

Annotated Checklist of the Terrestrial Gastropods of Nepal

Prem B. Budha^{1,4}, Fred Naggs², Thierry Backeljau^{3,4}

1 Tribhuvan University, Kirtipur, Kathmandu, Nepal **2** Natural History Museum, Cromwell Road, London, SW7 5BD, UK **3** Royal Belgian Institute of Natural Sciences, Vautierstraat 29, B-1000, Brussels, Belgium **4** University of Antwerp, Evolutionary Ecology Group, Groenenborgerlaan 171, B-2020, Antwerp, Belgium

Corresponding author: Prem B. Budha (pbbudha@cdztu.edu.np; prembudha@yahoo.com)

Academic editor: M. Schilthuizen | Received 26 December 2014 | Accepted 10 March 2015 | Published 30 March 2015

<http://zoobank.org/79C9A851-D8B3-4024-B5F1-C3EC84C6095E>

Citation: Budha PB, Naggs F, Backeljau T (2015) Annotated Checklist of the Terrestrial Gastropods of Nepal. ZooKeys 492: 1–48. doi: 10.3897/zookeys.492.9175

Abstract

This is the very first checklist of the terrestrial gastropods of Nepal. It includes 138 species and six subspecies, of which 22 species are endemic and four are introduced. It highlights 34 species recorded for the first time in Nepal and provides new distribution records for another 30 species.

Keywords

Gastropoda, checklist, endemic, Nepal

Introduction

The rich diversity of non-marine molluscs of the Indian subcontinent was explored by pioneering 19th century British malacologists. However, as foreigners were restricted from entering Nepal until 1951, the Nepalese malacofauna remained poorly known. *Pupa eurina* Benson, 1864 (now *Pupilla eurina*) may have been the first land snail recorded from Nepal (Budha 2005), but its type locality of ‘Tribeni Ghat’ has not been identified. The earliest confirmed records of terrestrial gastropods from Nepal were an unidentified *Nanina* species and *Anadenus* sp. [?= *A. giganteus* Heynemann] from Kathmandu Valley (Nevill 1878: p. 27 and 65 respectively). No publications on Nepa-

lese snails appeared for the following 95 years until the description of two new species and two new subspecies of *Hemiphaedusa* by Nordsieck (1973) and a chromosomal study on some ariophantids (Kiauta and Butot 1973). Subsequently, Schileyko and Frank (1994) described a new species (*Laevozebrinus nepalensis*), a new genus (*Nepaliena*) and a new enid subfamily (Pseudonapaeinae) from hills surrounding Kathmandu Valley. In addition, they described the reproductive anatomy of *Oxytesta orobia* (Benson, 1848). Since then, several occasional papers on the Nepalese terrestrial gastropods have been published (Kuznetsov 1996, Kuznetsov and Schileyko 1997, 1999, Schileyko and Kuznetsov 1998a, 1998b, Raut 1999, Schileyko 1999, Wiktor 2001a, Subba and Ghosh 2001, 2008, Wiktor and Bössneck 2004, Budha 2005, Kuzminykh and Schileyko 2005, Bössneck 2006, Budha and Naggs 2008, Gerber and Bössneck 2009, Budha et al. 2012, Schileyko and Balashov 2012, Khanal and Budha 2013). Despite the fact that the study of Nepalese terrestrial gastropods is still in its infancy, there is a need for at least a provisional checklist as a starting point for further study. The present paper aims at providing such a list.

The data included here are based on published records and field investigations from 2006–2010 by Prem Budha. Collected material has been deposited in the Central Department Zoology Museum of Tribhuvan University (CDZMTU), Kirtipur, Kathmandu, Nepal. The list provides taxonomic notes where needed, as well as distribution ranges of genera and species. The original names of the type species of genera and subgenera are provided. An attempt was made to standardize the use of geographical place names and local features but, owing to the nature of this data, it was not always possible to do so. The district name is mentioned for all species from Nepal with particular locations such as hill, forest, and village names wherever data are available. National park or conservation areas are given without district names because most national parks extend across more than one district. Particular locations within national parks are given where known. Indian states are given with particular location(s) wherever data are available. The systematic arrangement at family and more inclusive levels is based on Bouchet and Rocroi (2005). Family names are arranged according to Bouchet and Rocroi (2005), while genus and species names are arranged alphabetically. The list includes 138 species and six subspecies, including 22 endemic species, four introduced species, 34 new species for Nepal, and new distribution records for 30 species.

Systematics

Class: Gastropoda Cuvier, 1795

Clade: Caenogastropoda Cox, 1960

Superfamily: Cyclophoroidea J.E. Gray, 1847

Family: Cyclophoridae J.E. Gray, 1847

Subfamily: Cyclophorinae J.E. Gray, 1847

Genus: *Cyclophorus* Montfort, 1810¹

Distribution: Subtropical and tropical Asia (Gude 1921, Benthem Jutting 1948, Zilch 1956, Kongim et al. 2006).

Type species: *Helix volvulus* O.F. Müller, 1774

Subgenus: *Glossostylus* Kobelt & Möllendorff, 1897

Distribution: India; Sri Lanka; Myanmar; Thailand; Vietnam; Taiwan; Malaysia; Philippines (Gude 1921).

Type species: *Cyclostoma validum* Sowerby, 1842

Cyclophorus (*Glossostylus*) *fulguratus* (L. Pfeiffer, 1852)²

Distribution: Myanmar; Thailand; Vietnam (Gude 1921).

Nepal: Ilam, Jhapa, Morang, Sunsari, Dharan, Udayapur and Gulmi Districts (Subba and Ghosh 2001).

Subgenus: *Kobeltostylus* Egorov, 2006³

Distribution: Bangladesh; India; Sri Lanka; Myanmar; Philippines (Gude 1921).

Type species: *Helix involvulus* O.F. Müller, 1774

Cyclophorus (*Kobeltostylus*) *pyrotrema* Benson, 1854

Distribution: Bangladesh; India; Myanmar (Gude 1921).

Nepal: Lalitpur District-Phulchowki Hill (Kuznetsov and Schileyko 1997).

Subgenus: *Annularia* Schumacher, 1817⁴

Distribution: India; Sri Lanka; Myanmar; Philippines (Gude 1921).

Type species: *Annularia aurantiaca* Schumacher, 1817

Cyclophorus (*Annularia*) *aurantiacus* (Schumacher, 1817)⁵

Distribution: Thailand; Myanmar; W Malaysia (Nevill 1878, Gude 1921).

Nepal: Ilam, Morang, Sunsari, Dharan and Udayapur Districts (Subba and Ghosh 2001).

Genus: *Theobaldius* Nevill, 1878

Distribution: Sri Lanka; S and NE India; Myanmar (Gude 1921).

Type species: *Cyclophorus annulatus* L. Pfeiffer, 1847

Theobaldius sp.

New species record for Nepal: Shivapuri-Nagarjun and Langtang National Parks.

Genus: *Scabрина* W.T. Blanford, 1863⁶

Distribution: S and SE Asia (Gude 1921, Maassen 2006).

Type species: *Cyclophorus calyx* Benson, 1847.

Scabrina phaenotopicus (Benson, 1851)

Distribution: India: W Bengal-Darjeeling, Sikkim (Gude 1921).

Nepal: Raheem et al. (2010).

New distribution records from Nepal: Chitwan National Park, Tanahu District-Shiddha Cave area and Lalitpur District-Phulchowki Hill.

Genus: *Pterocyclos* Benson, 1832

Distribution: India; Sri Lanka; SE Asia (Raheem and Naggs 2006, Ramakrishna et al. 2010, Kongim et al. 2013).

Type species: *Pterocyclos rupestris* Benson, 1832

Pterocyclos cf. *brahmakundensis* Godwin-Austen, 1915

Distribution: India: Assam-Brahmakund (Gude 1921).

New species record for Nepal: Langtang National Park.

Subfamily: Alycaeinae W.T. Blanford, 1864⁷Genus: *Alycaeus* J.E. Gray, 1850

Distribution: India; Nepal; Myanmar; China; Japan; Taiwan; Korea; Thailand; Vietnam; Laos; Philippines; Indonesia; Malaysia; Australia (Gude 1921, Tarruella and Domènech 2011).

Type species: *Alycaeus eydouxi* Venmans, 1956⁸

Subgenus: *Alycaeus* J.E. Gray, 1850

Distribution: India; Myanmar; China; Malaysia; Japan (Gude 1921).

Type species: *Alycaeus eydouxi* Venmans, 1956

Alycaeus (Alycaeus) burti Godwin-Austen, 1874

Distribution: India: Arunachal Pradesh, Assam, Mizoram-Akha Hills, Dihiri Parbat; Bhutan (Gude 1921, Ramakrishna et al. 2010).

Nepal: Solukhumbu District (Kuznetsov and Schileyko 1997).

New distribution records from Nepal: Kathmandu District-Champadevi Hill, Lalitpur District-Phulchowki Hill and Shivapuri-Nagarjun National Park.

Alycaeus (Alycaeus) lohitisensis Godwin-Austen, 1914

Distribution: India: Assam, Arunachal Pradesh (Gude 1921, Ramakrishna et al. 2010).

Nepal: Lalitpur District-Phulchowki Hill (Kuznetsov 1996).

Alycaeus (Alycaeus) yamneyensis Godwin-Austen, 1914

Distribution: India: Arunachal Pradesh-Yamne Valley, Abor Hills (Gude 1921).

Nepal: Tarruella and Domènech (2011).

Genus: *Chamalycaeus* Kobelt & Möllendorff, 1897

Distribution: India; Nepal; Myanmar; China; Taiwan; Korea; Thailand; Vietnam; Laos; Philippines; Indonesia; Malaysia; Australia (Gude 1921, Tarruella and Domènech 2011).

Type species: *Alycaeus andamaniae* Benson, 1861

Subgenus: *Dicharax* Kobelt & Möllendorff, 1900

Distribution: NE India; Myanmar; China; Malaysia (Gude 1921).

Type species: *Alycaeus hebes* Benson, 1857

Chamalycaeus (Dicharax) bicrenatus (Godwin-Austen, 1874)

Distribution: NE India: Assam, Nagaland-Naga Hill (Ramakrishna et al. 2010).

Nepal: Lalitpur District-Phulchowki Hill (Kuznetsov 1996).

Chamalycaeus (Dicharax) digitatus (H.F. Blanford, 1871)

Distribution: NE India: W Bengal-Darjeeling, Sikkim-Richila Peak; W Bhutan (Gude 1921).

New species record for Nepal: Kathmandu District-Champadevi Hill, Lalitpur District-Phulchowki Hill, Shivapuri-Nagarjun National Park.

Chamalycaeus (Dicharax) inflatus (Godwin-Austen, 1874)

Distribution: NE India: Nagaland-Naga Hills (Ramakrishna et al. 2010).

Nepal: Shivapuri-Nagarjun National Park-Nagarjun Forest (Khanal and Budha 2013).

Chamalycaeus (Dicharax) notatus (Godwin-Austen, 1876)

Distribution: NE India: Nagaland-Naga Hills, Arunachal Pradesh-Dafla Hills (Gude 1921).

Nepal: Solukhumbu District (Kuznetsov and Schileyko 1997).

Chamalycaeus (Dicharax) plectochilus (Benson, 1859)

Distribution: NE India: W Bengal-Darjeeling, Sikkim-Damsang Peak; W Bhutan (Gude, 1921).

New species records for Nepal: Kathmandu District-Champadevi Hill, Shivapuri-Nagarjun and Langtang National Parks.

Chamalycaeus (Dicharax) strangulatus (L. Pfeiffer, 1846)⁹

Distribution: This is the only species of *Chamalycaeus (Dicharax)* recorded from the W Himalaya, NW India: Himachal Pradesh-Simla, Uttarakhand-Kumaon, Nainital (Ramakrishna et al. 2010).

New species record for Nepal: Shivapuri-Nagarjun National Park.

Chamalycaeus (Dicharax) styliifer (Benson, 1857)

Distribution: NE India: W Bengal-Darjeeling and Sikkim; Bhutan (Gude 1921).
New species records for Nepal: Lalitpur District-Phulchowki Hill, Shivapuri-Nagarjun and Langtang National Parks.

Subgenus: *Cyclorhynchus* Godwin-Austen, 1914

Distribution: NE India to Myanmar (Gude 1921).

Type species: *Alycaeus constrictus* Benson, 1851

Chamalycaeus (Cyclorhynchus) otiphorus (Benson, 1858)

Distribution: NE India: W Bengal-Darjeeling, Sikkim-Pankhabari, Meghalaya, Nagaland (Gude 1921, Ramakrishna et al. 2010).

Nepal: Lalitpur District-Phulchowki Hill (Kuznetsov 1996).

New distribution record from Nepal: Shivapuri-Nagarjun National Park.

Chamalycaeus (Cyclorhynchus) summus (Godwin-Austen, 1914)

Distribution: NE India: Sikkim-Richila Peak; W Bhutan (Gude 1921).

Nepal: Solukhumbu District (Kuznetsov and Schileyko 1997).

Family: Diplommatinidae L. Pfeiffer, 1856

Subfamily: Diplommatininae L. Pfeiffer, 1856

Genus: *Diplommatina* Benson, 1849¹⁰

Distribution: India; Nepal; China; Indonesia; Vietnam; Singapore; Malaysia; Japan; Philippines; Taiwan; Papua New Guinea; Fiji (Gude 1921, Zilch 1953, Schileyko and Kuznetsov 1997, Maassen 2002, Panha and Burch 2005, Webster et al. 2012).

Type species: *Bulimus folliculus* L. Pfeiffer, 1846

Subgenus: *Diplommatina* Benson, 1849

Distribution: N India; Nepal; China; Malaysia; Philippines; Japan; Taiwan; Papua New Guinea; Fiji (Gude 1921, Zilch 1953, Schileyko and Kuznetsov 1997, Panha and Burch 2005, Webster et al. 2012).

Type species: *Bulimus folliculus* L. Pfeiffer, 1846

Diplommatina (Diplommatina) exserta Godwin-Austen, 1886

Distribution: Myanmar: Damotha Cave, etc., Moulmein, now Mawlamyine (Gude 1921).

New species record for Nepal: Tanahu District-Siddha Cave area.

Diplommatina (Diplommatina) folliculus (L. Pfeiffer, 1846)

Distribution: NW India: Himachal Pradesh-Landour, Simla, Uttarakhand-Nainital (Naggs 1997, Ramakrishna et al. 2010).

New species records for Nepal: Lalitpur District-Phulchowki Hill, Shivapuri-Nagarjun and Langtang National Parks.

Diplommatina (Diplommatina) munipurensis Godwin-Austen, 1892

Distribution: NE India: Manipur; Myanmar (Gude 1921).

New species records for Nepal: Lalitpur District-Phulchowki Hill, Langtang National Park.

Diplommatina (Diplommatina) oviformis Fulton, 1901

Distribution: India: W Bengal-Darjeeling (Gude 1921).

Nepal: Solukhumbu District (Kuznetsov and Schileyko 1997).

New distribution records from Nepal: Hills surrounding Lalitpur and Kathmandu Districts, Shivapuri-Nagarjun and Langtang National Parks.

Diplommatina (Diplommatina) pachychilus Benson, 1857

Distribution: NE India: W Bengal-Darjeeling (Gude 1921).

Nepal: Solukhumbu District (Kuznetsov and Schileyko 1997).

New distribution records from Nepal: Shivapuri-Nagarjun and Langtang National Parks.

Diplommatina (Diplommatina) regularis Fulton, 1901.

Distribution: NE India: W Bengal-Darjeeling (Ramakrishna et al. 2010).

New species record for Nepal: Shivapuri-Nagarjun National Park-Baghdwar.

Diplommatina (Diplommatina) silvicola Godwin-Austen, 1886

Distribution: NE India: Assam-North Cachar, Jenta Hajuma Peak (Gude 1921, Ramakrishna et al. 2010).

New species record for Nepal: Shivapuri-Nagarjun National Park-Balaju, Pani Tanki.

Diplommatina (Diplommatina) sperata W.T. Blanford, 1862

Distribution: Myanmar (Gude 1921).

Nepal: Solukhumbu District (Kuznetsov and Schileyko 1997).

Subgenus: *Metadiancta* Möllendorff, 1898

Distribution: NE India: Assam, Manipur, Nagaland; Myanmar; Vietnam (Gude 1921).

Type species: *Diplommatina dohertyi* Godwin-Austen, 1892

Diplommatina (Metadiancta) miriensis Godwin-Austen, 1917

Distribution: NE India: Arunachal Pradesh-Miri Hills (Gude 1921).

New species records for Nepal: Shivapuri-Nagarjun and Langtang National Parks.

Subgenus: *Sinica* Möllendorff, 1885

Distribution: India; Nepal; Myanmar; China; Japan; Philippines; Indonesia; Malaysia; Papua New Guinea; Taiwan (Gude 1921, Zilch 1953, Kuznetsov and Schileyko 1997).

Type species: *Diplommatina collarifera* Schmacker and Boettger, 1877

Diplommatina (Sinica) canarica Beddome, 1875¹¹

Distribution: India: Western Ghats, Karnataka, Maharashtra (Ramakrishna et al. 2010, Raheem et al. 2014).

Nepal: Solukhumbu District (Kuznetsov and Schileyko 1997).

Family: Pupinidae L. Pfeiffer, 1853

Subfamily: Pupininae L. Pfeiffer, 1853

Genus: *Schistoloma* Kobelt, 1902

Distribution: Indian Himalaya; Nepal; China; Thailand; W Malaysia; Sumatra; Borneo; Philippines (Gude 1921, Bartsch 1915, Tumpeesuwan and Panha 2008).

Type species: *Cyclostoma altum* Sowerby, 1842

Schistoloma cf. funiculalum (Benson, 1838)¹²

Distribution: India: W Bengal-Darjeeling (Gude 1921).

New species records for Nepal: Lalitpur District-Phulchowki Hill, Shivapuri-Nagarjun and Langtang National Parks.

Superfamily: Ellobioidea L. Pfeiffer, 1854 (1822)

Family: Ellobiidae L. Pfeiffer, 1854 (1822)

Subfamily: Carychiinae Jeffreys, 1830

Genus: *Carychium* O.F. Müller, 1773

Distribution: Very widely distributed from N and C America, Europe to S and SE Asia (Burch and Panha 2002, Thompson 2011).

Type species: *Carychium minimum* O.F. Müller, 1774

Carychium minusculum Gredler, 1888¹³

Distribution: China "aus Hope" (Gredler 1888).

Nepal: Langtang National Park-Syabru (Kuznetsov and Schileyko 1997), Kavre District-Chandeshwari (Nesemann et al. 2007).

Carychium sp.¹⁴

New species records for Nepal: Lalitpur District-Phulchowki Hill, Shivapuri-Nagarjun and Langtang National Parks.

Clade: Systellommatophora Pilsbry, 1948

Superfamily: Veronicelloidea J.E. Gray, 1840

Family: Veronicellidae J.E. Gray, 1840

Genus: *Laevicaulis* Simroth, 1913

Distribution: Pantropical (Stanisic 1998).

Type species: *Vaginulus alte* Férussac, 1822

Laevicaulis alte (Férussac, 1822)¹⁵

Distribution: The geographical origin of *L. alte* is uncertain, but it has been widely distributed in tropical and subtropical countries through human agency (Stanisic 1998). New distribution records from Nepal: Widely distributed throughout most districts of Tarai and inner Tarai.

Clade: Stylommatophora Schmidt, 1855

Superfamily: Succineoidea H. Beck, 1837

Family: Succineidae H. Beck, 1837

Subfamily: Catinellinae Odhner, 1950

Genus: *Quickia* Odhner, 1950

Distribution: W and E Africa; Mascarene Islands; Seychelles; Aldabra; India; Nepal (Patterson 1975, Schileyko 2007).

Type species: *Succinea concisa* Morelet, 1848

Quickia sp.

New species record for Nepal: Chitwan District-Sauraha (collected from flower vase at hotel).

Subfamily: Succeineinae H. Beck, 1837

Genus: *Succinea* Draparnaud, 1801

Distribution: Nearly circumglobal (Schileyko 2007), the Northern Hemisphere; Australia; some Pacific islands (Thompson 2011).

Type species: *Succinea amphibia* Draparnaud, 1801 (= *Helix putris* Linnaeus, 1758)

Succinea sp.

New species records for Nepal: Kathmandu and Lalitpur Districts.

Superfamily: Pupilloidea Turton, 1831

Family: Pupillidae Turton, 1831

Subfamily: Pupillinae Turton, 1831

Genus: *Pupilla* Fleming, 1828

Distribution: Temperate N America; Europe; Africa; Asia; Australia (Gude 1914, Pokryszko et al. 2009).

Type Species: *Pupa marginata* Draparnaud, 1801(= *Turbo muscorum* Linnaeus, 1758).

Pupilla annandalei Pilsbry, 1921¹⁶

Distribution: Pakistan.

Nepal: Pokryszko et al. (2009).

Pupilla eurina (Benson, 1864)¹⁷

Distribution: Endemic to Nepal.

Nepal: Tribeni Ghat (Blanford and Godwin-Austen 1908), Annapurna Conservation Area-Tukuche (Kuznetsov and Schileyko 1997).

New distribution record from Nepal: Langtang National Park-Gosainkund.

Pupilla triplicata (Studer, 1820)

Distribution: Europe and C Asia (Sysoev and Schileyko 2009).

Nepal: Annapurna Conservation Area-Tukuche (Kuznetsov and Schileyko 1997).

Family: Pyramidulidae Kennard & Woodward, 1914

Genus: *Pyramidula* Fitzinger, 1833

Distribution: Holarctic and S Asia (Gittenberger and Bank 1996, Schileyko and Balashov 2012).

Type species: *Helix rupestris* Draparnaud, 1801

Pyramidula humilis (Hutton, 1838)¹⁸

Distribution: NW India: Himachal Pradesh, Punjab, Uttarakhand (Ramakrishna et al. 2010)

Nepal: Shivapuri-Nagarjun National Park-Nagarjun Forest (Khanal and Budha 2013).

Pyramidula kuznetsovi Schileyko & Balashov, 2012¹⁹

Distribution: Endemic to Nepal.

Nepal: Mustang District-Muktinath (Schileyko and Balashov 2012).

Family: Valloniidae Morse, 1864

Genus: *Vallonia* Risso, 1826

Distribution: Holarctic (Gerber and Bössneck 2009).

Type species: *Vallonia rosalia* Risso, 1826 (= *Helix pulchella* O.F. Müller, 1774)

Vallonia costohimala Gerber & Bössneck, 2009

Distribution: Endemic to Nepal.

Nepal: Northern districts from Darchula to Panchthar (Gerber and Bössneck 2009).

Vallonia himalaevi Gerber & Bössneck, 2009

Distribution: Endemic to Nepal.

Nepal: Northern districts from Darchula to Panchthar (Gerber and Bössneck 2009).

Vallonia kathrinae Gerber & Bössneck, 2009

Distribution: Endemic to Nepal.

Nepal: Mugu and Mustang Districts (Gerber and Bössneck 2009).

Vallonia ladacensis (Nevill, 1878)

Distribution: India: Western Ghats, Jammu and Kashmir; Nepal; Tibet; Tianshan Turkey (Gerber and Bössneck 2009, Raheem et al. 2014).

Nepal: Bajura, Darchula, Humla and Mustang Districts (Gerber and Bössneck 2009).

Vallonia tenuilabris (A. Braun, 1843)

Distribution: Kazakhstan; Tajikistan; NW India: Jammu and Kashmir; Tibet; Siberia; N China; Mongolia to Russia (Gerber and Bössneck 2009).

Nepal: Solukhumbu and Taplejung Districts (Gerber and Bössneck 2009).

Family: Vertiginidae Fitzinger, 1833

Subfamily: Vertigininae Fitzinger, 1833

Genus: *Truncatellina* Lowe, 1852

Distribution: Holarctic (Schileyko 1998).

Type species: *Pupa linearis* Lowe, 1852

Truncatellina sp.

Nepal: Annapurna Conservation Area-Khobang (Kuznetsov and Schileyko 1997).

Subfamily: Gastrocoptinae Pilsbry, 1918

Genus: *Gastrocopta* Wollaston, 1878

Distribution: Almost cosmopolitan extending to all tropical and warm temperate continents but extinct in Europe (Pilsbry 1916–1918).

Type species: *Pupa acarus* Benson, 1856

Gastrocopta huttoniana (Benson, 1849)

Distribution: India: Western Ghats, Himachal Pradesh, Kashmir, Maharashtra (Ramakrishna et al. 2010, Raheem et al. 2014).

Nepal: Annapurna Conservation Area (Kuznetsov and Schileyko 1997).

Superfamily: Enoidea Woodward, 1903

Family: Enidae Woodward, 1903

Subfamily: Pseudonapaeinae Schileyko, 1978

Genus: *Pupinidius* Möllendorff, 1901

Distribution: W China; Nepal (Schileyko 1998, Wu and Zheng 2009).

Type species: *Buliminus pupinidius* Möllendorff, 1901

Pupinidius himalayanus Kuznetsov & Schileyko, 1999

Distribution: Endemic to Nepal.

Nepal: Mustang District, Tukuiche to Muktinath trekking route (Kuznetsov and Schileyko 1999).

Pupinidius siniayevi Kuznetsov & Schileyko, 1999

Distribution: Endemic to Nepal.

Nepal: Mustang District-Tukuche to Muktinath trekking route (Kuznetsov and Schileyko 1999).

Pupinidius tukuchensis Kuznetsov & Schileyko, 1997

Distribution: Endemic to Nepal.

Nepal: Mustang District-Tukuche (Kuznetsov and Schileyko 1997).

Genus: *Laevozebrinus* Lindholm, 1925

Distribution: Afghanistan; Iran; mountain regions of C Asia; N Pakistan and adjacent territories of India (Schileyko 1998).

Type species: *Buliminus urgutensis* Kobelt, 1902

Laevozebrinus mustangensis Kuznetsov & Schileyko, 1997

Distribution: Endemic to Nepal.

Nepal: Mustang District-Tukuche to Muktinath trekking route (Kuznetsov and Schileyko 1997).

Laevozebrinus nepalensis Schileyko & Frank, 1994

Distribution: Endemic to Nepal.

Nepal: Annapurna Conservation Area and hills surrounding Kathmandu District (Schileyko and Frank 1994).

Subspecies: *nepalensis* Schileyko & Frank, 1994

Distribution: Mustang District-Khobang, Tukuche, Marpha, Jomsom (Kuznetsov and Schileyko 1997).

Subspecies: *myagdiensis* Kuznetsov & Schileyko, 1997

Distribution: Myagdi District-Sukebagar, Titre, Dana (Kuznetsov and Schileyko 1997).

Genus: *Mirus* Albers, 1850

Distribution: India; Sri Lanka; Myanmar; E Asia; Japan (Kuznetsov and Schileyko 1997, Schileyko 1998, Raheem and Naggs 2006).

Type species: *Bulimus cantorii* Philippi, 1844²⁰

Mirus (?) *nilagiricus* (L. Pfeiffer, 1846)²¹

Distribution: India: Western Ghats, Tamil Nadu-Nilgiris, Arunachal Pradesh-Dafla Hill, Meghalaya-Khasi Hills; Myanmar (Gude 1914, Ramakrishna et al. 2010, Raheem et al. 2014).

Nepal: Solukhumbu District-Khari Khola (Kuznetsov and Schileyko 1997).

Genus: *Nepaliena* Schileyko & Frank, 1994

Distribution: Endemic to Nepal (Kuznetsov and Schileyko 1997).

Type species: *Bulimus ceratinus* Benson, 1849

Nepaliena ceratina (Benson, 1849)

Distribution: Endemic to Nepal.

Nepal: Kathmandu and Myagdi Districts, Annapurna Conservation Area (Schileyko and Frank 1994, Kuznetsov and Schileyko 1997).

Genus: *Subzebrinus* Westerlund, 1887

Distribution: SE Kazakhstan and adjacent territories of China; India; Japan; Nepal (Gude 1914, Schileyko 1998, Raheem et al. 2010).

Type species: *Buliminus labiellus* Martens, 1881

Subzebrinus rufistrigatus (Reeve, 1849)

Distribution: India: Kashmir between Jamuna and Sutlej River, Jhelum Valley (Gude 1914)

New species record for Nepal: Mugu District-Rogumba.

Family: Cerastidae Wenz, 1923

Genus: *Darwininitium* Budha & Mordan, 2012²²

Distribution: Endemic to Nepal.

Type species: *Darwininitium shiwalikianum* Budha & Mordan, 2012

Darwininitium shiwalikianum Budha & Mordan, 2012

Distribution: Endemic to Nepal.

Nepal: Shiwalik range of C Nepal, Chitwan National Park and Makwanpur District-Taubas, Bhaise (Budha et al. 2012).

Superfamily: Clausilioidea J.E. Gray, 1855

Family: Clausiliidae J.E. Gray, 1855

Subfamily: Phaedusinae A.J. Wagner, 1922

Genus: *Cylindrophaedusa* O. Boettger, 1877²³

Distribution: Pakistan; India; Nepal; Bhutan; Myanmar (Nordsieck 2002).

Type species: *Clausilia cylindrica* L. Pfeiffer, 1846

Subgenus: *Cylindrophaedusa* O. Boettger, 1877

Distribution: India: Punjab, W Bengal (Nordsieck 1973, 2002).

Type species: *Clausilia cylindrica* L. Pfeiffer, 1846

Cylindrophaedusa (*Cylindrophaedusa*) *cylindrica* (L. Pfeiffer, 1846)

Distribution: India: Punjab-Muree, W Bengal-Darjeeling (Nordsieck 1973, 2002).
New species record for Nepal: Dadeldhura District.

Subgenus: *Montiphaedusa* Nordsieck, 2002

Distribution: N Pakistan; Nepal; NE India; Bhutan; Myanmar (Nordsieck 2002).
Type species: *Clausilia ioes* Benson, 1852

Cylindrophaedusa (*Montiphaedusa*) *ioes* (Benson, 1852)

Distribution: N Pakistan; Nepal; NE India; Bhutan; Myanmar (Nordsieck 2002).

Subspecies: *jiriensis* (Nordsieck, 1973)

Distribution: Endemic to Nepal.
Nepal: Dolakha District-Jiri (Nordsieck 1973).

Cylindrophaedusa (*Montiphaedusa*) *kathmandica* (Nordsieck, 1973)

Distribution: Endemic to Nepal.
Nepal: Hills surrounding Kathmandu Valley (Nordsieck 1973).
New distribution records from Nepal: Lalitpur District-Phulchowki Hill, Shivapuri-Nagarjun and Langtang National Parks.

Cylindrophaedusa (*Montiphaedusa*) *martensiana* (Nordsieck, 1973)

Distribution: Endemic to Nepal.
Nepal: Lamjung, Myagdi and Mustang Districts (Nordsieck 1973).

Subspecies: *martensiana* (Nordsieck, 1973)

Distribution: Myagdi and Mustang Districts-Dhorpatan, Thakkhola, Lete, Gorepani (Nordsieck 1973).

Subspecies: *dhaulagirica* (Nordsieck, 1973)

Distribution: Lamjung District-Jaljala, Myagdi Khola, Muri (Nordsieck 1973).

Superfamily: Achatinoidea Swainson, 1840

Family: Achatinidae Swainson, 1840

Genus: *Lissachatina* Bequaert, 1950²⁴

Distribution: Originally from E Africa but now globally distributed in tropical to warm temperate areas, i.e. W Africa; N and S America; S and SE Asia; China; Japan; Caribbean countries; Oceania (Tillier et al. 1993, Raut and Barker 2002, EPPO 2013).

Type species: *Achatina fulica* Bowdich, 1822

Lissachatina fulica (Bowdich, 1822)

Distribution: See distribution of *Lissachatina*.

Nepal: Probably introduced into Nepal in the 1930s–40s (Raut 1999). It is now established as a pest in all districts of Tarai and the inner valleys causing significant damage to crops. It has spread into the mid hill districts: Kaski, Baglung, Makwanpur, Chitwan, Myagdi, Tanahun, Dhading, Palpa, Gulmi, Syangjha (Budha and Naggs 2008).

New distribution records from Nepal: Dang, Surkhet, Banke, Bardia, Kailali and Kanchanpur Districts.

Family: Ferussaciidae Bourguignat, 1883

Genus: *Ceciloides* Férussac, 1814²⁵

Distribution: Europe; Africa; S Asia; Philippines; Oceania; American tropics (Thompson 2011).

Type species: *Buccinum acicula* O.F. Müller, 1774

Ceciloides cf. *minuta* Mousson, 1874²⁶

Distribution: Drift debris of the Euphrates (type locality), Sarus River near Adana, SE Asia Minor (Pilsbry and Tryon 1908–1909).

New species record for Nepal: Baitadi District, Far W Nepal.

Family: Subulinidae P. Fischer & Crosse, 1877

Subfamily: Subulininae P. Fischer and Crosse, 1877²⁷

Genus: *Allopeas* H.B. Baker, 1935²⁸

Distribution: Tropical, subtropical, and many temperate regions of Africa, S and SE Asia (Schileyko 1999, Thompson 2011).

Type species: *Bulimus gracilis* Hutton, 1834 (= *Allopeas gracile* (Hutton, 1834))

Allopeas clavulinum (Potiez & Michaud, 1838)²⁹

Distribution: Bourbon Island (type locality), other islands of the Indian Ocean; Japan (Pilsbry 1946).

New species records for Nepal: Kathmandu, Kaski and Kailali Districts.

Allopeas gracile (Hutton, 1834)

Distribution: Tropics of both hemispheres, abundant in cultivated districts, perhaps the most widely ranging of all land snails (Pilsbry 1946).

New species records for Nepal: Chitwan and Dhading Districts.

Genus: *Curvella* Chapar, 1885

Distribution: S Africa; India; China; SE Asia (Gude 1914, Schileyko 1999).

Type species: *Curvella sulcata* Chapar, 1885

Curvella sikkimensis Gude, 1914

Distribution: India: W Bengal-Darjeeling, Sikkim (Gude 1914).

New species record for Nepal: Ilam District-Maipokhari.

Genus: *Paropeas* Pilsbry, 1906

Distribution: Widespread in the tropical Indo-Pacific regions (Naggs 1994).

Type species: *Bulimus acutissimum* Mousson, 1857

Paropeas achatinaceum (L.Pfeiffer, 1846)

Distribution: Widespread in disturbed habitats in tropical Indo-Pacific regions (Naggs 1994).

Nepal: Shivapuri-Nagarjun National Park-Nagarjun Forest (Khanal and Budha 2013).

New distribution record from Nepal: Ramechhap District.

Subfamily: Opeatinae Thiele, 1931

Genus: *Opeas* Albers, 1850³⁰

Distribution: Worldwide in tropical, subtropical and many temperate regions (Schileyko 1999, Thompson 2011).

Type species: *Helix goodallii* Miller, 1822

Opeas sp.

Nepal: Morang District (Subba and Ghosh 2008).

Subfamily: Glessulinae Godwin-Austen, 1920³¹Genus: *Bacillum* Theobald, 1870³²

Distribution: NE India: W Bengal-Darjeeling, Sikkim, Assam-North Cachar, Meghalaya-Khasi Hill, Nagaland-Naga Hills (Gude 1914, Ramakrishna et al. 2010).

Type species: *Achatina cassiaca* Reeve, 1849

Bacillum sp.³³

Nepal: Ilam and Panchthar District (Subba and Ghosh 2008).

Genus: *Glessula* Martens, 1860

Distribution: India; Sri Lanka; Thailand; Malaysia; Vietnam (Gude 1914, Godwin-Austen 1920, Schileyko 2011).

Nepal: Kathmandu District (Kuznetsov 1996, Schileyko and Kuznetsov 1996).

Type species: *Achatina ceylanica* L. Pfeiffer, 1845³⁴

Glessula orobia (Benson, 1860)

Distribution: India: W Bengal-Darjeeling (Gude 1914, Ramakrishna et al. 2010).

New species record for Nepal: Ilam District-Maipokhari.

Glessula subjerdoni Beddome, 1906³⁵

Distribution: S India: Western Ghats, Andhra Pradesh-Golconda Hill, Orissa-Jaypore (Gude 1914, Ramakrishna et al. 2010, Raheem et al. 2014).

Nepal: Kathmandu District-Nagarjun Forest (Kuznetsov 1996).

Genus: *Rishetia* Godwin-Austen, 1920

Distribution: India; Sri Lanka; Nepal; Myanmar; W Bhutan (Godwin-Austen 1920)³⁶.

Type species: *Glessula (Rishetia) longispira* Godwin-Austen, 1920

Rishetia hastula (Benson, 1860)

Distribution: India: W Bengal-Darjeeling (Gude 1914, Godwin-Austen 1920).

New species record for Nepal: Chitwan National Park.

Rishetia tenuispira (Benson, 1836)³⁷

Distribution: India: Western Ghats, W Bengal, Sikkim, Mizoram, Arunachal Pradesh, Maharastra; Myanmar; Bangladesh (Pilsbry and Tryon 1908-1909, Gude 1914, Ramakrishna et al. 2010, Raheem et al. 2014).

Nepal: Shivapuri-Nagarjun National Park-Nagarjun Forest, Balaju (Schileyko and Kuznetsov 1996).

New distribution record from Nepal: Lalitpur District-Phulchowki Hill.

Superfamily: Streptaxoidea J.E. Gray, 1860

Family: Streptaxidae J.E. Gray, 1860

Genus: *Gulella* L. Pfeiffer, 1856

Distribution: Africa; Indo-Pacific (Bruggen 2006, Cole and Herbert 2009, Herbert and Rowson 2011, Rowson et al. 2011).

Type species: *Pupa menkeana* L. Pfeiffer, 1853

Gulella bicolor (Hutton, 1834)³⁸

Distribution: Sri Lanka; throughout India; Myanmar (Blanford and Godwin-Austen 1908); Brazil (Pilsbry 1926, Simone 2013); SE China (Yen 1939); Cuba (Sarasúa 1944, Maceira et al. 2013); Caribbean Islands (Schalie 1948); Philippines; Indonesia (Bentham Jutting 1950); Andaman and Nicobar Islands; Malaysia; Singapore (Bentham Jutting 1961); Kenya (Clench 1964); Venezuela; French Guiana (Tillier 1980); Japan (Azuma 1982); Australia (Stanisic 1981); N America (Dundee and Baerwold 1984); Oman (Mordan 1988); Bel Air area of North Mahé; Seychelles (Naggs 1989); Jamaica (Rosenberg and Muratov 2006); Vietnam (Schileyko 2011).

New species record for Nepal: Chitwan District.

Family: Diapheridae Panha & Naggs, 2010

Subfamily: Enneinae Bourguignat, 1883

Genus: *Sinoennea* Kobelt, 1904

Distribution: Japan; China; Vietnam; Malaysia; Sumatra; India (Gude 1914).

Type species: *Pupa strophioides* Gredler, 1881

Subgenus: *Indoennea* Kobelt, 1904

Distribution: India; Malaysia; Sumatra (Schileyko 2000).

Type species: *Ennea blanfordiana* Godwin-Austen, 1872

Sinoennea (Indoennea) blanfordiana Godwin-Austen, 1872

Distribution: India: Assam-North Cachar (Ramakrishna et al. 2010).

New species record for Nepal: Lalitpur District-Phulchowki Hill.

Subgenus: *Sinoennea* Kobelt, 1904

Distribution: Foothills of Himalaya; S India; China; Malay Peninsula; Sumatra; Japan; S Korea (Schileyko 2000).

Type species: *Pupa strophioides* Gredler, 1881

Sinoennea (Sinoennea) stenopylis (Benson, 1860)

Distribution: NE India: Arunachal Pradesh, Sikkim, Assam, Manipur, Meghalaya, Nagaland (Ramakrishna et al. 2010).

Nepal: Solukhumbu District (Kuznetsov and Schileyko 1997).

Superfamily: Plectopyloidea Möllendorff, 1898

Family: Plectopylidae Möllendorff, 1898

Genus: *Endothyrella* Zilch, 1960³⁹

Distribution: Nepal; NE India: Arunachal Pradesh, Assam, Nagaland, Meghalaya, Manipur, Mizoram, Sikkim (Ramakrishna et al. 2010).

Type species: *Helix plectosoma* Benson, 1836

Endothyrella affinis (Gude, 1897)⁴⁰

Distribution: NE India: Arunachal Pradesh, Assam, Meghalaya-Khasi Hill, Mizoram (Gude 1914, Ramakrishna et al. 2010).

Nepal: Kathmandu District-Swoyambhunath Temple Forest (Kuznetsov and Schileyko 1997).

Endothyrella minor (Godwin-Austen, 1879)

Distribution: India: Manipur, Meghalaya, Nagaland, Sikkim, W Bengal (Gude 1914, Ramakrishna et al. 2010).

New species records for Nepal: Lalitpur District-Phulchowki Hill, Shivapuri-Nagarjun National Park-Chisapani, Baghdwar, Langtang National Park-Golphubhanjyang.

Superfamily: Gastrodontoidea Tryon, 1866

Family: Chronidae Thiele, 1931

Subfamily: Kaliellinae Thiele, 1931

Genus: *Kaliella* W.T. Blanford, 1863

Distribution: Indo-Malayan (Blanford and Godwin-Austen 1908).

Type species: *Helix barrakporensis* L. Pfeiffer, 1853⁴¹

Kaliella barrakporensis (L. Pfeiffer, 1853)

Distribution: India; Sri Lanka; Pakistan; Madagascar; Myanmar; Tropical E Africa and Eastern S Africa (Blanford and Godwin-Austen 1908, Herbert and Kilburn 2004, Verdcourt 2006, Ramakrishna et al. 2010), hot-house alien in Britain (Preece and Naggs 2014).

Nepal: Annapurna Conservation Area (Kuznetsov and Schileyko 1977).

New distribution records from Nepal: Shivapuri-Nagarjun National Park, Lalitpur District-Phulchowki Hill, Kathmandu District-Champadevi Hill, Kirtipur.

Kaliella dikrangensis Godwin-Austen, 1883

Distribution: India: Arunachal Pradesh (Blanford and Godwin-Austen 1908, Ramakrishna et al. 2010).

Nepal: Shivapuri-Nagarjun National Park (Khanal and Budha 2013).

Kaliella fastigiata (Hutton, 1838)

Distribution: India: Himachal Pradesh, Uttarakhand, W Bengal, Arunachal Pradesh, Nagaland; Madagascar; Myanmar (Blanford and Godwin-Austen 1908, Ramakrishna et al. 2010).

Nepal: Kathmandu District-Champadevi Hill (Khanal and Budha 2013).

New distribution record from Nepal: Lalitpur District-Phulchowki Hill.

Kaliella nana (Hutton, 1838)

Distribution: India: Uttarakhand, Himachal Pradesh, W Bengal (Blanford and Godwin-Austen 1908, Ramakrishna et al. 2010).

Nepal: Annapurna Conservation Area (Kuznetsov and Schileyko 1997), Shivapuri-Nagarjun National Park (Khanal and Budha 2013).

New distribution records from Nepal: Lalitpur District-Phulchowki Hill and Kathmandu District-Champadevi Hill.

Kaliella nongsteinensis Godwin-Austen, 1883

Distribution: India: Meghalaya-Khasi Hill (Blanford and Godwin-Austen 1908, Ramakrishna et al. 2010).

Nepal: Solukhumbu District (Kuznetsov and Schileyko 1997).

Family: Euconulidae H.B. Baker, 1928

Subfamily: Euconulinae H.B. Baker, 1928

Genus: *Euconulus* Reinhardt, 1883

Distribution: Holarctic (Roth and Sadeghian 2006).

Type species: *Helix fulva* O.F. Müller, 1774

Euconulus fulvus (O.F. Müller, 1774)⁴²

Distribution: Holarctic (Roth and Sadeghian 2006).

Nepal: Hills surrounding Kathmandu Valley (Kuznetsov and Schileyko 1997).

New distribution records from Nepal: Langtang National Park and Mustang District.

Family: Pristilomatidae Cockerell, 1891

Genus: *Hawaiiia* Gude, 1911⁴³

Distribution: N America from Alaska and Maine to Florida and south to Costa Rica, Cuba, Hispaniola, Jamaica, Puerto Rico, and the Virgin Islands; Europe; Japan; Australia (Kerney and Cameron 1979, Rosenberg and Muratov 2006, Sasaki 2008, Thompson 2011).

Type species: *Helix kawaiensis* Reeve, 1854 (= *Helix minuscula* Binney, 1841)

Hawaiiia sp.

Nepal: Annapurna Conservation Area (Kuznetsov and Schileyko 1997).

Superfamily: Helicarionoidea Bourguignat, 1877

Family: Helicarionidae Bourguignat, 1877

Subfamily: Durgelinae Godwin-Austen, 1888

Genus: *Durgella* W.T. Blanford, 1863

Distribution: India: Arunachal Pradesh, Assam, Andhra Pradesh, Orissa, Meghalaya, Manipur, Sikkim, W Bengal; Myanmar (Blanford and Godwin-Austen 1908, Ramakrishna et al. 2010).

Type species: *Helix levicula* Benson, 1859

Durgella sp.

New species records for Nepal: Chitwan National Park; Kathmandu and Pokhara Districts.

Genus: *Sitala* H. Adams, 1865

Distribution: India; Sri Lanka; Andaman Islands; SE Asia (Schileyko 2002).

Type species: *Helix infula* Benson, 1848

Sitala rimicola (Benson, 1859)

Distribution: India: Uttarakhand, W Bengal, Sikkim, Assam, Meghalaya, Nagaland (Ramakrishna et al. 2010).

Nepal: Mustang District (Kuznetsov and Schileyko 1997).

New distribution records from Nepal: Dadeldhura, Kathmandu, Rasuwa and Mustang Districts.

Genus: *Cryptaustenia* Cockerell, 1891⁴⁴

Distribution: India; Nepal; Bhutan; Myanmar; Thailand (Schileyko 2003).

Type species: *Vitrina planospira* Benson, 1859 (= *Vitrina succinea* Reeve, 1862)

Cryptaustenia cf. *globosa* (Godwin-Austen, 1876)

Distribution: India: Arunachal Pradesh (Ramakrishna et al. 2010).

Nepal: Kathmandu District, Annapurna Conservation Area (Kuznetsov and Schileyko 1997).

Cryptaustenia ovata (H.F. Blanford, 1871)

Distribution: India: W Bengal (Blanford and Godwin-Austen 1908).

Nepal: Kathmandu, Panchthar, Taplejung, Morang and Terhathum Districts (Subba and Ghosh 2008), Annapurna Conservation Area (Kuznetsov and Schileyko 1997). Shivapuri-Nagarjun National Park-Nagarjun Forest (Khanal and Budha 2013).

Genus: *Girasia* J.E. Gray, 1855

Distribution: India: Assam, Arunachal Pradesh, Himachal Pradesh, Meghalaya, Mizoram, Manipur, Nagaland, Sikkim; Myanmar (Blanford and Godwin-Austen 1908, Ramakrishna et al. 2010).

Type species: *Girasia hookeri* J.E. Gray, 1855

Girasia sp.

New species record for Nepal: Langtang National Park.

Family: Ariophantidae Godwin-Austen, 1888

Subfamily: Macrochlamydinae Godwin-Austen, 1888

Genus: *Macrochlamys* Benson in Godwin-Austen, 1883⁴⁵

Distribution: S and SE Asia (Blanford and Godwin-Austen 1908).

Type species: *Macrochlamys indica* Benson in Godwin-Austen, 1883

Macrochlamys indica Benson in Godwin-Austen, 1883

Distribution: India; Andaman Islands; Bangladesh; Sri Lanka (Ramakrishna et al. 2010).

Nepal: Ilam, Sunsari, Dharan, Kathmandu, Lalitpur, Gulmi, Kaski Districts (Subba and Ghosh 2001).

New distribution records from Nepal: Dadeldhura, Baitadi, and Kanchanpur Districts.

Macrochlamys lata Godwin-Austen, 1888

Distribution: India: Meghalaya (Ramakrishna et al. 2010).

Nepal: Annapurna Conservation Area (Kuznetsov and Schileyko 1997).

Macrochlamys longicauda Godwin-Austen, 1883

Distribution: India: Meghalaya (Ramakrishna et al. 2010).

Nepal: Kathmandu District, Annapurna Conservation Area (Kuznetsov and Schileyko 1997).

New distribution records from Nepal: Shivapuri-Nagarjun and Langtang National Parks.

Macrochlamys lubrica (Benson, 1852)

Distribution: India: W Bengal-Darjeeling, Sikkim, Meghalaya (Blanford and Godwin-Austen 1908, Ramakrishna et al. 2010).

Nepal: Mid hills of several districts of E Nepal (Subba and Ghosh 2008).

Macrochlamys nuda (L. Pfeiffer, 1852)

Distribution: NW India: Himachal Pradesh-Simla, Uttarakhand-Kumaon (Blanford and Godwin-Austen 1908).

Nepal: Annapurna Conservation Area (Schileyko and Kuznetsov 1996, 1998b).

Macrochlamys patane (Benson, 1859)

Distribution: NE India: W Bengal-Darjeeling, Sikkim (Blanford and Godwin-Austen 1908).

Nepal: Kathmandu District (Schileyko and Kuznetsov 1996).

Macrochlamys perpaula (Benson, 1859)

Distribution: India: Bihar, Jharkhand, Sikkim, W Bengal-Darjeeling (Ramakrishna et al. 2010).

Nepal: Shivapuri-Nagarjun National Park-Nagarjun Forest (Khanal and Budha 2013).

Macrochlamys sathilaensis Godwin-Austen, 1907

Distribution: NE India: Sikkim-Richila Peak; Bhutan (Blanford and Godwin-Austen 1908).

Nepal: Annapurna Conservation Area, Solukhumbu District (Kuznetsov and Schileyko 1997).

Macrochlamys sequax (Benson, 1859)

Distribution: India: W Bengal-Darjeeling (Blanford and Godwin-Austen 1908).

Nepal: Annapurna Conservation Area (Kuznetsov and Schileyko 1997).

Macrochlamys sequius Godwin-Austen, 1907

Distribution: India: W Bengal-Darjeeling (Blanford and Godwin-Austen 1908).

Nepal: Annapurna Conservation Area (Kuznetsov and Schileyko 1997).

Macrochlamys subjecta (Benson, 1852)

Distribution: India: Jharkhand-Rajmahal Hills, Orrissa-Cuttak (Blanford and Godwin-Austen 1908).

Nepal: Annapurna Conservation Area (Kuznetsov and Schileyko 1997).

New distribution records from Nepal: Widely distributed in W Tarai to the mid hills of C Nepal.

Macrochlamys tugurium (Benson, 1852)⁴⁶

Distribution: India: Manipur, Sikkim, W Bengal-Darjeeling (Ramakrishna et al. 2010).

Nepal: Kathmandu District (Kiauta and Butot 1972).

New distribution record from Nepal: Khaptad National Park.

Genus: *Euaustenia* Cockerell, 1891⁴⁷

Distribution: Afghanistan; Pakistan; NW and NE India: Uttarakhand, Sikkim (Blanford and Godwin-Austen 1908).

Type species: *Vitrina scutella* Benson, 1859 (= *Vitrina monticola* L. Pfeiffer, 1849⁴⁸)

Euaustenia cassida (Hutton, 1838)

Distribution: NW India: Himachal Pradesh, Kashmir, Uttarakhand-Kumaon (Blanford and Godwin-Austen 1908, Ramakrishna et al. 2010).

New species records for Nepal: Baitadi, Darchula, and Dadeldhura Districts.

Euaustenia monticola (L. Pfeiffer, 1849)

Distribution: NW India: Kashmir, Uttarakhand-Nainital (Ramakrishna et al. 2010).

Nepal: Kathmandu District (Schileyko and Frank 1994, Kuznetsov 1996), Annapurna Conservation Area (Kuznetsov and Schileyko 1997).

New distribution records from Nepal: Shivapuri-Nagarjun and Langtang National Parks.

Genus: *Bensonies* H.B. Baker, 1938

Distribution: Afghanistan; Pakistan; India: Uttarakhand, Sikkim (Blanford and Godwin-Austen 1908).

Type species: *Nanina monticola* Hutton, 1838

Bensonies convexa (Reeve, 1852)

Distribution: India: Himachal Pradesh, Uttarakhand (Blanford and Godwin-Austen 1908).

Nepal: Annapurna Conservation Area (Kuznetsov and Schileyko 1997).

