

DELIMITATION AND PHYLOGENETICS OF THE DIVERSE LAND-SNAIL FAMILY UROCOPTIDAE (GASTROPODA: PULMONATA) BASED ON 28S rRNA SEQUENCE DATA: A REUNION WITH *CERION*

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ABSTRACT

The extreme morphological diversity in the land-snail family Urocoptidae has complicated its delimitation from other land-snail families, and has obscured its intra- and interfamilial phylogenetic relationships. Using an independent dataset of 28S rRNA DNA-sequence data, I tested morphology-based hypotheses about these relationships. These data refute the recent placement of the Australian genus *Coelocion* within the Urocoptidae. Instead, they provide strong support for a North American/circum-Caribbean clade, to be named Urocoptoidea (new superfamily), which consists of the families Urocoptidae and Cerionidae. In all optimal trees (maximum likelihood, maximum parsimony and Bayesian), *Cerion* is nested among New World Urocoptidae, rather than occupying a basal position as their sister group. Even so, the monophyly of the New World Urocoptidae could not be statistically rejected. Judging from the fossil record, the superfamily Urocoptoidea originated in the southwestern part of the North American continent, where it was widespread by the late Cretaceous. The Antillean Urocoptoidea most likely constitute three separate lineages that may have been carried eastward on the proto-Antillean island arc, which started in the late Cretaceous from a position near the SW North American landmass. Shell characters used in urocoptid classification are re-evaluated in the light of these results, and consequences for taxonomy and implications for evolutionary research are discussed.

INTRODUCTION

The land-snail family Urocoptidae displays a staggering conchological and taxonomic diversity. Shells range from discoidal to highly conic, shell sculpture from smooth to strongly ribbed, and the columella can be solid or hollow, with enormous variation in the number and form of lamellae. The family contributes significantly to the land-snail diversity in the southwestern North American and circum-Caribbean regions. More than 500 species have been listed from Cuba alone (Jaume & de la Torre, 1976), which accounts for more than one-third of the total number of terrestrial snail species known from the island (Espinosa & Ortea, 1999). Up to 87 genera (Schileyko, 1999a) have been recognized, the exact number depending on the delineation of the family.

The family name Urocoptidae (+ Cyliindrellidae Tryon, 1868; see Bouchet *et al.*, 2005) was introduced by Pilsbry & Vanatta (1898) for an assemblage of high-spired New World land snails, including the Caribbean genus *Cerion* and the Brazilian genus *Megaspira*. These latter two genera were later each moved into their own family (Pilsbry, 1901–1902, 1904), leaving a group of circum-Caribbean and southwestern North American Urocoptidae. Pilsbry (1904) admitted that ‘few if any characters special to the group run through all [urocoptid] genera’, but argued ‘yet so interlaced are the varying combinations of structural peculiarities, that the whole is bound into one group of forms, undoubtedly of common ancestry’. Even

so, such a network of similarities is difficult to interpret in phylogenetic and taxonomic terms.

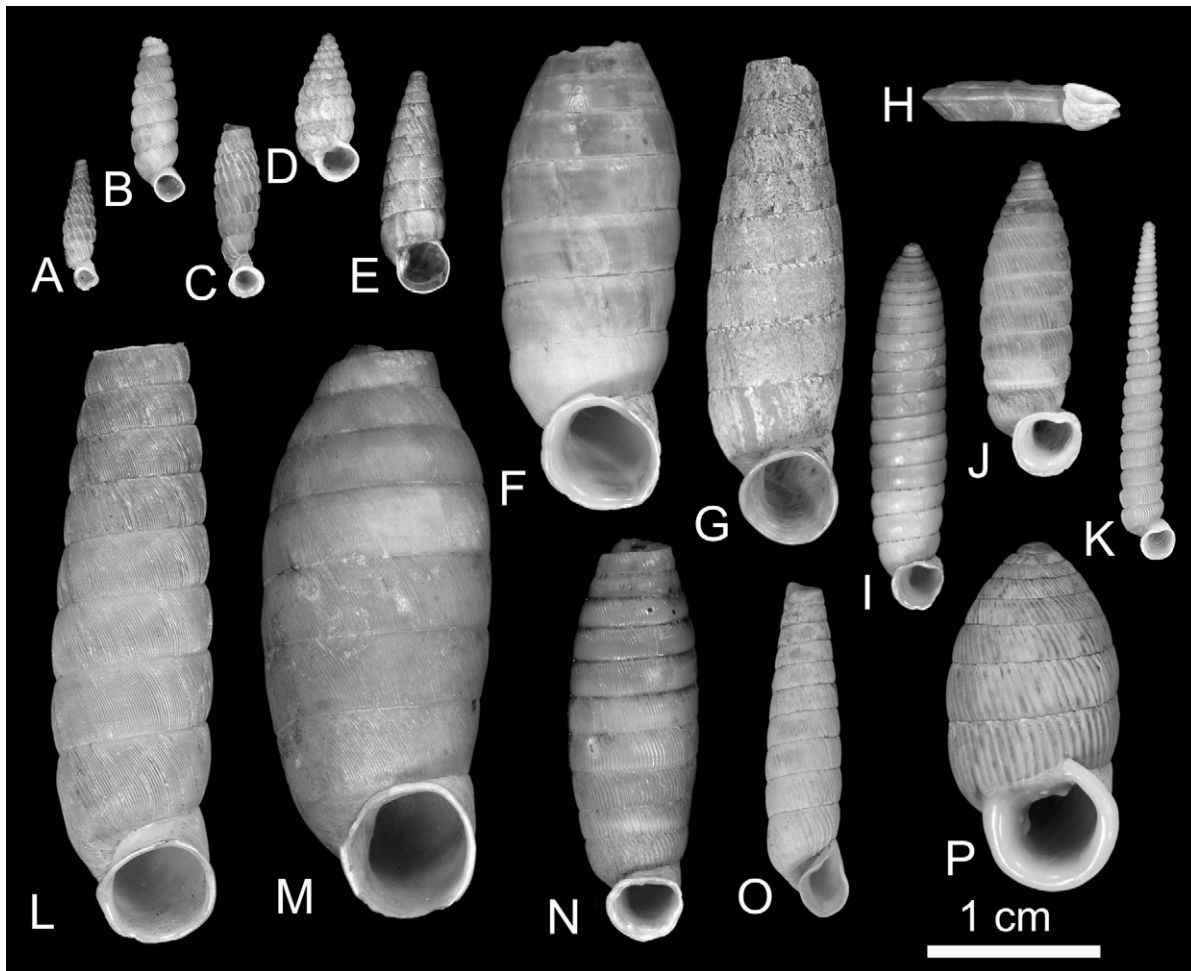
So far, urocoptid classification has been based on conchological characters as well as the morphology of the feeding apparatus, and scanty information about the soft anatomy. Genera have been identified as urocoptid based on the presence of one or more of the following conchological characters (Pilsbry, 1903, 1946; Schileyko, 1999a): (1) a high-spired shell with many narrow whorls; (2) the presence of columellar sculpture; (3) the breaking off (decollation) of the early whorls; (4) a circular or squarish aperture with an expanded or reflexed peristome. Taken separately, none of these conchological characters is unique to the family, or even present in all 87 genera that have been identified as urocoptid (Schileyko, 1999a). Although the family as a whole does not have any unique anatomical characters (see Schileyko, 1999a), genera have been included in the family (Dall, 1905) or removed from it (Christensen & Miller, 1975) based on soft-anatomical similarities with particular urocoptids or non-urocoptids, respectively. The latest revision of Urocoptidae (Schileyko, 1999a) recognizes eight subfamilies (Table 1): five predominantly Antillean subfamilies, two subfamilies from southwestern North America and one Australian subfamily. Not all authors agree with the identification of the North American and Australian subfamilies as urocoptid, however.

Central to urocoptid classification is a core group of Antillean genera (Fig. 1A–F), among which is the type genus *Urocoptis*, which are considered to have a specialized feeding apparatus (Pilsbry, 1904: 152, 1946: 109). All Antillean urocoptid genera examined by Pilsbry (1903, 1904), other than the Hispaniolan genus *Archegocoptis* (Fig. 1G) (see Pilsbry,

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Table 1. Subfamilies of Urocoptidae recognized by Schileyko (1999a), with their number of genera and distribution. Recognition of the plaited-jawed urocoptid group after Pilsbry (1904, 1946).

