Cranial osteology, taxonomic reassessment, and phylogenetic relationships of the Early Cretaceous (Aptian-Albian) turtle *Trinitichelys hiatti* (*Paracryptodira*)

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We describe the skull of the Early Cretaceous (Aptian-Albian) baenid turtle *Trinitichelys hiatti* using micro-computed tomography to provide new insights into the cranial anatomy of basal baenids and into the evolution of paracryptodires. We show that the validity of *Trinitichelys hiatti* versus *Arundelemys dardeni* still holds true, that the most basal known baenids for which skull material is known share an intriguing combination of features that are typical of either *Pleurosternidae* or *Baenidae*, and that the carotid system of *Trinitichelys hiatti* is intermediate to that of pleurosternids and more advanced baenids. Our expanded phylogenetic analysis confirms the traditional placement of *Arundelemys dardeni*, *Lakotemys australodakotensis*, and *Trinitichelys hiatti* as basal baenids, retrieves *Helochelydridae* along the stem of Baenoidea, but recovers *Dinochelys whitei*, *Glyptops ornatus*, *Dorsetochelys typocardium*, and *Uluops uluops* as basal branching *Paracryptodira*.

1   **Cranial osteology, taxonomic reassessment, and phylogenetic**

2   **relationships of the Early Cretaceous (Aptian-Albian) turtle**

3   ***Trinitichelys hiatti* (*Paracryptodira*)**

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16   **Abstract**

17   We describe the skull of the Early Cretaceous (Aptian-Albian) baenid turtle *Trinitichelys hiatti*

18   using micro-computed tomography to provide new insights into the cranial anatomy of basal

19   baenids and into the evolution of paracryptodires. We show that the validity of *Trinitichelys*

20   *hiatti* versus *Arundelemys dardeni* still holds true, that the most basal known baenids for which

21   skull material is known share an intriguing combination of features that are typical of either

22   *Pleurosternidae* or *Baenidae*, and that the carotid system of *Trinitichelys hiatti* is intermediate to

23 that of pleurosternids and more advanced baenids. Our expanded phylogenetic analysis confirms

24 the traditional placement of *Arundelemys dardeni*, *Lakotemys australodakotensis*, and

25 *Trinitichelys hiatti* as basal baenids, retrieves *Helochelydridae* along the stem of Baenoidea, but

26 recovers *Dinochelys whitei*, *Glyptops ornatus*, *Dorsetochelys typocardium*, and *Uluops uluops* as

27 basal branching *Paracryptodira*.

29 INTRODUCTION

30 *Baenidae* Cope, 1873 is a diverse clade of aquatic paracryptodiran turtles that lived in North

31 America from the Early Cretaceous to the Eocene (Hay, 1908; Gaffney, 1972; Joyce & Lyson,

32 2015). The clade includes all turtles more closely related to *Baena arenosa* Leidy, 1870 than

33 *Pleurosternon bullockii* (Owen, 1842) or any extant turtle (Lyson & Joyce, 2011). Along with

34 *Pleurosternidae*, *Baenidae* is included in the clades *Baenoidea* Williams, 1950 and

35 *Paracryptodira* Gaffney, 1975, which are defined as the least inclusive and most inclusive clades

36 containing *Baena arenosa* and *Pleurosternon bullockii* (Lyson & Joyce, 2011), respectively.

37 Additional groups of European and North American turtles have been found to have

38 paracryptodiran affinities, such as *Compsemydidae* Pérez-García, Royo-Torres & Cobos, 2015,

39 which have either been retrieved as basal branching paracryptodires (Pérez-García, Royo-Torres

40 & Cobos, 2015) or baenids (Rollot, Evers & Joyce, 2021a), and *Helochelydridae* Nopcsa, 1928,

41 which were found to be pleurosternids (Rollot, Evers & Joyce, 2021a).

42   *Baenidae* is particularly diverse from the Santonian to the Eocene (Joyce & Lyson, 2015), but

43 little is known about its most basal representatives in the Early Cretaceous. Only four taxa are

44 currently recognized in the Early Cretaceous fossil record as valid baenids: *Arundelemys dardeni*

45 Lipka et al., 2006 from the Aptian–Albian of Maryland, *Lakotemys australodakotensis* Joyce,

46   Rollot & Cifelli, 2020 from the Berriasian–Valanginian, *Protobaena wyomingensis* (Gilmore,

47   1920) from the Albian of Wyoming, and *Trinitichelys hiatti* Gaffney, 1972 from the Aptian–

48   Albian of Texas. New insights have recently been provided into the cranial anatomy of

49   *Arundelemys dardeni* (Evers, Rollot & Joyce, 2021) and *Lakotemys australodakotensis* (Rollot et

50   al., 2022), but many uncertainties remain about the anatomy of *Protobaena wyomingensis* and

51   *Trinitichelys hiatti*. *Trinitichelys hiatti* is exclusively known from the holotype, MCZ VPRA-

52   4070, a nearly complete skeleton that only lacks the mandible, the posterior part of the shell, the

53   caudal vertebrae, and the distal parts of the limbs. A brief diagnosis of the species along with a

54   few illustrations and reconstructions of the skull and shell were originally provided by Gaffney

55   (1972), but a detailed description of the holotype is still lacking. *Trinitichelys hiatti* has,

56   nevertheless, regularly been included in phylogenetic analyses of *Paracryptodira* and always is

57   retrieved as one of the most basal baenids (Lyson & Joyce, 2009a, 2009b, 2010, 2011; Pérez-

58   García, Royo-Torres & Cobos, 2015; Pérez-García et al., 2015; Lyson et al., 2016, 2021; Lyson,

59   Sayler & Joyce, 2019; Joyce & Rollot, 2020).

60   As part of a project that aims to provide detailed insights into the cranial anatomy of basal

61   baenids and better understand the evolution of paracryptodires, we provide a complete

62   description of the skull of the holotype of *Trinitichelys hiatti* based on μCT scans. We compare

63   our interpretation of the cranial osteology of *Trinitichelys hiatti* to the original work of Gaffney

64   (1972) and discuss similarities with *Arundelemys dardeni* and *Lakotemys australodakotensis*, as

65   well as the validity of those taxa. We also provide an expanded phylogenetic analysis of

66   paracryptodires that takes into account the latest discoveries and insights into paracryptodiran

67   anatomy and relationships.

69   MATERIAL AND METHODS

70   The skull of MCZ VPRA-4070 was scanned using a Bruker SkyScan 1173 at the Museum of

71   Comparative Zoology (MCZ) Digital Imaging Facility, Harvard University. The scan was

72   performed with a voltage of 130 kV, a current of 60 µA, and a 0.25 mm brass filter. A total of

73   2206 coronal slices were obtained with a voxel size of 29.2 µm. The specimen was segmented

74   using the software Amira (version 2021.2; https://www.fei.com/software). Bone-by-bone

75   reconstructions were obtained through interpolated slice-by-slice segmentations and the 3D

76   models were exported as .ply files. The software Blender 2.79b (https://www.blender.org) was

77   used to create the images for the figures. The µCT slice data and 3D models are archived on

78   MorphoSource under the MCZ Vertebrate Paleontology Organization

79   (https://www.morphosource.org/projects/000417478?).

80   The phylogenetic relationships of *Trinitichelys hiatti* were investigated by using the taxon-

81   character matrix of Rollot, Evers and Joyce (2021a). The matrix was expanded to include the

82   meiolaniformes *Peligrochelys walshae* from the Paleocene of Argentina (Sterli & de la Fuente,

83   2013, 2019) and *Chubutemys copelloi* from the Aptian–Albian of Argentina (Gaffney et al.,

84   2007; Sterli, de la Fuente & Umazano, 2015); the sichuanchelyids *Mongolochelys efremovi* from

85   the Maastrichtian of Mongolia (Sukhanov, 2000; Suzuki & Chinzorig, 2010) and *Sichuanchelys*

86   *palatodentata* from the Oxfordian of China (Joyce et al., 2016); the indeterminate early stem

87   turtle *Eileanchelys waldmani* from the Bathonian of Scotland, UK (Anquetin et al., 2009;

88   Anquetin, 2010); the recently described pleurosternid *Pleurosternon moncayensis* from the

89   Tithonian-Berriasian of Spain (Pérez-García et al., 2021); and the baenids *Lakotemys*

90   *australodakotensis* from the Berriasian-Valanginian of South Dakota, USA (Rollot et al., 2022),

91   *Neurankylus torrejonensis* from the Paleocene of New Mexico, USA (Lyson et al., 2016),

92 *Goleremys mckennai* from the Paleocene of California, USA (Hutchison, 2004), *Saxochelys*

93 *gilberti* from the Maastrichtian of North Dakota, USA (Lyson, Sayler & Joyce, 2019), and

94 *Palatobaena knellerorum* from the Paleocene of Colorado USA (Lyson et al., 2021). Although

95 not a global matrix with an exhaustive taxon set, our taxon additions ensure that critical groups

96 of turtles to test the content of Paracryptodira are included. Particularly, the addition of early

97 diverging turtle species and clades such as Meiolaniformes provide tests for the controversial

98 phylogenetic positions of *Kallokibotion bajazidi*, compsemydids and helochelydrids, which have

99 variously been found as paracryptodires or not (e.g., Joyce et al. 2016; Pérez-García & Codrea

100 2018; Rollot, Evers & Joyce 2021a).

101 In addition to taxonomic expansion, three characters were modified (characters 9, 11, and 26;

102 see Supplementary Information) and 2 were deleted (characters 5 and 25). A further 22

103 characters were run ordered, because they form morphoclines (characters 5, 9, 13, 15, 17, 25, 26,

104 29, 32, 37, 38, 39, 44, 46, 58, 61, 78, 86, 93, 95, 96, and 99). The character scoring for

105 *Arundelemys dardeni* and *Trinitichelys hiatti* were updated following the latest insights into the

106 cranial anatomy of these taxa (Evers, Rollot & Joyce, 2021; this study; see Supplementary

107 Information). The scoring for *Pleurosternon bullockii* were updated following recent

108 investigation of morphological variability in the shell of this taxon (Guerrero & Pérez-García,

109 2020, 2021; see Supplementary Information) and additional changes were implemented for

110 *Compsemys victa*, *Peckemys brinkman*, *Helochelydra nopcsai*, *Naomichelys speciosa*, and

111 *Kallokibotion bajazidi* (see Supplementary Information).

112 The final matrix included 48 species and 105 characters and was subjected to a traditional

113 parsimony analysis using TNT (version 1.5; Goloboff, Farris & Nixon, 2008). The first analysis

114 was performed under equal weighting and the second analysis was carried out with the

115   implementation of an implied weighting factor of K=12, following recommendations from

116   Goloboff, Torres & Arias (2018). One thousand random addition sequences were followed by a

117   round of tree bisection reconnection. Trees suboptimal by 10 steps and with a relative fit

118   difference of 0.1 were retained as part of the first search. A tree collapsing rule was implemented

119   with a minimum length of 0. *Proganochelys quenstedti* was chosen as the outgroup.

120

121   SYSTEMATIC PALAEONTOLOGY

122   TESTUDINATA Klein, 1760 [Joyce et al. 2020]

123   PARACRYPTODIRA Gaffney, 1975 [Joyce et al. 2021]

124   BAENOIDEA Williams, 1950 [Joyce et al. 2021]

125   BAENIDAE Cope, 1873 [Joyce et al. 2021]

126   TRINITICHELYS Gaffney, 1972

127   *Trinitichelys hiatti* Gaffney, 1972

128

129   **Holotype:** MCZ VPRA-4070, a partial skeleton, only lacking the mandible, the caudal vertebrae,

130   the distal parts of the limbs, and the posterior part of the shell (Gaffney, 1972, figs. 2–5, 47;

131   Gaffney, 1982, fig. 3; Figs. 1–6).

132

133   **Type locality and horizon:** 1 mile from Hardee, on road to Forestburg, Montague County,

134   Texas, USA. (Gaffney, 1972); Antlers Formation (Trinity Sands of Gaffney, 1972), Aptian-

135   Albian, Early Cretaceous (Joyce, Sterli & Chapman, 2014).

136

137 **Revised diagnosis:** *Trinitichelys hiatti* can be diagnosed as a baenid by a reduced, only

138 anteriorly developed lingual ridge, a ventral extension of the jugal, a deep upper temporal

139 emargination, a well-developed posterior process of the pterygoid with an extensive contact with

140 the basioccipital, absence of basipterygoid processes, absence of a second pair of anterior

141 tubercula basioccipitale, presence of axillary buttresses with an extensive contact with the

142 costals, presence of extensive inguinal buttresses, and the absence of epiplastral processes.

143 *Trinitichelys hiatti* is closer to *Lakotemys australodakotensis* than any other baenid and shares

144 with the latter an elongate skull, a small nasal, and a maximum combined width of the parietals

145 greater than their length. *Trinitichelys hiatti* can be differentiated from all other baenids by the

146 following combination of features: presence of a carotid pit, an articular surface of the condylus

147 occipitalis formed by the basioccipital only, a midline contact of the pterygoids for 40-70% of

148 their length, a pleurosternid-like skull sculpturing, nasals that extend as far anteriorly as the

149 premaxillae, vertebrals significantly wider than long, vertebral III narrower anteriorly than

150 posteriorly, gulars smaller than extragulars.

151

152 **Referred material:** none.

153

154 DESCRIPTION

155 **Skull.** The skull of MCZ VPRA-4070 is dorsoventrally crushed and diagonally distorted (Fig. 1).

156 Most palatal and braincase elements are damaged but the cheek area and skull roof bones are

157 overall well preserved. Damage to both otic capsules prevents any clear observation of their

158 internal anatomy. The cavum labyrinthicum could not be reconstructed. The right side of MCZ

159 VPRA-4070 is less affected by crushing than the left side, which allows for detailed descriptions

160   of almost every bone on this side. However, we are not able to rigorously differentiate the jugal

161   from the quadratojugal. These two bones are, therefore, left unresolved in the figures and models

162   (Fig. 1E).

