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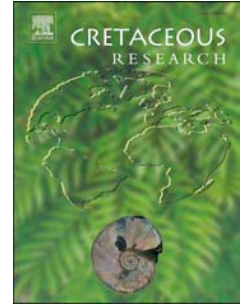
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# Accepted Manuscript

*Shajia*, a new genus of polyconitid rudist from the Langshan Formation of the Lhasa Block, Tibet, and its palaeogeographical implications

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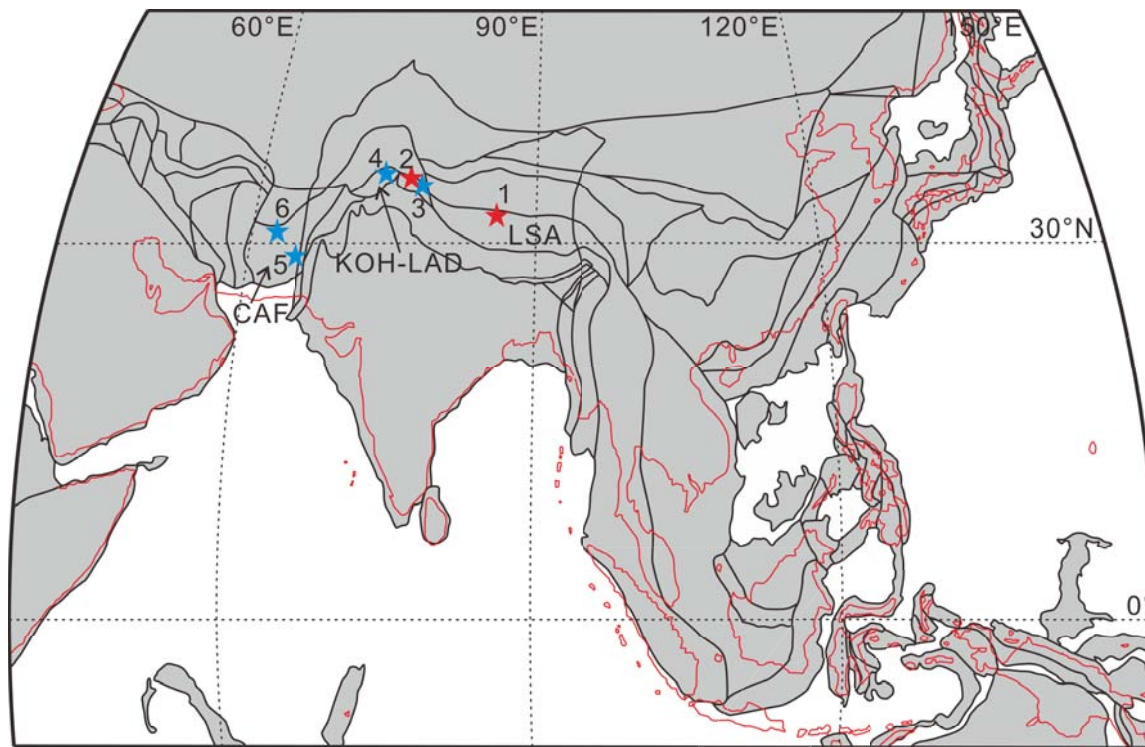
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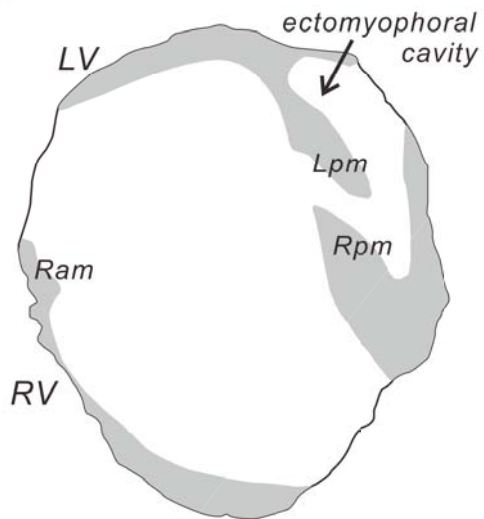
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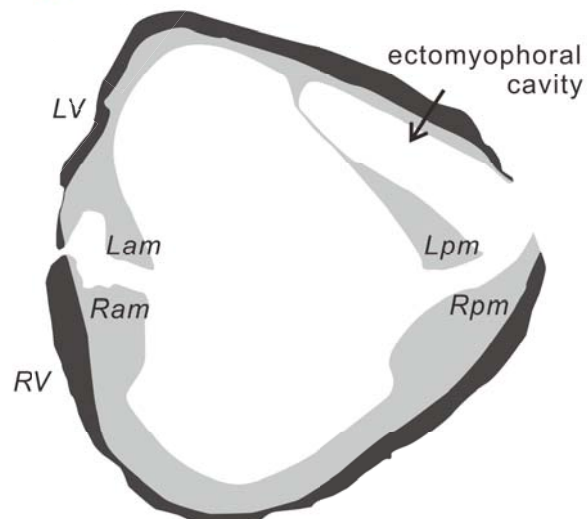
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★ *Horiopleura haydeni*



★ *Shajia tibetica* gen. et sp. nov.



1 ***Shajia*, a new genus of polyconitid rudist from the Langshan Formation of the**  
2 **Lhasa Block, Tibet, and its palaeogeographical implications**

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26 **Abstract.**

27 A new polyconitid rudist *Shajia tibetica* gen. et sp. nov., of late Aptian to Albian  
28 age, is described from the Langshan Formation of Nyima County, northern Lhasa  
29 Block, Tibet. Though comparable in size and external morphology with *Horiopleura*  
30 *haydeni* Douvillé, which is a common endemic species in southwestern Asia, *Shajia*  
31 differs from the latter species in its possession of an inwardly inclined, instead of  
32 outwardly facing, posterior myophore in the right valve. In addition, a single  
33 specimen from Ladakh, which was previously assigned to *Polyconites?* sp., on  
34 account of a similar myophoral distinction from *H. haydeni*, is transferred to the new  
35 genus. *Shajia* is considered most likely to have been derived from one of a group of  
36 *Horiopleura* species that lived on the southern margin of the Mediterranean Tethys.

37 The so-called 'Yasin fauna' represented by the late Aptian to Albian *Horiopleura*  
38 *haydeni*/*Auroradiolites gilgitensis* rudist association, is considered to be restricted to  
39 southwestern Asia, including Afghanistan, Kohistan in northern Pakistan and Ladakh  
40 in northern India, though those two species in particular have not so far been recorded  
41 from the Lhasa Block of Tibet. Nevertheless, *S. tibetica* co-occurs with *Auroradiolites*  
42 *biconvexus* (Yang et al.), which probably evolved directly from *A. gilgitensis*  
43 (Douvillé), and the age of the latter association is in accordance with the generally

44 accepted age of the Yasin fauna as late Aptian to Albian. Hence the *S. tibetica* and *A.*  
45 *biconvexus* association can be considered a regional variant of the Yasin fauna, which  
46 had evidently already dispersed to the Lhasa Block by the late Aptian. So the  
47 Langshan Formation can be considered palaeogeographically linked with other  
48 mid-Cretaceous shallow-marine carbonate deposits in adjacent southwestern Asian  
49 regions. These findings also provide new evidence that the age of the rudist  
50 assemblage of the Lhasa Block is late Aptian to Albian, although a slightly younger  
51 age cannot be excluded.

52 **Keywords:** Lhasa Block; Langshan Formation; mid-Cretaceous; Rudists;  
53 Polyconitidae; Yasin fauna

## 54 1. Introduction

55 Rudists are an extinct order of bivalves that flourished on the carbonate  
56 platforms of the Tethyan–Atlantic–Pacific oceanic realm during the Late Jurassic to  
57 Cretaceous (Skelton, 2018). The mid-Cretaceous rudists of southwestern Asia and the  
58 western Pacific region show great similarity and affinity (Sano and Masse, 2013;  
59 Skelton et al., 2013). Accordingly, the Southwest Asian/Pacific Faunal Province was  
60 proposed, covering Iran, Afghanistan, Kohistan in northern Pakistan, Ladakh in  
61 northern India, Tibet in China and Japan, as well as Cebu Island and the Japanese  
62 seamounts in the Pacific region (Rao et al., 2015, 2017). The rudist fauna of this  
63 province is dominated by the endemic radiolitid *Auroradiolites* Rao et al., 2015 and  
64 the polyconitid lineage of *Horiopleura haydeni* Douvillé, 1926–*Praecaprotina* Yabe

65 and Nagao, 1926– *Magallanesia* Sano et al., 2014, as well as some more widely  
66 dispersed taxa such as *Eoradiolites* Douvillé, 1909 and *Sellaea* Di Stefano, 1889  
67 (Skelton et al., 2013; Sano et al., 2014; Rao et al., 2015). The orbitolinid assemblage  
68 associated with these rudists is likewise composed of several endemic taxa such as  
69 *Mesorbitolina birmanica* (Sahni, 1937), *Palorbitolinoidea orbiculata* Zhang, 1986  
70 and *Palorbitolinoidea hedini* Zhang, 1986, together with cosmopolitan taxa such as  
71 *Mesorbitolina texana* (Roemer, 1849), *M. subconcava* (Leymerie, 1878) and *M. aperta*  
72 (Erman, 1854) (Cherchi and Schroeder, 2013; Schlagintweit and Wilmsen, 2014; Rao  
73 et al., 2015, 2017; Boudagher–Fadel et al., 2017).

