# On the phylogenetic relationships of the genus *Mexistrophia* and of the family Cerionidae (Gastropoda: Eupulmonata)

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## ABSTRACT

Phylogenetic analyses of partial DNA sequences of the mitochondrial COI and 16S rDNA genes derived from *Mexistrophia reticulata* Thompson, 2011, the type species of the genus *Mexistrophia*, indicate that this genus is sister taxon to all remaining living Cerionidae, and that the family Cerionidae is most closely related to Urocoptidae. Relationships among representative cerionid taxa are consistent with the zoogeographic hypothesis that *Mexistrophia* has been isolated from the remaining living Cerionidae since the Cretaceous, and suggest that the near-shore, halophilic habitat that has commonly been associated with this family is likely a Cenozoic adaptation that coincided with the transition from continental to island habitats. The genus *Protocerion* is described to include the Late Cretaceous species *Cerion acherontis* Roth and Hartman, 1998, as its retention in *Cerion* would render this genus paraphyletic.

## INTRODUCTION

The family Cerionidae comprises a well-studied group of terrestrial snails inhabiting islands of the tropical western Atlantic, ranging from the barrier islands of southeastern Florida, throughout the Bahamas, Greater Antilles, Cayman Islands, western Virgin Islands, and the Dutch Antilles, but absent from Jamaica, the Lesser Antilles, and coastal Central and South America. All are halophilic, confined to terrestrial vegetation growing in close proximity of the shore, but occasionally occur further inland in areas that can be reached by salt spray (Clench, 1957; Woodruff, 1978). Rare fossil taxa extend the range of Cerionidae to the Upper Cretaceous of Montana (Roth and Hartman, 1998) and the Paleocene of the Itaboraí Basin of Brazil (Salvador et al., 2011). More recently, the genus *Mexistrophia* was proposed within the Cerionidae to include three new species inhabiting cool coniferous forests in the highlands (2000–2600 m) of central Mexico (Thompson, 2011). Thompson (2011) compared the shell morphology, anatomy, and radula of *Mexistrophia reticulata*, the type species of *Mexistrophia*, with those of several species of *Cerion*, including *Cerion uva* (Linnaeus, 1758), the type species of the type genus of Cerionidae. He concluded that anatomical features of *Mexistrophia reticulata* are typical of Cerionidae and that radular morphology differs only slightly. However, *Mexistrophia* may be distinguished from species of *Cerion* in lacking lamellae and denticles along the columella at all stages of growth.

Harasewych (2012) reviewed the diversity of living and fossil Cerionidae from geographic and temporal perspectives and combined these data with paleogeographic reconstructions of the Caribbean region (Iturralde-Vinent, 2006) and a COI based phylogeny of a selection of cerionid taxa (Harasewych et al., 2011: fig. 17) to formulate a hypothesis for the zoogeographic history of the family Cerionidae from the earliest fossil record in the Late Cretaceous of Montana to the more widespread modern fauna. According to this hypothesis (Figure 1), *Mexistrophia* was an early offshoot that was isolated from the South American ancestors of all remaining cerionids during the Late Cretaceous by the formation of a seaway separating the faunas of North and South America.

The family Cerionidae has been assigned to a variety of superfamilies, among them Orthalicoidea (Thiele, 1931; Bouchet et al., 2005) Clausilioidea (Baker, 1961; Solem, 1978; Tillier, 1989) Cerioidea (Baker, 1955; Shileyko, 1979, 1999) and most recently Urocoptoidea (Uit de Weerd, 2008). In this paper we investigate the phylogenetic relationships of the genus *Mexistrophia* to other members of the Cerionidae as well as the placement of the family Cerionidae within Eupulmonata based on partial sequences for the COI and 16S genes.

