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Pathological caudal skeleton of an ichthyodectiform fish from the Upper Cretaceous Niobrara Formation of western Kansas, USA

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A series of 12 contiguous caudal vertebrae of an ichthyodectiform fish from the Smoky Hill Chalk Member of the Niobrara Formation is described. The vertebral centra exhibit extensive overgrowth of pathological bone and there is additional pathological bone within the centra and intervertebral spaces, which together resulted in the coossification of most centra. The extent of the pathology is greatest on preural vertebrae 1-3 and decreases anteriorly, which suggests that the pathology began posteriorly and progressed anteriorly. In addition to the pathological overgrowth on bones, the specimen preserves features interpreted as calcified and/or ossified soft tissues associated with the neural and haemal canals. The pathologies are unlike previously described examples of bony pathologies in fish, and it is suggested that they resulted from combined bacterial and fungal infections. As the pathologies developed, they would have adversely impacted the fish's swimming and feeding abilities, and presumably eventually led to the fish's death.

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16 LRH: S. C. BENNETT

17 RRH: PATHOLOGICAL FISH VERTEBRAE

18

19 Abstract:

20 A series of 12 contiguous caudal vertebrae of an ichthyodectiform fish from the Smoky Hill

21 Chalk Member of the Niobrara Formation is described. The vertebral centra exhibit extensive

22 overgrowth of pathological bone and there is additional pathological bone within the centra and

23   intervertebral spaces, which together resulted in the coossification of most centra. The extent of

24   the pathology is greatest on preural vertebrae 1-3 and decreases anteriorly, which suggests that

25   the pathology began posteriorly and progressed anteriorly. In addition to the pathological

26   overgrowth on bones, the specimen preserves features interpreted as calcified and/or ossified soft

27   tissues associated with the neural and haemal canals. The pathologies are unlike previously

28   described examples of bony pathologies in fish, and it is suggested that they resulted from

29   combined bacterial and fungal infections. As the pathologies developed, they would have

30   adversely impacted the fish's swimming and feeding abilities, and presumably eventually led to

31   the fish's death.

32

33   ADDITIONAL KEYWORDS: Hyperostosis – bacterial and fungal infection – vertebrae – fish

34   _____

35

36   **INTRODUCTION**

37   Although pathologies are not uncommon among extant fishes (Schlumberger and Lucké, 1948),

38   only a few types of pathologies have been described from fossil fishes. Most common are

39   hyperostoses of neural and haemal spines, fin pterygiophores, and ribs that resulted in large

40   rounded bony masses that are commonly known as 'Tilly bones' (Gervais, 1875; Konnerth, 1963;

41   Tiffany et al., 1980; Schlüter et al., 1992; Schlüter and Kohring, 2002; Capasso, 2005; Meunier

42   et al., 2010). Such pathologies are common in extant fishes (Smith-Vaniz et al., 1995; Jawad,

43   2013; Jawad et al., 2015; Chanet, 2018), and can also affect skull bones and vertebrae (Meunier

44   et al., 1999; Bearez et al., 2005). A possible notochordal chondroma was described in a Late

45   Cretaceous pycnodontid from Lebanon (Capasso, 2022), and though a soft tissue tumor, its

46 presence was indicated by the displacement of neural and haemal arches. Preservation of hard

47 nodules in the skin of fossil fish has also been reported (Petit, 2010; Petit and Khalloufi, 2012).

48 Here a pathological caudal skeleton of an ichthyodectiform fish from the Upper Cretaceous

49 Smoky Hill Chalk Member of the Niobrara Formation of western Kansas is described, which is

50 unlike previously described pathologies in fossil fishes and, in addition to the osseous

51 pathologies, preserves what are interpreted as calcified and/or ossified soft tissue associated with

52 the neural and haemal canals.

53

54   **MATERIAL AND METHODS**

55

56 The specimen, YPM VP 42619, is the pathological caudal skeleton of a large fossil fish collected

57 21 April 1876 by B. F. Mudge and his collecting party from the Santonian to early Campanian

58 Smoky Hill Chalk Member of the Niobrara Formation of southwestern Gove County, Kansas,

59 USA (Hattin, 1982). Other specimens collected on 20 and 21 April of that year (YPM VP 2390,

60 40541, and 40542) were identified as being collected from the 'southwest part' or 'southwest

61 corner' of Gove County, so that presumably was the case for this specimen as well. Note that by

62 late 1875, O. C. Marsh of the Yale Peabody Museum had told Mudge that he would no longer

63 pay for fish specimens other than 'snout fish', i.e., *Saurodon* (O. C. Marsh correspondence in

64 YPM archives), so the fact that the specimen was collected suggests that it was deemed unusual.

65   The specimen was cleaned of surrounding chalk matrix using low pressure sodium

66 bicarbonate air abrasive, and was examined with stereomicroscopes and photographed. A

67 horizontal sample of bone extending to the midline was removed from the left side of one

68 vertebral centrum, embedded, ground, and polished using standard methodology, and the

69   resulting thin section was examined and photographed with microscopes.

70   **Institutional Abbreviations**—USNM, United States National Museum, Washington,

71   D.C., USA; and YPM, Peabody Museum of Natural History, Yale University, New Haven,

72   Connecticut, USA.

73

74   **DESCRIPTION**

75

76   YPM VP 42619 consists of a series of 12 contiguous vertebral centra, two of which are free (i.e.,

77   not fused to adjacent centra) and ten of which are coossified, most of which have broken bases of

78   neural and haemal spines preserved in articulation with the centra (Fig. 1, 2), and four small

79   neural and haemal spine fragments. The entire series of 12 vertebrae exhibits extensive

80   overgrowth of pathological bone tissue. The anteriormost free vertebra is 34.4 mm wide x 27.7

81   mm high x 18.7 mm long, the posterior free vertebra is 35.6 x 31.0 x 18.4 mm, and the two free

82   vertebrae have a combined length of 36.9 mm. The series of ten coossified vertebrae is 172.8

83   mm long, and is broken into three sections: an anterior section of three vertebrae, 59.9 mm long

84   (~20 mm/centrum), 34.4 x 36.5 mm at the anterior end, and 34.2 x 29.6 mm at the posterior end,

85   with little taper; a middle section of four vertebrae 69.3 mm long (~17.3 mm/centrum) and 25.7

86   x 23.0 mm at the posterior end, with somewhat more taper; and a posterior section of three

87   vertebrae 43.6 mm long (~14.5 mm/centrum) and 13.4 mm x 16.2 mm at the posterior end, with

88   significant taper and a marked upward curvature posteriorly. The combined length of all 12

89   vertebrae is 209.7 mm. At the breaks between the sections of the coossified centra, calcite and/or

90   bone tissue can be seen filling the biconical space between the cotyles of the adjacent vertebrae

91   where the intervertebral disk would have been. The posteriormost vertebra has a small broken

92   and distorted posterior cotyle, 12.6 x 9.8 mm as preserved, which indicates that there was

93   another vertebra posterior to it, so the posteriormost vertebra is interpreted as the first ural

94   vertebra and the subsequent vertebra would have been the second ural. Given that the

95   posteriormost vertebra is the first ural, the other nine vertebrae of the coossified series are preural

96   vertebrae 1-9 and the two free vertebrae are preurals 10 and 11. The fragments of neural and

97   haemal spines not articulated with the vertebral centra consist of three 2-2.5 cm long sections of

98   individual spines and one ~3 cm long section of ~5 adhering spines, which show little evidence

99   of pathology.

