

# Biodiversity census of Lake St Lucia, iSimangaliso Wetland Park (South Africa): Gastropod molluscs

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## Abstract

The recent dry phase experienced by the St Lucia estuarine system has led to unprecedented desiccation and hypersaline conditions through most of its surface area. This has changed only recently, at the end of 2011, with the onset of a new wet phase that has already caused a major shift to oligo- and mesohaline conditions. The estuary mouth, however, remains closed to the ocean, making the weak connection recently established between the St Lucia and the Mfolozi estuaries the only conveyance for marine recruitment. As a result, only 10 indigenous and two alien aquatic gastropod species are currently found living in the St Lucia estuarine lake. This is out of a total of 37 species recorded within the system since the earliest survey undertaken in 1924, half of which have not been reported in the literature before. The tick shell, *Nassarius kraussianus*, which was consistently found in large abundance prior to the recent dry phase, appears to have temporarily disappeared from the system, probably as a result of the extinction of *Zostera* marine grasses inside the lake. Population explosions of the bubble shell *Haminoea natalensis*, with its distinct egg masses, were recorded seasonally until 2009, but the species has subsequently not been observed again. A molecular DNA analysis of the various populations previously reported as belonging to the same assimineid species, variably referred to as *Assiminea capensis*, *A. ovata*, or *A. bifasciata*, has revealed that the St Lucia assemblage actually comprises two very distinct taxa, *A. cf. capensis* and a species provisionally referred to here as “*A.*” aff. *capensis* or simply Assimineidae sp. In the mangroves, the climbing whelk *Cerithiidea decollata* is still found in numbers, while ellobiids such as *Cassidula labrella*, *Melampus semiaratus* and *M. parvulus* are present in low abundances and all previously recorded littorinids have disappeared. A number of alien freshwater species have colonized areas of the system that have remained under low salinity. These include the invasive thiarid *Tarebia granifera*, which can be found in concentrations exceeding 5000 ind.m<sup>-2</sup>, the lymnaeid *Pseudosuccinea columella* and the physid *Aplexa marmorata*.

**Keywords**

Mollusca, Gastropoda, biodiversity census, hypersalinity, iSimangaliso Wetland Park, illustrated checklist

**Introduction**

Lake St Lucia is a large, complex estuarine lake situated on the South African east coast. It has been extensively investigated since the late 1940s, as it is the largest such system in Africa, the oldest protected estuary in the world and a Ramsar Wetland of International Importance since 1986 (Porter 2013). It currently forms a crucial part of the iSimangaliso Wetland Park, which is South Africa's first UNESCO World Heritage Site. During the past century, the system has undergone a number of changes related to anthropogenic activities, which superimposed on an already complex and variable climate have escalated the magnitude of its regular shifts from wet to dry states (Perissinotto et al. 2013). Typically the system experiences sub-decadal alternations of droughts and anomalous wet conditions, at times resulting in severe floods. Recently, the system has undergone a major shift, from a prolonged dry phase during 2002–2011 to flood conditions during 2012–2013, which has resulted in the current predominance of oligohaline conditions through most of its basins (Raw et al. 2013; Peer et al. 2014).

The rich biodiversity of the St Lucia estuarine lake is one of the main drivers of its special conservation status. Species are the building-blocks of any ecosystem, yet in the St Lucia case there are many misidentifications and several groups of invertebrates remain poorly investigated or completely ignored. A few detailed taxonomic studies of selected invertebrate groups have already been undertaken, starting from 2010, using a combination of traditional morphological analyses and molecular DNA barcoding. These have consistently revealed the occurrence of species that were either previously confused with others or completely unknown to science (e.g. Daly et al. 2012; Gómez et al. 2012; Carrasco and Perissinotto 2012; Todaro et al. 2011, 2013). A systematic approach has been implemented recently, aimed at producing a modern “Biodiversity Census” for the estuarine lake. The main objective of the initial phase of the census is to add accurate checklists of as many aquatic invertebrate groups as possible to those already existing for the vertebrates and the macrophytes. As the diversity census of bivalve molluscs and true crabs have already been completed and published (Nel et al. 2012; Peer et al. 2014), this new contribution focused on the gastropod molluscs is regarded as the third of the series planned within the census.

The class Gastropoda is the most diverse among the molluscs and includes about 55000 extant aquatic species globally (Brusca and Brusca 2003). Gastropods play an integral part in the functioning of aquatic ecosystems (Carlén and Ólafsson 2002). In estuarine ecosystems such as St Lucia, gastropods are important components of food webs and energy pathways. They are mostly detritivores or herbivores, feeding on a large variety of decomposing organic materials or on benthic or epiphytic microalgae, protozoans,

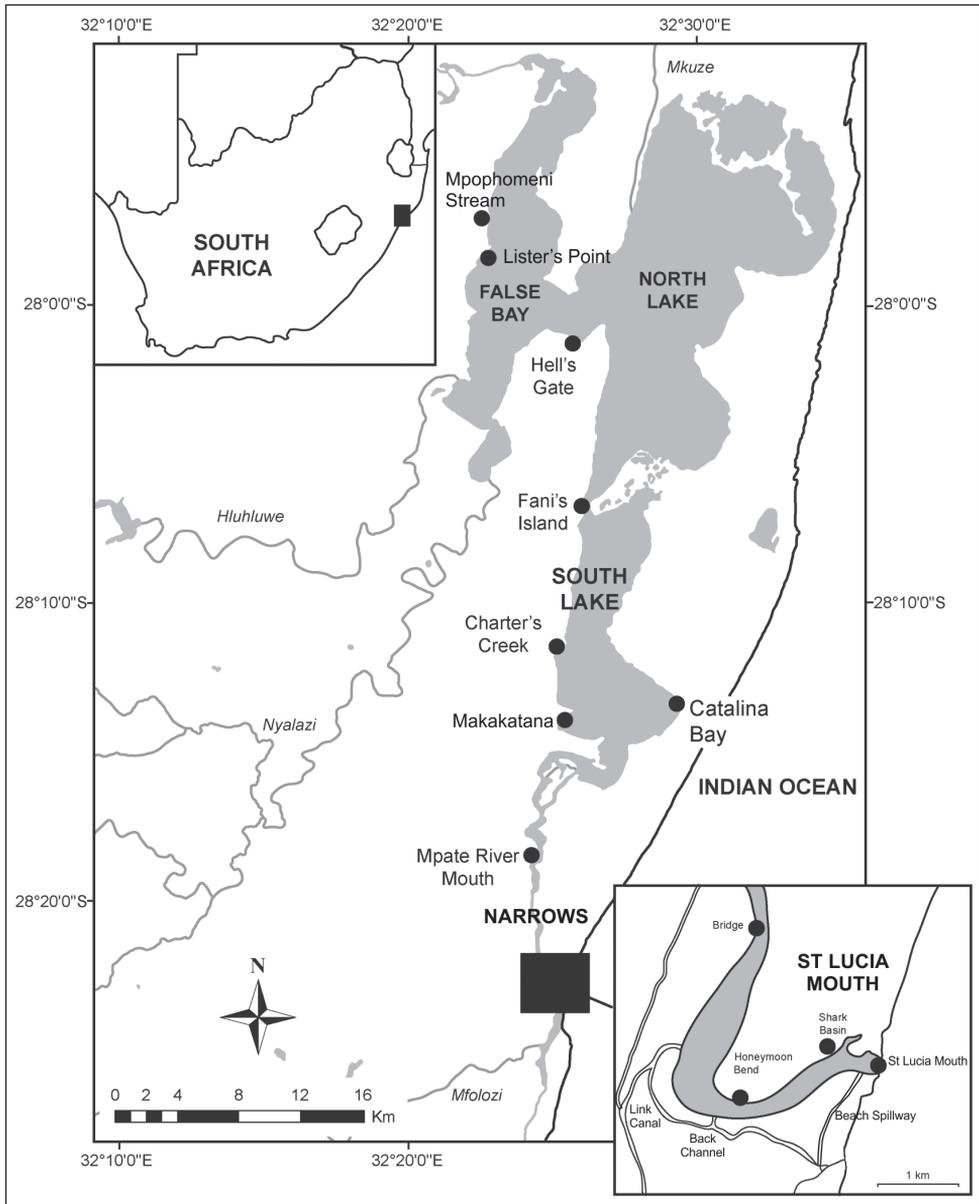
bacteria and fungi. There are also a few predatory or scavenger species, especially among the muricids, nassariids and naticids. Gastropods also play a key role in nutrient dynamics in mangrove ecosystems, where they graze on encrusting fauna and microalgae, thus cleaning the pneumatophores (Ghasemi et al. 2011). In turn, both snails and limpets are consumed by a variety of predators, including birds (Whitfield and Cyrus 1978; Hockey et al. 2005; Turpie et al. 2013), fish (Blaber and Blaber 1980; Whitfield 1998; Dyer et al. 2013), crabs (Sousa 1993; Schaefer and Zimmer 2013), leeches, larvae of marsh flies and aquatic beetles (Appleton 1996), as well as anemones (Daly et al. 2012). Some freshwater species living on the fringes of Lake St Lucia, or even entering the estuarine system in times of freshwater dominance, may be of veterinarian/medical importance as they act as vectors of parasites responsible for water-borne diseases, such as bilharzia, fascioliasis and paramphistomiasis (Appleton 1996). In estuaries, the diversity of gastropods is determined to a large extent by changes in physico-chemical conditions and the availability of detritus and microalgae as their primary food sources (Carlén and Ólafsson 2002).

The purpose of this study is thus to provide a comprehensive review of the diversity of gastropod molluscs in the St Lucia estuarine lake. This includes identifying species that are currently present in the system and comparing them with what was collected in past surveys. Changes in diversity over time are related to shifts in environmental and climatic conditions that have occurred during the past century. The compilation of an annotated and illustrated checklist of all gastropod species recorded so far within the system is designed to aid managers, researchers and visitors in the iSimangaliso Wetland Park with the identification of these important molluscs.

## Methods

The St Lucia estuarine lake is located on the north coast of KwaZulu-Natal, between 27°52' to 28°24'S and 32°21' to 32°34'E. The system has a surface area of approximately 350 km<sup>2</sup> (Taylor et al. 2006), with a perimeter of approximately 347 km at low water and depth of 0.9 m (Cyrus et al. 2011). It is subdivided into three lake basins, viz. False Bay, North and South lakes, which communicate with the mouth via a narrow channel known as “The Narrows” (Figure 1).

The first gastropod records from the St Lucia system date back to 1924, with specimens deposited in the KwaZulu-Natal Museum (NMSA), in Pietermaritzburg, ever since. Further collections were later undertaken during the two surveys of the University of Cape Town, in 1948–1949 and 1964–1965. Specimens collected during these surveys are currently deposited at the Iziko South African Museum (ISAM), in Cape Town. In 1982–1983, a dedicated collecting survey was undertaken throughout the lake system by the provincial conservation authority, the Natal Parks Board (NPB). The same authority, renamed Ezemvelo KwaZulu-Natal Wildlife (EKZNW), completed another similar survey during 2005, at the peak of the most recent drought. A number of publications containing gastropod records have also been published since 1954, mainly by researchers operating at the universities of KwaZulu-Natal, Zululand,



**Figure 1.** Map of the St Lucia estuarine lake, with position of main collection sites used in the study. Adapted from Peer et al. (2014).

Rhodes and Cape Town (e.g. Day et al. 1954; Millard and Broekhuysen 1970; Boltz 1975; Pillay and Perissinotto 2008, 2013; MacKay et al. 2010). Finally, a dedicated survey during 2012 and 2013 was conducted as part of this study, in order to establish the current status of gastropod diversity within the system.

## **Museum and literature data**

Specimens and data of gastropods collected at St Lucia in past surveys were obtained from the KwaZulu-Natal Museum in Pietermaritzburg and the Iziko South African Museum in Cape Town. Particularly rich collections from St Lucia were undertaken by the NMSA in 1987. Reference to specimens from either museum are here complemented with their accession numbers. Literature involving past macrobenthic surveys undertaken in the St Lucia Estuary (e.g. Day et al. 1954; Millard and Broekhuysen 1970; Bolt 1975; Weerts 1993; Pillay and Perissinotto 2008; MacKay et al. 2010) were reviewed to obtain information about gastropod diversity and the environmental conditions in which species were collected. Information such as synonyms, common name, size distribution and other records about the various species were used to annotate the illustrated checklist.

## **Historical surveys**

Both NPB 1982–1983 and EKZNW 2005 collecting surveys were conducted at the onset of extreme drought conditions, when organisms within the estuarine lake were experiencing mass kills in response to hypersaline conditions and lake fragmentation/desiccation. Dead gastropods were mainly found washed up along the shorelines of St Lucia. The Natal Parks Board surveyed the banks of the whole lake from December 1982 to April 1983, collecting freshly dead specimens. These were later identified to species level by the late R.N. Kilburn. Ezemvelo KZN Wildlife surveyed the St Lucia banks in 2005, taking samples at fixed points along a number of transects in both South and North lakes (Figure 1). On this occasion, gastropods were identified by D. Herbert and R.N. Kilburn. In all cases, no specialized equipment was used and specimens were collected by hand at the surface or within the sediment by using spades and/or mechanical grabs.

## **2012–2013 survey**

Two surveys were conducted in March and July 2012. The survey in March was conducted at Fani's Island, St Lucia Mouth, Hell's Gate, Makakatana, Lister's Point, the Bridge over the Narrows and along a transect from Catalina Bay to Charter's Creek. The Back Channel, Shark Basin and Mpathe Mouth were also visited (Figure 1, Table 1). Macrobenthic samples were taken using a Zabalocki-type Eckman grab with a sampling area of 0.0236 m<sup>2</sup> and depth of 15 cm. Each sample was made up of three grabs, with three replicate samples taken at each site. Replicate samples were emptied into 20 L buckets and water was added in each sample. Each sample was stirred vigorously to suspend benthic organisms and the supernatant was passed through a 500 µm sieve. This

**Table 1.** List of localities mentioned in the study with their coordinates and key biophysical characteristics.

Region	Site name	Latitude	Longitude	Comments
False Bay	Lister's Point	-27.9697	32.3847	Muddy and fossiliferous coquina substrate; sparse macrophyte cover.
	Mpophomeni Stream	-27.9519	32.3771	Brackish forest stream with muddy sand substrate.
North Lake	Hell's Gate	-28.0118	32.4438	Muddy and fossiliferous coquina substrate; sparse macrophyte cover.
South Lake	Catalina Bay	-28.2237	32.4839	Limestone flat, muddy sand substrate; freshwater seepage from dune aquifers; exhibiting sedges such as <i>Phragmites</i> , <i>Juncus</i> and <i>Schoenoplectus</i> .
	Charter's Creek	-28.1994	32.4162	Muddy sand substrate; submerged macrophytes such as <i>Ruppia</i> sp. frequently recorded.
	Fani's Island	-28.1091	32.4341	Muddy sand substrate; historic presence of <i>Zostera capensis</i> from this site southwards.
	Makakatana	-28.2364	32.4199	Sandy substrate, brackish conditions and relatively low turbidity; submerged macrophytes such as <i>Ruppia cirrhosa</i> frequently recorded.
Narrows	Mpate River Mouth	-28.2945	32.4012	Muddy substrate, fringed by intertidal reeds <i>Phragmites australis</i> and mangroves.
	St Lucia Bridge	-28.3689	32.4096	Muddy substrate, fringed by mangroves <i>Avicennia marina</i> and <i>Bruguiera gymnorhiza</i> and some <i>Hibiscus tiliaceus</i> ; submerged macrophytes such as <i>Stuckenia pectinata</i> generally present.
St Lucia Mouth	Honeymoon Bend	-28.3871	32.4032	Tidal influence; muddy substrate, fringed by
	Mfolozi Back Channel	-28.3922	32.4094	<i>Phragmites</i> reeds and mangroves <i>Avicennia marina</i> and <i>Bruguiera gymnorhiza</i> .
	Mfolozi Link Canal	-28.3945	32.3943	
	Mfolozi-St Lucia Beach Spillway	-28.3892	32.4238	Sandy substrate; recent shallow link between St Lucia Mouth and Mfolozi River; influenced by tide.
	Shark Basin	-28.3831	32.4203	Sandy mud substrate; fringed by reeds and sedges as well as mangroves; influenced by tides and freshwater draining from adjacent areas to the north.

procedure was repeated five times for each replicate sample. Material that was retained on the sieve was emptied into plastic jars. Sediments that were left in the bucket were washed through a 2 mm sieve. Samples were preserved in 4% phloxin-stained formalin. Qualitative samples were also collected with a D-net. At each site, the net was pushed over the sediment surface for a distance of approximately 5 m. At least one D-net sample was collected from each site. Macrofauna retained on the D-net were emptied into plastic jars and 4% phloxin-stained formalin was added. Both sampling methods (grab and D-net) were used at Fani's Island, St Lucia Mouth, Hell's Gate, Makakatana and along a transect from Catalina Bay to Charter's Creek, while only D-net samples were collected from the Bridge and the Back Channel (Figure 1, Table 1).

The survey also included the manual collection of dead gastropod shells along the shoreline of the lake, within close proximity of the sampling stations. Further collections on an opportunistic basis were undertaken throughout 2013. In the laboratory, each

sample was emptied into a sorting tray and gastropods were separated and identified with the aid of specialized literature and, where necessary, external taxonomy experts. Suitable specimens and shells were photographed in a standardized way, so as to show morphological characteristics that aid in their identification in an illustrated checklist.

## Results

A total of 20 families and 37 species of gastropods have been found in the St Lucia estuarine system since 1924, with half of the species not previously recorded in the literature. These include *Afrolittorina africana*, *Alaba pinnae*, *Bulinus natalensis*, *Cerithium dialeucum*, *Ergalatax heptagonalis*, *Jujubinus suarezensis*, *Littoraria coccinea glabrata*, *L. intermedia*, *L. pallescens*, *L. subvittata*, *Lymnaea natalensis*, *Melampus parvulus*, *Murex brevispinus*, *Neritina gagates*, *N. natalensis*, *Phalium areola*, *Pterotrachea* cf. *hippocampus* and *Purpura bufo* (Table 2, Appendix).

The earliest records of gastropod specimens collected in the St Lucia system are from the KwaZulu-Natal Museum (NMSA) and date back as far as 1924. Seventeen species originating from St Lucia are currently deposited in its collections, mostly obtained during dedicated surveys conducted in 1987 (Table 2). Of these, 11 are among the new records reported here, as they were never included in previous reports or publications on Lake St Lucia. Another two of the new records were collected during surveys undertaken by the provincial conservation authority, EKZNW, while the other six were only revealed during the latest survey of 2012–2013. Although three among the latter were only recorded as dead shells (i.e. *Cerithium dialeucum*, *Murex brevispinus*, *Purpura bufo*), they were found in sufficient number and deep enough in the upper reaches of the estuarine lake to suggest with reasonable confidence they were once established within the system, rather than accidentally introduced there.

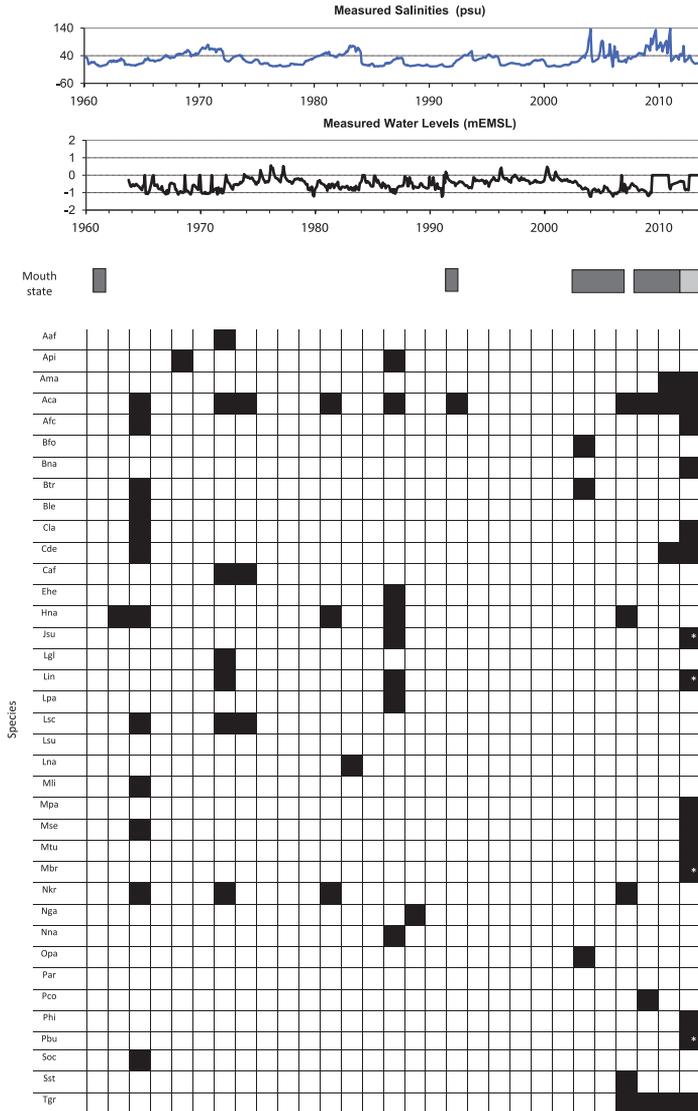
Only 12 species were found alive within the system during the recent 2012–2013 survey. These include *Aplexa marmorata*, *Assimineea* cf. *capensis*, *Assimineidae* sp., *Bulinus natalensis*, *Cassidula labrella*, *Cerithidea decollata*, *Lymnaea natalensis*, *Melampus parvulus*, *M. semiaratus*, *Melanooides tuberculata*, *Pterotrachea* cf. *hippocampus* and *Tarebia granifera* (Figure 2). Among them, five are freshwater dwellers (*A. marmorata*, *B. natalensis*, *L. natalensis*, *M. tuberculata* and *T. granifera*) that have entered the system only recently, in response to the establishment of a new wet phase after the prolonged drought of 2002–2011. *Melanooides tuberculata* was found in high abundance at Shark Basin, at shallow depths in permanently submerged channels, as well as in a tributary stream (Mpophomeni) at False Bay (Tables 1–2, Appendix). Two of these freshwater species, i.e. *A. marmorata* and *T. granifera*, are actually alien invasives that have spread from colonies initially restricted to the seepage points around Catalina Bay (Appendix). *T. granifera* was recorded in high abundance at Makakatana in March 2012, spreading subsequently throughout the Narrows to the south and at least as far as Charter's Creek to the north-west (Figure 1, Table 1).

**Table 2.** Gastropod species originally recorded from the St Lucia estuarine lake. Reference codes: B: Bolt (1975); BKJC: Blaber, Kure, Jackson and Cyrus (1983); DMB: Day, Millard and Broekhuysen (1954); EKW: Ezemvelo KwaZulu-Natal Wildlife Survey Record (2005); ISAM: Iziko South African Museum Collection Record (Accession No.); NMSA: KwaZulu-Natal Museum Collection Record (Accession No.); MB: Millard and Broekhuysen (1970); MCR: MacKay, Cynus and Russell (2010); MPAl: Miranda, Perissinotto and Appleton (2010); MPA2: Miranda, Perissinotto and Appleton (2011); MET: Miranda et al. (2014); NMPO: Nelson Miranda Personal Observation (2013); NPB: Natal Parks Board Survey Record (1982/83, 1988); OF: Owen and Forbes (1997); PMRP: Recorded During This Study (2014); PP: Pillay and Perissinotto (2008); RMP: Raw, Miranda and Perissinotto (2013); V: Vrdoljak (2004); W: Weerts (1993). The classification scheme follows Bouchet and Rocroi (2005). (\* = New record for Lake St Lucia).

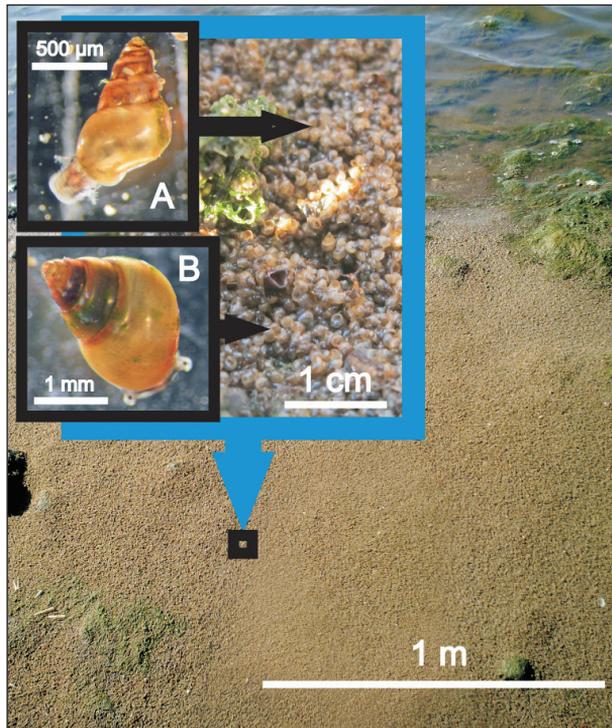
Species (original record)	Current valid name	Record year(s)	Reference(s)
<b>TROCHIDAE</b>			
<i>Jujubinus suarezensis</i> (P. Fischer, 1878)	Idem*	1987, Jul–Nov 2012	NMSA (E2145), PMRP 2014
<b>NERITIDAE</b>			
<i>Neritina gagates</i> Lamarck, 1822	Idem*	1988	NPB 1988
<i>Neritina natalensis</i> Reeve, 1855	Idem*	1924, 1987	NMSA (B7378, D5947)
<b>THIARIDAE</b>			
<i>Melanoides tuberculata</i> (Müller, 1774)	Idem	Jul 2012–Nov 2013	RMP 2013
<i>Tarebia granifera</i> (Lamarck, 1822)	Idem	2006, Apr–Jul 2007, Feb 2007–Mar 2011, 2010	PP 2008, MPA 2010, MPA 2011, NMSA (W8287)
<b>CERTHIDAE</b>			
<i>Cerithium diluacum</i> Philippi, 1849	Idem*	Nov 2013	PMRP 2014
<b>LITIOPIIDAE</b>			
<i>Alaba pinnae</i> (Krauss, 1848)	Idem*	1967, 1987	NMSA (8083, E2164)
<b>POTAMIDIDAE</b>			
<i>Cerithidea decollata</i> (Linnaeus, 1767)	Idem	Jul 1948–Jul 1951, Jul 1964 & Jan 1965, 2011–2013	NMSA (A6384), ISAM (STL60), DMB 1954, MB 1970, PMRP 2014
<b>LITTORINIDAE</b>			
<i>Afrolittorina africana</i> (Krauss in Philippi, 1847)	Idem*	1971	NMSA (A1635)
<i>Littoraria glabrata</i> (Philippi, 1846)	<i>Littoraria coccinea glabrata</i> (Philippi, 1846)*	1971	NMSA (A1636)
<i>Littoraria intermedia</i> (Philippi, 1846)	Idem*	1971, 1987, Mar 2012	NMSA (A1634, D9983, E460), PMRP 2014
<i>Littoraria pallens</i> (Philippi, 1846)	Idem*	1987	NMSA (D9980)
<i>Littoraria subvittata</i> (Reid, 1986)	Idem*	Not reported ( <i>sine die</i> )	NMSA (7128)

Species (original record)	Current valid name	Record year(s)	Reference(s)
<i>Litonotaria scabra</i> (Linnaeus, 1758)	Idem	Jul 1948–Jul 1951, Jul 1964 & Jan 1965, Jan–Jul 1972 & Jan 1973	ISAM (STL50B), DMB 1954, MB 1970, B 1975
<b>PTEROTRACHEIDAE</b>			
<i>Pterotrachea</i> cf. <i>hippocampus</i> Philippi, 1836	Idem*	Aug 2013	PMRP 2014
<b>ASSIMINEIDAE</b>			
<i>Assiminea</i> sp. Fleming, 1828	Probably comprising both <i>Assiminea</i> cf. <i>capensis</i> and <i>Assiminea</i> sp.	Jul 1948–Jul 1951, Aug 1981–Jul 1982, Oct 2005	DMB 1954, BKJC 1983, PP 2008
<i>Assiminea bifasciata</i> Nevill, 1880	<i>Assiminea</i> cf. <i>capensis</i> Bartsch, 1915	Jul 1964 & Jan 1965, Jan–Jul 1972 & Jan 1973	ISAM (STL104G), MB 1970, B 1975
<i>Assiminea durbanensis</i>	<i>Assiminea</i> sp. or “ <i>Assiminea</i> ” aff. <i>capensis</i> (Sowerby, 1892)*	Jan & May 1992	W 1993
<i>Assiminea</i> cf. <i>ovata</i> (Krauss, 1848)	<i>Assiminea</i> cf. <i>capensis</i> Bartsch, 1915	2007–2009	MPA2 2011
<i>Assiminea</i> cf. <i>capensis</i> Bartsch, 1915	Idem	Jan 1927, 1987, 2011–2013	NMSA (1987), RMP 2013, WPPC 2014
<i>Coriandria durbanensis</i> (Tomlin, 1916)	<i>Assiminea</i> sp. or “ <i>Assiminea</i> ” aff. <i>capensis</i> (Sowerby, 1892)*	Jul 1948–Jul 1951, Jul 2012–May 2013	ISAM (STL18A), DMB 1954, RMP 2013, MET 2014
<i>Syncaea</i> sp. Gray, 1821	<i>Nomen nudum</i> ; probably confused with <i>Assiminea</i> sp.	Jul 1948, Jul 1964 & Jan 1965	ISAM (STL64A), MB 1970
<b>CASSIDAE</b>			
<i>Phalium areola</i> (Linnaeus, 1758)	Idem*	Not reported ( <i>sine die</i> )	NMSA (B4786)
<b>NASSARIIDAE</b>			
<i>Nassa kraussiana</i> (Dunker, 1846)	<i>Nassaritis kraussianus</i> (Dunker, 1846)	Jul 1964 & Jan 1965	MB 1970
<i>Nassaritis kraussianus</i> (Dunker, 1846)	Idem	Jul 1948–Jul 1951, Feb 1971, Dec 1972, Jan–Jul 1972 & Jan 1973, Dec 1981, Aut 2005 & Spr 2006	NMSA (B5533, W1752, 9144), ISAM (STL6C), DMB 1954, B 1975, MCR 2010
<b>MURICIDAE</b>			
<i>Ergalutax heptagonalis</i> (Reeve, 1846)	Idem*	1987	NMSA (D5772)
<i>Murex brevispinus</i> Lamarck, 1822	Idem*	Jul–Nov 2012	PMRP 2014
<i>Purpura bufo</i> Lamarck, 1822	Idem*	Jul 2013	PMRP 2014
<b>HAMINOEIDAE</b>			
<i>Cylichna africana</i> Bartsch, 1915	<i>Haminoea natalensis</i> (Krauss, 1848) or <i>Cylichna tubulosa</i> Gould, 1859	Jul 1972 & Jan 1973	B 1975
<i>Haminoea gracilis</i> (Sowerby, III 1897)	<i>Haminoea natalensis</i> (Krauss, 1848)	Jul 1964 & Jan 1965	MB 1970

Species (original record)	Current valid name	Record year(s)	Reference(s)
<i>Haminooea natalensis</i> (Krauss, 1848)	Idem	Jul 1948–Jul 1951, Dec 1962, Apr 1963, Apr 1965, Jun 1987, 2006, 2007	NMSA (A2362, A2228, D9971, E478), ISAM (STL6B), DMB 1954, PP 2008, MPA2 2011
<i>Haminooea petersi</i> (Martens, 1879)	<i>Haminooea natalensis</i> (Krauss, 1848)	Aug 1981–Jul 1982	BKJC 1983
<b>APLYSIIDAE</b>			
<i>Barnardalecia cirrhifera</i> (Quoy & Gaimard, 1832)	<i>Bursatella leachii</i> Blainville, 1817	Jul 1948–Jul 1951	DMB 1954
<i>Notarchus cirrhifera</i> (Quoy & Gaimard, 1832)	<i>Bursatella leachii</i> Blainville, 1817	Jul 1964 & Jan 1965	MB 1970
<i>Silicocheilus striatus</i> (Quoy & Gaimard, 1832)	Idem	May 2007	MPA2 2011
<b>SIPHONARIIDAE</b>			
<i>Siphonaria oculus</i> Krauss, 1848	Idem	Jul 1948–Jul 1951, Jul 1964 & Jan 1965	ISAM (STL43A), DMB 1954, MB 1970
<b>PLANORBIDAE</b>			
<i>Bulinus natalensis</i> (Krauss in Küster, 1841)	Idem*	Nov. 2012	PMRP 2014
<i>Bulinus tropicus</i> (Krauss, 1848)	Idem	Jul 1948, Jul 1964 & Jan 1965, May 2002–Apr 2003	ISAM (STL104G), DMB 1954, MB 1970, PM 2013; YMT May 2002–Apr 2003
<i>Bulinus forskalii</i> (Ehrenberg, 1831)	Idem	May 2002–Apr 2003	V 2004
<b>PHYSIDAE</b>			
<i>Aplexa marmorata</i> (Guilding, 1828)	Idem	Aug 2009, 2009–2010	MPA1 2010, MPA2 2011
<b>LYMNAEIDAE</b>			
<i>Lymnaea natalensis</i> (Krauss, 1848)	Idem*	1982–1983	NPB 1982–1983
<i>Pseudosuccinea columella</i> (Say, 1817)	Idem	Aug 2009	MPA1 2010
<b>SUCCINEIDAE</b>			
<i>Oxyloma patentesissima</i> (Menke in Pfeiffer, 1853)	Idem	May 2002–Apr 2003	V 2004
<b>ELLOBIIDAE</b>			
<i>Cassidula labrella</i> (Deshayes, 1830)	Idem	Jul 1964 & Jan 1965	ISAM (STL237M), MB 1970, PMRP 2014
<i>Melampus ordinaris</i> Melvill & Ponsorby, 1901	<i>Melampus lividus</i> (Deshayes, 1830)	Jul 1964 & Jan 1965	ISAM (STL237Y), MB 1970
<i>Melampus parvulus</i> Pfeiffer, 1856	Idem*	2012–2013	PMRP 2014
<i>Melampus semianatus</i> Connolly, 1912	Idem	Jul 1964 & Jan 1965, Mar 2012	ISAM (STL237N), MB 1970



**Figure 2.** Records of gastropod species collected at Lake St Lucia in relation to changes in salinity, water levels and mouth state during the period 1960-present. Dark gray bar indicates closed mouth, light gray bar indicates intermittent connection with the ocean. No continuous physico-chemical measurements are available for the period prior to 1960. Species codes: Aaf: *Afrolittorina africana*; Api: *Alaba pinnae*; Ama: *Aplexa marmorata*; Aca: *Assimineae cf. capensis*; Afc: *Assimineidae sp. ("Assimineae" aff. capensis)*; Bfo: *Bulinus forskalii*; Bna: *Bulinus natalensis*; Btr: *Bulinus tropicus*; Ble: *Bursatella leachii*; Cla: *Cassidula labrella*; Cde: *Cerithidea decollata*; Cdi: *Cerithium dialaecum*; Ehe: *Ergalatax heptagonalis*; Hna: *Haminoea natalensis*; Jsu: *Jujubinus suarezensis*; Lgl: *Littoraria coccinea glabrata*; Lin: *Littoraria intermedia*; Lpa: *Littoraria pallescens*; Lsc: *Littoraria scabra*; Lsu: *Littoraria subvittata*; Lna: *Lymnaea natalensis*; Mli: *Melampus lividus*; Mpa: *Melampus parvulus*; Mse: *Melampus semiaratus*; Mtu: *Melanoides tuberculata*; Mbr: *Murex brevispinus*; Nkr: *Nassarius kraussianus*; Nga: *Neritina gagates*; Nna: *Neritina natalensis*; Opa: *Oxyloma patentissima*; Par: *Phalium areola*; Pco: *Pseudosuccinea columella*; Phi: *Pterotrachea cf. hippocampus*; Pbu: *Purpura bufo*; Soc: *Siphonaria oculus*; Sst: *Stylocheilus striatus*; Tgr: *Tarebia granifera*.



**Figure 3.** Assimineidae sp. (A) and *Assiminea* cf. *capensis* (B): thick layer of snails washed up on the shoreline of Lister’s Point at False Bay in July 2012 (Photo: Nelson AF Miranda).

*Cassidula labrella*, *Cerithidea decollata*, *Melampus parvulus* and *M. semiaratus* are the only mangrove species that have been able to survive within the system, despite the closed mouth conditions that have prevailed since 2002. *Cerithidea decollata* was the only one among them to be found in abundance at all mangrove sites, including the St Lucia Bridge, Back Channel, Honeymoon Bend (Narrows) and Shark Basin near the St Lucia Mouth (Figure 1, Table 1). On the other hand, *C. labrella*, *M. parvulus* and *M. semiaratus* were only found in the mangroves at Shark Basin and in very low numbers, on shaded mud surfaces and under fallen wood.

Of the typical estuarine species recorded in all surveys undertaken in the past in Lake St Lucia, only *Assiminea* cf. *capensis* and Assimineidae sp. persisted through the latest survey (Miranda et al. 2014). Large aggregations of *A. cf. capensis* and Assimineidae sp. were found in various areas of the estuarine system, with the former generally preferring salinities below 30 and the latter dominating under hypersaline conditions, mainly at Lister’s Point (False Bay). In July 2012, accumulations of hundreds of thousands of live individuals, mainly belonging to Assimineidae sp., were observed along the shoreline of Lister’s Point, apparently washed up by wind-driven wave motion (Figure 3). Similar aggregations, but this time dominated by *A. cf. capensis*, were observed the following year, in May 2013, in the bay just south of Lister’s Point, fol-



**Figure 4.** *Haminoea natalensis*: Aggregation of egg masses spawned during September 2006 in the shallows of Catalina Bay, on the Eastern Shores of South Lake (Photo: Lynette Clennell).

lowing the onset of a wet cycle with flooding and consequent drop in salinity to about 15–20 throughout False Bay. The oceanic pelagic heteropod *Pterotrachea* cf. *hippocampus* was only recorded on one occasion in August 2013, while netting zooplankton in the beach spillway connecting the Mfolozi to the St Lucia Mouth.

