

EARLY ORDOVICIAN TRILOBITES FROM THE NAZARENO AREA, NORTHWESTERN ARGENTINA

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ABSTRACT—The upper part of the Santa Rosita Formation (Ordovician, Tremadocian) in the Nazareno area, Cordillera Oriental, northwestern Argentina, records the vertical passage of high-energy, shallow water platform environments to offshore settings. Eighteen trilobite species are described from this locality for the first time. Although the taxa from the lower part of the succession (*Leptoplastides* sp., *Asaphellus* sp.) are scarce and non-age diagnostic, those from the upper part include diverse assemblages partially assigned to the late Tremadocian *Notopeltis orthometopa* Zone. Systematic descriptions of several species (*Geragnostus nesossii* Harrington and Leanza, *G. callaveiformis* Harrington and Leanza, *Asaphellus jujuanus* Harrington, *Notopeltis orthometopa* [Harrington], *Mekynophrys nanna* Harrington, *Ceratopyge forficuloides* Harrington and Leanza, *Apatokephalus tibicen* Přibyl and Vaněk) are improved, the genus *Nileus* Dalman (including *N. australis* n. sp.) is first reported from the Tremadocian of western Gondwana, and new species of *Asaphellus* Callaway (*A. nazarenensis* n. sp.), *Conophrys* Callaway, and *Apatokephalus* Brøgger are described. The trilobites have their closest affinities with faunas from Norway and Sweden. *Notopeltis orthometopa* and *Mekynophrys nanna* are restricted to the uppermost part of the succession, well above the first records of most other trilobites recognized.

INTRODUCTION

THE UPPER Tremadocian (Lower Ordovician) of the Cordillera Oriental in northwestern Argentina is represented by the upper part of the Santa Rosita Formation and coeval units, which are characterized by highly fossiliferous shales and sandstones deposited in storm-dominated, open marine environments (Turner, 1960, 1964; Harrington and Leanza, 1957; Moya et al., 2003; Buatois and Mángano, 2003; Astini, 2003, 2008; Buatois et al., 2006; Moya, 2008). The classic localities, such as Santa Victoria, Incamayo, and the areas to the east of Tilcara, to the west of Purmamarca, and around Salta city, discontinuously extend over a strip of nearly 250 km in length, between the border with Bolivia and the vicinity of Salta city (Fig. 1). Trilobites are the dominant element of the fossil assemblages, followed by brachiopods, gastropods, echinoderms, bivalves, cephalopods, graptolites, conodonts, and acritarchs (e.g., Benedetto, 2003 and references).

Harrington and Leanza (1957) presented a comprehensive revision of the Ordovician trilobites of northwestern Argentina and proposed a helpful zonal scheme based on these organisms. However, although subsequent authors provided important supplementary information on the trilobites of the Cordillera Oriental, there are many aspects which still merit further attention. With regard to the upper Tremadocian, Waisfeld and Vaccari (2003, 2008) pointed out the need to improve the taxonomic knowledge of several index species, to establish their exact stratigraphic positions, and to revise the validity of the current "Bienvillia tetragonalis-Shumardia minutula" and Notopeltis orthometopa zones. In that direction, Buatois et al. (2006 and references), Zeballo et al. (2005, 2008), Zeballo and Tortello (2005), and Zeballo and Albanesi (2013) recently provided accurate stratigraphic data from the classic sections of east of Tilcara (Alfarcito) and west of Purmamarca (Coquena/ Chalala), with main focus on conodont faunas and, to a lesser extent, trilobites and graptolites.

The upper part of the Santa Rosita Formation is well exposed in the Nazareno area, about 30 km southwest of Santa Victoria village (Fig. 1). At this locality, a 660-m-thick section consists mainly of sandstones, mudstones, and shales reflecting the vertical passage of lower shoreface environments to offshore settings. Invertebrates are well preserved and very abundant along the succession, but they are still poorly known. Manca et al. (1995) identified acritarchs and conodonts from the late Tremadocian Paltodus deltifer Zone and provided a preliminary list of trilobites, brachiopods, and gastropods, and Benedetto (2007) described a new orthid brachiopod. Recently, Giuliano et al. (2013) illustrated more conodonts of the P. deltifer Zone, and a monotonous graptolite fauna of the Bryograptus kjerulfi Zone. The purpose of this paper is to describe the trilobites from Nazareno for the first time. A few species studied herein are new, whereas many others represent common taxa of the Cordillera Oriental for which more refined data about their systematics and stratigraphic positions were needed.

GEOGRAPHIC AND STRATIGRAPHIC SETTING

The Cordillera Oriental (Central Andean Basin, northwestern Argentina) consists of abruptly rising mountain ranges of northsouth trend separated by deep valleys (Turner and Mon, 1979). This geological province is characterized by large thrust belts of lower Paleozoic rocks (Cambrian quartzites of the Mesón Group; late Furongian–Early Ordovician sandstones and shales of the Santa Victoria Group—Santa Rosita and Acoite formations and equivalents) juxtaposed on a Neoproterozoic– early Cambrian basement of slates and meta-graywackes of the Puncoviscana Formation (Harrington and Leanza, 1957; Turner, 1960; Moya, 1999; Sánchez, 1999; Astini, 2003).

The Santa Rosita Formation consists of a complex mosaic of late Furongian—late late Tremadocian rocks that represent a wide variety of sedimentary environments (Turner, 1960; Moya, 1988; Moya et al., 2003; Buatois and Mángano, 2003; Astini, 2003). The unit is divided into different members that include



FIGURE 1—Map of the Nazareno area, showing the location of the field locality (star) just southeast of Nazareno village (redrawn from Manca et al., 1995).

fluvio-estuarine sediments and open-marine shoreface, offshore transition, offshore, and shelf deposits which accumulated on a gently dipping shelf (Buatois and Mángano, 2003 and references). Exposures show the greatest thickness in the Santa Victoria region, where they are about 2300 m thick (Fig. 1). In addition, other formation names have been proposed in some localities of the Cordillera Oriental (e.g., Río Iturbe; west of Purmamarca) for equivalent units (Harrington *in* Harrington and Leanza, 1957).

The trilobite faunas described herein come from the Santa Rosita Formation exposed at the Nazareno locality (eastern flank of the Santa Victoria Range, Salta Province), about 30 km southwest of Santa Victoria village and \sim 3200 m above sea level (Fig. 1). Vilela (1960), Manca et al. (1995), and Salfity et al. (1998) provided a geological sketch of the area surrounding Nazareno. There, the Tremadocian shales and sandstones of the Santa Rosita Formation unconformably overlie the Cambrian tide-dominated quartzites of the Mesón Group (Turner, 1960),

and are unconformably overlain by the Late Cretaceous– Paleogene non-marine rocks of the Salta Group (Turner, 1959) and Quaternary alluvial deposits. Manca et al. (1995) and Giuliano et al. (2013) recovered conodonts from this succession that belong to the *Paltodus deltifer* Zone (early late Tremadocian). In addition, Benedetto (2007) described the new orthid brachiopod *Euorthisina? nazarenensis*, and Giuliano et al. (2013) reported the graptolite *Bryograptus* cf. *B. kjerulfi* Lapworth, 1880.

The 660 m-thick section studied herein, measured from a minor fault developed along the Nazareno River, corresponds only to the upper part of the Santa Rosita Formation. The lower half of the succession is composed of sandstone whereas the upper half is dominated by mudstone (Fig. 2). The former displays gray, fine- to very fine-grained quartzose sandstones in erosive-based beds, 5 to 60 cm thick that are interbedded with gray and green, massive and thinly laminated mudstones (facies C and D). Internally, the sandstone beds exhibit planar-



FIGURE 2—Columnar section of the Santa Rosita Formation at Nazareno, northwestern Argentina, displaying facies succession and distributions of trilobites identified. Facies: A, black shale; B, green to greenish gray mudstone; C, mudstone and combined-flow rippled sandstone; D, interbedded hummocky cross-stratified sandstone; E, amalgamated hummocky cross-stratified sandstone.

lamination, combined-flow ripple cross-lamination (facies C), and hummocky cross-stratification (facies D). The bases of the sandstone layers commonly show scours, whereas the tops have symmetric to nearly symmetric ripples and occasional indications of bioturbation. Lenticular bioclastic concentrations up to 9 cm thick are preserved locally. Intercalated mudstone beds range from a few centimeters to 4 m thick, though they are absent in the upper part of this interval, where amalgamated sandstone beds occur. Laminated mudstones bear a low diversity trilobite assemblage composed of *Leptoplastides* sp. and *Asaphellus* sp.

The presence of hummocky cross-stratification indicates a storm origin for the sandstone beds. The record of amalgamated hummocky cross-stratified deposits (facies E), bioclastic concentrations, and low percentages of mudstones suggests a high-energy, shallow water platform setting (offshore transition to lower shoreface).

On the other hand, the upper half of the succession consists mainly of black, thinly laminated shales (facies A) and yellowish-green and greenish-gray, massive and laminated mudstones, with intercalations of light gray, parallel laminated, and massive silty sandstone beds 1 to 3 cm thick (facies B). The latter may display small load casts and tool marks on the base, and symmetric to nearly symmetric ripples on the top. The shale and mudstone intervals contain diverse trilobites in association with inarticulate and articulate brachiopods, echinoderms, gastropods, cephalopods, and bivalves. In addition, disarticulated exoskeletons and fossil concentrations were recorded from sandstone beds in the middle part of the sequence.

The accumulation of thick packages of shales and mudstones of the upper interval is mainly attributed to low-energy, suspension fallout deposition in an offshore to shelf environment, occasionally punctuated by deposition of silty sandstone beds. The latter display structures produced by rapid, episodic sedimentation, and wave activity, representing storm deposition immediately above the storm wave base.

IMPLICATIONS OF THE FAUNAS

The fauna of the lower part of the section is limited to indeterminate species of Leptoplastides Raw, 1908 and Asaphellus Callaway, 1877 that provide little biostratigraphic information. In contrast, the trilobites from the upper mudstones are much more diverse and include metagnostids, shumardiids, olenids, ceratopygids, nileids, kainellids, orometopids, pliomerids, and several asaphids (Fig. 2). A number of them (Geragnostus nesossii Harrington and Leanza, 1957, G. callaveiformis Harrington and Leanza, 1957, Asaphellus jujuanus Harrington, 1937, Notopeltis orthometopa [Harrington, 1938], Mekynophrys nanna Harrington, 1938, Ceratopyge forficuloides Harrington and Leanza, 1957) represent typical late Tremadocian species of the Cordillera Oriental whose systematic descriptions needed to be improved or clarified (Harrington and Leanza, 1957, p. 151; Wright et al., 1994, p. 463; Waisfeld and Vaccari, 2003). In addition, the genus Nileus Dalman, 1827 (with N. australis n. sp.) is reported from the Tremadocian of western Gondwana for the first time, and new forms of Asaphellus, Conophrys Callaway, 1877, and Apatokephalus Brøgger, 1896 are described below.

Harrington and Leanza (1957, p. 27) pointed out that several late Tremadocian trilobites from northwestern Argentina have their closest affinities with species from Britain and Scandinavia. In the Nazareno section these include *Geragnostus callaveiformis*, which mostly resembles *G. crassus* Tjernvik, 1956, from the *Apatokephalus serratus* Zone of Sweden and Norway (Tjernvik, 1956; Ahlberg, 1992; Ebbestad, 1999); *Conophrys* cf. *C. pusilla*, which has direct morphological affinities with *C. pusilla* (Sars, 1835), from the *C. pusilla* and *Apatokephalus serratus* zones of Norway; and *Parabolinella triarthroides* Harrington, 1938, which shows a striking similarity with *Parabolinella lata* Henningsmoen, 1957, from the upper Tremadocian of Norway (Henningsmoen, 1957; Rushton, 1988; Ebbestad, 1999).

