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# The phacopid trilobite *Echidnops taphomimus* n. sp. from the Lower Devonian of Argentina: insights into infaunal molting, eye architecture and geographic distribution

Q1 Juan José **Rustán**,<sup>1,2</sup> and Diego **Balseiro**<sup>1</sup>

5 <sup>1</sup>CICTERRA, CONICET and Universidad Nacional de Córdoba, Av. Vélez Sarsfield 1611, Ciudad Universitaria, X5016GCA, Córdoba,  
6 Argentina (juanjorustan@gmail.com)

7 <sup>2</sup>Universidad Nacional de La Rioja, Av. René Favaloro s/n 5300, La Rioja, Argentina (d.balseiro@conicet.gov.ar)

8 **Abstract.**—Some Silurian-Devonian Argentinian trilobites characterized by infaunal behavior during molting are  
10 considered. After a taxonomic reappraisal, a species previously referred to a lineage of the phacopid *Paciphacops*  
11 is proposed as *Echidnops taphomimus* new species, from the Lower Devonian (probably late Lochkovian) of the  
12 Talacasto Formation, Argentine Precordillera. The visual surface of *E. taphomimus* indicates that a irregular pattern  
13 of lens arrangement, typical of early phacopids such as the Ordovician *Ormathops*, can also be recognized in more  
14 derived Devonian relatives, providing new insights on some evolutionary aspects of visual development. *Echidnops*  
15 is recognized in Australia and Argentina, recording an unusual distribution pattern in trilobites from the Lower  
16 Devonian of southern South America, otherwise mostly linked to faunas of related Gondwanan, austral circum-polar  
17 Devonian basins of the Malvinokaffric Realm. In accordance with proposed increasing predation pressure in the  
18 context of the Mid Paleozoic Marine Revolution, evidence indicates that the infaunal molting behavior, as defensive  
19 strategy, arose in several trilobite groups during Silurian-Devonian times, rather than in a single endemic lineage  
20 of *Paciphacops* species.

## 21 Introduction

22  
23  
24 During the Early and Middle Devonian, a particular marine  
25 fauna mostly recognized based on brachiopods and trilobites  
26 developed in southwestern Gondwana, which justified the  
27 recognition of the Malvinokaffric Realm. This major paleobi-  
28 ogeographical region had an almost circumpolar distribution,  
29 being recorded in southern South America, Antarctica, and  
30 South Africa (Boucot and Racheboeuf, 1993). Trilobites are  
31 fundamental to understand biogeographic patterns and para-  
32 digmatic evolutionary events in this realm (Eldredge and  
33 Ormiston, 1979; Abe and Lieberman, 2012). Most of the studies  
34 on trilobites, however, have been conducted on calmoniids, an  
35 entirely endemic family emblematic of the Malvinokaffric  
36 Realm that radiated spectacularly during the Early Devonian  
37 (Abe and Lieberman, 2012), whereas phacopid trilobites,  
38 common and well-known elements of Devonian marine  
39 communities of Laurussian basins, have received less attention.

40 Devonian marine strata in Argentina, particularly those  
41 from the Precordillera Basin, are well developed and yield  
42 a diverse Malvinokaffric trilobite fauna, particularly in the  
43 Precordillera Basin (Baldis, 1975). In this basin, only few pha-  
44 copids have been reported, namely “*Phacops*” *chavelai* Baldis  
45 and Longobucco, 1977, from the Middle Devonian Chigua  
46 Formation, and *Reedops* cf. *bronni* (Barrande, 1846) by Hollo-  
47 way and Rustán (2012) together with a couple of species of  
48 *Paciphacops* Maksimova, 1972 (Rustán et al., 2011a, 2011b),  
49 from the Lower Devonian Talacasto Formation.

50 *Paciphacops* species received renewed interest as they  
51 were interpreted as representing new Devonian species forming  
52 part of a Malvinokaffric Silurian-Devonian lineage that showed  
53 a particular infaunal moulting habit (Rustán et al., 2011b). This  
54 behavior, together with a trend toward increasing size and  
55 spinosity, were interpreted as anti-predator adaptations, that  
56 evolved during an increase in global marine durophagous  
57 predation recorded in the Devonian (Rustán et al., 2011b)  
58 known as the Paleozoic Marine revolution (Signor and Brett,  
59 1984). Moreover, those features evinced compellingly that  
60 trilobites were actively involved as preys in this major global  
61 bioevent (Rustán et al., 2011b). However, the fact that infaunal  
62 moulting was limited to a few of phylogenetically related  
63 species prevented further inferences about the evolution of  
64 such behavior and the actual scope of the Marine Paleozoic  
65 Revolution.

66 Here we report on the taxonomic reappraisal of some  
67 of these Argentinian specimens, previously reported as  
68 *Paciphacops* n. sp. (Rustán et al., 2011a) and *Paciphacops*  
69 n. sp. B (Rustán et al., 2011b), based on new and better materials  
70 from the Lochkovian of the Talacasto Formation. The fossils  
71 support a reassignment to a new species of the genus *Echidnops*  
72 Sandford, 2002 previously restricted to eastern Gondwana  
73 (Australia), refusing the previously supposed *Paciphacops*  
74 lineage (Rustán et al., 2011b). In addition, new morphological  
75 information on the particular lens arrangement of this new  
76 *Echidnops* species, contributes to a discussion on the visual  
77 system of phacopids. In turn, paleobiogeographic implications



78 of this first non-Australian *Echidnops* record in the  
79 Malvinokaffric context are discussed. The recognition of  
80 infaunal moulting in other taxa than *Paciphacops*, provides  
81 new insights into the extent of ethological predator-deterrent  
82 strategies among Devonian trilobites and some linked  
83 evolutionary aspects.

#### 84 Geological setting

85 The Lower Devonian Talacasto Formation (Padula et al., 1967)  
86 is mainly exposed in the Central Argentine Precordillera of San  
87 Juan Province (Fig. 1), although isolated outcrops are also  
88 known in the northernmost part of the Precordillera, in La Rioja  
89 Province (Rustán et al., 2011a). This formation is composed  
90 of a marine succession of intensely bioturbated greenish-gray  
91 mudstones with intercalated sandstones. It begins with dark,  
92 fine-grained, muddy levels, passing upwards into sandy levels  
93 (Fig. 1). In its type locality at Quebrada de Talacasto, Sierra de  
94 Talacasto, in the San Juan Province (Fig. 1), the formation  
95 reaches around 300 m in thickness, but a maximum of more  
96 than 1000 m is recorded to the north at the Loma de los Piojos  
97 section, near Jáchal city.

98 The Talacasto Formation represents a muddy shelf  
99 depositional system developed during a highstand. This forma-  
100 tion overlies the mainly Silurian shelf succession of the  
101 Los Espejos Formation (Astini, 1991) and is overlaid by the  
102 turbiditic system of the upper Lower-lower Upper? Devonian  
103 Punta Negra Formation (Bracaccini, 1949; Bustos, 1996; Bustos  
104 and Astini, 1997). The Talacasto Formation is the source of  
105 most of the Devonian macrofossils described from Argentina,  
106 sometimes exceptionally preserved. The main fossil groups  
107 include brachiopods, trilobites, bivalves, gastropods, cephalo-  
108 pods, echinoderms, corals, tentaculitids, ostracods, hyoliths,  
109 conulariids, abundant ichnofossils, and scarce plant remains.

110 According to brachiopod and palynological information  
111 (Benedetto et al., 1992; Herrera, 1993; Racheboeuf and Herrera,  
112 1994; Herrera and Bustos, 2001; García-Muro and Rubinstein,  
113 2015), the Talacasto Formation spans from the Lochkovian to  
114 the Emsian. The base of the Devonian is missing at most places  
115 due to the presence of a discontinuity between the Los Espejos  
116 and Talacasto formations. However, the Silurian-Devonian  
117 boundary can be recognized in the uppermost interval of the  
118 Los Espejos Formation in a few localities toward the north of the  
119 Talacasto area, at Cerro del Fuerte, La Chilca (Benedetto  
120 et al., 1992; Carrera et al., 2013), and Jáchal river sections  
121 (García-Muro and Rubinstein, 2015).