New distribution records from Nepal: Lalitpur District-Phulchowki Hill, Kathmandu District- Champadevi Hill, Shivapuri-Nagarjun and Langtang National Parks.

Bensonies jacquemonti (Martens, 1869)

Distribution: Pakistan: Murree; NW India: Himachal Pradesh, Kashmir, Punjab, Uttarakhand (Blanford and Godwin-Austen 1908, Ramakrishna et al. 2010).

New species record for Nepal: Baitadi District.

Bensonies monticola (Hutton, 1838)

Distribution: NW India: Kashmir, Punjab, Uttarakhand (Blanford and Godwin-Austen 1908, Ramakrishna et al. 2010).

New species record for Nepal: Khaptad National Park.

Bensonies nepalensis (W.T. Blanford, 1904)⁴⁹

Distribution: Endemic to Nepal, where it is common in Kathmandu Valley (Blanford 1904, Blanford and Godwin-Austen 1908).

New distribution records from Nepal: Lalitpur, Kavre, Chitwan, Kaski, Gulmi, Syangjha, Parbat, and Myagdi Districts.

Bensonies theobaldiana (Godwin-Austen, 1888)

Distribution: NW India: Himachal Pradesh-Simla, Uttarakhand (Blanford and Godwin-Austen 1908, Ramakrishna et al. 2010).

New species record for Nepal: Khaptad National Park.

Genus: *Himalodiscus* Kuznetsov, 1996

Distribution: Endemic to Nepal.

Nepal: C and W Nepal.

Type species: *Himalodiscus aculeatus* Kuznetsov, 1996

Himalodiscus aculeatus Kuznetsov, 1996⁵⁰

Distribution: Endemic to Nepal.

Nepal: Lalitpur District-Phulchowki Hill (Kuznetsov 1996).

New distribution record from Nepal: Shivapuri-Nagarjun National Park.

Himalodiscus echinatus Schileyko & Kuznetsov, 1998

Distribution: Endemic to Nepal.

Nepal: Annapurna Conservation Area. Only reported from the type locality Lete (Schileyko and Kuznetsov 1998b).

Genus: *Khasiella* Godwin-Austen, 1899

Distribution: E Himalaya from Nepal and India to Myanmar (Blanford and Godwin-Austen 1908).

Type species: *Helix vidua* Hanley & Theobald, 1875⁵¹

Khasiella ornatissima (Benson, 1859)

Distribution: India: W Bengal, Sikkim (Blanford and Godwin-Austen 1908), Uttar Pradesh (Ramakrishna et al. 2010).

Nepal: Lalitpur District-Phulchowki Hill (Kuznetsov 1996).

New distribution records from Nepal: Chitwan National Park, Chitwan and Nawalparasi Districts.

Khasiella pansa (Benson, 1856)⁵²

Distribution: Myanmar: Ayeyarwady Valley, Sullivan Island, Mergui Archipelago (Blanford and Godwin-Austen 1908).

Nepal: Ilam, Jhapa, Morang, Sunsari, Dharan, Saptari, Udayapur, Kaski, Rupandehi and Kailali Districts (Subba and Ghosh 2001, Subba 2003, Surana et al. 2004).

Genus: *Oxytesta* Zilch, 1956

Distribution: E Himalaya from Nepal and NE India to Myanmar and Laos (Blanford and Godwin-Austen 1908).

Type species: *Helix oxytes* Benson, 1836

Oxytesta blanfordi (Theobald, 1859)

Distribution: India: W Bengal-Darjeeling, Sikkim (Blanford and Godwin-Austen 1908, Ramakrishna et al. 2010).

Nepal: Mustang (Kuznetsov and Schileyko 1997, Schileyko and Kuznetsov 1998b).

New distribution records from Nepal: Rasuwa and Parbat Districts.

Oxytesta cyclopax (Benson, 1852)

Distribution: India: Sikkim (Ramakrishna et al. 2010).

Nepal: Solukhumbu District (Kuznetsov and Schileyko 1997).

New distribution record from Nepal: Sankhuwasabha District.

Oxytesta orobia (Benson, 1848)⁵³

Distribution: India: W Bengal-Darjeeling (Ramakrishna et al. 2010).

Nepal: Hills surrounding Kathmandu Valley (Schileyko and Frank 1994, Kuznetsov and Schileyko 1997).

New distribution records from Nepal: Shivapuri-Nagarjun and Langtang National Parks, Sankhuwasabha District.

Oxytesta sylvicola (W.T. Blanford, 1880)

Distribution: NE India: Assam-Burail range, North Cachar, Nagaland (Blanford and Godwin-Austen 1908, Ramakrishna et al. 2010).

Nepal: Ilam, Morang, Dharan, Udayapur, Kaski, Kathmandu, Lalitpur and Terhathum Districts (Subba and Ghosh 2001).

Genus: *Rotungia* Godwin-Austen, 1918

Distribution: India: Arunachal Pradesh-Abor Hill; Myanmar-Upper Rotung (Ramakrishna et al. 2010).

Type species: *Rotungia williamsoni* Godwin-Austen, 1918

Rotungia williamsoni Godwin-Austen, 1918

Distribution: India: Arunachal Pradesh-Abor Hill (Ramakrishna et al. 2010)

Nepal: Taplejung and Terhathum Districts (Subba and Ghosh 2008).

Genus: *Syama* Blanford & Godwin-Austen, 1908

Distribution: India (Blanford and Godwin-Austen 1908).

Type species: *Nanina (Macrochlamys) prona* Nevill, 1878.

Syama prona (Nevill, 1878)

Distribution: NW India: Himachal Pradesh, Uttarakhand (Blanford and Godwin-Austen 1908, Ramakrishna et al. 2010).

Nepal: Shivapuri-Nagarjun National Park-Nagarjun Forest (Khanal and Budha 2013).

Subspecies: *prona* (Nevill, 1878)

Distribution: Annapurna Conservation Area (Kuznetsov and Schileyko 1997, Schileyko and Kuznetsov 1998b).

Genus: *Rasama* Laidlaw, 1932⁵⁴

Distribution: NE India; W Bhutan (Blanford and Godwin-Austen 1908).

Type species: *Macrochlamys kala* Godwin-Austen, 1883

Rasama kala (Godwin-Austen, 1883)

Distribution: India: Sikkim-Damsang Peak, Dalling Hills; W Bhutan (Blanford and Godwin-Austen 1908).

New species record for Nepal: Ilam District-Maipokhari.

Genus: *Taphrospira* W.T. Blanford, 1905

Distribution: India: Assam; Andaman Islands; Myanmar (Blanford and Godwin-Austen 1908).

Type species: *Helix convallata* Benson, 1856

Taphrospira compluvialis (W.T. Blanford, 1865)

Distribution: India: Assam; Andaman Islands; Myanmar (Blanford and Godwin-Austen 1908).

Nepal: Panchthar, Taplejung and Terhathum Districts (Subba and Ghosh 2008).

Taphrospira convallata (Benson, 1856)

Distribution: Myanmar (Blanford and Godwin-Austen 1908).

New species record for Nepal: Shivapuri-Nagarjun National Park.

Superfamily: Limacoidea Lamarck, 1801

Family: Limacidae Lamarck, 1801

Subfamily: Limacinae Lamarck, 1801

Distribution: W Palearctic region (Wiktor and Bössneck 2004).

Genus: *Limax* Linnaeus, 1758

Distribution: Palearctic region (Wiktor and Bössneck 2004).

Type species: *Limax maximus* Linnaeus, 1758

Limax seticus Wiktor & Bössneck, 2004

Distribution: This is the only *Limax* species recorded from the Himalaya (Wiktor and Bössneck 2004).

Nepal: Endemic to Nepal; probably the slug species with the highest elevation range (up to 5000 m) in the world. This species was reported only from Bajura District.

Genus: *Turcomilax* Simroth, 1901

Distribution: India and Nepal (Wiktor et al. 1999, Bössneck 2006).

Type species: *Gigantomilax (Turcomilax) nanus* Simroth, 1901

Subgenus: *Kasperia* Godwin-Austen, 1914⁵⁵

Distribution: India: Kashmir (Godwin-Austen, 1914).

Type species: *Limax (Kasperia) mayae* Godwin-Austen, 1914 (= *Limax turkestanus* Simroth, 1898)

Turcomilax (Kasperia) oli Wiktor, Naggs & Gupta, 1999⁵⁶

Distribution: India: Kumaun Himalaya (Wiktor et al. 1999).

Nepal: Darchula District (Bössneck 2006).

Family: Agriolimacidae Wagner, 1935

Subfamily: Agriolimacinae Wagner, 1935

Genus: *Deroceras* Rafinesque, 1820

Distribution: Holarctic. From Sahara to NE America and S Asia (Wiktor et al. 2000, Thompson 2011).

Type species: *Limax laevis* O.F. Müller, 1774

Deroceras laeve (O.F. Müller, 1774)

Distribution: Holarctic. From Sahara to NE America. It has been introduced worldwide (Wiktor et al. 2000).

Nepal: Kathmandu, Taplejung and Panchthar Districts (Bössneck 2006).

New distribution record from Nepal: Lalitpur District.

Superfamily: Arionoidea J.E. Gray, 1840

Family: Anadenidae Pilsbry, 1948

Genus: *Anadenus* Heynemann, 1863

Distribution: S China; southern slopes of the Himalaya from Pakistan eastward to Sikkim (Wiktor 2001a).

Type species: *Anadenus giganteus* Heynemann, 1863 [Currently replaced by: *Limax altivagus* Theobald, 1862]⁵⁷

Anadenus altivagus (Theobald, 1862)⁵⁸

Distribution: Southern slopes of the Himalaya from Rawalpindi in the west of N Pakistan through Kashmir and Nepal to Sikkim in NE India (Wiktor 2001a).

Nepal: Bajura, Darchula, Humla and Rasuwa Districts (Bössneck 2006).

New distribution records from Nepal: Langtang National Park-Dhunge-Gosainkund-Chisapani trekking route.

Anadenus nepalensis Wiktor, 2001

Distribution: Endemic to Nepal.

Nepal: Hills of Darchula, Dolpa, Humla, Jumla, Lamjung, Kaski, Palpa and Kathmandu Districts (Wiktor 2001a, Bössneck 2006).

Subgenus: *Sagarmathia* Kuzminykh & Schileyko, 2005

Distribution: Endemic to Nepal (Kuzminykh and Schileyko 2005).

Type species: *Anadenus (Sagarmathia) kuznetsovi* Kuzminykh & Schileyko, 2005

Anadenus (Sagarmathia) kuznetsovi Kuzminykh & Schileyko, 2005

Distribution: Endemic to Nepal.

Nepal: Only reported from the type locality, Phuiyan Khola, Solukhumbu District (Kuzminykh and Schileyko 2005).

Family: Philomycidae J.E. Gray, 1847

Genus: *Meghimatium* van Hasselt, 1823

Distribution: Russia; China; Korea; Japan; Borneo; Sumatra; Java; Celebes; Philippines (Wiktor and Jurkowska 2007).

Type species: *Meghimatium striatum* van Hasselt, 1823

Meghimatium cf. *pictum* (Stoliczka, 1873)⁵⁹

Distribution: China; India (Wiktor et al. 2000).

Nepal: Chitwan National Park (Bössneck 2006).

Superfamily: Helicoidea Rafinesque, 1815

Family: Bradybaenidae Pilsbry, 1934

Subfamily: Bradybaeninae Pilsbry, 1934

Genus: *Bradybaena* Beck, 1837

Distribution: India; Bangladesh; Nepal; China; Myanmar; Thailand; Laos; Vietnam; Cambodia; Indonesia; Malaysia; Singapore (Hoong 1995, Panha 1995–1996, Wu 2002, 2004, Kuznetsov and Schileyko 1997, Ramakrishna et al. 2010, Schileyko 2011); the type species, *B. similis* is widely introduced in other regions (Carvalho et al. 2008).

Type species: *Helix similis* Férussac, 1821

Bradybaena radiculicola (Benson, 1848)

Distribution: NW to NE India: Himachal Pradesh, Uttarakhand, Sikkim (Ramakrishna et al. 2010).

Nepal: Annapurna Conservation Area-Kokhethanti, Lete Khola (Kuznetsov and Schileyko 1997, Schileyko and Kuznetsov 1998a, 1998b).

Bradybaena ? thakkholaensis Schileyko & Kuznetsov, 1998a⁶⁰

Distribution: Endemic to Nepal.

Nepal: Annapurna Conservation Area. Only known from Thakkhola, the type locality (Schileyko and Kuznetsov 1998a).

Genus: *Plectotropis* Martens, 1860

Distribution: India; China; Japan; Sumatra (Schileyko 2004, Ramakrishna et al. 2010).

Type species: *Helix elegantissima* L. Pfeiffer, 1849

Plectotropis tapeina (Benson, 1836)⁶¹

Distribution: India; Bangladesh; Myanmar (Ramakrishna et al. 2010).

Nepal: Ilam and Panchthar Districts (Subba and Ghosh 2008).

Family: Camaenidae Pilsbry, 1895

Subfamily: Camaeninae Pilsbry, 1895

Genus *Landouria* Godwin-Austen, 1918

Distribution: Sri Lanka; NE India; Nepal; Indonesia; Philippines (Schileyko and Kuznetsov 1998a).

Type species: *Helix huttonii* L. Pfeiffer, 1842⁶²

Landouria aborensis Godwin-Austen, 1918

Distribution: India: Arunachal Pradesh-Abor Hill (Ramakrishna et al. 2010).

Nepal: Dolakha, Lalitpur, Ramechhap and Solukhumbu Districts (Kuznetsov and Schileyko 1997, Schileyko and Kuznetsov 1998a).

Landouria coeni (Preston, 1914)⁶³

Distribution: India: Nagaland (Gude 1914).

Nepal: Solukhumbu District (Schileyko and Kuznetsov 1998a).

Landouria dhaulagirica Schileyko & Kuznetsov, 1998a

Distribution: Endemic to Nepal.

Nepal: Annapurna Conservation Area-Larjung, Kokhethanti, Kalopani (Schileyko and Kuznetsov 1998a).

Landouria huttonii (L. Pfeiffer, 1842)

Distribution: India: Himachal Pradesh, Uttarakhand, W Bengal, Assam, Nagaland (Ramakrishna et al. 2010).

Nepal: Kaski and Myagdi Districts (Kuznetsov and Schileyko 1997, Schileyko and Kuznetsov 1998a).

Landouria rhododendronis Schileyko & Kuznetsov, 1998a

Distribution: Endemic to Nepal.

Nepal: Annapurna Conservation Area-Gorepani, Parbat District (Schileyko and Kuznetsov 1998a).

Landouria savadiensis (Nevill, 1877)

Distribution: Myanmar: Sawady (Nevill, 1877).

Nepal: Shivapuri-Nagarjun National Park-Nagarjun Forest, Tare-Bhir (Schileyko and Kuznetsov 1998a).

Genus: *Ganesella* W.T. Blanford, 1863

Distribution: India; Myanmar; Thailand; Cambodia (Ramakrishna et al. 2010).

Type species: *Helix capitium* Benson, 1848

Ganesella sp.

Nepal: Shivapuri-Nagarjun National Park (Khanal and Budha 2013).

New distribution record from Nepal: Lalitpur District-Phulchowki Hill.

Notes

- ¹ Eight subgenera of *Cyclophorus* were recognized by Kobelt (1902), one of which, the African *Maizania* Bourguignat, 1889, was elevated to family level Maizanidae by Tielecke (1940) (see Bouchet and Rocroi 2005: 248). Gude (1921) mentioned only five subgenera viz.: *Glossostylus* Kobelt and Möllendorff, 1897 (S and SE Asia), *Litostylus* Kobelt & Möllendorff, 1897 (S and SE Asia), *Salpingophorus* Kobelt and Möllendorff, 1897 (S and SE Asia), *Cyclophorus* Montfort, 1810 (S and SE Asia) and *Cyclohelix* Mörch, 1852 (Andaman and Nicobar Islands). Wenz

- (1939: 458–460) replaced *Salpingophorus* by *Annularia* Schumacher, 1817 and *Cyclohelix* by *Otopoma* Gray, 1850, while Egorov (2006) replaced *Litostylus* by *Kobeltostylus* Egorov, 2006. In this list we follow Gude (1921) but with the adapted names proposed by Wenz (1939) and Egorov (2006). Note that Egorov and Greke (2007) also recognized five subgenera, but they regarded *Salpingophorus* as a junior synonym of *Cyclophorus*, while maintaining *Cricophorus* Kobelt and Möllendorff, 1897 as separate subgenus, next to *Cyclophorus*, *Glossostylus*, *Cyclohelix* and *Kobeltostylus*.
- ² Allozyme data of *Cyclophorus fulguratus* populations in Thailand suggest that this is a species complex (Prasankok et al. 2009). It remains to be investigated how the Nepalese populations fit into this picture.
 - ³ The name *Litostylus* Kobelt & Möllendorff, 1897 is a junior homonym of *Litostylus* Faust, 1893 (= Insecta, Coleoptera, Curculionidae). Egorov (2006) therefore replaced the molluscan name by *Kobeltostylus*.
 - ⁴ Wenz (1939) replaced the name *Salpingophorus* Kobelt & Möllendorff, 1897 by *Annularia* Schumacher, 1817, while Egorov and Greke (2007) regarded both these names as junior synonyms of *Cyclophorus* Montfort, 1810 (see note ¹).
 - ⁵ *Cyclophorus* (*A.*) *aurantiacus* is distributed in SE Asia, so that its presence in Nepal is doubtful and requires confirmation.
 - ⁶ Nevill (1878) regarded *Scabrina* W.T. Blanford, 1863 as a subgenus of *Cyclophorus* Montfort, 1810. Kobelt and Möllendorff (1897) raised *Scabrina* to genus rank. *Cyclophorus pinnulifer* Benson, 1857 was fixed as the type species of *Scabrina* by Nevill (1878).
 - ⁷ Some authors have erroneously attributed the Alycaeinae to Gray, 1850 (Minato 2005, Tarruella and Domènech 2011). However, according to Bouchet and Rocroi (2005) the correct authorship is 'W. Blanford, 1864'. Alycaeinae comprises four genera (Tarruella and Domènech 2011) namely *Alycaeus* J.E. Gray, 1850, *Chamalycaeus* Kobelt & Möllendorff, 1897, *Cipangocharax* Shintaro, 1934 and *Dioryx* Benson, 1859. The generic names *Alycaeus* and *Chamalycaeus* have been applied by recent authors (Panha and Burch 2005, Maassen 2006, Dumrongrojwattana and Maassen 2008, Lee et al. 2008, Tarruella and Domènech 2011). Conversely, *Cycloryx* Godwin-Austen, 1914, *Dicharax* Kobelt & Möllendorff, 1900 and *Raptomphalus* Godwin-Austen, 1914 are treated as subgenera of *Chamalycaeus* by Gude (1921). We apply Gude's (1921) generic categories.
 - ⁸ The name of the type species of *Alycaeus* J.E. Gray, 1850, by original designation *Cyclostoma gibbum* Férussac, 1838, is a junior homonym of *Cyclostoma gibbum* Draparnaud, 1805 (Hydrobiidae). Therefore, it has been replaced by *Alycaeus eydouxii* Venmans, 1956.
 - ⁹ Some authors attribute authorship of *Chamalycaeus* (*D.*) *strangulatus* to Hutton such as Pfeiffer (1846), Nevill (1878), Hanley and Theobald (1878) but without indicating the publication year. Hutton's name was, however, a manuscript name of no nomenclatural standing. Gude (1921) and Tarruella and Domènech (2011) were correct in assigning authorship to 'Pfeiffer'.

- ¹⁰ Seven subgenera have been recognized within *Diplommatina* (Kobelt 1902, Kuroda 1928): *Benigoma* Kuroda, 1928, *Diplommatina* Benson, 1849, *Diploptychia* Möllendorff, 1895, *Metadiancta* Möllendorff, 1898, *Moussonia* Semper, 1865, *Pseudopalaina* Möllendorff, 1898, and *Sinica* Möllendorff, 1885.
- ¹¹ *Diplommatina* (*S.*) *canarica* is endemic to the Western Ghats (Raheem et al. 2014). Hence, the identification of the Nepalese specimens by Kuznetsov and Schileyko (1997) needs to be verified.
- ¹² In the original description of *Schistoloma funicularum* Benson (in Hutton and Benson 1838) distinguished this species from the European fossil species *C. mumia* by ‘the rounder and more reflected orange peristome, and by its central position at the base, as well as by the delicate sculpture, and an embossed spiral cord which winds from above the umbilicus to the base, whence the species has received the trivial appellation of ‘Funiculalum’. It is the first known Indian species belonging to pupaeform or subcylindric division of *Cyclostoma*’. Sowerby (1850) changed the spelling ‘*funiculalum*’ to ‘*funiculatum*’ without giving any reason. Gude (1921) considered Benson’s (1838) ‘*funiculalum*’ to be a nomen nudum because of the spelling error (*funiculalum*, laps). Many authors have used ‘*funiculatum*’ (e.g. Gray in Baird 1850, Pfeiffer 1853, Hanley and Theobald 1870, Nevill 1878, Kobelt and Möllendorff 1897, Gude 1921, Ramakrishna et al. 2010). This was, however, an unjustified emendation (ICZN Article 32.2, 32.3) and thus Benson’s name stands. Nepalese specimens differ in possessing a whitish, instead of orange peristome, but the significance of this is unknown.
- ¹³ *Carychium minusculum* Gredler, 1888 was originally described from China, “aus Hupe” (type locality), which is the Chinese Province Hubei (= Hupeh) (See Zilch 1974). The correct publication year is ‘1888’ instead of ‘1887’ as is sometimes mentioned (e.g. Zilch 1974, Nesemann et al. 2007). In Nepal, this species was recorded from two different localities, viz. Kavre District by Nesemann et al. (2007) and Langtang National Park-Syabru by Kuznetsov and Schileyko (1997). PB checked specimens from these two localities (Nesemann’s specimen and an image of Kuznetsov and Schileyko 1997). The shells from these two localities differ by size, shape and sculpture and may be two distinct taxa.
- ¹⁴ *Carychium* shells collected by PB from Phulchowki, Shivapuri-Nagarjun and Langtang National Parks have very fine and strong radial ribs, as well as slender apical whorls. As such they differ from the shells of Nesemann et al. (2007), which are comparatively smooth and smaller. They are therefore, tentatively regarded as separate taxa. The Phulchowki specimen was also compared with images of Schileyko’s *C. minusculum* specimen from Langtang National Park deposited in ZMMU No. Lc-39251 and *C. minusculum* in Zilch (1974: Fig. 13). The peristome along the umbilicus region is more or less straight in the Phulchowki taxon, while it is strongly reflected in Schileyko’s *minusculum*.
- ¹⁵ According to Kennard (1942) the name *Vaginulus alte* was published in 1822, instead of 1821 as is often mentioned in the literature or 1823 as mentioned in Sherborn (1923: 230). The spelling ‘*altae*’ in e.g. Bössneck (2006) and Raheem et al. (2010) is erroneous.

- ¹⁶ The type locality of *Pupilla annandalei* Pilsbry, 1921 was doubtfully recorded as Ava (Myanmar) in the Indian Museum (Nevill 1878). Pilsbry (1920-21) speculated that the holotype may have been collected in Nepal because he associated it with central Asian species. However, confirmed records are restricted to granite mountains between 2,000 and 2,800 m in northern Pakistan (Pokryszko et al. 2009).
- ¹⁷ Pilsbry (1920-21: 204) asserted that *Pupa eurina* Benson, 1864 was collected in Nepal. If correct, Benson's record would be the earliest scientific report of a land snail from Nepal (Budha 2005). Benson (1864: 139) gave the locality in Latin as '*ad Tribeni Ghât fluminis Gogra*', but we have not been able to identify this locality, since 'Tribeni' refers to several localities where two rivers meet and 'ghat' refers either to a place where cremations take place or to sites where people cross a river along a trail by using locally made wooden boats. Godwin-Austen (1899: 260) expanded on Benson's locality information 'the typical specimens were found in the exuviae of the River Gogra at Tribeni Ghat. This river rises in the Tibetan plateau, and these shells may have been brought down thus from far back in the mountain range'. The downstream course of the Karnali river in Nepal is known as Gogra (= Ghaghara) in India immediately after the two branches of Karnali river meet at the Nepal-India border at Katarniya ghat, Uttar Pradesh, India. The confluence of Seti and Karnali river is called Tribeni which is approx. 100 km upstream (north) from the Nepal-India border. There is no clear evidence that William Theobald ever entered Nepal. However, Joseph Hooker, who was among the earliest Europeans to venture into Nepal to investigate its biota, did spend time with Theobald in India (Hooker 1854: 37, 57) and so it is possible that Hooker passed on samples of *Pupa eurina* to Theobald.
- ¹⁸ Hutton and Benson (1838) attributed the authorship of *Helix humilis* to Hutton, but Gude (1914) and Ramakrishna et al. (2010) incorrectly cite 'Benson' while Sherborn (1927: 3062) cited 'Hutton & Benson', 1838 as authors.
- ¹⁹ *Pyramidula kuznetsovi* was misidentified as *P. humilis* by Schileyko and Kuznetsov (1997). Kuznetsov's collections were recently reviewed and Schileyko and Balashov (2012) redescribed the samples as a new species.
- ²⁰ The correct spelling is '*cantorii*' and not '*cantori*' as some authors mention (e.g. Zilch 1959, Schileyko 1998).
- ²¹ The type locality of *Mirus nilagiricus* (L. Pfeiffer, 1846) is Nilgiris, South India. Although Kuznetsov and Schileyko (1997) reported this species from Nepal, they question whether the Himalayan species belongs to *Mirus*, though without suggesting an alternative generic placement.
- ²² Shortly after the description of *Darwininitium shiwalikianum*, Dr. Somsak Panha communicated that he and Dr. Chirasak Sutcharit (both Chulalongkorn University Bangkok, Thailand) noticed the conchological similarity between this species and *Helix capitum* Benson, 1848, type species of the camaenid genus *Ganesella* W.T. Blanford, 1863. Further anatomical and DNA studies are needed to verify whether *D. shiwalikianum* and *G. capitum* are conspecific. Moreover, the family level affiliations of *Darwininitium* and *Ganesella* remain to be assessed since the

- Camaenidae may not be monophyletic (e.g. Scott 1996) and the phylogenetic relationships of the Camaenidae are still poorly resolved (Wade et al. 2007). If *D. shiwalikianum* is related or identical to *G. capitum*, then it does not represent a pseudosigmurethrous orthurethran condition as was originally claimed by Budha et al. (2012). It would also mean that *Darwininitium* Budha & Mordan, 2012 will be a junior synonym of *Ganesella* W.T. Blanford, 1863.
- ²³ Nordsieck (1973) assigned Nepalese Phaedusinae to the genus *Hemiphaedusa* and this was followed by Raheem et al. (2010). Later, Nordsieck (2002) described the new subgenus *Montiphaedusa* Nordsieck, 2002 of the genus *Cylindrophaedusa* and grouped all Himalayan clausiliids in *Montiphaedusa*.
- ²⁴ Although E African *Lissachatina* is distinguished from W African *Achatina* (Bequaert 1950, Mead 1995), both generic names have been applied to this species. This list follows Budha and Naggs (2008) and Raheem et al. (2010, 2014), who used *Lissachatina* at genus level for reasons further explained by Raheem et al. (2014).
- ²⁵ *Cecilioides* is the name used in the original description but it has been variously spelled by different authors. Hermannsen (1846) emended it to *Caecilioides*, which was followed by Pilsbry and Tryon (1908–1909) and Gude (1914). *Cecilioides* has been placed on the official list of generic names (ICZN Opinion 335) and all other spellings are invalid.
- ²⁶ Only a single *Cecilioides* shell was collected in Nepal (Baitadi District). It measures about 2 mm, has four whorls, and resembles *C. minuta*.
- ²⁷ Many subulinid genera, such as *Opeas*, *Beckianum*, *Leptopeas*, *Lamellaxis* and *Leptinaria* have been confusingly interpreted (Thompson 2011), even if they are conchologically relatively well-differentiated and anatomical data are available for several of them.
- ²⁸ Baker (1935) erected *Allopeas* as a subgenus of *Lamellaxis* Strebel & Pfeiffer, 1882.
- ²⁹ Schileyko and Kuznetsov (1997) identified a Nepalese specimen as *Allopeas mauritianum prestoni* (Sykes, 1898) from Annapurna Conservation Area. Sykes (1898) original combination was *Opeas prestoni*. Naggs and Raheem (2000) placed ‘prestoni’ under *Allopeas*. Pilsbry and Tryon (1906) placed *Opeas prestoni* Sykes, 1898 under *O. mauritianum* (Pfeiffer, 1852) as var. *prestoni*. Brodie and Barker (2011) and Bouchet and Cosel (1991) also placed ‘mauritianum’ under *Opeas*. Some authors assign ‘prestoni’ to *Lamellaxis* (e.g. Deisler and Abbott 1984, Nekola 2014). Griffiths and Florens (2006) suggested that *Allopeas mauritianum* is a junior synonym of *A. clavulinum*. The type locality of this species is Mauritius. FN examined the syntype of *mauritanus* and confirmed that it is identical with material identified as *Allopeas clavulinum*. It has been spread by commerce throughout the tropics but its native range is not known (Hanna 1966, Deisler and Abbott 1984).
- ³⁰ As for subulinids in general, *Opeas* species have been confusingly interpreted and have been assigned variously to different genera such as *Allopeas*, *Lamellaxis*, *Paropeas* and *Prosopeas* (although this latter may not even be a subulinid) (Naggs 1994).
- ³¹ We follow Bouchet and Rocroi (2005) and regard Glessulinae as a subfamily of the Subulinidae.

- ³² The relationships of *Bacillum* are still unclear. Schileyko (1999) placed the genus in the Rishetiinae Schileyko, 1999, together with *Eutomopeas* Pilsbry, 1946, *Tortaxis* Pilsbry, 1906 and *Rishetia* Godwin-Austen, 1920. Based on the half exposed reproductive parts of a specimen labeled as *Bacillum* sp. Godwin-Austen (1920: 7) states 'The very recent and extended knowledge of the animals of *Bacillum* and *Glessula* shows that the two genera come next to each other....' (Godwin-Austen (1920: 7). But the same specimen (NHM) from a lot of 3 specimens from Assam, leg. S.L. Hora, Godwin-Austen coll. (Acc. 1830), Reg. 20120113) examined by PB confirmed that it is closer to *Rishetia* than to *Glessula* since it has an elongated flagellum. Because of its truncated columella, and elongately turreted shell, we provisionally retain *Bacillum* in the Glessulinae.
- ³³ Subba and Ghosh (2008) recorded *Bacillum* sp. from E Nepal without a description or figure.
- ³⁴ Although Martens (1860) designated *Cionella gemma* Benson, 1850 as the type species of *Glessula* (e.g. Zilch 1959), the correct type species is *Achatina ceylanica* L. Pfeiffer, 1845 (Gude 1914, Raheem et al. 2014). This is because *A. ceylanica* is the type species (by monotypy) of the genus *Electra* Albers, 1850, which is a junior homonym of *Electra* Lamouroux, 1816 (Ectoprocta). Therefore *Electra* Albers, 1850 was replaced by *Glessula* Martens, 1860 and in such cases ICZN Art. 67.8 rules that the type species of the replaced genus name is automatically also the type species of the new genus name.
- ³⁵ The type locality of *Glessula subjerdoni* is S India: Jaypore and Golconda Hills (Beddome 1906). Specimens from NE India (Darjeeling) were erroneously identified as *G. subjerdoni* by Gude (1914) and were subsequently assigned to *G. crassula* (Reeve, 1850) by Godwin-Austen (1920). Nevertheless, later authors (Kuznetsov 1996, Dey and Mitra 2000, Ramakrishna et al. 2010) have followed Gude (1914). Raheem et al. (2014) consider *G. subjerdoni* to be a 'nomen dubium'.
- ³⁶ The distribution range of *Rishetia* in this list is based on unpublished anatomical data of specimens from Nepal and Sri Lanka. For example, Dinarzarde Raheem's unpublished figures of dissected specimen of *Glessula capillacea* (L. Pfeiffer, 1855) from Sri Lanka indicate that it belongs to *Rishetia* because it has an elongated flagellum typical of *Rishetia*.
- ³⁷ Specimens of *Rishetia tenuispira* from Nepal were first described under the genus name *Ranibania* Schileyko & Kuznetsov, 1996. *Ranibania* was subsequently synonymized with *Rishetia* (Schileyko, 1999). However, Schileyko's (1999) *Rishetia tenuispira* (Benson) from Nepal differs from Benson's *R. tenuispira* from the type locality, Khasi Hills NE India and is similar to Godwin-Austen's *Rishetia longispira* Godwin-Austen, 1920. Khanal and Budha (2013) identified specimens of the same locality as Schileyko (1999; Balaju, Raniban, Nepal) as *R. cf. longispira*. Godwin-Austen (1920) gave a very confusing and conflicting account on *longispira* and *tenuispira* (p. 33 same animal characters including reproductive anatomy) but the distribution range of *longispira* was recorded as westward from Bhutan to Sikkim and Darjeeling, whereas *tenuispira* was recorded from the Khasi and Garo Hills (p. 11–12).

- ³⁸ *Gulella bicolor* was originally described as *Pupa bicolor* Hutton, 1834 but Blanford and Godwin-Austen (1908) assigned it to *Ennea* H. Adams & A. Adams, 1855. The species has also been included in the Indo-Chinese streptaxid genus *Sinoennea* Kobelt, 1904. DNA sequence data, however, suggest that *Pupa bicolor* comes within *Gulella* (Rowson et al. 2011).
- ³⁹ The record of *E. plectosoma* (Benson, 1836) from Pegu (=Bamo, Myanmar) (Gude 1914: 81) is probably erroneous (Páll-Gergely et al. unpublished manuscript).
- ⁴⁰ Kuznetsov and Schileyko (1997) recorded *E. affinis* from Swoyambhunath temple forest area, but the material from this area may be a different species (Páll-Gergely et al. unpublished manuscript).
- ⁴¹ Some authors '1852' as the publication year of *Kaliella barrakporensis* (e.g. Godwin-Austen 1882, Blanford and Godwin-Austen 1908). Raheem et al. (2014) pointed out that part 20 p. 156 of the Proceedings of the Zoological Society of London was published in 1854, 1852 being the date when the proceedings were presented at the Society's meetings (see Duncan 1937). Therefore this publication was preceded by Pfeiffer's '*Helix barrakporensis* 1853 Monographia Heliceorum Viventium 3: 59'. So the correct publication year is 1853, not 1852.
- ⁴² According to Falkner et al. (2002) *Euconulus fulvus* is a species complex.
- ⁴³ The genus *Hawaiiia* is assigned to the Vitrinidae by Vaught (1989), to the Zonitidae by Riedel (1980) and to the Pristilomatidae by Anderson (2005). This later placement is followed in this list.
- ⁴⁴ Cockerell (1891, 1893) published the name as '*Cryptausteniae*' (plural), while in 1898 he corrected it to '*Cryptaustenia*' (singular). However, according to Art 11.8 and 33.2.2 of ICZN, the publication date of the corrected name remains '1891'.
- ⁴⁵ There is still much nomenclatural and taxonomic confusion with respect to the genus *Macrochlamys* and its type species. This list follows Raheem et al. (2014) in applying the current genus-level interpretation of *Macrochlamys* sensu Godwin-Austen (1883) with *Macrochlamys indica* Benson in Godwin-Austen, 1883 as its type species.
- ⁴⁶ According to Kiauta and Butot (1973) *Macrochlamys tugurium* would be the most common land gastropod of Kathmandu Valley but so far PB has not recorded *M. tugurium* in this area. The most common land gastropod in the Kathmandu Valley is *Bensonies nepalensis*, because of its similar shell shape and size, may have been misidentified as *M. tugurium*.
- ⁴⁷ Cockerell (1891, 1893) published the name as '*Euausteniae*' (plural), while in 1898 he corrected it to '*Euaustenia*' (singular). According to Art. 11.8 and 33.2.2 of the ICZN, the publication date of the corrected name remains '1891'.
- ⁴⁸ The publication date of *Vitrina monticola* L. Pfeiffer is '1849' not '1848' as cited by some authors mention (e.g. Blanford and Godwin-Austen 1908, Schileyko 2003, Mitra et al. 2005, Ramakrishna et al. 2010). See Duncan (1937) for the publication date of the *Proceedings of the Zoological Society of London* part 16:107; see also Sherborn (1928).

- ⁴⁹ *Bensonies nepalensis* shows a remarkable shell colour polymorphism that seems to correlate with altitude: at lower altitudes in C Nepal (Chitwan District) the body whorl of shells shows a dark brown band on a chocolate brown or white background. They co-occur with banded shells which are similar to mid hill specimens (PB, unpublished observations).
- ⁵⁰ *Himalodiscus aculeatus* was originally assigned to the Discidae by Kuznetsov (1996) based on conchological features, but based on anatomical data Schileyko and Kuznetsov (1998b) re-assigned it to Ariophantidae.
- ⁵¹ The type species '*Helix vidua*' has been confusingly cited. Zilch (1960) mentions '*Euplecta vidua* W.T. Blanford', but Schileyko (2002) mentions '*Euplecta vidua* Hanley and Theobald, 1875'. Godwin-Austen (1876) mentions '*Euplecta (Rotula) vidua* Blanford', whereas Blanford and Godwin-Austen (1908) list '*K. vidua* Blanford' in the same book under its species description as '*Khasiella vidua* H. & T. (Blf. MSS) (*Helix*)'. We follow Coan and Kabat (2012) in referring the type species to as *Helix vidua* Hanley & Theobald, 1875.
- ⁵² The identification of Nepalese *Khasiella pansa* needs to be verified.
- ⁵³ Schileyko and Frank (1994) and Kuznetsov and Schileyko (1997) reported *Oxyteta orobia* from the neighbourhood of Kathmandu, Nepal. PB checked the syntypes in NHM and specimens available at RBINS and compared these with Nepalese shells and concluded that the Nepalese specimens belong to a different species.
- ⁵⁴ *Sarama* Blanford and Godwin-Austen, 1908 is a junior homonym of *Sarama* Moore, 1887. *Saramina* Wenz, 1947 is a junior synonym of *Rasama* Laidlaw, 1932.
- ⁵⁵ The subgeneric name *Taulimax* Wiktor and Likharev, 1980 is a junior synonym of *Kasperia* Godwin-Austen, 1914 (Wiktor 2001b).
- ⁵⁶ Bössneck (2006) and Raheem et al. (2010) misspelled the genus name as *Turcolimax*.
- ⁵⁷ Although *Anadenus giganteus* Heynemann, 1863 is the type species of *Anadenus* Heynemann, 1863 (Zilch 1959, Wiktor et al. 2000), Wiktor (2001a) proposed to replace it by *Limax altivagus* Theobald, 1862, because he regarded *A. giganteus* Heynemann, 1863 as a 'nomen dubium'. For the time being, we nevertheless maintain *A. giganteus* as the type species as Simroth (1901) did provide anatomical data, including figures of *A. giganteus*.
- ⁵⁸ Three paratypes of *Anadenus nepalensis* from Langtang National Park in fact belong to *A. altivagus* viz. one specimen from 'Chandrabar (= Chandanbari), 3,300 m a.s.l., fir forest' and two specimens from 'Gosainkund, 4,200 m a.s.l.' both collected on 27.09.1981 by A. Kuska (see Wiktor 2001a) (A. Wiktor, pers.comm. 13.10.2009). This was confirmed by their reproductive anatomy (with its typical spines inside the penis) examined by PB.
- ⁵⁹ Wiktor et al. (2000) figured the reproductive anatomy of *Meghimatium* cf. *pictum* (Stoliczka, 1873) and *M. bilineatum* (Benson, 1842) based on Chinese specimens but found no clear differences and hence were undecided as to whether or not *M.* cf. *pictum* is a distinct species. The reproductive organs of a specimen from Nepal resemble those of Chinese *M.* cf. *pictum*.

- ⁶⁰ *Bradybaena* (?) *thakkeholensis* was described on the basis of a few juvenile shells by Schileyko and Kuznetsov (1998a), its anatomy is unknown.
- ⁶¹ Subba and Ghosh (2008) misspelled this species name as *Aegista* (*Placetotropis*) *tapeina*.
- ⁶² The correct spelling is '*huttonii*' (Raheem et al. 2014; see Pfeiffer 1842: 82), not '*huttoni*' as mentioned by e.g. Zilch (1960) and Schileyko (2004).
- ⁶³ *Landouria coeni* was placed in the subgenus *Plectotropis* of the genus *Aegista* by Ramakrishna et al. (2010). However, these two taxa were treated as distinct genera by Preston (1914), Gude (1914), and Schileyko (2004).

Acknowledgements

PB Budha received a faculty research grant from the University Grants Commission, Sanathimi Bhaktapur, Nepal. This work could not have been undertaken without the support of the Darwin Initiative programme *Developing land snail expertise in South and Southeast Asia*. PB gratefully acknowledges the Royal Belgian Institute of Natural Sciences (RBINS), Brussels, for financial support. We would like to thank the following colleagues for providing specimens and/or advice: Jonathan Ablett (Natural History Museum, London), Dinarzade Raheem (RBINS), Alexander Sysoev (Zoological Museum of Moscow University, Moscow), Andrzej Wiktor (Museum of Natural History, Wrocław University, Poland), Rose Sablon (RBINS) and Hasko Nesemann (Aquatic Ecology Centre, Kathmandu University, Nepal). We are grateful to Ramesh Devkota, Srijana Khanal, Sunita Khatiwara and Naresh Kohar for support in the field work. Sanjan Thapa, Hari P. Sharma, Bharat Babu Shrestha, Ripu Kunwar and Janak Khatiwada provided samples from Khaptad National Park, Mugu, Taplejung and Dhading Districts.

References

- Anderson R (2005) An annotated list of the non-marine Mollusca of Britain and Ireland. *Journal of Conchology* 38(6): 607–638.
- Azuma M (1982) Colored illustrations of the land snails of Japan. Hoikusha, Osaka.
- Baird W (1850) Nomenclature of Molluscos Animals and Shells in the collection of the British Museum Part 1. Cyclophoridae. Spottiswoodes and Shaw, London. doi: 10.5962/bhl.title.59531
- Baker HB (1935) Jamaican Land Snails. *The Nautilus* 48(3): 83–88
- Bartsch P (1915) The Philippine land shells of the genus *Schistoloma*. *Proceedings of the United States National Museum* 49(2104): 195–204. doi: 10.5479/si.00963801.49-2104.195
- Beddome RH (1906) Notes on Indian and Ceylonese species of *Glessula*. *Proceedings of the Malacological Society of London* 6: 160–172.
- Benson WH (1864) Characters of *Coilostele*, an undescribed genus of Auriculacea (?), and of species *Helix*, *Pupa*, and *Ancylus*, from India, West Africa, and Ceylon. *Annals and Magazine of Natural History* (3) 13: 136–140.

- Bentham Jutting WSS van (1961) The Malayan Streptaxidae Genera *Huttonella* and *Sinoennea*. Bulletin of the Raffles Museum, Singapore 26: 5–33.
- Bentham Jutting WSS van (1948) Systematic studies on the non-marine Mollusca of the Indo-Australian Archipelago I. Critical Revision of the Javanese Operculate Land-shells of the Families Hydrocenidae, Helicinidae, Cyclophoridae, Pupinidae and Cochlostomatidae. Treubia 19: 539–604.
- Bentham Jutting WSS van (1950) Systematic studies on the non-marine Mollusca of the Indo-Australian Archipelago II. Critical Revision of the Javanese Pulmonate Land-shells of the Families Helicarionidae, Pleurodontidae, Fruticolidae and Streptaxidae. Treubia 20: 381–505.
- Bequaert JC (1950) Studies in the Achatininae, a group of African land snails. Bulletin of the Museum of Comparative Zoology, Harvard 105: 1–216.
- Blanford WT (1904) Description of Indian and Burmese land shells referred to the genera *Macrochlamys*, *Bensonina* and *Taphrospira* (gen. nov.), *Microcystina*, *Euplecta* and *Polita*. Proceedings of the Zoological Society of London 2: 441–447.
- Blanford WT, Godwin-Austen HH (1908) The fauna of British India, including Ceylon and Burma. Mollusca, Testacellidae and Zonitidae. London, 311 pp.
- Bössneck U (2006) Ökologie und Verbreitung der Nacktschnecken im Nepal-Himalaya (Mollusca: Gastropoda: Pulmonata). In: Hartmann M, Weipert J (Eds) Biodiversität und Naturausstattung im Himalaya. Bandung 2, 39–48.
- Bouchet P, Rocroi JP (2005) Classification and nomenclator of gastropod families. Malacologia 47: 1–397.
- Bouchet P, Cosel B von (1991) Les Mollusques terrestres et fluviatiles des Départements d'Outre-Mer. Muséum national d'Histoire naturelle, Paris, 109 pp.
- Brodie G, Barker GM (2011) Introduced land snails in the Fiji Islands: Are there risks involved? In: Veitch CR, Clout MN, Towns DR (Eds) Island Invasives: eradication and management. IUCN, Gland, Switzerland, 32–36.
- Bruggen AC van (2006) *Gulella johannae* spec. nov. (Gastropoda, Pulmonata, Streptaxidae), a new land snail from the Drakensberg range in Limpopo Province, South Africa, with notes on *G. johannesburgensis* (M. & P.). Zoologische Mededelingen 80(1): 63.
- Budha PB (2005) Nepalese malacology trails behind “Catch up”. Himalayan Journal of Sciences 3(5): 9–10.
- Budha PB, Mordan PB, Naggs F, Backeljau T (2012) *Darwininitium* – a new fully pseudosigmurethrous orthurethran genus from Nepal (Gastropoda, Pulmonata, Cerastidae). ZooKeys 175: 19–26. doi: 10.3897/zookeys.175.2755
- Budha PB, Naggs F (2008) The Giant African Land Snail *Lissachatina fulica* (Bowdich) in Nepal. The Malacologist 50: 19–21.
- Burch JB, Panha S (2002) The land snail genus *Carychium* (Pulmonata: Carychiidae) in Thailand. Walkerana 9(22): 171–175.
- Carvalho CDM, Bessa ECA, D'Ávila S (2008) Life history strategy of *Bradybaena similaris* (Férussac, 1821) (Mollusca: Pulmonata: Bradybaenidae). Molluscan Research 28(3): 171–174.
- Chaijirawong R, Nuamsee K, Dumrongrojwattana P (2008) Shell and radula morphology and reproductive anatomy of the introduced carnivorous snail *Gulella bicolor* (Pulmonata: Streptaxidae) from Chong Buri Province. Kasetsart Journal (Natural Science) 42: 251–255.

- Clench WJ (1964) *Gulella bicolor* (Hutton). The Nautilus 77: 142–143.
- Coan EV, Kabat AR (2012) The malacological works and taxa of Sylvanus Hanley (1819–1899). Malacologia 55(2): 285–359. doi: 10.4002/040.055.0208
- Cockerell TDA (1891) On the geographical distribution of slugs. Proceedings of the Zoological Society of London 59(2): 214–226. doi: 10.1111/j.1096-3642.1891.tb01744.x
- Cockerell TDA (1893) A checklist of the slugs with appendix and notes by Walter E Collinge. The Conchologist 2(7–8): 168–176, 185–232.
- Cole ML, Herbert DG (2009) Description of four new species of *Gulella* Pfeiffer, 1856 from Eastern Cape, South Africa, with additional notes on two poorly known species (Mollusca: Eupulmonata: Streptaxidae). Zoologische Mededelingen 83: 547–564.
- Deisler JE, Abbott RT (1984) Range extensions of some introduced land mollusks in the Bahama Islands, with first reports for four species. The Nautilus 98(1): 12–17.
- Dey A, Mitra SC (2000) Mollusks of the Himalaya. Records of the Zoological Survey of India 98(2): 5–50.
- Dumrongrojwattana P, Maassen WJM (2008) Two new species of *Alycaeus* from Eastern Thailand (Gastropoda, Caenogastropoda, Cyclophoridae). The Thailand Natural History Museum Journal 3(1): 1–4.
- Duncan FM (1937) On the dates of publication of the Society's 'Proceedings', 1859–1926. Proceedings of the Zoological Society of London 107: 71–84.
- Dundee DS, Baerwold RJ (1984) Observations on a micropredator, *Gulella bicolor* (Hutton) (Gastropoda: Pulmonata: Streptaxidae). The Nautilus 98: 63–68.
- Egorov RV (2006) *Kobeltostylus* nom. nov., a replacement name for *Litostylus* Kobelt & Möllendorff, 1897 (non Faust, 1893) (Gastropoda: Littoriniformes: Cyclophoridae) with a revised diagnosis of the subgenus. Club Conchylia Informationen 37: 54–55.
- Egorov RV, Greke K (2007) The genus *Cyclophorus* Montfort, 1810: systematics and nomenclature. Club Conchylia Informationen 38: 57–64.
- EPPO (2013) PQR database. European and Mediterranean Plant Protection Organization, Paris, France. <http://www.eppo.int/DATABASES/pqr/pqr.htm>
- Falkner G, Ripken Th EJ, Falkner M (2002) Mollusques continentaux de France. Liste de référence annotée et bibliographie. Patrimoines naturels 52, 350 pp.
- Gerber J, Bössneck U (2009) The genus *Vallonia* in Nepal (Gastropoda: Pulmonata: Valloniidae). Archiv für Molluskenkunde 138(1): 43–52.
- Gittenberger E, Bank RA (1996) A new start in *Pyramidula* (Gastropoda, Pulmonata: Pyramidulidae). Basteria 60: 71–78.
- Godwin-Austen AA (1876) On the Helicidae collected during the expedition into the Daffa Hills, Assam. The Journal of the Asiatic Society of Bengal 45(2): 311–318.
- Godwin-Austen AA (1882) Land and freshwater Mollusca of India including South Arabia, Baluchistan, Afghanistan, Kashmir, Nepal, Burmah, Pegu, Tenasserim, Malay Peninsula, Ceylon, and other islands of the Indian Ocean. Taylor and Francis, London. Conchologia Indica 1(2): 19–65.
- Godwin-Austen AA (1883) Land and freshwater Mollusca of India including South Arabia, Baluchistan, Afghanistan, Kashmir, Nepal, Burmah, Pegu, Tenasserim, Malay Peninsula,

- Ceylon, and other islands of the Indian Ocean. Taylor and Francis, London. *Conchologia Indica* 1(3): 67–94.
- Godwin-Austen AA (1899) Land and freshwater Mollusca of India including South Arabia, Baluchistan, Afghanistan, Kashmir, Nepal, Burmah, Pegu, Tenasserim, Malay Peninsula, Ceylon, and other islands of the Indian Ocean. Taylor and Francis, London. *Conchologia Indica* 2(9): 87–146.
- Godwin-Austen AA (1914) Land and freshwater Mollusca of India including South Arabia, Baluchistan, Afghanistan, Kashmir, Nepal, Burmah, Pegu, Tenasserim, Malay Peninsula, Ceylon, and other islands of the Indian Ocean. Taylor and Francis, London. *Conchologia Indica* 2(12): 311–442.
- Godwin-Austen AA (1920) Land and freshwater Mollusca of India including South Arabia, Baluchistan, Afghanistan, Kashmir, Nepal, Burmah, Pegu, Tenasserim, Malay Peninsula, Ceylon, and other islands of the Indian Ocean. Taylor and Francis, London. *Conchologia Indica* 3(1): 1–65.
- Gredler PV (1888) Zur Conchylien-Fauna von China. XIII Stück. *Jahrbücher der Deutschen-malakozoologischen Gesellschaft* 14: 343–373.
- Griffiths OL, Florens VFB (2006) A field guide to the non-marine molluscs of the Mascarene Islands (Mauritius, Rodrigues, and Réunion) and the northern dependencies of Mauritius. Bioculture Press.
- Gude GK (1914) The Fauna of British India, including Ceylon and Burma, Mollusca, Vol II (Trochomorphidae-Janellidae). Today and Tomorrow's Printers and Publishers, New Delhi.
- Gude GK (1921) The Fauna of British India, including Ceylon and Burma, Mollusca, Volume III: Land Operculates (Cyclophoridae, Truncatellidae, Assimineidae, Helicinidae). Today and Tomorrow's Printers and Publishers, New Delhi.
- Hanley S, Theobald W (1870) Illustrations of the land and freshwater shells of British India. *Conchologia Indica*, part 1: 1–10, plates 1–20.
- Hanley S, Theobald W (1875) Illustrations of the land and freshwater shells of British India. *Conchologia Indica*. Part 7: 49–56, plates 121–140.
- Hanna GD (1966) Introduced mollusks of western North America. Occasional papers of the California Academy of Sciences 48, 108 pp.
- Herbert D, Kilburn D (2004) Field Guide to the land snails and slugs of eastern South Africa. Natal Museum, Pietermaritzburg.
- Herbert DG, Rowson B (2011) *Pupa menkeana* Pfeiffer, 1853, type species of the speciose land snail genus *Gulella* Pfeiffer, 1856: correction of longstanding misidentification and designation of neotype (Mollusca: Eupulmonata: Streptaxidae). *African Invertebrates* 52(2): 1–10. doi: 10.5733/afin.052.0201
- Hermannsen AN (1846) *Indicis generum malacozoorum primordia*. Fischer Cassel 1: 1–104.
- Hooker JD (1854) Notes of a naturalist in Bengal, the Sikkim and Nepal Himalayas, the Khasia Mountains, &c. *Himalayan Journals* 1: 1–408.
- Hoong HW (1995) A review of the land snail fauna of Singapore. *The Raffles Bulletin of Zoology* 43(1): 91–113.
- Hutton T, Benson WH (1838) On the land and freshwater shells of the Western Himalaya. *The Journal of the Asiatic Society of Bengal* 7: 211–218.

