Phylogeny and life history evolution of Blaberoidea (Blattodea)

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Abstract. Blaberoidea, comprised of Ectobiidae and Blaberidae, is the most speciose cockroach clade and exhibits immense variation in life history strategies. We analysed the phylogeny of Blaberoidea using four mitochondrial and three nuclear genes from 99 blaberoid taxa. Blaberoidea (excl. Anaplectidae) and Blaberidae were recovered as monophyletic, but Ectobiidae was not; Attaphilinae is deeply subordinate in Blattellinae and herein abandoned. Our results, together with those from other recent phylogenetic studies, show that the structuring of Blaberoidea in Blaberidae, Pseudophyllodromiidae **stat. rev.**, Ectobiidae **stat. rev.**, Blattellidae **stat. rev.**, and Nyctiboridae **stat. rev.** (with "ectobiid" subfamilies raised to family rank) represents a sound basis for further development of Blaberoidea systematics. Relationships in Blaberidae are widely incongruent with current classification, but more congruent with geographic distribution, with large Afrotropical, Neotropical, and Indo-Malayan clades. We further investigate evolutionary trends and correlations of various life history traits: wing development, body size, microhabitat, mating pattern, ootheca handling, and clutch size.

Key words. Blaberidae, Ectobiidae, Attaphilinae, character mapping, character correlation, habitat, wing reduction, body size, clutch size, reproductive behaviour.

1. Introduction

Blattodea (cockroaches including termites) includes about 7600 species and is divided into three superfamilies: Blaberoidea, Blattoidea, and Corydioidea. Blaberoidea (Figs. 1B–H, 2) contains nearly half of the species and is distributed worldwide. It is classified in two families: Ectobiidae, the most speciose blattodean family (2326 species, Fig. 1B–F, Beccaloni & Eggleton 2013; often called 'Blattellidae'); and Blaberidae, the third most speciose family (1201 species, Figs. 1G,H, 2, Beccaloni & Eggleton 2013; Termitidae is the second most speciose family). Roth (2003a) classified Ectobiidae in 6 subfamilies: Attaphilinae (1 genus), Blattellinae (77 genera), Ectobiinae (11), Nyctiborinae (10), Pseudophyllodromii-nae (63), and Anaplectinae (2); 60+ further genera are not assigned to subfamily (Beccaloni 2014). Blaberidae is classified into 12 subfamilies: Blaberinae (23 genera), Diplopterinae (1), Epilamprinae (47), Geoscapheinae (4), Gyninae (5), Oxyhaloinae (17), Panchlorinae (5), Panesthiinae (7), Paranauphoetinae (1), Perisphaerinae (19), Pycnoscelinae (3), and Zetoborinae (14); 23 additional genera are not assigned to subfamily (Beccaloni 2014).

Members of Blaberoidea have been included in most phylogenetic studies of Blattodea or Dictyoptera (which additionally includes Mantodea, the praying mantids), either using morphological (e.g. McKittrick 1964; Grandcolas 1996; Klass & Meier 2006), molecular (e.g. In-

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WARD et al. 2007; PELLENS et al. 2007a; DJERNÆS et al. 2012; LEGENDRE et al. 2015; WANG et al. 2017; BOURGUIGNON et al. 2018; EVANGELISTA et al. 2019), or combined data sets (WARE et al. 2008; DJERNÆS et al. 2015). EVANGELISTA et al. (2019) included a smaller blaberoid taxon sample than other recent studies, but is the first based on a huge transcriptomic data set. These studies have generally agreed on the monophyly of Blaberoidea. However, DJERNÆS et al. (2015), WANG et al. (2017), and BOURGUIGNON et al. (2018), who included the rarely sampled Anaplectinae (Fig. 1A), all placed this group in Blattoidea (called BLATCI clade in DJERNÆS et al. 2015); DJERNÆS et al. (2015) excluded Anaplectinae from Ectobiidae and Blaberoidea, and ranked it as a family, Anaplectidae.

All of the aforementioned studies also agreed on the monophyly of Blaberidae. However, several of the blaberid subfamilies appeared non-monophyletic in previous studies (Fig. S1), and there is little consensus regarding the relationships among the subfamilies. Points of agreement are: **(1)** some Blaberinae are more closely related to Zetoborinae than to other Blaberinae (e.g. McKITTRICK 1964; LEGENDRE et al. 2014, 2017; BOURGUIGNON et al. 2018); **(2)** Panesthiinae is paraphyletic with respect to Geoscapheinae, while Panesthiinae + Geoscapheinae is monophyletic (e.g. LEGENDRE et al. 2014, 2017; LO et al. 2016); **(3)** Oxyhaloinae is monophyletic (e.g. LEGENDRE et al. 2014, 2017; BOURGUIGNON et al. 2018).

For Ectobiidae, even with exclusion of Anaplectinae, monophyly has not been demonstrated and there have long been indications of its paraphyly with respect to Blaberidae (e.g. McKITTRICK 1964; GRANDCOLAS 1996; KLASS & MEIER 2006; INWARD et al. 2007; PELLENS et al. 2007a; DJERNÆS et al. 2012, 2015; BOURGUIGNON et al. 2018; EVANGELISTA et al. 2019). The subfamilies Blattellinae (Fig. 1C,D), Ectobiinae (Fig. 1B), Nyctiborinae, and Pseudophyllodromiinae (Fig. 1E,F) were by and large recovered as monophyletic, but this was based on the inclusion of very few genera of each. However, McKITTRICK (1964), KLASS & MEIER (2006), LEGENDRE et al. (2015), and WANG et al. (2017) found Pseudophyllodromiinae to be non-monophyletic, and McKITTRICK (1964), DJERNÆS et al. (2012), BOURGUIGNON et al. (2018), and EVANGELISTA et al. (2019) found Blattellinae to be non-monophyletic as one genus disassociated from the remaining blattellines. So far, authors have rarely argued for family status for the various ectobiid subfamilies (but see GRANDCOLAS 1996), mainly due to lack of clarity whether or to what extent this classification reflects phylogenetic relationships. For the relationships among the various ectobiid subfamilies (and Blaberidae), multiple different combinations were found in phylogenetic studies, all with little support. Yet, most studies (McKITTRICK 1964, in part; KLASS & MEIER 2006; INWARD et al. 2007; DJERNÆS et al. 2015; EVANGELISTA et al. 2019) agree on a sister group relationship between Blattellinae and Nyctiborinae. All the existing hypotheses on the monophyly and phylogenetic relationships of the ectobiid subfamilies suffer from very limited taxon sampling, which is especially striking with regard to the speciose Blattellinae and Pseudophyllo-

dromiinae. Lack of inclusion in phylogenetic studies also concerns some taxa with aberrant life history, such as the minute myrmecophilous *Attaphila*, which was classified in a separate subfamily (Attaphilinae) by ROTH (2003a), but transferred to Blattellinae by DJERNÆS (2018).

Blattodea exhibit a huge variety of reproductive and other life history strategies as well as wide ranges of body size and wing development, and the Blaberoidea make the most significant contribution to this diversity. Cockroaches are found in a range of habitats from tropical forests over temperate heathlands to deserts, and they occur in a wide variety of microhabitats, e.g. leaf litter, soil, dead wood, ant nests, caves, or up in the canopy (BELL et al. 2007; LEGENDRE et al. 2014). Body size in cockroaches ranges from 2.5 mm to 78 mm, with both the largest and some of the smallest species belonging to Blaberoidea (GURNEY 1937, 1959). Wing reduction has occurred in many groups of cockroaches, and macropterous, brachypterous, and apterous species occur in all three superfamilies (Corydioidea, Blattoidea, and Blaberoidea). With regard to reproduction, three basic mating patterns are known in cockroaches (usually following initial courtship): A) The male raises his wings (if present), the female mounts the male, and the male engages the genitalia while underneath the female, moving backwards if necessary; the animals then assume an end-to-end position, in which mating is completed. B) The male mounts the female and engages the genitalia from this position before assuming the end-to-end position. C) No mounting is performed; the male and female engage genitalia directly end to end and remain in this position. All three patterns are known in Blaberoidea (SRENG 1993). Cockroaches employ several ways of handling their eggs, which are usually assembled in an ootheca: simply producing and depositing an ootheca (oviparity A); carrying the ootheca externally until the eggs hatch (oviparity B); carrying the ootheca internally until hatch (ovoviviparity A); not producing an ootheca and carrying the eggs internally until hatch (ovoviviparity B); and carrying a (thin-walled) ootheca internally, providing substantial nourishment to the developing embryos (viviparity). All five modes occur in Blaberoidea (BELL et al. 2007). Cockroaches also exhibit large variation in clutch size (number of eggs per ootheca), from 3 to 243 eggs, with both extremes occurring in Blaberoidea (ROTH 1995a; GRANDCOLAS & DELEPORTE 1998). Blaberoidea furthermore includes taxa with some other aberrant life history characteristics, such as the jumping *Saltoblattella* (BOHN et al. 2010), semiaquatic *Rhabdoblatta*, *Opisthoplatia*, and *Epilampra* species, *Perisphaerus* and *Pseudoglomeris* species rolling themselves up, and *Schultesia lampyridiformis* mimicking fireflies (BELL et al. 2007).

One aim of the present study is to produce a phylogeny of the higher taxa in Blaberoidea. Although it is by far not yet possible to sample the majority of its genera, we include a wide selection of genera. This will lead to significant progress in outlining principal lineages both in Blaberoidea and in Blaberidae and thus provide a much better estimate of the usefulness of the ectobiid and blab-

erid subfamilies as taxonomic units. Some of the sampled genera have not been included in previous phylogenetic studies; of these, we especially want to place the tiny myrmecophilous *Attaphila*. Additionally, we will use our phylogenetic results to map geographic distribution and examine evolutionary trends of and potential correlations between life history traits to improve evolutionary scenarios of Blaberoidea.

2. Materials and methods

2.1. Taxonomy

We generally follow the taxonomy of the Cockroach Species File (BECCALONI 2014). Yet, we will propose a few changes, mainly concerning the usage of names for subfamily and family level groupings of Blaberoidea outside Blaberidae. This needs some comments: In the Cockroach Species File, the four subfamilies Blattellinae, Ectobiinae, Nyctiborinae, and Pseudophyllodromiinae (alternatively called Plectopterinae) comprise the family Ectobiidae (alternatively called Blattellidae). (Attaphilinae is included in Blattellinae.) GRANDCOLAS (1996) ranked the four subfamilies as families: Blattellidae, Ectobiidae, Nyctiboridae, and Pseudophyllodromiidae, hence the same rank as Blaberidae. Therefore, 'Ectobiidae' and 'Blattellidae' both have a wider and a narrower meaning. To both taxon names we add 's.l.' when referring to the wider meaning and 's.s.' when referring to the narrower meaning (though 'Blattellidae s.l.' is not further used herein, as we call this grouping 'Ectobiidae s.l.'). In addition, we put Ectobiidae s.l., as it is most likely non-monophyletic, in double quotes or call this grouping 'non-blaberid Blaberoidea'. The authority and year for all named species included in the data set are given in Table S1.

2.2. Molecular data

The data set consists of partial sequences of seven genes: the mitochondrial 12S (~ 400 nucleotides = nt), 16S (~ 430 nt), and COI + COII [1] (~ 2030 nt, but most sequences ~ 740 nt or ~ 1600 nt), and the nuclear 18S (~ 1850 nt), 28S (~ 2200 nt, but most sequences ~ 610 nt), and H3 (~ 330 nt). The total length of the aligned data set is 9684 nt. Most of the included sequences are from Gen-Bank; the *Attaphila* sequences are new and were produced using standard methods (see DJERNÆS et al. 2015 for details).

The taxon sample consists of 99 ingroup taxa (Blaberoidea), 25 near outgroup taxa (other Dictyoptera), and 5 far outgroup taxa (other Polyneoptera) for a total of 129 taxa (Table S1). Selection of near outgroup taxa aimed to include three representatives for each of the other major dictyopteran lineages (Mantodea, Nocticolidae, Corydiidae, Blattidae, Lamproblattidae, Tryonicidae, and Cryptocercidae + Isoptera), but six for Anaplectidae (formerly in Blaberoidea, now in Blattoidea, see Introduction). The five polyneopteran taxa were used to root Dictyoptera.

The sequences were aligned in MAFFT 7.146b (KATOH et al. 2005; KATOH & STANDLEY 2013; http://mafft. cbrc.jp/alignment/server/) using the Q-INS-i algorithm, which considers secondary structure, except the H3 sequences, for which the G-INS-i algorithm was used due to the lack of secondary structure (COI+COII includes tRNA-leu, which has secondary structure). Based on preliminary alignments, parts of two sequences were excluded as they were unalignable, with no clear matches on GenBank: second segment (nt 470–1074) of *Dendroblatta* sp. FL-2014 28S (KF372442) and second segment (nt 463–1011) of *Isoldaia* sp. FL-2014 28S (KF372443). NJ trees were produced for each alignment to check for incorrectly identified GenBank sequences, but no misidentifications were evident on this basis. Some 28S and COI sequences were misaligned by MAFFT; these sequences were aligned in Mesquite v. 2.74 (MADDISON & MADDISON 2010) using the Pairwise Aligner tool: *Metoligotoma bidens* 28S was aligned against *Bacillus rossius* 28S; *Margattea nimbata* 28S against *Balta longicercata* 28S; *Cyrtonotula secunda* 28S, *C. tertia* 28S, and *Paranauphoeta pullata* 28S against *Gromphadorhina portentosa* 28S; *Chaeteessa valida* COI against *Mantoida schraderi* COI; *Calolampra* sp. BL40 COI against *Monastria* sp. FL-2014 COI; *Thanatophyllum akinetum* COI against *Schultesia lampyridiformis* COI. All alignments were checked visually and manual corrections were made. All characters in the alignments were included in the phylogenetic analyses (no excluded characters).

On the one hand, we used the entire ("***complete***") data set for analyses. However, as our taxon sampling approach produced a data set with large amounts of missing data, we also analysed a reduced ("***trimmed***") data set with data-deficient taxa removed. First, we defined the marker-related core of the data set by excluding those genes or gene regions with a particularly large proportion of missing data: **(1)** A small part of the included 16S fragment. **(2)** The part of the 28S fragment exceeding the ~ 610 nt fragment produced by INWARD et al. (2007) and DJERNÆS et al. (2012, 2015). **(3)** All parts of COI. The marker-related core thus contained the genes or gene regions with sequence data for more than 65% of the total included taxa: 12S (302 parsimony-informative characters = pic), most of 16S (294 pic), 18S (697 pic), part of 28S (272 pic), COII (462 pic), and H3 (127 pic), with a total of 2154 pic. Second, balancing the inclusion of taxa against gene(-region) coverage, we removed taxa whose sequence data covered less than 50% of the 2154 core pic (i.e. coverage calculated based on a pic-per-gene basis, not on a nucleotides-per-gene basis). This procedure resulted in the removal of 12 species from the complete

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[1] Including tRNA-Leu (between COI and COII) and parts of tRNA-Lys (3' end of COII).
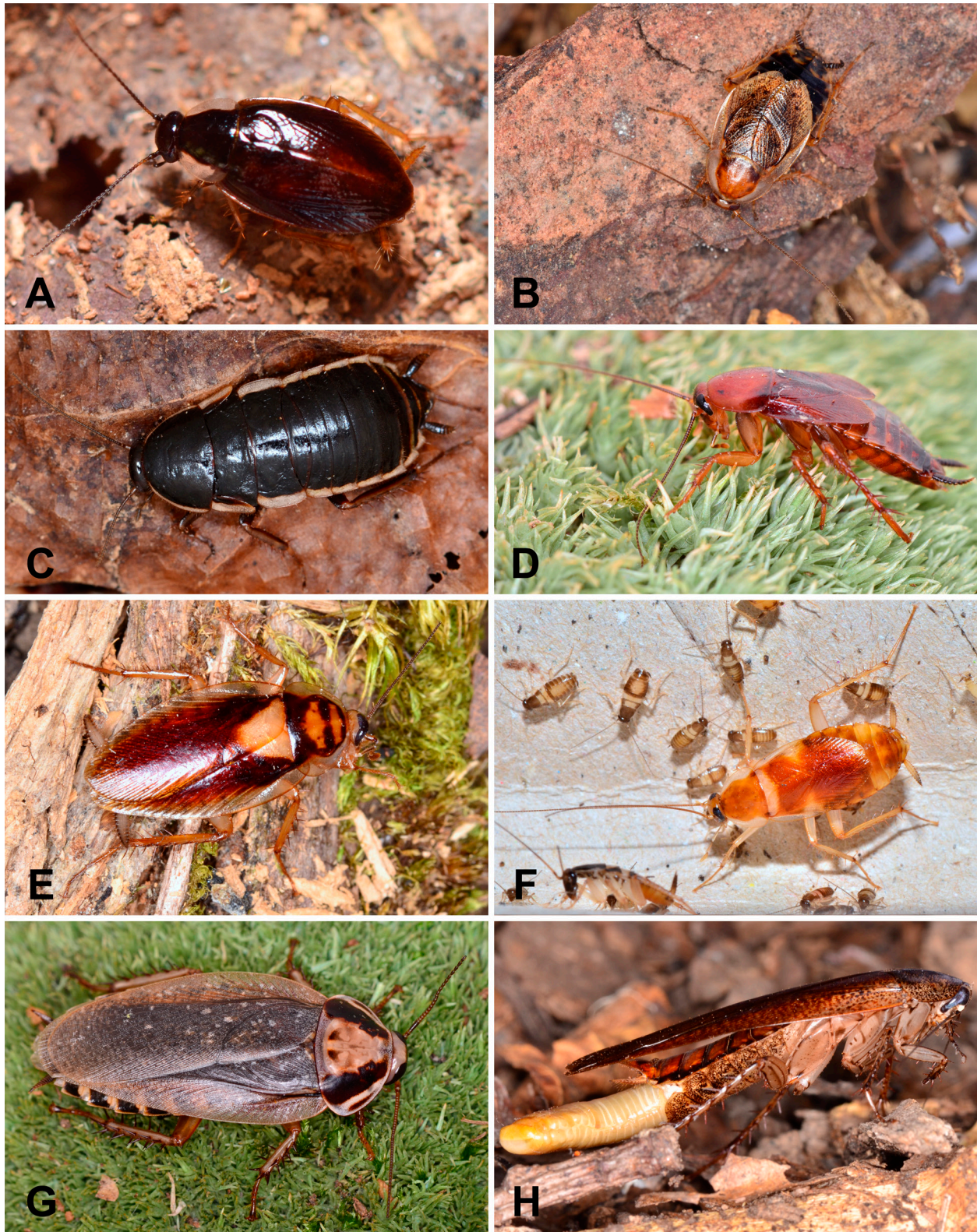
Fig. 1. Blaberoidea of various subgroups, and an Anaplectidae. **A**: *Anaplecta* sp. (Anaplectidae) female from Cameroon. **B**: *Ectobius* sp. (Ectobiidae s.s.) female from Croatia. **C**: *Loboptera decipiens* (Blattellidae s.s.) female from Croatia. **D**: *Paratemnopteryx couloniana* (Blattellidae s.s.) male from culture (original provenance unknown). **E**: *Dendroblatta* sp. (Pseudophyllodromiidae) female from French Guiana. **F**: *Supella longipalpa* (Pseudophyllodromiidae) female and larvae in loose aggregation from Greece. **G**: *Henschoutedenia flexivitta* (Blaberidae: Oxyhaloinae) male from Cameroon. **H**: *Epilampra* sp. (Blaberidae: Epilamprinae) female from French Guiana, retracting ootheca into brood sac. — (Sub-)family-level taxonomy following changes introduced herein. Photographs by Zuzana Kotyková Varadínová.

Fig. 2. Blaberoidea of various subgroups. **A**: *Gyna capucina* (Blaberidae: Gyninae) male (top) and female (bottom) from Cameroon. **B**: *Lanxoblatta emarginata* (Blaberidae: Zetoborinae) female from French Guiana. **C**: *Aptera fusca* (Blaberidae: Epilamprinae) female from South Africa, displaying brooding behaviour. **D**: *Bantua* sp. (Blaberidae: Perisphaerinae) female from South Africa. **E**: *Corydidarum pygmaea* (Blaberidae: Perisphaerinae) female from culture (original provenance unknown), displaying brooding behaviour. **F**: *Perisphaerus* sp. (Blaberidae: Perisphaerinae) male from the Philippines. **G**: *Paranauphoeta formosana* (Blaberidae: Paranauphoetinae) male from culture (original provenance unknown). **H**: *Panesthia angustipennis angustipennis* (Blaberidae: Panesthiinae) female (left) and larva (right) from the Philippines. — (Sub-)family-level taxonomy following changes introduced herein. Photographs by Zuzana Kotyková Varadínová.

data set to produce the trimmed data set: *Blattella bisignata*, *Parcoblatta pensylvanica*, *P. lata*, and *Saltoblattella montistabularis* ("Ectobiidae s.l.": Blattellinae); *Balta longicercata*, *Margattea nimbata*, *Isoldaia* sp. FL-2014, *Nahublattella fraterna*, and *N. nahua* ("Ectobiidae s.l.": Pseudophyllodromiinae); *Paranauphoeta pullata* (Blaberidae: Paranauphoetinae); *Cyrtonotula secunda* and *C. tertia* (Blaberidae: Epilamprinae). For the species included in the trimmed data set, we included all our available sequence data, except for *Dendroblatta* sp. FL-2014, see above. Running analyses on the trimmed data set allowed us to evaluate whether the overall tree structure and support values were influenced by the high proportion of missing data in the complete data set.

2.3. Data partitioning and phylogenetic analyses

The complete and trimmed data sets were analysed both unpartitioned and partitioned by gene, with tRNA-leu and tRNA-lys treated as a single partition (8 partitions: 12S, 16S, 18S, 28S, COI, COII, tRNAs, H3). We used PartitionFinder v.1.1.1 (LANFEAR et al. 2012) to choose a partitioning scheme and models (models limited to those available in MrBayes 3.1.2) with model selection based on AIC. PartitionFinder did not combine any partitions and recommended a GTR + G + I model for all partitions, which we used in all analyses.

Maximum likelihood (ML) analyses were run in Garli 2.01 (ZWICKL 2006) on Cipres XSEDE (MILLER et al. 2010) with 1 and 8 partitions for both the complete and the trimmed data set. When analysing 8 partitions, the model and the overall rate (subsetspecificrates) were unlinked across partitions. *Timema podura* was specified as outgroup to facilitate production of consensus trees. The analyses were set to terminate after 20,000 generations without significant change of topology, with 8 independent runs, from which a majority rule consensus tree was produced in Mesquite. Bootstrap analyses were run for each partitioning scheme with 100 bootstrap repetitions and 1 search repetition per bootstrap repetition, settings otherwise as above. Bootstrap values were calculated in Mesquite.

