Journal of Paleontology, 90(5), 2016, p. 923–958

0022-3360/16/0088-0906
doi: 10.1017/jpa.2016.104

Journal of PALEONTOLOGY
A JOURNAL OF THE PALEONTOLOGICAL SOCIETY

Early Ordovician trilobites from the Iruya area (Cordillera Oriental, northwestern Argentina) and their stratigraphic significance

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Abstract.—The middle part of the Santa Rosita Formation (Tremadocian) is well exposed in the Iruya area, northwestern Argentina. At the Pantipampa and Rodeo Colorado localities, it is composed of shale and sandstone representing a wave-dominated shelf with influence of storm activity. Twenty-two trilobite species are described from these localities. Low-diversity assemblages from the lower part of the succession (*Kainella meridionalis* Kobayashi, *Asaphellus catamarcensis* Kobayashi, *Leptoplastides marianus* [Hoek]) are diagnostic of the early Tremadocian *Kainella meridionalis* Zone. Trilobites from the middle part of the sequence are much more diverse. *Kainella teiichii* Vaccari and Waisfeld, *Gymnagnostus kobayashii* n. sp., *Conophrys* sp. indet., *Asaphellus clarksoni* n. sp., *A. stenorhachis* (Harrington), *A. isabelae* Meroi Arcerito, Waisfeld and Balseiro, *Ogygiocaris*? *iruyensis* n. sp., *Niobe* (*Niobella*) *inflecta* (Harrington and Leanza) n. comb., *Metayuepingia riccardii* n. sp., *Pseudokainella keideli* Harrington, *Apatokephalus rugosus* n. sp., *Onychopyge acenolazai* n. sp., *O. gonzalezae* n. sp., *Nileus cingolanii* n. sp., *N. erici* n. sp., *Leptoplastides marianus*, *Parabolinella* sp. indet., *Hapalopleura* sp. indet., and Ceratopygidae gen. et sp. indet., occur at different levels of the *Kainella teiichii* Zone. This biostratigraphic unit includes the oldest records of *Nileus* Dalman and *Ogygiocaris*? Angelin; *Metayuepingia* Liu, *Niobe* (*Niobella*) Reed, and *Onychopyge* Harrington are here first reported from the Tremadocian of southwest Gondwana. Finally, the uppermost part of the succession is characterized by the absence of the genus *Kainella* Walcott and the occurrence of *Bienvillia tetragonalis* (Harrington), *Asaphellus stenorhachis*, *Pseudokainella keideli* and *Leptoplastides* sp. indet., which are indicative of the middle Tremadocian *Bienvillia tetragonalis* Zone. The trilobites described in this paper provide a basis for the refinement of correlations with other Lower Ordovician sections of the Cordillera Oriental. The genera recognized have their closest affinities with faunas from Scandinavia, Great Britain, and China.

Introduction

The Cordillera Oriental (Central Andean Basin, northwestern Argentina) is characterized by large thrust belts of lower Paleozoic rocks that include late Furongian–late Tremadocian sandstone and shale of the Santa Rosita Formation (Turner, 1960). This formation represents a wide variety of sedimentary environments and has yielded numerous fossils such as trilobites, brachiopods, graptolites, gastropods, echinoderms, bivalves, cephalopods, conodonts, and acritarchs (e.g., Benedetto, 2003; Buatois and Mángano, 2003). Because of their abundance and good state of preservation, the trilobites led to a useful biostratigraphic chart that was originally proposed by Harrington and Leanza (1957) and further refined by subsequent authors (e.g., Tortello et al., 2002; Waisfeld and Vaccari, 2003, 2008; Vaccari et al., 2010). Fossiliferous sections of the Santa Rosita Formation are well exposed in the Santa Victoria, Nazareno, Iruya, Abra de Zenta, Quebrada de Moya, El Perchel, Tilcara, and Purmamarca areas (Fig. 1.1).

The Iruya area comprises a long strip between the village of Rodeo Colorado and the small town of Iruya (Fig. 1.2, 1.3). This region has attracted the attention of paleontologists since the late nineteenth century, when Kayser (1897) provided one of the first descriptions of trilobites from Argentina (*Leiagnostus*? *iruyensis* [Kayser, 1897], *Angelina hyeronimi* [Kayser, 1876], *Beltella ulrichi* [Kayser, 1897]) based on material from the surroundings of the town of Iruya. Later, Harrington (1938) and Harrington and Leanza (1957) revised the material studied by Kayser and, in addition, described a trilobite assemblage dominated by *Parabolina* (*Neoparabolina*) *frequens argentina* (Kayser, 1876) from San Isidro Creek. These faunas characterize the lower part of the Santa Rosita Formation and the *P. frequens argentina* Zone (uppermost Cambrian). Similar trilobites have recently been reported from the lower Iruya River (Spagnuolo et al., 2005) and the San Isidro River (Esteban and Tortello, 2009).

In addition, the Iruya area contains abundant Early Ordovician trilobites; however, the information on their systematics and occurrence is not yet adequate because it is based largely on isolated findings whose precise location is uncertain (Harrington and Leanza, 1957, p. 239). Harrington (1938) and Harrington and Leanza (1957) described a low diversity assemblage composed of *Kainella meridionalis* Kobayashi, 1935, *Leptoplastides marianus*

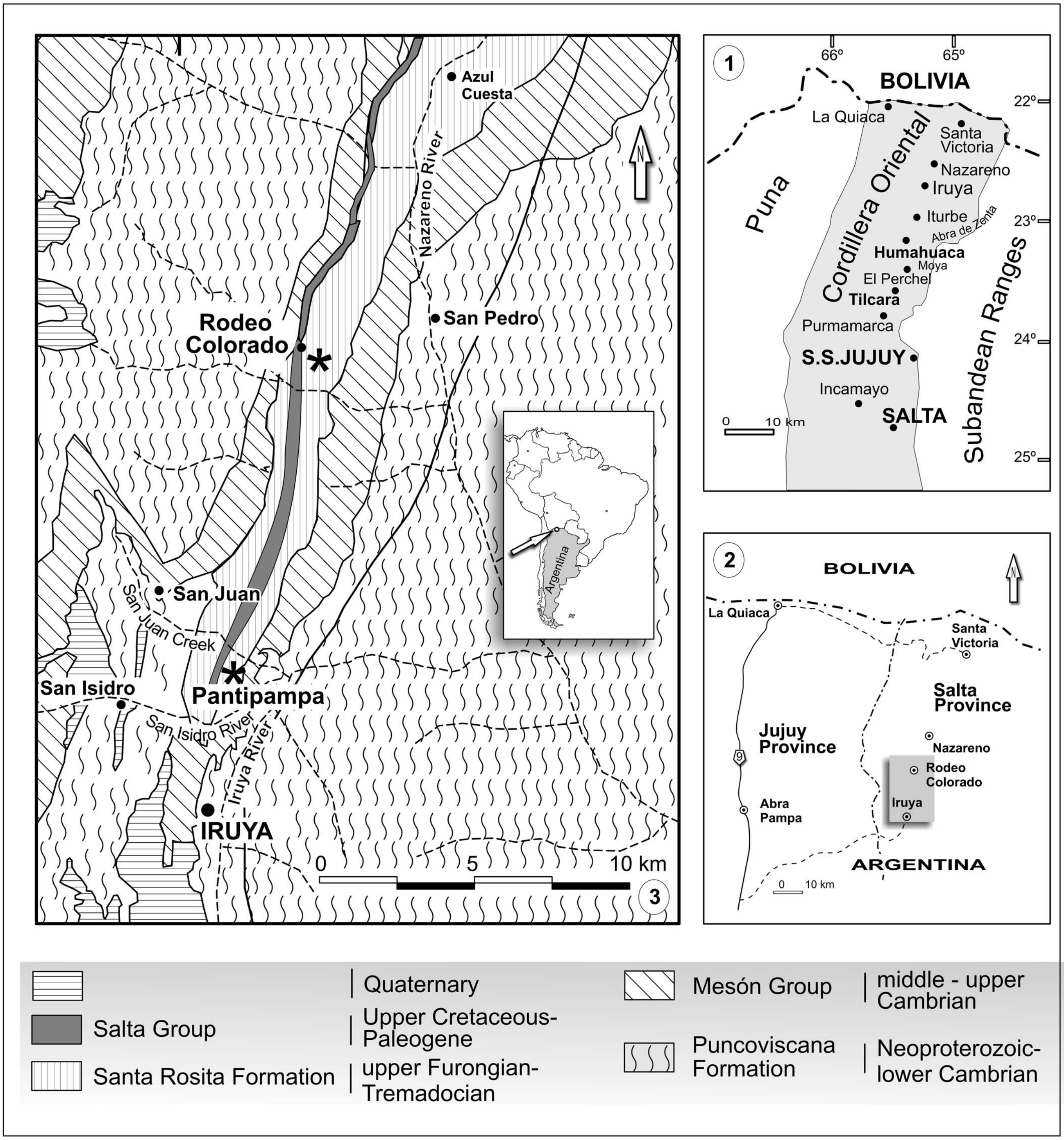

Figure 1. Location map and geologic framework of the Iruya area. **(1)** Simplified map of the Cordillera Oriental, northwestern Argentina, showing classic fossil localities of the Santa Rosita Formation; **(2)** location map of the Iruya area; **(3)** geological sketch of the Iruya area, with the locations (asterisks) of the Pantipampa and Rodeo Colorado sections (after Figueroa Caprini, 1955, unpublished; Vilela, 1960; Turner, 1964; Astini, 2003).

(Hoek in Steinmann and Hoek, 1912), and *Asaphellus catamarcensis* Kobayashi, 1935 from the "Quebrada Colorada" (= San Juan Creek; Figueroa Caprini, 1955, unpublished), whereas Harrington and Leanza (1957) reported other *Kainella* faunas from undetermined localities along the San Pedro River (= Nazareno River). Similar assemblages were also recognized by Figueroa Caprini (1955, unpublished) in Rodeo Colorado. All of these trilobites were originally assigned to the lower Tremadocian "*Kainella meridionalis* Zone" Harrington and Leanza (1957); a unit that has been revised recently by Vaccari et al. (2010).

Vaccari and Waisfeld (2010) and Vaccari et al. (2010) provide a comprehensive systematic revision of the genus *Kainella* Walcott, 1925 in northwestern Argentina and southern Bolivia, emend the diagnosis of *K. meridionalis* sensu

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Harrington and Leanza (1957), and propose a new biostratigraphic scheme that includes the successive early Tremadocian *K. meridionalis* and *K. teiichii* zones. These units were mainly defined on the occurrence of their eponymous species at the El Perchel locality (Fig. 1.1; Vaccari et al., 2010; Meroi Arcerito et al., 2015). Because the Iruya area also reveals valuable data on these biozones, the trilobites from two well-exposed sections, Pantipampa and Rodeo Colorado, are described herein. Specimens of *Kainella* occur here in association with high diversity assemblages, which include asaphids, ceratopygids, olenids, richardsonellids, kainellids, nileids, shumardiids, hapalopleurids, and agnostoids. Nine species are new, four are left in open nomenclature, whereas nine represent taxa that have previously been reported from northwestern Argentina but whose stratigraphic ranges are refined.

Geologic setting

The Argentinian Cordillera Oriental is a high relief thrust system that is bounded to the east by the Subandean Ranges and to the west by the Puna Plateau (Fig. 1.1). Neoproterozoic–early Cambrian metasedimentary rocks of the Puncoviscana Formation, Cambrian quarzite of the Mesón Group, as well as late Furongian–Early Ordovician sandstone and shale of the Santa Victoria Group (Santa Rosita and Acoite formations and equivalents) are well exposed in remarkable ranges extending from the Santa Victoria area in the north to the south of Salta Province (Harrington and Leanza, 1957; Turner, 1960; Turner and Mon, 1979; Moya, 1988, 2008; Astini, 2003).

The Santa Rosita Formation (upper Furongian–Tremadocian) and equivalents (Harrington and Leanza, 1957) record a complex history of sea level changes and a wide variety of sedimentary environments, from tide-dominated estuarines to open marine settings affected by waves (Buatois and Mángano, 2003; Moya et al., 2003; Buatois et al., 2006). Lateral variations in thickness are significant between different localities of the Cordillera Oriental. Exposures show greater thickness toward the north, in the Santa Victoria region, where they are ∽2300 m thick.

Turner (1964), Figueroa Caprini (1955, unpublished), Vilela (1960), and Turner and Mon (1979) provided valuable information on the geology of the Iruya area (Iruya Department, Salta Province). There, shale and sandstone of the Santa Rosita Formation constitute narrow thrust belts which unconformably overlie the Cambrian quarzite of the Mesón Group (Turner, 1960), and are unconformably overlain by the Late Cretaceous–Paleogene continental sandstone of the Salta Group (Turner, 1959) and Quaternary alluvial deposits (Fig. 1.3). The trilobites described herein come from the middle part of the Santa Rosita Formation at the Pantipampa and Rodeo Colorado localities, approximately 5 km and 15 km north northeast of Iruya town, respectively (Fig. 1.3).

The lower parts of the sections studied (Figs. 2, 3) display dark and greenish gray, massive to thinly laminated shale, mudstone and silty mudstone (Facies 1), which are occasionally interbedded with gray, massive, very fine-grained silty sandstone in sharp-based, tabular beds 1–3 cm thick (Facies 2). Facies 1 generally passes vertically from dark shale to greenish gray silty mudstone. Bioturbation is very rare. Many trilobites described herein were collected from this facies, in association with brachiopods, gastropods, bivalves, cephalopods, and echinoderms.

Dark gray to greenish gray, fine to very fine sandstone and calcareous sandstone beds containing bioclastic concentrations have been recognized throughout the Pantipampa and Rodeo Colorado sections (Facies 3). The sandstone beds are 3–15 cm thick and exhibit tabular or lenticular geometry, undulating and erosive bases, and undulating tops with symmetrical or near-symmetrical ripples. Internally, the beds usually display either parallel-lamination or small-scale combined-flow ripple cross-lamination. Scour marks (flute and gutter casts) are common at the bases of these layers. Additionally, small load casts are locally present. The top of some sandstone packages exhibit weak indications of bioturbation.

Bioclastic concentrations generally appear at the bases of the calcareous sandstone beds, constituting lenses and layers up to 4 cm thick. They are easily observable because of their brownish to yellowish color and consist mainly of fragmented brachiopods and trilobites. Occasionally, concentrations occur at the tops of the sandstone beds. Some coquinites contain conodonts of great biostratigraphic value (see below).

Light gray, fine- to very fine-grained sandstone with hummocky cross-stratification in erosive-based beds 5–20 cm thick, are restricted to the lower interval of the Rodeo Colorado section (Facies 4). A typical bed of Facies 4 shows parallel lamination, ripple cross-lamination, and low-angle microhummocky cross-lamination. Laminae develop hummocks and swales; wavelength is 10–20 cm; amplitude is 0.5–1.0 cm. Poorly preserved flute and gutter casts are present at the bases of beds. Bioturbation appears at the tops of some packages.

Facies 1 mostly records continuous background sedimentation. The shale and mudstone of this facies accumulated under low-energy suspension conditions below storm wave base. The abundance of trilobites and other organisms in Facies 1 indicates a suitable environment for the development of benthic life at the sediment-water interface. However, the dark color of some unbioturbated beds may reflect low-oxygen conditions during their deposition (Bottjer and Savrda, 1993).

Facies 2, 3, and 4 reflect event sedimentation. Clearly defined, sharp-based silty sandstone beds of Facies 2 indicate relatively rapid, episodic deposition superimposed upon the more continuous background sedimentation. These deposits are characteristic of muddy shelf areas and are interpreted as extremely distal members of storm sedimentation (Reineck and Singh, 1972; Pedersen, 1985). Facies 2 is regarded as having been deposited below storm wave base (Aigner, 1985; Brenchley et al., 1993).

The occurrence of lenticular and laterally extensive fine- to very fine-grained sandstone and calcareous sandstone of Facies 3 and 4 represents a sudden short-term change from low- to moderately high-energy conditions. These facies record sedimentation above storm wave base, on a platform affected by fair weather and storm waves. The presence of combined-flow ripple cross-lamination, symmetrical to near-symmetrical ripples, and flute and gutter casts in Facies 3 reflects deposition from combined and purely oscillatory flows. The records of bioclastic concentrations (Facies 3) and hummocky cross-stratification (Facies 4) clearly indicate a storm origin for these deposits

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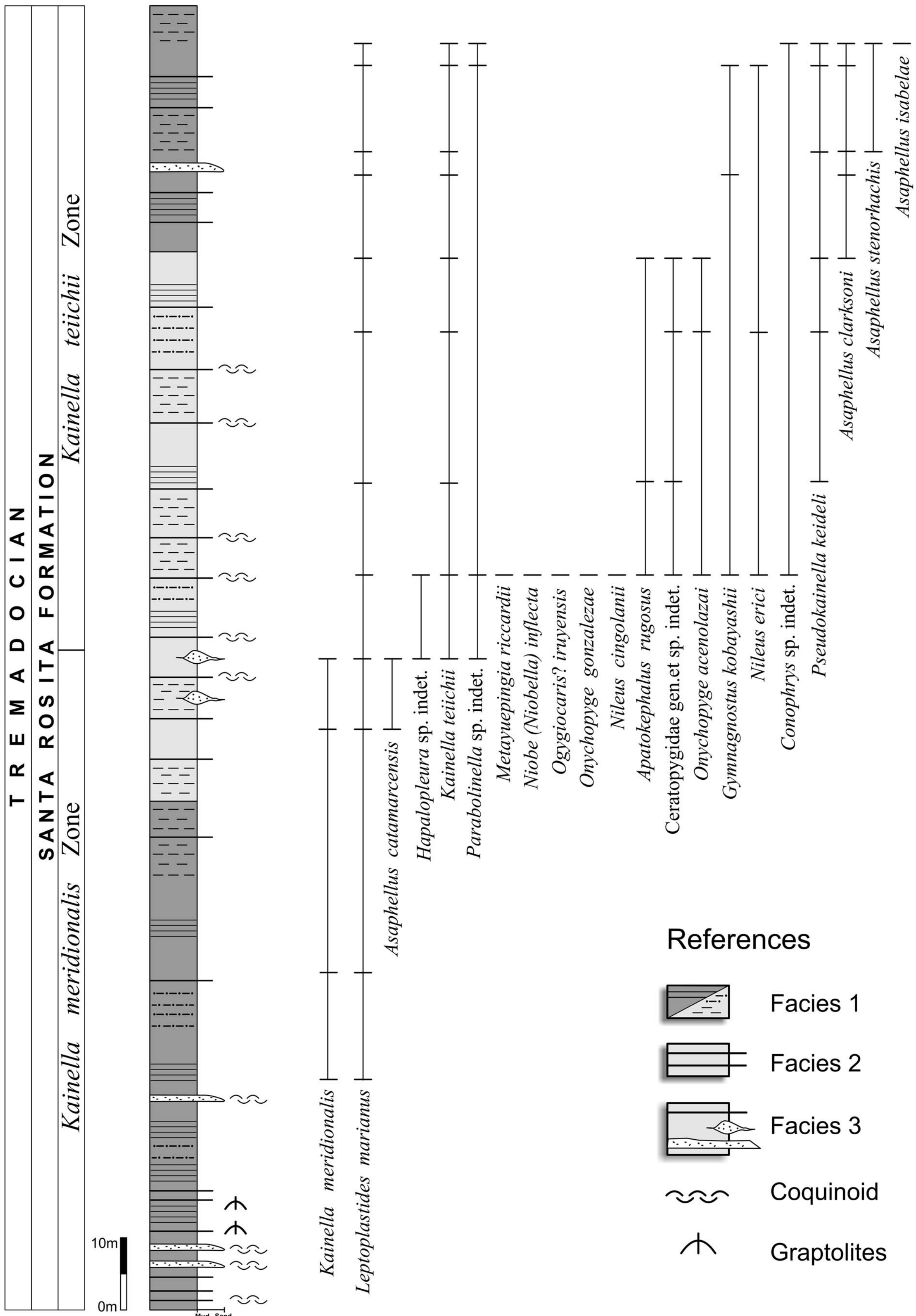

Figure 2. Columnar section of the Santa Rosita Formation at the Pantipampa locality (Iruya area, northwestern Argentina) displaying facies succession and distributions of trilobites identified.

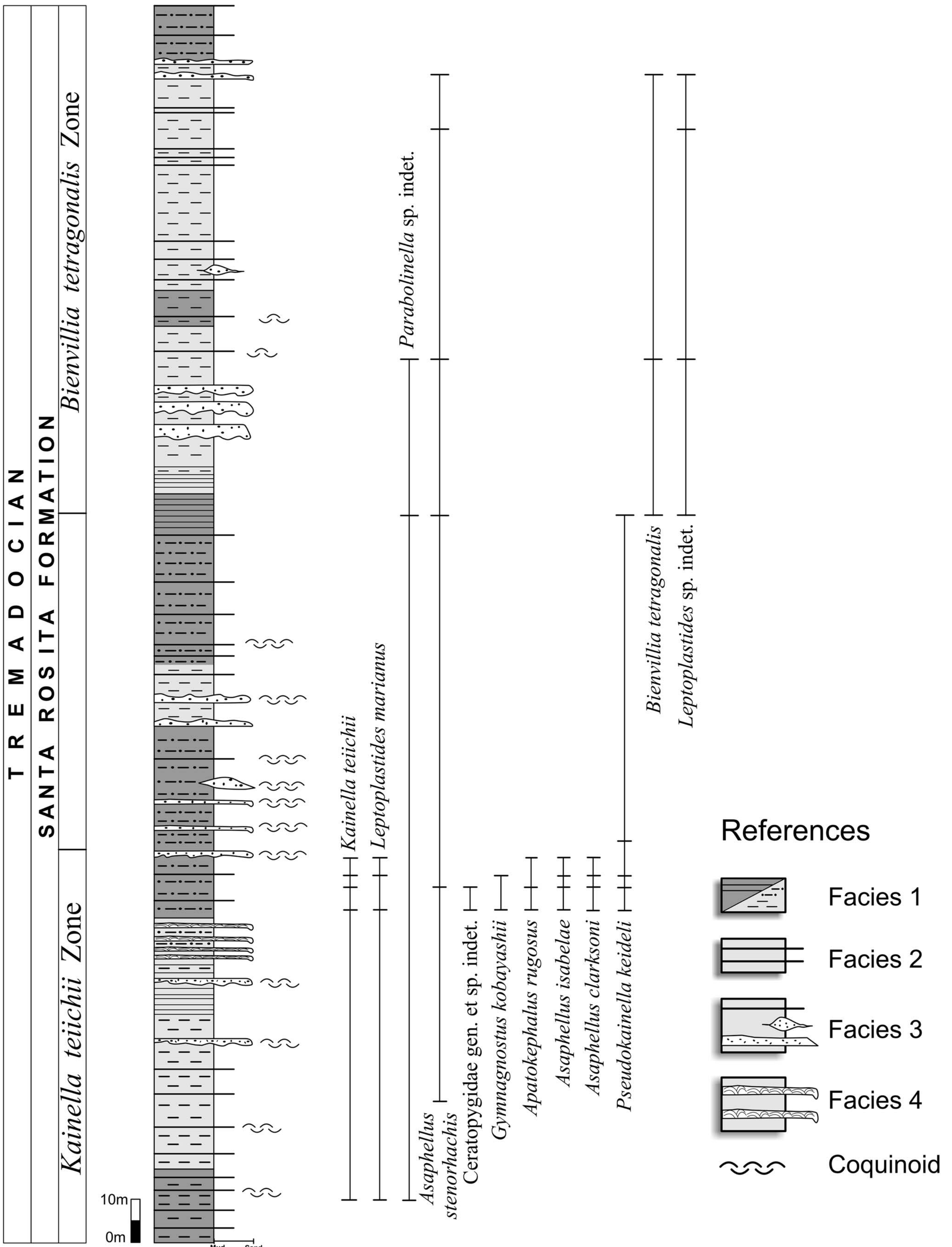

Figure 3. Columnar section of the Santa Rosita Formation at the Rodeo Colorado locality (Iruya area, northwestern Argentina) displaying facies succession and distributions of trilobites identified.

