

The Middle Ordovician conodonts *Eoplacognathus robustus* Bergström and *E. lindstroemi* (Hamar): Taxonomy and apparatus reconstruction

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ABSTRACT. The Middle-Upper Ordovician Ponón Trehué Formation cropping out in the San Rafael Block (Argentina) provided a large collection of conodonts which have been published years ago. The species *Eoplacognathus robustus* and *Eoplacognathus lindstroemi* recovered from these strata have been revised and restudied. In this contribution we describe M and S elements that were assigned previously to *Baltoniodus prevariabilis* and *Baltoniodus variabilis* as belonging to the *E. robustus* and *E. lindstroemi* apparatuses. The morphological characters of the P, S and M elements as part of these late *Eoplacognathus* apparatus were analyzed and support the proposal of a new reconstruction of it. We have compared this apparatus with the *Baltoniodus* apparatus and suggest the inclusion of the *Eoplacognathus* genus into the Balognathidae family. The new architecture of the *Eoplacognathus* apparatus is comparable to the genus *Lenodus*. This analysis improves the knowledge about this index conodont group allowing a new insight on the evolution, phylogeny and paleobiology of this lineage.

Keywords: Cuyania, Ordovician, *Eoplacognathus*, Taxonomy.

RESUMEN: Los Conodontes *Eoplacognathus robustus* Bergström y *E. lindstroemi* (Hamar) del Ordovícico Medio: taxonomía y reconstrucción de sus aparatos. La Formación Ponón Trehué del Ordovícico Medio-Superior que aflora en el Bloque de San Rafael (Argentina) ha provisto una gran colección de conodontes que se han dado a conocer a través de los años. Las especies *Eoplacognathus robustus* y *Eoplacognathus lindstroemi* recuperadas de estos estratos han sido revisadas y reestudiadas. En esta contribución describimos los elementos M y S que se asignaron previamente a *Baltoniodus prevariabilis* y *Baltoniodus variabilis* como pertenecientes a los aparatos *E. robustus* y *E. lindstroemi*. Se analizaron los caracteres morfológicos de los elementos P, S y M de estos *Eoplacognathus* tardíos que apoyan la propuesta de una nueva reconstrucción de sus aparatos. Se lo ha comparado con el aparato *Baltoniodus* y sugerimos la inclusión del género *Eoplacognathus* en la familia Balognathidae. La nueva arquitectura del aparato de *Eoplacognathus* es equiparable con la del género *Lenodus*. Este análisis mejora el conocimiento sobre este grupo de conodontes guía permitiendo una nueva visión sobre la evolución, filogenia y paleobiología de este linaje.

Palabras clave: Cuyania, Ordovícico, *Eoplacognathus*, Taxonomía.

1. Introduction

The *Eoplacognathus* apparatus was first described and their species defined as zonal and subzonal index conodonts by Bergström (1971), supporting this proposal on the P elements. This original description is only based on the oral shape of these P elements. The key conodonts *E. robustus* Bergström and *E. lindstroemi* (Hamar) document the homonymous subzones for the conodont-bearing strata.

The Middle-Upper Ordovician strata of Ponón Trehué outcrops, exposed in the San Rafael Block (Fig. 1), provided a large collection of conodonts. Previous contributions on this conodont fauna were carried out by Heredia (1982, 1998, 2001, 2002) and Lehnert *et al.* (1999). Recently Heredia *et al.* (2014) and Heredia and Mestre (2015) restudy the conodont collection from the Ponón Trehué Formation presenting a new interpretation of the conodont apparatus of *Eoplacognathus*. A deeper revision of these materials allow us to assign S and M elements previously assigned to the *Baltoniodus* species as belonging to the *E. robustus* and *E. lindstroemi* apparatuses.

The main purpose of this contribution is to analyze the morphological characters and taxonomy of P elements of *Eoplacognathus robustus* and *E. lindstroemi*, and include S and M elements as part of the *Eoplacognathus* apparatus, thereby proposing a new reconstruction of it; additionally, we compare it to the *Baltoniodus* apparatus.