Bayesian inference (BI) analyses were run in MrBayes 3.2.2 (RONQUIST et al. 2012) on Cipres XSEDE. An unpartitioned analysis of the complete data set was run for 40 mio. generations sampled every 2000 generations, with burnin set to 5000 trees and burninfrac set to 25%, but did not quite reach convergence (average standard deviation of split frequencies 0.010656). This analysis had taken 163 hours (run on 8 parallel processors) and a longer run on Cipres XSEDE was thus not possible (maximum run lenght 168 hours). An unpartitioned analysis of the trimmed data set was run for 20 mio. generations, with burnin set to 5000 trees and burninfrac set to 25%. A partitioned analysis of the trimmed data set (8 partitions; statefreq, revmat, shape, and pinvar unlinked; ratepr allowed to vary) had not reached convergence af-

ter 60 mio. generations (average standard deviation of split frequencies 0.029539). This analysis had taken 143 hours (run on 8 parallel processors), and based on the likelihood (overlay) plot for the two runs, it would not be possible to reach convergence within the maximum of 168 hours allowed on Cipres XSEDE. Attempting to use MrBayes 3.2.2 Restart on XSEDE was not successful (huge fall in likelihood at restart point). A partitioned Bayesian analysis of the complete data set was not attempted. The various phylogenetic trees are shown in Figs. 3 and S2 – S7.

We tested the placement of *Attaphila* in Blattellinae in MrBayes using Bayes factors (KASS & RAFTERY 1995) by constraining Blattellinae excluding *Attaphila* as monophyletic. The test was performed on the trimmed, unpartitioned data set; apart from the constraint, the settings for the constrained analysis were identical to those for the unconstrained analysis. The Bayes factor was calculated based on the harmonic mean likelihoods from the constrained analysis relative to the unconstrained analysis.

2.4. Data collecting and definition of characters and states

2.4.1. Geographic distribution data

Data were collated from a number of sources. With the exception of widespread pest species, data for named species described prior to 1970 were taken from Princis' catalogue (PRINCIS 1962, 1963a, 1964, 1965, 1966, 1967, 1969, 1971), and data for named species described after 1970 were taken from original descriptions. Data for various unnamed species ('sp.' herein) were taken from DJERNÆS et al. (2012, 2015), DNA extraction data table from INWARD et al. (2007, data table unpublished) and original collecting data (*Attaphila* sp. A and sp. B). Distribution data for other 'sp.' species (*Latindia* sp., *Isoldaia* sp., *Dendroblatta* sp., *Monastria* sp., *Calolampra* sp., *Epilampra* sp., *Henschoutedenia* sp., Panesthiinae sp., *Laxta* sp., *Pseudoglomeris* sp., *Zetobora* sp.) for which we did not have access to locality data were taken from Cockroach Species File (BECCALONI, Nov. 2014) based on distribution of genus / subfamily. Distribution of widespread pest species (*Blatta orientalis*, *Blattella germanica*, *Symploce pallens*, *Supella longipalpa*, *Phoetalia pallida*, *Nauphoeta cinerea*, *Rhyparobia maderae*, *Pycnoscelus surinamensis*) was scored as inapplicable (Table S2).

Our definitions of biogeographic regions generally follow the definitions of World Wildlife Fund (OLSON et al. 2001), but we divided Palearctic in East and West (along the Ural Mountains), and included all of Mexico in the Neotropical region, all of China (unless more specific locality information was available) in East Palearctic, and the Oceanic region in Australasia. Thus we employ seven biogeographic regions: 1) Afrotropics, 2) West Palearctic, 3) East Palearctic, 4) Indo-Malayan,

5) Australasia, 6) Neotropics, and 7) Nearctic. These are used in the character mapping and the initial heuristic check for potential correlations (see 2.5. and 2.6.) as the seven states of the categorical character "geographic distribution". Species reported to occur in several regions are scored for all respective regions (except for the pest species, see above).

2.4.2. Body size data

Data were mainly extracted from the taxonomic literature, but some species were measured by the authors. References for each set of measurements are given in Table S3. When available, we included total body length (up to posterior tip of abdomen, excluding overhanging parts of wings and cerci) and pronotum length for both males and females; both measured distances are here subsumed as 'body size'. The measurements are based on either dried or alcohol preserved individuals. Based on the available data, the size values to be used in mapping and correlation analyses were determined in the following ways: **(1)** When only a single value was given for each measured distance (e.g. an average or only one individual measured), we used this value. **(2)** When a range of values was given (e.g. male body length 28.7−31.9 mm), we report the range and used its midpoint (here 30.3 mm), as an estimated average. **(3)** When several individual values or a mixture of individual values and ranges of values were given, we report a range including the largest and smallest value given, as well as an estimated average, which was then used (estimate reached by adding all individual values as well as upper- and lowermost values of a range, divided by the number of measured specimens). The estimated averages are also shown in Tables S3 and S4. The single values determined according to (1)−(3) represent the values of the quantitative characters 'body length' and 'pronotum length'; see 2.5. and 2.6. for scoring of character states for mapping and correlation analyses. When doing correlation analyses between various measured distances, we only included species for which data for all distances included in the relevant analysis were present and from the same source (e.g. if data for males and females of a particular species were from different sources, we did not use these data for correlation analyses between male and female size).

We calculated the average size difference between the sexes for all individual species as the ratio male body length / female body length, using the values obtained according to (1)−(3) above. Then we used the resulting values for the species **(1)** to calculate the average size difference for Blattodea as a whole and for selected subgroups; and **(2)** to calculate the percentage of species in Blattodea and selected subgroups for which females are larger than males.

2.4.3. Wing development data

Data are from original observations and from the literature; the source(s) for each species are given in Ta-

ble S4. Males and females of each species are categorised as 1) macropterous (tegmina and wings present and reaching at least to the end of the abdomen; Figs. 1A,E,G,H, 2A,B,F,G,H), 2) brachypterous (tegmina and wings present, but not reaching the end of the abdomen; Figs. 1B,C,D,F), or 3) apterous (tegmina and wings completely absent; Figs. 2C,D,E). These are used in the mapping and correlation analyses as the three states of the categorical character "wing development". There was no taxon with more than one of these states in one sex. Wing data for species only identified to genus are based on a selected substitute species or the general pattern in the genus (Table S4).

2.4.4. Microhabitat data

Data were mainly extracted from the literature; the source(s) for each species are given in Table S4. We scored 11 microhabitat categories: 1) Soil: burrowing in the soil. 2) Epigean: living in leaf litter or under stones. 3) Herbage: found on low herbaceous vegetation. 4) Dead wood: living in galleries in dead wood. 5) Loose bark: living under loose bark on dead or alive trees, standing or on the ground, or living under fallen dead trees. 6) Tree cortex: living on the surface of tree trunks (cortical). 7) Cavities: living in treeholes, crevices, or other types of holes. 8) Caves: living in caves (cavernicolous). 9) Canopy: living in the canopy on foliage or on/in epiphytes. 10) Insect nests: living in nests of social insects (inquiline). 11) Bird nests: living in bird nests (scored as 'unknown' due to Mesquite only allowing 10 discrete character states). These are used in the mapping and correlation analyses as the 11 states of the categorical character "microhabitat". Species reported to occur in several microhabitats are scored for all respective microhabitats for character mapping; the scoring for correlation analyses differs (see 2.6.).

2.4.5. Reproductive data

Data on mating pattern, egg/ootheca handling, and clutch size were mainly extracted from the literature; the sources for each species are given in Table S5, and an overview of the data at family/subfamily level in Table 1.

The ***mating pattern*** definitions follow SRENG (1993): 1) Type A: female mounts male. 2) Type B: male mounts female. 3) Type C: no mounting but direct end-to-end contact (see Introdution). These are used in the mapping and correlation analyses as the three states of the categorical character "mating pattern". There was no taxon with more than one of these states.

The ***egg/ootheca handling*** definitions follow BELL et al. (2007): 1) Oviparity A: ootheca dropped well before hatch, although it might be carried externally for several days prior to deposition. 2) Oviparity B: ootheca carried externally until hatch. 3) Ovoviviparity A: ootheca carried internally until hatch, without significant provision of nutrients from mother. 4) Ovoviviparity B: no ootheca, eggs carried internally until hatch, without significant

Table 1. Family/subfamily overview of data on mating type, reproductive mode and clutch size included in the present study. ***Mating type*** definitions follow SRENG (1993): Type A: female mounts male. Type B: male mounts female. Type C: no mounting, male and female simply make direct contact end to end. ***Reproductive mode*** definitions follow BELL et al. (2007: table 7.1): Oviparity A = OP-A: ootheca dropped well prior to hatch. Oviparity B = OP-B: ootheca carried externally until hatch. Ovoviviparity A = OVP-A: ootheca carried internally until hatch. Ovoviviparity B = OVP-B: no ootheca, eggs carried internally until hatch. Viviparity = VP: ootheca carried internally until hatch, eggs receive significant nutrients from mother during gestation. ***Clutch sizes*** are based on ranges of average/typical clutch sizes for included species; for instance, in Blattidae, the species with the smallest clutch size have an average of 14 eggs per ootheca, while the species with the largest clutch size have an average of 21 eggs. For some species, the clutch size is estimated based on the number of live hatchlings, see section 2.4.5.; in these cases the relevant reference is marked with *. See Tables S5 and S6 for data on individual species. The family/subfamily names and designations in this table do not reflect the taxonomic changes in the present paper. 'n.d.' indicates the lack of data. [1] Preserved females carrying mature, non-rotated ootheca observed in genus. [2] A single included species, *Temnopteryx phalerata*, produces 68 eggs per ootheca. [3] A single included species, *Paratropes bilunata*, exhibits either oviparity A or B. [4] A single included species, *Lucihormetica grossei*, exhibits either ovoviviparity or viviparity. [5] A single included species, *Aptera fusca*, exhibits either ovoviviparity A or B and produces 28 eggs per ootheca.

Family / Subfamily	Mating type	Reproductive mode	Clutch size	References (M: mating, R: reproductive mode, C: clutch size)
Nocticolidae	n.d.	OP-A	4	M. Robinson, pers. comm. to MD (R, C)
Corydiidae	A & C	OP-A	8−14	ROTH 1971 (C); LIVINGSTONE & RAMANI 1978 (M, R, C); FRITZSCHE 1996 (M, R); GRANDCOLAS 1997b (R, C)
Blattidae	A	OP-A	14−21	ROTH & WILLIS 1952 (M), 1954 (M, R, C), 1955a (R); WILLIS et al. 1958 (C); McKITTRICK 1964 (R); BARTH 1968b (M), 1970 (M); ROTH 1971 (C)
Lamproblattidae	n.d.	OP-A	16	McKITTRICK 1964 (R); LAWSON 1967 (C); ROTH 1968a (C)
Tryonicidae	n.d.	OP-A	14	GRANDCOLAS 1997c (R); GRANDCOLAS et al. 2002 (R, C)
Anaplectidae	n.d.	OP-B[1]	5−10	McKITTRICK 1964 (R); ROTH 1971 (C)
Cryptocercidae	A	OP-A	32	NALEPA 1988 (M, R, C)
Mastotermitidae	n.d.	OP-A	20	NALEPA & LENZ 2000 (R, C); GRIMALDI & ENGEL 2005 (C)
Ectobiidae				
Blattellinae	A	OP-A&B	11−44 (11−68)[2]	RAU 1947 (R, C); ROTH & WILLIS 1952 (M), 1954 (M), 1957a (M); EDMUNDS 1953 (R); POPE 1953 (R); WILLIS et al. 1958 (C); McKITTRICK 1964 (R); ROTH 1967b (R), 1968a (C), 1968c (R), 1971 (C); BARTH 1968c (M); WENDELKEN & BARTH 1971 (M); COCHRAN 1986 (R, C); GRANDCOLAS 1992a (R); APPEL et al. 1998 (C); TSAI & LEE 2001 (R; C*); HORN & HANULA 2002 (R); BOHN et al. 2010 (R, C); BUJANG & LEE 2010 (C); LAIDLER 2012 (R, C)
Pseudophyllodromiinae	A	OP-A	15−37	POPE 1953 (C); McKITTRICK 1964 (R); ROTH 1967b (R), 1968a (C), 1971 (C); WILLIS 1969 (C); 1970 (M); HALES & BREED 1983 (R); SHAKILA & BHOOPATHY 1996 (M); BOYER & RIVEAULT 2004 (R, C)
Ectobiinae	A	OP-A	11−17	BROWN 1952 (R, C); ROTH & WILLIS 1957b (M, R, C); McKITTRICK 1964 (R); ROTH 1968a (C); DREISIG 1971 (R); BROWN 1973a (R, C), b (R); PAYNE 1973 (M)
Nyctiborinae	A	OP-A[3]	24−38	McKITTRICK 1964 (R); BARTH 1968c (M); ROTH 1968a (C); DEANS & ROTH 2003 (R); ZV pers. obs (R, C)
Attaphilinae	n.d.	OP-A or B	6	ROTH 1995a (R, C)
Blaberidae				
Blaberinae	A	OVP-A[4]	24−34	ROTH & WILLIS 1957a (R); WILLIS et al. 1958 (C); BARTH 1964 (M); ROTH & BARTH 1967 (M); ROTH 1968a (R, C), c (M, R, C); GRILLOU 1973 (M); WENDELKEN & BARTH 1987 (M); GRANDCOLAS 1992b (R, C); VETTER & HINTZE-PODUFAL 1993 (M, R); HINTZE-PODUFAL & VETTER 1996 (R); PELLENS & GRANDCOLAS 2003 (R, C); FRITZSCHE 2003 (R, C*); GREVEN & ZWANZIG 2013 (M); ZV & MK pers. obs. (C)
Diplopterinae	A	VP	12	ROTH & WILLIS 1955 (M, R), ROTH & HAHN 1964 (C)
Epilamprinae	A & C	OVP-A[5]	50−77 (28−77)[5]	BARTH 1968c (M); BARTH in ROTH 1969 (M); ROTH 1970a (R); FISK & SCHAL 1981 (M, R, C); PICKER et al. 2004 (R, C*); ZHU & TANAKA 2004 (R, C*); NORIYUKI 2013 (C), 2014 (C)
Geoscapheinae	C	OVP-B	20	RUGG & ROSE 1984c (R), 1991 (M, R); WALKER & ROSE 1998 (R, C)
Gyninae	n.d.	OVP-A	62−128	GRANDCOLAS 1994 (C); GRANDCOLAS & DELEPORTE 1998 (R, C)
Oxyhaloinae	A & C	OVP-A	28−51	ROTH & WILLIS 1954 (R); WILLIS et al. 1958 (C); ENGELMANN 1962 (R); ROTH & BARTH 1967 (M); ROTH 1968a (R, C), c (R); ZIEGLER 1972 (M, R); FRASER & NELSON 1984 (M); SRENG 1984 (M), 1993 (M); P.E. Bragg, pers. comm. to MD (R); ZV & MK pers. obs. (R, C)
Panchlorinae	C	OVP-A	31−57	ROTH & WILLIS 1957a (M, R, C); WILLIS 1966 (M, R)
Panesthiinae	C	OVP-A	15−25	REDHEUIL 1973 in ROTH 1979a (M); ROTH 1979b (R); RUGG & ROSE 1984c (R, C); O'NEILL et al. 1987 (M); OBATA 1988 in MAEKAWA et al. 2008 (C); WALKER & ROSE 1998 (R, C); MAEKAWA et al. 2008 (R)
Perisphaerinae	n.d.	OVP-A	14−32	ROTH 1981 (R, C), 1992 (R, C); ZV & MK pers. obs. (R, C)
Pycnoscelinae	B	OVP-A	26	ROTH & WILLIS 1954 (R), 1957a (R); WILLIS et al. 1958 (C); ROTH & BARTH 1967 (M)
Zetoborinae	A	OVP-A&B	25−43	BARTH 1968c (M); ROTH 1968c (R, C), 1970a (R), 1973 (M, R, C); BARTH in ROTH 1969 (M); GRANDCOLAS 1991 (R, C), 1993b (R, C*); GRANDCOLAS & PELLENS 2002 (R); PELLENS et al. 2002 (C); MONCEAU & VAN BAAREN 2012 (M)
Paranauphoetinae	n.d.	n.d.	n.d.	−

provision of nutrients from mother. 5) Viviparity: eggs/ootheca carried internally until hatch, eggs receive significant amounts of nutrients from mother. These are used in the mapping and correlation analyses as the five states of the categorical character "egg/ootheca handling". There was no taxon with more than one of these states.

Clutch size refers to the number of eggs contained in one ootheca, or to the number of eggs simultaneously incubated in the brood sac (for the few Blaberidae that do not form an ootheca), or to the number of live larvae simultaneously associated with their mother (for some Blaberidae only this number is available). In the two former cases, numbers were directly taken as the clutch size. In the case of live larvae we assumed that the hatching percentage was 75% (based on studies on hatching percentage in Blaberidae: WILLIS et al. 1958; PELLENS & GRANDCOLAS 2003) and extrapolated the number of eggs accordingly. Number of eggs or live larvae per clutch are given as in the source literature in Table S6, i.e. either as a single number (can represent a single observation or a typical or average number), or as several numbers (from several individual observations), or as a range, or any combination of these. For some species, egg numbers were estimated by M. Djernæs based on published pictures of oothecae (primarily in ROTH 1968a, 1971; the number of egg chambers is usually visible from the relief of the ootheca). For calculating statistical correlations between quantitative characters, we needed a single number denoting clutch size for each relevant species. When a single number was supplied, we used this. When several numbers or a range were supplied, M. Djernæs estimated the typical egg number for the species. The single numbers represent the values of the quantitative character "clutch size", see 2.5. and 2.6. for scoring of character states for mapping and correlation analyses.

2.5. Character mapping

We used a tree primarily based on the majority rule consensus tree from the partitioned maximum likelihood analysis of the trimmed data set (ML-T-P, Fig. 3). Sampled taxa not included in the trimmed data set were added to the ML-T-P tree according to their placement relative to neighbouring taxa in the partitioned maximum likelihood analysis of the complete data set (ML-C-P, Fig. S4).

We mapped the following characters in Mesquite 3.03 (build 702; MADDISON & MADDISON 2015): the categorical characters geographic distribution, wing development (separately for males and females), microhabitat, mating pattern, and egg/ootheca handling; the quantitative characters of body size (body and pronotum length, each separately for males and females) and clutch size. In the few cases in which it was impossible to find data for the exact species included in the phylogenetic analyses (especially the various "sp.") , we used data available for a congener.

In the quantitative characters referring to body size and clutch size, we divided the range of occurring values into a limited number of discrete character states by defining intervals with 50% numerical increase within each interval. The intervals are as follows: Body length (in mm): 2.0–2.9, 2.9–4.4, 4.4–6.6, 6.6–10.0, 10.0–15.0, 15.0–22.5, 22.5–33.8, 33.8–50.6, 50.6–75.9. Pronotum length (in mm): 0.7–1.0, 1.0–1.5, 1.5–2.3, 2.3–3.4,

3.4–5.1, 5.1–7.6, 7.6–11.4, 11.4–17.1, 17.1–25.6. Clutch size: 3–4, 5–6, 7–10, 10–15, 15–22, 23–34, 35–50, 51–75, 76–113, 114–170. If a species has a value defining the boundary between two intervals, e.g. 15 eggs per ootheca, it is scored for both intervals bracketing the boundary.

We treated categorical characters as unordered and quantitative characters (with the defined discrete states) as ordered and reconstructed ancestral states for all nodes using parsimony.

2.6. Correlation analyses

Due to the size of the data set, the mirror tree function in Mesquite did not work to compare the distribution of states of different characters over the mapping trees. Instead, we compared identical trees with different characters mapped pairwise (using two identical files), the trees set up to mirror each other (one tree oriented Right, and the other Left). We used the mirrored trees as a heuristic visual method to look for correlations between characters. Potential correlations were tested for significance in Mesquite using either PAGEL's (1994) correlation test (part of the Correl Package; MIDFORD & MADDISON 2015) or the PDAP Package v. 1.16 (MIDFORD et al. 2010). We used PAGEL's (1994) correlation test if one or both characters in a potential correlation were categorical, e.g. microhabitat (categorical) and female body length (quantitative). We used PDAP:PDTREE if both characters in a potential correlation were quantitative, e.g. female body length and clutch size. In each correlation test, we only included species for which we had data for both of the characters examined for correlation. In the few cases in which it was impossible to find data for the exact species included in the phylogenetic analyses (especially the various "sp."), we used data available for a congener (see 2.5.). Sometimes different congeners were used with regard to different characters, e.g. *Xestoblatta* sp. 1 was replaced with *X. agautierae* Grandcolas, 1992 in the analyses of correlation between body length (both male and female) and microhabitat, but with *X. festae* (Griffini, 1896) in the analyses of correlation between female body length and clutch size. Due to their unstable placement in the tree, both *Nahublattella* species were excluded from the correlation analyses.

PAGEL's (1994) correlation test only works for binary characters, thus multistate characters involved in potential correlations had to be converted to binary characters, e.g. microhabitat with states non-epigean (0) versus epigean (1), or female body length with states not 5–20 mm (not medium sized) (0) versus 5–20 mm (medium sized) (1). The intervals here created by dividing ranges into discrete states in quantitative characters are independent, and different, from those in character mapping. Furthermore, PAGEL's (1994) correlation test cannot handle the occurrence of more than one scoring per character and taxon, e.g. microhabitat both epigean and non-epigean, while we have several such polymorphic scorings for

Table 2. Results of correlation analyses (PDAP) between different measures of body size, between male and female body size, and between female body size and number of eggs per ootheca. See section 2.6. for details about the analyses and trees. In first column, F = female, M = Male. 'n.s.' indicates that no significant correlation was found. * indicates that these values should be treated with caution as the tree showed a significant lack of fit ($P < 0.005$) to the M / F data (screens 1+2 in PDAP Package), but none of the other tested branch lengths (see section 2.6) provided a better fit to the data.

