



# Two middle Cambrian diceratocephalid trilobites, *Cyclolorenzella convexa* and *Diceratocephalus cornutus*, from Korea: development and functional morphology

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Silicified sclerites of the latest middle Cambrian trilobites, *Cyclolorenzella convexa* and *Diceratocephalus cornutus*, have been recovered from the Sesong Formation, Korea. Their morphological similarity and stratigraphic occurrences suggest that *D. cornutus* is a descendant of *C. convexa*. The ontogenies of both trilobites demonstrate that a pair of long frontal horns in the cephalon of *D. cornutus* is an evolutionarily novel structure. It is inferred that redeployment of some pre-existing regulatory gene played a significant role in constructing the frontal horns of *D. cornutus*. The frontal horns may have been a defensive structure to deter predators. The facial suture of *D. cornutus*, which extends onto the frontal horns and splits them into the dorsal and ventral halves, was a solution to enable easier forward egression during ecdysis. □ *Functional morphology, Korea, Middle Cambrian, ontogeny, trilobites.*

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Silicified trilobite faunas have provided important insights into trilobite evolution and phylogeny by revealing previously unknown morphology. They provide not only detailed juvenile morphology which has been considered crucial for elucidation of higher level classification (Whittington 1957; Chatterton 1980; Chatterton *et al.* 1994; Chatterton & Speyer 1997; Fortey 2001), but also valuable information on complex and intricate mature morphology which is difficult to observe in crack-out specimens (e.g. Whittington 1959; Chatterton *et al.* 1997; Adrain & Westrop 2005). Such detailed information on morphology could also advance our understanding of the life mode and functional morphology of trilobites.

The silicified trilobites from the Sesong Formation, Taebaeksan Basin, Korea, allow us to examine the detailed morphology of two late middle Cambrian diceratocephalid trilobites: *Cyclolorenzella convexa* (Resser & Endo *in* Endo & Resser 1937) and *Diceratocephalus cornutus* (Endo *in* Endo & Resser 1937). *Diceratocephalus cornutus* differs from *C. convexa* in having a pair of anteriorly projecting spines on the frontal part of the cephalon (hereafter, 'the frontal horns'). To date, only a small number of fragmentary crack-out specimens have been reported from China, and thus our understanding of the morphology of *Diceratocephalus* remains incomplete.

This paper presents the morphologic features and post-protaspid ontogenies of *C. convexa* and *D. cornutus*, based on silicified sclerites from the Sesong Formation. We explore the developmental origin and functional morphology of an evolutionarily novel structure, the frontal horns. The function of facial suture of *D. cornutus* which runs along the lateral margin of the frontal horns is also discussed.

## Locality and geology

The Taebaeksan Basin is located in the mid-eastern part of the Korean Peninsula (Fig. 1A) and comprises the Cambrian–Ordovician Joseon Supergroup and the Carboniferous–Permian Pyeongan Supergroup. The Joseon Supergroup is divided into the Taebaek, Yeongwol, Yongtan, Pyeongchang and Mungyeong groups on the basis of different lithologic successions in different regions (Choi 1998). The Taebaek Group occupies the eastern part of the Taebaeksan Basin (Fig. 1B) and is thought to have been deposited in a shallow marine environment (Chough *et al.* 2000). The Taebaek Group consists of, in ascending order, the Jangsan/Myeonsan, Myobong, Daegi, Sesong, Hwajeol, Dongjeom, Dumugol, Makgol, Jigunsan and Duwibong formations, with the

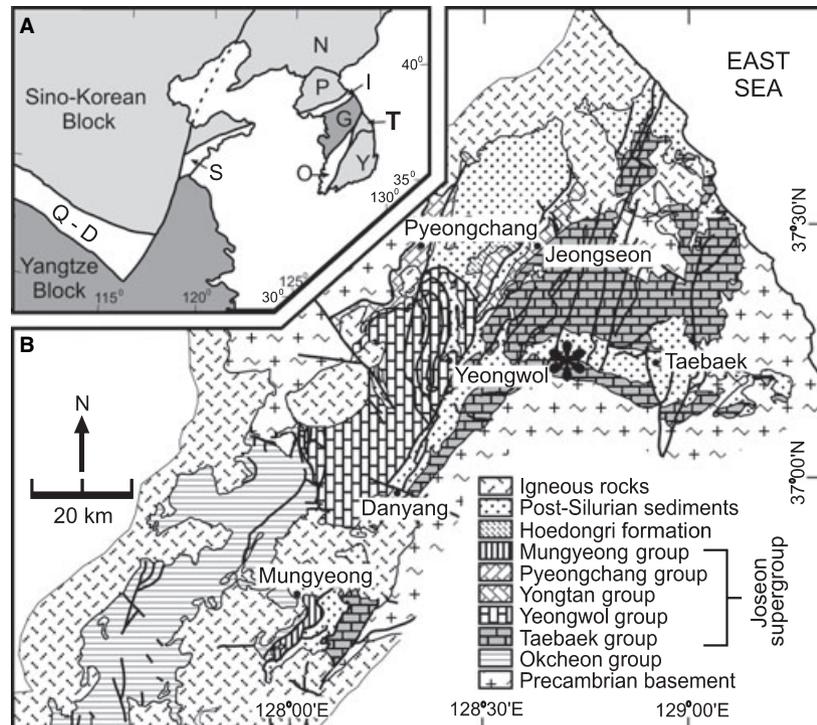


Fig. 1. Index maps. A, tectonic map of Korean peninsula and surrounding area showing the location of the Taebaeksan Basin. Key: Q-D, Qinling–Dabie belt; S, Sulu Belt; N, Nangnim Massif; P, Pyeongnam Basin; I, Imjingang Belt; G, Gyeonggi Massif; O, Okcheon Belt; T, Taebaeksan Basin; Y, Yeongnam Massif. B, simplified geological map of the Taebaeksan Basin showing the distribution of the lower Palaeozoic Joseon Supergroup in the Taebaeksan Basin. The location of the Jikdong section is indicated by an asterisk. Modified from Choi *et al.* (2001).

Cambrian–Ordovician boundary lying within the Dongjeom Formation (Choi *et al.* 2004).

The material considered in this study comes from the lower part of the Sesong Formation in the Jikdong section which is exposed along a mountain trail located about 20 km west from Taebaek City (Fig. 1B). The Sesong Formation is late middle Cambrian to early Furongian in age, and contains five biozones: the *Stephanocare*, *Neodrepanura*, *Prochuangia*, *Chuangia* and *Kaolishania* zones in ascending order (Sohn & Choi 2005). The Jikdong section exposes most of the Sesong Formation, which consists mainly of fine-grained sandstone and shale with a coarsening upward trend: the lower part is represented by limestone nodule-bearing dark-grey shale with frequent intercalations of limestone conglomerate beds, while the upper part is largely of light grey laminated sandstone. The middle Cambrian–Furongian boundary lies about 30 m above the base of the Sesong Formation in the Jikdong section.

The Jikdong section consists of two separate subsections: i.e. Jikdong A (JDA) and Jikdong B (JDB) sections (Fig. 2). The JDA section (37°10′31.1″ N and 128°46′30.8″ E) exposes the lower 60 m of the Sesong Formation, but the 14-m interval above the base is covered by vegetation. The JDB section (37°10′28.0″ N and 128°46′56.2″ E) is located about

0.2 km east of the JDA section and comprises a 7-m-thick succession. Fossil occurrences suggest that the JDB section is stratigraphically older than the JDA section (Fig. 2).

## Materials and methods

Samples for this study were collected from the lower part of the Sesong Formation, exposed in the JDA and JDB sections. *Cyclolorenzella convexa* was collected from the nine fossiliferous horizons in the JDB section and from JDA 2 and 2.1 horizons of the JDA section (Fig. 2). *Diceratocephalus cornutus* was recovered from the JDA 3 horizon to JDA 9 horizon of the JDA section (Fig. 2).