163   The skull of MCZ VPRA-4070 resembles *Pleurosternon bullockii* (Evers, Rollot & Joyce,

164   2020) by being longer than wide (Fig. 1A) but still appears to be less elongate than *Glyptops*

165   *ornatus* (*Glyptops plicatulus* of Gaffney, 1979a) and differs from the wedge-shaped skull of

166   baenodds (Joyce & Lyson, 2015). The approximate length between the anterior tip of the

167   premaxillae and the condylus occipitalis is 54 mm, and the approximate width between the

168   squamosals dorsal to the cavum tympani is 44 mm. The skull surface of *Trinitichelys hiatti* is

169   sculptured by low and irregular pits that are particularly well preserved on the skull roof and the

170   lateral surface of the maxillae. The surface texture is similar to *Arundelemys dardeni* (Lipka et

171   al., 2006; Evers, Rollot & Joyce, 2021) but differs from the irregular tubercles of *Glyptops*

172   *ornatus* (Gaffney, 1979a), *Pleurosternon bullockii* (Evers, Rollot & Joyce, 2020), *Pleurosternon*

173   *moncayensis* (Pérez-García et al., 2021), and *Uluops uluops* (Rollot, Evers & Joyce, 2021a), or

174   the fine crenulations in *Dorsetochelys typocardium* (DORCM G 23). The surface texture along

175   the posterior portion of the parietals of *Trinitichelys hiatti* shows a slightly more striated pattern,

176   albeit less pronounced than the ridge-like arrangement exhibited in the same area in

177   *Pleurosternon bullockii* (Evers, Rollot & Joyce, 2020).

178   Only a few scute sulci are preserved on the right side of the skull roof (see Fig. 2), but those

179   do not allow reconstruction of the cranial scute pattern. Following the scute nomenclatural

180   system of Sterli and de la Fuente (2013), we tentatively identify some cranial scutes by

181   comparing them to the scute pattern of *Arundelemys dardeni* (Evers, Rollot & Joyce, 2021) and

182   *Eubaena cephalica* (Rollot, Lyson & Joyce, 2018). The dorsal process of the prefrontal is

183   mediolaterally crossed by a sulcus that separates scute Z anteriorly from scute Y posteriorly (Fig.

184   2). The second sulcus can be traced from the posterior aspect of the orbit margin, extending

185   posteriorly on the postorbital, before crossing the parietal transversally just posterior to the

186   frontal-parietal suture (Fig. 2). The sulcus separates scute F_2 from scute D posteriorly and F_3

187   laterally, respectively. The third sulcus is located along the posterior part of the parietal, which it

188   crosses sagittally to reach the posterior skull roof margin, and we interpret this sulcus to separate

189   scute A medially from scute H laterally (Fig. 2A).

190   Despite shearing to the skull, the orbits can be interpreted as being vertically oriented (Figs.

191   1A, 1C), which resembles the condition observed in *Compsemys victa* (Lyson & Joyce, 2011),

192   *Arundelemys dardeni* (Lipka et al., 2006; Evers, Rollot & Joyce, 2021), *Lakotemys*

193   *australodakotensis* (Rollot et al., 2022), and *Saxochelys gilberti* (Lyson, Sayler & Joyce, 2019)

194   but contrasts with *Eubaena cephalica* (Rollot, Lyson & Joyce, 2018), *Palatobaena cohen* (Lyson

195   & Joyce, 2009a), *Palatobaena knellerorum* (Lyson et al., 2021), and *Cedrobaena putorius*

196   (Lyson & Joyce, 2009b). The cheek emargination is moderately deep, formed by the maxilla,

197   jugal, and quadratojugal, and just reaches the level of the lower margin of the orbit (Fig. 1E).

198   The cheek emargination of MCZ VPRA-4070 is slightly less deep than that of *Pleurosternon*

199   *bullockii* (Evers, Rollot & Joyce, 2020), *Uluops uluops* (Rollot, Evers & Joyce, 2021a), and

200   *Arvinachelys goldeni* (Lively, 2015), but overall resembles that of *Lakotemys australodakotensis*

201   (Rollot et al., 2022) and the baenodds *Plesiobaena antiqua* (Brinkman, 2003), *Chisternon*

202   *undatum* (Gaffney, 1972), *Eubaena cephalica* (Rollot, Lyson & Joyce, 2018). A well-developed

203   processus pterygoideus externus with a large vertical flange is present as in *Pleurosternon*

204   *bullockii* (Evers, Rollot & Joyce, 2020), *Uluops uluops* (Rollot, Evers & Joyce, 2021a),

205   *Arundelemys dardeni* (Lipka et al., 2006; Evers, Rollot & Joyce, 2021), and *Lakotemys*

229   *typocardium* (Evans & Kemp, 1976), *Glyptops ornatus* (Gaffney, 1979a), *Uluops uluops* (Rollot,

230   Evers & Joyce, 2021a), and most baenodds (Joyce & Lyson, 2015), but unlike *Pleurosternon*

231   *bullockii* (Evers, Rollot & Joyce, 2020), *Arundelemys dardeni* (Lipka et al., 2006; Evers, Rollot

232   & Joyce, 2021), *Lakotemys australodakotensis* (Rollot et al., 2022) and *Neurankylus*

233   *torrejonensis* (Lyson et al., 2016). The crushing and shearing of the anteriormost portion of the

234   skull does not allow us to infer with confidence if a contact was present between the nasal and

235   the maxilla, but our 3D reconstructions suggest that a nasal-maxilla contact is prevented on the

236   right side by an unusual anterior prefrontal process that reaches the dorsolateral margin of the

237   apertura narium externa (see prefrontal; Figs. 1A, 1C), as is the case in *Lakotemys*

238   *australodakotensis* (Rollot et al., 2022), but we also note that this lack of a contact may be the

239   result of damage to the anterior margin of the nasal. The left side is not informative in this regard

240   as its morphology is obscured by damage. Almost all paracryptodires with distinct nasals exhibit

241   a nasal-maxilla contact along the anteriormost aspect of the skull (Gaffney, 1972; Evans &

242   Kemp, 1975, 1976; Lyson & Joyce, 2011; Joyce & Lyson, 2015; Lively, 2015; Rollot, Evers &

243   Joyce, 2021), with the exception of *Naomichelys speciosa* and *Helochelydra nopcsai*, where the

244   prefrontal prevents the two bones from contacting each other (Joyce et al., 2011; Joyce, Sterli &

245   Chapman, 2014). This contact may be absent in numerous baenodds as well (e.g., *Chisternon*

246   *undatum*, Gaffney, 1972), but difficult to assess, given that the nasal is often fused to the frontal

247   (Gaffney, 1972).

248

249   **Prefrontal.** The prefrontal forms the anterodorsal margin of the orbit and perhaps contributes to

250   the posterolateral margin of the external nares (Figs. 1A, 1E, and 3A). The dorsal plate of the

251   prefrontal is clearly exposed on the skull roof but is prevented from contacting its counterpart by

252   the anterior process of the frontal that reaches the nasal (Fig. 1A). This strongly contrasts with

253   the original description of Gaffney (1972), which asserts that the prefrontal does not contribute

254   to the dorsal skull roof at all. An exposure of the prefrontal on the skull roof dorsal to the orbit is

255   generally present among paracryptodires, including *Arundelemys dardeni* (Lipka et al., 2006;

256   Evers, Rollot & Joyce, 2021), *Lakotemys australodakotensis* (Rollot et al., 2022), *Compsemys*

257   *victa* (Lyson and Joyce, 2011), *Dorsetochelys typocardium* (Evans & Kemp, 1976), *Arvinachelys*

258   *goldeni* (Lively, 2015), *Neurankylus eximius* (Brinkman & Nicholls, 1993), *Neurankylus*

259   *torrejonensis* (Lyson et al., 2016), *Pleurosternon bullockii* (Evers, Rollot & Joyce, 2020), or

260   *Uluops uluops* (Rollot, Evers & Joyce, 2021a), but is greatly reduced to absent in baenodds

261   (Brinkman & Nicholls, 1991; Joyce & Lyson, 2015). The dorsal plate of the prefrontal bears an

262   anterior process that anteriorly inserts between the nasal and the maxilla. Although our 3D

263   models show that this process prevents the nasal from contacting the maxilla, it is unclear to us if

264   this is genuine (see nasal). The dorsal plate of the prefrontal contacts the nasal anteromedially,

265   the maxilla anterolaterally, and the frontal posteromedially and posteriorly (Figs. 1A, 1E, and

266   3A). The descending process of the prefrontal forms the anteromedial wall of the fossa orbitalis

267   (Figs. 1E and 3A). Despite damage that affects the ventral portions of the prefrontal and vomer,

268   the arrangement of these bones in that area allows us to suggest that the descending process

269   likely contributes to the margin of the enlarged foramen orbito-nasale. Within the orbit, the

270   prefrontal-frontal contact forms a W-shaped suture in ventral view, which reminds of the

271   condition observed in *Uluops uluops* (Rollot, Evers & Joyce, 2021a), albeit weaker interdigitated

272   as in the latter. The descending process of the prefrontal contacts the ascending process of the

273   maxilla anteriorly and laterally and the vomer ventromedially (Figs. 1E and 3A). A contact

274   between the descending process of the prefrontal and the palatine within the fossa orbitalis is not

275   preserved as is, but the interpolation of the intact margins of the foramen orbito-nasale suggests

276   that this contact was present, as in the vast majority of turtles. The descending process of the

277   prefrontal of *Trinitichelys hiatti* seems to slightly extend medially within the nasal cavity, but a

278   sheet-like ridge, as identified in *Arundelemys dardeni* (Evers, Rollot & Joyce, 2021) and

279   *Lakotemys australodakotensis* (Rollot et al., 2022), is not apparent.

280

281   **Frontal.** The frontal is broad posteriorly and abruptly narrows anteriorly by way of a process

282   that starts anterior to its orbital contribution and extends medially to the dorsal process of the

283   prefrontal to reach the nasal (Fig. 1A). The frontal is about twice as long anteroposteriorly as it is

284   wide mediolaterally at its posterior contact with the parietal. The frontal forms a short process at

285   about mid-length that extends laterally to contribute to the dorsal margin of the orbit. This

286   process inserts between the dorsal process of the prefrontal anteriorly and the postorbital

287   posteriorly, thus preventing both bones from contacting each other (Figs. 1A, 1C, 1E, and 3A). A

288   frontal contribution to the orbit margin is present in a broad selection of paracryptodires,

289   including *Arundelemys dardeni* (Lipka et al., 2006, Evers, Rollot & Joyce, 2021), *Lakotemys*

290   *australodakotensis* (Rollot et al., 2022), *Dorsetochelys typocardium* (Evans & Kemp, 1976),

291   *Helochelydra nopcsai* (Joyce et al. 2011), *Naomichelys speciosa* (Joyce, Sterli & Chapman,

292   2014), *Neurankylus torrejonensis* (Lyson et al., 2016), *Pleurosternon bullockii* (Evers, Rollot &

293   Joyce, 2020), *Uluops uluops* (Rollot, Evers & Joyce, 2021a), and most baenodds (Gaffney,

294   1982), but is notably absent in *Arvinachelys goldeni* (Lively, 2015), *Compsemys victa* (Lyson &

295   Joyce, 2011), *Hayemys latifrons* (Gaffney, 1972), and *Gamerabaena sonsalla* (Lyson & Joyce,

296   2010). The anterior process of the frontal represents about half of its length and prevents the

297   prefrontals from contacting one another along the midline of the skull (Fig. 1A). The anterior

298   process contacts the nasal anteriorly and the prefrontal anterolaterally and laterally (Fig. 1A).

299   The frontal otherwise contacts its counterpart medially along its full length, the parietal

300   posteriorly, and the postorbital posterolaterally (Figs. 1A, 1C, 1E and 3). Each frontal ventrally

301   bears a poorly developed crista cranii, which collectively form the shallow sulcus olfactorius.

302   The crista cranii level off posteriorly on the underside of the frontal and are not directly

303   continuous with the margin of the descending process of the parietal, as is also the case in

304   *Arundelemys dardeni* (Evers, Rollot & Joyce, 2021), *Lakotemys australodakotensis* (Rollot et al.,

305   2022), *Pleurosternon bullockii* (Evers, Rollot & Joyce, 2020), and *Uluops uluops* (Rollot, Evers

306   & Joyce, 2021a). The overall shape of the frontal differs significantly from the original

307   description of Gaffney (1972) who illustrated it to be a rectangular bone that has a straight

308   anterior suture with the nasal and that contributes broadly to the margin of the orbit.

309

310   **Parietal.** The parietal is about twice as long as wide and forms the medial and posterior portions

311   of the skull roof (Fig. 1A). Its shape and contacts broadly conform to the skull reconstructions

312   provided by Gaffney (1972). The dorsal plate of the parietal roofs the braincase and forms most

313   of the upper temporal emargination (Figs. 1A and 3B), of which the extent is described above

314   (see Skull). On the dorsal skull roof, the dorsal plate contacts the frontal anteriorly, the

315   postorbital laterally, and the supraoccipital posteromedially (Figs. 1A, 1C, 1E, and 3). Although

316   reduced, a clear contact of the parietal with the squamosal is visible along the posterolateral tip

317   of the parietal on the right side of the skull (Fig. 1A), contra Gaffney (1972). A parietal-

318   squamosal contact is known to be present in *Lakotemys australodakotensis* (Rollot et al., 2022),

319   *Dorsetochelys typocardium* (Evans & Kemp, 1976), *Pleurosternon bullockii* (Evans & Kemp,

320   1975; Evers, Rollot & Joyce, 2020), *Uluops uluops* (Rollot, Evers & Joyce, 2021a),

321 *Helochelydra nopcsai* (Joyce et al., 2011), *Naomichelys speciosa* (Joyce, Sterli & Chapman,

322 2014), and *Neurankylus torrejonensis* (Lyson et al., 2016). Among baenodds, it is generally

323 absent, with exception of *Baena arenosa* and *Chisternon undatum* (Gaffney, 1972). The

324 descending process of the parietal forms the posterior margin of the foramen interorbitale, the

325 anterior part of the lateral wall of the cavum cranii, and the medial margin of the fossa temporalis

326 (Fig. 3). The parietal slightly underlies the postorbital for a short distance at the base of the

327 processus inferior parietalis. At the level of this underlying sheet of bone and slightly posterior to

328 the ventral process of the postorbital, the parietal bears a low mediolateral ridge, which forms the

329 posterior margin of the roof of the sulcus palatino-pterygoideus (Fig. 4A), as observed in

330 *Arundelemys dardeni* (Evers, Rollot & Joyce, 2021), *Lakotemys australodakotensis* (Rollot et al.,

331 2022), *Pleurosternon bullockii* (Evers, Rollot & Joyce, 2020), and *Uluops uluops* (Rollot, Evers

332 & Joyce, 2021a). However, this feature is comparatively poorly developed with regard to the

333 aforementioned taxa. As the ventral half of the processus inferior parietalis is strongly damaged

334 on both sides, the bony contributions to the foramen nervi trigemini and the extent of the contact

335 of the processus inferior parietalis with the pterygoid and purported epipterygoid cannot be

336 assessed precisely (Figs. 3A and 4A). Within the upper temporal fossa, a broad contact with the

337 prootic and a broad posterolateral contact with the supraoccipital can nevertheless be identified

338 with confidence (Fig. 3A).

