Doubled helix: Sagdoidea is the overlooked sister group of Helicoidea (Mollusca: Gastropoda: Pulmonata)

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We performed multi-locus, time-calibrated phylogenetic analyses of Jamaican Pleurodontidae to infer their relationships within pulmonate land snails. These analyses revealed that Sagdoidea, with about 200 species in the Caribbean Basin and neighbouring regions, is the sister group of Helicoidea with about 4700 species worldwide and that these superfamilies diverged 61–96 Ma. Morphological disparity in Sagdoidea is similar to that in Helicoidea despite its much lower species richness. Helicoidea originated in the New World and colonized the Old World 46–64 Ma. Pleurodontids and sagdids colonized Jamaica 15.0–18.4 and 12.8–16.5 Ma, respectively, consistent with geological estimates of Jamaican subaerial emergence by mid-Miocene. Allopatric convergence in shell morphologies required caution in using fossils from outside the geographic range of ingroup taxa to calibrate molecular clock estimates. Estimates of ages of clades varied by 24–55%, depending on the calibration points included. We use these results to revise Helicoidea and Sagdoidea. Pleurodontids from Jamaica and the Lesser Antilles were reciprocally monophyletic but other putative pleurodontids grouped basally in Helicoidea as Labyrinthidae (new family), or with Sagdidae. Newly recognized members of Sagdoidea are Solaropsinae and Caracolinae (Solaropsidae), Polydontinae (Sagdidae) and Zachrysiidae (new family). Pleurodontidae is restricted to two subfamilies, Pleurodontinae, in the Lesser Antilles, with Gonostomopsinae, a synonym, and Lucerninae resurrected for the Jamaican endemic genera *Lucerna*, *Dentellaria*, *Thelidomus* and *Eurycratera*. *Lucerna* and *Dentellaria* have been treated as subgenera of *Pleurodonte*, but rendered it paraphyletic in our analyses.

ADDITIONAL KEYWORDS: Caribbean – convergence – disparity – fossil calibration – Jamaica – phylogeny – Pleurodontidae – Sagdidae.

INTRODUCTION

Interactions among phenotypic, functional, and lineage diversifications have long intrigued evolutionary biologists. Within Mollusca, the second largest metazoan phylum, of particular interest is determining the degree to which convergent shell morphologies are due to similar ecological opportunities, as seen in adaptive radiation, or simply due to constraint in the range of possible shell morphologies (Hirano *et al.*, 2015; Stankowski, 2015). Unlike well-studied taxa, such in-depth evolutionary studies of land snails have been held back due to the lack of a robust phylogenetic framework. Many molluscan taxa are still defined by shell and anatomical characters, which may be under strong selective forces. For studies of phenotypic diversification (e.g. Triantis *et al.*, 2016) and biogeography (e.g. Scott, 1996), homoplasy mistaken for synapomorphy may obscure true patterns where classifications have not yet been corroborated with molecular data sets.

Convergence in shell form has bedevilled the classification of the helicoid land snails for generations. Many of the species treated here were first named in the genus *Helix* Linnaeus, 1758, typified by *Helix pomatia* Linnaeus, 1758, the escargot, which has a shape many people associate with the prototypical 'garden snail'. Anatomical studies began in earnest with the work of Pilsbry (1895), who recognized multiple genera in the Helicidae, dividing them into the newly named subfamilies Polygyrinae, Acavinae, Sagdinae and Camaeninae, in addition to the nominotypical Helicinae. Since then each of these subfamilies has been elevated to family level, and Acavoidea, Sagdoidea and, in some classification, Polygyroidea have been excluded from Helicoidea. Currently 17 families are recognized in Helicoidea but no consensus has been reached on their interrelationships (Bouchet *et al.*, 2005).

Our own interest in helicoid phylogeny began with an investigation of the Jamaican taxa within the Pleurodontidae Ihering, 1912. This family contains the largest endemic Jamaican snail species, with shells 20–70 mm in width, and crawling animals sometimes exceeding 100 mm in length. Since the outgroup of Pleurodontidae was unknown, we constructed a molecular phylogeny of Jamaican pleurodontid species using one nuclear and two mitochondrial genes, with multiple outgroups across and outside the helicoid families. The results proved to be of general interest for helicoid phylogeny, as they also shed light on previously hypothesized superfamilial relationships of many eupulmonate families (Table 1).

The West Indies has been an exceptionally fertile ground for investigating many aspects of biogeography and macroevolution (Ricklefs & Birmingham, 2008). Radiations of land snails in Jamaica are also of general interest as they represent natural experiments in which independent taxa evolving across the same landscape can be used to test many ideas in evolution and ecology. Jamaica has more than 560 named species of terrestrial gastropods, a remarkable diversity that for its area (11 000 km^2) is as high as any place on earth (Rosenberg & Muratov, 2006). Overall 90% of Jamaican species are endemic and 97–100% of species in the eight most diverse families (25 or more species) are endemic: Helicinidae, Neocyclotidae, Annulariidae and Truncatellidae among the operculates, and Oleacinidae, Urocoptidae, Sagdidae and Pleurodontidae among the pulmonates. However, among terrestrial gastropods in the West Indies, to date, only Urocoptidae has been subjected to molecular phylogenetic analysis (Uit de Weerd, Robinson & Rosenberg, 2016).

Jamaica is thought never to have been in contact with another land mass since its emergence in the Miocene (Buskirk, 1985; Mitchell, 2008), so current diversity results from a limited, but unknown, number of colonization events and subsequent evolutionary radiations. Here, we test the hypothesis that Jamaican pleurodontids are monophyletic, representing a single colonization that resulted in four endemic genera: *Dentellaria* Schumacher, 1817, *Lucerna* Swainson, 1840, *Eurycratera* Beck, 1837 and *Thelidomus* Swainson, 1840. This hypothesis conflicts with the classifications by Cuezzo (2003), who grouped *Eurycratera* and *Thelidomus* with

Table 1. Comparison of superfamily-level classification by Zilch (1960), Tillier (1989), Bouchet *et al.* (2005) and Schileyko (1998, 2000, 2003, 2004, 2005, 2006)

Family	Zilch	Tillier	Bouchet & Rocroi	Schileyko
Helicidae	Helicacea	Helicoidea	Helicoidea	Helicoidea
Hygromiidae*	Helicacea	Helicoidea	Helicoidea	Hygromioidea
Helicodontidae*	Helicacea	Helicoidea	Helicoidea	Hygromioidea
Geomitridae†	Helicacea	Helicoidea	Helicoidea	Hygromioidea
Cochlicellidae‡	Helicacea	Helicoidea	Helicoidea	Xanthonychoidea
Sphincterochilidae*	Helicacea	Helicoidea	Helicoidea	Xanthonychoidea
Bradybaenidae	Helicacea	Helicoidea	Helicoidea	Xanthonychoidea
Helminthoglyptidae	Helicacea	Helicoidea	Helicoidea	Xanthonychoidea
Cepolidae§	Helicacea	Helicoidea	Helicoidea	Xanthonychoidea
Camaenidae	Camaenacea	Helicoidea	Helicoidea	Camaenoidea
Pleurodontidae	Camaenacea	Helicoidea	Helicoidea	Polygyroidea
Polygyridae	Polygyracea	Helicoidea	Helicoidea	Polygyroidea
Sagdidae	Polygyracea	Helicoidea	Sagdoidea	Sagdoidea
Systrophiidae	Rhytidacea	Endodontoidea	Rhytidoidea	Rhytidoidea

*Classified as Helicidae in Zilch (1960) and Tillier (1989).
†Classified as Helicidae in Zilch (1960) and Tillier (1989) and as a subfamily of Hygromiidae in Schileyko (2005).
‡Classified as Helicidae in Zilch (1960) and Tillier (1989) and as a tribe of Geomitridae in Razkin *et al.* (2015).
§Classified as a subfamily of Helminthoglyptidae in Zilch (1960), Tillier (1989) and Schileyko (2004).

Polydontes Montfort, 1810 rather than with *Pleurodonte* Fischer von Waldheim, 1807, and Schileyko (2006), who included both Jamaican and Lesser Antillean species in *Pleurodonte*. These classifications both imply at least two colonization events of Jamaica.

Previous classifications have generally agreed that *Lucerna* and *Dentellaria* are closely related to the Lesser Antillean *Pleurodonte*, sometimes being treated as subgenera within it (e.g. Baker, 1935). Since we end up concluding that *Lucerna* and *Dentellaria* should be ranked as full genera, independent of *Pleurodonte*, we treat them as full genera in the Results for simplicity and refer to *Pleurodonte* excluding *Lucerna* and *Dentellaria* as *Pleurodonte s.s.* for clarity. Placement of *Eurycratera* and *Thelidomus* has been more equivocal. Pilsbry (1895), Baker (1935), Zilch (1960) and Cuezzo (2003) considered them more closely related to Greater Antillean *Polydontes* rather than Lesser Antillean *Pleurodonte*, while Wurtz (1955a) and Schileyko (2006) placed them with *Pleurodonte*. Both Pilsbry (1895) and Wurtz (1955a) noted the lack of characters to discern evolutionary relationships of the native Jamaican genera. Similarly, Cuezzo's (2003) morphological cladistic analysis of Pleurodontidae (as American Camaenidae) did not find anatomical characters that unite Jamaican pleurodontid genera.

MATERIAL AND METHODS

TAXON SAMPLING

A total of 70 Jamaican pleurodontid specimens and 52 additional pleurodontid and helicoid specimens were used for molecular analysis (Table 2). These included the type species of each of the four Jamaican genera. Many nominal taxa have been treated as junior synonyms of *Lucerna lucerna* (Müller, 1774) (e.g. by Rosenberg & Muratov, 2006), which has been considered a morphologically variable species, or species complex, widespread in Jamaica (Goodfriend, 1983). After a preliminary analysis (Blake, 2007) revealed more than 10% genetic divergence in 16S sequences, we decided to include more than 20 operational taxonomic units (OTUs) from the *L. lucerna* species complex, since greater taxon sampling reduces errors in phylogenetic reconstruction (Zwickl & Hillis, 2002). Some OTUs could not be confidently identified with nominal taxa and so were identified as 'cf.' or assigned a letter (e.g. sp. A). Our sampling included 25 of 31 native pleurodontid taxa listed as valid by Rosenberg & Muratov (2006), four OTUs identified as 'cf.' and 19 identified by letter.

Non-Jamaican pleurodontids included the type species of *Caracolus* Montfort, 1810, *Coloniconcha* Pilsbry, 1933, *Gonostomopsis* Pilsbry, 1889, *Granodomus* Pilsbry, 1931, *Hispaniolana* Pilsbry, 1933, *Isomeria*

Albers, 1850, *Lissembryon* Pilsbry, 1933, *Luquillia* Crosse, 1892 and *Pleurodonte*. Non-type species of pleurodontid genera from outside Jamaica included *Labyrinthus quadridentatus*, *Parthena obliterata*, *Zachrysia provisoria* and *Z. havanensis*. The sampled pleurodontids included species from all of the Greater Antilles, the Lesser Antilles (*Gonostomopsis*, *Pleurodonte s.s.*), Central America (*Labyrinthus* Beck, 1837) and South America (*Isomeria* and *Solaropsis* Beck, 1837). Since the phylogenetic position of Jamaican pleurodontids is uncertain, we included members of 11 pulmonate families as immediate outgroups: Bradybaenidae, Camaenidae, Cepolidae, Helicidae, Helicodontidae, Helminthoglyptidae, Geomitridae, Hygromiidae, Polygyridae, Sagdidae and Sphincterochilidae, representing more than half of the families in superfamily Helicoidea Rafinesque, 1815. We used previously published sequences for 23 helicoid taxa in phylogenetic analyses from GenBank (Wade *et al.*, 2007; Uit de Weerd, 2008; Hugall & Stanisic, 2011; Table 2). *Tamayoa decolorata* (Drouët, 1859), a scolodontid in superfamily Rhytidoidea Pilsbry, 1893, was used as a non-helicoid outgroup. Wade, Mordan & Clarke (2001) identified *Haplotrema* Ancey, 1881, also a rhytidoid, to be a sister taxon to the Helicoidea.

To determine which putative pleurodontid and polygyrid fossils to include as calibration points, GR and MS visited the invertebrate paleontology collection at the United States National Museum. They examined type material of relevant taxa under a dissecting microscope and compared them with the recent members of Pleurodontidae, Polygyridae and other helicoids from the ANSP collection.

DNA EXTRACTION, AMPLIFICATION AND SEQUENCING

We used DNeasy Tissue Kit (QIAGEN, Valencia, CA) to extract genomic DNA from individual snails preserved in 70% ethanol. A small piece of foot was used for most taxa. We sequenced two mitochondrial genes [cytochrome *c* oxidase subunit II (*COII*) and 16S *rRNA*] and one nuclear gene (28S *rRNA*). Polymerase chain reactions (PCRs) were performed using Apex Master Mix (Genesee Scientific, San Diego, CA) to amplify approximately 510 bp of *COII*, 440 bp of 16S and 425 bp of 28S. Primers and reaction conditions are indicated in Tables 3 and 4. Initially, PCR products were purified with ExoSAP-IT (USB, Cleveland, OH), sequenced with BigDye Terminator v3.1 Cycle Sequencing Kit, cleaned with BigDye Xterminator Purification Kit (Applied Biosystems, Carlsbad, CA) and sent for Sanger sequencing at University of Pennsylvania. Later, PCR products were purified and sequenced at Functional Biosciences, Inc. (Madison, WI). We were unable to amplify all genes

