A new genus of sinogaleaspids (Galeaspida, stem-Gnathostomata) from the Silurian Period in Jiangxi, China

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Galeaspida are an endemic clade of jawless stem-gnathostomes known as ostracoderms. Their existence illuminates how specific characteristics developed in jawed vertebrates. Sinogaleaspids are of particular interest among the galeaspids but their monophyly is controversial because little is known about *Sinogaleaspis xikengensis*. Newly discovered sinogaleaspids from the Lower Silurian of Jiangxi, China provide a wealth of data and diagnostic features used to establish the new genus, *Rumporostralis* gen. nov., for *Sinogaleaspis xikengensis*. A morphological study showed that t he sensory canal system of sinogaleaspids had mosaic features similar to those of three known galeaspids. There are 3-8 pairs of transverse canals in the Sinogaleaspidae, which suggests that the sensory canal system of galeaspid probably had a grid distribution with transverse canals arranged throughout the cephalic division. Phylogenetic analysis of Galeaspida supports the monophyly of the Sinogaleaspidae , consisting of *Sinogaleaspis*, *Rumporostralis,* and *Anjiaspis*. However, *Shuyu* and *Meishanaspis* form another monophyletic group, Shuyuidae fam. nov., which is outside all other eugaleaspidiforms. We propose a cladistically-based classification of Galeaspida based on our analysis.

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16 **ABSTRACT**

17   Galeaspida are an endemic clade of jawless stem-gnathostomes known as ostracoderms. Their existence
18 illuminates how specific characteristics developed in jawed vertebrates. Sinogaleaspids are of particular interest
19 among the galeaspids but their monophyly is controversial because little is known about *Sinogaleaspis xikengensis*.
20 Newly discovered sinogaleaspids from the Lower Silurian of Jiangxi, China provide a wealth of data and diagnostic
21 features used to establish the new genus, *Rumporostralis* gen. nov., for *Sinogaleaspis xikengensis*. A morphological
22 study showed that the sensory canal system of sinogaleaspids had mosaic features similar to those of three known
23 galeaspids. There are 3-8 pairs of transverse canals in the Sinogaleaspidae, which suggests that the sensory canal
24 system of galeaspid probably had a grid distribution with transverse canals arranged throughout the cephalic
25 division. Phylogenetic analysis of Galeaspida supports the monophyly of the Sinogaleaspidae, consisting of
26 *Sinogaleaspis*, *Rumporostralis,* and *Anjiaspis*. However, *Shuyu* and *Meishanaspis* form another monophyletic group,
27 Shuyuidae fam. nov., which is outside all other eugaleaspidiforms. We propose a cladistically-based classification of
28 Galeaspida based on our analysis.

30 **INTRODUCTION**
31   The Silurian–Devonian armored galeaspids were a prevalent and diverse clade of jawless stem-gnathostomes
32 (Fig.1A) that exhibited traits thought to belong to jawed gnathostomes (Gai et al., 2011; Gai & Zhu, 2012; Gai et al.,
33 2019a). They contribute to our understanding of the conformation of the gnathostome body, which is significant to
34 vertebrate evolution (Sansom et al., 2008). The family Sinogaleaspidae of the Eugaleaspidiformes within the
35 Galeaspida, from the Lower Silurian of Xiushui, Jiangxi province and Changxing, Zhejiang province, is an
36 important early clade (Fig.1B-D) possessing the characteristics that demonstrate the step-by-step transitions from
37 jawless to jawed vertebrates. SRXTM provides an example of the cranial anatomy of *Shuyu*, a sinogaleaspid, and
38 other important characteristics that may be compared with other early vertebrate groups (Gai et al. 2011; Gai & Zhu
39 2012; Gai et al. 2019a). However, the phylogeny and morphology of its constituents are still disputed.
40   The family Sinogaleaspidae was proposed by Pan and Wang (1980), and morphologically includes the species
41 *Sinogaleaspis*, *S. shankouensis, Meishanaspis* and *Anjiaspis*, and '*S.*' *xikengensis*, and '*S.*' *zhejiangensis* (Pan &
42 Wang, 1980; Pan, 1986a; Wang, 1991; Gai & Zhu, 2005; Gai et al., 2005; Liu et al., 2015). It remains unknown
43 whether Sinogaleaspidae is a monophyletic group (Fig.1B-D) (Zhu, 1992; Gai et al., 2005; Zhu & Gai, 2006; Gai et
44 al., 2018). Gai et al. (2005) suggested that the three species assigned to *Sinogaleaspis* formed a paraphyletic group
45 instead of a monophyletic group (Fig.1C). *S. shankouensis* is more closely related to *Yunnanogaleaspis* and higher

46 eugaleaspids than to '*S.' zhejiangensis* and *'S.' xikengensis* (Fig.1C; Gai et al., 2005), whereas '*S.' zhejiangensis*
47 was determined as the sister to all other eugaleaspididiforms in later phylogenetic analyses (Fig.1D; Zhu & Gai,
48 2006; Gai et al., 2018). Gai et al. (2011) determined the genus *Shuyu* for '*S.' zhejiangensis* based on novel material,
49 especially the three-dimensional images of the neurocrania. However, the systematic position of '*S.' xikengensis*
50 (Pan & Wang, 1980) is still unresolved due to its poor preservation and large amounts of missing data, especially
51 related to its sensory canal system.
52
53
54   Five excavations of the Lower Silurian region of Xiushui, Jiangxi province have been organized since 2003.
55 This location is the primary site of *'S.' xikengensis* discovery and an abundance of Silurian fish remains have been
56 found here, including sinogaleaspids, xiushuiaspids, and sclerites of dayongaspids and hanyangaspids. Our study
57 describes newly discovered sinogaleaspid fossils and discusses their importance to the phylogeny of the
58 Eugaleaspidiformes.
59
60 **GEOLOGICAL SETTING**
61   The Silurian strata in the northwestern Jiangxi province are subdivided into six formations: the Lishuwo,
62 Dianbei, Qingshui, Xiajiaqiao, Xikeng, and Xiaoxi formations (Zhao et al., 2009; Zhao & Zhu, 2010; Wang et al.,
63 2018; Rong et al., 2019). New sinogaleaspid material was collected from two fossil sites in the Xikeng formation at
64 Taiyangsheng, Xiushui County, Jiangxi province near Xikeng village (Fig.2A) and a newly discovered location on
65 the side of Shipan Reservoir (Fig.2A). The Xikeng formation is mainly composed of medium- to thin-bedded
66 yellow-green and purple siltstone and mudstone intercalated with fine sandstone. It is conformably underlaid by the
67 Xiajiaqiao formation and unconformably overlaid by the Xiaoxi formation (Fig. 2B) (Wang et al., 2018). The
68 galeaspids from the Xikeng formation include *Sinogaleaspis shankouensis*, 'S'. *xikengensis*, *Xiushuiaspis*
69 *jiangxiensis,* and *X. ganbeiensis* (Pan & Wang, 1980; Pan & Wang, 1983). The early vertebrate fossil assemblage
70 was referred to as either the *Sinogaleaspis–Xiushuiaspis* assemblage (Pan, 1986b) or the Maoshan Assemblage
71 (Zhao & Zhu, 2010) and it is consistent with the assemblage found in the Maoshan formation of the northwestern
72 Zhejiang province (Pan, 1986b; Pan, 1988; Wang, 1991). The fish-bearing Xikeng formation is known as the Upper
73 Red Beds (URBs) and is the equivalent of the Huixingshao formations in Chongqing and Guizhou, and the Maoshan
74 formations in the Jiangsu and Zhejiang provinces. Although the precise age of the URBs in the western part of the
75 Yangtze Platform is difficult to determine, it is thought to be from the middle-late Telychian period due to evidence
76 from the underlying Xiushan formation with its invertebrate fauna and sequence stratigraphic analyses (Zhao et al.,
77 2009; Zhao & Zhu, 2010; Wang et al., 2018; Rong et al., 2019). The age of the fish-bearing Xikeng formation is
78 thought to be from the middle-late Telychian age of the Llandovery epoch during the Silurian period like those of
79 the Huixingshao and Maoshan formations in South China (Fig. 2B).
80
81
82 **MATERIAL AND METHODS**
83   The newly discovered sinogaleaspid material includes four head-shields of *Rumporostralis xikengensis* gen. nov.
84 (IVPP V25136.1–4), and one head-shield of *Rumporostralis shipanensis* gen. et sp. nov. (IVPP V26114). All
85 specimens are permanently housed in the collections of the Institute of Vertebrate Paleontology and
86 Paleoanthropology (IVPP), Chinese Academy of Sciences and are accessible for examination. The holotypes of
87 *Sinogaleaspis shankouensis* (GMC V1751) and *Rumporostralis xikengensis* (GMC V1753) are permanently housed
88 in the collections of the Geological Museum of China (GMC) and were used for comparison and measurement.
89   All specimens were prepared mechanically using a Vibro-tool with a tungsten-carbide bit or a needle. Some
90 specimens were reversed in latex casts. Specimens were measured with a digital vernier calliper, studied under

