

# Diversification of *Asaphellus* Callaway, 1877 (Asaphidae: Trilobita) during the Tremadocian in South West Gondwana (Cordillera Oriental, Argentina)

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## ABSTRACT

*Asaphellus* Callaway, 1877 is the earliest widespread genus of the family Asaphidae Burmeister, 1843, and although its systematics bears several problematic issues, an input to overcome these difficulties has been attempted. Our main focus is a group of strongly effaced *Asaphellus* species from the Cordillera Oriental (NW Argentina), including new material from the Santa Rosita Formation (Furongian-Tremadocian), mainly belonging to Alfarcito and Rupasca members (Quebrada del Arenal, Perchel, Jujuy Province). *Asaphellus* is reconsidered herein in order to restrict some features and discuss others not taken in account before. Moreover, several problematic Argentinean species are revised. The poorly known, but extensively cited, *A. catamarcensis* Kobayashi, 1935 is assessed here upon the type series in order to clarify its taxonomy and previous assignments. A reappraisal of *A. stenorbachis* (Harrington, 1938), another enduring problematic taxon, is proposed. Besides, *A. isabellae* n. sp., a unique species within the genus mainly due to its extreme effacement is defined herein. Other species left in open nomenclature are also described. Regarding local random occurrences in the Furongian, the genus radiated locally from the early Tremadocian (Tr1) onwards, however, taxonomic diversification was not mirrored by the abundance of *Asaphellus* in local communities. From the middle Tremadocian (Tr2) this diversification is associated with an increase in abundance, and even dominance of the taxon in numerous assemblages, further expanding its environmental range into shallower settings. The increase of *Asaphellus* diversity (Tr1- early Tr2) is decoupled from the records of local increase in Asaphidae diversity since the late Tremadocian (Tr3) and Floian, underscoring the complex pattern of diversification at different taxonomic levels.

KEY WORDS  
Asaphidae,  
*Asaphellus*,  
Trilobites,  
Tremadocian,  
Argentina,  
new species.

## RÉSUMÉ

*Diversification d'Asaphellus Callaway, 1878 (Asaphidae: Trilobita) au cours du Trémadocien dans le sud-ouest du Gondwana (Cordillère Orientale, Argentine).*

*Asaphellus* Callaway, 1877 est le plus ancien genre appartenant à la famille Asaphidae Burmeister, 1843 à présenter une importante extension géographique. La présente contribution propose une résolution de plusieurs problèmes de définition au niveau de la systématique de ce groupe. Ce travail se concentre sur un groupe d'espèces ayant une surface très lisse et peu ornementée. Ces *Asaphellus* de la Cordillère Orientale (NO de l'Argentine) incluent du matériel nouveau de la Formation Santa Rosita (Furongien-Trémadocien) et proviennent principalement des membres Alfarcito et Rupasca (Quebrada del Arenal, Perchel, Province de Jujuy). La définition du genre a été modifiée afin de restreindre certains caractères et complétée par d'autres qui n'avaient pas été considérés auparavant. De plus, certaines espèces problématiques d'Argentine ont été revues. Notamment, *A. catamarcensis* Kobayashi, 1935 extrêmement citée mais finalement peu connue, est redécrite ici à partir de son matériel type, afin de clarifier sa taxinomie et les précédentes assignations. Une évaluation de *A. stenorhachis* (Harrington), 1938, autre taxon durablement problématique, est proposée. Une nouvelle espèce, *A. isabelae* n. sp., particulière au sein du genre par son ornementation extrême faible est ici décrite. Enfin, d'autres espèces laissées en nomenclature ouverte sont également présentées. Après une distribution restreinte et morcelée au Furongien, le genre connaît une radiation locale au tout début du Trémadocien basal (Tr1), mais la diversification taxinomique ne se reflète pas par l'abondance des *Asaphellus* dans les communautés locales. À partir du Trémadocien moyen (TR2), cette diversification est associée à une augmentation de l'abondance et même d'une domination de ce genre dans de nombreux assemblages, plusieurs espèces développant une tolérance environnementale aux milieux peu profonds. L'augmentation de la diversité des *Asaphellus* (Tr1-Tr2 inférieur) est découplée de l'augmentation locale des enregistrements de la diversité des Asaphidae depuis le Trémadocien supérieur (Tr3) et le Floien, soulignant un modèle complexe de diversification à différents niveaux taxinomiques.

## MOTS CLÉS

Asaphidae,  
*Asaphellus*,  
Trilobites,  
Trémadocien,  
Argentine,  
espèce nouvelle.

## INTRODUCTION

The systematics of the Family Asaphidae has long proved to be problematic, perhaps as a result of a number of different effaced homeomorphs, occupying similar ecozones in different palaeocontinents (Turvey 2007). Convergence at different taxonomic levels obscures the understanding of natural relationships, hence, and despite recent efforts (Bell & Braddy 2012), the phylogeny of this complex group is far from being resolved.

Among the early representatives of the Asaphidae, *Asaphellus* Callaway, 1877 is an important genus in helping to resolve the diversification of the family, and as currently conceived is remarkably rich in species, with nearly 70 (e.g., Harrington 1938; Harrington & Leanza 1957; Courtessole *et al.* 1985; Zhou & Zhang 1985; Fortey & Owens 1987, 1991, 1992; Peng 1990; Vidal 1998). Moreover, *Asaphellus* is also one of the earliest asaphids with a worldwide distribution, whereas most early genera such as *Golasaphus* Shergold, 1971, *Griphasaphus* Öpik, 1967, *Norinia* Troedsson, 1937 were geographically restricted (Pärnaste & Bergström 2013). *Asaphellus* is also particularly interesting due to its long stratigraphic range, originating in the Furongian and persisting until the Darrivillian (Fortey & Owens 1987). However, its wide geographic distribution and extended stratigraphical range may well be a result of taxonomic uncertainties, mainly caused by its simple and conservative morphology, in addition to a variable degree of effacement. Furthermore, *Asaphellus* might be considered a taxonomic “wastebasket” form (*sensu* Plotnick & Wagner

2006), being a very large and heterogeneous genus, characterized by quite general morphologies and wide temporal and geographic distributions. The lack of diagnostic autapomorphic features, and abundant homoplasies, mostly result in a weakly supported taxonomy. The scenario is complicated even more by the fact that previous workers (e.g., Kobayashi 1935, Harrington 1938, Harrington and Leanza 1957) used to refer poorly preserved Tremadocian asaphids to *Asaphellus*, resulting either in many very weakly based species, or left in open nomenclature.

In the context of the evolutionary trilobite fauna proposed by Adrain *et al.* (1998), the importance of this family is paramount, as it played a central role in the development of the Ibx II fauna, which behaved as a cohort, declining since the middle Ordovician and disappearing at the end of Ordovician during a mass extinction event (Adrain *et al.* 1998). Hence, the study of the diversification of this family throughout regional and global records is fundamental for the comprehension of trilobite evolution during the Early Ordovician (Adrain *et al.* 2004).

Asaphids have been widely documented in the Furongian-Ordovician of the Cordillera Oriental (Harrington 1938; Harrington & Leanza 1957; Tortello & Rao 2000; Tortello *et al.* 2002; Aceñolaza *et al.* 2003; Waisfeld & Vaccari 2003; Tortello & Aceñolaza 2010); however, a detailed taxonomic study is still pending. In this contribution, we revise *Asaphellus* with special focus on the species present in the early and middle Tremadocian successions of the Argentinean Cordillera Oriental. We also revise the type material of *Asaphellus cata-*



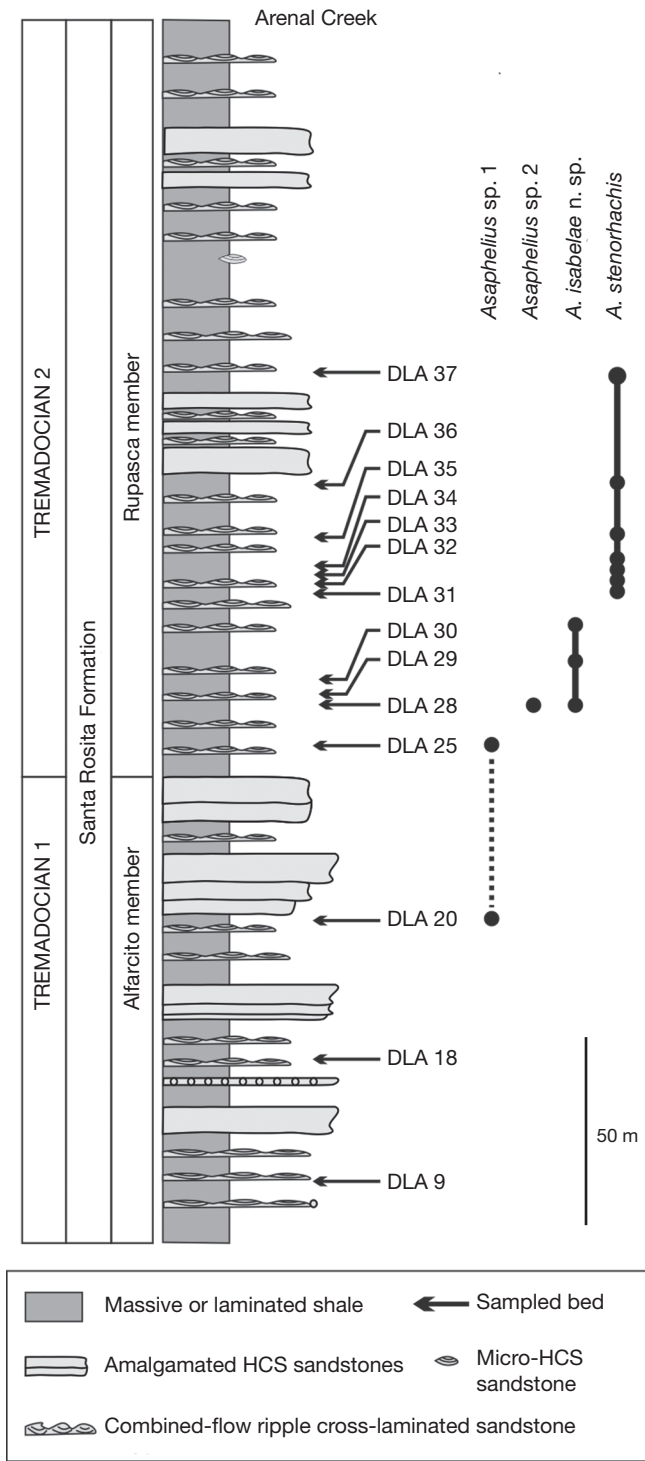


FIG. 2. — Stratigraphic log of Alfarcito and Rupasca members in the Quebrada del Arenal, with detailed position of the fossil samples and the stratigraphic ranges of the studied taxa.

basis of the records of the *Paltodus deltifer pristinus* conodont subzone (Zeballos & Albanesi 2012) and the *Kainella teiichii* Zone in its lower part, and the *Bienvilleia tetragonalis* Zone in its upper part (Vaccari *et al.* 2010).

The succession exposed in the Quebrada del Arenal is about 300 m thick. Both members are represented by several coarsen-

ing up cycles ranging from lower offshore to lower shoreface settings (Balseiro *et al.* 2011a). In other localities, however, the Rupasca Member is represented by deeper environments ranging from lower offshore to open shelf.

The type material of *Asaphellus catamarcensis* re-illustrated herein originates in the Pascha-Incamayo area (Angosto de Pascha, Quebrada del Toro, 40 km to the northwest of Salta). The Cambrian-Ordovician succession exposed in this area is stratigraphically complex, and lateral relationships with coeval successions of the Cordillera Oriental are not fully understood. Astini (2003) revised local stratigraphy, which included Sococha, Lampazar, Cardonal, Devendeus, Saladillo, and Parcha formations, the latter four units being of Tremadocian age.