100   The bone is mostly brown, though paler in places, presumably as a result of weathering,

101   and parts, particularly the dorsal surfaces, are encrusted with orange ferruginous deposits.

102   Masses of somewhat darker ferruginous particulate matter with an appearance that resembles

103   sintered porous bronze are present within some depressions on the centra (Fig. 3.1). The material

104   seems not to be osseous, and presumably was derived from the surrounding matrix, but it resisted

105   removal by the air abrasive when the specimen was prepared.

106   Anterior and posterior views of preural vertebra 11 show that the centrum is

107   amphicoelous with an hourglass shaped cross-section typical of fishes (Fig. 1). In lateral view,

108   the contours of the external surface of the centrum are evident despite the bony overgrowth, and

109   include a prominent lateral longitudinal ridge bounded above and below by longitudinal grooves.

110   That morphology is typical of ichthyodectiform fishes (Bardack, 1965; Cavender, 1966), which

111   are represented in the Smoky Hill Chalk by *Ichthyodectes*, *Gillicus*, and *Xiphactinus*, and the

112   morphology of the caudal skeleton of YPM VP 42619 compares well with the '*Ichthyodectes*

113   type' caudal skeleton described and illustrated by Cavender (1966, fig. 1).

114   The outer margin of the anterior cotyle of preural vertebra 11 is 22.4 mm wide x 21.2 mm

115   high, but the centrum proper is surrounded by ~5 mm of bony overgrowth. That bone has a dense

116   surface with an intricate reticulate pattern of ridges and grooves and many small pores opening

117   onto the surface (Fig. 3.1). Preural vertebra 10 is similar to preural 11 and is shown articulated

118   with preural 11 in Figure 1.3. There is a gap between the outer parts of the overgrowing bone at

119   the posterior end of preural 11 and the anterior end of preural 10, and the bony overgrowth on

120   either side of the gap is thickened and coarsely textured with projections and pits. Because there

121   was no contact between the bony overgrowth of the two vertebrae, the bony overgrowth would

122   not have prevented movement between the two vertebrae. However, some bone tissue is present

123   in the intervertebral space between preurals 10 and 9, which suggests that movement between

124   those vertebrae was reduced.

125   The centra of the anterior section of the coossified series of vertebrae also exhibit gaps

126   between the outermost bony overgrowth of adjacent centra. However, the gaps are narrower than

127   those between the free vertebrae, ~2 mm or less, and at their bottoms there are sinuous grooves

128   where the posterior surface of the bony overgrowth of the anterior vertebra meets the anterior

129   surface of the overgrowing bone of the posterior vertebra. The grooves presumably are sinuous

130   because they are between the bony overgrowths of the centra rather than the centra themselves

131   and the rate of deposition of the bony overgrowth was not uniform. In some places, the bony

132   overgrowth of adjacent vertebrae is fused and the groove obliterated, but despite the fact that in

133   most places the bony overgrowth is not fused, the close correspondence of the shapes of the

134   surfaces of the adjacent vertebrae meeting at the grooves suggests that no significant movement

135   was possible. The base of the haemal arch of preural vertebra 9 is better preserved than any other

136   and exhibits some bony overgrowth, though to a lesser extent than the vertebral centra.

137   The extent of fusion of the centra increases posteriorly, and by the middle section of the

138   coossified series of 10 vertebrae the gaps have disappeared and the narrow grooves between the

139   bony overgrowth are at the surface of the bony overgrowth on each centrum (Fig. 3.2). On the

140   posterior section of the coossified series, the bone is fully fused and the grooves obliterated. The

141   external surface of the bony overgrowth on the posterior section appears very dense, but retains a

142   little of the reticulate surface structure seen on the more anterior vertebrae. Examination of the

143   intervertebral spaces between the three sections of coossified centra found that there was bone

144   tissue within the spaces.

145   Longitudinal structures are preserved on the dorsal and ventral midlines of the centra, and

146   are presumably associated with the neural and haemal canals. The ventral structure passes

147   between the articular surfaces for, or the bases of, the haemal spines, and is best seen on the

148   ventral midline of preural vertebrae 7-9 (Fig. 3.4). The structure is ~2.5 mm wide over the

149   middle of the centrum and ~4.0 mm wide over the intervertebral joint. At the anterior end of

150   preural vertebra 9, the structure has a flattened suboval cross-section and does not exhibit a

151   lumen. A similar, but somewhat smaller dorsal longitudinal structure is preserved passing

152   between the articular surfaces for, or the bases of, the neural spines. The structures cannot be

153   interpreted as any normally osseous part of the vertebral column proper. It seems likely that they

154   represent calcified or ossified soft tissues associated with the haemal and neural canals, though

155   the fact that the ventral structure widens and narrows makes it unlikely that it is the caudal vein

156   that passes through the haemal arches in fishes (Schultze and Arratia, 1989). However, an

157   alternative interpretation would be that they are pathological bone tissue that preferentially

158   invaded and grew along the canals. If the longitudinal structures represent soft tissues, their

159   calcification or ossification presumably was related to the osseous pathologies of the caudal

160   skeleton, but it is not clear whether the structures were calcified or ossified, and if so, how.

161

162   ***Thin section***

163   Figure 4 shows a horizontal thin section of the left side of the centrum of preural vertebra 10

164   from the midline to the external surface. The conical anterior cotyle is intact and apparently was

165   unaffected by pathology, whereas the medialmost ~25% of the posterior cotyle is missing.

166   Between the cotyles, cancellous bone infilled with calcite occupies much of the centrum's

167   volume, but the lateral part of the centrum is occupied by denser bone. The anterior cotyle

168   exhibits fine striations parallel to its anterior surface that presumably are growth lines reflecting

169   cyclical changes in the rate of deposition of bone tissue (Fig. 5A). A linear feature exhibiting

170   similar striations that presumably were formed in a similar manner extends posteriorly at least 4

171   mm from the anterior cotyle's lateral margin and is interpreted as the former external surface of

172   the centrum upon which pathological bone tissue was deposited. Posteriorly, there are additional

173   features farther back that may also represent the original external surface. Based on that

174   interpretation, the bony overgrowth surrounding the centrum ranged from 4.0 to 5.3 mm thick.

