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Relationships of Henicopidae (Chilopoda: Lithobiomorpha): New molecular data, classification and biogeography*

by

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ABSTRACT

Phylogenetic relationships in the lithobiomorph family Henicopidae are analysed based on sequence data for five molecular markers and 58 morphological characters. The character sample includes two nuclear ribosomal genes (complete 18S rRNA and the D3 region of 28S rRNA) and three mitochondrial genes, two ribosomal (16S rRNA and 12S rRNA) and one protein-coding (cytochrome *c* oxidase subunit I). Terminal taxa include six outgroup species of Lithobiidae and 41 exemplars of Henicopidae representing 33 species.

Analysis of the combined dataset using Direct Optimization and exploring stability of clades to a range of gap:substitution and transversion:transition costs yields a most congruent (minimal ILD) cladogram that is largely congruent with the shortest molecular cladogram. Morphology, however, contributes additional nodes to the strict consensus of all explored parameters. The morphological cladogram resolves the Oriental *Shikokuobius* as sister to a gondwanan clade of Anopsobiinae, whereas the sequence data place *Shikokuobius* as sister to Henicopinae or all Henicopidae. Henicopinae *sensu* Attems is monophyletic for combined analyses for all parameters, being retrieved amongst the shortest morphological cladograms and by all molecular parameter sets, but the traditionally defined Zygethobiini is polyphyletic for several parameter sets. For the most congruent parameters, the nearctic *Zygethobius* is resolved in the expected position as sister to Henicopini, but the oriental *Cermatobius* nests within the Henicopini. Henicopini divides into two clades: one unites *Henicops* and *Lamyctes* (stable for all combined analyses as well as for morphological and molecular data alone) and the other unites the four gondwanan subgenera of *Paralamyctes*. In most analyses, South African species of *Paralamyctes* unite as a clade, with Cape endemics each others' closest relatives. Most parameter sets for the molecular and combined data resolve a group that includes the Australasian *Paralamyctes* (*Thingathinga*) and *P.* (*Haasiella*) together with Patagonian species formerly placed in *P.* (*Nothofagobius*).

INTRODUCTION

Henicopidae comprise most of lithobiomorph diversity in the southern temperate regions of the world. Relationships within Henicopidae have been analysed based on evidence from morphology together with sequences from five molecular loci (Edgecombe *et al.* 2002). These markers were nuclear ribosomal RNAs 18S and 28S, mitochondrial ribosomal RNAs 12S and 16S, and the mitochondrial coding gene, cytochrome *c* oxidase subunit I (COI hereafter). As much as 3500 bp of sequence information is available for most species.

The present study expands the taxonomic sampling used by Edgecombe *et al.* (2002) and Edgecombe & Giribet (2003) in order to explore additional questions in henicopid systematics and biogeography. Taxa added to the molecular dataset and their significance are as follows:

*Note that all Tables are presented at the end of the paper.

- *Zygethobius pontis* Chamberlin, 1911, a nearctic member of the Tribe Zygethobiini. Sequence data have only been available for an oriental zygethobiine, *Cermatobius* (= *Esastigmatobius*) *japonicus* (Silvestri, 1909). The monophyly and systematic position of Zygethobiini are contentious, the group nesting within the Tribe Henicopini in previous analysis (Edgecombe *et al*. 2002);
- *Shikokuobius japonicus* (Murakami, 1967), one of the few non-gondwanan taxa assigned to the Subfamily Anopsobiinae, and two Australian species of *Dichelobius* Attems, 1911. Previously sequence data for Anopsobiinae have been available only for species of a single genus, *Anopsobius*. Anopsobiinae has been attributed particular importance in chilopod systematics by the theory that their male genital characters are primitive relative to all other pleurostigmophoran Chilopoda (Prunescu 1996). The studies of Edgecombe *et al*. (1999) and Edgecombe & Giribet (2002) placed Anopsobiinae as the sister group to other Henicopidae, consistent with traditional classifications (Henicopidae *sensu* Attems 1928; Desmopleura Verhoeff 1925), and Lithobiomorpha was found to be monophyletic;
- Three species of *Paralamyctes* from South Africa (*P. spenceri* Pocock, 1901; *P. asperulus* Silvestri, 1903; *P. prendinii* Edgecombe, 2003*a*). Sequence data have previously been available for only one South African species, *P. weberi* Silvestri, 1903. The new sequences allow a more stringent test of the biogeographic affinities of southern African species in the context of this gondwanan genus;
- The first molecular data for *Paralamyctes* from Madagascar (*P. tridens* Lawrence, 1960);
- Two species of *Paralamyctes* from Chile, *P. chilensis* (Gervais in Walckenaer & Gervais, 1847) and *P. wellingtonensis* Edgecombe, 2003*c*, and a putatively allied species from eastern Australia, *P.* (*Nothofagobius*) *cassisi* Edgecombe, 2001. These species allow the biogeographic affinities of southern South American species relative to those from Australia and other parts of Gondwana to be more rigorously explored.

In addition, we include sequence data for a second member of the lithobiid Subfamily Ethopolyinae (*Eupolybothrus fasciatus* Newport, 1844). Six species of Lithobiidae (four Lithobiinae and two Ethopolyinae) are used as outgroups for Henicopidae. All sequence data have been generated by the authors except for sequences of *Lithobius forficatus*, sourced from GenBank.

These taxa are sequenced for the 18S, 28S, 12S, 16S rRNA and COI loci, and coded for their morphological characters using the morphology dataset of Edgecombe (2003*b*), modified from that of Edgecombe *et al*. (2002). Taxonomic sampling in this analysis is restricted to species for which multiple molecular markers are available.

DATA AND METHODOLOGY

Molecular data

Procedures for DNA isolation, amplification, sequencing and editing are as detailed by Edgecombe *et al*. (2002: 33–34). A list of the taxa sampled, loci sequenced, and GenBank accession codes is provided in Table 1.

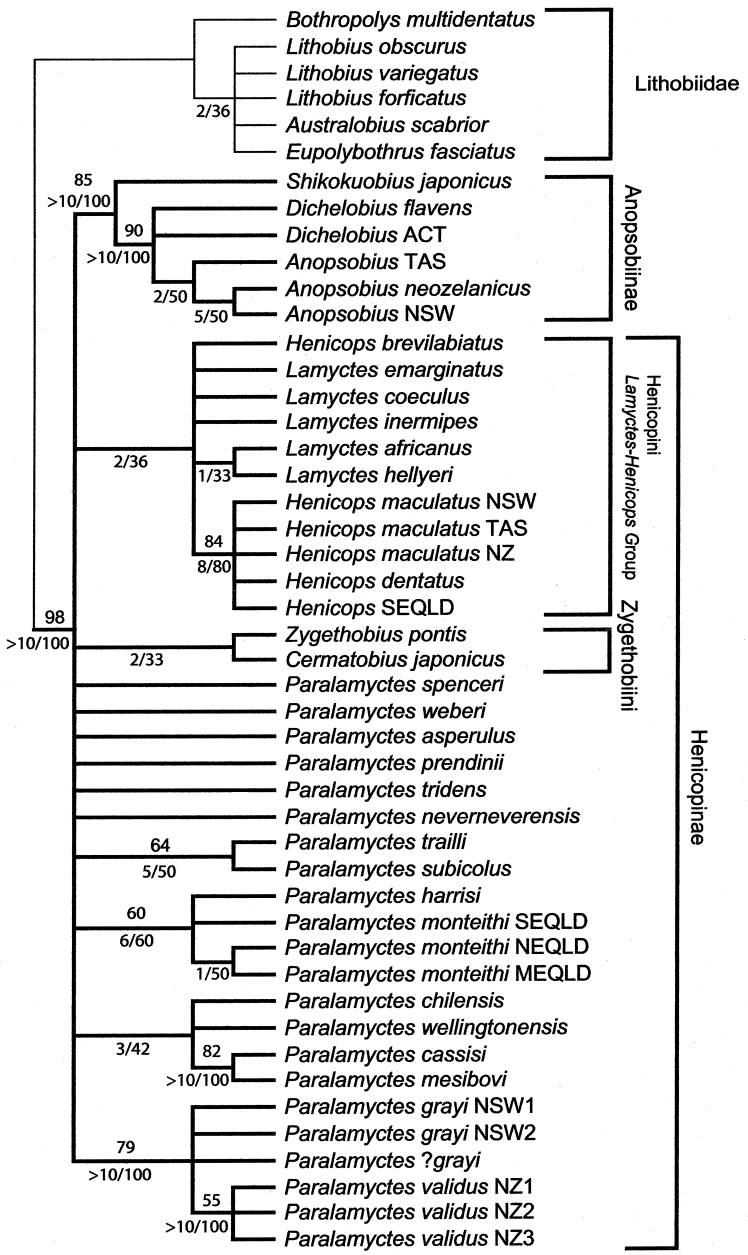

Fig. 1. Strict consensus of 10 000 shortest cladograms based on morphological data (134 steps; CI = 0.56; RI = 0.86). Branches for the ingroup (Henicopidae) appear darker than those for the outgroup (Lithobiidae). Numbers above branches indicate jackknife frequencies; numbers below branches indicate absolute Bremer support and relative fit difference, RFD, shown as a percentage (see text for a description of these support measures). Labels on branches indicate groups recovered in all morphological analyses (Anopsobiinae, *Lamyctes-Henicops* Group within Henicopini, Zygethobiini) and traditional membership of Henicopinae. *Paralamyctes* (unresolved) is traditionally assigned to Henicopini.

Morphological data

All taxa for which molecular data are available are coded for 58 morphological characters (Table 2 and Appendix 1). Characters 1–51 follow the character state descriptions of Edgecombe (2003*b*) except for adding a state to the description of maxillipede coxosternal shape to accommodate *Paralamyctes prendinii* (character 11, state 8), and adding a state for male gonopod segmentation to incorporate *Eupolybothrus* (character 44, state 2). Seven new characters are added to describe the modified cephalic margin of most Lithobiidae (character 52), the reduced number of spiracle-bearing segments in *Dichelobius* (character 53), the coxal pore arrangement of Ethopolyinae (character 54), the tarsal segmentation of *Henicops* (character 55), and three modifications of the pretarsal claws (characters 56–58).