Subfamily	Number of genera	Distribution	
Coelociontinae	1	Queensland, Australia	
Holospirinae	15	SW USA, Mexico, Belize, Guatemala	New World Urocoptidae
Eucalodiinae	4	Central and S Mexico, Guatemala	
Urocoptinae	9	<i>Archeogocoptis</i> : Hispaniola	plaited-jawed urocoptids
		Other: Cuba, S-Florida, Jamaica, Hispaniola	
Apominae	6	Jamaica, Swan and Grand Cayman islands, Haiti	
Brachypodellinae	1	Antilles, Northern S America, Central America, S Mexico	
Microceraminae	6	S Florida, S Texas to Costa Rica, Bahamas, Dutch Leeward Antilles	
Tetrentodontinae	45	Cuba and adjacent Bahamas, Hispaniola	
Total	87	SW North America, circum-Caribbean area, Australia	

**Figure 1.** Shells of genera classified with the Urocoptidae (A–O) and Cerionidae (P). See Table 1 for the higher-level classification of these genera. Asterisks indicate specimens from populations sampled in this study. A. *Brachypodella dominicensis gabbi**. B. *Simplicivex inornata**. C. *Torrecoptis holguinensis**. D. *Microceramus pontificus**. E. *Macroceramus microdon**. F. *Archeogocoptis menkeana*. G. *Archeogocoptis crenata*. H. *Hendersoniella palmeri simplex*. I. *Coelostemma* sp. nov.* J. *Holospira goldfussi*. K. *Epirobia polygyra*. L. *Eucalodium speciosum*. M. *Anisospira liebmanni*. N. *Dissotropis* sp.* O. *Coelocentrum australis*. P. *Cerion striatellum**.

1903: 302), were found to have a very thin high-arched jaw consisting of many narrow converging plates ('plaited jaw') which form a V-shape in its centre (Pilsbry, 1904: 152, 1946: 109) (Fig. 2A), as well as a radula with a narrow median tooth (Pilsbry, 1904: 152, 1946: 109). These genera and the genera allied with them on the basis of conchological similarity have

been placed in five different subfamilies: Apominae Paul, 1982, Brachypodellinae Baker, 1956, Microceraminae Pilsbry 1904 (*sensu* Schileyko, 1999a), Tetrentodontinae Bartsch, 1943 and Urocoptinae Pilsbry, 1898. In contrast to Pilsbry (1903, 1904, 1946), Schileyko (1999a) included *Archeogocoptis* within the otherwise plaited-jawed subfamily Urocoptinae, assuming that

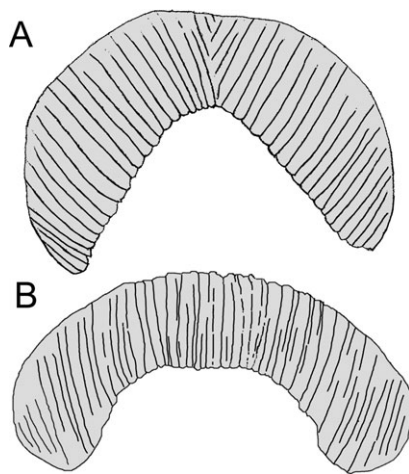


Figure 2. Example of (A) a high-arched plaited jaw (*Microceramus pontificus*) and (B) a non-plaited-jaw (*Archeogocoptis crenata*). Both drawings are modified from those by Pilsbry (1904: pl. 14, fig. 4; 1903: pl. 63, fig. 46; no scale bar provided), which were used to distinguish the groups.

differences in the feeding apparatus ‘reflect predominantly the dietary specialization’. He did not list characters supporting this rearrangement. Excluding *Archeogocoptis*, the five subfamilies combined contain 66 genera, an assemblage hereafter referred to as the plaited-jawed urocoptid group. Of these, 59 are endemic to the Greater Antilles, and 63 to the West Indian islands as a whole. Only three genera of the plaited-jawed urocoptid group have a range extending into the continental regions surrounding the Caribbean.

No uniquely shared characters have been reported that support the placement of *Archeogocoptis* (Fig. 1G) and of the two southwestern North American subfamilies, Holospirinae Pilsbry, 1946 (Fig. 1H–K) and Eucalodiinae Fischer & Crosse, 1873 (Fig. 1L–N) in the family Urocoptidae together with the plaited-jawed urocoptid group. Both North American subfamilies and *Archeogocoptis* have a striate, non-plaited jaw (Fig. 2B), and a normal, helicid-like radula, which constitute ‘the archaic type of mouth parts’ according to Pilsbry (1903: 302). He assigned *Archeogocoptis* to the subfamily Eucalodiinae based on conchological similarities with the genus *Eucalodium*. Based on their feeding apparatus, the North American urocoptid genera were initially (Crosse & Fischer, 1870) assigned to the family Helicidae, whereas the Antillean genera studied were placed in the Cylindrellidae (Crosse & Fischer, 1870). This study did not include *Archeogocoptis*. Later Morrison (1953) suggested that the subfamilies Holospirinae and Eucalodiinae, including *Archeogocoptis*, are more closely related to the North American family Polygyridae, based on their essentially North American distribution and on ‘anatomical features including the radula’. He placed these subfamilies in the family Eucalodiidae. Elucidating the phylogenetic position of the Holospirinae and Eucalodiinae is important not only for nomenclatorial reasons (Roth, 2000), but also for a better understanding of the evolution and biogeography of these subfamilies and the Antillean urocoptids.

A final taxon of uncertain affinity with the Urocoptidae is the Australian genus *Coelocion* (Fig. 1O). Schileyko (1999a) transferred this genus to the Urocoptidae, including the Eucalodiinae and Holospirinae, on the basis of conchological similarity. Its shell has the same shape and size as that of the Urocoptidae, and it has a wide, hollow columella carrying spiral lamellae (see Schileyko, 1999a: fig. 566), a combination of characters otherwise only found in various holospirine

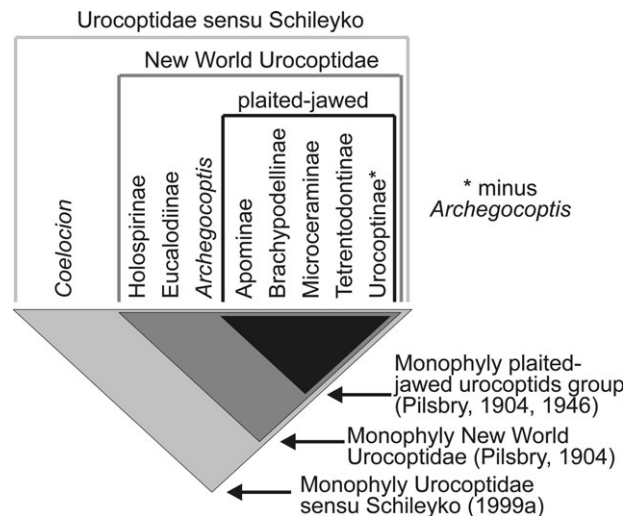


Figure 3. Hypotheses tested. Monophyly of New World Urocoptidae after Pilsbry (1904). Monophyly of plaited-jawed urocoptid group after Pilsbry (1904, 1946). For further information about both these groups, see Table 1. *Urocoptinae minus *Archeogocoptis*.

species. Only its Australian distribution and its elongated ovate aperture distinguish *Coelocion* from the Urocoptidae. Others (Nordsieck, 1986; followed by Bouchet *et al.*, 2005) included both *Coelocion* and the Urocoptidae in the larger superfamily Orthalicoidea, but within this assigned *Coelocion* to a separate family, the Coelociontidae Iredale 1937 (+ Coelociidae Nordsieck, 1986). This family also includes the genus *Perrieria* from New Guinea. Nordsieck (1986) defined ‘Coeloci[on]tidae’ on the basis of its Australian–New Guinean distribution and its fold system: ‘if fully developed with palatal plica, columellar lamellae simple’ (but see Schileyko, 1999b: 540; Pilsbry, 1906: 36). Besides Urocoptidae and Coeloci[on]tidae Nordsieck (1986) recognized three additional extant orthalicooid families: Orthaliciidae (Orthaliciidae + Placostylidae *sensu* Bouchet *et al.*, 2005; Bulimulidae *s.l.* *sensu* Herbert & Mitchell, in press), Cerionidae (but see Wade, Mordan, & Naggs, 2006) and Megaspiridae. He does not present explicit hypotheses about the phylogenetic interrelationships between these families, but stated that ‘Urocoptidae and Ceri[on]tidae are related’ (Nordsieck, 1985). This conclusion was based on unspecified similarities in the male part of the genitalia. Such genital–anatomical data are lacking for *Coelocion*, however, and the genus’ systematic position and that of the so-called family Coelociontidae remain uncertain (Nordsieck, 1986).

