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Roth, S., Balvín, O., Siva-Jothy, M.T. orcid.org/0000-0001-9699-887X et al. (12 more authors) (2019) Bedbugs evolved before their bat hosts and did not co-speciate with ancient humans. Current Biology, 29 (11). 1847-1853.e4. ISSN 0960-9822

https://doi.org/10.1016/j.cub.2019.04.048

Bedbugs (Cimicidae) Evolved Before Their Bat Hosts and Did Not Co-Speciate with Ancient Humans

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[**] Author deceased during manuscript preparation. Osvaldo di Iorio (1959-2016) contributed substantial material of the Haematosiphoninae and discussions about the evolution of bird-associated Cimicidae, his specialty. For an obituary see (Oliva M (2016) Obituario: Osvaldo Rubén Di Iorio (1959-2016). *Bol Soc Entomol Argent* 27:32.

Keywords: Ashford hypothesis, bed bug, Chiroptera, evolution of generalism, hematophagy, human parasite, specialization, speciation

All 100+ bedbug species (Cimicidae) are obligate blood-sucking parasites [1, 2]. In general, blood-sucking (haematophagy) is thought to have evolved in generalist feeders adventitiously taking blood meals [3, 4] but those cimicid taxa currently considered ancestral are putative host specialists [1, 5]. Bats are believed to be the ancestral hosts of cimicids [1] but a cimicid fossil [6] predates the oldest known bat fossil [7] by >30 MY. The bedbugs that parasitize humans [1, 8] are host generalists, so their evolution from specialist ancestors is incompatible with the 'resource efficiency' hypothesis, and only partially consistent with the 'oscillation' hypothesis [9–16]. Because quantifying host shift frequencies of hematophagous specialists and generalists may help to predict host associations when vertebrate ranges expand by climate change [17], livestock and pet trade in general, and because of the previously proposed role of human pre-history in parasite speciation [18-20], we constructed a fossil-dated, molecular phylogeny of the Cimicidae. This phylogeny places ancestral Cimicidae to 115 MYA as haematophagous specialists with lineages that later frequently populated bat and bird lineages. We also found that the clades including the two major current urban pests, *Cimex lectularius* and *C. hemipterus* separated 47 MYA, rejecting the notion that the evolutionary trajectories of *Homo* caused their divergence [18-21].

Results and Discussion

The molecular phylogeny

The consensus tree (Figure 1) of five DNA sequence segments of four genes from recently collected species (Table S1) i) shows that the Cimicidae are monophyletic and firmly placed within the Cimicomorpha [4, 22-25], (ii) provides robust resolutions of other debated relationships (Figure 1), including the paraphyly of the groups that parasitize swallows (martin bugs, previously genus *Oeciacus*) [21] and robustly identifies *Primicimex*+*Bucimex* iii) as a monophyletic clade (Figure 1) (supporting morphological arguments [1] and a concurrent investigation [26]) and (iv) as the sister of the remaining extant Cimicidae, solving a long-standing problem in insect systematics [22-25, 27, 28]. v) The biogeographical distribution (Figure 1) shows continent-restricted ranges of higher cimicid taxa that may relate to either occasional cross-continent host dispersal or geological events. Supporting the latter, we observed that all ancestral clades are found only on continents that developed from Pangaea, that India has not been colonized until 75 MYA, Europe not before 50 MYA and that the Wallacea line represents a distribution border. Consistent with dispersal by hosts is some degree of host conservatism (see results below) and a (near) cosmopolitan distribution only for human-associated species. On the other hand, it is striking that a continuous form of cross-continent dispersal by hosts has not altered the biogeographic distribution of those cimicids that parasitise swallow species: neither the North American *C. vicarius* nor the European *C. hirundinis* have been recorded in the winter grounds of their hosts, South America and sub-saharan Africa, respectively.

Enigmatic ancestral host and multiple colonization events of bats

Independently dating the phylogenetic tree using a fossil from the related family Vetanthocoridae (152 MYA) [25] rejects the widely-held view [1] that the Cimicidae evolved on bat hosts. Our mean estimate of 115 MYA (74-170, 95 % highest posterior density (HPD) interval) for the stem of the Cimicidae supports the idea of a minimum age of the group of 100 MYA based on fossil evidence [6]. The origin of the Cimicidae crown group with a mean of 93.8 (56-137 95% HPD) MYA is placed 30-50 MY before the earliest known bats [7, 27-29] (Figure 2) and 20 MY before the earliest inferred bats (73 (64-81, 95 %) MYA) [29]. Our estimate appears robust: Employing the oldest known cimicid fossil as an additional calibration point places the stem species at 122 MYA (111-150 MYA, 95 % HPD, relaxed molecular clock estimation of lineage divergence points within the family) and the crown divergence at 102 MYA (91-114 MYA, 95 % HPD) (Figure 2). Our estimate is also robust against previous suggestions that the Vetanthocoridae might be the sister group to all Cimicoidea [30] (Figure S1).

All four ancient bedbug lineages predate the evolution of bats (Figure 2) but were reconstructed to ancestral bat hosts (Figure 3A). This suggests that bats were colonized several times independently, unless the evolutionary origin of bats [7, 27–29] has been grossly underestimated. Thus, the stem species of bedbugs evolved 115-122 MYA, well before the K-T mass extinction boundary, a key event in vertebrate diversification. The identity of the ancestral host(s) from which bats were colonized repeatedly, is unknown.

Evolution of hematophagy

Our phylogeny does not support ancestral host generalism (G) in cimicids (Figure 3B), so we propose the commonly assumed evolution of haematophagy from facultative blood-feeding by ancestral predators [3, 4] did not occur. This result is robust against variation in the definition of species along the host specialist (S)/host generalist (G) axis depending on the specialization metrics or recording intensity [9-16]. For example, technically, all specialists are ‘putative specialists’ until additional hosts may eventually be found. In any case, the derived state of G holds true if broadly defined by the phylogenetic distance of their hosts [16], i.e., as using more than one of the four major, phylogenetically deeply diverged host groups of waterfowl (Galloanseres) and other birds (Neoaves), as well as bats (Chiroptera) and humans (Figure 3A). It also holds true for a tighter definition of G accounting for variability within taxonomic groups [16] as being those parasites recorded from more than three host genera (Figure S3) and if the number of currently known host genera is used (Figure S2). Therefore, haematophagy likely evolved within the true bugs (Heteroptera), in insects that were already specialists and gave rise to the Cimicidae. This result is compatible with the view that the specialist blood-sucking Polyctenidae are the sister group of the Cimicidae [4, 22].

Pattern of host shifts

Of the 29 species on our tree that allow a classification, most (24/29, 83%) are S (broadly defined - Figure 3B), or 55% (15/27), using tighter definitions (Figure S3). Five cimicid species on our molecular tree are G (broadly defined). [1]).

Host shifts between bat taxa were common by ancient bat specialists since most extant bat-parasitic cimicid lineages evolved before their extant hosts’ lineages (Table S2). Host switches from bats to birds also occurred; we identified at least three such independent events (Figure 3A). Our host reconstruction indicates that parasite diversification is not generally driven by co-speciation with hosts [14, 15, but see 31] for either bat or bird hosts (Figures S4, S5). Together these observations suggest that the extant pattern of G/S distribution in cimicids is the result of evolutionarily dynamic host transitions.

When examining host transitions at all 31 subterminal nodes on our tree that are classifiable as G or S, we found the highest number (9/31, or 29%) involved host specialists switching host but staying specialist (S→S). Two nodes were G→S transitions (6%) and five (16%) were S→G transitions (or 7/31 (23%) if specialists are defined more strictly) (Figures 3B, S3).

The paucity of G→S transitions departs from the general pattern in mammalian parasites [16], and indicates that the "resource efficiency" hypothesis (where host specialists (S) evolve from generalists (G) by fitness advantages on specific hosts [9-11]) does not appear to apply to cimicids. An extension of this idea, the "oscillation" hypothesis, proposes that genetic variation or phenotypic plasticity maintained in S species allows them to add hosts to their portfolio (and so become G again), depending on ecological opportunities [12, 14, 16]. While this hypothesis allows for any number of S/G transitions, S→G transitions should be evenly distributed across evolutionary time, if they are regularly oscillating. This prediction was rejected: all seven S→G transitions occurred in a short period, between 10 and 20 MYA (cf. Figures 2, 3B).

Acceptance of unusual hosts under ecological opportunities (such as laboratory-forced host feeding) can serve as an indicator of plasticity or genetic variation in host preference [14]. Such propensity to switch hosts has only been recorded in G (Figures 3, S3) but not in S species [5, 32] - which the "oscillation hypothesis" requires - but few experimental tests exist. Anecdotal acceptances of unusual hosts outside the laboratory suggested to mimic ecological opportunities created by humans have been reported during guano-mining, chicken-breeding or pet-keeping; again, however, in G, or unscorable, but not in S species. Unless future systematic screening of such events would reveal a massive usage of unusual hosts by S species, there is little current evidence to suggest that S species commonly oscillate to evolve into G species, nor that host specialization in the Cimicidae is driven by selection for resource efficiency.

S→S transitions (host switches without extensions in host breadth, or so-called "musical chairs" pattern [12]) are the common pattern in cimicids. The "musical chairs" hypothesis makes no further predictions [12] but S→S transitions can, like S→G, be based on the ecological opportunities new hosts present [14, 15], such as after major (e.g. inter-continental) dispersal events [16]. In support, for example, two of the three bat-to-bird host shifts in cimicids concerned the Haematosiphoninae and *Paracimex* where bird hosts replaced bats, rather than having been added (Figure 3). Both examples simultaneously involved the colonisation of another continent (South America and Southeast Asia). However, other S→S transitions are not related to intercontinental shifts.

The only temporary association of cimicids with the host body would be expected to increase opportunities for alternative host use, and hence generalism (such as in mosquitoes). However, the widespread and ancient specialization reported here (predicted for parasites with tight host associations that cannot readily exploit new hosts, such as lice) finds a parallel in selection on salivary proteins [33] and divergence in endosymbionts [34], which aid blood digestion.

In conclusion, several bedbug lineages specialized on bats in ancient times, but subsequent host shifts were frequent and the switches (and expansions of host portfolio) that can be explained by current models of host specialization, are related to the ecological opportunities that human activity or inter-continental dispersal provided. As general models of host specialization only had limited ability to predict patterns of host use in cimicids, we examined more specific ideas developed for their colonization of human hosts.

Human colonization and Ashford's hypothesis

Three bedbug species routinely use humans as hosts (*C. lectularius*, *C. hemipterus* and *Leptocimex boueti*) [1, 3, 8] representing three independent events (Figure 3A). All are G, all are recent, and all represent expansions of the host portfolio, rather than replacements, i.e. they represent the somewhat more unusual S→G transitions among mammalian parasites [16] (Figure 3). The three colonization events of humans are non-randomly captured by these S→G transitions, which represent just 16% (or broad definition: 23%) of transitions [Fisher's exact test, *P*=0.0022 (or broad definition of G: *P*=0.0078)]. Thus, humans represent an important, nonrandom, target for specialist cimicid species.

Our finding that the *C. hemipterus* and *C. lectularius* lineages diverged ~47 MYA, clearly rejects Ashford's hypothesis [18], which predicts a divergence that coincides with the split between the *H. sapiens* and the *H. erectus* clades around 1.6 MYA. Our results show that *C. lectularius* belongs to a bat-associated lineage and *C. hemipterus* to a bird-parasitic lineage [21, Figure 3A], so Ashford's idea would require a series of independent host shifts from birds and bats to *Homo* lineages. With one species pair of human parasites showing contrary [lice: 19, 20] and one no support (cimicids) for Ashford's hypothesis, this idea should be rejected, or re-tested by dating the split of other species pairs of human parasites.

C. lectularius specifically has also been hypothesized to have colonized humans, or *H. sapiens*, when ancient man started to use caves regularly and so represented a predictable food source [1]. Our analysis shows all clades parasitizing humans had diverged at least 5-10 MY before the oldest known *Homo* species [35, 36]. The spatial and temporal coexistence of several lineages of hominids [34] allows several transmission scenarios and host shifts. However, because bedbugs are not known from other extant hominids, or other primates, colonization likely took place in the hominin lineages. Thus, no matter when hominids first entered caves, bat- and bird-parasitizing *C. lectularius* were already there and ready to exploit the new opportunity. Thus although the fact that bat- and human-associated lineages of *C. lectularius* diverged between 99,000-867,000 years ago [37] provides us with a hint of when humans acquired *C. lectularius*, it does not tell us which of the *Homo* lineages, or their cave-dwelling behaviour was the initial driver for contact. Our work shows that the driver for the association suggested by Ashford is too simplistic.

Conclusion

Our phylogenetic reconstruction shows that bedbugs (Cimicidae) evolved before bats, their previously assumed primary hosts and colonized them on several subsequent occasions. It supports the view that generalism can evolve when ecological opportunities arise, even after long periods of specialization and shows that all colonizations of human hosts conform to this view. The phylogeny also served to elucidate debated taxonomic relationships and rejects Ashford hypothesis.

Author Contributions

S.R., M.S-J., E.H.M., and K.R. designed the study, S.R., O.B., O.D.I., M.S-J., P.B., O.C., E.F., M.M., R.N., N.S., E.H.M., F.A.A.K., M.P.L. and K.R. extensively contributed material or sequences, S.R. carried out the molecular work, S.R., E.W., and K.R. analyzed the data, S.R., and K.R. wrote the first draft, S.R., O.B., M.S-J., M.L.P., E.H.M, E.W., and K.R. carried out the first revision. All authors, except O.D.I. contributed to all subsequent revisions.

Acknowledgments

We thank M. Lehnert, M. Stoneking, N. Tatarnic, E. Vargo and three reviewers for comments on the manuscript, all people mentioned in Table S1 for providing samples and L. Lindblom, K. Meland, D. Rees for help with molecular work, and B. Jordal and R. Mally for help with data analysis. For specimen loan or opportunity for inspection or DNA extraction we thank Museum Senckenberg Frankfurt, Naturalis Biodiversity Center Leiden, Natural History Museum London, Tel Aviv University Department of Zoology, Universidad Nacional Autónoma de México Instituto de Biología, Universiti Malaysia Sarawak Zoology Department, Field Museum Chicago and University of Texas Insect Collection. The Forest Department of Sarawak provided permits (Research: #NCCD 907.4.4 (JLD.12)-85; Park # 209/2015 and Export #16001). Supported by Meltzer Research Fund (S.R.), NERC (M.S-J), Ministry of Education Malaysia (NRGS/1087/2013(01) - 1088/2013(02)) (F.A.A.K.), Royal Society URF (E.H.M.), DFG (K.R., Zukunftskonzept to TU Dresden).

Declaration of Interests

Richard Naylor is owner of CimexStore (UK). All other authors declare no competing interests.

Main figure titles and legends

Figure 1. **Phylogeny of the bedbug family (Cimicidae).** Bayesian consensus tree based on five gene sequences showing the biogeographical distribution (branch colours) and classical taxonomy at the subfamily level. Photographs show morphologically typical representatives of each subfamily. Numbers beside the nodes indicate posterior probability values. The branch lengths scale represents the number of estimated nucleotide substitutions per site. Sample codes refer to Table S1. Sequences of outgroups, boxed in shaded grey, were taken from GenBank.

Figure 2. Chronogram of the bedbug family (Cimicidae). Bayesian consensus tree of the Cimicidae and selected outgroup taxa in relation to geological age (MYA) (x-axis). A relaxed clock model [38] was used to date the tree based on two calibration points, fossil Vetanthocoridae (152 MYA) [25] and the oldest known fossil cimicid (100 MYA) [6]. Numbers below nodes represent Bayesian posterior probability values, blue bars represent 95% highest posterior density intervals of the time estimates in million years (MYA). Scale in millions of years. The Cimicidae are boxed in shaded blue. 'gr.' stands for group, a taxonomic aggregate. The time estimates returned a mean age of 103 MY for the crown group of the Cimicidae and are robust against alternate taxonomic assumptions of the Vetanthocoridae (Figure S1).

Figure 3. Ancestral bedbug hosts. Mirror trees showing (A) systematic host groups, and (B) their classification as putative host specialist or generalist (see main text for classification; Figure S3). In A), colours indicate different host types reported [1, 39-41, Table S1]. In B) putatively specialized (black) or generalist (white) host uses were reconstructed with (unordered) parsimony. Separate analyses with MrBayes [42] confirmed specialized host use as the ancestral state for all Cimicidae. The result did not change if the two lineages with the highest uncertainty about their ancestral state, i.e. Cimicinae and (Cacodminae + Haematosiphoninae) were analysed separately by setting all other clades to an unknown state of G or S (probabilities of bats as ancestral host 98%, and ancestral specialist 85% for the Cimicinae, and 96%, and 98%, respectively for the Cacodminae+Haematosophinae. *Leptocimex duplicatus* was analysed as *Leptocimex* spec. to demonstrate human host use in this genus. Results were identical if ancestral analysis host and specialization employed bats or bats + human). The results also did not change if classes of the exact number of currently known host genera was employed (Figure S2).

STAR Methods text

CONTACT FOR REAGENT AND RESOURCE SHARING

Further Information and Requests may be directed to the corresponding author, Steffen Roth (Steffen.Roth@uib.no).

METHOD DETAILS

Sample origin

We obtained material from three main sources over the course of 15 years. First, we contacted the major natural history museums in the world as several species are known only from a single collection from their type locality. However, most of this material dated from the 1960s and 1980s and was too old for our analysis, museum material from only two species could be used, material for one of which was subsequently obtained otherwise. Second, between 2002 and 2015, we contacted researchers with requests for specimens. Researchers working on cimicids provided material from 10 species. We also contacted approximately 500 researchers that work in caves, on cave-dwelling bats or other putative bedbug hosts, such as swallows and swiftlets. Approximately half the people responded, and about 30 respondents promised to send material. From those who did send material, an extra 18 species were obtained. Third, between 2000 and 2014, the authors undertook field trips to obtain material, adding 10 species. This resulted in a total of 38 species, of which 34 species from 62 localities yielded sufficient DNA for the analysis (Table S1). Unfortunately, existing *Latrocimex* material from Brazil [43] was not at our disposal to be analyzed.

Taxon sampling

In total, 34 species of Cimicidae were analysed, representing 17 genera from 5 out of 6 currently recognized subfamilies [1]. The most closely related families were chosen as outgroups: Nabidae, Anthocoridae, Plokiophilidae, Microphysidae, Curaliidae, and Joppeicidae [4, 23-25], except the Polyctenidae (for which we obtained no material). We also included representatives of two more distant outgroups, the Tingidae and Miridae. All outgroup taxa sequences were obtained from GenBank (Table S1).

DNA extraction, PCR amplification, and DNA sequencing

Nuclear and mitochondrial genomic DNA was extracted from 70-96% ethanol-preserved specimens using a QIAGEN DNAEasy blood and tissue kit (Qiagen Inc., Hilden, Germany) following the manufacturer's instructions and standard methods for DNA extraction and purification. If high-quality amplicons were not acquired, a set of ambiguous primers with universal sequencing adaptors was used (Table S3). The total volumes of PCR reactions were 10 µl (0.25 µl Promega GoTaq Flexi DNA Polymerase (5 U/µl); ddH2O; 5x Colorless buffer; 2 mM MgCl2; 0.2 mMdNTP; 0.5 µM of each primer), with 1–2 µ DNA template. PCR thermal conditions are shown in Table S3. PCR products were purified using ExoSAP-IT (Thermo Fisher Scientific). Sequencing reactions for both strands of the amplified genes were performed using

BigDye Terminator v3.1 Cycle Sequencing Kit (Thermo Fisher Scientific). Products were sequenced using Applied Biosystems automated sequencer.

Sequences were amplified from cytochrome *c* oxidase subunit I (COI), 16S rRNA, the D3 region of 28S rRNA (28S D3 rRNA) and two segments of 18S rRNA There was no overlap of the two 18S rRNA fragments in some taxa. Therefore, the two fragments were treated as separate data sets (called 18S part1 and part2) in all analyses. Sequence contigs were assembled and visually inspected for ambiguous sites in Sequencher v. 4.5 (Gene Codes, Ann Arbor, Michigan).

