestri 2003, 58, 77–85.
15. Polilov, A.A. At the Size Limit—Effects of Miniaturization in Insects; Springer International Publishing: Cham, Switzerland, 2016; p. 325.
16. Minelli, A.; Fusco, G. No limits: Breaking constrains in insect miniaturization. *Arthropod Struct. Dev.* 2019, 48, 4–11. [CrossRef] [PubMed]
17. Makarova, A.A.; Polilov, A.A.; Chklovskii, D.B. Small brains for big science. *Curr. Opin. Neurobiol.* 2021, 71, 77–83. [CrossRef]
18. Polilov, A.A. Anatomy of adult *Megaphragma* (Hymenoptera: Trichogrammatidae), one of the smallest insects, and new insight into insect miniaturization. *PLoS ONE* 2017, 12, e0175566. [CrossRef]
19. Makarova, A.; Polilov, A.; Fischer, S. Comparative morphological analysis of compound eye miniaturization in minute hymenoptera. *Arthropod Struct. Dev.* 2015, 44, 21–32. [CrossRef]
20. Diakova, A.V.; Makarova, A.A.; Polilov, A.A. Between extreme simplification and ideal optimization: Antennal sensilla morphology of miniaturized *Megaphragma* wasps (Hymenoptera: Trichogrammatidae). *PeerJ* 2018, 6, e6005. [CrossRef]
21. Diakova, A.V.; Polilov, A.A. Porous or non-porous? The challenge of studying unusual placoid sensilla of *Megaphragma* wasps (Hymenoptera, Trichogrammatidae) with electron microscopy. *J. Hymenopt. Res.* 2021, 84, 69–73. [CrossRef]
22. Boudinot, B.E.; Beutel, R.G.; Gorb, S.N.; Polilov, A.A. Functional diversity of attachment and grooming leg structures is retained in all but the smallest insects. *J. Zool.* 2020, 313, 99–113. [CrossRef]
23. Nedoluzhko, A.V.; Sharko, F.S.; Boulygina, E.S.; Tsygankova, S.V.; Sokolov, A.S.; Mazur, A.M.; Polilov, A.A.; Prokhortchouk, E.B.; Skryabin, K.G. Mitochondrial genome of *Megaphragma amalphitanum* (Hymenoptera: Trichogrammatidae). *Mitochondrial DNA Part A* 2016, 27, 4526–4527. [CrossRef]
24. Nedoluzhko, A.V.; Sharko, F.S.; Tsygankova, S.V.; Boulygina, E.S.; Sokolov, A.S.; Rastorguev, S.M.; Kadnikov, V.V.; Mardanov, A.V.; Ravin, N.V.; Mazur, A.M.; et al. Metagenomic analysis of microbial community of a parasitoid wasp *Megaphragma amalphitanum*. *Genom. Data* 2017, 11, 87–88. [CrossRef] [PubMed]
25. Sharko, F.S.; Nedoluzhko, A.V.; Le, B.M.; Tsygankova, S.V.; Boulygina, E.S.; Rastorguev, S.M.; Sokolov, A.S.; Rodriguez, F.; Mazur, A.M.; Polilov, A.A.; et al. A partial genome assembly of the miniature parasitoid wasp, *Megaphragma amalphitanum*. *PLoS ONE* 2019, 14, e0226485. [CrossRef]
26. Polilov, A.A. First record of *Megaphragma* (Hymenoptera, Trichogrammatidae) in Columbia, and third animal species known to have anucleate neurons. *J. Hymenopt. Res.* 2017, 60, 181–185. [CrossRef]
27. Polilov, A.A.; Makarova, A.A.; Pang, S.; Shan Xu, C.; Hess, H. Protocol for preparation of heterogeneous biological samples for 3D electron microscopy: A case study for insects. *Sci. Rep.* 2021, 11, 4717. [CrossRef] [PubMed]
28. Polilov, A.A.; Department of Entomology, Faculty of Biology, Lomonosov Moscow State University, Moscow, Russia. 2021; *Unpublished data*.
29. Loomans, A.J.M.; van Lenteren, J.C. Biological control of thrips pests: A review on thrips parasitoids. *Wagening. Agric. Univ. Pap.* 1995, 95, 89–201.
30. Loomans, A.J.M. *Parasitoids as Biological Control Agents of Thrips Pests*; Wageningen University: Wageningen, The Netherlands, 2003; p. 215.
31. Prokhortchouk, E.B.; Nedoluzhko, A.V.; Sharko, F.S.; Tsygankova, S.V.; Boulygina, E.S.; Rastorguev, S.M.; Sokolov, A.S.; Mazur, A.M.; Polilov, A.A.; Skryabin, K.G. Genome sequencing and transcriptome assembly of the parasitoid wasp *Megaphragma amalphitanum* (Hymenoptera: Trichogrammatidae). *Mosc. Univ. Biol. Sci. Bull.* 2017, 72, 30–32. [CrossRef]