Samples of limestone conglomerate and limestone nodules were digested with 7% hydrochloric acid and silicified trilobite sclerites were recovered from the residues. Apart from *C. convexa* and *D. cornutus*, the collected trilobite sclerites include *Neodrepanura premesnili* (Bergeron 1899), *Bergeronites ketteleri* (Monke 1903), *Shantungia spinifera* Walcott 1905; *Blackwelderia* sp., *Liostracina* sp., *Pseudagnostus* sp. and *Clavagnostus* sp. This faunal assemblage indicates that the studied interval belongs to the *Neodrepanura* Zone (formerly *Drepanura* Zone, see Özdikmen 2006)

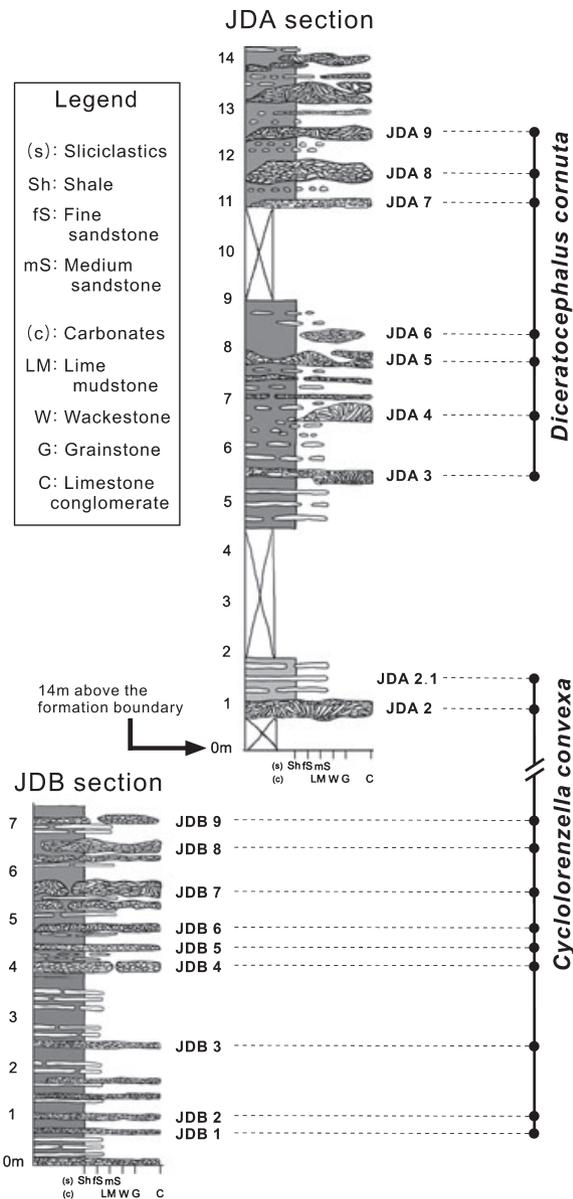


Fig. 2. Lithological columns of the Sesong Formation exposed in the Jikdong A and B sections, with stratigraphic occurrences of *Cyclorenzella convexa* (Resser & Endo in Endo & Resser 1937) and *Diceratocephalus cornutus* (Endo in Endo & Resser 1937).

of the Sesong Formation, which is latest middle Cambrian in age.

*Cyclorenzella convexa* is represented by 49 cranidia, 32 librigenae and 34 pygidia, while *D. cornutus* is represented by 33 cranidia, 20 librigenae and 21 pygidia. Small specimens were mounted on stubs, sputter-coated with gold and examined under a scanning electron microscope. The images of larger specimens were obtained using a digital camera. All of the specimens used in this study are housed in the palaeontological collections of Seoul National University, Korea, under the registered SNUP numbers.

## Notes on taxonomy and phylogeny

The genus *Cyclorenzella* was established by Kobayashi (1960) with the type species, *Lorezella quadrata* Kobayashi 1935; from the Sesong Formation, Korea. Subsequently more than 20 species have been referred to the genus from the upper middle Cambrian of China. Park *et al.* (2008) emended the generic concept of *Cyclorenzella* to include the forms having a short frontal area with convex preglabellar boss defined by parallel-sided longitudinal furrows. Accordingly, *Cyclorenzella* comprises only two species, *C. quadrata* and *C. convexa* (Resser & Endo in Endo & Resser 1937), whilst most of the species previously assigned to *Cyclorenzella* were transferred to *Jiulongshania* Park *et al.* 2008. *Cyclorenzella convexa* is differentiated from *C. quadrata* by its pustulose prosopon.

*Diceratocephalus* Lu 1954 was erected to accommodate cranidia bearing a pair of long frontal horns from the *Neodrepanura* Zone of Liaoning Province, North China. Seven species were assigned to *Diceratocephalus*: namely, the type species *D. armatus* Lu 1954; *D. latifrons* Lu 1954; *D. ezhuangensis* Qiu & Liu in Qiu *et al.* 1983; *D. dongyushanensis* Zhang & Wang 1985; *D. spinosus* Luo in Guo *et al.* 1996; *D. angustilimbatus* Guo & Luo in Guo *et al.* 1996 and *Blackwelderia* (?) *cornuta* Endo in Endo & Resser 1937 (*cf.* Guo *et al.* 1996). These species were differentiated on the basis of subtle differences in the shape of the frontal horns, relative length of the frontal area and surface sculpture. In this study, we suggest that all of the species referred to *Diceratocephalus* belong to a single species that shows a range of intraspecific variation. *Diceratocephalus cornutus* has a nomenclatural priority over all the other species.

*Cyclorenzella convexa* and *D. cornutus* share many morphological features such as a subtrapezoidal glabella, a convex preglabellar boss on the frontal area defined by parallel-sided longitudinal furrows, small palpebral lobes located posteriorly and a triangular occipital ring with a prominent occipital spine. The main difference lies in the presence of a pair of frontal horns in *D. cornutus*. The morphological correspondence between *Cyclorenzella* and *Diceratocephalus* was noted by Zhang & Jell (1987) who also suggested that *Diceratocephalus* may have evolved from *Cyclorenzella*. The fact that *C. convexa* shows no significant autapomorphies and the stratigraphic occurrence in which *C. convexa* precedes *D. cornutus* supports the phylogenetic interpretation of Zhang & Jell (1987): *C. convexa* is ancestral to *D. cornutus*.

## Ontogeny

No protaspis has been recognized for either *C. convexa* or *D. cornutus*, and therefore the description of ontogeny is limited to post-protaspis sclerites. Most of the specimens are disarticulated and thus the placement of cranial specimens into meraspid and holaspid stages is not possible. The bivariate plots of cranial length versus width do not reveal any biologically reasonable clustering of instars (Fig. 3). Consequently, the ontogenetic development of the cranidia in this study focuses only on shape changes with growth.

The trilobite trunk underwent dynamic changes in morphology during ontogeny with the generation of

new segments near the rear end of trunk and the release of thoracic segments from the anterior part of meraspid pygidia. Without any fully articulated specimens, it is generally difficult to distinguish meraspid and holaspid pygidia, and even more so for the recognition of meraspid degrees. However, for some trilobites having persistent structures such as macropleural segments or axial spine-bearing segments, the dynamics of ontogenetic development of the pygidium can be understood by observing the relative position of these structures during ontogeny (see Hughes 2003; Hughes *et al.* 2006). In the diceratocephalid trilobites, the persistent structure on the pygidium is the sculptural ridges running obliquely forward on the pleural field. Given the fixed position of the segment from