In conclusion, the assignment of taxa to the family Urocoptidae and the family’s delimitation are based almost exclusively on conchological characters and those of the feeding apparatus. Since these are the characters that can be expected to interact most directly with the environment, they could be prone to parallel or convergent evolution (Pilsbry, 1904). Here I present the first test of the hypotheses about urocoptid (inter)relationships, using an independent DNA-sequence dataset. Using sequences of more than half of the nuclear large subunit ribosomal RNA gene, I will test the following nested hypotheses (from bottom to top in Fig. 3):

- (1) Monophyly of the Urocoptidae *sensu* Schileyko (1999a): the New World Urocoptidae form a monophyletic group with the genus *Coelocion*, to the exclusion of Cerionidae.
- (2) Monophyly of the New World Urocoptidae (Pilsbry, 1904): the subfamilies Eucalodiinae and Holospirinae, and the genus *Archeogocoptis*, constitute a monophyletic group

together with the plaited-jawed urocoptid group, to the exclusion of the Polygyridae.

- (3) Monophyly of the plaited-jawed urocoptid group (Pilsbry, 1904, 1946): all plaited-jawed urocoptids form a clade, thus separating *Archegocoptis* from the subfamily Urocoptinae.

MATERIAL AND METHODS

Given the nested nature of the hypotheses to be tested (Fig. 3), samples spanning a range of taxonomic levels were included in the analyses (see Table 2). All eight urocoptid subfamilies as recognized by Schileyko (1999a) are represented, as well as the former subfamily Macroceraminae, which he merged into the Microceraminae. Of the subfamilies Eucalodiinae and Holospirinae three and four samples, respectively, were included. This was done because their position might be basal to the other Urocoptidae subfamilies (Pilsbry, 1904: xxiv), in which case they would represent an important part of the genetic diversity within the family. In order to test for a close relationship of the Eucalodiinae and Holospirinae with the Polygyridae (Morrison, 1953), two genera from this family were included. The sampling of other non-urocoptid groups is based on previous classifications of stylommatophoran land snails combined with insights from Wade *et al.* (2006) and on availability. Genera of the Clausilioidea and Orthalicoidea clades (Wade *et al.*, 2006) were sampled to represent these two superfamilies. The Urocoptidae have been associated with either of these two superfamilies (cf. Nordsieck, 1986;

Tillier, 1989), as have the Cerionidae and the Megaspiridae. Cerionidae was represented in the analyses, but no tissue could be obtained of the Brazilian family Megaspiridae. It is unlikely that the omission of the Megaspiridae introduces a bias, since new DNA-sequence data (Ueshima, personal communication) indicate that the family is not closely related to the Urocoptidae. To further accommodate for the uncertainty about the position of the Urocoptidae, five stylommatophoran sequences representing other superfamilies of stylommatophoran pulmonates were either retrieved from GenBank or sequenced as part of this study. Of these, the sequence of *Lamellaxis*, being part of the basal 'achatinooid' clade (Wade, Mordan & Clarke, 2001; Wade *et al.*, 2006) served to root the phylogeny.

Total genomic DNA was extracted (DNAeasy[®] Tissue Kit, Qiagen) from 1 to 4 mm³ tissue, using either the foot or the entire animal when small. Shells were kept as vouchers. DNA thus extracted was dissolved in 300 µl buffer. The 5' part of the 28S rRNA gene, spanning regions D1 to D7b (Hassouna, Michot & Bachellerie, 1984), was PCR-amplified and sequenced directly using various combinations of primers (see Table 3). For each sample, the 28S regions amplified overlapped, with variable positions in their region of overlap, as a control against possible sample swapping further in the process. Depending on the quantity of DNA, the PCRs consisted of 40–45 cycles (1 min denaturation at 94°C, 1 min annealing at 60°C and 1 min extension at 72°C), preceded by 4 min denaturation at 94°C, and followed by 10 min extension at 72°C. The 25-µl PCR mix (Qiagen Taq PCR Core Kit) for each reaction contained 1 × Q solution, 1 × PCR buffer, 0.4 µM of each primer,

Table 2. Species sampled in this study.

Taxonomic position		Species	GenBank	Location	
Superfamily	Family	Subfamily			
Orthalicoidea	Urocoptidae	Apominae	<i>Simplicivervix inornata</i> (C.B. Adams, 1849)	EU409894	Jamaica
		Brachypodellinae	<i>Brachypodella dominicensis gabbi</i> Pilsbry, 1904	EU409895	Barahona, Dominican Rep.
		Coelociontinae*	<i>Coelocion australis</i> (Forbes, 1851)	EU409896	Queensland, Australia
		Eucalodiinae	<i>Anisospira liebmanni</i> (L. Pfeiffer, 1846)	EU409897	Oaxaca, Mexico
			<i>Dissotropis</i> sp. nov. Solem, 1957	EU409899	Guerrero, Mexico
			<i>Eucalodium</i> sp. (<i>speciosum/boucardi</i> complex)	EU409900	Veracruz, Mexico
			<i>Coelostemma</i> sp. nov.	EU409901	San Luis Potosi, Mexico
		Holospirinae	<i>Epirobia polygyra</i> (L. Pfeiffer, 1856)	EU409902	Veracruz, Mexico
			<i>Hendersoniella lux lux</i> Thompson & Correa S., 1991	EU409903	San Luis Potosi, Mexico
			<i>Holospira fortisculpta</i> Thompson & Mihalcik, 2005	EU409904	Puebla, Mexico
			<i>Macroceramus microdon</i> (L. Pfeiffer, 1853)	EU409905	Distrito Arecibo, Puerto Rico
		Microceraminae	<i>Macroceramus pontificus</i> (Gould, 1848)	EU409906	Florida, USA
			Tetrentodontinae	<i>Torrecoptis holguinensis</i> (Aguayo, 1934)	EU409907
		Urocoptinae	<i>Autocoptis menkeana</i> (L. Pfeiffer, 1853)	EU409908	Bahoruco, Dominican Rep.
			<i>Archegocoptis crenata</i> (Weinland & von Martens, 1859)	EU409898	Département de l'Ouest, Haiti
			<i>Cerion striatellum</i> Guerin-Meneville, 1829	EU409909	Puerto Rico
Cerionidae	<i>Bulimulus diaphanus</i> (L. Pfeiffer, 1854)	EU409910	Clarendon Parish, Jamaica		
	Orthalicoidea	<i>Lamellaxis gracilis</i> (Hutton, 1834)	DQ256733 ¹		
Achatinoidea	Subulinidae	<i>Arion silvaticus</i> Lohmander, 1937	AY145392 ²		
Arionoidea	Arionidae	<i>Nenia tridens</i> (Schweigger, 1786)	EU409911	Distrito de Bayamón, Puerto Rico	
Clausilioidea	Clausiliidae	<i>Polygyra cereolus</i> (Megerle von Mühlfeld, 1818)	EU409912	Grand Cayman	
Helicoidea	Polygyridae	<i>Praticolella martensiana</i> (Pilsbry, 1907)	DQ256730 ¹		
		<i>Deroceras reticulatum</i> (Müller, 1774)	AY145404 ²		
Limacoidea	Agriolimacidae	<i>Helicodiscus parallelus</i> (Say, 1821)	DQ256731 ¹		
Punctoidea	Helicodiscidae	<i>Sagda spei</i> Pilsbry & Brown, 1910	EU409913	Manchester Parish, Jamaica	
Sagdoidea	Sagdidae	<i>Mesomphix globosus</i> (MacMillan, 1940)	DQ256732 ¹		
Zonitoidea	Zonitidae				

Sub-familial assignment of the urocoptid species according to Schileyko (1999a), classification of other taxa following Bouchet *et al.* (2005). *Considered a separate orthalicooid family by Bouchet *et al.* (2005). All sequences were determined as part of this study, except for those with superscript numbers, which were retrieved from GenBank: (1) by Holznagel & Lydeard, submitted in 2005; (2) by Passamaneck, Schander & Halanych (2004).

Table 3. PCR and sequencing primers used in this study.