Correlation between	Tree 1		Tree 2	
	Probability	Coefficient of determination	Probability	Coefficient of determination
F pronotum length **vs** F body length	$P = 0.0$	$R^2 = 0.860$	$P = 0.0$	$R^2 = 0.862$
F pronotum length / F body length **vs** F body length	n.s.	$R^2 = 0.013$	n.s.	$R^2 = 0.013$
M pronotum length **vs** M body length	$P = 0.0$	$R^2 = 0.828$	$P = 0.0$	$R^2 = 0.830$
M pronotum length / M body length **vs** M body length	n.s.	$R^2 < 0.001$	n.s.	$R^2 < 0.001$
M body length **vs** F body length	$P = 0.0$	$R^2 = 0.909$	$P = 0.0$	$R^2 = 0.906$
M body length / F body length **vs** F body length	n.s.	$R^2 = 0.011$	n.s.	$R^2 = 0.009$
M pronotum length **vs** F pronotum length	$P = 0.0$	$R^2 = 0.934$	$P = 0.0$	$R^2 = 0.934$
M pronotum length / F pronotum length **vs** F pronotum length	n.s.*	$R^2 = 0.002$*	n.s.*	$R^2 = 0.002$*
Eggs per ootheca **vs** F body length	$P < 0.001$	$R^2 = 0.272$	$P < 0.001$	$R^2 = 0.269$
Eggs per ootheca / F body length **vs** F body length	$P < 0.001$	$R^2 = 0.224$	$P < 0.001$	$R^2 = 0.229$
Eggs per ootheca **vs** F pronotum length	$P < 0.001$	$R^2 = 0.295$	$P < 0.001$	$R^2 = 0.288$
Eggs per ootheca / F pronotum length **vs** F pronotum length	$P < 0.001$	$R^2 = 0.243$	$P < 0.001$	$R^2 = 0.254$

microhabitat (see 2.4.4.). When converting this character to a series of binary characters, we scored all species showing e.g. the state "epigean" as epigean, even if they also occur in other microhabitats. In each correlation test, we used 1000 simulations with 10 iterations each. When we obtained a *P*-value between 0.04 and 0.06, or when > 75% of the simulation sets included constant characters (as defined by the software), we used 10000 simulations. The tree used for Pagel's correlation test was the same as that used for mapping, but with *Nahublattella* removed, and with *Saltoblattella* + *Ectobius* + Pseudophyllodromiinae placed as sister to Blaberidae (without *Nahublattella* the polytomy at the base of Blaberoidea was resolved according to results from the partitioned maximum likelihood analysis of the trimmed data set). Each analysis was run twice, once using branch lengths based on the actual branch lengths from the partitioned maximum likelihood analysis of the complete data set, and once with all branch lengths equal to 'one'.

We used PDAP to calculate correlations between various measures of body size (body length and pronotum length) in males and females and between female body size measures and clutch size. We report the *P*-value for Pearson product-moment correlation coefficient and the *R*²-value for least-squares regression (chart 9). All measurement values were log10 transformed for these correlation analyses. Prior to log transformation, pronotum length was increased by a factor 10. The log10 values were rounded to three decimal places. We investigated sexual size dimorphism using log (male size / female size) versus log female size (both body length and pronotum length). We investigated relative pronotum length using log (pronotum length / body length) versus log body length. We investigated relative clutch size using log (clutch size / female body size) versus log female body size. See Table 2 for all correlations tested using PDAP. The tree used for the PDAP correlation tests was primarily based on the tree used for mapping, but with

Nahublattella removed. However, when using phylogenetically independent contrasts as in PDAP, polytomies reduce the number of degrees of freedom in the analyses, which is otherwise determined by the number of species (data points) in the tree (GARLAND 2006). One approach is to run the correlation tests using different topologies (resolving polytomies in different ways), which we did. In Blaberidae, our mapping tree (see Fig. 5) included a polytomy at the base of clade **c24** involving *Thanatophyllum*, *Diploptera*, *Epilampra*, *Gyna*, and the large clades **c27** and **c35**. We resolved this polytomy in two different ways based on the results from our analyses, shown in Figs. S3 and S6: **(1)** (*Thanatophyllym* + **c27**) + **c35** and *Diploptera* + (*Epilampra* + *Gyna*) [as in analyses ML-T-unP and ML-C-unP] resulting in Tree 1. **(2)** (*Gyna* + **c27**) + **c35** and *Epilampra* + (*Diploptera* + *Thanatophyllym*) [as in analysis BI-T-P and partially supported by analyses ML-T-P and BI-T-unP] resulting in Tree 2. We set all branch lengths equal to 'one', which according to the diagnostics included in PDAP (screens 1+2) provides the best overall fit to the tip data. Other sets of branch lengths tested included: branch lengths based on the actual branch lengths from the partitioned maximum likelihood analysis of the complete data set; actual branch lengths with exponential transform: actual branch lengths logN transformed; branch length method of Nee; branch length method of Nee with exponential transform; branch length method of Grafen; and tree arbitrarily ultrametric.

3. Results and discussion

3.1. Results of phylogenetic analyses

The analyses of the trimmed data set generally provided better resolution and higher support values. We consider these analyses more reliable based on their lower pro-

portion of missing data compared to the analyses with the complete data set. The seven trees resulting from the various possible combinations of **(1)** maximum likelihood (ML) vs. Bayesian inference (BI), **(2)** trimmed (T) vs. complete (C) data set, and **(3)** partitioned (P) vs. unpartitioned (unP) data are shown in Figs. 3 and S2–S7; an overview consensus tree of the results is given in Fig. 4. A partitioned Bayesian analysis of the complete data set was not attempted due to computational constraints (see 2.3.). In the following, we abbreviate the analyses and trees by concatenating the abbreviations given above (e.g. the unpartitioned maximum likelihood analysis of the trimmed data set is abbreviated ML-T-unP). The support values for selected clades in these trees are listed in Table 3; we abbreviate support values as bs (= bootstrap support) and pp (= posterior probability). To avoid repetitions of long strings of taxonomic names and to provide easier cross-reference to the trees, we address clades of interest as "c + number" (e.g. clade **c08**), the sequence of numbering is arbitrary. The clade IDs are included in Fig. 5 and Table 3. We call the presence of a clade 'uncontested' if no analysis showed a grouping contradictory to it, while the clade may be absent in some analyses due to lack of resolution (i.e. its subclades having separate origins from a polytomy). The seven trees are largely identical, although the same clades can have very different levels of support. Most differences among the trees concern the resolution of a few specific nodes and disjunct placements of a few "rogue taxa".

3.1.1. Relationships in Blaberoidea

Blaberoidea (*sensu* Djernæs et al. 2015, i.e. excl. Anaplectidae), clade **c03**, appeared as monophyletic in all our analyses (bs 55–76, pp 58–100). All our analyses excluded Anaplectidae (represented by species of *Anaplecta*, see Fig. 1A) from Blaberoidea and placed it in a strongly supported Blattoidea (**c01**; bs 88–96, pp 100). There it appeared in a clade with Tryonicidae and Lamproblattidae, and this clade (**c02**) was sister to Cryptocercidae + Isoptera; support values were low to moderate for these relationships (**c02**; bs < 50–52, pp 96–100).

Within Blaberoidea, our analyses yielded five more or less stable principal clades of varied inclusiveness, which roughly corresponded to taxonomic units: **c16** (Blaberidae), **c06** (Blattelline incl. *Attaphila*), **c14** (Pseudophyllodromiinae excl. *Nahublattella*), **c12** (Ectobiinae + *Saltoblattella*), **c05** (Nyctiborinae). The relationships between these clades were not clearly resolved.
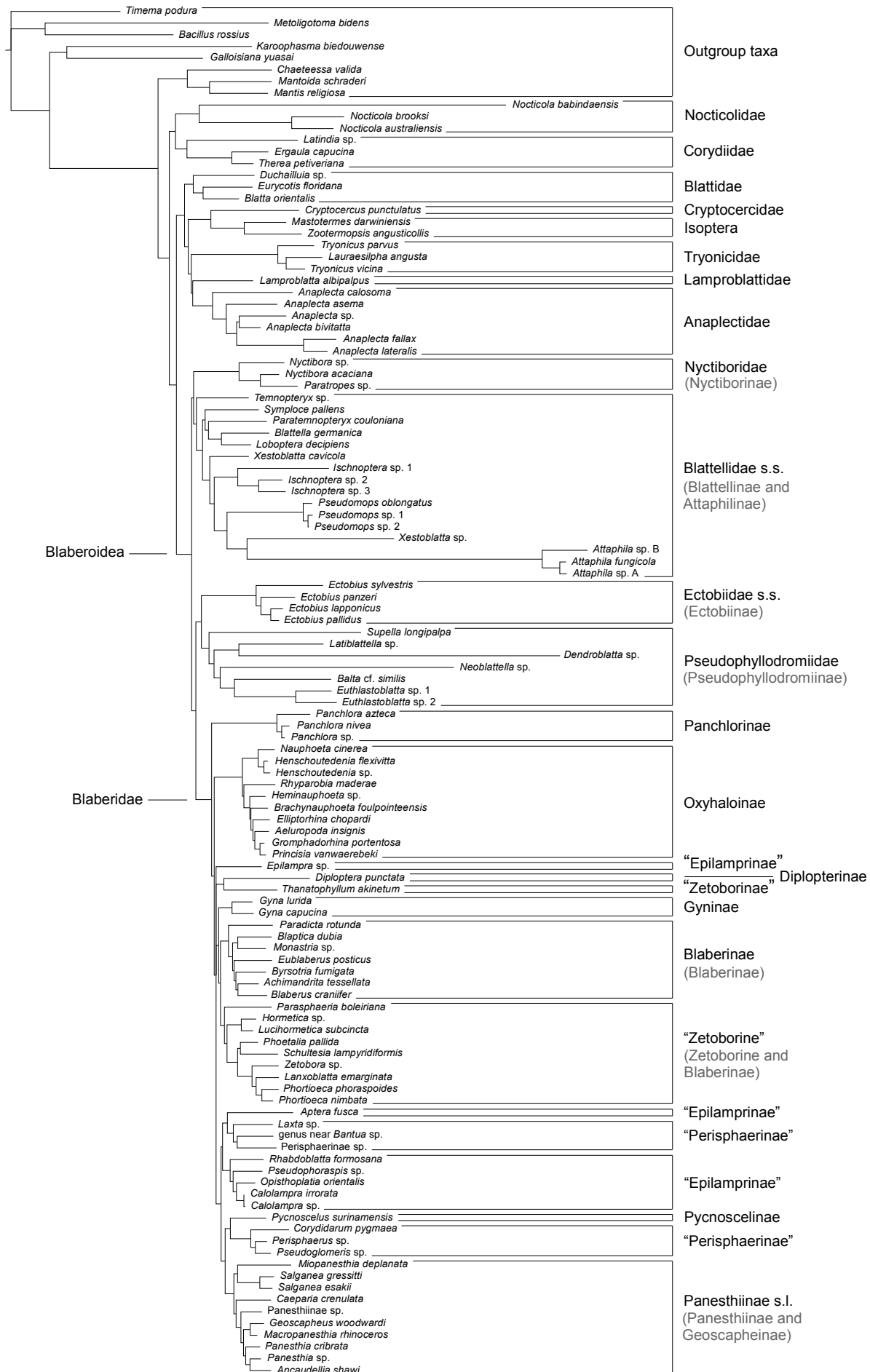
The largest principal clade was the strongly supported and consistently obtained clade **c16** (bs 81–100, pp 100), which included all sampled Blaberidae (Figs. 1G,H, 2). Relationships within Blaberidae are detailed below (see 3.1.2.). Another very strongly supported principal (but small) clade is **c05** (bs 100, pp 100 in all analyses), comprised of *Nyctibora* and *Paratropes*, our sampled Nyctiborinae. The third principal clade was the small **c12**, which combined *Saltoblattella* (only included in complete data set) and *Ectobius* (Fig. 1B), but only

with moderate support (bs < 50, pp 90 in analyses ML-C-P, BI-C-unP). This clade was not consistently found, as analysis ML-C-unP placed *Saltoblattella* in a contradictory deep clade together with the pseudophyllodromiines *Neoblattella* and *Nahublattella* (bs < 50). This is likely to involve some artefact (such as long branch attraction, see below for *Neoblattella*). The three sampled *Ectobius* species always formed a strongly supported subclade (**c13**; bs 100, pp 100).

Support was fairly low for the fourth principal clade **c06** (bs < 50, pp 67–99), which included all sampled Blattellinae (Fig. 1C,D) and *Attaphila* (Attaphilinae), whereas support was stronger for the uncontested clade **c07** (bs < 50–78, pp 83–100), which differs from **c06** only by exclusion of *Temnopteryx*. *Temnopteryx* was in most analyses obtained as the sister group of the core blattelline clade **c07**; but in analysis ML-C-unP it was sister to the nyctiborine clade **c05** (bs < 50), and in ML-C-P it originated separately from a polytomy at the base of Blaberoidea. The genus appears to be an early offshoot of the blattelline clade with limited affinity to other Blattellinae. Clade **c09** (bs < 50–65, pp 75–97) comprised *Attaphila*, *Xestoblatta* sp., *Pseudomops*, and *Ischnoptera*. Within **c09**, *Attaphila* + *Xestoblatta* sp. + *Pseudomops* (**c10**; bs < 50–71, pp 74–100) appeared in all trees, usually with *Xestoblatta* sp. as sister to *Attaphila*. *Xestoblatta cavicola* was variously associated with either **c09** or the other major blattelline subclade (**c08**), but always separated from *Xestoblatta* sp., the genus thus appearing polyphyletic. We tested the placement of *Attaphila* within the blattelline clade **c06** using Bayes factors by constraining "Blattellinae" as monophyletic, and obtained a Bayes factor of 34 in favour of the unconstrained analysis, a highly significant difference (Kass & Rafferty 1995).

Support was also fairly low for the fifth principal clade **c14** (bs < 50, pp 56–72), which included all sampled Pseudophyllodromiinae (Fig. 1E,F) except *Nahublattella*, and for a clade **c15** (bs < 50, pp 64–90), which differs from **c14** only by exclusion of *Neoblattella*. Either **c14**, **c15**, or both (*Neoblattella* sister to remaining pseudophyllodromiines in BI-T-unP) were present in all analyses. We consider it plausible that either clade **c14** or **c15** is reliable, and that the weak support for both was an effect of *Neoblattella* (a long branch) weakening support of **c14** when placed deeply inside it (mostly with a consistent position) and weakening support of **c15** when placed outside of it (either as its sister or disjunct). *Supella* (Fig. 1F) appeared in different positions in the pseudophyllodromiine clade.

The worst case of unstable placement in "Ectobiidae s.l." was the pseudophyllodromiine *Nahublattella*, which due to the availability of only 12S and 16S could only be included in the complete data set (in Table 3 its position is indicated by the superscript 'Na'). It was never associated with the pseudophyllodromiine clade **c14** (nor **c15**), but was either found in a clade with *Saltoblattella* and *Neoblattella* (analysis ML-C-unP; see above), or subordinate in the blattelline clade **c06** (BI-C-unP; see above), or it arose from a polytomy at the base of Blaberoidea (ML-C-P).

Timema podura
Metoligotoma bidens
Bacillus rossius
Karoophasma biedouwense
Galloisiana yuasai
Chaeteessa valida
Mantoida schraderi
Mantis religiosa

Outgroup taxa

Nocticola babindaensis
Nocticola brooksi
Nocticola australiensis

Nocticolidae

Latindia sp.
Ergaula capucina
Therea petiveriana

Corydiidae

Duchailluia sp.
Eurycotis floridana
Blatta orientalis

Blattidae

Cryptocercus punctulatus

Cryptocercidae

Mastotermes darwiniensis
Zootermopsis angusticollis

Isoptera

Tryonicus parvus
Lauraesilpha angusta
Tryonicus vicina

Tryonicidae

Lamproblatta albipalpus

Lamproblattidae

Anaplecta calosoma
Anaplecta asema
Anaplecta sp.
Anaplecta bivitatta
Anaplecta fallax
Anaplecta lateralis

Anaplectidae

Nyctibora sp.
Nyctibora acaciana
Paratropes sp.

Nyctiboridae
(Nyctiborinae)

Temnopteryx sp.
Symploce pallens
Paratemnopteryx couloniana
Blattella germanica
Loboptera decipiens
Xestoblatta cavicola
Ischnoptera sp. 1
Ischnoptera sp. 2
Ischnoptera sp. 3
Pseudomops oblongatus
Pseudomops sp. 1
Pseudomops sp. 2
Xestoblatta sp.
Attaphila sp. B
Attaphila fungicola
Attaphila sp. A

Blattellidae s.s.
(Blattellinae and Attaphilinae)

Blaberoidea

Ectobius sylvestris
Ectobius panzeri
Ectobius lapponicus
Ectobius pallidus

Ectobiidae s.s.
(Ectobiinae)

Supella longipalpa
Latiblattella sp.
Dendroblatta sp.
Neoblattella sp.
Balta cf. *similis*
Euthlastoblatta sp. 1
Euthlastoblatta sp. 2

Pseudophyllodromiidae
(Pseudophyllodromiinae)

Panchlora azteca
Panchlora nivea
Panchlora sp.

Panchlorinae

Nauphoeta cinerea
Henschoutedenia flexivitta
Henschoutedenia sp.
Rhyparobia maderae
Heminauphoeta sp.
Brachynauphoeta foulpointeensis
Elliptorhina chopardi
Aeluropoda insignis
Gromphadorhina portentosa
Princisia vanwaerebeki

Oxyhaloinae

Blaberidae

Epilampra sp.

"Epilamprinae"

Diploptera punctata
Thanatophyllum akinetum

Diplopterinae

"Zetoborinae"

Gyna lurida
Gyna capucina

Gyninae

Paradicta rotunda
Blaptica dubia
Monastria sp.
Eublaberus posticus
Byrsotria fumigata
Achimandrita tessellata
Blaberus craniifer

Blaberinae
(Blaberinae)

Parasphaeria boleiriana
Hormetica sp.
Lucihormetica subcincta
Phoetalia pallida
Schultesia lampyridiformis
Zetobora sp.
Lanxoblatta emarginata
Phortioeca phoraspoides
Phortioeca nimbata

"Zetoborine"
(Zetoborine and Blaberinae)

Aptera fusca

"Epilamprinae"

Laxta sp.
genus near *Bantua* sp.
Perisphaerinae sp.

"Perisphaerinae"

Rhabdoblatta formosana
Pseudophoraspis sp.
Opisthoplatia orientalis
Calolampra irrorata
Calolampra sp.

"Epilamprinae"

Pycnoscelus surinamensis

Pycnoscelinae

Corydidarum pygmaea
Perisphaerus sp.
Pseudoglomeris sp.

"Perisphaerinae"

Miopanesthia deplanata
Salganea gressitti
Salganea esakii
Caeparia crenulata
Panesthiinae sp.
Geoscapheus woodwardi
Macropanesthia rhinoceros
Panesthia cribrata
Panesthia sp.
Ancaudellia shawi

Panesthiinae s.l.
(Panesthiinae and Geoscapheinae)

The relationships among the blaberid (**c16**), pseudo-phyllodromiine (**c14**), ectobiine (**c12**), blattelline (**c06**), and nyctiborine (**c05**) principal clades (and *Nahublattella*) were less clear. Yet, our trimmed analyses consistently placed the ectobiine **c12** and the pseudophyllodromiine **c14** as sister groups (clade **c11**; bs < 50, pp 56−79), and the blattelline **c06** and the nyctiborine **c05** (clade **c04**; bs < 50, pp 75−95) as sister groups.

3.1.2. Relationships in Blaberidae

The trees had a consistent underlying phylogenetic structure for Blaberidae (**c16**), see Fig. 4; the deep relationships appeared clearer than for the base of Blaberoidea, although support values were mostly low (**c18**, **c24**, **c35**, **c36**, **c41**; bs ≤ 51, pp 51−100, see Table 3).

We found a basalmost dichotomy between our sampled panchlorines (**c17**, only represented by 3 Neotropical *Panchlora* species; bs 100, pp 100) and all other Blaberidae (**c18**; bs ≤ 51, pp 100) in all our analyses, albeit with only moderate support. The following dichotomy separated a strongly supported, purely Afrotropical clade (**c19**; bs 99−100, pp 100) that included all sampled oxyhaloines (Fig. 1G) from the remaining Blaberidae (**c24**; bs < 50, pp 58−93) – with the exception of analysis BI-T-unP (see below).

Blaberidae excluding the panchlorine and oxyhaloine clades (clade **c24**) fell into two large and one small subclade and three single terminal taxa with ambiguously resolved relationships. One large subclade was the almost exclusively Neotropical **c27** including all blaberines and most zetoborines (bs < 50−67, pp 99−100, absent only in analysis BI-C-unP due to lack of resolution). The other large subclade was the predominantly Indo-Malayan clade **c35** (bs < 50, pp 67−100, absent only in analysis ML-C-P due to lack of resolution), which included all sampled Panesthiinae, Geoscapheinae, Perisphaerinae, Pycnoscelinae, and Paranauphoetinae, as well as Epilamprinae with the sole exception of *Epilampra*. The small subclade **c26** (bs 100, pp 100) included the two sampled Gyninae (Afrotropical *Gyna* species, Fig. 2A). The three singletons are our sole sampled *Epilampra* (Fig. 1H), *Diploptera punctata* (our sole sampled Diplopterinae), and the zetoborine *Thanatophyllum*. The relationships among these three clades and three singletons within **c24** are conflicting. Four analyses (ML-T-P, ML-C-P, BI-T-unP, BI-T-P) showed a *Diploptera + Thanatophyllum* clade (**c25**; bs < 50, pp 98); *Epilampra* was partly sister to this clade (BI-T-P and BI-T-unP, pp 77−99), and Gyninae (**c26**) was often sister to the Blaberinae + Zetoborinae clade **c27** (ML-T-P, BI-T-P, and BI-T-unP, bs < 50, pp 98−100). In other analyses, *Thanatophyllum* either

clustered with clade **c27** (ML-T-unP, ML-C-unP) forming **c28** (bs < 50) or was close to the other Zetoborinae sampled herein (BI-C-unP, **c32**; pp 59). However, these placements of *Thanatophyllum* were poorly supported. In the latter three analyses, *Diploptera* formed a poorly supported clade together with *Epilampra* and *Gyna* (bs < 50, pp 74), which was placed as sister to the rest of clade **c24** (ML-T-unP, ML-C-unP) or in a polytomy (BI-C-unP). Due to this situation, we consider the base of **c24** as an unresolved polytomy of *Epilampra*, *Gyna*, *Diploptera*, *Thanatophyllum*, and the large clades **c27** and **c35**.

