Hydrobiologia (2012) 688:125–138
DOI 10.1007/s10750-011-0658-8

Contribution to the taxonomy, distribution and paleoecology of the early representatives of *Penthesilenula* Rossetti & Martens, 1998 (Crustacea, Ostracoda, Darwinulidae) from Argentina, with the description of a new species

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Published online: 17 March 2011

Abstract Early Mesozoic Argentinian darwinuloids, now re-assigned to the genus *Penthesilenula* (*incae* group), are described and illustrated. These records seem to constitute the oldest known for the genus. The close similarities between the studied species and those described from eastern Asia enlarge the geographical distribution of *Penthesilenula* (*incae* group), which, although restricted to the southern Hemisphere in Recent and Holocene times, may have had a wider distribution in the past. Additional information on the paleoecology, plus a preliminary account on the distribution of darwinulid species from Argentina are also offered. One new species is described: *Penthesilenula loana* sp. nov.

Guest Editors: D. A. Do Carmo, R. L. Pinto & K. Martens / Ostracoda – Biostratigraphy and Applied Ecology

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Keywords Darwinulidae · Triassic · Jurassic · Argentina · Taxonomy · Paleoecology

Introduction

The Darwinulidae are the only surviving post-Palaeozoic family of the non-marine superfamily Darwinuloidea.

Recent Darwinulidae have been revised in detail by Rossetti & Martens (1998) who recognized five genera on both soft part and valve features; they are, the type genus *Darwinula* Brady & Robertson, *Microdarwinula* Danielopol and three genera created by Rossetti and Martens (op. cit.): *Alicenula*, *Vestalenula* and *Penthesilenula*. The data with morphological characteristics derived from the revision mentioned above have been later used for a cladistic analysis, whose results together with the molecular-based phylogeny, confirmed the five genera recognized by Rossetti and Martens (Martens et al., 2005). Recently, a new genus, *Isabenula*, has been described by Rossetti et al. (2009).

As all these genera have been characterized on both soft part and valve features, Rossetti & Martens (1998, p. 59) suggested that it should be possible to allocate at least the Mesozoic and the Cenozoic species of the former *Darwinula* s. l. to one of these new genera (*Darwinula* s. s. is now, as far as extant fauna is concerned, monospecific, comprising the type species *Darwinula stevensoni*). Taking this into

account, a preliminary re-examination of the Argentinian darwinuloid records using the same criteria was discussed by Ballent et al. (2005).

This paper revises the position of the early Mesozoic darwinulid species from Argentina which are now re-assigned to the genus *Penthesilenula* and provides information on the taxonomy and distribution of living and fossil species, paleoecology, and depositional environment. *Penthesilenula loana* sp. nov. is described.

Materials and methods

The studied material comes from a number of localities in both Patagonia and west-central Argentina (Fig. 1).

1. Cañadón Asfalto Basin (in central extra-Andean Patagonia). The continental volcano-sedimentary sequences of mainly siliciclastic lacustrine strata of the Late Jurassic (Oxfordian-Tithonian) Cañadón Asfalto Formation, from different localities in the middle Chubut river in central extra-Andean Patagonia (between 42°36′, 44°00′S and 70°00′, 68°30′W), have provided abundant microfaunas including darwinulid ostracods.
2. Section from the eastern slope of Cerro Corona (40°10′S, 70°21′W), in Neuquén Province. This fossiliferous locality is situated on the right bank of the Cañadón La Pintada and along the eastern slope of the Cerro Corona (Ballent, 1987). The studied levels occur in the Piedra Pintada Formation (cf. Damborenea & Manceñido, 1993) (or Los Molles Formation sensu Gulisano & Pando, 1981) and comprise nearly 50 m of olive grey and greenish brown claystones (massive at the bottom and laminated towards the top of the section), intercalated with greenish brown fine grained, calcareous sandstones. Stromatolites, conchostracans, plant and coal remains are more frequent in the lower part of the section. This is a deposit which is thought of late Pliensbachian age because of its associations with strata elsewhere of marine facies containing invertebrates (Gulisano & Pando, 1981).
3. Internal moulds of darwinulids recovered from a conventional core sample in the southern Mendoza Province (northern Neuquén Basin, between 37°00′, 37°20′S and 69°00′, 69°30′W). The ostracods are recovered from lacustrine pelites of the Los Molles Formation; the intercalated marine microfossils indicate an Early Jurassic age for this sample.
4. Darwinulids recovered from the Lower Jurassic (pre-Toarcian) sediments of the middle member (up to 19 m thick) of the Remoredo Formation at Arroyo Montañesito, southern Mendoza province (northern Neuquén Basin, approximately 35°30′S, 70°00′W). These deposits are represented by massive to upward-coarsening, dark grey, oncoidal wackestones, associated with a well preserved

