

Huncalotis, an enigmatic new pectinoid genus (Bivalvia, Late Jurassic) from South America

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Abstract The extensive outcrops of the Late Jurassic–Early Cretaceous Vaca Muerta Formation black shales and marls in the Neuquén Basin have yielded very few bivalves, and these are not well known. The material described here was collected in central Neuquén, from late Tithonian calcareous levels within the black shales, between beds with *Substeueroceras* sp. and with *Argentiniceras noduliferum* (Steuer). The material is referred to the new genus *Huncalotis* and to the new species *H. millaini*. The strongly inequivalve shells, the ligamental area with a triangular slightly prosocline resilifer, the right valve with ctenolium and a very deep byssal notch, and the lack of radial ornamentation make the shell of this new genus strikingly similar to the Triassic pectinid *Pleuronectites*. This resemblance may be due to either phylogenetic relationships or convergence. *Obliquipecten peruanum* Rivera from central Peru is tentatively referred to *Huncalotis*. The Neuquén specimens are found in two main preservation types. Most of the material occurs in shell pavements, with equally abundant right and left valves and wide size range, within “beef” or “sandwich concretions”. These specimens are commonly complete but disarticulated, and show radial fractures

orientated at right angles to the shell margins. A few specimens were found on the outside of large calcareous concretions within black shales; these are often articulated, complete shells, which preserve the original convexity of the valves. In some cases these articulated shells seem to be associated with large ammonite shells, suggesting an epibyssate (possibly also pseudoplanktonic) lifestyle.

Keywords Late Tithonian · Neuquén Basin · Vaca Muerta Formation · Argentina · Peru · Bivalvia · Pectinoidea · Pectinidae

Kurzfassung Die reichlich zutage tretenden Schwarzschiefer und Mergel der spätjurassisch–frühkretazischen Vaca Muerta-Formation des Neuquén-Beckens haben bisher nur sehr wenige Muscheln geliefert, die ungenügend bekannt sind. Das hier beschriebene Material wurde im Zentrum der Provinz Neuquén aufgesammelt und stammt aus kalkigen Lagen innerhalb der Schwarzschiefer des späten Tithoniums, mit den Ammoniten *Substeueroceras* sp. und *Argentiniceras noduliferum* (Steuer). Das Bivalvenmaterial wird der neuen Gattung *Huncalotis* mit der neuen Art *H. millaini* zugeordnet. Die stark ungleichklappigen Schalen ähneln aufgrund verschiedener morphologischer Charakteristika (dreieckiges leicht prosoklines Resilium im Ligamentbereich, Vorhandensein eines Ctenoliums und einer sehr tiefen byssalen Kerbe in der rechten Klappe sowie Fehlen einer radialen Ornamentierung) der triassischen pectiniden Muschelgattung *Pleuronectites*. Diese auffallende Ähnlichkeit kann entweder durch phylogenetische Beziehungen oder Konvergenz verursacht worden sein. *Obliquipecten peruanum* Rivera aus Zentral-Peru wird vorläufig ebenso der Gattung *Huncalotis* zugewiesen. Von den Exemplaren aus dem Neuquén-Becken wurden zwei Erhaltungstypen gefunden. Das meiste Material kommt in Muschelpflastern

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(mit gleichermaßen häufig vorkommenden rechten und linken Klappen sowie einem weiten Größenspektrum), in sogenannten “beef”- oder “sandwich”-Konkretionen vor. Solche Schalen sind gewöhnlich vollständig, jedoch disartikulierte und mit radial angeordneten Bruchstellen (in rechtem Winkel zum Schalenrand) versehen. Einige Exemplare wurden an der Außenseite von Kalkkonkretionen gefunden, wobei diese oft artikuliert sind und die ursprünglichen konvexen Schalen zeigen. In einigen Fällen scheinen solche artikulierten Schalen zusammen mit großen Ammonitengehäusen vorzukommen, so daß eine epibyssate (oder möglicherweise auch pseudoplanktonische) Lebensweise angenommen werden kann.

Schlüsselwörter Bivalvia · Pectinoidea · Pectinidae · Tithonium · Neuquén-Becken · Vaca Muerta-Formation · Argentinien · Peru

Resumen *Huncalotis*, un enigmático nuevo género de pectinoideo (Bivalvia, Jurásico Tardío) de América del Sur. Las pelitas oscuras y margas bituminosas de la espesa Formación Vaca Muerta (Jurásico Tardío - Cretácico Temprano) se hallan ampliamente distribuidas en la cuenca neuquina pero los registros de bivalvos, y de faunas bentónicas en general, son escasos en esta unidad. El material descripto proviene de niveles fosilíferos de edad tithoniana tardía, entre niveles con *Substeueroceras* sp. y con *Argentiniceras noduliferum* (Steuer), conteniendo abundantes restos de una nueva especie de bivalvo referida al nuevo género *Huncalotis*. La conchilla fuertemente inequivalva, las aurículas anteriores de la valva derecha limitadas por una profunda escotadura bisal con ctenolio, el área ligamentaria con resilífero triangular y levemente prosocline y la ausencia de ornamentación radial, hacen que las conchillas de este género sean muy similares a las del pectínido Triásico *Pleuronectites*. Esta similitud puede deberse a relaciones filogenéticas o simplemente a convergencia. *Obliquipecten peruanum* Rivera, especie de las cercanías de Lima, Perú, se incluye con dudas en *Huncalotis*. El material de Neuquén se halla preservado de dos modos diferentes. La mayoría se presenta como pavimentos de conchillas, con valvas derechas e izquierdas igualmente abundantes y un amplio rango de tamaños, en concreciones tipo “beef”. Estos ejemplares se hallan completos pero desarticulados, y presentan fracturas radiales perpendiculares a los márgenes de las conchillas. Otros ejemplares aparecen en el exterior de grandes concreciones calcáreas dentro de pelitas negras; éstos están comúnmente articulados, preservan la convexidad original de las valvas, y en varios casos valvas articuladas muestran estrecha relación con grandes conchillas de amonites, lo que indicaría un modo de vida epibisado, incluso pseudoplanktónico.

Fig. 1 **a** Location map within the Neuquén Basin. **b** Geological map of the Arroyo Rahuecú region (modified from Gulisano and Gutiérrez-Pleimling 1995). **c** Geological map of the Huncal region (from Leanza et al. 2003; Leanza and Hugo 2005). Fossiliferous localities: 1 Arroyo Rahuecú; 2 Huncal, north of Arroyo Coihueco; 3 Huncal, south of the suspension bridge over Arroyo Coihueco; 4 Huncal, road to Loncopué

Palabras clave Tithoniano tardío · Cuenca Neuquina · Formación Vaca Muerta · Argentina · Perú · Bivalvia · Pectinoidea · Pectinidae

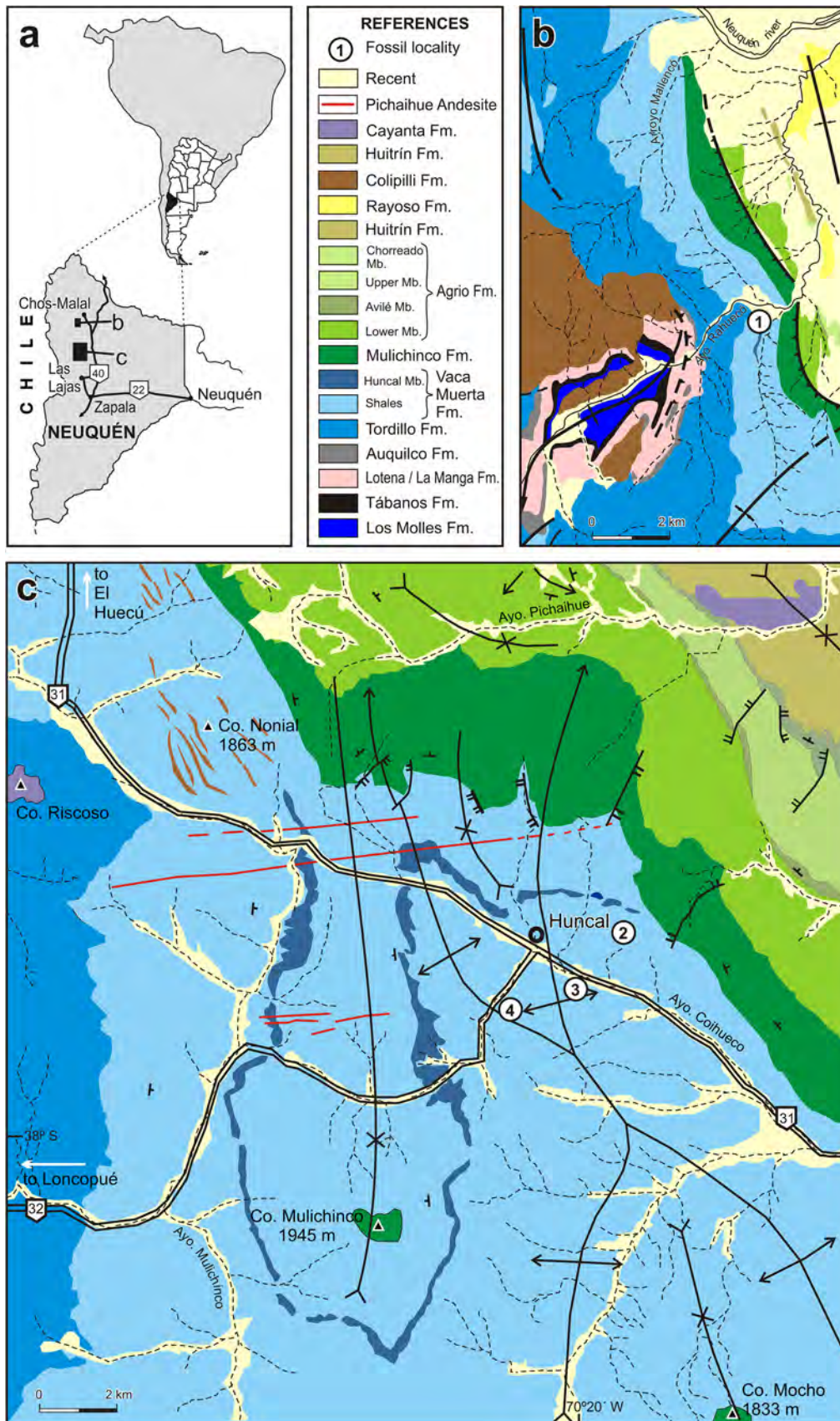
Introduction

Late Jurassic–Early Cretaceous pectinoidean and monotoid bivalves from South America are poorly known and in need of revision. Although some species have been reported from Colombia, Peru and Argentina, previous descriptions are incomplete and illustrations poor (Lisson 1907; Royo y Gómez 1945; Sokolov 1946; Rivera 1951; Romero et al. 1995), and only the material described by Rivera (1951) could be located and revised. We analyse here material from the Vaca Muerta Formation in the Neuquén Basin (Argentina) which shows a unique combination of shell characters that suggests it should be referred to a new pectinoid genus and species of uncertain systematic affinities. The peculiar mode of preservation in “sandwich concretions” is also discussed, since it adds to the knowledge of the diagenetic history of the sediments involved.

The Vaca Muerta Formation contains a rich ammonite fauna (Leanza and Hugo 1978; Leanza and Wiedmann 1989; Leanza 1981a, b; Zeiss and Leanza 2010; Riccardi et al. 2011) but few other macrofossils. Several levels also bear bivalves, among them monotoid species described a long time ago (Sokolov 1946) but not revised since then. The material described here was collected from three localities near the settlement of Huncal (Damborenea and Leanza 2004) and one locality near Rahuecú, all of them in Neuquén Province, west-central Argentina (Fig. 1).