Table 2. List of specimens sequenced

Taxon	Locality	Catalogue number	GenBank accession number		
			COII	16S	28S
Helicoidea: Pleurodontidae: Lucerninae					
Dentellaria amabilis (C. B. Adams, 1850)	Trelawny Parish, Jamaica	ANSP 448754	KF246775	KF246883	KF207604
"	Trelawny Parish, Jamaica	ANSP 449140	KF246776	KF246884	
Dentellaria atavus (Pfeiffer, 1845)	Westmoreland Parish, Jamaica	ANSP 449145	KF246777	KF246885	KF207605
Dentellaria bronni (Pfeiffer, 1846)	Trelawny Parish, Jamaica	ANSP 403293	KF246778	KF246886	KF207606
Dentellaria candescens C. B. Adams, 1850	Saint Ann Parish, Jamaica	ANSP 448671	KF246779	KF246887	KF207607
Dentellaria invalida (C. B. Adams, 1850)	Saint Andrew Parish, Jamaica	ANSP 402520	KF246780	KF246888	KF207608
Dentellaria okeniana (Pfeiffer, 1845)	Westmoreland Parish, Jamaica	ANSP 448828	KF246781	KF246889	KF207609
"	Westmoreland Parish, Jamaica	ANSP 449163	KF246782	KF246890	
"	Hanover Parish, Jamaica	ANSP 448749	KF246783	KF246891	
Dentellaria pallescens (C. B. Adams, 1851)	Trelawny Parish, Jamaica	ANSP 448743	KF246784	KF246892	KF207610
Dentellaria peracutissima (C. B. Adams, 1845)	Manchester Parish, Jamaica	ANSP 406240	KF246785	KF246893	KF207611
"	Saint Catherine Parish, Jamaica	ANSP 448684	KF246786	KF246894	
Dentellaria picturata (C. B. Adams, 1849)	Hanover Parish, Jamaica	ANSP 448691	KF246787	KF246896	KF207612
Dentellaria schroeteriana (Pfeiffer, 1845)	Hanover Parish, Jamaica	ANSP 449033	KF246800	KF246909	KF207621
Dentellaria simson (Pfeiffer, 1852)	Portland Parish, Jamaica	ANSP 402407	KF246789	KF246898	KF207614
"	Saint Catherine Parish, Jamaica	ANSP 404204	KF246790	KF246899	
"	Saint Andrew/Saint Mary Parish, Jamaica	ANSP 448967	KF246791	KF246900	
Dentellaria cf. *D. simson*	Hanover Parish, Jamaica	ANSP 449274	KF246792	KF246901	KF207615
Dentellaria sinuata (Müller, 1774)	Westmoreland Parish, Jamaica	ANSP 448876	KF246793	KF246902	KF207616
"	Hanover Parish, Jamaica	ANSP 449001	KF246794	KF246903	
Dentellaria cf. *D. sinuata* (Müller, 1774)	Saint Elizabeth Parish, Jamaica	ANSP 405612	KF246795	KF246904	KF207617
Dentellaria sloaneana (Pfeiffer, 1868)	Portland Parish, Jamaica	ANSP 402320	KF246796	KF246906	KF207619
"	Hanover Parish, Jamaica	ANSP 448894	KF246797	KF246907	
Dentellaria strangulata (C. B. Adams, 1849)	Portland Parish, Jamaica	ANSP 409730	KF246798	KF246908	
"	Portland Parish, Jamaica	ANSP 449377	KF246799		

Table 2. *Continued*

Taxon	Locality	Catalogue number	GenBank accession number		
			COII	16S	28S
Dentellaria tridentina (Férussac, 1832)	Westmoreland Parish, Jamaica	ANSP 448960	KF246801	KF246910	
"	Hanover Parish, Jamaica	ANSP 448971	KF246802	KF246911	
"	Westmoreland Parish, Jamaica	ANSP 449292	KF246803	KF246912	
"	Westmoreland Parish, Jamaica	ANSP 449224	KF246804	KF246913	
"	Hanover Parish, Jamaica	ANSP 449172	KF246805	KF246914	
Dentellaria valida (C. B. Adams, 1850)	Saint Thomas Parish, Jamaica	ANSP 402504	KF246806	KF246915	KF207622
"	Portland Parish, Jamaica	ANSP 448905	KF246807	KF246916	
"	Saint Thomas Parish, Jamaica	ANSP 449390	KF246808	KF246917	
"	Saint Thomas Parish, Jamaica	ANSP 449071	KF246809	KF246918	
Eurycratera jamaicensis (Gmelin, 1791)	Saint Ann Parish, Jamaica	ANSP 450340	KF246839	KF246951	KF207652
"	Hanover Parish, Jamaica	ANSP 450059	KF246840	KF246952	
Lucerna bainbridgii (Pfeiffer, 1845)	Trelawny Parish, Jamaica	ANSP 448881	KF246811	KF246920	KF207624
"	Saint Elizabeth Parish, Jamaica	ANSP 449106	KF246812	KF246921	
Lucerna chemnitziana (Pfeiffer, 1845)	Portland Parish, Jamaica	ANSP 409155	KF246813	KF246922	KF207625
Lucerna lamarckii (Férussac, 1821)	Saint Thomas Parish, Jamaica	ANSP 409635	KF246814	KF246923	KF207626
"	Portland Parish, Jamaica	ANSP 409265	KF246815	KF246924	
Lucerna lucerna (Müller, 1774)	Saint Ann Parish, Jamaica	ANSP 451304	KF246827	KF246938	KF207639
Lucerna cf. *L. lucerna* (Müller, 1774)	Saint Andrew Parish, Jamaica	ANSP 402237	KF246816	KF246925	KF207627
Lucerna mora (Griffith & Pidgeon, 1834)	Saint Andrew Parish, Jamaica	ANSP 402247		KF246926	KF207628
"	Saint Thomas Parish, Jamaica	ANSP 449273	KF246817	KF246927	
Lucerna sublucerna (Pfeiffer, 1889)	Saint Catherine Parish, Jamaica	ANSP 450319	KF246838	KF246950	KF207651
Lucerna cf. *L. sublucerna* (Pfeiffer, 1889)	Saint Thomas Parish, Jamaica	ANSP 449339	KF246819	KF246929	KF207630
Lucerna vacillans (Vendryes, 1902)	Saint Andrew Parish, Jamaica	ANSP 402542	KF246818	KF246928	KF207629
Lucerna sp. A	Portland Parish, Jamaica	ANSP 450022		KF246930	KF207631
Lucerna sp. B	Clarendon Parish, Jamaica	ANSP 450256	KF246820	KF246931	KF207632
Lucerna sp. C	Manchester Parish, Jamaica	ANSP 450064	KF246821	KF246932	KF207633

Table 2. *Continued*

Taxon	Locality	Catalogue number	COII	16S	28S
Lucerna sp. D	Saint Ann Parish, Jamaica	ANSP 450271	KF246822	KF246933	KF207634
Lucerna sp. E	Trelawny Parish, Jamaica	ANSP 450219	KF246823	KF246934	KF207635
Lucerna sp. F	Saint James Parish, Jamaica	ANSP 450323	KF246824	KF246935	KF207636
Lucerna sp. G	Saint James Parish, Jamaica	ANSP 450279	KF246825	KF246936	KF207637
Lucerna sp. H	Saint James Parish, Jamaica	ANSP 450042	KF246826	KF246937	KF207638
Lucerna sp. J	Saint Ann Parish, Jamaica	ANSP 450039	KF246828	KF246939	KF207640
Lucerna sp. K	Saint Ann Parish, Jamaica	ANSP 449992	KF246829	KF246940	KF207641
Lucerna sp. L	Saint Ann Parish, Jamaica	ANSP 450157	KF246830	KF246941	KF207642
Lucerna sp. M	Saint Ann Parish, Jamaica	ANSP 450117		KF246942	KF207643
Lucerna sp. N	Saint Mary Parish, Jamaica	ANSP 451076	KF246831	KF246943	KF207644
Lucerna sp. O	Westmoreland Parish, Jamaica	ANSP 451262	KF246832	KF246944	KF207645
Lucerna sp. P	Westmoreland Parish, Jamaica	ANSP 450246	KF246833	KF246945	KF207646
Lucerna sp. Q	Hanover Parish, Jamaica	ANSP 450109	KF246834	KF246946	KF207647
Lucerna sp. R	Westmoreland Parish, Jamaica	ANSP 450283	KF246835	KF246947	KF207648
Lucerna sp. S	Hanover Parish, Jamaica	ANSP 449988	KF246836	KF246948	KF207649
Lucerna sp. T	Saint Elizabeth Parish, Jamaica	ANSP 450362	KF246837	KF246949	KF207650
Thelidomus aspera (Férussac, 1821)	Saint Elizabeth Parish, Jamaica	ANSP 407417	KF246841	KF246953	KF207653
"	Saint Catherine Parish, Jamaica	ANSP 405101	KF246842	KF246954	
Thelidomus cognata (Férussac, 1821)	Hanover Parish, Jamaica	ANSP 450138	KF246843	KF246955	KF207654
Helicoidea: Pleurodontidae: Pleurodontinae					
Gonostomopsis auridens (Rang, 1834)	Martinique	USDA 131164	KF246855	KF246969	KF207670
Pleurodonte dentiens (Férussac, 1822)	St. Mark Parish, Dominica	USDA 110730	KF246844	KF246956	KF207655
Pleurodonte guadeloupensis dominicana (Pilsbry & Cockerell, 1937)	St. George Parish, Dominica	USDA 110296	KF246847	KF246959	KF207658
Pleurodonte isabella (Férussac, 1821)	St. James Parish, Barbados	USDA 131167	KF246848	KF246960	KF207659
Pleurodonte lychnuchus (Müller, 1774)	Basse-Terre, Guadeloupe	USDA 131171	KF246850	KF246963	KF207663
Helicoidea: Bradybaenidae					
Bradybaena similaris (Férussac, 1822)	Rio Grande do Sul, Brazil	USDA 131199		KF247037	KF207741

Table 2. *Continued*

Taxon	Locality	Catalogue number	GenBank accession number		
			COII	16S	28S
"	Queensland, Australia		GQ851264	GQ851001	AY014138
Helicoidea: Camaenidae					
Austrochloritis agamemnon (Gude, 1906)	Queensland, Australia		GQ851314	GQ851060	GQ850887
Austrochloritis porteri (Cox, 1866)	Queensland, Australia		GQ851256	GQ850994	GQ850888
Basedowena gigantea Solem, 1993	South Australia, Australia		GQ851260	GQ850998	GQ850889
Chloritisanax banneri (Pfeiffer, 1863)	Queensland, Australia		GQ851266	GQ851003	GQ850891
Cupedora lincolnensis (Pfeiffer, 1864)	South Australia, Australia			GQ851157	
Cupedora lorioliana (Crosse, 1863)	South Australia, Australia		GQ851323	GQ851070	
Cupedora luteofusca (Cox, 1868)	South Australia, Australia			GQ851075	
Cupedora patruelis (Angas, 1868)	South Australia, Australia			GQ851069	
Cupedora sub001lorioliana (Pilsbry, 1890)	South Australia, Australia			GQ851217	
Hadra barneyi (Cox, 1873)	Queensland, Australia		GQ851308	GQ851047	GQ850912
Jacksonena delicata Hedley, 1912	Queensland, Australia		GQ851398	GQ851229	GQ850897
Mussonena campbelli Iredale, 1938	Queensland, Australia		GQ851287	GQ851025	GQ850900
Noctepuna cerea (Hedley, 1894)	Queensland, Australia		GQ851292	GQ851030	GQ850901
Noctepuna mayana (Hedley, 1899)	Queensland, Australia		GQ851293	GQ851031	GQ850897
Obsteugenia inflecta (Hedley, 1912)	Queensland, Australia		GQ851339	GQ851091	GQ850903
Papuexul bidwilli (Reeve, 1853)	New South Wales, Australia		GQ851294	GQ851032	GQ850905
Rhynchotrochus macgillivrayi (Forbes, 1851)	Queensland, Australia		GQ851298	GQ851036	GQ850907
Satsuma jacobii (Pilsbry, 1900)	Gifu, Japan		GQ851277	GQ851015	GQ850899
Spurlingia forsteriana (Reeve, 1852)	Queensland, Australia		GQ851350	GQ851105	GQ850913
Sphaerospira fraseri (Griffith & Pidgeon, 1833)	Queensland, Australia		GQ851300	AY151067	GQ850908
Sphaerospira volgiola (Iredale, 1933)	Queensland, Australia		GQ851328	GQ851076	GQ850894
Trozena morata Iredale, 1938	Queensland, Australia		GQ851306	GQ851045	GQ850911
Helicoidea: Cepolidae					
Cepolis definita (Fulton, 1908)	Pedernales, Dominican Republic	USDA 131190		KF247018	KF207721
Dialeuca nemoraloides (C. B. Adams, 1845)	Saint Thomas Parish, Jamaica	ANSP 451012	KF246876	KF247020	KF207723
Helicoidea: Geomitridae					
Cernuella cisalpina (Rossmässler, 1837)	North Carolina, USA	USDA 142070	KF246872	KF247012	KF207715
Cochlicella acuta (O. F. Müller, 1774)	Nabeul, Tunisia	USDA 131187	KF246874	KF247015	KF207718
Cochlicella barbara (Linnaeus, 1758)	Vizcaya, Spain	USDA 131188	KF246875	KF247016	KF207719
Disculella maderensis (Wood, 1828)	Madeira, Portugal	USDA 131189		KF247017	KF207720
Helicoidea: Hygromiidae					
Monacha cantiana (Montagu, 1803)	Italy	USDA 140816	KF246873	KF247013	KF207716

Table 2. *Continued*

Taxon	Locality	Catalogue number	GenBank accession number		
			COII	16S	28S
Trochulus hispidus (Linnaeus, 1758)	Maine, USA	USDA 131186		KF247014	KF207717
Helicoidea: Helicidae					
Cornu aspersum (O. F. Müller, 1774)	Colorado, USA	USDA 131197	KF246878	KF247035	KF207739
Helix pomatia Linnaeus, 1758	Ljubljana, Slovenia	USDA 131198		KF247036	KF207740
Cepaea nemoralis (Linnaeus, 1758)	Denmark	USDA 131204	KF246877	KF247034	KF207738
Helicoidea: Helicodontidae					
Helicodonta obvoluta (O. F. Müller, 1774)	Italy	USDA 131202		KF247043	KF207748
Helicoidea: Helminthoglyptidae					
Plesarionta stearnsiana (Gabb, 1867)	California, USA	USDA 110439		KF247027	KF207730
Helicoidea: Labyrinthidae (new family)*					
Isomeria oreas (Koch, 1844)	Valle del Cauca, Colombia		KF246861	KF246980	KF207682
Labyrinthus quadridentatus (Broderip, 1832)	Puntarenas, Costa Rica		KF246862	KF246981	KF207683
"	Puntarenas, Costa Rica		KF246863	KF246982	
Helicoidea: Polygyridae					
Polygyra cereolus (Mühlfeld, 1816)	Cayman Islands	USDA 131205		KF247038	EU409912
Praticolella mexicana Perez, 2011	Westmoreland Parish, Jamaica	ANSP 450907	KF246879	KF247039	KF207742
Helicoidea: Sphincterochilidae					
Sphincterochila candidissima (Draparnaud, 1801)	Spain	USDA 131200		KF247040	KF207743
Sagdoidea: Sagdidae: Platysuccineinae					
Platysuccinea n. sp. (Shuttleworth, 1854)	Ponce, Puerto Rico	USDA 131185		KF247011	KF207714
Sagdoidea: Sagdidae: Polydontinae*					
Coloniconcha prima Pilsbry, 1933	Sud-Est, Haiti	UF 47737	KF246859	KF246976	KF207677
Granodomus lima (Férussac, 1821)	Trujillo Alto, Puerto Rico	UF 28178		KF246977	KF207678
Hispaniolana undulata (Férussac, 1819)	Grand-Anse, Haiti	UF 46656			KF207681
Lissembryon dilatata (Pfeiffer, 1846)	La Altagracia, Dominican Republic	UF 336785	KF246864	KF246983	KF207684
Luquillia luquillensis (Shuttleworth, 1854)	Rio Grande, Puerto Rico	UF 191184	KF246865	KF246984	KF207685
Parthena obliterata (Férussac, 1821)	Sud, Haiti	UF 46184	KF246866	KF246986	KF207687
"	Sud-Est, Haiti	UF 46592	KF246867	KF246987	
Sagdoidea: Sagdidae: Sagdinae					
Aerotrochus mcnabianus (Chitty, 1853)	Hanover Parish, Jamaica	ANSP 451227		KF246995	KF207695
Corneosagda immunda (C. B. Adams, 1849)	Portland Parish, Jamaica	ANSP A22931		KF246996	KF207696
Hyalosagda arboreoides (C. B. Adams, 1845)	Saint Thomas Parish, Jamaica	ANSP 451023		KF246998	KF207699

