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SHORT COMMUNICATION

PUNCTOIDEA, DISCOIDEA OR LIMACOIDEI? TAXONOMIC POSITION OF THE GENUS *HIRASEA* PILSBRY, 1902 ENDEMIC TO THE OCEANIC OGASAWARA ISLANDS, WITH A PRELIMINARY NOTE ON ITS RELATIONSHIP WITH JAPANESE MAINLAND TAXA

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ABSTRACT: The Ogasawara Islands are oceanic islands in the Pacific Ocean, known for evolutionary radiations, especially in land snails and plants. The endemic genus *Hirasea* has been assigned to several different taxa. Some malacologists classified this genus within Limacoidei, while others placed it within either Punctoidea or Discoidea. In this study, the phylogenetic position of *Hirasea* was investigated using a nuclear 28S rRNA marker. Our results demonstrate that species of *Hirasea* belong to Limacoidei, rather than Punctoidea or Discoidea.

KEY WORDS: molecular phylogeny; the Ogasawara Islands

The Ogasawara Islands, also known as the Bonin Islands, are oceanic islands where evolutionary radiations of organisms, particularly in land snails and plants, have occurred (e.g., ITO 1998, CHIBA 1999). The group consists of approximately 30 islands and forms part of the Izu-Bonin-Mariana arc system in the northwest Pacific Ocean. The Ogasawara Islands are located approximately 1,000 km south of Honshu Island, approximately 650 km south of the oceanic Izu Islands, approximately 750 km north of the Mariana Islands, and approximately 4,000 km west of the Hawaiian Islands. The land snail fauna of these islands is particularly diverse, with over 110 recorded indigenous species, exhibiting an exceptionally high level of endemism (more than 90%) (CHIBA 2009a). The genus *Hirasea* Pilsbry, 1902 is endemic to the Ogasawara Islands and exhibits remarkable diversification in shell morphology among species (CHIBA 2009b). This genus was originally described as a member of Zonitidae Mörch, 1864 within Zonitoidea Mörch, 1864, but has subsequently been assigned to multiple taxonomic groups. Some malacologists have classified *Hirasea* within Limacoidei, specifically under Trochomorphidae Möllendorff, 1890 and Euconulidae Baker, 1928 of Trochomorphoidea Mörch, 1864 (e.g., KURODA 1930, UESHIMA & KUROZUMI 1988), as well as Helicarionidae Bourguignat, 1877 of Helicarionoidea Bourguignat, 1877 (HIRANO et al. 2018). Others have placed it within Punctoidea Morse, 1864, assigning it to Endodontidae Pilsbry, 1895 or Charopidae Hutton, 1884 (e.g., HABE 1969, MOLLUSCABASE 2021). Still others have classified it within Discidae Thiele, 1931 of Discoidea Thiele, 1931 (e.g., KURODA 1958). To date, molecular phylogenetic approaches have been applied to this genus in two studies. HIRANO et al. (2018) focused on the phylogenetic relationships within *Hirasea* and used taxa classified within Helicarionidae as an out-

group. COLGAN & STANISIC (2023) primarily included Punctoidea in their analysis and failed to identify any taxon closely related with *Hirasea*. Therefore, the taxonomic position of *Hirasea* remains unresolved. In this study, we conducted a phylogenetic analysis of the genus using a broad range of stylommatophoran land snail species to clarify its taxonomic position.

Specimens of *Hirasea* (Figs 1–2) were collected on the Ogasawara Islands under permits issued by the Agency for Cultural Affairs and the South Kanto branch, Ministry of the Environment. Additionally, specimens from ten genera belonging to Trochomorphoidea were collected from the Japanese mainland (Table 1). The specimens examined in this study were identified based on the taxonomic descriptions provided in the literature including AZUMA (1982), IIJIMA (2018) and NISHI & NISHI (2018). The specimens used in this study were pre-