QUANTIFICATION AND STATISTICAL ANALYSIS

Sequence alignments

Alignment was conducted using the MUSCLE [44] algorithm implemented in MEGA v. 6 [45] with the following settings: -400 gap opening penalty, -50 gap extension penalty. We used GBlocks V.0.91b [46] to test and where required to eliminate poorly aligned positions in the original alignments and used this dataset for an alternative analysis (Figures S6A,B).

Since saturation in substitutions can lead to incorrect phylogenetic inferences [47], the positions 1-3 were evaluated for substitution saturation by DAMBE V 5.2.13 [48] in the whole dataset. Saturation was not observed for any but the third position in only the COI dataset. As there was no conflict in topology of the separate gene trees (see below) we ran the analysis with all three positions included.

Phylogenetic analyses

Models of evolution for each sequence set were selected in MEGA v. 6 [45] based on Akaike Information Criterion (Table S4). Preliminary analysis of single gene sets was unable to recover stable clades at different depths of the tree but did not show any conflict among the separate gene trees (see Figures S7A-E). Therefore, phylogenetic Bayesian analyses (BA) were conducted on the concatenated data set in MrBayes 3.2.1. [42]. Model parameter values for the partitions were estimated independently using the "unlink" command and relative site-specific rates for all gene fragments were estimated by setting the prior for "ratepr" to "variable". For all analyses, Markov Chain Monte Carlo (MCMC) sampling was conducted with two independent and simultaneous runs for 10,000,000 generations. Trees were saved every 1000 generations. Likelihood values and effective sample size were observed with Tracer v1.4 [49], and all trees sampled before the likelihood values stabilized were discarded as burn-in. Stationarity was reassessed using the convergence diagnostics in MrBayes (i.e., the average standard deviation of split frequencies (values <0.01) and the potential scale reduction factor (values ≈ 1.00)). A burn-in of 25% of all sampled trees was sufficient to ensure that suboptimal trees were excluded. The remaining trees were used to construct a 50% majority rule consensus tree.

Bayesian and other trees were formatted for presentation using either TreeView (Win32) 1.6.6 [50], FigTree 1.4.1 [51], or Mesquite 3.5. [52] In order to test the robustness of our dataset we performed additional analyses using different outgroups. We found no effect on topology and support values for the ingroup clades (results not shown except Figure S8 for a selection of the closest outgroup taxa). Removing *Paracimex* had no effect on the relationships of other taxa confirming the absence of long-branch attraction [21].

In order to compare the tree from Bayesian inference with Maximum Likelihood (ML) analysis we ran the same partitioned dataset by using RAxML 7.4.2. [53]. Since RaxML does not allow the use of mixed nucleotide models, we used the GTR gamma invariant (GTRGAMMAI) for all partitions. ML with rapid bootstrap was performed in 1000 iterations and obtained bootstrap values were placed on a consensus tree (Figure S9).

Molecular Dating

We used Beast 1.8.4 [38] with 82 sequences, including 20 outgroups to infer the divergence dates of the sequences under a Yule speciation process (a pure birth process) and an uncorrelated relaxed molecular clock [38].

First, we constrained the Cimicoidea as a monophyletic group and used a lognormal prior mean age of 152.2 million years (MY) with standard deviation 0.2 MY as calibration point for the group based on a fossil flower bug (Heteroptera: Cimicomorpha: Cimicoidea: Vetanthocoridae) from the late Jurassic [25]. In this analysis, we wanted to test if our molecular dating of the family Cimicidae is in concordance with oldest known cimicid fossil, *Quasicimex eilapinastes* Engel, 2008 from the mid Cretaceous (ca. 100 MYA) [6]. Our estimates placed the origin of Cimicidae at 93.8 MYA with a 95% highest probability density interval of 56-137 MYA (tree not shown). Accepting the fossil as a proxy for the minimum age of the Cimicidae, this clock estimate appeared as a reasonable result. To better account for variable evolutionary rates over the whole tree, we used the minimum age of *Q. eilapinastes* as an additional calibration point, setting a lognormal prior with a mean of 102.5 MYA and standard deviation 0.06 MY for the diversification of the Cimicidae. The root in both analyses was given a weak uniform prior ranging from 0 to 350 MYA. We ran two successive MCMC chains with 100 million generations, sampling every 1000 generations. All chains had reached equilibrium at two million generations. When discarding 20% of the initial tree samples the consensus trees from each run produced the same topologies and the same branch support. We pooled samples from the two runs with the program "logcombiner" implemented in BEAST [38] by discarding 50% of the initial trees from each run and computed a consensus chronogram based on 10000 resampled trees. Parameter estimates, including posterior probabilities and mean node ages with highest probability density intervals, were calculated in TreeAnnotator (implemented in BEAST [38]) and displayed with FigTree [51].

These model settings were conservative and returned a stem age of 121.6 MYA and a crown group age of 102.2 MYA for the Cimicidae (Figure 2). Running the analysis with a birth-death instead of a Yule model, and using uniform instead of lognormal priors returned a mean estimate of 145 MYA for the stem of Cimicidae and 121 MY for the first divergence of the family.

Our phylogeny corresponds very well with a cladistic analysis [30] placing the Vetanthocoridae within the Cimicoidea. To explore effects of earlier ideas [30] that the vetanthocorid fossil may represent the sister group of all other Cimicoidea, we defined the divergence of Cimicoidea and Nabidoidea as a calibration point, leaving the Microphysidae, Joppelicidae and Miridoidea as members of the outgroup, in accordance with our previous findings of branching patterns. Using a uniform prior with minimum age 152.2 million years for the split of Cimicoidea from Nabidoidea in MCMC runs of up to 18 million generations returned a mean age of the Cimicidae stem of 127.4 MY while the crown group was estimated to 103.6 MY (Figure S1). This date estimate for the age of the Cimicidae crown group is just one million years older than the age we used as prior in the clock estimates with two calibrations points, indicating that the age estimates for the ingroup are robust. Moreover, the taxonomic constraint in these calculations resulted in lower support values of some branch compared to our initial, unconstrained estimate.

Ancestral host character state reconstruction

We mapped ancestral host characters on the tree with time estimated nodes. We used Mesquite version 3.5 [52] to prune the outgroup taxa from the tree and to collapse zero-length terminal branches. We coded terminal taxa with discrete trait characters according to the known host groups of each species: bats, birds (divided into Neoaves and Galloanseres) and humans. We then used the ‘trace ancestral character’ function to estimate ancestral states of nodes with maximum likelihood (Figure 3A). A simple one-parameter Markov model [54], implemented in [38] was applied with these calculations, estimating the rate of state changes directly from the data [52]. In a second approach, we coded terminal taxa with the discrete trait characters 'specialist' or 'generalist' (Figure 3B). We then used the ‘trace ancestral character’ function to estimate ancestral states of nodes with maximum parsimony.

We also used the number of currently known host genera for each of the cimicid species as a meristic character. We traced the character states on the phylogeny using linear meristic parsimony reconstruction with Mesquite (Figure S2). In addition, we inferred ancestral states at ancestral nodes using the full hierarchical Bayesian approach (integrating uncertainty concerning topology and other model parameters) as described in [55] and integrated in MrBayes 3.2. The ancestral host character for the selected lineages (i.e. Cimicinae and (Haematosiphoninae + Cacodminae) at the KT boundary (the time of their assumed first colonization of bats) was also inferred using the full hierarchical Bayesian approach in MrBayes 3.2 [38]. All terminal taxa not belonging to one of these two lineages were coded as character “unknown host”.

Supplemental item titles

Figure S1. Chronogram of the Cimicoidea, using Vetanthocoridae as the sister group to the Cimicoidea Using the Cimicoidea + Nabidoidea divergence as calibration point dates the Cimicidae ancestor to 127 MYA and the first divergence of the crown group to 103 MYA, very similar to the situation that the Vetanthocoridae are aprt of the Cimcoidea. The topological constraint for the calibration changed the position of *Afrocimex* and devaluated the support for some of the clades that were well supported from unconstrained phylogenetic estimates. Support values are shown over branches and dating values in MYA (in italics) at nodes. For terminals no values are shown for the purpose of clarity.

Figure S2. Evolution of the host spectrum in cimicids using the currently known number of host genera. The ancestral state is reconstructed as 1 or 2 host species, confirming ancestral host specialization. The methods are exactly those used for Figure 3.

Figure S3. Host reconstruction using a stricter definition of generalism. Here, host generalism is defined as utilizing more than three host genera (species shaded in grey). The host spectrum was obtained from the same sources as for Figure 3, with an additional record for *C. sparsilis* on domestic dog [56].

Figure S4. Host relationships (tanglegram) of the Haematosophinae. Primary hosts (solid line) and secondary hosts (long dashed line) [after 57]. Dotted branches are species that were not analyzed in our study. The Haematosiphoninae (diverged around 50 MYA) and the bird-parasitic *Paracimex* (around 15 MYA) or *Cimex vicarius* (around 18 MYA) all appeared long after their respective swift or swallow host groups had appeared in the early Eocene [58, 59]. Phylogram of birds from [60]. Hosts were compiled from [1, 39–41, Table S1].

Figure S5. Host relationships (tanglegram) of Cimicidae parasitic on bats. Specialists having only one species or genus as hosts are shown with green connectors, generalists with a wider range of host taxa are shown with red connectors; *Leptocimex* and *Stricticimex* utilize hosts except *Noctilio* that phylogenetically are wide apart (orange). Bat phylogeny according to [26], host spectrum after [1,39–41, Table S1].

Figure S6. GBlock alignment tests for trees using strict and relaxed models. Neighbor Joining (NJ) tree for the combined data set with original alignment set and GBlocks data set with tree strict (a) and relaxed (b) model using default settings of Gblocks V.0.91b [46]. NJ analysis was performed in MEGA v.6 [45]. NJ analysis using strict (a) and relaxed GBlock alignments (b) of all molecular markers separately showed no significant effect of alignments and no need to eliminate poorly aligned positions and divergent regions, except some outgroup taxa. The original alignment data set was used for further analysis. Samples C41 and outgroup taxa *Curalium cronini* were removed from this analysis because of missing sequences.

Figure S7 a-e Bayesian analysis (BA) of phylogenetic relationships of the Cimicidae inferred from individual genes. The analysis was carried out using MrBayes v.3.2.1 [42] for individual genes, substitution models were as chosen in the combined data set analysis (Table S4). Details for settings in MrBayes for single genes BA can be requested from the authors. Consensus trees inferred from the single gene fragments (18S rDNA part1 and part 2, COI, 16S rDNA, 28S D3 rDNA- Table S4) shows their different phylogenetic information but also that single gene analyses are unable to recover phylogenetic relationship.

Figure S8 MrBayes consensus tree using one representative species of the closest phylogenetic taxa (e.g. Anthocoridae, Nabidae and Plokiophillidae) within our outgroup sampling. The tree is a Bayesian consensus tree based on four genes (see Material & Methods). Numbers beside the nodes indicate posterior probability values. Topology and support value of the Cimicidae clades did not change due to different outgroup sampling (see Figure1).

Figure S9. Maximum Likelihood analysis of the combined molecular data set. The Maximum Likelihood analysis confirmed the results of the BA (Figure S3) but the sister relationship of Cacodminae and Haematosiphoninae was not resolved. There was also low support for the node (*Leptocimex*+*Stricticimex*) + (*Aphrania*+*Cacodmus*).

Supplementary Tables

Table S1. List of samples of the 34 species, covering 30% of extant species described to date from 6 out of 7 recognized subfamilies, or 17 out of 26 genera described to date [2].

Table S2. Evolutionary occurrence of extant bedbug lineages and their host genera, as extracted from our phylogenetic tree. (*) indicates molecular ages which are confirmed by oldest fossils (less than ±10 MYA). Mean age, 95% lower and upper highest posterior distribution inferred by BEAST [38] is reported. Event-, distance- or topology-based cophylogenetic tests were not applied because the molecular and phylogenetic resolution differed between host and parasite trees and because over-precision should be avoided (see *Results and Discussion*).

Table S3 List of primers used and PCR conditions.

Table S4 Characteristics of sequences used. To implement Kimura's two-parameter model (K2) in BEAST 1.8.4 [38] we selected the Hasegawa-Kishino-Yano (HKY) model and set “base frequencies” to “All Equal”. For many taxa sampled, the two 18S fragments did not overlap. Therefore, the two fragments were analyzed separately.

Table S5. Alignment file.

- see separate upload -

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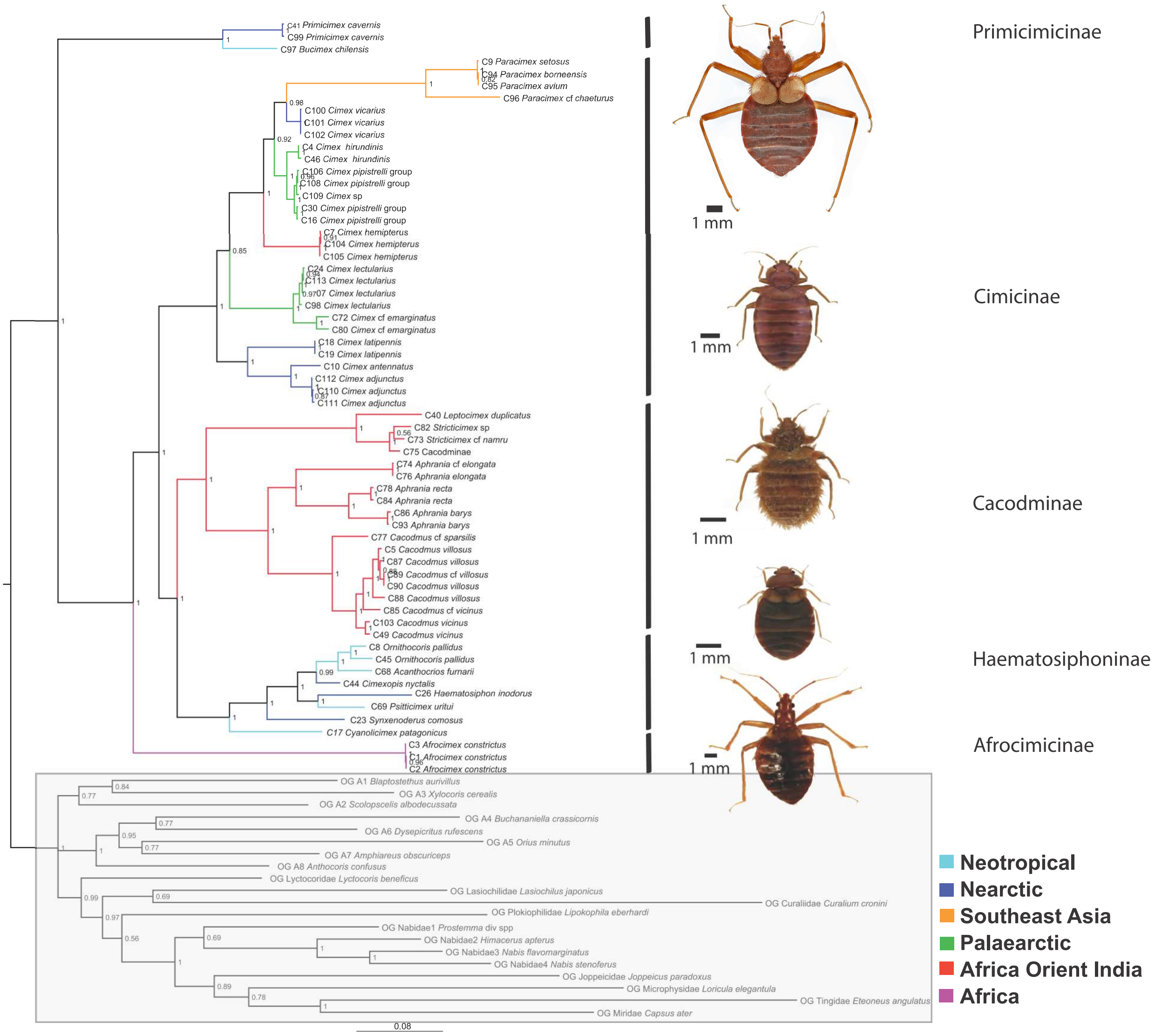
Figure1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C99 Primicimex cavernis
C97 Bucimex chilensis
C9 Paracimex setosus
C94 Paracimex borneensis
C95 Paracimex avium
C96 Paracimex cf chaeturus
C100 Cimex vicarius
C101 Cimex vicarius
C102 Cimex vicarius
C4 Cimex hirundinis
C46 Cimex hirundinis
C106 Cimex pipistrelli group
C108 Cimex pipistrelli group
C109 Cimex sp
C30 Cimex pipistrelli group
C16 Cimex pipistrelli group
C7 Cimex hemipterus
C104 Cimex hemipterus
C105 Cimex hemipterus
C24 Cimex lectularius
C113 Cimex lectularius
C107 Cimex lectularius
C98 Cimex lectularius
C72 Cimex cf emarginatus
C80 Cimex cf emarginatus
C18 Cimex latipennis
C19 Cimex latipennis
C10 Cimex antennatus
C112 Cimex adjunctus
C110 Cimex adjunctus
C111 Cimex adjunctus
C40 Leptocimex duplicatus
C82 Stricticimex sp
C73 Stricticimex cf namru
C75 Cacodminae
C74 Aphrania cf elongata
C76 Aphrania elongata
C78 Aphrania recta
C84 Aphrania recta
C86 Aphrania barys
C93 Aphrania barys
C77 Cacodmus cf sparsilis
C5 Cacodmus villosus
C87 Cacodmus villosus
C89 Cacodmus cf villosus
C90 Cacodmus villosus
C88 Cacodmus villosus
C85 Cacodmus cf vicinus
C103 Cacodmus vicinus
C49 Cacodmus vicinus
C8 Ornithocoris pallidus
C45 Ornithocoris pallidus
C68 Acanthocrios furnarii
C44 Cimexopis nyctalis
C26 Haematosiphon inodorus
C69 Psitticimex uritui
C23 Synxenoderus comosus
C17 Cyanolicimex patagonicus
C3 Afrocimex constrictus
C1 Afrocimex constrictus
C2 Afrocimex constrictus
OG A1 Blaptostethus aurivillus
OG A3 Xylocoris cerealis
OG A2 Scolopscelis albodecussata
OG A4 Buchananiella crassicornis
OG A6 Dysepicritus rufescens
OG A5 Orius minutus
OG A7 Amphiareus obscuriceps
OG A8 Anthocoris confusus
OG Lyctocoridae Lyctocoris beneficus
OG Lasiochilidae Lasiochilus japonicus
OG Curaliidae Curalium cronini
OG Plokiophilidae Lipokophila eberhardi
OG Nabidae1 Prostemma div spp
OG Nabidae2 Himacerus apterus
OG Nabidae3 Nabis flavomarginatus
OG Nabidae4 Nabis stenoferus
OG Joppeicidae Joppeicus paradoxus
OG Microphysidae Loricula elegantula
OG Tingidae Eteoneus angulatus
OG Miridae Capsus ater
0.08
Primicimicinae
Cimicinae
Cacodminae
Haematosiphoninae
Afrocimicinae
1 mm
1 mm
1 mm
1 mm
1 mm
Neotropical
Nearctic
Southeast Asia
Palaearctic
Africa Orient India
Africa