339

340 **Postorbital.** The postorbital is an elongate, plate-like bone that forms the posterior margin of the

341 orbit and the dorsolateral aspect of the skull roof (Figs. 1A, 1C, 1E, and 3A). A mediolaterally

342 thickened, ventral process is developed along the anterior portion of the postorbital that rests on

343 the jugal and maxilla. Along with the medial process of the jugal, the ventral process of the

344   postorbital forms the well-developed posterior wall of the fossa orbitalis that constricts the

345   passage from the temporal fossa posteriorly to the orbital fossa anteriorly (Fig. 1C). The ventral

346   process of the postorbital is thus very similar to that of *Pleurosternon bullockii* and *Uluops*

347   *uluops* (Evers, Rollot & Joyce, 2020) and is reminiscent of the septum orbitotemporale of

348   pleurodires (Gaffney, Tong & Meylan, 2006). Within the orbital fossa, the postorbital contacts

349   the jugal ventromedially and the maxilla ventrolaterally. The medial process of the jugal prevents

350   any contact of the postorbital with the palatine and the pterygoid. Along the skull roof, the width

351   of the postorbital overall gradually decreases towards the posterior (Figs. 1A, 1E). The

352   postorbital contacts the maxilla anteroventrally along the posteroventral margin of the orbit,

353   which prevents the jugal from contributing to the latter (see jugal; Figs. 1E and 3A) and contrasts

354   with the initial observations of Gaffney (1972), who highlighted a clear jugal contribution to the

355   orbit. The postorbital contacts the frontal anteromedially, the parietal medially, the jugal

356   anteroventrally along a sinusoid-shape suture, the quadratojugal posteroventrally, and the

357   squamosal posteriorly (Figs. 1A, 1C, 1E, and 3A). A short contact between the parietal and

358   squamosal posterior to the postorbital prevents the latter from contributing to the upper temporal

359   emargination (Fig. 1A), as in *Dorsetochelys typocardium* (Evans & Kemp, 1976), *Helochelydra*

360   *nopcsai* (Joyce et al., 2011), *Naomichelys speciosa* (Joyce, Sterli & Chapman, 2014),

361   *Pleurosternon bullockii* (Evans & Kemp, 1975; Evers, Rollot & Joyce, 2020), and *Uluops uluops*

362   (Rollot, Evers & Joyce, 2021a), but also the baenids *Lakotemys australodakotensis* (Rollot et al.,

363   2022), *Baena arenosa* (Gaffney, 1972), *Chisternon undatum* (Gaffney, 1972), and *Neurankylus*

364   *torrejonensis* (Lyson et al., 2016).

365

366   **Jugal-quadratojugal.** In the µCT data, we are not able to detect a clear suture between the jugal

367   and the quadratojugal and thus segmented these two bones as a single mesh (Fig. 1E). The

368   approximate extent of both bones can be assessed, with the exception of the posterior-most

369   portion of the jugal and the anterior limit of the anterior process of the quadratojugal. Here, we

370   figure and describe both bones together. The anterior third of this bony complex likely

371   corresponds to the jugal, which forms the posteroventral part of the fossa orbitalis and the

372   anterodorsal margin of the cheek emargination (Figs. 1C, 1E). The medial process of the jugal

373   rests upon the posterior portion of the maxilla, and contacts the palatine medially, the pterygoid

374   posteromedially, and the ventral process of the postorbital dorsally. Within the orbit, the medial

375   process of the jugal contacts the maxilla along a V-shaped suture of which the anterior tip ends

376   just posterior to the foramen supramaxillare (Fig. 1A). Along the lateral skull surface, the jugal

377   contacts the maxilla anteroventrally, the postorbital anterodorsally and dorsally along a sinusoid-

378   shape suture, and the quadratojugal posteriorly (Figs. 1A, 1C, and 1E). In his restoration,

379   Gaffney (1972) suggested a broad contribution of the jugal to the orbit. Although the area of

380   interest is crossed by various cracks, we are confident that the piece of bone originally identified

381   as belonging to the jugal actually corresponds to the posterior part of the maxilla. The small

382   contact now apparent between the postorbital and the maxilla in the posteroventral corner of the

383   orbit margin thus prevents the jugal from contributing to the margin of the orbit (Fig. 1E), as in

384   *Arundelemys dardeni* (Lipka et al., 2006; Evers, Rollot & Joyce, 2021), *Lakotemys*

385   *australodakotensis* (Rollot et al., 2022), *Glyptops ornatus* (Gaffney, 1979a), *Pleurosternon*

386   *bullockii* (Evers, Rollot & Joyce, 2020), and a wide selection of baenodds (see Brinkman &

387   Nicholls, 1991; Brinkman, 2003; Lyson & Joyce, 2010; Lively, 2015; Rollot, Lyson & Joyce,

388   2018; Lyson, Sayler & Joyce, 2019). The quadratojugal portion of the jugal-quadratojugal

389   complex likely is a triradiate element that nearly forms the entire posterior margin of the cheek

390   emargination (Fig. 1E). The posterior margin of the quadratojugal is concave, contacts the

391   quadrate, but does not contribute to the anterior margin of the cavum tympani (Fig. 1E),

392   confirming initial observations by Gaffney (1972). The dorsal process of the quadratojugal

393   extends dorsally above the cavum tympani between the quadrate and postorbital to contact the

394   squamosal and has a similar extent above the cavum tympani than most paracryptodires (Figs

395   1A, 1E), with the exception of some palatobaenines (Brinkman, 2003; Lyson & Joyce, 2009a,

396   2009b) and *Compsemys victa* (Lyson & Joyce, 2011), in which the process is shorter or absent.

397   The posteroventral process extends ventrally along the anteroventral margin of the quadrate and

398   almost reaches the condylus mandibularis (Fig. 1E). The anterior process contacts the postorbital

399   dorsally and the jugal anteriorly (Figs. 1A, 1C, and 1E).

400

401   **Squamosal.** The squamosal is a cone-shaped element that forms the posterodorsolateral portion

402   of the skull, the lateral margin of the upper temporal emargination, the posterodorsal margin of

403   the cavum tympani, and most of the deep and voluminous antrum postoticum (Figs. 1A, 1D–E,

404   and 3A). A broad concavity is developed along the ventrolateral margin of the posterior process

405   of the squamosal. On the dorsal skull surface, the squamosal contacts the parietal anteromedially,

406   the postorbital anteriorly, the quadratojugal anterolaterally, and the quadrate laterally (Figs. 1A,

407   1E, and 3A). Within the temporal fossa, the squamosal contacts the quadrate anteriorly and

408   anteromedially and the paroccipital process of the opisthotic posteromedially (Figs. 1A, 1D). The

409   dorsal margin of the squamosal forms the posterolateral margin of the upper temporal

410   emargination. Its edge is medially curved to overhang the temporal fossa (Fig. 1A).

411

412   **Premaxilla.** The premaxilla forms the anteriormost part of the skull, ventrally contributes to the

413   apertura narium externa and to the anterior aspect of the labial ridge, and floors the anteromedial

414   portions of the fossa nasalis (Figs. 1B–C, 1E, 3, and 4B–C). The premaxilla forms a median

415   ridge with its counterpart that slightly protrudes from below into the fossa nasalis and likely

416   served as an insertion surface for the internarial septum. In ventral view, the premaxillae and

417   vomer jointly form a "tongue groove," a distinct depression at the front of the palate that is

418   laterally framed by the triturating surfaces, and in which the anterior portion of the tongue is

419   inferred to have been located (Fig. 1B). Among paracryptodires, such a tongue groove is

420   otherwise developed in *Arundelemys dardeni* (Evers, Rollot & Joyce, 2021) and numerous

421   baenodds (e.g., Lyson & Joyce, 2009a, 2009b; Rollot, Lyson & Joyce, 2018; Lyson, Sayler &

422   Joyce, 2019). The premaxilla contacts its counterpart medially along the skull midline, the

423   maxilla laterally, and the vomer posteriorly (Figs. 1B–C, 1E, and 3). The foramen praepalatinum

424   is entirely formed by the premaxilla and is located at the posteriormost portion of the latter, very

425   close to the suture with the vomer (Figs. 1B and 4C). A foramen praepalatinum exclusively

426   formed by the premaxilla is also present in *Arundelemys dardeni* (Lipka et al., 2006),

427   *Dorsetochelys typocardium* (DORCM G 23), *Pleurosternon bullockii* (Evans & Kemp, 1975;

428   Evers, Rollot & Joyce, 2020), and a broad set of eubaenines (Gaffney, 1972), while a

429   contribution from the vomer and/or maxilla is apparent in *Arvinachelys goldeni* (Lively, 2015)

430   and palatobaenines (Gaffney, 1972; Archibald & Hutchison, 1979; Brinkman, 2003; Lyson &

431   Joyce, 2009a, 2009b). The labial margin of the premaxilla is even and does not form a distinct

432   hook (Fig. 1C) as seen in *Compsemys victa* (Lyson & Joyce, 2011).

433

434 **Maxilla.** The maxilla forms the lateral margins of the apertura narium externa, the anterolateral

435 wall of the fossa nasalis, as well as the anteroventral and ventral aspects of the orbital margin and

436 fossa orbitalis (Figs. 1A–C, 1E, and 3). The maxilla has an ascending process that extends

437 dorsally to cover the lateral aspect of the descending process of the prefrontal (Figs. 1C, 1E, and

438 3A). The ascending process of the right maxilla is minorly exposed on the skull roof anterodorsal

439 to the orbit, but its left counterpart is not apparent in dorsal view because of the damage and

440 shearing that affects this area (Fig. 1A). Although such an extent for this process is highly

441 unusual for a paracryptodire, we conclude that this interpretation is the one best supported by the

442 μCT scans. The ascending process of the maxilla contacts the prefrontal dorsally and posteriorly,

443 but contact with the nasal is barely prevented by the elongate anterior process of the prefrontal

444 dorsal to the maxilla (Figs. 1A, 1C, 1E, and 3A). In lateral view, the maxilla forms the

445 anteroventral margin of the cheek emargination and contacts the jugal posteriorly along an S-

446 shaped suture and the postorbital posterodorsally (Figs. 1E and 3A). Within the fossa orbitalis,

447 the maxilla forms the lateral margin of the relatively large foramen orbito-nasale and contacts the

448 prefrontal anterodorsally, the vomer anteromedially, the palatine posterolaterally, and the jugal

449 posteriorly (Figs. 1A, 1E, and 3A). The foramen supramaxillare is entirely formed by the maxilla

450 and located just anterior to the V-shaped suture of the latter with the jugal (Fig. 1A). The canalis

451 alveolaris superior can be traced for most of its length within the maxilla and the foramen

452 alveolare superius is located medially at the base of the ascending process of the maxilla. The

453 flat, but ventrodorsally rounded triturating surface is almost entirely formed by the maxilla, with

454 extremely minor contributions from the premaxilla anteriorly and palatine laterally (Fig. 1B).

455 The triturating surfaces anteriorly frame a tongue groove (see Premaxilla above). The triturating

456 surface is relatively narrow anteriorly, but slightly expands posteriorly (Fig. 1B). Its dimensions

457   are similar to that of *Arundelemys dardeni* (Lipka et al., 2006; Evers, Rollot & Joyce, 2021),

458   *Lakotemys australodakotensis* (Rollot et al., 2022), *Chisternon undatum* (Gaffney, 1972),

459   *Arvinachelys goldeni* (Lively, 2015), *Pleurosternon bullockii* (Evans & Kemp, 1975; Evers,

460   Rollot & Joyce, 2020), and *Uluops uluops* (Rollot, Evers & Joyce, 2021a), but differs from

461   broader surfaces of baenodds such as *Eubaena cephalica* (Rollot, Lyson & Joyce, 2018),

462   *Palatobaena* spp. (Archibald & Hutchison, 1979; Lyson & Joyce, 2009a), *Saxochelys gilberti*

463   (Lyson, Sayler & Joyce, 2019), and *Stygiochelys estesi* (Gaffney, 1972). The maxilla is bordered

464   laterally by a high labial ridge, which forms a weak curve visible in lateral view along the

465   anteroposterior length of the maxilla (Figs. 1E and 3A), as in *Baena arenosa* (Gaffney, 1972),

466   *Boremys pulchra* (Brinkman & Nicholls, 1991), *Arvinachelys goldeni* (Lively, 2015),

467   *Compsemys victa* (Lyson & Joyce, 2011), and *Glyptops ornatus* (Gaffney, 1979a). The lingual

468   ridge of *Trinitichelys hiatti* is low. The right maxilla has what seems to be a short accessory ridge

469   near its contact with the premaxilla. However, a mirroring ridge is absent on the left side, so that

470   it remains unclear if this ridge represents some abnormality or taphonomic feature, or a

471   polymorphically developed accessory ridge.