The uppermost part of the section studied yields two asaphids, Notopeltis orthometopa and Mekynophrys nanna, which indicate assignment to the late Tremadocian Notopeltis orthometopa Zone (Harrington and Leanza, 1957, p. 28). Harrington and Leanza (1957) originally reported the Notopeltis orthometopa Zone from several localities of the Cordillera Oriental, though in most cases data about the exact stratigraphic ranges of its species were not provided. An exception is the Santa Victoria River section (Harrington and Leanza, 1957, fig. 2), where there are well-documented records of N. orthometopa in association with M. nanna, Pyrimetopus pyrifrons (Harrington, 1938), Apatokephalus tibicen Přibyl and Vaněk, 1980, Parabolinella triarthroides, Bienvillia rectifrons (Harrington, 1938), Rossaspis rossi (Harrington and Leanza, 1957), and Ceratopyge forficuloides. Similar assemblages are recognized in the upper 100 m of the Nazareno section; however, it is important to note that most of the trilobites described from Nazareno first occur ~ 250 m below N. orhometopa.

A situation comparable to that of Nazareno is known from the upper member of the Coquena Formation in the Coquena-Chalala creeks, western Purmamarca (Harrington and Leanza, 1957; Moya, 1999; Benedetto and Carrasco, 2002; Zeballo and Albanesi, 2013). There, Harrington and Leanza (1957) described the trilobites Geragnostus callaveiformis, Asaphellus jujuanus, Notopeltis orthometopa, Mekynophrys nanna, Pyrimetopus pyrifrons, Apatokephalus tibicen, Parabolinella triarthroides, and Bienvillia rectifrons (among others), from an interval assignable to the conodont Paltodus deltifer deltifer Zone (Zeballo and Albanesi, 2013). Recent resampling has shown that *N. orthometopa* occurs only at the top of the Coquena Formation (Notopeltis orthometopa Zone), well above the first records of Parabolinella triarthroides and Pyrimetopus pyrifrons (Zeballo et al., 2008; Zeballo and Albanesi, 2013). We follow Zeballo and Albanesi (2013) in provisionally regarding strata with trilobites below the FAD of Notopeltis orthometopa as an unnamed zone (Fig. 2).

Another interval assignable with confidence to the *Notopeltis* orthometopa Zone is at Huacalera (Humacha section, Jujuy Province). There, *Notopeltis orthometopa* and *Mekynophrys* nanna co-occur in upper beds of the Santa Rosita Formation, from levels assigned to the *Paltodus deltifer deltifer* Zone (Zeballo et al., 2008; Zeballo and Albanesi, 2013). These beds also correlate with the uppermost Santa Rosita Formation at Nazareno.

MATERIAL AND REPOSITORY

The results presented here are based on the study of nearly seven hundred trilobites collected in the field. Most of the specimens are preserved as delicate exoskeletons or molds, which were whitened with magnesium oxide vapors before photographing. The material is housed in the Museo de Ciencias Naturales de La Plata (La Plata, Argentina) with the prefix MLP. Slabs containing more than one specimen are labeled with both a collection number and additional letters.

SYSTEMATIC PALEONTOLOGY

The morphological terms used in this paper have been mostly defined by Moore (1959), 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 Metagnostidae Jaekel, 1909 Genus Geragnostus Howell, 1935

Type species.—Agnostus sidenbladhi Linnarsson, 1869, from the upper Tremadocian (*Conophrys pusilla* and *Apatokephalus serratus* zones) of south-central and southern Sweden, and southern Norway (by original designation) (Tjernvik, 1956; Ahlberg, 1989a, 1992; Ebbestad, 1999).

Remarks.—*Geragnostus* Howell is a geographically widespread Ordovician genus which has been extensively discussed during the last three decades (e.g., Fortey, 1980; Zhou, 1987; Ahlberg, 1989a, 1992; Peng, 1990a, 1990b; Nielsen, 1997; Tortello et al., 2006). The type species was redescribed and discussed in detail by Ahlberg (1989a). The generic concept adopted here is that of Fortey (1980) and Ahlberg (1989a, 1989b, 1990, 1992), so that the partially effaced genera *Geragnostella* Kobayashi, 1939, *Neptunagnostella* Pek, 1977, and *Geratrinodus* Kobayashi and Hamada, 1978, are regarded as subjective junior synonyms of *Geragnostus*.

As stated by Fortey (1980), the parietal glabellar surface of *Geragnostus* is characterized by a median node lying immediately behind the median part of the transglabellar furrow. The outer ends of F3 are forward- and outward-curving furrows, which represent the anterior margin of the 6P glabellar muscle scar. This cephalic pattern is also present in the Ordovician genus *Trinodus* M'Coy, 1846, although the latter mostly differs from *Geragnostus* by having a shorter pygidial axis in which the length of M3 is much less than the combined lengths of M1 + M2 (Ahlberg, 1989a, 1992 and references; Owen and Parkes, 2000).

GERAGNOSTUS CALLAVEIFORMIS Harrington and Leanza, 1957 Figure 3.1–3.3

1937 Agnostus sp. indet. HARRINGTON, p. 110, pl. 5, fig. 7.

1938 Geragnostus sp. a indet. HARRINGTON, p. 161, pl. 4, fig. 4.

- 1957 Geragnostus (Micragnostus) callaveiformis HARRING-TON AND LEANZA, p. 71, figs. 13.1–13.5, 14.
- 1996a Geragnostus callaveiformis; TORTELLO, p. 206, pl. 1, figs. 6–8.
- 2003 Geragnostus (Geragnostus) callaveiformis; WAISFELD AND VACCARI, p. 316, pl. 19, figs. 12, 13.

Diagnosis.—Geragnostus with a proportionately short glabella; lateral portions of F3 curved only slightly forward abaxially; pygidial axis carrying a conspicuous axial tubercle; posteroaxis large, semiovate; border furrows relatively wide (sag.); pygidial border with minute posterolateral spines (emended from Harrington and Leanza, 1957).

Material.—Fourteen (14) cephala and 10 pygidia (MLP 34198–34204, 34205a) from the Nazareno area, Cordillera Oriental, northwestern Argentina. Upper part of the Santa Rosita Formation (upper Tremadocian).

Remarks.—Harrington and Leanza (1957) provided a complete description of *G. callaveiformis* on the basis of material from the upper Tremadocian of west of Purmamarca and Río Iturbe. In addition, Tortello (1996a) reported this species from the Santa Victoria area, near the Bolivian border.

The overall morphology of *Geragnostus callaveiformis* mostly resembles that of *G. crassus* Tjernvik, 1956, from the upper Tremadocian (*Apatokephalus serratus* Zone) of Sweden and Norway (Tjernvik, 1956, pl. 1, fig. 8; Ahlberg, 1992, fig. 7a–7r;

Ebbestad, 1999, fig. 17). However, the Argentinian species differs by having a longer (sag.) posteroaxis. *Geragnostus callaveiformis* also resembles *G. callavei* (Raw *in* Lake, 1906), from the upper Tremadocian of the Lake District, Shropshire and North Wales, United Kingdom (Lake, 1906, pl. 2, fig. 20; Rushton, 1988, pl. 66, figs. 1, 2, 4, 5, 11; Fortey and Owens, 1991, fig. 3k), although the former is distinguished by its shorter (sag.) and tapered glabella, and its slightly shorter (sag.) posteroaxis (cf. Harrington and Leanza, 1957).

Furthermore, *G. callaveiformis* is comparable with *G.* cf. *G. yangtzeensis* Lu, 1975, from the Tremadocian of northwestern Hunan, China (Peng, 1990a, pl. 1, figs. 1-8), but the cephalic acrolobe of the latter is constricted and its border furrow is much wider (sag.; exsag.).

Geragnostus Nesossii Harrington and Leanza, 1957 Figure 3.10, 3.11

1957 Geragnostus (Geragnostus) nesossii Harrington and Leanza, p. 65, figs. 9.1–9.5, 10.

- 1996a Geragnostus nesossii; TORTELLO, p. 206, pl. 1, fig. 9.
- 1996b Geragnostus nesossii; TORTELLO, p. 21, fig. 4.1-4.12.
- 2003 Geragnostus (Geragnostus) nesossii; WAISFELD AND VACCARI, p. 316, pl. 19, fig. 15.

Diagnosis.—A species of *Geragnostus* with a semiovate cephalon, longer than wide; glabella long, gently tapered forward; F3 laterally effaced; cephalic border furrow very wide and shallow, widest anterolaterally (emended from Harrington and Leanza, 1957, and Tortello, 1996b).

Material.—One cephalon and three pygidia (MLP 34184–34186, 34205b) from the Nazareno area, Cordillera Oriental, northwestern Argentina. Upper part of the Santa Rosita Formation (upper Tremadocian).

Remarks.—Although Harrington and Leanza (1957) originally assigned the *Geragnostus nesossii* type locality (Quebrada de Pingüiyal, south of Salta city) to the latest Cambrian *Parabolina frequens argentina* Zone, subsequent studies demonstrated that it is late Tremadocian in age (González, 1983; Tortello, 1996b; Waisfeld and Vaccari, 2003). *Geragnostus nesossii* has proved to be a recurrent element in late Tremadocian fossil assemblages of the Cordillera Oriental (Santa Victoria area; Quebrada de Coquena and Quebrada de Chalala, west of Purmamarca; Tortello, 1996b), although it is generally represented by very small numbers of specimens. Such is the case in the Nazareno area, where to date only one cephalon and three fragmentary pygidia have been found.

The pygidium of *G. nesossii* is difficult to distinguish from that of the type species *G. sidenbladhi* Linnarsson, 1869, from the upper Tremadocian of Sweden and Norway (Tjernvik, 1956, textfig. 27A, pl. 1, figs. 5, 6; Ahlberg, 1989a, figs. 1A–1K, 2A–2C, 3A–3G; Ahlberg, 1992, fig. 6a–6f; Ebbestad, 1999, fig. 16A– 16L), because both share a subquadrate outline, a shallow border furrow, weakly convex pleural fields, and a proportionately short (sag.) axis with a weakly constricted M2 and a posteriorly rounded to slightly truncate M3. In contrast, the cephalon of *G. nesossii* is diagnostic. It differs from that of *G. sidenbladhi* and other species of the genus mainly in possessing a semiovate shape, a very wide (sag; exsag.) border furrow, and a long and conical glabella.

Genus GALBAGNOSTUS Whittington, 1965

Type species.—Agnostus galba Billings, 1865, from the middle Table Head Formation (Middle Ordovician) of Newfoundland, Canada (by original designation).