Figure 2

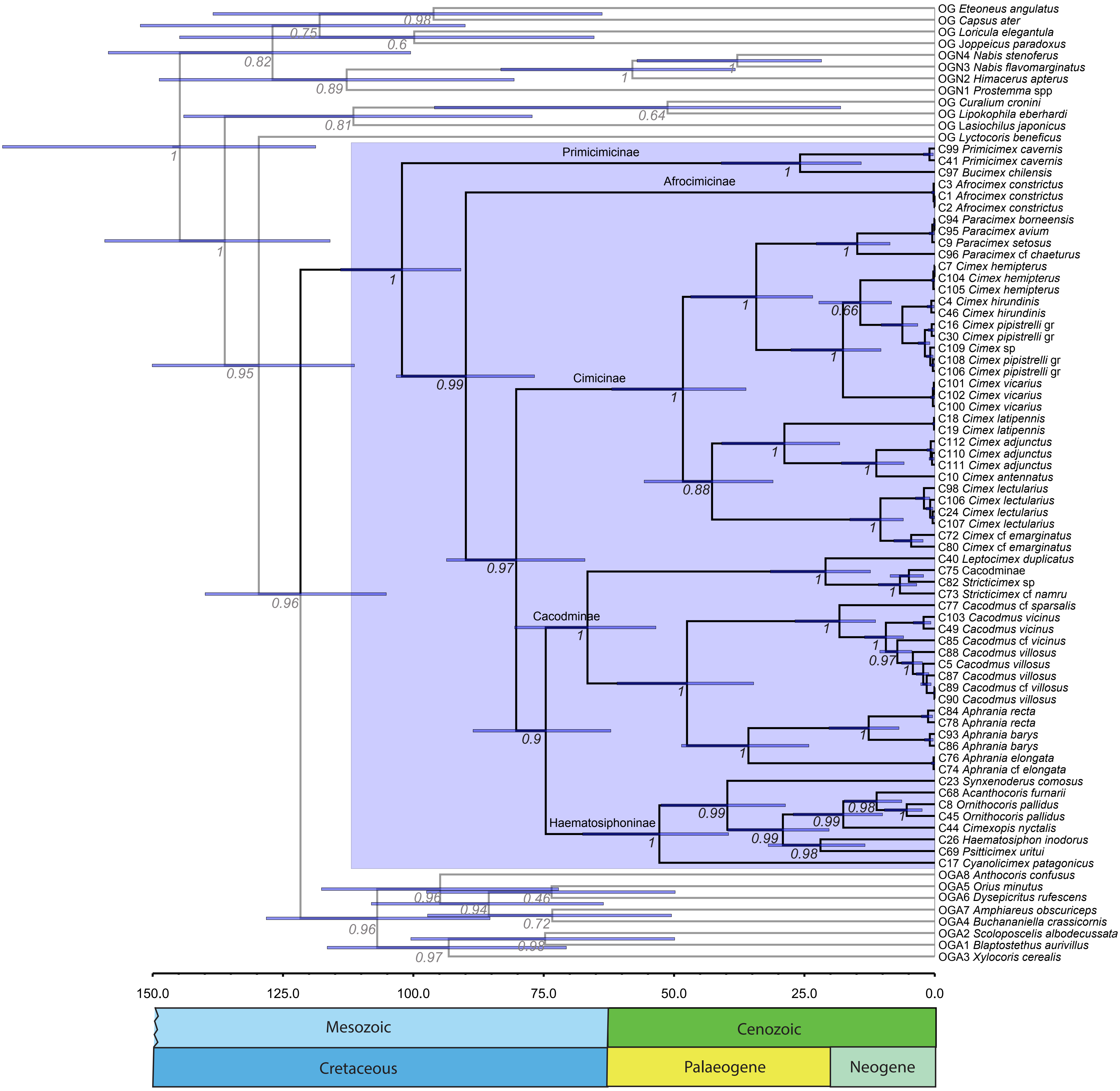
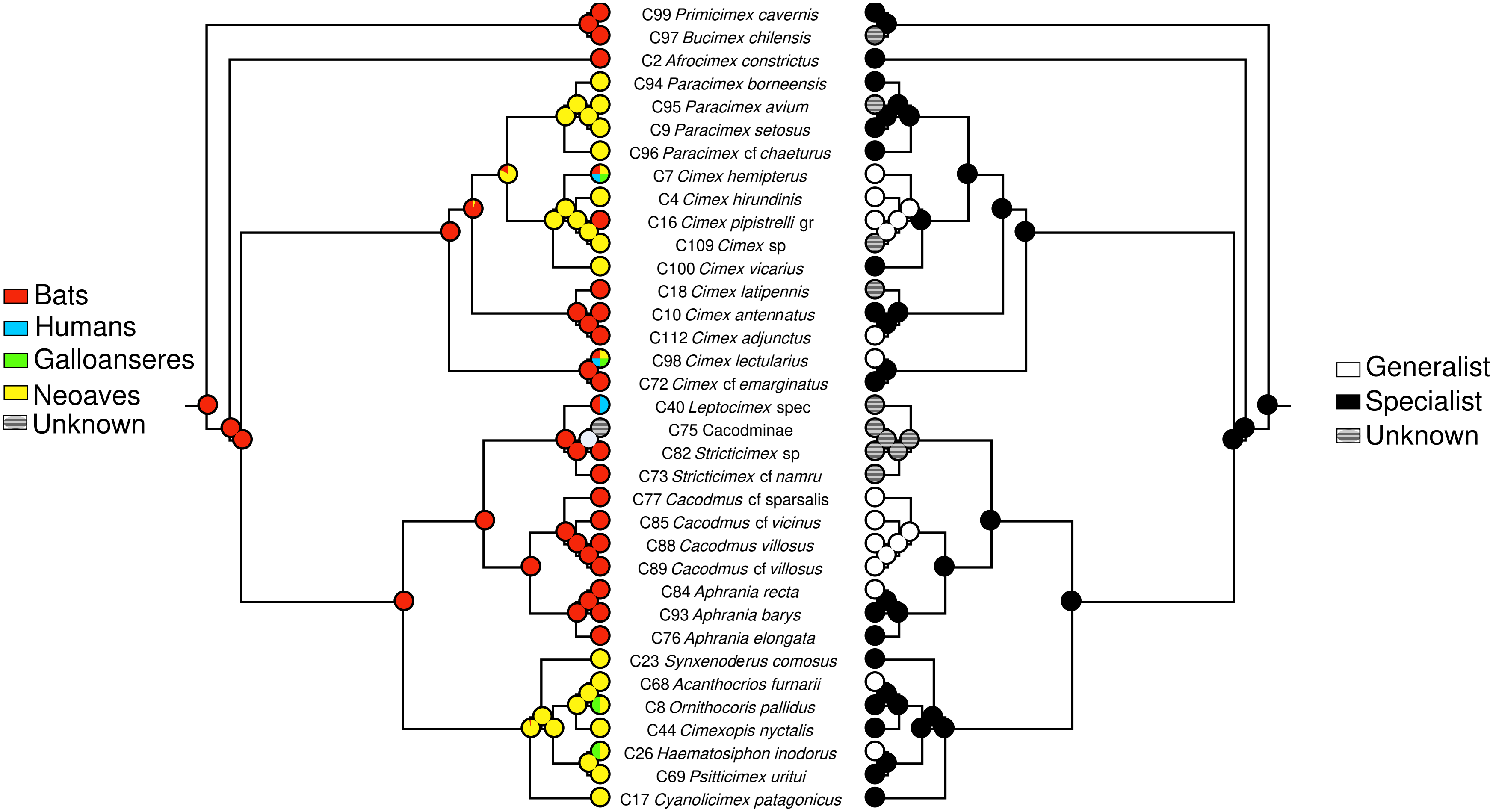

OG *Eteoneus angulatus*
OG *Capsus ater*
OG *Loricula elegantula*
OG *Joppeicus paradoxus*
OGN4 *Nabis stenoferus*
OGN3 *Nabis flavomarginatus*
OGN2 *Himacerus apterus*
OGN1 *Prostemma* spp
OG *Curalium cronini*
OG *Lipokophila eberhardi*
OG *Lasiochilus japonicus*
OG *Lyctocoris beneficus*
C99 *Primicimex cavernis*
C41 *Primicimex cavernis*
C97 *Bucimex chilensis*
C3 *Afrocimex constrictus*
C1 *Afrocimex constrictus*
C2 *Afrocimex constrictus*
C94 *Paracimex borneensis*
C95 *Paracimex avium*
C9 *Paracimex setosus*
C96 *Paracimex* cf *chaeturus*
C7 *Cimex hemipterus*
C104 *Cimex hemipterus*
C105 *Cimex hemipterus*
C4 *Cimex hirundinis*
C46 *Cimex hirundinis*
C16 *Cimex pipistrelli* gr
C30 *Cimex pipistrelli* gr
C109 *Cimex* sp
C108 *Cimex pipistrelli* gr
C106 *Cimex pipistrelli* gr
C101 *Cimex vicarius*
C102 *Cimex vicarius*
C100 *Cimex vicarius*
C18 *Cimex latipennis*
C19 *Cimex latipennis*
C112 *Cimex adjunctus*
C110 *Cimex adjunctus*
C111 *Cimex adjunctus*
C10 *Cimex antennatus*
C98 *Cimex lectularius*
C106 *Cimex lectularius*
C24 *Cimex lectularius*
C107 *Cimex lectularius*
C72 *Cimex* cf *emarginatus*
C80 *Cimex* cf *emarginatus*
C40 *Leptocimex duplicatus*
C75 Cacodminae
C82 *Stricticimex* sp
C73 *Stricticimex* cf *namru*
C77 *Cacodmus* cf *sparsalis*
C103 *Cacodmus vicinus*
C49 *Cacodmus vicinus*
C85 *Cacodmus* cf *vicinus*
C88 *Cacodmus villosus*
C5 *Cacodmus villosus*
C87 *Cacodmus villosus*
C89 *Cacodmus* cf *villosus*
C90 *Cacodmus villosus*
C84 *Aphrania recta*
C78 *Aphrania recta*
C93 *Aphrania barys*
C86 *Aphrania barys*
C76 *Aphrania elongata*
C74 *Aphrania* cf *elongata*
C23 *Synxenoderus comosus*
C68 *Acanthocoris furnarii*
C8 *Ornithocoris pallidus*
C45 *Ornithocoris pallidus*
C44 *Cimexopis nyctalis*
C26 *Haematosiphon inodorus*
C69 *Psitticimex uritui*
C17 *Cyanolicimex patagonicus*
OGA8 *Anthocoris confusus*
OGA5 *Orius minutus*
OGA6 *Dysepicritus rufescens*
OGA7 *Amphiareus obscuriceps*
OGA4 *Buchananiella crassicornis*
OGA2 *Scoloposcelis albodecussata*
OGA1 *Blaptostethus aurivillus*
OGA3 *Xylocoris cerealis*
Primicimicinae
Afrocimicinae
Cimicinae
Cacodminae
Haematosiphoninae
0.98
0.75
0.6
0.82
1
0.89
1
0.64
0.81
1
1
1
0.95
1
0.99
1
1
0.66
1
1
1
1
0.88
1
0.97
0.96
1
1
1
1
0.97
1
1
0.9
1
1
0.99
0.98
1
0.99
0.99
0.98
1
0.96
0.46
0.94
0.72
0.96
0.98
0.97
150.0
125.0
100.0
75.0
50.0
25.0
0.0
Mesozoic
Cenozoic
Cretaceous
Palaeogene
Neogene

Figure 3



C99 *Primicimex cavernis*
C97 *Bucimex chilensis*
C2 *Afrocimex constrictus*
C94 *Paracimex borneensis*
C95 *Paracimex avium*
C9 *Paracimex setosus*
C96 *Paracimex* cf *chaeturus*
C7 *Cimex hemipterus*
C4 *Cimex hirundinis*
C16 *Cimex pipistrelli* gr
C109 *Cimex* sp
C100 *Cimex vicarius*
C18 *Cimex latipennis*
C10 *Cimex antennatus*
C112 *Cimex adjunctus*
C98 *Cimex lectularius*
C72 *Cimex* cf *emarginatus*
C40 *Leptocimex* spec
C75 Cacodminae
C82 *Stricticimex* sp
C73 *Stricticimex* cf *namru*
C77 *Cacodmus* cf sparsalis
C85 *Cacodmus* cf *vicinus*
C88 *Cacodmus villosus*
C89 *Cacodmus* cf *villosus*
C84 *Aphrania recta*
C93 *Aphrania barys*
C76 *Aphrania elongata*
C23 *Synxenoderus comosus*
C68 *Acanthocrios furnarii*
C8 *Ornithocoris pallidus*
C44 *Cimexopis nyctalis*
C26 *Haematosiphon inodorus*
C69 *Psitticimex uritui*
C17 *Cyanolicimex patagonicus*
Bats
Humans
Galloanseres
Neoaves
Unknown
Generalist
Specialist
Unknown

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Chemicals, Peptides, and Recombinant Proteins		
QIAGEN DNAEasy blood and tissue kit	Qiagen Inc., Hilden, Germany	(QIAGEN, RRID:SCR_008539)
ExoSAP-IT	Thermo Fisher Scientific	(Thermo Fisher Scientific, RRID:SCR_008452)
BigDye Terminator v3.1 Cycle Sequencing Kit	Thermo Fisher Scientific	(Thermo Fisher Scientific, RRID:SCR_008452)
Full list of primers	Table S3	
Deposited Data		
Age of fossil	[6], [25]	
Host spectrum	[1, 39–41], Table S1	
Bat phylogeny	[27]	
Phylogram of birds	[60]	
Outgroup taxa	Table S1	
A list of species analyzed	Table S1	
Software and Algorithms		
Sequencher v. 4.5	Gene Codes, Ann Arbor, Michigan	http://www.genecodes.com/ (Sequencher, RRID:SCR_001528)
MrBayes 3.2.1.	[42]	http://mrbayes.sourceforge.net/ (MrBayes, RRID:SCR_012067)
Tracer 1.7	[49]	http://tree.bio.ed.ac.uk/software/tracer/
TreeView (Win32) 1.6.6	[50]	http://en.bio-soft.net/tree/TreeView.html (TreeView, RRID:SCR_013503)
FigTree 1.4.1	[51]	http://tree.bio.ed.ac.uk/ (FigTree, RRID:SCR_008515)
Mesquite 3.2	[52]	https://www.mesquiteproject.org/
RAxML 7.4.2.	[53]	https://sco.h-its.org/exelixis/web/software/raxml/ (RAxML, RRID:SCR_006086)
MEGA v. 6	[45]	http://en.bio-soft.net/tree/MEGA.html (MEGA Software, RRID:SCR_000667)
GBlocks V.0.91b	[46]	http://molevol.cmima.csic.es/castresana/Gblocks_server.html (Gblocks, RRID:SCR_015945)
DAMBE V 5.2.13	[48]	http://dambe.bio.uottawa.ca/DAMBE/dambe.aspx
Beast 1.8.4	[38]	http://www.beast2.org/ (BEAST, RRID:SCR_010228)


C41 Primicimex cavernis
C99 Primicimex cavernis
C97 Bucimex chilensis
C111 Cimex adjunctus
C110 Cimex adjunctus
C112 Cimex adjunctus
C10 Cimex antennatus
C18 Cimex latipennis
C19 Cimex latipennis
C107 Cimex lectularius
C24 Cimex lectularius
C106 Cimex lectularius
C98 Cimex lectularius
C72 Cimex cf emarginatus
C80 Cimex cf emarginatus
C100 Cimex vicarius
C101 Cimex vicarius
C102 Cimex vicarius
C30 Cimex pipistrelli gr
C16 Cimex pipistrelli gr
C106 Cimex pipistrelli
C108 Cimex pipistrelli
C109 Cimex sp
C46 Cimex hirundinis
C4 Cimex hirundinis
C7 Cimex hemipterus
C104 Cimex hemipterus
C105 Cimex hemipterus
C94 Paracimex borneensis
C95 Paracimex avium
C9 Paracimex setosus
C96 Paracimex cf chaeturus
C17 Cyanocimex patagonicus
C68 Acanthocoris furnarii
C45 Ornithocoris pallidus
C8 Ornithocoris pallidus
C44 Cimexopis nyctalis
C69 Psitticimex uritui
C26 Haematosiphon inodorus
C23 Synxenoderus comosus
C2 Afrocimex constrictus
C1 Afrocimex constrictus
C3 Afrocimex constrictus
C75 Cacodominae
C82 Stricticimex sp
C73 Stricticimex cf namru
C40 Leptocimex duplicatus
C84 Aphrania recta
C78 Aphrania recta
C93 Aphrania barys
C86 Aphrania barys
C76 Aphrania elongata
C74 Aphrania cf elongata
C88 Cacodmus villosus
C5 Cacodmus villosus
C89 Cacodmus cf villosus
C90 Cacodmus villosus
C87 Cacodmus villosus
C85 Cacodomus cf vicinus
C103 Cacodmus vicinus
C49 Cacodomus vicinus
C77 Cacodmus cf sparsalis
OGA2 Scoloposcelis albodecussata
OGA3 Xylocoris cerealis
OGA1 Blaptostethus aurivillus
OGA4 Buchananiella crassicornis
OGA6 Dysepicritus rufescens
OGA7 Amphiareus obscuriceps
OGA5 Orius minutus
OGA8 Anthocoris confusus
OG Lyctocoris beneficus
OG Lipokophila eberhardi
OG Curalium cronini
OG Lasiochilus japonicus
OGN4 Nabis stenoferus
OGN3 Nabis flavomarginatus
OGN2 Himacerus apterus
OGN1 Prostemma spp
OG Joppeicus paradoxus
OG Loricula elegantula
OG Capsus ater
OG Eteoneus angulatus
175
150
125
100
75
50
25
0

Figure S1. Chronogram of the Cimicoidea, using Vetanthocoridae as the sister group to the Cimicoidea Using the Cimicoidea + Nabidoidea divergence as calibration point dates the Cimicidae ancestor to 127 MYA and the first divergence of the crown group to 103 MYA, very similar to the situation that the Vetanthocoridae are part of the Cimcoidea. The topological constraint for the calibration changed the position of *Afrocimex* and devaluated the support for some of the clades that were well supported from unconstrained phylogenetic estimates. Support values are shown over branches and dating values in MYA (in italic) at nodes. For terminals no values are shown for the purpose of clarity.