472

473   **Vomer.** The vomer is an unpaired bone that forms the posteroventral part of the fossa nasalis, the

474   anteromedial margin of the foramen orbito-nasale, and the medial margin of the apertura narium

475   interna (Figs. 1B and 3). The anterior half of the vomer is significantly broadened between the

476   maxillae while the posterior half is narrow and extends posteriorly to reach the anterior process

477   of the pterygoids (Fig. 1B). The vomer contacts the premaxilla anteriorly, the maxilla

478   anterolaterally, the palatine posterolaterally, and the pterygoid posteriorly (Figs. 1B and 3). The

479   posterior portion of the vomer is relatively short because the anterior process of the pterygoids

480 extends anterior to the level of the foramen palatinum posterius (see Pterygoid below). A similar

481 arrangement is present in *Arundelemys dardeni* (Evers, Rollot & Joyce, 2021), *Dorsetochelys*

482 *typocardium* (Evans & Kemp, 1976), *Uluops uluops* (Rollot, Evers & Joyce, 2021a), but is

483 absent in *Compsemys victa* (Lyson & Joyce, 2011) and baenodds (Gaffney, 1972). The shape and

484 contacts of the vomer are similar to those of *Arundelemys dardeni* (Evers, Rollot & Joyce, 2021).

485 The posterior contact of the vomer with the anterior process of the pterygoids prevents the

486 palatines from contacting their counterparts medially (Fig. 1B). At about mid-length, the vomer

487 bears low, dorsolaterally-directed processes for articulation with the descending process of the

488 prefrontals (Fig. 3A). Similar processes and vomer-prefrontal contacts are found in *Arundelemys*

489 *dardeni* (Evers, Rollot & Joyce, 2021), *Compsemys victa* (Lyson & Joyce, 2011), *Glyptops*

490 *ornatus* (Gaffney, 1979a), *Pleurosternon bullockii* (Evans & Kemp, 1975), and *Uluops uluops*

491 (Rollot, Evers & Joyce, 2021a).

492

493 **Palatine.** The palatine is a laminar bone that forms the posteromedial part of the fossa orbitalis,

494 the posterior margin of the apertura narium interna, the posterior portion of the foramen orbito-

495 nasale, and the anterior and medial margin of the foramen palatinum posterius (Figs. 1B, 3B, and

496 4D). The lateral aspect of the palatine between the foramen orbito-nasale and the foramen

497 palatinum posterius contacts the maxilla ventrolaterally and contributes minorly to the triturating

498 surface (Fig. 3B). The palatine contacts the descending process of the prefrontal anteriorly, the

499 vomer medially, the pterygoid posteromedially and posteriorly, and the jugal posterolaterally

500 (Figs. 1B, 3, and 4D).

501

502   **Pterygoid.** The anterior half of the pterygoid contacts its counterpart medially, the palatine

503   anterolaterally along a curved and concave suture, the jugal laterally along the anterior portion of

504   the well-developed processus pterygoideus externus, and the vomer anteriorly by means of its

505   anterior process (Figs. 1B, 3B, and 5A–B). The posterior half of the pterygoid contacts by means

506   of its posterior process the parabasisphenoid medially, the basioccipital and exoccipital

507   posteromedially, and the quadrate laterally (Figs. 1B, 1D). In the trigeminal region, the pterygoid

508   contacts the purported epipterygoid anterodorsally, the prootic posterodorsally, and the quadrate

509   posteriorly (Fig. 3A). A contact with the descending process of the parietal may have been

510   present but the crushing of the latter does not allow clear observation of that area. The pterygoid

511   forms the posterolateral margin of the foramen palatinum posterius, the ventral margin of the

512   canalis cavernosus, and floors the cavum acustico-jugulare (Figs. 1B and 5B–C).

513   The pterygoid bears a long anterior process that reaches the posteriormost portion of the

514   vomer, and prevents the palatines from contacting each other (Figs. 1B and 3B). This process

515   ends slightly anterior to the level of the anteriormost margin of the foramen palatinum posterius

516   and is about half as long as the palatine anteroposteriorly (Fig. 1B). Such an extensive anterior

517   process is also found in *Arundelemys dardeni* (Evers, Rollot & Joyce, 2021), *Lakotemys*

518   *australodakotensis* (Rollot et al., 2022), *Dorsetochelys typocardium* (Evans & Kemp, 1976), and

519   *Uluops uluops* (Rollot, Evers & Joyce, 2021a), and appears to differ from other known

520   paracryptodires (Gaffney, 1972, 1979a; Evers, Rollot & Joyce, 2020; Lyson & Joyce, 2011). In

521   some palatobaenines, the pterygoid-palatine suture is located slightly more anteriorly than in

522   other baenodds and the pterygoid marginally protrudes anteriorly within the palatine (Gaffney,

523   1972; Archibald & Hutchison, 1979; Lyson & Joyce, 2009a). This process is however greatly

524   reduced in comparison to the anterior process of *Trinitichelys hiatti*. The pterygoid of

525   *Trinitichelys hiatti* forms a well-developed processus pterygoideus externus that extends into the

526   subtemporal fossa (Figs. 3A and 5). The process is dorsoventrally expanded into a robust,

527   vertical flange that is similar to that of *Arundelemys dardeni* (Evers, Rollot & Joyce, 2021),

528   *Lakotemys australodakotensis* (Rollot et al., 2022), *Glyptops ornatus* (Gaffney, 1979a),

529   *Pleurosternon bullockii* (Evers, Rollot & Joyce, 2020), *Pleurosternon moncayensis* (Pérez-

530   García et al., 2021), and *Uluops uluops* (Rollot, Evers & Joyce, 2021a), but also the processus

531   trochlearis pterygoidei of pleurodires. The crista pterygoidei is low and forms the lateral border

532   for the sulcus cavernosus (Fig. 5C). The pterygoid-epipterygoid contact, if real, is inferred to be

533   located along the anterior part of the crista pterygoidei. The canalis cavernosus could not be

534   reconstructed because of the crushing that affects the relevant region of the skull, but the

535   pterygoid clearly exhibits a groove along its dorsal surface that extends posterolaterally for most

536   of its length (Figs. 5B–C and 6A–B). The anterior portion of this groove is the sulcus cavernosus

537   and the posterior portion corresponds to the ventral margin of the canalis cavernosus. The

538   foramen cavernosum is likely located slightly posteroventral to the anterior limit of the prootic

539   and the pterygoid ventrally contributes to the formation of that foramen. We are not able to

540   determine the exact bony contributions to the foramen nervi trigemini because of the

541   dorsoventral crushing of the skull, but the 3D models suggest that the pterygoid and parietal

542   likely contributed to it (Fig. 3A).

543   At mid-length along the parabasisphenoid-pterygoid suture, the pterygoid forms the lateral

544   part of a carotid pit (sensu Evers, Rollot & Joyce, 2021; Fig. 5A and 6C), which is roughly half

545   the size of that of *Uluops uluops* (Rollot, Evers & Joyce, 2021a). The carotid pit of *Trinitichelys*

546   *hiatti* is posteriorly constricted by extensions of the pterygoid and parabasisphenoid that partially

547   cover the posterior aspect of the pit and separate it from a narrow, posteriorly directed carotid

548   groove (Figs. 6C–D). In that regard, *Trinitichelys hiatti* differs from *Uluops uluops*, where the

549   carotid pit is fully confluent posteriorly with the carotid groove and lacks the extensions of the

550   pterygoid and parabasisphenoid that constrict the posterior margin of the carotid pit (Rollot,

551   Evers & Joyce, 2021a). The basicranium of *Trinitichelys hiatti* thus might exhibit an

552   intermediate ossification stage between that of *Uluops uluops* and baenodds, in which a foramen

553   posterius canalis carotici interni and canalis caroticus internus are present (see Discussion

554   below). The carotid pit of *Trinitichelys hiatti* contains two foramina that we identify as the

555   foramen posterius canalis nervi vidiani and the foramen posterius canalis carotici

556   basisphenoidalis (Figs. 5D and 6D). The foramen posterius canalis nervi vidiani is located along

557   the anterolateral margin of the carotid pit and is formed by the pterygoid (Figs. 5D and 6D). The

558   foramen posterius canalis nervi vidiani leads to the canalis nervus vidianus, which extends

559   anteriorly through the pterygoid (Figs. 6B, 6D). The canalis nervus vidianus exits the skull along

560   the dorsal surface of the pterygoid by means of the foramen anterius canalis nervi vidiani, which

561   is located posterolaterally to the anterior process of the pterygoid (Figs. 6B and 6D). The second

562   foramen found in the carotid pit is the foramen posterius canalis carotici basisphenoidalis,

563   through which the cerebral artery enters the parabasisphenoid (Fig. 6D). The foramen posterius

564   canalis carotici basisphenoidalis is located along the medial margin of the carotid pit and formed

565   by the pterygoid laterally and the parabasisphenoid medially. There is no evidence for the

566   presence of a canal for the palatine artery, the canalis caroticus lateralis. When present, this canal

567   generally extends anteriorly along the pterygoid-parabasisphenoid suture and exits the skull

568   through the foramen anterius canalis carotici lateralis (see Rollot, Evers & Joyce, 2021b), usually

569   located within the sulcus cavernosus. In *Uluops uluops* and *Lakotemys australodakotensis*, the

570   only known paracryptodires for which a canalis caroticus lateralis can unambiguously be

571   identified, the entrance point of the palatine artery into the skull, the foramen posterius canalis

572   carotici lateralis, is located between the foramen posterius canalis nervi vidiani and the foramen

573   posterius canalis carotici basisphenoidalis (Rollot, Evers & Joyce, 2021a; Rollot et al., 2022). In

574   *Trinitichelys hiatti*, we are not able to identify any additional foramen in the carotid pit than the

575   posterior foramina for the canals for the vidian nerve and cerebral artery and cannot observe any

576   canal that extends along the pterygoid-parabasisphenoid suture. We consider the canalis

577   caroticus lateralis and the palatine artery to be absent in *Trinitichelys hiatti*. The circulation

578   system of *Trinitichelys hiatti* therefore demonstrably resembles that of *Arundelemys dardeni*

579   (Lipka et al., 2006; Evers, Rollot & Joyce, 2021), *Eubaena cephalica* (Rollot, Lyson & Joyce,

580   2018), and *Pleurosternon bullockii* (Evers, Rollot & Joyce, 2020), taxa in which the canalis

581   caroticus lateralis has been shown to be absent by the use of micro-CT scans. The foramen

582   distalis nervi vidiani is located along the lateral margin of the carotid sulcus just posterior to the

583   extensions of the pterygoid and parabasisphenoid that constrict the carotid pit (Fig. 5D). The

584   foramen distalis nervi vidiani allows the passage of the vidian nerve from the canalis pro ramo

585   nervi vidiani into the carotid sulcus (Fig. 6D).

586   The pterygoid fossa on the ventral surface of the posterior process of the pterygoid is

587   moderately deep (Fig. 5A). The posterior process of the pterygoid is long and has an elongate

588   contact medially with the basioccipital (Figs. 1B, 5B, and 5D), similar to that of baenodds

589   (Gaffney, 1972; Brinkman & Nicholls, 1991, 1993; Joyce & Lyson, 2015), *Arundelemys dardeni*

590   (Lipka et al., 2006), and *Lakotemys australodakotensis* (Rollot et al., 2022), but which contrasts

591   with that of *Dorsetochelys typocardium* (Evans & Kemp, 1976), *Glyptops ornatus* (Gaffney,

592   1979a), *Pleurosternon bullockii* (Evans & Kemp, 1975), *Pleurosternon moncayensis* (Pérez-

593   García et al., 2021), and *Uluops uluops* (Rollot, Evers & Joyce, 2021a), in which the posterior

594 process of the pterygoid does not extend beyond the posterior limit of the parabasisphenoid. The

595 posterior process of the pterygoid also contacts the exoccipital posterodorsally as in *Arundelemys*

596 *dardeni* (Evers, Rollot & Joyce, 2021) and *Saxochelys gilberti* (Lyson, Sayler & Joyce, 2019).

597 The ventral surface of the posterior process of the pterygoid is smooth as anterior tubercula

598 basioccipitale are absent (Figs. 5A and 6C). Within the cavum acustico-jugulare, the pterygoid

599 contacts the prootic anterodorsomedially and the quadrate laterally. A contact with the opisthotic

600 is not preserved but was likely present dorsomedially.

601

602 **Epipterygoid.** The area of the descending process of the parietal is badly crushed (Fig. 4A).

603 Numerous fragmentary bony pieces can be found in the matrix surrounding this region of the

604 skull and an attribution of these to either the parietal, pterygoid, or a potential epipterygoid is not

605 possible with certainty. We are unable to determine if a separate, ossified epipterygoid is present

606 in *Trinitichelys hiatti*, but note that an intriguing piece of bone, located medial to the processus

607 pterygoideus externus, may represent a portion of an epipterygoid (Fig. 3A). Its bony

608 components have been segmented and are described herein. The piece of bone of interest is

609 laterally thick and parasagittaly crossed by a suture that is visible along the lateral surface where

610 the bony element is the thickest. The thickening and position of the suture is similar to the

611 epipterygoid of *Uluops uluops* and its suture with the parietal. The epipterygoid of *Uluops*

612 *uluops* has a lateral bulge at its dorsal process, which extends as a thick ridge over the lateral

613 surface of the epipterygoid, and the suture with the parietal is located just dorsal to that (Rollot,

614 Evers & Joyce, 2021a). If the conformation is the same in *Trinitichelys hiatti*, then the bone

615 located dorsomedially to the suture within the bony element belongs to the parietal, and the

616 ventrolateral bone corresponds to the epipterygoid. An alternative interpretation is that the bone

617   medial to the suture is actually part of an expanded crista pterygoidea, and that the bone lateral to

618   the suture corresponds to the ventralmost aspect of the descending process of the parietal that

619   laterally rests on the pterygoid. As we are not able to favor one hypothesis over the other, we

620   consider the presence or absence of an epipterygoid in *Trinitichelys hiatti* to be unknown.

