# Exploring the shell-based taxonomy of the Sri Lankan land snail *Corilla* H. and A. Adams, 1855 (Pulmonata: Corillidae) using mitochondrial DNA

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## Abstract

The land-snail genus *Corilla* is endemic to Sri Lanka and India's Western Ghats. The ten extant Sri Lankan species belong to two distinct shell forms that are associated respectively with lowland and montane rainforest. We here present the first molecular phylogenetic analysis for *Corilla*. Our dataset includes nine

nominal Sri Lankan species and is based on three mitochondrial genes (CO1, ND1 and 16S). Although the deeper nodes in the trees are not fully resolved, the results do suggest speciation in *Corilla* has involved repeated, ecologically-driven convergence in shell form. The mtDNA data agree with the current shell-based taxonomy for *C. adamsi*, *C. beddomeae*, *C. carabinata*, *C. humberti* and *C. colletti*, consistently supporting the first four as monophyletic, and supporting the last also as monophyletic in nearly all analyses. *Corilla adamsi*, *C. beddomeae* and *C. colletti* may each contain at least one additional, previously-undescribed species. The relationship between northern and eastern *C. odontophora* couldn't be reliably resolved, but our results suggest that they are distinct species and that there is further species-level or intraspecific (geographical) differentiation within eastern *C. odontophora*. The current, morphologically-defined species limits of the three remaining nominal species, *C. gudei*, *C. erronea* and *C. fryae*, are inconsistent with the mtDNA sequence data. Northern and southern *C. gudei* appear to be distinct species: the sister taxon of southern *C. gudei* is *C. humberti*, and in the Bayesian trees alone the sister taxon of northern *C. gudei* is the lowland *C. carabinata*. *Corilla erronea* and *C. fryae* constitute a well supported clade in which both nominal species are paraphyletic. While most intra-clade CO1 *p*-distances are moderate to relatively large, the phylogenetic structuring within the clade does not seem to correspond to any obvious morphological, elevational or geographical patterns. These results are difficult to interpret, and further detailed study is needed before the taxonomic status of *C. erronea* and *C. fryae* can be resolved.

## 1. Introduction

The native land-snail fauna of the Western Ghats-Sri Lanka biodiversity hotspot is phylogenetically diverse and is dominated by species endemic to the region, many of them belonging to genera endemic or largely endemic to the Western Ghats and Sri Lanka (Raheem et al., 2014). One of the genera endemic to the hotspot is *Corilla* H. & A. Adams, 1858, the sole representative of the stylommatophoran family Corillidae, a putative Gondwanan relict (Naggs & Raheem, 2005). Species of *Corilla* inhabit tropical rainforest and moist monsoon forest, where they are usually found on the forest floor, among leaf litter and decaying wood. The current species-level taxonomy for *Corilla* largely follows Gude's (1896a, 1896b, 1914) revisionary work,

and is based entirely on shell morphology, the key characters being shell shape and size, the form of the lip, the arrangement of the folds inside the mouth of the shell (the palatal and parietal folds) and shell sculpture. Species identification within this taxonomic framework is generally straightforward, but the status of these nominal species as monophyletic taxa has not been investigated and molecular phylogenetic studies of this genus have still to be carried out.

Taxonomic diversity in *Corilla* is concentrated in Sri Lanka, where ten of the 11 extant species occur, all endemic to the island (Gude, 1914; Barnacle, 1956) and all highly restricted in distribution (**Figs. 1A, B**). The Sri Lankan species belong to two distinct shell forms that are associated respectively with the forests of the lowlands (lowland rainforest and moist monsoon forest occurring up to an elevation of 1000 m, Legg and Jewell, 1995) and the mountains (submontane and montane rainforest above elevations of 1000 m, Legg and Jewell, 1995). The lowland species are *Corilla adamsi* (Gude, 1914), *C. carabinata* (Férussac, 1821), *C. colletti* Sykes, 1897 and *C. lesleyae* Barnacle, 1956, all of which are parapatric/allopatric. The montane species comprise three parapatric/allopatric taxa, *C. gudei* Sykes, 1897, *C. humberti* (Brot, 1864), *C. odontophora* (Benson, 1865), and three partly sympatric ones, *C. beddomeae* (Hanley in Hanley & Theobald, 1876), *C. erronea* (Albers, 1853) and *C. fryae* Gude, 1896. The shells of the lowland species are wide-lipped and dull yellow or red-brown in colour, whereas montane species possess narrow-lipped shells that are black or dark brown (**Figs. 1C, D**). These differences may have evolved once, reflecting sustained independent diversification within lowland and montane rainforest regions. Or, they may have evolved several times with closely-related species diverging in bioclimatic distribution and morphology and distantly related species converging on similar bioclimatic distributions and morphology. Exploring the evolutionary basis of these differences will provide new insights into the relationship between species diversification and the evolution of habitat-specific morphological characters in rainforest taxa. This is a neglected topic in rainforest research (but see Dowle et al., 2015) – the major focus among workers has been on issues such as the phylogenetic relationships between lowland and montane taxa, the role of specific extrinsic factors (e.g. palaeo-climatic change, tectonic changes such as mountain uplift) in speciation, and the timing and rate of diversification (e.g. Moritz et al., 2000; Elias et al., 2009; Santos et al., 2009; Fjeldså et al., 2012; Leubert and Wiegand, 2014).

Here we explore the taxonomy and diversification of Sri Lankan *Corilla* using a phylogenetic analysis of three mitochondrial gene fragments. We focus on two questions:

1. Did the lowland and montane shell forms evolve once or several times?
2. To what extent do the current, shell-based species-level taxa (nominal species) correspond to well supported mtDNA clades?

## 2. Material and methods

The ingroup consisted of nine of the ten nominal species of Sri Lankan *Corilla* (the other Sri Lankan species, *C. lesleyae* and the Indian species *Corilla anax* (Benson, 1865) were not sampled), and four other land stylommatophoran taxa, *Albinaria caerulea* (Deshayes, 1835) (Clausiliidae), *Cornu aspersum* (Müller, 1774) (Helicidae), *Sculptaria damarensis damarensis* H. Adams, 1870 (Sculptariidae) and *Halongella schlumbergeri* (Morlet, 1886) (Plectopylidae) (**Table1**). *Lissachatina fulica* (Bowdich, 1822) (Achatinidae) was used as the outgroup. The inclusion of *Sculptaria* and the plectopylid *Halongella* in the ingroup was based on the classifications of Nordsieck (1986) and Bouchet and Rocroi (2005). These authors treated the Corillidae, Sculptariidae and Plectopylidae as three distinct, but putatively-related families and placed them together to form the superfamily Plectopyloidea. The other ingroup taxa and the outgroup were selected on the basis of Wade et al.'s (2001, 2006) molecular phylogenetic trees for stylommatophoran pulmonates. For *Corilla*, the monophyly of the nine nominal species was evaluated by sampling two to six populations from across the range of each species, with 42 individuals being sampled in total (**Table1**). The type localities of *C. colletti* ("Balangoda, Ceylon", Sykes, 1897) and *C. fryae* ("Albion Estate, Lindula District", Gude, 1896a) were sampled. *Corilla odontophora* was originally described from three localities ("Near Fort McDonald, Bandarawella and Bibiligamua, at 4,500 feet", Benson, 1865) and we sampled in the vicinity of two of these (i.e. haplotypes *C. odontophora* 1a and 1b are from "Bibiligamua" and haplotype *C. odontophora* 2 from "Fort McDonald"). The type locality of *C. carabinata* is unknown (Férussac, 1821) and data are inadequate or inaccurate for the remaining sampled species. For *C. adamsi*, *C. erronea* and *C. humberti* the type locality was simply indicated as 'the island of Ceylon' (Albers, 1853; Pfeiffer, 1854; Brot, 1864). The type localities

for *C. beddomeae* ("Haycock Mountain", a hill in southern Sri Lanka with a maximum elevation of 661 m, Gude, 1896b) and *C. gudei* ("Kurunegala, at 1,500 feet", Sykes, 1897) are almost certainly incorrect; these two localities lie well outside the known range of *C. beddomeae* and *C. gudei*, both of which are montane rainforest species and have not been recorded below 900 m (≈2950 ft).

Phylogenetic analyses were based on nucleotide sequences of three mtDNA gene fragments: the protein-coding cytochrome *c* oxidase 1 (CO1, ~680 bp) and NADH dehydrogenase 1 (ND1, ~470 bp), and the ribosomal 16S rRNA (16S, ~480 bp) (**Table 2**). New sequence data were generated for *Corilla*, *Halongella* and *Sculptaria*; data for *A. caerulea*, *Cornu aspersum* and *L. fulica* were obtained from GenBank (**Table 1**). For each individual, genomic DNA was extracted from a *c.* 6-10 $mm^3$ piece of foot tissue with the Nucleospin® Tissue kit (Macherey-Nagel, Düren, Germany), following the manufacturers's standard protocol, or using a CTAB (hexadecyltrimethylammonium bromide) protocol (Goodacre and Wade, 2001). PCR amplifications were done by adding 1 µl of DNA extract to 10-µl volumes containing 1 µl of 10x Qiagen® CoralLoad PCR Buffer (including 1.5 mM $MgCl_2$), 0.2 mM of dNTP (GE Healthcare, Buckinghamshire, U.K.), 0.2 µM of each of the primers, 0.25 U of Qiagen® Taq DNA polymerase (Qiagen, Venlo, the Netherlands), and 0.625 mM of Qiagen® $MgCl_2$ solution (i.e. with the $MgCl_2$ in the buffer the total was 2.125 mM $MgCl_2$ per reaction volume). When amplifying ND1, the amount of $MgCl_2$ solution was increased to 1.25 mM (i.e. total of 2.75 mM $MgCl_2$ per reaction volume). For CO1 the PCR mix also contained 5.5 µg of Ambion® Ultrapure Bovine Serum Albumin (Life Technologies, Ghent, Belgium). The PCR temperature profile for 16S consisted of: first, an initial denaturation for 5 min at 95 ºC; then, 35 cycles of 45 s at 95 ºC, 30 s at an annealing temperature of 45 ºC, and 2 min at 72 ºC; and finally, an extension step of 10 min at 72 ºC. These conditions were the same for the other markers apart from the annealing temperature (i.e. 40-45 ºC for CO1 and 50 ºC for ND1). Amplification products were purified using the GFX PCR DNA Purification Kit (GE Healthcare), following the manufacturer's instructions, and purified DNA was diluted in 15 µl of sterile water.

Both DNA strands were sequenced on an ABI3130xl Genetic Analyzer using ABI PRISM BigDye® Teminator v. 1.1. Cycle Sequencing Kit (Life Technologies). Sequences have been deposited in GenBank (**Table 1**, accession numbers: CO1 XXXXXXXX–XXXXXX; ND1 XXXXXXXX–XXXXXX; 16S

XXXXXXXX–XXXXXX). Sequence data for each of the marker regions were assembled using SeqScape v. 2.5 (Life Technologies) and the chromatograms were checked by eye for inconsistencies. Assembled data were aligned using MAFFT v. 7 (Katoh and Standley, 2013) and trimmed to equal length. Alignments were carried out with default parameters on the MAFFT online server (http://mafft.cbrc.jp/alignment/server), using the Q-INS-i alignment strategy for the 16S data and the L-INS-i strategy for the other data. Using BioEdit v. 7.0.9.0 (Hall, 1999), alignments were checked by eye, all alignment gaps were removed and concatenated datasets were assembled. Alignments are available at the NHM data portal (http://data.nhm.ac.uk).