The large Neotropical Blaberinae + Zetoborinae clade **c27** fell into two subclades that were yielded consistently; one comprised only blaberines (**c29**; bs 98−100, pp 99−100), and one comprised both zetoborines and some blaberines (**c31**; bs < 50−68, pp 84−100). The zetoborine *Thanatophyllum* was in some trees sister either to the whole **c27** or to its zetoborine-dominated subclade **c31** (see above).

The very inclusive, predominantly Indo-Malayan clade **c35** mostly had low support, but was present in all trees, except in ML-C-P due to lack of resolution. It consisted of two subclades (**c36** and **c41**) that were again poorly supported, but uncontested – except that one taxon, the epilamprine *Aptera* (Fig. 2C), jumped between the two clades (in Table 3 its presence in a clade is indicated by the superscript '+Ap'). Clade **c36** comprised all respective Epilamprinae (except *Epilampra* and sometimes *Aptera*, see above) and part of the Perisphaerinae (bs < 50, pp 84, absent in analyses ML-C-P, BI-T-P, and BI-C-unP due to lack of resolution); clade **c41** comprised all Panesthiinae, Geoscaphaeinae, Paranauphoetinae, and Pycnoscelinae as well as the remaining Perisphaerinae and sometimes *Aptera* (bs < 50, pp 51−88, retrieved in all analyses).

Clade **c36** was further divided in two consistently retrieved subclades. One of these, **c37**, was purely epilamprine (with *Rhabdoblatta*, *Pseudophoraspis*, *Opisthoplatia*, *Calolampra*, and *Cyrtonotula*, the latter only included in the complete data set). Support for this clade was low when *Cyrtonotula* was included (bs < 50, pp < 50), but clade **c38** (identical to **c37** but for the exclusion of *Cyrtonotula*) was very strongly supported (bs 95−100, pp 100). The other subclade, **c40**, was either purely perisphaerine (*Laxta*, genus near *Bantua* sp., see *Bantua* in Fig. 2D, and Perisphaerinae sp.) or additionally included *Aptera* (analyses ML-T-P and ML-C-P) as its basalmost branch. Support for **c40** was low (bs < 50, pp 60−93), but *Laxta* + genus near *Bantua* sp. + Perisphaerinae sp. appeared in all analyses.

Clade **c41** was further divided in two almost consistently obtained subclades. The first subclade (**c42**; bs < 50, pp 83−84) was composed of *Paranauphoeta*

Table 3. Clade support for relevant clades found in the various analyses (partly formal taxonomic units at superfamily, family or subfamily level). The clade numbers are included in Fig. 5; a clade placed in parentheses has no direct equivalent in this tree, but the approximate position is indicated. — *Analyses*: ML-T-unP: Maximum Likelihood, trimmed data set, data unpartitioned (Fig. S2). ML-T-P: Maximum Likelihood, trimmed data set, data partitioned (Fig. 3). ML-C-unP: Maximum Likelihood, complete data set, data unpartitioned (Fig. S3). ML-C-P: Maximum Likelihood, complete data set, data partitioned (Fig. S4). BI-T-unP: Bayesian inference, trimmed data set, data unpartitioned (Fig. S5). BI-T-P: Bayesian inference, trimmed data set, data partitioned (Fig. S6). BI-C-unP: Bayesian inference, complete data set, data unpartitioned (Fig. S7). [1] Analysis did not converge within the available time (average standard deviation of split frequencies 0.029539). [2] Analysis did not quite converge within the available time (average standard deviation of split frequencies 0.010656). — *Clades and support values*: Presence of a clade in a particular analysis with a support value of ≥ 50 is indicated by a support value: bootstrap value (bs) for maximum likelihood analyses and posterior probability (pp) for Bayesian inference analyses; presence of a clade in a particular ML analysis with a bs < 50 is indicated by ++. If a 'rogue taxon' is included in addition to the specification of the clade, the abbreviation of the taxon is added to the support value or the ++ as a superscript preceded by '+' ([+Na] = *Nahublattella*; [+Ne] = *Neoblattella*; [+Xec] = *Xestoblatta cavicola*; [+Ap] = *Aptera*); relevant absence of a rogue taxon in a clade is indicated by the same superscript preceded by '−'. Absence of a clade in an analysis, due to lack of resolution or contradictory placement, is indicated by a '*'. Taxa written in grey were not included in the trimmed data set, thus only have to be considered as part of a specified clade in the analyses whose columns are shown grey; lacking evidence with regard to a clade in a trimmed analysis (as a defining component of the clade is missing after trimming) is indicated by 'na' (not applicable). — *Parts of blaberid subfamilies*: Blaberinae (pars1): *Paradicta*, *Blaptica*, *Monastria*, *Eublaberus*, *Byrsotria*, *Archimandrita*, *Blaberus*; Blaberinae (pars2): *Hormetica*, *Lucihormetica*, *Phoetalia*; Zetoborinae (major): *Parasphaeria*, *Schultesia*, *Zetobora*, *Lanxoblatta*, *Phortioeca* (majority of Zetoborinae, i.e. all excl. *Thanatophyllum*); Perisphaerinae (pars1): *Laxta*, sp. near *Bantua*, Perisphaerinae sp.; Perisphaerinae (pars2): *Corydidarum*, *Pseudoglomeris*, *Perisphaerus*; Epilamprinae (major): *Rhabdoblatta*, *Pseudophoraspis*, *Opisthoplatia*, *Calolampra*, *Cyrtonotula*. The (sub-)family names and designations in this table do not reflect the taxonomic changes in the present paper.

Clade (code)	Clade (by classificatory units)	ML-T-unP (bs)	ML-T-P (bs)	ML-C-unP (bs)	ML-C-P (bs)	BI-T-unP (pp)	BI-T-P[1] (pp)	BI-C-unP[2] (pp)
c01	Blattoidea incl. Anaplectidae	90	88	96	92	100	100	100
c02	Anaplectidae + Tryonicidae + Lamproblattidae	++	52	++	++	96	100	98
c03	Blaberoidea excl. Anaplectidae	76	75	55	61	100	58	100
c04	Nyctiborinae + Blattellinae incl. Attaphilinae	++	++	*	*	75	95	*
c05	Nyctiborinae (*Nyctibora* + *Paratropes*)	100	100	100	100	100	100	100
c06	Blattellinae incl. Attaphilinae	++	++	*	*	99	73	67 [+Na]
c07	Blattellinae incl. Attaphilinae excl. *Temnopteryx*	78	58	++	++	100	97	83 [+Na]
c08	*Paratemnopteryx* + *Loboptera* + *Blattella* + *Symploce* + *Parcoblatta pennsylvanica*	++	51	++ [+Xec]	++	100	100	86 [+Xec]
c09	Attaphilinae + *Xestoblatta* sp. + *Pseudomops* + *Ischnoptera*	65	++	++	++	80	97 [+Xec]	75 [+Na]
c10	Attaphilinae + *Xestoblatta* sp. + *Pseudomops*	71	65	53	++	100	98	74 [+Na]
c11	*Ectobius* + *Saltoblattella* + Pseudophyllodromiinae excl. *Nahublattella*	++	++	++ [+Na]	*	79	56	78 [-Ne]
c12	Ectobiinae (*Ectobius* + *Saltoblattella*)	na	na	*	++	na	na	90
c13	*Ectobius*	100	100	100	100	100	100	100
c14	Pseudophyllodromiinae excl. *Nahublattella*	++	++	*	++	72	56	*
(c15)	Pseudophyllodromiinae excl. *Neoblattella*, excl. *Nahublattella*	*	*	++	*	64	*	90
c16	Blaberidae	100	93	95	81	100	100	100
c17	Panchlorinae (*Panchlora*)	100	100	100	100	100	100	100
c18	Blaberidae excl. Panchlorinae	51	++	++	++	100	100	100
c19	Oxyhaloinae	100	99	100	100	100	100	100
c20	*Nauphoeta* + *Henschoutedenia*	100	100	100	100	100	100	100
c21	*Rhyparobia* + *Brachynauphoeta* + *Heminauphoeta* + *Elliptorhina* + *Aeluropoda* + *Gromphadorhina* + *Princisia*	64	++	76	++	98	88	94
c22	*Brachynauphoeta* + *Heminauphoeta* + *Elliptorhina* + *Aeluropoda* + *Gromphadorhina* + *Princisia*	100	99	100	100	100	100	100
c23	*Elliptorhina* + *Aeluropoda* + *Gromphadorhina* + *Princisia*	83	83	83	77	100	100	100
c24	Blaberidae excl. Panchlorinae & Oxyhaloinae	++	++	++	++	*	93	58
c25	Diplopterinae (*Diploptera*) + *Thanatophyllum*	*	++	*	++	98	98	*
c26	Gyninae (*Gyna*)	100	100	100	100	100	100	100
c27	Blaberinae + Zetoborinae (major)	++	67	++	54	99	100	*
(c28)	Blaberinae + Zetoborinae incl. *Thanatophyllum*	++	*	++	*	*	*	*
c29	Blaberinae (pars1)	100	100	98	99	100	100	99
c30	*Eublaberus* + *Byrsotria* + *Archimandrita* + *Blaberus*	++	++	++	++	79	90	60
c31	Blaberinae (pars2) + Zetoborinae (major)	++	66	++	68	100	84	89
(c32)	Blaberinae (pars2) + Zetoborinae (major) + *Thanatophyllum*	*	*	*	*	*	*	59
c33	*Phoetalia* + *Schultesia* + *Zetobora* + *Lanxoblatta* + *Phortioeca*	100	100	100	99	100	100	100
c34	*Zetobora* + *Lanxoblatta* + *Phortioeca*	100	100	100	99	100	100	100
c35	Epilamprinae (major) + *Aptera* + Perisphaerinae (pars1) + Panesthiinae + Geoscapheinae + Pycnoscelinae + Paranauphoetinae + Perisphaerinae (pars2)	++	++	++	*	100	78	67

Table 3 continued.

Clade (code)	Clade (by classificatory units)	ML-T-unP (bs)	ML-T-P (bs)	ML-C-unP (bs)	ML-C-P (bs)	BI-T-unP (pp)	BI-T-P[1] (pp)	BI-C-unP[2] (pp)
c36	Epilamprinae (major) + Perisphaerinae (pars1)	++	++ [+Ap]	++	*	84	*	*
c37	Epilamprinae (major) incl. *Cyrtonotula*	na	na	++	++	na	na	*
c38	Epilamprinae (major) excl. *Cyrtonotula*	99	100	99	95	100	100	100
c39	*Opisthoplatia* + *Calolampra*	97	96	99	96	100	100	100
c40	Perisphaerinae (pars1)	++	++ [+Ap]	++	++ [+Ap]	93	77	60
c41	Panesthiinae + Geoscapheinae + Pycnoscelinae + Paranauphoetinae + Perisphaerinae (pars2)	++ [+Ap]	++	++ [+Ap]	++	88 [+Ap]	64	51 [+Ap]
c42	Pycnoscelinae + Paranauphoetinae + Perisphaerinae (pars2)	++ [+Ap]	++	++ [+Ap]	++	84 [+Ap]	83	*
c43	Perisphaerinae (pars2)	99	100	100	100	100	100	100
c44	Panesthiinae + Geoscapheinae	100	100	97	100	100	100	100
c45	Geoscapheinae + *Panesthia* + *Ancaudellia* + Panesthiinae sp.	76	82	74	85	100	100	100
c46	Geoscapheinae (*Geoscapheus* + *Macropanesthia*)	100	98	100	100	100	100	100
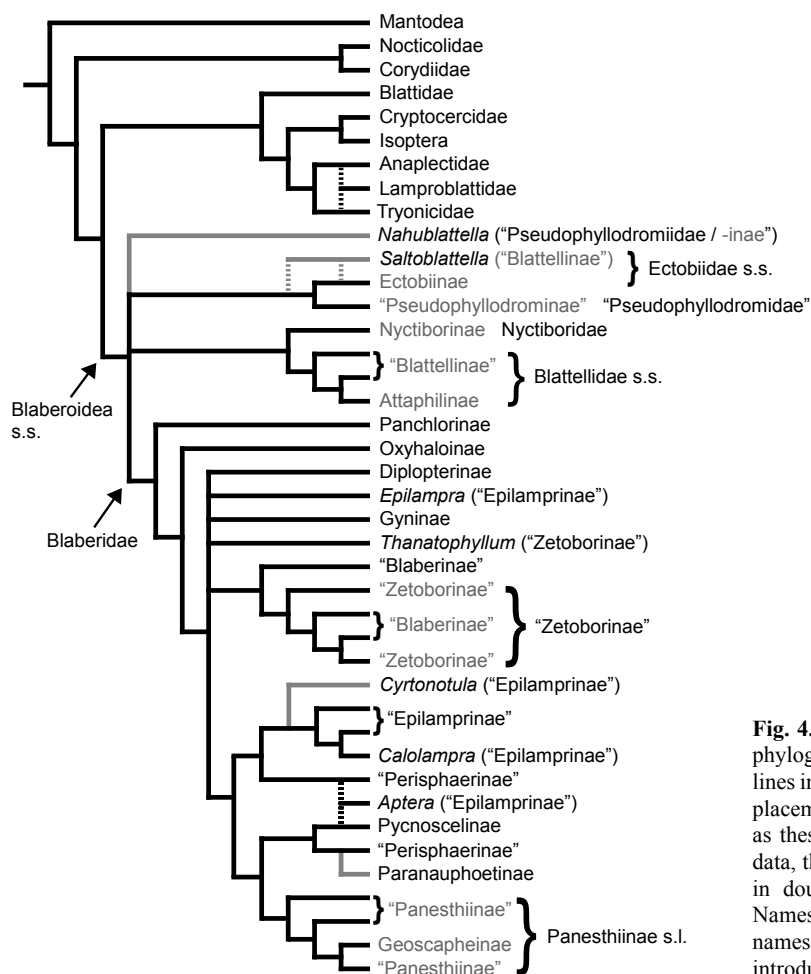
Fig. 4. Consensus tree of Dictyoptera based on all our phylogenetic trees (Figs. 3, S2–S7, Table 3). Stippled lines indicate alternative placements. Grey lines indicate placements of taxa not included in the trimmed data set; as these placements are based on a limited amount of data, they should be treated with caution. Taxon names in double quotes address non-monophyletic groups. Names in grey are 'old' taxon names, while the black names replacing them reflect the revised classification introduced herein.

(Fig. 2G; representing the monogeneric Paranauphoetinae, only in complete data set), *Pycnoscelus* (the only sampled Pycnoscelinae), and some perisphaerines (*Corydidarum* Fig. 2E, *Perisphaerus* Fig. 2F, and *Pseudoglomeris*), and it sometimes additionally included *Aptera* (analyses ML-T-unP, ML-C-unP, and BI-T-unP) as sister to *Pycnoscelus*. Apart from the issue of *Aptera*, clade **c42** was present in all analyses, except in BI-C-unP due to lack of resolution. Part of **c42**, clade **c43**, which comprised the three perisphaerine genera, formed a strongly supported subclade (bs 99–100, pp 100). The second major subclade of clade **c41**, clade **c44**, included all sampled Panesthiinae (Fig. 2H) and Geoscapheinae and was very strongly supported (bs 97–100, pp 100). Within **c44** the two geoscapheines and the panesthiines *Panesthia*, *Ancaudellia*, and Panesthiinae sp. formed a well-supported, consistently present monophylum (**c45**; bs 74–85, pp 100). The two geoscapheines formed a strongly supported subclade of this (**c46**; bs 98–100, pp 100).

3.2. Comparison with previous phylogenetic results and classification

With regard to the comparison of our phylogenetic results with current classification and with previous phylogenetic studies, two points should be noted: **(1)** Any statement of some classificatory unit (e.g. some 'subfamily') appearing as monophyletic refers solely to the representatives that we have sampled, or other authors have sampled for their study. It is well possible that a classificatory unit is non-monophyletic considering further members of it. **(2)** Different studies have used similar to very different taxon samples (of similar or different size) to represent certain classificatory units. Accordingly, results of mono- or non-monophyly of a classificatory unit can differ among studies even if they have obtained identical phylogenetic results for the taxa sampled in both. (The trees in Fig. S1 must be seen on this background.) Therefore, the aim of the following paragraphs is not discussing the (non-)monophyly of current classificatory units, but rather outlining groups of genera that form clades and can thus be used as cores for building up monophyletic classificatory units in the future. Yet, we have to refer to the current classificatory units as a framework for the discussion – also to indicate necessary changes in Blaberoidea systematics when approaching a phylogeny-based classification. For formal reasons, genera that gave their names to classificatory units of higher rank (type genera) play a particular role in this effort. We essentially discuss assignment of *genera* to clades, while we are aware that caution is advised in this in view of some genera appearing as polyphyletic in phylogenetic studies (e.g. *Parcoblatta*, *Xestoblatta*, and *Balta* herein; *Symploce* in WANG et al. 2017). In Table 4 we summarise which genera can presently be assigned – with varied degree of support – to one of the principal blaberoid lineages (not done for the uncontroversial Blaberidae).

The monophyly of **Blaberoidea** (**c03**; excl. Anaplectidae) in all our analyses is consistent with nearly all previous studies (e.g. INWARD et al. 2007; ROTH et al. 2009; DJERNÆS et al. 2012, 2015; WANG et al. 2017; BOURGUIGNON et al. 2018; EVANGELISTA et al. 2019). This also applies to the studies only including morphological data (MCKITTRICK 1964; GRANDCOLAS 1996; KLASS & MEIER 2006), as they placed Anaplectidae as sister to the remaining Blaberoidea. Our placement of **Anaplectidae** in Blattoidea and in a clade with Tryonicidae, Lamproblattidae, and Cryptocercidae + Isoptera is consistent with the results of DJERNÆS et al. (2015), WANG et al. (2017), and BOURGUIGNON et al. (2018, with a different position of Tryonicidae as sister group of Blattidae). We thus consider the separation of Anaplectidae from Blaberoidea as confirmed. The placement of an *Anaplecta* deeply within Blaberoidea, as sister to a group of pseudophyllodromiine species, in the molecular study of LEGENDRE et al. (2015) is exceptional. While the outline of Blaberoidea is thus well established by now, one main task in the group is the delimitation of its principal, deep lineages.

3.2.1. Blattellinae and Attaphilinae

We found moderate support for a monophyletic Blattellinae (**c06**, including the type genus *Blattella*) – with one noteworthy exception: Our phylogenetic study is the first to include members of the myrmecophilous *Attaphila*, the sole genus of the subfamily Attaphilinae created by ROTH (2003a). Our finding that *Attaphila* is deeply subordinate in the blattelline clade contradicts subfamily status for this genus. Thus, we sink "Attaphilinae" and place *Attaphila* in Blattellinae (as stated before in DJERNÆS 2018 and in a not formally published conference abstract, see Blattodea Species File). GRANDCOLAS' (1992a) suggestion of a close relationship among *Ischnoptera*, *Pseudomops*, and *Xestoblatta* was supported by our results, but we add *Attaphila* to this group (**c09**). In other recent molecular studies with a meaningful blaberoid sample most of the blattellines were also assembled in a clade (LEGENDRE et al. 2015; WANG et al. 2017; BOURGUIGNON et al. 2018; EVANGELISTA et al. 2019); the taxon samples are partly quite different, but *Blattella* and a few other genera are shared, which allows to claim the correspondence of these clades in the different studies (see Table 4). A noteworthy exception is the association of the blattelline *Anallacta* Shelford, 1908 with the ectobiine taxa in BOURGUIGNON et al. (2018) and with pseudophyllodromiine taxa in EVANGELISTA et al. (2019), which suggests a shift of the genus to Ectobiinae or Pseudophyllodromiinae (the latter preferred herein based on the stronger data in EVANGELISTA et al. 2019; see Table 4). Another exception is the placement of *Pseudomops* and a *Xestoblatta* (and two other blattelline genera) in a pseudophyllodromiine clade in LEGENDRE et al. (2015), which also separates these taxa from *Ischnoptera* – a significant contradiction of our results (see also below). The predominant position of *Temnopteryx* as a basal branch of the blattelline clade (**c06**) in our study agrees with the result of LEGENDRE et al. (2015), the only other study having sampled this taxon.

3.2.2. Pseudophyllodromiinae

We found low support for a monophyletic Pseudophyllodromiinae (**c14**) as another principal clade, but did consistently find clade **c14** under exclusion of *Nahublattella* (which, however, was only represented by very limited data), and with occasional exclusion of *Neoblattella* (likely based on long branch attraction). A clear pseudophyllodromiine clade was also detected in three of the four recent studies with a decent sample of the group (WANG et al. 2017; BOURGUIGNON et al. 2018; EVANGELISTA et al. 2019); the taxon samples are very different, only the shared inclusion of *Balta* in these papers and our study allows to regard the pseudophyllodromiine clades as corresponding (*Supella* and *Euthlastoblatta* additionally shared between EVANGELISTA et al. 2019 and the present study; see Table 4). A noteworthy exception is the association of the pseudophyllodromiine *Latiblattella* with the nyctiborines in WANG et al. (2017), which contradicts our well-supported placement of the genus deeply inside the

Table 4. State of the art for the assignment of blaberoid genera to the four principal blaberoid clades Pseudophyllodromiidae, Ectobiidae, Blattellidae, and Nyctiboridae (former ectobiid subfamilies raised to family rank; Blaberidae not included), based on a synthesis of the results from the present paper = Dj(tp) and other recent molecular or combined phylogenetic studies with a meaningful sample across the principal blaberoid lineages: Evangelista et al. (2019) = Ev(19); Bourguignon et al. (2018) = Bo(18); Wang et al. (2017) = Wa(17); Legendre et al. (2015) = Le(15). (?) is added to a genus name if the assignment is highly questionable (e.g. due to evident problems in the respective part of a phylogenetic tree, see section 3.2.2.). Type genera of family-level clades are indicated; missing for Pseudophyllodromiidae, as *Pseudophyllodromia* has not yet been included as a terminal taxon in a phylogenetic study. * = transfer from Attaphilinae to Blattellinae in Blattodea Species File was made in anticipation of the present publication. The names and definitions of the genera are in accord with the Blattodea Species File; however, their inclusion in this table does not refer to the type species of a genus but to the species (or unidentified member of a genus) sequenced by the authors of the associated publication(s).

