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A specimen of *Paralycoptera* Chang & Chou 1977 (Teleostei: Osteoglossoidei) from Hong Kong (China) with a potential Late Jurassic age that extends the temporal and geographical range of the genus

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We identify an osteoglossoid teleost fish - *Paralycoptera* - from Late Jurassic volcanoclastic mudstones from the Lai Chi Chong Formation of Hong Kong, China. This partially preserved postcranial skeleton represents the first Mesozoic fish from Hong Kong and the most southerly *Paralycoptera* to date. A radiometric date for the Lai Chi Chong Formation of ~146 Ma implies a temporal range expansion for *Paralycoptera* of approximately 40 million years back from the Early Cretaceous (~110Ma). However, spores found in the Formation suggest an Early Cretaceous age that is consistent with the existing age assignment to *Paralycoptera*. We argue that the proposed temporal range extension is genuine because it is based on recent precise and accurate radiometric data, but given the discrepancies with the biostratigraphic ages further investigation is needed to confirm this. This study provides an important step towards revealing Hong Kong's Mesozoic vertebrate fauna and understanding its relationship to well-studied mainland Chinese ones.

1 **A specimen of *Paralycoptera* Chang & Chou 1977 (Teleostei: Osteoglossoidei) from Hong**
2 **Kong (Guangdong, China) with a potential Late Jurassic age that extends the temporal and**
3 **geographical range of the genus**

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11 **Abstract** We identify an osteoglossoid teleost fish - *Paralycoptera* - from Late Jurassic
12 volcanoclastic mudstones from the Lai Chi Chong Formation of Hong Kong, China. This partially
13 preserved postcranial skeleton represents the first Mesozoic fish from Hong Kong and the most
14 southerly *Paralycoptera* to date. A radiometric date for the Lai Chi Chong Formation of ~146 Ma
15 implies a temporal range expansion for *Paralycoptera* of approximately 40 million years back
16 from the Early Cretaceous (~110Ma). However, spores found in the Formation suggest an Early
17 Cretaceous age that is consistent with the existing age assignment to *Paralycoptera*. We argue
18 that the proposed temporal range extension is genuine because it is based on recent precise and
19 accurate radiometric data, but given the discrepancies with the biostratigraphic ages further
20 investigation is needed to confirm this. This study provides an important step towards revealing
21 Hong Kong's Mesozoic vertebrate fauna and understanding its relationship to well-studied
22 mainland Chinese ones.

23 **Keywords** Jurassic, fish, osteoglossomorph, *Paralycoptera*, Hong Kong, Lai Chi Chong
24 Formation, lacustrine, volcanism

25 **1 Introduction**

26 In the summer of 2013, a fish fossil - SHGM L275 - labelled as a plant was discovered in the
27 collections of the Stephen Hui Geological Museum (SHGM) at the University of Hong Kong
28 (HKU). The fossil (~2 cm long) is hosted within a small mudstone fragment (5 cm by 3cm) that
29 was supposedly collected from the Lai Chi Chong Formation (荔枝莊組) of Lai Chi Chong, Sai
30 Kung, north-eastern New Territories, Hong Kong (**Fig. 1**). This provenance information is based
31 on the specimen label, which appears to be correct, given that all fossils with the same catalogue
32 number are lithologically similar and match the locality's expected lithologies (see Section 4). It
33 is not mentioned in the literature - probably because of its incorrect specimen label - unlike a
34 fossil fish specimen from associated rocks in Shek Pik (石壁), Lantau Island, which has a passing
35 mention in Lee *et al.* (1997) (**Fig. 1**). The latter specimen is supposed to be in the SHGM
36 collections, but as it could not be located, it is assumed to have been lost. A fossil fish is also
37 known from Lantau Peak (鳳凰山), Lantau Island (C.M. Lee, personal communication, July
38 19th, 2014) (**Fig. 1**). The rocks from this site, Shek Pik and the Lai Chi Chong Formation all
39 belong to the Lantau Volcanic Group, so all three fossils should have similar ages (Sewell *et al.*
40 2000) (**Fig. 1**). The fish fossil assemblages of Lai Chi Chong and Lantau Island are therefore
41 important to compare, but unfortunately, the whereabouts of the Lantau Peak fossil is also

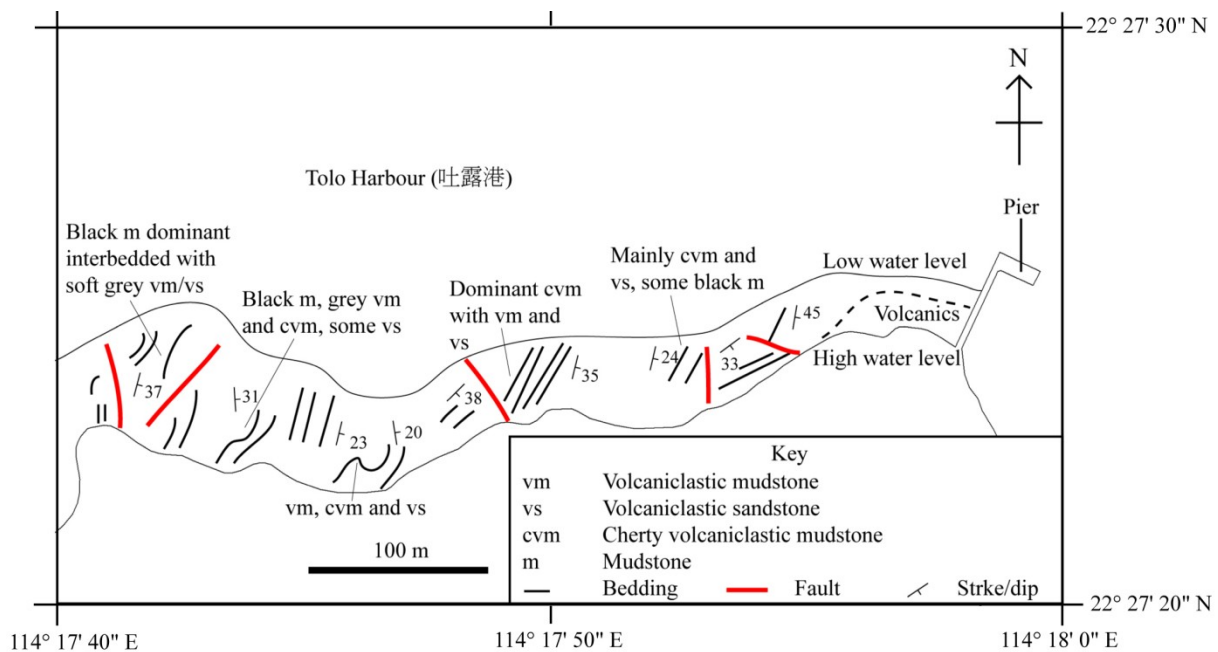
42 unknown, so this comparison is not currently possible.