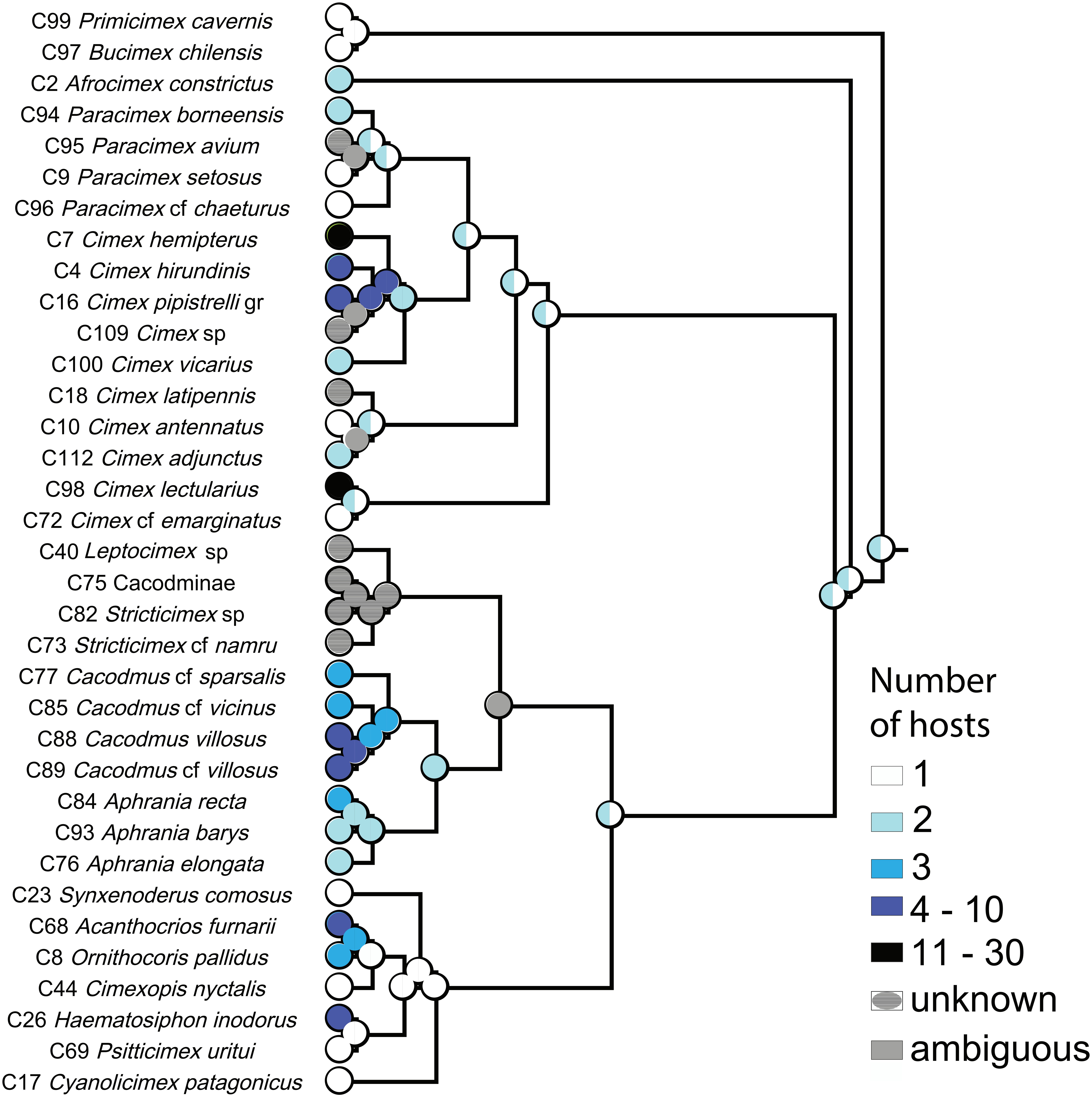

C99 *Primicimex cavernis*
C97 *Bucimex chilensis*
C2 *Afrocimex constrictus*
C94 *Paracimex borneensis*
C95 *Paracimex avium*
C9 *Paracimex setosus*
C96 *Paracimex* cf *chaeturus*
C7 *Cimex hemipterus*
C4 *Cimex hirundinis*
C16 *Cimex pipistrelli* gr
C109 *Cimex* sp
C100 *Cimex vicarius*
C18 *Cimex latipennis*
C10 *Cimex antennatus*
C112 *Cimex adjunctus*
C98 *Cimex lectularius*
C72 *Cimex* cf *emarginatus*
C40 *Leptocimex* sp
C75 Cacodminae
C82 *Stricticimex* sp
C73 *Stricticimex* cf *namru*
C77 *Cacodmus* cf *sparsalis*
C85 *Cacodmus* cf *vicinus*
C88 *Cacodmus villosus*
C89 *Cacodmus* cf *villosus*
C84 *Aphrania recta*
C93 *Aphrania barys*
C76 *Aphrania elongata*
C23 *Synxenoderus comosus*
C68 *Acanthocrios furnarii*
C8 *Ornithocoris pallidus*
C44 *Cimexopis nyctalis*
C26 *Haematosiphon inodorus*
C69 *Psitticimex uritui*
C17 *Cyanolicimex patagonicus*
Number of hosts
1
2
3
4 - 10
11 - 30
unknown
ambiguous

Figure S2. Evolution of the host spectrum in cimicids using the currently known number of host genera. The ancestral state is reconstructed as 1 or 2 host species, confirming ancestral host specialization. The methods are exactly those used for Figure 3.

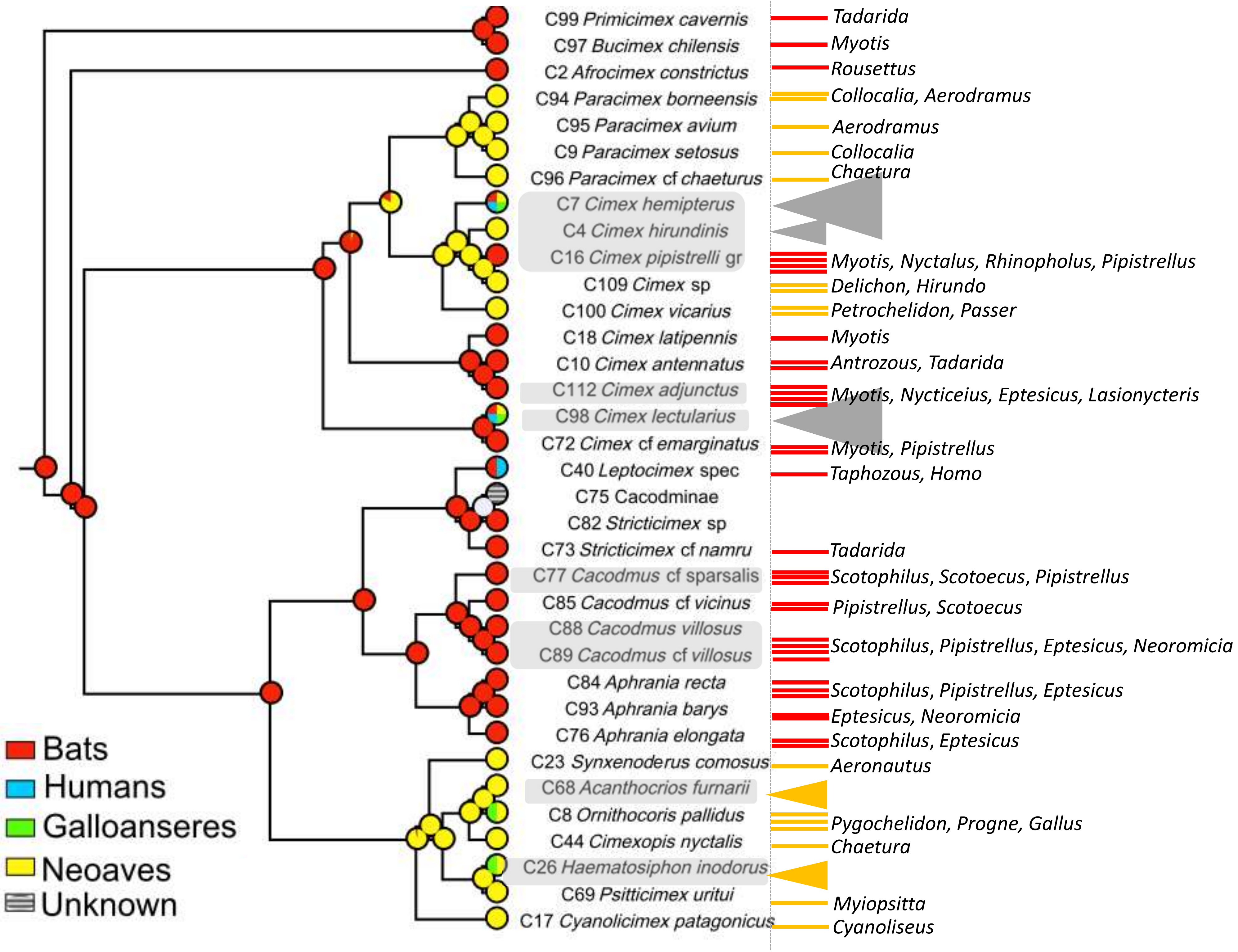

C99 Primicimex cavernis
Tadarida
C97 Bucimex chilensis
Myotis
C2 Afrocimex constrictus
Rousettus
C94 Paracimex borneensis
Collocalia, Aerodramus
C95 Paracimex avium
Aerodramus
C9 Paracimex setosus
Collocalia
C96 Paracimex cf chaeturus
Chaetura
C7 Cimex hemipterus
C4 Cimex hirundinis
C16 Cimex pipistrelli gr
Myotis, Nyctalus, Rhinopholus, Pipistrellus
C109 Cimex sp
Delichon, Hirundo
C100 Cimex vicarius
Petrochelidon, Passer
C18 Cimex latipennis
Myotis
C10 Cimex antennatus
Antrozous, Tadarida
C112 Cimex adjunctus
Myotis, Nycticeius, Eptesicus, Lasionycteris
C98 Cimex lectularius
C72 Cimex cf emarginatus
Myotis, Pipistrellus
C40 Leptocimex spec
Taphozous, Homo
C75 Cacodminae
C82 Stricticimex sp
C73 Stricticimex cf namru
Tadarida
C77 Cacodmus cf sparsalis
Scotophilus, Scotoecus, Pipistrellus
C85 Cacodmus cf vicinus
Pipistrellus, Scotoecus
C88 Cacodmus villosus
C89 Cacodmus cf villosus
Scotophilus, Pipistrellus, Eptesicus, Neoromicia
C84 Aphrania recta
Scotophilus, Pipistrellus, Eptesicus
C93 Aphrania barys
Eptesicus, Neoromicia
C76 Aphrania elongata
Scotophilus, Eptesicus
C23 Synxenoderus comosus
Aeronautus
C68 Acanthocrios furnarii
C8 Ornithocoris pallidus
Pygochelidon, Progne, Gallus
C44 Cimexopis nyctalis
Chaetura
C26 Haematosiphon inodorus
C69 Psitticimex uritui
Myiopsitta
C17 Cyanolicimex patagonicus
Cyanoliseus
🟥 Bats
🟦 Humans
🟩 Galloanseres
🟨 Neoaves
▤ Unknown

Figure S3. Host reconstruction using a stricter definition of generalism. Here, host generalism is defined as utilizing more than three host genera (species shaded in grey). The host spectrum was obtained from the same sources as for Figure 3, with an additional record for *C. sparsilis* on domestic dog [56].

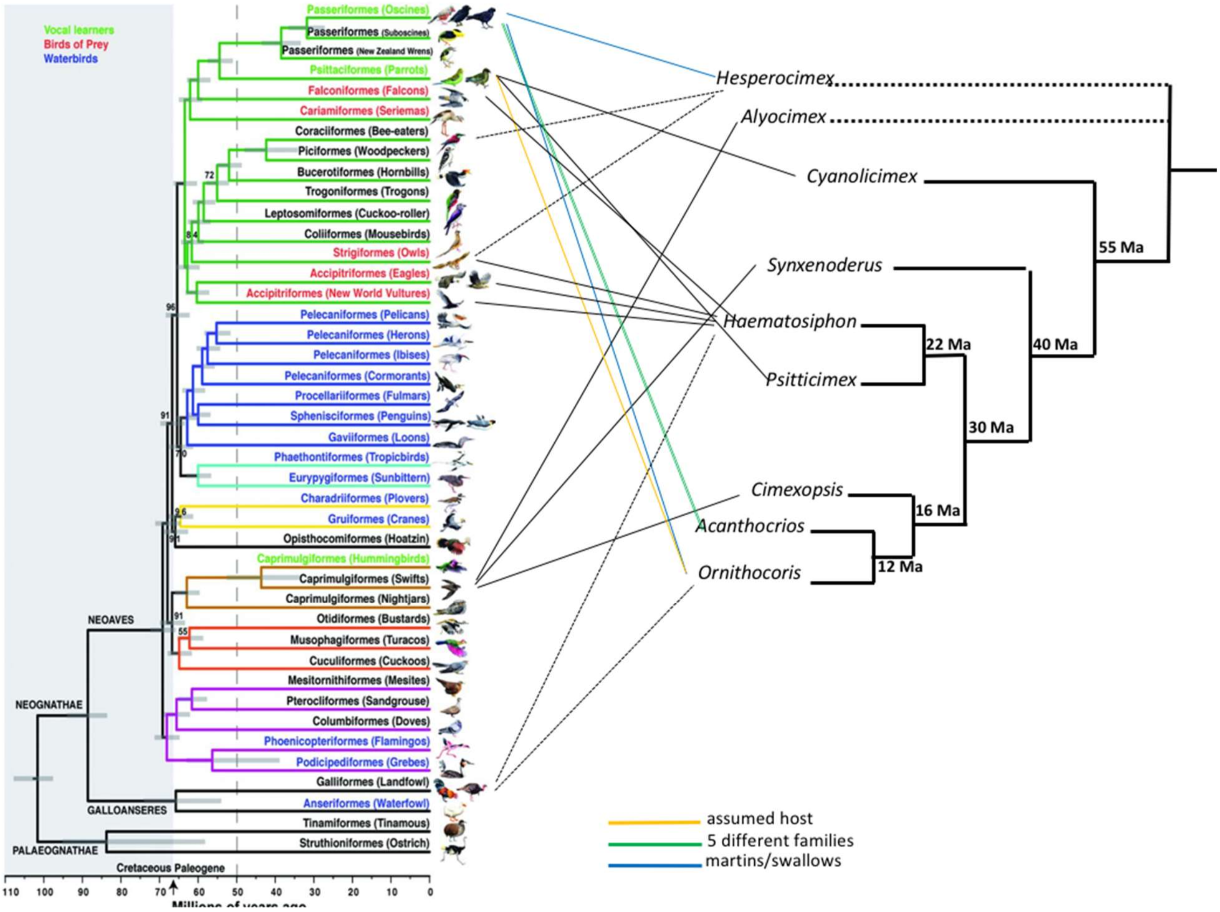


Figure S4. Host relationships (tanglegram) of the Haematosophinae. Primary hosts (solid line) and secondary hosts (long dashed line) [after 57]. Dotted branches are species that were not analyzed in our study. The Haematosiphoninae (diverged around 50 MYA) and the bird-parasitic *Paracimex* (around 15 MYA) or *Cimex vicarius* (around 18 MYA) all appeared long after their respective swift or swallow host groups had appeared in the early Eocene [58, 59]. Phylogram of birds from [60]. Hosts were compiled from [1, 39–41, Table S1].

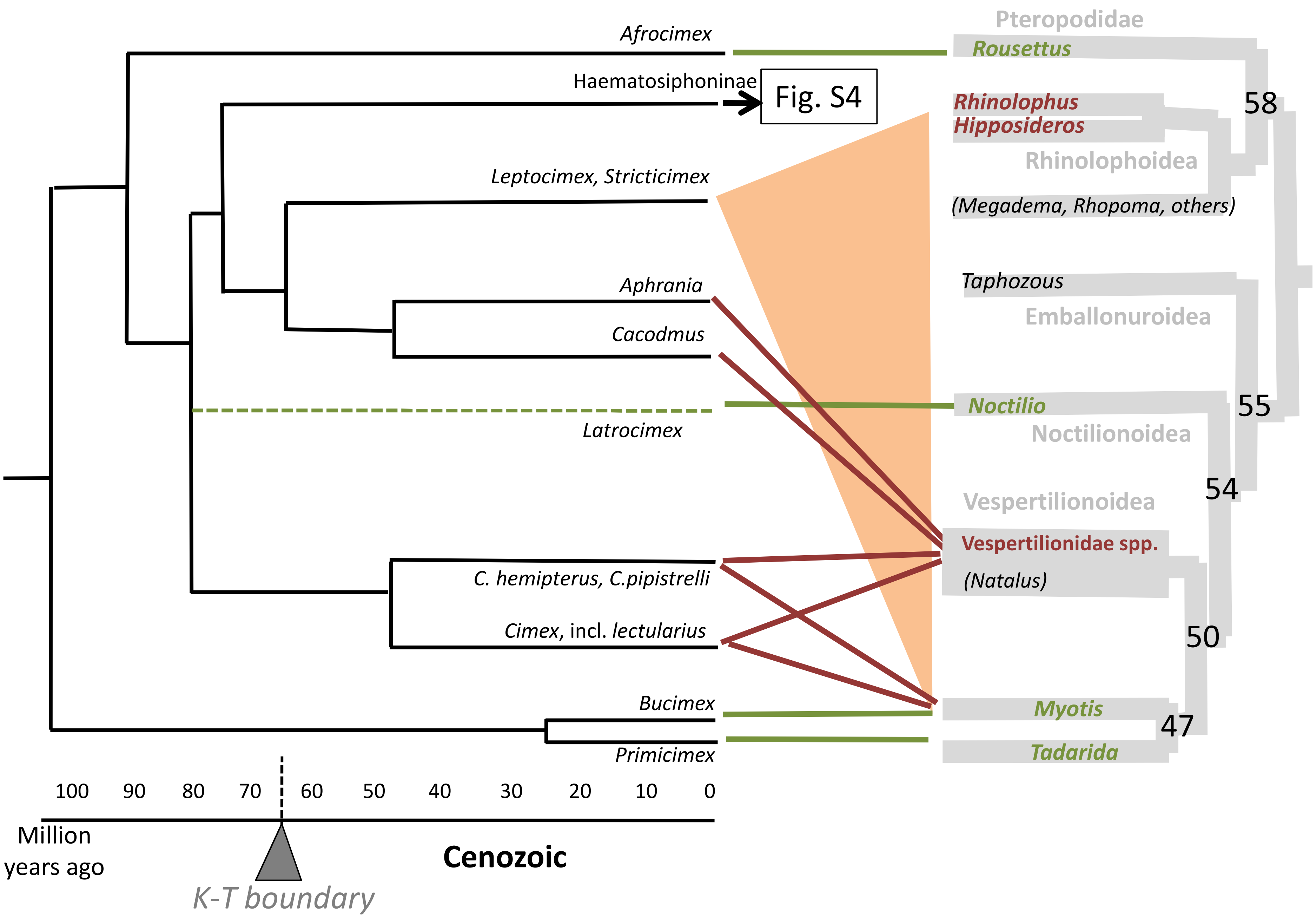
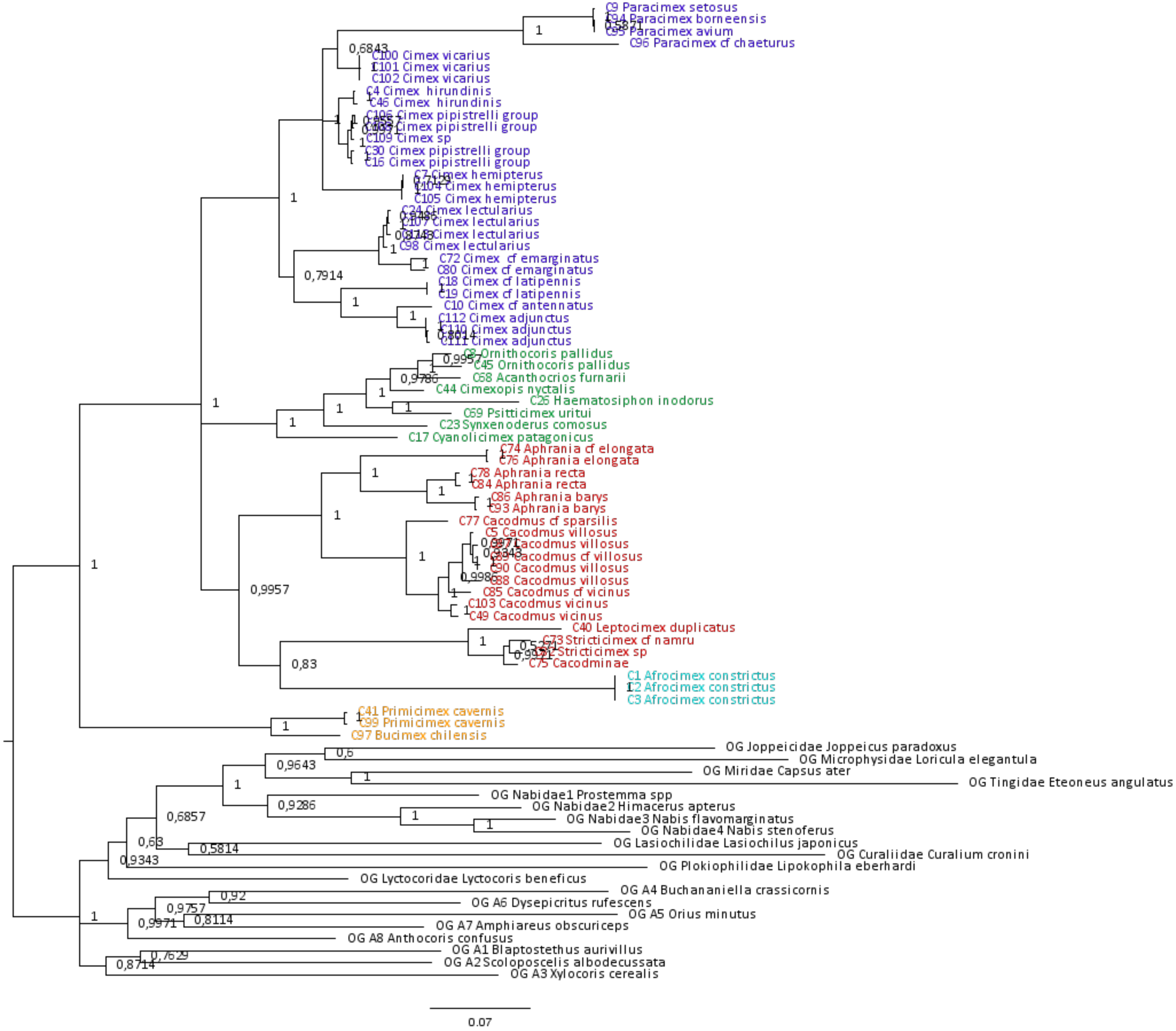

Afrocimex
Haematosiphoninae
Fig. S4
Leptocimex, Stricticimex
Aphrania
Cacodmus
Latrocimex
C. hemipterus, C.pipistrelli
Cimex, incl. lectularius
Bucimex
Primicimex
100
90
80
70
60
50
40
30
20
10
0
Million years ago
K-T boundary
Cenozoic
Pteropodidae
Rousettus
Rhinolophus
Hipposideros
Rhinolophoidea
(Megadema, Rhopoma, others)
Taphozous
Emballonuroidea
Noctilio
Noctilionoidea
Vespertilionoidea
Vespertilionidae spp.
(Natalus)
Myotis
Tadarida
58
55
54
50
47

Figure S5. Host relationships (tanglegram) of Cimicidae parasitic on bats. Specialists having only one species or genus as hosts are shown with green connectors, generalists with a wider range of host taxa are shown with red connectors; *Leptocimex* and *Stricticimex* utilize hosts except *Noctilio* that phylogenetically are wide apart (orange). Bat phylogeny according to [26], host spectrum after [1,39–41, Table S1].