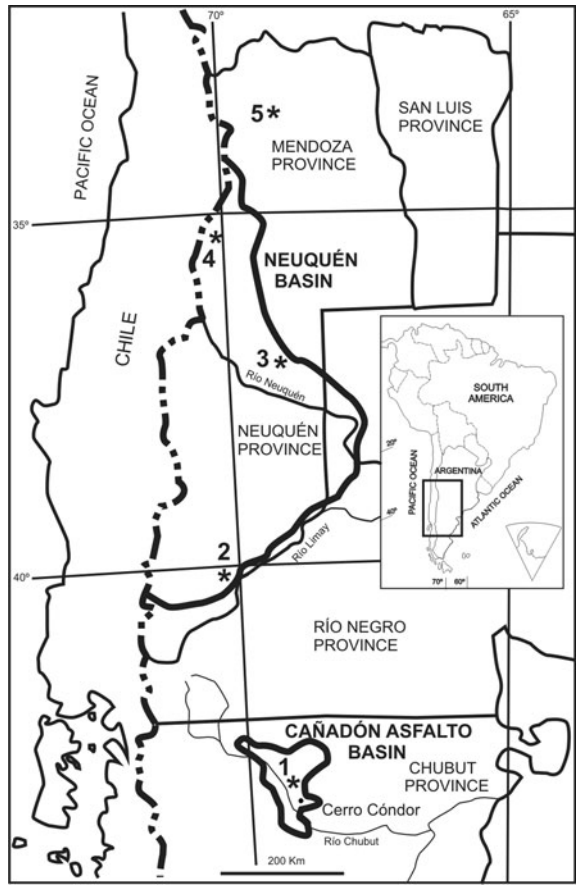


Fig. 1 Location map showing the position of the fossiliferous localities (modified from Volkheimer et al., 2008). Cañadón Asfalto Basin: *1* Several sections in central extra-Andean Patagonia; Neuquén Basin: *2* Eastern slope of Cerro Corona, Neuquén Province; *3* Conventional core sample in the southern Mendoza Province; *4* Arroyo Montañesito, Mendoza Province; *5* Quebrada del Arbolito, in the Quebrada de San Isidro, Mendoza Province

assemblage of fragmented bivalves and freshwater ostracods (Lanés & Palma, 1998).

5. A low diversity microfauna containing cypridoids and one species of darwinulid has been recovered from lacustrine sediments of the upper part of the Cerro de Las Cabras Formation (late Middle Triassic) from Quebrada del Arbolito, in the Quebrada de San Isidro, Precordillera, west of Mendoza city, Mendoza Province, Argentina (Hünicken & Chaia, 1992).

The samples were processed with 10% hydrogen peroxide for 24 h or (where indurated rocks) treated with anhydrous sodium sulphate (several days for full disintegration) and then washed over a 63 μm sieve, and oven dried (30°C). Selected specimens were mounted on stubs using carbon conductive adhesive tape and gold-coated for examination by a scanning electron microscope (SEM) at the Servicio de Microscopía Electrónica del Museo de La Plata. Type and figured specimens are deposited in the collections of the Museo de La Plata, Argentina-Sección Micropaleontología (MLP-Mi 482–499, 571, 572, 1808, 1809, 1810) and División Zoología Invertebrados (MLP 26209), and Laboratorio de Micropaleontología, Facultad de Ciencias Exactas y Naturales, Buenos Aires, Argentina (FCEN-LM 3090).

Results

Diagnosis and some remarks of the genus *Penthesilenula*

The genus *Penthesilenula* was described by Rossetti & Martens (1998) with *P. incae* (Delachaux) as the type species. According to the diagnosis, the valves of adult specimens are small to large in size, elongate or sub-rectangular in lateral view, with dorsal margin straight over at least part of length, anterior margin narrowly rounded, posterior margin bluntly rounded and with the caudal brooding cavity externally visible. Left valve generally overlapping right valve on all margins, except dorsal margin. Valve surface smooth. Hinge adont, central muscle scars with a variable number of spots arranged in a circular rosette. Left valve either with two rounded internal teeth (anteroventral and posteroventral in the *africana* group) or with posterior internal teeth in the *incae* group. Right valve without postero-ventral keel. It differs from *Darwinula* in the sub-rectangular shape of the valves and in the presence of internal teeth in the left valve. In *Darwinula stevensoni* the *L*/*H* ratio is nearly 2.50 while in *Penthesilenula incae* the *L*/*H* ratio is lower (2.06–2.08). *Penthesilenula* differs from *Vestalenula* with the latter smaller in size and possessing an anteroventral tooth near to the inner margin of the left valve and a postero-ventral external keel in the right valve. *Penthesilenula* differs from *Alicenula* with the latter possessing a more elongate and medium-sized carapace. *Alicenula*, although not originally described as having teeth in the left valve, has been shown to have an antero-ventral ridge-like tooth near the edge of the inner margin and a posterior caudal tooth (see *A. leguminella* in Martens et al., 2003, figure 3).

Systematic descriptions

The adopted suprageneric classification is that proposed by Horne et al. (2002); for the genera within the Darwinulidae, we follow the systematic review of Rossetti & Martens (1998). The following conventions are employed: L = length, H = height, W = width; very small (less than 0.400 mm), small (0.400–0.500 mm), medium (0.510–0.700 mm), large (0.710–0.900 mm), very large (more than 0.900 mm).

Class Ostracoda Latreille, 1806
Subclass Podocopa G. W. Müller, 1894
Order Podocopida Sars, 1866
Suborder Darwinulocopina Sohn, 1988
Superfamily Darwinuloidea Brady & Norman, 1889
Family Darwinulidae Brady & Norman, 1889
Genus *Penthesilenula* Rossetti & Martens, 1998
Type species. *Darwinula incae* Delachaux, 1928 (in Rossetti et al., 1996: 35–40) from the Recent of Lake Huaron (Region of Huancavelica, Department of Junin, Peru).

Penthesilenula sarytirmenensis (Sharapova) sensu Mandelstam, 1947 *(Fig. 2A–G)*

1975. *Darwinula* sp. sensu Musacchio, pl. II, figs 1–2.

1990. *Darwinula* sp. sensu Musacchio et al., pl. II, figs 1–4.

1990. *Darwinula* sp. 2 sensu Musacchio et al., pl. II, figs 5–7.

1995. *Darwinula sarytirmenensis* (Sharapova), Musacchio, pl. I, fig. 11.

Studied material: fifty carapaces, plus a few poorly preserved valves.

Repository: MLP-Mi 459, 482–491.

