

Article

Phylogenetic Position of African Punctoid Snails (Stylommatophora, Punctoidea, Trachycystinae)

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Abstract: The punctoid land snail family Charopidae, as currently defined, is a paraphyletic assemblage of taxa with Gondwanan distribution. It is represented in Africa largely by the pinwheels (genus *Trachycystis* and allies) and afrodontas (genus *Afrodonta* and allies), as well as a few additional genera, such as *Reticulapex*, *Pilula*, and *Helenoconcha*. Herein, a Bayesian inference phylogenetic analysis (using four molecular markers) is conducted to test whether these taxa belong to the Charopidae and, if so, what their position is in the phylogenetic tree. It is concluded that *Reticulapex* and *Pilula* do not belong to the Punctoidea and are thus transferred to the Acavidae and Helicarionoidea, respectively. The pinwheels and afrodontas form a monophyletic group, the most basal branch of “Charopidae”, here classified as the subfamily Trachycystinae. It possibly represents an old southern African lineage potentially dating back to the split of Gondwana, while the remaining “Charopidae” and Punctidae can be found in Zealandia and Australia, and later, in the Americas and Europe. If further studies support the present findings, the elevation of Trachycystinae to the family level might be warranted. Finally, Flammoconchinae is also identified as a New Zealand subfamily of “Charopidae”.

Keywords: Charopidae; Flammoconchinae; Gastropoda; Gondwana; molecular phylogenetics



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1. Introduction

The land snail family Charopidae, as currently defined, has a Gondwanan distribution [1], being represented in Africa largely by two groups: the pinwheels and the afrodontas [2]. The pinwheel snails have discoid or low conical (helicoid) shells that lack apertural dentition and have been historically classified in the genus *Trachycystis* Pilsbry, 1893 (type species: *Helix bisculpta* Benson, 1851). Presently, the several previously accepted subgenera of *Trachycystis* are considered full genera [3,4]. The afrodontas, on the other hand, have smaller discoid shells bearing apertural dentition and have been historically classified in the genus *Afrodonta* Melville & Ponsonby, 1908 (type species: *Afrodonta bilamellaris* Melville & Ponsonby, 1908, by subsequent designation of [5]). Like *Trachycystis* above, *Afrodonta* has recently been split into several genera [6].

Both pinwheels and afrodontas were originally assigned to the family Endodontidae (e.g., [7–11]), but were later transferred to the Charopidae when that taxon was elevated to family level by Solem [11,12]. Both the Charopidae and Endodontidae belong to the superfamily Punctoidea, alongside the families Punctidae and Cystopeltidae [1]. Solem [12] was mainly interested in the Pacific Punctoidea and proposed—based solely on penial anatomy—that both *Afrodonta* and *Trachycystis* were closely related to *Graeffedon* Solem, 1983, from Samoa and Tonga (currently in Charopinae). Schileyko [13] established the family Trachycystidae to allocate *Trachycystis*, but subsequently [14] returned that genus to the Endodontidae within the subfamily Trachycystinae (*Afrodonta* was kept in subfamily Endodontinae).

Most subsequent authors (e.g., [15–17]), however, followed Solem’s classification. Hence, Trachycystinae has typically been considered synonymous with Charopinae [16,17], and sometimes includes taxa from places other than southern Africa, such as Saint Helena and South America (e.g., [4,12]).

In the molecular phylogenetic analysis of Punctoidea conducted by [1], there was a single African representative, belonging to the genus *Chalcoecystis* Watson, 1934. Those authors showed that *Chalcoecystis* did not belong to the Charopinae; rather, it was the most basal branch of the clade comprised of a paraphyletic Charopidae and the family Punctidae. They remarked that the subfamily Trachycystinae could have some biological reality, provided that the group was circumscribed solely to African taxa. Therefore, herein, that assertion is tested by including newly sequenced Trachycystinae species in the molecular framework of [1].