Species that were not found alive during the 2012–2013 survey, but have been previously documented as dominant within the system include *Nassarius kraussianus* and *Haminoea natalensis*. Both were only recorded as dead shells during 2012–2013, but in very large numbers and throughout the lake basins, particularly at Charter’s Creek, Catalina Bay and Fani’s Island (South Lake) (Figure 1, Table 1). While the last live record of *N. kraussianus* during the recent closed mouth phase of the estuary dates back to the spring of 2006 (MacKay et al. 2010), *H. natalensis* was found alive in large abundance at least until 2011. In the South Lake, at Charter’s Creek and Catalina Bay dense aggregations of freshly-spawned egg masses were observed in the spring of 2006 (Figure 4).

Among the mangrove dwellers that were present in the past but have recently disappeared entirely from the system are all the *Littoraria* species, i.e. *L. coccinea glabrata*, *L. intermedia*, *L. pallescens*, *L. subvittata* and *L. scabra* (Table 2, Figure 2). Although the estuarine lake has experienced a large freshwater inflow since late 2011, several

freshwater species that were previously found within the system were not recorded alive in 2012–2013. These include both *Neritina* species, i.e. *N. gagates* and *N. natalensis*, as well as *Bulinus tropicus*, *B. forskalii*, *Pseudosuccinea columella* and *Oxyloma patentissima* (Figure 2, Appendix).

Typical estuarine and/or coastal marine species that are also among the new records may have entered the system only on sporadic occasions and/or for short periods of time under open mouth conditions. They include *Afrolittorina africana*, *Alaba pinnae*, *Ergalatax heptagonalis* and *Phalium areola*. All of them are represented in past collections from the KwaZulu-Natal Museum (Table 2). The common coffee-bean snail *Melampus lividus*, the estuarine limpet *Siphonaria oculus* and the opisthobranch *Bursatella leachii* were already reported in the earliest surveys of the University of Cape Town (Day et al. 1954; Millard and Broekhuysen 1970) (Table 2, Figure 2, Appendix). A second opisthobranch species, *Stylocheilus striatus*, was only recorded at Catalina Bay for a few months, immediately after the seaward mouth breach of March 2007. Finally, coastal marine species that were clearly once established in the northern lakes and have only been recorded in the latest survey from dead shells include whelks such as *Murex brevispinus* and *Purpura bufo*, and the cerithiid *Cerithium dialeucum* (Table 2, Appendix).

## Discussion

### Gastropod diversity and hydrological phases

Major climatic events and hydrodynamic processes control the gastropod species richness and abundance in the St Lucia estuarine lake (Figure 2). The highest diversity reported so far coincides with the period Jul 1964 – Jan 1965, when the second survey by the University of Cape Town (UCT) was conducted on the system. On that occasion, 12 gastropod species were recorded at a time when the estuarine lake was under tidal influence, with a normal salinity gradient decreasing from the estuary basin to the northern lakes (Millard and Broekhuysen 1970). Other major surveys undertaken by UCT in 1948–1951 and by NMSA in 1987 resulted in total records of 7 and 8 species, respectively (Day et al. 1954; Figure 2). These were periods characterized respectively by the first hypersaline event recorded in the system and a flood peak flow occurrence (Stretch et al. 2013).

During the last decade, St Lucia has undergone some of the most dramatic shifts ever recorded in the region. These have caused an unprecedented crisis and triggered a burst of fresh research activity on the system. It is thus not surprising that of the total 37 species of gastropod recorded within the estuarine lake, 19 are new records arising from the recent escalation in analyses and collecting efforts. During the latest dedicated gastropod survey, undertaken between Jan 2012 and Nov 2013, a total of 15 species were recorded, with only 12 found still alive and four in reasonable abundance, even if intermittently. Among the latter group, two are actually alien invasive species, i.e. *Tarebia granifera* and *Aplexa marmorata* (Figure 2).

## Response to recent dry and wet phases

In 2002, a sand berm closed off the St Lucia Estuary from the ocean, leading to a prolonged period of mouth closure, which still persists currently. The mouth was breached from the seaward side for a brief period of six months, between March and August 2007, by a combination of extreme events linked to Cyclone Gamede (Whitfield and Taylor 2009). Between 2002 and 2011, prolonged closure and low rainfall resulted in frequent periods of hypersaline conditions in the northern lakes, with complete desiccation of some areas at times (Perissinotto et al. 2013). These events led to the virtual disappearance of the entire gastropod community, with the exception of few mangrove dwellers and the most tolerant estuarine species, namely *Assimineea* cf. *capensis*, *Assimineidae* sp. and *Haminoea natalensis*. These were actually able to thrive, as little competition for resources remained at the onset of the harsh conditions (Figures 2-4). Alien invasive species, such as *Tarebia granifera* and *Aplexa marmorata*, were also able to take advantage of this situation and occupy vacant habitats and under-utilized resources in freshwater seepage areas.

Since the end of 2011, the system has entered a wet phase, with above average rainfall leading to occasional flooding and the prevalence of oligo- to polyhaline conditions throughout the extent of the system. This was compounded by the excavation of a beach spillway in July 2012, which has since contributed substantial freshwater inflow from the Mfolozi River into the St Lucia system and also partial exchange of water with the open ocean (Nel 2014, van Elden et al. in press). These changes have led to the appearance of a number of new gastropod species of brackish to freshwater origin, including *Bulinus natalensis*, *Cassidula labrella*, *Melampus parvulus*, *M. semiaratus* and *Melanooides tuberculata* (Figure 2). While the presence of the heteropod *Pterotrachea* cf. *hippocampus* in recent plankton collections clearly indicates marine penetration into the St Lucia, although the beach spillway connection to the Mfolozi mouth has failed so far to result in significant recruitment of typical coastal gastropod species from the ocean.

## Historical trends

Historical collections and surveys have, however, recorded numerous species of euryhaline marine and estuarine species, even in the uppermost reaches of the estuarine lake. For instance, the tick shell *Nassarius kraussianus* is present in all museum collections from St Lucia and has been recorded as abundant in all previous studies in the area (Table 2, Figure 2). Despite the numerous dead shells retrieved during the past few years throughout the system, it has not been found alive since 2006 (MacKay et al. 2010). *Nassarius kraussianus* is known as being generally associated with *Zostera* beds (Marais and Seccombe 2010) and its recent disappearance from the system has coincided with the extinction of the *Zostera* beds inside the lake basins after 2005, following the closure of the mouth in 2002 (Adams et al. 2013). Similarly dependent on marine grasses are typical estuarine species, such as *Alaba pinnae*, which is generally attached to *Zostera*

blades (Kilburn and Rippey 1982), and the top-shell *Jujubinus suarezensis* and the whelk *Murex brevispinus*, both tidal mudflat dwellers living among submerged seagrasses (e.g. *Thalassodendron* in Mozambique, Kilburn and Rippey 1982). Only old specimens of these species were found repositied in the KwaZulu-Natal Museum (Table 2) and only dead shells were retrieved in the latest survey. Therefore, it seems most likely that these too may have died out shortly after the closure of the St Lucia mouth. Other mouth closure episodes have been recorded in the past, e.g. 1959-1961 and 1992-1993 (Figure 2), however they never persisted uninterruptedly for such a long period of time and never created conditions severe enough to cause the complete extinction of the *Zostera* beds from the system (Millard and Broekhuysen 1970; Adams et al. 2013).

Apart from causing the disappearance of marine grasses, prolonged mouth closure would also lead to the eventual death of barnacle and oyster beds (Nel et al. 2012), on which several species of gastropods depend for their food. For instance, the two whelks retrieved at False Bay and Charter's Creek (South Lake) as dead shells in recent collections, *Ergalatax heptagonalis* and *Purpura bufo*, are known to be associated with barnacles and most probably depended on the dense barnacle beds that proliferated on the Cretaceous rock platforms prior to mouth closure (Kilburn and Rippey 1982; Marais and Seccombe 2010).

### Mangrove communities

Among the 20 species not previously recorded from the St Lucia estuarine lake are typical mangrove dwellers, such as *Littoraria intermedia*, *L. pallescens*, *L. subvittata*, *L. scabra* and *Melampus parvulus*. St Lucia mangroves have undergone significant deterioration since the mouth closed in 2002, as persistent low salinity in the Narrows and near the mouth has favoured the development of reeds at the expense of mangrove vegetation (Adams et al. 2013). This has inevitably impacted on the once rich mangrove-dependent gastropod community (Day et al. 1954; Millard and Broekhuysen 1970). Indeed, of all the typical mangrove species reported here, only the resilient *Cerithidea decollata* was found in reasonable numbers during the latest survey. The other three species still present, *M. semiaratus*, *M. parvulus* and *Cassidula labrella*, occurred sporadically in very low numbers and only near the St Lucia Mouth. Surprisingly, the giant mangrove whelk, *Terebralia palustris* was never recorded at St Lucia, despite having been reported as well-established and common both to the south (e.g. Richards Bay, Durban Bay) and to the north (Mgobezeleni, Kosi Bay) of this system, at least in the past (Macnae 1963; Berjak et al. 2011).

### Key and indicator species

Population explosions of the bubble shell *Haminoea natalensis* with its distinct egg masses were recorded seasonally until 2009 (Figures 2 and 4). The observed trend of

population explosions followed by high mortality and dwindling numbers is typical for opisthobranchs. Environmental conditions during the different seasons as well as the recruitment of *H. natalensis*, are the most important factors driving its population biology (Malaquias and Sprung 2005; Miranda et al. 2011). *Haminoea natalensis* has not been observed in St Lucia again after 2009. However, when favorable higher salinity conditions return, the species will probably again be found along the shores in shallow water, feeding on microphytobenthic mats (Miranda and Perissinotto 2012).

The taxonomy of assimineids, or sentinel snails, is poorly understood and currently under revision in South Africa. In the St Lucia Estuary, there are inconsistencies in the literature in terms of what species of *Assiminea* occur in the system. This is not surprising given the morphological and ecological similarities as well as spatial overlap between different assimineids. Earlier literature refers to *A. bifasciata* as the only species present in the system (Day et al. 1954; Millard and Broekhuysen 1970; Bolt 1975; Whitfield and Blaber 1978). Recent literature reports *A. ovata* (Miranda et al. 2011, Carrasco et al. 2012, Daly et al. 2012) and *A. globifera* (Taylor et al. 2006) and *A. durbanensis* (Weerts 1993) have also been reported from St Lucia. Three species of assimineids are listed by MacKay et al. (2010) in St Lucia, while Pillay and Perissinotto (2008) and Owen et al. (2010) make reference to *Assiminea* sp.. Millard and Broekhuysen (1970) reported the occurrence of *A. bifasciata* as well as *Syncera* sp. *Syncera* Gray, 1821 is *nomen nudum* and a synonym of *Assiminea* (Fukuda and Ponder 2003). The most recent genetic and morphological study conducted in the St Lucia Estuary has confirmed the existence of two species: *A. cf. capensis* and *Assimineidae* sp. ("*A.*" aff. *capensis* in Miranda et al. 2014). These two species exhibit patterns of spatial overlap that appear to vary depending on environmental parameters, particularly salinity. *Assimineidae* sp. is an assimineid in the broader sense, but belongs in an as yet unnamed genus and subfamily (Winston Ponder pers. comm.). Perhaps what Millard and Broekhuysen (1970) reported as *Syncera* sp. was in fact *Assimineidae* sp.. This false sentinel snail seems to prefer the more saline conditions in the northern parts of St Lucia and has been previously referred to as *Coriandria durbanensis* or *A. durbanensis* (Raw et al. 2013; Weerts 1993). It is clear that *A. cf. capensis* and *Assimineidae* sp. have been misidentified and confused in the past because of poor taxonomic knowledge and their morphological variability and similarities.

### **Alien invasive species**

Three of the five predominant alien invasive freshwater gastropods in South Africa have been recently recorded from St Lucia: *Aplexa marmorata*, *Pseudosuccinea columella* and *Tarebia granifera*. Previously, under hypersaline conditions these species were restricted to freshwater seepage areas on the Eastern Shores of the South Lake and along the Narrows (Miranda et al. 2010). However, the oligohaline conditions which currently persist following an increased volume of freshwater entering the system potentially favour the expansion of these species to new areas. This has already been observed with

*T. granifera*, which due to its unexpected high salinity tolerance (Miranda et al. 2010) has recently been recorded, albeit at low densities, from Charter's Creek and Makakata on the Western Shores of South Lake.

As the freshwater-dominated phase of St Lucia continues, the potential for alien invasive gastropods to enter and spread within the system increases. The consequences of these expansions vary depending on the species. *Pseudosuccinea columella* in South Africa is susceptible to the liver flukes (*Fasciola* spp.) which infect livestock, although it has not been confirmed as an intermediate host (Appleton 2003). *Aplexa marmorata* is widespread in KwaZulu-Natal, however its potential impacts are largely unknown. Similarly, although not reported from St Lucia, is *Physa acuta* (de Kock and Wolmarans 2007) and *Helisoma duryi* (Appleton 2003). The latter has however been recorded from artificial environments in the region. The greatest potential impact is that of *Tarebia granifera*, which displaces native gastropods and attains very large densities (Miranda et al. 2011; Raw et al. 2013). As *T. granifera* is so successful, this species poses a threat to native malacofauna, such as the *Bulinus* species group, which would be expected to expand their range during a freshwater-dominated phase.

In addition to the threats from freshwater alien invasive species, estuaries are also threatened by the invasion of marine species from coastal sources (Nehring 2006). The majority of marine alien invasive species are introduced through ship fouling or ballast water (Picker and Griffiths 2011) and the proximity of an estuary to intensive international shipping increases its risk to introduced species (Nehring 2006). For St Lucia, the largest threat comes from the shipping activities at the industrial port of Richards Bay. Presently, there are no records of marine alien species in St Lucia due to the prolonged closure of the mouth to the Indian Ocean. The recent re-establishment of a connection through the beach spillway with the Mfolozi River may allow previously reported native marine species to re-enter the system, but also increase the risk of introduction of alien species. The continuous monitoring and assessment of potential impacts that these species may have on the ecosystem at large is necessary, given the significance of St Lucia as the largest estuarine lake in Africa and South Africa's first World Heritage Site.

## Conclusions

Throughout its history, the St Lucia estuarine lake has experienced drastic shifts in hydrological states, from extreme dry conditions accompanied by hypersalinity and desiccation, to floods followed by freshwater dominance. The state of the mouth has also varied from an extended open bay joined to the Mfolozi River to extreme constriction and prolonged closure. The latest period of closure has been unprecedented and virtually uninterrupted since 2002. Although the monitoring of gastropod diversity within the system has been erratic until recently, there are clear indications that higher diversity has coincided with periods when the estuarine lake was under tidal influence, with

a normal salinity gradient decreasing from the estuary basin to the northern lakes (e.g. 1964–1965). Drastic declines were observed when the system experienced hypersaline (e.g. 1948–1951) or flood conditions (e.g. 1987), with a closed mouth state compounding the problem by preventing any recruitment from the ocean. During the last decade, St Lucia has undergone some of the most dramatic shifts ever recorded in the region. Despite the intense, dedicated gastropod surveys undertaken in 2012–2013, only 12 species were found still alive, with four in reasonable abundance. Among these, unfortunately two are actually alien invasive species, i.e. *Tarebia granifera* and *Aplexa marmorata*, with the first spreading at alarming rates as low salinity conditions now prevail throughout the system.

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Note: The number in square brackets at the end of a reference corresponds to the in-text citations used in the Appendix.

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## Appendix

### Annotated and Illustrated Checklist of the Gastropod Molluscs of Lake St Lucia

#### Family: Trochidae

##### *Jujubinus suarezensis* (P. Fischer, 1878)

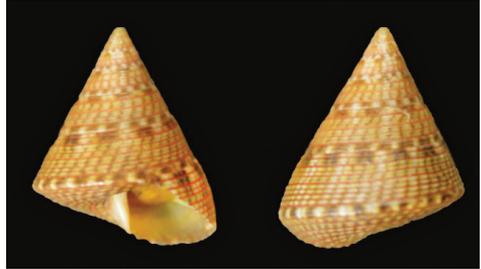
**Common name.** Square top –snail.

**Size.** Maximum shell height 12 mm<sup>(1)</sup>.

**Remarks.** Occurs on protected mudflats<sup>(1)</sup>.

**Distribution.** East African distribution including Madagascar. Common in Mozambique extending south to Durban in South Africa<sup>(1)</sup>.

**St Lucia records.** Not previously reported from St Lucia; collected in 1987 (NMSA). Only dead shells collected in 2012 from Fani's Island (South Lake).



*Jujubinus suarezensis* (P. Fisher, 1978)  
17 mm, Inhaca Island, Jul 1970  
RN Kilburn leg.

#### Family: Neritidae

##### *Neritina gagates* Lamarck, 1822

**Common name.** Brown nerite or Zebra nerite.

**Size.** Maximum shell height 22 mm<sup>(2)</sup>.

**Remarks.** Occurs on stones in streams that are tidally influenced<sup>(2)</sup>.

**Distribution.** Southeastern coast of Africa from Mozambique to Mzamba in the Eastern Cape Province of South Africa<sup>(3)</sup>. Also reported from the Comoro Islands, Madagascar and Seychelles<sup>(2)</sup>.

**St Lucia records.** Not previously reported from St Lucia; collected in 1988 from the St Lucia Mouth (NPB). Not found during the recent survey.



*Neritina gagates* Lamarck, 1822  
19 mm, Mhlanga Estuary, Feb 2013  
NAF Miranda leg.

***Neritina natalensis* Reeve, 1855**

**Common name.** Spotted nerite.

**Size.** Maximum shell height 20 mm<sup>(2)</sup>.

**Remarks.** Reportedly occurs within mangroves<sup>(2)</sup> and on *Phragmites* stems in estuaries.

**Distribution.** East African coast from Somalia extending south to the Umzimkulu River on the KwaZulu-Natal coast of South Africa<sup>(2)</sup>. Also reported from the Mtamvuna River<sup>(3)</sup>.

**St Lucia records.** Not previously reported from St Lucia; collected in 1924 and 1987 (NMSA) from False Bay. Not recorded in the recent survey.



*Neritina natalensis* Reeve, 1855  
23 mm, St Lucia False Bay, Oct 1924  
HWB Marley leg.

**Family: Thiaridae*****Melanooides tuberculata* (Müller, 1774)**

**Common name.** Red-rimmed melania.

**Size.** Maximum shell height 45 mm<sup>(3)</sup>.

**Remarks.** Predominantly parthenogenetic species<sup>(3)</sup> which inhabits fresh and brackish water<sup>(2)</sup>.

**Distribution.** Natural Indo-Pacific distribution includes much of Africa with a southern limit at Port Elizabeth<sup>(2)</sup> and extending east to southern Asia and northern Australia<sup>(3)</sup>. Introduced to regions of North America<sup>(4)</sup> and New Zealand<sup>(5)</sup>.

**St Lucia records.** Reported in 2012<sup>(6)</sup> from Shark Basin (St Lucia Mouth). Recently recorded from the Mpophomeni Stream (False Bay).



*Melanooides tuberculata* (Müller, 1774)  
23 mm, St Lucia False Bay, Feb 2013  
NAF Miranda leg.



*Melanooides tuberculata* (Müller, 1774)  
14 mm, St Lucia Mouth, Feb 2013  
NAF Miranda leg.

***Tarebia granifera* (Lamarck, 1822)**

**Common name.** Quilted melania<sup>(7)</sup>.

**Size.** Maximum shell height 29.5 mm<sup>(7)</sup>.

**Remarks.** Alien invasive species first recorded in northern KwaZulu-Natal in 1999<sup>(8)</sup>. Indigenous to southeastern Asia<sup>(7)</sup> but has also been introduced to the Caribbean<sup>(9)</sup>, the Americas<sup>(4,10)</sup> and Israel<sup>(11)</sup>.

**St Lucia records.** Reported from St Lucia in 2006<sup>(12)</sup>, 2007<sup>(13)</sup> and between 2010 and 2013<sup>(6,13,14)</sup>. Reported in the recent survey from the mangroves at the St Lucia Bridge (Narrows) as well as Makakatana, Catalina Bay and Charter's Creek (South Lake).



*Tarebia granifera* (Lamarck, 1822)  
21 mm, St Lucia Catalina Bay, Feb 2010  
NAF Miranda leg.

**Family: Cerithiidae*****Cerithium dialeucum* Philippi, 1849**

**Common name.** White-studded cerith.

**Size.** Up to 30.5 mm.

**Remarks.** Dead shells collected at Lister's Point in March 2012.

**Distribution.** Indo-Pacific distribution with southwestern reports from Mozambique<sup>(15)</sup>, Madagascar<sup>(16)</sup> and Mauritius<sup>(17)</sup>. South African distribution restricted to coastline from Kosi Bay to Durban<sup>(18)</sup>.

**St Lucia records.** Not previously reported.



*Cerithium dialeucum* Philippi, 1849  
30.5 mm, St Lucia False Bay, Mar 2012  
R Perissinotto leg.

**Family: Litiopidae*****Alaba pinnae* (Krauss, 1848)**

**Common name.** Pinnated litiopid.

**Size.** Maximum shell height 11 mm<sup>(1)</sup>.

**Remarks.** Common estuarine species which varies in plumpness<sup>(1)</sup>.

**Distribution.** Still Bay to Zululand coast<sup>(1)</sup>.

**St Lucia records.** Not previously reported from St Lucia; collected at Charter's Creek (South Lake) in 1967 and 1987 respectively (NMSA). Not found in the recent survey.



*Alaba pinnae* (Krauss, 1848)  
9.3 mm, St Lucia Charter's Creek, 1967  
R Kilburn leg.

**Family: Potamididae*****Cerithidea decollata* (Linnaeus, 1767)**

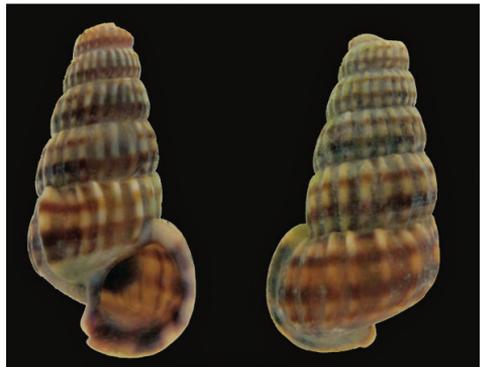
**Common name.** Truncated mangrove snail<sup>(19)</sup>.

**Size.** Maximum shell height 36 mm<sup>(1)</sup>.

**Remarks.** Common mangrove climbing whelk also found in salt marshes on mud beneath vegetation<sup>(1)</sup>, although less abundant<sup>(19)</sup>. Shells tend to have a characteristically decollated apex.

**Distribution.** Indo-pacific mangrove species. South African distribution extends from Knysna along southeastern coast into Mozambique<sup>(19)</sup>.

**St Lucia records.** Reported in previous surveys from 1948–51<sup>(20)</sup>, 1964–65<sup>(21)</sup>. Found in the recent survey at Shark Basin, at the Mfolozi Back Channel (St Lucia Mouth), and at the St Lucia Bridge (Narrows).



*Cerithidea decollata* (Linnaeus, 1767)  
36 mm, St Lucia Bridge, Nov 2012  
NAF Miranda leg.

**Family: Littorinidae*****Afrolittorina africana* (Krauss in Philippi, 1847)****Common name.** African periwinkle<sup>(19)</sup>.**Size.** Shell height 5–8 mm<sup>(19)</sup>.**Remarks.** Typical high intertidal species which occurs in large numbers usually on exposed rocks<sup>(1)</sup>.**Distribution.** Southwestern Indian Ocean<sup>(22)</sup> from Durban to southern Mozambique<sup>(19)</sup> as well as southeastern Madagascar<sup>(22)</sup>.**St Lucia records.** Not previously reported from St Lucia; collected in 1971 from “St Lucia River Estuary” (NMSA). Not recorded in the recent survey.

*Afrolittorina africana* (Krauss in Philippi, 1847)  
7.8 mm, Zululand, Sep 1971  
R Kilburn leg.

***Littoraria coccinea glabrata* (Philippi, 1846)****St Lucia synonyms.** *Littorina glabrata* Philippi, 1846.**Common name.** Striped periwinkle<sup>(19)</sup>.**Size.** Maximum shell height 24 mm<sup>(1)</sup>.**Remarks.** High resistance to desiccation<sup>(19)</sup> enables habitation of exposed regions<sup>(1)</sup> above high spring-tide level in sub-tropical regions.**Distribution.** Tropical and subtropical Indian Ocean distribution<sup>(1)</sup> with a southern limit at Port Elizabeth<sup>(1)</sup> on the South African coast.**St Lucia records.** Not previously reported from St Lucia; collected in 1971 (NMSA) from the St Lucia Estuary. Not found during the recent survey.

*Littoraria coccinea glabrata* (Philippi, 1846)  
14 mm, St Lucia Estuary, Nov 1971  
R Kilburn leg.

***Littoraria intermedia* (Philippi, 1846)**

**Common name.** Estuarine periwinkle<sup>(19)</sup>.

**Size.** Shell height 14–26 mm<sup>(23)</sup>.

**Remarks.** Associated with roots and trunks of *Rhizophora* and occasionally *Bruguiera* mangrove trees<sup>(23)</sup>.

**Distribution.** Tropical and subtropical Indo-Pacific distribution from the east African coast including the Red Sea and east to Polynesia<sup>(23)</sup>, with a southern limit at Port Elizabeth on the Eastern Cape coast of South Africa<sup>(19)</sup>.

**St Lucia records.** Not previously reported from St Lucia; collected in 1971 and 1987 (NMSA) from St Lucia Estuary and Shark Basin respectively. Only dead shells retrieved recently from Shark Basin (St Lucia Mouth).



*Littoraria intermedia* (Philippi, 1846)  
13 mm, St Lucia River Estuary, Nov 1971  
RN Kilburn leg.

***Littoraria pallescens* (Philippi, 1846)**

**Common name.** Pale periwinkle

**Size.** Shell height 15–25 mm<sup>(23)</sup>.

**Remarks.** Commonly occurs on the leaves of *Rhizophora* in mangrove forests<sup>(23)</sup>.

**Distribution.** Tropical to sub-tropical Indo-Pacific distribution extending from east African coast to Samoa<sup>(23)</sup>.

**St Lucia records.** Not previously reported from St Lucia; collected in 1987 (NMSA) from the St Lucia Estuary. Not found during the recent survey.



*Littoraria pallescens* (Philippi, 1846)  
15 mm, St Lucia Estuary, Aug 1987  
RH Taylor leg.

***Littoraria subvittata* (Reid, 1986)**

**Common name.** Aldabra periwinkle.

**Size.** Shell height 13–34 mm<sup>(23)</sup>.

**Remarks.** Occurs in mangroves and marsh grass habitats as well as on sheltered rocks<sup>(23)</sup>.

**Distribution.** Coastal Indian Ocean distribution from Aden, Yemen<sup>(23)</sup>, in the north to the Swartkops River mouth<sup>(24)</sup> at Port Elizabeth, South Africa. Range extends east to Mauritius, Maldives and Cocos Islands<sup>(23)</sup>.

**St Lucia records.** Not previously reported from St Lucia; collected by NMSA at unknown date. Not found during the recent survey.



*Littoraria subvittata* (Reid, 1986)

18 mm, Lake St Lucia  
Burnup Collection.

***Littoraria scabra* (Linnaeus, 1758)**

**Common name.** Mangrove periwinkle.

**Size.** Shell height 25–35 mm<sup>(23)</sup>.

**Remarks.** Characteristic mangrove and estuarine species found above high water<sup>(1)</sup>. Usually found on trunks, roots<sup>(23)</sup> and branches of mangrove trees<sup>(1)</sup>.

**Distribution.** Tropical and sub-tropical Indo-Pacific distribution extending from the eastern African coast across to Samoa and Hawaii<sup>(23)</sup>. The southern limit of the species is Algoa Bay at Port Elizabeth in South Africa<sup>(1,19)</sup>.

**St Lucia records.** Reported from St Lucia in 1948–51<sup>(20)</sup>, 1964–55<sup>(21)</sup> and 1972–73<sup>(25)</sup> however the species has not been recorded recently.

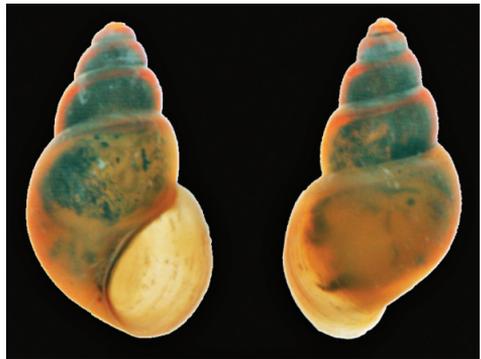


*Littoraria scabra* (Linnaeus, 1758)

14 mm, Kosi Bay Estuary, July 1987  
DG Herbert leg.

**Family: Pterotracheidae*****Pterotrachea* cf. *hippocampus* Philippi, 1836****Common name.** Sea elephant.**Size.** Up to 34 mm.**Remarks.** Pelagic marine species related to *Charonia* spp. (Ranellidae). The species is expected to occur more frequently in the system as the marine connection is maintained.**Distribution.** Circumtropical distribution including the Gulf of Mexico<sup>(26)</sup>, the Mediterranean Sea<sup>(27)</sup> and the North Atlantic<sup>(28)</sup>.**St Lucia records.** Not previously reported from St Lucia; recorded in the recent survey in 2013 from the Mfolozi-St Lucia Beach Spillway (St Lucia Mouth).

*Pterotrachea* cf. *hippocampus* Philippi, 1836  
34 mm, Mfolozi Channel, Aug 2013  
NK Carrasco leg.

**Family: Assimineidae****Assimineidae sp.****St Lucia synonyms.** *Assimineia bifasciata* Nevill, 1880; *Coriandria durbanensis* (Tomlin, 1916); *Rissoa capensis* Sowerby, 1892.**Common name.** False sentinel.**Size.** Up to 2.22 mm.**Remarks.** Taxon under revision. Provisional name based on genetics and shell morphometrics<sup>(29)</sup>. Small size and sympatric occurrence with *Assimineia* spp. caused previous confusion and misidentification. Forms dense aggregations on firm mud.**Distribution.** East coast of southern Africa.**St Lucia records.** Probably combined in the 1948–51<sup>(4)</sup> survey with *Assimineia* spp. Reported in 2012 as *Coriandria durbanensis* (Tomlin 1916)<sup>(6)</sup> from Lister's Point (False Bay). Found in the recent survey from Charter's Creek (South Lake), Hell's Gate (North Lake) and Lister's Point (False Bay).

Assimineidae sp.  
0.8 mm, St Lucia False Bay, Jul 2012  
NAF Miranda leg.

***Assiminea* cf. *capensis* Bartsch, 1915**

**St Lucia synonyms.** *Assiminea bifasciata* Nevill, 1880; *Assiminea* cf. *ovata* (Krauss, 1848); *Syncera* sp. Gray, 1821;

**Common name.** Sentinel snail.

**Size.** Maximum shell height 7 mm<sup>(1,19)</sup>.

**Remarks.** Dominant in estuaries on the east coast<sup>(19)</sup> forming large colonies on firm mud sheltered by mangroves or salt marsh<sup>(19)</sup>. Species listed as “*capensis*” following the recommendation of W. Ponder, as the taxonomy of this group is currently under review.

**Distribution.** Southern African species extending from Langebaan to Mozambique<sup>(19)</sup>.

**St Lucia records.** Previous records in 1948–51<sup>(20)</sup>, 1981–2<sup>(30)</sup> and 2005<sup>(12)</sup> probably comprised both *A.* cf. *capensis* and “*A.*” aff. *capensis*. Reported as *Syncera* sp. in 1964–5<sup>(21)</sup> and *A. durbanensis* in 1993<sup>(31)</sup>. Identified as *A.* cf. *ovata* in 2007–9<sup>(14)</sup> following Appleton 1996<sup>(3)</sup>. Reported as *A.* cf. *capensis* in 2012<sup>(6)</sup> and found during the recent survey from the Mfolozi Back Channel (St Lucia Mouth), Catalina Bay and Charter’s Creek (South Lake) as well as Lister’s Point (False Bay).



*Assiminea* cf. *capensis* Bartsch, 1915  
2 mm, St Lucia Catalina Bay, Nov 2012  
NAF Miranda leg.

**Family: Cassidae*****Phalium areola* (Linnaeus, 1758)**

**Common name.** Checkerboard bonnet.

**Size.** Maximum shell height 69 mm<sup>(1)</sup>.

**Remarks.** Inhabits sandy environments, known to bury itself in the substrate<sup>(1)</sup>. Subtidal species which was most likely washed into the system.

**Distribution.** Indo-Pacific distribution including the KwaZulu-Natal coast<sup>(1)</sup>. Reported from Mozambique<sup>(15)</sup> and Tanzania<sup>(32)</sup>.

**St Lucia records.** Not previously reported from St Lucia; single specimen collected from the St Lucia Mouth by NMSA at an unspecified date. Not reported in the recent survey.



*Phalium areola* (Linnaeus, 1758)  
55 mm, St Lucia Bay, 1978  
M Lavoipierre leg.

**Family: Nassariidae*****Nassarius kraussianus* (Dunker, 1846)**

**St Lucia synonyms.** *Nassa kraussiana* (Dunker, 1846).

**Common name.** Tick shell<sup>(19)</sup>.

**Size.** Shell height 7.5–10 mm<sup>(1)</sup>.

**Remarks.** Characteristic estuarine species found in salt marshes and lagoonal mudbanks<sup>(19)</sup> where it forms dense colonies. Occurs within shallow pools often among eelgrass<sup>(1)</sup>.

**Distribution.** Southern African distribution from the Namaqualand coast<sup>(2)</sup> extending along KwaZulu-Natal<sup>(19)</sup>. Also reported from southern Mozambique<sup>(15)</sup>.

**St Lucia records.** Reported in 1948–51<sup>(20)</sup>, 1972–73<sup>(25)</sup> and 2010<sup>(33)</sup>. Recorded in 1964–65<sup>(21)</sup> as *N. kraussiana*. Dead shells retrieved during the recent survey from South and North Lake shores, as well as False Bay.



*Nassarius kraussianus* (Dunker, 1846)  
11 mm, St Lucia Charter's Creek, Mar 2012  
NAF Miranda leg.

**Family: Muricidae*****Ergalatax heptagonalis* (Reeve, 1846)****Common name.** Heptagonal rock snail.**Size.** Maximum shell length 30 mm<sup>(1)</sup>.**Remarks.** Common under rocks or logs on muddy sand of estuarine bays<sup>(1)</sup>.**Distribution.** Indo-pacific distribution including the KwaZulu-Natal coast<sup>(1)</sup> extending to Mozambique as well as Madagascar<sup>(15)</sup>.**St Lucia records.** Not previously reported from St Lucia; collected in 1987 (NMSA) from the Mfolozi Link Canal (St Lucia Mouth). The specimen collected was probably exposed after excavation of the Link Canal as it is a Pleistocene subfossil. Not found during the recent survey, however the species may re-colonize St Lucia if the marine connection is maintained.*Ergalatax heptagonalis* (Reeve, 1846)

25 mm, Mission Rocks, Apr 1987

R Kilburn leg.

***Murex brevispinus* Lamarck, 1822****Common name.** Short spined murex<sup>(19)</sup>.**Size.** Maximum shell height 82 mm<sup>(1)</sup>.**Remarks.** Occurs on protected intertidal sandbanks, often among eelgrass<sup>(1,19)</sup>. Forms dense mating aggregations<sup>(19)</sup>.**Distribution.** Indian Ocean distribution along the eastern coast of Africa extending from Kenya to Durban<sup>(1,15,19)</sup>.**St Lucia records.** Not previously reported from St Lucia; only dead shells retrieved from Lister's Point (False Bay) and Fani's Island (South Lake) in the recent survey.*Murex brevispinus* Lamarck, 1822

71 mm, Durban, Aug 1968

BJ Young leg.

***Purpura bufo* Lamarck, 1822**

**Common name.** Toad purpura.

**Size.** Maximum shell height 70 mm.

**Remarks.** Common in rock pools on the KwaZulu-Natal coast. Specimen illustrated is a sub-adult.

**Distribution.** Tropical and sub-tropical Indian Ocean<sup>(15,32)</sup> with southern limit in the eastern Transkei<sup>(1,19)</sup>.

**St Lucia records.** Not previously collected or reported from St Lucia. Only one dead shell was found at False Bay during the recent survey.



*Purpura bufo* Lamarck, 1822  
52 mm, St Lucia False Bay, Jul 2013  
NAF Miranda leg.

**Family: Haminoeidae*****Haminoea natalensis* (Krauss, 1848)**

**St Lucia synonyms.** *Haminoea petersi* (Martens, 1879); *Haminoea gracilis* (Sowerby, 1897); *Cylichna africana* Bartsch, 1915; *Cylichna tubulosa* Gould, 1859.

**Common name.** Natal bubble shell.

**Size.** Maximum shell length 19 mm<sup>(1)</sup>.

**Remarks.** Inhabits shallow water including tidal rock pools<sup>(34)</sup>.

**Distribution.** On the South African coast, replaces *H. alfredensis* from the Transkei into northern KwaZulu-Natal<sup>(1)</sup>. Occurs from Port Alfred to Mozambique and is likely synonymous with other Indo-Pacific species<sup>(34)</sup>.

**St Lucia records.** Probably misidentified in 1972–73<sup>(25)</sup> as *C. africana*, as misspelled *H. gracilis* in 1964–65<sup>(21)</sup> and as misspelled *H. petersi* in 1981–82<sup>(30)</sup>. Reported in 1948–51<sup>(20)</sup>, as well as in 2006<sup>(12)</sup> and 2007<sup>(14)</sup>. Only dead shells retrieved during the recent survey.



*Haminoea natalensis* (Krauss, 1848)  
18 mm, St Lucia Charter's Creek, Apr 1963  
AC van Bruggen leg.



