

# REASSESSMENT OF THE SPINOSE POLYTOECHIID BRACHIOPOD *PINATOTOECHIA* BENEDETTO FROM THE LOWER ORDOVICIAN OF WESTERN ARGENTINA

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**Key words.** Brachiopods. Billingsellida. Lower Ordovician. W Puna. Famatina. Argentina.

*PINATOTOECHIA* (type species *Pinatotoechia acantha* Benedetto, 2001a) is a peculiar spinose polytoechiid hitherto confined to the Famatina-Puna volcanic-arc system fringing the Andean margin of Gondwana during the Ordovician (Benedetto, 1998) (Fig. 1). This genus was originally described from the volcanosedimentary Aguada de la Perdiz Formation exposed west of Salar del Rincón in the Puna region of NW Argentina, a few kilometers from the international border with Chile (Benedetto, 2001a). According to the associated trilobites, as well as the graptolites from correlatable units, the age of these beds is latest Floian–early Dapingian (Koukharsky *et al.*, 1996; Monteros *et al.*, 1996; Brussa *et al.*, 2003; Toro *et al.*, 2015). New and better preserved specimens of *Pinatotoechia acantha* were subsequently collected from the nearly coeval volcanoclastic Suri Formation of the Famatina Range (Benedetto, 2003) (Fig. 1).

Rubel (2007), in the supplement of the revised *Treatise*, synonymized *Pinatotoechia* Benedetto with *Tritoechia* Ulrich and Cooper, 1936, arguing that the spines of the former are, in fact, identical to the aditicles of the type species *Tritoechia typica* (Schuchert and Cooper, 1932). The purpose of this paper is to present conclusive evidence on the presence of true hollow spines erected on the tops of costellae in order to support the validity of the genus and to improve its description and illustration. Likewise, the ventral interior of *Pinatotoechia* is redescribed and reillustrated to show that its pseudospondylium and ventral muscle pattern clearly differ from those of *Tritoechia*.

High-resolution optical images of spines were obtained using an OLYMPUS LEXT OLS4000 confocal laser scanning microscopy available in the Laboratory of Electronic Microscopy and X-ray Analysis (LAMARX), Consejo Nacional de Investigaciones Científicas y Técnicas and Universidad Nacional de Córdoba, Argentina.

## SYSTEMATIC PALEONTOLOGY

Illustrated specimens are deposited in the paleontological collection of the Centro de Investigaciones en Ciencias de la Tierra (CICTERRA), CONICET–Universidad Nacional de Córdoba. All the types and figured specimens appear with the institutional abbreviation **CEGH-UNC**.

Class STROPHOMENATA Williams *et al.*, 1996  
Order BILLINGSSELLIDA Schuchert, 1893  
Suborder BILLINGSSELLIDINA Öpik, 1934  
Superfamily POLYTOECHIOIDEA Öpik, 1932  
Family POLYTOECHIIDAE, Öpik, 1934

**Remarks.** In this paper we support the criteria exposed by Popov *et al.* (2001, 2007) and Topper *et al.* (2013) for recognizing two families among the Polytoechioidea, Tritoechiidae and Polytoechiidae. In the former the entire ventral muscle field rests directly on the floor of the delthyrial cavity or it is raised on a pseudospondylium not undercut anteriorly. In contrast, in the Polytoechiidae the pseu-

dospondylium is free anteriorly and supported medially and laterally by septa resembling the spondylium triplex of gonambonitids (Vinn and Rubel, 2000). Since *Antigonambonites* Öpik, 1934, and *Raunites* Öpik, 1939, formerly attributed to the Gonambonitidae, possess a pseudospondylium of polytoechiid type instead of a true spondylium, Topper *et al.* (2013) placed them in the family Polytoechiidae. In their phylogenetic analysis *Antigonambonites* appears, together with *Polytoechia* Hall and Clarke, 1892, as a derived polytoechiid. As will be shown below, the pseudospondylium of *Pinatotoechia* is undercut anteriorly and supported by a median septum and a pair of lateral septa, and therefore this genus is attributed here to the redefined Family Polytoechiidae. Based on important differences in the ontogeny, Popov *et al.* (2007) suggested that Polytoechioidea should be placed in the order Billingsellida outside the suborder Clitambonitidina. According to these authors the embryonic development and mode of attachment in the polytoechioidean *Antigonambonites* Öpik are comparable to those of