Two main sets of replicated phylogenetic analyses were run: one using the complete dataset (46 ingroup sequences and one outgroup) and a second omitting two of the samples of *C. colletti*, *C. colletti* 5 and 6 (44 ingroup sequences and one outgroup). The second set of analyses was carried out because support for the basal split within *Corilla* declined when *C. colletti* 5 and 6 were included. In order to assess the stability of relationships within *Corilla* in the absence of the five other stylommatophoran genera, all phylogenetic analyses were re-run using the *Corilla* sequences alone; trees were rooted on *C. beddomeae* (recovered as the sister clade of all other Sri Lankan *Corilla* in the analyses that also included the five other stylommatophorans).

Phylogenetic analyses were carried out employing Bayesian (Huelsenbeck et al., 2001) and Maximum Likelihood (ML; Felsenstein, 1981) approaches, the software programmes used being respectively MrBayes v. 3.2 (Ronquist et al., 2012) and RAxML v. 8 (Stamatakis, 2014a). Analyses were run on the CIPRES Science Gateway v. 3.3 (http://www.phylo.org/index.php, Miller et al., 2010). The concatenated mtDNA dataset was divided into seven data blocks: six separate blocks for the first, second and third codon positions of CO1 and ND1 and a seventh block for 16S. This scheme was analysed using PartitionFinder version 1.1.1 (Lanfear et al., 2012) and the best-fit combinations of partitioning schemes and nucleotide substitution models were selected. The settings common to all PartitionFinder analyses were branchlengths = linked, model_selection = BIC (Bayesian Information Criterion), and search = all. For MrBayes datasets the models option in PartitionFinder was set at ‘mrbayes’ (i.e. the option specifying the 24 nucleotide models available

in MrBayes), and for RAxML datasets this option was set at 'GTR+G' (the GTR model with gamma-shaped rate variation across sites), with RAxML also being implemented at the command line (Lanfear, 2013).

Each MrBayes analysis involved two independent MCMC runs (with four chains per run) for 20-40 million generations, sampling every 1000 generations, and discarding the first 25% of samples as burn-in; each analysis was repeated at least once. All analyses were run until the average standard deviation of split frequencies dropped and remained below 0.01; convergence was also assessed by examining the other diagnostics (i.e. the Potential Scale Reduction Factor for the various model parameters including the branch and node parameters) and summary statistics (e.g. plot of the generation vs. the log probability of the data given the parameter values) reported to the MrBayes log file, as well as by analysing the trace files generated by the MCMC runs using Tracer v. 1.6 (Rambaut et al., 2014). Each RAxML analysis involved a single programme run and consisted of a rapid bootstrap analysis with the extended majority rule boot stopping criterion (maximum of 1000 bootstrap replicates), followed by a search for the best-scoring ML tree (Stamatakis et al., 2008; Pattengale et al., 2010; Stamatakis, 2014b); each run was repeated at least once. As recommended by Stamatakis (2014b), the model of nucleotide substitution used for the RAxML analyses was GTR+G. Trees were rooted on the outgroup taxon *L. fulica* using the tree-viewing software FigTree (v. 1.4, Rambaut, 2006-2012). Branches with bootstrap values ≥70% and posterior probabilities ≥0.95 were considered to be well/strongly supported (Hillis and Bull, 1993; Alfaro and Holder, 2006), and we treated branches with bootstrap values <70% and posterior probabilities <0.95 as not being reliably resolved.

Substitution saturation of the third codon position of CO1 and ND1 was assessed for the 42 *Corilla* sequences using Xia's method (Xia et al., 2003; Xia and Lemey, 2009) and the software DAMBE v.5.5.1 (Xia, 2013). For both CO1 and ND1, there was little saturation of the third codon position assuming a symmetrical topology ($Iss < Iss.c$, $p < 0.01$, number of OTUs = 8), but substantial saturation assuming an asymmetrical tree topology ($Iss < Iss.c$, $p > 0.01$, number of OTUs = 8). Therefore, all Bayesian and ML analyses were undertaken both including and excluding the third codon position of CO1 and ND1.

Pairwise uncorrected *p*-distances were calculated for CO1 using MEGA6 (Tamura et al., 2013) and were summarised on the basis of selected clades/samples. Additional support for these clades/samples was obtained by examining the 16S and ND1 alignments of *Corilla* (42 sequences) for differences in indels.

## 3. Results

The phylogenetic analyses of the two mtDNA datasets (including and excluding the two samples of *C. colletti*, 5 and 6, see **Table 3** for properties) yielded similar results (**Table 4**). When the third codon positions of the protein coding genes were excluded the resulting trees were less well resolved and branch support generally declined (**Table 4**). Nevertheless, the results were consistent with the analyses based on the complete CO1 and ND1 datasets, so unless stated otherwise we focus here on the complete datasets.

The monophyly of *Corilla* was well supported in all our analyses (**Table 4**, **Fig. 2**). The relationships among *Corilla* and the other ingroup taxa (*A. caerulea*, *Cornu aspersum*, *H. schlumbergeri* and *S. damarensis damarensis*) were not reliably resolved in the ML analyses. In the Bayesian analyses, while *Corilla* always formed a well supported clade with *Cornu aspersum* and *A. caerulea*, the relationships among *Corilla*, *S. damarensis damarensis* and *H. schlumbergeri* were not reliably resolved.

The sister-group relationship between *C. beddomeae* and all other Sri Lankan *Corilla* was consistently well supported in the Bayesian analyses. It was well supported (bootstrap value ≥76%) in the ML analyses only when *C. colletti* 5 and 6 were excluded (analyses 4 and 8 in **Table 4)**. This sister-group relationship was only weakly supported in the ML analysis of the complete dataset (analysis 2, **Table 4**), whereas all the deeper nodes within *Corilla* were not reliably resolved in the ML analysis excluding the CO1 and ND1 third codon positions (analysis 6, **Table 4**). While most of the deeper nodes within the sister clade of *C. beddomeae* (Clade A of **Fig. 2**) were not reliably resolved in both Bayesian and ML analyses, the Bayesian analyses (analyses 1, 3, 5 and 7 in **Table 4**) always recovered a well supported sister-group relationship between the lowland *C. adamsi* and all the remaining species in Clade A (Clade B in **Fig. 2**).

The monophyly of four of the nine nominal species, *C. adamsi*, *C. beddomeae*, *C. carabinata* and *C. humberti*, was consistently well supported. The monophyly of a fifth nominal species, *C. colletti*, was also well supported in nearly all analyses. When all the samples of *C. colletti* were included (analyses 1, 2, 5 and 6 in **Table 4**) two deeply-divergent and well supported sister clades were usually recovered for *C. colletti*: one clade from the western part of the range (*C. colletti* 1-4) and one from the east (*C. colletti* 5 and 6). In the ML analysis excluding the CO1 and ND1 third codon positions, the western clade of *C. colletti* was well supported, but relationships between it and *C. colletti* 5 and 6 were not reliably resolved.

Our results are consistent with the non-monophyly of each of the remaining nominal species of *Corilla*. Both *C. erronea* and *C. fryae* were paraphyletic and together formed a well supported clade (*C. erronea-fryae* clade of **Fig. 2**) with substantial mtDNA diversity (e.g. compare with *C. carabinata*). In the case of *C. gudei*, the southern haplotype (*C. gudei* 3) was consistently well supported as sister to *C. humberti*, whereas in the analyses including the complete CO1and ND1 datasets (analyses 1-4 in **Table 4**), the two northern haplotypes (*C. gudei* 1 and 2) formed a well supported sister-group relationship with *C. carabinata*. For *C. odontophora*, the three eastern haplotypes (*C. odontophora* 1a, 1b and 2) formed a well supported clade, but their relationship to the northern haplotype (*C. odontophora* 3) was not reliably resolved.

*Corilla beddomeae* comprised two relatively deeply divergent and well supported clades, corresponding to haplotypes from the western extremity of the range (*C. beddomeae* 1a and 1b) vs. all the other haplotypes (*C. beddomeae* 2a-5). *Corilla adamsi* also comprised two relatively deeply divergent lineages, the northern haplotype (*C. adamsi* 1) vs. a well supported clade of the southern haplotypes (*C. adamsi* 2-4). Less marked divergences were present in the southern clade of *C. adamsi* (*C. adamsi* 2 vs. 3 and 4), and in eastern *C. odontophora* (one population represented by *C. odontophora* 2 vs. a second population, *C. odontophora* 1a and 1b). *Corilla carabinata* comprised a well supported clade of northern haplotypes (*C. carabinata* 2-5) and its sister, the haplotype from the south (*C. carabinata* 1).

The Bayesian and ML analyses of the 42 sequences of *Corilla* on their own (see Supplementary Table S1 for dataset properties and Supplementary Table S2 for support values of selected clades) were consistent

with the analyses of *Corilla* and the five other stylommatophoran genera. The key findings were that clades A and B (**Fig. 2**) were consistently well supported and that the clade comprising *C. carabinata* and northern *C. gudei* was well supported in all but one of the analyses.

*P*-distances for the CO1 gene (see **Table 5** for summary, and Supplementary Table S3 for data in full) were large between the two sister clades within *C. beddomeae* (range = 0.126-0.150, mean = 0.136), between northern and southern *C. adamsi* (range = 0.150-0.179, mean = 0.167), and between eastern and western *C. colletti* (range = 0.111-0.131, mean = 0.122). These *p*-distances are comparable, in most cases, to *p*-distances among nominal species (e.g. *C. adamsi* vs. *C. beddomeae*, range = 0.176-0.218, mean = 0.194). *P*-distances were also large between northern and southern *C. gudei* (range = 0.157-0.163, mean = 0.160), between northern and eastern *C. odontophora* (range = 0.166-0.170, mean = 0.168), between *C. adamsi* 2 and each of the two haplotypes *C. adamsi* 3 and 4 (range = 0.124-0.126, mean = 0.125), and between *C. odontophora* 2 and each of the two haplotypes *C. odontophora* 3a and 3b (0.181). In comparison, *p*-distances were smaller between *C. humberti* and southern *C. gudei* (range = 0.070-0.072, mean = 0.071); these were more similar to the *p*-distances among the haplotypes of species such as *C. carabinata* (range = 0-0.041, mean = 0.022) and among the haplotypes of certain, other clades (e.g. western *C. colletti*, range = 0.002-0.089, mean = 0.069). Although *p*-distances between southern and northern *C. carabinata* were relatively small (range = 0.037-0.041, mean = 0.038), they were nevertheless two orders of magnitude greater than those between the two haplotypes of northern *C. carabinata* (range = 0-0.009, mean = 0.005). *P*-distances between *C. colletti* 3 and the other members of the western clade of *C. colletti* (1, 2 and 4) were larger (range = 0.057-0.089, mean = 0.078), but of a similar order of magnitude to the *p*-distances among the latter three haplotypes of *C. colletti* (range = 0.002-0.089, mean = 0.060). *P-distances* among sequences in the *C. erronea-fryae* clade varied substantially (range = 0.002-0.102, mean = 0.070), with most being in the range = 0.078-0.102; *p*-distances were small only between haplotypes *C. erronea* 3 and *C. fryae* 2 (0.037) and among haplotypes *C. erronea* 1 and 2 and *C. fryae* 1a and 1 b (range = 0.002-0.015).