74 Within the SW Asian/Pacific Faunal Province, the so-called ‘Yasin fauna’ of  
75 rudists represented by the late Aptian–Albian *Horiopleura haydeni/Auroradiolites*  
76 *gilgitensis* association had a widespread distribution in southwest Asia including Iran,  
77 Afghanistan, Kohistan, and Ladakh (Douvillé, 1926; Rossi Ronchetti, 1965; Montenat  
78 et al., 1982; Upadhyay, 2001, 2014; Skelton et al., 2005; Sha and Cestari, 2016). In  
79 the mid-Cretaceous, these fossil sites were all located on blocks/terrane arrays  
80 along, or offshore from the southern Asian margin on the northern side of the eastern  
81 Neo-Tethyan Ocean (Rao et al., 2017). The Yasin fauna, as such, has not previously  
82 been recorded from the Lhasa Block, which occupied a similar geographical and  
83 tectonic position to the blocks/terrane arrays mentioned above. Instead, *Auroradiolites*  
84 *biconvexus*, probably derived directly from *A. gilgitensis*, and the canaliculate  
85 polyconitid genus *Magallanesia* were found there (Rao et al., 2015; 2017).

86 In this study, a new polyconitid genus, *Shajia*, which is superficially comparable

87 with *Horiopleura haydeni*, is described, based on articulated specimens collected  
88 from the Langshan Formation of Nyima County, Lhasa Block. A single specimen  
89 collected in Ladakh and formerly assigned to *Polyconites?* sp., by Masse and  
90 Fenerci-Masse (2017) is also reappraised in the light of the new material from the  
91 Lhasa Block. The relationship of *Shajia* with the Yasin fauna and its  
92 palaeogeographical implications are evaluated and the age of the rudist fauna from the  
93 Langshan Formation revised accordingly.

## 94 **2. Geological setting**

95 The Qinghai–Tibet plateau is generally regarded as a complex tectonic collage of  
96 several blocks; from north to south they are the Songpan–Ganze–Hoh Xil, Qiangtang,  
97 Lhasa and Tethyan–Himalayan blocks, which are separated from each other by  
98 sutures (Yin and Harrison, 2000; Zhu et al., 2013). These blocks rifted from  
99 Gondwana, drifted northward, and finally accreted to the Asian continent successively  
100 during the late Palaeozoic and Mesozoic eras, prior to the India–Asia collision (Pan et  
101 al., 2012; Li et al., 2017). Today, the Lhasa Block is bounded by the Bangong–Nu  
102 suture to the north and the Indua–Yarlung suture to the south (Fig. 1A; Yang et al.,  
103 2015). It rifted from the India–Gondwana continent in the Late Triassic, and collided  
104 with Asia in latest Jurassic–earliest Cretaceous times (Yin and Harrison, 2000;  
105 Metcalfe, 2006).

106 [Figure 1 hereabouts]

107 In the late Early to early Late Cretaceous (Barremian–Cenomanian), the Lhasa



108 Block had already collided with the Qiangtang Block, and was located on the north  
109 side of the eastern Tethys Ocean. At this time, shallow marine carbonate deposits,  
110 represented by the Langshan Formation, were widely distributed along the northern  
111 portion of this block (Leier et al., 2007; Rao et al., 2015). The Langshan Formation  
112 crops out as a nearly east-west-oriented belt extending from Baingoin County in the  
113 east to Rutog County in the west (XZBGM, 1993). It is dominated by dark-grey to  
114 black limestone sometimes interbedded with siltstone and mudstone (Zhang et al.,  
115 2004; Leier et al., 2007). The thickness of the Langshan Formation is poorly  
116 constrained and has considerable lateral variation; in this paper, we regard it as about  
117 1000 m, referring to Zhang et al. (1986), Leeder et al. (1988), and Leier et al. (2007).

118 Abundant fossils have been recorded from the Langshan Formation, dominated  
119 by orbitolinids (Zhang, 1982, 1986, 1991; Boudagher-Fadel et al., 2017), rudists  
120 (Yang et al., 1982; Gou and Shi, 1998, Scott et al., 2010; Rao et al., 2015, 2017),  
121 gastropods (Yu and Xia, 1985) and corals (Löser and Liao, 2001; Deng and Wang,  
122 2013). The age of the Langshan Formation is mainly constrained by foraminifers,  
123 especially large benthic orbitolinids. Deposition started from the Early Barremian  
124 based on the occurrence of *Eopalorbitolina charollaisi* Schroeder and Conrad, 1968  
125 (Rao et al., 2015), and extended to the Early Cenomanian, as indicated by the  
126 appearance of *Daxia cenomana* Cuvillier and Szakall, 1949, *Nezzazata conica* (Smout,  
127 1956), *Cuneolina* cf. *cylindrica*, *Orbitolina qatarica* Henson, 1948, *Conicorbitolina*  
128 sp. A and *Pseudedomia* sp. (Boudagher-Fadel et al., 2017).

129 The polyconitid specimens described herein were collected from the Langshan

130 Formation on the western side of Dangqiong Lake in southern Nyima County (Fig.  
131 1B). This fossil site is located in the southern Nyima Basin, about 450 km northwest  
132 of Lhasa (DeCelles et al., 2007; Kapp et al., 2007). No palaeontological data have  
133 previously been published from the Langshan Formation of the Nyima Basin.  
134 According to the observations of Tong Zhang and Zhaoxiong Ma during field work,  
135 these specimens were collected from the lower part of the upper Langshan Formation.  
136 Furthermore, several large specimens of *Auroradiolites* were collected from the same  
137 bed as these polyconitid specimens. Although the left valves of these *Auroradiolites*  
138 specimens were not preserved, they are most likely attributable to *A. biconvexus*  
139 because of the large size of the right valves. As the age range of *A. biconvexus* was  
140 revised to late Aptian–Albian (Rao et al., 2017), and the geological range of the upper  
141 Langshan Formation is late Aptian to early Cenomanian (Rao et al., 2015), a late  
142 Aptian to Albian age can be assumed for these polyconitid specimens.

### 143 **3. Systematic palaeontology**

144 This published work and the nomenclatural acts it contains have been registered  
145 in Zoobank: <http://www.zoobank.org/References/xxxxxx>

146 The numbered specimens are housed at the Nanjing Institute of Geology and  
147 Palaeontology, Chinese Academy of Sciences, 39 East Beijing Road, Nanjing 210008,  
148 China (NIGPAS).

149 Abbreviations: *at*, anterior tooth; *ct*, central tooth; *Lam*, anterior myophore of left  
150 valve; *Lig*, Ligamentary infolding; *Lpm*, posterior myophore of left valve; *LV*, left  
151 valve; *ol*, outer shell layer; *pt*, posterior tooth; *Ram*, anterior myophore of right valve;

152 *Rpm*, posterior myophore of right valve; *RV*, right valve.

153 Quantitative characters (Fig. 2): *Dap*, antero–posterior commissural diameter,

154 *Ddv*, dorso–ventral commissural diameter; *Hd*, dorsal height of *RV*; *Hv*, ventral height

155 of *RV*; *LVc*, convexity of the *LV*.

156 The suprageneric classification used herein follows Skelton (2013a, b).

157 [Figure 2 hereabouts]

158 **Order** HIPPURITIDA Newell, 1965 (*nom. correct.* Scarlato & Starobogatov, 1971,

159 *pro* Order Hippuritoida Newell, 1965; emend. Bouchet *et al.* 2010)

160 **Suborder** HIPPURITIDINA Newell, 1965 (Skelton, 2013b)

161 **Superfamily** RADIOLITOIDEA d’Orbigny, 1847

162 **Family** POLYCONITIDAE Mac Gillavry, 1937

163 **Genus** SHAJIA gen. nov.

164 *LSID*. urn:lsid:zoobank.org:act: xxxxxx

165 **Type species.** *Shajia tibetica* gen. et sp. nov.

166 **Derivation of name.** The new genus is named for Professor Jingeng Sha, a

167 well-known Chinese palaeontologist who has made extensive studies of Mesozoic

168 bivalves and of the geological evolution of the Qinghai–Xizang Plateau (Tibet). In

169 recent years, he has focused on reviewing the rudist record of China, including

170 publication of an important paper in *Cretaceous Research* to revise the late Aptian–

171 Albian Yasin-type rudist fauna of the Himalayan area (Sha and Cestari, 2016). We

172 chose his name as the root for the new genus erected herein in honour of his

173 contributions to Himalayan, and especially Tibetan rudist research.

174 **Diagnosis.** Large-sized polyconitid (antero-posterior commissural diameter can reach  
175 90mm). *RV* conical and slightly twisted, *LV* low capuloid with dorsally over-hanging  
176 umbo. Ventral height of *RV* is less than twice the dorsal height, resulting in a dorsally  
177 inclined commissure. Outer shell layer is relatively thick, especially in the *RV* where  
178 its thickness may reach nearly 10 mm, on which longitudinal ribs are also developed.  
179 Subequal teeth of *LV* (*at* > *pt*) straddling the straight and erect central tooth of *RV*.  
180 Ligamentary infolding strongly developed. *LV* anterior myophore a narrow, flat-ended  
181 buttress projecting in from the anterior valve wall and facing onto the shelf-like  
182 anterior myophore of the *RV*, which is formed by a thickening of the inner shell layer.  
183 Posterior myophore in *LV* is a plate projected subparallel to the posterior valve wall,  
184 from which it is thus separated by a sub-rectangular ectomyophoral cavity; the  
185 adductor insertion surface on the broad tip of the *Lpm* is inclined somewhat outwards  
186 so as to face onto the depressed, inwardly sloping surface of the *RV* posterior  
187 myophore, which is formed by a pillow-like swelling of the inner shell layer.

