# Phylogenetic relationships and classification of Solaropsidae (Gastropoda: Stylommatophora)

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**Abstract.** The classification of terrestrial sundial snails has a long and contentious history; they have been diversely classified in Camaenidae, Pleurodontidae, Polygyridae, and also in their own family, Solaropsidae. Two genera have been recently removed from Solaropsidae (*Polygyratia* Gray, 1847 and *Ridleya* Ancey, 1901), but the status of its 3 remaining genera (*Solaropsis* H. Beck, 1837, *Olympus* Simone, 2010, and *Psadara* K. Miller, 1878) is still uncertain. We have sequenced 4 mitochondrial and nuclear markers of species belonging to those 3 genera and included them in a phylogenetic framework of all helicoid snails (Sagdoidea and Helicoidea). Our analysis supports a monophyletic Solaropsidae within Sagdoidea, as well as its internal division into Solaropsinae and Caracolinae. *Solaropsis* and *Psadara* are both paraphyletic and include the monotypic *Olympus*. Thus, we consider the latter 2 genera synonymous with *Solaropsis*. We also present a summary of the fossil record of the family, excluding from it the genus *Hodopoeus* Pilsbry & Cockerell, 1945 (now classified in Labyrinthidae) and discussing the paleobiogeographic history of Sagdoidea and of early branches of Helicoidea. Finally, Epiphragmophoridae (formerly a subfamily of Xanthonychidae) is supported as a distinct family-level clade within Helicoidea.

**Key words.** Epiphragmophoridae, Helicoidea, Neotropics, paleobiogeography, Sagdoidea, *Solaropsis*, sundial snails.

## Introduction

Sundial snails are large Neotropical terrestrial gastropods belonging to the Stylommatophora, or "pulmonate" snails. They have been subject to a complex classification history. The genus *Solaropsis* H. Beck, 1837 and its allied forms were first classified within the Helicidae sensu lato (Pilsbry 1894 in 1893–1895, Ihering 1900) but have been subsequently assigned to Pleurodontidae (Ihering 1912, Thiele 1931, Morretes 1949, 1953, Bouchet et al. 2005, Massemin et al. 2009, Cuezzo et al. 2018), Camaenidae (Zilch 1960 in 1959–1960, Richardson 1985, Abbott 1989, Tillier 1989, Cuezzo 2002, 2003, Salgado & Coelho 2003, Simone 2010, Birckolz et al. 2016), Polygyridae (Schileyko 2006), and also to their own family, Solaropsidae (Nordsieck 1986, Simone 2006, Bouchet et al. 2017, Sei et al. 2017, Salvador 2019a).

Typically, Solaropsidae included 5 genera: *Solaropsis*, *Psadara* K. Miller, 1878, *Olympus* Simone, 2010, *Polygyratia* Gray, 1847, and *Ridleya* Ancey, 1901. The latter 2 have recently been excluded from that family and reassigned to Scolodontidae (Salvador 2019b, Salvador & Cavallari 2020). The status of the other 3 remained contentious, with some authors considering them valid whereas others judged all 3 as synonymous with one another (e.g., Simone 2006, Birckolz et al. 2016, Cuezzo et al. 2018, Salvador 2019a).

The affinities of the solaropsids with other American "helicoids" has also been problematic (Tillier 1989), and during their history they have been placed in close relationship to most other American helicoid genera, most often *Pleurodonte* Fischer de Waldheim, 1807, *Epiphragmophora* Doering, 1874, *Labyrinthus* H. Beck, 1837, and *Isomeria* Albers, 1850. More recently, Sei et al. (2017) have included the subfamily Caracolinae within Solaropsidae, which in turn was placed within Sagdoidea, the sister taxon to Helicoidea.

Until the work of Sei et al. (2017), most molecular phylogenetic works had a poor sampling of American helicoids other than Pleurodontidae (e.g., Wade et al. 2006, 2007). Even the phylogeny of Sei et al. (2017) lacked a thorough representation of solaropsid genera and of possibly allied forms such as *Labyrinthus* and *Epiphragmophora*. Meanwhile, morpho-anatomical phylogenies (Tillier 1989, Cuezzo 2003, Cuezzo et al. 2018) have indicated different groupings than molecular ones, likely due to the complexity in assigning character states for anatomical features in *Solaropsis* (Tillier 1989) and to the different groups used in each analysis. Here we present a better sampling of these taxa and include the Solaropsidae into a broad phylogenetic analysis using a multi-locus approach. Furthermore, we investigate the taxonomic status of its 3 component genera and also present an account of its fossil record.

## Material and Methods

Fifteen specimens from 12 different species of South American "helicoid" snails were sampled for genetic sequencing, representing the Solaropsidae (6 species) and 2 potentially related genera, *Labyrinthus* and *Epiphragmophora* (Table 1). For 3 species, we had 2 samples as there were doubts about whether they represented the same taxon. Tissue samples (a piece of the foot) were obtained from the malacological collections of the following institutions: Museu de Zoologia da Universidade de São Paulo (MZSP, São Paulo, Brazil), Natural History Museum (NHMUK, London, UK), Universidade Federal do Acre (UFAC, Rio Branco, Brazil), and Instituto de Biodiversidad Neotropical, CONICET – Universidad Nacional de Tucumán (IBN, Tucumán, Argentina).

Data for 51 additional species (excluding outgroups) were gathered from NCBI GenBank (Table 2), representing all family-level taxa of Sagdoidea and Helicoidea, with a greater focus on those groups potentially related to Solaropsidae. Preference was given to nominate genera and to more complete sequence data. The outgroup was selected to include both basal and more derived stylommatophorans and consists of: *Succinea manaosensis* Pilsbry, 1926 (Succineidae), *Rhytida greenwoodi* (Gray, 1950) (Rhytididae), and *Discus rotundatus* (O.F. Müller, 1774) (Discidae); sequence data were sourced from GenBank (Table 2).

DNA extraction was conducted using QIAGEN DNeasy® Blood & Tissue Kit. Four markers were targeted for this study: (1) the barcoding fragment of the

**Table 1.** Species with markers sequenced for this study, with GenBank accession numbers, voucher data, and locality of provenance.