*Haminoea natalensis* (Krauss, 1848)  
11 mm, St Lucia Catalina Bay, May 2007  
L Clennell leg.

**Family: Aplysiidae*****Bursatella leachii* Blainville, 1817**

**St Lucia synonyms.** *Barnardaclesia cirrhifera* (Quoy & Gaimard, 1832); *Notarchus cirrhifera* (Quoy & Gaimard, 1832).

**Common name.** Shaggy Sea Hare, Ragged Sea Hare.

**Size.** Maximum length 130 mm<sup>(34)</sup>.

**Remarks.** Common estuarine species which also occurs in tide pools<sup>(19)</sup>.

**Distribution.** Circumtropical species reported from the east coast of Africa<sup>(19)</sup>, the Mediterranean Sea<sup>(27)</sup>, the North Atlantic region<sup>(28)</sup> as well as the Caribbean<sup>(35)</sup>.

**St Lucia records.** Reported as *B. cirrhifera* in 1948–51<sup>(20)</sup> and as *N. cirrhifera* in 1964–65<sup>(21)</sup>. Not recorded during the recent survey.



*Bursatella leachii* Blainville, 1817  
175 mm, Salt Rock, Aug 2009  
DG Herbert leg.

***Stylocheilus striatus* (Quoy & Gaimard, 1832)**

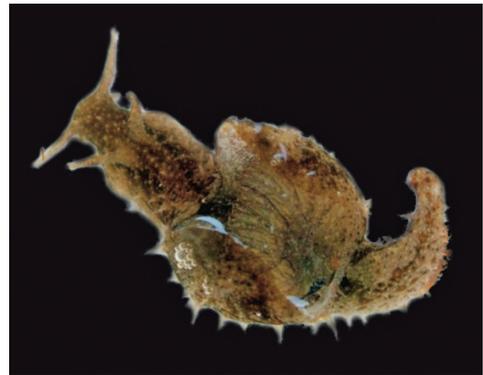
**Common name.** Lined Sea Hare.

**Size.** 28 mm<sup>(33)</sup>.

**Remarks.** Occurs in sheltered pools and estuaries, often sympatric with *Bursatella leachii*.

**Distribution.** Circumtropical distribution including Cape Verde<sup>(36)</sup> and the Caribbean Sea<sup>(35)</sup>. Southern African distribution extends from Mngazana in the Eastern Cape to southern Mozambique<sup>(34)</sup>.

**St Lucia records.** Recorded in 2007<sup>(14)</sup> after the overtopping and mouth breaching event. Not reported in the recent survey.



*Stylocheilus striatus* (Quoy & Gaimard, 1832)  
53 mm, St Lucia Estuary, Apr 2007  
C Fox leg.

**Family: Siphonariidae*****Siphonaria oculus* Krauss, 1848****Common name.** Eyed false-limpet<sup>(19)</sup>.**Size.** Maximum length 33 mm<sup>(1)</sup>.**Remarks.** Locally common species which is found on sheltered rocks in lagoons and estuaries<sup>(1)</sup>.**Distribution.** Southern African distribution extends along the coast from False Bay in the Western Cape Province to Mozambique<sup>(1)</sup>.**St Lucia records.** Reported in 1948–51<sup>(20)</sup> and 1964–65<sup>(21)</sup> from the St Lucia Mouth. Not recorded in the recent survey.

*Siphonaria oculus* Krauss, 1848  
30 mm, Durban Bay, Sep 1972  
BJ Young leg.

**Family: Planorbidae*****Bulinus natalensis* (Krauss in Küster, 1841)****Common name.** Natal bladder snail**Size.** 9.6 × 8.5 mm (depressed form) 9.5 × 6.5 mm (high spired form)<sup>(2)</sup>.**Remarks.** Wide range of habitats including small pools, slow flowing rivers and lakes<sup>(2)</sup>.**Distribution.** East African distribution extending from Ethiopia to the northern coastal region of KwaZulu-Natal<sup>(2)</sup> where it occurs predominantly on the eastern lowlands<sup>(24)</sup>.**St Lucia records.** Not previously reported from St Lucia; recorded in the recent survey at Catalina Bay (South Lake) in 2012.

*Bulinus natalensis* (Krauss in Küster, 1841)  
14 mm, St Lucia Catalina Bay, Nov 2012  
JL Raw leg.

***Bulinus tropicus* (Krauss, 1848)**

**Common name.** Tropical bladder snail.

**Size.** 12.3 × 7.8 mm (slender form), 10.6 × 8.3 mm (more globose form)<sup>(2)</sup>.

**Remarks.** Commonly occurs in small earth dams and residual pools of seasonally flowing streams<sup>(2)</sup>.

**Distribution.** Eastern and southern Africa, extending from Ethiopia to Namibia and the Western Cape of South Africa. Not commonly found on the eastern coastal region of South Africa<sup>(2)</sup>.

**St Lucia records.** Reported in 1948<sup>(20)</sup>, 1964–65<sup>(21)</sup> and 2002–03<sup>(37)</sup>. Only dead shells retrieved from the lake shores at Lister's Point (False Bay), Hell's Gate (North Lake), Fani's Island (South Lake) and Mpate Mouth (Narrows) during the recent survey.



*Bulinus tropicus* (Krauss, 1848)  
16 mm, Durban, Mar 2002  
D Nadasan leg.

***Bulinus forskalii* (Ehrenberg, 1831)**

**Common name.** Forskål's bladder snail.

**Size.** 17 × 5.4 mm<sup>(2)</sup>.

**Remarks.** Ability to aestivate allows this species to commonly inhabit seasonal pools<sup>(24)</sup>.

**Distribution.** Afrotropical distribution extending south from the Egyptian Mediterranean region to Namibia<sup>(2)</sup>. Also reported from Madagascar<sup>(2)</sup>.

**St Lucia records.** Reported in 2002–03<sup>(37)</sup> from the South Lake Eastern Shores. Not reported during the recent survey.



*Bulinus forskalii* (Ehrenberg, 1831)  
8.1 mm, Uvongo, Mar 1996  
M Coke leg.

**Family: Physidae*****Aplexa marmorata* (Guilding, 1828)**

**Common name.** Slender bladder snail<sup>(7)</sup>.

**Size.** 15 × 8 mm<sup>(3)</sup>.

**Remarks.** Alien species introduced from South America<sup>(3)</sup>. Commonly colonizes lentic waterbodies and the backwaters of rivers<sup>(24)</sup>. Recent work assigns this species to the genus “*Aplexa*” rather than “*Physa*”<sup>(38)</sup>.

**Distribution.** Occurs in isolated populations in KwaZulu-Natal, Mpumalanga and Limpopo<sup>(24)</sup>.

**St Lucia records.** Reported in 2005<sup>(39)</sup> from a pan on the Western Shores (South Lake). Recorded in 2009<sup>(13)</sup>, 2010<sup>(14)</sup> and in the recent survey in 2012 from Catalina Bay (South Lake).



*Aplexa marmorata* (Guilding, 1828)  
12 mm, St Lucia Catalina Bay, Feb 2010  
NAF Miranda leg.

**Family: Lymnaeidae*****Lymnaea natalensis* (Krauss, 1848)**

**Common name.** Natal pond snail.

**Size.** Maximum shell height 25 mm<sup>(2)</sup>.

**Remarks.** Occurs in permanent streams<sup>(2)</sup>. Major intermediate host of the giant liver fluke, *Fasciola gigantica*<sup>(3)</sup>. Debated whether this species should be assigned to the genus *Radix*.

**Distribution.** East African distribution including the highlands of Ethiopia<sup>(2)</sup>. Southern range includes the Orange, Okavango and Zambezi Rivers<sup>(24)</sup>.

**St Lucia records.** Not previously reported from St Lucia; collected in 1982 (NPB). Reported in the recent survey from Catalina Bay (South Lake) in 2012.



*Lymnaea natalensis* (Krauss, 1848)  
12 mm, St Lucia Catalina Bay, Nov 2012  
NAF Miranda leg.

***Pseudosuccinea columella* (Say, 1817)**

**Common name.** Reticulate pond snail.

**Size.** 17 × 9 mm<sup>(2)</sup>.

**Remarks.** Alien species introduced from North America. Occurs on damp mud at the water-air interface<sup>(24)</sup>. Intermediate host for *Fasciola hepatica* and *F. gigantica*<sup>(24)</sup>.

**Distribution.** Widely introduced to many areas, including Puerto Rico, Europe and New Zealand. First reported from Africa in 1944 from the Western Cape Province of South Africa<sup>(2)</sup>.

**St Lucia records.** Reported in 2009<sup>(13)</sup> from freshwater seepage area in Catalina Bay (South Lake). Not recorded in the recent survey.



*Pseudosuccinea columella* (Say, 1817)  
11 mm, St Lucia Catalina Bay, Jul 2009  
NAF Miranda leg.

**Family: Succineidae*****Oxyloma patentissima* (Menke in Pfeiffer, 1853)**

**Common name.** Twisted amber snail<sup>(40)</sup>.

**Size.** Maximum shell length 10 mm<sup>(3)</sup>.

**Remarks.** Typically occurs on emergent vegetation alongside water<sup>(3)</sup>.

**Distribution.** Southern African distribution includes Mozambique, northern Botswana and Zimbabwe<sup>(17)</sup>. Found on the KwaZulu-Natal coastal belt between Park Rynie and Lake Sibaya<sup>(40)</sup>.

**St Lucia records.** Reported in 2002–03<sup>(37)</sup> from South Lake Eastern Shores. Not recorded in the recent survey.



*Oxyloma patentissima* (Menke in Pfeiffer, 1853)  
8.8 mm, Mhlanga Lagoon, Dec 1995  
D Herbert & L Davis leg.

**Family: Ellobiidae*****Cassidula labrella* (Deshayes, 1830)**

**Common name.** Keeled coffee-bean snail.

**Size.** 12 × 7.5 mm<sup>(2)</sup>.

**Remarks.** Typically found on the surface of firm mud in mangroves and salt marshes<sup>(24)</sup>.

**Distribution.** East African coastal distribution from the Massawa region of the Red Sea to Port Elizabeth in South Africa<sup>(2)</sup>.

**St Lucia records.** Reported in 1964–65<sup>(21)</sup> as well as during the recent survey at the mangroves near the St Lucia Estuary Mouth.



*Cassidula labrella* (Deshayes, 1830)  
12 mm, St Lucia Mouth, Mar 2012  
N Peer leg.

***Melampus lividus* (Deshayes, 1830)**

**Common name.** Common coffee-bean snail<sup>(40)</sup>.

**Size.** Maximum shell height 18 mm<sup>(40)</sup>.

**Remarks.** Reported as *Melampus ordinarius* Melvill & Ponsonby, 1901 from deep vertical cracks in high level outcrops at Mission Rocks<sup>(40)</sup>.

**Distribution.** Tropical to subtropical Indian Ocean distribution extending from East London north along the KwaZulu-Natal coast<sup>(40)</sup>.

**St Lucia records.** Reported in 1964–65<sup>(21)</sup>. Not recorded in the recent survey.



*Melampus lividus* (Deshayes, 1830)  
18 mm, St Lucia Mission Rocks, Apr 1988  
D Brink leg.

***Melampus parvulus* Pfeiffer, 1856**

**Common name.** Dwarf coffee-bean snail<sup>(40)</sup>.

**Size.** Maximum shell height 13 mm<sup>(40)</sup>.

**Remarks.** Found on firm mud in lagoons and estuaries where individuals form dense colonies<sup>(40)</sup>.

**Distribution.** Tropical Indo-Pacific distribution including Indian Ocean islands. South African distribution extends from KwaZulu-Natal to Port Alfred<sup>(40)</sup>.

**St Lucia records.** Not previously reported from St Lucia; recorded from the mangroves at Shark Basin (St Lucia Mouth) in the recent survey.



*Melampus parvulus* Pfeiffer, 1856  
10 mm, St Lucia Mouth, Mar 2013  
SM Ngubane leg.

***Melampus semiaratus* Connolly, 1912**

**Common name.** Half-grooved coffee-bean snail<sup>(40)</sup>.

**Size.** Maximum shell height 12 mm<sup>(40)</sup>.

**Remarks.** Mangrove species which occurs in the burrows of crabs up to a depth of 150 mm as well as on the surface of the mud<sup>(24)</sup>.

**Distribution.** East African distribution ranging from the Giuba River in Tanzania to the Umkomaas River on the southern coast of KwaZulu-Natal in South Africa<sup>(2)</sup>.

**St Lucia records.** Reported in St Lucia in 1964–65<sup>(21)</sup> as well as in the recent survey from the mangroves at Shark Basin (St Lucia Mouth) in 2012.



*Melampus semiaratus* Connolly, 1912  
12 mm, St Lucia Mouth, Mar 2013  
SM Ngubane leg.



# Description of two new species and redescription of one species of agnarid terrestrial isopods (Oniscidea, Agnaridae) from western Iran

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## Abstract

The present study reports on three species of terrestrial isopods from western Iran. The genus *Mongoloniscus* Verhoeff, 1930 is recorded for the first time from Iran, with description of a new species: *M. persicus* **sp. n.** *Protracheoniscus ehsani* **sp. n.** is described and *P. darevskii* Borutzky, 1975 is redescribed based on Iranian specimens. The diagnostic characters of these species are figured and their geographical distribution is presented on a map.

## Keywords

Oniscidea, Agnaridae, new species, Iran

## Introduction

The terrestrial isopods of the family Agnaridae Schmidt, 2003 are distributed from the Mediterranean region to eastern and southern Asia (Schmidt 2003, 2008). The German author postulated an Indian origin for the family. He considered the internal lungs with spiracles located on the lateral margin of all pleopod exopodites as the only autapomorphy of the family.

According to world catalogue of terrestrial isopods (Schmalfuss 2003), Agnaridae include 15 nominal genera. Former studies recorded two genera in Iran: *Hemilepistus*



**Figure 1.** Map of Iran indicating the sampling localities of *Mongoloniscus persicus* sp. n. (in black), *Protracheoniscus ehsani* sp. n. (in blue) and *P. darevskii* (in red).

Budde-Lund, 1879 and *Protracheoniscus* Verhoeff, 1917 (Kashani et al. 2010, 2013, Kashani 2014). In this study, three agnarid species are reported from western Iran, of which two are new species. The genus *Mongoloniscus* is found for the first time in Iran. *Protracheoniscus darevskii* Borutzky, 1975 is reported for the first time from Iran. Since the type specimens are lost, a redescription of the species is presented based on Iranian specimens. Moreover, two new species, namely *Mongoloniscus persicus* sp. n. and *Protracheoniscus ehsani* sp. n. are described. Sampling localities for these species are presented on the map (Fig. 1).

## Material and methods

The material examined was collected in many localities from western Iran (Fig 1). Specimens were collected by hand and preserved in 96% ethanol. The isopods were dissected and body parts were slide-mounted in Euparal. Drawings were made using

a drawing tube fitted on a SaIran ZSM-100 dissecting stereomicroscope and on a Nikon Y-IDT compound microscope. Type material of the newly described species is deposited in the Zoological Museum, University of Tehran (ZUTC), Staatliches Museum für Naturkunde, Stuttgart (SMNS), Iranian Research Institute of Plant Protection (IRIPP) and in the author personal collection (PCGMK). All the other specimens are kept in PCGMK.

## Taxonomy

**Order Isopoda Latreille, 1817**

**Suborder Oniscidea Latreille, 1802**

**Family Agnaridae Schmidt, 2003**

**Genus *Mongoloniscus* Verhoeff, 1930**

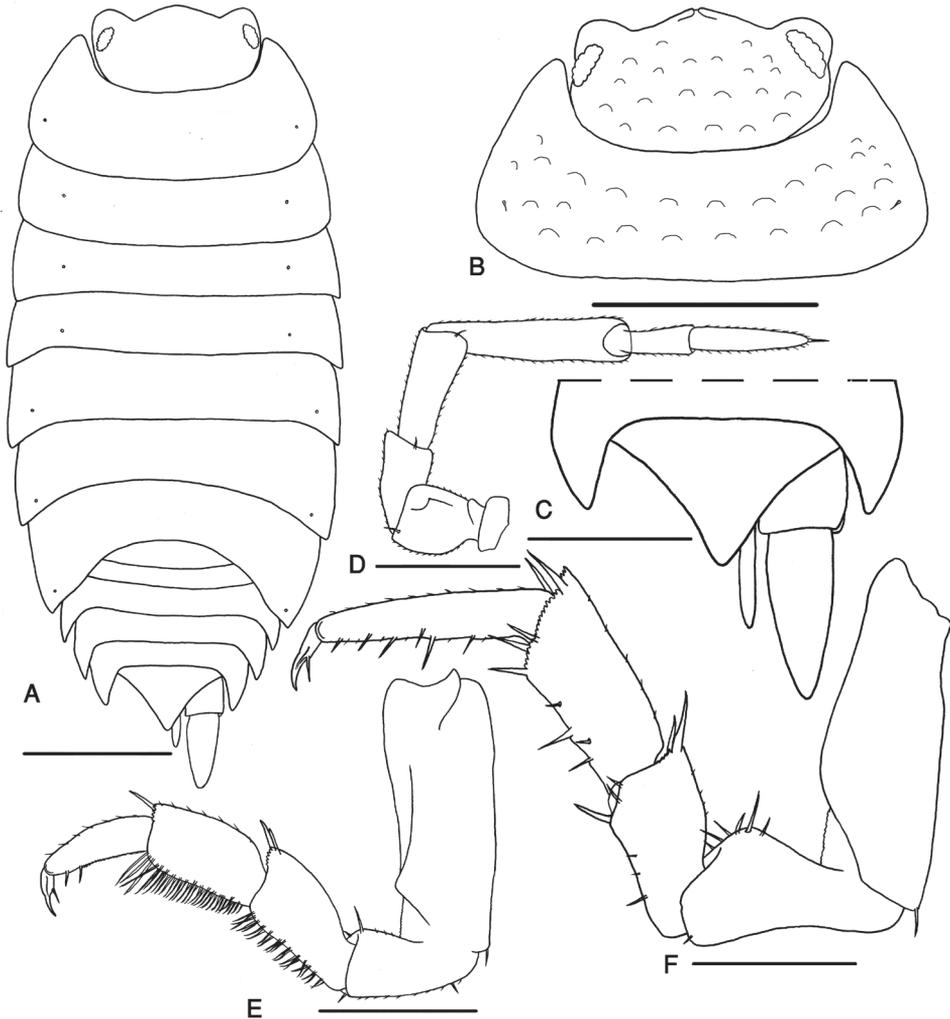
**Diagnosis.** Kwon (1993) discussed in details the characteristics of the genus *Mongoloniscus* and considered it as a good genus. He mentioned the granulated dorsum and triangular median lobe of the head as differentiating characters of the genus from *Protracheoniscus*. According to the eco-morphological classification proposed by Schmalzfuss (1984), the members of the genus are clinger type.

***Mongoloniscus persicus* sp. n.**

<http://zoobank.org/7AD9DA60-17E6-418B-AEE6-346289578E08>

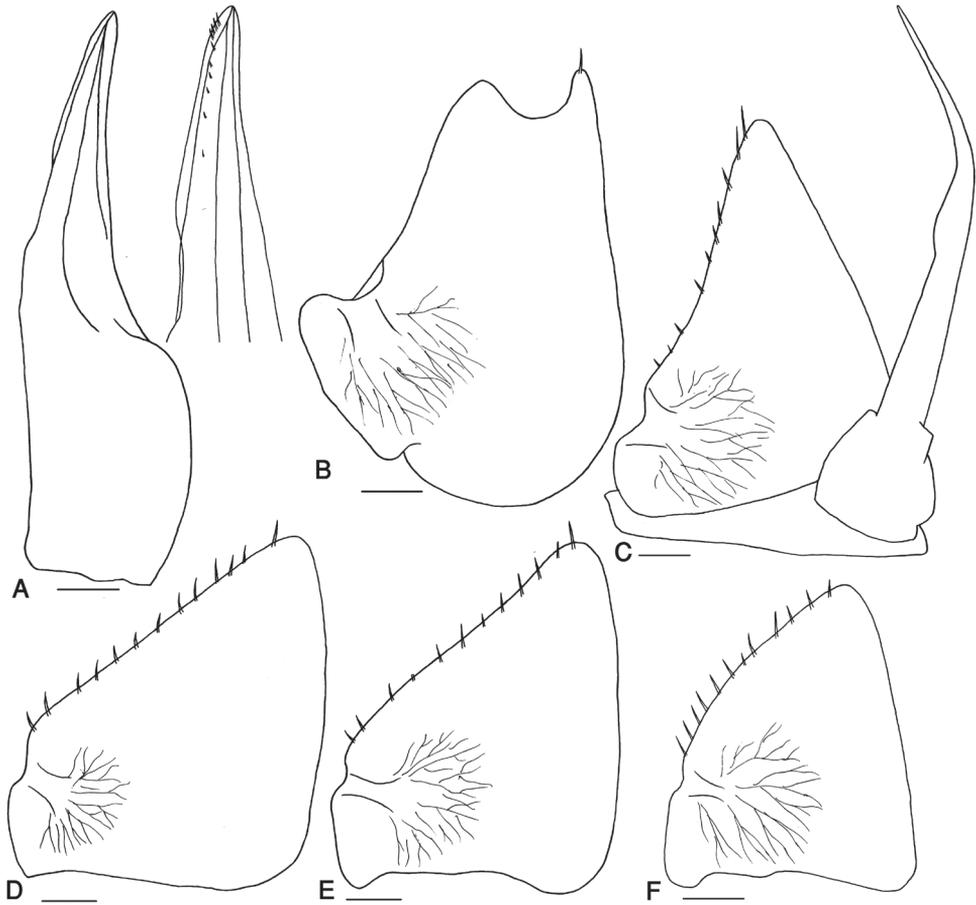
**Material examined.** Holotype: male, 5.5 mm, **Zanjan**, the University of Zanjan campus, 13 June 2011, leg. G.M. Kashani (ZUTC Iso.1121).

Paratypes: **Zanjan**, same data as holotype, two males and two females (IRIPP Iso-1051); same data as holotype, five males and six females (PCGMK1530); Mellat Park, 36°39.5'N, 48°31.5'E, 19 September 2011, leg. G.M. Kashani, one male (SMNS T308); Mellat Park, 36°39.5'N, 48°31.5'E, 19 September 2011, leg. G.M. Kashani, one female (SMNS T309); Mellat Park, 36°39.5'N, 48°31.5'E, 19 September 2011, leg. G.M. Kashani, one female (PCGMK1534); Mahneshan, 26 March 2012, leg. R. Sayadi, three males and five females (PCGMK1535); Mahneshan, 27 March 2012, leg. R. Sayadi, two males and eight females (PCGMK1536); Mahneshan, 25 April 2012, leg. R. Sayadi, ten males and ten females (PCGMK1540); Mahneshan, 26 April 2012, leg. R. Sayadi, two males and one female (PCGMK1541); Mahneshan, 26 April 2012, leg. R. Sayadi, two males and one female (IRIPP Iso-1046); Mahneshan, 6 July 2011, leg. Z. Rostami, three males and two females (PCGMK1597); Tarom, 4 April 2012, leg. A. Ayoubi, six males and five females (PCGMK1519); Qeydar, Panjeh-Ali Mount, 18 April 2013, two males and four females (PCGMK1609); Taham Dam, 6 Km to Golahrood Village, 28 April 2013,



**Figure 2.** *Mongoloniscus persicus* sp. n., male, paratype. **A** body outline indicating the position of noduli laterales **B** cephalon and first pereonite **C** telson and uropods **D** antenna **E** pereopod 1 **F** pereopod 7. Scale = **A–B** 1 mm; **C–G** 0.5 mm.

five males and six females (PCGMK1611); 10 Km N Halab, 36°18.7'N, 48°07.0'E, 29 September 2008, leg. G.M. Kashani & E. Entezari, three males and one female (PCGMK1715); **Kurdistan**, Saghez to Saheb, 36°12.0'N, 46°25.6'E, 1 October 2008, leg. G.M. Kashani & E. Entezari, two males and two females (PCGMK1346); **West Azarbaijan**, Piranshahr to Oshnavieh, Soufian Village, 2 October 2008, leg. G.M. Kashani & E. Entezari, four males and one female (PCGMK1361); **Qazvin**, Bojn Zahra, 30 June 2008, leg. G.M. Kashani, one male (PCGMK1627); **Tehran**, Pishva, 35°12.4'N, 51°48.4'E, 24 June 2008, leg. G.M. Kashani, two males, four females and two juvenile (PCGMK1434); **Qom**, Langrood Village, 2 April 2011,



**Figure 3.** *Mongoloniscus persicus* sp. n., male, paratype. **A** pleopod endopodite 1 **B** pleopod exopodite 1 **C** pleopod 2 **D** pleopod exopodite 3 **E** pleopod exopodite 4 **F** pleopod exopodite 5. Scale = 0.1 mm.

leg. G.M. Kashani, two males (PCGMK1593); Qanavat, 1 August 2013, leg. G.M. Kashani, seven males and ten females (PCGMK1678); Qom City, 1 August 2013, leg. G.M. Kashani, two males and two females (PCGMK1679).

**Diagnosis.** Head with well developed lateral and median lobes. Male pereopod VII ischium with concave ventral margin. Male pleopod exopodite I with a deep hollow at apex.

**Description.** Maximum length, male and female, 6 mm. Color pale brown with the usual pale muscles spots. Body outline as in Fig. 2A. Cephalon with well developed lateral and median lobes; frons with an incision in the middle, vertex with faint tubercles (Fig. 2B). Antenna surpassing the posterior margin of pereon-tergite I but not reaching the posterior margin of pereon-tergite II; fifth article of peduncle as long as flagellum, with length:width ratio 4:1; flagellum with two articles, proximal one shorter, flagellar articles ratio 1:1.5 (Fig. 2D).

Pereon covered with faint tubercles. Pereon-tergite I with rounded posterolateral margin. Noduli laterales on pereonites II to IV distinctly more distant from the lateral margins than those on pereonites I and V to VII (Fig. 2A).

Pleon slightly narrower than pereon (Fig. 2A). Telson triangular with slightly concave sides and rounded apex, surpassing uropod-protopodites but not reaching the middle of uropod-exopodites. Uropod-exopodites short, almost as long as telson (Fig. 2C). Pleopod exopodites I–V with monospiracular covered lungs (Fig. 3B–F).

Male: Pereopods I–III merus and carpus with brushes of trifid setae (Fig. 2E). Pereopod I ischium triangular, carpus with depression on rostral surface equipped with slender scales; propodus narrow and long, proximal part of sternal margin with dense small scales, distal part bearing strong setae; dactylus with one dactylar and one unguis seta (Fig. 2E). Pereopod VII ischium with concave ventral margin, straight in smaller specimens; propodus narrow and long; dactylus with one dactylar and one unguis seta (Fig. 2F). Pleopod exopodite I with long hind lobe bearing a deep hollow and one short seta at apex, outer margin with no setae (Fig. 3B); endopodite I straight with triangular apical part slightly bent outwards and some short setae (Fig. 3A). Pleopod endopodite II longer than exopodite; exopodite triangular with a line of strong setae on outer margin (Fig. 3C). Pleopod exopodites III–V as in Fig. 3D–F.

**Etymology.** Due to the broad geographical distribution of the species in Iran, the name of the species is after the old name of the country, Persia.

**Remarks.** Prior to this study, the genus *Mongoloniscus* was only reported from eastern Asia (Kwon 1993; Schmalzfuss 2003). *Mongoloniscus persicus* sp. n. is the first species of the genus *Mongoloniscus* to be reported from western Asia. It has a broad geographical distribution in the central and western parts of Iran. Ecologically, this species is well adapted to cultivated areas and exists in huge numbers in some habitats.

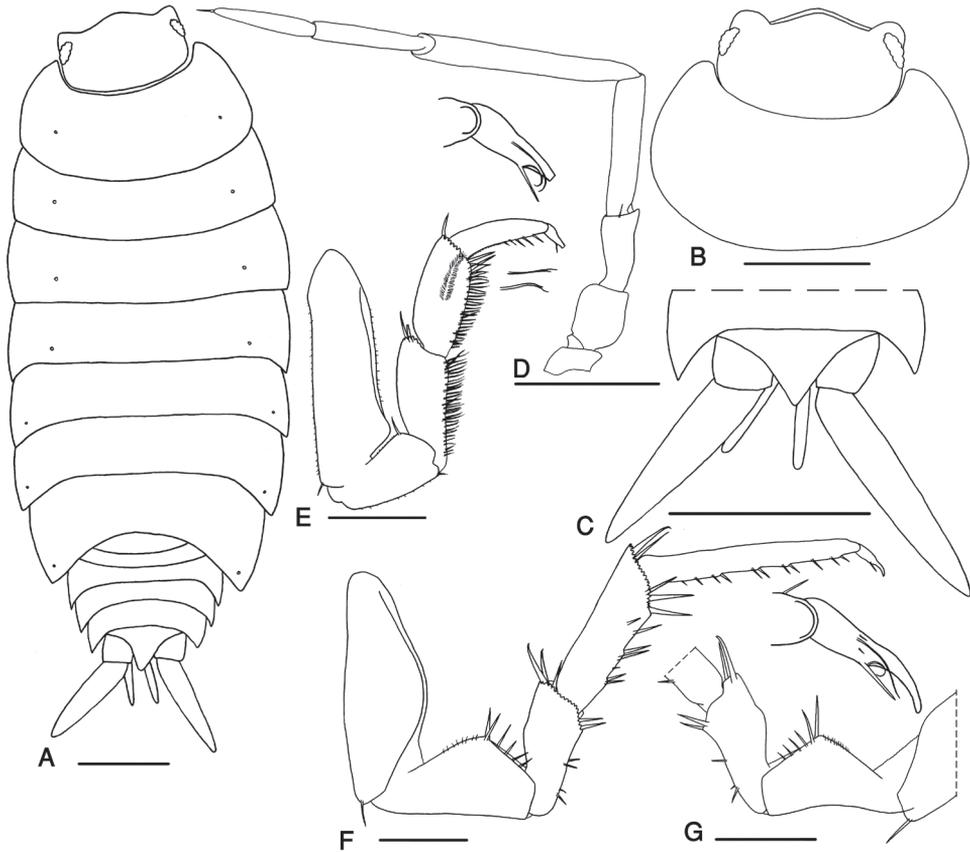
**Distribution.** Iran.

### **Genus *Protracheoniscus* Verhoeff, 1917**

**Diagnosis.** Body length variable, up to 25 mm; tergites always smooth; head with short or developed lateral lobes; antenna variable in size, with flagellum of two articles; pereon epimera I with rounded posterolateral corner; telson triangular with more or less concave sides; male pleopod exopodite I with short to long hind lobe, endopodite I straight; clinger or runner type according to the eco-morphological classification proposed by Schmalzfuss (1984).

### ***Protracheoniscus darevskii* Borutzky, 1975**

**Material examined.** West Azarbaijan, 58 Km N Mahabad, 37°07.9'N, 45°26.3'E, 4 October 2008, leg. G.M. Kashani & Ehsan Entezari, eleven males, eight females and one juvenile (PCGMK1374); Urumiah to Miandoab, 36°54.7'N, 45°44.9'E, 4 Octo-

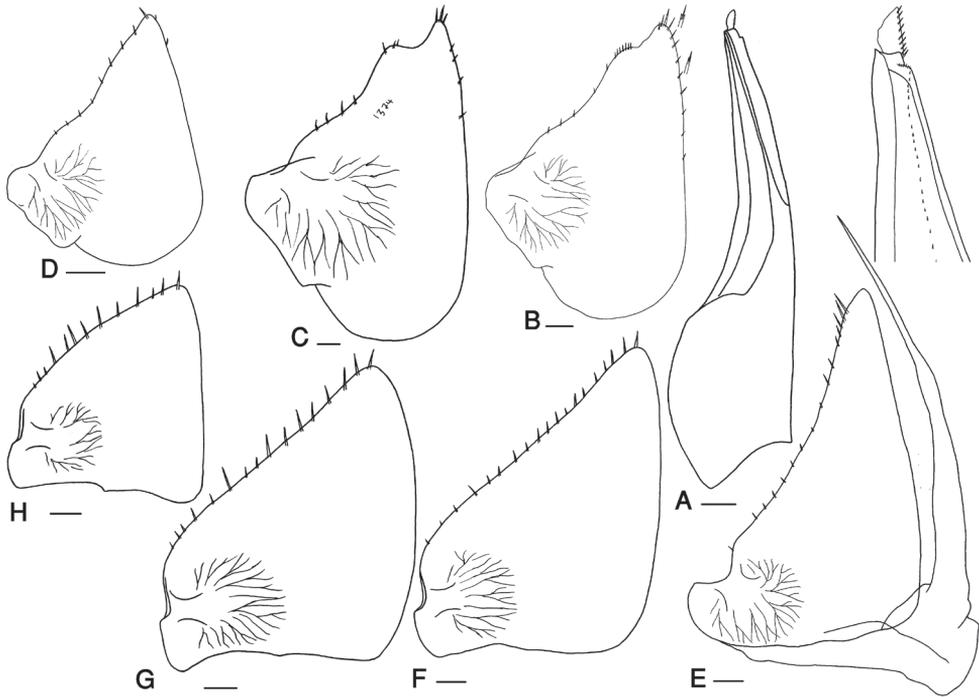


**Figure 4.** *Protracheoniscus darevskii* Borutzky, 1975, male. **A** body outline indicating the position of noduli laterales **B** cephalon and first pereonite **C** telson and uropods **D** antenna **E** pereopod 1 **F** pereopod 7 **G** pereopod 7 ischium. Scale = **A–C** 1 mm; **D–G** 0.5 mm.

ber 2008, leg. G.M. Kashani & E. Entezari, one male and one female (PCGMK1377); 5 Km S Miandoab, 36°56.9'N, 46°09.9'E, 4 October 2008, leg. G.M. Kashani & E. Entezari, one male (PCGMK1381); **Zanjan**, Mahnesan, 26 April 2012, leg. R. Sayadi, one male (PCGMK1546); Mahnesan, 6 July 2011, leg. Z. Rostami, one male and one female (PCGMK1599); **Kurdistan**, 10 Km N Bijar, 30 August 2013, leg. E. Jazimagh, one male and one female (PCGMK1610); 10 Km N Bijar, 25 June 2013, leg. E. Jazimagh, ten males and fifteen female (PCGMK1677); 10 Km N Bijar, 30 August 2013, leg. E. Jazimagh, one male and one female (IRIPP Iso-1047).

**Diagnosis.** Head with developed rounded lateral and median lobes. Male pereopod VII ischium with straight or concave ventral margin. Male pleopod exopodite I with a deep hollow or obliquely truncate apex. Endopodite I with an apical lobe equipped with small setae.

**Redescription.** Maximum length, male and female, 10 mm. Color dark brown with the usual pale muscles spots. Body outline as in Fig. 4A. Cephalon with rounded



**Figure 5.** *Protracheoniscus darevskii* Borutzky, 1975, male. **A** pleopod endopodite 1 **B–D** pleopod exopodite 1 **E** pleopod 2 **F** pleopod exopodite 3 **G** pleopod exopodite 4 **H** pleopod exopodite 5. Scale = 0.1 mm.

lateral lobes not protruding compared with broadly rounded frons (Fig. 4B). Antenna long, surpassing the posterior margin of pereon-tergite III; fifth article of peduncle as long as flagellum, with length:width ratio 7:1; flagellum with two articles, proximal article as long as the distal one (Fig. 4D).

**Pereon smooth.** Pereon-tergite I with rounded posterolateral margin. Noduli laterales on pereonites I to IV distinctly more distant from the lateral margins than those on pereonites V to VII (Fig. 4A).

Pleon narrower than pereon (Fig. 4A). Telson triangular with slightly concave sides and acute distal part (Fig. 4C). Uropod exopodites long, almost 2.5 times as long as telson (Fig. 4C). Pleopod exopodites I–V with monospiracular covered lungs (Fig. 5B–H).

Male: Pereopods I–III merus and carpus with brushes of setae (Fig. 4E). Pereopod I ischium triangular, carpus with depression on rostral surface equipped with slender scales; propodus narrow and long, proximal part of sternal margin with dense small scales, distal part bearing strong setae; dactylus with one dactylar and one unguis seta (Fig. 4E). Pereopod VII ischium with straight or concave ventral margin, merus with a short crest on dorsal margin, propodus narrow and long, dactylus with one dactylar and one unguis seta (Fig. 4F, G). Pleopod exopodite I with long hind lobe bearing a deep hollow at apex, in smaller specimens with an obliquely truncate apex; outer margin with several spine setae (Fig. 5B–D); endopodite I straight with an apical lobe

equipped with small setae (Fig. 5A). Pleopod endopodite II longer than exopodite; exopodite triangular with a line of strong setae on outer margin (Fig. 5E). Pleopod exopodites III–V as in Fig. 5F–H.

**Remarks.** During the examination of type material of terrestrial isopods deposited in Zoological Museum of Moscow State University (ZMMU), it was revealed that the type material of *P. darevskii* is possibly lost. Borutzky (1975) described the species from Armenia and figured its diagnostic characters. *Protracheoniscus darevskii* is here redescribed on the new material from western Iran (Fig. 1).

This species is characterized by the male pleopod exopodite I possessing a deep hollow at apical part of distal margin and endopodite I with an apical lobe bearing small setae.