43 **Figure 1:** A map of Hong Kong showing the location of the Lai Chi Chong Formation in Sai
44 Kung, as well as the broader Lantau Volcanic Group. The locations of fossil fish discoveries in
45 Hong Kong are also marked. Scale bar = 10 km (modified from Sewell *et al.* 2000).

46 The plant fossils discovered within the Lai Chi Chong Formation e.g. *Cyathidites*, *Classopollis*
47 and *Cicatricosisporites* suggest that it has an Early Cretaceous age (Lee *et al.* 1997). However,
48 U-Pb zircon dating of coarse crystalline tuff from the upper Lai Chi Chong Formation suggests
49 that the Formation is actually 146.6 ± 0.2 million years old, which corresponds to the Tithonian
50 stage of the Late Jurassic (Campbell *et al.* 2007), some 40 million years earlier. The high
51 sampling and analytical standards that were met in obtaining the absolute age at Lai Chi Chong
52 (see Campbell *et al.* 2007 for details) suggests that it is unequivocal and that the plant fossil
53 evidence deserves further detailed investigation.

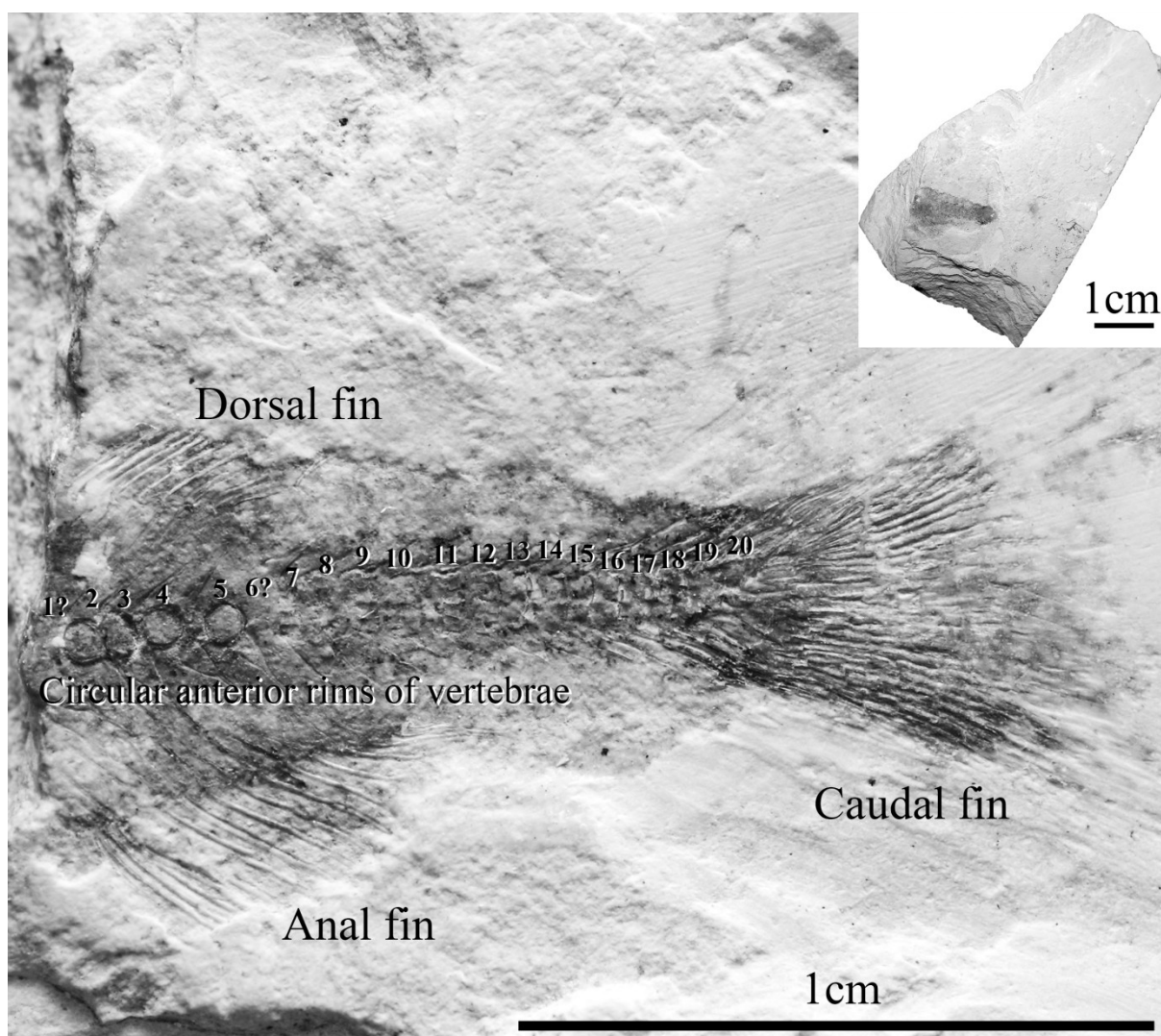
54 This study focuses on the identification of SHGM L275 and understanding its ecology in the
55 context of the palaeoenvironment of the Lai Chi Chong Formation, that has been inferred from its
56 geology and plant fauna (Lee *et al.* 1997) (**Fig. 2**).



57 **Figure 2:** A simplified geological field sketch of the type locality of the Lai Chi Chong
 58 Formation at Lai Chi Chong, Sai Kung, NE New Territories, Hong Kong (simplified from
 59 Workman 1991).