Geological setting

Several hundred metres of dark bituminous shales, marls and limestones known as the Vaca Muerta Formation (Weaver 1931) were accumulated during the Late Jurassic–Early Cretaceous in the Neuquén Basin (Leanza et al. 1978; Gulisano et al. 1984; Legarreta and Uliana 1991; Leanza et al. 2011). Although this unit forms an apparently monotonous sequence of black shales intercalated with marls with high organic content (Legarreta and Uliana



1996), several facies associations were recognized (Leanza 1973; Mitchum and Uliana 1985; Kietzmann and Vennari 2013; Kietzmann et al. 2014, and references therein). The Vaca Muerta Formation crops out extensively in central Neuquén Province, and its biostratigraphy is based on ammonites (Leanza 1981a; Leanza and Hugo 1978; Riccardi 2008a, b; Riccardi et al. 2000, 2011; Aguirre-Urreta et al. 2011; Riccardi 2015). Recent cyclostratigraphic analyses (Kietzmann et al. 2011) provide additional age control and contribute to the calibration of the ammonite zones.

The succession of the Vaca Muerta Formation in the Nonial–Huncal area (central part of the Neuquén Basin) was studied by Leanza et al. (2003, fig. 4; Leanza et al. 2006).

Age of the fauna

According to Leanza et al. (2003, fig. 2; Leanza et al. 2006, fig. 4), the material described here was found below the Huncal Member of the Vaca Muerta Formation in calcareous levels which occur within the black shales typical of this unit, 110 m above limestones with *Substeuerocheras*, and 425 m below levels with *Argentiniceras noduliferum* (Steuer) (Fig. 2), at least at three localities around Huncal (Damborenea and Leanza 2004, fig. 1c). Weighting the stratigraphic distance to the levels with *A. noduliferum*, which is true Berriasian in age, against the proximity to levels with *Substeuerocheras*, and taking the finding of *Substeuerocheras* cf. *S. striolatissimum* (Steuer) in one of the calcareous concretions (Fig. 8e, f) into account, a late Tithonian age is assigned to the bivalve beds. In the Andes, *Substeuerocheras* cf. *striolatissimum* (Steuer) occurs in association with himalayitids (e.g. *Himalayites andinus* Leanza 1975) at the very base of the *Substeuerocheras koeneni* ammonite biozone (see Leanza 1981b), which largely excludes a Berriasian age for the studied bivalves.

The material from Rahuecú was also found below the Huncal Member in a similar stratigraphic position (Fig. 1b).

Materials and methods

Most of the specimens were found in shell pavements, where the valves are isolated but, due to the peculiar preservation mode in shales with “beef” (discussed below), only the external surface is seen and the specimens are somewhat flattened by compaction. A few specimens were found in calcareous concretions, and in this case are not deformed and occasionally have both valves

articulated. Specimens were coated with ammonium chloride or with magnesium oxide before photographing, unless the natural contrast between shell and matrix enhanced the feature to be illustrated.

Abbreviations preceding catalogue numbers of examined specimens are as follows: MLP: invertebrate palaeontology collection at La Plata Natural Sciences Museum, La Plata, Argentina; ING: fossil collection at the Instituto Geológico, Minero y Metalúrgico del Perú (INGEMMET), Lima, Peru.

Descriptive terminology of shells follows Waller (1984), Hautmann (2004) and Carter et al. (2012).

Systematic palaeontology

Subclass **Pteriomorphia** Beurlen, 1944

Order **Pectinida** J. Gray, 1854

Superfamily **Pectinoidea** Rafinesque, 1815, emend. Waller 1978

Genus **Huncalotis** gen. nov.

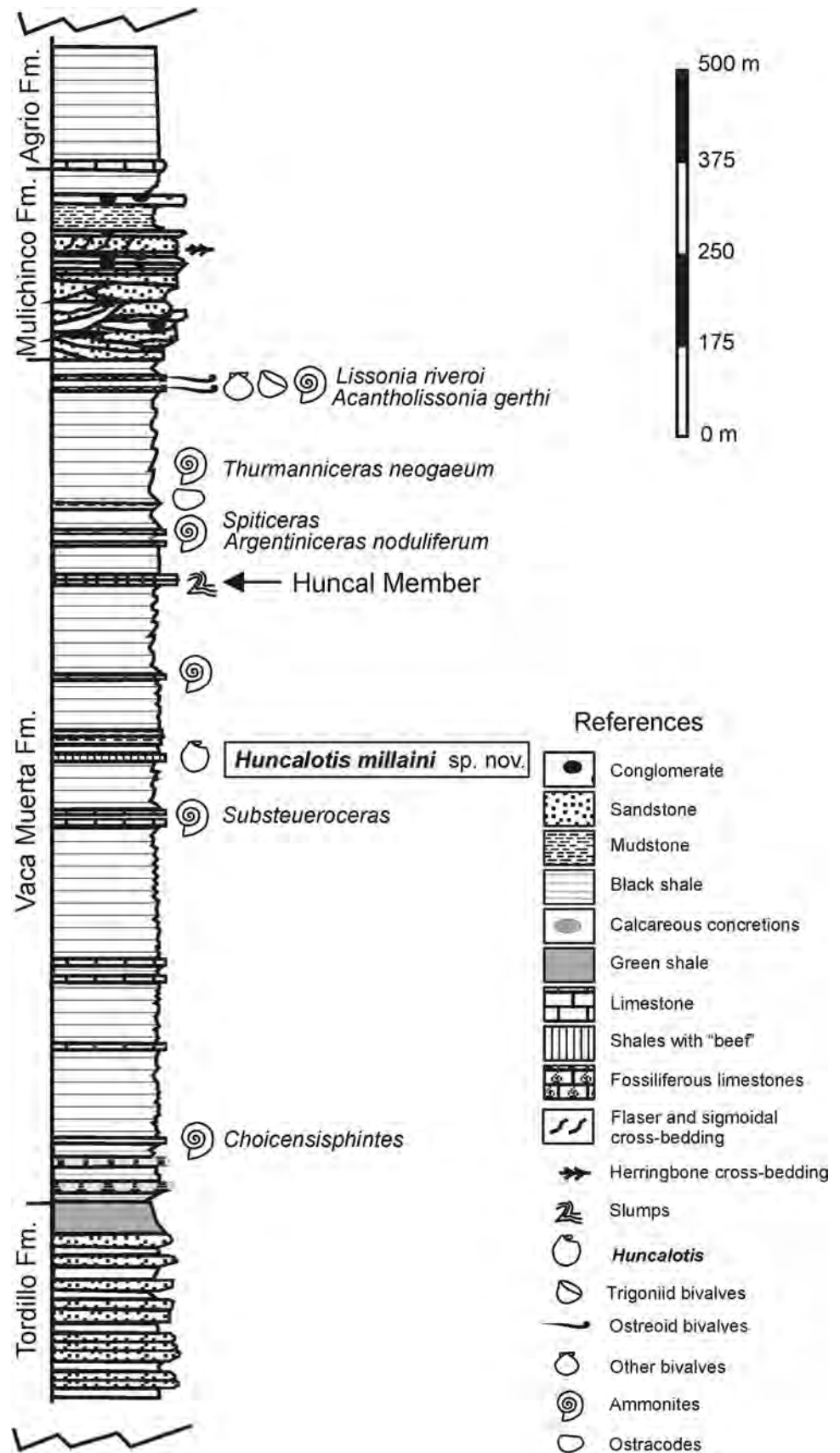
Etymology. The name refers to the type locality of the type species, Huncal in central Neuquén, Argentina.

Type species. *Huncalotis millaini* sp. nov., described herein, from the late Tithonian of central Neuquén, Argentina (Figs. 3, 4, 5, 9).

Diagnosis. Inequivalve shells, moderately inflated, left valve more convex than right valve. Valves inequilateral with slightly opisthocline (prorescent) discs. Right anterior auricle well developed, long and narrow, separated from disc by a deep and wide byssal notch and byssal fasciole, with functional ctenolium. Right posterior auricle short; not delimited from disc. Left valve with poorly differentiated anterior and posterior auricles. Right valve hinge plate offset from commissural surface, with central, slightly prosocline triangular resilifer and narrow anterior and posterior bourrelets. Exterior with regular commarginal ornamentation on both valves.

Discussion. Besides the type species, *Obliquipecten peruanum* Rivera (1951: 48–49, pl. 6, figs. 6, 7, 8; see also Lisson 1907: 31, pl. 3, fig. 4, as *Synclonema* sp.), from Tithonian–Berriasian beds near Lima, Peru is tentatively included in *Huncalotis*. These specimens were previously referred to *Arctotis* by Romero et al. (1995: 122). The material from Colombia described by Royo y Gómez (1945: 220, pl. 29, fig. 2) as “*Pseudavicula*? sp. nov.” is tentatively assigned to *Huncalotis*? *peruana*. Part of the type material of *Obliquipecten peruanum* was examined at the INGEMMET collections in Lima, Peru (see Fig. 6). Because some of the diagnostic characters, such as the

Fig. 2 Section of the Vaca Muerta Formation at Huncal, Neuquén (from Leanza et al. 2003), and biostratigraphic framework for beds containing *Huncalotis millaini* sp. nov.



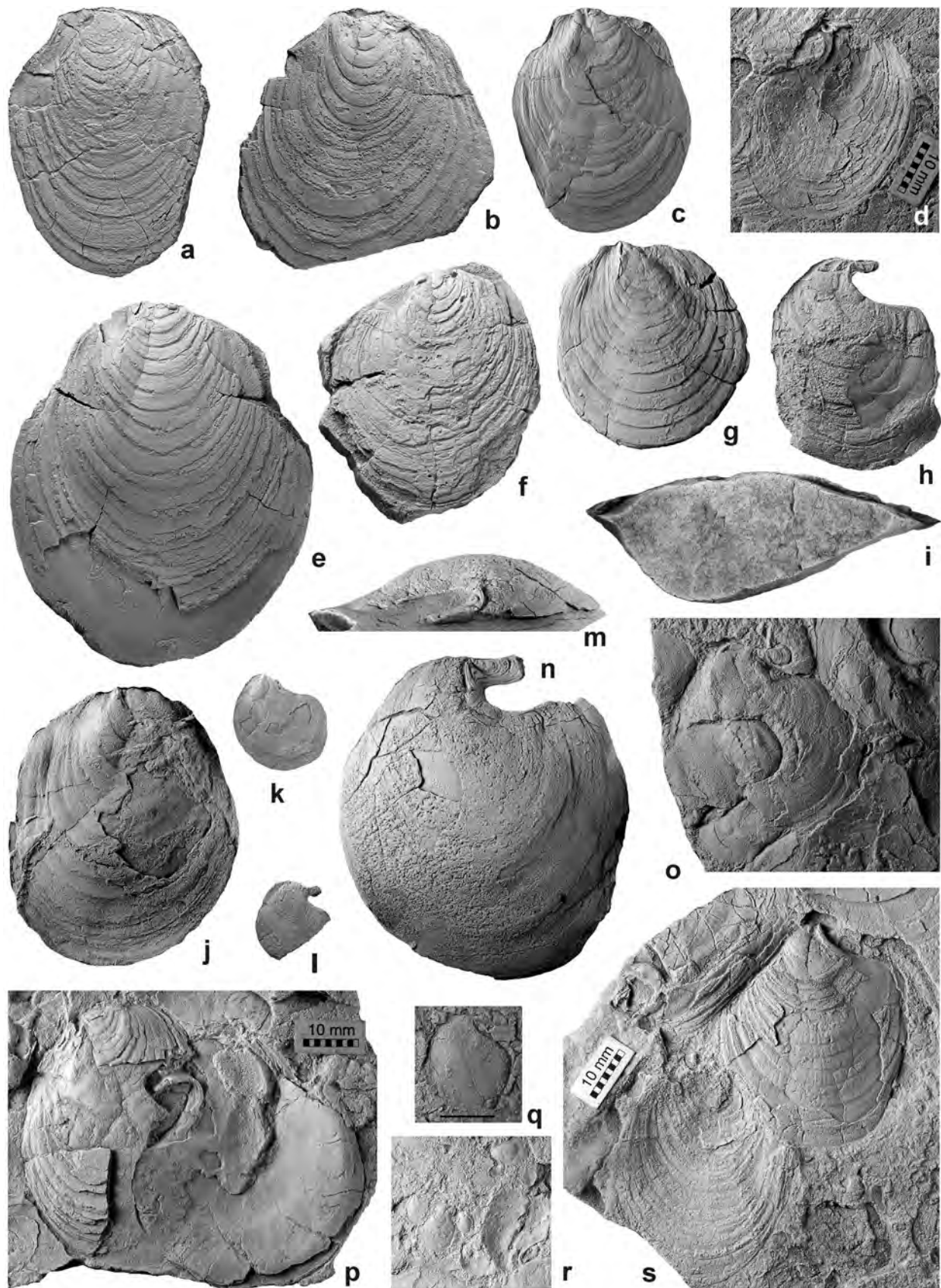


Fig. 3 *Huncalotis millaini* sp. nov. **a** MLP 35402, paratype, left valve; **b** MLP 35421b, paratype, left valve; **c** MLP 35403, paratype, left valve; **d** MLP 35405, paratype, right valve *internal view*; **e** MLP 35420, paratype, left valve; **f** MLP 35421a, paratype, left valve; **g** MLP 35412, paratype, left valve; **h** MLP 35406, right valve; **i** MLP 35423, paratype, cross section of specimen with both valves, *dorsal view* with left valve above; **j** MLP 35425a, left valve; **k** MLP 35432, incomplete young right valve showing ctenolium; **l** MLP 35426, paratype, young right valve; **m**, **n** MLP 35439, paratype, complete right valve in *dorsal* and *lateral views*; **o** MLP 35429a, holotype, right valve showing ctenolium; **p** MLP 35414, paratype, *outer view* of fragmentary left valve and *inner view* of right valve; **q** MLP 35434, paratype, young right valve; **r** MLP 35430, paratype, several young specimens; **s** MLP 35406a, right (*top*) and left valves. All figures natural size (graphic scale on figures). Localities: **m**, **n**: Rahucó; all others: Huncal

