Phylogeny of Henicopidae (Chilopoda: Lithobiomorpha): a combined analysis of morphology and five molecular loci

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Abstract. Relationships in Henicopidae, the dominant southern temperate clade of Lithobiomorpha, are appraised based on parsimony analysis of forty-nine morphological characters and sequence data from five loci (nuclear ribosomal RNAs 18S and 28S, mitochondrial ribosomal RNAs 12S and 16S, protein-coding mitochondrial cytochrome c oxidase I). A combined analysis of these data used direct character optimization, and tested stability of hypotheses through parameter-sensitivity analysis. The morphology dataset highlighted the mandibles as a source of new characters. Morphology, as well as the most congruent parameters for the sequence data and combined analysis, resolved Zygethobiini within Henicopini. Groups retrieved by combined analysis of the sequences and combination with morphology for all parameters include Anopsobiinae/Henicopinae, Lamyctes + Lamyctinus + Henicops, Paralamyctes (Paralamyctes), and a clade that groups the southeastern Australian/New Zealand Paralamyctes (Haasiella) and P. (Thingathinga). Paralamyctes (including Haasiella) is a Gondwanan clade in the most congruent cladograms based on all molecular data and combination with morphological data. Biogeographic analysis of subtrees for Paralamyctes resolved the interrelationships of Gondwana as (Patagonia ((New South Wales + southeastern Queensland) ((Tasmania) (southern Africa + India) (New Zealand + north Queensland))).

Introduction

The chilopod family Henicopidae is distributed on all continents except Antarctica, but is most characteristic of the southern temperate regions, where it largely replaces Lithobiidae (Eason, 1992). The last comprehensive treatment of henicopid systematics was by Attems (1928) in his monograph on the South African Myriapoda. Generic concepts in Henicopidae have changed little since Attems’ revision. The monophyly of some of the larger and more geographically widespread genera of Henicopidae, such as Lamyctes Meinert, 1868, and Paralamyctes Pocock, 1901, as conceived by Attems (1928) and subsequent workers (Archey, 1937; Lawrence, 1955, 1960), is not well established. Attems’s (1928) key to henicopid genera employed few characters that could be regarded as convincing synapomorphies, and very little discussion of relationships within Henicopidae has been presented. In the present work, we attempt to redress this situation by appraising morphological and molecular sequence evidence for henicopid phylogeny. The molecular dataset employed in this study consists of five loci and totals as much as 3500 bp per taxon. These data are analysed in concert with morphological homologies, those employed by previous workers and many which are newly documented by electron microscopy.

This study emphasizes Henicopidae in the faunas of Australia and New Zealand. Whereas New Zealand henicopid systematics was put on a sound footing by Archey (1937), the fauna of Australia has been nearly ignored. However, recent work (Edgecombe, 2001) has initiated a systematic appraisal of Australian Henicopidae. Biogeographic patterns within Paralamyctes are of particular interest because this group has representatives on each of the major fragments of Gondwana (southern South America, southern Africa, Madagascar, India, New Zealand and Australia). A phylogeny for Paralamyctes that includes detailed biogeographic patterns...
for Australasian species, undertaken in the context of a cladistic analysis of Henicopidae, provides a basis for appraising Gondwanan area relationships.

Materials and methods

Terminal taxa

The modern classification of Henicopidae (Eason, 1992) remains that advanced by Attems (1928). In this scheme, Henicopidae is composed of two subfamilies, Anopsobiinae and Henicopinae, although some workers (Chamberlin, 1962; Hoffman, 1982) have advocated separate familial status for Anopsobiinae (see Murakami, 1967; Table 1 for a comparison of classificatory schemes). Henicopinae consists of tribes Henicopini and Zygethobiini. The monophyly of Henicopidae was challenged by Prunescu (1996), who put forward two characters of the male genital system for which Anopsobiinae is interpreted as sharing a character state with Scutigeromorpha (i.e. a sympleiomorphy), whereas Henicopinae is thought to share the derived homologue with Lithobiidae and Epimorpha. Edgecombe et al. (1999) included Prunescu’s (1996) hypotheses for these two characters in their analysis of chilopod phylogeny, but concluded that a larger body of molecular and morphological evidence supported Lithobiomorpha and Henicopidae (= Anopsobiinae + Henicopinae) as monophyletic groups. In this study, Lithobiidae was considered to be sister group of Henicopinae (Edgecombe et al., 1999) and lithobids were employed as outgroup for rooting henicopid phylogeny.

As noted above, Lithobiidae is the most appropriate outgroup for Henicopidae, among currently accepted groupings within Lithobiidae (Eason, 1992), molecular data are available for representatives of subfamilies Lithobiinae (Lithobius obscurus, Lithobius variegatus rubriceps, Australobius scabrior) and Ethopoliinae (Bothrolypus multidentatus). These taxa were coded as terminals for morphological and molecular analyses.

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The present morphological analysis emphasizes numerous characters that have not previously been surveyed or used taxonomically, e.g. details of the mandibular aciculae, fringe of bristles, accessory denticles and furry pad. Many such details are undescribed or unillustrated for species that we were not able to study directly, and ‘absence’ codings were not justified based on old published accounts. For example, the
structure of mandibular aciculae is drawn in published accounts (Silvestri, 1917; Arche, 1937) as simple when electron and compound microscopy of the species reveals branching. To ensure the accuracy and comparability of codings, the taxonomic sample for this analysis was limited to populations that we surveyed by electron microscopy, with the addition of *Paralamyctes newtonii*, for which the holotype was examined under a compound microscope. Coding all characters (morphological and molecular) based on direct observation of the specimens allowed the strictest test for monophyly of all the taxonomic categories here evaluated (from species, when more than one population was studied, to the family level). Using several populations of a species was the only way to detect putative non-monophyletic species, and permit their rediagnosis.

Thus, for a few Australian and New Zealand species we collected molecular data from multiple populations throughout the geographical range of the species. *Paralamyctes monteithi* was sampled from the Wet Tropics of northeastern Queensland, the Eungella region of middle eastern Queensland, and from the Kenilworth region of southeastern Queensland. *Paralamyctes gruiyi* was represented by two samples from New South Wales. Samples for *Paralamyctes validus* were from North Island (Waitakere Ranges and Ohakune) and South Island (Banks Peninsula), New Zealand. *Henicops maculatus* was sampled from Tasmania, the Blue Mountains of New South Wales and New Zealand.

The complete list of taxa coded for the morphological character set and the available sequence data for these taxa are summarized in Appendix 1. Collection data for all specimens employed in the molecular sampling are detailed in Appendix 2, which also cites taxonomic authorship for all species.

**Morphological characters**

Forty-nine morphological characters are described in *Morphological characters and observations*. Illustration of morphology in this work attempts to highlight species erected in the older literature that have not previously been figured photographically. Australian species of *Paralamyctes* are illustrated by Edgecombe (2001). Codings for morphological data are provided in Appendix 3.

**Molecular data**

**DNA isolation.** Genomic DNA samples were obtained from fresh, frozen or ethanol-preserved tissues in a solution of guanidinium thiocyanate homogenization buffer following a modified protocol for RNA extraction (Chirgwin et al., 1979). The tissues were homogenized in 400 μl of 4 M guanidinium thiocyanate and 0.1 M β-mercaptoethanol for 1 h, followed by a standard protocol of phenol purification and 3 M sodium acetate precipitation.

**DNA amplification.** The 18S rDNA loci were PCR-amplified in two or three overlapping fragments of about 950, 900 and 850 bp each, using primer pairs 1F–5R, 3F–18Sh1 and 5F–9R, respectively. Primers used in amplification and sequencing were described in Giribet et al. (1996) and Whiting et al. (1997). The 28S rDNA fragment was amplified and sequenced using primers 28Sa (5′–GAC CCG TCT TGA AAC ACG GA–3′) and 28Sb (5′–TCG GAA GGA ACC AGC TAC–3′) (Whiting et al., 1997). The COI fragment was amplified and sequenced using primers LCO1490 (5′–GTT CAA CAA ATC ATA AAG ATA TTG G–3′) and HCO2198 (5′–TAA ACT TCA GGG TGA CCA AAA AAT CA–3′) (Folmer et al., 1994). The 16S rRNA fragment was amplified and sequenced using primers 16Sr (5′–CGC CTT TTT ATC AAA AAC AT–3′) (Xiong & Kocher, 1991) and 16Sb (5′–CTC CGG TTT GAA CTC AGA TCA–3′). The 12S rRNA fragment was amplified and sequenced using primers 12Sai (5′–AAA CTA GGA TTA GAT ACC CTA TTA T–3′) and 12Sbi (5′–AAG AGC GAC GGG CGA TGT GT–3′) (Kocher et al., 1989).

Amplification was carried out in a 50-μl volume reaction, with 1.25 units of AmpliTaq® DNA polymerase (Perkin Elmer, Foster City, CA, U.S.A.), 200 μM of dNTPs and 1 μM of each primer. The PCR program consisted of an initial denaturing step at 94°C for 60 s, 35 amplification cycles (94°C for 15 s, 49°C for 15 s, 72°C for 15 s), and a final step at 72°C for 6 min in a GeneAmp® PCR System 9700 (Perkin Elmer). The annealing temperature to amplify the COI fragment was 46°C.

**DNA sequencing.** PCR amplified samples were purified with the GENECLEAN® III kit (BIO 101 Inc., Vista, CA, U.S.A.) or with the AGTC® gel filtration cartridges (Edge Biosystems, Gaithersburg, MD, USA), and directly sequenced using an automated ABI Prism® 377 DNA sequencer or an ABI Prism® 3700 DNA analyser. Cycle-sequencing with AmpliTaq® DNA polymerase, FS (Perkin-Elmer) using dye-labelled terminators (ABI PRISM™ BigDye™ Terminator Cycle Sequencing Ready Reaction Kit, Foster City, CA, U.S.A.) was performed in a GeneAmp® PCR System 9700 (Perkin Elmer). The sequencing reaction was carried out in a 10-μl volume reaction: 4 μl of Terminator Ready Reaction Mix, 10–30 ng/ml of PCR product, 5 pmoles of primer and dH2O to 10 μl. The cycle-sequencing program consisted of an initial step at 94°C for 3 min, 25 sequencing cycles (94°C for 10 s, 50°C for 5 s, 60°C for 4 min) and a rapid thermal ramp to 4°C and hold. The BigDye-labelled PCR products were isopropanol-p precipitated following manufacturer protocol, or cleaned with AGTC® Gel Filtration Cartridges (Edge BioSystems).

**DNA editing.** Chromatograms obtained from the automated sequencer were read and contigs made using the sequence editing software Sequencher™ 3.0. Complete sequences were edited in GDE, where they were split according to primer-delimited regions and secondary structure features. The external primers 1F and 9R (for the 18S rDNA loci), 28Sa and 28Sb (for the 28S fragment), LCO1490 and HCO2198 (for the COI fragment), 16Sr and 16Sb (for the 16S rDNA fragment) and 12Sai and 12Sbi (for the 12S rDNA fragment) were excluded from the analyses. All the new sequences were deposited in GenBank (see accession codes in Appendix 1).