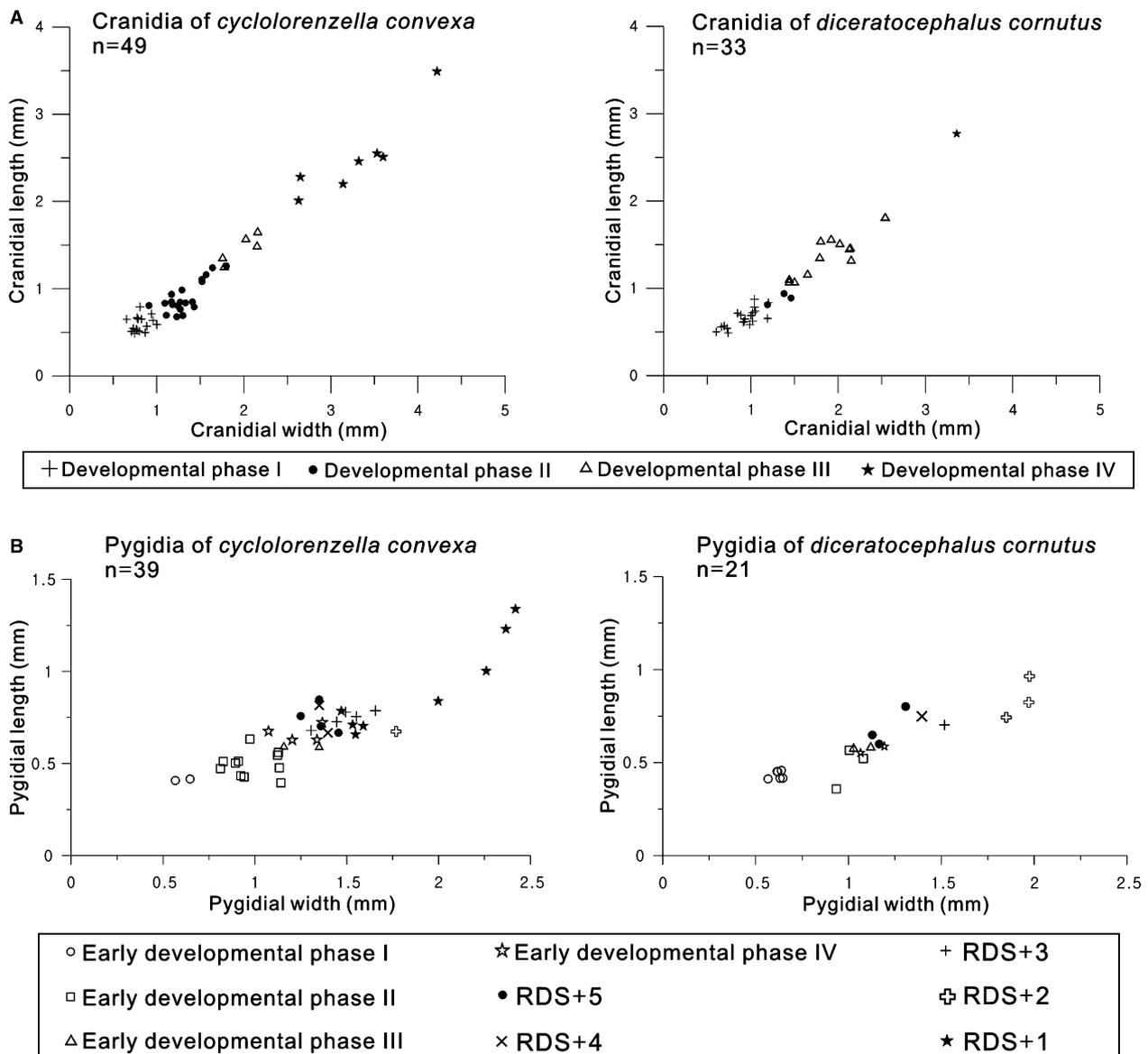


Fig. 3. Scatter plots of length versus width for cranidia and pygidia of *Cyclolorenzella convexa* (Resser & Endo in Endo & Resser 1937) and *Diceratocephalus cornutus* (Endo in Endo & Resser 1937). A, scatter plots for post-protaspis cranidia. B, scatter plots for meraspid and holaspid pygidia.

which the sculptural ridges diverge (hereafter 'the ridge-diverging segment', RDS) in holaspid pygidia, once the sculptural ridges appear on the meraspid pygidium during ontogeny, the number of segments in front of the RDS on the pygidium enables us to determine the meraspid degree to which the concerned meraspid pygidium belongs. There seems to be no more segment release from the pygidium after the RDS has become the second anteriormost segment in *C. convexa* (Fig. 6W–AB), while in *D. cornutus* no more segment release is observed after the RDS has become the third anteriormost segment (Fig. 9N, P and also see Lu *et al.* 1965, pl. 43, figs 22, 25). Nevertheless, without any definitive evidence of holaspid pygidial morphology, we will use the 'RDS +  $n$ ' ( $n$  = the number of segments in front of the RDS) scheme to indicate the ontogenetic stages of pygidia. Therefore, the supposed holaspid pygidium of *Cyclolorenzella* may correspond to the RDS + 1, while in *Diceratocephalus* the pygidium in holaspid phase may belong to the RDS + 2. The small immature pygidia in which the RDS is yet to be generated or the number of segments in front of the RDS is ambiguous are referred to the 'early developmental phase', which is divided, in turn, into four phases according to morphologic changes with growth.

## *Cyclolorenzella convexa*

### *Development of cranidium*

Park *et al.* (2008) described the mature cranidial morphology of *C. convexa* in detail. This study focuses only on morphologic changes in the post-protaspid cranidia (Fig. 4). For the purpose of description, the post-protaspid cranidia are divided into four developmental phases according to size and morphologic features.

The developmental phase I (Fig. 4A–C) contains small cranidia, 0.49–0.79 mm long and 0.65–0.96 mm wide. This phase displays features as follows: surface smooth; glabella slender, parallel-sided to slightly tapering forward; glabella ca. 21–24% of cranidial width; axial furrow shallow to moderately incised; a pair of longitudinal furrows on the frontal area; posterior border furrow shallow; occipital furrow weakly incised; occipital spine tumid, 25–33% of cranidial length, directed posteriorly upward; palpebral lobes are not recognizable in smaller specimens (Fig. 4A) but weakly visible in larger specimens (Fig. 4C); and preglabellar field 12–20% of cranidial length. In the developmental phase II (Fig. 4D, E), cranidia are 0.69–1.26 mm long and 0.91–1.80 mm wide. The surface is granulose in this phase: larger specimens (Fig. 4E) display conspicuous rows of thorn-like

pustules on the posterior margin of the occipital ring, the posterior margin of the posterior border, and the anterior margin of the cranidium. The glabella tapers slightly forward and is ca. 30% of the cranidial width. Paired longitudinal furrows on the frontal area are deeply incised. The palpebral lobes are clearly recognizable and the posterior border furrows are moderately incised. The developmental phase III (Fig. 4F–H) cranidia are 1.26–1.66 mm long and 1.75–2.16 mm wide. The thorn-like pustules are reduced in relative length. The glabella tapers moderately forward, and is defined by deep and wide axial furrows. The posterior border furrows are wider and deeper than those of the developmental phase II cranidia. The developmental phase IV cranidia (Fig. 4I–O) are thought to be morphologically mature. The glabella tapers moderately forward. Granules are variable in size and distribution. The length of the occipital spine is ca. 40% of the cranidial length. The largest specimen, 3.49 mm in length (Fig. 4N, O), displays randomly distributed thorn-like pustules on the surface.

### *Development of librigena*

The smallest specimen (Fig. 5A) has a smooth surface and a relatively narrow genal field. Morphological changes with growth include increase in granulosity; appearance of a row of pustules on lateral margin of genal field which continues along lateral margin of genal spine; appearance of a row of pustules on posterior margin of posterior border; enlargement of genal field; appearance of shallow lateral border furrow; inward-curving of genal spine; and downward-curving of cephalic doublure adaxially (Fig. 5D).

### *Development of pygidium*

The early developmental phase I includes small pygidia which are about 0.4–0.5 mm in length (Fig. 6A, B). One short axial spine projects from the middle part of pygidium, which is directed posteriorly upward. The posterior border is narrow, defined by a faint shallow posterior border furrow. During the early developmental phase II (Fig. 6C–L), the anteriormost segment possesses a long axial spine which is generally curved rearward. This phase II may contain several instars, taking into account the differences in size and morphology. In the early developmental phase III (Fig. 6M, N), however, a relatively short axial spine is expressed in the anteriormost segment, and transaxial furrows, pleural furrows and inter-pleural furrows are weakly developed. The axis comprises four or five axial rings. Several pustules are present on the surface. Pygidia in early developmental phase IV (Fig. 6O, P) display the sculptural ridges running