Figs 1–2. Living animal and shell morphology of *Hirasea*: 1 – *Hirasea operculina*; 2 – *Hirasea diplomphalus* (photographed on 14 March 2009 at Anijima Island, Tokyo, Japan)

served in 99.5% ethanol and deposited in the collection of Tohoku University (Table 1). Genomic DNA was isolated from a piece of foot using DNeasy Blood and Tissue kits (Qiagen, CA, USA) according to the manufacturer's instructions. Partial fragments (about 1,000 bp) of the large subunit 28S rRNA gene were amplified and sequenced using the universal primers 28SC1 and 28SD3 (Vonnemann et al. 2005). The condition used for the polymerase chain reaction (PCR) was as follows: 94 °C for 3 min, (94 °C for 30 s, 50 °C for 30 s and 72 °C for 1.25 min) × 35, and 72 °C for 5 min. The PCR products were purified using Exo-SAP-IT (Amersham Biosciences, Little Chalfont, Buckinghamshire, UK). Sequencing was performed using an ABI 3130xl sequencer (Applied Biosystems, Carlsbad, CA, USA). The resulting 28S sequences have been deposited in the DDBJ/EMBL/GenBank database (Table 1). In addition to these newly obtained sequences, sequence data from Wade et al. (2001), which analysed a wide range of stylommatophoran species, were obtained from GenBank and included in our phylogenetic analyses (Appendix 1).

DNA sequences were aligned with MUSCLE v3.8 (Edgar 2004). To eliminate any uncertainty in the 28S, trimAl 1.2 with automated option (Capella-Gutiérrez et al. 2009) was used to exclude ambiguous alignment regions. Phylogenetic trees were constructed for the 28S dataset (375 bp) using maximum likelihood (ML) and Bayesian inference (BI) methods. Prior to the ML and BI analyses, ModelFinder (Kalyaanamoorthy et al. 2017) was used to select the appropriate models for sequence evolution. As a result, the following models were selected: GTR+F+R4 in the ML analysis; GTR+G in the BI analysis. ML analysis was performed with IQ-TREE (v. 1.6.12) using the option of a perturbation strength of 0.7 (Nguyen et al. 2015, Chernomor et al. 2016). For the ML analyses, we assessed nodal support by performing ultrafast bootstrap analyses with 10,000 replications (Hoang et al. 2018). BI analysis was performed using MrBayes (v. 3.1.2) with two simultaneous runs (Ronquist & Huelsenbeck 2003). Each run consisted of four simultaneous chains for 20 million generations and sampling of trees every 1,000 generations. We confirmed the convergence of runs and sufficient effective sample sizes using Tracer (v. 1.6; Rambaut et al. 2013). Then we discarded the first 2,000 trees as burn-in and used the remaining samples to estimate tree topology, branch length, and substitution parameters.

The phylogenetic analyses using ML and BI methods yielded phylogenetic trees with nearly identical topology. Only well-supported clades (ultrafast bootstrap support values ≥ 95% or posterior probabilities ≥ 0.95) are considered hereafter. Our phylogenetic analyses showed that species of *Hirasea* belong to Limacoidei, rather than to Punctoidea or Discoidea (Fig. 3). *Hirasea* was placed in Clade A together with Euconulidae and Chronidae Thiele, 1931, whereas Trochomorphidae was not included in this clade (Fig. 3). However, our analyses did not support the monophyly of either Euconulidae or Chronidae. This result is consistent with the findings of Pholyotha et al. (2023), who focused on Euconulidae in Thailand. Therefore, a taxonomic revision of both Euconulidae and Chronidae is needed to determine the family to which *Hirasea* belongs. Our analyses included only a few species from Punctoidea and Discoidea, and did not include Geotrochidae Schileyko, 2002 and Staffordiidae Thiele, 1931 of Trochomorphoidea. Since Staffordiidae is restricted to the Dafla Hills at the foot of the Eastern Himalayas and remains a poorly understood family (Hausdorf 2000), we are unable to discuss this family in detail in this study. The monophyly of each of Punctoidea, Discoidea, and the