ligament area and ctenolium, are inadequately known, the species is only tentatively included in the new genus. The Peruvian species is currently under revision by Vera Alleman (pers. commun. 2014).

The systematic position of *Huncalotis* within the Pectinida is difficult to establish. Incomplete left valves were preliminarily referred to the Inoceramoidea and Monotoidea (Leanza et al. 2003; Damborenea and Leanza 2004; Rodrigues et al. 2009), but recently discovered well-preserved material indicates relationships with the Pectinoidea (see below). Key characters for the assignment to the Aviculopectinoidea vs. Pectinoidea are the ligament type, details of the right anterior auricle and the presence of either a ctenolium or pseudoctenolium.

Ligamental characters are not completely preserved in *Huncalotis*, but seem to be intermediate between alivincular-areate and alivincular-alate types (sensu Hautmann 2004), i.e. between Aviculopectinoidea and Pectinoidea ligaments, respectively. *Huncalotis* right valve ligament area is steeply inclined with respect to the commissural plane; it has a well-defined triangular resilifer, which slightly projects ventrally into the body cavity, and is flanked posteriorly by a long and longitudinally striated bourrelet; an anterior bourrelet may also be present (Fig. 4e, f). Left valve ligamental area is unfortunately unknown in *Huncalotis*, and therefore it is not possible to determine whether the resilium of the alivincular ligament was internal (and thus close to the alivincular-alate ligament system typical of pectinoids) or external. Although the first possibility is suggested by the inclination of the right valve ligamental area and the convexity of the left valve umbonal region, this question cannot be settled on the basis of the available material.

The right anterior auricle is long and spatulate, and while most of it lies on the commissural plane, in large specimens it curves ventrally towards the interior of the left valve (Figs. 3m, 5c, 9m). The left valve anterior auricle has a concave inner surface (Figs. 3a, 4d, 5c),

probably to accommodate the inclined right anterior auricle. A right anterior auricle inclined or offset towards the left valve is regarded as a significant feature to discuss the phylogeny of early Buchiidae by Wasmer et al. (2012). Nevertheless, the presence of ctenolium in *Huncalotis*, together with the large size of the byssal gape, and the prominent byssal fasciole, suggests that the inclination of its anterior auricle may have evolved convergently to the Buchiidae, perhaps due to morphological constraints related to the strong byssal attachment.

A true functional ctenolium is only known in the Pectinidae, whilst a disc-type pseudoctenolium is present in some Buchiidae, Oxytomidae and Monotidae (all Aviculopectinoidea, see Waller 1984; Monotidina according to Carter et al. 2011). The character in the studied material is here interpreted as a true ctenolium with numerous (up to at least 10) active teeth, as it appears to be formed on the outward-turned inner surface of the disc rather than on the disc itself (see Figs. 4a, b, 9j–m). Again, *Huncalotis* material does not allow performing detailed shell microstructure analysis to confirm this, but several characteristics reinforce our interpretation: denticles originate early in ontogeny and were evidently functional through all growth stages. The hook-shaped denticles are strong and cover a substantial portion of the right valve antero-dorsal margin, in some specimens being discernible on the suture close to the byssal fasciole up to the umbo. All these features are indicative of a particularly strong and efficient byssal attachment.

As a result, *Huncalotis* is assigned to the Pectinoidea, following Waller's (1984) criteria. Nevertheless, several important features are different from those seen in typical pectinoid shells, such as the absence of any radial ornamentation, the already mentioned ligamental area and the lack of cardinal and auricular crura. As discussed below, several diagnostic features are close to those of the family Pleuronectitidae Hautmann (in Carter et al. 2011). However, other key characters, such as shell microstructure (see Carter and Hautmann 2011), are not yet known in *Huncalotis*, and it is not referred to any particular pectinoid family herein.

Huncalotis is closely similar to the Triassic genus *Pleuronectites* Schlotheim, recently discussed by Waller (in Waller and Stanley 2005), Hautmann (2010) and Carter and Hautmann (2011) with regard to shell shape, size, valve inflation and ligament features. However, *Pleuronectites* is characterized by a smooth shell surface with occasional low radial costae (see discussion in Waller and Stanley 2005: 39, and revised diagnosis in Hautmann 2010), whilst *Huncalotis* bears regular commarginal ornamentation only. The right posterior auricle is well delimited in *Pleuronectites*, but not in *Huncalotis*. *Pleuronectites* is characterized by a prominent auricular scroll on the right

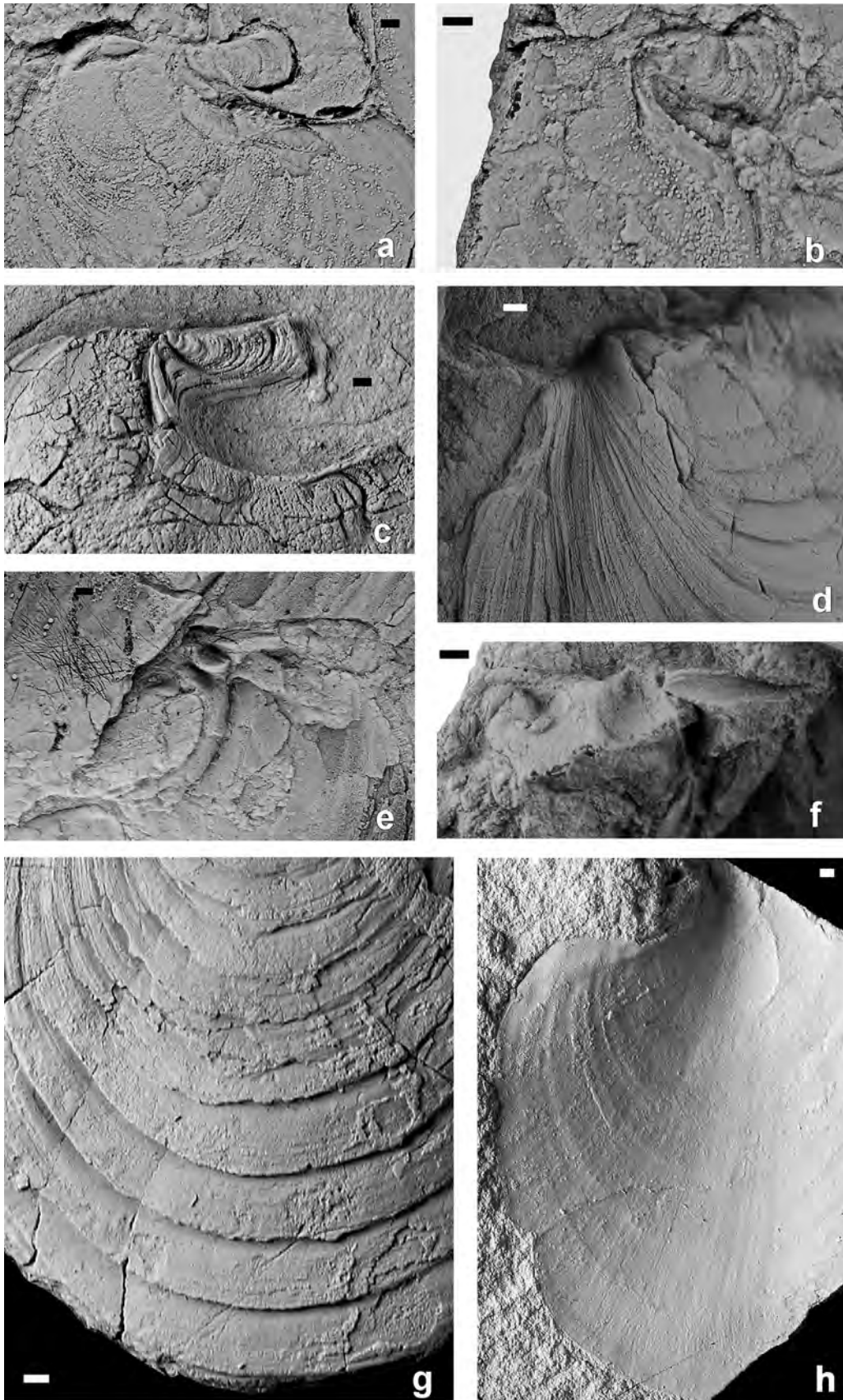


Fig. 4 *Huncalotis millaini* sp. nov. **a, b** exterior view of right valves showing ctenolium, **a** MLP 35429a, holotype; **b** MLP 35429b, paratype. **c** MLP 35439, paratype, exterior of right valve showing almost complete anterior auricle and byssal fasciole. **d** MLP 35412, paratype, oblique view of left valve exterior showing curved anterior auricle. **e** MLP 35405, paratype, right valve inner view of ligamental area. **f** MLP 35411, paratype, right valve inner view of ligamental area. **g** MLP 35412, paratype, detail of left valve ornamentation. **h** MLP 35431, detail of inner (?) surface of right valve showing faint radial lines. Scale bar 1 mm

anterior auricle, which is not evident in *Huncalotis*. Despite these differences, which justify assignment to two different genera, the shells of both taxa appear morphologically very similar and thus may be closely related.