Descriptions of most characters are provided by Edgecombe *et al*. (2002).

Data analysis

The morphological analyses were executed with the parsimony-based computer program NONA v. 2.0 (Goloboff 1998), using a heuristic search strategy with 1000 random addition replicates using tbr (tree bisection-reconnection) branch swapping, and retaining up to 10 trees per replicate (**hold10000;hold/10;mult*1000**). The results of this first round of searches were submitted to tbr swapping without limiting the number of trees (**max***). Relative support, measured by the relative fit difference (RFD) (Goloboff & Farris 2001), was calculated with the computer program TNT (Goloboff *et al*. 2000). Bremer support (Bremer 1988) generates absolute values of the degree to which a tree is suboptimal compared to another. A limitation of that method is that it does not always take into account the relative amounts of evidence contradictory and favourable to the group. This problem is diminished if the support for the group is calculated as the ratio between the amounts of favourable and contradictory evidence, as proposed by Goloboff & Farris (2001). Relative support varies between 0 and 1; for example, if the RFD is 0.25, the amount of contradictory evidence is 75 % the amount of favourable evidence. RFD has been used in previous analyses of morphological data (Giribet & Boyer 2002), but has not yet been implemented in POY.

Molecular data and combined analyses of morphology and molecules were analysed using direct optimisation under parsimony (Wheeler 1996) in the computer program POY, version poy_test4 (Wheeler *et al*. 2002). Direct optimisation was executed in parallel on a Linux cluster of 28 nodes at 1 GHz each at Harvard University (darwin.oeb.harvard.edu). Each analysis consisted of 100 random addition replicates with spr and tbr branch swapping, each replicate executed in a node. Analyses were performed for 12 analytical parameters [as in our previous study (Edgecombe *et al*. 2002)] varying the gap:change ratio and the transversion:transition ratio. Parsimony jackknife (Farris et al. 1996; Farris 1997) values have been calculated for the molecular and the combined analyses with POY, using 1000 random addition replicates and 36 % character deletion. For more details on the analytical procedures we refer readers to our previous studies (Giribet *et al*. 2001; Edgecombe *et al*. 2002).

Presentation of phylogenetic hypotheses

As in previous studies on chilopod phylogeny (Edgecombe *et al*. 1999 2002; Edgecombe & Giribet 2002 2003), we explore the data by evaluating hypotheses under

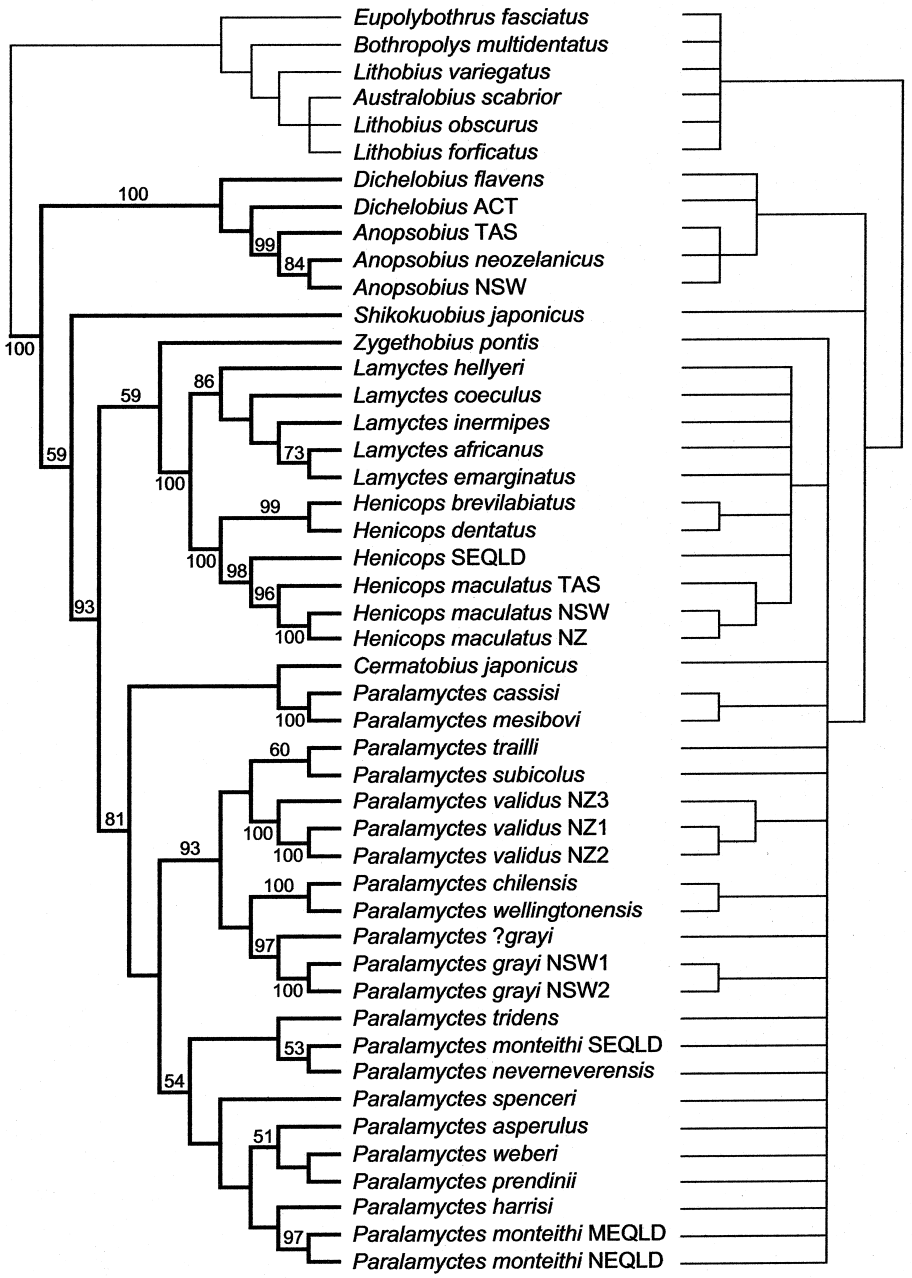

Fig. 2. Cladograms based on the combined analysis of all molecular data. Cladogram at left is the single tree at 7174 steps obtained for the most congruent parameter set (111); cladogram at right is strict consensus for all 12 parameter sets. Numbers on branches indicate jackknife frequencies.

multiple optimisation parameter sets (sensitivity analysis *sensu* Wheeler 1995) and identify the combined analysis tree for the parameter set that minimises overall incongruence among all partitions, as measured by the Incongruence Length Difference (ILD), as our working hypothesis. This 'best corroborated' tree provides a hypothesis that serves as a basis for interpreting evolutionary patterns. Support measures on the branches of that tree provide some extra information on top of the pattern recovered, this being strictly equivalent to what most systematists present in their studies. The strict consensus of all the hypotheses obtained under all the explored analytical parameters is also presented to report the strictest test of nodal stability. Given the severity of these tests, poor resolution in the consensus of all parameters should not be misconstrued as indicating poor resolution in the data. The strict consensus of all analysed parameters indicates nodes that are especially stable and parameter-independent, such nodes being excellent candidates for taxonomic propositions even though in certain cases they may present low nodal support values. Unresolved nodes in a strict consensus can originate in many ways, including rampant conflict among trees under different analytical parameters, the presence of a single unstable taxon, or by a single contradictory hypothesis under a suboptimal parameter set. To distinguish between these alternatives, detailed exploration of each hypothesis becomes a necessity. Some of the unstable taxonomic relationships are presented via graphic plots (Fig. 4) where a black square represents monophyly and a white square non-monophyly. The analytical parameter sets explored are represented in two axes, one for the gap:change ration and another for the transversion:transition ratio.

RESULTS

Morphological data

Analysis of the data in Table 2 finds 10 000 shortest cladograms of 134 steps (CI = 0.56; RI = 0.86) (10 000 was set as the upper limit for trees to save). The strict consensus of these 10 000 trees is shown in Figure 1. Analysis of the same data under a driven search (Goloboff 2002) executed in TNT, making a consensus twice every five hits to minimum length, results in a stable consensus identical to that presented in Figure 1, indicating that no extra nodes may be collapsed if a buffer limit higher than 10 000 were specified. The strict consensus (Fig. 1) shows little basal resolution, with neither Henicopinae nor Henicopini resolved in all minimal length cladograms. Ambiguity in the Henicopini involves some trees in which Anopsobiinae is allied to a *Lamyctes-Henicops* Group, as well as variable patterns of inter-relationship between the subgenera of *Paralamyctes*, and particularly labile relationships within *P*. (*Paralamyctes*). That subgenus (*sensu* Edgecombe 2001; Edgecombe *et al*. 2002) is not always monophyletic, and poorer resolution compared to a previous morphological analysis (Edgecombe 2003b) is produced by addition of South African members, which are labile based on the morphological data alone. *Shikokuobius* is strongly supported as sister to gondwanan Anopsobiinae (i.e., a clade uniting *Dichelobius* and *Anopsobius*) (Bremer support >10; RFD 1.0). Zygethobiini is monophyletic (Bremer support 2; RFD 0.33); though usually resolved as sister group of Henicopini, in some cladograms it is allied to *Paralamyctes*. The *Lamyctes-Henicops* Group is retrieved, albeit with weak support (Bremer support 2; RFD 0.36). *Paralamyctes sensu* Edgecombe (2001) is monophyletic in most minimal length cladograms, but finds some conflict in the variable position of Zygethobiini.