91 optical zoom, and photographed with a Canon EOS 5D Mark III camera with a Canon macro photo lens (MP-E
92 65mm 1:2.8 1-5×).
93
94 **RESULTS**
95 **Systematic paleontology:**
96   **Subclass** Galeaspida Tarlo, 1967
97   **Order** Eugaleaspiformes (Liu, 1965) Liu, 1980
98   **Family** Shuyuidae fam. nov.
99   **Differential diagnosis.** Shuyuidae differs from other families of Eugaleaspiformes in the splayed posterior
100 supraorbital canals and absence of U-shaped median dorsal canals.
101   **Type genus.** *Shuyu* Gai et al., 2011
102   **Referred genera.** *Meishanaspis*
103   **Remarks.** Newly discovered sinogaleaspid material provides a wealth of data and reliable diagnostic features to
104 erect the new genus *Rumporostralis* gen. nov. for '*Sinogaleaspis*' *xikengensis*. Our phylogenetic analysis of
105 Galeaspida shows that *Shuyu* and *Meishanaspis* are not included in Sinogaleaspidae and form another monophyletic
106 group. A new family, Shuyuidae fam. nov., was created for *Shuyu* and *Meishanaspis*. Shuyuidae is positioned in the
107 new cladogram as the sister to all other Eugaleaspididiformes with synapomorphies including a subtriangular head-
108 shield and longitudinal oval or wedge-shaped median dorsal opening.
109
110   **Family** Sinogaleaspidae Pan & Wang, 1980
111   **Differential diagnosis.** Sinogaleaspidae differs from other families of Eugaleaspiformes in the V-shaped
112 posterior supraorbital canals and more than 2 pairs of median transverse canals (autapomorphy).
113   **Type genus.** *Sinogaleaspis*. Pan & Wang, 1980
114   **Referred genera.** *Rumporostralis* gen. nov., *Anjiaspis*
115   **Remarks.** The amended Sinogaleaspidae, including *Sinogaleaspis shankouensis*, *Rumporostralis xikengensis*, *R.*
116 *shipanensis,* and *Anjiaspis reticularis* is monophyletic with synapomorphy (U-shaped median dorsal canals) and
117 autapomorphy (more than 2 pairs of median transverse canals).
118
119   Genus *Rumporostralis* gen. nov.
120
121
122 **Etymology.** *Rumpo* latin, state of being dehiscent or split; *rostralis*, Latin, snout, in referring to the rostral margin of
123 the head-shield split by the anterior end of median dorsal opening.
124 **Type species.** *Rumporostralis xikengensis* (Pan & Wang, 1980)
125 **Referred species**. *Rumporostralis shipanensis* gen. et sp. nov.

126 **Differential diagnosis.** *Rumporostralis* differs from other Eugaleaspiformes by an unclosed rostral margin of the

127 head-shield, indicating autapomorphy.

128 **Remarks.** The genus including *R. xikengensis and R. shipanensis* is uniquely characterized by the unclosed rostral
129 margin.

130
131 **Holotype.** A nearly complete head-shield GMC V1753A, B
132 **Referred specimens.** A nearly complete head-shield IVPP V25136.1, three incomplete head-shields IVPP
133 V25136.2–4.

134 **Type locality and horizon.** Xikeng village and Shipan reservoir, Taiyangsheng Town, Xiushui County, Jiangxi
135 Province, China; Xikeng formation, Telychian, Llandovery, Silurian.
136 **Differential diagnosis.** *R. xikengensis* differs from the other species *R. shipanensis* in the small size of the head-
137 shield.
138
139   *Rumporostralis shipanensis* gen. et sp. nov.
140
141 **Holotype.** An incomplete head-shield IVPP V26114.1a, b
142 **Type locality and horizon**. Shipan reservoir, Taiyangsheng Twon, Xiushui County, Jiangxi Province, China;
143 Xikeng formation, Telychian, Llandovery, Silurian.
144 **Differential diagnosis.** *R. shipanensis* differs from the type species *R. xikengensis* by the large size of the head-
145 shield.
146
147 **Description**
148 ***Rumporostralis xikengensis***
149 *Rumporostralis xikengensis* is a small-sized sinogaleaspid with a subtriangular head-shield (Figs.3, 4, 6B). The
150 rostral margin of the head-shield is disrupted by the anterior end of the median dorsal opening. The measurements of
151 4 specimens of *R. xikengensis* indicate that the size of the head-shield is consistent (Table 1). The head-shield is longer
152 than it is wide with a length-to-width ratio of about 1:2. The head-shield protrudes caudally into a pair of cornual and
153 inner cornual processes. The cornual processes are oriented caudo-laterally (or postero-laterally) and are short and
154 rapidly taper off in the holotype and the newly discovered specimen IVPP V25136.1 (c, Figs. 3A, B, 4A, B). The
155 inner cornual processes, which are completely preserved in the holotype and new specimen IVPP V25136.1 (ic, Figs.
156 3A, B, 4A, B), are small, spine-like, and caudally-oriented. The inner cornual processes are much smaller than the
157 cornual processes.
158   The median dorsal opening (md.o) (Figs. 3, 4, 6B) is fairly long and wedge-shaped or longitudinally elliptic in
159 outline along the midline. The length-to-width ratio of the opening is less than 6 (Table 1). The anterior end of the
160 median dorsal opening disrupts the rostral margin of the head-shield and its posterior end is positioned anterior to
161 the level of the orbital opening (md.o) (Figs. 3, 4, 6B).
162   The orbital openings are dorsally positioned on the head-shield (Figs. 3, 4, 6B) and are round with a diameter of
163 about 1.5 mm among the four specimens (Table 1). The orbital opening on the left side of specimen IVPP V25136.1
164 is longitudinal oval, which may be due to a deformation caused during preservation.
165   The pineal opening is clearly preserved in specimen IVPP V25136.2. It is level with the posterior margin of the
166 orbital opening in the midline of the head-shield (Figs. 3D, E, 6B). The pineal opening is small and round with a
167 diameter of 0.7 mm (Table 1). The ratio of the length of the pre-pineal and post-pineal region is about 1:2.
168   The sensory canal system is difficult to reconstruct in *Rumporostralis xikengensis* because it is preserved in
169 only one specimen (IVPP V25136.1) (Figs. 4A-B). The identified sensory canals consist of posterior supraorbital
170 canals (soc_2), infraorbital canals (ifc), lateral dorsal canals (ldc), lateral transverse canals (ltc), median dorsal canals
171 (mdc), and median transverse canals (mtc) (Figs. 4A, B, 6B). The posterior supraorbital canals (Figs. 4A, B, 6B) are
172 V-shaped. These canals originate from the anterior margin of the orbital opening, extend posteriorly along the inner
173 side of the orbital opening, and meet behind the pineal opening. The median dorsal canals (Figs. 4A, B, 6B) are U-
174 shaped and connect anteriorly with the posterior supraorbital canals level with the pineal opening and curve inward
175 to converge with the opposite one on the midline of head-shield (Figs. 4A, B, 6B). The infraorbital canals (Figs. 4A,
176 B, 6B) are an inverted S-shape. These canals originate on the lateral margin of the head-shield, pass through the
177 lateral side of the orbital opening, and connect with the lateral dorsal canals. There are at least four pairs of lateral
178 transverse canals (Figs. 4A, B, 6B) and three pairs of median transverse canals (Figs. 4A, B, 6B). The anterior three