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(tempestites) (Brenner and Davies, 1973; Walker et al., 1983; Brenchley, 1985). However, the absence of amalgamated hummocky cross-stratified beds, and the presence of microhummocky structures and small-sized scour marks suggest moderate energy conditions.

The Pantipampa and Rodeo Colorado sections are interpreted as having formed in a wave-dominated shelf with influence of storm activity. Background sedimentation was punctuated by storm deposition in an upper offshore to offshore-transition setting.

Biostratigraphy

The occurrence and biostratigraphic importance of *Kainella* in South America was first pointed out by Kobayashi (1935), who described in detail an Early Ordovician assemblage composed of *Kainella meridionalis*, *Leptoplastides marianus* (=*Andesaspis argentinensis* Kobayashi, 1935), *Asaphellus catamarcensis* and *Pseudokainella* from the Incamayo area (Fig. 1.1). This trilobite association is characteristic of the "*Kainella meridionalis* Zone"; a unit that was formally proposed by Harrington and Leanza (1957, p, 26, fig. 2, table 1) on material from a detailed section of Santa Victoria and other selected localities of the Cordillera Oriental, including the Iruya area. In the last five decades, new localities of this biozone have been cited in several papers (e.g., Přibyl and Vaněk, 1980; Salfity et al., 1984; Moya, 1988; Rao and Tortello, 1998; Moya and Albanesi, 2000; Tortello and Aceñolaza, 2010). Partial correlations of the "*K. meridionalis* Zone" with the early Tremadocian *Cordylodus angulatus* Zone were indicated by Tortello and Rao (2000), while Moya et al. (1994) and Aceñolaza et al. (2003) reported material of *Kainella* in association with *Rhabdinopora flabelliformis* cf. *socialis* (Salter, 1858), *R. flabelliformis flabelliformis* (Eichwald, 1840), and age-diagnostic acritarchs.

As stated above, Vaccari and Waisfeld (2010) recently provided a full systematic revision of *Kainella* in northwestern Argentina and southern Bolivia, restricted the diagnosis of *Kainella meridionalis* and described new species of the genus, which allowed for the subdivision of the *Kainella meridionalis* Zone sensu Harrington and Leanza (1957) into three successive biostratigraphic units: *K. andina*, *K. meridionalis*, and *K. teiichii* zones (Vaccari et al., 2010). The *K. meridionalis* and *K. teiichii* zones are formally defined by the first appearances of their eponymous species at the type localities in El Perchel area (Fig. 1.1). Although knowledge about the trilobite species that are associated with *Kainella* in each zone is still incomplete, conodonts and graptolites provide crucial biostratigraphic information, which is noted in Figure 4. The *K. meridionalis* Zone and the lower part of the *K. teiichii* Zone correlate with the early Tremadocian *Cordylodus angulatus* and "*Rhabdinopora flabelliformis anglica*" zones, whereas the upper part of the *K. teiichii* Zone is equivalent to the *Paltodus deltifer* and *Bryograptus* zones (Vaccari et al., 2010). The *K. teiichii* Zone is overlain by the trilobite *Bienvillia tetragonalis* Zone; a unit mainly characterized by the disappearance of *Kainella* and the presence of *B. tetragonalis* (Harrington, 1938) (Harrington and Leanza, 1957; see also Waisfeld and Vaccari, 2008).

In the Iruya area, the lower part of the Pantipampa section is characterized by the occurrence of the graptolite *Rhabdinopora*

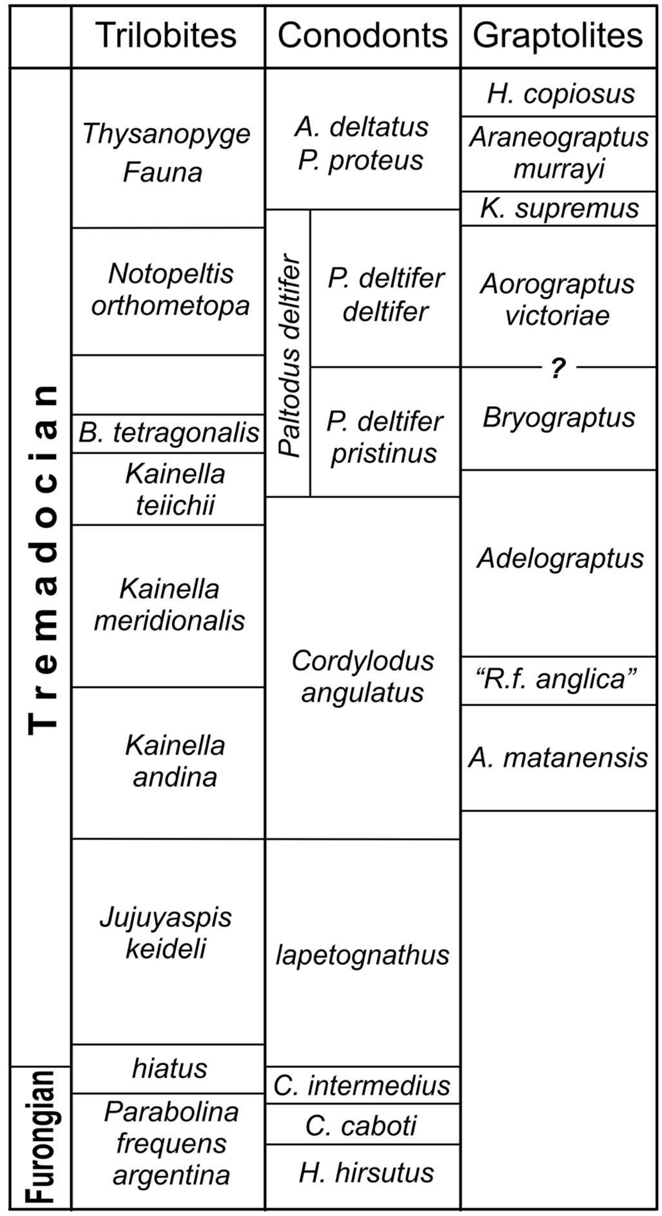

Figure 4. Correlation chart of the latest Furongian-Tremadocian trilobite, conodont, and graptolite zones of northwestern Argentina (modified from Ortega and Albanesi, 2005; Albanesi et al., 2008; Waisfeld and Vaccari, 2008; Vaccari et al., 2010).

Eichwald, 1855, as well as *Kainella meridionalis* in association with *Leptoplastides marianus* and *Asaphellus catamarcensis*, and therefore it is assigned to the *Kainella meridionalis* Zone (Fig. 2). Tortello and Aceñolaza (2010) described an identical trilobite assemblage from Abra de Zenta (Fig. 1.1), from levels with acritarchs of early Tremadocian age (Aráoz, 2009).

The middle and upper parts of the Pantipampa section, as well as the lower part of the Rodeo Colorado section, are characterized by the presence of the zonal species *Kainella teiichii* Vaccari and Waisfeld, 2010. The base of this unit still includes *K. meridionalis* and *Asaphellus catamarcensis*, in association with *Leptoplastides marianus* (Fig. 2). A similar assemblage was originally described by Kobayashi (1935) from the Incamayo area, where *Leptoplastides marianus* and

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Asaphellus catamarcensis occur in association with conodonts of the *Cordylodus angulatus* Zone (Rao and Tortello, 1998; Tortello and Rao, 2000; Albanesi et al., 2008).

The high diversity documented at ∽103 m above the base of the Pantipampa section is remarkable. Five species are unique to this horizon (*Metayuepingia riccardii* n. sp., *Ogygiocaris*? *iruyensis* n. sp., *Niobe* (*Niobella*) *inflecta* [Harrington and Leanza, 1957], *Onychopyge gonzalezae* n. sp., *Nileus cingolanii* n. sp.), whereas other taxa extend toward upper levels of the succession (e.g., *Apatokephalus rugosus* n. sp., *Gymnagnostus kobayashii* n. sp., *Onychopyge acenolazai* n. sp., *Nileus erici* n. sp., *Conophrys* sp. indet.) (Fig. 2). A conodont assemblage of the *Cordylodus angulatus* Zone was recorded at 83 m above the base of the Pantipampa section (personal communication, J. Carlorosi, 2015).

Leptoplastides marianus, *Gymnagnostus kobayashii*, *Parabolinella* sp. indet., *Pseudokainella keideli* (Harrington, 1938), *Apatokephalus rugosus*, Ceratopygidae gen et sp. indet., *Asaphellus clarksoni* n. sp., *Asaphellus isabelae* Meroi Arcerito, Waisfeld and Balseiro, 2015, and *Asaphellus stenorhachis* (Harrington, 1938) occur in different levels of the *K. teiichii* Zone at both the Pantipampa and Rodeo Colorado sections (Figs. 2, 3). The stratigraphic range of *Asaphellus stenorhachis*, assigned only to the *Bienvillia tetragonalis* Zone by Meroi Arcerito et al. (2015), is extended herein to the upper part of the *K. teiichii* Zone. This also applies to the range of *Pseudokainella keideli* (Harrington, 1938; Harrington and Leanza, 1957).

The upper part of the Rodeo Colorado section is characterized by the disappearance of the genus *Kainella* and the appearance of *Bienvillia tetragonalis*, which occurs in association with *Asaphellus stenorhachis*, *Parabolinella* sp. indet., *Pseudokainella keideli*, hyolithids, as well as some poorly preserved specimens assignable to *Leptoplastides* sp. indet. (Fig. 3). *Bienvillia tetragonalis* is a species of great biostratigraphic value within the Cordillera Oriental. Assemblages composed of *B. tetragonalis*, *Pseudokainella keideli*, and *Leptoplastides granulosa* (Harrington, 1938), typify the *Bienvillia tetragonalis* Zone in the Tilcara and El Perchel areas (e.g., Buatois et al., 2006; Waisfeld and Vaccari, 2008).

Systematic paleontology

This paper is based on the study of nearly 600 trilobites collected by the authors from the Pantipampa and Rodeo Colorado localities. In addition, selected specimens from Rodeo Colorado that were obtained by Figueroa Caprini during the 1950s (Figueroa Caprini, 1955, unpublished) are illustrated in Figures 5.17, 5.24, 5.26, 11.6, 11.8, 11.9, 11.11, 11.18–11.20, and 13.27. The material is housed in the Museo de La Plata (Argentina) with the prefix MLP. Slabs containing more than one specimen are labeled with both a collection number and additional letters. Before photography, the specimens were coated with magnesium oxide.

The morphological terms used below have been mostly defined by Moore (1959), Henninngsmoen (1960), Robison (1964), Shergold et al. (1990), and Whittington and Kelly (1997). Several aspects of the suprageneric classification adopted were discussed by Fortey (1980, 1997, 2001) and Shergold et al. (1990).

Order Agnostida Salter, 1864
Superfamily Agnostoidea M‘Coy, 1849
Family Agnostidae M‘Coy, 1849
Subfamily Agnostinae M‘Coy, 1849
Genus *Gymnagnostus* Robison and Pantoja-Alor, 1968

Type species.—*Gymnagnostus gongros* Robison and Pantoja-Alor, 1968, from the upper Furongian–lower Tremadocian of Mexico, by original designation.

Remarks.—In many agnostoid trilobites the dorsal furrows of the exoskeleton are secondarily effaced, resulting in several smooth or nearly smooth lineages that are difficult to differentiate (e.g., Robison and Pantoja-Alor, 1968; Ahlberg, 1988). Early Ordovician highly effaced agnostoids have been variously assigned to *Litagnostus* Rasetti, 1944, *Leiagnostus* Jaekel, 1909, and *Gymnagnostus* Robison and Pantoja-Alor, 1968 (Nielsen, 1997). Based on the study of juvenile specimens and parietal morphology, Palmer (1955) and Robison and Pantoja-Alor (1968) noted that *Litagnostus* represents a diplagnostid genus characterized by having indications of a long “pseudagnostid-type” pygidial axis, whereas *Gymnagnostus* bears a shorter, parallel-sided posteroaxis of “geragnostid” aspect (see also Shergold et al., 1990; Fortey and Owens, 1991; Nielsen, 1997). As stated by Ahlberg (1988), *Gymnagnostus* is morphologically very close to *Leiagnostus*, but the cephalon of the former is distinguished by its well-defined cephalic border and its faintly outlined basal lobes.

Gymnagnostus kobayashii new species
Figure 5.1–5.7

Diagnosis.—A *Gymnagnostus* species with a moderately developed cephalic border; vestiges of axial furrows on the pygidial anteroaxis; a variably defined axial pygidial node; a shallow, proportionately wide pygidial border furrow, which is represented by an abrupt change in exoskeletal slope; and a pygidial border lacking marginal spines.

Description.—Cephalon convex, subcircular in outline, subequal in length and width; acrolobe highly effaced, with faint indications of a delicate axial node, which is situated approximately one-third cephalic length from posterior margin; basal lobes partially outlined, indistinct anteriorly; cephalic border narrow, slightly convex, narrowing slightly laterally; cephalic border furrow shallow and narrow. Largest observed cephalon 3.4 mm long (sag.).

Pygidium convex, semiovate in outline, approximately as wide as long; acrolobe highly effaced, slightly constricted, with vestiges of axial furrows on M1 lobe; axial node variably developed, situated approximately one-third pygidial length from anterior margin; pygidial border narrow, weakly convex, lacking marginal spines; border furrow shallow, proportionately wide, represented by an abrupt change in exoskeletal slope; anterolateral corners of pygidium nearly right-angled; articulating half-ring narrow (sag.), arched, separated from the acrolobe by a very narrow articulating furrow. Largest observed pygidium 4 mm long (sag.).

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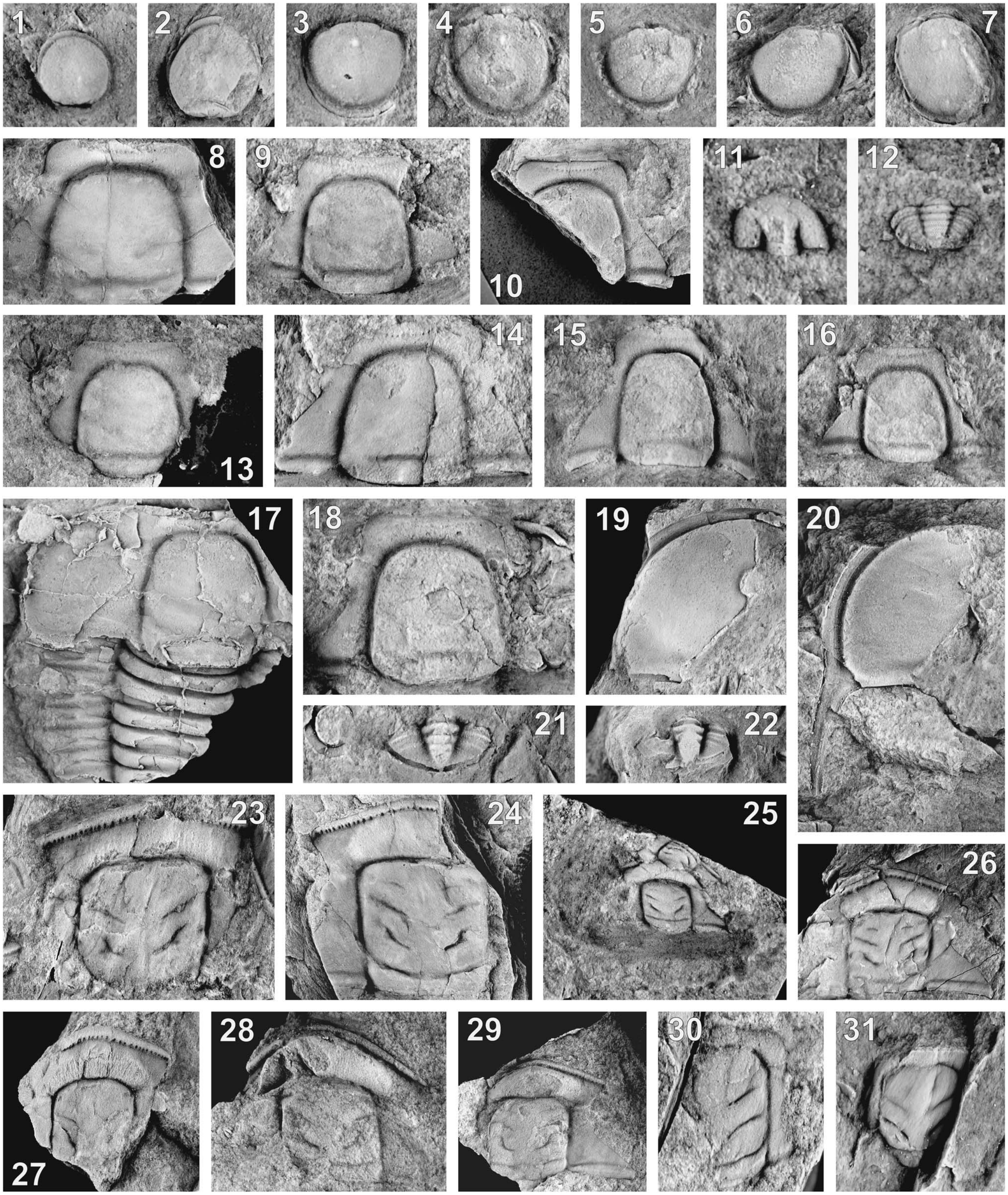

Figure 5. Agnostoids, shumardiids and olenids from the Santa Rosita Formation in the Iruya area, northwestern Argentina. (**1–7**) *Gymnagnostus kobayashii* n. sp.: (**1**) cephalon, MLP 35062a, ×5.3, Pantipampa (P); (**2**) cephalon, MLP 35035a, ×5.3, P; (**3**) pygidium (holotype), MLP 35144, ×5.3, P; (**4**) pygidium, MLP 35318c, ×4.3, Rodeo Colorado (RC); (**5**) pygidium, MLP 35324b, ×5.3, RC; (**6**) pygidium, MLP 35256, ×5.3, P; (**7**) pygidium, MLP 35189b, ×5, P. (**8–10**) *Leptoplastides marianus* (Hoek in Steinmann and Hoek, 1912): (**8**) cranidium, MLP 35185, ×3.4, P; (**9**) cranidium, MLP 35029, ×4, P; (**10**) fragmentary cranidium, MLP 35019, ×4, P. (**11, 12**) *Conophrys* sp. indet.: (**11**) cranidium, latex cast, MLP 35158b, ×11, P; (**12**) pygidium, latex cast, MLP 35283c, ×11, P. (**13–22**) *Leptoplastides marianus* (Hoek in Steinmann and Hoek, 1912): (**13**) cranidium, latex cast, MLP 35032, x4, P; (**14**) cranidium, MLP 35098, ×4, P; (**15**) cranidium, MLP 34998, ×4, P; (**16**) cranidium, MLP 35000, ×4, P; (**17**) fragmentary cephalon and thorax, latex cast, MLP 4937, ×3.4, RC; (**18**) cranidium, MLP 34990, ×3.4, P; (**19**) librigena, MLP 35015, ×2.4, P; (**20**) librigena, MLP 34999, ×3.4, P; (**21**) pygidium, MLP 35239, ×4, P; (**22**) pygidium, MLP 35149, ×4, P. (**23–29**) *Parabolinella* sp. indet.: (**23**) cranidium, MLP 35270, ×1.9, P; (**24**) cranidium, MLP 4953, ×1.9, RC; (**25**) two small cranidia, MLP 35368a,b, ×3.4, RC; (**26**) cranidium, MLP 4934, ×2, RC; (**27**) cranidium, MLP 35243, ×2, P; (**28**) cranidium, MLP 35375, ×2, RC; (**29**) cranidium, latex cast, MLP 34972, ×2, P. (**30, 31**) *Bienvillia tetragonalis* (Harrington, 1938): (**30**) cranidium, MLP 35360, ×4.2, RC; (**31**) cranidium, latex cast, MLP 35399, ×4.2, RC.

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Etymology.—In honor of Teiichi Kobayashi, who provided one of the first comprehensive discussions on the systematics of smooth agnostoids (Kobayashi, 1937).

Types.—Holotype, pygidium, MLP 35144 (Fig. 5.3), length 3.2 mm, width 3.3 mm; paratypes, three cephala and eight pygidia (MLP 35035a, 35061, 35062a, 35189b, 35209, 35248a, b, 35256, 35318c, 35323b, 35324b).

Occurrence.—Pantipampa and lower Rodeo Colorado sections, Iruya area, northwestern Argentina, Santa Rosita Formation, lower Tremadocian, *Kainella teiichii* Zone.

Remarks.—The best known species of *Gymnagnostus* from South America is *G. bolivianus* (Hoek in Steinmann and Hoek, 1912); a taxon that was fully described from the upper Furongian (*Parabolina frequens argentina* Zone) of the Cordillera Oriental (e.g., Harrington and Leanza, 1957, figs. 21.2a, b, 23; Tortello and Esteban, 2003, fig. 4.K–N, P–S; Esteban and Tortello, 2007, Fig. 9A). The cephalon of *G. bolivianus* is identical to that of *Gymnagnostus kobayashii* n. sp., but the pygidium of the latter is distinguished by its wider border furrow and its slightly constricted acrolobe. Similarly, *Gymnagnostus kobayashii* differs from *Gymnagnostus mexicanus* Robison and Pantoja-Alor, 1968, from the uppermost Furongian of Mexico (Robison and Pantoja-Alor, 1968, pl. 97, figs. 15, 16, 19–22) and western Newfoundland, Canada (Fortey in Fortey et al., 1982, pl. 2, fig. 6; Pratt, 1988, fig. 6Q), by having a shallow, relatively wide pygidial border furrow.

Gymnagnostus perinflatus (Harrington and Leanza, 1957) from the upper Furongian of the Famatina Range and western Cordillera Oriental (Harrington and Leanza, 1957, fig. 21.3; Tortello and Esteban, 1999, figs. 5.P–T; Esteban and Tortello, 2007, fig. 9.F), as well as *Leiagnostus* aff. *turgidulus* Harrington and Leanza, 1957 from the lower Tremadocian of South Wales (Owens et al., 1982, pl. 1, figs. b–d, f), further differ from *Gymnagnostus kobayashii* mainly in having a very narrow cephalic border. The type species, *G. gongros* Robison and Pantoja-Alor, 1968 (pl. 97, figs. 24–33) from the upper Furongian–lower Tremadocian of Mexico, is easily distinguished by showing a conspicuous pygidial axial node, a narrow pygidial border furrow, and well-defined posterolateral spines.

Harrington and Leanza (1957, p. 239) cited two fragmentary specimens of *Gymnagnostus* associated with *Kainella*, *Leptoplastides marianus* and *Hapalopleura clavata*, from an indeterminate locality of the Iruya area. Although this material was originally assigned to *Gymnagnostus bolivianus* (= "*Gallagnostus*" *bolivianus*), a further revision may show that it is conspecific with *G. kobayashii*.

Order Ptychopariida Swinnerton, 1915
Suborder Ptychopariina Swinnerton, 1915
Family Shumardiidae Lake, 1907
Genus *Conophrys* Callaway, 1877

Type species.—*Conophrys salopiensis* Callaway, 1877, from the upper Tremadocian of England, Wales and Nova Scotia, Canada, by subsequent monotypy.

Remarks.—Fortey and Owens (1987) regarded the presence of small to moderate-sized anterolateral glabellar lobes, a macropleural thoracic segment, and a transversely oval pygidium with an extended axis, as diagnostic features of *Conophrys* Callaway, 1877. As stated by Fortey and Owens (1987) and Waisfeld et al. (2001), the closely related taxon *Shumardia* Billings, 1862 differs from *Conophrys* mainly in having larger, swollen anterolateral glabellar lobes, a subtriangular pygidium and a shorter pygidial axis, and in lacking macropleural spines and a well-defined pygidial rim. Although *Conophrys* was often regarded as a subgenus of *Shumardia* in the past, we follow Waisfeld et al. (2001) and consider it at a generic level.