188 [Figure 3 hereabouts]

189 **Discussion.** The thickening of the outer shell layer, especially of the *RV*, the subequal  
190 teeth of the *LV* (*at* > *pt*) and reflexed plate-like *Lpm* with adjacent ectomyophoral  
191 cavity, all observed in the Nyima specimens (Figs. 3A; 4-6) are diagnostic characters  
192 of the family Polyconitidae Mac Gillavry, 1937 (Skelton, 2013a). Comparisons thus  
193 need to be made with the handful of known genera in that family, starting with those

194 most easily excluded from further consideration.

195 The lack of sub-division into multiple canals of the *LV* posterior ectomyophoral cavity  
196 of the *Nyima* specimens (Figs. 3A) rules out the genus *Magallanesia* Sano et al., 2014  
197 (= ‘Polyconitid new taxon 1’ in Skelton et al., 2013) (Fig. 3F). The genus *Polyconites*  
198 Roulland, 1830, can also be excluded as the *LV* of this genus is nearly flat  
199 (operculiform), the external surface of the shell lacks ribbing, and the posterior  
200 myophore of the *RV* is generally represented only by a slight thickening of the inner  
201 shell layer, at least in more derived species (Fig. 3D) (Masse et al., 1998; Skelton and  
202 Masse, 1998; Skelton, 2013a), although it is a little more prominent in juvenile shells  
203 of more primitive species (Skelton et al., 2010).

204 The external morphology of the *Nyima* specimens is similar to that of the genus  
205 *Horiopleura*, including the sparse, subdued longitudinal ribs (Fig. 4D), similar to  
206 those described from the Himalayan species *Horiopleura haydeni* by Douvillé (1926)  
207 and Rossi Ronchetti (1965). Moreover, the anterior myophoral arrangement of *Shajia*  
208 differs little from that seen in *Horiopleura* species (e.g., Fig. 3C). However, the  
209 depressed, inwardly sloping *Rpm* in the *Nyima* specimens (Fig. 3A) contrasts sharply  
210 with that in *Horiopleura haydeni*, which projects upward so as to face back onto the  
211 inner face of the *Lpm* (Fig. 3B). The same contrast is observed, moreover, in the type  
212 species of *Horiopleura*, *H. lamberti* Douvillé, 1889 (Fig. 3C), as well as in the more  
213 derived genera *Praeacprotina* (Fig. 3E), and ‘Polyconitid new taxa 2 and 3’ (Skelton  
214 et al., 2013), both of the latter additionally showing only a weakly convex *LV*.

215 Otherwise, both *Tepeyacia* and ‘Polyconitid new taxon 4’ (Skelton et al., 2013) are  
216 characterized by distinctive pleated infoldings of the *RV* outer shell layer, not  
217 observed in the Nyima specimens, while the polyconitid affinity of *Douvillelia* and  
218 *Jerjesia* is in any case questionable (Skelton, 2013a; Masse et al., 2015) as neither  
219 appears to possess the diagnostic *LV* posterior ectomyophoral cavity.

220 In a recent review of the genus *Horiopleura*, however, Masse and Fenerci-Masse  
221 (2017, p. 54) noted that the outwardly inclined (facing towards the posterior side)  
222 and/or concave upward form of the *Rpm* (as in Fig. 3B, C) is ‘reported in the group of  
223 large, advanced species, e.g. *Horiopleura lamberti*; [whereas] in the group of small,  
224 putative primitive species, the inclination may be inwards (towards the anterior side),  
225 but a posterior shoulder is always present, a character that differentiates it from  
226 *Polyconites*’. All the figured specimens of the ‘putative primitive species’ assigned to  
227 *Horiopleura* by Masse and Fenerci-Masse (2017; e.g., Figs. 7C, 8E, F, 9A, B, 13A3  
228 therein) indeed show this ‘shoulder’ to be a consistent attribute, such that adductor  
229 insertion area on the *Rpm* invariably forms a distinct ledge (either flat or slightly  
230 concave) that is oriented sub-parallel to the commissural plane.

231 Nevertheless, an Albian specimen from Parnassus, Greece, described by Masse and  
232 Fenerci-Masse (2017; Fig. 19B therein) and assigned by them to *H. distefanoi* Parona,  
233 1909, does show an inwardly sloping *Rpm* with a correspondingly suppressed internal  
234 shoulder – a feature accordingly incorporated in their diagnosis for the species: ‘RV  
235 ledge like posterior myophore sloping inwards’ (Masse and Fenerci-Masse, 2017; p.

236 72). Accordingly, we suggest that the species that includes that specimen, if not *H.*  
237 *distefanoi* itself (pending confirmation the myophoral condition cited above in that  
238 species), might be allied with the new genus proposed herein, as an intermediate form,  
239 on the grounds that it differs from other species of *Horiopleura* by the marked inward  
240 inclination of the *Rpm* with associated suppression of the internal shoulder. This  
241 myophoral distinction is analogous to that which was used diagnostically to separate  
242 the earliest species of *Polyconites*, *P. hadriani*, from its inferred ancestral species of  
243 *Horiopleura* (Skelton et al., 2010), though additionally accompanied in that case by  
244 the pronounced flattening of the LV, in contrast to *Shajia*. Likewise, we propose that a  
245 single specimen from Ladakh that was assigned to *Polyconites?* sp., by Masse and  
246 Fenerci-Masse (2017), and which shows remarkably similar characteristics to those of  
247 the Nyima specimens (see below), should also be transferred to the genus *Shajia*.

248 **Age and distribution.** Late Aptian to Albian for the rudist-bearing limestone bed of  
249 Nyima County in Tibet (China), and late Aptian for the single specimen recorded from  
250 Ladakh (northern India); therefore, a late Aptian to Albian age should be assigned to  
251 this new genus based on current records.

252

253 *Shajia tibetica* sp. nov.

254 Figures 4–6

255 *LSID.* urn:lsid:zoobank.org:act: xxxxxx

256 ? aff. 2017 *Horiopleura distefanoi* (Parona, 1909) Masse and Fenerci-Masse, fig. 19B

257 2017 *Polyconites* ? sp. Masse and Fenerci-Masse, fig. 20

258 **Derivation of name.** From Tibet, the type locality where the new species was found.

259 **Material.** Two articulated specimens (NIGP. 110522-110523), with the outer shell  
260 layer partially worn. The *RV* apices of both specimens were broken.

261 **Holotype.** Articulated specimen (NIGP. 110522; Figs. 4, 5). Two antero-posterior  
262 sections cutting through both valves were made (Fig. 4C), the more ventral section  
263 (Fig. 5A-B) oblique to the commissural plane and the more dorsal section (Fig. 5C-D)  
264 sub-perpendicular to it.

265 **Paratype.** Articulated specimen (NIGP. 110523; Fig. 6). Three obliquely transverse  
266 sections were made (Fig. 6A): the upper one cuts through both valves (the  
267 over-hanging dorsal part of the *LV* and the ventral part of the *RV*, Fig. 6C); the middle  
268 one cuts mainly across the *RV*, though including the umbonal tip of the *LV* (Fig. 6D,  
269 E); and the lower section cuts across the *RV* only (Fig. 6F).

270 **Localities.** The specimens were collected from the Langshan Formation of Nyima  
271 County, Tibet. The fossil site is located at the west side of Dangqiong Lake (E  
272  $86^{\circ}27'23''$ , N  $31^{\circ}36'53''$ ; Fig. 1B).

273 **Diagnosis.** As for genus.

274 [Figures 4–6 hereabouts]

275 **Description.**



276 **External morphology.** The two specimens are relatively large; although both *RV*  
277 apices are broken, values of *Hd* can be estimated at about 70 mm, and of *Hv* up to 120  
278 mm, creating a dorsally inclined commissure. The *RV* is slightly twisted and curved  
279 and the *LV* is of low capuloid form, becoming gradually lower from the dorsal to  
280 ventral parts (Fig. 4C). The commissure is sub-rounded in the holotype, with a 90 mm  
281 diameter, whereas in the paratype it is elliptical because of dorso-ventral compression,  
282 with a 90 mm *Dap* and a 50 mm *Ddv*. Although the *ol* is partly worn or encrusted,  
283 blunt longitudinal ribs could be observed in each *RV* (Figs. 4D, 6B); rib width is about  
284 2 mm. In the *LV*, fine costae radiate from the apex to the commissural rim.

285 The invaginated ligament, supported on an infolding of the dark outer shell layer,  
286 created a longitudinal furrow on the dorsal flank of the *RV* (Fig. 6A, F). The extent of  
287 external wear of the specimens precludes the possibility of recognizing radial bands  
288 either in the transverse sections, or on the natural surfaces of the shells.

289 **Internal organization.** The thickness of the dark outer shell layer may approach 10  
290 mm in parts of the *RV* (Figs. 5, 6C-F). In the *LV*, in contrast, it is only a few mm thick,  
291 thickening slightly towards the commissure (Fig. 5). The inner shell layer is thick,  
292 especially in the myocardial area, and has been replaced by white to pale grey calcite  
293 spar (Figs. 5, 6 C, D, F). In the oblique transverse section of the paratype *RV*, the *ol*  
294 infolding associated with the invaginated ligament is about 3 mm wide and 6 mm in  
295 length, and a small ligamentary cavity wraps around its truncated inner tip (Fig. 6F).