Families *assigned genera*	according to phylogenetic study of	taxonomic assignment in Blattodea Species File	assignment in column 1 contradicted in	therein resulting as
Pseudophyllodromiidae				
Balta	Dj(tp), Ev(19), Bo(18), Wa(17), Le(15)	Pseudophyllodromiinae		
Margattea	Dj(tp)	Pseudophyllodromiinae		
Euthlastoblatta	Dj(tp), Ev(19), Le(15)	Pseudophyllodromiinae		
Neoblattella	Dj(tp)	Pseudophyllodromiinae		
Isoldaia	Dj(tp), Le(15)	Pseudophyllodromiinae		
Latiblattella	Dj(tp), Le(15)	Pseudophyllodromiinae	Wa(17)	Nyctiborinae
Dendroblatta	Dj(tp), Le(15)	Pseudophyllodromiinae		
Supella	Dj(tp), Ev(19), Le(15)	Pseudophyllodromiinae		
Sorineuchora Caudell, 1927	Wa(17)	Pseudophyllodromiinae		
Allacta Saussure & Zehntner, 1895	Bo(18), Wa(17)	Pseudophyllodromiinae		
Shelfordina Hebard, 1929	Wa(17)	Pseudophyllodromiinae		
Ellipsidion Saussure, 1863	Ev(19), Bo(18)	Pseudophyllodromiinae		
Euphyllodromia	Bo(18)	Pseudophyllodromiinae		
Amazonina Hebard, 1929	Bo(18)	Pseudophyllodromiinae		
Sundablatta Hebard, 1929	Ev(19)	Pseudophyllodromiinae		
Cariblatta Hebard, 1916	Ev(19)	Pseudophyllodromiinae		
Anallacta	Ev(19)	Blattellinae	Bo(18)	Ectobiinae
Anisopygia (?)	Le(15)	incertae sedis		
Pseudoanaplectinia (?)	Le(15)	Blattellinae		
Paramuzoa (?)	Le(15)	Nyctiborinae		
Ectobiidae				
Ectobius (**type genus**)	Dj(tp), Bo(18), Wa(17), Le(15)	Ectobiinae		
Phyllodromica	Bo(18)	Ectobiinae		
Ectoneura	Bo(18)	Ectobiinae		
Saltoblattella	Dj(tp)	Blattellinae		
Blattellidae				
Blattella (**type genus**)	Dj(tp), Ev(19), Bo(18), Wa(17), Le(15)	Blattellinae		
Loboptera	Dj(tp), Ev(19), Le(15)	Blattellinae		
Parcoblatta	Dj(tp), Bo(18), Le(15)	Blattellinae		
Paratemnopteryx	Dj(tp), Ev(19), Bo(18), Le(15)	Blattellinae		
Symploce	Dj(tp), Ev(19), Bo(18), Wa(17), Le(15)	Blattellinae		
Haplosymploce Hanitsch, 1933	Wa(17)	Blattellinae		
Episymploce Bey-Bienko, 1950	Ev(19), Wa(17)	Blattellinae		
Ischnoptera	Dj(tp), Ev(19), Bo(18), Wa(17), Le(15)	Blattellinae		
Pseudomops	Dj(tp)	Blattellinae	Le(15)	Pseudophyllodromiinae
Xestoblatta	Dj(tp), Le(15) (in part)	Blattellinae	Le(15) (in part)	Pseudophyllodromiinae
Attaphila	Dj(tp)	Blattellinae* / Attaphilinae		
Symplocodes Hebard, 1929	Wa(17)	Blattellinae		
Hemithyrsocera Saussure, 1893	Wa(17)	Blattellinae		
Lobopterella Princis, 1957	Ev(19), Bo(18), Wa(17)	Blattellinae		
Anaplectoidea Shelford, 1906	Wa(17)	Blattellinae		
Sigmella Hebard, 1940	Wa(17)	Blattellinae		
Temnopteryx	Dj(tp), Le(15)	Blattellinae		
Asiablatta Asahina, 1985	Ev(19), Bo(18)	Blattellinae		
Carbrunneria Princis, 1954	Bo(18)	Blattellinae		
Beybienkoa Roth, 1991	Bo(18)	Blattellinae		
Nyctiboridae				
Nyctibora (**type genus**)	Dj(tp), Ev(19), Wa(17), Le(15)	Nyctiborinae		
Paratropes	Dj(tp), Wa(17), Le(15)	Nyctiborinae		
incertae sedis	**sampled in**			
Nahublattella	Dj(tp)	Pseudophyllodromiinae		
Megaloblatta	Bo(18)	Nyctiborinae		

pseudophyllodromiine clade. In LEGENDRE et al. (2015) the matter is ambiguous, as the sampled pseudophyllodromiines (a similar selection as in our study) are assembled in a clade, but this additionally includes an anaplectid (*Anaplecta* sp.), two "ectobiid s.l." incertae sedis (two *Anisopygia* Saussure, 1893), a nyctiborine (*Paramuzoa* Roth, 1973), and some blattellines (*Pseudoanaplectinia* Roth, 1995 and a *Pseudomops* + *Xestoblatta* clade). Our results contradict this placement of *Pseudomops* and *Xestoblatta* (see Blattellinae clade above), while the placement of *Anisopygia*, *Paramuzoa*, and *Pseudoanaplectinia* to this clade remains untested (see (?) behind taxon names in Table 4). EVANGELISTA et al.'s (2019) finding of *Anallacta* belonging to the pseudophyllodromiine clade (as the sister group of the remaining pseudophyllodromiines) is of particular interest (see section 3.2.1.).

There has been a conflict regarding the status of Pseudophyllodromiinae based on morphological work: GRANDCOLAS (1996) assumed monophyletic Pseudophyllodromiinae, including *Nahublattella*, *Supella*, and *Euphyllodromia* Shelford, 1908. KLASS & MEIER (2006) also included these taxa and suggested the group to be paraphyletic, as they found *Nahublattella* + (*Supella* + (*Euphyllodromia* + remaining Blaberoidea [Ectobiinae not included])). Our results cannot support or contradict either hypothesis with regard to *Nahublattella* (poor data) or *Euphyllodromia* (not included herein). *Euphyllodromia* was included, however, in BOURGUIGNON et al. (2018), where it is in the clade around *Balta*, while *Supella* is included in our pseudophyllodromiine clade (i.e., also around *Balta*). This suggests that *Supella* and *Euphyllodromia* belong to the same principal blaberoid lineage, contra KLASS & MEIER (2006). We further note that the type genus *Pseudophyllodromia* Brunner von Wattenwyl, 1865 has never been included as a terminal taxon in a phylogenetic analysis (character scoring was done at the "(sub)family"-level in GRANDCOLAS 1996; see KLASS 2001 for problems in the character matrix). Therefore, the use of the name 'Pseudophyllodromiinae' for this principal blaberoid clade is actually problematic.

3.2.3. Ectobiinae

We received moderate support for a principal clade **c12** comprising *Ectobius*, the type genus of Ectobiinae, and *Saltoblattella*. *Saltoblattella* was provisionally assigned to Blattellinae when described (BOHN et al. 2010), but the authors noted several similarities with Ectobiinae. DJERNÆS et al. (2012) placed *Saltoblattella* as sister to *Ectobius*, but, due to their limited sampling of non-blaberid Blaberoidea, did not perform any taxonomic change. The present study includes a much broader sample of non-blaberid Blaberoidea (39 versus 7 species) and blattellines (while additional ectobiine genera could not be included). With this sample, Blattellinae incl. *Attaphila* and excl. *Saltoblattella* is generally monophyletic in the analyses (clade **c06**; except for the dissociation of *Temnopteryx* in some analyses). Consequently, we remove *Saltoblattella* from Blattellinae and place it provision-

ally in Ectobiinae. Further genera traditionally assigned to Ectobiinae have only been sampled in BOURGUIGNON et al. (2018): *Phyllodromica* Fieber, 1853 and *Ectoneura* Shelford, 1907, which formed a clade together with *Ectobius*, the genus *Anallacta* (see but see section 3.2.2.) being sister to this clade.

3.2.4. Nyctiborinae

Our finding of strong support for Nyctiborinae (**c05**), with *Paratropes* and the type genus *Nyctibora* sampled, as one of the principal lineages of Blaberoidea is consistent with previous studies, with the same two genera sampled (INWARD et al. 2007; DJERNÆS et al. 2015; LEGENDRE et al. 2015; WANG et al. 2017). However, this is far from demonstrating the monophyly of Nyctiborinae, as the majority of its 10 genera have remained unsampled. Also note that LEGENDRE et al. (2015) placed the nyctiborine *Paramuzoa* in their pseudophyllodromiine clade (see section 3.2.2.), far remote from their *Paratropes* + *Nyctibora* clade. BOURGUIGNON et al. (2018) only sampled one nyctiborine, *Megaloblatta* Dohrn, 1887, whose relationship to *Nyctibora* and *Paratropes* thus remains open.

3.2.5. Blaberidae

We found very strong support for a monophyletic Blaberidae (**c16**), which is the most extensively sampled principal lineage of Blaberoidea. This result agrees with all previous studies (e.g. MCKITTRICK 1964; GRANDCOLAS 1996; INWARD et al. 2007; PELLENS et al. 2007a; ROTH et al. 2009; DJERNÆS et al. 2012; LEGENDRE et al. 2015; WANG et al. 2017; BOURGUIGNON et al. 2018; EVANGELISTA et al. 2019).

Regarding the **deeper relationships** in Blaberidae, our result of Panchlorinae (**c17**) being sister to the remaining Blaberidae (**c18**) is congruent with some recent studies (e.g. LEGENDRE et al. 2014, 2015). In contrast, LEGENDRE et al. (2017) found a clade in this position that, in addition to Panchlorinae, includes *Thanatophyllum* and two epilamprines not sampled herein. Our result of Oxyhaloinae (**c19**) being the next branch agrees with LEGENDRE et al. (2017), while the next branch is Diplopterinae + Oxyhaloinae in LEGENDRE et al. (2014), and Diplopterinae alone in LEGENDRE et al. (2015). With regard to Blaberidae excl. Panchlorinae and Oxyhaloinae (i.e. clade **c24**), the large Neotropical Blaberinae + Zetoborinae clade **c27** (incl. or excl. *Thanatophyllum*) agrees with some previous studies (e.g. LEGENDRE et al. 2014: fig. S2, 2017), whereas others have not recovered this clade (e.g. LEGENDRE et al. 2014, fig. 1, 2015; BOURGUIGNON et al. 2018). For the other large clade, **c35** (including Perisphaerinae, Epilamprinae excl. *Epilampra*, Pycnoscelinae, Paranauphoetinae, Panesthiinae, and Geoscapheinae), congruence with the literature is limited: LEGENDRE et al. (2014) found a Perisphaerinae + Pycnoscelinae + Panesthiinae incl. Geoscapheinae clade, but placed *Rhabdoblatta* and *Calolampra* (Epilamprinae) well away from it. WANG et al. (2017) found a Perisphaerinae + Epilampri-

nae + Pycnoscelinae + Paranauphoetinae + Panesthiinae + Diplopterinae clade which, apart from the inclusion of Diplopterinae, is similar to our clade **c35**. Bourguignon et al. (2018) also found a similar clade, but placed Paranauphoetinae as sister to two Neotropical epilamprines. In Legendre et al. (2017) our clade **c35** is entirely absent. Evangelista et al. (2019) only used a small blaberid sample of 7 species, whereby its contribution to internal relationships in Blaberidae is very limited. The most noteworthy point is that Diplopterinae + Oxyhaloinae is sister to the remaining blaberids, whereas Panchlorinae is more subordinate, being sister to *Gyna*. Their *Blaberus* + *Schultesia* branch is congruent with our clade **c27**, but this has little bearing as besides *Gyna* and *Diploptera* these are the only representatives of our entire clade **c24** (which only excludes Panchlorinae and Oxyhaloinae).

Among the blaberid subfamilies, Panchlorinae, Gyninae, Pycnoscelinae, Paranauphoetinae, and Diplopterinae were only represented by a single genus each in our sample (*Calolampra* herein regarded as an epilamprine, not a diplopterine) – all by the type genus. The same was the case in every recent study including any of these subfamilies (also in Legendre et al. 2017, who, however, found the genus *Gynopeltis* Gerstaecker, 1869, classified as Blaberidae incertae sedis, associated with *Gyna*). Consequently, we cannot contribute anything to the question whether Panchlorinae, Gyninae, Pycnoscelinae, Paranauphoetinae, and Diplopterinae as currently outlined are monophyletic or not, although this point is of limited relevance for the two latter subfamilies, which are monogeneric. Yet, the inclusion of additional species (and genera) from all these subfamilies in future studies is desired. Among the subfamilies with more than one genus sampled herein, only two were obtained as monophyletic: Oxyhaloinae and Geoscapheinae, both with strong support. All others – Blaberinae, Epilamprinae, Panesthiinae, Perisphaerinae, and Zetoborinae – appeared as para- or polyphyletic. While this is in contrast to some previous studies (Grandcolas 1993a, 1997a), the level of agreement with molecular and combined studies is quite high when taxon sampling is taken into account.

The very strong and consistent support for monophyletic **Oxyhaloinae** was one of our few results fully congruent with current taxonomy as well as with previous studies (e.g. Legendre et al. 2014, 2015, 2017; Bourguignon et al. 2018). Congruence with the clade *Nauphoeta* + *Princisia* in Evangelista et al (2019) is also relevant, as these two genera represent the two principal subclades of Oxyhaloinae (**c20** and **c21**) in our study.

While we retrieved neither **Blaberinae** nor **Zetoborinae** as a monophyletic unit, the combination Blaberinae + Zetoborinae (excl. *Thanatophyllum*) formed a moderately supported clade (**c27**). Its basal split in a strongly supported blaberine (**c29**) and a moderately supported blaberine-zetoborine (**c31**) subclade can be used for a revised outline of the two subfamilies (alternatively, both could be comprised within an expanded Blaberinae and separated at tribal level). In this sense, we transfer *Phoetalia*, *Lucihormetica*, and *Hormetica* from Blaberinae

to Zetoborinae. This is consistent with other molecular and combined studies (Legendre et al. 2014, 2015, 2017) and the morphological study by McKittrick (1964). The only phylogenetic study supporting the placement of the transfer candidates in Blaberinae is Grandcolas' (1993a) morphological study. Although *Thanatophyllum* clustered with the remaining Zetoborinae or Blaberinae + Zetoborinae only in some of our analyses, we leave it in Zetoborinae. Its transfer to Diplopterinae (see above) or into yet another blaberid subfamily near Panchlorinae (as suggested by the results of Legendre et al. 2017: fig. 1(1)) are alternative options to be tested in future studies.

Our strong support for the monophyly of a clade **c44** comprising the sampled panesthiines and geoscapheines agrees with the results from other studies (Legendre et al. 2014, 2015, 2017; Bourguignon et al. 2018). In our study **Panesthiinae** was consistently paraphyletic with regard to **Geoscapheinae** (clade **c46**). The deeply subordinate position of the latter within the former was well supported by some strong nodes (mainly of clade **c45**). Geoscapheinae subordinate in Panesthiinae was also found in every phylogenetic study with a sufficient taxon sampling (e.g. Legendre et al. 2014, 2015). Furthermore, a recent comprehensive study of the phylogeny of Australian Panesthiinae and Geoscapheinae (Lo et al. 2016) showed the subfamilies to be mutually paraphyletic as species of the highly polyphyletic genus *Panesthia* are scattered over the geoscapheine part of the tree – a result also supported by Legendre et al. (2017). Rugg & Rose (1984a) erected the subfamily Geoscapheinae for species previously placed in Panesthiinae, as they presumed these species to form the sister group of the remaining Panesthiinae. As phylogenetic studies consistently contradict this, we follow Roth (2003a) and sink Geoscapheinae and return the included species to Panesthiinae. In the following we refer to Panesthiinae incl. Geoscapheinae as Panesthiinae s.l.

Perisphaerinae was never retrieved herein as monophyletic, but was consistently split in two clades (**c40** and **c43**) embedded in different superordinate clades (**c36** versus **c41**, which together form clade **c35**). The strongly supported perisphaerine clade **c43** comprises *Corydidarum*, *Perisphaerus*, and *Pseudoglomeris*. The much more weakly supported perisphaerine clade **c40**, including 'Perisphaerinae sp.', 'genus near *Bantua* sp.', and *Laxta* sp., is more amorphous, especially as only one of three species is even identified to genus. Grandcolas' (1997a) morphology-based support of a monophyletic Perisphaerinae, including *Laxta*, is in conflict with our results. Recent molecular and combined studies (Legendre et al. 2014, 2015, 2017; Bourguignon et al. 2018) also contradict a monophyletic Perisphaerinae; the distribution of sampled perisphaerines over the disparate clades varies among the studies, only Legendre et al. (2017) found a pattern concordant with our results. In view of this evidence, "Perisphaerinae" evidently requires subdivision in at least two subfamilies, possibly in accordance with the two "perisphaerine" clades **c40** and **c43**. "Perisphaerinae" will then be limited to the members of **c43** (in-

cluding taxa found to belong there in future studies), as it includes the type genus *Perisphaerus*. However, these taxonomic changes are not done here; they should await evidence from an increased sampling of Perisphaerinae – a clear priority for future studies.

Epilamprinae was likewise not monophyletic in our analyses: Most epilamprines formed a strongly supported clade **c38** comprised of *Rhabdoblatta*, *Pseudophoraspis*, *Opisthoplatia*, and a deeply subordinate *Calolampra*. The epilamprine *Cyrtonotula* appeared as its sister group (together clade **c37**) with weak support. *Epilampra* sp., our sole representative of the type genus of the subfamily, was clearly disjunct from this clade, either isolated or variously associated with *Diploptera*, *Thanatophyllum*, and *Gyna* with low support. *Aptera* jumped between the two disjunct perispherine-dominated clades **c40** (being the sister group of the perisphaerines) and **c42** (being the sister group of *Pycnoscelus*); when associated with **c40**, which we obtained as sister to the main epilamprine clade **c37**, *Aptera* would at least be near epilamprines. There are several issues in this: **(1)** The phylogenetic disunity of *Epilampra* and (some) other epilamprines was also found in other studies with a suitable taxon sample (LEGENDRE et al. 2014, 2015; BOURGUIGNON et al. 2018). LEGENDRE et al. (2017) even found four disjunct epilamprine clades: one only including *Epilampra* species, a large one resembling our clade **c37**, one only including *Aptera* species, and an additional one including *Colapteroblatta* Hebard, 1919 and *Galiblatta* Hebard, 1926 (not sampled herein) as sister group of an otherwise isolated *Thanatophyllum* (plus a fifth "clade" represented by a *Rhabdoblatta* very remote from its putative congeners). **(2)** In the studies that have included *Aptera*, LEGENDRE et al. (2017) found this taxon as sister to *Pycnoscelus*, this clade being sister to the perisphaerines around *Perisphaerus*; INWARD et al. (2007) found *Aptera* associated with Perisphaerinae sp. and genus near *Bantua* sp. (both placed in **c40** herein). These placements are consistent with our two alternatives. As a third alternative, LEGENDRE et al. (2015) placed *Aptera* as sister to the only included *Epilampra* (the same *Epilampra* specimen as herein), with *Aptera* + *Epilampra* far remote from the majority of the included epilamprines. *Aptera* was moved from Perisphaerinae to Epilamprinae by GRANDCOLAS (1997a), but in view of the recent unanimous phylogenetic disunity of both subfamilies this transfer is of limited relevance. **(3)** PRINCIS (1967) placed *Cyrtonotula* in Epilamprinae. ROTH (2003a) removed it from Epilamprinae and classified it as Blaberidae incertae sedis without argument. MAVROPULO et al. (2015) returned *Cyrtonotula* to Epilamprinae based on DNA analyses and genital characters showing a close relationship to the epilamprines *Rhabdoblatta*, *Pseudophoraspis* (both sampled herein) and *Morphna* Shelford, 1910. This is supported by our ML analyses (see clade **c37**). **(4)** For *Calolampra* our results support, like other recent studies (LEGENDRE et al. 2014, 2015, 2017), assignment to Epilamprinae (i.e. clade **c37**) as in MCKITTRICK (1964), the Cockroach Species File (BECCALONI 2014), and ROTH (2003a) versus GRANDCOLAS'

(1993a) placement in Diplopterinae. As a conclusion, we here maintain the subfamily "Epilamprinae" as comprising *Epilampra*, the members of **c37** (including *Calolampra* and *Cyrtonotula*), and *Aptera*. However, we note that new subfamilies need to be created in the future at least for **c37**, and possibly for *Aptera*. Prior to such taxonomic rearrangement, the sampling of epilamprines needs to be increased, including additional representatives of the type genus, preferably including the type species *E. brasiliensis* Fabricius, 1775.

Independent of the question of monophyly, **Panchlorinae**, **Diplopterinae**, and **Gyninae** clearly deserve the status of separate subfamilies, as we found their members to have originated from fairly deep splitting events in Blaberidae. Whether *Thanatophyllum* has to be transferred from Zetoborinae to Diplopterinae remains open – we leave it provisionally in Zetoborinae. Gyninae as a separate subfamily agrees with GRANDCOLAS (1993), whereas we cannot confirm the placement of *Gyna* in Perisphaerinae as proposed by MCKITTRICK (1964) and ROTH (1972) – independent of Perisphaerinae itself not having been retrieved herein as a monophyletic unit. Other recent studies (LEGENDRE et al. 2014, 2015, 2017; BOURGUIGNON et al. 2018) also support the placement of *Gyna* outside Perisphaerinae.

In contrast, subfamily status might not be appropriate for **Paranauphoetinae** and **Pycnoscelinae**, as these are likely both part of a more apical clade (**c42**) otherwise including a subclade (**c43**) consisting of the perisphaerine genera *Corydidarum*, *Pseudoglomeris*, and the type genus *Perisphaerus*. Paranauphoetinae and Pycnoscelinae could then be downranked to tribes within Perisphaerinae (s.s., i.e. *Perisphaerus* and relatives), in partial agreement with ROTH's (1999) placement of *Paranauphoeta* in Perisphaerinae. However, the placement of the two taxa in recent studies is quite contradictory. For *Pycnoscelus* the same relationship was found in LEGENDRE et al. (2017; *Paranauphoeta* not sampled), though with additional inclusion of the epilamprine *Aptera* as the sister taxon of *Pycnoscelus* (as in our ML-T-unP, ML-C-unP, and BI-T-unP). WANG et al. (2017) placed *Pycnoscelus* and *Paranauphoeta* as sister taxa and their clade as sister to some epilamprines and *Diploptera*. *Pycnoscelus* was placed as sister to Panesthiinae s.l. in LEGENDRE et al. (2015), and to Panesthiinae s.l. plus some epilamprines and perisphaerines in BOURGUIGNON et al. (2018). ANISYUTKIN (2003) placed *Paranauphoeta* as sister to Perisphaerinae + Panesthiinae (his reason for removing *Paranauphoeta* from Perisphaerinae and creating for it a subfamily Paranauphoetinae). BOURGUIGNON et al. (2018) placed *Paranauphoeta* as sister to two epilamprines, but due to differences in taxon sampling it is not clear whether this result is in conflict with our results. A taxonomic rearrangement thus has to await further phylogenetic evidence.