Table 2. *Continued*

Taxon	Locality	Catalogue number	COII	16S	28S
Sagda cf. *S. epistylioides* (Férussac, 1821)	Westmoreland Parish, Jamaica	ANSP 451188		KF247005	KF207708
Stauroglypta anthoniana (C. B. Adams, 1849)	Hanover Parish, Jamaica	ANSP 450929		KF247006	KF207709
Zaphysema olivaceum H. B. Baker, 1935	Portland Parish, Jamaica	ANSP 409733	KF246871	KF247010	KF207713
Sagdoidea: Solaropsidae: Caracolinae*					
Caracolus caracollus (Linnaeus, 1758)	Jayuya, Puerto Rico	UF 133476	KF246856	KF246970	KF207671
Caracolus gaskoini (Reeve, 1851)	Independencia, Dominican Republic	UF 257921		KF246971	KF207672
Caracolus bornii (Pfeiffer, 1846)	Trujillo Alto, Puerto Rico	UF 28177		KF246972	KF207673
Caracolus sagemon (Beck, 1837)	Holguín, Cuba	UF 296189	KF246857	KF246973	KF207674
"	Camagüey, Cuba	ANSP A22935	KF246858	KF246974	KF207675
Caracolus sarcocheila (Mörch, 1850)	La Altagracia, Dominican Republic	UF 22572		KF246975	KF207676
Sagdoidea: Solaropsidae: Solaropsinae					
Solaropsis cf. *S. gibboni* (Pfeiffer, 1846)	Cundinamarca, Colombia			KF246988	KF207688
Solaropsis heliaca (d'Orbigny, 1835)	Santa Cruz, Bolivia	UF 212799	KF246868	KF246989	KF207689
Solaropsis sp.	El Zarza, Ecuador	UF 215393	KF246869	KF246990	KF207690
Solaropsis sp.	Concepción, Paraguay			KF246991	KF207691
Sagdoidea: Zachrysiidae (new family)*					
Zachrysia havanensis (Pilsbry, 1894)	Mayagüez, Puerto Rico	USDA 131181		KF246992	KF207692
Zachrysia provisoria (Pfeiffer, 1858)	Grand Cayman, Cayman Islands	ANSP 400324	KF246870	KF246993	KF207693
Rhytidoidea: Scolodontidae					
Tamayoa decolorata (Drouët, 1859)	Hanover Parish, Jamaica	ANSP 451152	KF246882	KF247045	KF207750

The higher classification shown is what we have adopted as the result of the analyses.
*Clades formerly placed in Pleurodontidae.

for all specimens. After sequences from GenBank were added, the *COII* alignment consisted of 115 sequences, the 16S alignment consisted of 143 sequences and the 28S alignment consisted of 145 sequences. We deposited new sequences in GenBank under accession numbers KF207604–KF207750 and KF246775–KF247045 (Table 2).

PHYLOGENETIC RECONSTRUCTION

The rDNA sequences were aligned with MAFFT 6.822 (Katoh & Toh, 2008) as implemented on the CIPRES Portal v3.1 (Miller, Pfeiffer & Schwartz, 2010) and ClustalX 2.0.11 (Larkin *et al.*, 2007) using optimum gap opening and gap extension penalties for ribosomal DNA described in Wilm, Maintz & Steger (2006).

We then manually adjusted alignments further in MacClade 4.08 (Maddison & Maddison, 2005). We used ALISCORE 2.0 (Misof & Misof, 2009; Kück *et al.*, 2010) to screen for randomly similar regions in aligned sequences on 16S. We used PartitionFinder v1.1.1 (Lanfear *et al.*, 2012) to determine that five partitions are the best fit for the data: the three codon positions of the *COII* gene, and the 16S and 28S genes. The best-fitting models of molecular evolution were determined using jModelTest 2.1.1 for each partition (Guindon & Gascuel, 2003; Darriba *et al.*, 2012) under the corrected Akaike Information Criterion (Akaike, 1974).

Maximum parsimony analysis was performed in PAUP* 4.0b10 (Swofford, 2002) with equal weighting, using the heuristic search option of 1000 random addition sequences with tree bisection-reconnection

Table 3. Primers used in this study

Gene	Primer	Sequence 5′–3′	Source
COII	LCOIIshort	ATG CTA TTT CAT GAY CAY GC	Modified from Hugall *et al.* (2002)
	HCOIIshort	GCT CCG CAA ATC TCT GA	Modified from Hugall *et al.* (2002)
16S *rRNA*	16Sa-L	CGG CCG CCT GTT TAT CAA AAA CAT	Palumbi *et al.* (1991)
	16Sbr-H	GGA GCT CCG GTT TGA ACT CAG ATC	Palumbi *et al.* (1991)
28S *rRNA*	D23F	GAG AGT TCA AGA GTA CGT G	Park & Ó Foighil (2000)
	D4R	TGT TAG ACT CCT TGG TCC GTG T	Park & Ó Foighil (2000)

Table 4. Amplification conditions and temperature profiles

Gene	Primer pair	Amplification conditions	Temperature profile
COII	LCOIIshort & HCOIIshort	Total volume 20 µL with 1× Apex Master Mix*, 0.25 µM of each primer	1 cycle of 4 min at 95 °C 13 cycles 1 min at 95 °C 30 s at 50 °C, decreasing by 1 °C every cycle 2 min at 72 °C 30 cycles 1 min at 95 °C 30 s at 38 °C 2 min at 72 °C 1 cycle of 10 min at 72 °C
16S *rRNA*	16Sa-L & 16Sbr-H	Total volume 20 µL with 1× Apex Master Mix, 3.5 mM MgCl$_2$, 0.4 mM BSA, 0.25 µM of each primer	1 cycle of 2 min at 93 °C 40 cycles 45 s at 93 °C 1 min at 48 °C 1 min at 68 °C 1 cycle of 7 min at 68 °C
28S *rRNA*	D23F & D4R	Total volume 20 µL with 1× Apex Master Mix, 0.25 µM of each primer 1.0 mM MgCl$_2$, 0.4 mM BSA and 5% DMSO were added to amplify non-Jamaican samples	1 cycle of 4 min at 95 °C 7 cycles 1 min at 95 °C 1 min at 60 °C, decreasing by 1 °C every cycle 90 s at 72 °C 30 cycles 1 min at 95 °C 1 min at 54 °C 90 s at 72 °C 1 cycle of 10 min at 72 °C

BSA, bovine serum albumin; DMSO, dimethyl sulfoxide.
*MgCl$_2$ (1.5 mM).

(TBR) branch-swapping and holding a maximum of 10 equally parsimonious trees at each step. Bootstrap frequencies were calculated based on 1000 replicates, each analyzed with a single random addition sequence and TBR swapping. Frequencies were calculated based on the strict consensus of all trees saved from each replicate, providing a conservative estimate of boot-strap support (Davis *et al.*, 2004).

We used RAxML v7.3.0 (Stamatakis, 2006) as implemented on the CIPRES Portal v3.1 to perform a maximum likelihood (ML) analysis. The data were partitioned into (1) *COII* first, (2) second, (3) third codon positions, (4) 16S and (5) 28S. The tree search and non-parametric bootstrap analysis were conducted simultaneously using 1000 replicates of the full boot-strap algorithm. During the tree search, the GTR + CAT model with 25 rate categories was fitted to each data partition. Branch lengths and model parameters were then optimized on the ML tree identified under GTR + CAT using the GTR + G model (GTRMIX option). We created a bootstrap consensus tree in PAUP* v4.0b (Swofford, 2002) and used Figtree v1.3.1 (Rambaut, 2009) to map an output tree file in vector graphics format.

We used MrBayes 3.1.2 (Huelsenbeck, Ronquist & Hall, 2001; Ronquist & Huelsenbeck, 2003) as implemented on the CIPRES Portal v3.1 to perform a Bayesian analysis. The data were partitioned as in the ML analysis. The analysis was performed by running two parallel analyses, consisting each of six Markov chains of 20 000 000 generations each with a sampling frequency of one tree per 1000 generations. The

number of swaps was set to one, and the chain temperature at 0.2. One different GTR + G model each with six substitution categories and a gamma-discrete category was applied for each partition. A consensus tree was calculated after omitting the first 5000 trees as burn-in. We evaluated the convergence of each analysis by examining the Potential Scale Reduction Factor and standard deviation (SD) of split frequencies in the standard output. We considered a clade to be moderately supported if it had bootstrap support values (B) between 75 and 89 and posterior probability (PP) between 0.95 and 0.97, and highly supported when B ≥ 90 and PP ≥ 0.98.

DIVERGENCE TIME ANALYSIS

The combined partition set was used during BEAST v1.7.4 (Drummond *et al.*, 2012) analysis to estimate divergence times. We excluded the outgroup *Tamayoa* following the recommendation in Drummond & Bouckaert (2015: 98) and redetermined the best substitution models for each gene with jModelTest v2.1.1 (TVM + G for *COII*, 010023 + G + F for 16S and 011230 + G + F for 28S) after the exclusion. We edited the Bayesian tree in Mesquite v2.75 (Maddison & Maddison, 2011) to create an ultrametric starting tree. We created the input file using BEAUti v1.7.4 (Drummond *et al.*, 2012), editing it to add the ultrametric starting tree and substitution models other than GTR. We modelled the gamma distribution with four categories and estimated base frequencies and used a relaxed molecular clock with rates for each branch drawn independently from a lognormal distribution (Drummond *et al.*, 2006). The tree model used a lognormal distribution for the Yule 'meanRate' prior (initial = 1.0).

Table 5 lists the calibration points used in the analysis. We chose the 'include stem' option for fossil-based calibration points so that the divergence time would be for the parent node of the most recent common ancestor (i.e. the bottom of the stem leading to the clade) except for the origin of *Lucerna* Clade B. The presence of two species at the Pliocene (*Lucerna bowdeniana* and *L. bernardi*) suggests that they belong to the crown group. For fossil-based calibration points, we chose a lognormal prior for the time to the most recent common ancestor (t_{MRCA}). The offsets of lognormal distributions were chosen as the younger bound of the fossils' ages. We used mean of 0.5 and SD of 1.0 for lognormal priors, except for the origin of *Labyrinthus s.l.*, for which the SD was set to 1.5 to account for the greater uncertainty of the age of *Labyrinthus obtusus* (Anderson & Hanna, 1925). We used normal distributions without hard bounds for geologic calibration points based on subaerial emergence of Jamaica and chose mean of 15 Ma

and SD of 1.0 Ma. Time of last emergence of Jamaica has been controversial, with estimates ranging from ≤10 Ma (Donovan, 2002; Graham, 2003) to 35 Ma (Iturralde-Vinent & MacPhee, 1999), with 10 Ma used to calibrate some phylogenies (e.g. Hedges, Couloux & Vidal, 2009; Burbrink, Ruane & Pyron, 2012). A 10 Ma age is likely too young: a number of authors have indicated middle Miocene emergence (Steineck, 1974; Hendry, 1987; Donovan & Paul, 2013), which at latest would be 11.6 Ma. Uit de Weerd *et al.* (2016) used an earliest date of 16 Ma for Jamaican emergence for their biogeographical analysis of Urocoptidae. Some of the differences may stem from different readings of the same underlying sources. For example, Robinson (1971) said (p. 7), 'Although there may have been elevation of the northern part of Central Jamaica in the Early Miocene, the major part of the region was raised above sea level some 10 million years ago'. Mitchell *et al.* (2016) noted that the age of zircons reported by Comer, Naeser & McDowell (1980) from bauxite deposits overlying guano-derived phosphorites show that the Manchester and St. Ann Plateaus were subaerially exposed by mid-Miocene.

Because we were not confident about the taxonomic placement of the oldest fossils (see Discussion) and the timing of the last emergence of Jamaica, we performed four BEAST runs, combinations of with and without the Eocene calibration points and the Jamaican geologic calibration point. Each MCMC chain was run for 200 000 000 generations with convergence confirmed using Tracer v1.7.4 (Drummond *et al.*, 2012) when effective sample size reached 200 or more for all parameters. After discarding the first 10% of the states as a burn-in, the samples from the posterior were summarized using TreeAnnotator v1.7.4 (Drummond *et al.*, 2012), using a maximum clade credibility (MCC) tree, a PP limit of 0.5 and mean node height as settings. We used FigTree v1.3.1 (Rambaut, 2009) to visualize the output.

Acronyms: AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences of Philadelphia, Drexel University, Philadelphia; BMNH, Natural History Museum, London; CAS, California Academy of Sciences, Geology type collection, San Francisco; HNC, Haus der Natur Cismar, Cismar, Germany; RMNH, Naturalis Biodiversity Center, Leiden; SDSNH, San Diego Natural History Museum, San Diego; SMF, Naturmuseum Senckenberg, Frankfurt am Main; TMM, Texas Memorial Museum, Austin; UF, University of Florida, Gainesville; USDA, United States Department of Agriculture, National Malacology Laboratory, Philadelphia; USNM, United States National Museum, Washington, D.C.; ZMUC, Zoological Museum, University of Copenhagen.