296 The myocardial complex is well displayed in both specimens despite some  
297 localized boring and minor disruption by narrow, spar-filled fractures and stylolites.

298 The *Lpm* is prominent, pedunculate, and reflexed so as to lie nearly parallel to the  
299 over-arching posterior shell wall of the *LV*, from which it is thus separated by an  
300 ectomyophoral cavity of sub-rectangular shape in section (Fig. 5C, D); a narrow  
301 annexe extends dorsally from the latter cavity above the *pt* (Figs. 5A, 6C, 'o'). The tip  
302 of the *Lpm*, where the adductor muscle attached, faces outwards onto the depressed  
303 and inwardly sloping face of the *Rpm*, which is formed by a swelling of the *RV* inner  
304 shell layer (Fig. 5C, D). The *Rpm* thus appears in transverse section simply as a solid  
305 thickening of the posterior inner shell, lacking any indication of an ectomyophoral  
306 cavity behind it (Fig. 6D-F). The *Lam* is a protruding buttress with a bluntly  
307 sub-rectangular termination in section, separated from the anterior valve wall by a  
308 narrow gutter (Figure 5D). Its counterpart in the *RV*, the *Ram*, is formed by a  
309 shelf-like thickening of the inner shell layer (Figs. 5C, D, 6D-F). The *ct* in the *RV* is  
310 an erect, robust ridge interposed between the *at* and *pt* of the *LV* (Fig. 5A; 6D, E); *at*  
311 is slightly larger than *pt* (Fig. 6D-F).

312 **Remarks.** The single Ladakh specimen, which was assigned to *Polyconites* ? sp., by  
313 Masse and Fenerci-Masse (2017; Fig. 20 therein), is closely comparable with the  
314 Nyima specimens. It is similar to them in terms of the external morphology of the  
315 shell (including the low capuloid form of the *LV*), the longitudinal ribbing of the *RV*,  
316 and the myocardial apparatus, with, in particular, a depressed, inward-sloping *Rpm*  
317 lacking a prominent internal shoulder (hence the appearance of 'strong affinity with  
318 *Polyconites*' noted by Masse and Fenerci-Masse, 2017, p. 72). Though somewhat  
319 smaller than the Nyima specimens, this specimen is virtually identical in form to the

320 type material found in Tibet and can thus be considered conspecific.

321 As noted earlier, in the discussion of the genus, the specimen assigned to *Horiopleura*  
322 *distefanoi* by Masse and Fenerci-Masse (2017) and thus perhaps that species – of  
323 similar age to *Shajia* – likewise shows a comparable myophoral configuration, as well  
324 as a *LV* of low capuloid shape. Taken together with other associated forms discussed  
325 by them, such similarities may bear upon the evolutionary origin of the new genus.

326 *Age and distribution.* As for genus.

## 327 **4. Discussion**

### 328 **4.1 Phylogenetic relationship of *Shajia* to other polyconitids**

329 At first sight, *Shajia* appears to have a chimaeric combination of characters from both  
330 *Horiopleura* and *Polyconites*: while its external shell form and ornamentation are very  
331 similar to those of the larger species of *Horiopleura*, the posterior myophoral  
332 arrangement, in particular, approaches that of *Polyconites*. Notwithstanding its  
333 distinction from both of those genera, derivation from either of them appears plausible:  
334 i.e., either from *Horiopleura*, through progressive inward inclination and depression  
335 of the *Rpm*, analogously to that proposed for the earlier origination of *P. hadriani*  
336 from an older *Horiopleura* sp. (Skelton et al., 2010), though without flattening of the  
337 *LV* and loss of ribbing; or, alternatively, from a *Polyconites* sp., through reversal of  
338 the *LV* flattening, to re-acquire a *Horiopleura*-like external shell shape, meanwhile  
339 retaining a depressed, inwardly-inclined *Rpm* – in contrast to the pronounced  
340 posteriorward tilt of the *Rpm* in the more derived species of *Horiopleura*.

341 Although *Shajia* is externally quite similar to the co-eval SW Asian *H. haydeni* in size,  
342 morphology, longitudinal ribs on the *RV*, as well as with respect to dentition, on the  
343 evidence of the few specimens known so far, it differs sharply from the latter species  
344 in its posterior myophoral organisation. Specifically, 1) the *Lpm* of *Shajia* is strongly  
345 reflexed posteriorly, such that it is nearly parallel to the posterior *LV* shell wall,  
346 forming a narrow sub-rectangular ectomyophoral cavity between them, whereas in *H.*  
347 *haydeni*, the *Lpm* protrudes more directly down into the *RV*; 2) correspondingly, the  
348 *Rpm* of *Shajia* is formed by the low, inward-facing swelling on the inner shell layer,  
349 whereas in *H. haydeni*, the *Rpm* is tilted backwards to form an erect plate with the  
350 adductor insertion surface on its posterior side (contrast Fig. 3A and B). As noted  
351 earlier, a similar contrast is seen also with respect to *H. lamberti*, as well as other,  
352 more derived polyconitid genera (Fig. 3 C, E, F).

353 On the other hand, co-eval species of *Polyconites* differ markedly from *Shajia* not  
354 only in their external form and ornamentation, as noted above, but also in the more  
355 extreme deflation of the *Rpm* (Fig. 3D). Furthermore, Sha and Cestari (2016) have  
356 drawn attention to the remarkable lack of records to date of *Polyconites* from the SW  
357 Asian Province (with the single exception of an unconfirmed mention of '*Polyconites*  
358 sp.', from Ladakh, by Mathur et al., 2008), weakening the circumstantial case for the  
359 derivation of *Shajia* from the latter genus.

360 Thus, by default, on the basis of the currently available evidence the most likely  
361 contender for the progenitor of *Shajia* is the species (or another, similar) represented  
362 by the specimen referred to *H. distefanoi* by Masse and Fenerci-Masse (2017; Fig.

363 19B therein), as discussed above. According to this scenario, *Shajia* would represent  
364 an iterative derivation of a *Polyconites*-like posterior myophoral organization from  
365 one of the 'third group' of *Horiopleura* species from the southern margin of the  
366 Mediterranean Tethys (extending to Oman) recognized by Masse and Fenerci-Masse  
367 (2017; pp. 75–76 therein). If correct, such a derivation would present an intriguing  
368 parallel with the appearance of another typically central to southern Tethyan form,  
369 *Sellaea* sp., in the Langshan fauna (Rao et al., 2015).

#### 370 **4.2. The composition and age of the rudist fauna of the Langshan Formation**

371 Study of rudists from the Langshan Formation was first conducted by Yang et al.  
372 (1982). Six species assigned to four genera were described from Rutog County,  
373 including *Toucasia* sp., *Requienia?* sp., *Rutonia bangonghuensis* Yang et al., 1982 and  
374 three species of *Praeradiolites*, *P. hedini* Douvillé, 1916, *P. biconvexus* Yang et al.,  
375 1982 and *P. ngariensis* Yang et al., 1982. Gou (1994) and Gou and Shi (1998)  
376 described eight new species plus an undetermined ninth, assigned to three genera,  
377 from the Langshan Formation of Coqen, Bangoin and Gegyai counties, comprising  
378 seven species placed in *Praeradiolites*, *P. gegyainensis* Gou, 1994, *P. exiguous* Gou,  
379 1994, *P. perbellus* Gou, 1994, *P. gregareus* Gou, 1994, *P. daxungensis* Gou and Shi,  
380 1998, *P. bangoinensis* Gou and Shi, 1998, *P. coquenensis* Gou and Shi, 1998, together  
381 with *Coralliochama anomalusa* Gou and Shi, 1998, and *Gyropleura?* sp.

382 Scott et al. (2010) restudied the specimens described by Yang et al. (1982) and  
383 considered the rudist assemblage of the Langshan Formation to be Albian to  
384 Cenomanian in age. They suggested that *Monopleura* sp., had been mistaken for

385 *Toucasia* sp., by Yang et al. (1982); they assigned *Praeradiolites ngariensis* to  
386 *Eoradiolites gilgitensis* based mainly on the structure of the anterior and posterior  
387 radial bands; and they attributed *P. biconvexus* to the genus *Sphaerulites* based on the  
388 external morphology.

389 Rao et al. (2015, 2017) revised the rudist taxa of the Langshan Formation  
390 described by Yang et al. (1982), Gou (1994), and Gou and Shi (1998). A new genus,  
391 *Auroradiolites*, was proposed for the endemic grouping of SW Asian to Japanese  
392 radiolitid species characterised by a compact *ol*, which were formerly attributed to  
393 *Praeradiolites* by Yang et al. (1982), Gou (1994), and Gou and Shi (1998).  
394 *Eoradiolites cf. hedini*, *Magallanesia rutogensis* and *Sellaea* sp. were also recognized,  
395 based on newly collected specimens. The age of the rudist assemblage reported by  
396 Rao et al. (2015, 2017) is most likely late Aptian to Albian, as the age range of *A.*  
397 *biconvexus* was revised to late Aptian to Albian by Rao et al. (2017).