122 *Localities*.—Most of the fossils studied herein come from the  
123 Quebrada de Las Aguaditas, Sierra de Los Blanquitos,  
124 approximately 12 km southwest of Jáchal, San Juan Province  
125 (Fig. 1). Fossiliferous horizons correspond to the same  
126 stratigraphic interval of the muddy lower part of the Talacasto  
127 Formation from which Edgecombe et al. (1994), described  
128 calmonioid trilobites such as *Talacastops zarelae*. Additional  
129 specimens come from equivalent layers of an isolated outcrop in  
130 the Sierra de Las Minitas, near Jagüé town, northernmost  
131 Precordillera, La Rioja Province (Rustán et al., 2011a). All  
132 specimens are preserved in dark grey to black nodules, included  
133 in a greenish-dark grey to black pelitic bioturbated interval,

reported as Facies Association A by Astini (1991). Co-occurring  
trilobites include dalmanitids, odontopleurids, proetids, and  
calmoniids (Edgecombe et al., 1994; Rustán et al., 2011a). This  
characteristic trilobite association is dominated by *Echidnops*  
*taphomimus* n. sp., which is mainly represented as articulated  
exuviae, whereas all other trilobites are preserved as  
disarticulated exoskeletal parts. The accompanying fauna, either  
in nodules or in the surrounding matrix, includes corals,  
crinoids, hyoliths, brachiopods, bivalves, cephalopods, con-  
ulariids, gastropods, and vertebrates (a small fragment of bone).

*Age*.—Brachiopod data indicated an early Lochkovian age  
for the fossiliferous interval at the Las Aguaditas locality  
(Edgecombe et al. 1994; Herrera 1995 and references therein).  
Equivalent strata from the Sierra de Las Minitas (Rustán et al.,  
2011a), have been dated as late Lochkovian based on palyno-  
logical content (Rubinstein et al., 2010). The presence of the  
phacopid *Reedops cf. bronni* in proximity to the fossiliferous  
locality bearing *E. taphomimus* at Sierra de Las Minitas  
(Holloway and Rustán, 2012), suggest that the succession  
would range into the Pragian.

#### Systematic paleontology

Illustrated specimens are housed in Argentina, in the paleonto-  
logical collections of the CIPAL (Centro de Investigaciones  
Paleobiológicas), at the CICTERRA (Centro de Investigaciones  
en Ciencias de la Tierra: CONICET-Universidad Nacional  
de Córdoba), Córdoba (CEGH-UNC) Additional material is  
housed in the paleontological repository of the Museo de  
Ciencias Naturales at the Universidad Nacional de La Rioja,  
La Rioja (PULR).

Order Phacopida Salter 1864

Suborder Phacopina Struve in Richter et al., 1959

Superfamily Phacopoidea Hawle and Corda, 1847

Family Phacopidae Hawle and Corda, 1847

Subfamily Phacopininae Hawle and Corda, 1847

Genus *Echidnops* Sandford, 2002

*Type species*.—*Echidnops wrighti* Sanford, 2002 from the  
Lochkovian of the Humevale Formation, central Victoria,  
Australia, by original designation.

*Echidnops taphomimus* new species

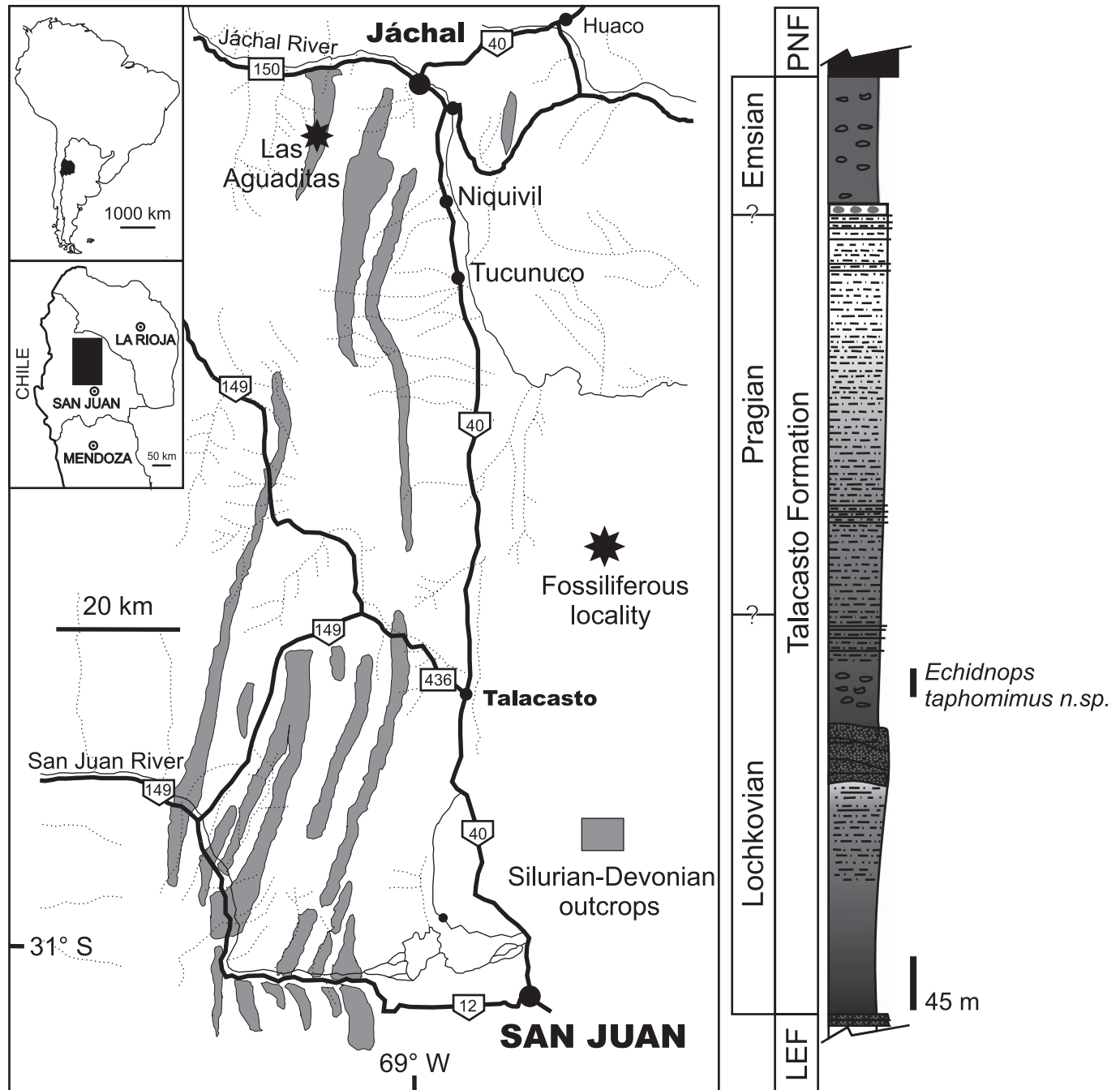
Figures 2.1–2.13, 3.1–3.10, 4.1–4.13, 5.1–5.9

2011a *Paciphacops (Paciphacops)* n. sp. Rustán et al.,  
p. 229, pl. 2, figs. 1–9.

2011b *Paciphacops (Paciphacops)* n. sp. B Rustán et al.,  
p. 496, pl. 2, figs. A–D, DR 4.

*Holotype*.—CEGH-UNC 24082, a nearly complete infaunal  
exuvia from the lower interval of the Talacasto Formation  
(Lochkovian) at Quebrada de Las Aguaditas, Sierra de  
Los Blaquitos, San Juan Province, Argentina (Fig. 2).