Table 5. Fossil-based calibration points for divergence analysis

Calibration point	Basis	Locality and stratigraphic period	Age (Ma)	Used in all analyses?	Reference
Origin of *Pleurodonte* s.s.	*Pleurodonte lehneri* Jung, 1971; BMNH GG 4501	Point St. Hilaire, Carriacou, Granada; Grand Bay Formation	16.0–11.6	Yes	Jung (1971); Donovan *et al*. (2003)
Origin of Pleurodontidae	*Pleurodonte wilsoni* Roth, 1984; TMM 40840–50	Presidio County: Chalk Gap Draw, TX, USA. Upper part of Chambers Tuff, Vieja Group, Chadronian	37.8–36.7	No	Roth (1984); Prothero (1996)
Origin of *Lucerna* Clade B	*Lucerna bowdeniana* (Simpson, 1895); MO115718, MO115719 *Lucerna bernardi* (Kimball, 1947); 1947/1 Inst. Jam. Coll.	Bowden shell beds, St. Thomas Parish, Jamaica. Bowden Formation, Lower Coastal Group, the end of Zanclean - Piacenzian	3.8–2.7	Yes	Goodfriend (1993); Aubry (1993)
Origin of *Labyrinthus* s.l.	*Labyrinthus obtusus* (Anderson & Hanna, 1925); CAS 1016	Kern County: Live Oak Creek, CA, USA; Tejon Formation, Ypresian to Bartonian	52.5–39.0	No	Roth (1988); Niemi *et al*. (2013)
Origin of *Caracolus*	*Caracolus aquilonaris* Bishop, 1979; AMNH 28814	Sheridan County: about 3 miles south of White Clay, NE, USA; White River Group, Whitney Member, Brule Formation	32.0–30.0	No	Bishop (1979); Prothero & Emry (2004)
Origin of *Zachrysia*	*Zachrysia fraterna* Roth, 1988; SDSNH 28388	SDSNH 3278, Murphy Canyon Road, San Diego, CA, USA; transition between Friars and Scripps Formations, Late Bridgerian-Earliest Uintan	47.2–45.2	No	Roth (1988); Walsh, Prothero & Lundquist (1996); Alroy (2000)
Origin of Cepolidae	*Polymita texana* Roth, 1984; TMM 40276-1	Presidio County: mouth of Capote Creek north of Candelaria, TX, USA; Colmena Tuff, Vieja Group, Chadronian	41.2–37.8	No	Roth (1984); Prothero (1996)
Origin of Helminthoglyptidae	*Xerarionta waltmilleri* Roth, 1984; TMM 40209-1006	Presidio County: Reeves Bone Bed, 96 Ranch, TX, USA; upper part of Chambers Tuff, Vieja Group, Chadronian	37.8–36.7	No	Roth (1984); Prothero (1996)
Origin of *Cupedora*	*Cupedora lloydi* (McMichael, 1968)	11 miles NE of Deep Well homestead, Northern Territory, Australia; Ulta Limestone Formation	28.4–23.0	Yes	Megirian *et al*. (2004); Schwartz (2006)
Origin of *Cepaea*	*Cepaea subglobosa* (Grateloup, 1828)	Lariey, Saucats, Gironde, France; Falun de Saucats Formation, Aquitanian	23.0–20.4	Yes	Lozouet, Lesport & Renard (2001); Cahuzac & Janssen (2010)
Origin of Polygyrini	*Linisa adamnis* (Dall, 1890); USNM 111959	Ballast Point, Hillsborough County, Fl, USA; Tampa Limestone Member, Arcadia Formation, Chattian	28.4–20.4	Yes	Mansfield (1937); Scott *et al*. (2001)

Catalog numbers and collection locality numbers are listed if available.

RESULTS

Sequences were obtained for 79, 99 and 100% of the 122 individuals for *COII*, 16S and 28S gene fragments, respectively; some of these were reported by Blake (2007, unpublished thesis), who worked in our laboratory. The lengths of fragments are: *COII* gene: 484–505 bp, 16S gene: 412–476 bp, 28S gene: 416–429 bp. The best models of evolution for five partitions are shown in Table 6: the three codon positions in *COII* and two ribosomal subunit genes.

Because alignments by MAFFT and ClustalX resulted in identical topologies and near-identical bootstrap support values, we report results obtained from MAFFT-aligned data only. Incongruences in topology recovered with the three phylogenetic reconstruction methods were limited to poorly supported groups and outgroup taxa (Figs 1–3).

The three analyses did not recover Pleurodontidae as a monophyletic group because other helicoid families intervened. Figure 4 shows how the subfamilies of Pleurodontidae as defined by Schileyko (2006) are dispersed across the tree. Pleurodontidae *s.s.*, which includes *Pleurodonte*, *Gonostomopsis* and Jamaican pleurodontids, formed a moderately or strongly supported clade with Bradybaenidae, Camaenidae, Cepolidae, Geomitridae, Helicidae, Helicodontidae, Helminthoglyptidae, Hygromiidae, Labyrinthidae, Polygyridae and Sphincterochilidae (maximum parsimonary bootstrap [MPB] = 86; maximum likelihood bootstrap [MLB]= 97; posterior probablity [PP] =1). ML and Bayesian analyses recovered *Caracolus*, *Solaropsis*, *Zachrysia*, Sagdinae, Platysuccineinae Baker, 1940 and Polydontinae Schileyko, 2006 as a moderately to strongly supported monophyletic group (MLB/PP = 84/1). Jamaican sagdids, which belong to the subfamily Sagdinae, were strongly supported (MPB/MLB/PP = 100/99/1) as a clade, but *Platysuccinea* n. sp., the sole representative of the sagdid subfamily Platysuccineinae in this study, grouped with Polydontinae (MPB/MLB/PP = 77/79/1). Jamaican sagdids as a sister clade to Polydontinae + Platysuccineinae was moderately to strongly supported (MPB/MLB/PP = 85/82/1). *Solaropsis* and *Caracolus* were recovered as a monophyletic group by ML and Bayesian analyses (MLB/PP = 76/1). Maximum parsimony analysis placed *Zachrysia* at the most basal position, while ML and Bayesian analyses weakly associated it with Solaropsidae (MLB/PP = 53/0.51).

All of the phylogenetic reconstruction methods recovered a single Jamaican pleurodontid clade (MPB/MLB/PP = 94/96/1), with *Thelidomus* and *Eurycratera* basal. The clade *Lucerna* + *Dentellaria* was moderately to strongly supported (MPB/MLB/PP = 87/94/1). Within *Lucerna*, the exclusively eastern clade (*Lucerna* Clade A: MPB/MLB/PP = 87/97/1) and other *Lucerna* except *L. bainbridgii* (*Lucerna* Clade B: MPB/MLB/PP = 94/99/1) were moderately to strongly supported. *Dentellaria* exclusive of *D. strangulata* and *D. okeniana* was strongly supported by ML and Bayesian analysis (MPB/MLB/PP = 55/89/1). *Dentellaria peracutissima* and *D. tridentina* were not recovered as monophyletic species. *Dentellaria candescens* and *D. simson*, which are treated as synonymous in Rosenberg & Muratov (2006) due to their morphologically similar apertural teeth, are not sister species. The relationships between *L. bainbridgii* with *Lucerna* Clades A and B are uncertain. It grouped with Clade A under ML and with Clade B under maximum parsimony and Bayesian analyses, but none gave robust support for the grouping (MPB/MLB/PP = 66/<50/0.68). Although relationships within *Dentellaria* are not well resolved, *Dentellaria* exclusive of *Lucerna* may not be monophyletic.
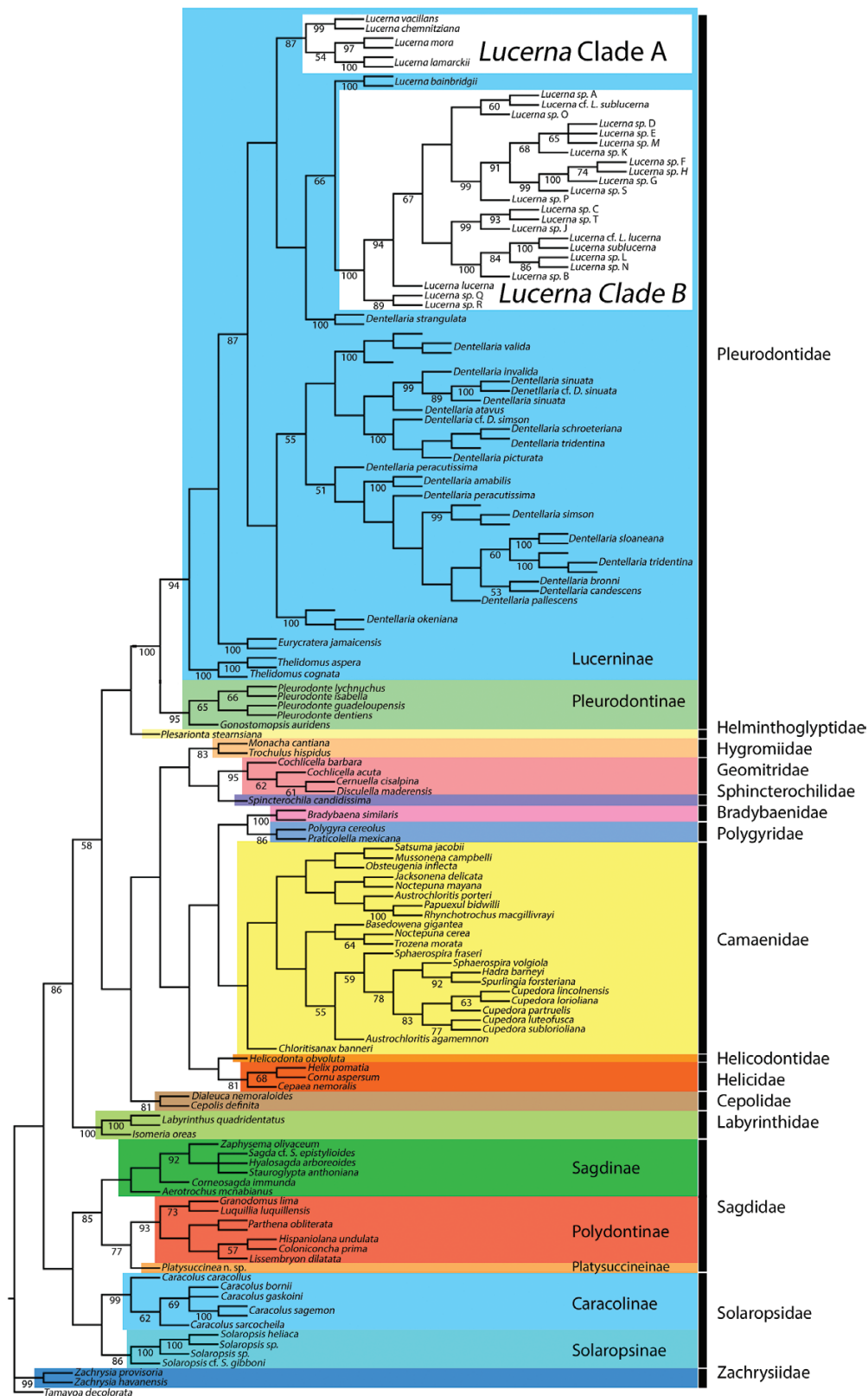
The sister clade of Jamaican Pleurodontidae was *Pleurodonte s.s.* + *Gonostomopsis*, both from the Lesser Antilles (MPB/MLB/PP = 100/99/1). *Pleurodonte s.s.* and *Gonostomopsis auridens* formed a monophyletic group (MPB/MLB/PP = 95/92/1). *Pleurodonte s.s.* had only weak support under maximum parsimony analysis (MPB = 65) and was paraphyletic under the other methods because of inclusion of *Gonostomopsis*. Blake (2007) also found a sister relationship between Jamaican and Lesser Antillean pleurodontids using a subset of the sequences reported here.

Table 6. The best models of evolution for each gene or partition as determined using the corrected Akaike Information Criterion Tests in jModelTest v2.1.1. (Darriba *et al.*, 2012; Guindon & Gascuel, 2003) including all the taxa listed in Table 2

|	Model	AICc	α
COII, first codon position	TrN + G	9039.16	0.35
COII, second codon position	010110 + G	3951.66	0.35
COII, third codon position	HKY + G	26308.13	1.82
16S	HKY + G	32540.44	0.36
28S	011230 + G + F	8950.17	0.43

G allows rate variation among sites, and F allows unequal base frequencies; α is the shape parameter for the gamma distribution of rates among sites. The six-digit numerical code for a particular model (e.g. 012130) denotes the six substitution rate parameters.