398 As the age range of the Langshan Formation goes no younger than the early  
399 Cenomanian, according to orbitolinid data (Boudagher-Fadel et al., 2017), the rudist  
400 assemblage described from the Langshan Formation by Rao et al. (2015, 2017) is  
401 most probably late Aptian–Albian in age, though a younger age cannot be excluded.

#### 402 **4.3. Palaeobiogeographic implications**

403 *Horiopleura haydeni*, and *Auroradiolites gilgitensis*, which together constitute  
404 the ‘Yasin-type’ rudist fauna (Skelton et al., 2005), were both first described by  
405 Douvillé (1926) as new species from the Yasin Group of the Gilgit region, northern  
406 Pakistan. This fossil site (Table 1, No. 4) is located in the northern Kohistan terrane,

407 next to the North Suture Zone, which separates Kohistan from the Asian continent  
408 (Karakoram) to the north (Searle et al., 1999; Robertson and Collins, 2002; Khan et  
409 al., 2009). Subsequently, Pudsey et al. (1985) described rudists and orbitolinids from  
410 Kohistan, and proposed that the rudist-bearing limestone was of latest Aptian and/or  
411 early to middle Albian age.

412 [Table 1 hereabouts]

413 In the adjacent Ladakh terrane, *Horiopleura* sp., tentatively compared with *H.*  
414 *haydeni* by Upadhyay (2001), also co-occurs with *Auroradiolites gilgitensis*. This  
415 rudist assemblage was identified from limestones within the Saltoro Formation near  
416 the village of Shukur (Table1, No. 3) in the Nubra-Shyok valley region along the  
417 Shyok Suture Zone, which separates Ladakh from the Karakoram to the north  
418 (Upadhyay 2001, 2014). Upadhyay (2014) suggested a latest Aptian to early Albian  
419 age for this rudist assemblage.

420 Further west in Afghanistan, *Horiopleura haydeni* has been reported from two  
421 localities: Montenat et al. (1982) identified *H. haydeni* from the upper Aptian strata at  
422 the Adi Gar Mountains, about 30km north-northwest of Spin Boldak in the Kandahar  
423 region (Table1, No. 5); Rao et al. (2017) described two *H. haydeni* specimens, which  
424 were found together with *Auroradiolites gilgitensis*, from the Khist hills, south of  
425 Khash Rud, in central Afghanistan (Table1, No. 6).

426 *Horiopleura haydeni* thus has a relatively wide distribution extending along a  
427 nearly east-west-oriented belt in southwestern Asia, including central Afghanistan,

428 Kohistan in northern Pakistan and Ladakh in northern India (Fig. 7). These Yasin  
429 fauna species, *per se*, have not so far been recorded from the Lhasa Block, but instead  
430 *A. biconvexus* – probably derived from *A. gilgitensis* – and the canaliculate  
431 polyconitid genus *Magallanesia* were found there (Rao et al., 2015, 2017).

432 [Fig. 7 hereabouts]

433 *Shajia tibetica* was first recorded from Ladakh, as '*Polyconites* sp.', without  
434 detailed locality information, by Masse and Fenerci-Masse (2017). The specimens of  
435 *S. tibetica* recorded herein from the Langshan Formation of Nyima County, northern  
436 Lhasa Block (Fig. 7), were found in association with *A. biconvexus*, implying a late  
437 Aptian to Albian age (Rao et al., 2015), which is in broad agreement, moreover, with  
438 the generally accepted age of the Yasin fauna (Skelton et al., 2005; Sha and Cestari,  
439 2016). Hence we conclude that *S. tibetica* and *A. biconvexus* can be regarded to be  
440 regional variants of the 'Yasin fauna'. Our material thus demonstrates that the Yasin  
441 fauna had already dispersed to the Lhasa Block by the late Aptian, which links the  
442 Langshan Formation palaeogeographically with other mid-Cretaceous sites of  
443 shallow-marine carbonate deposition in adjacent southwestern Asian regions.

444 The Kohistan–Ladakh terrane was situated between Asia to the north and India to  
445 the south in mid-Cretaceous times (Rolland et al., 2002). Although the exact timings  
446 of the collisions of the Kohistan–Ladakh terrane with Asia and with India,  
447 respectively, are still controversial (Rehman et al., 2011), it is generally accepted that  
448 the terrane itself was then located on the northern side of the Neo-Tethyan Ocean



449 (Chen et al., 1993; Searle et al., 1999). Meanwhile, according to the palaeogeographic  
450 reconstruction of Asia, central Afghanistan was situated on the southern Asian margin  
451 by mid-Cretaceous times (Chen et al., 1993; Zaman and Torii, 1999). At that time, the  
452 Lhasa Block had already collided with the Asian continent, and was also located at the  
453 northern margin of the Neo-Tethyan (Zhang, 2000; Leier et al., 2007). Therefore, all  
454 the localities that have yielded Yasin fauna were arrayed along or offshore from the  
455 southwestern Asian margin on the northern side of the Neo-Tethyan Ocean in the  
456 mid-Cretaceous.

457 As discussed above, in the SW Asian/Pacific Faunal Province, *Shajia* and  
458 *Horiopleura haydeni* were restricted to the southwestern Asia region. The genus  
459 *Praecaprotina* of late Aptian–Albian age has only been recorded from Japan and the  
460 Daiichi–Kashima Guyot in the Northwest Pacific (Masse and Shiba, 2010). The  
461 canaliculate polyconitid genus *Magallanesia*, of likely late Albian age, was found not  
462 only on Cebu Island and Takuyo–Daini Seamount, both located in the Pacific region  
463 (Sano et al., 2014), but also on the Lhasa Block in southwestern Asia (Rao et al.,  
464 2015). These polyconitid taxa, are all endemic to the combined southwestern Asia and  
465 Pacific regions, and mostly co-occur with the radiolitid genus *Auroradiolites*, which is  
466 characterised by an entirely compact outer shell layer and is also restricted to these  
467 regions (Rao et al., 2017). Hence these findings suggest strong endemism in the rudist  
468 fauna of the SW Asian/Pacific Faunal Province during the late Aptian to Albian  
469 interval.

## 470 **5. Conclusions**

471 *Shajia tibetica* gen. et sp. nov., a new polyconitid rudist, is described from the  
472 Langshan Formation of Nyima County in the northern Lhasa Block of Tibet. It is  
473 similar in external form to *Horiopleura haydeni* Douvillé, 1926, an abundant species  
474 of late Aptian to Albian age that is endemic to southwestern Asia, including  
475 Afghanistan, Kohistan in northern Pakistan, and Ladakh in northern India. However,  
476 *Shajia* differs from the latter species in its posterior myophoral arrangement: 1) *Lpm*  
477 is strongly bent posteriorly, such that it is nearly parallel to the over-arching posterior  
478 shell wall of the *LV*, thereby forming a sub-rectangular ectomyophoral cavity between  
479 them; 2) *Rpm* is formed by an inward-inclined swelling of the inner shell layer,  
480 without forming a projecting plate. A single specimen from Ladakh which was  
481 assigned to *Polyconites?* sp. by Masse and Fenerci-Masse (2017), is reappraised and  
482 transferred to *Shajia*. It was most likely derived from one of a small group of  
483 *Horiopleura* species that dwelt on the southern margin of the Mediterranean Tethys  
484 (extending to Oman) and which show a posterior myophoral arrangement approaching  
485 that of *Shajia*. The geological range of *Shajia* is probably Upper Aptian to Albian,  
486 combining the records from the Lhasa Block and Ladakh.

487 *S. tibetica* is associated with *A. biconvexus*, and as the age of the association is  
488 basically in accordance with that of the Yasin fauna (*H. haydeni* and *A. gilgitensis*) it  
489 may thus be considered as a regional variant of the latter association. This new  
490 material thus shows that the Yasin fauna had already dispersed to the Lhasa Block by  
491 the late Aptian, making the Langshan Formation comparable palaeobiogeographically  
492 with other mid-Cretaceous shallow-water carbonate deposits in adjacent southwestern

493 Asia regions.

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774 **Table caption**

775 Table 1. Localities yielding *Shajia* and *Horiopleura haydeni* in the SW Asian/Pacific  
776 Faunal Province, with currently assigned ages. See Fig. 7 for the geographical  
777 distribution of these localities.

778

779 **Figure Captions**

780 1. Location of study area. (A) Map showing the tectonic framework of Tibet and the  
781 outcrops of the Langshan Formation (grey) in the Lhasa Block (after XZBGM,  
782 1993; Wang et al., 2013). (B) Locality map for *Shajia* in Nyima County (red  
783 rectangle in A). *Abbreviations*: BNS, Bangong–Nu Suture; IYS, Indus–Yarlung  
784 Suture.

785 [in colour]

786 2. Abbreviations of quantitative characters used for the description of *Shajia* (*LV*,  
787 left valve; *RV*, right valve): *Dap*, antero-posterior commissural diameter, *Ddv*,  
788 dorso–ventral commissural diameter; *Hd*, dorsal height of *RV*; *Hv*, ventral height  
789 of *RV*; *Lvc*, convexity of the *LV*.