**Distribution.** Southern Armenia: Megri District; western Iran.

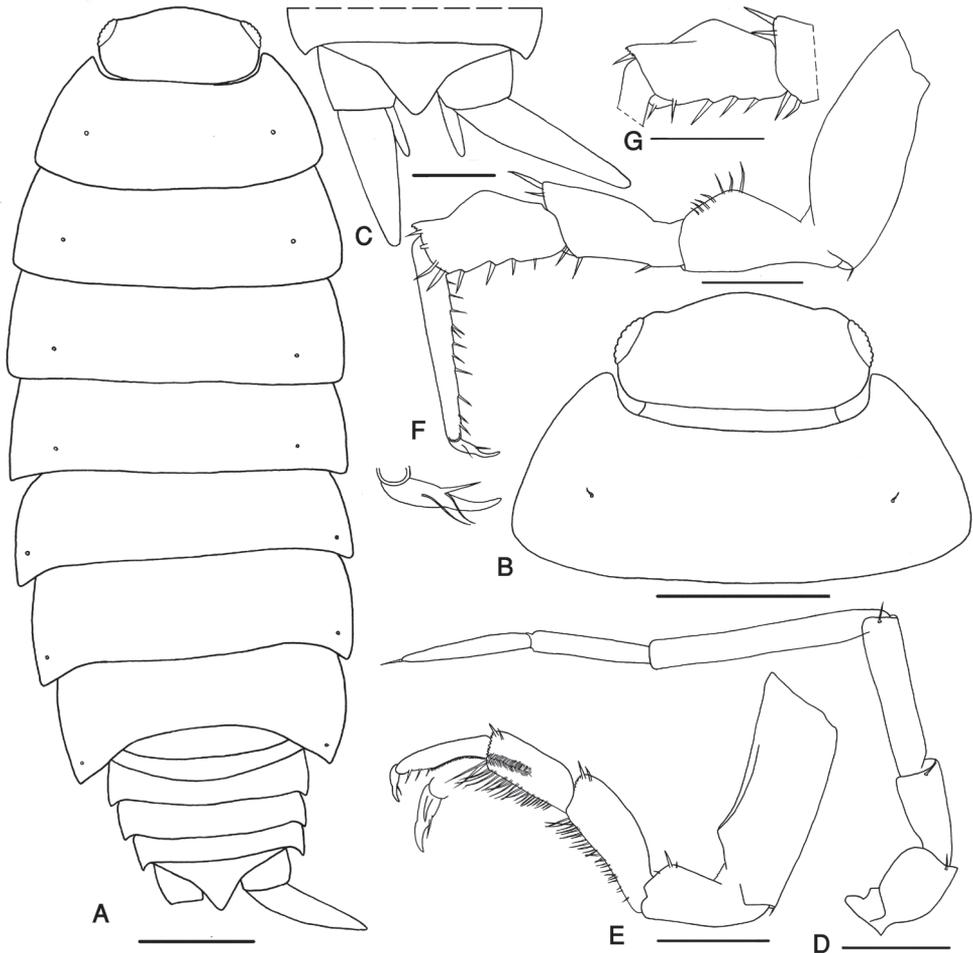
***Protracheoniscus ehsani* sp. n.**

<http://zoobank.org/2860DC91-D00D-41BE-B230-A51943AE76D0>

**Material examined.** Holotype: male, 8 mm, **Markazi**, Saveh to Boin-Zahra, Vardeh, 35°15.3'N, 50°16.5'E, 18 July 2013, leg. G.M. Kashani & B. Eshaghi (ZUTC Iso.1122).

Paratypes: **Markazi**, same data as holotype, one male and one female (IRIPP Iso.1049); same data as holotype, five males and seven females, some with marsupium (PCGMK 1652); Shazand, 9 October 2004, leg. G.M. Kashani, one male (PCGMK 1109); **Qazvin**, 20 Km N Qazvin, 36°20.7'N, 50°10.7'E, 19 July 2013, leg. G.M. Kashani & B. Eshaghi, one male (SMNS T310); 20 Km N Qazvin, 36°20.7'N, 50°10.7'E, 19 July 2013, leg. G.M. Kashani & B. Eshaghi, one female with marsupium (SMNS T311); 20 Km N Qazvin, 36°20.7'N, 50°10.7'E, 19 July 2013, leg. G.M. Kashani & B. Eshaghi, two males and seven females (PCGMK 1675); Qazvin to Razmian, Barajin village, 19 July 2013, leg. G.M. Kashani & B. Eshaghi, two females (IRIPP Iso.1048); Qazvin to Razmian, Barajin village, 19 July 2013, leg. G.M. Kashani & B. Eshaghi, eight females, two males and seven juveniles (PCGMK 1669); **Zanjan**, 25 km to Chavarzaq from Zanjan, 28 April 2013, leg. G.M. Kashani, one male (PCGMK 1614); 25 km to Chavarzaq from Zanjan, 6 May 2013, leg. G.M. Kashani, one male and five females (PCGMK 1615); Abhar, 36°09.4'N, 49°15.4'E, 12 September 2013, leg. G.M. Kashani & B. Eshaghi, four males and four females (PCGMK 1697); Abhar to Darasajin, 36°03.6'N, 49°13.2'E, 12 September 2013, leg. G.M. Kashani & B. Eshaghi, three males and one female (IRIPP Iso.1050); Abhar to Darasajin, 36°03.6'N, 49°13.2'E, 12 September 2013, leg. G.M. Kashani & B. Eshaghi, five males and four females (PCGMK 1699).

**Diagnosis.** Head with developed rounded median lobe much more protruding than lateral ones. Male pereopod VII carpus with a triangle ridge on dorsal margin. Male pleopod endopodite I with two rows of long setae at apex.

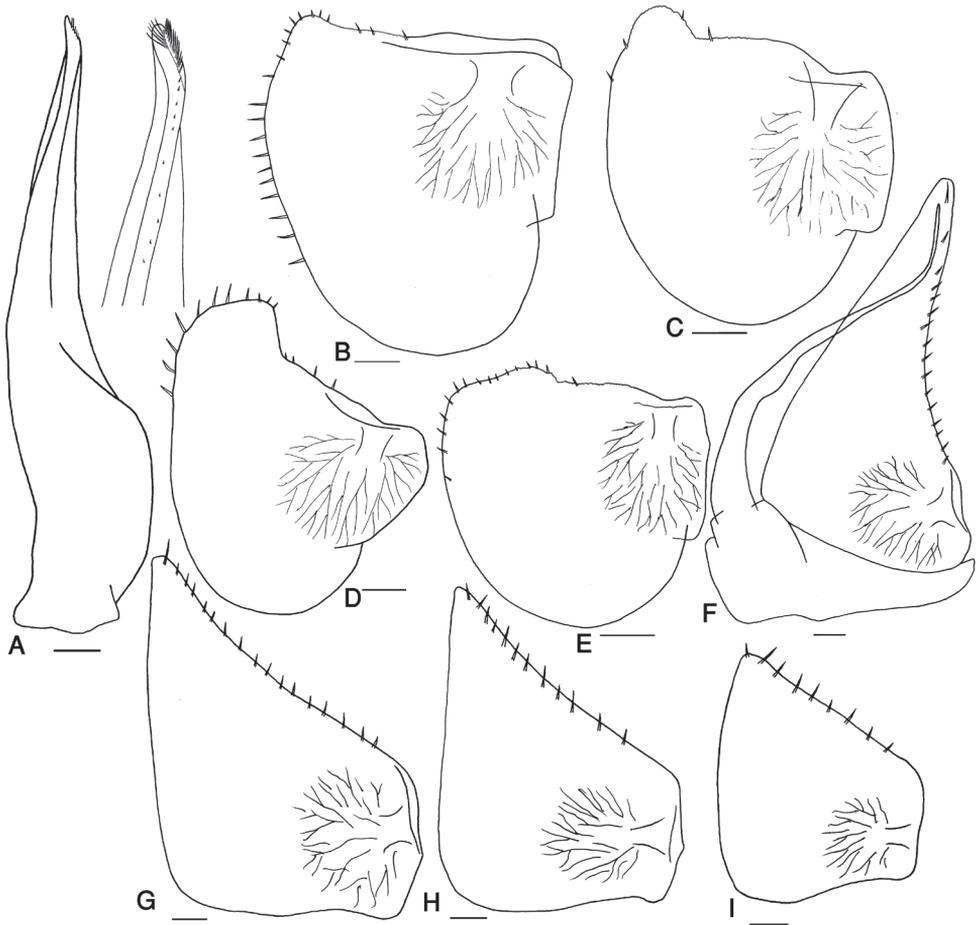


**Figure 6.** *Protracheoniscus ehsani* sp. n., male, paratype. **A** body outline indicating the position of noduli laterales **B** cephalon and first pereonite **C** telson and uropods **D** antenna **E** pereopod 1 **F** pereopod 7 **G** pereopod 7 ischium. Scale = **A–B** 1 mm; **C–G** 0.5 mm.

**Description.** Maximum length, male 8 mm and female 11 mm. Color dark brown with the usual pale muscles spots. Body outline as in Fig. 6A. Cephalon with very small lateral lobes not protruding compared with broadly rounded frons (Fig. 6B). Antenna long, surpassing the posterior margin of pereon tergite III; fifth article of peduncle as long as flagellum, with length:width ratio 7:1; flagellum with two articles, proximal article as long as the distal one (Fig. 6D).

**Pereon smooth.** Pereon tergite I with rounded posterolateral margin. Noduli laterales on pereonites I to IV distinctly more distant from the lateral margins than those on pereonites V to VII (Fig. 6A).

Pleon narrower than pereon (Fig. 6A). Telson triangular in distal part, with rounded apex, slightly surpassing uropod protopodites (Fig. 6C). Uropod exopodites long,



**Figure 7.** *Protracheoniscus ehsani* sp. n., male, paratype. **A** pleopod endopodite 1 **B–E** pleopod exopodite 1 **F** pleopod 2 **G** pleopod exopodite 3 **H** pleopod exopodite 4 **I** pleopod exopodite 5. Scale = 0.1 mm.

almost two times as long as telson (Fig. 6C). Pleopod exopodites I–V with monospiracular covered lungs (Fig. 7B–I).

Male: Pereopods I–III merus and carpus with brushes of setae (Fig. 6E). Pereopod I ischium triangular, carpus with depression on rostral surface equipped with slender scales; propodus narrow and long, proximal part of sternal margin concave with dense small scales, distal part bearing strong setae; dactylus with one dactylar and one unguis seta (Fig. 6E). Pereopod VII ischium with concave ventral margin, carpus with a triangle ridge in dorsal margin, propodus narrow and long, dactylus with one dactylar and one unguis seta (Fig. 6F,G). Pleopod exopodite I hind lobe variable in shape, with rounded short to truncate long distal margin; outer margin equipped with few to several strong setae (Fig. 7B–E); endopodite I straight with apical part slightly bent inwards bearing two rows of long setae (Fig. 7A). Pleopod endopodite II longer than

exopodite; exopodite triangular, outer margin convex equipped with a line of strong setae (Fig. 7F). Pleopod exopodites III–V as in Fig. 7G–I.

**Etymology.** The name of the species is after my late friend, Ehsan Entezari, who unfortunately passed away tragically during a field study.

**Remarks.** *Protracheoniscus ehsani* sp. n. is characterized by short lateral lobes of head, a triangle ridge on dorsal margin of male pereopod VII carpus, and two rows of long setae at apical part of male pleopod endopodite I. This species is similar to *P. darevskii*, but differs from that in the shape of pleopod endopodite and exopodite I, and in the conspicuous ridge on the dorsal margin of carpus of pereopod VII.

**Distribution.** Central Iran.

## Acknowledgments

I cordially thank Dr. Helmut Schmalfuss for his invaluable advice and comments on the draft of the manuscript and Dr. Stefano Taiti for improving the text scientifically. This study was financially supported by a grant from the University of Zanjan (Research Project, code 9147).

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# The deep phylogeny of jumping spiders (Araneae, Salticidae)

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## Abstract

In order to resolve better the deep relationships among salticid spiders, we compiled and analyzed a molecular dataset of 169 salticid taxa (and 7 outgroups) and 8 gene regions. This dataset adds many new taxa to previous analyses, especially among the non-salticoid salticids, as well as two new genes – *wingless* and myosin heavy chain. Both of these genes, and especially the better sampled *wingless*, confirm many of the relationships indicated by other genes. The cocalodines are placed as sister to lapsiines, in a broader clade with the spartaeines. Cocalodines, lapsiines, and spartaeines are each supported as monophyletic, though the first two have no known morphological synapomorphies. The lyssomanines appear to be non-monophyletic, of three separate groups: (1) *Lyssomanes* plus *Chinoscopus*, (2) *Onomastus*, and (3) the remainder of Old World species. Several previously-inferred relationships continue to be supported: hisponines as sister to the Salticoida, Amycoidea as sister to the remaining Salticoida, and Saltafresia as monophyletic. The relationship of *Salticus* with *Philaeus* and relatives is now considered well enough corroborated to move the latter into the subfamily Salticinae. A new clade consisting of the Plexippoida + Aelurilloida + Leptorche-steae + Salticinae is recognized. *Nungia* is found to be an astioid, and *Echeclus*, *Gedea* and *Diplocanthopoda* to be hasariines. The euophryines are corroborated as monophyletic. The agoriines *Agorius* and *Synagelides* are salticoids, within the sister group to amycoids, but their further placement is problematical, perhaps because of their nuclear ribosomal genes' high GC bias, as also seen in the similarly problematic *Eupoa*.

## Keywords

Jumping spiders, Salticidae, phylogeny, systematics

## Introduction

Salticid spiders, remarkable for their excellent vision (Land 1969, Blest et al. 1990), include more than 5000 species (Platnick 2014) with a great diversity of body forms and behaviours. While this diversity has long resisted phylogenetic organization, recent molecular studies (Maddison and Hedin 2003, Su et al. 2007, Maddison et al. 2008, Bodner and Maddison 2012, Zhang and Maddison 2013), aided by compilations of morphological taxonomic knowledge (Prószyński 2013) have resolved much of the phylogenetic structure of the family. One of the best-supported clades is the Salticoida, recognized by both morphological and molecular data (Maddison 1996, Maddison and Hedin 2003) and containing about 95% of the known species in the family. Within the Salticoida, large groups such as the Amycoidea, Astioida, Marpissoida and Plexippoida are well-corroborated (Maddison and Hedin 2003, Maddison et al. 2008). However, many of the deeper relationships of salticoids have been poorly resolved. Outside the Salticoida are the spartaeines, lyssomanines, and hisponines, showing ancestral features like limited tracheal systems, complex palpi, and the retention of a tarsal claw on the female palp. These non-salticoids (often called “basal salticids”) have been studied phylogenetically (Su et al. 2007), but with limited taxon sampling.

In this work we attempt to resolve more firmly the basic structure of the family by increasing the taxon sampling, especially among non-salticoid salticids, and by using additional genes. Two of the genes, *wingless* and myosin heavy chain, are new to salticid molecular phylogenetics. By building a dataset that has a greater number of genes among selected species, we hoped to obtain a phylogenetic resolution with stronger confidence.

## Methods

### Taxon sampling

Taxa included in the analysis are 169 species of salticids and representatives of four dionychnan families as outgroups (Table 1, Suppl. material 1). Based on previous phylogenetic work (Maddison and Hedin 2003, Maddison et al. 2008, Bodner and Maddison 2012, Zhang and Maddison 2013, in press), about 70 species of salticids from the major clade Salticoida were selected because they would represent most known major lineages, and because several genes are available for each (Table 1, Suppl. material 1). In addition, a few salticoids were added because their placement was unclear: *Agorius*, *Diplocanthopoda*, *Echeclus*, *Gedea*, *Nungia*, *Phaulostylus*, and *Synagelides*.

Our sample targeted especially the non-salticoid salticids, those that lie outside the major clade of familiar salticids (Maddison and Needham 2006). We included

most available data from non-salticoid salticids, both new data and data previously published by Su et al. (2007) and others (Maddison and Hedin 2003, Maddison and Needham 2006, Maddison et al. 2007, Bodner and Maddison 2012, Ruiz and Maddison 2012, Zhang and Maddison 2013, Maddison and Piascik, in press). Included for the first time in a molecular phylogeny are the cocalodines (Wanless 1982, Maddison 2009), which are Australasian non-salticoid salticids. Also analyzed for the first time are the lyssomanine genera *Chinoscopus* and *Pandisus*, the lapsiine *Lapsias*, and the spartaeines *Brettus*, *Meleon*, *Sparbambus*, and *Taraxella*.

Some previously-published data from non-salticoid salticids was either excluded or represented under a different species name here. Excluded are sequences of *Hispo* cf. *frenata*, because its limited data made it unstable in the analyses (see Maddison and Piascik 2014), "*Portia labiata*" from Su et al. (2007), because its identification is in doubt and no voucher specimen is available, and the actin 5C sequence of *Tomomingi* sp. voucher d243, which we discovered to have been a contaminant from the euophryine *Ilargus*. The species labeled as *Phaeacius yixin* by Su et al. (2007) is included here as "*Phaeacius* sp. [Hainan]", because the specimen was a juvenile female and thus identified with doubt; by its DNA we suspect it is *P. lancearius*. The specimen labeled as *Mintonia ramipalpis* by Su et al. (2007) is actually a female *M. silvicola*. This misidentification arose because of an error in male-female matching by Wanless (1984), whose female "*M. ramipalpis*" is actually the female of *M. silvicola*. The correct match of male and female *M. silvicola* is evident by intimate co-collecting in a recent expedition to Sarawak (Maddison and Piascik, unpublished) and in DNA sequence comparison. We have therefore blended data from Su et al.'s female with that from our males to represent *M. silvicola*.

Some of the species studied appear to be undescribed, or are doubtfully the same as described species. Following the usual convention, the names of some of our specimens includes "cf." to indicate that they may be the same as the mentioned species, "aff." to indicate that they are close to, but distinctly different from, the mentioned species. Figures 1–13 give illustrations of some of the undescribed species, in order to facilitate future association of our data with a species name. The species we refer to as "cf. *Phaeacius* [Sarawak]" (Figs 1, 2) is known from a single female and juvenile from Lambir Hills, Sarawak. It resembles *Phaeacius* but the legs are shorter, and the epigynum is distinctively different. *Phaeacius* sp. [Sarawak] (Figs 3, 4) is a fairly typical *Phaeacius* whose epigynum resembles that of *P. leytensis* Wijesinghe, 1991, but with the atria elongated posteriorly. *Onomastus* sp. [Guangxi] is shown in Fig. 5. *Sonoita* aff. *lightfooti* (Fig. 6) has longer grooves for the openings of the epigynum than *S. lightfooti*, and is distinctive in gene sequences as well. *Gelotia* sp. [Guangxi] (Fig. 7) has a palp resembling *G. syringopalpis*, but the tibial apophyses are much shorter. *Echeclus* sp. [Selangor] (Figs 8, 9) was identified as an *Echeclus* by the distinctive form of the palp tibia, and the embolus hidden behind a ledge of the tegulum, through which several dark sclerites can be seen (Prószyński 1987). It might equally well have been identified, by the same features, as a *Curubis* species (Zabka 1988). Indeed, the two genera are likely synonyms. "*Echeclus*" is used as that is the older name. *Taraxella* sp. [Johor]

**Table 1.** Specimens and sequences used in phylogenetic analyses, with GenBank numbers indicated. \* marks previously published sequences. Specimen localities given in Suppl. material 1.

Outgroups	Reference	28s	18s	wingless	myosin HC	actin 5c	histone 3	COI	16sNDI
Anyphaenidae: <i>Hibana</i> sp.	s318	AY297295*	KM033091		KM032961	KM032929		AY297422*	AY297295 / AY297358*
Gnaphosidae: <i>Cesonia</i> sp.	s319	AY297293; EF201663*		KM032996		EU522700*	DQ665720*	AY297420*	AY296711 / AY297356*
Miturgidae: <i>Chetivacanthium</i> sp.	s321	AY297294; EF201664*		KM032997		KM032928		AY297421*	AY296712 / AY297357*
Oxyopidae: <i>Oxyopes birmanicus</i> Thorell, 1887	Su et al. 2007	EF419032 / EF419065*	EF418998*				EF419126*	EF419097*	EF418969 / EF419150*
Philodromidae: <i>Philodromus duacensis</i> Keyserling, 1884	GR011	KM033130	KM033092	KM032998	KM032962				
Thomisidae: <i>Misumenops nepenthicola</i> (Pocock, 1898)	Su et al. 2007	EF419029 / EF419062*	EF418996*				EF419123*	EF419094*	EF418967 / EF419148*
Thomisidae: <i>Xysticus</i> sp.	s316	AY297296; EF201665*	KM033093			EU522701*	DQ665704*	AY297296*	AY296714 / AY297359*
<b>Lysosmanines</b>									
<i>Asemonea sichuanensis</i> Song & Chai, 1992	SC-03-0055		EF418986*					EF419082*	
<i>Asemonea sichuanensis</i> Song & Chai, 1992	MRB084	KM033131				KM032931			
<i>Asemonea</i> cf. <i>stella</i> Wanless, 1980	MRB083	JX145767*	KM033094			KM032930		JX145686*	
<i>Asemonea tenuipes</i> (O. P.-Cambridge, 1869)	d186	KM033132	KM033095	KM032999	KM032963	KM032932			
<i>Chinocopus</i> cf. <i>flavus</i> (Peckham, Peckham & Wheeler, 1889)	d273	KM033133	KM033096						KM032888
<i>Goleba lyna</i> Maddison & Zhang, 2006	d051	DQ665768*	KM033097	KM033000		EU522709*	DQ665707*	DQ665755*	
<i>Lysosmanes amazonicus</i> Peckham & Wheeler, 1889	ECU11-6112	KM033134							KM032889
<i>Lysosmanes anillanus</i> Peckham & Wheeler, 1889	d298	KM033135		KM033001					
<i>Lysosmanes</i> cf. <i>benderi</i> Logunov, 2002	ECU11-5402	KM033136							KM032890
<i>Lysosmanes</i> cf. <i>jeminus</i> Peckham & Wheeler, 1889	ECU11-5682	KM033137							KM032891
<i>Lysosmanes longipes</i> (Taczanowski, 1871)	MRB086	KM033138				KM032933		KM033208	KM032892
<i>Lysosmanes pauper</i> Mello-Leitão, 1945	d297	KM033139		KM033002					
<i>Lysosmanes taczanowskii</i> Galiano, 1980	ECU11-4193	KM033141							KM032894
<i>Lysosmanes tenuis</i> Peckham & Wheeler, 1889	ECU11-4869	KM033142							KM032895
<i>Lysosmanes viridis</i> (Walckenaer, 1837)	s160	AY297231*						AY297360*	AY296652 / AY297297*



	Reference	28s	18s	wingless	myosin HC	actin 5c	histone 3	COI	16sNDI
<i>Gelotia syringopalpis</i> Wanless, 1984	MRB105			KM033019				KM033212	KM032903
<i>Gelotia</i> sp. [Guangxi]	MRB199			KM033018		KM032939		KM033210	
<i>Gelotia</i> sp. [Yunnan]	LiD002-053-05		KM033102 <sup>s</sup>				KM033196 <sup>s</sup>	KM033211 <sup>s</sup>	
<i>Holcolaetis velleera</i> Simon, 1910	Su et al. 2007	EF419025 / EF419058*	EF418992*				EF419119*	EF419090*	EF418963 / EF419144*
<i>Holcolaetis cf. zuluensis</i> Lawrence, 1937	d036	DQ665770*	KM033103			EU522711*	DQ665721*	DQ665757*	
<i>Melcon aff. kenti</i> (Lessert, 1925)	d287	KM033159				KM032940			
<i>Mintonia mackiei</i> Wanless, 1984	SWK12-4202	KM033161							
<i>Mintonia cf. melinaensis</i> Wanless, 1984	d441	KM033160							
<i>Mintonia ramipalpis</i> (Thorell, 1890)	SWK12-1442	KM033162							
<i>Mintonia sibiricola</i> Wanless, 1987	d104			KM033020					KM032904
<i>Mintonia sibiricola</i> Wanless, 1987	SWK12-1653	KM033163							
<i>Mintonia sibiricola</i> Wanless, 1987	Su et al. 2007		EF418995*				EF419122*	EF419093*	
<i>Mintonia tauricornis</i> Wanless, 1984	d249	KM033164		KM033021		KM032941			KM032905
<i>Neobrettus tibialis</i> (Proszynski, 1978)	LiD-001-055-05	EF419030 / EF419063*					EF419124*	EF419095*	
<i>Neobrettus</i> sp. [Sarawak]	SWK12-1040	KM033165							
<i>Paracrypha wanlessi</i> Zabka & Kovac, 1996	Su et al. 2007	EF419033 / EF419066*	EF418999*					EF419098*	
<i>Phaeacius lancearius</i> (Thorell, 1895)	d111	DQ665775*		KM033022				DQ665759*	
<i>Phaeacius malayensis</i> Wanless, 1981	Su et al. 2007	EF419034 / EF419067*	EF419000*					EF418970 / EF419151*	
<i>Phaeacius</i> sp. [Guangxi]	LQ-24-06	KM033166 <sup>s</sup>	KM033104 <sup>s</sup>					KM033213 <sup>s</sup>	KM032906 <sup>s</sup>
<i>Phaeacius</i> sp. [Hainan]	Su et al. 2007	EF419035 / EF419068*	EF419001*						EF418971 / EF419152*
<i>Phaeacius</i> sp. [Sarawak]	SWK12-4541	KM033167							
<i>Portia africana</i> (Simon, 1886)	Su et al. 2007	EF419037 / EF419069*	EF419003*				EF419128*	EF419101*	
<i>Portia crassipalpis</i> (Peckham & Peckham, 1907)	SWK12-2354	KM033168							
<i>Portia fimbriata</i> (Doleschall, 1859)	LiD-001-04	EF419038 / EF419070*	EF419004*				EF419129*	EF419102*	EF418973 / EF419154*
<i>Portia heteroidea</i> Xie & Yin, 1991	Su et al. 2007	EF419039 / EF419071*	EF419005*				EF419130*	EF419103*	EF418974 / EF419155*

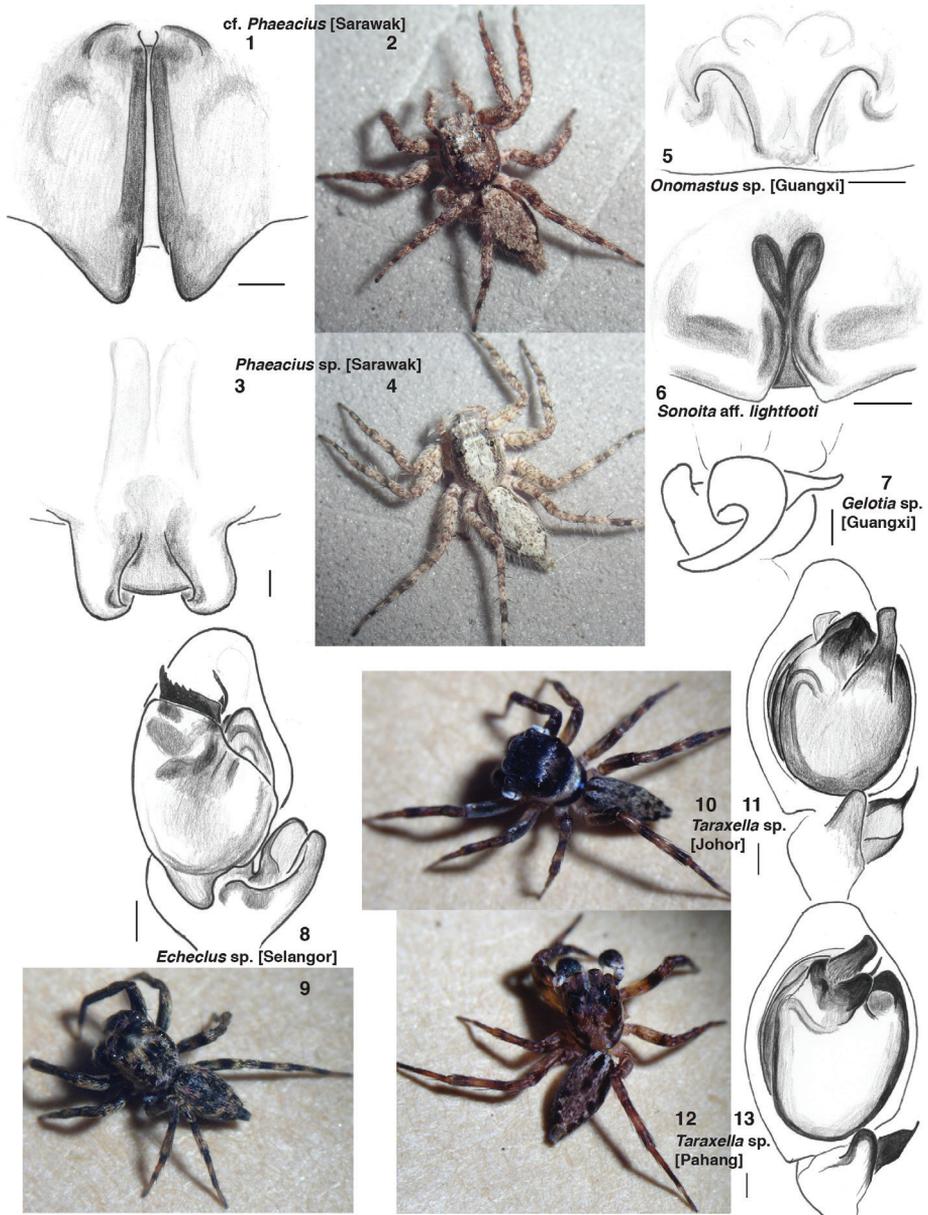
	Reference	28s	18s	wingless	myosin HC	actin 5c	histone 3	COI	16sNDI
<i>Portia jianfeng</i> Song & Zhu, 1998	Su et al. 2007	EF419040 / EF419072*	EF419006*				EF419104*	EF418975 / EF419156*	
<i>Portia labiata</i> (Thorell, 1887)	S206	AY297232*					AY297361*	AY296653 / AY297298*	
<i>Portia cf. schultzei</i> Karsch, 1878	d131	DQ665776*	KM033105	KM033023	KM032967	EU522718*	DQ665708*		
<i>Portia quei</i> Zabka, 1985	Su et al. 2007	EF419042 / EF419074*	EF419008*				EF419132*	EF418977 / EF419158*	
<i>Portia taiwanica</i> Zhang & Li, 2005	MRB103	KM033169			KM032942		KM033214	KM032907	
<i>Portia</i> sp. [Sichuan]	SC-03-0011	EF419043 / EF419075*	EF419009*				EF419133*	EF418978 / EF419159*	
<i>Sonoita lighfooti</i> Peckham & Peckham, 1903	d226	KM033170					KM033215		
<i>Sonoita</i> aff. <i>lighfooti</i> Peckham & Peckham, 1903	MRB200	JX145791*					JX145705*	JX145927*	
<i>Sparanobus gombakensis</i> Zhang, Woon & Li, 2006	d251	KM033171		KM033024		KM032943			
<i>Spartaeus jianfengensis</i> Song & Chai, 1991	Su et al. 2007	EF419045 / EF419076*	EF419011*				EF419109*	EF418980 / EF419161*	
<i>Spartaeus plamicki</i> Song, Chen & Gong, 1991	SC-03-069	EF419046 / EF419077*	EF419012*				EF419135*	EF418981 / EF419162*	
<i>Spartaeus spinimanus</i> (Thorell, 1878)	S199						KM033216	KM032908	
<i>Spartaeus thalamicus</i> Wanless, 1984	BV-004	EF419047 / EF419078*	EF419013*				EF419136*	EF418982 / EF419163*	
<i>Spartaeus uplandicus</i> Barrion & Litsinger, 1995	S185/S186	AY297233*					AY297363*	AY296655*	
<i>Spartaeus wildtruckeri</i> Wanless, 1987	Su et al. 2007	EF419048 / EF419079*	EF419014*				EF419137*	EF418983 / EF419164*	
<i>Taraxella</i> sp. [Johor]	d246	KM033172			KM032944			KM032909	
<i>Taraxella</i> sp. [Pahang]	d248	KM033173			KM032945				
<i>Taraxella</i> sp. [Pahang]	LiD-001-003-06		KM033106 <sup>s</sup>				KM033217 <sup>s</sup>	KM032910 <sup>s</sup>	
<i>Yaginumanis wanlessi</i> Zhang & Li, 2005	Su et al. 2007	EF419050 / EF419081*	EF419016*				EF419139*	EF418985 / EF419166*	
<b>Lapsines</b>									
<i>Galianona bryicola</i> Maddison, 2006	d124	DQ665771*	DQ665741*	KM033025		EU522706*	DQ665717*	DQ665758*	DQ665727*
<i>Galianona sacha</i> Maddison, 2006	d116	DQ665766*	DQ665734*	KM033026	KM032968	EU522707*	DQ665716*	DQ665754*	
<i>Lapsias camandea</i> Maddison, 2012	d442	KM033174							
<i>Lapsias guamanti</i> Maddison, 2012	UBC-SEM AR00191	KM033175		KM033027					

	Reference	28s	18s	wingless	myosin HC	actin 5c	histone 3	COI	16sNDI
<i>Lapsias lorax</i> Maddison, 2012	UBC-SEM AR00194	KM033176		KM033028					
<i>Socioladeopaktus lyra</i> Ruiz & Maddison, 2012	GR130	JQ312077		KM033029	JQ312074*				JQ312079*
<i>Thnandina bellavista</i> Maddison, 2012	d396	KM033177		KM033030					
<i>Thnandina cosanga</i> Maddison, 2012	d395	KM033178							
<i>Thnandina parocula</i> Maddison, 2006	d123	DQ665779*	KM033107			EU522720*	DQ665718*	DQ665761*	DQ665726*
<i>Thnandina parocula</i> Maddison, 2006	d394			KM033031	KM032969				
<b>Eupoa</b>									
<i>Eupoa nezha</i> Maddison & Zhang, 2007	d220/MRB102	EF201648*	EF201666*	KM033032				EF201668*	EF201667*
<b>Hisponines</b>									
cf. <i>Tomocyba</i> sp. [Madagascar]	d305	KM032881*							
<i>Hispo macfarlanei</i> Wanless, 1981	d404	KM032882*		KM032970					
<i>Hispo</i> sp. [Madagascar]	d309	KM032883*							
<i>Jerzego</i> cf. <i>alboguttatus</i> Simon, 1903	SWK12-4787	KM032884*							
<i>Jerzego corticicola</i> Maddison, 2014	SWK12-2900	KM032885*							KM032887*
<i>Massagris contortuplicata</i> Wsólowska & Haddiad, 2013	d082	DQ665772*	KM033108	KM033033			DQ665705*		DQ665722*
<i>Massagris schisma</i> Maddison & Zhang, 2006	d081	DQ665762*	KM033109	KM033034					DQ665728*
<i>Tomobella andasibe</i> (Maddison & Zhang, 2006)	d127	DQ665780*	DQ665752*	KM033035			KM033198		DQ665725*
<i>Tomocyba</i> sp. [Madagascar]	d306	KM032886*							
<i>Tomomingi</i> sp. [Gabon]	MRB243	JX145764*	KM033110	KM033036	KM032971	JX145850*		JX145684*	
<b>Salpicoida</b>									
<b>Agonines</b>									
<i>Agorius constrictus</i> Simon, 1901	d172					KM032953			
<i>Agorius constrictus</i> Simon, 1901	d213		KM033119	KM033072					KM032921
<i>Agorius</i> sp. [Selangor]	d299	KM033189		KM033073					
<i>Synagelides</i> cf. <i>lshanensis</i> Xie & Yin, 1990	d214			KM033074					
<i>Synagelides</i> cf. <i>palpalis</i> Zabka, 1985	MRB050								KM032922
<i>Synagelides</i> cf. <i>palpalis</i> Zabka, 1985	d225	KM033190						KM033226	
<b>Amycoids</b>									
<i>Cotinus</i> sp. [Ecuador]	MRB024	JX145746*	KM033120	KM033075	KM032987	JX145832*		JX145671*	JX145896*
<i>Hurtius vulpinus</i> Simon, 1901	S213	AY297239*						AY297368*	AY296662 / AY297306*

	Reference	28s	18s	wingless	myosin HC	actin 5c	histone 3	COI	16sNDI
<i>Hirtius cf. vulpinus</i> Simon, 1901	d156			KM033076		EU522712*	KM033203		
<i>Hypaeus aff. miles</i> Simon, 1900 [Ecuador]	d130	EU815499*	KM033121	KM033077	KM032988	EU522702*			KM032923
<i>Sarinda cutleri</i> (Richman, 1965)	MRB193	JX145744*		KM033078		KM032954		JX145669*	JX145895*
<i>Stiticus floricola polustris</i> (Peckham & Peckham, 1883)	d030	DQ665778*	KM033122	KM033079	KM032989		KM033204	DQ665760*	DQ665729*
<b>Astoids</b>									
<i>Anasia mollicomma</i> (L. Koch, 1880)	d046	EU815483*	EU815532*		KM032990	JX145834*	KM033205	EU815598*	EU815550*
<i>Helpis minitabunda</i> (L. Koch, 1880)	d265		KM033123	KM033080	KM032991	KM032955		KM033227	
<i>Ligura latidans</i> (Doleschall, 1859)	d175	JX145749*		KM033081		JX145835*		EF419091*	JX145898*
<i>Ligura latidans</i> (Doleschall, 1859)	LiD-001-027-05		EF418993*					EF419120*	
<i>Mopsis mormon</i> Karsch, 1878	d018	EU815470*	EU815529*	KM033082		JX145836*	KM033206	EU815586*	EU815565*
<i>Myrmanachne</i> sp. [Pahang]	d162	EU815507*	KM033124	KM033083	KM032992	JX145837*		EU815616*	
<i>Neon reticulatus</i> (Blackwall, 1853)	d283	KM033191	KM033125	KM033084	KM032993	KM032956			
<i>Nungia epignynidis</i> Zabka, 1985	d221	KM033192							KM032924
<i>Simaetha</i> sp.	d027	EU815477*	KM033126	KM033085		JX145839*		EU815592*	EU815546*
<i>Trite pennata</i> Simon, 1885	d035	EU815478*		KM033086	KM032957		KM033207	EU815593*	EU815547*
<b>Bavines</b>									
<i>Bavia aff. aerieps</i> Simon, 1877 [Sabah]	d079	EU815490*	KM033127			KM032958		EU815603*	KM032925
<i>Stagetus</i> sp. [Selangor]	MRB079	KM033193		KM033087		KM032959			KM032926
<b>Marjissoids</b>									
<i>Afromaregus</i> sp. [Gabon]	MRB262	JX145758*	KM033128	KM033088	KM032994	JX145842*		JX145682*	JX145905*
<i>Dendryphantus hastatus</i> (Clerck, 1757)	d043	EF201646*	KM033129	KM033089				KM033228	KM032927
<i>Platyrypus californicus</i> (Peckham & Peckham, 1888)	d316	KM033194		KM033090	KM032995	KM032960		KM033229	
<i>Rbene</i> sp. [Pahang]	LiD-001-021-05	EF419044*	EF419010*					EF419134*	EF418979 / EF419160*
<i>Tisaniba mulu</i> Zhang & Maddison, 2014	SWK12-1244	KM032876*							KM032880*
<b>Saltafresians</b>									
<i>Aelurillus cf. ater</i> (Kroneberg, 1875)	d140	EU815504*	EU815536*	KM033037	KM032972	JX145831*	KM033199	EU815615*	EU815564*
<i>Amphidarius complexus</i> Zhang & Maddison, 2012	JXZ035	KC615380*		KM033038		KC616069*		KC615640*	KC615806*
<i>Athamas cf. whitmei</i> O. P. Cambridge, 1877	JXZ345					KC616286*		KC615649*	KC615822*
<i>Baccharella pavida</i> Saïts & Jocqué, 2001	d195	EU815511*	EU815538*	KM033039	KM032973	KM032946		EU815618*	EU815569*
<i>Bathippus macrognathus</i> (Thorell, 1881)	JXZ372	KC615407*		KM033040		KC616305*			KC615835*