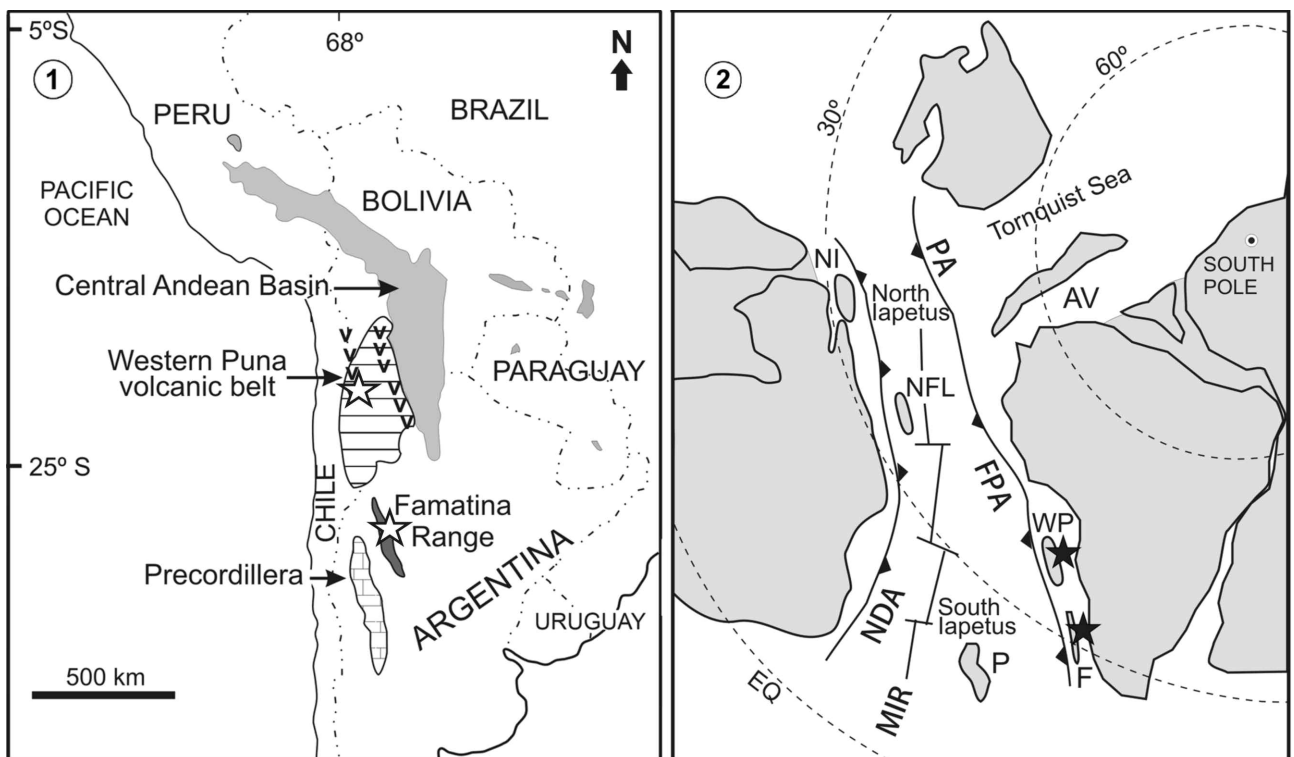
strophomenates and differ substantially from those of rhynchonellates. Popov *et al.* (2007) consider that clitambonitidines derived from the order Protorthida, which places them outside the Strophomenata.

Genus *Pinatotoechia* Benedetto, 2001a

**Type species.** *Pinatotoechia acantha* Benedetto, 2001a. Aguada de la Perdiz Formation, Vega Pinato, western Puna region, Salta Province, NW Argentina.