The stratigraphical provenance of the type material of *A. catamarcensis* is unknown, although evidence based on other trilobite taxa (discussed below) point to the possibility that it is from the Cardonal Formation. This unit is composed of meter-scale sandy packages with frequent tidal structures alternating with debris flows and conglomerates. Vaccari *et al.* (2010) suggested an early Tremadocian to early-middle Tremadocian age for this unit.

#### SPATIO-TEMPORAL DISTRIBUTION OF *ASAPHELLUS* IN THE CORDILLERA ORIENTAL

The *Asaphellus* species described herein represent a distinct group of largely effaced forms ranging in age from the latest early Tremadocian (Tr1) to middle Tremadocian (Tr2). However, the history of the genus in the basin can be traced further back; *A. cf. A. aspinus* Robison & Pantoja-Alor, 1968, *A. convexus* Benedetto, 1977, and *Asaphellus* sp. from the Lampazar Formation (*Parabolina (N.) frequens argentina* Zone) were recorded (Tortello & Esteban 2003; Esteban & Tortello 2007) as the oldest known *Asaphellus* species in the Furongian successions, exposed on the western flank of the Cordillera Oriental. In the early Tremadocian (Tr1), four *Asaphellus* species occurred within the *Kainella meridionalis* Zone (*sensu* Vaccari *et al.* 2010). These include: *Asaphellus catamarcensis*, which, as revised herein, is present in the Pascha-Incamayo area; *A. isabelae* n. sp. from Quebrada del Arenal, also recognized in the Cardonal Formation; *Asaphellus* sp. recently reported by Tortello *et al.* (2013) from the Alfarcito Member (Quebrada Moya), and *Asaphellus* sp. 1 described below. Apart from the latter records, we report here four species occurring in the middle Tremadocian (Tr2), into the *Kainella teiichii* and *Bienvilleia tetragonalis* zones (Fig. 3). According to our taxonomic revision, *Asaphellus* sp. 1 has been widely reported in several localities of the Cordillera Oriental, and its range extends to the lower part of the Tr2 (*Kainella teiichii* Zone). *A. isabelae* n. sp. is abundant in the Rupasca Member (Quebrada del Arenal), with a restricted vertical range in the creek, constrained to the upper part of the *K. teiichii* Zone. *A. stenorbachis* is recognized in several localities of the Alfarcito-Tilcara area, associated with trilobites of the *Bienvilleia tetragonalis* Zone. The third species reported here in open nomenclature (*Asaphellus* sp. 2) is so far restricted to the *K. teiichii* Zone.

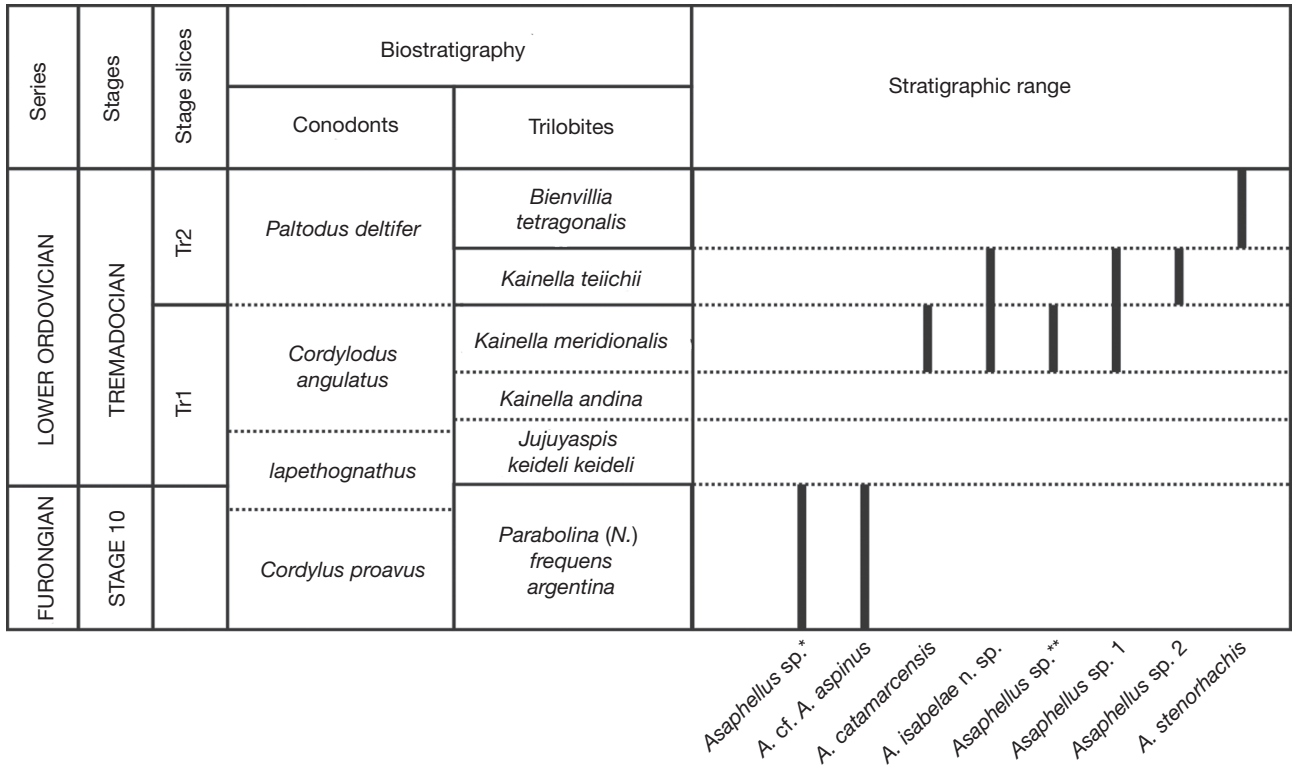


FIG. 3. — Biostratigraphic scheme for Cordillera Oriental and ranges of the different *Asaphellus* Callaway, 1877 species recognized in the basin from *Parabolina (N.) frequens argentina* Zone to *Bienvillia tetragonalis* Zone. Biostratigraphy modified from Albanesi *et al.* (2008) and Vaccari *et al.* (2010). *Asaphellus* cf. *aspinus* in Tortello & Esteban (2003); *Asaphellus* sp. in: \*, Tortello & Esteban 2007; \*\*, Tortello *et al.* 2013.

*Asaphellus* diversified during the Tr1 with at least four species, a diversity that was maintained during the Tr2 (Fig. 3). This pattern of rise in the number of species, however, is not mirrored by the abundance of *Asaphellus* in local communities. *Asaphellus* was a rare element in Cambrian communities of Cordillera Oriental (Balseiro *et al.* 2011b), where it is always noted in low abundance (Fig. 4). During Tr1, the genus was still a minor component of local communities; however, at the beginning of the Tr2 there was a sharp rise in the abundance of *Asaphellus* in local communities. In this interval, *Asaphellus* became a common genus, and was occasionally the dominant one in shallower environments, reaching its greatest abundance in upper offshore and lower shoreface facies, but it was almost absent in deep-water (Fig. 5).

From a temporal viewpoint, the decoupling between the diversity of *Asaphellus* and its abundance in local communities is quite interesting. In palaeoecological literature, taxonomic diversity is usually used as a proxy for abundance, implying that if a given taxon diversifies, its abundance should also increase (Adrain *et al.* 2000). One possible explanation for such decoupling of our data could be that the rather high diversity of *Asaphellus* during Tr1 does not reflect the pattern in local communities on a regional scale, because different *Asaphellus* species rarely, if ever, co-occur in local communities. Only after a regional increase in diversity during the Tr1, the genus reached a high abundance in local communities in Tr2.

This pattern of diversity and abundance at generic level cannot be rearranged to higher taxonomic (family) levels. In the case of *Asaphellus*, the genus is the only member of the Asaphidae during Tr1 and early Tr2. Only during late Tr2 and Tr3, Asaphidae diversified on a regional scale (Waisfeld & Astini 2003; Balseiro *et al.* 2010; Meroi *et al.* 2012). Hence, at family level, Asaphidae first reached a high abundance in local communities (in the early Tr2), and only later the family diversified; reaching 11 genera (in the late Tr2 to the Tr3) (Meroi *et al.* 2012). This is the opposite pattern compared to *Asaphellus*, thus, this example highlights the complex relationship between diversity and abundance at different taxonomic levels.

From an environmental viewpoint, the high abundance of *Asaphellus* in upper offshore and lower shoreface facies is also of significance; Balseiro *et al.* (2011b) discussed the rarity of *Asaphellus* in the Furongian of the Cordillera Oriental and showed that the genus was restricted to intermediate environments. Current data indicate that the rise in abundance in Tr2 is also related to such environments because *Asaphellus* dominates local communities only in environments between normal and storm wave base (Fig. 5). Indeed, we can now confidently state that the abundance of *Asaphellus* in deeper environments is significantly delayed compared to shallow settings, because in Tr2 when the genus was already quite frequent in shallow environments, it also was still virtually absent in deeper settings (Balseiro *et al.* 2011a).

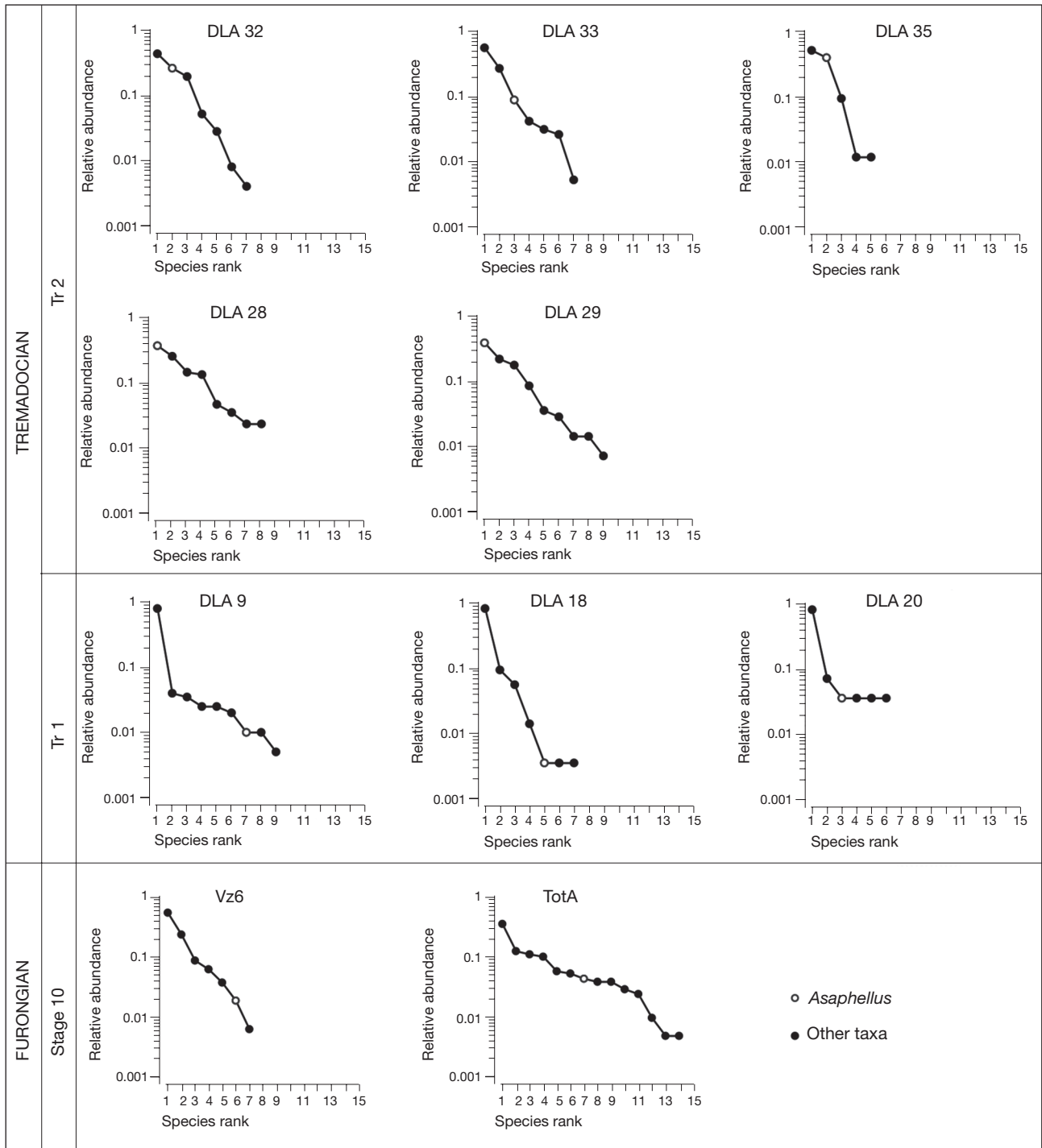


FIG. 4. — Trilobite rank-ordered abundance distributions for different samples from the offshore facies in Cordillera Oriental. Relative abundance is logged on the y axis, and taxa are ordered according to their relative abundance on the x axis. *Asaphellus* Callaway, 1877 is indicated in white. DLA stands for the Quebrada del Arenal (Tremadocian), Vz stands for the Quebrada Vizcacha (Cambrian Stage 10), and TotA stands for the Quebrada Totora (Cambrian Stage 10). The data, nomenclature, and sample location for the Cambrian outcrops come from Balseiro *et al.* (2011b).