2. Material and Methods

2.1. Taxon Sampling

The present species selection contains 13 species (from nine genera) representing not only pinwheels and afrodontas, but also another two genera that have been included in the Trachycystinae [3,4,18]: *Reticulapex* Emberton & Pearce, 2000 and *Pilula* E. von Martens, 1898. Unfortunately, no suitable specimens of *Helenoconcha* Pilsbry, 1892 could be procured; this genus is endemic to Saint Helena and it is potentially related to *Trachycystis* sensu lato, according to [12].

Furthermore, sequences from four genera of New Zealand Charopidae that are considered basal within the family (F. Brook, pers. comm. 2021) were also included: *Cavellia* Iredale, 1915, *Flammoconcha* Dell, 1952, *Pseudaliodiscus* Climo, 1971, and *Therasiella* Powell, 1948. This was conducted to further put to test whether Trachycystinae is the most basal branch of Charopidae, as suggested by [1].

The full set of taxa used here can be seen in Table 1. Samples were obtained from the following collections: NMSA = Kwa-Zulu Natal Museum (Pietermaritzburg, South Africa); OZD = Department of Zoology, University of Otago (Dunedin, New Zealand); and UF = Florida Museum of Natural History (Gainesville, USA). DNA sequences of other Punctoidea were obtained from NCBI GenBank (from the study of Salvador et al., 2020; Table 2). The family-level classification of Punctoidea used here follows Salvador et al. (2020).

Table 1. List of species used in this study, with GenBank accession numbers for each marker, and voucher data (registration number and locality of provenance). * Fragmentary sequences, excluded from final analysis.

Species	COI	16S	ITS2+28S	Voucher	Provenance
African Charopidae					
<i>Afrodonta bilamellaris</i> Melvill & Ponsonby, 1908	ON365470	ON374086	ON376035	NMSA-Mol 0W9618	South Africa, KwaZulu-Natal, Port Shepstone, Four Man's Hill
<i>Chalcoecystis viridula</i> (Connolly, 1939)	—	ON374088	ON376037	NMSA-Mol 0W9407	South Africa
<i>Chilocystis calorama</i> (Melvill & Ponsonby, 1899)	ON365472	ON374089	ON376038	NMSA-Mol 0W9636	South Africa, KwaZulu-Natal, Port Shepstone, Simuma Hill
<i>Chilocystis scolopendra</i> (Melvill & Ponsonby, 1903)	ON365473	ON374090	ON376039	NMSA-Mol 0W7837	South Africa, KwaZulu-Natal, Port Shepstone, Hlokoohloko Valley
<i>Phortion oconnori</i> (Preston, 1912)	ON365475	ON374092	ON376041	NMSA-Mol 0W8889	South Africa, Western Cape, Bainskloof Pass
<i>Psichion inclara</i> (Morelet, 1889)	ON365478	ON374095	ON376043	NMSA-Mol 0W9163	South Africa, Eastern Cape, Woody Cape Nature Reserve
<i>Trachycystis bathycoele</i> (Melvill & Ponsonby, 1892)	ON365481	—	—	NMSA-Mol 0P0178	South Africa, Limpopo, Entabeni Forest
<i>Trachycystis glanvilliana</i> (Ancey, 1890)	ON365482	ON374097	ON376047	NMSA-Mol 0W7149	South Africa, KwaZulu-Natal, Karkloof Falls
<i>Trachycystis tollini</i> (Benson, 1856)	—	—	ON376048 *	NMSA-Mol 0W9407	South Africa, Western Cape, Platbos Forest Reserve
<i>Xerocystis capensis</i> (L. Pfeiffer, 1841)	—	—	ON376049 *	NMSA-Mol 0W8893	South Africa, Western Cape, De Hoop Nature Reserve

Table 1. Cont.