**Emended Diagnosis.** Ventribiconvex multicostellate polytoechiid with simple rows of subvertical tubular hollow spines on the top of costellae. Ventral interior with anteriorly free pseudospondylium supported by a median septum and a pair of side septa.

**Morphological remarks.** *Tritoechia typica* (Schuchert and Cooper) is the type species of *Tritoechia* and is characterized by a peculiar ornament of discontinuous swollen hollow costellae. A detail of a dorsal valve bearing such 'tubular



**Figure 1.** 1, Map of southwestern South America showing the Cambro-Ordovician geological units mentioned in the text showing *Pinatotoechia acantha* localities (with stars); 2, Early Ordovician paleogeographic reconstruction of the Iapetus Ocean and intervening terranes. AV, Avalonia; F, Famatina Range; FPA, Famatina-Puna volcanic island-arc system; MIR, Mid-Iapetus ridge; NDA, Notre Dame arc; NFL, Central Newfoundland; NI, Northwest Ireland; P, Precordillera terrane; PA, Penobscot arc; WP, Western Puna volcanic arc. Black stars: *Pinatotoechia acantha* occurrences (modified from Benedetto, 1998; Iapetus terranes after Harper *et al.*, 1996, and Van Staal *et al.*, 1998).

costellae' was illustrated by Ulrich and Cooper (1938, pl. 33, fig. 26). It should be noted that this kind of ornamentation is not evident neither in other North American species (Ulrich and Cooper, 1938) nor in species from the Laurentian-derived Precordillera terrane (Benedetto, 1987, 2001b), Wales (Neuman and Bates, 1978), Famatina Range (Benedetto, 1994, 2003), Kazakhstan (Popov *et al.*, 2001), Tasmania (Laurie, 1980, 1991) and Iran (Ghobadi Pour *et al.*, 2011), thus this feature is distinctive of the type species only and, as stated before (Benedetto, 1987), it cannot be considered diagnostic of the genus *Tritoechia*. In the gonambonitid *Estlandia marginata* (Pahlen, 1877), from the lower Sandbian of Estonia, costellae are crossed by strong growth lamellae which form anteriorly directed arches, or may be directed almost perpendicular to the shell surface and joined anteriorly appearing as a series of holes aligned along ribs; when raised upwards may form short hollow spines (Wright and Rubel, 1996: pl. 2, fig. 5). These authors interpreted the 'tubular costae' of clitambonitoids as aditicles. However, compared with the better known aditicles of plaesiomyids (Jin *et al.*, 2007) there seems to have substantial differences. As defined by these authors, aditicles are proportionally large, anteriorly tilted tubular perforations developed along the crests and slopes of costae or costellae and confined largely to the outer shell layer. The diameter of aditicles measured in the specimen of *Plaesiomys anticostiensis* (Shaler, 1865) illustrated by Jin *et al.* (2007: fig. 6.5) is approximately of 75 µm. Aditicles are always tubular shell perforations and they do not originate spinose structures. Epipunctae are another kind of perforations which are setigerous tubules that can be distinguished from aditicles in their five to ten time smaller sizes and in their uniform distribution on ribs and in interspaces. Epipunctae have not yet been described in the clitambonitidines.

The hollow tubular spines of *Pinatotoechia acantha* are morphologically comparable to those of the tritoechiid *Acanthotoechia hibernica* Williams and Curry, 1985. In both species the spines can be viewed as extreme variants of the *Estlandia*-type 'tubular costellae'. When broken at their base, they appear as a series of subcircular depressions aligned on costellae. However, when preserved complete, the spines are relatively long, subvertical or slightly inclined, sharpened to a point.