Table 1. Limacoidei species newly sequenced in this study

Species	Locality	Specimen ID	28S
Hirasea			
Hirasea chichijimana Pilsbry, 1902	Anijima Island, Tokyo, Japan	TUMC-KC190001	LC871374
Hirasea operculina (Gould, 1859)	Anijima Island, Tokyo, Japan	TUMC-KC190005	LC871375
Chronidae			
Ceratochlamys ceratodes (Gude, 1900)	Kochi, Kochi, Japan	TUMC-KC190124	LC871373
Gastrodontella stenogyra (Adams, 1868)	Sendai, Miyagi, Japan	TUMC-KC105545	LC871379
Japanochlamys cerasina (Pilsbry, 1902)	Sendai, Miyagi, Japan	TUMC-KC106844	LC871381
Nipponochlamys hakusanus (Pilsbry et Hirase, 1907)	Toyone, Aichi, Japan	TUMC-KC105487	LC871378
Parakaliella harimensis (Pilsbry, 1901)	Tanabe, Wakayama, Japan	TUMC-KC190011	LC871376
Takemasaia eikoae (Azuma, 1983)	Okinawa Island, Okinawa, Japan	TUMC-KC105650	LC871380
Trochochlamys crenulata (Gude, 1900)	Toyone, Aichi, Japan	TUMC-KC105463	LC871377
Yamatochlamys circumdata (Pilsbry, 1902)	Kanuma, Tochigi, Japan	TUMC-KC106906	LC871382
Euconulidae			
Coneuplecta sp.	Sendai, Miyagi, Japan	TUMC-KC107065	LC871383
Parasitala reinhardti (Pilsbry, 1900)	Shizuoka, Shizuoka, Japan	TUMC-KC190009	LC871384

individual families within Trochomorphoidea – except for Euconulidae, Chronidae, and Staffordiidae – has been strongly supported by molecular analyses (SALVADOR et al. 2020, PHOLYOTHA et al. 2023). Therefore, the inclusion of additional species from these taxa is unlikely to affect the conclusions drawn in the present study.

Our analyses also revealed a taxon closely related with *Hirasea* on the Japanese mainland. The ancestors of certain indigenous land snails of the Ogasawara Islands are thought to have been derived from the Japanese mainland (e.g., CHIBA 1999), and this could be the case for the focal genus. However, dispersal from the Oceanian Islands has also contributed to the development of the land snail fauna on the Ogasawara Islands (e.g., GOULDING et al. 2023). Therefore, further analyses using additional specimens from both the Japanese mainland and the Oceanian Islands are needed to infer the route by which the ancestors of *Hirasea* reached the Ogasawara Islands.

This study provided preliminary insights into the molecular phylogenetic relationships of Trochomorphoidea in Japan, although approximately half of Japanese genera of this superfamily remain to be examined in future studies. For example, HORSÁKOVÁ et al. (2020) suggested that the Holarctic genus *Euconulus* Reinhardt, 1883 could have a close relationship with *Parakaliella* Habe, 1946