	Reference	28s	18s	wingless	myosin HC	actin 5c	histone 3	COI	16sNDI
<i>Bianor maculatus</i> (Keyserling, 1883)	d017	EU815469*		KM033041			KM033200	EU815585*	EU815542*
<i>Bristowia afra</i> Szűts, 2004	JXZ363	KC615409*				KC616301*			
<i>Bristowia afra</i> Szűts, 2004	MIR230							KM033218	
<i>Cheliceroides longipalpis</i> Zabka, 1985	d222		KM033111	KM033043		JX145830*		KM033219	EU815579*
<i>Cheliceroides</i> cf. <i>longipalpis</i> Zabka, 1985	d415	KM033179					KM033201	EU815581*	
<i>Chinuatius parvulus</i> (Banks, 1895)	d009	EU815464*	EU815525*	KM033044		JX145848*			
<i>Chinophrys pengi</i> Zhang & Maddison, 2012	JXZ145	KC615416*		KM033045		KC616146*			KC615843*
<i>Coryphalia lacuples</i> (Simon, 1888)	JXZ315	KC615390*		KM033046		KC616260*		KC615645*	KC615816*
<i>Cosmophasis umbratica</i> Simon, 1903	Su et al. 2007	EF419020*					EF419117*	EF419085*	EF418960 / EF419141*
<i>Gyaca nimbatia</i> (Thorell, 1881)	JXZ229	KC615474*		KM033047		KC616197*		KC615693*	KC615899*
<i>Diolenius varicus</i> Gardzińska & Zabka, 2006	JXZ349	KC615480*		KM033048		KC616290*		KC615695*	KC615905*
<i>Diplocanthopoda marina</i> Abraham, 1925	d209	KM033180				KM032947		KM033220	KM032911
<i>Eburneana</i> sp. [Gabon]	MIR231	KM033181		KM033049		JX145858*		KM033221	KM032912
<i>Echeilus</i> sp. [Selangor]	MIR089	KM033182				KM032948		KM033222	KM032913
<i>Euophrys frontalis</i> (Wälckenaer, 1802)	JXZ137	KC615536*		KM033050		KC616139*			KC615960*
<i>Evarcha prozysnyskii</i> Marusik & Logunov, 1998	d096	DQ665765*	KM033112			EU522704*			DQ665723*
<i>Evarcha prozysnyskii</i> Marusik & Logunov, 1998	d323			KM033051	KM032974				
<i>Freya deconata</i> (C. L. Koch, 1846)	d211	EU815521*	EU815539*		KM032975	EU522705*			JX145908*
<i>Gedeo</i> cf. <i>tibialis</i> Zabka, 1985	MIR090	KM033183				KM032949		KM033223	KM032914
<i>Habrocestum</i> cf. <i>albimanum</i> Simon, 1901	d132	EU815500*						EU815611*	EU815562*
<i>Habronattus borealis</i> (Banks, 1895)	d207	KM033184		KM033052	KM032976	KM032950		KM033224	KM032915
<i>Hasarius adansonii</i> (Audouin, 1826)	d295		KM033113	KM033053	KM032977				
<i>Hasarius adansonii</i> (Audouin, 1826)	S130/S131/S324	AV297281*						AV297409*	
<i>Heliophanus cupreus</i> (Wälckenaer, 1802)	d044	DQ665769*	KM033114			EU522710*	DQ665710*	DQ665756*	KM032916
<i>Idastrandia</i> cf. <i>orientalis</i> (Szombathy, 1915)	d108	EU815535; EU815496*	EU815535*			JX145852*		EU815608*	EU815560*
<i>Langerra</i> aff. <i>longicymbium</i> Song & Chai, 1991	d182	KM033185		KM033054					KM032917
<i>Lepioncheutes berolinensis</i> (C. L. Koch, 1846)	d086	EU815491*	EU815534*	KM033055				EU815604*	EU815556*
<i>Longarenus brachycephalus</i> Simon, 1903	MIR258	JX145798*		KM033056	KM032978	KM032951		JX145707*	KM032918
<i>Nannenus</i> sp. [Pahang]	d105	EU815493*		KM033057	KM032979	JX145853*			EU815558*
<i>Naphrys pulex</i> (Hentz, 1846)	JXZ081	JX145760*	KM033115		KM032980	JX145844*		KC615749*	JX145907*

	Reference	28s	18s	wingless	myosin HC	actin 5c	histone 3	COI	16sNDI
<i>Omoedus orbiculatus</i> (Keyserling, 1881)	d008							KC615792*	
<i>Omoedus orbiculatus</i> (Keyserling, 1881)	JXZ136	JX145762*	KM033116	KM033058		JX145846*	KM033202		
<i>Omoedus papuanus</i> Zhang & Maddison, 2012	JXZ286	KC615619*		KM033059		KC616234*		KC615790*	KC616042*
<i>Pellenes peninsularis</i> Emerton, 1925	d057	DQ665774*	KM033117	KM033060		JX145864*	DQ665712*		
<i>Pellenes peninsularis</i> Emerton, 1925	d400				KM032981				
<i>Phalostylus grammicus</i> Simon, 1902	d304	KM033186		KM033061					
<i>Philalena chrysops</i> (Poda, 1761)	d025	EU815475*	EU815530*	KM033062		JX145855*		EU815590*	EU815545*
<i>Phintella</i> sp. [Gabon]	d402	KM033187		KM033063					
<i>Plexippus paykulli</i> (Audouin, 1826)	LiD-001-029-05		EF419002*				EF419127*		
<i>Plexippus paykulli</i> (Audouin, 1826)	MRB016	JX145784*		KM033064		EU522713*			
<i>Plexippus paykulli</i> (Audouin, 1826)	S73							AY296674 / AY297384*	AY297317*
<i>Pochyta</i> cf. <i>paumosa</i> Simon, 1903	MRB257	JX145806*		KM033065		KM032983		JX145715*	KM032919
<i>Saitis barbipes</i> (Simon, 1868)	JXZ147	KC615589*		KM033066		KC616147*		KC615767*	KC616011*
<i>Salicicus senicus</i> (Clerck, 1757)	d003	DQ665777*	KM033118	KM033067		EU522719*	DQ665713*	JX145663*	AY296707 / AY297352*
<i>Thiania bhannoensis</i> Thorell, 1887	LiD-001-028-05	EF419049 / EF419080*	EF419015*				EF419138*	EF419113*	EF418984 / EF419165*
<i>Trydarsus</i> cf. <i>nobilitatus</i> (Nicolet, 1849)	MRB270	KM033188		KM033068		KM032985		KM033225	KM032920
<i>Tasitola hyrata</i> (Simon, 1903)	MRB226	JX145771*		KM033069		JX145856*		JX145689*	JX145912*
<i>Yllenus arenarius</i> Menge, 1868	d013		EU815527*					EU815583*	EU815541*
<i>Yllenus arenarius</i> Menge, 1868	JXZ173	JX145766*		KM033070		KM032986			
<i>Zabkattus fircatus</i> Zhang & Maddison, 2012	JXZ218	KC615503*		KM033071		KC616190*			KC615928*



**Figures 1–13.** Specimens of undescribed species. **1, 3, 5, 6** are of epigyna, ventral view; **8, 11, 13** of left palps, ventral view; **7** of the right palp tibia, retrolateral view. Scale bar 0.1 mm. **1–2** Female cf. *Phaeacius* [Sarawak], voucher SWK12–3728 **3–4** Female *Phaeacius* sp. [Sarawak], voucher SWK12–4541 **5** female *Onomastus* sp. [Guangxi], voucher MRB085 **6** Female *Sonoita* aff. *lightfooti*, voucher MRB200. **7** male *Gelotia* sp. [Guangxi], voucher MRB199. The drawing is reversed so as to appear to be the left palpus **8–9** Male *Echeclus* sp. [Selangor], voucher MRB089 **10–11** Male *Taraxella* sp. [Johor], voucher d246 for the palpus. The photo of the living male may or may not be of the same specimen **12–13** Male *Taraxella* sp. [Pahang], voucher d248. The photo of the living male may or may not be of the same specimen. Figures **1–13** are copyright ©2014 W.P. Maddison, released under a Creative Commons Attribution (CC-BY) 3.0 license.

(Figs 10, 11) and *Taraxella* sp. [Pahang] (Figs 12, 13) are typical species of *Taraxella*. The specimen MRB024 identified as *Cotinusa* sp. is the same as that named “unidentified thiodinine” by Bodner and Maddison (2012). The *Hypaeus* specimen (d130) was formerly identified as *Acragas* sp. (Bodner and Maddison 2012). The specimen d105 labeled as “*Nannenus lyriger*” by Maddison et al. (2008) is not *N. lyriger*, but another apparently undescribed species of *Nannenus*. The data for *Chelicerooides longipalpis* comes from two specimens, d222 which is clearly *C. longipalpis*, and d415 which may be a different but very closely related species. Notes on the undescribed hisponines are given by Maddison and Piascik (2014), whose data we use.

Specimens whose voucher ID’s (Table 1, Suppl. material 1) are of the form S###, d###, MRB###, or JXZ###, SWK12-####, or ECU11-####, where # is a digit, are deposited in the Spencer Entomological Collection of the Beaty Biodiversity Museum, University of British Columbia. The remaining vouchers are in the Lee Kong Chi-an Natural History Museum (formerly Raffles Museum for Biodiversity Research or RMBR), National University of Singapore.

In addition to analyses done on all 176 sampled taxa (“Complete”), subsets of taxa were analyzed alone. A first subset (“Salticoida”) of 78 taxa highlighted the Salticoida, with just 7 non-salticoid outgroup taxa (4 hisponines, 1 spartaeine, 1 coclodine, 1 lapsiine), in order to obtain an alignment that was less perturbed by highly divergent non-salticoids. A second subset highlighted the non-salticoids (“Non-salticoid”, 120 taxa), to obtain an alignment primarily for non-salticoid salticids, and also to be able to explore their relationships in more detail.

## Gene choice and sequencing

Eight genes were used for this analysis. Two are nuclear ribosomal genes, 28s and 18s (Maddison and Hedin 2003, Maddison et al. 2008). Four are nuclear protein coding genes: actin 5C (Vink et al. 2008, Bodner and Maddison 2012), *wingless* (Blackledge et al. 2009), myosin heavy chain (“myosin HC”, Blackledge and Hayashi, unpublished), and histone 3 (Su et al. 2007). Two mitochondrial regions were also used, CO1 and another region including 16s and NADH1 (“16sND1”, Hedin and Maddison 2001, Maddison and Hedin 2003). Following Bodner and Maddison (2012), the intron region of actin 5C was deleted from the analyses as it is highly variable and difficult to align.

The sequencing protocols for *wingless* and myosin HC are described below. For other genes, sequences marked “s” in Table 1 and Suppl. material 1 were obtained by the protocols of Su et al. (2007), all others by the protocols of Bodner and Maddison (2012) and Zhang and Maddison (2013).

For most *wingless* sequences, the forward and reverse primers used were respectively Spwgf1 and Spwgr1 (Blackledge et al. 2009). PCR amplification included a 2 min 94 °C denaturation and 35 cycles of 30 s at 94 °C, a 30 s annealing step at 52–57 °C, 30 s at 72 °C and one 3 min extension step at 72 °C. For some specimens this did not succeed in amplifying *wingless*, and for those we used a nested protocol starting

with outer primers wg550F and wgABRz (Wild and Maddison 2008). The resulting product was then amplified using two internal primers, forward Wnt8MBf1 5'-TGT-GCTACTCARACKTGYTGG-3' and reverse Wnt8MBr3 5'-ACAAWGTTCTGCA ACTCATRCG-3'. For both the external and internal reactions amplification was done with 2 min 94 °C denaturation and 37 cycles of 20 s at 94 °C, a 20 s annealing step at 52 °C (wg550F/wgABRz) or 56 °C (wnt8MBf1/wnt8MBr3), and 2 min at 72 °C, and no final extension. The nested protocol obtained sequences for *Bavia* aff. *aericeps* (voucher d389), *Hasarius adansonii* (d295), *Philodromus* sp. (GR011), *Simaetha* sp. (d027), and *Yllenus arenarius* (JXZ173). In other specimens, the nested protocol often resulted in amplification of a different member of the *wingless* family (e.g. WNT-8), but these were readily detected (and excluded) by BLASTing them to other genes in the NCBI database (<http://www.ncbi.nlm.nih.gov>).

The region of myosin HC sequenced corresponds mostly to an intron. Primers used are (forward) Myhc1f 5'-ACAACAATTCTTCAACCATCAC-3' and (reverse) Myhc5r 5'-CTTCCTCAAGGATGGACA-3' (Blackledge and Hayashi, unpublished). PCR amplification included a 2 min 95 °C denaturation and 35 cycles of 20–45 s at 95 °C, a 45 s annealing step at 52 °C, 1 min at 72 °C and one 10 min extension step at 72 °C. The boundary between the exon and intron was determined by aligning the salticid implicit amino acid translations against the known transcript for myosin HC in *Cyrtophora citricola* (Genbank accession AAM97635.1; Ruiz-Trillo et al. 2002).

Two small single-nucleotide errors in the sequences were corrected after the analyses but before submission to Genbank. These are near the ends of CO1 of MRB199 (*Gelotia* sp. [Guangxi]) and MRB231 (*Eburneana* sp. [Gabon]). Given that CO1 had little resolution, these are unlikely to have affected the results.

## Sequence alignment

Automatic multiple sequence alignment was performed by MAFFT (Katoh et al. 2002, 2005), run via the align package of Mesquite (prerelease of version 3, Maddison and Maddison 2014), aided by Mesquite for manual corrections and for alignment by amino acid. Coding regions were easily aligned by hand according to amino acid translations. This was done starting with an initial automated nucleotide alignment, followed by hand correction in Mesquite using the Color Nucleotide By Amino Acid function to reveal amino acid translation. Non-coding regions (28s, 18s, noncoding region of 16sND1, myosin HC intron) were aligned by MAFFT using the L-INS-i option (--localpair --maxiterate 1000). Mesquite was used to color the matrix via the option “Highlight Apparently Slightly Misaligned Regions” so as to identify regions that needed correction. These were almost always near the ends of sequences.

Alignment was done separately on the Complete, Non-salticoid and Salticoida datasets. Following the MAFFT alignment, the Salticoida dataset required 5 small realignments by hand in 18s. The first 60 positions in the initial alignment of 16s were also realigned locally, and in addition 8 minor shifts by one or two positions were made by hand. The Non-salticoid dataset required three simple hand fixes in 28s. The

first 24 positions of 16s in the initial alignment were realigned by MAFFT in isolation because of several obvious misalignments. The Complete dataset appeared poorly aligned in 28s from sites 375 to 489 in the initial alignment, which were therefore realigned by MAFFT in isolation. The first 60 positions in the initial alignment of 16s were also realigned locally, and in addition 8 minor shifts by one or two positions were made by hand. Five small shifts were performed by hand for 18s. Many analyses were done with different variants of the alignments as this study was progressing, and the phylogenetic trees remained substantially consistent.

### **Phylogenetic analysis**

Phylogenetic analyses using maximum likelihood were run using RAxML version 7.2.8alpha (Stamatakis 2006a, 2006b). The protein coding genes and 16sND1 were each divided into partitions. Protein coding regions were divided into one partition for 1st and 2nd codon positions, and another partition for third codon positions. Introns and non-coding regions were treated as separate partitions. For the fused 8 gene analyses, there were 7 partitions total: (1) 1st + 2nd codon positions in nuclear genes, (2) 3rd codon position nuclear, (3) nuclear intron, (4) nuclear ribosomal, (5) 1st + 2nd codon positions mitochondrial, (6) 3rd codon position mitochondrial, (7) noncoding mitochondrial. Each partition was permitted to have its own model parameters.

Analyses were done for each gene region separately with the Complete taxon set. In addition, analyses fusing all 8 genes were done for the Non-salticoid and Salticoida taxon sets. For all of these, RAxML runs assuming the GTRCAT model were used with 100 search replicates, to seek maximum likelihood trees. In addition, likelihood bootstrap analysis was performed with 500-1500 bootstrap replicates (as indicated in the figures), each involving a single search replicate. Phylogenetic analyses using GARLI version 1.0.699 (Zwickl 2006) under the model GTR+gamma+I were also done but are not reported; they resulted in substantially similar trees.

### **Data resources**

The data underpinning the analyses reported in this paper are deposited in the Dryad Data Repository at doi: 10.5061/dryad.v53h1.

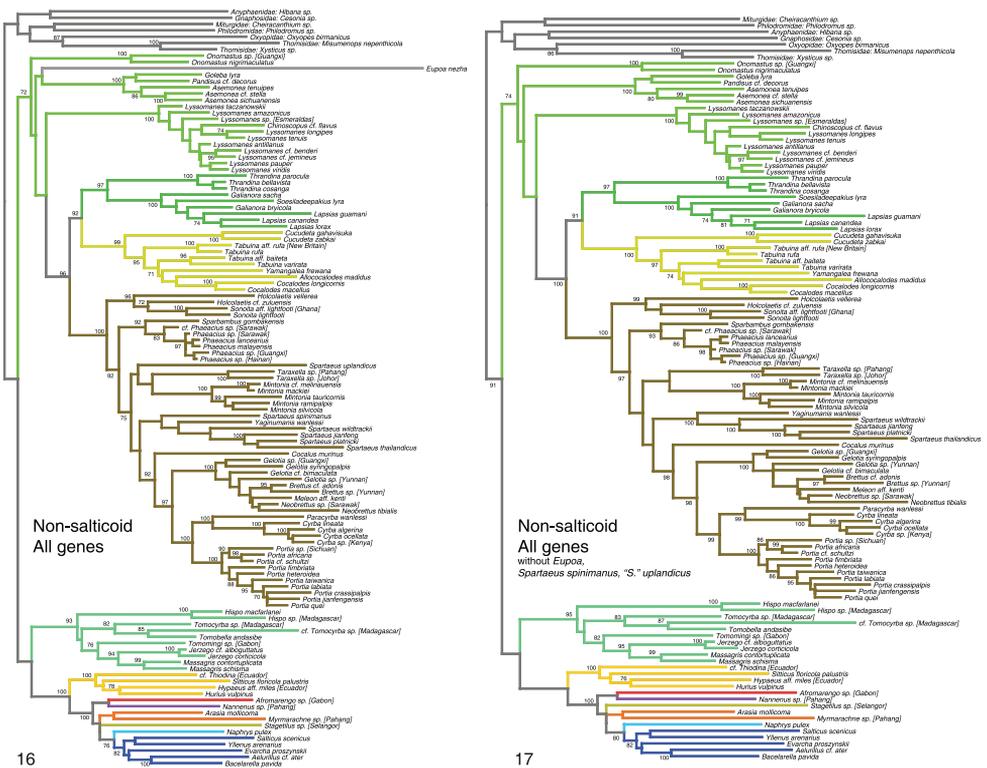
### **Results**

Sequences obtained and used in analyses are indicated in Table 1 and Suppl. material 1, along with those sequences taken from the literature.

Figure 14 summarizes the results of the phylogenetic analyses, which are given in more detail in Figures 15–27. Colors assigned to clades in Figure 14 are shown in the remaining figures. Figures 15–19 show the All Genes results for the Complete, Non-



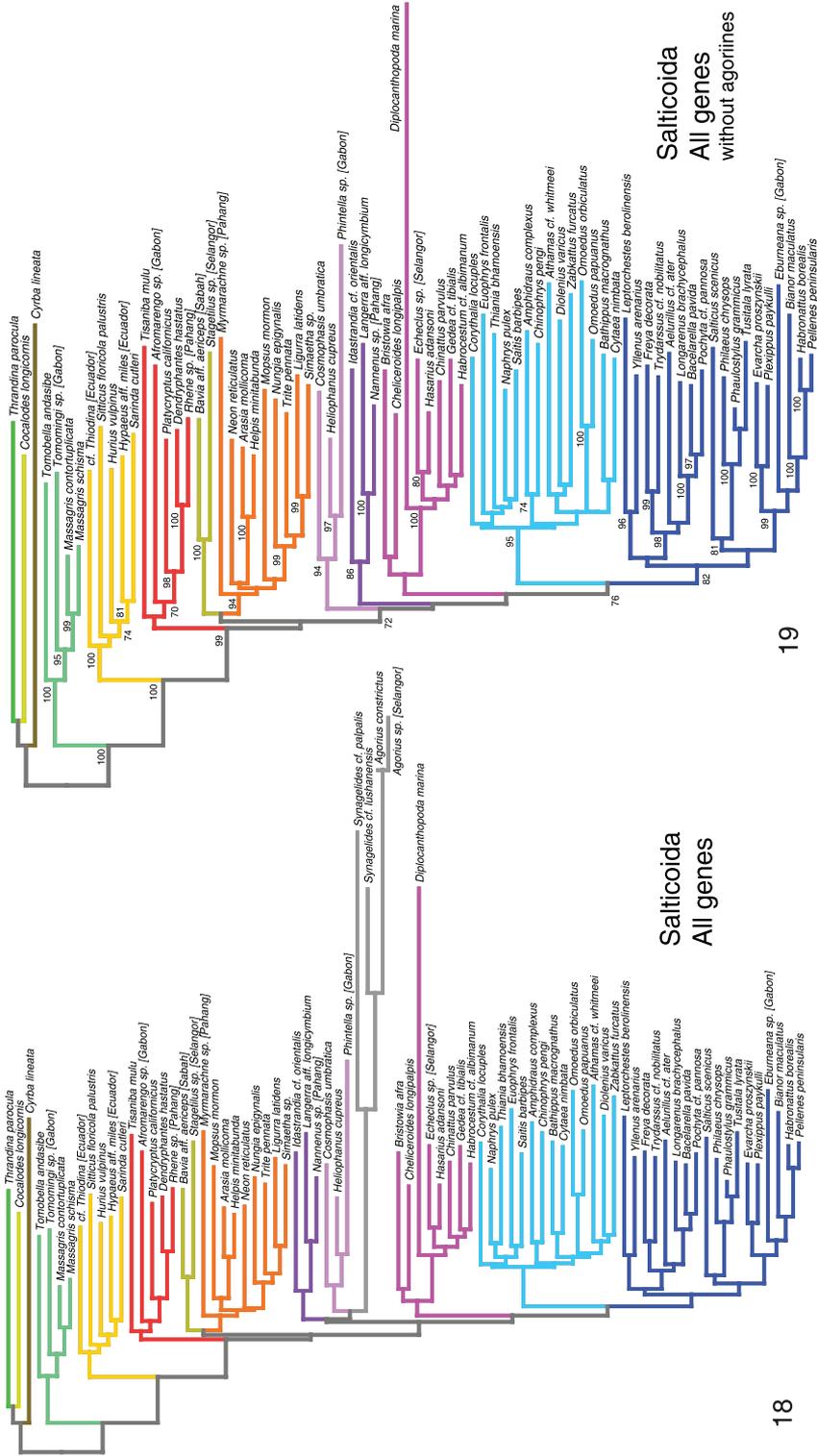




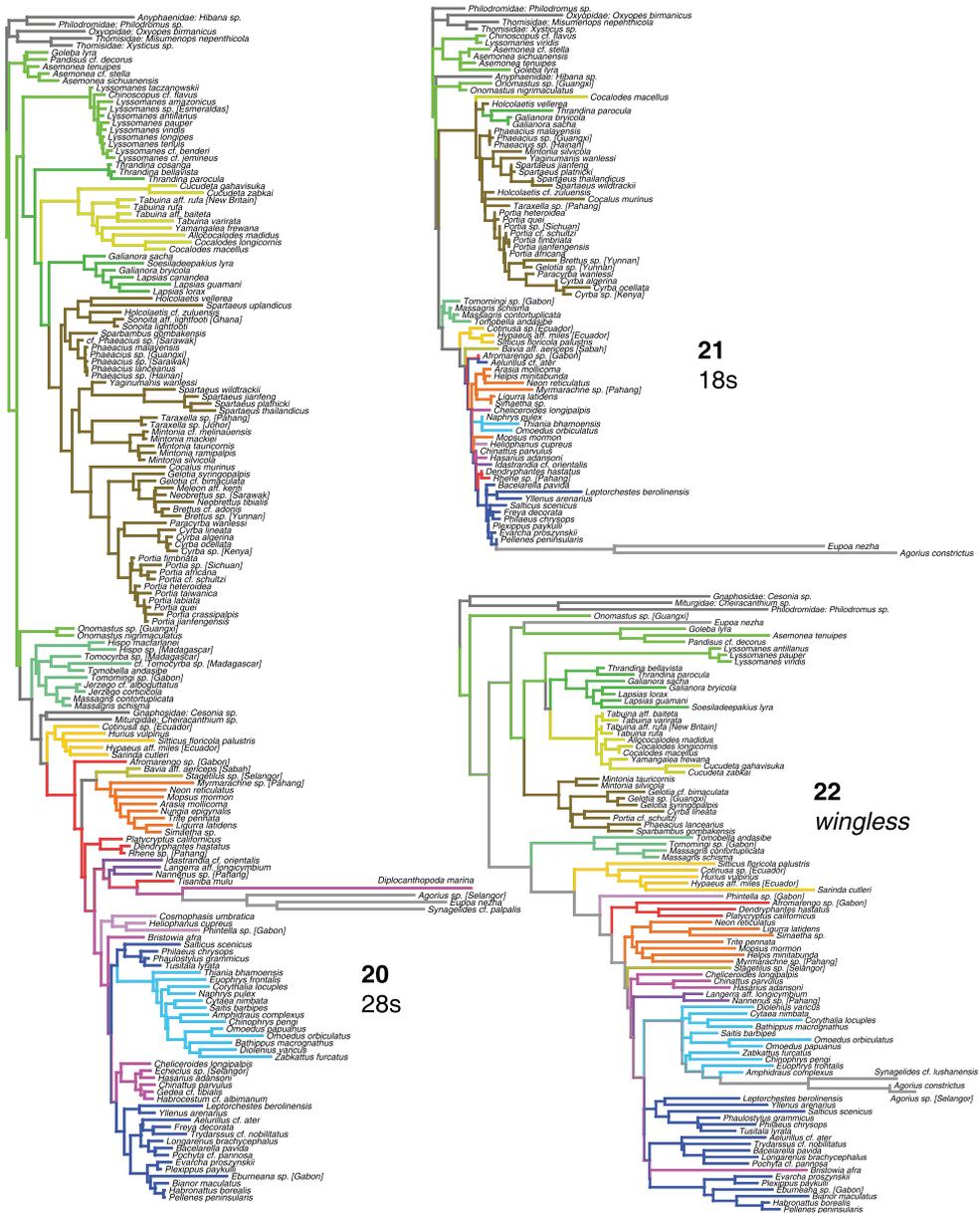
**Figures 16–17.** Phylogeny from Non-salticoid dataset, All Genes analysis. Numbers beside branches show percentage of RAxML likelihood bootstrap replicates with clade. **16** Non-salticoid analysis with all taxa included (1500 bootstrap replicates used) **17** Non-salticoid analysis with *Eupoidea*, *Sparteaus spinimanus*, and “S.” *uplandicus* excluded (500 bootstrap replicates used). Colors of branches are the same as those highlighting taxa in Fig. 14.

salticoid and Salticoida datasets. Figures 20–27 show the results for individual genes analyzed separately.

Several taxa stood out as being problematical, especially for nuclear ribosomal genes. *Eupoidea* was not only difficult to sequence (Maddison et al. 2007) but its 28s and 18s genes stand as outliers in alignments, remarkably different from other salticoids. The same holds for the agoriniines *Agorius* and *Synagelides* and, in 28s, for the hasariine *Diplocanthopoda*. These sequences do not appear to be contaminants, as they BLAST in the NCBI database to salticids. In analyses with just 28s or 18s, these taxa tend to appear on long branches, wandering to different parts of the salticid phylogeny in different analyses, attaching themselves together and to clearly inappropriate relatives (e.g. within the pellenines, Fig. 21). This instability and unexpected placement are likely artifacts due to long branch attraction (Felsenstein 1978), possibly related to compositional bias (Hasegawa and Hashimoto 1993). *Eupoidea* and the agoriniines have the highest GC bias of the sample (0.72–0.78, compared to 0.60–0.69 for all other species) in 28s, and are similar outliers in 18s. With *wingless*, *Eupoidea* appears on a normal-length branch



**Figures 18–19.** Phylogeny from Salticoida dataset, All Genes analysis. **18** Salticoida analysis with all taxa included **19** Salticoida analysis with *Agorinus* and *Synagelides* excluded. Numbers beside branches show percentage of 1000 RAxML likelihood bootstrap replicates with clade. Colors of branches are the same as those highlighting taxa in Fig. 14.



**Figures 20–22.** Phylogeny from gene regions analyzed alone, complete taxon sample. **20** 28s **21** 18s **22** *wingless*. Colors of branches are the same as those highlighting taxa in Fig. 14.

(Fig. 22). However, the agoriines with *wingless* are on a long branch in an unlikely place, within the euphryines (Fig. 22). Their placement is unstable: in slight variants of the analyses they come out in other places. There is nothing obviously unusual about the *wingless* sequences in agoriines, but whatever has shifted the GC bias in the nuclear ribosomal genes might also be affecting the rest of the genome. When *Eupo* and the



are generally those for analysis with *Eupoia* and the agoriines excluded. *Diplocanthopoda* was left in the bootstrap analyses, because CO1, actin 5C and 16sND1 all agree on a clear placement in the hasariines.

## Discussion

Many of the salticid clades now recognized by molecular data had been previously recognized by morphological data. For instance, Wanless (1980, 1984, 1985) recognized the three distinct lyssomanine groups and the Spartaeinae. The Salticoida was strongly supported by many morphological characters (Maddison 1988, 1996, Maddison and Hedin 2003), except that the status of the hisponines was unclear. Wanless (1981) implicitly included the hisponines within the salticoids, while Maddison (1996) did not consider the hisponines in his listing of salticoid synapomorphies. Other groups whose previous formulation by morphology mostly or entirely matches their current boundaries by molecular data are the marpissines (Barnes 1958), euophryines (Prószyński 1976), amycines (Galiano 1968), heliophanines (Maddison 1987), dendryphantines (Maddison 1996), and plexippines (Maddison 1988). At the finer scale, morphological systematics gave us concepts for many genera that are concordant with more recent data.

However, the first molecular data for salticid phylogeny as a whole (Maddison and Hedin 2003) uncovered several unanticipated groups, including the Amycoidea, Plexippoida, and Marpissoida. Further data revealed the Astioida and Aelurilloida (Maddison et al. 2008), and later the Saltafresia (Bodner and Maddison 2012). These are major groups within the Salticoida, each uniting several subfamilies.

## Deepest relationships

Our results help resolve or add strength to relationships at the deepest level of salticid phylogeny. Wanless (1980) recognized three major subdivisions of lyssomanines: (1) the New World genera *Lyssomanes* and *Chinoscopus*, (2) the Asian *Onomastus*, and (3) the remaining Old World genera including *Asemonea*. He suggested these three groups are so distinct that they may not belong together. The molecular data agree: the three groups' divisions are so deep that their relationships have not yet been recovered, and it is possible, even likely, that they do not form a monophyletic group. Different analyses give different results of the relationships of these three, with some showing the New World genera as sister to the spartaeine-lapsiine-cocalodine clade (as recovered by Su et al. 2007), other results showing *Onomastus* in that role, and others showing the three lyssomanine groups together.

Spartaeines, lapsiines and cocalodines form a clade (node 1, Fig. 14). Although Rodrigo and Jackson (1992) concluded that spartaelines, *Holcolaetis* and the *Cocalodes* group form a clade (they were unaware of lapsiines), our analysis provides the first support for such an arrangement – their analysis included only a single taxon outside the

group, and therefore it could not speak to the monophyly of the group. Our new result is intuitively appealing, as it groups together all of the extant medium-sized generalized non-salticoids/non-hisponines that are typically brown or gray. However, these presumably are or could be plesiomorphic traits; there had been no obvious reason to expect the spartaeines, lapsiines and cocalodines should have fallen together. There is no known morphological synapomorphy of this clade.

Within this spartaeine-lapsiine-cocalodine clade, the subclade historically best known by morphology is Wanless's (1984) narrow version of the Spartaeinae, delimited by the presence of a tegular furrow (Wanless 1984). The Spartaeinae sensu stricto is primarily Afro-Eurasian, with a few Australasian species. Outside of this clade, there are no clear morphological synapomorphies defining subclades, and yet there is a striking geographical pattern: all of the Neotropical species belong to a clade, thus forming the lapsiines, while all of the Australasian species belong to a clade, thus forming the cocalodines. It is unsatisfying that we lack morphological synapomorphies for the lapsiines or cocalodines. The data suggest that the lapsiines and cocalodines are sister groups, with spartaeines more distant (Fig. 14).

Our results continue to support the relationship of hisponines with the Salticoida (node 2, Fig. 14; Figs 15–17; Maddison and Needham 2006, Bodner and Maddison 2012).

The placement of *Eupoa* remains unclear. As noted under Results, the 28s and 18s genes of *Eupoa* may be unreliable phylogenetically, although Maddison et al. 2007 found those genes to place *Eupoa* among non-salticoid salticids. In our results *Eupoa* likewise has no clear placement, except for being outside the clade of Salticoida+Hisponinae. This result appears in the Non-salticoid and Complete datasets, and with the separate analyses of *wingless*, CO1, and 16sND1.

## Spartaeinae

Our results strongly support the monophyly of the Spartaeinae sensu Su et al. (2007), placing *Holcolaetis* and *Sonoita* together with the Spartaeinae in the narrow sense. This is concordant with Wanless's (1985) hypothesis that *Holcolaetis* and *Sonoita* formed a clade with the spartaeines to the exclusion of *Cocalodes*. The analyses of Su et al. (2007) did not sample *Sparbambus*, *Taraxella*, *Brettus* or *Meleon*, but otherwise their results were largely concordant with ours, which are: (1) *Phaeacius* (with *Sparbambus*) diverge deep, (2) *Yaginumanus* is sister to *Spartaeus*, (3) *Gelotia*, *Neobrettus*, *Brettus* and *Meleon* are monophyletic, (4) *Paracyrba* and *Cyrba* are sisters, (5) *Portia* is sister to *Cyrba* and *Paracyrba*. There is strong support for *Gelotia* through *Cyrba* as a monophyletic group, and for their relationship with *Cocalus*. By our data the exact placements of *Taraxella* and *Mintonia* are unclear.

A few spartaeine taxa in our analyses were problematical in appearing unstable, having different placements by different analyses. One of these is *Spartaeus spinimanus*, for which we have only 16sND1 and CO1 data, both gene regions that appear to evolve too quickly for reliable phylogenetic placement at this level (Bodner and Maddison 2012, Zhang and

Maddison 2013). The other is “*Spartaeus*” *uplandicus*, whose 28s sequence appears strongly divergent from others. This sequence is from Maddison and Hedin (2003, as “unidentified spartaeine”, vouchers 185 and 186), and it groups “*S.*” *uplandicus* with one species of *Holcolaetis*, against the placements by morphology, CO1 and 16sND1. There is a chance that this gene was mis-sequenced in “*S.*” *uplandicus*. Because of the instability generated, we excluded *S. spinimanus* and “*S.*” *uplandicus* from our analyses giving bootstrap results.

Because of the concordance of our phylogenetic results with those of Su et al. (2007), our phylogeny continues to support their conclusions on the stepwise evolution of a complex predatory strategy in spartaeines.

### Deep Salticoid relationships

The Salticoida’s basal divergence places the primarily-Neotropical Amycoida as sister group to an unnamed clade (node 3, Fig. 14) that contains most of salticid diversity. This surprising result, first discovered by Maddison and Hedin (2003), had very strong support in the analyses of Bodner and Maddison (2012). We here add support from two new genes, *wingless* and myosin HC, both of which independently resolve both the Amycoida and its sister group as monophyletic.

There have been hints of a clade uniting the Marpissoida, Astioida and baviines (Bodner and Maddison 2012). In our analyses the clade does not receive bootstrap support above 50% in the Complete or Salticoida analyses. The maximum likelihood trees either show the three as monophyletic or not, depending on taxon inclusion and details of the analysis (e.g., Figs 15 and 18). At present we must conclude the relationship between these three and the Saltafresia is unresolved.

### Astioida

The astioids as delimited by Maddison et al. (2008) continue to be resolved as a clade, with new support from myosin HC and *wingless* (Figs 18, 22, 23). Although the body form of *Nungia* resembles that of baviines and the marpissoid *Metacyrba*, our data clearly place it as an astioid.