790 [in black and white]

791 3. Diagrammatic antero-posterior sections across both valves of *Shajia* and other  
792 similar polyconitids (outer shell layer shown in black; inner shell, in grey). A,  
793 *Shajia* (based on Fig. 5D herein); B, *Horiopleura haydeni* (after Rossi Ronchetti,  
794 1965, Plate 38, fig. 1; outer shell layer worn, and image reversed to facilitate  
795 comparison); C, *Horiopleura lamberti* (after Skelton and Smith, 2000, Fig. 7); D,  
796 *Polyconites* (after Skelton, 2013a, Fig. 7A); E, *Praecaprotina yaegashii* (after



797 Sano et al., 2014, Fig. 2); F, *Magallanesia canaliculata* (after Sano et al., 2014,  
798 Fig. 4D). Abbreviations: *Lam*, anterior myophore of left valve; *Lpm*, posterior  
799 myophore of left valve; *LV*, left valve; *Ram*, anterior myophore of right valve;  
800 *Rpm*, posterior myophore of right valve; *RV*, right valve.

801 [in black and white]

802 4. *Shajia tibetica* gen. et sp. nov., holotype articulated specimen (NIGP. 110522). A,  
803 dorsal view showing overhanging umbo of *LV*. B, ventral view. C, anterior view  
804 showing the oblique commissure and the convexity of the *LV*; red lines show the  
805 two sections made on this specimen; a, b, c, and d represent the positions of the  
806 sections shown in Figs. 5A–D respectively. D, posterior view of *RV* showing the  
807 longitudinal ribs (inset: magnified view of red rectangle).

808 [in colour]

809 5. *Shajia tibetica* gen. et sp. nov., holotype (NIGP. 110522): A–D, successively  
810 more ventrally situated antero-posterior sections of both valves, as indicated either  
811 side of the red lines in Fig. 4C (B and D are reversed so that all images are viewed  
812 looking dorsally, for ease of comparison): A–B show the dentition; C–D show the  
813 myophoral organisation. Abbreviations: *at*, anterior tooth (from *LV*); *ct*, central  
814 tooth (from *RV*); *Lam*, anterior myophore of left valve; *Lpm*, posterior myophore  
815 of left valve; *LV*, left valve; *o*, annexe extending dorsally from the ectomyophoral  
816 cavity; *pt*, posterior tooth (from *LV*); *Ram*, anterior myophore of right valve; *Rpm*,  
817 posterior myophore of right valve; *RV*, right valve.

818 [in colour]

819 6. *Shajia tibetica* gen. et sp. nov., paratype articulated specimen (NIGP. 110523). A,  
820 dorsal view, commissure indicated by dashed red line; solid red lines show the  
821 three transverse sections made of this specimen. B, anterior view showing the  
822 longitudinal ribs on the *RV*. C, D–E and F show the three successively lower  
823 transverse sections indicated in A, all in adumbonal view of the *RV*, revealing the  
824 myocardial organisation.

825 Abbreviations: *at*, anterior tooth (from *LV*); *ct*, central tooth (from *RV*); *Lig*,  
826 infolding of outer shell layer associated with invaginated ligament; *Lpm*, posterior  
827 myophore of left valve (dorsalmost part only); *LV*, left valve; *o*, annexe extending  
828 dorsally from the ectomyophoral cavity; *ol*, outer shell layer (of *RV*); *pt*, posterior  
829 tooth (from *LV*); *Ram*, anterior myophore of right valve; *Rpm*, posterior myophore  
830 of right valve; *RV*, right valve.

831 [in colour]

832 7. Present-day geographical map showing the fossil localities bearing *Shajia* and  
833 *Horiopleura haydeni*, represented by red and blue stars respectively (see Table 1  
834 for details). The base map was generated using the ODSN online Plate Tectonic  
835 Reconstruction Service (Hay et al., 1999). CAF, central Afghanistan; KOH–LAD,  
836 Kohistan–Ladakh terrane; LSA, Lhasa block.

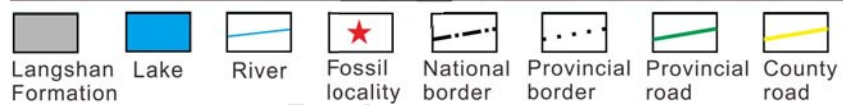
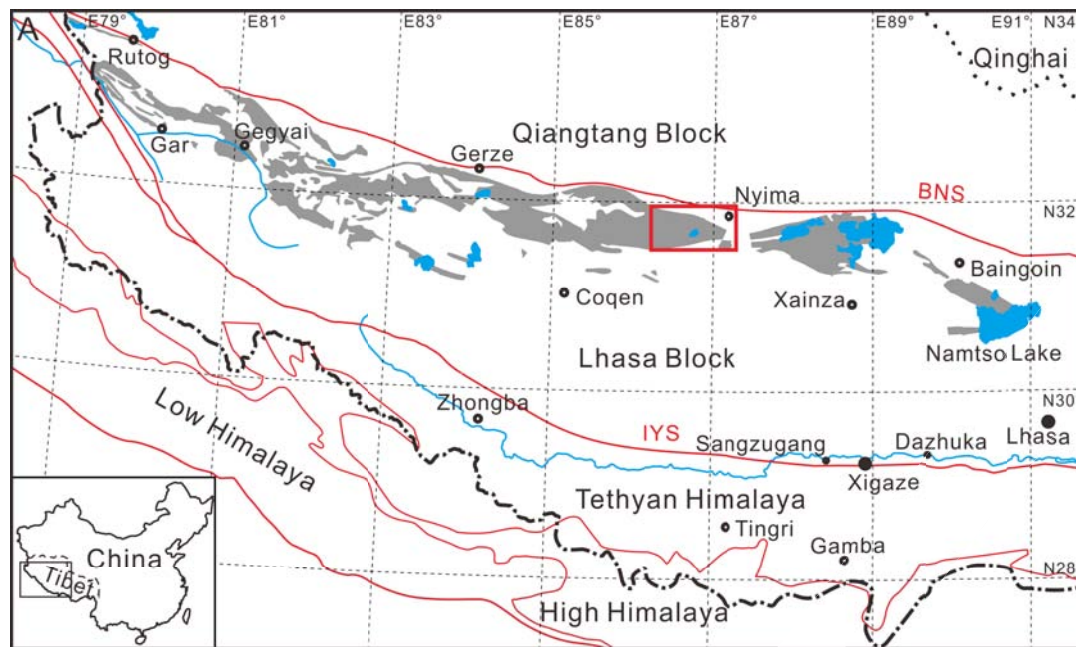
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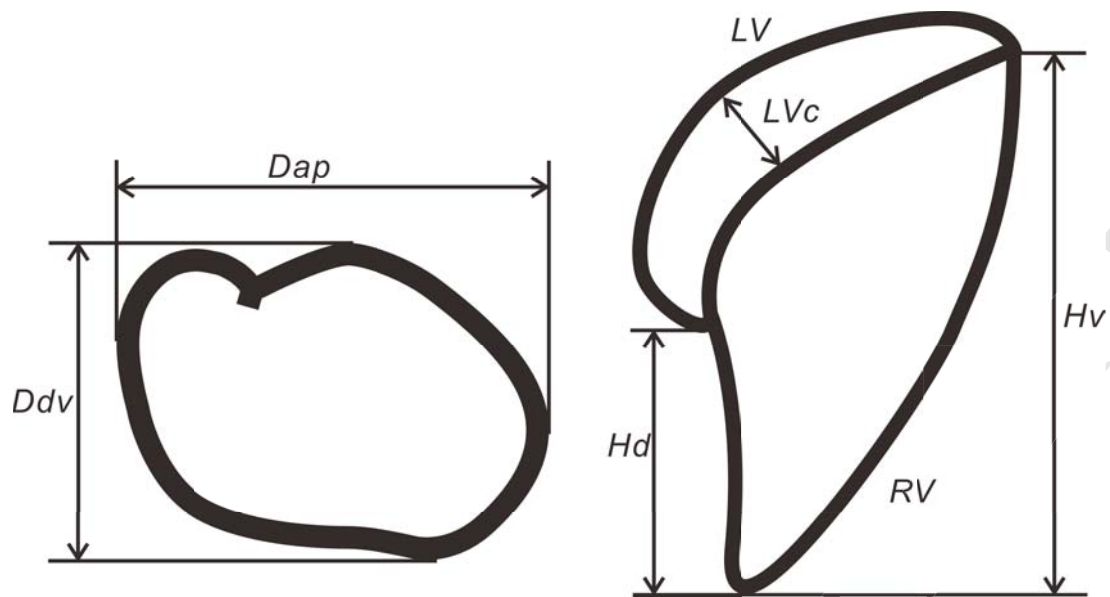
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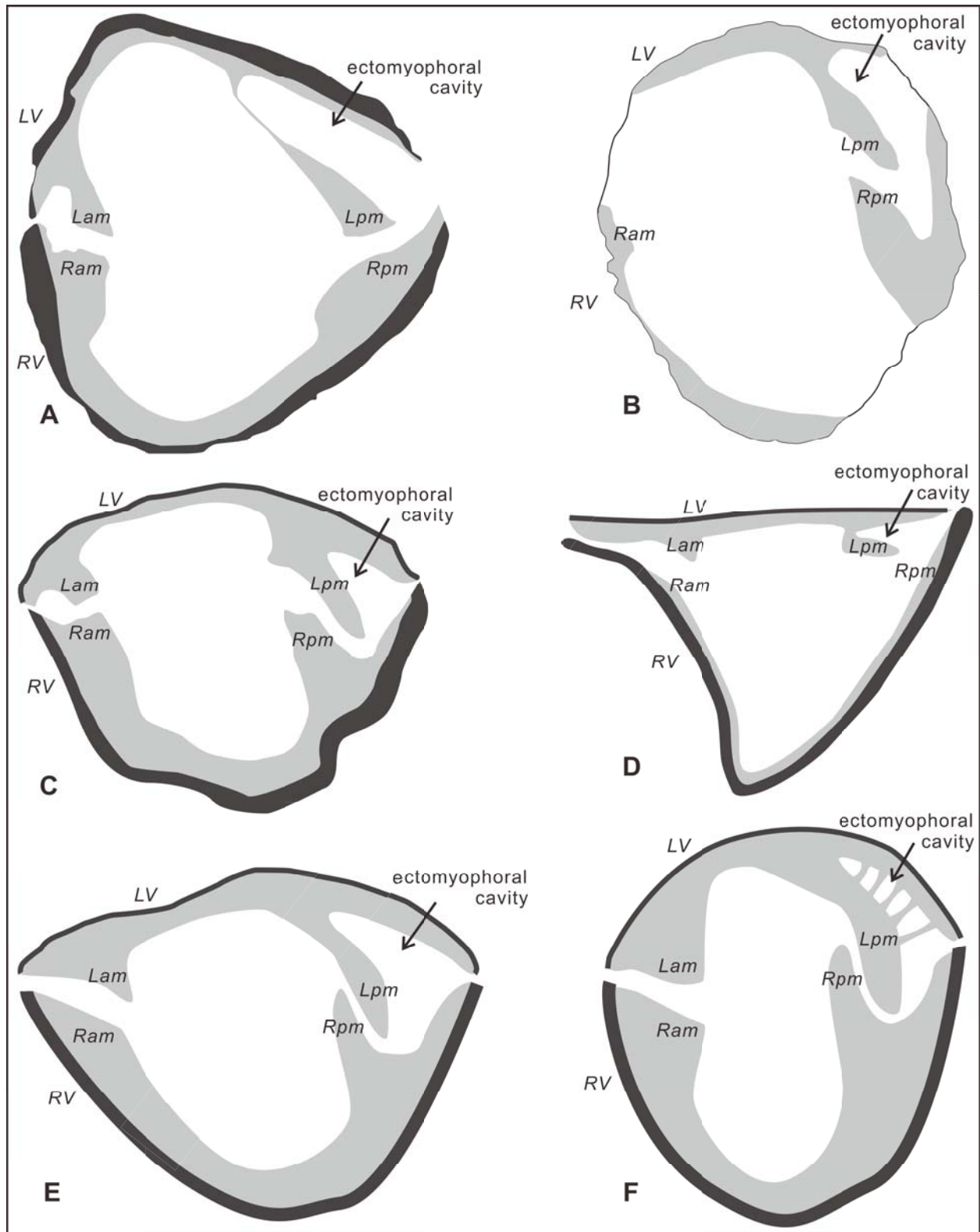
Table 1