621

622   **Quadrate.** The quadrate forms most of the cavum tympani and antrum postoticum, the condylus

623   mandibularis, the lateral portion of the cavum acustico-jugulare, and the incisura columella auris

624   (Figs. 1D–E and 3A). In lateral view, the quadrate contacts the quadratojugal along a convex

625   suture and the squamosal posterodorsally (Figs. 1E and 3A). The cavum tympani is deep and

626   visually separated from the voluminous antrum postoticum by a ridge formed by the quadrate.

627   Within the lower temporal fossa, the quadrate has an elongate contact with the pterygoid

628   medially. Within the upper temporal fossa, the quadrate contacts the prootic anteromedially, the

629   opisthotic posteromedially, and the squamosal posterolaterally (Figs. 1A and 3A). The presence

630   of a potential contact between the supraoccipital and quadrate is unclear. A small piece of bone

631   is located between the supraoccipital, prootic, opisthotic, and quadrate on the floor of the upper

632   temporal fossa, but are unable to determine with confidence which element it represents (Fig.

633   1A, right side). Its attribution to the supraoccipital or quadrate would suggest a point contact

634   between these two bones, attribution to the opisthotic or prootic would preclude such a contact,

635   even though both bones would still approach one another closely. A supraoccipital-quadrate

636   contact is commonly present in paracryptodires, varying from an elongate contact as in

637   *Compsemys victa* (Lyson & Joyce, 2011) and *Eubaena cephalica* (Rollot, Lyson & Joyce, 2018),

638   to a point contact, as in *Chisternon undatum* (Gaffney, 1972) and, likely, *Pleurosternon bullockii*

639   (Evers, Rollot & Joyce, 2020). The presence of a supraoccipital-quadrate contact in *Trinitichelys*

640   *hiatti*, even if reduced, would thus correspond to the usual condition found in paracryptodires.

641   The quadrate forms the lateral margin of the foramen stapedio-temporale, canalis stapedio-

642   temporalis, and aditus canalis stapedio-temporalis, and the posterodorsal margin of the canalis

643   cavernosus and the associated posterior foramen. Two facets separated by a shallow sulcus are

644   present on the left condylus mandibularis for the articulation with the mandible (Fig. 1B). The

645   quadrate forms the lateral half of the processus trochlearis oticum, which seems somewhat more

646   prominent than in *Arundelemys dardeni* (Evers, Rollot & Joyce, 2021). Within the cavum

647   acustico-jugulare, the quadrate contacts the opisthotic dorsomedially and the pterygoid

648   ventromedially.

649

650   **Prootic.** The prootic is badly crushed on both sides of the skull. We are able to determine the

651   contacts of the prootic with surrounding bones, but its contributions to internal structures can

652   only be estimated. The prootic contacts the parietal anteromedially, the pterygoid

653   anteroventrally, the quadrate laterally and posterolaterally, the supraoccipital posteromedially,

654   and the opisthotic posteriorly below the skull surface (Figs. 1A and 3A). A point contact with the

655   opisthotic is perhaps present within the upper temporal fossa (see Quadrate above). A

656   contribution of the prootic to the foramen nervi trigemini remains unclear as this area is damaged

657   (Fig. 3A). Within the upper temporal fossa, the prootic forms the medial margin of the foramen

658   stapedio-temporale (Fig. 1A), which leads to the cavum acustico-jugulare by means of the

659   canalis stapedio-temporalis and aditus canalis stapedio-temporalis that are medially bordered by

660   the prootic as well. Within the cavum acustico-jugulare, the prootic borders the canalis

661   cavernosus dorsomedially. The prootic also forms the dorsal margin of the foramen cavernosum.

662   The prootic contributes to the anterolateral part of the cavum cranii, but dorsoventral crushing

663   obscures the fossa acustico-facialis and the canals for the facial (VII) and acoustic nerves (VIII).

664   The canals for the vidian nerve, which are located in the pterygoid (see above), however, provide

665   clues about the path of the facial nerve and the relative position of the geniculate ganglion. The

666   vidian nerve extends ventromedially from the medial part of the pterygoid that housed the lateral

667   head vein to the carotid groove ventrally (Figs. 5D, 6B, and 6D), meaning that the geniculate

668   ganglion was likely located within the canalis cavernosus, and that the facial nerve, which is

669   usually medial to the ganglion, extended laterally from the fossa acustico-facialis to the canalis

670   cavernosus. This is also the case in *Arundelemys dardeni* (Evers, Rollot & Joyce, 2021),

671   *Lakotemys australodakotensis* (Rollot et al., 2022), *Eubaena cephalica* (Rollot, Lyson & Joyce,

672   2018), *Pleurosternon bullockii* (Evers, Rollot & Joyce, 2020), *Pleurosternon moncayensis*

673   (Pérez-García et al., 2021), and *Uluops uluops* (Rollot, Evers & Joyce, 2021a). The prootic

674   otherwise forms the anterior part of the cavum labyrinthicum and the anterior half of the canalis

675   semicircularis anterior and horizontalis. The fenestra ovalis is not well preserved in the

676   specimen, making it impossible to judge if it was completely surrounded by the prootic and

677   opisthotic ventrally.

678

679   **Opisthotic.** The right opisthotic is well-preserved and only shows minor signs of damage that

680   affect its most anterior part and the processus interfenestralis, which is almost completely

681   missing. The anterior part of the opisthotic contacts the supraoccipital anteromedially, the prootic

682   anteriorly below the skull surface, and the quadrate anterolaterally (Fig. 1A). The

683   posterolaterally oriented paroccipital process contacts the exoccipital ventromedially and the

684   squamosal anterolaterally, roofs the cavum acustico-jugulare, and forms the dorsal margin of the

685   fenestra postotica (Figs. 1B, 1D). The paroccipital process bears a ridge along its posterodorsal

686 surface that extends posterolaterally and disappears close to the suture with the squamosal (Fig.

687 1D). A near-identical ridge is present on the paroccipital process of *Lakotemys*

688 *australodakotensis* (Rollot et al., 2022) and *Uluops uluops* (Rollot, Evers & Joyce, 2021a), but

689 absent in *Arundelemys dardeni* (Evers, Rollot & Joyce, 2021). The opisthotic of *Trinitichelys*

690 *hiatti* does not contribute to the foramen stapedio-temporale, but a small contribution to the

691 canalis stapedio-temporalis cannot be excluded. The opisthotic forms the posterior part of the

692 cavum labyrinthicum, the posterior half of the canalis semicircularis horizontalis and canalis

693 semicircularis posterior, and the foramen externum nervi glossopharyngei (IX) at the base of the

694 broken processus interfenestralis. Due to the abovementioned damage, we are not able to

695 comment on the anatomy of the fenestra perilymphatica, the foramen jugulare anterius, the

696 recessus scalae tympani, the fenestra ovalis, and the foramen internum nervi glossopharyngei.

697

698 **Supraoccipital.** The supraoccipital forms the posterior tip of the skull roof, roofs the cavum

699 cranii, and forms the dorsal margin of the foramen magnum and the medial margin of the upper

700 temporal fossa (Figs. 1A, 1D, and 3B). The supraoccipital contacts the parietal anteromedially,

701 the prootic anterolaterally, the opisthotic posterolaterally, and the exoccipital posteroventrally

702 (Figs. 1A, 1D, and 3). A medial point contact with the quadrate might be present as well (see

703 Quadrate above). We note that in *Arundelemys dardeni* and *Lakotemys australodakotensis*, with

704 which *Trinitichelys hiatti* shares a large amount of features (Evers, Rollot & Joyce, 2021; Rollot

705 et al., 2022; this study) and that were regularly found close to the latter in paracryptodiran

706 phylogenies (Lyson & Joyce, 2011; Pérez-García et al., 2015; Rollot, Evers & Joyce, 2021a), the

707 supraoccipital is prevented from contacting the quadrate by a prootic-opisthotic contact just

708 lateral to the latter (Lipka et al., 2006; Rollot et al., 2022). If the bony piece of interest is part of

709   the prootic in *Trinitichelys hiatti*, then the bone arrangement within its upper temporal fossa

710   would be nearly identical to that of *Arundelemys dardeni* and *Lakotemys australodakotensis*. On

711   the other hand, if the bony piece belongs to the supraoccipital, the latter would then have a long,

712   pointed lateral process that would be unique among paracryptodires, with the exception of one

713   specimen of *Palatobaena cohen* (DMNH EPV.97017), in which differences within that portion

714   of the skull are attributed to intraspecific or ontogenetic variation (Lyson and Joyce, 2009a). As

715   we are unable to favor one hypothesis over the other and both seem equally admissible to us, we

716   choose to not attribute the small piece of bone in the center of the upper temporal fossa of

717   *Trinitichelys hiatti* to either the supraoccipital or prootic. The crista supraoccipitalis is a vertical

718   sheet of bone developed between the foramen magnum and the skull roof (Fig. 3B). In dorsal

719   view, the crista supraoccipitalis is short and posteriorly only slightly extends beyond the level of

720   the condylus occipitalis, but does not reach the level of the posterior tip of the squamosals (Fig.

721   1A). The crista supraoccipitalis is mediolaterally thin and the ventrodorsal depth of the upper

722   temporal fossa is intermediate (Fig. 1D), as in *Pleurosternon bullockii* (Evers, Rollot & Joyce,

723   2020). On the skull roof, the parietals cover the crista supraoccipitalis almost completely. The

724   posterodorsal tip of the crista supraoccipitalis is apparent just posterior to the parietals on the

725   skull roof and forms the posteromedial end of the latter (Fig. 1A). The contribution of the crista

726   supraoccipitalis to the skull roof is, however, extremely minor, and is similar to the condition

727   observed in *Cedrobaena putorius* (Lyson & Joyce, 2009b), *Neurankylus eximius* (Brinkman &

728   Nicholls, 1993), and *Pleurosternon bullockii* (Evers, Rollot & Joyce, 2020), but differs from

729   *Dorsetochelys typocardium* (Evans & Kemp, 1976), *Eubaena cephalica* (Rollot, Lyson & Joyce,

730   2018), and *Uluops uluops* (Rollot, Evers & Joyce, 2021a), in which the posterodorsal aspect of

731   the crista supraoccipitalis is developed as a large plate. The supraoccipital roofs the cavum

732   labyrinthicum and forms the posterior portion of the canalis semicircularis anterior and the

733   anterior portion of the canalis semicircularis posterior.

734

735   **Basioccipital.** The basioccipital is an unpaired, quadrangular element that forms the

736   posteroventromedial portion of the skull, floors the posterior part of the cavum cranii and forms

737   the ventral margin of the foramen magnum (Figs. 1B, 1D, and 3B). In posterior view, the

738   basioccipital contacts the exoccipital dorsolaterally and the pterygoid laterally and forms the

739   complete articular surface of the condylus occipitalis (Fig. 1D), as in *Arundelemys dardeni*

740   (Evers, Rollot & Joyce, 2021), *Glyptops ornatus* (Gaffney, 1979a), but also *Compsemys victa*,

741   *Dorsetochelys typocardium*, *Kallokibotion bajazidi*, and *Uluops uluops* (Rollot, Evers & Joyce,

742   2021a), but likely not baenodds (Rollot, Evers & Joyce, 2021a). The basioccipital bears a low

743   crista dorsalis basioccipitalis along its anterodorsal surface and laterally forms short tubercula

744   basioccipitale to which the exoccipital and pterygoid contribute as well (Fig. 1D). In ventral

745   view, the basioccipital contacts the parabasisphenoid anteriorly and the pterygoid laterally along

746   nearly straight sutures (Fig. 1B). The ventral surface of the basioccipital is nearly flat and only a

747   weak depression is apparent posterior to the contact with the parabasisphenoid. We are not able

748   to identify a canalis basioccipitalis within that depression. The basioccipital likely contacted the

749   processus interfenestralis of the opisthotic along its anterodorsal surface, but the exact extent of

750   this contact could not be assessed as the process is not preserved.

751

752   **Exoccipital.** The exoccipital in *Triniticelys hiatti* is not fused to the basioccipital and remains a

753   separate bony element (Figs. 1D and 3B), contra most baenodds (Gaffney, 1982). The

754   exoccipital forms the posterolateral part of the cavum cranii, the lateral margin of the foramen

755   magnum, the posteromedial part of the cavum acustico-jugulare, the medial margin of the

756   fenestra postotica, and the posterior margin of the foramen jugulare anterius (Figs. 1D and 3B).

757   In posterior view, the exoccipital contacts the supraoccipital dorsomedially, the paroccipital

758   process of the opisthotic dorsally and dorsolaterally, the pterygoid ventrolaterally, and the

759   basioccipital ventrally (Fig. 1D). The exoccipital contributes to the tuberculum basioccipitale

760   dorsolaterally (Fig. 1D), which is typical in baenodds (Gaffney, 1982), but different from

761   *Neurankylus torrejonensis*, where they are formed by the basioccipital only (Lyson et al., 2016).

762   The exoccipital does not contribute to the formation of the functional articular surface of the

763   condylus occipitalis (see Basioccipital above). Within the cavum acustico-jugulare, the

764   exoccipital contacts the opisthotic anteriorly, the pterygoid anterolaterally and laterally, and rests

765   on the dorsal surface of the basioccipital. We are not able to determine the number of foramina

766   nervi hypoglossi because of the dorsoventral crushing of that area, but note the presence of at

767   least one canal for the hypoglossal nerve that crosses the left exoccipital mediolaterally.

768

769   **Parabasisphenoid.** The parabasisphenoid is a single element that forms the ventral margin of the

770   cavum cranii (Fig. 3B). The parabasisphenoid contacts the pterygoid laterally along its entire

771   length, the prootic dorsolaterally posterior to the level of the foramen nervi trigemini, and the

772   basioccipital posteriorly (Figs. 1B and 3B). A contact with the palatine and vomer is absent (Fig.