Remarks.—The parietal glabellar surface of *Galbagnostus* shows a particular arrangement of six muscle impressions (1P–



FIGURE 3—Agnostoids, shumardiids, and olenids from the Santa Rosita Formation at Nazareno, northwestern Argentina. *1–3, Geragnostus callaveiformis* Harrington and Leanza, 1957: *1*, cephalon, MLP 34204, ×5.7; *2*, pygidium, MLP 34201, ×5.1; *3*, pygidium, MLP 34203, ×4.7; *4*, *5*, *Galbagnostus* sp.: *4*, cephalon, MLP 34189, ×5; *5*, pygidium, MLP 34187, ×5.3; *6–9, Conophrys* cf. *C. pusilla* (Sars, 1835): *6*, cranidium, MLP 34193, ×8.3; *7*, cranidium, latex mold, MLP 34194, ×6.9; *8*, cranidium, MLP 34191, ×6.6; *9*, pygidium, latex mold, MLP 34197, ×8.1; *10*, *11*, *Geragnostus nesossii* Harrington and Leanza, 1957: *10*, cephalon, MLP 34184, ×4; *11*, pygidium, MLP 34185, ×4; *12–15, Leptoplastides* sp.: *12*, cranidium, MLP 34076, ×3.7; *13*, cranidium, latex mold, MLP 34071, ×4.1; *14*, small cranidium, MLP 34073, ×3.8; *15*, meraspid cranidium, MLP 34075, ×5.2; *16–23*, *25*, *Bienvillia rectifrons* (Harrington, 1938): *16*, cranidium, MLP 34291, ×2; *17*, cranidium, MLP 34283, ×2.8; *18*, cranidium, MLP 34293, ×2.9; *23*, cranidium and fragmentary thorax, MLP 34373, ×2.4; *25*, pygidium, MLP 34292, ×3.9; *24*, *26–33*, *Parabolinella triarthroides* Harrington, 1938: *24*, cranidium and fragmentary thorax, MLP 34373, ×2.4; *25*, pygidium, MLP 34308, ×2.9; *27*, cranidium, MLP 34301, ×2.3; *28*, cranidium, MLP 34304, ×3.3; *29*, cranidium, MLP 34300, ×3.5; *30*, cranidium, MLP 34309, ×3.1; *31*, cranidium, MLP 34374, ×4.4; *32*, cranidium, MLP 34375, ×2.9; *33*, cephalon and fragmentary thorax, MLP 34376, ×2.6.

6P) that is homologous with the configuration of *Geragnostus/ Trinodus* (Fortey, 1980, fig. 4). However, in *Galbagnostus* the anteroglabella is appreciably reduced and therefore the 6P muscle scar extends almost to the anterior end of the glabella, and the axial glabellar node is located in an exceptionally advanced position (Fortey, 1980). Shergold et al. (1990) and Nielsen (1997) regarded the presence of a short glabella, a very forwardly situated axial glabellar node, a short and tapered pygidial axis, a conspicuous pygidial tubercle, and a transverse, trapeziform posteroaxis with an indistinct median ridge, as the most diagnostic features of *Galbagnostus*; concepts that are followed here.

GALBAGNOSTUS sp. Figure 3.4, 3.5

Description.—Cephalon moderately convex, subcircular in outline, wider than long. Glabella short and proportionately narrow, scarcely rising above level of genae, gently tapered forward, faintly constricted at midlength, rounded anteriorly, well defined by narrow axial furrows, occupying 50 percent of the total cephalic length (sag.) and about one third of the maximum cephalic width (tr.); axial node very weak, situated close to the anterior end of the glabella; F3 indistinct; glabellar culmination broadly rounded. Basal lobes entire, subtriangular, much wider than long. Acrolobe unconstricted and genae smooth, confluent, of uniform width, rounded anteriorly. Border furrow shallow and narrow, uniform in width anteriorly and anterolaterally; cephalic border gently convex, relatively narrow; sagittally, border + border furrow occupies about 12 percent of the cephalic length. Posterior border convex (exsag.), without spines.

Pygidium convex, subcircular in outline, wider than long. Axis convex, trilobed, tapered backward, subrounded posteriorly, defined by narrow axial furrows; it is subequal in length and width, and occupies about 62 percent of the total pygidial length. M1 as long as M2 (exsag.), divided into two trapezoidal lateral lobes and a central ridge; M2 carrying a conspicuous central tubercule that encroaches over M3 and constitutes the highest point of the pygidium; F1 and F2 shallow but distinct; M3 transverse, trapeziform, shorter (sag.) than M1 + M2, with faint indications of an axial ridge and an almost imperceptible deepening of axial furrow behind this ridge. Pleural fields convex, smooth, confluent, of uniform width. Border and border furrow imperfectly preserved. Articulating half-ring narrow (sag.) and convex, separated from the axis by a transverse, deep ring furrow.

Material.—Two cephala and one pygidium (MLP 34187–34189) from the Nazareno area, Cordillera Oriental, northwestern Argentina. Upper part of the Santa Rosita Formation (upper Tremadocian).

Remarks.—The material studied includes only two cephala and one pygidium characterized by having a short (sag.) glabella, an effaced glabellar F3, a very advanced glabellar node, and a proportionately small, trapezoidal posteroaxis with weak indications of an axial ridge; therefore, they are confidently assigned to *Galbagnostus* sp.

Galbagnostus sp. shows strong similarities with *Galbagnostus* saltaensis (Harrington and Leanza, 1957), from the upper Tremadocian of the Cordillera Oriental (Harrington and Leanza, 1957, fig. 17.2a–17.2e; Fortey, 1980, p. 25; Tortello, 1996a, pl. 1, figs. 1–4; Waisfeld and Vaccari, 2003, pl. 19, figs. 10, 11, 14), but the former seems to have a larger pygidial axis with a posteriorly rounded M3. It differs from the type species *Galbagnostus galba* (Billings, 1865), from the middle Table Head Formation of western Newfoundland, Canada (Whittington, 1965, pl. 2, fig. 24, pl. 3, figs. 1–15, pl. 4, figs. 1–10, text-fig. 2; Shergold et al., 1990, fig. 18.1a, 18.1b), mainly in showing a shorter, narrower glabella and a rounded glabellar culmination.

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 (by subsequent monotypy).

Remarks.—Fortey and Owens (1987) proposed a diagnosis for *Conophrys*, which was partially modified by Peng (1990a). Fortey and Owens (1991) fully revised the morphology and ontogeny of the type species *C. salopiensis* Callaway, 1877, and provided valuable criteria for distinguishing it from *C. pusilla* (Sars, 1835) from the upper Tremadocian of Norway (Fortey and Rushton, 1980; Ebbestad, 1999).

Although most of the above-mentioned authors regarded *Conophrys* as a subgenus of *Shumardia* Billings, 1862, we follow Waisfeld et al. (2001) and recognize it at generic level.

CONOPHRYS cf. C. PUSILLA (Sars, 1835) Figure 3.6–3.9

Description.-Cranidium semicircular in outline, gently convex (tr., sag.), nearly twice as wide (tr.) as long (sag.), lacking surface sculpture. Glabella little elevated above genal region, long, occupying 90-95 percent of the total cephalic length, with well defined, teardrop-shaped anterolateral lobes; preglabellar furrow ogival or obtusely pointed, shallower and narrower than axial furrows, which are wide (tr.) and deep; anterior lateral glabellar furrow faint and long, running forward and inward from axial furrows, not reaching preglabellar furrow; anterolateral lobes protruding outward beyond level of lateral margins of occipital ring, with their posterior edges just behind midlength of the cranidium; lateral glabellar furrows S1 and S2 indistinct; occipital furrow faint, transverse and straight; occipital ring somewhat wider (tr.) than the rest of the glabella, broadly rounded posteriorly, with indications of a median node at posterior extremity. Fixed cheek wide (tr.), convex, semicircular in outline, merging with a transverse anterior cephalic margin; preglabellar field narrow (sag.). Posterior border, posterior border furrow and genal angles too poorly preserved for description.

Pygidium subtrapezoidal, about twice as wide (tr.) as long (sag.), with a slightly forward curvature at posterior margin sagittally. Axis transversely convex, somewhat tapered, rounded posteriorly, well defined by discrete axial furrows, with four axial rings and a very tiny terminal piece, occupying about 75 percent of the total pygidial length (excluding articulating half ring) and one third of the maximum pygidial width. Articulating half ring crescentic, defined by a shallow, transverse articulating furrow. Pleural fields gently convex, divided into four pleurae by faint, uniformly curved outward and backward interpleural furrows. Border and border furrow indistinct. Pygidial sculpture of one row of coarse granules on each axial ring and pleural rib, as well as on the pygidial margin.

Material.—Eight cranidia and one pygidium (MLP 34190–34197) from the Nazareno area, Cordillera Oriental, northwestern Argentina. Upper part of the Santa Rosita Formation (upper Tremadocian).

Remarks.—Until complete cephala and additional pygidia are recovered, the specimens studied herein are left under open nomenclature. *Conophrys* cf. *C. pusilla* has direct morphological affinities with *C. pusilla* (Sars, 1835), from the upper Tremadocian (*C. pusilla* and *Apatokephalus serratus* zones) of Norway (e.g., Bulman and Rushton, 1973, pl. 6, figs. 1–4; Fortey and Owens, 1991, fig. 8s–8w; Ebbestad, 1999, figs. 24A–24J, 25A), mainly in sharing a well-defined front of the glabella, teardropshaped anterolateral glabellar lobes, a pygidial axis with four axial rings, and a similar pattern of tubercles on the pygidium. The holotype cranidium of *C. pusilla* (Fortey and Owens, 1991, fig. 8u; Ebbestad, 1999, fig. 24A) shows a longer (sag.) preglabellar field and relatively wider (tr.) lateral glabellar lobes, though Ebbestad (1999) demonstrated that these characters are rather variable in this species. The pygidium of *Conophrys pusilla* more clearly differs from the material from Nazareno in having a proportionately wider (tr.), transversely elongate outline, and pleural furrows and ribs that are flexed backward distally.

Conophrys cf. *C. pusilla* is distinguished from the type species *C. salopiensis* (Callaway), from the upper Tremadocian (*C. salopiensis* Biozone) of England, Wales and eastern Canada (e.g., Fortey and Owens, 1991, figs. 8m–8r, 13a–13j), because the former bears proportionately larger anterolateral glabellar lobes, and a perceptible preglabellar furrow.

Waisfeld and Vaccari (2003) revised in detail *Conophrys minutula* (Harrington, 1938), from the upper Tremadocian of northwestern Argentina, and regarded its long glabella, the welldeveloped anterolateral lobes, its narrow and distinct preglabellar furrow, and the pattern of granules on the pygidium as its most diagnostic features. Although *C. minutula* was originally considered widespread in the Cordillera Oriental, Waisfeld and Vaccari (2003) showed that reliably identified material of this species occurs only in its type locality (Quebrada de Coquena, west of Purmamarca) (Harrington, 1938, pl. 9, figs. 6, 8, 15, ?16; Harrington and Leanza, 1957, p. 79, 80, fig. 24.1c, 24.1d (only); Waisfeld and Vaccari, 2003, p. 327, pl. 29, figs. 14–16). *Conophrys* cf. *C. pusilla* is differentiated from *C. minutula* mainly by having a shorter (sag.) glabella, and narrower (tr.) anterolateral glabellar lobes.

Conophrys cf. *C. pusilla* further differs from *C. gaoluoensis* (Zhou), from the Tremadocian of northwestern Hunan, China (Peng, 1990a, pl. 2, figs. 1–15, text-fig. 6), because the latter possesses a distinctive pitted cranidium, an evenly rounded anterior margin, a longer (sag.) preglabellar field, a deeper occipital furrow, and a more developed pygidial axis.

A large group of species of *Conophrys* (e.g., *C. sulcata* Malanca, 1996; *C. alata* [Robison and Pantoja-Alor, 1968]; *C. changshanensis* [Lu *in* Lu et al., 1976]; *C. acutifrons* [Liu *in* Zhou et al., 1977]; *C. rushtoni* Waisfeld et al., 2003; *C. fabiani* Waisfeld et al., 2003; *C. wrighty* Waisfeld et al., 2001) is characterized by having very small anterolateral glabellar lobes, and therefore it is easily distinguished from *C. cf. C. pusilla*.