C9 Paracimex setosus
C94 Paracimex borneensis
C95 Paracimex avium
C96 Paracimex cf chaeturus
0,5871
1
0,6843
C100 Cimex vicarius
C101 Cimex vicarius
C102 Cimex vicarius
C4 Cimex hirundinis
C46 Cimex hirundinis
C106 Cimex pipistrelli group
Cimex pipistrelli group
0,8557
0,9971
C109 Cimex sp
C30 Cimex pipistrelli group
C16 Cimex pipistrelli group
C7 Cimex hemipterus
0,7129
C104 Cimex hemipterus
C105 Cimex hemipterus
C24 Cimex lectularius
0,9486
C107 Cimex lectularius
Cimex lectularius
0,8748
C98 Cimex lectularius
C72 Cimex cf emarginatus
C80 Cimex cf emarginatus
C18 Cimex cf latipennis
C19 Cimex cf latipennis
C10 Cimex cf antennatus
C112 Cimex adjunctus
C110 Cimex adjunctus
C111 Cimex adjunctus
0,8014
0,7914
C8 Ornithocoris pallidus
0,9957
C45 Ornithocoris pallidus
0,9786
C68 Acanthocrios furnarii
C44 Cimexopis nyctalis
C26 Haematosiphon inodorus
C69 Psitticimex uritui
C23 Synxenoderus comosus
C17 Cyanolicimex patagonicus
C74 Aphrania cf elongata
C76 Aphrania elongata
C78 Aphrania recta
C84 Aphrania recta
C86 Aphrania barys
C93 Aphrania barys
C77 Cacodmus cf sparsilis
C5 Cacodmus villosus
0,9971
Cacodmus villosus
0,9343
Cacodmus cf villosus
C90 Cacodmus villosus
0,9986
C88 Cacodmus villosus
C85 Cacodmus cf vicinus
C103 Cacodmus vicinus
C49 Cacodmus vicinus
0,9957
C40 Leptocimex duplicatus
C73 Stricticimex cf namru
0,5271
Stricticimex sp
0,9921
C75 Cacodminae
0,83
C1 Afrocimex constrictus
C2 Afrocimex constrictus
C3 Afrocimex constrictus
C41 Primicimex cavernis
C99 Primicimex cavernis
C97 Bucimex chilensis
OG Joppeicidae Joppeicus paradoxus
0,6
OG Microphysidae Loricula elegantula
0,9643
OG Miridae Capsus ater
OG Tingidae Eteoneus angulatus
OG Nabidae1 Prostemma spp
0,9286
OG Nabidae2 Himacerus apterus
OG Nabidae3 Nabis flavomarginatus
OG Nabidae4 Nabis stenoferus
0,6857
0,63
OG Lasiochilidae Lasiochilus japonicus
0,5814
OG Curaliidae Curalium cronini
0,9343
OG Plokiophilidae Lipokophila eberhardi
OG Lyctocoridae Lyctocoris beneficus
OG A4 Buchananiella crassicornis
0,92
OG A6 Dysepicritus rufescens
0,9757
OG A5 Orius minutus
0,8114
0,9971
OG A7 Amphiareus obscuriceps
OG A8 Anthocoris confusus
OG A1 Blaptostethus aurivillus
0,7629
OG A2 Scoloposcelis albodecussata
0,8714
OG A3 Xylocoris cerealis
0.07

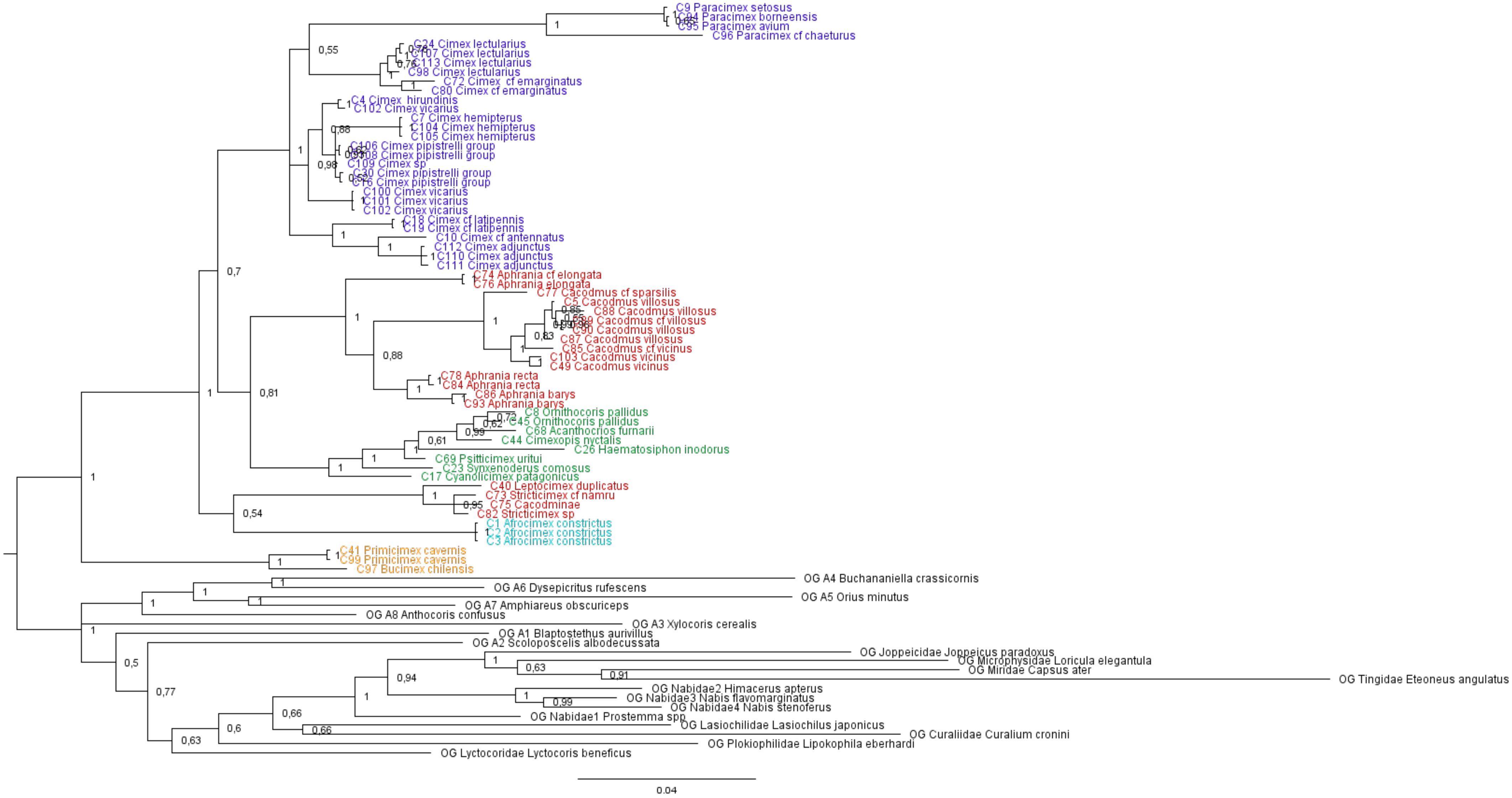
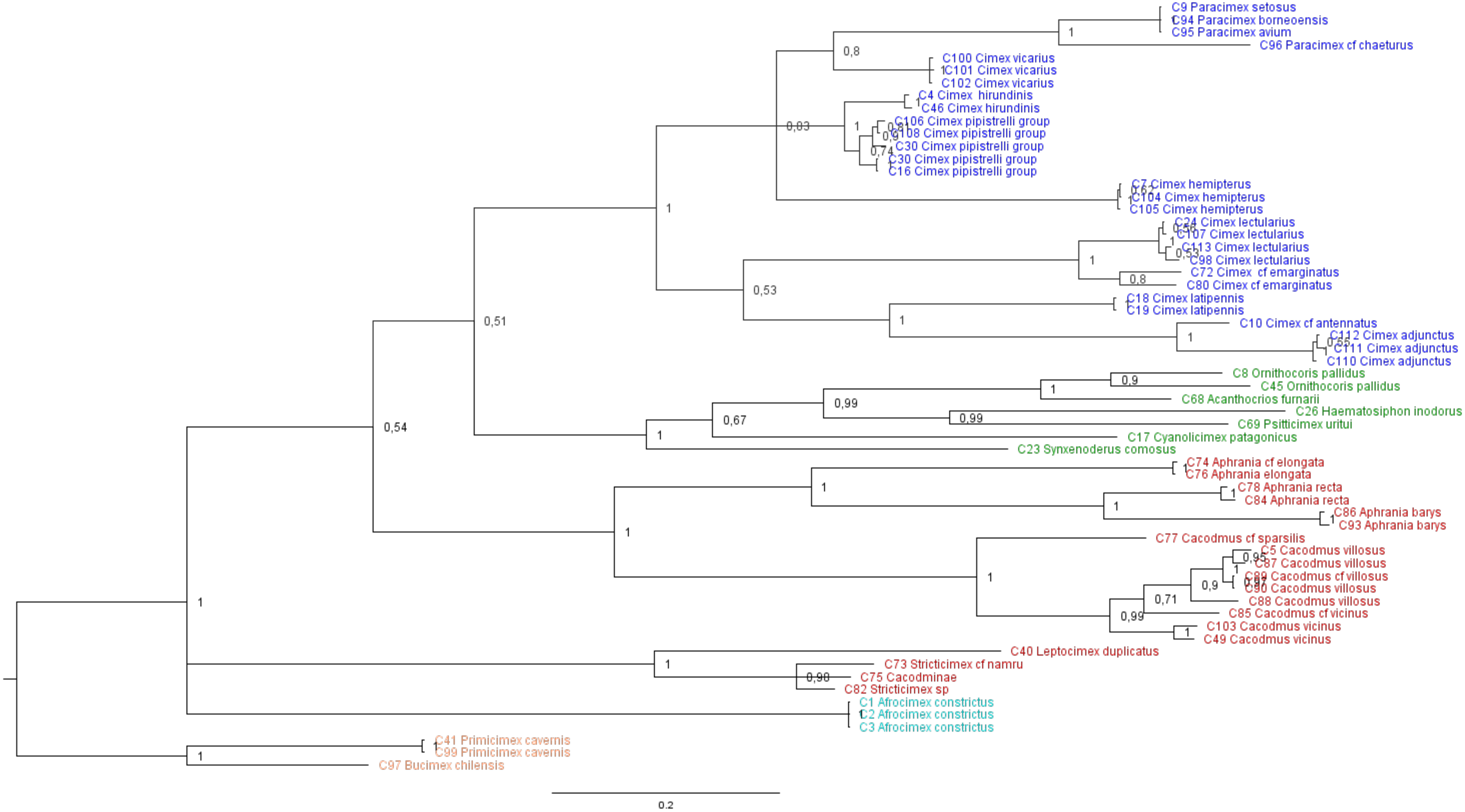
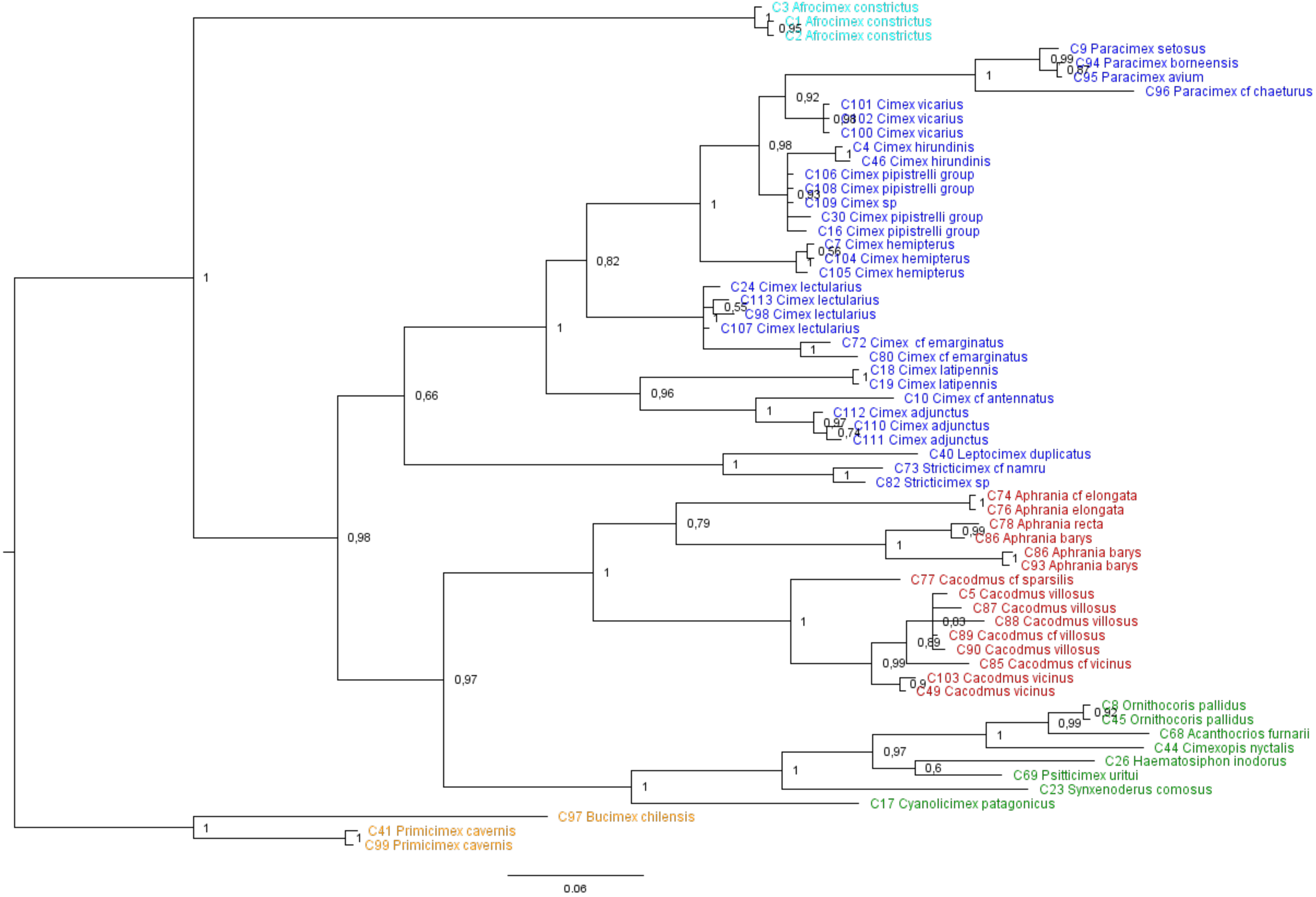

C9 Paracimex setosus
C94 Paracimex borneensis
C95 Paracimex avium
C96 Paracimex cf chaeturus
C24 Cimex lectularius
C107 Cimex lectularius
C113 Cimex lectularius
C98 Cimex lectularius
C72 Cimex cf emarginatus
C80 Cimex cf emarginatus
C4 Cimex hirundinis
C102 Cimex vicarius
C7 Cimex hemipterus
C104 Cimex hemipterus
C105 Cimex hemipterus
C106 Cimex pipistrelli group
C108 Cimex pipistrelli group
C109 Cimex sp
C30 Cimex pipistrelli group
C16 Cimex pipistrelli group
C100 Cimex vicarius
C101 Cimex vicarius
C102 Cimex vicarius
C18 Cimex cf latipennis
C19 Cimex cf latipennis
C10 Cimex cf antennatus
C112 Cimex adjunctus
C110 Cimex adjunctus
C111 Cimex adjunctus
C74 Aphrania cf elongata
C76 Aphrania elongata
C77 Cacodmus cf sparsilis
C5 Cacodmus villosus
C88 Cacodmus villosus
C89 Cacodmus cf villosus
C90 Cacodmus villosus
C87 Cacodmus villosus
C85 Cacodmus cf vicinus
C103 Cacodmus vicinus
C49 Cacodmus vicinus
C78 Aphrania recta
C84 Aphrania recta
C86 Aphrania barys
C93 Aphrania barys
C8 Ornithocoris pallidus
C45 Ornithocoris pallidus
C68 Acanthocrios furnarii
C44 Cimexopis nyctalis
C26 Haematosiphon inodorus
C69 Psitticimex uritui
C23 Synxenoderus comosus
C17 Cyanolicimex patagonicus
C40 Leptocimex duplicatus
C73 Stricticimex cf namru
C75 Cacodminae
C82 Stricticimex sp
C1 Afrocimex constrictus
C2 Afrocimex constrictus
C3 Afrocimex constrictus
C41 Primicimex cavernis
C99 Primicimex cavernis
C97 Bucimex chilensis
OG A4 Buchananiella crassicornis
OG A6 Dysepicritus rufescens
OG A5 Orius minutus
OG A7 Amphiareus obscuriceps
OG A8 Anthocoris confusus
OG A3 Xylocoris cerealis
OG A1 Blaptostethus aurivillus
OG A2 Scoloposcelis albodecussata
OG Joppeicidae Joppeicus paradoxus
OG Microphysidae Loricula elegantula
OG Miridae Capsus ater
OG Tingidae Eteoneus angulatus
OG Nabidae2 Himacerus apterus
OG Nabidae3 Nabis flavomarginatus
OG Nabidae4 Nabis stenoferus
OG Nabidae1 Prostemma spp
OG Lasiochilidae Lasiochilus japonicus
OG Curaliidae Curalium cronini
OG Plokiophilidae Lipokophila eberhardi
OG Lyctocoridae Lyctocoris beneficus
0.04

Figure S6. GBlock alignment tests for trees using strict and relaxed models. Neighbor Joining (NJ) tree for the combined data set with original alignment set and GBlocks data set with tree strict (a) and relaxed (b) model using default settings of Gblocks V.0.91b [46]. NJ analysis was performed in MEGA v.6 [45]. NJ analysis using strict (a) and relaxed GBlock alignments (b) of all molecular markers separately showed no significant effect of alignments and no need to eliminate poorly aligned positions and divergent regions, except some outgroup taxa. The original alignment data set was used for further analysis. Samples C41 and outgroup taxa *Curalium cronini* were removed from this analysis because of missing sequences.