- Kennard AS (1942) The Histoire and Prodrome of Férussac Part III. Proceedings of the Malacological Society of London 25: 111–118.
- Kerney MP, Cameron RAD (1979) A field guide to the land snails of Britain and north-west Europe. Collins, London.
- Khanal S, Budha PB (2013) Terrestrial gastropod fauna of Nagarjun forest, Shivapuri-Nagarjun National Park, Kathmandu, Nepal. Journal of Institute of Science and Technology, Tribhuvan University 18(1): 113–119.
- Kiauta B, Butot LJM (1973) The chromosomes of *Macrochlamys tугurium* (Benson, 1852) from Nepal (Stylommatophora, Sigmurethra: Ariophantidae). Basteria 37: 145–148.
- Kobelt W (1902) Das Tierreich. Eine Zusammenstellung und Kennzeichnung der rezenten Tierformen. Mollusca: Cyclophoridae, Lief. 16. Berlin.
- Kobelt W, Möllendorff OF von (1897) Catalog der gegenwärtig lebend bekannten Pneumonopomen. Nachrichtenblatt der Deutschen Malakozoologischen Gesellschaft 1(3): 73–192.
- Kongim B, Panha S, Naggs F (2006) Karyotype of land operculate snails of the genus *Cyclophorus* (Prosobranchia: Cyclophoridae). Invertebrate Reproduction & Development 49: 1–8. doi: 10.1080/07924259.2006.9652188
- Kongim B, Sutcharit C, Tongkerd P, Panha S (2013) Karyotypes of the snorkel snail genera *Pterocyclos* and *Rhiostoma* (Prosobranchia: Cyclophoridae). The Raffles Bulletin of Zoology 61(1): 13–20.
- Kuroda T (1928) Catalogue of the shell bearing Mollusca of Amami-Oshima (Oshima, Osumi). Special publication of the Kagoshima-Ken Educational Investigation Committee, Kagoshima, Japan, 126 pp.
- Kuzminykh AA, Schileyko AA (2005) Slugs of the family Anadenidae Pilsbry, 1948, (Gastropoda: Pulmonata) with description of two new subgenera and three new species. Ruthenica 15(2): 109–118.
- Kuznetsov AG (1996) *Himalodiscus aculeatus* Kuznetsov, gen. et sp. nov. (Pulmonata, Endodontidae) from Nepal. Ruthenica 5(2): 163–165.
- Kuznetsov AG, Schileyko AA (1997) New data on Enidae (Gastropoda, Pulmonata) of Nepal. Ruthenica 7(2): 133–140.
- Kuznetsov AG, Schileyko AA (1999) Two new species of the genus *Pupinidius* Moellendorff, 1901 (Enidae, Pulmonata), and the distribution of the genus in Nepal. Ruthenica 9(2): 117–121.
- Lee YC, Leu KY, Wu WL (2008) A molecular phylogenetic investigation of *Cyathopoma* (Prosobranchia: Cyclophoridae) in East Asia. Zoological Studies 47(5): 591–604.
- Maassen WJM (2002) Remarks on Diplommatinidae from Sumatra, Indonesia with descriptions of eleven new species (Gastropoda, Prosobranchia). Basteria 66: 163–182.
- Maassen WJM (2006) Remarks on *Alycaeus* species from South-East Asia, with the descriptions of four new species with keeled shells (Gastropoda, Caenogastropoda, Cyclophoridae). Basteria 70: 133–139.
- Maceira D, Miquel SE, Espinosa J, Virgillito M, Lauranzon B (2013) Moluscos terrestres exóticos y primera cita de la familia Punctidae (Mollusca: Pulmonata: Gastropoda) y de su especie *Paralaoma servilis* para Cuba. Solenodon 11: 95–102.

- Martens E von (1860) Die Heliceen, nach natürlicher Verwandtschaft systematisch geordnet von Joh. Christ. Albers. Zweite Ausgabe nach dem hinterlassenen Manuskript besorgt von Eduard von Martens. Wilhelm Engelmann, Leipzig.
- Mead AR (1995) Anatomical studies reveal new phylogenetic interpretations in *Lissachatina* (Pulmonata: Achatinidae). *Journal of Molluscan Studies* 61: 257–273. doi: 10.1093/mollus/61.2.257
- Minato H (2005) Two new species of *Chamalycaeus* (Gastropoda: Alycaeidae) from Miyazaki Prefecture, Southeastern Kyushu, Japan. *Venus* 64(1–2): 39–44.
- Mitra SC, Dey A, Ramkrishna (2005) Pictorial handbook: Indian land snails, Zoological Survey of India, 344 pp.
- Mordan PB (1988) Land Molluscs of the Wahiba Sands. *Journal of Oman Studies*. Special Report no. 3.
- Naggs F (1989) *Gulella bicolor* (Hutton) and its implications for the taxonomy of streptaxids. *Journal of Conchology* 33: 165–168.
- Naggs F (1994) The reproductive anatomy of *Paropeas achatinaceum* and new concept of *Paropeas* (Pulmonata: Achatinoidea: Subulinidae). *Journal of Molluscan Studies* 60: 175–191. doi: 10.1093/mollus/60.2.175
- Naggs F (1997) William Benson and the early study of land snails in British India and Ceylon. *Archives of Natural History* 24(1): 37–88. doi: 10.3366/anh.1997.24.1.37
- Naggs F, Raheem DC (2000) Land snail diversity in Sri Lanka. The Natural History Museum, London, UK, 216 pp.
- Nekola JC (2014) Overview of the North American terrestrial gastropod fauna. *American Malacological Bulletin* 32(1): 1–35.
- Nesemann H, Sharma S, Sharma G, Khanal SN, Pradhan B, Shah DN, Tachamo RD (2007) Aquatic Invertebrates of the Ganga River basin Vol 1 - Mollusca, Annelida, Crustacea (in part). Published by Hasko Nesemann. ISBN 978-99946-2-674-8
- Nevill G (1877) The list of the Mollusca brought back by Dr J Anderson from Yunnan and Upper Burma with description of new species. *The Journal of the Asiatic Society of Bengal* 46: 14–41.
- Nevill G (1878) Hand list of Mollusca in the Indian Museum Calcutta, Part I. Gastropoda, Pulmonata and Prosobranchia-Neurobranchia. Calcutta, 338 pp. doi: 10.5962/bhl.title.23978
- Nordsieck H (1973) Zur Anatomie und Systematik der Clausilien, XII, Phaedusinae, I: Phaedusinaus Nepal und ihre systematische Stellung innerhalb der Unterfamilie. *Archiv für Molluskenkunde* 103: 63–85.
- Nordsieck H (2002) Annotated checklist of the South East Asian Phaedusinae with the description of new taxa (Gastropoda, Pulmonata, Clausiliidae). *Basteria* 66: 85–100.
- Panha S (1995–1996) A checklist and classification of the terrestrial pulmonate snails of Thailand. *Walkerana* 8(19): 31–40.
- Panha S, Burch JB (2005) An introduction to the microsnailes of Thailand. *Malacological Review* 37/38: 1–155.
- Patterson CM (1975) *Quickia aldabraensis* (Mollusca, Gastropoda: Pulmonata, Succineidae), a new species of land snail from Aldabra atoll, western Indian Ocean. *Bulletin of the British Museum (Natural History) Zoology* 28: 177–186.

- Pfeiffer L (1842) *Symbolae ad historiam heliceorum. Sectio altera*. Fischer, Cassel.
- Pfeiffer L (1846) Nachtrag zur Revision der Gattung *Cyclostoma*. *Zeitschrift für Malakozoologie* 3: 86.
- Pfeiffer L (1853) Die gedeckelten Lungenschnecken (Helicinacea et Cyclostomacea) in Abbildungen nach der Natur. *Systematisches Conchylien-Cabinet* 1(19): 8–400.
- Pilsbry HA (1916–1918) Pupillidae (Gastrocoptinae). *Manual of Conchology, Second Series: Pulmonata* 24. Academy of Natural Sciences of Philadelphia, 1–380.
- Pilsbry HA (1920–1921) Pupillidae (Vertiginidae and Pupillinae). *Academy of Natural Sciences of Philadelphia. Manual of Conchology, Second Series: Pulmonata* 26: 1–254.
- Pilsbry HA (1926) The land mollusks of the Republic of Panama and the Canal zone. *Proceedings of the Academy of Natural Sciences of Philadelphia* 78: 57–126.
- Pilsbry HA (1946) Notes on the anatomy of Australian and Galapagos Bulimulidae (Mollusca, Pulmonata). *Notulae Naturae of the Academy of Natural Sciences of Philadelphia* 168: 1–4.
- Pilsbry HA, Tryon GW (1906) Achatinidae: Stenogyrinae and Coeliaginae. *Academy of Natural Sciences of Philadelphia. Manual of Conchology, Second Series: Pulmonata* 18: 1–357.
- Pilsbry HA, Tryon GW (1908–1909) Structural and Systematic with illustrations of the species: *Caeciloides*, *Glessula* and Partulidae. *Academy of Natural Sciences of Philadelphia. Manual of Conchology, Second Series: Pulmonata* 20(77–78): 1–154.
- Pokryszko BM, Auffenberg K, Hlaváč JC, Naggs F (2009) Pupilloidea of Pakistan (Gastropoda: Pulmonata): Truncatellininae, Vertigininae, Gastrocoptinae, Pupillinae (in part). *Annales Zoologici (Warszawa)* 59(4): 423–458. doi: 10.3161/000345409X484847
- Prasankok P, Sutcharit C, Tongkerd P, Panha S (2009) Biochemical assessment of the taxonomic diversity of the operculate land snail, *Cyclophorus fulguratus* (Gastropoda: Cyclophoridae) from Thailand. *Biochemical Systematics and Ecology* 36: 900–906. doi: 10.1016/j.bse.2008.11.005
- Preece RC, Naggs F (2014) *Kaliella barrakporensis* (Pfeiffer), a new hot-house alien in Britain. *Journal of Conchology* 41(6): 781–782.
- Preston HB (1914) Characters of new land and freshwater shells from the Naga Hills, Assam. *Proceedings of the Malacological Society of London* 11: 19–24.
- Raheem DC, Budha PB, Naggs F, Preece RC (2010) An illustrated guide to the terrestrial snails of Nepal. *Natural History Museum, London*.
- Raheem DC, Taylor H, Ablett J, Preece RC, Aravind NA, Naggs F (2014) A systematic revision of the land snails of the Western Ghats of India. *Tropical Natural History, Supplement* 4. Chulalongkorn University, Bangkok, Thailand, 1–285.
- Raheem DC, Naggs F (2006) An illustrated guide to the land snails of Sri Lankan natural forest and cultivated habitats. *Natural History Museum, London*.
- Ramakrishna, Mitra SC, Dey A (2010) Annotated checklist of Indian land molluscs. *Zoological Survey of India, Kolkata*.
- Raut SK (1999) The giant African land snail *Achatina fulica* Bowdich in Nepal and Bhutan. *Journal of the Bombay Natural History Society* 96(1): 173.
- Raut SK, Barker GM (2002) *Achatina fulica* Bowdich and other Achatinidae as pests in tropical agriculture. In: Barker GM (Ed.) *Molluscs as crop pests*. CAB International, 55–114.
- Riedel A (1980) *Genera zonitidarum*. Dr. W. Backhuys, Publisher, Rotterdam.

- Rosenberg G, Muratov IV (2006) Status report on the terrestrial Mollusca of Jamaica. Proceedings of the Academy of Natural Sciences, Philadelphia 155: 117–161. doi: 10.1635/i0097-3157-155-1-117.1
- Roth B, Sadeghian PS (2006) Checklist of the land snails and slugs of California, Second Edition. Contributions in Science, Santa Barbara Museum of Natural History 3: 1–82.
- Rowson B, Tattersfield P, Symondson WOD (2011) Phylogeny and biogeography of tropical carnivorous land-snails (Pulmonata: Streptaxoidea) with particular reference to East Africa and Indian Ocean. Zoologica Scripta 40(1): 85–98. doi: 10.1111/j.1463-6409.2010.00456.x
- Sarasúa PH (1944) Los Moluscos de los Jardines Cubanos. Revista de la Sociedad Malacológica “Carlos de la Torre” 2(2): 59–63.
- Sasaki T (2008) Micromolluscs in Japan: taxonomic composition, habitats, and future topics. Zoosymposia 1: 147–232. doi: 10.11646/zoosymposia.1.1.12
- Schalie H van der (1948) The land- and freshwater mollusks of Puerto Rico. Miscellaneous Publications, Museum of Zoology, University of Michigan No. 70. University of Michigan Press, 134 pp.
- Schileyko AA (1998) Treatise on recent terrestrial pulmonate molluscs Part 2. Gastrocoptidae, Hypselostomatidae, Vertiginidae, Truncatellinidae, Pachnodidae, Enidae, Sagdidae. Ruthenica, Supplement 2: 129–256.
- Schileyko AA (1999) Treatise on recent terrestrial pulmonate molluscs Part 4. Draparnaudiidae, Caryodidae, Macrocyclidae, Acavidae, Clavatoridae, Dorcasidae, Sculptariidae, Corillidae, Plectopylidae, Megalobulimidae, Strophocheilidae, Cerionidae, Achatinidae, Subulinidae, Glessulidae, Micractaeonidae, Ferrussaciidae. Ruthenica, Supplement 2: 437–556.
- Schileyko AA (2000) Treatise on recent terrestrial pulmonate molluscs Part 6. Rhytididae, Chlamydephoridae, Systrophidae, Haplotrematidae, Streptaxidae, Spiraxidae, Oleacinidae, Testacellidae. Ruthenica, Supplement 2: 731–880.
- Schileyko AA (2002) Treatise on recent terrestrial pulmonate molluscs Part 9. Helicarionidae, Gymnarionidae, Rhysotinae, Ariophantidae. Ruthenica, Supplement 2: 1167–1302.
- Schileyko AA (2003) Treatise on recent terrestrial pulmonate molluscs Part 11. Trigonochlamyidae, Papillodermidae, Vitrinidae, Limacidae, Bielziidae, Agriolimacidae, Boettgeriidae, Camaenidae. Ruthenica, Supplement 2: 1467–1626.
- Schileyko AA (2004) Treatise on recent terrestrial pulmonate molluscs Part 12. Bradybaenidae, Monadeniidae, Xanthonychidae, Epiphragmophoridae, Helminthoglyptidae, Etonidae, Humboldtianidae, Sphincterochilidae, Cochlicellidae. Ruthenica, Supplement 2: 1627–1763.
- Schileyko AA (2007) Treatise on recent terrestrial pulmonate molluscs Part 15. Oopeltidae, Anadenidae, Arionidae, Philomycidae, Succineidae, Athoracophoridae. Ruthenica, Supplement 2: 2049–2210.
- Schileyko AA (2011) Checklist of land pulmonate molluscs of Vietnam (Gastropoda: Stylomatophora). Ruthenica 21(1): 1–68.
- Schileyko AA, Balashov IA (2012) *Pyramidula kuznetsovi* sp. nov. a new species of land molluscs from Nepal (Pulmonata, Pyramidulidae). Ruthenica 22(1): 41–45.

- Schileyko AA, Frank C (1994) Some terrestrial Mollusca of the Nepalesian fauna. *Archiv für Molluskenkunde* 123(1/6): 127–136.
- Schileyko AA, Kuznetsov AG (1996) A new genus of the Subulinidae (Pulmonata) from Nepal. *Ruthenica* 5(2): 158–160.
- Schileyko AA, Kuznetsov AG (1998a) Land snails of the genus *Landouria* Godwin-Austen, 1918 and some other Bradybaenidae of Nepal (Gastropoda, Pulmonata). *Ruthenica* 8(1): 43–54.
- Schileyko AA, Kuznetsov AG (1998b) On the taxonomic position of the genus *Himalodiscus* Kuznetsov, 1996 with a description of a new species. *Ruthenica* 8(1): 85–88.
- Scott B (1996) Phylogenetic relationships of the Camaenidae (Pulmonata: Stylommatophora: Helicoidea). *Journal of Molluscan Studies* 62: 65–73. doi: 10.1093/mollus/62.1.65
- Sherborn CD (1923) Index Animalium Part II. Index Aff.-Anus, 129–384. http://www.sil.si.edu/digitalcollections/indexanimalium/volumes/pagedisplay.cfm?filename=SIL34_02_02_0104&recordid=74260
- Sherborn CD (1927) Index Animalium Part XII. Index haani-implicatus, 2881–3136. http://www.sil.si.edu/digitalcollections/indexanimalium/volumes/pagedisplay.cfm?filename=SIL34_02_12_0184&recordid=207160
- Sherborn CD (1928) Index Animalium Part XVI. Index melanophysa-munchissoni, 3971–4194. http://www.sil.si.edu/digitalcollections/indexanimalium/volumes/pagedisplay.cfm?filename=SIL34_02_16_0188&recordid=262638
- Simone LRL (2013) Anatomy of predator snail *Huttonella bicolor*, an invasive species in Amazon rainforest, Brazil (Pulmonata, Streptaxidae). *Papéis Avulsos de Zoologia* 53(3): 47–58.
- Simroth H (1901) [1902] Die Nacktschneckenfauna des Russischen Reiches. Kaiserlichen Akademie der Wissenschaften, St. Petersburg. doi: 10.5962/bhl.title.46383
- Sowerby GB (1850) Descriptions of some additional species of the genus *Cyclostoma*. *Thesaurus Conchyliorum* 1(1): 157–168.
- Stanisic J (1981) The Carnivorous Land Snail *Gulella* (*Huttonella*) *bicolor* (Hutton, 1834) in Australia (Pulmonata: Streptaxidae). *Journal of the Malacological Society of Australia*, 5(1–2): 84–86. doi: 10.1080/00852988.1981.10673939
- Stanisic J (1998) Systellommatophora. In: Beesly PL, Ross GJB, Wells A (Eds) *Mollusca: The Southern Synthesis. Fauna of Australia. Volume 5*. CSIRO Publishing, Part B, 1060–1067.
- Subba BR (2003) Molluscan checklist of Ghodaghodi Tal area, Kailali District. *Our Nature* 1: 1–2.
- Subba BR, Ghosh TK (2001) Terrestrial mollusks from Nepal. *Journal of the Bombay Natural History Society* 98(1): 58–61.
- Subba BR, Ghosh TK (2008) Report on some terrestrial molluscs from different regions of Nepal. *Journal of Natural History Museum, Tribhuvan University* 23: 78–81.
- Surana R, Subba BR, Limbu KP (2004) Report of mollusks from Chimdi Lake (Birju Tal), Sunsari District eastern Nepal. *Our Nature* 2: 45–46.
- Sutcharit C, Naggs F, Wade CM, Fontanilla I, Panha S (2010) The new family Diapheridae, a new species of *Diaphera* Albers from Thailand, and the position of the Diapheridae within a molecular phylogeny of the Streptaxoidea (Pulmonata: Stylommatophora). *Zoological Journal of the Linnean Society* 160: 1–16.

- Sykes ER (1898) List of the species of *Cataulus* found in Ceylon with descriptions of some new land-shells from that Island. Proceedings of the Malacological Society of London 3: 65–74.
- Sysoev A, Schileyko A (2009) Land snails and slugs of Russia and adjacent countries. Pensoft Series Faunistica No 87. Sofia, Bulgaria, 312 pp., 142 plates.
- Tarruella A, Domènech JL (2011) Listado taxonómico ilustrado de la familia Cyclophoridae J.E. Gray, 1847 (Mollusca: Gastropoda): Parte 2. La subfamilia Alycaeinae J.E. Gray, 1850. Spira 4(1): 71–76.
- Thompson FG (2011) An annotated checklist and bibliography of the land and freshwater snails of Mexico and Central America. Bulletin of the Florida Museum of Natural History 50(1): 1–299.
- Tielecke H (1940) Anatomie, Phylogenie und Tiergeografie der Cyclophoriden. Berlin.
- Tillier S (1980) Gastéropodes terrestres et fluviatiles de Guyane Française. Mémoires du Muséum national d'histoire naturelle. Paris, Sér. A, Zoologie 118: 1–19.
- Tillier S, Jackson GVH, MacFarlane R (1993) Giant African snail, 2nd edition. Pest Advisory Leaflet - South Pacific Commission, No. 6: 4.
- Tumpeesuwan S, Panha S (2008) First record of the genus *Schistoloma* Kobelt, 1902 (Prosobranchia: Pupinidae) in Thailand. The Natural History Journal of Chulalongkorn University 8(1): 65–67.
- Vaught KC (1989) A classification of the living Mollusca. American Malacologists, Melbourne, Florida, 195 pp.
- Venmans LAWC (1956) Notes on *Alycaeus*. Proceedings of the Malacological Society of London 32(8): 81–87.
- Verdcourt B (2006) A revised list of the non-marine Mollusca of East Africa (Kenya, Uganda and Tanzania, excluding Lake Malawi). Published by the author, Maidenhead, England, 75 pp.
- Wade CM, Hudelot C, Davison A, Naggs F, Mordan PB (2007) Molecular phylogeny of the helicoid land snails (Pulmonata: Stylommatophora: Helicoidea), with special emphasis on the Camaenidae. Journal of Molluscan Studies 73(4): 411–415. doi: 10.1093/mollus/eym030
- Webster NB, Van Dooren TJ, Schilthuizen M (2012) Phylogenetic reconstruction and shell evolution of the Diplommatinidae (Gastropoda: Caenogastropoda). Molecular Phylogenetics and Evolution, 63(3): 625–638. doi: 10.1016/j.ympev.2012.02.004
- Wenz W (1939) Allgemeiner Teil und Prosobranchia. In: Schindewolf OH (Ed.) Handbuch der Paläozoologie, Band 6, Gastropoda. Berlin, 481–720.
- Wiktor A (2001a) A review of Anadenidae (Gastropoda: Pulmonata) with a description of a new species. Folia Malacologica 9(1): 3–26. doi: 10.12657/folmal.009.002
- Wiktor A (2001b) Taxonomic position of *Kasperia* Godwin-Austen, 1914 (Gastropoda: Pulmonata: Limacidae). Folia Malacologica 9(1): 37–38. doi: 10.12657/folmal.009.004
- Wiktor A, Bössneck U (2004) *Limax (Limax) seticus* n. sp. from high mountains in Nepal (Gastropoda: Pulmonata: Limacidae). Folia Malacologica 12(4): 183–187. doi: 10.12657/folmal.012.017
- Wiktor A, Chen De-Niu, Wu M (2000) Stylommatophoran slugs of China (Gastropoda: Pulmonata) *Prodromus*. Folia Malacologica 8(1): 3–35. doi: 10.12657/folmal.008.002

- Wiktor A, Jurkowaska J (2007) The collection of terrestrial slugs (Gastropoda: Pulmonata) at the Museum of Natural History, Wroclaw University (Poland). *Folia Malacologica* 15(2): 83–93.
- Wiktor A, Naggs F, Gupta PK (1999) *Turcomilax (Taulimax) oli* sp. n. from the Kumaun Himalaya, India (Gastropoda: Pulmonata: Limacidae). *Malakologische Abhandlungen* 19: 225–231.
- Wu M (2002) Study on Bradybaenid land snails in NW Sichuan (Gastropoda: Pulmonata: Stylommatophora). *Zoological Research* 23(6): 504–513.
- Wu M (2004) Preliminary phylogenetic study of Bradybaenidae (Gastropoda: Stylommatophora: Helicoidea). *Malacologia* 46(1): 79–125.
- Wu M, Zheng W (2009) A review of Chinese *Pupinidius* Moellendorff (Gastropoda, Stylommatophora: Enidae), with the description of new species. *Zootaxa* 2053: 1–31.
- Yen TC (1939) Die chinesischen Land- und Süßwasser-Gastropoden des Natur-Museums Senckenberg. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 444: 1–233.
- Zilch A (1953) Die Typen und Typoide des Natur-Museums Senckenberg, 9: Mollusca, Cyclophoridae, Diplommatininae. *Archiv für Molluskenkunde* 82: 1–47.
- Zilch A (1956) Die Typen und Typoide des Natur-Museums Senckenberg, 17: Mollusca, Cyclophoridae, Cyclophorinae-Cyclophoreae (3). *Archiv für Molluskenkunde* 85: 33–54.
- Zilch A (1959) Euthyneura. *Handbuch der Paläozoologie Band 6, Gastropoda* 1–2: 1–400.
- Zilch A (1960) Euthyneura. *Handbuch der Paläozoologie Band 6, Gastropoda* 3–4: 401–835.
- Zilch A (1974) Vinzenz Gredler und die Erforschung der Weichtiere Chinas durch Franziskaner aus Tirol. *Archiv für Molluskenkunde* 104(4–6): 171–228.

Illustrated type catalogue of *Amphidromus* Albers, 1850 in the Natural History Museum, London, and descriptions of two new species

Chirasak Sutcharit¹, Jonathan Ablett², Piyoros Tongkerd¹,
Fred Naggs², Somsak Panha¹

1 Animal Systematics Research Unit, Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok 10330, Thailand **2** Division of Higher Invertebrates, Natural History Museums, London, SW7 5BD, United Kingdom

Corresponding authors: Chirasak Sutcharit (jirasak4@yahoo.com); Somsak Panha (somsak.pan@chula.ac.th)

Academic editor: Eike Neubert | Received 23 September 2014 | Accepted 9 March 2015 | Published 30 March 2015

<http://zoobank.org/334F0DAA-1CD1-40F4-9B8C-A62E4A97A732>

Citation: Sutcharit C, Ablett J, Tongkerd P, Naggs F, Panha S (2015) Illustrated type catalogue of *Amphidromus* Albers, 1850 in the Natural History Museum, London, and descriptions of two new species. ZooKeys 492: 49–105. doi: 10.3897/zookeys.492.8641

Abstract

The collection of the Southeast Asian tree snail genus *Amphidromus* Albers, 1850 at the Natural History Museum, London includes more than 100 lots of type specimens representing 85 name-bearing types, 9 paratypes and 6 paralectotypes, and one *nomen nudum*. Lectotypes are here designated for *A. cambojiensis*, *A. perakensis globosus*, *A. columellaris gloriosa*, *A. maculiferus inflata*, *A. lepidus*, *A. sinistralis lutea*, *A. moniliferus*, *A. maculiferus obscura*, *A. sinistralis rosea* and *A. sinensi vicaria*. In addition, the missing types of A.A. Gould were discovered and their type status is discussed. A complete catalogue of these types, including colour photographs is provided for the first time. After examining these type specimens, two new *Amphidromus* species, *Amphidromus* (*Syndromus*) *globonevilli* Sutcharit & Panha, **sp. n.** and *Amphidromus* (*Syndromus*) *principalis* Sutcharit & Panha, **sp. n.** were recognized and are described herein.

Keywords

Tree snails, systematics, molluscs, type specimen, Southeast Asia, NHM, taxonomy

Introduction

Amphidromus Albers, 1850 is a genus of tree dwelling snails; the members of this genus are distributed in the region from Assam in India throughout Indochina, the southern of the Philippines, Indonesia (east of Weber's line) with a single species occurring in the Northern Territory of Australia (Pilsbry 1900, Solem 1959, 1983, Laidlaw and Solem 1961, Sutcharit and Panha 2006). This diverse genus of large snails with colorful shells has long been known to malacologists. The first revision of *Amphidromus* by Fulton (1896a) arranged nominal species into 19 species groups, and included descriptions of new species with illustrations. Pilsbry's revision (1900) provided more complete descriptions and redescriptions and figured species, some for the first time, becoming the standard identification guide for the group. Laidlaw and Solem (1961) gathered and documented further information on previously recognised species and provided a list of all species-group names applied to *Amphidromus*. The most significant issue of Laidlaw and Solem (1961) was the recording of the primary type specimens, the institution where they were deposited and registration number for all the species within the entire genus. More than 300 nominal species-group names have been applied to this genus (Richardson 1985), but only 75 were recognized as distinct species in Laidlaw and Solem (1961), since then an additional 16 species have been described and validated (see Solem 1983, Dharma 1993, 2007, Panha 1996, Lehmann and Maassen 2004, Severns 2006, Sutcharit and Panha 2006b, 2011, Chan and Tan 2010, Cilia 2013). This indicates that *Amphidromus* are morphologically variable, especially in shell colour, which has led to an over-description of some taxa, and species recognition based solely on published descriptions and figures are being difficult. Therefore, type specimens are the ultimate reference point for species identification, and represent an international standard providing the basis of nomenclatural stability when following the International Code of Zoological Nomenclature (ICZN). Comparison with the primary type specimens will minimise this difficulty, at least within the constraints of morphological taxonomy.

The Natural History Museum in London (hereafter the NHM), formerly the British Museum (Natural History), is one of the oldest and largest museum collections with mollusc specimens acquired from many varied sources and collectors (Dance 1986). Two collections that contain important type material of the genus *Amphidromus* are those of Hugh Cuming (containing 27 type specimens of *Amphidromus* described by L. Pfeiffer and L. Reeve) and Hugh Fulton (included 60 type specimens of *Amphidromus*). These two collections were deposited at the NHM and form the largest collection of primary type specimens of *Amphidromus*, being comprised of 87 taxa (~one-fourth of the currently known *Amphidromus* taxa). Until now, many of these types have not been figured or adequately figured (Laidlaw and Solem 1961). The second largest collection of *Amphidromus* type material is in the Senckenberg Forschungsinstitut und Naturmuseum in Frankfurt (51 taxa), where all the specimen lots have been catalogued and illustrated (Zilch 1953). Thirty-three type lots of *Amphidromus*

are housed in the National Museum of Natural History, Smithsonian Institution the remaining type lots are distributed amongst other museums. However, the primary types of 57 taxa had not previously been traced (Laidlaw and Solem 1961). Some of these ‘missing’ lots have subsequently been traced such as those located at the National Museum of Wales, Cardiff (Wood and Gallichan 2008).

Recent research on *Amphidromus* systematics including detailed morphological studies of reproductive anatomy and molecular phylogenetics (Sutcharit et al. 2007) needs to be integrated with a critical assessment of type material. This will allow for the correct application of nomenclature and the recognition of suitable voucher specimens that can act as surrogates of type specimens for DNA and additional morphological work, since historical species were often described based solely on shells. The aim of this paper is to evaluate the type status of *Amphidromus* type specimens in the NHM collections and to figure specimens and designate lectotypes in accordance with ICZN (1999: Art. 74) guidelines. Evaluating species as biological entities is largely outside of the scope of this study. However, examination of these type collections, revealed two *Amphidromus* species that we consider to be new and these are described herein.

Materials and methods

Collections: The primary type specimens (i.e. holotype, lectotype and syntype/syn-types) along with the paratype(s) and paralectotype(s) of *Amphidromus* described from the early 19th century until 2013 and deposited at the NHM were examined. Those specimens that were confirmed as forming part of the type series of species, where a unique type had not been designated, were considered to be syntype lots. In cases where a holotype was not explicitly designated but where in the original publication the species name was clearly based on an individual shell, these were taken to be the holotype fixed by monotypy. Lectotypes mentioned in this catalogue have been designated by Laidlaw and Solem (1961), unless otherwise stated, and conform to the ICZN guidelines (1999).

From the published list of Gould’s type specimens, Johnson (1964) presumed that some of the unlocated types were probably to be found in the NHM. Although, most of A. Gould’s types can be found in the Museum of Comparative Zoology, Harvard University, there was a record that Gould presented the specimens of some species that he had described to Hugh Cuming (Johnson 1964). Among Gould’s types that were unequivocally recognized in the NHM, the original labels are obviously marked with “Type” and their locality is congruent with the recorded type locality. For example, Johnson (1964: 88) certainly accepted the type specimen of “*Anodonta horda* Gould, 1855” was in the H. Cuming collection and designated a specimen (NHMUK registration no. 196465) as the lectotype (Fig. 1A). Such evidence is, therefore, taken into account in order to distinguish Gould’s type specimens.



Figure 1. Original labels of the type specimens. **A** Evidence of the original labels of Gould's type specimens in the H. Cuming collection. Label of *Anodonta horda* Gould, 1855, lectotype (NHMUK 196465) designated by Johnson (1964: 88). The original label marked with "Type" does not frequently occur in H. Cuming's collection, which suggests that the specimen was received from Gould **B** Label of *A. atricallosus* (Gould, 1843), the printed label attached on the top is typical of the way that Reeve used to indicate the specimen examined and figured in the *Conchologica Iconica* **C** Label of *A. bataviae* (Grateloup, 1840) **D** Label of *A. bulowi* Fruhstorfer, 1905 **E** Label of *A. cruentatus* (Morelet, 1875) **F** Label of *A. hosei* Smith, 1895.

This illustrated catalogue provides the shell measurements and photographs of the name-bearing types. All specimens considered as forming part of the type series were photographed in the standard position, apertural and abapertural views. Additional views were also photographed for the taxa that have unique shell characters. The original labels were photographed and checked with the original description (Figs 1, 2). Measurements of any holotype and lectotype material were taken in mm with digital calipers. Those taxa where the primary type is housed in a different institution to the NHM, but where paratypes or paralectotypes are kept in the NHM, are also included in this illustrated catalogue.

Structure of the illustrated catalogue: The taxa in this illustrated type catalogue were checked against the original publications and are listed as given in the original description regardless of termination or incorrect original spelling, and the authorship(s) and date. Additional comments, such as the print date, availability of the name or corrected subsequent spelling, are provided in square brackets. The synonymy tabulation and the usage of each taxon name are provided in Pilsbry (1900), Laidlaw and Solem (1961) and Richardson (1985). Only the original combination of the taxon name with reference to pages, plate and/or figures are mentioned. The type locality is given verbatim as stated in the original publication. If possible, the modern name and/or regional names of the type locality are provided in square brackets. If any incongruence between the published type locality and that given on the original label occurred, this is mentioned in the comments under the remarks of those taxa. Under the type materials, primary type specimens with the NMH registration number (registered specimens are cited as NHMUK), the measurements of shell height (H) and shell width (W), and the figures are given. In addition, if the paratypes or paralectotypes of that taxa are available then the respective registration number, number of specimens with a dextral (D) or sinistral (S) coiling direction, and figures of a representative specimen are given. If necessary, remarks are given on the status of type specimens, authorships, availability of name, notes on the type locality, and other necessary comments. Full bibliographic references are provided at the end of this paper.

Institutional abbreviation: Abbreviations of the museum collections used the lists of taxa and species descriptions are listed as follows:

| | |
|--------------|---|
| CUMZ | Chulalongkorn University, Museum of Zoology, Bangkok, Thailand |
| MCZ | Museum of Comparative Zoology, Harvard University, Cambridge, UK |
| MNHN | Muséum National d'Histoire Naturelle, Paris, France |
| MZB | Museum Zoologicum Bogoriense, Indonesia |
| NHMUK | Natural History Museum, London, UK |
| RMNH | National Museum of Natural History, Leiden, Netherlands |
| SMF | Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt a.m., Germany |
| UMZC | University Museum of Zoology Cambridge, Cambridge, UK |
| ZMA | Zoological Museum of Amsterdam, Amsterdam, Netherlands |



Figure 2. Original labels of the type specimens. **A** Label of *A. lepidus* (Gould, 1856), with Pfeiffer's handwritten "sinensis Bens. var." **B** Bottom of a box with *A. adamsii luteofasciata* type specimens. The two larger glued labels are Fulton's original handwritten ones. On the right side, the vertical lines indicate an unambiguously designated lectotype in Laidlaw and Solem (1961) with reference to Fulton's (1896) original figures **C** Label of *A. masoni* (Godwin-Austen, 1876), with Godwin-Austen's handwritten the species and locality names **D** Label of *A. melanomma* (Pfeiffer, 1852), with Pfeiffer's handwritten of the specie name in blue ink **E** Label of *A. moniliferus* (Gould, 1846), the name "theobaldianus, Reeve – from type" was subsequently added up later **F** Label of *A. andamanicus nicobarica* Godwin-Austen, 1895.

Results

There are 210 type specimens representing 100 available names within the genus *Amphidromus* in the NHM collections. Only one species name “*globosa* Nevill, 1878” is considered as an unavailable nominal taxon (ICZN 1999: Art. 12). Among these available names, the NHM retained 85% of the name-bearing types exclusively as 10 holotypes, 70 lectotypes and five lots of syntype material. Of the 10 holotype lots, a lot of “*nicobarica* Godwin-Austen, 1895” was recently discovered in the general collections and recognized as the holotype (fixed by monotypy). The five syntypes are “*gracilior* Fulton, 1896”, “*melanomma* Pfeiffer, 1852”, “*robustus* Fulton, 1896”, “*rubiginosa* Fulton, 1896” and “*theobaldianus* Benson, 1857”. Among the 70 lectotype lots, ten lots were recently designated from the original type series of W. Collinge “*globosus* Fulton, 1903” and type series of H. Fulton as “*gloriosa* Fulton, 1896”, “*inflata* Fulton, 1896”, “*lutea* Fulton, 1896”, “*obscura* Fulton, 1896”, “*rosea* Fulton, 1896” and “*vicaria* Fulton, 1896”. The three long unrecognized type series of H. Cuming “*cambojiensis* Reeve, 1860”, “*lepidus* Gould, 1856” and “*moniliferus* Gould, 1846” are discovered. They are acknowledged as lectotypes to clarify their type status and promote the stability of the taxon name. The history and type evidences are summarized under each taxon.

The remaining 15% are paratypes and paralectotypes, whose name-bearing types had been designated and housed elsewhere. The original type series of six nominal taxa (“*atricallosus* Gould, 1843”, “*begini* Morlet, 1886”, “*romaensis* Rolle, 1903”, “*roseotincta* Möllendorff, 1894”, “*singalangensis* Rolle, 1908” and “*ventrosulus* Möllendorff, 1900”) are recently recognized taxa in the NHM, and are considered as paralectotypes. The other nine nominal taxa of “*abbasi* Chan and Tan, 2010”, “*albulus* Sutcharit and Panha, 2006”, “*babiensis* Laidlaw, 1954”, “*banksi* Butot, 1955”, “*classarius* Sutcharit and Panha, 2006”, “*dextrochlorus* Sutcharit and Panha, 2006”, “*iunior* Cilia, 2013”, “*rottinensis* Chan and Tan, 2010” and “*simalurensis* Laidlaw, 1954” have only the paratypes available at the NHM.

Alphabetical list of the taxa

Amphidromus abbasi Chan & Tan, 2010

Amphidromus abbasi Chan & Tan, 2008: 7, 8, fig. 1. [*nomen nudum*, ICZN 1999: Arts 8.6 and 11.1].

Amphidromus abbasi Chan & Tan, 2010: 246, fig. 1a–c.

Type locality. Approximately 1.2 km from coast, Laggaliru, Southwest Sumba, Indonesia.

Type material. Holotype MZB-Gastropoda 14.232, paratypes NHMUK 20080623 (2S, Fig. 3A).

Remarks. Chan and Tan (2008) described “*abbasi*” in the Occasional Molluscan Papers which does not fulfill the ICZN guidelines and could not be made available

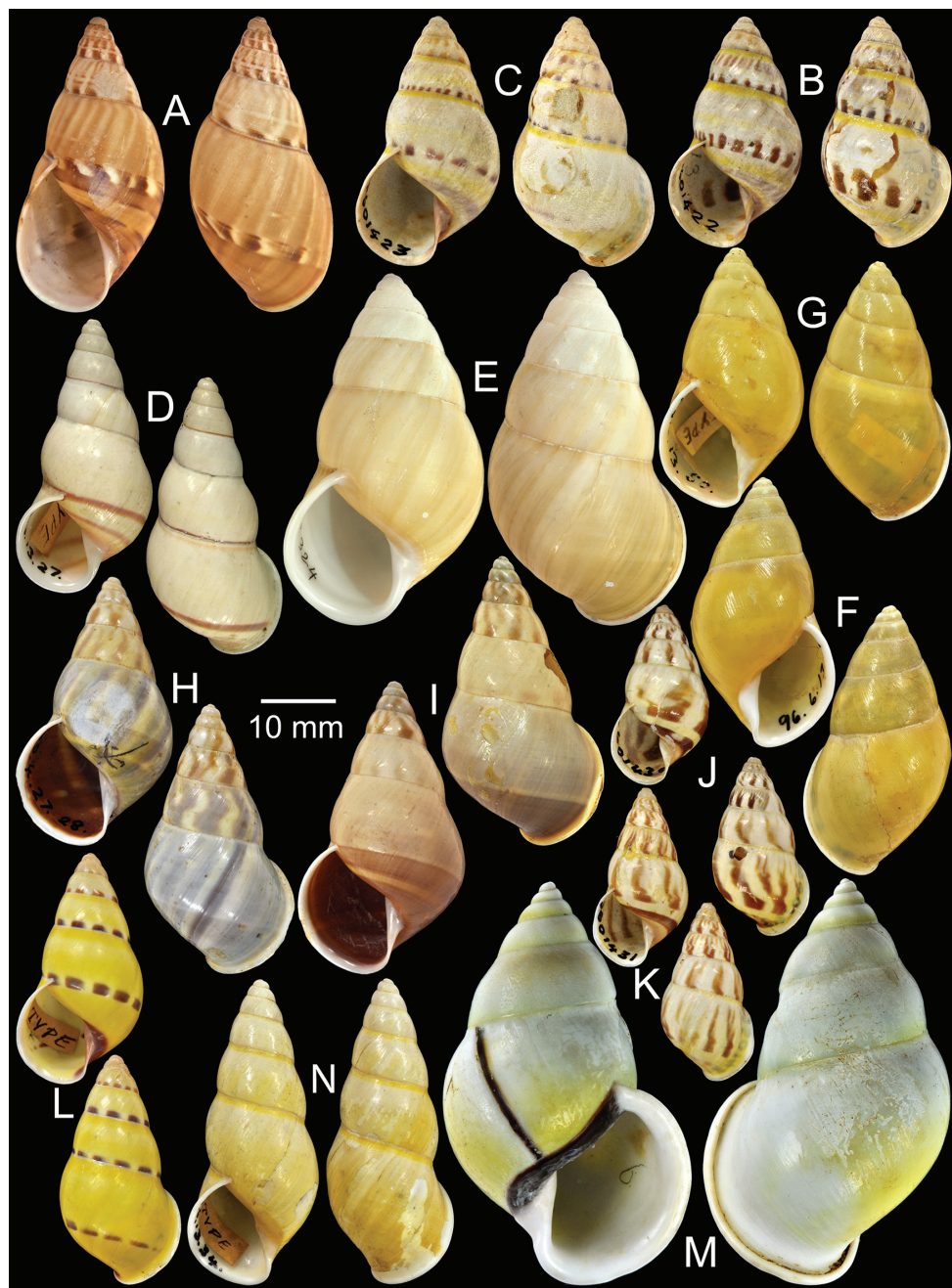


Figure 3. Type specimens of *Amphidromus* spp. **A** Paratype of *A. abbasi* **B–C** *A. adamsii*, **B** lectotype and **C** paralectotype **D** Lectotype of *A. suspectus albolabiatus* **E** Paratype of *A. inversus albulus* **F–G** *A. alticola*, **F** lectotype and **G** paralectotype **H–I** *A. angulatus*, **H** lectotype and **I** paralectotype **J–K** *A. areolatus*, **J** lectotype and **K** paralectotype **L** Lectotype of *A. adamsii articulata* **M** Paralectotype of *A. atricallosus* **N** Lectotype of *A. adamsii aureocincta*.

(ICZN 1999: Arts 8.6 and 11.1). However, “*abbasi*” was later published correctly (ICZN 1999: Art. 8) and made available in Chan and Tan (2010).

The authors stated that three specimens were housed in the NHM under this paratype lot, but only two are registered in the NHM collections (Chan and Tan 2010).

***Amphidromus adamsii* (Reeve, 1848)**

Bulimus adamsii Reeve, 1848: *Bulimus* plate 13, species 73, fig. 73a–d.

Type locality. Eastern Coast of Borneo (on a tall tree in an islet between Banguey and Balamangan).

Type material. Lectotype NHMUK 19601422 (Fig. 3B; H=30.0 mm, W=16.8 mm), paralectotypes NHMUK 19601423 (2S, Fig. 3C).

Remarks. There is a variation in the spelling of the species name, of which “*adamsi*” is considered as an incorrect subsequent spelling. References of the subsequent use of the incorrect spelling have been compiled in Laidlaw and Solem (1961: 597). The original and correct spelling is “*adamsii*”.

***Amphidromus suspectus albolabiata* Fulton, 1896**

Amphidromus suspectus var. *albolabiatus* Fulton, 1896a: 79, pl. 6, fig. 9.

Type locality. Timor.

Type material. Lectotype NHMUK 1896.6.3.27 (Fig. 3D; H=36.9 mm, W=17.8 mm).

***Amphidromus inversus albulus* Sutcharit & Panha, 2006**

Amphidromus inversus albulus Sutcharit & Panha, 2006a: 80–82, figs 2–4.

Type locality. Kapas Island (Pulau Kapas), Marang, Terengganu, peninsular Malaysia.

Type material. Holotype CUMZ 2323, paratypes CUMZ 2299 (3D + 8S), CUMZ 2300 (5D + 17S), CUMZ 2324 (4D + 1S), CUMZ 2327 (14D + 20S), NHMUK 20050160 (1D + 1S, Fig. 3E), SMF 327982 (1D + 1S).

***Amphidromus alticola* Fulton, 1896**

Amphidromus alticola (Boettger, MSS.), Fulton 1896a: 70, pl. 6, fig. 5, 5a.

Type locality. Java.

Type material. Lectotype NHMUK 1896.6.13.49 (Fig. 3F; H=34.7 mm, W=18.8 mm), paralectotype NHMUK 1896.6.13.50 (1D, Fig. 3G).

Remarks. Fulton wrote “Boettger, MSS.” after the species name, but it appears that there was no description by O. Boettger. The taxon is, therefore, attributed solely to Fulton.

***Amphidromus angulatus* Fulton, 1896**

Amphidromus angulatus Fulton, 1896a: 84, 85, pl. 6, fig. 3.

Type locality. Sarawak.

Type material. Lectotype NHMUK 1889.4.27.28 (Fig. 3H; H=35.1 mm, W=19.2 mm), paralectotypes NHMUK 1889.4.27.29 (2S, Fig. 3I).

***Amphidromus areolatus* (Pfeiffer, 1861)**

Bulimus areolatus Pfeiffer, 1861: 194.

Type locality. Siam [Thailand].

Type material. Lectotype NHMUK 19601430 (Fig. 3J; H=22.5 mm, W=11.9 mm), paralectotype NHMUK 19601431 (1S, Fig. 3K).

***Amphidromus adamsii articulata* Fulton, 1896**

Amphidromus adamsi var. *articulata* Fulton, 1896a: 82, pl. 5, fig. 7.

Type locality. Banguay Island [Sabah, Malaysia].

Type material. Lectotype NHMUK 1896.6.13.2 (Fig. 3L; H=31.0 mm, W=16.0 mm).

***Amphidromus atricallosus* (Gould, 1843)**

Bulimus atricallosus Gould, 1843: 140.

Bulimus atricallosus—Gould 1844: 457, pl. 24 fig. 3.

Type locality. Tavoy, British Burma [Dawei, Tanintharyi Region, Myanmar].

Type material. Lectotype (designated by Johnson 1964: 44), MCZ 169050, paralectotype NHMUK 20110203 (Figs 1B, 3M; H=54.1 mm, W=33.3 mm).

Remarks. Gould (1844: 457) mentioned that two specimens were the basis for the species description, but did not explicitly designate a holotype. Johnson (1964:

44) stated that “figured holotype MCZ 169050”, but this specimen does not match with the original figure, especially in the differing location of the dark varix (Gould 1844: pl. 24, fig. 3). The holotype that Johnson specified seems to be inappropriate, and should be interpreted as a lectotype designation (ICZN 1999: Art. 74.6) to stabilise the name. In addition, the “paratype FMNH 72403” mentioned in Sutcharit and Panha (2006b: 14) is misinterpreted. This specimen from the Laidlaw ex. Fulton collection from the type locality should be considered as a topotype.

The dextral specimen, from the H. Cuming collection and figured in Reeve (1848), has an original label stating “type” and the locality is congruent with the type locality (Fig. 1B). This supports that supposition that the specimen likely came from Gould’s type series and is, therefore, considered as the paralectotype. In addition, Johnson (1964: 88) recognized a sinistral specimen as “paratype MCZ 169051”. However, if this sinistral specimen originated from the original type series, Gould would have most likely mentioned the sinistral specimen in the original description and is in the opinion of the authors unlikely to be type material.

***Amphidromus aureocincta* Fulton, 1896**

Amphidromus adamsi var. *aureocincta* Fulton, 1896a: 83, 84, pl. 5 fig. 3, 3a.

Type locality. North Borneo.

Type material. Lectotype NHMUK 1896.6.13.34 (Fig. 3N; H=41.0 mm, W=17.2 mm), paralectotypes SMF 7551 (2S).

***Amphidromus webbi babiensis* Laidlaw, 1954**

Amphidromus webbi babiensis Laidlaw, 1954: 76–78, fig. 1.

Type locality. Poeloe Babi Island, Sumatra [Babi Island, Aceh, Indonesia].

Type material. Holotype in RMNH, paratype NHMUK 1957.11.18.1 (1S, Fig. 4A).

***Amphidromus banksi* Butot, 1955**

Amphidromus banksi Butot, 1955: 127–129, fig. 29a, pl. 5, figure top left.

Type locality. Mt. Kadam region, Pualu Panaitan, West Java [Pulau Panaitan, Banten, Indonesia].

Type material. Holotype ZMA Moll. 137447, paratypes NHMUK 1957.11.18.3 (1S, Fig. 4B), SMF 153479 (11S).