REMARKS ON *ASAPHELLUS ISABELAE* N. SP.

*Asaphellus isabelae* n. sp. represents a rare case within *Asaphellus*, as it possesses an extremely thin cuticle. This feature is possible to be observed by the visual detection of rock rugosity on the surface of the specimens. Although most

of our studied fossils are internal moulds, a few of them preserve fragments of the cuticle; therefore, for the purpose of estimating its cuticle thickness, six thin sections were made in specimens of *A. isabelae* n. sp. and *A. stenorrhachis*. Measurements were taken using a metric ocular

microscope; these were confirmed by checking them on the photographs, using the program Image J software. The results reveal that *A. isabelae* n. sp. has a cuticle thickness of 10 µm on average, compared with 19 µm in *A. stenorhachis*. These values are an average, since cuticle thickness varies by about 2-3 µm along the sclerites, even between specimens of the same species (see Fortey & Wilmot 1991). In contrast with what Wilmot (1988) observed in proetids, the effacement increases and the thickness of the cuticle decreases throughout ontogeny, becoming extremely thin in larger specimens.

According to Fortey & Wilmot (1991), the thickness of the trilobite cuticle may be correlated with sea depth, following an environmental gradient with progressively thicker cuticles in increasingly inshore sites. Under this assumption, and considering its very thin cuticle, we would expect to find *A. isabelae* n. sp. in deeper environments. However, contrary to such expectations, this species reaches its higher abundances in rather shallow and oxygenated environments (upper offshore). Interestingly, the case of *Asaphellus isabelae* n. sp. does not seem to be an exception in the Tremadocian of the Cordillera Oriental, because the entire bathymetric gradient is dominated by trilobites with thin cuticles such as olenids (Balseiro *et al.* 2011a). Therefore, this feature cannot be understood only as a consequence of the environment, at least for trilobites from the Cordillera Oriental. The amount of environmental influence on the phenotype for this character needs to be further studied, and perhaps no general assumption within Trilobita can be made.

Despite the fact that a thin cuticle could have made the individuals more exposed to predators, such a disadvantage was apparently not of critical importance for *A. isabelae* n. sp., perhaps some other trait provided defense from predators. Considering that this species attained a very large size, between 10-15 cm long (sag.) in adults, it was the largest trilobite known from the Cordillera Oriental during Tr1 and lower Tr2, a possible explanation could be that it reached a “size refugia” against predators (Paine 1976; Richards & Leighton 2012), thus avoiding predation because of its large size. Such a benefit from size alone could imply that investing in a thicker cuticle did not have a clear advantage, in terms of increasing fitness, due to its high physiological cost (Flenner *et al.* 2009). There are two lines of evidence that support our hypothesis: 1) all the other trilobites that co-occur with *A. isabelae* n. sp. are smaller and have a thicker cuticle; this would indicate that smaller trilobites could reach higher fitness from thicker cuticles; and 2) the cuticle of *A. isabelae* n. sp. became thinner throughout ontogeny, which might suggest that predatory forces decreased as this species grew in size. Hence, it seems to be a trade-off among size, cuticle thickness, and fitness. Other explanations could be also erected, for instance, a shallow burrowing life-style or a pigmented cuticle could provide camouflage or shelter as protection from predators, and therefore a thin cuticle would be possible. Unfortunately available data are not enough to test these last two hypotheses.

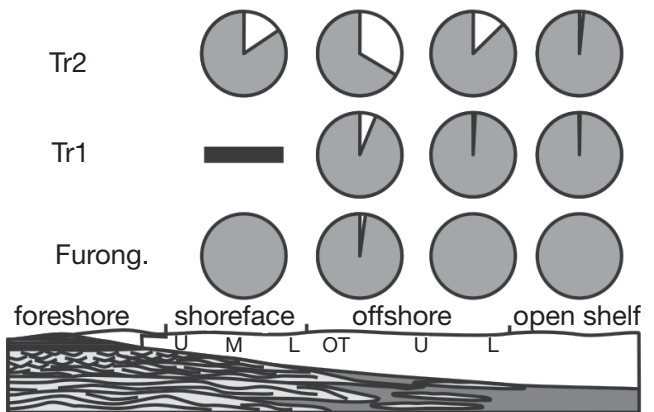


FIG. 5. — Trends in the relative abundance of *Asaphellus* Callaway, 1877 across different depositional environments in Cordillera Oriental. Each pie-chart is based on the mean relative abundance of all samples coming from the given environment. *Asaphellus* abundance is indicated in white and other genera in grey. The Tr1 shoreface is not recorded. Data from Balseiro *et al.* (2011a, b) and Balseiro & Waisfeld (2014).

## SYSTEMATIC PALAEOONTOLOGY

The specimens described herein are housed in the palaeontological collection of the Centro de Investigaciones Paleobiológicas (CIPAL) of the Universidad Nacional de Córdoba (Córdoba, Argentina), prefix CEGH-UNC. The type material of *Asaphellus catamarcensis* is housed in the National Museum of Natural History, Smithsonian Institution (Washington DC, United States), prefix USNM-PAL.

Family ASAPHIDAE Burmeister, 1843  
Subfamily ISOTELINAE Angelin, 1854

Genus *Asaphellus* Callaway, 1877

*Asaphelloides* Kobayashi, 1937: 497.

*Hemigyraspis* Raymond, 1910: 41.

*Megalaspidella* Kobayashi, 1937: 499, 500.

*Plesiomegalaspis* Thorall, 1946: unnamed pages.

TYPE SPECIES. — *Asaphus homfrayi* Salter, 1866, by original designation, Lower Ordovician, upper Tremadocian Stage of Porthmadog, Gwynedd, North Wales, UK.

## REMARKS

Asaphids' taxonomy is a problematic field into systematic, mainly because effacement is regarded as one of the most polyphyletic characters among trilobites (Fortey & Shergold 1984; Turvey 2007). In addition, there are many different isotelina taxa in which effacement appears as a morphological trend (e.g., Jaanusson 1959; Nielsen 1995; Turvey 2007, among others).

It is important to note that, as *Asaphellus* has become a “waste-basket” taxon for the Early Ordovician (mostly Tremadocian) asaphids, an excessive expansion of its diagnosis exacerbates

the problem even more (Fortey & Owens 1987). However, some species indicate a wide range of intrageneric variation. Among them, *A. whittardi* (Bates, 1969) from South Wales (Fortey & Owens 1987) exhibits a remarkably prominently segmented pygidium for the genus, with 10 well-defined axial rings, 8 pairs of ribs, and visible interpleural furrows. Besides, its glabella is bounded by shallow but well impressed axial furrows. At the other extreme of morphological variability within the genus, in such species as *A. yanbeensis* Yin *in* Yin & Shanji, 1978 (see Peng 1990) and *A. isabellae* n. sp., whose segmentation is nearly completely obscured by effacement, with the preglabellar furrow as an exception, because of it remains visible as a shallow furrow or a change in slope. Between these extremes, several species show very lightly impressed but discernible furrows, as in *A. stenorbachis*, or a diverse effacement, either of the cranidium or the pygidium. In this latter respect, *A. cf. A. trinodosus* Chang, 1949 from the Tremadocian of Tasmania (Jell & Stait 1985), has an effaced cranidium but a distinct pygidial axis bounded by well-defined axial furrows. In addition, there are other cases contributing to the variability of the genus. For instance, usually the pygidial axis decreases unevenly in width and tapers backwards, however, *A. lugneensis* Courtessole *et al.*, 1985 and *A. fezouataensis* Vidal, 1998 are examples where the pygidial axis decreases in width evenly.

*Asaphellus acutululus* Zhou & Zhang, 1978 from China has the entire hypostoma covered with terrace ridges (see Zhou & Zhang 1985: pl. 10, figs 4, 5), a feature that is also present in *A. fezouataensis* (Vidal 1998: pl. 1, figs 2, 3), *A. tataensis* Vidal, 1998 (Vidal 1998: pl. 5, fig. 2), and *A. inflatus* Lu, 1959 (see Peng 1990: pl. 6, fig. 8). Thus, although a terraced lateral border of hypostoma is common for the genus, a hypostoma fully covered by terraced ridges seems also a relatively frequent feature. Another consideration concerns the inner margin of pygidial border, which is not subparallel to the margin in *A. stenorbachis*, which condition is not common within the genus. Finally, there are examples of anomalous features as for instance in *A. stubbsi* Fortey, 2009 from the Lower Fezouata Formation, where the genal spines curve outwards at genal angles before curving backwards distally, the anterior facial suture meets the anterior border without forming an ogive, and it shows rounded, forward-facing pleural extremities in its thorax. Thus, despite the apparent lack of characters of *Asaphellus* due to variable effacement, there is still a wide range of morphological variety.

Some species of *Asaphellus* have been erected upon poorly preserved material or upon juvenile specimens which are in need of revision. Among them, *A. nanchuanensis* Lu, 1975 is based upon an incomplete cranidium, a juvenile pygidium and a hypostoma. The same applies to *A. inflatus longus* Lu, 1975, which was based upon very small juvenile material. Hutchison & Ingham (1967) defined *Asaphoon pithogastron* upon very small specimens (about 4 mm maximum widths of both pygidium and cranidium). Later, Owens *et al.* (1982: pl. 2, fig. g) and Fortey & Owens (1991) suggested that this material should be a young *Asaphellus* meraspid. However, we suggest that the meraspid material figured in Owens *et al.*

(1982: pl. 2, fig. g) and Hutchison & Ingham (1967: pl. 8, figs 11, 13), which includes the holotype, does not belong to *Asaphellus* meraspid. Only the pygidium of Hutchison & Ingham (1967: pl. 8, fig. 14) may be considered as a meraspid or an early holaspid stage of *Asaphellus*. The specimens of Hutchison & Ingham (1967: pl. 8, fig. 13) and Owens *et al.* (1982: pl. 2, fig. g), differ mainly in the pygidial border. On the other hand, the pygidium shown in Hutchison & Ingham (1967: pl. 8, fig. 13) differs from the specimen illustrated by them (1967: pl. 8, fig. 14) in several respects, and likely they do not belong to the same species. Moreover, *Asaphoon pithogastron* might belong to a genus different from *Asaphellus*.