Although the dorsal interior of *Pinatotoechia* is closely comparable to that of *Tritoechia* and other tritoechiids, some well-preserved ventral internal molds associated to spinose exteriors from both W Puna and Famatina Range clearly show that the anterior portion of the pseudospondylium is free and that it is supported medially by a thick septum and laterally by a pair of subvertical septa, becoming sessile posteriorly (Fig. 2.1–5). On the other hand, the adductor scars are located in a deep, U-shaped median depression separated from the flanking diductor scars by a pronounced break in the slope of the pseudospondylium surface, resembling the muscle pattern of the clitambonitoid *Estlandia*. The subcircular thickening localized in the posterior third of the pseudospondylium (Fig. 2.3) can be interpreted as a pedicle callist, but another possibility is that it corresponds to the proximal part of a 'pedicle sheath' like that present in juvenile specimens of *Antigonambonites planus* (Pander, 1830) (Popov *et al.*, 2007); this structure, however, is tubular and much smaller than the scar present in *Pinatotoechia*.

*Pinatotoechia acantha* Benedetto, 2001a

Fig. 2.1–17

**Referred material.** In addition to the material listed by Benedetto (2001a, 2003), the following new specimens are illustrated: CEGH-UNC 18446 and 18447 from Vega Pinato, western Puna, Salta Province.

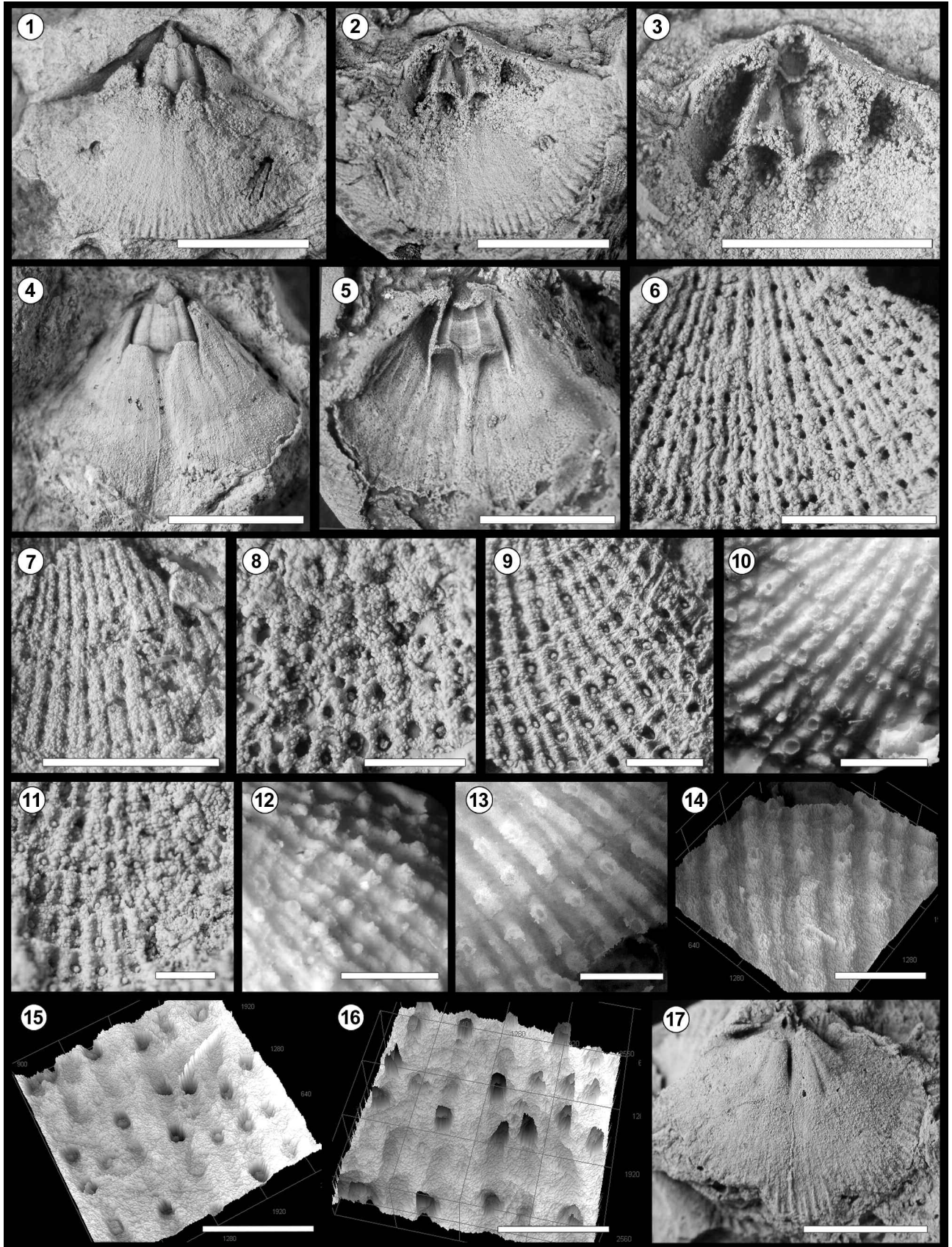
**Stratigraphic occurrence.** Aguada de la Perdiz Formation, western Puna region, upper Floian–lower Dapingian; upper part of the Suri Formation, Famatina Range, Floian (Fig. 1).