Primer name (order from 5' to 3')	Direction	Sequence	Origin
28S2	Forward	GACCTCAGATCGGRCGAGATTAC	Ueshima (personal communication)
28S800	Forward	GCAGAGWGCCACAACCGGTT	Ueshima (personal communication)
28S599Apr	Reverse	ACCCACCAGGCTTGTCRCC	This study
28SAlb607R	Reverse	GGACGCGAGCGCCCCACCTAC	This study
28S1128	Forward	CGTCTTGAAACACGGACCAAG	Ueshima (personal communication)
28S1145	Reverse	GAACCTCCACCAGAGTTTCCTC	Ueshima (personal communication)
28S1489F	Forward	TGTAACAACCTCACCTGCCGAATCA	This study
28S2119R	Reverse	GCTACTACCACCAAGATCTGC	Ueshima (personal communication)
28S2210R	Reverse	GACCCAGCCCTCAGAGCCAATCC	This study

0.2 μ M of each dNTP, 2.5 U of *Taq* DNA polymerase, and 1–3 μ l DNA-extraction product. Depending on the specificity of the PCR, PCR-product was either directly purified, or gel-purified, using Qiagen columns. Following the appropriate single-extension reactions, DNA was sequenced directly either by the author, using a CEQTM 8000 sequencer (Beckman Coulter), or at Macrogen Korea, using an ABI3730XL or ABI3700 sequencer.

Sequences were assembled and checked using the programs Pregap 4 and Gap 4, respectively. Both programs are part of the Staden Package (Staden, Beal & Bonfield, 2000). Sequence alignment was accomplished using the program CLC Free Workbench, Version 4.0.1 (CLC bio A/S). Ambiguously aligned regions were excluded from the analyses, using as boundaries the nearest invariable positions. The alignment was submitted to treeBASE. The model of sequence evolution for subsequent model-based analyses was selected by MrModeltest version 2.2 (Nylander, 2004), after running the standard MrModeltest modelblock in PAUP*4.0b10 (Swofford, 2002).

Bayesian analyses were performed using MrBayes version 3.1.2. (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). These analyses consisted of two parallel runs of 10,000,000 generations each, using the model selected by MrModeltest 2. Trees were sampled every 100 generations, and the first 5,000,000 generations of each analysis were discarded as a burn-in period. After this burn-in period, the standard deviation of the split frequencies had dropped permanently below 0.0057. The remaining 100,000 post burn-in trees of the combined runs were used to construct a majority rule consensus tree and to assign posterior probabilities to clades identified. Posterior probabilities of a priori hypotheses were obtained by filtering the set of post burn-in trees using constraint topologies representing the hypothesis in question.

Neighbour-joining (NJ), maximum likelihood (ML) and maximum parsimony (MP) analyses were performed using PAUP* Version 4.0b10 (Swofford, 2002). The model selected by MrModeltest version 2 was used in the NJ and ML analyses. The MP and ML trees were obtained through heuristic searches. The MP heuristic search consisted of 10,000 random addition replicates using TBR and steepest descent. In the case of ML analyses, each heuristic search for the ML tree was preceded by a short heuristic search consisting of a stepwise addition followed by TBR, using empirical base frequencies and estimating all other relevant parameters. This was done in order to find the optimal setting for these model parameters and implement them in the subsequent search (100 random addition replicates, TBR) for the ML tree.

NJ bootstrap analyses consisted of 10,000 bootstrap replicates, using the model of choice from MrModeltest 2. To make a ML bootstrap analysis amenable, not only the model but also its parameter settings were implemented according to MrModeltest 2. These ML bootstrap analyses consisted of 100

bootstrap replicates (five random addition replicates and TBR for each). MP bootstrap analyses were based on informative characters only, and consisted of 1,000 replicates (heuristic search with five random addition replicates and TBR with steepest descent).

In order to test the three hypotheses about urocoptid inter-relationships (Fig. 3), for each hypothesis the ML and MP trees with that particular topology were evaluated against the optimal ML and MP trees, respectively. Any alternative hypothesis was likewise tested. Trees compatible with a particular hypothesis were obtained through ML and MP searches with the appropriate topological constraints, using otherwise the same method as in the unconstrained search. The side-by-side log-likelihood scores for each set of ML trees compared were calculated in PAUP 4.0b10, using the same model as in previous ML analyses with empirical base frequencies. Based on these scores, probabilities were assigned to the trees using the approximately unbiased (AU) test (Shimodaira, 2002) and the weighted Shimodaira-Hasegawa (WSH) test (Shimodaira & Hasegawa, 1999; Shimodaira, 2002), as implemented in CONSEL 0.1i (Shimodaira & Hasegawa, 2001). Both tests were used because of their different qualities. The UA-test is less conservative than the WSH test, but unlike the WSH test it may break down when likelihood differences between the trees tested are small (Shimodaira, 2002). Whenever the optimal parameter settings were different for the trees compared, all calculations were performed twice using each parameter setting in turn, to check the effect of these differential settings on the probability scores of both trees. The MP trees were compared using the Templeton test (Templeton, 1983) as implemented in PAUP.

RESULTS

Dataset

The 28S sequences determined in this study varied in length from 2,131 bp in *Bulimulus* to 2,190 bp in *Eucalodium*. The indels responsible for this length variation were concentrated in 10 highly variable regions that were excluded from the analyses because of alignment ambiguities. The final dataset contained 11 one-base indels, and a single three-base indel. All of these indels were unique, except for one, viz. a shared one-base gap in the sequence of *Simplicervix* and *Brachypodella*. Initially, a 394 bp gap was found in *Archeogocoptis* in the 3' part of the 28S region studied. This missing part included the priming side of reverse primer 28S2119R that had previously been used for successful amplification. It was assumed that this gap was an artefact of the amplification process, perhaps caused by PCR-jumping between two identical 5-bp stretches (GGTGC, inferred from other taxa) on both sides of the missing region. A new primer (Arch28SF: CCCGGGTGCAGATCTTGGT

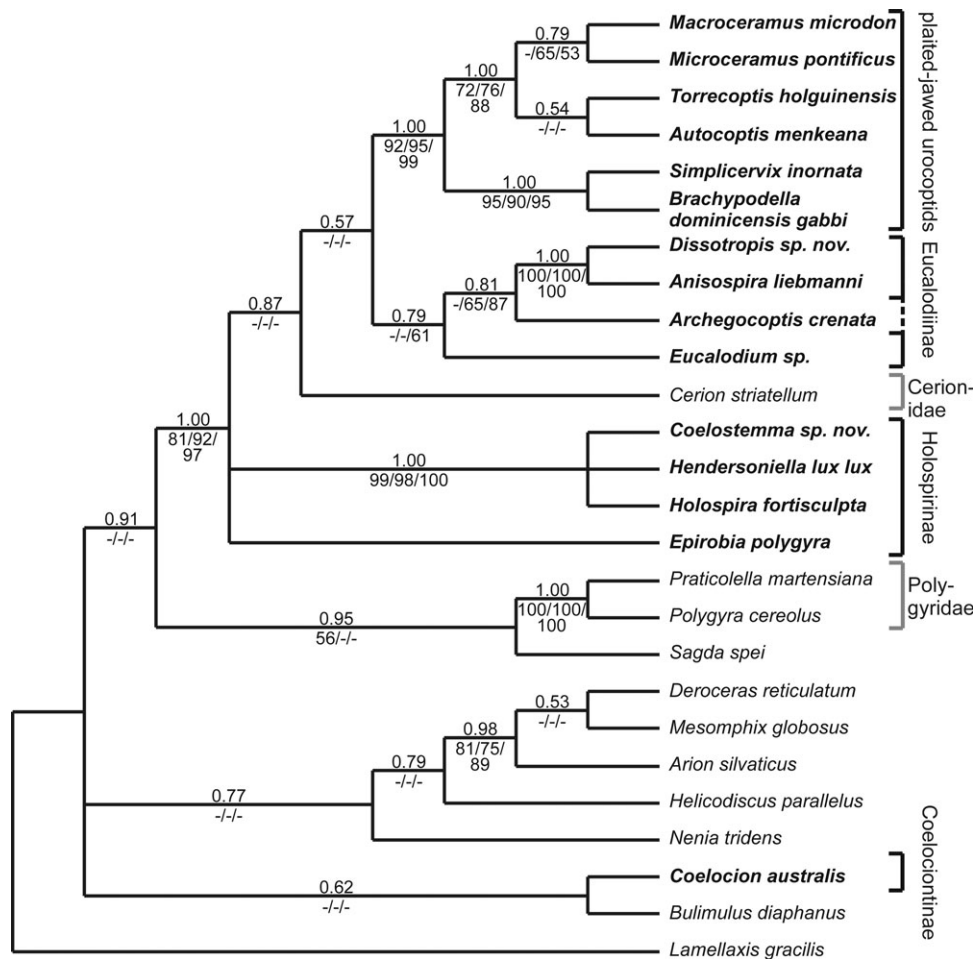


Figure 4. Majority rule consensus tree of the post burn-in trees from the Bayesian analysis. Names of species belonging to urocoptid genera according to Schileyko (1999a) are indicated in bold. Posterior probabilities are shown above branches. ML, MP and NJ bootstrap support values are shown, in that order, below branches. Dashes indicate bootstrap support values below 50%.