2. Geological setting

Within the Ponón Trehué region is located the only preserved record in all Cuyania of the Lower Paleozoic carbonate-siliciclastic succession in depositional contact with basement rocks. This basement is interpreted to be of Grenvillian (late Mesoproterozoic) age (Ramos, Vujovich and Dallmeyer, 1996; Cingolani and Varela, 1999) and constitutes the Cerro La Ventana Formation.

The outcrops in the Ponón Trehué area allow for the recognition of three different units. One is composed entirely of the Mesoproterozoic basement. The other two are sedimentary units that include varying amounts of reworked basement rocks. A well-established Ordovician clastic succession of

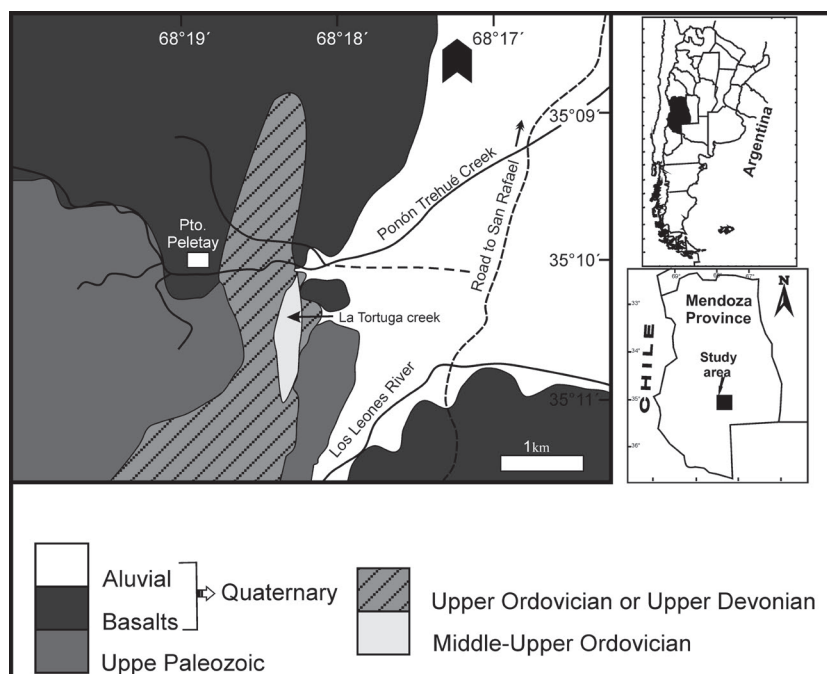


FIG. 1. Location map of the Ponón Trehué region (Mendoza Province) showing studied section, La Tortuga creek (Modified from Heredia and Mestre, 2017).

the Ponón Trehué Formation (upper Darrivilian to lower Sandbian) is composed of granite conglomerate, sandstone and thin-bedded, fossiliferous limestone. A significant unconformity can be traced between the Ordovician clastic sequence and the underlying basement, exposed to the east. The dominant features of these Mesoproterozoic and Ordovician rocks are their isolate, discontinuous and dispersed outcrops in a green shale matrix suggesting an olistostromic origin for these deposits (Heredia and Mestre, 2017). Astini (2002) considered that the limestone outcrops of the Ponón Trehué Formation (*sensu* Bordonaro, Keller and Lehnert, 1996) were blocks and fragmentary carbonate bodies discontinuously exposed, floating in arkose conglomerate, in agreement with Heredia (1998, 2001), Beresi and Heredia (2000) and Heredia and Mestre (2017). In spite of these interpretations these deposits are informative about their fossil record and history.

The Ordovician outcrops in Ponón Trehué represent a depositional cycle from shallower to deeper environments. This succession involves two different deposits: the lower one comprises coarse siliciclastic deposits and the upper one consists of fine, dark carbonate–fine clastic deposits. The biostratigraphy of these Ordovician outcrops has been based on conodonts, recognizing two biozones: the *Pygodus serra* Zone and *Pygodus anserinus* Zone (Heredia, 1982; Bordonaro, Keller and Lehnert, 1996; Heredia, 1996; Lehnert *et al.*, 1999; Heredia, 2001; Cingolani and Heredia, 2001; Heredia and Mestre, 2017) (Fig. 2). Brachiopods, sponge spicules (Beresi and Heredia, 2000), bryozoans, ostracodes, crinoids, trilobites and algae fragments were also recovered from the analyzed samples.

