

# New insights into the early diversification of the Ostracoda: Tremadocian ostracods from the Cordillera Oriental, Argentina

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New species of ostracods from the Tremadocian in the northwest region of Argentina are described. These are among the earliest well-documented records of ostracods, which shed new light onto the early diversification of the group. The described fauna consists of seven species, five of which are new: *Saltite uchuy* sp. nov., *Saltite kuraq* sp. nov., *Concho-primitia? iglesiasi* sp. nov., *Orechina violeatae* sp. nov., and *Orechina catalinae* sp. nov. The fauna consists primarily of soanellids, a non-dimorphic family of palaeocopids, and of binodicopids. One factor leading to diversification of the group in this region may have been the complex configuration of the northwest basin, which had a restricted pattern of circulation. The distribution of the first ostracods is largely restricted to Gondwana and peri-Gondwana regions. Accordingly, it is possible to envision that the origin or at least an important radiation of the group was centred in this region. Both the Soanellidae and the genus *Orechina* would have originated in Gondwana and would have become widespread later during the Middle Ordovician. The Tremadocian fauna located in Argentina show significant affinities with fauna located in the warm-water setting of the east Gondwana, mainly in Australia and China.

Key words: Ostracoda, early diversification, Tremadocian, Andes, Argentina.

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## Introduction

Ostracods are an abundant and diverse component of marine assemblages from the Ordovician to the present, that have an exceptionally well-documented fossil record. The first diversification of ostracods took place during the Middle Ordovician, between the Floian and Darriwilian. They reached maximum diversity during the Late Ordovician, when all the modern orders were already present (Schallreuter in Braddy et al. 2004). Since the Ordovician, ostracods have continued their diversification and have colonized almost the entire spectrum of the present-day aquatic ecosystem.

Despite their high diversity, the first records of ostracods during the Tremadocian (Early Ordovician), are scarce and patchy (Williams et al. 2008), and their origin remains unknown. The origin and position of ostracods within the crustacean phylogeny are intensely debated issues. Some of these include: molecular analysis that places the first ostracods in either the latest Proterozoic or Early Cambrian (Regier et al. 2005), the question of whether the origin of the group is monophyletic or polyphyletic (e.g., Regier et al. 2005; Newman 2005), and if the possible origin of ostracods could be from some bradoriids (Salas et al. 2007; Williams et al.

2008). A more complete synthesis is discussed in Williams et al. (2008) and references therein. The first ostracod with its soft anatomy preserved is actually recorded in the Silurian. Prior to the Silurian the identification of the earliest ostracods is possible only through the carapace. Since the first records of ostracods are present during the Tremadocian, this period is important to understanding the first stage of diversification of the group.

Thus far the ostracods have been represented in the Tremadocian by three genera and five defined species, and by some undetermined forms widespread in several regions (Salas et al. 2007; Williams et al. 2008). Here we describe five new species from the Tremadocian in Argentina, and two more genera are recorded, deepening our understanding of the early diversification of the group.

*Institutional abbreviations.*—CEGH-UNC, CIPAL-Centro de Investigaciones Paleobiológicas, CICTERRA, Córdoba, Argentina; JUY-P, Museo de Geología, Minería y Paleontología, Instituto de Geología y Minería, Universidad Nacional de Jujuy, San Salvador de Jujuy, Argentina.

*Other abbreviations.*—L, maximum length of the valve; L:H, Length:Height ratio; L1–L4, lobes from the anterior

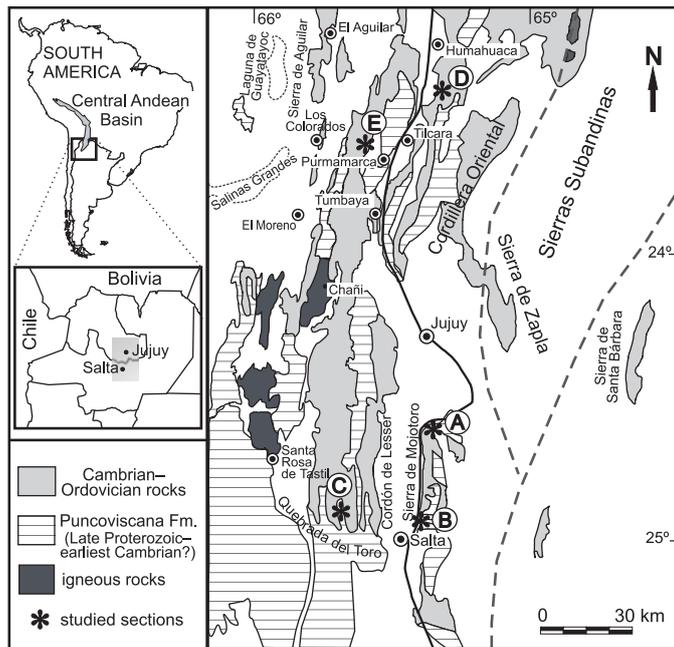


Fig. 1. Geological setting and location of ostracod localities (asterisks): Abra de Santa Laura (A), Cerro San Bernardo in Sierra de Mojotoro (B), Pascha-Incamayo area (C), Quebrada de Humacha (D), and Purmamarca area (E). Modified after Salas et al. (2007).

one to the posterior one; N1, anterior node; N2, preadductor node; S1–S3, sulci from the anterior to the posterior one; Tr1–Tr3, stage slice of the Tremadocian, from Bergström et al. (2009).

## Material and methods

### Geological setting and origin of the material

Tremadocian sequences are widely exposed in the Central Andean Basin, represented in the northwest Argentina (Salta and Jujuy provinces) by the Puna, Cordillera Oriental and Sierras Subandinas regions. These sequences of thousands of meters are deposited in a foreland basin that developed along the western margin of Gondwana. The Cordillera Oriental is a forebulge, where platform deposits developed into a low gradient ramp-like setting influenced by a large scale prograding deltaic system from the east, and by an active volcanic arc complex in the west, represented in the Puna region (Bahlburg 1990, 1991; Bahlburg and Furlong 1996; Astini 2003). Within this framework a variety of depositional environments, ranging from outer shelf to shoreface, tide or wave dominated are represented in the basin (Astini 2003; Buatois et al. 2006). This variation of environments led to a complex stratigraphy, generating a varied nomenclature, with many formal and informal names for the units. The most accepted nomenclature is by Turner (1960), who identified the whole Ordovician sequence as the Santa Victoria Group, and the Upper Cambrian–Tremadocian succession as the Santa Rosita Formation.

Biostratigraphical data based on trilobites, graptolites, and conodonts have been obtained in some areas (Harrington and Leanza 1957; Tortello and Rao 2000; Albanesi et al. 2001; Ortega and Albanesi 2002, 2003; Zeballo et al. 2003, 2008; Waisfeld et al. 2006; Waisfeld and Vaccari 2008a); this data has contributed to the regional correlation of the different units. The ostracod fauna has been collected from different Tremadocian sections of the Cordillera Oriental: Sierra de Mojotoro (Abra Santa Laura, Cerro San Bernardo), Pascha-Incamayo area, Quebrada de Humacha section, and Purmamarca area: Quebrada Chalala section (Figs. 1, 2).

**Sierra de Mojotoro.**—A thick Tremadocian sequence outcrop within the Sierra de Mojotoro, situated in the southeastern part of the Cordillera Oriental. The Sierra de Mojotoro sequence is divided in several units, identified from bottom to top as: La Pedrera, San José, La Caldera, Floresta, Áspero, and San Bernardo formations (Moya 1998). The studied ostracod fauna come from two formations found in two different locations: the Floresta Formation in Abra de Santa Laura, and the San Bernardo Formation in the Cerro San Bernardo (Figs. 1, 2).

*Abra de Santa Laura/Dique La Ciénaga:* The studied material of Floresta Formation comes from two different collections. The first, completed by Saturnino Iglesias in 1949, is housed in the Museo de Geología, Minería y Paleontología, Instituto de Geología y Minería, Universidad Nacional de Jujuy (unpublished material). Iglesias identified the location of the collection to be on the left margin of the Nacional Rout N° 9 to 13 km from the Dique La Ciénaga. This location was recently re-discovered by one of the authors (NEV) and placed by the National Road N° 9, 2 km northeast of the Abra de Santa Laura locality (24°29'21.91"S 65°17'53.40"W) (Fig. 1). The outcrops in this locality are partly covered by the rain forest, so the measured thickness of the section is an estimation. The Floresta Formation consists of mostly light green siltstone interbedded with some fine-grained sandstone beds; while the upper part of the sequence contains intercalated coquinas levels (Fig. 3A). The ostracods come from the siltstone beds, where they are preserved like moulds, and from the coquinas, where they are phosphatised. In the siltstone the fauna consists of the bivalves *Intihuarella simplicidentata* Sánchez and *Ucumaris conradoi* Sánchez in Sánchez and Vaccari, 2003; and the trilobites *Bienvillia* sp., *Parabolinella* sp. nov., and *Asaphelus* sp. The brachiopod *Lipanorthis santalaurae* Benedetto in Benedetto and Carasco, 2002 is recorded in the coquinas. The presence of *Parabolinella* sp. nov., is important for determining the age of the fauna, as it is the most abundant species in the *Bienvillia tetragonalis* Biozone in the Rupasca Member of the Santa Rosita Formation. The age of this biozone was recently fixed according to conodonts, and assigned to the upper part of the *Paltodus deltiifer* Biozone (*P. deltiifer pristinus* Subzone; Zeballo et al. 2003; Zeballo and Tortello 2005). The biozone indicates a Tr2 age (Fig. 2).