*Paratypes*.—CEGH-UNC 12740-42, 12744, 24081, 24083-84,  
24088, 26130, 26151-52.



**Figure 1.** Location map and schematic stratigraphic column of the fossil locality recording *Echidnops taphomimus* n. sp. Lochkovian of the Talacasto Formation, Quebrada de Las Aguaditas, Sierra de Los Blanquitos, San Juan Province, Argentina.

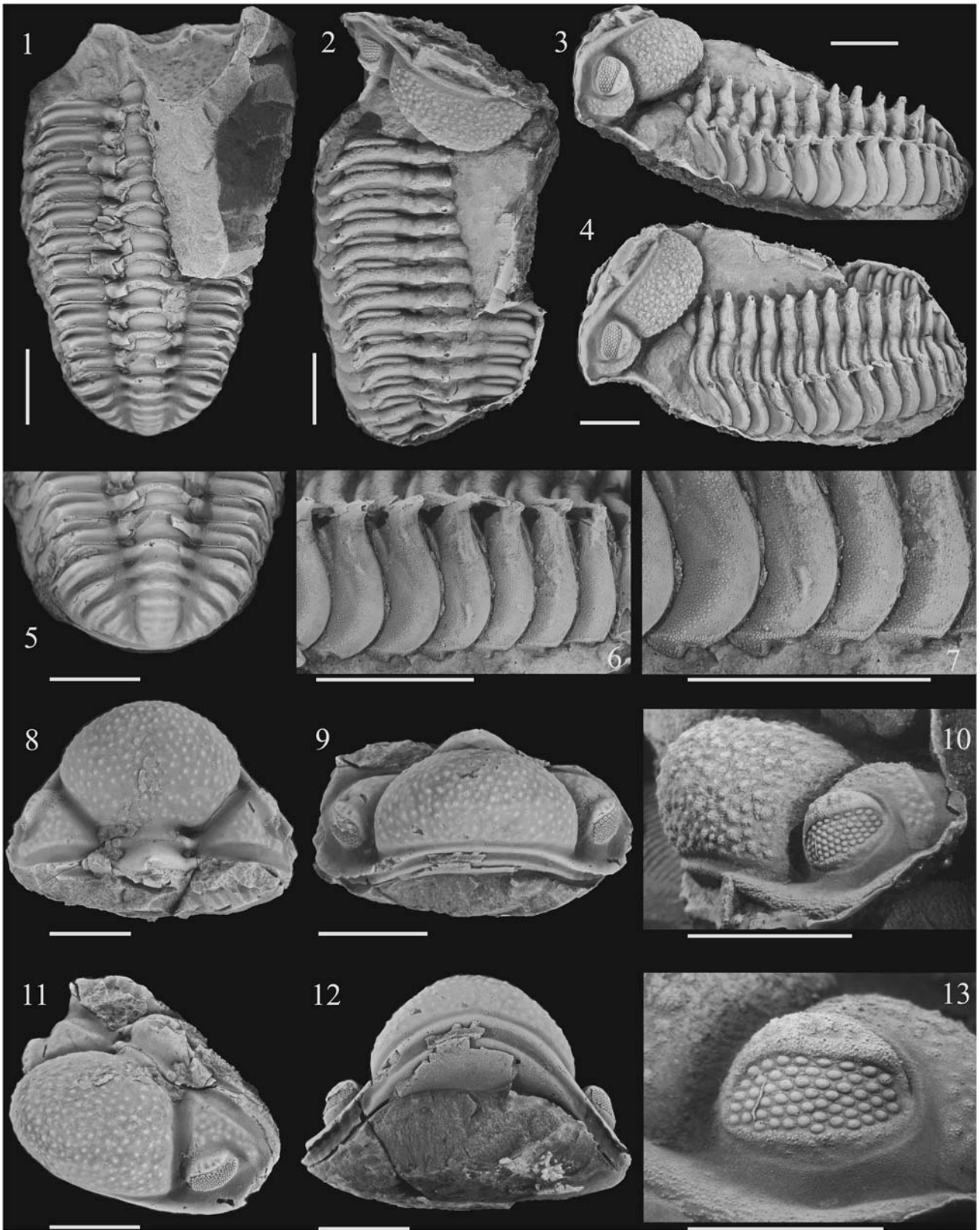
185 *Diagnosis.*—Large *Echidnops* (more than 9 cm of maximum  
 186 total length) with upturned cephalic anterior region; small eyes  
 187 with 50 up to 60 lenses, distributed in an irregular pattern of  
 188 10–14 poorly defined vertical files, with a maximum of six to  
 189 seven lenses; arcuate and crenulated palpebral lobe; very stout  
 190 and wide-based genal, intergenal, and occipital cephalic spines,  
 191 and similar axial and fulcral thoracic ones; lateral lobe of the  
 192 thoracic axial ring just weakly separated by a couple of shallow  
 193 fossulae (not by a clear furrow); anterior pleural band very  
 194 narrow (ridge-like), nearly straight and transversely oriented;  
 195 posterior pleural band inflated and very wide (exsag.).

*Occurrence.*—Lower part of the Talacasto Formation (probably  
 late Lochkovian) at Quebrada de Las Aguaditas, Sierra de Los  
 Blaquitos (San Juan Province) and Sierra de Las Minitas,  
 La Rioja Province, Argentine Precordillera.

*Description.*—Rustán et al. (2011a) gave an description of  
*E. taphomimus* n. sp. based on fossils from Las Minitas, here we  
 focus on new information provided by materials from the  
 Quebrada de Las Aguaditas.

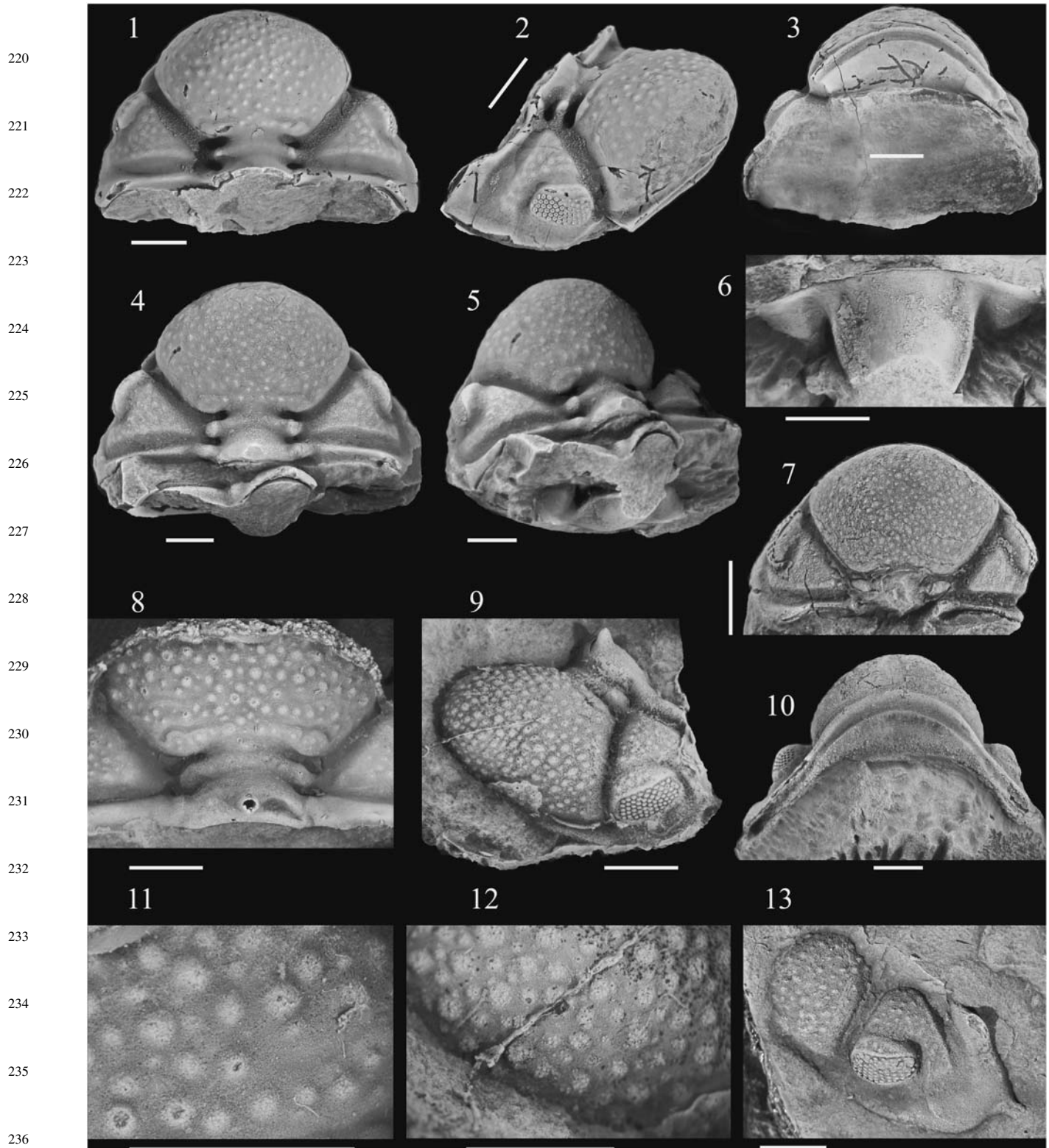
Known maximum length of toracopygidium (CEGH-UNC  
 7057) ~62 mm, and cephalon (CEGH-UNC 26135) ~25 mm.