| Species | CO1 | 16S | ITS2+28S | Voucher | Provenance |
|---|---|---|---|---|---|
| **Solaropsidae** | | | | | |
| *Solaropsis punctata* (J.A. Wagner, 1827) | MT080619 | MT080824 | — | MZSP 63653 | Brazil: Bahia, Porto Seguro, Parque Nacional Monte Pascoal |
| *Psadara* cf. *peruviana* (Haas, 1951) #1 | MT080615 | MT080823 | MT080839 | UFAC IA-779 | Brazil: Acre, Rio Branco, Bairro Universitário |
| *Psadara* cf. *peruviana* (Haas, 1951) #2 | MT080616 | MT080813 | MT080840 | UFAC 1091 | Brazil: Acre, Rio Branco, Bairro Universitário, 09.9476° S, 067.8864° W |
| *Psadara juruana* (Ihering, 1905) | MT080614 | MT080821 | MT080838 | MZSP 104242 | Brazil: Pará, Altamira, Usina de Belo Monte |
| *Psadara rosaria* (L. Pfeiffer, 1849) | MT080617 | MT080825 | MT080841 | MZSP 136827 | Brazil: Goiás, São Domingos, Parque Estadual da Terra Ronca |
| *Psadara rugifera* (Dhorn, 1882) | MT080618 | MT080822 | MT080842 | MZSP 131922 | Brazil: Roraima, Porto Velho |
| *Olympus nimbus* Simone, 2010 | MT080613 | MT080826 | MT080837 | MZSP 87151 | Brazil: Amazonas, São Gabriel da Cachoeira, Pico da Neblina, Cachoeira do Tucano |
| **Labyrinthidae** | | | | | |
| *Labyrinthus bifurcatus* (Deshayes, 1838) | MT080611 | MT080820 | MT080836 | NHMUK 20190592 | Ecuador: Nuevo Corrientes (river?) |
| *Labyrinthus diminutus* Gude, 1903 | MT080612 | MT080819 | — | UFAC IA-746 | Brazil: Acre, Sena Madureira, Reserva Florestal do Antimary |
| **Epiphragmophoridae** | | | | | |
| *Epiphragmophora parodizi* Fernández & Rumi, 1984 | MT080605 | MT080818 | MT080831 | IBN 806 | Argentina: Tucumán, Trancas, Gonzalo close to Hualinchay, 26.3224° S, 065.5374° W |
| *Epiphragmophora tomsici* Fernández & Rumi, 1984 | MT080606 | MT080815 | MT080832 | IBN 807 | Argentina: Tucumán, Trancas, Rearte River margin, 26.3814° S, 065.5268° W |
| *Epiphragmophora trenquelleonis* (Grateloup, 1851) #1 | MT080607 | MT080817 | — | IBN 659 | Argentina: Córdoba, Punilla, La Falda, 31.0968° S, 064.5038° W |
| *Epiphragmophora trenquelleonis* (Grateloup, 1851) #2 | MT080608 | MT080816 | MT080833 | IBN 894 | Argentina: Córdoba, Cruz del Eje, Sierra San Marcos, 30.7900° S, 064.6332° W |
| *Epiphragmophora trigrammephora* (d'Orbigny, 1835) #1 | MT080609 | MT080812 | MT080834 | IBN 340 | Argentina: Córdoba, Totoral, 5km S. Santa Catalina, 30.8572° S, 064.2600° W |
| *Epiphragmophora trigrammephora* (d'Orbigny, 1835) #2 | MT080610 | MT080814 | MT080835 | IBN 844 | Argentina: Jujuy, Ledesma, Calilegua National Park, 23.6212° S, 064.5886° W |

**Table 2.** List of specimens retrieved from GenBank used in phylogenetic analyses, with accession numbers, provenance data, and reference to original publications. The sequences from SEI et al. (2017) do not include the ITS2 marker.

| Species | CO1 | 16S | ITS2+28S | Provenance | References |
|---|---|---|---|---|---|
| **Sagdoidea: Sagdidae** | | | | | |
| *Sagda* cf. *epistylioides* (A. Férussac, 1821) | — | KF247005 | KF207708 | Jamaica: Westmoreland Parish | SEI et al. 2017 |
| *Hyalosagda arboreoides* (C.B. Adams, 1845) | — | KF246998 | KF207699 | Jamaica: St. Thomas Parish | SEI et al. 2017 |
| *Lacteoluna selenina* (Gould, 1848) | — | KF246999 | KF207700 | USA: Florida | Rosenberg et al. unpublished |
| *Polydontes acutangula* (Burrow, 1815) | — | KF246985 | KF207686 | Puerto Rico: Rio Grande | Rosenberg et al. unpublished |
| *Polydontes angustata* (Gray, 1828) | — | KF246978 | KF207679 | Dominican Republic: Samana | Rosenberg et al. unpublished |
| *Platysuccinea portoricensis* (Shuttleworth, 1854) | — | KF247011 | KF207714 | Puerto Rico: Ponce | SEI et al. 2017 |
| **Sagdoidea: Solaropsidae** | | | | | |
| *Solaropsis* cf. *gibboni* (L. Pfeiffer,1846) | — | KF246988 | KF207688 | Colombia: Cundinamarca | SEI et al. 2017 |
| *Solaropsis heliaca* (d'Orbigny,1835) | — | KF246989 | KF207689 | Bolivia: Santa Cruz | SEI et al. 2017 |
| *Solaropsis* sp. 1 | — | KF246990 | KF207690 | Ecuador: El Zarza | SEI et al. 2017 |
| *Solaropsis* sp. 2 | — | KF246991 | KF207691 | Paraguay: Concepción | SEI et al. 2017 |
| *Caracolus caracollus* (Linnaeus, 1758) | — | KF246970 | KF207671 | Puerto Rico: Jayuya | SEI et al. 2017 |
| *Caracolus sagemon* (H. Beck, 1837) | — | KF246973 | KF207674 | Cuba: Holguin | SEI et al. 2017 |
| *Caracolus gaskoini* (Reeve, 1851) | — | KF246971 | KF207672 | Dominican Republic: Independencia | SEI et al. 2017 |
| *Caracolus sarcocheila* (Mörch, 1850) | — | KF246975 | KF207676 | Dominican Republic: La Altagracia | SEI et al. 2017 |
| **Sagdoidea: Zachrysiidae** | | | | | |
| *Zachrysia havanensis* (Pilsbry, 1894) | — | KF246992 | KF207692 | Puerto Rico: Mayaguez | SEI et al. 2017 |
| *Zachrysia provisoria* (L. Pfeiffer, 1858) | — | KF246993 | KF207693 | Cayman Islands: Grand Cayman | SEI et al. 2017 |
| **Helicoidea: Bradybaenidae** | | | | | |
| *Bradybaena similaris* (A. Férussac, 1822) | MN022742 | GQ851001 | AY014138 | Undetermined / Australia: Queensland, Brisbane / Sri Lanka | SAADI & WADE 2019, SEI et al. 2017, WADE et al. 2001 |
| **Helicoidea: Camaenidae** | | | | | |
| *Austrochloritis porteri* (Cox, 1866) | MN512679 | GQ850994 | GQ850888 | Australia / Australia: Queensland, Lamington | KÖHLER et al. 2020, HUGALL & STANISIC 2011 |
| *Papuexul bidwilli* (Reeve, 1853) | — | GQ851032 | GQ850905 | Australia: New South Wales, Port Macquarie | SEI et al. 2017 |
| **Helicoidea: Canariellidae** | | | | | |
| *Canariella giustii* Ibáñez & Alonso, 2006 | KY818423 | KY818447 | KY818561 | Spain: Canary Islands, Tenerife, Teno | NEIBER et al. 2017 |
| **Helicoidea: Cepolidae** | | | | | |
| *Cepolis definita* (Fulton, 1908) | — | KF247018 | KF207721 | Dominican Republic: Pedernales | SEI et al. 2017 |
| *Dialeuca nemoraloides* (C.B. Adams, 1845) | — | KF247020 | KF207723 | Jamaica: St. Thomas Parish | SEI et al. 2017 |
| **Helicoidea: Elonidae** | | | | | |
| *Elona quimperiana* (Blainville, 1821) | FJ786457 | FJ786408 | JQ805023 | Spain: Gipuzkoa, Aránzazu | GÓMEZ-MOLINER et al. 2013 |
| **Helicoidea: Geomitridae** | | | | | |
| *Cochlicella barbara* (Linnaeus,1758) | MK228708 | KF247016 | KJ458633 | France: Landes, Mimizan / Spain: Vizcaya / undetermined | JOURDAN et al. 2019, SEI et al. 2017, RAZKIN et al. 2015 |
| *Cochlicella acuta* (O.F. Müller, 1774) | KP727359 | KF247015 | AY014126 | Undetermined / Tunisia: Nabeul / undetermined | RAZKIN et al. 2017, SEI et al. 2017, WADE et al. 2001 |
| **Helicoidea: Helicidae** | | | | | |
| *Helix pomatia* Linnaeus, 1758 | KX241543 | KF247036 | AY841333 | Italy: Piedmont, Morozzo / Slovenia: Ljubljana / undetermined | CESARONI et al. 2017, SEI et al. 2017, WADE et al. 2006 |
| *Cornu aspersum* (O.F. Müller, 1774) | MK883428 | KF247035 | AY014128 | Algeria / USA: Colorado / undetermined | BOUAZIZ-YAHIATENE et al. 2019, SEI et al. 2017, WADE et al. 2001 |
| **Helicoidea: Helicodontidae** | | | | | |
| *Helicodonta obvoluta* (O.F. Müller, 1774) | JF717801 | KR704980 | KR705057 | Netherlands / Germany: Sachsen — Anhalt, Ruebeland | GROENENBERG et al. 2011, NEIBER et al. 2017 |
| **Helicoidea: Hygromiidae** | | | | | |
| *Monacha cantiana* (Montagu, 1803) | MG208932 | MG209003 | AY841332 | Italy: Lombardy, Rezzato / undetermined | PIEŃKOWSKA et al. 2018, WADE et al. 2006 |
| *Trochulus hispidus* (Linnaeus, 1758) | KY818415 | KY818541 | KY818647 | Undetermined | NEIBER et al. 2017 |