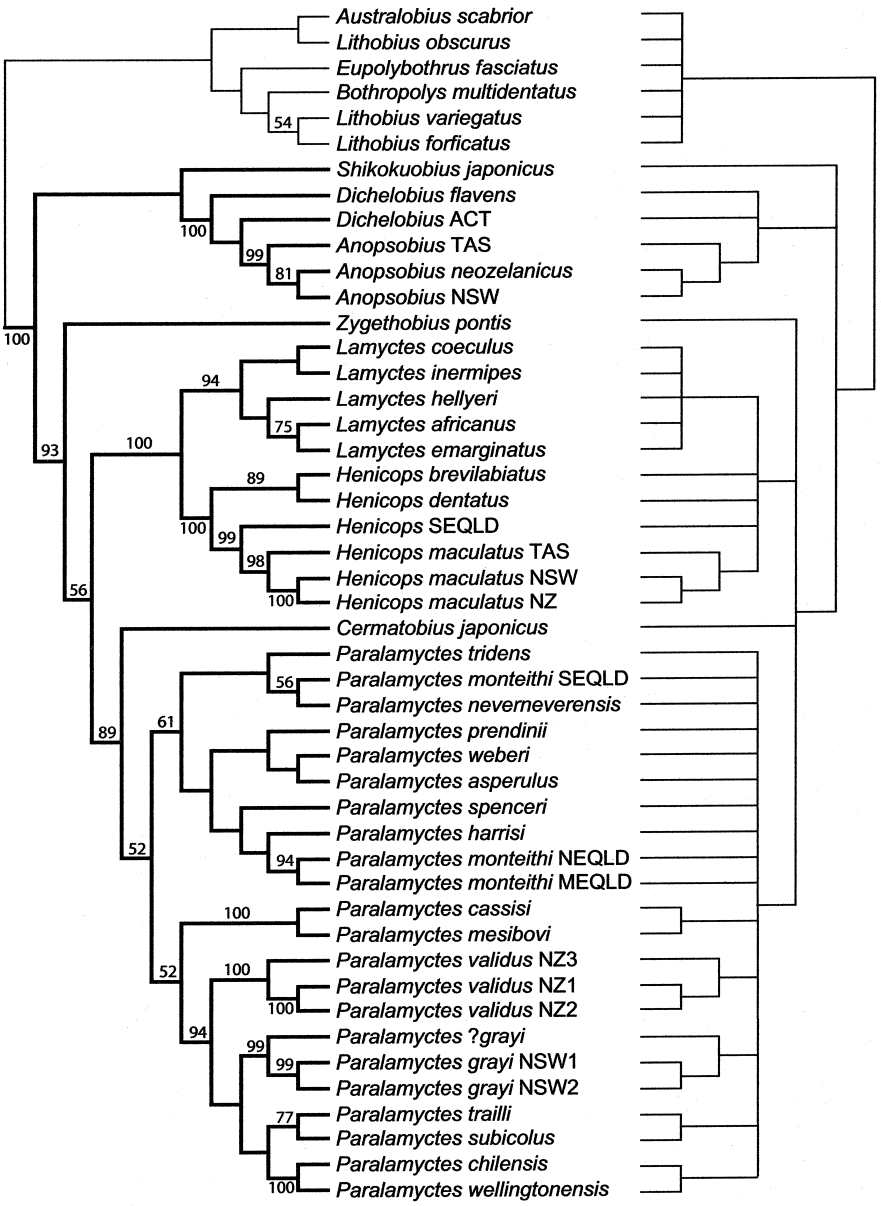

Fig. 3. Cladograms based on the combined analysis of all data (morphological + molecular). Cladogram at left is the single shortest tree of 7343 steps obtained for the most congruent parameter set (111); cladogram at right is strict consensus for all 12 parameters. Numbers on branches indicate jackknife frequencies.

Molecular data

Figure 2 (left cladogram) shows the shortest cladogram of 7174 steps for combined molecular data for the parameter set (111) that minimises incongruence between all data partitions. This tree length was obtained after tree fusing (Goloboff 1999), and not through regular random addition replicate searches with SPR and TBR. A majority of the resolved nodes in Henicopidae based on the molecular data (Fig. 2, cladogram at left) are compatible with the morphological cladograms, i.e. the nodes are generally present among the morphological cladograms. In particular, nodes in the molecular cladogram that withstand all 12 parameter sets (Fig. 2, cladogram at right) are also resolved in or compatible with the morphological cladogram, except for the node uniting *Henicops dentatus* and *H. brevilabiatus*. In other words, incongruence between the molecular and morphological data is mostly confined to groups that are parameter-sensitive. For higher-level relationships, noteworthy cases of congruence are the *Lamyctes-Henicops* Group and a clade composed of *Dichelobius* and *Anopsobius*, which are retrieved for all molecular parameter sets, have a 100 % jackknife frequency for parameter set 111, and are also resolved by all morphological cladograms.

In general, cladograms from single markers are unstable to parameter set variation, with few nodes other than grouped populations of single species being stable for all 12 explored parameters for individual markers. The *Lamyctes-Henicops* Group and *Dichelobius* + *Anopsobius* are stable to parameter variation for the 16S rRNA partition. Even for a single parameter set (e.g. 111, which minimises incongruence between the five genes and morphology; see below), the strict consensus of the trees for some markers is largely unresolved (trees not shown).

Combined morphological and molecular data

The parameter set that minimises incongruence between the five molecular markers and morphology is 111, for which all transformations are equally weighted (ILD 0.0301; see Table 3 for comparison of ILDs for each parameter set). This parameter set yielded a single tree at 7343 steps (Fig. 3), and was hit twice out of 100 replicates. Tree fusing did not improve the length of the tree nor find any other trees of the same length. The minimal ILD combined cladogram for the ingroup, Henicopidae, (Fig. 3, left cladogram) is largely congruent with the molecular cladogram for the same parameter set (Fig. 2). Though relatively few nodes withstand all explored parameters (Fig. 3, right cladogram), some of those that do are major clades, such as Henicopinae, the *Lamyctes-Henicops* Group, and *Paralamyces*. In adddition, several other groups are represented across most of parameter space [see Fig. 4; e.g. see plots for *Shikokuobius* + gondwanan Anopsobiinae, *P.* (*Paralamyctes*), *P.* (*Thingathinga*), *P.* (*Haasiella*) + *P.* (*Thingathinga*)].

For the nodes in the molecular-only cladogram (Fig. 2, left) that conflict with the morphology-only cladogram (Fig. 1), in most instances the combined analysis is resolved in favour of the molecular cladogram. An example is provided by the morphological grouping of Chilean *Paralamyctes* species with the Australian subgenus *Nothofagobius*, versus the molecular (and combined) grouping of these species with the Australasian subgenera *Haasiella* and *Thingathinga*. The morphological grouping has a Bremer support of 3 and jackknife frequency of only 42 % whereas the molecular grouping of the Chilean species with *P.* (*Thingathinga*) and *P.* (*Haasiella*) has a jackknife frequency of 93/94 % for the molecular and combined analyses, respectively. However, in the

case of *Shikokuobius*, in which a morphological alliance with Anopsobiinae has strong support (Bremer support >10), the combined analysis is resolved in favour of morphology.

DISCUSSION

Relative contribution of the morphological and molecular data

As discussed above, the molecular tree and the combined tree for parameter set 111 are largely congruent. This congruence need not be construed as 'swamping' of the morphological character set by the larger sequence dataset, because a majority of nodes

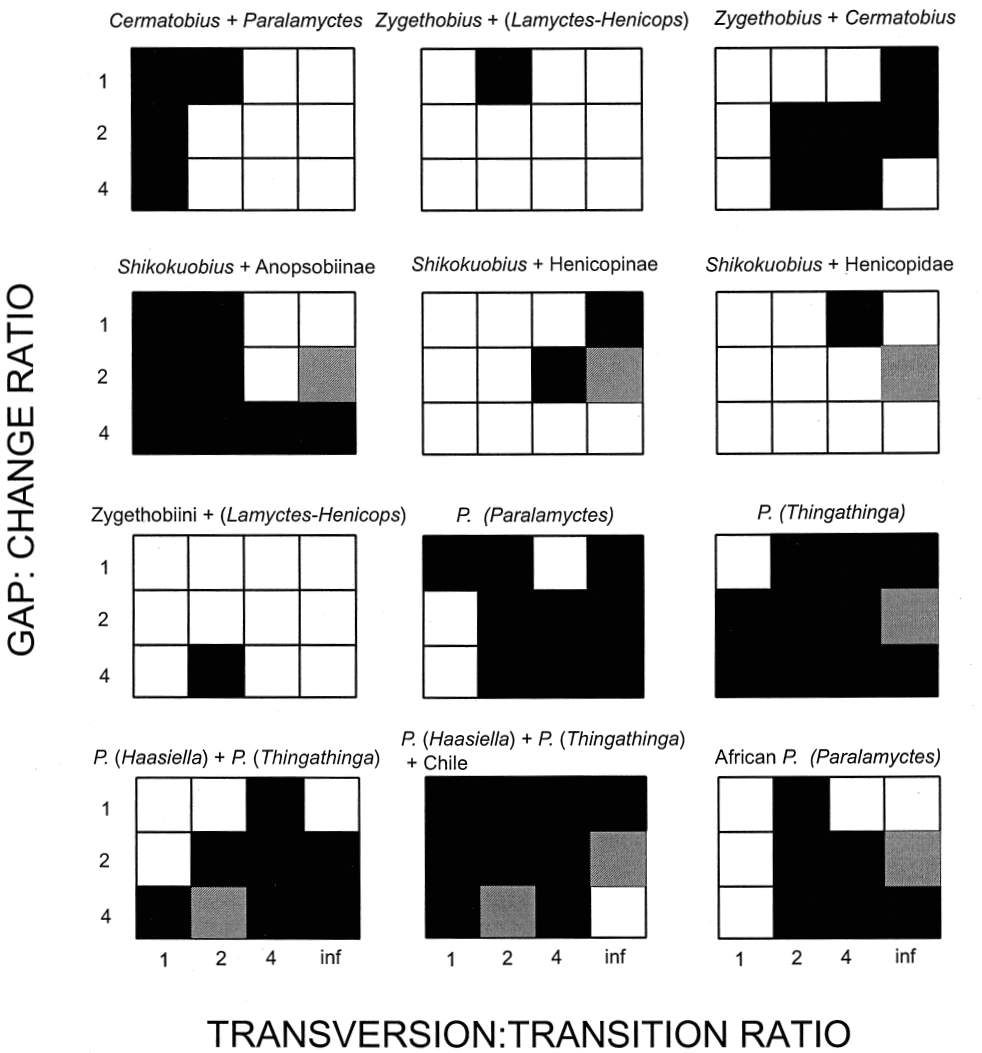

Fig. 4. Graphic plots of sensitivity analyses. Black square = monophyly of indicated clade under gap cost and transversion:transition ratio shown along the axes; grey square = monophyly in some minimal length cladograms; white square = non-monophyly.

in the combined analysis are also present among the large number of trees from the morphological data. Also, in some cases the combined analysis favours the morphological resolution, e.g. *Shikokuobius* as an anopsobiine rather than a basal henicopine or basal henicopid. The morphological data make a positive contribution to most nodes in the combined analysis.

