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Schellwienella clarkei (Orthotetida, Brachiopoda): a new species from the Devonian of the Paraná Basin, Brazil

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Abstract.—Devonian orthotetides from South America have often been uncritically assigned to a limited number of broadly described species. *Schellwienella clarkei* n. sp. is described from the Ponta Grossa Formation, Paraná Basin, southern Brazil. These brachiopods had been identified as *Schuchertella agassizi*. *Schellwienella clarkei* n. sp. differs from *Schuchertella agassizi* on the basis of shell structure, dental plates, and cardinalia.

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Introduction

The first faunal inventory and taxonomic description of Devonian brachiopoda from the Paraná Basin (Brazil) was by Clarke (1913). It included species classified at present within the order Orthotetida Waagen, 1884, with the occurrence of *Schuchertella agassizi* (Rathbun, 1874), *Schuchertella sulivani* (Morris and Sharpe, 1846), and *Schuchertella sancticrucis* Clarke, 1913. *Schuchertella agassizi*, the most abundant species, was identified based on ornamentation pattern similarities with specimens from the Middle Devonian Ererê Formation (Amazonas Basin, Brazil). *Schuchertella sulivani* was originally described from the Falkland Islands, Fox Bay Formation (Pragian-Emsian, Stone, 2016) by Morris and Sharpe (1846) and, later, by Sharpe (1856) for the Bokkeveld Group (Emsian-Givetian, Penn-Clarke, 2019) in South Africa, based on growth patterns. *Schuchertella sancticrucis* species was named by Clarke (1913) for the Santa Cruz shales, São Domingos Member (now the São Domingos Formation), Givetian (Melo, 1988; Grahn et al., 2013), Paraná Basin, Brazil.

Generally orthotetide brachiopods include taxa considered broadly, a taxonomic viewpoint subsequently shown to be incorrect; e.g., "*Schuchertella*," (Isaacson, 1977). Schuchert (1929) recognized that specimens then classified within the subfamily Orthotetinae Waagen, 1884 consisted of strophomenide, orthide and orthotetide fragmentary samples and considered of questionable validity.

Cooper and Grant (1974) broadly revised the suborders Strophomenidina Öpik, 1934 and Orthotetidina Waagen, 1884. They reassigned the impunctate families Davidsoniidae King, 1850 (currently atrypides) and Fardeniidae Williams, 1965 (currently a junior synonym of Chilidiopsidae Boucot, 1959a) to the suborder Strophomenidina. Suborder Orthotetidina, (the pseudopunctate forms), characteristic of the post Devonian Paleozoic, were returned to the superfamily Orthotetacea Waagen, 1884.

"Schuchertella" misidentifications.—*Schuchertella* was first described by Girty (1904), based on the type species being *Streptorhynchus lens* White, 1862. This included orthotetide forms of *Streptorhynchus,* previously assigned to *Orthotetes* Fisher de Waldheim, 1830, which possessed neither a median septum nor dental plates (Weller, 1914; Easton, 1962; Stigall Rode, 2005).

A strong median septum in ventral valve led Fisher de Waldheim in 1850 to classify specimens as *Orthotetes;* however, Hall and Clarke (1892) argued that these samples should probably belong to *Derbyia*. After a careful study of Fisher de Waldheim's figured specimens, Girty (1904), based on characteristics shared with the type species, agreed with their type structure as belonging to *Derbyia*, suggesting a synonymy between both genera. As an attempt to solve the problems related to the absence of a generic name for specimens previously assigned as *Orthotetes*, Girty (1904*)* erected the genus *Schuchertella*.

Streptorhynchus agassizi Rathbun, 1874 was described from the Middle Devonian Ererê Formation, highlighting the presence of dental plates and a thin, bilobed cardinal process (Rathbun, 1874). Even after Girty's description some problems remained with the new genus's description and *Streptorhynchus agassizi*. Nevertheless, the species was relocated to Girty's genus as *Schuchertella agassizi* in all three Devonian units (Ponta Grossa, Maecuru and Ererê formations), in which its occurrence was known (Rathbun, 1874, 1879; Clarke, 1913; Rezende et al., 2019a).

The common practice of ascribing Orthotetida specimens to *Schuchertella* led different authors to propose new taxa to

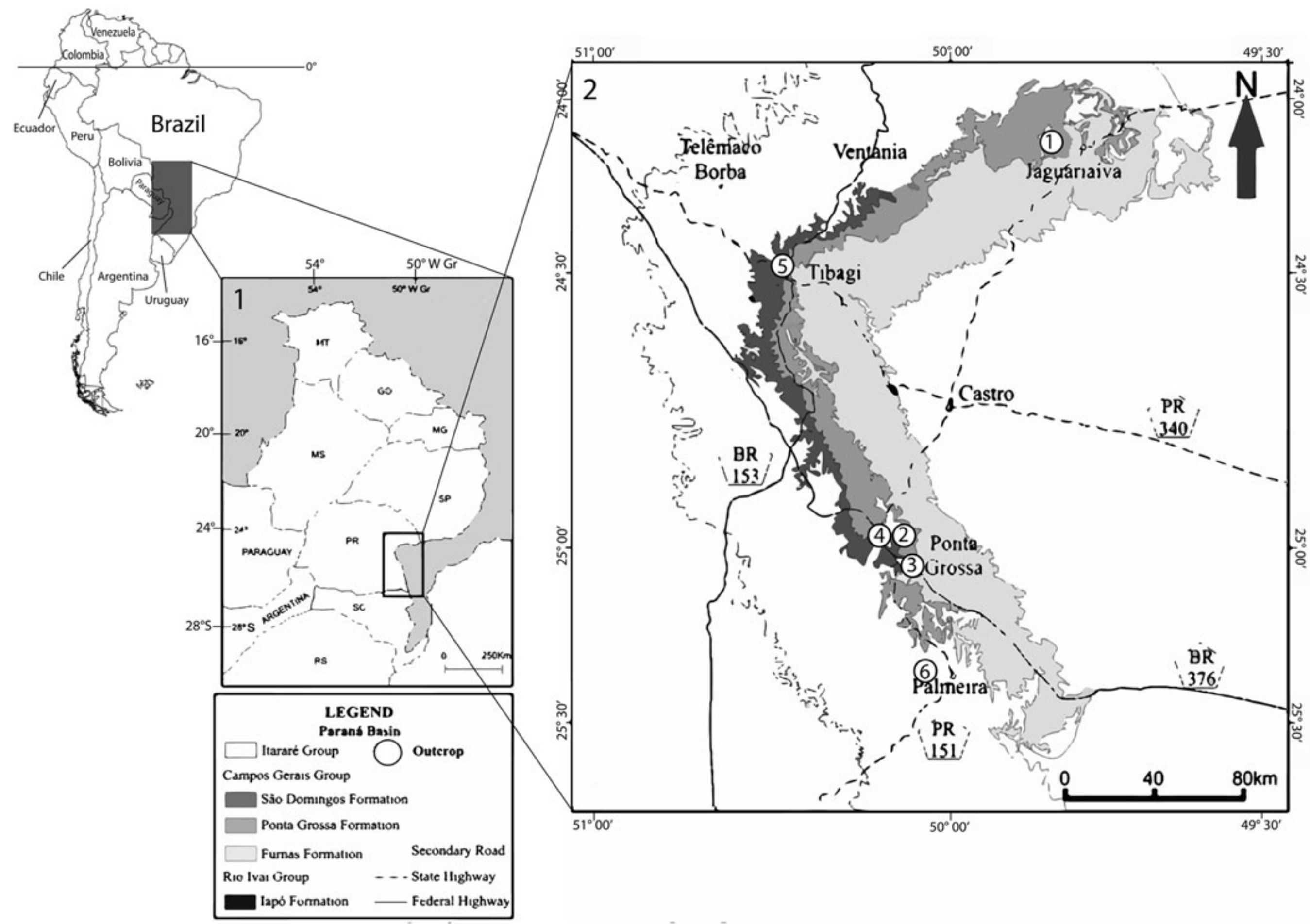

Figure 1. Modified from Grahn et al., 2013. Map of the studied area. (**1**) Paraná Basin distribution in Brazil; (**2**) Apucarana Sub-Basin formations, Outcrops: 1 – Jaguariaíva-Arapoti Railroad; 2 – Fazanda Rivadávia; 3 – Ponta Grossa Municipality; 4 -First curve of the railroad track; 5 Tibagi Municipality; 6 – Fazenda Santa Cruz, Palmeira Municipality (?).

include morphologies that did not fit its diagnosis. Dunbar and Condra (1932) described dental plates in specimens classified as *Schuchertella*, thereby defending its relocation to *Schellwienella* Thomas, 1910.

Schuchertella was considered an impunctate genus (Williams, 1965 *apud* Stigall Rode, 2005). However, extropunctation was later recognized in specimens of *Streptorhynchus lens* (G. A. Cooper in a written commun. to J. G. Johnson, dated Dec. 28, 1965; see Boucot and Johnson, 1968). Nevertheless, even recognizing this feature, Boucot and Johnson (1968) and Thomas (1971) chose to keep *Schuchertella*'s diagnosis as impunctate, but adding quotation marks until more an appropriate genus might be found. More recently, Williams and Brunton in Williams et al. (2000) followed by Stigall Rode (2005) considered *Schuchertella* an extropunctate genus.