**Table 2.** Continued.

| Species | CO1 | 16S | ITS2+28S | Provenance | References |
|---|---|---|---|---|---|
| **Helicoidea: Labyrinthidae** | | | | | |
| *Labyrinthus quadridentatus* (Broderip, 1832) | — | KF246981 | KF207683 | Costa Rica: Coto Brus | Sei et al. 2017 |
| *Isomeria oreas* (Koch, 1844) | — | KF246980 | KF207682 | Colombia: Valle del Cauca | Sei et al. 2017 |
| **Helicoidea: Pleurodontidae** | | | | | |
| *Pleurodonte dentiens* (A. Férussac, 1822) | — | KF246956 | KF207655 | Dominica: St. Mark Parish | Sei et al. 2017 |
| *Pleurodonte isabella* (A. Férussac, 1821) | — | KF246960 | KF207659 | Barbados: St. James Parish | Sei et al. 2017 |
| *Dentellaria sinuata* (O.F. Müller, 1774) | — | KF246902 | KF207616 | Jamaica: Westmoreland Parish | Sei et al. 2017 |
| *Lucerna lucerna* (O.F. Müller, 1774) | — | KF246938 | KF207639 | Jamaica: St. Ann Parish | Sei et al. 2017 |
| *Lucerna sublucerna* Pilsbry, 1889 | — | KF246950 | KF207651 | Jamaica: St. Catherine Parish | Sei et al. 2017 |
| *Gonostomopsis auridens* (Rang, 1834) | — | KF246969 | KF207670 | Martinique | Sei et al. 2017 |
| **Helicoidea: Polygyridae** | | | | | |
| *Polygyra cereolus* (Megerle von Mühlfeld, 1818) | — | KF247038 | EU409912 | Cayman Islands | Sei et al. 2017 |
| *Polygyra septemvolva* Say, 1818 | DQ086069 | DQ085984 | — | USA: Florida, Hillsborough State Park | Perez 2011 |
| *Praticolella mexicana* Perez, 2011 | — | KF247039 | KF207742 | Jamaica: Westmoreland Parish | Sei et al. 2017 |
| **Helicoidea: Sphincterochilidae** | | | | | |
| *Sphincterochila candidissima* (Draparnaud, 1801) | FJ786500 | KF247040 | KJ458637 | Spain | Gómez-Moliner et al. 2013, Sei et al. 2017, Razkin et al. 2015 |
| **Helicoidea: Trichodiscinidae** | | | | | |
| *Trichodiscina coactiliata* (A. Férussac, 1838) | — | KF247023 | KF207726 | Belize | Rosenberg et al. unpublished |
| **Helicoidea: Trissexodontidae** | | | | | |
| *Caracollina lenticula* (Michaud, 1831) | FJ786455 | FJ786406 | JQ805003 | Italy | Gómez-Moliner et al. 2013 |
| **Helicoidea: Xanthonychidae** | | | | | |
| *Xanthonyx* sp. | — | KF247024 | KF207727 | Mexico: Nuevo Leon | Rosenberg et al. unpublished |
| *Helminthoglypta greggi* Willett, 1931 | KY986379 | KY986341 | — | USA: California, Soledad Mountain | Goodward et al. 2017 |
| *Helminthoglypta umbilicata* (Pilsbry, 1898) | KC254708 | KC254722 | — | USA: California, Landels-Hill Big Creek Reserve | Gilbertson et al. 2013 |
| *Bunnya metli* Araiza-Gómez et al., 2019 | KY886473 | KY886472 | MG000150 | Mexico: Zinacantepec, San Juan de las Huertas | Araiza-Gómez et al. 2019 |
| *Humboldtiana queretaroana* (Dall, 1897) | | DQ324491 | DQ324515 | Mexico: Querétaro | Mejía & Zúñiga 2007 |
| *Plesarionta stearnsiana* (Gabb, 1867) | — | KF247027 | KF207730 | USA: California | Sei et al. 2017 |
| *Monadenia fidelis* (Gray, 1834) | MN022743 | KF247021 | AY014142 | Undetermined / USA: Washington / USA: Oregon | Saadi & Wade 2019, Rosenberg et al. unpublished, Wade & Mordan 2000 |
| **Outgroup** | | | | | |
| *Succinea manaosensis* Pilsbry, 1926 | MN186467 | MN186468 | MN186473 | Brazil: Paraíba, Areia | Salvador et al. 2020 |
| *Discus rotundatus* (O.F. Müller, 1774) | FJ917285 | FJ917265 | FJ917240 | Germany: Hesse, Frankfurt am Main | Dinapoli & Klussmann-Kolb 2010 |
| *Rhytida greenwoodi* (Gray, 1850) | KT970868 | KT970900 | KP230525 | New Zealand: Waikato, Raglan | Moussalli & Herbert 2016 |