Molecular data were collected for thirty-one specimens belonging to twenty-three morphologically defined species (Appendices 1 and 2). The molecular loci used in this study are the following.

(1) 18S rRNA: The complete sequence of the small nuclear ribosomal subunit proved to be useful in previous studies of chilopod phylogenetics (Edgecombe et al., 1999; Giribet et al., 1999), and was chosen as the ‘skeleton’ of the cladogram. This locus was sampled for thirty specimens, and the total length (excluding primer pairs 1F and 9R) ranges between 1814 and 2272 bp. The 18S rRNA sequences were divided into thirty-one fragments, according to primer regions and secondary structure features (see Edgecombe et al., 1999). Two of these regions showed large sequence length heterogeneity (fragment H18S5 ranges from 22–100 bp; fragment H18S24 ranges from 56–458 bp), and were excluded from the analyses.

(2) 28S rRNA: The D3 fragment of the large nuclear ribosomal subunit was also used in previous analyses of chilopod phylogeny (Edgecombe et al., 1999; Giribet et al., 1999). We used sequences for twenty-eight specimens, of a total length (excluding primers 28Sa and 28Sb) ranging between 301 and 442 bp. The fragment was divided into eight pieces, one of which (H28S3, ranges between 82 and 220 bp) was excluded from the analyses.

(3) 16S rRNA: A fragment of the mitochondrial ribosomal large subunit ranging between 486 and 516 bp was sequenced for twenty-eight specimens. The gene fragment was divided into eight fragments, all of which were included in the analyses.

(4) 12S rRNA: A fragment of the mitochondrial ribosomal small subunit ranging between 337 and 349 bp was sequenced for seventeen specimens. The gene fragment was divided into eleven fragments, all of them included in the analyses.

(5) COI: A fragment of 657 bp of the mitochondrial protein coding gene cytochrome c oxidase I was sequenced for twenty-two taxa. This fragment was analysed as a single, previously aligned, piece due to the fact that it is a coding fragment that does not present sequence length variation.

In total, we included ca. 3500 bp of sequence data per complete taxon. Difficulties in amplifying some of the most variable fragments for certain clades (the 12S partition is missing for most outgroup taxa as well as for all the members of Lamycetes and Henicops) should not affect their final outcome in the cladogram, because the intention of using such gene fragments was to address potential problems within the clade including Paralamycetes.

**Analytical methods**

Morphological data (Appendix 3) were analysed using the parsimony program NONA version 2.0 (Goloboff, 1998). Multistate characters are unordered except for character 8. The search strategy used tbr branch swapping on a series of 1000 random addition replicates retaining up to ten cladograms per replicate (h/10; mult*1000). As 741 of the 1000 replicates found cladograms of minimum length, no further search strategies were adopted. This strategy found 130 cladograms of 105 steps, which were swapped to completion (to report all the cladograms present in the islands found) using tbr (max*).

Bremer support values were estimated using the heuristic procedure implemented in NONA, retaining up to 10 000 cladograms in the buffer. The number of extra steps required to force monophyly of a group was calculated in NONA by moving the branches to the desired position (command mv n m; where n is the node to be moved to node m), and swapping on all the tree nodes except the one that is constrained as monophyletic (force + n; max/ were n is the node forced to be monophyletic), then taking the difference between the constrained cladogram and the shortest one.

Molecular data were analysed using the direct optimization method of Wheeler (1996) as implemented in the computer program POY (Gladstein & Wheeler, 1997–2000). Each gene was analysed independently and in combination with (1) all other molecular data and (2) all available data (molecular and morphological). A parameter space of two variables (gap/ change ratio and transversion/transition ratio) was explored, totalling twelve parameter sets analysed per partition, and for each of the combined analyses (molecular and total evidence). Therefore, eighty-four independent analyses were performed (sensitivity analysis sensu Wheeler, 1995).

The POY analyses were run in a cluster of 256 pentium III processors at 500 MHz (65 536 Mb of RAM) connected in parallel using pvm software and the parallel version of POY (commands -parallel -jobsperrnode 2 in effect). Each analysis started from the best of 100 ’quick’ random addition sequence builds (-multibuild 100 -buildspr -buildtbr -approxbuild -buildmaxtrees 1), followed by spr and tbr branch swapping holding one cladogram per round of spr (-sprmaxtrees 1) and tbr (-tbrmaxtrees 1). Two rounds of tree fusing (Goloboff, 1999) (commands -treefuse -fuselimit 10 -fusemingroup 5) and swapping on suboptimal cladograms (commands -slop 5 -checkslop 10) were used to make more aggressive searches; holding up to fifty cladograms per round (-maxtrees 50) and using the command -fitchtrees, which saves the most diverse cladograms that it can find for each island. This search strategy was repeated for a minimum of ten times and then up to 1000 times or until minimum cladogram length is hit three times (commands -random 1000 -stopat 3 -minstop 10). The option -multirandom was in effect, which does one complete replication in each processor instead of parallelizing every search. This strategy is implemented for the first time in a POY analysis, and tries to increase the chances of finding minimum length cladograms. The parameter sets were specified through stepmatrices (-molecularmatrix ‘name’). Other commands in effect were -noleading -norandomizeoutgroup.

Bremer support values were estimated using the heuristics procedure implemented in POY (-bremer -constraint ‘filename’ -topology ‘treetopology-in-parenthetical-notation’).

Character congruence was used to choose the combined analysis that minimized incongruence among partitions (as in Wheeler, 1995). However, a more conservative estimate of the phylogenetic hypothesis was presented via the strict consensus of all the parameter sets. Congruence among partitions (morphological and molecular) was measured by the ILD metrics (Mickevich & Farris, 1981; Farris et al., 1995). This
value is calculated from the difference between the overall cladogram length and the sum of its data components:

\[
ILD = \frac{\text{Length}_{\text{Combined}} - \sum \text{Length}_{\text{Individual Sets}}}{\text{Length}_{\text{Combined}}}
\]

Character congruence is used thus as an optimality criterion to choose our ‘best’ cladogram; the cladogram that minimizes conflict among all the data. This is understood as an extension of parsimony; in the same sense that parsimony tries to minimize the number of overall steps in a cladogram, the ‘character congruence analysis’ attempts to find the parameter set that maximizes congruence for all the data sources.

**Morphological characters and observations**

1. **Ocelli:** (0) cluster of ocelli; (1) single ocellus; (2) ocelli absent.
   Lithobiidae (except for some blind cave species) possess a cluster of ocelli/stemmata (state 0: Fig. 1E), whereas Henicopidae have either a single ocellus on each side of the head (state 1: Fig. 1A) or lack ocelli (state 2).

2. **Convexity of ocellus:** (0) bulging; (1) flattened.
   Most henicopids have a bulging (or domed) ocellus (Fig. 1A). *Paralamyctes* (*Thingathinga*) from New South Wales and *P. (Haasiella)* sp. from Tasmania have a distinctly flattened ocellus (Fig. 1B). Coding is restricted to species that have a single ocellus (ch. 1 : 1).

3. **Antennal segmentation:** (0) 17 or more segments; (1) 15 segments.
   Antennal segment counts have a range from fifteen to seventy-one segments within Henicopidae, and this variation is nearly continuous across the family as a whole. Despite this, antennal segmentation is considerably restricted within most groups (e.g. genera) defined on the basis of other characters, and both ends of the distribution are correlated with high-level (subfamilial, tribal) groupings. State 1 (15 segments) is restricted to Anopsobiinae. State 0 accommodates the range of lithobiid segmentation, and is shared by all Henicopidae. Whereas *Zygethobius* has up to 71 antennomeres, *Lamyctes* and *Paralamyctes* have between 15 and 25 antennomeres.

4. **Change in lengths of antennomeres:** (0) gradual change in length along antenna; (1) markedly uneven in proximal part of antenna, with short, paired antennomeres interspersed between longer ones.
   *Lamyctes*, *Analamyctes* and *Henicops* share a peculiar modification of the antennae, there being a few much shortened antennomeres that irregularly alternate with longer antennomeres, the shortened antennomeres typically being developed in pairs. This condition is observed in *L. africanus* (Fig. 1D) and *L. emarginatus*, and was noted by Chamberlin (1912) in his diagnosis of *Lamyctes*. Most henicopids have a more even length distribution; whereas a pair of shorter antennomeres is not uncommonly present, these species do not consistently have multiple pairs of ringlike articles.

5. **Long, tubular antennomeres:** (0) some antennomeres equally wide and long, proximal 2 antennomeres much larger than succeeding few; (1) all antennomeres longer than wide, proximal 2 antennomeres not substantially larger than succeeding few.
   *Paralamyctes harrisi* has all very elongate antennomeres. *Paralamyctes monteithi* most closely approaches this condition, and these species can be segregated based on having all antennomeres longer than wide.

6. **Tömösváry organ:** (0) on small sclerotization anteroventral to ocelli; (1) near margin of cephalic pleurite; (2) situated near midwidth of cephalic pleurite.
   The morphology and positioning of the Tömösváry organ differ between Lithobiidae and Henicopidae. State 0 describes Lithobiidae (Fig. 1E), whereas states 1 (Fig. 1F) and 2 (Fig. 1G) encompass variation in position of the Tömösváry organ in Henicopidae. *Henicops* differs from other henicopids in the medial, rather than lateral, position of the organ on the pleurite. The medial position bears similarity to that of *Craterostigmus* (Fig. 1H). Size of the Tömösváry organ varies considerably within Henicopidae but variation is continuous, and meaningful character states have not been identified.

7. **Cephalic pleurite:** (0) pleurite approximately horizontal, with Tömösváry organ opening on surface of the pleurite; (1) pleurite inclined, constricted just behind Tömösváry organ, which lies on ventral margin of head shield.
   Edgecombe (2001) described a peculiar modification of the sutures that delimit the cephalic pleurite in *Paralamyctes* from Queensland, the pleurite being greatly constricted behind the Tömösváry organ (Fig. 1K). This character was cited as an autapomorphy of *P. (Paralamyctes) monteithi*.