Considering all the problems related to these classifications, new genera were proposed for morphologies that did not fit within *Schuchertella* (sensu stricto) definition. Consideration was given not only shell structure but also details from the cardinalia, and ornamentation. Following these criteria, Gratsianova (1974) described the genus *Eoschuchertella*, while Cooper and Dutro (1982) described the genus *Floweria,* from the Late Devonian of New Mexico, USA. Both are impunctate, and they are distinguished by their cardinal process, in which *Floweria* possesses a more recurved cardinalia rather than that in *Eoschuchertella*.

For specimens from Brazilian sedimentary basins, Rathbun (1879) presented variations within *Schuchertella agassizi* from the Ererê and Maecuru formations (Rathbun, 1874, 1879). This species was recognized by Clarke (1913) from the Ponta Grossa Formation due to similarities in ornamentation, but Clarke disregarded the problems described by Rathbun. Decades later, Melo (1985) suggested that these specimens may not belong to *Schuchertella* but did not offer any other classification.

Within South America, the species "*Schuchertella*" *agassizi* has been described from Brazil (Maecuru and Ererê formations, Amazonas Basin; Ponta Grossa Formation, Paraná Basin), South Africa (Bokkeveld Group), Argentina (Jachal – Talacasto, Porongal and Rio Pescado formations), Bolivia (Icla Formation), Paraguay (Santa Rosa Formation) and Uruguay (Cordobés Formation), from the Early to Middle Devonian (Emsian to Eifelian) (Melo, 1985).

Few studies regarding taxonomy related to Devonian orthotetide brachiopods have been published recently, leaving many gaps of information, especially about late Paleozoic species,

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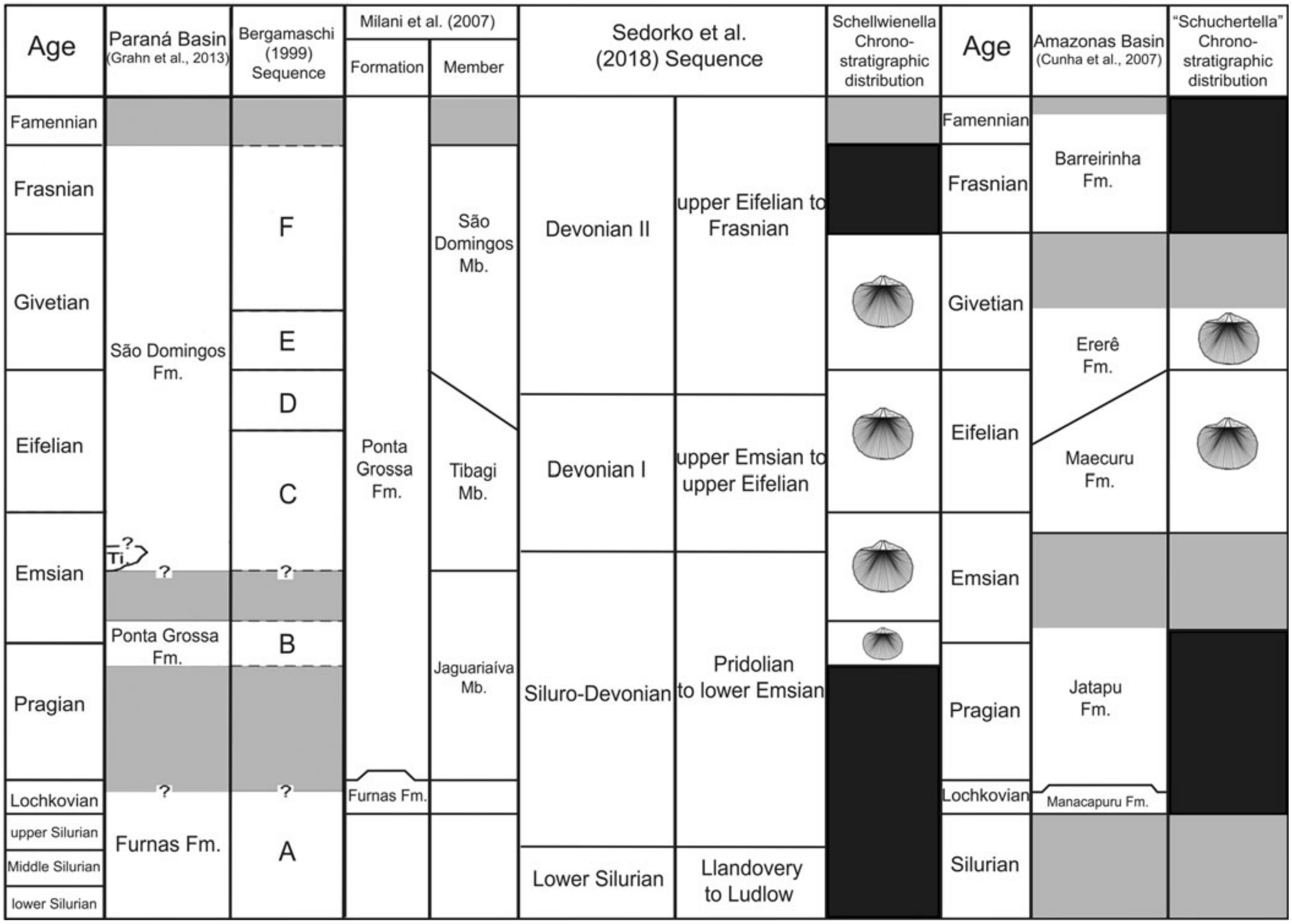

Figure 2. Stratigraphic nomenclature and correlations of key Devonian formations in the Paraná and Amazonas basins (Brazil). Modified from Bergamaschi (1999), Cunha et al. (2007), Grahn et al. (2013), Schemm-Gregory and Henriques (2013), and Horodyski et al. (2018). Gray bars represent no geologic record; black bars represent absence of Orthotetide brachiopods.

Table 1. Stratigraphic description of Ponta Grossa and São Domingos formations.

Stratigraphic unit	Stratigraphic sequence *sensu* Berhamaschi (1999)	Stratigraphic sequence *sensu* Sedroko et al. (2018)	Litology and sedimentary structure	Age	Paleoenvironment	Taxa	References
Ponta Grossa Formation	"B"	Siluro-Devonian	Interbedded sandstones-siltstones followed by sandy shales with rare limestones or sandy clay nodules and bioturbaded siltstones and pyritic black shales	late Pragian - early Emsian	interpreted as shallow marine (shoreface to offshore)	Marine invertebrates and ichnofossils	Melo (1988) Grahn et al. (2013) Horodyski (2014) Horodyski et al. (2018) Rezende et al. (2019b)
São Domingos Formation	"C"; "D"; "E"; "F"	Devonian I Devonian II	Thick and extensive clay shales interbedded with siltstones, with a greater occurrence of sandstone bodies upwards	late Emsian – middle Frasnian	Towards the top, the finely laminated black shales are interpreted as the transgressive pulse the corresponds to the Kacak event, responsible for the Middle Devonian mass extinction event	Marine invertebrates, Ichonofossils (*Zoophycus*), fish remains	Bosetti et al. (2010) Grahn et al. (2013) Horodyski (2014) Richer et al. (2017) Horodyski et al. (2018) Rezende et al. (2019b)

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focusing mostly on North American specimens (Melo, 1985, Rezende et al., 2019a).

We propose a systematic re-evaluation of the Malvinokaffric Realm (now called Malvinoxhosan Realm by Penn-Clarke and Harper, 2020) species "*Schuchertella*" *agassizi* through the descriptions of specimens from the Ponta Grossa and São Domingos formations, and the identification of a new species for the Lower Devonian Paraná Basin, just as for Lower and Middle Devonian Icla, Belén, Gamoneda and Huamampampa formations, Bolivia.

Geological setting

The Paraná Basin is a wide sedimentary area that encompasses parts of Brazil, eastern Paraguay, northeastern Argentina and northern Uruguay encompassing an area of approximately 1.5 million km^2 (Milani et al., 2007).

In Brazil (Fig. 1) it is distributed over the States of Mato Grosso, Mato Grosso do Sul, Goiás, São Paulo, Paraná, Santa Catarina and Rio Grande do Sul, and it is classified as an intracratonic basin. Six supersequences are recognized in the basin, with the "Paraná" corresponding to the Siluro-Devonian time span. Within this supersequence three formations are described: Furnas, Ponta Grossa and São Domingos (Milani et al., 2007; Grahn et al., 2013). The samples discussed here belong to the Apucarana Sub-Basin, Ponta Grossa (former Jaguariaíva Member) and São Domingos (former Tibagi and São Domingos members) formations (Fig. 2; Table 1).

Material and methods

Taxonomic description and material photography.—Sixty one specimens were described and analyzed with a stereoscopic microscope, measured with a caliper, and all were compared with each other and with the original description of "*Schuchertella*" *agassizi.* The diagnostic characters of *Schuchertella* and other taxa from the order Orthotetida were also included in the analysis in order to define which diagnostic character characterizes each taxon and provide a taxonomic (species) re-evaluation.