mitochondrial CO1 gene (primers LCO and HCO: Folmer et al. 1994), c. 650 bp; (2) mitochondrial 16S rRNA gene (primers 16SarL and 16SbrH: Simon et al. 1994), c. 450 bp; (3) and (4) a continuous fragment of nuclear DNA encompassing the 3′ end of the 5.8S rRNA gene, the ITS2 region, and the 5′ end of the 28S rRNA gene, c. 1,300 bp overall, amplified in 2 fragments (primers LSU-1 and LSU-3 for first section, and LSU-2 and LSU-5 for second section: Wade & Mordan 2000, Wade et al. 2006). PCR amplification for CO1 and 16S consisted of: initial denaturation at 96 °C (2 min); 35 cycles of denaturation at 94 °C (30 s), annealing at 48 °C (1 min) and extension at 72 °C (2 min); final extension at 72 °C (5 min). PCR protocol for ITS2+28S was: initial denaturation at 95 °C (3 min); 40 cycles of denaturation at 95 °C (30 s), annealing at either 50 °C (ITS2 section) or 45 °C (28S section) (1 min) and extension at 72 °C (2 min); final extension at 72 °C (4 min). Minor variations of these protocols affecting annealing temperature or the durations of steps of the cycles were used in repeat trials when initial amplification failed. PCR products were quantified using agarose-gel electrophoresis, cleaned, and sent to the Massey Genome Service (Massey University, Palmerston North, New Zealand) for Sanger sequencing.

Sequences were assembled, quality-assessed to judge the necessity of repeats, trimmed in Geneious Prime (v. 2019.0.3, Biomatters Ltd), and uploaded to GenBank (Table 1). Sequences were aligned in Geneious Prime using the MUSCLE plugin (EDGAR 2004) with default settings (i.e., optimized for accuracy). The resulting alignments were then submitted to Gblocks (TALAVERA & CASTRESANA 2007), with the least constraining setting, to eliminate poorly aligned and divergent regions that could interfere with the analysis. Sequences of each marker (CO1, 16S, and ITS2+28S) were then concatenated for phylogenetic analyses, having first been analyzed separately to reveal any significant conflicts between resulting trees (none were found).

A phylogenetic analysis by Bayesian inference (**BI**) was performed with MrBayes (v. 3.2.7: RONQUIST et al. 2012) via the CIPRES Science Gateway (v. 3.3: MILLER et al. 2015): 2 concurrent analyses were run, each with 4 Markov chains of 10 million generations (the first 20% discarded as "burn-in"), default priors, nst = 6, rates = invgamma, with substitution model parameters (default) unlinked across the 3 markers. Convergence was assessed by examining standard deviation of split frequencies (<0.01) and also by analyzing the likelihood plots in Tracer (v. 1.7.1: RAMBAUT et al. 2018). A maximum-likelihood (**ML**) analysis was also performed via the PhyML 3.0 online portal (GUINDON et al. 2010), using smart model selection (LEFORT et al. 2017) with the Akaike Information Criterion (AIC), subtree pruning-regrafting branch swapping, and 2,000 bootstrap replicates.

# Results

Our analysis was based on sequence data from taxa within Sagdoidea and Helicoidea, the 2 superfamilies in which solaropsids have been historically classified. Besides the 3 outgroup species, 66 terminal taxa were used (Tables 1, 2). CO1 sequences were c. 680 bp long, 16S c. 520 bp long, and ITS1+28S c. 1604 bp long. After elimination of poorly aligned regions and invariant sites using Gblocks, CO1 sequences consisted of 616 bp, 16S of 386 bp, and ITS1+28S of 1130 bp. Thus, the concatenated sequences used for the analyses were 2132 bp long.

The resulting BI phylogenetic tree is presented in Figure 1 and will be the only one discussed here. The ML tree had mostly the same topology (and overall similar support) for the groups of interest, so ML bootstrap values are also presented in Figure 1. There were minor differences in the internal arrangement of crown Solaropsidae and of Epiphragmophoridae; they are shown in Figure 2.

Overall, the separation of Solaropsidae from other "helicoid" families had strong support (Fig. 1). Both Sagdoidea and Helicoidea form strongly supported monophyletic clades (posterior probability [**PP**] = 1.0), except for the position of *Bunnya metli* Araiza-Gómez et al., 2019 in relation to both clades, which remains unresolved (it was

placed within Helicoidea in SEI et al. 2017). The inner split within Sagdoidea (into Sagdidae + Zachrysiidae and Solaropsidae) was well supported (PP = 1.0), with strong support also for the split between Sagdidae and Zachrysiidae (PP = 0.99). The split within Solaropsidae between Caracolinae and Solaropsinae is well supported (PP = 0.97), with each of the subfamilies monophyletic (PP = 1.0). The many internal branches within Solaropsinae vary in support, from weakly to strongly supported; they show both *Solaropsis* and *Psadara* as currently defined to be polyphyletic assemblages (Figs 1, 2). The arrangements of the subfamilies within Sagdidae are strongly supported (PP = 1.0 in all cases; see Discussion below).

The most basal clade within Helicoidea is moderately supported (PP = 0.96), being composed of the strongly supported Cepolidae and Labyrinthidae (PP = 1.0 each). The remaining Helicoidea form a well-supported clade (PP = 1.0), but its internal branching is poorly resolved, with a basal polytomy. This was expected given the diversity of the group and the partial dataset (including very short lengths of some GenBank sequences; Table 2); in any event, the crown helicoids were not the focus of this study. Nevertheless, some groups were strongly supported (all PP = 1.0): (1) Camaenidae + Bradybaenidae + Polygyridae; (2) Epiphragmophoridae; (3) Helicidae; and (4) Pleurodontidae. The Epiphragmophoridae and the most basal branch of the Helicoidea are of particular interest and will be the only Helicoidea taxa discussed in more detail below.

# Discussion

## Systematics — Sagdoidea

This superfamily is well supported and largely well resolved, being divided into Zachrysiidae, Sagdidae, and Solaropsidae (Fig. 1).

**Zachrysiidae Robinson, Sei & Rosenberg, 2017 in SEI et al. 2017.** This family was recovered here as the sister taxon of Sagdidae (PP = 0.99), while it was recovered as the sister taxon of Solaropsidae (PP < 0.8) in the work of SEI et al. (2017). SEI et al. (2017) erected the family Zachrysiidae to contain just *Zachrysia*. However, given the strong support and position observed in our phylogeny, we suggest that this taxon might be more appropriately treated as a subfamily of Sagdidae rather than a monotypic family. Further work with improved taxa sampling should help clarify this issue.