GGTAG), used in combination with primer 2210R, allowed for amplification of a region spanning only one of these two identical 5-bp stretches. Thus 379 of the missing 394 bp were recovered.

The dataset consisted of 2,035 positions that could be aligned unambiguously. Of these, 258 positions were variable (12.7%). The 3' part of the sequences turned out to be relatively highly conserved, with only 28 of the last 385 bases being variable (7.3%). The GTR + I + Γ model was selected as the best model of sequence evolution by both the hierarchical likelihood ratio test and the Akaike information criterion implemented in MrModeltest 2.2. All analyses produced trees that are congruent in their well-supported clades (Bayesian posterior probability >0.95; bootstrap value >70) (Fig. 4), with the exception of the branch grouping *Sagda* with the two Polygyridae (*Praticolella* and *Polygyra*), which has a high posterior probability but low bootstrap support.

Monophyly of the Urocoptidae (sensu Schileyko, 1999a)

In contrast to Schileyko's classification (Schileyko, 1999a), all analyses place the Australian genus *Coelocion* outside a well-supported (Bayesian posterior probability, BPP = 1.0; ML bootstrap support, MLB = 81%; MP bootstrap support, MPB = 92%; NJ bootstrap support, NJB = 97) clade of New World Urocoptidae plus *Cerion* (Fig. 4). According to the Bayesian analysis, the genus *Coelocion* is only distantly related

to the New World Urocoptidae. In the majority rule consensus tree from the Bayesian analysis, it groups with *Bulimulus* (BPP = 0.618) instead of with the New World Urocoptidae + *Cerion* (BPP = 0.000). Although these two clades together represent the superfamily Orthalicoidea, they do as such not constitute a monophyletic group according to the Bayesian analysis (BPP = 0.00013). In the ML tree *Coelocion* also clusters with *Bulimulus* (MLB < 50), whereas in the MP trees *Coelocion* is the sister group of all other ingroup taxa included, with the exception of *Helicodiscus* which branches off more basally. Neither in the ML nor in the MP tree does the New World Urocoptidae + *Cerion* clade form a monophyletic orthalicoid group with *Bulimulus* and/or *Coelocion*. Constraining the Urocoptidae including *Coelocion* to be monophyletic significantly decreases the likelihood and parsimony score compared to these unconstrained trees for all three tests ($P < 0.01$; Table 4). Thus the monophyly of the Urocoptidae *sensu* Schileyko (1999a) is rejected.

Monophyly of the New World Urocoptidae

As part of the New World Urocoptidae plus *Cerion* clade, the Eucalodiinae, the Holospirinae and *Archegocoptis* are more closely related to plaited-jawed urocoptids than to the Polygyridae (Fig. 4). Even so, none of the optimal trees retrieved the New World urocoptids as monophyletic, due to the unexpected nested position of *Cerion* among these

Table 4. *P*-values for the ML and MP topologies representing hypotheses of urocoptid (inter)relationships as compared to the optimal ML and MP tree.

Taxon	Topologies tested	ML analyses (GTR + I + Γ)			MP analyses	
		Δ log-li	<i>P</i> -value		Steps	Templeton (<i>P</i> , 1-tailed)
			AU test	WSH test		
Urocoptidae sensu Schileyko, 1999a	Optimal: non-monophyletic: ((NW Uroc. + Cerionidae), <i>Coelocion</i> , rest)	(-5878.0)	>0.99	>0.99	536	Optimal
	H ₀ : monophyletic (after Schileyko, 1999a): ((NW Urocoptidae + <i>Coelocion</i>), Cerionidae, rest)	46.3/46.1	<0.01**	<0.01**	554	<0.01**
NW Urocoptidae	Optimal: non-monophyletic: Cerionidae nested within NW Urocoptidae	(-5878.0)	0.96	0.92	536	Optimal
	H ₀ : monophyletic (after Pilsbry, 1904): ((Eucalodiinae + Holospirinae + <i>Archeogoc.</i> + other NW Uroc.), Polyg., rest)	3.6–3.7	0.08	0.38	537	0.16 < <i>P</i> < 0.41
	H ₁ : non-monophyletic (after Morrison, 1953): ((Eucalodiinae + Holospirinae + <i>Archeogoc.</i> + Polyg.), other NW Uroc., rest)	21.6–21.9	0.04*; 0.06 ^{H0}	0.06; 0.07 ^{H0}	544	0.04 < <i>P</i> < 0.07; 0.06 < <i>P</i> < 0.08 ^{H0}
Plaited-jawed urocoptid group	Optimal = H ₀ : monophyletic (after Pilsbry 1904; 1946): ((Urocoptinae + other plaited-jawed urocoptids), <i>Archeogocoptis</i> , rest)	(-5878.0)	>0.99	>0.99	536	Optimal
	H ₁ : non-monophyletic (after Schileyko, 1999a): ((Urocoptinae + <i>Archeogocoptis</i>), other plaited-jawed urocoptids, rest)	50.1/49.6	<0.01**	<0.01**	551	≤0.01**

Optimal trees are described in as far as they are similar for the ML and MP analyses, for further details see text. Values between parentheses are the log-likelihood scores of the optimal ML tree. *Significant at 5% level; **significant at 1% level. ^{H0}When compared with H0 only. Abbreviations: Polyg., Polygyridae; NW Uroc., New World Urocoptidae. *Archeogoc.*, *Archeogocoptis*

urocoptids. The basal phylogenetic relationships within the clade of New World Urocoptidae plus *Cerion* remain relatively unresolved. According to the Bayesian analysis, most probably the Holospirinae occupy a position basal to a clade (BPP = 0.867) comprising *Cerion* plus the sistergroups (BPP = 0.569) Eucalodiinae (including *Archeogocoptis*) and plaited-jawed urocoptids. Both clades are also retrieved in the maximum likelihood tree, but are poorly bootstrap supported (MLB < 50%). In the seven MP trees (length 536), *Cerion* is placed either (1) again as a sistergroup to the clade of Eucalodiinae and the plaited-jawed urocoptids (MPB < 50%) or (2) as sistergroup to the Holospirinae (MPB < 50%, but NJB = 54%).

The posterior probability of a clade of the New World Urocoptidae to the exclusion of *Cerion* is very low (BPP = 0.022), but it is not rejected by the AU and WSH tests (*P* > 0.05; Table 4). In the MP analyses only one additional transformation (537 vs 536) is required in order to have *Cerion* branch off basally to a clade of New World Urocoptidae (*P* > 0.16; Table 4).

Monophyly of the plaited-jawed urocoptid group

All plaited-jawed urocoptids are placed in a highly supported clade (BPP = 1.0; MLB = 92%; MPB = 95%; NJB = 99%) excluding the genus *Archeogocoptis*, which groups with the Eucalodiinae genera *Dissotropis* and *Anisospira* in all optimal trees (BPP = 0.811; MLB < 50%; MPB = 65; NJB = 87). Bayesian posterior probabilities support the monophyly of Eucalodiinae only when *Archeogocoptis* is included in this otherwise North American subfamily (BPP = 0.790 vs BPP = 0.046 without *Archeogocoptis*). The AU, the WSH and the Templeton test all refute a position of *Archeogocoptis* with the Urocoptinae (*P* ≤ 0.01; Table 4).