3. Previous Considerations On Taxonomy

The family Polyplacognathidae Bergström, 1983 including *Polyplacognathus* Stauffer, 1935; *Eoplacognathus* Hamar, 1966; *Cahabagnathus* Bergström, 1983 (Sweet, 1981). All these genera are characterized exclusively by bimembrate apparatuses with bilaterally asymmetrical stelliplanate Pa element (polyplacognathiform element) and pastiniplanate Pb element (Sweet, 1988). Later, Stouge and Bagnoli (1999) included to *Polonodus* Dzik, 1976; *Yangtzeplacognathus* Zhang, 1998; and *Baltoplacognathus* Zhang, 1998, into this family without any reference to the basal cavity morphology.

These are well known from numerous studies of abundant material throughout Middle Ordovician sections in Baltoscandia, North America, Argentina and China.

Bergström (1971) provided the first description of the *Eoplacognathus* apparatus based only on P elements of the species *Eoplacognathus lindstroemi* (Hamar, 1964), namely two ambalodiform (Pb) and one polyplacognathiform (Pa) elements. Lindström (in Ziegler, 1973) presented a reviewed diagnosis recognizing two ambalodiform (Pb) and one amorphognathiform (Pa) elements. This author changed drastically the idea of the genus *Eoplacognathus* from polyplacognathiform (stelliplanate) to amorphognathiform (pastiniscaphate) elements (Lindström in Ziegler, 1973).

Dzik (1976) considered that the evolution process of the *Eoplacognathus* species led only platform elements (Pa and Pb) in the apparatus. Later, Dzik (1994) described a multielemental apparatus for the earliest species of the genus *Eoplacognathus*: *E. zgierzensis* Dzik, conformed by Pa, Pb, S and M elements.

Stouge and Bagnoli (1990) reported for the first time S and M elements in the apparatus of *Eoplacognathus pseudoplanus* proposing a change in this genus name to *Lenodus pseudoplanus*, including the genus *Lenodus* to the Balognathidae Family. Stouge and Bagnoli (1999) kept the genus *Eoplacognathus* in the Polyplacognathidae. However, Löfgren and Zhang (2003) continue to use the designation *Eoplacognathus pseudoplanus*, and they recognized S and M elements for this species. Melgren *et al.* (2012) recognized S elements in the *E. foliaceus* apparatus.

A detailed review of the P elements basal cavity from the *Eoplacognathus* species showed that is different in earlier representatives comparing with later ones, been the first ones scaphate (*E. pseudoplanus* to *E. robustus* species) and the later ones are planate (*E. lindstroemi* and *E. elongatus* species). This character appeared earlier in the *E. robustus* sinistral Pa element. We propose that this feature can be used as tool for species recognition between *E. robustus* and *E. lindstroemi*.

Zhang (1998) studied the Polyplacognathidae family proposing changes in its interpretation, recognizing two new genera *Baltoplacognathus* and *Yangtzeplacognathus*, together with *Eoplacognathus*–*Polyplacognathus* and *Cahabagnathus* represent