773   1B). The anterior half of the parabasisphenoid, which forms the rostrum basisphenoidale, is

774   developed as a thin sheet of bone that rests on the pterygoid for all of its length, forms the medial

775   margin of the sulcus cavernosus, gradually broadens towards the posterior, and is bordered by

776   the sella turcica posteriorly and the retractor bulbi pits dorsolaterally (Fig. 6A). The sella turcica

777   forms a moderately deep depression that houses the two foramina anterius canalis carotici

778   basisphenoidalis, which are relatively widely spaced, and is overhung by the dorsum sellae (Fig.

779   6B). Most of the clinoid processes is missing, but their bases are preserved and show that those

780   are broad and that the clinoid processes likely extended anterolaterally to the dorsum sellae. The

781   retractor bulbi pits of *Trinitichelys hiatti* are located ventrally to the base of the clinoid processes

782   and form shallow depressions, as in *Arundelemys dardeni* (Evers, Rollot & Joyce, 2021), that

783   contrast with the great depth of the retractor bulbi pits observed in *Pleurosternon bullockii*

784   (Evers, Rollot & Joyce, 2020) and *Uluops uluops* (Rollot, Evers & Joyce, 2021a). The posterior

785   part of the parabasisphenoid is dorsoventrally thick and its dorsal surface forms a deep concavity

786   that contained parts of the brain. The foramen posterius canalis nervi abducentis is located along

787   the anterolateral aspect of the dorsal surface of the parabasisphenoid (Fig. 6A). The short canalis

788   nervus abducentis extends anteriorly through the parabasisphenoid and exits the latter by means

789   of the foramen anterius canalis nervi abducentis, which is located within the retractor bulbi pits

790   (Fig. 6B). The foramen anterius canalis nervi abducentis, canalis nervus abducentis, and foramen

791   posterius canalis nervi abducentis are solely formed by the parabasisphenoid (Figs. 6A–B). A

792   contribution of the pterygoid to the formation of these structures, as observed in *Arundelemys*

793   *dardeni* (Evers, Rollot & Joyce, 2021), *Pleurosternon bullockii* (Evers, Rollot & Joyce, 2020),

794   and *Uluops uluops* (Rollot, Evers & Joyce, 2021a), is absent. The lateral margins of the posterior

795   part of the parabasisphenoid form raised surfaces for the articulation with the prootic and likely

796   bordered the hiatus acusticus ventrally. A crista basis tuberculi basalis is not fully preserved in

797   *Trinitichelys hiatti*, but a small portion of the parabasisphenoid that is slightly raised

798   posteromedially just anterior to the suture with the basioccipital indicates that at least a short

799   crista basis tuberculi basalis was present, as in *Arundelemys dardeni* (Evers, Rollot & Joyce,

800   2021) and *Lakotemys australodakotensis* (Rollot et al., 2022).

801   In ventral view, the parabasisphenoid forms the medial margin of the small carotid pit at mid-

802   length along the suture with the pterygoid (Figs. 1B and 6C). The foramen posterius canalis nervi

803   vidiani and foramen posterius canalis carotici basisphenoidalis are present within this cavity (see

804   Pterygoid above). The foramen posterius canalis carotici basisphenoidalis is located along the

805   medial margin of the carotid pit and formed by the pterygoid laterally and the parabasisphenoid

806   medially (Fig. 6D). As mentioned in the pterygoid section, no canal other than the canalis nervus

807   vidianus and canalis caroticus basisphenoidalis extends through the basicranium. The palatine

808   artery and canalis caroticus lateralis are therefore considered absent, as is the case in

809   *Arundelemys dardeni* (Lipka et al., 2006), *Pleurosternon bullockii* (Evers, Rollot & Joyce, 2020),

810   *Eubaena cephalica* (Rollot, Lyson & Joyce, 2018), and likely all baenodds (Rollot, Evers &

811   Joyce, 2021a). In *Pleurosternon bullockii* (Evers, Rollot & Joyce, 2020) and *Uluops uluops*

812   (Rollot, Evers & Joyce, 2021a), the parabasisphenoid bears a basipterygoid process that extends

813   laterally into the pterygoid and roofs the carotid pit for its entire length. In *Trinitichelys hiatti*,

814   the dorsal aspect of the carotid pit is fully formed by the pterygoid and we are not able to observe

815   a lateral process of the parabasisphenoid in that area of the skull (Figs. 4A and 5C). The

816   basipterygoid process is thus considered absent in this taxon, as is also the case in *Arundelemys*

817   *dardeni* (Evers, Rollot & Joyce, 2021), *Lakotemys australodakotensis* (Rollot et al., 2022), and

818   advanced baenids (Gaffney, 1982). Posterior to the carotid pit, the parabasisphenoid forms along

819   with the pterygoid a groove that extends posteriorly on the ventral surface of the skull and that

820   likely housed the internal carotid artery (Fig. 6C). The posterolateral surface of the

821   parabasisphenoid is smooth and anterior tubercula basioccipitale are absent (Figs. 1B and 6C).

822

823   **Stapes.** The right stapes is partially preserved and shattered into four pieces that do not preserve

824   its more medial and lateral parts. The four pieces are oval shaped in cross-section, have a similar

825   width and show no sign of expansion, suggesting that they belong to the central aspect of the

826   stapes.

827

828   **Hyoid apparatus.** Portions of the first pair of ceratobranchials are preserved on the underside of

829   the skull of *Trinitichelys hiatti*. The right ceratobranchial is complete (see Fig. 7) while only the

830   posterior part is preserved for the left one. Both ceratobranchials appear to be slightly shifted

831   towards the right. Ceratobranchial I is elongate and curved. Its anterior portion extends to the

832   level of the processus pterygoideus externus and its posterior portion reaches the level of the

833   posterior margin of the opisthotic. The ceratobranchial I is overall circular in cross-section

834   posteriorly and broadens progressively towards the anterior, to become dorsoventrally broader

835   along its anterior half. The anterior and posterior articulation facets are not preserved.

836

837   DISCUSSION

838   **Comparison with the original description of Gaffney (1972)**

839   *Trinitichelys hiatti* was originally named and figured by Gaffney (1972) based on a partial

840   skeleton, which only lacks the lower jaw, the caudal vertebrae, the distal parts of the limbs, and

841   the posterior part of the shell (Gaffney, 1972; Joyce & Lyson, 2015). Gaffney (1972) provided

842   illustrations of the skull that showed some bony contacts in dorsal and left lateral views, but did

843   not provide a description beyond the characters listed in his diagnosis. A detailed documentation

844   of the skull was, therefore, lacking prior to the present study.

845   We were able to identify most cranial sutures from the available µCT slice data, allowing us

846 to highlight in detail all bony contacts with exception of the one between the jugal and

847 quadratojugal. Our reconstruction shows several stark differences with the original one of

848 Gaffney (1972). The sutures on the skull surface are extremely difficult, if not impossible, to

849 interpret directly on the specimen, and we were only able to trace them with confidence by using

850 µCT scans and digitally reconstructing the skull bone by bone. We suspect that most of the

851 sutures identified by Gaffney actually correspond to cracks, of which a multitude cross the skull.

852 This explains the differences between his original interpretation and our reconstruction of the

853 skull. We here take the opportunity to review these differences based on the original restored

854 dorsal, ventral, and lateral views provided by Gaffney (1972; Fig. 8).

855   In dorsal view, Gaffney (1972) identified a large nasal that slightly contributes to the

856 anterodorsal margin of the orbit and contacts the maxilla laterally and the frontal dorsally (Fig.

857 8B). Although some uncertainty remains for the presence of a nasal-maxilla contact (see Nasal in

858 the Description section above), the nasal appears to be about half the size of that inferred by

859 Gaffney (1972) and contacts the prefrontal posterolaterally and the frontal posteriorly (Fig. 8C).

860 The posterior extent of the nasal is reduced compared to Gaffney's (1972) reconstruction and the

861 nasal is prevented from contributing to the orbital margin by an extended contact between the

862 prefrontal and the maxilla. Gaffney (1972) also interpreted the interorbital space as being fully

863 occupied by the frontals, the latter forming most of the dorsal margin of the orbit, and the dorsal

864 plate of the prefrontals as being reduced and not exposed on the dorsal skull (Fig. 8B). Our

865 reconstruction of that area alternatively shows that the dorsal plate of the prefrontal is actually

866 moderately exposed on the skull roof, forming the anterior half of the dorsal aspect of the orbital

867 margin, and that the frontal only slightly contributes to the latter by means of a short lateral

868   process (Fig. 8C). Gaffney (1972), additionally, inferred a point contact between the parietal and

869   squamosal along the anterolateral part of the upper temporal emargination on the left side of the

870   skull, while on the right side, this contact seems to be prevented by an extremely small

871   contribution of the postorbital to the upper temporal emargination (Fig. 8B). Instead, we identify

872   a contact between the parietal and squamosal on the right side of the skull, albeit small, but note

873   that too much damage affects the same area on the left side to allow a clear observation of the

874   contact there (Fig. 8C).

875   In ventral view, Gaffney (1972) only showed a maxilla-palatine contact along the medial

876   margin of the triturating surface and an opisthotic-quadrate contact posterior to the incisura

877   columella auris (Fig. 8E), which we are able to confirm. Gaffney (1972) furthermore traced

878   dashed lines posteromedially to the foramina palatinum posterius, indicating the likely position

879   of the pterygoid-pterygoid, pterygoid-palatine, and pterygoid-vomer sutures, with the anterior

880   limit of the pterygoids being located just posterior to the foramina palatinum posterius (Fig. 8E).

881   Our interpretation of that area differs in that we identify an anterior process of the pterygoids that

882   anteriorly protrudes between the palatines and contacts the vomer anterior to the anterior margin

883   of the foramina palatinum posterius (Fig. 8F). The suture between the pterygoid and vomer is,

884   therefore, located more anteriorly than Gaffney (1972) inferred, and the vomer appears to be

885   anteroposteriorly reduced compared to the original interpretation of that specimen.

886   In lateral view, the main difference lies in the interpretation of the sutures, contacts, and shape

887   of the jugal. Gaffney (1972) identified a rather anteroposteriorly elongate jugal that contributes

888   to the orbital margin and contacts the maxilla anteroventrally, the postorbital dorsally, and the

889   quadratojugal posteriorly (Fig. 8H). Instead, we suggest that the jugal is located slightly more

890   posterodorsal to what Gaffney (1972) interpreted, and is prevented from contributing to the orbit

891   by a short contact between the postorbital and maxilla along the posteroventral corner of the

892   orbit (Fig. 8I). We are also unable to identify a suture between the jugal and quadratojugal, and

893   suggest that the feature identified by Gaffney (1972) actually corresponds to a crack. Although

894   those differences and new interpretations do not considerably affect the previously suggested

895   affinities and phylogenetic position of *Trinitichelys hiatti* (see Phylogenetic relationships below),

896   our description and interpretations provide new insights into the anatomy of that taxon, allowing

897   us to compare it in detail to other known basal baenids and highlight intriguing similarities

898   shared by basal baenids with both pleurosternids and more advanced baenids (see Similarities

899   with pleurosternids and advanced baenids section below).

900

901   **Validity of *Arundelemys dardeni*, *Lakotemys australodakotensis*, and *Trinitichelys hiatti***

902   The reinterpretation of the cranial anatomy of *Trinitichelys hiatti* raises questions regarding the

903   validity of the subsequently named Early Cretaceous *Arundelemys dardeni* and *Lakotemys*

904   *australodakotensis*, as these two taxa were named presuming *Trinitichelys hiatti* to have a

905   morphology that indeed is very different, but herein shown to be incorrect. While several

906   features clearly distinguish *Lakotemys australodakotensis* from both *Arundelemys dardeni* and

907   *Trinitichelys hiatti*, such as the presence of a canalis caroticus lateralis, the absence of a lateral

908   process of the frontal, the ventral exposure of the parabasisphenoid for most of its length, the

909   formation of the foramen palatinum posterius by the palatine, and its older occurrence relative to

910   the other two taxa (Berriasian to Valanginian), the reconstructions of *Trinitichelys hiatti* and

911   *Arundelemys dardeni* show greater similarity that warrant further exploration. We therefore

912   thoroughly compare and discuss the differences and variation between these species based on

913   available 3D segmented skull models (Evers, Rollot & Joyce, 2021; this study), and provide a

914   rationale for retaining both as valid taxa.

915   While *Lakotemys australodakotensis* can easily be distinguished from *Arundelemys dardeni*

916   and *Trinitichelys hiatti*, the differences between the latter two are more subtle and we are not

917   able to identify clear differences in terms of bony contacts or bony contributions to most cranial

918   structures. We are nonetheless able to identify a multitude of more subtle differences that

919   generally pertain to the size and shape of several bones or bony structures: *Trinitichelys hiatti*

920   has a smaller orbit, a greater height of the maxilla below the orbit, smaller nasals that contact one

921   another for most of their length, a greater exposure of the prefrontal on the skull roof, a foramen

922   praepalatinum located closer to the premaxilla-vomer suture, a protruding ridge formed by the

923   nasals ventromedially that divides the nasal cavity into left and right halves, a taller premaxilla,

924   more transversely oriented canalis caroticus basisphenoidalis, a medial extension of the

925   descending process of the prefrontals within the nasal cavity but sheet-like ridge absent, a more

926   prominent processus trochlearis oticum, a transverse ridge along the posterodorsal surface of the

927   paroccipital process of the opisthotic, a poorly developed mediolateral ridge of the parietal

928   (which forms the posterior margin of the roof of the sulcus palatino-pterygoideus), absence of a

929   pterygoid contribution to the foramen anterius canalis nervi abducentis and canalis nervus

930   abducentis (which are completely formed by the parabasisphenoid), a slightly more reduced

931   ventral exposure of the parabasisphenoid, and a narrower incisura columella auris. Additionally,

932   the frontal of *Trinitichelys hiatti* has a straight suture anteriorly with the nasal, whereas the

933   frontal clearly protrudes anteriorly between the nasals in *Arundelemys dardeni* (Evers, Rollot &

934   Joyce, 2021), separating the latter along the midline for half of their length. Some of these

935   differences pertain to features known to vary intraspecifically in extant turtles (the trionychid

936   *Apalone ferox*: Dalrymple, 1977; the emydid *Pseudemys texana*: Bever, 2009a, the kinosternid

937   *Sternotherus odoratus*: Bever, 2009b) or to features that have been interpreted as such for fossils

938   (the protostegid *Rhinochelys pulchriceps*: Evers, Barrett & Benson, 2019). Some elements of

939   discussion have also been provided for baenids, such as *Palatobaena cohen* (Lyson & Joyce,

940   2009a) and *Saxochelys gilberti* (Lyson, Sayler & Joyce, 2019), but only the variable ventral

941   exposure of the parabasisphenoid that was observed in specimens of *Eubaena cephalica* is

942   relevant to us here (Rollot, Lyson & Joyce, 2018). We, therefore, base the following

943   comparisons on these studies.