175   The bone tissue of the overgrowth is quite dense, but exhibits various bone textures. Much of the

176   outermost ~1 mm of bone tissue exhibits closely spaced slender subparallel canals, ~30 μm in

177   diameter with occasional rounded expansions, and subperpendicular to the external surface such

178   that the sectioned tissue resembles a palisade (Fig. 5B). Examination of preural vertebra 10

179   reveals that the palisade-like tissue is associated with the presence of the reticulate pattern on the

180   external surface (Fig. 3A), and the small pores that are part of the reticulate pattern of that

181   surface may be openings of the slender canals. A dark line at the base of the palisade-like layer

182   and subparallel to the external surface may be a growth? line. Deep to the palisade-like layer, the

183   bone tissue is generally quite dense and without any discernible pattern, but there are many

184 spaces that are interpreted as large vascular canals. In places there are also slender subparallel

185 canals that may represent a second palisade-like layer, and deep to them a second dark growth?

186 line. Traces of a third layer of similar tissue with subparallel canals are visible to the left in

187 Figure 5B, deep to the second layer. It is not clear whether the specimen preserves successive

188 layers of palisade-like tissue with the deeper layers being less distinct because of remodeling or

189 the specimen records increasing expression of the palisade-like character in successive layers

190 deposited sequentially.

191   The thin section also shows bone tissue in the biconical intervertebral space where the

192 intervertebral disk would have been. The tissue is cancellous, but denser than the normal

193 cancellous bone within the vertebral centrum that was described above. The intervertebral bone

194 appears to be continuous with bone tissue that extends through the gap in the posterior cotyle and

195 into the centrum near the midline (Fig. 6). The latter bone tissue exhibits a rather linear character

196 with subparallel bands of bone and several rather large roughly longitudinal vascular canals that

197 converge anteriorly, extend through the gap, and diverge within the centrum, where they appear

198 to be continuous anteriorly with rather dense cancellous bone tissue similar to that near the

199 middle of the intervertebral space. It is not clear which direction the pathological bone may have

200 grown, but it seems more likely that it was growing into the centrum from the intervertebral

201 space, in which case, pathological bone may have been growing anteriorly through successive

202 centra and intervertebral spaces, with what is seen in preural vertebra 10 being the leading end of

203 what might have continued to grow into preural vertebra 11 if the fish had lived longer. One last

204 feature of note is a large suboval void surrounded by a ring of rather dense dark appearing bone

205 and filled with fractured calcite, which is lateral to the pathological bone passing through the gap

206 in the posterior cotyle and just anterior to the remaining part of the cotyle (Fig. 4, 6). Presumably

207   the void represents an abscess that resulted from an infection that destroyed all trabeculae of the

208   cancellous bone within the ring of dense bone, but it is not clear how that process was related to

209   the deposition of the pathological bone of the ring and elsewhere.

210

211   **DISCUSSION**

212

213   Cavender (1966) stated that the caudal peduncles of *Ichthyodectes* and *Gillicus* appeared slightly

214   more constricted than those of *Xiphactinus*, but stated that except where extreme large size

215   indicated a specimen pertained to *Xiphactinus*, the caudal skeletons of *Ichthyodectes*, *Gillicus*,

216   and *Xiphactinus* were indistinguishable. However, Bardack (1965) differentiated the vertebrae of

217   *Gillicus* and *Ichthyodectes* from those of *Xiphactinus* on the basis of differences in the

218   dorsoventral height of the lateral ridge between the two prominent longitudinal grooves. He

219   noted that in *Xiphactinus* the ridge is twice the width of the grooves, whereas in *Ichthyodectes*

220   and *Gillicus* the lateral ridge is about the width of the grooves. Unfortunately, in YPM VP 42619

221   it is not possible to assess the relative width of the longitudinal ridge and grooves because of

222   extensive bony overgrowth, so the specimen must be viewed as an indeterminate

223   ichthyodectiform. Comparing the preserved length of the series of 12 vertebrae to an essentially

224   complete mounted 155 cm long specimen of *Ichthyodectes* (USNM 12358; Bardack, 1965)

225   suggests that YPM VP 42619 had a fork length of ~1.4 m and, if *Ichthyodectes*, was not quite

226   half grown.

227   The pathologies of YPM VP 42619 can be categorized as: 1) overgrowing pathological

228   bone tissue that seems to have been deposited on the external surface of the centra; 2) dense

229   cancellous bone in the intervertebral space and within the centrum; and 3) what are interpreted as

230   calcified or ossified soft tissues associated with the haemal and neural canals. The overgrowing

231   pathological bone and the dense cancellous bone of YPM VP 42619 are unlike Tilly bones, i.e.,

232   the common hyperostoses of spines, pterygiophores, etc. of fishes, which typically appear as

233   greatly swollen parts of bones. Although Tilly bones exhibit a characteristic swollen appearance,

234   their histology varies considerably: in *Euthynnus* they were described as consisting of greatly

235   thickened lamellar cortical bone surrounding spongy medullary bone (Béarez et al., 2005); in

236   *Caranx* as acellular bone (Chanet, 2018); and in *Prionotus* as spongy bone (Meunier et al.,

237   1999). Interestingly, in unidentified fossil fishes from a Plio-Pleistocene paleolake in Tanzania

238   Tilly bones consisted of dense bone with multiple thick annual? layers and have a finely ridged

239   external surface with many small pores opening between the ridges (Schlüter and Kohring,

240   2002), and the multiple bone layers remind one of the palisade-like layers in YPM VP 42619

241   whereas the ridged surface with small pores are somewhat similar to the reticulate surface in

242   YPM VP 42619. Despite the histological variation, in most cases, the histology of Tilly bones,

243   other than being greatly thickened, appears similar to that of the adjacent unaffected bone tissue.

244   It has been suggested that Tilly bones are a response to abnormal environmental conditions

245   (Schlüter and Kohring, 2002). Tilly bones of the unidentified fishes from a Plio-Pleistocene

246   paleolake in Tanzania had high levels of fluorine, and it was suggested that the fishes dealt with

247   high levels of fluorine in the lake's waters by increasing the quantity of bone tissue in the body

248   and depositing fluorine within the hyperostotic bone tissue. However, there is sufficient variation

249   in the histology of Tilly bones that it seems likely that they can result from more than one cause.

250   Regardless, the overgrowing bone of YPM VP 42619 does not exhibit the swollen appearance

251   typical of Tilly bones, and the histology of the pathologies differs from that of adjacent

252   unaffected bone tissue.

253   The overgrowing bone of YPM VP 42619 somewhat resembles diffuse idiopathic

254   skeletal hyperostosis (DISH) and spondylosis deformans of mammals, which often affect the

255   vertebral column of older individuals (Kuperus et al., 2020; Kranenburg et al., 2011). DISH is

256   characterized by formation of a continuous solid bone bridge ventral to the vertebral centrum and

257   bridging an unaffected intervertebral disc, whereas spondylosis deformans consists of small bone

258   spurs to bone bridges across the disc space but not covering the entire ventral surface of the

259   centrum. The overgrowing bone of YPM VP 42619 differs from DISH and spondylosis

260   deformans in that it is not confined to the ventral surface of the vertebrae, and in humans and

261   dogs, DISH normally occurs in older individuals, whereas the ichthyodectiform fish in this study

262   seems to have been less than half grown. DISH is usually visualized by X-ray, and it is difficult

263   to compare both the three dimensional fossil and the histological thin section of YPM VP 42619

264   to such images. However, Kranenburg et al. (2011, fig. 5) illustrated a sagittally sectioned series

265   of fused vertebrae of a dog exhibiting DISH and also histological sections of vertebrae exhibiting

266   DISH and spondylosis deformans, and it is apparent that the pathological bone bridging between

267   vertebral centra is cancellous bone very similar to the normal bone tissue within the centra,

268   which is unlike what is seen in YPM VP 42619.