The clades within *C. adamsi*, *C. beddomeae*, *C. carabinata* and *C. colletti* are characterised by differences in 16S indels (**Table 6**). Northern and southern *C. adamsi* differed at seven indel positions, the two sister clades within *C. beddomeae* at eight indels, southern and northern *C. carabinata* at two indels and

western and eastern *C. colletti* at one indel. In addition, northern and southern *C. gudei* differed from each other at seven indels and eastern and northern *C. odontophora* at five indels. The ND1 sequence alignment of *Corilla* (440 bp in length) contained an indel at positions 383-385 and only *C. colletti* 3 had a codon (GAA) at this indel.

## 4. Discussion

The monophyly of *Corilla* was well supported in both Bayesian and ML analyses. Although the Bayesian analyses suggest that the Plectopyloidea (the superfamily comprising the Plectopylidae, Corillidae and Sculptariidae, Nordsieck, 1986, Bouchet and Rocroi, 2005) are non-monophyletic, overall our data shed little light on the relationships among *Halongella* (Plectopylidae), *Sculptaria* (Sculptariidae) and *Corilla* (Corillidae).

We found strong support for the montane species *C. beddomeae* being sister to all other Sri Lankan *Corilla*. Several studies on the diversification of rainforest taxa have shown that while montane taxa have frequently evolved from lowland ancestors (Moritz et al., 2000; Fjeldså et al., 2012; Wesener et al., 2011), some diverse lowland taxa have a montane origin (Elias et al., 2009; Santos et al., 2009; Fjeldså et al., 2012; Leubert & Wiegand, 2014). The pattern for *Corilla* is unclear because the deeper nodes in both Bayesian and ML trees were not reliably resolved. Nevertheless, the results do suggest that lowland and montane shell forms have evolved on at least two separate occasions. Speciation thus appears to have involved repeated, ecologically-driven convergence in shell morphology; to our knowledge the only broadly comparable data are for two distantly-related lineages of the pulmonate land snail *Placostylus* on New Caledonia (Dowle et al., 2015). Improving phylogenetic resolution is essential for a clearer understanding of diversification in *Corilla*.

The mtDNA data agree with the current shell-based taxonomy for *C. adamsi*, *C. beddomeae*, *C. carabinata*, *C. humberti* and *C. colletti*, supporting the first four as monophyletic, and supporting the last as

monophyletic in most analyses. The relatively deep phylogenetic divergences within *C. adamsi*, *C. beddomeae* and *C. colletti* are reflected in large CO1 *p*-distances (i.e. comparable to those among most nominal species) and are characterised by differences in one or more 16S indels. This evidence suggests that these three nominal species may each contain at least one additional species that has yet to be described.

The presence of an extra codon in the ND1 sequence of *C. colletti* 3 together with the relatively small CO1 *p*-distances among members of the western clade of *C. colletti* suggest a possible case of intraspecific geographic differentiation. *C. colletti* 3 is from a site (~1200 m) close to the summit of the Rakwana Massif (**Fig. 1A**), whereas all the other members of the western clade of *C. colletti* are from lowland sites to the south and north. The shallow divergence between southern and northern *C. carabinata* may also indicate intraspecific geographical differentiation. The relationship between the northern haplotype and eastern clade of *C. odontophora* was not reliably resolved. Nonetheless, the mean CO1 *p*-distance between these two groups is similar to most interspecific *p*-distances and to *p*-distances between the deeply-divergent clades within *C. adamsi*, *C. beddomeae* and *C. colletti*. This coupled with the differences in 16S indels points to the possibility that northern and eastern *C. odontophora* are separate species. The deep divergence within eastern *C. odontophora* (*C. odontophora* 2 vs. 1a and 1b, **Fig. 2**) and the correspondingly large mean CO1 *p*-distance also suggests a further species-level split or possible geographical differentiation.

The current, morphologically-defined species limits of the three remaining nominal species, *C. gudei*, *C. erronea* and *C. fryae*, are inconsistent with the mtDNA sequence data. *Corilla gudei* is a montane species restricted to the Knuckles Massif (**Fig. 1A**), an isolated mountain range located to the north of the Central Highlands, and haplotypes from the northern and southern parts of this range were included in the study. The sister taxon of southern *C. gudei* is *C. humberti* from the Central Highlands and in the Bayesian trees alone the sister taxon of northern *C. gudei* is the lowland *C. carabinata*. These findings suggest that northern and southern *C. gudei* are distinct species; the high mean CO1 *p*-distance between northern and southern *C. gudei* and the differences observed at seven 16S indel positions provide further support for this. Preliminary data also indicate that the shells of northern and southern *C. gudei* differ very subtly. The shell sculpture of all *Corilla* (**Figs. 1E, F**) consists of striae (shallow incised lines) and/or ribs (raised lines) corresponding to

the direction of growth of the shell and running parallel to the edge of the lip (i.e. collabral sculpture *sensu* Cox, 1960). In northern *C. gudei* the collabral sculpture is generally stronger than in southern *C. gudei.*

The divergence between *C. humberti* and southern *C. gudei* is noticeably shallow in comparison to all other interspecific divergences in the tree (**Fig. 2**) and this is reflected in a relatively small mean CO1 *p*-distance (7.1%); there were also no differences in 16S indels. We would argue, however, that because southern *C. gudei* and *C. humberti* are conchologically very different (*C. humberti* is the only montane species without palatal folds in the mouth of the shell) they are distinct species. These snails also occur in disjunct mountain ranges and have distinct elevational ranges (southern *C. gudei*, 1180-1370 m, *C. humberti*, 1640-2025 m).

*Corilla erronea* and *C. fryae* are confusingly similar in their shell morphology (see descriptions by Albers, 1853; Gude, 1896a), with both species sharing a previously unreported, yet highly distinctive character not found in other extant *Corilla* species (the collabral sculpture of the shell is intersected by faint striae running in the opposite direction, **Fig. 1E**). Following traditional usage and as followed here, *C. fryae* is the name used for specimens from the southwestern sector of the Central Highlands, whereas *C. erronea* refers to individuals from other montane areas. Our results show that specimens identified as *C. erronea* and *C. fryae* constitute a well supported clade in which both nominal species are paraphyletic. The mean CO1 *p*-distance among members of the *C.erronea-fryae* clade is small, but most values range from 7.8%-10.2% and are thus larger than the mean CO1 *p*-distance between *C. humberti* and southern *C. gudei*. While these moderate to relatively large CO1 *p*-distances reflect substantial mtDNA sequence diversity, the phylogenetic structuring within the *C.erronea-fryae* clade does not seem to correspond to any obvious morphological, elevational or geographical patterns. These results are difficult to interpret, and further detailed study is needed before the taxonomic status of *C. erronea* and *C. fryae* can be resolved.

Future research needs to address three crucial issues. First, phylogenetic resolution has to be improved, likely through additional sampling of loci. Second, more populations need to be sampled. Many/most of the populations sampled for this study are represented by only a single haplotype, and most species have been inadequately sampled across their geographical range. For example, southern *C. gudei* was represented by

only a single individual, and only two of the three localities given in the original description of *C. odontophora* were sampled in this study. Third, detailed studies are needed on the internal anatomy of *Corilla*. Apart from brief descriptions of the genitalia and radula of *C. erronea* and *C. humberti* (Semper, 1870, pp. 100-102; Pilsbry, 1894, p. 147-149; Pilsbry, 1905; Godwin-Austen, 1907, p. 199-201), published data on the anatomy of *Corilla* are scarce. At present we do not know which internal anatomical characters if any correspond with key shell-based characters and how useful such anatomical characters might be in discriminating between taxa that are morphologically very similar.

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**References**


Albers, J.C., 1853. Ueber *Helix Rivolii* Desh. und eine damit verwechselte Art. Zeitschrift für Malakozoologie 10, 105-109.

Alfaro, M.E., Holder, M.T., 2006. The posterior and the prior in Bayesian phylogenetics. Annual Review of Ecology, Evolution, and Systematics 37, 19-42.

Barnacle, G.A.S., 1956. A new species of *Corilla* from Ceylon. Journal of Conchology 24, 95-96.

Benson, W.H., 1865. Description of *Helix odontophora*, a new Species of the *Corilla* type, from Upper Ouvah, in Ceylon. Annals and Magazine of Natural History, Series 3, 15, 175-176.

Brot, A., 1864. Description de trois espèces nouvelles. Journal de Conchyliologie 12, 19-22.

Bouchet, P., Rocroi, J.-P., 2005. Classification and Nomenclator of Gastropod Families. Malacologia 47 (1-2), 1-397.

Cooray, P.G., 1984. An introduction to the geology of Sri Lanka (Ceylon). Second (revised) edition. National Museums of Sri Lanka, Colombo.

Cox, L.R., 1960. General characteristics of Gastropoda. In: Moore, C. (Ed.), Treatise on Invertebrate Palaeontology Part I, Mollusca 1. Geological Society of America and University of Kansas Press, USA, pp. I84-I169.

Dowle, E.J., Morgan-Richards, M., Brescia, F., Trewick, S.A., 2015. Correlation between shell phenotype and local environment suggests a role for natural selection in the evolution of *Placostylus* snails. Molecular Ecology 24, 4205-4221.

Elias, M., Joron, M., Willmott, K., Silva-Brandao, K. L., Kaiser, V., Arias, C. F., Pinerez, G. L. M., Uribe, S., Brower, A. V. Z., Freitas, A. V. L., Jiggins, C. D., 2009. Out of the Andes: patterns of diversification in clearwing butterflies. Molecular Ecology 18, 1716-1729.

Felsenstein, J., 1981. Evolutionary trees from DNA sequences: a maximum likelihood approach. Journal of Molecular Evolution 17, 368-376.

Férussac, A.E.J. D'Audebard de., 1821. Tableaux Systématiques Des Animaux Mollusques Classés En Familles Naturelles, Dans Lesquels On A Établi La Concordance De Tous Les Systèmes; Suivis D'un Prodrome Général Pour Tous Les Mollusques Terrestres Ou Fluviatiles, Vivants Ou Fossiles. Deuxième Partie, Tableaux Particuliers Des Mollusques Terrestres Et Fluviatiles, Presentant Pour Chaque Famille Les Genres Et Espèces Qui La Composent. Classe Des Gastéropodes. II., Tableau De La Famille Des Limaçons. Arthus Bertrand, Paris.

Fjeldså, J., Bowie, R.C.K., Rahbek, C., 2012. The role of mountain ranges in the diversification of birds. Annual Review of Ecology, Evolution, and Systematics 43, 249-265.

Folmer, O., Black, M., Hoeh, W., Lutz, R., Vrijenhoek, R., 1994. DNA primers for amplification of mitochondrial cytochrome C oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3, 294-299.

Gaitán-Espitia J.D., Nespolo R.F., Opazo J.C., 2013. The Complete Mitochondrial Genome of the Land Snail *Cornu aspersum* (Helicidae: Mollusca): Intra-Specific Divergence of Protein-Coding Genes and Phylogenetic Considerations within Euthyneura. PLoS ONE 8(6), e67299.

Gaston, K. J., 1991. How large is a species' geographic range? Oikos 61, 434-438.