Pleuronectites has a time range from the Middle to Late Triassic (Anisian to Carnian, see Hayami 1975; Waller 2006) and an apparently wide geographical distribution in the Tethys and circum-Pacific areas (Waller and Stanley

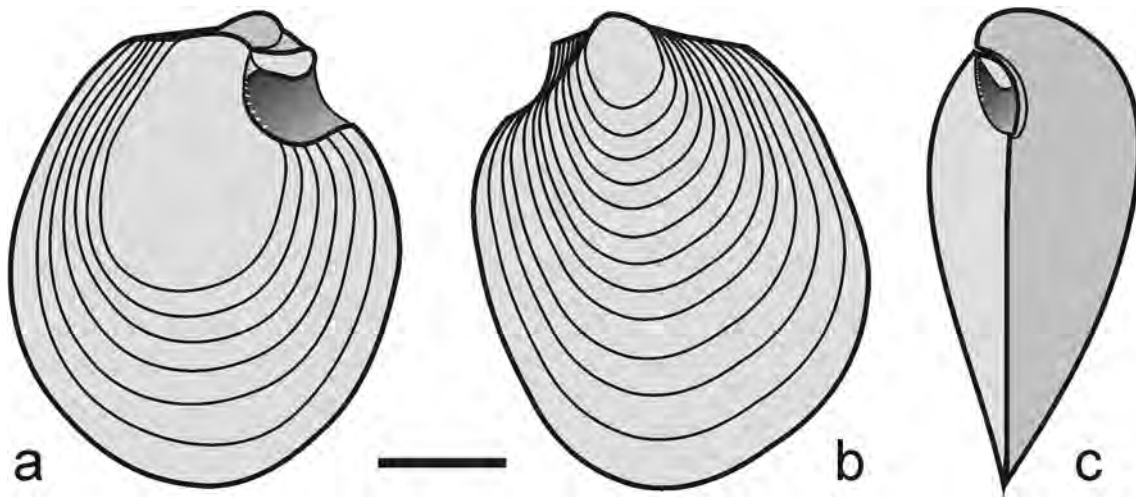


Fig. 5 *Huncalotis millaini* sp. nov., reconstruction of external features. **a** Right valve; **b** left valve; **c** anterior view. Scale bar 1 cm

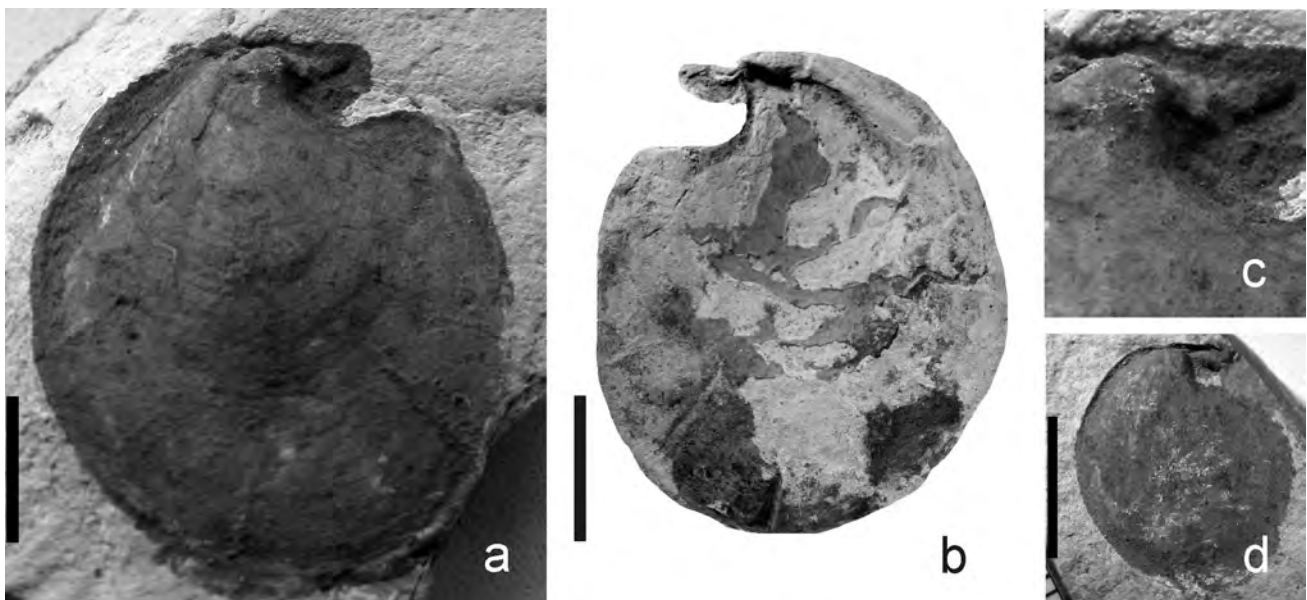


Fig. 6 *Huncalotis? peruana* (Rivera), syntypes. **a, c** Composite mould of right valve, ING530a; **b** inner view of right valve, ING530b; **d** internal mould of right valve, ING530c. Scale bars 1 cm

2005; Waller 2006; Ros et al. 2014, fig. 36), although Hautmann (2010) is sceptical regarding most assignments to *Pleurnectites* in the literature, apart from those referring to the type species, and thus its range could be constrained. The Lower Triassic *Pleurnectites meeki* Newell and Boyd 1995 was regarded as an entoliid rather than a pectinid by Waller (in Waller and Stanley 2005), because it lacks a ctenolium.

There is an earlier record of a *Pleurnectites* species from the Late Jurassic of NE Africa (*P. aubryi* Douvillé 1886: 228, pl. 12, fig. 3), but this was subsequently referred to *Eopecten*, see Stefanini (1939), Cox (1965) and Kiessling et al. (2011). Consequently, if *Pleurnectites* and *Huncalotis* are phylogenetically related, it is evident that there is a huge time gap between them (Carnian–Tithonian, i.e. more than 80 Ma). Some of the characters they share, such as the inequivalve shells, persistent functional ctenolium and lack or poor development of radial ribbing, are considered as derived ones within Pectinoidea (Waller 2006: 332), whilst others, such as a ligamental area with bourrelets, are clearly primitive (Hautmann 2004, 2010). Already Allasinaz (1972: 205, 323) regarded the ligamental area of *Pleurnectites* as of a peculiar type, intermediate between what he called “*Aviculopecten*-like” ligament (=alivincular-areate sensu Hautmann 2004) and “*Pecten*-like” ligament (=alivincular-alate sensu Hautmann 2004). Hautmann (2010) discussed this question in detail: he mentioned the narrow bourrelets in *Pleurnectites*, but stated that the resilifer is entirely internal and thus referred this ligament to his alivincular-alate type; yet he recognized that the narrow bourrelets may indicate derivation from an ancestor with an alivincular-areate ligament. Nevertheless, details of the ligamental area are difficult to evaluate phylogenetically since they are imperfectly known or unknown in many early Mesozoic pectinoid species.

On the other hand, the morphological similarity between *Pleurnectites* and *Huncalotis* may be just due to convergence, which is known in other bivalves and is seemingly common in pectinoids, to the point of being “a major problem for reconstructing their phylogenetic history” (Carter and Hautmann 2011: 467); see Alejandrino et al. (2011) and Serb et al. (2011) for a discussion of this aspect in living Pectinidae which suggests that iterative morphological evolution may be more prevalent in the family than previously thought. More and better-preserved specimens of the new genus are needed to adequately address this question; among the pending information, the microstructure of the shell may be significant (Carter and Hautmann 2011), but unfortunately the available material is not suitable to perform microstructure analysis. A similar relationship involving homoeomorphy in epibyssate bivalves separated in time was proposed by Kemper (1982) for the pair of monotoidean genera *Buchia* Rouillier 1845

(extinguished in the Hauterivian) and *Aucellina* Pompeckj, 1901 (known from the late Barremian).

The genus *Periclarara* Li and Ding (1981), from the Middle Triassic of southern China, was referred to the Pectinidae due to the presence of a ctenolium-like structure on the right valve (see Chen and Komatsu 2002, fig. 2 and pls. 1–3), but differs from *Huncalotis* by having a small subcircular shell with radial ornamentation, by the smaller right anterior auricle and narrow byssal gape.

In fact, some key characters of *Huncalotis*, such as the inequivalve shell, the poorly defined left valve auricles, the lack of radial ornamentation and the right anterior auricle ventrally curved towards the interior of the left valve, allow comparison with some buchioidean and oxytomoidean genera. *Huncalotis* general shell shape and ornamentation are similar to those of *Malayomaorica* (Jeletzky 1963), a Late Jurassic Indo-Pacific genus. However, *Huncalotis* has a ctenolium, lacks radial ornament and differs in having a clearly defined left anterior auricle, and in details of the ligamental area. The regular commarginal ornamentation of *Huncalotis millaini* is reminiscent of certain species of *Buchia* of similar age, such as *B. keyserlingi* (Trautschold) as figured by Surlyk and Zakharov (1982, pl. 76, figs. 2, 3), but all other significant shell features (e.g., ligament, auricle shape and size) are quite different. The lack of radial ornamentation, and the large right anterior auricle with wide byssal fasciole distinguish species of this new genus from those of *Aucellina* Pompeckj, some of which present a young shell with disc-type pseudoctenolium (see illustrations of this feature in Kemper 1982, pls. 1, 2).

Other comparable genera are those traditionally referred to the subfamily Camptonectinae, and thought by some authors to have evolved from *Pleurnectites* (see for instance Johnson 1984: 113). Waller and Marincovich (1992) emended the diagnosis of this subfamily to include pectinids with a distinctly concave antero-dorsal margin of the disc in lateral view, and with a wide range of shell ornamentation (smooth, antimarginal, radial, commarginal, or combination of these), and placed *Pleurnectites* within it, though later (Waller and Stanley 2005) it was referred to the Chlamydiae. Nevertheless, the widely separated commarginal step-like ornamentation of *Huncalotis* (Fig. 4g) is quite different from the commarginal flanges in Camptonectinae, and similarities between *Huncalotis* and members of this subfamily are regarded as convergent. However, the ornamentation of some smooth or commarginally sculptured *Camptochlamys* species may be compared to *Huncalotis*, for instance the boreal species *C. obscurus* (Sowerby; see Johnson 1984, pl. 4, figs. 17–22, 24, 25) from the Aalenian to Hauterivian of Europe, or *C. alaskaensis* Waller and Marincovich (1992, figs. 4.1–4.16), from the Late Cretaceous of Alaska. Large species referred to *Camptonectes* (*Boreionectes*) by

Zakharov (1966, pls. 8–15), from the Late Jurassic–Early Cretaceous of Siberia, have a somewhat similar commarginal ornamentation, and *Canadonectites paucicostatus* Aberhan (1998, pl. 13, figs. 1, 2, 3, text-fig. 7), from the Sinemurian–Pliensbachian boundary of western Canada, has a mostly smooth shell, but all these species have more equilateral valves, much better delimited auricles on both valves and always at least traces of radial or antimarginal ornamentation.

***Huncalotis millaini* sp. nov.**

Figures 3, 4, 5, 9

Etymology. Dedicated to the Millaín Mapuche community that inhabits the region around Huncal.

Type material. **Holotype:** MLP 35429a, nearly complete right valve (Figs. 3o, 4a); **paratypes:** specimens MLP 35402, 35403, 35405, 35407, 35409–35415, 35417, 35420, 35421, 35423, 35426–35428, 35429b, 35430, 35433, 35434, 35436, 35439.

Type locality and horizon: Vaca Muerta Formation, late Tithonian; south of Arroyo Coihueco near Huncal, Neuquén, Argentina (loc. 3 in Fig. 1c).

Material. Approximately 130 specimens: 40 right valves, 67 left valves, 5 specimens with articulated valves and numerous fragments (MLP 35402 to 35441) from three localities near Huncal and one locality near Rahuecó (Fig. 1). Doubtfully included: MLP 32689 (right valve), and MLP 32699 (left valve), from the Vaca Muerta Formation at Tres Esquinas, southern Mendoza Province, collected by D. Kietzmann.

Diagnosis. Large (up to 70 mm high) *Huncalotis* with regular commarginal step-like costae on both valves, but more pronounced on left valves; both valves internally smooth.

Description. Large inequivalve shells, higher than long, moderately inflated, with left valve more convex than right one (Fig. 3i). Hinge line straight and long, about half of the total shell length. Narrow and low prosogyrous umbones centrally placed. Right valve disc prorescent, antero-dorsal margin concave forming a deep byssal notch, meeting the evenly convex ventral margin at a right angle (Fig. 3h, n); posterior margin only slightly convex. Dorsal part of anterior margin in the left valve slightly concave in lateral view (Fig. 3c).

The left valve has blunt anterior and posterior auricles, without a clear separation from the disc. The left valve anterior auricle is not on the commissural plane, but has a convex outer surface, probably to accommodate part of the right anterior auricle (Figs. 3a, 4d, 5c), and lacks a distinct byssal sinus. The right valve has a very deep and wide

byssal notch and a well-defined, spatulate, long and narrow anterior auricle with a distinct byssal fasciole (Figs. 3n, 4c, 9m). The dorsal margin of this auricle protrudes distally above the hinge axis, but not forming a prominent auricular scroll; the dorsal part of this auricle is on the commissural plane, but the ventral part is curved inwards (Figs. 3m, 5c, 9m). The shell has a ctenolium originating early in ontogeny and consisting in a row of small stout spines or denticles along the suture and the ventral byssal notch shell margin, from the umbo to reach approximately the length of the auricle (Figs. 4a, b, 9j–m). In the best-preserved specimens denticles are curved and hook-like, whilst in most specimens their tips are worn. Up to 10 inactive denticles on the suture close to the byssal fasciole, and between 6 and 10 active denticles on the free ventral margin of the byssal notch are preserved in the largest specimens. The ctenolium is preserved in about one-third of the available right valves of the whole size range and all preservation types. The right posterior ear is indistinct and short (Fig. 4c).