60 2 Methods and Materials

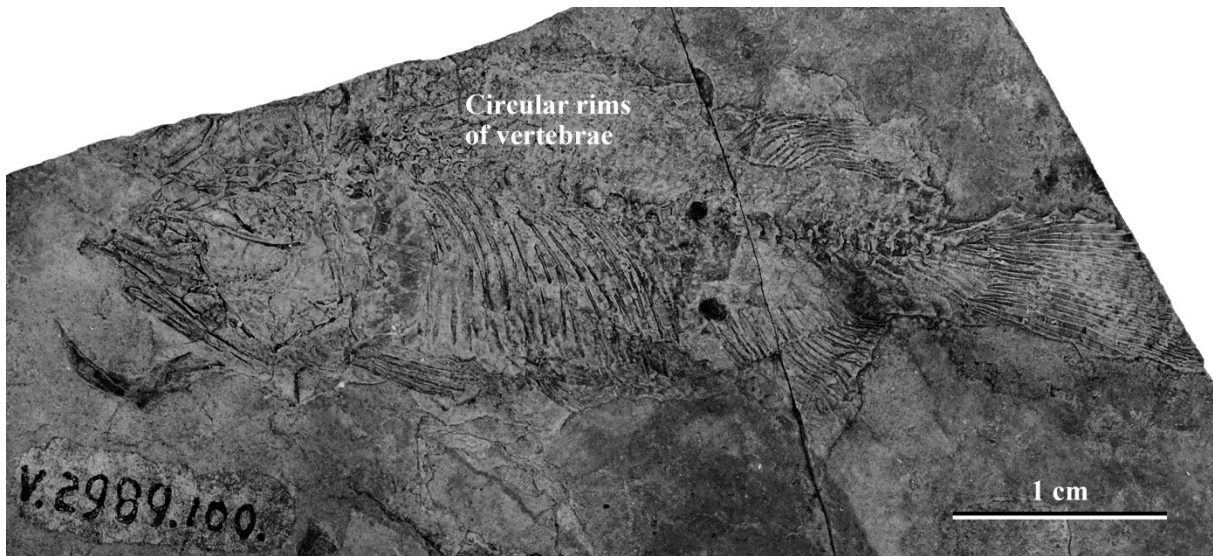
61 The studied fossil specimen, SHGM L275, is a partially-preserved articulated bony fish skeleton
 62 that is missing its anterior portion (**Fig. 3**). The specimen shows the dorsal, anal and caudal fins
 63 and is preserved in a laminated, non-fissile, pale grey orange-spotted mudstone from the Lai Chi
 64 Chong Formation (**Fig. 3**). SHGM L275 is now deposited in the collections of the Stephen Hui
 65 Geological Museum (SHGM) at the University of Hong Kong. The specimen was prepared
 66 mechanically using a thin needle and was examined under a *Leica S8APO* stereomicroscope
 67 which has a magnification range of 10-80x. Photographs were taken of the specimen using a
 68 range of focal points with a Nikon D610 DSLR camera mounted to the stereomicroscope. The
 69 images were uploaded into the open-access computer software *CombineZP*
 70 (www.combinezp.software.informer.com/) to focus-stack them into fully-focused composite
 71 images. Based on a preliminary comparative study against Nelson (2006), SHGM L275 was
 72 diagnosed as an osteoglossomorph fish based on the possible presence of an epural and 15
 73 principal branched caudal fin rays (Xu & Chang 2009). The specimen was then compared by
 74 standard methods with other Chinese Mesozoic osteoglossomorph fish from the collections of the
 75 Institute Vertebrate Paleontology and Paleoanthropology (IVPP; Beijing, China) and the Stephen
 76 Hui Geological Museum (SHGM (HKU), Hong Kong) (see **Supplemental Table S1** in the
 77 Supplementary Information). The specimen's features were then coded against character lists
 78 from osteoglossomorph-specific phylogenetic analyses (Shen 1996; Zhang 2006; Li & Wilson
 79 1996; Wilson & Murray 2008; Xu & Chang 2009). The review of the osteoglossoid
 80 osteoglossomorph *Paralycoptera* by Xu & Chang (2009) was particularly important towards the
 81 referral of SHGM L275 to this genus because of its details on anatomical variation.



82 **Figure 3:** Magnified image (10.5x) of the specimen SHGM L275. The upper right image was
 83 taken before further preparation. The circular features in the anterior portion of the specimen
 84 appear to be the anterior rims of vertebrae. Identified vertebrae are numbered from 1 to 20, with 1
 85 being an abdominal vertebra, and the rest (19) – caudal vertebrae. Scale bar = 1 cm.

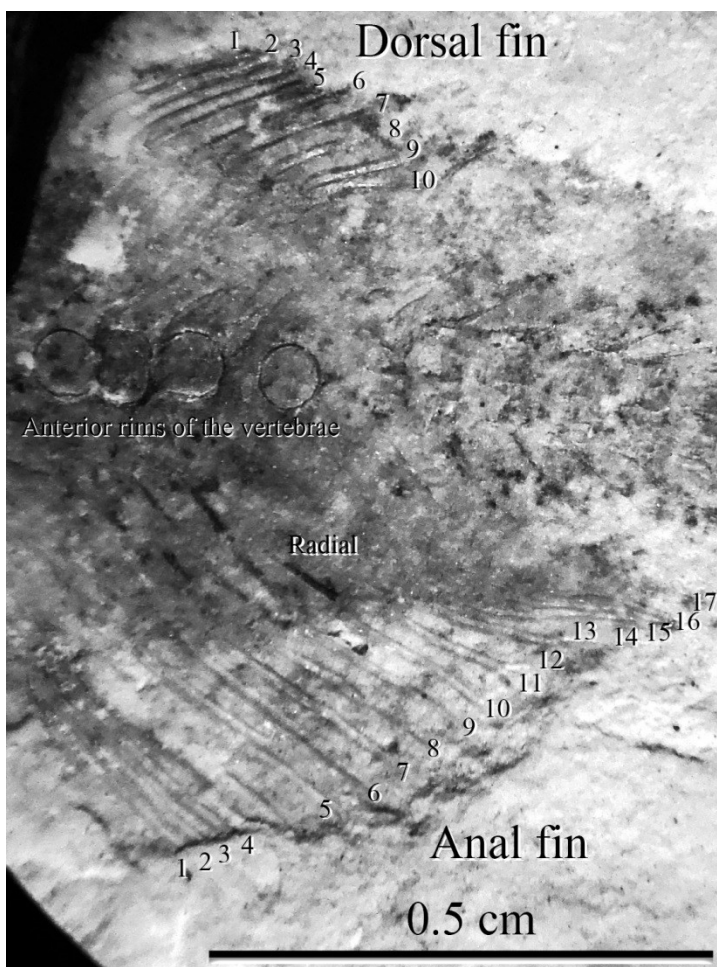
86 3 Results

87 The specimen SHGM L275 is a rather small fish. The preserved part corresponds to the caudal
 88 portion of the fish, with the head and abdominal portion missing. The total length of the
 89 preserved part, including the caudal fin, is approximately 18 mm. Twenty vertebrae are identified
 90 in this portion (**Fig. 3**) between the anterior part of the dorsal and anal fins and the caudal fin,
 91 with the anteriormost preserved one being an abdominal vertebra, and the rest (19) – caudal
 92 vertebrae. The number of caudal vertebrae is comparable to many stem osteoglossomorphs, like
 93 *Huashia gracilis* and *Jinanichthys longicephalus* (Wilson & Murray 2008). Most of the vertebral
 94 centra are dorsoventrally deeper than anteroposteriorly long, which may allow easier lateral
 95 movements during propulsion, as in most fish. In the anterior part of the specimen, there are four
 96 circular features directly on the vertebral column (**Fig. 3**) - these are the anterior rims of the
 97 vertebrae. This feature is also identified in the osteoglossoid osteoglossomorph *Paralycoptera*
 98 *wui*, IVPP V2989.100 (**Fig. 4**), and in other studied osteoglossomorph specimens like *Yanbiania*
 99 *wangqingica*, IVPP V6767-1, and *Tongxinichthys microdus*, IVPP 2332.1 (Wilson & Murray



101 **Figure 4:** *Paralycoptera*, IVPP V2989.100, has a partially disarticulated vertebral column that
 102 reveals numerous circular vertebral rims (most of them are impressions), as in SHGM L275.
 103 Scale bar = 1 cm.