179   pairs of lateral transverse canals extend across the lateral dorsal canals to connect with the median transverse canals
180   (Figs. 4A, B, 6B). The fourth lateral transverse canal is near the posterior edge of the head-shield and extends
181   posterolaterally (Figs. 4A, B, 6B).
182   The endoskeletal roof of the oralobranchial chamber was poorly preserved in the internal mold of holotype
183   GMC V1753B, but there are indications of at least 5 pairs of transversely elongated branchial fossae (Fig.3B).
184   Impressions for the subcutaneous vascular plexus are also preserved on the endoskeletal roof of the oralobranchial
185   chamber in the internal mold of holotype GMC V1753B (Fig.3B). There is an extensive endoskeletal postbranchial
186   wall in specimen IVPP V25136.1, 2, (Figs. 3D, 4A, B) that closes the oralobranchial chamber posteriorly. The
187   postbranchial wall is penetrated by a large pore in the midline of the head-shield for the passage of the neural canal
188   to the body (Figs. 3D, F, 4A–C).
189   The lateral margin of the head-shield is smooth and the surface of the head-shield is ornamented with closely
190   set, coarse, granular tubercles (Fig.3C). There are about 10 tubercles per square millimeter.
191
192   *Rumporostralis shipanensis*
193   *Rumporostralis shipanensis* is a medium-sized sinogaleaspid. The longest known head-shield is 52.4 mm; the widest
194   known head-shield is 63.0 mm, and the length of its head-shield along the midline is 34.5 mm (Table 1). The rostral
195   margin of the head-shield is unclosed. The holotype of this species is 12.6 mm along the long axis of the median
196   dorsal opening (Fig. 5A, B) and 4.9 mm along the short axis. The diameter of the orbital opening (Fig. 5A, B) is 5.8
197   mm in the holotype. The orbital opening on the left side is a longitudinal oval, which may be due to a deformation
198   during preservation. The distance between the paired orbital openings is 8.0 mm in the holotype. The lateral margin
199   of the head-shield is smooth and the exoskeleton of the head-shield is ornamented with closely set, coarse granular
200   tubercles (Fig. 5C). There are about 1.5 tubercles per square millimeter.
201
202   **Comparison**
203   *Rumporostralis* is similar to *Shuyu*, *Meishanaspis*, *Anjiaspis*, and *Sinogaleaspis* with a subtriangular head-shield, a
204   wedge-shaped or longitudinal oval-shaped median dorsal opening, and spine-like cornual and inner cornual processes.
205   It is comparable to *Sinogaleaspis* in its V-shaped posterior supraorbital canals, U-shaped medial dorsal canal, and at
206   least 3 pairs of median transverse canals (Figs. 6A, B,7). It is markedly different from *Sinogaleaspis* in the following
207   aspects: 1) the head-shield of *Rumporostralis* is more slender than that of *Sinogaleaspis*, which has a wider-than-long
208   head-shield (Figs. 6A, B,7); 2) the posterior end of the median dorsal opening is in front of the level of orbital openings
209   in *Rumporostralis* but behind the level of the center of orbital openings in *Sinogaleaspis* (Figs. 6A, B,7); 3) the anterior
210   end of the median dorsal opening reaches the anterior margin of the head-shield and disrupts the margin in
211   *Rumporostralis*, but in *Sinogaleaspis* it separates from the rostral margin of the head-shield (Figs. 6A, B, 7); 4) the
212   pineal opening is level with the posterior margin the orbital opening in *Rumporostralis* but the opening is more posterior
213   in *Sinogaleaspis* (Figs. 6A, B, 7); 5) the ornamentations of *Rumporostralis* are coarse granular tubercles (Figs. 6B, 7)
214   but are tiny granular tubercles in *Sinogaleaspis* (Figs. 6A, 7). There are some differences in the sensory canal systems
215   of *Rumporostralis* and *Sinogaleaspis* (Figs. 6A, B, 7). For example, there are 3 pairs of median transverse canals
216   identified in *Rumporostralis xikengensis* (Figs. 6B, 7) but up to 6 pairs have been identified in *Sinogaleaspis*
217   *shankouensis* (Figs. 6A, 7) whose sensory canal system was comprehensively reconstructed based on 11 specimens (Gai
218   et al., 2019b). It is difficult to determine whether these differences are caused by the incomplete preservation of
219   *Rumporostralis* or from another cause.
220
221
222   *Rumporostralis shipanensis* resembles *Rumporostralis, R. xikengensis* in its unclosed rostral margin, the
223   position of the median dorsal more anteriorly than the orbital openings, and its ornamentation of coarse granular

224 tubercles. However, the head-shield of the former is about three times larger than the latter. Growth variations have
225 been observed in some tessellate osteostracans, notably *Escuminaspis* and *Superciliaspis* (Sansom, 2007; Hawthorn,
226 2008; Keating et al., 2012; Scott & Wilson, 2012), but the relative size of the head-shield seems to be a reliable
227 species diagnostic tool in osteostracans and galeaspids (Moy-Thomas & Miles, 1971; Janvier, 1996). Galeaspids
228 have no cranial tesserae with ringed growth lines and have no clear growth series observed from the rich collection
229 of *Shuyu zhejiangensis* in Zhejiang and *Sinogaleaspis shankouensis* in Jiangxi (Gai et al., 2005, Gai et al., 2019b).
230 There is only about a 10 percent variation in the length of the head-shield which indicates that the armored
231 galeaspids either could not grow or became ossified only when they reached their definitive adult size, which is
232 typical of most osteostracans (Westoll, 1945; Denison, 1952; Moy-Thomas & Miles, 1971; Janvier, 1996). The large
233 size difference (up to 300 per cent variation in head-shield length) between *R. xikengensis* and *R. shipanensis* is
234 beyond the known range of intraspecific differences.
235
236 **Phylogenetic analysis and results**
237   We conducted a new phylogenetic analysis to explore the position of *Rumporostralis* and *Sinogaleaspis* within
238 Galeaspida based on its known dataset (Gai & Zhu, 2005; Zhu & Gai, 2006; Gai et al., 2018) and new data from
239 Sinogaleaspidae (Gai et al., 2019b). Three taxa and five new characteristics were added to the data matrix presented
240 by Gai et al. (2018) (S1 File). The newly added characteristics are as follows:
241   [55] The unclosed rostral margin: (0) absent; (1) present.
242   [56] The ornamentation of the head-shield: (0) star-shaped tubercles; (1) tiny granular tubercles; (2) coarse
243 granular tubercles.
244   [57] Pineal organ: (0) on front of or level with the posterior margin of orbital opening; (1) behind posterior
245 margin of orbital opening.
246   [58] Pre-pineal region longer than the post-pineal region in mid-line of head-shield: (0) absent; (1) present.
247   [59] Preorbital commissure: (0) absent; (1) present.
248   Phylogenetic data entry and formatting were performed using Mesquite version 3.6 (Maddison & Maddison
249 2015). The phylogenetic analysis was conducted using PAUP 4.0b 10 with the parsimony analysis package and the
250 heuristic search option (1000 replicates, random addition sequence) (Swofford 2003). All characteristics were
251 unordered and weighted equally, as in the earlier versions of this dataset. An early plesiomorphic osteostracan
252 *Ateleaspis* was selected as the outgroup for our phylogenetic analysis (Sansom, 2019). Our analysis yielded 6
253 equivalent most-parsimonious trees (Fig.8) with a tree length of 160, consistency index (CI) of 0.4562, and retention
254 index (RI) of 0.7825 (S2 File).
255 **DISCUSSION**
256 **Taxonomy of Eugaleaspidiformes**
257   The Sinogaleaspidae family was established by Pan and Wang (1980), and five species *Sinogaleaspis*
258 *shankouensis*, *Rumporostralis xikengensis*, *Shuyu zhejiangensis*, *Meishanaspis lehmani*, and *Anjiaspis reticularis* are
259 morphologically assigned to this family (Pan & Wang, 1980, Pan, 1986, Wang, 1991, Zhu, 1992, Gai & Zhu, 2005,
260 Liu et al., 2015). The previously morphologically recognized Sinogaleaspidae was paraphyletic in our cladogram.
261 We restricted Sinogaleaspidae including *Sinogaleaspis shankouensis, Anjiaspis reticularis*, *Rumporostralis*
262 *xikengensis*, and *R. shipanensis* (Fig.8) and the amended Sinogaleaspidae are characterized by U-shaped median
263 dorsal canals, V-shaped posterior supraorbital canals, and more than two median transverse canals. Sinogaleaspidae
264 is more closely related to *Yunnanogaleaspis* and higher eugaleaspids by their typical eugaleaspid-pattern sensory
265 canals. However, *Shuyu zhejiangensis* and *Meishanaspis lehmani* are not included in Sinogaleaspidae and form
266 another monophyletic group altogether. We named the clade to a new family, Shuyuidae fam. nov. (Fig.8). The new
267 clade represents the deepest branching of the Eugaleaspidiformes with more primitive characteristics seen in the
268 outgroup of Eugaleaspidiformes, such as the absence of the typical eugaleaspid-pattern sensory canals, splayed