Godwin-Austen, H.H., 1897-1914. Land and Freshwater Mollusca of India, including South Arabia, Baluchistan, Afghanistan, Kashmir, Nepal, Burmah, Pegu, Tenasserim, Malay Peninsula, Ceylon, and other

islands of the Indian Ocean. Supplementary to Messrs. Theobald and Hanley's Conchologia Indica. Volume 2. Taylor and Francis, Red Lion Court, Fleet Street, London.

Goodacre, S.L., Wade, C.M., 2001. Molecular evolutionary relationships between partulid land snails of the Pacific. Proceedings of the Royal Society of London Series B 268, 1-7.

Gude, G.K., 1896a. Armature of Helicoid Landshells; and a new species of *Corilla*. Science-gossip, new series, 3, 88-92.

Gude, G.K., 1896b. Armature of Helicoid Landshells. Science-gossip, new series, 3, 126-128.

Gude, G.K., 1914. The Fauna of British India including Ceylon and Burma. Mollusca - II. Trochomorphidae-Janellidae. Taylor and Francis, London.

Hall, T.A., 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symposium Series 41, 95-98.

Hatzoglou, E., Rodakis, G.C., Lecanidou, R., 1995. Complete sequence and gene organisation of the mitochondrial genome of the land snail *Albinaria coerulea*. Genetics 140, 1353-1366.

He, Z. P., Dai, X. B., Zhang, S., Zhi, T. T., Lun, Z. R., Wu, Z. D., Yang, T. B., 2014. Complete mitochondrial genome of the giant African snail, *Achatina fulica* (Mollusca: Achatinidae): a novel location of putative control regions (CR) in the mitogenome within Pulmonate species. Mitochondrial DNA Part A 27, 1084-1085.

Hillis, D.M., Bull, J.J., 1993. An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. Systematic Biology 42, 182-92.

Huelsenbeck, J.P., Ronquist, F.R., Nielsen, R., Bollback, J.P., 2001. Bayesian inference of phylogeny and its impact on evolutionary biology. Science 294, 2310-2314.

Katoh, K., Standley, D.M., 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Molecular Biology and Evolution 30, 772-780.

Lanfear, R., 2013. PartitionFinder v1.1.0 and PartitionFinderProtein v1.1.0 Manual. Available from <http://www.robertlanfear.com/partitionfinder>.

Lanfear, R., Calcott, B., Ho, S.Y.W., Guindon S., 2012. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. Molecular Biology and Evolution 29, 1695-1701.

Legg, C., Jewell, N., 1995. A 1:50,000-scale forest map of Sri Lanka: the basis for a National Forest Geographic System. The Sri Lanka Forester, Special Issue (Remote Sensing), 3-24.

Luebert, F., Weigend, M., 2104. Phylogenetic insights into Andean plant diversification. Frontiers in Ecology and Evolution 2, 27.

Miller, M.A., Pfeiffer, W., Schwartz, T., 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: Proceedings of the Gateway Computing Environments Workshop (GCE), 14 Nov. 2010, New Orleans, LA, pp. 1- 8.

Moritz, C., Patton, J.L., Schneider, C.J., Smith, T.B., 2000. Diversification of rainforest faunas: an integrated molecular approach. Annual Review of Ecology, Evolution, and Systematics 31, 533-563.

Naggs, F., Raheem, D., 2005. Sri Lankan snail diversity: faunal origins and future prospects. Records of the Western Australian Museum Supplement 68, 11-29.

Nordsieck, H., 1986. The system of the Stylommatophora (Gastropoda), with special regard to the systematic position of the Clausiliidae, II. Importance of the shell and distribution. Archiv für Molluskenkunde 117, 93-116.

Pattengale, N., Alipour, M., Bininda-Emonds, O.R.P., Moret, B.M.E., Gottlieb, E.J., Stamatakis, A., 2010. How many Bootstrap Replicates are necessary? Journal of Computational Biology 17, 337-354.

Pfeiffer, L., 1854. Descriptions of nineteen new species of Helicea, from the collection of H. Cuming, Esq. Proceedings of the Zoological Society, proceedings for 1853,127-128.

Pilsbry, H.A., 1894. Helicidae (Volume 7). Manual of Conchology, Second Series: Pulmonata, Volume 9. The Conchological Department, Academy of Natural Sciences of Philadelphia.

Pilsbry, H.A., 1905. Anatomical and systematic notes on *Dorcasia*, *Trigonephrus*, n.gen., *Corilla*, *Thersites*, and *Chloritis*. Proceedings of the Malacological Society of London 6, 286-291.

Quinteiro, J., Rodriguez-Castro, J., Castillejo, J., Iglesias-Pineiro, J., Rey-Mendez, M., 2005. Phylogeny of slug species of the genus *Arion*: evidence of Iberian endemics and of the existence of relict species in Pyrenean refuges. Journal of Zoological Systematics and Evolutionary Research 43, 139-148.

Raheem, D.C., Taylor, H., Ablett, J., Preece, R.C., Aravind, N.A., Naggs, F., 2014. A systematic list of the land snails of the Western Ghats of India. Tropical Natural History Supplement 4, 1-294.

Rambaut, A., 2006-2012. FigTree. Tree Figure Drawing Tool Version 1.4.0. Institute of Evolutionary Biology, University of Edinburgh. Available from <http://tree.bio.ed.ac.uk/software/figtree>.

Rambaut, A., Suchard, M.A., Xie, D., Drummond, A.J., 2014. Tracer v1.6. Available from <http://beast.bio.ed.ac.uk/Tracer>.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A., Huelsenbeck, J.P., 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61, 539-542.

Santos, J.C., Coloma, L.A., Summers, K., Caldwell, J.P., Ree, R., Cannatella, D.C., 2009. Amazonian amphibian diversity is primarily derived from late Miocene Andean lineages. PLoS Biology 7, 0448-0461.

Semper, C., 1870. Reisen im Archipel der Philippinen. Theil 2. Wissenschaftliche Resultate. Dritter Band. Landmollusken. C. W. Kreidel, Wiesbaden.

Simon, C., Frati F., Beckenbach, A., Crespi, B., Liu, H., Flook, P., 1994. Evolution, weighting and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction "primers". Annals of the Entomological Society of America 87, 651-701.

Stamatakis, A., 2014a. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30, 1312-1313.

Stamatakis, A., 2014b. The RAxML v8.1.X Manual. Heidelberg Institute for Theoretical Studies. Available from <http://www.exelixis-lab.org>.

Stamatakis, A., Hoover, P., Rougemont, J., 2008. A Rapid Bootstrap Algorithm for the RAxML Web Servers. Systematic Biology 57, 758-771.

Sykes, E.R., 1897. Description of some new species of helicoid and operculate land-shells from Ceylon. Proceedings of the Malacological Society of London 2, 233-237.

Tamura, K., Stecher, G., Peterson, D., Filipski, A., Kumar, S., 2013. MEGA6: molecular evolutionary genetics analysis version 6.0. Molecular Biology and Evolution 30, 2725-2729.

Wade, C.M., Mordan, P.B., Clarke B.C., 2001. A phylogeny of the land snails (Gastropoda: Pulmonata). Proceedings of the Royal Society of London Series B 268, 413-422.

Wade, C. M., Mordan, P. B., Naggs, F., 2006. Evolutionary relationships among the Pulmonate land snails and slugs (Pulmonata, Stylommatophora). Biological Journal of the Linnean Society 87, 593-610.

Wesener, T., Raupach, M. J., Decker, P. 2011. Mountain refugia play a role in soil arthropod speciation on Madagascar: a case study of the endemic Giant fire-millipede genus *Aphistogoniulus*. PLoS ONE 6, e28035.

Xia, X., 2013. DAMBE5: a comprehensive software package for data analysis in molecular biology and evolution. Molecular Biology and Evolution 30, 1720-1728.

Xia, X., Lemey, P., 2009. Assessing substitution saturation with DAMBE. In: Lemey, P., Salemi, M., Vandamme, A.M., (Eds.), The Phylogenetic Handbook. Cambridge University Press, Cambridge, pp. 615-630.

Xia, X., Xie, Z., Salemi, M., Chen, L., Wang, Y., 2003. An index of substitution saturation and its application. Molecular Phylogenetics and Evolution 26, 1-7.

**Figure Captions (Fig. 1 to appear in colour, Fig. 2 in black-and-white)**

**Figure 1. A, B.** Sampled localities (symbols) and distributional limits (dashed lines) of Sri Lankan *Corilla* (see **Table 1** for sample codes). The distributional limits (approximating to extent of occurrence *sensu* Gaston, 1991) are based on unpublished distributional data from field surveys and museum collections (primarily two Sri Lankan institutions the Colombo Museum and the University of Peradeniya, and the Natural History Museum, London, UK). These data consist of >200 individual records and date mainly from the last 3 decades. **A**, the 3 lowland species (*C. adamsi*, *C. carabinata* and *C. colletti*) and 3 of the montane species (*C. beddomeae*, *C. gudei* and *C. humberti*); **B**, the 3 other montane species (*C. erronea*, *C. fryae* and *C. odontophora*). The type localities of *C. colletti*, *C. fryae* and *C. odontophora* (Benson, 1865; Gude, 1896a; Sykes, 1897) are shown by open circles and are numbered if they have been sampled in this study. Although they are almost certainly incorrect, the type localities for *C. beddomeae* (□) and *C. gudei* (◇) are also shown. The Central Highlands, Knuckles Massif and Rakwana Massif are the three main mountain masses of Sri Lanka (Cooray, 1984). **C-F.** Shell morphology of *Corilla*: **C**, shell of the lowland *C. adamsi*; **D**, shell of the montane *C. erronea*; **E**, collabral sculpture (black arrows) of *C. erronea* and striae running in opposing direction (white arrows); **F**, collabral sculpture (black arrows) of *C. gudei*.

**Figure 2.** Bayesian majority consensus tree of the complete concatenated CO1-ND1-16S sequence dataset for *Corilla* and some other stylommatophorans with *Lissachatina fulica* as the outgroup (see **Table 3**). Support values are given as posterior probabilities for Bayesian analyses (only values ≥0.95 are shown) and as bootstrap percentages for ML analyses (only values ≥70% are shown); maximal support (Bayesian = 1, ML = 100%) is indicated by an asterisk. Montane and lowland taxa are indicated by black and grey shading respectively, and clades A and B by arrows.