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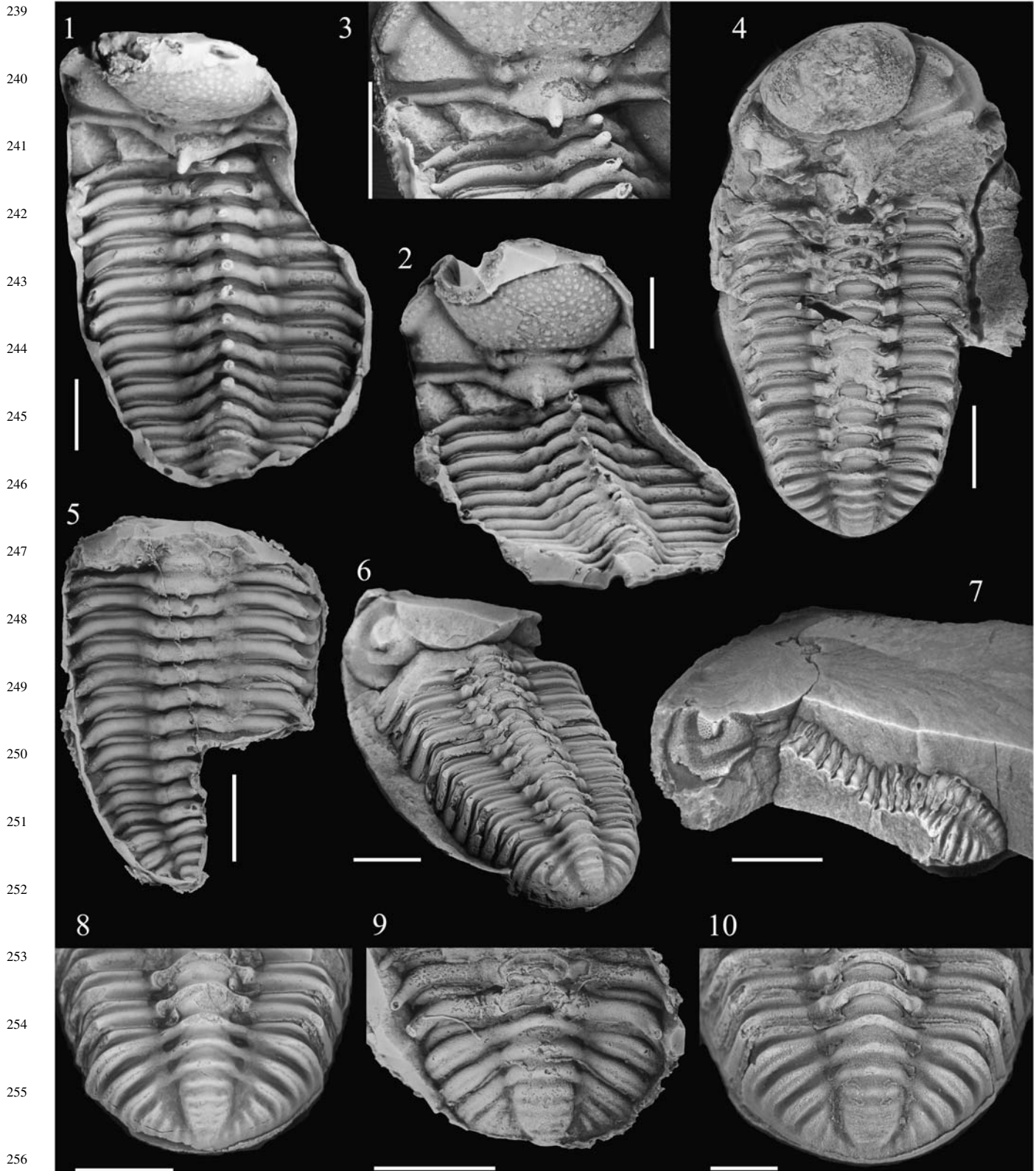


**Figure 2.** *Echidnops taphomimus* n. sp., holotype CEGH-UNC 24082, Lochkovian, Talacasto Formation, Quebrada de Las Aguaditas, Sierra de Los Blanquitos, San Juan Province, Argentina: (1) internal mold, dorsal view; note the infaunal molt pattern; (2) latex cast of external mold, (3) lateral view; (4) latero-dorsal view; (5) pygidium, dorsal view; (6) detail of thoracic fulcral spines and pleural tips in lateral view; (7) detail of ornamentation and unciniate ventral processes of pleural tips; (8) internal mold of cephalon, dorsal view; (9) internal mold of cephalon, frontal view; (10) latex cast of cephalon external mold, lateral view; (11) internal mold of cephalon, latero-dorsal view; (12) internal mold of cephalon, ventral view; (13) external mold of cephalon, detail of the eye, nearly antero-lateral view. Scale bars represent 1 cm in all photographs except (13), where represents 0.5 cm.