In *A. fezouataensis* and *Asaphellus cf. fezouataensis* Vidal, 1998; the pygidial border is almost indistinct, just slightly indicated by a change in slope, whereas the cephalon exhibits a well-defined border. Moreover, *A. inflatus* (see Lu 1975: pl. 14, fig. 17, and Peng 1990) exhibits no border, therefore, in all respects, this species seems closer to *Paramegalaspis* Thoral, 1935 (Jaanusson 1956; Peng 1990) or *Notopeltis* Harrington & Leanza, 1957 rather than *Asaphellus*.

Although *Asaphellus* includes a wide morphological variety, some assigned species do not comply with the general features of the generic diagnosis (Fortey & Owens 1987): for instance, *A. coreanicus* Kobayashi, 1934 (see Choi *et al.* 2003) is closer to *Hunnebergia* Tjernvik, 1956; whereas *Asaphellus tomkokensis* Kobayashi, 1934 in Choi *et al.* (2003), *A. communis* Robison & Pantoja-Alor, 1968, and *A. pricensis* Legg, 1976 are closer to *Golasaphus* Shergold, 1971. Other species such as *Asaphellus* sp. (Courtessole *et al.* 1985), and *A. cuervoae* Corbacho & Lopez-Soriano, 2012, also do not match the diagnosis of *Asaphellus* (Fortey & Owens 1987). In addition, *A. toledanus* Rabano, 1990 (see also Pillet 1992) resembles *Pseudomegalaspis* Jaanusson, 1953 mainly in the cranidial and pygidial doublure (see Rabano 1990: fig. 4). However, the border of the cephalon and pygidium, and the hypostoma features of *A. toledanus* resemble *Asaphellus*. Hence, the generic status of this species requires a revision.

*Asaphellus catamarcensis* Kobayashi, 1935  
(Fig. 6)

*Asaphellus? catamarcensis* Kobayashi, 1935: 65, pl. 11, figs 11-15; *non Asaphellus jujuanus* Harrington, 1937: 115; *non Asaphellus (Asaphelloides) americanus* Kobayashi, 1937: 14; *non* Kobayashi, 1937a: 497; *non Asaphellus catamarcensis* Kobayashi *in* Harrington, 1938: 246; *non* Harrington & Leanza, 1957: 147-151; *non* Tortello & Rao, 2000: 72; *non* Tortello, Esteban & Aceñolaza, 2002: 137; *non* Aceñolaza, Aráoz, Vergel, Tortello & Nieva, 2003: 23-28; *non* Waisfeld & Vaccari, 2003: 319; *non* Tortello & Aceñolaza, 2010: 162.

LECTOTYPE (HERE DESIGNATED). — One pygidium without precise stratigraphic horizon, from Angosto de Pascha, Pascha-Incamayo area, Salta Province, USNM-PAL94136D (Fig. 6A).

MATERIAL. — The type material illustrated by Kobayashi (1935: pl. 9, figs 11-15) housed in the Smithsonian Museum (USNM-PAL94136) comprises one cranidium, one free cheek, and two pygidia. This is refigured herein, except for the cranidium, which is lost, all from the type locality.



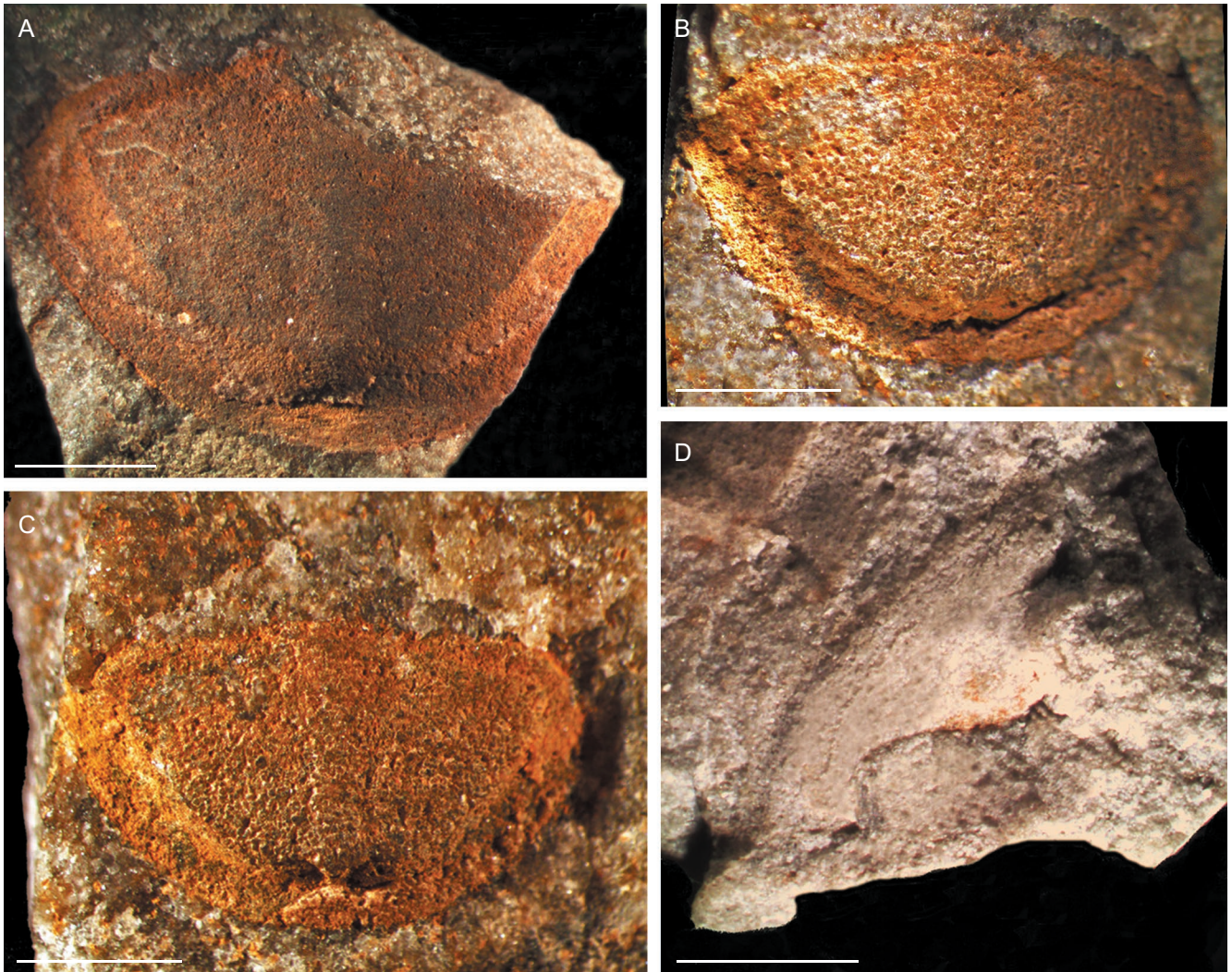


FIG. 6. — Type specimens of *Asaphellus catamarcensis* Kobayashi, 1935 (USNM 94136), Angosto de Pascha, Pascha-Incamayo area: **A**, lectotype in dorsal view (USNM 94136D); **B**, **C**, pygidium in dorsal view (USNM 94136C); **D**, free cheek in dorsal view (USNM 94136B). Scale bars: A, D, 0.5 cm; B, C, 0.25 cm.

#### REMARKS

*A. catamarcensis* is a much-quoted *Asaphellus* species from the Argentine Cordillera Oriental that has been apparently recognized in several different localities, and employed either in local or international comparisons. However, this species constitutes a remarkable nomenclatural problem and is in need of revision. It was erected by Kobayashi (1935) and placed with doubt within *Asaphellus*, no diagnosis and description but only general comparisons were provided. So far, the main problems are the incomplete and poorly preserved type material, and the range of specimens showing a wide spectrum of variability that have been assigned to *A. catamarcensis* since 1935 (e.g., Harrington & Leanza 1957; Tortello & Rao 2000; Tortello *et al.* 2002; Waisfeld & Vaccari 2003; Tortello & Aceñolaza 2010). In addition, this scenario becomes even more complex when the stratigraphic unclarity of the type locality is regarded.

The stratigraphic provenance of *A. catamarcensis* is uncertain. Kobayashi (1935) explicitly noted that he received the

fossils for study without locality details, except for the label (Praire Catamarca, i.e. Angosto de Pascha). According to Kobayashi (1935: 60), these fossils, preserved in a “light brown quartzite”, included *Kainella meridionalis* Kobayashi, 1935; *Kainella conica* Kobayashi, 1935; *Kainella lata* Kobayashi, 1935; *Leptoplastides argentinensis* (Kobayashi 1935), and *Asaphellus catamarcensis* (Kobayashi 1935). Since Kobayashi’s work, *A. catamarcensis* has been considered a common member of the “*Kainella* Fauna”. Waisfeld & Vaccari (2003) and Vaccari *et al.* (2010) revised *K. meridionalis* and reinterpreted the definition of the “*Kainella* Fauna”. According to these revisions, *K. meridionalis* is restricted to some boulders of the Cardonal Formation, whereas the “*Kainella* Fauna” may occur either in the reworked boulders within debris flow deposits of the Cardonal and the Devendeus formations, or in the lower heterolithic levels of the Saladillo Formation.

From the reworked boulders of the Cardonal Formation, Waisfeld & Vaccari (2003) and Vaccari *et al.* (2010) reported at least two of the species listed by Kobayashi (1935): *Kainella*

*meridionalis* and “*Kainella*” *conica*. Hence, it is highly probable that *A. catamarcensis* comes also from the boulders included in this unit. Alternatively, and less likely, *A. catamarcensis* might come from the debris flow deposits of the Devendeus Formation. The record of another *Kainella* species (*K. cf. K. teiichii*) in a boulder of coarse quartzitic sandstone of the Devendeus Formation (cf. Vaccari & Waisfeld 2010: figs 9.1-9.7) suggests that the provenance of *A. catamarcensis* from this unit cannot be ruled out.

Unfortunately the holotype cranidium figured by Kobayashi (1935: pl. 11, fig. 11) is lost, hence, a possible comparison of this sclerite is restricted to Kobayashi’s drawing. We re-illustrate here a free cheek and two pygidia from the type series. The material is fragmentary and poorly preserved. The free cheek is subtriangular and the genal spine is broken off, however, a medium size might be inferred considering the width of the base. Within the type material, we are uncertain whether the two pygidia are conspecific, and because one of them is a juvenile, we have selected the specimen illustrated in Fig. 6A herein as the lectotype of *A. catamarcensis*. The latter is semicircular, convex, with a well-marked, anteriorly wide (tr.), and slightly funnel-shaped axis. The pygidium has a remarkably wide border (sag., exag., and tr.), being among the widest known in the genus; the doublure is wider than the border and strongly terraced.

Harrington (1938) and Harrington & Leanza (1957) redescribed the species, and gave a diagnosis, but expanding the concept of *A. catamarcensis* including a wide array of features exhibited by different morphotypes from more than ten localities (from Salta, Jujuy, and La Rioja provinces) ranging in age from the Furongian to the late Tremadocian (cf. Waisfeld & Vaccari 2003). Also Hoel (1999) mentioned two morphological variants, one younger than the other, both assigned to *A. catamarcensis* among the illustrations provided by Harrington & Leanza (1957). The incomplete nature of some material largely prevents accurate comparisons and assignments, however, the shape and definition of the axis, the effacement of the axial rings and pleural furrows, and the wide border of the pygidium selected as the lectotype pygidium suggest that none of the specimens illustrated by these authors can be considered to be conspecific with *A. catamarcensis*.