**Description.** See Benedetto (2001a) and Benedetto (2003).

**Diagnosis.** The same as the genus by monotypy.

**Discussion.** The only other known spinose polytoechiid is the monotypic genus *Acanthotoechia* Williams and Curry, 1985, from the Lower Ordovician Tourmakeady Formation of Ireland. As stated previously (Benedetto 2001a) this genus can be easily distinguished from *Pinatotoechia* by its definitely parvicostellate ornamentation and its gently concave dorsal valve. Concerning to the ornament, the diameter of tubular spines in *Pinatotoechia acantha* ranges from 180 to 230 µm, their maximum measured height is about 460 µm, and spacing between spines measured along a rib is of 500–600 µm. In *Acanthotoechia hibernica* Williams and





Curry, 1985, the diameter of tubular spines is about three to four times smaller than in *P. acantha*, those on the primary ribs having a mean diameter of 80 µm, and those on the finer intercalated ribs of 60 µm. Moreover, in the Irish genus the primary costellae bear two rows of laterally tilted spines (in anterior view), which near to the anterior margin may be united at their base appearing as bifid (Williams and Curry, 1985: fig. 159); the finer intercalated ribs bear a single row of smaller simple spines.

Internally, the dorsal valve of *Acanthotoechia* clearly differs from that of *Pinatotoechia* in having a well-defined subperipheral rim comparable to that of *Pomatotrema* Ulrich and Cooper in Schuchert and Cooper (1932), *Platytoechia* Neuman, 1964, and *Martellia* Wirth, 1936 (Popov *et al.*, 2001; Percival *et al.*, 2009). Unlike *Pinatotoechia*, the pseudospondylium in *Acanthotoechia* is entirely sessile and the adductor field is raised on a prominent median ridge. The sessile pseudospondylium supports the assignment of the Irish genus to the family Tritoechiidae.

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**Figure 2.** 1–17, *Pinatotoechia acantha* Benedetto. 1–3, 6, CEGH-UNC 15900 (Famatina Range), ventral internal mold (1), latex cast (2), detail of pseudospondylium (3), and external mold showing spinose ornamentation (6). 4–5, holotype CEGH-UNC 18445 (W Puna), ventral internal mold (4) and latex cast (5). 7, CEGH-UNC 18447 (W Puna), fragmentary ventral external mold. 8, CEGH-UNC 18446 (W Puna), detail of fragmentary ventral external mold. 9–10, CEGH-UNC 15901 (Famatina Range), detail of ventral external mold and latex cast showing hollow spines. 11, CEGH-UNC 18448 (W Puna), fragmentary ventral external mold. 12, latex cast of the external mold illustrated in figure 6, oblique view showing spines. 13–14, latex cast illustrated in figure 12 photographed using confocal laser scanning microscope perpendicular to shell surface (13) and oblique view (14). 15–16, 3D images of the latex cast (oblique views) displayed in the height (15) and unevenness inverted (16). 17, CEGH-UNC 15847 (Famatina Range), internal mold of dorsal valve. Scale bars 1–6, 17= 5mm; 6, 7= 2mm; 8–16= 1mm.



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