Species	COI	16S	ITS2+28S	Voucher	Provenance
African taxa, not Charopidae					
<i>Pilula cordemoyi</i> (G. Nevill, 1870)	ON365476	ON374093	—	UF 415477	Réunion Island, Basse Valley
<i>Reticulapex michellae</i> K.C. Emberton et al., 2010	ON365479	—	ON376044	UF 421124	Madagascar, Andriantantely Massif
<i>Reticulapex</i> sp.	—	—	ON376045	UF 421119	Madagascar, Andriantantely Massif
New Zealand Charopidae					
<i>Cavellia buccinella</i> (Reeve, 1852)	ON365471	ON374087	ON376036	OZD Cabuc-1	New Zealand, Northland, Kaipara
<i>Flammoconcha cumberi</i> (Powell, 1941)	ON365474	ON374091	ON376040	OZD FB29	New Zealand, West Coast, Grange Ridge
<i>Pseudallodiscus ponderi</i> Climo, 1971	ON365477	ON374094	ON376042	OZD Ppond-1	New Zealand, Auckland, Pahiatua Hill Scenic Reserve
<i>Therasiella celinde</i> (Gray, 1850)	ON365480	ON374096	ON376046	OZD FB116	New Zealand, Waikato, Pokeno

Table 2. List of species used in the phylogenetic analysis for which data were retrieved from GenBank, with accession numbers for each marker, and provenance data of the voucher specimen.

Species	COI	16S	ITS2+28S	Provenance of Voucher
Charopidae				
<i>Allodiscus dimorphus</i> (Reeve, 1852)	MN792581	MN756708	MN782439	New Zealand, Auckland, Waitakere Ranges, Titirangi, Atkinson Track
<i>Alsolemia longstaffae</i> (Suter, 1913)	MN792582	MN756709	MN759313	New Zealand, Southland, Colac Bay
<i>Chalcocystis aenea</i> (F. Krauss, 1848)	MN792590	MN756717	MN782447	South Africa, KwaZulu-Natal, Hluhluwe
<i>Charopa coma</i> (Gray, 1843)	MN792591	MN756718	MN782448	New Zealand, Auckland, Waitakere Ranges, Titirangi, Paturoa Stream
<i>Fectola infecta</i> (Reeve, 1852)	MN792600	MN756727	MN782457	New Zealand, Waikato, Coromandel Peninsula, Port Charles
<i>Flammulina zebra</i> (Le Guillou, 1842)	MN792601	MN756728	MN782458	New Zealand, Tasman, Lake Daniells
<i>Mitodon wairarapa</i> (Suter, 1890)	MN792607	MN756732	MN782464	New Zealand, Southland, Stewart Island, Mason Bay, Gutter
<i>Mocella eta</i> (Pfeiffer, 1853)	MN792608	MN756733	MN782465	New Zealand, Northland, Umuheke Bay
<i>Neophenacohelix giveni</i> (Cumber, 1961)	MN792609	MN756743	MN782466	New Zealand, Northland, Whangarei, Coronation Reserve
<i>Otoconcha dimidiata</i> (L. Pfeiffer, 1853)	MN792614	MN756738	MN782471	New Zealand, Northland, Whangarei, Bream Head
<i>Phacussa helmsi</i> (Hutton, 1882)	MN792618	MN756742	MN782475	New Zealand, West Coast, Greymouth, Point Elizabeth
<i>Phenacohelix pilula</i> (Reeve, 1852)	MN792619	MN756744	MN782476	New Zealand, Northland, Whangaruru North Head
<i>Radioconus amoenus</i> (Thiele, 1927)	MN792623	MN756749	MN782481	Brazil, Santa Catarina, Florianópolis, Gruta do Triângulo
<i>Radiodiscus</i> sp.	MN792625	MN756751	MN782483	Brazil, Bahia, Ilhéus
<i>Radiodiscus</i> sp.	MN792626	MN756752	MN782484	Chile, Chiloé, Chiloé National Park, Chepu
<i>Ranfurlya constanceae</i> Suter, 1903	MN792627	MN756753	MN782485	New Zealand, Auckland Islands, Adams Island
<i>Sinployea atiensis</i> (Pease, 1870)	MN792628	MN756754	MN782486	Cook Islands, Rarotonga, Tupapa Valley
<i>Stenacapha hamiltoni</i> (Cox, 1868)	MN792629	MN756755	MN782487	Australia, Tasmania, Central Plateau, Viorny
<i>Suteria ide</i> (Gray, 1850)	MN792630	MN756756	MN782488	New Zealand, Manawatu-Wanganui, Bushy Park
<i>Therasia thaisa</i> Hutton, 1883	MN792631	MN756757	MN782489	New Zealand, Southland, Clifden, Clifden Limestone Cave System