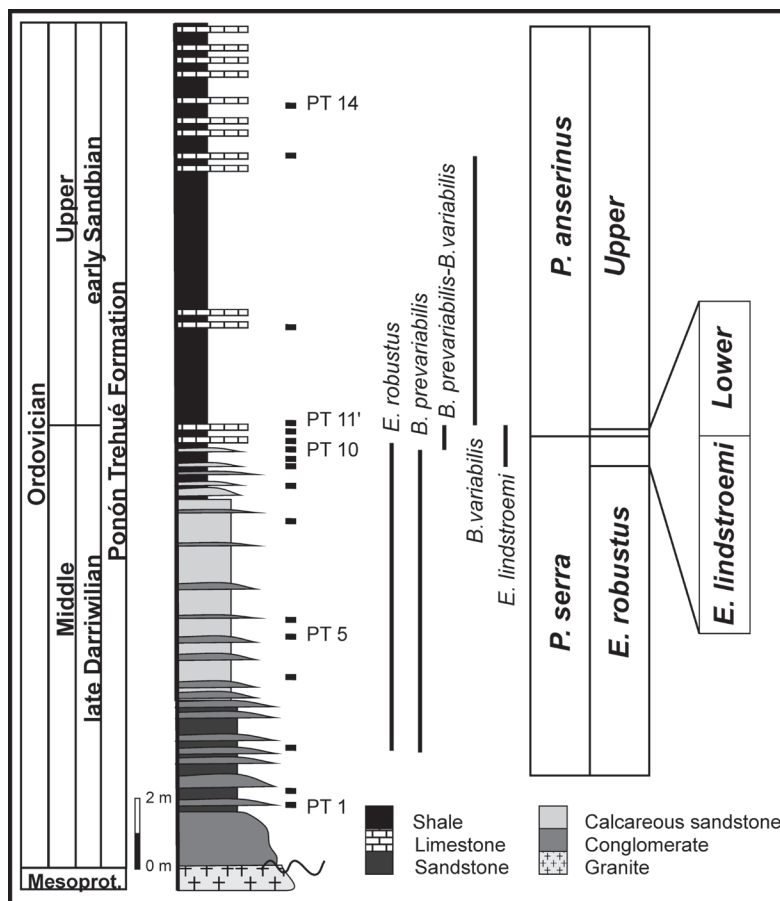


FIG. 2. Stratigraphic column in La Tortuga section with the ranges of the selected conodont species and conodont biostratigraphical scheme for the Ponón Trehué Formation (Modified from Heredia and Mestre, 2017).

four evolutionary lineages in the Middle Ordovician. The index species *Yangtzeplacognathus foliaceus*, *Baltoplacognathus reclinatus*, *B. robustus*, *E. lindstroemi* and *E. elongatus* were redefined among others. Zhang (1998) supported this proposal based on differences on the morphological features of the Pa elements (*Baltoplacognathus*) or Pb elements (*Yangtzeplacognathus*), linking them discontinuously. Especially the differences between both genera are expressed mainly in the length and width of the processes and angles between them, whereas the differences between species of the first genus lie on the denticles row of the processes (Zhang, 1998).

Several elements identified as *E. robustus*-*E. lindstroemi* transitional forms were recovered from the PT10 sample, in the Ponón Trehué section (Heredia, 2002). These types of elements are defined as a transitional form due to the features that exhibit

such as size and shape of the processes and lobes. There is a trend that can be followed in the Pa element morphology of the species *E. robustus*-*E. robustus*/*E. lindstroemi* transition- *E. lindstroemi*. Based on this evidence, we reject the use of the genus *Baltoplacognathus* for the species *robustus*.

The basal cavity of the *Eoplacognathus* P elements was shortly described by Bergström (1971). He mentioned that the basal cavity is scaphate in juvenile specimens and planate in mature specimens for the most of species of this genus, except *E. lindstroemi* and *E. elongatus*. These descriptions do not reflect the true morphology of the basal cavity, after that we consider the necessity of taxonomical revision of this genus. Descriptions of the P element basal cavities are herein developed, it is worth noting that they are different in the early *E. robustus* species when compared to the descendent *E. lindstroemi*, being the

first one scaphate and the later one are planate. We propose that this feature could be used as an additional tool for diagnosing between *E. robustus* and *E. lindstroemi*.

4. Taxonomy

The synonymy lists are condensed, mostly containing only the original citations of species names incorporated in each multielement taxon. In the descriptions, we have used the conventional orientational terms -anterior, posterior, and lateral-noting these do not relate to the anatomical orientation of elements (see Purnell *et al.*, 2000).

The S elements location in the *Baltoniodus* apparatus follows the Stouge and Bagnoli (1999) interpretation of it.

Order Prioniodontida Dzik, 1976

Superfamily Prioniodontacea Bassler, 1925

Family Balognathidae Hass, 1959

Genus *Eoplacognathus* Hamar, 1966

Type species. *Ambalodus lindstroemi* Hamar, 1964

***Eoplacognathus robustus* Bergström**

Fig. 3, A-J

1971. *Eoplacognathus robustus* n. sp. Bergström, p. 140, Pl. 1, 14-16.