269   The slender subparallel canals with occasional rounded expansions seen in the palisade-

270   like layers of the overgrowing bone of YPM VP 42619 bring to mind the hyphae of fungi, so the

271   possibility that the pathologies of YPM VP 42619 could have resulted from a fungal infection

272   should be considered. Fungal infections of the spine of humans are rare, but typically develop as

273   combined bacterial and fungal infections of the spine in immunocompromised humans with

274   fungus in both the vertebral centra and intervertebral disks (Williams et al., 1999; Tay et al.,

275   2002; Caldera et al., 2016). Studies of the combined infections are usually visualized by X-ray

276   and MRI, which makes comparisons to the three dimensional fossil and the histological thin

277   section of YPM VP 42619 difficult. However, Cimerman et al. (1999, fig. 1) illustrated fungal

278   hyphae within femoral bone tissue, which appear quite similar to the slender subparallel canals

279   of YPM VP 42619, but do not exhibit any regular or subparallel arrangement. Two species of the

280   fungal genus *Aspergillus* were cultured from the tissue and exhibited hyphae and vesicles

281   ranging from 20 to 40 μm in diameter. Given the similarity of the fungal hyphae and the slender

282   subparallel canals of YPM VP 42619 and the fact that fungal infections of the centrum and

283   intervertebral disk occur in humans, the pathologies of YPM VP 42619 are tentatively

284   interpreted as resulting from a combined bacterial and fungal infection, in which the presence of

285   different infectious agents may explain the different morphologies of the pathologies.

286   The 11 preural vertebrae and one ural vertebra of YPM VP 42619 represent ~14% of the

287   fish's fork length, and presumably it was the most important 14% in regard to function of the

288   caudal fin in propulsion because lateral flexion of the caudal peduncle adjusts the angle of the

289   caudal fin as it moves through the water so as to maximize thrust. The fusion of the centra would

290   have had a marked adverse affect on the fish's swimming ability. In addition, the calcification

291   and/or ossification of the tissues associated with the neural and haemal canals may have impaired

292   the blood supply to and innervation of the caudal region leading to paralysis of muscles and loss

293   of sensation. As a result, although swimming must have been possible for the fish to have lived

294   long enough for the pathology to become widespread, it presumably was inefficient and would

295   have affected the fish's ability to feed. Most likely, the onset of the adverse effects of the

296   pathologies was gradual, but as they progressed, the fish's health would have declined and the

297   positive feedback of reduced feeding ability and declining health would have led to the fish's

298   death.

299

CONCLUSION

301

302 The series of 12 vertebral centra of YPM VP 42619 exhibit extensive overgrowing pathological

303 bone deposited on and surrounding the centra, cancellous bone that is denser than in the

304 intervertebral space and within the centrum, and what are interpreted as calcified or ossified soft

305 tissues associated with the haemal and neural canals. The pathologies are unlike any previously

306 described in fossil or extant fishes, and although they are somewhat similar to the diffuse

307 idiopathic skeletal hyperostosis (DISH) and spondylosis deformans of mammals, there are

308 significant differences as well, and it is most likely that the pathologies resulted from combined

309 bacterial and fungal infections. As the pathologies developed, they would have adversely

310 impacted the fish's swimming and feeding abilities, and presumably eventually led to the fish's

311 death.

312

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314

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REFERENCES

319

320 **Bardack D. 1965.** Anatomy and evolution of chirocentrid fishes. University of Kansas

321   Paleontological Contributions, Vertebrata, Article 10, 88 pp.

322   **Béarez P, Meunier FJ, Kacem A, 2005.** Description morphologique et histologique de

323   l'hyperostose vertébrale chez la thonine noire, *Euthynnus lineatus* (Teleostei: Perciformes:

324   Scombridae). CBM-Cahiers de Biologie Marine., 46, 21–28.

325   **Caldera G, Cahueque M, Cobar A, Gómez G, Rodríguez O. 2016.** Fungal spondylodiscitis:

326   review. Journal of Spine, 5, 1000302.

327   **Capasso LL, 2005.** Antiquity of cancer. International Journal of Cancer, 113, 2–13.

328   **Capasso L, 2022.** Possible notochordal chondroma in a fossil fish from the Late Cretaceous of

329   Lebanon. International Journal of Paleopathology, 37, 6–8.

330   **Cavender T, 1966.** The caudal skeleton of the Cretaceous teleosts *Xiphactinus*, *Ichthyodectes*,

331   and *Gillicus*, and its bearing on their relationship with *Chirocentrus*. Occasional Papers of

332   the Museum of Zoology of the University of Michigan, 650, 1–15.

333   **Chanet B, 2018.** Swollen bones in jacks and relatives (Teleostei: Acanthomorphata:

334   Carangidae). Cybium : Revue Internationale d'Ichtyologie, 42, 99–103,

335   10.26028/cybium/2018-421-010. hal-03971149.

336   **Cimerman M, Gunde-Cimerman N, Zalar P, Perkovic T, 1999.** Femur osteomyelitis due to a

337   mixed fungal infection in a previously healthy man. Journal of clinical microbiology, 37,

338   1532–1535.

339   **Gervais P, 1875.** De l'hyperostose chez l'homme et chez les animaux. Journal de Zoologie, 4,

340   272–284 & 445–462.

341   **Hattin DE, 1982.** Stratigraphy and depositional environment of Smoky Hill Chalk Member,

342   Niobrara Chalk (Upper Cretaceous) of the type area, western Kansas. Kansas Geological

343   Survey, Bulletin, 225, 1–108.

344   **Jawad LA, 2013.** Hyperostosis in three fish species collected from the Sea of Oman. The

345   Anatomical Record, 296, 1145–1147.

346   **Jawad L, Wallace A, Dyck W, 2015.** Documentation of the case of hyperostosis in the silver

347   bream, *Pagrus auratus* (Forster, 1801) sampled from waters around New Zealand. Boletim

348   do Instituto de Pesca, São Paulo, 41, 1043–1047.

349   **Konnerth A, 1966.** Tilly bones. Oceanus, 12, 6–9.

350   **Kranenburg HJC, Voorhout G, Grinwis GC, Hazewinkel HA, Meij BP, 2011.** Diffuse

351   idiopathic skeletal hyperostosis (DISH) and spondylosis deformans in purebred dogs: a

352   retrospective radiographic study. The Veterinary Journal, 190, e84–e90.