C9 Paracimex setosus
1
C94 Paracimex borneoensis
C95 Paracimex avium
1
C96 Paracimex cf chaeturus
0,8
C100 Cimex vicarius
1
C101 Cimex vicarius
C102 Cimex vicarius
C4 Cimex hirundinis
1
C46 Cimex hirundinis
0,83
1
C106 Cimex pipistrelli group
0,81
C108 Cimex pipistrelli group
0,9
C30 Cimex pipistrelli group
0,74
C30 Cimex pipistrelli group
1
C16 Cimex pipistrelli group
C7 Cimex hemipterus
0,62
1
C104 Cimex hemipterus
C105 Cimex hemipterus
1
C24 Cimex lectularius
0,56
C107 Cimex lectularius
1
C113 Cimex lectularius
0,53
C98 Cimex lectularius
1
C72 Cimex cf emarginatus
0,8
C80 Cimex cf emarginatus
0,53
C18 Cimex latipennis
1
C19 Cimex latipennis
0,51
1
C10 Cimex cf antennatus
1
C112 Cimex adjunctus
0,55
1
C111 Cimex adjunctus
C110 Cimex adjunctus
C8 Ornithocoris pallidus
0,9
C45 Ornithocoris pallidus
1
C68 Acanthocrios furnarii
0,99
C26 Haematosiphon inodorus
0,99
C69 Psitticimex uritui
0,54
0,67
1
C17 Cyanolicimex patagonicus
C23 Synxenoderus comosus
C74 Aphrania cf elongata
1
C76 Aphrania elongata
1
C78 Aphrania recta
1
C84 Aphrania recta
1
C86 Aphrania barys
1
C93 Aphrania barys
1
C77 Cacodmus cf sparsilis
C5 Cacodmus villosus
0,95
C87 Cacodmus villosus
1
1
C89 Cacodmus cf villosus
0,97
0,9
C90 Cacodmus villosus
0,71
C88 Cacodmus villosus
0,99
C85 Cacodmus cf vicinus
C103 Cacodmus vicinus
1
C49 Cacodmus vicinus
1
C40 Leptocimex duplicatus
1
C73 Stricticimex cf namru
0,98
C75 Cacodminae
C82 Stricticimex sp
C1 Afrocimex constrictus
1
C2 Afrocimex constrictus
C3 Afrocimex constrictus
C41 Primicimex cavernis
1
C99 Primicimex cavernis
1
C97 Bucimex chilensis
0.2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1
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0,95
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0,99
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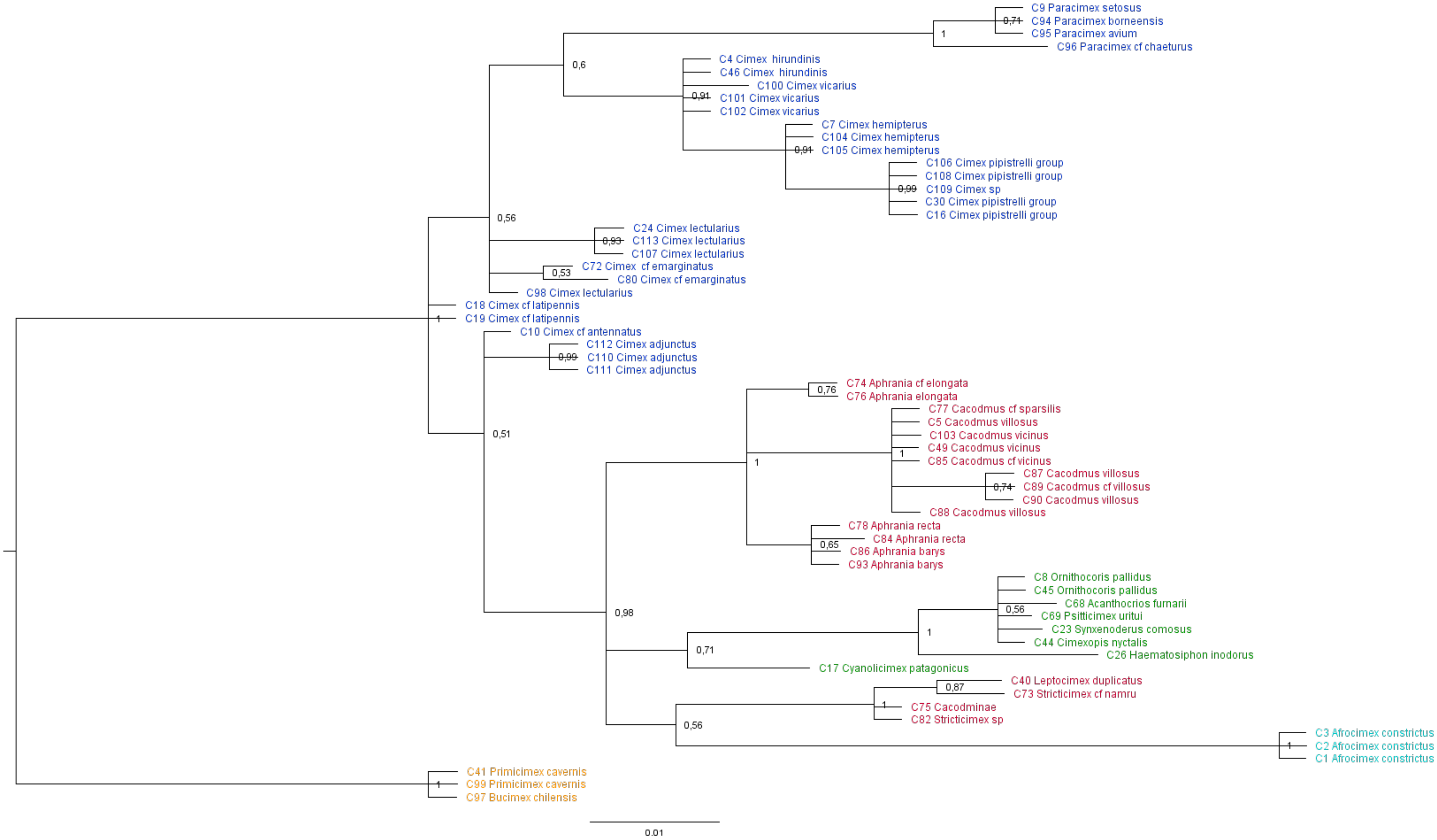
0,87
C95 Paracimex avium
1
C96 Paracimex cf chaeturus
0,92
C101 Cimex vicarius
0,98
C102 Cimex vicarius
C100 Cimex vicarius
0,98
C4 Cimex hirundinis
1
C46 Cimex hirundinis
C106 Cimex pipistrelli group
C108 Cimex pipistrelli group
0,93
C109 Cimex sp
1
C30 Cimex pipistrelli group
C16 Cimex pipistrelli group
C7 Cimex hemipterus
0,56
C104 Cimex hemipterus
1
C105 Cimex hemipterus
0,82
1
C24 Cimex lectularius
C113 Cimex lectularius
0,55
C98 Cimex lectularius
1
C107 Cimex lectularius
1
C72 Cimex cf emarginatus
1
C80 Cimex cf emarginatus
C18 Cimex latipennis
1
C19 Cimex latipennis
0,66
0,96
C10 Cimex cf antennatus
1
C112 Cimex adjunctus
0,97
C110 Cimex adjunctus
0,74
C111 Cimex adjunctus
C40 Leptocimex duplicatus
1
C73 Stricticimex cf namru
1
C82 Stricticimex sp
C74 Aphrania cf elongata
1
C76 Aphrania elongata
0,79
C78 Aphrania recta
0,99
C86 Aphrania barys
0,98
1
C86 Aphrania barys
1
C93 Aphrania barys
1
C77 Cacodmus cf sparsilis
C5 Cacodmus villosus
C87 Cacodmus villosus
0,83
C88 Cacodmus villosus
1
C89 Cacodmus cf villosus
0,89
C90 Cacodmus villosus
0,99
C85 Cacodmus cf vicinus
0,97
C103 Cacodmus vicinus
0,9
C49 Cacodmus vicinus
C8 Ornithocoris pallidus
0,92
0,99
C45 Ornithocoris pallidus
C68 Acanthocrios furnarii
1
0,97
C44 Cimexopis nyctalis
C26 Haematosiphon inodorus
0,6
1
C69 Psitticimex uritui
1
C23 Synxenoderus comosus
C17 Cyanolicimex patagonicus
C97 Bucimex chilensis
1
C41 Primicimex cavernis
1
C99 Primicimex cavernis
0.06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0,6
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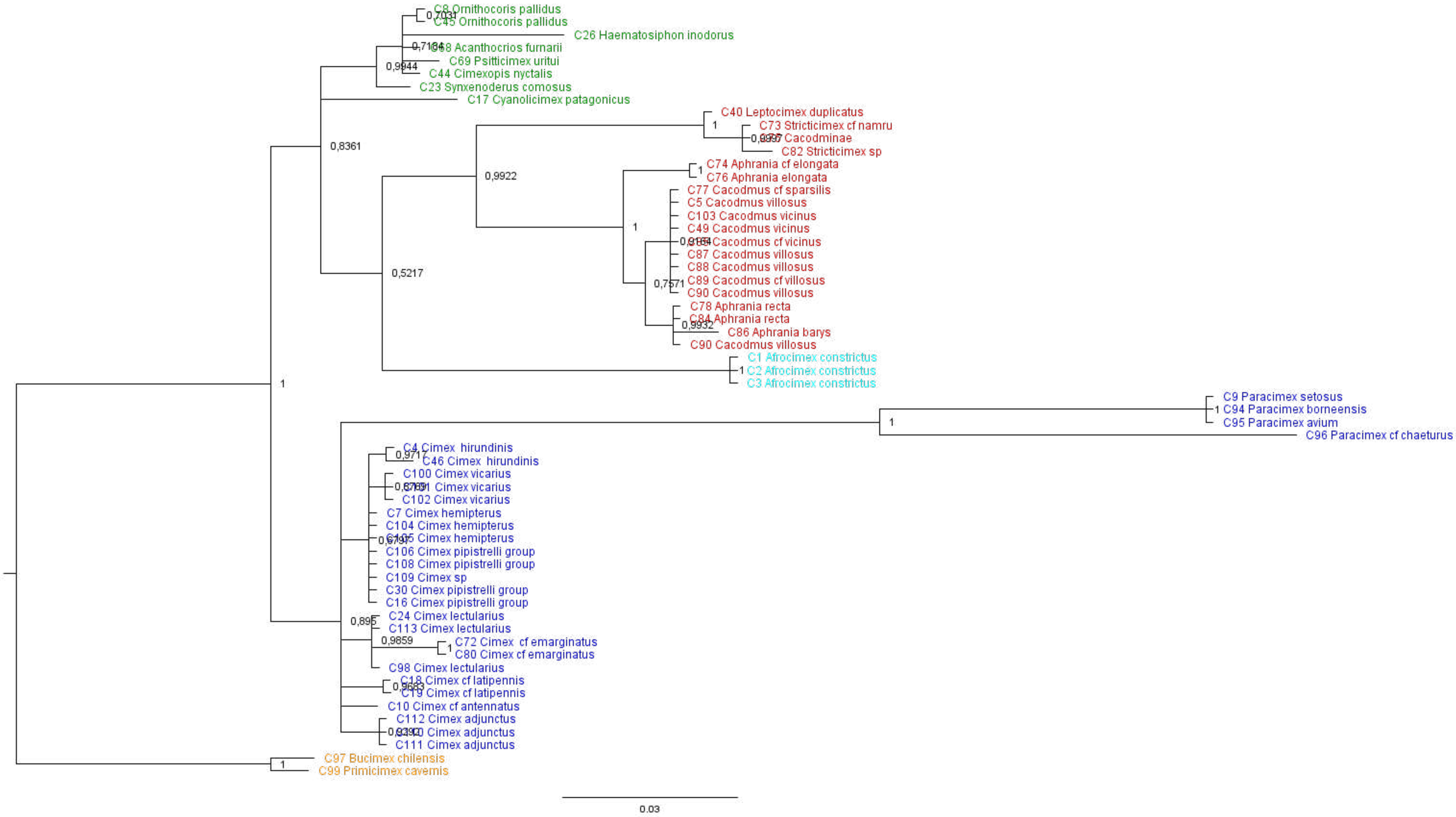
C46 Cimex hirundinis
C100 Cimex vicarius
0,91
C101 Cimex vicarius
C102 Cimex vicarius
C7 Cimex hemipterus
C104 Cimex hemipterus
0,91
C105 Cimex hemipterus
C106 Cimex pipistrelli group
C108 Cimex pipistrelli group
0,99
C109 Cimex sp
C30 Cimex pipistrelli group
C16 Cimex pipistrelli group
0,56
C24 Cimex lectularius
0,93
C113 Cimex lectularius
C107 Cimex lectularius
C72 Cimex cf emarginatus
0,53
C80 Cimex cf emarginatus
C98 Cimex lectularius
C18 Cimex cf latipennis
1
C19 Cimex cf latipennis
C10 Cimex cf antennatus
C112 Cimex adjunctus
0,99
C110 Cimex adjunctus
C111 Cimex adjunctus
C74 Aphrania cf elongata
0,76
C76 Aphrania elongata
C77 Cacodmus cf sparsilis
C5 Cacodmus villosus
0,51
C103 Cacodmus vicinus
1
C49 Cacodmus vicinus
C85 Cacodmus cf vicinus
1
C87 Cacodmus villosus
0,74
C89 Cacodmus cf villosus
C90 Cacodmus villosus
C88 Cacodmus villosus
C78 Aphrania recta
C84 Aphrania recta
0,65
C86 Aphrania barys
C93 Aphrania barys
C8 Ornithocoris pallidus
C45 Ornithocoris pallidus
C68 Acanthocrios furnarii
0,56
C69 Psitticimex uritui
0,98
C23 Synxenoderus comosus
1
C44 Cimexopis nyctalis
C26 Haematosiphon inodorus
0,71
C17 Cyanolicimex patagonicus
C40 Leptocimex duplicatus
0,87
C73 Stricticimex cf namru
1
C75 Cacodminae
C82 Stricticimex sp
0,56
C3 Afrocimex constrictus
1
C2 Afrocimex constrictus
C1 Afrocimex constrictus
C41 Primicimex cavernis
1
C99 Primicimex cavernis
C97 Bucimex chilensis
0.01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C26 Haematosiphon inodorus
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C69 Psitticimex uritui
0,9944
C44 Cimexopis nyctalis
C23 Synxenoderus comosus
C17 Cyanolicimex patagonicus
0,8361
C40 Leptocimex duplicatus
1
C73 Stricticimex cf namru
0,9997
C75 Cacodminae
C82 Stricticimex sp
0,9922
C74 Aphrania cf elongata
1
C76 Aphrania elongata
C77 Cacodmus cf sparsilis
C5 Cacodmus villosus
C103 Cacodmus vicinus
1
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0,9164
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C87 Cacodmus villosus
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0,5217
0,7571
C89 Cacodmus cf villosus
C90 Cacodmus villosus
C78 Aphrania recta
C84 Aphrania recta
0,9932
C86 Aphrania barys
C90 Cacodmus villosus
C1 Afrocimex constrictus
1
C2 Afrocimex constrictus
C3 Afrocimex constrictus
1
C9 Paracimex setosus
1
C94 Paracimex borneensis
C95 Paracimex avium
1
C96 Paracimex cf chaeturus
C4 Cimex hirundinis
0,9717
C46 Cimex hirundinis
C100 Cimex vicarius
0,8769
C101 Cimex vicarius
C102 Cimex vicarius
C7 Cimex hemipterus
C104 Cimex hemipterus
0,6797
C105 Cimex hemipterus
C106 Cimex pipistrelli group
C108 Cimex pipistrelli group
C109 Cimex sp
C30 Cimex pipistrelli group
C16 Cimex pipistrelli group
0,895
C24 Cimex lectularius
C113 Cimex lectularius
0,9859
C72 Cimex cf emarginatus
1
C80 Cimex cf emarginatus
C98 Cimex lectularius
C18 Cimex cf latipennis
0,9683
C19 Cimex cf latipennis
C10 Cimex cf antennatus
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C110 Cimex adjunctus
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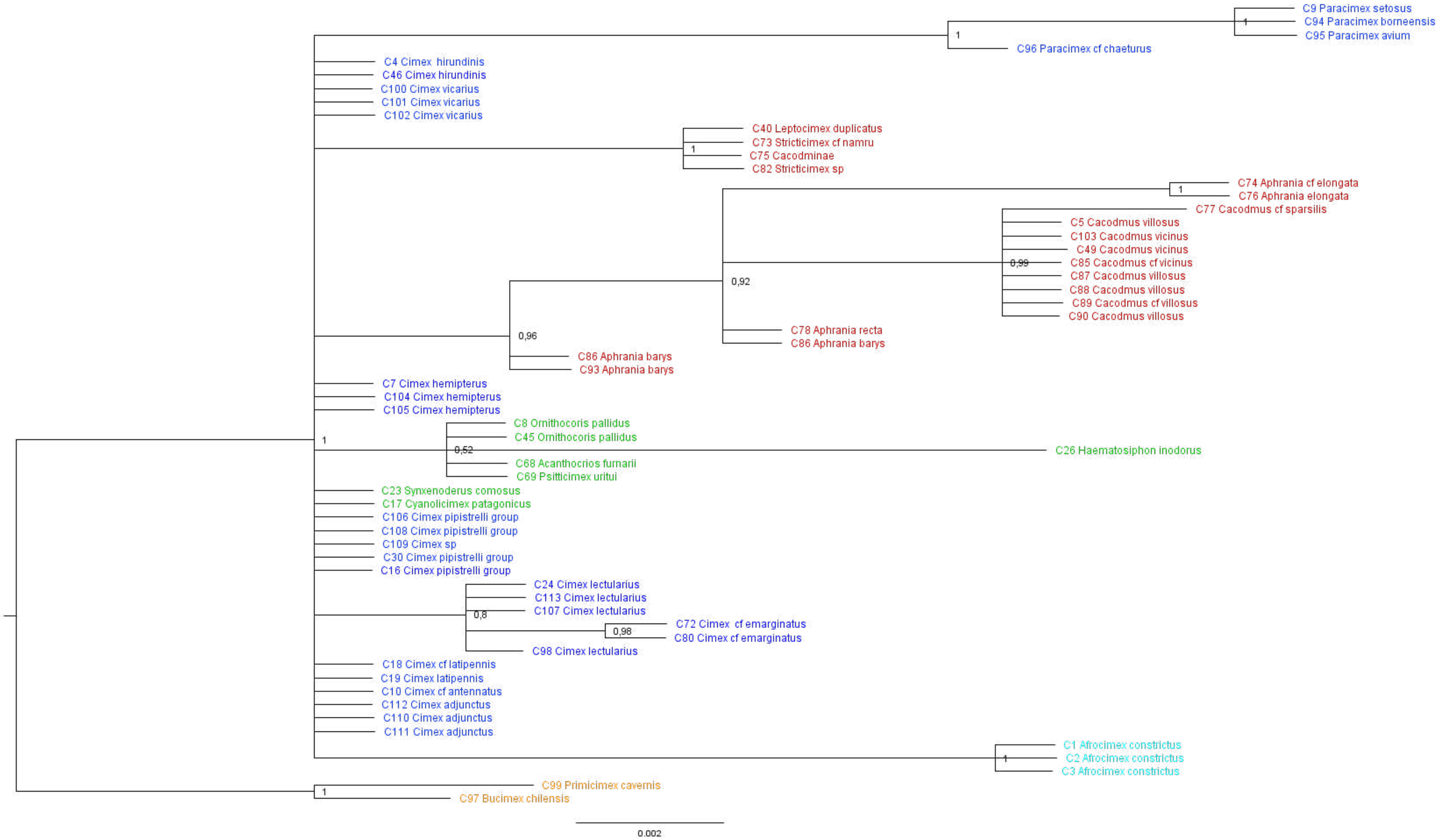
1
C99 Primicimex cavernis
0.03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C94 Paracimex borneensis
C95 Paracimex avium
1
1
C96 Paracimex cf chaeturus
C4 Cimex hirundinis
C46 Cimex hirundinis
C100 Cimex vicarius
C101 Cimex vicarius
C102 Cimex vicarius
C40 Leptocimex duplicatus
C73 Stricticimex cf namru
1
C75 Cacodminae
C82 Stricticimex sp
C74 Aphrania cf elongata
1
C76 Aphrania elongata
C77 Cacodmus cf sparsilis
C5 Cacodmus villosus
C103 Cacodmus vicinus
C49 Cacodmus vicinus
0,99
C85 Cacodmus cf vicinus
C87 Cacodmus villosus
C88 Cacodmus villosus
C89 Cacodmus cf villosus
C90 Cacodmus villosus
0,92
C78 Aphrania recta
C86 Aphrania barys
0,96
C86 Aphrania barys
C93 Aphrania barys
C7 Cimex hemipterus
C104 Cimex hemipterus
C105 Cimex hemipterus
C8 Ornithocoris pallidus
C45 Ornithocoris pallidus
1
0,52
C26 Haematosiphon inodorus
C68 Acanthocrios furnarii
C69 Psitticimex uritui
C23 Synxenoderus comosus
C17 Cyanolicimex patagonicus
C106 Cimex pipistrelli group
C108 Cimex pipistrelli group
C109 Cimex sp
C30 Cimex pipistrelli group
C16 Cimex pipistrelli group
C24 Cimex lectularius
C113 Cimex lectularius
C107 Cimex lectularius
0,8
C72 Cimex cf emarginatus
0,98
C80 Cimex cf emarginatus
C98 Cimex lectularius
C18 Cimex cf latipennis
C19 Cimex latipennis
C10 Cimex cf antennatus
C112 Cimex adjunctus
C110 Cimex adjunctus
C111 Cimex adjunctus
C1 Afrocimex constrictus
1
C2 Afrocimex constrictus
C3 Afrocimex constrictus
C99 Primicimex cavernis
1
C97 Bucimex chilensis
0.002

Figure S7 a-e Bayesian analysis (BA) of phylogenetic relationships of the Cimicidae inferred from individual genes. The analysis was carried out using MrBayes v.3.2.1 [42] for individual genes, substitution models were as chosen in the combined data set analysis (Table S4). Details for settings in MrBayes for single genes BA can be requested from the authors. Consensus trees inferred from the single gene fragments (18S rDNA part1 and part 2, COI, 16S rDNA, 28S D3 rDNA- Table S4) shows their different phylogenetic information but also that single gene analyses are unable to recover phylogenetic relationship.