Left and right valves ornamented with regularly spaced commarginal, flat-topped, step-like costae (Fig. 4g). Density of ornament varies from 2 to 4 costae per cm; most commonly 3 costae per cm occur. The shell lacks radial ornamentation, but some decorticated shells show a faint radial lineation from inside (Fig. 4h). Inner shell surface and margin smooth (Fig. 3p).

Ligamental area only visible in a few specimens. Right valve hinge plate offset from commissural surface (inclined about 60°). Central, deep and short, very slightly prosocline, triangular resilifer (Fig. 4e, f), with regularly curved ventral margin which slightly extends into the body cavity and is supported by a low but strong internal shell thickening which can be regarded as a resilial buttress. Posterior to the ligamental pit there is a narrow triangular, long and longitudinally striated area (posterior bourrelet, Fig. 4f). All specimens with a preserved ligamental area are fractured along a line parallel to the posterior margin of the resilial pit, but a very low thickening of the posterior area at the resilifer border seems to be present (Fig. 4e), although the material is not adequately preserved to identify this structure as a resilial tooth (in the sense of Waller 1986). A similar flat triangular area (anterior bourrelet) is imperfectly seen anterior to the resilifer. The left valve ligamental area is unknown.

No muscle scars could be identified.

Dimensions. Large shells reach about 7 cm high and 5.5 cm long. Table 1 includes measurements of well-preserved types; see Fig. 7 for abbreviations. In the shell pavements all sizes categories are preserved; see Fig. 7c.

Comparison. There are several previous references of material from South America which should be taken into

Table 1 Measurements of the best-preserved specimens (in mm)

MLP	Type	Valve	L	H	pdl	adl	W	Costae/2 cm
35402	Paratype	l ext	35.00	48.15	11.30	5.10		4
35403	Paratype	l ext	32.10	40.95	11.50	5.00		5
35409	Paratype	r ext	48.90	57.65	12.60	(9.00)		6
35410	Paratype	l ext	32.15	45.10	13.20	10.55		8
35412	Paratype	l ext	34.35	38.35	12.30	6.70		7
35414	Paratype	r int	41.60	48.10	8.69	11.55		
35414	Paratype	l ext	38.90	48.45	12.05	6.89		7
35417	Paratype	r ext	27.50	27.90	4.30	5.50		7
35420	Paratype	l ext	55.45	68.20				5
35421	Paratype	l ext	49.00	(55.00)	13.00	7.65		6
35423	Paratype	b ext	40.75	45.10			13.70	5
35423	Paratype	l int	35.00	(48.00)			8.10 (lv)	
34528	Paratype	r int	19.55	20.95	4.55	5.50		
35429a	Holotype	r ext	35.85	35.20	4.95	7.00		
35430	Paratype	l ext	32.80	43.45	7.90	5.10		
35434	Paratype	r int	14.30	16.50	2.95	4.00		
35436	Paratype	r ext	44.05	45.10	5.00	8.20		
35439	Paratype	r ext	51.50	59.15	7.35	9.00	8.60 (rv)	

For abbreviations see Fig. 7. Data between parentheses indicate estimated dimensions in incomplete specimens. Valve: *l* left, *r* right, *b* both, *ext* outer view, *int* inner view. Commarginal costae were counted along a 2-cm radial line in the middle portion of the shell

account for comparison, although illustrations are very poor. The new species is very similar in shape to specimens described as *Obliquipecten peruanum* Rivera (1951: 48–49, pl. 6, figs. 6, 7, 8; previously described by Lisson 1907: 31, pl. 3, fig. 4, as *Synclonema* sp.; later referred to *Arctotis* by Romero et al. 1995: 122; see Fig. 6 here), from Tithonian–Berriasian beds near Lima, Peru, and potentially also to *Pseudoavicula?* sp. from equivalent beds in Colombia (Royo y Gómez 1945: 220, pl. 29, fig. 2). However, in these species, the ligamental characters are unknown, the presence of ctenolium is not clear, and also the commarginal ornamentation is more regular in the material described herein. The type specimens of *Obliquipecten peruanum* are also smaller and have a relatively shorter hinge line. All these features suggest that they belong to a different species, but probably should be included in the same genus. It is interesting to mention that Rivera (1951) referred her new species *O. peruanum* only provisionally to the Palaeozoic genus *Obliquipecten*, and stated that it most probably belonged to a new genus. In the specimen illustrated as *Aucella* aff. *blanfordiana* Stoliczka by Romero et al. (1995, pl. 17, fig. 2), which also comes from Tithonian–Berriasian beds near Lima, the ornamentation of the disc seems to consist of commarginal folds rather than regular steps.

The species here described is remarkably similar to Triassic species referred to *Pleuronectites*, especially to its type species, *Pleuronectites laevigatus* Schlottheim (1820: 217; Schlottheim 1823: 111, pl. 35, fig. 2; Philippi 1900,

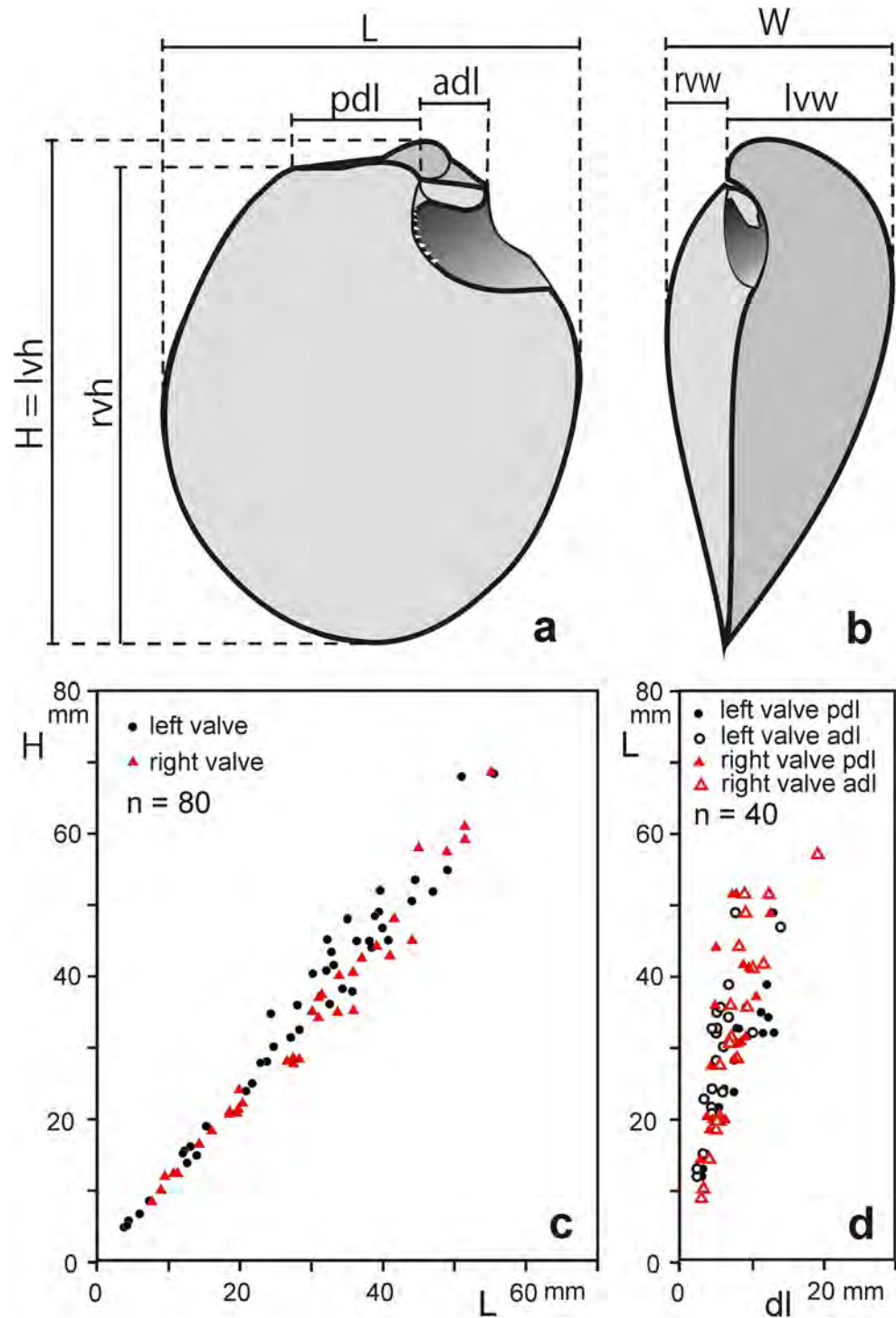
t-figs. 1, 1a; Salomon 1900, pl. 14, figs. 1, 2), with regard to shell shape, deep byssal notch with ctenolium and general shape of right anterior auricle. However, *Pleuronectites* has larger, more inequivalve shells, lacks commarginal ornamentation and occasionally has low radial costae; it also differs from *Huncalotis millaini* sp. nov. in its larger posterior auricles, which are clearly separated from the disc (Hagdorn 1995; Hautmann 2010, fig. 1). Several other nominal species of *Pleuronectites* were either regarded as synonyms of *P. laevigatus* or referred to other genera (see Waller and Stanley 2005; Hautmann 2010). *Pleuronectites meeki* Newell and Boyd (1995: 72, fig. 52), from the Early Triassic of Nevada, USA, has a much smaller shell with wider anterior auricles without byssal fasciole; the ctenolium is unknown; the species probably does not belong to *Pleuronectites* (see Waller and Stanley 2005, p. 39).

Other comparisons were mentioned in the generic discussion above.

Preservation

There are two main preservation modes at the studied localities (Fig. 8b). Most of the material comes from shell pavements, with equally abundant right and left valves, and only preserved at levels with “beef” (Fig. 9). Some specimens were found in the outer part of large calcareous concretions within the black shales (Fig. 8e, f).

Fig. 7 Measurements of the dimensions of the shell of *Huncalotis*. **a** Right valve view; **b** anterior view; **c**, height/length relationship of right and left valves; **d**, length/dorsal length relationship of right and left valves. *L* maximum length, *H* maximum height, *W* total width (both valves), *adl* length of anterior auricle, *pdl* length of posterior dorsal margin, *lvh* left valve height, *rvh* right valve height, *rvw* right valve width, *lvw* left valve width



Shales with “beef”

Within the Vaca Muerta Formation there are several levels with fibrous calcite veins within a 30–50 m thickness of black shale (Fig. 8b-1). The veins consist of calcite crystals arranged perpendicular to the plane of the vein. They have been reported to contain large amounts of bitumen at La

Valenciana, Mendoza (Parnell and Carey 1995; Parnell et al. 2000; Cobbold and Rodrigues 2007) and were recently studied in a tectonic context (Rodrigues et al. 2009; Cobbold et al. 2013; Zanella et al. 2015).

These structures are known as “shales with beef” or “beef in shale” (Lang et al. 1923; David 1952; Bonte 1952; Tarney and Schreiber 1977; Stoneley 1983) and are



Fig. 8 Taphonomy. **a** Huncal locality 2 seen from locality 3. **b** Detail of black shales of the Vaca Muerta Formation at locality 4, showing some “beef” levels (1) and one concretion level (2); hammer for scale. **c** Upper surface of a “beef” level lacking shelly fauna; pen is 15 cm long. **d** Calcite “beef” being used as building stone at Huncal, Neuquén, showing the two (upper and lower) “beef” zones. **e** Big calcareous concretion with a large *Substeueroceas* cf.