Figure 1

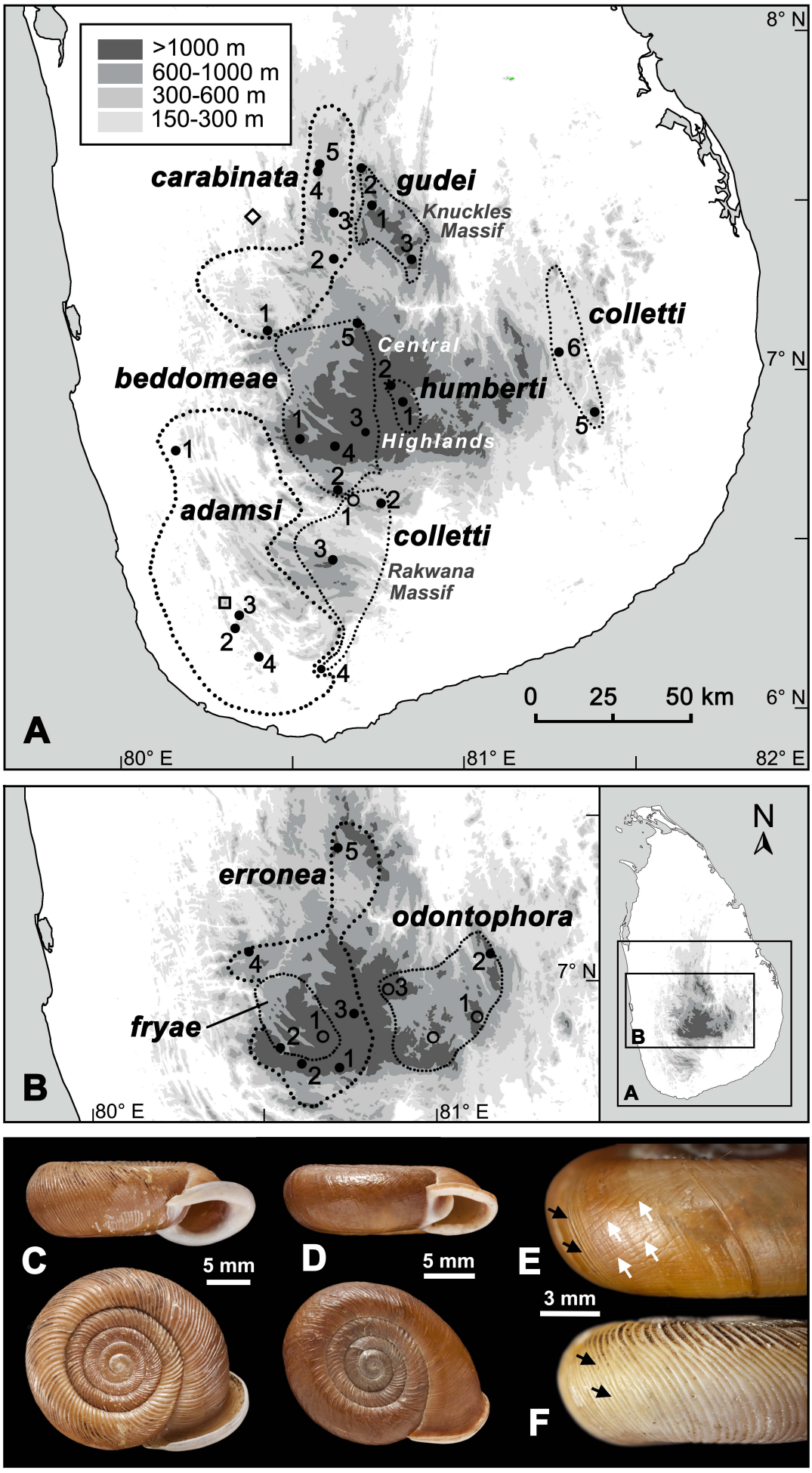
>1000 m
600-1000 m
300-600 m
150-300 m
carabinata
gudei
Knuckles Massif
colletti
Central
beddomeae
humberti
Highlands
adamsi
colletti
Rakwana Massif
8° N
7° N
6° N
0 25 50 km
A
80° E
81° E
82° E
erronea
odontophora
fryae
B
7° N
80° E
81° E
N
A
B
C
5 mm
D
5 mm
E
3 mm
F

**Figure 2**


carabinata 5a
carabinata 5b
carabinata 3
carabinata 4
carabinata 2a
carabinata 2b
carabinata 1
gudei 1
gudei 2
colletti 1
colletti 2
colletti 4
colletti 3
colletti 6
colletti 5
odontophora 3
odontophora 1a
odontophora 1b
odontophora 2
fryae 1a
fryae 1b
erronea 2
erronea 1
erronea 4
erronea 5
erronea 3
fryae 2
humberti 1
humberti 2
gudei 3
adamsi 3
adamsi 4
adamsi 2
adamsi 1
beddomeae 2a
beddomeae 2b
beddomeae 4a
beddomeae 4b
beddomeae 5
beddomeae 3
beddomeae 1a
beddomeae 1b
Cornu aspersum
Albinaria caerulea
Sculptaria damarensis damarensis
Halongella schlumbergeri
Lissachatina fulica
Corilla carabinata
Corilla gudei north
Corilla colletti
Corilla odontophora north
Corilla odontophora east
Corilla erronea-fryae
Corilla humberti
Corilla gudei south
Corilla adamsi
Corilla beddomeae
A
B
0.99
90
85
76
82
99
87
98
92
97
73
0.3

**Table 1.** Taxa used in this study with sample codes, localities and GenBank accession numbers. Taxonomy for *Corilla* follows Gude (1914). Sampled type localities are indicated by an asterisk. The DNA sequence data for *Albinaria caerulea*, *Cornu aspersum* and *Lissachatina fulica* are from complete mt genomes generated respectively by Hatzoglou et al. (1995), Gaitán-Espitia et al. (2013) and He et al. (2014).

| **Taxon, Sample Code & Locality** | **GenBank Accession Number** | | |
|---|---|---|---|
| | **CO1** | **ND1** | **16S** |
| ***Corilla adamsi*** | | | |
| **1**: 1.6 km ne Ingiriya, Kalutara District | pending | pending | pending |
| **2**: Homadola, near Udugama, Galle District | pending | pending | pending |
| **3**: Kospelaketiya, Kanneliya, Galle District | pending | pending | pending |
| **4:** Nakiyadeniya, Galle District | pending | pending | pending |
| ***Corilla beddomeae*** | | | |
| **1a, 1b**: Adam's Peak (eastern face), Nuwara Eliya District | pending | pending | pending |
| **2a, 2b**: 4.8 km n Opanayaka, Hunuwalakanda, Ratnapura District | pending | pending | pending |
| **3**: 4 km se Agrapatana, Nuwara Eliya District | pending | pending | pending |
| **4a, 4b**: 7.5 km se Maskeliya, Nuwara Eliya District | pending | pending | pending |
| **5**: 4.5 km se Pupuressa, Kandy District | pending | pending | pending |
| ***Corilla carabinata*** | | | |
| **1**: 1.6 km ne Dedugala, Kegalle District | pending | pending | pending |
| **2a, 2b**: Kandy, Kandy District | pending | pending | pending |
| **3**: Matale, Matale District | pending | pending | pending |
| **4**: 5.1 km e Dodangaslanda, Matale District | pending | pending | pending |
| **5a, 5b**: Ambokka-Neugala range, above Selagama, Matale District | pending | pending | pending |
| ***Corilla colletti*** | | | |
| **1***: Balangoda, Ratnapura District | pending | pending | pending |
| **2**: Rajawaka, Ratnapura District | pending | pending | pending |
| **3**: above Bulutota, Rakwana, Ratnapura District | pending | pending | pending |
| **4**: Makandura, Matara District | pending | pending | pending |
| **5**: Maragalakanda range, Moneragala District | pending | pending | pending |
| **6**: 5.4 km se Lunugala, Badulla District | pending | pending | pending |
| ***Corilla erronea*** | | | |
| **1**: above Northcove Estate, Bogowantalawa, Nuwara Eliya District | pending | pending | pending |
| **2**: 7.5 km se Maskeliya, Nuwara Eliya District | pending | pending | pending |
| **3**: 4.8 km nw Ambawela, Nuwara Eliya District | pending | pending | pending |
| **4**: 5.1 km sw Aranayaka, Kegalle District | pending | pending | pending |
| **5**: Galheeria Estate, above Elkaduwa, Matale District | pending | pending | pending |
| ***Corilla fryae*** | | | |
| **1a*, 1b***: Albion Estate, 7km sw Lindula, Nuwara Eliya District | pending | pending | pending |
| **2**: Adam's Peak (eastern face), Nuwara Eliya District | pending | pending | pending |
| ***Corilla gudei*** Sykes, 1897 | | | |
| **1**: Laggala, above Illukkumbura, Matale District | pending | pending | pending |
| **2**: 2.2 km ne Gammaduwa, Matale District | pending | pending | pending |
| **3**: Nawanagala, Kandy District | pending | pending | pending |
| ***Corilla humberti*** | | | |
| **1**: Between Nuwara Eliya and Hakgala, Nuwara Eliya District | pending | pending | pending |
| **2**: Nuwara Eliya, Nuwara Eliya District | pending | pending | pending |
| ***Corilla odontophora*** | | | |
| **1a*, 1b***: Namunukula, above Bibilegama (="Bibiligamua"), Badulla District | pending | pending | pending |
| **2**: 5.7 km nw Lunugala, Badulla District | pending | pending | pending |
| **3***: 4 km nw historic site of "Fort McDonald", Paranagama, Nuwara Eliya District | pending | pending | pending |
| ***Albinaria caerulea*** Locality not indicated | NC_001761 | NC_001761 | NC_001761 |
| ***Cornu aspersum*** Chile | NC_021747.1 | NC_021747.1 | NC_021747.1 |
| ***Lissachatina fulica*** Locality not indicated | NC_024601.1 | NC_024601.1 | NC_024601.1 |
| ***Halongella schlumbergeri*** Cat Ba National Park, Vietnam | pending | pending | pending |
| ***Sculptaria damarensis damarensis*** Khubis Springs, Namibia | pending | pending | pending |

**Table 2.** Primers used in the study. Sources: 1, Simon et al. (1994); 2, Folmer et al. (1994); 3, primers designed for this study by S. T. Williams; 4, Quintero et al. (2005).

| Marker | Primer | Direction | Annealing temperature | Sequence (5'-3') | Fragment size |
|---|---|---|---|---|---|
| 16S | 16Sar[1] | Forward | 45 °C | CGCCTGTTTAACAAAAACAT | ~450 bp |
| | 16Sbr[1] | Reverse | 45 °C | CCGGTCTGAACTCAGATCACGT | ~450 bp |
| CO1 | LCO1490[2] | Forward | 40-45 °C | GGTCAACAAATCATAAAGATATTGG | ~650 bp |
| | HCO2198[2] | Reverse | 40-45 °C | TAAACTTCAGGGTGACCAAAAAATCA | ~650 bp |
| | CORR-CO1-F[3] | Forward | 45 °C | TGATGTGGTATAGTAGGAAC | ~460 bp |
| | CORR-CO1-R[3] | Reverse | 45 °C | TAATAGCACCTGCTAAGACTG | ~460 bp |
| ND1 | MOL-NAD1F[4] | Forward | 50 °C | CGRAARGGMCCTAACAARGTTGG | ~430 bp |
| | MOL-NAD1R[4] | Reverse | 50 °C | GGRGCACGATTWGTCTCNGCTA | ~430 bp |

**Table 3.** Properties of the two concatenated datasets. The first dataset consists of 42 *Corilla* samples and 5 other taxa, *Albinaria caerulea*, *Cornu aspersum*, *Lissachatina fulica* (outgroup), *Halongella schlumbergeri* and *Sculptaria damaraensis damaraensis*; the second contains all these samples apart from *C. colletti* 5 and 6. The original concatenated alignments (i.e. including indels) for these two datasets were respectively 2166 bp (with 29 indels in 16S and 1 indel in ND1) and 2163 bp (with 31 indels in 16S and 1 indel in ND1).