104 In SHGM L275, the anal fin is larger than the dorsal fin like those in *Paralycoptera wui* (Chang
 105 & Chou 1977; Xu & Chang 2009). Seventeen fin rays were observed in the anal fin whilst 10
 106 were observed in the dorsal fin, although the actual number of fin rays may be higher because the
 107 anterior ends of both fins are incomplete (**Fig. 5**). However, the fin ray counts - as they are - are
 108 the same as those of *Paralycoptera wui* IVPP V2989.100 and .105, although the fins of the latter
 109 specimen are also incomplete, as in SHGM L275. For both the anal and dorsal fins, the lengths of
 110 the fin rays are longer in the anterior portion of the fin than in the posterior portion giving them a
 111 sub-triangular shape. The preserved anterior margins of the anal and dorsal fins are opposite to
 112 each other and are rather close to the caudal fin suggesting that the dorsal fin is posteriorly
 113 situated along the fish. Such features, together with the shape of the fins, are seemingly similar to
 114 the posterior portion of *Lycoptera*, but in the latter taxon the size difference between the anal and
 115 dorsal fin is not significant compared to SHGM L275. Between the fins and the vertebrae,
 116 pterygiophores supporting the fin rays are observed (**Fig. 5**). The number of pterygiophores is
 117 more or less the same as the number of fin rays because the ends of each pterygiophore preserved
 118 leads to the base of a fin ray.

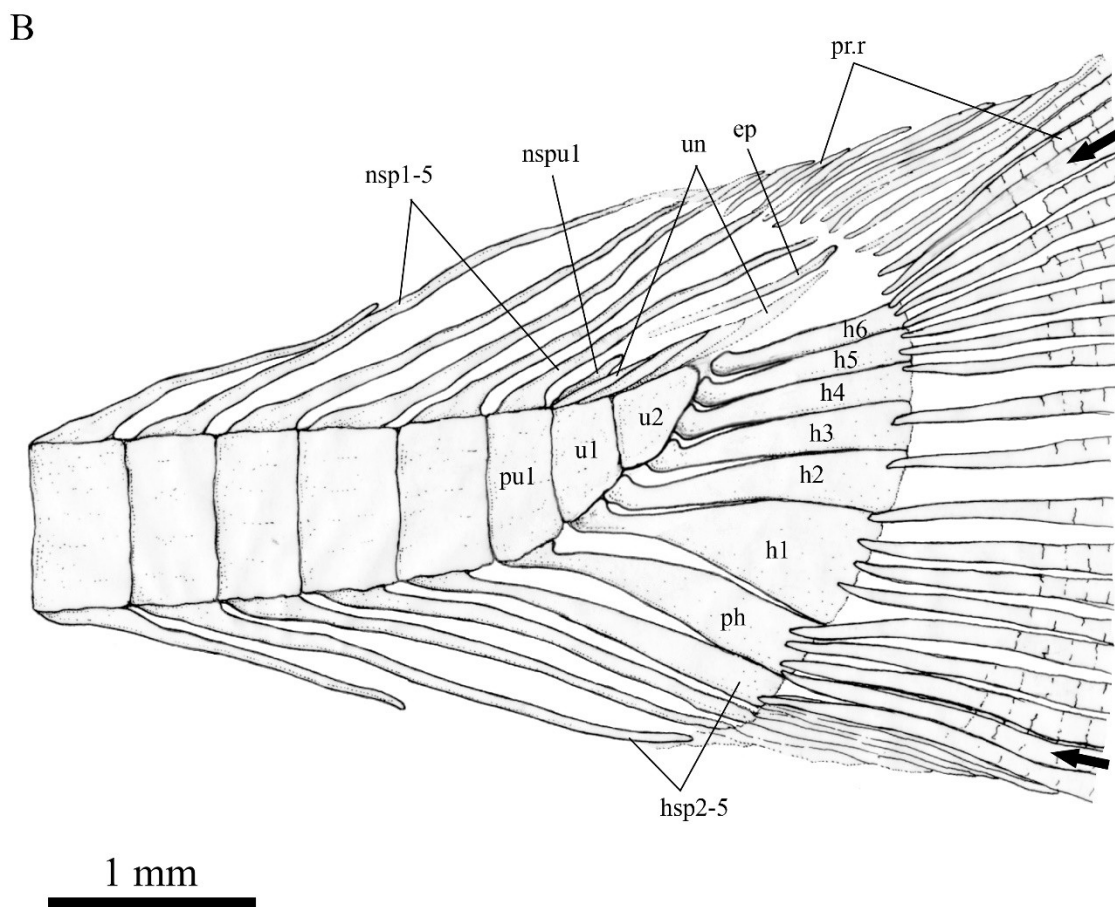
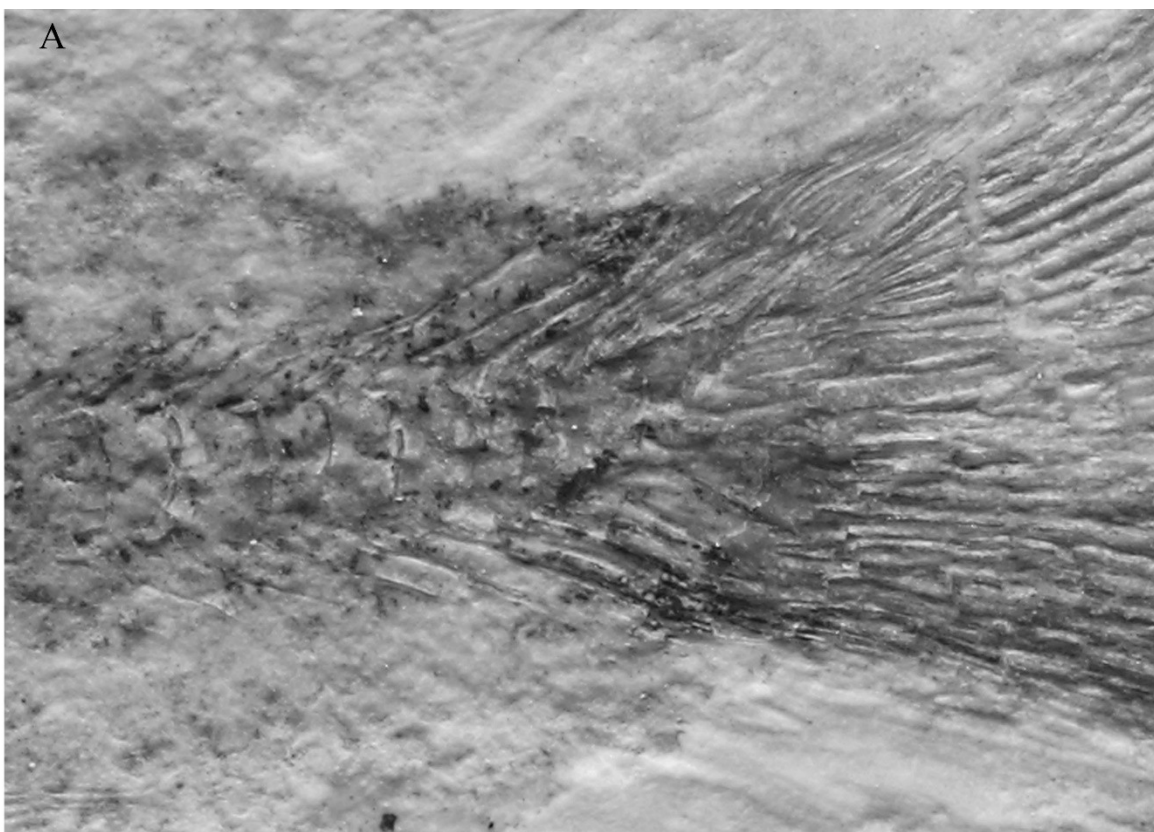


119 **Figure 5:** Magnified image (10.5x) of the anterior portion of SHGM L275 showing the position
 120 of the fin rays in the anal and dorsal fins. Scale bar = 0.5 cm.