Table 2. Cont.

Species	COI	16S	ITS2+28S	Provenance of Voucher
Cystopeltidae				
<i>Cystopelta bicolor</i> Petterd & Hedley, 1909	MN792592	MN756719	MN782449	Australia, Tasmania, Bronte Park
<i>Diemenoropa kingstonensis</i> (Legrand, 1871)	MN792616	MN756740	MN782473	Australia, Tasmania, Skullbone Plains, Kenneth Lagoon
<i>Lilloiconcha</i> cf. <i>gordurasensis</i> (Thiele, 1927)	MN792604	MN756731	MN782461	Brazil, Alagoas, Pedra Talhada Biological Reserve
<i>Lilloiconcha gordurasensis</i> (Thiele, 1927)	MN792605	—	MN782462	Brazil, São Paulo, São Paulo, Burle Marx Park
<i>Lilloiconcha superba</i> (Thiele, 1927)	MN792606	—	MN782463	Brazil, Alagoas, Pedra Talhada Biological Reserve
<i>Scelidoropa officeri</i> (Legrand, 1871)	MN792617	MN756741	MN782474	Australia, Tasmania, Flinders Island, Brougham Sugarloaf
<i>Zilchogyra</i> sp.	MN792632	—	MN782490	Brazil, São Paulo, Cotia, Morro Grande Reserve
Endodontidae				
<i>Libera fratercula</i> (Pease, 1867)	MN792603	MN756730	MN782460	Cook Islands, Rarotonga, Tupapa
Punctidae				
<i>Laoma leimonias</i> (Gray, 1850)	MN792602	MN756729	MN782459	New Zealand, Northland, Kaihu, Maropiu Road
<i>Paralaoma seroilis</i> (Shuttleworth, 1852)	MN792615	MN756739	MN782472	New Zealand, Southland, Colac Bay
<i>Phrixgnathus celia</i> Hutton, 1883	MN792620	MN756745	MN782477	New Zealand, Southland, Stewart Island, Mason Bay
<i>Punctum californicum</i> Pilsbry, 1898	MN792621	MN756746	MN782478	USA, California, San Francisco, Presidio, Lincoln Boulevard
<i>Punctum pygmaeum</i> (Draparnaud, 1801)	MN812719	MN756747	MN782479	UK, Monmouthshire, Monmouth, Pentwyn Farm
<i>Punctum randolphii</i> (Dall, 1895)	MN792622	MN756748	MN782480	Canada, British Columbia, Pemberton, Riverside Trail, Lillooet River
Helicarionoidea				
<i>Antiquarion evelynensis</i> Hyman & Köhler, 2020	MN654044	MN654081	—	Australia, Queensland, Millaa Millaa
<i>Antiquarion ravenshoe</i> Hyman & Köhler, 2020	MN654053	MN654089	—	Australia, Queensland, Tully
<i>Mysticarion insuetus</i> Iredale, 1941	KY662466	KY662376	—	Australia, New South Wales, Newcastle
<i>Nitor subrugatus</i> (Reeve, 1852)	MH248130	MH255873	—	Australia, New South Wales, Tooloom National Park
<i>Sarika resplendens</i> (Philippi, 1847)	MT364982	MT365763	MT365707	Thailand
<i>Stanisicarion freycineti</i> (Férussac, 1821)	MN073628	MN073747	—	Australia, Queensland, Eastern Escarpment Conservation Area
Rhytidoidea				
<i>Acavus phoenix</i> (L. Pfeiffer, 1854)	—	—	AY014083	Unknown
<i>Ampelita lamarei</i> (L. Pfeiffer, 1853)	—	—	KP230504	Madagascar, Msoala Peninsula
<i>Embertoniphanta goudotiana</i> (Férussac, 1839)	—	—	KP230517	Madagascar, Tsingy Beanka, Belitsaka
<i>Rhytida greenwoodi</i> (Gray, 1850)	KT970868	KT970900	KP230525	New Zealand, Waikato, Raglan
Trochomorpoidea				
<i>Asperitas trochus</i> (O. F. Müller, 1774)	MT654630	MT651546	MT651601	Indonesia
<i>Dyakia hugonis</i> (L. Pfeiffer, 1864)	MT803064	MT741748	MT741915	Malaysia, Sabah, Segaliud Lokan Forest Reserve
<i>Rhinocochlis nasuta</i> (Metcalf, 1852)	MT803094	MT741771	MT741938	Malaysia, Sarawak, Sibul, Lanjak Entimau