1976. *Eoplacognathus lindstroemi robustus* Bergström, Dzik: Text-fig. 32 A-C.

1985. *Eoplacognathus robustus* Bergström, Bergström and Orchard: Pl. 2.2, 8, 12.

1994. *Eoplacognathus robustus* Bergström, Dzik: p. 98, Pl. 21, figs. 3-5, text. 23.

1998. *Eoplacognathus robustus* Bergström, Heredia: p. 341, Pl. I, fig. 3-11, text-fig. 3.

1998. *Baltoplacognathus robustus* (Bergström), Zhang: text-fig. 7, H-N.

1999. *Baltoplacognathus robustus* (Bergström), Stouge and Bagnoli: Pl. 2, fig. 9-12.

2001. *Eoplacognathus robustus* Bergström, Heredia: Pl.1, fig. 3

2011. *Baltoplacognathus robustus* (Bergström), Viira: fig. 9, F.

2012. *Baltoplacognathus robustus* (Bergström), Hints, Viira and Nõlvak: fig. 5, D-F.

2016. *Baltoplacognathus robustus* (Bergström), Wu *et al.*: fig. 3, 6.

2016. *Baltoplacognathus robustus* (Bergström), Stouge *et al.*: fig. 3, H-I.

Materials. Fifty four elements. Seventeen Pa, eighteen Pb, six S, and three M elements.

Description. The dextral and sinistral Pa and Pb elements are pastinacaphate with wide basal cavity that occupies all the aboral side (Fig. 3 E). These elements agree well with Bergström's (1971) oral description.

M. The M element is represented by a modified geniculate morphology. The cusp is erect and has a central carina on the inner side, and is longer than the anterior margin. The angle between anterior margin of the cusp and the anterior margin of the base is greater than 180°. The angle between anterior and oral margins is less than 90° and has a U-like shape.

Sa. The Sa element has an alate morphology. The element has three regularly denticulate processes. The denticles are fused in the base and climb through the cusp.

Sb. The teriopede element, clearly asymmetrical. The cusp is short, erect to the tip. The three processes have regular proclined denticles toward the cusp.

Sd. The symmetrical quadriramate elements has a short cusp and all processes are regularly denticulate and they are connecting with the cusp through a carina.

***Eoplacognathus lindstroemi* (Hamar, 1964)**

Fig. 4, A-G

1964. *Ambalodus lindstroemi* n. sp. Hamar, p. 258, Pl. 5, 1, 4, 7-8, 10-11, text-fig. 5, 1, 3-4.

1971. *Eoplacognathus lindstroemi* (Hamar), Bergström: p. 139, Pl. 2, 15-18.

1985. *Eoplacognathus lindstroemi* (Hamar), Bergström and Orchard: Pl. 2.2, 11, 13.

1994. *Eoplacognathus lindstroemi* (Hamar), Dzik: p. 98, Pl. 21, 6-9, text-fig. 23.

1998. *Eoplacognathus lindstroemi* (Hamar), Zhang: text-fig. 8, A-K.

1999. *Eoplacognathus lindstroemi* (Hamar), Stouge and Bagnoli: Pl. 2, fig. 5-8.

2001. *Eoplacognathus lindstroemi* (Hamar), Heredia: Pl. 3, 6, 13.

2011. *Eoplacognathus lindstroemi* (Hamar), Viira: fig. 9, G.

2012. *Eoplacognathus lindstroemi* (Hamar), Hints, Viira and Nõlvak: fig. 5, G-I.

2016. *Eoplacognathus lindstroemi* (Hamar), Stouge *et al.*: fig. 3, N-P.