Harrington (1938: pl. 13, figs 3-6, 8-10, 16) referred several specimens from different localities to *A. catamarcensis*: the material illustrated in his figures 3 and 8 comes from the Quebrada de Iruya and it is possibly associated with *K. meridionalis* (according to the revision by Vaccari & Waisfeld 2010). The pygidium in Figure 3 resembles *A. stenorbachis* here defined, mainly in the indistinct segmentation and morphology of the border. The latter characters distinguish it from those of the lectotype of *A. catamarcensis*. The hipostomes (Harrington 1938: pl. 13, figs 4, 6) are from Angosto de Pascha, the type locality of *A. catamarcensis*, the one illustrated in Fig. 6 does not appear to belong to an *Asaphellus* species. The rest of the pictures assigned to *A. catamarcensis* in Harrington (1938: pl. 13) match with new species under study from Quebrada de Humacha and

also some of them were discussed recently in Tortello & Esteban (2014).

*Megalaspis americana* (*Asaphellus* (*Asaphelloides*) *americanus* Hoek in Steinman & Hoek, 1912) *sensu* Kobayashi (1937) is a poorly known species from Cuesta de Erquis (Tarija Department, Bolivia). Harrington (1938: pl. 13, figs 19, 20) assigned two distorted pygidia from Río Volcancito (Sierra de Famatina, La Rioja) to *Asaphellus* (*Asaphelloides*) *americanus* and Harrington & Leanza (1957: figs 65.3, 5) referred the same specimens to *A. catamarcensis* considering that the Bolivian species and *A. catamarcensis* were synonymous. Among other features, the well-impressed segmentation of the pleural fields suggests that the material from Río Volcancito is not conspecific with *A. catamarcensis*, whereas the validity of *Megalaspis americana* requires further corroboration.

The material illustrated by Harrington & Leanza (1957: figs 65.7, 8) from Quebrada de Los Canchos (Caldera Department, Salta) was the basis for the concept of *A. catamarcensis* of Tortello & Rao (2000), Tortello *et al.* (2002), Aceñolaza *et al.* (2003), and Tortello & Aceñolaza (2010). The outline, shape of the axis and the border, and segmentation of the pygidia do not conform to the lectotype of *A. catamarcensis*. Instead, this material is referred here to *Asaphellus* sp. 1 (Fig. 7C-F) from the Quebrada del Arenal, Rupasca Member, *Kainella teiichii* Zone (Vaccari *et al.* 2010). In addition, Tortello & Aceñolaza (2010) also referred to *A. catamarcensis* two cranidia that the authors considered very close to the type cranidium illustrated by Kobayashi (1935). The cranidia from Abra de Zenta (Tortello & Aceñolaza 2010; Fig. 4A, B) shows features such as a strongly tapering glabella with a pronounced lateral constriction at midlength (exsag.), and a quite deeply impressed preglabellar furrow. Despite the fragmentary nature of the cranidium figured by Kobayashi (1935) that prevents detailed comparisons, neither the lateral constriction nor the deeply impressed preglabellar furrow are visible. Hence, we do not agree with the assignment of these sclerites to *A. catamarcensis*. In addition, the pygidium in Harrington (1938: pl. 13, fig. 10) from Angostura de Parcha is identical to that of *Asaphellus* sp. 1 reported herein.

Several of the specimens referred to *A. catamarcensis* by Harrington & Leanza (1957: figs 65.2, 4, 6; 64.4, 5, 6) come from the upper Tremadocian successions of the Quebrada de Coquena, Quebrada de Chalala, and Río Santa Victoria. They are apparently close to a new species that it is now under revision by the authors from the upper middle Tremadocian successions exposed in Quebrada de Humacha and Quebrada de Chalala, and also close to the recent published asaphids in Tortello & Esteban (2014).

Likewise, the pygidia from Río Volcancito (La Rioja, Furongian, *Parabolina* (*N.*) *frequens argentina* Zone, Harrington & Leanza 1957: figs 65.3) are distinguished from that of *A. catamarcensis* in a fairly segmented, shorter, and wider axis. Finally, the pygidia from Quebrada Colorada (Iruya, *K. meridionalis* Zone), referred to *A. catamarcensis* by Harrington & Leanza (1957: pl. 64.1, 65. 1), differ from the lectotype pygidium in a more well-segmented axis and narrower border.

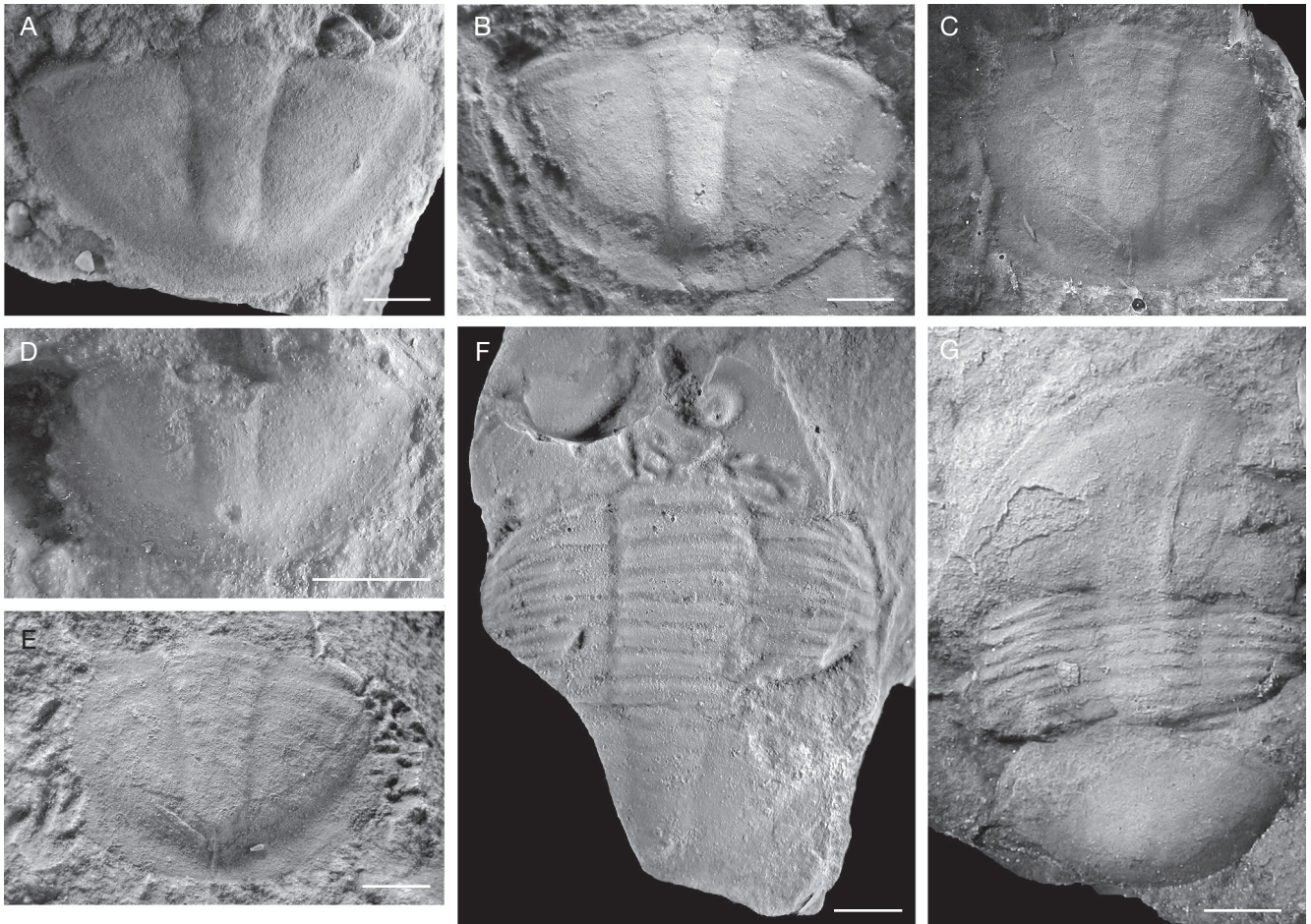


FIG. 7. — **A, B**, *Asaphellus* sp. 2, pygidia in dorsal view: **A**, CEGH-UNC 25763; **B**, CEGH-UNC 25764; **C-F**, *Asaphellus* sp. 1, CEGH-UNC 25765–25768; **C**, pygidium, latex cast, dorsal view, CEGH-UNC 25765; **D**, pygidium, dorsal view, CEGH-UNC 25766; **E**, pygidium, dorsal view, CEGH-UNC 25765; **F**, pygidium and thorax, dorsal view, CEGH-UNC 25767; **G**, *A. isabelae* n. sp., articulated juvenile, latex cast, dorsal view, CEGH-UNC 25762. Scale bars: A-F, 0.5 cm; G, 0.25 cm. All specimens come from the Quebrada del Arenal, Santa Rosita Formation, Santa Victoria Group: A, B, G, from DLA 28; C, E, from DLA 25; D, F, from DLA 20.

Waisfeld & Vaccari (2003: pl. 22, figs 3–6) assigned to *A. catamarcensis* some material derived from a sandstone boulder of the Cardonal Formation in the Pascha-Incamayo region. This boulder comes from the alleged type locality of Kobayashi's material and contains *K. meridionalis*. The pygidium figured by Waisfeld & Vaccari (2003: pl. 22, figs 4, 5) is similar to the lectotype in several respects, however, the axis is less-defined and more parallel sided; the border is incomplete but appears to be narrower than the lectotype. The pygidium of Waisfeld & Vaccari (2003: pl. 22, fig. 4, 5) is reinterpreted here as *A. isabelae* n. sp.

*Asaphellus stenorbachis* (Harrington, 1938)  
(Figs 8A–M, 9A)

*Illaenus stenorbachis* Harrington, 1938: 182 pl. 5, fig. 18.

*Illaenopsis stenorbachis* – Harrington & Leanza 1957: 183, figs 93.3; non figs 93.1, 2, 4.

HOLOTYPE. — CPBA (collection of the UBA – Universidad Nacional de Buenos Aires) no. 4165 (Harrington 1938: pl. 5, fig. 18; Harrington & Leanza 1957: fig. 93.3), Quebrada de Rupasca, Alfarcito region, Rupasca Member, Santa Rosita Formation, Santa Victoria Group, lower Tr2.

MATERIAL. — 57 fragmentary specimens including 3 partially complete individuals, 21 cranidia, 27 pygidia, 15 free cheeks, 8 specimens with thoracic segments, and 3 hypostomas. Illustrated material CEGH-UNC 25736–25748.

OCCURRENCE AND AGE. — Quebrada del Arenal (levels from DLA 31 to DLA 37). Quebrada Rupasca, and Angosto de Chucalezna, J. Til.-2 in Harrington & Leanza (1957). Quebrada Colorada and Angosto de Chucalezna, S. Iru.4 in Harrington (1938). Rupasca Member, Santa Rosita Formation, Santa Victoria Group. Middle Tremadocian (Tr2), *B. tetragonalis* Zone.

EMENDED DIAGNOSIS. — Exoskeleton elongated and elliptical, about 70% longer than wide. Cranidium smooth, glabella almost indistinct laterally, preglabellar furrow ill-defined, convex forward. Genal spines widely based, and short (about 20% of free cheek maximum length). Pygidial border flat to slightly concave, wider anteriorly than posteromedially, barely defined axis in the anterior third of the pygidium.

DESCRIPTION

Cephalon semicircular, slightly convex, wide and depressed frontal area without differentiated anterior border, 1.8 times wider than long and 40% of the total body length, wide (tr.) posterolateral projection. Lateral border broad and well-

marked by a change in slope, posterior border defined by a wide (exsag.), shallow, and transverse posterior border furrow.