944   As the holotype skull of both species are nearly identical in size (a 58 mm full skull length for

945   *Arundelemys dardeni* likely from the premaxilla to the posterior margin of what is preserved

946   from the skull, slightly posterior to the base of the condylus occipitalis according to Lipka et al.,

947   2006; a 56 mm premaxilla-condylus occipitalis length for *Trinitichelys hiatti* according to

948   Gaffney, 1972), we can dismiss the possibility that variation between them results from

949   ontogenetic changes. A ventromedially protruding ridge that separates the nasal cavity into left

950   and right halves, as observed in *Trinitichelys hiatti* but not in *Arundelemys dardeni*, is variably

951   present or absent in the *Pseudemys texana* specimens used by Bever (2009a), and this feature

952   therefore appears to be a poor taxonomic delineator. This is maybe unsurprising, as the ridge

953   likely serves as the attachment for an internarial septum, and soft tissue attachment sites are

954   known to frequently vary.

955   The degree of closure of the fissura ethmoidalis has been shown to exhibit some variability as

956   well, as it can be closed, partially closed, or narrowly open, and has its ventral margin that

957   continues to ossify late in postnatal ontogeny in *Pseudemys texana* (Bever, 2009a). In

958   *Arundelemys dardeni* and *Trinitichelys hiatti*, the medial extension of the descending process of

959   the prefrontal frames the fissura ethmoidalis. The fissura ethmoidalis is narrower in *Trinitichelys*

960   *hiatti*, which might be due to the presence of a sheet-like ridge on the medial extension of the

961   descending process, reminding of the differences observed between specimens of *Pseudemys*

962   *texana* (Bever, 2009a).

963   On the skull roof, the nasals of *Arundelemys dardeni* are larger than that of *Trinitichelys hiatti*

964   and they differ in shape, and the frontal of *Arundelemys dardeni* clearly protrudes anteriorly to

965   separate the nasals along the midline for half of their length, while the frontal of *Trinitichelys*

966   *hiatti* has an anterior straight suture with the nasals. The anterior process of the frontal, including

967   its anterior apex, have been shown to exhibit a great degree of variability in size and shape in

968   specimens of *Pseudemys texana* (Bever, 2009a), leading others to also consider great nasal

969   variation to be of limited taxonomic importance in a set of specimens of the fossil *Rhinochelys*

970   *pulchriceps* (Evers, Barrett & Benson, 2019).

971   On the otic capsule, the processus trochlearis oticum appears to be more prominent in

972   *Trinitichelys hiatti* than in *Arundelemys dardeni*, a difference that could potentially be a result of

973   sexual dimorphism, as is the case in *Pseudemys texana* in which the processus trochlearis oticum

974   is more distinctively sculptured in adult males than females (Bever, 2009a), but we are not able

975   to determine sexual dimorphism herein given that we only have two skulls for study and no

976   particular way to determine their sex. In *Apalone ferox*, Dalrymple (1977) similarly noticed

977   differences in the size of the processus trochlearis oticum, but suggested that these differences,

978   along with variation of other cranial features such as the size and shape of triturating surfaces,

979   height and width of the supraoccipital crest, and width of the temporal passageway, are actually

980   linked to the feeding mechanism.

981   Despite damage to the quadrate in *Arundelemys dardeni*, the incisura columella auris appears

982   to be intact and is broader than that of *Trinitichelys hiatti*. Variation to this feature has been

983   reported in *Sternotherus odoratus*, in which the incisura columella auris can be open, restricted

984   caudally by a descending secondary process of the quadrate, or restricted by an ascending

985   secondary process of the quadrate (Bever, 2009b). The foramen anterius canalis nervi abducentis

986   and anteriormost portion of the canalis nervus abducentis are completely formed by the

987   parabasisphenoid in *Trinitichelys hiatti*, while a pterygoid contribution to these structures is

988   present in *Arundelemys dardeni*. The amount of variation for this character is still poorly known

989   in paracryptodires, but in *Pseudemys texana*, in which the foramen anterius canalis nervi

990   abducentis and canalis nervus abducentis are generally completely formed by the

991   parabasisphenoid, at least one specimen has been observed to exhibit a pterygoid contribution to

992   the latter structures (Bever, 2009a). Finally, in the baenid *Eubaena cephalica*, the

993   parabasisphenoid of a newly discovered specimen has been shown to be slightly more elongate

994   than that of the holotype (Rollot, Lyson & Joyce, 2018), a very similar difference to that

995   observed between *Arundelemys dardeni* and *Trinitichelys hiatti*.

996   Among the 15 anatomical differences we observed between *Arundelemys dardeni* and

997   *Trinitichelys hiatti*, 8 have previously been described as variable features in some other turtles.

998   The remaining 7 differences have not been identified as being subject to variation in this

999   selection of turtles, which does not necessarily mean that other populations of the same species

1000   or other species of turtles could not actually show variability in some or all of these aspects of

1001   cranial morphology. Unfortunately, studies of cranial variation (postnatal ontogeny, sexual

1002   dimorphism, individual) remain extremely rare in turtles and assessing whether differences as

1003   observed herein between two fossil skulls are part of intraspecific variation or may actually

1004   represent interspecific variation is extremely challenging. More studies such as those on

1005   *Pseudemys texana* (Bever, 2009a) and *Sternotherus odoratus* (Bever, 2009b) are needed to better

1006   understand cranial morphological variability in turtles. While waiting for more insights into this

1007   subject, the numerous differences identified herein, albeit minor, are sufficient for now to keep

1008   both species as separate taxonomic entities, but we are aware that future studies on cranial

1009   morphological variability or additional fossil discoveries of material of *Arundelemys dardeni* and

1010   *Trinitichelys hiatti* might provide new arguments rather in favor of a synonymy.

1011   Finally, obtaining more precise data about the age of *Arundelemys dardeni* and *Trinitichelys*

1012   *hiatti* could help solving this issue. *Arundelemys dardeni* and *Trinitichelys hiatti* were found in

1013   Aptian-Albian layers of Maryland and Texas, respectively, but a more constrained age is not

1014   known yet, which impedes synonymizing or clearly distinguishing both taxa based on temporal

1015   considerations. *Arundelemys dardeni* was originally described as being late Albian to early

1016   Aptian in age (Lipka et al., 2006) but this was likely a typographical error, as a late Aptian to

1017   early Albian age was more recently mentioned for the layers in which the skull had been found

1018   (Frederickson, Lipka & Cifelli, 2018). *Trinitichelys hiatti* was first described as Albian in age by

1019   Gaffney (1972), although he also mentioned a slightly more precise age for the latter as being

1020   early Albian, based on Stephenson et al. (1942). Recent work, however, on the stratigraphy of

1021   Early Cretaceous formations in Arkansas, Oklahoma, and Texas, rather suggest a global Aptian-

1022   Albian age for the Antlers Formation, in which *Trinitichelys hiatti* was found (for additional

1023   geological information and summaries, see Cifelli et al., 1997; Nydam & Cifelli, 2002; Suarez et

1024   al., 2021). Given that the Aptian and Albian span over a time period of about 30 Mya and a

1025   restricted occurrence time is lacking for both taxa, synonymizing them appears to be out of the

1026   question until detailed stratigraphical data allow a determination of a precise age for

1027   *Arundelemys dardeni* and *Trinitichelys hiatti*.

1028

1029   **Similarities with pleurosternids and advanced baenids**

1030   The basal baenids *Arundelemys dardeni* and *Lakotemys australodakotensis* have recently been

1031   shown to share an intriguing combination of features either typical of pleurosternids or of

1032   baenids (Rollot et al., 2022). The redescription of *Trinitichelys hiatti* we provide herein allows

1033   extending these preliminary comparisons to the latter, and all basal baenid skulls known to date

1034   share this combination of features. The features of interest are summarized in Table 1 and we

1035   briefly discuss them here again. *Arundelemys dardeni*, *Lakotemys australodakotensis*, and

1036   *Trinitichelys hiatti* notably share with pleurosternids an anterior process of the pterygoid, a well-

1037   developed external process of the pterygoids, an ossified epipterygoid, relatively narrow

1038   triturating surfaces, and a moderate exposure of the prefrontal on the skull roof. Typical features

1039   of more advanced baenids that are shared by *Arundelemys dardeni*, *Lakotemys*

1040   *australodakotensis*, and *Trinitichelys hiatti* but not with pleurosternids are the presence of a

1041   posterior process of the pterygoid with an elongate contact with the basioccipital (reduced

1042   contact in pleurosternids), the absence of secondary basioccipital tubera formed by the

1043   parabasisphenoid along the posterior portion of its suture with the pterygoid (present in

1044   pleurosternids), and the absence of a basipterygoid process (present in pleurosternids). Given this

1045   combination of features, *Arundelemys dardeni* and *Lakotemys australodakotensis* were suggested

1046   to be morphological intermediates between pleurosternids and more advanced baenids (Rollot et

1047   al., 2022) and the fact that *Trinitichelys hiatti* shares with the latter two taxa the same similarities

1048 reinforces this hypothesis, which is discussed later in this paper (see Phylogenetic relationships

1049 below).

1050

1051 **Circulatory system**

1052 The circulatory system has been extensively used in turtle systematics for decades and the

1053 position of the foramen posterius canalis carotici interni was used to distinguish the primary

1054 groups of turtles from one another (McDowell, 1961; Gaffney, 1975; Sterli & de la Fuente,

1055 2010). Different interpretations for the circulatory system of paracryptodires, however, have

1056 recently been proposed, especially for the internal carotid artery and the presence versus absence

1057 of the palatine artery (Rollot, Evers & Joyce, 2021a). While a canal for the palatine artery, the

1058 canalis caroticus lateralis, was consistently identified in most described paracryptodires

1059 (Gaffney, 1972; Brinkman and Nicholls, 1991, 1993; Brinkman, 2003), a recent review of the

1060 circulatory system of that clade revealed that the palatine artery is actually lost in most

1061 paracryptodires, with the exception of the Late Jurassic pleurosternid *Uluops uluops* (Rollot,

1062 Evers & Joyce, 2021a). A canalis caroticus lateralis was also recently identified in the basal

1063 baenid *Lakotemys australodakotensis* (Rollot et al., 2022), and a canal for the palatine artery,

1064 therefore, is unambiguously present in two paracryptodires only. Although the putative repeated

1065 independent loss of the palatine artery within paracryptodires might appear surprising at first,

1066 independent losses of that artery have been documented in other turtle clades such as

1067 testudinoids, in which it is variably present, but greatly reduced in size, or absent (Rollot, Evers

1068 & Joyce, 2021a). In addition to this new source of variability identified within paracryptodires,

1069 we here also document differences in the morphology of the carotid pit and closure of the

1070 circulatory system between members of that clade that are relevant for the understanding of the

1071 evolution of the basicranial area of paracryptodires in particular, but also have the potential to

1072 provide new insights into the evolution of the basicranium in turtles in general. In the

1073 pleurosternids *Pleurosternon bullockii* (Evers, Rollot & Joyce, 2020) and *Uluops uluops* (Rollot,

1074 Evers & Joyce, 2021a), the carotid pit is posteriorly confluent with a sulcus that extends on the

1075 ventral surface of the skull along the pterygoid-parabasisphenoid suture and which likely held

1076 the internal carotid artery. The carotid pit of *Trinitichelys hiatti* differs from that condition in that

1077 it is slightly smaller than that of *Pleurosternon bullockii* and *Uluops uluops*, and posteriorly

1078 constricted by extensions of the pterygoid and parabasisphenoid that partially cover the posterior

1079 aspect of the cavity and separates it from a narrow, posteriorly directed carotid groove. In

1080 *Lakotemys australodakotensis*, it appears that a true carotid pit and carotid groove are absent and

1081 the foramen posterius canalis nervi vidiani, foramen posterius canalis carotici lateralis, and

1082 foramen posterius canalis carotici basisphenoidalis are located in a shallow depression instead

1083 (Rollot et al., 2022). In *Arundelemys dardeni*, on the left side, a relatively large carotid pit is

1084 present, but is posteromedially slightly constricted by a small medial extension of the pterygoid

1085 (Evers, Rollot & Joyce, 2021), a similar morphology to that of *Trinitichelys hiatti*. We interpret

1086 the observed constriction along the posterior margin of the carotid pit in *Arundelemys dardeni*

1087 and *Trinitichelys hiatti* as a putative intermediate ossification stage of the basicranium between

1088 the fully open carotid pit of pleurosternids and the anteriorly completely enclosed circulatory

1089 system of more advanced baenids. This hypothesis is also supported by differences between

1090 pleurosternids and baenids regarding the ventral exposure of the foramen distalis nervi vidiani. In

1091 *Uluops uluops*, the foramen distalis nervi vidiani, which allows the passage of the vidian nerve

1092 from the canalis pro ramo nervi vidiani into either the carotid groove or the canalis caroticus

1093 internus, is located in the carotid groove at the posterior end of the carotid pit (Rollot, Evers &

1094   Joyce, 2021a), while in more advanced baenids, the foramen distalis nervi vidiani is not ventrally

1095   exposed and the vidian nerve, by means of the canalis pro ramo nervi vidiani, joins the canalis

1096   caroticus internus just anterior to the foramen posterius canalis carotici interni (Brinkman &

1097   Nicholls, 1991; Brinkman & Nicholls, 1993; Brinkman, 2003; Rollot, Lyson & Joyce, 2018;

1098   Rollot, Evers & Joyce, 2021a). An increased ossification of the basicranium in advanced

1099   baenids, therefore, might have led to the complete enclosure of the circulatory system and the

1100   presence of a true canalis caroticus internus and foramen posterius canalis carotici interni,

1101   ventrally covering the junction point between the canalis pro ramo nervi vidiani and internal

1102   carotid artery system.