Where the morphological data make a more obvious contribution is seen with respect to clade stability, using the strict consensus of all 12 parameter set as the most severe test of stability. Inclusion of the morphological data increases resolution in the consensus of all the parameters (16 resolved nodes within Henicopidae for combined analysis versus 12 for the molecular analyses). Though this difference may seem quantitatively underwhelming, the extra nodes contributed by morphology include some fundamental groupings, such as monophyly of *Lamyctes*, *Paralamyctes*, and *P.* (*Haasiella*).

Support for major clades

***Shikokuobius* + Gondwanan Anopsobiinae -** A clade composed of the gondwanan Anopsobiinae, here represented by *Dichelobius* and *Anopsobius*, is stable and strongly supported. This grouping is retrieved with morphology alone (Fig. 1), combined molecular data for all 12 parameter sets (Fig. 2), all data for all parameter sets (Fig. 3), under the optimal (111) parameter set for the 18S and 12S partitions, and for all parameters for the 16S partition. The jackknife frequency for this clade is 100 % for the molecular and combined analyses. Unambiguous morphological synapomorphies are an elongate median furrow in the head shield (character 8), coxal pores restricted to legs 14 and 15 (character 34), an extended spur-bearing process on the first article of the female gonopod (character 46), and indistinct scutes on the proximodorsal surface of the main pretarsal claw (character 58).

The sister group relationships of the gondwanan Anopsobiinae are more contentious. The morphological data strongly favour *Shikokuobius* as sister group of gondwanan Anopsobiinae (RFD 1.00). Unambiguous apomorphies of Anopsobiinae (including *Shikokuobius*) in Fig. 3 are rounded tergite margins (character 17), a transverse margin of tergite 8 (character 19), the lobate coxal process on leg 15 (character 32), the single ventral spur on the prefemur of leg 15 (character 33), undivided tarsi on legs 1–12 (character 38), and the tuberculate accessory denticles on the mandibular teeth (character 51). With delayed transformation, the group is also supported by the fringe of branching bristles on the mandible terminating at the aciculae (character 23) and the ventral bristles having a wide base (character 24). The 18S and 12S partitions, however, instead resolve *Shikokuobius* as sister to Henicopinae or sister to all other Henicopidae, respectively, for parameter set 111. These are the alternative placements for combined molecular data (Fig. 2), with *Shikokuobius* + Henicopinae being favoured in 10 of 12 parameter sets for the molecular data. A sister group relationship between *Shikokuobius* and gondwanan anopsobiines is favoured by combination of all data (Fig. 3), being present in 8 of 12 explored parameters for the combined dataset. Suboptimal resolutions that place *Shikokuobius* as sister to Henicopinae or Henicopidae (Fig. 4) reflect the contribution of the 18S and 12S partitions. Because most combined analyses, including the most congruent hypothesis and the nearest suboptimal ones (e.g. parameter sets 211 and 121), resolve *Shikokuobius* as a basal anopsobiine, this is considered to be a reasonably stable hypothesis.

Zygethobiini - Previous analysis (Edgecombe *et al*. 2002) lacked molecular data for nearctic Zygethobiini. The current dataset incorporates sequences for four genes for the eastern North American *Zygethobius pontis* together with four genes for the Japanese *Cermatobius japonicus*. The single morphological character classically (Chamberlin 1912; Attems 1914, 1928) used to distinguish Zygethobiini from Henicopini (lack of spiracles on the first pedigerous segment: character 20) is a symplesiomorphy. Additional morphological support for a zygethobiine clade (Fig. 1) is all based on homoplastic characters, also occurring within Henicopini, and some morphological apomorphies are confined to *Paralamyctes* and *Cermatobius* but not shared by *Zygethobius* (Edgecombe *et al*. 2002: 50–51).

The least incongruent molecular (Fig. 2) and combined (Fig. 3) cladograms both resolve Zygethobiini as a polyphyletic group: *Zygethobius* is sister to all other Henicopinae for combined data (sister to *Lamyctes* + *Henicops* for the molecular data), whereas *Cermatobius* nests within Henicopini. A sister group relationship between *Zygethobius* and *Cermatobius* (i.e. monophyly of Zygethobiini) is resolved in six of 12 parameter sets for the combined data, though these are all suboptimal with respect to ILD and include the more extreme parameters. Most of the remaining six parameter sets (minimal ILD and the immediately suboptimal parameters, including 211 and 121) favour *Cermatobius* being more closely related to Henicopini than is *Zygethobius*. Characters shared by *Zygethobius* and *Cermatobius* (subquadrate posterior emargination of tergite 7: character 18; coxal pore row in a deep cuticular fold: character 35) map onto Fig. 3 as convergences. Thus, though the present data favour non-monophyly of Zygethobiini using partition congruence as an optimality criterion, the resolution of a zygethobiine clade in many analyses indicates that the group's status remains an open question.

***Lamyctes-Henicops* Group -** As found in previous analysis (Edgecombe *et al*. 2002), monophyly of a clade that includes *Lamyctes* and *Henicops* is one of the most clearcut results in henicopid systematics. Morphological data suggest that *Lamyctopristus* Attems, 1928, and *Analamyctes* Chamberlin, 1955, also belong to this clade (Edgecombe 2003b), but this remains untested with molecular data.

The *Lamyctes-Henicops* Group is monophyletic under the following tests: morphology alone; minimal ILD parameter set for 18S rRNA; all parameter sets for 16S rRNA; combined molecular data (stable for all 12 parameter sets; 100 % jackknife frequency for the minimal ILD parameters); combined morphological and molecular data (stable for all 12 parameter sets; 100 % jackknife frequency for the minimal ILD parameters). The resolution of this clade from separate data partitions and its stability and strength of support in a simultaneous analysis regime make it an ideal candidate for formal taxonomic recognition. The group is identified by the intercalation of pairs of short antennal articles between groups of longer articles (character 4), an abrupt transition between plumose bristles and rows of scale-like bristles along the mandibular gnathal edge (character 25), and several small insertions plus a large insertion in the 18S rRNA sequence (Edgecombe *et al*. 1999: table 4).

The internal resolution of the *Lamyctes-Henicops* Group has a few stable groupings. In the combined analysis, all explored parameters retrieve the monophyly of *Lamyctes* (Fig. 3, right cladogram), and all but one resolve the monophyly of *Henicops* if *H. brevilabiatus* is assigned to the genus. *Lamyctes* is defined morphologically by a tooth-

like pseudoporodont (character 13) and flattened, multifurcating scales in the mandibular accessory denticle field (character 51). However, relationships among members of the *Lamyctes* group are unstable (see Edgecombe & Giribet 2003 for cladograms based on individual molecular markers). *Lamyctes coeculus* (type species of *Lamyctinus* Silvestri, 1909) is sister to other congeners in only one parameter set for the combined data. The combined data, which generally nest *L. coeculus* within *Lamyctes*, lead us to classify *Lamyctinus* as a synonym of *Lamyctes*, despite the distinctive antennal segmentation and leg numbers in the first larval stage of *L. coeculus* (Andersson 1979).

***Paralamyctes* -** The gondwanan genus *Paralamyctes* Pocock, 1901, as delimited by Edgecombe (2001 2003*b*) is ambiguous for morphological data alone (Fig. 1), although