## MATERIALS AND METHODS

Specimens of *Mexistrophia reticulata* Thompson, 2011 were collected west of Pinal de Amoles, Querétaro State, Mexico (21°07′ 26.52″ N, 99°40′59.58″ W), not far from the type locality for this species. The shells were cracked,

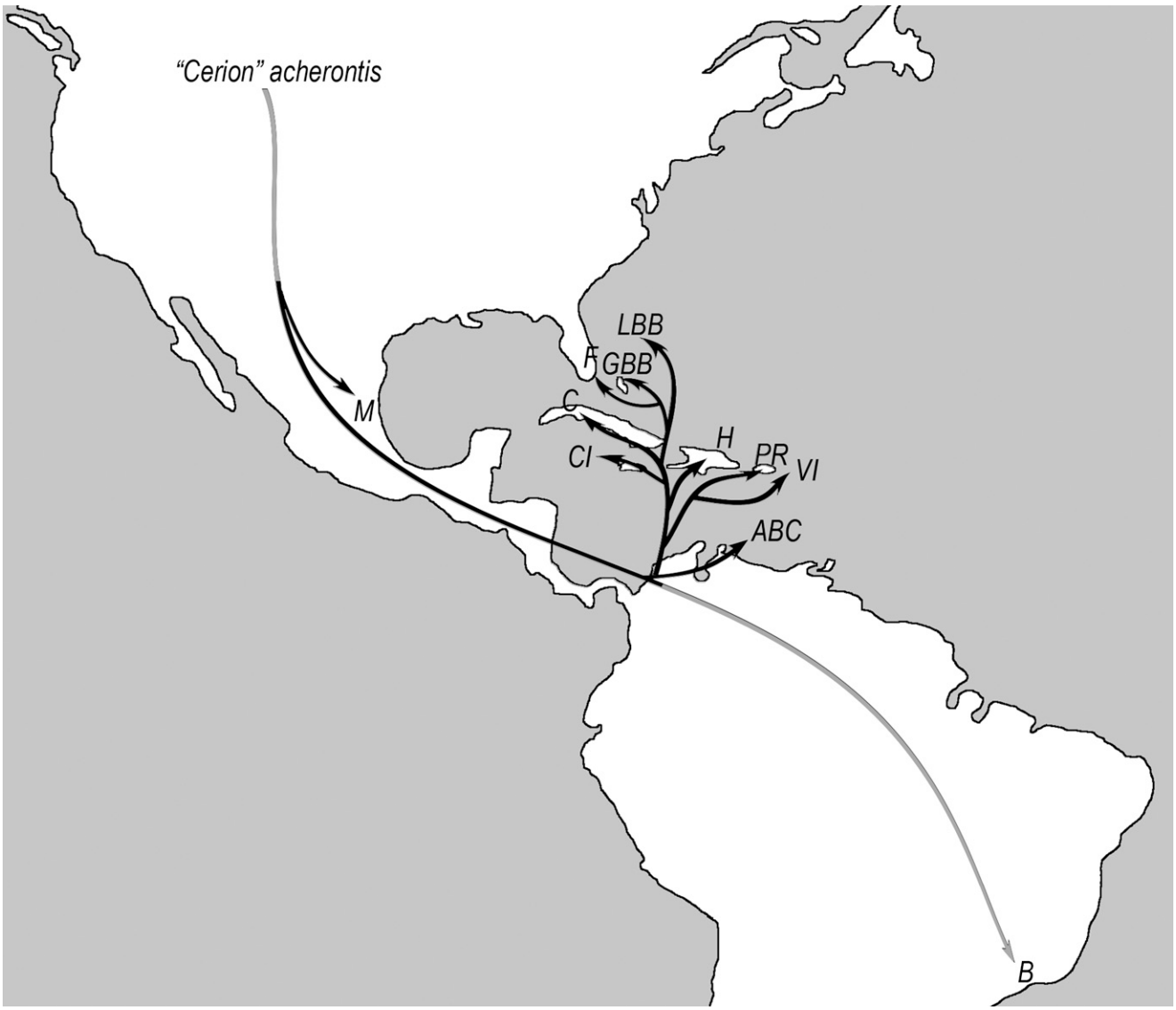


**Figure 1.** Hypothesized zoogeographic history of the family Cerionidae (after Harasewych 2012:fig. 12). Grey portions based on fossil taxa. *ABC*, Aruba, Bonaire and Curaçao; *B*, Brazil; *C*, Cuba; *CI*, Cayman Islands; *F*, Florida; *GBB*, Great Bahama Bank; *H*, Hispaniola; *LBB*, Little Bahama Bank; *M*, Mexico; *PR*, Puerto Rico, *VI*, western Virgin Islands.