All specimens consist of interior, exterior, composite molds and counter-molds of ventral and dorsal valves. Considering the available material in scientific collections, figured "UNIRIO" specimens were coated with magnesium oxide and "GP/1E" specimens were coated with ammonium chloride prior to photographing, in order to enhance the contrast between high and low surfaces in the preserved characters (Cerri, 2013; Zambito and Schemm-Gregory, 2013). (Note: "UNIRIO" = Universidade Federal do Estado do Rio de Janeiro; "GP/1E" = Universidade de São Paulo). The photographs were taken with a digital camera, Canon EOS50, and described according to the terms applied by Rathbun (1874, 1879), Williams and Brunton in Williams et al. (2000), Stigall Rode (2005), and Bassett and Bryant (2006).

Repositories and institutional abbreviations.—The studied material consists of specimens from the Ponta Grossa and São Domingos formations (Paraná Basin, Brazil; Fig. 2) included in the scientific collection "Fósseis Paleozoicos" at the Universidade Federal do Estado do Rio de Janeiro (UNIRIO), Laboratório de Estudo de Comunidades Paleozoicas (LECP). Others specimens are from the scientific collections from the Instituto de Geociências of the Universidade de São Paulo (IGeo – USP), and from the Museu de Ciências da Terra (MCTer/DGM). From Bolivia (Icla, Belén, Gamoneda and Huamampampa formations), the studied material consists of samples from the U.S. National Museum (USNM) analyzed and described by one of the authors (P. Isaacson), figured and described in Isaacson (1977, 1993).

Systematic paleontology

Class Strophomenata Williams et al., 1996
Order Orthotetida Waagen, 1884
Suborder Orthotetidina Waagen, 1884
Superfamily Orthotetoidea Waagen, 1884
Family Pulsiidae Cooper and Grant, 1974
Genus *Schellwienella* Thomas, 1910

Type species.—*Spirifera crenistria* Phillips, 1836; lower Carboniferous (Pendleside Limestone Group, Viséan) of Bowland, Yorkshire, England.

Schellwienella clarkei new species
Figure 3–5

1856 *Strophomena baini* Sharpe, p. 208, pl. 26, fig. 13.
1874 *Streptorhynchus agassizi* Rathbun, p. 248, pl. 9, figs. 3, 4, 10, 16, 17, 23, 25, 26, 28-30.
1879 *Streptorhynchus agassizi* Rathbun, p. 24. pl. 9, fig. 4 in Rathbun, 1874.
1908 *Orthotetes chemungensis* Knod [non Conrad], p. 541, pl. 26, figs, 13, 14, 14a; pl. 27, fig. 5.
1913 *Schuchertella agassizi* (Hartt) Clarke, p. 276, pl. 23, figs. 5-8, 10-13 [non 9].
1916 *Schuchertella woolworthana* Williams and Breger [non Hall], p. 35.
1923 *Shchuchertella agassizi* (Hartt) Kozlowski, p. 85, pl. 9, fig. 30.
1925 *Schuchertella baini* (Sharpe) Reed, p. 42.
1933 *Orthotetes agassizi* (Hartt and Rathbun) Katzer, p. 183, 189, 197, pl. 11, figs. 6a-c.
1938 *Schuchertella agassizi* (Hartt) Méndez-Alzola, p. 22, pl. 6, fig. 1-3
1939 *Schellwienella agassizi* (Hartt) Caster, p. 113–116.
1954 *Schellwienella agassizi* (Hartt) Lange, p. 33, 42, 77, 81.
1972 *Streptohynchus agassizi* (Hartt) Carvalho, p. 67, pl. 8, fig. 5–12.
1977 *Schellwienella agassizi* (Hartt) Copper, p. 175-185.
1985 "*Schuchertella*" *agassizi* (Hartt) Melo, appendix 1 and 2, p. 93-99.

Holotype.—UNIRIO 0505-BQ A and B (Mold and Counter-mold) illustrated in Figure 3.5–3.6

Diagnosis.—Ventral valve with pseudopunctae in an apparently random pattern; short dental plates; triangular muscle field

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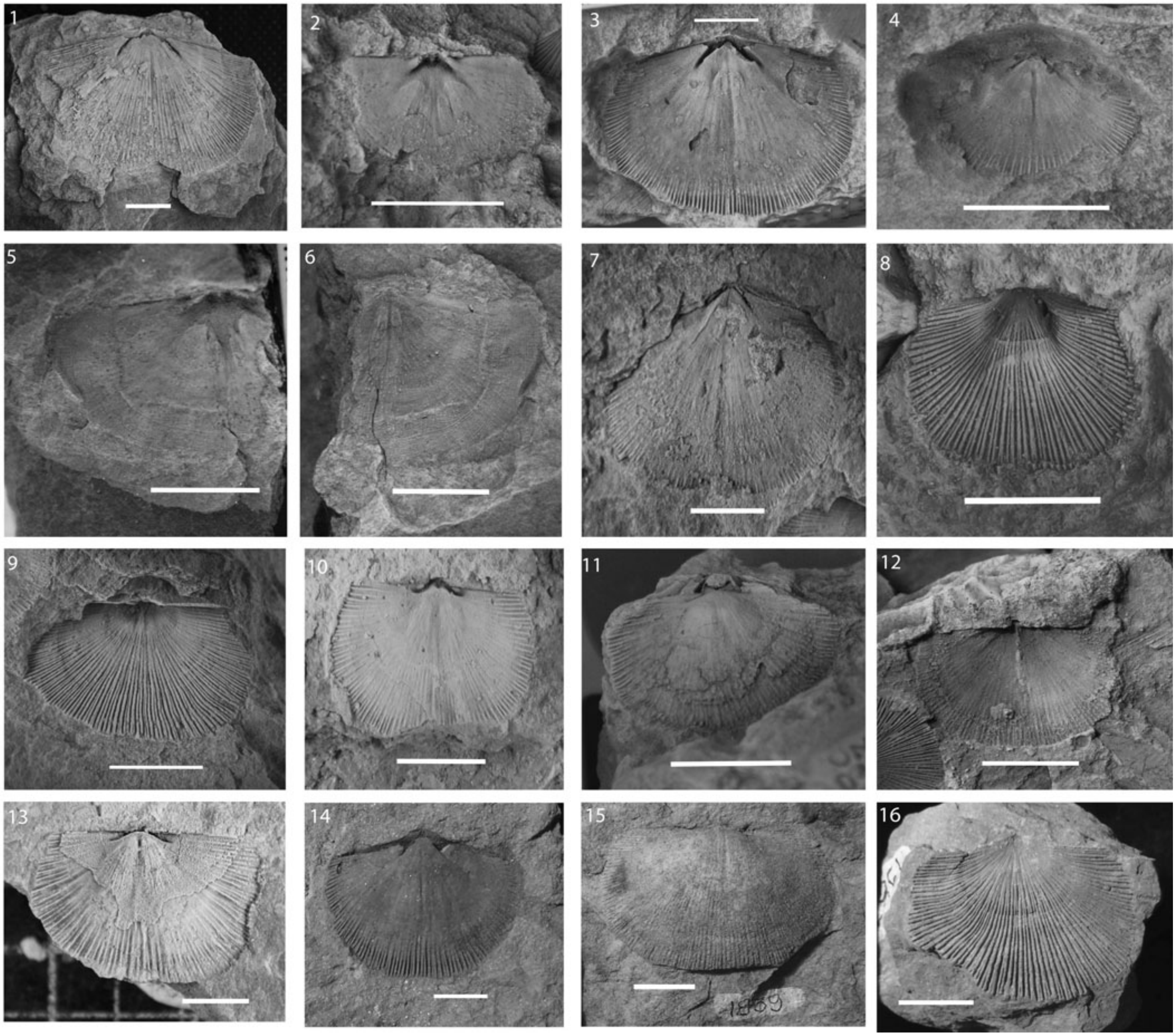

Figure 3. *Schellwienella clarkei* n. sp. from Ponta Grossa and São Domingos formations, Paraná state, Brazil: (**1**) UNIRIO 0065 – BQ. Ventral interior mold, Lower Devonian, Ponta Grossa Formation. Scale = 10 mm; (**2**) UNIRIO 0051 – BQ. Ventral interior conter-mold, Lower Devonian. Ponta Grossa Formation. Scale = 10 mm; (**3**) UNIRIO 0187 – BQ. Ventral interior mold, Lower Devonian. Ponta Grossa Formation. Scale = 10 mm; (**4**) UNIRIO 0199 – BQ B. Ventral interior mold, Lower Devonian. Ponta Grossa Formation. Scale = 10 mm; (**5**) Holotype UNIRIO 0505 – BQ A. Ventral interior conter-mold, Lower Devonian. Ponta Grossa Formation. Scale = 10 mm; (**6**) Holotype UNIRIO 0505 – BQ B. Ventral interior mold, Lower Devonian. Ponta Grossa Formation. Scale = 10 mm; (**7**) GP/1E 7790. Ventral interior mold, Lower Devonian. Ponta Grossa Formation. Scale = 10 mm; (**8**) UNIRIO 0101- BQ A. Ventral composite mold, Lower Devonian. Ponta Grossa Formation. Scale = 10 mm; (**9**) GP/1E 7790. Dorsal exterior mold, Lower Devonian. Ponta Grossa Formation. Scale = 10 mm; (**10**) GP/1E 7919. Interior dorsal mold, Lower Devonian. Ponta Grossa Formation. Scale = 10 mm; (**11**) UNIRIO 0186 – BQ. Interior dorsal mold, Lower Devonian. Ponta Grossa Formation. Scale = 10 mm; (**12**) UNIRIO 0571 – BQ. Interior dorsal mold, Lower Devonian. Ponta Grossa Formation. Scale = 10 mm; (**13**) GP/1E 7655. Interior dorsal mold, Lower Devonian. Ponta Grossa Formation. Scale = 10 mm; (**14**) DGM 1804 – I. Interior ventral mold, Lower Devonian. Ponta Grossa Formation. Scale = 10 mm; (**15**) DGM 1839 – I. Interior ventral mold, Lower Devonian. Ponta Grossa Formation. Scale = 10 mm; (**16**) DGM 1987 – I. Exterior dorsal mold, Lower/Middle Devonian. São Domingos Formation. Scale = 10 mm.

separated by a median septum that extends until approximately ½ the length of the valve. Costae increase by bifurcation and intercalation.