Description: carapace very large, elongate-ovate in lateral view. Greatest length immediately below mid-height, greatest height in the posterior third of the valves. Anterior margin narrowly rounded; posterior margin bluntly rounded. Dorsal margin straight in the mid-third, ventral margin concave anteromedially. Left valve overlaps right valve along all the periphery. In dorsal view the carapace is an elongate ovoid, with the greatest width in the mid-third of the valve. Valve surface smooth. Hinge adont. Central muscle scars in a circular pattern situated immediately in front of the mid-length and at mid-height of the valve (the number of the individual scars is not possible to count). Other internal features not observed.

Measurements (mm): (figured specimens)

MLP-Mi 482 $L = 1.080$, $H = 0.465$, $W = 0.380$; MLP-Mi 483 $L = 1.000$, $H = 0.465$, $W = 0.400$; MLP-Mi 484 $L = 0.995$, $H = 0.450$, $W = 0.420$; MLP-Mi 485 $L = 1.090$, $H = 0.493$, $W = 0.400$; MLP-Mi 486 $L = 0.992$, $H = 0.435$, $W = 420$; MLP-Mi 487 $L = 0.980$, $H = 0.445$, $W = 0.400$; MLP-Mi 489 $L = 0.865$, $H = 0.400$, $W = 0.370$.

Distribution and age: this species has been described from the Middle Jurassic of the Mangishlaka Peninsula, ex USSR (Mandelstam, 1947) and also recorded from the Middle and Late Jurassic of several localities in China (including Li, 1985; Zheng, 1995) and south-eastern India (Govindan, 1975). In Argentina, it has been recorded from the Late Jurassic (Oxfordian-Tithonian) of several localities in the Chubut Province, "Estratos de Almada", El Barrancal (near to Paso de Indios), El Capricho (near to Cerro Cóndor), "Estancia La Sin Rumbo" (Musacchio et al., 1990; Musacchio, 2001; Gallego et al., 2011).

Remarks: a phylogenetically related species to *Penthesilenula sarytirmenensis* is *P. eosarytirmenensis* (Ye, 1977) from the Upper Triassic of Yunnan Province, China, which is very similar in outline and overlap, although it differs from the former in its smaller carapace. The studied sample population of *P. sarytirmenensis* comprises large number of adults, plus juvenile instars which go well back into the ontogeny of the species.

Fig. 2 **A–G** *Penthesilenula sarytirmenensis* (Sharapova). All carapaces: **A** MLP-Mi 482, right lateral view; **B** MLP-Mi 484, dorsal view; **C** MLP-Mi 483, left lateral view; **D** MLP-Mi 485, right lateral view; **E** MLP-Mi 486, left lateral view; **F** MLP-Mi 487, right lateral view; **G** MLP-Mi 489, left lateral view. **H–K** *Penthesilenula loana* sp. nov. All carapaces: **H** MLP-Mi 492, Holotype, adult, right lateral view; **I** MLP-Mi 494, Paratype, juvenile, dorsal view; **J** MLP-Mi 493, Paratype, adult, left lateral view, **K** MLP-Mi 572, adult, right lateral view. **L–R** *Penthesilenula* sp. A: **L–M** MLP-Mi 496, carapace, left lateral view and detail muscle scars; **N–O** MLP-Mi 497, fragment, right lateral view) and detail of the muscle scars; **P** MLP-Mi 498, fragment, right lateral view; **Q** MLP-Mi 499, fragment, left lateral view, **R** MLP-Mi 1808, fragment, right lateral view. **S** *Penthesilenula* sp. B FCEN-LM 3090, carapace, left lateral view. **T** *Penthesilenula*? sp. MLP-Mi 1809, carapace, juvenile, left lateral view. **U** *Penthesilenula incae* (Delachaux) MLP-Mi 1810, Holocene, left valve, internal view. **V–X** *P. incae* MLP 26209, Recent, left valve, internal view and details showing caudal tooth and muscle scars. *Scale bar* = 0.100 mm (in figures **W**, **X**, the *bar* represents 0.050 and 0.010 mm, respectively)

Penthesilenula loana sp. nov. *(Fig. 2H–K)*

1987 *Darwinula* sp. Ballent, p. 102, pl. 4, figs 11a, b.

Type locality and type level: eastern slope of Cerro Corona (40°10′S, 70°21′W), Neuquén Province, Argentina, level 1058, late Pliensbachian (Early Jurassic).

Type material:

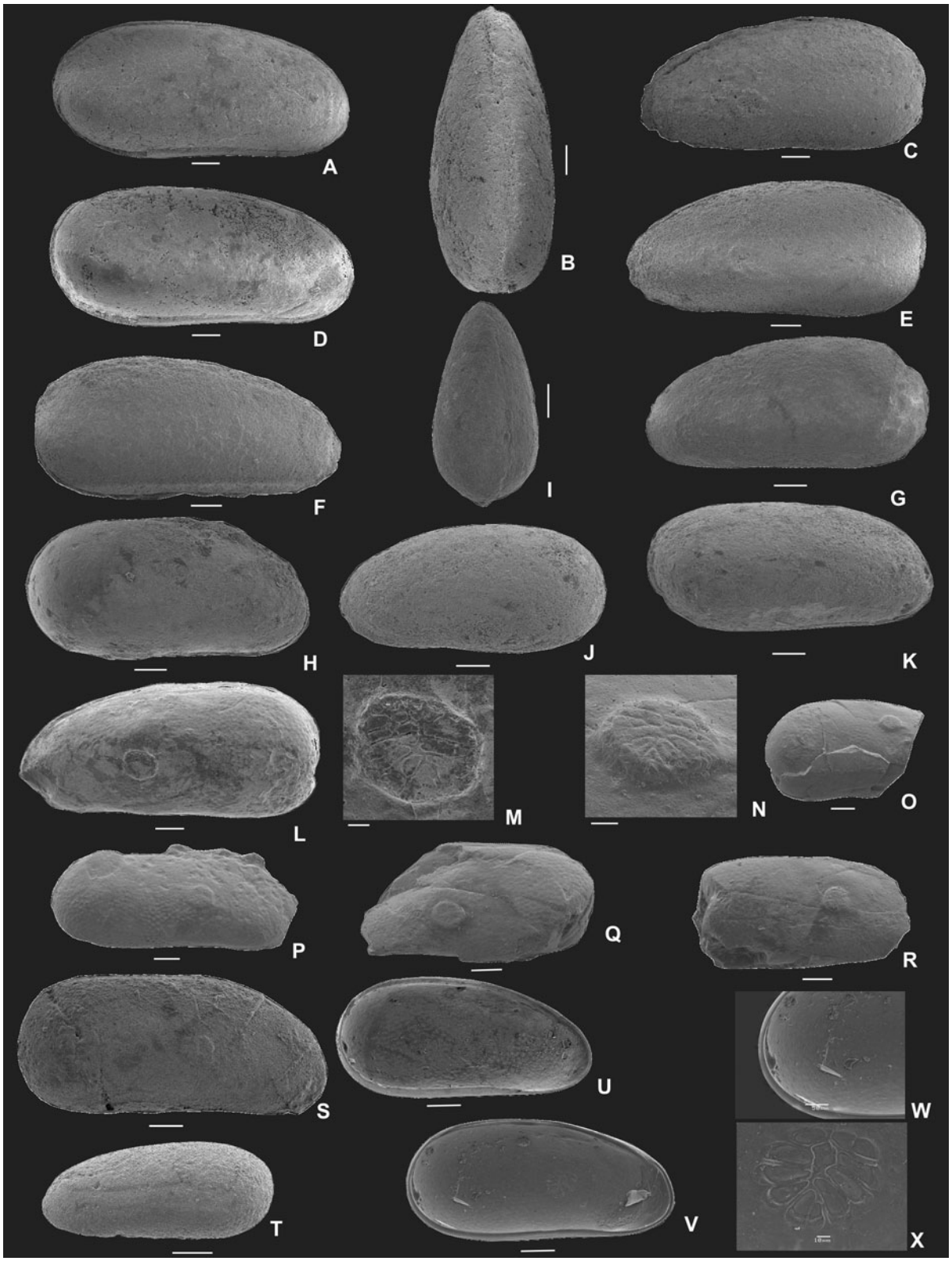
Holotype: female carapace, MLP-Mi 492 figured in Fig. 2H.

Paratypes: female carapaces, MLP-Mi 571, 572, 495 and juvenile carapaces MLP-Mi 493, 494; all from the eastern slope of Cerro Corona (40°10′S, 70°21′W), Neuquén Province, Argentina, level 1058.

Studied material: thirty carapaces, adults and juveniles.

Derivation of the name: from the aboriginal Mapuche word *loan* meaning guanaco, a camelid (mammal, ruminant) native to the mountainous regions of South America, very common in Argentinian and Chilean Patagonia.

Diagnosis: a species of *Penthesilenula* which is very large and robust, elongated sub-rectangular in lateral view, a dorsal margin which is straight along its posterior two-third, plus a smooth valve surface.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Description: carapace very large and robust, elongated sub-rectangular in lateral view with the posterior third broadly enlarged, slightly truncated. Greatest length in the lower third and greatest height in the posterior third of the valves. Anterior margin narrow and obliquely rounded, pointed downwards. Posterior margin bluntly rounded. Dorsal margin straight in the posterior two-third of the valves. Ventral margin slightly concave anteromedianly. Left valve overlapping right valve along entire periphery, except along the posterior part of the dorsal margin where in some carapaces the overlap is reversed. Large caudal brooding cavity visible externally. In dorsal view the carapace is ovoid in outline, posteriorly broadly rounded, anteriorly rather convex and with the greatest width in the posterior third of the valve. Smooth valve surface. Internal features not observed.

Measurements (mm): (specimens figured)

Holotype MLP-Mi 492 $L = 0.877$, $H = 0.436$, $W = 0.450$.

Paratypes MLP-Mi 493 $L = 0.789$, $H = 0.380$, $W = 0.450$; MLP-Mi 494 $L = 0.580$, $H = 0.\ 250$, $W = 0.310$; MLP-Mi 572 $L = 0.935$, $H = 0.440$; $W = 0.500$.

Age and distribution: late Pliensbachian, eastern slope of Cerro Corona, Neuquén Province, Argentina.

Remarks: the new species resembles *P. magna* (Jiang, 1963) from the Middle-Late Jurassic of China. Both species are elongated sub-rectangular in lateral view although the latter is somewhat more strongly concave anteroventrally and has greater *H*:*L* ratio (the height is more than half length, nearly 0.600 in *P. magna* and nearly 0.480 in *P. loana* sp. nov.). Population of this new species comprises adults and juvenile instars which go well back into the ontogeny of the species. Valves with "cup in cup" structure, in which progressively smaller valves occur one within another, are frequent in the studied samples.

Penthesilenula sp. A *(Fig. 2L–R)*

Repository: MLP-Mi 496–499, 1808.

Measurements (mm): specimens figured MLP-Mi 496 $L = 1.030$, $H = 0.465$, $W = 0.400$; MLP-Mi 497, fragment $L = 0.595$; MLP-Mi 498, fragment $L = 0.930$; MLP-Mi 499, fragment $L = 0.640$; MLP-Mi 1808, fragment $L = 0.690$.

Age and distribution: Early Jurassic; conventional core sample in the southern Mendoza Province (northern Neuquén Basin, between 37°00′, 37°20′S and 69°00′, 69°30′W), Argentina.