353   **Kuperus JS, Hoesein FAM, de Jong PA, Verlaan JJ, 2020.** Diffuse idiopathic skeletal

354   hyperostosis: Etiology and clinical relevance. Best Practice & Research Clinical

355   Rheumatology, 34, 101527, 12 pp.

356   **Meunier FJ, Bearez P, Francillon-Vieillot H, 1999.** Some morphological and histological

357   aspects of hyperostosis in the eastern Pacific marine fish *Prionotus stephanophrys*

358   Lockington, 1880 (Triglidae). In: Sérel, B. and Sire, Y., eds., 5th Indo-Pacific Fish

359   Conference, Proceedings. Paris, Société Francaise d'Ichtyologie, 125–133.

360   **Meunier FJ, Gaudant J, Bonelli E, 2010.** Morphological and histological study of the

361   hyperostoses of *Lepidopus albyi* (Sauvage, 1870), a fossil Trichiurideae from the

362   Tortonian (Upper Miocene) of Piedmont (Italy). Cybium, 34, 293–301.

363   **Petit G, 2010.** Skin nodules in fossil fishes from Monte Bolca (Eocene, northern Italy).

364   Geodiversitas, 32, 157–163.

365   **Petit G, Khalloufi B, 2012.** Paleopathology of a fossil fish from the Solnhofen Lagerstätte

366   (Upper Jurassic, southern Germany). International Journal of Paleopathology, 2, 42–44.

367   **Schlumberger HG, Lucké B, 1948.** Tumors of fishes, amphibians, and reptiles. Cancer

368   Research, 8, 657–753.

369   **Schlüter T, Kohring R, 2002.** Palaeopathological fish bones from phosphorites of the Lake

370   Manyara Area, Northern Tanzania – Fossil evidence of a physiological response to

371   survival in an extreme biocenosis. Environmental Geochemistry and Health, 24, 131–140.

372   **Schlüter T, Kohring R, Mehl J, 1992.** Hyperostotic fish bones ('Tilly bones') from presumably

373   Pliocene phosphorites of the Lake Manyara area, northern Tanzania. Paläontologische

374   Zeitschrift, 66, 129–136.

375   **Schultze HP, Arratia G, 1989.** The composition of the caudal skeleton of teleosts

376   (Actinopterygii: Osteichthyes). Zoological journal of the Linnean Society, 97, 189–231.

377   **Smith-Vaniz WF, Kaufman LS, Glowacki J, 1995.** Species-specific patterns of hyperostosis in

378   marine teleost fishes. Marine Biology, 121, 573–580.

379   **Tay BK, Deckey J, Hu SS, 2002.** Spinal infections. JAAOS-Journal of the American Academy

380   of Orthopaedic Surgeons, 10, 188–197.

381   **Tiffany WJ III, Pelham RE, Howell Winter FW, 1980.** Hyperostosis in Florida fossil fishes:

382   Florida Scientist, 43(1), 44–49.

383   **Williams RL, Fukui MB, Meltzer CC, Swarnkar A, Johnson DW, Welch W, 1999.** Fungal

384   spinal osteomyelitis in the immunocompromised patient: MR findings in three

385   cases. American Journal of Neuroradiology, 20, 381–385.

386

387   **FIGURE CAPTIONS**

388

389   **Figure 1**. Ichthyodectiform fish YPM VP 42619. Photographs of pathological vertebrae that

390   were not coossified with adjacent vertebrae. Preural vertebra 11 in (A) anterior and (B) posterior

391 views, and (C) preural vertebrae 11 and 10 articulated in dorsal view. Abbreviations: hs, haemal

392 spine; mc, margin of cotyle; nct, calcified or ossified neural canal soft tissues; ns, neural spine;

393 and pu, preural vertebra. Scale bar = 3 cm. Page width, 6340 x 2218 @ 900 dpi]

394

395 **Figure 2**. Ichthyodectiform fish YPM VP 42619. Photographs of pathological series of

396 coossified preural vertebrae 1-9 and ural vertebra 1 in: (A) dorsal; (B) ventral; and (C) left lateral

397 views. Abbreviations: co, cotyle of ural vertebra 1; hct, calcified or ossified haemal canal soft

398 tissues; hs, haemal spine; lg, lateral groove; lr, lateral ridge; nct, calcified or ossified neural canal

399 soft tissues; pu, preural vertebra; and u, ural vertebra. Scale bar = 5 cm. [Page width, 6375 x

400 4984 @ 900 dpi]

401

402 **Figure 3**. Ichthyodectiform fish YPM VP 42619. Detail photographs of selected features: (A)

403 reticulate pattern of fine ridges and grooves on lateral surface of preural vertebra 10, and

404 ferruginous particulate matter in longitudinal groove; (B) narrow sinuous groove between preural

405 vertebrae 8 and 7 in ventral view (compare to Fig. 2C); (C) pathological bone tissue on right

406 lateral surface of preural vertebra 2 through ural vertebra 1 and remnant of sinuous groove

407 between preural vertebra 1 and ural vertebra 1; and (D) soft tissues of haemal canal on preural

408 vertebrae 8 and 7 in ventral view with anterior to the right (compare to Fig. 2C). Abbreviations:

409 hct, calcified or ossified haemal canal soft tissues; lg, longitudinal groove; pm, particulate

410 matter; rb, reticulate bone; and sg, sinuous groove. Scale bars = 1 cm. [Page width, 6377 x 5740

411 @ 900 dpi]

412

413   **Figure 4**. Ichthyodectiform fish YPM VP 42619. Photograph of horizontal thin section of the left

414   side of centrum of preural vertebra 10 extending laterally from the midline with anterior to the

415   left. Numbered rectangles show the location of detail photographs in Fig. 5 and 6. The arrow at

416   left indicates the presumed external surface of the centrum upon which pathological bone was

417   deposited. Abbreviations: ac, anterior cotyle; ivb, intervertebral bone tissue; pc, posterior cotyle;

418   pl, palisade-like layer; and vo, large void. Scale bar = 5 mm. [Page width, 6378 x 5338 @ 900

419   dpi]

420

421   **Figure 5**. Ichthyodectiform fish YPM VP 42619. Detail photographs of the thin section of the

422   centrum of preural vertebra 10 in Fig. 4 showing: (A) striations of presumably stratified bone of

423   the anterior cotyle and similarly stratified bone of the presumed former external surface of the

424   centrum upon which overgrowing bone tissue was deposited; and (B) thin palisade-like layer at

425   the lateral surface with closely spaced slender subparallel canals. The arrow at left in A indicates

426   the presumed external surface of the centrum upon which pathological bone was deposited.