Table 2. Cont.

Species	COI	16S	ITS2+28S	Provenance of Voucher
Outgroup				
<i>Gulella caryatis</i> (Melvill & Ponsonby, 1898)	HQ328133	HQ328323	GQ330510	Namibia
<i>Subulina octona</i> (Bruguière, 1789)	JX988066	JX988353	MF444887	Palau

Based on the observed morphological features of the shell and soft body, it was suspected that *Reticulapex* and *Pilula* were not members of the Punctoidea. They seem to more closely resemble, respectively, members of the Acavidae and Helicarionoidea/Trochomorpoidea. DNA sequences of species belonging to those groups were obtained from GenBank (Table 2) and included in the analysis. The classification of Acavidae, Helicarionoidea, and Trochomorpoidea used here follows [18].

The outgroup for the phylogenetic analysis (see below) was composed of species from basal lineages within the Stylommatophora: Achatinidae, Rhytididae, and Streptaxidae. DNA sequences of members of those families were likewise obtained from GenBank (Table 2).

2.2. DNA Extraction, Amplification and Sequencing

The specimens used herein were fixed and preserved in ethanol (70% to 98%). Larger specimens had a small section of their foot clipped for DNA extraction, while very minute specimens were used completely. DNA extraction followed the standard protocol of the QIAGEN DNEasy® Blood & Tissue Kit, with a repetition of the final step to increase the yield.

The same markers used by [1] were adopted herein: (1) the barcoding fragment of the mitochondrial COI gene (primers LCO/HCO of [19]), which was circa 650 bp long; (2) the mitochondrial 16S rRNA gene (primers 16SarL/16SbrH of [20]), circa 450 bp; and (3) a continuous fragment of nuclear DNA, amplified in two fragments, encompassing the 3' end of the 5.8S rRNA gene, the ITS2 region, and the 5' end of the 28S rRNA gene (primers LSU-1/LSU-3 and LSU-2/LSU-5 of [21,22]), circa 1300 bp in total.

The settings of the PCR amplification were as follows. COI and 16S: initial denaturation at 96 °C (3 min); 35 cycles of denaturation at 95 °C (30 s), annealing at either 48 °C (COI) or 50 °C (16S) (1 min), and extension at 72 °C (2 min); and final extension at 72 °C (5 min). ITS2+28S: initial denaturation at 95 °C (3 min); 40 cycles of denaturation at 95 °C (30 s), annealing at either 50 °C (ITS2 section) or 45 °C (28S section) (1 min), and extension at 72 °C (5 min for ITS2 section or 2 min for 28S section); and final extension at 72 °C (4 min). Small variations in the protocol were pursued regarding the annealing temperatures and number of cycle steps for repeats of the samples that failed to amplify in the first round.