Remarks: the studied material is poorly preserved and consists of a few carapaces and numerous fragments of carapaces, all of them as internal moulds. Carapace very large, subrectangular in lateral view, with dorsal and ventral margins almost subparallel to each other. Greatest length slightly below mid-height and greatest height in the posterior third of the valves. Anterior margin obliquely rounded and posterior margin bluntly rounded. Dorsal margin slightly arcuate to almost straight in the posterior half of the valve. Ventral margin slightly concave medially and almost subparallel to the dorsal margin. Adductor muscle scars comprise a circular "rosette", with 12–14 elongated spots positioned anteriorly and variably situated immediately below or above of half of the greatest height of the valves. As they are internal moulds, a pointed posterior incision in the left valve (that could correspond to the caudal internal tooth that characterizes the *incae* group) is observed in some specimens. *Penthesilenula* sp. A resembles *P. subparallela* (Ye, 1977) from the Late Jurassic of China, the latter of which, however, has more elongated carapace.

Penthesilenula sp. B *(Fig. 2S)*

Repository: FCEN-LM 3090.

Measurements (mm): specimens figured FCEN-LM 3090, carapace $L = 0.905$, $H = 0.400$, $W = 0.350$.

Age and distribution: Early Jurassic (pre-Toarcian); Remoredo Formation at Arroyo Montañesito, southern Mendoza province (northern Neuquén Basin, approximately 35°30′S, 70°00′W), Argentina.

Remarks: the studied material comprises only one carapace and numerous fragments. Carapace very large, subrectangular in lateral view, with dorsal and ventral margins almost subparallel to each other. Greatest length below mid-height. In dorsal view the carapace is subovate, compressed and with both margins subparallel in the posterior third of the carapace. Valve surface smooth. Adductor muscle scars comprise a circular "rosette", positioned anteriorly and above of the greatest length of the valves. The present specimen resembles *Penthesilenula loana* sp. nov., although it is narrower in dorsal view.

Penthesilenula? sp. *(Fig. 2T)*

Repository: MLP-Mi 1809.

Measurements (mm): specimen figured, MLP-Mi 1809, $L = 0.780$, $H = 370$, $W = 0.300$.

Age and distribution: late Middle Triassic, Quebrada del Arbolito, in the Quebrada de San Isidro, Precordillera at west of Mendoza city, Mendoza Province, Argentina.

Remarks: this species is left in open nomenclature due to the fact that the material consists of a few juvenile specimens. Carapace medium, subovate in lateral view, with dorsal margin straight in the posterior half of the valve, anterior margin narrowly rounded, while the posterior margin is nearly straight. Left valve overlapping right valve on all margins. Valve surface smooth. Other internal features not observed.

Discussion

Taxonomy and morphology

The material of *P. sarytirmenensis*, *P. loana* sp. nov. and *Penthesilenula* sp. B analyzed in this present study comprise carapaces which are filled with material which does not allow for observation of the internal features. An incision that probably indicates the presence of the caudal tooth in the left valve is observed in some specimens of *Penthesilenula* sp. A (as internal moulds). However, the external features of these species, such as the very large size, the sub-rectangular elongate shape in lateral view, the dorsal margin straight over at least part of its length, the posterior margin nearly straight, and the left valve overlapping right valve, are enough to accommodate them in *Penthesilenula incae* group.

Regarding the size of the carapace, we observe that extant species of *Penthesilenula* are generally 0.80–0.90 mm long, while own fossils species are larger, reaching 1 mm or more.

Distribution

The geographical distribution of the fossil and extant Darwinulidae has been discussed by Martens et al. (1997) and Rossetti & Martens (1998).

Darwinula stevensoni has a cosmopolitan distribution. The majority of the extant known *Vestalenula* are distributed in the Southern Hemisphere, mainly at low latitudes (except *V. boteai* from Romania, *V. cornelia* from Japan and *Vestalenula* sp. B from Tunisia). However, the fossil record of *Vestalenula* is widely known from the Neogene and Quaternary deposits of both Europe and western Asia. These records have been recently summarized and updated by Ligios et al. (2009).

Alicenula occurs in South and Central America, and also in Africa (Martens & Rossetti, 2002). However, the origin of this genus dates back to at least 170–160 million years, with *A. leguminella* (Forbes) from the latest Jurassic of England (Martens et al., 2003); and the taxa originally assigned to *Darwinula* in Wakefield (1994) from the Bathonian of the Inner Hebrides, Scotland, which are now included in *Alicenula* (*A. palmo*, *A. phaselus*, *A. protensa, A. cicatricosa* all of Wakefield, 1994 and *A. incurva* (Bate), see Wakefield, 2009). Also, a re-examination of *D. martinsi* Silva from the Early Cretaceous of the Araripe Basin, northern Brazil (re-description in Do Carmo et al., 2004) shows that it is better accommodated in *Alicenula* (Ballent & Díaz, unpublished results).

Species belonging to the *Penthesilenula africana* group are widely distributed (Europe, Africa, Oceania and Brazil in South America), including Quaternary records from the Fiji Islands and Tasmania (Martens & Rossetti, 2002), and the Pleistocene from southern Portugal (Cabral et al., 2005). Species belonging to the *incae* group are more restricted, occurring in the Southern Hemisphere: South America (Peru, Bolivia, Argentina) and New Zealand (Martens & Rossetti, 2002).

Studies on the Darwinulidae in Argentina have been poorly investigated up to this present study with contemporaneous works dealing with the taxonomic aspects of the cypridoids. To begin the study on the former family, a preliminary list of extant and fossil darwinulid species from Argentina is presented in Table 1. Data were extracted from the literature, from re-examination of specimens deposited in the collections of the Museo de La Plata and unpublished results from the present authors.