Record	Locality	Age	Species	References
1	Nyima County, Tibet, Southeast China	late Aptian to Albian	<i>Shajia tibetica</i>	This paper
2	Ladakh, North India	late Aptian	<i>S. tibetica</i>  (= ' <i>Polyconites</i> sp.')	Masse and Fenerci-Masse, 2017
3	Shukur, Nubra-Shyok valley, Ladakh, North India	latest Aptian to early Albian	<i>Horiopleura</i>  <i>haydeni</i>	Upadhyay, 2001, 2014
4	Yasin, Gilgit region, Kohistan, Northwest Pakistan	latest Aptian to middle Albian	<i>H. haydeni</i>	Douvillé, 1926; Rossi Ronchetti, 1965; Pudsey et al., 1985; Sha and Cestari, 2016
5	Adi Gar Mt. (about 30 km N.N.W. from Spin Boldak) in Kandahar, Central Afghanistan	late Aptian	<i>H. haydeni</i>	Montenat et al., 1982
6	Khrist hills, south of Khash Rud, Central Afghanistan	latest Aptian to middle Albian	<i>H. haydeni</i>	Rao et al., 2017

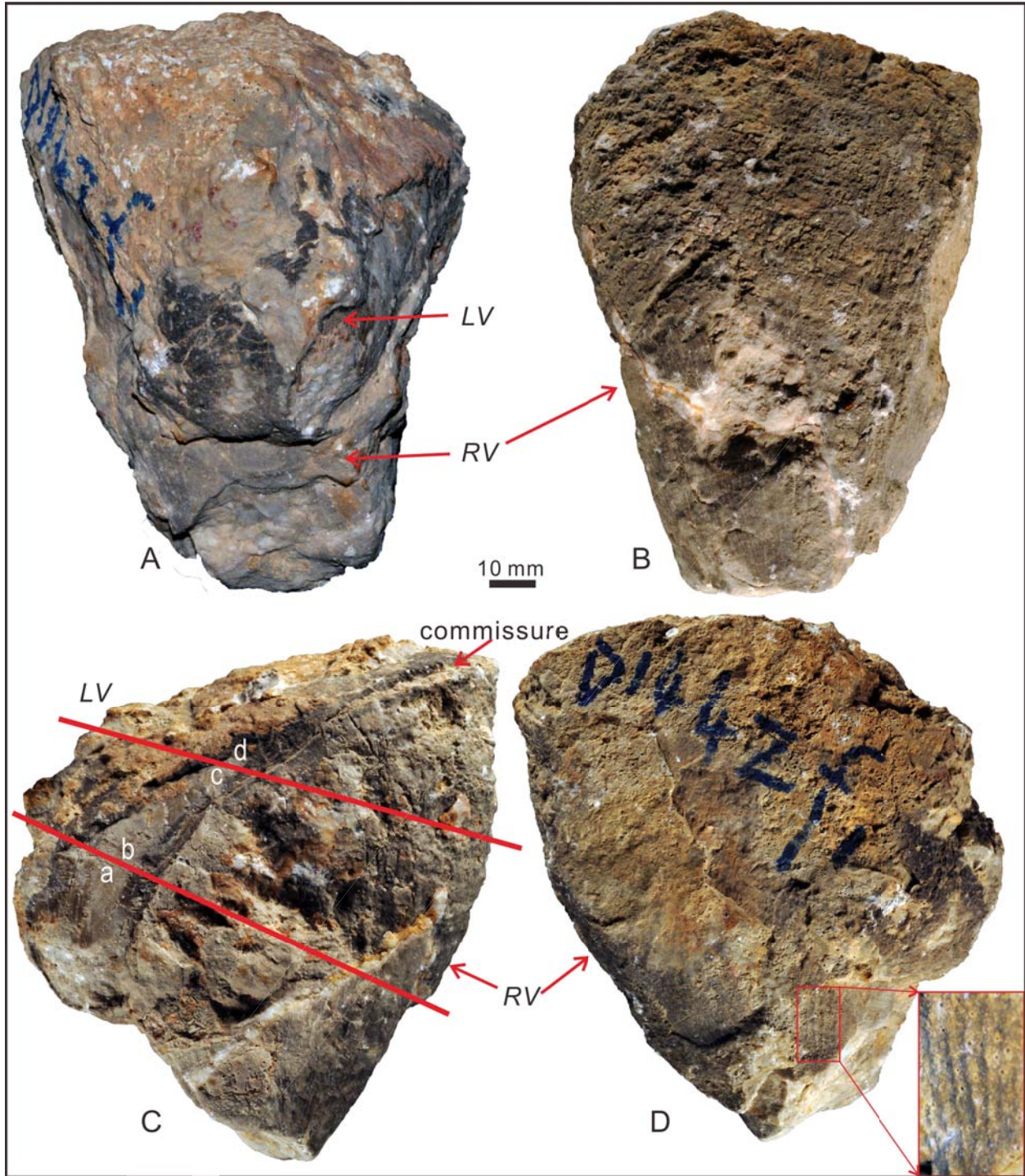


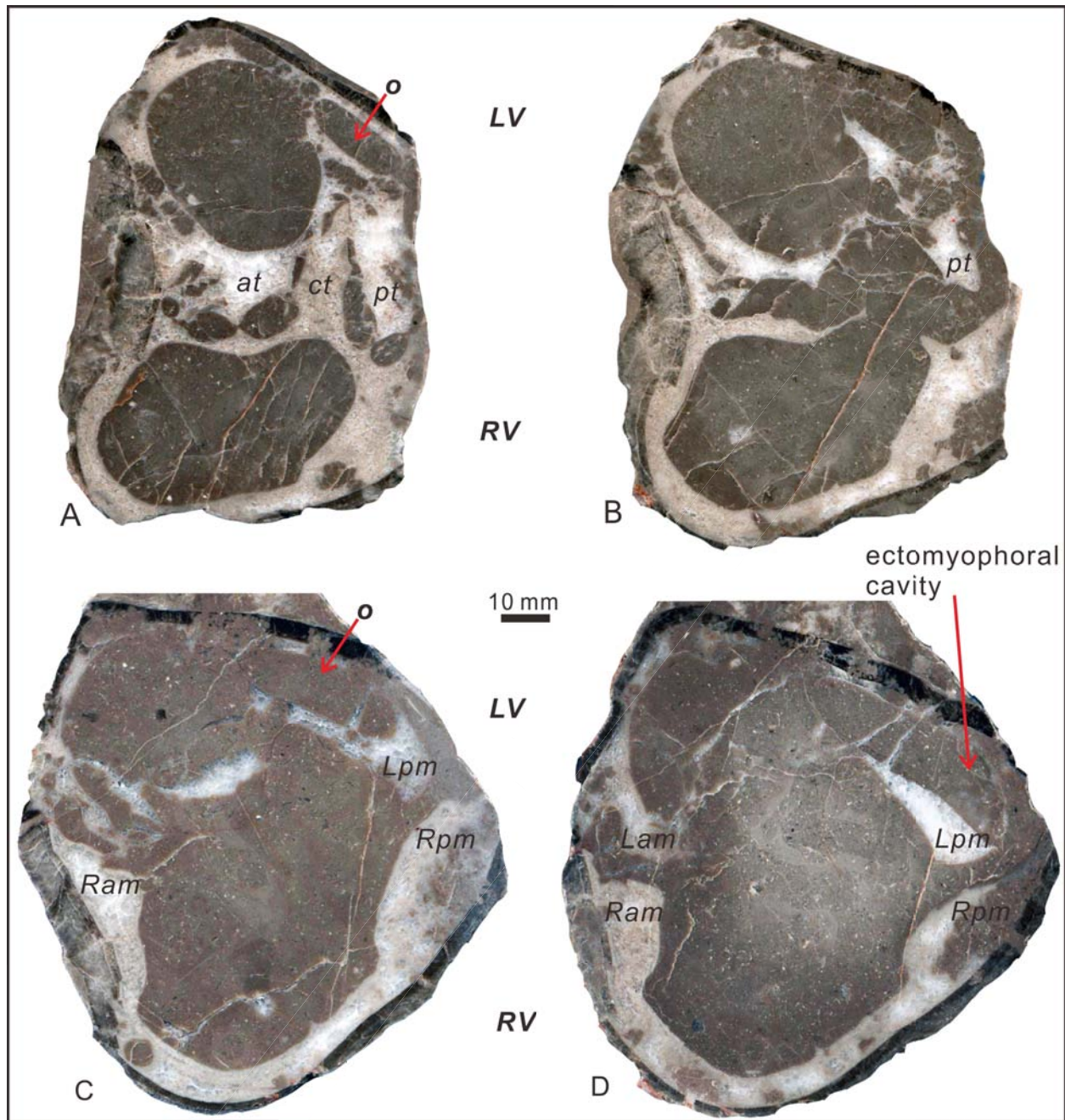