Occurrence.—Ponta Grossa Formation (Pragian-Emsian); São Domingos Formation (Emsian-Frasnian) (Brazil); Icla, Belén, Gamoneda and Huamampampa formations (late Pragian-mid Eifelian) (Bolivia).

Type horizon.—Ponta Grossa Formation

Type locality.—Railroad section, railway branch of Jaguariaíva-Arapoti between km 2.2 and 6.6, Jaguariaíva Municipality (SIGEP 65). Geological and paleobiological site has typical Devonian Malvinoxhosan Realm fossils, microfossils, trace fossils and plant debris of great paleobiogeographic importance. Difined by SIGEP (Comissão Brasileira de Sítios Geológicos e Paleontológicos), a Brazilian commission responsible for identifing geological and paleobiological sites of exceptional scientific value.

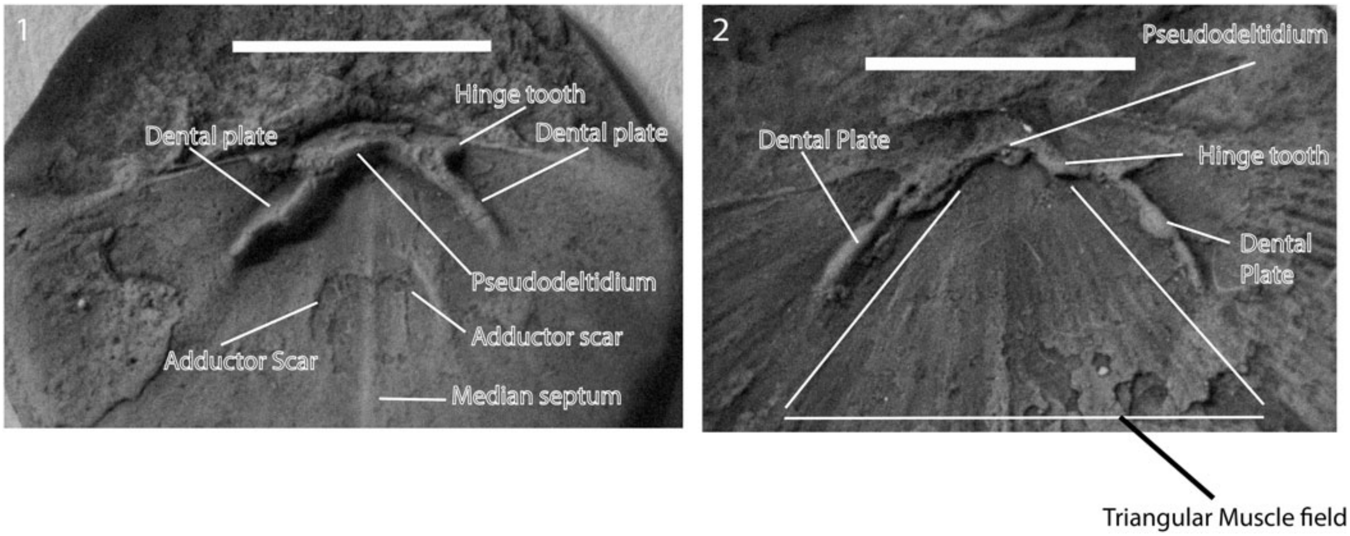

Figure 4. *Schellwienella clarkei* n.sp. from Ponta Grossa Formation. (**1**) Ventral interior counter-mold (cast in modeling clay). UNIRIO 017-BQ. Scale = 10 mm.; (**2**) Ventral interior counter-mold (cast in modeling clay). UNIRIO 0065-BQ. Scale = 10 mm.

Description.—Shell with subcircular to circular outline. Moderate size, length varying from 4 to 27 mm and width varying from 5 to 38 mm. Biconvex to plano-convex. Hinge line straight, ventral beak small, erect and pointed, when compared to a more concave and broadened as is the one on the dorsal valve. Costellae by intercalation and bifurcation or exclusively by one or another, which are separated by a reduced interspace. Proportions of length to width about as 0.65 to 0.75. Pseudopunctate shell.

Ventral interior.—Delthyrium completely closed by the pseudodeltidium (large, convex); triangular-shaped stout hinge teeth, wider in the base and narrowing towards the apex, supported by short and posteriorly divergent dental plates. The latter, in juvenile specimens can be less developed, with greater angle of divergence (120-110°), becoming smaller in ontogeny (100-70°). Wide triangular muscle field, reaching about one-third to half the length of the valve, with both adductor and diductor scars anteriorly striated with a sub-circular shape narrowing anteriorly, completely surrounding the flabellate adductor scars. These are well impressed lanceolate scars, separated by a low median septum that extends about half the length of the valve. Fimbriate micro-ornamentation next to the anterior commisure. Pseudopunctation, in random pattern.

Dorsal interior.—Bilobed cardinal process with stout, triangular lobes and a median groove facing each lobe, delimited by a small chilidium. Notothyrium anteriorly open, in order to expose the attachment of cardinal process lobes. Dental sockets triangular in shape supported by short and weakly curved socket plates. Well impressed lanceolate adductor muscle scar, posteriorly striated. Median septum dividing adductor scar, that extends half the length of the valve. (Figs. 4 and 5)

Etymology.—Species dedicated to John Mason Clarke, pioneer paleontologist with extensive studies of Devonian invertebrates from the Paraná Basin.

Materials.—Sixty one specimens (molds, exclusively) collected in different outcrops in Brazil and Bolivia; see Table 2 for details.

Dimensions.—See Table 3 and Figure 6.

Remarks.—This species was included in the genus *Schuchertella* by Clarke (1913) on the basis of similarities between exterior molds, as are mostly preserved in Orthotetida genera from South America. This kind of preservation makes generic assignment problematic regarding this group (Williams and Brunton, 1993). The present authors include it in the genus *Schellwienella* on the basis of interior molds containing important diagnostic features such as shell's microstructure (pseudopunctation), cardinalia, and dental plates. The recognition of these features also helps to differentiate many "*Schuchertella*" *agassizi* records in Brazil by the erection of a new species for the Paraná Basin. The new species *Schellwienella clarkei* resembles *Schuchertella agassizi* in ornamentation, but differs in shell's microstructure and between the divergence angle of the dental plates. Regarding the species *Schellwienella sulivani*, the Brazilian specimens possess larger and heavier shells (varying from 27 to 35 mm in length to 40–55 mm in width), and more ovate adductor scars when compared to *S. clarkei*. Meanwhile, *Schellwienella sancticrucis* is the most different one, with rounded outline, coarser ornamentation and bigger muscle field when compared to *S. clarkei.*

Discussion

Taxonomic history: ornament, microstructure and cardinalia.—Classification of specimens from the Ponta Grossa Formation as "*Schuchertella*" *agassizi* (Clarke, 1913) is based on ornamentation pattern, which develops from the beak to the anterior margin, with primary and secondary costae gradually originating through bifurcation. This feature is also present on the original description of the species from the Ererê Formation. However, it is not the most significant diagnostic character, and therefore Clarke's classification needs to be reconsidered.