Facial suture isoteliform, anterior branch slightly divergent in front of eyes, meeting anteriorly in a tiny ogive; posterior branch sigmoidal, runs outwards and backwards behind the eyes, and slightly inwards cutting posterior border close to the genal angle.

Cranidium almost flat; palpebral, preocular, and postocular areas barely discernible. Preglabellar area flat, defined by a gentle change in slope, reaching about 15% of cranial maximum length (sag.). Wide posterior area of fixigena (exag., tr.). Glabella smooth, defined by indistinct axial furrows, with no differential convexity compared with the rest of the cranidium (Fig. 8A, B); occipital ring reduced, poorly defined by a shallow furrow, slightly convex forward, set close to posterior margin. Median node located at about 1/5 of the cranial maximum length from posterior margin.

Palpebral lobe of medium size, flat, broadly arcuate, located at cranial midlength, palpebral furrow nearly effaced; eye length (exag.)/cranial maximum length (sag.) about 0.22 (n = 7).

Free cheek subtriangular, broadly arcuate external margin; doublure subparallel to the margin, lateral border defined by broad and shallow furrow, diminishing in width and fading out towards genal angle, depressed with respect to genal field, border narrow and weakly convex. Genal spine broad-based, and short (about 20% of the librigena length), strongly tapering and directed straight backwards (Fig. 8B, E).

Hypostoma elongate (sag.) and suboval, with rounded posterior margin; wide posterolateral borders with strong and closely spaced terrace lines. Median body gently convex, longer than wide, posterior lobe crescentic, maculae sharply impressed, transverse, and deep; anterior wings wide (tr.) and subrounded.

Thorax with 8 segments, about the same length (sag.) as the pygidium, decreasing slightly in width (tr.) backwards. Axis weakly convex, about 35% of the total width (tr.), defined by well impressed and slightly backwards-tapering axial furrows; articulating furrow narrow and deep; articulating half-ring short (tr.). Pleural region moderately wide (about 65% of thoracic maximum width); pleural furrow deeper and wider medially, runs toward anterior margin of pleura, shallower and narrower adaxially, lightly impressed abaxially, anterior pleural band slightly wider (exag.) than posterior pleural band. Pleural extremities obliquely truncated and facing backwards, well-marked pleural fulcra.

Pygidium slightly convex, about 55% wider than long. Border flat, well-defined by a shallow furrow and a change in slope, decreasing progressively in width backwards, narrowest posteromedially. Anterolateral corner of pygidium (articulating facet) subtriangular. Inner margin of doublure subparallel to the margin. Fine and closely spaced terrace lines visible on doublure (on exfoliated material). Axis gently convex (tr., sag.), about 20% of pygidial width, bounded by weak axial furrows, indistinct posteriorly (Fig. 8E, G, K), almost effaced in some specimens (Fig. 8L, J, L, M), evenly tapering backwards, posterior tip slightly raised, terminat-

ing in advance of border furrow. Articulating half-ring of even width, defined by a transverse furrow. 2-3 anterior axial rings slightly impressed in specimens preserved in mudstone, defined by narrow and shallow ring furrows, up to eight faint rings visible in some specimens (mostly internal moulds).

Pleural field wide, subtriangular; inner part gently convex (tr.), then steeply curving down to border furrow; anterior half-rib well defined by distinct furrow, wider medially, abruptly terminating at border furrow, remainder ribs and furrows faint or indistinct.

#### REMARKS

Harrington (1938) erected *Iliaenus stenorbachis* on the basis of a single pygidium with four attached thoracic segments from the Quebrada Rupasca (Alfarcito area). Later, Harrington & Leanza (1957: 183, 184) included in this species additional material from other localities of the Cordillera Oriental (Quebrada Lampazar and Quebrada Pingüiyal), and accommodated it in *Iliaenopsis* Salter, 1867. Waisfeld & Vaccari (2003) noted that the holotype is an asaphid, and hence the name *stenorbachis* should be restricted to it. Although the holotype (Harrington 1938: pl. 5, fig. 18; Harrington & Leanza 1957: fig. 93.3) is slightly distorted, the *Asaphellus* material from the Quebrada del Arenal studied herein closely resembles it in an identical pygidial outline, mostly indistinct axial and pleural furrows (except for the first pleural furrow), and the uneven width of the border, wider laterally than posteromedially. Hence, the material from Quebrada del Arenal is referred herein to *Asaphellus stenorbachis*. *Asaphellus stenorbachis* is similar to the type species *A. homfrayi* Salter, 1866 from the late Tremadocian Garth Hill and Shineton Shale formations (North Wales and Shropshire, UK) (Lake 1942; Fortey & Owens 1991) in the general effacement of the exoskeleton and the anterior course of the facial suture with a similar variation range between the anterior and posterior branches (90-110°). However, in *A. stenorbachis* the glabella is less defined laterally, the preglabellar field is narrower (sag., exsag.), the postocular fixigena is wider (tr.), the genal spine is shorter, the pygidial border is of uneven width (sag., exsag., tr.) and finally, the pygidial axis is less distinct and less raised above the pleural field.

Several species of *Asaphellus* are known from north western Argentina. *A. catamarcensis*, herein restricted to the type material, distinguishes from *A. stenorbachis* in the pygidial outline, wider border, well-defined axis, and more segmented pleural fields.

*Asaphellus jujuanus* Harrington, 1937 is a poorly known species from the upper Tremadocian of the Quebrada Coquena, Jujuy Province (Harrington 1937, 1938; Harrington & Leanza 1957: figs 66, 6-12; Waisfeld & Vaccari 2003). It differs from *A. stenorbachis* mainly in the cranial features, such as a narrower (exsag.) and shorter (tr.) posterior fixigenal area, larger eyes, and more distinct axial furrows defining the glabella.

*Asaphellus kayseri* (Kobayashi, 1937) is another Argentinean species in need of revision; its age and stratigraphic position

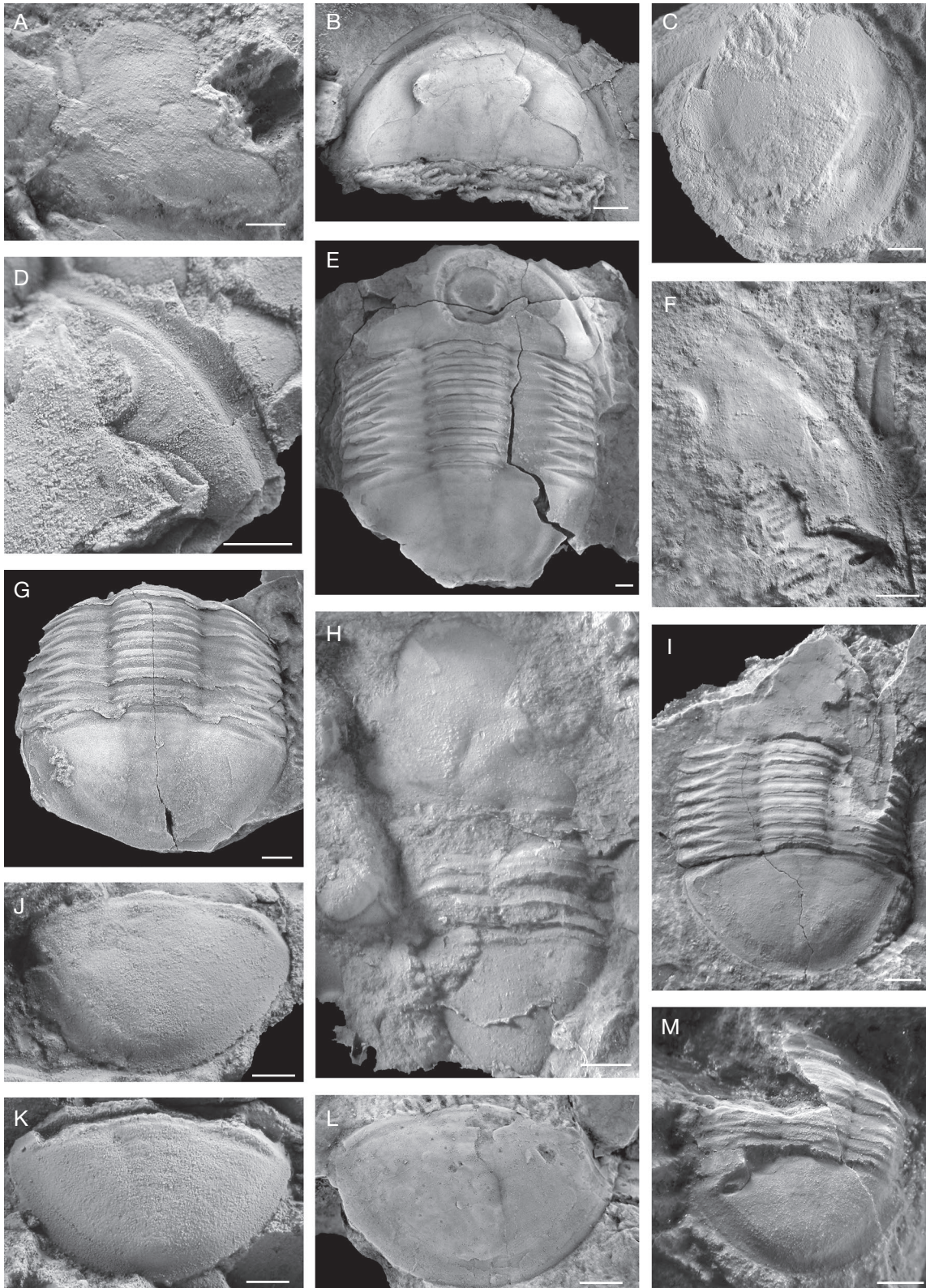


FIG. 8. — *Asaphellus stenorhachis* (Harrington, 1938): **A**, cranium, dorsal view, CEGH-UNC 25736; **B**, cephalon, latex cast, dorsal view, CEGH-UNC 25737; **C**, hypostoma, dorsal view, CEGH-UNC 25738; **D**, right free cheek, dorsal view, CEGH-UNC 25739; **E**, dorsal view of a complete specimen, CEGH-UNC 25740; **F**, right free cheek, dorsal view, CEGH-UNC 25741; **G**, pygidium and articulated thorax, dorsal view, CEGH-UNC 25742; **H**, cranium with incomplete thorax and fragmentary pygidium, latex cast, dorsal view, CEGH-UNC 25743; **I**, cranium with articulated thorax and pygidium, dorsal view, CEGH-UNC 25744; **J-L**, pygidia, dorsal view; **J**, CEGH-UNC 25745; **K**, CEGH-UNC 25746; **L**, CEGH-UNC 25747; **M**, pygidium and fragmentary articulated thorax, dorsal view, CEGH-UNC 25748. **A**, **D**, **J**, **K**, are preserved in coquinas. All specimens come from Quebrada del Arenal, Santa Rosita Formation, Santa Victoria Group; **A-C**, **E**, **G-I**, **L**, come from DLA 32; **D**, **J**, **K**, from DLA 37; **F**, from DLA 34; **M**, from DLA 31. Scale bars: **B**, **E-G**, **I**, **L**, 0.5 cm; **A**, **C**, **D**, **H**, **J**, **K**, **M**, 0.25 cm.

are uncertain (cf. Waisfeld & Vaccari 2003: 320). *A. kayseri* (*sensu* Harrington & Leanza 1957: figs 75, 1-9) differs from *A. stenorhachis* in a well impressed axial glabellar furrows, subparallel anterior sections of the facial suture, and a better segmented pygidial axis and pleural fields.

Finally, the general effacement of the glabella, course of the anterior facial suture, pygidial outline and pygidial furrows of *A. stenorhachis* clearly distinguishes it from *A. riojanus* Harrington & Leanza, 1957 from the Furongian of the Famatina Range (Volcancito Formation; Tortello & Esteban 2007), mainly in the course of the anterior suture and the general outline of the pygidium.