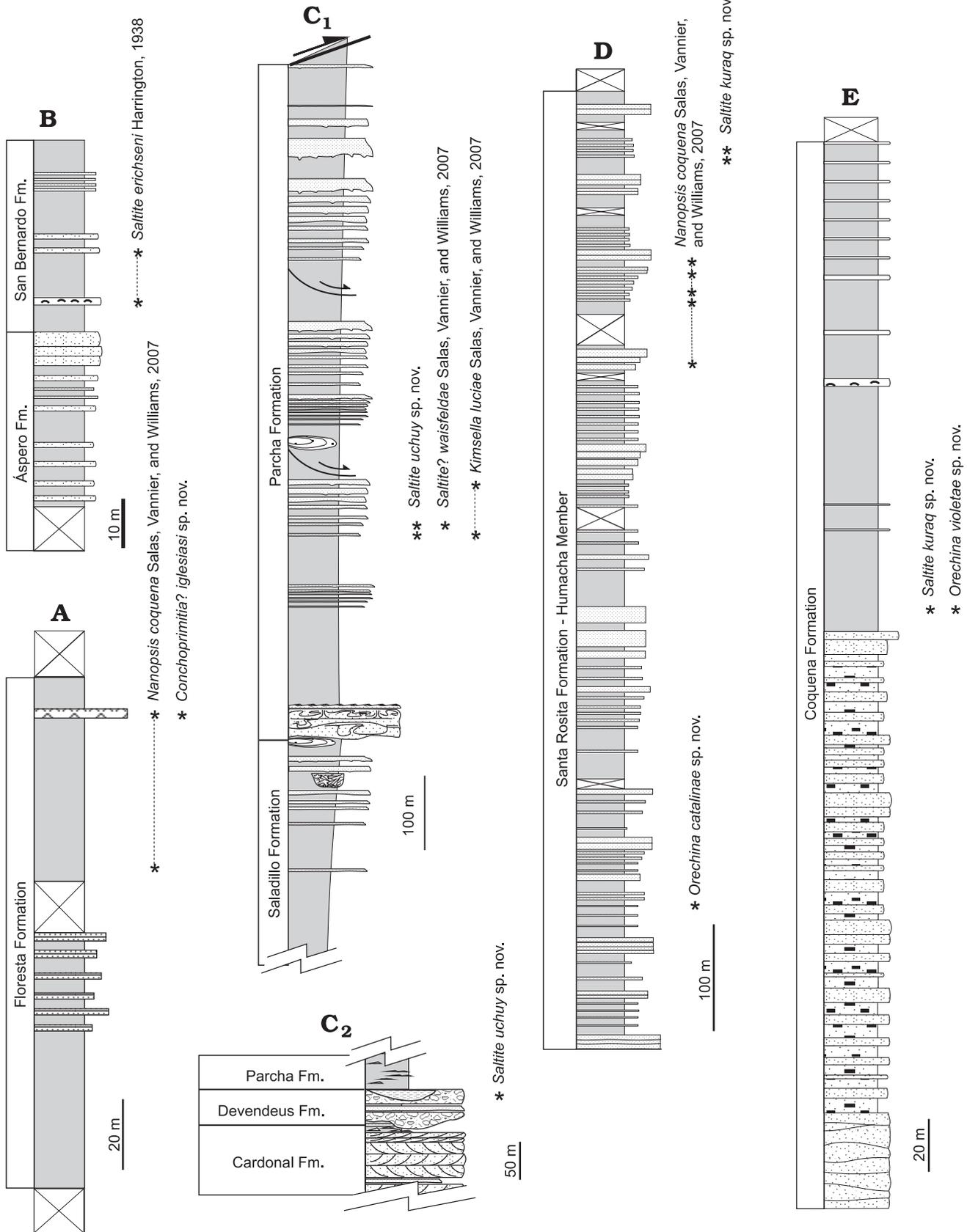


Fig. 3. Lithologic columns indicating ostracod-bearing levels (asterisks) of the studied sections. **A.** Abra de Santa Laura section. **B.** San Bernardo Formation (redrawn from Benedetto and Carrasco 2002). **C.** Pascha-Incamayo area, 1, western flank section; 2, eastern flank section (redrawn from Astini 2003). **D.** Quebrada de Humacha section (redrawn from Muñoz 2009). **E.** Quebrada Chalala (redrawn from Benedetto and Carrasco 2002).

lower levels with ostracods are located in an interval without definition of biozone of trilobites between *Bienvillia tetragonalis* and *Notopeltis orthometopa* biozones (Waisfeld and Vaccari 2008a), corresponding to the Late Tremadocian. In the upper levels of the unit the ostracods were recovered from black shale, associated with trilobites, brachiopods, gastropods, and bivalves, and attributed by Zeballos et al. (2008) to *Aorograptus victoriae* Biozone, partly equivalent with *Acodus deltatus*–*Paroistodus proteus* biozones. This indicates a late Tremadocian age (Tr3) (Fig. 2).

**Purmamarca area: Quebrada Chalala section.**—The Quebrada Chalala is situated near to the town of Purmamarca (ca. 50 km north from Jujuy City) (Fig. 1). Here ostracods were collected in the Coquena Formation. Benedetto and Carrasco (2002) subdivide the Quebrada Chalala section in a lower heterolithic unit primarily consists of fine-grained sandstone beds with hummocky stratification, which are overlain by thick packages of sandstone and siltstone. The lower unit is interpreted to be a storm-dominated shoreface whereas the overlying sandstone and siltstone correspond to a lower shoreface to inner shelf transition environment. The upper unit is equivalent to the “Coquena shales” sensu Harrington and Leanza (1957), and is characterized by grey bioturbated mudstone that represent inner-shelf deposits (Fig. 3E). The studied material was collected from the lower part of the second member of the unit and was associated with the trilobite *Notopeltis orthometopa* Harrington and Leanza, 1957, and the brachiopods *Nanorthis brachymyaria* Benedetto, 2002, *Lipanorthis andinus* Benedetto, 2002, and *Astraborthis quebradensis* Benedetto in Benedetto and Carrasco (2002). Zeballos et al. (2008) recognized the *A. deltatus*–*P. proteus* biozones in the uppermost Coquena Formation, associated with the trilobite *Notopeltis orthometopa* indicating a Tr3 age (Fig. 2).

## Techniques of study

The studied material was collected during successive field expeditions. Additionally, some of the ostracods in the Floresta Formation are from the Iglesias Collection, deposited in the Museo de Geología, Minería y Paleontología, Instituto de Geología y Minería, Universidad Nacional de Jujuy. Specimens of Floresta, Parcha, and Santa Rosita (Humacha Member) formations were recovered from acid residues obtained by processing calcarenite samples with 10% acetic acid. The ostracod valves or internal moulds are preserved in phosphate (apatite) and many show exquisite detailing of their three-dimensional morphology and exoskeletal ornament. The phosphate is secondary. The material from the Coquena, San Bernardo, and Santa Rosita (Humacha Member) formations appear either with the original carapace preserved or as internal moulds.

Specimens were studied by means of Scanning Electron Microscopy (SEM) at the LABMEN of the University of San Luis, Argentina.

## Systematic palaeontology

Subclass Ostracoda Latreille, 1806

Order Beyrichiocopida Pokorný, 1953

Suborder Palaeocopina Henningsmoen, 1953

Superfamily Tetradelloidea Swartz, 1936

Family Soanellidae Kanygin, 1967

Genus *Saltite* Rossi de García and Proserpio, 1976

1976 *Bernardite* Rossi de García and Proserpio (gen. nov.); Rossi de García and Proserpio 1976: 559–560, pl. 1: 1, 2.

1976 *Nortite* Rossi de García and Proserpio (gen. nov.); Rossi de García and Proserpio 1976: 561–562, pl. 1: 5.

1993 *Eopilla* Schallreuter (gen. nov.); Schallreuter 1993: 117–120, pl. 20.

*Type species: Drepanellina erichseni* Harrington, 1938. San Bernardo Formation at the Cerro San Bernardo, northwest Argentina, Late Tremadocian.