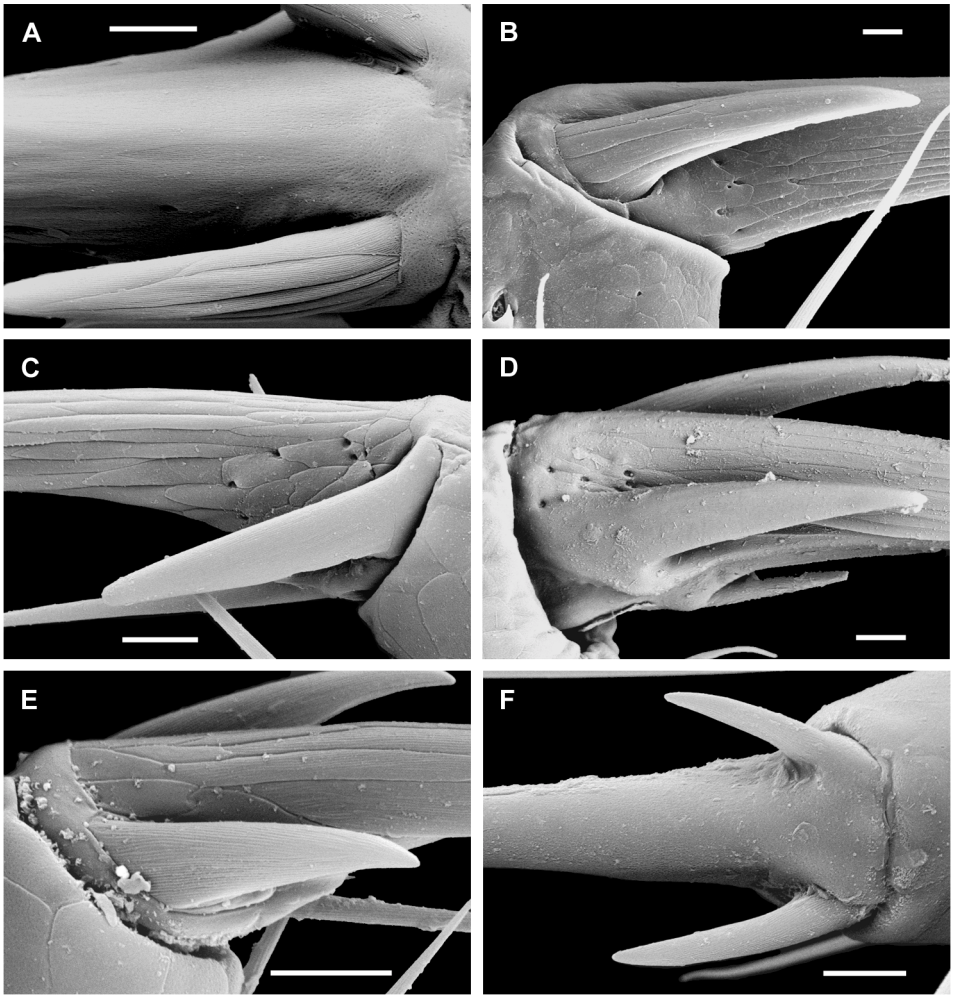

Fig. 5. Details of the pretarsus of Henicopidae, showing characters 57 and 58 in Appendix 1. A. *Paralamyctes* (*Thingathinga*) *grayi*, dorsal view. B. *Paralamyctes* (*Thingathinga*) *validus*, anterior view. C. *Paralamyctes* (*Haasiella*) *trailli*, anterior view. D. *Cermatobius japonicus*, posterior view. E. *Lamyctes emarginatus*, anterior view. F. *Anopsobius neozelanicus*, dorsal view. All scales 10 µm.

it is monophyletic in most of the shortest morphological cladograms. For the minimal ILD parameter set for the combined molecular analysis (Fig. 2), *Paralamyctes* is paraphyletic. Its monophyly is violated by *Cermatobius* falling inside *Paralamyctes*, specifically allying with the Australian subgenus *P*. (*Nothofagobius*). However, this paraphyletic resolution of *Paralamyctes* is highly dependent on specific analytical parameters, and is in fact found for no parameter set other than 111. All other explored parameters retrieve a monophyletic *Paralamyctes*, as is the case for all parameters when the morphological data are included (Fig. 3, right cladogram). The behaviour of *Cermatobius* (which allies with *Paralamyctes* under some parameter sets but is sister group to *Zygethobius* under most others) can perhaps be attributed to the aberrant (highly autapomorphic, with numerous small insertions) 18S rRNA partial sequence for *Zygethobius*.

Groups within *Paralamyctes* - The nominate subgenus *P*. (*Paralamyctes*), is identified by a unique structure of its mandibular aciculae (Edgecombe 2001; Edgecombe *et al*. 2002), though the species sharing the diagnostic series of pinnules along the dorsal side of each acicula (character 21) do not unite in all minimal length cladograms based on morphology alone (Fig. 1). However, *P*. (*Paralamyctes*) is retrieved by combined molecular data for the most congruent parameter set (Fig. 2, left cladogram), as well as in all but one of the 11 suboptimal parameter sets, and is retrieved in the optimal parameter set (111) by both 18S and 16S rRNA. For the combined morphological and molecular data, it is found across three-quarters of the explored parameters [Fig. 4, *P*. (*Paralamyctes*) plot], including the most congruent ones (Fig. 3, left cladogram) with a jackknife frequency of 61 %.

For simultaneous analysis (Fig. 3, left cladogram), the other large clade within *Paralamyctes* groups species of *P*. (*Haasiella*) within *P*. (*Thingathinga*), as the latter was delimited morphologically (Fig. 1). As discussed above, a pair of species from Chile, *P. chilensis* and *P. wellingtonensis*, are also nested within the morphologically-delimited *P*. (*Thingathinga*). However, the apparent paraphyly of *P*. (*Thingathinga*) in the optimal cladogram (Fig. 3, left cladogram) is unique to this one parameter set; in ten parameter sets the morphologically-delimited subgenus is monophyletic (as it is in some of the cladograms for the remaining parameter set) [see Fig. 4: *P*. (*Thingathinga*) plot]. Monophyly of *P*. (*Thingathinga*) is enhanced by two new characters of the pretarsus (characters 57–58 in Appendix 1): strong scutes on the accessory claws, and indistinct scutes on the dorsoproximal surface of the main claw (Fig. 5A, B). A group composed of the Australian and New Zealand *P*. (*Thingathinga*) and *P*. (*Haasiella*) and the Chilean clade, is represented in 9 of 12 parameter sets for combined analysis (Fig. 4), only missing in one extreme parameter set (and variably present in two others), and is accordingly regarded as a stable grouping.

The grouping of the two morphologically similar Australian species of *P*. (*Nothofagobius*), *P. cassisi* and *P. mesibovi*, is strongly supported by molecular data as well (jackknife frequency 100 %). Because Chilean species formerly assigned to *P*. (*Nothofagobius*) based on morphological similarities (Edgecombe 2001) are now robustly allied with *P*. (*Thingathinga*) and *P*. (*Haasiella*), *P*. (*Nothofagobius*) is restricted to its two Australian members.

The inter-relationships of the three major clades *P*. (*Paralamyctes*), *P*. (*Nothofagobius*) and *P*. (*Thingathinga*) + *P*. (*Haasiella*) are unstable and rather weakly supported. The

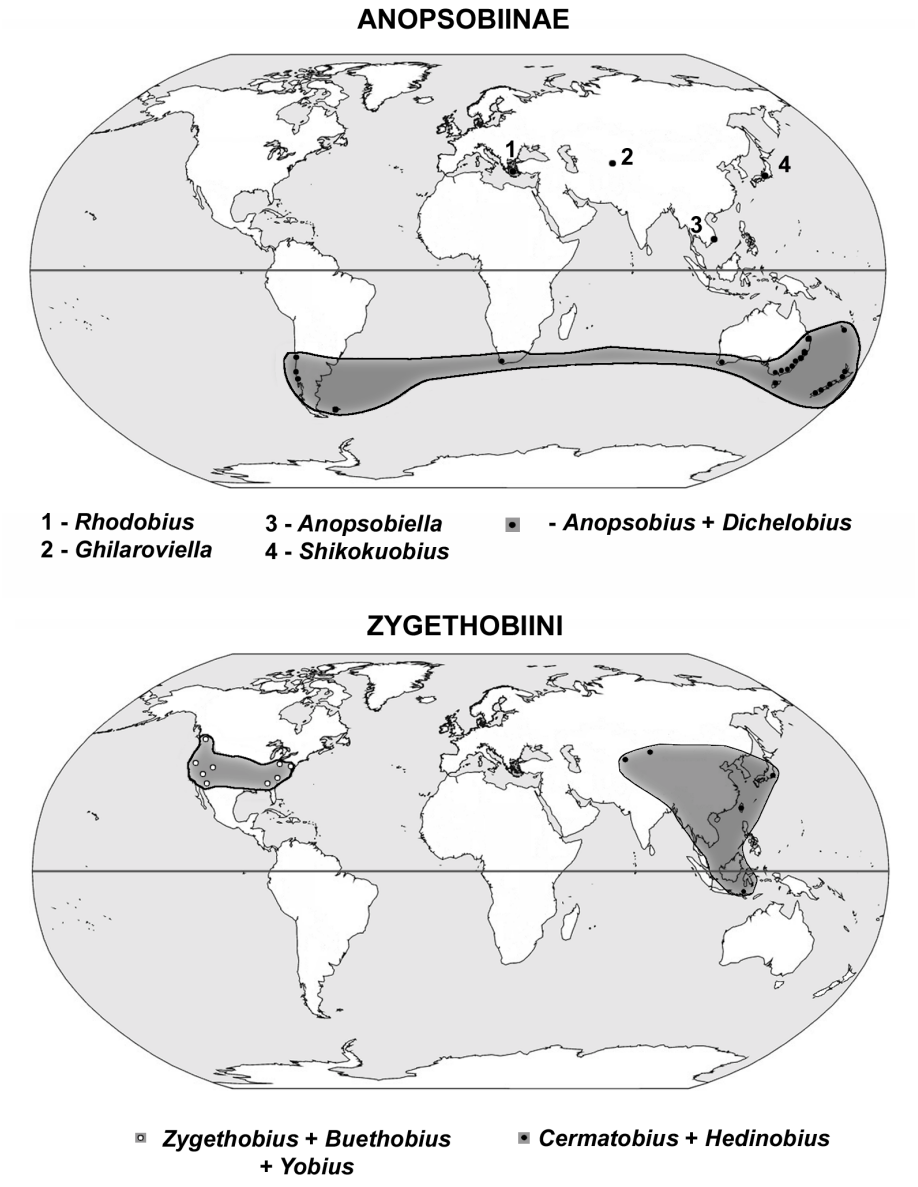

Fig. 6. Distributions of Anopsobiinae and Zygethobiini.

combined analyses for the two lowest ILD parameter sets, 111 and 211, favour a sister group relationship between *P*. (*Nothofagobius*) and *P*. (*Thingathinga*) + *P*. (*Haasiella*). Morphological characters that optimise as synapomorphies at this node are simple aciculae (character 22) and distal spinose projections on the tibia of leg 15 (character 37, state 4), but both of these are forced to reverse within the group, and the jackknife frequency for combined data is only 52 % for parameter set 111. Of the alternative resolutions, *P*. (*Paralamyctes*) is sister to *P*. (*Thingathinga*) + *P*. (*Haasiella*) for five parameter sets, as well as for the minimal ILD parameter set for the molecular data (Fig. 2, left cladogram).