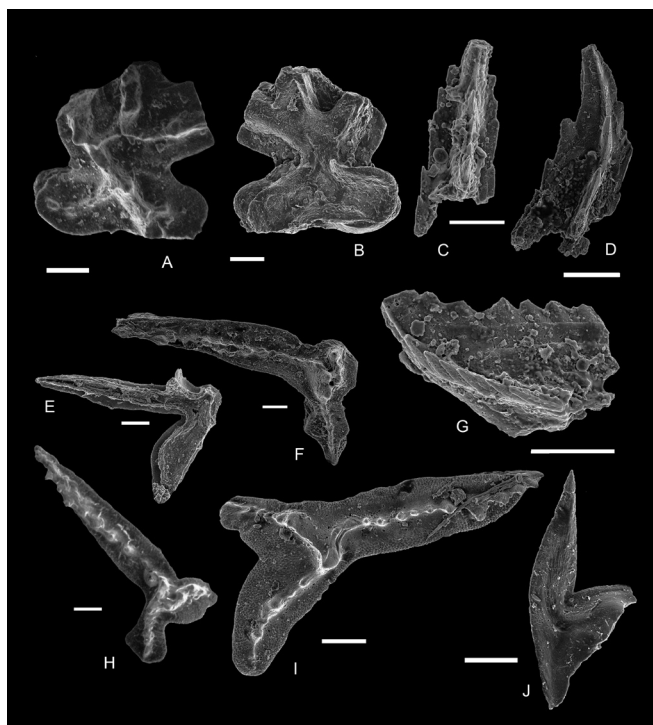


FIG. 3. Scanning electron microscope photomicrographs, scale bar 0,1 mm. 1-10. **A-J:** *Eoplacognathus robustus* Bergström. **A.** dextral Pa element, oral view, CORD MP 2228(1), PT 8. **B.** dextral Pa element, aboral view, CORD MP 2228(1), PT 8. **C.** Sa element, posterior view, CORD MP 2292(3), PT9. **D.** Sd element, lateral view, CORD MP 2292(4), PT9. **E.** dextral Pa element, aboral view, CORD MP 2225(2), PT 9. **F.** sinistral Pb element, oral view, CORD MP 2229 (4), PT 9. **G.** Sb element, lateral view, CORD MP 2229 (2) PT9. **H.** sinistral Pb, oral view, CORD MP 2229(1) PT9. **I.** dextral Pb element, oral view, CORD MP 2223(5), PT 9. **J.** M element, lateral view, CORD MP 2292(1), PT9.

Materials. Four hundred eighty five elements. Three hundred Pa, one hundred seventy three Pb, eight S, and four M elements.

Description. We have nothing to add to the description by Bergström (1971) on the Pa and Pb elements.

M. The M element is represented by modified geniculate morphology. The cusp is erect and is longer than the anterior margin. The angle between anterior margin of the cusp and the anterior margin of the base is greater than 180° and the anterior margin is thin and short. The angle between anterior and oral margins is less than 90° and has a U-like shape.

Sa. The Sa element has an alate morphology. The element has three regularly denticulate processes. The denticles are fused in the base and climb through the cusp.

Sb. The teriopedate element, clearly asymmetrical with a short cusp and erect to the tip. The three processes have regular and similar in shape procline denticles. These denticles appear high on the cusp.

Sd. The symmetrical quadriramate element with a short cusp. All the processes are regularly denticulate and connecting with the cusp through a carina.

Sd and Sa element present bad preservation, for this reason, we did not illustrate these both element.

5. Remarks

The *Eoplacognathus* apparatuses herein described are composed by six elements: Pa, Pb, M, Sa, Sb, and Sd. The P elements are abundant but the S and M elements are very poor in number. The recovering of S and M elements is possible when the collection of *Eoplacognathus* is large. The absence of the Sc element and decreasing number of the other S and the M elements could be explained following Löfgren and Zhang (2003) observation; these authors suggested a decrease of S elements in evolutionary trends between *Lenodus*-*Yangzeplacognathus*-*Eoplacognathus*



FIG. 4. Scanning electron microscope photomicrographs, scale bar 0,1 mm. **A-G.** *Eoplacognathus lindstroemi* (Hamar), all the elements from PT11'. **A.** mature dextral Pa element, oral view, CORD MP 2364 (1). **B.** juvenile dextral Pa element, aboral view, CORD MP 2364(2). **C.** mature sinistral Pa element, oral view, CORD MP 2364(3). **D.** sinistral Pb element, oral view, CORD MP 2362(2). **E.** M element, lateral view, CORD MP 2290(6). **F.** dextral Pb element, oral view, CORD MP 2361(2). **G.** Sc element, lateral view, CORD MP 2290(2).

apparatuses and the progressive disappearance of the bipennate element into these apparatuses.