121 In the caudal skeleton of SHGM L275 (**Fig. 6**), six hypurals were identified. The first one is
 122 posteriorly broader, giving a fan-like shape, whereas the second is comparatively narrow. These
 123 hypurals articulate with the first ural centrum, and support the rays of the lower lobe of the caudal
 124 fin. Under the first hypural, the parhypural, articulating with the preural centrum 1, also has a
 125 somewhat fan-shaped broader posterior portion. The second ural centrum is triangular in shape
 126 and is slightly upturned towards the upper lobe of the fin. The third to sixth hypurals are
 127 rectangular rod-shaped, articulating with the second ural centrum, and supporting the rays of the
 128 upper lobe of the caudal fin. Comparing ural centrum 2 with ural centrum 1 and neighbouring
 129 vertebral centra, ural centrum 2 is anteroposteriorly longer than dorsoventrally deep whilst the
 130 others are dorsoventrally deeper than anteroposteriorly long. In the area above the ural centra 1
 131 and 2, traces of uroneurals can be seen, though it is difficult to estimate their number (possibly
 132 two or three). The anterior tip(s) of the uroneurals extend to the posterodorsal end of the preural
 133 centrum 1. An epural is probably present above the uroneurals. No urodermals were found.

134 Even though the caudal fin rays are poorly-preserved, the caudal fin appears to be symmetrical
 135 because the vertebral column only bends slightly towards the upper lobe. Thus, the specimen is
 136 likely to possess a homocercal tail, which is a trait of all teleostean fish (Nelson 2006). We were
 137 able to find out the approximate counts of the caudal fin rays: 17 principal fin rays are
 138 recognized, seven branched rays with one unbranched ray at the upper margin in the upper lobe,
 139 and eight branched rays with one unbranched ray at the lower margin in the lower lobe. Besides,

140 about 5-6 and 3-4 short, procurrent rays are observed in front of the upper and lower lobe
141 respectively. Five neural spines on the 1st-5th preural centra and four haemal spines under 2nd-
142 5th preural centra are prolonged, the posterior ones of which are in support of the procurrent rays.
143 The ural centrum 1, perhaps, also carries a short neural spine (**Fig. 6**).



144 **Figure 6:** Magnified image of the caudal skeleton and bases of caudal fin rays in SHGM L275,

145 the arrows point to the outermost (unbranched) principal caudal fin rays. Abbreviations: ep,
 146 epural; h1-6, hypurals 1-6; hsp2-5, haemal spines on preural centrum 2-5; nsp1-5, neural spines
 147 on preural centrum 1-5; nspu1, neural spine on u1; ph, parhypural; pr.r, procurent rays; pu1,
 148 preural 1; u1, u2, ural centra 1 and 2; un, uroneurals. Scale = 1 mm.

149 Based on the features described above, especially that a possible epural is present, the number of
 150 branched caudal fin rays is 15 and the dorsal fin is posteriorly situated, SHGM L275 most likely
 151 belongs to the order Osteoglossiformes (Shen 1997, Xu & Chang 2009), under the superorder
 152 Osteoglossomorpha (Greenwood *et al.* 1966).

153 SHGM L275 was added to the osteoglossomorph phylogenetic data matrices of Shen (1996),
 154 Zhang (2006), Wilson & Murray (2008), and Xu & Chang (2009) (**Table 1**) and in all four
 155 analyses the taxon that has the most similar codings was *Paralycoptera*. However, for the Zhang
 156 (2006) matrix, SHGM L275 has more closely matched codings to *Singida* than to *Paralycoptera*.
 157 The Eocene temporal range of *Singida* (Xu & Chang 2009) is at odds with the Late Jurassic age
 158 of SHGM L275, but it might be possible that the new specimen supports an extremely large range
 159 extension. However, SHGM L275 is referable to *Paralycoptera* based on additional details of the
 160 caudal skeleton: the two hypurals in the lower lobe of *Paralycoptera* are separated and unfused
 161 (Shen 1996) like in SHGM L275, whilst those in *Singida* are partially fused (Murray & Wilson
 162 2005). In addition, *Singida* has a falcate anal fin instead of the triangular one in *Paralycoptera*
 163 (Murray & Wilson 2005) and SHGM L275.

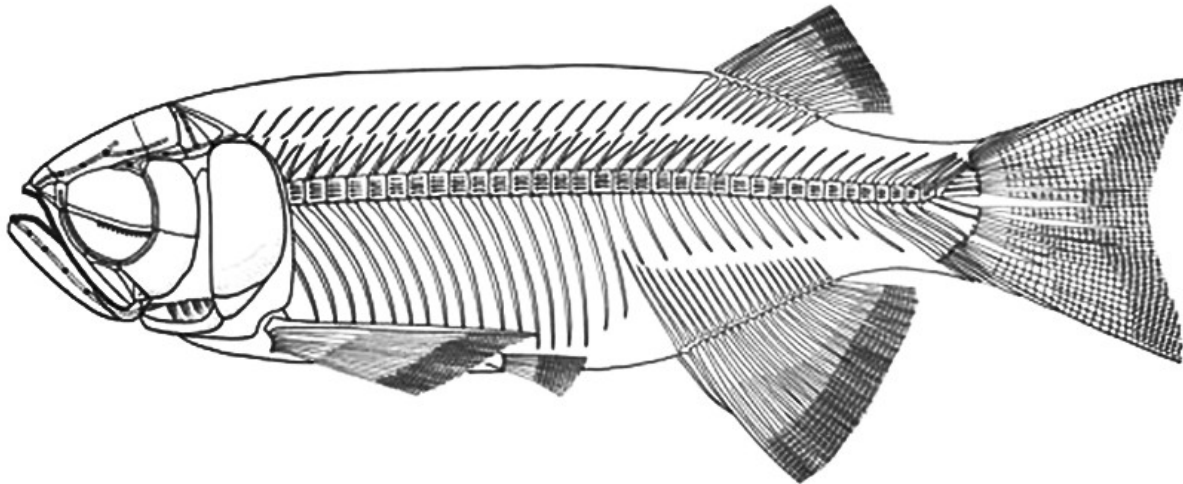
164 **Table 1:** The applicable characters from Shen (1996), Zhang (2006), Wilson & Murray (2008)
 165 and Xu & Chang (2009) to SHGM L275, coding similarities with the most closely-matched
 166 genus – *Paralycoptera* (○ = matched; x = not matched). For the codings of the individual studies
 167 please see **Supplemental Tables S2-S5** in the Supplemental Information).