8. **Median furrow on head shield:** (0) absent or faint; (1) deep and continuous between anterior margin of head and transverse suture; (2) extended behind transverse suture to middle of head shield.
   *Paralamyctes* (including *Haasiella*) species have a median furrow that is well impressed and continuous to the transverse suture (Fig. 1B). The lithobiids used as outgroup taxa have at most an incomplete median depression (e.g. *Australobius*). The median depression is faint in *Zygethobius*, whereas in *Henicops* (Fig. 1A), *Analamyctes* and *Lamyctes* it is indistinct.
Fig. 1. A-C, Anterior part of head shield, showing presence (B,C) or absence (A) of median furrow. A, Henicops maculatus; B, Paralamyctes (Thingathinga) ?grayi; C, N, Esastigmatobius japonicus; D, Lamyctes africanaus, proximal part of antenna; E, Bothropolyca multidentatus, ocelli and Tömösiváry organ in ventral view; F–K, cephalic pleurite with Tömösiváry organ in ventral view; F, Paralamyctes validus; G, Henicops maculatus; H, Craterostigmus tasmanianus; I, Paralamyctes (Haasiella) trailli; J, Lamyctinus coeculus; K, Paralamyctes (Paralamyctes) monteithi. L–N, Labrum, showing variation in inner margin. L, Paralamyctes (Paralamyctes) spenceri; M, Paralamyctes (Paralamyctes) harrisi. Scales = 20 μm (J), 40 μm (K), 50 μm (H,I,L,N), 100 μm (A,B,D,G,M), 200 μm (C).
or, at most, confined to the anteriormost part of the head shield. Anopsobius and Esastigmatobius japonicus, however, have a sharply incised median furrow. The furrow in Esastigmatobius (Fig. 1C) differs from that of Paralamyctes only in terminating in advance of the transverse suture. Archey (1937) cited the median furrow ‘continued as a depression through sulcus nearly to middle of head’ in the diagnosis of Haastiella, and the Tasmanian species shares this state (state 2 above) with the three named New Zealand species of Paralamyctes (Haastiella). Although Archey (1937: Pl. 20, Figs 1, 3) drew Paralamyctes validus as having a median furrow running behind the transverse suture, the structure is actually a shallow depression that is present in other species, and not a well defined furrow as observed in Paralamyctes (Haastiella). The topological relationship between the three states justifies their ordering (0-1-2).

9. **Shoulder in labral margin:** (0) absent; (1) present.

The New Zealand species Paralamyctes harrisi and P. validus share a more pronounced flexure of the labral margin (Fig. 1M) than most congeners. The margin forms a bulge (shoulder) adjacent to the midpiece which is sclerotized comparable to the midpiece; the posterior part of the shoulder is subtransverse or oblique, and the margin is abruptly flexed backward where the fringe of labral bristles projects. A gently curved margin, without a shoulder, is general for Henicopidae (Fig. 1L). Other species possessing the strongly flexed state are *P. grayi* from New South Wales and *P. monteithi* from Queensland; in the latter, the inner portion varies from oblique to nearly transverse. Some Lithobiidae (e.g. Australobius, Bothropoly) have a pronounced curvature in the labral margin, but they lack a shoulder near the midpiece. A particularly modified labral margin characterizes *Esastigmatobius japonicus* (Fig. 1N). A bulging ‘shoulder’ is positioned farther backward than in *Paralamyctes*, and a large field of bristles fills a prominent notch behind this shoulder. The course of the margin in *Esastigmatobius* may be an elaboration of a shallow notch observed in the region that underlies the bristles in *Anopsobius*, whereas in *Paralamyctes* the corresponding extent of the labral margin is straight. As such, we do not regard the ‘shoulder’ in *Esastigmatobius* to be homologous with that in *Paralamyctes*.

10. **Pleurites of maxillipede segment connected ventrally,**

forming a continuous band between maxillipede coxosternite and sternite of first pedigerous segment: (0) pleurites discontinuous; (1) pleurites continuous.

State 1 is observed in all taxa referred to Henicopidae (= Anopsobiinae + Henicopinae), and contrasts with the ventral interruption of the maxillipede pleurites in Lithobiidae (Chamberlin, 1912; subsequent workers). Outgroup comparison with Scutigeromorpha, Craterostigmus and Epimorpha s.s. suggests that the henicopid state is a synapomorphy.

11. **Shape of maxillipede coxosternite:** (0) subtriangular coxosternite with narrow, curved dental margin (Fig. 2A); (1) subtrapezoidal coxosternite with narrow, straight dental margin (Fig. 2B); (2) narrow dental margin, markedly V-shaped, with deep median notch (Fig. 2C); (3) subsemicircular coxosternite with wide, convex dental margin (Fig. 2D); (4) trapezoidal coxosternite with narrow, curved dental margin (Fig. 2E); (5) wide, subtransverse dental margin (Fig. 2F); (6) narrow, straight dental margin projected forward (Fig. 3A); (7) trapezoidal coxosternite with moderately wide, weakly V-shaped dental margin (Fig. 3B).

The shape of the maxillipede coxosternite is summarized by the width and relative curvature of the dental margin. We have elected to code for variation in coxosternal shape by recognizing numerous character states, each of which is illustrated in Figs 2 and 3A,B. Development of a median notch is correlated with the character states based on dental margins; a deep median notch (Fig. 2C) is present in species with a V-shaped dental margin (state 2), whereas the median notch is suppressed in species with a wide, transverse dental margin (state 5). Variation in the median notch has not been coded as an independent character.

12. **Teeth on dental margin of maxillipede coxosternite:** (0) large, pointed teeth as extensions of the coxosternite; (1) small, blunt knobs with independent sclerotization from coxosternite.

The morphology of forcipular teeth and their delimitation on the dental margin permit systematic resolution within Paralamyctes. Paralamyctes chilensis, *P. cassisi* and *P. mesibovi* have few, large, sharp teeth that are direct extensions of the coxosternite. This state is shared by Henicops (Figs 2B, 3G), Lamycetes (Fig. 2A) and Lithobiidae (Fig. 3C). Paralamyctes weberi, however, resembles other species from Australia (*P. grayi*, *P. hornerae* and *P. monteithi*) (Fig. 2D,F) and New Zealand (*P. harrisi* and *P. validus*) (Fig. 3D,H) in having the teeth developed as small, blunt bulbs that are encircled by a narrow rim. Sclerotization is markedly greater on the bulbs than on the rims. Silvestri’s (1917: Fig.VI.2) figure of *P. newtoni* indicates that this species has small, blunt knobs rather than large, sharp teeth. In *P. (Haastiella) trailli*, the dental margin is swollen as a rim (Fig. 3E). The teeth, however, have the same style of independent sclerotization as in many other Paralamyctes. All species with a wide, subtransverse dental margin (ch. 11 : 5) possess the knob-like teeth, but they are also present in species with other coxosternal shapes. The teeth in *Esastigmatobius japonicus* are small knobs as in *Paralamyctes*.

13. **Paired cusps on teeth on maxillipede coxosternite:** (0) absent (unpaired, conical teeth); (1) present.

Anopsobius neozelanicus and Anopsobius sp. from New England National Park (New South Wales) have each tooth on the maxillipede coxosternite developed as two cusps, one directly above the other (Fig. 3F). Anopsobius from Tasmania has conical teeth, without this pairing of cusps, and in this respect resembles other hemicopids.

14. **Porodont:** (0) present; (1) absent.

Lithobiidae and Anopsobiinae have a translucent seta (= porodont) at the outer edge of the maxillipede teeth (most Lithobius species and Anopsobiinae) or between the teeth (Australobius). The homology of the so-called ectodont (Chamberlin, 1955) of species of Lamycetes and Lamycinus with a porodont was endorsed by Zaleskaja (1994), whereas Negrea & Matic (1996) referred to this structure as a
pseudoporodont. Because the positioning and enlarged socket of the pseudoporodont in *Lamyctes, Lamycitus* (Fig. 3K) and *Analamyctes* (Fig. 3J) conform to those of the porodont of Anopsobiinae (Fig. 3I), coding herein regards them as homologous. A porodont/ectodont is not differentiated in other Henicopini (Fig. 3D,E,G) or in the examined Zygetobiini.

15. *Proportions of maxillipedal tarsungulum:* (0) pretarsal section of approximately equal length to tarsal section; (1) pretarsal section much longer than tarsal section.

Elongation of the maxillipedal tarsungulum as a slender fang is characteristic of certain Australian (Fig. 2D,F) and New Zealand (Fig. 3H) species of *Paralamyctes*, and is also observed in *Esastigmatobius japonicus*. In particular, the...
The distal (pretarsal) part of the tarsungulum is elongated, being considerably longer than the proximal (tarsal) section. The delimitation of the two parts is marked by a variably defined suture on the inner edge of the tarsungulum and the concentration of setae on the tarsal part. Similar proportions of the pretarsus and tarsus are observed in some species that have a relatively shorter tarsungulum, such as *P. (Paralamyctes)* *weberi* and *P. (Haasiella)* *trailli*. *Henicops* (Fig. 3G), *Lamyctes* (Fig. 2A) and some other species of *Paralamyctes* (*P. chilensis*, Fig. 2E; *P. mesibovi*, *P. cassisi*, *P. validus*, *Lithobius obscurus*, *Paralamyctes validus*; *Paralamyctes (Haasiella) trailli*; *Anopsobius* sp. G,H, Tarsungulum and dental margin of maxillipepe: G, *Henicops maculatus*; H, *Paralamyctes (Paralamyctes) harrisi*. I–K, Lateral corner of dental margin of maxillipepe, showing porodont: I, *Anopsobius* sp.; J, *Analamyctes andinus*; K, *Lamycinus coeculus*. Scales = 2 μm (J), 4 μm (K), 5 μm (F), 10 μm (I), 30 μm (E), 100 μm (A,C,D,G), 200 μm (B,H).
P. neverneverensis) have relatively short tarsungula with about equal tarsal and pretarsal sections.

16. Dense setation on inner part of maxillipe tibial and femur: (0) absent; (1) present.

Paralamyctes harrisi (Fig. 3H) and P. monteithi (Fig. 2D) share a denser concentration of relatively long setae on the inner part of the forcipule than other terminals in this study, most obviously on the tibia and femur. Many henicopids (Fig. 3A) and lithobiids (Fig. 3B) have the setation on the inner part of the telopod not substantially denser than on the outer part.

17. Body narrowed across anterior part of trunk: (0) T1 of similar width to head and T3; (1) T1 narrower than head and T3.

Paralamyctes chilensis resembles P. mesibovi and P. cassisi in the relative narrowness of the anterior part of the trunk, cited by Edgecombe (2001) in the diagnosis of P. (Nothofagobius). In other congeners and other henicopid genera, T1 is larger (of about equal width to the head and T3).

18. Angulation of posterolateral corners of tergites: (0) some angular/toothed; (1) all rounded.

The New South Wales species, Anopsobius margin. Shallow concavity (Attems, 1928) that comprises the pectinate lamella is referred to as aciculae. Following Chamberlin (1912), these vary considerably with respect to their structure (ch. 22), as well as their number (as few as four in Lamycites and Lamycitus to fifteen in some Paralamyctes), although the latter varies continuously and does not readily provide an informative character. The paired teeth on the mandible bear rows of scale- or peglike structures for which we employ the term ‘accessory denticles’ (Lawrence, 1960). The ‘fringe of branching bristles’ refers to the row of bristles that skirts most or all of the gnathal lobe of the mandible. This fringe varies in its extent (chs 23, 26) and in the structure of its bristles (chs 24, 25). The cluster of bristles on the dorsal edge of the mandible is called a furry pad, after Attems (1928) (= pulvillus of Crabill, 1960). The accessory denticles may intergrade with the furry pad or be differentiated from it (ch. 28).