**Sagdidae Pilsbry, 1895.** Sagdidae is divided into 3 strongly supported subfamilies: Platysuccineinae H.B. Baker, 1940, Polydontinae Schileyko, 2006, and Sagdinae Pilsbry, 1895. Following the reasoning mentioned above for Zachrysiidae, the subfamily Polydontinae could potentially be synonymized with the monotypic Platysuc-
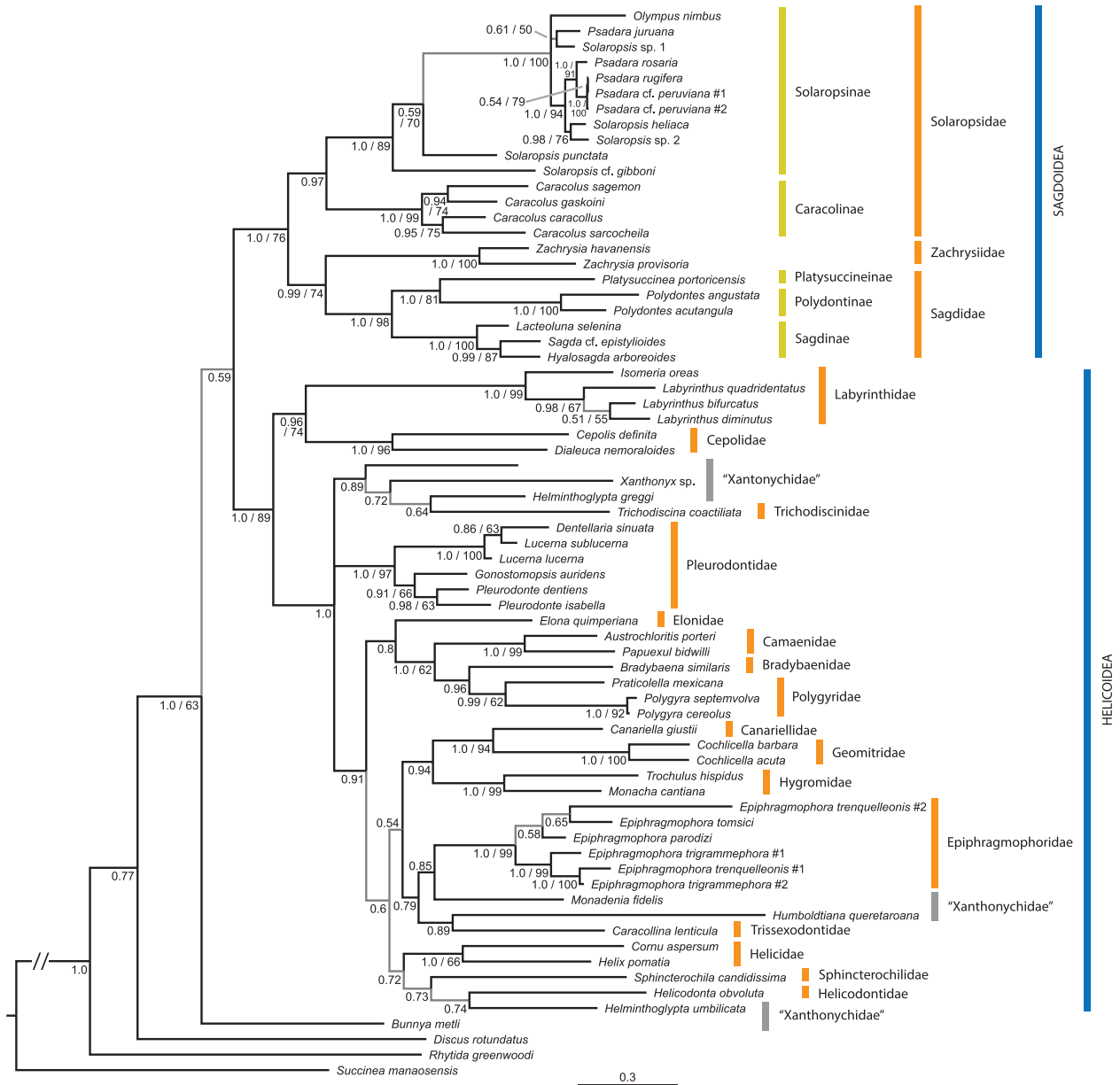
**Figure 1.** Bayesian-inference phylogenetic tree based on CO1, 16S, and ITS2+28S with a focus on Solaropsidae. Posterior probabilities (≥0.5), as well as bootstrap values (≥50%) from the ML analysis, are shown on nodes. Branches with posterior probabilities below 0.75 are shown in grey. Scale bar is substitutions per site.

cineinae, given that both form a single clade well separated from Sagdinae (PP = 1.0).

Cuezzo (2003) did not include Sagdinae or Platysuccineinae in the cladistic analysis of what at that time was considered the "American Camaenidae", but found that the presence of an accessory flagellum was a synapomorphy supporting a sister relationship between *Polydontes* Montfort, 1810 and *Zachrysia* Pilsbry, 1926. Here, Zachrysiidae is the sister group of Sagdidae, so that character state could potentially be a synapomorphy of the clade formed by both families. Anatomical information about these subfamilies is scant, so further studies could potentially shed light on the evolution of these taxa.

**Solaropsidae Nordsieck, 1986.** Wurz (1955), based on his anatomical revision of the "American Camaenidae",

already maintained that *Solaropsis* was a representative of an ancient stock whose affinities at that time were not known. We confirmed the assertion of Wurz (1955) and the molecular results of Sei et al. (2017) that Solaropsidae is not directly related to the other typical helicoid groups within which it has been historically classified (i.e., Pleurodontidae, Camaenidae, and Labyrinthidae). Instead, it is nested with strong support within the Sagdoidea.

Our phylogeny supports 2 subfamilies within Solaropsidae: Solaropsinae Nordsieck, 1986 (PP = 1.0; Fig. 3A–C) and Caracolinae Cuezzo, 2003 (PP = 1.0; Fig. 3D–F), consistent with the work of Sei et al. (2017). It is, however, necessary to highlight that anatomically *Caracolus* Montfort, 1810 is very different from *Solaropsis* (Cuezzo 2002, 2003, Schileyko 2006, Cuezzo et al.
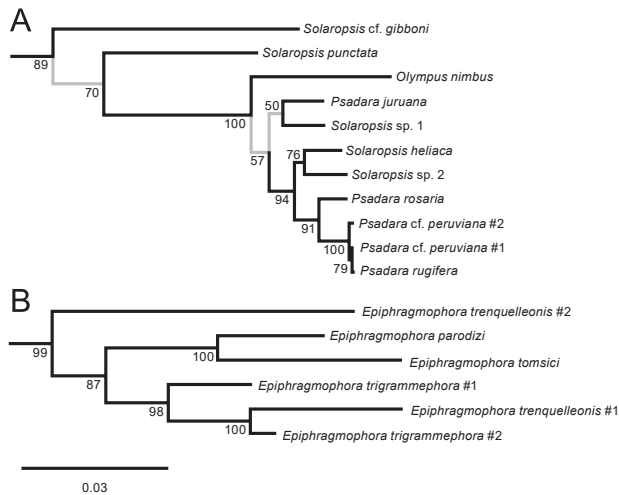
**Figure 2.** Excerpts of the maximum-likelihood tree showing internal arrangements of subfamily Solaropsinae (A) and family Epiphragmophoridae (B), which differ slightly from the BI topologies (Fig. 1). Branches with bootstrap values below 75% are shown in grey. Scale bar is substitutions per site.