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Figure 1. Majority rule consensus of the 14 most parsimonious trees (length = 9877 steps, consistency index = 0.19, retention index = 0.61) from the combined data. Bootstrap support values ≥50% are indicated below the branches.
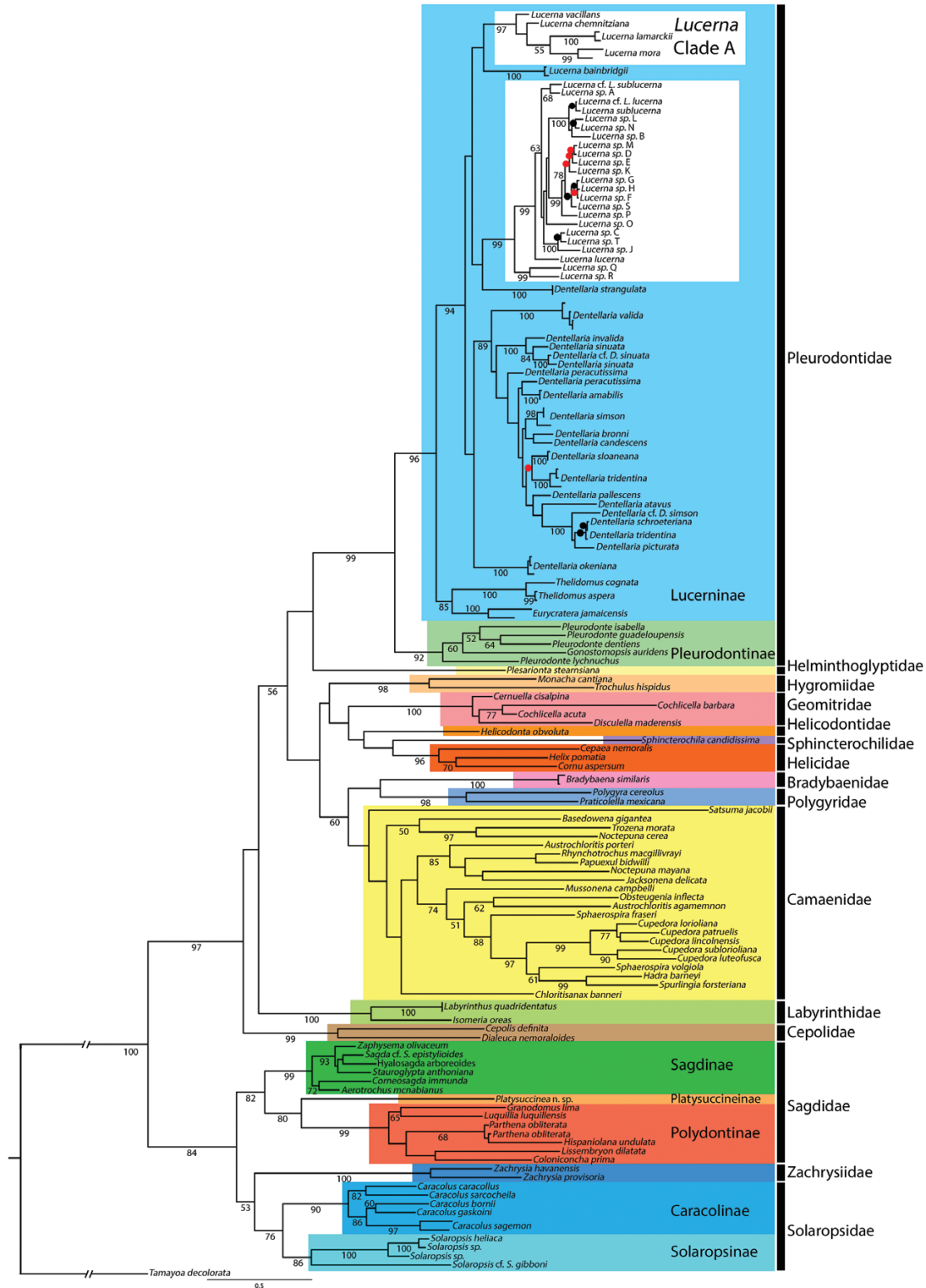
Figure 2. Maximum likelihood tree of species relationships based on the combined data, under the GTR + G evolutionary model fitted separately to each partition. Branch lengths are drawn proportional to the average probability of substitution per site under this model. Non-parametric bootstrap values ≥50% are indicated below or next to the branches. Where branch lengths are very short, bootstrap support is indicated with coloured dots (red: between 50 and 75%; blue: between 75 and 89%; black: ≥90%). Scale bar in substitution/site.
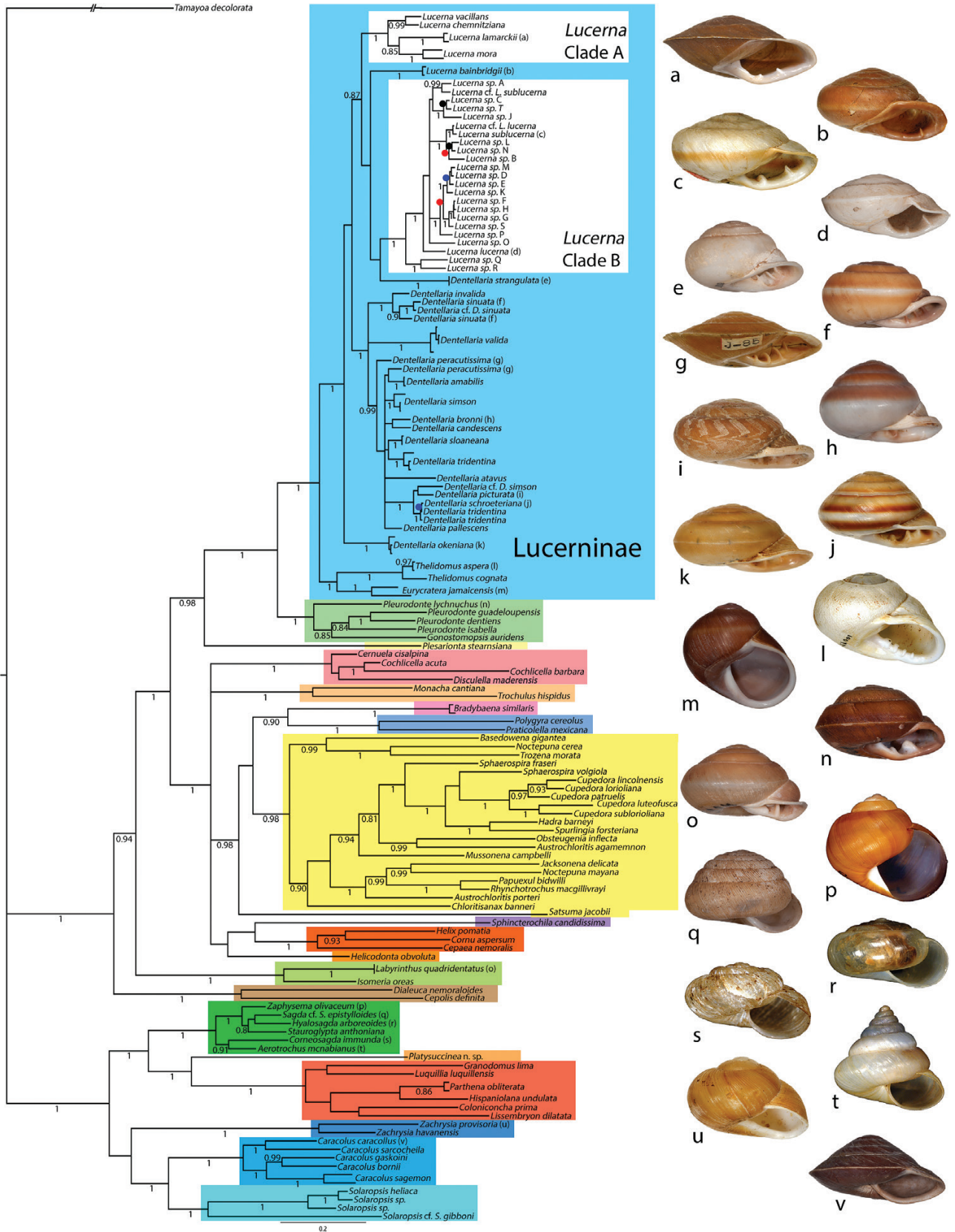
EXAMINATION OF FOSSIL TAXA

Type material of the following fossil taxa was examined at USNM: *Helix adamnis* (USNM 111959), *H. crusta* (USNM 111946, 111948, 646926), *H. cunctator* (USNM 111947, 111949, 111950, 646255), *H. diespiter* (USNM 111951, 111952, 111953, 111954, 646927, 646928, 646929), *H. direpta* (USNM 111955, 111956, 130354), *H. haruspica* (USNM 111957, 165005), *H. instrumosa* (USNM 111945, 646253, 646254) and *H. latebrosa* (USNM 111944), all named by Dall (1890) from Ballast Point, Florida (Arcadia Formation); *Pleurodonte kendrickensis* Mansfield, 1937 (USNM 495996) also from the Arcadia Formation in Florida and *Pleurodonte bowdeniana* Simpson, 1895 (USNM 115718, 115719) from the Bowden Formation in Jamaica. Mansfield (1937) classified *H. adamnis* as *Polygyra* and *H. crusta*, *H. cunctator*, *H. diespiter*, *H. direpta*, *H. haruspica* and *H. instrumosa* as *Pleurodonte*.

Dall (1890) placed his *H. adamnis* in section *Daedalochila* of subgenus *Polygyra* (these are currently recognized as full genera) and compared it with the recent *Po. ventrosula* and *Po. hindsii*, which are currently classified as *Linisa* by Emberton (1995). Emberton (1995) tentatively referred *H. adamnis* to *Linisa* and Perez *et al.*'s (2014) phylogenetic reconstruction recovered a monophyletic clade containing *Daedalochila*, *Polygyra* and *Linisa*, so it is reasonable to calibrate the branch representing Polygyrini (*Polygyra cereolus*) with this fossil.

Our examination of *H. crusta*, *H. cunctator*, *H. diespiter*, *H. direpta*, *H. instrumosa* and *H. latebrosa* shows that they possess apertural characters like those of some polygyrids and cepolids, namely a ridge behind the adult aperture formed by the lip turning in to constrict the aperture and then reflecting back out, with thickening of the inner shell layer along the ridge, but no thickening of the outer shell layer at the outer lip itself. In the Jamaican pleurodontids, the outer lip flares at maturity and thickens so that both inner and outer shell layers are involved in the thickening and the thickening does not constrict the aperture. In *Pleurodonte s.s.*, the outer lip may or may not flare at maturity, but thickening involves both inner and outer shell layers, in some cases constricting the aperture. This constriction, however, is not homologous to that seen in the Floridian fossils and occurs at the growing edge of the outer lip, rather than on an internal ridge behind it. *Helix haruspica* and *Pl. kendrickensis* do not have the internal ridge, but thickening of the lip involves only the inner shell layer; also, they lack the pustulate microsculpture of pleurodontids.

Our examination of *Pl. bowdeniana* confirmed that it is a pleurodontid; it has thickening of the outer lip involving both internal and external shell layers, and it has pustulate microsculpture, as shown by Goodfriend (1993: fig. 1D). Goodfriend referred *Pl. bowdeniana* to the *Pleurodonte lucerna* species-group, and we concur with that placement. Goodfriend also referred *Pl. bernardi* to that species group although it has four apertural teeth, which is more characteristic of *Dentellaria* species; however, it lacks the basal grooves leading to the teeth, so we accept Goodfriend's placement. These taxa were used to calibrate the node for *Lucerna* Clade B, which corresponds to the *Pl. lucerna* species-group. No other calibrations were used within *Pleurodonte* as we could not confirm any of the Floridian fossils referred to *Pleurodonte* as members of the clade.

DIVERGENCE TIME ANALYSIS

Because we have reservations about the validity of calibration points in the Eocene (see Discussion), we report the divergence dates estimated without them (Fig. 4). See Table 7 for the comparison of divergence dates estimated with and without the Eocene fossils and with and without the last emergence of Jamaica. Divergence time estimates based on our molecular data (Fig. 4; Table 7), when calibrated with the age of the last emergence of Jamaica, place the origin of Jamaican Pleurodontidae (i.e. Lucerninae; Node H) at approximately 16.7 Ma [t_{MRCA}; 95% posterior credibility interval (PCI): 15.0–18.4 Ma]. Jamaican Sagdidae

Figure 3. Best Bayesian tree of species relationships based on the combined data. Branch lengths are drawn proportional to the average probability of substitution per site under the evolutionary model fitted separately to each partition. Posterior probabilities >0.8 are indicated below or next to the branches. Where branch lengths are very short, bootstrap support is indicated with coloured dots (red: between 0.8 and 0.94; blue: between 0.95 and 0.97; black: ≥0.98). Scale bar in substitution/site. The specimens figured are not the individuals sequenced, and the figures are not to scale. Taxa shown to the right: (a) *Lucerna lamarckii* (ANSP 162727, standard diameter: 61.6 mm), (b) *Lu. bainbridgii* (ANSP 162738, 55.7 mm), (c) *Lu. sublucerna* (ANSP 4295, 34.0 mm), (d) *L. lucerna* (ZMUC-GAS-556, 31.9 mm), (e) *Dentellaria strangulata* (ANSP 766, 26.2 mm), (f) *D. sinuata* (ANSP 1289, 26.2 mm), (g) *D. peracutissima* (ANSP 162697, 42.2 mm), (h) *D. bronni* (ANSP 770, 23.1 mm), (i) *D. picturata* (ANSP 8961, 26.7 mm), (j) *D. schroeteriana* (ANSP 782, 26.2 mm), (k) *D. okeniana* (ANSP 159730, 34.8 mm), (l) *Thelidomus aspera* (ANSP 100737, 47.0 mm), (m) *Eurycratera jamaicensis* (ANSP 162171, 49.6 mm), (n) *Pleurodonte lychnuchus* (ANSP 1006, 26.3 mm), (o) *Labyrinthus quadridentatus* (ANSP 45553, 20.6 mm), (p) *Zaphysema olivaceum* (ANSP 165680, 25.5 mm), (q) *Sagda* cf. *S. epistylioides* (ANSP 461700, 11.6 mm), (r) *Hyalosagda arboreoides* (ANSP 28244, 12.0 mm), (s) *Corneosagda immunda* (ANSP 168487, 11.6 mm), (t) *Aerotrochus mcnabianus* (ANSP 868, 9.0 mm), (u) *Zachrysia provisoria* (ANSP 451224, 29.7 mm), (v) *Caracolus caracollus* (ANSP 337205, 60.8 mm).
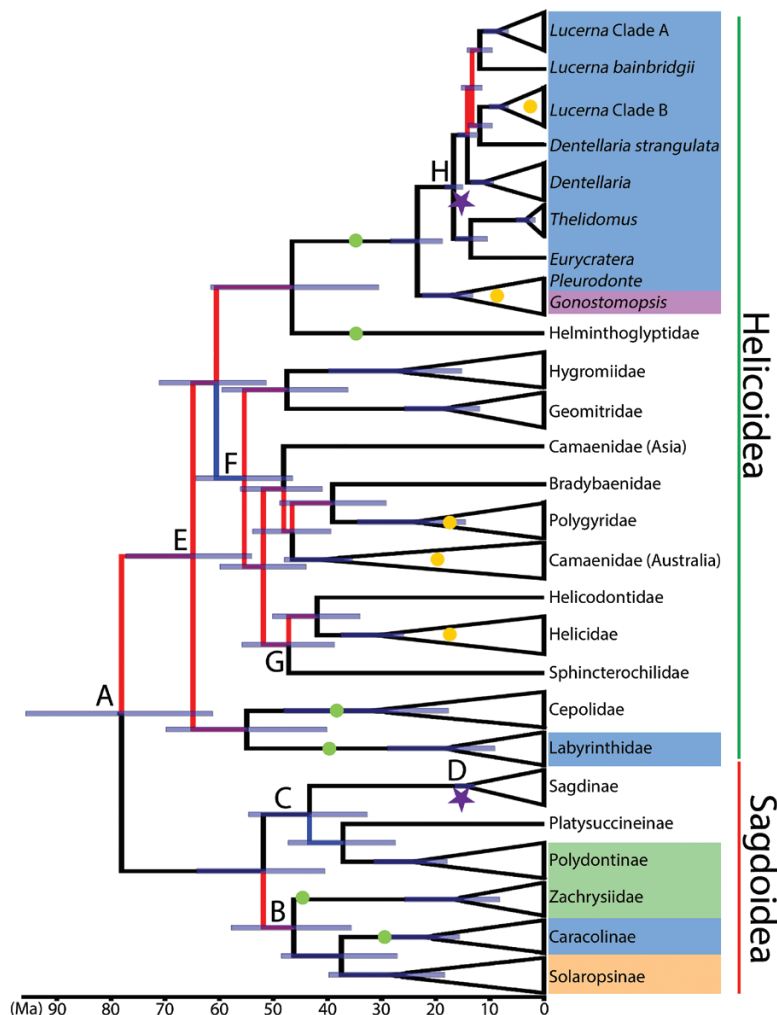
Figure 4. Maximum Clade Credibility (MCC) chronogram inferred using the non-autocorrelated model of rate evolution in BEAST and without the Eocene calibration points (see Table 5). Error bars (blue) represent 95% posterior credibility intervals and are only given for nodes that were present on more than 50% of the posterior sampled trees. The colour of branches indicates Bayesian posterior probabilities shown as black >0.98, blue 0.95–0.98, red <0.95. Subfamilies of Pleurodontidae in Schileyko (2006) are highlighted: Pleurodontinae: blue, Polydontinae: green, Gonostomopsinae: purple. Solaropsinae, shown in orange, was classified as a subfamily of Polygyridae in Schileyko (2006). Yellow dots indicate the minimum ages of fossils used as calibration points younger than the Eocene. Green dots indicate the minimum ages of fossils in the Eocene. Purple stars indicate the mean of the prior based on the last emergence of Jamaica.

might have arisen slightly later (Node D, t_{MRCA} 14.7 Ma, PCI: 12.8–16.5 Ma). The split of Helicoidea and Sagdoidea is estimated to have occurred at 78.1 Ma (Node A, PCI: 61.2–95.7 Ma), between late Cretaceous and middle Paleocene. The diversification of Helicoidea is estimated to have occurred around 64.9 Ma (Node E, PCI: 54.0–77.3 Ma), between late Cretaceous and early Eocene. Exclusion of the calibration points based on the Eocene fossils resulted in generally older estimates across the MCC tree, and the oldest estimates were consistently found when both the Eocene and Jamaican emergence calibration points were excluded (Table 7). Depending on what calibration points were included, estimated mean ages of nodes varied by 24% [Node B, min. 47.6 Ma (the Eocene calibration points included and the Jamaican geologic calibration point excluded), max. 58.8 Ma (both the Eocene and Jamaican geologic calibration points excluded)] to 55% [Node H, min. 16.5 Ma (both the Eocene and Jamaican geologic calibration points included), max. 25.5 Ma (both the Eocene and Jamaican geologic calibration points excluded)]. The differences between replicated BEAST runs were negligible.