427   Abbreviations: ac, anterior cotyle; dl, dark growth? line; pl, palisade-like layer; str, striations;

428   and ssc, slender subparallel canals. Scale bar = 1 mm. [Page width, 6193 x 3138 @ 900 dpi]

429

430   **Figure 6**. Ichthyodectiform fish YPM VP 42619. Detail photograph of the thin section of the

431   centrum of preural vertebra 10 in Fig. 4 showing pathological bone tissue within the centrum and

432   intervertebral disk. Abbreviations: ivb, intervertebral bone tissue; lvc, longitudinal vascular

433   canal; pc, posterior cotyle; and vo, large void. Scale bar = 1 mm. [Page width, 6193 x 3138 @

434   900 dpi]

435

Figure 1

Free vertebrae

Figure 1. Ichthyodectiform fish YPM VP 42619. Photographs of pathological vertebrae that were not coossified with adjacent vertebrae. Preural vertebra 11 in (A) anterior and (B) posterior views, and (C) preural vertebrae 11 and 10 articulated in dorsal view. Abbreviations: hs, haemal spine; mc, margin of cotyle; nct, calcified or ossified neural canal soft tissues; ns, neural spine; and pu, preural vertebra. Scale bar = 3 cm.
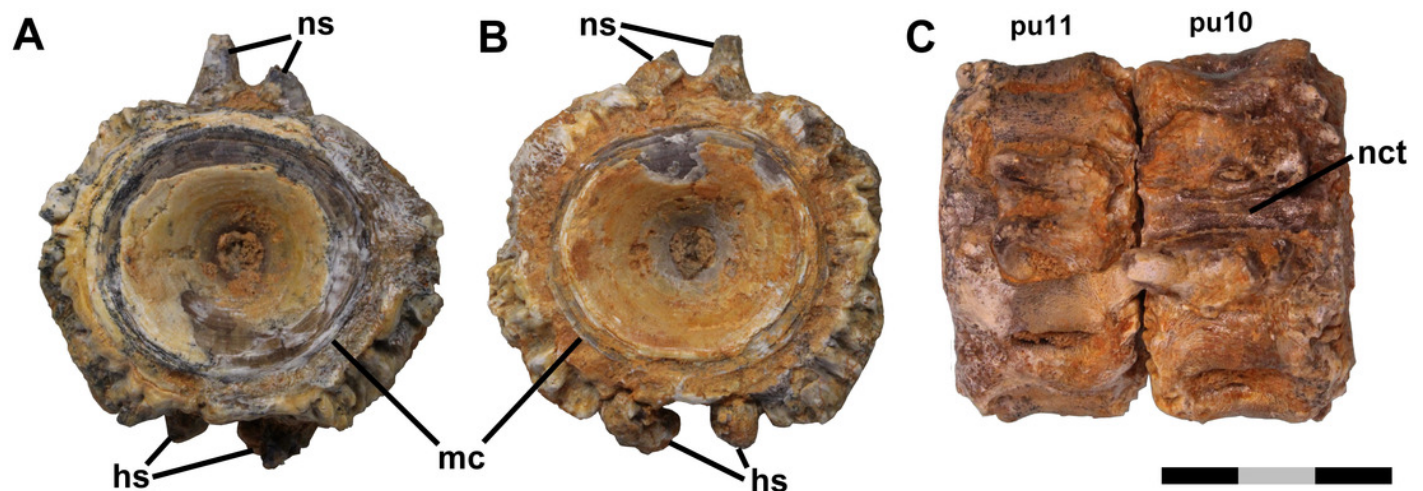
Figure 2

Fused vertebrae

Figure 2. Ichthyodectiform fish YPM VP 42619. Photographs of pathological series of coossified preural vertebrae 1-9 and ural vertebra 1 in: (A) dorsal; (B) ventral; and (C) left lateral views. Abbreviations: co, cotyle of ural vertebra 1; hct, calcified or ossified haemal canal soft tissues; hs, haemal spine; lg, lateral groove; lr, lateral ridge; nct, calcified or ossified neural canal soft tissues; pu, preural vertebra; and u, ural vertebra. Scale bar = 5 cm.
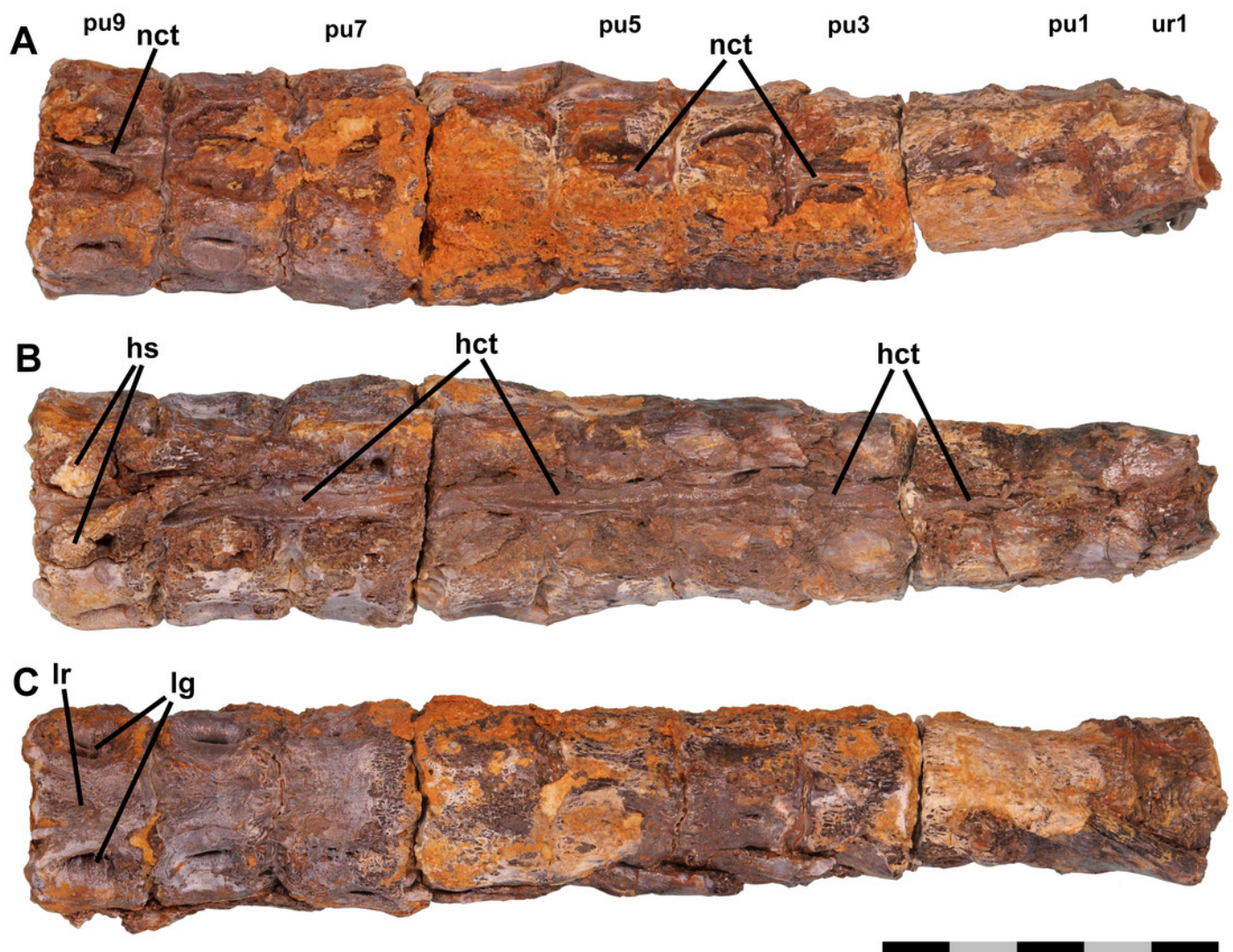
Figure 3