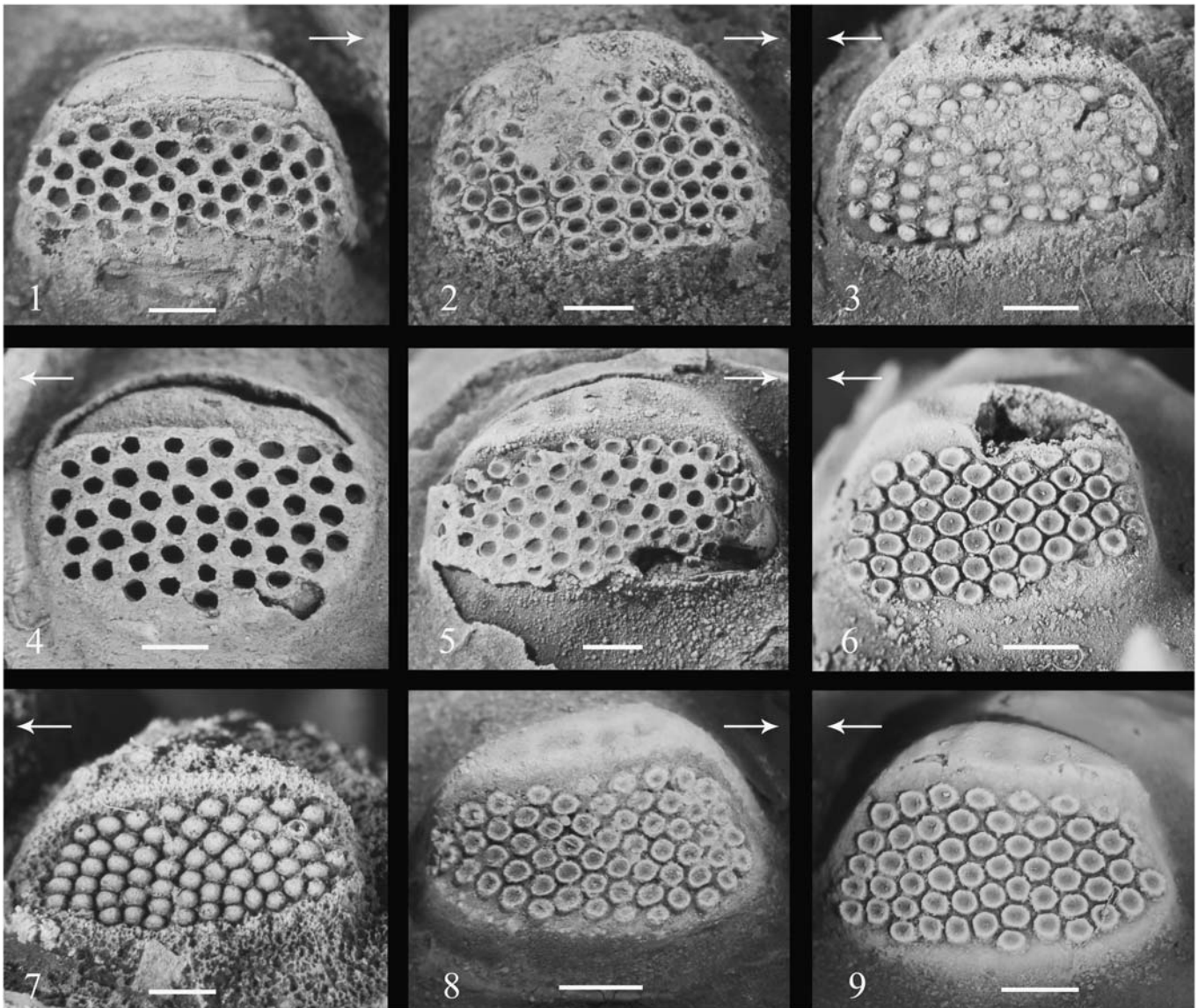
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**Figure 3.** Cephalic morphology of *Echidnops taphomimus* n. sp., Lochkovian, Talacasto Formation, Quebrada de Las Aguaditas, the Sierra de Los Blanquitos, San Juan Province, Argentina: (1–3) cephalon, internal mold (paratype CEGH-UNC 24088), dorsal, anterodorsal and ventral views; (4, 5) cephalon, internal mold (paratype CEGH-UNC 12744), dorsal and postero-dorsal views; note the three dimensional arrangement, diagnostic of the infaunal molt pattern, involving the hypostome obliquely detached and the cephalon rotated up and backward; (6) the same specimen, detail of the (incomplete) hypostome; (7) cephalon, internal mold, dorsal view (paratype CEGH-UNC 26130); (8) latex cast of cephalon external mold, dorsal view, note S2 and S3 (paratype CEGH-UNC 26152); (9) latex cast of cephalon external mold, antero-dorsal view (paratype CEGH-UNC 12742); (10) cephalon, internal mold, ventral view (paratype CEGH-UNC 12740); (11) the same as (8), detail of tuberculation, note thick granulation of tubercles; (12) the same as (9), detail of tuberculation, note granulation and central pits in larger tubercles; (13) latex cast of cephalon external mold, dorso-lateral view, note the genal spine, (paratype CEGH-UNC 12741). Scale bars represent 5 mm in all photographs except in (12) and (13), where represents 1 mm.



**Figure 4.** Examples of typical infaunal molt patterns, and thoracic morphology of *Echidnops taphomimus* n. sp., Lochkovian, Talacasto Formation, Quebrada de Las Aguaditas, Sierra de Los Blanquitos, San Juan Province, Argentina: (1) latex cast of a nearly complete specimen, dorsal view, note the nearly vertical position of the cephalon over the thorax (paratype CEGH-UNC 24081); (2) the same in postero-dorsal view; (3) the same, detail of the nearly 90 degrees angle in the contact between the occipital ring lying over the first thoracic segment, (4) a nearly complete specimen, internal mold (paratype CEGH-UNC 12740); (5) latex cast of a nearly complete thoracopygidium, dorsal view, note the nearly vertical position of the cephalon over the thorax (paratype CEGH-UNC 26151); (6) a nearly complete specimen, internal mold, postero-dorsal view (paratype CEGH-UNC 24084); (7) a nearly complete specimen, internal mold, postero-lateral dorsal view (paratype CEGH-UNC 24083); (8) pygidium, internal mold, dorsal view (CEGH-UNC 26132); (9) latex cast of pygidium external mold, dorsal view (CEGH-UNC 12745); (10) the same as (4), detail of pygidium, dorsal view. Scale bars represent 1cm.



**Figure 5.** Eye morphology of *Echidnops taphomimus* n. sp., Lochkovian, Talacasto Formation, Quebrada de Las Aguaditas, Sierra de Los Blanquitos, San Juan Province, Argentina. Note the irregular arrangement (files are obscurely defined) and similar size of lenses: (1) right eye, internal mold, lateral view (CEGH-UNC 26131); (2) right eye, internal mold, lateral view (CEGH-UNC 12741); (3) left eye, with lenses preserved, lateral view (CEGH-UNC 12741); (4) left eye, internal mold, lateral view (CEGH-UNC 26130); (5) right eye, internal mold, lateral view (CEGH-UNC 26129); (6) left eye, internal mold, lateral view (CEGH-UNC 26133); (7) left eye, latex cast mold, lateral view (CEGH-UNC 12742); (8) right eye, internal mold, lateral view (CEGH-UNC 12740); (9) left eye, internal mold, lateral view (holotype CEGH-UNC 24082). Arrows point anteriorly. Scale bars represent 1 mm.

259 Cephalon usually representing ~30% of total length. Glabella  
 260 with frontal lobe markedly inflated and directed upward,  
 261 outstanding forward and projecting beyond the preglabellar  
 262 furrow in lateral view (Figs. 2.8–2.12, 3.1–3.5, 3.7, 3.10).  
 263 Cephalic tubercles bearing granules and usually a wide funnel-  
 264 like depressed central area (Fig. 3.11, 3.12) that corresponds to a  
 265 central pit in internal molds (Fig. 3.1). Anterior cephalic region  
 266 upturned. Axial furrows highly divergent forward (70°–80°).  
 267 Palpebral lobe narrow (tr.), sloping anterolaterally, gently  
 268 arcuate to semilunar in outline, with large fossulae disposed  
 269 nearly in a row laterally, giving it a crenulated appearance.  
 270 Medium to small eye with length (exsag.) (~30%–40% of  
 271 sagittal cephalic length); visual surface with an irregular lenses  
 272 arrangement, 10–14 poorly defined dorso-ventral files of lenses

and a maximum of six to seven lenses (total lens number usually  
 between 50 and 60, see Table 1). Cephalic posterior border as  
 a strong ridge, deflected postero-laterally abaxial to fulcrum,  
 which bears a stout, dorsolaterally-directed intergenal spine  
 transversely elliptical in cross section at its base. Genal spine  
 small, stout, slightly flattened in cross section at its base and  
 posterolaterally directed. Vincular furrow well impressed, with  
 anterior and posterior edges clearly defined, evenly arched  
 upward in frontal view (Fig. 2.9), narrowest and shallowest  
 immediately below the anterior ends of the axial furrows  
 (Figs. 2.12, 3.3, 3.10), becoming distinctly crenulated posteriorly.