2018), and no morphological synapomorphies have yet been found that reflect this grouping.

The arrangement of taxa within Solaropsinae is in part poorly resolved, but clearly shows that both *Solaropsis* and *Psadara* are polyphyletic (Figs 1, 2). Given that there are no obvious morphological differences between the solaropsine branches, the most parsimonious resolution is to consider *Psadara* and *Olympus* as junior synonyms of *Solaropsis* (CUEZZO 2002, 2003, CUEZZO et al. 2018). In that case *Solaropsis* H. Beck, 1837 possesses the following synonyms (see also ZILCH 1960 in 1959–1960): *Eupsadara* Pilsbry, 1926; *Olympus* Simone, 2010; *Ophiodermis* Agassiz, 1846; *Ophiospila* Ancey, 1887; *Psadara* K. Miller, 1878; *Psadariella* Weyrauch, 1956; *Solarium* Spix, 1827 [non Lamarck, 1799]. In accordance, we propose the new combination for the single species in *Olympus*: *Solaropsis nimbus* (Simone, 2010) comb. nov. (there is no change in the epithet, given that "nimbus" is a noun in apposition).

Even so, it is worthwhile to note that the 2 most basal species of Solaropsinae in our tree (*Solaropsis* cf. *S. gibboni* (L. Pfeiffer, 1846) and *S. punctata* (Wagner, 1827)) are the only species to have a strong keel on the median-apical region of the body whorl and are well outside the genetic variation found within their sister group in the subfamily Solaropsinae (Figs 1, 2). A basal position of *S. gibboni* in the tree would agree with the morphological results from CUEZZO et al. (2018). It is possible that these "keeled *Solaropsis*" might form a separate genus-level group within this subfamily and warrant the resurrection of one of the synonyms listed above. Unfortunately, we could not procure a specimen of *S. pellisserpentis* (Gmelin, 1791), the type species of the genus. The keel-less shell of that species (e.g., SIMONE 2006: fig. 929) is more in line with the *Solaropsis* crown-group recovered here (PP = 1.0), which includes the more centrally angulated

and rounded shell forms of *Solaropsis* s.s. as well as "*Psadara*" and "*Olympus*" (Fig. 3A–C).

*Solaropsis nimbus* retains a noticeably large genetic distance from its congeners (Fig. 1), as could be expected from its distinct morphology (i.e., narrower shell and taller spire, Fig. 3C), which hitherto has granted it its own genus (SIMONE 2010). In contrast, *Solaropsis rugifera* and *Solaropsis* cf. *S. peruviana* are genetically close to one another (Figs 1, 2), which might indicate a possible synonymy, a matter for future studies. A joint analysis of morphological and molecular characters, incorporating more species, would be desirable to resolve the phylogenetic relationships within Solaropsinae.

## Systematics — Helicoidea

The Helicoidea were included to investigate a potential relationship to Solaropsidae, as explained above. No relationship was evident, but there are some results observed within this group that warrant further discussion.

**Labyrinthidae Borerro, Sei, Robinson & Rosenberg, 2017 in SEI et al. 2017.** Like SEI et al. (2017), we recovered a basal and well-resolved helicoid clade formed by Cepolidae and Labyrinthidae (0.96 PP, with 1.0 PP for each family). This is the sister taxon of all other Helicoidea and thus has some implications for biogeography (see below). However, in the ML tree of SEI et al. (2017), Cepolidae has a more basal position than Labyrinthidae.

**Xanthonychidae Strebel & Pfeffer, 1879.** Xanthonychidae is widely polyphyletic, with branches scattered through the phylogenetic tree. *Bunnya metli* in particular (presently classified in Humboldtianinae) was placed externally to the Sagdoidea and Helicoidea, which could indicate that it represents a distinct family. That, as well as the position of other Humboldtianinae, should be further investigated.

The polyphyly of Xanthonychidae has been previously indicated by the study of morphological characters (CUEZZO 1998). Although solving the classification of this "family" is far from the objective of the present study, our results show there is still much work to be done. SEI et al. (2017) have already proposed some new families for a few branches previously classified in Xanthonychidae, but to establish a solid classification a study with a larger sample size (including type species) and increased marker coverage is necessary.