*Species included: Saltite uchuy* sp. nov., *Saltite kuraq* sp. nov., *Saltite ingelora* (Schallreuter, 1993), and *Saltite? waisfeldae* Salas, Vannier, and Williams, 2007. Possibly *Ctenobolbina sinensis* Hou, 1953a, *C. sinensis wangi* Hou, 1953a, and *C. taitzehoensis* Hou, 1953a from the Late Tremadocian of China. The last tentative assignment of Schallreuter (1993) was made from very poor photographic illustrations (Hou 1953a), so the confirmation of whether *Saltite* occurs in the Tremadocian of China demands further analysis.

*Remarks.*—*Saltite* Rossi de García and Proserpio, 1976, from northwest Argentina, and *Eodominina* Schallreuter, 1993, from Australia, are both monospecific genera, and have been revised with detailed synonymy and description by Schallreuter and Hinz-Schallreuter (2004, 2007) and Salas et al. (2007). Schallreuter and Hinz-Schallreuter (2007) compared *Saltite erichseni* (Harrington, 1938) with *Eopilla ingelora* Schallreuter, 1993 and proposed that *Eopilla* might be a subgenus of *Saltite*. Here, new and abundant material from the Tremadocian of northwest Argentina is examined, and new species are defined, concluding that *Eopilla* is a junior synonym of *Saltite*. According to Schallreuter and Hinz-Schallreuter (2007) the only difference between the genera are the broad lobes and slit-like sulci in *Saltite* and the small and ridge-like lobes and broader sulci in *Eopilla*. However, the width of the lobes is variable between the new species defined here, supporting the synonymy of the genera. The genus includes three species from Argentina, one species from Australia, and a possible species from China; the main difference between the species is the width of lobes and the sulci. With respect to *Eopilla waisfeldae* Salas, Vannier, and Williams, 2007 is not comparable with the species included in the genus *Saltite*. The main differences between *Eopilla waisfeldae* and the other species are the presence of a tiny and rounded node instead of L2, the indistinct L4, the prominent and very sharp L1 and L3, and the flat lateral surface of the valves. The species would be compared with *S. ingelora* by its very narrow lobes and by the poorly defined L4. Due to the mentioned differences, until more material of *Saltite? waisfeldae* is available the species will be assigned with doubt to the genus *Saltite*.

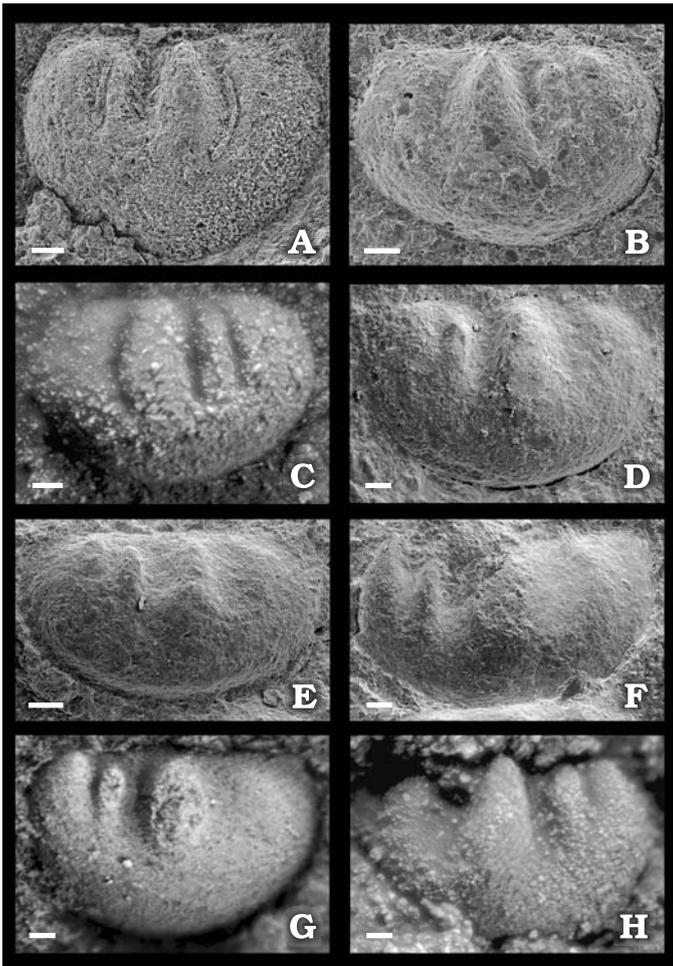


Fig. 4. Late Tremadocian soanellid ostracods from the Cordillera Oriental Argentina. A–C. *Saltite erichseni* (Harrington, 1938). San Bernardo Formation from Cerro San Bernardo section. A. CEGH-UNC 21150, internal mould of left valve, lateral view. B. CEGH-UNC 21149, internal mould of right valve, lateral view. C. CEGH-UNC 23994, external mould of right valve, lateral view. D–H. *Saltite kuraq* sp. nov. Humacha Member of Santa Rosita Formation from Humacha section. D. CEGH-UNC 24004, internal mould of left valve, lateral view. E. Holotype CEGH-UNC 23999, internal mould of left valve, lateral view. F. CEGH-UNC 24000, internal mould of left valve, lateral view. G. CEGH-UNC 24002, external mould of left valve, lateral view. H. CEGH-UNC 24005, external mould of right valve, lateral view. Scale bars 100  $\mu$ m.

*Stratigraphic and geographic distribution.*—Northwest Argentina, Western Australia, and probably Northeast China in the Late Tremadocian.

#### *Saltite erichseni* (Harrington, 1938)

Fig. 4A–C.

*Material.*—Several pieces of rock with hundreds of internal and external moulds, and latex cast, including the figured specimens CEGH-UNC 21149–50, 23994. Specimens we have examined range from 0.68 mm to 1.20 mm in length.

*Remarks.*—*Saltite erichseni* (Harrington, 1938), from San Bernardo Formation, was described and reassigned generically on successive occasions by, Harrington (1938), Rossi

de García and Proserpio (1976), and Schallreuter and Hinz-Schallreuter (2007). Additional material assigned to *Saltite erichseni* is illustrated here. The presence of four strong lobes in the valves, of which L3 is the strongest, and the slit-like sulci are diagnostic features of the species.

*Stratigraphic and geographic distribution.*—Known only from San Bernardo Formation in the Cerro San Bernardo, northwest Argentina. Tr3, *A. murrayi* Biozone.

#### *Saltite uchuy* sp. nov.

Fig. 5.

*Etymology:* From Quechua language *uchuy*, small, in reference to the small size of the species.

*Holotype:* CEGH-UNC 24007, left valve (Fig. 5B).

*Type locality:* Pascha-Incamayo area, northwest Argentina.

*Type horizon:* Coquina levels of the Parcha Formation, in the Angosto de Pascha section. Tr3, *Hunnegraptus copiosus* Biozone.

*Diagnosis.*—*Saltite* species with small and sub-elliptical valves, long and narrow lobes and broad and deep sulci. L3 is rather wide.

*Description.*—Valves amplete to slightly postplete, with an elliptical outline. Maximum length situated in mid-height of valves. Average L:H = 1.52. Dorsal margin straight, and only slightly shorter than maximum length of valves. Ventral and lateral margins evenly rounded. Cardinal angles obtuse. The valves have four long finger-like lobes, of which L2 does not reach the dorsal margin. L1 is adjacent to anterior margin of the valve, and is curved, with the concavity towards the posterior side. L2 is shorter than the others, straight, and vertical to slightly oblique to the dorsal margin. L3 is by far the most prominent lobe in the valve and stands just behind mid-height. Its anterior margin is straight and the posterior curved in most of the specimens. L4 is crescent-like with the concavity towards the anterior half of the valve. S1 is narrow and relatively short; S2 is broad and deep, with its margins straight and parallel. Marginal structures are lacking. The lateral surface is smooth, and in the internal moulds some specimens have sharp dots in the extra lobular surface.

*Material.*—About 300 specimens, shells and internal moulds, including the figured material CEGH-UNC 24006–08, 24010–13. Specimens we have examined range from 0.50 mm to 0.90 mm in length.

*Discussion.*—*Saltite uchuy* sp. nov. was described as undetermined binodicope by Salas et al. (2007). Here, new and abundant material, such as valves and internal moulds, is described allowing its taxonomic assignment to the genus *Saltite* Rossi de García and Proserpio, 1976. Characters like the quadri lobate valves, with L3 biggest than the others lobes are the main features of the genus.

*Saltite uchuy* sp. nov. differs from *S. erichseni* (Harrington, 1938), which is present in San Bernardo Formation, in its relatively small size (in *S. uchuy* sp. nov. the maximum length is ca. 0.90 mm and in *S. erichseni* L is ca. 1.20 mm), and in the outline of the valves, elliptic in the new species and circular in *S. erichseni*. Although, the main difference be-

tween the two species are the lobes and sulci, in *S. uchuy* sp. nov. the lobes are finger-like and sulci are wide, mainly S2, whereas in *S. erichseni* the lobes are all together, only separated by slit-like sulci. In *S. erichseni* L3 is broader. *S. uchuy* sp. nov. resembles *S. kuraq* sp. nov., from the Humacha Member (Santa Rosita Formation) in the Humacha section, in their relatively narrow lobes and broad sulcus, however, *S. uchuy* sp. nov. is smaller, its fourth lobe is very well defined similar to L1, and L2 is longer whereas in *S. kuraq* sp. nov. is short and is joined to L1. *S. uchuy* sp. nov. differs from the Australian species, *S. ingeloriae* (Schallreuter, 1993), by its relatively shorter lobes, and by its more defined L4. Moreover, in the Australian species L1 and L2 are very close, whereas the other sulci are broader. *S. uchuy* sp. nov. differs from *S.?* *waisfeldae* Salas, Vannier and Williams, 2007 mainly in its lobes, L1 and L3 have a too sharp relief, L2 is node-like, and L4 is very faint.