| | **46 ingroup + 1 outgroup** | **44 ingroup + 1 outgroup** |
|---|---|---|
| **Number of *Corilla* samples** | 42 | 40 |
| **Markers** | CO1 + ND1 + 16S | CO1 + ND1 + 16S |
| **Number of haplotypes** | 47 (43 + 44 + 43) | 45 (41 + 42 + 41) |
| **Total number of sites** | 1277 (459 + 429 + 389) | 1281 (459 + 429 + 393) |
| **Number of invariable sites** | 502 (238 + 93 + 171) | 503 (238 + 93 + 172) |
| **Number of variable sites** | 775 (221 + 336 + 218) | 778 (221 + 336 + 221) |

**Table 4.** Patterns of support for selected clades recovered in phylogenetic analyses of *Corilla*, *Albinaria caerulea*, *Cornu aspersum*, *Lissachatina fulica*, *Halongella schlumbergeri* and *Sculptaria damaraensis damarensis* (all alignments gaps have been excluded). Analyses excluding the 3rd codon position of CO1 and ND1 are presented for comparison. Clades follow **Fig. 2**. For properties of the mtDNA datasets including all codon positions of CO1 and ND1see **Table 3**. The datasets excluding the 3rd codon position of CO1 and ND1 have the following composition: dataset of 46 ingroup sequences + 1 outgroup, CO1 = 306 bp, ND1 = 286 bp, 16S = 389 bp; dataset of 44 ingroup sequences + 1 outgroup, CO1 = 306 bp, ND1 = 286 bp, 16S = 393 bp. Support values are given as posterior probabilities for Bayesian analyses and as bootstrap percentages for ML; maximal support (Bayesian = 1, ML = 100%) is indicated by an asterisk. Apart from one of the ML analyses (all deeper nodes not reliably resolved in analysis 6 below), *C. beddomeae* was consistently recovered as sister to all other *Corilla*. Abbreviations are: nr, relationships not reliably resolved; na, support value not available because the relevant samples were excluded from the analysis.

| **Dataset** | C01 (all codon positions), ND1 (all codon positions), 16S | | | | C01 (codon positions 1+2), ND1 (codon positions 1+2), 16S | | | |
|---|---|---|---|---|---|---|---|---|
| **Constituent samples** | 46 ingroup + 1 outgroup | | 44 ingroup + 1 outgroup | | 46 ingroup + 1 outgroup | | 44 ingroup + 1 outgroup | |
| **Method** | 1. Bayesian | 2. ML | 3. Bayesian | 4. ML | 5. Bayesian | 6. ML | 7. Bayesian | 8. ML |
| **Clade** | | | | | | | | |
| *Corilla* | * | * | * | * | * | * | * | 99 |
| A | * | 65 | * | 76 | 0.95 | nr | * | 78 |
| B | * | 63 | * | 63 | 0.96 | nr | * | 66 |
| *C. beddomeae* | * | * | * | * | * | * | * | * |
| *C. adamsi* | * | 98 | * | 96 | * | 90 | * | 90 |
| *C. erronea-fryae* | * | 92 | * | 84 | * | 84 | * | 79 |
| *C. humberti* + *C. gudei* South | * | 98 | * | 97 | * | * | * | 99 |
| *C. humberti* | * | 97 | * | 98 | * | * | * | * |
| *C. carabinata* + *C. gudei* North | 0.99 | 85 | 0.99 | 79 | nr | nr | nr | 49 |
| *C. carabinata* | * | * | * | * | * | * | * | * |
| *C. gudei* North | * | * | * | * | * | * | * | * |
| *C. colletti* | * | 76 | * | 93 | 0.96 | nr | * | 90 |
| *C. odontophora* East | * | * | * | * | * | 98 | * | 99 |
| *C. adamsi* (2-4) | * | * | * | * | * | * | * | 99 |
| *C. beddomeae* (1a, 1b) | * | * | * | * | * | * | * | * |
| *C. beddomeae* (2a-5) | * | * | * | * | * | * | * | * |
| *C. carabinata* (2a-5b) | 0.99 | 90 | 0.98 | 88 | * | 98 | 0.99 | 97 |
| *C. colletti* (1-4) | * | 82 | * | 93 | 0.99 | 73 | * | 90 |
| *C. colletti* (5, 6) | * | 87 | na | na | 0.97 | nr | na | na |
| *C. odontophora* (1a, 1b) | * | * | * | * | * | * | * | * |

**Table 5.** p-distances between 42 *Corilla* sequences based on CO1 (459 bp). Distances have been pooled to correspond with the clades/groups shown in **Fig. 2**, and are gives as ranges (in plain font) and as means (bold font). Distances for members of the same clade/group are in the shaded cells. The letters N, S and E indicate north, south and east respectively.

| | *C. adamsi* (1) | *C. adamsi* (2-4) | *C. beddomeae* (1a, 1b) | *C. beddomeae* (2a-5) | *C. gudei* N (1, 2) | *C. carabinata* (1) | *C. carabinata* (2a-5b) | *C. colletti* (5, 6) | *C. colletti* (1-4) | *C. erronea-fryae* | *C. gudei* S (3) | *C. humberti* | *C. odontophora* N (3) | *C. odontophora* E (1a-2) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *C. adamsi* (1) | - **-** | 0.150-179 | 0.179 | 0.176-0.194 | 0.172-0.181 | 0.224 | 0.218-0.220 | 0.207-0.216 | 0.200-0.214 | 0.172-0.190 | 0.196 | 0.183 | 0.207 | 0.181-0.198 |
| *C. adamsi* (2-4) | **0.167** | 0.022-0.124 **0.091** | 0.200-0.207 | 0.196-0.218 | 0.176-0.190 | 0.185-0.205 | 0.192-0.218 | 0.207-0.218 | 0.185-0.209 | 0.187-0.214 | 0.187-0.207 | 0.176-0.187 | 0.185-0.198 | 0.183-0.214 |
| *C. beddomeae* (1a, 1b) | **0.179** | **0.203** | 0.004 **0.004** | 0.126-0.150 | 0.176-0.187 | 0.220-0.222 | 0.216-0.220 | 0.222-0.229 | 0.198-0.218 | 0.176-0.207 | 0.19 | 0.168-0.172 | 0.216-0.218 | 0.192-0.235 |
| *C. beddomeae* (2a-5) | **0.186** | **0.208** | **0.136** | 0.000-0.050 **0.038** | 0.192-0.214 | 0.218-0.233 | 0.218-0.240 | 0.200-0.227 | 0.181-0.220 | 0.172-0.209 | 0.196-0.216 | 0.181-0.205 | 0.207-0.214 | 0.166-0.242 |
| *C. gudei* N (1, 2) | **0.176** | **0.182** | **0.182** | **0.201** | 0.015 **0.015** | 0.161-0.163 | 0.166-0.170 | 0.168-0.179 | 0.163-0.185 | 0.137-0.159 | 0.157-0.163 | 0.153-0.163 | 0.153-0.159 | 0.159-0.172 |
| *C. carabinata* (1) | **0.224** | **0.193** | **0.221** | **0.225** | **0.162** | - **-** | 0.037-0.041 | 0.192-0.196 | 0.187-0.192 | 0.174-0.203 | 0.192 | 0.194-0.198 | 0.168 | 0.179-0.205 |
| *C. carabinata* (2a-5b) | **0.219** | **0.200** | **0.218** | **0.230** | **0.168** | **0.038** | 0-0.009 **0.005** | 0.198-0.205 | 0.181-0.196 | 0.172-0.198 | 0.192-0.194 | 0.194-0.200 | 0.174-0.181 | 0.176-0.200 |
| *C. colletti* (5, 6) | **0.211** | **0.212** | **0.225** | **0.215** | **0.171** | **0.194** | **0.202** | 0.017 **0.017** | 0.111-0.131 | 0.172-0.194 | 0.172-0.183 | 0.174-0.190 | 0.17 | 0.179-0.190 |
| *C. colletti* (1-4) | **0.204** | **0.196** | **0.207** | **0.199** | **0.173** | **0.190** | **0.189** | **0.122** | 0.002-0.089 **0.069** | 0.155-0.190 | 0.146-0.168 | 0.133-0.176 | 0.157-0.179 | 0.170-0.192 |
| *C. erronea-fryae* | **0.179** | **0.201** | **0.188** | **0.185** | **0.148** | **0.184** | **0.182** | **0.182** | **0.172** | 0.002-0.102 **0.07** | 0.157-0.168 | 0.139-0.181 | 0.148-0.163 | 0.092-0.179 |
| *C. gudei* S (3) | **0.196** | **0.200** | **0.190** | **0.207** | **0.160** | **0.192** | **0.192** | **0.178** | **0.157** | **0.167** | - **-** | 0.070-0.072 | 0.168 | 0.157-0.190 |
| *C. humberti* | **0.183** | **0.184** | **0.170** | **0.191** | **0.158** | **0.196** | **0.197** | **0.182** | **0.155** | **0.155** | **0.071** | 0.004 **0.004** | 0.161-0.163 | 0.153-0.168 |
| *C. odontophora* N (3) | **0.207** | **0.194** | **0.217** | **0.210** | **0.156** | **0.168** | **0.177** | **0.170** | **0.166** | **0.155** | **0.168** | **0.162** | - **-** | 0.166-0.170 |
| *C. odontophora* E (1a-2) | **0.192** | **0.196** | **0.220** | **0.208** | **0.167** | **0.190** | **0.186** | **0.184** | **0.180** | **0.147** | **0.179** | **0.162** | **0.168** | 0.011-0.181 **0.124** |

**Table 6.** Indels in the aligned 16S region of *Corilla* (42 sequences, 462 bp) that define some of the clades discussed in the text. Shading indicates indels consisting of ≥2 base positions. Clades/groups follow **Fig. 2**. The letters N, S and E indicate north, south and east respectively.

| | **12** | **13** | **43** | **44** | **46** | **50** | **51** | **157** | **163** | **198** | **243** | **244** | **245** | **246** | **283** | **284** | **285** | **299** | **303** | **304** | **305** | **306** | **307** | **312** | **325** | **326** | **327** | **346** | **432** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *C. adamsi* (1) | - | A | T | T | A | A | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | G | - | - | - | T | - |
| *C. adamsi* (2-4) | C/- | T | T | T | - | A | - | - | - | T | G/- | - | - | - | A | - | - | T | - | - | - | - | - | T | - | - | T | T | - |
| *C.beddomeae* (1a, 1b) | - | A | - | - | - | T | - | - | - | T | - | - | - | T | - | - | - | A | A | T | T | T | T | T | - | T | T | C | - |
| *C. beddomeae* (2a-5) | - | - | T | C/T | - | T | - | - | - | T | T | A | T | T | T | - | - | A | - | - | - | A/T | A/T | C/T/- | - | - | T | T | T |
| *C. carabinata* (1) | - | - | T | T | - | A | C | - | - | - | - | - | - | - | A | A | T | A | - | - | - | - | A | A | - | T | T | T | - |
| *C. carabinata* (2a-5b) | - | - | T | T | - | A | C | - | - | - | T | - | - | - | A | A | T | A | - | - | - | - | G | A | - | T | T | T | - |
| *C. colletti* (1-4) | - | - | T | T | - | A | T | - | - | - | T/- | - | T/- | A/- | A | A/G | T | A | - | - | - | - | - | A | - | C/T | T | C/T | - |
| *C. colletti* (5, 6) | - | - | T | T | - | G | T | - | - | - | - | - | - | - | A | A | T | A | - | - | - | - | - | A | - | T | T | C | - |
| *C. erronea-fryae* | - | - | T | T | - | A/T | C/T | - | T/- | - | - | - | - | - | A | A/T | - | A | - | - | - | - | A/G/T | A | - | T | T | T | - |
| *C. gudei* N (1, 2) | - | - | T | T | - | - | T | - | - | - | - | - | - | - | A | A/G | C | G | - | - | - | - | G | A | - | C | T | T | - |
| *C. gudei* S (3) | - | - | T | T | - | A | T | C | - | - | - | - | - | - | A | T | - | A | - | - | - | - | T | A | - | T | T | - | - |
| *C. humberti* | - | - | T | T | - | A | T | C | - | - | - | - | - | - | A | T | - | A | - | - | - | - | T | A | - | T | T | - | - |
| *C. ondontophora* E (1a-2) | - | - | T | T | - | A | - | - | - | - | T | - | - | - | A | A | - | A | - | - | - | - | A | A | - | T | T | C | - |
| *C. odontophora* N (3) | - | - | T | T | - | G | T | - | - | - | - | - | - | - | A | G | - | A | - | - | - | - | - | A | T | T | T | C | - |