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 Shineton Shale Formation (upper Tremadocian) in South Shropshire, England (by original designation) (Fortey and Owens, 1991).

LEPTOPLASTIDES sp. Figure 3.12–3.15

Description.—Cranidium subtrapezoidal, slightly convex, with straight to backwardly curved anterior margin and downsloping fixed cheeks. Glabella large, moderately elevated above genal region, slightly longer (sag.) than wide (tr.), somewhat tapered and broadly rounded anteriorly, surrounded by well-defined axial furrows; occupies about 85–88 percent of the total cranidial length and a half of maximum width of the cranidium; S1 and S2 oblique backward, almost imperceptible on large holaspides; occipital ring with rounded posterior margin and a weak median node; occipital furrow very shallow, straight medially and somewhat oblique forward laterally. Preglabellar field short (sag.); anterior border much shorter (sag.) than preglabellar field, little upturned, widest (sag.) medially, delimited by a shallow, straight to slightly curved backward border furrow; anterior facial suture somewhat convergent; palpebral area of the fixigena narrow (tr.), 0.3 width of adjacent glabella; palpebral lobe about one-fifth length of cranidium, little elevated above fixigena, forward of cranidial midpoint, surrounded by a very faint palpebral furrow; eye ridge indistinct on large holaspides; posterior facial suture strongly divergent, sinuous; posterior fixigena relatively wide (tr.), with a shallow border furrow and a narrow (exsag.) posterior border.

A meraspid cranidium (Fig. 3.15) has proportionately large palpebral lobes, a perceptible eye ridge, faint but distinct lateral glabellar furrows, a backwardly curved occipital furrow, and a delicate occipital spine.

Material.—Thirteen (13) cranidia and two incomplete librigenae (MLP 34066–34077) from the Nazareno area, Cordillera Oriental, northwestern Argentina. Santa Rosita Formation (Tremadocian).

Remarks.—Assemblages dominated by Leptoplastides are very common in different Tremadocian depositional environments of the Cordillera Oriental (e.g., Balseiro and Marengo, 2008; Tortello et al., 2013). In the Nazareno area, this genus is restricted to the lower beds of the succession, which are interpreted as high-energy shallow marine deposits. Leptoplastides sp. differs from L. marianus (Hoek in Steinmann and Hoek, 1912), from the lower Tremadocian of northwestern Argentina (e.g., Harrington and Leanza, 1957, fig. 30.1, 30.7-30.9; Tortello and Aceñolaza, 2010, figs. 2a-2n, 3a-3e, and references), mainly in having a shorter (sag.) frontal area, a non-pitted anterior border furrow, and an anteriorly rounded glabella. Also, it is distinguished from Leptoplastides granulosa (Harrington, 1938), from the upper Tremadocian of Alfarcito, east of Tilcara, Cordillera Oriental (Harrington, 1938, pl. 8, figs. 13, 18, 21; Harrington and Leanza, 1957, figs. 29, 30.2, 30.4, 30.6, 30.10; Waisfeld and Vaccari, 2003, pl. 10, figs. 8-10; Zeballo and Tortello, 2005, fig. 4M, 4P-4R), by showing larger palpebral lobes, a fairly tapered glabella, and wider (tr.) fixed-cheeks.

Leptoplastides sp. bears a strong resemblance with *Leptoplastides* sp. nov. A, from the uppermost Tremadocian of Great Britain (Fortey and Owens, 1992, fig. 3k, 3l, 3n–3p), by having a very short anterior cranidial border; however, the latter is distinguishable by its narrower (tr.) palpebral area of the fixigena.

> 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.—Ludvigsen and Tuffnell (1983) provided a comprehensive systematic revision of the closely allied olenid genera *Triarthrus* Green, 1832, *Bienvillia* Clark, 1924, and *Porterfieldia* Cooper, 1953, pointing out that the arrangement of transverse cephalic furrows in front of the glabella is of great taxonomic importance. *Triarthrus* lacks an anterior border furrow on the cranidium, whereas *Bienvillia* is characterized by having a welldefined anterior cranidial furrow, which is separated from the preglabellar furrow by a discernible, inflated preglabellar field. Thus, several Tremadocian species from Argentina originally referred to *Triarthrus* by Harrington and Leanza (1957) have been reassigned to *Bienvillia* (*B. parchaensis, B. tetragonalis, B. rectifrons*) (e.g., Henningsmoen, 1957; Fortey, 1974; Ludvigsen and Tuffnell, 1983).

> BIENVILLIA RECTIFRONS (Harrington, 1938) Figure 3.16–3.23, 3.25

- 1938 Triarthrus angelini var. rectifrons HARRINGTON, p. 209, pl. 8, figs. 17, 19–21.
- 1938 Peltura? sp. HARRINGTON, p. 215, pl. 8, fig. 17.
- 1957 *Triarthrus rectifrons*; HARRINGTON AND LEANZA, p. 115, fig. 43.2a–43.2g.
- 1980 Triarthrus rectifrons; Přibyl and Vaněk, p. 18, pl. 9, figs. 6, 7.
- 2003 Bienvillia rectifrons (Harrington); WAISFELD AND VACCARI, p. 329, pl. 31, figs. 15–17.

Material.—Twenty-seven (27) cranidia, three cranidia and thoracic fragments, one incomplete thorax, one thoracopygon, and two pygidia (MLP 34282–34296, 34297a, 34298[1–6], 34299[1–7], 34372, 34373) from the Nazareno area, Cordillera Oriental, northwestern Argentina. Upper part of the Santa Rosita Formation (upper Tremadocian).

Remarks.—The material examined is characterized by a subquadrate glabella bearing elongated (tr.), distinct and backwardly directed S1 and S2 furrows, a short (sag.) and convex anterior cephalic border, a well-defined anterior border furrow on the cranidium, and a discrete, inflated preglabellar field; features that are representative of *Bienvillia* Clark, 1924 (Ludvigsen and Tuffnell, 1983). Besides, the presence of a short (sag.) preglabellar field and moderately long (exsag.) palpebral lobes indicates correspondence with *B. rectifrons* (Harrington, 1938), from the upper Tremadocian of the Cordillera Oriental (Santa Victoria area, Salta Province; Quebrada de Coquena, west of Purmamarca, Jujuy Province).

Harrington and Leanza (1957, p. 115, fig. 43.2a–43.2g) provided a detailed description of *B. rectifrons*, and Waisfeld and Vaccari (2003) illustrated additional material from the type locality (Quebrada de Coquena, west of Purmamarca). Waisfeld and Vaccari (2003) regarded the convergent preocular sections of the facial suture as one of the most diagnostic attributes of this species. Although many specimens studied herein have this character, others seem to show a subparallel anterior facial suture (Fig. 3.20), variations that may lack crucial taxonomic significance.

Bienvillia rectifrons differs from the type materials of B. tetragonalis (Harrington, 1938), from the upper Tremadocian of Alfarcito, east of Tilcara (Harrington and Leanza, 1957, fig. 42.2, 42.3; see additional specimens from the type locality in Waisfeld and Vaccari, 2003, pl. 31, figs. 18–20), mainly in having a shorter (sag.) preglabellar field. As stated by Ludvigsen and Tuffnell (1983, p. 574), the preglabellar field of *B. parchaensis* (Harrington and Leanza), from the upper Tremadocian of the Incamayo area, Cordillera Oriental (Harrington and Leanza, 1957, figs. 43.1a-43.1h, 44.1a-44.1e; Waisfeld and Vaccari, 2003, pl. 31, figs. 12-14), is similar to that of B. rectifrons, but the former species is distinguished by its larger (exsag.) palpebral lobes. Alternatively, Bienvillia angelini (Linnarsson, 1869), from the upper Tremadocian of Norway (Henningsmoen, 1957, pls. 8, 11.8-11.10; Ebbestad, 1999, figs. 36A-36L, 37), exhibits a rounded preglabellar furrow, and a narrower (tr.) anterior part of the fixed cheeks (Ebbestad, 1999).

Subfamily OLENINAE Burmeister, 1843 Genus Parabolinella Brøgger, 1882

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

PARABOLINELLA TRIARTHROIDES Harrington, 1938 Figure 3.24, 3.26–3.33

1938 Parabolinella triarthroides HARRINGTON, p. 194, pl. 7, figs. 10, 11.

- 1957 Parabolinella triarthroides; HARRINGTON AND LEANZA, p. 105, 107, fig. 39.1a, 39.1b.
- 2003 *Parabolinella triarthroides*; WAISFELD AND VACCARI, p. 330, pl. 32, figs. 14–18.
- 2008 Parabolinella triarthroides; ZEBALLO, ALBANESI AND ORTEGA, fig. 5.8.

Material.—Fifty-four (54) cranidia, one cephalon and thorax, one cranidium and thorax, and one fragmentary thorax (MLP 34300–34312, 34313[1–10], 34314[1–5], 34315[1–5], 34374–34376) from the Nazareno area, Cordillera Oriental, northwestern Argentina. Upper part of the Santa Rosita Formation (upper Tremadocian).

Remarks.—The specimens studied exhibit a quadrate glabella, medially disconnected and backwardly directed S1 and S2 furrows with a bifurcate S1, a narrow (sag.) and convex anterior cephalic border, a pitted anterior border furrow, a well-defined preglabellar field, moderately divergent anterior sections of the facial suture, palpebral lobes situated anterior from cephalic midpoint, wide (tr.) posterior fixigenae, and librigenae with long genal spines that continue curvature of lateral cephalic margins; therefore, they essentially agree with the diagnosis of Parabolinella Brøgger, 1882 (Henningsmoen, 1957; Robison and Pantoja-Alor, 1968; Ludvigsen, 1982). In addition, the small size (largest observed cranidium 9 mm in length) and the presence of straight, subparallel axial furrows, a tumid preglabellar field, appreciable, forwardly curved ocular ridges, well-differentiated palpebral lobes, and very wide (tr.) posterior fixigenae, indicate close affinities with P. triarthroides Harrington, 1938, a taxon previously described from the upper Tremadocian of the Quebrada de Coquena, west of Purmamarca (Harrington, 1938, pl. 7, figs. 10, 11; Harrington and Leanza, 1957, fig. 39.1a, 39.1b; Waisfeld and Vaccari, 2003, pl. 32, figs. 14-18). Some cranidia (Fig. 3.32) show weak indications of fine, irregularly anastomosing striae on the preglabellar field, a sculpture that was regarded as distinctive of this species by Waisfeld and Vaccari (2003, pl. 32, fig. 17). The exoskeleton of P. triarthroides is very delicate and most of the specimens from Nazareno have suffered partial distortion (e.g., compare Fig. 3.26 and 3.30).

Although sclerites of *P. triarthroides* were reported from the upper Cambrian of Vermont and the basal Ordovician of Texas (Shaw, 1951; Winston and Nichols, 1967), Rushton (1988) reconsidered their identity and removed them from the synonymy list of the species. In addition, Rushton (1988, text-fig. 3C) assigned a small cephalon and fragments of thorax from the upper Tremadocian of England to *P. triarthroides*. However, these specimens seem to differ from the Argentinian material in showing a little longer (sag.) preglabellar field, less divergent anterior sections of facial suture, slightly curved cephalic axial furrows, and a proportionately narrower (tr.) glabella. Thus, the occurrence of *P. triarthroides* in England should be treated with scepticism.