DISCUSSION

Phylogenetic relationships and evolution of characters used in urocoptid classification

The finding that the Australian alleged urocoptid *Coelocion* represents a lineage separate from the other, New World, Urocoptidae, suggests that an high-spired urocoptid-like shell with lamellae evolved independently on both continents. *Coelocion* is not unique in exhibiting a misleading conchological similarity to New World Urocoptidae. The Mexican genera *Berendtia* and *Spartocentrum* were once placed in the Urocoptidae as well, based on their high-spired urocoptid-like shells with spiral sculpture, until genital-anatomical studies revealed them to be members of the Bulimulidae (Christensen & Miller, 1975). Similar shells are also found in the Achatinoid clade, in the family Coeliacidae, which even itself is not monophyletic (Wade *et al.*, 2006). The recurrent evolution of high-spired shells with spiral lamellae may result from biomechanical selection pressures. High-spired shells that are raised to a horizontal position when the snail is moving experience more torque (Cain, 1977), an effect that may be compensated by spiral lamellae that offer extra support for the columellar muscle (Schileyko, 1979). According to the phylogeny found in this study, spiral lamellae must have evolved four times within the clade of New World Urocoptidae plus *Cerion* (Fig. 5). Moreover, this reconstruction underestimates the amount of homoplasy in this character, since even at the genus level there may be species with and without spiral lamellae, i.e. *Brachypodella* (Pilsbry, 1904: 67–88) and *Coelostemma* (Thompson, 1988). Likewise, according to the Bayesian consensus tree the other characters that *Coelocion* has in common with some of the New World Urocoptidae, shell-decollation and columella-type, are homoplasious characters even within the clade of New World Urocoptidae and *Cerion*. Within this

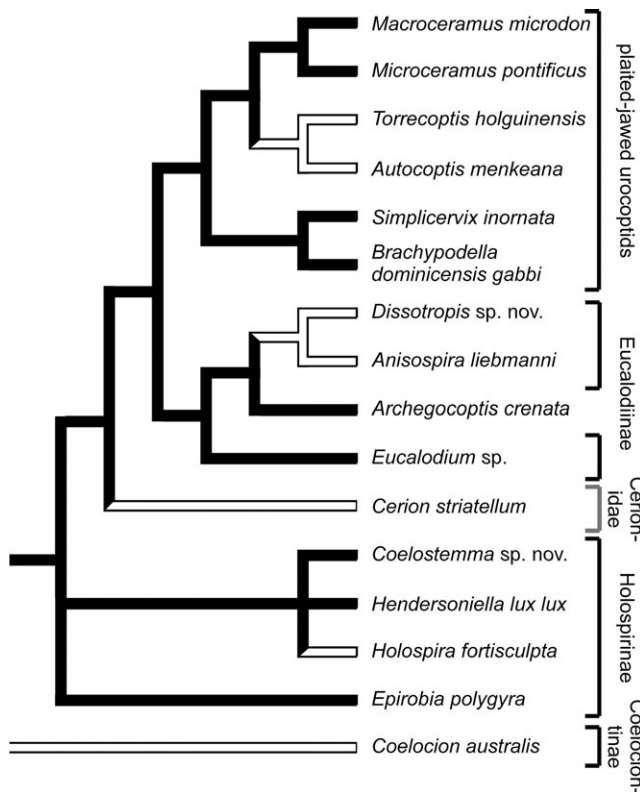


Figure 5. Inferred evolution of spiral lamellae among the Urocoptidae and *Cerion*, based on their presence (≥ 1) or absence in species sampled (see Pilsbry, 1901–1902, 1903, 1904; Thompson, 1968; Schileyko, 1999a, b), and the phylogenetic relationships of these species according to the majority-rule consensus tree of the post burn-in trees from the Bayesian analyses (Fig. 4). The (inferred) presence of ≥ 1 lamella is indicated by white branches, absence by black branches.

clade, the shell evolved from non-decollate to decollate to non-decollate again (Fig. 6). The columella either changed from hollow to solid to hollow within the clade of New World Urocoptidae plus *Cerion*, or alternatively it changed from solid to hollow at least twice (Fig. 7).

The observation that the family Cerionidae occupies a position nested within the New World Urocoptidae or at the very least is their sister group, necessitates a reinterpretation of the morphological characters that were used to separate *Cerion* from the Urocoptidae. The Cerionidae were initially set apart as a family in their own right, on the basis of unique genital characters and their ‘short, oblong kidney, with very extensive lumen’ (Pilsbry, 1901–1902: 176). Other authors reached different conclusions. Nordsieck (1985) stressed the genital-anatomical similarity between Cerionidae and Urocoptidae rather than the differences. The diagnostic value of kidney length in *Cerion* was questioned by Tillier (1989: 69), who pointed out the considerable variation between *Cerion* species. Thus these characters do not contradict the results of the current study.

Among Urocoptidae, *Cerion* is most similar to the Holospirinae. The so-called (Gould, 1989) triphasic shell of *Cerion* (Fig. 1P) resembles the cylindrical shell with a conic upper part found in the holospirine genera *Coelostemma* (Fig. 1I) and *Holospira* (Fig. 1J) (see also Schileyko, 1999a). The genus *Hendersoniella*, which is closely related to these two genera according to all analyses, is discoid and resembles the ‘button-like’ shell characteristic of the juveniles of some *Cerion* species (Gould, 1989). More generally, *Cerion* resembles the subfamily Holospirinae (see Thompson & Mihalcik, 2005)

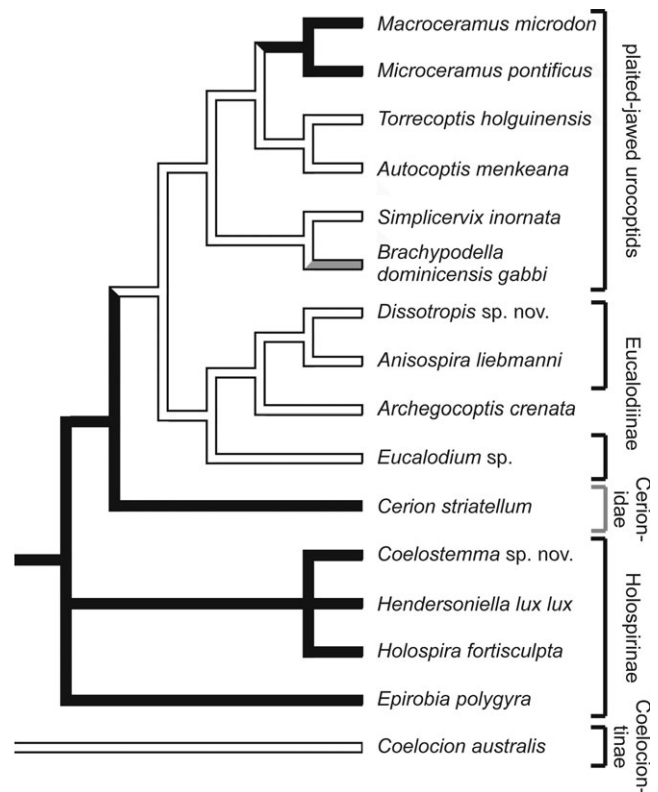


Figure 6. Inferred evolution of decollation among the Urocoptidae and *Cerion*, based on its occurrence in species sampled (see Pilsbry, 1901–1902, 1903, 1904; Schileyko, 1999a, b) and the phylogenetic relationships between these species according to the majority rule consensus tree of the post burn-in trees from the Bayesian analysis (Fig. 4). Black branches represent an inferred non-decollated shell, white ones an inferred decollated one. The grey branch indicates polymorphism in this trait in *Brachypodella dominicensis* (see Pilsbry, 1904).

in its non-decollate shell, which retains the apex at maturity. This feature is found in none of the other species in the clade of New World Urocoptidae plus *Cerion*, except on the branch representing Microceraminae (genera *Macroceramus* and *Microceramus*), which is nested among decollating species (Fig. 7), and occasionally in *Brachypodella dominicensis* (Pilsbry, 1904: 86). *Cerion* species also have a hollow columella at least in their early whorls (Pilsbry, 1901–1902: 174). Unlike the Holospirinae, however, in many species of *Cerion* the columella becomes solid in the later whorls (Pilsbry, 1901–1902: 174). The combination of spiral and parietal lamella observed in most *Cerion* species (Schileyko, 1999b) is also found in many Holospirinae (Thompson & Mihalcik, 2005), although in that subfamily the parietal lamella is located further from the aperture. No parietal lamella ever occurs in other Urocoptidae. *Cerion* also resembles the Holospirinae also genital-anatomically in characters of its male ducts (Nordsieck, 1985). These similarities are consistent with the position of *Cerion* and the Holospirinae in the phylogenetic trees. They can be considered either symplesiomorphic or synapomorphic, depending upon whether *Cerion* and the Holospirinae are a paraphyletic group with respect to the other New World Urocoptidae (Bayesian analyses, ML analyses, some MP trees), or constitute a monophyletic group nested among these taxa (NJ bootstrap analysis, some MP trees). It should be noted however that none of these basal relationships is highly supported. Any resemblance to *Cerion* among the plaited-jawed urocoptids (e.g. in *Autocoptis*, Fig. 1F) is superficial, accomplished by decollation of the slender upper part of the shell.