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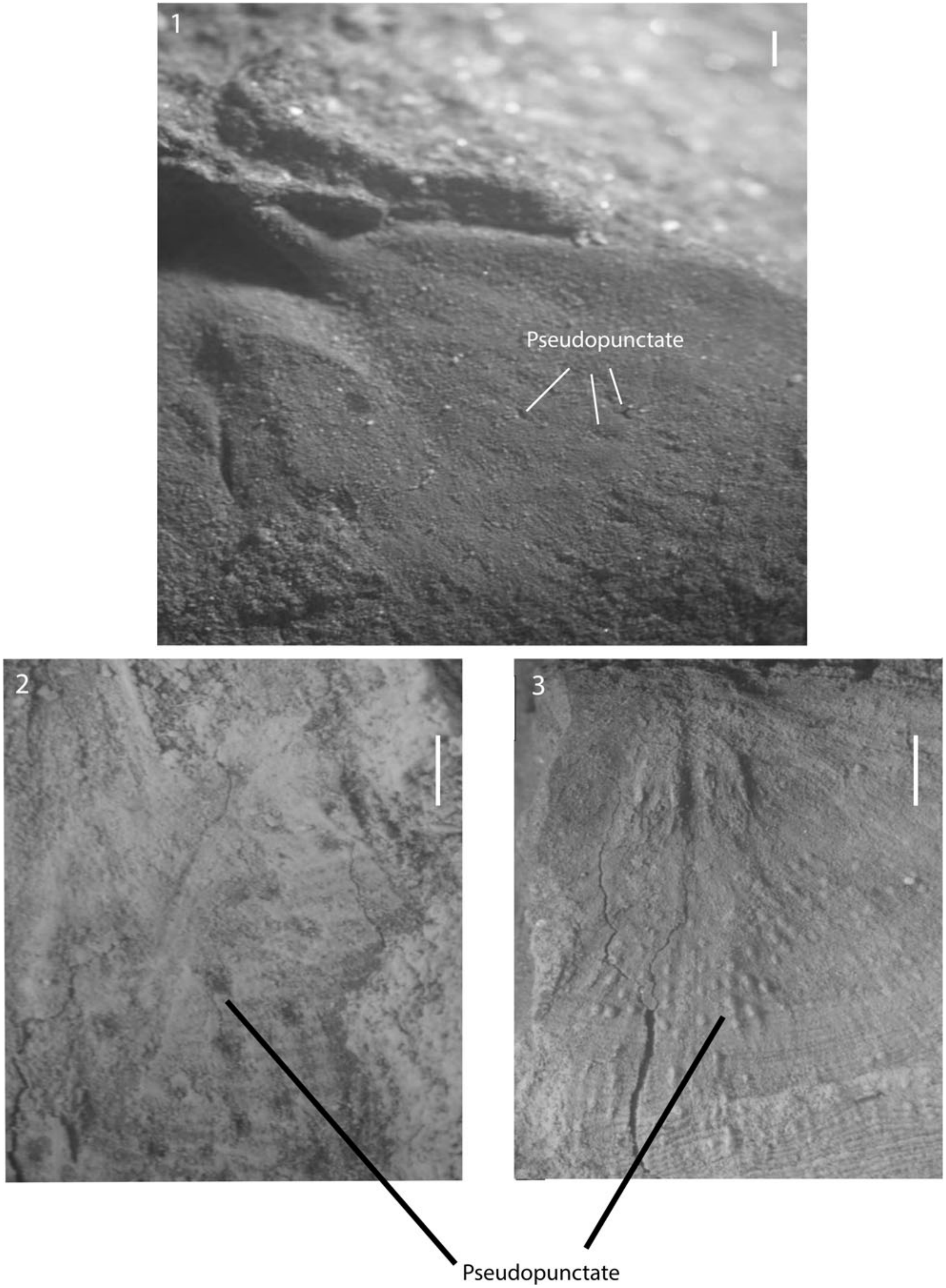

Figure 5. *Schellwienella clarkei* n.sp. from Ponta Grossa Formation. (**1**) Ventral interior counter-mold highlighting the presence of pseudopunctae in the surface. UNIRIO 0051-BQ B. Scale = 1 μm.; (**2**) Ventral interior mold highlighting the presence of pseudopunctae in the surface. UNIRIO 0505-BQ A. Scale = 1 mm.; (**3**) Ventral interior counter-mold highlighting the presence of pseudopunctae in the surface. UNIRIO 0505-BQ B. Scale = 1 mm.

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Table 2. Sample numbers, stratigraphic position and outcrops.

Stratigraphy	Locality (outcrop)	Sample numbers
Ponta Grossa Formation	Fazenda Rivadávia	UNIRIO 0549-BQ, 0571
Ponta Grossa Formation	Ponta Grossa Municipality	DGM 1533, 1534, 1535, 1536
Ponta Grossa Formation	Railroad track, First Curve	UNIRIO 0065-BQ, 0067, 0070 A e B
Ponta Grossa Formation	Jaguariaíva-Arapoti branch, former Jaguariaíva-Jacarezinho branch	UNIRIO 0051-BQ A and B, 0052-BQ, 0075-BQ, 0186-BQ, 0187-BQ, 0199-BQ A and B, 0237-BQ, 0505-BQ, 0513, ||DGM 1749, 1751, 1764, 1792, 1804, 1805, 1819, 1852, 1857, 1908, 1909, 1917, GP/1E 5641, 7551 A and B, 7554 A and B, 7556, 7557, 7562, 7655 A and B, 7702, 7712, 7790, 7804, 7809, 7867 A and B, 7919, ||DGM 1839, 1944
São Domingos Formation	Tibagi Municipality	DGM 1611, 1620, 1987, 3854, 4856
São Domingos Formation	Santa Cruz, Palmeira Municipality	||DGM 1960, 1961
Icla, Belén, Gamoneda and Huamampampa formations	Bolivia	USNM 209058, 209140, 209158; 209159, 209160, 209161, 209163, 209164

Table 3. Measurements (in mm) of the species *Schellwienella clarkei* and *Schuchertella agassizi* Rathbun. ML = Mean length; MW = Mean width; MdL = Median length; MdW = Median width; MnL = Minimum length; MnW = Minimum width; MxL = Maximum length; MxW = Maximum width; SDL = Standard deviation length; SDLW = Standard deviation width.

Species	Number of measured specimens	MdL	MdW	MnL/MxL	MnW/MxW	M ± SDL	M ± SDW
Schellwienella clarkei (Paraná Basin)	20	18.275	26.915	3.38/28	5.17/38.09	19.5 ± 7.043	28.16 ± 8.953
Schellwienella clarkei (Bolivia)	30	16.476	23.246	4.5/31.8	8.7/41.6	16 ± 7.555	23.25 ± 10.192
Schellwienella clarkei (Paraná and Bolivia)	50	17.196	24.714	3.38/31.8	5.17/41.6	17.1 ± 7.404	24.845 ± 9.873
Schuchertella agassizi (Amazonas Basin)	23	6.869	9.934	2.5/15	5/18	7 ± 3.193	10 ± 3.619

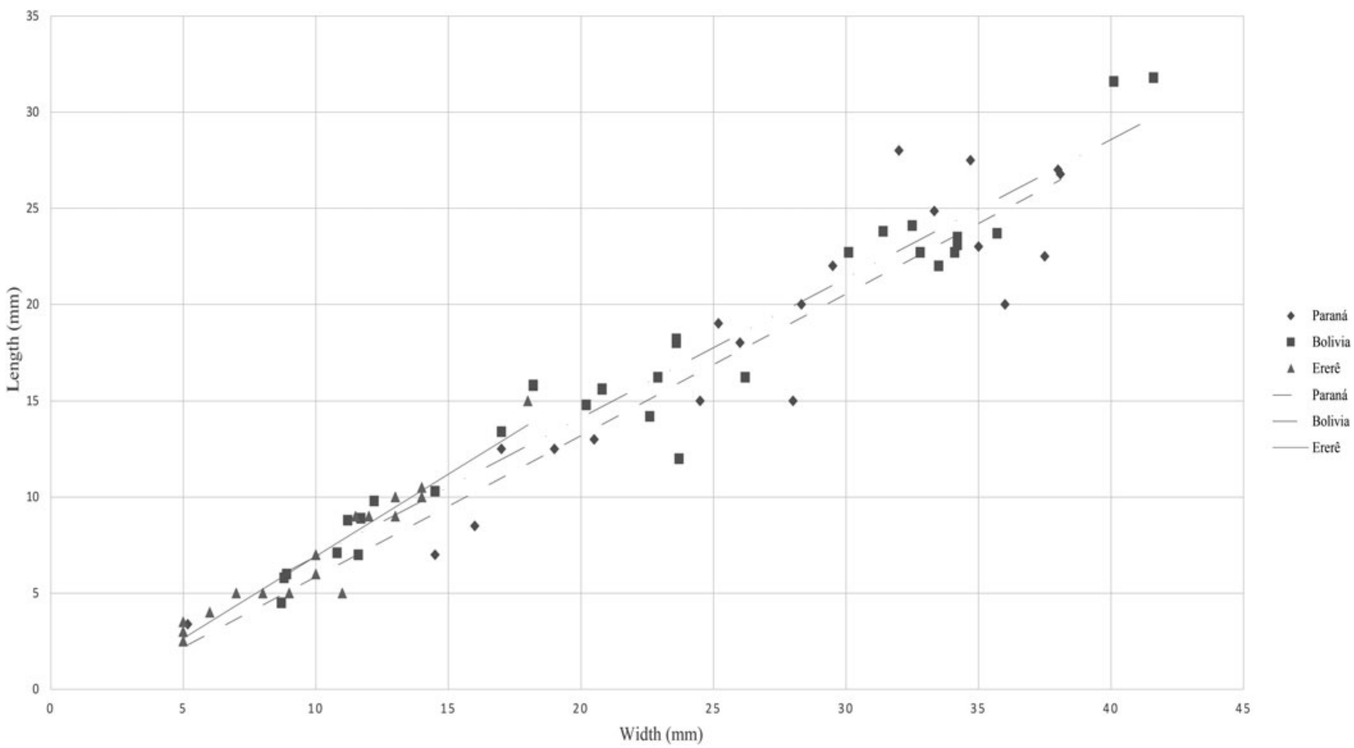

Figure 6. Scatter diagram plotting length to width of *Schellwienella clarkei* from Paraná Basin, Brazil; *Schellwienella clarkei* from Bolivian formations; *Schuchertella agassizi* from Ererê Formation, Amazonas Basin, Brazil.