and the animals preserved in RNAlater and stored at −70°C (voucher material USNM 1283835). As the Cerionidae had most recently been included in Urocoptoidea on the basis of molecular data (Uit de Weerd, 2008), tissue from living specimens of *Microceramus pontificus* (Gould, 1848) from South Miami, Florida (voucher specimens USNM 1283834) were also sequenced in order to include a member of the family Urocoptidae in this analysis.

Genomic DNA was extracted from buccal muscle dissected from preserved or living specimens using the DNAeasy Tissue Kit (Qiagen) according to the manufacturer's animal tissue protocol.

Portions of two mitochondrial genes were amplified: a 655 bp region of the cytochrome c oxidase I gene using the primers JgLCO1490 (Geller et al., 2013) and C1-N-2191R (aka NancyCOIR) (Simon et al., 1994) and a 510 bp region of the 16S ribosomal gene using the primers 16S-ar and 16S-br (Palumbi, 1996). For each gene, the Promega GoTaq hot start master mix (Promega M7132) was utilized at concentrations according to manufacturer's instructions, but modified to reduce reaction volume to 20 µL. Cycling parameters for each gene region were optimized as follows: COI – initial denaturation for 7 min at 95°C + 45 cycles (30 sec at 95°C + 45 sec at 42°C +1 min at 72°C) + 3 min at 72°C; 16S – initial denaturation for 7 min at 95°C + 35 cycles (30 sec at 95°C + 45 sec at 48°C +1 min at 72°C) + 5 min at 72°C. PCR products were visualized by agarose gel electrophoresis (1.5% agarose) and purified with ExoSAP-IT (Affymetrix) according to manufacturer's protocols prior to sequencing.

Sequencing reactions for 16S were performed using 1 µL of purified PCR product in a 10 µL reaction containing 0.5 µL primer, 1.75 µL Big Dye buffer and 0.5 µL Big Dye (Life Technologies); for COI the volume of Big Dye was increased to 0.75µL. The sequencing reaction was carried out under standard cycling conditions (25 cycles of 5 sec at 95 °C + 10 sec at 50 °C + 4 min at 60 °C). Reactions were purified using Millipore Sephadex plates (MAHVN-4550) according to the manufacturer's instructions and sequenced on an ABI 3730XL automated DNA sequencer. Sequencher v. 4.7 (GeneCodes, Ann Arbor, MI, USA) was used to visualize, trim, edit, and assemble contigs from forward and reverse sequences. All PCR, sequencing, and analytics were carried out at the Laboratories of Analytical Biology at the National Museum of Natural History. The sequences have been deposited in GenBank (NCBI). Accession numbers are listed in Table 1.

Partial sequences for the mitochondrial COI and 16S genes of *Mexistrophia reticulata* and *Microceramus pontificus* were aligned against a range of euthyneuran taxa for which both COI and 16S sequences were available (Table 1), most derived from complete mitochondrial genomes. Representative species of Cerionidae were selected to span the previously documented phylogenetic diversity within the family (Harasewych et al., 2011: fig. 17).

Alignments of COI and 16S were obtained using the L-INS-i alignment strategy in MAFFT (Katoh et al., 2002)] for 16S and MUSCLE (Multiple Sequence Comparison by Log-Expectation) (Edgar, 2004) for COI. The aligned sequences were concatenated using Geneious version 7.1.2 (Kearse et al., 2012) In the concatenated data set, positions 1-554 are 16S, and positions 555 to 1212 are COI.

A best-fit model of nucleotide sequence evolution (compatible with MrBayes) and partitioning arrangement for each locus was determined using MrAIC (Nylander, 2004). The GTR+I+G model was chosen for both loci.