### Saltafresia

Bodner and Maddison (2012) proposed a clade, the Saltafresia, containing salticoids other than amycoids, astioids, baviines and marpissoids. They found this clade reasonably well supported – 0.78 likelihood bootstrap and 1.0 posterior probability – but no single gene supported it on its own. Our data here continue to support it when all genes are combined. Two genes support it separately, with the exception of single taxa: 28s (but *Tisaniba* is included) and *wingless* (but *Phintella* is excluded).

## Hasarieae

Previous work had established *Habrocestum* and *Chinattus* as close relatives of *Hasarius* (Maddison et al. 2008). We here add several more genera to the group, all Asian. These are *Gedeia*, *Echeclus* and *Diplocanthopoda*. The relationships among these genera are not clearly resolved except for a well-supported relationship between *Hasarius* and *Echeclus* (Figs 14, 19).

## Salticinae

The relationship between *Salticus* and the *Philaeus* group proposed by Maddison et al. (2008) receives additional support from *wingless*, along with previously-demonstrated support from 28s and actin. With high posterior probabilities (Bodner and Maddison 2008) and reasonable likelihood bootstrap values (Figs 15, 19), and supported by different genes independently (Figs 20, 22, 24), this relationship can now be considered sufficiently secure that we here formally place the genera of the *Philaeus* group into a subfamily – the Salticinae. In addition to genera previously analyzed (*Salticus*, *Philaeus*, *Carrhotus*, *Tusitala*, *Mogrus*, and *Pignus*) the subfamily also includes *Phaulostylus*, which is related to *Tusitala* (Fig. 14).

## Plexippoida+Aelurilloida+Leptorchestae+Salticinae (Node 5)

A set of four major groups (plexippoids, aelurilloids, leptorchestines and the Salticinae) form a clade in our analyses (node 5, Fig. 14). This group is resolved in the All Genes analyses with high bootstrap values, and it appears, almost, in the independent analyses of each of three genes (18s, *wingless*, myosin HC). We say “almost” because three of the genes have one or two taxa missing from or added to the group (Fig. 14). While we believe the evidence is good that these form a clade, there is a possibility that the Euophryinae might also fall nested within it. For instance, in the analyses of Bodner and Maddison (2012) the euophryines were placed as sister to the plexippoids. In our analyses the Euophryinae is placed as sister to the Plexippoida + Aelurilloida + Leptorchestae + Salticinae.

This major clade is almost entirely Afro-Eurasian, with the plexippoid *Habronattus* being the only exception with more than a handful of species (others are *Pellenes*, *Sibianor*, *Evarcha*, *Phlegra*, *Paramarpissa* and *Salticus*, each with fewer than 15 described New World species).

## Euophryinae

The 14 euophryine taxa in the analyses are resolved strongly as a monophyletic group. This is a stronger test of monophyly than that of Zhang and Maddison (2013), because

it includes additional genes and more non-euophryine taxa. The All Genes analyses, along with *wingless* and myosin HC individually, suggest that the euophryines are the sister group to node 5 (Fig. 14).

### Agoriines

Morphologically, the antlike agoriines *Agorius* and *Synagelides* are puzzling, with strangely contorted legs and unusual genitalia (Szüts 2003, Logunov and Hereward 2006, Prószyński 2009). While they appear to be salticoids, morphology has given little guidance as to their placement. As noted already, their 28s and 18s genes appear anomalous, and give no clear indication as to their relationships. In the All Genes analysis their placement is ambiguous, though they appear to be salticoids. In an attempt to determine their placement, an additional analysis was done, using a dataset that included *Agorius constrictus* and a chimera of *Synagelides* cf. *lushanensis* and *S.* cf. *palpalis* (to have a single *Synagelides* taxon with three genes). The aberrant nuclear ribosomal genes of agoriines were excluded from the analysis. The other taxa included were the 70 taxa having at least 4 genes other than CO1 and histone 3. A RAxML likelihood analyses placed *Agorius* and *Synagelides* within the sister group of the Amycoidea (node 3, Figure 14) with high support (bootstrap percentage 88), but exactly where was highly unstable. Among the 100 likelihood non-bootstrap search replicates were 7 different placements: sister to leptorchestines, sister to baviines, sister to node 5 in Figure 14, sister to the Saltafresia, sister to astioids+marpissoids+baviines, sister to node 3, or sister to node 3 without the baviines. While a relationship with the leptorchestines is appealing, as it would allow their antlike body forms to be homologous, the best we can say at present is that agoriines likely belong within the sister group of amycoids (node 3).

### Generic limits

Most of the genera for which we have multiple species – e.g., *Asemonea*, *Portia*, *Mintonia*, *Phaeacius*, *Cyrba* – are inferred to be monophyletic in our analyses, corroborating existing concepts based on morphology. The clearest exception is *Tabuina*, in which *T. rufa* and the similar *T.* aff. *rufa* fall apart from the type species *T. varirata*, which had been anticipated as a possibility by Maddison (2009). *Lyssomanes*, *Galianora*, and *Gelotia* are reconstructed as paraphyletic, but in each case the bootstrap values are low.

The placement of cf. *Phaeacius* [Sarawak] as sister to *Phaeacius*, with strong molecular divergence from the other species, would justify establishing a new genus for it.

### Behaviour of individual genes

Previous work (Maddison and Hedin 2003, Bodner and Maddison 2012) has suggested that 28s and actin 5C are phylogenetically informative to a reasonable degree for

deeper salticid phylogeny, insofar as their results are concordant with summed genes analyses, morphological resemblances, and biogeographical patterns. 16sND1 is useful at the shallower levels (Hedin and Maddison 2001) but has difficulties recovering deeper relationships, while CO1 struggles through both shallow and deep levels (Maddison and Hedin 2003, Bodner and Maddison 2012).

One surprise in our analyses was the informative behaviour of CO1 in deeper relationships among the non-salticoid salticids. Although CO1 is almost nonsensical in its inferred relationships within the Salticoida, it succeeds in recovering the Spartaeinae, the Spartaeinae sensu Wanless, the lapsiines, and the Salticoida as monophyletic.

Two new genes added, *wingless*, myosin HC, both show clear concordance with the 28s and previous all genes analyses. *Wingless* supports many of the previously recognized clades, including the Salticoida, Amycoida, the sister clade to Amycoida, Plexippoida, Marpissoida (in part), Astioida (in part), Spartaeinae sensu Wanless, and lapsiines. We find it encouraging that a haphazardly chosen protein-coding gene, independent from 28s, supports previous molecular results in Salticidae. There are still, however, many aspects of salticid relationships yet to be resolved, such as the deepest relationships in the family, including the relationships among the three subgroups of lyssomanines, the placement of *Eupoa* and the agoriines, and the relationships among astioids, marpissoids, baviines and the *Saltafresia*. With the coming era of genomic data, we expect large quantities of new data will be available for exploring these relationships.

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## **Supplementary material I**

### **Specimens used in phylogenetic analyses, with localities and GenBank numbers of sequences indicated.**

Authors: Wayne Maddison, Daiqin Li, Melissa Bodner, Junxia Zhang, Xu Xin, Qingqing Liu, Fengxiang Liu

Data type: Occurrence; geographic locality; sex.

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# A taxonomic revision of the *Neoserica* (sensu lato) *pilosula* group (Coleoptera, Scarabaeidae, Sericini)

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## Abstract

Nine new species of the *Neoserica* (sensu lato) *pilosula* Moser, 1915, group are described from China: *Neoserica curvipennis* sp. n., *N. emeishanensis* sp. n., *N. lincangensis* sp. n., *N. ludingensis* sp. n., *N. lushuiana* sp. n., *N. rangshuiensis* sp. n., *N. shennongjiaensis* sp. n., *N. tianeana* sp. n., and *N. weibaoshanica* sp. n. The lectotype of *Neoserica pilosula* Moser, 1915, is designated. Habitus and male genitalia are illustrated, a key to the species of the group and a map of species distribution are given.

## Keywords

Beetles, chafers, *Neoserica*, China, new species

## Introduction

*Neoserica* Brenske, 1897 is one of the most species-rich groups of Sericini. It comprises nearly 200 taxa. Since the designation of the type species of *Neoserica* (Pope 1960) and the redefinition of the genus based on a first revision of close allies of the type species (Ahrens 2003), many species are so far grouped under *Neoserica* being not directly related

to *Neoserica* sensu stricto (Ahrens 2003). We preliminarily consider them in *Neoserica* sensu lato (e.g. Ahrens 2004), a collective group that was found to be neither monophyletic (Ahrens and Vogler 2008) nor related to *Neoserica* sensu stricto (Ahrens 2003). The current study continues a series of the taxonomic revisions of *Neoserica* species groups (Ahrens et al. 2014a, Ahrens et al. 2014b, Ahrens et al. in press) based on which hopefully their relationship and their right classification can be subsequently established.

In the present paper we explore the taxonomy of the representatives related to *Neoserica pilosula* Moser, 1915, originally described from Yunnan (China). According to our present knowledge, the species group is restricted to the mountain areas of Southwest China. The species of this group are characterised by a bidentate protibia, an antennal club composed of four antennomeres in both sexes, a short labrum that bears a transverse rim of very dense, short and robust setae, and by a densely setose dorsal surface of the body. The *Neoserica pilosula* group shares the transverse rim of setae on labrum with most species of the *Neoserica* (s.l.) *lubrica* group (Ahrens 2004). The species of the latter group, however, have a glabrous dorsal surface and an antennal club composed of three antennomeres in females. Here, nine new species are described, all originating from Southwest China.

## Material and methods

The terminology and methods used for measurements, specimen dissection and genital preparation follow Ahrens (2004). Data from specimens examined are cited in the text with original label contents given in quotation marks verbatim, multiple labels are separated by a “/”. Descriptions, if not otherwise stated, are based on the holotype specimen. Male genitalia were glued to a small pointed card and photographed in both lateral and dorsal view using a stereomicroscope Leica M125 with a Leica DC420C digital camera. A number of single images were combined in order to obtain an entirely focused image using the automontage software as implemented in Leica Application Suite (V3.3.0). The resulting images were subsequently digitally edited to eliminate background using Artweaver software. Based on the geographical coordinates obtained from the labels and Google map (<https://www.google.de/maps/>), the distribution map was generated using Q-GIS 2.0.1 and Adobe Photoshop CS4 software.

Type specimens and additional material examined are deposited in the following institutions:

- CPPB** Collection P. Pacholátka, Brno, Czech Republic;
- HBUM** Museum of Hebei University, Baoding (Hebei Prov.), China;
- IZAS** Institute of Zoology, Chinese Academy of Sciences, Beijing, China;
- NMPC** National Museum Prague (Natural History), Czech Republic;
- ZFMK** Zoologisches Forschungsmuseum A. Koenig, Bonn, Germany;
- ZMHB** Museum für Naturkunde, Berlin, Germany.

**Key to species groups of *Neoserica* (*sensu lato*)**

- 1 Hypomeron not carinate..... *Tetraserica* Ahrens, 2004  
 1' Hypomeron carinate..... 2  
 2 Antennal club in female composed of 3 antennomeres.....  
 ..... *Neoserica* (s.l.) *vulpes* group, *N.* (s.l.)  
*calva* group, *N.* (s.l.) *lubrica* group, *Anomalophylla* Reitter, 1887, *Gynaecoserica* Brenske, 1896, *Leuroserica* Arrow, 1946, *Sericania* Motschulsky, 1860, *Calloserica* Brenske, 1894, *Lasioserica* Brenske, 1896, *Gastroserica* Brenske, 1897, *Neoserica* (s.str.) Brenske, 1894, *Trioserica* Moser, 1922, *Microserica* Brenske, 1894, *Oxyserica* Brenske, 1900, other *Neoserica* (s.l.)  
 2' Antennal club in female composed of more than 3 antennomeres..... 3  
 3 Labrum without a transverse rim of very dense, short and robust setae ..... 4  
 3' Labrum short, with a transverse rim of very dense, short and robust setae.  
 Dorsal surface densely setose..... *N.* (s.l.) *pilosula* group  
 4 Metatibia slender and long..... 5  
 4' Metatibia short and wide ..... *Neoserica*  
 (s.l.) *uniformis* group & *N.* (s.l.) *multifoliata* group (from Indochina)  
 5 Antennal club of males with 7 antennomeres..... 6  
 5' Antennal club of males with 7, 6 or less antennomeres ..... 7  
 6 Metafemur with a continuously serrated line adjacent to the anterior margin  
 of metafemur. Protibia more or less distinctly tridentate .....  
 ..... *Neoserica* (s.l.) *septemlamellata* group  
 6' Metafemur without a continuously serrated line adjacent to the anterior margin  
 of metafemur. Protibia always distinctly bidentate ..... *Nepaloserica* Frey, 1965  
 7 Basis of labroclypeus dull. Antennal club of males with 6 antennomeres..... 8  
 7' Antennal club of males with 5 or 4 antennomeres..... 9  
 8 Angle between basis of hypomeron and that of pronotum strongly rounded,  
 angle of surfaces of hypomeron and pronotum basally blunt. Hypomeron  
 basally strongly produced ventrally and transversely sulcate .....  
 ..... *Lepidoserica* Nikolaev, 1979  
 8' Angle between basis of hypomeron and that of pronotum sharp, angle of sur-  
 faces of hypomeron and pronotum sharp. Hypomeron basally not produced  
 ventrally and not sulcate ..... *Neoserica* (s.l.) *abnormis* group  
 9 Body surface strongly shiny. Body small (5.7–6.6 mm) .....  
 ..... *Neoserica* (s.l.) *speciosa* group  
 9' Body surface dull. Body larger (8 mm) ..... *Chrysoserica* Brenske, 1897

**Key to species of *Neoserica* (s.l.) *pilosula* group (♂ ♂)**

- 1 Antennal club as long as remaining antennomeres combined..... 2  
 1' Antennal club 1.2 times as long as remaining antennomeres combined ..... 6

2	Eyes smaller: ratio diameter/interocular distance $\sim 0.6$ . <i>N. ludingensis</i> sp. n.
2'	Eyes larger; ratio diameter/interocular distance $> 0.7$ ..... 3
3	Metatibia shorter and wider: ratio metatibial width/length $< 1/2.9$ ..... 4
3'	Metatibia longer and narrower: ratio metatibial width/length $> 1/3.2$ ..... ..... <i>N. curvipenis</i> sp. n.
4	Right paramere subequal in length to left or longer ..... 5
4'	Right paramere spherical, much shorter than left ..... <i>N. pilosula</i> Moser
5	Right paramere longer than left ..... <i>N. lincangensis</i> sp. n.
5'	Right paramere subequal in length to left ..... <i>N. tianeana</i> sp. n.
6	Right paramere spherical, much shorter than left. Median apical process between parameres trifid ..... <i>N. weibaoshanica</i> sp. n.
6'	Right paramere long, subequal in length to left or longer ..... 7
7	Right paramere in dorsal view straight ..... 8
7'	Right paramere in dorsal view strongly curved externally ..... 9
8	Right paramere with a filiform spine internally at middle. Left paramere more abruptly narrowed towards apex ..... <i>N. shennongjiaensis</i> sp. n.
8'	Right paramere without a filiform spine internally. Left paramere evenly narrowed towards apex ..... <i>N. rangshuiensis</i> sp. n.
9	Right paramere distinctly longer than width of phallobase at apex ..... ..... <i>N. emeishanensis</i> sp. n.
9'	Right paramere as longer as width of phallobase at apex ..... <i>N. lushuiana</i> sp. n.

## Systematics

### *Neoserica* (s.l.) *pilosula* Moser, 1915

Figs 1A–D, 5

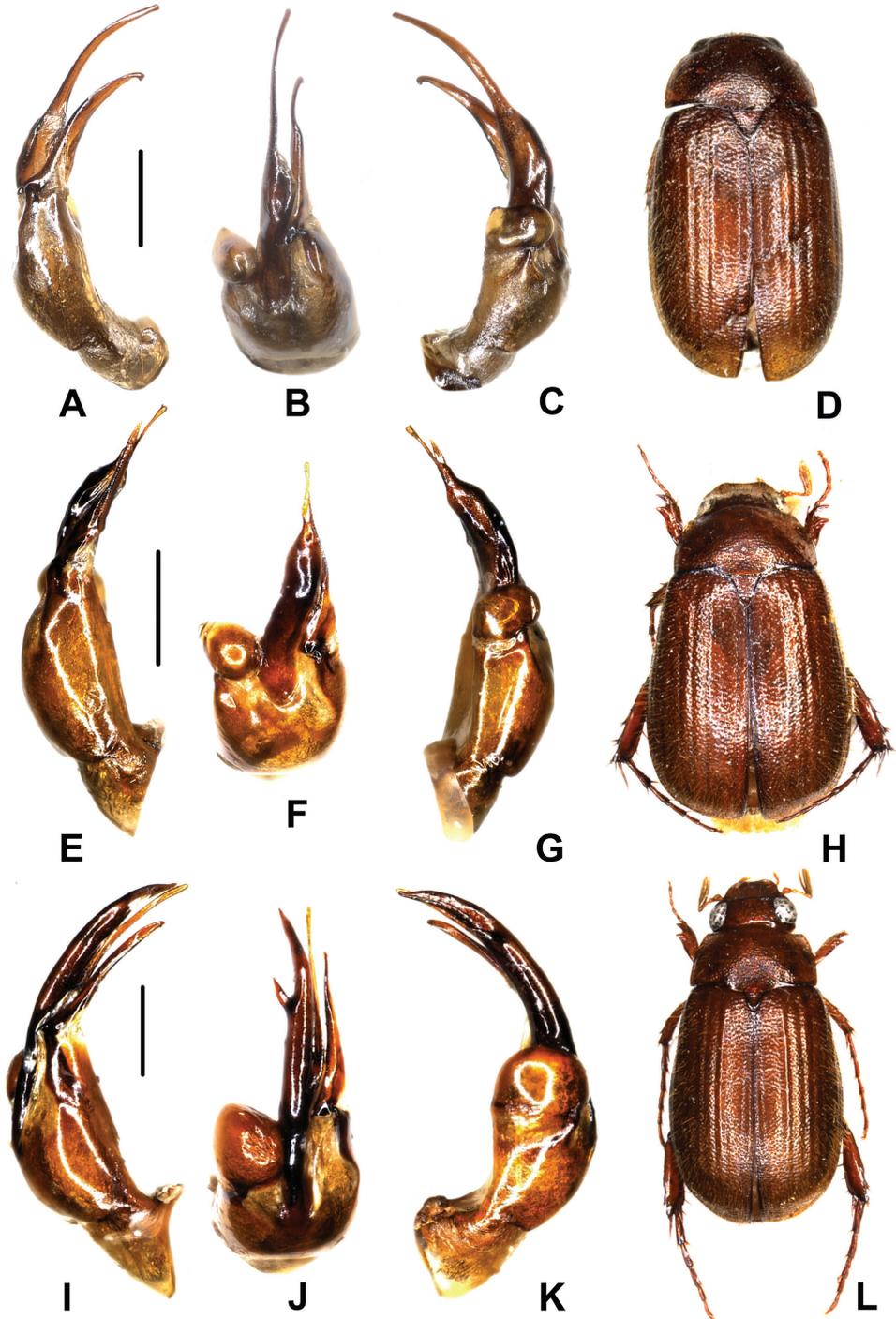
*Neoserica pilosula* Moser, 1915: 377.

**Type material examined.** Lectotype (here designated) @ “Yünnan China/ *Neoserica pilosula* Type Mos./ *pilosula* Mos.” (ZMHB).

**Additional material examined.** 1 ♂ “China C-Yunnan 60km SE Kunming Shilin (Stone forest) lgt. D. Král 3.–4.VII.90” (NMPC), 3 ♂♂, 1 ♀ “Mts. Junzishan, Shizong, Yunnan, 14.VII.2006, leg. Mao Benyong etc.” (HBMU).

**Redescription of lectotype.** Body length: 7.5 mm, length of elytra: 5.7 mm, width: 4.2 mm. Body oblong, reddish brown, antennal club yellowish brown, dorsal surface shiny, densely covered with fine, semi-erect setae (Fig. 1D).

Labroclypeus subtrapezoidal, widest at base; lateral margins weakly convex and moderately convergent towards moderately rounded anterior angles; anterior margin shallowly sinuate medially; margins moderately reflexed; surface moderately elevated medially, coarsely and densely punctate, densely setose. Frontoclypeal suture finely incised, weakly elevated and moderately angled medially. Smooth area anterior to



**Figure 1.** A–D *Neoserica pilosula* Moser, 1915 (Lectotype) E–H *N. ludingensis* sp. n. (holotype) I–L *N. weibaoshanica* sp. n. (holotype). A, E, I aedeagus, left side lateral view C, G, K aedeagus, right side lateral view B, F, J parameres, dorsal view D, H, L habitus. Scale: 0.5 mm, habitus not to scale.

eye three times as wide as long. Ocular canthus moderately long, finely and sparsely punctate, with a few setae. Frons with coarse and moderately dense punctures, with dense setae being bent posteriorly. Eyes large, ratio diameter/interocular width: 0.76. Antenna with ten antennomeres, club with four antennomeres and straight, as long as remaining antennomeres combined. Mentum elevated and slightly flattened anteriorly. Labrum short and almost straight anteriorly, with a transverse rim of very dense, short and robust setae.

Pronotum widest at base, lateral margins evenly convex and convergent anteriorly; anterior angles distinctly produced and sharp; posterior angles blunt, rounded at tip; anterior margin with fine, complete marginal line, weakly produced medially; surface densely and finely punctate, densely setose; anterior and lateral borders with sparse but longer setae; hypomeron carinate at base. Scutellum with fine, dense punctures and a few fine setae, on basal midline punctures less dense.

Elytra oblong, widest behind middle, striae weakly impressed, finely and densely punctate, intervals nearly flat, with fine, dense punctures, densely covered with fine, moderately long setae. Epipleural edge fine, ending at moderately curved external apical angle of elytra; epipleura densely setose, apical border with a wide membranous rim of microtrichomes (visible at magnification 100 $\times$ ).

Ventral surface shiny, finely and densely punctate. Metasternum with short, fine setae. Metacoxa glabrous, with a few single setae laterally. Abdominal sternites finely and densely punctate and finely setose, with a transverse row of coarse punctures each bearing a robust long seta. Mesosternum between mesocoxae as wide as mesofemur. Ratio of length of metepisternum/metacoxa: 1/1.74. Pygidium moderately convex and shiny, finely and densely punctate, without smooth midline; shortly and densely setose, with sparse long and erect setae on disc and beside the apical margin.

Legs slender; femora with two longitudinal rows of setae, finely and densely punctate. Anterior margin of metafemur acute, without adjacent serrated line; posterior margin of metafemur smooth, dorsally and ventrally, in apical half moderately widened. Metatibia wide and moderately long, widest at two thirds of metatibial length; ratio of width/length: 1/2.86; dorsal margin sharply carinate, with two groups of spines; basal group at half of metatibial length, apical group at three quarters of metatibial length; basally with a few strong short single setae; lateral face densely and coarsely punctate, shortly setose; ventral edge finely serrated, with four robust equidistant setae; medial face impunctate; apex weakly truncate interiorly near tarsal articulation. Tarsomeres ventrally with sparse, short setae; not carinate laterally, impunctate dorsally; metatarsomeres with a strongly serrated ventral ridge; first metatarsomere distinctly shorter than following two tarsomeres combined and as long as dorsal tibial spur. Protibia moderately long, bidentate; anterior claws symmetrical, basal tooth of inner claw sharply truncate at apex.

Aedeagus: Fig. 1A–C.

**Variation.** Body length: 7.5–7.7 mm, length of elytra: 5.7–5.8 mm. Female: antennal club composed of four antennomeres, as long as the remaining antennomeres combined.

***Neoserica* (s.l.) *ludingensis* sp. n.**

<http://zoobank.org/44F58E1B-DCD6-4423-8380-F7D6A3208BCB>

Figs 1E–H, 5

**Type material examined.** Holotype: ♂ “China West Sichuan Moximian Luding Co. 13.–18.7.94 Benes [sic]” (ZFMK). Paratypes: 2 ♂♂ “Yanzigou, Xinxing, Luding, Sichuan, 7.VIII.2004, 1560m, leg. Zhang Yong” (IZAS, ZFMK), 1 ♂ “Yanzigou, Xinxing, Luding, Sichuan, 7.VIII.2004, 1560m, leg. Bai Ming, Wan Xia” (IZAS), 1 ♂ “Hailuogou, Luding, Sichuan, 11.VIII.2004, 1900m, leg. Bai Ming” (IZAS), 1 ♂ “Huangjing, Luzhou, Sichuan, 17.VII.2002, leg. Bai Ming, Wang Jianfeng” (HBUM).

**Description.** Body length: 7.2 mm, length of elytra: 5.3 mm, width: 4.3 mm. Body oblong, reddish brown, antennal club yellowish brown, dorsal surface shiny, densely covered with fine, semi-erect setae (Fig. 1H).

Labroclypeus subtrapezoidal, widest at base; lateral margins weakly convex and moderately convergent towards moderately rounded anterior angles; anterior margin shallowly sinuate medially; margins moderately reflexed; surface moderately elevated medially, coarsely and densely punctate, densely setose. Frontoclypeal suture finely incised, weakly elevated and moderately angled medially. Smooth area anterior to eye 2.5 times as wide as long. Ocular canthus moderately long, impunctate, with one or two single setae. Frons with coarse and moderately dense punctures, with dense setae being bent posteriorly. Eyes moderately large, ratio diameter/interocular width: 0.6. Antenna with ten antennomeres, club with four antennomeres and straight, as long as remaining antennomeres combined. Mentum elevated and slightly flattened anteriorly. Labrum short and almost straight anteriorly, with a transverse rim of very dense, short and robust setae.

Pronotum widest at base, lateral margins evenly convex and convergent anteriorly; anterior angles distinctly produced and sharp; posterior angles blunt, rounded at tip; anterior margin with fine, complete marginal line, weakly produced medially; surface densely and finely punctate, densely setose; anterior and lateral borders with sparse but longer setae; hypomeron carinate at base. Scutellum with fine, dense punctures and a few fine setae, on basal midline punctures less dense.

Elytra oblong, widest behind middle, striae weakly impressed, finely and densely punctate; intervals nearly flat, odd ones slightly convex; intervals with fine, dense punctures, densely covered with fine, moderately long setae. Epipleural edge fine, ending at moderately curved external apical angle of elytra; epipleura densely setose, apical border with a wide membranous rim of microtrichomes (visible at magnification 100×).

Ventral surface shiny, finely and densely punctate. Metasternum with short, fine setae. Metacoxa glabrous, with a few single setae laterally. Abdominal sternites finely and densely punctate, finely setose, with a transverse row of coarse punctures each bearing a long seta. Mesosternum between mesocoxae as wide as mesofemur. Ratio of length of metepisternum/metacoxa: 1/1.35. Pygidium moderately convex and shiny, finely and densely punctate, without smooth midline; shortly and densely setose, with sparse long and erect setae on disc and beside the apical margin.

Legs slender; femora with two longitudinal rows of setae, finely and densely punctate. Anterior margin of metafemur acute, without adjacent serrated line; posterior margin of metafemur smooth, dorsally and ventrally, in apical half moderately widened. Metatibia wide and moderately long, widest at two thirds of metatibial length; ratio of width/length: 1/3.2; dorsal margin sharply carinate, with two groups of spines; basal group shortly behind middle of metatibial length, apical group at three quarters of metatibial length; basally with a few strong short single setae; lateral face densely and coarsely punctate, sparsely and shortly setose; ventral edge finely serrated, with four robust equidistant setae; medial face impunctate; apex weakly truncate interiorly near tarsal articulation. Tarsomeres ventrally with sparse, short setae; not carinate laterally, impunctate dorsally; metatarsomeres with a strongly serrated ventral ridge; first metatarsomere distinctly shorter than following two tarsomeres combined and slightly longer than dorsal tibial spur. Protibia moderately long, bidentate; anterior claws symmetrical, basal tooth of inner claw sharply truncate at apex. Female unknown.

Aedeagus: Fig. 1E–G.

**Diagnosis.** *Neoserica ludingensis* sp. n. differs from *N. pilosula* by the slightly smaller eyes and by the shape of the aedeagus: the median lobe between the parameres is shorter and thicker, the left paramere is in lateral view nearly straight.

**Etymology.** The new species is named after its occurrence in Luding county area.

**Variation.** Body length: 7.2–7.3 mm, length of elytra: 5.3–5.4 mm, width: 4.3–4.4 mm.

***Neoserica* (s.l.) *weibaoshanica* sp. n.**

<http://zoobank.org/BFEC3D38-CAF6-41F2-92FC-DEC18AB189F2>

Figs 1I–L, 5

**Type material examined.** Holotype: ♂ “Yunnan 2000–2800m 25.11N, 100.24E Weibaoshan mts. W slope 25–28/6.92 Vit Kubáň leg./ Coll. Milan Nikodým, Praha” (ZFMK). Paratypes: 1 ♂ Yunnan 2000–2800m 25.11N 100.24E Weibaoshan mts. W slope 25–28/6.92 Vit Kubáň leg./ Coll. Milan Nikodým, Praha” (ZFMK), 2 ♂♂, 1 ♀ “Yunnan 2000–2500m 25.42N 100.08E Cangshan mts. E slope 21.VI.92 David Král leg.” (NMPC), 3 ♂♂ “China (N-Yunnan) Dali Bai Nat. Aut. Pref., 1 km W of Dali old town, creek valley at foothill of Diancang Shan, 2170m, 25°41.9'N/ 100°08.4'E (along creek under stones, plant roots, in soil) 19./23.VI.2005 D.W. Wrase [13A]” (ZFMK), 1 ♂ “Yunnan 2500–2700m 25.58N, 100.21E Jizu Shan 6–10.7. Vit Kubáň leg. 1994” (CPPB), 1 ♂ “China- Yunnan prov. 22–27 July 1998 Dali old tower env. Zd. Jindra lgt.” (ZFMK), 2 ♂♂, 3 ♀♀ “China, N.Yunnan, env. Xiaguan, 2400m, 29.vii.2002, leg. S. Murzin, I. Shokhin” (CPPB, ZFMK).

**Description.** Body length: 7.5 mm, length of elytra: 5.0 mm, width: 3.8 mm. Body oblong, reddish brown, antennal club yellowish brown, dorsal surface shiny, densely covered with fine, semi-erect setae (Fig. 1L).

Labroclypeus short and subtrapezoidal, widest at base; lateral margins weakly convex and moderately convergent towards strongly rounded anterior angles; anterior margin shallowly sinuate medially; margins moderately reflexed; surface moderately elevated medially, coarsely and finely but densely punctate, sparsely setose. Frontoclypeal suture finely incised, weakly elevated and moderately angled medially. Smooth area anterior to eye 2.5 times as wide as long. Ocular canthus narrow and moderately long, sparsely punctate, with one or two single setae. Frons with coarse and moderately dense punctures, with dense setae being bent posteriorly. Eyes large, ratio diameter/interocular width: 0.76. Antenna with ten antennomeres, club with four antennomeres and straight, 1.2 times as long as remaining antennomeres combined. Mentum elevated and slightly flattened anteriorly. Labrum short and almost straight anteriorly, with a transverse rim of very dense, short and robust setae.

Pronotum widest at base, lateral margins evenly convex and moderately convergent anteriorly; anterior angles moderately produced and sharp; posterior angles blunt, rounded at tip; anterior margin with robust, complete marginal line, weakly produced medially; surface densely and finely punctate, densely setose; anterior and lateral borders with sparse but longer setae; hypomerion carinate at base. Scutellum with fine, dense punctures and a few fine setae.

Elytra oblong, widest behind middle, striae weakly impressed, finely and densely punctate; intervals nearly flat, odd ones slightly convex; intervals with fine, dense punctures, densely covered with fine, moderately long setae. Epipleural edge fine, ending at moderately curved external apical angle of elytra; epipleura densely setose, apical border with a wide membranous rim of microtrichomes (visible at magnification 100×).

Ventral surface shiny, finely and densely punctate. Metasternum with short, fine setae. Metacoxa glabrous, with a few single setae laterally. Abdominal sternites finely and densely punctate, finely setose, with a transverse row of coarse punctures each bearing a long seta. Mesosternum between mesocoxae as wide as mesofemur. Ratio of length of metepisternum/metacoxa: 1/1.59. Pygidium moderately convex and shiny, finely and densely punctate, without smooth midline; with dense, moderately long setae on disc and beside the apical margin.

Legs slender; femora with two longitudinal rows of setae, finely and densely punctate. Anterior margin of metafemur acute, without adjacent serrated line; posterior margin of metafemur smooth, dorsally and ventrally, in apical half moderately widened, dorsal posterior margin with dense and thick, evenly long setae. Metatibia wide and moderately long, widest at two thirds of metatibial length; ratio of width/length: 1/3.0; dorsal margin sharply carinate, with two groups of spines; basal group shortly behind middle of metatibial length, apical group at three quarters of metatibial length; in basal half with a continuously serrated line and some single punctures each bearing a short seta; lateral face densely and coarsely punctate, densely and shortly setose; ventral edge finely serrated, with four robust equidistant setae; medial face impunctate; apex weakly truncate interiorly near tarsal articulation. Tarsomeres ventrally with sparse, short setae; not carinate laterally, impunctate dorsally; metatarsomeres with a strongly serrated ventral ridge; first metatarsomere distinctly shorter than following

two tarsomeres combined and slightly longer than dorsal tibial spur. Protibia moderately long, bidentate; anterior claws symmetrical, basal tooth of inner claw sharply truncate at apex.

Aedeagus: Fig. 11–K.

**Diagnosis.** *Neoserica weibaoshanica* sp. n. differs from *N. pilosula* by the longer antennal club, the shorter labroclypeus, and the shape of trifold median lobe of aedeagus bearing a long filiform process on the left side shortly after the base and a short spine on the right side before the apex.

**Etymology.** The new species is named after its type locality in Weibaoshan Mts.

**Variation.** Body length: 6.9–7.9 mm, length of elytra: 4.4–5.5 mm, width: 3.6–4.4 mm. Female: antennal club composed of four antennomeres, as long as the remaining antennomeres combined.

***Neoserica* (s.l.) *tianeana* sp. n.**

<http://zoobank.org/450EBD39-435E-4517-A66B-F5352E46E9BF>

Figs 2A–D, 5

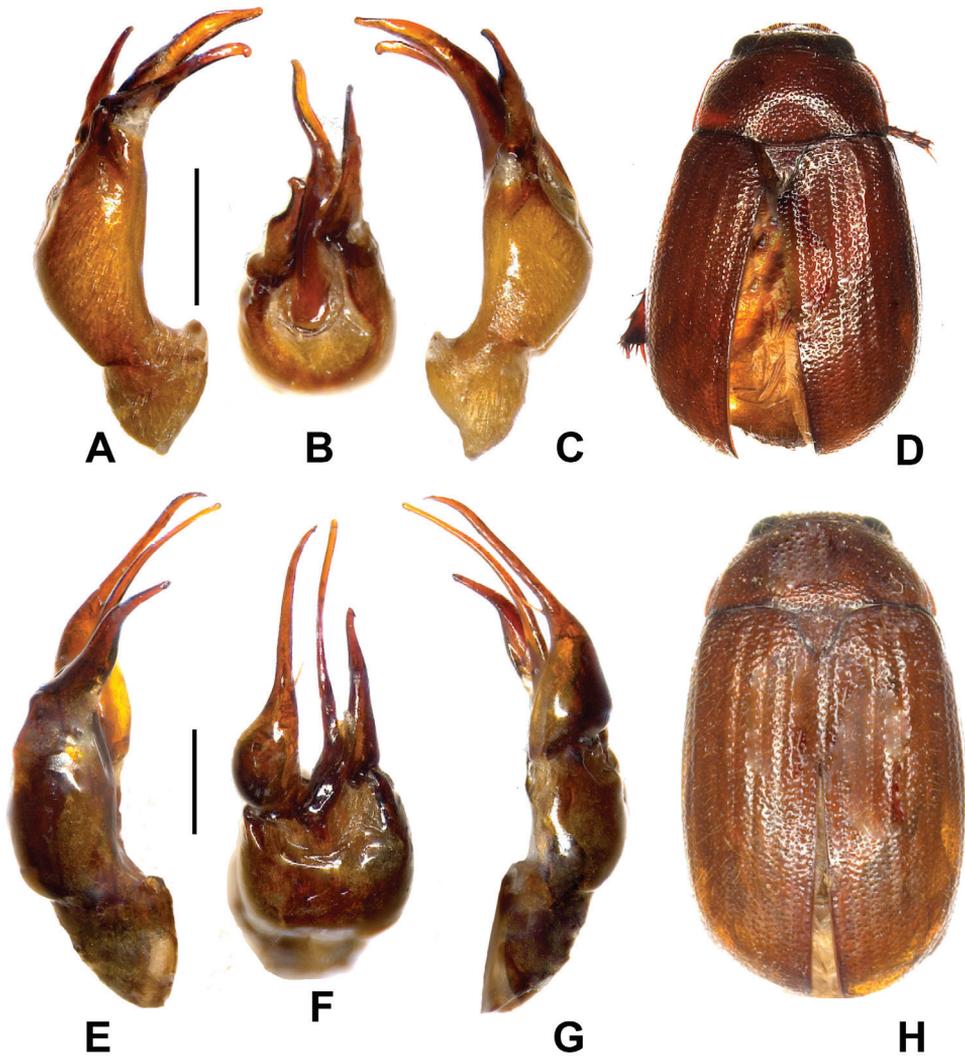
**Type material examined.** Holotype: ♂ “Dashan Forestry Farm, Tian’e, Guangxi, 3.VIII.2002, 1100m, leg. Jiang Guofang” (IZAS).

**Description.** Body length: 7.2 mm, length of elytra: 5.2 mm, width: 3.9 mm. Body oblong, reddish brown, antennal club yellowish brown, dorsal surface shiny, densely covered with fine, semi-erect setae (pilosity partly abraded; Fig. 2D).