PCR success was assessed via agarose gel electrophoresis. The PCR products were cleaned with ExoSAP-IT™ (Affymetrix Inc., Santa Clara, CA, USA) following the manufacturer's protocol. Samples were sent out to Massey Genome Service (Massey University, Palmerston North, New Zealand) to be Sanger sequenced.

2.3. Sequence Assembly and Alignment

Sequences were quality proofed and assembled in Geneious Prime (v.2020.2.2, Biomatters Ltd., Auckland, New Zealand), and the consensus was uploaded to GenBank. See Table 1 for the registration numbers.

Alignment of the consensus sequences was likewise conducted in Geneious Prime using the MAFFT plugin (v.7.450; [23,24]) with the default settings. The resulting alignment of each marker (COI, 16S, and ITS+28S) was visually proofed for inconsistencies. The alignment was then run through Gblocks [25], using the least restrictive settings, to eliminate poorly aligned or data-deficient positions that could interfere with the analyses. The resulting alignments were then concatenated for a single phylogenetic analysis.

2.4. Phylogenetic Analysis

Phylogenetic analyses were performed via Bayesian inference using MrBayes (v.3.2.7 [26]) via the CIPRES Science Gateway (v. 3.3 [27]). Two concurrent analyses were run, each with 4 Markov chains of 60 million generations (the first 20% discarded as 'burn-in'), the default priors, nst = 6, rates = invgamma, temperature parameter = 0.1, sampling every 1000 generations, and with the substitution model parameters unlinked across the markers (COI, 16S, and ITS+28S). MCMC convergence was assessed by examining the standard deviation of split frequencies (~0.01) and the potential scale reduction factor (PSRF~1.0), as well as trace plots in Geneious [28].

3. Results

Including the outgroup, 64 terminal taxa were used in the analysis (Tables 1 and 2). After the exclusion of positions with Gblocks (see above), the resulting COI sequences were 653 bp long, 16S were 405 bp long, and ITS2+28S were 1055 bp long. Thus, the concatenated sequences used for the analyses were 2011 bp long.

In a first trial, the African species *Trachycystis tollini* and *Xerocystis capensis* (Table 1) formed a sister pair with very long branches inside the clade formed by all other Trachycystinae (Figure 1). This was deemed an artefact due to the short and fragmentary sequences of both species (Table 1), and they were thus removed from further analyses, as they were likely confounding the relationships within the Trachycystinae. Their exclusion did not change the topology of the tree outside of the Trachycystinae.