Table 7. The comparison of posterior probabilities and the divergence date estimates for the major clades estimated with and without the calibration points in the Eocene and the last emergence of Jamaica (Table 5)

Node	Eocene fossils included				Eocene fossils excluded			
	With Jamaica		Without Jamaica		With Jamaica		Without Jamaica	
	PP	Mean (95% PCI)	PP	Mean (95% PCI)	PP	Mean (95% PCI)	PP	Mean (95% PCI)
A. Helicoidea/Sagdoidea split	1.0	75.4 (63.2, 89.9)	0.99	78.3 (65.2, 94.6)	1.0	78.1 (61.2, 95.7)	1.0	98.3 (74.0, 124.0)
B. Zachrysiidae/Solaropsidae split	0.74	47.7 (45.9, 50.1)	0.82	47.6 (46.0, 50.4)	0.68	51.8 (40.5, 64.2)	0.7	58.8 (42.9, 75.6)
C. Sagdinae/Polydontinae + Platysuccineinae split	1.0	43.9 (35.8, 51.8)	1.0	45.2 (37.2, 53.9)	1.0	43.3 (32.6, 54.6)	1.0	55.4 (40.2, 71.5)
D. Diversification of Sagdinae	1.0	14.6 (12.7, 16.4)	1.0	13.2 (8.7, 18.6)	1.0	14.7 (12.8, 16.5)	1.0	16.4 (10.5, 23.2)
E. Diversification of Helicoidea	1.0	57.9 (50.0, 66.0)	0.99	60.7 (52.5, 70.5)	0.90	64.9 (54.0, 77.3)	0.95	80.2 (63.4, 99.4)
F. Diversification of Old World helicoids	0.73	52.5 (44.6, 60.4)	0.7	55.1 (46.5, 64.5)	0.96	55.4 (46.5, 64.4)	0.98	67.6 (53.5, 81.6)
G. Diversification of Sphincterochilidae + Helicodontidae + Helicidae	0.84	45.6 (37.3, 53.6)	0.76	48.0 (39.7, 57.0)	0.77	47.2 (38.7, 55.8)	0.77	56.9 (44.1, 69.9)
H. Diversification of Lucerninae	1.0	16.5 (14.9, 18.2)	1.0	20.7 (17.1, 25.2)	1.0	16.7 (15.0, 18.4)	1.0	25.5 (19.1, 32.1)

Mean ages and 95% posterior credibility intervals are shown in Ma.

DISCUSSION

PHYLOGENETIC RELATIONSHIPS AND CLASSIFICATION OF HELICOIDEA AND SAGDOIDEA

Our molecular phylogeny revealed that many taxa previously classified as pleurodontids grouped with Sagdidae. Sagdidae has been considered anatomically distinct from helicoids and classified as a divergent taxon (see Table 1) with rank as high as infraorder (Sagdoinei Schileyko & Starobogatov, in Golikov & Starobogatov, 1989). We found that most supposed pleurodontids do not group with *Pleurodonte*, but with Sagdidae, including all members of Polydontinae in the classification of Schileyko (2006), and many taxa placed in Caracolinae by Cuezzo (2003) (see Table 8) including *Solaropsis*. Based on molecular evidence, Wade, Mordan & Naggs (2006) and Wade *et al.* (2007) found that Pleurodontidae was not monophyletic, with '*Pleurodonte*' (corresponding to *Dentellaria* herein) and *Thelidomus* grouping with Hygromiidae, and '*Polydontes*' (corresponding to *Granodomus* and *Hispaniolana* herein) and *Zachrysia* grouping with Sagdidae. Our results support and amplify this finding (Figs 1–4) and provide further confirmation that the Camaenidae should be restricted to the Old World, contrary to Cuezzo (2003), but in agreement with Scott (1996) and Wade *et al.* (2006, 2007), who found

paraphyly of the Old and New World taxa. Although we used relatively short fragments of one nuclear and two mitochondrial genes, our results are concordant with prior molecular results where there is taxonomic overlap, and we found robust support for major clades (e.g. Helicoidea, Sagdoidea, Pleurodontidae). A preliminary phylogeny of Helicoidea and Sagdoidea based on 58 exon loci (ca. 20 kbp total) by Sei *et al.* (2014) following the methodology in Teasdale *et al.* (2016) also recovered a similar overall topology, but with much less extensive taxon sampling.

Sagdoidea as previously constituted contained mainly small-bodied taxa. Of 21 genera treated by Schileyko (1998), only two have any species in which maximum shell dimension exceeds 20 mm (*Zaphysema* Pilsbry, 1894 and *Sagda* Beck, 1837), yet all the taxa that we found to group with Sagdidae have members with maximum shell dimension greater than 25 mm (Polydontinae, *Caracolus*, *Solaropsis*, *Zachrysia*). Sagdinae in Sagdoidea thus seems analogous to Hygromiidae and Geomitridae in Helicoidea as a radiation exploiting small body size. Platysuccineinae and two other subfamilies of Sagdidae, Aquebaninae Baker, 1940 and Yunqueinae Baker, 1961, which are not represented in our analyses, also have small body size.

In addition to high levels of divergence in anatomy and shell morphology obscuring relationships,

Table 8. Classification of New World Pleurodontidae by Zilch (1960), Cuezzo (2003) and Schileyko (2006)

Zilch (1960)	Cuezzo (2003)	Schileyko (2006)
Camaenidae	Camaenidae	Pleurodontidae
	Pleurodontinae	Pleurodontinae
Pleurodonte	*Pleurodonte*	*Pleurodonte*
(Pleurodonte)	*(Pleurodonte)*	*Dentellaria*
(Dentellaria)	*(Dentellaria)*	
	Caracolinae	
(Caracolus)	*Caracolus*	*Caracolus*
(Gonostomopsis)	–	*
Labyrinthus		*Labyrinthus*
(Labyrinthus)	*Labyrinthus*	*(Labyrinthus)*
(Isomeria)	*Isomeria*	*(Isomeria)*
Eurycratera		*Eurycratera*
(Eurycratera)	*Eurycratera*	
(Thelidomus)	*Thelidomus*	*Thelidomus*
		Polydontinae
	Polydontes	*Polydontes*
(Granodomus)	*(Granodomus)*	*Granodomus*
(Parthena)	*(Parthena)*	*Parthena*
Polydontes		
(Polydontes)	*(Polydontes)*	
(Luquillia)	*(Luquillia)*	*Luquillia*
(Hispaniolana)	*(Hispaniolana)*	*Hispaniolana*
(Lissembryon	–	*Lissembryon*
Zachrysia	*Zachrysia*	*Zachrysia*
		Gonostomopsinae
		*Gonostomopsis**
		Polygyridae
		Solaropsinae
Solaropsis	*Solaropsis*	*Solaropsis*

Dashes (–) indicate a taxon that was not treated in a particular classification.
*Movement such that the linear order could not be preserved.

convergence has also played a role. Wurtz (1955a) noted multiple shared anatomical characters among species of *Caracolus*, *Labyrinthus s.l.* and *Pleurodonte s.l.* (e.g. size of ovotestis, origin of free retractors, apical angle of lung and ureter) and Cuezzo (2003) reported that *Caracolus* and *Labyrinthus s.l.* exhibited similarity in morphology of alveoli and phallic sheath. *Caracolus*, *Labyrinthus* and *Lucerna* also share discoidal, keeled shells. They were all previously placed in the Pleurodontinae, but our study places them in three different families.

Homoplasy in shell characters due to ecological adaptations is well documented in gastropods (e.g. Australian camaenids: Criscione & Köhler, 2013; Köhler & Criscione, 2015; *Placostylus* in New Caledonia: Dowle *et al.*, 2015 and hydrobioids in New Zealand: Haase, 2008). Homoplasy in anatomical characters has been reported so often in helicoids that Neiber, Razkin & Hausdorf (2017) suggest that parallel evolution in genital characters is a rule rather

than an exception. Extensive homoplasy of some characters and rapid divergent evolution of others have confounded the systematics of Pleurodontidae and of helicoids generally. This may explain why our results differ substantially from those of Cuezzo (2003), who produced the only prior phylogenetic analysis of the New World helicoids, based on shell morphology and internal anatomy. She recognized Pleurodontinae for *Pleurodonte* (containing *Pleurodonte s.s.*, *Dentellaria* and *Lucerna*) and Caracolinae for *Eurycratera* (including *Thelidomus*), *Polydontes* (including *Granodomus*, *Lissembryon*, *Luquillia* and *Parthena*), *Zachrysia*, *Caracolus*, *Solaropsis*, *Isomeria* and *Labyrinthus*. Our analyses did recover the core group that Cuezzo placed in Caracolinae, but exclude the basal (*Eurycratera*) and crown groups (*Labyrinthus* and *Isomeria*) of her phylogenetic tree. Cuezzo (2003) did not include sagdids, or small-bodied helicoids such as Thysanophoridae and Hygromiidae in her analysis, and some of the shell characters coded in her matrix can be variable within

species (e.g. whether the umbilicus is open or not), or intergrade so as not to be consistently scorable (e.g. general shape of aperture). We also found that some characters for *Zachrysia* were scored erroneously. For example, character 25 (flagellum) was scored as 'long straight, thin, even' when *Zachrysia* actually has a thick flagellum (Pilsbry, 1929). Furthermore, some of the outgroups were scored with the common state of characters, rather than as polymorphic (e.g. Helicidae), so the entire matrix needs to be re-evaluated before it can be re-analyzed to understand if there is genuine conflict between molecules and morphology.

The clade containing Sagdidae is the sister group of Helicoidea, so we rank it as superfamily Sagdoidea. In addition to Sagdidae, Sagdoidea contains Solaropsidae Nordsieck, 1986, including subfamily Caracolinae (transferred from Pleurodontidae), and Zachrysiidae Robinson, Sei & Rosenberg, new family (diagnosed below). Sagdidae includes Polydontinae (transferred from Pleurodontidae) and Platysuccineinae. These are all Neotropical taxa: Sagdidae has centre of diversity in Jamaica, with 56 endemic species there, and is restricted to the Caribbean Basin and neighbouring areas (Florida, Bahamas, Bermuda); Caracolinae and Polydontinae are native to the Greater Antilles, but not Jamaica; Zachrysiidae is native to Cuba and Solaropsinae is restricted to South America. The phylogeny implies that Sagdoidea have been present continuously in the Greater Antilles since the early Eocene or early Oligocene (Fig. 4 and Table 7, Node B, 51.8 Ma, PCI: 40.5–64.2 Ma and Node C, 43.3 Ma, PCI: 32.6–54.6 Ma). It thus joins Urocoptidae, another group of land snails, as one of the oldest elements of the Caribbean biota (Uit de Weerd *et al.*, 2016).

The clade containing *Pleurodonte* does not group with Sagdoidea, but with Helicoidea, sister to Helminthoglyptidae. Even the restricted Pleurodontinae recognized by Schileyko (2006) proves to be polyphyletic, with *Caracolus* grouping with Sagdoidea and *Labyrinthus* and *Isomeria* basal to most other families in Helicoidea, separate from Jamaican and Lesser Antillean Pleurodontinae, which are the only remaining members of Pleurodontidae. We propose Labyrinthidae Borrero, Sei, Robinson & Rosenberg, new family (diagnosed below), for *Labyrinthus* and *Isomeria*. Labyrinthidae is sister to Cepolidae in our calibrated phylogeny (Fig. 4), but Cepolidae is the basal clade of Helicoidea in our ML and Bayesian trees (Figs 2, 3). The phylogenetic analysis of Old World helicoids by Razkin *et al.* (2015: fig. 3) also found Cepolidae as the basal clade in Helicoidea. Their investigation included several other New World taxa, but none of those here classified in Sagdoidea.

The relaxed molecular clock analysis dates the divergence of the Helicoidea and Sagdoidea between late

Cretaceous and middle Paleocene (PCI: 61.2–95.7 Ma, Node A in Fig. 4). Helicoidea diversified in the New World around 64.9 Ma (PCI: 54.0–77.3 Ma, Node E) and colonized the Old World between 46.5 and 64.4 Ma (Node F). All three analyses show a single colonization of the Old World, but this is strongly supported only in the Bayesian analysis. The alternate scenario is two colonizations of the Old World. The main difference between these scenarios is placement of Polygyridae: trees showing one colonization have Polygyridae nested in Bradybaenidae/Camaenidae, indicating that it recolonized the New World, whereas trees with two colonizations have Polygyridae basal, indicating a New World origin.

We found a substantially younger age for the origin of Helicoidea than did Razkin *et al.* (2015), who estimated 107 Ma (PCI: 82.7–138.0). This is likely due to their inclusion of a Jurassic (150 Ma) calibration point for the origin of Stylommatophora, although there is no fossil evidence to support this age, which resulted in Helicoidea being more than twice as old as any of the fossils they used to calibrate helicoid families. Jörger et al. (2010) estimated the divergence of Orthurethra and Stylommatophora (which includes Helicoidea) at about 80 Ma, and Neiber *et al.* (2017) suggests Razkin *et al.*'s (2015) age of Helicoidea may be an overestimation. Razkin *et al.*'s (2015) fossil calibrations are compatible with nodes in our tree, for example Helicidae (33.9 Ma) and Helicodontidae (28.1 Ma) vs. 38.7–55.8 Ma PCI for divergence of Sphincterochilidae, Helicodontidae and Helicidae (Node G). Moreover, it is difficult to judge if some of the fossils used in Razkin *et al.* (2015) are genuinely members of the families they are attributed to, for example, *Loganiopharynx* (Hygromiidae) and *Dentellocaracolus* (Sphincterochilidae) (see discussion of fossils below). Another problem with the calibrated phylogeny in Razkin *et al.* (2015) is that it contains taxa not included in their main analyses (Pleurodontidae, Cepolidae, Monadeniidae and Polygyridae) and their calibrated and uncalibrated analyses recovered different clades among taxa that were included (e.g. Sphincterochilidae + Elonidae and Helicidae + Trissexodontidae; fig. 2 vs. fig. 3).