Conophrys sp. indet.
Figure 5.11, 5.12

Description.—Cranidium semicircular in outline, gently convex (tr., sag.), sagittal length half posterior width, lacking surface sculpture; glabella little elevated above genal region, long, occupying ~85% of the total cephalic length and one third of the posterior cephalic width; anterolateral glabellar lobes moderate-sized, not inflated nor extended back, protruding outward slightly beyond level of lateral margins of occipital ring, with their posterior edges behind midlength of the cranidium; preglabellar furrow weakly defined, very narrow and shallow, strongly pointed anteriorly; axial furrows parallel sided, relatively wide (tr.) and deep; occipital furrow faint, slightly convex forward medially; lateral furrows S1 and S2 incised proximally; occipital ring a little wider (tr.) than the rest of the glabella, slightly rounded posteriorly; fixed cheek wide (tr.), convex, semicircular in outline, merging with a rounded anterior cephalic margin; posterior margin transverse; posterior border furrow distinct, defining a narrow (exsag.) posterior border. Largest observed cranidium 1.2 mm long (sag.).

Pygidium subtrapezoidal, nearly twice as wide (tr.) as long (sag.), with a slightly forward curvature at posterior margin sagittally; axis somewhat tapered, rounded posteriorly, with four axial rings and a terminal piece, occupying ~80% of the total pygidial length (excluding articulating half ring) and one third of the maximum pygidial width; articulating half ring crescentic, defined by a distinctive, forwardly curved articulating furrow; pleural fields gently convex, divided into five pleurae by deep, curved outward and backward interpleural furrows; border and border furrow indistinct; pygidial sculpture of coarse granules on both axial rings and pleural ribs. Available pygidium 0.9 mm long (sag.).

Materials.—Nine cranidia and one pygidium (MLP 35035b, 35053a, 35059b,c, 35062b, 35068b,c, 35115, 35158b, 35283c) from the Pantipampa locality, Iruya area, northwestern Argentina, Santa Rosita Formation, lower Tremadocian, *Kainella teiichii* Zone.

Remarks.—*Conophrys* sp. indet. belongs to a group of species of *Conophrys* that is characterized by having small anterolateral glabellar lobes. Within this group, *Conophrys* sp. indet. compares closely with those species that show a very faint preglabellar furrow, a smooth cranidium, and a sculpture of coarse granules on the pygidium.

http://dx.doi.org/10.1017/jpa.2016.104

Conophrys erquensis (Kobayashi, 1937) was originally described by Kobayashi (1937, pl. 6, figs. 1–3) on the basis of scarce, poorly preserved specimens from the lower Tremadocian ("*Kainella* shales") of southern Bolivia. Additionally, Harrington and Leanza (1957, fig. 24.2a, b) assigned to *C. erquensis* several cranidia and one pygidium from the lower Tremadocian of Tilcara (Fig. 1.1) which show high correspondence with *Conophrys* sp. indet. The cranidia described above (Fig. 5.11) share a glabellar outline, relative development of glabellar furrows, and proportions of the occipital ring with those of *C. erquensis* from Tilcara (Harrington and Leanza, 1957, fig. 24.2b), whereas the pygidium (Fig. 5.12) slightly differs in the relative length (sag.) of the axis (compare with Harrington and Leanza, 1957, fig. 24.2a). Although this difference may lack crucial taxonomic significance, the specimens studied herein are left in open nomenclature pending the recovery of more pygidia and a comprehensive revision of the type material of *C. erquensis*.

Conophrys sp. indet. is distinguished from *C. fabiani* Waisfeld et al., 2001, from the lower Tremadocian of the Argentine Puna (Waisfeld et al., 2001, fig. 13.1–13.12), by having an anteriorly pointed glabella, a longer preglabellar area, and an ill-defined pygidial rim. *Conophrys* sp. indet. differs from *Conophrys alata* Robison and Pantoja-Alor, 1968, from the upper Furongian–lower Tremadocian of Mexico (Robison and Pantoja-Alor, 1968, pl. 99, figs. 13–18), because the former exhibits the posterior edges of the anterolateral glabellar lobes behind midlength of the cranidium, a longer and narrower pygidium, an indistinct pygidial rim, and a less indented posterior margin. The type species, *C. salopiensis* from the upper Tremadocian (*C. salopiensis* Biozone) of England, Wales and eastern Canada (e.g., Fortey and Owens, 1991, figs. 8m–r, 13a–j; Ebbestad, 1999, fig. 25.B), hardly differs from *Conophrys* sp. indet. except by showing slightly larger, better delineated anterolateral glabellar lobes.

Conophrys sulcatus Malanca, 1996, from the lower Tremadocian in the vicinity of the city of Salta, Cordillera Oriental (Malanca, 1996, pl. 1, figs. 1–12, pl. 2, figs. 1–14; Waisfeld and Vaccari, 2003, pl. 29, fig. 17), also compares closely with *Conophrys* sp. indet.; however, the former is distinguished by its longer (sag.) glabella, its well-defined occipital furrow, and a little longer (sag.) postaxial region. *Conophrys changshanensis* Lu in Lu et al., 1976, from the lower Tremadocian of northwestern Hunan, China (Peng, 1990b, pl. 5, fig. 7–11), differs mainly by having a deeper preglabellar furrow, and lacking granules on the pygidium. *Conophrys rushtoni* Waisfeld et al., 2001, from the lower Tremadocian of north Wales (Rushton, 1982, pl. 3, figs. 13–17, 19, 21; Waisfeld et al., 2001, p. 854–857) exhibits a more rounded and firmly impressed preglabellar furrow, a more transverse anterior margin of the cranidium, a transversely elongate pygidium, and a shorter pygidial axis.

Conophrys wrighti Waisfeld et al., 2001, from the lower Tremadocian of New Zealand (Wright et al., 1994, fig. 8.A–H; Waisfeld et al., 2001, p. 857), differs from *Conophrys* sp. indet. mainly in having a sculpture of fine nodes on the cranidium. A group of species of *Conophrys* (e.g., *C. pusilla* [Sars, 1835]; *C. gaoluoensis* Zhou in Zhou et al., 1977, illustrated by Peng, 1990a; *C. minutula* [Harrington, 1938]) is characterized by having large, teardrop-shaped anterolateral glabellar lobes, and therefore it is easily distinguished from the material studied herein.

Suborder Olenina Burmeister, 1843
Family Olenidae Burmeister, 1843
Subfamily Pelturinae Hawle and Corda, 1847
Genus *Leptoplastides* Raw, 1908

Type species.—*Conocoryphe salteri* Callaway, 1877, from the upper Tremadocian of England, by original designation (Fortey and Owens, 1991).

Remarks.—Henningsmoen (1957, p. 264) fully revised *Leptoplastides* Raw, 1908, and regarded *Parabolinopsis* Hoek in Steinmann and Hoek, 1912 and *Andesaspis* Kobayashi, 1935 as junior synonyms. These concepts were followed by Robison and Pantoja-Alor (1968).

Leptoplastides marianus (Hoek in Steinmann and Hoek, 1912)
Figure 5.8–5.10, 5.13–5.22

1912 *Parabolinopsis mariana* Hoek in Steinmann and Hoek, p. 226, pl. 7, figs. 1–3.
1935 *Andesaspis argentinensis* Kobayashi, p. 67, pl. 11, figs. 1, 2 (only).
1957 *Parabolinopsis mariana*; Harrington and Leanza, figs. 30.1, 30.7, 30.9 (only).
1957 *Leptoplastides marianus*; Henningsmoen, p. 266.
2010 *Leptoplastides marianus*; Tortello and Aceñolaza, p. 157–159, figs. 2.a–n, 3.a–e (see for further synonymy).
2013 *Leptoplastides marianus*; Tortello, Zeballo and Esteban, figs. 6.1–6.11, 7.1–7.8.

Holotype.—Complete specimen from the Tremadocian of Cuesta de Iscayachi, southern Bolivia (Kobayashi, 1937, pl. 4, fig. 15).

Diagnosis.—A species of *Leptoplastides* with a glabella defined by moderately converging axial furrows and a straight or slightly curved preglabellar furrow; anterior cranidial border furrow represented by a backwardly directed row of tiny pits; preglabellar field short (sag.) but distinct, of similar length or slightly longer (sag.) than anterior border; palpebral lobes moderately developed, situated opposite anterior third of glabella; pygidium with a tapering axis, 2 pairs of faint pleural furrows, and entire posterior margin. Largest observed cranidium 9.5 mm long (sag.).

Materials.—One fragmentary axial shield, 55 cranidia, 46 librigenae and 12 pygidia (MLP 4937, 4947, 34968a, 34969b, 34970b, 34971, 34973b, 34975, 34977b, 34979b, 34980b, 34981b, 34982, 34983, 34988, 34990, 34991, 34993, 34994, 34997–35000, 35004a, 35005–35007, 35008b, 35009–35015, 35017–35019, 35022–35024, 35026, 35028, 35029, 35030b, 35032, 35037, 35055b, 35057b, 35067, 35098, 35129, 35130b, 35133, 35141, 35142a, 35149, 35150b, 35153b, 35157b, 35162, 35184, 35185, 35188, 35202b, 35205, 35216, 35239, 35246, 35251, 35263, 35267, 35276, 35280, 35287, 35302, 35304, 35308, 35309, 35311, 35312b, 35318b, 35321b,

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35323a, 35332, 35350, 35352, 35353c, 35355b) from the Pantipampa and lower Rodeo Colorado sections, Iruya area, northwestern Argentina, Santa Rosita Formation, lower Tremadocian, *Kainella meridionalis* and *Kainella teiichii* zones.

Remarks.—Harrington and Leanza (1957) revised *Leptoplastides marianus* in detail and regarded it as "one of the most abundant species in the Argentinian and Bolivian Tremadocian" (Harrington and Leanza, 1957, p. 91). Although they synonymized it with both "*Andesaspis*" *argentinensis* Kobayashi, 1935 from the lower Tremadocian of the Incamayo area, and "*Protopeltura*" *granulosa* Harrington, 1938 from the ?upper Tremadocian of Tilcara, Waisfeld and Vaccari (2003) showed that the latter represents a valid species of *Leptoplastides*, which is distinguished from *L. marianus* mainly by its smaller, more forwardly situated palpebral lobes, and its shorter (sag.) preglabellar field. In addition, *Leptoplastides granulosus* seems to have delicate marginal spines on the pygidium (Harrington, 1938, pl. 8, figs. 13, 18, 21; Harrington and Leanza, 1957, figs. 29, 30.4, 30.6, 30.8).

Leptoplastides marianus is reported from different facies at several localities of the Cordillera Oriental but in most cases the material collected consists only of cranidia and librigenae (e.g., Rao and Tortello, 1998; Tortello and Rao, 2000; Tortello and Aceñolaza, 2010; Tortello et al., 2013). Fortunately, the collections studied herein include some pygidia, which exhibit a tapering axis with two or three rings and a terminal piece, two faint pleural ribs, and an entire margin (Fig. 5.21, 5.22).

Cranidia of *L. marianus* from the Iruya area show slight variations in the length (sag.) of the preglabellar field (Fig. 5.9, 5.16), the course of the preglabellar furrow (Fig. 5.10, 5.17), and the degree of expression of the lateral glabellar furrows (Fig. 5.13, 5.14); a specific variability that was also documented in material from the lower Tremadocian of Abra de Zenta, Quebrada de Moya, and Incamayo (Tortello et al., 2013 and references therein). Although the palpebral lobes of the specimens from the Quebrada de Moya (Tortello et al., 2013, figs. 6.1–6.8, 7.1–7.7) are a little larger than those of material from other localities, such a difference may lack specific significance.

Leptoplastides marianus differs from the type species *L. salteri* (Callaway, 1877), from the upper Tremadocian of England (Henningsmoen, 1957, pl. 2, fig. 14; Fortey and Owens, 1991, figs. 8.c–j, 9), because the latter bears a slightly shorter (sag.) preglabellar field, more anteriorly located genal spines, and deeper pleural furrows on the pygidium.

Subfamily Oleninae Burmeister, 1843
Genus *Parabolinella* Brøgger, 1882

Type species.—*Parabolinella limitis* Brøgger, 1882, from the uppermost part of the Alum Shale Formation in the Oslo region, Norway (subsequently designated by Bassler, 1915).

Parabolinella sp. indet.
Figure 5.23–5.29

Materials.—Twenty-eight cranidia (MLP 4934, 4953, 34972, 34976, 35142b, 35243, 35269, 35270, 35273, 35275, 35282, 35284, 35285, 35289, 35298, 35312a, 35313, 35361, 35362, 35368a,b, 35371–35375) from the Pantipampa and Rodeo Colorado localities, Iruya area, northwestern Argentina, Santa Rosita Formation, Tremadocian, *Kainella teiichii* and *Bienvillia tetragonalis* zones.

Remarks.—Waisfeld and Vaccari (2003) noted the need to revise the morphologic range of *Parabolinella argentinensis* Kobayashi, 1936, which has been widely reported from many lower and upper Tremadocian localities of northwestern Argentina, and provisionally restricted this species to specimens from the type locality (Purmamarca; lowest Tremadocian, *Jujuyaspis keideli* Zone) (Kobayashi, 1936, pl. 15, figs. 1–5; Harrington, 1938, pl. 7, figs. 1, 8; Harrington and Leanza, 1957, fig. 38.3; Waisfeld and Vaccari, 2003, pl. 32, figs. 9–13). Recently, Monti and Confalonieri (2013) and Monti (2015, unpublished) conducted a cladistic analysis of *Parabolinella* and regarded material from the lower Tremadocian of Santa Victoria and Iruya, previously assigned to *P. argentinensis* by Harrington and Leanza (1957, figs. 37.1, 37.2, 37.5–37.7, 38.4–38.6), as a new species characterized mainly by having a long (sag.), inflated preglabellar field, and an angular anterior cranidial margin. *Parabolinella* specimens studied herein seem to be conspecific with that material. Further specimens were described by Tortello et al. (2013, figs. 7.9–7.11, 8.1–8.10) from the lower Tremadocian of the Quebrada de Moya locality.

Subfamily Triarthrinae Ulrich, 1930
Genus *Bienvillia* Clark, 1924

Type species.—*Dikelocephalus*? *corax* Billings, 1865, from a late Cambrian limestone boulder in the Levis Formation at Levis in Quebec, Canada, by original designation.

Remarks.—The closely allied olenid genera *Triarthrus* Green, 1832, *Bienvillia* Clark, 1924, and *Porterfieldia* Cooper, 1953 are distinguished by the arrangement of transverse cephalic furrows in front of the glabella (Ludvigsen and Tuffnell, 1983). *Bienvillia* is characterized by having a well-defined anterior cranidial furrow, which is separated from the preglabellar furrow by a discernible, inflated preglabellar field. The *Bienvillia* species of northwestern Argentina include *B. tetragonalis* (Harrington, 1938), *B. rectifrons* (Harrington, 1938) and *B. parchaensis* (Harrington and Leanza, 1957) (e.g., Henningsmoen, 1957; Fortey, 1974; Waisfeld and Vaccari, 2003).

Bienvillia tetragonalis (Harrington, 1938)
Figure 5.30, 5.31

1938 *Parabolinella tetragonalis* Harrington, p. 196, 197, pl. 7, figs. 3, 4.
1957 *Triarthrus tetragonalis*; Harrington and Leanza, p. 113–115, figs. 42.2–42.4 (only).
1957 *Bienvillia tetragonalis tetragonalis*; Henningsmoen, p. 144.
2003 *Bienvillia tetragonalis*; Waisfeld and Vaccari, p. 329, pl. 31, figs. 18–20.
2005 *Bienvillia tetragonalis*; Zeballo and Tortello, p. 137, fig. 4.S–T.

http://dx.doi.org/10.1017/jpa.2016.104

Holotype.—Cranidium from the Tremadocian of the Tilcara area, Cordillera Oriental, Argentina (Harrington and Leanza, 1957, fig. 42.2).

Description.—Cranidium subtrapezoidal, weakly convex, with straight to forwardly curved anterior margin and slightly downsloping fixed cheeks; glabella large, subquadrate, slightly longer (sag.) than wide (tr.), poorly elevated above genal region, surrounded by subparallel axial furrows and a medially curved backward preglabellar furrow; lateral glabellar furrows S1 and S2 subequal in development, deep, oblique backward, disconnected medially and not reaching axial furrows; occipital furrow deep and narrow, straight medially and somewhat oblique forward laterally; preglabellar field flat or slightly convex, occupying ∽13%–17% of the total cephalic length; anterior cephalic border very short (sag.), slightly upturned, delimited by a narrow (sag.) border furrow; anterior facial suture subparallel; eye ridge faint but visible, short, oblique backward; palpebral area of the fixigena narrow (tr.); palpebral lobe approximately one-fourth length of cranidium, with its anterior edge just in front of lateral extremities of S2, surrounded by a very faint palpebral furrow; posterior fixigena with a shallow border furrow and a narrow (exsag.) posterior border. Largest observed cranidium 6.8 mm long (sag.).

Materials.—Five cranidia (MLP 35360, 35369, 35370, 35398, 35399) from the upper part of the Rodeo Colorado section, Iruya area, northwestern Argentina, Santa Rosita Formation, Tremadocian, *Bienvillia tetragonalis* Zone.

Remarks.—The cranidia examined are few but clearly represent a species of *Bienvillia* with a proportionately long (sag.) preglabellar field, a subparallel anterior facial suture, a moderately developed palpebral lobe, and a glabella that is slightly longer than wide. Therefore, this material is assigned to *Bienvillia tetragonalis* (Harrington, 1938), which is well known from the eponymous zone in both the type locality (Alfarcito, east of Tilcara; Harrington, 1938; Harrington and Leanza, 1957; Waisfeld and Vaccari, 2003; Zeballo and Tortello, 2005) and El Perchel area (Waisfeld and Vaccari, 2008).

Bienvillia rectifrons (Harrington, 1938), from the upper Tremadocian of northwestern Argentina (Harrington, 1938, pl. 8, figs. 17, 19–21; Harrington and Leanza, 1957, fig. 43.2a–g; Přibyl and Vaněk, 1980, pl. 9, figs. 6, 7; Waisfeld and Vaccari, 2003, pl. 31, figs. 15–17; Tortello and Esteban, 2014, fig. 3.16–3.23, 3.25), differs from *B. tetragonalis* mainly in possessing a longer (sag.) preglabellar field. *Bienvillia parchaensis* (Harrington and Leanza, 1957), from the upper Tremadocian of the Incamayo area, southern Cordillera Oriental (Harrington and Leanza, 1957, figs. 43.1a–h, 44.1a–e; Waisfeld and Vaccari, 2003, pl. 31, figs. 12–14), shows, in addition, larger (exsag.) palpebral lobes (Harrington and Leanza, 1957; Ludvigsen and Tuffnell, 1983).

Order Asaphida Salter, 1864 emend. Fortey and Chatterton, 1988
Superfamily Asaphoidea Burmeister, 1843
Family Asaphidae Burmeister, 1843
Subfamily Isotelinae Angelin, 1854

Genus *Asaphellus* Callaway, 1877

Type species.—*Asaphus homfrayi* Salter, 1866, from the Tremadocian of North Wales, by original designation.

Remarks.—Meroi Arcerito et al. (2015) discussed the morphological variability of *Asaphellus* and, based mainly on material from El Perchel area, described in detail several representative species from the Tremadocian of the Cordillera Oriental (e.g., *A. stenorhachis* [Harrington, 1938]; *A. isabelae* Meroi Arcerito, Waisfeld and Balseiro, 2015; *Asaphellus* sp. 1 sensu Meroi Arcerito, Waisfeld and Balseiro, 2015). As shown below, the Pantipampa and Rodeo Colorado sections include well-preserved specimens of these taxa.

Asaphellus catamarcensis Kobayashi, 1935
Figure 6.1–6.15

1935 *Asaphellus*? *catamarcensis* Kobayashi, p. 65, 66, pl. 11, figs. 11–15.
1957 *Asaphellus catamarcensis*; Harrington and Leanza, p. 147, fig. 65.7, 65.8 (only).
2000 *Asaphellus catamarcensis*; Tortello and Rao, p. 72, 73, fig. 3T–V.
2010 *Asaphellus catamarcensis*; Tortello and Aceñolaza, p. 162, fig. 4.a–4.i (see for further synonymy).
2015 *Asaphellus catamarcensis*; Meroi Arcerito, Waisfeld and Balseiro, fig. 6.A–D.

Lectotype.—Pygidium from the lower Tremadocian of the Incamayo area, Cordillera Oriental, Argentina (Kobayashi, 1935, pl. 11, fig. 14; Meroi Arcerito et al., 2015, fig. 6A).

Description.—Cranidium gently convex (sag., tr.), wider than long, with pointed anterior margin and moderately downsloping fixed cheeks; glabella very long, unfurrowed, weakly elevated above genal region, poorly defined by weak axial and preglabellar furrows, constricted between palpebral lobes, rounded anteriorly, reaching anterior border furrow; posterior half of the glabella much wider (tr.) than anterior half; glabellar length (sag.) represents ∽80%–84% of the total length of the cranidium; axial node absent; occipital ring not differentiated; socket for reception of first thoracic articulating half-ring very short (sag.), well defined by a delicate furrow; anterior cranidial border slightly convex, delimited by an anterior border furrow which is represented by a change in slope of exoskeleton; anterior facial suture diverging at an angle of 45º to the exsagittal line; palpebral area of the fixigena narrow (tr.); eyes small, situated adjacent to mid-length of cranidium; posterior facial suture oblique backward and outward, sinuous; posterior fixigena wide (tr.), with a shallow border furrow and a narrow (exsag.), convex posterior border; librigenae with wide and depressed border, which narrows backward; genal angles produced into long spines continuing curvature of lateral margin. Largest observed cranidium 27.5 mm long (sag.).