3.2.6. Deep relationships in Blaberoidea

Our analyses yielded limited resolution between the five principal clades: (Ectobiinae **c12** + Pseudophyllo-

dromiinae **c14**) + (Nyctiborinae **c05** + Blattellinae **c06**) + Blaberidae **c16**; the sister group to Blaberidae differed between analyses. Bourguignon et al. (2018) found (Ectobiinae + Pseudophyllodromiinae) + (Nyctiborinae + (Blattellinae + Blaberidae)) (but note that from Nyctiborinae only *Megaloblatta* was sampled therein, for which a relationship with *Nyctibora* remains undemonstrated). Legendre et al. (2015) essentially found (Nyctiborinae + Blattellinae) + ((Ectobiinae + Pseudophyllodromiinae) + Blaberidae) (though with irregularities regarding the pseudophyllodromiine clade, see 3.2.2.). Wang et al. (2017) basically found Ectobiinae + ((Blattellinae + Pseudophyllodromiinae) + (Nyctiborinae + Blaberidae)); and Evangelista et al. (2019) found Ectobiinae + (Pseudophyllodromiinae + ((Nyctiborinae + Blattellinae) + Blaberidae)). The more recent studies converge on a single point of near-consensus: there is a clade Nyctiborinae + Blattellinae. The sole point of full consensus among all these studies is that there is no evidence for a phylogenetic unit 'Ectobiidae s.l.' in the sense of comprising all non-blaberid Blaberoidea (see also Klass & Meier 2006; Inward et al. 2007; Pellens et al. 2007a); the taxon name 'Ectobiidae' should consequently no longer be used in this wide sense.

In sum, there is now increasing consensus that Blaberoidea falls into five major clades reflecting the taxonomic units Pseudophyllodromiinae (Fig. 1E,F), Ectobiinae (Fig. 1B), Blattellinae (Fig. 1C,D), Nyctiborinae, and Blaberidae (Figs. 1G,H, 2) (while Anaplectidae, Fig. 1A, is no longer included, and Attaphilinae clearly had to be merged in Blattellinae). In view of the lack of a consensus regarding the relationships among these five lineages, the structuring of Blaberoidea into these five taxonomic units represents a sound basis for further development of Blaberoidea systematics. For the four controversial, formerly "Ectobiidae s.l." clades we have summarised the state-of-the-art taxon content (referring to genera) in Table 4, which, however, is still very provisional. The respective "Ectobiidae s.l." subfamilies deserve family status (like Blaberidae, as suggested by Grandcolas 1996). With this, the name 'Ectobiidae' now refers to the former 'Ectobiinae'; it should include those taxa that are likely to belong to the same principal lineage (**c12** herein) of non-blaberid Blaberoidea as its type genus *Ectobius*. To avoid confusion, we refer herein to 'Ectobiidae' in the old sense as "Ectobiidae s.l." and to 'Ectobiidae' in the new sense as Ectobiidae s.s. The other former "Ectobiidae s.l." subfamilies will be referred to as Pseudophyllodromiidae, Nyctiboridae, and Blattellidae s.s. There may be reason for a further family-level taxon to accommodate *Nahublattella*, but this clearly needs more evidence. In view of the still very limited work on Blaberoidea systematics, both the detection of further deep lineages and an ongoing shift of genera between subfamilies and families would not be surprising.
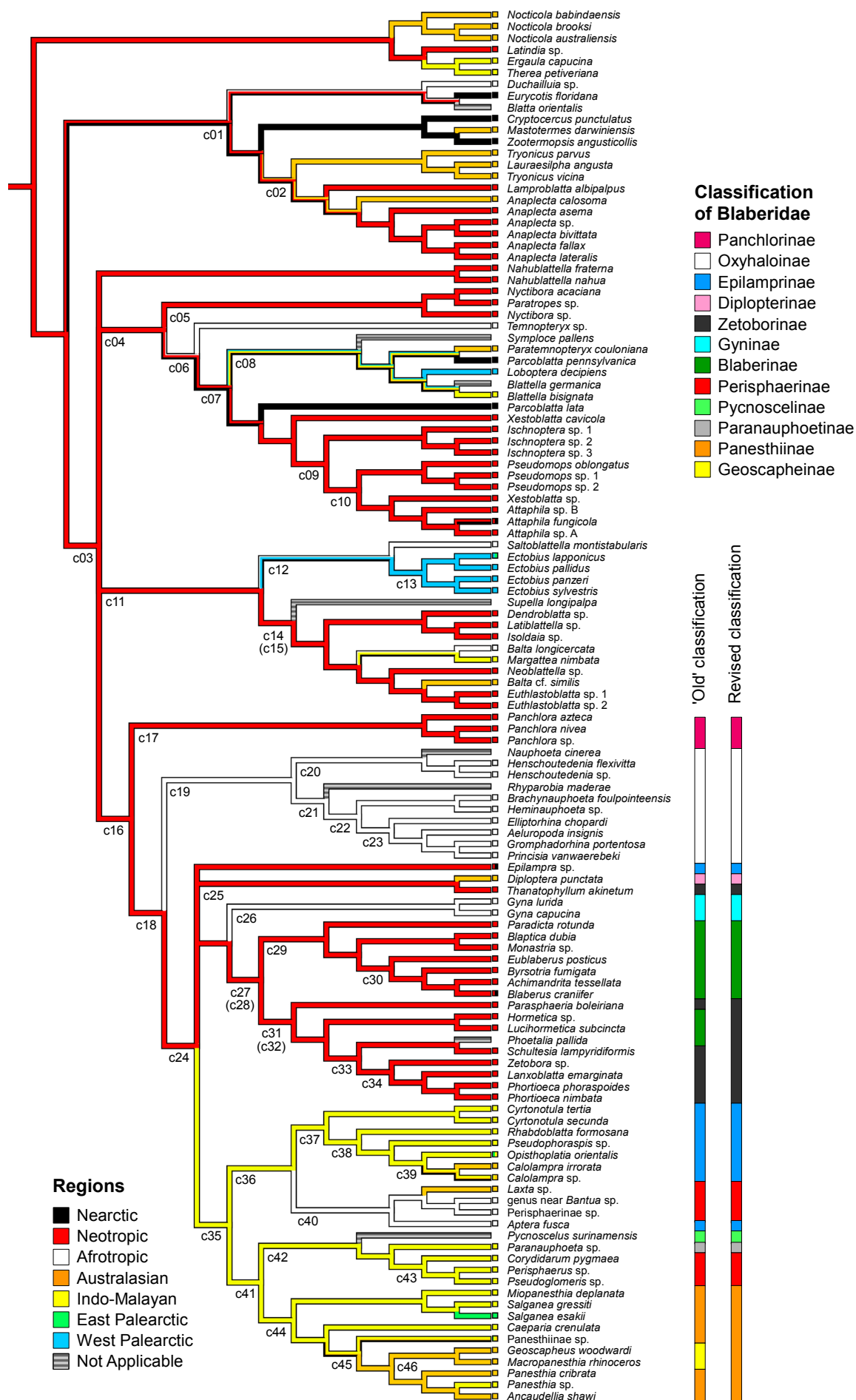
3.3. Mapping

3.3.1. Distribution

The non-blaberid part of the Blaberoidea tree does not show a clear biogeographic pattern (Fig. 5), probably because sampling is not dense enough. The reconstructed Neotropical origin for Blaberoidea could result from this and geographic sampling bias. On the other hand, the lack of a biogeographic pattern in the tree might partly reflect the presence of an undivided Gondwana or even Pangaea at the time of the early diversification of Blaberoidea ca. 130–210 mya (Djernaes et al. 2015: ca. 190–210 mya; Wang et al. 2017: ca. 160–190 mya; Bourguignon et al. 2018: ca. 150–180 mya; Evangelista et al. 2019 ca. 130–170 mya). Faunal exchange between present-day Neotropical, Afrotropical, Indo-Malayan, and Australasian regions was likely easier then. Yet, there is one interesting case in the non-blaberid part: The Neotropical myrmecophilous *Attaphila* (though with *A. fungicola* extending to Nearctic Texas) is subordinate in a clade **c09** of likewise Neotropical Blattellidae s.s. (*Xestoblatta* sp., *Ischnoptera*, and *Pseudomops*). The myrmecophilous life habits of *Attaphila* thus most likely originated in the Neotropics.

The blaberid part of the tree, with much denser sampling, shows a fairly clear biogeographic pattern (Fig. 5) in the way that all principal clades are limited to or strongly focused on one of the defined biogeographic regions. Essentially, there is a large purely Afrotropical clade **c19** (Oxyhaloinae), a large purely Neotropical clade **c27** (Blaberinae[1] plus most Zetoborinae), and a large mostly Indo-Malayan clade **c35** (including several subfamilies). Clade **c35** includes two independent, strongly subordinate extensions into the neighbouring Australasian region within its subclades **c37** (Epilamprinae: within *Calolampra*) and **c45** (a branch of Panesthiinae s.l.); and a subordinate extension into the neighbouring East Palearctic region in its subclade **c44** (within *Salganea*). However, **c35** furthermore includes a change into the remote Afrotropics at the base of or within its subclade **c40** (including some Perisphaerinae and possibly *Aptera*); another extension into the Australasian region (*Laxta*) is part of this clade. Regarding the smaller remaining blaberid clades, the monogeneric clade **c26** (*Gyna*) has little bearing. The Neotropical clade **c17** has, in spite of being monogeneric (*Panchlora*), some bearing, as it indicates that the earliest diversification of Blaberidae took place in the region that at present constitutes the Neotropics[2]. The geographic disjunctness of clade **c25** (*Diploptera* + *Thanatophyllum*) is of little relevance, as this clade only appears in some of the analyses. The phylogenetic disunity of the

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[1] The sampled *Blaberus craniifer* also occurs in Nearctic Florida, but it is disputed whether it is native or introduced in that area, see Atkinson et al. (1990).

[2] Four species of the large genus *Panchlora* occur in the Afrotropics (Gurney & Roth 1972), but these have never been included in a phylogenetic study.

Classification of Blaberidae

- ■ Panchlorinae
- □ Oxyhaloinae
- ■ Epilamprinae
- ■ Diplopterinae
- ■ Zetoborinae
- ■ Gyninae
- ■ Blaberinae
- ■ Perisphaerinae
- ■ Pycnoscelinae
- ■ Paranauphoetinae
- ■ Panesthiinae
- ■ Geoscapheinae

Regions

- ■ Nearctic
- ■ Neotropic
- □ Afrotropic
- ■ Australasian
- ■ Indo-Malayan
- ■ East Palearctic
- ■ West Palearctic
- ■ Not Applicable

epilamprines makes sense from a biogeographic point of view, as the main epilamprine clade **c37** is included in the Indo-Malayan and Australasian superordinate clade **c35**, whereas the genus *Epilampra* is mainly Neotropical with a few Nearctic representatives. The much clearer geographic structure of the blaberid part of the tree compared to the non-blaberid part might, in addition to the denser taxon sampling, in part be caused by the break-up of Gondwana, which was well under way at the time of the early diversification of Blaberidae ca. 60–160 mya (Djernæs et al. 2015: ca. 120–160 mya; Wang et al. 2017: 100–140 mya; Bourguignon et al. 2018: ca. 90–130 mya; Evangelista et al. 2019: 60–90 mya).

In several parts of the blaberid tree, geographic distribution is more congruent with phylogeny than the current classification is (Fig. 5), especially when considering the phylogenetically disjunct placement of members of the taxonomic units Epilamprinae and Perisphaerinae. Recent research on, for instance, Mantodea (e.g. Svenson & Whiting 2009) and Phasmatodea (e.g. Bradler & Buckley 2018: p. 289) is characterised by similar findings. In these taxa, incongruence between 'traditional' classification and recent results on phylogeny is evidently based on multiple convergence of superficial morphological characters in the course of adaptation to similar life habits (e.g. Svenson & Whiting 2009) – while classification has long been based on such characters. In Blattodea, the genus *Cryptocercus* provides an instructive example of the same matter. It was originally placed in or near the blaberid Panesthiinae (e.g. Brunner von Wattenwyl 1865; Kirby 1904). Later detailed morphological studies of the male and female genitalia (McKittrick 1964; Klass 1995; also influential in the morphology-based phylogenetic analyses of Deitz et al. 2003 and Klass & Meier 2006) suggested *Cryptocercus* to be phylogenetically far from Blaberidae, but close to Isoptera. Still later, the latter placement was consistently confirmed by molecular phylogenies (first by Lo et al. 2000, then by e.g. Inward et al. 2007 and Pellens et al. 2007). The earlier misclassification was based on similarity of external morphology (as explained by McKittrick 1964), likely caused by similar life styles (both *Cryptocercus* and Panesthiinae live in dead wood).

3.3.2. Body size

Overall phylogenetic trends in body size are similar in males and females using either body length or pronotum length as proxies for body size. We present here the mapping of female and male body lengths (Fig. S8). Non-blaberid Blaberoidea are on average distinctly smaller than blaberids, but with size ranges overlapping (e.g. Djernæs 2018). Our results support this, even though our reconstruction of ancestral body lengths for Blaberoidea and Blaberidae (10–22.5 mm) are identical. The size increase in Blaberidae happens in **c18** (Blaberidae excl. Panchlorinae), which has an ancestral body length of 22.5–33.8 mm. The ancestral body lengths for the other principal blaberoid clades are 15–22.5 mm in **c06** (Blattellidae s.s.) and **c05** (Nyctiboridae), 6.6–15 mm in **c14** (Pseudophyllodromiidae), and 6.6–10 mm in **c12** (Ectobiidae s.s.).

Some interesting points according to our reconstruction are: **(1)** A body length of 10–22.5 mm is widespread in non-blaberid Blaberoidea. Females are on average slightly larger, and thus the reconstructed plesiomorphic body length of Blaberoidea is 10–15 mm for males but 15–22.5 mm for females. **(2)** Throughout most of the non-blaberid part of the tree, there are at most minor changes to this (e.g. body lengths of 6.6–10 mm) – but with the striking exception of the minute myrmecophilous *Attaphila*. Based on our limited taxon sampling, mapping suggests that miniaturisation only happened at the base of *Attaphila* (with a drastic decrease from 6.6–22.5 mm to 2–4.4 mm), not gradually at the nodes preceding it, as members of the related genera *Xestoblatta*, *Pseudomops* and *Ischnoptera* are normally sized. This tentatively suggests that myrmecophily evolved simultaneously with body size reduction, and not in a group that already had acquired small body size long before as a prerequisite. **(3)** The larger size of blaberids is shown as rooted at the base of clade **c18** (Blaberidae excl. *Panchlora*), where size increases significantly from 10–15 mm to 22.5–33.8 in males and from 15–22.5 mm to 22.5–33.8 mm in females. This means that the size increase is not coincident with the acquisition of ovoviviparity at the base of Blaberidae, clade **c16**. *Panchlora* has retained the plesiomorphic moderate size of 10–22.5 mm body length. Following the base of clade **c18**, there are multiple cases of both decreasing and increasing size in Blaberidae. In a few cases these trends correlate with phylogenetic relationships: increasing size in clades **c23** (*Gromphadorina* and relatives), **c30** (*Blaberus* and relatives), and, less clearly, clade **c45** (*Macropanesthia* and relatives); decreasing size in clade **c43** (Perisphaerinae pars 2). A very large body length of more than 50.6 mm has been reached three times in the evolution of Blaberidae (in clades **c23** and **c30**, and in *Macropanesthia*), but not in any of our sampled non-blaberid Blaberoidea. However, members of the nyctiborid genus *Megaloblatta* (not included herein) can reach body lengths of at least 66 mm (Bell et al. 2007); while the placement of this genus in Nyctiborinae has

← **Fig. 5.** Tree showing geographical distribution of Blattodea and classification of Blaberidae into subfamilies. The numbers on the tree are the clade numbers used in the text and in Table 3; numbers in parentheses refer to a similar clade that is not present in this tree (but specified in Table 3 and in the text). Within Blaberidae, phylogeny is generally more congruent with geographical distribution patterns than with classification. See section 2.4.1. for definition of regions and Table S2 for more detailed information on distribution. The tree is based on those from analyses ML-T-P (Fig. 3) and ML-C-P (Fig. S4), see section 2.5. for details. Both the 'old' classification of Blaberidae and the revised classification introduced herein are shown.

never been tested (see 3.2.4.), it clearly belongs among the non-blaberid Blaberoidea (BOURGUIGNON et al. 2018).

The ratio between male (M) and female (F) body sizes did not show a clear phylogenetic trend (Fig. S9). However, male body length decreases slightly compared to female body length at the base of Blaberidae (**c16**) and males being distinctly shorter than females (M < 75% F) is more widespread in Blaberidae. However, in clades **c19** (Oxyhaloine) and **c44** (Panesthiinae s.l.) males are generally nearly as long as or even longer than females. This relatively large male body size is likely due to sexual selection over access to mates and/or territories. Males of representatives of both clades are known to fight each other (BARTH 1968a; RUGG & ROSE 1991; CLARK & MOORE 1995; Z. Varadínová & M. Kotyk pers. obs.) and, at least in *Gomphadorhina portentosa*, larger males are more frequent winners in these contests (BARTH 1968a; CLARK & MOORE 1995). No trends in the relative size of males and females are apparent when looking at pronotum length. Variation in the ratio between pronotum length and body length is distributed evenly across the phylogenetic tree in case of the males (average 27%, range 16−42%), but with regard to females (average 29%, range 18−52%) congruence with phylogeny is seen in some parts of the tree: **(1)** A relatively short female pronotum (≤ 25% of body length) has been acquired at the bases of clades **c19** (Oxyhaloinae) and **c44** (Panesthiinae s.l.), but in each clade there is a reversal to a normal ratio: *Gomphadorhina* in **c19**, and *Geoscapheus* + *Macropanesthia* in **c44**. **(2)** Relatively long female pronota have evolved independently in *Gyna* (> 36% of body length) and in clade **c43** (perisphaerines *Corydidarum*, *Perisphaerus*, *Pseudoglomeris*; ≥ 34% of body length).

3.3.3. Wing development

Our raw data on wing development confirm ROFF's (1990, 1994) observation that brachypterous and apterous conditions are more common in females than in males. Mapping of wing development on the tree shows that wing reduction or loss have occurred very often in Blaberoidea (as in Blattodea as a whole; Figs. S10, S11). In some parts of the blaberoid tree, however, the density of taxa with brachypterous or apterous females is so high that the reconstruction (Fig. S11) shows a deep event of wing reduction in females combined with later reversal(s) to full wing development as a plausible alternative to multiple wing reduction (e.g. clade **c11**, Ectobiidae s.s. + Pseudophyllodromiidae, and its subclades **c12** and **c14**; clade **c44**, Panesthiinae s.l.) or even as the preferred hypothesis (clade **c06**, Blattellidae s.s.) when losses and gains are treated as equally likely. There are no such cases with regard to the males (Fig. S10), with the minor exception of a reversal from apterous to brachypterous in *Brachynauphoeta*. For neither sex the reconstruction shows any unambiguous reversal from apterous to macropterous, as suggested for Phasmatodea by WHITING et al.'s (2003) analyses.

In the somewhat larger clades that consistently show some degree of wing reduction, the evolutionary succes-

sion of wing reduction in the two sexes varies strongly: In most of these clades, wing reduction in the female precedes wing reduction in the male, i.e. all taxa in the clade concerned show brachyptery or aptery in the female, but only some show such conditions in the male; examples are clades **c08** (*Blattella* and relatives) and **c39** (*Calolampra* and *Opisthoplatia*). In some clades, brachyptery or aptery have remained limited to females, such as in **c43** (*Pseudoglomeris* and relatives, with aptery in females). In other clades, wing reduction or loss has occurred simultaneously in both sexes, either to a weaker degree in males than in females, as in the *Attaphila* clade, or to the same extent in both sexes, as in clade **c22** (*Gromphadorina* and relatives). However, there are no clades in our trees in which wing reduction in the male precedes wing reduction in the female, or in which wing reduction is limited to the male. Furthermore, no cases of cockroaches with macropterous females and brachypterous or apterous males are known; however, when both sexes have reduced wings, females can have slightly longer wings (BELL et al. 2007).

ROFF (1986) suggested that a trade-off between flight ability and reproductive capacity might lead to wing reduction in females (with macroptery retained in males). Across the neopteran insects, brachypterous/flightless females generally have a higher reproductive output than macropterous/flight-capable females of the same species (CISPER et al. 2000; GUERRA 2011). ROFF (1989) also found increased egg production in female crickets following experimental wing removal. In contrast, KOTYK & VARADÍNOVÁ (2017) found no effect of experimental removal of wings on fecundity of macropterous female cockroaches. Yet it may make a difference whether females are genuinely wingless or have become deprived of their wings (i.e. have previously invested in the flight apparatus), thus it is still possible that female cockroaches are subjected to a trade-off between flight ability and reproductive capacity. Interestingly, KOTYK & VARADÍNOVÁ (2017) did find a marked negative effect of wing removal on mating success in macropterous males. They thus propose that there is positive selection for macroptery in male cockroaches, causing males to retain their wings while the females lose theirs.

3.3.4. Microhabitat

The microhabitat data on Blaberoidea have limitations, as a great proportion is based on incidental observations. The few focused studies show that microhabitat preferences often differ between day and night, between males and females, and between adults and larvae (SCHAL et al. 1984; GAUTIER & DELEPORTE 1986). Thus, many of the species for which we have microhabitat data are likely to occur in additional microhabitats. Keeping these limitations in mind, epigean, including leaf litter, is the most common microhabitat in non-blaberid Blaberoidea and was reconstructed as ancestral for Blaberoidea (and for Blattodea as a whole; Fig. S12). Despite the limitations, there are some fairly striking cases of microhabitat

change in the reconstruction. They concern either soft changes that likely require little adaptive modification, but are quite stable throughout larger clades; or drastic changes to divergent microhabitats that require considerable adaptation.