The pygidium referred by Harrington (1938: pl. 13, fig. 3) to *A. catamarcensis* from Quebrada Colorada (Iruya area) resembles that of *A. stenorhachis* in several aspects, such as the general outline, degree of effacement, and shape of the border. It is possibly conspecific with *A. stenorhachis*, but better preserved material is required in order to be certain of this assignment.

Suárez Soruco (1975: pl. 2, figs 1, 2) defined *A. palquiensis* from the *Kainella andina* Zone, lower Tremadocian (Tr1) of South Bolivia (Vaccari *et al.* 2010). *A. palquiensis* differs from *A. stenorhachis* in a much longer genal spines, a better defined preglabellar area, and stronger segmentation of the pygidium.

Among other non-Argentinean species of *Asaphellus*, Robison & Pantoja-Alor (1968) described three species from the Tiñú Formation (Tremadocian, Oaxaca, Mexico); of these, only *A. artus* bears some resemblance to *A. stenorhachis*. The smoothness and posteromedian decrease in width of the pygidium of the latter, resembles the external moulds of the Mexican species (Robison & Pantoja-Alor 1968: pl. 99, figs 1-6), however, the exfoliated material of *A. artus* displays a well-defined and segmented pygidial axis, and distinctly furrowed pleural fields. Besides, *A. artus* has larger eyes, a well-defined frontal area, and larger genal spines.

Another similar species is *A. cf. graffi* Thorol, 1946 (Fortey & Owens 1992: fig. 4) from the Habberley Formation (late Tremadocian, Welsh basin, UK), however, the outline of the pygidium, the well-defined axis, and a broader border clearly distinguishes it from *A. stenorhachis*.

A group of Tremadocian species of *Asaphellus* from China described as *A. inflatus* Lu, 1959; *A. tungtzuensis* Sheng, 1958; and *A. yanheensis* Yin *in* Yin & Shanji, 1978) from the Nantsinkwan Formation of the Yangtze Platform (Peng 1990) display a very faint segmentation in the pygidium, thus resembling *A. stenorhachis*, however, the hypostoma of the latter has a non-terraced median body and more marked cephalic and pygidial borders defined by a change in slope.

The nature of the pygidial border of *A. acutulus* Zhou & Zhang, 1985 from the Tremadocian of the Jilin region, north-east China, closely resembles that of *A. stenorhachis* (particularly the specimens illustrated by Zhou & Zhang 1985: pl. 10, figs 7, 8), nonetheless, considering several differences in the cranial features, the general outline of the pygidium, the axis that is not funnel-shaped and decreases steadily backwards in width, distinguishes this from *A. stenorhachis*.

### *Asaphellus isabelae* n. sp.

(Figs 7G; 9B; 10)

*Asaphellus catamarcensis* – Waisfeld & Vaccari 2003: pl. 22, fig. 5; *non* Kobayashi, 1935.

HOLOTYPE. — CEGH-UNC 25751 (Fig. 10E). Type horizon DLA 28, lower Tr2, Quebrada del Arenal creek, lower Rupasca Member, Santa Rosita Formation, Santa Victoria Group.

MATERIAL. — 140 fragmentary specimens, including 1 partly complete individual, 20 cranidia, 48 pygidia, 28 free cheeks, 7 specimens with thoracic segments, and 12 hypostomas. Illustrated material CEGH-UNC 25749-25761.

OCCURRENCE AND AGE. — DLA 28, DLA 29, DLA 30, lower part of the Rupasca Member, Quebrada del Arenal, *K. teiichii* Zone, middle Tremadocian (Tr2); reworked boulder of the Cardonal Formation, Pascha-Incamayo area, *K. meridionalis* Zone, lower Tremadocian (Tr1).

ETYMOLOGY. — After FR Meroi Arcerito's grandmother Isabel Olivares.

### DIAGNOSIS

Flat and large species of *Asaphellus*. Cuticle very thin, high degree of smoothness and effacement, except for the lightly impressed preglabellar furrow, pygidial axis indistinct.

### DESCRIPTION

Exoskeleton large, subelliptical and flat. Isopygous with flat cephalic and pygidial borders. Cephalon semicircular, with wide border, diminishing in width towards the genal angle. Doublure subparallel to the margin. Cranidium depressed or flat; axial furrow indistinct. Glabella almost indistinguishable, faint traces of convex anterior preglabellar furrow in some specimens (Fig. 10E, F). Wide and subtriangular (exsag.) posterolateral projection. Posterior border and occipital ring reduced, poorly defined, and very close to posterior margin. Palpebral lobes of medium size, located at cranial midlength. Anterior section of facial suture diverges gently forwards, bends smoothly adaxially, and converges medially to form an obtuse point sagittally in an ogive. Posterior section of facial suture curves backwards, bends downwards and slightly inwards at the level of the posterior border.

Free cheek long and relatively narrow, subtriangular with rounded external margin. Broad-based and long genal spine (55% of the total librigena length), slightly divergent from external margin.

Hypostoma elongated, oval in outline (sag.), with rounded posterior margin. Wide posterolateral border, with fine terraced lines. Median body widest (tr.) at midlength, anterior lobe convex (sag., tr.), posterior lobe short (sag.), crescentic, maculae transverse, sharply impressed.

Thorax incompletely known; almost indistinguishable from *A. stenorhachis* but less convex. Axis weakly convex, about 35% of the total width (tr.), defined by well impressed and slightly backward-tapering furrows; articulating furrow narrow and deep; articulating half-ring short (tr.). Pleural region moderately wide (about 65% of thoracic maximum width); pleural furrow deeper and wider medially, runs toward the anterior margin of pleura, shallower and narrower adaxially, lightly

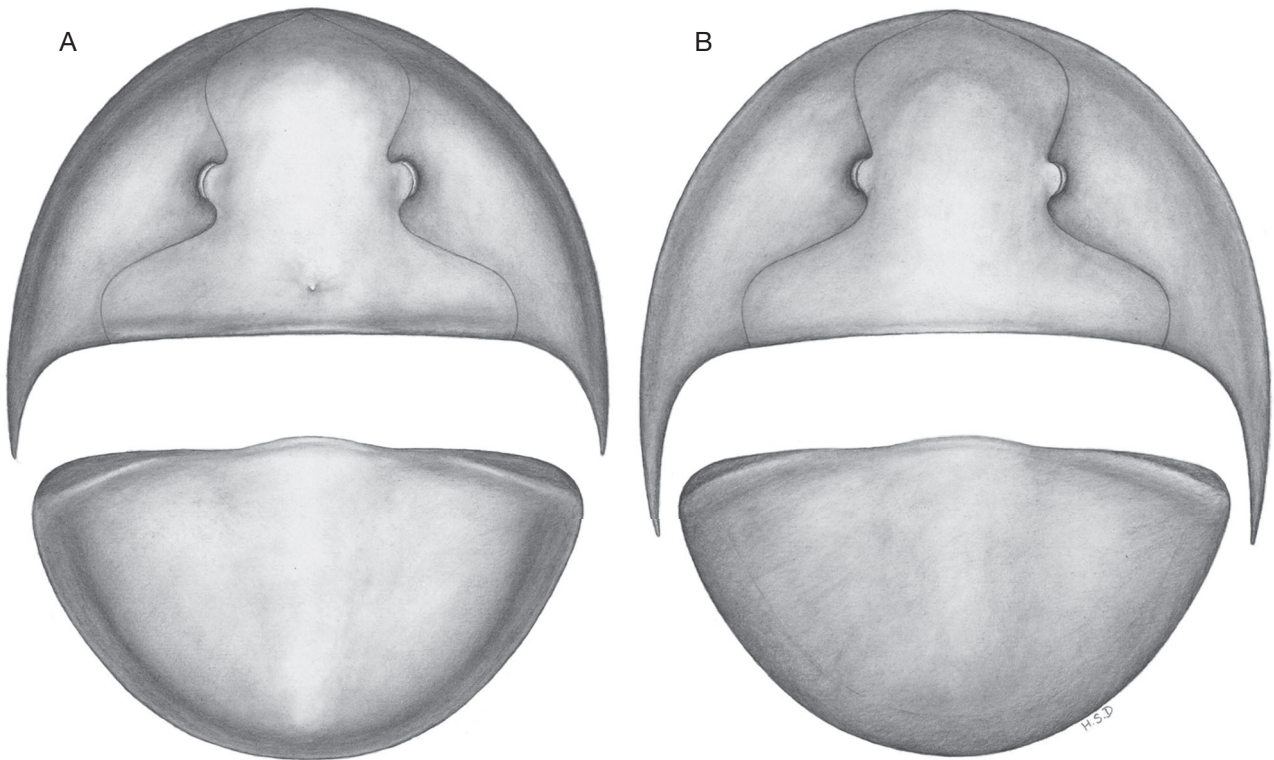


FIG. 9. — **A**, reconstruction of *A. stenorhachis* (Harrington, 1938); **B**, reconstruction of *A. isabelae* n. sp. Drawing by Santiago Druetta.

impressed abaxially. Pleural extremities obliquely truncated and backward-facing, faint marked pleural fulcra.

Pygidium of very low convexity, 57% wider than long ( $n=14$ ), border and border furrow indistinct. Doublure evenly wide, about 10% length of pygidium ( $n = 11$ ), subparallel to the pygidial margin along its extension. Anterior half-ring narrow (sag.), slightly convex forward. Articulating facet subtriangular, long (tr.). Anterior half-rib defined by narrow and shallow pleural furrow, remaining pleural furrows and ribs not visible.

#### REMARKS

*Asaphellus isabelae* n. sp. appears to represent an extreme in effacement, flatness, and reduction of the cuticle thickness within the group. The latter character is noteworthy, as even the sediment roughness is reproduced on the surface of the exoskeleton. Despite effacement complicates taxonomy, the extreme smoothness and flatness might be considered as an autoapomorphic character for this species.

Such a combination of characters has seldom been recorded in other *Asaphellus* species. For example, *Asaphellus yanheensis* Yin in Yin & Shanji, 1978 (Peng 1990: pl. 7, figs 6-13) from the Nantsinkwan Formation (Tremadocian, NW Hunan, China) exhibits a thorough effacement, with blurred furrows either in the cranidia or pygidia. Though the pygidium of the Chinese species exhibits great resemblance to *A. isabelae* n. sp., the cranidium of the former differs in several significant respects, such as a better defined anterior ogive, a median node that is placed more forwardly, a subparallel preocular facial sutures, and postocular sutures running straight backwards.

Other species also show effacement either on the cranidium or the pygidium. *Asaphellus tungtzuensis* (Sheng 1958) (Peng 1990: pl. 8, figs 1, 2) from the Tremadocian of north west Hunan resembles *A. isabelae* n. sp. in the general effacement of the cranidium, however, the pygidium shows traces of axial furrows delimiting a weak axis along its length. The cranidium of *Asaphellus* cf. *A. trinodosus* Chang, 1949 (Jell & Stait 1985) from the Florentine Valley Formation (Tremadocian, Tasmania) is largely effaced; however, the pygidial axial furrows distinctly outline a convex axis. Among the Argentinean species of *Asaphellus*, only *A. stenorhachis* (see above) exhibits a general effacement though not to the degree of that of *A. isabelae* n. sp. *Asaphellus stenorhachis* differs from the new species in the higher convexity mainly of the pygidium, a better definition of the pygidial axis in its anterior third, and the presence of some furrows, lightly impressed but discernible (for instance the border furrows in the cephalon and pygidium).