Details of pathology

Figure 3. Ichthyodectiform fish YPM VP 42619. Detail photographs of selected features: (A) reticulate pattern of fine ridges and grooves on lateral surface of preural vertebra 10, and ferruginous particulate matter in longitudinal groove; (B) narrow sinuous groove between preural vertebrae 8 and 7 in ventral view (compare to Fig. 2C); (C) pathological bone tissue on right lateral surface of preural vertebra 2 through ural vertebra 1 and remnant of sinuous groove between preural vertebra 1 and ural vertebra 1; and (D) soft tissues of haemal canal on preural vertebrae 8 and 7 in ventral view with anterior to the right (compare to Fig. 2C). Abbreviations: hct, calcified or ossified haemal canal soft tissues; lg, longitudinal groove; pm, particulate matter; rb, reticulate bone; and sg, sinuous groove. Scale bars = 1 cm.
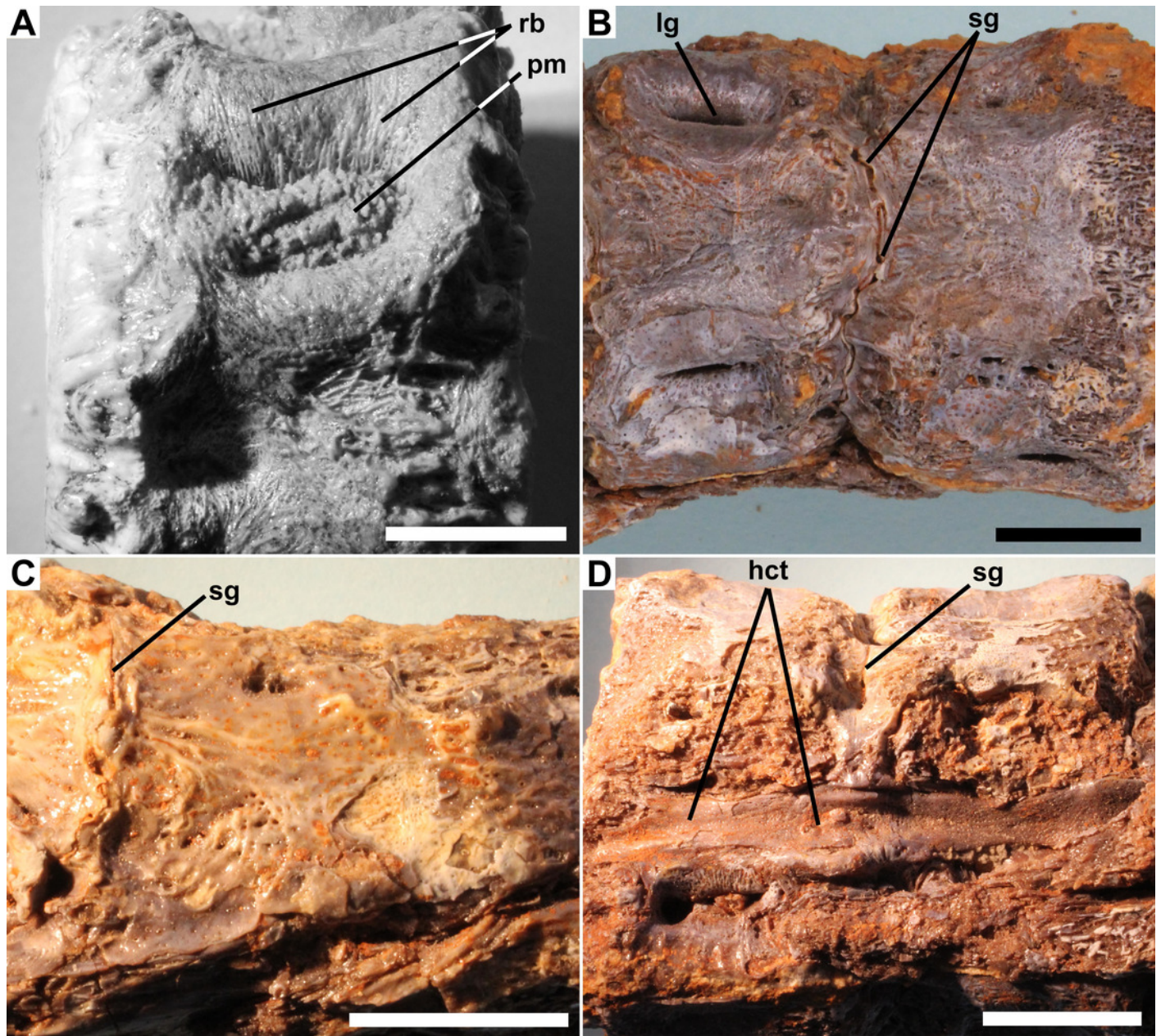
Figure 4