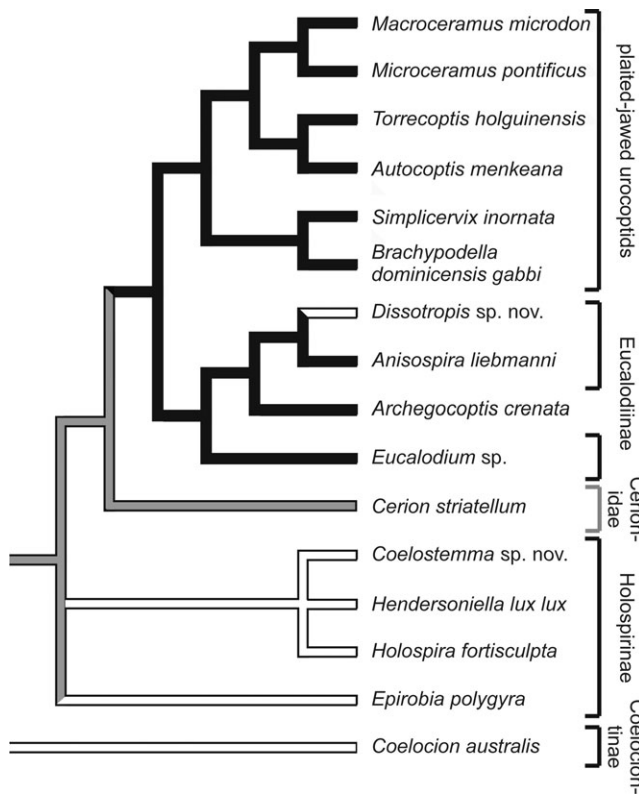


Figure 7. Inferred evolution of a hollow/solid columella among the Urocoptidae and *Cerion* species sampled, based on the type of columella in these species (see Pilsbry, 1901–1902, 1903, 1904; Thompson, 1968; Schileyko, 1999a, b), and the phylogenetic relationships between these species according to the majority rule consensus tree of the post burn-in trees from the Bayesian analysis (Fig. 4). Black branches represent a solid columella, white branches a hollow one. Grey branches indicate ambiguity between these two character states. Thus the occurrence of an at least partially hollow columella in *Cerion* is indicated in grey. The open umbilicus in *Hendersoniella* is interpreted here as a hollow columella.

Unlike the conchological characters that have been used to identify and group species as urocoptid, the plaited jaw is non-homoplasiously synapomorphic. It is unique to a clade consisting of all Antillean genera sampled other than *Archegocoptis*, as assumed by Pilsbry (1903, 1904, 1946). The clade of plaited-jawed urocoptids has undergone a major radiation, and harbours the majority (66) of genera within the family. This radiation and the additional sampling of supposedly plaited-jawed urocoptids will be the focus of another paper (Uit de Weerd, in preparation). On the other hand, the radular characteristics that the more basal New World Urocoptidae, viz. Holospirinae, Eucalodiinae and *Archegocoptis*, share with the Polygyridae rather than with the plaited-jawed urocoptid clade may be symplesiomorphic.

Palaeogeography

The distribution of its extant taxa suggests that the clade of New World Urocoptidae plus *Cerion* has always been confined to the western hemisphere. This notion is congruent with the earliest fossils that were assigned to taxa belonging to the clade, which make their first appearance in the late Cretaceous of southwestern North America. Fossils assigned to the extant genus *Holospira* have been described from Upper Cretaceous sediments in present-day southwestern Canada (Tozer, 1956)

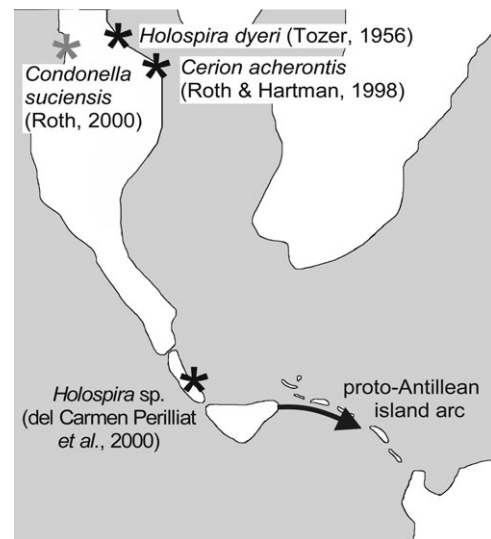


Figure 8. Late Cretaceous (Maastrichtian) distribution of landmasses and fossils identified as Urocoptidae or Cerionidae, and the approximate position of the proto-Antillean island arc. The locality of the earlier, Campanian, fossil *Condonella suciensis* is indicated in dark grey. Location of the proto-Antillean island arc after Iturralde-Vinent (2006).

and southern Mexico (del Carmen Perilliat, Vega, & Corona, 2000). The genus has a more extensive record in the Tertiary, with Palaeocene (Hartman, 1981) and in particular many Eocene-Oligocene fossils (Gardner, 1945; Russell, 1955; McKenna, Robinson & Taylor, 1962; Roth & Megaw, 1989; Pierce & Constenius, 2001) that bridge the geographic gap between the Cretaceous sites. The oldest probable species of *Cerion* was described from the late Cretaceous of Montana (Roth & Hartman, 1998). While the fossil is most similar to extant *Cerion* species, the authors note that it also resembles some Urocoptidae in its elongate-ovate shell shape, which complicates its assignment to either family. Assignment of fossils to the subfamily Eucalodiinae is more controversial. The enigmatic discoid genus *Condonella* from the upper Cretaceous of Washington was assigned to the ‘Eucalodiidae’ on the basis of similarities in whorl shape and sculpture with the Eucalodiinae *Coelocentrum* and *Dissotropis* (Roth, 2000). A more recent, lower Eocene, species from Wyoming was described as *Eucalodium* (Cockerell, 1915), but this assignment has been disputed (Russell, 1931; Hartman & Roth, 1998). The data on first appearances in the fossil record are consistent with the Bayesian consensus and ML trees found in this study, in which holospirine lineages and *Cerion* present the basal-most branches in the clade of New World Urocoptidae plus Cerionidae (Fig. 4).

The Cretaceous fossils predate the Antillean islands. At that time, only a precursory proto-Antillean island arc existed, situated at the east-end of the southwestern part of the North American landmass in the late Cretaceous (Pindell, 1994; Iturralde-Vinent, 2006) (Fig. 8). From this position, the proto-Antillean island arc moved northeastwards during the early Tertiary, until it was stopped in the Middle Eocene by its collision with the Bahamas platform (Pindell, 1994; Iturralde-Vinent & MacPhee, 1999), which resulted in the formation of most of the Greater Antilles (Pindell, 1994; Iturralde-Vinent & MacPhee, 1999). Based on such palaeogeological data and on the distribution of non-gastropod groups, Rosen (1976, 1985) suggested a vicariance model, which assumes that the eastwards movement of the proto-Antillean island arc may have carried lineages originating in North

America to a present position on the Greater Antilles. This vicariance model would account for the unexpected identification of no fewer than three separate Caribbean lineages within the Urocoptidae plus Cerionidae clade (Fig. 9): (1) the plaited-jawed urocoptid clade; (2) *Archegocoptis*; and (3) *Cerion*. The co-occurrence of these lineages in the Caribbean area would be more difficult to explain if assuming isolated random dispersal events from North America. Such a vicariance model has its own complications, however. First, the proto-Antilles are generally thought of as volcanic (Pindell, 1994). Most Urocoptidae presently found on the Greater Antilles dwell on limestone only, although they can be found on vegetation growing on calc-alkaline volcanic substrate in the Lesser Antilles (Robinson, personal communication). Second, the ranges of the plaited-jawed urocoptid clade and the North American Urocoptidae touch or even overlap in Texas, Eastern Mexico and Guatemala. The plaited-jawed urocoptid clade is represented there by two genera only, *Brachypodella* and *Microceramus*. *Microceramus* is thought to have colonized North America from the Greater Antilles (Pilsbry, 1904: 153). In contrast, the continental species of *Brachypodella* may occupy a relatively basal position within the genus (Paul, 1989). Although the phylogeographic reconstruction (Fig. 9) indicates that the plaited-jawed urocoptids diverged on the Greater Antilles and subsequently colonized North America, it relies on only a few branches, some of which are poorly supported. The phylogeography of the plaited-jawed urocoptid clade will be tested in more detail elsewhere (Uit de Weerd, in preparation). A third complication of a vicariance scenario is its assumption that at