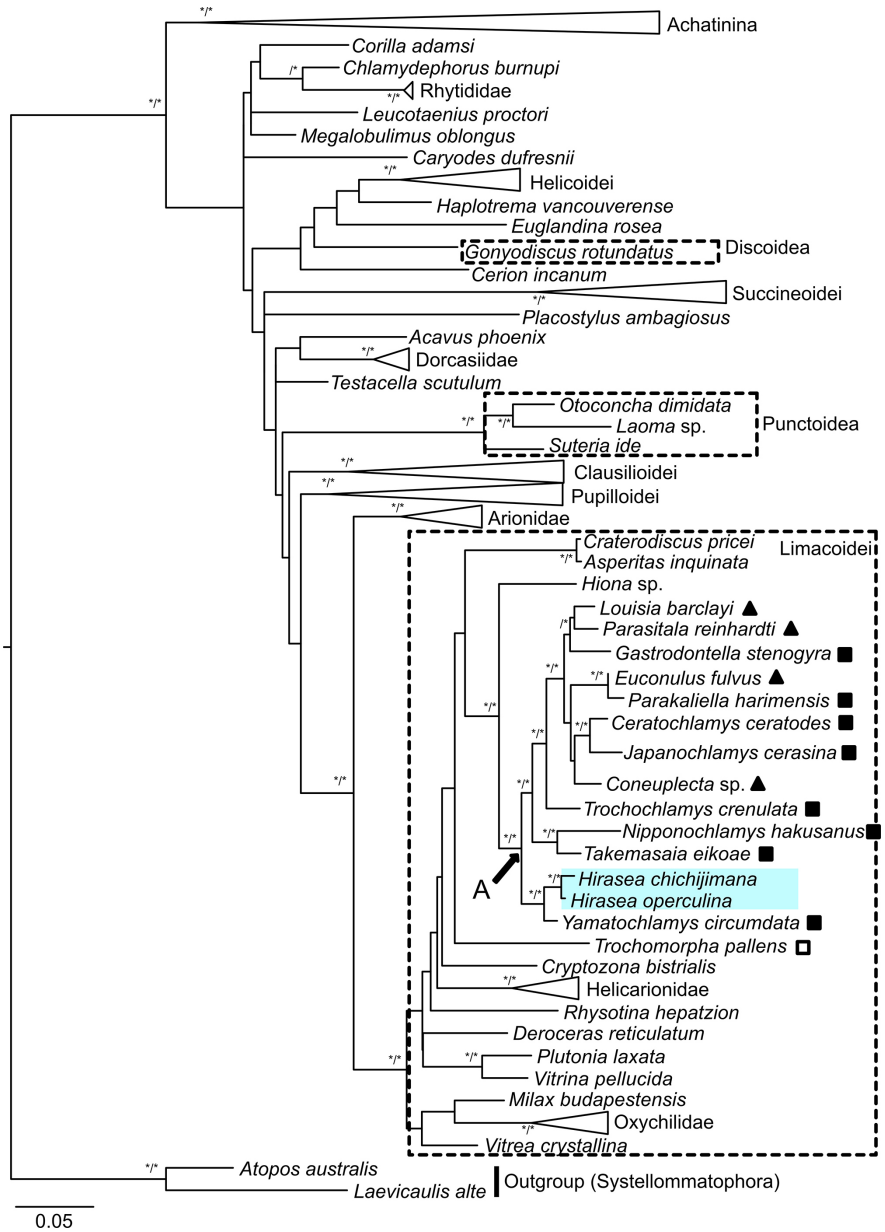

Fig. 3. Maximum likelihood tree of stylommatophoran land snails based on the 28S rRNA gene. Asterisks on branches indicate high ultrafast bootstrap values (≥ 95%, left) and Bayesian posterior probabilities (≥ 0.95, right). The shaded box highlights species of *Hirasea*. Filled triangles, filled squares, and open square represent Euconulidae, Chronidae, and Trochomorphidae, respectively. Clade A represents a well-supported clade comprising *Hirasea*, Euconulidae, and Chronidae

based on similarities in shell morphology, and this hypothesis was supported by our findings (Fig. 3).

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APPENDIX 1.

List of species and corresponding sequence data obtained from WADE et al. (2001)

Family	Species	Location	28S
Acavidae	*Acavus phoenix* (Pfeiffer, 1854)	Kitugula, Sri Lanka	AY014083
	Leucotaenius proctori (Sowerby, 1894)	Beheloa, Madagascar	AY014085
Achatinidae	*Achatina fulica* Bowdich, 1822	Unknown (Zool. Soc. Lond, colln)	AY014069
	Archachatina marginata (Swainson, 1821)	Nigeria (NHM collection)	AY014071
	Bocageia sp.	Sao Thomé	AY014062
	Glessula ceylanica (Pfeiffer, 1845)	Colombo, Sri Lanka	AY014064
	Limicolaria sp.	Somalia (NHM collection)	AY014072
	Rumina decollata (Linnaeus, 1758)	Sicily	AY014065
	Xerocerastus sp.	Otjiwarongo, Namibia	AY014067
	Zootecus insularis (Ehrenberg, 1831)	Dubai, United Arab Emirates	AY014068
Amastridae	*Leptachatina lepida* Cooke, 1910	Hawaii Island, Hawaii	AY014022
Arionidae	*Arion ater* (Linnaeus, 1758)	Kirk Ireton, Derbyshire, UK	AY014144
	Arion hortensis (Férussac, 1819)	Kirkdale, Derbyshire, UK	AY014143
	Geomalacus maculosus (Allman, 1843)	Unknown	AY014145
Ariophantidae	*Cryptozona bistrialis* (Beck, 1837)	Sri Lanka	AY014107
Athoracophoridae	*Athoracophorus bitentaculatus* (Quoy et Gaimard, 1832)	Mere Mere, New Zealand	AY014018
Bothriembryontidae	*Placostylus ambagiosus* Suter, 1906	Manaaki Whenua, New Zealand	AY014059
Buliminidae	*Buliminus labrosus* (Olivier, 1804)	Saladin's Castle, Syria	AY014034
	Macaronapaeus vulgaris (Morelet et Dronet, 1857)	San Miguel, Azores	AY014037
	Mastus pupa (Linnaeus, 1758)	Sicily	AY014039
	Pene sidonensis (Férussac, 1821)	Saladin's Castle, Syria	AY014035
Camaenidae	*Aegista vulgivaga* (Schumacher et Boettger, 1890)	Osaka City, Japan	AY014139
	Bradybaena similaris (Férussac, 1821)	Sri Lanka	AY014138
	Euhadra amaliae (Kobelt, 1875)	Osaka City, Japan	AY014140
	Euhadra sandai (Pilsbry, 1928)	Osaka City, Japan	AY014141
	Polydontes undulata (Férussac, 1821)	Dominican Republic	AY014121
	Satsuma japonica (Pfeiffer, 1847)	Osaka City, Japan	AY014122
Caryodidae	*Caryodes dufresnii* Leach, 1815	Mt Wellington, Hobart, Tasmania	AY014086
Cerastidae	*Cerastus schweinfurthii* (Martens, 1895)	Al-Mahuit, N. Yemen	AY014040
	Pachnodus silhouettanus Van Mol et Coppois, 1980	Silhouette Island, Seychelles	AY014041
Cerionidae	*Cerion incanum* (Binney, 1851)	Florida Keys, USA	AY014060
Charopidae	*Suteria ide* (Gray, 1850)	Waitomo, New Zealand	AY014095
Chlamydephoridae	*Chlamydephorus burnupi* (Smith, 1892)	Pevensey, Natal	AY014089
Chondrinidae	*Chondrina avenacea* (Bruguière, 1792)	Verdon Gorge, France	AY014032
	Chondrina clienta (Westerlund, 1883)	Villach, Austria	AY014031
	Solatopupa similis (Bruguière, 1792)	Verdon Gorge, France	AY014033
Clausiliidae	*Albinaria xantostoma* (Boettger, 1883)	Crete	AY014048
	Clausilia bidentata (Strøm, 1765)	Kirkdale, Derbyshire, UK	AY014051
	Cochlodina laminata (Montagu, 1803)	South Downs, East Sussex, UK	AY014047
	Macrogastra rolphii (Turton, 1826)	South Downs, East Sussex, UK	AY014052
	Mundiphaedusa decapitata (Pilsbry, 1902)	Osaka City, Japan	AY014055
	Papillifera papillaris (Müller, 1774)	Sicily	AY014050
	Stereophaedusa japonica (Crosse, 1871)	Yamaguchi City, Japan	AY014053
Cochlicopidae	*Cochlicopa lubricella* (Porro, 1838)	San Miguel, Azores	AY014020
	Cochlicopa lubrica (Müller, 1774)	Box Hill, Dorking, UK	AY014019
Cocliaxidae	*Pyrgina umbilicata* Greeff, 1882	Sao Thomé	AY014073