**Appendix A. Supplementary Material.**

**Table S1.** Properties of the two concatenated datasets consisting of *Corilla* alone. The first dataset comprises 42 samples and the second 40 samples (i.e. excluding *C. colletti* 5 and 6). The original concatenated alignments (i.e. including indels) for these two datasets were respectively 1361 bp (with 31 indels in 16S and 1 indel in ND1) and 1360 bp (with 29 indels in 16S and 1 indel in ND1).

| | **42 *Corilla* samples** | **40 *Corilla* samples** |
|---|---|---|
| **Markers** | CO1 + ND1 + 16S | CO1 + ND1 + 16S |
| **Number of haplotypes** | 42 (38 + 39 + 40) | 40 (36+ 37 + 38) |
| **Total number of sites** | 1327 (459 + 437 + 431) | 1328 (459 + 437 + 432) |
| **Number of invariable sites** | 668 (261 + 162 + 245) | 673 (261 + 165 + 247) |
| **Number of variable sites** | 659 (198 + 275 + 186) | 655 (198 + 272 + 185) |

**Table S2.** Patterns of support for selected clades recovered in phylogenetic analyses of *Corilla* alone (all alignments gaps have been excluded). Analyses excluding the 3rd codon position of CO1 and ND1 are presented for comparison. Clades follow **Fig. 2**. For properties of the mtDNA datasets including all codon positions of CO1 and ND1see **Table S1**. The datasets excluding the 3rd codon position of CO1 and ND1 have the following composition: dataset of 42 *Corilla* samples, CO1 = 306 bp, ND1 = 291 bp, 16S = 431 bp; dataset of 40 *Corilla* samples, CO1 = 306 bp, ND1 = 291 bp, 16S = 432 bp. Support values are given as posterior probabilities for Bayesian analyses and as bootstrap percentages for ML. Maximal support (Bayesian = 1, ML = 100%) is indicated by an asterisk and 'na' indicates that values were not available because the relevant samples were excluded from the analysis. Trees were rooted on *C. beddomeae* so this taxon is not considered here.

| **Dataset** | C01 (all codon positions), ND1 (all codon positions), 16S | | | | C01 (codon positions 1+2), ND1 (codon positions 1+2), 16S | | | |
|---|---|---|---|---|---|---|---|---|
| **Constituent samples** | 42 *Corilla* samples | | 40 *Corilla* samples | | 42 *Corilla* samples | | 40 *Corilla* samples | |
| **Method** | 1. Bayesian | 2. ML | 3. Bayesian | 4. ML | 5. Bayesian | 6. ML | 7. Bayesian | 8. ML |
| **Clade** | | | | | | | | |
| A | * | * | * | * | * | * | * | * |
| B | * | 98 | * | 98 | * | 91 | * | 93 |
| *C. adamsi* | * | 99 | * | * | * | 98 | * | * |
| *C. erronea-fryae* | * | 98 | * | 96 | * | 88 | * | 88 |
| *C. humberti* + *C. gudei* South | * | 99 | * | * | * | * | * | * |
| *C. humberti* | * | 97 | * | * | * | * | * | * |
| *C. carabinata* + *C. gudei* North | * | 94 | * | 94 | 0.94 | 76 | 0.96 | 78 |
| *C. carabinata* | * | * | * | * | * | * | * | * |
| *C. gudei* North | * | * | * | * | * | * | * | * |
| *C. colletti* | * | 99 | * | * | * | * | * | * |
| *C. odontophora* East | * | * | * | * | * | * | * | * |
| *C. adamsi* (2-4) | * | * | * | * | * | * | * | * |
| *C. carabinata* (2a-5b) | 0.97 | 84 | 0.96 | 87 | 0.99 | 94 | 0.99 | 76 |
| *C. colletti* (1-4) | * | 96 | * | * | 0.99 | 87 | * | * |
| *C. colletti* (5, 6) | * | * | na | na | * | * | na | na |
| *C. odontophora* (1a, 1b) | * | * | * | * | * | 90 | * | 83 |

**Appendix A. Supplementary Material**

**Table S3.** *P*-distances between 42 Corilla sequences based on CO1 (459 bp). Shading indicates distances among members of the same clade and/or nominal species.