Parabolinella triarthroides strongly resembles Parabolinella lata Henningsmoen, 1957, from the upper Tremadocian of Norway (Henningsmoen, 1957, pl. 12, fig. 8; Ebbestad, 1999, fig. 38A–38G), by sharing a similar glabellar outline, an inflated preglabellar field, as well as distinct, curved ocular ridges; the Argentinian species can be distinguished only by its narrower (tr.) palpebral area of the fixigena (cf. Rushton, 1988). Parabolinella triarthra (Callaway, 1877), from the Shineton Shales of Shropshire, England (e.g., Henningsmoen, 1957, pl. 12, figs. 6, 7; Owens et al., 1982, pl. 1, fig. k), differs from *P. triarthroides* in having less differentiated palpebral lobes. The type species *Parabolinella limitis* Brøgger, 1882, from the Tremadocian of Norway (Henningsmoen, 1957, pl. 1, fig. 8, pl. 12, figs. 1–5), further differs in possessing a glabella that is somewhat longer than wide, and backwardly directed ocular ridges.

Order Asaphida Salter, 1864 emend. Fortey and Chatterton, 1988 Superfamily Asaphoidea Burmeister, 1843 Family Asaphidae Burmeister, 1843 Genus Notopeltis Harrington and Leanza, 1957

Type species.—Megalaspidella orthometopa Harrington, 1938, from the upper Tremadocian of northwestern Argentina (by original designation).

NOTOPELTIS ORTHOMETOPA (Harrington, 1938) Figures 4.1–4.18, 5.1–5.18

- 1938 Megalaspidella orthometopa HARRINGTON, p. 239, pl. 12, figs. 1–8.
- 1938 Megalaspidella pumila HARRINGTON, p. 241, pl. 11, figs. 5, 7, pl. 12, figs. 12–14.
- 1957 *Notopeltis orthometopa* (Harrington); HARRINGTON AND LEANZA, p. 155, figs. 67, 68.1–68.11, 69.1–69–5.
- 2003 Notopeltis orthometopa; WAISFELD AND VACCARI, pl. 23, figs. 3–7.
- 2008 Notopeltis orthometopa; ZEBALLO, ALBANESI AND ORTE-GA, fig. 5.5, 5.6.

Description—Thorax with eight segments; axis subparallel sided to slightly tapered backward, narrower (tr.) than pleurae, about 0.25 of total thoracic width, surrounded by well-defined axial furrows, without axial nodes; pleurae with distal fulcrum, oblique furrow and pointed extremities, ending in very short spines.

Material.—Five exoskeletons, three axial shields, seven cephala, 33 cranidia, 10 librigenae, three hypostomes, 12 thoracopyga and 67 pygidia (MLP 34086–34137, 34138a, 34139a, 34140a, 34141a, 34142[1–22], 34143[1–13], 34144[1–5], 34145[1–9], 34146[1–12]) from the Nazareno area, Cordillera Oriental, northwestern Argentina. Upper part of the Santa Rosita Formation (upper Tremadocian). Largest observed pygidium 14.5 mm in length.

Remarks.—Harrington and Leanza (1957) revised the synonymy of *Notopeltis orthometopa* (Harrington) and described in great detail its cephalon and its pygidium on the basis of numerous specimens from the Quebrada de Coquena, west of Purmamarca, preserved in both limestone and shale. These specimens are mainly characterized by lacking a pygidial border furrow and a concave border, and having a differentiated, very long glabella, a noticeable cephalic border, and well-defined genal spines. It is important to note that Harrington and Leanza (1957) identified certain variability with respect to the pygidial convexity and shape (e.g., compare figs. 68.9, 68.11, 69.4, 69.5, and figs. 68.10, 69.3 of Harrington and Leanza, 1957), which was interpreted as variations in conservation and distortion.

The material studied herein conforms in all fundamental features with the diagnosis of *Notopeltis orthometopa* (Harrington). The pygidium illustrated in Figure 4.12 shows little indication of flattening and compares closely with those from the Quebrada de Coquena figured by Harrington and Leanza (1957, figs. 68.9, 68.11, 69.2 [paratype], 69.4 [paratype], 69.5) and Waisfeld and Vaccari (2003, pl. 23, fig. 5). On the other hand, many specimens from Nazareno exhibit signs of compression (e.g., Fig. 4.14, 4.18), longitudinal distortion (e.g., Figs. 4.16, 5.4, 5.12, 5.17) and transversal deformation (e.g., Fig. 4.10, 4.17), demonstrating substantial resemblance with individuals from Purmamarca illustrated by Harrington (1938, fig. 11.7) and Harrington and Leanza (1957, figs. 68.10, 69.3).

Genus MEKYNOPHRYS Harrington, 1938

Type species.—*Mekynophrys nanna* Harrington, 1938, from the upper Tremadocian of northwestern Argentina (by original designation).

Description.-Exoskeleton of moderate to large size; anterior cephalic border narrow (sag.), convex, raised; preglabellar field long (sag.), depressed, with a raised sagittal ridge extending from glabella to anterior cephalic border; glabella subcylindrical, expanded (tr.) posteriorly, with a posterior mesial node; S1 furrow deeper, more oblique backward-inward than S2 and S3; lateral preoccipital glabellar lobes raised along axial furrows in rounded crest oblique backward-outward; occipital furrow deepest at sides and shallow on midline, curved backward medially; anterior branches of facial suture divergent in front of eyes; palpebral area of the fixigena narrow (tr.); posterior fixigena wide (tr.) and short (exsag.); pygidium sub-semicircular in outline; axis long and narrow (tr.), slightly tapering backward, with indistinct posterior rings and a blunt terminal piece; pleural fields crossed by weak, slightly oblique pleural furrows; pygidial border wide, concave; doublure very wide, with fine terrace ridges subparallel to margin.

MEKYNOPHRYS NANNA Harrington, 1938 Figure 6.1–6.21

- 1938 Mekynophrys nanna Harrington, p. 207, pl. 6, figs. 7, 16–18.
- 1938 Basiliella carinata HARRINGTON, p. 247, pl. 13, figs. 12, 14, 15, 18 (only).
- 1957 *Mekynophrys nanna*; HARRINGTON AND LEANZA, p. 119, fig. 44.3.
- 1957 *Basiliella carinata*; HARRINGTON AND LEANZA, p. 145, figs. 61.1–61.9, 62.1–62.9 (see for further synonymy).
- 1980 Basiliella (Carinobasiliella) carinata; PŘIBYL AND VANĚK, p. 25, pl. 13, figs. 3–5, text-fig. 4.
- 2003 Mekynophrys nanna; WAISFELD AND VACCARI, p. 320, pl. 23, figs. 9–12.
- 2008 *Mekynophrys nanna*; ZEBALLO, ALBANESI AND ORTEGA, fig. 5.12.

Description.—Hypostome large, subpentagonal in outline, as long (sag.) as wide (tr.); anterior lobe of median body large, moderately convex, ovate, as long as wide, occupying about 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 rounded; anterior margin of hypostome broadly rounded; anterior wings subtriangular, broad; lateral border wide posterolaterally, converging anteriorly to merge with the median body opposite the middle of the hypostome; the surface of the median body of the hypostome shows a complex pattern of dactylogram-like wrinkles, and the lateral border exhibits 8–12 terrace lines subparallel to margin.

Material.—Twenty-six (26) cranidia, 11 librigenae, three hypostomes and 25 pygidia (MLP 34139b, 34140b, 34141b, 34147–34180, 34181[1–9], 34182[1–5], 34183[1–7]) from the Nazareno area, Cordillera Oriental, northwestern Argentina. Upper part of the Santa Rosita Formation (upper Tremadocian). Largest observed pygidium 25 mm in length.

Remarks.—Mekynophrys nanna Harrington, 1938 was originally described on the basis of juvenile cranidia from the Quebrada de Coquena that proved to be conspecific with *Basiliella carinata* Harrington, 1938 (*M. nanna* regarded as senior synonym; Waisfeld and Vaccari, 2003). Based of numerous specimens from west of Purmamarca and additional localities of the Cordillera Oriental (e.g., Santa Victoria), Harrington and Leanza (1957) provided a detailed description of *B. carinata*, pointing out its preglabellar ridge, its pattern of furrows and lobes on the glabella, its narrow pygidial axis, the well-differentiated, concave pygidial border, and its conspicuous doublure. In addition, Waisfeld and Vaccari (2003, pl. 23, fig. 11) documented a particular sculpture of delicate anastomosing ridges



FIGURE 4—Notopeltis orthometopa (Harrington, 1938) from upper part of Santa Rosita Formation at Nazareno, northwestern Argentina: *1*, cranidium, MLP 34115, ×3.2; *2*, cranidium, MLP 34112, ×2.3; *3*, cranidium, MLP 34091, ×2.6; *4*, librigena, MLP 34142, ×2.5; *5*, cranidium, MLP 34134, ×3.1; *6*, cranidium, MLP 34132, ×2; *7*, cranidium, MLP 34137, ×1.8; *8*, hypostome, MLP 34088, ×2.7; *9*, exoskeleton, MLP 34113, ×2; *10*, exoskeleton, MLP 34091, ×2.6; *i*, thoracopygon, MLP 34101, ×2.8; *12*, thoracopygon, MLP 34129, ×2.5; *13*, thoracopygon, MLP 34100, ×2; *14*, thoracopygon, MLP 34093, ×1.8; *15*, librigena, MLP 34137, ×3.5; *16*, pygidium and thoracic fragment, MLP 34106, ×2.3; *17*, pygidium and fragmentary thorax, MLP 34126, ×2.7; *18*, pygidium and fragmentary thorax, MLP 34138a, ×1.4.



FIGURE 5—Pygidia of *Notopeltis orthometopa* (Harrington, 1938) from upper part of Santa Rosita Formation at Nazareno, northwestern Argentina: *1*, MLP 34124, ×2.7; *2*, MLP 34114, ×3; *3*, MLP 34131, ×2.4; *4*, MLP 34123, ×2.2; *5*, MLP 34092, ×3; *6*, MLP 34096, ×3.2; *7*, MLP 34120, ×2.5; *8*, MLP 34117, ×2.7; *9*, MLP 34105, ×2.6; *10*, MLP 34107, ×2.7; *11*, MLP 34111, ×3.8; *12*, MLP 34128, ×2.8; *13*, MLP 34116, ×4; *14*, MLP 34130, ×3.6; *15*, MLP 34094, ×3.5; *16*, MLP 34097, ×2.1; *17*, latex mold, MLP 34133, ×2; *18*, MLP 34103, ×2.9.

on the exoskeleton. The hypostome of the species is described herein for the first time.

The pygidia from Nazareno show variations in the length of the axis, which occupies 65–80 percent of the total pygidial length, and the degree of expression of the pleural furrows, which are less marked in large specimens.

Genus Asaphellus Callaway, 1877

Type species.—Asaphus homfrayi Salter, 1866, from the Tremadocian Series in Gwynedd, North Wales (by original designation).

Asaphellus jujuanus Harrington, 1937 Figure 7.1–7.19

- 1937 Asaphellus jujuanus HARRINGTON, p. 115, pl. 5, figs. 5, 9, 10, 14.
- 1938 Asaphellus jujuanus; HARRINGTON, p. 242, pl. 12, fig. 15, pl. 13, figs. 1, 2 (only).
- 1938 Asaphellus catamarcensis Kobayashi; HARRINGTON, p. 244, pl. 13, figs. 5, 16 (only).
- 1957 Asaphellus jujuanus; HARRINGTON AND LEANZA, p. 151, fig. 66.7, ?66.10, 66.12 (only).