Classification

The discussion above indicates support for the assignment of *Shikokuobius* to Anopsobiinae. Other Northern Hemisphere taxa with coxal pores on legs 12–15, *Rhodobius* Silvestri, 1933, and *Ghilaroviella* Zalesskaja, 1975, are also likely basal anopsobiines. The monophyly of Henicopinae can be regarded as well supported, especially given that the group is stable for all explored parameters for combined analysis (Fig. 3, right cladogram). Apomorphies for Henicopinae in Fig. 3 (left cladogram) are the lack of a porodont (character 13) and merger of the coxal process and telopod on the first maxilla (character 30). However, the status of Zygethobiini and Henicopini has not been settled. The most congruent molecular and combined analyses reject Zygethobiini, with *Cermatobius* possibly being a member of the Henicopini, sister to *Paralamyctes* under several parameter sets. That resolution optimises shared morphological characters of *Cermatobius* and *Paralamyctes*, such as the elongate median furrow in the head shield (Edgecombe *et al*. 2002, fig. 1B C), an elongate pretarsal section of the maxillipede tarsungulum (character 14), and a large, bell-shaped first maxillary sternite (character 29: see Edgecombe *et al*. 2002, fig. 8C–E) as synapomorphies. Henicopini as traditionally defined (Attems 1928) by the presence of a spiracle on the first pedigerous segment is monophyletic under six parameter sets, but contradicted in six others.

The two fundamental groupings within the traditional Henicopini are the *Lamyctes-Henicops* Group, discussed above, and *Paralamyctes*. Both groups are present under all parameter sets for the combined data. A more conclusive result on the status of Zygethobiini is required before the higher level classification of Henicopini is revised (e.g. splitting the group into the *Lamyctes-Henicops* Group and a *Paralamyctes* or *Paralamyctes* + *Cermatobius* Group).

Biogeography

The persisting controversies in henicopid systematics (relationships of basal Anopsobiinae and the monophyly, paraphyly or polyphyly of Zygethobiini) involve groups with disjunct biogeographic distributions (Fig. 6). Basal anopsobiines such as *Shikokuobius japonicus* from Japan (and *Ghilaroviella valiachmedovi* from Tajikistan) are assigned to an otherwise mostly gondwanan group with members in southern South America, southern Africa, temperate and subtropical Australia, New Zealand and New Caledonia. Zygethobiini is a grouping of nearctic (*Zygethobius*, *Buethobius* and the possibly synonymous *Yobius*) and oriental (*Cermatobius*, *Hedinobius*) taxa separate from a predominantly southern temperate group (Henicopini). The fact that the relationships between gondwanan and non-gondwanan taxa and basal relationship within

subfamilies continue to be particularly difficult problems might be expected if the extant Northern Hemisphere taxa are relictual members of pangean groups pruned by geographic extinction. The non-monophyly of Zygethobiini in several parameter sets, which involves closest relationships between oriental members (*Cermatobius*) and exclusively gondwanan (*Paralamyctes*) or largely gondwanan (Henicopini) taxa, allows that the Nearctic-Oriental distribution of Zygethobiini (Fig. 6) may be a taxonomic artefact. Determining the biogeographic significance of Zygethobiini and its apparent trans-Pacific distribution requires a more conclusive answer on the group's monophyly.

Previous analysis of henicopid biogeography focused on geographic patterns in *Paralamyctes* (Edgecombe *et al*. 2002), in large part because this group has been most intensively sampled at the species and population levels throughout its geographic range (versus, as an example, *Lamyctes*, in which dozens of species from vast extents of the tropics and temperate realms have not yet been subjected to phylogenetic analysis). The larger taxonomic sample now available for *Paralamyctes*, especially the addition of previously unavailable molecular data for species from Madagascar, Chile and several more species from South Africa, warrants a reappraisal of geographic patterns in this genus.

The best estimate of species relationships for *Paralamyctes* is provided by the most congruent combined cladogram (Fig. 3, left cladogram). An area cladogram for *Paralamyctes* (Fig. 7) is based on this taxonomic cladogram. Areas of endemism for Australia are as specified previously (Edgecombe *et al*. 2002: fig. 17); New Zealand is treated as a single area because relevant species have largely sympatric, widespread distributions. The area 'Cape region' includes Table Mountain and the Knysna Forest (*sensu* Griswold 1991: Fig. 1) because the species in those areas are shared (*P. asperulus*, *P. weberi* and *P. spenceri* occurring in both). 'Eastern South Africa' refers to other parts of the distribution of *P. spenceri* and includes the Natal-Zululand Coast, Transkei-Natal Midlands, Natal Drakensberg and Transvaal Drakensberg areas of Griswold (1991).

As indicated in discussion above, some of the geographically-informative nodes in the area cladogram are based on phylogenetic hypotheses that are stable across much or all of parameter space (Fig. 4). Here we include: monophyly of a group of Cape region endemics; monophyly of the Australia-New Zealand-Patagonia group based on *P*. (*Thingathinga*) and *P*. (*Haasiella*); monophyly of the Australasian clade *P*. (*Haasiella*); monophyly of the Tasmanian-New South Wales clade *P*. (*Nothofagobius*). Less reliable are the nodes that split Australian species of *P*. (*Paralamyctes*), including the closer relationship between the southern African clade and a *harrisi* + *monteithi* (partim) group. *Paralamyctes monteithi* is instead monophyletic under five parameter sets (110, 121, 410, 411, 421), and united with *P. neverneverensis* in parameter sets 110, 121 and 411, a resolution that indicates monophyly of Australian occurrences of *P*. (*Paralamyctes*). In fact, 6 of 12 parameter sets include *P. neverneverensis*, *P. monteithi*, *P. tridens* and *P. harrisi*, with the South African species excluded, and six parameter sets unite the four South African species as a clade. Nine parameter sets support an alliance between species from Madagascar and New Zealand (*P. tridens* and *P. harrisi*, respectively). These examples demonstrate that biogeographic interpretations based on nodes in Fig. 7 that withstand few parameters, must be used cautiously.

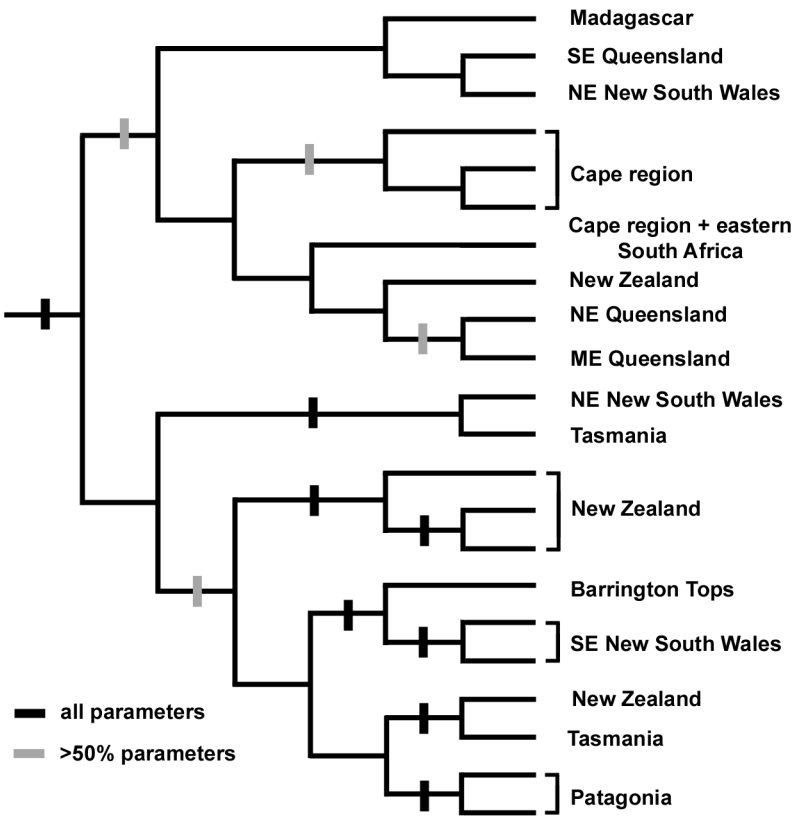

Fig. 7. Area cladogram for *Paralamyctes* based on relationships under most congruent parameters for combined morphological and molecular data (Fig. 3, left cladogram). Stable clades are indicated (present in at least six parameter sets for the combined data).

Considering only those nodes in Fig. 7 that are present in most parameter sets, the two main clades within *Paralamyctes* [= *P*. (*Haasiella*) + *P*. (*Thingathinga*) and *P*. (*Paralamyctes*)] have largely non-overlapping distributions. Sympatry between the two clades is confined to North Island, New Zealand, and middle eastern and northeastern Queensland [the relevant species of *P*. (*Haaasiella*), *P*. (*H*.) *cammooensis*, lacks molecular data and was not included in this analysis]. The stable components of the *P*. (*Haasiella*) + *P*. (*Thingathinga*) clade (Fig. 7) summarise as ((New Zealand + Tasmania)(Patagonia)(Barrington Tops + SE New South Wales)). The area relationships of NE New South Wales, Queensland, South Africa, Madagascar and New Zealand based on *P*. (*Paralamyctes*) are for the most part parameter sensitive, but the monophyly of the whole clade is quite stable (Fig. 4). Morphological data indicate that southern India [occurrence of *P*. (*P*.) *newtoni* Silvestri; Edgecombe (2001)] is also part of the distribution of *P*. (*Paralamyctes*). The alternative affinities for species from New Zealand (and north Queensland) may reflect geographic patterns of different ages that can be compared to geological models for gondwanan fragmentation (Lawver *et al*. 1992). For

example, the distribution involving Australia, New Zealand and Patagonia could involve the later connection between southern South America and East Gondwana (via Antarctica) compared to the older connection of these areas with West Gondwana [including Africa, Madagascar and India, all of which host species of *P*. (*Paralamyctes*)].