269 posterior supraorbital canals, and more lateral transverse canals from the infraorbital canals.
270   Eugaleaspidae was established by Liu (1980) to replace Galeaspidae for the junior homonym between the
271 generic names *Galeaspis* in Agnatha and Trilobita (Liu, 1965). In the first cladistically-based classification of the
272 Galeaspida, Zhu and Gai (2006) proposed that the species of Eugaleaspidae include *Eugaleaspis changi* (Liu, 1965),
273 *E. xujiachongensis* (Liu, 1975), *E. lianhuashanensis* (Liu, 1986a), *E. xiushanensis* (Liu, 1983), *Yunnanogaleaspis*
274 *major* (Pan & Wang, 1980), and *Nochelaspis maeandrine* (Zhu, 1992; Zhu & Gai 2006). Zhu et al. (2012) described
275 a new member of Eugaleaspidae *Dunyu longiforus* from the Ludlow (Silurian) Kuanti Formation of Qujing, Yunnan,
276 and suggested that *E. xiushanensis* from the middle-late Telychian Huixingshao formation of Chongqing should be
277 reassigned to *Dunyu* based on new data from the type specimen. Liu (1986) established Tridensaspidae for
278 *Tridensaspis magnoculus* after considering its highly specialized rostral process and lateral projecting process which
279 differed from other Eugaleaspidiformes. Our phylogenetic analysis indicated that *Pterogonaspis yuhaii* should be
280 reassigned to Tridensaspidae to form a monophyletic group (Fig.8) as it is more closely related to *Tridensaspis*
281 *magnoculus* with the synapomorphies of the long rostral process and lateral projecting cornual process as in
282 previous parsimony-based cladograms (Zhu, 1992; Gai et al., 2005; Zhu & Gai, 2006). Tridensaspidae is more
283 closely related to *Dunyu* plus *Eugaleaspis* than *Yunnanogaleaspis* and *Nochelaspis* (Fig.8)*. The continued grouping
284 of *Yunnanogaleaspis* and *Nochelaspis* to Eugaleaspidae as proposed by Zhu and Gai (2006), will cause
285 Eugaleaspidae to be a polyphyletic group and the family Eugaleaspidae should be further modified to represent a
286 morphologically inclusive group. Therefore, we propose the removal of *Yunnanogaleaspis* and *Nochelaspis* from
287 Eugaleaspidae (Fig.8) to maintain the diagnostic stability of Eugaleaspidae which is mainly based on *Eugaleaspis*
288 (Liu, 1965).
289
290 **Sensory canal system of Sinogaleaspidae**
291   The sensory canal system, also called the lateral line system in modern aquatic vertebrates, is a system of
292 sense organs that serves to detect movements, vibration, and pressure gradients in the surrounding water
293 (Bleckmann, 1993; Coombs & Montgomery, 1999; Bleckmann & Zelick, 2009; Mogdans & Bleckmann, 2012). It is
294 unique to aquatic vertebrates from cyclostome fishes (lampreys and hagfish) (Fernholm, 1985) to amphibians
295 (Schlosser, 2002). It is prevalent in the armored jawless fishes such as galeaspids, osteostracans, and heterostracans,
296 and jawed placoderms during the Silurian-Devonian period (Fig.9) (Jollie, 1962; Piveteau, 1964; Denison, 1978;
297 Northcutt, 1985; Liu, 1986b; Northcutt, 1989; Janvier, 1996). The sensory canal system of galeaspids exhibits a
298 characteristic festooned pattern consisting of two pairs of longitudinal stems and a varied number of transverse
299 canals issuing from the stems (Liu, 1986b; Janvier, 1996). Its general pattern is comparable with other vertebrate
300 groups. For example, most stem canals such as supraorbital canals, median dorsal canals, infraorbital canals, and
301 lateral dorsal canals have their corresponding homologous parts in lampreys, heterostracans, osteostracans, and
302 placoderms (Fig. 9A–J) (Stensiö, 1932; Ritchie, 1967; Elliott, 1984; Northcutt, 1985; Liu, 1986b; Janvier, 1996).
303 The number, placement, and branching pattern of the sensory canals in galeaspids varies significantly among
304 different groups, even if the species are closely related (Fig. 9E–J) (Liu 1986b). Three patterns of sensory canals are
305 generally recognized in galeaspids: 1) two median transverse canals with more lateral transverse canals issuing from
306 the infraorbital canals and undeveloped supraorbital canals as in plesiomorphic taxa Dayongaspidae,
307 Hanyangaspidae, and Xiushuiaspidae (Fig. 9E,G); 2) a V-shaped posterior supraorbital canal and one median
308 transverse canal (dorsal commissures) as in Huananaspiformes and Polybranchiaspidiformes (Fig. 9H, J); 3) the U-
309 shaped median dorsal canals anteriorly fused with the posterior supraorbital canals as in Eugaleaspidiformes (Fig.
310 9F, I) (Liu, 1986b; Wang, 1991).
311
312

313   The sensory canal patterns of sinogaleaspids are different from those of all other known galeaspids. The
314   sensory canals of sinogaleaspids are a typical eugaleaspid-pattern with a U-shaped median dorsal canal (Figs. 6, 9F)
315   which is a dignostic characteristic of Eugaleaspidiformes (Fig. 9I). The U-shaped median dorsal canals were thought
316   to be lost in Polybranchiaspidiformes and Huananaspidiformes, but their vestiges are sometimes visible as a pair of
317   short canals crossing with the dorsal commissure in *Polybranchiaspis*, *Damaspis*, and *Laxaspis* (Fig. 9H) (Liu,
318   1986). Sinogaleaspids also exhibit the mosaic features of two other known patterns. For example, they have two
319   additional lateral transverse canals issuing from the infraorbital canals ($ltc_{a,b}$) (Fig. 9F), which may be regarded as a
320   plesiomorphic characteristic of galeaspids, since 3-4 lateral transverse canals are found on the infraorbital canal in
321   the plesiomorphic taxa such as Dayongaspidae, Hanyangaspidae, and Xiushuiaspidae (ltc_{a-c}) (Fig. 9E, G). The
322   number of lateral transverse canals tends to decrease in later evolution, but the vestiges of these canals can
323   sometimes be observed on the infraorbital canals in *Eugaleaspis changi* (Fig. 9I) and *Laxaspis qujingensis* (Fig. 9H).
324   Sinogaleaspids bear the typical V-shaped posterior supraorbital canal (Figs. 6, 9F) which is a derived characteristic
325   uniquely shared by Polybranchiaspidiformes and Huananaspidiformes (Fig. 9H, J). The preorbital commissure and
326   central canal in sinogaleaspids are also found in some members of Huananaspidiformes and
327   Polybranchiaspidiformes including *Laxaspis* and *Sanchaspi*s (Fig. 9F, H, J).
328   The sinogaleaspid sensory canal system is notable for the presence of more than two pairs of median
329   transverse canals (Pan & Wang, 1980; Gai & Zhu, 2005) which has been questioned by Wang (1991) and Liu et al.
330   (2014). However, newly discovered sinogaleaspids confirm their presence (Gai et al., 2019b). Among three genera
331   referred to sinogaleaspids, *Sinogaleaspis* has 6 pairs of median transverse canals (Fig. 6A) (Gai et al., 2019b),
332   *Anjiaspis* has 8 pairs (Gai & Zhu, 2005), and *Rumporostralis* has at least 3 (Fig. 6B) and more likely 6 pairs, like
333   *Sinogaleaspis*. Among about 80 described galeaspid species, this feature occurs uniquely in sinogaleaspids but is
334   very common in heterostracans (Fig. 9A; Kiaer, 1932; Kiaer & Heintz, 1935; Stensiö, 1964; Blieck, 1984; Liu,
335   1986b). Liu (1986b) observed a general grid-like pattern of the sensory canal system for plesiomorphic vertebrates
336   composed of 2-3 pairs of longitudinal stems linked by transverse branches; this is a common pattern among the
337   different types of sensory canal systems in various vertebrate groups. The sensory canal system of heterostracans is
338   regarded as the ideal model for a general pattern (Blieck, 1984; Liu, 1986b).
339   The median transverse canals of sinogaleaspids occur in the post-orbital region of the head-shield and are level
340   with the anterior, central, and posterior margins of the orbital opening as in *Anjiaspis* and *Sinogaleaspis* (Gai & Zhu,
341   2015; Gai et al., 2019b). The grid distribution of the sensory canal system on the dorsal side of the head-shield in
342   sinogaleaspids is made up of 4 longitudinal canals intercrossed with 3-8 pairs of transverse canals, reflecting the
343   assumed plesiomorphic condition of vertebrates.
344
345   **CONCLUSION**
346   The newly discovered sinogaleaspids from the Lower Silurian in Jiangxi, China provides a wealth of new data
347   and reliable diagnostic features to assign the new genus, *Rumporostralis* gen. nov., to '*Sinogaleaspis*' *xikengensis*.
348   This in-depth morphological study determined that the sensory canal system of sinogaleaspids exhibits the mosaic
349   features of three known galeaspid patterns. The presence of 3-8 pairs of transverse canals in Sinogaleaspidae
350   suggests that the sensory canal system of galeaspids probably displayed a grid distribution with transverse canals
351   arranged throughout the cephalic division. An extended phylogenetic analysis of Galeaspida corroborates the
352   monophyly of Sinogaleaspidae, which consists of *Sinogaleaspis*, *Rumporostralis,* and *Anjiaspis*. *Shuyu* and
353   *Meishanaspis* were excluded from Sinogaleaspidae to form the monophyletic group Shuyuidae fam. nov., which is
354   the sister of all other Eugaleaspididiformes. We propose a cladistically-based classification of the Galeaspida.
355
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359 Figure 8.