Schuchertella was erected by Girty (1904), type species *Streptorhynchus lens*, for specimens that lacked a median septum and dental plates (Weller, 1914; Easton, 1962; Stigall Rode, 2005). The recognition of extropunctation in *Streptorhynchus lens*, previously described as impunctate, resulted in a modification of *Shuchertella*'s diagnosis, restricting it to extropunctate forms (Thomas, 1971; Stigall Rode, 2005). The identification of shell structure is essential in Orthotetidina's taxonomic hierarchy. According to Williams and Brunton (1993) the details of microstructure can be synapomorphies of certain groups. Also, the articulation apparatus and muscle field are considered just as essential to ensure a precise taxonomic identification. Three groups of microstructure are recognized, impunctate (e.g. Chilidiopsidae, Areostrophiidae),

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pseudopunctate (e.g Pulsiidae), extropunctate (e.g Schuchertellidae) (William and Brunton, 1993; Long and Brunton, 2005).

Small dental plates supporting hinge teeth in *Schuchertella* specimens were discussed by Boucot (1959b), who disagreed with this classification, mentioning that such plates are present in *Schellwienella* and not in *Schuchertella*. Details from the cardinalia were used by Cooper and Grant (1974), Bassett and Bryant (2006) and Sun and Baliński (2008) to justify the inclusion of *Schuchertella* and *Schellwienella* within Orthotetacea. They assigned two subfamilies, Pulsinae and Schuchertellinae to this superfamily. The Pulsinae would include Schuchertellidae specimens with dental plates (*e.g. Pulsia* and *Schellwienella*) and the Schuchertellinae would not have dental plates (*e.g Schuchertella*). Another important structure from the cardinalia to be considered when ascribing brachiopods to *Schellwienella* is the presence and size of a pseudodeltidium (Isaacson, 1977, 1993), in which specimens possess a large and convex pseudodeltidium (Halamski and Baliński, 2009; Mottequin and Simon, 2017).

The main reasons that warrant familial separation are details from shell microstructure, which according to Williams and Brunton (1993) would have priority during taxonomic classification of Orthotetacea, along with structures from the articulation apparatus and presence or absence of dental plates (as discussed by Cooper and Grant, 1974; Bassett and Bryant, 2006). The Pulsiidae are described as possessing pseudopunctae and dental plates variable in angle and length, and Schuchertellidae as possessing extropunctae and bearing hinge teeth unsupported by dental plates (Williams and Brunton, 1993; Williams and Brunton in Williams et al., 2000; Long and Brunton, 2005), therefore it is inappropriate to keep Pulsiinae as a subfamily within Schuchertellidae.

Shell microstructure.—Pseudopunctation was already reported for *Schellwienella* by Boucot (1959a) in juvenile specimens and was used by Brice et al. (2013) as a criterion of differentiation from *Schuchertella*.

Microstructure preservation is complex, which sometimes enables a precise identification within a taxonomic group. Studied molds' preservation can provide equivocal information (presence or absence) of this structure (Cerri, 2013). However, differentiating pseudopunctae and extropunctae is a taphonomic-related issue (Williams and Brunton, 1993). Pseudopunctation consists of inwardly directed conical deflections, which may or may not possess calcite rods (taleolae). These can appear as tubercles on the valve interiors. Extropunctae occur as a depression on the interior of the valve. During fossilization, these features are often filled by fine sediment or diagenetic precipitates. When the extropunctae are filled, pseudopunctate microstructure can be misidentified. Here, microstructure is considered as pseudopunctate, since similar tubercles are found, along with its origin as discussed herein. In association with other diagnostic characters that fit *Schellwienella*, the diagenetic precipitation hypothesis is currently discarded.

The recognition of extropunctae in *Schuchertella lens* led Cooper and Dutro (1982) to create a new genus *Floweria*, which resembles *Schuchertella* in outline and ornamentation, but with a reduced interarea and impunctate fabric. This genus also resembles *Eoschuchertella*, also impunctate, but bearing differences in the cardinalia and the ornamentation pattern (Cooper and Dutro, 1982; Mottequin, 2008).

Taxa comparison.—Schuchertella, Floweria, Eoschuchertella, Schellwienella are similar regarding its external morphology, which led Stigall Rode (2005) to give greater evolutionary importance to shell microstructure and to species chronostratigraphy, as presented in Table 4. Cooper and Grant (1974) described a single species, *Schuchertella subvexa* which occurred from latest Devonian (Famennian) to Upper Permian. They did not consider the divergences between the generic description and the morphology observed in typical Devonian specimens. More recently, *Schuchertella bassa* by Grant (1995), also studied by Shen and Claphan (2008), recognized the cemented life habit in this species. This is similar to what is observed in orthotetoids from the late Paleozoic (Brett and Walker, 2002). Pedicle atrophy during the early stages of life led to an unattached stock and, consequently, an epibenthic (lying on the sea floor) mode of life, was found in genera such as *Pulsia, Schellwienella* and *Orthotetes*, in the lower Paleozoic (Williams, 1953; Williams and Brunton, 1993). This questioned the viability of the genus's presence in for a wider stratigraphic distribution. For these reasons, it is not possible to attribute the Paraná specimens to any *Schuchertella* species, due to not only its chronostratigraphic distribution, but also the microstructure details and paleoecological characteristics.

Generic evolutionary relations.—Even though Williams (1956) was not able to identify pseudopunctae in Silurian orthotetacid specimens, Boucot (1959a), through written communication with Williams in 1957, highlighted its presence in juvenile specimens of *Schellwienella*. The 'schuchertellid' brachiopods lack dental plates, having their first known occurrence for the Lochkovian, possibly from a schellwienellid ancestor. The older *Schellwienella*-like species is known from England's upper Silurian (Boucot, 1959a). Girty (1904, 1908) and Campbell (1957) suggested that its origin was in the Silurian, becoming pseudopunctate in the Lower Devonian (Williams et al., 1970), with greater development during the Late Devonian/Early Mississipian.

The ancestral relationships within Orthotetacea were also debated by Campbell (1957), following the criteria also used by Girty (1908) and Dunbar and Condra (1932), without including the reduction and development of dental plates. Evolutionary relationships of shell microstructure could have been responsible for the outwardly directed extropunctae to be derived from the inwardly directed pseudopunctae, due to a change in its organic components (Williams and Brunton, 1993). Considering a recent taxonomic classification, the single extropunctate family is Schuchertellidae, which had its origin in the lower Paleozoic, followed by greater diversification during the Carboniferous and Permian.

Schellwienella clarkei *n. sp. distribution.*—The occurrence of *Schellwienella* in the Paraná Basin had already been mentioned by Copper (1977) with no description of its diagnostic characters. The specimens found in the Ponta Grossa and São Domingos formations belong to *Schellwienella*, given the presence of pseudopunctae, dental

Table 4. Comparative morpho-anatomic data of each Late Paleozoic Orthotetida genera. Pr = Profile, Int = Interarea, CP = Cardinal Process, DPl = Dental Plates, MS = Median Septum, MF = Muscle Field, SF = Shell's Fabric, Chronostrat = Chronostratigraphy, References.