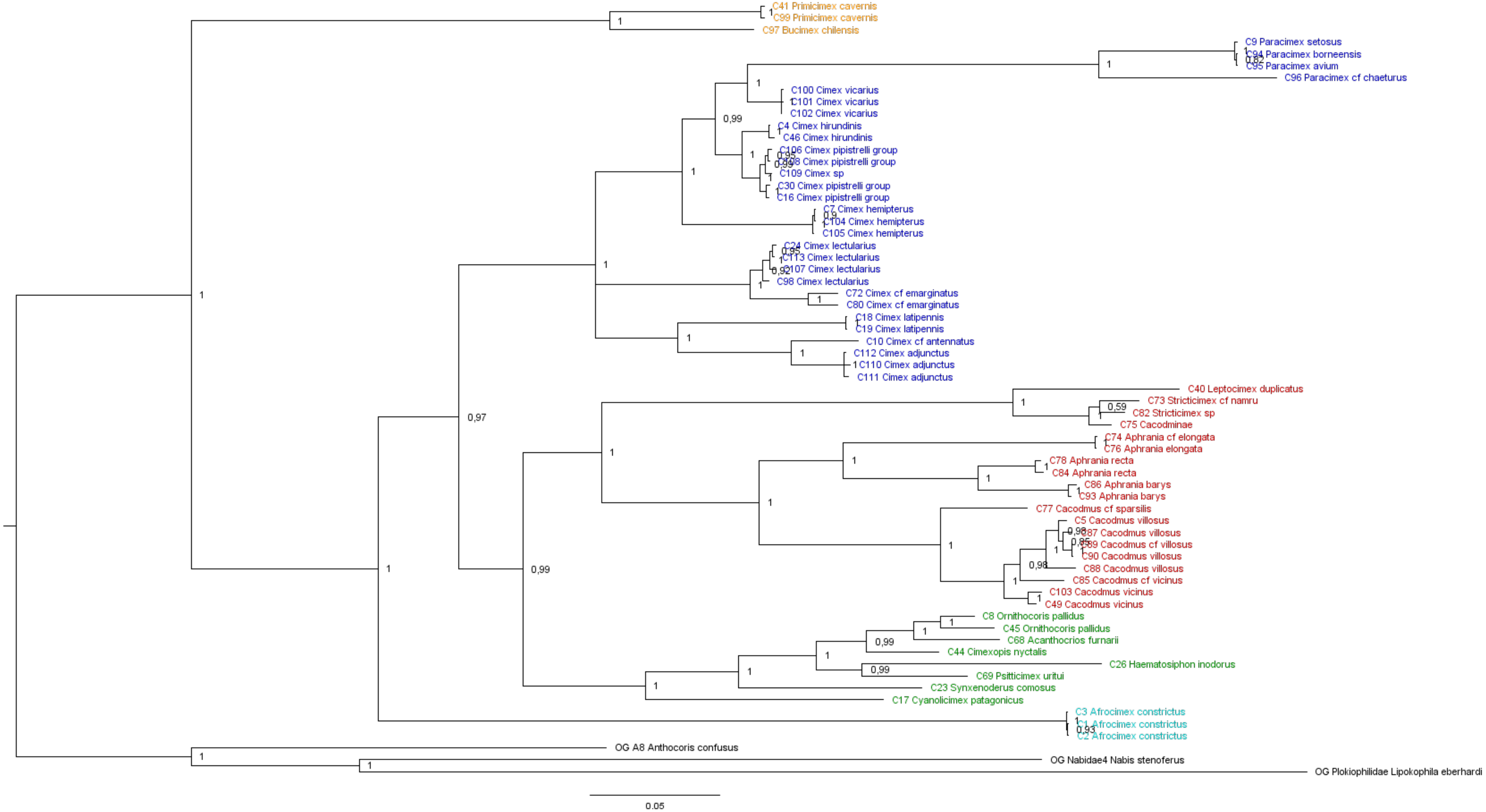
C41 Primicimex cavernis
C99 Primicimex cavernis
C97 Bucimex chilensis
C9 Paracimex setosus
C94 Paracimex borneensis
C95 Paracimex avium
C96 Paracimex cf chaeturus
C100 Cimex vicarius
C101 Cimex vicarius
C102 Cimex vicarius
C4 Cimex hirundinis
C46 Cimex hirundinis
C106 Cimex pipistrelli group
C108 Cimex pipistrelli group
C109 Cimex sp
C30 Cimex pipistrelli group
C16 Cimex pipistrelli group
C7 Cimex hemipterus
C104 Cimex hemipterus
C105 Cimex hemipterus
C24 Cimex lectularius
C113 Cimex lectularius
C107 Cimex lectularius
C98 Cimex lectularius
C72 Cimex cf emarginatus
C80 Cimex cf emarginatus
C18 Cimex latipennis
C19 Cimex latipennis
C10 Cimex cf antennatus
C112 Cimex adjunctus
C110 Cimex adjunctus
C111 Cimex adjunctus
C40 Leptocimex duplicatus
C73 Stricticimex cf namru
C82 Stricticimex sp
C75 Cacodminae
C74 Aphrania cf elongata
C76 Aphrania elongata
C78 Aphrania recta
C84 Aphrania recta
C86 Aphrania barys
C93 Aphrania barys
C77 Cacodmus cf sparsilis
C5 Cacodmus villosus
C87 Cacodmus villosus
C89 Cacodmus cf villosus
C90 Cacodmus villosus
C88 Cacodmus villosus
C85 Cacodmus cf vicinus
C103 Cacodmus vicinus
C49 Cacodmus vicinus
C8 Ornithocoris pallidus
C45 Ornithocoris pallidus
C68 Acanthocrios furnarii
C44 Cimexopis nyctalis
C26 Haematosiphon inodorus
C69 Psitticimex uritui
C23 Synxenoderus comosus
C17 Cyanolicimex patagonicus
C3 Afrocimex constrictus
C1 Afrocimex constrictus
C2 Afrocimex constrictus
OG A8 Anthocoris confusus
OG Nabidae4 Nabis stenoferus
OG Plokiophilidae Lipokophila eberhardi
0,99
0,97
0,99
0,95
0,99
0,9
0,95
0,92
0,62
0,59
0,98
0,85
0,98
0,99
0,99
0,93
0.05

Figure S8 MrBayes consensus tree using one representative species of the closest phylogenetic taxa (e.g. Anthocoridae, Nabidae and Plokiophillidae) within our outgroup sampling. The tree is a Bayesian consensus tree based on four genes (see Material & Methods). Numbers beside the nodes indicate posterior probability values. Topology and support value of the Cimicidae clades did not change due to different outgroup sampling (see Figure1).

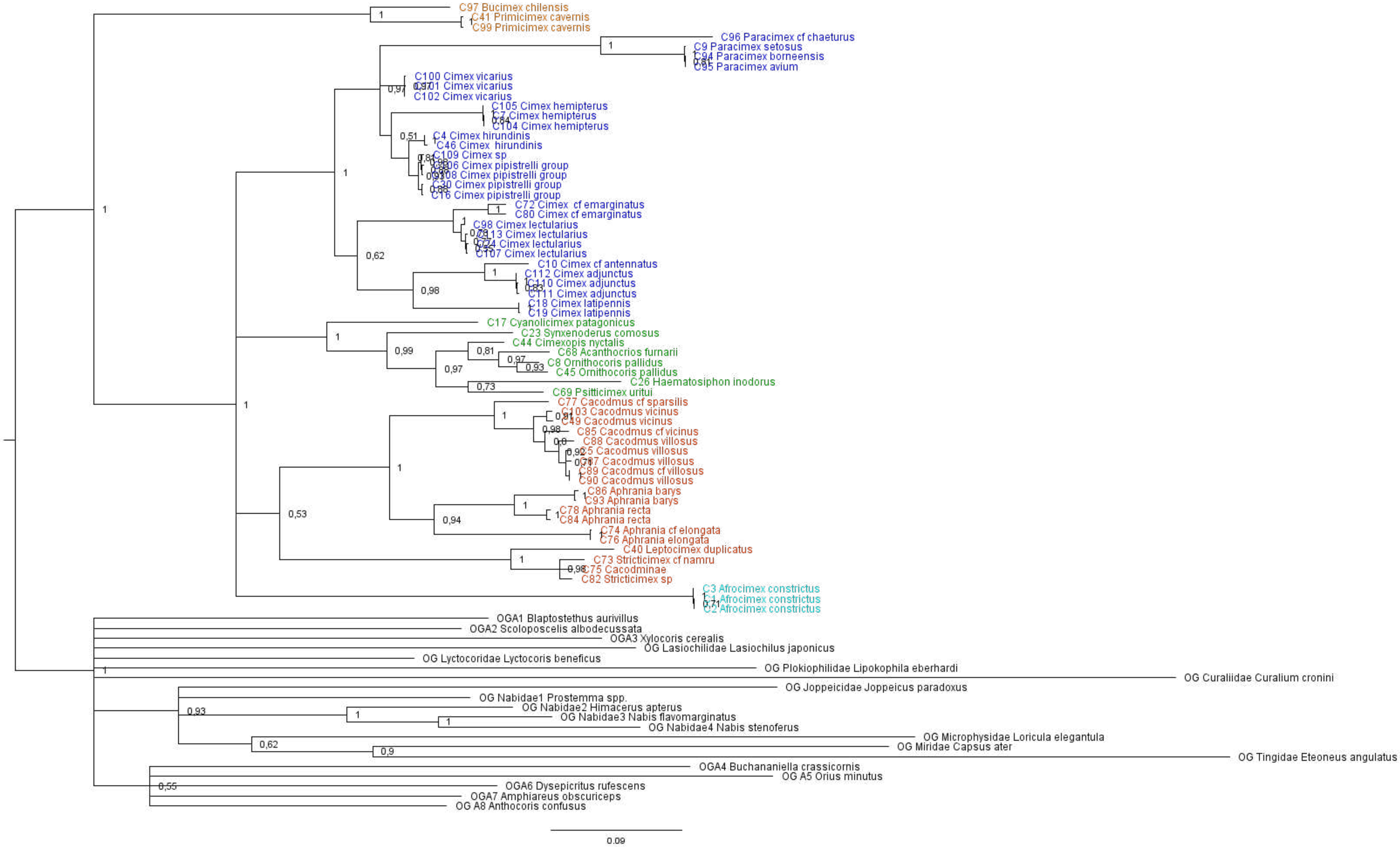
C97 Bucimex chilensis
C41 Primicimex cavernis
C99 Primicimex cavernis
C96 Paracimex cf chaeturus
C9 Paracimex setosus
C94 Paracimex borneensis
C95 Paracimex avium
C100 Cimex vicarius
C101 Cimex vicarius
C102 Cimex vicarius
C105 Cimex hemipterus
C7 Cimex hemipterus
C104 Cimex hemipterus
C4 Cimex hirundinis
C46 Cimex hirundinis
C109 Cimex sp
C106 Cimex pipistrelli group
C108 Cimex pipistrelli group
C30 Cimex pipistrelli group
C16 Cimex pipistrelli group
C72 Cimex cf emarginatus
C80 Cimex cf emarginatus
C98 Cimex lectularius
C113 Cimex lectularius
C24 Cimex lectularius
C107 Cimex lectularius
C10 Cimex cf antennatus
C112 Cimex adjunctus
C110 Cimex adjunctus
C111 Cimex adjunctus
C18 Cimex latipennis
C19 Cimex latipennis
C17 Cyanolicimex patagonicus
C23 Synxenoderus comosus
C44 Cimexopis nyctalis
C68 Acanthocrios furnarii
C8 Ornithocoris pallidus
C45 Ornithocoris pallidus
C26 Haematosiphon inodorus
C69 Psitticimex uritui
C77 Cacodmus cf sparsilis
C103 Cacodmus vicinus
C49 Cacodmus vicinus
C85 Cacodmus cf vicinus
C88 Cacodmus villosus
C25 Cacodmus villosus
C87 Cacodmus villosus
C89 Cacodmus cf villosus
C90 Cacodmus villosus
C86 Aphrania barys
C93 Aphrania barys
C78 Aphrania recta
C84 Aphrania recta
C74 Aphrania cf elongata
C76 Aphrania elongata
C40 Leptocimex duplicatus
C73 Stricticimex cf namru
C75 Cacodminae
C82 Stricticimex sp
C3 Afrocimex constrictus
C1 Afrocimex constrictus
C2 Afrocimex constrictus
OGA1 Blaptostethus aurivillus
OGA2 Scoloposcelis albodecussata
OGA3 Xylocoris cerealis
OG Lasiochilidae Lasiochilus japonicus
OG Lyctocoridae Lyctocoris beneficus
OG Plokiophilidae Lipokophila eberhardi
OG Curaliidae Curalium cronini
OG Joppeicidae Joppeicus paradoxus
OG Nabidae1 Prostemma spp.
OG Nabidae2 Himacerus apterus
OG Nabidae3 Nabis flavomarginatus
OG Nabidae4 Nabis stenoferus
OG Microphysidae Loricula elegantula
OG Miridae Capsus ater
OG Tingidae Eteoneus angulatus
OGA4 Buchananiella crassicornis
OG A5 Orius minutus
OGA6 Dysepicritus rufescens
OGA7 Amphiareus obscuriceps
OG A8 Anthocoris confusus
1
0,97
0,51
0,84
0,62
0,98
0,99
0,81
0,97
0,93
0,73
0,53
0,94
0,98
0,8
0,92
0,71
0,93
0,55
0,62
0,9
0.09

Figure S9. Maximum Likelihood analysis of the combined molecular data set. The Maximum Likelihood analysis confirmed the results of the BA (Figure S3) but the sister relationship of Cacodminae and Haematosiphoninae was not resolved. There was also low support for the node (*Leptocimex*+*Stricticimex*) + (*Aphrania*+*Cacodmus*).

Supplementary Tables

Table S1. List of samples of the 34 species, covering 30% of extant species described to date from 6 out of 7 recognized subfamilies, or 17 out of 26 genera described to date [2], their localities and genbank admission numbers. In addition to the collectors mentioned we thank M.I.M. Azhar, P. Bize, H. Brailovsky, P. Christe, A. Gueorguieva, G. Kyle, C. Lausen, R. Mally, E. McArthur, L. Mollis, J. Rasgon, W. Reeves, M. Ševčík, S. Stoffberg, and M. Webb for providing specimens or helped in obtaining them.