360
361
362   **Reference**

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Figure 1

Phylogenetic placement (A) and interrelationships (B-D) of galeaspids.

(A) galeaspids are attributed to the major armored, jawless fossil vertebrates (or 'ostracoderms', purple bar) (phylogenetic scenario adapted from Sansom et al., 2010, Artwork credit: Dinghua Yang and Nobu Tamura). (B-D) summary of previous hypotheses of galeaspid phylogeny showing controversy on the monophyly of Sinogaleaspidae (B simplified from Zhu, 1992; C simplified from Gai et al., 2005; D simplified from Zhu & Gai 2006, Gai et al., 2018)
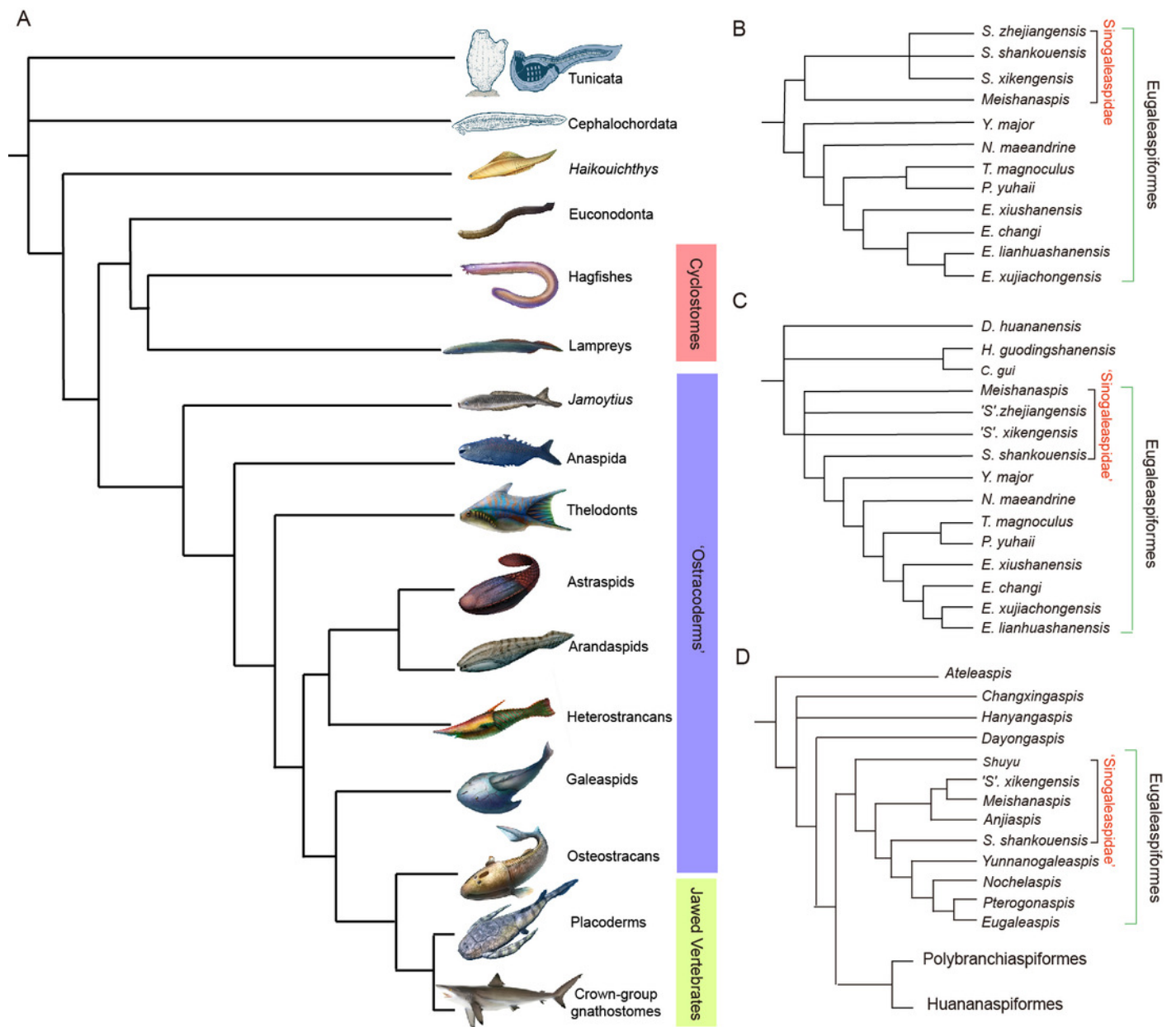
Figure 2

Maps of the two fossil localities of *Rumporostralis* (A) and the fish-bearing lithological
column (B) in Xiushui County, Jiangxi Province, China.
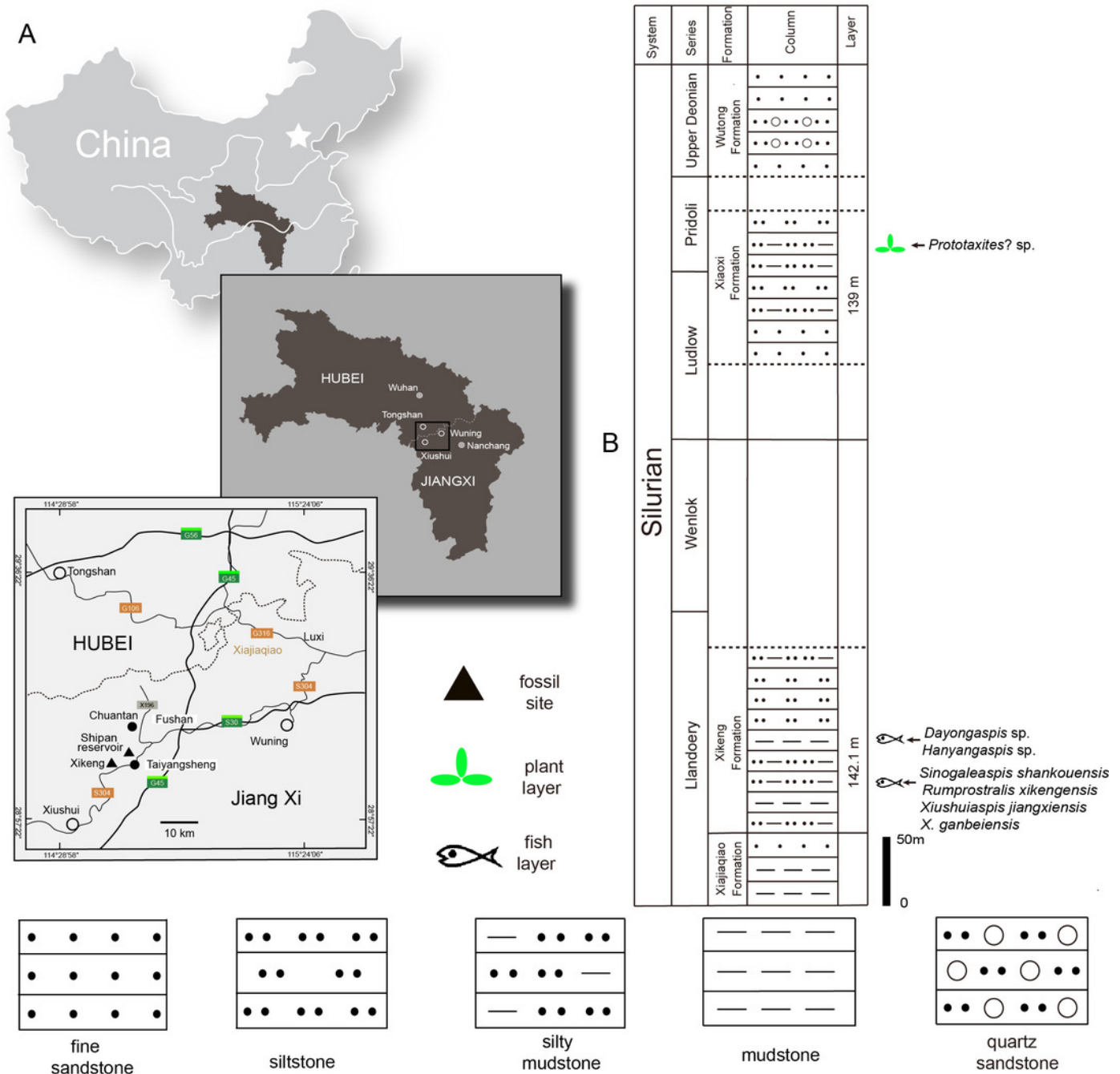
Figure 3

Photographs of *Rumporostralis xikengensis* gen. nov.