22. Type of aciculae of mandible: (0) bipinnulate; (1) simple; (2) pinnules along dorsal side only.

Pinnulate aciculae are present in most lithobiomorphs, although the details of the branching arrangements vary. Lithobiidae such as Australobius and Lithobius (Fig. 5D) have blunt scalloping of the margin of the aciculae. In Anopsobius, the aciculae are less flattened distally than in many Henicopinae and bipinnulate branching of the margin is shown as rather subdued branches (Fig. 6A). Within Henicopinae, a bipinnulate margin is seen in Henicops (H. maculatus, Fig. 5C), Lamycites (L. emarginatus, Fig. 5A, L. africanus), Lamycitus, Analamycites (Edgecombe, 2001; Fig. 3B), Paralamyctes (Haasiella) (P. trailli, Fig. 5B) and P. (Nothofagobius) (P. chilensis: Edgecombe, 2001; Fig. 22K).

The pinnules are particularly large in Lamycites (Fig. 5A) and Lamycitus but relatively small in Henicops. This distribution, coupled with evidence from Zygethobiinae (bipinnulate aciculae described in Zygethobius and Buethobius by Chamberlin, 1912; confirmed here for Zygethobius pontis, Fig. 5H, and Esastigmatobius japonicus), Anopsobinae (Anopsobius above), and Lithobiidae, suggests that the bipinnulate state is a symplesiomorphy for Henicopidae/ Henicopinae/Henicopini. Considering outgroups, the aciculae of Craterostigmus bear two rows of short barbs; the homology of these and the pinnules on each side of the aciculae in Lithobiomorpha is probable.

‘Simple’ aciculae (state 1) are developed in species of Paralamyctes from Australia (Edgecombe, 2001) and in P. validus from New Zealand (Fig. 5G).

In Paralamyctes spenceri, Attems (1928; Fig. 448) showed the aciculae to bear a row of short pinnules along one side only. Our observations confirm Attems’ description (Fig. 5E), with only the occasional acicula being bipinnulate. A single series of pinnules is also seen in ‘Tripobriobius’ (Paralamyctes) newtoni, P. harrisi (Figs 4B, 5F), P. monteithi (Edgecombe, 2001: Fig. 3LJ), P. neverneverensis (Edgecombe, 2001: Fig. 8J) and in P. weberi.

23. Fringe of branching bristles on mandible: (0) extends along entire gnathal margin, skirting aciculae; (1) terminates at aciculae.

All Henicopini (Figs 4, 5C, 6D) and Lithobiidae examined have a continuous fringe of branching bristles (state 0). Anopsobius displays a strikingly different distribution of the branching bristles, which terminate where the aciculae origin-
ate (state 1; Fig. 6A). This morphology has not been noted in descriptions of *Anopsobius* or in other Anopsobiinae. *Zygethobius*, however, shows the same state as *Anopsobius*; the bristles abruptly terminate where the aciculae originate (Fig. 5H). This state is not consistently developed in *Zygethobiini*; *Esastigmatobius japonicus* has the bristles skirting the aciculae as in *Henicopini* (Fig. 6B).

24. **Ventral bristles in fringe on mandible with a wide base:** (0) absent; (1) present.

In most *henicopids* and in *lithobiids*, the branching bristles on the ventral half of the mandibular fringe have narrow bases (Fig. 5I). In *Anopsobiinae* (*Anopsobius*, Fig. 6A) and *Zygethobiini* (*Zygethobius*, Fig. 6C), these bristles are flattened and widened at their bases. These basal parts lack pectinations, whereas the bristles are branching along their lengths in other taxa (Fig. 5C,I). *Lithobius variegatus rubriceps* lacks pectinations basally on the many bristles on the ventral end of the fringe, but the bristles are narrow-based as in other *Lithobiidae*.

25. **Differentiation of branching bristles on mandible:** (0) branching structure of bristles grades evenly along fringe; (1) abrupt transition between scalelike bristles and plumose bristles.

*Lithobiids* and most *henicopids* display a constant or evenly grading structure of branching bristles along the mandible; these may evenly increase in length ventrally (e.g. *Paralamyctes*, Fig. 6E) or have a narrow region in which length of the bristles increases somewhat more strongly. In *Henicops* (Fig. 4A), *Lamyctes/Lamyctinus* (Edgecombe, 2001: Fig. 3C), the structure of the bristles changes abruptly, from simple bristles that splay from scalelike bases on the dorsal half of the mandible to typical plumose bristles along the ventral half of the mandible.

26. **Width of fringe of branching bristles dorsally:** (0) fringe narrowed dorsally, not developed along all bristles of furry pad; (1) fringe wide, dense, developed along whole length of furry pad.

*Paralamyctes validus* is distinguished by the considerable width of the mandibular bristle fringe dorsally, adjacent to the furry pad. The fringe is composed of several bristle rows, and is present along the bases of all bristles in the furry pad (Fig. 7A). In most *henicopids*, the fringe narrows dorsally (Fig. 7B, E, F).

27. **Accessory denticles on mandible:** (0) interrupted by grooved ridge running along teeth; (1) continuous field of accessory denticles, without grooved ridge on teeth.

*Paralamyctes cassisi* (Edgecombe, 2001: Fig. 17D) and *P. mesibovi* (Fig. 6F) share a continuous field of accessory denticles on the mandibular teeth. In most other *henicopids* (Figs 6D, E; 7A) and in *lithobiids* (Fig. 7C), the field of accessory denticles is interrupted between each tooth by a groove incised along the ventral edge. The groove is also lacking in *P. monteithi* and in *Zygethobiini* (both *Zygethobius pontis* and *Esastigmatobius japonicus*, Fig. 7E).

28. **Furry pad intergrades with accessory denticles:** (0) absent; (1) present.

In *Paralamyctes spenceri*, *P. weberi*, *P. newtoni*, *P. monteithi*, *P. harrisi* (Fig. 7F) and *Zygethobius pontis* (Fig. 7E), the accessory denticles grade evenly into the furry pad, the distal projections of the furry pad merely being progressively elongated. In other *henicopids* and in *lithobiids*, the furry pad is well differentiated from the accessory denticles. This involves either an abrupt elongation of the elements of the furry pad (Fig. 7A, D), or an intervening smooth region that lacks either scale- or setalike morphology (Fig. 7C).

29. **Shape of first maxillary sternite:** (0) small, wedge-shaped, with median suture; (1) large, bell-shaped, coxae not merged anterior to sternite, suture between coxa and sternite confined to posterior edge of maxilla.

An enlargement and bell shape of the first maxillary sternite in all species of *Paralamyctes* (Fig. 8C), including subgenus *Haasiella* (Fig. 8D), is distinctive relative to other *Henicopini*. Outgroup *lithobiids* (e.g. *Australobius*, Fig. 8A) possess a smaller, triangular sternite similar to that of

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**Fig. 4.** Gnathal lobe of mandible. A, *Henicops maculatus*; B, *Paralamyctes* (*Paralamyctes*) *harrisi*. Scales = 20 μm. ac = aciculae; ad = accessory denticles; fp = furry pad; fr = fringe of branching bristles.
Fig. 5. A–H, Mandibular aciculae: A, Lamycetes emarginatus; B, Paralamyctes (Haasiella) trailli; C, Henicops maculatus; D, Lithobius obscurus; E, Paralamyctes (Paralamyctes) spenceri; F, Paralamyctes (Paralamyctes) harrisi; G,I, Paralamyctes validus. Aciculae and fringe of branching bristles: H, Zygethobius pontis. Scales = 2 µm (A), 5 µm (B,D,G), 10 µm (C,E,F,H,I).
Henicops (Fig. 8B) and Lamyctes. A large, bell-shaped sternite is observed in *P. (Haasiella) munroi* (see Archey, 1937: Pl. 22, Fig. 5), *P. (H.) trailli* (Fig. 8D) and an undescribed *P. (Haasiella)* species from Tasmania. In addition to the size and shape, the sternite of *Paralamyctes* is distinctive for the less complete fusion of its sutures than in other lithobiomorphs. These sutures serve to distinguish *Paralamyctes* from *Anopsobius*, which also has a relatively large sternite (see Attems, 1911: Fig. 2 for *Dichelobius*). However, the morphology of the maxillary
sternite in *Esastigmatobius japonicus* (Fig. 8E) is the same as observed in *Paralamyctes*.

30. *Basal joint of telopodite of first maxilla fused on inner side to coxal process*: (0) telopodite distinctly demarcated; (1) telopodite fused to adjacent part of coxa.

Fusion of the maxillary telopodite to the coxal process is a diagnostic character for Henicopinae (Attem, 1928).

31. *Setae on coxal process of first maxilla*: (0) dense cluster of differentiated setae; (1) mostly simple setae.

Chamberlin (1912) contrasted Lithobiidae and Henicopidae by the presence of plumose setae on the coxal process of the first maxilla in the former vs simple or partly lacinate setae in the latter. Described more precisely, Lithobiidae have a dense, brushlike setal cluster that includes plumose setae, simple

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striated setae and complex setae composed of slender strands (Fig. 8F). Archey (1917, 1937) documented a few plumose setae in New Zealand material referred by him to Henicops maculatus, and considered this feature to distinguish Henicops from all other henicopids (Archey, 1917). The same condition is observed in typical Henicops maculatus from Tasmania (Fig. 8H). Whereas most henicopids have exclusively simple setae (Fig. 8G), some examples of one or two lacininate or plumose setae amidst otherwise simple setae are known. Zygethobius pontis has predominantly simple setae. A particularly large specimen of Paralamyctes harrisi (New Zealand Arthropod Collection) has a few plumose setae in its cluster of simple setae. No henicopids have a brushlike setal cluster as in lithobiids.

32. Coxa of leg 15 with long, lobate process ending in a spine: (0) absent; (1) present.
An anal leg coxal process is shared by all Anopsobiinae. The supposed zygetobiine Hedinoebius hummelti (Verhoeff, 1934; Pl. 5, Fig. 9a) also has a coxal process.

33. Prefemur of leg 15 with spurs: (0) spurs absent; (1) single ventral spur; (2) several spurs in a whorl.
A single, strong ventral spur on the anal leg prefemur unites all Anopsobiinae to the exclusion of Catanopsobius Silvestri, 1909. According to Verhoeff (1934), Hedinoebius has a spur on the trochanter and prefemur of the anal leg. State 2 codes for the characteristic whorl of spurs in Lithobiidae.