Osteoglossomorph study	Equivalent character numbers							
Shen (1996)	28	29	33	34	35	36		
Zhang (2006)	47	48	49	53	54	61	60	
Wilson & Murray (2008)	69	67	68	71		65	64	
Xu & Chang (2009)	54	55	56				62	
SHGM L275 compared to <i>Paralycoptera</i>	○	x	x	○	○	○	○	

168 In comparing SHGM L275 and *Paralycoptera* based on the above analyses (**Tables 1, S2-S5**),
 169 there were a few character state discrepancies. These unmatched characters include: (1) the
 170 condition of the neural spine on ural centrum 1 – whether the neural spine is complete or
 171 rudimentary, and (2) the number of epurals. According to Wilson & Murray (2008), the neural
 172 spine on the first ural centrum of *Paralycoptera* should be absent or rudimentary, whereas Shen
 173 (1996) and Xu & Chang (2009) observe a completely developed neural spine. Zhang (2006) is
 174 uncertain about the relative development of this spine, but in SHGM L275 a rudimentary neural
 175 spine is present. The number of epurals present in *Paralycoptera* remains controversial. Shen
 176 (1996) identified a single epural in *Paralycoptera* whereas Xu & Chang (2009) noted its absence.
 177 In specimens IVPP V2989.65, .100 and .105 of *Paralycoptera*, we also identified no epurals, like
 178 Xu & Chang (2009). An ‘x’ was been marked in **Table 1** for this character, even though the
 179 character state used by Xu & Chang (2009) - ‘one or absent’ - should justify the use of a ‘○’ mark
 180 instead. We therefore advocate the separation of this state in future work in accordance with
 181 Greenwood (1970) and the epural characters of Shen (1996), Zhang (2006) and Wilson & Murray
 182 (2008). There is a possible epural in SHGM L275. Zhang (2006) and Wilson & Murray (2008)

183 both record uncertainty in the number of epurals in *Paralycoptera*. The first preural centrum of
184 SHGM L275 has a complete neural spine, as identified in *Paralycoptera* by all four
185 aforementioned analyses, but Xu & Chang (2009) mistakenly recorded a ‘rudimentary or absent’
186 neural spine in their data matrix. Excluding the aforementioned discrepancies, the four studies
187 otherwise converge on SHGM L275 being a specimen of *Paralycoptera*. However, Xu &
188 Chang’s (2009) observations of individual anatomical variation within *Paralycoptera* actually
189 explain the differences in the caudal skeleton observed by Shen (1996), Zheng (2006) and Wilson
190 & Murray (2008). This therefore confirms that SHGM L275 is a specimen of *Paralycoptera* (**Fig.**
191 **7**), which in our opinion negates the need for a numerical phylogenetic analysis. Xu & Chang
192 (2009) synonymised the genus into one species *P. wui* whose features in SHGM L275 are:

- 193
194 (1) a completely developed neural spine on the first preural centrum;
195 (2) two or three uroneurals;
196 (3) four upper hypurals and two lower hypurals, and
197 (4) all hypurals are independent.



198 **Figure 7:** Reconstruction of *Paralycoptera* (Xu & Chang, 2009; used with the permission of the
199 authors).

200 Systematic Palaeontology

201 SUBDIVISION TELEOSTEI MÜLLER, 1846
202 SUPERORDER OSTEOGLOSSOMORPHA GREENWOOD *ET AL.*, 1966
203 ORDER OSTEOGLOSSIFORMES REGAN, 1909
204 SUBORDER OSTEOGLOSSOIDEI REGAN, 1909
205 GENUS †*PARALYCOPTERA* CHANG & CHOU, 1977
206 †*PARALYCOPTERA* sp. CHANG & CHOU, 1977

207 4 Discussion

208 4.1 Ecology of *Paralycoptera*

209 *Paralycoptera* is a member of both northern China’s *Lycoptera* Fauna and south-eastern China’s
210 *Mesochlupea* Fauna (Chang & Jin 1996). It has been discovered in Jilin, Liaoning, Shandong,
211 Zhejiang and Fujian provinces (Xu & Chang 2009) and now in Guangdong Province too (this

212 study) (**Fig. 8**). This geographical range is impressive given that the northern part of China has
213 been separated from the south by the Qinling-Dabie Shan orogenic belt since the Late Triassic
214 (Hacker *et al.* 2004), and the 20° difference in latitude between the southernmost and
215 northernmost localities - Hong Kong, Guangdong Province and Tonghua, Jilin Province
216 respectively - a distance of over 2000 km. This geographic distribution may imply that
217 *Paralycoptera* was adaptable to a wide range of environments compared to other members of the
218 two faunas. However, climate variability over this geographical area was not very significant in
219 the Late Mesozoic - climate change towards more temperate and humid conditions is reflected by
220 geochemical weathering indices (Ohta *et al.* 2014) with temperatures between 5 °C and 25 °C
221 reconstructed from oxygen isotope data from sedimentary rocks in north-eastern China (Wang *et al.*
222 *et al.* 2013). However, occasional semi-arid periods are indicated by the appearance of the arid
223 plants *Ephedripites* and *Classopollis* in Hong Kong (Lee *et al.* 1997), as well as oxygen isotope
224 data from sedimentary rocks in north-eastern China, including from Jilin and Liaoning provinces
225 (Wang *et al.* 2013). Therefore, *Paralycoptera* most likely lived in areas with a tropical-
226 subtropical climate similar to many modern osteoglossoids, such as *Scleropages formosus*
227 (Kottelat 2011).



228 **Figure 8:** The locations of *Paralycoptera* discoveries within China (Locations from Chang &
229 Miao, 2004).