Family	Species	Location	28S
Corillidae	*Corilla adamsi* Gude, 1914	Sri Lanka	AY014092
Discidae	*Gonyodiscus rotundatus* (Müller, 1774)	Kirkdale, Derbyshire, UK	AY014097
Dorcasiidae	*Trigonephrus globulus* (Müller, 1774)	Natal, South Africa	AY014081
	Dorcasia alexandri Gray, 1938	Windhoek, Namibia	AY014079
Dyakiidae	*Asperitas inquinata* (Müller, 1774)	Java	AY014108
Euconulidae	*Euconulus fulvus* (Müller, 1774)	Kirkdale, Derbyshire, UK	AY014098
	Louisia barclayi (Benson, 1850)	Mauritius	AY014102
Haplotrematidae	*Haplotrema vancouverense* (Lea, 1839)	Eugene, Oregon	AY014090
Helicarionidae	*Fastosarion brazieri* (Cox, 1864)	Royal National Park, NSW	AY014099
	Harmogenanina argentea (Reeve, 1852)	Reunion	AY014101
	Plegma caelatura (Férussac, 1821)	Reunion	AY014103
Helicellidae	*Cernuella virgata* (Da Costa, 1778)	Porthcurnick, Cornwall, UK	AY014127
	Cochlicella acuta (Müller, 1774)	Porthcurnick, Cornwall, UK	AY014126
Helicidae	*Arianta arbustorum* (L., 1758)	Deepdale, Derbyshire, UK	AY014136
	Cantareus apertus (Born, 1778)	Sicily	AY014129
	Cantareus aspersa (Müller, 1774)	Kettering, Northants, UK	AY014128
	Cepaea hortensis (Müller, 1774)	Marlborough Downs, Wiltshire, UK	AY014131
	Cepaea nemoralis (L., 1758)	Marlborough Downs, Wiltshire, UK	AY014130
	Helicigona lapicida (L., 1758)	Deepdale, Derbyshire, UK	AY014137
	Marmorana scabriuscula (Deshayes, 1830)	Sicily	AY014133
	Theba pisana (Müller, 1774)	Sicily	AY014135
Helminthoglyptidae	*Monadenia fidelis* (Gray, 1834)	Oregon	AY014142
Hygromiidae	*Craterodiscus pricei* McMichael, 1959	Ravenshoe, NE Qld, Australia	AY014123
	Trichia hispida (Linnaeus, 1758)	Deepdale, Derbyshire, UK	AY014125
	Trichia striolata (Pfeiffer, 1828)	Deepdale, Derbyshire, UK	AY014124
Limacidae	*Deroceras reticulatum* (Müller, 1774)	Kirkdale, Derbyshire, UK	AY014119
Megalobulimidae	*Megalobulimus oblongus* (Müller, 1774)	Antigua (Zool. Soc. Lond. colln)	AY014078
Microcystidae	*Hiona* sp.	Moorea	AY014105
Milacidae	*Milax budapestensis* (Hazay, 1881)	Kirkdale, Derbyshire, UK	AY014117
Orculidae	*Orcula austriaca* Zimmerman, 1932	Kuhberg, Austria	AY014028
Otoconchidae	*Otoconcha dimidiata* Pfeiffer, 1853)	Waitakere New Zealand	AY014096
Partulidae	*Eua zebrina* (Gould, 1848)	Samoa	AY014046
	Partula suturalis Pfeiffer, 1855	Moorea	AY014042
	Samoana conica (Gould, 1848)	Samoa	AY014045
Polygyridae	*Vespericola columbiana* (Lea, 1838)	Eugene, Oregon, USA	AY014120
Punctidae	*Laoma* sp.	Mannacau Harbour, New Zealand	AY014093
Pupillidae	*Lauria cylindracea* (da Costa, 1778)	Mullaghmore, Co. Sligo, Ireland	AY014023
	Lauria fasciolata (Morelet, 1860)	San Miguel, Azores	AY014024
Pyramidulidae	*Pyramidula rupestris* (Draparnaud, 1801)	Mullaghmore, Co. Sligo, Ireland	AY014030
Rathouisiidae	*Atopos australis* (Heynemann, 1876)	Malanda, Queensland, Australia	AY014152
Rhytididae	*Rhytida stephenensis* Powell, 1930	Manaaki Whenua, New Zealand	AY014087
	Schizoglossa sp.	Kaikarangi, New Zealand	AY014088
Spiraxidae	*Euglandina rosea* (Férussac, 1821)	Moorea (Zool. Soc. Lond, colln)	AY014074