Vestalenula is recognized from the Late Pleistocene, while *Alicenula* occurs from the Early Cretaceous through the Neogene. To our knowledge, neither living nor Holocene species of both genera

Table 1 List of extant and fossil species of darwinulids from Argentina with their geographical location, (paleo)environments and stratigraphical range

Genus	Species/distribution/(paleo)environment	Age	References
Darwinula	*D. stevensoni* (Brady & Robertson). Wide distribution (northern Argentina, Patagonia, Buenos Aires Province). Temporary and permanent ponds; hot springs	Living Living	Laprida et al. (2006) Díaz (unpubl.), Laprida (2006)
Microdarwinula	As *Darwinula* sp. (tentatively included in *Microdarwinula*). Patagonia (Lago Cardiel area, 48°–49°S, 70°71°W). Springs (MLP-Mi 1407–1411)	Living	Cusminsky et al. (2005)
Vestalenula	*V. plagiolii* (Pinto & Kotzian). Buenos Aires Province. Temporary ponds	Living	Laprida (2006)
	As *D. plagiolii* (Entre Ríos Province, 32°00′S, 58°30′W). Lacustrine	Late Pleistocene/ Holocene	Zabert & Herbst (1986)
Alicenula	As *Darwinula* sp. (La Rioja Province, aprox. 37°S, 67°W). Lacustrine, freshwater/oligohaline?	Late Miocene	Cusminsky et al. (2006)
	As *D.* aff. *stevensoni* and *Darwinula* sp. (Río Negro Province, between 41°28′S, 70°45′W and 41°30′S, 70°53′W). Lacustrine (freshwater to oligohaline)	Oligocene	Bertels-Psotka & Cusminsky (1999)
	As *D.* aff. *kwangoensis* Grékoff (Río Negro and Neuquén Provinces, 39°00′S, 68°70°W). Non-marine (MLP-Mi 81/2)	Late Cretaceous	Musacchio (1973)
	As *Darwinula* sp. (San Juan Province, 31°40′6″S, 67°11′64″W). Shallow lacustrine (MLP-Mi 1268)	Early Cretaceous (Albian)	Prámparo et al. (2005)
	Alicenula sp. (Santa Cruz Province, 49°31′52″S, 71°28″W). Lacustrine. (MLP-Mi 1820)	E. Cretaceous (Albian)	Ballent (unpublished)
	As *D.* aff *oblonga* Roemer and *Darwinula* sp. A (Neuquén Province, approx. 39°30′S, 70°00′W). Freshwater to brackish (MLP-Mi 24, 25)	E. Cretaceous (Hauterivian–Barremian)	Musacchio (1970), Simeoni & Musacchio (1986)
Penthesilenula	*Penthesilenula* sp. Chaco Province (27°48′S, 59°16′W) and Misiones Provinces. Temporary ponds	Living	Díaz & Ballent (under study)
	P. incae (Delachaux). Patagonia (Lago Cardiel area, 48°–49°S, 70°71°W); Laguna Cari-Laufken area, 41°–41°30′S, 68°69°W); Arroyo Telsen, 42°14′S, 67°04′W; Northern Argentina. Temporary and permanent ponds; hot springs; small swamps	Living	Cusminsky et al. (2010) Laprida et al. (2006) Ballent & Díaz (2009)
	P. incae. Southern Buenos Aires Province (38°34′S, 58°42′W). Freshwater to estuarine	Holocene	Ferrero (1996)
	P. incae. San Juan Province (appr. 32°S, 70°W). Lacustrine	Holocene	This paper
	P. sarytirmenensis (Sharapova). Chubut Province. East Asia. Lacustrine	Middle-Late Jurassic	This paper
	P. loana sp. nov. Neuquén Province. Lacustrine	Early Jurassic (Pliensbachian)	This paper
	Penthesilenula sp. A. Mendoza Province (area 37°00′, 37°20′S, 69°00, 69°30′W). Lacustrine	Early Jurassic	This paper
	Penthesilenula sp. B. Mendoza Province (approx. 35°30′S, 70°00′W). Lacustrine	Early Jurassic	This paper
	Penthesilenula? sp. Mendoza Province. Lacustrine	Late Middle Triassic	This paper

have been recorded in Argentina, although this may be due to an insufficient sampling of known outcrops.

Living species of *Penthesilenula* (in *incae* group) have been found in temporary ponds along the National Route 11 (Chaco Province, see Table 1) and in the water entrapped in the leaf cups of the Apiaceae *Eryngium* cf. *pandanifolium* at the National Park of Iguazú, Misiones Province (Ballent & Díaz, 2009) both of which are currently under study. Laprida et al. (2006) recognized *Penthesilenula incae*

in an isolated hot spring from the southern Altiplano of Argentina. In Patagonia, the type species has been known as *P. setosa* (Daday, 1902), which has to be considered as senior synonym of *P. incae* (Rossetti & Martens, 1998). Recently, the species has been found in several localities in Río Negro Province (Cusminsky et al., 2010) and in small swamps near a stream (Arroyo Telsen, Chubut Province, Fig. 2V–X).

Holocene records of *P. incae* are noted from Quebrada de Zonda, San Juan Province (Fig. 2U) and from southern Buenos Aires Province (see Table 1).

It is interesting to note the close similarities between the species of *Penthesilenula* recorded in this paper and others from the eastern Asia. *P. sarytirmenensis* (Sharapova) has been recognized from the Middle-Late Jurassic of Russia, China and India. *P. loana* sp. nov. is very similar to *P. magna* (Jian) from the Middle-Upper Jurassic of China, while *Penthesilenula* sp. resembles *P. subparallela* (Ye) from the Late Jurassic of China. Likewise, species identified as *Darwinula* sp. referred to by Sohn & Chatterjee (1979, for example the specimen illustrated in plate 1, fig. 6) from a presumably reptilian coprolite collected in the Upper Triassic Maleri Formation (central India) are externally similar to *Penthesilenula* rather than to *Darwinula*.