Hypostome subpentagonal in outline, as long (sag.) as wide (tr.); anterior lobe of median body large, slightly convex, ovate, as long as wide, with an incision sagitally close to its apex,

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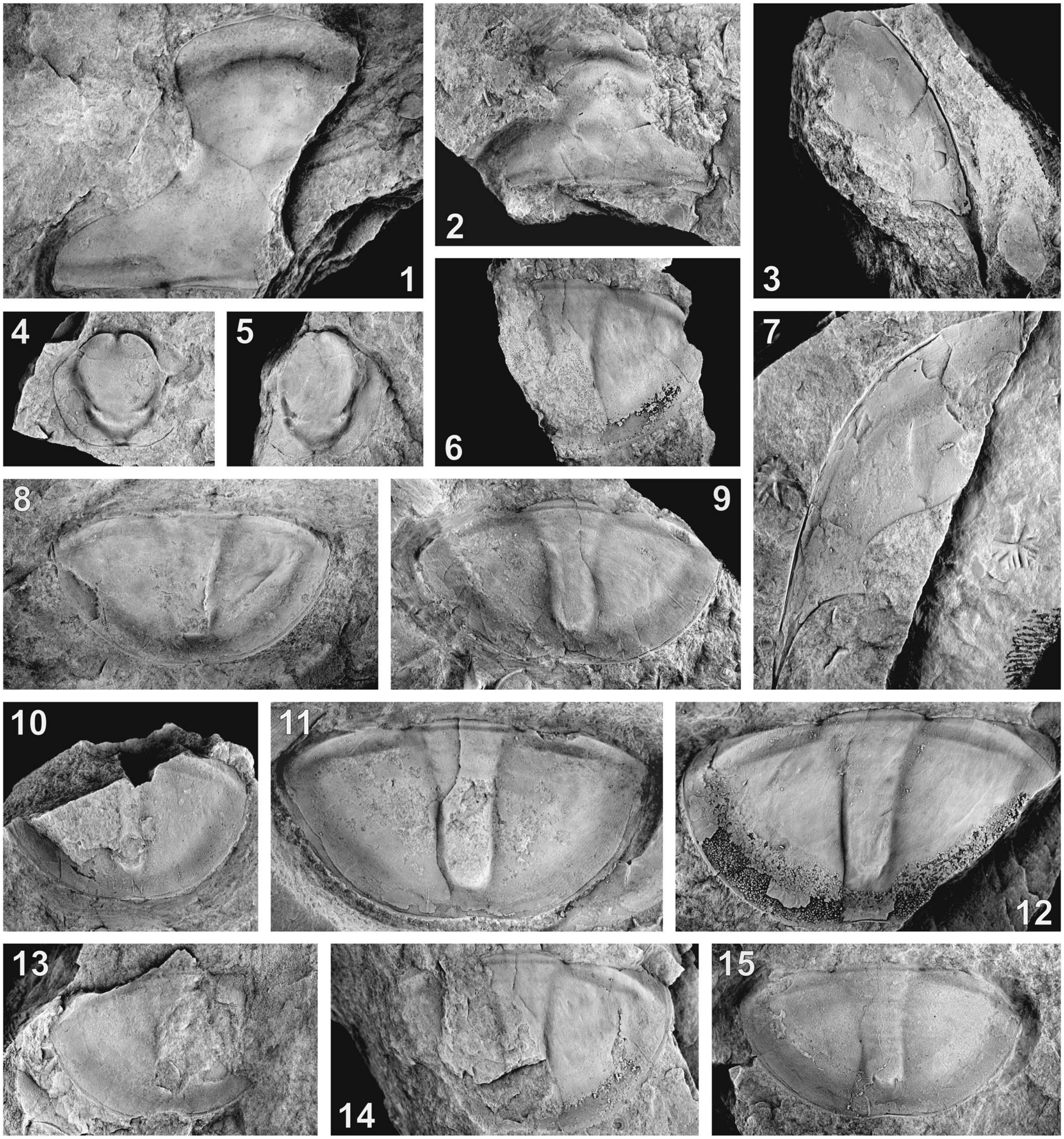

Figure 6. *Asaphellus catamarcensis* Kobayashi, 1935 from the Santa Rosita Formation in the Iruya area, northwestern Argentina: (**1**) cranidium, MLP 34985, ×1.7; (**2**) cranidium, MLP 34992, ×1.7; (**3**) librigena, MLP 35003, ×1.7; (**4**) hypostome, MLP 34980a, ×1.7; (**5**) hypostome, MLP 35025, ×1.7; (**6**) pygidium, latex cast, MLP 34970a, ×1.7; (**7**) librigena, MLP 34989, ×1.7; (**8**) pygidium, MLP 34979a, ×1.7; (**9**) pygidium, MLP 34973a, ×1.7; (**10**) pygidium, MLP 34996, ×1.7; (**11**) pygidium, MLP 34977a, ×1.7; (**12**) pygidium, MLP 34984, ×1.7; (**13**) pygidium, MLP 35031, ×1.7; (**14**) pygidium, MLP 35002, ×1.7; (**15**) pygidium, MLP 34986, ×1.7. All specimens from Pantipampa.

occupying approximately two-thirds of the total length of the hypostome, tapering posteriorly to meet with a pair of maculae; posterior lobe short (sag.) and weakly convex, with its posterior margin slightly pointed backward; anterior wings subtriangular, broad; lateral border wide, depressed, of uniform width; posteromedian margin having an indentation.

Pygidium semielliptical in outline, much wider than long, somewhat convex; pygidial axis long and narrow, little elevated above level of pleural fields, delimited by variably developed axial furrows, ∽23%–26% of total width of pygidium at anterior extremity, tapering toward posterior at anterior half and nearly parallel sided at posterior half, with traces of segmentation on its anterior part, ending in a more or less inflated point which reaches posterior border furrow; length of axis ∽85% of that of pygidium on sagittal line; articulating half ring very narrow (sag.), delimited by a straight and shallow furrow; pleural field smooth, downsloping; anterior border narrow (exsag.) and convex, clearly delimited by a shallow furrow; lateral and posterior border furrow weak, represented by a change of slope of the exoskeleton; lateral and posterior border variably developed, weakly concave to flat; posterior margin can show a small indentation. Largest observed pygidium 22 mm long (sag.).

Materials.—Two cranidia, seven librigenae, two hypostomes, and 17 pygidia (MLP 34970a, 34973a, 34974, 34977a, 34978, 34979a, 34980a, 34981a, 34984, 34985, 34986, 34987b, 34989, 34992, 34995, 34996, 35001–35003, 35004b, 35008a, 35020, 35025, 35027, 35031) from the middle part of the Pantipampa section, Iruya area, northwestern Argentina, Santa Rosita Formation, lower Tremadocian, *Kainella meridionalis* Zone and basal *K. teiichii* Zone.

Remarks.—Kobayashi (1935) briefly described *Asaphellus catamarcensis* on the basis of one fragmentary cranidium, one free cheek, one hypostome, and two pygidia from the Incamayo area. Subsequently Harrington and Leanza (1957) redescribed *A. catamarcensis* and reported it from numerous upper Furongian and lower and upper Tremadocian localities of the Cordillera Oriental, as well as from the uppermost Furongian of the Famatina System in the La Rioja Province. Because the morphologic range recognized by Harrington and Leanza (1957) is quite wide, Waisfeld and Vaccari (2003) pointed out the need to critically revise the diagnosis and stratigraphic position of this species.

Because the original description was insufficient for a complete understanding of *Asaphellus catamarcensis*, Meroi Arcerito et al. (2015, fig. 6) re-illustrated the type series and designated a pygidium as the lectotype. Such specimens exhibit small eyes, genal spines continuing curvature of lateral cephalic margin, a faint but perceptible pygidial axis, and a well-developed pygidial border. Among the numerous specimens assigned by Harrington and Leanza (1957) to *A. catamarcensis*, only the pygidia illustrated in their figs. 65.7 and 65.8 accord with the type material. In addition, specimens from Incamayo and Abra de Zenta were described by Tortello and Rao (2000, fig. 3.T–3.V) and Tortello and Aceñolaza (2010, fig. 4.a–4.i), respectively, in association with *Leptoplastides marianus*, *Pseudokainella* and *Kainella meridionalis*.

Furthermore, *A. catamarcensis* from the Iruya area is restricted to the lower part of the Pantipampa section (Fig. 2). As in material from Incamayo and Abra de Zenta, the pygidia studied herein show variations in the degree of expression of the axial furrows (Fig. 6.10, 6.12, 6.13), the width (tr.) of the border (compare Fig. 6.8, 6.11, 6.12), and the outline of the axis, which ends in a more or less inflated point (Fig. 6.9, 6.12). A similar variability is seen in the type series of *A. catamarcensis* (see Meroi Arcerito et al., 2015, fig. 6.A–C). Although Meroi Arcerito et al. (2015) prefer to restrict *A. catamarcensis* to the type series from Incamayo (Kobayashi, 1935), we regard it as a taxon with a wider representation in the lower Tremadocian (*Cordylodus angulatus* Zone) of northwestern Argentina.

Asaphellus catamarcensis differs from *A. jujuanus* Harrington, 1938, from the upper Tremadocian of the Cordillera Oriental (e.g., Harrington and Leanza, 1957, fig. 66.7, 66.12; Tortello and Esteban, 2014, fig. 7.1–7.19), in having a more oblique posterior facial suture, longer genal spines, smooth pleural fields, and a less depressed pygidial border. It is distinguished from *A. nazarenensis* Tortello and Esteban, 2014, from the upper Tremadocian of northwestern Argentina (Tortello and Esteban, 2014, fig. 8.1–8.6), in possessing a narrower (tr.) palpebral area of the fixigena and a more developed pygidial border; and from *A. kayseri* (Kobayashi, 1937) sensu Harrington and Leanza (1957, figs. 74, 75) (Waisfeld and Vaccari, 2003, pl. 22, figs. 7–9) by lacking pleural furrows on the pygidium and having smaller palpebral lobes and a wider pygidial border. *Asaphellus catamarcensis* further differs from partially effaced species of *Asaphellus* (e.g., *A. inflatus* Lu in Wang, 1962; *A. yanheensis* Yin in Yin and Li, 1978; *A. homfrayi* [Salter, 1866]; *A. isabelae* Meroi Arcerito, Waisfeld and Balseiro, 2015) in showing perceptible axial furrows on the pygidium.

Asaphellus clarksoni new species
Figure 7.1–7.15

Diagnosis.—A species of *Asaphellus* with an effaced cranidium, a well-defined pygidial axis, faint but perceptible pleural furrows, and a distinct, concave pygidial border.

Description.—Cranidium effaced, slightly convex (sag., tr.), wider than long, pointed anteriorly, with moderately downsloping fixed cheeks; glabella highly effaced; axial node weak, situated close to the posterior cranidial margin; socket for reception of first thoracic articulating half-ring very short (sag.), defined by a delicate furrow; anterior border furrow very shallow, delimiting a slightly upturned anterior border; anterior facial suture clearly diverging in front of eyes, meeting mesially in broad ogive; palpebral area of the fixigena narrow (tr.); palpebral lobe arcuate, situated at or slightly behind cranidial midpoint, occupying ∽15% of the total length (sag.) of the cranidium; posterior facial suture oblique backward and outward, sinuous; posterior fixigena with a very wide (exsag.) and shallow border furrow and a linear posterior border; librigenae showing a low eye socle, a wide and concave border, and a broad-based, short genal spine that continues curvature of lateral margin. Largest observed cranidium 23 mm long (sag.).

Pygidium semicircular in outline, scarcely convex, width approximately twice length; axis elevated above level of pleural fields, ∽25% of total width of pygidium at anterior extremity, slightly tapered at anterior half and nearly parallel sided at posterior part, with faint indications of seven rings and a bulbous terminal piece; length of axis ∽83%–85% of that of pygidium on sagittal line; articulating half ring extremely narrow (sag.), crescentic; pleural field only slightly downsloping, with two or three faint but perceptible wide shallow pleural furrows, among which the first is the most distinct; border furrow indicated by an abrupt change of slope of the exoskeleton; border well-developed, concave; border plus

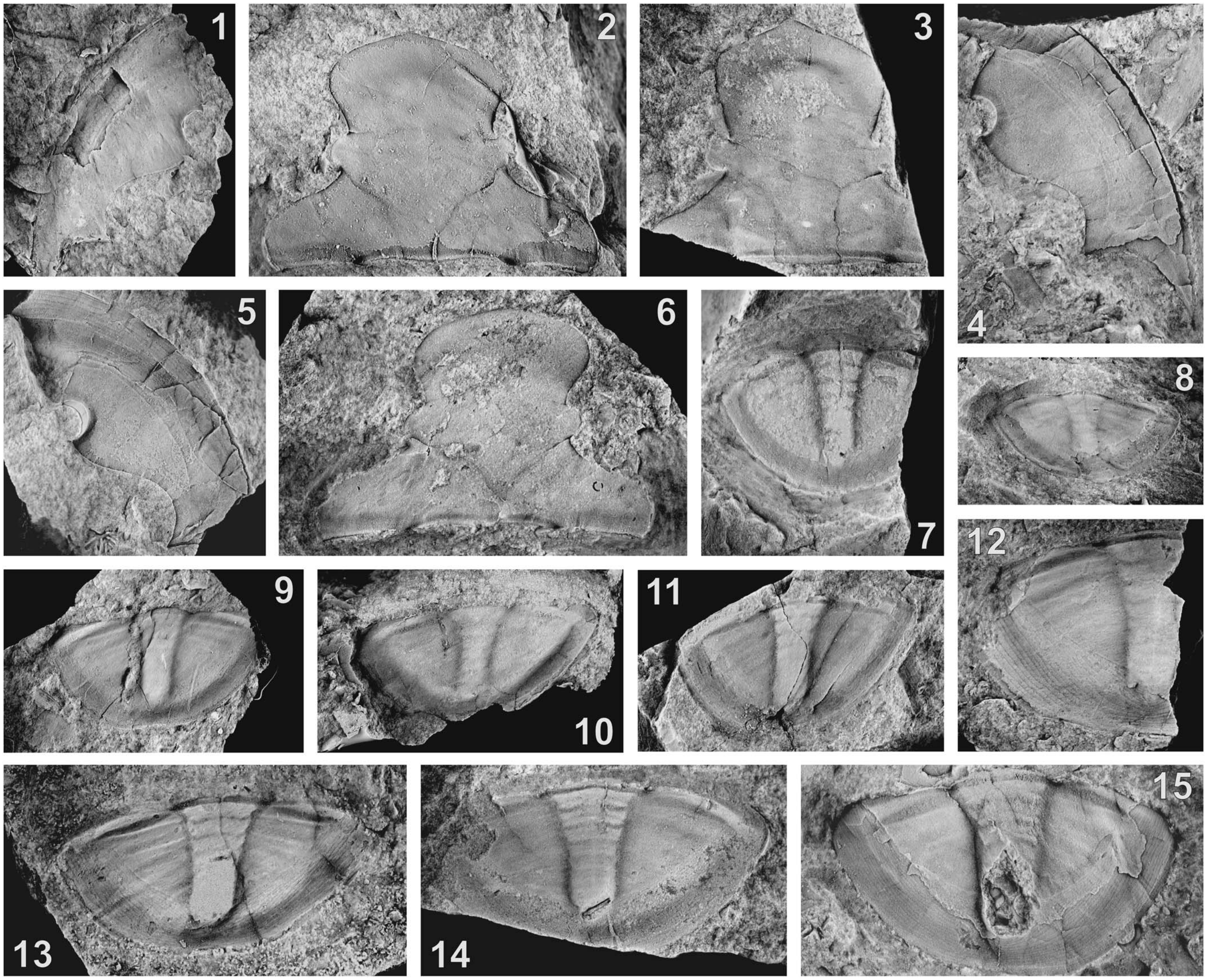

Figure 7. *Asaphellus clarksoni* n. sp. from the Santa Rosita Formation in the Iruya area, northwestern Argentina: **(1)** librigena, latex cast, MLP 35224, ×2.2, Pantipampa (P); **(2)** cranidium, MLP 35327, ×1.8, Rodeo Colorado (RC); **(3)** cranidium, MLP 35325, ×2.2, RC; **(4)** librigena, MLP 35349a, ×2.2, RC; **(5)** librigena, MLP 35335, ×1.8, RC; **(6)** cranidium, MLP 35324a, ×2.2, RC; **(7)** pygidium, MLP 35199, ×2.5, P; **(8)** pygidium, MLP 35260, ×2.5, P; **(9)** pygidium, latex cast, MLP 35200, ×2.5, P; **(10)** pygidium, latex cast, MLP 35253, ×2.5, P; **(11)** pygidium, MLP 35244, ×2.2, P; **(12)** fragmentary pygidium, MLP 35279, ×2.2, P; **(13)** pygidium (holotype), MLP 35252, ×2.2, P; **(14)** pygidium, MLP 35206, ×2.2, P; **(15)** pygidium, MLP 35355a, ×2.2, RC.

border furrow occupies ∽15%–17% of the total pygidial length; doublure broad, covered with 15–18 terrace ridges following the doublural contour. Largest observed pygidium 15.5 mm long (sag.).

Etymology.—Dedicated to Dr Euan N. K. Clarkson (University of Edinburgh, Scotland).

Types.—Holotype, pygidium, MLP 35252 (Fig. 7.13), length 10.5 mm, width 20 mm; paratypes, 7 cranidia, 12 librigenae, 1 thorax and 25 pygidia (MLP 35199, 35200, 35206, 35207, 35210, 35217–35224, 35235, 35238, 35241, 35242, 35244, 35245, 35253, 35257–35262, 35278, 35279, 35286, 35306, 35324a, 35325, 35327, 35335, 35336, 35338, 35344, 35348, 35349a, 35351, 35355a).

Occurrence.—Upper Pantipampa and lower Rodeo Colorado sections, Iruya area, northwestern Argentina, Santa Rosita Formation, lower Tremadocian, *Kainella teiichii* Zone.

Remarks.—Harrington and Leanza (1957) assigned several specimens to *A. catamarcensis* whose affinity needs to be revised. A complete exoskeleton from the lower Tremadocian of the Santa Victoria area shows an effaced cranidium, traces of pygidial pleural furrows and a distinct pygidial border (Harrington and Leanza, 1957, fig. 64.3), and therefore it may be conspecific with *A. clarksoni* n. sp. Similarly, some pygidia of *Asaphellus* sp. from the El Perchel area (Meroi Arcerito et al., 2015, fig. 7.B, C, E) exhibit a well-developed border and vestiges of pleural furrows which resemble those of *A. clarksoni*.

Beds with *A. clarksoni* lie above those containing *A. catamarcensis* (Fig. 2). The latter species is particularly similar to *A. clarksoni*, but differs in having a better defined

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anterior cranidial border furrow and pleural fields without furrows. The new species from Iruya also shows similarities with *Asaphellus jujuanus* Harrington, 1938, from the upper Tremadocian of the Cordillera Oriental (e.g., Harrington and Leanza, 1957, fig. 66.7, 66.12; Tortello and Esteban, 2014, fig. 7.1–7.19), which possesses a pygidium with faint indications of pleural furrows and a broad border. *Asaphellus clarksoni* differs by having an indistinct glabella, smaller palpebral lobes, a more oblique posterior facial suture, and fewer rings on the pygidial axis.

Asaphellus clarksoni is distinguished from *A. kayseri* (Kobayashi, 1937), from the Tremadocian of northwestern Argentina (Harrington and Leanza, 1957, figs. 74, 75; Waisfeld and Vaccari, 2003, pl. 22, figs. 7–9), by having a less defined glabella, a more developed pygidial border, and fewer axial rings on the pygidium. It differs from *Asaphellus nazarenensis* Tortello and Esteban, 2014, from the upper Tremadocian of the Nazareno area, Cordillera Oriental (Tortello and Esteban, 2014, fig. 8.1–8.6), because the latter shows a perceptible glabella, pleural fields lacking furrows, and a narrower pygidial border.

The type species, *Asaphellus homfrayi* (Salter, 1866) from the upper Tremadocian of Great Britain (e.g., Fortey and Owens, 1991, figs. 3.l–u, 7.a–g, 8.a, b), differs from *A. clarksoni* mainly by its pleural fields without furrows. *Asaphellus graffi* (Thoral, 1946), from the Floian of southern France (Courtessole et al., 1985, pl. 11, figs. 1–4), exhibits a better delineated glabella and a shorter (sag.), uniformly tapered pygidial axis. *Asaphellus* cf. *graffi*, from the upper Tremadocian of Wales (Fortey and Owens, 1992, fig. 4a–g), is similar in most of the essential features to *A. clarksoni*, although the former has a more concave frontal area. *Asaphellus stenorhachis* (Harrington, 1938) is easily distinguished by showing a highly effaced pygidum (see below).

Asaphellus stenorhachis (Harrington, 1938)
Figure 8.1–8.17

1938 *Illaenus stenorhachis* Harrington, p. 182, 183, pl. 5, fig. 18.
1957 *Asaphellus jujuanus* Harrington and Leanza, fig. 66.6, 66.8, 66.9 (only).
2015 *Asaphellus stenorhachis*; Meroi Arcerito, Waisfeld and Balseiro, p. 141–144, figs. 8.A–M, 9.A (see for further synonymy).

Holotype.—Fragmentary thorax and pygidium from the Tremadocian of the Tilcara area, Cordillera Oriental, Argentina (Harrington, 1938, pl. 5, fig. 18; Harrington and Leanza, 1957, fig. 93.3).

Materials.—Ten cranidia, eight librigenae and twenty-six pygidia (MLP 35211–35215, 35272a, 35305, 35314–35316, 35358, 35359, 35363–35367, 35376–35380, 35381a–e, 35382–35386, 35388–35397) from the upper Pantipampa and Rodeo Colorado sections, Iruya area, northwestern Argentina, Santa Rosita Formation, Tremadocian, *Kainella teiichii* and *Bienvillia tetragonalis* zones.

Remarks.—The material studied shows undefined cephalic axial furrows; a slightly divergent anterior facial suture; arcuate, distinct palpebral lobes; and extremely faint pygidial axial furrows. Thus, it is assigned to *Asaphellus stenorhachis* (Harrington, 1938); a highly effaced asaphid that has been fully revised by Meroi Arcerito et al. (2015).

Asaphellus stenorhachis compares most closely with partially effaced species of *Asaphellus* (see a complete discussion in Meroi Arcerito et al., 2015). It strongly resembles *Asaphellus* sp., from the Tremadocian of the Nazareno area, Cordillera Oriental (Tortello and Esteban, 2014, fig. 8.8–8.12), in sharing an effaced, semicircular pygidium with a moderately developed border and very faint indications of a long tapering axis; however, the cranidium of *A. stenorhachis* seems to differ from that of *Asaphellus* sp. by its proportionately larger palpebral lobes.

Two cranidia from the *Bienvillia tetragonalis* Zone of Río Iturbe (Cordillera Oriental), originally referred to as *Asaphellus jujuanus* by Harrington and Leanza (1957, fig. 66.6, 66.9), exhibit a fully effaced glabella and anterior border furrow, and an oblique posterior facial suture; therefore, they are reassigned herein to *A. stenorhachis*. In addition, an associated librigena showing a distinct eye socle and a small genal spine (Harrington and Leanza, 1957, fig. 66.8) is considered conspecific.

Asaphellus isabelae Meroi Arcerito, Waisfeld and Balseiro, 2015
Figure 8.18–8.20

2015 *Asaphellus isabelae* Meroi Arcerito, Waisfeld and Balseiro, p. 144, figs. 7G, 9B, 10A–M.

Holotype.—Cranidium from the Tremadocian of Quebrada del Arenal, El Perchel area, Cordillera Oriental, Argentina (Meroi Arcerito et al., 2015, fig. 10E).

Materials.—Eight pygidia and a few fragmentary, delicate cranidia (MLP 35283b, 35288, 35290, 35291, 35301, 35303, 35320, 35357) from the uppermost Pantipampa section and the lower Rodeo Colorado section, Iruya area, northwestern Argentina, Santa Rosita Formation, lower Tremadocian, *Kainella teiichii* Zone.

Remarks.—A few asaphid specimens collected from the Iruya area have a proportionately large size (largest available pygidium 25 mm long), a semicircular outline, a very low and uniform convexity, and completely obliterated furrows, showing a degree of effacement that is higher than that of *Asaphellus stenorhachis*. This material accords with *Asaphellus isabelae*; a delicate, smooth asaphid recently described in great detail by Meroi Arcerito et al. (2015, figs. 7G, 8.B, 10.A–M) from the *Kainella meridionalis* and *K. teiichii* zones of El Perchel, Cordillera Oriental.

Subfamily Ogygiocarinidae Raymond, 1937
Genus *Ogygiocaris* Angelin, 1854

Type species.—*Trilobus dilatatus* Brünnich, 1781, from the Middle Ordovician of Baltica, by original designation.