Labroclypeus subtrapezoidal, widest at base; lateral margins weakly convex and moderately convergent towards moderately rounded anterior angles; anterior margin shallowly sinuate medially; margins moderately reflexed; surface moderately elevated medially, coarsely and finely, densely punctate, densely setose. Frontoclypeal suture finely incised, weakly elevated and moderately angled medially. Smooth area anterior to eye three times as wide as long. Ocular canthus moderately long, impunctate, with two or three setae. Frons with coarse and dense punctures, with dense setae being bent posteriorly. Eyes large, ratio diameter/interocular width: 0.75. Antenna with ten antennomeres, club with four antennomeres and straight, as long as remaining antennomeres combined. Mentum elevated and slightly flattened anteriorly. Labrum short and almost straight anteriorly, with a transverse rim of very dense, short and robust setae.

Pronotum widest at base, lateral margins weakly convex and convergent anteriorly; anterior angles distinctly produced and moderately sharp; posterior angles blunt, rounded at tip; anterior margin with fine, complete marginal line, weakly produced medially; surface densely and finely punctate, densely setose; anterior and lateral borders with sparse but longer setae; hypomerion carinate at base. Scutellum with fine, dense punctures and a few fine setae.

Elytra oblong, widest behind middle, striae weakly impressed, finely and densely punctate; intervals nearly flat, odd ones slightly convex; intervals with fine, dense punc-



**Figure 2.** **A–D** *Neoserica tianeana* sp. n. (holotype) **E–H** *N. shennongjiaensis* sp. n. (holotype). **A, E** aedeagus, left side lateral view **C, G** aedeagus, right side lateral view **B, F** parameres, dorsal view **D, H** habitus. Scale: 0.5 mm, habitus not to scale.

tures, densely covered with fine, moderately long setae. Epipleural edge fine, ending at moderately curved external apical angle of elytra; epipleura densely setose, apical border with a wide membranous rim of microtrichomes (visible at magnification 100 $\times$ ).

Ventral surface shiny, finely and densely punctate. Metasternum with short, fine setae. Metacoxa glabrous, with a few single setae laterally. Abdominal sternites finely and densely punctate, finely setose, with a transverse row of coarse punctures each bearing a long seta. Mesosternum between mesocoxae as wide as mesofemur. Ratio of length of metepisternum/metacoxa: 1/1.73. Pygidium strongly convex and shiny,

finely and densely punctate, without smooth midline; shortly and densely setose, with sparse long and erect setae on disc and beside the apical margin.

Legs slender; femora with two longitudinal rows of setae, finely and densely punctate. Anterior margin of metafemur acute, without adjacent serrated line; posterior margin of metafemur smooth, dorsally and ventrally, in apical half moderately widened. Metatibia wide and moderately long, widest at middle; ratio of width/length: 1/2.7; dorsal margin sharply carinate, with two groups of spines; basal group at middle, apical group at three quarters of metatibial length; in basal half with a few strong and short single setae in coarse punctures beside a undulated serrated line; lateral face densely and coarsely punctate, densely and shortly setose; ventral edge finely serrated, with four robust equidistant setae; medial face impunctate; apex weakly truncate interiorly near tarsal articulation. Meso- and metatarsomeres of holotype also missing. Protibia moderately long, bidentate; anterior claws symmetrical, basal tooth of inner claw sharply truncate at apex. Female unknown.

Aedeagus: Fig. 2A–C.

**Diagnosis.** *Neoserica tianeana* sp. n. differs from *N. pilosula* and the other previous species by the long, non-spherical right paramere being subequal in length to the left one.

**Etymology.** The new species is named after the type locality, Tian'e.

***Neoserica* (s.l.) *shennongjiaensis* sp. n.**

<http://zoobank.org/CF4AEAAC-BB7A-4CE7-8D8E-4C36CB51E38C>

Figs 2E–H, 5

**Type material examined.** Holotype: ♂ “Honghua, Shennongjia, Hubei, 26.VII.1980, 900, leg. Yu Peiyu” (IZAS). Paratypes: 1 ♀ “Honghua, Shennongjia, Hubei, 26.VII.1980, 900, leg. Yu Peiyu/ LW-617” (IZAS), 1 ♂ “Mts. Zhongtiaoshan, Shanxi, 30.VII.1995, 550m, leg. Li Wenzhu” (IZAS), 1 ♂ “Hetouzhai, Jinping, Yunnan, 15.V.1956, 1700m, leg. Huang Keren” (ZFMK), 1 ♂ “Dashahe, Daozhen, Guizhou, 17–21.VIII.2004, leg. Yang Xiujuan, Hua Huiran” (HBUM), 1 ♂ “Mt. Baiyunshan, Songxian County, Henan, 14–17.VIII.2008, leg. Ren Guodong, Wu Qiqi etc.” (HBUM).

**Description.** Body length: 7.5 mm, length of elytra: 5.7 mm, width: 4.2 mm. Body oblong, reddish brown, antennal club yellowish brown, dorsal surface shiny, densely covered with fine, semi-erect setae (Fig. 2H).

Labroclypeus subtrapezoidal, widest at base; lateral margins weakly convex and moderately convergent towards strongly rounded anterior angles; anterior margin distinctly sinuate medially; margins moderately reflexed; surface moderately elevated medially, coarsely and finely but densely punctate, sparsely setose. Frontoclypeal suture finely incised, weakly elevated and moderately angled medially. Smooth area anterior to eye 2.5 times as wide as long. Ocular canthus narrow and moderately long, sparsely punctate, with one or two single setae. Frons with coarse and moderately dense punctures, with dense setae being bent posteriorly. Eyes large, ratio diameter/interocular width: 0.73. Antenna with ten antennomeres, club with four antennomeres and

straight, 1.2 times as long as remaining antennomeres combined. Mentum elevated and slightly flattened anteriorly. Labrum short and almost straight anteriorly, with a transverse rim of very dense, short and robust setae.

Pronotum widest at base, lateral margins evenly convex and moderately convergent anteriorly; anterior angles moderately produced and sharp; posterior angles blunt, rounded at tip; anterior margin with fine, complete marginal line, weakly produced medially; surface densely and finely punctate, densely setose; anterior and lateral borders with sparse but longer setae; hypomerion carinate at base. Scutellum with fine, dense punctures and a few fine setae.

Elytra oblong, widest behind middle, striae weakly impressed, finely and densely punctate; intervals nearly flat, odd ones slightly convex; intervals with fine, dense punctures, densely covered with fine, moderately long setae. Epipleural edge fine, ending at moderately curved external apical angle of elytra; epipleura densely setose, apical border with a wide membranous rim of microtrichomes (visible at magnification 100×).

Ventral surface shiny, finely and densely punctate. Metasternum with short, fine setae. Metacoxa glabrous, with a few single setae laterally. Abdominal sternites finely and densely punctate, finely setose, with a transverse row of coarse punctures each bearing a long seta. Mesosternum between mesocoxae as wide as mesofemur. Ratio of length of metepisternum/metacoxa: 1/1.62. Pygidium weakly convex and shiny, finely and densely punctate, without smooth midline; with dense, long setae on disc and beside the apical margin.

Legs slender; femora with two longitudinal rows of setae, finely and densely punctate. Anterior margin of metafemur acute, without adjacent serrated line; posterior margin of metafemur smooth, dorsally and ventrally, in apical half moderately widened, dorsal posterior margin with fine setae. Metatibia wide and moderately long, widest at two thirds of metatibial length; ratio of width/length: 1/2.7; dorsal margin sharply carinate, with two groups of spines; basal group shortly behind middle of metatibial length, apical group at three quarters of metatibial length; in basal half with a continuously serrated line and some single punctures each bearing a short seta; lateral face densely and coarsely punctate, densely and shortly setose; ventral edge finely serrated, with four robust equidistant setae; medial face impunctate; apex weakly truncate interiorly near tarsal articulation. Tarsomeres ventrally with sparse, short setae; not carinate laterally, impunctate dorsally; metatarsomeres with a strongly serrated ventral ridge; metatarsomeres 2-5 and dorsal tibial spur of holotype also missing. Protibia moderately long, bidentate; anterior claws symmetrical, basal tooth of inner claw sharply truncate at apex.

Aedeagus: Fig. 2E–G.

**Diagnosis.** *Neoserica shennongjiaensis* sp. n. differs from *N. tianeana* sp. n. by the significantly longer right paramere.

**Etymology.** The new species is named after the type locality, Shennongjia.

**Variation.** Body length: 7.5–8.0 mm, length of elytra: 5.1–5.7 mm, width: 3.8–4.2 mm. First metatarsomere distinctly shorter than following two tarsomeres combined and slightly longer than dorsal tibial spur. Female: antennal club composed of four antennomeres, as long as the remaining antennomeres combined.

***Neoserica* (s.l.) *lincangensis* sp. n.**

<http://zoobank.org/9B76942F-5E0D-4141-A78A-82295FC18F49>

Figs 3A–D, 5

**Type material examined.** Holotype: ♂ “Yunnan, Lincang, Mt. Wulaoshan, 2010-VII-31, N23.90648, E100.15944, 1807m/ LW-1324” (IZAS). Paratype: 1 ♀ “Yunnan, Lincang, Mt. Wulaoshan, 2010-VII-31, N23.90648, E100.15944, 1807m/ LW-1324b” (ZFMK).

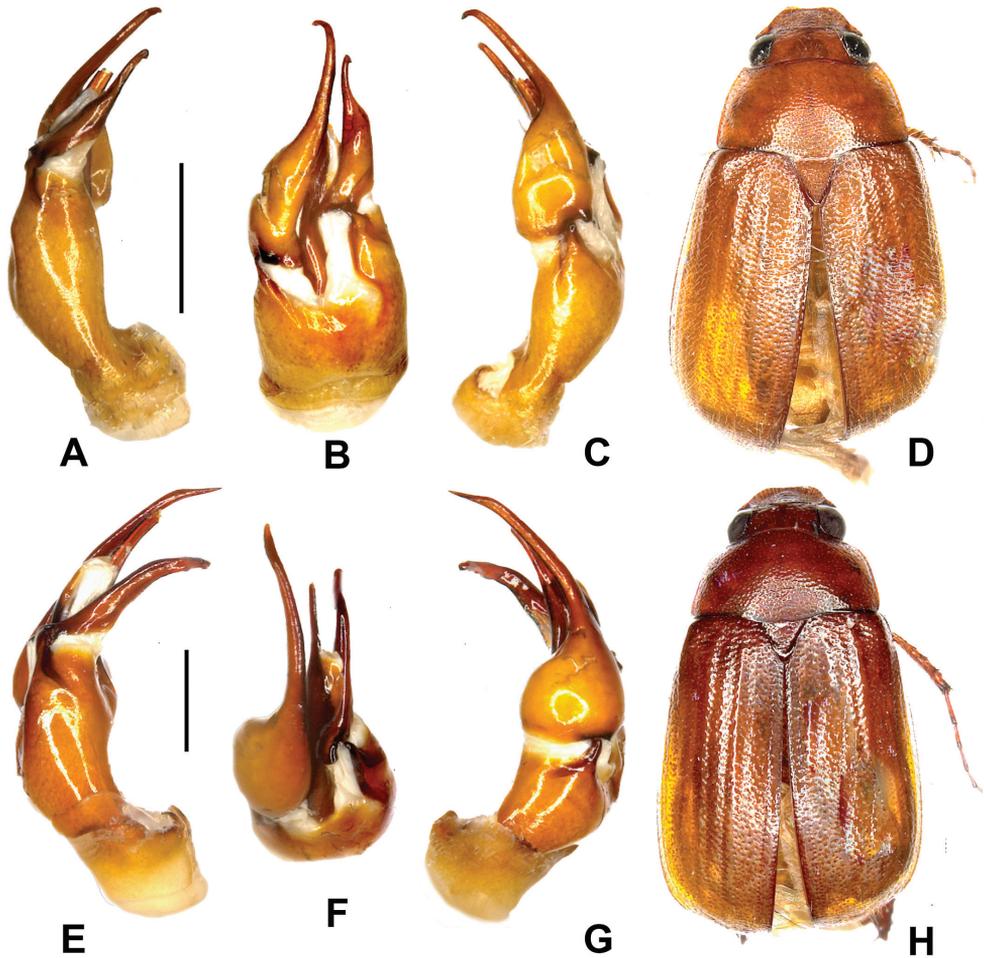
**Description.** Body length: 6.7 mm, length of elytra: 4.8 mm, width: 3.8 mm. Body oblong, reddish brown, antennal club yellowish brown, dorsal surface shiny, densely covered with fine, semi-erect setae (Fig. 3D).

Labroclypeus subtrapezoidal, widest at base; lateral margins weakly convex and moderately convergent towards strongly rounded anterior angles; anterior margin distinctly sinuate medially; margins moderately reflexed; surface moderately elevated medially, coarsely and finely but densely punctate, sparsely setose. Frontoclypeal suture finely incised, weakly elevated and moderately angled medially. Smooth area anterior to eye twice as wide as long. Ocular canthus narrow and moderately long, sparsely punctate, with two long setae. Frons with coarse and moderately dense punctures, with dense setae being bent posteriorly. Eyes large, ratio diameter/interocular width: 0.74. Antenna with ten antennomeres, club with four antennomeres and straight, as long as remaining antennomeres combined. Mentum elevated and slightly flattened anteriorly. Labrum short and almost straight anteriorly, with a transverse rim of very dense, short and robust setae.

Pronotum widest at base, lateral margins evenly convex and moderately convergent anteriorly; anterior angles moderately produced and sharp; posterior angles blunt, rounded at tip; anterior margin with fine, complete marginal line, weakly produced medially; surface densely and finely punctate, around midline punctures very dense, partly fusing with each other transversely, densely setose; anterior and lateral borders with sparse but longer setae; hypomerion carinate at base. Scutellum with fine, dense punctures and a few fine setae.

Elytra oblong, widest behind middle, striae weakly impressed, finely and densely punctate; intervals nearly flat, odd ones slightly convex; intervals with fine, dense punctures, densely covered with fine, moderately long setae. Epipleural edge fine, ending at moderately curved external apical angle of elytra; epipleura densely setose, apical border with a wide membranous rim of microtrichomes (visible at magnification 100×).

Ventral surface shiny, finely and densely punctate. Metasternum with short, fine setae. Metacoxa glabrous, with a few single setae laterally. Abdominal sternites finely and densely punctate, finely setose, with a transverse row of coarse punctures each bearing a long seta. Mesosternum between mesocoxae as wide as mesofemur. Ratio of length of metepisternum/metacoxa: 1/1.57. Pygidium weakly convex and shiny, finely and densely punctate, without smooth midline; with dense, long setae on disc and beside the apical margin.



**Figure 3.** **A–D** *Neoserica lincangensis* sp. n. (holotype) **E–H** *N. rangshuiensis* sp. n. (holotype). **A, E** aedeagus, left side lateral view **C, G** aedeagus, right side lateral view **B, F** parameres, dorsal view **D, H** habitus. Scale: 0.5 mm, habitus not to scale.

Legs slender; femora with two longitudinal rows of setae, finely and densely punctate. Anterior margin of metafemur acute, without adjacent serrated line; posterior margin of metafemur smooth, dorsally and ventrally, in apical half moderately widened, dorsal posterior margin with fine setae. Metatibia wide and moderately long, widest at two thirds of metatibial length; ratio of width/length: 1/2.7; dorsal margin sharply carinate, with two groups of spines; basal group shortly behind middle of metatibial length, apical group at three quarters of metatibial length; in basal half with a undulated, nearly continuously serrated line and beside it some single punctures each bearing a short seta; lateral face moderately densely and coarsely punctate, shortly setose; ventral edge finely serrated, with four robust equidistant setae; medial

face impunctate; apex weakly truncate interiorly near tarsal articulation. Tarsomeres ventrally with sparse, short setae; not carinate laterally, impunctate dorsally; metatarsomeres with a strongly serrated ventral ridge; first metatarsomere distinctly shorter than following two tarsomeres combined and slightly longer than dorsal tibial spur. Protibia moderately long, bidentate; anterior claws symmetrical, basal tooth of inner claw sharply truncate at apex.

Aedeagus: Fig. 3A–C.

**Diagnosis.** *Neoserica lincangensis* sp. n. is most similar to *N. shennongjiaensis* sp. n. but differs from it by the shorter antennal club and the shape of the parameres: the right paramere is basally strongly enlarged and abruptly curved at apex.

**Etymology.** The new species is named after its occurrence in the Lincang county.

**Variation.** Body length: 6.4–6.7 mm, length of elytra: 4.5–4.8 mm, width: 3.0–3.8 mm. Female: antennal club composed of four antennomeres, as long as the remaining antennomeres combined.

***Neoserica* (s.l.) *rangshuiensis* sp. n.**

<http://zoobank.org/3104170D-10E8-4C3C-898F-CEF1C2CB7D42>

Figs 3E–H, 5

**Type material examined.** Holotype: ♂ “Guizhou, Kuankuoshui Nature Reserve, Rangshui, 2010-VIII-15, 1527m, N28.22, E107.19 daytime/ LW-1380” (IZAS). Paratype: 1 ♂ “Guizhou, Zunyi, Kuankuoshui Nature Reserve, Rangshui, 2010-VIII-16, 860m/ LW-1032” (ZFMK).

**Description.** Body length: 7.3 mm, length of elytra: 5.2 mm, width: 3.9 mm. Body oblong, reddish brown, antennal club yellowish brown, dorsal surface shiny, densely covered with fine and short, semi-erect setae (in part abraded; Fig. 3H).

Labroclypeus subtrapezoidal, widest at base; lateral margins weakly convex and moderately convergent towards moderately rounded anterior angles; anterior margin shallowly sinuate medially; margins moderately reflexed; surface convexly elevated medially, coarsely and finely but densely punctate, sparsely setose. Frontoclypeal suture finely incised, weakly elevated and moderately angled medially. Smooth area anterior to eye 2.5 times as wide as long. Ocular canthus narrow and moderately long, sparsely punctate, with a single short terminal seta. Frons with coarse and sparse punctures, with numerous setae being bent posteriorly. Eyes large, ratio diameter/interocular width: 0.78. Antenna with ten antennomeres, club with four antennomeres and straight, 1.2 times as long as remaining antennomeres combined. Mentum elevated and slightly flattened anteriorly. Labrum short and almost straight anteriorly, with a transverse rim of very dense, short and robust setae.

Pronotum widest at base, lateral margins nearly straight and convergent, slightly convex anteriorly and moderately convergent towards moderately produced and sharp anterior angles; posterior angles blunt, rounded at tip; anterior margin with fine, com-

plete marginal line, weakly produced medially; surface densely and finely punctate, except on disc (probably abraded) densely setose; anterior and lateral borders with sparse but longer setae; hypomerion carinate at base. Scutellum with fine, dense punctures and a few fine setae.

Elytra oblong, widest behind middle, striae weakly impressed, finely and densely punctate; intervals nearly flat, odd ones slightly convex; intervals with fine, dense punctures, punctures on odd intervals concentrated along striae, densely covered with fine, moderately long setae. Epipleural edge fine, ending at moderately curved external apical angle of elytra; epipleura densely setose, apical border with a wide membranous rim of microtrichomes (visible at magnification 100×).

Ventral surface shiny, finely and densely punctate. Metasternum with short, fine setae. Metacoxa glabrous, with a few single setae laterally. Abdominal sternites finely and densely punctate, finely setose, with a transverse row of coarse punctures each bearing a long seta. Mesosternum between mesocoxae as wide as mesofemur. Ratio of length of metepisternum/metacoxa: 1/1.57. Pygidium strongly convex and shiny, finely and densely punctate, without smooth midline; with dense, long setae on disc and beside the apical margin.

Legs slender; femora with two longitudinal rows of setae, finely and densely punctate. Anterior margin of metafemur acute, without adjacent serrated line; posterior margin of metafemur smooth, dorsally and ventrally, in apical half moderately widened, dorsal posterior margin with fine setae. Metatibia wide and moderately long, widest at two thirds of metatibial length; ratio of width/length: 1/2.7; dorsal margin sharply carinate, with two groups of spines; basal group shortly behind middle of metatibial length, apical group at three quarters of metatibial length; in basal half with a undulated, nearly continuously serrated line and beside it single coarse punctures each bearing a short robust seta; lateral face moderately densely and coarsely punctate, shortly setose; ventral edge finely serrated, with four robust equidistant setae; medial face impunctate; apex weakly truncate interiorly near tarsal articulation. Tarsomeres ventrally with sparse, short setae; not carinate laterally, impunctate dorsally; metatarsomeres missing in holo- and paratype. Protibia moderately long, bidentate; anterior claws symmetrical, basal tooth of inner claw sharply truncate at apex.

Aedeagus: Fig. 3E–G.

**Diagnosis.** *Neoserica rangshuiensis* sp. n. is most similar to *N. lincangensis* sp. n. but differs from it by the slightly longer antennal club and the shape of the parameres: the right paramere is only in the basal third strongly enlarged (not in basal half as in *N. lincangensis* sp. n.) and slightly bent at the apex only (not curved); the left paramere is evenly curved (not straight or double-bent).

**Etymology.** The new species is named after its type locality, Rangshui.

**Variation.** Body length: 7.3–7.4 mm, length of elytra: 5.2–5.3 mm. Metatarsomeres of the paratype with a strongly serrated ventral ridge; first metatarsomere distinctly shorter than the following two tarsomeres combined and slightly longer than the dorsal tibial spur.

***Neoserica* (s.l.) *lushuiana* sp. n.**

<http://zoobank.org/B8FBBBE0-C613-4BA3-B62C-B3C847FFD79C>

Figs 4A–D, 5

**Type material examined.** Holotype: ♂ “Lushui, Yunnan, 9.VI.1981, 1810m, leg. Wang Shuyong, No.17” (IZAS).

**Description.** Body length: 6.2 mm, length of elytra: 4.5 mm, width: 3.2 mm. Body oblong, reddish brown, antennal club yellowish brown, dorsal surface shiny, densely covered with fine, semi-erect setae (Fig. 4D).

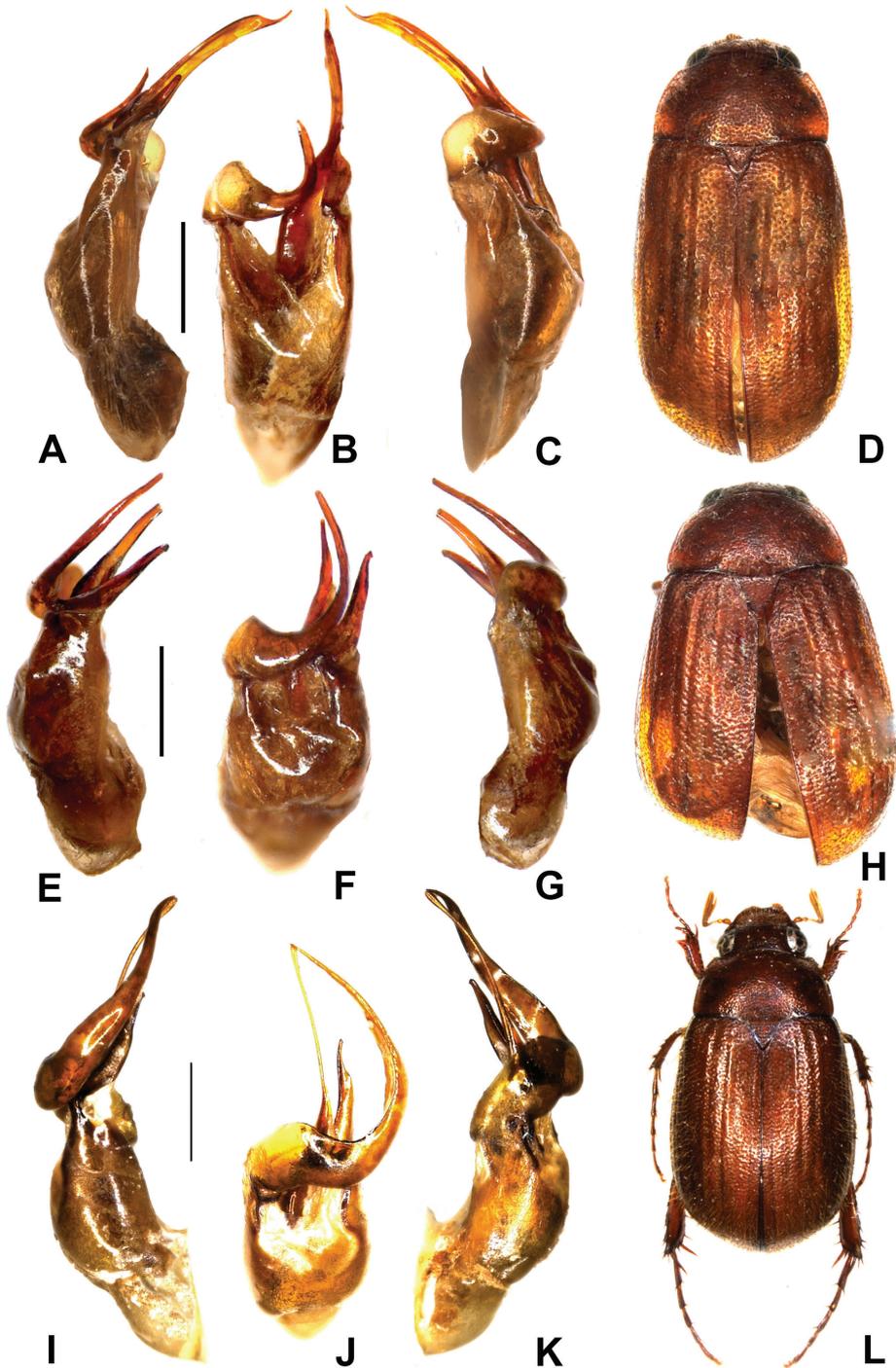
Labroclypeus subtrapezoidal, widest at base; lateral margins weakly convex and moderately convergent towards moderately rounded anterior angles; anterior margin shallowly sinuate medially; margins moderately reflexed; surface moderately convex medially, coarsely and finely but densely punctate, sparsely setose. Frontoclypeal suture finely incised, weakly elevated and moderately angled medially. Smooth area anterior to eye 2.5 times as wide as long. Ocular canthus narrow and moderately long, sparsely punctate, with a single short terminal seta. Frons with coarse and dense punctures, with dense setae being bent posteriorly. Eyes large, ratio diameter/interocular width: 0.71. Antenna with ten antennomeres, club with four antennomeres and straight, 1.2 times as long as remaining antennomeres combined. Mentum elevated and slightly flattened anteriorly. Labrum short and almost straight anteriorly, with a transverse rim of very dense, short and robust setae.

Pronotum widest at posterior third, lateral margins evenly convex, moderately convergent posteriorly and towards moderately produced and sharp anterior angles; posterior angles blunt, rounded at tip; anterior margin with fine, complete marginal line, weakly produced medially; surface densely and finely punctate, densely setose; anterior and lateral borders with dense, long setae; hypomeron carinate at base. Scutellum small, with fine, dense punctures and a few fine setae.

Elytra oblong, widest behind middle, striae weakly impressed, finely and densely punctate; intervals flat, odd ones slightly convex; intervals with fine, dense punctures, punctures on odd intervals concentrated along striae, densely covered with fine, moderately long setae. Epipleural edge fine, ending at moderately curved external apical angle of elytra; epipleura densely setose, apical border with a wide membranous rim of microtrichomes (visible at magnification 100×).

Ventral surface shiny, finely and densely punctate. Metasternum with short, fine setae. Metacoxa glabrous, with a few single setae laterally. Abdominal sternites finely and densely punctate, finely setose, with a transverse row of coarse punctures each bearing a long seta. Mesosternum between mesocoxae as wide as mesofemur. Ratio of length of metepisternum/metacoxa: 1/1.55. Pygidium moderately convex and shiny, finely and densely punctate, without smooth midline; with dense, long setae on disc and beside the apical margin.

Legs slender; femora with two longitudinal rows of setae, finely and densely punctate. Anterior margin of metafemur acute, without adjacent serrated line; posterior margin of metafemur smooth, dorsally and ventrally, in apical half moderately wid-



**Figure 4.** A–D *Neoserica lushuiana* sp. n. (holotype) E–H *N. emeishanensis* sp. n. (holotype) I–L *N. curvipennis* sp. n. (holotype). A, E, I aedeagus, left side lateral view C, G, K aedeagus, right side lateral view B, F, J parameres, dorsal view D, H, L habitus. Scale: 0.5 mm, habitus not to scale.

ened, dorsal posterior margin with sparse, fine setae. Metatibia wide and moderately long, widest at two thirds of metatibial length; ratio of width/length: 1/3.0; dorsal margin sharply carinate, with two groups of spines; basal group shortly behind middle of metatibial length, apical group at three quarters of metatibial length; in basal half with a slightly undulated, nearly continuously serrated line and beside it single coarse punctures each bearing a short robust seta; lateral face moderately densely and coarsely punctate, shortly setose; ventral edge finely serrated, with four robust equidistant setae; medial face impunctate; apex weakly truncate interiorly near tarsal articulation. Tarsomeres ventrally with sparse, short setae; not carinate laterally, impunctate dorsally; metatarsomeres with a strongly serrated ventral ridge; first metatarsomere distinctly shorter than following two tarsomeres combined and slightly longer than dorsal tibial spur. Protibia moderately long, bidentate; anterior claws symmetrical, basal tooth of inner claw sharply truncate at apex. Female unknown.

Aedeagus: Fig. 4A–C.

**Diagnosis.** *Neoserica lushuiana* sp. n. differs from all other species of the *N. pilosula* group by having the right paramere strongly curved externally (in dorsal view).

**Etymology.** The new species is named after its type locality, Lushui.

***Neoserica* (s.l.) *emeishanensis* sp. n.**

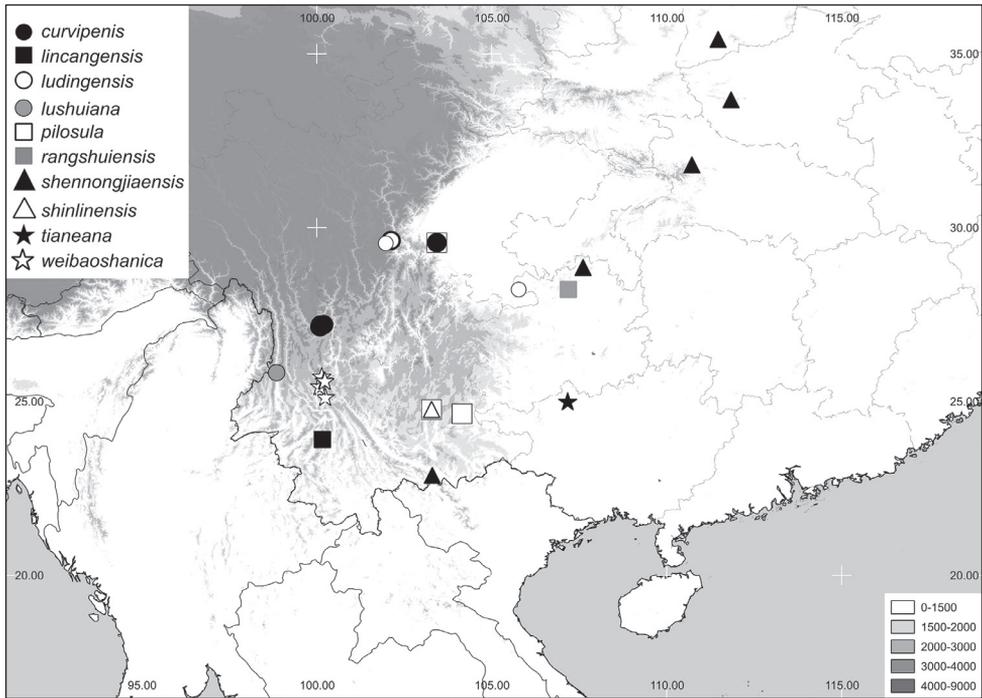
<http://zoobank.org/FD694F41-71E6-4D4D-922F-1B7C45E4D001>

Figs 4E–H, 5

**Type material examined.** Holotype: ♂ “Qingyin’ge, Mts. Emeishan, Sichuan, 21.IX.1957, 800–1000m, leg. Zhu Fuxing/ LW-670” (IZAS). Paratypes: 2 ♂♂ “Qingyin’ge, Mts. Emeishan, Sichuan, 21.IX.1957, 800–1000m, leg. Zhu Fuxing” (IZAS, ZFMK).

**Description.** Body length: 6.6 mm, length of elytra: 5.1 mm, width: 4.0 mm. Body oblong, reddish brown, antennal club yellowish brown, dorsal surface shiny, elytra densely covered with fine, semi-erect setae; setae on head and pronotum abraded in type specimens (Fig. 4H).

Labroclypeus subtrapezoidal, widest at base; lateral margins weakly convex and moderately convergent towards moderately rounded anterior angles; anterior margin distinctly sinuate medially; margins moderately reflexed; surface moderately convex medially, coarsely and finely but densely punctate, sparsely setose. Frontoclypeal suture finely incised, weakly elevated and moderately angled medially. Smooth area anterior to eye twice as wide as long. Ocular canthus narrow and moderately long, sparsely punctate, glabrous. Frons with coarse and dense punctures, with a few moderately long setae beside eyes. Eyes moderately large, ratio diameter/interocular width: 0.68. Antenna with ten antennomeres, club with four antennomeres and straight, 1.2 times as long as remaining antennomeres combined. Mentum elevated and slightly flattened anteriorly. Labrum short and almost straight anteriorly, with a transverse rim of very dense, short and robust setae.



**Figure 5.** Distribution of the species of the *Neoserica pilosula* group.

Pronotum widest at base, lateral margins evenly convex, moderately convergent towards moderately produced and sharp anterior angles; posterior angles blunt, rounded at tip; anterior margin with fine, complete marginal line, weakly produced medially; surface densely and finely punctate, sparsely setose; anterior and lateral borders with sparse, long setae; hypomerion carinate at base. Scutellum small, with fine, dense punctures and a few fine setae.

Elytra oblong, widest behind middle, striae weakly impressed, finely and densely punctate; intervals flat, odd ones slightly convex; intervals with fine, dense punctures, punctures on odd intervals concentrated along striae, densely covered with fine, moderately long setae. Epipleural edge fine, ending at moderately curved external apical angle of elytra; epipleura densely setose, apical border with a wide membranous rim of microtrichomes (visible at magnification 100×).

Ventral surface shiny, finely and densely punctate. Metasternum with short, fine setae. Metacoxa glabrous, with a few single setae laterally. Abdominal sternites finely and densely punctate, finely setose, with a transverse row of coarse punctures each bearing a long seta. Mesosternum between mesocoxae as wide as mesofemur. Ratio of length of metepisternum/metacoxa: 1/1.61. Pygidium moderately convex and shiny, shortly and densely punctate, without smooth midline; with dense, long setae beside the apical margin.

Legs slender; femora with two longitudinal rows of setae, finely and densely punctate. Anterior margin of metafemur acute, without adjacent serrated line; posterior margin

of metafemur smooth, dorsally and ventrally, in apical half moderately widened, dorsal posterior margin with sparse, fine setae. Metatibia wide and moderately long, widest at two thirds of metatibial length; ratio of width/length: 1/2.85; dorsal margin sharply carinate, with two groups of spines; basal group shortly behind middle of metatibial length, apical group at three quarters of metatibial length; in basal half with a slightly undulated, nearly continuously serrated line and beside it single coarse punctures each bearing a short robust seta; lateral face moderately densely and coarsely punctate, shortly setose; ventral edge finely serrated, with four robust equidistant setae; medial face impunctate; apex weakly truncate interiorly near tarsal articulation. Tarsomeres ventrally with sparse, short setae; not carinate laterally, impunctate dorsally; metatarsomeres missing in holotype. Protibia moderately long, bidentate; anterior claws symmetrical, basal tooth of inner claw sharply truncate at apex. Female unknown.

Aedeagus: Fig. 4E–G.

**Diagnosis.** *Neoserica emeishanensis* sp. n. is most similar to *N. lushuiana* sp. n. but differs from it by the longer right paramere (in dorsal view) being much longer than the phallobase width.

**Etymology.** The new species is named after its type locality, Mt. Emeishan.

**Variation.** Body length: 6.6–7.0 mm, length of elytra: 5.1–5.4 mm, width: 4.0–4.2 mm.

**Remarks.** Metatarsomeres are missing in all paratypes.

***Neoserica* (s.l.) *curvipennis* sp. n.**

<http://zoobank.org/8AB9299A-AACB-4B78-9364-E287FF85F2B4>

Figs 4I–L, 5

**Type material examined.** Holotype: ♂ “Yunnan 2000–3000m 27.20N 100.11E Habashan mts. SE slope 10-13/7. Vit Kubáň leg. 92/ [ex] coll. Milan Nikodým, Praha” (ZFMK). Paratypes: 1 ♀ “Yunnan 2000-3000m 27.20N 100.11E Habashan mts. SE slope 10-13/7. Vit Kubáň leg. 92/ [ex] coll. Milan Nikodým, Praha” (ZFMK), 1 ♂ “Yunnan cca 2000m 27.15N 100.09E Hutiao gorge Jinsha r. 18-22/7. leg. Vit Kubáň leg. 92” (ZFMK), 1 ♂ “China West Sichuan Moximian Luding Co. 13.–18.7.94 Benes” (ZFMK), 1 ♂ “China; Yunnan prov.; Daju – 50km N Lijiang; 27,21N 100,19E; S. Bečvář leg.; 21.–27.vi.1993” (CPPB), 2 ♂♂, 1 ♀ “China Yunnan 2000-3000m 27°20’N 100°11’E Habashan Mts. SE slope, 10.[-]13.7.1992. D. Král lgt.” (NMPC), 1 ♂ “Yunnan ca. 2000m 27.15N 100.09E Hutiao gorge Jinsha r. 18–22.7.92 leg. David Král” (NMPC), 1 ♂ “Qingyinge, Emeishan, Sichuan, 22.IX.1957, 800–1000m, leg. Zhu Fuxing” (IZAS).

**Description.** Body length: 7.6 mm, length of elytra: 5.2 mm, width: 4.0 mm. Body oblong, reddish brown, antennal club yellowish brown, dorsal surface shiny, densely covered with fine, semi-erect setae (Fig. 4L).