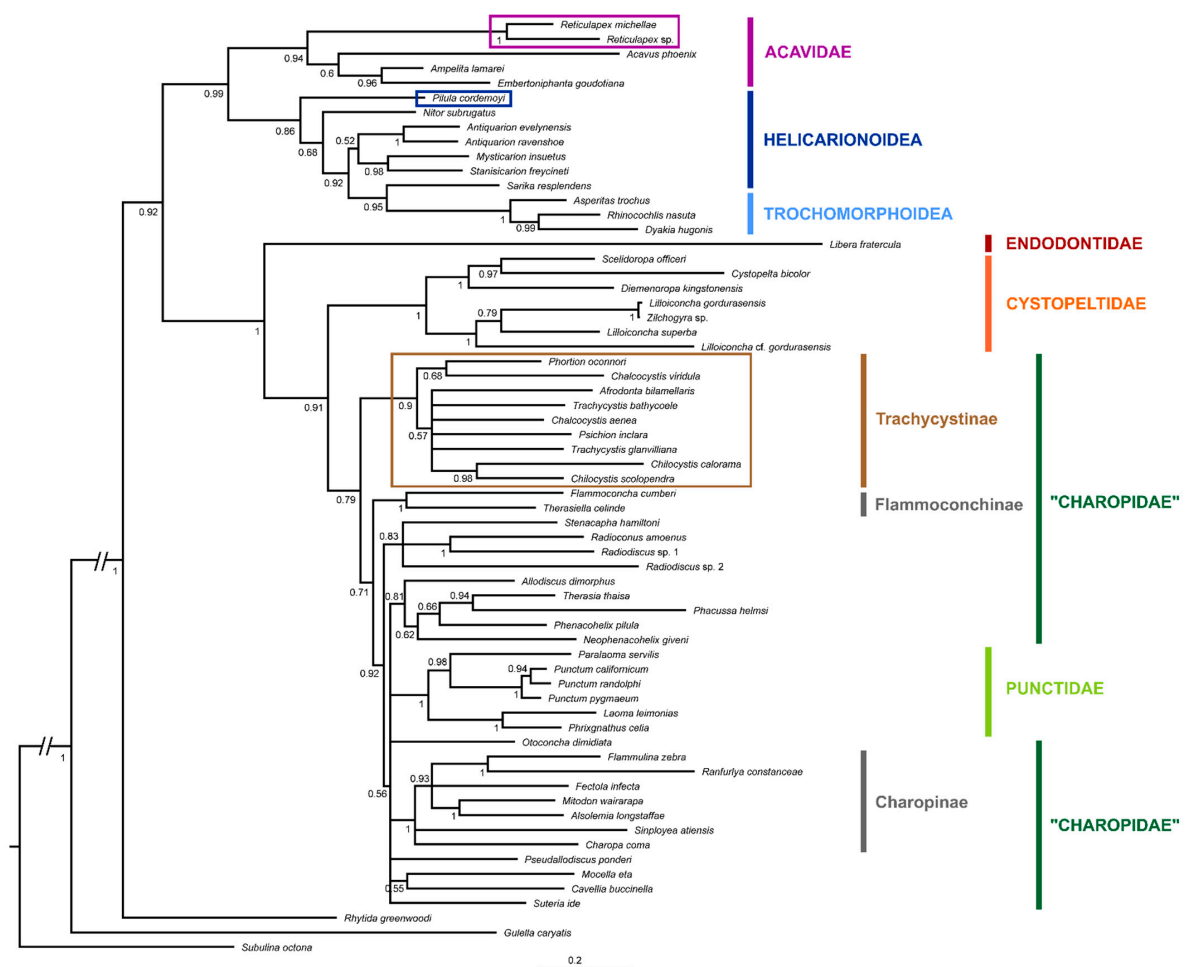


Figure 1. Bayesian inference phylogenetic tree based on COI, 16S, and ITS2+28S with a focus on African taxa. Posterior probabilities are shown on nodes. Scale bar = substitutions per site.

As hypothesized based on the overall morphology, *Reticulapex* and *Pilula* are not members of the Trachycystinae, or even the Punctoidea. *Reticulapex* belongs to the family Acavidae, with good support (posterior probability or PP = 0.94; Figure 1). The position of *Pilula* is not so clear; however, it seems more closely related to the superfamily Helicarionoidea (PP = 0.86), recovered as paraphyletic here (Figure 1).

The arrangement of the Punctoidea is similar to that of [1], with Endodontidae being the first branch, followed by the Cystopeltidae (including Australian and South American branches), and a paraphyletic Charopidae that includes the Punctidae. Nevertheless, the addition of African species and potentially basal New Zealand Charopidae to the dataset has brought more resolution to the “Charopidae”.

Trachycystinae was recovered as a monophyletic group with some support (PP = 0.90; Figure 1) and the most basal branch of the “Charopidae” and Punctidae clade, though with low support (PP = 0.79; Figure 1). A well-supported group formed by the New Zealand *Flammoconcha* and *Therasiella* (both represented by their type species) was recovered as basal to all other “Charopidae” and Punctidae (PP = 1.0; Figure 1).

Charopinae and Punctidae were recovered as monophyletic, as per [1], but there was a curious group formed by Australian *Stenacapha* B.J. Smith & Kershaw, 1985 and South American charopids, albeit with low support (PP = 0.83; Figure 1).