S. striolatissimum (Steuer) eroded external mould and at least 11 specimens of *Huncalotis millaini* n. sp. (arrows), probably initially byssally attached to the ammonite umbilical region and periphery; penknife is 9 cm long. **f** Detail of **e**, slightly displaced valves of probably the same specimen; pen is 8 mm thick, *l* external view of dorsal portion of left valve, *r* internal view of right valve



Fig. 9 Preservation of *Huncalotis millaini* sp. nov. in sandwich concretions; **a–c** MLP 35406, upper, lower and lateral views of shell pavement preserved in beef; the slab contains convex-up (x) and concave-up (v) shells, shell (s) and internal moulds (im) on top of the lower beef zone, secondary moulds (sm) at the bottom of the lower beef zone; **d, e** MLP 35404, recrystallized right valve, showing detail (e) of calcite crystals, some of them zoned; **f** MLP 35403, paratype, left valve showing radial cracks (white arrows) due to compaction; **g** MLP 35406, right valve showing part preserved as an internal mould (im) on the beef and part as shell (s); **h, i** MLP 35413, paratype, left valve in dorsal (h) and lateral (i) views showing part

preserved as a subinternal mould (sim) on the lower beef zone, part as recrystallized shell (s) on the median suture between the two beef zones and part as a secondary mould (sm) on top of the upper beef zone preserving a blurred replica of the shell; broken line in **h** indicates median suture of beef; **j–m** ontogenetic sequence (scale 1 mm) of differently preserved right valves showing functional ctenolium at all stages and progressive curvature of anterior shell margin, **j** MLP 35430a (paratype), **k** MLP 35430b (paratype), **l** MLP 35426a, **m** MLP 35439 (paratype). Graphic scales 10 mm, except in **e** and **j–m** 1 mm

widespread in both space and time, and not limited to fully marine sediments (see for instance Hudson and Andrews 1987). It is agreed that they were formed by the presence of layers of overpressurized fluids (Sellés-Martínez 1996; Cobbold and Rodrigues 2007), but controversy still remains as to the time of formation, and several mechanisms have been proposed (see discussion in Marshall 1982). If overpressuring occurs during burial and compaction of the shale, the source of the calcite should be within the shales themselves (Stoneley 1983), but overpressure can also occur relatively late during diagenesis as a result of post-burial uplift and unloading of the sediments (Marshall 1982). In petroleum source rocks, such as the Vaca Muerta Formation, this type of fibrous calcite veins may indicate primary oil migration pathways (Mann 1994; Parnell et al. 2000). Calcite “beef” beds are widespread in the Neuquén Basin, but appear to be limited to certain levels of the *Substeuero-ceras koeneni* Zone in the studied area. “Beef” levels are sometimes as regular and extensive as to be quarried by local people for building (Fig. 8d).

The most common preservation of the described species is on one internal surface of these calcite levels, which occur within the black shale (see Rodrigues et al. 2009, fig. 7a, b). Potentially, the shell pavements acted as an anisotropic surface to facilitate beef formation on both sides (Cobbold and Rodrigues 2007; Rodrigues et al. 2009, fig. 7; Cobbold et al. 2013), and the surface is pushed aside by calcite crystals (Fig. 9a–c, h–i). The thickness of the calcite crust varies between 1 and 100 mm, and preserves the surface structure (such as ripples, see Fig. 8c, or even shell ornamentation, see Fig. 9i) of bivalve and ammonite shells (see Rodrigues et al. 2009, fig. 7). Even in the thickest examples the underside shows a blurred replica of the shell mould (Fig. 9b). Fossil impressions on such calcite veins have also been reported from a wide range of ages and locations (i.e., Eocene fish in Brown 1954; Cambrian trilobites in Seilacher 2001; Early Jurassic ammonites in Marshall 1982). This peculiar preservation of the material is superficially similar to the padded trilobites, such as those from the Middle Cambrian Wheeler Shales of Utah (Bright 1959; Seilacher 2001). In contrast with these trilobite examples, the layer spreads beyond the margin of the shells, encompassing the whole sedimentary surface. The orientation of the calcite crystals is not controlled by the morphology of the shell, and calcite grows irrespective of whether the convex side of the shell is upwards or downwards in original position (Fig. 9a). In this respect, the “beef” levels from the Vaca Muerta Formation can be regarded as equivalent to the “calcite layers” which occasionally preserve fossils and have been termed “sandwich concretions” (Seilacher 2001).

Radial fractures, oriented at right angles to the shell margins (Fig. 9f), were probably produced during

compaction by cracking of a convex valve lying flat and concordant to the bedding (Müller 1979; analogous to “splayed pattern” in Alexander and Gibson 1993). These fractures are present in both left and right valves (Fig. 9f, g).

In several specimens the original shell was replaced or overgrown by disordered prismatic, long, hexagonal calcite crystals, some of them showing concentric zonal growth (Fig. 9d, e).

According to Rodrigues et al. (2009: 701), the original shell is seen in thin sections at the suture, and the calcite “fibres project the inner or outer moulds of the shells onto the outer surfaces of the beef”; “where the fibres are oblique, the moulds are offset laterally across the vein, by exactly the projected amount”; and “the fibres are not in optical and textural continuity with the original shell”. The presence of displaced fossils in the Vaca Muerta Formation indicates that the calcite veins grew into relatively plastic sediments (Marshall 1982), but this should have occurred after compaction, since the fossil shells were already fractured when the veins formed.

Calcareous concretions

Several complete specimens from the Huncal and Rahuec6 localities occur on the external surface of very large calcareous concretions (Fig. 8b–2). These specimens show the actual shell convexity and have no radial fractures (Figs. 3i, m, n, 8f).

Occasionally, *Huncalotis* valves are found on and around large ammonite shells, such as the illustrated specimen (Fig. 8e, f), which is determined as *Substeuero-ceras* cf. *striolatissimum* (Steuer). Preservation of articulated or slightly displaced right and left valves of the same specimen is common in this context (Fig. 8f).

Palaeoecology

Huncalotis millaini was an epifaunal pleurothetic bivalve. Its mode of life was most probably epibyssate throughout life, as suggested by the large byssal notch with functional ctenolium present at all growth stages. The strength of the ctenolium is usually correlated with the strength and persistence of byssal attachment (Waller 1984). Some specimens of *Huncalotis* were found on or near large ammonites, concentrated in both the umbilical and ventral regions of the ammonite shell, in a position indicating an epifaunal life habit on living ammonites (Fig. 8e). The largest *Huncalotis* specimens are positioned near the ammonite umbilicus, suggesting sequential epifaunal fixation during ammonite ontogeny. No bivalves occur on the flanks of the ammonites, which would have to be expected if the large ammonite would have acted as a “benthic

island". The proposed life habit of *Huncalotis* is similar to the bivalves of the *Torquatisphinctes*–oxytomid assemblage from the Late Jurassic of the Antarctic Peninsula (Doyle and Whitham 1991), the lower Toarcian Posidonienschiefer of SW Germany (Schmid-Röhl and Röhl 2003) or to *Pleuronectites laevigatus* (Schlotheim) on nautiloid shells from the Triassic of southern Germany (Klug and Lehmkuhl 2004), i.e. epibyssate and possibly pseudoplanktonic.

The extreme abundance of pectinids at certain levels and complete absence at others is thought to be a result of the preservation enhanced by the calcite beef levels. Nevertheless, the crowded shell pavements, with a wide range of sizes and both left and right valves represented, can be interpreted as the result of an opportunistic strategy. These clusters have very low diversity (are nearly monospecific) but show high abundance of complete isolated valves of all sizes. Left valves are clearly more abundant than right ones. Some epibyssate Pectinida (among them *Buchia* and *Aucellina*) were regarded as opportunists (Kauffman 1976; Hallam 1977; MacDonald 1982; Sha and Fürsich 1994), even able to tolerate low oxygen levels. The black shales of the Vaca Muerta Formation were deposited in anaerobic to dysaerobic bottom conditions (Legarreta et al. 1991; Kietzmann et al. 2014), comparable to the environment suggested for beds of the Nordenskjöld Formation from Antarctica containing the already mentioned *Torquatisphinctes*–oxytomid assemblage (Doyle and Whitham 1991).

In both the shell pavements and the calcareous concretions the only accompanying fauna are large ammonites and a few undeterminable oysters, which encrusted the ammonites. *Huncalotis* shells do not show any sign of encrusting or other traces of epizoan organisms, and they also lack predation marks.

Conclusions

The new pectinoid genus *Huncalotis* from South America is described based on abundant and well-preserved material of late Tithonian age from the Neuquén Basin in Argentina. *Obliquipecten peruanus* Rivera from Tithonian–Berriasian beds in Peru is tentatively included in the new genus, which thus probably had a wide geographical distribution but a short stratigraphical range.

Huncalotis species lived fixed by a strong byssus throughout life; evidence suggests an epibyssate life habit.

The type species, *H. millaini* sp. nov., has a peculiar set of shell characters, some of which are used to characterize different bivalve families and even superfamilies. The presence of both a functional ctenolium at all growth stages and an alivincular ligament points to relationships with the

Pectinoidea. Nevertheless, the ligament area, though incompletely preserved, seems to be intermediate between alivincular-areate, typical of Aviculopectinoidea, and alivincular-alate, characteristic of Pectinoidea. Furthermore, other characters, such as the poorly defined left valve auricles, the lack of radial ornamentation and the right anterior auricle ventrally curved towards the interior of the left valve, allow comparison with some buchioidean and oxytomoid genera. This combination of primitive and derived key characters is of considerable importance for analysis of bivalve phylogeny, and its discussion in that context may add to our knowledge about early pectinoid evolution.

The inequivalve shells with regular commarginal ornamentation, the long and narrow right anterior auricle with a functional ctenolium and very large byssal gape resemble the shells of the Middle Triassic *Pleuronectites*, from which however it is separated in time by more than 80 million years. If their morphological resemblance is due to phylogenetic relationships, *Huncalotis* could be regarded as a Lazarus taxon within Pleuronectitidae, but the alternative possibility that shell similarities result from homoeomorphic convergence cannot be dismissed.

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References

- Aberhan, M. 1998. Early Jurassic Bivalvia from western Canada. Part I. subclasses Palaeotaxodonta, Pteriomorpha, and Isofilibranchia. *Beringeria* 21: 57–150.
- Aguirre-Urreta, B., D.G. Lazo, M. Griffin, V. Vennari, A.M. Parras, C. Cataldo, R. Garberoglio, and L. Luci. 2011. Megainvertebrados del Cretácico y su importancia bioestratigráfica. In: *Geología y Recursos Naturales de la Provincia del Neuquén*, eds. H.A. Leanza, C. Arregui, O. Carbone, J.C. Daniela, and J.M. Vallés, 18° Congreso Geológico Argentino, Neuquén, Relatorio, pp. 465–488.
- Alejandrino, A., L. Puslednik, and J.M. Serb. 2011. Convergent and parallel evolution in life habit of the scallops (Bivalvia: Pectinidae). *BMC Evolutionary Biology* 11: 164–172.
- Allasinaz, A. 1972. Revisione dei Pettinidi triassici. *Rivista Italiana di Paleontologia* 78(2): 189–428.
- Alexander, R.R., and M.A. Gibson. 1993. Paleozoic brachiopod autecology based on taphonomy: example from the Devonian Ross Formation of Tennessee (USA). In: *Brachiopod and Molluscan Biogeography, Palaeoecology and Stratigraphy*, ed.