**Stratigraphic and geographic distribution.**—*Saltite uchuy* sp. nov. is known from the Parcha Formation and from the matrix of the Devendeus Formation in Pascha-Incamayo area, northwest Argentina. *Acodus deltatus*–*Pariostodus proteus* biozones, Late Tremadocian.

***Saltite kuraq* sp. nov.**

Fig. 4D–H.

**Etymology:** from Quechua language *kuraq*, the biggest, in reference to the big size of the species.

**Holotype:** CEGH-UNC 23999, internal mould of left valve (Fig. 4G).

**Type locality:** Quebrada de Humahuaca area, in Quebrada de Humacha section, northwest Argentina.

**Type horizon:** PN sample, *A. victoriae* Biozone, partly equivalent with *A. deltatus*–*P. proteus* biozones, Tr3, Humacha Member of the Santa Rosita Formation.

**Diagnosis.**—*Saltite* species with L2 short and tilted to the anterior half of the valves, L2 meets with L1.

**Description.**—Valves amplete and sub-elliptical in lateral outline. L:H ratio is 1.57. The maximum length is situated near the dorsal margin. The dorsal margin is straight and slightly shorter than L. The lateral margins are rounded to lightly straight and the ventral margin is rounded. Well defined and obtuse cardinal angles, with the anterior slightly bigger than the posterior one. The valves are quadri lobated. The lobes are well defined and perpendicular to dorsal margin or slightly tilted away from it. L1 and L2 are in the anterior half of the valves, they are generally thin and rounded. L1 reaches or overreaches dorsal margin, L2 is shorter and is tilt to the anterior half of valves and meets with L1. In some specimens the lobes are shorter, only well defined in the dorsal half of the valves. Axis of L3 corresponds approximately to midline of valve or is slightly behind it. L3 is the most prominent lobe, it overreaches the dorsal margin, and it is broad in the base and tapering to the dorsal end. L4 varies from well defined to a faint elevation near the posterior end of the valves. The lateral surface is punctuated, however, this feature is visible in only two specimens, the preservation of the material is not so good.

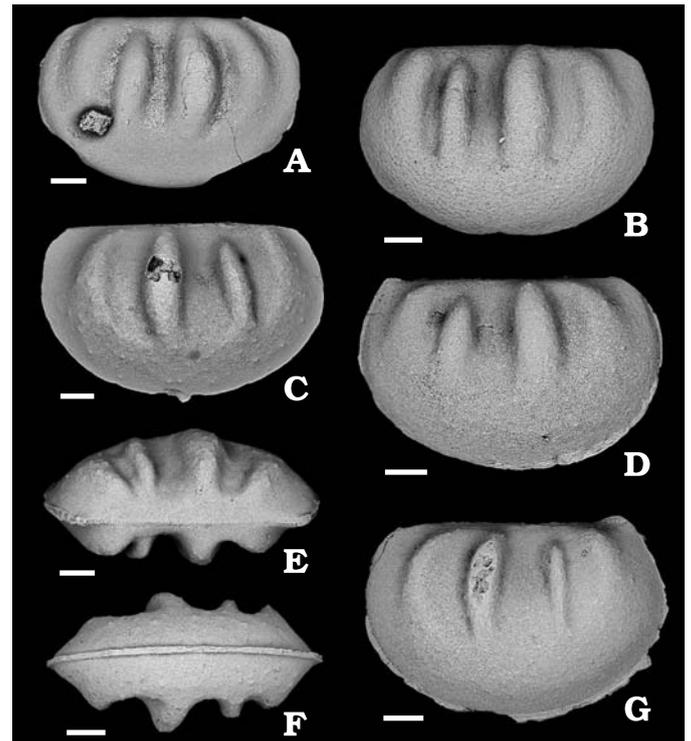


Fig. 5. Late Tremadocian soanellid ostracod *Saltite uchuy* sp. nov. from the Parcha Formation in the Pascha-Incamayo area of Cordillera Oriental, Argentina. **A.** CEGH-UNC 24006, left valve in lateral view. **B.** Holotype CEGH-UNC 24007, left valve in lateral view. **C.** CEGH-UNC 24012, internal mould of right valve in lateral view. **D.** CEGH-UNC 24008, internal mould of left valve in lateral view. **E.** CEGH-UNC 24010, internal mould in dorsal view. **F.** CEGH-UNC 24011, internal mould in ventral view. **G.** CEGH-UNC 24013, internal mould of right valve, lateral view. Scale bars 100  $\mu$ m.

**Material.**—Around 100 specimens of internal and external moulds, and latex cast, including the figured material CEGH-UNC 23999–24000, 24002, 24004–05. Specimens we have examined range from 0.53 mm to 1.4 mm in length.

**Discussion.**—The main difference between *Saltite kuraq* sp. nov. and the other species of the genus is the joint between L1 and L2, a feature that is not observed in any of the other forms. Moreover, *S. kuraq* sp. nov. differs from *S. uchuy* sp. nov., from the Parcha Formation, in the posterior lobe. In the described species L4 varies from poorly defined to very well defined; there are specimens in which L4 is a faint lobe. In *S. uchuy* sp. nov. L4 is always well developed and similar to L1. On the other side, *S. kuraq* sp. nov. is bigger than the Pascha specimens. *S. kuraq* sp. nov. varies from *S. erichseni* mainly in its narrower lobes and broader sulcus. In the new species the valves are sub-elliptic whereas in *S. erichseni* the valves are subcircular. The length of the valves is similar in the two species, however, *S. kuraq* sp. nov. is larger in size. *S. ingeloriae* (Schallreuter, 1993), the Australian species, has very long and thin lobes, with wide sulci between each other, and is smaller than the Argentinian species.

**Stratigraphic and geographic distribution.**—Known from the upper part of the Humacha Member in the Quebrada de

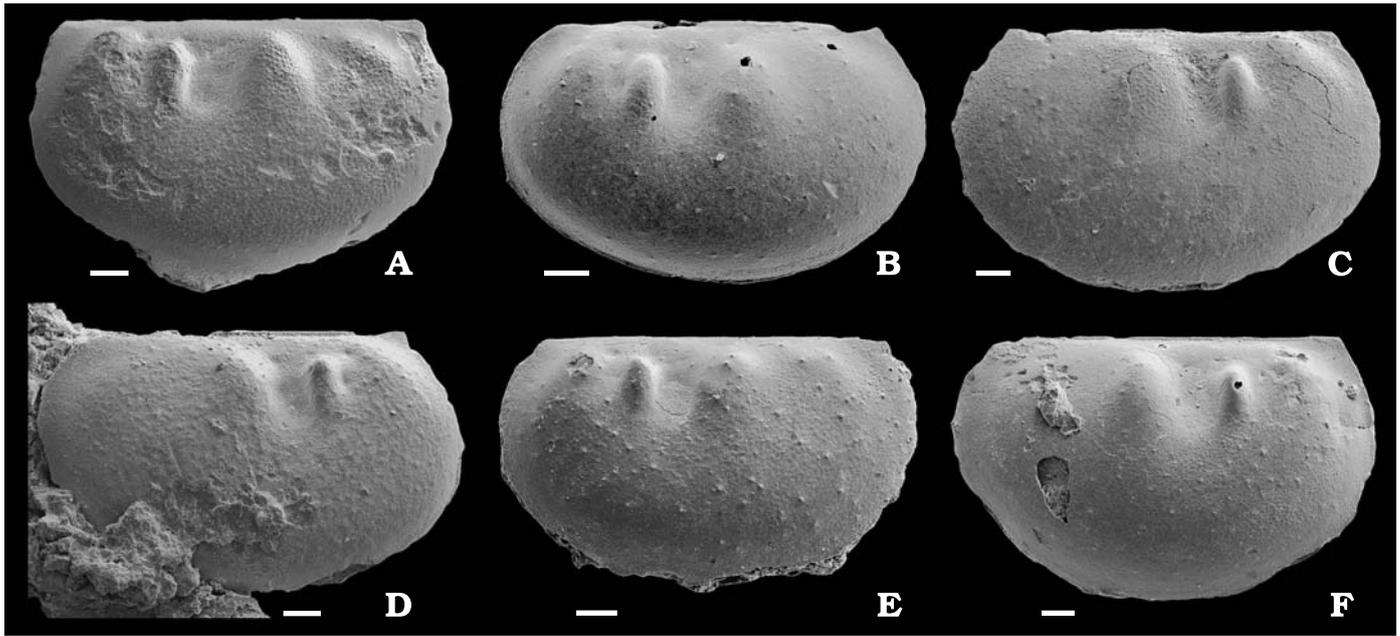


Fig. 6. Late Tremadocian ostracod *Nanopsis coquena* Salas, Vannier, and Williams, 2007 from the Cordillera Oriental Argentina. **A, B, D–F.** Humacha Member, middle levels of the Humacha section. **A.** CEGH-UNC 24015, left valve in lateral view. **B.** CEGH-UNC 24018, left valve in lateral view. **C.** Iglesias collection, Floresta Formation, Abra de Santa Laura section; JUY-P 045, internal mould of right valve, lateral view. **D.** CEGH-UNC 24021, right valve in lateral view. **E.** CEGH-UNC 24019, left valve in lateral view. **F.** CEGH-UNC 24023, right valve in lateral view. Scale bars 100  $\mu$ m.