| | *C. adamsi* 1 | *C. adamsi* 2 | *C. adamsi* 3 | *C. adamsi* 4 | *C. beddomeae* 1a | *C. beddomeae* 1b | *C. beddomeae* 2a | *C. beddomeae* 2b | *C. beddomeae* 5 | *C. beddomeae* 4a | *C. beddomeae* 4b | *C. beddomeae* 3 | *C. gudei* 1 | *C. gudei* 2 | *C. carabinata* 1 | *C. carabinata* 2a | *C. carabinata* 2b | *C. carabinata* 3 | *C. carabinata* 4 | *C. carabinata* 5a | *C. carabinata* 5b | *C. colletti* 3 | *C. colletti* 1 | *C. colletti* 4 | *C. colletti* 2 | *C. colletti* 6 | *C. colletti* 5 | *C. erronea* 1 | *C. erronea* 2 | *C. fryae* 1a | *C. fryae* 1b | *C. erronea* 5 | *C. erronea* 4 | *C. erronea* 3 | *C. fryae* 3 | *C. gudei* 3 | *C. humberti* 1 | *C. humberti* 2 | *C. odontophora* 2 | *C. odontophora* 1a | *C. odontophora* 1b | *C. odontophora* 3 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *C. adamsi* 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *C. adamsi* 2 | 0.150 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *C. adamsi* 3 | 0.179 | 0.124 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *C. adamsi* 4 | 0.172 | 0.126 | 0.022 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *C. beddomeae* 1a | 0.179 | 0.203 | 0.207 | 0.200 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *C. beddomeae* 1b | 0.179 | 0.200 | 0.207 | 0.200 | 0.004 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *C. beddomeae* 2a | 0.194 | 0.211 | 0.216 | 0.218 | 0.150 | 0.150 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *C. beddomeae* 2b | 0.192 | 0.214 | 0.214 | 0.216 | 0.146 | 0.146 | 0.009 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *C. beddomeae* 5 | 0.192 | 0.203 | 0.209 | 0.216 | 0.135 | 0.133 | 0.044 | 0.046 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *C. beddomeae* 4a | 0.176 | 0.200 | 0.203 | 0.205 | 0.129 | 0.131 | 0.046 | 0.048 | 0.039 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *C. beddomeae* 4b | 0.176 | 0.200 | 0.203 | 0.205 | 0.129 | 0.131 | 0.046 | 0.048 | 0.039 | 0.000 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *C. beddomeae* 3 | 0.183 | 0.196 | 0.209 | 0.211 | 0.126 | 0.129 | 0.050 | 0.052 | 0.022 | 0.044 | 0.044 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *C. gudei* 1 | 0.181 | 0.176 | 0.190 | 0.185 | 0.187 | 0.185 | 0.214 | 0.209 | 0.203 | 0.203 | 0.203 | 0.207 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *C. gudei* 2 | 0.172 | 0.176 | 0.185 | 0.181 | 0.179 | 0.176 | 0.203 | 0.198 | 0.192 | 0.192 | 0.192 | 0.198 | 0.015 | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *C. carabinata* 1 | 0.224 | 0.205 | 0.190 | 0.185 | 0.222 | 0.220 | 0.233 | 0.229 | 0.227 | 0.218 | 0.218 | 0.227 | 0.161 | 0.163 | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *C. carabinata* 2a | 0.220 | 0.207 | 0.192 | 0.196 | 0.218 | 0.216 | 0.231 | 0.240 | 0.231 | 0.218 | 0.218 | 0.231 | 0.166 | 0.168 | 0.037 | | | | | | | | | | | | | | | | | | | | | | | | | | |
| *C. carabinata* 2b | 0.220 | 0.207 | 0.192 | 0.196 | 0.218 | 0.216 | 0.231 | 0.240 | 0.231 | 0.218 | 0.218 | 0.231 | 0.166 | 0.168 | 0.037 | 0.000 | | | | | | | | | | | | | | | | | | | | | | | | | |
| *C. carabinata* 3 | 0.218 | 0.209 | 0.194 | 0.198 | 0.218 | 0.216 | 0.235 | 0.240 | 0.235 | 0.222 | 0.222 | 0.235 | 0.168 | 0.170 | 0.037 | 0.004 | 0.004 | | | | | | | | | | | | | | | | | | | | | | | | |
| *C. carabinata* 4 | 0.218 | 0.209 | 0.194 | 0.198 | 0.218 | 0.216 | 0.235 | 0.240 | 0.235 | 0.222 | 0.222 | 0.235 | 0.168 | 0.170 | 0.037 | 0.004 | 0.004 | 0.000 | | | | | | | | | | | | | | | | | | | | | | | |
| *C. carabinata* 5a | 0.218 | 0.214 | 0.194 | 0.198 | 0.220 | 0.218 | 0.233 | 0.237 | 0.233 | 0.220 | 0.220 | 0.233 | 0.168 | 0.170 | 0.041 | 0.009 | 0.009 | 0.004 | 0.004 | | | | | | | | | | | | | | | | | | | | | | |
| *C. carabinata* 5b | 0.218 | 0.214 | 0.194 | 0.198 | 0.220 | 0.218 | 0.233 | 0.237 | 0.233 | 0.220 | 0.220 | 0.233 | 0.168 | 0.170 | 0.041 | 0.009 | 0.009 | 0.004 | 0.004 | 0.000 | | | | | | | | | | | | | | | | | | | | | |
| *C. colletti* 3 | 0.200 | 0.185 | 0.198 | 0.200 | 0.214 | 0.214 | 0.209 | 0.207 | 0.220 | 0.211 | 0.211 | 0.209 | 0.179 | 0.176 | 0.190 | 0.194 | 0.194 | 0.196 | 0.196 | 0.196 | 0.196 | | | | | | | | | | | | | | | | | | | | |
| *C. colletti* 1 | 0.200 | 0.187 | 0.190 | 0.200 | 0.198 | 0.198 | 0.196 | 0.194 | 0.185 | 0.183 | 0.183 | 0.179 | 0.163 | 0.163 | 0.190 | 0.185 | 0.185 | 0.187 | 0.187 | 0.183 | 0.183 | 0.089 | | | | | | | | | | | | | | | | | | | |
| *C. colletti* 4 | 0.214 | 0.194 | 0.203 | 0.209 | 0.218 | 0.216 | 0.209 | 0.207 | 0.211 | 0.207 | 0.207 | 0.203 | 0.185 | 0.183 | 0.192 | 0.192 | 0.192 | 0.194 | 0.194 | 0.194 | 0.194 | 0.057 | 0.089 | | | | | | | | | | | | | | | | | | |
| *C. colletti* 2 | 0.203 | 0.190 | 0.192 | 0.203 | 0.200 | 0.200 | 0.198 | 0.196 | 0.187 | 0.185 | 0.185 | 0.181 | 0.166 | 0.166 | 0.187 | 0.183 | 0.183 | 0.185 | 0.185 | 0.181 | 0.181 | 0.087 | 0.002 | 0.087 | | | | | | | | | | | | | | | | | |
| *C. colletti* 6 | 0.216 | 0.214 | 0.216 | 0.218 | 0.229 | 0.227 | 0.227 | 0.224 | 0.216 | 0.220 | 0.220 | 0.205 | 0.170 | 0.179 | 0.196 | 0.203 | 0.203 | 0.205 | 0.205 | 0.205 | 0.205 | 0.131 | 0.124 | 0.124 | 0.122 | | | | | | | | | | | | | | | | |
| *C. colletti* 5 | 0.207 | 0.207 | 0.207 | 0.209 | 0.224 | 0.222 | 0.218 | 0.216 | 0.211 | 0.211 | 0.211 | 0.200 | 0.168 | 0.168 | 0.192 | 0.200 | 0.200 | 0.203 | 0.203 | 0.198 | 0.198 | 0.126 | 0.120 | 0.111 | 0.118 | 0.017 | | | | | | | | | | | | | | | |
| *C. erronea* 1 | 0.181 | 0.209 | 0.190 | 0.190 | 0.187 | 0.185 | 0.192 | 0.185 | 0.174 | 0.179 | 0.179 | 0.181 | 0.144 | 0.139 | 0.176 | 0.181 | 0.181 | 0.183 | 0.183 | 0.183 | 0.183 | 0.176 | 0.155 | 0.172 | 0.157 | 0.183 | 0.176 | | | | | | | | | | | | | | |
| *C. erronea* 2 | 0.179 | 0.207 | 0.187 | 0.187 | 0.179 | 0.179 | 0.190 | 0.183 | 0.174 | 0.176 | 0.176 | 0.179 | 0.142 | 0.137 | 0.179 | 0.174 | 0.174 | 0.176 | 0.176 | 0.176 | 0.176 | 0.176 | 0.155 | 0.176 | 0.157 | 0.187 | 0.181 | 0.011 | | | | | | | | | | | | | |
| *C. fryae* 1a | 0.179 | 0.207 | 0.196 | 0.196 | 0.181 | 0.179 | 0.187 | 0.181 | 0.174 | 0.179 | 0.179 | 0.181 | 0.146 | 0.142 | 0.179 | 0.174 | 0.174 | 0.176 | 0.176 | 0.176 | 0.176 | 0.185 | 0.159 | 0.181 | 0.161 | 0.192 | 0.185 | 0.015 | 0.009 | | | | | | | | | | | | |
| *C. fryae* 1b | 0.176 | 0.205 | 0.194 | 0.194 | 0.179 | 0.176 | 0.185 | 0.179 | 0.172 | 0.176 | 0.176 | 0.179 | 0.144 | 0.139 | 0.176 | 0.172 | 0.172 | 0.174 | 0.174 | 0.174 | 0.174 | 0.183 | 0.157 | 0.179 | 0.159 | 0.190 | 0.183 | 0.013 | 0.007 | 0.002 | | | | | | | | | | | |
| *C. erronea* 5 | 0.183 | 0.205 | 0.194 | 0.196 | 0.194 | 0.192 | 0.196 | 0.198 | 0.190 | 0.190 | 0.190 | 0.194 | 0.155 | 0.153 | 0.174 | 0.174 | 0.174 | 0.176 | 0.176 | 0.176 | 0.176 | 0.174 | 0.174 | 0.179 | 0.176 | 0.183 | 0.172 | 0.081 | 0.078 | 0.078 | 0.081 | | | | | | | | | | |
| *C. erronea* 4 | 0.190 | 0.203 | 0.209 | 0.214 | 0.207 | 0.205 | 0.190 | 0.192 | 0.181 | 0.181 | 0.181 | 0.187 | 0.155 | 0.148 | 0.203 | 0.194 | 0.194 | 0.192 | 0.192 | 0.192 | 0.192 | 0.190 | 0.170 | 0.183 | 0.168 | 0.185 | 0.174 | 0.102 | 0.096 | 0.100 | 0.098 | 0.098 | | | | | | | | | |
| *C. erronea* 3 | 0.172 | 0.211 | 0.196 | 0.200 | 0.198 | 0.196 | 0.209 | 0.207 | 0.194 | 0.198 | 0.198 | 0.192 | 0.155 | 0.150 | 0.190 | 0.190 | 0.190 | 0.187 | 0.187 | 0.187 | 0.187 | 0.187 | 0.168 | 0.185 | 0.170 | 0.183 | 0.172 | 0.085 | 0.083 | 0.087 | 0.085 | 0.085 | 0.102 | | | | | | | | |
| *C. fryae* 3 | 0.176 | 0.209 | 0.205 | 0.209 | 0.183 | 0.181 | 0.196 | 0.194 | 0.181 | 0.181 | 0.181 | 0.183 | 0.159 | 0.155 | 0.196 | 0.196 | 0.196 | 0.198 | 0.198 | 0.194 | 0.194 | 0.187 | 0.161 | 0.190 | 0.163 | 0.194 | 0.179 | 0.083 | 0.081 | 0.085 | 0.083 | 0.089 | 0.102 | 0.037 | | | | | | | |
| *C. gudei* 3 | 0.196 | 0.187 | 0.207 | 0.207 | 0.190 | 0.190 | 0.216 | 0.216 | 0.203 | 0.205 | 0.205 | 0.196 | 0.157 | 0.163 | 0.192 | 0.192 | 0.192 | 0.194 | 0.194 | 0.192 | 0.192 | 0.168 | 0.146 | 0.168 | 0.148 | 0.183 | 0.172 | 0.166 | 0.166 | 0.166 | 0.168 | 0.157 | 0.181 | 0.168 | 0.163 | | | | | | |
| *C. humberti* 1 | 0.183 | 0.187 | 0.185 | 0.176 | 0.168 | 0.172 | 0.205 | 0.203 | 0.192 | 0.187 | 0.187 | 0.185 | 0.157 | 0.163 | 0.198 | 0.198 | 0.198 | 0.200 | 0.200 | 0.198 | 0.198 | 0.170 | 0.137 | 0.176 | 0.139 | 0.190 | 0.179 | 0.155 | 0.150 | 0.157 | 0.155 | 0.157 | 0.181 | 0.157 | 0.144 | 0.070 | | | | | |
| *C. humberti* 2 | 0.183 | 0.187 | 0.185 | 0.181 | 0.168 | 0.172 | 0.200 | 0.198 | 0.187 | 0.183 | 0.183 | 0.181 | 0.153 | 0.159 | 0.194 | 0.194 | 0.194 | 0.196 | 0.196 | 0.194 | 0.194 | 0.170 | 0.133 | 0.176 | 0.135 | 0.185 | 0.174 | 0.150 | 0.146 | 0.153 | 0.150 | 0.153 | 0.176 | 0.153 | 0.139 | 0.072 | 0.004 | | | | |
| *C. odontophora* 2 | 0.181 | 0.214 | 0.209 | 0.209 | 0.194 | 0.192 | 0.183 | 0.181 | 0.170 | 0.166 | 0.166 | 0.172 | 0.159 | 0.159 | 0.205 | 0.198 | 0.198 | 0.200 | 0.200 | 0.196 | 0.196 | 0.181 | 0.170 | 0.192 | 0.172 | 0.185 | 0.179 | 0.107 | 0.107 | 0.111 | 0.109 | 0.102 | 0.115 | 0.094 | 0.092 | 0.157 | 0.157 | 0.153 | | | |
| *C. odontophora* 1a | 0.196 | 0.187 | 0.183 | 0.190 | 0.233 | 0.233 | 0.240 | 0.242 | 0.224 | 0.216 | 0.216 | 0.220 | 0.170 | 0.172 | 0.179 | 0.179 | 0.179 | 0.176 | 0.176 | 0.176 | 0.176 | 0.181 | 0.176 | 0.185 | 0.176 | 0.190 | 0.183 | 0.163 | 0.161 | 0.166 | 0.163 | 0.172 | 0.179 | 0.168 | 0.174 | 0.190 | 0.168 | 0.163 | 0.181 | | |
| *C. odontophora* 1b | 0.198 | 0.192 | 0.187 | 0.194 | 0.235 | 0.235 | 0.237 | 0.240 | 0.222 | 0.218 | 0.218 | 0.218 | 0.170 | 0.172 | 0.185 | 0.185 | 0.185 | 0.183 | 0.183 | 0.179 | 0.179 | 0.185 | 0.176 | 0.190 | 0.176 | 0.190 | 0.179 | 0.161 | 0.159 | 0.163 | 0.161 | 0.174 | 0.176 | 0.170 | 0.172 | 0.190 | 0.168 | 0.163 | 0.181 | 0.011 | |
| *C. odontophora* 3 | 0.207 | 0.185 | 0.198 | 0.198 | 0.218 | 0.216 | 0.214 | 0.214 | 0.209 | 0.207 | 0.207 | 0.209 | 0.153 | 0.159 | 0.168 | 0.174 | 0.174 | 0.176 | 0.176 | 0.181 | 0.181 | 0.172 | 0.157 | 0.179 | 0.157 | 0.170 | 0.170 | 0.148 | 0.159 | 0.159 | 0.157 | 0.150 | 0.163 | 0.150 | 0.153 | 0.168 | 0.163 | 0.161 | 0.170 | 0.166 | 0.168 |


| | *C. adamsi* 1 | *C. adamsi* 2 | *C. adamsi* 3 | *C. adamsi* 4 | *C. beddomeae* 1a | *C. beddomeae* 1b | *C. beddomeae* 2a | *C. beddomeae* 2b | *C. beddomeae* 5 | *C. beddomeae* 4a | *C. beddomeae* 4b | *C. beddomeae* 3 | *C. gudei* 1 | *C. gudei* 2 | *C. carabinata* 1 | *C. carabinata* 2a | *C. carabinata* 2b | *C. carabinata* 3 | *C. carabinata* 4 | *C. carabinata* 5a | *C. carabinata* 5b | *C. colletti* 3 | *C. colletti* 1 | *C. colletti* 4 | *C. colletti* 2 | *C. colletti* 6 | *C. colletti* 5 | *C. erronea* 1 | *C. erronea* 2 | *C. fryae* 1a | *C. fryae* 1b | *C. erronea* 5 | *C. erronea* 4 | *C. erronea* 3 | *C. fryae* 3 | *C. gudei* 3 | *C. humberti* 1 | *C. humberti* 2 | *C. odontophora* 2 | *C. odontophora* 1a | *C. odontophora* 1b | *C. odontophora* 3 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|