- M.O. Manceñido, *Palaeogeography, Palaeoclimatology, Palaeoecology* 100(1–2): 25–35.
- Beurlen, K. 1944. Beiträge zur Stammesgeschichte der Muscheln. *Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Abteilung der Bayerischen Akademie der Wissenschaften zu München* 1944(1–2): 133–145.
- Bonte, A. 1952. Réflexions sur le “beef”, à propos d’une note de M.L. David. *Compte Rendu Sommaire des Séances, Société Géologique de France* 7–8: 110–112.
- Bright, R.C. 1959. A paleoecologic and biometric study of the middle Cambrian trilobite *Elrathia kingii* (Meek, Utah). *Journal of Paleontology* 33(1): 83–98.
- Brown, R. 1954. How does cone-in-cone material become emplaced? *American Journal of Science* 252: 372–376.
- Carter, J.G., and M. Hautmann. 2011. Shell microstructure of the basal pectinid *Pleurometites laevigatus*: implications for pectinoid phylogeny (Mollusca: Bivalvia: Pteriomorpha). *Journal of Paleontology* 85(3): 464–467.
- Carter, J.G., C.R. Altaba, L.C. Anderson, R. Araujo, A.S. Biakov, A.E. Bogan, D.C. Campbell, M. Campbell, J. Chen, J.C.W. Cope, G. Delvene, H.H. Dijkstra, Z. Fang, R.N. Gardner, V.A. Gavrilova, I.A. Goncharova, P.J. Harries, J.H. Hartman, M. Hautmann, W.R. Hoeh, J. Hylleberg, B. Jiang, P. Johnston, L. Kirkendale, K. Kleemann, J. Koppka, J. Kříž, D. Machado, N. Malchus, A. Márquez-Aliaga, J.-P. Masse, C.A. McRoberts, P.U. Middelfart, S. Mitchell, L.A. Nevesskaja, S. Özer, J. Pojeta Jr, I.V. Polubotko, J.M. Pons, S. Popov, T. Sánchez, A.F. Sartori, R.W. Scott, I.I. Sey, J.H. Signorelli, V.V. Silantiev, P.W. Skelton, T. Steuber, J.B. Waterhouse, G.L. Wingard, and T. Yancey. 2011. A synoptical classification of the Bivalvia (Mollusca). *University of Kansas Paleontological Contributions* 4: 1–47.
- Carter, J.G., P.J. Harries, N. Malchus, A.R. Sartori, L.C. Anderson, R. Bieler, A.E. Bogan, E.V. Coan, J.C.W. Cope, S.M. Cragg, J.R. García-March, J. Hylleberg, P. Kelley, K. Kleemann, J. Kříž, C. McRoberts, P.M. Mikkelsen, J. Pojeta jr., I. Temkin, T. Yancey, and A. Zieritz. 2012. Part N, Revised, Volume 1, Chapter 31: Illustrated Glossary of the Bivalvia. *Treatise Online* (Kansas University Paleontological Institute) 48: 1–209.
- Chen, J.-H., and T. Komatsu. 2002. So-called Middle Triassic “Claraia” (Bivalvia) from Guangxi. *South China. Acta Palaeontologica Sinica* 41(3): 434–447.
- Cobbold, P.R., and N. Rodrigues. 2007. Seepage forces, important factors in the formation of horizontal hydraulic fractures and bedding-parallel fibrous veins (‘beef’ and ‘cone-in-cone’). *Geofluids* 7(3): 313–322.
- Cobbold, P.R., A. Zanella, N. Rodrigues, and H. Loseth. 2013. Bedding-parallel fibrous veins (beef and cone-in-cone): World-wide occurrence and possible significance in terms of fluid overpressure, hydrocarbon generation and mineralization. *Marine and Petroleum Geology* 43: 1–20.
- Cox, L.R. 1965. Jurassic Bivalvia and Gastropoda from Tanganyika and Kenya. *Bulletin of the British Museum (Natural History) Geology. Supplement* 1: 1–213.
- Damborenea, S.E. and H.A. Leanza. 2004. Bivalvos monotoides tithonianos de la Formación Vaca Muerta, norte de Neuquén, Argentina. *Ameghiniana* 41, *Suplemento Resúmenes*: 9R.
- David, L. 1952. Présence de la structure “beef” et “cone-incone” dans le Crétacé de l’Est-Constantinois (Algérie). *Comptes Rendus de la Société Géologique de France* 3: 51–52.
- Douvillé, H. 1886. Examen des fossils rapportés du Choa par M. Aubry. *Bulletin de la Société Géologique de France*, 3^{ème} sér., 14: 223–241.
- Doyle, P. and A.G. Whitham. 1991. Palaeoenvironments of the Nordenskjöld Formation: an Antarctic Late Jurassic-Early Cretaceous black shale-tuff sequence. In: *Modern and Ancient Continental Shelf Anoxia*, eds. R.V. Tyson and T.H. Pearson, *Geological Society of London Special Publication* 58: 397–414.
- Gray, J.E. 1854. A revision of the arrangement of the families of bivalve shells (Conchifera). *The Annals and Magazine of Natural History (series 2)* 13(77): 408–418.
- Gulisano, C.A. and A.R. Gutiérrez-Pleimling. 1995. Field Guide. The Jurassic of the Neuquén Basin, a) Neuquén Province. *Publicación Dirección Nacional del Servicio Geológico* 158 (=Serie E, *Asociación Geológica Argentina*, 2): 1–111.
- Gulisano, C.A., A.R. Gutiérrez Pleimling, and R.E. Digregorio. 1984. Análisis estratigráfico del intervalo Tithoniano-Valanginiense (Formaciones Vaca Muerta, Quintuco y Mulichinco) en el suroeste de la provincia de Neuquén. *9 Congreso Geológico Argentino. Actas* 1: 221–235.
- Hagdorn, H. 1995. Farbmuster und Pseudoskulptur bei Muschelkalzfossilien. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 195 (Seilacher Festschrift): 85–108.
- Hallam, A. 1977. Jurassic bivalve biogeography. *Paleobiology* 3: 58–73.
- Hautmann, M. 2004. Early Mesozoic evolution of alivincular bivalve ligaments and its implications for the timing of the “Mesozoic marine revolution”. *Lethaia* 37: 167–172.
- Hautmann, M. 2010. The first scallop. *Paläontologische Zeitschrift* 84(2): 317–322.
- Hayami, I. 1975. A systematic survey of the Mesozoic Bivalvia from Japan. *Bulletin of the University Museum, University of Tokyo* 10(1–249): 1–10.
- Hudson, J.D., and J.E. Andrews. 1987. The diagenesis of the Great Estuarine Group, Middle Jurassic, Inner Hebrides, Scotland. In: *Diagenesis of Sedimentary Sequences*, ed. J.D. Marshall, *Geological Society of London Special Publication* 36: 259–276.
- Jeletzky, J.A. 1963. *Malayomaorica* gen. nov. (Family Aviculopectinidae) from the Indo-Pacific Upper Jurassic; with comments on related forms. *Palaeontology* 6(1): 148–160.
- Johnson, A.L.A. 1984. The palaeobiology of the bivalve families Pectinidae and Propeamussiidae in the Jurassic of Europe. *Zitteliana* 11: 1–235. Taf. 1–11.
- Kauffman, E.G. 1976. Deep-sea Cretaceous macrofossils: Hole 317A, Manihiki Plateau. In: Schlanger, S.O., Jackson, E.D. et al. (Eds.), *Initial Reports of the Deep Sea Drilling Project*, 33: 503–535.
- Kemper, E. 1982. Die Aucellinen des Apt und Unter-Alb Nordwestdeutschlands. *Geologisches Jahrbuch* A65: 579–595.
- Kiessling, W., D.K. Pandey, M. Schemm-Gregory, H. Mewis, and M. Aberhan. 2011. Marine benthic invertebrates from the Upper Jurassic of northern Ethiopia and their biogeographic affinities. *Journal of African Earth Sciences* 59: 195–214.
- Kietzmann, D.A., and V.V. Vennari. 2013. Sedimentología y estratigrafía de la Formación Vaca Muerta (Tithoniano-Berriasiano) en el área del cerro Domuyo, norte de Neuquén, Argentina. *Andean Geology* 40: 41–65.
- Kietzmann, D.A., J. Martín-Chivelet, R.M. Palma, J. López-Gómez, M. Lescano, and A. Concheyro. 2011. Evidence of precessional and eccentricity orbital cycles in a Tithonian source rock: the mid-outer carbonate ramp of the Vaca Muerta Formation, Northern Neuquén Basin, Argentina. *AAPG Bulletin* 95: 1459–1474.
- Kietzmann, D.A., R.M. Palma, A.C. Riccardi, J. Martín-Chivelet, and J. López-Gómez. 2014. Sedimentology and sequence stratigraphy of a Tithonian-Valanginian carbonate ramp (Vaca Muerta Formation): a misunderstood exceptional source rock in the Southern Mendoza area of the Neuquén Basin, Argentina. *Sedimentary Geology* 302: 64–86.
- Klug, C., and A. Lehmkuhl. 2004. Soft-tissue attachment structures and taphonomy of the Middle Triassic nautiloid *Germanonautilus*. *Acta Palaeontologica Polonica* 49(2): 243–258.
- Lang, J.D., L.F. Spath, and W.A. Richardson. 1923. Shales-with-“beef”, a sequence in the Lower Lias of the Dorset coast.