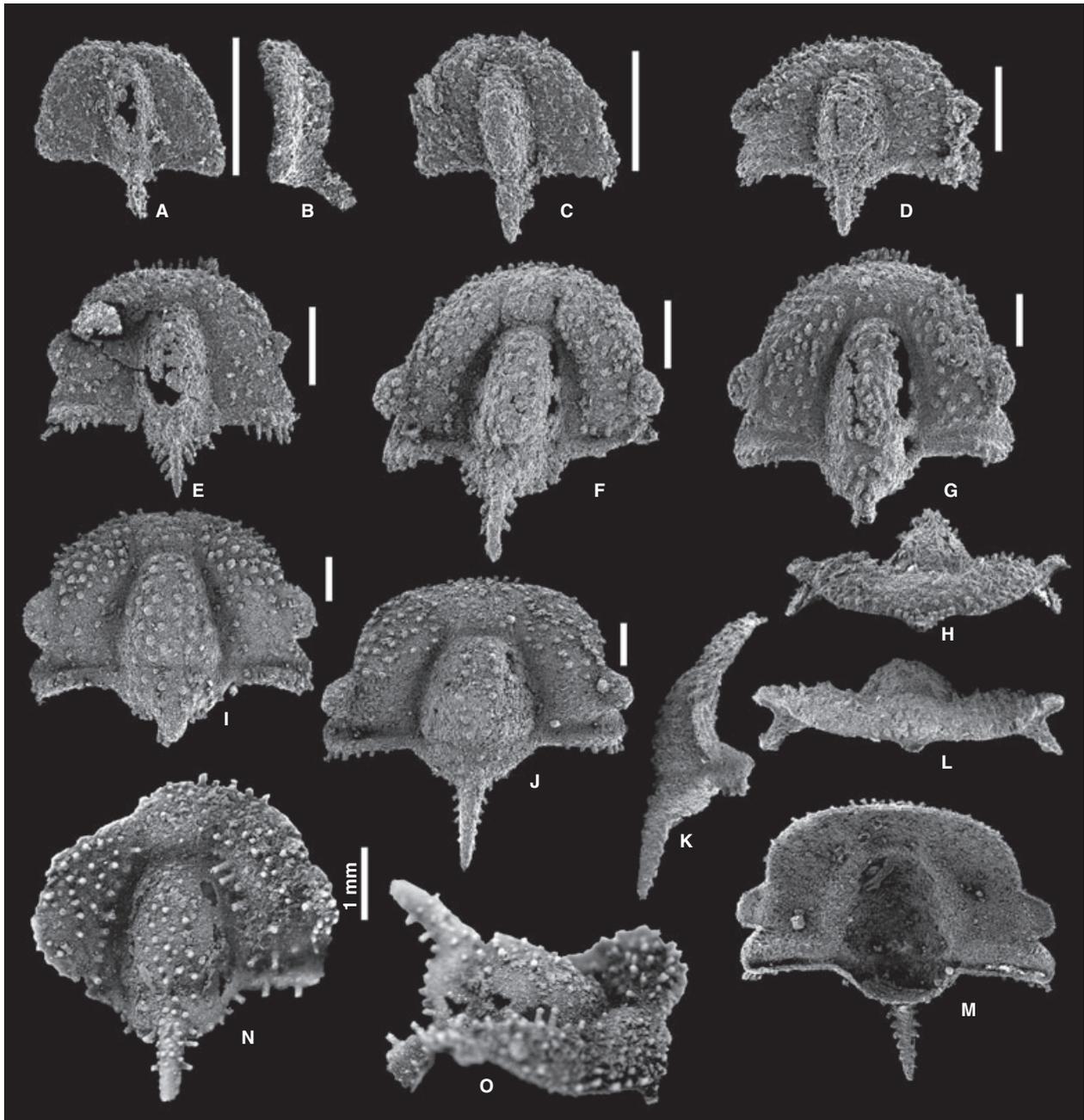


Fig. 4. Cranidia of *Cyclolorenzella convexa* (Resser & Endo in Endo & Resser 1937). A–C, developmental phase I. A–B, SNUP4700, dorsal and lateral views. C, SNUP4701. D–E, developmental phase II. D, SNUP4702. E, SNUP4504. F–H, Developmental phase III. F, SNUP4501. G–H, SNUP4502, dorsal and anterior views. I–O, developmental phase IV. I, SNUP4503. J–M, SNUP4504, dorsal, lateral, anterior, and ventral views. N–O, SNUP4703, dorsal, and oblique antero-lateral views. Scale bars are 0.5 mm long, if not mentioned otherwise.

obliquely forward from the posteriormost axial ring; ridges are slightly removed from the posterior pygidial margin. Five or six axial rings are recognizable in front of the RDS. The posterior margin is slightly indented dorsally in posterior view (Fig. 6P).

In the RDS + 5 pygidia (Fig. 6Q, R), five axial rings are visible in front of the RDS. The pleural and interpleural furrows are better developed than those of pygidia in the previous stages. Thorn-like pustules are distributed on the pleural field. The RDS + 4 pygidia

(Fig. 6S) exhibit four axial rings in front of the RDS. The RDS + 3 pygidia (Fig. 6T, U) have three axial rings in front of the RDS and the axis is posteriorly rounded. Pustules are not present on the area behind the sculptural ridges. The RDS + 2 pygidia are represented by one poorly preserved specimen (Fig. 6V), which has two axial rings in front of the RDS. Pustules are visible only in the anteriormost segment. The RDS + 1 pygidia (Fig. 6W–AB) are characterized by having only one axial ring in front of the RDS. As no

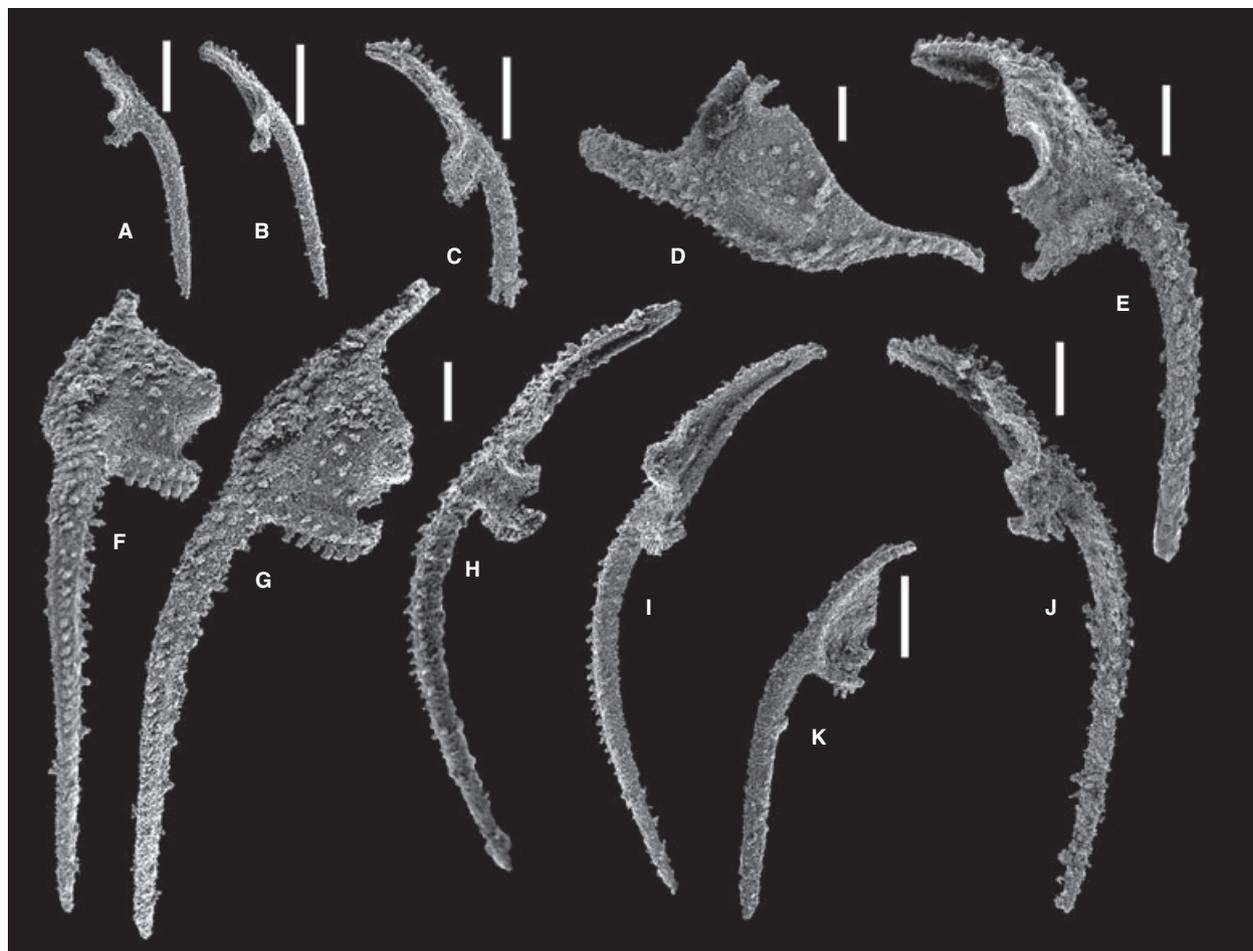


Fig. 5. Librigenae of *Cyclolorenzella convexa* (Resser & Endo in Endo & Resser 1937). A–B, SNUP4704, oblique lateral, and dorsal views. C, SNUP4705. D, SNUP4510. E, SNUP4706. F–I, SNUP4508, posterolateral view, oblique lateral view, dorsal view and oblique lateral view from right-hand side respectively. Note that the visual surface is retained. J, SNUP4509. K, SNUP4707. Scale bars are 0.5 mm long.

more segment release is observed, it probably represents the start of the holaspid phase. The RDS + 1 pygidia are 0.66–1.34 mm long and 1.55–2.42 mm wide. No pustules are present on the surface. The sculptural ridges diverging from the rear margin of terminal piece are visible (Fig. 6W, Z) but are faintly developed in the largest pygidium (Fig. 6AA).

It is noteworthy that the size of the pygidium remains more or less constant from the RDS + 5 stage to the early phase of the RDS + 1 stage (Fig. 3B). Although it is difficult to count the number of axial segments behind the RDS in the pygidia of *C. convexa*, this stability in pygidial size during development may represent a depletion phase in which segment release from the anterior part of the pygidium into the thorax continued after the generation of new segments in the posterior part of the pygidium had ceased (Hughes *et al.* 2006). Simpson *et al.* (2005, fig. 9) reported the pygidial development of *Hintzeia plicamarginis* Simpson *et al.* 2005 and showed that there was no significant increase in the immature pygidial size during the

depletion phase. In the depletion phase of the pygidium of *H. plicamarginis*, the net increase in the size of the remaining segments of the pygidium compensated for the decrease in size due to the loss of segments during development (Simpson *et al.* 2005, p. 533). The mode of segmental development of *C. convexa* can be referred to as ‘protomeric’, in which onset of the epimorphic phase preceded onset of the holaspid phase (Hughes *et al.* 2006).