34. Coxal pores: (0) on legs 14 and 15 only; (1) on legs 13–15 only; (2) on legs 12–15 only; (3) on legs 11–15.
The distribution of coxal pores on legs 12–15 in Lithobiidae (state 2 above) suggests that this arrangement is plesiomorphic for Henicopidae. It is present in most Henicopinae and in some Anopsobiinae (Ghilaroviella Zalesskaja, 1975 and Shikokuobius Shinohara, 1982). Paralamyctes (= ‘Triporobius’) newtoni lacks coxal pores on leg 12, although homology with absence of pores on this leg in Anopsobiinae is not forced by our unordered multistate coding. This coding strategy is favoured so as not to make an assumption of progressive loss.

Presence of coxal pores on leg 11 (state 3) is restricted to Hedinoebius and Zygethobius. Verhoeff (1934) claimed that Attems erred in attributing coxal pores on leg 11 to Zygethobius, citing Chamberlin in support of his claim that

Fig. 8. A,F, Australobius scabrior. A, Coxa and sternite of first maxilla; F, setae on coxal process of first maxilla. B,H, Henicops maculatus. B, coxa and sternite of first maxilla; H, simple and laciniate setae on coxal process of first maxilla. C, Paralamyctes (Paralamyctes) monteithi, coxa and sternite of first maxilla; D, Paralamyctes (Haasiella) trailli, first maxilla; E, Esastigmatobius japonicus, first maxilla; G, Paralamyctes validus, simple setae on coxal process of first maxilla; I, Lamycetes africanus, male first genital sternite and gonopods. Scales = 5 μm (G), 10 μm (F,H), 50 μm (A–E,I).
Zygethobius has coxal pores on legs 12–15 only. The source for this information is evidently Chamberlin (1911). Examination of Zygethobius pontis confirms the coxal pores on leg 11, as was observed by Chamberlin (1912).

35. Coxal pores set in deep groove, largely concealed by anteroventral face of coxa in ventral view: (0) absent; (1) present.

Many Paralamyctes species share a partial covering of the coxal pores, particularly distally (e.g. developed to some extent in P. weberi, P. harrisi and P. monteithi). The concealment of the coxal pores in a deep groove is more pronounced in P. grayi and P. validus. The coxal pores are likewise set in a deep, folded-over groove in Zygethobius and Easistigmatobius.

36. Distal spinose projection on tibia of legs 1–11: (0) absent; (1) present.

All Henicopidae possess tibial projections on at least the first 11 legs, and they are variably present on legs 12–15. Tibial projections are absent in Lithobiidae and all other chilopods. The most conspicuous variation observed in the structure of tibial projections is the prominent basal articulation of a sharp, spinelike spur in Easistigmatobius vs fusion of the projection in other henicopids, including Zygethobius. We have not coded for the presence of a tibial projection on leg 12 because it is polymorphic within certain henicopid species (Ghilarioviella vialiachmedovi Zalesskaja, 1975).

37. Distal spinose projection on tibia of leg 13: (0) absent; (1) present.

A tibial projection is present on leg 13 in henicopids except for many species of Lamyctes, Lamycytinus and Anopsobiinae. The systematic distribution of a tibial projection on leg 14 does not covary with spurs on leg 13. The projection is absent on leg 14 in Easistigmatobius japonicus and in some species of Paralamyctes, such as P. newtoni, P. spenceri and P. (Haasiella) spp.

38. Distal spinose projection on tibia of leg 14: (0) absent; (1) present.

The systematic distribution of a tibial projection on leg 14 is more or less symmetrical across the posterior accessory claws, whereas Lithobiidae have only the posterior accessory claw (Eason, 1964). Anopsobius and Zygethobiini have symmetrical accessory claws as in Henicopini. The polarity of the character is ambiguous with outgroup comparison, sclerendromorphs having symmetrical anterior and posterior accessory claws, whereas Craterostigmus has a posterior accessory claw and a ventral accessory spur but not an anterior accessory claw.

39. Distal spinose projection on tibia of leg 15: (0) absent; (1) present.

Within Henicopini, a tibial projection on leg 15 is confined to some Australian and New Zealand species of Paralamyctes (P. mesibovi, P. cassisi, P. validus, P. ?grayi, P. neverneversis). Chamberlin’s (1912) description of a tibial projection on leg 15 in Zygethobius pontis was regarded by Crabbil (1981) as a likely error. Crabbil’s description is followed here.

40. Tarsus of legs 1–12: (0) divided into basitarsus and distitarsus; (1) undivided.

Coding for Easistigmatobius japonicus is problematic. The tarsi are divided into numerous weak tarsomerses, but the position of the basitarsus-distitarsus joint is uncertain. This and the following character are coded as missing data.

41. Articulation between basitarsus and distitarsus on anterior pairs of legs: (0) distinct on dorsal side of leg; (1) fused on dorsal side of leg, distinct ventrally.

Paralamyctes validus, P. grayi and P. hornerae have the tarsal articulation distinct ventrally but fused across a narrow extent dorsally on the anterior few pairs of legs. In other species of Paralamyctes, the articulation is continuous dorsally and flexure is more pronounced than in P. validus and similar species. The articulation is continuous dorsally in lithobiid outgroups and in Zygethobius. Henicops, however, displays a narrow fused sector on the dorsal side of the leg.

42. Subdivision of basitarsus indicated by paired larger setae: (0) absent; (1) present.

Edgcombe et al. (1999; their ch. 69) described a pattern of paired larger setae on the basitarsus in Henicops. We have not coded with an assumption that a bipartite tarsus is a necessary precursor to the presence of the setae, i.e. taxa with a unipartite tarsus, such as Anopsobius and Lamycytes, are coded for the absence of paired larger setae.

43. First tarsal segment bisegmented (tripartite tarsus): (0) absent; (1) present.

A three-segmented tarsus (bipartite basitarsus) is present in Henicops maculatus and Henicops species from Western Australia.

44. Accessory apical claws: (0) anterior and posterior accessory claws; (1) posterior accessory claw only.

Henicopidae have more or less symmetrical accessory claws on each side of the apical claw, whereas Lithobiidae have only the posterior accessory claw (Eason, 1964). Anopsobius and Zygethobiini have symmetrical accessory claws as in Henicopini. The polarity of the character is ambiguous with outgroup comparison, sclerendromorphs having symmetrical anterior and posterior accessory claws, whereas Craterostigmus has a posterior accessory claw and a ventral accessory spur but not an anterior accessory claw.

45. First genital sternite of male divided longitudinally: (0) undivided; (1) divided.

Attems (1928) diagnosed Lamycytes by its bipartite genital sternite in the male (Fig. 81). The same condition is observed in all species of Henicops (see Borucki, 1996: Fig. 102), but in no other henicopids (the state in Lamycytinus is undescribed due to the lack of male specimens for examination). Lithobiidae have an undivided sternite. In Analamycytes tucumanus, the sternite has a median longitudinal band of decreased sclerotization, but does not form two discrete sclerites as in Henicops and Lamycytes.

46. Segmentation of male gonopod: (0) 4 segments with a setalike terminal process; (1) stout gonopod with 1 or 2 segments.

As Edgecombe et al. (1999) noted, male gonopods composed of four segments, the last being a setalike process, are shared by all henicopids and are unique to Henicopidae. The only counterevidence to this segmentation pattern being a synapomorphy is a belief that flabelliform gonopods are likely to be plesiomorphic because they are more leglike, and ‘As a rule, in Chilopoda, the evolution presents a tendency [sic] to simplify the features of different systems or organs’ (Prunescu, 1996). ‘Flabelliform’ gonopods may indeed be plesiomorphic, but we see no reason to necessarily dismiss the precise segmental correspondence as a henicopid autapomorphy.

47. Number of spurs on female gonopod: (0) 2; (1) 3.

Two spurs on the female gonopod is the general and widespread state in Lithobiomorpha. Exceptions in the Henicopini are in Tasmanian/New South Wales Paralamyctes (Nothofagobius) (three spurs) and
Numerous Lithobiidae, though two spurs are certainly the basal spurs. The three-spurred (or more) condition is developed in displays more polymorphism than do henicopids (three to five spurs). The three-spurred (or more) condition is developed in having a process bearing the spurs on the female gonopod (Edgecombe, 2001: Figs 16B, 19B, 21B).

48. Claw of female gonopod: (0) simple (unipartite); (1) tripartite, dorsal and ventral accessory denticles present.

Results

Morphological data

With the analytical parameters described above, 144 minimal length cladograms of 105 steps (C.I. 0.58; R.I. 0.85) were found. Figure 9 is the strict consensus of these cladograms.

Morphological data support the traditional division of Henicopidae (bs > 5) into Anopsobiinae (bs > 5) and Henicopinae (bs = 3), but reject the division of the latter clade into Henicopini and Zygethobiini. Zygethobiini (bs = 3) is instead resolved within Henicopini, indeed within cladistic structure of Paralamyctes sensu Edgecombe (2001). This resolution results from the presence of both synapomorphies of Paralamyctes (chs 8 : 1, 29 : 1) in Esastigmatobius, as well as additional characters that are otherwise confined to parts of Paralamyctes (chs 12 : 1, 15 : 1). These apomorphies are absent in Zygethobiini.

The basal nodes within Henicopinae are problematic due to optimization issues. Blindness (ch. 1 : 2) optimized at the base of Henicopinae, is shared by Lamycinus and Anopsobiinae. However, this optimization is challenged by outgroup evidence from Craterostigmus, which has a single ocellus like most Henicopinae (ch. 1 : 1). We have not forced a character state tree that prohibits the reappearance of ocelli from absence. Missing data may also affect the position of Lamycinus. A putative synapomorphy of Henicops + Lamycinus is the division of the first genital sternite in the male (ch. 45 : 1). The status of this character in Lamycinus is uncertain, males not being present in our collections and the state undescribed in the literature.

Clades within Paralamyctes correspond to three subgenera recognized in Edgecombe’s (2001) classification, P. (Nothofagobius), P. (Thingathinga) and P. (Haasiella), although the branch support for each subgenus is only 1. The monophyly of P. (Paralamyctes) is, however, not supported by all minimal length cladograms.

Molecular data

In consideration of cladograms for each molecular partition, we distinguish between hypotheses that are supported for all of the analytical parameters that were explored and those supported by the most congruent set of parameters. The most congruent parameter set for combined analysis of all data is 111 (Appendix 4). The following discussion therefore refers to the strict consensus of cladograms using 111 weights for each locus as well as the consensus of cladograms for all parameters.