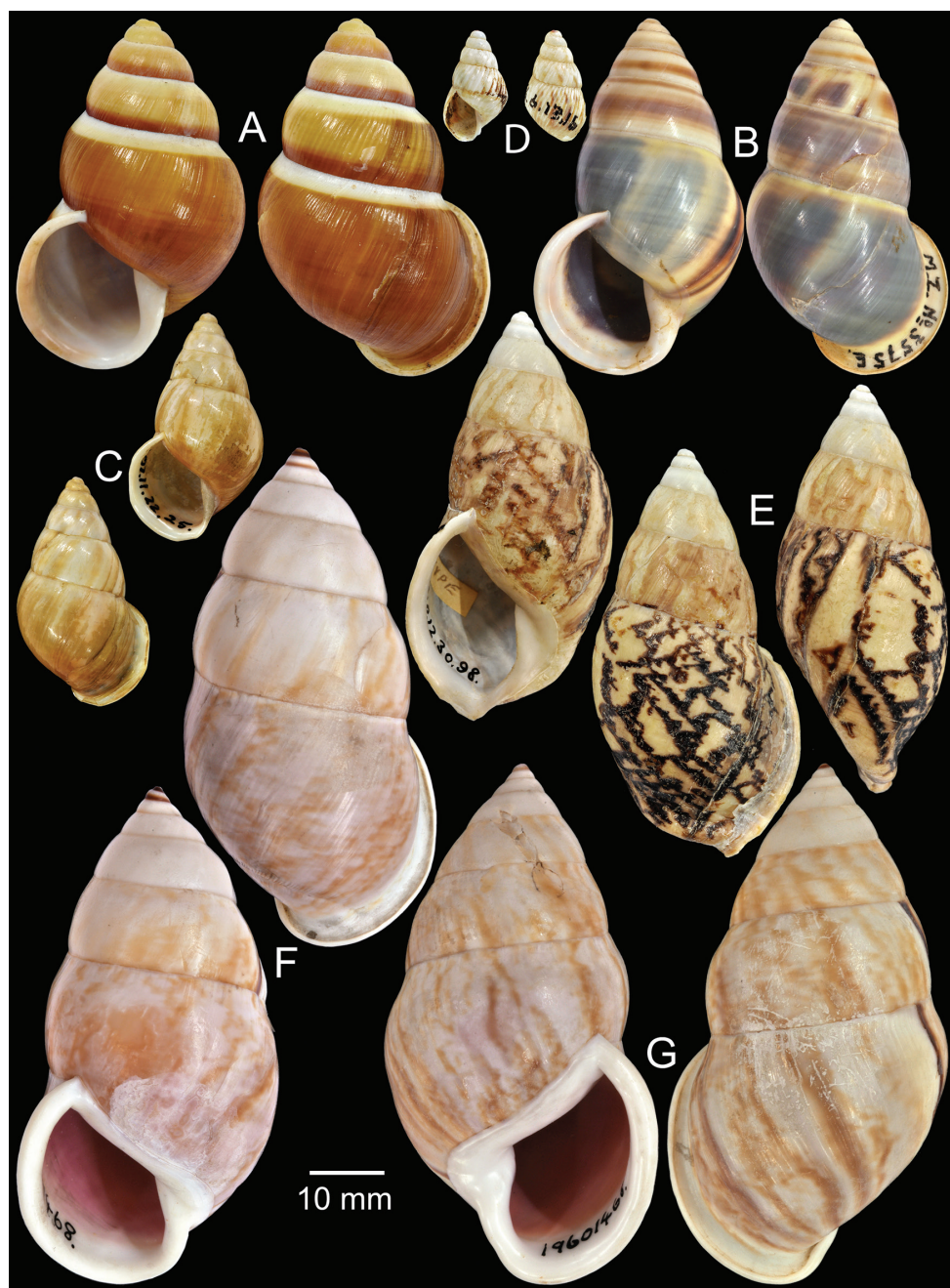


Figure 4. Type specimens of *Amphidromus* spp. **A** Paratype of *A. webbi babiensis* **B** Paratype of *A. banksi* **C** Lectotype of *A. bataviae* **D** Paralectotype of *A. begini* **E** Lectotype of *A. bulowi* **F–G** *A. cambojiensis* **F** lectotype and **G** paralectotype.

***Amphidromus bataviae* (Grateloup, 1840)**

Bulimus bataviae Grateloup, 1840b (March): 165.

Partula bataviae Grateloup, 1840a (November): 425, pl. 2, fig. 12.

Type locality. Batavia [Jakarta, Indonesia].

Type material. Lectotype NHMUK 1907.11.22.25 (Figs 1C, 4C; H=30.3 mm, W=17.3 mm).

Remarks. Jean P.S. de Grateloup described “*Bulimus bataviae*” in March 1840. Consecutively, he redescribed this taxon including an illustration in November 1840 as “*Partula bataviae*” (Fig. 1C). However, the previous published name was referred to in the November publication. Therefore, the *Bulimus* name confers the availability, and agrees with Sherborn’s (1922) list which was made available in Grateloup’s March publication (1840b).

***Amphidromus begini* (Morlet, 1886)**

Bulimus begini Morlet, 1886: 74.

Type locality. Plateau de Stang-Trang, Cambodge [Stung Treng Plateau, Cambodia].

Type material. Lectotype (designated by Fischer-Piette 1950: 158) MNHN-IM 2000-1832, paralectotype NHMUK 1896.6.13.16 (1S juvenile, Fig. 4D).

Remarks. The original description does not include an illustration, however Morlet (1889: 177, 178, pl. 6, fig. 4) re-published the description and included illustrations of the species. Fischer-Piette (1950: 158) cited a specimen in the Muséum National d’Histoire Naturelle, Paris collections as the “holotype, 25 mm” which we consider an inadvertent lectotype designation (ICZN 1999: Art. 74.5). The NHM specimen is from the H. Fulton collection ex. Dautzenberg and ex. Morlet and gives “Cambodia” as the collection locality. It is considered to be a paralectotype.

***Amphidromus bulowi* Fruhstorfer, 1905**

Amphidromus bülowi Fruhstorfer, 1905: 83, 84, pl. 1 fig. 2 (lectotype is lower figure).

Type locality. West Sumatra.

Type material. Lectotype NHMUK 1910.12.30.98 (Figs 1E, 4E; H=54.5 mm, W=27.9 mm).

***Amphidromus cambojiensis* (Reeve, 1860)**

Bulimus cambojiensis Reeve, 1860: 204.

Type locality. Cambojia [Cambodia].

Type material. Lectotype (design. n.), NHMUK 19601468/1 (Fig. 4F; H=66.6 mm, W=35.1 mm), paralectotypes NHMUK 19601468/2-3 (1S + 1D, Fig. 4G).

Remarks. *Bulimus cambojiensis* Reeve, 1860 was described from a specimen collected by H. Mouhot. When describing *Bulimus cambojiensis*, Reeve did not designate a unique type. Fulton (1896a) figured this species for the first time, but did not clearly state their syntype status. The specimen that most closely matches the original description (Reeve 1860: 204) and the figure in Fulton (1896a: pl. 7, fig. 7) is designated here as the lectotype to stabilise the name.

Variation in the spelling of the species name is found as “*cambodjensis*” or “*cambojiensis*”, but both are considered as incorrect subsequent spellings (Morelet 1875: 260, Pfeiffer 1877: 23). The correct original spelling “*cambojiensis*” is here highlighted to be maintained as proper usage.

***Amphidromus chloris* Reeve, 1848**

Bulimus chloris Reeve, 1848: *Bulimus* plate 37, species 223, fig. 223.

Type locality. Eastern Islands [probably in the area of Mindanao Islands, Philippines].

Type material. Lectotype NHMUK 19601424 (Fig. 5A; H=50.7 mm, W=22.9 mm), paralectotypes NHMUK 19601425 (4S, Fig. 5B), SMF 28065 (2S).

Remarks. The locality on the original label of the type series states the sample was collected from the Philippine Islands. The type locality is, therefore, confined to the Philippines Islands. This is congruent with the known distribution of this species from the Mindanao and Sulu archipelagoes of the Philippines (Bartsch 1917).

***Amphidromus atricallosus classarius* Sutcharit & Panha, 2006**

Amphidromus atricallosus classarius Sutcharit & Panha, 2006b: 22, figs 4h, i, 11d–f, 12d, 13d, 14e, f.

Type locality. Koh Tachai, Pangnga, southern Thailand in the Andaman sea.

Type material. Holotype CUMZ 2215, paratypes CUMZ 2011 (10S), 2232 (5S), NHMUK 20050158 (1S, Fig. 5C), SMF 327980 (1S).

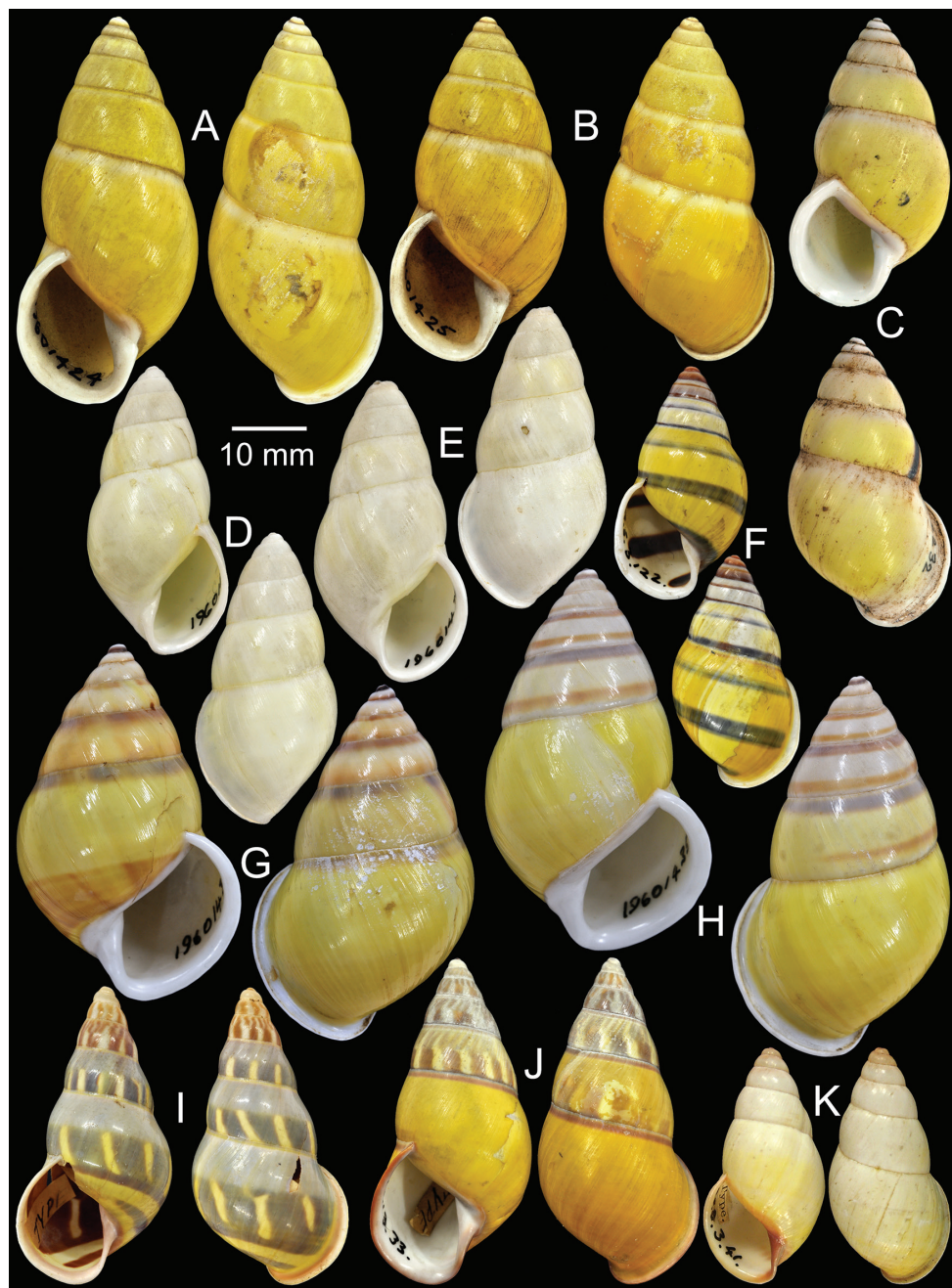


Figure 5. Type specimens of *Amphidromus* spp. **A–B** *A. chloris* **A** lectotype and **B** paralectotype **C** Paratype of *A. atricallosus classarius* **D–E** *A. cochinchinensis*, **D** lectotype and **E** paralectotype **F** Holotype of *A. cognatus* **G–H** *A. comes*, **G** lectotype and **H** paralectotype **I** Lectotype of *A. pictus concinna* **J** Lectotype of *A. everetti connectens* **K** Lectotype of *A. consobrinus*.

***Amphidromus cochinchinensis* (Pfeiffer, 1857)**

Bulimus cochinchinensis Pfeiffer, 1857a [1856]: 331, 332.

Type locality. Cochin China [Southern Vietnam].

Type material. Lectotype NHMUK 19601432 (Fig. 5D; H=38.5 mm, W=19.0 mm), paralectotype NHMUK 19601433 (1D, Fig. 5E).

***Amphidromus cognatus* Fulton, 1907**

Amphidromus cognatus Fulton, 1907: 151, pl. 9, fig. 7.

Type locality. unknown.

Type material. Holotype NHMUK 1907.5.3.122 (Fig. 5F; H=31.0 mm, W=16.5 mm).

Remarks. The type locality was said to be unknown. However, Solem (1983: 154) examined the specimens from precisely known localities, and confined the type locality to be from Port Essington, Cobourg Peninsula, Northern Territory, Australia.

***Amphidromus comes* (Pfeiffer, 1861)**

Bulimus comes Pfeiffer, 1861: 193, 194.

Type locality. Camboja [Cambodia].

Type material. Lectotype NHMUK 19601434 (Fig. 5G; H=46.7 mm, W=28.1 mm), paralectotypes NHMUK 19601435 (2D, Fig. 5H).

***Amphidromus concinna* Fulton, 1896**

Amphidromus pictus var. *concinna* Fulton, 1896a: 85, pl. 5, fig. 9.

Type locality. Kina Balu, North Borneo [Sabah, Malaysia].

Type material. Lectotype NHMUK 1896.6.13.18 (Fig. 5I; H=35.4 mm, W=17.8 mm).

***Amphidromus everetti connectens* Fulton, 1896**

Amphidromus everetti var. *connectens* Fulton, 1896a: 87, pl. 5, fig. 17 [= fig. 18 on the plate].

Type locality. North Borneo.

Type material. Lectotype NHMUK 1896.6.13.33 (Fig. 5J; H=43.1 mm, W=20.8 mm).

***Amphidromus consobrinus* Fulton, 1897**

Amphidromus consobrinus Fulton, 1897: 211, 212, pl. 6, fig. 3.

Type locality. South Flores Island [East Nusa Tenggara, Indonesia]; Sumba Island [East Nusa Tenggara, Indonesia].

Type material. Lectotype NHMUK 1897.8.3.41 (Fig. 5K; H=31.9 mm, W=15.5 mm), paralectotype NHMUK 1897.8.3.42 (1S) from South Flores.

Remarks. Fulton stated in the original description that the type series were from two localities. The specimen figured in the original description was designated as the lectotype by Laidlaw and Solem (1961: 611). As a result the type locality of this taxon is restricted to “South Flores Island, East Nusa Tenggara, Indonesia”, the locality of the lectotype.

***Amphidromus contusus* (Reeve, 1848)**

Bulimus contusus Reeve, 1848: *Bulimus* plate 37, species 220, fig. 220.

Type locality. Eastern Islands.

Type material. Lectotype NHMUK 19601426 (Fig. 6A; H=49.4 mm, W=25.9 mm), paralectotypes NHMUK 19601427 (3S, Fig. 6B).

***Amphidromus costifer* Smith, 1893**

Amphidromus costifer Smith, 1893: 12 with text fig.

Type locality. Annam [Central Vietnam].

Type material. Holotype NHMUK 1893.2.26.4 (Fig. 6C; H=46.5 mm, W=29.0 mm).

***Amphidromus crassa* Fulton, 1899**

Amphidromus contrarius var. *crassa* Fulton, 1899a: 213, 215, pl. 11, fig. 8.

Type locality. Timor Island.

Type material. Lectotype NHMUK 1898.12.3.324 (Fig. 6D; H=40.4 mm, W=19.4 mm), paralectotype NHMUK 1898.12.3.323 (1S, Fig. 6E).

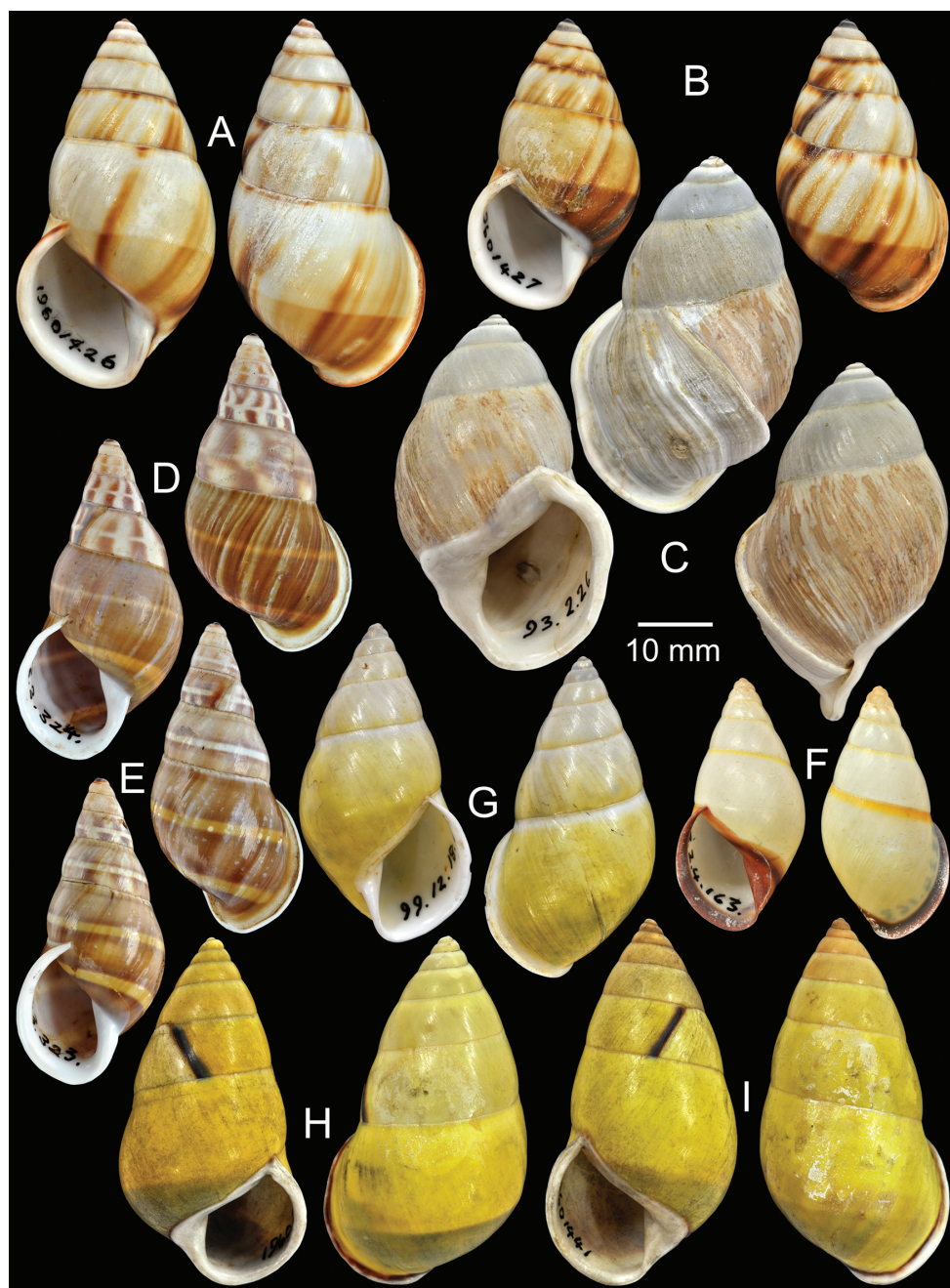


Figure 6. Type specimens of *Amphidromus* spp. **A–B** *A. contuses* **A** lectotype and **B** paralectotype **C** Holotype of *A. costifer* **D–E** *A. contrarius crassa* **D** lectotype and **E** paralectotype **F** Holotype of *A. cruentatus* **G** Holotype of *A. dautzenbergi* **H–I** *A. dohni* **H** lectotype and **I** paralectotype.

***Amphidromus cruentatus* (Morelet, 1875)**

Bulimus cruentatus Morelet, 1875: 264, 265, pl. 13, fig. 5.

Type locality. Cambodje [Cambodia].

Type material. Holotype NHMUK 1893.2.4.163 (Figs 1D, 6F; H=33.4 mm, W=16.5 mm).

***Amphidromus dautzenbergi* Fulton, 1899**

Amphidromus dautzenbergi Fulton, 1899b: 303, fig. 3.

Type locality. Tonkin [Central Vietnam].

Type material. Holotype NHMUK 1899.12.18.38 (Fig. 6G; H=42.9 mm, W=22.6 mm).

***Amphidromus schomburgki dextrochlorus* Sutcharit & Panha, 2006**

Amphidromus schomburgki dextrochlorus Sutcharit & Panha, 2006b: 23–26, figs 4m, 16d–f, 17f.

Type locality. Ban Khok Klang, Tao Ngoi District, Sakonnakhon, northeastern Thailand.

Type material. Holotype CUMZ 2296, paratypes CUMZ 2017 (19D), NHMUK 20050149 (1D, Fig. 7A), SMF 327973 (1D).

***Amphidromus dohrni* (Pfeiffer, 1864)**

Bulimus dohrni Pfeiffer, 1864 [1863]: 525.

Type locality. Cochin-China [Southern Vietnam].

Type material. Lectotype NHMUK 19601440 (Fig. 6H; H=46.3 mm, W=24.3 mm), paralectotypes NHMUK 19601441 (1D + 1S, Fig. 6I).

***Amphidromus dubius* Fulton, 1896**

Amphidromus dubius Fulton, 1896a: 86–87, pl. 6, figs 1, 1a.

Type locality. Balabac Island [Palawan, Philippines].

Type material. Lectotype NHMUK 1896.6.13.6 (Fig. 7B; H=31.4 mm, W=17.7 mm), paralectotype NHMUK 1896.6.13.7 (1S, Fig. 7C).

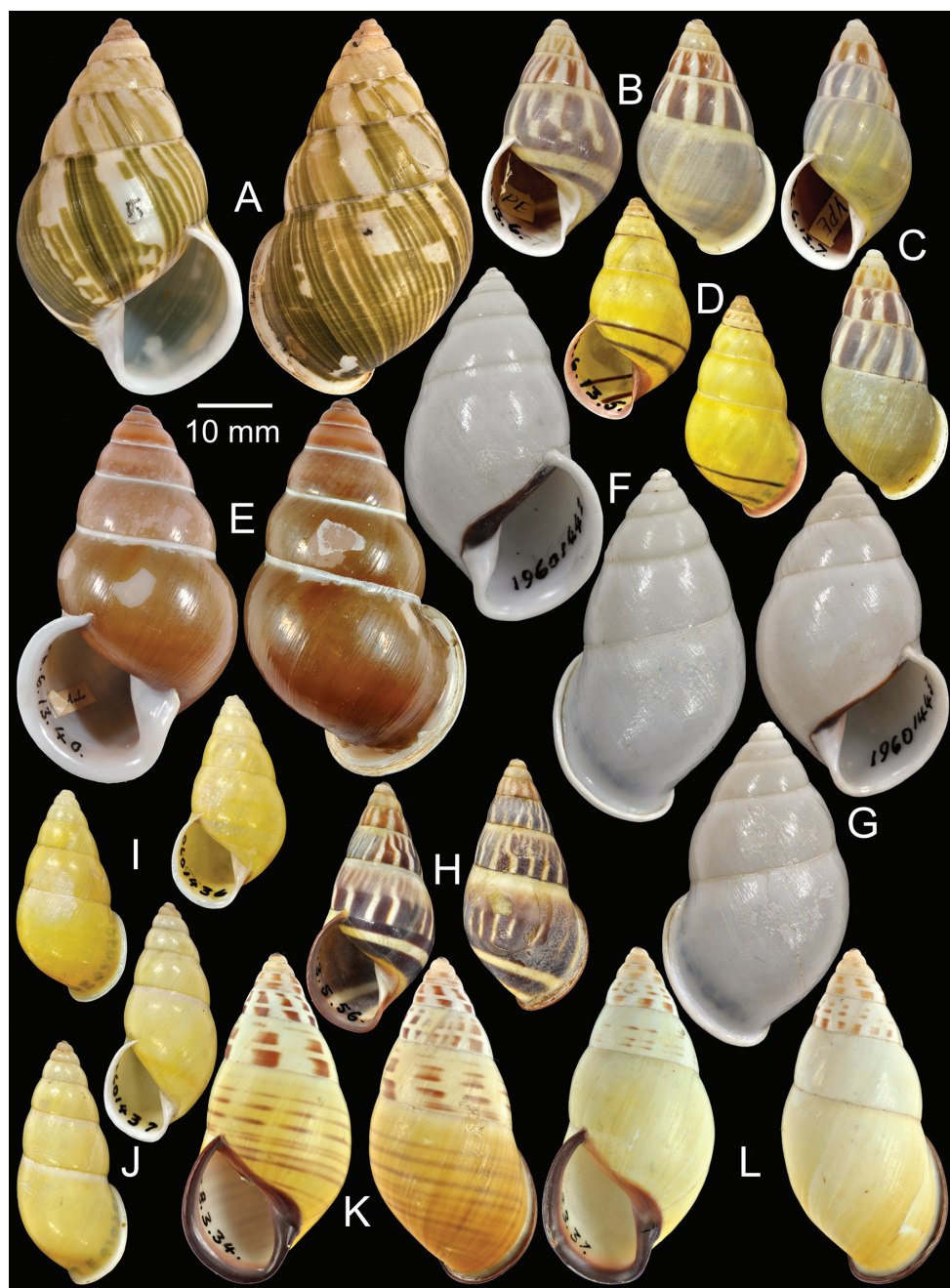


Figure 7. Type specimens of *Amphidromus* spp. **A** Paratype of *A. schomburgki dextrochlorus* **B–C** *A. dubius* **B** lectotype and **C** paralectotype **D** Holotype of *A. adamsii duplocincta* **E** Lectotype of *A. enganoensis* **F–G** *A. eques* **F** lectotype and **G** paralectotype **H** Lectotype of *A. everetti* **I–J** *A. flavus* **I** lectotype and **J** paralectotype **K–L** *A. floresianus*, **K** lectotype and **L** paralectotype.

***Amphidromus adamsii duplocincta* Fulton, 1896**

Amphidromus adamsi var. *duplocincta* Fulton, 1896a: 82, pl. 5, fig. 4.

Type locality. Banguay Island [Sabah, Malaysia].

Type material. Holotype NHMUK 1896.6.13.5 (Fig. 7D; H=29.2 mm, W=15.7 mm).

***Amphidromus enganoensis* Fulton, 1896**

Amphidromus enganoensis Fulton, 1896a: 71, pl. 6, fig. 11.

Type locality. Engano Island, West Sumatra.

Type material. Lectotype NHMUK 1896.6.13.40 (Fig. 7E; H=50.5 mm, W=29.2 mm).

Remarks. The original description was based on more than one specimen and three sets of measurements were given. The unique type was not explicitly designated, and the single specimen that remained in Fulton's collection could not be implied to be the unique type (ICZN 1999: Art. 74.6). The "holotype" referred to in Laidlaw and Solem (1961) is explicit with a unique indication that constitutes a valid lectotype designation. Therefore, this specimen should be recognized as the lectotype to stabilise the name.

***Amphidromus eques* (Pfeiffer, 1857)**

Bulimus eques Pfeiffer, 1857b: 158.

Type locality. Cochinchina [Southern Vietnam].

Type material. Lectotype NHMUK 19601442 (Fig. 7F; H=47.8 mm, W=26.2 mm), paralectotypes NHMUK 19601443 (2D, Fig. 7G).

***Amphidromus everetti* Fulton, 1896**

Amphidromus everetti Fulton, 1896a: 87.

Type locality. Palawan [Philippines].

Type material. Lectotype NHMUK 1893.3.5.56 (Fig. 7H; H=33.9 mm, W=16.5 mm), paralectotypes SMF 7558 (2S), SMF 7575 (1S), SMF 7663 (1S).

Remarks. The type locality in the original description was given as Palawan. However, the locality on the label of the lectotype is Balabac Island, the southernmost of the Palawan Islands.

***Amphidromus flavus* (Pfeiffer, 1861)**

Bulimus flavus Pfeiffer, 1861: 194.

Type locality. Siam [Thailand].

Type material. Lectotype NHMUK 19601436 (Fig. 7I; H=27.6 mm, W=14.5 mm), paralectotypes NHMUK 19601437 (1S, Fig. 7J).

***Amphidromus floresianus* Fulton, 1897**

Amphidromus floresianus Fulton, 1897: 211, pl. 6, fig. 2.

Type locality. South Flores [Indonesia].

Type material. Lectotype NHMUK 1897.8.3.34 (Fig. 7K; H=44.0 mm, W=21.8 mm), paralectotypes NHMUK 1897.8.3.35–7 (3S, Fig. 7L), SMF 7554 (1S).

***Amphidromus glaucolarynx* (Dohrn, 1861)**

Bulimus glaucolarynx Dohrn, 1861: 207, pl. 26, fig. 7.

Type locality. In regno Siam [Thailand].

Type material. Lectotype NHMUK 19601454 (Fig. 8A; H=44.2 mm, W=20.1 mm), paralectotypes NHMUK 19601455 (1D + 2S, Fig. 8B).

***Amphidromus sinensis globosa* Nevill, 1878 [*nomem nudum*, ICZN (1999: Art. 12)].**

Amphidromus sinensis var. *globosa* Nevill, 1878: 126 [*nomem nudum*].

Type locality. Chittagong [now in Bangladesh].

Type material. Original specimen NHMUK 1903.7.1.1921 (1S, H=25.1 mm, W=16.5 mm).

Remarks. The name “*globosa*”, an unavailable name, was included in this catalog in order to indicate the history of the taxon. This name was introduced without a description or indication and therefore failed to conform to the ICZN guidelines (1999: Art. 12) and could not be made available by Nevill (1878). Later, this name was cited in Pilsbry (1900: 191) and Richardson (1985: 44). They cited this name without validating the taxon, and so this name could not be made available in subsequent works (ICZN 1999: Arts 11.5.2, 12).

We have surveyed for *Amphidromus* in western Thailand and collected a number of specimens with similar shell morphology to Nevill’s (1878) original specimen. It

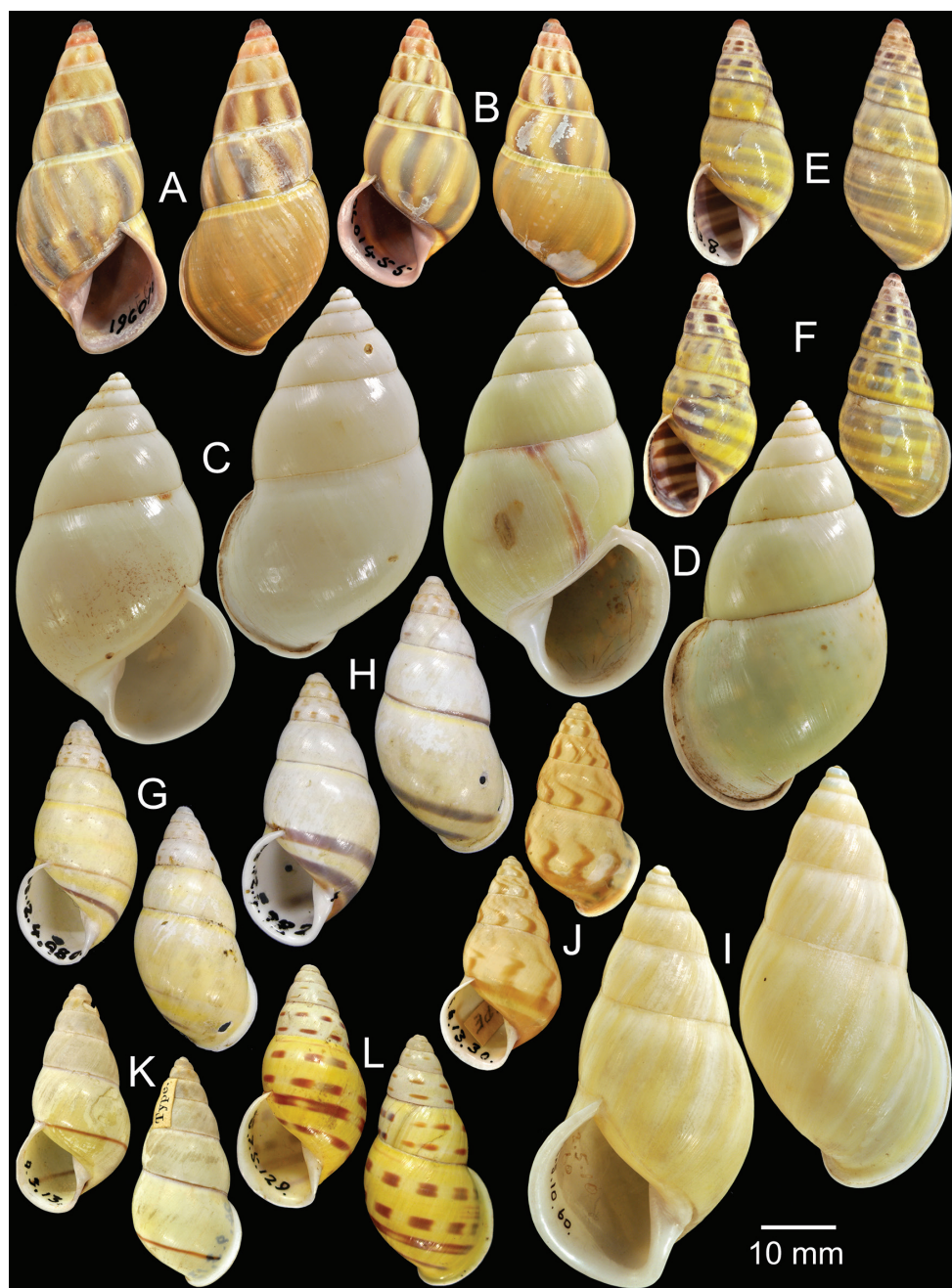


Figure 8. Type specimens of *Amphidromus* spp. **A–B** *A. glaucolarynx* **A** lectotype and **B** paralectotype **C–D** *A. perakensis globosus*, **C** lectotype and **D** paralectotype **E–F** *A. columellaris gloriosa* **E** lectotype and **F** paralectotype **G–H** *A. sinensis gracilis* **G** lectotype and **H** paralectotype **I** Possible syntype of *A. maculiferus garcilior* **J** Lectotype of *A. hamatus* **K** Holotype of *A. hosei* **L** Holotype of *A. inconstans*.

appear to be an undescribed species, therefore, we provide a species description and description of genitalia anatomy as *Amphidromus* (*Syndromus*) *globonevilli* Sutcharit and Panha, sp. n. (see description below).

***Amphidromus perakensis globosus* Fulton, 1903**

Amphidromus perakensis var. *globosus* Fulton in Collinge, 1903: 211, 212.

Type locality. Biserat, Jalor [Yala, Thailand].

Type material. Lectotype (design. n.), NHMUK 1904.5.26.24 (Fig. 8C; H=50.0 mm, W=28.5 mm), paralectotypes NHMUK 1904.5.26.25–30 (4D adults + 2D juveniles, Fig. 8D).

Remarks. This species was described based on specimens from Annandale and Robinson's collection in the Malay Peninsula. Laidlaw and Solem (1961: 622) stated "... the location of the material is unknown." We located seven specimens in the NHM general collections with an original label stating that they were purchased from Annandale and Robinson, with the locality "Biserat State of Jalor, Malay Peninsula". We consider these specimens to be the syntypes. The specimen that most closely matches the original description is here designated as the lectotype.

Regarding the authorship of this name, Collinge (1903: 211, 212) clearly stated that H. Fulton provided him with the brief definition and the species name. Fulton, therefore is solely attributed the authorship (ICZN 1999: Art. 50.1.1).

***Amphidromus columellaris gloriosa* Fulton, 1896**

Amphidromus columellaris var. *gloriosa* Bttg. Fulton 1896a: 79.

Type locality. Sierah Island, Tenimber Laut [Tanimbar Islands, Indonesia].

Type material. Lectotype (design. n.), NHMUK 1894.5.23.8 (Fig. 8E; H=32.5 mm, W=14.1 mm), paralectotypes NHMUK 1894.5.23.7 (Fig. 8F), SMF 7555 (3S).

Remarks. Authorship was originally attributed to O. Boettger from a manuscript name. However, since O. Boettger did not write the description, the taxon is attributed to Fulton only. The brief original description clearly implied that it was based on more than one specimen. However, no illustration or measurements were provided, and the unique type was not designated in the original publication. Two specimens from NHM collection accompanied with Fulton's handwritten label stating the taxon name and collection locality are considered to be syntypes. The specimen that most closely matches with the description is here designated as the lectotype to stabilise the name.

***Amphidromus sinensis gracilis* Fulton, 1896**

Amphidromus sinensis var. *gracilis* Fulton, 1896a: 80, pl. 6, fig. 10.

Type locality. Pegu, Burma [Bago, Myanmar].

Type material. Lectotype NHMUK 1888.12.4.980 (Fig. 8G; H=26.7 mm, W=13.0 mm), paralectotypes NHMUK 1888.12.4.981–2 (2S, Fig. 8H).

***Amphidromus maculiferus gracilior* Fulton, 1896**

Bulimus maculiferus var. β . Pfeiffer, 1853: 319. Küster and Pfeiffer 1854: pl. 40, fig. 9.
Amphidromus maculiferus var. *gracilior* Pfeiffer, Fulton 1896a: 74, 75.

Type locality. Mindanao Island [Philippines].

Type material. Possible syntype NHMUK 1842.5.10.60 (1S, Fig. 8I; H=56.3 mm, W=28.8 mm).

Remarks. Fulton (1896a: 74, 75) attributed the authorship of this species to L. Pfeiffer. However, “Gracilior” in Pfeiffer (1853: 319) is only the first word of the description which is not a valid name (ICZN 1999: Art. 11.9). Therefore, Fulton (1896a: 74) is the sole author of this species.

The specimens that Pfeiffer used as the basis for “*Bulimus maculiferus* var. β .”, were examined and used by Fulton, and are acknowledged as the type series (ICZN 1999: Art 72.4). A single specimen in the NHM from H. Cuming’s collection with Fulton’s handwritten labels bearing the taxon name and the locality “Mindanao, Philippines” is considered to be a possible syntype. This specimen corresponds closely with the figure in Küster and Pfeiffer (1854: pl. 40, fig. 9). However, the specimen is much smaller in size than the specimens quoted in Pfeiffer (1853: 319). Therefore, we treat the NHM specimen as a possible syntype.

***Amphidromus hamatus* Fulton, 1896**

Amphidromus hamatus Fulton, 1896a: 84, pl. 5, fig. 13.

Type locality. Labuan Island [Sabah, Malaysia].

Type material. Lectotype NHMUK 1896.6.13.30 (Fig. 8J; H=27.7 mm, W=15.0 mm).

***Amphidromus hosei* Smith, 1895**

Amphidromus hosei Smith, 1895: 115, pl. 3, fig. 20.

Type locality. Meri, Sarawak.

Type material. Holotype NHMUK 1894.9.3.13 (Figs 1F, 8K; H=30.6 mm, W=14.5 mm).

***Amphidromus winteri inauris* Fulton, 1896**

Amphidromus winteri var. *inauris* (Bttg. MSS.) Fulton 1896a: 74, pl. 6, figs 12, 12a.

Type locality. Java.

Type material. Lectotype NHMUK 1896.6.13.13 (Fig. 9A; H=50.3 mm, W=27.5 mm), paralectotype NHMUK 1896.6.13.14 (1S, Fig. 9B), SMF 7638 (1S).

Remarks. Fulton wrote “Bttg. MSS.” after the variety name, but did not appear to give O. Boettger credit for the description. Therefore, authorship is attributed to Fulton.

***Amphidromus inconstans* Fulton, 1898**

Amphidromus inconstans Fulton, 1898: 10, text fig.

Type locality. Alor (= Ombai) Island, Malayan Archipelago [East Nusa Tenggara, Indonesia].

Type material. Holotype NHMUK 1898.7.5.129 (Fig. 8L; H=36.8 mm, W=18.8 mm), paratypes SMF 7563 (4S).

***Amphidromus maculiferus inflata* Fulton, 1896**

Amphidromus maculiferus var. *inflata* Fulton, 1896a: 75.

Type locality. Baranda Philippines Islands.

Type material. Lectotype (design. n.), NHMUK 19601466/1 (Fig. 9C; H=64.2 mm, W=34.2 mm), paralectotypes NHMUK 19601466/2-3 (2S, Fig. 9D).

Remarks. Three specimens originally from the Fulton collection with his handwritten label bearing the taxon and the type locality were located in the NHM collections. The largest shell (64.2 × 34.2 mm) clearly corresponds to the original description and Fulton’s measurements (66 × 38 mm) and so is here designated as the lectotype to stabilise the name.

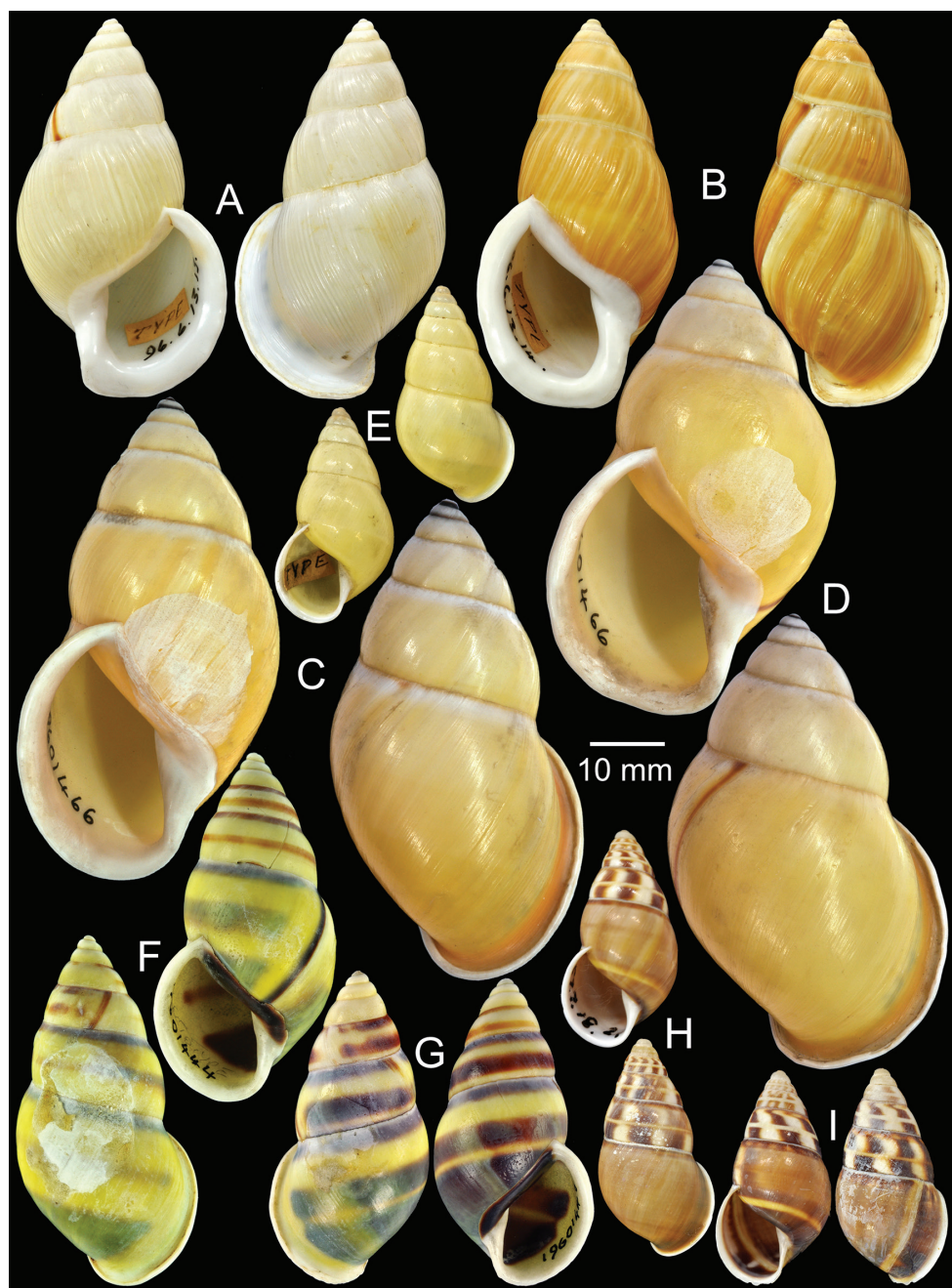


Figure 9. Type specimens of *Amphidromus* spp. **A–B** *A. winteri inauris* **A** lectotype and **B** paralectotype **C–D** *A. maculiferus inflata* **C** lectotype and **D** paralectotype **E** Holotype of *A. adamsii inornata* **F–G** *A. janus* **F** lectotype and **G** paralectotype **H–I** *A. filozonatus jucunda* **H** lectotype and **I** paralectotype.

***Amphidromus adamsii inornata* Fulton, 1896**

Amphidromus adamsi var. *inornata* Fulton, 1896a: 83, pl. 5, fig. 6.

Type locality. North Borneo.

Type material. Lectotype NHMUK 1896.6.13.12 (Fig. 9E; H=27.3 mm, W=14.6 mm).

***Amphidromus iunior* Cilia, 2013**

Amphidromus (Syndromus) iunior Cilia, 2013: 264–266, figs 1–6.

Type locality. Mangili village, east part of Sumba Island, East Nusa Tenggara, Indonesia.

Type material. Holotype MNHN 23265, paratypes FMNH 328120 (2S), MNHN 23266 (2S), NHMUK 20120044 (3S).

***Amphidromus janus* (Pfeiffer, 1854)**

Bulimus janus Pfeiffer, 1854 [1852]: 85.

Type locality. in Novis Hebridibus [New Hebrides].

Type material. Lectotype NHMUK 19601444 (Fig. 9F; H=46.6 mm, W=24.0 mm), paralectotypes NHMUK 19601445 (1D + 1S, Fig. 9G).

Remarks. The type locality “New Hebrides” seems to be an error, since this is beyond the known range of *Amphidromus*. Subsequent collections and reports confine the species distribution to Burma from the Tavoy and Mergui archipelagos (Nevill 1878, Pilsbry 1900, Gude 1914, Laidlaw and Solem 1961).

***Amphidromus filozonatus jucunda* Fulton, 1896**

Amphidromus filozonatus var. *jucunda* Fulton, 1896a: 78, pl. 7, fig. 8.

Type locality. Macassar, Celebes [Makassar, South Sulawesi, Indonesia].

Type material. Lectotype NHMUK 1857.7.18.2/1 (Fig. 9H; H=28.0 mm, W=14.3 mm), paralectotype NHMUK 1857.7.18.2/2 (1S, Fig. 9I).

***Amphidromus kalaoensis* Fulton, 1896**

Amphidromus kalaoensis Fulton, 1896b: 102.

Type locality. Kalao Island [South Sulawesi, Indonesia].

Type material. Holotype NHMUK 1896.5.16.153 (Fig. 10A; H=31.9 mm, W=15.6 mm), paratypes NHMUK 1896.5.16.154–6 (3S, Fig. 10B).

***Amphidromus lepidus* (Gould, 1856)**

Bulimus lepidus Gould, 1856: 12.

Type locality. Mergui Islands [Mergui Archipelago, Tanintharyi Region, Myanmar].

Type material. Lectotype (design. n.), NHMUK 19601486 (Figs 2A, 10C; H=22.0 mm, W=14.0 mm).

Remarks. Johnson (1964: 28, 29) indicated that some of the unlocated specimens from Gould's type catalogue were probably in the NHM, since Gould presented some specimens to H. Cuming. No specimens of *Bulimus lepidus* Gould, 1856 could be located by Johnson (1964: 100). There is a specimen in the NHM from the H. Cuming collection marked with "Type" and the locality "Mergui Islands" (Fig. 2A) which corresponds to the type locality, and the shell matches the measurements given in the original description (height 22.5 mm, width 12.5 mm). In addition, Fulton (1896a: 80) stated that "the type" of *Bulimus lepidus* is in the British Museum (now the NHM). This specimen is, therefore, considered as the syntype, and is here designated as the lectotype to stabilise the name. It is figured here for the first time since it was described.

***Amphidromus lindstedti* (Pfeiffer, 1857)**

Bulimus lindstedti Pfeiffer, 1857c [1856]: 388.

Type locality. Malacca.

Type material. Lectotype NHMUK 19601448 (Fig. 10D; H=38.9 mm, W=18.4 mm).

Remarks. Fulton (1896a: 85) described the type as being bleached in condition, and suggested that the specimen should have a color pattern if it were not bleached. We examined the lectotype but, in contrast, consider it to be entirely white in shell colour and not bleached. In addition, Laidlaw and Solem (1961) suggested that *Amphidromus quadrasi* Hidalgo, 1887 and *Amphidromus versicolor* Fulton, 1896 from the Philippines were probably junior synonyms of this species. With a unique straight columella, thickened parietal callus and elongated aperture, *Amphidromus lindstedti* (Pfeiffer, 1857) is clearly distinct from both species. However, new collections from precise localities will help elucidate whether this is a distinct species or a colour form of the other taxa.

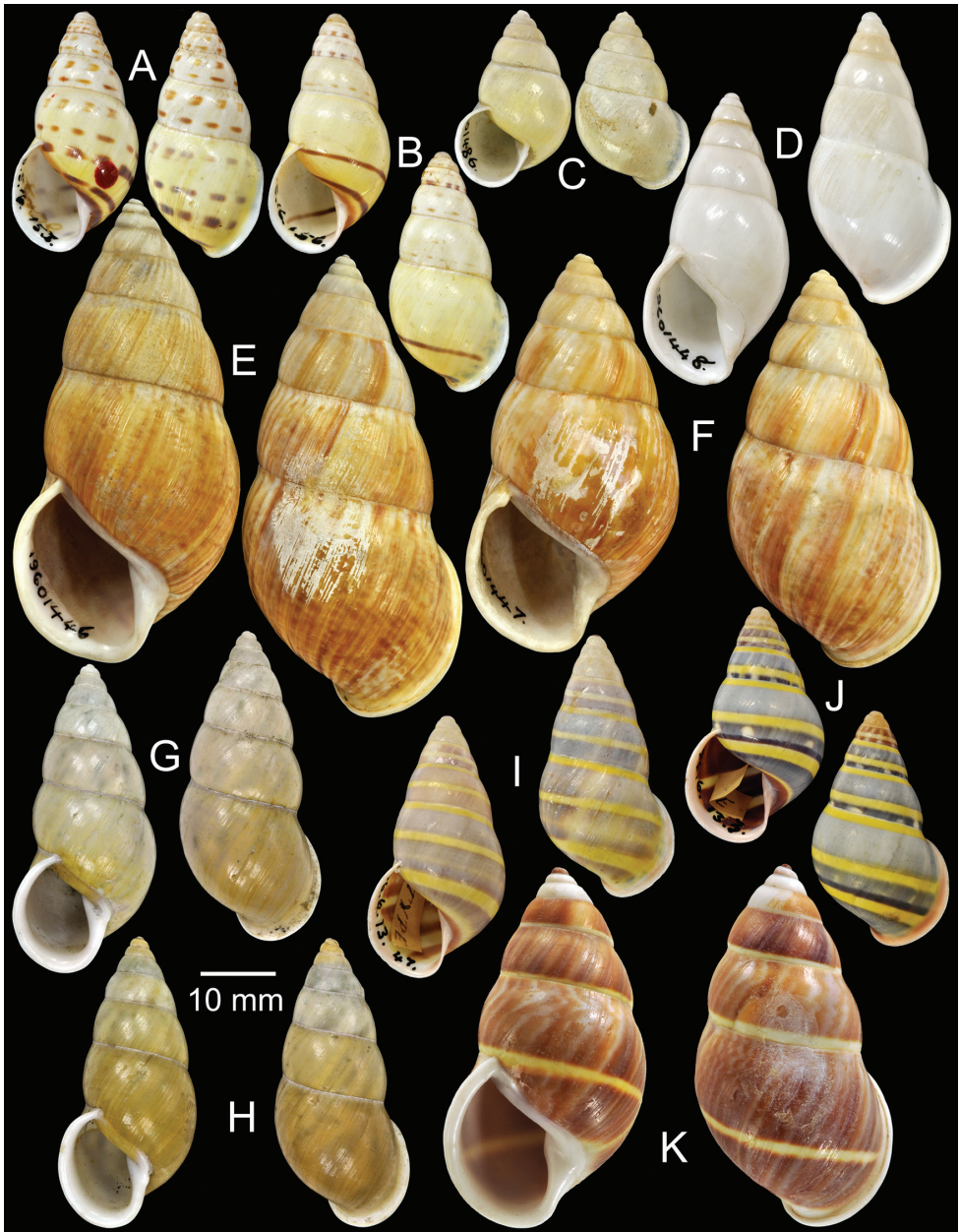


Figure 10. Type specimens of *Amphidromus* spp. **A–B** *A. kalaoensis* **A** holotype and **B** paratype **C** Lectotype of *A. lepidus* **D** Lectotype of *A. lindstedti* **E–F** *A. loricatus* **E** lectotype and **F** paralectotype **G–H** *A. sinistralis lutea* **G** lectotype and **H** paralectotype **I–J** *A. adamsii luteofasciatus* **I** lectotype and **J** paralectotype **K** Possible syntype of *A. melanomma*.