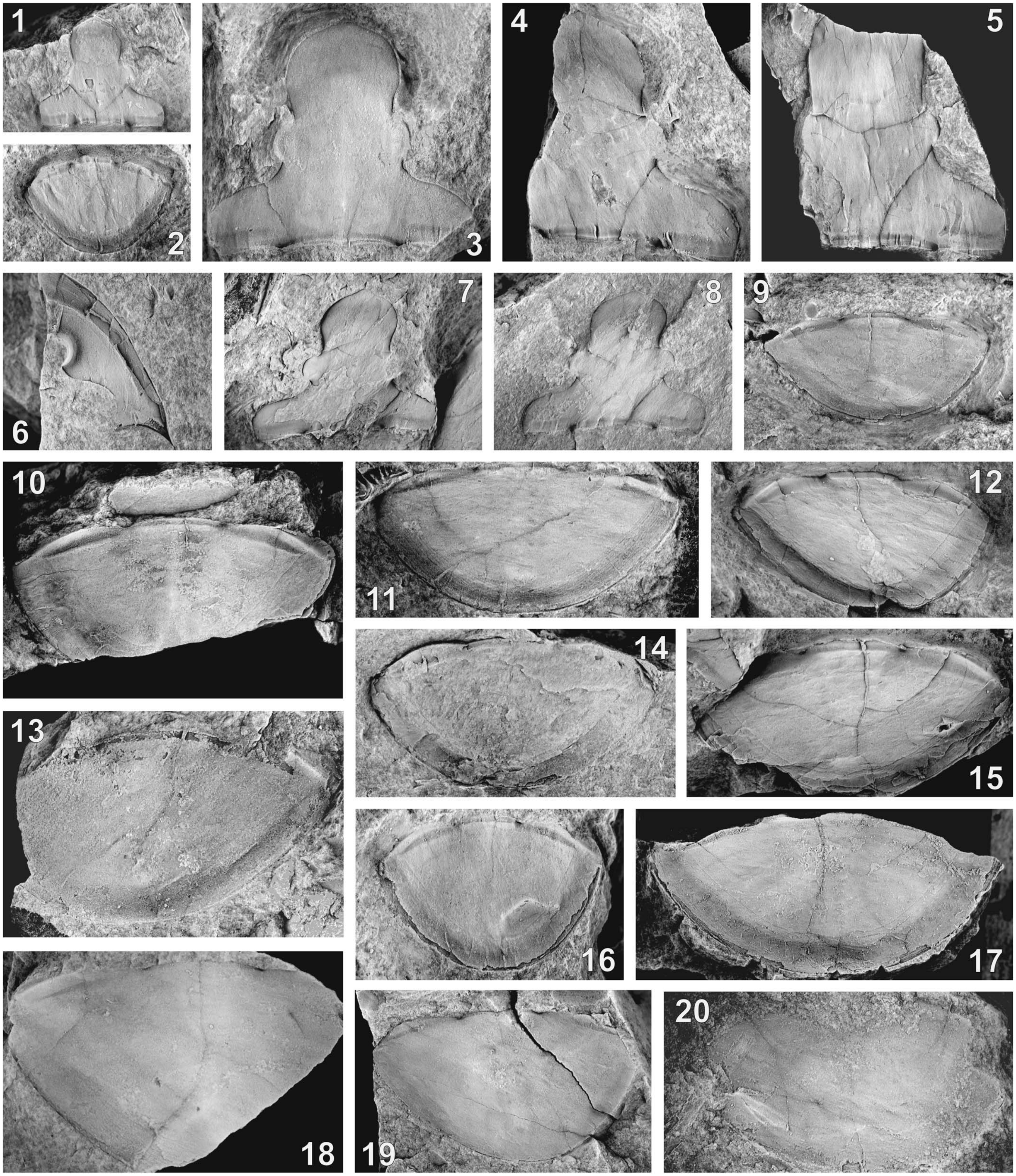

Figure 8. Asaphids from the Santa Rosita Formation in the Iruya area, northwestern Argentina. **(1–17)** *Asaphellus stenorhachis* (Harrington, 1938): **(1)** cranidium, MLP 35396, ×2.2, Rodeo Colorado (RC); **(2)** pygidium, MLP 35383, ×3, RC; **(3)** cranidium, MLP 35367, ×2.2, RC; **(4)** fragmentary cranidium, MLP 35385, ×2.2, RC; **(5)** cranidium, MLP 35384, ×1.4, RC; **(6)** librigena, MLP 35316, ×2.2, RC; **(7)** cranidium, MLP 35381a, ×2.2, RC; **(8)** cranidium, MLP 35381b, ×2.2, RC; **(9)** pygidium, MLP 35314, ×2.2, RC; **(10)** pygidium, MLP 35364, ×2.2, RC; **(11)** pygidium, MLP 35211, ×2.2, Pantipampa (P); **(12)** pygidium, MLP 35382, ×2.2, RC; **(13)** pygidium, MLP 35272a, ×2.2, P; **(14)** pygidium, MLP 35386, ×2.2, RC; **(15)** pygidium, MLP 35381c, ×2.2, RC; **(16)** pygidium, MLP 35358, ×2.2, RC; **(17)** pygidium, MLP 35376, ×1.6, RC. **(18–20)** *Asaphellus isabelae* Meroi Arcerito, Waisfeld and Balseiro, 2015: **(18)** pygidium, MLP 35291, ×2, P; **(19)** pygidium, MLP 35303, ×2, P; **(20)** pygidium, MLP 35290, ×2, P.

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Remarks.—Harrington and Leanza (1957), Henningsmoen (1960), Fortey and Owens (1978), Waisfeld and Vaccari (2006) and Hansen (2009) discussed in detail the diagnostic features of *Ogygiocaris*. Waisfeld and Vaccari (2006) regarded both *Ogygiocarella* Harrington and Leanza, 1957 and *Araiorhachis* Přibyl and Vaněk, 1980 as junior synonyms of *Ogygiocaris*, which is followed here.

Ogygiocaris? *iruyensis* new species
Figure 9.1–9.8

Diagnosis.—A species of *Ogygiocaris*? with an anteriorly pointed glabella; pygidial axis with marked anterior five rings and extremely faint or indistinct posterior four rings, ending in blunt point; pleural fields crossed by five oblique furrows, which are shallow, straight to slightly curved, and end at level of doublural margin; anterior part of the doublural margin slightly undulating; paradoublural line indistinguishable.

Description.—Cranidium somewhat convex, wider than long, with slightly downsloping fixed cheek; glabella large, unfurrowed, moderately elevated above genal region, a little constricted (tr.) medially and pointed anteriorly, surrounded by narrow and shallow axial furrows; it occupies ∽78% of the total length of the cranidium; occipital brim extremely narrow (sag.), delimited by a shallow, transverse furrow; anterior cephalic border convex, slightly widened sagittally, length (sag.) approximately half the length of preglabellar field, differentiated by change in slope of exoskeleton; preglabellar field depressed, with lateral margins moderately divergent; anterior facial suture somewhat divergent forward; posterior facial suture transverse, strongly directed outward; posterior fixigena very wide (tr.) and short (exsag.), with a shallow border furrow and a slender (exsag.), convex posterior border; palpebral area of the fixigena too poorly preserved for description. Available cranidium 14.5 mm long (sag.).

Librigenae, hypostome and thorax unknown.

Pygidium semicircular in outline, flat to somewhat convex transversely and longitudinally, width approximately twice length, margin entire; axis long and very narrow, hardly elevated above level of pleural fields, surrounded by narrow axial furrows, ∽15%–17% of total width of pygidium at anterior extremity, slightly tapered at anterior half and nearly parallel sided at posterior half, with marked anterior five rings and extremely faint or indistinct posterior four rings, ending in blunt point; length of axis ∽81%–83% of that of pygidium on sagittal line; articulating half-ring narrow (sag.), crescentic; pleural fields flat or weakly convex, crossed by five straight to slightly curved, oblique pleural furrows ending at level of the doublural margin; doublure wide, covered with 14 terrace lines; the anterior part of the doublural margin is slightly crenulate (Fig. 9.8); paradoublural line indistinguishable; some specimens show a well-defined, fairly flat pygidial border of uniform width (Fig. 9.5, 9.7, 9.8), which represents only 6%–8% of the total pygidial length (sag.). Largest observed pygidium 19.5 mm long (sag.).

Etymology.—Refers to the Iruya area, Salta Province, Argentina.

Types.—Holotype, pygidium, MLP 35158a (Fig. 9.3), length 7 mm; paratypes, one cranidium and seven pygidia (MLP 35043a, 35053b, 35154, 35156a, 35159–35161, 35163).

Occurrence.—Pantipampa section, Iruya area, northwestern Argentina, Santa Rosita Formation, lower Tremadocian, *Kainella teiichii* Zone.

Remarks.—The specimens described above show a long glabella, a posteriorly located palpebral area of the fixigena, a very wide (tr.) and short (exsag.) posterior fixigena, a narrow pygidial axis, and vestiges of an undulating doublural margin. Thus, they are allied to *Ogygiocaris* Angelin, 1854, which was previously described from the Middle Ordovician of Scandinavia and Great Britain, as well as from the upper Tremadocian of northwestern Argentina (e.g., Harrington and Leanza, 1957; Henningsmoen, 1960; Fortey and Owens, 1978; Waisfeld and Vaccari, 2006 and references; Hansen, 2009). However, the pygidia studied exhibit only nine axial rings and five pairs of pleural furrows which are shallow and not distally curved, so the generic affinity is tentative.

The pygidia of both *Ogygiocaris*? *iruyensis* n. sp. and *O. araiorhachis* Harrington and Leanza, 1957 sensu Waisfeld and Vaccari (2006), from the upper Tremadocian of the Incamayo area, Cordillera Oriental (Harrington and Leanza, 1957, figs. 71.1–71.3, 71.6, 72.2; Waisfeld and Vaccari, 2003, pl. 23, figs. 16, 17; 2006, fig. 1.A–I), show a very slightly undulating anterior doublural margin, which is more evident in well preserved specimens, and lack paradoublural lines. Nevertheless, *O.*? *iruyensis* differs in possessing slightly more divergent anterior branches of the facial sutures, an anteriorly pointed glabella, and a smaller number of pygidial axial rings and pleural furrows.

The new species most closely resembles "*Thysanopyge*"? *latelimbata* Harrington and Leanza (1957, fig. 84.1) and a group of pygidia of "*Ogygiocaris araiorhachis*" (Harrington and Leanza, 1957, figs. 71.4, 71.5, 72.2, 72.3; see Waisfeld and Vaccari, 2006, p. 733), from the upper Tremadocian of the Cordillera Oriental. *O.*? *iruyensis* is distinguished by its slightly pointed preglabellar furrow, the wider (tr.) glabella, its less divergent anterior facial sutures, and its fewer pygidial axial rings and pleural furrows.

The type species, *Ogygiocaris dilatata* (Brünnich, 1781) from the Middle Ordovician of Norway (Henningsmoen, 1960, pl. 1, figs. 1–7, pl. 2, figs. 1–6; Hansen, 2009, pl. 1, figs. 1–8), differs from *O.*? *iruyensis* in having a larger pygidium with 11 discrete axial rings, 7 deep pleural furrows, an apparent paradoublural line, and a clear indentation on the posterior margin. Similarly, many other species of *Ogygiocaris* (*O. debuchii* [Brongniart, 1822]; *O. sarsi* Angelin, 1854; *O. striolata* Henningsmoen, 1960; *O. seavilli* Whittard, 1964; *O. macrops* Rushton and Hughes, 1981; *O. henningsmoeni* Hansen, 2009) can be distinguished by having a conspicuous paradoublural line, a longer pygidial axis, and prominent pygidial pleural furrows, which are generally more numerous, longer and deeper than those of *O.*? *iruyensis* and show backwardly flexed extremities (Henningsmoen, 1960; Whittard, 1964; Hughes, 1979; Rushton and Hughes, 1981).

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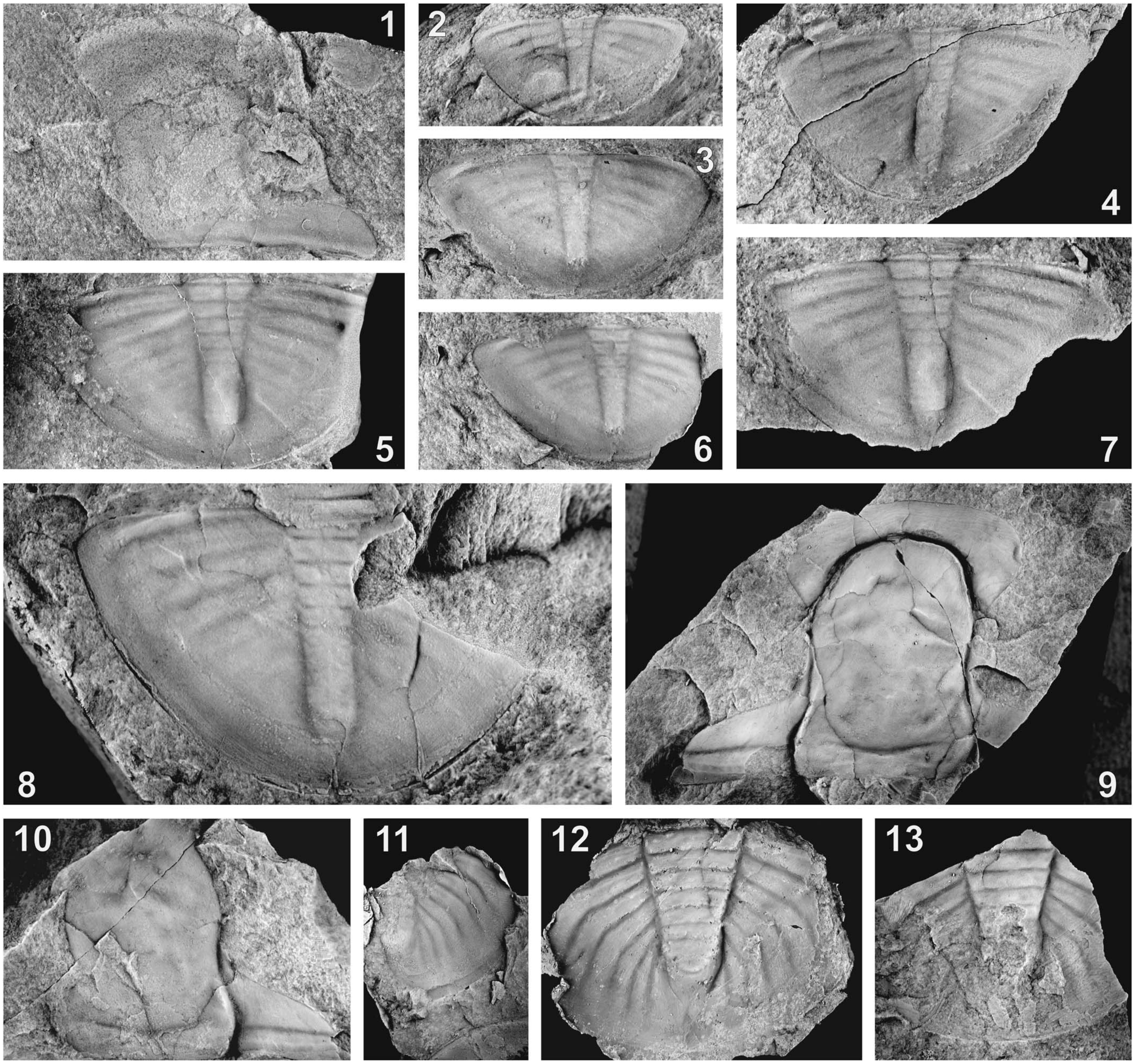

Figure 9. *Ogygiocaris*? *iruyensis* n. sp. and *Niobe* (*Niobella*) *inflecta* (Harrington and Leanza, 1957) from the Santa Rosita Formation in the Iruya area, northwestern Argentina. **(1–8)** *Ogygiocaris*? *iruyensis* n. sp.: **(1)** cranidium, MLP 35163, ×2.6; **(2)** pygidium, MLP 35161, ×3; **(3)** pygidium (holotype) MLP 35158a, ×3; **(4)** pygidium, MLP 35160, ×3; **(5)** pygidium, latex cast, MLP 35159, ×3; **(6)** pygidium, MLP 35053b, ×3; **(7)** pygidium, MLP 35154, ×3; **(8)** pygidium, MLP 35043a, ×2.3. **(9–13)** *Niobe* (*Niobella*) *inflecta* (Harrington and Leanza, 1957): **(9)** cranidium, MLP 35054, ×1.3; **(10)** cranidium, MLP 35050b, ×1.3; **(11)** pygidium, latex cast, MLP 35089b, ×1.3; **(12)** pygidium, latex cast, MLP 35109, ×1.3; **(13)** pygidium, MLP 35094, ×1.3. All specimens from Pantipampa.

Subfamily Niobinae Jaanusson (*in* Moore, 1959)
Genus *Niobe* Angelin, 1854
Subgenus *Niobe* (*Niobella*) Reed, 1931

Type species.—*Niobe homfrayi* Salter, 1866, from the lower Tremadocian of North Wales, by original designation.

Niobe (*Niobella*) *inflecta* (Harrington and Leanza, 1957) new combination
Figure 9.9–9.13

1957 *Hypermecaspis inflecta* Harrington and Leanza, p. 125, fig. 48.1, 48.2.

Holotype.—Pygidium from the lower Tremadocian of the Santa Victoria area, Cordillera Oriental, Argentina (Harrington and Leanza, 1957, fig. 48.2).

Description.—Cranidium large, subtrapezoidal in outline, wider than long; glabella scarcely raised above level of fixigena, elongate, well defined by narrow axial furrows, widest posteriorly, narrowest at midlength and sub-truncate in front,

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occupying ∽88% of the total cranidial length; median glabellar node very weak, situated at level of the posterior end of the palpebral area; occipital ring narrows (sag.) medially, occupying 10% of the total glabellar length (sag.); occipital furrow shallow at sides and deepest on midline, curved backward medially; frontal area depressed, lacking differentiated border furrow, covered with sinuous terrace ridges subparallel to anterior cranidial margin; anterior facial suture diverging at an angle of 45º to the exsagittal line; posterior fixigenae wide (tr.), defined by sigmoidal sutures, with a distinct border furrow; palpebral area of the fixigena not preserved for description. Largest observed cranidium 34 mm long (sag.).

Materials.—Two incomplete cranidia and four pygidia (MLP 35042c, 35050b, 35054, 35089b, 35094, 35109) from the Pantipampa section, Iruya area, northwestern Argentina, Santa Rosita Formation, lower Tremadocian, *Kainella teiichii* Zone.

Remarks.—Harrington and Leanza (1957, p. 125, fig. 48.1, 48.2) erected *Hypermecaspis inflecta* on the basis of a set of large pygidia (holotype 25 mm length) from the Santa Victoria area (Cordillera Oriental) which, according to Ebbestad (1999, p. 32), differ from those of other species of *Hypermecaspis* Harrington and Leanza, 1957 in having a semicircular outline and a less tapering rachis, which is bluntly rounded posteriorly. Ebbestad (1999) tentatively reassigned *H. inflecta* to *Cermatops* Shergold, 1980, and pointed out its high degree of similarity with the pygidium of *C. thalastus* Jell, Hughes and Brown, 1991, from the Furongian of western Tasmania (Jell et al., 1991, fig. 7F–H).

The cranidium of "*H*". *inflecta* (Fig. 9.9, 9.10) is described herein for the first time, which allowed for a further understanding of the affinities of this species. Although the material examined is scarce, it clearly shows a smooth, flat frontal area, and palpebral lobes extremely close to the glabella. Therefore, its general aspect suggests closer correspondence with *Niobe* (*Niobella*) Reed, 1931; a taxon characterized by having a depressed frontal area; gently divergent anterior branches of facial sutures; a straight-sided or slightly constricted, non-bacculate glabella; palpebral lobes placed in contact with the axial furrow; and a flat pygidial border (e.g., Whittington, 1965; Shergold and Sdzuy, 1984; Peng, 1990b). Following Ebbestad (1999 and references), we recognize *Niobella* at subgeneric level.

Niobe (*Niobella*) *inflecta* most closely resembles *N.* (*N.*) *shenjiawanensis* Peng, 1990b, from the lower Tremadocian (*Onychopyge*-*Hysterolenus* Assemblage Zone) of China (Peng, 1990b, pl. 12, figs. 6, 7), which was originally based on three cranidia showing a long (sag.), medially constricted glabella, gently divergent anterior facial sutures, a moderately developed frontal area, and oblique posterior facial sutures. The Argentinian species differs in having a better defined occipital furrow.

Genus *Metayuepingia* Liu in Zhou et al., 1977

Type species.—*Metayuepingia angustilimbata* Liu in Zhou et al., 1977 from the Lower Ordovician of China, by original designation.

Metayuepingia riccardii new species
Figure 10.1–10.27

Diagnosis.—A species of *Metayuepingia* with an oblique posterior facial suture, a poorly defined posterior cranidial border, a tapering pygidial axis with five to six rings, and a proportionately wide pygidial border.

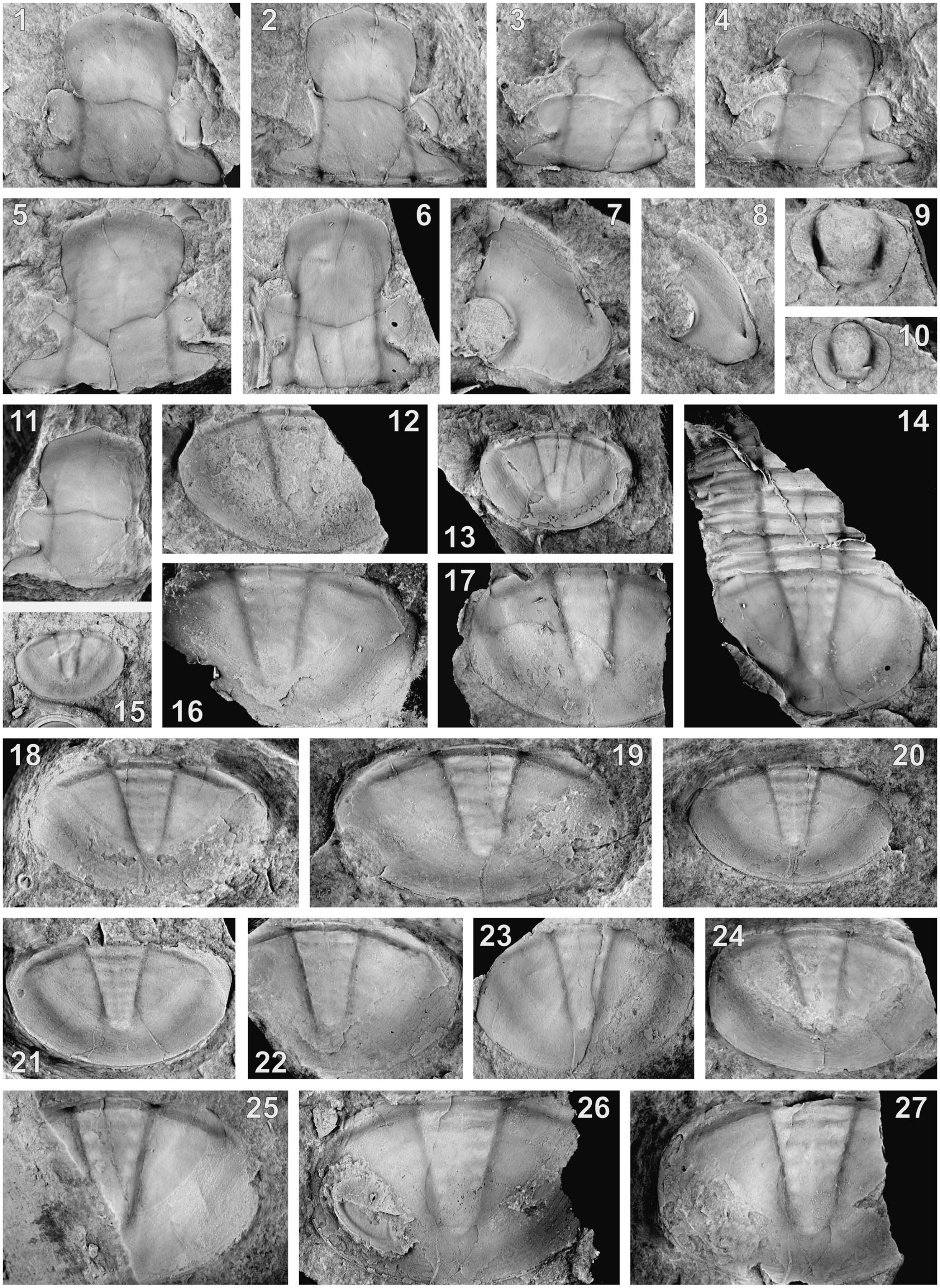
Description.—Cranidium subtrapezoidal in outline, gently convex, with concave frontal area and pointed anterior margin; glabella elongate, unfurrowed, slightly constricted (tr.) at level of palpebral areas, surrounded by shallow and narrow axial furrows, ill-defined anteriorly where it grades into preglabellar field; it occupies approximately four-fifths length of cranidium and a half of maximum cranidial width (tr.); median glabellar node delicate, situated opposite posterior part of palpebral lobes; occipital brim extremely narrow (sag.), delimited by a faint band furrow; anterior facial suture slightly diverging in front of eyes, meeting mesially in pointed ogive; palpebral area of the fixigena narrow (tr.); palpebral lobe prominent, arcuate, situated behind cranidial midpoint, occupying ∽23%–25% of the total length (sag.) of the cranidium; posterior facial suture oblique backward and outward, sigmoidal; posterior fixigena wide (tr.), triangular; librigenae with wide, concave lateral border and rounded genal angle; posterior border furrow weak; hypostome with wide (tr.) lateral borders, covered with terrace lines. Largest observed cranidium 15 mm long (sag.).