The *Eoplacognathus robustus* and *E. lindstroemi* apparatuses from Ponón Trehué were compared to *Eoplacognathus pseudoplanus* and *E. suecicus* apparatuses from the Precordillera (Heredia, 2012; Mestre, 2012; Mestre and Heredia, 2013) (Table 1, Fig. 5). The analysis of these data inform that there is a great increasing of P elements over the S and M elements, and the early representatives of the genus neither provided Sc elements.

We have recognized that the S and M elements from *E. robustus* and *E. lindstroemi* can be identified as belonging to mature specimens. This datum allows inferring that the S and M elements representing juvenile and adult specimens are missing. Dzik (1976) proposed that the evolutionary process of the *Eoplacognathus* species let only platform elements in the apparatuses by the progressive demineralization of the S and M elements. Perhaps the S and M mature elements from our collection are mineralized as part of the ontogenetic process.

The S and M elements of the *E. robustus* and *E. lindstroemi* (early and late form) apparatuses were compared with those of *Baltoniodus prevariabilis*

TABLE 1. COMPARATIVE TABLE OF *EOPLACOGNATHUS* APPARATUS ELEMENTS. (*)

	E. p.	E. s.	E. r.	E. l.
P	47	33	45	473
S	18	5	6	8
M	7	1	3	4
Total	72	39	54	485
P	65,3	84,6	83,3	97,5
S	25,0	12,8	11,1	1,6
M	9,7	2,6	5,6	0,8
Total	100,0	100,0	100,0	100,0

(*) Elements recovered from **E. p.** (*Eoplacognathus pseudoplanus*), **E. s.** (*Eoplacognathus suecicus*); **E. r.** (*Eoplacognathus robustus*) and **E. l.** (*Eoplacognathus lindstroemi*) from the Precordillera and Ponón Trehué, respectively; amount and percentage of elements from each species displayed on figure 5.

and *B. variabilis* (Fig. 6). The main differences in the S elements of these two genera are the orientation, shape, distribution and height of the denticles and the absence/presence of micro-striation on the cusps.

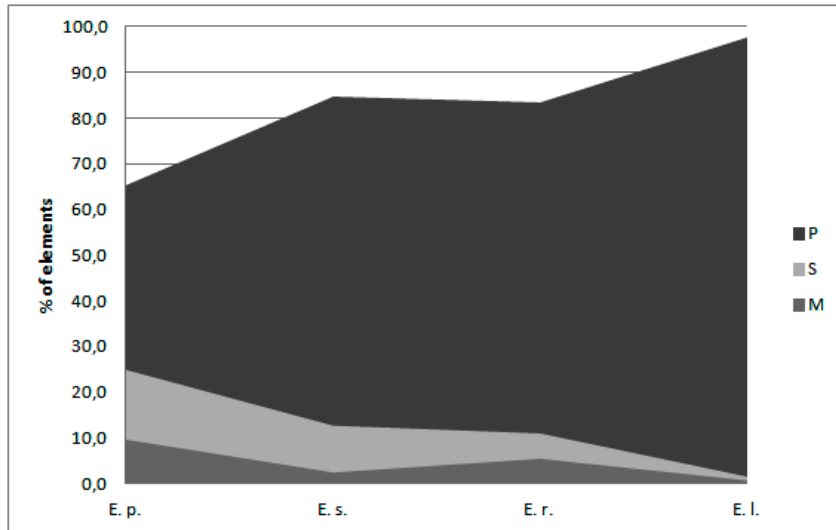


FIG. 5. Percentage of elements on the apparatuses of **E. p.** (*Eoplacognathus pseudoplanus*), **E. s.** (*Eoplacognathus suecicus*), **E. r.** (*Eoplacognathus robustus*) and **E. l.** (*Eoplacognathus lindstroemi*) from the Precordillera and Ponón Trehué.