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TABLE 1.

Taxon sampling used in the analyses and molecular partitions used for every taxon. 18S (complete 18S rRNA); 28S (D3 region of the 28S rRNA); COI (750 bp fragment of the cytochrome *c* oxidase I gene); 16S (500 bp fragment of the 16S rRNA); 12S (400 bp fragment of the 12S rRNA); *P.* = *Paralamyctes*.

	18S rRNA	**28S rRNA**	**COI**	**16S rRNA**	**12S rRNA**
Lithobiidae					
Lithobiinae					
Australobius scabrior	AF173241	AF173272			
Lithobius variegatus rubriceps	AF000773	AF000780	AF334311	AY84071	
Lithobius obscurus	AF334271	AF334292		AF334333	AF334361
Lithobius forficatus	X90653-4	X90656	AJ270997	AJ270997	AJ270997
Ethopolyinae					
Bothropolys multidentatus	AF334272	AF334293	AF334334		
Eupolybothrus fasciatus	AY213718	AY3123737	AY214420	AY214365	AY212328
Henicopidae					
Anopsobiinae					
Shikokuobius japonicus	AY213719	AY213738	AY214366	AY212329	
Anopsobius sp. TAS	AF173247	AF173273	AF334312	AF334336	AF334363
Anopsobius neozelanicus	AF173248	AF173274	AF334313	AF334337	AF334364
Anopsobius sp. NSW	AF334273	AF334294		AF334335	AF334362
Dichelobius flavens	AY213720	AY213739	AY214421	AY214367	AY212330
Dichelobius sp. ACT	AY213721	AY213740	AY214422	AY214368	
Henicopinae					
Zygethobiini					
Cermatobius japonicus	AF334291		AF334332	AF334360	AF334377
Zygethobius pontis	AY213722-3	AY213741	AY214423	AY214369	
Henicopini					
Lamyctes inermipes	AY213726	AY213743	AY214425	AY214371	
Lamyctes africanus	AF334274	AF334295	AF334314	AY214373	
Lamyctes emarginatus	AF173244	AF173276	AF334338		

TABLE 1 (continued).

	18S rRNA	28S rRNA	COI	16S rRNA	12S rRNA
Lamyctes coeculus	AF334275	AF334296	AF334315	AF334339	
Lamyctes hellyeri	AY213736	AY213746	AY214428	AY214375	
Henicops dentatus	AY213724-5	AY213742	AY214424	AY214370	
Henicops maculatus NSW	AF173245	AF173275	AF334316	AF334340	
Henicops maculatus TAS	AF334276	AF334297	AF334317	AF334341	
Henicops maculatus NZ	AF334277	AF334298	AF334318	AF334342	
Henicops sp. SE QLD	AF334299	AF334319	AF334343		
Henicops brevilabiatus	AY213734	AY213744	AY214426	AY214372	
P. (*Nothofagobius*) *cassisi*	AY213733	AY213747	AY214429	AY214376	
P. (*Nothofagobius*) *mesibovi*	AF334284	AF334306	AF334325	AF334350	AF334369
P. (*Haasiella*) *trailli*	AF173246	AF173279	AF334326	AF334351	
P. (*Haasiella*) *subicolus*	AF334285	AF334307	AF334327	AF334352	AF334370
P. (*Thingathinga*) *validus* NZ1	AF334289	AF334310	AF334329	AF334357	AF334374
P. (*Thingathinga*) *validus* NZ2	AF334290	AF334330	AF334358	AF334375	
P. (*Thingathinga*) *validus* NZ3	AF173243	AF173278	AF334331	AF334359	AF334376
P. (*Thingathinga*) *grayi* NSW1	AF334287	AF334354			
P. (*Thingathinga*) *grayi* NSW2	AF173242	AF173277		AF334355	AF334372
P. (*Thingathinga*) *?grayi*	AF334288	AF334309	AF334328	AF334356	AF334373
P. chilensis	AY213731	AY213748	AY214430	AY214377	AY212331
P. wellingtonensis	AY213732	AY213749	AY214431	AY214378	AY212332
P. (*Paralamyctes*) *harrisi*	AF334278	AF334300	AF334320	AF334344	AF334365
P. (*Paralamyctes*) *monteithi* NE QLD	AF334279	AF334301	AF334345		
P. (*Paralamyctes*) *monteithi* ME QLD	AF334280	AF334302	AF334321	AF334346	
P. (*Paralamyctes*) *monteithi* SE QLD	AF334281	AF334303	AF334322	AF334347	AF334366
P. (*Paralamyctes*) *neverneverensis*	AF334283	AF334305	AF334324	AF334349	AF334368
P. (*Paralamyctes*) *weberi*	AF334282	AF334304	AF334323	AF334348	AF334367
P. (*Paralamyctes*) *asperulus*	AY213728	AY213750	AY214432	AY214379	AY212333
P. (*Paralamyctes*) *prendinii*	AY213729	AY213751	AY214433	AY214380	AY212334
P. (*Paralamyctes*) *spenceri*	AY213727	AY213752	AY214434	AY214381	AY212335
P. (*Paralamyctes*) *tridens*	AY213730	AY213753		AY214382	

TABLE 2.

Morphological character matrix. Characters 1–51 from Edgecombe (2003*b*); characters 52–58 described in Appendix 1. A = polymorphism: 0 + 1.

	1	**11**	**21**	**31**	**41**	**51**
Australobius scabrior	0-0000-000	7010000000	0000000000	002200-000	0101101000	01000-00
Lithobius variegatus rubriceps	0-0000-000	7011000000	0000000000	002200-000	0101000000	01000-00
Lithobius obscurus	0-0000-000	0011000000	0000000000	002200-000	0101001000	01000-00
Lithobius forficatus	0-0000-000	7011000000	0000000000	002200-000	0101001000	01000-00
Bothropolys multidentatus	0-0010-000	2011000000	0000000000	002200-000	0101001000	00010-00
Eupolybothrus fasciatus	0-0000-000	7011000100	0000000000	002200-000	0102000000	01010-00
Shikokuobius japonicus	—00010001	0010001010	0010010000	11120101-0	0000000000	20000000
Anopsobius neozelanicus	—10010101	2110001000	0010010000	11100111-0	0000010000	20000001
Anopsobius NSW	—10010101	2110001010	0010010000	11100111-0	0000010000	20000001
Anopsobius TAS	—10010101	2010001010	0010010000	11100111-0	0000010000	20000001
Dichelobius flavens	—00010101	2010001010	0010010000	11100101-0	0000010000	20100001
Dichelobius ACT	—10010101	2010001010	0010010000	11100101-0	0000010000	20100001
Cermatobius japonicus	1100010001	3001000100	0000010111	1002112??0	0000100000	00001000
Zygethobius pontis	1000010001	3000000100	0010010101	1003113000	0000000000	00000000
Lamyctes inermipes	1001010001	0020001001	0001000001	10020121-0	0000000000	10000000
Lamyctes africanus	1001010001	0020001001	0001000001	10020111-0	0010000000	10000000
Lamyctes emarginatus	1001010001	0020001001	0001000001	10020101-0	0000000000	10000000
Lamyctes coeculus	—00010001	0020001001	0001000001	10020101-0	00??000100	10000000
Lamyctes hellyeri	—01010001	0020001001	0001000001	00020111-0	00??000000	10000000
Henicops dentatus	1000010001	1000000101	0001000001	2002013011	1010000001	00001000
Henicops maculatus NSW	1001020001	1000000001	0001000001	2002013011	1010000001	00001000
Henicops maculatus TAS	1001020001	1000000001	0001000001	20020130A1	1010000001	00001000

TABLE 2 (continued).

	1	**11**	**21**	**31**	**41**	**51**
Henicops maculatus NZ	1001020001	1000000001	0001000001	2002013011	1010000001	00001000
Henicops SE QLD	1001020001	1000000001	0001000001	2002013011	0010000001	00001000
Henicops brevilabiatus	1001010001	3001101001	0001000001	20020121-0	0010000000	00000000
Paralamyctes (*N.*) *cassisi*	1000010101	4000010001	0100001011	1002014000	0000110000	00000000
Paralamyctes (*N.*) *mesibovi*	1000010101	4000010001	0100001011	1002014000	0000110000	00000000
Paralamyctes (*H.*) *trailli*	—00010101	6001000011	0000000011	10020121-0	0000000110	00000000
Paralamyctes (*H.*) *subicolus*	1100010101	5001000011	0000000011	10020131-0	0000000010	00000000
Paralamyctes (*T.*) *validus* NZ1	1000010111	5001000001	0100100011	1002114010	0000000000	00000011
Paralamyctes (*T.*) *validus* NZ2	1000010111	5001000001	0100100011	1002114010	0000000000	00000011
Paralamyctes (*T.*) *validus* NZ3	1000010111	5001000001	0100100011	1002114010	0000000000	00000011
Paralamyctes (*T.*) *grayi* NSW1	1100010111	5001000101	0100000011	1002113010	0000000000	00000011
Paralamyctes (*T.*) *grayi* NSW2	1100010111	5001000101	0100000011	1002113010	0000000000	00000011
Paralamyctes (*T.*) ?*grayi*	1100010111	5001000101	0100000011	1002014010	0000000000	00000011
Paralamyctes chilensis	1000010101	4000010001	0000000011	1002013000	0000010000	00000000
Paralamyctes wellingtonensis	1000010101	4000000001	0000000011	1002013000	0000010000	00000000
Paralamyctes (*P.*) *harrisi*	1000111111	3001100001	1000000111	1002013000	0000000000	00000000
Paralamyctes (*P.*) *monteithi* NE QLD	1000111111	3001100001	1000000111	1002013000	0000000000	00000100
Paralamyctes (*P.*) *monteithi* ME QLD	1000111111	3001100001	1000000111	1002013000	0000000000	00000100
Paralamyctes (*P.*) *monteithi* SE QLD	1000111111	3001100001	1000000111	1002013000	0000000000	00000000
Paralamyctes (*P.*) *neverneverensis*	1000010101	4000000001	1000000111	1002014000	0000000000	00000000
Paralamyctes (*P.*) *weberi*	1000010101	4001000001	1000000111	1002013000	0000000000	00000100
Paralamyctes (*P.*) *asperulus*	1000010101	4001000101	1000000111	1002012000	0000000000	00000100
Paralamyctes (*P.*) *prendinii*	1000010001	8001000001	1000000111	10?2012000	0000000000	0000?000
Paralamyctes (*P.*) *spenceri*	1000010101	4001000001	1000000111	1002012000	0000000000	00000000
Paralamyctes (*P.*) *tridens*	1000011101	3001000001	1000000111	1002012000	0000000000	00000000

TABLE 3.