230 *Paralycoptera* localities were all continental basins (**Fig. 8**) where fluvial or lacustrine deposits

231 dominated (Chang & Jin 1996) and these have similar lithologies (see **Table 2**). Vigorous
 232 tectonic activity and episodes of volcanism were common in these localities during the late
 233 Mesozoic (Chang & Jin 1996; Chang & Chou 1977; Li & Li 2007). The Lai Chi Chong
 234 Formation of Hong Kong consists of mainly tuff and tuffaceous sedimentary rocks (Lai *et al.*
 235 1996). A shallow freshwater lake environment subject to the influence of volcanic activity is
 236 indicated by fluvial-lacustrine and volcanoclastic sedimentary facies (Workman 1991; Sewell *et*
 237 *al.* 2000), predominantly turbidites (Lai *et al.* 1996), and the discovery of terrestrial freshwater
 238 plant fossils including *Equisetites*, *Cladophlebis exiliformis*, *Gleichenites gladius* and
 239 *Carpolithus* (Lee *et al.* 1997). According to Lin & Lee (2012), the ‘parallel laminated fine
 240 sandstone and mudstone’ facies is the most likely origin of SHGM L275 as the only light-
 241 coloured mudstone unit is confined to this facies (grey volcanoclastic mudstone from the western
 242 portion of the Lai Chi Chong locality; **Fig. 2**). This facies contains fine-grained, cross-laminated,
 243 white and grey coloured mudstone representing a depositional environment below the wave base,
 244 where suspension currents might affect deposition (Lin & Lee 2012). The similarities in the
 245 palaeoenvironment between Lai Chi Chong and existing *Paralycoptera* localities (Workman
 246 1991; Chang *et al.* 2008; Hu *et al.* 2012; P.J. Chen 1983) provides additional support for the
 247 inference that *Paralycoptera* from Lai Chi Chong lived in shallow freshwater lakes near areas of
 248 active volcanism. One potential hypothesis to explain the association of *Paralycoptera* discovery
 249 sites with volcanism is that *Paralycoptera* may have thrived on the higher nutrient levels in the
 250 lake caused by the influx of volcanoclastic material, and/or the warmer water temperatures
 251 provided by thermo-tectonic activities. The sedimentary rocks preserved at Lai Chi Chong
 252 frequently show syn-sedimentary structures including microfaults, slumps, convolute bedding,
 253 load and flame structures, suggesting the occurrence of mass flows that might have been
 254 triggered by episodic volcanic and seismic activity directly related to the local subduction
 255 tectonic setting (Sewell *et al.* 2000). This implies that the habitat of *Paralycoptera* was subjected
 256 to episodic catastrophic events and was not a prolonged quiet, tranquil water body. This habitat is
 257 possibly similar to the turbid and swift-water habitat of Hiodontiformes - a closely related group
 258 to Osteoglossiformes (Gray 1988). These episodic conditions could indicate that *Paralycoptera*
 259 had a high tolerance to environmental stress (highly variable sediment and nutrient input and
 260 possible changes in water temperature). However, the association of the fish with volcanism may
 261 more simply reflect the higher fossil preservation potential by volcanoclastic sediments,
 262 especially give that only one specimen is known among the strata so far. Crucially, the laminated
 263 mudstone that SHGM L275 is preserved in represents a relatively stable rather than unstable
 264 depositional setting. This also fits the living environments of most modern osteoglossoid fish
 265 which tend to prefer still water bodies e.g. *Pantodon buchholzi* and *Scleropages formosus*
 266 (Moelants 2010; Kottelat 2011). It therefore seems more plausible that *Paralycoptera* lived in
 267 relatively stable water body like their modern counterparts and probably migrated in times of
 268 environmental stress (no evidence of mass fish mortality in the rocks showing synsedimentary
 269 structures).

270 **Table 2:** Lithological characteristics of the formations preserving *Paralycoptera*.

Formation	Province	Age	Major lithology (those that yield <i>Paralycoptera</i> are in bold font)
Lai Chi Chong	Guangdong	~146 Ma, Tithonian, Late Jurassic (Campbell <i>et al.</i> 2007)	Light grey thickly laminated tuffaceous mudstone , massive black cherty mudstone, alternatively light and dark thickly laminated and cross-bedded coarse sandstone, conglomerate; greenish grey fine

			ash crystal tuff and rhyolite (Lai <i>et al.</i> 1996; Lin & Lee 2012)
Fenshuiling	Shandong	Late Jurassic to Early Cretaceous (Li 1998)	Mudstone, shale, siltstone, sandstone, conglomerate and tuff (Wang 1985)
Guantou	Zhejiang	~110 Ma, Early Cretaceous (Xu & Chang 2009)	Purplish grey, greyish green and greyish yellow tuffaceous siltstone , dark grey mudstone , purple sandstone ; andesite and tuff breccia (Q.S. Chen 1983; Hu <i>et al.</i> 2012)
Hengtongshan	Jilin	Early Cretaceous (Han <i>et al.</i> 2013)	Black mudstone, oil shale and tuffite (Han <i>et al.</i> 2013)
Baiyashan	Fujian	Early Cretaceous (Zhang 2009)	Purplish red conglomerate, siltstone and sandstone (Zhang 2009)

271 4.2 Geographical distribution of *Paralycoptera* and the biogeography of the *Mesoclupea* Fauna

272 The discovery of *Paralycoptera* in Hong Kong extends the geographical range (**Fig. 8**) of the
 273 genus ~700 km further south of the previously most southerly locality in the Baiyashan
 274 Formation of Fujian Province (Xu & Chang 2009). This implies that *Paralycoptera* was much
 275 more widespread than previously thought and suggests that the genus may also be present in
 276 other similarly-aged lacustrine deposits in southeastern China (**Fig. 8**). *Paralycoptera* is a typical
 277 member of the *Mesoclupea* Fauna (Chang & Jin 1996) so it is possible that the other members of
 278 this fauna such as *Mesoclupea*, *Sinamia* and *Paraclupea* could be found in Hong Kong in the
 279 future.

280 4.3 Age of the Lai Chi Chong Formation and osteoglossomorph evolution and biogeography

281 Another implication of SHGM L275 arises from the age of the Lai Chi Chong Formation. A
 282 Jurassic age was originally proposed by Workman (1991) based on the identification of the fossil
 283 plants *Cladophlebis* and *Equisetites*. However, subsequent studies of spore fossils (including
 284 *Cicatricosisporites*, *Klukisporites*, *Cyaathidites*, *Classopollis* and *Pinuspollenite*) from exposures
 285 of the Formation at Cheung Sheung (嶂上), Sai Kung - ~2.5 km south of Lai Chi Chong - suggest
 286 that the Formation was deposited between the Valanginian to Barremian stages of the Early
 287 Cretaceous (Lee *et al.* 1997) (**Table S6**). This age determination is closer to the Aptian age of
 288 other *Paralycoptera* specimens found elsewhere in China, based on absolute dating of volcanic
 289 units (Xu & Chang 2009) (**Table 2**). However, as mentioned in the introduction (see section 1),
 290 an Early Cretaceous age is not corroborated by the Late Jurassic radiometric age of the Formation
 291 (Campbell *et al.* 2007). The small degree of uncertainty in the radiometric data (see Campbell *et al.*
 292 *et al.* 2007) suggests that the Formation - and so SHGM L275 - date to the Tithonian stage of the
 293 Late Jurassic (**Fig. 9**), but its discrepancy with the biostratigraphic ages warrants further
 294 investigation. Thus, a Late Jurassic age is cautiously assigned to SHGM L275 pending the
 295 discovery of an *in situ* specimen - the formation and locality information of SHGM L275 are
 296 based on its specimen label only, as it was not possible to verify this with the fossil's discoverer
 297 because they are not known. This conclusion has a profound impact on the origins of
 298 osteoglossomorphs as it shows that *Paralycoptera* and *Lycoptera* were contemporaneous. This

299 new evidence therefore rejects Chang & Chou's (1977) hypothesis that *Lycoptera* gave rise to
300 *Paralycoptera*. According to Chang & Chou (1977), *Paralycoptera* is more derived than
301 *Lycoptera*, despite their many similarities, because of features including a dorsoventrally deeper
302 body and a larger anal fin compared to dorsal fin. However, as found in this study, the age of
303 *Paralycoptera* is comparable to the age of *Lycoptera*, so the many morphological similarities
304 between *Paralycoptera* and *Lycoptera* described in Chang & Chou (1977) were likely results of
305 convergence, given their relatively disparate phylogenetic relationships (Xu & Chang 2009).