Hypostome large, widest (tr.) across anterior wings  
 (Fig. 3.6). Hypostomal suture smooth, even, and gently bowed  
 forward. Anterior wings very large, laterally extended and

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**Table 1.** Some measurements of the head and eyes of *Echidnops taphomimus* n. sp.

Specimen Repository (CEGH-UNC)	Cephalic Length, mm	No. of Files (putative)	Maximum Lens per File (putative)	Total Lens
7056	16	12?	5	–
7067	–	10	6	–
7071	–	11	6	55?
12740	20	11	5	46
12741	16	11	7	61?
12742	14	12	6	59
12744	16	12	6	55
12746	20?	10	6?	–
12748	20	12	–	–
24081	19	9?	6	–
24082	20	12	6	55
26129	–	14?	6	60?
26130	15	11	6	49
26131	–	13	5	56
26133	–	11	6	51

287 disposed in a very high angle that is almost transversely oriented  
 288 respect of the hypostomal median body; with a strong distal  
 289 inflation and separated by large and very deep lateral notches,  
 290 more or less exsagittally oriented. Median body, slightly longer  
 291 than wide (although its posterior part is broken), considerably  
 292 inflated adventrally. Anterior lobe barely inflated, defined by a  
 293 very faint furrow. Maculae not evident. Lateral border furrow  
 294 moderately wide and deep. Small and shallow fossulae  
 295 anterolaterally on the lateral border furrow, at junction between  
 296 the anterior wings and the anterior lobe. Lateral border narrow  
 297 and moderately high.

298 Distal portion of thoracic pleurae with a nearly blunt  
 299 ventral uncinata-like process, posteriorly directed and separated  
 300 from the lateral side of the pleural tip by a, transverse, nearly  
 301 straight granulose ridge (Fig. 2.6, 2.7). Lateral side of the pleural  
 302 tip with rounded posterior edge, exhibiting in the anterior side a  
 303 nearly concave and sparsely granulose articulating facet, which  
 304 shows a shallow and wide (dorsoventral) furrow posterolaterally  
 305 directed, intersected by the curved (anteriorly concave) incision  
 306 of the pleural furrow ending (Fig 2.6).

307 Lateral lobe of the thoracic axial ring rather weakly  
 308 separated from it by a pair of shallow notches (Figs. 2.2,  
 309 4.1–4.2).

310 *Etymology.*—After the greek *taphos*: tomb, and *mimos*:  
 311 imitator/mimic. In regarding the infaunal molt behavior,  
 312 whereby articulated exoskeletal remains are buried by the  
 313 trilobite during molting, thus generating a “false tomb.”

314 *Materials.*—CEGH-UNC 7055-67, 7071-77, 12739, 12743,  
 315 12745-50, 24085-87, 24089, 26129, 26131-26150, 26153 from  
 316 Quebrada de Las Aguaditas and PULR 118-126 from the Sierra  
 317 de Las Minitas (Rustán et al., 2011a).

318 *Remarks.*—In accordance with the diagnosis by Sandford  
 319 (2002), Argentinian studied specimens show the main mor-  
 320 phological features of *Echidnops*, namely: median spines on the  
 321 occipital ring, thoracic axial rings and the first pygidial axial  
 322 ring; eyes short, ~30%–40% cephalic length, placed with  
 323 anterior margin opposite ~60% cephalic length (measured from  
 324 posterior to anterior), dorso-ventral files of lenses with up to six

to seven lenses, and a moderately thickened sclera; wide (tr.)  
 glabella ~55% cephalic width; axial furrows diverging forward  
 ~75°–80°; vincular furrow deep medially with lateral notches  
 very well impressed, and first pygidial axial rings bearing spine-  
 like ridges transversally. Genal, intergenal, and fulcral spines,  
 frequently present in *Echidnops*, are also clearly exhibited by  
*E. taphomimus* n. sp.

Rustán et al. (2011a), already noted the continuing  
 problem of differentiating *Paciphacops*, *Kainops* Ramsköld  
 and Werdelin, 1991, *Viaphacops* Maksimova, 1972 and  
*Ananaspis* Campbell, 1977 (overlooking references to  
*Echidnops*). Shared cephalic characters used for the assignment  
 to *Paciphacops* included those originally proposed as diagnostic  
 of *Paciphacops* (*Paciphacops*) by Maksimova (1972): preocci-  
 pital furrow bent forward and shallowest in its middle portion;  
 more or less reduced preoccipital lobe appressed to the base of  
 the glabella, and cut off behind by a straight occipital furrow;  
 anterolateral angles of glabella drawn out; occipital ring broad  
 (sag., exsag.); and pygidium moderately well segmented with  
 rounded-triangular shape. Additional characters included a  
 thickened sclera (character 23 as was suggested by Ramsköld  
 and Werdelin, 1991). From the new available evidence, it is  
 clear that these characters in particular are not sufficient for  
 recognizing *Paciphacops* because most of them are shared with  
*Echidnops*, as was already noted by Sandford (2002). In fact,  
 taking into account cephalic characters except occipital, fulcral,  
 and genal spines, most of the species currently assigned to  
*Echidnops* were previously included in *Paciphacops*  
 (i.e., *E. taphomimus* n. sp., *E. crawfordae*, and *E. serratus*  
 (see Wright and Haas, 1990; Ramsköld and Werdelin, 1991;  
 Ebach, 2002; Rustán et al., 2011a, 2011b). The actual  
 taxonomic concept of *Echidnops* highlights the relevance of  
 postcephalic characters in phacopid systematic, as was already  
 stated by Sandford (2002). In this regard, we consider that the  
 knowledge of some additional postcephalic, characters in  
*Echidnops* would help to better separate it from its close  
 relatives such as *Paciphacops*, *Kainops*, *Viaphacops*, and  
*Ananaspis*. Relevant postcephalic characters include a thick  
 exoskeleton, the strong downward deflection of the thoracic  
 pleurae through almost 90° at the fulcrum, and a trend to  
 develop fulcral shoulders and spines.

Our taxonomic reappraisal besides suggests that some  
 cephalic characters of alleged taxonomic relevance are only of  
 relative importance. For example, perforated tubercles, tradi-  
 tionally regarded as associated with large-eyed morphs, have  
 been regarded as diagnostic of *Paciphacops* (Campbell, 1977;  
 Wright and Haas, 1990). However, *E. taphomimus* n. sp., which  
 has relatively small eyes, clearly exhibits perforated glabellar  
 tubercles (Fig. 3.11). We have not included this character in the  
 diagnosis of *E. taphomimus* n. sp. because it seems to be present  
 in other congeneric species (see Wright and Haas, 1990, fig. 3A  
 and Sandford, 2002, figs. 6B, 6C, 7R, 8F–8Q, and 10A).

In addition, we recognized a wide continuum of  
 morphological cephalic variation in holaspides of *Echidnops*  
*taphomimus* belonging to a single population from the same  
 stratigraphic level (nodules from a single narrow interval in the  
 Quebrada de Las Aguaditas and Sierra de Las Minitas), ranging  
 from slender and narrow (tr.) cephalata to wider (tr.) and more  
 robust ones. Such variation, classically taken into account for

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384 recognition of morphs, would indicate intraspecific variability,  
 385 rather than sexual, ontogenetic, or taxonomic differences as  
 386 previously proposed (Campbell, 1977, p. 10). Given that all  
 387 specimens are preserved in nodules, undistorted, a possible  
 388 taphonomic or collecting bias is also definitely disregarded.