Conchostracans are crustacean that as darwinulids inhabit small and temporary water bodies and warm temperatures littoral areas of lakes. The existence of large shallow lakes interconnected repeatedly during periods of high lake levels from the Late Permian of the Plate Russian created favourable ecological niches for darwinulid diversity (Molostovskaya, 2000). Also, the "megamonsoonal" circulation with trans-equatorial winds as a dispersal agent created by the geographical configuration of the Pangea (Parrish, 1993) explains the presence of closely related species of other ostracod taxa (Musacchio, 2001) as well as conchostracan families and floras (Gallego & Melchor, 2000) in eastern Laurussia and Gondwana.

Paleoecology-Environment of deposition

Recent *Penthesilenula* belonging to the *incae* group have been recovered in a wide range of aquatic environments, including semi-terrestrial and terrestrial habitats. The type species *P. incae* is a bottom-dweller, and is especially abundant in coarse-grained sediments containing abundant organic matter. It has also been found in shallow hot springs, pools and canals in largely dry lakes, with many algae, in 10–20 cm water depths at the southern Altiplano in Perú and Bolivia (Rossetti et al., 1996). Other living species of *Penthesilenula* have been recovered from both saturated and unsaturated terrestrial habitats, such as leaf litter in forests or in water pouches in bromeliads in São Paulo State, Brazil (Pinto et al., 2004). Likewise, a broad salinity tolerance (from distilled water to 25 g–30 g/l) of species of *Penthesilenula* has been demonstrated by Van Doninck et al. (2003).

Laprida et al. (2006) recognized *Penthesilenula incae* in an isolated hot spring (30°C) at 4000 m asl, inhabiting humid coarse-grained sands at 20 cm water depth from the southern Altiplano of Argentina. In this case *P. incae* is associated with *D. stevensoni* and cypridoids (*Candona* sp., *Hemicypris panningi*, *Heterocypris* sp. and *Cypridopsis fuhrmanni*). Holocene records of this species are recovered from lacustrine greyish and white-yellowish siltstones and fine sandstones with sporadic intercalated coarse sandstones at Quebrada de Zonda, San Juan Province. The charophytes *Chara* cf. *hispida* var. *major* and *C.* cf. *papillosa*, plus the ostracods *Cypridopsis* sp., *Eucypris* sp. and *Chlamydotheca incisa* are also abundant in this association (García, 1996). *P. incae* has been recognized (although scarcely) in freshwater to estuarine sediments from southern Buenos Aires Province by Ferrero (1996, pl. I, fig. 4). In this case the microfauna is represented by freshwater and brackish species such as *Heterocypris* cf. *incongruens*, *Limnocythere staplini*, *Cyprideis multidentata* and *C. hartmanni*, among others.

Penthesilenula sarytirmenensis recovered from the lacustrine limestones, calcareous sandstones and volcanic tuffs of the Late Jurassic, Cañadón Asfalto Formation, in the Chubut Province occurs in association with the freshwater ostracod *Theriosynoecum barrancalensis*, and a rich biota of abundant mega and microflora, freshwater invertebrates, amphibians, turtles, dinosaurs and mammals. The megaflora is dominated by conifers, arborescent ferns and equisetaleans (Escapa et al., 2008). Warm and relatively humid climatic conditions are indicated by the high percentages of the thermophilic Cheirolepidiaceae, associated with Araucariaceae, which need moist conditions (Volkheimer et al., 2008). Palaeoenvironmental conditions were controlled by climatic

changes which resulted in expansion and contraction cycles of the hydrologically closed water bodies that were influenced by rainfall changes (Cabaleri & Armella, 2005).

Penthesilenula loana sp. nov. from the late Pliensbachian of the eastern slope of Cerro Corona in Neuquén Province occurs with freshwater cypridoids and conchostracans, as well as with abundant plant and coal remains (Ballent, 1987). Intercalated layered accretionary structures—stromatolites—formed in shallow water are also frequent. Moist climatic conditions, as shown by the frequency of coal and well preserved fossil floras (Equisetales, Filicales, Bennetitales, Coniferales, Araucariaceae) prevail in this locality (Gnaedinger, 2006; Volkheimer et al., 2008). Valves with "cup in cup" structure are present in this ostracod species. This arrangement of ostracod valves has been reported on several occasions from a number of fossil sequences (Wakefield & Athersuch, 1990; Wakefield, 1995; Boomer et al., 2001; Carignano & Ballent, 2009). Fontana & Ballent (2005) documented this phenomenon in a recent cypridid from southern Buenos Aires Province, Argentina. This type of record has been associated with shallow water depositional environments and seems to occur at the shoreline by the action of wavelets; it is favoured by monospecific assemblages and high number of individuals (Guernet & Lethiers, 1989).

Specimens of *Penthesilenula* sp. A have been recovered from the Early Jurassic lacustrine pelites rich in kerogens which are the source hydrocarbon rocks in the southern Mendoza Province (Villar et al., 2008). *Penthesilenula* sp. B from the Early Jurassic at Arroyo Montañesito, southern Mendoza province, is associated with cypridoids and fragments of bivalves in a shallow lacustrine environment (Lanés & Palma, 1998).