Sagdoidea occupies the Caribbean Basin and northern to central South America, while Helicoidea is distributed in all continents except Antarctica. Sagdoidea is much less species rich than Helicoidea, with about 200 species, vs. about 4700 [tallied from Richardson (1980, 1982, 1983, 1984, 1985, 1986), with genera placed in the superfamilies used herein; see Rosenberg (2014); Table 7]. Despite low species richness, however, the magnitude of morphological disparity in Sagdoidea is similar to that in Helicoidea (Table 9; Fig. 5); for example, the range of shell widths in Sagdoidea entirely encompasses the range of widths

Table 9. Comparison of morphological disparity of Helicoidea and Sagdoidea

Feature	Helicoidea			Sagdoidea
Maximum height (mm)	*Helicostyla woodiana*	**79**	52	*Hispaniolana gigantea*
Minimum height (mm)	*Atenia quadrasi*	2.4	**1.5**	*Vilitas omissa*
Maximum width (mm)	*Lysinoe ghiesbreghti*	**75**	85	*Solaropsis gibboni*
Minimum width (mm)	*Ripkeniella petrophila*	3.5	**2.6**	*Trifaux triodon*
Maximum whorls	*Buliminidius hirsutus*	**13**	11	*Sagda* cf. *S. grandis*
Minimum whorls	*Metostracon mima*	**<1**	2.5	*Coloniconcha prima*
Maximum H/W	*Buliminidius hirsutus*	**3.9**	1.1	*Sagda* cf. *S. grandis*
Minimum H/W	*Polygyra septemvolva*	0.25	**0.24**	*Polygyratia polygyrata*

The species with the greatest or least measure for each given feature for each superfamily is shown. The more extreme value is shown in bold for each comparison, with five favouring Helicoidea and three favouring Sagdoidea. The minimum width for sagdids is not certain; Schileyko (2006) classifies *Trifaux* as a polygyrid, but we consider it a sagdid as no polygyrids are native to Jamaica; on the other hand, Schileyko (1998) classified *Xenodiscula* as a sagdid (height 0.55, width 1.6 mm), but noted that it might be a zonitoid. The smallest width of an undoubted sagdid is 3.1 mm, for *Vilitas omissa*. The minimum height width ratio for sagdoids is also uncertain. Schileyko (2006) placed *Polygyratia* in Solaropsinae, but its systematic position is controversial (see Cuezzo, 2003). If *Polygyratia* proves not to be a sagdoid, then *Corneosagda ptychodes* is the next flattest species, with H/W = 0.35, and six of the comparisons favor Helicoidea. The figured specimens are exemplars of the species, except for *Sagda* cf. *S. grandis*, which is the actual specimen with greatest number of whorls and greatest H/W ratio known thus far in the Sagdoidea
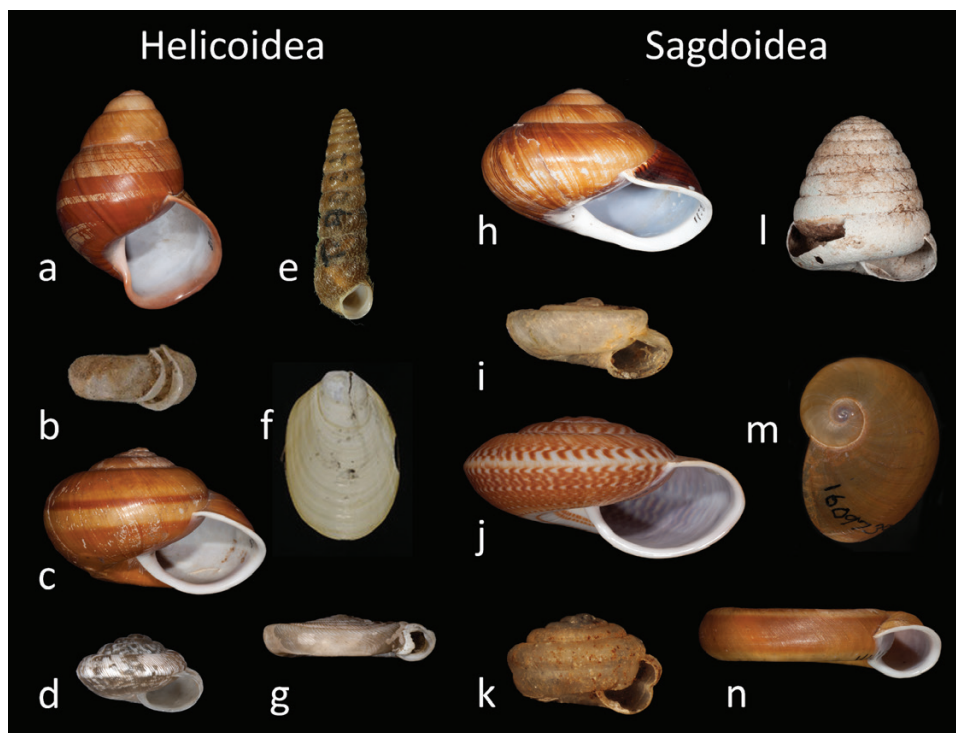
Figure 5. Comparison of morphological disparity of Helicoidea (a–g) and Sagdoidea (h–n) presented in Table 9. Taxa shown: (a) *Helicostyla woodiana* (ANSP 3142), (b) *Atenia quadrasi* (HNC 41159), (c) *Lysinoe ghiesbreghti* (ANSP 33555), (d) *Ripkeniella petrophila* (RMNH.MOL.57268), (e) *Buliminidius hirsutus* (SMF-9022), (f) *Metostracon mima* (ANSP 77245), (g) *Polygyra septemvolva* (ANSP 149810), (h) *Hispaniolana gigantea* (ANSP 1132), (i) *Vilitas omissa* (ANSP 5612), (j) *Solaropsis gibboni* (ANSP 411023), (k) *Trifaux triodon* (ANSP 163915), (l) *Sagda* cf. *S. grandis* (ANSP 139396), (m) *Coloniconcha prima* (ANSP 160973), (n) *Polygyratia polygyrata* (ANSP 217111).

in Helicoidea. Both groups have semislugs, and species with periostracal hairs, apertural barriers, axial ribs and shell shapes ranging from discoid to globose to pyramidal, evidently due to convergent evolution.

ORIGIN AND COMPOSITION OF PLEURODONTIDAE

Our phylogenetic analyses show that the four Jamaican genera form a monophyletic group, sister to pleurodontids from the Lesser Antilles. All other

supposed pleurodontids grouped with Sagdidae, or, in the case of *Labyrinthus* and *Isomeria*, did not group with either Pleurodontidae or Sagdidae. Our analyses did not determine the biogeographic origin of Jamaican Pleurodontidae despite inclusion of many potential outgroups. All three analyses recovered *Plesarionta stearnsiana*, a helminthoglyptid from California, as a sister taxon to the pleurodontids, although strong support was found only with the Bayesian analysis. Razkin *et al.* (2015: fig. 3) found Pleurodontidae (represented by *Dentellaria* and *Thelidomus*) sister to a clade containing Humboldtianidae and Monadeniidae, with those three families sister to the clade containing Helicidae. Their analysis did not contain Helminthoglyptidae; whereas ours did not contain Humboldtianidae or Monadeniidae, but the latter two families are often ranked as subfamilies of Helminthoglyptidae, and all of them were included in Superfamily Xanthonychoidea by Schileyko (2006). All of the 'xanthonychoid' families were represented in Sei *et al.*'s (2014) preliminary phylogeny, and Xanthonychidae, Helminthoglyptidae, Monadeniidae, Humboldtianidae, Epiphragmophoridae and Pleurodontidae formed a well-supported clade. *Trichodiscina coactiliata* (Férussac, 1839), a xanthonychid that inhabits central Mexico to northern South America, was found to share the most recent common ancestor with Pleurodontidae. Future research should seek the sister group of Pleurodontidae among the members of that group, namely Xanthonychidae, Monadeniidae, Helminthoglyptidae and Epiphragmophoridae.

There is no strong evidence for the occurrence of Pleurodontidae outside the Caribbean Basin. The conchological characteristics of helicoid fossil species described by Dall (1890) and Mansfield (1937) from Florida agree with polygyrids or cepolids, as shown in Results. Nordsieck (2014) reclassified *Pleurodonte norica* Binder, 2004 from the Lower Miocene of Austria as a *Galactochilus* and *Pleurodonte michalkovaci* Binder & Harzhauser in Harzhauser, Gross & Binder (2008) from the Middle Miocene of Austria as a *Pseudochloritis*. Nordsieck (2014) placed both *Galactochilus* and *Pseudochloritis* in Elonidae (Helicoidea). Kadolsky, Binder & Neubauer (2016) showed that *Galactochilus* had been misapplied to European species and suggested that *Pl. norica* might belong to their new genus *Agalactochilus* which they placed in Helicidae. When Cockerell (1914) described *Pleurodonte eohippina* (Paleocene, Wyoming), he suggested an affinity to *Labyrinthus* (which we exclude from Pleurodontidae). Russell (1931) doubted Cockerell's (1914) original generic assignment and noted that its morphology was within the range of *Polygyra* or *Ashmunella*, whereas Hartman & Roth (1998) classified it in Helicinidae. Thus, difficulty in delineating Pleurodontidae within

Helicoidea (e.g. Richardson, 1985), in addition to over-reliance on general shell shape without close attention to detailed character states, have muddled fossil classifications and cladistics of Pleurodontidae and other helicoids as well.

Pleurodontids colonized Jamaica approximately 16.7 Ma (PCI: 15.0–18.4 Ma) and Sagdidae colonized in a similar time frame (14.7 Ma, PCI: 12.8–16.5 Ma). Both of these molecular clock estimates are consistent with geological estimates for the emergence of Jamaica at 14–15 Ma (Mitchell, 2008; James-Williamson, Mitchell & Ramsook, 2014). Both Jamaican pleurodontids and sagdids have varied shell morphologies (Fig. 3), ranging from low-spired, sharply keeled to globose, and, in Sagdidae, pyramidal. The pleurodontid radiation is consistent with a single colonization of Jamaica. This colonization resulted in more than 30 endemic species, with an array of morphologies suggestive of adaptive radiation. However, there has been only one study of Jamaican taxa aimed at detecting adaptive trait variation: Goodfriend (1987) found a strong positive correlation between mean shell diameter and mean annual rainfall.

The Jamaican taxa usually classified as *Pleurodonte* did not group with *Pleurodonte s.s.* from the Lesser Antilles and are reclassified here as *Dentellaria* and *Lucerna*, which were considered subgenera of *Pleurodonte* by Baker (1935). We resurrect the subfamily Lucerninae Swainson, 1840; it contains *Lucerna*, *Dentellaria*, *Thelidomus* and *Eurycratera*, all of which are endemic to Jamaica (see Taxonomic Actions below). The subfamily Pleurodontinae is restricted to the Lesser Antilles. Gonostomopsinae Schileyko, 2006 is a synonym of Pleurodontinae, as *Gonostomopsis* grouped within *Pleurodonte* in the Bayesian and ML analyses. We did not have material of the monotypic subfamily Discolepinae (Schileyko, 2006) to assess whether it belongs in Pleurodontidae. Solem (1959) suggested that *Discolepis* Ancey, 1904, from Martinique, was derived from *Trichodiscina*, which Sei *et al.* (2014) suggested was related to Pleurodontidae.

With the removal of the Lesser Antillean taxa, it becomes easier to delineate morphological patterns among the Jamaican taxa that were historically classified as *Pleurodonte*. *Lucerna* generally have large shells (>35 mm) with either no or one tooth on the outer part of the basal lip and *Dentellaria* have smaller shells (<35 mm) with two teeth on the outer part of the basal lip. The teeth in *Lucerna* are confined to the lip, in *Dentellaria* they extend farther into the aperture, so that external grooves corresponding to at least some of the teeth are visible basally. When *Lucerna* are small, they have thicker shells than *Dentellaria* of similar size. Other trends are that *Dentellaria* always have three or four (or rarely five) apertural teeth, whereas

all *Lucerna*, except *Lu. chemnitziana*, have two or fewer. Some *Dentellaria* have the aperture strongly deflected so that the lip edge is raised onto the basal region; this does not occur in *Lucerna*.

Our analyses do not support the monophyly of these genera, but neither do they strongly contradict them, and the taxa that prevent monophyly are the most aberrant morphologically. All three analyses show two clades in *Lucerna*; Clade A is eastern in distribution and Clade B is largely west of A, with *Lu. bainbridgii* of uncertain placement between them. All three analyses show *Dentellaria* monophyletic, except for two taxa of uncertain placement: *D. okeniana* and *D. strangulata*. The former was found to be the sister clade of *Dentellaria* exclusive of *D. strangulata* or basal to *Lucerna* + *Dentellaria*, and the latter was recovered as the sister clade of *Lucerna* Clade B or *Lucerna* Clade B and *Lu. bainbridgii*, but all combinations lacked strong support. *Dentellaria okeniana* is the only *Dentellaria* that has only one outer tooth instead of two, and *D. strangulata* has an extremely constricted aperture, with teeth diverging rather than paralleling each other in the aperture. These could both be put in monotypic genera if further study confirms their position outside *Dentellaria*.

Although *Lucerna* Clade B includes only two currently recognized species (i.e. *L. lucerna* and *L. sublucerna*; Rosenberg & Muratov, 2006), morphological diversity (e.g. size, body whorl profile, basal tooth morphology, soft tissue colour pattern) and up to 21% divergence in *COII* and 14.9 % divergence in 16S sequences within this group strongly suggest the presence of numerous overlooked and cryptic species. Identification of these OTUs with nominal taxa will be the subject of a separate paper.

VARIATION, ECOTYPES AND IMPLICATIONS FOR FOSSIL CALIBRATIONS

The Jamaican radiations of Pleurodontidae and Sagdidae show that 15 million years is sufficient for radical change in shell form in land snails, with shapes ranging from flattened lenticular to globose (Fig. 3g–m and 3p–s). But morphological change can occur much more rapidly than that. Several recent studies have shown substantial variation of the spire index (length to width ratio) within species of land snails. Uit de Weerd & Velázquez (2017) demonstrated rapid increase in spire height in *Tenuistemma* (Urocoptidae) in Cuba, and *Ainohelix editha* (Bradybaenidae) in Hokkaido, Japan, has forms ranging from flat-spired to globular (index 0.38–0.81, measured from Teshima *et al.*, 2003: fig. 1). Morii *et al.* (2015) suggested that introgressive hybridization between *A. editha* and *Ezohelix gainesi* showed that adaptive morphological

differences were evolving more rapidly than reproductive isolation.