389 Rustán et al. (2011a) discussed *E. crawfordae* (Wright and  
 390 Haas, 1990) from the late Pragian Rosedale Shale, New South  
 391 Wales, Australia, as the most closely related species to  
 392 *E. taphomimus* n. sp.. However, the strong similarities with  
 393 *E. wrighti* Sandford, 2002 from the late Lochkovian of the  
 394 Humevale Formation, New South Wales, were overlooked by  
 395 these authors. These three species are clearly the most closely  
 396 related, mainly on the basis of the strong spine development and  
 397 spine distribution pattern, while all remaining members of the  
 398 group lack either the genal (*E. serratus* Sandford, 2002) or the  
 399 fulcral spines (*E. sherwini* Sandford, 2002 and *E. hollowayi*  
 400 Sandford, 2002).

401 Apart from its larger size, *E. taphomimus* n. sp. can be  
 402 differentiated from both *E. crawfordae* and *E. wrighti* by  
 403 a series of fossulae toward the external edge of the palpebral  
 404 lobe (Fig. 2.8–2.10, 2.13), just a pair of shallow fossulae (not a  
 405 true furrow) separating weakly the lateral lobes on the thoracic  
 406 axial rings; and the nearly straight and ridge-like anterior pleural  
 407 band (which is orientated nearly 90° with respect to the axial  
 408 axis). Moreover, *E. taphomimus* n. sp. differs from *E. wrighti* in  
 409 having smaller eyes, fewer dorso-ventral files of lenses  
 410 (approximately 10–14 versus nearly 16, respectively), less  
 411 tuberculated glabella, fulcral pleural region ~90° angle in  
 412 transverse section, and pygidium with spine-like ridges on the  
 413 first axial rings instead of nodes.

## 414 Discussion

415 *Lens arrangement.*—A striking character of *Echidnops tapho-*  
 416 *mimus* n. sp. is the irregular arrangement of lenses on the visual  
 417 surface of the eye. Difficulties in recognizing files and counting  
 418 lenses (at least in holaspides) are caused by a progressive  
 419 curvature of the upper (dorsal) part of each lens file, as well as to  
 420 the intercalation of lenses between files, particularly near the  
 421 central-upper region of the visual surface (Fig. 5). Curvature of  
 422 lens files is particularly noticeable when counting them from  
 423 anterior to posterior and vice versa. As a result, the usual  
 424 phacopid regular hexagonal close packing of lenses is not  
 425 recognizable in *E. taphomimus*, so that reporting a complete lens  
 426 formula cannot be assured. Nevertheless, we present approxi-  
 427 mate lens formulae for several specimens (Table 1) because  
 428 this provides an idea of the overall arrangement, and allows  
 429 comparisons with previous reports of closely related species.

430 Irregular packing of lenses is also present in most of  
 431 *Echidnops* species, including *E. crawfordae* (see Wright and  
 432 Haas, 1990, figs. 3B, 3J, 4D), *E. hollowayi* (Sandford, 2002,  
 433 fig. 8I, 8N), and *E. serratus* (Sandford, 2002, fig. 10G, 10H).  
 434 It is not present in *E. wrighti* or *E. sherwini* (Sandford, 2002,  
 435 figs. 6N, 9H).

436 The phylogenetic significance of this character is not clear,  
 437 pending a cladistic analysis to explore its taxonomic relevance  
 438 in distinguishing less spinose species of *Echidnops* from those  
 439 belonging to closely allied genera such as *Paciphacops*,  
 440 *Kainops*, or *Viaphacops*.

441 Although irregularities of lens arrangement have been  
 442 reported in other members of Phacopina, such contributions  
 443 have focused on considering them particular isolated exceptions  
 444 to the regularity or bilateral symmetry, and thus, their taxonomic  
 445 value has been not explored (see cases cited by Crônier and  
 446 Clarkson, 2001: 110). Apart from, mostly unsupported, early  
 447 hypotheses on sexual dimorphism, they have been attributed  
 448 either to variation in timing of lens emplacement led by a not  
 449 absolutely deterministic program of development, or abnorm-  
 450 alities, stress or injuries during development (Thomas 1998;  
 451 Crônier and Clarkson, 2001; Crônier et al., 2004; Feist et al.,  
 452 2009, and references therein). In contrast, the clear pattern of  
 453 general irregularity of lens arrangement in *Echidnops* is stable at  
 454 a specific level (observable in all individuals belonging to each  
 455 species that exhibits the character), suggesting that it might be of  
 456 taxonomic relevance.

457 Significantly, an irregular lens pattern seems to be present  
 458 in other trilobites also at a specific level. For example *Reedops*  
 459 *bronni* (Barrande, 1846) exhibits this feature as illustrated by  
 460 Alberti (1970, pl.14, fig. 2b), Chlupáč (1977, pl. XXII, figs. 4,  
 461 9–11, 17), McKellar and Chatterton (2009, l.1, figs. 1, 3, 7, 11),  
 462 and Holloway and Rustán (2012, pl.2, fig. 6); whereas other  
 463 species, such as *R. cephalotes* (Alberti, 1983) and *R. pembertoni*  
 464 McKellar and Chatterton, 2009, clearly exhibit a regular lens  
 465 pattern.

466 Another analogous case seems to be *Struveaspis* Alberti,  
 467 1966, according to illustrations from Chlupáč (1977, pls. 30 and  
 468 31), Alberti (1970, pl. 13, fig. 10), Alberti (2000, pl. 2 fig. 1b),  
 469 and Corbacho et al. (2014, pl. 1, fig. 10).

470 The irregular lens pattern observed in *Echidnops* species  
 471 resembles particularly that of the Ordovician basal phacopine  
 472 *Ormathops* Delo, 1935. Clarkson (1971) recognized two  
 473 different kinds of eye disruptions in *Ormathops*, namely: (1)  
 474 blocks of lenses with different orientation separated by vertical  
 475 lines called caesurae, and (2) changes in the way lenses are  
 476 packed in the upper part of the visual surface, allowing lens  
 477 packing changes and curving of the files over toward the top.  
 478 Although caesurae are not present in *Echidnops*, the lens  
 479 distribution in *Echidnops* is identical to the second type of  
 480 disruption (i.e., packing changes) observed in *Ormathops* by  
 481 Clarkson (1971). *Echidnops taphomimus* n. sp. further shares  
 482 with *Ormathops* a roughly constant lens size from the top to the  
 483 bottom of the eye, which is a unique feature among schizochroal  
 484 eyes (Crônier and Clarkson, 2001). As noted by Clarkson  
 485 (1971), a constant lens size would cause a geometrical constraint  
 486 to a regular lens packing because the visual surface approxi-  
 487 mates a cone segment. Therefore, the lens packing irregularities  
 488 observed in *Echidnops* and *Ormathops* are a simple conse-  
 489 quence of a constant lens size.

490 Clarkson (1971) argued that the lens arrangement present  
 491 in *Ormathops* was an intermediate step in the early rapid  
 492 evolution of schizochroal eyes, which never reappeared in the  
 493 entire history of the clade, most probably because it was not as  
 494 efficient as a fully regular eye. This hypothesis was later  
 495 supported by Henry et al. (1992) who recognized parallel  
 496 evolutionary trends in *Ormathops* and *Toletanaspis* Rábano  
 497 1989 characterized by older Ordovician species with irregular  
 498 eye patterns and younger Ordovician ones with “true”  
 499 schizochroal regular eyes. Moreover, the alleged parallelism



500 reported by these authors would suggest a markedly  
501 polyphyletic origin for the schizochroal eyes.

502 The irregular lens distribution in derived Devonian  
503 phacopids such as *Echidnops*, challenges the idea that a regular  
504 pattern would be the best spatial option for forming a proper  
505 image, and that an irregular pattern would be simply an  
506 evolutionary step towards regular eyes. It seems plausible that  
507 such irregular eyes were an alternative viable solution to  
508 functional efficiency of the schizochroal eye, which is in turn  
509 a more parsimonious interpretation since it does not involve  
510 a polyphyletic origin for a complex structure as schizochroal  
511 eyes. These new insights deserve further investigation.