A nearly complete external (A) and internal (B) mould of head-shield, holotype, GMC V1753A, B. (C) close-up of coarse granular tubercles (180 degrees rotation of box region of Figure 2A). (D) a nearly complete external mould of the head-shield, IVPP V25136.2a. (E) close-up of the anterior part of head-shield (box region 1 of Fig. 3D).(F) close-up of the posterior part of head-shield (box region 2 of Fig. 3D). (G) An incomplete internal mould of the head-shield, IVPP V25136.4. Abbreviations: br.c. branchial chamber; c. cornual process; ic. inner cornual process; md.o. median dorsal opening; nc.p. pore for the passage of the neural canal; orb. orbital opening; pi. pineal opening; pb.w. postbranchial wall; va.p. subcutaneous vascular plexus; vr. ventral rim.
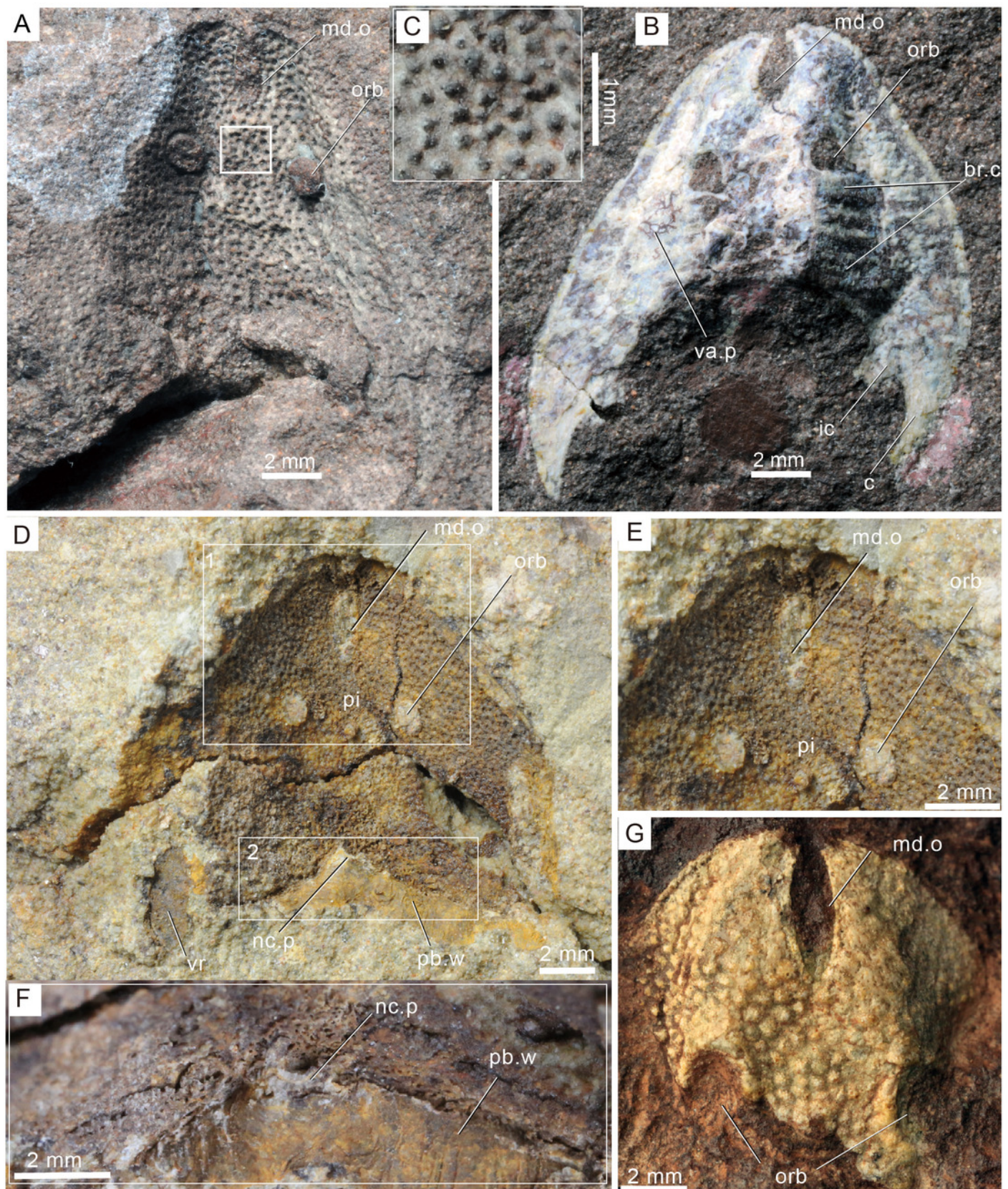
Figure 4

Photographs (A) and interpretative drawing (B) of *Rumporostralis xikengensis* gen. nov., IVPP V25136.1.

(C) close-up of postbranchial wall and pore on it for passage of the neural canal (box region of Fig. 4A). Abbreviations: c. cornual process; ic. inner cornual process; ifc. infraorbital canal; ldc. lateral dorsal canal; ltc. lateral transverse canal; mdc. median dorsal canal; md.o. median dorsal opening; mtc. median transverse canal; nc.p. pore for passage of the neural canal; orb. orbital opening; pi. pineal opening; pb.w. postbranchial wall; soc1. anterior supraorbital canal; soc2. posterior supraorbital canal. ifc. infraorbital canal; ldc. lateral dorsal canal; ltc. lateral transverse canal; mdc. median dorsal canal.
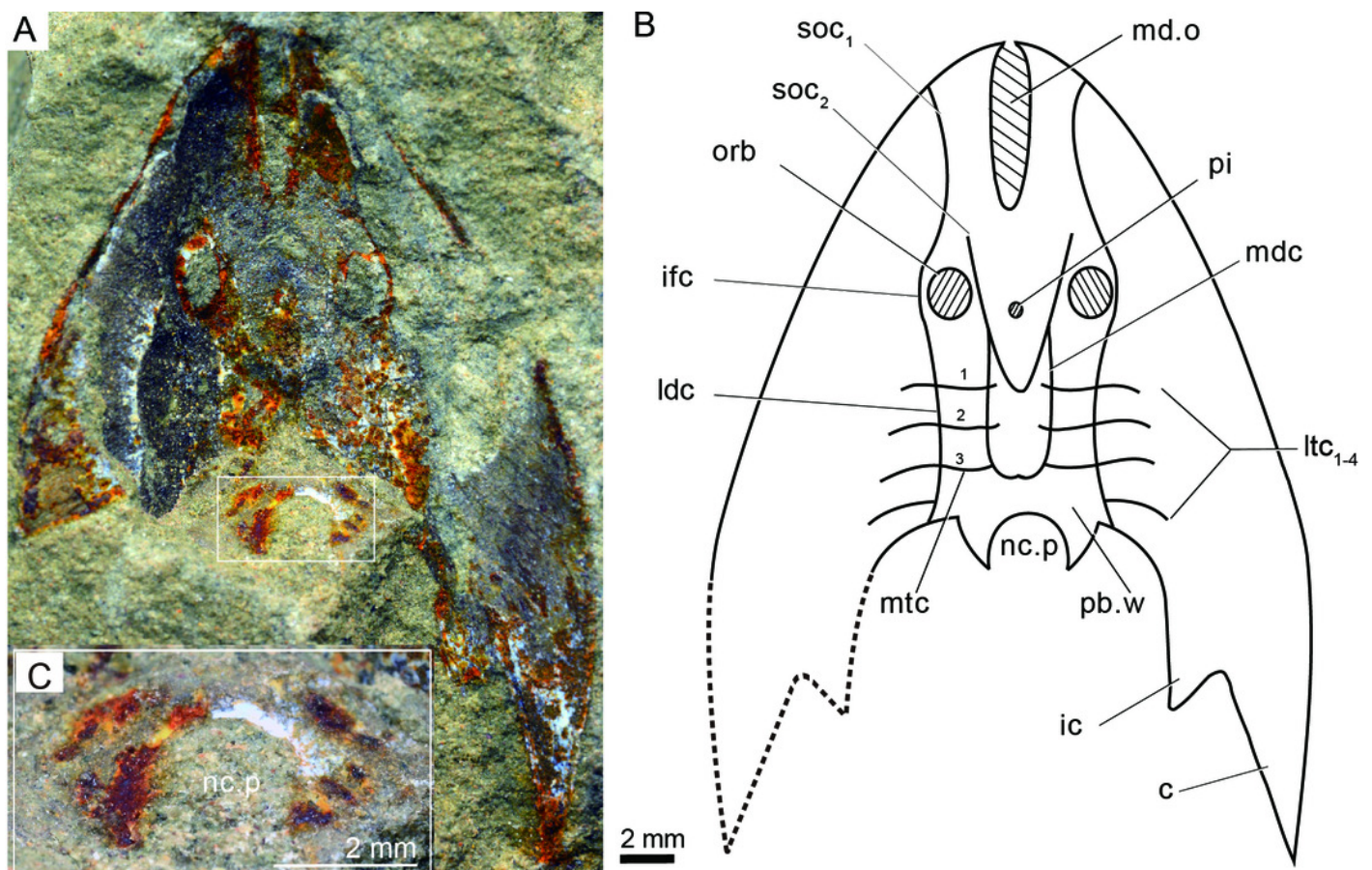
Figure 5

Photograph and interpretative drawing of *Rumporostralis shipanensis* gen. et sp. nov.