- 1957 Asaphellus catamarcensis; HARRINGTON AND LEANZA, p. 147, figs. 64.4, ?64.6, 65.4 (only).
- 2003 Asaphellus jujuanus; WAISFELD AND VACCARI, p. 319, pl. 22, figs. 1, 2.

Diagnosis.—A species of *Asaphellus* with exoskeleton of large size, flat or very slightly convex; posterior facial suture transverse, strongly directed outward; genal spines small; pygidial axis long and narrow, with traces of five rings on its anterior part; pleural fields smooth or with very faint indications of five or six pleural furrows; pygidial border well-developed, depressed (emended from Harrington and Leanza, 1957).

Material.—Two exoskeletons, 12 cranidia, five librigenae, two hypostomes, and 45 pygidia (MLP 34316–34371) from the Nazareno area, Cordillera Oriental, northwestern Argentina. Upper part of the Santa Rosita Formation (upper Tremadocian). Largest observed pygidium 31 mm in length.

Remarks.—Asaphellus jujuanus was originally described by Harrington (1937) on the basis of specimens from the Quebrada de Chalala that are available in Harrington and Leanza collection, University of Buenos Aires. The examination of that material proved that it is compatible in all details with a collection of complete exoskeletons, cranidia, librigenae, and pygidia from the middle part of the Nazareno section. The presence of a transverse posterior facial suture, short genal spines, a flat pygidium, a narrow pygidial axis, and a conspicuous, depressed border, are considered herein as characteristic features of this species.

As indicated by Waisfeld and Vaccari (2003), the definition and scope of most of the species of *Asaphellus* from northwestern Argentina need to be critically revised. In that regard, it is important to note that Harrington and Leanza (1957) assigned to *A. jujuanus* some specimens which seem to be different from the type material of that species. Two cranidia and one hypostome from the Tremadocian of Rio Uturbe, Jujuy Province (Harrington and Leanza, 1957, fig. 66.6, 66.9, 66.11) differ from *A. jujuanus* in having an imperceptible anterior border furrow and a much narrower posterolateral border, respectively. Besides, a distorted pygidium from the upper Tremadocian of Santa Victoria, Salta Province (Harrington and Leanza, 1957, fig. 66.10), shows an imperfectly preserved axis and therefore its specific affinity is doubtful.

On the other hand, some specimens from west of Purmamarca that were referred to as *Asaphellus catamarcensis* Kobayashi by Harrington (1938, pl. 13, figs. 5, 16) and Harrington and Leanza (1957, figs. 64.4, 65.4) are reassigned herein to *A. jujuanus*. A longitudinally distorted exoskeleton from the upper Tremadocian of Santa Victoria (Harrington and Leanza, 1957, fig. 64.6) is also very similar to the specimens described herein and is probably conspecific with them.

Asaphellus jujuanus differs from Asaphellus catamarcensis Kobayashi, from the lower Tremadocian of the Cordillera Oriental (Kobayashi, 1935, pl. 11, figs. 11–15; Harrington and Leanza, 1957, fig. 65.7, 65.8; Tortello and Aceñolaza, 2010 and references), mainly in having a transverse posterior facial suture, and more rings on the pygidial axis.

Asaphellus nazarenensis new species Figure 8.1–8.6

Diagnosis.—An *Asaphellus* species with perceptible axial furrows, a moderately wide (tr.) palpebral area of the fixigena, and a narrow (sag.) pygidial border.

Description.—Cranidium slightly convex, with pointed anterior margin and moderately downsloping fixed cheeks; glabella broad, unfurrowed, little elevated above genal region, subparallel sided to slightly tapered forward and rounded anteriorly, slightly constricted between palpebral lobes, surrounded by faint but perceptible axial furrows and an almost indiscernible preglabellar furrow; it occupies about 85 percent of the total length of the cranidium; posterior glabellar node very weak or 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 little upturned, pointed anteriorly, differentiated by change in slope of exoskeleton; anterior facial suture somewhat divergent forward; palpebral area of the fixigena rather wide (tr.); eyes situated adjacent to mid-length of cranidium; posterior facial suture oblique backward and outward, sinuous; posterior fixigena relatively wide (tr.), with a welldefined border furrow and a narrow (exsag.), convex posterior border.

Librigenae, hypostome, and thorax unknown.

Pygidium semicircular in outline, transversely elongate, somewhat convex, width about twice length; axis little elevated above level of pleural fields, about 25 percent of total width of pygidium at anterior extremity, tapered at anterior half and nearly parallel sided at posterior half, with slightly marked anterior 4 or 5 rings and indistinct posterior rings, ending in blunt point; length of axis about 85 percent of that of pygidium on sagittal line; articulating half ring very narrow (sag.), crescentic; pleural field smooth, only slightly downsloping; border furrow weak, poorly defined; border very narrow, fairly convex to flat, occupying only 7 percent of the total pygidial length (sag.).

Etymology.—Refers to Nazareno village, Salta Province, Argentina.

Types.—Holotype, pygidium, MLP 34215a (Fig. 8.3), length 8.7 mm, width 19 mm; paratypes, six cranidia and eleven pygidia (MLP 34210b, 34212–34214, 34215b, 34216–34220, 34297b).

Occurrence.—Middle part of the Nazareno section, Cordillera Oriental, northwestern Argentina. Upper Santa Rosita Formation (upper Tremadocian).

Remarks.—This new species differs from *A. jujuanus* Harrington, from the upper Tremadocian of the Cordillera Oriental (see above), by having a wider (tr.) palpebral area of the fixigena, a more oblique posterior facial suture, a smaller number of pygidial axial rings, and a narrower pygidial border. *Asaphellus naza-renensis* differs from *A. catamarcensis* Kobayashi, from the lower Tremadocian of northwestern Argentina (Kobayashi, 1935, pl. 11, figs. 11–15; Harrington and Leanza, 1957, fig. 65.7, 65.8; Tortello and Aceñolaza, 2010 and references), in having a shorter pygidial border, and from *A. kayseri* (Kobayashi) sensu Harrington and Leanza (1957, figs. 74, 75) (Waisfeld and Vaccari, 2003, pl. 22, figs. 7–9) by possessing a wider (tr.) palpebral area, and lacking pleural furrows on the pygidium.

Asaphellus nazarenensis can be easily differentiated from A. aspinus Robison and Pantoja-Alor, from the Tremadocian of Mexico (Robison and Pantoja-Alor, 1968, pl. 98, figs. 1–11), by possessing smaller palpebral lobes, a quite convex anterior cranidial border, a tapered pygidial axis, and a narrower pygidial border. Because the Argentinian species bears noticeable axial furrows, it is further distinguished from a number of partially effaced species of Asaphellus from Mexico (A. artus Robison and Pantoja-Alor), China (e.g., A. inflatus Lu; A. yanheensis Yin), and Great Britain (A. homfrayi [Salter]).

In the Nazareno section, *Asaphellus nazarenensis* is recorded below the first appearance of *Notopeltis orthometopa*, from which it is distinguished mainly by its shallower frontal area and its differentiated pygidial border.

Asaphellus sp. Figure 8.8–8.12

Description.—Exoskeleton highly effaced; cephalic axial furrows undefined; frontal area concave, proportionately long (sag.); anterior facial suture somewhat divergent forward;



palpebral lobes small, lying just behind mid-length of cranidium; posterior facial suture oblique backward and outward, sinuous.

Pygidium semicircular, slightly convex, length about 0.6 width; axial furrow extremely faint; axis tapered backward, little elevated above level of pleural fields, with weak indications of seven or eight rings and a long terminal piece, occupying about 85–90 percent of the total pygidial length; pleural fields effaced; border narrow, imprecisely defined by a broad shallow border furrow.

Material.—One fragmentary cephalon and thorax, and nine pygidia (MLP 34078–34085) from the Nazareno area, Cordillera Oriental, northwestern Argentina. Santa Rosita Formation (Tremadocian).

Remarks .--- Since the cephalon is known only from a fragmentary specimen, this material is referred to in open nomenclature. The specimens examined compare most closely with highly effaced species of Asaphellus Callaway, 1877. Asaphellus sp. and Asaphellus artus Robison and Pantoja-Alor, from the Tremadocian of Mexico (Robison and Pantoja-Alor, 1968, pl. 99, figs. 1-6), share a pygidium of similar outline and degree of effacement, but the cephalon of the latter exhibits a more clearly defined glabella and a noticeable anterior cephalic border. Asaphellus homfrayi (Salter), from the upper Tremadocian of Great Britain (e.g., Fortey and Owens, 1991, figs. 31-3u, 7a-7g, 8a, 8b), is distinguished by its proportionately larger palpebral lobes. Asaphellus inflatus Lu (e.g., Peng, 1990a, pl. 6, figs. 3-19, pl. 7, figs. 1-5) and A. vanheensis Yin (Peng, 1990a, pl. 7, figs. 6-13), from the Tremadocian of China, are similar to Asaphellus sp. by showing minute palpebral lobes; however, the Chinese species differ mainly in having a shorter (sag.) frontal area and an ill-defined pygidial border.

Family CERATOPYGIDAE Linnarsson, 1869 Genus CERATOPYGE Hawle and Corda, 1847

Type species.—Olenus forficula Sars, 1835, from the upper part of the Alum Shale Formation (Tremadocian) in Oslo, Norway (Ebbestad, 1999) (by original designation).

CERATOPYGE FORFICULOIDES Harrington and Leanza, 1957 Figure 9.1–9.10

- 1957 Ceratopyge forficuloides HARRINGTON AND LEANZA, p. 185, fig. 94.1–94.9.
- 2003 *Ceratopyge forficuloides*; WAISFELD AND VACCARI, p. 323, pl. 26, figs. 6–8.

Diagnosis.—A *Ceratopyge* species with a wide (sag.) anterior cephalic border; preglabellar field narrow (sag.); lateral glabellar furrows effaced; median glabellar node delicate, located close to the occipital ring; anterior facial suture diverging at an angle of 45° to the exsagittal line; pygidial axis with four rings and a terminal piece (emended from Harrington and Leanza, 1957).

Description.—Hypostome subrectangular, longer than wide; median body large, strongly convex, ovoid in outline, width about 0.6 of length, lacking well-differentiated anterior and posterior lobes; maculae small, situated far back; posterolateral border narrow (tr.), concave, merging with median body anterior of its center; anterior wings proportionately large, subtriangular; anterior margin broadly rounded, with a raised border.

Material.-Two cephala, nine cranidia, two librigenae, three

hypostomes, and 15 pygidia (MLP 34211b, 34229b, 34230b, 34231b, 34232–34243, 34244[1–10]) from the Nazareno area, Cordillera Oriental, northwestern Argentina. Upper part of the Santa Rosita Formation (upper Tremadocian). Largest observed cranidium 11 mm in length.

Remarks.—The specimens examined show all the typical features of *Ceratopyge forficuloides*, a taxon described by Harrington and Leanza (1957) on the basis of relatively scarce material from the Santa Victoria and Incamayo areas (Cordillera Oriental). Illustrations of additional material from Nazareno, a description of the hypostome, and a revised diagnosis of this species are provided herein. The preglabellar field of the specimens from Nazareno is slightly longer than that of the type material (Harrington and Leanza, 1957, fig. 94.7, 94.9; Waisfeld and Vaccari, 2003, pl. 26, figs. 6, 7), a variation that is not accorded taxonomic significance.