18S rRNA. The 18S cladogram for parameter set 111 (Fig. 10) (single cladogram of 630 steps; 170 replicates performed) shows monophyly of Henicopidae, Anopsobius and (Lamycinus + Lamycinus)(Henicops). However, Henicopini is paraphyletic, with the zygethobine Esastigmatobius nested within Paralamyctes sensu Edgecombe (2001). Among the subgenera recognized by Edgecombe (2001), P. (Paralamyctes), including P. (Nothofagobius), is sister group to Esastigmatobius, whereas P. (Thingathinga) and P. (Haasiella) are paraphyletic with respect to each other. Paralamyctes (P.) monteithi, as diagnosed morphologically, appears as a polyphyletic species, with the population from southeastern Queensland grouping separate from the populations in middle eastern and northeastern Queensland.

Monophyly of Henicopidae, Anopsobius, Henicopinae and Henicops are stable to parameter change, being monophyletic in all the parameter sets here examined (Fig. 10). The lack of resolution in the strict consensus of all parameters is mainly due to the lack of population-level information in the 18S gene, especially for those parameters where transitions are not counted, which result in hundreds of equally parsimonious cladograms. However, the stability of the deep (subfamilial) divergences, and the marked degree of congruence between the 18S cladogram under the optimal parameter set and the total evidence cladogram, shows the usefulness of this gene for inference of chilopod relationships.

28S rRNA. These data are particularly sensitive to analytical parameters, no clades withstanding the entire range of explored weights. With the most congruent parameter set (111) (Fig. 11; strict consensus of forty-nine cladograms of 114 steps; 181 replicates performed), monophyletic groups include Henicopidae, Anopsobius, a Lamycinus + Lamycinus + Henicops clade, Henicops and a clade composed of Paralamyctes (Haasiella) and P. (Thingathinga). Paralamyctes (Nothofagobius) mesibovi is sister to Haasiella + Thingathinga. Among species represented by multiple exemplars, the monophyly of neither P. (P.) monteithi nor P. (T.) validus is resolved in the consensus cladogram.

16S rRNA. These data for the optimal parameter set (a single cladogram of 1333 steps, Fig. 12; minimum-cladogram length hit five times out of 146 replicates) show monophyly of Henicopidae and Anopsobiinae, but not for Henicopinae. (Lamycinus + Lamycinus) Henicops form a monophyletic
Fig. 9. Strict consensus of 144 cladograms of 105 steps based on a parsimony analysis of morphological characters. Numbers above branches indicate Bremer support values calculated up to five extra steps. Subgenera of *Paralamyctes* as proposed by Edgecombe (2001) are indicated in the cladogram irrespective of their monophyletic status.
Phylogeny of Henicopidae (Chilopoda)  

Lithobius variegatus  
Lithobius obscurus  
Australobius  
Bothropolyx  
Anopsobius TAS  
Anopsobius neozelandicus  
Anopsobius NSW  
Lamyctinus coeculus  
Lamyctes emarginatus  
Lamyctes africanaus  
Henicops maculatus TAS  
Henicops maculatus NSW  
Henicops maculatus NZ  
Esastigmatobius  
P. monteithi SE QLD  
P. weberi  
P. neverneverensis  
P. harrisi  
P. mesibovi  
P. monteithi NE QLD  
P. monteithi ME QLD  
Haasiella tralli  
Haasiella TAS  
P. grayi NSW  
P. grayi NSW1  
P. grayi  
Haasiella NZ  
P. validus NZ1  
P. validus NZ2  
P. validus NZ3  

Fig. 10. Cladograms corresponding to the 18S rRNA sequence data analyses. At left is single cladogram of 630 steps obtained for the most congruent parameter set (111); cladogram at right is strict consensus for all twelve parameter sets.

group that is sister to Anopsobius. The only species of Nothofagobius for which molecular data are available, P. (N.) mesibovi, is sister to Esastigmatobius. Subgenus Paralamyctes is nonmonophyletic, forming a basal grade within Henicopidae. Subgenera Haasiella and Thingathinga form a clade, although each is resolved as paraphyletic with respect to the other. Regarding species-level monophyly, 16S supports monophyly of P. (P.) monteithi and P. (T.) grayi, but not the monophyly of P. (T.) validus, in which is nested P. (Haasiella) sp. from New Zealand.

Henicopidae, (Lamyctes + Lamyctinus + Henicops), Anopsobius, P. (T.) grayi + P. (Thingathinga) from the Barrington Tops, and the clade comprising P. (T.) validus and the Haasiella species from New Zealand are stable to all the parameter sets examined here (Fig. 12).

12S rRNA. The 12S cladogram for the parameter set that minimizes incongruence (one cladogram of 646 steps; minimum length hit 121 times out of 191 replicates) shows monophyly of Henicopidae, Anopsobiinae + Henicopini, Anopsobius, Henicopini (sampling confined to Paralamyctes sensu Edgecombe, 2001) and subgenus Paralamyctes (Fig. 13). The remaining Paralamyctes form a grade of Thingathinga including Haasiella and P. (Nothofagobius) mesibovi. Paralamyctes validus is monophyletic, and sister group to Haasiella from New Zealand, whereas P. grayi is resolved as paraphyletic. The basal position of Esastigmatobius may be sensitive to rooting problems, as only a single lithobiid outgroup was available for this gene and no data are available for Henicops, Lamyctes or Lamyctinus.

Few clades withstand all analytical parameters (Fig. 13), these being Anopsobius and the clade containing Paralamyctes validus and P. (Haasiella) from New Zealand.

COI. The cytochrome c oxidase I data for the most congruent parameter set (Fig. 14) (one cladogram of 1453 steps; minimum length hit 129 times out of 170 replicates) show monophyly of Henicopidae, Henicops + (Lamyctes + Lamyctinus) and P. validus. Genus Paralamyctes and
subgenus *P.* (Paralamyctes) as recognized by Edgecombe (2001) are polyphyletic. Sampled species of subgenera Haasiella and Thingathinga, however, unite as clades. Monophyly of Anopsobius or Henicops, obtained for almost all parameters for the other partitions, is not supported by the COI data. This could lead us to think that the COI gene is not very ‘useful’ for resolving henicopid relationships. However, when all the parameter sets are condensed, all the clades obtained except one (a clade in which *P.* mesibovi nests with species of subgenus Paralamyctes) are compatible with the total evidence cladogram. This may indicate that the COI gene contains some relevant information at the level here studied.

All molecular data

The combined analysis of all molecular data (18S + 28S + 16S + 12S + COI) for the parameter set that minimizes incongruence (Fig. 15; one cladogram of 4254 steps; minimum length hit 128 times out of 240 replicates) shows monophyly of Henicopidae, Anopsobius, ((Lamycites + Lamycites) Henicops), Paralamyctes sensu Edgecombe (2001) and subgenus Paralamyctes. *Esastigmatobius* is sister to *Paralamyctes*, rendering Henicopini a grade that includes Zygethobiini. *Paralamyctes* (Nothofagobius) mesibovi is sister to a clade containing subgenera Haasiella + Thingathinga, neither of which is itself monophyletic. Among the species represented in the molecular dataset by more than one specimen, *Henicops maculatus*, *P.* (T.) validus and *P.* (T.) grayi are monophyletic, but *P.* (P.) monteithi is nonmonophyletic. For *Henicops maculatus* as well as *Anopsobius*, the exemplars from New Zealand and New South Wales are more closely related to each other than either is to the exemplar from Tasmania. Within *P.* (T.) validus, the samples from North Island (Waitakere Ranges and Ohakune) are more closely related than either is to the sample from Banks Peninsula on South Island. This resolution is present in the most congruent parameters for 12S (Fig. 13) and for all parameters for 16S (Fig. 12) and COI (Fig. 14).

These combined results are in general stable to parameter variation. Groups found across all the parameters here studied are Henicopidae, Anopsobini, Lamycites + Lamycites + Henicops, subgenus Paralamyctes and the clade composed of subgenera Thingathinga and Haasiella. *Henicops maculatus* and *P.* (T.) grayi + *P.* (Thingathinga) from the Barrington Tops are monophyletic in all the parameter sets studied.

The deeper relationships of Henicopidae as resolved based on the combination of the five genes (Fig. 15) agree with the morphological cladogram (Fig. 9) with respect to the sister-group relationship between Anopsobini and Henicopinae, as well as the non-monophyly of Henicopini. Both sources of data resolve the zygethobiine *Esastigmatobius* more closely related to *Paralamyctes* than either of these taxa is to *Lamycites*, Lamycites and Henicops.

Simultaneous analysis

The simultaneous analysis of all the data for the parameter that minimizes overall incongruence (Fig. 16) is entirely compatible with the best cladogram for all the molecular data analysed in combination (Fig. 15), except for the relative positions of *P.* weberi and *P.* harrisi, which are inverted. The position of certain taxa with morphological data only are more resolved in the simultaneous analysis cladogram than in the morphological cladogram (see the positions of *P.* hornerae and *P.* newtoni), but Zygethobiini, supported by the morphological analysis, is paraphyletic in the combined analysis, its monophyly requiring an extra step. This is affected by molecular support for resolution of *Esastigmatobius* with *Paralamyctes* along with morphological characters shared by *Esastigmatobius* and *Paralamyctes* but not Zygethobiini (Ch. 8:1; Ch. 29:1).

Common features to the cladogram obtained under the optimal parameter set and the strict consensus of all the parameters examined are the monophyly of Henicopidae, Anopsobius, Henicopinae, (Lamycites + Lamycites) (Henicops) (Analamyctes) and the monophyly of Paralamyctes subgenus Paralamyctes, Nothofagobius and the clade composed of Haasiella + Thingathinga. Haasiella from New Zealand is sister group to *P.* validus under all parameter sets, and New South Wales species of *P.* (Thingathinga) are invariably a clade.

The simultaneous analysis cladogram resolves some regions of conflict between the optimal combined molecular cladogram (Fig. 15) and the morphological cladogram (Fig. 9) in favour of the former. In particular, the relationships of the four subgenera of *Paralamyctes* are resolved in favour of *P.* (Nothofagobius) being most closely related to *P.* (Haasiella) and *P.* (Thingathinga), with *P.* (Paralamyctes) the basally derived clade within the genus.

Discussion

The following discussion highlights the contentious relationships of Zygethobiini, examines the most consistently resolved taxa within Henicopini, and amends henicopid classification to conform to the inferred phylogeny.

Status of Zygethobiini

The relationships of Zygethobiini emerge as the most problematic issue in henicopid systematics. Monophyly of Zygethobiini is not well established. Traditional treatments (Chamberlin, 1912; Attems, 1914, 1928) defined the group based on a single character, absence of a spiracle on segment I, which is sympleiomorphic for Henicopinae. A large number of antennal articles is potentially synapomorphic for Zygethobiini, but intraspecific variation in Henicopini prevented its use as a cladistically informative character (see discussion of ch. 3). Few characters are identified as morphological synapomorphies, and those optimized as synapomor-
Phylogeny of Henicopidae (Chilopoda)

Fig. 12. Cladograms corresponding to the 16S rRNA sequence data analyses. At left is single cladogram of 1333 steps obtained for the most congruent parameter set (111); cladogram at right is strict consensus for all twelve parameter sets.