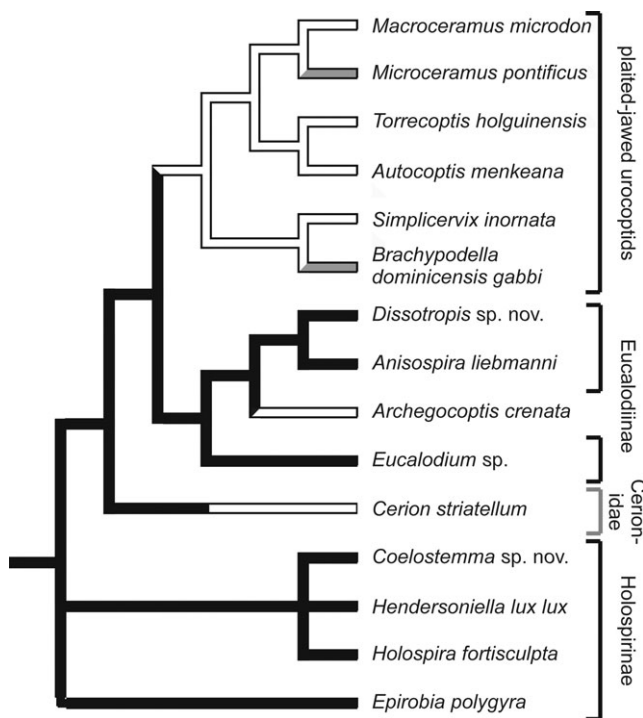


Figure 9. Phylogeography of the clade of New World Urocoptidae plus *Cerion*, based on the current and fossil distribution of the genera, and on the majority rule consensus tree of the post burn-in trees from the Bayesian analysis (Fig. 4). Black branches indicate an inferred distribution in the southwestern part of the North American continent (present-day Guatemala, Mexico and southwestern USA), white branches indicate a more eastern distribution on the Antilles, Bahamas and in south Florida. The basal part of the *Cerion*-lineage is shown as southwestern North American, based on the oldest fossil assigned to the genus, *Cerion acherontis* (Roth & Hartman, 1998).

least some of the proto-Antilles were above water at any point from the Cretaceous/early Tertiary onward to formation of the Greater Antilles. This seems unlikely given all the dynamics involved (Iturralde-Vinent & MacPhee, 1999). The oldest evidence for Urocoptidae on the Greater Antilles is the cast of a species from allegedly Miocene sediments in the Dominican Republic (Pilsbry & Olsson, 1954) that is similar in appearance, and is considered related, to snails now placed in the extant genus *Autocoptis* from that area. If this determination and date are correct, it suggests that by the Miocene the plaited-jawed urocoptids had undergone a major diversification into the main groups now recognized.

Taxonomy

The results necessitate several taxonomic revisions. First, the genus *Archegocoptis* should be removed from the Urocoptinae and be restored to its previous position in the Eucalodiinae. The family Urocoptidae should now include only the New World Urocoptidae. *Coelocion* should be excluded from the Urocoptidae. The present study was not designed to test the alternative classification of *Coelocion* with *Perrieria* (Nordsieck, 1986; Bouchet *et al.*, 2005) and, pending new data to the contrary, that classification should be maintained. As a name for the family containing both genera, Coelociontidae Iredale, 1937 (see earlier references) has precedence. As long as significant support for a placement of *Cerion* within the Urocoptidae is lacking, the current classification cannot be rejected and Cerionidae should be maintained as a separate family.

Several alternative superfamilial classifications of the families Cerionidae and Urocoptidae have been proposed (Table 5), depending on the anatomical or conchological characters examined, and on the interpretation of interfamilial differences and similarities in these characters. Most authors have classified Cerionidae and Urocoptidae in either the superfamily Clausilioidea (=Clausiliacea) or Orthalicoidea (=Bulimuloidea; =Bulimulacea), although not always together. Previous molecular phylogenetic studies (Wade *et al.*, 2006; Herbert & Mitchell, in press) applied these two names to two highly supported clades, neither of which contain *Cerion*. Those studies, which did not sample Urocoptidae, failed to identify any (super)families closely related to Cerionidae, and the family was not assigned to a superfamily. Based on these findings and the position of *Cerion* in a well supported clade with the Urocoptidae, I propose to classify the Urocoptidae and Cerionidae in a superfamily of their own. This superfamily should then be named Urocoptoidea, since the name Urocoptidae (Pilsbry & Vanatta, 1898) has precedence over Cerionidae (Pilsbry, 1901–1902). The Orthalicoidea (*sensu* Bouchet *et al.*, 2005) minus Urocoptidae and Cerionidae, consists of the families Orthalicidae, Placostylidae (both united as Bulimulidae *s.l.* by Herbert & Mitchell, in press), Coelociontidae and Megaspiridae. Pending evidence to the contrary, Orthalicoidea is maintained as a superfamily in this configuration. As such, the superfamily Orthalicoidea is more inclusive than the so-called orthalicoid clade identified by Herbert & Mitchell (in press), but it has a similar Gondwanan distribution.

Implications for future research

The finding that the Urocoptidae are closely related to *Cerion*, can help to place the many studies on evolution within *Cerion* (e.g. Woodruff, 1978; Gould, 1989; Goodfriend & Gould, 1996) in a phylogenetic framework and in a broader perspective. Such studies have been hampered by the absence of a known closest relative that can serve as an outgroup for *Cerion* (Roth & Hartman, 1998), and have been criticized for lacking

Table 5. Previous superfamilial placement of Cerionidae and Urocoptidae in stylommatophoran classification schemes.

Author	Family	Superfamily	Based on
Thiele (1931)	Cerionidae	Bulimulacea (=Orthalicoidea)	Combination of shell and anatomical characters (foot, respiratory vein, kidney, genitals)
	Urocoptidae	Bulimulacea (=Orthalicoidea)	
Baker (1955, 1956, 1957)	Cerionidae	Cerioidea	Ureter (Baker, 1955)
	Urocoptidae	Orthalicoidea (=Orthalicoidea)	Thiele (1931: 667–676)
Zilch (1960)	Cerionidae	Bulimulacea (=Orthalicoidea)	Shell
	Urocoptidae	Bulimulacea (=Orthalicoidea)	Shell
Baker (1961)	Cerionidae	Clausilioidea/Clausiliacea	Genital anatomy
	Urocoptidae	–	–
Taylor & Sohl (1962); Solem (1978); Boss (1982)	Cerionidae	Clausiliacea (= Clausilioidea)	Baker (1961)
	Urocoptidae	Bulimulacea (=Orthalicoidea)	Zilch (1960)
Schileyko (1979)	Cerionidae	Cerioidea	Ureter
	Urocoptidae	Clausilioidea	Genital-anatomy + shell
Nordsieck (1986); Bouchet <i>et al.</i> (2005)	Cerionidae	Orthalicoidea	Genital-anatomy + shell (Nordsieck, 1985)
	Urocoptidae	Orthalicoidea	Zilch (1960)
Tillier (1989)	Cerionidae	Clausilioidea	Overall anatomy
	Urocoptidae	Clausilioidea	Overall anatomy
Schileyko (1999a, b); Millard (2003)	Cerionidae	Cerionoidea	Schileyko (1979)
	Urocoptidae	Bulimuloidea (=Orthalicoidea)	Unspecified

a phylogenetic context (Stone, 1996). Research on *Cerion* has focused on patterns of variation in shell form and size. These have either been attributed to selection (Quensen & Woodruff, 1997), or have been described as non-adaptive consequences of structural (Gould, 1984, 1992) and historical constraints (Gould, 1989). The explanatory power of these hypotheses can now be tested for the Urocoptoidea as a whole, which holds a much greater variation in shell form and size than the genus *Cerion* alone. The impact of historical constraints on shell form in *Cerion* can only be evaluated in the light of the phylogenetic position of the genus. In short, the reunion of *Cerion* with the Urocoptidae will enable researchers to look beyond the boundaries of the genus, allowing for a better interpretation of their results in an evolutionary context.

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