Blaberidae as a whole has generally left the ancestral epigean microhabitat, with early and extensive diversification of microhabitat preferences. Indeed, according to our sample, clade **c37** (larger part of Epilamprinae) is the only significant remainder of the epigean life habit in Blaberidae. Two soft microhabitat changes in Blaberidae are noteworthy: a strong tendency to live in cavities is present in clade **c29** (larger part of Blaberinae) and a change to life under loose bark is found in clade **c34** (*Lanxoblatta* + *Phortioeca* + *Zetobora*).

Blaberid clade **c44** (Panesthiinae s.l.) is one example of a more drastic microhabitat change to life in dead wood, which required considerable adaptation. The reconstruction (Fig. S12) suggests that this change originated from the context of the plesiomorphic epigean life habit, although this point of the reconstruction does not appear very reliable (i.e., could be sensitive to the addition of further blaberid taxa). On the other hand, an epigean origin is also reconstructed for the clade comprised of *Cryptocercus* and Isoptera (where it appears more reliable). In neither instance is there any indication that the adaptation to dead wood might instead have originated from some other hidden wood-related microhabitat, such as life in pre-existing tree holes or under loose bark, though any of these could have played a role in the stem groups of clades **c44** and *Cryptocercus* + Isoptera. Another drastic change, the adaptation to soil burrowing, has originated in a subordinate clade of the dead-wood clade **c44**, in *Geoscapheus* + *Macropanesthia* (**c46**). This change could have its basis in an extension of galleries from dead wood down into the soil, with subsequent limitation to the latter. According to Lo et al. (2016) the change from dead wood to soil occurred several times within Panesthiinae s.l., with aridification as the driving factor. It is noteworthy that the shift from dead wood to soil has also occurred within the *Cryptocercus* + Isoptera clade, where *Cryptocercus* and several termite taxa construct galleries in dead wood, while many other termites expand this into the soil, and still others have acquired methods of nest-building independent of wood (Noirot & Darlington 2000).

Another drastic change is that to insect nests as found in *Attaphila*. The reconstruction suggests that it started from the plesiomorphic epigean life habits, or perhaps from life on herbage, as these are the life habits of the closest relatives of *Attaphila*. It appears thus plausible that first adaptive steps of *Attaphila* for regulating contact with ants have taken place in leaf litter or herbage and related to foraging ants. The alternative that the association with ants started from a preference for microhabitats similar to an ant nest (such as cavities), and that first adaptive steps occurred in ant nests, where *Attaphila* ancestors often showed up when searching for crevices, is not suggested by the reconstruction.

3.3.5. Mating

In contrast to the situation in microhabitats, incidental observations can be considered to be sufficient for categorising the mating pattern of a species, but not even these are available for the majority of the taxa in our sample. The reconstruction (Fig. S13) thus shows numerous gaps. Type A (female mounts male) is by far the most common mating pattern observed in Blaberoidea and was unambiguously reconstructed as ancestral for Blaberoidea (and for Blattodea as a whole). Type B (male mounts female) is here only included for *Pycnoscelus surinamensis* (based on observations on *P. indicus* (Fabricius, 1775), the sexual parent species for the parthenogenetic *P. surinamensis*). Type C (no mounting) is only reported for some Blaberidae (except for the polyphagid *Therea*); according to our reconstruction it has clearly originated four times independently from type A within Blaberidae: in the basalmost offshoot clade **c17** (*Panchlora*), in clade **c23** (subclade of **c19**, Oxyhaloinae), in (part of) clade **c44** (Panesthiinae s.l.), and in part of *Epilampra* (*E. involucris* Fisk & Schal, 1981). In none of these cases a reversal to type A is evident.

Our results agree with those of Sreng (1993) in that type A is the most widespread and probably ancestral type of mating and that types B and C are quite unusual and have evolved several times, mostly in Blaberidae. However, our results do not support Sreng's hypothesis that type B is an intermediate state between types A and C. Instead they show that both types B and C arose independently from type A. Evolutionary explanations of transitions from mating type A to B or C are mostly unclear and might differ between particular cases. In clade **c44** (Panesthiinae s.l.) the occurrence of type C could be attributed to confined spaces of the deadwood and soil galleries; however, *Cryptocercus*, which also live in deadwood galleries, have maintained type A.

3.3.6. Egg/ootheca handling

Similar to the mating pattern, incidental observations can suffice for categorising the reproductive mode of a species, but these must usually refer to the final stage of ootheca handling. Such data are available for most of the taxa sampled. Oviparity A (dropping the egg case well before hatch) is by far the most common reproductive mode in non-blaberid Blaberoidea and was unambiguously reconstructed as ancestral for Blaberoidea (and for Blattodea as a whole; as also claimed in Roth 1989a and Bell et al. 2007) (Fig. S14). In contrast, in Blaberidae ovoviviparity A (ootheca carried internally until hatch) is predominant (see also McKittrick 1964; Roth 1968a; Bell et al. 2007) and was unambiguously reconstructed as ancestral for this group. These results are consistent with those of Evangelista et al. (2019: fig. 3b,c, albeit with different categories of ootheca handling). The other modes occur only in very few, strongly subordinate taxa of our sample, having been acquired independently in each of the following cases: **(1)** oviparity B (carrying oo-

theca externally until hatch) in the *Blattella* species arose from oviparity A within clade **c06** (Blattellidae s.s.); **(2)** ovoviviparity B (no ootheca, eggs carried internally until hatch) in clade **c46** (*Geoscapheus* + *Macropanesthia*) arose from ovoviviparity A within clade **c44** (Panesthiinae s.l.); and **(3)** viviparity (eggs carried internally until hatch, provision of nutrients) in *Diploptera punctata* also arose from ovoviviparity A. An interesting point is that ovoviviparity A of Blaberidae (**c16**) evolved in a different corner of the blaberoid tree than oviparity B (within **c06**, Blattellidae s.s.), although the longer retention of the ootheca in the latter would appear as an ideal evolutionary starting point for the retraction of the ootheca in the former.

The picture of how the ootheca is handled in the non-blaberid Blaberoidea is enriched by data on taxa not sampled herein, which are assigned partly to Pseudophyllodromiidae and partly to Blattellidae s.s. First, while in our data set oviparity B only clearly occurs in *Blattella*, it has also been reported for *Chorisia* Princis, 1951 (Blattellidae s.s., considered as closely related to *Blattella*) and for some *Lophoblatta* Hebard, 1929 (Pseudophyllodromiidae) (Roth 1968a,b, 1983). Second, ovoviviparity A has been reported for the following taxa: **(1)** *Sliferia* Roth, 1989 (Pseudophyllodromiidae) retracts nearly the entire ootheca into the abdomen (incomplete ovoviviparity A; Roth 1989a, 2003b). Complete retraction of the ootheca into the abdomen is found in **(2)** *Pseudobalta* Roth, 1997 (Pseudophyllodromiidae; ootheca membranous and transparent as is typical for ovoviviparous species producing an ootheca: Roth 1997), **(3)** *Stayella* Roth, 1984 (Blattellidae s.s.; Roth 1982a), and **(4)** *Pseudoanaplectinia* (Blattellidae s.s.; small transparent ootheca with 3−5 eggs; Roth 1995a). Members of the first three ovoviviparous genera have not yet been included in any well-documented morphology- or DNA-based phylogenetic study (taxa only listed in Grandcolas' 1996 morphology-based analysis, but without documentation of their characters; see Klass 2001 for a discussion of that study). *Pseudoanaplectinia* is represented in Legendre et al. (2015), where, however, it was placed in a doubtful clade including mainly pseudophyllodromiids but also blattellids s.s. and an anaplectid (see 3.2.2.). Consequently, the phylogenetic positions of all four genera in Blaberoidea are fairly unclear. It cannot be ruled out that some of them are closest to Blaberidae and their ovoviviparity A goes back to the same origin as for Blaberidae. Yet it appears likely that ovoviviparity A has evolved several times in Blaberoidea, but not in other cockroaches (Blattoidea and Corydioidea). Then, some factor likely predisposed Blaberoidea to ovoviviparity. Rotation of the completed ootheca by 90°, likely present in all Blaberoidea except Pseudophyllodromiidae (also present in *Ectobius*, contra Evangelista et al. 2019: fig. 3a; see e.g. Brown 1973a),

was viewed by Roth (1967a) and Bell et al. (2007) as a key factor in the evolution of ovoviviparity. As an ootheca is usually higher than wide, a rotated ootheca fits better with the transverse format of the cockroach and thus improves the mother's ability to move through vertically constricted spaces. It also fits better with the transverse format of the vestibulum (the perigenitalic space above the subgenital plate, where the ootheca is built), which eases its retraction into the vestibulum (where its frontal end is held horizontally after rotation). This brings the anterior eggs in contact with the walls of the mother's vestibulum, and with increasing retraction based on the concurrent evolution of a brood sac from the anteroventral part of the vestibulum more eggs get the option for such contact. However, *Sliferia* and *Pseudobalta* do not rotate the ootheca (Roth 1989a, 1997); in *Sliferia* the ootheca is wider than high, which can be seen as an adaptive alternative to rotation (Roth 1989a).

It is worth noting that oviparity B might also occur in Anaplectidae, which would be unique within Blattoidea. McKittrick (1964) observed preserved specimens of several *Anaplecta* species which were carrying a mature (unrotated) ootheca. However, more information is needed on whether *Anaplecta* species carry the ootheca externally until hatch or drop it well prior to hatch as several species exhibiting oviparity A are known to carry the ootheca for several days before dropping it (e.g. *Ectobius panzeri*, Brown 1973a).
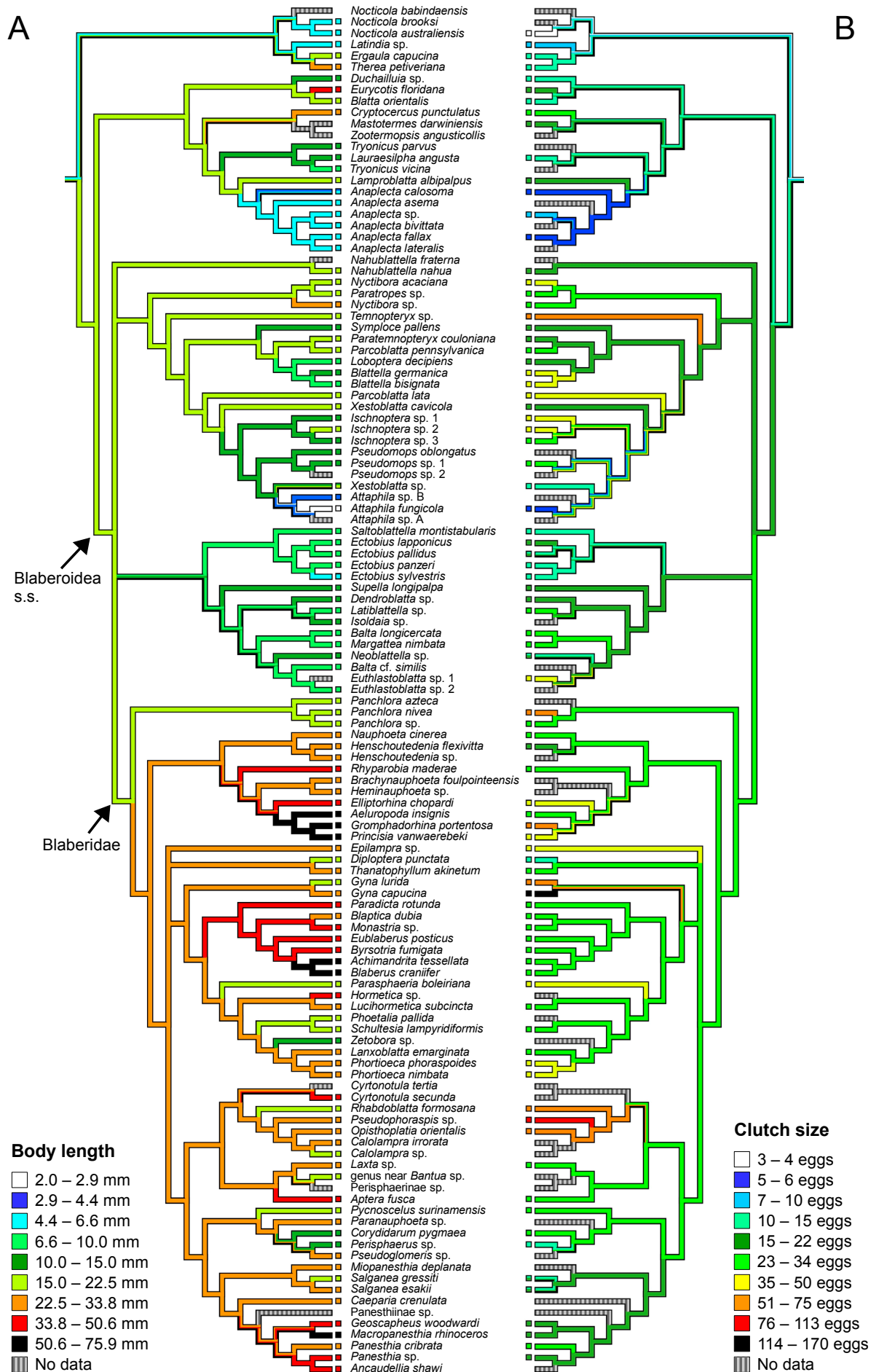
3.3.7. Clutch size

Data on clutch size can be gained, by counting egg chambers, from a completed ootheca found either in isolation or in association with the mother, and thus by any incidental finding of such an ootheca. In contrast, data on the complete number of eggs produced by a female during her lifetime (total egg number = number of oothecae × clutch sizes) need long-time observation, and are thus much sparser.

Mapping of clutch size on the tree does not show any clear pattern, although there is a slight increase in clutch size at (or near) the base of Blaberidae: a low-moderate number of 15−22 eggs is reconstructed as ancestral for Blaberoidea, but a slightly higher number of 23−34 eggs as ancestral for Blaberidae (Fig. 6). Clutch size is also overall higher in Blaberidae, with 75% of the species producing oothecae averaging 20−57 eggs (median 31), than in non-blaberid Blaberoidea, with 75% of the species producing oothecae averaging 14−38 eggs (median 23). However, clutch size relative to body size is generally lower in Blaberidae than in non-blaberid Blaberoidea (Fig. S15).

The large clutch sizes in Blaberidae are surprising at first glance, as by practising ovoviviparity blaberids have

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→ **Fig. 6.** Trees showing female body length (**A**) compared to clutch size (**B**). Note the increase in body size in Blaberidae excl. Panchlorinae and the congruence between body size and clutch size. See Tables S4 and S5 for details on body size and clutch size. The tree is based on those from analyses ML-T-P (Fig. 3) and ML-C-P (Fig. S4), see section 2.5. for details.

A

B

Nocticola babindaensis
Nocticola brooksi
Nocticola australiensis
Latindia sp.
Ergaula capucina
Therea petiveriana
Duchailluia sp.
Eurycotis floridana
Blatta orientalis
Cryptocercus punctulatus
Mastotermes darwiniensis
Zootermopsis angusticollis
Tryonicus parvus
Lauraesilpha angusta
Tryonicus vicina
Lamproblatta albipalpus
Anaplecta calosoma
Anaplecta asema
Anaplecta sp.
Anaplecta bivittata
Anaplecta fallax
Anaplecta lateralis
Nahublattella fraterna
Nahublattella nahua
Nyctibora acaciana
Paratropes sp.
Nyctibora sp.
Temnopteryx sp.
Symploce pallens
Paratemnopteryx couloniana
Parcoblatta pennsylvanica
Loboptera decipiens
Blattella germanica
Blattella bisignata
Parcoblatta lata
Xestoblatta cavicola
Ischnoptera sp. 1
Ischnoptera sp. 2
Ischnoptera sp. 3
Pseudomops oblongatus
Pseudomops sp. 1
Pseudomops sp. 2
Xestoblatta sp.
Attaphila sp. B
Attaphila fungicola
Attaphila sp. A
Saltoblattella montistabularis
Ectobius lapponicus
Ectobius pallidus
Ectobius panzeri
Ectobius sylvestris
Supella longipalpa
Dendroblatta sp.
Latiblattella sp.
Isoldaia sp.
Balta longicercata
Margattea nimbata
Neoblattella sp.
Balta cf. *similis*
Euthlastoblatta sp. 1
Euthlastoblatta sp. 2
Panchlora azteca
Panchlora nivea
Panchlora sp.
Nauphoeta cinerea
Henschoutedenia flexivitta
Henschoutedenia sp.
Rhyparobia maderae
Brachynauphoeta foulpointeensis
Heminauphoeta sp.
Elliptorhina chopardi
Aeluropoda insignis
Gromphadorhina portentosa
Princisia vanwaerebeki
Epilampra sp.
Diploptera punctata
Thanatophyllum akinetum
Gyna lurida
Gyna capucina
Paradicta rotunda
Blaptica dubia
Monastria sp.
Eublaberus posticus
Byrsotria fumigata
Achimandrita tessellata
Blaberus craniifer
Parasphaeria boleiriana
Hormetica sp.
Lucihormetica subcincta
Phoetalia pallida
Schultesia lampyridiformis
Zetobora sp.
Lanxoblatta emarginata
Phortioeca phoraspoides
Phortioeca nimbata
Cyrtonotula tertia
Cyrtonotula secunda
Rhabdoblatta formosana
Pseudophoraspis sp.
Opisthoplatia orientalis
Calolampra irrorata
Calolampra sp.
Laxta sp.
genus near *Bantua* sp.
Perisphaerinae sp.
Aptera fusca
Pycnoscelus surinamensis
Paranauphoeta sp.
Corydidarum pygmaea
Perisphaerus sp.
Pseudoglomeris sp.
Miopanesthia deplanata
Salganea gressiti
Salganea esakii
Caeparia crenulata
Panesthiinae sp.
Geoscapheus woodwardi
Macropanesthia rhinoceros
Panesthia cribrata
Panesthia sp.
Ancaudellia shawi

Blaberoidea s.s.

Blaberidae

Body length

- ☐ 2.0 – 2.9 mm
- ■ 2.9 – 4.4 mm
- ■ 4.4 – 6.6 mm
- ■ 6.6 – 10.0 mm
- ■ 10.0 – 15.0 mm
- ■ 15.0 – 22.5 mm
- ■ 22.5 – 33.8 mm
- ■ 33.8 – 50.6 mm
- ■ 50.6 – 75.9 mm
- ▦ No data

Clutch size

- ☐ 3 – 4 eggs
- ■ 5 – 6 eggs
- ■ 7 – 10 eggs
- ■ 10 – 15 eggs
- ■ 15 – 22 eggs
- ■ 23 – 34 eggs
- ■ 35 – 50 eggs
- ■ 51 – 75 eggs
- ■ 76 – 113 eggs
- ■ 114 – 170 eggs
- ▦ No data

reached a higher level of brood care than non-blaberid blaberoids, which predominantly practise oviparity A. On the other hand, the picture could well be different when considering total egg number: In taxa practising oviparity A, oothecae can be produced in rapid succession, whereby a high total egg number can be reached. In contrast, in taxa practising ovoviviparity, a retracted ootheca blocks the production of further oothecae for a longer period, whereby total egg number could be relatively low (oviparity A: a new ootheca every 2–15 days; oviparity B: every 21–35 days; ovoviviparity A and B: every 39–90 days; viviparous *Diploptera punctata*: every 70–100 days; data in RAU 1940, WILLIS et al. 1958, BOYER & RIVAULT 2004).

Even when comparing different taxa showing oviparity A, clutch size is not an accurate measure of reproductive investment and potential. It might be more advantageous for some oviparous taxa to produce many small oothecae, and for others to produce few larger ones. This is essentially a matter of after how many eggs an ootheca is terminated and dropped, and a new one is started. The changes of clutch size in the non-blaberid part of the Blaberoidea tree must be seen in this light, including the fact that the intervals between instances of ootheca completion vary at least by a factor 7 (see above). Data on the total egg numbers are needed for assessing reproductive potential.

In contrast, when comparing different ovoviviparous taxa, clutch size is probably a more significant measure, as each clutch must be carried by the mother until the eggs are ready to hatch; the intervals between completion (i.e. extrusion) of individual retracted oothecae vary only by a factor 2.25 (see above). Thus, both the increase of clutch size within clade **c38** (*Rhabdoblatta* and relatives) to > 51 and the (secondary) decrease in clade **c44** (Panesthiinae s.l.) to < 22 are likely biologically relevant changes. The decrease in clutch size in **c44** might be correlated with increased reproductive investment in the form of parental care as several panesthiines s.l. care for their offspring after hatch (e.g. stomodeal feeding in *Salganea taiwanensis* Roth, 1979, MAEKAWA et al. 2008; shelter and provisions in *Macropanesthia rhinoceros*, RUGG & ROSE 1991). However, other panesthiines s.l. such as *Panesthia cribrata* seem to have very limited or no post-hatch parental care (RUGG & ROSE 1984b).

3.4. Statistical correlations between characters

3.4.1. Body size: pronotum – body length and male – female size

Correlation analyses (PDAP) of body size show that body length and pronotum length are very strongly correlated in each sex ($P = 0.0$): Body length explains more than 80% of the size variance in pronotum length ($R^2 > 0.8$). Relative length of the pronotum (compared to body

length) is not significantly correlated with body length in either sex. This means that the ratio between body length and pronotum length does not vary regularly depending on body size. Male and female body size are very strongly correlated ($P = 0.0$) whether measured as total body length or pronotum length (Fig. S8): The size of one sex explains more than 90% of the size variance in the other sex ($R^2 > 0.9$). Table 2 shows more precise R^2 and *P*-values. The ratio between male and female body size is not correlated with female body size, whether measured as total body length or pronotum length. This means that the ratio between body sizes of males and females does not vary regularly depending on body size.

BELL et al. (2007) suggested that female cockroaches are usually larger than conspecific males, and our data confirm this with females being the larger sex in ca. 65% of the species in Blattodea and Blaberoidea, and in 79% of species in Blaberidae; male body length is on average 95% of female body length in Blattodea and Blaberoidea, but 91% of female body length in Blaberidae. Such female-biased sexual size dimorphism (SSD) is widespread in insects (TEDER & TAMMARU 2005). The degree of SSD is sometimes correlated with body size, i.e. SSD decreases with increasing size in taxa with female-biased SSD and increases with increasing size in taxa with male-biased SSD (Rensch's rule). Such relationships were found in e.g. Heteroptera and some Diptera, but not in the studied polyneopteran taxa (BLANCKENHORN et al. 2007; BIDAU et al. 2016). Our data set confirms the absence of agreement with Rensch's rule (or its opposite) for the polyneopteran cockroaches.