(A) an incomplete internal mould of head-shield, holotype, IVPP V26114.1a, in dorsal view.
(B) interpretative drawing. (C) close-up of the coarse granular tubercles (box region of
Figure.5A). Abbreviations: md.o. median dorsal opening; orb. orbital opening.
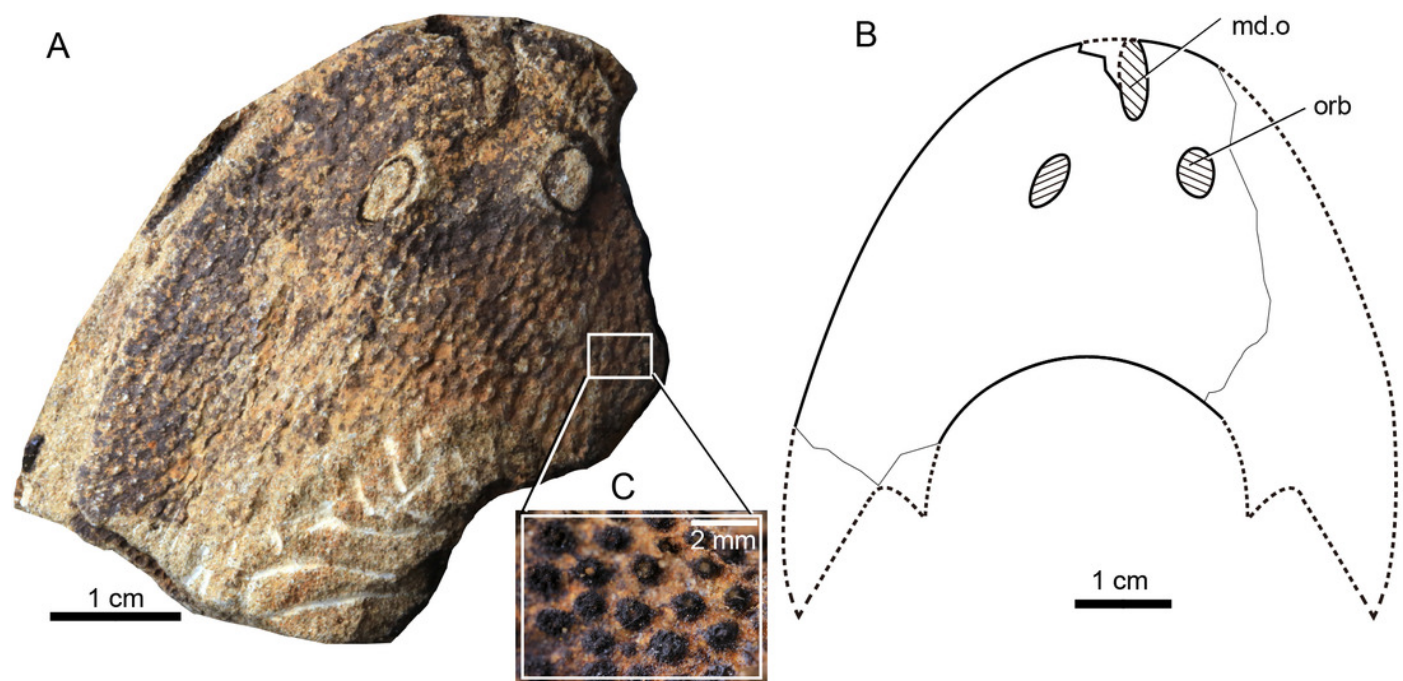
Figure 6

Comparison of *Sinogaleaspis shankouensis* (A) and *Rumporostralis xikengensis* (B)

Artwork credit: Xiaocong Guo
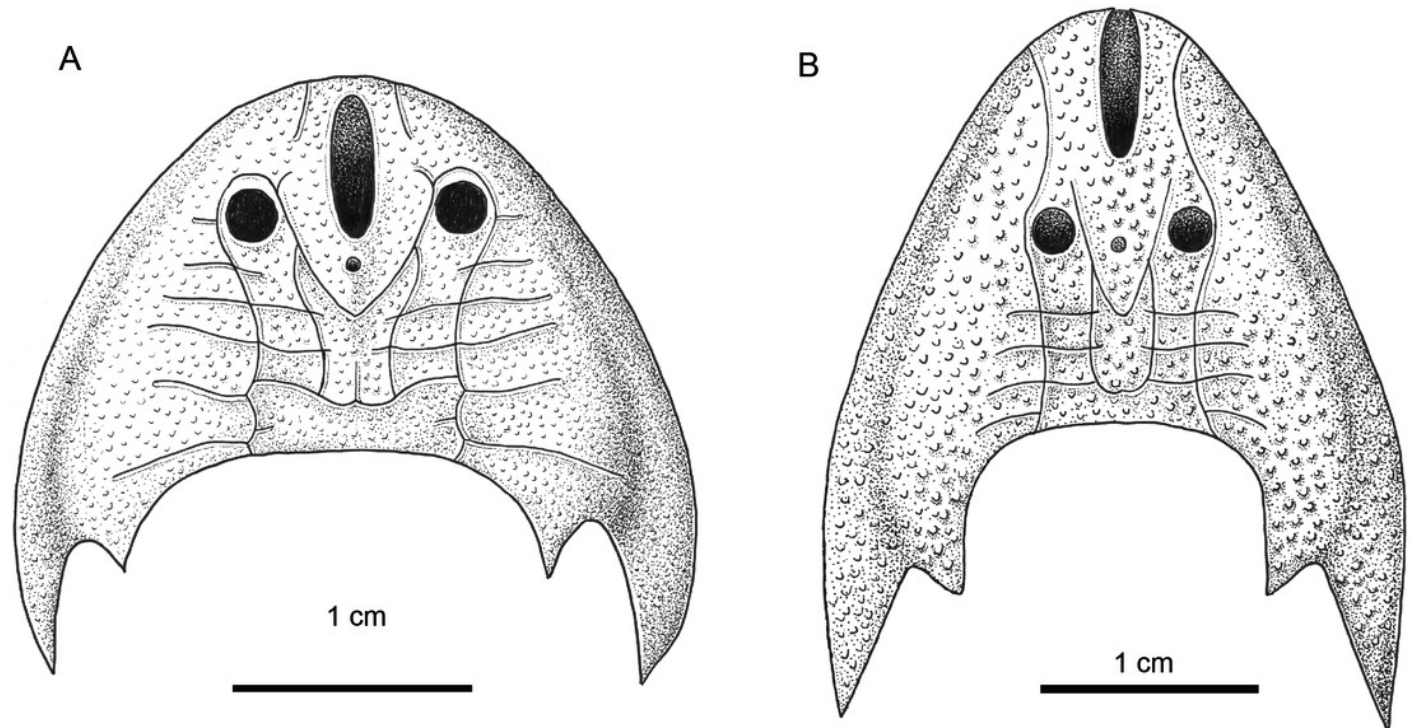
Figure 7

Life restoration of *Sinogaleaspis shankouensis* (left) and *Rumporostralis xikengensis* (right) in a fresh river.

Artwork credit: Xiaocong Guo.

Figure 8

Strict consensus tree of 6 most parsimonious trees and cladistically-based classification of the Galeaspida

Tree length =160, consistency index (CI) = 0.4562, retention index (RI) = 0.7825。Numbers on branches denote bootstrap frequencies (above node) and Bremer support values (below node), bootstrap frequencies below 50 are not shown, analysis based on the dataset revised from Zhu & Gai, 2006, Gai et al. 2018. Artwork credit: Dinghua Yang.