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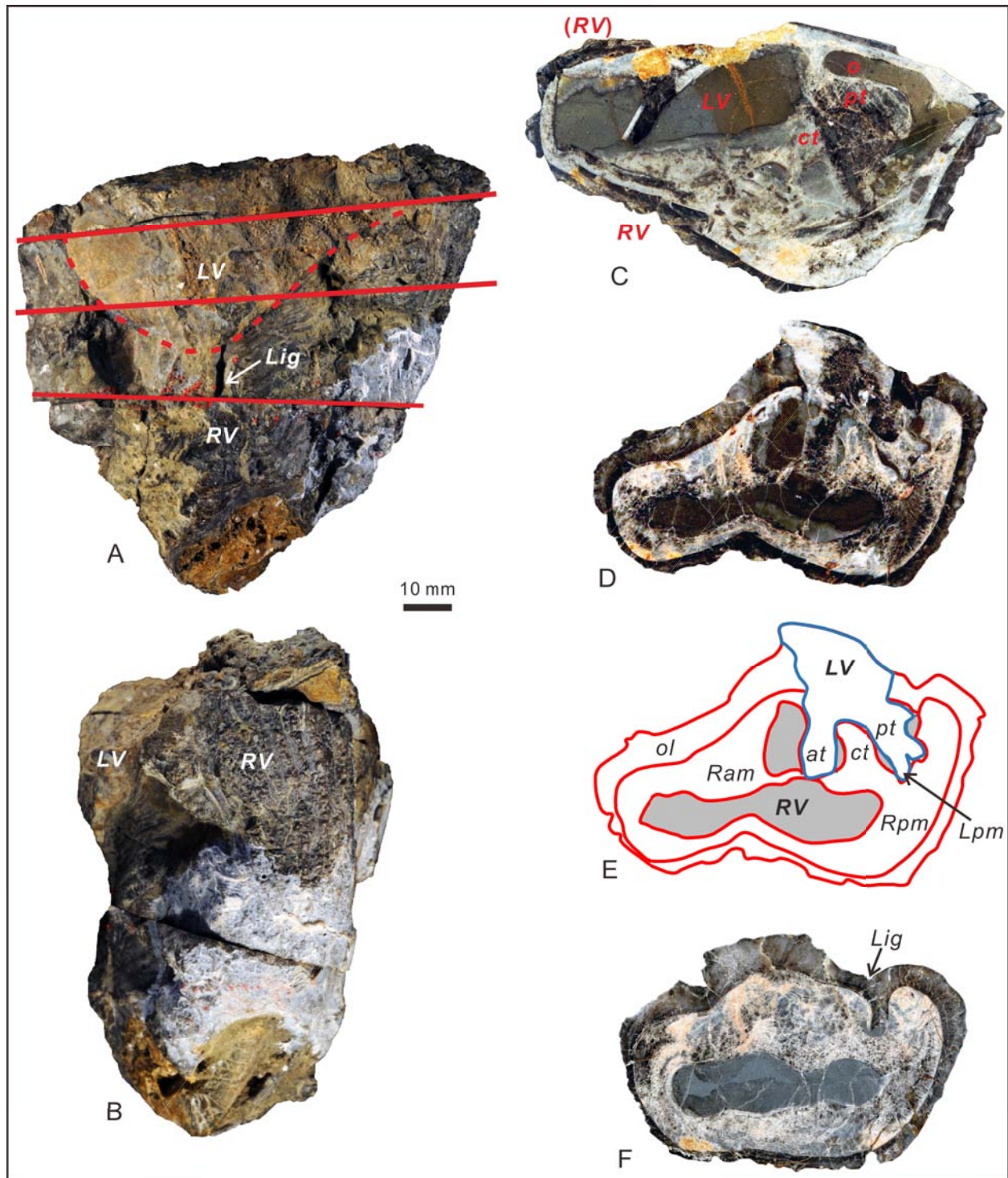


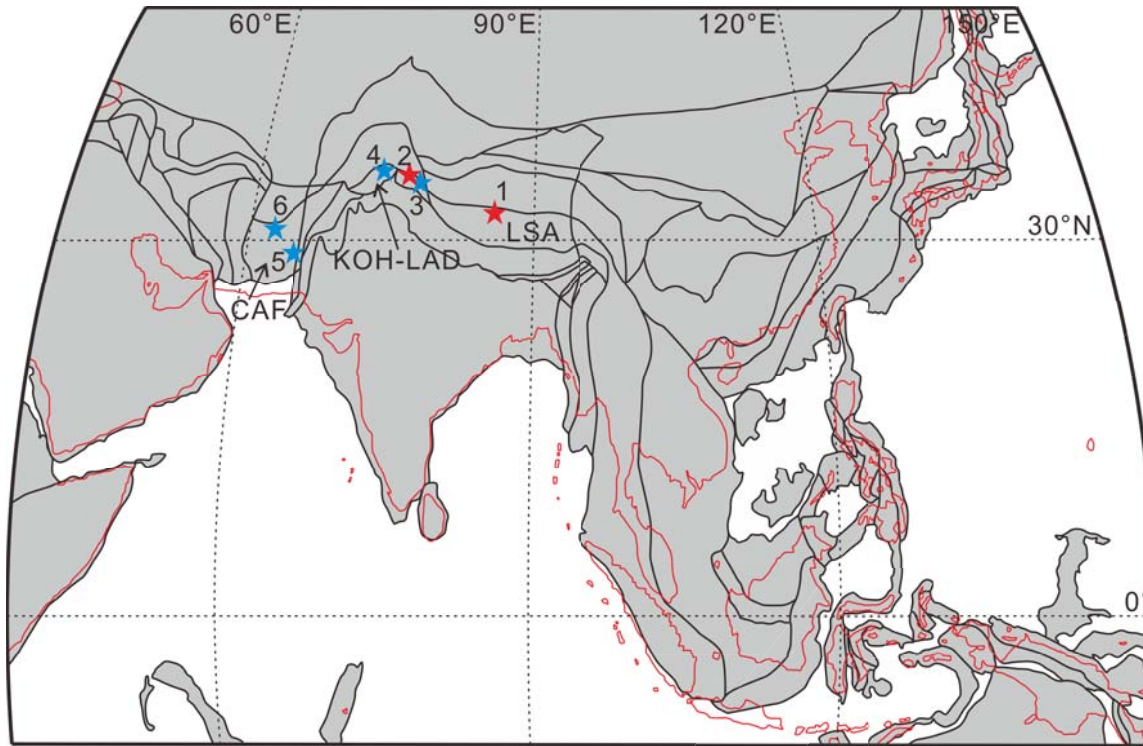












**1 Highlights**

- 2 1. A new polyconitid rudist *Shajia tibetica* gen. et sp. nov., likely late Aptian to  
3 Albian in age, is described from the Langshan Formation of Nyima County, Tibet.
- 4 2. *Shajia* is externally comparable with *Horiopleura haydeni* Douvillé, 1926, but  
5 differs in its possession of an inwardly inclined, instead of outwardly facing,  
6 posterior myophore in the right valve
- 7 3. A single specimen from Ladakh that was assigned to *Polyconites?* sp. by Masse and  
8 Fenerci-Masse (2017), is revised and transferred to *Shajia*.
- 9 4. The *Shajia tibetica* /*Auroradiolites biconvexus* rudist association can be considered  
10 a regional variant of the Yasin fauna.

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