***Amphidromus loricatus* (Pfeiffer, 1855)**

Bulimus loricatus Pfeiffer, 1855 [1854]: 293.

Type locality. unknown.

Type material. Lectotype NHMUK 19601446 (Fig. 10E; H=61.5 mm, W=29.2 mm), paralectotype NHMUK 19601447 (1S, Fig. 10F).

Remarks. The original description gave the type locality as “unknown”. However, the original label accompanying the lectotype states it was collected from Java. The type locality of this taxa is, therefore, confined to Java.

***Amphidromus sinistralis lutea* Fulton, 1896**

Bulimus sinistralis var. B. Martens, 1867: 355, pl. 21, fig. 2b.

Amphidromus sinistralis var. *lutea* Martens, Fulton 1896a: 76.

Type locality. Moluccas [probably in the area of Maluku and North Maluku, Indonesia].

Type material. Lectotype (design. n.), NHMUK 20140752/1 (Fig. 10G; H=40.8 mm, W=18.9 mm), paralectotypes NHMUK 20140752/2–8 (7S, Fig. 10H).

Remarks. Fulton (1896a) correctly nominated this name, but attributed the authorship to von Martens. However, von Martens (1867: 355) described the subspecific name as ‘B’ which is an invalid (ICZN 1999: Art. 11.9). Therefore, the authorship of this taxon should be attributed to Fulton.

The original description was very brief, without any measurements or illustrations, and did not indicate that a unique type was designated. The NHM holds a lot with eight shells from the Da Costa collection, with the original label stating “Fulton co-types” which are considered syntypes. The specimen that has a small label with Fulton’s handwritten glued inside the aperture is designated here as the lectotype to stabilise the name. The paralectotypes are the other seven specimens from the same lot.

***Amphidromus adamsii luteofasciata* Fulton, 1896**

Amphidromus adamsi var. *luteofasciata* Fulton, 1896a: 82, pl. 5, figs 2, 2a.

Type locality. Banguay Island [Sabah, Malaysia].

Type material. Lectotype NHMUK 1896.6.13.47 (Figs 2B, 10I; H=34.4 mm, W=17.2 mm), paralectotypes NHMUK 1896.6.13.3 (1S, Figs 2B, 10J), SMF 7549 (2S).

***Amphidromus contrarius maculata* Fulton, 1896**

Amphidromus contrarius var. *maculata* Fulton, 1896a: 78, pl. 7, fig. 4.

Type locality. Macassar [Makassar, South Sulawesi, Indonesia].

Type material. Lectotype NHMUK 19601456 (Fig. 11A; H=32.1 mm, W=16.9 mm), paralectotype NHMUK 19601457 (1S, Fig. 11B), SMF 28294 (1S).

***Amphidromus masoni* (Godwin-Austen, 1876)**

Bulimus masoni Godwin-Austen, 1876: 316.

Type locality. Dihiri Parbat, 2000 feet [Dafla Hills, Assam, India].

Type material. Lectotype (design. n.), NHMUK 1903.7.1.1908 (Figs 2C, 11C; H=30.7 mm, W=17.7 mm).

Remarks. Godwin-Austen (1876) stated that there were two specimens in the type series. Only a single specimen from the Godwin-Austen type lot remains in the NHM collections (Fig. 2C). Laidlaw and Solem (1961: 639) considered this specimen to be the holotype. This should be interpreted as an inadvertant lectotype designation (ICZN 1999: Art. 74.6). The apex of the lectotype has been damaged at around the second and third whorls and the shell height is much smaller than it would have been if undamaged.

***Amphidromus melanomma* (Pfeiffer, 1852)**

Bulimus melanomma Pfeiffer, 1852: 95.

Type locality. insulis Moluccis [= the islands of the Moluccas].

Type material. Possible syntype NHMUK 20140753/1 (Figs 2D, 10K; H=47.8 mm, W=26.3 mm).

Remarks. The original description by Pfeiffer (1852: 95) did not give an illustration of the species but a set of measurements were provided. Küster and Pfeiffer (1854: 135, 136, pl. 39, figs 28, 29; pl. 41, figs 1, 2, 7, 8) re-published the description, and figured the nominal species and included two varietal forms.

The NHM holds a lot that has an original label in Pfeiffer's handwriting giving the species name (in blue ink) and the collection locality of "Malacca". The words "*B. melanoma* var γ Pfr. Mon. Hel. III p. 310", not written by Pfeiffer, were added to the label at a later time (Fig. 2D). The specimen illustrated in Küster and Pfeiffer (1854: pl. 39, figs 27, 28) is recognized by the sinistral shell, with a yellow peripheral band on the periphery of the last whorl and the dimensions are very close to those given in the original description. Since the lot contains two other dextral specimens which were not mentioned in the original description, we refrain from designating this as a lectotype,

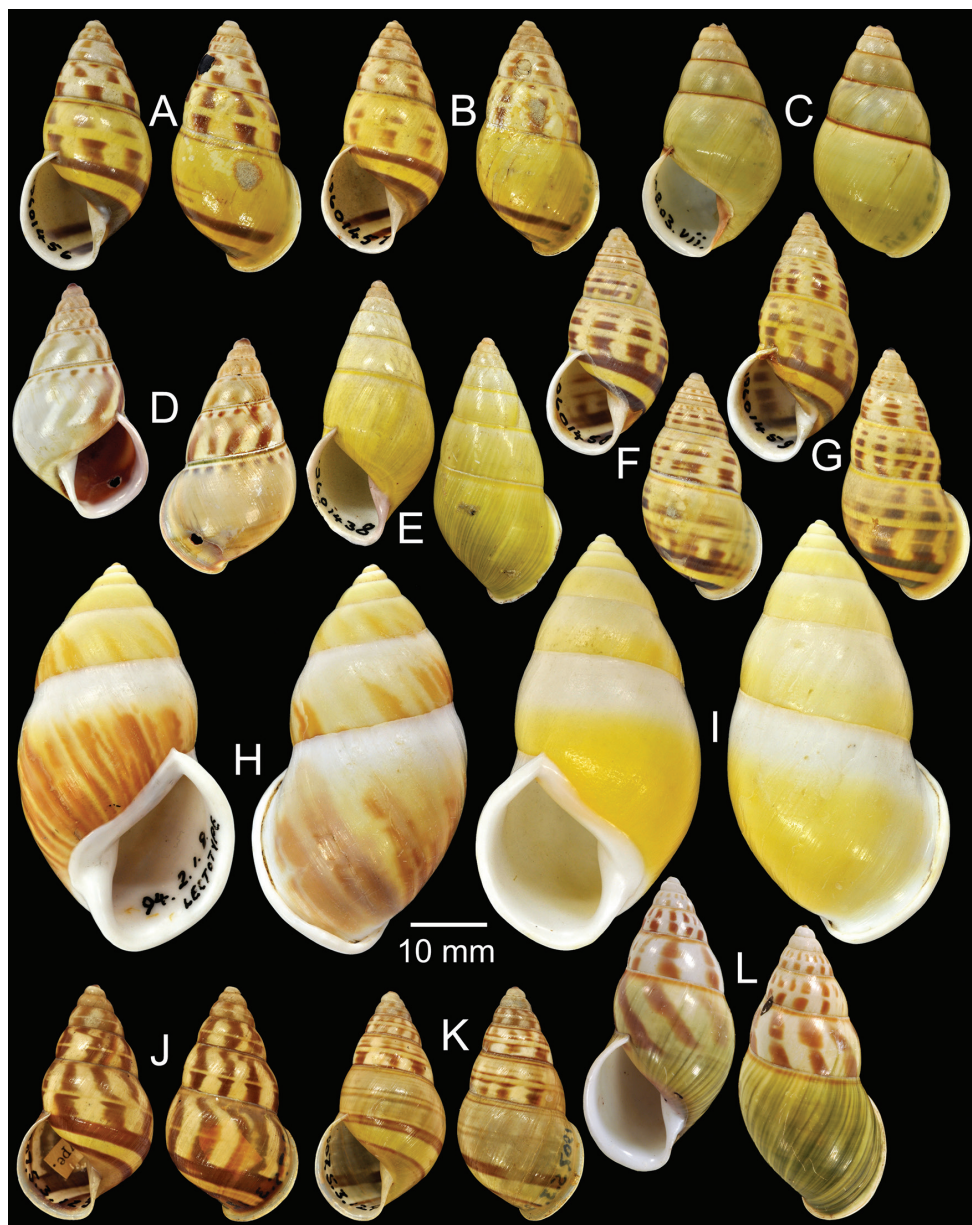


Figure 11. Type specimens of *Amphidromus* spp. **A–B** *A. contrarius maculata* **A** lectotype and **B** paralectotype **C** Lectotype of *A. masoni* **D** Lectotype of *A. moniliferus* **E** Lectotype of *A. mouhoti* **F–G** *A. contrarius multifasciata* **F** lectotype and **G** paralectotype **H–I** *A. perversus natunensis* **H** lectotype and **I** paralectotype **J–K** *A. niasensis* **J** lectotype and **K** paralectotype **L** Holotype of *A. nicobarica*.

considering the sinistral specimen to be a possible syntype. The other two dextral shells (NHMUK 20140753/2-3) that are contained in the lot are excluded from the type series (ICZN 1999: Art. 72.4.1).

***Amphidromus moniliferus* (Gould, 1846)**

Bulimus moniliferus Gould, 1846: 99.

Type locality. Tavoy [Dawei, Tanintharyi Region, Myanmar].

Type material. Lectotype (design. n.), NHMUK 20120009 (Figs 2E, 11D; H=29.3 mm, W=16.5 mm).

Remarks. Gould noted that he received several specimens (dextral and sinistral) from F. Mason, and he wrote his original description from the sinistral specimen (Gould 1846). However, in the catalogue of Gould's type specimens, Johnson (1964) could not locate any type material of *Bulimus moniliferus*. A single specimen was found in the NHM from the H. Cuming collection with "Type" written on it and the locality "Tavoy" which corresponds to the type locality in the original description (Fig. 2E). In addition, F. Mason, the original collector who presented specimens to Gould, mentioned that local people (Karen ladies) often strung the shells of *A. atricallosus* and others congeners from their necklaces (Mason 1850: 400). Evidence of a hole remains on the basal lip of the lectotype of *Bulimus atricallosus* (MCZ 169050) and in the NHM type specimen of *Bulimus moniliferus* Gould, 1846. This specimen is, therefore, designated as the lectotype to stabilise the name.

***Amphidromus mouhoti* (Pfeiffer, 1861)**

Bulimus mouhoti Pfeiffer, 1861: 194.

Type locality. Siam [Thailand].

Type material. Lectotype NHMUK 19601438 (Fig. 11E; H=34.2 mm, W=16.1 mm).

***Amphidromus contrarius multifasciata* Fulton, 1896**

Amphidromus contrarius var. *multifasciata* Fulton, 1896a: 78, pl. 7, fig. 5.

Type locality. Cambodia.

Type material. Lectotype NHMUK 19601458 (Fig. 11F; H=29.4 mm, W=15.1 mm); paralectotypes NHMUK 19601459 (2S, Fig. 11G).

***Amphidromus perversus natunensis* Fulton, 1896**

Amphidromus perversus var. *natunensis* Fulton, 1896a: 69.

Type locality. Natuna Islands [Indonesia].

Type material. Lectotype NHMUK 1894.2.1.8 (Fig. 11H; H=51.7 mm, W=26.9 mm), paralectotypes NHMUK 1894.2.1.9–19 (5D + 6S, Fig. 11I).

***Amphidromus niasensis* Fulton, 1907**

Amphidromus niasensis Fulton, 1907: 151–152, pl. 9, fig. 9.

Type locality. Nias Island, Sumatra.

Type material. Lectotype NHMUK 1907.5.3.123 (Fig. 11J; H=30.1 mm, W=16.5 mm), paralectotype NHMUK 1907.5.3.124 (1S, Fig. 11K).

***Amphidromus andamanicus nicobarica* Godwin-Austen, 1895**

Amphidromus andamanicus var. *nicobarica* Godwin-Austen, 1895: 443, 450.

Type locality. Katchall [island in Andaman and Nicobar Islands, India].

Type material. Holotype NHMUK 1888.8.6.31 (Figs 2F, 11L; H=38.4 mm, W=19.0 mm).

Remarks. Godwin-Austen clearly stated that this taxon was described based on only one specimen. Therefore a single specimen ex. Röepstorff (Fig. 2F) in the NHM collections is recognized as the holotype fixed by monotypy (ICZN 1999: Art. 73.1.2).

***Amphidromus maculiferus obscura* Fulton, 1896**

Amphidromus maculiferus var. *obscura* Fulton, 1896a: 75.

Type locality. Mindanao Island.

Type material. Lectotype (design. n.), NHMUK 19601535/1 (Fig. 12A; H=61.4 mm, W=31.5 mm), paralectotypes NHMUK 19601535/2-3 (1D + 1S, Fig. 12B).

Remarks. The original description was based on more than one specimen, since Fulton stated “...remarkable that this is the only form of *maculiferus* of which *dextral* specimens have been found...”. A unique type was not indicated in the original description. The NHM holds a lot that consists of three specimens (2D, 1S) from the H. Cuming collection with an original label in Fulton’s handwriting. The dextral specimen closely matches with the original description and is here designated as the lectotype to stabilise the name.

***Amphidromus adamsii ornata* Fulton, 1896**

Amphidromus adamsii var. *ornata* Fulton, 1896a: 82, 83, pl. 5, fig. 14.

Type locality. Banguay Island, Borneo [Sabah, Malaysia].

Type material. Lectotype NHMUK 1893.6.7.3 (Fig. 12C; H=33.8 mm, W=19.4 mm), paralectotypes NHMUK 1893.6.7.4–5 (2S, Fig. 12D).

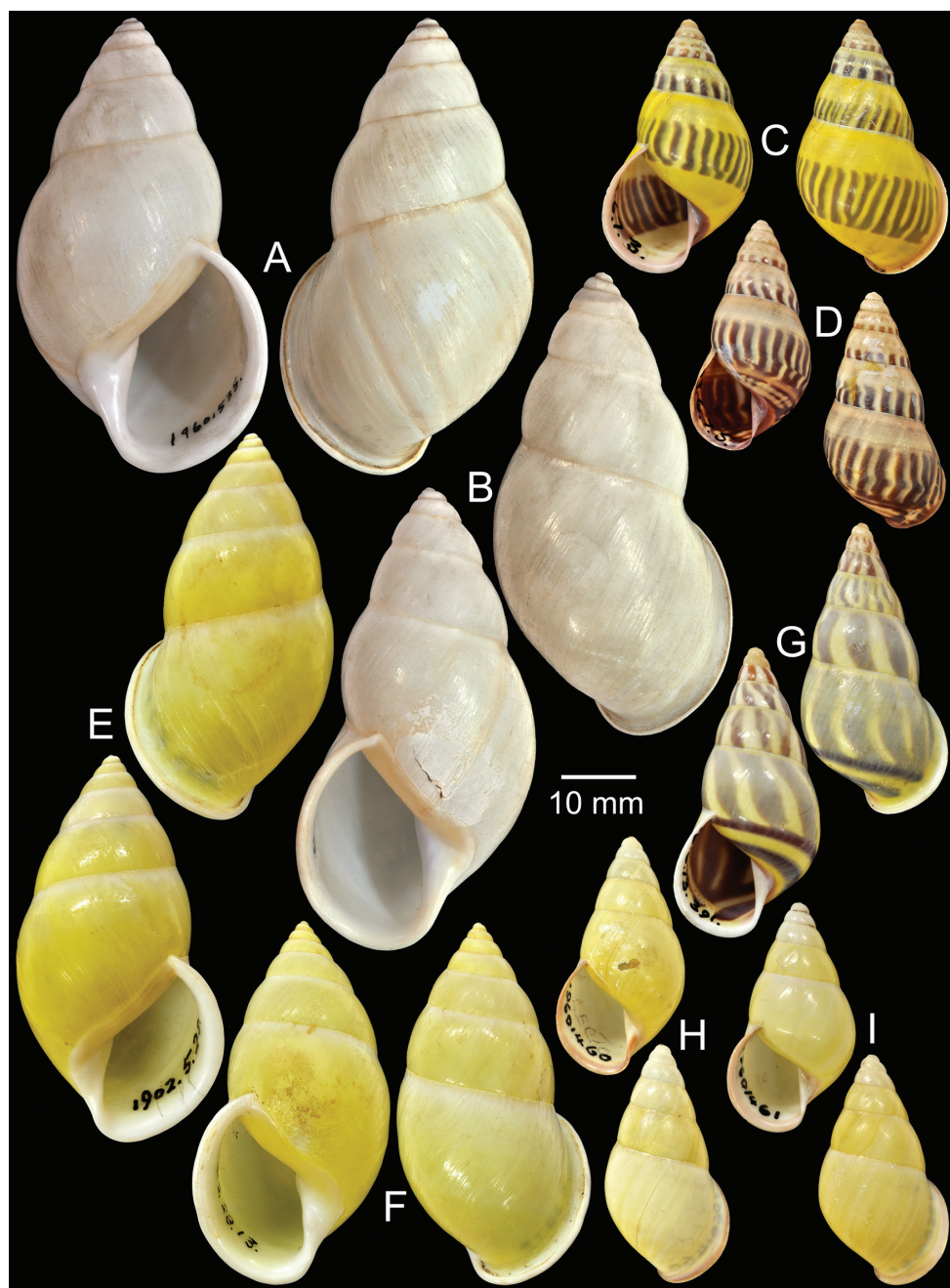


Figure 12. Type specimens of *Amphidromus* spp. **A–B** *A. maculiferus obscura* **A** lectotype and **B** paralectotype **C–D** *A. adamsii ornata* **C** lectotype and **D** paralectotype **E–F** *A. perakensis*, **E** lectotype and **F** paralectotype **G** Holotype of *A. pictus* **H–I** *A. placidus* **H** lectotype and **I** paralectotype.

***Amphidromus perakensis* Fulton, 1901**

Amphidromus perakensis Fulton, 1901: 104, pl. 9, figs 8–10.

Type locality. Perak [Peninsular Malaysia].

Type material. Lectotype NHMUK 1902.5.28.12 (Fig. 12E; H=51.0 mm, W=26.9 mm), paralectotypes NHMUK 1902.5.28.13 (1S, Fig. 12F), SMF 7595 (3D + 2S).

***Amphidromus pictus* Fulton, 1896**

Amphidromus pictus Fulton, 1896a: 85, pl. 5, fig. 8.

Type locality. Kina Balu, North Borneo.

Type material. Lectotype NHMUK 96.6.13.391 (Fig. 12G; H=38.1 mm, W=18.6 mm).

***Amphidromus placidus* Fulton, 1896**

Amphidromus placidus Fulton, 1896a: 84, pl. 5, fig. 11.

Type locality. East Boneo.

Type material. Lectotype NHMUK 19601460 (Fig. 12H; H=31.5 mm, W=16.2 mm), paralectotypes NHMUK 19601461 (2S, Fig. 12I).

***Amphidromus poecilochroa* Fulton, 1896**

Amphidromus poecilochroa Fulton, 1896a: 77, pl. 6, fig. 7.

Type locality. Sumbawa Island [West Nusa Tenggara, Indonesia].

Type material. Lectotype NHMUK 1896.6.13.29 (Fig. 13A; H=36.1 mm, W=20.0 mm), paralectotypes NHMUK 1895.12.19.13-14 (2S, Fig. 13B), SMF 7594 (2S).

***Amphidromus flavus proxima* Fulton, 1896**

Amphidromus flavus var. *proxima*, Fulton 1896a: 81, pl. 6, fig. 4.

Type locality. unknown.

Type material. Holotype NHMUK 1896.6.13.48 (Fig. 13C; H=32.6 mm, W=16.1 mm).

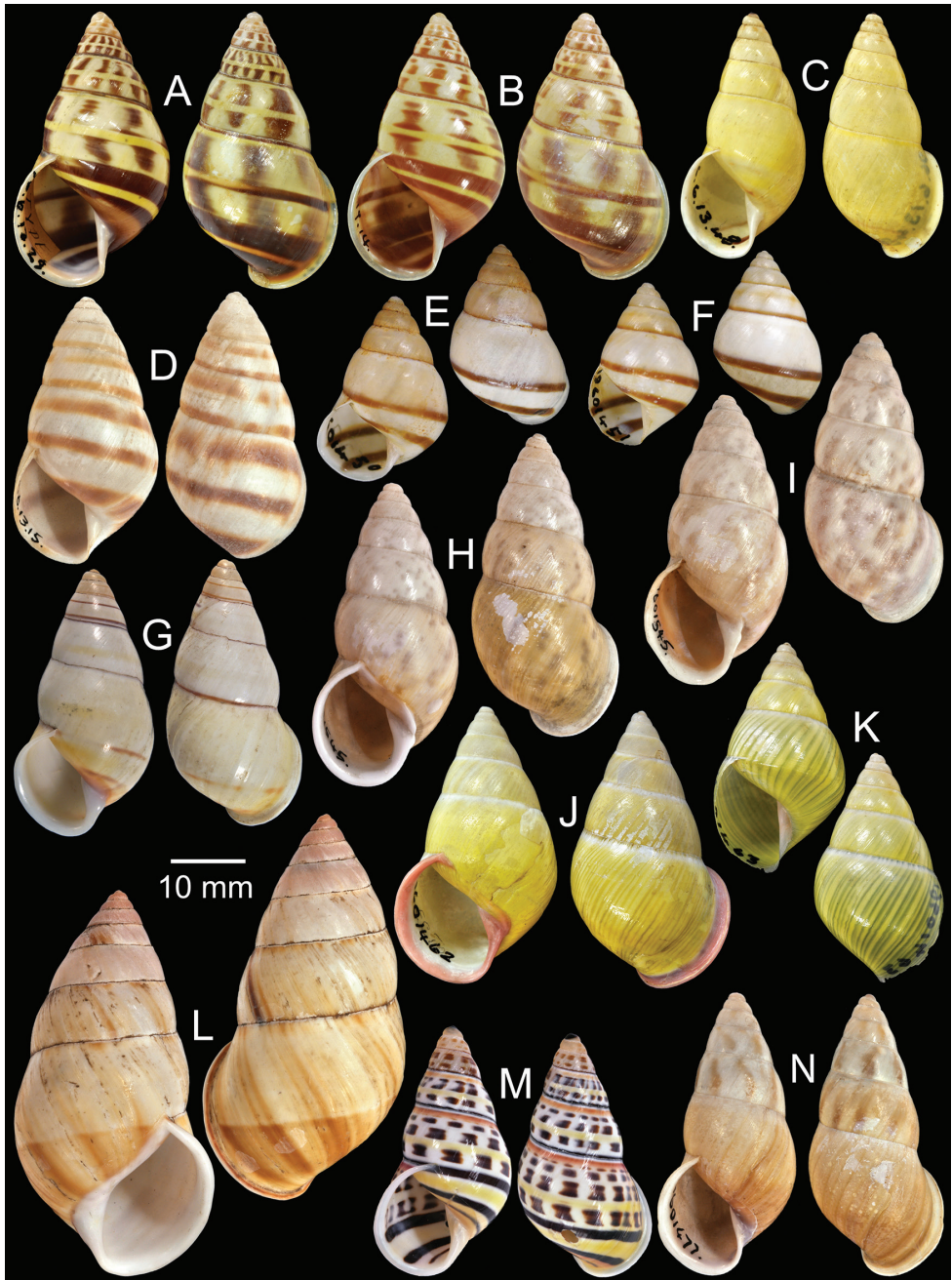


Figure 13. Type specimens of *Amphidromus* spp. **A–B** *A. poecilochroa* **A** lectotype and **B** paralectotype **C** Holotype of *A. flavus proxima* **D** Syntype of *A. robustus* **E–F** *A. roemeri* **E** lectotype and **F** paralectotype **G** Paralectotype of *A. laevus romaensis* **H–I** *A. sinistralis rosea* **H** lectotype and **I** paralectotype **J–K** *A. roseolabiatus* **J** lectotype and **K** paralectotype **L** Paralectotype of *A. annamiticus roseotincta* **M** Paratype of *A. rottiensis* **N** Probable syntype of *A. adamsii rubiginosa*.

***Amphidromus robustus* Fulton, 1896**

Amphidromus robustus Fulton, 1896a: 73.

Type locality. Java.

Type material. Syntype NHMUK 1896.6.13.15 (1D juvenile, Fig. 13D; H=35.3 mm, W=18.8 mm).

Remarks. The specimen from Fulton's collection with an accompanied label bearing a handwritten taxon and locality is considered to be a syntype (ICZN 1999: Art. 72.4). However, in the original description, Fulton provided the measurements of an adult specimen, yet only a juvenile specimen was located in the NHM.

***Amphidromus roemeri* (Pfeiffer, 1863)**

Bulimus römeri Pfeiffer, 1863 [1862]: 274, pl. 36, fig. 4.

Type locality. Lao Mountains, Cambodia [=Cambodia].

Type material. Lectotype NHMUK 19601450 (Fig. 13E; H=23.1 mm, W=15.0 mm), paralectotypes NHMUK 19601451 (2S juveniles, Fig. 13F).

***Amphidromus laevis romaensis* Rolle, 1903**

Amphidromus laevis var. *romaensis* Rolle, 1903: 157.

Type locality. Insel Roma, Timor.

Type material. Lectotype (designated by Zilch 1953: 133, pl. 22, fig. 11), SMF 7574a, paralectotypes SMF 7574b-c, NHMUK 1908.7.6.78 (1S, Fig. 13G).

Remarks. The original description was very brief and H. Rolle never designated a unique name-bearing type. Later, Zilch (1953) designated the lectotype from H. Rolle's collection in the Senckenberg Museum. The NHM registration records show that a specimen was purchased from Sowerby and Fulton's collection with the original label stating "Co-type" and giving the locality "Roma I.". Therefore, we consider this specimen to be a paralectotype.

***Amphidromus sinistralis rosea* Fulton, 1896**

Amphidromus sinistralis var. *rosea* Fulton, 1896a: 76.

Type locality. Nördliches Celebes [Northern Sulawesi, Indonesia].

Type material. Lectotype (design. n.), NHMUK 19601545/1 (Fig. 13H; H=40.1 mm, W=19.2 mm), paralectotypes NHMUK 19601545/2-3 (2S, Fig. 13I).

Remarks. Fulton attributed the authorship to von Martens. However, von Martens (1867: 356, pl. 21, fig. 2c) only describe this varietal form with a letter “*Bulimus sinistralis* var. C.” which is not a valid name (ICZN 1999: Art. 11.9). Therefore, Fulton (1896a: 76) is the sole author of this species.

The NHM holds a lot with Fulton’s handwritten labels bearing the taxon and type locality. The specimen that corresponds most closely with the original description is designated as the lectotype.

***Amphidromus roseolabiatatus* Fulton, 1896**

Amphidromus roseolabiatatus Fulton, 1896a: 89, pl. 6, fig. 8.

Type locality. Siam [Thailand].

Type material. Lectotype NHMUK 19601462 (Fig. 13J; H=36.5 mm, W=20.7 mm), paralectotype NHMUK 19601463 (1S, Fig. 13K).

***Amphidromus annamiticus roseotincta* Möllendorff, 1894**

Amphidromus annamiticus var. *roseotincta* Möllendorff, 1894: 150.

Type locality. near Chaya [Chaiya, Suratthani, Thailand].

Type material. Lectotype (designated by Zilch 1953: 135, pl. 23, fig. 26), SMF 7546, paralectotypes SMF 7547 (7D), SMF 28241 (10D), SMF 82356 (2D), SMF 82357 (4S), NHMUK 1894.2.26.45–46 (2D, Fig. 13L).

Remarks. Möllendorff (1894) provided a very brief definition of the taxon without figures. The type locality as written on the lectotype label was “Tschaya”. The NMH possess a lot of two shells purchased from H. Rolle, which are considered to be probable paralectotypes.

***Amphidromus rottiensis* Chan & Tan, 2010**

Amphidromus rottiensis Chan, Tan & Abbas, 2008: 2, 3, fig. 1. [*nomen nudum*, ICZN (1999: Arts 8.6 and 11.1)].

Amphidromus rottiensis Chan & Tan, 2010: 246, fig. 1G–I.

Type locality. Southwest central plateau portion (Busalangga) of Rotti Island (Pulau Rote), Indonesia.

Type material. Holotype MZBGst.15.047 (Ex NHMUK 20080621), paratypes NHMUK 20080622 (3S, Fig. 13M).

Remarks. Chan et al. (2008) described “*rottiensis*” in the Occasional Molluscan Papers which does not fulfil the ICZN (1999: Art. 8.6) guidelines, and could not

be made available (ICZN 1999: Art. 11.1). However, the same species name was later published correctly (ICZN 1999: Art. 8) and made available in Chan and Tan (2010).

***Amphidromus adamsii rubiginosa* Fulton, 1896**

Amphidromus adamsi var. *rubiginosa* Fulton, 1896a: 84.

Type locality. N. Borneo.

Type material. 2 probable syntypes NHMUK 19601477 (2S, Fig. 13N).

Remarks. There are two specimens from H. Cuming's collection accompanied with Fulton's handwritten label stating the taxon name. The type locality in the original publication was given as N. Borneo, but this lot has no locality. However, these specimens closely match the original description, especially in colour pattern and so it seems likely that these were indeed the shells that Fulton based the species description upon. Therefore, on this basis, we consider these specimens to be probable syntypes.

***Amphidromus adamsii rufocincta* Fulton, 1896**

Amphidromus adamsi var. *rufocincta* Fulton, 1896a: 83, pl. 5, fig. 1.

Type locality. Borneo.

Type material. Lectotype NHMUK 1896.6.13.11 (Fig. 14A; H=34.2 mm, W=17.7 mm).

***Amphidromus schomburgki* (Pfeiffer, 1860)**

Bulimus schomburgki Pfeiffer, 1860: 137, pl. 51, fig. 9.

Type locality. Siam [Thailand].

Type material. Lectotype NHMUK 19601452 (Fig. 14B; H=48.0 mm, W=25.5 mm), paralectotypes NHMUK 19601453 (1D + 1S, Fig. 14C).

***Amphidromus webbi simalurensis* Laidlaw, 1954**

Amphidromus webbi var. *simalurensis* Laidlaw, 1954: 78, 79.

Type locality. Soea Lamatau, Simalur Island [Simeulue Island, Aceh, Indonesia].

Type material. Holotype in RMNH, paratype NHMUK 1957.11.18.2 (1S, Fig. 14D).

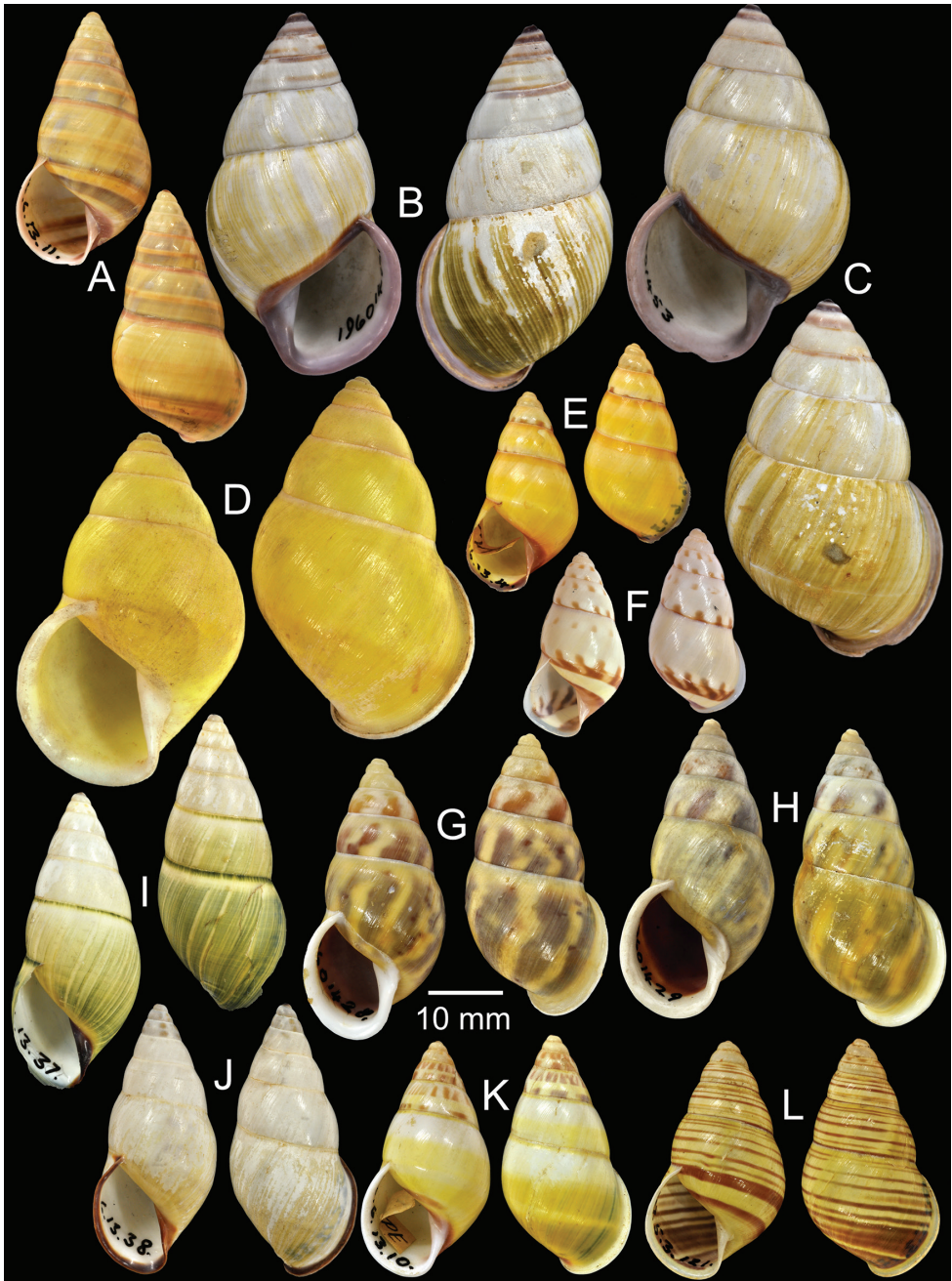


Figure 14. Type specimens of *Amphidromus* spp. **A** Lectotype of *A. adamsii rufocincta* **B–C** *A. schomburgki* **B** lectotype and **C** paralectotype **D** Paratype of *A. webbi simalurensis* **E** Lectotype of *A. adamsii simplex* **F** Paralectotype of *A. singalangensis* **G–H** *A. sinistralis* **G** lectotype and **H** paralectotype **I–J** *A. smithii* **I** lectotype and **J** paralectotype **K** Lectotype of *A. quadrasi solida* **L** Lectotype of *A. sowerbyi*.

***Amphidromus adamsii simplex* Fulton, 1896**

Amphidromus adamsi var. *simplex* Fulton, 1896a: 83, pl. 5, fig. 12.

Type locality. Banguay Island [Sabah, Malaysia].

Type material. Lectotype NHMUK 1896.6.13.4 (Fig. 14E; H=26.1 mm, W=13.4 mm).

***Amphidromus singalagensis* Rolle, 1908**

Amphidromus singalagensis Rolle, 1908: 67.

Type locality. Ostabhang des Singalang, West Sumatra [Eastern slope of Mount Singalang, West Sumatra, Indonesia].

Type material. Lectotype (designated by Zilch 1953: 133, pl. 23, fig. 20), SMF 7671, paralectotypes NHMUK 1908.7.6.85-86 (2S, Fig. 14F), SMF 7672 (5S).

Remarks. The lectotype was designated from H. Rolle's collection (Zilch 1953: 133, pl. 23, fig. 20). The NHM holds one lot of 2 specimens from the type series, labeled as "co-type", and these are considered paralectotypes.

***Amphidromus sinistralis* (Reeve, 1849)**

Bulimus sinistralis Reeve, 1849: *Bulimus*, plate 81 species 603, fig. 603.

Type locality. Java.

Type material. Lectotype NHMUK 19601428 (Fig. 14G; H=37.3 mm, W=18.5 mm), paralectotypes NHMUK 19601429 (2S, Fig. 14H).

***Amphidromus smithii* Fulton, 1896**

Amphidromus smithii Fulton, 1896a: 88, 89, pl. 7, figs 12, 12a.

Type locality. Annam [Central Vietnam].

Type material. Lectotype NHMUK 1896.6.13.37 (Fig. 14I; H=39.2 mm, W=16.5 mm), paralectotype NHMUK 1896.6.13.38 (1S, Fig. 14J).

***Amphidromus quadrasi solida* Fulton, 1896**

Amphidromus quadrasi var. *solida* Fulton, 1896a: 86, pl. 5, fig. 16.

Type locality. Palawan [Philippines].

Type material. Lectotype NHMUK 1896.6.13.10 (Fig. 14K; H=31.5 mm, W=16.3 mm).

***Amphidromus sowerbyi* Fulton, 1907**

Amphidromus sowerbyi Fulton, 1907: 152, pl. 9, fig. 10.

Type locality. Nias Island, Sumatra.

Type material. Lectotype NHMUK 1907.5.3.121 (Fig. 14L; H=31.1 mm, W=17.2 mm).

***Amphidromus adamsii subunicolor* Fulton, 1896**

Amphidromus adamsii var. *subunicolor* Fulton, 1896a: 82, pl. 5, fig. 5.

Type locality. Banguay Island [Sabah, Malaysia].

Type material. Lectotype NHMUK 1896.6.13.46 (Fig. 15A; H=30.1 mm, W=16.8 mm).

Remarks. Fulton attributed the authorship of this variety to von Martens (1867: 357). However, von Martens only describe this varietal form with a letter “*Bulimus adamsii* var. D.”, which is not a valid name (ICZN 1999: Art. 11.9). Later “*subunicolor*” was appropriately described and figured in Fulton (1896a). The basal lip or bottom of the aperture of the lectotype was damaged and so the shell height given here is much smaller than the actual specimen size.

***Amphidromus sumbaensis* Fulton, 1896**

Amphidromus sumbaensis Fulton, 1896a: 102.

Type locality. Sumba (Soemba) Island [Sumba Island, East Nusa Tenggara, Indonesia].

Type material. Lectotype NHMUK 96.6.13.41 (Fig. 15B; H=34.1 mm, W=16.6 mm), paralectotype NHMUK 1896.6.13.42 (1S).

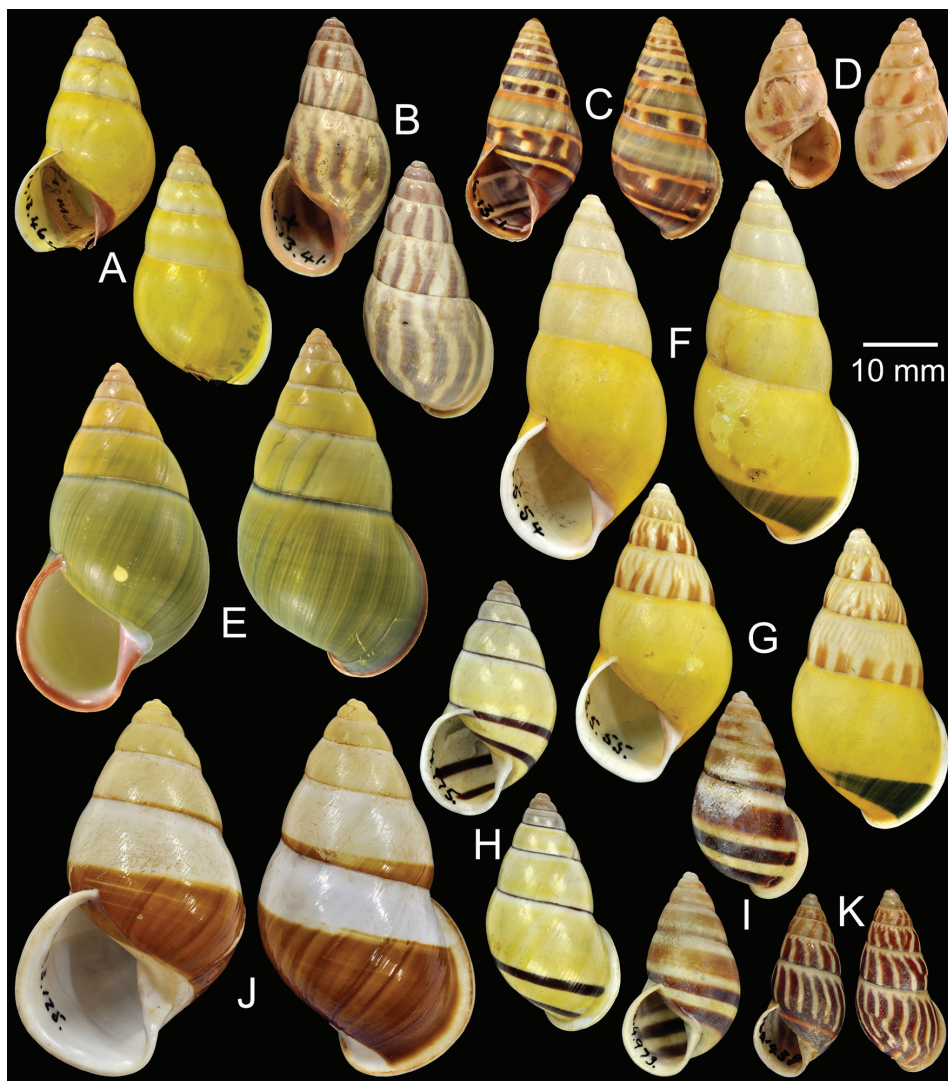


Figure 15. Type specimens of *Amphidromus* spp. **A** Lectotype of *A. adamsii subunicolor* **B** Lectotype of *A. sumbaensis* **C** Lectotype of *A. adamsii superba* **D** Possible syntype of *A. theobaldianus* **E** Paralectotype of *A. smithi ventrosulus* **F–G** *A. versicolor* **F** lectotype and **G** paralectotype **H–I** *A. sinensis vicaria* **H** lectotype and **I** paralectotype **J** Holotype of *A. webbi* **K** Lectotype of *A. zebrinus*.

***Amphidromus adamsii superba* Fulton, 1896**

Amphidromus adamsi var. *superba* Fulton, 1896a: 83, pl. 5, fig. 10.

Type locality. Banguay Island [Sabah, Malaysia].

Type material. Lectotype NHMUK 1896.6.13.1 (Fig. 15C; H=29.4 mm, W=14.4 mm).

***Amphidromus theobaldianus* (Benson, 1857)**

Bulimus theobaldianus Benson, 1857: 329, 330.

Type locality. Yanglaw, Tenasserim [in the area of Tanintharyi Region, Myanmar].

Type material. Possible syntype NHMUK 1907.11.21.64 (1D juvenile; Fig. 15D; H=22.3 mm, W=12.4 mm).

Remarks. The original description seems to be based on one specimen and a single set of measurements was given. Benson (1857: 329) stated “peristomate tenui?” [=peristome thin?], and Theobald (1876: 187) also stated “...described by Benson from an imperfect example”, which we have interpreted as meaning that the type specimen is an immature shell. The NHM holds a lot containing a juvenile specimen figured in Hanley and Theobald (1870: pl. 19, fig. 10), and the label states “from Hanley coll. figd in Con. Ind. pl. 19, fig. 10”. The collection locality states “Tenasserim” which agrees with the original description. However, this specimen is larger than the dimensions given, so we refrain from designating it as the lectotype.

***Amphidromus smithi ventrosulus* Möllendorff, 1900**

Amphidromus smithi ventrosulus Möllendorff, 1900: 132, 133.

Type locality. Phuc-son, Annam [Tan Yen District, Bac Giang Province, northeastern Vietnam].

Type material. Lectotype (designated by Zilch 1953: 133, pl. 23, fig. 19), SMF 7643 (1S), paralectotypes SMF 7642/6 (6S), NHMUK 1902.3.22.20-21 (2S, Fig. 15E).

Remarks. Möllendorff indicated that the specimens examined in the original description were from H. Fruhstorfer’s collection. The lectotype was designated by Zilch (1953: 133) and is housed in the Senckenberg Museum. The NHM registration records show that the two specimens were purchased from H. Fruhstorfer. The specimen locality is “Annam” which matches with the type locality. We therefore consider these specimens to be paralectotypes.

***Amphidromus versicolor* Fulton, 1896**

Amphidromus versicolor Fulton, 1896a: 86.

Type locality. Balabac [Balabac Island, Palawan, Philippines].

Type material. Lectotype NHMUK 1893.3.5.54 (Fig. 15F; H=48.7 mm, W=21.8 mm), paralectotype NHMUK 1893.3.5.55 (1S, Fig. 15G).

***Amphidromus sinensis vicaria* Fulton, 1896**

Amphidromus sinensis var. *vicaria* Fulton, 1896a: 80.

Type locality. Pegu [Bago, northeast of Yangon, Myanmar]; Chittagong [in Bangladesh].

Type material. Lectotype (design. n.), NHMUK 1888.12.4.975 (Fig. 15H; H=30.3 mm, W=16.7 mm), paralectotypes NHMUK 1888.12.4.971–974 (4S, Fig. 15I), NHMUK 1888.12.4.976–979 (4S) from Pegu; SMF 7639 (1S), SMF 175769 (2S) from Chittagong.

Remarks. Fulton clearly stated in the original description that the type series was composed of two lots from Pegu, and Chittagong. No specimens from Chittagong were located in the NHM collections. However, the specimen that most closely matched with the original description in Fulton (1896a: 80) and is figured in Hanley and Theobald (1876: pl. 21, fig. 5) is designated here as the lectotype, NHMUK 1888.12.4.975. The type locality of these taxa is here restricted to “Pegu”, the locality of the lectotype.

***Amphidromus webbi* Fulton, 1907**

Amphidromus webbi Fulton, 1907: 152–153, pl. 9, fig. 8.

Type locality. Nias Island, Sumatra [North Sumatra, Indonesia].

Type material. Holotype NHMUK 1907.5.3.125 (Fig. 15J; H=51.1 mm, W=29.8 mm).

***Amphidromus zebrinus* (Pfeiffer, 1861)**

Bulimus zebrinus Pfeiffer, 1861: 194.

Type locality. Siam [Thailand].

Type material. Lectotype NHMUK 19601439 (Fig. 15K; H=24.7 mm, W=11.6 mm).

Descriptions

Genus *Amphidromus* Albers, 1850

Subgenus *Syndromus* Pilsbry, 1900

Type-species. *Helix contraria* Müller, 1774 by subsequent designation of Zilch (1960: 623).

***Amphidromus (Syndromus) globonevilli* Sutcharit & Panha, sp. n.**

<http://zoobank.org/B2747236-D3C2-427E-9FE1-CE1F986CF037>

Figs 16A, C–F, 17A, B

Amphidromus sinensis var. *globosa* Nevill, 1878: 126. [*nomen nudum*]. Type locality: Chittagong [Bangladesh]. Pilsbry 1900: 191. Richardson 1985: 44.

Type material. Holotype CUMZ 4925 (height 21.9 mm, width 14.2 mm, whorls $5\frac{3}{4}$; Fig. 16C), paratypes CUMZ 4926 (13 shells), CUMZ 4927 (6 shells; Fig. 16D–F), CUMZ 4928 (12 shells), CUMZ 4929 (4 shells), NHMUK 20140707 (2 shells), SMF (2 shells).

Measurement of 37 paratypes; height range 18.3–23.3 mm, mean 21.08 ± 1.18 ; width range 11.9–15.3 mm, mean 13.59 ± 0.69 ; height/width ratio 1.46–1.62, mean 1.55 ± 0.04 ; whorls 5–6.

Other material. Chittagong [now in Bangladesh] original specimen of “*globosa* Nevill, 1878” NHMUK 1903.7.1.1921.

Type locality. Wat Phothikhun, Maesod, Tak, Thailand ($16^{\circ}45'42.2''\text{N}$, $98^{\circ}38'49''\text{E}$).

Diagnosis. This new species can be distinguished from *A. sinensis* (Benson, 1851) by having a smaller, more ovate conic shell (Fig. 16G–I). It differs from *A. flavus* (Pfeiffer, 1861) which exhibits an elongated conic shell a faint yellowish spiral band below the periphery, and an elongated aperture (Fig. 7I, J). It differs from *A. lepidus* (Gould, 1856) and *A. roemeri* (Pfeiffer, 1863) by having a yellowish shell colour with two dark brown spiral bands below the periphery, while *A. roemeri* have a more ovate to stout shell, whitish in colour with reddish-brown spiral bands below the periphery (Fig. 13E, F) and *A. lepidus* has a monochrome whitish shell (Fig. 10C).

Description. Shell. Shell small, sinistral, ovate conic, rather thin; umbilicus perforate. Apex acute without black spot; spire short; suture depressed and wide. Whorls slightly convex; last whorl round to ovate. Periostracum thin and transparent. Shell colour yellowish, paler near apex; subsutural band white and with darker yellow band below. Last whorl with two brown spiral bands below periphery. Aperture wide and ovate; columella straight; lip white and little expanded; parietal callus thin and transparent.

Genital organs. Atrium (at) short ($n = 5$). Penis (p) long, cylindrical and enlarged near penial retractor muscle. Epiphallus (e) smaller than penis and almost similar to penis length; flagellum (fl) similar length to epiphallus; appendix absent. Penial retractor muscle (pr) short and relatively thin. Vas deferens (vd) narrow tube extending from free oviduct (fo) and connected to epiphallus (Fig. 17A).

Internal wall of penis almost smooth surfaced, corrugated into a series of thickened; proximal to genital orifice, with swollen longitudinal penial pilasters (pp). Penial verge (pv) large, elongated conical shape, about two-thirds of penis length and with smooth surface (Fig. 17B).

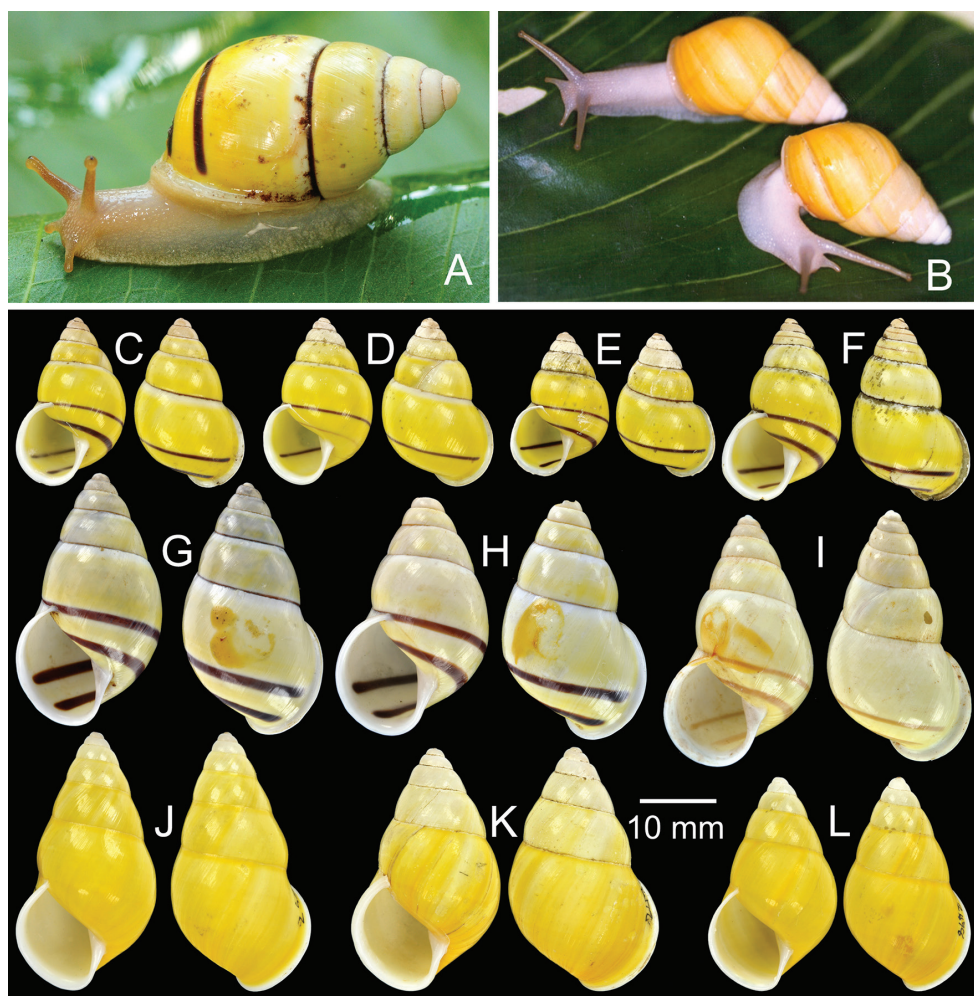


Figure 16. Shells and live snails characteristics. **A** Living snail of *A. (Syndromus) globonevilli* Sutcharit and Panha, sp. n. from the type locality with a shell height of approximately 20 mm **B** Living snail of *A. (Syndromus) principalis* Sutcharit and Panha, sp. n. from the type locality with a shell height of approximately 25 mm **C–F** *A. (Syndromus) globonevilli* Sutcharit and Panha, sp. n. **C** holotype CUMZ 4925 and **D–F** paratypes CUMZ 4927 **G–I** Syntypes UMZC of *A. sinensis* (Benson, 1851) from China **J–L** *A. (Syndromus) principalis* Sutcharit and Panha, sp. n. **J** holotype CUMZ 2543 and **K, L** paratypes CUMZ 2478.