In addition to the problem of monophyly of Zygethobiini, the position of the group in Henicopidae also demands further consideration. Combined analysis of sequence and morphological data (Fig. 16) concludes that Zygethobiini is nested within Henicopini, rather than being its sister group as the traditional classification implies. This result is retrieved based on morphology alone (Fig. 9) and with the most congruent parameter set for the sequence data alone (Fig. 15). However, we urge caution because sequences are available for only a single exemplar of Zygethobiini, and the position of Esastigmatobius is very labile when the cladograms from each sequence partition are compared. For the most congruent parameter set, Esastigmatobius is resolved as sister to Paralamyctes (Thingathinga) for COI, as sister to P. (Nothofagobius) for 16S, as sister to all other Henicopidae for 12S, and as sister to P. (Paralamyctes) and

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P. (Nothofagobius) for 18S. Sequence data from North American exemplars of Zygetobiini (Zygetobius, Buethobius Chamberlin, 1911; Yobius Chamberlin, 1945) are necessary before a position of Zygetobiini within Henicopini can be accepted. Even so, from evidence at hand, we posit that Henicopini is paraphyletic with respect to Zygetobiini and that Zygetobiini is itself of doubtful monophyly.

Monophyly of Lamyctes + Lamyctinus + Henicops + Analamyctes

The monophyly of a group including Lamyctes, Lamyctinus and Henicops is one of the most consistently resolved and stable components in the molecular analyses. This clade is present in analyses of 16S sequences for all explored parameters, and is present for the most congruent parameters for all the genes for which molecular data are available (no data are available for 12S to test the group). The combined sequences and pooling of all data support the monophyly of the clade including Lamyctes + Lamyctinus + Henicops for all parameters here explored, although the morphological data alone are not able to obtain this clade (Fig. 9). This group, with Analamyctes branching between Lamyctes and Henicops, is resolved as a basal grade within Henicopinae based on morphology alone. Three extra steps are required to force monophyly of Lamyctes + Lamyctinus + Henicops + Analamyctes for the morphological data. As discussed above, the paraphyly of this group based on morphology alone may be affected by optimization problems involving blindness and missing data for the male first genital sternite in Lamyctinus. Characters that place Lamyctinus and Lamyctes basally are perhaps correlated with small body size. These two genera resemble Anopsobiinae in the lack of tergite projections (ch. 18) and lack of tarsal joints (ch. 40). Within Lithobiidae, small body size is likewise associated with the absence of tergite projections and tarsal joints (e.g. in Garibius) (Crabill, 1957), such that these characters may be functionally correlated in Lithobiomorpha.

Presence of the Lamyctes + Lamyctinus + Henicops group for the optimal parameters for all four available genes, and its stability for the 16S data in particular, provide strong evidence for monophyly. Combination of morphological data indicates that Analamyctes is a member of this group, although Bremer support is greatly diminished by the addition of the morphological codings for Analamyctes. In analyses excluding Analamyctes, the Lamyctes + Lamyctinus + Henicops clade is the best supported supraspecific taxon in the most congruent total evidence cladogram (Bremer support = 55), whereas addition of Analamyctes decreases Bremer support to 3.

Monophyly of Paralamyctes (Paralamyctes)

Monophyly of P. (Paralamyctes) sensu Edgecombe (2001) is not upheld in all morphological cladograms, despite the restriction of some apomorphic states to this group (e.g. pinnules present only on the dorsal side of the mandibular aciculae: ch. 22 : 2). This is due to the position of Esastigmatobius, which sometimes appears as sister group to a clade formed by the non-Nothofagobius Paralamyctes (subgenera Paralamyctes, Haasiella and Thingathinga), whereas in other instances it appears as ingroup P. (Paralamyctes). However, P. (Paralamyctes) is present under all parameters for the combined analysis of the molecular data on their own (Fig. 15) and is likewise present in all analyses of the combined morphological and sequence data (Fig. 16); the group is stable in a simultaneous analysis regime, and depicts a Bremer support value of 14 in the total evidence cladogram for the parameter set that maximizes congruence. Molecular support for the monophyly of P. (Paralamyctes) is contributed

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by 12S and 18S sequences in particular. In the former, the four sampled species are a clade for the most congruent parameter set, and for the latter the six sampled terminals are united with *P. mesibovi*.

*Monophyly of Paralamyctes (Haasiella) + P. (Thingathinga)*

Within *Paralamyctes*, a clade restricted to or including the species assigned to subgenera *Haasiella* and *Thingathinga* by
Edgecombe (2001) is present for the most congruent parameter set for most analyses (bs = 10 in the total evidence cladogram, Fig. 16). The 111 parameter sets for 18S, 28S and 16S all retrieve the Haasiella + Thingathinga group, and the clade is present in some (but not all) minimal length cladograms based on morphology. The same parameter set for 12S also unites these species but places *P. (Nothofagobius) mesibovi* within the group. Simultaneous analysis of all sequence and morpho-

Fig. 16. Cladograms based on the combined analysis of all data (morphological + molecular). At left is single shortest cladogram of 4376 steps obtained for the most congruent parameter set (111); cladogram at right is strict consensus for all twelve parameters.
logical data supports the *Haasiella* + *Thingathinga* clade for all parameters, although in each case the morphologically defined subgenera are resolved as paraphyletic when the sequence data are added. Only the morphological data on their own yield *Haasiella* and *Thingathinga* as clades. As such, the status of the two subgenera is less stable than is the more inclusive clade that unites them within *Paralamyctes*. A particularly stable component is a clade composed of the new *P.* (*Haasiella*) species from Ruato, New Zealand and *P.* (*T.*). *validus*. This grouping is supported by the optimal cladogram for 18S, by all parameter sets for 16S, 12S and combined molecular data, and simultaneous analysis with morphology. Two other well supported clades in the total evidence cladogram are a group of *Haasiella* species (*H.* *trailli* and the Tasmanian species; bs = 16 for the 111 parameter set) and a group uniting New South Wales species of *P.* (*Thingathinga*) (bs = 21 for the 111 parameter set). Both of these groups are stable for all explored parameters.

### Classification

The simultaneous analysis cladogram (Fig. 16) is taken as the best basis for emending henicopid classification to reflect the group’s phylogeny. Groups that warrant recognition in the...
classification are those that are monophyletic in a simultaneous analysis regime. Clades that are stable to analytical parameters and well supported (e.g. have high Bremer support) are particularly worthy of taxonomic recognition. With these considerations, the classification of Henicopidae analysed in this study may be summarized as in Table 1.

Paralaymctes and Gondwanan biogeography

The cladogram used as a basis for interpreting biogeographic history of Paralaymctes is that based on combined analysis of all available data, for the most congruent parameters (Fig. 16). This cladogram (as well as the most congruent cladogram based on the combined sequence data, Fig. 15) identifies Paralaymctes sensu Edgecombe (2001) as a monophyletic group endemic to Gondwana, with the Neartic-Oriental Zygethobiini as most closely allied outgroup taxa. These relationships are consistent with a Pangean distribution for the more inclusive clade that unites these taxa.

For biogeographic analysis, seven areas of endemism are recognized in eastern Australia based on Paralaymctes distributions (Fig. 17). The range of P. monteithi in Queensland is divided into three analytical areas corresponding to the three allopatric populations sampled. The sequence data indicate geographical differentiation in this species that is not detected morphologically, notably for the southeastern population, which has a unique relationship to P. neverneverensis from northeastern New South Wales. These relationships are consistent with a Pangean distribution for the more inclusive clade that unites these taxa.

The cladogram for Paralaymctes is shown in Fig. 18, based on the taxonomic cladogram in Fig. 16. Clades endemic to the same area have been collapsed to a single terminal, e.g. the New Zealand clade of P. (Haesiella) sp. and P. validus. The informative nodes in this cladogram are assessed using subtree analysis (Nelson & Ladiges, 1996). This approach is particularly critical of information derived from redundant areas, or areas repeated on the cladogram ‘(areas of sympatry’
of Enghoff, 1996). Nelson & Ladiges compare area redundancy to paralogy in molecular systematics, and argue that geographical data are not necessarily associated with nodes involving redundancy, or ‘paralogous nodes’. The informative nodes in a taxon-area cladogram may be summarized via subtrees that are ‘paralogy-free’. Three such subtrees are present in the Paralamyctes cladogram, one derived from each of P. (Paralamyctes), P. (Notohaegobius) and the P. (Haussellia)/P. (Thingaihinga) clade (Fig. 19). The three subtrees are entirely congruent with respect to the cladistic information they imply (as expressed in terms of their three-taxon statements of area relationship) and combine to produce a minimal tree (sensu Ladiges et al., 1997) with several resolved nodes (Fig. 20).

Aspects of the minimal tree are incongruent with the sequence of Gondwanan fragmentation, which is generally resolved as (Africa (India (New Zealand + Patagonia + Australia))) (Lawver et al., 1992) or (Africa + India) (New Zealand + Patagonia + Australia) (Linder & Crisp, 1995). Most noteworthy are the basal resolution of Patagonia relative to other parts of Gondwana and the composite, rather than monophyletic, nature of Australia. The minimal tree for Paralamyctes recognizes parts of southeastern Australia (southeastern Queensland to southeastern New South Wales) as separate from much of the rest of Gondwana (grouping including Tasmania, southern Africa + India, and New Zealand + northern Queensland). The complex patterns resolved for areas within Australia underscores the importance of analysing small intracontinental areas of endemism where the data permit, rather than making assumptions of continent ‘monophyly’ based on geological models (Weston & Crisp, 1994).

The standard geological/climatic model for area relationships permits, rather than making assumptions of continent ‘monophyly’ based on geological models (Weston & Crisp, 1994). The informative nodes in a taxon-area cladogram may be summarized via subtrees that are ‘paralogy-free’. Three such subtrees are present in the Paralamyctes cladogram, one derived from each of P. (Paralamyctes), P. (Notohaegobius) and the P. (Haussellia)/P. (Thingaihinga) clade (Fig. 19). The three subtrees are entirely congruent with respect to the cladistic information they imply (as expressed in terms of their three-taxon statements of area relationship) and combine to produce a minimal tree (sensu Ladiges et al., 1997) with several resolved nodes (Fig. 20).

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The standard geological/climatic model for area relationships in eastern Australia dates the split from southern South America (via Antarctica) at 35–50 million years, then predicts the vicariance sequence (Tasmania (northern Queensland + southeastern Australia)) (Weston & Crisp, 1994). The minimal tree for Paralamyctes differs from this sequence, including its relationship between New Zealand and northern Queensland (rather than the latter being related to southeastern Australia) and the anomalously basal placement of southern South America relative to Africa + India and East Gondwana (areas within Australia and New Zealand).