Phylogenetic analyses were performed on a concatenated dataset (16S + COI) using Bayesian Inference (BI) performed with MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003) and Maximum Likelihood (ML) with RAxML (Stamatakis, 2006). All analyses were run on the Smithsonian Institution high performance computing cluster (SI/HPC). BI analysis was carried out for 10 million

**Table 1.** List of taxa and their GenBank reference numbers for the gene sequences used in phylogenetic analyses. Asterisk (*) denotes that both COI and 16S sequence data were derived from a complete mitochondrial genome sequence.

| Taxon | COI GenBank No. | 16S GenBank No. | Superfamily | Family |
|---|---|---|---|---|
| **Euthyneura** | | | | |
| **Euopisthobranchia** | | | | |
| *Aplysia californica* | NC005827* | | Aplysioidea | Aplysiidae |
| **Panpulmonata** | | | | |
| *Siphonaria pectinata* | AY345049* | | Siphonarioidea | Siphonariidae |
| *Salinator rhamphidia* | JN620539* | | Amphiboloidea | Amphibolidae |
| **Hygrophila** | | | | |
| *Biomphalaria glabrata* | AY380531* | | Planorboidea | Planorbidae |
| *Physella acuta* | NC023253* | | Planorboidea | Physidae |
| *Galba pervia* | JN564796* | | Lymnaeoidea | Lymnaeidae |
| **Eupulmonata** | | | | |
| *Ovatella vulcani* | JN615139* | | Ellobioidea | Ellobiidae |
| *Trimusculus reticulatus* | JN632509* | | Trimusculoidea | Trimusculidae |
| *Platevindex mortoni* | GU475132* | | Onchidioidea | Onchidiidae |
| *Onchidella celtica* | NC012376* | | Onchidioidea | Onchidiidae |
| *Peronia peronii* | JN619346* | | Onchidioidea | Onchidiidae |
| *Vertigo pusilla* | NC026045* | | Pupilloidea | Vertiginidae |
| *Gastrocopta cristata* | KC185403* | | Pupilloidea | Pupillidae |
| *Pupilla muscorum* | NC026044* | | Pupilloidea | Pupillidae |
| *Albinaria caerulea* | X83390* | | Clausilioidea | Clausiliidae |
| *Achatina fulica* | NC024601* | | Achatinoidea | Achatinidae |
| *Camaena cicatricosa* | NC025511* | | Helicoidea | Camaenidae |
| *Mastigeulota kiangsinensis* | NC024935* | | Helicoidea | Bradybaenidae |
| *Cylindrus obtusus* | JN107636* | | Helicoidea | Helicidae |
| *Cepaea nemoralis* | CMU23045* | | Helicoidea | Helicidae |
| *Helix aspersa* | JQ417194* | | Helicoidea | Helicidae |
| *Microceramus pontificus* | KT272166 | KT272164 | Urocoptoidea | Urocoptidae |
| *Mexistrophia reticulata* | KT272165 | KT272163 | Urocoptoidea | Cerionidae |
| *Cerion uva* | KJ624975 | KJ636144 | Urocoptoidea | Cerionidae |
| *Cerion striatellum* | KJ934716 | KJ636083 | Urocoptoidea | Cerionidae |
| *Cerion malonei* | KJ934718 | KJ636085 | Urocoptoidea | Cerionidae |
| *Cerion stevensoni* | KJ934720 | KJ636087 | Urocoptoidea | Cerionidae |
| *Cerion caerulescens* | KJ934722 | KJ636089 | Urocoptoidea | Cerionidae |
| *Cerion incanum* | NC025645* | | Urocoptoidea | Cerionidae |

generations with two independent runs, each with four chains, and with trees sampled every 1000th generation. Model parameters (tratio, statefreq, shape, pinvar) were unlinked among partitions, and the rate prior (prset ratepr) was set to "variable". Convergence was determined when the average standard deviation of split frequencies was <0.01 and the potential scale reduction factor (PSRF) was 1.00. To calculate posterior probabilities, a "burn-in" of 25% of the total trees sampled per run adequately removed trees prior to convergence. ML options for RAxML included the GTRCAT model of nucleotide evolution (-m), rapid bootstrap analysis, and search for best-scoring ML tree (-f a), and 1000 bootstrap replicates.