Pygidium sub-semicircular in outline, gently to moderately convex transversely and longitudinally, wider than long; axis evenly tapering backward, scarcely elevated above level of pleural fields, surrounded by narrow axial furrows, with slightly marked five to six rings and terminal piece, rounded at posterior end; it occupies ∽25% of total width of pygidium at anterior extremity, and 69%–71% of length of pygidium on sagittal line; pleural fields moderately convex, smooth; border broad, concave, not well defined by border furrows; doublure very wide, covered with 12 terrace ridges following the doublural contour. Largest observed pygidium 18.5 mm long (sag.).

Etymology.—Dedicated to Dr Alberto C. Riccardi (Museo de La Plata).

→

Figure 10. *Metayuepingia riccardii* n. sp. from the Santa Rosita Formation in the Iruya area, northwestern Argentina: **(1)** cranidium, latex cast of specimen figured in **(2)** MLP 35070, ×2.5; **(2)** cranidium, MLP 35070, ×2.5; **(3)** cranidium, latex cast of specimen figured in **(4)** MLP 35048, ×2.5; **(4)** cranidium (holotype) MLP 35048, ×2.5; **(5)** cranidium, MLP 35401, ×2.5; **(6)** cranidium, latex cast, MLP 35042a, ×2.5; **(7)** librigena, latex cast, MLP 35126, ×2.5; **(8)** librigena, MLP 35155, ×3.5; **(9)** hypostome, MLP 35146, ×2.5; **(10)** hypostome, MLP 35081, ×2.5; **(11)** cranidium, MLP 35087, ×2.5; **(12)** pygidium, MLP 35073a, ×2.1; **(13)** pygidium, MLP 35136, ×2.1; **(14)** fragmentary thoracopygon, latex cast, MLP 35058, ×1.7; **(15)** pygidium, latex cast, MLP 35057a, ×2.1; **(16)** pygidium, latex cast, MLP 35085, ×2.1; **(17)** pygidium, latex cast, MLP 35089a, ×1.7; **(18)** pygidium, MLP 35071, ×2.1; **(19)** pygidium, MLP 35086, ×2.1; **(20)** pygidium, MLP 35039, ×2.1; **(21)** pygidium, MLP 35063, ×2.1; **(22)** pygidium, MLP 35093, ×1.7; **(23)** pygidium, latex cast, MLP 35044, ×2.1; **(24)** pygidium, MLP 35045, ×2.1; **(25)** pygidium, MLP 35082, ×2.1; **(26)** pygidium, latex cast, MLP 35056a, ×2.1; **(27)** pygidium, MLP 35092a, ×2.1. All specimens from Pantipampa.



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Types.—Holotype, cranidium, MLP 35048 (Fig. 10.4), length 11.3 mm; paratypes, 13 cranidia, 8 librigenae, 4 hypostomes, 1 fragmentary thoracopygon and 24 pygidia (MLP 35034b, 35036a, 35038, 35039, 35041, 35042a, 35043b, 35044, 35045, 35047, 35055a, 35056a, 35057a, 35058, 35063, 35069, 35070, 35071, 35073a, 35076a, 35081, 35082, 35083b, 35085–35087, 35089a, 35092a, 35093, 35099, 35101b, 35108, 35113b, 35116, 35122, 35126, 35134, 35136, 35137, 35139, 35146, 35151, 35152, 35155, 35157a, 35401).

Occurrence.—Pantipampa section, Iruya area, northwestern Argentina, Santa Rosita Formation, lower Tremadocian, *Kainella teiichii* Zone.

Remarks.—The presence of a large, medially constricted glabella; a glabellar node located opposite posterior part of palpebral lobes; an absent occipital furrow; prominent and medially placed palpebral lobes; an anteriorly up-turned frontal area; an isoteliform facial suture; a tapering, segmented pygidial axis; smooth pleural fields; and a broad concave pygidial border are characters of *Metayuepingia* Liu in Zhou et al., 1977, a taxon previously described from the Lower Ordovician of China (Zhou et al., 1977; Peng, 1990b). Although the pygidial axis of the material studied is slightly longer, and the pygidial border is somewhat wider than those of other species of *Metayuepingia*, we feel that these variations lack generic significance.

Metayuepingia latilimbata Liu in Zhou et al., 1977, from the upper Tremadocian (*Shumardia* (*Conophrys*) *acutifrons-Asaphopsoides* Zone) of China (Zhou et al., 1977, pl. 64, figs. 5, 6; Peng, 1990b, pl. 14, figs. 12–16), differs from *M. riccardii* in having a transverse posterior facial suture, a better defined posterior border of the fixigena, a slightly shorter (sag.) pygidial axis with four rings and terminal piece, and a proportionately narrower pygidial border. The type species, *Metayuepingia angustilimbata* Liu in Zhou et al., 1977, from the Tremadocian (*Apatokephalus latilimbatus-Taoyuania affinis* and *Shumardia* [*Conophrys*] *acutifrons-Asaphopsoides* zones) of China (Zhou et al., 1977, pl. 64, figs. 1–3; Peng, 1990b, pl. 13, figs. 10–13; pl. 14, figs. 1–11) shows, in addition, a less tapered pygidial axis.

Metayuepingia divergens Peng, 1990b, from the upper Tremadocian (*Shumardia* [*Conophrys*] *acutifrons-Asaphopsoides* Zone) of China (Peng, 1990b, pl. 15, figs. 2, 3), was described on the basis of two distorted cranidia which differ from *M. riccardii* in having a more divergent anterior facial suture, a wider (tr.) anterior fixigena, and a gently convex frontal area.

Superfamily Remopleuridioidea Hawle and Corda, 1847
Family Richardsonellidae Raymond, 1924
Genus *Kainella* Walcott, 1925

Type species.—*Hungaia billingsi* Walcott, 1924, from the lower Survey Peak Formation in British Columbia, Canada, by original designation.

Kainella meridionalis Kobayashi, 1935
Figure 11.22, 11.23

1935 *Kainella meridionalis* Kobayashi, p. 65, pl. 11, figs. 5–7 (only).

1957 *Kainella meridionalis*; Harrington and Leanza, p. 127, fig. 50.1–50.8.

2010 *Kainella meridionalis*; Vaccari and Waisfeld, p. 275, figs. 1.1–1.3, 2.1–2.14, 3, 9.22 (see for further synonymy).

Lectotype.—Cranidium from the lower Tremadocian of the Incamayo area, Cordillera Oriental, Argentina (Kobayashi, 1935, pl. 11, fig. 7; Vaccari and Waisfeld, 2010, fig. 1.2).

Materials.—Three fragmentary cranidia and one pygidium (MLP 34965–34967, 35021) from the lower part of the Pantipampa section, Iruya area, northwestern Argentina, Santa Rosita Formation, lower Tremadocian, *Kainella meridionalis* Zone and basal *K. teiichii* Zone.

Remarks.—Vaccari and Waisfeld (2010) emended the diagnosis and scope of *Kainella meridionalis* Kobayashi, 1935 from northwestern Argentina, and regarded the presence of four pairs of anastomosing ridges on the preglabellar field as one of its most characteristic features. Since *Kainella* specimens from the lower part of the Pantipampa section show this character, they are assigned confidently to this species. Vaccari and Waisfeld (2010) discussed the affinities of *K. meridionalis* with other species of *Kainella* from the Cordillera Oriental of Argentina and Bolivia (e.g., *K. teiichii* Vaccari and Waisfeld, 2010, see below; *K. andina* Suárez-Soruco, 1975; *K. morena* Vaccari and Waisfeld, 2010), North America, Korea, China, and New Zealand.

Kainella teiichii Vaccari and Waisfeld, 2010
Figure 11.1–11.21

2010 *Kainella teiichii* Vaccari and Waisfeld, p. 278, figs. 1.5, 4.1–4.14, 5 (see for further synonymy).

Holotype.—Pygidium from the Tremadocian of the Tilcara area, Cordillera Oriental, Argentina (Vaccari and Waisfeld, 2010, fig. 4.13).

Materials.—Thirty cranidia, eighteen librigenae and twenty pygidia (MLP 4929, 4935, 4942, 4954, 4959, 4960, 4970, 34977c, 34987a, 35060, 35066, 35072, 35080, 35088, 35090, 35105a, 35107, 35125, 35164, 35179, 35182, 35187, 35189a, 35202a, 35203, 35204, 35208, 35225–35228, 35231–35234, 35236, 35237, 35240, 35247, 35249, 35250, 35254, 35255, 35268, 35271, 35272b, 35307, 35310, 35317, 35318d, 35319a, 35326, 35328–35331, 35333, 35334, 35337, 35340–35342, 35349b, 35353a, 35354) from the Pantipampa and lower Rodeo Colorado sections, Iruya area, northwestern Argentina, Santa Rosita Formation, Tremadocian, *Kainella teiichii* Zone.

Remarks.—The specimens examined represent a distinctive *Kainella* species of the upper Pantipampa and lower Rodeo Colorado sections. They are characterized by having a single pair of well-defined oblique ridges on the preglabellar field, slightly curved genal spines, a pygidial axis ∽1.5 times longer

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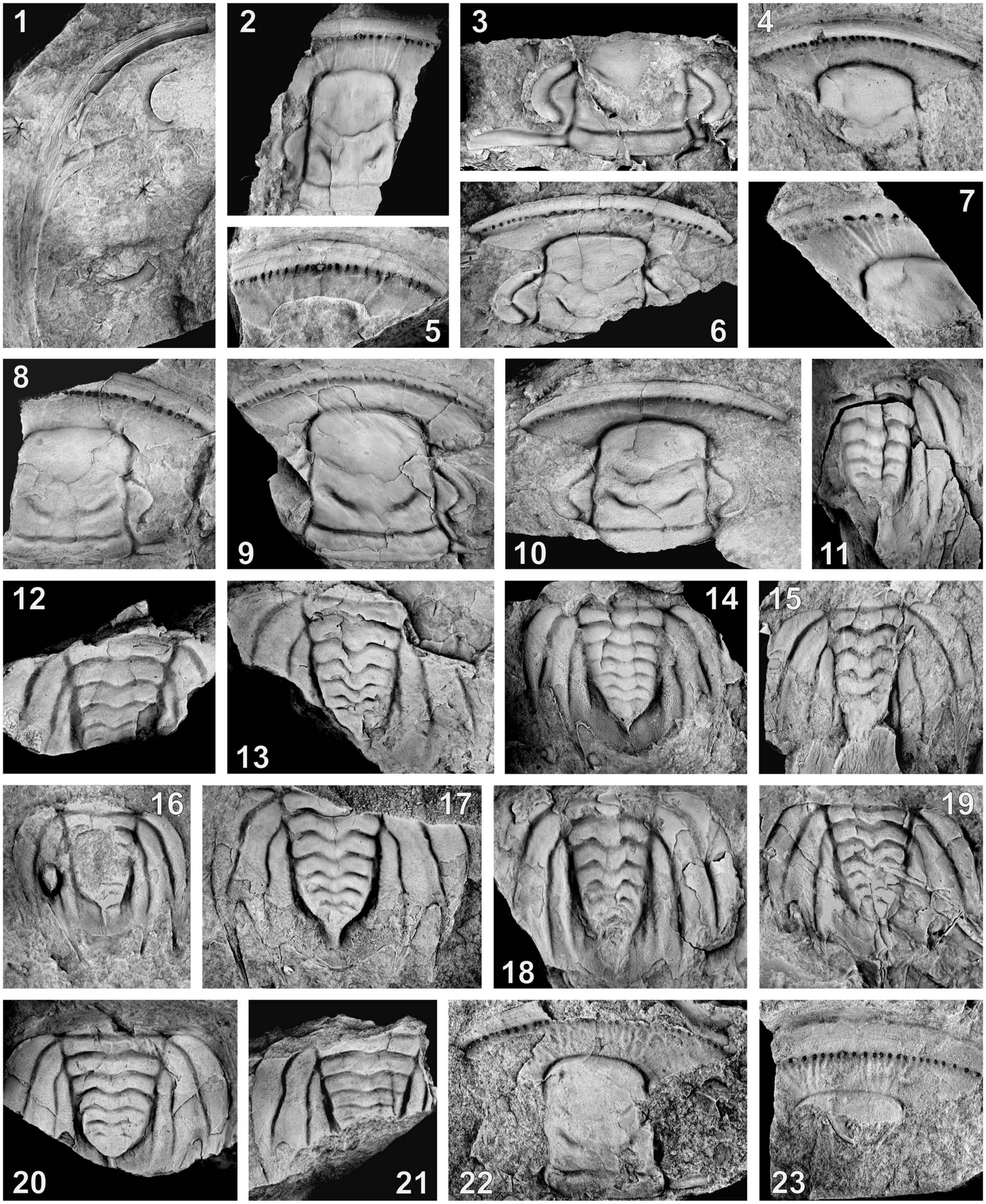

Figure 11. Richardsonellids from the Santa Rosita Formation in the Iruya area, northwestern Argentina. (**1–21**) *Kainella teiichii* Vaccari and Waisfeld, 2010: (**1**) librigena, MLP 35353a, ×1.4, Rodeo Colorado (RC); (**2**) cranidium, latex cast, MLP 35240, ×1.4, Pantipampa (P); (**3**) cranidium, latex cast, MLP 35179, ×1.6, P; (**4**) cranidium, MLP 35317, ×2.5, RC; (**5**) fragmentary cranidium, MLP 35319a, ×1.4, RC; (**6**) cranidium, latex cast, MLP 4929, ×1.9, RC; (**7**) fragmentary cranidium, MLP 35254, ×1.4, P; (**8**) cranidium, MLP 4942, ×1.4, RC; (**9**) cranidium, MLP 4970, ×1.4, RC; (**10**) cranidium, latex cast, MLP 35333, ×2.2, RC; (**11**) pygidium, MLP 4954, ×1, RC; (**12**) pygidium, MLP 35227, ×1.8, P; (**13**) pygidium, MLP 35326, ×1.6, RC; (**14**) pygidium, latex cast, MLP 35189a, ×2.2, P; (**15**) pygidium, latex cast, MLP 35354, ×2.2, RC; (**16**) pygidium, MLP 35088, ×2.2, P; (**17**) pygidium, MLP 35164, ×1.6, P; (**18**) pygidium, MLP 4960, ×1.6, RC; (**19**) pygidium, MLP 4935, ×2.2, RC; (**20**) pygidium, MLP 4959, ×2.2, RC; (**21**) pygidium, MLP 35331, ×2.2, RC. (**22, 23**) *Kainella meridionalis* Kobayashi, 1935: (**22**) cranidium, MLP 35021, ×1.7, P; (**23**) fragmentary cranidium, MLP 34966, ×1.7, P.

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than wide, and backwardly oblique pygidial pleural furrows. Therefore, according to the diagnosis of Vaccari and Waisfeld (2010), they are assignable to *Kainella teiichii*. This species is very similar to *K. meridionalis* Kobayashi, 1935, from the lower Tremadocian of the Cordillera Oriental, but the latter differs mainly by showing anastomosing preglabellar ridges, more strongly curved genal spines, and a proportionately longer (sag.) pygidial axis (Vaccari and Waisfeld, 2010). Kainellids collected from Rodeo Colorado by Figueroa Caprini (1955) were added to the present study (Fig. 11.6, 11.8, 11.9, 11.11, 11.18, 11.19, 11.20; see also Tortello et al., 2002, fig. 5.E–H) and assigned to *K. teiichii*.

Genus *Pseudokainella* Harrington, 1938

Type species.—*Pseudokainella keideli* Harrington, 1938, from the Tremadocian of the Cordillera Oriental, Argentina, by original designation.

Remarks.—After the original description of Harrington (1938) and Harrington and Leanza (1957), *Pseudokainella* was revised by Jell (1985), who regarded it as a kainellid having a preglabellar field of variable length, a variable angle of divergence of the anterior facial suture, and three, four, or five pairs of pygidial marginal spines which decrease in size posteriorly (see also Peng, 1990b; Tortello and Esteban, 2007). Thus, *Elkanaspis* Ludvigsen, 1982 and *Fatocephalus* Duan and An in Guo et al., 1982 could be considered as junior synonyms of *Pseudokainella* (Jell, 1985).

Alternatively, Ludvigsen (1982) and Ludvigsen et al. (1989) prefer to limit *Pseudokainella* to species having a particularly short (sag.) preglabellar field, a widely divergent anterior facial suture, and a very long anterior pair of pygidial spines. In accordance with this criterion, Waisfeld and Vaccari (2003) restricted the concept of *Pseudokainella* to the type species *P. keideli* Harrington.

Pseudokainella keideli Harrington, 1938
Figure 12.1–12.6

1938 *Pseudokainella keideli* Harrington, p. 174, pl. 5, figs. 11–15.
1957 *Pseudokainella keideli*; Harrington and Leanza, p. 131–132, figs. 51, 52.5–52.10.
2003 *Pseudokainella keideli*; Waisfeld and Vaccari, p. 325, pl. 27, figs. 13–16.
2005 *Pseudokainella keideli*; Zeballo and Tortello, p. 139, figs. 5G–H.

Holotype.—Complete specimen from the Tremadocian of the Tilcara area, Cordillera Oriental, Argentina (Harrington, 1938, pl. 5, fig. 14; Harrington and Leanza, 1957, fig. 52.6).

Materials.—One cephalon, twenty cranidia, one librigena and fifteen pygidia (MLP 4926, 4927, 4952a, 35178, 35180, 35182, 35193, 35194a, 35195–35198, 35229, 35230, 35264, 35265, 35274, 35277, 35281, 35283a, 35292–35297, 35299, 35300, 35323c, 35339, 35343, 35345, 35347) from the Pantipampa and Rodeo Colorado localities, Iruya area, northwestern Argentina, Santa Rosita Formation, Tremadocian, *Kainella teiichii* and *Bienvillia tetragonalis* zones.

Remarks.—As stated by Harrington and Leanza (1957), *Pseudokainella keideli* Harrington is characterized by having a long and conical glabella with 2 or 3 oblique lateral furrows, an extremely short (sag.) preglabellar field, strongly divergent anterior branches of facial sutures, narrow (tr.) palpebral area of the fixigena, genal angles in a slightly advanced position, a tapering pygidial axis composed of four rings and a terminal piece, and four pairs of pygidial marginal spines, among which the anterior pair is much longer than the others. Although the material studied herein is not perfectly preserved, it shows such diagnostic features and is therefore assigned to this species.

Pseudokainella keideli has been previously described from the *Bienvillia tetragonalis* Zone of the Tilcara region (Harrington, 1938; Harrington and Leanza, 1957; Waisfeld and Vaccari, 2003; Zeballo and Tortello, 2005). This report provides the first record from the northern Cordillera Oriental, from both the *Kainella teiichii* Zone and the *Bienvillia tetragonalis* Zone.

Family Kainellidae Ulrich and Resser, 1930
Genus *Apatokephalus* Brøgger, 1896

Type species.—*Trilobites serratus* Boeck, 1838, from the upper Tremadocian in Oslo, Norway (subsequently designated by Bassler, 1915).

Remarks.—Ebbestad (1999) discussed in detail the concept of the cosmopolitan genus *Apatokephalus* Brøgger, 1896 and redescribed the type species *A. serratus* (Boeck, 1838) based on well-preserved material from Norway. *Apatokephalus* is characterized by having a bell-shaped glabella with a long (sag.) frontal lobe, three pairs of lateral furrows, large palpebral lobes very close to the glabella, librigenal spines in an advanced position, and a small, serrate pygidium (Peng, 1990b). The numerous species of this genus show variations in the length (sag.) of the preglabellar field, the outline of the glabellar furrows, the sculpture of the glabella, and the direction of the anterior and posterior facial sutures (Peng, 1990b; Ebbestad, 1999).

Apatokephalus rugosus new species
Figure 12.7–12.13

Diagnosis.—A species of *Apatokephalus* with a sculpture of raised granules of different sizes on the test, a very short (sag.) preglabellar field, sigmoidal anterior facial sutures curving backward laterally, and a pygidium with four pairs of apparent pleural furrows and five broad-based marginal spines.

Description.—Cranidium with slightly pointed anterior margin; glabella bell-shaped, moderately convex, slightly rounded anteriorly, occupying ∽86% of the total cranidial length, clearly expanded (tr.) between palpebral lobes; frontal glabellar lobe subquadrate, occupying approximately one-fourth of the glabellar length; lateral glabellar furrows distinct, medially disconnected, only anterior two pairs connecting with axial

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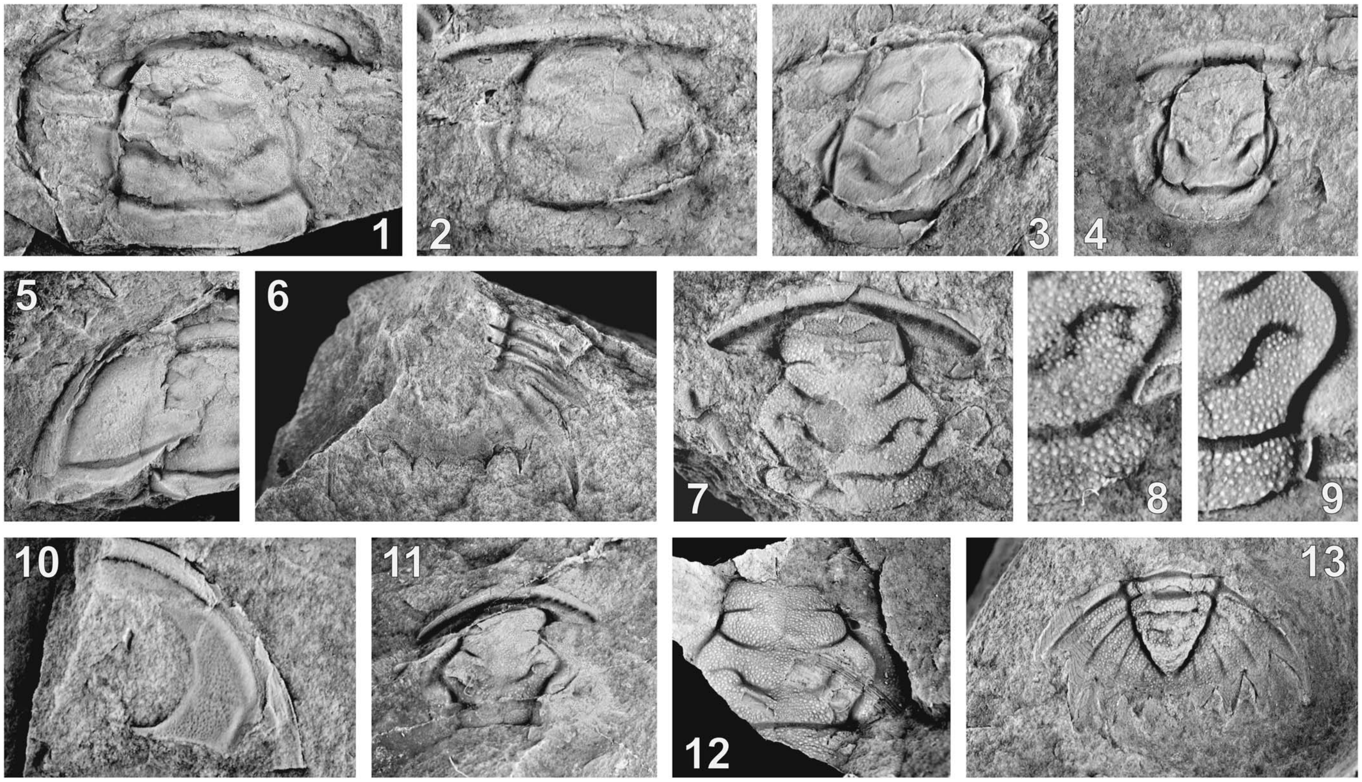

Figure 12. Richardsonellids and kainellids from the Santa Rosita Formation in the Iruya area, northwestern Argentina. **(1–6)** *Pseudokainella keideli* Harrington, 1938: **(1)** cranidium, MLP 35180, ×2.3, Pantipampa (P); **(2)** cranidium, MLP 35197, ×2.3, P; **(3)** cranidium, MLP 35264, ×2.3, P; **(4)** cranidium, MLP 35265, ×2.3, P; **(5)** librigena, MLP 35194a, ×2.3, P; **(6)** posterior thorax and pygidium, MLP 35297, ×2.3, P. **(7–13)** *Apatokephalus rugosus* n. sp.: **(7)** cranidium (holotype) MLP 35322, ×3.4, Rodeo Colorado (RC); **(8)** detail of glabellar granulation, latex cast, MLP 35322, ×6.9, RC; **(9)** detail of glabellar granulation, latex cast, MLP 35186b, ×6.8, P; **(10)** librigena, MLP 35186a, ×3.4, P; **(11)** small cranidium, MLP 35186b, ×4.5, RC; **(12)** cranidium, latex cast, MLP 35150, ×3.4, P; **(13)** pygidium, MLP 35130a, ×3.4, P.

furrows; S1 long, sigmoidal, directed obliquely inward and backward, situated opposite middle (sag.) of palpebral lobes; S2 straight to slightly curved backward, approximately parallel to the preoccipital furrow; S3 shorter than S1 and S2, transverse, straight to slightly curved forward; occipital furrow distinct, of uniform depth, slightly curved forward medially and laterally; occipital ring somewhat wider (tr.) than the anterior lobe of the glabella, broadly rounded posteriorly, occupying ∽18% of the total glabellar length; preglabellar field very short (sag.), depressed; anterior cranidial border much longer (sag.) than preglabellar field, upturned, with open-spaced terrace ridges subparallel to margin, separated from the preglabellar field by a pitted border furrow; anterior sections of facial suture sigmoidal, curving backward laterally; palpebral lobes large, crescentic, extending from the occipital furrow to the third lateral glabellar lobe (L3); palpebral lobe furrow deeply incised; librigenae with long genal spines continuing curvature of lateral margins; genal angles moderately advanced; eye socle semi-circular, very narrow, elevated above flat genal field; posterior facial suture transverse, extending outward from posterior end of eye socle; lateral cephalic border with 5–6 fine terrace lines subparallel to margin, delimited by a shallow border furrow; external surface of exoskeleton covered with variably developed raised tubercules, which are less distinct on the small holaspides (Fig. 12.11). Largest observed cranidium 8.8 mm long (sag.).