Rhagada (Camaenidae) from Rosemary Island, Western Australia has a range of morphologies similar to that seen in *A. editha* (index 0.37–0.80, measured from Stankowski, 2011: fig. 7) and has been presented as a model of ecological speciation (Stankowski, 2013). The full range of morphologies in this *Rhagada* species is represented in a cline of only 200 m, with low-spired forms associated with rocky outcrops, where their shape may help them shelter in crevices. The most dramatic variation within a species was reported by Breure (2008): the type series of *Bostryx multiconspectus* has spire index varying from 0.45 to 1.00, and his figure 4 shows a range up to 1.39 in the material examined.

The distribution of spire indices in land snails is generally thought to have adaptive significance. Cain (1977) showed that the distribution is bimodal with modes around 0.5 and 3, and few species have values around 1. Cain argued that the non-random distribution of values could be explained only by natural selection. He speculated that having length similar to width was less stable in crawling animals. Subsequent research has shown that snails of different spire indices have preferred orientations (horizontal or vertical surfaces) (Cook & Jaffar, 1984), that high- and low-spired shells are more balanced than globose shells (Okajima & Chiba, 2011) and that deflection of the aperture in formation of the adult lip brings the shell into a position more balanced with respect to gravity than in juveniles (Okajima & Chiba, 2013). The typical pleurodontid shape is near the mode of 0.5 that Cain observed for low spired shells, so the frequent convergence on this shell form is not surprising.

Cain's (1977) data show considerable variation in spire index within species (his fig. 2), so there is ample scope for natural selection to act on shell shape in many species. Many authors have demonstrated variation in shell shape in snail species and populations, including Brown (1911) and Goodfriend (1983) for Jamaican pleurodontids, Crampton (1932) for Society Islands partulids and Welch (1938) for Hawaiian achatinellids. In more recent years, some studies of land snails have recognized ecotypes. In *Mandarina* (Bradybaenidae) in the Bonin Islands, there are arboreal, semiarboreal, exposed ground and sheltered ground ecotypes, with arboreal snails having lower spires than ground dwelling ones, among other differences (Chiba, 2004; Davison & Chiba, 2006). In *Placostylus* (Dowle *et al.*, 2015) in New Caledonia, lower-spired shells with narrower apertures are associated with warmer, drier forests and higher-spired shells with wider apertures with cooler, wetter forests. *Rhagada* (Stankowski, 2013), discussed above, shows repeated evolution of a

flat-spired keeled ecotype in rocky elevated areas from a more globose ecotype in the surrounding plain.

The diversity of ecological associations in these few examples suggests that the shapes in pulmonate land snails overall cannot be explained as a set of ecomorphs as has been done with *Anolis* lizards (Williams, 1983; Losos, 2009), but consistent ecomorphs may yet be identified in subclades within various pulmonate groups. For example, Uit de Weerd *et al.* (2016) found that urocoptid genera group by geographic region rather than nominal subfamily (as we found with pleurodontids) and that independent radiations of urocoptids developed similar suites of forms, including large, bullet-shaped terrestrial forms, slender arboreal forms with reduced peristome, and elongate forms that live on rock faces. More than 100 years ago, Pilsbry (1903) proposed that these represented 'independent local adaptive radiations'.

Under the ecological opportunity hypothesis of adaptive radiation (Schluter, 2000), morphological variation within species should be highest in the initial phases of adaptive radiation, but it should then decrease as it becomes increasingly constrained by interspecific competition as lineages accumulate (Parent & Crespi, 2009). Assigning fossil land snails to modern radiations is thus inherently risky, since the current array of morphologies may not represent the initial array, and convergence is likely in the limited morphospace of snail shells.

The geographical cohesion of subclades observed in the Helicoidea, Sagdoidea and Urocoptoidea, along with the degree of morphological change that can occur over time periods much less than 15 million years, casts doubt on the generic identification of North American pre-Miocene land snail fossils that have been attributed to *Pleurodonte* (Roth, 1984), *Caracolus* (Bishop, 1979), *Zachrysia* and *Labyrinthus* (both in Roth, 1988), which may represent convergent morphologies. Comparison of fossil and extant species becomes inherently more problematic if they are allopatric, since there is no potential for stratigraphic continuity. However, excluding calibration points based on these fossils from our analysis did not substantially change the molecular clock estimates.

Sauquet *et al.* (2012) noted three methods employed in assessing the relationships of fossils used in calibrations: intuitive, apomorphy-based and phylogenetic. The phylogenetic method is not feasible with land snails: since features of soft anatomy rarely fossilize, fossil snail taxa cannot readily be included in a phylogenetic analysis with recent ones. The apomorphy-based method is also problematic, as few uniquely apomorphic characters of the shell have ever been defined in land snails. Although the phylogenetic and apomorphy-based approaches are not feasible for the fossil taxa considered herein, there are approaches beyond the merely intuitive that can be employed. One

is combinations of characters: Roth (1988) in assigning his new Eocene taxon to *Zachrysia* described a set of characters shared with *Zachrysia*, including layers of the shell structure, so his classification was not intuitive, but argued as well as the available data could support. Even now, we do not reject the placement in *Zachrysia*, but point out that it is biogeographically unlikely. Another consideration in choosing fossils for calibrations is to prefer fossils within the current geographic range of the relevant clade, and to consider the effect on the analysis of excluding extralimital fossils.

TAXONOMIC ACTIONS AND CONCLUSIONS

Pleurodontidae is restricted to genera *Pleurodonte*, *Dentellaria*, *Lucerna*, *Eurycratera* and *Thelidomus*. The genus *Pleurodonte* as traditionally recognized is paraphyletic. It is here restricted to the Lesser Antilles. Schileyko (2006) had already raised *Dentellaria* to a full genus which we confirm; we here remove *Lucerna* from the synonymy of *Pleurodonte* and recognize it as a full genus endemic to Jamaica.

We found that the type species of *Lucerna*, *Carocolla acutissima* Lamarck, 1822, is an older name for *Helix ingens* C. B. Adams, 1850, based on the photographed type in Mermod (1951: 706). When he introduced the name *acutissima*, Lamarck did not state that it was a replacement name for *Helix acuta* Lamarck, 1816 (non Müller, 1774), which was included in its synonymy. Similarly, *H. acuta* Lamarck, 1816 was included in synonymy of *Helix lamarckii* Férussac, 1821, also without statement that it was preoccupied. We designate the specimen illustrated by Mermod as the lectotype of *H. acuta* Lamarck, 1816, *H. lamarckii* Férussac, 1821 and *C. acutissima* Lamarck, 1822, rendering them objective synonyms. The correct name for the taxon is *Lucerna lamarckii* (Férussac, 1821).

We synonymize *Gonostomopsis* with *Pleurodonte*, since it grouped within *Pleurodonte* in the Bayesian and ML analyses. In that topology, maintaining it as a distinct genus would require transferring all the included *Pleurodonte* species to *Gonostomopsis*, except the type species, *Pl. lychnuchus*, which is basal. This also results in Gonostomopsinae being synonymized with Pleurodontinae. If further analysis including more of the Lesser Antillean species shows a need to subdivide *Pleurodonte*, the name *Gonostomopsis* should not be resurrected. It is an unnecessary replacement name for *Chrysodon* Ancey, 1887 (non Oken 1815) – Oken's work is not available, having been rejected in ICZN Opinion 417.

Under ICZN Article 23.9, we declare Pleurodontidae Ihering, 1912 to be a nomen protectum and use it as the valid name for the family, giving it precedence over its senior synonym Lucernidae Swainson, 1840. We also

declare Pleurodontinae a nomen protectum in relation to the senior homonym Pleurodontinae Conrath, 1887 (Bivalvia), which is a nomen oblitum. The following 26 works have used Pleurodontinae or Pleurodontidae as valid for the gastropod clade since 1977: Bertrand (2001), Borrero (2012), Borrero & Araujo (2012), Bouchet *et al.* (2005), Breure (2010), Breure *et al.* (2016), Capinera (2012, 2013), Ciomperlik *et al.* (2013), Coan & Petit (2011), Cuezzo (2003), Hugall & Stanisic (2011), Johnson *et al.* (2004), Mulieri & Mello-Patiu (2013), Nekola (2014), Razkin *et al.* (2015), Robinson *et al.* (2009), Rosenberg & Muratov (2006), Roth (2001), Salvador & Simone (2015), Schileyko (2006), Smith & Silagyi (2009), Takeda (1980), Takeda & Tsuruoka (1979), Tang & Tang (1977) and Willig *et al.* (2013); additional works could be cited. We have found no evidence that Lucernidae or Lucerninae Swainson, 1840 or Pleurodontinae Conrath, 1887 has been used as valid since 1899.

DESCRIPTION OF LABYRINTHIDAE BORRERO, SEI, ROBINSON & ROSENBERG, NEW FAMILY

urn:lsid:zoobank.org:act:25A32F13-DF56-42FD-8A38-2B81F1E38915

Type genus: *Labyrinthus* Beck, 1837

The shell is discoidal, ranging from 10 to 60 mm in width in *Labyrinthus*, and 18 to 75 mm in *Isomeria* (Cuezzo, 2006). An umbilicus is always present in juveniles, but ranges among species from fully open to closed in adults. Most species have conspicuous apertural barriers in the form of denticles and lamella of various levels of development. In general, *Labyrinthus* species have more complex apertural barriers on the palatal and parietal areas, with more numerous and/or larger teeth and lamella than those of *Isomeria*, and the shells tend to be less inflated, including some lentiform taxa.

Feeding apparatus has been described for only a few species. The central radular tooth is monocuspid and the lateral and marginal teeth are mono- or bicuspid. The jaw is simple, with either low irregular longitudinal ribs, or weak concentric striations.

The only unique morphological synapomorphies for the family are those reproductive characters noted by Cuezzo (2003, 2006) as shared by *Labyrinthus* and *Isomeria*: the presence of denticles in the interior walls of the vagina in addition to those in the phallus, and the free oviduct branching at an angle with the vagina rather than being continuous with it.

The close relationship between *Labyrinthus* and *Isomeria* is supported by conchological, anatomical and molecular data, yet this clade does not group with pleurodontids or sagdoids, but rather branches basally in Helicoidea. The grouping with *Caracolus* and *Solaropsis* found by Cuezzo (2003) is not supported, so we recognize this clade at the family level.

The name Lampadiidae Winckworth, 1945, based on *Lampadion* Röding, 1798 previously has been considered available for this clade (Bouchet *et al.*, 2005), but is a *nomen nudum*, as shown by Bouchet *et al.* (2017). Rather than validating Winckworth's name, we have named the taxon Labyrinthidae, for two reasons: (1) *Lampadion* is not a name in current use, although it is regarded as a senior synonym of *Labyrinthus* Beck, 1837 by a few authors (e. g., Rehder, 1967; Abbott, 1989). Wurtz (1955b) designated a lectotype for *Lampadion* that rendered it a *nomen dubium*, but Rehder (1967) disputed the validity of this action. As the situation is unresolved, we prefer to base the family name on the well-known genus *Labyrinthus* and (2) Schileyko (2006) introduced the family-group name Lampadiini as a tribe in Helicidae, based on *Lampadia* Albers, 1854. To avoid homonymy with this name, we would need to choose a different stem than the one used by Winckworth to introduce a name based on *Lampadion* (ICZN Article 29.6). Labyrinthidae has been used in Pisces but is not available as it is not based on genus name (ICZN Article 11.7.1); it is not recognized in van der Laan, Eschmeyer & Fricke's (2014) list of family-group names of fish.

Labyrinthidae includes 60–70 species of Neotropical mainland distribution, mostly in northwestern South America, but extending east to French Guyana and northeastern Brazil, and north into southern Central America (Panama and Costa Rica). To the south, its distribution extends into Peru, and includes mostly Andean regions, with some Amazonian habitats. Highest species diversity is in western Colombia, Ecuador and northern Peru.

DESCRIPTION OF ZACHRYSIIDAE ROBINSON, SEI & ROSENBERG, NEW FAMILY

urn:lsid:zoobank.org:act:FC1250C0-D6D6-41B8-A062-F08F64D9A26B

Type genus: *Zachrysia* Pilsbry, 1894

The shell is solid and thick, 16–70 mm in width (Schileyko, 2006), generally globose but depressed, and somewhat eccentrically and unevenly coiled. The protoconch consists of one and half whorls that are polished and shiny, with faint microscopic spiral lines. The teleoconch consists of four to four and a half whorls, and can be sharply and finely ribbed to almost smooth in sculpture. There may be a microsculpture of closely crowded granules, sometimes arranged in irregular spiral striae. The oblique aperture is downturned at maturity, with a thickened, reflexed

lip and the baso-columellar margin expanded with a slight tooth. The shell colour can be pale yellow to orange. Adults are not umbilicate, while juveniles are minutely so.

The reproductive anatomy of the Zachrysiidae is unique, quite distinct from all other taxa previously included in the Pleurodontidae and New World Camaenidae. The right ommatophoral retractor muscle does not pass between the phallus and the oviduct, but rather to the left of the genitalia. The phallus is thick, lacks a verge, but the phallus chamber contains one to two fleshy structures (in most species), referred to as 'stimulus' (Pilsbry, 1929; Cuezzo, 2003) or stimulators (Schileyko, 2006), but whose functions are debatable and may differ in different species. The epiphallus is very short (in some species barely discernable). There is a thick flagellum that may be short or long, but does not taper but ends rather bluntly, plus there is (in most species) what Pilsbry (1929) called an accessory flagellum and what Schileyko (2006) called the penial caecum, attached separately to the phallus; again, its function is unknown. The gametolytic gland duct is coiled around the phallus retractor muscle, is separate from the oviduct throughout its length, that is, not coiled together, nor running down to the phallic-oviducal angle, all characteristics unknown in other helicoids. The gametolytic gland duct is short, swollen basally and the gametolytic gland reservoir relatively large. The ovotestis or gonad is made up of very elongated acini, and there is no vagina, again characters that differ with those of other Pleurodontidae.

The Zachrysiidae consists of some 14 known species included in a single genus *Zachrysia* with several subgenera, all native to Cuba. Three species have been introduced outside of Cuba: two are established in Florida, and two have spread to several islands in the West Indies, the Yucatan Peninsula of Mexico and Panama. Outside of their native range, *Zachrysia* species are serious horticultural pests (Fields & Robinson, 2004).

Cuezzo (2003) placed *Zachrysia* in Caracolinae, with several genera that we here place in Pleurodontidae *s.s.* (*Eurycratera*), Sagdidae (*Polydontes*) and Labyrinthidae (*Labyrinthus* and *Isomeria*). Our ML and Bayesian phylogenies do show Zachrysiidae as sister to the remaining taxa that Cuezzo placed in Caracolinae (*Caracolus* and *Solaropsis*) but this is weakly supported (Figs 2, 3).

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