Ateleaspis

100

Changxingaspis — Xiushuiaspidae
Hanyanaspis — Hanyangaspidae
Dayongaspis — Dayongaspidae

Meishanaspis ⎤ Shuyuidae fam. nov.
Shuyu ⎦

more than 2 mtc
V-shaped soc$_2$

Anjiaspis ⎤
Sinogaleaspis ⎥ Sinogaleaspidae
61 *R. xikengensis* ⎥
1 *R. shipanensis* ⎦

U-shaped mdc

Yunnanogaleaspis ⎤ Incertae familiae
Nochelaspis ⎦

71 *Tridensaspis* ⎤ Tridensaspidae
3 *Pterogonaspis* ⎦

68 *Dunyu* ⎤ Eugaleaspidae
2 *Eugaleaspis* ⎦

Eugaleaspiformes

79

Geraspis ⎤ Geraspididae
1 *Kwangnanaspis* ⎦

Gumuaspis ⎤
61 *Platyventaspis* ⎥ Gumauspidae
2 *Nanningaspis* ⎦

Microhoplonaspis ⎤ Pentathyraspidae
1 *Pentathyraspis* ⎦

Duyunolespis ⎤ Duyunolepidae
2 *Lopadaspis* ⎦

Bannhuanaspis ⎤
Dongfangaspis ⎥
1 *Polybranchiaspis* ⎥ Polybranchiaspidae
1 *Damaspis* ⎥
1 *Laxaspis* ⎦

Polybranchiaspiformes

V-shaped soc$_2$

Wenshanaspis ⎤ Zhaotongaspididae
2 *Zhaotongaspis* ⎦

Antiquisagittaspis ⎤ Sanchaspidae
2 *Sanchaspis* ⎦

Gantarostraspis ⎤ Gantarostraspidae
1 *Wumengshanaspis* ⎦

Sanqiaspis — Sanqiaspidae

Asiaspis ⎤
Nanpanaspis ⎥
1 *Stephaspis* ⎦ Huananaspidae

Hunanaspis ⎤
1 *Lungmenshanaspis* ⎥
1 *Qingmenaspis* ⎥ Macrothy-
59 *Macrothyraspis* ⎥ raspinae
2 *Sinoszechuanaspis* ⎦

Huananaspiformes

Galeaspida
Polybranchiaspidida

Figure 9

The sensory canal system in early vertebrates.

(A) Heterostracan *Anchipteraspis crenulata* (redrawn from Elliott 1984). (B) Petromyzontid *Lampetra fluviatilis* (redrawn from Stensiö 1932). (C) Osteostracan *Ateleaspis tessellate* (redrawn from Ritchie 1967). (D) Placoderm *Radotina prima* (redrawn from Denison, 1978). (E-J) Galeaspids: (E) *Dayongaspis hunanensis* (redraws from Pan & Zeng 1985); (F) *Sinogaleaspis shankouensis* (redrawn from Gai et al. 2019b); (G) *Hanyangaspis guodingshanensis* (redrawn from P'an et al. 1975); (H) *Laxaspis qujingensis* (redrawn from Liu 1975); (I) *Eugaleaspis changi* (redrawn from Liu 1965); (J) *Sanchaspis magalarostrata* (redrawn from Pan & Wang 1981)**.** Abbreviations: c. cornual process; cc. central canal; ic. inner cornual process; ifc. infraorbital canal; ldc. lateral dorsal canal; lf. lateral field; ltc. lateral transverse canal; mdc. median dorsal canal ; md.o. median dorsal opening; mf. median field; mtc. median transverse canal; nhf. naso-hypophysial foramen; no, nasal opening; orb. orbital opening; pi. pineal opening; poc. preorbital commissure; soc. supraorbital canal; soc_1. anterior supraorbital canal; soc_2. posterior supraorbital canal; ro. rostral process; v.mdc, vestige of median dorsal canal.
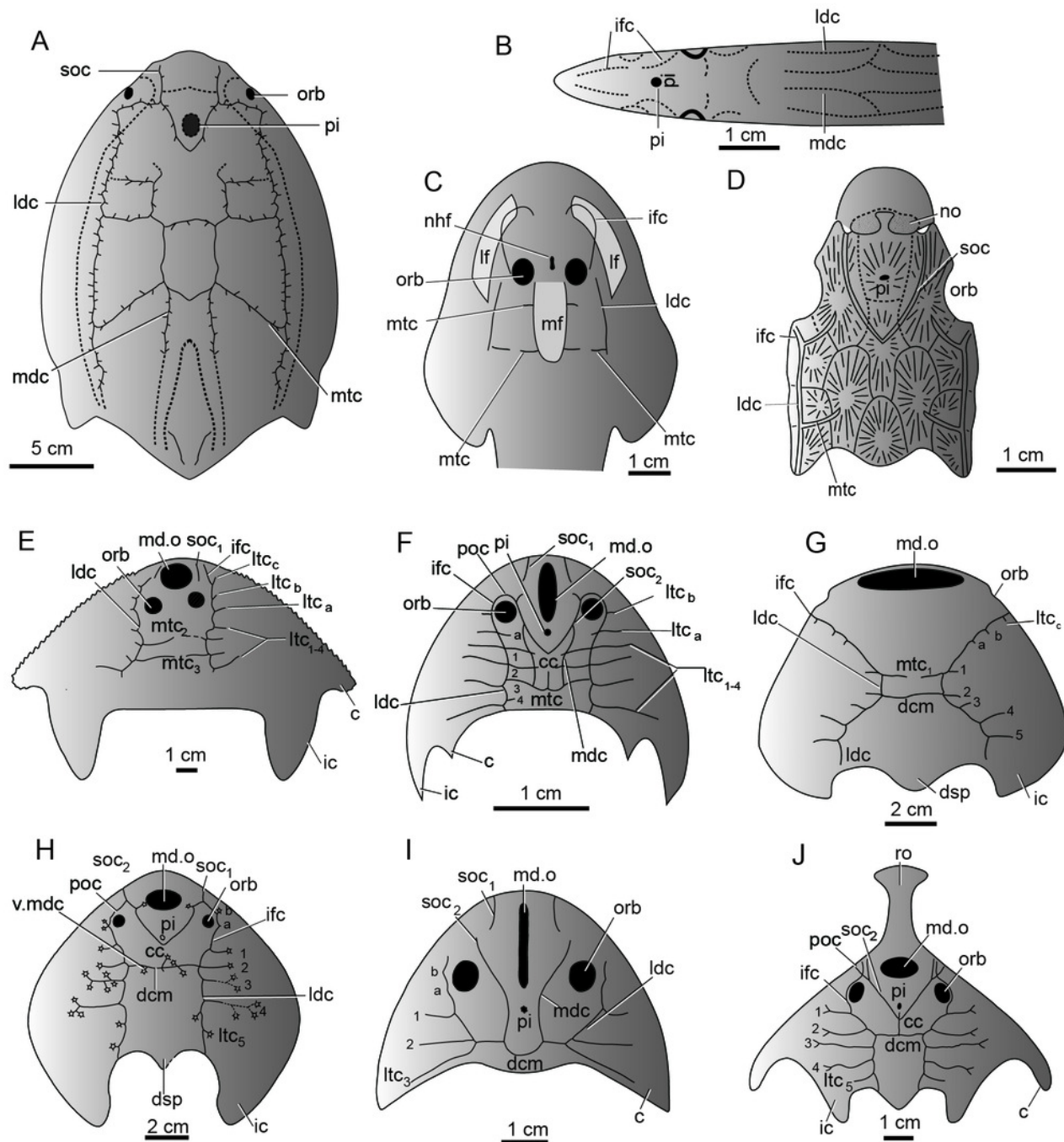
Table 1 Measurements of *Rumporostralis xikengensis* and *R. shipanensis* (mm)

Specimen Item	Rumporostralis xikengensis					R.shipanensis
	V1753	V25136.1	V25136.2	V25136.3	V25136.4	V26114
Maximum length of the head-shield	19.1	27.8	25.5	–	–	–
Maximum width of the head-shield	17.8	21.5	19.1	16.6	–	63.0
Length of the head-shield in midline	11.0	17.2	14.6	11.5	–	34.5
Diameter of the orbital opening	1.7	2.5	1.8	1.7	2.1	5.8
Distance between the orbital openings	3.3	4.4	4.3	2.8	4.0	8.0
Long axis of the median dorsal opening	3.0	6.5	5.5	4.0	4.6	12.6
Short axis of the median dorsal opening	1.1	1.3	1.1	1.0	1.4	4.9
Length of the pre-pineal region in midline	5.5	10.6	6.8	6.5	9.2	18.5
Length of the post-pineal region in midline	4.5	6.6	5.8	5.0	–	16.0