306 Given the freshwater habitats of osteoglossomorphs, migration across an oceanic barrier was
307 unlikely, so these fish should have a Pangean origin (Xu & Chang 2009). However, the location
308 of their origins, whether in Africa or Asia, has been debated (Wilson & Murray 2008; Xu &
309 Chang 2009). The Late Jurassic occurrence of *Paralycoptera* in Hong Kong provides additional
310 evidence to support the hypothesis (Xu & Chang 2009) that osteoglossomorphs originated from
311 eastern Asia, as the oldest representatives of this clade are all known from the Late Jurassic of
312 China, e.g. *Lycoptera* and *Tongxinichthys* (Chang & Jin 1996) instead of Africa, which instead
313 has members with more derived anatomical traits (Xu & Chang 2009).



314 **Figure 9:** Jurassic fish localities in SE Asia and the localities of *Paralycoptera* (Modified from
 315 Chang & Miao, 2004).

316 4.4 New phylogenetic characters

317 In our study a numerical phylogenetic analysis was not performed because existing data made it
 318 possible to unequivocally assign SHGM L275 to *Paralycoptera*. However, in the course of this
 319 study it was noted that *Singida* was not easily distinguishable from *Paralycoptera* on the basis of

320 existing characters relating to the posterior skeleton. Anatomical characteristics such as the
321 degree of fusion in the hypurals and the shape of the anal fin that were not included in existing
322 phylogenetic character lists would therefore be useful to include in future phylogenies:

323 - Hypurals in the lower lobe: [0] = independent; [1] = partially fused; [2] = fully fused.

324 - Anal fin shape: [0] = triangular; [1] = falcate.

325 4.5 Limitations and future work

326 The taxonomic identification of SHGM L275 was difficult because the fossil is incomplete, and
327 is the only specimen of its kind from Hong Kong. Thus, further discoveries of *Paralycoptera* in
328 the city (in Lai Chi Chong and on Lantau Island) would help to facilitate further anatomical
329 comparisons with mainland Chinese specimens providing additional insights into anatomical
330 variation in this taxon. To resolve the current discrepancies between the biostratigraphic and
331 radiometric ages of the Lai Chi Chong Formation, and confirm the proposed temporal range
332 extension for *Paralycoptera*, a reappraisal of current biostratigraphic evidence is required.
333 Radiometric dating of fossil-bearing strata within the Formation will be particularly valuable, if
334 suitable rocks can be identified in the future. However, both of these aspects are beyond the scope
335 of this paper to address further. More detailed petrological analysis of the matrix of SHGM L275
336 using scanning electron microscopy would be valuable for corroborating its facies assignment
337 (the ‘parallel laminated fine sandstone and mudstone’ facies with the scheme of Lin & Lee (2012)
338 and the volcanoclastic sedimentary facies of Workman (1991)) and facilitating comparisons with
339 the sedimentary facies of other *Paralycoptera* localities in mainland China, such as in Liaoning
340 province (P.J. Chen 1983). These facies investigations, in addition to comparisons between the
341 floras at these different localities, will be important towards elucidating the palaeoenvironment of
342 *Paralycoptera* (and its co-inhabitants) in greater detail, particularly in relation to neighbouring
343 volcanic activity. Future fossil collection and petrological analysis of non-Lai Chi Chong
344 Formation Lantau Volcanic Group sediments, such as those on Lantau Island, will improve our
345 understanding of local variations in the palaeoenvironment of *Paralycoptera*, and will potentially
346 provide evidence of how this taxon (and its co-inhabitants) responded to the well-documented
347 episodes of Jurassic volcanism in Hong Kong (Sewell *et al.* 2000). The latter narrative therefore
348 makes Hong Kong an ideal place to understand the biotic response of Mesozoic fossils to
349 significant environmental stress, so it is hoped that this will lead to further development of
350 palaeontological studies in Hong Kong.

351 5 Conclusions

352 A fossil fish, SHGM L275, from Lai Chi Chong, Hong Kong was rediscovered in the fossil
353 collections of Stephen Hui Geological Museum at the University of Hong Kong. This specimen is
354 identified as *Paralycoptera* based on the following four anatomical characteristics:

- 355 (1) a completely developed neural spine on the first preural centrum;
- 356 (2) two or three uroneurals;
- 357 (3) four upper hypurals and two lower hypurals, and
- 358 (4) all hypurals are independent.

359 The discovery of *Paralycoptera* in Late Jurassic-aged strata in Hong Kong - the city’s only
360 Mesozoic vertebrate – appears to extend the temporal range of the genus back by ~40 million
361 years. However, discrepancies between the biostratigraphic and radiometric ages of the strata,

362 which belongs to the Lai Chi Chong Formation, warrants a cautious treatment of the proposed
363 temporal range extension, pending further geochronological investigation. However, our
364 discovery unequivocally extends *Paralycoptera*'s geographical range approximately 700 km
365 southwards, potentially affecting the *Mesoclupea* Fish Fauna. In the context of the geological
366 literature on the Lai Chi Chong Formation and our knowledge of the fossil's matrix, it is
367 suspected that *Paralycoptera* lived in freshwater lakes in close proximity to volcanic
368 environments that experienced episodic earthquakes and volcanic eruptions that greatly affected
369 the lake's regime. This palaeoenvironment appears to match those of other *Paralycoptera*
370 localities in mainland China inspiring the conclusion that this taxon was potentially tolerant of
371 high environmental stresses and may even have thrived on higher nutrient levels and changeable
372 water temperatures in the lake, during times of volcanic activity.

373 This study makes an important contribution to our understanding of Hong Kong's fossil heritage,
374 given that the city has a relatively poor fossil record and limited sedimentary rock exposures (Lee
375 *et al.* 1997). This study is the first on Hong Kong fossils in over 15 years (Lee *et al.* 1997) so it is
376 hoped that it can help to promote further interest in Hong Kong's palaeontology, particularly
377 given the rare opportunity to study the biotic response to long-lived and accurately-dated
378 Mesozoic volcanic events.

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391 TKT and MP collected and analysed the data and also wrote the paper, MMC had some input in
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