### *Diceratocephalus cornutus*

#### *Remarks on morphology*

*Diceratocephalus cornutus* is morphologically closely comparable with *C. convexa* but differs in having a pair of frontal horns in the cephalon and two axial rings in front of the RDS in the presumed holaspid pygidium. A single poorly preserved exoskeleton is preserved in partly enrolled posture (Fig. 7O, P). The poor preservation of

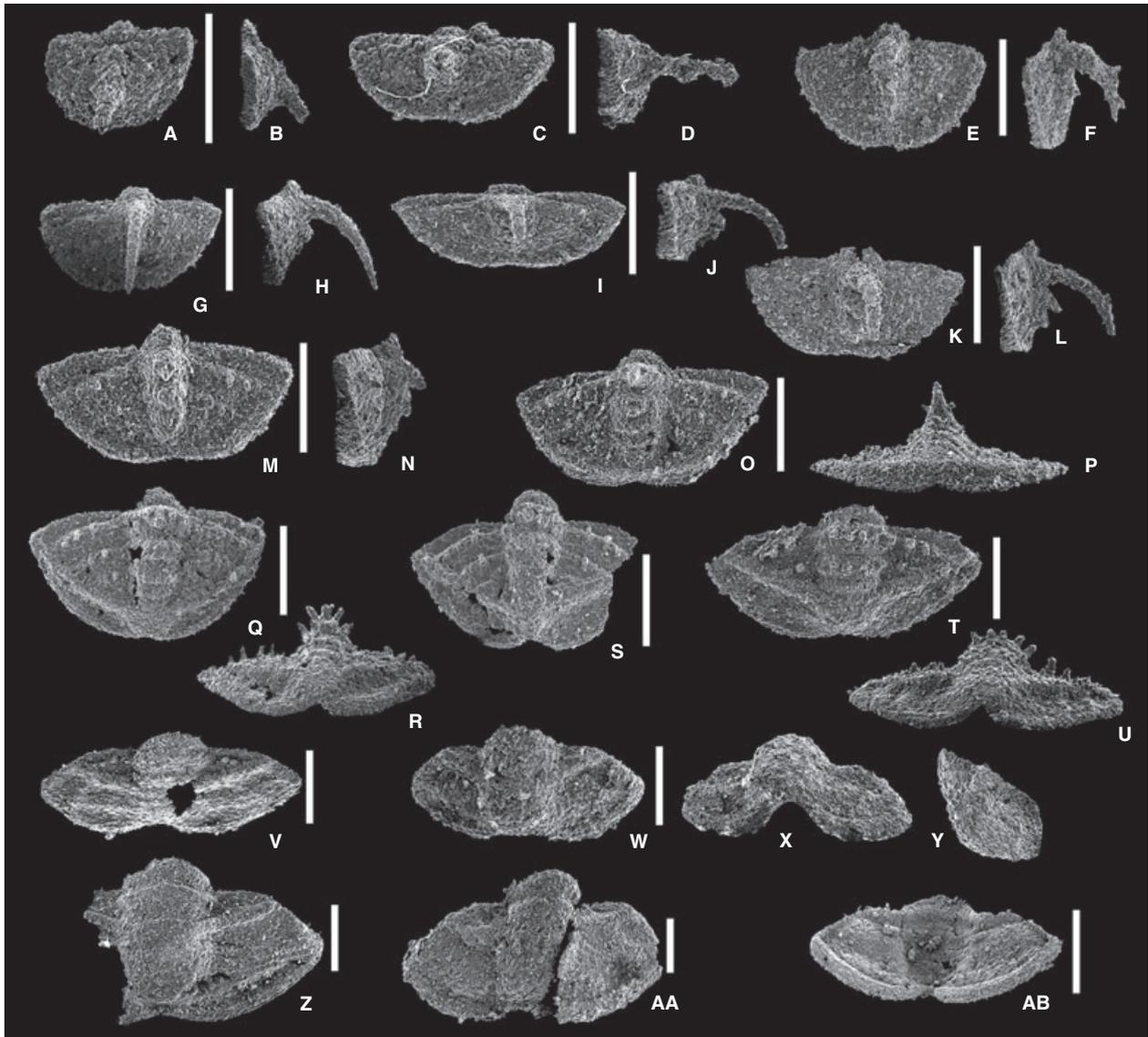


Fig. 6. Pygidia of *Cyclolorenzella convexa* (Resser & Endo in Endo & Resser 1937). A–B, pygidium at the early developmental phase I; SNUP4709, dorsal and lateral views. C–L, pygidia at the early developmental phase II. C–D, SNUP4710, dorsal and lateral views. E–F, SNUP4711, dorsal and lateral views. G–H, SNUP4712, dorsal and lateral views. I–J, SNUP4713, dorsal and lateral views. K–L, SNUP4714, dorsal and lateral views. M–N, pygidium at the early developmental phase III; SNUP4715, dorsal and lateral views. O–P, pygidium at the early developmental phase IV; SNUP4716, dorsal and posterior views. Q–R, RDS + 5 pygidium; SNUP4717, dorsal and posterior views. S, RDS + 4 pygidium; SNUP4718. T–U, RDS + 3 pygidium; SNUP4719 dorsal and posterior views. V, RDS + 2 pygidium; SNUP4720. W–AB, RDS + 1 pygidia which are assumed to be in the holaspis phase. W–Y, dorsal, posterior, and lateral views respectively. SNUP4513. Z, SNUP4721. AA, SNUP4514. AB, SNUP4722, ventral view. Scale bars are 0.5 mm long.

the specimen hinders counting the number of thoracic segments, but nine or ten axial rings appear to be situated in front of the RDS, which would make seven or eight thoracic segments in holaspis. However, without any certainty, we will use the 'RDS +  $n$ ' to denote the developmental stages of pygidia.

#### *Cranidium ontogeny*

Despite the similar cranidial morphology to *C. convexa*, the four developmental phases of *D. cornutus* may not be directly equated with those of *C. convexa*.

The developmental phase I (Fig. 7A–D) includes all small cranidia without the frontal horns. The cranidia are 0.49–0.86 mm long and 0.60–1.20 mm wide. The occipital spine is 28–36% of the cranidial length. The large specimen (Fig. 7D) possesses a row of thorn-like pustules on either side of the occipital spine. Morphological features and changes with growth at this phase are similar to those of *C. convexa*. Developmental phase II (Fig. 7E) is defined as the stage in which short frontal horns appear. Three cranidia are assigned to this phase (Fig. 3A) and are 0.81–0.94 mm long and 1.19–1.46 mm wide. The frontal horn is ca. 10% of the cranidial length and the occipital spine is