- Quarterly Journal of the Geological Society of London 79(1): 47–99.
- Leanza, H.A. 1973. Estudio sobre los cambios faciales de los estratos limítrofes Jurásico-Cretácicos entre Loncopué y Picún Leufú, provincia del Neuquén, República Argentina. *Revista de la Asociación Geológica Argentina* 28(2): 97–132.
- Leanza, H.A. 1975. *Himalayites andinus* n. sp. (Ammonitina) del Tithoniano superior del Neuquén, Argentina. *1° Congreso Argentino de Paleontología y Bioestratigrafía* (San Miguel de Tucumán). *Actas* 1: 581–588.
- Leanza, H.A. 1981a. The Jurassic-Cretaceous boundary beds in West Central Argentina and their ammonite zones. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 161(1): 62–92.
- Leanza, H.A. 1981b. Faunas de ammonites del Jurásico y Cretácico inferior de América del Sur, con especial consideración de la Argentina. In: *Cuencas Sedimentarias de América del Sur*, W. Volkheimer and E. Musacchio, eds, 2: 559–597. Buenos Aires.
- Leanza, H.A., and C.A. Hugo. 1978. Sucesión de amonites y edad de la Formación Vaca Muerta y sincrónicas entre los paralelos 35° y 40° Ls. Cuenca Neuquina-Mendocina. *Revista de la Asociación Geológica Argentina* 32(4): 248–264.
- Leanza, H.A., and C.A. Hugo. 2005. Hoja Geológica 3969-I. Zapala. Provincia del Neuquén. Programa Nacional de Cartas Geológicas de la República Argentina 1:250.000. *Boletín Servicio Geológico Minero Argentino* 275: 1–132, 1 geological map.
- Leanza, H.A., and J. Wiedmann. 1989. Nuevos ammonites del Berriasiano/Valanginiano (Cretácico inferior) del Neuquén, Argentina. In: *Cretaceous of the western Tethys*. ed. J. Wiedmann, Proceedings of the 3rd International Cretaceous System Symposium (Tübingen 1987), pp. 793–810. Schweizerbart. Stuttgart.
- Leanza, H.A., H.G. Marchese, and J.C. Riggi. 1978. Estratigrafía del Grupo Mendoza con especial referencia a la Formación Vaca Muerta entre los paralelos 35° y 40° L.S., cuenca neuquina-mendocina. *Revista de la Asociación Geológica Argentina*, 32(3): 190–208.
- Leanza, H.A., C.A. Hugo, D. Repol, and M. Salvarredy Aranguren. 2003. Miembro Huncal (Berriasiano inferior): un episodio turbidítico en la Formación Vaca Muerta, Cuenca Neuquina, Argentina. *Revista de la Asociación Geológica Argentina* 58(2): 248–254.
- Leanza, H.A., D. Repol, C.A. Hugo, and P. Sruoga. 2006. Hoja Geológica 3769-31, Chorriaca, provincia del Neuquén. Programa Nacional de Cartas Geológicas de la República Argentina a escala 1: 100.000. *Instituto de Geología y Recursos Minerales. SEGEMAR. Boletín* 354: 1–93. Buenos Aires.
- Leanza, H.A., F. Sattler, R. Martinez, and O. Carbone. 2011. La Formación Vaca Muerta y Equivalentes (Jurásico Tardío–Cretácico Temprano) en la Cuenca. Neuquina. In: *Geología y Recursos Naturales de la Provincia del Neuquén*, eds. H.A. Leanza, C. Arregui, O. Carbone, J.C. Daniela, J.M. Vallés, 18° Congreso Geológico Argentino, Neuquén, Relatorio, pp. 113–129.
- Legarreta, L., and M.A. Uliana. 1991. Jurassic–Cretaceous marine oscillations and geometry of back-arc basin fill, central Argentine Andes. In: *Sea Level Changes at Active Plate Margins: Process and Product*, ed. D.I.M. McDonald, *International Association of Sedimentologists, Special Publication* 12: 429–450.
- Legarreta, L., and M.A. Uliana. 1996. The Jurassic succession in west-central Argentina: stratal patterns, sequences and paleogeographic evolution. *Palaeogeography, Palaeoclimatology, Palaeoecology* 120(3–4): 303–330.
- Legarreta, L., E. Kozłowski, and A. Boll. 1991. Esquema estratigráfico y distribución de facies del Grupo Mendoza en el ámbito surmendocino de la Cuenca Neuquina. *Actas 8° Congreso Geológico Argentino* 3: 389–409.
- Li, J.H., and B.L. Ding. 1981. Two new lamellibranch genera from Lower Triassic of Anhui. *Acta Palaeontologica Sinica* 20(4): 325–330.
- Lisson, C.I. 1907. *Contribución a la geología de Lima y sus alrededores*. Librería e Imprenta Gil. 124 pp., 13 pl. Lima.
- Macdonald, D.I.M. 1982. Palaeontology and ichnology of the Cumberland Bay Formation, South Georgia. *Bulletin of the British Antarctic Survey* 57: 1–14.
- Mann, U. 1994. An integrated approach to the study of primary petroleum migration. In: *Geofluids: Origin, Migration and Evolution of Fluids in Sedimentary Basins*, ed. J. Parnell. *Geological Society of London Special Publication* 78: 233–260.
- Marshall, J. 1982. Isotopic composition of displacive fibrous calcite veins: reversal in pore-water composition trends during burial diagenesis. *Journal of Sedimentary Petrology* 52(2): 615–630.
- Mitchum, R.M. and M.A. Uliana. 1985. Seismic stratigraphy of carbonate depositional sequences. Upper Jurassic/Lower Cretaceous. Neuquén Basin, Argentina. In: *Seismic stratigraphy, II. An integrated approach to hydrocarbon analysis*, eds. B.R. Berg and D.G. Woolverton. *American Association of Petroleum Geologists, Memoir* 39: 255–274.
- Müller, A.H. 1979. Fossilization (Taphonomy). In: *Treatise on Invertebrate Paleontology. Part A. Introduction*, eds. R.A. Robison, and C. Teichert, Geological Society of America and University of Kansas Press. Lawrence, Kansas, pp. A2–A78.
- Newell, N.D., and D.W. Boyd. 1995. Pectinoid bivalves of the Permian-Triassic crisis. *Bulletin of the American Museum of Natural History* 227: 1–95.
- Parnell, J., and P.F. Carey. 1995. Emplacement of bitumen (asphaltite) veins in the Neuquén Basin, Argentina. *Bulletin American Association of Petroleum Geologists* 79(12): 1798–1816.
- Parnell, J., C. Honghan, D. Middleton, T. Haggan, and P. Carey. 2000. Significance of fibrous mineral veins in hydrocarbon migration: fluid inclusion studies. *Journal of Geochemical Exploration* 69–70: 623–627.
- Philippi, E. 1900. Beiträge zur Morphologie und Phylogenie der Lamellibranchier. II. Zur Stammesgeschichte der Pectiniden. *Zeitschrift der Deutschen geologischen Gesellschaft* 52(1): 64–117.
- Pompeckj, J.F. 1901. Über Aucellen und Aucellen-ähnliche Formen. *Neues Jahrbuch für Mineralogie und Paläontologie, Beilage-Bände* 14: 319–368.
- Rafinesque, C.S. 1815. *Analyse de la Nature ou Tableau de l'University et des Corps Organisés, etc.* Palermo: Jean Barravecchia. 233 pp.
- Riccardi, A.C. 2008a. The marine Jurassic of Argentina: a biostratigraphic framework. *Episodes* 31: 326–335.
- Riccardi, A.C. 2008b. El Jurásico de Argentina y sus amonites. *Revista de la Asociación Geológica Argentina* 63(4): 625–643.
- Riccardi, A.C. 2015. Remarks on the Tithonian–Berriasian ammonite biostratigraphy of west central Argentina. *Volumina Jurassica* 13(2): 23–52.
- Riccardi, A.C., H.A. Leanza, S. Damborenea, M. Manceñido, S. Ballent, and A. Zeiss. 2000. Marine Mesozoic biostratigraphy of the Neuquén Basin. In: *Geoscientific Cooperation with Latin America*, eds. H. Miller, and F. Hervé, 31st International Geological Congress (Rio de Janeiro). *Zeitschrift für Angewandte Geologie, Sonderheft* 1: 103–108.
- Riccardi, A.C., S.E. Damborenea, M.O. Manceñido, and H.A. Leanza. 2011. Megainvertebrados jurásicos y su importancia geobiológica. In: *Geología y Recursos Naturales de la Provincia del Neuquén*, eds. H.A. Leanza, C. Arregui, O. Carbone, J.C.

- Daniela, and J.M. Vallés, 18^o Congreso Geológico Argentino, Neuquén, Relatorio, pp. 441–464.
- Rivera, R. 1951. La Fauna de los Estratos Puente Inga, Lima. *Boletín de la Sociedad Geológica del Perú* 22: 1–53, lám. 1–9.
- Rodrigues, N., P.R. Cobbold, H. Loseth, and G. Ruffet. 2009. Widespread bedding-parallel veins of fibrous calcite ('beef') in mature source rock (Vaca Muerta Fm, Neuquén Basin, Argentina): evidence for overpressure and horizontal compression. *Journal of the Geological Society, London* 166: 695–709.
- Romero, P.L., M.A. Aldana, C.Z. Rangel, E.R. Villavicencio, and J.A. Ramírez. 1995. Fauna y flora fósil del Perú. *Instituto Geológico Minero y Metalúrgico de Perú, Serie D: Estudios Especiales, Boletín* 17: 1–332.
- Ros, S., A. Márquez-Aliaga, and S. Damborenea. 2014. Comprehensive database on Induan (Early Triassic) to Sinemurian (Early Jurassic) marine bivalve genera and their paleobiogeographic record. *University of Kansas Paleontological Contributions* 8: 1–219.
- Rouillier, K. 1845. Untitled article proposing the genus *Buchia* for *Avicula mosquensis*. *Bulletin de la Société Impériale des Naturalistes de Moscou* 18: 289.
- Royo y Gómez, J. 1945. Fósiles carboníferos e infracretácicos del oriente de Cundinamarca. *Compilación de los estudios geológicos oficiales en Colombia* 4: 193–242.
- Salomon, W. 1900. Ueber *Pseudomonotis* und *Pleuronectites*. *Zeitschrift der Deutschen Geologischen Gesellschaft* 52: 348–359.
- Schlotheim, E.F.V. 1820. *Die Petrefactenkunde auf ihrem jetzigen Standpunkte durch die Beschreibung seiner Sammlung versteinerter und fossiler Überreste des Thier- und Pflanzenreichs der Vorwelt erläutert*. Gotha: Becker.
- Schlotheim, E.F.V. 1823. *Nachträge zur Petrefactenkunde, zweite Abtheilung*. Gotha: Becker.
- Schmid-Röhl, A., and H.J. Röhl. 2003. Overgrowth on ammonite conchs: environmental implications for the Lower Toarcian Posidonia Shale. *Palaeontology* 46(2): 339–352.
- Seilacher, A. 2001. Concretion morphologies reflecting diagenetic and epigenetic pathways. *Sedimentary Geology* 143: 41–57.
- Sellés-Martínez, J. 1996. Concretion morphology, classification and genesis. *Earth-Science Reviews* 41(2): 177–210.
- Serb, J.M., A. Alejandrino, E. Otárola-Castillo, and D.C. Adams. 2011. Morphological convergence of shell shape in distantly related scallop species (Mollusca: Pectinidae). *Zoological Journal of the Linnean Society* 2011: 1–14.
- Sha, J., and F.T. Fürsich. 1994. Bivalve faunas of eastern Heilongjiang, northeastern China. II. The Late Jurassic and Early Cretaceous buchiid fauna. *Beringeria* 12: 3–93.
- Sokolov, D.N. 1946. Algunos fósiles suprajurásicos de la República Argentina. *Revista de la Sociedad Geológica Argentina* 1(1): 7–16.
- Stefanini, G. 1939. Molluschi del Giurassio della Somalia. *Palaeontographia Italica* 32(Suppl. 4): 103–270.
- Stoneley, R. 1983. Fibrous calcite veins, overpressures, and primary oil migration. *The American Association of Petroleum Geologists Bulletin* 67: 1427–1428.
- Surlyk, F., and V.A. Zakharov. 1982. Buchiid bivalves from the Upper Jurassic and Lower Cretaceous of East Greenland. *Palaeontology* 25(4): 727–753.
- Tarney, J., and B.C. Schreiber. 1977. Cone-in-cone and beef-in-shale textures from DSDP Site 330, Falkland Plateau, South Atlantic. *Initial Reports of the Deep Sea Drilling Project* 36: 865–870.
- Waller, T.R. 1978. Morphology, morphoclines and a new classification of the Pteriomorpha (Mollusca, Bivalvia). *Philosophical Transactions of the Royal Society of London B* 284: 345–365.
- Waller, T.R. 1984. The ctenolium of scallop shells: functional morphology and evolution of a key family-level character in the Pectinacea (Mollusca: Bivalvia). *Malacologia* 25(1): 203–219.
- Waller, T.R. 1986. A new genus and species of scallop (Bivalvia: Pectinidae) from off Somalia, and the definition of a new tribe Decatopectinini. *The Nautilus* 100(2): 39–46.
- Waller, T.R. 2006. Phylogeny of families in the Pectinoidea (Mollusca: Bivalvia): importance of the fossil record. In: Bieler, R. (Ed.), *Bivalvia— a look at the Branches. Zoological Journal of the Linnean Society* 148: 313–342.
- Waller, T.R., and L. Marincovich jr. 1992. New species of *Campitochlamys* and *Chlamys* (Mollusca: Bivalvia: Pectinidae) from near the Cretaceous/Tertiary boundary at Ocean Point, North Slope, Alaska. *Journal of Paleontology* 66(2): 215–227.
- Waller, T.R., and G.D. Stanley. 2005. Middle Triassic pteriomorphian Bivalvia (Mollusca) from the New Pass Range, west-central Nevada: systematics, biostratigraphy, paleoecology, and paleobiogeography. *Journal of Paleontology* 79 (Supplement to no. 1). *The Paleontological Society Memoir* 61: 1–64.
- Wasmer, M., M. Hautmann, E. Hermann, D. Ware, G. Roohi, K. Ur-Rehman, A.- Yaseen, and H. Bucher. 2012. Olenekian (Early Triassic) bivalves from the Salt Range and Surghar Range, Pakistan. *Palaeontology* 55(5): 1043–1073.
- Weaver, C. 1931. Paleontology of the Jurassic and Cretaceous of west central Argentina. *Memoir, University of Washington* 1: 1–469. Seattle.
- Zakharov, V.A. 1966. *Pozdneyskies i rannemelovye dvustvorchatye molluski severa Sibiri i uslovia ikh sushchestvovaniya (Otryad Anisomyaria)*. [Late Jurassic and Early Cretaceous bivalve molluscs of north Siberia], 189. Sibirskoe Otdelenie: Akademiya Nauk SSSR.
- Zanella, A., P.R. Cobbold, G. Ruffet, and H.A. Leanza. 2015. Geological evidence for fluid overpressure, hydraulic fracturing and strong heating during maturation and migration of hydrocarbons in Mesozoic rocks of the northern Neuquén Basin, Mendoza Province, Argentina. *Journal of South American Earth Sciences* 62: 229–242.
- Zeiss, A., and H.A. Leanza. 2010. Upper Jurassic (Tithonian) ammonites from the lithographic limestones of the Zapala region, Neuquén Basin, Argentina. *Beringeria* 41: 23–74.