Family	Species	Location	28S
Streptaxidae	*Gonaxis quadrilateralis* Preston, 1910	Reunion	AY014076
	Gonospira sp.	Mauritius	AY014077
Subulinidae	*Subulina striatella* (Rang, 1831)	Kew Gardens, UK (introduced)	AY014061
Succincidae	*Succinea putris* (Linnaeus, 1758)	Southampton, UK	AY014057
Testacellidae	*Testacella scutulum* Sowerby, 1821	North London, UK	AY014075
Trochomorphidae	*Trochomorpha pallens* Pease, 1870	Faatoai Valley, Moorea	AY014110
Urocyclidae	*Rhysotina hepatizon* (Gould, 1848)	Sao Thomé	AY014100
Valloniidae	*Vallonia costata* (Müller, 1774)	San Miguel, Azores	AY014025
	Vallonia excentrica Sterki, 1892	San Miguel, Azores	AY014026
Veronicellidae	*Laevicaulis alte* (Férussac, 1823)	Dubai, United Arab Emirates	AY014151
Vertiginidae	*Vertigo antivergo* (Draparnaud, 1801)	Chuett. Arnoldstein, Austria	AY014027
Vitreidae	*Vitrea crystallina* (Müller, 1774)	New Forest, Hampshire, UK	AY014113
Vitrinidae	*Plutonia laxata* (Morelet, 1860)	San Miguel, Azores	AY014112
	Vitrina pellucida (Müller, 1774)	Kirkdale, Derbyshire, UK	AY014111
Zonitidae	*Oxychilus alliarius* (Müller, 1822)	Deepdale, Derbyshire, UK	AY014114
	Oxychilus cellarius (Müller, 1774)	Co. Kerry, Ireland	AY014116
	Oxychilus helveticus (Blum, 1881)	Kirkdale, Derbyshire, UK	AY014115