32. Gillespie, J.J.; Munro, J.B.; Heraty, J.M.; Yoder, M.J.; Owen, A.K.; Carmichael, A.E. A secondary structural model of the 28S rRNA expansion segments D2 and D3 for chalcidoid wasps (Hymenoptera: Chalcidoidea). *Mol. Biol. Evol.* 2005, 22, 1593–1608. [CrossRef]
33. Owen, A.K.; George, J.; Pinto, J.D.; Heraty, J.M. A molecular phylogeny of the Trichogrammatidae (Hymenoptera: Chalcidoidea), with an evaluation of the utility of their male genitalia for higher level classification. *Syst. Entomol.* 2007, 32, 227–251. [CrossRef]
34. Noyes, J.S. Collecting and preserving chalcid wasps (Hymenoptera: Chalcidoidea). *J. Nat. Hist.* 1982, 16, 315–334. [CrossRef]
35. Cruaud, A.; Nidelet, S.; Arnal, P.; Weber, A.; Fusu, L.; Gumovský, A.; Huber, J.; Polaszek, A.; Rasplus, J.-Y. Optimized DNA extraction and library preparation for minute arthropods: Application to target enrichment in chalcid wasps used for biocontrol. *Mol. Ecol. Resour.* 2019, 19, 702–710. [CrossRef]
36. Park, J.K.; O’Foighil, D. Sphaeriid and corbiculid clams represent separate heterodont bivalve radiations into freshwater environments. *Mol. Phylogenet. Evol.* 2000, 14, 75–88. [CrossRef] [PubMed]
37. Whiting, M.F.; Carpenter, J.C.; Wheeler, Q.D.; Wheeler, W.C. The Strepsiptera problem: Phylogeny of the holometabolous insect orders inferred from 18S and 28S ribosomal DNA sequences and morphology. *Syst. Biol.* 1997, 46, 1–68. [CrossRef] [PubMed]
38. Nunn, G.B.; Theisen, B.F.; Christensen, B.; Arctander, P. Simplicity correlated size growth of the nuclear 28S ribosomal RNA D3 expansion segment in the crustacean order Isopoda. *J. Mol. Evol.* 1996, 42, 211–223. [CrossRef]
39. Holmer, O.; Black, M.; Hoeh, W.; Lutz, R.; Vrijenhoek, R. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Mol. Mar. Biol. Biotech.* 1994, 3, 294–299.
40. Hebert, P.D.N.; Cywinska, A.; Ball, S.L.; DeWaard, J.R. Biological identifications through DNA barcodes. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* 2003, 270, 313–321. [CrossRef]
41. Dascálu, M.M.; Caba, F.G.; Fusu, L. DNA barcoding in Dorcadionin (Coleoptera, Cerambycidae) uncovers mitochondrial-morphological discordance and the hybridogenic origin of several subspecies. *Org. Divers. Evol.* 2022, 22, 205–229. [CrossRef]
42. Fusu, L.; Polaszek, A. Description, DNA barcoding and phylogenetic placement of a remarkable new species of *Eopelma* (Hymenoptera: Eupelmidae) from Borneo. *Zootaxa* 2017, 4263, 557–566. [CrossRef]
43. Meusnier, I.; Singer, G.A.; Landry, J.F.; Hickey, D.A.; Hebert, P.D.; Hajibabaei, M. A universal DNA mini-barcode for biodiversity analysis. *BMC Genom.* 2008, 9, 214. [CrossRef]
74. Polaszek, A. Egg parasitism in the Aphelinidae (Hymenoptera: Chalcidoidea) with special reference to *Centrodora* and *Encarsia* species. *B. Entomol. Res.* 1991, 81, 97–106. [CrossRef]

75. Polaszek, A.; Kimani, S.W. *Telenomus* species (Hymenoptera: Scelionidae) attacking eggs of pyralid pests (Lepidoptera) in Africa: A review and guide to identification. *B. Entomol. Res.* 1990, 80, 57–71. [CrossRef]

76. Fatouros, N.E.; Cusumano, A.; Bin, F.; Polaszek, A.; van Lenteren, J.C. How to escape from insect egg parasitoids: A review of potential factors explaining parasitoid absence across the Insecta. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* 2020, 287, 20200344. [CrossRef]

77. Al khatib, F.; Cruaud, A.; Fusu, L.; Genson, G.; Rasplus, J.-Y.; Ris, N.; Delvare, G. Multilocus phylogeny and ecological differentiation of the “*Eupelmus urozonus* species group” (Hymenoptera, Eupelmidae) in the West-Palaearctic. *BMC Evol. Biol.* 2016, 16, 1–20. [CrossRef]