Taxa	Pr	Int	CP	DPl	MS	MF	SF	Chronostrat	References
Schuchertella	Biconvex?	Ventral interarea high and linear (anacline), chilidium convex	Bilobed	Absent	Absent	Flabellate ventral muscle scars	Extrapunctate	Upper Devonian (Famennian) – upper Permian	Girty (1904); Williams and Brunton in Williams et al. (2000); Stigall Rode (2005)
Schellwienella	Biconvex to planoconvex	Ventral interea with delthyrium completely covered by a convex pseudodeltidium. Dorsal interarea with notothyrium anteriorly opened, covered by small chilidium.	Bilobed	Present	Present	Triangular ventral field. Lanceolate adductor scar.	Pseudopunctate	Lower Devonian (Praguian-Emsian) – Lower Carboniferous	Williams and Brunton in Williams et al. (2000); Bassett and Bryant (2006)
Floweria	Planoconvex to unequally biconvex	Ventral interarea moderately long (longitudinally). Dorsal interarea greatly reduced.	Bilobed, with low lobes, medially grooved	Present	Present (dorsal low myophragm)	Ventral muscle field subcircular. Adductor roundly flabellate	Impunctate	Lower Devonian – Upper Devonian (Frasnian)	Cooper and Dutro (1982); Williams and Brunton in Williams et al. (2000); Stigall Rode (2005)
Eoschuchertella	Strongly ventribiconvex	Ventral interarea low (apsacline), covered by convex pseudodeltidium. Dorsal interarea low and weakly noticeable, covered by reuced chilidial plates.	Lobes low and grooved. Less developed	Present	Present (weak dorsal myophragm)	Muscle scar ill defined	Impunctate	Lower Devonian (Emsian) – Middle Devonian (Eifelian)	Cooper and Dutro (1982); Herrera et al. (1998); Williams and Brunton in Williams et al. (2000)
Iridistrophia	Planoconvex to Concavoconvex	Pseudodeltidium convex. Chilidium reduced or vestigial	Bilobed, with well-developed lobes	Present	Absent	Indistict muscle scar.	Impunctate	Lower Devonian	Herrera et al. (1998); Williams and Brunton in Williams et al. (2000); Jansen (2001, 2016)
Schuchertellopsis	Irregular ventral profile. Dorsal valve plane to weakly convex	Ventral interarea with arched pseudodeltidium. Dorsal interarea weak.	Uncertain (poorly known dorsal valves)	Absent	Present – in one subgenus (weak ventral myophragm)	Indistict muscle scar.	Pseudopunctate/ Extrapunctate	Middle Devonian (Eifelian) – Upper Devonian (Frasnian)	Williams and Brunton in Williams et al. (2000); Long and Brunton (2005)
Streptorhynchus	Ventribiconvex	Ventral interarea apsacline. Pseudodeltidium with monticulus. Chilidium small.	High, with occasionally with short median or node at base	Absent	Absent	Flabellate ventral muscle scars. Dorsal muscle scar faintly impressed.	Extrapunctate	Carboniferous - Permian	Williams and Brunton in Williams et al. (2000)
Xystostrophia	Biconvex	Ventral interarea apsacline, high convex pseudodeltidium. Dorsal interarea anacline, low chilidium	Thin, bilobed, posteriorly projected	Present	Present	Large, rhomboidal diductor scar	Impunctate	Middle Devonian	Williams and Brunton in Williams et al. (2000); Stigall Rode (2005); Halamski (2009); Halamski and Balínski (2013)
Derbyia	Planoconvex, convexi-concave or biconvex	Ventral interea with flat pseudodeltidium and triangular delthyrium. Small chilidium, occasionally with median groove	Long or short cardinal process, bifid at free end	Present	Present	Ventral muscle scar flabellate; dorsal subcircular adductor scars	Pseudopunctate	Lower Carboniferous – Upper Permian	Cooper and Grant (1974); Williams and Brunton in Williams et al. (2000); Torres-Martínez et al. (2018)

plates supporting hinge teeth, a median septum in the ventral valve, and a triangular muscle field. Therefore, it is impractical to retain the name *Schuchertella agassizi*, a species from the Ererê Formation (Rathbun, 1874), which has divergences between the descriptions, especially regarding the absence of a median septum and pseudopunctation. Hence, it is here described as a new species named *Schellwienella clarkei* n. sp.

Considering that the origin of the first 'Schellwienellid' occurrence is from the late Early Silurian (Boucot, 1959a), the occurrence of *Schellwienella* in southern Brazil supports the origin of pseudopunctate *Schellwienella* in Lower Devonian (Williams et al., 1970). Based on samples described herein from the Ponta Grossa strata (Pragian-Emsian), it is possible to infer that the origin of pseudopunctate orthotetoids could be in the Southern Hemisphere (southwestern Gondwana).

A large number of specimens studied by Clarke (1913) were assigned to the species *Schuchertella agassizi*, originally from the Amazonas Basin, based strictly on the similarity of exterior molds, which show both intercalation and bifurcation. The original description of the species by Rathbun (1874) indicates differences between the material from the Amazonas and Paraná Basin. According to Rathbun (1874) the ornamentation pattern occurs by intercalation, which is different than *S. clarkei* n. sp.

Besides the difference of exterior molds, features of the interior are diagnostic, such as the divergence between the angle of the dental plates in *Schuchertella agassizi* and *Schellwienella clarkei* n. sp., of 135 degrees in the former and of 70 to 110 degrees in the latter. Even considering that this angle in juvenile specimens becomes smaller in ontogeny, the greatest angle measured so far was of 120 degrees, maintaining the difference between *Schuchertella agassizi* and *Schellwienella clarkei*. Another internal feature that separates the Amazonian *S. agassizi* from the southern *S. clarkei* pertains to the kind of microstructure, which not only differentiates species, but also supports in generic differences between *Schuchertella* and *Schellwienella*. Even though Rathbun (1874) did not describe the texture of Amazonian specimens, some samples from the Ererê Formation have been seen by the first author, in which no punctation or pseudopunctation were observed. Meanwhile, the pseudopunctae occur in Paraná specimens, establishing the difference between both species. Another distinguishing feature seen in samples is regarding the absence of a dorsal septum in *S. agassizi*, (not specified in Rathbun, 1874), however present in *S. clarkei* n. sp. specimens.

The species *Schuchertella sulivani* was identified by Clarke (1913) from the Ponta Grossa Formation as the same as described by Morris and Sharpe (1846) from the Falkland Islands, Fox Bay Formation, Lower Devonian (Stone, 2010; 2016) and by Sharpe (1856) to its equivalent unit in the Bokkeveld Group, South Africa (Penn-Clarke, 2019). The species *S. sulivani* in both Fox Bay Formation and Bokkeveld Group are described by Morris and Sharpe (1846) and by Sharpe (1856) as identical and possessing ornamentation in a bifurcation pattern; however, that assigned by Clarke (1913) possesses a pattern similar to "*Schuchertella*" *agassizi,* having bifurcation and intercalation. Nevertheless, it is not the purpose herein to discuss this matter, and we accept the species *Schuchertella sulivani* as occurring in all three Malvinoxhosan Realm regions.

The specimens assigned by Clarke (1913) as *Schuchertella sulivani* (Fig. 7) were described as of larger and heavier shells than "*Schuchertella*" *agassizi* (*Schellwienella clarkei* n. sp. herein), but also possibly different ontogenetic stages. The species *Schuchertella sulivani* was relocated to *Schellwienella* by Caster (1939) and followed by Lange (1954). Even though no formal description was offered to justify this re-assignment; following works have retained this classification without question (Aldiss and Edwards, 1999; Stone, 2010, 2012, 2016; Stone and Rushton, 2013). Since the exterior molds possess a similar ornamentation pattern in both *Schellwienella sulivani* (Ponta Grossa Formation) and *Schellwienella clarkei* n. sp., thereby presenting a possible intraspecific variation, the main differences consist mostly on the shape of the dorsal adductor scar, which assumes a lanceolate form in *S. clarkei* and an ovate form in *S. sulivani*. However, since there are few specimens of *Schellwienella sulivani* a conclusion can only be tentative at this time. More specimens need to be studied in order to enumerate the differences between the new species *Schellwienella clarkei, Schellwienella sulivani* from Ponta Grossa Formation and *Schellwienella sulivani* from other Malvinoxhosan Realm areas. Meanwhile, we accept both as different species, with its main difference regarding the interior dorsal mold.

Another species described by Clarke (1913) was *Schuchertella sancticrucis* (Fig. 7) from the Santa Cruz shales, São Domingos Formation, Santa Rosa Member, currently São Domingos Formation, Givetian in age (Melo, 1988; Grahn et al., 2013). Caster (1939) proposed closer similarity between *Schuchertella sancticrucis* and *Schellwienella sulivani* (from the Falkland Islands) due to internal characters, which led to the former's reassignment as *Schellwienella sancticrucis*. These criteria were also followed by Lange (1954) but without detailed taxonomic discussion. Based on elements provided by Clarke (1913), *Schellwienella sancticrucis* possesses a coarser costa and shows little evidence of multiplication, along with a nearly circular outline. The interior is described as presenting a very large flabellate scar, however it is an ill-defined muscle field. Clarke (1913) stated that such features did not allow an in-depth comparison to other species. Yet, they do offer distinctions to the new species *S. clarkei*, which possesses a different ornamentation pattern and a different outline. In addition, according to the analysis of Clarke's holotype, there are slight differences between *Schellwienella clarkei* n. sp. and *Schellwienella sancticrucis* muscle field, with a more prominent adductor scar in the latter. Again, the lack of sufficient specimens leads us here to agree with Clarke (1913), reinforcing the need of more in-depth studies about *Schellwienella sancticrucis* for further comparisons.

Beyond Paraná State, Quadros (1987) reported a possible first occurrence of "*Schuchertella*" specimens from the outcrops of Serra do Atimã, in Chapada dos Guimarães municipality, Mato Grosso State, northwest of the Paraná Basin (Chapada series; Alto-Garças sub-Basin). Even though the Quadros (1987) specimens are described as impunctate, based on the figured fossils, interior mold structures resemble pseudopunctae (Quadros, 1987, pl. 3, figs. 3, 4, 9). Also, the dental plates and muscle scars are split by a median septum. Another similarity is shown in the ornamentation pattern, described by Quadros (1987) as showing ontogenetic bifurcation and, more rarely, by intercalation.