Thin section of preural 10

Figure 4. Ichthyodectiform fish YPM VP 42619. Photograph of horizontal thin section of the left side of centrum of preural vertebra 10 extending laterally from the midline with anterior to the left. Numbered rectangles show the location of detail photographs in Fig. 5 and 6. The arrow at left indicates the presumed external surface of the centrum upon which pathological bone was deposited. Abbreviations: ac, anterior cotyle; ivb, intervertebral bone tissue; pc, posterior cotyle; pl, palisade-like layer; and vo, large void. Scale bar = 5 mm.
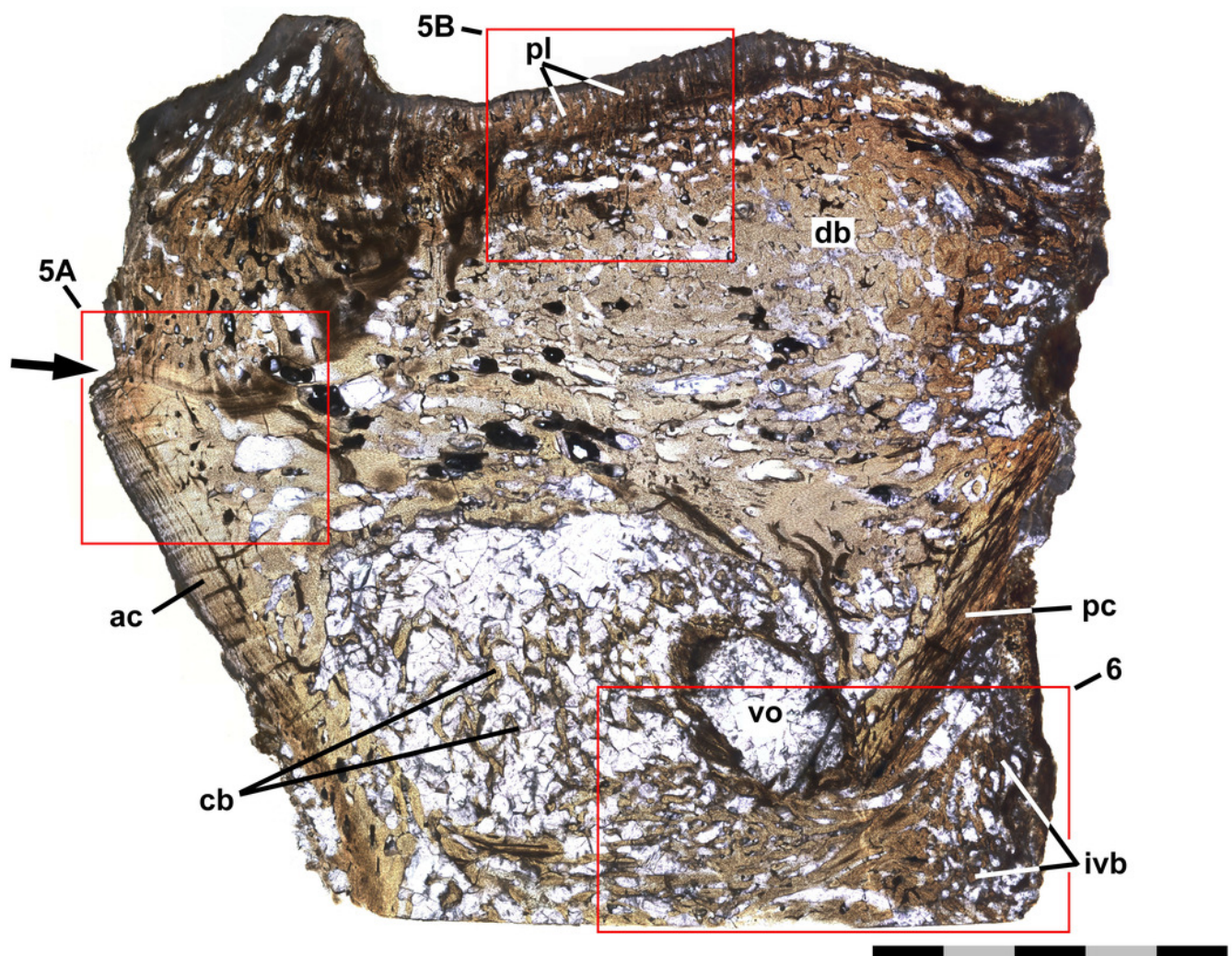
Figure 5

Growth lines and palisade-like layer

Figure 5. Ichthyodectiform fish YPM VP 42619. Detail photographs of the thin section of the centrum of preural vertebra 10 in Fig. 4 showing: (A) striations of presumably stratified bone of the anterior cotyle and similarly stratified bone of the presumed former external surface of the centrum upon which overgrowing bone tissue was deposited; and (B) thin palisade-like layer at the lateral surface with closely spaced slender subparallel canals. The arrow at left in A indicates the presumed external surface of the centrum upon which pathological bone was deposited. Abbreviations: ac, anterior cotyle; dl, dark growth? line; pl, palisade-like layer; str, striations; and ssc, slender subparallel canals. Scale bar = 1 mm.
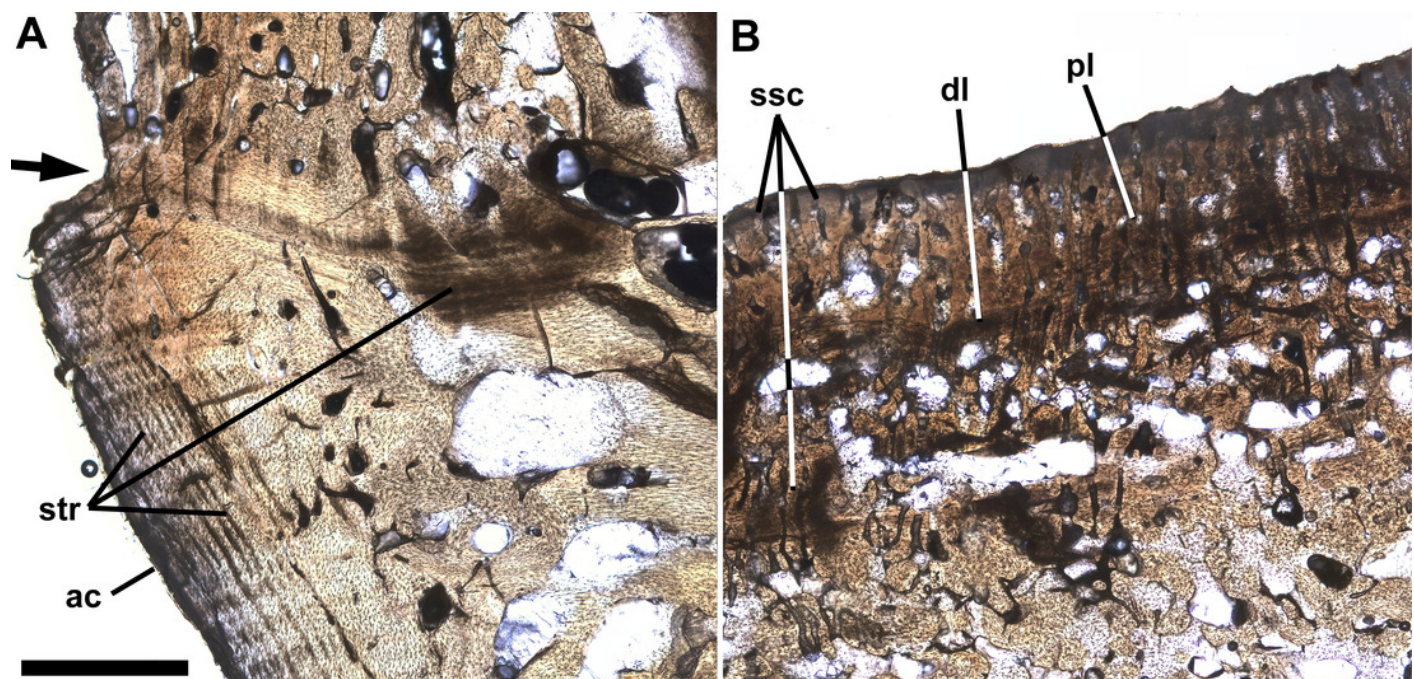
Figure 6

Intervertebral bone

Figure 6. Ichthyodectiform fish YPM VP 42619. Detail photograph of the thin section of the centrum of preural vertebra 10 in Fig. 4 showing pathological bone tissue within the centrum and intervertebral disk. Abbreviations: ivb, intervertebral bone tissue; lvc, longitudinal vascular canal; pc, posterior cotyle; and vo, large void. Scale bar = 1 mm.