Pygidium semielliptical in outline, approximately twice as wide (tr.) as long (sag.); axis transversely convex, tapering backward, well defined by discrete axial furrows, divided into four rings and a triangular terminal piece that continues backward into a weak posterior ridge, occupying ∽80% of the total pygidial length (excluding articulating half ring) and one-third of the maximum pygidial width; articulating half ring very narrow (sag.), delimited by a conspicuous furrow; pleural fields only slightly downsloping, with four pairs of distinct pleural furrows and five pairs of broad-based lateral spines derived from pleurae, which decrease in size posteriorly; doublure wide, covered with 10–12 terrace lines; external surface of axial rings and pleural fields with densely spaced tubercles. Largest observed pygidium 5 mm long (sag.).

Etymology.—Latin *rugosus*, referring to the sculpture of the exoskeleton.

Types.—Holotype, cranidium, MLP 35322 (Fig. 12.7), length 8.8 mm; paratypes, six cranidia, three librigenae, and three pygidia (MLP 35057c, 35076b, 35078, 35114, 35123, 35130a, 35131, 35150a, 35186a,b, 35353b).

Occurrence.—Pantipampa and Rodeo Colorado sections, Iruya area, northwestern Argentina, Santa Rosita Formation, lower Tremadocian, *Kainella teiichii* Zone.

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Remarks.—The specimens examined exhibit a variably developed sculpture on the external surface of the test. Small cranidia show sparse openly spaced granules (Fig. 12.11), whereas late holaspides have larger tubercles, which are of different sizes and more or less densely packed (compare Fig. 12.7–12.9 and 12.12).

Apatokephalus rugosus closely resembles *A. sarculum* Fortey and Owens, 1991, from the upper Tremadocian of north England (Fortey and Owens, 1991, fig. 12.a–j, l, o), mainly in having a surface sculpture of distinct granules, well-defined glabellar furrows, a short (sag.) preglabellar field, and a sigmoidal and transverse facial suture. However, *A. sarculum* differs in its much shorter (sag.) pygidial axis. *Apatokephalus canadensis* Kobayashi, 1953, from the Tremadocian of western Canada (Kobayashi, 1953, pl. 3, figs. 1–4; Dean, 1989, pl. 24, figs. 6, 9), exhibits a well-developed ornamentation and a very short preglabellar field, but differs from *A. rugosus* in lacking broad-based pygidial spines.

The type species *Apatokephalus serratus* (Boeck, 1838), from the upper Tremadocian of Norway (Fortey and Owens, 1991, fig. 12k, m, p, q; Ebbestad, 1999, figs. 41A, 42A–O), differs from *A. rugosus* in having a glabella covered with more prominent and more openly spaced tubercles, and six pairs of delicate marginal spines on the pygidium. The pygidium of *Apatokephalus exiguus* Harrington and Leanza, 1957, from the upper Tremadocian of the Cordillera Oriental (Harrington and Leanza, 1957, figs. 57, 58.1–58.5), is distinguished from that of *A. rugosus* mainly in its shorter (sag.) axis and its minute marginal spines.

Apatokephalus tibicen Přibyl and Vaněk, 1980, from the upper Tremadocian of the Cordillera Oriental (Harrington and Leanza, 1957, fig. 56.1, 56.3–56.8, 56.10; Přibyl and Vaněk, 1980, pl. 12, figs. 3, 4; Tortello and Esteban, 2014, figs. 9.11–9.15, 9.19), is distinguished from *A. rugosus* mainly by its longer (sag.) preglabellar field. In addition, the anterior facial suture is transverse or strongly diverging forwardly in *A. tibicen*, while it curves backward laterally in *A. rugosus*.

Apatokephalus levisensis (Rasetti, 1943), from the lower Ordovician of Quebec, eastern Canada (Fortey and Owens, 1991, fig. 12n, r), differs from *A. rugosus* in the presence of a longer (sag.) preglabellar field. The preglabellar field is even larger in *A. longifrons* Dean, 1989, from the Tremadocian of Canada (Dean, 1989, pl. 24, figs. 1, 2, 4, 7), and *Apatokephalus* sp. (Tortello and Esteban, 2014, fig. 9.16, 9.20), from the upper Tremadocian of the Nazareno area, Cordillera Oriental.

Apatokephalus latilimbatus Peng, 1990b, from the Tremadocian of China (Peng, 1990b, pl. 11, figs. 1–14, pl. 12, figs. 4, 5, 9), further differs from *A. rugosus* in its wider (sag.) anterior border, its strongly advanced genal spines, and its smaller pygidial axis. *Apatokephalus dubius* (Linnarsson, 1869), from the upper Tremadocian of Scandinavia (Ebbestad, 1999, figs. 41B, 42A–G), is distinguished mainly by having a fine fingerprint-like ornament on the glabella. Similarly, the skeleton of *A. incisus* Dean, 1966, from the Lower Ordovician of the Montagne Noire, southern France, lacks tuberculate sculpture.

Family Ceratopygidae Linnarsson, 1869
Genus *Onychopyge* Harrington, 1938

Type species.—*Onychopyge riojana* Harrington, 1938, from the upper Furongian of La Rioja Province, Argentina, by original designation.

Remarks.—Although the original diagnosis of *Onychopyge* was based on very fragmentary material from Argentina (Harrington, 1938; Harrington and Leanza, 1957), the concept of the genus was later improved with new and better preserved material mainly from Mexico (Robison and Pantoja-Alor, 1968), Australia (Jell, 1985) and China (Qian, 1986). *Onychopyge* has exceptionally large palpebral lobes with their inner ends adjacent to axial furrows, a subrectangular glabella with faint to moderately developed lateral furrows, a tapered pygidial axis of five to seven rings extended into a postaxial ridge, and a large anterior pygidial segment showing a pair of wide pleural furrows and a pair of prominent marginal spines. Posterior pleural furrows of the pygidium are faint or absent (Harrington and Leanza, 1957; Robison and Pantoja-Alor, 1968; Jell, 1985).

The material of *Onychopyge* described to date from Argentina comes from the upper Furongian (*Parabolina frequens argentina* Zone) of both the Famatina Range (Harrington, 1938; Harrington and Leanza, 1957; Tortello and Esteban, 2007) and the Cordillera Oriental (Harrington and Leanza, 1957; Benedetto, 1977; Zeballo and Tortello, 2005; Esteban and Tortello, 2007). The first Tremadocian material is described below.

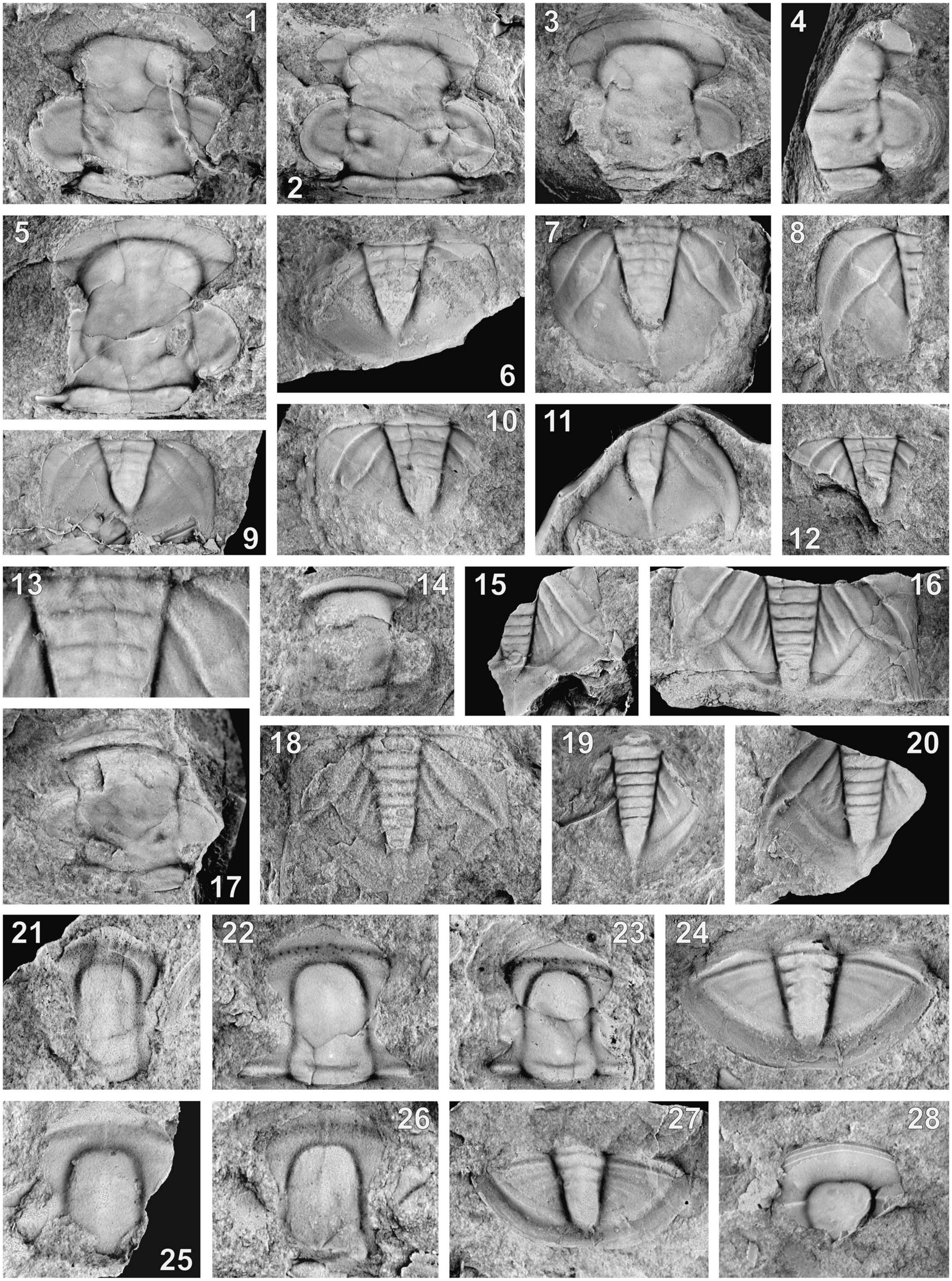
Onychopyge acenolazai new species
Figure 13.1–13.13

Diagnosis.—A species of *Onychopyge* with a laterally expanded frontal glabellar lobe, a frontal area bounded posteriorly by a shallow accessory furrow which is interrupted by the anterior end of the glabella, a short (tr.) and bifurcate lateral glabellar furrow S1, and a strongly tapered pygidial axis of five rings and terminal piece. External surface of exoskeleton covered with Bertillon pattern of delicate lines.

Description.—Cranidium of low convexity in both anterior and lateral profiles, subtrapezoidal in outline, as long as wide;

Figure 13. Ceratopygids and hapalopleurids from the Santa Rosita Formation in the Iruya area, northwestern Argentina. **(1–13)** *Onychopyge acenolazai* n. sp.: **(1)** cranidium, MLP 35040, ×2.5, Pantipampa (P); **(2)** cranidium (holotype) MLP 35091, ×2.7, P; **(3)** cranidium, MLP 35096, ×2.7, P; **(4)** fragmentary cranidium, MLP 35074b, ×2.7, P; **(5)** cranidium, MLP 35166, ×2.5, P; **(6)** pygidium, MLP 35117, ×2.7, P; **(7)** pygidium, latex cast, MLP 35167, ×2.4, P; **(8)** pygidium, MLP 35075b, ×2.7, P; **(9)** pygidium, latex cast, MLP 35059a, ×2.7, P; **(10)** pygidium, latex cast, MLP 35119, ×2.7, P; **(11)** pygidium, latex cast, MLP 35118, ×2.7, P; **(12)** pygidium, MLP 35097, ×2.7, P; **(13)** detail of pygidial surface, latex cast, MLP 35167, ×5. **(14–20)** *Onychopyge gonzalezae* n. sp.: **(14)** cranidium, MLP 35079, ×3.5, P; **(15)** pygidium, latex cast, MLP 35143, ×2.7, P; **(16)** pygidium (holotype) MLP 35147, ×2.7, P; **(17)** cranidium, MLP 35049a, ×2.7, P; **(18)** pygidium, MLP 35046, ×2.7, P; **(19)** pygidium, MLP 35064, ×2.7, P; **(20)** pygidium, latex cast, MLP 35124, ×2.7, P. **(21–27)** Ceratopygidae gen. et sp. indet.: **(21)** cranidium, latex cast, MLP 35319b, ×4.1, Rodeo Colorado (RC); **(22)** cranidium, MLP 35176, ×4.2, P; **(23)** cranidium, MLP 35181, ×4.3, P; **(24)** pygidium, MLP 35175, ×3.5, P; **(25)** cranidium, latex cast, MLP 35127b, ×4.3, P; **(26)** cranidium, MLP 35318a, ×4.3, RC; **(27)** pygidium, MLP 4961a, ×4.3, RC. **(28)** *Hapalopleura* sp. indet.: cranidium, latex cast, MLP 35111, ×2.7, P.

http://dx.doi.org/10.1017/jpa.2016.104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glabella large, subrectangular in outline, longer than wide, slightly raised above level of fixigenae, delimited by sinuous axial furrows, clearly expanded (tr.) both at glabellar lateral lobe L2 and frontal lobe, with rounded anterolateral corners and slightly curved anterior margin, occupying ∽85%–88% of the total cranidial length, with a discrete lateral furrow S1 and extremely faint indications of S2 and S3; S1 disconnected at middle and separated from axial furrows, short, bifurcate, with greatest depth at point of adaxial bifurcation; glabellar median node very delicate, located in preoccipital segment; occipital furrow deepest at sides and shallow on midline, slightly curved backward medially; occipital ring wider (tr.) than the rest of the glabella, broadly rounded posteriorly, occupying ∽13% of the total glabellar length; anterior facial suture divergent before converging inward along the anterior cranidial margin; frontal area distinct, slightly convex, bounded posteriorly by a shallow, backwardly oblique brim furrow (= "accessory furrow") that is interrupted by the anterior end of the glabella; palpebral lobes large, semicircular, approximately one-half length of glabella; palpebral furrows shallow but distinct; posterior limbs narrow (exsag.) and strap-like. Bertillon pattern of fine lines covers the external surface of the cranidium. Largest observed cranidium 15 mm long (sag.).

Librigenae fragmentary, insufficient for description. Hypostome and thorax unknown.

Pygidium subparabolic in ouline, wider than long, with slightly pointed posterior margin; axis convex, elevated above pleural fields, anterior width one third maximum width of pygidium, tapered backward, surrounded by narrow axial furrows, occupying ∽65%–70% of the total pygidial length (sag.); it is composed of a short (sag.) articulating half-ring, five rings and a terminal piece that are defined by shallow, forwardly curved transaxial furrows; a narrow postaxial ridge extends from the axis to the posterior pygidial margin; pleural fields weakly convex; anterior pleural furrow wide, extended posterolaterally into a pair of stout marginal spines; posterior pleural furrows indistinct; border furrow absent; doublure wide, carrying 10–12 fine, openly spaced terrace lines following the doublural contour; external surface of pygidium covered with Bertillon pattern of delicate lines. Largest observed pygidium 12.5 mm long (sag.).

Etymology.—Dedicated to Dr Florencio G. Aceñolaza (Universidad Nacional de Tucumán).

Types.—Holotype, cranidium, MLP 35091 (Fig. 13.2), length 12.4 mm; paratypes, nine cranidia, one fragmentary librigena, and eleven pygidia (MLP 35035d, 35040, 35059a, 35068a, 35074b, 35075b, 35083a, 35096, 35097, 35104, 35105b, 35117–35119, 35138, 35165–35167, 35169, 35191, 35201).

Occurrence.—Pantipampa section, Iruya area, northwestern Argentina, Santa Rosita Formation, lower Tremadocian, *Kainella teiichii* Zone.

Remarks.—The presence of a posteriorly located brim furrow, which is interrupted by the anterior end of the glabella, is one of the most diagnostic attributes of the new species *Onychopyge acenolazai*. *Onychopyge parkerae* Jell, 1985, from the Tremadocian of Australia (Jell, 1985, pl. 23, figs. 1–16, pl. 24, figs. 1–4), differs from *O. acenolazai* in having a brim furrow that is concurrent with the preglabellar furrow, and a shorter (sag.) pygidial axis, which occupies only a little more than half pygidial length. *Onychopyge depressa* Qian, 1986, from the Cambrian–Ordovician boundary interval of China (Qian, 1986, pl. 80, figs. 1–6, 11, text-fig. 116), also differs by its more anteriorly located brim furrow and, in addition, its better defined lateral glabellar furrows, the smaller palpebral lobes, and its much shorter (sag.) post-axial region.

As with many other species of the genus, *Onychopyge austrina* Peng, 1984, from the lower Tremadocian of China (Peng, 1984, pl. 6, figs. 1–3, pl. 7, figs. 1, 2; Peng, 1990b, pl. 18, figs. 8–10), differs from *O. acenolazai* in lacking an apparent brim furrow. Besides, the former is distinguished by having a very narrow, abruptly upturned anterior cranidial border.

Onychopyge acenolazai is differentiated from the type species, *Onychopyge riojana* Harrington, 1938, from the upper Furongian of La Rioja, Argentina (Harrington, 1938, pl. 5, fig. 30; Harrington and Leanza, 1957, figs. 95, 96.2a–c; Tortello and Esteban, 2007, figs. 7.5–7.14), because the latter shows a less distinct preglabellar furrow, a longer (sag.) pygidial axis which is composed of seven segments instead of five, and noticeable posterior pleural furrows on the pygidium. Additionally, *Onychopyge* sp. aff. *O. riojana*, from the Tremadocian of New Zealand (Wright et al., 1994, fig. 15B–G), exhibits considerably smaller palpebral lobes.

Onychopyge acenolazai and *O. argentina* Harrington and Leanza, 1957, from the upper Furongian of the Cordillera Oriental (Harrington and Leanza, 1957, fig. 96.1a–d), share a pygidium with a tapered axis of five segments, and an acutely rounded posterior margin. However, the cranidium of *O. acenolazai* shows a longer (sag.) frontal area, as well as more posteriorly located palpebral lobes. *Onychopyge acenolazai* differs from *O. harringtoni* Benedetto, 1977, from the upper Furongian of the western Cordillera Oriental (Benedetto, 1977, pl. 2, figs. 14, 15, text-fig. 10), in having a non-tapered glabella, indistinct glabellar lateral furrows S2 and S3, longer (exsag.) palpebral lobes, and five pygidial axial rings instead of six.

The exoskeleton of *Onychopyge sculptura* Robison and Pantoja-Alor, 1968, from the upper Furongian-lower Tremadocian of Mexico (Robison and Pantoja-Alor, 1968, pl. 100, figs. 1–7, 10), exhibits a Bertillon pattern of raised lines which is very similar to that of *O. acenolazai*. Nevertheless, the Argentinian species differs by its non-tapered glabella, its more distinct preglabellar furrow, and its wider (tr.) pygidium. *Onychopyge branisi* Suárez-Soruco, 1975, from the lower Tremadocian of southern Bolivia (Suárez-Soruco, 1975, pl. 1, fig. 7, pl. 2, figs. 7–8), is distinguished by having a deep lateral glabellar furrow S2, proportionately larger palpebral lobes, and six axial rings on the pygidium.

Onychopyge assula Shergold, 1975, from the lower Tremadocian (*Cordylodus proavus* Zone) of Australia (Shergold, 1975, pl. 46, figs. 3–4), was erected on the basis of fragments of one cranidium and one pygidium, which seem to differ from *O. acenolazai* by having a well developed lateral glabellar furrow S2, and a more prominent post-axial ridge.

Onychopyge gonzalezae new species
Figure 13.14–13.20

Diagnosis.—Member of *Onychopyge* with a convex, short (sag.) frontal area; brim furrow concurrent with preglabellar furrow; pygidial axis very long (sag.) and narrow (tr.), composed of seven rings and an elongate terminal piece; posterior pygidial pleural furrows distinct.

Description.—Cranidium moderately convex, subtrapezoidal in dorsal view, broadly rounded anteriorly; glabella large, subrectangular in outline, longer than wide, slightly elevated above genal area, delimited by sinuous axial furrows; it occupies ∽85% of the total length of the cranidium; lateral glabellar furrow S1 represented by a rounded pit-like depression close to the axial furrow; S2 and S3 indistinct; occipital furrow slightly curved backward; occipital ring somewhat wider (tr.) than the rest of the glabella, broadly rounded posteriorly, occupying ∽15% of the total glabellar length (sag.); frontal area short (sag.), convex, of uniform length, delimited posteriorly by a transverse, shallow but distinct brim furrow which is concurrent with the preglabellar furrow; anterior facial suture divergent; palpebral lobes large, semicircular, ∽50% length of glabella (sag.), lacking a well defined palpebral furrow. Largest observed cranidium 11 mm long (sag.).

Librigenae, hypostome and thorax unknown.

Pygidium subparabolic in ouline, wider than long, with rounded corners at intersection of anterior and lateral margins, obtusely pointed posteriorly; axis very long, convex, elevated above pleural fields, slightly tapered backward, anterior width 22% maximum width of pygidium, surrounded by narrow axial furrows; it occupies ∽70% of the total pygidial length and is composed of a short (sag.) articulating half-ring, seven axial rings and a long triangular terminal piece; transaxial furrows deep, transverse; pleural fields flat or weakly convex; anterior pleural furrow clearly marked, wide and sinuous, directed posterolaterally, extended into pair of long marginal spines; posterior three pleural furrows distinctive, straight, directed posterolaterally; a delicate postaxial ridge extends from the axis to the posterior pygidial margin; doublure wide, carrying openly spaced terrace lines following the doublural contour. Largest observed pygidium 11.5 mm long (sag.).

Etymology.—The species is named for Analía González (Director of School 4424, Salta Province), who offered her hospitality during field work.