The subfamily Epiphragmophorinae Hoffmann, 1928 (Fig. 3G–I), was previously classified within Xanthonychidae (CUEZZO 2006, BOUCHET et al. 2017). It was not present in the study of SEI et al. (2017). Our results show that it is significantly separated from any representative of Xanthonychidae (with the possible exception of *Monadenia* Pilsbry, 1895, classified in its own subfamily Monadeniinae Nordsieck, 1987). Given the strong support recovered for this group (1.0 PP) and its position in our phylogeny (Fig. 1), we return it to the family level as Epiphragmophoridae (NORDSIECK 1986, SCHILEYKO
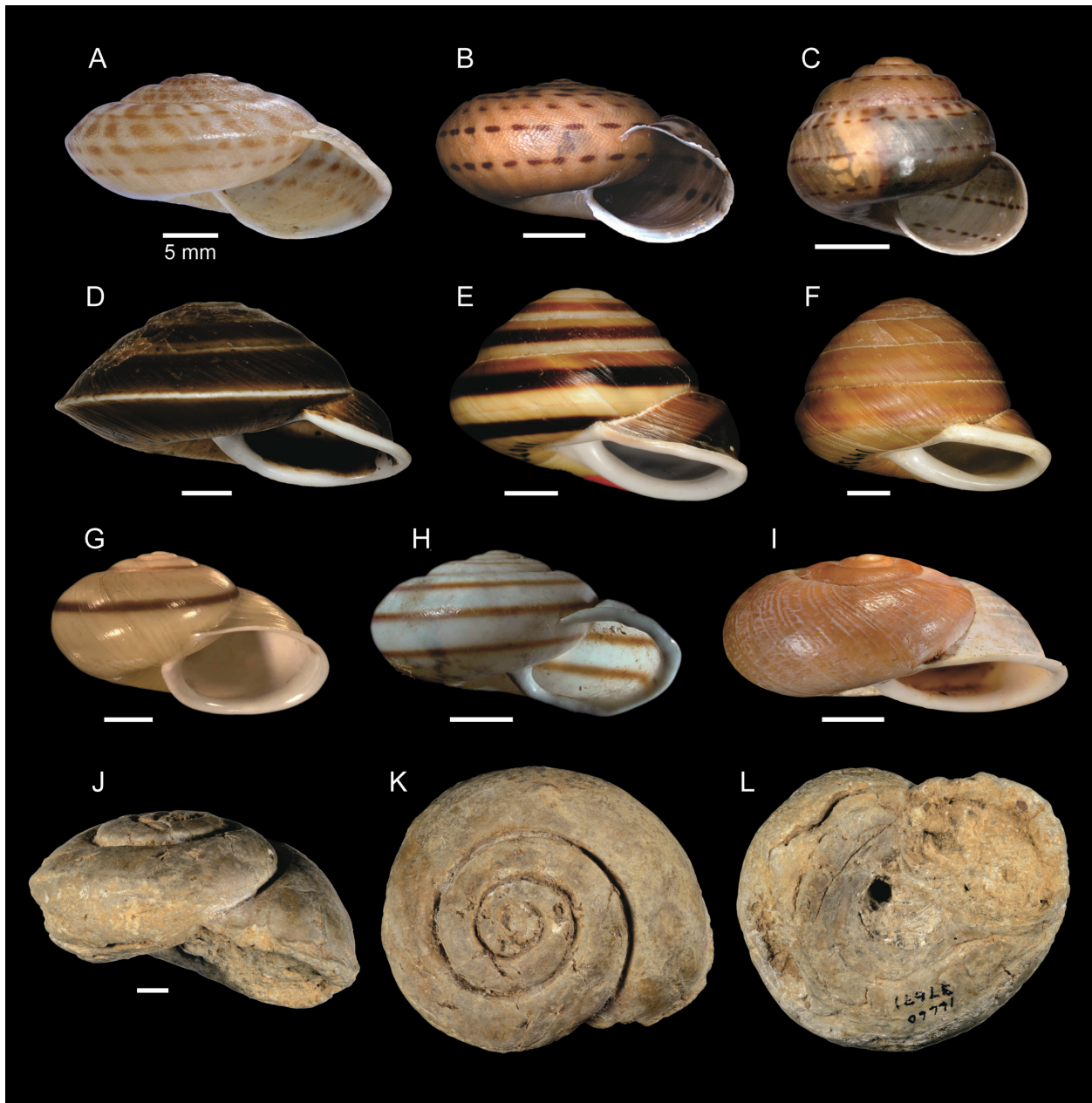
**Figure 3.** Examples of Solaropsidae (A–F), Epiphragmophoridae (G–I), and fossil Labyrinthidae (J–L); all scale bars = 5 mm. **A–C.** Subfamily Solaropsinae. **A.** *Solaropsis heliaca* (d'Orbigny, 1835), from Mato Grosso do Sul state, Brazil; NMW 1458, syntype of *Solaropsis paravicinii* Ancey, 1897 (shell width = 30.2 mm). **B.** *Solaropsis rosaria* (L. Pfeiffer, 1849), from Tocantins state, Brazil; MZSP 114871 (width = 23.8 mm); previously assigned to *Psadara*. **C.** *Solaropsis nimbus* (Simone, 2010), from Amazonas state, Brazil; MZSP 87151, holotype (width = 15.7 mm); previously assigned to *Olympus*. **D–F.** Subfamily Caracolinae. **D.** *Caracolus marginella* (Gmelin, 1791), from Mayagüez municipality, Puerto Rico; ANSP 20861, lectotype of *Caracolus marginella mayaguezi* H.B. Baker, 1961 (width = 35 mm). **E.** *Caracolus goodrichi* Ramsden, 1914, from Guantánamo province, Cuba; ANSP 110771, lectotype of (width = 28 mm). **F.** *Caracolus lowei* Pilsbry, 1929, from Guantánamo province, Cuba; ANSP 147372, lectotype (width = 29 mm). **G–I.** Family Epiphragmophoridae. **G.** *Epiphragmophora trenquelleonis* (Grateloup, 1851), from the foothills of Sierras de Córdoba, Argentina; SMF 7708, lectotype (width = 28.5 mm). **H.** *Epiphragmophora trigrammephora* (d'Orbigny, 1835), from Valle Grande, Santa Cruz department, Bolivia; MNHN unnumbered, syntype (width = 24.2 mm). **I.** *Epiphragmophora tomsici* Fernández & Rumi, 1984, from Andalgalá department, Catamarca province, Argentina; FML 530, holotype (width = 27.2 mm). **J–L.** Fossil Labyrinthidae *Hodopoeus crassus* Pilsbry & Cockerell, 1945, from the Tertiary of southern USA; ANSP 16660, holotype (width = 57 mm). **J.** Apertural view. **K.** Apical view. **L.** Umbilical view.

1991). Whether the North American *Monadenia* spp. would be better allocated to their own family or to a subfamily of Epiphragmophoridae, remains a matter for further investigation. *Monadenia* exhibits substantial anatomical differences from *Epiphragmophora* in its genitalia, especially the dart apparatus; *Epiphragmophora* possesses 2 dissimilar mucous glands while *Monadenia* has only 1 (M.G. Cuezzo, pers. obs.). Shell characters of *Monadenia fidelis* and some *Epiphragmophora* spp. are indeed similar, but this could simply

represent convergence, as observed between other helicoid lineages.

The monophyly of the genus *Epiphragmophora* Doering, 1874, the main component of the Epiphragmophoridae, has been previously demonstrated on the basis of morphological characters in a cladistic analysis (CUEZZO 2006). According to that author, broadly distributed species such as *E. trenquelleonis* (Grateloup, 1851) and *E. trigrammephora* (d'Orbigny, 1835) (Fig. 3G and 3H, respectively) could in fact be species complexes, as suggested by their high morphological variability. Here we provide more evidence that these species are complexes, as members of each belong to different branches in our phylogeny (Figs 1, 2); we intend to study this matter in more detail.

## Paleobiogeography

The fossil record of American "helicoids" is quite sparse. The oldest "Camaenidae" fossil known from the Americas is typically considered to be *Kanabohelix kanabensis* (White, 1876), from the Late Cretaceous of Utah, USA (Point of Rocks Groups, Laramie Formation; WHITE 1876, PILSBRY 1927 in 1927–1935, SOLEM 1978). However, we agree with the assessment of WENZ (1943 in 1938–1944) and BISHOP (1980) that *K. kanabensis* actually belongs in Helicinidae (Neritimorpha). As such, there is no fossil Sagdoidea or Helicoidea known from the final Mesozoic of the Americas, even though this is thought to be the original distribution of the group and is the estimated time of their divergence (SEI et al. 2017). The basal position of the Mexican *Bunnya metli* (Figs 1, 2) is a further indication of the origin of the entire Sagdoidea + Helicoidea complex in the Americas. Further fossil records are discussed under their respective sections below.

**Sagdoidea.** The oldest record, *Hodopoeus crassus* Pilsbry & Cockerell, 1945, dates from the Paleocene/Eocene of the southern USA (New Mexico or Texas, locality uncertain). It was originally classified in Camaenidae (ZILCH 1960 in 1959–1960, SOLEM 1978, MOLLUSCABASE 2018). TRACEY et al. (1993), however, tentatively included it in Solaropsidae, albeit without giving any explanation for their decision. Given the morphological features of the monotypic genus *Hodopoeus* Pilsbry & Cockerell, 1945 (Fig. 3J–L), here we classify it instead in Labyrinthidae (see discussion in the Appendix).