## RESULTS

The region of the 16S gene sequenced for *Mexistrophia reticulata* and *Microceramus pontificus* corresponded to positions 564–1069 of the 16S gene in *Cerion incanum*. The length was 486 bp in *Mexistrophia* and 476 bp in *Microceramus*. The alignment containing the taxa in Table 1 spanned 554 positions, of which 174 (31.4%) were constant and 326 (58.8%) were parsimony informative. The 655 bp portion of the COI gene sequenced for *Mexistrophia reticulata* and *Microceramus pontificus* corresponded to positions 39–693 of the COI gene in *Cerion incanum*. The COI alignment of the taxa in Table 1 spanned 658 bp, of which 310 (47.1%) were constant and 302 (45.9%) were parsimony informative.

Phylogenetic analyses of the concatenated 16S + COI data using maximum likelihood and Bayesian inference resulted in a single, fully resolved and well supported tree (Figure 2). *Mexistrophia* emerged as the sister taxon to all remaining living Cerionidae, and the family Cerionidae as sister taxon to the single representative

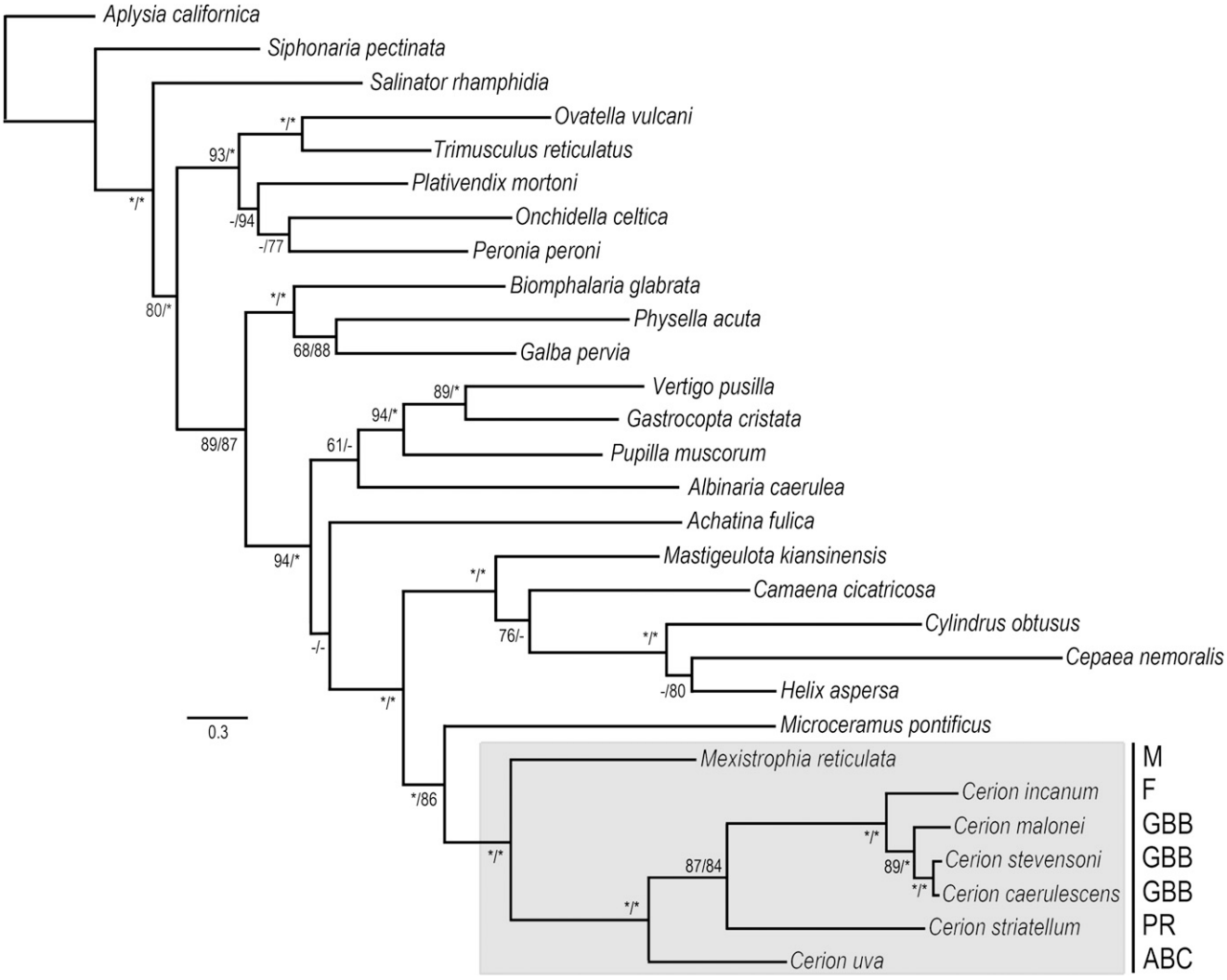


**Figure 2.** Molecular phylogenetic tree from analyses of concatenated 16S and COI sequence data, represented as a maximum likelihood phylogram with maximum likelihood bootstrap values/ Bayesian posterior probabilities. (* ≥ 95% support, - ≤ 50% support). The family Cerionidae is in gray. Letters to the right of the bar correspond to the geographic localities / island groups identified in figure 1.

of the family Urocoptidae. Cerionidae and Urocoptidae (both in Urocoptoidea) are most closely related to the Helicoidea, a clade represented by multiple families in our study.

## DISCUSSION

Molecular data strongly supports the inclusion of the genus *Mexistrophia* in the Cerionidae, an assignment originally based on anatomical data and shell morphology. The topology of the phylogram of the Cerionidae is concordant with the branching patterns in the zoogeographic hypothesis for the distribution of Cerionidae (Figure 1), although several geographic regions are not yet represented by molecular data.