Vagina (v) cylindrical, longer than penis, held in position with series of thin muscles originating from foot floor. Vaginal pouch and stimulator pilaster absent. Gametolytic duct (gd) long, slender; proximal to genital orifice enlarged same diameter as vagina, and distal to genital orifice tapering to small tube connected to gametolytic sac (gs). Oviduct (ov) and albumen gland (ag) enlarged; hermaphroditic gland (hg) multilobed and connected with hermaphroditic duct (hd) (Fig. 17A).

Internally, vaginal wall sculptured with longitudinal vaginal pilasters (vp); proximal to genital orifice with smooth and continuous ridges about two-third of its length, and pilasters at distal to genital orifice interrupted by transverse divisions (Fig. 17B).

Etymology. The specific name comes from the Latin word “*globous*” meaning “ball or sphere” and the name of Dr. Geoffroy Nevill, who first recognized this as a new species and introduce the name “*globosa*” but was unavailable (see Remark of “*globosa*”).

Distribution. This new species is known from the type locality in Tak Province, western Thailand. In addition, NHM specimens indicate that this species is also found from Chittagong, Bangladesh.

Remarks. The type specimen of *A. sinensis* s.s. was presumed to be lost (Pilsbry 1900, Laidlaw and Solem 1961). Recently, we have located one lot of three shells in Benson’s collection at UMZC with the collection locality of “China”, which we consider to be possible syntypes. Photographs of these three shells (Fig. 16G–I) are shown here for further comparison. The shell that most closely matches the original description of Benson’s (1851: 264) and Benson’s specimen figured in Küster and Pfeiffer (1853: pl. 20, figs 1, 2) is illustrated in Figure 16G.

***Amphidromus (Syndromus) principalis* Sutcharit & Panha, sp. n.**

<http://zoobank.org/27D54FEF-42E2-4F30-B04A-A6DF503FC18F>

Figs 16B, J–L, 17C, D

Type material. Holotype: CUMZ 2543 (height 33.9 mm, width 17.9 mm, whorls 6; Fig. 16J), paratypes CUMZ 2478 (3 shells, Fig. 16K, L), CUMZ 2386 (19 shells), CUMZ 2387 (18 shells), NHMUK 20140708 (2 shells) and SMF (2 shells).

Measurement of 27 paratypes; height range 25.2–36.0 mm, mean 30.60 ± 2.38 ; width range 14.5–18.9 mm, mean 16.43 ± 1.09 ; height/width ratio 1.69–2.00, mean 1.86 ± 0.07 ; whorls $5\frac{3}{4}$ – $6\frac{3}{4}$.

Other material. From the type locality CUMZ 2401, 2422.

Type locality. Koh Kra, about 30 km off the east coast of Pak Phanang, Nakhon Srithammarat in the Gulf of Thailand (8°23'55"N, 100°44'2"E).

Diagnosis. This new species is distinguished from *A. globonevilli* Sutcharit and Panha, sp. n. by having a more ovate to elongated conic shell of entirely uniform bright yellow colour. The reproductive organ lacks a vaginal pouch, the penial verge is small and conical. Living snails have an entirely whitish to creamy body; only older snails are likely to have a pale brown head-foot. Superficially, this new species resembles *A. flavus* from northern Thailand and Laos. However, this new species exhibits a bright yellow, slightly ovate shell, shorter expanded lip and thickened shell, while *A. flavus* has a slender, pale yellow shell, wide expanded lip with faint spiral band below periphery (Fig. 7I, J).

Description. Shell. Shell ovate to slightly elongate conic, glossy, smooth, sinistral and rimate. Apex obtuse with brown to black spot on the tip. Shell uniform golden yellow (without any bands). Last whorl darker yellow than earlier whorls. Spire conic with

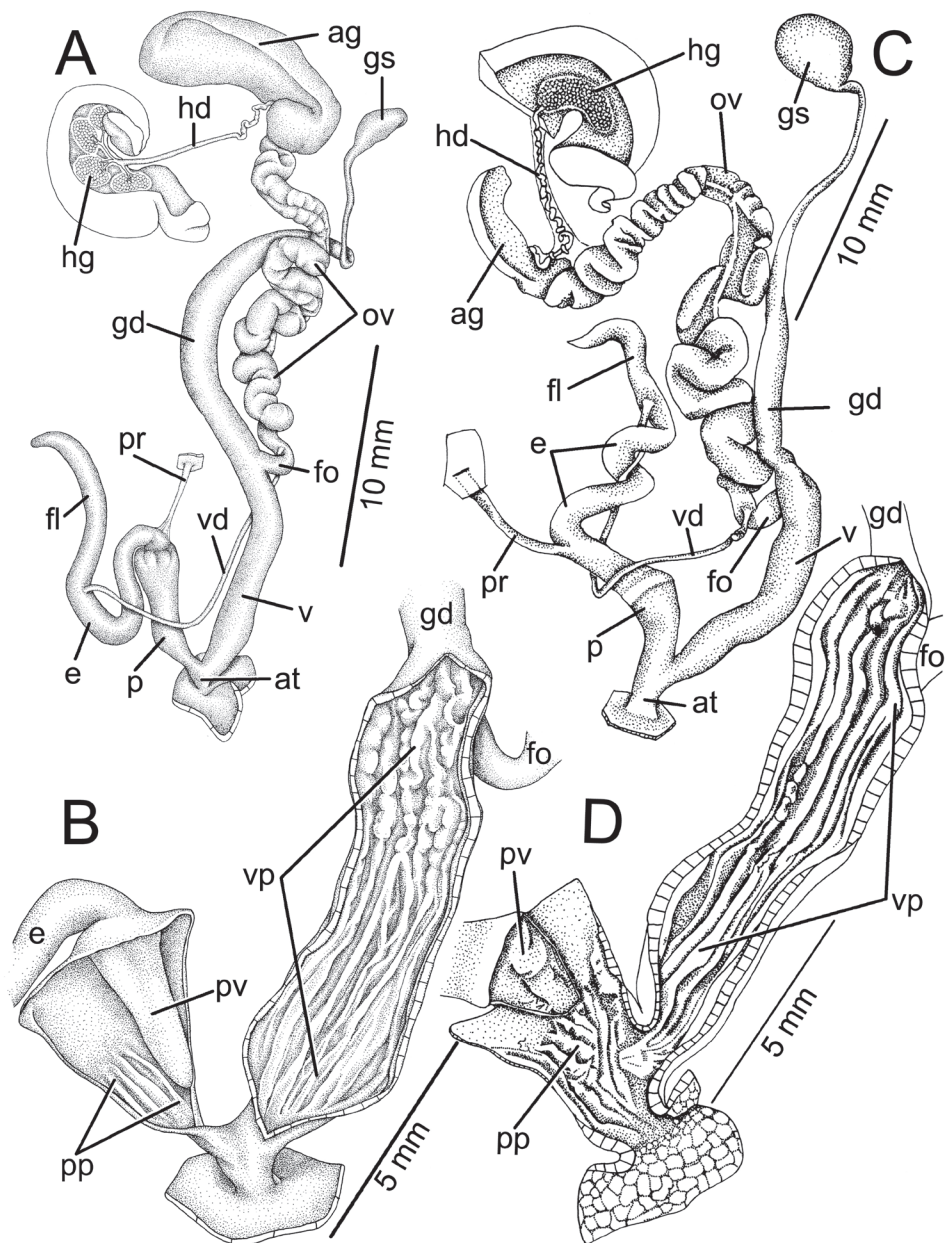


Figure 17. A–B Genitalia of *A. (Syndromus) globonevilli* Sutcharit and Panha, sp. n. showing the reproductive system and interior structures of the penis and vaginal chamber **C–D** Genitalia of *A. (Syndromus) principalis* Sutcharit and Panha, sp. n. showing the general characteristics of the genital system and the interior structures of the penis, atrium and vagina chamber. Anatomical abbreviations are as described in Sutcharit and Panha (2006a, b, 2011): ag, albumin gland; ap, appendix; at, atrium; e, epiphallus; fl, flagellum; fo, free oviduct; gd, gametolytic duct; gs, gametolytic sac; hd, hermaphroditic duct; hg, hermaphroditic gland; o, oviduct; p, penis; pp, penial pilaster; pm, penial retractor muscle; pv, penial verge; v, vagina; vd, vas deferens; vp, vaginal pilaster.

slightly depressed suture. Aperture ovate; peristome white, narrowly expanded and not reflected. Columella white, straight and perpendicular. Parietal callus thin and translucent.

Genital organ. Atrium (at) slightly long ($n = 10$). Penis (p) long, cylindrical and enlarged in middle. Epiphallus (e) longer than penis length; flagellum (fl) shorter than epiphallus; appendix absent. Penial retractor muscle (pr) thickened and relatively long (Fig. 17C). Vas deferens (vd) small tube and connected between epiphallus and free oviduct.

Internal wall of penis corrugated into series of thin and longitudinal penial pilasters (pp), which form a thin fringe around penial verge. Penial verge (pv) short conic, surface with thin irregular furrow (Fig. 17C).

Female reproductive organ similar to former described species but differs in that vagina internal wall possesses swollen and nearly smooth longitudinal vaginal pilaster (Fig. 17C, D).

Etymology. The specific epithet is derived from the Latin “*principalis*” meaning “leader” and refers to Her Royal Highness Princess Maha Chakri Sirindhorn who chaired the Plant Genetic Conservation Project as a Royal Initiation to support biodiversity in Thailand. The malacological survey on Koh Kra in 2000 was part of an expedition supported by this project.

Distribution. This new species is known only from the type locality.

Remarks. *Amphidromus principalis* Sutcharit & Panha, sp. n. is known only from the type locality, the granitic island. The forestation type on the island was dry evergreen forest, the snails were found crawling on the tree leaves, trunks or branches of almost all trees up to 10 m height. We also explored two other satellite islands but found no *Amphidromus* on these islands or any other terrestrial snails other than subulinids.

Acknowledgements

We thank the Plant Genetic Conservation Project Under the Royal Initiation of Her Royal Highness Princess Maha Chakri Sirindhorn and the Navy Special Warfare Unit, The Royal Thai Navy for help and encouragement that made our fieldwork possible. We are indebted to A.J. Baldinger (MCZ, Harvard) and R. Piece (UMZC, Cambridge) for the loan of type specimens. We are grateful to the ASRU members for collecting specimens. We are especially grateful to N. Kitana and S. Natsupakpong for providing copies of important literatures, and F. Köhler for photographing type materials. This project was funded by the TRF Senior Research Scholar 2012-2015 (RTA5580001); Ratchadaphiseksomphot Endowment Fund of Chulalongkorn University (RES 560530658-FW); the Darwin Initiative Project (no. 14-653).

References

Albers JC (1850) Die Heliceen, nach natürlicher Verwandtschaft systematisch geordnet. Verlag von TCF Enslin, Berlin, 266 pp.

- Bartsch P (1917) The Philippine land shells of the genus *Amphidromus*. Bulletin of the United State National Museum 100: 1–47.
- Benson WH (1851) Description of new landshells from St. Helens, Ceylon, and China. Annals and Magazine of Natural History, Series 2 vol. 7: 262–265.
- Benson WH (1857) New species of *Bulimus* from India, Burma, and the Mauritius. Annals and Magazine of Natural History, Series 2 vol. 19: 327–330.
- Butot LJM (1955) The mollusk fauna of Pualau Panaitan (Prinseneiland) land and freshwater molluscs. Treubia 23: 69–135.
- Chan SY, Tan SK (2008) On a new species of *Amphidromus* (*Syndromus*) (Gastropoda: Pulmonata: Camaenidae) from Sumba Island, Indonesia. Occasional Molluscan Papers 1: 6–10.
- Chan SY, Tan SK (2010) On two new species of *Amphidromus* (Gastropoda: Camaenidae) from the Lesser Sunda Islands, Indonesia. Raffles Bulletin of Zoology 58: 245–249.
- Chan SY, Tan SK, Abbas J (2008) On a new species of *Amphidromus* (*Syndromus*) (Gastropoda: Pulmonata: Camaenidae) from Rotti Island, Indonesia. Occasional Molluscan Papers 1: 1–5.
- Cilia DP (2013) Description of a new species of *Amphidromus* Albers, 1850 from Sumba, Indonesia (Gastropoda Pulmonata Camaenidae). Biodiversity Journal 4: 263–268.
- Collinge WE (1903) Report on the non-operculate land Mollusca. Fasciculi Malayensis Zoology 2: 205–218.
- Dance SP (1986) A history of shell collecting. EJ Brill-Dr. W Backhuys, Leiden, 265 pp.
- Dharma B (1993) Description of two new species of *Amphidromus* from Sumatra, Indonesia (Gastropoda: Pulmonata: Camaenidae). Apex 8: 139–143.
- Dharma B (2007) Report of fossil *Amphidromus* and description of new species and new subspecies of recent and fossil *Amphidromus* from Indonesia (Gastropoda: Pulmonata: Camaenidae). Schriften zur Malakozoologie 23: 45–78.
- Dohrn H (1861) Descriptions of new shells from the collection of H. Cuming, Esq. Proceedings of the Zoological Society of London 29: 205–207.
- Duncan FM (1937) On the dates of publication of the Society's 'Proceedings' 1859–1926, with an appendix containing the dates of publication 1830–1858, compiled by F.H. Waterhouse; also of the 'Transactions' 1833–1869 by Henry Peavot, originally published in P.Z.S. 1893, 1913. Proceedings of the Zoological Society of London, Series A 107: 71–84.
- Fischer-Piette E (1950) Liste des types décrits dans le Journal de Conchyliologie et Conservés dans la collection de ce journal. Journal de Conchyliologie 90: 149–180.
- Fruhstorfer H (1905) Ein neuer *Amphidromus*. Nachrichtenblatt der Deutschen Malakozoologischen Gesellschaft 37: 83–84.
- Fulton H (1896a) A list of the species of *Amphidromus* Albers, with critical notes and descriptions of some hitherto undescribed species and varieties. Annals and Magazine of Natural History, Series 6 vol. 17: 66–94.
- Fulton H (1896b) Descriptions of new species of *Nanina*, *Helix*, *Amphidromus* and *Porphyrobaphe*. Annals and Magazine of Natural History, Series 6 vol. 18: 100–104.
- Fulton H (1897) Descriptions of two new species of *Amphidromus*. Annals and Magazine of Natural History, Series 6 vol. 20: 211–212.
- Fulton H (1898) Description of *Amphidromus inconstans* n. sp. from the Malay Archipelago. Proceedings of the Malacological Society of London 3: 10.

- Fulton H (1899a) A list of the species of land Mollusca collected by Mr. W. Doherty in the Malay archipelago; with descriptions of some supposed new species and varieties. Proceedings of the Malacological Society of London 3: 212–219.
- Fulton H (1899b) Descriptions of supposed new species of *Streptaxis* and *Amphidromus*. Proceedings of the Malacological Society of London 3: 302–303.
- Fulton H (1901) Descriptions of new species of *Xesta*, *Amphidromus* and *Cyclostoma* from Madagascar and Perak. Journal of Malacology 8: 103–104.
- Fulton H (1907) Description of new species of *Trochomorpha*, *Cochlostyla*, *Amphidromus*, *Bulimus*, *Drymaeus*, *Placostylus*, *Stenogyra*, *Leptopoma*, *Cyclophorus*, *Cyclotus* and *Alycaeus*. Annals and Magazine of Natural History, Series 7 vol. 19: 149–157.
- Godwin-Austen HH (1876) On the Helicidae collected during the expedition into the Dafla Hills, Assam. Journal of the Asiatic society of Bengal 45: 311–318.
- Godwin-Austen HH (1895) List and distribution of the land Mollusca of the Andaman and Nicobar Islands, with Descriptions of some supposed new species. Proceedings of the Zoological Society of London 63: 438–457.
- Gould AA (1843) Description of land mollusks from the province of Tavoy, in British Burmah. Proceedings of the Boston Society of Natural History 1: 137–141.
- Gould AA (1844) Description of land mollusks from the province of Tavoy, in British Burmah. Boston Journal of Natural History 4: 452–459.
- Gould AA (1846) Descriptions of shells, sent from Tavoy, in Burmah, by the Rev. Mr. Mason. Proceedings of the Boston Society of Natural History 2: 98–100.
- Gould AA (1855) New species of land and fresh-water shells from Western (N.) America. Proceedings of the Boston Society of Natural History 1855: 128–129.
- Gould AA (1856) Descriptions of new shells. Proceedings of the Boston Society of Natural History 6: 11–16.
- Grateloup JPS de (1840a) Description de plusieurs coquilles nouvelles ou peu connues de mollusques exotiques vivants. Actes de la Société Linnéenne de Bordeaux 11: 394–455.
- Grateloup JPS de (1840b) Note sur un memoire relatif à des mollusques exotiques nouveaux ou peu connus. Actes de la Société Linnéenne de Bordeaux 11: 161–170.
- Gude GK (1914) Mollusca II (Trochomorphidae – Janellidae). In: Shipley AE, Marshall GAK (Eds) The Fauna of British India, including Ceylon and Burma. Taylor and Francis, London, 520 pp.
- Hanley SCT, Theobald W (1870–1876) Conchologia Indica: Illustrations of the Land and Fresh-water Shells of British India. Savill, Edward and Co., London, i–xviii + 65 pp., 160 pl. [p. 1–18, pls 1–40 [1870]; p. l–xviii [1876]] [Published in parts, dates after Prashad (1927)]
- Hidalgo JG (1887) Description d'un *Amphidromus* et d'un *Cyclophorus* nouveaux, provenant des îles Philippines. Journal de Conchyliologie 35: 36–37.
- International Commission on Zoological Nomenclature (ICZN) (1999) International Code of Zoological Nomenclature, Forth Edition. London, International Trust for Zoological Nomenclature, 306 pp. <http://iczn.org/node/40200> [accessed 28 January 2015]
- Johnson RI (1964) The recent Mollusca of Augustus Addison Gould: Illustrations of the types described by Gould with a bibliography and catalog of his species. United States National Museum Bulletin 239: 1–182. doi: 10.5479/si.03629236.239

- Küster HC, Pfeiffer L (1845–1855) Die Gattungen *Bulimus*, *Partula*, *Achatinella*, *Achatina* und *Azece*. In: Abbildungen nach der Natur mit Beschreibungen. Systematisches Conchylien-Cabinet von Martini und Chemnitz 1 (13) [(1)]: iii–xix, 1–395, pls 1–70. [p. 49–96, pls 19–24 [1853]; p. 97–232, pls 30–52 [1854]] [Published in parts, dates follow Welter-Schultes (1999)]
- Laidlaw FF (1954) Notes on species of the genus *Amphidromus* (Mollusca: Pulmonata: Pleurodontidae) from island laying off the west coast of Sumatra, with description of new races. *Zoologische Mededelingen* 33: 75–81.
- Laidlaw FF, Solem A (1961) The land snail genus *Amphidromus*: A synoptic catalogue. *Fieldiana: Zoology* 41: 507–677.
- Lehmann H, Maassen WJM (2004) A new species of *Amphidromus* from Laos (Gastropoda: Pulmonata: Camaenidae). *Basteria* 68: 17–20.
- Martens E von (1867) Die Preussische Expedition nach Ost-Asien. Verlag der Königlichen Geheimen Ober-Hofbuchdruckerei, 477 pp.
- Mason F (1850) The Natural productions of Burmah, or notes on the fauna, flora and minerals of the Tenasserim province and the Burman empire. American Mission Press, Maulmain, 712 pp.
- Möllendorff OF von (1894) On a collection of land-shells from the Samui Islands, Gulf of Siam. *Proceedings of the Zoological Society of London* 1894: 146–156.
- Möllendorff OF von (1900) Zur Binnenmollusken-Fauna Annams III. *Nachrichtenblatt der Deutschen Malakozoologischen Gesellschaft* 32: 117–139.
- Morelet A (1875) Series Conchyliologiques, comprenant L'énumération de mollusques terrestres et fluviatiles, recueillis pendant le cours de différents voyages, ainsi que la description, de plusieurs espèces nouvelles. IV. 4e livraison Indo Chine, 227–377.
- Morlet L (1886) Diagnoses molluscorum novorum Cambodgiae. *Journal de Conchyliologie* 34: 74–75.
- Morlet L (1889) Catalogue des coquilles recueillies, par M. Pavie dans le Cambode et le Royaume de Siam, et description d'espèces nouvelles (1). *Journal de Conchyliologie* 37: 121–199.
- Müller OF (1774) Vermium terrestrium et fluviatilium, seu animalium infusoriorum, helminthicorum, et testaceorum, non marinorum, succincta historia, 2. Heineck and Faber, Hauniae et Lipsiae, 214 pp.
- Nevill G (1878) Hand list of Mollusca in the Indian Museum, Calcutta. Calcutta, Trustees, 338 pp. doi: 10.5962/bhl.title.6561
- Panha S (1996) A new species of *Amphidromus* from Thailand (Stylommatophora: Camaenidae). *Malacological Review* 29: 131–132.
- Petit RE (2007) Lovell Augustus Reeve (1814–1865): Malacological author and publisher. *Zootaxa* 1648: 1–120.
- Pfeiffer L (1852) Diagnosen neuer Heliceen. *Zeitschrift für Malakozoologie* 9: 91–95.
- Pfeiffer L (1853) Monographia Heliceorum Viventium. Volume 3. F.A. Brockhaus, Lipsiae, 711 pp.
- Pfeiffer L (1854) Descriptions of eighteen new species of land shells from the collection of H. Cuming, Esq. *Proceedings of the Zoological Society of London* 20 [1852]: 83–87. [Published in parts, dates follow Duncan (1937)]

- Pfeiffer L (1855) Descriptions of fifty-seven new species of Helicea Mr. H. Cuming's collection. Proceedings of the Zoological Society of London 22 [1854]: 286–298. [Published in parts, dates follow Duncan (1937)]
- Pfeiffer L (1857a) Descriptions of fifty-eight new species of Helicea from the collection of H. Cuming, Esq. Proceedings of the Zoological Society of London 24 [1856]: 324–336. [Published in parts, dates follow Duncan (1937)]
- Pfeiffer L (1857b) Diagnosen neuer Landschnecken. Malakozoologische Blätter 4: 155–158.
- Pfeiffer L (1857c) Descriptions of thirty-three new species of land shells from the collection of H. Cuming, Esq. Proceedings of the Zoological Society of London 24 [1856]: 385–392. [Published in parts, dates follow Duncan (1937)]
- Pfeiffer L (1860) Descriptions of thirty-six new species of land shells from Mr. H. Cuming's collection. Proceedings of the Zoological Society of London 28 [1860]: 133–141. [Published in parts, dates follow Duncan (1937)]
- Pfeiffer L (1861) Descriptions of new land shells in the collection of Mr. H. Cuming Esq. Proceedings of the Zoological Society of London 29 [1861]: 190–196. [Published in parts, dates follow Duncan (1937)]
- Pfeiffer L (1863) Descriptions of thirty-six new land shells from the collection of H. Cuming, Esq. Proceedings of the Zoological Society of London 30 [1862]: 268–278. [Published in parts, dates follow Duncan (1937)]
- Pfeiffer L (1864) Descriptions of fifteen new species of land shells from the collection of H. Cuming, Esq. Proceedings of the Zoological Society of London 31 [1863]: 523–526. [Published in parts, dates follow Duncan (1937)]
- Pfeiffer L (1877) Monographia Heliceorum Viventium. Volume 8. F.A. Brockhaus, Lipsiae, 729 pp.
- Pilsbry HA (1900) Manual of Conchology, Structure and Systematic, with Illustrations of the Species, 2nd Series, Vol. 13. Academy of Natural Science Philadelphia, PA, 253 pp.
- Prashad B (1927) On the dates of publication of Hanley and Theobald's "Conchologica Indica". Journal and Proceedings of the Asiatic Society of Bengal, new series 22: 129–130.
- Reeve L (1848–1850) Conchologia Iconica: Illustrations of the shells of molluscous animals. Volume 5, Monograph of the genera *Bulimus*, *Achatina*, *Dolium*, *Cassis*, *Turritella*, *Mesalia*, *Eglisia*, *Cassidaria*, *Oniscia*, *Eburna*, pls 1–57. Reeve, Benham, and Reeve, King William Street, Strand, London, 147 plates. [pls 1–57 [1848]; pls 58–84 [1849]] [Published in parts, dates follow Petiti (2007)]
- Reeve L (1860) On two new species of shells from Cambojia. Annals and Magazine of Natural History, Series 3 vol 6: 203–204.
- Richardson L (1985) Camaenidae: Catalog of species. Tryonia 12: 1–479.
- Rolle H (1903) Neue Landschnecken von Niederländisch Indien. Nachrichtenblatt der Deutschen Malakozoologischen Gesellschaft 35: 156–157.
- Rolle H (1908) Zur Fauna von West-Sumatra. Nachrichtenblatt der Deutschen Malakozoologischen Gesellschaft 40: 63–70.
- Sherborn CD (1922) Index Animalium, Part I. Introduction, bibliography and Index A—Aff. The Trustees of the British Museum, London, 1–128.

- Severns M (2006) A new species and a new subspecies of *Amphidromus* from Atauro Island, East Timor (Gastropoda: Pulmonata: Camaenidae). *Basteria* 70: 23–28.
- Smith EA (1893) Descriptions of six new species of land shells from Annam. *Proceedings of the Malacological Society of London* 1: 10–13. doi: 10.3853/j.0067-1975.35.1983.315
- Smith EA (1895) On a collection of land-shells from Sarawak, British North Borneo, Palawan, and other neighboring islands. *Proceedings of the Zoological Society of London* 63 [1895]: 97–127.
- Solem A (1959) Zoogeography of the land and fresh-water molluscs of the New Hebrides. *Fieldiana: Zoology* 43: 241–359.
- Solem A (1983) First record of *Amphidromus* from Australia with anatomical note on several species (Mollusca: Pulmonata: Camaenidae). *Records of the Australian Museum* 35: 153–166.
- Sutcharit C, Panha S (2006a) A new subspecies of *Amphidromus* (A.) *inversus* (Müller, 1774) from Peninsular Malaysia. *Journal of Conchology* 39: 79–83.
- Sutcharit C, Panha S (2006b) Taxonomic review of the tree snails *Amphidromus* Albers, 1850 (Pulmonata: Camaenidae) in Thailand and adjacent areas: Subgenus *Amphidromus*. *Journal of Molluscan Studies* 72: 1–30. doi: 10.1093/mollus/eyi044
- Sutcharit C, Asami T, Panha S (2007) Evolution of whole-body enantiomorphy in the tree snail genus *Amphidromus*. *Journal of Evolutionary Biology* 20: 661–672. doi: 10.1111/j.1420-9101.2006.01246.x
- Sutcharit C, Panha S (2011) Neotype designation and re-description of the vanishing tree snail, *Amphidromus* (*Amphidromus*) *mundus* (Pfeiffer, 1853) (Pulmonata: Camaenidae). *Raffles Bulletins of Zoology* 59: 139–143.
- Theobald W (1876) Descriptions of some new land and freshwater shells from India and Burmah. *Journal of the Asiatic Society of Bengal* 45: 184–189.
- Welter-Schultes FW (1999) Systematisches Conchylien-Cabinet von Martini und Chemnitz (1837–1920), bibliography of the volumes in Göttingen. *Archives of Natural History* 26: 157–203. doi: 10.3366/anh.1999.26.2.157
- Wood H, Gallichan J (2008) The new molluscan names of César-Marie-Felix Ancey including illustrated type material from the National Museum of Wales. *Studies in Biodiversity and Systematics of Terrestrial Organism from the National Museum of Wales. Biotir Report* 3, 162 pp.
- Zilch A (1953) Die Typen und Typoide des Natur-Museums Senckenberg 10: Mollusca, Pleurodontidae (I). *Archiv für Molluskunkunde* 82: 131–140.
- Zilch A (1960) Gastropoda, Euthyneura. In: Schindewolf OH (Ed.) *Handbuch der Paläozoologie*, Band 6, Gastropoda. Gebrüder Borntraeger, Berlin, 601–834.

Assembly of a micro-hotspot of caenogastropod endemism in the southern Nevada desert, with a description of a new species of *Tryonia* (Truncatelloidea, Cochliopidae)

Robert Hershler¹, Hsiu-Ping Liu², Jeffrey S. Simpson²

1 Department of Invertebrate Zoology, Smithsonian Institution, P.O. Box 37012, Washington, DC 20013-7012, USA **2** Department of Biology, Metropolitan State University of Denver, Denver, CO 80217, USA

Corresponding author: Robert Hershler (hershler@si.edu)

Academic editor: T. Backeljau | Received 13 January 2015 | Accepted 16 March 2015 | Published 30 March 2015

<http://zoobank.org/8C3C5DD3-7424-49EC-9444-E07917D82DBE>

Citation: Hershler R, Liu H-P, Simpson JS (2015) Assembly of a micro-hotspot of caenogastropod endemism in the southern Nevada desert, with a description of a new species of *Tryonia* (Truncatelloidea, Cochliopidae). ZooKeys 492: 107–122. doi: 10.3897/zookeys.492.9246

Abstract

Newly obtained and previously published sequences of the cytochrome *c* oxidase subunit I (COI) gene were analyzed to examine the biogeographic assembly of the caenogastropod fauna (belonging to the families Assimineidae, Cochliopidae, and Hydrobiidae) of an isolated spring along the lower Colorado River in southern Nevada (Blue Point Spring). Based on available COI clock calibrations, the three lineages that comprise this fauna are 2.78–1.42 million years old, which is roughly coeval or slightly younger than the age of Blue Point Spring (inferred from local fossil spring deposits). Two of the lineages—endemic *Pyrgulopsis coloradensis* and *Assiminea* aff. *infima*—are most closely related to snails in the Death Valley area (well to the west) and likely colonized Blue Point Spring by transport on birds. A single haplotype was detected in both of these snails, suggesting that they may have only recently colonized Blue Point Spring. The third lineage—endemic *Tryonia infernalis*, newly described herein based on morphological and molecular evidence—is most closely related to a geographically proximal species in a lower Colorado River tributary (*T. clathrata*); the split between these taxa may be the product of vicariance (severance of a prior drainage connection) or a separate jump dispersal event. The considerable genetic diversity in *T. infernalis* (three haplotypes differing by 0.6% mean sequence divergence) suggests a possibly lengthy history of local differentiation. Our findings also identify Blue Point Spring as a new micro-hotspot of groundwater-dependent biodiversity in Nevada and will assist ongoing efforts to protect and conserve these imperiled ecosystems.

Keywords

Gastropoda, Assimineidae, Hydrobiidae, western United States, aquatic snails, biogeography, taxonomy, conservation

Introduction

The desert region of southeastern California and southwestern Nevada, encompassing portions of the Great Basin and lower Colorado River watershed, contains distinctive assemblages of tiny caenogastropods—belonging to the families Assimineidae (genus *Assiminea*), Cochliopidae (*Tryonia*) and Hydrobiidae (*Pyrgulopsis*)—that have been a recent focus of biogeographic study using mtDNA sequence data (e.g., Hershler et al. 1999a, b, Hershler and Liu 2008a, b). These assemblages broadly overlap geographically and are tightly linked with spring habitats; their biogeographic histories do not well correlate with surface drainage and have likely been shaped, at least in part, by overland dispersal on waterfowl (e.g., Liu et al. 2003, Hershler et al. 2005, Liu and Hershler 2007, Hershler and Liu 2008a). The biogeographic patterns of these assemblages also differ in important respects. The regional assimineids (referred to herein as the *Assiminea infima* complex) are amphibious animals that typically live on riparian vegetation along the margins of springs and spring runs. This assemblage belongs to a single lineage that diverged from marine (Pacific) coastal progenitors during the late Pliocene (Hershler and Liu 2008a). The other two assemblages are entirely aquatic: *Tryonia* is restricted to thermal waters while *Pyrgulopsis* lives in ambient temperature and thermal habitats. Both of these assemblages are composed of multiple lineages, some having long histories of diversification within the region (Hershler et al. 1999a, Hershler et al. 2011). The *Tryonia* assemblage is composed of a few subgroups that have close relationships with congeners from the lower Colorado River basin (*T. angulata* Hershler), northern Great Basin and western California (*T. margae* Hershler, *T. salina* Hershler), and northeastern Mexico (*T. porrecta* [Mighels, 1845]; clade composed of *T. elata* Hershler, *T. ericae* Hershler, *T. variegata* Hershler) (Hershler et al. 1999a, Hershler et al. 2011). The *Pyrgulopsis* assemblage contains a much larger number of lineages which have close relationships to taxa from western California, the lower Colorado River basin, and other portions of western North America (Hershler and Liu 2008b, Hershler et al. 2013).

The *A. infima* complex is subdivided into a clade that is distributed in the Death Valley region (this lineage also contains a population from the head of the Gulf of California) and a genetically divergent population (*A. aff. infima* Berry) in Blue Point Spring (Hershler and Liu 2008a), which is located along Lake Mead ca. 150 km to the east-southeast (Fig. 1). Blue Point Spring also contains an endemic species of *Pyrgulopsis* (*P. coloradensis* Hershler) and a population of *Tryonia* that was previously assigned to widely ranging *T. porrecta* (Hershler 2001), neither of which have been previously studied genetically. Here we analyze newly obtained and previously published DNA sequences to examine the intersection of the biogeographic histories of the three con-

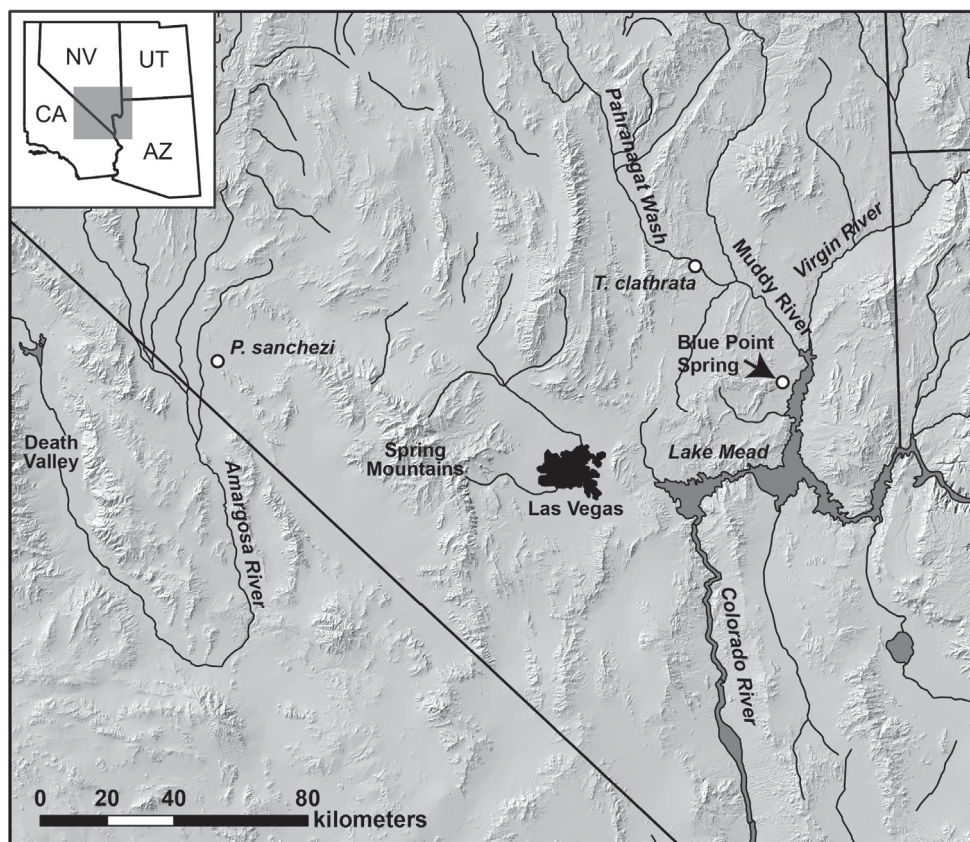


Figure 1. Map showing the location of Blue Point Spring relative to other geographic areas discussed in the text. The collecting localities for specimens of *Pyrgulopsis sanchezi* and *Tryonia clathrata* (sister taxa of Blue Point Spring endemics) used in the molecular phylogenetic analyses are also shown.

trasting groups of snails at this isolated spring. We also describe the Blue Point *Tryonia* as a new, endemic species based on molecular and morphologic evidence. Our results reveal a complex historic assembly of the Blue Point Spring snail fauna; and delineate this water body as another micro-hotspot of groundwater-dependent biodiversity in the region, which will assist ongoing efforts to protect and conserve these imperiled ecosystems (Greenwald and Bradley 2008, Abele 2011).

Methods

Fresh material was collected from Blue Point Spring by RH in May, 2014, and preserved in 90% ethanol for genetic analysis; a portion of the *T. porrecta* sample was relaxed with menthol crystals, fixed in dilute (4%) formalin, and preserved in 70% ethanol for anatomical study. Genomic DNA was extracted from entire snails (*A. aff. infima*, six

specimens; *P. coloradensis*, four specimens; *T. porrecta*, six specimens) using a CTAB protocol (Bucklin 1992); each specimen was analyzed for mtDNA separately. LCO1490 and HCO2198 (Folmer et al. 1994) were used to amplify a 710 base pair (bp) fragment of the cytochrome *c* oxidase subunit I gene (COI). Amplification conditions and sequencing of amplified polymerase chain reaction product were those of Liu et al. (2003). Sequences were determined for both strands and then edited and aligned using SEQUENCHER™ version 5.0.1. Novel haplotypes were not detected in the newly sequenced specimens of *A. aff. infima* and thus we did not update our previously published phylogenetic analysis of the *A. infima* complex (Hershler and Liu 2008a). The newly sequenced specimens of Blue Point Spring *Tryonia* were analyzed together with previously published sequences from 30 congeners and closely related *Minckleyella balnearis* Hershler, Liu & Landye (a monotypic genus from northern Mexico), with *Mexipyrgus carranzae* Taylor used to root the phylogenetic tree (per Liu et al. 2001). Given that *Pyrgulopsis* is a large genus containing 139 species (Hershler et al. 2014), most of which have been previously sequenced, we restricted our analysis of the relationships of *P. coloradensis* to the newly sequenced specimens from Blue Point Spring, and sequences of 18 congeners from adjacent areas (including those that were found to be most similar to the newly obtained haplotypes using a BLAST search) to obtain a readable tree. The phylogenetic tree for this dataset was rooted with *Floridobia winkleyi* (Pilsbry) (per Hershler et al. 2003). One example of each haplotype detected in a given sample was used in the phylogenetic analyses. The new sequences from Blue Point Spring populations were deposited in GenBank (accession numbers KP899916–KP899919).

MRMODELTEST 2.3 (Nylander 2004) was used to obtain an appropriate substitution model (using the Akaike Information Criterion) and parameter values for the molecular phylogenetic analyses. MRMODELTEST selected GTR + I + G model parameters as the best fit model for both the *Tryonia* and *Pyrgulopsis* datasets. Phylogenetic analyses were performed using four different methodologies—distance, maximum parsimony (MP), maximum likelihood (ML) and Bayesian inference. The distance, MP, and ML analyses were performed using PAUP*4.ob10 (Swofford 2002), and the Bayesian analyses were conducted using MRBAYES 3.2.3 (Ronquist and Huelsenbeck 2003). For the distance analyses, GTR distance was used to generate a neighbor-joining (NJ) tree (Saitou and Nei 1987). The MP analyses were conducted with equal weighting, using the heuristic search option with tree bisection reconnection branch-swapping and 100 random additions. The ML analyses were performed using GTR + I + G model. A GTR distance based NJ tree was used as the initial topology for branch-swapping. Node support was evaluated by 10,000 bootstrap pseudo-replicates except for the ML analysis, in which support values were based on 100 replications. For the Bayesian analyses Metropolis-coupled Markov chain Monte Carlo simulations were run with four chains (using the model selected through MRMODELTEST) for 3,000,000 generations for *Tryonia*, and 2,000,000 generations for *Pyrgulopsis*. Markov chains were sampled at intervals of 10 generations to obtain 300,000 and 200,000 sample points, respectively. We used the default settings for the priors on topologies and the GTR + I + G model parameters selected by MRMODELTEST as the best fit model for both analyses. At the

end of the analyses, the average standard deviation of split frequencies was less than 0.01 (0.0036 and 0.0033, respectively) and the Potential Scale Reduction Factor (PSRF) was 1, indicating that the runs had reached convergence. The sampled trees with branch lengths were used to generate a 50% majority rule consensus tree, with the first 25% of the samples removed to ensure that the chain sampled a stationary portion.

Genetic distances within and between samples were calculated using MEGA6 (Tamura et al. 2013), with standard errors estimated by 1,000 bootstrap replications with pairwise deletion of missing data. Since MEGA does not contain the GTR model that was selected by MRMODELTEST, we used the maximum composite likelihood distance, which is the nearest model. Tajima relative rate tests of local clock-like behavior (Tajima 1993) were performed using MEGA6. The posterior Bayes factor was used to test a global clock assumption (MRBAYES 3.2.3).

Large, adult females were used for shell measurements. The total number of shell whorls (WH) was counted for each specimen; and the height and width of the entire shell (SH, SW), body whorl (HBW, WBW), and aperture (AH, AW) were measured from camera lucida outline drawings using a digitizing pad (see Hershler 1989). In addition, three ratios were generated from the raw data (SW/SH, HBW/SH, AH/SH). Descriptive statistics were generated using Systat for Windows 11.00.01 (SSI 2004). Sexual dimorphism in shells, which is commonly observed in *Tryonia* species (Taylor 1987), could not be quantified owing to the small sample size. Variation in the number of cusps on the radular teeth ($n = 5$) was assessed using the method of Hershler et al. (2007a). Descriptive terminology follows that of Taylor (1987) and Hershler (2001). The brief taxonomic description of the new species focuses on diagnostic features of external morphology. Types and other voucher material were deposited in the Smithsonian Institution's National Museum of Natural History (USNM) collection.

Results

The phylogenetic analyses congruently depicted a sister relationship between *P. coloradensis* and *P. sanchezi* Hershler, Liu & Bradford, which is distributed in the Death Valley area (Fig. 1). This relationship was strongly supported (1.0 posterior probability) only in the Bayesian analysis (the Bayesian tree is shown in Fig. 2). This clade in turn was depicted as sister to *P. deserta* (Pilsbry) (distributed along the Colorado River upflow from Blue Point Spring), albeit without support (0.70). The four sequenced specimens of *P. coloradensis* shared the same haplotype which differed from sequences of the other congeners included in the analysis by 4.5–11.4%.

The phylogenetic analyses of the *Tryonia* dataset congruently delineated a well-supported sister relationship between Blue Point Spring population and *T. clathrata*, which is also distributed in the lower Colorado River basin (Fig. 1). The Bayesian tree is shown in Fig. 3. (Note that the haplotype detected in near topotypes of *T. porrecta* was positioned in another portion of the tree.) The depicted sister relationship between this clade and *T. gilae* Taylor (which is also distributed in the lower Colorado River basin) was not

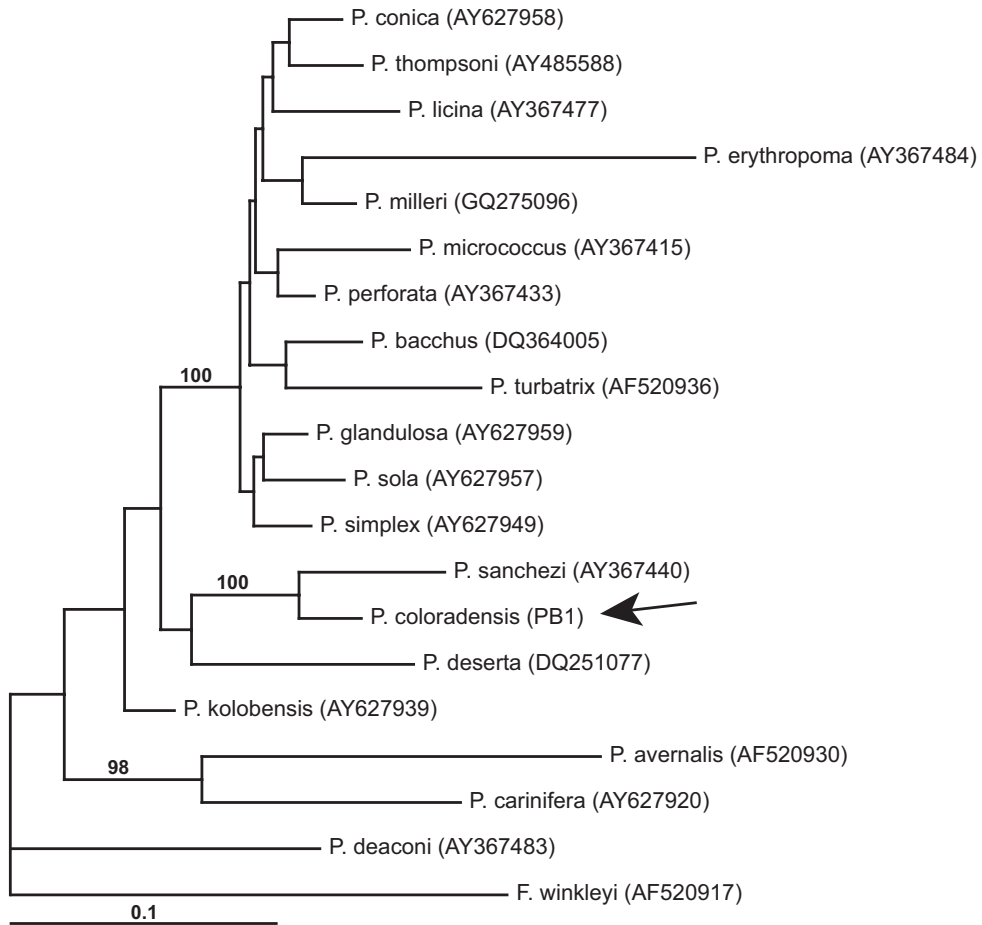


Figure 2. Bayesian tree based on COI data delineating the phylogenetic relationships of *P. coloradensis* (sequence identified by arrow). Posterior probabilities for nodes are indicated when >95%. GenBank accession numbers for haplotypes are given in parentheses.

well supported. Three haplotypes (BPB-D) differing by 3–7 bps were detected in the six sequenced specimens of the Blue Point Spring *Tryonia*. The average divergence between these haplotypes and those of the other congeners included in the analysis was 3.9–9.0%. The Blue Point Spring population of *Tryonia* is morphologically diagnosable (as detailed below) in addition to being phylogenetically independent and substantially divergent genetically. We describe this distinct evolutionary lineage as a new species below.

The eight sequenced specimens of *A. aff. infima* shared the same haplotype which differed from sequences of the other members of the *A. infima* complex by 2.6 ± 0.5%.

Tajima's relative rate test did not reject clocklike behavior for the datasets of interest. The posterior Bayes factor also strongly favored the molecular clock model, indicating that the application of a molecular clock is appropriate for these data.

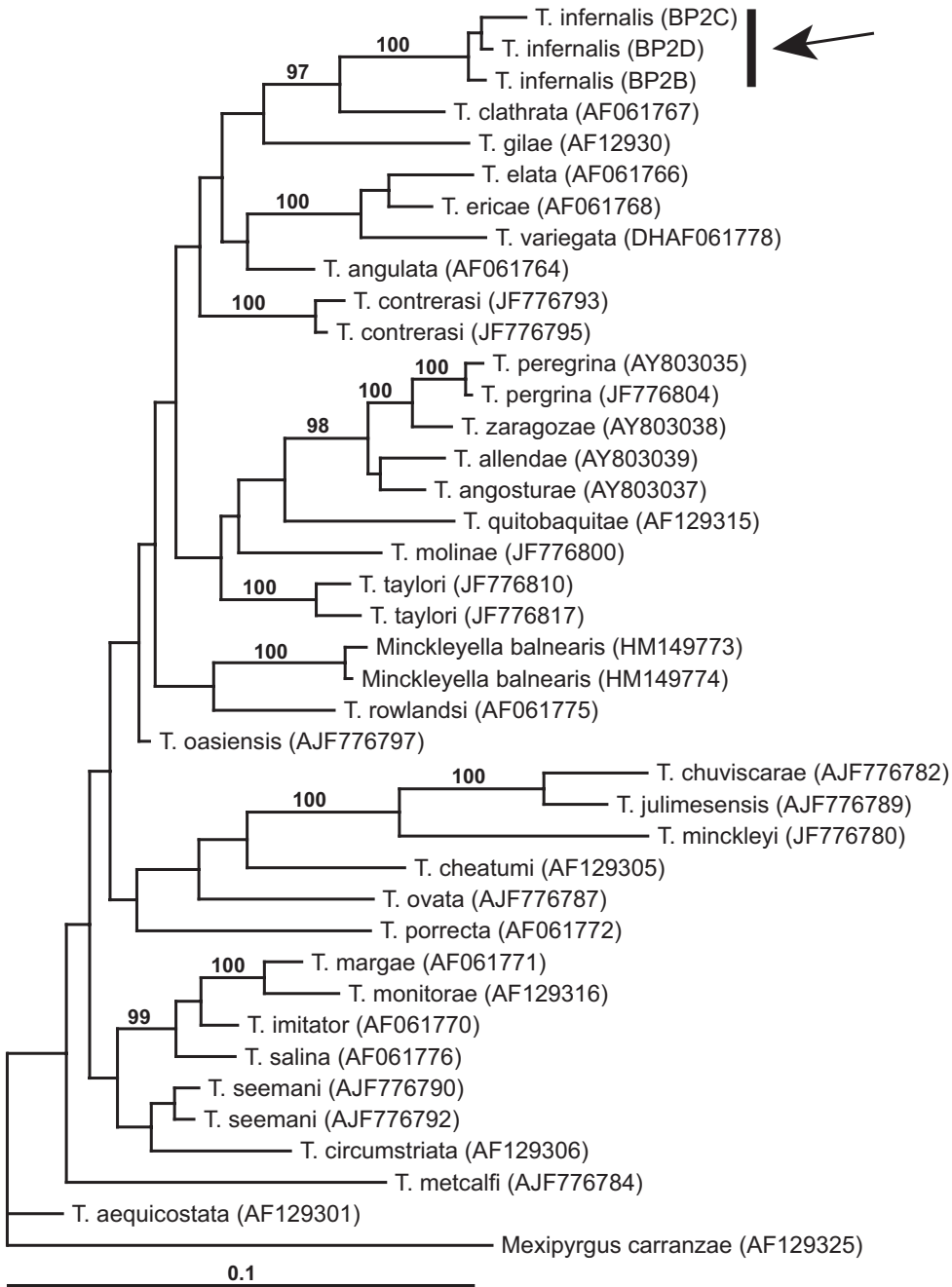


Figure 3. Bayesian tree based on COI data delineating the phylogenetic relationships of the Blue Point Spring *Tryonia* (lineage highlighted by arrow). Posterior probabilities for nodes are indicated when >95%. GenBank accession numbers for haplotypes are given in parentheses.