Tree lengths for the individual data sets (18S: 18S rRNA; 28S: 28S rRNA; 16S: 16S rRNA; 12S: 12S rRNA; COI: cytochrome *c* oxidase I; MOR: morphology) and combined data sets (MOL: molecular [18S + 28S + 16S + 12S + COI]; TOT: combined [18S + 28S+ 16S + 12S + COI + mor]) at different parameter set values, and ILDs for the combined analyses of all data (ILD), at parameter (PAR) sets 110 to 441. Numbers in italics reflect the minimum incongruence among data sets as measured by ILD. PAR indicates ratio between gap-cost : transversion cost: transition cost (e.g. 110 indicates a gap: transversion ratio of 1, and a transversion: transition ratio of infinity, or gap cost = 1, transversion.

PAR	18S	28S	16S	12S	COI	MOR	MOL	TOT	ILD
110	504	68	1227	559	1055	134	3539	3703	0.04213
111	*1070*	*159*	*2270*	*1000*	*2489*	*134*	*7174*	*7343*	*0.03010*
121	1602	240	3556	1592	3607	268	10882	11209	0.03069
141	2634	392	6021	2728	5749	536	18041	18703	0.03438
210	621	89	1424	660	1055	268	4014	4334	0.05007
211	1210	188	2524	1119	2489	268	7715	8042	0.03034
221	1850	290	3999	1806	3607	536	11867	12513	0.03396
241	3123	488	6855	3137	5749	1072	19966	21223	0.03765
410	812	117	1708	822	1055	536	4764	5406	0.06585
411	1427	230	2833	1277	2489	536	8509	9149	0.03902
421	2278	376	4613	2107	3609	1072	13434	14698	0.04375
441	3970	656	8088	3739	5757	2144	23116	25590	0.04830

APPENDIX 1.

Notes on morphological characters.

Characters 1–51 in Table 2 use the character state descriptions of Edgecombe (2003*b*, Appendix), except for adding an additional state to each of characters 11 and 44 to incorporate variation in species newly added in the present study, as follows, along with seven new characters.

Character 11. Shape of maxillipede coxosternite: (8) wide, gently convex margin with shallow V (Edgecombe 2003*a*: fig. 2G).

Character 44. Segmentation of male gonopod: (2) single, elongated segment (Attems 1926: fig. 453).

Character 52. Lateral margin of head shield interrupted at anterior limit of marginal ridge: (0) not interrupted; (1) interrupted.

Lithobiidae coded here, except for *Bothropolys multidentatus*, have the lateral margin of the head interrupted (*sensu* Eason 1982). Henicopidae and *B. multidentatus* (Chamberlin 1925: pl. 1, fig. 1) have an uninterrupted margin.

Character 53. Spiracle on eighth pedigerous segment: (0) present; (1) absent.

All analysed species except *Dichelobius flavens* and *Dichelobius* sp. ACT have a spiracle on segment 8.

Character 54. Coxal pore arrangement: (0) in single file; (1) scattered pore field.

Scattered coxal pores (state 1) unite Ethopolyinae (here *Bothropolys* and *Eupolybothrus*). The ontogeny of *Bothropolys* shows a transformation from state 0, as in non-ethopolyine Lithobiidae and all Henicopidae, to state 1 (Chamberlin 1925: pl. 2, figs 4, 5).

Character 55. Distitarsus of leg 15 divided: (0) undivided (single tarsomere); (1) divided into two or more tarsomeres.

Character 56. Insertion of anterior pretarsal accessory claw: (0) dorsolaterally on main claw; (1) ventrolaterally on main claw.

Most henicopids have the anterior and posterior accessory claws originating dorsolaterally on the main claw (all species in Fig. 5). Some species of *Paralamyctes* (*Paralamyctes*) have the anterior accessory claw originating near the ventral margin of the main claw.

Character 57. Definition of scutes on pretarsal accessory claws: (0) absent or weak; (1) strong.

Species of *Paralamyctes* (*Thingathinga*) have scutes strongly delimited by sutures on both accessory claws (Fig. 5A, B), whereas other henicopids (Fig. 5C–F) either lack scutes or have them faintly defined. Lithobiomorph accessory claws are ornamented by fine ridges and grooves (Fig. 5A, E), regardless of whether or not scutes are defined.

Character 58. Definition of scutes on dorsoproximal part of main pretarsal claw: (0) distinct; (1) indistinct.

Most henicopids and lithobiids have distinct, often strong, sutures delimiting scutes on the dorsoproximal surface of the main claw (Figs 5C–E). In *Paralamyctes* (*Thingathinga*) (Fig. 5A) and in gondwanan Anopsobiinae (Fig. 5F) sutures and scutes are undefined in this region.

APPENDIX 2.

Voucher data for specimens used in molecular analyses. All other vouchers documented by Edgecombe *et al.* (2002: Appendix 2).

Eupolybothrus fasciatus (Newport, 1844)
Monte Fogliano (600 m), Viterbo, Lazio, Italy
23 March 2000; M. Zapparoli
MCZ DNA100281

Shikokuobius japonicus (Murakami, 1967)
Shizen-Kyoiku-en, Meguro-ku, Tokyo, Japan
23 August 2001; M. Takano
MCZ DNA100463

Dichelobius flavens Attems, 1911
34º58'S 116º53'E
Valley of the Giants Road, 600 m S Tree Top Walk, Walpole-Nornalup National Park, Western Australia
26 February 2001; G. D. Edgecombe and Z. Johanson
AM KS 77587, MCZ DNA100380

***Dichelobius* sp.** ACT
35º21'S 148º50'E
Brindabella Road, 1 km NE Piccadilly Circus, Australian Capital Territory
26 November 2000; G. D. Edgecombe and Z. Johanson
AM KS 77588, MCZ DNA100248

Zygethobius pontis Chamberlin, 1911
Buffalo Mountain Natural Area Preserve, W Martinsville, Floyd County, Virginia, USA
27 February 2001; R. Hoffman
MCZ DNA100359

Lamyctes hellyeri Edgecombe & Giribet, 2003
41º07'04"S 146º04'40"E
Penguin, Tasmania, Australia
7 August 2001; R. Mesibov
MCZ DNA100639

Lamyctes inermipes (Silvestri, 1897)
27º5'1.3"S 65º39'56.5"W
Road to Tafí del Valle, Tucumán Province, Argentina
16 September 2001; G. Giribet
MCZ DNA100478

Henicops brevilabiatus (Ribaut, 1923)
21º47'S 166º04'E
Mt Do summit, New Caledonia
27 November 2000; G. B. Monteith
MCZ DNA100381

Henicops dentatus Pocock, 1901
34º27'S 116º01'30"E
Karri Bush Walk, Pemberton Forest Park, Pemberton, Western Australia
24 February 2001; G. D. Edgecombe & Z. Johanson
AM KS 77589, MCZ DNA100378

Paralamyctes chilensis (Gervais in Walckenaer & Gervais, 1847)
Anticara, Parque Nacional Puyehue, Región de Los Lagos, Chile
30 December 2000; G. Hormiga
MCZ DNA100405

Paralamyctes wellingtonensis Edgecombe, 2003*c*
50º56'45"S 72º55'00"E
Near Refugio Chileno, Parque Nacional Torres del Paine,
Esperanza Province, Región de Magallanes, Chile
8 December 2000; J. Miller & I. Agnarsson
MCZ DNA100408

Paralamyctes* (*Nothofagobius*) *cassisi Edgecombe, 2001
29º28'S 152º21'E
Washpool Walk, Washpool National Park, New South Wales, Australia
26 February 2002; G. D. Edgecombe & Y.-y. Zhen
AM KS 77590, MCZ DNA100540

Paralamyctes* (*Paralamyctes*) *asperulus Silvestri, 1903
33º56'S 18º28'E
Newlands Forest, eastern slope of Table Mountain,
Cape Town, Western Cape Province, South Africa
9 April 2001; G. Giribet & L. Prendini
MCZ DNA100401

Paralamyctes* (*Paralamyctes*) *prendinii Edgecombe, 2003*a*
33º56'S 18º28'E
Newlands Forest, eastern slope of Table Mountain,
Cape Town, Western Cape Province, South Africa
9 April 2001; G. Giribet & L. Prendini
MCZ DNA100399

Paralamyctes* (*Paralamyctes*) *spenceri Pocock, 1901
28º44'39"S 31º08'15"E
Nkandhla Forest, Kwazulu-Natal, South Africa
4 April 2001; G. Giribet & L. Prendini
MCZ DNA100402

Paralamyctes* (*Paralamyctes*) *tridens Lawrence, 1960
18º28'24"S 47º57'36"E
3 km NE Andranomay, Antananarivo Province, Madagascar
5 December 2000; C. Griswold *et al*.
CAS-ENT-BLF2545, MCZ DNA100539