Although *C. forficuloides* was originally considered as occurring in lower and upper Tremadocian strata, Waisfeld and Vaccari (2003) noted that the associated fauna reported by Harrington and Leanza (1957, p. 242) suggests only a late Tremadocian age. The record of *C. forficuloides* in the middle part of the Nazareno section is consistent with that stratigraphic position.

Ceratopyge forficuloides differs from the type species *C. forficula* (Sars, 1835), from the Tremadocian of Norway and Sweden (e.g., Ebbestad, 1999, fig. 57), because the latter has a narrower (sag.) anterior cephalic border, a distinct S1 lateral glabellar furrow, and a more anteriorly located median glabellar node (Harrington and Leanza, 1957; Ebbestad, 1999). *Ceratopyge acicularis* (Sars and Boeck, 1838) from the Tremadocian of Scandinavia (e.g., Ebbestad, 1999, figs. 58, 59) shows, in addition, a longer pygidial axis.

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).

NILEUS AUSTRALIS new species Figure 8.7, 8.13–8.20

Diagnosis.—A *Nileus* species with a subrectangular, anteriorly truncate glabella; palpebral lobes small for the genus; test surface of pygidium with weak indications of a few terrace lines on anterolateral part of pleural fields; pygidial axis vaguely perceptible on internal molds, with undifferentiated axial rings; pygidial border very narrow; doublure covered with 14 terrace lines.

Description.—External surface of exoskeleton smooth. Cranidium gently convex (sag., tr.), wider than long, with maximum width between the palpebral lobes. Glabella very broad, gently arched (sag., tr.), longer than wide, unfurrowed, slightly tapering forward immediately in front of eyes and expanding laterally close to the anterior margin, truncate anteriorly; median glabellar node delicate, situated opposite posterior parts of palpebral lobes; axial furrows delimiting glabella from palpebral lobes wide and shallow; occipital ring defined only on internal molds, extremely

FIGURE 6—Mekynophrys nanna Harrington, 1938 from upper part of Santa Rosita Formation at Nazareno, northwestern Argentina: *1*, *5*, cranidium, latex cast and mold, MLP 34147, ×2.9; *2*, cranidium, MLP 34173, ×2; *3*, cranidium, latex mold, MLP 34157, ×3.1; *4*, cranidium, MLP 34156, ×2; *6*, cranidium, MLP 34152, ×2.6; *7*, cranidium, MLP 34162, ×4; *8*, cranidium, MLP 34154a, ×4.4; *9*, librigena, MLP 34168, ×1.7; *10*, hypostome, MLP 34155, ×2; *11*, pygidium, latex mold, MLP 34149, ×2; *12*, pygidium, latex mold, MLP 34179, ×3.6; *13*, pygidium, latex mold, MLP 34164, ×1.4; *14*, pygidium, latex mold, MLP 34160, ×4.2; *15*, pygidium, latex mold, MLP 34163, ×2.5; *17*, pygidium, MLP 34167, ×2.3; *18*, pygidium, latex mold, MLP 34166, ×4.6; *19*, pygidium, latex mold, MLP 34178, ×2.1; *20*, pygidium, MLP 34154b, ×1.6; *21*, pygidium, MLP 34175, ×5.1.



FIGURE 7—Asaphellus jujuanus Harrington, 1937 from the Santa Rosita Formation at Nazareno, northwestern Argentina: 1, exoskeleton, MLP 34369, ×1.9; 2, cranidium, MLP 34329, ×2.7; 3, cranidium, MLP 34371, ×1.9; 4, librigena, MLP 34368, ×0.8; 5, cranidium, MLP 34324, ×2.4; 6, cranidium, latex mold, MLP 34340, ×1.9; 7, hypostome, MLP 34355, ×2.2; 8, pygidium, MLP 34330, ×1.7; 9, pygidium, MLP 34338, ×1.7; 10, pygidium, MLP 34332, ×1.8; 11, pygidium, MLP 34349, ×1.6; 12, pygidium, MLP 34362, ×1.4; 13, pygidium, MLP 34323, ×2; 14, pygidium, MLP 34334, ×2; 15, pygidium, MLP 34321, ×1.9; 16, pygidium, MLP 34354, ×2.3; 17, pygidium, MLP 34319, ×1.5; 18, pygidium, MLP 34320, ×1.3; 19, pygidium, MLP 34361, ×1.

narrow (sag.), with faint, transverse occipital furrow; the lateral extremities of the occipital ring bear a tiny pit. Palpebral lobes small for the genus, arcuate, gently convex, slightly backward of glabellar midpoint, occupying one-third of the total length of the

cranidium and about 30 percent of the maximum cranidial width; posterior branches of facial suture strongly divergent, short, almost straight; posterior fixed cheeks short (tr.), triangular, downsloping, confluent with glabella.



FIGURE 8—Asaphids and nileids from the Santa Rosita Formation at Nazareno, northwestern Argentina. *1–6, Asaphellus nazarenensis* n. sp.: *1*, cranidium, MLP 34216, ×2.6; *2*, cranidium, MLP 34215b, ×2.4; *3*, pygidium (holotype), MLP 34215a, ×3.2; *4*, pygidium, MLP 3421bb, ×3; *5*, cranidium, MLP 34217, ×2.6; *6*, pygidium, MLP 34218, ×5.8; *8–12, Asaphellus* sp.: *8*, pygidium, latex mold, MLP 34085, ×3.2; *9*, pygidium, MLP 34080, ×3.6; *10*, pygidium, MLP 34079, ×1.1; *11*, pygidium, MLP 34082, ×2.2; *12*, fragmentary cephalon and thorax, MLP 34078, ×1.1; *7*, *13–20*, *Nileus australis* n. sp.: *7*, cranidium, MLP 34222, ×3.9; *13*, cranidium (right) and pygidium (left), MLP 34231a, ×3.2; *14*, cranidium, MLP 34228, ×3; *15*, pygidium (holotype), MLP 34226, ×4; *16*, pygidium, MLP 34225, ×3.8; *17*, pygidium, MLP 34221, ×2.7; *18*, pygidium retaining exoskeleton, MLP 34223, ×3.8; *19*, pygidium, latex mold, MLP 34227, ×7; *20*, pygidium, MLP 34224, ×4.4.



Pygidium semielliptical in outline, about twice as wide as long, somewhat convex, with short (sag.) articulating half-ring, rounded anterolateral corners and entire posterior margin; test surface almost smooth, with weak indications of a few terrace lines on anterolateral part of pleural fields. Axis invisible on testaceous material and vaguely perceptible on internal molds, strongly tapering, rounded at posterior end, little elevated above level of pleural fields, occupying about 60–65 percent of the total length (sag.) of the pygidium. Pleural field smooth, only slightly downsloping; border very narrow, imperfectly indicated by a change of slope of the exoskeleton; doublure exceptionally broad, with its anterior margin slightly curved forward, covered with 14 terrace ridges following the doublural contour.

Etymology.—Alluding to its occurrence in the Southern Hemisphere.

Types.—Holotype, pygidium, MLP 34226 (Fig. 8.15), length 6.5 mm, width 12.5 mm; paratypes, three cranidia and eight pygidia (MLP 34221–34228, 34229a, 34230a, 34231a).

Occurrence.—Middle part of the Nazareno section, Cordillera Oriental, northwestern Argentina. Upper Santa Rosita Formation (upper Tremadocian).

Remarks.—The material described above is characterized by having an effaced exoskeleton with a sagittally convex glabella, arcuate palpebral lobes, minute posterior fixed cheeks, and a transversely elongate pygidium. In addition, internal molds show a median glabellar node opposite posterior parts of palpebral lobes, a short and rapidly tapering pygidial axis, and a broad pygidial doublure with its anterior margin slightly curved forward. Therefore, it is consistent with the definition of *Nileus* Dalman, 1827 (Fortey, 1975; Nielsen, 1995). The presence of only a few terrace lines on the test of the anterolateral part of the pygidium (Fig. 8.18, 8.19) indicates affinities with the "*exarmatus* group" of Nielsen (1995).

Nileus australis n. sp. is among the oldest species of the genus. It clearly differs from *N. limbatus* Brøgger, from the upper Tremadocian (*Megistaspis armata* and lower *Megistaspis planilimbata* zones) of Norway and Sweden (e.g., Ebbestad, 1999, figs. 63A–63O, 64A–64G and references), by having a truncate anterior cranidial margin, an almost imperceptible, narrow pygidial border, and a pygidium with undifferentiated axial rings on internal molds.

Nileus exarmatus Tjernvik, from the Floian and Dapingian of Scandinavia (e.g., Tjernvik, 1956, text-fig. 33B, pl. 2, figs. 16–21; Nielsen, 1995, figs. 164A–164N, 165A–165J and references), and *N. australis* share a similar pattern of terrace lines on the test of the pygidium, but the former is distinguished by its distinctly curved anterior cranidial margin, its larger palpebral lobes, a concave, wider pygidial border, and a pygidial axis with a positive relief on both internal molds and testaceous specimens. *Nileus orbiculatoides* Schrank, 1972, from the Middle Ordovician of Scandinavia (Nielsen, 1995, figs. 169A–169M, 170A–170P, 172A–172L and references), differs from *N. australis* mainly by having a mesial boss on the anterior cranidial margin, longer (exsag.) palpebral lobes, a well defined, concave pygidial border, and more terrace lines on the pygidial doublure. The type species *N. armadillo* (Dalman, 1827) (Nielsen, 1995, figs. 147A–147N, 148A–148O, 149A–149M, 150A–150N and references) is also distinguished by possessing a pygidium with a concave border of variable width, and a doublure with an increased number of terrace lines.

Nileus porosus Fortey, from the Valhallfonna Formation of Spitsbergen (Fortey, 1975, pl. 12, figs. 1–14), is very similar to *N. australis* because of its relatively small palpebral lobes, its indistinct pygidial border, and the presence of 12–15 terrace lines on the pygidial doublure; however, the dorsal surface of the former exhibits terrace lines behind the articulating facet and, also, around the posterior margin of the pygidium. *Nileus orbiculatus* Tjernvik, from the Floian (*Megistaspis* aff. *M. estonica* Zone) of Sweden (Tjernvik, 1956, pl. 11, figs. 22, 23), is a rare, small species that is differentiated by having a medially widened (tr.) glabella.

Superfamily REMOPLEURIDIOIDEA Hawle and Corda, 1847 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).

Apatokephalus tibicen Přibyl and Vaněk, 1980 Figure 9.11–9.15, 9.19

- 1938 Apatokephalus dubius (Linnarsson); HARRINGTON, p. 171, pl. 5, figs. 6–10.
- 1957 *Apatokephalus serratus* (Boeck); HARRINGTON AND LEANZA, p. 135, fig. 56.1, 56.3–56.8, 56.10.
- 1980 Apatokephalus tibicen Přibyl and Vaněk, p. 23, pl. 12, figs. 3, 4.

Material.—One imperfectly preserved exoskeleton, nine cranidia, four librigenae, and 13 pygidia (MLP 34259–34271, 34272[1–4], 34273[1–7], 34377) from the Nazareno area, Cordillera Oriental, northwestern Argentina. Upper part of the Santa Rosita Formation (upper Tremadocian). Largest observed cranidium 7.5 mm in length.

Remarks.—Přibyl and Vaněk (1980, pl. 12, figs. 3, 4) erected *Apatokephalus tibicen* on the basis of material from several Tremadocian localities of the Argentinian Cordillera Oriental that had been previously referred to as *A. serratus* (Boeck, 1838) by Harrington (1938) and Harrington and Leanza (1957). More recently, Waisfeld and Vaccari (2003, p. 324) pointed out the presence of variations in the morphology of many specimens illustrated by Harrington and Leanza (1957, fig. 56.1–56.10), drawing attention to the possible existence of more that one species in those collections.