Population age structures

The presence of large numbers of adults and of juvenile instars well back into the ontogeny of *P. sarytirmenensis* and in *P. loana* sp. nov. can be interpreted as the product of a low energy regime, typified (in modern analogues) by the Histogram of Type A of Whatley (1983). These characteristics agree with the low diversity of the studied assemblages. In the case of the microfaunas from the Cañadón Asfalto Basin in Chubut Province, the percentage of the total individuals made up by the two most abundant species (*P. sarytirmenensis* and *T. barrancalensis*) reaches near 90% of the total of specimens, which characterizes freshwater associations (Whatley, 1983). All of the studied microfaunas are composed of carapaces (articulated valves). It is argued that, if a high percentage of adult specimens are articulated, these have not been subject to any great amount of post-mortem transportation (which is valid in our study) or this can indicate rapid burial before biological activity and/or tissue decay can bring about disarticulation. However, the fact that certain species have been encountered as carapaces and others as valves, as demonstrated by Whatley (1988), may be due to biological and morphological reasons of the species in question rather than taphonomical ones. Also, there exists the strong possibility that the adductor muscles of some species contract on death while in others they relax. Darwinulids are brooders (eggs, plus the first two or three instars are retained in the carapace). For this reason it is important how tightly the valves can close. They possess marginal structures such as internal teeth (in the left valve in *Penthesilenula*) which prevent them from closing too much and so crushing eggs and juveniles, and the brood pouch becomes obscured (Martens et al., 2003). However, the closing valves must be safe enough to prevent them from opening which would cause the death of the animal and progeny.

Adductor muscle scars

The central (or adductor) muscle scars are the most conspicuous group of scars caused by the attachment of the closing muscles which run from valve to valve transversely through the body of the ostracod. They are situated immediately in front of the middle of the valve, which is functionally the most efficient position. The number and the arrangement of the individual scars vary considerably in different groups and certain basic patterns are restricted to the higher systematic categories (scars arranged in the shape of a rosette in Darwinuloidea). This character becomes of relative value for some species as has been referred to by Pinto & Kotzian (1961). These authors demonstrated that in darwinulid species (*Vestalenula plagiolii*, *Penthesilenula brasiliensis*, *Alicenula serricaudata*) from Río Grande do Sul, Brazil, the number

and disposition of muscle scars vary, not only among individuals of the same species, but also among valves of the same individual.

In the present study, in *Penthesilenula* sp. A the adductor muscle scars comprise a circular "rosette" with 12–14 elongated spots positioned anteriorly; the arrangement is similar in number of scars to that of the type species, although they are smaller (Fig. 2M, N).

In *Penthesilenula incae* from the Holocene sediments of San Juan Province, the central muscle scars consist of 13–14 small spots arranged in a nearly circular rosette. However, in the same species living forms recovered from small swamps near Arroyo Telsen (Chubut Province), the muscle scars are larger and of a reduced number (9–11) with some individual scars exhibiting one or two prominent sutures (Fig. 2X).

The confirmed presence of males in one darwinulid species (*Vestalenula cornelia*, Yakushima, Japan) does challenge the view that the Darwinulidae is one of the oldest asexual lineages in the animal kingdom (Smith et al., 2006). The apparent absence of darwinulid males in the fossil record since the Triassic has been determined using a combination of three morphological criteria in the preserved carapaces (Martens et al., 2003): size dimorphism, an absence of a brood pouch and the position of central muscle scars (presumed to be more centrally placed in males due to the lack of brood chamber). However, male carapaces of *V. cornelia* are of similar size and shape to the A-1 juvenile females of the same species, suggesting that the males may have been dismissed as A-1 juveniles in fossil species (Smith et al., 2006).

In this study, although we do not have much evidence yet, we have observe that in the case of *P. sarytirmenensis* the central muscle scars are always situated in front of the mid-length or at mid-height of the valve. In *Penthesilenula* sp. A the adductor muscle scars are positioned in front of the centre and variably somewhat below or above of half of the greatest height of each valve. Likewise, *P. sarytirmenensis* and *P. loana* nov. sp., including the smallest specimens, show the greatest width situated at the posterior part of the carapace which may be interpreted as a clearly visible brood pouch. Taking all this into account we interpret that in the present study all-female populations are recognized.

Conclusions

Five early Mesozoic darwinulid species from lacustrine sediments of the Cañadón Asfalto and the Neuquén Basins in Argentina are reviewed and reassigned to the genus *Penthesilenula* Rossetti & Martens (*incae* group). One of these species is formally described: *Penthesilenula loana* sp. nov. To our knowledge, these are the first confirmed Mesozoic records of the genus and, thus, its origin could date back to at least nearly 200 million years ago (Early Jurassic).

Populations of *P. sarytirmenensis* (Sharapova) and *P. loana* sp. nov. comprise large number of adults and of juvenile instars well back into the ontogeny of the species. In both species only all-female populations are recognized. This leads us to believe (which coincides with Martens et al., 2003) that Darwinulidae are ancient asexuals which have survived for at least 200 million years without their male counterparts.

In all localities, the studied species occur associated with other freshwater ostracods, invertebrates and a rich biota of abundant mega and microflora, coal remains, as well as terrestrial vertebrates. The environment of deposition corresponds to a shallow and low energy lacustrine regime with warm and relatively humid climatic conditions. Recent species show similar ecological conditions.

The coeval occurrence of *P. sarytirmenensis* in central extra-Andean Patagonia, Argentina and ex USSR, China and India as well as the close similarities between the studied species and others from eastern Asia further support faunal exchanges during the early Mesozoic. The "megamonsoonal" circulation created by the geographical configuration of the Pangea could have favoured floral and faunal exchange between Asia and Gondwana at that time.

As regards the occurrences of darwinulids, we conclude that the genera *Penthesilenula* and *Alicenula* would seem to have a wide fossil Mesozoic record at least in the southern South America.

Although our results are preliminary, we like to think that they will be one more step closer to clarifying some aspects related to the taxonomy and biology of the earliest Mesozoic darwinuloids.

Acknowledgements We are especially thankful to O. Gallego (Corrientes, Argentina) for providing us with samples from the Chubut Province to our study and specialized literature.

A. Benialgo (La Plata, Argentina) is acknowledged for drafting Fig. 1. To the guest editors of this volume, who made a pertinent first revision of this paper. We thank Nigel Ainsworth and David Horne for their helpful criticisms and comments to improve the manuscript. Funding for this study was provided by Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and the Universidad Nacional de La Plata, Argentina (PIP 0819 and N589, respectively).

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