3.4.2. Microhabitat – wing development

BELL et al. (2007) suggested that cockroaches living in enclosed microhabitats (soil, dead wood, crevices) were most likely to have lost or reduced their wings. This seems to apply to some of the clades characterised by wing reduction or loss: *Attaphila* with brachypterous males and apterous females live enclosed in ant nests and the two genera in clade **c46** (*Geoscapheus* + *Macropanesthia*) live in burrows in the soil. However, we did not find any correlation between brachyptery or aptery and any of our habitat categories (or combination of categories). Yet, it should be noted that some macropterous species living in enclosed microhabitats shed their wings, thus achieving effective brachyptery; this is the case for all termites and several species of Panesthiinae s.l. (BELL et al. 2007; ROTH 1979a and references therein). This could obscure a correlation between wing reduction and living in enclosed microhabitats.

3.4.3. Microhabitat – body size

Our correlation analyses (PAGEL's 1994) found several correlations between microhabitat and body size (Table 5).

Being small to medium sized (body length 5–15 mm, 5–20 mm, 5–25 mm, or 5–30 mm) was correlated with

Table 5. Results (*P*-values) of correlation analyses (Pagel's 1994) between microhabitat and body length. See section 2.6. for details about the analyses. In first column, F = female, M = Male. 'n.s.' indicates that no significant correlation was found. Actual* branch lengths were based on the branch lengths from the ML-C-P tree. [a] indicates that the *P* value was based on 10,000 simulations.

Correlation between	Actual* branch lengths	Branch lengths = 1
Habitat = epigean ***vs*** F body length 5 – 30 mm	*P* = 0.001	*P* = 0.010
Habitat = epigean ***vs*** F body length 5 – 25 mm	*P* = 0.005	*P* = 0.023
Habitat = epigean ***vs*** F body length 5 – 20 mm	*P* = 0.023	*P* = 0.007
Habitat = epigean ***vs*** F body length 5 – 15 mm	*P* < 0.003[a]	*P* = 0.004
Habitat = epigean ***vs*** M body length 5 – 30 mm	*P* = 0.010	n.s.
Habitat = epigean ***vs*** M body length 5 – 25 mm	*P* = 0.021	n.s.
Habitat = epigean ***vs*** M body length 5 – 20 mm	n.s.	n.s
Habitat = epigean ***vs*** M body length 5 – 15 mm	*P* = 0.006	*P* = 0.012
Habitat = inquiline ***vs*** F body length < 5 mm	*P* = 0.010	*P* < 0.001[a]
Habitat = inquiline ***vs*** F body length < 4 mm	*P* = 0.003	*P* = 0.0
Habitat = inquiline ***vs*** M body length < 5 mm	*P* = 0.019	*P* = 0.004
Habitat = inquiline ***vs*** M body length < 4 mm	*P* = 0.033	*P* < 0.001[a]
Habitat = loose bark ***vs*** F body length 10 – 40 mm	n.s.	n.s.
Habitat = loose bark ***vs*** F body length 15 – 35 mm	n.s.	n.s.[a]
Habitat = loose bark ***vs*** M body length 10 – 40 mm	*P* = 0.030	*P* = 0.039
Habitat = loose bark ***vs*** M body length 15 – 35 mm	n.s.	*P* = 0.026

being epigean for females, whether actual branch lengths[1] or all branch lengths = 1 were used. In males, the correlation was only significant in some cases (body length 5 – 25 mm or 5 – 30 mm with actual branch lengths; body length 5 – 15 mm with both types of branch lengths). For something shaped like a typical cockroach this might be the optimal size range for moving through the leaf litter and being able to avoid predators. Our character mapping (see 3.3.2. and 3.3.4.) shows epigean as the ancestral microhabitat for Blaberoidea (and for Blattodea), and the ancestral body length for Blaberoidea as 10 – 15 mm in males and 15 – 22.5 mm in females. This can be taken as agreeing with the correlation between 5 – 30 mm body length and epigean microhabitat, as long as leaf litter in the times of early diversification of Blaberoidea was of similar structure as today.

Being medium sized (body length 15 – 35 mm or 10 – 40 mm) was correlated with living under loose bark for males (except for body length 15 – 35 mm when actual branch lengths were used, see Table 5), while females showed no significant correlation between these size intervals and living under loose bark.

A correlation between small body size and living in insect nests was already proposed by Wheeler (1900). He noted that both *Attaphila* and an inquiline cricket, *Myrmecophilus* Berthold, 1827, which were then the only polyneopterans known to live closely associated with ants, were very small. Today several additional species of cockroaches are known to live in ant or termite nests, such as members of the genera *Myrmecoblatta* Mann, 1914 (Corydiidae), *Pseudoanaplectinia* (Blattellidae s.s.), and *Nocticola* (Nocticolidae). They are all diminutive (body length < 6 mm, Hebard 1917a; Roth 1988, 1995a; Table S3). In our analyses of the entire Blattodea (including inquiline *Attaphila* but only non-inquiline *Nocticola*) we found a strong positive correlation between having a very small body size (body length 2 – 5 mm) and living in insect nests. Bell et al. (2007) suggested that small size facilitates integration of the inquiline cockroaches into the colony life of their hosts. *Attaphila fungicola* rides on large soldiers as well as on queens of the host *Atta texana* (Buckley) during mating flights (Moser 1964; Phillips et al. 2017), and this is only possible as *Attaphila* is distinctly smaller (body length ≈ 2.5 mm) than the soldiers and queens. Thus, the ability to spread vertically (following the line of descent) with the host by riding queens on their mating flight may select for small size. Small size might also ease squeezing into nooks and crannies in the host's nest and thus remain unnoticed. However, *A. fungicola* is not that much smaller than the minor workers (body length ≈ 3.5 mm) (Moser 1964). Additionally, *Attaphila* seem to employ chemical mimicry to be accepted by their hosts (Nehring et al. 2016). Wheeler (1900) thought that inquilines had originally been diminutive and that this facilitated adaptation to their current lifestyle – rather than size reduction having occurred during the adaptation to this lifestyle. However, size reduction in *Attaphila* has more likely occurred during adaptation to the inquiline lifestyle as its closest relatives are much larger (see 3.3.2.; Fig. S8).

3.4.4. Clutch size – body size

Correlation analyses (PDAP, Table 2) found a strong positive correlation (*P* < 0.001) between clutch size and female body size measured as either body length or pronotum length for the entire Blattodea (Figs. 6, S16): Body size statistically explains about 25 – 30% of the variance in clutch size (R^2 = 0.3). This means that larger females tend to produce larger clutches. A positive correlation between female body size and number of eggs across species was found in Orthoptera (Stauffer & Whitman

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[1] Branch lengths based on the branch lengths from the partitioned Maximum Likelihood analysis of the complete data set.

1997) and Diptera, but not in Hymenoptera and Coleoptera (BERRIGAN 1991). In our data for Blattodea, however, we refer to clutch size (eggs per ootheca), not to the entire number of eggs produced by a female (see 3.3.7.); this makes comparison with the cited results complicated.

One aspect of the correlation between female body size and clutch size in Blattodea is the abovementioned phylogenetic trend of slightly increased clutch size in the overall larger Blaberidae (20–57 eggs) compared to non-blaberid Blaberoidea (14–38 eggs) (Fig. 6). In this part of the tree, the question is whether further factors are involved in this interplay, which is the driving factor, and what are the underlying functional correlations. As argued in 3.3.7., clutch size in Blaberidae is plausibly affected by their ovoviviparity. Two interrelated points are relevant in the interplay between body size, clutch size, and ovoviviparity: **(1)** The phylogenetic origin of increased body size was found at the base of clade **c18** (Blaberidae excluding *Panchlora*), whereas the increase of clutch size (less clearly) and the origin of ovoviviparity A (very clearly) are reconstructed at the base of Blaberidae (**c16**). **(2)** Ovoviviparity in Blaberidae might affect the total lifetime egg number in three ways by keeping the ootheca within the body: First, actual length of the abdomen likely limits the ability to increase ootheca size and thus clutch size; second, due to the longer intervals required between successive oothecae it reduces the number of oothecae that can be produced during a female's life; and third, due to the higher level of brood care for the individual eggs, some reduction of egg number is likely possible. The data suggest that these three factors together resulted in selection towards a slight increase of clutch size, i.e. brood care could apparently not compensate the lower frequency of ootheca production. One plausible way to allow for larger clutch size is to increase body length. Another (less common) way is to fold or bend the ootheca, which has been observed in the genus *Gyna*: *G. capucina* and *G. henrardi* Hanitsch, 1950 have the largest clutch sizes known in cockroaches, up to 144 and 243 eggs per ootheca, respectively – much larger than other species of *Gyna* (28–62 eggs) (GRANDCOLAS & DELEPORTE 1998). *G. capucina* and *G. henrardi* fold the ootheca like a Z in order to fit it into the abdomen; this zigzag folding is not known from any other cockroach (GRANDCOLAS & DELEPORTE 1998). *Panchlora nivea* employs a similar but less elaborate strategy: it produces 53–60 eggs per ootheca (ROTH & WILLIS 1957a), a relatively large number compared to its body size, and has an ootheca curved like the letters J or C (ROTH & WILLIS 1957a; ROTH 1968a).

In conclusion, ovoviviparity might have been the original driving force in the evolution of the three traits in Blaberidae and might have affected clutch size and body size as follows: **(1)** Ovoviviparity selected for increased clutch size to maintain a sufficiently high total lifetime egg number. **(2)** In clade **c18** (Blaberidae excl. Panchlorinae) this could have led to an increase of body size, which enabled an increase of ootheca length and thus clutch size. **(3)** In *G. capucina* (*G. henrardi* not included in the present study) and *P. nivea*, the same selection could have led to a folding of the ootheca, by which it could be longer without increase in body length. This could explain why the increase in clutch size precedes the increase in body length in Blaberidae. On the other hand, however, Blaberidae generally have lower clutch size *relative to body size* than non-blaberid Blaberoidea (see 3.3.7., Fig. S15). In view of this, the increase of body size in **c18** could alternatively have occurred for other reasons, but could have been a factor *allowing* for an increase of clutch size. It is also noteworthy that the subclades of Blaberidae showing exceptionally large body length are not characterised by exceptionally high clutch sizes (Fig. 6).

4. Conclusions

Our phylogenetic analyses using Bayesian inference and Maximum Likelihood yielded five principal lineages within Blaberoidea, the relationships among which remain unclear: Blaberidae, Pseudophyllodromiidae, Ectobiidae s.s., Blattellidae s.s., and Nyctiboridae (while Anaplectidae are confirmed to belong to Blattoidea). This classification provides a solid foundation for future work on Blaberoidea systematics. It essentially agrees with the findings in other recent molecular studies of Blattodea and with previous taxonomic divisions – although with exceptions. Compared to previous classification, the consistently unsupported "Ectobiidae s.l.", comprising the non-blaberid lineages, is abandoned and its subfamilies raised to family rank; and Attaphilinae, included in a molecular study for the first time, is sunk in Blattellidae s.s., in which it is deeply subordinate.

In all four non-blaberid families the number of genera sampled in our and other recent studies is still very limited (see Table 4), and a significant increase of this number should be a major focus of forthcoming studies. The inclusion of "ectobiid s.l." genera specified as "incertae sedis" (i.e. without assignment to subfamily, e.g. in the "Blattodea Species File") and of sub-saharan Ectobiidae s.s. is of particular interest. In addition, the inclusion of genera with specialised biological features would be of great interest, such as the beetle-mimicking members of the genus *Prosoplecta* (see SHELFORD 1912). The detection of further principal lineages of Blaberoidea in such work would not be surprising. *Nahublattella*, usually assigned to Pseudophyllodromiinae/-idae, is one candidate for representing such a lineage, but the currently available data are too poor for a solid placement.

In Blaberidae, we found that the phylogenetic structuring into large clades shows a striking correlation with the occurrence in the main biogeographic regions; this resembles recent results in Mantodea and Phasmatodea. Among the well-sampled blaberid "subfamilies" (with several genera), some are supported in phylogenetic analyses, either alone (Oxyhaloinae), or at least in groups of two (Blaberinae + Zetoborinae; Panesthiinae + Geo-

scaphaeinae). Two other subfamilies appear as polyphyletic: **(1)** In Epilamprinae our single sampled *Epilampra* was far remote from the other sampled epilamprines; other recent studies suggest an even stronger phylogenetic fragmentation of Epilamprinae. **(2)** Perisphaerinae was split in two disjunct clades. Epilamprinae and Perisphaerinae thus require a new structuring in subfamilies; to reach this, many more of their genera should be sampled – in view of the distinct biogeographic pattern of the blaberid tree best from all biogeographic regions where they occur. In addition, there are some smaller clades and isolated terminals in our analyses that represent subfamilies with only one or a few genera (Panchlorinae, Diplopterinae, Gyninae, Pycnoscelinae), and some members of the larger subfamilies behave as rogue taxa (*Aptera*, *Thanatophyllum*). For these taxa the sampling of further genera or (if monogeneric) species is also desirable – from different biogeographic regions if this is applicable; Afrotropical Panchlorinae is a case in point. We further recommend the inclusion of genera so far specified as "incertae sedis" (without assignment to subfamily). As for Blaberoidea as a whole, the detection of further principal lineages of Blaberidae would not be surprising.

Our mapping of life-history traits on the phylogenetic trees and the statistical evaluation of correlations between some of these traits yielded some interesting results on the evolution of microhabitat choice, wing development, mating type, mode of ootheca handling, clutch size, body size, and male-female size dimorphism. Resulting hypotheses are quite straightforward in terms of wing reduction, which in different taxa occured in both sexes simultaneously or first in females, and in mating type, with a plesiomorphic and two independent apomorphic types. On the other hand ootheca handling, clutch size, and body size show some complicated interrelationships, but some plausible explanations for these are presented here. However, besides the limited representation of blaberoid genera in the phylogenetic hypotheses detailed above, much more data are needed on life-history traits. This concerns traits for which incidental observations are already informative, e.g. on aggregation or on flight capability, but especially traits that require medium- or long-term observations, such as microhabitat selection at different times of the day and by different instars and sexes, total egg production (sum of eggs in all oothecae produced), parental behaviour, or territoriality. There is a particular shortcoming with regard to the natural diet of cockroach species (a trait thus not included in the present paper; see DjernÆs 2018), which can only be obtained by observation in nature (not in cultures with standardised food), or by analyses of gut contents of specimens caught in nature. To expand our knowledge of cockroach life-history characteristics is thus an important challenge for future studies of the evolution of Blattodea. We thus encourage researchers to publish any life-history related observations, and we underline the desirability of targeted life-history studies. Future studies of evolutionary trends and correlations between life-history traits in Blattodea might either look at non-blaberoids (sparsely sampled in this paper), or focus on blaberoid clades identified here as exhibiting large variation in one or more of these traits (e.g. Oxyhaloinae, with large variation in body size, clutch size, and wing development).

5. Acknowledgements

6. References

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DOI: 10.26049/ASP78-1-2020-03/1

Fig. S1. Previous hypotheses regarding the relationships between the various subfamilies of Blaberoidea s.l. Assignment of taxa to subfamilies based on Cockroach Species file (BECCALONI 2014) and not always congruent with the assignments used by the authors of the respective studies. For further details on taxon sampling for the various trees, refer to the respective studies.

Fig. S2. Tree from Maximum Likelihood analysis of the unpartitioned trimmed data set (ML-T-unP). See section 2.3. for details about the analysis.

Fig. S3. Tree from Maximum Likelihood analysis of the unpartitioned complete data set (ML-C-unP). See section 2.3. for details about the analysis.

Fig. S4. Tree from Maximum Likelihood analysis of the complete data set using eight partitions (ML-C-P). See section 2.3. for details about the analysis.

Fig. S5. Tree from Bayesian Inference analysis of the unpartitioned trimmed data set (BI-T-unP). See section 2.3. for details about the analysis.

Fig. S6. Tree from Bayesian Inference analysis of the trimmed data set using eight partitions (BI-T-P). See section 2.3. for details about the analysis.

Fig. S7. Tree from Bayesian Inference analysis of the unpartitioned complete data set (BI-C-unP). See section 2.3. for details about the analysis.

Fig. S8. Mapping of body length of males and females. See Table S3 for information on body length as well as information on pronotum length. The tree is based on the ML-T-P (Fig. 3) and ML-C-P (Fig. S4) trees, see section 2.5. for details.

Fig. S9. Mapping of body length of males in relation to that of conspecific females. The more reddish the colour, the longer the males are compared to conspecific females. The more blueish the colour, the shorter the males are compared to conspecific females. The numbers beside the coloured boxes are log10 (M body length / F body length). Negative numbers indicate that males are shorter than conspecific females while positive numbers indicate that males are longer than conspecific females. See Table S3 for actual body lengths. The tree is one of two trees used for PDAP correlation analyses, based on the ML-T-P (Fig. 3) and ML-C-P (Fig. S4) trees, see sections 2.5. and 2.6. for details. Note that the clade consisting of *Diploptera*, *Epilampra* and *Gyna*, a clade that seems to be defined by relatively short males, is not present in many of our phylogenetic trees, e.g. ML-T-P (Fig. 3), nor in the other tree used in our PDAP correlation analyses.

Fig. S10. Mapping of wing development in males. See Table S4 for information on wing development. The tree is based on the ML-T-P (Fig. 3) and ML-C-P (Fig. S4) trees, see section 2.5. for details.

Fig. S11. Mapping of wing development in females. See Table S4 for information on wing development. The tree is based on the ML-T-P (Fig. 3) and ML-C-P (Fig. S4) trees, see section 2.5. for details.

Fig. S12. Mapping of microhabitat of adults. If a species is known from more than one type of habitat, all the different microhabitats are reflected in the coding. See section 2.4.4 for definitions and Table S4 for information on microhabitat. The tree is based on the ML-T-P (Fig. 3) and ML-C-P (Fig. S4) trees, see section 2.5. for details.

Fig. S13. Mapping of mating pattern. See section 2.4.5. and Table S5 for information on mating patterns. The tree is based on the ML-T-P (Fig. 3) and ML-C-P (Fig. S4) trees, see section 2.5. for details.

Fig. S14. Mapping of reproductive mode. Oviparity A: ootheca dropped well before hatch. Oviparity B: ootheca carried externally until hatch. Ovoviviparity A: ootheca carried internally until hatch. Ovoviviparity B: no ootheca, eggs carried internally until hatch. Viviparity: eggs/ootheca carried internally until hatch, eggs receive significant amounts of nutrients from the mother during gestation. See Table S5 for information on reproductive modes. The tree is based on the ML-T-P (Fig. 3) and ML-C-P (Fig. S4) trees, see section 2.5. for details.

Fig. S15. Mapping of clutch size (number of eggs per ootheca) in relation to female body length. The more reddish the colour, the larger the number of eggs produced in a single clutch compared to female body length. The more blueish the colour, the smaller the number of eggs produced in a single clutch compared to female body length. The numbers beside the coloured boxes are log10 (number of eggs / F body length). The value zero is equal to one egg per mm body length. See Table S3 for actual body lengths and Table S6 for actual clutch sizes. The tree is one of two trees used for PDAP correlation analyses, based on the ML-T-P (Fig. 3) and ML-C-P (Fig. S4) trees, see sections 2.5. and 2.6. for details.

Fig. S16. Phylogenetically independent contrasts regression of clutch size versus female body length illustrating the positive correlation between clutch size and female body length. Note the extremely large clutch size in *Gyna capucina*. The observed states of terminal taxa are shown against the regression line (black), confidence intervals (95% CI: red; 90% CI: orange) and prediction intervals (95%: green; 90%: cyan) generated by PDAP:PDTREE. This chart is based on one of the two trees used for PDAP correlation analyses (see e.g. Fig. S15), based on the ML-T-P (Fig. 3) and ML-C-P (Fig. S4) trees, see sections 2.5. and 2.6. for details.

Table S1. Taxa included in the phylogenetic analyses with GenBank accession numbers. Authority and year of description given for all named species. Taxa marked in blue were not included in the trimmed data set, see section 2.2. for details. The (sub-)family names and designations in this table do not reflect the taxonomic changes in the present paper.

Table S2. Available data on geographical distribution for all included species. Our definitions of biogeographic regions generally follow the definitions of World Wildlife Fund (OLSON et al. 2001), but we divided Palearctic in East and West (along the Ural Mountains), and included all of Mexico in the Neotropical region, all of China (unless more specific locality information was available) in East Palearctic, and the Oceanic region in Australasia. The (sub-) family names and designations in this table do not reflect the taxonomic changes in the present paper.

Table S3. Available data on ranges of body length (up to posterior tip of abdomen, excluding overhanging parts of wings and cerci) and of pronotum length, both for females and males, and for all included species or selected substitute species. The measurements are based on either dried or alcohol-preserved individuals. The (sub-) family names and designations in this table do not reflect the taxonomic changes in the present paper.

Table S4. Available data on biogeographical regions, body size, wing length and microhabitat for all included species or selected substitute species. For more information on regions or body size, see Tables S2 and S3 respectively. The (sub-)family names and designations in this table do not reflect the taxonomic changes in the present paper.

Table S5. Available data on mating type, reproductive mode and eggs per ootheca for all included species or selected substitute species. ***Mating type*** definitions follow SRENG (1993): Type A: female mounts male. Type B: male mounts female. Type C: no mounting, the male and female simply make direct contact end to end. ***Reproductive mode*** definitions follow BELL et al. (2007: table 7.1): Oviparity A: ootheca dropped prior to hatch. Oviparity B: ootheca carried externally until hatch. Ovoviviparity A: ootheca carried internally until hatch. Ovoviviparity B: no ootheca, eggs carried internally until hatch. Viviparity: eggs receive significant nutrients from mother during gestation. ***Clutch sizes*** are (estimated) average/ typical number of eggs, for ranges of clutch sizes etc., see Table S6. The (sub-)family names and designations in this table do not reflect the taxonomic changes in the present paper.

Table S6. Available data on clutch sizes (eggs or live larvae per ootheca) for all included species or selected substitute species. Eggs per ootheca are in several cases estimated based on photographs of oothecae, in these cases the reference is listed as 'inferred from', e.g. 'inferred from ROTH 1971'. In some blaberids, only data on number of live larvae per clutch was available, in these cases we assumed that the average number of larvae was 75% of the average number of eggs (see hatching percentages at bottom of table). The column 'Average for calculations' is the (estimated) typical egg number for each species used for analyses, see section 2.4.5. for details. The (sub-)family names and designations in this table do not reflect the taxonomic changes in the present paper.