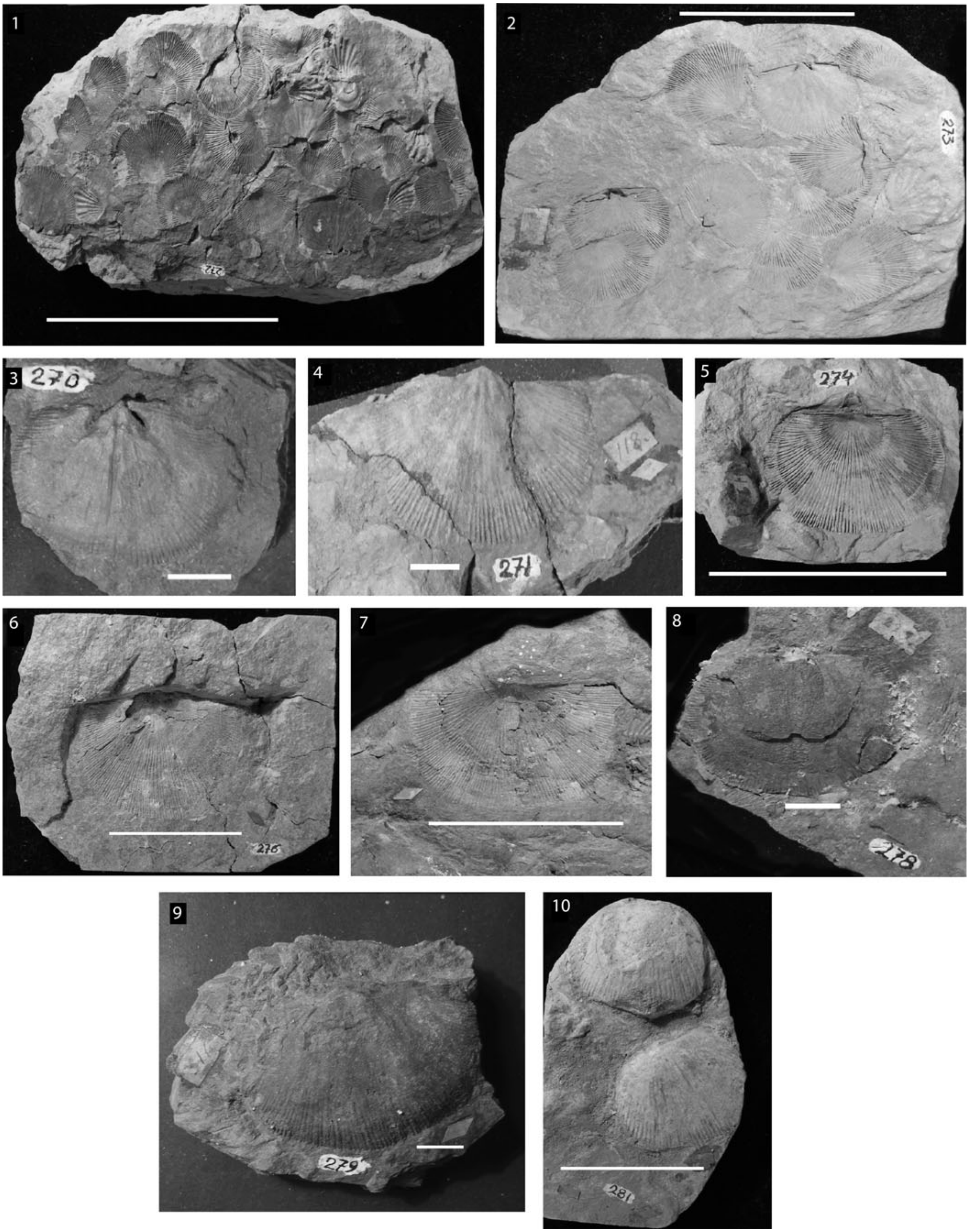

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Figure 7. Brazilian Devonian orthotetides coeval with *Schellwienella clarkei* sp.n. (**1**) DGM 272 – I. "*Schuchertella*" *agassizi*. Clarke (1913). Plate 23, fig. 6, 8, 12, 13. Lower Devonian. Ponta Grossa Formation. Scale = 100 mm; (**2**) DGM 273 – I. "*Schuchertella*" *agassizi*. Clarke (1913). Plate 23, fig. 5. Lower Devonian. Ponta Grossa Formation. Scale = 50 mm; (**3**) DGM 270 – I. "*Schuchertella*" *agassizi*. Clarke (1913). Plate 23, fig. 11. Lower Devonian. Ponta Grossa Formation. Scale = 10 mm; (**4**) DGM 271 – I. "*Schuchertella*" *agassizi*. Clarke (1913). Plate 23, fig. 7. Lower Devonian. Ponta Grossa Formation. Scale = 10 mm; (**5**) DGM 274 – I. "*Schuchertella*" *agassizi*. Clarke (1913). Plate 23, fig. 10. Lower Devonian. Ponta Grossa Formation. Scale = 50 mm; (**6**) DGM 276 – I. "*Schuchertella*" *sulivani*. Clarke (1913). Plate 23, fig. 21. Lower Devonian. Ponta Grossa Formation. Scale = 50 mm; (**7**) DGM 277 – I. "*Schuchertella*" *sulivani*. Clarke (1913). Plate 23, fig. 23. Lower Devonian. Ponta Grossa Formation. Scale = 50 mm; (**8**) DGM 278 – I. "*Schuchertella*" *sulivani*. Clarke (1913). Plate 23, fig. 16. Lower Devonian. Ponta Grossa Formation. Scale = 10 mm; (**9**) DGM 279 – I. "*Schuchertella*" *sulivani*. Clarke (1913). Plate 23, fig. 22. Lower Devonian. Ponta Grossa Formation. Scale = 10 mm; (**10**) DGM 281 – I. "*Schuchertella*" *sancticrucis*. Clarke (1913). Plate 23, figs 14–15. Middle Devonian. São Domingos Formation. Scale = 50 mm.

Therefore, the Quadros (1987) specimens are here considered as belonging to *Schellwienella* cf *S. clarkei*.

Morphological similarities between the external molds of other Orthotetida were responsible for equivocal taxonomic classification of "*Schuchertella.*" In the Malvinoxhosan Realm, this taxon is usually designated as "*Schuchertella*" (Boucot et al., 2001; Rezende et al., 2019a). This assumption allowed Boucot (1975) to suggest this genus was cosmopolitan.

In other South American localities, Méndez-Alzola (1938) described the species *S. agassizi* from the Devonian of Uruguay as of relatively small size, with costae increasing by bifurcation or by intercalation. Even though the Uruguayan samples diverge from the original species *Schuchertella agassizi* from the Ererê Formation and possess the same intraspecific variation as the new species *S. clarkei*, the lack of internal characters in its description do not allow inclusion into the new species.

Isaacson (1977, 1993) described samples from the Icla, Belén, Gamoneda, and Huamampampa formations in Bolivia attributing it to "*Schuchertella*" sp., since no better taxon was available. This description mentions an ontogenetic change of the divergence angle of the dental plates, which tends to become smaller. The same ontogenetic change was observed in Ponta Grossa specimens (Fig. 2.1–2.5, 2.7, 2.14). Isaacson (1977, 1993) mentioned two of the three species established by Clarke (1913) (*Schuchertella sulivani and Schuchertella agassizi*) and criteria to distinguish both species based on size and number of costae; however, the former applied the presence or absence of dental plates as a criteria for the Bolivian fossils. In addition, Isaacson (1977, 1993) pointed out the obsolescent chilidium as an unlikely feature in *Schellwienella*. Nevertheless, the presence of bilobed dental plates, cardinal process and the pseudopunctation are enough to support its generic relocation to *Schellwienella*.

The taxonomic classification for the Brazilian specimens applies to those of Isaacson (1977, 1993) from the Icla, Belén, Gamoneda and Huamampampa formations in Bolivia. Occurrences of the same species in these formations supports marine connections between the Paraná Basin, the Andean (Bolivia) and Chaco (Northwestern Argentina and Paraguay) basins during lower Devonian (Barrett and Isaacson, 1988; Melo, 1988; Grahn et al., 2016; Penn-Clarke, 2019), from which the species would have migrated.

Conclusion

Brachiopods from the Ponta Grossa and São Domingos formations (Brazil) described by Clarke (1913) as *Schuchertella agassizi* are identified herein as *Schellwienella clarkei* n. sp. The generic assignment is supported by the presence of pseudopunctae, dental plates supporting hinge teeth, a median septum in the ventral valve, and a triangular muscle field. This new classification is also known from coeval deposits of Bolivia.

Shell microstructure is confirmed as an important taxonomic criterion within orthotetides. Published studies on orthotetides dealt mostly with North American material and their results were applied uncritically to South American taxa; the revision of the latter seems a fruitful subject of future work.

Scarcity of information regarding Brazilian orthotetide fossils is an issue for proper, in-depth, taxonomic studies. Most of the published works are based on North American late Paleozoic specimens, possibly maintaining gaps of information and identification mistakes about this group (Melo, 1985). Herein, the efforts are aimed at taxonomic clarifications for orthotetide systematics, a group to which varying assignments were made, and further detailed studies regarding the southern hemisphere specimens are needed.

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