512 *Paleobiogeography.*—The Devonian, particularly the Lower  
513 Devonian, southern South American basins, have highly  
514 endemic trilobite fauna shared with South Africa, Ghana,  
515 Malvinas Islands and Antarctica. The faunal similarities led to  
516 the proposal of a nearly circumpolar, southern paleobiogeographic  
517 major area, known as the Malvinokaffric Realm  
518 (Richter and Richter, 1942). The Malvinokaffric Realm was  
519 later also recognized based on the distribution of other marine  
520 groups (Boucot and Racheboeuf, 1993), such as brachiopods  
521 (Boucot et al., 1969), ostracods (Lethiers et al., 2001; Salas  
522 et al., 2013), and hyoliths (Malinky and Racheboeuf, 2011). The  
523 Gondwanan records of New Zealand and Australia were  
524 excluded from the Malvinokaffric Realm because of their  
525 unrelated Early Devonian marine faunas (Boucot and  
526 Racheboeuf, 1993).


527 The endemic distribution of Early Devonian Malvinokaffric  
528 trilobites is notable and observed even at a familial level in  
529 calmoniids (Eldredge and Ormiston, 1979; Abe and Lieberman,  
530 2009), dalmanitids (Braniša and Vaněk, 1973; Holloway and  
531 Carvalho, 2009; Rustán and Vaccari, 2012a), and homalonotids  
532 (Simões et al., 2009). Endemicity is even recorded within  
533 cosmopolitan genera already present during the Silurian, which  
534 record radiations within the Malvinokaffric Realm in the Lower  
535 Devonian, as is the case of the endemic aulacopleurid  
536 *Maurotarion (Malvinotarion)* Rustán and Vaccari, 2010.

537 In this paleobiogeographical context, *Echidnops* exhibits  
538 an unusual distribution. All *Echidnops* species except the  
539 Argentinian *E. taphomimus* n. sp., are known from Australia  
540 (Sandford, 2002). Thus, *Echidnops* represents the first trilobite  
541 connecting the Early Devonian Australian basins with the South  
542 American Malvinokaffric coeval ones, and clearly suggest  
543 a particular link between the Precordillera Basin and South-  
544 eastern Australia.

545 Although unique, this striking Australian-Andean distribu-  
546 tion pattern is consistent with a few other cases such as the  
547 brachiopod *Boucotia* Gill 1969 (according Herrera, 1995).  
548 Among trilobites from the Argentine Precordillera indicating  
549 extra-Malvinokaffric affinities, the probably late Pragian  
550 aulacopleurid *Maurotarion megacephalum* Rustán and Vaccari  
551 2012b, suggests a biogeographical connection with the Eastern  
552 Americas Realm because it was considered most closely allied  
553 to *Maurotarion periergum* (Haas, 1969), from the Pragian of the  
554 Great Basin, United States (Adrain, 2009; Rustán and Vaccari,  
555 2012b). Independent evidence is also provided by the distribu-  
556 tion of other Pragian trilobites such as *Reedops*, a cosmopolitan  
biostratigraphical indicator recorded in slightly higher

stratigraphical intervals than *Echidnops taphomimus* n. sp.  
(Holloway and Rustán, 2012).

The remarkable distribution pattern of *Echidnops* challenge  
the classical paleobiogeographical interpretations about these  
basins as isolated by means of dispersal barriers, particularly  
during periods of low sea levels, such as the Pragian (Rustán and  
Vaccari, 2010). In accordance, recent data on Lower-Middle  
Devonian trilobites from northern South American basins  
(including records from Colombia and Venezuela) indicate the  
presence of Malvinokaffric elements in faunal associations  
otherwise paleobiogeographically linked to the Devonian  
Eastern Americas Realm (Morzadec et al., 2015).

 *Infaunal molting and its role in the mid Paleozoic marine  
revolution.*—Infaunal molting behavior in trilobites has been  
only recently recognized mainly based on specimens of  
*E. taphomimus* n. sp. studied herein (Rustán et al., 2011b).  
The infaunal molting pattern is typically characterized by an  
articulated thoracopygidium, frequently exhibiting a gentle  
dorsal concave-up bending; the cephalon separated and placed  
in front of and slightly above the first thoracic segment, being  
nearly perpendicularly oriented up to clearly rotated backward;  
and the hypostome being displaced. Because no other  
taphonomic agents can be invoked for explaining such a distinct  
three-dimensional arrangement as generated onto the sea  
bottom, this preservational pattern has been interpreted as  
biologically produced because of the trilobite being entirely  
buried in soft sediment during the molting process (Rustán et al.  
2011b, fig 2.6, and Fig. 4.1–4.7). The three-dimensional pattern  
described, provide unequivocal evidence of this ethological  
feature, in contrast with, earlier, functional inferences based on  
plausible life style of blind trilobites (Becker and Schreiber,  
1994).

Because the exuviation process is the most vulnerable  
period of the trilobite adult life, this behavior was understood as  
an evolutionary acquisition related to a predator-deterrent active  
(ethological) strategy (Rustán et al., 2011b).

The infaunal molting pattern was originally recognized in  
a hypothetical late Silurian-Early Devonian phacopid lineage,  
involving three species of *Paciphacops* from western Argentina,  
namely *P. argentinus*, *P. sp A* and *P. sp B* (Rustán et al. 2011a,  
2011b). In addition, an evolutionary defensive trend toward  
a thickening of the carapace, a development of spinosity and an  
increasing size was documented for this putative lineage.  
However, the present reassignment to *Echidnops* rejects the  
idea of a Siluro-Devonian evolutionary trend of *Paciphacops*, as  
suggested by Rustán et al. (2011a, 2011b). Hence, on the one  
hand, morphological characters in *E. taphomimus* n. sp. might  
be interpreted as plesiomorphies and not necessarily as adaptive  
responses against predation coupled to infaunalism. On the  
other hand, this implies that infaunal molting should have  
evolved independently several times. In accordance, prelimin-  
ary reports (Rustán et al., 2012a, 2012b) indicated that infaunal  
molting is also present in the phacopid *Viaphacops orurensis*  
(Bonarelli, 1921) and in the calmoniid *Pennaia*, from the  
Middle Devonian (Givetian?) of the Sica Sica Formation  
in Bolivia. Additional support comes from the phacopid  
“*Phacops*” *chavelai* and the calmoniid *Punillaspis argentina*,  
from the Middle Devonian Chigua Formation of Argentina  
(Rustán et al., 2015). In addition, Błazejowski et al. (2015)

616 recently reported an exceptional specimen of the blind phacopid  
 617 *Trimerocephalus*, from the Late Devonian of Poland, caught in  
 618 the act of molting infaunally. Finally, a number of molt  
 619 ensembles coming (mainly) from the Lower Devonian of  
 620 Germany-Luxemburg (Alberti 2015a, 2015b), although in many  
 621 cases differ from the typical infaunal molt pattern reported  
 622 herein, suggest it could also be present in acastid, homalonotid,  
 623 and proetid trilobites. Thus, evidences support that infaunal  
 624 molting evolved independently in many different groups in mid  
 625 Paleozoic seas as an analogue of the enrollment and coaptive  
 626 structures earliest in the history of the trilobites (Esteve et al.,  
 627 2011). This clear defensive conduct can be interpreted as  
 628 evidence of escalation, in concert with the evolutionary-  
 629 ecological context of the so-called mid Paleozoic marine  
 630 revolution (Signor and Brett, 1984), a major bio-event related  
 631 to the sudden appearance of several groups of predators that  
 632 greatly intensified predation pressure in Silurian-Devonian  
 633 marine ecosystems, simultaneously triggering defensive evolu-  
 634 tionary trends in a number of prey groups (Brett and Walker,  
 635 2002; Brett, 2003; Klug et al 2010). According the phylogenetic  
 636 patterns preliminary observed in this major paleoecological  
 637 scenario, trilobites probably played an active role in a more  
 638 similar way to the evolution of infaunalism in bivalves than in  
 639 irregular echinoids during the Mesozoic (Harper, 2003).

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