Humacha section, and in the Coquena Formation in the Quebrada de Chalala section, northwest Argentina. Tr3 (*Ara-neograptus victoriae*, *Acodus deltatus*–*Pariostodus proteus* biozones).

#### Family uncertain

#### Genus *Nanopsis* Henningsmoen, 1954

*Type species:* *Beyrichia nanella* Moberg and Segerberg, 1906. Ceratopyge Shale, Ventlinge, Öland, Sweden; original designation. Late Tremadocian.

*Species included:* *Nanopsis coquena* Salas, Vannier, and Williams, 2007, and *Nanopsis pilloides* (Schallreuter, 1998).

*Discussion.*—*Nanopsis* is characterized by a very simple morphology of nodes and sulci restricted to the dorsal half of the valves, and by the absence of any marginal structures. So far three species would be included in the genus: *Nanopsis nanella* (Moberg and Segerberg, 1906) from the Baltic region (Henningsmoen 1954; Tinn and Meidla 2004), *Nanopsis coquena* Salas, Vannier, and Williams, 2007 from the northwest of Argentina (Salas et al. 2007) and *Bumire pilloides* Schallreuter from Western Australia (Schallreuter 1998). *Bumire* Schallreuter, 1998 is a monospecific genus from the Floian of Australia that shares with *Nanopsis* its main features, suggesting that it should be regarded as a junior synonym of *Nanopsis*. Both forms share the same simple morphology. The valves are subelliptical and amplete to slightly postplete. They are bi or tri sulcate, the sulci are restricted to the dorsal half of the valves, S1 is poorly developed, S2 is the deepest and longest sulcus and S3 is poorly

defined if it is present. Admarginal structures and dimorphism are absent.

Salas et al. (2007) also mentioned a possible synonymy with a Chinese Tremadocian species, however, the confirmation of this demands further analysis.

*Stratigraphic and geographic distribution.*—Norway and Sweden, and northwest Argentina in Tr2 (*Paltodus deltifer* Biozone), and Western Australia in Floian. Possibly in the Tremadocian of China.

#### *Nanopsis coquena* Salas, Vannier, and Williams, 2007

Fig. 6.

*Material.*—Over 100 specimens including the figured material CEGH-UNC 24015, 24018–19, 24021, 24023 and JUY-P 045. The specimens we have examined range from 0.53 mm to 1.41 mm in length.

*Remarks.*—This species was described by Salas et al. (2007), the authors defined the species having only few specimens from the Floresta and Coquena formations. Here, new and abundant material from the Floresta Formation and from the Humacha Member of the Santa Rosita Formation provides additional morphological information which allows the recognition of the species with its intraspecific variations. The valves bear three well defined and short lobes that not reach the ventral half of the valves. L1 and L2 are in the anterodorsal part of valves. L1 is rounded, adjacent to anterior margin, and could reach the dorsal margin, L2 is shorter, and narrower, and is immediately behind L1. L3 is bigger than the other lobes, bulbous, and it generally reaches the dorsal margin. L4 is a very

faint elevation, more visible in the valves than in the internal moulds (Figs. 6A, C). The main variation in the species is the development of the lobes, which are more or less visible on the surface of the valves. The most variable lobe is L4 which is very faint in some specimens, and mainly in the internal moulds. On the basis of the new material found, some specimens illustrated by Salas et al. (2007: figs. 4.1–4.4) should be removed from the species due to their too prominent and long lobes that reach the ventral half of the valve. Moreover, these specimens have a punctuated surface not observed in the rest of the material.

With respect to the other species of the genus, *Nanopsis coquena* differs from *N. nanella* (Moberg and Segerberg, 1906) and *N. pilloides* (Schallreuter, 1998) in that *N. coquena* is larger in size (L reaches the 1.41 mm) and mainly in the well-developed sulcus S3, which is not present in the other species.

*Stratigraphic and geographic distribution.*—*Nanopsis coquena* is known from the Floresta Formation (Tr2, *Paltodus deltifer* Biozone) along the Road N° 9 (km 1,651.5 km), and from the Humacha Member, Santa Rosita Formation, in the middle part of the Humacha section (Tr3). Northwest Argentina.

#### Suborder Eridostracina Adamczak, 1961

#### Family Conchoprimitiidae Henningsmoen, 1953

#### Genus *Conchoprimitia* Öpik, 1935

*Type species:* *Conchoprimitia gammae* Öpik, 1935. Tallinn, Estonia, Late Dapingian–Early Darriwilian.

#### *Conchoprimitia?* *iglesiassi* sp. nov.

Fig. 7.

*Etymology:* This species is named for Saturnino Iglesias, an Argentinian geologist who collected the specimens of *N. coquena* and this species.

*Holotype:* JUY-P 043 left valve (Fig. 7C).

*Type locality:* Road N° 9 (km 1,651.5 km), between Salta and Jujuy cities, northwest Argentina.

*Type horizon:* Floresta Formation, 24°29'21.91"S 65°17'53.40"E. *Paltodus deltifer* Biozone, Tr2.

*Diagnosis.*—Subcircular and postplete outline. Valves with a tiny and rounded preadductorial node and a short and poorly defined sulcus.

*Description.*—Valves subcircular and postplete in outline. Average L:H = 1.56. Dorsal margin straight and long, only slightly shorter than maximum length of valves. The maximum length is at the mid-height of the valves. Cardinal angles obtuse, with the posterior one bigger than the anterior one. Lateral and ventral margins evenly rounded. The valves bear a tiny, and rounded preadductorial node. The node is in the anterior half of the valve near the dorsal margin. Immediately behind, there is a short, straight, and poorly defined sulcus, perpendicular to the dorsal margin. Marginal surface rather steep in the anterior half, where the valves are wider. In juveniles the marginal surface is steep in the posterior half too. Lateral surface smooth.

*Material.*—Twenty specimens collected by Saturnino Igle-

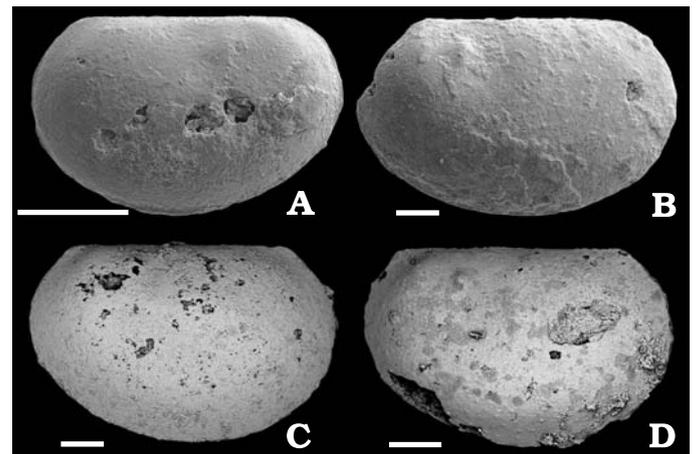


Fig. 7. Late Tremadocian conchoprimitid ostracod *Conchoprimitia?* *iglesiassi* sp. nov. Iglesias collection, from the Floresta Formation, Abra de Santa Laura section of the Cordillera Oriental Argentina. A. JUY-P 041, internal mould of right valve, lateral view. B. JUY-P 042, internal mould of left valve, lateral view. C. Holotype JUY-P 043, left valve in lateral view. D. JUY-P 044, left valve in lateral view. Scale bars 200  $\mu$ m.

sias, including the figured material JUY-P 041–044. Specimens we have examined range from 0.56 mm to 1.48 mm in length.