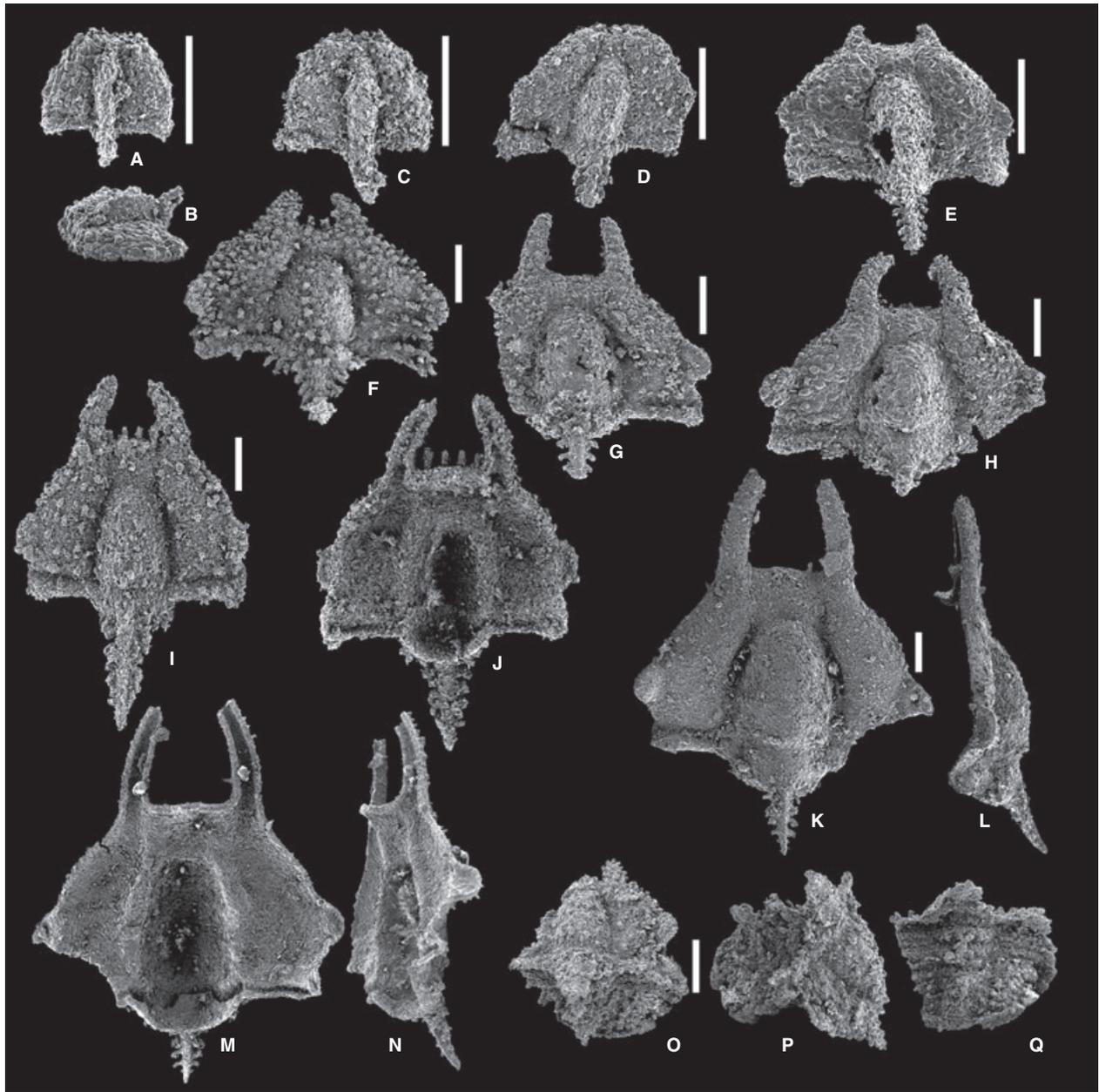


Fig. 7. Cranidia of *Diceratocephalus cornutus* (Endo in Endo & Resser 1937). A–D, developmental phase I. A–B, SNUP4723, dorsal and oblique lateral views. C, SNUP4724. D, SNUP4725. E, Developmental phase II, SNUP4726. F–J, Developmental phase III. F, SNUP4727. G, SNUP4728. H, SNUP4729. I–J, SNUP4730, dorsal and ventral views. K–N, developmental phase IV, SNUP4731, dorsal, lateral, ventral and ventro-lateral views. O–Q, poorly preserved partially enrolled meraspid specimen with articulated trunk; SNUP4732. O, dorsal view. P, oblique lateral view. Q, dorsal view of the trunk. Scale bars are 0.5 mm long.

34–41% of the cranidial length. During developmental phase III (Fig. 7F–J), the frontal horns measure 23–36% of the cranidial length. The cranidia are 1.08–1.82 mm long and 1.44–2.54 mm wide. Some specimens (Figs 7F, I) have a strongly granulate prosopon, while others have subdued pustules (Figs 7G, H). The occipital spine is 41–54% of the cranidial length. The largest specimen (Fig. 7K–N) is 2.77 mm long and belongs to developmental phase IV. The incomplete frontal horns are 43% of the cranidial length. The surface is smooth. The

occipital spine is ca. 30% of the cranidial length. To sum up, the cranidial ontogeny of *D. cornutus* is closely similar to that of *C. convexa*, except for the presence of frontal horns and the slightly longer occipital spine during early ontogeny.

#### *Ontogeny of librigenae*

Librigenae include the ventral half of the frontal horns which match the dorsal half of the horns in cranidia.

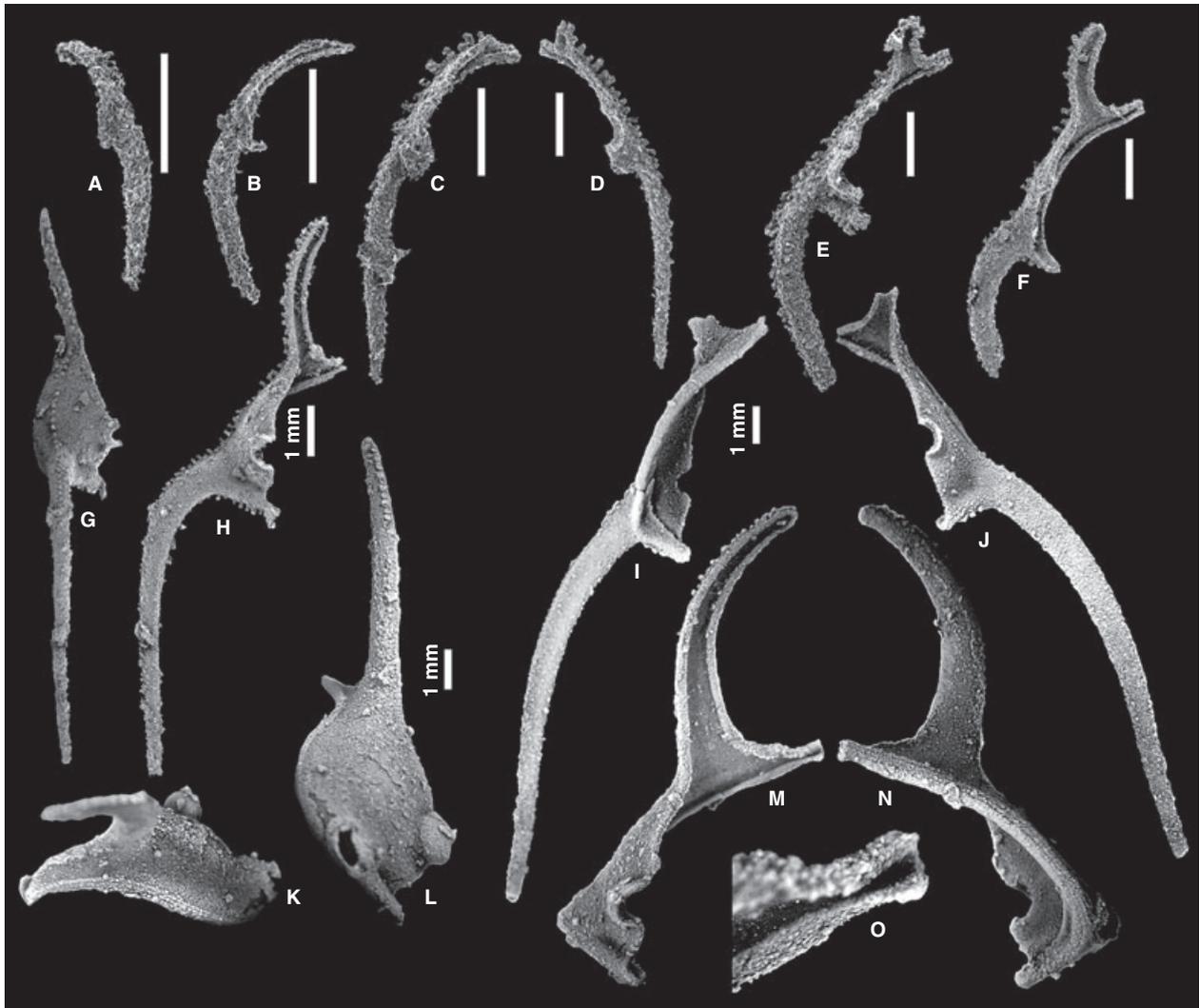


Fig. 8. Librigenae of *Diceratocephalus cornutus* (Endo in Endo & Resser 1937). A, SNUP4733. B, SNUP4734. C, SNUP4735. D, SNUP4736. E, SNUP4737. F, SNUP4738. G–H, SNUP4739, lateral and dorsal views. I–J, SNUP4740, dorsal and ventral views. K–N, SNUP4741, anterior, lateral, dorsal and ventral views respectively. O, magnified view of cephalic doublure of SNUP4741. Scale bars are 0.5 mm long, if not indicated otherwise.

The small librigenae (Fig. 8A, B) lacking the frontal horns may correspond to developmental phase I cranidia. The complete librigena (Fig. 8G, H) bears a row of pustules running from the anterior tip of the frontal horn along the lateral margin of genal field to the anterior lateral margin of the genal spine. However, in the larger fragmentary specimens (Fig. 8K–N), pustules are only present on the anterior part of the lateral margin of the frontal horn.

#### *Pygidium ontogeny*

The ontogeny of pygidia of *D. cornutus* (Fig. 9) is similar to that of *C. convexa*. Smaller immature pygidia at the early developmental phases I–IV (Fig. 9A–J) show

a similar trend in morphologic development to those of *C. convexa*, but the long axial spine in the anterior-most segment tends to curve rearward more abruptly in pygidia of *D. cornutus*. The holaspid phase of *D. cornutus* seems to have two axial rings in front of the RDS (RDS + 2). The specimens referred to the RDS + 2 stage (Fig. 9N–P) are 0.74–0.96 mm long and 1.85–1.97 mm wide. The previously reported larger specimens of *D. cornutus* (Lu *et al.* 1965; pl. 43, figs 22, 25) also possess two axial rings in front of the RDS, suggesting that there was no more segment release after the RDS + 2 stage. Accordingly, the RDS + 3 specimen with three axial rings in front of the RDS (Fig. 9M) would be the meraspid degree just before the holaspid phase.