The specimens studied herein represent an *Apatokephalus* species with a slightly angulate anterior cranidial margin, a preglabellar field as wide (sag.) as the anterior border, a pitted anterior border furrow, well defined glabellar furrows, a broad (sag.) occipital ring, greatly divergent anterior branches of the facial suture, non-advanced genal spines, a tapering pygidial axis

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FIGURE 9—Ceratopygids, kainellids, orometopids, and pliomerids from the Santa Rosita Formation at Nazareno, northwestern Argentina. *1–10, Ceratopyge forficuloides* Harrington and Leanza, 1957: *1*, cranidium, MLP 34230b, ×3.5; *2*, cephalon, MLP 34231b, ×2.7; *3*, cranidium, MLP 34235, ×4.7; *4*, cranidium, MLP 34229b, ×4.1; *5*, pygidium, MLP 34233, ×3.3; *6*, pygidium, latex mold, MLP 34232, ×5; *7*, librigena, MLP 34211b, ×4.1; *8*, hypostome, MLP 34238, ×4; *9*, pygidium, MLP 34237, ×5.2; *10*, pygidium, latex mold, MLP 34240, ×4.5; *11–15, 19, Apatokephalus tibicen* Přibyl and Vaněk, 1980: *11*, cranidium, Iatex mold, MLP 34265, ×4.8; *12*, cranidium, MLP 34263, ×3.8; *14*, librigena, MLP 34262, ×4.3; *15*, pygidium, latex mold, MLP 34266, ×4.1; *19*, fragmentary thoracopygon, MLP 34261, ×3.5; *16, 20, 21, Apatokephalus* sp.: *16*, cranidium, MLP 34276a, ×2.5; *20*, cranidium, MLP 34278, ×3.3; *21*, pygidium, latex mold, MLP 34263, ×3.8; *23*, cranidium, MLP 34206, ×4.1; *24*, cranidium, MLP 34210a, ×4.8; *23–28*, *Rossaspis*? sp.: *23*, cranidium, MLP 34250, ×3.4; *24*, fragmentary cranidium, MLP 34249, ×3.5; *25*, disarticulated exoskeleton, MLP 34255, ×3.2; *26*, cranidium, latex mold, MLP 34253, ×5.2; *27*, pygidium, MLP 34248, ×3; *28*, exoskeleton, latex mold, MLP 34245, ×3.

with 4 rings and an elongate terminal piece, four distinct pygidial pleural furrows, and five pairs of marginal spines of different size. The specimens show evidence of distortion, which affected the glabellar shape and the exact configuration of the lateral glabellar furrows. On the other hand, the best preserved individuals exhibit a set of four or five terrace lines on the anterior cephalic border, and the testaceous cranidia have, in addition, a surface sculpture of crowded, fine tubercles (Fig. 9.13). In general, these characters are compatible with the holotype of A. tibicen (Harrington and Leanza, 1957, fig. 56.1; Přibyl and Vaněk, 1980, pl. 12, fig. 3; Waisfeld and Vaccari, 2003, pl. 27, fig. 17). Although the latter has a less acuminate anterior cranidial margin and a more transverse lateral glabellar furrow S3, these characters may lack specific significance. Several specimens illustrated by Harrington and Leanza (1957, fig. 56.3-56.8, 56.10), despite being imperfectly preserved, seem to be conspecific with the material studied here.

The type species *Apatokephalus serratus* (Boeck, 1838), from the upper Tremadocian of Scandinavia (e.g., Ebbestad, 1999, figs. 41A, 42A–42O and references), differs from *A. tibicen* by having a cephalic sculpture of sparse, coarse tubercles, a shorter (sag.) preglabellar field, advanced genal spines, and more numerous marginal pygidial spines. The cranidium of *Apatokephalus sarculum* Fortey and Owens, from the upper Tremadocian of England (Stubblefield and Bulman, 1927, pl. 4, fig. 7; Hutchison and Ingham, 1967; Fortey and Owens, 1991, fig. 12a–12j, 12l, 12o), is very similar to that of *A. tibicen*, but the English species is distinguished by its advanced genal spines and its shorter pygidium. *Apatokephalus dactylotypos* Ebbestad, from the upper Tremadocian of Norway (Ebbestad, 1999, figs. 41C, 44), can be also distinguished by the presence of a median bulge on the frontal glabellar lobe.

As stated by Wright et al. (1994), A. aff. A. tibicen, from the Lower Ordovician of New Zealand, differs from A. tibicen in having a shorter (sag.) frontal area and more advanced genal spines. Apatokephalus dubius (Linnarsson), from the upper Tremadocian of Baltica (e.g., Ebbestad, 1999, figs. 41B, 43 and references), is different because it shows a rounded anterior cranidial margin, a shorter preglabellar field, as well as a fine, raised fingerprint-like sculpture on the glabellar test. Apatokephalus exiguus Harrington and Leanza, from the upper Tremadocian of Cerrillos, southern Salta (Harrington and Leanza, 1957, figs. 57, 58; Waisfeld and Vaccari, 2003) lacks a well developed preglabellar field, and possesses a narrower (sag.) cranidial border and a shorter (sag.) pygidium.

Although *A. latilimbatus* Peng, from the Lower Ordovician of China (Peng, 1990b, pl. 11, figs. 1–14, pl. 12, figs. 4, 5, 9), bears an angulate anterior cranidial margin, it differs considerably from *A. tibicen* by having a broader (sag.) anterior cranidial border, genal spines in a very advanced position, and a smaller pygidium.

APATOKEPHALUS sp. Figure 9.16, 9.20

Description.—Apatokephalus with raised, very narrow (sag.) anterior cranidial border and broad (sag.) preglabellar field; anterior border furrow pitted; glabella bell-shaped, slightly rounded to truncate anteriorly, occupying about 80 percent of the total cranidial length (sag.); with three pairs of distinct, medially disconnected lateral furrows, only anterior two pairs connecting with axial fields; S1 sigmoidal, bifurcated, directed obliquely inward and backward; S2 straight, approximately parallel to preoccipital furrow; S3 well defined, slightly oblique inward and backward; glabellar median node delicate, located in front of S3, only visible on internal molds; occipital furrow straight, transverse, deepest laterally and shallow and narrow on

midline; occipital ring narrow (sag.), with its posterior margin strongly bowed forward; anterior sections of facial suture very divergent in front of eyes; palpebral lobes large, crescentic, occupying more than two-thirds of the total glabellar lengh, extending from the occipital furrow to the frontal glabellar lobe; the external cranidial surface is densely but finely tuberculate. Largest observed cranidium 9.2 mm in length.

Material.—Nine cranidia (MLP 34138, 34274–34281) from the Nazareno area, Cordillera Oriental, northwestern Argentina. Upper part of the Santa Rosita Formation (upper Tremadocian).

Remarks.—A very narrow anterior cranidial border, a long preglabellar field, and the particular shape of the occipital ring are the most distinctive features of this taxon. The pygidium illustrated in Figure 9.21 could be conspecific, although there is not complete certainty about this. Until more is known about the librigenae and the post-cephalic exoskeleton of the species, we refer the present specimens to *Apatokephalus* sp.

Superfamily TRINUCLEOIDEA Hawle and Corda, 1847 Family OROMETOPIDAE Hupé, 1955 Genus Pyrimetopus Přibyl and Vaněk, 1980

Type species.—Orometopus pyrifrons Harrington, 1938, from the upper Tremadocian of northwestern Argentina (by original designation).

Pyrimetopus pyrifrons (Harrington, 1938) Figure 9.17, 9.18, 9.22

- 1938 Orometopus pyrifrons HARRINGTON, p. 219, pl. 10, figs. 3–5, 8, 9, 13.
- 1957 Orometopus pyrifrons; HARRINGTON AND LEANZA, p. 197, fig. 105.1–105.7.
- 1980 Pyrimetopus pyrifrons (Harrington); PŘIBYL AND VANĚK, p. 44, text-fig. 13.
- 2003 *Pyrimetopus pyrifrons*; WAISFELD AND VACCARI, pl. 28, figs. 11–15.
- 2008 *Pyrimetopus pyrifrons*; ZEBALLO, ALBANESI AND ORTE-GA, fig. 5.10.

Material.—Eight cranidia (MLP 34206–34209, 34210a, 34211a) from the Nazareno area, Cordillera Oriental, northwestern Argentina. Upper part of the Santa Rosita Formation (upper Tremadocian). Largest observed cranidium 4.2 mm in length.

Remarks.-Přibyl and Vaněk (1980) erected the genus Pyrimetopus to accommodate Orometopus pyrifrons Harrington from the upper Tremadocian of the Argentinian Cordillera Oriental (Harrington, 1938, pl. 10, figs. 3-5, 8, 9, 13; Harrington and Leanza, 1957, fig. 105.1-105.7). Additional material of Pyrimetopus pyrifrons from the type locality (Quebrada de Coquena, west of Purmamarca) was illustrated by Waisfeld and Vaccari (2003, pl. 28, figs. 11-15). A set of small cranidia from Nazareno is characterized by having a clavate, strongly convex and forwardly expanded glabella, which is well defined by deep axial furrows; an occipital ring with rounded posterior margin; a straight, shallow occipital furrow, normal to axis; a proportionately short (sag.) frontal area, lacking border; subparallel anterior branches of facial suture; a moderately narrow (tr.) palpebral area of the fixigena; faint, backwardly oblique eye ridges; and a distally widened (exsag.) posterior border furrow. Some specimens show faint indications of an axial node behind the glabellar midpoint. Thus, these cranidia conform in all fundamental features with the diagnosis of P. pyrifrons.

> Order PHACOPIDA Salter, 1864 Suborder CHEIRURINA Harrington and Leanza, 1957 Family PLIOMERIDAE Raymond, 1913 Genus Rossaspis Harrington, 1957

Type species.—Protopliomerops superciliosa Ross, 1951, from

the Garden City Formation, Idaho, U.S.A. (by original designation).

Rossaspis? sp. Figure 9.23–9.28

- 1937 *Protopliomerops primigenus* (Angelin); HARRING-TON, p. 120, pl. 5, figs. 2, 3.
- 1938 *Protopliomerops primigenus* (Angelin); HARRINGTON, p. 183, pl. 6, figs. 9, 12, 14, 15, 20.

Material.—Two complete specimens, two cephala, seven cranidia, one cephalon and thorax, and five pygidia (MLP 34245–34258) from the Nazareno area, Cordillera Oriental, northwestern Argentina. Upper part of the Santa Rosita Formation (upper Tremadocian).

Remarks.—*Rossaspis*? sp. represents a plomerid trilobite which closely resembles *Rossaspis*? *rossi* (Harrington and Leanza) sensu Waisfeld and Vaccari (2003), from the upper Tremadocian of Potrero de Castillo River, Salta Province (Harrington and Leanza, 1957, fig. 119.3a–119.3d, 119.3f), though the latter slightly differs by showing a subelliptical glabella. The material studied seems to be even closer to, and likely conspecific with, an indeterminate pliomerinae from west of Purmamarca (Quebrada de Coquena; Quebrada de Chalala) originally studied by Harrington (1937, pl. 5, figs. 2, 3; 1938, pl. 6, figs. 9, 12, 14, 15) (Waisfeld and Vaccari, 2003). Since a comprehensive revision of the latter taxon is in preparation (Waisfeld and Vaccari, 2003, p. 319), the present material is left under open nomenclature.

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