*Discussion.*—The taxonomic position of this species is unclear. It is similar in lateral outline to the species of *Conchoprimitia*, however, other features differ rather considerably. The new species has a small, and rounded node, and an indistinct sulcus. The described material resembles several Early and Middle Ordovician species of *Conchoprimitia*, and even some Circulinidae like *Vogdesella* Baker, 1924. The Argentinian species is similar to *Conchoprimitia socialis* (Brögger, 1882) from the Middle Ordovician of the Oslo region in the subcircular outline of the valves, and in the presence of a node and a sulcus in the antero dorsal part of the carapace (Henningsmoen 1954: pl. 2: 1–6). However, the new species is smaller (L = 1.48 mm in *C.?* *iglesiassi* sp. nov., L = 4.45 mm in *C. socialis*), the valves are postplete, the nodes are more rounded and poorly defined, and the steepest area is anterodorsally whereas in the Baltic species is postero-ventrally. *Conchoprimitia* sp. (Tinn and Meidla 2004: fig. 5A–D) from the Dapingian of Baltic has a short and poorly defined sulcus, however, it is more elongated and has very well defined retention marks, unknown in the new species. *Conchoprimitia distincta* (Sarv, 1959) (in Schallreuter 1989: fig. 5.1–2) from the Darriwilian of Baltic has a circular and postplete outline, and a very indistinct sulcus, however, it has an important swell in the posterodorsal half of the valves, and the carapace is punctuated. *Conchoprimitia? polonica* Olempska, 1994 (Olempska 1994: pl. 47: 14–16), from the Darriwilian of Poland, has a postplete outline, a short and indistinct sulcus, and a weakly developed preadductorial node as *Conchoprimitia? iglesiassi* sp. nov. In the Argentinian species, however, L is longer, the cardinal corners are more defined and they are not rounded, the anterior margin is not so sharp, the valves are less

convex, and the preadductorial node is small and rounded. The new species also resembles *Vogdesella aequae* Olempska, 1994 (Olempska 1994: pl. 44: 10–12) from the Darriwilian of Poland, however, the Argentinian form is bigger, N1 is small and sharp, and N2 is not present or is very indistinct.

*Stratigraphic and geographic distribution.*—Known only from the type locality.

Suborder Binodicopina Schallreuter, 1972

Superfamily Aechminoidea Bouček, 1936

Family Circulinidae Neckaja, 1966

Genus *Orechina* Krůta, 1968

*Type species:* *Orechina punctata* Krůta, 1968. Ořech, middle Bohemia, Czech Republic, Late Ordovician.

*Orechina violetae* sp. nov.

Fig. 8A–C, E.

*Etymology:* For one of my (MJS) twins Violeta.

*Holotype:* CEGH-UNC 24029, right valve (Fig. 8A).

*Type locality:* Purmamarca area, Quebrada de Chalala section, northwest of Argentina.

*Type horizon:* Ch2 sample, Coquena Formation, Late Tremadocian.

*Diagnosis.*—Species of *Orechina* with a semicircular and amplete outline. Adductorial sulcus short, narrow and U-shaped. Valves reticulate, with rectangular cells. The dorsal area is smooth. Lateral surface of valves is convex.

*Description.*—The valves are sub-elliptical to semicircular and amplete in outline. The maximum length is situated at the mid-height of the valve. The average L:H is 1.54. The dorsal margin is straight and shorter than the maximum length. Lateral and ventral margins are rounded, the posterior one showing a sharper outline. The cardinal corners are both well defined, and obtuse (cardinal corners are ca. 140°). Valves unisulcate, the adductorial sulcus (S2) is in the antero-dorsal half of the valve. S2 is short, narrow, U-shaped, and poorly to well defined depending on the specimens. An oval muscle spot is present in the ventral end of the sulcus, in some specimens it is indistinct. In some exemplars, there is a poorly defined and small preadductorial node. The lateral surface of the valves is rather convex, with the maximum width in the posterior half of the valves. The lateral surface is reticulate with elongated cells (rectangular). The reticulation follows the free margin of the valve, and the cells are smaller towards the cardinal corners. The dorsal area is smooth as the marginal surface. In the internal moulds there is a well defined and short sulcus. Immediately in front of the sulcus is an oval node. The surface of the mould is smooth.

*Material.*—Over 20 specimens of valves and internal moulds, including the figured material CEGH-UNC 24029–31, 24036. Specimens we have examined range from 0.68 mm to 1.12 mm in length.

*Discussion.*—The studied material shared several features with the genus *Orechina*, i.e., the presence of an adductorial

sulcus S2, with a rounded muscle spot in its ventral part, the rounded outline of the valves, and the reticulated lateral surface, except for the dorsal area. The new species does not have a bend between the lateral and marginal surface of the valves, however, Schallreuter and Krůta (1987), in the emended diagnosis of the genus, include the bend as a normally present feature, and not as a diagnostic character. The convexity of the valves and the large angle (ca. 90°) between the marginal surface and the plane of the separation of the valves are not common features in the genus and in the family Circulinidae. However, the other characters of this form resemble the genus *Orechina*.

The genus *Orechina* has several species widespread in Bohemia, Baltic region, and Poland during the Middle to Late Ordovician. The presence of *Orechina* in the Upper Tremadocian levels of northwest Argentina would be the first mention of the genus in Gondwana and would extend its range to the first stage of diversification of ostracods. This new species is comparable with *Orechina procera* Schallreuter, 1980 (Schallreuter 1980: figs. 8.1–8.3; Schallreuter and Krůta 1987: figs. 2.1–2.2) from the Sandbian of Sweden, and with *Orechina krutai* Olempska, 1994 from the Middle Ordovician of Poland, based mainly on the lack of a bend between the lateral and marginal surface of the valves and on a ridge at the dorsal margin, as well as for the outline of the valves. However, the new species is larger, S2 is less defined (feature shared with *O. krutai*), and has a muscle spot in its ventral end, the valves are more convex, and the lateral surface is reticulate with rectangular cells. With respect to the Bohemian species, *Orechina punctata* Krůta, 1968 and *Orechina densipuncta* (Schmidt, 1941) (in Schallreuter and Krůta 1987: figs. 1–4), both from the Late Ordovician, the main difference is the presence of the bend between the lateral and marginal surfaces, and of the ridge in the dorsal margin.

The studied material is comparable too with *Mytoa klavava* Schallreuter and Krůta, 1988, from the Arenig of Bohemia, in the presence of a rounded muscle spot and in the indistinct sulcus. However, the Bohemian species is elongate, the lateral surface is flat, and the reticulation is not defined.

*Orechina violetae* sp. nov. differs from the other Argentinian species, *Orechina catalinae* sp. nov., in that it has wider valves, which are more convex, the reticulation more defined with rectangular cells and mainly in the presence of a muscle spot, absent in *O. catalinae* sp. nov.

*Stratigraphic and geographic distribution.*—Known only from the type locality.

*Orechina catalinae* sp. nov.

Fig. 8D, F–H.

*Etymology:* For one of my (MJS) twins Catalina.

*Holotype:* CEGH-UNC 24037, external mould of left valve (Fig. 8G).

*Type locality:* Quebrada de Humahuaca area, northwest Argentina.

*Type horizon:* V1f sample, lower levels of the Humacha Member, Santa Rosita Formation, Middle Tremadocian.

*Diagnosis.*—Subcircular and amplete in outline. Well defined, short, and V-shaped adductorial sulcus. Lateral sur-