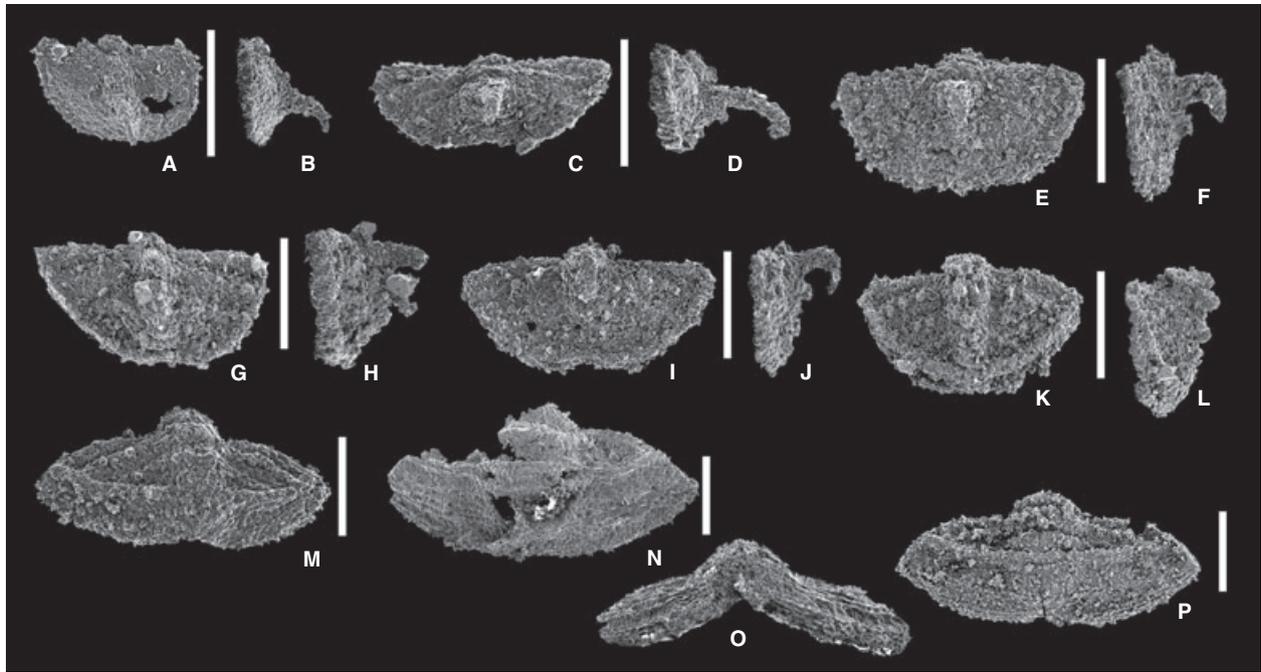


Fig. 9. Pygidia of *Diceratocephalus cornutus* (Endo in Endo & Resser 1937). A–B, pygidium at the early developmental phase I; SNUP4744, dorsal and lateral views. C–F, pygidia at the early developmental phase II. C–D, SNUP4745, dorsal and lateral views. E–F, SNUP4746, dorsal and lateral views. G–H, pygidium at the early developmental phase III; SNUP4747, dorsal and lateral views. I–J, pygidium at the early developmental phase IV; SNUP4748, dorsal and lateral views. K–L, RDS + 5 pygidium; SNUP4749, dorsal and lateral views. M, RDS + 3 pygidium; SNUP4750. N–P, RDS + 2 pygidia which are supposed to be in the holaspid phase. N–O, SNUP4751, dorsal and posterior views. P, SNUP4752. Scale bars are 0.5 mm long, if not mentioned otherwise.

## Discussion

Silicified material of two diceratocephalid species in this study offers an excellent opportunity to observe some unique morphological features of those trilobites with ancestor–descendant relationship. Accordingly, the novel evolutionary structure of the descendant species, *D. cornutus*, is discussed in terms of: (1) developmental origin of the frontal horns; (2) their functional morphology; and (3) functional morphology of the facial suture which splits the frontal horns into the dorsal and ventral halves.

### *How did Diceratocephalus cornutus gain its horns?*

The frontal horns of *D. cornutus* project anteriorly from the anterior margin of the cephalon, a feature unique to this trilobite. Other trilobite genera with a pair of horn-like structures projecting from the cephalon include the Silurian encrinurid *Perirehaedulus* Adrain & Edgecombe 1995 and the lower Cambrian eodiscoid *Dicerodiscus* Zhang 1964. However, the horn-like structures of *Perirehaedulus* emerge from the frontal lobe of the glabella, while those of *Dicerodiscus* are directed laterally and then curve rearward. Moreover, the ventral half of each frontal horn of *D.*

belongs to the doublure of the librigena (Fig. 8C–O). The frontal horns of *D. cornutus* have no homologues in the Class Trilobita and hence can be considered as an evolutionary novelty (*sensu* Müller & Wagner 1991; also see Raff 1996, p. 399; Arthur 2004; Carroll *et al.* 2005, p. 160).

The lack of any hint of frontal horns in the ontogenetic development of the ancestral species, *C. convexa*, discounts any explanation of their origin by heterochronic evolution. Other cases like heterotopy, heterotypy, heterometry and allometric repatterning (*sensu* Webster & Zelditch 2005) are also inapplicable as an explanation, because all these evolutionary modes revolve around the modification of structures that already existed in ancestral species.

The redeployment of already existing regulatory genes has been proved to be a powerful mechanism for generating evolutionary novelties (e.g. Raff 1996; True & Carroll 2002; Carroll *et al.* 2005), which may also apply for the evolution of frontal horns of *D. cornutus*. As an analogue to the horn-developmental process, recent works on the extant dung beetle genus *Onthophagus* are worth discussing. *Onthophagus* contains more than 2000 species, many of which have anteriorly projecting horns on their head and pronotum and show a wide range of variation in morphology and number of horns (Emlen *et al.* 2005). As

beetle horns lack any homologues in other groups of insects, the developmental process of beetle horns may provide a significant insight into the development of the frontal horns of *D. cornutus*. Moczek & Nagy (2005) discovered that, during development, the horns of *Onthophagus* share some of the same patterning genes with insect appendages and, among others, the *Distal-less* (*Dll*) gene plays a significant role in generating the horns; DLL protein was found to be expressed wherever the horns grow.

It is well known that the *Dll* gene causes distalization and outgrowth, encodes for distal structures, and provides information for establishing the proximal/distal coordinates of the leg (Williams 1998), and its expression has been utilized repeatedly in body wall outgrowth in different animals. As the *Dll* gene is so widespread and used for body wall outgrowth during development throughout the Bilateria, it is even inferred to have existed in the ancestral Urbilateria (Panganiban *et al.* 1997; Shubin *et al.* 1997; Carroll 2005). Trilobita, an ancient arthropod group, may have possessed and used this gene for limb and spine development, and for *D. cornutus* the easiest way to evolve the frontal horns might have been by redeploying the *Dll* gene.

#### Why did *Diceratocephalus cornutus* evolve the frontal horns?

Anteriorly oriented spine-pairs are displayed by many globular protaspides and have been interpreted as buoyancy-boosting structures (Speyer & Chatterton 1989). To balance the buoyancy over the body, pairs of spines are located in other regions of the body (Speyer & Chatterton 1989; Chatterton & Speyer 1997) and without exception, all the spines disappear during ontogeny, reflecting changes in mode of life from planktonic to nekto-benthic. Such anteriorly oriented spine-pairs remained until early meraspid stages in some trilobites such as *Olenelloides* Peach 1894; *Jujuyaspis keideli* Kobayashi 1936; *Leptoplastus salteri* (Callaway 1877), *Menoparia genalunata*, Ross 1951; and *Triarthrus latissimus* Månsson 1998 (see McNamara 1978 for ontogeny of *Olenelloides*; Tortello & Clarkson 2003 for ontogeny of *J. keideli*; Raw 1925 for

ontogeny of *L. salteri*; Ross 1952 for ontogeny of *M. genalunata*; and Månsson 1998 for ontogeny of *T. latissimus*).

Were the frontal horns of *D. cornutus* also a buoyancy-improving structure? In *D. cornutus*, the earliest immature cranidia do not show any trace of horns (Fig. 7A–D). The anteriorly projecting horn-pair first emerges when the cranidium measures ca. 0.8 mm in length (Fig. 7E), and subsequently gets longer throughout ontogeny until the horn becomes as long as the remainder of the cranidium. Therefore, the horns of *D. cornutus* must have been functional at maturity. The comparison of overall morphology of a poorly preserved articulated specimen (Fig. 7O, P) with those of pelagic trilobites (Fortey 1985) suggests that *D. cornutus* had probably a benthic mode of life, and hence the frontal horns were not used for boosting buoyancy.