Accepting the branching patterns in the minimal tree to be results of Gondwanan fragmentation (e.g. split between New Zealand and eastern Australia by opening of the Tasman Sea from 80 mya and split between southern Africa and East Gondwana by a spreading centre from 160 mya (Lawver et al., 1992), the biogeographic patterns implied for Patagonia and southeastern Australia might reflect aspects of an older history than is generally inferred for these areas. For example, the isolation of southernmost Australia and north Queensland may date to the Early Cretaceous fragmentation of Australia by epicontinental seaways (BMR Palaeogeographic Group, 1990). Reconciling the minimal tree with the conventional geological model can be made by postulating extinction of lineages of each subgenus on certain fragments of Gondwana, although this reconciliation is ad hoc.

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References


Newport, G. (1845) Monograph of the class Myriapoda, order


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Appendix 1. Taxon sampling used in the analyses and molecular partitions used for every taxon, with GenBank accession codes. 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); * indicates partial sequence fragments; *P. = *Paralamyctes*. Taxa without molecular data were used in the morphological and combined analyses.

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Appendix 2

Voucher data for specimens used in molecular analyses. Institutional abbreviations: AM, Australian Museum, Sydney; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge; QVM, Queen Victoria Museum and Art Gallery, Launceston.

**Lithobius variegatus rubriceps** Newport, 1845
Sant Llorenç (Barcelona, Spain)
7 November 1994; J. Pujade
MCZ 28608

**Lithobius obscurus** Meinert, 1872
33°56' S 18°28' E
Newlands Forest, E slope of Table Mountain, Cape Town (Cape District, Western Cape Province, South Africa)
11 November 1999; L. Prendini
Afromontane forest
MCZ 28610

**Australobius scabrior** Chamberlin, 1920
26°41’54” S 152°35’05” E
Intersection of Sunday Creek Road and Gigher Creek Road, Kenilworth area (Queensland, Australia)
7 May 1998; G.D. Edgecombe, S. Davis & G. Milledge
Under eucalypt bark; wet sclerophyll forest
AM KS 57956

**Bothropolys multidentatus** (Newport, 1845)
Columbia (Maryland, U.S.A.)
Autumn 1995; J.W. Shultz
MCZ 28611

**Anopsobius** sp., TAS
41°02' S 145°22' E
Dip Falls, CQ 633 555 (220 m) (Tasmania, Australia)
Under moss on rotting log; fire-regenerated wet eucalypt forest, *Eucalyptus obliqua over Pomaderris apetala* and *Acacia melanoxylon*
AM KS 57957

**Anopsobius neozelanicus** Silvestri, 1909
Purple Peak trackway, Hinewai Reserve, Banks Peninsula (South Island, New Zealand)
8 December 1998; G.D. Edgecombe, Z. Johanson & P.M. Johns
Under logs in *Nothofagus fusca* forest
AM KS 57958

**Anopsobius** sp., NSW
30°30' S 152°24' E
Tom’s cabin (1300 m), New England National Park (New South Wales, Australia)
*Nothofagus*-mossy cool temperate rainforest; litter sifting
AM KS 57959

**Esastigmatobius japonicus** Silvestri, 1909
Mt Men-noki (390 m), Tanbara-cho, Shuso-gun, Ehime Prefecture (Shikoku, Japan)
25 April 2000; T. Tsurusaki
MCZ 28612

**Lamyctes emarginatus** (Newport, 1844)
Australian Museum garden, Sydney (New South Wales, Australia)
27 August 1998; G.D. Edgecombe
AM KS 57960

**Lamyctes africanus** (Porat, 1871)
33°56’ E 18°28’ E
Newlands Forest, E slope of Table Mountain, Cape Town (Cape District, Western Cape Province, South Africa)
11 November 1999; L. Prendini
Afromontane forest
MCZ 28613

**Lamyctinus coeculus** (Broëlemann, 1889)
33°16’ S 150°41’ E
13.4 km N of Colo Heights work depot, Putty Road, Melling Long Reach (New South Wales, Australia)
14 March 2000; G.D. Edgecombe, G. Giribet & Z. Johanson
Soil and under eucalypt bark; dry eucalypt/Avocado forest
AM KS 57961

**Henicops maculatus** Newport, 1844, NSW
33°33’ S 150°25’ E
3 km W of Mount Tomah (New South Wales, Australia)
26 January 1996; G.D. Edgecombe & Z. Johanson
AM KS 57962

**Henicops maculatus** Newport, 1844, TAS
41°33’ S 145°45’ E
Upper Southwell River, CP 955 987 (700 m) (Tasmania, Australia)
10 February 1998; G.D. Edgecombe, Z. Johanson & R. Mesibov
Mossy rainforest
AM KS 57963

**Henicops maculatus** Newport, 1844, NZ
Ruato, 6.5 km E of Hell’s Gate, southern shore of Lake Rotoiti (North Island, New Zealand)
29 November 1998; G.D. Edgecombe & Z. Johanson
AM KS 57964

**Henicops** sp., QLD
26°40’11” S 152°36’35” E
Sunday Creek Road, 9.8 km W of Charlie Moreland Park, Kenilworth State Forest (Queensland, Australia)
6 May 1998; G.D. Edgecombe, S. Davis & G. Milledge
Wet sclerophyll forest
AM KS 57965

**Paralamyctes (Paralamyctes) harrisi** Archey, 1922
Ruato, 6.5 km E of Hell’s Gate, southern shore of Lake Rotoiti (North Island, New Zealand)
29 November 1998; G.D. Edgecombe & Z. Johanson
Paralamyctes (Paralamyctes) monteithi Edgecombe, 2001, NE QLD
17°25′29″ S 145°29′00″ E
The Crater, Mount Hypipamee National Park (Queensland, Australia)
25 April 1998; G.D. Edgecombe, G. Cassis, S. Davis & G. Milledge
Rainforest
AM KS 57901

Paralamyctes (Paralamyctes) monteithi Edgecombe, 2001, ME QLD
21°04′ S 148°34′30″ E
Dalrymple Road, 1.7 km NE of junction with Snake Road, Eugella National Park (Queensland, Australia)
21 April 1998; G.D. Edgecombe, S. Davis & G. Milledge
Rainforest
AM KS 57908

Paralamyctes (Paralamyctes) weberi Silvestri, 1903
33°56′ S 18°28′ E
Newlands Forest, E slope of Table Mountain, Cape Town (Cape District, Western Cape Province, South Africa)
11 November 1999; L. Prendini
Afromontane forest
MCZ 28614

Paralamyctes (Paralamyctes) neverneverensis Edgecombe, 2001
30°22′ S 152°44′ E
Wonga Walk, 200 m E of Tristania Falls, Dorrigo National Park (New South Wales, Australia)
Rainforest litter
AM KS 57955

Paralamyctes (Nothofagobius) mesibovi Edgecombe, 2001
41°31′03″ S 145°31′24″ E
Coldstream River CQ768027 (600 m) (Tasmania, Australia)
9 March 2000; R. Mesibov
Selectively logged old-growth rainforest, Nothofagus cunninghamii over Atherosperma moschatum and Dicksonia antarctica
QVM 23 : 41377

Paralamyctes (Haasiella) trailli (Archey, 1917)
Purple Peak trackway, Hinewai Reserve, Banks Peninsula (South Island, New Zealand)
8 December 1998; G.D. Edgecombe, Z. Johanson & P.M. Johns
Under logs in Nothofagus fusca forest
AM KS 57966

Paralamyctes (Haasiella) sp., TAS (= Wailamyctes sp. of Mesibov, 1986)
41°11′ S 145°28′ E
Southern Creek, CQ 708 405 (300 m) (Tasmania, Australia)
18 April 2000; R. Mesibov
Wet eucalypt forest, self-regenerated following heavy logging c. 40 years ago, Eucalyptus obliqua regrowth
QVM 23 : 41378

Paralamyctes (Haasiella) sp., NZ
Ruato, 6.5 km E of Hell’s Gate, southern shore of Lake Rotoiti (North Island, New Zealand)
29 November 1998; G.D. Edgecombe & Z. Johanson
AM KS 57967

Paralamyctes (Thingathinga) grayi Edgecombe, 2001, NSW1
33°46′ S 150°28′ E
Ingar picnic area, Blue Mountains National Park (New South Wales, Australia)
21 April 2000; G.D. Edgecombe, G. Giribet & Z. Johanson
AM KS 57936

Paralamyctes (Thingathinga) grayi Edgecombe, 2001, NSW2
34°42′ S 150°30′ E
6.8 km N of Hamptden Bridge, Mount Barrengarry (New South Wales, Australia)
13 November 1997; G.D. Edgecombe & Z. Johanson
Rainforest litter
AM KS 57932

Paralamyctes (Thingathinga) ?grayi Edgecombe, 2001
32°07′04″ S 151°25′33″ E
Mount Allyn Forest Park, Chichester State Forest, Barrington Tops (970 m) (New South Wales, Australia)
16 March 1999; G.D. Edgecombe & Z. Johanson
Rainforest
AM KS 57940

Paralamyctes (Thingathinga) validus Archey, 1917, NZ1
Mutukuru Reserve, Waitakere Ranges (North Island, New Zealand)
27 November 1998; G.D. Edgecombe & Z. Johanson
AM KS 57969

Paralamyctes (Thingathinga) validus Archey, 1917, NZ2
2.4 km W of Ohakune (610 m), Ohakune Lakes Reserve (North Island, New Zealand)
1–3 December 1998; G.D. Edgecombe & Z. Johanson
AM KS 57970

Paralamyctes (Thingathinga) validus Archey, 1917, NZ3
Purple Peak trackway, Hinewai Reserve, Banks Peninsula (South Island, New Zealand)
8 December 1998; G.D. Edgecombe, Z. Johanson & P.M. Johns
Under logs in Nothofagus fusca forest
AM KS 57968

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### Appendix 3. Morphological character matrix.

Characters 1–49 are as described in the text. A = polymorphism: 0 and 1.

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Appendix 4. Cladogram lengths for the individual datasets (18S: 18S rRNA; 28S: 28S rRNA; 16S: 16S rRNA; 12S: 12S rRNA; COI: cytochrome c oxidase I; MOR: morphology) and combined datasets (MOL: molecular – 18S + 28S + 16S + 12S + COI); TOT: combined (18S + 28S + 16S + 12S + COI + mor) at different parameter sets (PAR), and ILDs for the combined analyses of all molecular data (ILD-1) and all data (ILD-2), at parameter sets 110–441. ILD numbers in italics reflect the minimum incongruence among datasets. PAR indicates ratio between gap-cost : transversion-cost : transition-cost (i.e. 110 indicates a gap : transversion ratio of 1, and a transversion : transition ratio of infinity (gap cost = 1; transversion cost = 1; transition cost = 0); 241 indicates a gap : transversion ratio of 2, and a transversion:transition ratio of 4 (gap cost = 8; transversion cost = 4; transition cost = 1)).

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