Systematic description

Family Cochliopidae Tryon, 1866

Genus *Tryonia* Stimpson, 1865

Tryonia infernalis Hershler, Liu, & Simpson, sp. n.

<http://zoobank.org/F7DD4C5E-E128-48AC-BAAE-866B6980C869>

Undescribed [*Fontelicella* and] *Tryonia* species.—Williams et al. 1985: 32.

Tryonia porrecta.—Hershler 1999: 335.

Types. USNM 883884 (a dry shell), Blue Point Spring, just below source, Clark County, Nevada, 36.3894°N, 114.4329°W, 24 July 1988, R. Hershler. Paratypes (ca. 200 dry shell and alcohol preserved specimens), USNM 1266143 (from same lot).

Referred material. NEVADA. *Clark County*: USNM 883248 (coll. James J. Landye, 17-XII-1992), USNM 1098627 (coll. Donald W. Sada, 6-XII-2006), USNM 1146345 (coll. Andrew K. Schwaneflugel, 29-V-2008), USNM 1146420 (coll. DWS, 11-XII-2009), USNM 1248362 (coll. RH, 5–15–2014), USNM 854844 (coll. Saxon Sharpe, no date), Blue Point Spring.

Diagnosis. Shell medium-sized, conic to turritiform; penis having two distal papillae on the inner edge and a single basal papilla both on the inner and outer edges. Readily distinguished from geographically proximal and closely related *T. clathrata* by its smaller size, weaker shell sculpture, and smaller number of papillae on the inner edge of the penis. Differentiated from *T. gilae* (also distributed in the lower Colorado River basin) by its more convex teleoconch whorls, lateral expansion of distal bulb of penis, and in having a basal papilla on the inner edge of the penis. Differs from *T. porrecta*, with which it was previously confused, by its smaller size, consistently weak shell sculpture, and much greater frequency of males.

Description. Shell (Fig. 4A–B) up to 2.8 mm tall, large females having 5.00–5.75 whorls, spire height 100–133% width of shell, male shells smaller than those of females. Teleoconch whorls highly convex, evenly rounded. Aperture ovate, weakly angled adapically. Parietal lip complete, adnate, umbilicus narrow. Outer lip orthocline or prosocline, sometimes weakly sinuate. Sculpture of strong growth lines and a few weak spiral threads. Periostracum light brown. Shell parameters for a series of paratypes are given in Table 1.

Inner and outer sides of operculum smooth (Fig. 4C–D). Radula (Fig. 4E–G): dorsal edge of central teeth concave, basal tongue V-shaped, median cusps elongate, distally pointed, lateral cusps four–six, basal cusps one–two, usually two (innermost larger; Fig. 4F). Lateral teeth having three–five cusps on inner and five–seven cusps on outer side, length of outer wing about 200% width of cutting edge, central cusp pointed (Fig. 4G). Inner marginal teeth with 24–34 cusps, outer marginal teeth with 27–38 cusps. Radula data are from USNM 1266143.

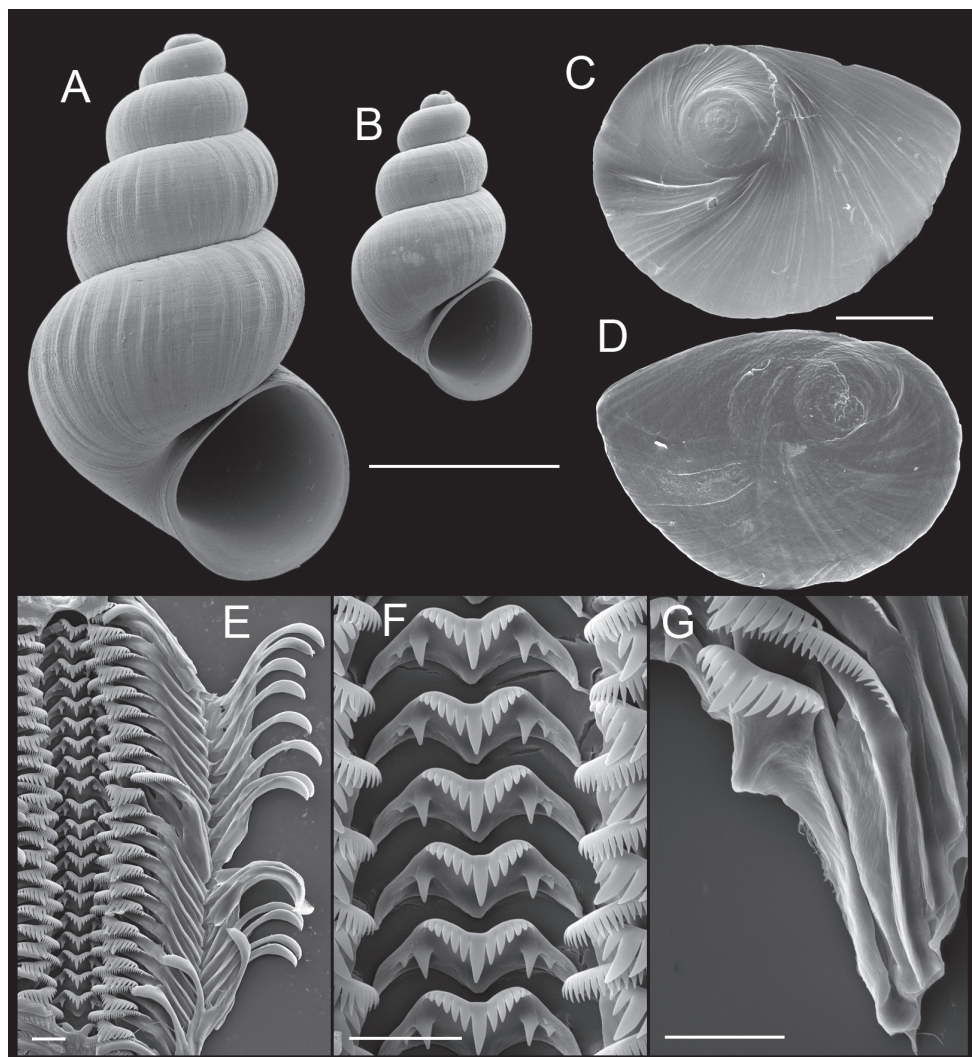


Figure 4. Shells, opercula and radula, *T. infernalis* sp. n. **A** Holotype, USNM 883884 **B** Male shell, USNM 1266143 **C, D** Opercula (outer, inner sides), USNM 1266143 **E** Portion of radular ribbon, USNM 1266143 **F** Central teeth, USNM 1266143 **G** Lateral and inner marginal teeth, USNM 1266143. Scale bars **A–B**: 1.0 mm; **C, D**: 200 µm; **E–G**: 10 µm.

Animal darkly pigmented. Penis (Fig. 5) having two distal and one basal papillae on inner edge and one basal papilla on outer edge (29 of 30 specimens); one specimen differed in having a single distal papilla along the inner edge. Distal bulb of penis expanded laterally on inner side, black; stylet small. Penial duct weakly undulating along most of length. Penial data are from USNM 1248362.

Etymology. The specific epithet (*infernalis*) is a Latin adjective meaning hellish, and refers to the Valley of Fire, which is closely proximal to the type locality.

Table 1. Shell parameters for *Tryonia infernalis*. Measurements are in mm.

| | WH | SH | SW | HBW | WBW | AH | AW | SW/SH | HBW/SH | AH/SH |
|---|-------|-------|-------|-------|-------|-------|-------|-------|--------|-------|
| Holotype, USNM 883884 | | | | | | | | | | |
| | 5.75 | 3.09 | 1.78 | 1.87 | 1.56 | 1.13 | 1.00 | 0.58 | 0.604 | 0.36 |
| Paratypes, USNM 1266143 (<i>n</i> = 9) | | | | | | | | | | |
| Mean | 5.33 | 2.61 | 1.41 | 1.60 | 1.25 | 0.95 | 0.80 | 0.54 | 0.61 | 0.37 |
| S.D. | 0.28 | 0.15 | 0.06 | 0.07 | 0.06 | 0.04 | 0.04 | 0.03 | 0.03 | 0.02 |
| Range | 5.00– | 2.41– | 1.33– | 1.46– | 1.13– | 0.91– | 0.75– | 0.49– | 0.58– | 0.34– |
| | 5.75 | 2.82 | 1.54 | 1.71 | 1.34 | 1.02 | 0.86 | 0.59 | 0.65 | 0.39 |

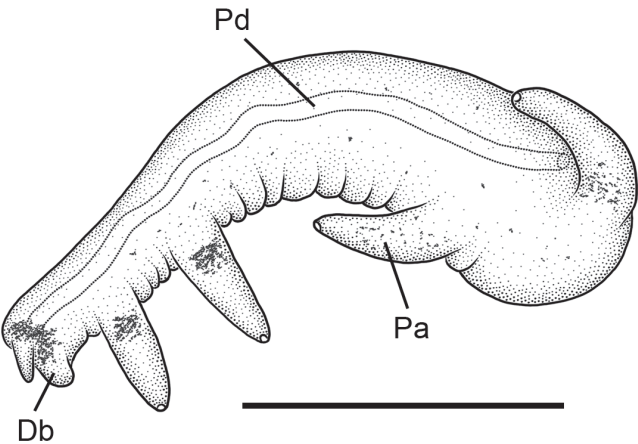


Figure 5. Penis (dorsal surface), *T. infernalis*, USNM 1248362. Scale bar: 500 μ m. **Db** distal bulb **Pa** distal papilla **Pd** penial duct.

Distribution and habitat. *Tryonia infernalis* is known only from its type locality, a thermal (ca. 30 °C) rheocene (discharging ca. 0.55 l/s; USGS 2007) whose outflow forms a narrow (ca. 0.3 m) stream (Fig. 6A). *Tryonia infernalis* is restricted to the upper 10 m of the spring run where it lives on silt and rocks. This species was considered to be extinct in 2002 following a series of unsuccessful searches, however it was subsequently “rediscovered” in a small, ponded reach above a weir plate associated with a USGS gaging station (Fig. 6B) in 2007 (Sada and Jacobs 2008; also see CCDCP 2002) and currently is abundant at this site (RH, personal observation).

Remarks. The reproductive anatomy of several females was studied to confirm that this species belongs to *Tryonia* as currently defined (Hershler 2001).

Discussion

Small assemblages of locally endemic spring-dwelling invertebrates are scattered throughout arid western North America (Williams et al. 1985, Shepard 1993, Myers and Resh

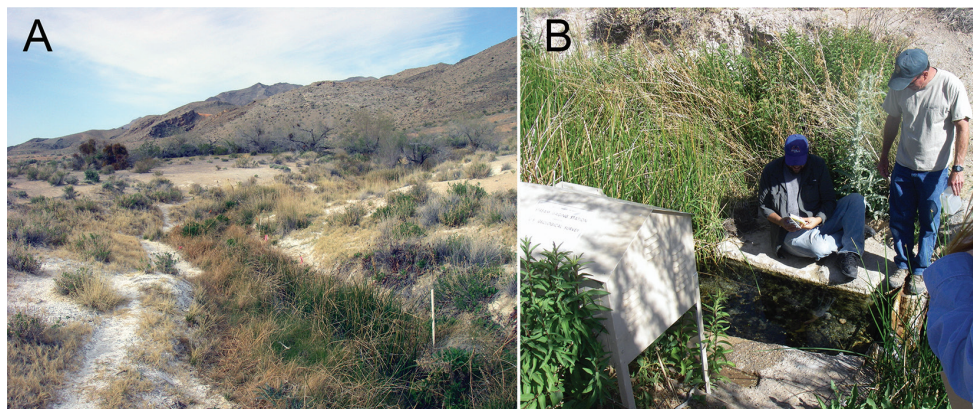


Figure 6. Photographs of Blue Point Spring. **A** Outflow channel; spring originates below one of the mesquite trees in the upper right (photograph taken on 24/III/2009) **B** Ponded area where *T. infernalis* occurs abundantly; the USGS gage house is in the lower left (15/V/2014).

1999). Although the biogeographic history of (some of) these taxa has been studied at spatial scales ranging from local watersheds (e.g., Hershler et al. 2007b) to major hydrographic basins (e.g., Witt et al. 2008) to the entire region (Liu and Hershler 2005), the origins of the endemic faunas of individual springs have been little investigated. The molecular phylogenetic evidence clearly points to a minimally dual origin of the Blue Point Spring fauna—*T. infernalis* is sister to a geographically close species from the lower Colorado River basin whereas *P. coloradensis* and the Blue Point Spring *Assimineea* are most closely related to taxa in the Death Valley region well to the west. (Note that Blue Point Spring harbors a divergent lineage of *Hyalella* amphipods that also is closely related to populations in the Death Valley region; Witt et al. 2006, provisional species HaPS11).

The use of a molecular clock to estimate divergence times is wrought with difficulties and is further complicated in this case by the absence of locally derived calibrations for *Assimineea* and *Tryonia*. Nevertheless, roughly calculated values provide useful insight into the biogeographic history of the Blue Point Spring fauna (note that we performed Bayes factor and Tajima's rate tests, both of which suggested that the assumption of a molecular clock is valid). Based on mtCOI clock calibrations of 1.83% per million years for European Hydrobiidae (Wilke 2003) and 1.62% per m.y. for *Pyrgulopsis* (Hershler and Liu 2008b), the estimated divergence times of the snail populations in Blue Point Spring ranged from 1.42–2.78 Ma (Table 2). Although the age of Blue Point Spring is not known with certainty, middle to lower Pleistocene (≤ 2.6 Ma) spring deposits (Beard et al. 2007, map unit Q2s) provide the earliest record of local groundwater discharge. Thus, the endemic lineages may be roughly with the same age as or slightly younger than Blue Point Spring. Lake Mead and the Death Valley region are separated by the intervening, north-south trending Spring Mountains (Fig. 1) and there is no record of a prior drainage connection between these areas during the Neogene; thus it would seem likely that *Assimineea* and *Pyrgulopsis* were transported to Blue Point Spring on waterbirds. The molecular data presented here suggests that

Table 2. COI sequence divergence and estimated ages of Blue Point Spring snail lineages based on two clock calibrations.

| Lineage | Per cent sequence divergence (sister taxon) | Estimated age (m.y.) | |
|------------------------|---|-------------------------------------|-------------------------------------|
| | | 1.83%/m.y. calibration ¹ | 1.62%/m.y. calibration ² |
| <i>A. aff. infima</i> | 2.6 (other members of <i>A. infima</i> complex) | 1.42 | 1.60 |
| <i>P. coloradensis</i> | 4.5 (<i>P. sanchezi</i>) | 2.46 | 2.78 |
| <i>T. infernalis</i> | 3.9 (<i>T. clathrata</i>) | 2.13 | 2.41 |

¹Wilke (2003)

²Hershler and Liu (2008b)

these two groups may have colonized Blue Point Spring at different times during the Pleistocene (Table 2). The sister taxon of *T. infernalis* (*T. clathrata*) is distributed in the White River Valley, which drains into Lake Mead (via the Muddy River) a few kilometers upflow from Blue Point Spring (Fig. 1). The split between these geographically close lineages could have been a product of vicariance (e.g., severance of a thermal stream connection per Hershler et al. 1999a) or dispersal of birds (per Wesselingh et al. 1999). Whereas only a single haplotype was detected for specimens of both *P. coloradensis* and the Blue Point Spring *Assimineae*, three well differentiated haplotypes (mean divergence, 0.6%) were observed in *T. infernalis*, suggesting a possibly longer history of *in-situ* diversification. Our findings imply a relatively complex assembly of the Blue Point Spring snail fauna. The mixture of a locally derived element that may have a relatively long history of diversification within the spring (*Tryonia infernalis*), and lineages that appear to have colonized this water body more recently (with no subsequent differentiation) follows a common pattern of community assembly (Emerson and Gillespie 2008).

The recognition of *T. infernalis* as a distinct, endemic species further highlights Blue Point Spring as a micro-hotspot of locally endemic aquatic biodiversity in Nevada. The Blue Point Spring *Assimineae* is probably a distinct species as well, but a formal taxonomic treatment is deferred pending completion of an ongoing revision of the *A. infima* complex (Hershler and Liu in preparation). Although this tiny aquatic ecosystem is on lands administered by the National Park Service (Lake Mead National Recreation Area), there may be a need for additional protection and conservation measures. The spring is located alongside a paved highway and public access is further facilitated by a small parking area near the lower end of the spring run. There is no fencing around the spring (or its run) and thus it is vulnerable to disturbance from foot traffic and other recreational activities. [We note in this context that Blue Point Spring harbors one of the few remaining populations of the relict leopard frog (*Rana onca* Cope), which requires open habitat maintained by ungulate grazing and thus may be negatively impacted by fencing (Bradford et al. 2004).] The spring run appears to have been “channelized” at one time in the past, which likely resulted in a reduction of the riparian habitat utilized by *Assimineae* (Landye 1973). The snail fauna may be further jeopardized by a suite of exotic fishes that were introduced through the use of the spring as an aquarium-fish rearing establishment (until the mid-1950’s) or by aquarium release

(Deacon et al. 1964); the convict cichlid (*Amatitlania nigrofasciata* [Günther]), which was discovered in the spring in the 1990's, may pose an especially serious threat owing to its omnivorous feeding habitats (Sada and Jacobs 2008). The red-rimmed melania (*Melanooides tuberculata* [Müller]), an invasive gastropod whose abundance appears to be negatively correlated with that of native snails in western springs based on anecdotal evidence, has also been introduced to the spring (Landye 1973).

Acknowledgements

This project was supported in part by funding from the National Park Service Mojave Desert Network Inventory and Monitoring Program (award # P13PG00412) that was facilitated by Geoffrey Moret. Sampling of Blue Point Spring snails in 2014 was made under the auspices of a scientific collecting permit from the National Park Service (Permit# LAKE-2014-SCI-0005). Kyle Simpson assisted with the fieldwork. The first author thanks Sue Beard for a useful discussion of the possible age of Blue Point Spring. Yolanda Villacampa measured shells and prepared scanning electron micrographs, and Freya Goetz prepared a digital version of the anatomical drawing. Ross Haley, Geoffrey Moret and Mark Sappington provided helpful comments on an early draft of this manuscript, which was also improved by input from two anonymous reviewers.

References

- Abele SL (Ed.) (2011) Nevada Springs Conservation Plan. Spring Conservation Working Group. The Nature Conservancy, Reno, Nevada. http://heritage.nv.gov/sites/default/files/library/springcons_1.pdf [accessed 8 December 2014]
- Beard LS, Anderson RE, Block DL et al. (2007) Preliminary geologic map of the Lake Mead 30' × 60' Quadrangle, Clark County, Nevada, and Mohave County, Arizona. United States Geological Survey Open-File Report 2007-1010. Plates 1–3, pamphlet. <http://pubs.usgs.gov/of/2007/1010/> [accessed 17 December 2014]
- Bradford DF, Jaeger JR, Jennings RD (2004) Population status and distribution of a decimated amphibian, the relict leopard frog (*Rana onca*). *Southwestern Naturalist* 49: 218–228. doi: 10.1894/0038-4909(2004)049<0218:PSADOA>2.0.CO;2
- Bucklin A (1992) Use of formalin-preserved samples for molecular analysis. *Newsletter of Crustacean Molecular Techniques* 2: 3.
- CCDCP (Clark County Desert Conservation Program) (2002) Biennium report for the 1999–2001 Biennium. <http://www.clarkcountynv.gov/Depts/dcp/Documents/Library/dcp%20reports/2002/99-01BiennRptwpicturesMDH.pdf> [accessed 18 December 2014]
- Deacon JE, Hubbs C, Zahuranec BJ (1964) Some effects of introduced fishes on the native fish fauna of southern Nevada. *Copeia* 1964: 384–388. doi: 10.2307/1441031

- Emerson BC, Gillespie RG (2008) Phylogenetic analysis of community assembly and structure over space and time. *Trends in Ecology and Evolution* 23: 619–630. doi: 10.1016/j.tree.2008.07.005
- Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3: 294–299.
- Greenwald N, Bradley C (2008) Assessing protection for imperiled species of Nevada, U.S.A.: are species slipping through the cracks of existing protections? *Biodiversity and Conservation* 17: 2951–2960. doi: 10.1007/s10531-008-9407-3
- Hershler R (1989) Springsnails (Gastropoda: Hydrobiidae) of Owens and Amargosa River (exclusive of Ash Meadows) drainages, Death Valley system, California-Nevada. *Proceedings of the Biological Society of Washington* 102: 176–248.
- Hershler R (1999) A systematic review of the hydrobiid snails (Gastropoda: Rissooidea) of the Great Basin, western United States. Part II. Genera *Colligyrus*, *Eremopyrgus*, *Fluminicola*, *Pristinicola*, and *Tryonia*. *Veliger* 42: 306–337.
- Hershler R (2001) Systematics of the North and Central American aquatic snail genus *Tryonia* (Rissooidea: Hydrobiidae). *Smithsonian Contributions to Zoology* 612: 1–53. doi: 10.5479/si.00810282.612
- Hershler R, Liu H-P (2008a) Phylogenetic relationships of assimineid gastropods of the Death Valley region: relicts of a late Neogene marine incursion? *Journal of Biogeography* 35: 1816–1825. doi: 10.1111/j.1365-2699.2008.01947.x
- Hershler R, Liu H-P (2008b) Ancient vicariance and recent dispersal of springsnails (Hydrobiidae: *Pyrgulopsis*) in the Death Valley system, California-Nevada. In: Reheis MC, Hershler R, Miller DM (Eds) *Late Cenozoic drainage history of the southwestern Great Basin and lower Colorado River region*. Geological Society of America Special Paper 439: 91–101. doi: 10.1130/2008.2439(04)
- Hershler R, Liu H-P, Bradford C (2013) Systematics of a widely distributed North American springsnail, *Pyrgulopsis micrococcus* (Caenogastropoda, Hydrobiidae), with descriptions of three new congeners. *ZooKeys* 330: 27–52. doi: 10.3897/zookeys.330.5852
- Hershler R, Liu H-P, Landye JJ (2011) New species and records of springsnails (Caenogastropoda: Cochliopidae: *Tryonia*) from the Chihuahuan Desert (Mexico and United States), an imperiled biodiversity hotspot. *Zootaxa* 3001: 1–32.
- Hershler R, Liu H-P, Mulvey M (1999a) Phylogenetic implications within the aquatic snail genus *Tryonia*: implications for biogeography of the North American Southwest. *Molecular Phylogenetics and Evolution* 13: 377–391. doi: 10.1006/mpev.1999.0659
- Hershler R, Liu H-P, Sada DW (2007b) Origin and diversification of the Soldier Meadow springsnails (Hydrobiidae: *Pyrgulopsis*), a species flock in the northwestern Great Basin, United States. *Journal of Molluscan Studies* 73: 167–183. doi: 10.1093/mollus/eym014
- Hershler R, Liu H-P, Thompson FG (2003) Phylogenetic relationships of North American nymphophiline gastropods based on mitochondrial DNA sequences. *Zoologica Scripta* 32: 357–366. doi: 10.1046/j.1463-6409.2003.00115.x

- Hershler R, Liu H-P, Frest TJ, Johannes EJ (2007a) Extensive diversification of pebblesnails (Lithoglyphidae: *Fluminicola*) in the upper Sacramento River basin, northwestern United States. *Zoological Journal of the Linnean Society* 149: 371–422.
- Hershler R, Mulvey M, Liu H-P (1999b) Biogeography in the Death Valley region: evidence from springsnails (Hydrobiidae: Tryonia). *Zoological Journal of the Linnean Society* 126: 335–354. doi: 10.1111/j.1096-3642.1999.tb01375.x
- Hershler R, Mulvey M, Liu H-P (2005) Genetic variation in the desert springsnail (*Tryonia porrecta*): implications for reproductive mode and dispersal. *Molecular Ecology* 14: 1755–1765. doi: 10.1111/j.1365-294X.2005.02522.x
- Hershler R, Ratcliffe V, Liu H-P, Hay C (2014) Taxonomic revision of the *Pyrgulopsis gilae* (Caenogastropoda, Hydrobiidae) species complex, with descriptions of two new species from the Gila River basin, New Mexico. *ZooKeys* 429: 69–85. doi: 10.3897/zookeys.429.7865
- Landye JJ (1973) Status of the inland aquatic and semi-aquatic mollusks of the American Southwest. [Unpublished] Report to the United States Department of the Interior, Bureau of Sport Fisheries and Wildlife, Office of Rare and Endangered Species, Washington, D.C.
- Liu H-P, Hershler R (2005) Molecular systematics and radiation of western North American nymphophiline gastropods. *Molecular Phylogenetics and Evolution* 34: 284–298. doi: 10.1016/j.ympev.2004.09.013
- Liu H-P, Hershler R (2007) A test of the vicariance hypothesis of western North American freshwater biogeography. *Journal of Biogeography* 34: 534–548. doi: 10.1111/j.1365-2699.2006.01611.x
- Liu H-P, Hershler R, Clift K (2003) Mitochondrial DNA sequences reveal extensive cryptic diversity within a western American springsnail. *Molecular Ecology* 12: 2771–2782. doi: 10.1046/j.1365-294X.2003.01949.x
- Liu H-P, Hershler R, Thompson FG (2001) Phylogenetic relationships of the Cochliopinae (Rissooidea: Hydrobiidae): an enigmatic group of aquatic gastropods. *Molecular Phylogenetics and Evolution* 21: 17–25. doi: 10.1006/mpev.2001.0988
- Myers MJ, Resh VH (1999) Spring-formed wetlands of the arid West; islands of aquatic invertebrate biodiversity. In: Batzer DP, Rader RB, Wissinger SA (Eds) *Invertebrates in freshwater wetlands of North America: ecology and management*. John Wiley and Sons, New York, 811–828.
- Nylander JAA (2004) MrModeltest v2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University.
- Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574. doi: 10.1093/bioinformatics/btg180
- Sada DW, Jacobs CA (2008) Environmental and biological characteristics of springs in Lake Mead National Recreation Area, Nevada and Arizona. Desert Research Institute, Las Vegas, NV. [Unpublished] Report to Lake Mead National Recreation Area, United States Park Service, Boulder City, Nevada and Great Basin Cooperative Ecosystem Studies Unit. Task Agreement No. J8R07060021. <http://irmafiles.nps.gov/reference/holding/146687?accessType=DOWNLOAD> [accessed 16 December 2014]

- Saitou N, Nei M (1987) The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Molecular Biology and Evolution* 4: 406–425.
- Shepard WD (1993) Desert springs—both rare and endangered. *Aquatic Conservation: Marine and Freshwater Ecosystems* 3: 351–359. doi: 10.1002/aqc.3270030409
- SSI (Systat Software, Inc.) (2004) Systat® for Windows®. Richmond, CA.
- Swofford DL (2002) PAUP*: phylogenetic analysis using parsimony (and other methods), version 4.08b10. Sinauer Associates, Sunderland, MA.
- Tajima F (1993) Simple methods for testing the molecular evolutionary clock hypothesis. *Genetics* 135: 599–607.
- Tamura K, Stecher G, Peterson D, Filipski A, Kumar S (2013) MEGA6: molecular evolutionary genetics analysis version 6.0. *Molecular Biology and Evolution* 30: 2725–2729. doi: 10.1093/molbev/mst197
- Taylor DW (1987) Fresh-water molluscs from New Mexico and vicinity. *New Mexico Bureau of Mines and Mineral Resources Bulletin* 116: 1–50.
- USGS (United States Geological Survey) (2007) Water-data Report 2007. 09419547 Blue Point Spring near Valley of Fire State Park, NV. <http://wdr.water.usgs.gov/wy2007/pdfs/09419547.2007.pdf> [accessed 16 December 2014]
- Wesselingh FP, Cadée GC, Renema W (1999) Flying high: on the airborne dispersal of aquatic organisms as illustrated by the distribution histories of the gastropod genera *Tryonia* and *Planorbarius*. *Geologie en Mijnbouw* 78: 165–174. doi: 10.1023/A:1003766516646
- Wilke T (2003) *Salenthydrobia* gen. nov. (Rissooidea: Hydrobiidae): a potential relict of the Messinian salinity crisis. *Zoological Journal of the Linnean Society* 137: 319–336. doi: 10.1046/j.1096-3642.2003.00049.x
- Williams JE, Bowman DB, Brooks JE et al. (1985) Endangered aquatic ecosystems in North American deserts with a list of vanishing fishes of the region. *Journal of the Arizona-Nevada Academy of Science* 20: 1–62.
- Witt JDS, Threlloff DL, Hebert PDN (2006) DNA barcoding reveals extraordinary cryptic diversity in an amphipod genus: implications for desert spring conservation. *Molecular Ecology* 15: 3073–3082. doi: 10.1111/j.1365-294X.2006.02999.x
- Witt JDS, Threlloff DL, Hebert PDN (2008) Genetic zoogeography of the *Hyaella azteca* species complex in the Great Basin: rapid rates of molecular diversification in desert springs. In: Reheis MC, Hershler R, Miller DM (Eds) Late Cenozoic drainage history of the southwestern Great Basin and lower Colorado River region. *Geological Society of America Special Paper* 439: 103–114. doi: 10.1130/2008.2439(05)

Revision of the genus *Epimesoplecia* Zhang, 2007 (Diptera, Nematocera, Protopleciidae) with five new species

Xiuqin Lin¹, Chungkun Shih¹, Dong Ren¹

¹ Key Lab of Insect Evolution and Environmental Change, College of Life Sciences, Capital Normal University, 105 Xisanhuanbeilu, Haidian District, Beijing 100048, China

Corresponding author: Dong Ren (rendong@mail.cnu.edu.cn)

Academic editor: V. Blagoderov | Received 18 December 2014 | Accepted 13 March 2015 | Published 30 March 2015

<http://zoobank.org/3DE583E5-6795-4A77-B70F-7B085B0A91F0>

Citation: Lin X, Shih C, Ren D (2015) Revision of the genus *Epimesoplecia* Zhang, 2007 (Diptera, Nematocera, Protopleciidae) with five new species. ZooKeys 492: 123–143. doi: 10.3897/zookeys.492.6852

Abstract

The genus *Epimesoplecia* Zhang, 2007 of Protopleciidae is revised based on five new species, *E. plethora* sp. n., *E. prosoneura* sp. n., *E. stana* sp. n., *E. macrostrena* sp. n., and *E. ambloneura* sp. n., described and illustrated from the Jiulongshan Formation of China. These new species, with clearly preserved characters of (1) compound eyes connected in males; (2) antennae, filiform or moniliform, with 16 segments; (3) r-m reaching the middle of the wing; (4) R_{4+5} ending very close to wing apex; (5) ratio of bRs/dRs ranging from 1.6 to 10.5; (6) M_2 more than 3 times as long as dM_{1+2} ; (7) legs thin and long, femur slender, almost equal to tibia; (8) tibial spurs minute; and (9) male genitalia (previously unknown), enable us to emend the diagnosis of *Epimesoplecia* Zhang, 2007. In addition, all described species of *Epimesoplecia* are characterized, their features summarized, and a key to *Epimesoplecia* species is given.

Keywords

Insects, fossil, taxonomy, Jiulongshan Formation, late Middle Jurassic

Introduction

Protopleciidae Rohdendorf, 1946, reported from the Jurassic, is a paraphyletic stem group to the Bibionidae (Blagoderov et al. 2002; Grimaldi and Engel 2005). Rohdendorf (1946) erected the Protopleciidae with three genera *Protoplecia* Handlirsch, 1906, *Mesoplecia* Rohdendorf, 1938 and *Mesopleciella* Rohdendorf, 1946 (Evenhuis 1994). Kovalev (1987) transferred 14 species in *Rhaetofungivora* Rohdendorf, 1964 of Pleciofungivoridae to Protopleciidae, but later, some of those were assigned to several different genera (Blagoderov 1996). The earliest record of the Protopleciidae is *Macropeza liasina* Geinitz, 1884 from the Early Jurassic in upper Liassic of Germany. Ansorge (1996) provided an updated description for *Protoplecia liasina* (Geinitz, 1884) and reported *Protoplecia klafackii* from the upper Liassic of Germany. Ansorge (1996) considered the affiliation of *Mesoplecia* and *Mesopleciella* with the Protopleciidae questionable based on the clearly shorter Sc, and suggested that *Archipleciomima* Rohdendorf, 1962 is the stem group of Pleciofungivoridae and Pleciomimidae due to long Rs stem. On the other hand, Lin (1976), Hong (1984), and Hong and Wang (1990) documented several genera and species in China, but many of them have been subsequently removed from this family (Blagoderov 1996). Recently, from the Jiulongshan Formation of China, Zhang (2007) described *Epimesoplecia* with two species, emended the diagnosis of *Mesoplecia* Rohdendorf, 1938, added two species to the genus, and excluded *Paraoligus exilis* Lin, 1976 and *Mesoplecia xinboensis* Hong, 1984 from this family, but stated that an alternative placement could not be suggested. Hao and Ren (2009) described three species of *Mesoplecia*. Lin et al. (2014) described two species as members of *Mesoplecia*, while transferring *M. antiqua* Hao & Ren, 2009 to Mesosciophilidae, because R_{2+3} of *M. antiqua* Hao & Ren, 2009 reaching R_1 forming a cell r, instead of reaching the anterior margin as all other protopleciids. After documented corrections and transfers, there are 33 species in seven genera described in Protopleciidae to date (Lin et al. 2014).

Herein, based on fourteen specimens collected from the Jiulongshan Formation in Daohugou Village, Ningcheng County, Inner Mongolia, China, five new species are described in *Epimesoplecia*, *E. plethora* sp. n., *E. prosoneura* sp. n., *E. stana* sp. n., *E. macrostrena* sp. n., and *E. ambloneura* sp. n. with ten specimens. One of the remaining four specimens is identified as a new material for *E. elenae* Zhang, 2007, while the other three cannot be assigned to species owing to lack of preserved diagnostic characters. These five new species are assigned to *Epimesoplecia* by a combination of the following characters: (1) antenna long, at least twice the head length; (2) wing narrow and long; (3) Sc elongate, nearly half of wing length; (4) R_{2+3} long, more than two-thirds of R_{4+5} length.

The Jiulongshan Formation of Inner Mongolia in China is very rich in fossil insects' record (Shi et al. 2011; Ren et al. 2010; Liu et al. 2012; Wang et al. 2013 and Li et al. 2013). Because of new calibrations for the Jurassic System, this deposit should be now considered as latest Middle Jurassic (late Callovian) in age (Walker

et al. 2013). The paleoenvironment reconstructed for that time was a volcanic region with mountains, streams and lakes under a humid and warm climate (Ren et al. 2002; Gao and Ren 2006).

Material and methods

All the type materials were collected from the Jiulongshan Formation (Fig. 1A) of Daohugou Village in Ningcheng County of Inner Mongolia, China (Fig. 1B) (after Ren et al. 2002). The specimens are housed in the Key Laboratory of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China (CNU; Dong Ren, Curator). The specimens were examined and photographed using a Leica MZ12.5 dissecting microscope with a Leica DFC 500 digital camera and illustrated with the aid of camera lucida attached to the microscope. The line drawings were drawn by Adobe Photoshop CS5. The wing venation nomenclature used in this paper is based on the interpretations and system proposed by Shcherbakov et al. (1995) and Wootton and Ennos (1989).

Systematic Paleontology

Order Diptera Linnaeus, 1758

Suborder Nematocera Latreille, 1825

Family Protopleciidae Rohdendorf, 1946

Genus *Epimesoplecia* Zhang, 2007

Type species. *Epimesoplecia shcherbakovi* Zhang, 2007

Species included. Type species, *E. elenae* Zhang, 2007, *E. plethora* sp. n., *E. prosononeura* sp. n., *E. stana* sp. n., *E. macrostrena* sp. n. and *E. ambloneura* sp. n.

Revised diagnosis. Compound eyes connected in males. Antennae filiform or moniliform, with 16 segments, at least twice of head length or slightly less than twice of head length; wings narrow and long; Sc elongate, at or near the same level of r-m; bRs at least 4 times as long as r-m; R_{2+3} long, more than two-thirds of R_{4+5} , R_{2+3} slightly sigmoidly curved or straight, reaching anterior margin distad of the apex of R_1 ; r-m reaching the middle of the wing; R_{4+5} ending very close to wing apex; M_{1+2} furcated distinctly proximad or distad of R_{2+3} ; M_2 more than 3 times as long as dM_{1+2} ; bM_{3+4} longer or slightly shorter than m-cu; pterostigma absent; bM_{1+2} longer or shorter than dM_{1+2} . Legs thin and long, femur slender, almost equal to tibia; tibial spurs minute. Male genitalia: abdomen cylindrical; genitalia complex, narrower than the 8th segment, with gonocoxites rounded; gonostylus elongated, shorter than gonocoxites. Female genitalia: the 8th segment smaller than preceding segments, genitalia simple, with 2-segmented cerci, the basal segment of cerci longer than the terminal one.

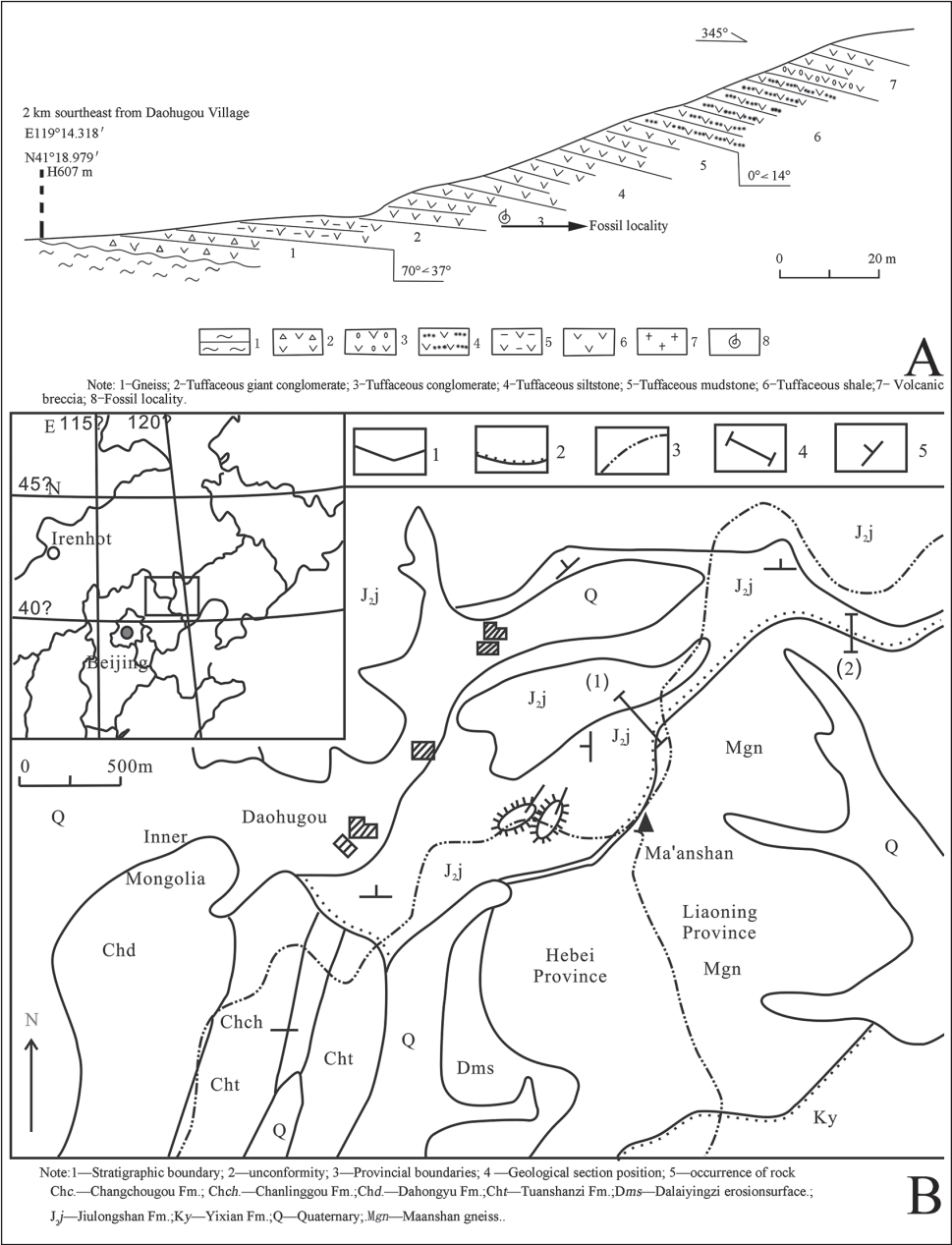


Figure 1. A Measured stratigraphic section at the Jiulongshan Formation of northeastern China **B** Map showing the fossil locality (after Ren et al. 2002).

***Epimesoplecia plethora* sp. n.**

<http://zoobank.org/86178CAD-809C-4637-B64A-33B6BFBA6030>

Figs 2–3

Etymology. The epithet of *plethora* is derived from the Greek word “plethore”, meaning “fullness”, emphasizing the body covered with dense pubescence. The specific epithet is a noun in apposition.

Diagnosis. Compound eyes crescent. Antennae moniliform. Sc very close to the level of r-m; fork of Rs distad of fork of M_{1+2} ; Rs distad of crossvein r-m; bRs less than 2 times (1.6–1.8) as long as dRs, the latter about 3 times (2.6–3) as long as r-m; R_{2+3} , sigmoidly curved, distinctly shorter than bRs and dRs combined; bM_{1+2} shorter than dM_{1+2} ; bM_{3+4} shorter than m-cu; cell bp as wide as cell ba terminally.

Material. Holotype: Female. NO. CNU-DIP-NN2013202, a well-preserved almost complete body with left haltere, both wings and part of legs (Fig. 2A). Paratype: NO. CNU-DIP-NN2013209p/c, part and counterpart, lateral view, only right wing and legs preserved, head and abdomen incomplete (Fig. 3A, B).

Horizon and locality. All specimens were collected from the Jiulongshan Formation, late Middle Jurassic age (Late Callovian) from Daohugou Village, Ningcheng County, Inner Mongolia Autonomous Region in China.

Description. Head (Fig. 2D, F): Ovipiform. Compound eyes crescent in females. Antennae: scape and pedicel thick and stout, 1st flagellomere slender, the remaining ones becoming thinner toward apex.

Thorax (Figs 2A, 3A, B): Scutum convex; scutellum clearly projecting; haltere depressed.

Legs (Figs 2A, 3A, B): Forelegs comparatively thin and slender, femur slightly thicker than tibia, covered with dense setae as preserved. The 1st tarsomere 2 times as long as the 2nd tarsomere; the 3rd to 5th tarsi gradually thinned, claws small. Mid legs: femur long and slender, almost equal to tibia, tibial spurs minute, claws well-preserved. Hind legs: femur more than four-fifths of tibia; distinctly longer than forelegs and mid legs, tibia less than 2 times as long as femur; the 1st tarsomere more than 2 times as long as the 2nd tarsomere; with two pretarsal claws.

Wings (Figs 2A, C and 3A): Wing long and narrow, 2.6–2.8 times as long as width (length 8.4–9.0 mm, width 3.0–3.4 mm); Sc terminating at the middle of the anterior margin, the costal field narrow; bRs 4–5 times as long as r-m; R_{2+3} slightly sigmoidly curved; Rs arising from one-fourth of wing length, furcating distal level of fork of M_{1+2} ; stem of Rs longer than stem R, the former longer than R_{2+3} ; R_{4+5} weakly curved upward medially, ending just below apex of wing; both R_{4+5} and M_1 subparallel; crossvein m-cu as long as r-m; CuA strongly curved, distad of M forking, ending at posterior margin of wing; A_1 not preserved.

Female genitalia (Fig. 2E, G): The 8th segment slightly smaller than preceding segments, genitalia simple, with 2-segmented cerci, the basal segment of cerci thicker and longer than the terminal one.

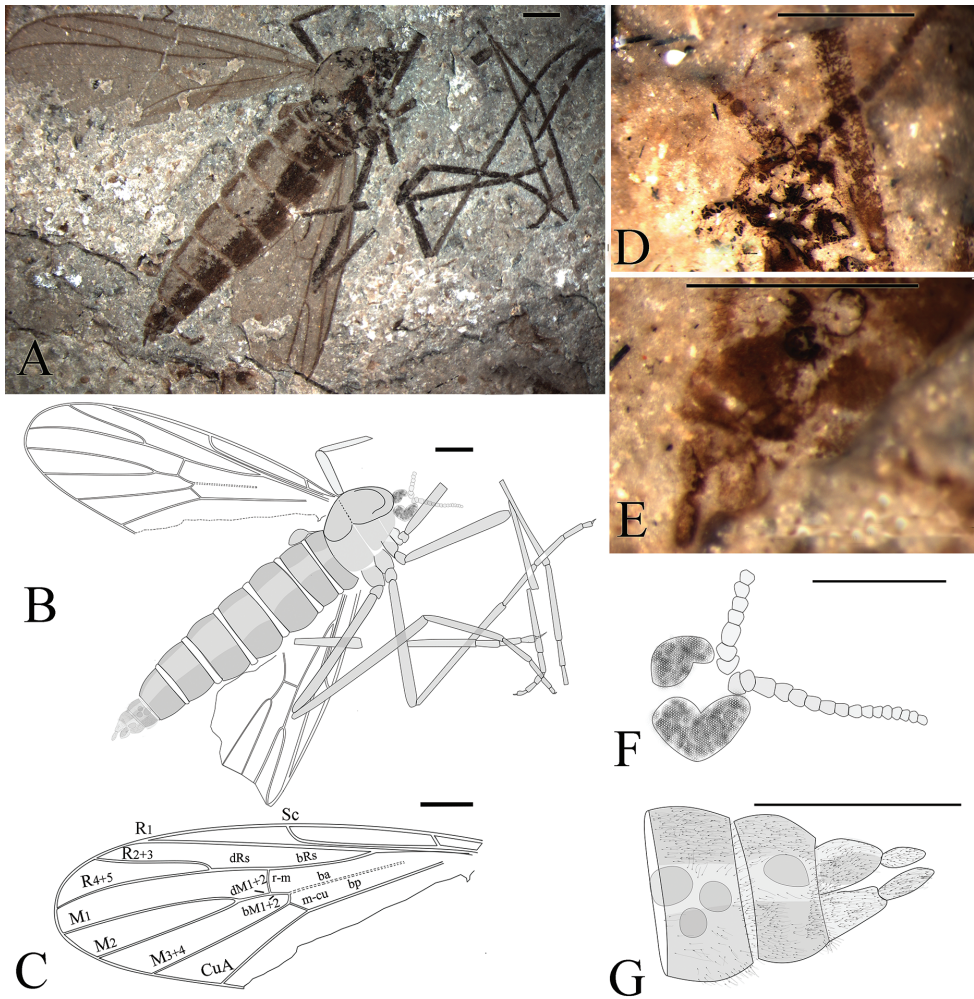


Figure 2. *Epimesoplecia plethora* sp. n. (CNU-DIP-NN2013202). Holotype. **A** Photograph of habitus; Line drawings of **B** Habitus **C** Left wing; Photographs of **D** Details of head (under alcohol) **E** Details of female genitalia (under alcohol); Line drawings of **F** Head **G** Female genitalia. Scale bars = 1 mm.

Dimensions (in mm). [Measurements for the paratype CNU-DIP-NN2013209p/c in brackets, if different]. Holotype: female. CNU-DIP-NN2013202, Body length 1.0 [5 as preserved], maximal width of body 2.2 [2.4]. Head length 0.6, width 0.8. Fore-legs: femur 1.7 as preserved [2.2]; tibia 1.4 as preserved [3.4]. Mid legs: femur 3 [2.8], tibia 3.5 [3]. Hind legs: femur 3.6 [4], tibia 4.4 [5]. Wing: length 9.0 [8.2], width 3.4 [3.0], R_{2+3} 2.4, bRs 2.2 [2.1], dRs 1.2, R_{4+5} 3 [3.4].

Remarks. The new species is differentiated from *E. shcherbakovi* Zhang, 2007 by the following features: bRs less than 2 times (1.6–1.7) as long as dRs (vs. bRs 4.5 times as long as dRs); Rs bifurcation distad to fork of M_{1+2} (vs. Rs bifurcation at the same level of fork of M_{1+2}); dm_{1+2} longer than bm_{1+2} (vs. dm_{1+2} shorter than bm_{1+2}). The

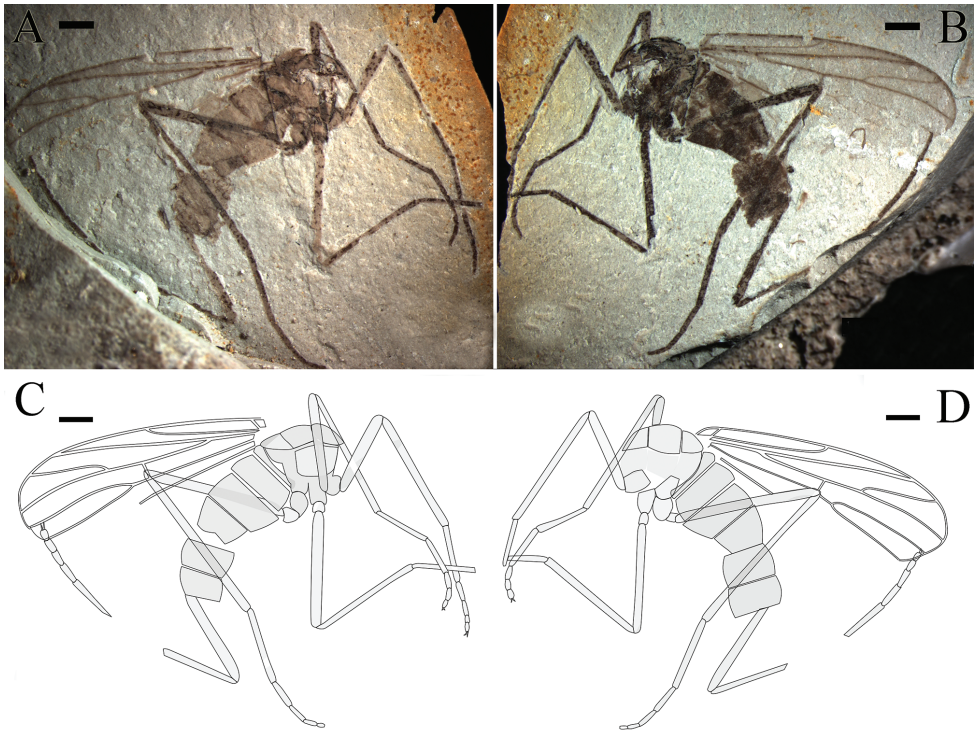


Figure 3. *Epimesoplecia plethora* sp. n. (CNU-DIP-NN2013209p/c). Paratype. **A, B** Photographs of part and counterpart **C, D** Line drawings of part and counterpart. Scale bars = 1 mm.

new species differs from *E. elenae* Zhang, 2007 in having antennae moniliform (vs. fili-form); bRs short, less than 2 times (1.6–1.7) as long as dRs (vs. bRs long, 2.5 times as long as dRs); bM_{3+4} clearly shorter than m-cu (vs. bM_{3+4} as long as m-cu). Comparisons with other species are listed in Table 1.

***Epimesoplecia prosoneura* sp. n.**

<http://zoobank.org/260A2E9B-8331-483A-9BBB-E67D58EB0B32>

Figs 4–5

Etymology. The epithet of *prosoneura* is derived from the Greek preposition “pro”, meaning “before”, and Greek word “neura”, meaning “string or sinew”, referring to proximal position of the fork of Rs. The specific epithet is a noun in apposition.

Diagnosis. Compound eyes crescent. Antennae moniliform. Sc exceeding the level of r-m or very close to r-m; fork of Rs proximad of fork of M_{1+2} ; R_{2+3} very close to crossvein r-m; R_{2+3} , almost straight, distinctly longer than bRs and dRs combined; bRs about 10 times (9.4–10.5) as long as dRs, the latter as long as r-m; bM_{1+2} shorter than dM_{1+2} ; bM_{3+4} shorter than m-cu; cell bp wider than cell ba terminally.