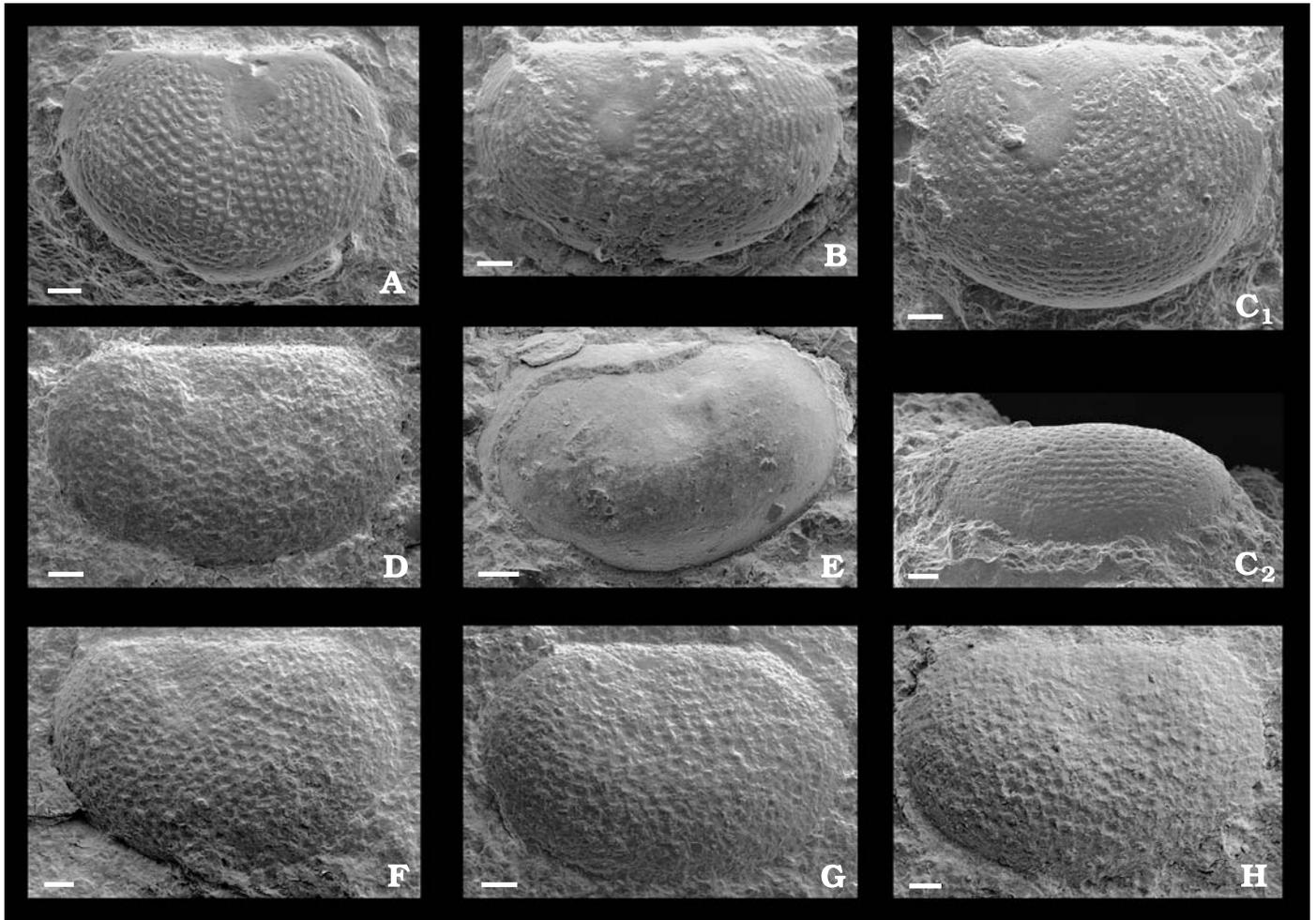


Fig. 8. Late Tremadocian binodicopids ostracods from the Northwest Basin of Argentina. **A–C, E.** *Orechina violeatae* sp. nov. Coquena Formation in Chalala section, Purmamarca area. **A.** Holotype CEGH-UNC 24029, right valve in lateral view. **B.** CEGH-UNC 24030, left valve in lateral view. **C.** CEGH-UNC 24031, right valve, lateral (**C<sub>1</sub>**) and ventral (**C<sub>2</sub>**) views. **E.** CEGH-UNC 24036, internal mould of right valve, lateral view. **D, F–H.** *Orechina catalinae* sp. nov. Humacha Member of the Santa Rosita Formation, lower part of the Humacha section. **D.** CEGH-UNC 24017, left valve in lateral view. **F.** CEGH-UNC 24027, left valve in lateral view. **G.** Holotype CEGH-UNC 24037, left valve in lateral view. **H.** CEGH-UNC 24028, right valve in lateral view. Scale bars 100  $\mu$ m.

face flat, without the bend between the lateral and marginal surface.

**Description.**—Sub-elliptic to circular outline, amplete. Average L:H 1.55. Maximum length at the mid-height of the valves. Dorsal margin straight and shorter than the maximum length. Lateral and ventral margin evenly rounded. Cardinal angles obtuse, the anterior is smaller and better defined than the posterior angle. The valves are unisulcate. The adductor sulcus (S2) is present in the anterodorsal half of the valve. It is well developed, short, does not reach the ventral half of the valve, is wide dorsally and V-shaped. The lateral surface is nearly flat, and reticulate.

**Material.**—More than 20 specimens from internal to external moulds, including the figured material CEGH-UNC 24017, 24027–28, 24037. Specimens we have examined range from 0.68 mm to 1.20 mm in length.

**Discussion.**—*Orechina catalinae* sp. nov. is similar to *Orechina violeatae* sp. nov. from the Coquena Formation of the

Chalala section but differs in the lack of a muscle spot, the more rounded cells of the reticulation and the flatter lateral surface. With respect to the others species included in the genus, *Orechina catalinae* sp. nov. is bigger (L reaches 1.20 mm), the reticulation takes up nearly all the valve surface, and the dorsal ridge, the bend between the lateral and marginal surfaces, and the muscle spot are absent.

**Stratigraphic and geographic distribution.**—Known only from the type locality.

## Affinities and diversity of the earliest ostracods

The first ostracods appear almost simultaneously in different regions during the *Paltodus deltifer* Biozone (Tr2); in the northwest Argentina (the southern extreme of the Central An-

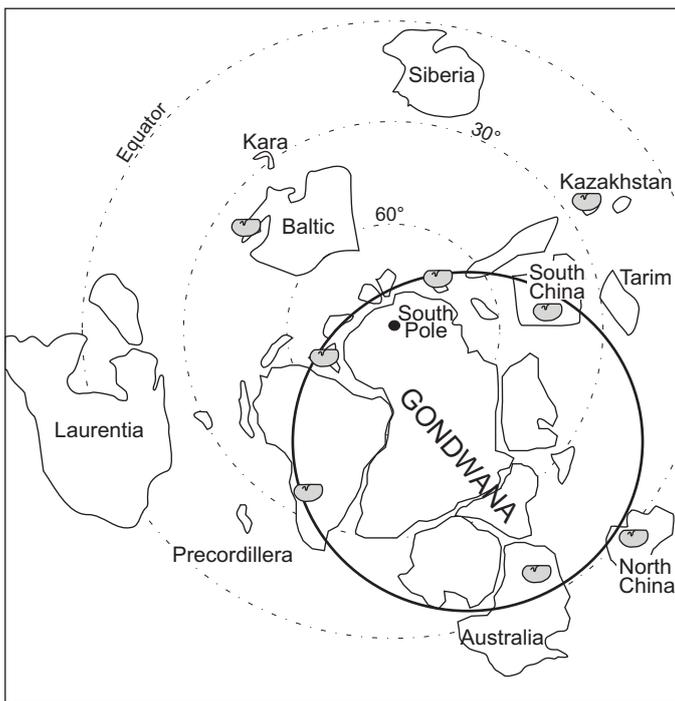


Fig. 9. Palaeogeographic distribution of ostracods in the Late Tremadocian. The circle embraced the Gondwana and peri-Gondwana Tremadocian records of ostracods. Modified from Williams et al. (2008).

dean Basin), in the Baltic region (Bjorkasholmen Formation, Norway and Alum Shale, Sweden, Henningsmoen 1954; Tinn and Meidla 2004), in Iran (Lashkarak Formation, Alborz region, Williams et al. 2008), in South Britain (Shinerton Shales Formation, Williams and Siveter 1998) and in Kazakhstan (Buru-Baital Formation, Melnikova et al. 2010). The ostracods appear somewhat later in southern China (Fenhsiang Formation = Ichang Formation in West. Hubei, Hou 1953b), northern China (Yehli Formation, Liaoning NE China, Hou 1953a), and Australia (lower levels of Emanuel Formation, in Canning Basin, Schallreuter 1993) (Figs. 2, 9).

This widespread geographical occurrence during the middle Tremadocian, suggests that ostracods originated in the Cambrian or at least earlier in the Tremadocian (Salas et al. 2007; Williams et al. 2008). Recently, a finding of some possible ostracods in the western Puna region of northwest Argentina, in levels assigned to the lowermost Tremadocian, would take the first record of the group to the Cambrian–Ordovician transition (Salas and Vaccari 2009). Moreover, a possible ostracod, podocopid or myodocopid, was recorded in the Early Tremadocian in England (Siveter et al. 1995).

All Tremadocian ostracods show, in general, a simple morphology of the carapace, subcircular to subelliptical outline, tri or quadri lobates valves, well to poorly-defined sulcus, and valves without marginal structure. One exception to these characteristics is a new genus, assigned to the Primitiidoidea, recently discovered in the Tremadocian of Kazakhstan (Melnikova et al. 2010).

In this context, as the record of Tremadocian ostracods is generally poor, northwest Argentina is an excellent location to study the early radiation of ostracods. The northwest basin contains five of the six genera known in the world, for the Tremadocian period, with 5 species of palaeocopids, 3 species of binodicopids and one possible species of eridostracin. This diversity may be due, at least in part, to the thick, well-exposed, and widespread marine platform facies suitable for ostracod colonization.