Results of this analysis also recovered a sister group relationship between Cerionidae and the urocoptid *Microceramus pontificus*, supporting the inclusion of Cerionidae within Urocoptoidea, as advocated by Uit de Weerd (2008), and contradict its placement within Clausilioidea (Baker, 1961; Solem, 1978; Tillier, 1989). To date, Cerionidae have been included in very few of the broader molecular studies of pulmonate phylogeny. Based on ribosomal RNA sequences, Wade and co-authors (2001: fig. 1) show *Cerion* as the sister taxon to Helicoidea + Spiraxidae + Haplotremidae, but do not include Urocoptidae among their sampled taxa. Topology of the more basal portions of our tree are generally consistent with results of other molecular studies on phylogenetic relationships among Pulmonata (e.g., Wade et al., 2006; Dayrat et al. 2011; White et al. 2011) when adjusted for taxon sampling and rooting.

The phylogenetic relationships within Cerionidae suggest that the near-shore, halophilic habitat that has commonly been associated with this family is likely a Cenozoic adaptation that coincided with the transition from continental to island habitats.

As reported by Thompson (2011: 190), *Mexistrophia* species inhabit cool mesic or submesic temperate forests, at elevations greater than 2000 m and distances in excess of 200 km from the nearest coastline. *Mexistrophia* is an early offshoot of a lineage that dates back to *"Cerion" acherontis* from the Hell Creek Formation [Upper Cretaceous (Maastrichtian)] of northeastern Montana. This species was part of a faunule that consisted almost entirely of fresh water forms (Roth and Hartman, 1998: Table 1). The habitat for this faunule has been interpreted as a subtropical, flat, forested floodplain. Similarly, the genus *Brasilennea* (Maury, 1935), recently transferred to the Cerionidae (Salvador et al., 2011), was endemic to the Middle to Late Paleocene Itaboraí Basin of Brazil. This genus was part of a fauna that included numerous terrestrial snails and mammals. Maury (1935: 4) commented that a crocodilian jaw was associated with the fossils she described. Salvador and Simone (2012: 49) noted that little is known about the paleoenvironment of the Itaboraí Basin, other than its high calcium carbonate availability, and cited reports that this basin had a wet and warm climate with copious vegetation.