Labroclypeus subtrapezoidal, widest at base; lateral margins convex and convergent towards moderately rounded anterior angles; anterior margin distinctly sinuate medi-

ally; margins moderately reflexed; surface weakly convex medially, coarsely and finely but densely punctate, densely setose. Frontoclypeal suture finely incised, weakly elevated and moderately angled medially. Smooth area anterior to eye 1.5 times as wide as long. Ocular canthus narrow and moderately long, sparsely punctate, with a few long setae. Frons with coarse and dense punctures mixed with sparse, fine ones, with dense setae being bent posteriorly. Eyes large, ratio diameter/interocular width: 0.71. Antenna with ten antennomeres, club with four antennomeres and straight, as long as remaining antennomeres combined. Mentum elevated and slightly flattened anteriorly. Labrum short and almost straight anteriorly, with a transverse rim of very dense, short and robust setae.

Pronotum widest at base, lateral margins evenly convex and moderately convergent towards moderately produced and sharp anterior angles; posterior angles blunt, rounded at tip; anterior margin with fine, complete marginal line, weakly produced medially; surface densely and finely punctate, densely setose; anterior and lateral borders with dense, long setae; hypomerion carinate at base. Scutellum small, with fine, dense punctures and dense, fine setae.

Elytra oblong, widest behind middle, striae weakly impressed, finely and densely punctate; intervals flat, odd ones slightly convex; intervals with fine, dense punctures, punctures on odd intervals concentrated along striae, densely covered with fine, moderately long setae. Epipleural edge fine, ending at moderately curved external apical angle of elytra; epipleura densely setose, apical border with a wide membranous rim of microtrichomes (visible at magnification 100×).

Ventral surface shiny, finely and densely punctate. Metasternum with short, fine setae. Metacoxa glabrous, with a few single setae laterally. Abdominal sternites finely and densely punctate, finely setose, with a transverse row of coarse punctures each bearing a long seta. Mesosternum between mesocoxae as wide as mesofemur. Ratio of length of metepisternum/metacoxa: 1/1.74. Pygidium moderately convex and shiny, finely and densely punctate, without smooth midline; with dense, long setae on disc and beside the apical margin.

Legs slender; femora with two longitudinal rows of setae, finely and densely punctate. Anterior margin of metafemur acute, without adjacent serrated line; posterior margin of metafemur smooth, dorsally and ventrally, in apical half moderately widened, dorsal posterior margin with sparse, fine setae. Metatibia wide and moderately long, widest at two thirds of metatibial length; ratio of width/length: 1/3.33; dorsal margin sharply carinate, with two groups of spines; basal group shortly behind middle of metatibial length, apical group at three quarters of metatibial length; basally with a few strong short single setae in coarse puncture with serrated borders; lateral face moderately densely and coarsely punctate, shortly setose; ventral edge finely serrated, with four robust equidistant setae; medial face impunctate; apex weakly truncate interiorly near tarsal articulation. Tarsomeres ventrally with sparse, short setae; not carinate laterally, impunctate dorsally; metatarsomeres with a strongly serrated ventral ridge; first metatarsomere distinctly shorter than following two tarsomeres combined and slightly longer than dorsal tibial spur. Protibia moderately long, bidentate; anterior claws symmetrical, basal tooth of inner claw sharply truncate at apex.

Aedeagus: Fig. 4I–K.

**Diagnosis.** *Neoserica curvipenis* sp. n. differs from the two previous species by the extremely widely curved right paramere exceeding significantly beyond the level of the left paramere (in dorsal view).

**Etymology.** The name of the new species is derived from the combined Latin words, *curvi* – curved, and *penis* – aedeagus, with reference to the curved shape of the right paramere.

**Variation.** Body length: 6.6–8.1 mm, length of elytra: 4.9–5.6 mm, width: 4.0–4.4 mm. Female: antennal club composed of four antennomeres, as long as the remaining antennomeres combined.

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# ***Neoplecostomus doceensis*: a new loricariid species (Teleostei, Siluriformes) from the rio Doce basin and comments about its putative origin**

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## **Abstract**

A new species of *Neoplecostomus* is described from the rio Doce basin representing the first species of this genus in the basin. The new species is distinguished from its congeners by having enlarged, fleshy folds between dentaries, two or three series of developed papillae anterior to premaxillary teeth and a adipose-fin membrane present, and by lacking enlarged odontodes along snout lateral margins in mature males, a well-developed dorsal-fin spinelet wider than dorsal-fin spine base, lower number of lateral-line plates and developed membrane on the dorsal portion of the first, second and third pelvic-fin branched rays. Additionally, we present a brief discussion of biogeographic scenarios that may explain the distribution of the new species in the rio Doce basin. We suggested that the ancestral lineage of the new species reached the rio Doce from the upper portions of rio Paraná drainages about 3.5 Mya (95% HPD: 1.6–5.5) indicating a colonization route of the *N. doceensis* ancestral lineage from the south end of Serra do Espinhaço, probably as a result of headwater capture processes between the upper rio Paraná and rio Doce basins.

## **Keywords**

Brazilian shield, catfishes, freshwater, ichthyology, Neoplecostominae, Neotropical fishes, Ostariophysi

## Introduction

Neoplecostominae currently includes six genera: *Neoplecostomus*, *Isbrueckerichthys*, *Kronichthys*, *Pareiorhaphis*, *Pareiorhina* and *Pseudotocinclus* (Armbruster 2004; Chiachio et al. 2008; Roxo et al. 2012a, b) and more than 50 valid species (Eschmeyer and Fong 2014) distributed throughout the southeastern drainage regions in South America, from Rio Grande do Sul to Bahia states, except for *Pareiorhaphis regani*, which occurs in the rio Negro, in the Amazon basin.

Since Langeani (1990), the genus *Neoplecostomus* has been diagnosed as having a conspicuous series of enlarged papillae just posterior to the dentary teeth, which are larger than those on the remaining portions of the lower lip, the abdomen covered with platelets forming either a pentagonal or hexagonal shield, and the canal bearing plate on the cheek and the dorsal locking mechanism absent. Presently, the genus includes 13 species (Eschmeyer 2014): *N. paranensis* Langeani, 1990, *N. corumba* Zawadzki, Pavanelli & Langeani, 2008, *N. selenae* Zawadzki, Pavanelli & Langeani, 2008, *N. yapo* Zawadzki, Pavanelli & Langeani, 2008, *N. botucatu* Roxo, Oliveira & Zawadzki, 2012, *N. bandeirante* Roxo, Oliveira & Zawadzki, 2012, *N. langeanii* Roxo, Oliveira & Zawadzki, 2012, all from the upper rio Paraná basin; *N. franciscoensis*, Langeani, (1990) from the rio São Francisco basin; *N. microps* (Steindachner, 1877), *N. variipictus* Bizerril, 1995, and *N. granosus* (Cuvier & Valenciennes, 1840) from the rio Paraíba do Sul basin; *N. espiritosantensis* Langeani, 1990 from rio Jacu basin and *N. ribeirensis* Langeani (1990) from rio Ribeira de Iguape basin.

An examination of the fish collections at the LBP (Laboratório de Biologia e Genética de Peixes de Botucatu – São Paulo); MCNIP (Museu de Ciências Naturais da PUC Minas – Minas Gerais); MZUSP (Museu de Zoologia de São Paulo – São Paulo); and NUP (Coleção Ictiológica do Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura, Universidade Estadual de Maringá – Paraná) revealed the existence of an undescribed species of *Neoplecostomus* from the rio Doce, the first species of the genus described from this basin. Additionally, we present a brief discussion of biogeographic scenarios that may explain the distribution of the new species in the rio Doce basin.

## Material and methods

Measurements and counts were taken on the left side of the specimens. Body plate nomenclature follows Schaefer (1997) and measurements follow Langeani (1990), modified by Zawadzki et al. (2008), and are shown in Table 1. All measurements were taken point to point with digital callipers to the nearest 0.1 mm. Specimens were cleared and stained (c&s) according to the method of Taylor and Van Dyke (1985). Dorsal-fin ray counts included the spinelet as the first unbranched ray. Vouchers were deposited in the collections of the (LBP) Laboratório de Biologia e Genética de Peixes, Universidade Estadual Paulista, Botucatu, Brazil; (MCNIP) Museu de Ciências Naturais da PUC Minas, Minas Gerais, Brazil; (MZUSP) Museu de Zoologia da Universidade de São

Paulo, São Paulo, Brazil; (NUP) Coleção Ictiológica do Nupélia, Universidade Estadual de Maringá, Maringá, Brazil. The scientific names of the species follow the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999).

## Results

### *Neoplecostomus doceensis* sp. n.

<http://zoobank.org/28057609-4191-4808-B6C0-7DABFD0E73D2>

Figure 1; Table 1

“*Neoplecostomus* sp. 9” – Roxo et al. 2012a: 2443 [phylogenetic relationships]. – Roxo et al. 2012b: 38 [phylogenetic relationships].

**Holotype.** MZUSP 115486 (1 male 101.1 mm SL), Brazil, Minas Gerais State, municipality of Ouro Preto, córrego Bananeiras, affluent of rio Gualaxo do Norte, rio Doce basin, 20°14'20"S, 43°28'40"W, Abril 2010, BP Maia.

**Paratypes.** All from Brazil, Minas Gerais State, rio Doce basin (97 specimens).

LBP 1098 (1 female 40.9, 1 male c&s 57.3 mm SL), municipality of Alto Rio Doce, rio Xopotó, 21°08'56"S, 43°23'58"W, October 2001, JC Oliveira, Al Alves, LR Sato. LBP 12261 (3 females 28.7–46.2 mm SL), municipality of Desterro do Melo, rio Xopotó, 21°09'09"S, 43°31'37"W, October 2011, A Ferreira, FF Roxo, GSC Silva. LBP 18981 (2 females 58.3–82.0 mm SL), uncertain location of the rio Piranga, 19 November 2000, JC Oliveira, OT Oyakawa. MCNIP 439 (3 males 80.6–86.7 mm SL), municipality of São José do Mantimento, rio José Pedro, affluent of rio Manhuaçu, 20°04'45"S, 41°44'00"W, 27 February 2012, TC Pessali, TA Barroso. MCNIP 1169 (1 female 59.4 mm SL, 4 males 75.0–100.3 mm SL), municipality of São José do Mantimento, rio José Pedro, affluent of rio Manhuaçu, 20°00'57"S, 41°44'07"W, 25 September 2013, TC Pessali, GM Santos. MZUSP 69368 (2 females 70.6–88.0 mm SL), municipality of Coroaci, rio Suaçuí Pequeno (at bridge of Procópio), 18°41'38"S, 42°12'50"W, 29 April 2001, AM Zanatta. MZUSP 80971 (3 males 70.8–96.3 mm SL), municipality of São Luiz, rio Manhuaçu, 20°20'11"S, 42°042'48"W, 21 April 2002, CBM Alves. MZUSP 94487 (1 female 54.1 mm SL), municipality of Alto Rio Doce, rio Xopotó, rio Doce basin, 21°04'04"S, 43°27'50"W, 11 July 2007, OT Oyakawa. MUZSP 94505 (6 females 31.4–40.5 mm SL) municipality of Desterro do Melo, rio Xopotó, rio Doce basin, 21°08'53"S, 43°30'46"W, 10 July 2007, OT Oyakawa. MUZSP 94514 (1 female 35.8 mm SL) municipality of Alto Rio Doce, rio Xopotó, rio Doce basin, 21°03'11"S, 43°26'46"W, 10 July 2007, OT Oyakawa. MUZSP 94527 (7 females 33.7–41.5 mm SL) municipality of Desterro do Melo, rio Xopotó, rio Doce basin, 21°09'10"S, 43°31'49"W, 10 July 2007, OT Oyakawa. MZUSP 94542 (1 male 53.1 mm SL, 7 females 37.7–53.9 mm SL) municipality of Desterro do Melo, rio Xopotó, rio Doce basin, 21°09'10"S, 43°31'28"W, 10 July 2007, OT Oyakawa.



**Figure 1.** *Neoplecostomus doceensis*, MZUSP 115486, male, 101.1 mm SL, holotype from the affluent of rio Gualaxo do Norte, rio Doce basin, municipality of Ouro Preto, Minas Gerais State, Brazil.

MZUSP 107368 (2 males 61.1–84.5 mm SL, 3 females 47.8–79.5 mm SL), uncertain location of the rio Piranga, 19 November 2000, JC Oliveira, OT Oyakawa. MZUSP 109327 (9 males 55.3–90.6 mm SL, 29 females 32.2–93.6 mm SL), municipality of Manhuaçu, affluent of the rio Manhuaçu, 20°17'34"S, 42°03'41"W, October 2008, TC Pessali. MZUSP 109339 (1 male 51.7 mm SL, 2 females 53.8–69.6 mm SL) collected with holotype. MUZUSP 110931 (2 males 63.7–80.7 mm SL), municipality of Mariana, rio Gualaxo do Sul, 20°30'17"S, 43°24'40"W, July 2012, LF Salvador, LAC Missiaggia. NUP 17003, (1 female 83.2 mm SL, 2 males 96.6–100.3 mm SL), municipality of São José do Mantimento, rio José Pedro, affluent of rio Manhuaçu, 20°00'57"S, 41°44'07"W, 25 September 2013, TC Pessali, GM Santos. NUP 17004, (3 males 89.4–97.7 mm SL), municipality of São José do Mantimento, rio José Pedro, affluent of rio Manhuaçu, 20°04'45"S, 41°44'00"W, 27 February 2012, TC Pessali, TA Barroso.

**Non-type specimens.** LBP 1096 (2 unsexed 54.4–57.7 mm SL), municipality of Alto Rio Doce, rio Xopotó, 21°08'56"S, 43°23'58"W, October 2001, JC Oliveira, AL Alves, LR Sato.

**Diagnosis.** *Neoplecostomus doceensis* is distinguished from all other congeners by having enlarged, fleshy folds between dentaries in all specimens, more evident in mature males, Fig. 2a (vs. absence of the enlarged fleshy folds, Fig. 2b). The new species can also be distinguished from all congeners by the presence of two or three series of well-developed papillae anterior to premaxillary teeth, Fig. 2c (vs. papillae poorly developed or absent Fig. 2d). Additionally, the new species can be distinguished from *N. botucatu* and *N. paranensis* by the presence of a fully-developed adipose fin (vs. lacking or reduced adipose fin); from *N. selenae* by moderately-sized odontodes along lateral margins of snout and snout without swollen skin in mature males (vs. presence of large-sized odontodes surrounded by swollen skin along lateral margins of snout in mature males); from *N. franciscoensis* and *N. ribeirensis* by having a well-developed dorsal-fin spinelet, wider than dorsal-fin spine base (vs. absent or narrower than dorsal-fin spine base); from *N. microps* and *N. variipictus* by a higher number of dentary teeth 12–35 (vs. 5–12 and 7 respectively); from *N. granosus* by having a lower number of lateral-line plates, 25–29 (vs. 34–43); from *N. langeanii* by the presence of a developed membrane on the dorsal portion of the first, second and third pelvic-fin branched rays (vs. lacking).

**Description.** Counts and measurements are presented in Table 1. Body robust, elongated and depressed, greatest width at cleithrum (25.8–28.7% SL), narrowing to caudal peduncle. Dorsal profile of the head elevating and gently convex from snout tip to posterior margin of nares, straight to slightly concave to posterior margin of parieto supraoccipital, straight to dorsal-fin origin. Dorsal profile of trunk slightly concave and descending from dorsal-fin origin to adipose-fin origin, almost straight and descending to first procurrent caudal-fin ray; greatest body depth at dorsal-fin origin (15.3–19.6% SL). Ventral profile slightly convex from snout tip to anal-fin origin; concave at anal-fin region, straight and ascending to lower caudal-fin ray. Trunk and caudal peduncle almost ellipsoid in cross-section, rounded laterally and almost flat dorsally and ventrally.

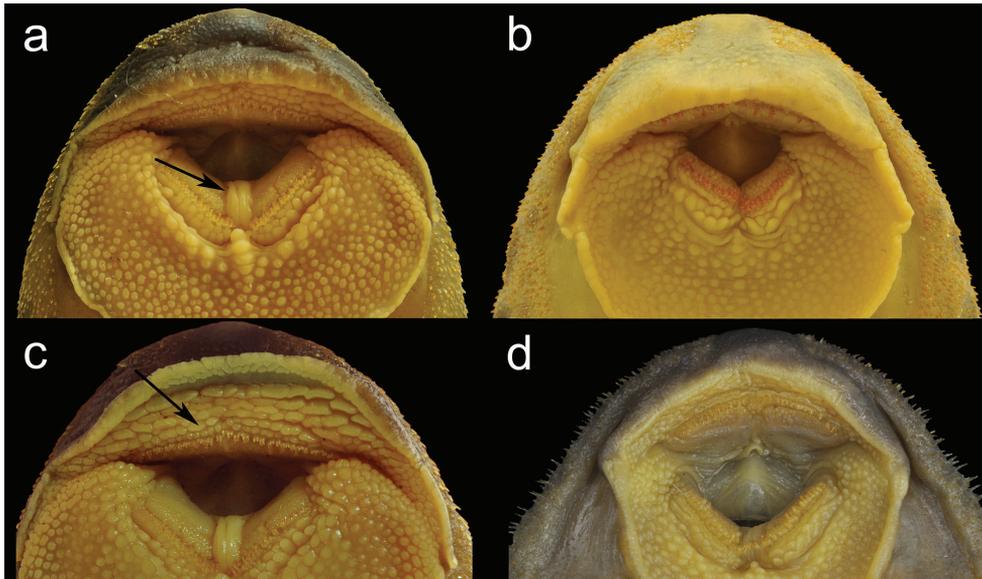
Dorsal body surface completely covered by dermal plates, except for a naked area around dorsal-fin base and a small naked area at snout tip. Ventral head surface naked except for a plate bearing odontodes in front of gill openings. Abdomen with conspicuous, small dermal platelets between insertions of pectoral and pelvic fins, forming a thoracic shield surrounded by naked areas. Abdominal platelets densely covered by backward-oriented odontodes, their tips round. Head wide (79.8–90.8% HL) and depressed (47.1–57.1% HL). Head and snout rounded in dorsal view; interorbital space straight to slightly concave in frontal view.

Snout tip with a weak ridge between nares, sometimes absent, more evident in larger specimens. A weak ridge from middle of snout to superior margin of orbit. Moderate-sized odontodes along lateral margins of snout, more evident in mature males. Eye moderately small (7.0–11.2% HL) and dorso-laterally placed; lips well developed and rounded; lower lip almost reaching pectoral girdle and covered with papillae, wider anteriorly. Enlarged fleshy folds among dentary, more evident in mature males (Fig. 2a). Two to three irregular and conspicuous rows of large and transversally flattened papillae along and posterior to dentary teeth and anterior to premaxillary

**Table 1.** Morphometric and meristics of *Neoplecostomus doceensis* (holotype and paratypes). SD = standard deviation.

	<i>Neoplecostomus doceensis</i> n = 26				
	Holotype	Min	Max	Mean	SD
SL	101.1	40.9	101.1	72.4	16.3
<b>Percents of SL</b>					
Predorsal length	43.2	42.5	47.0	43.8	0.9
Head length	31.1	31.0	33.1	32.3	0.6
Head width	28.2	25.7	28.5	27.5	0.7
Cleithral width	26.3	25.8	28.7	27.1	0.8
Occipital-dorsal distance	12.1	10.7	13.8	12.3	0.7
Thoracic length	17.9	14.6	18.6	17.2	1.1
Interdorsal length	19.9	16.9	22.0	18.9	1.3
Caudal peduncle length	28.3	27.3	38.7	31.3	3.2
Caudal peduncle depth	8.7	6.5	8.7	7.4	0.5
Body depth	19.6	15.3	19.6	17.5	1.2
Preanal length	65.1	59.0	67.0	64.3	1.9
<b>Percents of HL</b>					
Head width	90.7	79.8	90.8	85.2	2.6
Head depth	56.5	47.1	57.1	51.9	2.7
Snout length	69.1	62.7	69.2	65.9	1.9
Orbital diameter	7.9	7.0	11.2	8.8	1.2
Interorbital width	32.5	29.3	34.1	31.6	1.3
Mandibullary width	18.8	12.5	22.4	18.2	2.6
<b>Other percents</b>					
Snout length/Orbital diameter	11.4	10.6	17.7	13.3	1.9
Interorbital/Orbital diameter	24.3	23.3	33.7	27.8	3.4
Interorbital/mandibullary width	57.9	44.3	74.4	58.6	8.4
Predorsal length/first ds ray length	46.0	41.8	51.1	46.1	1.8
Caudal peduncle length/Caudal peduncle depth	30.6	18.5	30.7	23.7	3.0
Pelvic-fin length/Caudal peduncle depth	33.9	25.4	36.5	29.5	2.6
Lower cd spine/Caudal peduncle depth	31.6	22.3	35.4	26.7	2.8
<b>Meristics</b>	<b>Holotype</b>	<b>Min</b>	<b>Max</b>	<b>Mode</b>	<b>SD</b>
Lateral-line plates	27	25	29	27	1
Predorsal plates	6	4	7	6	1
Plates of dorsal-fin base	6	5	6	6	0
Plates between dorsal and caudal	15	15	18	16	1
Plates between adipose and caudal	5	5	6	5	0
Plates between an and caudal	11	10	13	12	1
Premaxillary teeth	26	14	33	22	6
Dentary teeth	20	12	35	20	6

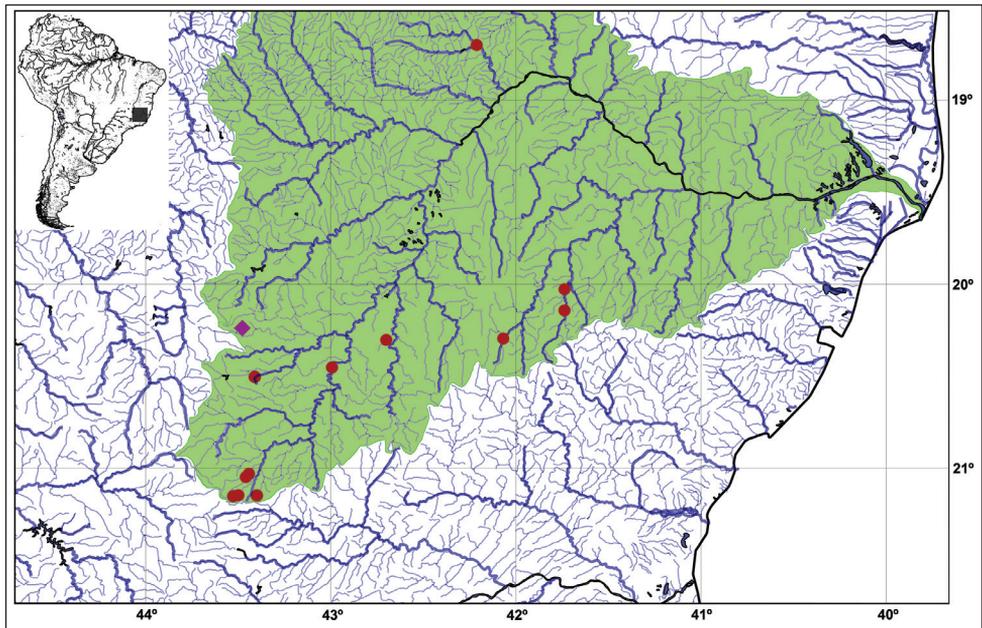
teeth (Fig. 2c). Maxillary barbel very short, coalesced, usually its tip not free from lower lip. Teeth long, slender and bicuspid; mesial cusp longer than lateral; dentary ramus forming an angle of approximately 125–130°.



**Figure 2.** **a** *Neoplecostomus doceensis*, MZUSP 115486, 101.1 mm SL, male, holotype, arrow showing the developed papillae between dentaries **b** *N. botucatu*, MZUSP 110364, 98.6 mm SL, male, paratype, lacking the papillae between dentaries **c** *N. doceensis*, MZUSP 115486, 101.1 mm SL (male), holotype, arrow showing the developed papillae series anterior to premaxillary teeth **d** *N. selенае*, MZUSP 51889, 101.7 mm SL, male, paratype, lacking the papillae series anterior to premaxillary teeth.

Dorsal fin II,7; origin slightly posterior to pelvic-fin origin; dorsal-fin spinelet semicircular and wider than dorsal-fin spine base (spinelet hardly visible in some specimens, but always present); dorsal-fin locking mechanism not functional; dorsal-fin posterior margin straight to slightly rounded, reaching end of pelvic-fin rays when adpressed. Adipose-fin well developed and always present, preceded by azygous plate. Pectoral-fin I,6; unbranched ray depressed and curved inward (more pronounced in larger specimens), shorter than longest branched ray; posterior margin slightly concave, almost reaching half pelvic-fin ray length when adpressed; unbranched ray anteroventrally covered with backward-oriented odontodes. Pelvic-fin I,5; posterior margin nearly straight, reaching anal-fin insertion when adpressed; pelvic-fin unbranched ray ventrally flattened, with dermal flap on its dorsal surface in males; first and second branched rays also with dermal flap on its dorsal surface in males; unbranched ray anteroventrally covered with backward-oriented odontodes. Anal-fin I,5; posterior margin nearly straight; unbranched ray ventrally covered with back-oriented odontodes. Caudal-fin I,7,7,I; bifurcated; lower spine longer than upper; pectoral spine and unbranched pelvic-fin rays with odontodes on lateral and ventral portions.

**Color in alcohol.** Ground color of dorsal surface of head and body dark brown to lighter brown in some specimens. Head with a pale spot on naked area of snout tip; orbital margin slightly lighter, mainly on its superior portion; small pale spot on interorbital space; lateral margin of snout usually lighter than rest of dorsal surface of



**Figure 3.** Map showing the type locality (pink diamond), 20°14'20"S, 43°28'40"W, and paratypes (red circles) of *Neoplecostomus doceensis* at the rio Doce basin (green highlighted drainages). See Distribution and Paratypes sections for details about each paratype localities.

head. Body dorsal color pattern in most specimens with four transverse light bands: first through supraoccipital, second in middle of dorsal-fin, third posterior to dorsal-fin, fourth posterior to adipose-fin. Body lateral portion with an upper darker and a lower lighter, just below lateral line. Dorsal, pectoral, pelvic, anal and caudal fins with hard visible irregular series of dark spots on rays. Ventral surface of head and body light brown.

**Sexual dimorphism.** Males with papilla at the urogenital opening and a membrane along the dorsal portion of the unbranched pelvic-fin ray. Males seem to reach a greater length.

**Distribution.** *Neoplecostomus doceensis* is known from thirteen localities: one at rio Gualaxo do Norte, one at rio Gualaxo do Sul, one at rio José Pedro, one at rio Piranga, three at rio Manhuaçu, one at rio Suaçuí Pequeno and five at rio Xopotó, all in the rio Doce Basin, Minas Gerais State, Brazil (Fig. 3).

**Ecological notes.** *Neoplecostomus doceensis* is found in clear water rivers, varying from small to medium sized, with rocky outcrops forming small waterfalls and substrates of rocks and sand. The species is found at the bottom of the rivers among the rocks.

**Etymology.** The specific name *doceensis* is a Latin noun meaning being located or having connection with the rio Doce basin. This hydrographic system is located in the southeastern region of Brazil and comprises a drainage area of 83,400 km<sup>2</sup>, on the border of Minas Gerais and Espírito Santo states.

## Discussion

### Taxonomy

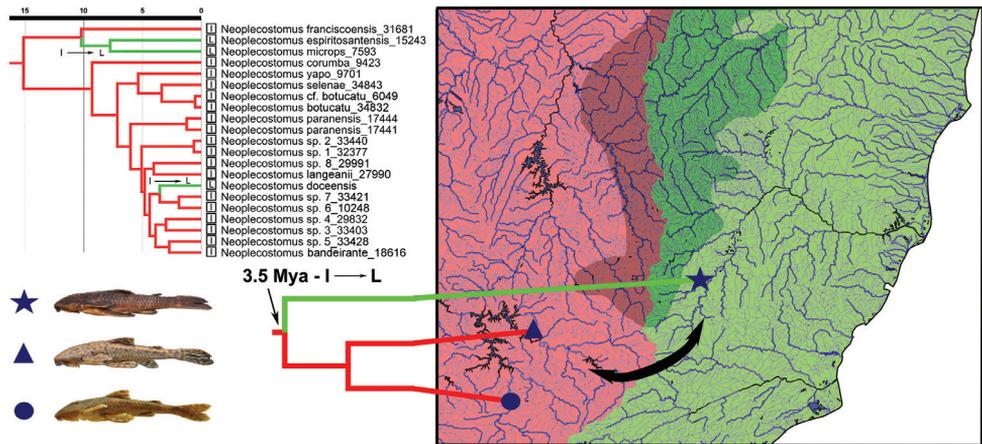
*Neoplecostomus doceensis* has a conspicuous series of enlarged papillae just posterior to the dentary teeth, which are larger than those on the remaining portions of the lower lip. The abdomen is covered with platelet shields of pentagonal, hexagonal or heptagonal shape. The canal bearing plate and the dorsal locking mechanism are absent, suggesting that this is a typical species of the genus *Neoplecostomus*, sensu Langeani (1990).

The main character used to distinguish the new species from its congeners is the enlarged fleshy folds between dentaries present in all specimens (Fig. 2a). Apparently, these folds can also be present in some large specimens of *N. selenae*, although it is poorly developed. Within *N. doceensis*, this character was observed in specimens of all sizes. However, it is more developed in mature males. Within *N. yapo*, we found variations of the folds between dentaries. In specimens of *N. yapo* of the rio Verde, municipality of Ponta Grossa (NUP 4300), this character is poorly developed, as in *N. selenae* and in specimens of the rio Atlântico, municipality of Mandaguaçu (NUP 4851), in which this character is absent. Several authors (e.g. Langeani 1990; Bizerril 1995; Zawadzki et al. 2008; Roxo et al. 2012c) have reported that the characters used to define the species of *Neoplecostomus* are influenced by both the sex and stage of ontogenetic development, which also occurs with the papillae between the dentary teeth.

The presence of two or three series of well-developed papillae anterior to the premaxillary teeth also distinguish the new species from its congeners (Fig. 2c). The presence of two or three series of conspicuous papillae just posterior to dentary teeth was previously discussed by Langeani (1990) and is used to diagnose the genus *Neoplecostomus*. Nevertheless, the papillae series anterior to premaxillary teeth have not previously been reported. Several species of *Neoplecostomus* such as *N. bandeirante*, *N. corumba* and *N. ribeirensis* have this character; however, it is best developed in *N. doceensis*. Apparently, this character is also influenced by sex and is enlarged in mature males.

### Biogeography and dispersal route

Roxo et al. (2012a, 2012b), in a phylogenetic study of the Neoplecostominae species, suggested that *Neoplecostomus* originated within “interior running drainages” (i.e., drainages of the upper rio Paraná, rio Iguaçu, and rio São Francisco). An exception was found for *N. ribeirensis*, which appeared as a sister group to *Isbrueckerichthys* and originated in littoral drainages (i.e., Northeastern Mata Atlântica rivers, rio Paraíba do Sul, rio Ribeira de Iguape, Southeastern Mata Atlântica river, and Fluminense river). The new species, *N. doceensis* (cited as *Neoplecostomus* sp. 9 in Roxo et al. 2012a), is closely related to two undescribed species of *Neoplecostomus*, *Neoplecostomus* sp. 6 (from córrego do Sapateiro) and *Neoplecostomus* sp. 7 (from córrego Tamborete) both from streams in the rio Grande basin, an Atlantic coastal drainage. Roxo et al. (2012a) suggested that



**Figure 4.** Distribution and time-calibrated phylogenetic tree of *Neoplecostomus* species, except *N. ribeirensis*, based on four mitochondrial (12S rRNA, 16SrRNA, COI, Cytb) and one nuclear marker (F-reticulon 4), modified from Figure 3 of Roxo et al. (2012a). The red coloration in the figure indicates the interior drainages (Upper Paraná, Iguassu, and São Francisco) and the green, the littoral drainages (Northeastern Mata Atlântica, Paraíba do Sul, Ribeira de Iguape, Southeastern Mata Atlântica and Fluminense). Based on our hypothesis, the ancestral lineage of *N. doceensis* dispersed from the upper rio Paraná to rio Doce drainages about 3.5 Mya (95% HPD: 1.6–5.5). See Table S1 in Roxo et al. (2012a) for all localities of undescribed species of *Neoplecostomus*.

the ancestor of *N. doceensis* (cited as *Neoplecostomus* sp. 9) reached the rio Doce basin about 3.5 million years ago (95% HPD: 1.6–5.5) indicating a colonization route of the *N. doceensis* ancestral lineage from southern Serra do Espinhaço (Fig. 4), probably as a result of headwater capture processes between the upper rio Paraná and rio Doce basins.

Ribeiro (2006) suggested that the south-eastern region of Brazil has undergone intensive geological activity and that the activations of ancient faults could have resulted in headwater captures between adjacent drainages during several periods of its geological history. The eastern Brazilian coastal drainages have probably resulted in the capture of several adjacent rivers, including the headwaters of the Tietê, Grande, São Francisco and Doce rivers. A river capture event at this approximate time and place is also consistent with the General Area Cladogram of fish taxa from tropical South America (Albert and Carvalho 2011). This process is likely to have influenced the movement of ancestral fish throughout the adjacent drainages, similar to the geodispersal of the ancestor of *N. doceensis* from the upper rio Paraná drainages to the rio Doce drainages about 3.5 Mya (95% HPD: 1.6–5.5).

### Comparative material

*Neoplecostomus bandeirante*: holotype, MZUSP 110363, 109.9 mm SL, rio Paraitinguinha, rio Tietê basin, paratypes, LBP 3921, 2, 88.0–94.9 mm SL, rio Paraitinguinha,

rio Tietê basin, LBP 2861, 8, 87.6–106.4 mm SL, rio Paraitinguinha, rio Tietê basin, NUP 6103, 1, 101.7 mm SL, rio Paraitinguinha, rio Tietê basin; *Neoplecostomus botucatu*: holotype, MZUSP 110364, 98.6 mm SL, córrego Águas de Madalena, rio Paranapanema basin, paratype, LBP 7525, 10, 80.3–102.2 mm SL, córrego Águas de Madalena, rio Paranapanema basin, LBP 8065, 12, 67.5–88.2 mm SL, córrego Águas de Madalena, rio Paranapanema basin, NUP 8016, 1, 69.8 mm SL, córrego Águas de Madalena, rio Paranapanema basin; *Neoplecostomus corumba*: holotype, DZSJRP 6713, 78.3 mm SL, córrego Gameleira, rio Paranaíba basin, paratypes, MZUSP 86208, 9, 45.7–77.6 mm SL, córrego Gameleira, rio Paranaíba basin; *Neoplecostomus espiritosantensis*: holotype, MZUSP 38573, 102.3 mm SL, rio Jucu, Coastal Drainage, LBP 2551, 2, 81.9–85.4 mm SL, rio Jucu, Coastal Drainage; *Neoplecostomus franciscoensis*: holotype, MZUSP 38577, 68.4 mm SL, affluent córrego Mutuca, rio São Francisco basin, LBP 6489, 50, 42.8–55.9 mm SL, rio das Velhas, rio São Francisco basin, MZUSP 107361, 7, 54.3–107.8 mm SL, rio Paraopeba, rio São Francisco basin; *Neoplecostomus langeanii*: holotype, MZUSP 110365, 85.5 mm SL, rio São Domingos, rio Grande basin, paratype, LBP 5931, 11, 48.4–69.6 mm SL, rio São Domingos, rio Grande basin, LBP 5947, 8, 56.6–73.5 mm SL, rio São Domingos, rio Grande basin; *Neoplecostomus microps*: LBP 6350, 4, 51.0–58.9 mm SL, rio Ribeirão Grande, rio Paraíba do Sul basin, LBP 8045, 31, 43.8–71.4 mm SL, ribeirão Piquete, rio Paraíba do Sul basin, LBP 8370, 17, 39.5–81.2 mm SL, rio Pomba, rio Paraíba do Sul basin; *Neoplecostomus paranensis*: holotype, MZUSP 38572, 71.4 mm SL, rio Cubatão, rio Grande basin, LBP 2732, 1, 70.5 mm SL, córrego Mocoquinha, rio Grande basin, MZUSP 10213, 2, 39.4–41.5 mm SL, rio Carandaí, rio Grande basin, MZUSP 35397, 1, 38.4 mm SL, rio São João, rio Grande basin, MZUSP 36583, 2, 52.0–62.4 mm SL, rio Cubatão, rio Grande basin, MZUSP 36625, 1, 56 mm SL, rio São Bartolomeu, rio Grande basin, MZUSP 38822, 1, 92.8 mm SL, rio Cubatão, rio Grande basin, MZUSP 38823, 1, 87.7 mm SL, rio Cubatão, rio Grande basin, MZUSP 38824, 1, 68.1 mm SL, rio Cubatão, rio Grande basin; *Neoplecostomus ribeirensis*: LBP 7384, 16, 37.7–79.2 mm SL, rio Água Doce, rio Ribeira de Iguape basin; *Neoplecostomus selenae*: holotype, MZUSP 51889, 101.7 mm SL, ribeirão das Batéias, rio Paranapanema basin, paratype, DZSJRP 7449, 4, 56.5–95.8 mm SL, ribeirão das Batéias, rio Paranapanema basin, MZUSP 52589, 4, 42.8–64.9 mm SL, ribeirão das Batéias, rio Paranapanema basin, NUP 3572, 5, 48.0–84.8 mm SL, ribeirão das Batéias, rio Paranapanema basin; *Neoplecostomus yapó*: holotype, DZSJRP 6714, 97.4 mm SL, riacho Fortaleza, rio Paranapanema basin, paratype, MZUSP 86211, 7, 63.8–105.2 mm SL, affluent of rio Yapó, rio Paranapanema basin, NUP 2609, 15, 48.4–109.6 mm SL, riacho Fortaleza, rio Paranapanema basin, NUP 4300, 5, 73.5–89.1 mm SL, rio Verde, rio Paranapanema basin, NUP 4851, 11, 39.2–73.8 mm SL, rio Atlântico, rio Paranapanema basin.

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