The Tremadocian of the Cordillera Oriental records a wide display of depositional environments, ranging from shelf to storm-dominated shallow-marine deposits, usually associated with deltaic systems, punctuated by conversions towards complex tide-dominated estuaries (Astini 2003; Buatois and Mángano 2003; Buatois et al. 2006). Most of the fauna recorded is present in the Tr3 stage-slice, and the diversification of the ostracods could have been a consequence of a regional flooding associated with a rise of the sea level during the Middle to Late Tremadocian (Astini 2003) (Fig. 10). Consequently, low energy sub-tidal environments would be generated in different areas of the Cordillera Oriental (Sierra de Mojotoro Range, Pascha-Incamayo). In addition, the peculiar basin configuration, represented by restricted, valley-fill sequences (Astini 2003; Buatois et al. 2006) may have generated a restricted circulation pattern that would have promoted the specific diversification observed in the region. In this context, the offshore environments were isolated from each other, and the small variations in depth and in levels of oxygenation would have been favourable to speciation. These features could explain how the genus *Saltite* has three well defined species, recorded nearly simultaneously at different locations within the basin. *Saltite erichseni* (Harrington, 1938) is recorded in the moderate-energy, shallow and well oxygenated successions in the San Bernardo Formation (Moya 1998; Waisfeld and Vaccari 2008b). *Saltite uchuy* sp. nov. is recorded in levels of phosphatised coquinas in the Parcha Formation and in the matrix of the conglomerate of the Devendous Formation, and *Saltite kuraq* sp. nov. is recorded in greenish shale, developed in lower energy conditions characteristic of a lower offshore in the Humacha Member (Santa Rosita Formation) (Buatois et al. 2006; Muños 2009). It is important to highlight that a similar regional pattern of speciation has been observed in *Thysanopyge*, an endemic genus of trilobite from the Central Andean Basin (Waisfeld and Vaccari 2008b, c).

Compared with the above-noted basins of the world, the Northwest Argentinean Basin contains a relatively abundant record of ostracods. However, the record is patchy and the ostracods appear only in some levels and localities. This fragmentary record could be related to taphonomic factors that caused the dissolution of the carapaces. In addition, our knowledge of the ostracods in this region is in its infancy and more sampling is necessary to fully explore this region.

During the Tremadocian all the main taxonomic groups are represented: palaeocopids, binodicopids, eridostracins,

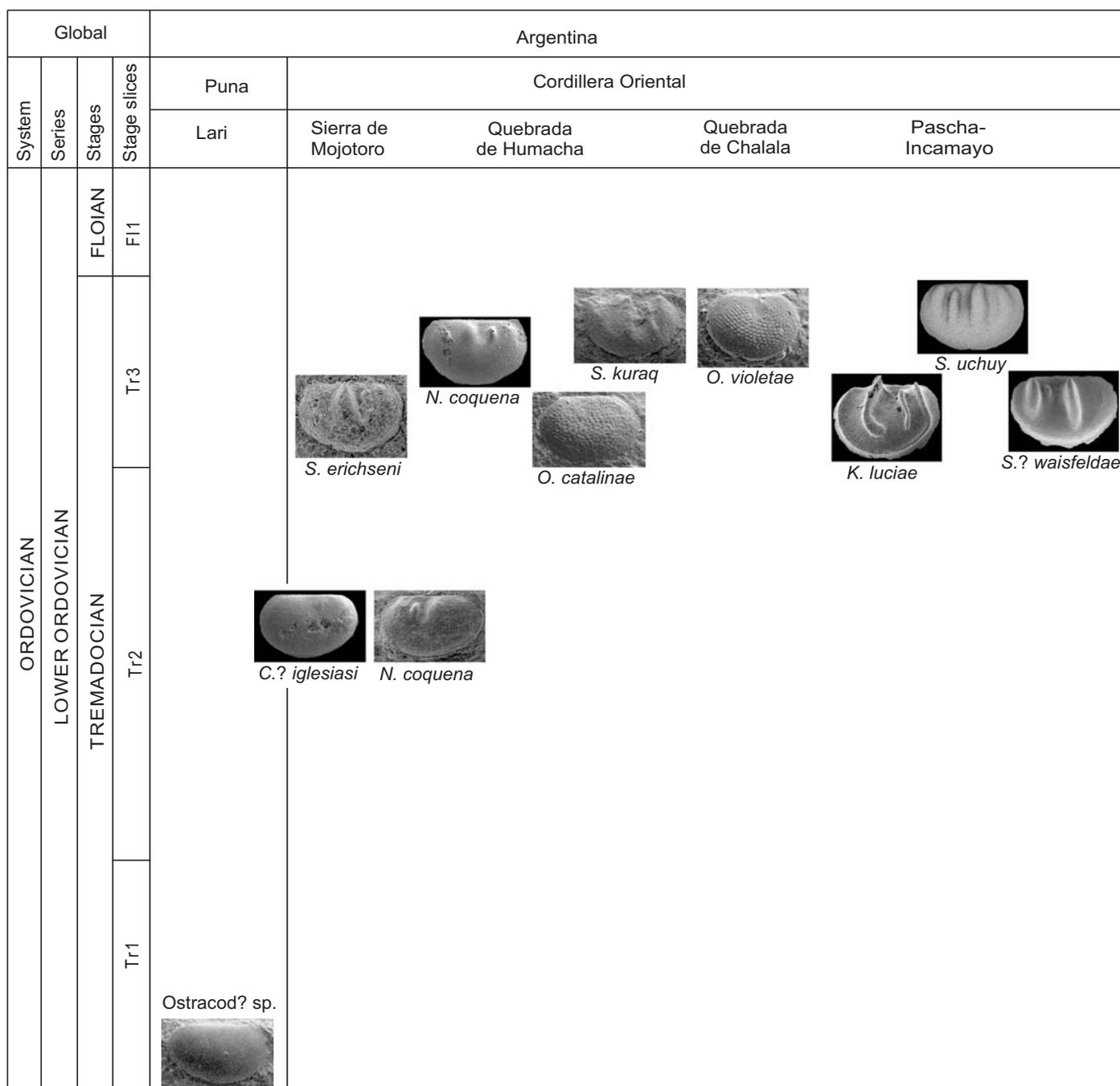


Fig 10. Temporal and spatial distribution of the ostracod species in the Tremadocian of the Northwest Argentinian Basin.

podocopids and myodocopids. Neither podocopids nor myodocopids are present in the Cordillera Oriental Argentina.

Among the present genera *Kimsella* is an endemic form. In contrast, *Saltite* has a more widespread distribution, and shows palaeogeographical affinities with Australia (Schallreuter 1993), and possible affinities with North China. *Conchoprimitia* is a widespread genus with many known species since the Floian, however during the Tremadocian it only appears associated with *Saltite* in Australia (Roger Schallreuter, personal communication 2005 in Salas et al. 2007)

and possibly in South China. With respect to the genus *Nanopsis*, it is present in the Tremadocian levels of north-west Argentina (*Nanopsis coquena*), Baltic region (*Nanopsis nanella*) and possibly in South China, since “*Sinoprimitia hupeiensis* resembles *Nanopsis*. In Australia, *Nanopsis* occurs later, in the Floian levels of the middle part of the Emanuel Formation (*Bumire pilloides* Schallreuter, 1998). Finally, the presence of *Orechina* in the Tremadocian levels of Argentina would be the oldest record of the genus, which is widespread in Bohemia, the Baltic region, and in Poland

during the Middle to Late Ordovician (Schallreuter and Krüta 1987). The Tremadocian fauna from the Cordillera Oriental Argentina show significant affinities with the Australian and Chinese species. Forms like *Saltite*, *Nanopsis*, and *Conchoprimitia* are shared by the three regions. The faunas from Iranian terranes and Avalonia (Southern Britain) (Siveter et al. 1995; Williams and Siveter 1998; Williams et al. 2008), although poorly known yet, are not comparable with the Argentinean forms. This palaeobiogeographical affinity with the warm water setting of the east Gondwana and Peri Gondwana has also been observed in trilobites (Vaccari et al. 2006; Vaccari and Waisfeld 2008).

The Tremadocian ostracods of the northwest Argentina are mainly represented by binodicopids, soanellids (family of non-dimorphic palaeocopids) and *Nanopsis*. This pattern, where fauna is dominated mainly by non-dimorphic palaeocopids, is observed in the rest of the Central Andean Basin at least until the Floian (Hughes et al. 1980; Přibyl 1984; Schallreuter and Hinz-Schallreuter 2004, 2007). Hinz-Schallreuter and Schallreuter (2007) and Schallreuter and Hinz-Schallreuter (2009) have defined three faunal provinces within the Gondwana and peri-Gondwana regions, by primarily analyzing the fauna of the middle to upper Ordovician. The defined provinces are Thuringian, Armorican, and Australian, including the Cordillera Oriental in the Australian province. Schallreuter and Hinz-Schallreuter (2009) further noted the relationship between the two regions during the Early Ordovician. According to the studied fauna it is possible to extend, at least the Australian province, until the Tremadocian due to the palaeogeographical affinities between Cordillera Oriental, Australia and probably China.

A noteworthy feature of the first radiation of the group is its palaeogeographical distribution, mainly restricted to Gondwana and peri-Gondwana regions (Williams et al. 2008), considering that only two species are known outside Gondwana (Fig. 9). This predominance of Tremadocian species in Gondwanan and peri-Gondwanan basins put the region in an important role for the early radiation of the group. Accordingly, it is possible to set out an origin or at least an important radiation of the group centred on this region. According to this distribution, both the soanellids and the genus *Orechina* would have originated in Gondwana and would have become widespread later during the Middle Ordovician.

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