Raphiophorid trilobites usually exhibit a single spine on the frontal glabellar lobe. Knell & Fortey (2005) suggested that the anterior spine of the Raphiophoridae might have been used as weaponry in intrasexual contests to overturn, push or lift rivals, just like beetle horns are used. They also believed it possible that the frontal horns of *Diceratocephalus* might have had a similar function. However, the frontal horns of *Diceratocephalus* are forwardly downsloping in lateral view: even the tip of the frontal horns may have touched the substrate surface (Fig. 10). It is doubtful if such forwardly downsloping horns are useful in lifting and/or overturning rivals in intrasexual contest. Knell & Fortey (2005, fig. 1) illustrated three-horned beetles as analogues, including *Oxysternon spiniferum* whose short pronotal horn slopes down forward, and they considered it as a case of weaponry. However, Moczek *et al.* (2006) revealed that such short pronotal horns are exaptations from pupal structures, which help the animal to shed the larval head capsule during pupation, rather than weaponry for intrasexual contest among adults. Therefore, the consideration by Knell & Fortey (2005) of the downsloping pronotal horn of *O. spiniferum* as weaponry can be discounted. Similarly, it is unlikely that the frontal horns of *D. cornutus* would have been used for intrasexual contests. In addition, there is no evidence of sexual dimorphism in *D. cornutus* which, if present,

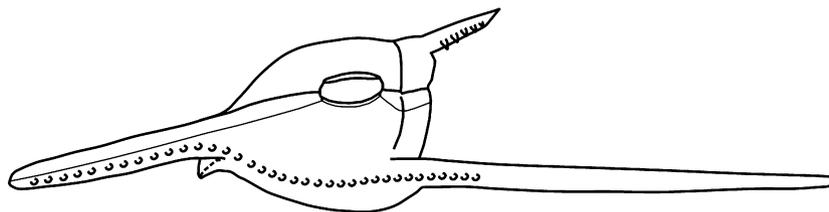


Fig. 10. Reconstruction of the cephalon of *Diceratocephalus cornutus* (Endo in Endo & Resser 1937) in lateral view. Note that the frontal horns slope gently downwards. The reconstruction is made mainly on the basis of SNUP4739 (Fig. 8G–H).

would have been a strong case for interpreting the horns as secondary sexual structures.

Why did *D. cornutus* evolve the anteriorly projecting horns? Morphologies of damesellid trilobites co-occurring with *D. cornutus* have led us to some ideas on the possible function of the frontal horns. The damesellids from the *Neodrepanura* Zone of Korea and China, such as *S. spinifera* Walcott 1905; *B. ketteleri* (Monke 1903), and *N. premesnili* (Bergeron 1899), possessed a pair of macropleural spines in the pygidium (see Zhang & Jell 1987; Guo *et al.* 1996). Notably, the backwardly directed macropleural spines of *B. ketteleri* and *N. premesnili* are so long that, when enrolled, the spines would have protruded forward beyond the anterior margin of the cephalon. Hence, in dorsal view, the enrolled animals would have looked as if they had a pair of spines projecting anteriorly from the cephalon (Fig. 11). We infer that, in terms of functional morphology, the anteriorly projecting frontal horns of *D. cornutus* played a role similar to the macropleural spines in the pygidia of *B. ketteleri* and *N. premesnili* in the enrolled position: these three contemporaneous trilobites came up with the same strategy. The role of these spines would have been to deter

predators from attacking and/or opening the enrolled individual.

#### Facial suture of *Diceratocephalus cornutus*

*Diceratocephalus cornutus* has a facial suture which extends forward along the lateral margin of the frontal horns. Therefore, during ecdysis, the horns split into dorsal and ventral halves. Why should the horns have been split in this manner during ecdysis? When trilobites underwent exuviation, the facial sutures were opened and the newly moulted animal emerged forwards through the anterior opening (Henningsmoen 1975; Whittington 1990). Because the newly moulted soft trilobite emerged 'forward' below the old exuvium, the old cranidium could not be allowed to form an exoskeletal 'anterior pocket' (*sensu* Henningsmoen 1975, p. 83). Otherwise, it would be difficult for the individual to extract itself forwards. Henningsmoen (1975, p. 83) considered that it was possible to avoid such a pocket by varying the location of the anterior branch of facial suture. Henningsmoen's (1975) anterior pocket hypothesis is quite reasonable in that most of the spinose structures of trilobites, such as genal spines, axial spines and pygidial spines are directed

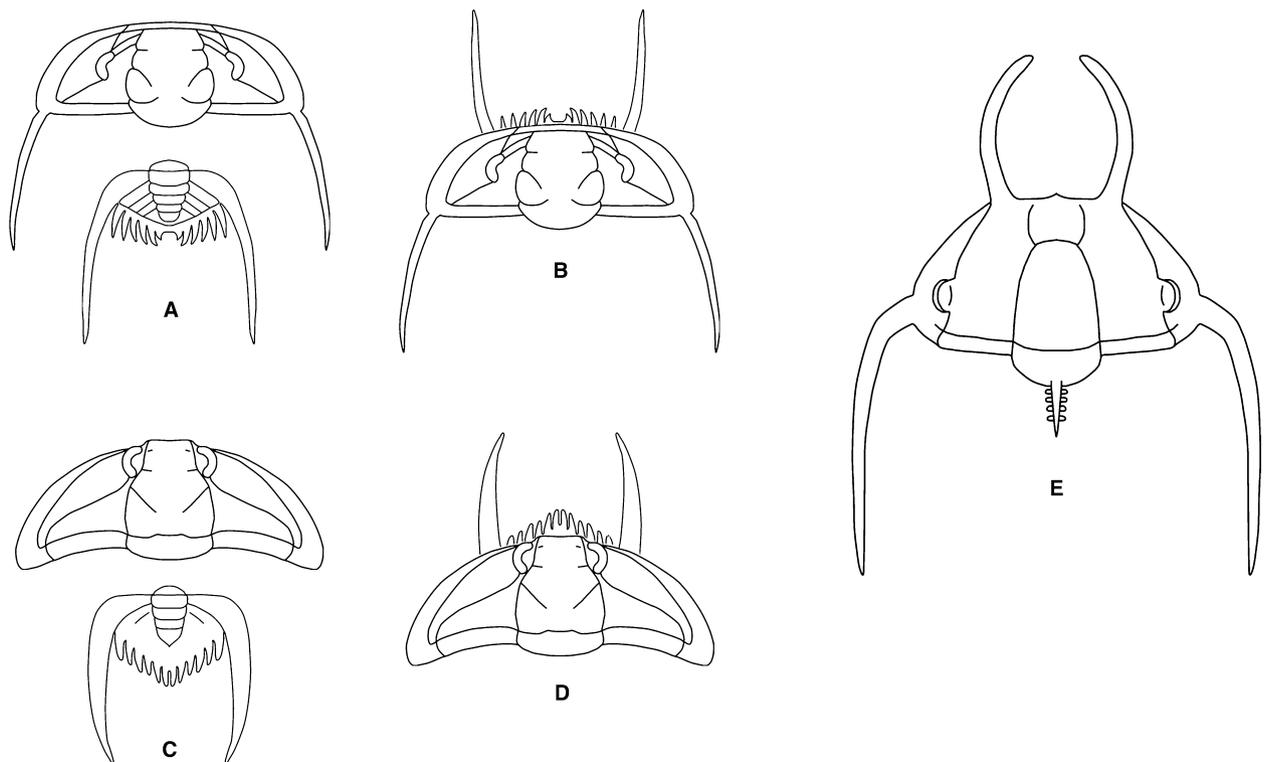


Fig. 11. Reconstructions of *Bergeronites ketteleri* (Monke 1903), *Neodrepanura premesnili* (Bergeron 1899) and *Diceratocephalus cornutus* (Endo *in* Endo & Resser 1937). Note that the long pygidial spines of *B. ketteleri* and *N. premesnili* poke forward out of the anterior margin of the cephalon in enrolled position. A, cephalon and pygidium of *B. ketteleri*. B, reconstruction of cephalon and pygidium of *B. ketteleri* in postulated enrolled position. C, cephalon and pygidium of *N. premesnili*. D, reconstruction of cephalon and pygidium of *N. premesnili* in postulated enrolled position. E, cephalon of *D. cornutus*.

'backward' and do not form any anterior 'dead end' for the advancing newly moulted animal. Henningsmoen (1975, fig. 2D) demonstrated that the anterior tip of the anteriorly projecting spine of *Megistaspidea* Jaanusson 1956 is divided by the anterior branch of facial suture, and hence there would not have been any barrier for the advance of the newly moulted animal. The same may have applied to *D. cornutus*. Having the anterior branch of the facial suture running along the lateral margin of the frontal horns, the newly moulted animal would not have been hindered in egressing forward during ecdysis.

## Conclusions

The silicified material of two diceratocephalid trilobites, *C. convexa* and *D. cornutus*, reveal detailed morphology as well as the partial ontogenies of these trilobites with ancestor–descendant relationship. Based on this information, the developmental origin and functional morphology of the frontal horns of *D. cornutus* are discussed. The pair of frontal horns of *D. cornutus* can be considered as an evolutionary novelty, and redeployment of pre-existing regulatory gene is credited with the formation of this novel structure. The frontal horns of *D. cornutus* may have been a defensive structure to deter predators during enrolment. The unusual course of the facial suture of *D. cornutus* was a solution for this anteriorly projecting horn-bearing animal to enable easier forward egression during ecdysis.

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