Table 1. Summary of data for all species of *Epimesoplecia* Zhang, 2007.

| Species | Specimen numbers | H/P | Sex | BL | WL | L/W | bRs/dRs | dRs/r-m | bM ₁₊₂ /dM ₁₊₂ | M ₇ /dM ₁₊₂ | bM ₃₊₄ /m-cu | bRs/r-m | Rs vs. M ₁₊₂ |
|------------------------------|-----------------------|-----|-----|--------|----------|-----|---------|---------|--------------------------------------|-----------------------------------|-------------------------|---------|-------------------------|
| <i>E. plethora</i> sp. n. | CNU-DIP-NN2013202 | H | ♀ | 10.6 | 9 | 2.6 | 1.6 | 2.6 | 0.6 | 4.2 | shorter | 4 | DS |
| | CNU-DIP-NN2013209 p/c | P | NA | 5 (ic) | 8.4 | 2.8 | 1.75 | 3 | 0.8 | 6 | NA | 5 | DS |
| <i>E. prosoneura</i> sp. n. | CNU-DIP-NN2013207 p/c | H | ♂ | 8.3 | 8 | 3.1 | 10.5 | 0.3 | 0.4 | 4.2 | shorter | 4.8 | PX |
| | CNU-DIP-NN2013214 | A | ♀ | 8.2 | 8.9 | 3.3 | 9.4 | 0.6 | 0.8 | 5.2 | shorter | 5.8 | PX |
| <i>E. stana</i> sp. n. | CNU-DIP-NN2013201 p/c | H | ♀ | 10.2 | 11.2 | 3.3 | 2.5 | 2 | 2.3 | 8 | shorter | 5.4 | DS |
| | DHG200384 | H | NA | 7 (ic) | 9.7 | 2.7 | 4.5 | 0.9 | 1.5 | 5 | longer | 4.6 | SL |
| <i>E. elenae</i> Zhang, 2007 | DHG200385 | H | ♀ | 10.5 | 10 | 2.4 | 2.5 | 1.8 | 0.6 | 5 | shorter | 4 | DS |
| | CNU-DIP-NN2013213 p/c | N | ♀ | 11.2 | 7.6 | 2.5 | 2.7 | 1.7 | 0.5 | 5.6 | shorter | 4.6 | DS |
| <i>E. macrostrena</i> sp. n. | CNU-DIP-NN2013211 | H | NA | 9 (ic) | 7.4 (ic) | >3 | 5 | 1.1 | 0.7 | ≈3 | NA | 5.6 | PX |
| | CNU-DIP-NN2013212 | P | ♀ | 10.3 | 7.1 | 2.5 | 4.7 | 1.1 | 0.7 | 3 | shorter | 4.6 | PX |
| | CNU-DIP-NN2013206 p/c | P | NA | 7 (ic) | 8 | 3.5 | 4.2 | 1.2 | 0.7 | 6.2 | longer | 4.4 | PX |
| <i>E. ambloneura</i> sp. n. | CNU-DIP-NN2013215 | H | ♀ | 12.7 | 9.1 | 2.5 | 7 | 0.7 | 2.8 | 11 | shorter | 5 | SL |
| | CNU-DIP-NN2013208 | P | NA | 5 (ic) | 7.4 | 2.3 | 6 | 0.7 | 1.3 | 8 | shorter | 5 | SL |

Notes: Abbreviations: 1. H = Holotype, P = Paratype, A = Allotype, N = New material; 2. BL = Body length (mm); 3. WL = Wing length (mm); 4. L/W = The ratio of wing length and width; 5. ic = incomplete; 6. p/c = Part and counterpart; 7. DS = Fork of Rs distad of fork of M₁₊₂; 8. PX = Fork of Rs proximad of fork of M₁₊₂; 9. NA = Not Available; 10. SL = Rs and M₁₊₂ at the same level.

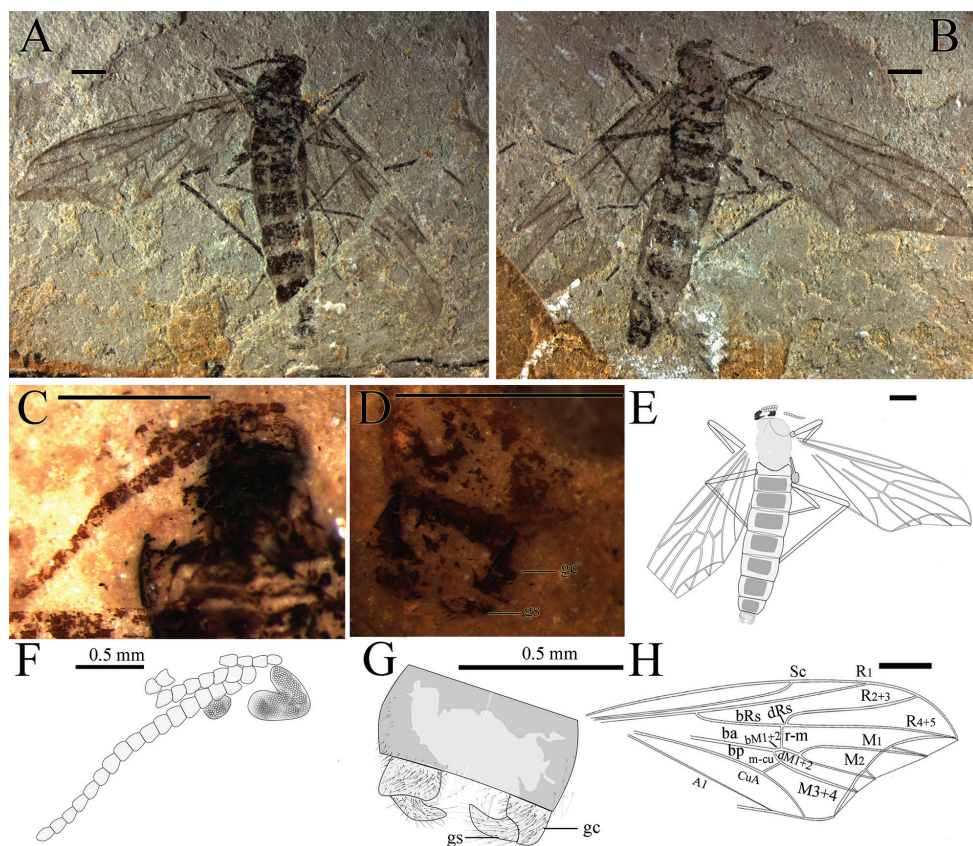


Figure 4. *Epimesoplecia prosoneura* sp. n. (CNU-DIP-NN2013207p/c). Holotype. Photographs of **A, B** Part and counterpart **C** Details of head (under alcohol) **D** Details of male genitalia (under alcohol); Line drawings of **E** Counterpart **F** Head **G** Male genitalia **H** Wing. Scale bars = 1 mm, gc—gonocoxite; gs—gonostylus.

Material. Holotype: male, NO. CNU-DIP-NN2013207p/c, part and counterpart, an almost complete specimen with well-preserved antennae, both wings and part of legs (Fig. 4A, B). Allotype (paratype): female. NO. CNU-DIP-NN2013214, in dorsal view, a specimen with well-preserved wings and body (Fig. 5A, B).

Horizon and locality. All specimens were collected from the Jiulongshan Formation, late Middle Jurassic age (Late Callovian) from Daohugou Village, Ningcheng County, Inner Mongolia Autonomous Region in China.

Description. Head (Figs 4C and 5C): Oviparous. Compound eyes protrusive in males. Antennae long, scape and pedicel thick and stout, the 1st flagellomere slender and long, the remaining ones becoming thinner toward apex.

Thorax (Figs 4A, B and 5A): Prothorax barely visible; scutum of mesothorax broad and oval, convex obviously; scutellum of metathorax projecting, semicircle; haltere depressed.

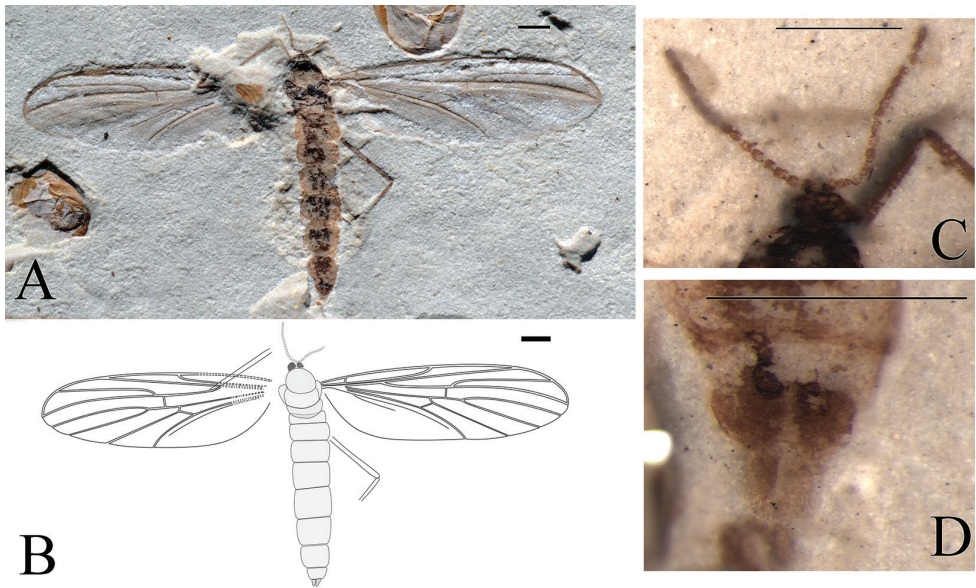


Figure 5. *Epimesoplecia prosoneura* sp. n. (CNU-DIP-NN2013214). Allotype. **A** Photograph of habitus **B** Line drawing of habitus; Photographs of **C** Details of head (under alcohol); **D** Details of female genitalia (under alcohol). Scale bars = 1 mm.

Legs (Figs 4A, B and 5A): Forelegs relatively slender; femur slender and long, covered with dense setae, slightly shorter than tibia; tarsi not preserved. Mid legs similar to forelegs, femur long and slender, tibia thinner than femur as preserved; Hind legs: femur slightly expanded, tibia slightly longer than femur as preserved.

Wings (Figs 4H and 5B): Wing long and narrow (length: 8–8.9 mm, width: 2.6–2.7 mm), apex of wings covering the abdominal terminalia. Costal field long and thin, Sc reaching C at the middle of anterior margin; Rs arising from basal one-fourth of wing length, furcating distad to fork of M_{1+2} ; bRs about 5 times (4.8–5.7) as long as r-m; crossvein m-cu slightly longer than r-m; CuA slightly curved, ending at posterior margin distad of mid wing; vein A_1 nearly straight, reaching posterior margin.

Male genitalia (Fig. 4G): Abdomen cylindrical; genitalia complex, slightly narrower than the 8th segment, with gonocoxites robust and rounded; gonostylus cylindrical and elongated, shorter than gonocoxites.

Female genitalia (Fig. 5D): The 8th segment slightly smaller than preceding segments, genitalia simple, with 2-segmented cerci, the basal segment of cerci longer than the terminal one.

Dimensions of holotype (in mm). [Measurements for the paratype CNU-DIP-NN2013214 in brackets, if different]. Holotype: male, CNU-DIP-NN2013207p/c, Body length 9.3 [8.2], maximal width of body 1.6 [1.4]. Antennae length: 1.8 (segments 1–16) [1.4 (segments 1–15)]. Foreleg: femur 1.6 as preserved; tibia 2.5 as preserved. Mid leg: femur 1.9 as preserved; tibia 2.7 as preserved. Hind leg: femur 2.2

as preserved [2 as preserved], tibia 3.5 as preserved [1.3 as preserved]. Wing: length 8 [8.9], width 2.6 [2.7]; R_{2+3} 3 [3.7]; bRs 1.9 [2.3]; dRs 0.1 [0.3]; R_{4+5} 3.6 [4].

Remarks. The new species is similar to *E. shcherbakovi* Zhang, 2007 but differs from the latter in having bRs about 10 times (9.4–10.5) as long as dRs (vs. 4.5 times); Rs bifurcation proximad of fork of M_{1+2} (vs. Rs bifurcation at the same level of fork of M_{1+2}); dM_{1+2} longer than bM_{1+2} (vs. dM_{1+2} shorter than bM_{1+2}); R_{2+3} , very close to the position crossvein r-m, distinctly longer than bRs and dRs combined (vs. R_{2+3} , distad of the position crossvein r-m, clearly shorter than bRs and dRs combined). The new species differs from *E. plethora* sp. n. in having bRs about 10 times (9.4–10.5) as long as dRs (vs. less than 2 times); bM_{3+4} clearly shorter than m-cu (vs. bM_{3+4} shorter than m-cu); Rs bifurcation proximad of fork of M_{1+2} (vs. Rs bifurcation distad of fork of M_{1+2}); dRs distinctly shorter than r-m (vs. dRs about 3 times as long as r-m); R_{2+3} , very close to the position crossvein r-m, distinctly longer than bRs and dRs combined (vs. R_{2+3} , sigmoidly curved, distinctly shorter than bRs and dRs combined). Comparisons with other species are listed in Table 1.

***Epimesoplecia stana* sp. n.**

<http://zoobank.org/323B8EC8-B13C-4360-BCFF-82E436529BB0>

Fig. 6

Etymology. The epithet is an arbitrary combination of letters used as a nun in apposition.

Diagnosis. Antennae moniliform. Sc very close to the level of r-m; fork of Rs distad of fork of M_{1+2} ; R_{2+3} distad of crossvein r-m; R_{2+3} , straight, distinctly less than bRs and dRs combined; bRs 2.5 times as long as dRs, the latter 2 times as long as r-m; bM_{1+2} significantly longer than dM_{1+2} (2.3 times); bM_{3+4} slightly longer than m-cu; cell bp narrower than cell ba terminally.

Material. Holotype: female, NO. CNU-DIP-NN-2013201p/c, in lateral view, a well-preserved body with partial antennae, almost complete wings and legs.

Horizon and locality. The specimen was collected from the Jiulongshan Formation, late Middle Jurassic age (Late Callovian) from Daohugou Village, Ningcheng County, Inner Mongolia Autonomous Region in China.

Description. Head (Fig. 6C): small, in lateral view; Antennae with segments 1–11 visible as preserved, moniliform. Maxillary palpi barely visible.

Thorax (Fig. 6A, B): Prothorax barely visible; scutum of mesothorax broad and oval, convex obviously; scutellum of metathorax projecting, semicircular; haltere depressed.

Legs (Fig. 6A, B): Forelegs relatively slender, femur slightly expanded, slightly shorter than tibia; tarsi not preserved. Mid legs similar to forelegs, femur thicker than tibia; tibial spurs minute; tarsi not preserved. Hind legs: femur slightly expanded, slightly shorter than tibia; tibia slender and long as preserved.

Wings (Fig. 6F): Wing long and narrow, more than 3 times as long as width (length: 11.2 mm, width: 3.4 mm as preserved); apex of wings covering the abdominal terminalia. Costal field long and thin, Sc reaching C very close to the position of r-m;

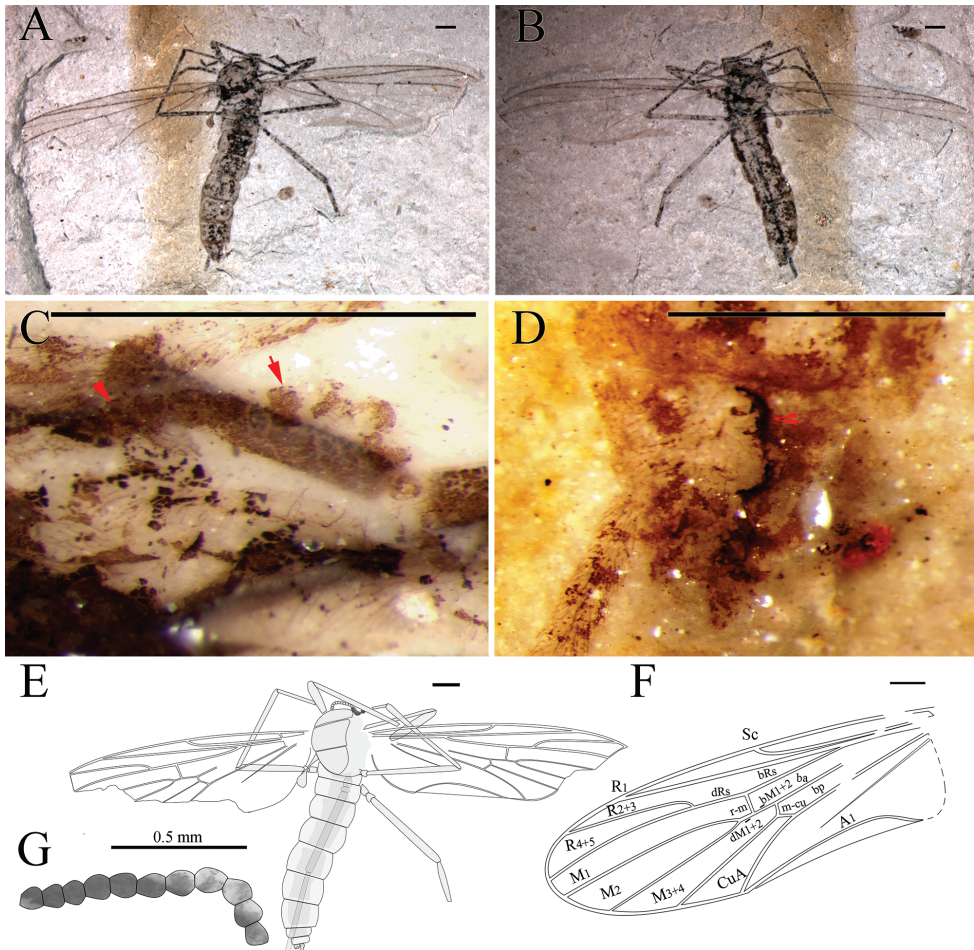


Figure 6. *Epimesoplecia stana* sp. n. (CNU-DIP-NN2013201p/c). Holotype. Photographs of **A**, **B** Part and counterpart; **C** Details of head (under alcohol) **D** Details of female genitalia (under alcohol); Line drawings of **E** Part **F** Left wing of counterpart **G** Partial antenna. Scale bars = 1 mm.

Rs arising from basal one-fourth of wing length, furcating distad to level of fork of M_{1+2} . Stem of Rs longer than stem of R, the former longer than R_{2+3} , bRs 5 times as long as r-m; crossvein r-m longer than m-cu; CuA slightly curved, ending at posterior margin; vein A_1 short, slightly longer than half of cell bp.

Female genitalia (Fig. 6D): The 8th segment slightly smaller than preceding segments, genitalia simple, cerci segments not visible.

Dimensions (in mm). Holotype: female, CNU-DIP-NN2013201p/c, Body length 10.2, maximal width of body 2.2. Antennae 1.1 (segments 1–11). Foreleg: femur 2.5; tibia 2.7. Mid leg: femur 3; tibia 3.4. Hind leg: femur 3.7, tibia 3.4. Wing: length 11.2, width 3.4; R_{2+3} 3; bRs 2.5; dRs 1.1; R_{4+5} 3.7.

Remarks. The new species having ratio of bRs/dRs of 2.5 is similar to *E. elenae* Zhang, 2007, but is distinguished from the latter by having Rs bifurcation

significantly distad of fork of M_{1+2} (vs. Rs bifurcation slightly distad of fork of M_{1+2}); bM_{1+2} distinctly longer than dM_{1+2} (vs. bM_{1+2} clearly shorter than dM_{1+2}); dM_{1+2} clearly shorter than r-m (vs. dM_{1+2} as long as r-m); dM_{1+2} short, almost one-eighth of M_2 (vs. dM_{1+2} long, one-fifth of M_2). Comparisons with other species are listed in Table 1.

***Epimesoplecia macrostrena* sp. n.**

<http://zoobank.org/8A937A8A-0349-45A6-B5FB-D5287856A37F>

Figs 7–8

Etymology. The epithet of *macrostrena* is derived from the Greek prefix “macro-”, meaning “large”, and Greek word “strenos”, meaning “insolence or excess of strength”, referring to the large wings and strong body of this species. The specific epithet is a noun in apposition.

Diagnosis. Antennae filiform. Sc very close to the level of r-m; fork of Rs proximal of fork of M_{1+2} ; R_{2+3} distad of crossvein r-m; R_{2+3} , straight, slightly shorter than bRs and dRs combined; bRs about 5 times (4.2–5) as long as dRs, the latter almost equal to r-m; bM_{1+2} shorter than dM_{1+2} (0.7 times); bM_{3+4} shorter than m-cu (barely longer than m-cu); cell bp slightly wider than cell ba terminally.

Materials. Holotype: sex unknown. NO. CNU-DIP-NN-2013211, in lateral view, a well-preserved specimen with partial antennae, wings and body as preserved (Fig. 7). Paratypes: CNU-DIP-NN-2013206p/c, sex unknown, a well-preserved specimen with almost complete wings and body (Fig. 8A, B), NO. CNU-DIP-NN-2013212, female, in ventral view, a well-preserved specimen with complete wings and body as preserved (Fig. 8E).

Horizon and locality. All specimens were collected from the Jiulongshan Formation, late Middle Jurassic age (Late Callovian) from Daohugou Village, Ningcheng County, Inner Mongolia Autonomous Region in China.

Description. Head (Figs 7C, D and 8C): Ovipositor and very small in lateral view; antennae filiform, segments 1–9 well-preserved, scape and pedicel slightly compressed; flagellar segments slender and long, becoming thinner and shorter toward apex (moniliform in CNU-DIP-NN-2013206p/c in Fig. 8C); maxillary palpi segments not visible.

Thorax (Figs 7A, B and 8E): Scutum well-developed, arched convex; scutellum depressed; haltere clearly depressed.

Legs (Figs 7A, B and 8E): Forelegs: femur thicker than tibia; almost four-fifths of tibia; the 1st tarsomere longer than half of tibia, the 2nd–5th greatly thinned than the former. Mid legs: femur slightly thicker than tibia; tibial spurs minute; the 1st tarsomere slightly longer than the 1st tarsomere of forelegs. Hind legs: femur expanded almost equal to tibia; tibial spurs minute; tarsi not preserved.

Wings (Figs 7E, 8D and F): Wing long and narrow (length: 7.1–8 mm, width: 2.3–3.2 mm), apex of wings not reaching the abdominal terminalia. Costal field long and thin, apex of Sc gradually tapering to the end; Rs arising almost from basal one-

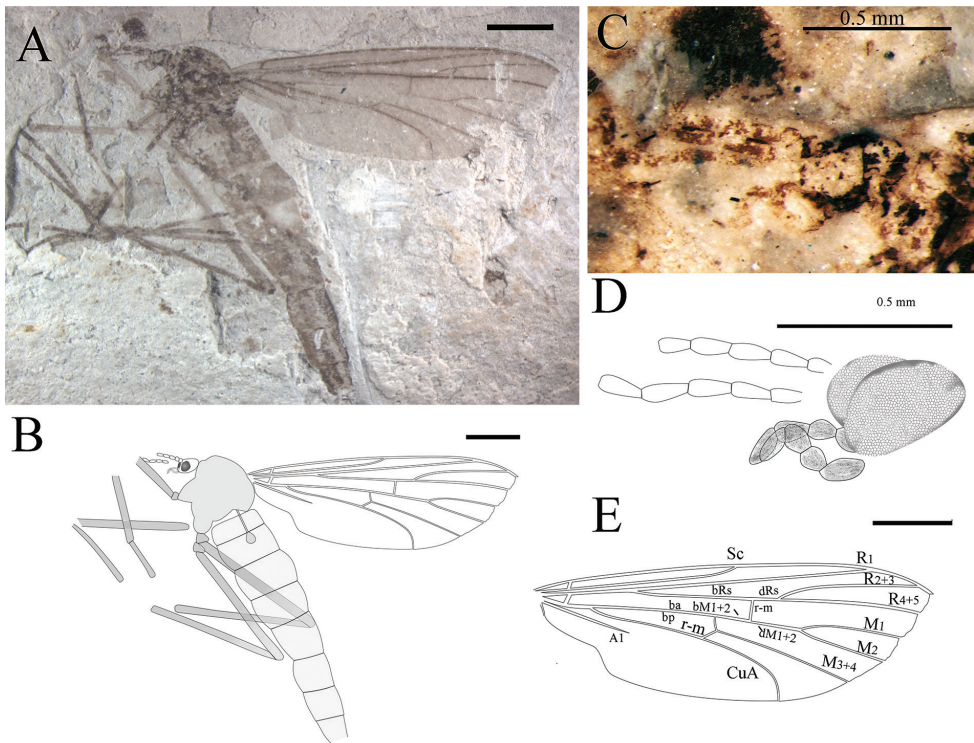


Figure 7. *Epimesoplecia macrostrena* sp. n. (CNU-DIP-NN2013211). Holotype. **A** Photograph of habitus **B** Line drawing of habitus **C** Photograph of details of head (under alcohol); Line drawings of **D** Head **E** Wing. Scale bars = 1 mm.

fifth of wing length, furcating proximad of fork of M_{1+2} bRs 4.4–5.6 times as long as r-m; crossvein m-cu slightly shorter than r-m; CuA arched near anal margin; vein A_1 nearly straight, reaching posterior margin.

Female genitalia (Fig. 8F): In lateral view, genitalia simple, with 2-segmented cerci.

Dimensions (in mm). [Measurements for the holotype in brackets]. Body length 7 (as preserved)–11.3 [10.3 as preserved]; antennae 0.9 (as preserved)–1.4 (segments 1–16) [0.9 segments 1–9]. Forelegs: femur 2.1–2.5 [1.8 as preserved]; tibia 2.9–3.1 [2.7 as preserved]. Mid leg: femur 2.4–3.8 as preserved [3.8 as preserved]; tibia 2.7–3.6 as preserved [3.6 as preserved]. Hind leg: femur 3.4–4.7 [4.7], tibia 3.8–4.8 [4.8]. Wing: length 7.1–8 [7.4 as preserved], width 2.3–3.3 [3.3]; R_{2+3} 2.4–3.2 [3.2]; bRs 1.9–2.9 [2.9]; dRs 0.5–0.8 [0.6]; R_{4+5} 3–3.7 [3.7].

Remarks. The new species is similar to *E. shcherbakovi* Zhang, 2007, but is differentiated from the latter by having Rs bifurcation proximad of fork of M_{1+2} (vs. Rs bifurcation at the same level of fork of M_{1+2}); b M_{1+2} shorter than d M_{1+2} (vs. b M_{1+2} longer than d M_{1+2}); dRs as long as r-m (vs. dRs clearly shorter than r-m); d M_{1+2} long, almost one-third of M_2 (vs. d M_{1+2} short, significantly less than one-third of M_2). Comparisons with other species are listed in Table 1.

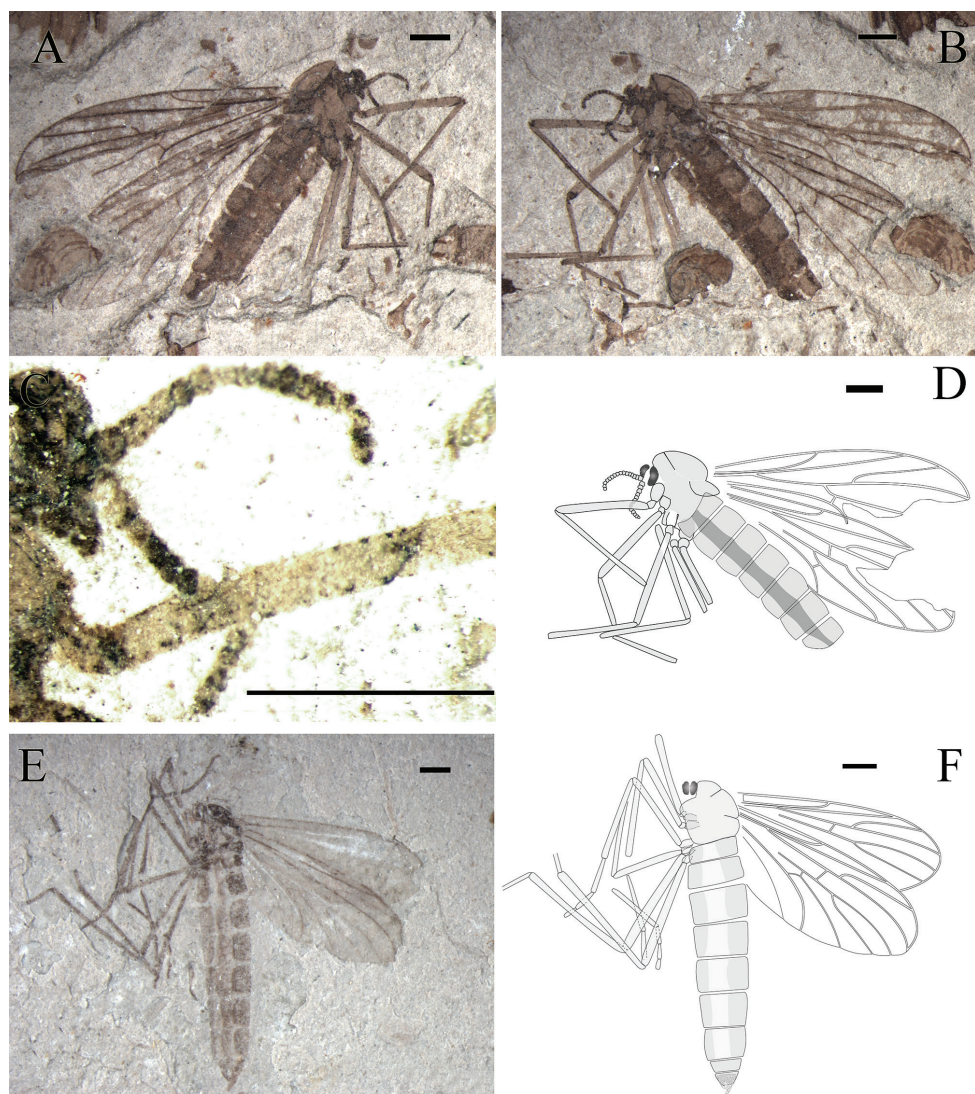


Figure 8. *Epimesoplecia macrostrena* sp. n. (CNU-DIP-NN2013206p/c). Paratype. Photographs of **A, B** Part and counterpart **C** Details of head; Line drawing of **D** Counterpart; (CNU-DIP-NN2013212) Paratype **E** Photograph of habitus **F** Line drawing of habitus. Scale bars = 1 mm.

***Epimesoplecia ambloneura* sp. n.**

<http://zoobank.org/268EE32F-E347-45C1-8FF7-F3DC03805D09>

Figs 9–10

Etymology. The epithet of *ambloneura* is derived from the Greek prefix “ambl-”, meaning “obtuse”, and Greek word “neura”, meaning “string or sinew”, referring to the blunt caudal vein of this species. The specific epithet is a noun in apposition.

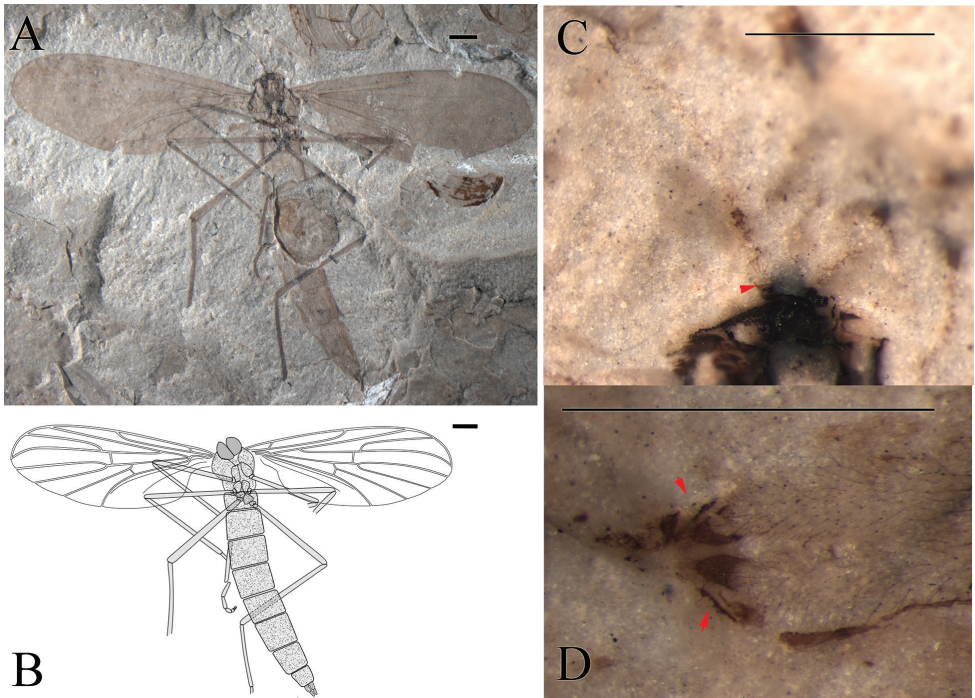


Figure 9. *Epimesoplecia ambloneura* sp. n. (CNU-DIP-NN2013215). Holotype. **A** Photograph of habitus **B** Line drawing of habitus; Photographs of **C** Details of head (under alcohol) **D** Details of female genitalia (under alcohol). Scale bars = 1 mm.

Diagnosis. Antennae filiform. Sc very close to the level of r-m; fork of Rs at the same level of fork of M_{1+2} ; R_{2+3} proximad of crossvein r-m; R_{2+3} , straight, distinctly longer than bRs and dRs combined; bRs about 6–7 times as long as dRs, the latter clearly shorter than r-m; bM_{1+2} significantly longer than dM_{1+2} (1.3–2.8 times); M_2 8–11 times as long as dM_{1+2} ; bM_{3+4} shorter than m-cu; cell bp slightly wider than cell ba terminally.

Materials. Holotype: male. NO. CNU-DIP-NN-2013215, in ventral view, a well-preserved specimen with partial antennae, complete wings and body (Fig. 9A). Paratype: sex unknown. NO. CNU-DIP-NN-2013208, in dorsal view, a specimen with only right wing well-preserved, but fragments of body as preserved (Fig. 10).

Horizon and locality. All specimens were collected from the Jiulongshan Formation, late Middle Jurassic age (Late Callovian) from Daohugou Village, Ningcheng County, Inner Mongolia Autonomous Region in China.

Description. Head (Fig. 9C): Ovoid and very small in lateral view; antennae long, with 16 segments, scape and pedicel slightly compressed; flagellar segments slender and long, becoming thinner and shorter toward apex; maxillary palpi segments barely visible.

Thorax (Figs 9A and 10A): Scutum well-developed, arched convex; scutellum depressed; haltere not visible.

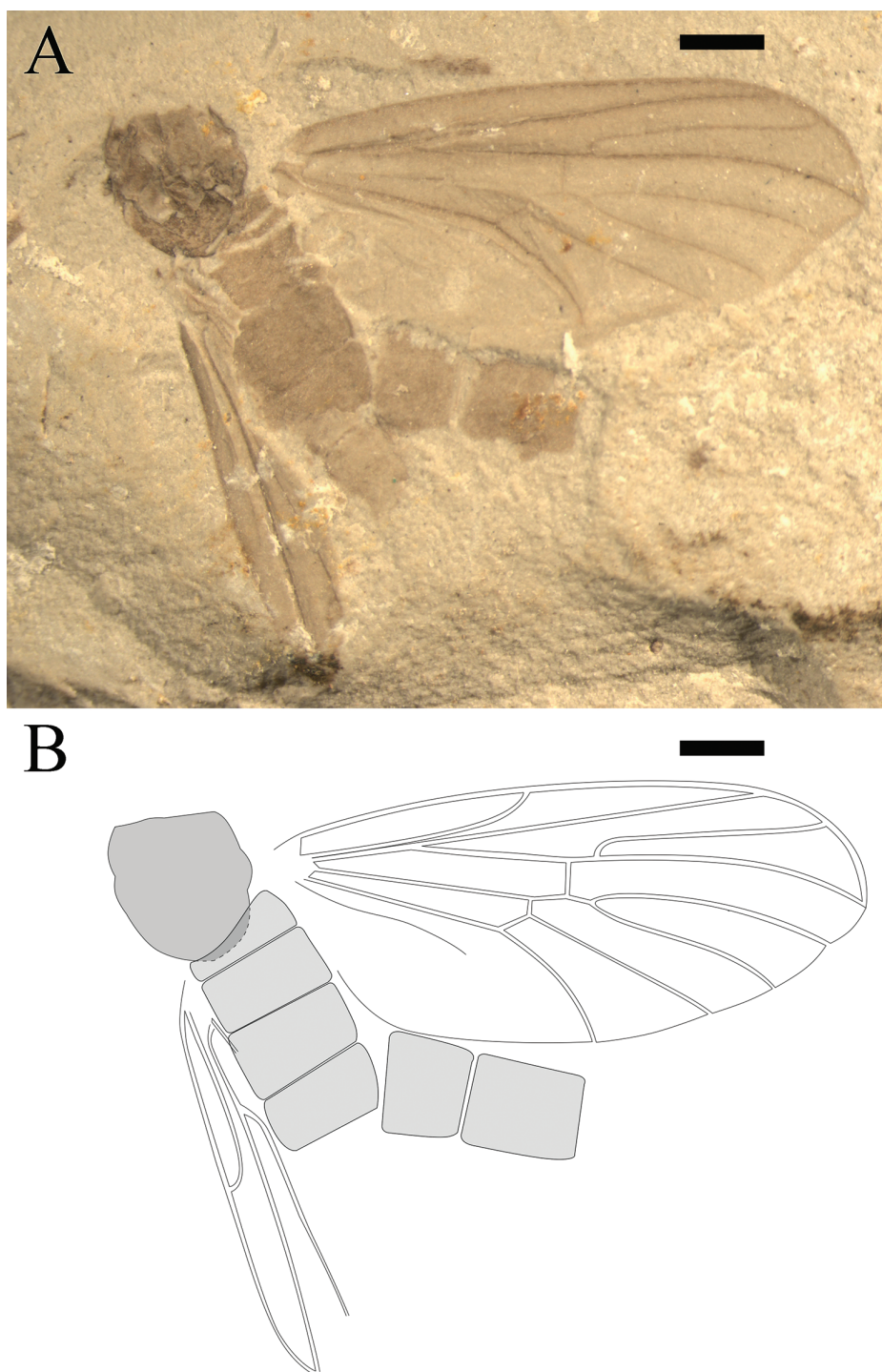


Figure 10. *Epimesoplecia ambloneura* sp. n. (CNU-DIP-NN2013208). Paratype. **A** Photograph of habitus **B** Line drawing of habitus. Scale bars = 1 mm.

Legs (Fig. 9A): Forelegs: femur slightly thicker than tibia; almost equal to tibia; tarsi not preserved. Mid legs: femur thicker than tibia; tibial spurs minute; tarsi not preserved. Hind legs: femur expanded, almost equal to tibia; tibial spurs minute; the 1st tarsomere longer than half of tibia; tarsi 2nd–5th not preserved.

Wings (Figs 9B and 10B): Wing long and narrow (length: 7.4–9.1 mm, width: 3.2–3.6 mm), apex of wings not reaching the abdominal terminalia. Costal field long and thin, apex of Sc gradually tapering to the end; Rs arising almost from basal one-fifth of wing length, furcating at the same level of fork of M_{1+2} ; bRs 5 times as long as r-m; CuA slightly oblique; vein A_1 nearly straight, not reaching posterior margin, exceeding the level of m-cu.

Female genitalia (Fig. 9D): Genitalia with 2-segmented cerci.

Dimensions of holotype (in mm). [Measurements for the paratype, CNU-DIP-NN2013208 in brackets]. Holotype: male. NO. CNU-DIP-NN-2013215, body length 12.7 as preserved [5 as preserved]; antennae 1.5 as preserved. Forelegs: femur 3.5 as preserved; tibia 3.9. Mid leg: femur 3.9; tibia 4.2. Hind leg: femur 4.2, tibia 4.8. Wing: length 9.1 [7.4], width 3.6 [3.2]; R_{2+3} 3.5 [2.9]; bRs 2.5 [1.9]; dRs 0.35 [0.3]; R_{4+5} 4 [3.3].

Remarks. The new species is similar to *E. shcherbakovi* Zhang, 2007, but differs from the latter in having bRs about 6–7 times as long as dRs (vs. 4.5 times); R_{2+3} clearly longer than bRs and dRs combined (vs. R_{2+3} significantly shorter than bRs and dRs combined); Rs bifurcation proximad of r-m (vs. Rs distad of r-m); M_2 8–11 times as long as dM_{1+2} (vs. 5 times); bM_{3+4} shorter than m-cu (vs. bM_{3+4} longer than m-cu). Comparisons with other species are listed in the Table 1.

Key to the species of *Epimesoplecia* Zhang, 2007

- | | | |
|---|--|------------------------------|
| 1 | Fork of Rs proximad fork of M_{1+2} | 2 |
| – | Fork of Rs distad or at same level fork of M_{1+2} | 3 |
| 2 | Fork of Rs proximad of r-m; bRs about 10 times as long as dRs | |
| | <i>E. prosoneura</i> sp. n. | |
| – | Fork of Rs distad of r-m; bRs significantly less than 10 times as long as dRs... | |
| | <i>E. macrostrena</i> sp. n. | |
| 3 | Fork of Rs at the same level of M_{1+2} ; dRs shorter than r-m..... | 4 |
| – | Fork of Rs distad of M_{1+2} ; dRs longer than r-m..... | 5 |
| 4 | R_{2+3} longer than Rs; bM_{1+2} clearly shorter than m-cu .. | <i>E. ambloneura</i> sp. n. |
| – | R_{2+3} distinctly shorter than Rs; bM_{1+2} longer than m-cu | |
| | <i>E. shcherbakovi</i> Zhang, 2007 | |
| 5 | bM_{1+2} longer than dM_{1+2} | <i>E. stana</i> sp. n. |
| – | bM_{1+2} distinctly shorter than dM_{1+2} | 6 |
| 6 | Antennae moniliform; bRs significantly less than 2.5 times as long as dRs.... | |
| | <i>E. plethora</i> sp. n. | |
| – | Antennae filiform; bRs 2.5 times as long as dRs..... | <i>E. elenae</i> Zhang, 2007 |

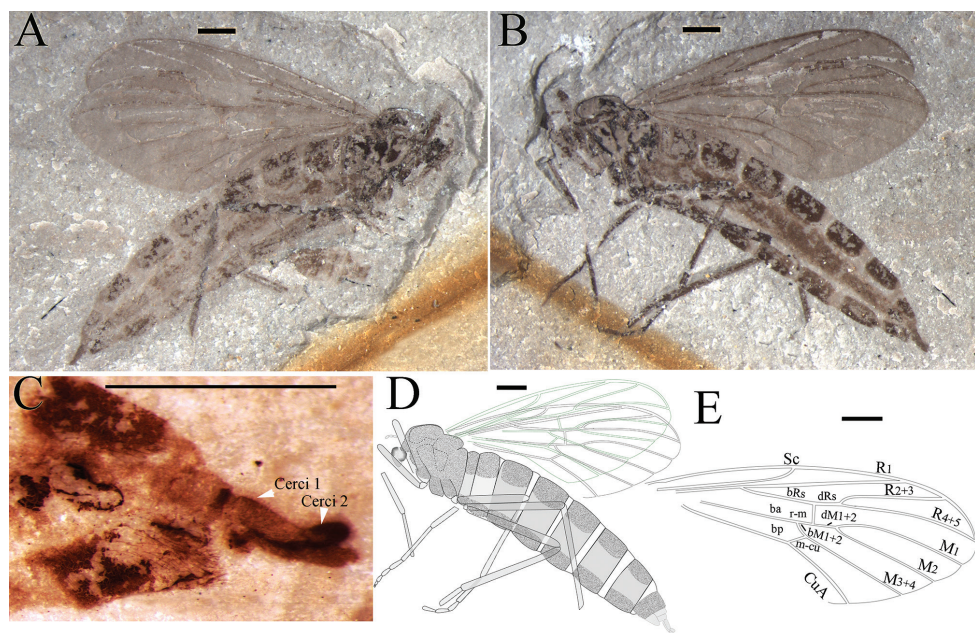


Figure 11. *Epimesoplecia elenae* Zhang, 2007. (CNU-DIP-NN2013213). New material. Photographs of **A, B** Part and counterpart **C** Details of female genitalia (under alcohol); Line drawings of **D** Counterpart **E** Wing. Scale bars = 1 mm.

Discussion

The generic diagnosis of *Epimesoplecia* Zhang, 2007 is revised based on eleven well-preserved new specimens, among which ten are used to describe the afore-mentioned five new species. One is identified as a new material for *E. elenae* Zhang, 2007 (Fig. 11). In total, seven species with 13 specimens have been described in *Epimesoplecia* so far, all from the Jiulongshan Formation of China (Table 1).

It is interesting to note that only one of the 13 specimens reported so far is male, ie. the holotype of *E. prosoneura* sp. n. (CNU-DIP-NN2013207 p/c) with well-preserved male genitalia. We also describe a female paratype of *E. prosoneura* sp. n. (CNU-DIP-NN2013214) with well-preserved female genitalia. Since both specimens have similar body size, wing length and venational characters, the sexual dimorphism of this species seems to be not significant.

The measurements of body length, wing length and other important characters of wings are summarised in Table 1. The data and information suggest that the following characters are stable within a species, but differ among different species: (1) fork of Rs vs. fork of M_{1+2} ; (2) ratio range of bRs and dRs; (3) dRs longer or shorter than r-m; (4) bM_{1+2} longer or shorter than m-cu; and (5) antennae moniliform or filiform. Based on these taxonomic characters, a key to the species of *Epimesoplecia* Zhang, 2007 is provided.

Acknowledgements

We sincerely appreciate comments and suggestion from Dr. Vladimir Blagoderov and two anonymous reviewers in improving this manuscript. We are grateful to Dr. Gao Taiping, Li Longfeng and Peng Yuanyuan for their constructive and critical comments on the manuscript. This research was supported by the National Basic Research Program of China (973 Program) (No. 2012CB821906), the National Natural Science Foundation of China (Nos. 31230065 and 41272006), Great Wall Scholar and KEY project of Beijing Municipal Commission of Education (KZ201310028033) and Program for Changjiang Scholars and Innovative Research Team in University (IRT13081).

References

- Ansorge J (1996) Insekten aus dem oberen Lias von Grimmen (Vorpommern/Norddeutschland). *Neue Paläontologische Abhandlungen* 2: 1–132.
- Blagoderov VA (1996) Revision of the Dipteran family Protopleciidae (Insecta, Diptera) from the Early Jurassic Soguty locality, Kyrgyzstan. *Paleontologicheskii Zhurnal*, 85–90.
- Blagoderov VA, Lukashevich ED, Mostovski MB (2002) Order Diptera Linné, 1758. The true flies (= Muscida Laicharting, 1781). In: Rasnitsyn AP, Quicke DLJ (Eds) *History of insects*. Kluwer Academic Publisher, Dordrecht, 227–240.
- Evenhuis NL (1994) *Catalogue of the Fossil Flies of the world (Insecta: Diptera)*. Backhuys Publishers, Leiden, 600 pp.
- Gao KQ, Ren D (2006) Radiometric Dating of Ignimbrite from Inner Mongolia Provides no Indication of a Post-Middle Jurassic Age for the Daohugou Beds. *Acta Geologica Sinica* 80: 42–45. [English Edition] doi: 10.1111/j.1755-6724.2006.tb00793.x
- Geinitz FE (1884) Über die Fauna des Dobbertiner Lias. *Zeitschrift der Deutschen Geologischen Gesellschaft* 36: 566–583.
- Grimaldi D, Engel MS (2005) *Evolution of the Insects*. Cambridge University Press, New York, 755 pp.
- Handlirsch A (1906) Die fossilen Insekten und die Phylogenie der rezenten Formen. Ein Handbuch für Paläontologen und Zoologen. Engelmann, Leipzig, 800 pp.
- Hao JY, Ren D (2009) Middle Jurassic Protopleciidae from Daohugou, Inner Mongolia, China. *Acta Zootaxonomica Sinica* 34(3): 554–559. [In Chinese, English summary]
- Hong YC (1984) Tracheata, Insecta. In: *The Tianjin Institute of Geology and Mineral Resources (Ed.) Palaeontological Atlas of North China II. Mesozoic Volume*. Geological Publishing House, Beijing, 128–185. [In Chinese]
- Hong YC, Wang WL (1990) Fossil insects from the Laiyang basin, Shandong province. Geological Publishing House, Beijing, 189 pp. [In Chinese, English summary]
- Kovalev VG (1987) Mesozoic Mycetophiloid Dipterans of the Family Pleciofungivoridae. *Paleontologicheskii Zhurnal* 2: 69–82. [In Russian]
- Latreille PA (1825) *Familles naturelles du règne animal, exposé succinctement et dans un ordre analytique avec l'indication de leurs genres*. J. B. Baillière, Paris, 570 pp.

- Li S, Shih CK, Wang C, Pang H, Ren D (2013) Forever love: The hitherto earliest record of copulating insects from the Middle Jurassic of China. *PLoS ONE* 8(11): e78188. doi: 10.1371/journal.pone.0078188
- Lin QB (1976) The Jurassic fossil insects from western Liaoning. *Acta Palaeontologica Sinica* 15(1): 97–116. [In Chinese, English summary]
- Lin XQ, Shih CK, Ren D (2014) Two new species of *Mesoplecia* (Insecta: Diptera: Protopleciiidae) from the late Middle Jurassic of China. *Zootaxa* 3838(5): 545–556. doi: 10.11646/zootaxa.3838.5.3
- Linnaeus C (1758) Tomus I. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Editio decima, reformata. Laurentii Salvii, Holmiae, 824 pp.
- Liu LX, Shih CK, Ren D (2012) Two new species of Ptychopteridae and Trichoceridae from the Middle Jurassic of northeastern China (Insecta: Diptera: Nematocera). *Zootaxa* 3501: 55–62.
- Ren D, Gao KQ, Guo ZG, Ji SA, Tan JJ, Song Z (2002) Stratigraphic division of the Jurassic in the Daohugou Area, Ningcheng, Inner Mongolia. *Geological Bulletin of China* 21: 584–591. [In Chinese, English abstract]
- Ren D, Shih CK, Gao TP, Yao YZ, Zhao YY (2010) Silent stories-insect fossil treasures from dinosaur era of the northeastern China. Science Press, Beijing, 324 pp.
- Rohdendorf BB (1938) Mesozoic Diptera from Karatau. I Brachycera and some Nematocera. *Trudy paleontologicheskogo instituta akademii nauk SSSR, Moscow* 7(3): 29–67, text fig. 1–21.
- Rohdendorf BB (1946) The evolution of the Wing and the Phytogeny of Oligoneura (Diptera, Nematocera). *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR Moscow, Leningrad*, 1–108. [In Russian, with English summary]
- Rohdendorf BB (1964) Historical development of the Diptera. *Trudy Paleontologicheskogo Instituta. Akademii Nauk SSSR* 100: 1–311. [In Russian]
- Shi CF, Yang Q, Ren D (2011) Two new fossil lacewing species from the Middle Jurassic of Inner Mongolia, China (Neuroptera: Grammolegiidae). *Acta Geologica Sinica* 85(2): 482–489. [English Edition] doi: 10.1111/j.1755-6724.2011.00416.x
- Shcherbakov DE, Lukashevich ED, Blagoderov VA, (1995) Triassic Diptera and initial radiation of the order. *International Journal of Dipterological Research* 6(2): 75–115.
- Walker JD, Geissman JW, Bowring SA, Babcock LE (2013) The Geological Society of America Geologic Time Scale. *Geological Society of America Bulletin* 125: 259–272. doi: 10.1130/B30712.1
- Wang Q, Shih CK, Ren D (2013) The Earliest Case of Extreme Sexual Display with Exaggerated Male Organs by Two Middle Jurassic Mecopterans. *PLoS ONE* 8(8): e71378. doi: 10.1371/journal.pone.0071378
- Wootton RJ, Ennos AR (1989) The implications of function on the origin and homologies of the dipterous wing. *Systematic Entomology* 14: 507–520. doi: 10.1111/j.1365-3113.1989.tb00300.x
- Zhang JF (2007) New Mesozoic Protopleciiidae (Insecta: Diptera: Nematocera) from China. *Cretaceous Research*, 289–296. doi: 10.1016/j.cretres.2006.05.009