ID/Species	**Country, Locality**	**Host**	**Date**	**Legit/Coll**	**N**	**M**	**Genbank accession no.**				
							COI	**16S**	**18S part 1**	**18S part 2**	**28S**
Primicinae: *Primicimex cavernis* Barber, 1941											
C41	USA, Texas, Vel Verde County, Fern cave	*Tadarida brasiliensis*	27.06.2003	Jim Kennedy			MG596838	MG596875	n.a.	n.a.	n.a.
C99	Mexico, Sonora Dessert	*Tadarida brasiliensis*	Sept. 2015	Omar Calva			MG596839	MG596876			MG763734
Primicinae: *Bucimex chilensis* Usinger 1963											
C97	Chile, R. de los Rios Mariquina, Valdivia, Pelchuquin	unknown	02.01.2013	J.F. Campodonico			MG596840	MG596877			MG763735
Afrocimicinae: *Afrocimex constrictus* Ferris and Usinger 1957											
C1	Kenya, Mount Elgon National Park	*Rousettus aegyptiacus*	March 2005	Reinhardt et al. 2007			MG596804	MG596841			MG763685
C2	Kenya, Mount Elgon National Park	*Rousettus aegyptiacus*	March 2005	Reinhardt et al. 2007			MG596805	MG596842			MG763686
C3	Kenya, Mount Elgon National Park	*Rousettus aegyptiacus*	March 2005	Reinhardt et al. 2007			MG596806	MG596843			MG763687
Haematosiphoninae: *Ornithocoris pallidus* Usinger 1959											
C8	USA, South Carolina, Ilse of Palms			Mary Pringle			MG596827	MG596863			MG763715
C25, C45	USA, South Carolina, Ilse of Palms	Martin (nest)	August 2010	Mary Pringle			MG596828	MG596864			MG763716
Haematosiphoninae: *Haematosiphon inodorus* (Dugés 1892)											
C26	USA, Idaho, Snake River Birds of Prey National Conservation Area	*Falco mexicanus* (nest)	1994	Mary Mc Fadzen			MG596829	MG596865			MG763717
Haematosiphoninae: *Acanthocrios furnarii (Cordero and Vogelsang 1928)*											
C68	Brazil, Canuelas	*Furnarius rufus* (nest)	12.10.2010	Osvaldo Di Iorio			MG596830	MG596866			MG763718
Haematosiphoninae: *Psitticimex uritui* (Lent and Abalos 1946)											
C69	Argentina, Buenes Aires, Junin	*Myiopsitta monachus*	20.06.2008	Osvaldo Di Iorio			MG596831	MG596867			MG763719
Haemotosiphoninae: *Synxenoderus comosus* List 1925											
C23	USA, California, Los Angeles County	*Aeronautes saxatalis* (nest)	02 .06. 2000	C.T. Collins			MG596832	MG596868			MG763720
Haematosiphoninae: *Cyanolicimex patagonicus* Carpintero, Di Iorio, Masello and Turienzo 2010											
C17	Argentina, Rio Negro, El Condor (Patagonia)	*Cyanoliseus patagonus*	20.12.2003	Petra Quillfeldt			MG596833	MG596869			MG763721
Haematosiphoninae: *Cimexopis nyctalis* List 1925											
C12, C44	USA, Texas, Travis County, NW of Austin, TX.	*Chaetura pelagica*	Sept. 1997	Paul D. Kyle			n.a.	MG596870	K	n.a.	MG763722
Cacodminae: *Leptocimex duplicatus* Usinger 1959											
C40	Israel, Kalia Cave, 31°44‘N 35°28‘ E		12.10.2012	Shumulik Landau			MG596810	MG596847			MG763694
Cacodminae: *Stricticimex* cf *namru* Usinger 1960											
C73	Iran, Ilam Province, Dehloran Cave (nymph)	mixed colony of *Asellia tridens, Rhinopoma microphyllum*, and *R. hardwickii*	17.10.2011	Petr Benda			MG596811	MG596848			MG763695
Cacodminae: *Stricticimex* spec.											
C82	Oman, Al Batinah Ash Shamal Province, Ghab, Wadi Al Hawasina (nymph)	*Nyctinomus thomasi*	07.04.2011	Petr Benda			MG596817	MG596853			MG763702
Cacodminae: Cacodminae spec.											
C75	Oman, Ash Sharqiyah Al Janub Province, Jaalan Bani Bu Ali (nymph)	*Taphozous nudiventris*	02.04.2011	Petr Benda			MG596814	n.a.			MG763697
Cacodminae: *Cacodmus* cf. *sparsilis* (Rothschild 1912)											
C77	Oman, Dhofar Province, Wadi Hannah	*Pipistrellus dhofarensis*	13.10.2008	Petr Benda			MG596813	MG596850			MG763699
Cacodminae: *Cacodmus vicinus* Horvath1934											
C103	Jordan, Zarqa Province, Azraq Wetland Reserve	*Pipistrellus kuhlii*	13.10.2008	Petr Benda			KF018762	KF018728	KF018714	KF018714	MG763701
C49	Spain, Caceres province, Plasencia	*Pipistrellus* sp.	19.09.2006	Unknown			MG596816	MG596852			MG763700
C85	Senegal, Fatick Province, Fathala Reserve	*Scotoecus hirundo*	14.02.2012	Radek Lučan			MG596819	MG596855			MG763705

Cacodminae: *Cacodmus villosus* (Stål 1855)											
C5	Kenya, Mount Elgon National Park	unknown	20.03.2005	Michael Siva-Jothy			MG596815	MG596851			MH181391
C87	Ethiopia, 4 km S of Korem	*Pipistrellus hesperidus*	28.10.2012	Petr Benda			MG596821	MG596857			MG763707
C88	Ethiopia, Suba Menagesha Forest	*Pipistrellus hesperidus*	25.10.2014	Petr Benda			MG596822	MG596858			MG763708
C89	Namibia, Kavango, East Province, Ncaute	*Neoromicia capensis*	22.01.2012	Petr Benda			MG596823	MG596859			MG763709
C90	Namibia Oshikoto Province, Ghaub farm	*Neoromicia capensis*	15.07.2014	Petr Benda			MG596824	MG596860			MG763710
Cacodminae: *Aphrania barys* Jordan and Rothschild 1912											
C86	Namibia, Zambezi Province, Kongola	*Neoromicia capensis*	28.01.2012	Petr Benda			MG596820	MG596856			MG763706
C93	South Africa, Northern Cape Province, Tswalu Private Nature Reserve	*Neoromicia capensis*	01.01.2009	Samantha Stoffberg			MG596825	MG596861			MG763711
Cacodminae: *Aphrania recta* Ferris and Usinger1957											
C78	Mauritania, Brakna Province, Bogué	*Nycticeinops schlieffenii*	14.10.2010	Petr Benda			KF018764	KF018730	KF018716	KF018716	MG763704
C84	Senegal, Fatick Province, Fathala Reserve	*Neoromicia* cf. *guineensis*	14.02.2012	Radek Lučan			MG596818	MG596854			MG763703
Cacodminae: *Aphrania elongata* Usinger 1966											
C74	Senegal, Fatick Province, Fathala Reserve	unknown	February 2012	Radek Lučan			MG596812	MG596849			MG763696
C76	Mauritania, Brakna Province, Bogué	*Scotophilus leucogaster*	14.10. 2010	Petr Benda			KF018763	KF018729	KF018715	KF018715	MG763698
Cimicinae: *Cimex pipistrelli* group: Europe											
C30	Laboratory population (5 yrs), originally from Hanau (Germany)	*Nyctalus noctula*	05.06.2004	Klaus Reinhardt, Dieter Kock			MG596834	MG596871			MG763723
C106	U.K. Rindleford, Bridgnorth, Shropshire	*Pipistrellus* spec.	14.xii.1999	John Mason			GU985534	GU985556	K	K	MG763726
C16	Huelva, Spain	bat	1 July 2003	Juan Quetglas			MG596835	MG596872			MG763725
C108	Bulgaria, Červen, Ruse region	*Nyctalus noctula*	1.10.2005	Ivailo Borissov			GU985530	GU98555	K	K	MG763724
Cimicinae: *Cimex* sp. *cf Cimex pipistrelli* group (see ref (*64*) for details)											
C109	Japan, Konda, Sasayama-City, Hyogo prefecture	*Delichon dasypus,* *Hirundo daurica japonica*	9.3.2008	Nobuhiko Kataoka			GU985542	GU985564	KF018708	KF018708	MG763727
Cimicinae: *Cimex adjunctus* Barber 1939											
C110	USA, Washington county, North Carolina1	*Nycticeius humeralis*	7.6.2005	Matina Kalcounis-Ruppell		1	GU985536	GU985558	KF018712	KF018712	MG763737
C111	USA, Galesburg, Kalamazoo county, Michigan	*Eptesicus fuscus*	6.7.2005	Lee Johnson		1	GU985535	GU985557			MG763736
C112	USA, Fulton, Kalamazoo county, Michigan	*Eptesicus fuscus*	19.6.2005	Lee Johnson		1	GU985537	GU985559			MG763738
Cimicinae: *Cimex* cf. *antennatus* Usinger and Ueshima 1965											
C10	USA, Antelope Valley, California		15.8.2002	A.C. Lohmann		1	KF018760	KF018732	KF018718	KF018718	MG763739
Cimicinae: *Cimex* cf. *latipennis* Usinger and Ueshima 1965											
C18	Canada, Hope, British Columbia, Canada	*Myotis lucifugus*	unknown	T. Luszczell		1	KF018758	KF018734	KF018720	KF018720	MG763740
C19	Canada, Hope, British Columbia, Canada	*Myotis volans*	unknown	T. Luszczell		1	KF018757	KF018733	KF018719	KF018719	MG763741
Cimicinae: *Cimex hemipterus* Fabricius 1803											
C7	Kenya, Mombasa	human		Oliver Otti			MG596826	MG596862			MG763712
C104	Malaysia, Melaca	human	15.12.2011	Hana Šípková	1	1	KF018754	KF018724	KF018710	KF018710	MG763713
C105	India, Tamil Nadu	human	6.12.2010	Robert Vlk	4	1	KF018755	KF018725	KF018710	KF018710	MG763714
Cimicinae: *Cimex lectularius* (Linnaeus 1758)											
C113	Czech Republic, Olomouc, stock	human	autumn 2005	Libor Mazánek	2	2	GU985524	GU985546	KF018711	KF018711	MG763730
C107	Czech Republic, Brandýs nad Orlicí	*Myotis myotis*	21.6.2006	Ondřej Balvín	2	2	GU985526	GU985548	KF018711	KF018711	MG763729
C24	long standing (>40 yrs) laboratory stock, London, UK	human		Klaus Reinhardt			MG596836	MG596873			MG763728
C98	Iran, Golestan province, picnic grass field	unknown host	27.05.2006	Jiří Hájek, Pavel Chvojka			MF680527	MF680518			MG763731
Cimicinae: *Cimex* cf. *emarginatus* Simov, Ivanova & Schunger, 2006											
C72	Bulgaria, Malashevska planina Mt., Monastery of the Saints Archangels, N 41.8564/ E22.99197	*Myotis* cf. *alcathoe*	10.09.2011	Leg. B. Petrov, I.. Alexandova, coll Nikolay Simov			MG596837	MG596874			MG763732
C80	Morocco, Bouhachen, Rif	*Pipistrellus pipistrellus*	06.05.2013	Tomáš Bartonička			MF680526	MF680517			MG763733
Cimicinae: Cimex (former *Oeciacus) hirundinis* (Lamarck 1816)											
C4	Switzerland	unknown	unknown	Pierre Bize			MG596808	MG596845			MG763692
C46	Czech Republic, Žíteč, Jindřichův Hradec	*Delichon urbica*	23.11.2007	Jaroslav Cepák			MG596809	MG596846			MG763693
Cimicinae: Cimex (former *Oeciacus) vicarius* (Horvath 1890)											

C100	USA, Sarben, Keith County, Nebraska	*Petrochelidon pyrrhonota*	2.10.2008	Charles R. Brown		3	GU985541	GU985563	KF018709	KF018709	MG763742
C101	USA, Keystone, Keith County, Nebraska	*Petrochelidon pyrrhonota*	3.10.2008	Charles R. Brown	16	2	KF018753	KF018723	KF018709	KF018709	MG763743
C102	USA, Keystone, Keith County, Nebraska	*Petrochelidon pyrrhonota*	3.10.2008	Charles R. Brown		1	KF018752	KF018722	KF018709	KF018709	MG763744
Cimicinae: *Paracimex setosus* Ferris and Usinger 1957											
C9	Malaysia	*Aerodromus vanikorensis* or *fuciphagus*		Dale Clayton		1	KF018761	KF018735	KF018721	KF018721	MG763689
Cimicinae: *Paracimex borneoensis* Usinger 1959											
C94	Malaysia, Borneo, Niah cave	*Aerodramus salanganus*	26.6.2015	Steffen Roth, Adrian Scheidt			KF018761	MF680519			MG763690
Cimicinae: *Paracimex avium* Kiritshenko 1913											
C95	Indonesia, Sumatra, Aceh, Takengon, Buffalo Cave (brass Koro), N 4.605577/Ep6.882463, 4.5km ESE of Takengon south bank of the lake	*Aerodramus salanganus*	3.6.2105	Adrian Scheidt			MG596807	MG596844			MG763688
Cimicinae: *Paracimex cf chaeturus* Ueshima 1968											
C96	China, Cave near Jiangshui, Yunnan province	*Aerodramus brevirostris*	May 2015	Ondřej Balvín			MF680531	MF680520			MG763691
OUTGROUP TAXA - DNA sequences from GenBank							**COI**	**16S**	**18SI**	**18SII**	**28S**
OGA1	Anthocoridae: *Blaptostethus aurivillus* Kazutaka 2008						KF36463	GQ258388	GQ258400	GQ258400	GQ258440
OGA2	Anthocoridae: *Scoloposcelis albodecussata* Yamada, Kazutaka & Hirowatari, Toshiya 2005						GQ292129	GQ258376	GQ258422	GQ258422	GQ258457
OGA3	Anthocoridae: *Xylocoris cerealis* Yamada & Yasunaga 2006						GQ292172	GQ258384	GQ258395	GQ258395	GQ258459
OGA4	Anthocoridae: *Buchananiella crassicornis* Carayon 1958						GQ292145	GQ258364	GQ258407	GQ258407	GQ258441
OGA5	Anthocoridae: *Orius minutus* (Linnaeus 1758)						KR040183	GQ258372	GQ258417	GQ258417	GQ258452
OGA6	Anthocoridae: *Dysepicritus rufescens* (Costa 1847)						GQ292210	GQ258386	GQ258399	GQ258399	GQ258444
OGA7	Anthocoridae: *Amphiareus obscuriceps* (Poppius 1909)						GQ292178	GQ258358	GQ258393	GQ258393	GQ258429
OGA8	Anthocoridae: *Anthocoris confusus* Reuter 1884						KM022525	GQ258359	GQ258401	GQ258401	GQ258431
OGNab1	Nabidae: *Prostemma div.* spp.						JQ782833	JQ782833	JQ782787	JQ782787	JQ7828081
OGNab2	Nabidae: *Himacerus apterus* (Fabricius 1798)						KR034788	GQ258381	GQ258425	GQ258425	GQ258435
OGNab3	Nabidae: *Nabis flavomarginatus* Scholtz 1847						KM022694	GQ258380	GQ258424	GQ258424	GQ258433
OGNab4	Nabidae: *Nabis stenoferus* Hsiao, 1964						GQ292211	GQ258379	GQ258426	GQ258426	GQ258434
OG	Joppeicidae: *Joppeicus paradoxus* Reuter, 1910						AY252951	AY252688	EU6831471	n.a.	AY252455
OG	Lasiochilidae: *Lasiochilus japonicus* Hiura, 1967						GQ292187	GQ258367	GQ258410	GQ258410	GQ258445
OG	Lyctocoridae: *Lyctocoris beneficus* (Hiura, 1959)						GQ292284	GQ258369	GQ258412	GQ258412	GQ258447
OG	Microphysidae: *Loricula elegantula* (Baerensprung, 1858)						KM022867	EU683098	EU683151	EU683151	AY252557
OG	Plokiophilidae: *Lipokophila eberhardi* Schuh, 1993						n.a.	AY252661	AY252148	n.a.	AY252432
OG	Curaliidae: *Curalium cronini* Schuh, Weirauch, Henry & Halbert, 2008						n.a.	n.a.	EU683128	EU683128	n.a.
OG	Tingidae: *Eteoneus angulatus* Drake & Maa 1953						EF523481	EF487290	EF487311	EF487311	EF487321
OG	Miridae: *Capsus ater* (Linnaeus, 1758)						AY252977	AY252712	EU683117	EU683117	AY252483

Table S2. Evolutionary occurrence of extant bedbug lineages and their host genera, as extracted from our phylogenetic tree. (*) indicates molecular ages which are confirmed by oldest fossils (less than ±10 MYA). Mean age, 95% lower and upper highest posterior distribution inferred by BEAST [38] is reported. Event-, distance- or topology-based cophylogenetic tests were not applied because the molecular and phylogenetic resolution differed between host and parasite trees and because over-precision should be avoided (see *Results and Discussion*).

Current Host	Time (MYA)	Bug Taxon	Time (MYA)
Rousettus	23 (26-18)	*Afrocimex*	90 (103-77)[xx]
Myotis	20*, (25-16)[x]	*Bucimex*	26 (42-13)
Tadarida	22[x] (27-17)	*Primicimex*	26 (42-13)
Vespertillionidae	54 (60-50)	Cimicinae+Cacodminae+ Haematosiphoninae	80 (94-65)
Vespertillionoidea	54 (60-50)	Cimicidae	123 (140-110*)

[x] *Tadarida-Myotis* split: 47MYA

[xx] 73 MYA according to different tree estimate (Figure 2)

Table S3 List of primers used and PCR conditions.

Gene	Abbreviation	Direction of primer	Primer name	Sequence from 5′ to 3′	Reference	Annealing temperature
Cytochrome oxidase subunit I	COI	F	Lep1Fdeg	ATTCAACCAATCATAAAGATATNGG	[61] modified	42°C
	COI	F	Lep1F	ATTCAACCAATCATAAAGATATTGG	[61]	48°C
	COI	R	Lep3R	TATACTTCAGGGTGTCCGAAAAATCA	[61] modified	42°/48°C
	COI	F	jgHCO	TITCIACIAAYCAYAARGAYATTGG	[62]	42°C
	COI	R	jgLCO	TAIACYTCIGGRTGICCRAARAAYCA	[62]	42°C
16S ribosomal	16S	F	16S LR-J	TTA CGC TGT TAT CCC TAA	[63]	48°C
	16S	R	16S LR-N	CGC CTG TTT ATC AAA AAC AT	[64]	48°C
	16S	F	16Ar	CGCCTGTTTATCAAAAACAT	[65]	48°C
	16S	R	16Br	CGGTCTGAACTCAGATCACG	[65]	48°C
18S ribosomal	18S	F	18S-1	CTG GTT GAT CCT GCC AGT AGT	[66]	48°C
	18S	R	18S-3	GGT TAG AAC TAG GGC GGT ATC T	[66]	48°C
	18S	F	18S-2	AGA TAC CGC CCT AGT TCT AAC	[66]	48°C
	18S	R	18S-4	GAT CCT TCT GCA GGT TCA CC	[66]	48°C
	18S	F	329	TAATGATCCTTCCGCAGGTT	[67]	44°/48°C
	18S	R	328	CCTGGTTGATCCTGCCAG	[67]	44°/48°C
28s ribosomal	28S (D3)	F	1274	GACCCGTCTTGAAACACGGA	[68]	48°C
28s ribosomal	28S (D3)	R	1275	TCGGAAGGAACCAGCTACTA	[68]	48°C

Table S4 Characteristics of sequences used. To implement Kimura's two-parameter model (K2) in BEAST 1.8.4 [38] we selected the Hasegawa-Kishino-Yano (HKY) model and set “base frequencies” to “All Equal”. For many taxa sampled, the two 18S fragments did not overlap. Therefore, the two fragments were analyzed separately.

Gene	Sequence length (bp)	Number of missing taxa	Alignment position	Parsimony informative	Variable sites	Evolution model
COI	591-659	2	659	335	359	GTR+G+I
16S rDNA	361-519	1	571	311	395	TN93+G+I
28S rDNA	301-337	1	363	82	121	K2+H
18S rDNA part 1	561-988	2	1121	266	415	K2+G+I
18S rDNA part 2	598-697	3	711	78	144	K2+G+I

Table S5. Alignment file.

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>C1 Afrocimex constrictus
TTCGGAAGGAACCAGCTACTAGATGGTTCGATTGGTCTTTCGCCCCTATACCCAGCTCCGACGATCGATTTGC
ACGTCAGAATCGCTGCGGACCTCCACCAGGGTTTCCCCTGGCTTCGTCCTGGCCAGGCATAGTTCACCATCTT
TCGGGTATCAGCGTGTGCGCTACAGGTGCGCCTCCACTCGTAATGAGAAAGAGACGCCCCGGGAGTGCGGGAC
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CGTAGGACTCCTTTCACTTTCATTGCGCCTTTAGGTTTT-C-
CACCCTATGACTCGCGCACACGCTAAACTCCTTGGTCCGTCTTTTAGATTT---
TATTTAAAGTTTAACCTGCCCTATGATA-----
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ATGGTTTGACGAGAAAAAGACTTTCTTTA-
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CTT----TATTA-AATATTAAAAAATA-AATATTTTAGATA----GT---TTAATAT---CTTT--
ATTTACTATTT--AATTTTGTTGGGGGGACAGGTAAATTTAATTAACTTT---ATTTA---TT--TTA-AT--
CGTTAATTAACGTGT-TTTTTGATCCATTT-ATA----ATGGGAATAAGATTAAGTTACTTTA---
GGGATAACAGCGTTATTTTGTTGGAGAGTTCATATTAATAATAAAGTTTGCGACCTCGATGTTGG-ATTAA-
AATAAGTATTT-
GGTGTAGGTGCTGCATTACTAGGTCTGTTCGACCTTTAATTTTTTACGTGATCTGATTTACTTTGTACTTTTT
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ACCATTCG--TGGTCAGGGCGCTTTTATCA-GAACAAGACCAATCGCCCGGCGAAGCCGG------
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>C2 Afrocimex constrictus
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ANNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNnnn
nnnnnnnnnnnnnnnnnnnnnnnnnnnnGGTATACTAGGAACATCATTAAGTTGACTAATTCGTATTGAATTA
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AGTAAGTATAT-
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