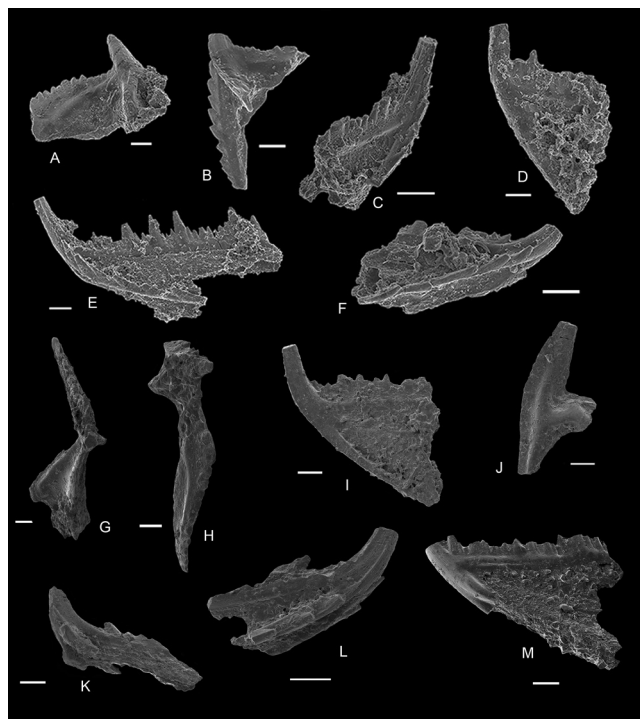


FIG. 6. Scanning electron microscope photomicrographs, scale bar 0,1 mm. **A-F.** *Baltoniodus variabilis* (Bergström), all elements from PT11'. **A.** Pa element, outer view, CORD MP-2259(1). **B.** Pb element, inner view, CORD MP-2259(2). **C, E.** Sa element, posterior view, CORD MP-2259(3). Lateral view, CORD MP-2259(4). **D.** Sc element, lateral view, CORD MP-2259(5). **F.** Sd element, lateral view, CORD MP-2259(6); **G-M.** *Baltoniodus prevariabilis* (Fähræus), all elements from PT 9, **G.** Pa element, oral view, CORD MP-2257(1). **H, K.** Pb element. **H.** oral view, CORD MP-2257(2). **K.** lateral view, CORD MP-2257(3). **I.** Sc element, lateral view, CORD MP-2257(4). **J.** M element, lateral view, CORD MP-2257(5). **L.** Sd element, lateral view, CORD MP-2257(6). **M.** Sb element, lateral view, CORD MP-2257(7).

For instance, the denticles are procline and uniform in height in the S elements of *Eoplacognathus*; on the other hand, *Baltoniodus* shows denticles erect that irregularly alternate in height on the posterior process. The cusp orientation of S elements in *Eoplacognathus* is procline, while in *Baltoniodus* is erect. The Sb elements (tertiopedate) of *Eoplacognathus* and *Baltoniodus* are very different, the first shows the three processes denticulate and the second has denticles only in the posterior process (Figs. 3, 4, 6). All these differences allow a correct identification of the S elements of *Eoplacognathus*.

The M elements of the *Eoplacognathus* present the obtuse angle between anterior margin of the cusp and the anterior margin of the base, similar that the M elements of genus *Lenodus*, in contrast the M element of *Baltoniodus* this angle is straight (Figs. 3, 4, 6).

6. Conclusions

The apparatuses of *E. robustus* and *E. lindstroemi* are described and illustrated for first time. The S and M elements added to these apparatuses allow proposing that the genus is composed by six elements. The Sc element (bipennate) was not retrieved. We note the main differences between the S and M elements from the coeval *Eoplacognathus* and *Baltoniodus* apparatuses for discriminating these both genera composition, allowing an accurate identification of the S elements of *Eoplacognathus*.

We propose considering the P element basal cavity as one of the main features of this group. This character could define among others the boundary between these two species, as already was suggested by Mestre and Heredia (2017). Further studies on the transitional form of *E. robustus* and *E. lindstroemi* would show if this feature can define a different species or genus between them.

Finally, we suggest the inclusion of the *Eoplacognathus* into the Balognathidae family. The new architecture of the *Eoplacognathus* apparatus is comparable to the genus *Lenodus* (*sensu* Löfgren and Zhang, 2003), where S and M elements keep the morphology and location through time, allowing a new insight on the evolution, paleobiology and phylogeny of this lineage.

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