4. Discussion

The present results support Trachycystinae as a valid clade at the subfamily level, restricted to African taxa of afrodontas and pinwheels. Other African taxa tested (*Reticulapex* and *Pilula*) that had been previously assigned to the Punctoidea [3,4,18] are excluded from this superfamily and transferred to the Acavidae and Helicarionoidea, respectively.

Trachycystinae is a monophyletic group, the most basal one in the family “Charopidae” (Figure 1). It possibly represents an old southern African lineage potentially dating back to the split of Gondwana, while the Cystopeltidae were distributed in Australia and South America, and the remaining “Charopidae” in Zealandia and Australia (and later, in the Americas, and eventually Europe with the Punctidae) [1]. The restricted distribution of the Trachycystinae in southern Africa is a common pattern shared by other relict family and subfamily-level taxa of land snails [29]. There is no fossil record available of Trachycystinae dating from the Cretaceous or Paleogene, when the split might have occurred [29,30]. To my knowledge, the oldest fossils currently known are three species of *Trachycystis* from the Early Miocene in Kenya [31], which imply a different and possibly broader geographic distribution of the subfamily in the past. Further fossil records belong to the extant species *Xerocystis capensis* and to “*Trachycystis*” sp. from the Pliocene of South Africa [32,33].

If further studies support the present findings, the elevation of the Trachycystinae to the family level (as sister to the “Charopidae” and Punctidae) might be warranted, similar to the status of the recently redefined Cystopeltidae [1].

It was not possible, however, to obtain a clear internal structure of the Trachycystinae (Figure 1). It is uncertain at this point whether this is due to missing sequences of some markers for a few species or to a lack of further species. Nevertheless, the present phylogeny hinted that the genus-level classification of some species (in the *Chalcocystis* and *Trachycystis*), as well as the validity of some genera, might warrant further attention in future studies.

Finally, even though it was not part of the objectives of this study, the arrangement of the present phylogeny (Figure 1) indicates that Flammoconchinae is a valid taxon in the subfamily level within the “Charopidae”. Excluding Trachycystinae, this newly defined Flammoconchinae is basal to all other “Charopidae” and Punctidae (Figure 1). It is endemic to New Zealand and contains the genera *Flammoconcha* and *Therasiella*, both of which have similar shells to some species of African pinwheels. The phylogenetic position of the genus *Calymna* F.W. Hutton, 1883, often classified in this subfamily, requires further investigation. No fossil record of this subfamily is known [1].

5. Conclusions

Based on the present results, the following revised taxonomic classification, listing only the genera that were present in the analysis, is proposed:

- Superfamily Rhytidoidea Pilsbry, 1893
 - Family Acavidae Pilsbry, 1895
 - Genus *Reticulapex* Emberton & Pearce, 2000
- Superfamily Punctoidea Morse, 1864
 - Family Endodontidae Pilsbry, 1895
 - Family Cystopeltidae Cockerell, 1891
 - Family Punctidae Morse, 1864
 - Family “Charopidae” Hutton, 1884
 - Subfamily Charopinae Hutton, 1884
 - Subfamily Flammoconchinae Schileyko, 2001
 - Genus *Flammoconcha* Dell, 1952
 - Genus *Therasiella* Powell, 1948
 - Subfamily Trachycystinae Schileyko, 1986
 - Genus *Afrodonta* Melvill & Ponsonby, 1908
 - Genus *Chalcocystis* H. Watson, 1934
 - Genus *Chilocystis* H. Watson, 1934
 - Genus *Phortion* Preston, 1910
 - Genus *Psichion* Gude, 1911
 - Genus *Trachycystis* Pilsbry, 1893
 - Genus *Xerocystis* H. Watson, 1934
- Superfamily Helicarionoidea Bourguignat, 1877
 - Helicarionoidea *incertae sedis*
 - Genus *Pilula* E. von Martens, 1898

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