Types.—Holotype, pygidium, MLP 35147 (Fig. 13.16), length 8.4 mm; paratypes, three cranidia and eight pygidia (MLP 35046, 35049a, 35064, 35065, 35079, 35112, 35124, 35135, 35140a, 35143, 35400).

Occurrence.—Pantipampa section, Iruya area, northwestern Argentina, Santa Rosita Formation, lower Tremadocian, *Kainella teiichii* Zone.

Remarks.—Although the material described above accords with many of the diagnostic features of *Onychopyge* Harrington, 1938 (see diagnosis in Harrington and Leanza, 1957; Robison and Pantoja-Alor, 1968; Jell, 1985), it differs from most species of this genus by its slightly convex frontal area and its long pygidial axis composed of seven rings and a very elongate (sag.) terminal piece. The type species, *O. riojana*, from the upper Furongian of La Rioja, Argentina (Harrington, 1938, pl. 5, fig. 30; Harrington and Leanza, 1957, figs. 95, 96.2a–c; Tortello and Esteban, 2007, figs. 7.5–7.14), shows a proportionately long pygidial axis, distinct posterior pleural furrows, and an obtusely pointed posterior pygidial margin (see especially Tortello and Esteban, 2007, fig. 7.5); however, it differs from *O. gonzalezae* n. sp. in having a concave frontal area lacking an anterior brim furrow. *Onychopyge* sp. aff. *O. riojana*, from the Tremadocian of New Zealand (Wright et al., 1994, fig. 15B–G), is distinguished, in addition, by its much smaller palpebral lobes.

Onychopyge argentina from the upper Furongian of Jujuy (Harrington and Leanza, 1957, fig. 96.1a–d), as well as *O. acenolazai* from the lower Tremadocian of the Pantipampa section (Fig. 13.1–13.13), are distinguished from *O. gonzalezae* mainly by their shorter (sag.) pygidial axes, less distinct posterior pleural furrows, and less angular posterior pygidial margin. In addition, the cranidium of *O. acenolazai* has a laterally expanded frontal glabellar lobe, and a more posteriorly located brim furrow.

Onychopyge harringtoni, from the upper Furongian of the western Cordillera Oriental (Benedetto, 1977, pl. 2, figs. 14, 15, text-fig. 10), differs from *O. gonzalezae* in having a concave frontal area, a tapered glabella, and more developed lateral glabellar furrows. As in *O. gonzalezae*, *O. parkerae*, from the Tremadocian of Australia (Jell, 1985, pl. 23, figs. 1–16, pl. 24, figs. 1–4), exhibits a brim furrow which is concurrent with the preglabellar furrow; however, the Australian species is clearly distinguished by its shorter pygidial axis. Other species of *Onychopyge* having a relatively short pygidial axis and a concave frontal area (*O. sculptura* Robison and Pantoja-Alor, 1968; *O. assula* Shergold, 1975; *O. depressa* Qian, 1986; *O. austrina* Peng, 1984) are also easily differentiated from *O. gonzalezae*.

Ceratopygidae gen. indet. sp. indet.
Figure 13.21–13.27

Description.—Cranidium subtrapezoidal in outline, approximately as long as wide, with pointed anterior margin; glabella elongate, smooth, fairly elevated above genal region, subparallel sided, subtruncate anteriorly, occupying ∽75%–79% of the total cranidial length; median glabellar node delicate, located close to the occipital ring; occipital furrow slightly bowed backward, indistinguishable laterally; anterior cranidial border faintly convex, subequal in length (sag.) to a little shorter or longer than preglabellar field, delimited by a shallow, slightly curved forward border furrow having row of tiny pits; anterior facial suture somewhat divergent; palpebral area of fixigena narrow (tr.); palpebral lobe approximately one-fifth length of cranidium, slightly elevated above fixigena, located at level of glabellar midpoint; posterior fixigena having shallow posterior border furrow and relatively narrow (exsag.) posterior border. Largest observed cranidium 8.2 mm long (sag.).

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Pygidium semiellitical in outline, somewhat convex, width approximately twice length, posterior margin entire; axis elevated above level of pleural fields, surrounded by deep and narrow axial furrows, evenly tapering backward, with slightly marked anterior three rings, rounded at posterior end, extending to posterior border; length of axis ∽78%–80% of that of pygidium on sagittal line; pleural field slightly convex, with faint indications of two pairs of oblique pleural furrows; border furrow weak, differentiated by change in slope of exoskeleton; border wide, fairly concave, becoming a little wider posterolaterally; posteromedian margin having a slender indentation. Largest observed pygidium 7 mm long (sag.).

Materials.—Seven cranidia and eight pygidia (MLP 4961a, 35033b, 35049b, 35127b, 35128, 35148, 35174–35177, 35181, 35192, 35318a, 35319b, 35321a) from the Pantipampa and Rodeo Colorado sections, Iruya area, northwestern Argentina, Santa Rosita Formation, lower Tremadocian (*Kainella teiichii* Zone).

Remarks.—The material examined compares with *Pseudohysterolenus* Harrington and Leanza (1957, p. 191), from the lower Tremadocian of northwestern Argentina, in having a parallel-sided, anteriorly subtruncate glabella, eyes close to glabella, a semielliptical pygidium with a tapered, segmented axis, and a wide pygidial border lacking marginal spines. However, *Pseudohysterolenus* differs mainly by having indications of lateral glabellar furrows, and a less differentiated anterior cranidial border.

Charchaqia Troedsson, 1937 (= *Aplotaspis* Henderson, 1976; Bao and Jago, 2000), from the uppermost Cambrian of North America, China, Australia, and Tasmania (e.g., Troedsson, 1937; Taylor, 1976; Jago, 1991; Bao and Jago, 2000), is similar to the material described above in having an isopygous exoskeleton with low relief, a long and parallel sided glabella without lateral furrows, a tapered pygidial axis, and slight indications of two or three pygidial pleural furrows. Some species show, in addition, a proportionately wide, concave pygidial border. However, *Charchaqia* is differentiated by its anteriorly placed palpebral lobes. The present material represents a new ceratopygid which is provisionally left under open nomenclature.

Superfamily Trinucleoidea Swinnerton, 1915
Family Hapalopleuridae Harrington and Leanza, 1957
Genus *Hapalopleura* Harrington and Leanza, 1957

Type species.—*Hapalopleura clavata* Harrington and Leanza, 1957, from the lower Tremadocian of the Cordillera Oriental, Argentina, by original designation.

Hapalopleura sp. indet.
Figure 13.28

Materials.—Two incomplete cranidia and one fragmentary thorax (MLP 35030a, 35103, 35111) from the Pantipampa section, Iruya area, northwestern Argentina, Santa Rosita Formation, lower Tremadocian, *Kainella teiichii* Zone.

Remarks.—Despite the efforts made to increase the number of specimens of this taxon, only two imperfect cranidia and one fragmentary thorax were collected from the middle part of the Pantipampa section. They are characterized by having a forwardly expanded and truncate glabella; a wide (sag.) preglabellar field; a downsloping anterior border showing three distinct terrace lines subparallel to margin; and long (tr.) and narrow (exsag.) ocular ridges normal to axis. Therefore, these specimens are assigned to *Hapalopleura*; a genus (type species: *H. clavata* Harrington and Leanza, 1957) originally described from the lower Tremadocian of the Cordillera Oriental, in association with *Kainella*, *Leptoplastides*, *Pseudokainella*, and *Apatokephalus*, among others (Harrington and Leanza, 1957). The material examined herein is restricted to two levels of the *Kainella teiichii* Zone (Fig. 2).

Superfamily Cyclopygoidea Raymond, 1925
Family Nileidae Angelin, 1854
Genus *Nileus* Dalman, 1827

Type species.—*Asaphus* (*Nileus*) *armadillo* Dalman, 1827, from the Floian Holen Limestone beds in Östergötland, Sweden, by original designation.

Remarks.—Nielsen (1995) fully revised the diagnosis of the widespread genus *Nileus* Dalman and described several representative Baltoscandian species, which are mostly Middle Ordovician in age. The early Tremadocian taxa described below are two of the oldest species of the genus.

Nileus cingolanii new species
Figure 14.1–14.11, 14.14

Diagnosis.—A *Nileus* species with a glabella clearly constricted (tr.) at level of palpebral areas; palpebral lobes comparatively large, with their posterior corners located far from glabella; palpebral furrows extremely faint; librigenae having acute genal angles; pygidial axis clearly tapered at anterior half and slightly tapered or nearly parallel sided at posterior half, with four rings and a blunt terminal piece; pygidial border undifferentiated; doublure covered with 14–16 terrace lines.

Description.—External surface of exoskeleton without ornamentation; cephalon parabolic in outline, quite convex (sag., tr.), with broadly rounded anterior cranidial margin; cranidium wider than long, with maximum width between the palpebral lobes; glabella very broad, gently arched (sag., tr.), longer than wide, unfurrowed, delimited by faint but perceptible axial furrows, clearly constricted at level of palpebral areas and slightly expanded in front of eyes at a low angle to sagittal line; median glabellar node delicate, situated opposite posterior third of palpebral lobe; occipital brim extremely narrow (sag.), defined by a faint, transverse band furrow; the lateral extremities of the occipital brim show a tiny pit; palpebral lobes conspicuous, pronouncedly arcuate, gently convex, slightly behind of glabellar midpoint, occupying ∽40% of the total length of the cranidium, delimited by extremely faint palpebral furrows, with their posterior corners located far from glabella;

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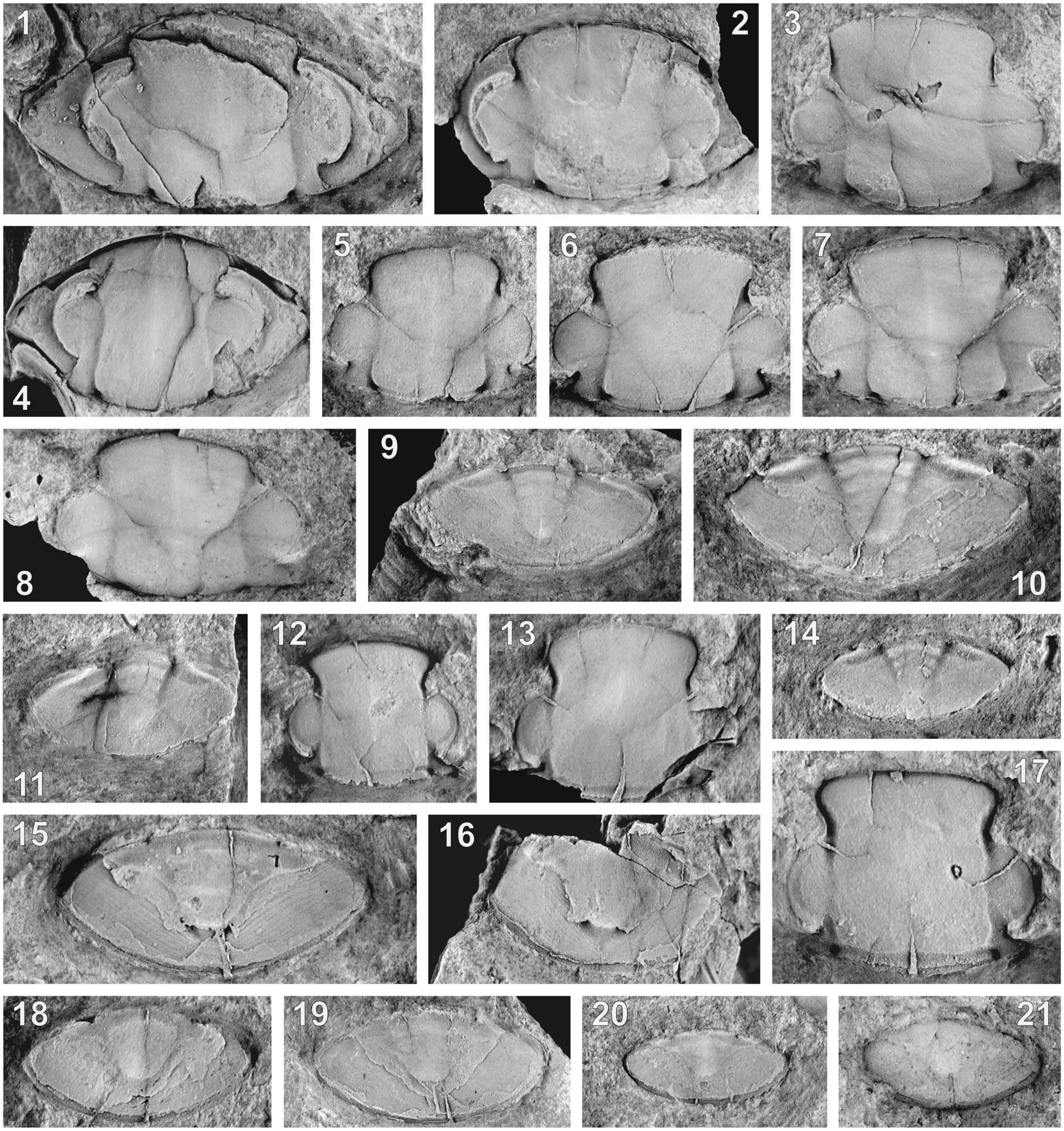

Figure 14. *Nileus* from the Santa Rosita Formation in the Iruya area, northwestern Argentina. **(1–11, 14)** *Nileus cingolanii* n. sp.: **(1)** cephalon, MLP 35050a, ×4; **(2)** cephalon, MLP 35172, ×4.2; **(3)** cranidium, MLP 35171, ×4; **(4)** cephalon, MLP 35173, ×4.2; **(5)** cranidium (holotype) MLP 35036b, ×4.2; **(6)** cranidium, MLP 35101a, ×4.2; **(7)** cranidium, MLP 35100, ×4.2; **(8)** cranidium, latex cast, MLP 35102, ×4.2; **(9)** pygidium, MLP 35074a, ×4.2; **(10)** pygidium, MLP 35052, ×4.2; **(11)** pygidium, MLP 35120a, ×4.2; **(14)** pygidium, MLP 35056b, ×4.2. **(12, 13, 15–21)** *Nileus erici* n. sp.: **(12)** cranidium, MLP 35084a, ×4.2; **(13)** cranidium, MLP 35095, ×4.2; **(15)** pygidium, MLP 35170, ×4.2; **(16)** fragmentary pygidium, MLP 35062c, ×4.2; **(17)** cranidium (holotype) MLP 35033a, ×4.2; **(18)** pygidium, MLP 35084b, ×4.2; **(19)** pygidium, MLP 35145, ×4.2; **(20)** pygidium, MLP 35121, ×4.2; **(21)** pygidium, latex cast, MLP 35120b, ×4.2. All specimens from Pantipampa.

posterior branches of facial suture arched, running obliquely backward-outward from posterior corners of palpebral lobes; posterior fixigena triangular, proportionately large, bent slightly down, representing 18% of the total cranidial length; librigena lacking posterior border; genal angle acute, spineless; cephalic doublure possessing at least 12 terrace lines. Largest observed cranidium 8.4 mm long (sag.).

Hypostome and thorax unknown.

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Pygidium semielliptical in outline, approximately twice as wide as long, somewhat convex, with well-developed articulating half-ring, rounded anterolateral corners and entire posterior margin; axis little elevated above level of pleural fields, clearly tapered at anterior half and slightly tapered or nearly parallel sided at posterior half, ∽28%–30% of total width of pygidium at anterior extremity; it is composed of four rings, of which only the first two pass completely across the axis, and a blunt terminal piece; length of axis ∽70% of that of pygidium on sagittal line; pleural fields smooth, slightly convex; border undifferentiated; doublure very broad, covered with 14–16 terrace ridges following the doublural contour. Largest observed pygidium 5.5 mm long (sag.).

Etymology.—Dedicated to Dr Carlos Cingolani (Museo de La Plata).

Types.—Holotype, cranidium, MLP 35036b (Fig. 14.5), length 5.9 mm; paratypes, three cephala, eleven cranidia, one librigena, eight pygidia (MLP 35034a, 35050a, 35051a,b, 35052, 35056b, 35073b, 35074a, 35077, 35100, 35101a, 35102, 35110, 35120a, 35127a, 35132, 35153a, 35168, 35171–35173).

Occurrence.—Pantipampa section, Iruya area, northwestern Argentina, Santa Rosita Formation, lower Tremadocian, *Kainella teiichii* Zone.

Remarks.—Nielsen (1995) pointed out that the outline of the central part of the glabella of *Nileus* is a useful taxonomic character at specific level. Certainly, the presence of a glabella constricted (tr.) in the middle is one of the most diagnostic features of *N. cingolanii* n. sp. The type species *N. armadillo* (Dalman, 1827) (Nielsen, 1995, figs. 147.A–N, 148.A–O, 149. A–M, 150.A–N; Hansen, 2009, pl. 16, figs. 14–18, pl. 17, figs. 1–11, text-fig. 54) differs from *N. cingolanii* mainly by having almost straight cephalic axial furrows and, in addition, rounded genal angles, a concave pygidial border of variable width, and an increased number of doublural terrace lines.

Nileus australis Tortello and Esteban, 2014, from the upper Tremadocian of the Nazareno area, Cordillera Oriental (Tortello and Esteban, 2014, fig. 8.7, 8.13–8.20), is characterized by having a non-constricted glabella, proportionately small palpebral lobes, and a short pygidial axis, and therefore it is easily distinguished from *N. cingolanii*. Additionally, *Nileus porosus* Fortey, 1975, from the Valhallfonna Formation of Spitsbergen (Fortey, 1975, pl. 12, figs. 1–14), exhibits well developed terrace lines on the dorsal surface of the pygidium.

Nileus limbatus Brøgger, 1882, from the upper Tremadocian (*Megistaspis armata* and lower *Megistaspis planilimbata* zones) of Norway and Sweden (e.g., Ebbestad, 1999, figs. 63. A–O, 64.A–G), differs from *N. cingolanii* mainly by showing a parallel-sided glabella between palpebral lobes, and a slightly shorter (sag.) pygidial axis. *Nileus orbiculatus* Tjernvik, 1956, from the Floian of Sweden (Tjernvik, 1956, pl. 11, figs. 22, 23), is readily distinguished by its medially widened (tr.) glabella.

The absence of a concave, fairly wide pygidial border differentiates *N. cingolanii* from a large group of species of the genus (e.g., *N. exarmatus* Tjernvik, 1956; *N. orbiculatoides* Schrank, 1972; *N. depressus* [Boeck, 1838]).

Nileus erici new species
Figure 14.12, 14.13, 14.15–14.21

Diagnosis.—Member of *Nileus* with a glabella subparallel sided on its posterior two thirds, tapering forward just in front of eyes, and expanding laterally toward the anterior margin; palpebral area of the fixigena relatively narrow (tr.), separated from the glabella by slightly sinuous axial furrow; palpebral furrows faint but distinct; posterior fixigena slender, pointed, and triangular; pygidial axis vaguely perceptible on testaceous material and more evident on internal molds, tapered uniformly, with traces of three rings and a rounded terminal piece; border extremely narrow; doublure covered with 14 terrace lines.

Description.—Cranidium slightly wider than long, with maximum width between the palpebral lobes, rather straight anteriorly; glabella subrectangular, gently convex (sag., tr.), longer than wide, subparallel sided on its posterior two thirds, tapering forward just in front of eyes, and expanding laterally toward the anterior margin; median glabellar node almost imperceptible, situated opposite posterior part of palpebral lobes; occipital brim extremely narrow (sag.), showing a pair of lateral pits and a shallow, transverse band furrow; palpebral area of the fixigena relatively narrow (tr.), occupying ∽34%–38% of the maximum cranidial width, separated from the glabella by delicate, slightly sinuous axial furrows; palpebral lobes arcuate, gently convex, slightly behind of glabellar midpoint, occupying ∽44% of the total length of the cranidium, delimited by faint but distinct palpebral furrows; posterior branches of facial suture short, strongly divergent backward; posterior fixigena minute, pointed triangular, downsloping. Largest observed cranidium 8.5 mm long (sag.).

Librigenae, hypostome and thorax unknown.

Pygidium semielliptical in outline, approximately twice as wide as long, somewhat convex, with short (sag.) articulating half-ring, rounded anterolateral corners and entire posterior margin; test surface smooth; axis vaguely perceptible on testaceous material and more evident on internal molds, tapered uniformly, rounded at posterior end, slightly elevated above level of pleural fields, occupying approximately two-thirds of the total length (sag.) of the pygidium, with traces of three rings and a rounded terminal piece; pleural field smooth, slightly downsloping; border extremely narrow, imperfectly indicated by a change of slope of the exoskeleton; doublure very broad, with its anterior margin curved forward, covered with 14 terrace ridges following the doublural contour. Largest observed pygidium 6.8 mm long (sag.).

Etymology.—The species is named for Eric Gómez Hasselroth, who has assisted in collecting the specimens studied in this paper.

Types.—Holotype, cranidium, MLP 35033a (Fig. 14.17), length 7.8 mm; paratypes, seven cranidia and ten pygidia (MLP 35062c, 35075a, 35084a,b, 35092b, 35095, 35106, 35120b, 35121, 35140b, 35145, 35156b, 35170, 35190, 35194b,c, 35266).

Occurrence.—Pantipampa section, Iruya area, northwestern Argentina, Santa Rosita Formation, lower Tremadocian, *Kainella teiichii* Zone.

Remarks.—*Nileus erici* n. sp. is primarily distinguished from the associated *N. cingolanii* (Fig. 14.1–14.11, 14.14) in the almost straight cephalic axial furrows, narrower (tr.) palpebral area of the fixigena, more distinct palpebral furrows, smaller posterior fixigena, wider (tr.) pygidial axis, and smaller number of pygidial axial rings.

Nileus erici is comparable with *Nileus australis*, from the upper Tremadocian of the Nazareno area, Cordillera Oriental (Tortello and Esteban, 2014, fig. 8.7, 8.13–8.20), in the general outline of the glabella and the configuration of the pygidium, but the species from Nazareno can be differentiated by the smaller (exsag.) palpebral lobes.

Nileus limbatus, from the upper Tremadocian (*Megistaspis armata* and lower *Megistaspis planilimbata* zones) of Norway and Sweden (e.g., Ebbestad, 1999, figs. 63.A–O, 64.A–G), differs from *N. erici* in having a broadly rounded anterior cephalic margin, an almost transverse posterior rachial termination, and an apparent pygidial border. *Nileus porosus*, from the Valhallfonna Formation of Spitsbergen (Fortey, 1975, pl. 12, figs. 1–14), is distinguished mainly by its more anteriorly placed palpebral lobes.

Nileus latifrons Nielsen, 1995, from the Middle Ordovician (upper *Megistaspis limbata* and *Asaphus expansus* zones) of Scandinavia (Nielsen, 1995, figs. 152–160), differs from *N. erici* by having gently arcuate cephalic axial furrows and a variably developed pygidial border. The cranidium of the type species, *Nileus armadillo* (Nielsen, 1995, figs. 147.A–N, 148. A–O, 149.A–M, 150.A–N; Hansen, 2009, pl. 16, figs. 14–18, pl. 17, figs. 1–11, text-fig. 54) is very like that of *N. erici*; however, the pygidium of the former exhibits a well developed border and more numerous terrace ridges. The presence of a concave, fairly wide pygidial border is a distinctive feature of many other species of the genus (e.g., *N. exarmatus*; *N. orbiculatoides*; *N. depressus*).

Acknowledgments

We are grateful to E. Gómez Hasselroth and M. H. Benítez for their help during field work. B. Ventura kindly shared logistic information, and A. González and all the staff of School 4424 (Rodeo Colorado, Provincia de Salta) offered their warm hospitality in the Rodeo Colorado locality. S. Peng provided advice on the genus *Metayuepingia*. F. Filippini, S. Gomba, and N. Valdez assisted in the cataloguing of specimens collected. We are also greatly indebted to L. Amati and an anonymous referee for their helpful comments and suggestions for improving the manuscript, and to S. Marcus, B. Pratt, and S. Westrop for their accurate editorial work. This research was supported by the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET, Project 0166), the Instituto Superior de Correlación Geológica (CONICET – Universidad Nacional de Tucumán, Project CIUNT26G-401_3), and the Universidad Nacional de La Plata, Argentina.

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Accepted 4 May 2016