#### *Asaphellus* sp. 1 (Fig. 7C-F)

*Asaphellus catamarcensis* – Harrington 1938: 246, pl. 13, fig. 10. non pl. 13, figs 3-6, 8, 9. — Harrington & Leanza 1957: 147-151, figs 65.7, 65.8; non figs 65.1-6; 64.1-6. — Tortello & Rao 2000: 72, 73, figs 3T-V. — Tortello, Esteban & Aceñolaza 2002: 137, figs 5C, D. — Aceñolaza, Aráoz, Vergel, Tortello & Nieva 2003: 23-28, pl. 1A; non pl. 1B. — Tortello & Aceñolaza 2010: 162, figs 4 D-H; non figs 4 A-C, I.

**MATERIAL.** — 4 pygidia; 1 fragmentary pygidium with attached thorax and free cheek. CEGH-UNC 25765-25767.

**OCCURRENCE AND AGE.** — Horizon DLA 20, DLA 25. Upper Alfarcito Member and lower Rupasca Member of the Santa Rosita Formation, Santa Victoria Group. Late Tr1 and early Tr2.

#### REMARKS

This species is scanty in our samples; it differs from all others described herein in a semicircular outline, a well-defined wide axis, with up to five rings visible on some specimens, a well-defined border, and a wide subparallel doublure (on average about twice wider than the border). Specimens of this morphotype have been referred to *A. catamarcensis* by different authors, among them, one pygidium illustrated by Harrington (1938: pl. 13, fig. 10) from Angosto de Parcha (Pascha-Incamayo area, Salta), and two pygidia figured by Harrington & Leanza (1957: fig. 65.7, 8) from Sierra de Mojotoro (Quebrada de los Canchos, Caldera Department, Salta). Later, Tortello & Rao (2000), Tortello *et al.* (2002), Aceñolaza *et al.* (2003), and Tortello & Aceñolaza (2010) accommodated the material from Angosto de Lampazar (Pascha-Incamayo area) and Abra de Zenta in *A. catamarcensis*, based on the resemblance with the pygidia from Sierra de Mojotoro that Harrington & Leanza (1957: pl. 65, figs 7, 8) referred to that species. However, the type pygidium of *A. catamarcensis* reillustrated herein differs from these previous assignments (see *A. catamarcensis* remarks). In addition, the cranidium refer in Tortello & Aceñolaza (2010: figs 4a, b) doubtfully could be assigned to *Asaphellus* (see *A. catamarcensis* remarks). Thus, we refer the material mentioned above tentatively to *Asaphellus* sp. 1. Nonetheless, additional material would be required in order to be certain about the generic assignment of this material.

*Asaphellus* sp. 1 resembles *A. verus* Zhou *in* Chen, Zhou, Zou, Lin, Yang, Wang, Qi, Wang & Lu, 1980, from the Hebei Province, China (Zhou & Fortey 1986: pl. 8, figs 9-24, pls 9, 1-3, 6) mainly in the pygidial outline and proportions, and the shape of the axis, however, in the Chinese species the axis is better segmented along its length and the pleural fields are wider (tr.).

#### *Asaphellus* sp. 2 (Fig. 7A, B)

**MATERIAL.** — Two pygidia CEGH-UNC 25763, 25764.

**OCCURRENCE AND AGE.** — Horizon DLA 28. Lower part of the Rupasca Member, Quebrada del Arenal, *K. teiichii* Zone, Santa Rosita Formation, Santa Victoria Group, middle Tremadocian (Tr2).

#### DESCRIPTION

Pygidium semicircular, 60% wider than long, gently convex with a well-defined, flat border of uniform width. Axis defined by narrow and well impressed axial furrows, about 18% of maximum pygidial width, raised above pleural fields, increasingly elevated above pleurae posteriorly, tapering backwards and funnel shaped, with rounded posterior tip, terminating

in advance of border furrow; three anterior axial rings barely visible. Broad (tr.) and gently convex pleural field, with faint indication of 3-4 pleural furrows, inner part gently convex (tr.), steeply sloping down to border abaxially. Inner margin of doublure subparallel to the pygidial margin.

#### REMARKS

*Asaphellus* sp. 2 resembles *A. catamarcensis* (as revised herein) mainly in the definition of the axis and in being well raised above pleural field. However, the pygidial outline is 61% wider than long, the axis is more parallel-sided, the border is wider, and the doublure widens posteromedially (lying well in advance of the posterior tip of the axis).

The well-defined and raised pygidial axis and the evenly wide border clearly distinguish this material from *A. stenorhachis* and *A. isabelae* n. sp. The latter occurs in the same beds in the Quebrada del Arenal. Also, *Asaphellus* sp. 2 differs from *A. kayseri* (Kobayashi, 1937) (Waisfeld & Vaccari 2003) in a poorly segmented axis and pleural field, and a wider border.

The Argentinean material resembles *Asaphellus?* sp. from the Saint-Chinean Formation, lower Tremadocian, Montagne Noire (Vidal 1996), however, *Asaphellus* sp. 2 exhibits a narrower border and doublure. Also, *Asaphellus* sp. 2 is close to *Asaphellus* sp. 1 (herein) and *A. verus* (Zhou & Fortey 1986, Upper Yehli Formation, Tremadocian, Hebei province, China), however, *Asaphellus* sp. 2 differs from both in a more marked, more convex, and less funnel-shaped axis. In addition, the doublure is subparallel to the border in *Asaphellus* sp. 2, instead of slightly subtriangular as in *Asaphellus* sp. 1.

#### CONCLUSIONS

*Asaphellus isabelae* n. sp. occurs in the *Kainella teiichii* and *Kainella meridionalis* Zones, and *A. stenorhachis* in the *Bienvillia tetragonalis* Zone, providing new information on asaphids diversity during the transition between zones within the Rupasca Member.

A faintly marked glabella lacking furrows or a change in slope, and the absence of pygidial furrows, makes *A. isabelae* n. sp. distinctive, and this is an apparent consequence of extreme effacement. We interpret this feature as an autapomorphy of this lineage within *Asaphellus*.

Remarkably; a thin cuticle, not reported until now in previous papers on *Asaphellus*, constitutes a rare case of study; this attribute could be due to low predatory pressure, perhaps as a result of size refugia reached by adults.

Apparently, the *Asaphellus* radiation is positively related to a wider bathymetric range, due to its occurrence in various bathymetric niches. In addition, locally in *Asaphellus*, first an increase in diversity is observed and subsequently an increase in abundance. Perhaps, during Tr1, *Asaphellus* does not reflect the pattern in diversity of local communities but at regional scale. This pattern of diversity and abundance at the generic level, however, cannot be extrapolated to higher taxonomic ranks (family).



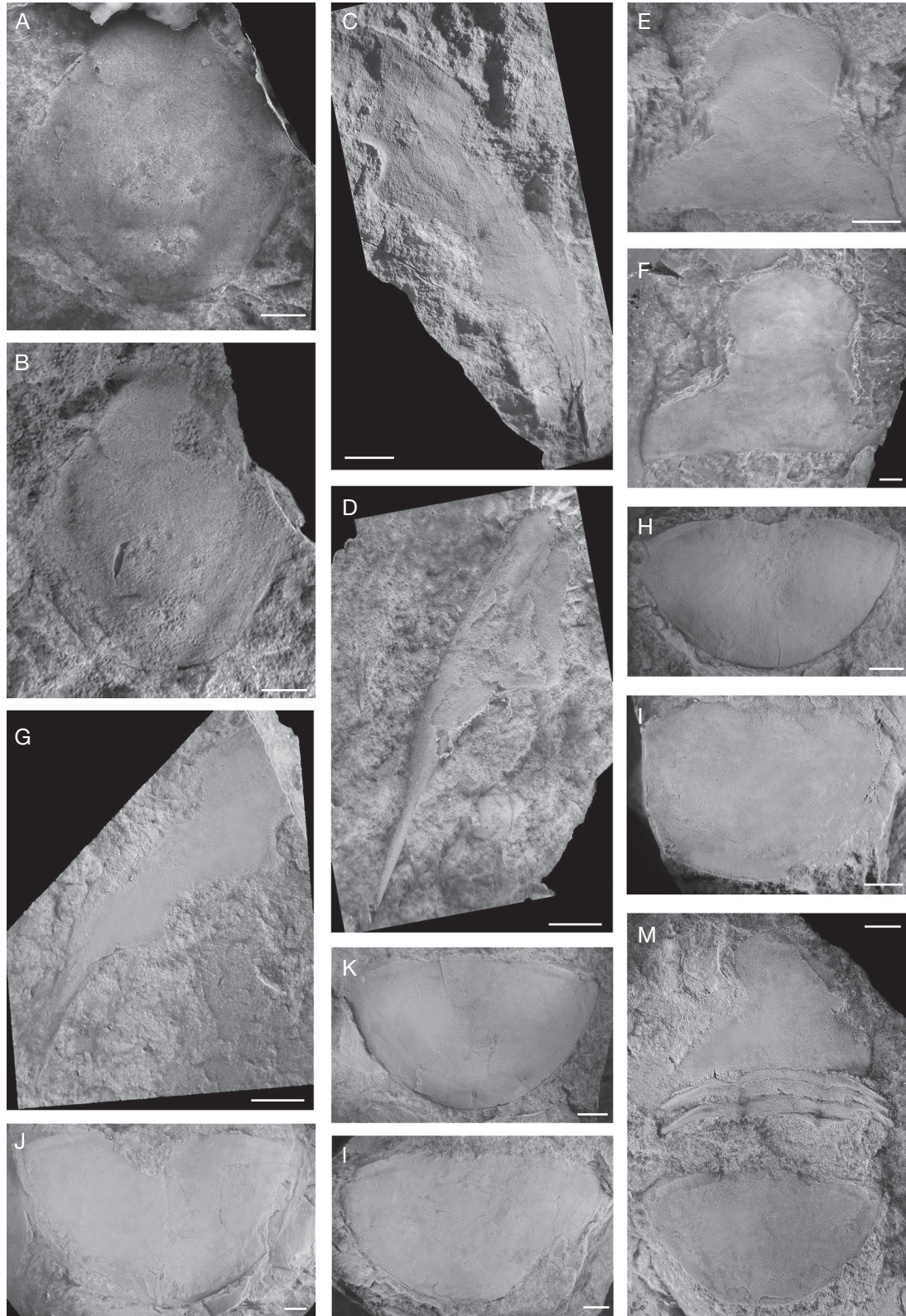


FIG. 10. — *Asaphellus isabelae* n. sp.: **A**, hypostoma, latex cast, dorsal view, CEGH-UNC 25749; **B**, hypostoma, dorsal view, CEGH-UNC 25752; **C**, right free cheek, dorsal view, CEGH-UNC 25750; **D**, left free cheek, latex cast, dorsal view, CEGH-UNC 25756; **E**, holotype cranidium, dorsal view, CEGH-UNC 25751; **F**, cranidium, latex cast, dorsal view, CEGH-UNC 25753; **G**, left free cheek, dorsal view, CEGH-UNC 25754; **H-J, L, pygidia, dorsal view; H**, CEGH-UNC 25755; **I**, CEGH-UNC 25758; **J**, CEGH-UNC 25757; **L**, CEGH-UNC 25760; **K**, pygidium, latex cast, dorsal view, CEGH-UNC 25759; **M**, almost complete moult, dorsal view, CEGH-UNC 25761. All specimens come from the Quebrada del Arenal, Santa Rosita Formation, Santa Victoria Group; **A, C-E, G-J, L, M**, come from DLA 28; **B, F, K**, come from DLA 30. Scale bars: **A, B**, 0.25 cm; **C-M**, 0.5 cm.

*A. catamarcensis* has had nomenclatural problems. Since 1957, the taxon has encompassed a wide range of forms with high morphological variety. Here we attempt to preserve nomenclatural stability of the taxon, restricting it to the type series of Kobayashi (1935).

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