Thus, there is no known fossil Solaropsinae. For Caracolinae, the oldest record dates from the Oligocene White River Group of Nebraska, USA (BISHOP 1979): *Caracolus aquilonaris* Bishop, 1979. The oldest Zachrysiidae fossil, *Zachrysia fraterna* Roth, 1988 dates from the Eocene of southern California (Friars Formation; ROTH 1988). The other 3 subfamilies in Sagdidae, however, have no known fossils other than Quaternary material (e.g., GOODFRIEND 1986). Note that all Sagdoidea fossils have been assigned to extant genera (as have

most of the fossil Helicoidea discussed here, see below).

SEI et al. (2017) calculated the times of the major splits of sagdoid and helicoid clades, using different models and input from the fossil record; however, they were confronted by an incomplete set of fossils, sometimes with unreliable identification and/or dating. Nevertheless, those authors' divergence dates are within reasonable limits compared to fossil evidence, such as their proposed late Paleocene to late early Eocene date of the split between Sagdidae and Solaropsidae, which is compatible with the dating of *Caracolus aquilonaris* and *Zachrysia fraterna*.

**Helicoidea.** Exploring the full breadth of helicoid biogeography is outside the scope of the present article; those discussions can be found elsewhere (e.g., SCOTT 1997, RAZKIN et al. 2015). However, the fact that Sagdoidea and the basal branch of Helicoidea are North American in origin has some implications for Helicoidea biogeography. Thus, we offer below a few new insights into the American helicoids based on our molecular tree and information from the fossil record.

The most basal branch of Helicoidea (Fig. 1) in our phylogeny is formed by the 2 American families Cepolidae and Labyrinthidae. As noted above, the oldest record of the latter is *Hodopoeus crassus* from the Paleocene/Eocene of southern USA. Nevertheless, given the uncertainties regarding that fossil's age, the second option is *Labyrinthus obtusus* (Anderson & Hanna, 1925) from the Eocene Tejon Formation in California (ROTH 1988). Fossil *Cepolis* spp. are known from the late Oligocene of Florida (Arcadia Formation, Tampa Member; DALL 1890 in 1890–1903). Given the basal position of the Labyrinthidae–Cepolidae clade and the purported Cretaceous split between Sagdoidea and Helicoidea (see above), it is very likely this Labyrinthidae–Cepolidae clade was around since a date prior to the Eocene. This clade became locally extinct north of Mexico, dispersing to, and surviving in, Central and South America (PILSBRY & COCKERELL 1945).

The oldest known (but putative) record of presumably non-Labyrinthidae helicoid snails in South America is *Helix* sp. from the Miocene Pebas Formation in the Brazilian Amazon (MAGALHÃES & MEZZALIRA 1953). The assignment to this genus is obviously incorrect and was used to indicate a general helicoid form, which, given the present knowledge, could belong to either Helicoidea or Sagdoidea. The original material of MAGALHÃES & MEZZALIRA (1953) could not be found (SALVADOR et al. 2018), and their work seems to be the only mention of such fossils in the literature, which is unusual for this otherwise well-studied formation (e.g., WESSELINGH et al. 2002, 2006, WESSELINGH 2006 for studies on non-Brazilian outcrops of the Pebas Formation). Thus, this record must be treated with caution.

Other than that, fossil Epiphragmophoridae (*Epiphragmophora* spp.) are known from the late Miocene of northern Argentina (SALVADOR et al. 2018), which is

an indication that by that time the family had already reached a similar range as is presently known for living representatives.

## Systematic Conclusions

Solaropsidae Nordsieck, 1986 belongs within superfamily Sagdoidea Pilsbry, 1895 and contains the subfamilies Solaropsinae Nordsieck, 1986 and Caracolinae Cuezzo, 2003. It is the sister family of a group formed by Zachrysiidae Robinson, Sei & Rosenberg, 2017 and Sagdidae Pilsbry, 1895; the latter contains subfamilies Platysuccineinae H.B. Baker, 1940, Polydontinae Schileyko, 2006, and Sagdinae Pilsbry, 1895. The genera *Psadara* K. Miller, 1878 and *Olympus* Simone, 2010 are considered synonymous with *Solaropsis* H. Beck, 1837. The fossil genus *Hodopoeus* Pilsbry & Cockerell, 1945 is excluded from Solaropsidae. Finally, Epiphragmophoridae Hoffmann, 1928 is considered a family-level taxon instead of a subfamily within Xanthonychidae Strebel & Pfeffer, 1879 (Helicoidea).

## Acknowledgements

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# Appendix

**Family Labyrinthidae**

**Genus *Hodopoeus* Pilsbry & Cockerell, 1945**

*Hodopoeus crassus* **Pilsbry & Cockerell, 1945**

**Holotype.** ANSP 16660 (Fig. 3J–L), from the collection of the Academy of Natural Sciences of Drexel University (Philadelphia, USA).

**Type locality.** Southern USA: New Mexico or Texas (locality uncertain).

**Discussion.** The only known fossil of this species is an internal cast (Fig. 3J–L). However, it displays conchological features that still allow its classification within the American "helicoids". Even though some features, like the helicoid shell, large prosocline aperture tilted abapically, and the indication of a keel on the body whorl, are consistent with most American lineages of "helicoids" (Sagdidae, Solaropsidae, Labyrinthidae, and Epiphragmophoridae), it is most similar to either the labyrinthid genus *Isomeria* Albers, 1850 or the solaropsid genus *Solaropsis* Beck, 1837. When all characters are taken together, the classification favors Labyrinthidae given that the fossil (Fig. 3J–L) shares almost all features with *Isomeria* (as noted by SOLEM 1978): centrally to adapically positioned keel on body whorl; presence of a narrow umbilicus; flattened spire with whorls gradually increasing in size; body whorl close to aperture flared; contraction of body whorl immediately behind the peristome; large, strongly prosocline aperture tilted abapically; high and round whorls; large size (>5 cm).

There is no real indication, however, of apertural dentition, which is a feature of *Isomeria* and labyrinthids in general. SOLEM (1978) interpreted the apparent indentation on the palatal region of the aperture as the mark of a tooth, but it might be simply an accident

of preservation. Also regarding preservation problems, there is an apparent constriction in the mid-section of the body whorl, which might be caused by erosion; however, this feature is characteristic of some species of *Solaropsis*, such as *S. johnsoni* Pilsbry, 1933, *S. rosaria* (L. Pfeiffer, 1849), and *S. undata* (Lightfoot, 1786), so

this might still prove itself a meaningful character when more fossils are found.

Despite the features shared with *Isomeria*, we retain *Hodopoeus* Pilsbry & Cockerell, 1945 as a separate genus, diagnosable by its large size, strongly tilted aperture, and apparent lack of apertural barriers.