*Cerion uva* represents the most basal lineage within the Cerionidae that is limited to island habitats. This species is endemic to the islands of Aruba, Bonaire and Curaçao, and is widely distributed throughout these islands (Harasewych, 2014: fig. 4), occurring on limestone plateaus along the coast, as well as further inland, even at elevations of 200 m or more. There are few places on these hot, arid islands that are more than 5 km from the ocean. Windborne salt spray and salt particles reach most or all parts of these islands. All remaining species of Cerionidae are limited to islands ranging from southern Florida throughout the Bahamas, Cuba, Cayman Islands, Hispaniola, Puerto Rico and the western Virgin Islands, where they occur on or near living or dried terrestrial vegetation, generally at low elevations and in close proximity to the shoreline. Some populations occur at elevations of tens of meters, usually near the edges of coastal cliffs. Populations of some normally coastal species may occasionally be found several kilometers inland, generally on the windward sides of islands.

When the progenitors of *Cerion* were first isolated on small, arid islands, most likely in the early to mid-Tertiary, selection favored animals that were salt tolerant and able to withstand heat, exposure to sun, and prolonged periods of desiccation. Descendants of these animals colonized the islands of the Greater Antilles along the GAARlandia land bridge during the late Eocene-early Oligocene and later the Bahamas via a stochastic accumulation of hurricane-borne propagules (Ituarralde-Vinent, 2006: figs. 6, 13; Harasewych, 2012: 123).

Although *Cerion acherontis* Roth and Hartman, 1998, the Cretaceous ancestor of Cerionidae, was provisionally described in the genus *Cerion*, its inclusion in *Cerion* would render this genus paraphyletic due to the intervening phylogenetic positions of the genera *Mexistrophia* and *Brasilennea*. We therefore propose *Protocerion* as a new genus for this Cretaceous species.

### ***Protocerion*** **new genus**

**Type Species:** *Cerion acherontis* Roth and Hartman, 1998. (By original designation)

**Diagnosis:** Shell of moderate size (~ 23 mm), pupiform in shape, apically rounded, elongate-ovate (shell length/shell width ~ 2.7). Protoconch and early whorls unknown. Teleoconch of 4+ smooth, weakly convex whorls, with impressed suture. Sculpture of faint growth lines. Umbilicus imperforate. Aperture rounded, slightly higher than wide, ~ 3/8 of shell length. Peristome adpressed, forming thin parietal callus and thickened, axial columellar lip, smoothly rolled outward. Lacking columellar or parietal folds.

**Distribution:** Known only from a single, fractured and compressed specimen (Figure 3) collected ~ 29.8 m above the base of the Hell Creek Formation, Garfield County, Montana (106°56′47″ N, 47°34′10″ N). Late Cretaceous (Late Maastrichtian).


**Figure 3.** The holotype and only known specimen of *Cerion acherontis* Roth and Hartman, 1998, the type species of ***Protocerion* new genus**. USNM 491763, Hell Creek Formation, Garfield County, Montana [106°56′47″ N, 47°34′10″ W]. Late Cretaceous (Late Maastrichtian).

**Remarks:** As noted by Roth and Hartman (1998), *Protocerion acherontis* more closely resembles the smooth-shelled morphotype exemplified by the Recent species *Cerion incanum* (Leidy, 1851) than any of the ribbed morphotypes (e.g., *Cerion uva*). Both *Protocerion* and *Mexistrophia* lack columellar or axial folds, which are present in *Brasillenea* and all species of *Cerion*. These folds are an apomorphy for *Brasillenea* + *Cerion* that is lacking in *Protocerion* and *Mexistrophia*. Their absence in *Protocerion* distinguishes this genus from *Cerion*.

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