1103

1104   **Phylogenetic relationships**

1105   The first phylogenetic analysis under equal weighting resulted in 2497 most parsimonious

1106   trees with 360 character-state transitions. The strict consensus tree is shown in Fig. 9A. Several

1107   polytomies are apparent at the base of the tree, at the base of baenoids, and within baenodds. The

1108   "pruned trees" function in TNT was used to identify three rogue taxa in the tree, namely

1109   *Pleurosternon moncayensis*, *Scabremys ornata*, and *Goleremys mckennai*. The obtained reduced

1110   most parsimonious tree has 477 character-state transitions. The new reduced strict consensus tree

1111   obtained without these taxa is shown in Fig. 9B and the time-calibrated tree with occurrence

1112   times plotted to stratigraphic time in Fig. 10. The exclusion of the aforementioned problematic

1113   taxa allowed a better resolution at the base of baenoids, with the resolution of the relationships

1114   between *Riodevemys inumbragigas*, *Toremys cassiopeia*, and *Pleurosternon bullockii*, and

1115   slightly improved the resolution within baenodds, by grouping *Denazinemys nodosa*, *Boremys*

1116   *grandis*, and *Boremys pulchra* together. The second phylogenetic analysis was performed under

1117   implied weighting with a K value of 12 and resulted in 10 most parsimonious trees. The strict

1118   consensus tree is shown in Fig. 11A. *Pleurosternon moncayensis* and *Scabremys ornata* were

1119   identified as problematic taxa, and the new reduced strict consensus tree obtained without them

1120   is shown in Fig. 11B. The tree with occurrence times plotted to stratigraphic time is shown is

1121   Fig. 12. The new strict consensus tree is almost fully resolved, with only one polytomy

1122   remaining between *Neurankylus eximius*, *Neurankylus torrejonensis*, and baenodds.

1123   The results of the two sets of analyses are overall similar with regard to the topology of

1124   *Helochelydridae* and *Baenoidea* as both of them retrieved helochelydrids as basal-branching

1125   *Paracryptodira* in a more inclusive position than *Baenoidea*. Within *Baenoidea*, *Baenidae*

1126   include *Lakotemys australodakotensis*, *Trinitichelys hiatti*, and *Arundelemys dardeni* as basal

1127   branching taxa and the clade is well-supported (10 synapomorphies in the reduced equally

1128   weighted strict consensus tree, 9 in the reduced implied-weighted one). Despite the subtle nature

1129   of morphological variation we identified between *Arundelemys dardeni* and *Trinitichelys hiatti*

1130   (see above), *Trinitichelys hiatti* is retrieved as sister taxon to *Lakotemys australodakotensis* at the

1131   base of *Baenidae* in both analyses, whereas *Arundelemys dardeni* is always retrieved in a less

1132   inclusive position relative to the latter two taxa within baenids. These results corroborate our

1133   suggestion to keep both taxa as separate taxonomic entities, but we note that different

1134   optimizations of shell-based characters in *Arundelemys dardeni*, in which the carapace and

1135   plastron are unknown, might yield to different affinities between *Lakotemys australodakotensis*,

1136   *Trinitichelys hiatti*, and *Arundelemys dardeni* at the base of baenids. *Pleurosternidae*, the sister

1137   group to *Baenidae*, contain *Riodevemys inumbragigas*, *Toremys cassiopeia*, and *Pleurosternon*

1138   *bullockii*. *Dinochelys whitei*, *Glyptops ornatus*, *Dorsetochelys typocardium*, and *Uluops uluops*,

1139   taxa that were often interpreted as pleurosternids, are retrieved in both analyses as basal

1140   branching paracryptodires in a paraphyletic succession outside of *Baenoidea*. We note that both

1141   *Pleurosternidae* and *Baenoidea* are only supported by one and two synapomorphies,

1142   respectively, and that the characters of interest are not universally preserved in the taxa retrieved

1143   as *Pleurosternidae* or just outside of *Baenoidea* (see below for further discussion about the

1144   synapomorphies). *Helochelydridae* are well-supported in both analyses (10 synapomorphies

1145   retrieved for the reduced equally weighted strict consensus tree versus 7 in the reduced implied

1146   weighted one), but their position as basal branching paracryptodires differs from latest insights

1147   into paracryptodiran relationships that retrieved helochelydrids deeply nested within

1148   *Pleurosternidae* (Rollot, Evers & Joyce, 2021a). This difference can be explained by the

1149   inclusion of additional stem testudinatans (i.e., meiolaniforms, sichuanchelyids, *Eileanchelys*

1150   *waldmani*) that likely pulled *Helochelydridae* outside of *Pleurosternidae* and *Baenoidea*, but still

1151   recovering them as *Paracryptodira*.

1152   The main difference between the analyses presented herein is the placement of

1153   *Compsemydidae*, which are retrieved either as the most basal branching clade of *Paracryptodira*

1154   (Fig. 11B) or outside of *Paracryptodira* in a polytomy with *Peligrochelys walshae*, *Chubutemys*

1155   *copelloi*, *Mongolochelys efremovi*, *Sichuanchelys palatodentata*, and *Eileanchelys waldmani*. As

1156   for the placement of *Helochelydridae*, the addition of basal testudinatans likely dragged

1157   *Compsemydidae* down from the previously suggested more advanced position within baenids

1158   (Rollot, Evers & Joyce, 2021a). Despite the inclusion of basal turtles, *Kallokibotion bajazidi* is

1159   still retrieved as the most basal member of *Compsemydidae*, confirming a previous hypothesis of

1160   its phylogenetic affinities (Rollot, Evers & Joyce, 2021a), and *Compsemydidae* are well

1161   supported in both analyses (13 synapomorphies in the reduced equally weighted strict consensus

1162   tree, 8 in the reduced implied weighted one). In the case where *Compsemydidae* are not retrieved

1163   as *Paracryptodira*, i.e., in the reduced equally weighted strict consensus tree, *Paracryptodira*,

1164   with *Helochelydridae* as its most basal branching clade, are united by 8 synapomorphies. In the

1165   reduced implied weighted strict consensus tree, only 2 synapomorphies unite paracryptodires

1166   with *Compsemydidae* as they are the most basal representatives, but the synapomorphies that

1167   unite helochelydrids with less inclusive paracryptodires are nearly identical to those in the

1168   former analysis. Future studies that include a larger sample of basal turtles and possibly basal

1169   *Testudines* are expected to clarify the phylogenetic placement of *Compsemydidae* and its

1170   affinities with *Paracryptodira*.

1171   As already mentioned above, our analyses consistently retrieved the same topologies for

1172   *Helochelydridae* and *Baenoidea*, and the synapomorphies uniting *Helochelydridae*, *Baenoidea*,

1173   *Baenidae*, and *Pleurosternidae* are nearly if not fully identical. *Baenidae* are well-supported by

1174   at least 9 synapomorphies in both the equally weighted and implied weighted strict consensus

1175   trees: a reduced lingual ridge, only developed anteriorly (character 5, state 1; absent in

1176   *Palatobaena* spp.), a ventral extension of the jugal (character 18, state 0; absent in some baenids

1177   but mostly due to intraspecific variation), a well-developed posterior process of the pterygoid

1178   with an extensive contact with the basioccipital (character 26, state 3), nasals that extend as far

1179   anteriorly as the premaxillae (character 68, state 0; nasal do not extend as far anteriorly as the

1180   premaxillae in baenodds), present and extensive contact of the axillary buttresses with the costals

1181   (character 84, state 1), present and extensive inguinal buttresses (character 85, state 1), a deep

1182   upper temporal emargination relative to the incisura columella auris (character 95, state 2),

1183   absence of basipterygoid processes (character 96, state 2), and absence of a second pair of

1184   anterior tubercula basioccipitale (character 97, state 0). A single additional synapomorphy is

1185   found in the equally weighted strict consensus tree and not the implied weighted one, the absence

1186   of epiplastral processes (character 45, state 1). The presence of extensive axillary and inguinal

1187   buttresses, the elongate pterygoid-basioccipital contact, and the absence of epiplastral processes

1188   are features that have been commonly used to distinguish *Baenidae* from *Pleurosternidae* within

1189   *Baenoidea*, and retrieving them as synapomorphies for *Baenidae* therefore does not come as a

1190   surprise. The character pertaining to the depth of the upper temporal emargination was modified

1191   recently (see Rollot, Evers & Joyce, 2021a) in order to take into account more precisely the

1192   extent of the upper emargination, and our analyses retrieved a deep upper temporal emargination

1193   as a synapomorphy of baenids (with the exception of *Hayemys latifrons* and *Palatobaena*

1194   *gaffneyi*). All the other turtles in our dataset are characterized by an upper emargination that is

1195   shallow to absent, with the exception of *Pleurosternon bullockii*, in which it is moderate and, in

1196   lateral view, ends between the anterior margin of the cavum tympani and the incisura columella

1197   auris. Similarly, the absence of a basipterygoid process unambiguously characterizes all baenids,

1198   which contrasts with the condition observed in pleurosternids and basal branching

1199   paracryptodires just outside of *Baenoidea*, in which the basipterygoid process is still present

1200   albeit reduced. The presence versus absence of anterior tubercula basioccipitale has recently

1201   been introduced as a character in matrices built to investigate paracryptodiran relationships

1202   (Rollot, Evers & Joyce, 2021a), and the tubercula are unambiguously absent in baenids, but

1203   present in all other paracryptodires with the exception of *Compsemydidae*. The extension of the

1204   nasals as far anteriorly as the premaxillae is retrieved as a synapomorphy for *Baenidae*, but this

1205   feature is only observed in basal baenids, as baenodds but also various basal branching

1206   paracryptodires and pleurosternids have nasals that do not extend as far anteriorly as the

1207   premaxillae. Finally, baenids are also united by a reduced lingual ridge (complete in *Peckemys*

1208 *brinkman*; absent in *Palatobaena* spp.), but this character seems to be somewhat more variable

1209 outside of *Baenidae* in our sample.

1210   The clades *Pleurosternidae* and *Baenoidea* are both weakly supported in our analyses.

1211 *Pleurosternidae* are only supported by one synapomorphy, wider than long vertebrals (character

1212 39, state 0), while *Baenoidea* are united by two synapomorphies, a moderately deep upper

1213 temporal emargination relative to the incisura columella auris (character 95, state 1) and the

1214 absence of a canal for the palatine artery (character 100, state 1). Our analyses retrieved

1215 exclusively cranial characters as synapomorphies for *Baenoidea*, but the pleurosternids

1216 *Riodevemys inumbragigas* and *Toremys cassiopeia* are actually solely known by shell material.

1217 These characters could, therefore, not be originally scored in our matrix for the aforementioned

1218 taxa, and were optimized *a posteriori* by the software as synapomorphies for *Baenoidea* despite

1219 the lack of information for *Riodevemys inumbragigas* and *Toremys cassiopeia*. A similar issue

1220 affects the placement of *Uluops uluops*, a taxon that was commonly found as a member of

1221 *Pleurosternidae* in phylogenetic analyses of paracryptodiran relationships, but that is retrieved as

1222 a basal branching paracryptodire just outside of *Baenoidea* in our analyses. The dimensions of

1223 the vertebral scutes, of which character state 0 (wider than long) is identified as the unique

1224 synapomorphy of *Pleurosternidae*, remain unknown for *Uluops uluops* as this taxon is

1225 exclusively known by cranial material. It is therefore likely that small changes in the matrix

1226 could bring some of the taxa retrieved just outside of *Baenoidea* into *Pleurosternidae*, and vice

1227 versa, and the addition of stem Testudinata in our matrix might have dragged down some

1228 paracryptodiran taxa, again, which results in *Pleurosternidae* to only include three taxa in our

1229 analyses.

1230   Our analyses recovered *Helochelydridae* as basal branching paracryptodires in a more

1231   inclusive position than *Dinochelys whitei*, *Glyptops ornatus*, and the clade formed by

1232   *Dorsetochelys typocardium* and *Uluops uluops*. We retrieved 10 synapomorphies that unite

1233   helochelydrids in the equally weighted strict consensus tree versus 7 in the implied weighted

1234   strict consensus tree. The 7 synapomorphies retrieved in the implied weighted strict consensus

1235   tree are all also found in the equally weighted strict consensus tree, and those common

1236   synapomorphies are as follows: a large contribution of the frontal to the orbit (character 15, state

1237   2), absence of a labial ridge on the mandible (character 70, state 1), presence of articular surfaces

1238   on the cervical vertebrae (procoelous or opisthocoelous; character 76, state 1), a shell sculpturing

1239   made of raised tubercles that easily break (character 78, state 2), presence of three suprapygals

1240   (character 86, state 2), presence of an entoplastral scute (character 102, state 1), and presence of

1241   V-shaped anterior peripherals (character 103, state 1). The three additional synapomorphies in

1242   the equally weighted strict consensus tree are the absence of epiplastral processes (character 45,

1243   state 1), large mandibular condyles (character 60, state 1), and a large external narial opening

1244   (character 73, state 1). The frontal contribution to the orbit appears to be quite variable in our

1245   dataset. The absence of a labial margin on the mandible seems, at first glance, to be a relatively

1246   solid character among our sample as all turtles in a more basal position than helochelydrids and

1247   for which this character can be scored, actually possess a labial margin on the mandible.

1248   However, we note that this feature is homoplastically shared with some baenids and that lots of

1249   missing data (about 50%) remain in our dataset for this character. The presence of articular

1250   surfaces on the cervical vertebrae is even more poorly characterized in our matrix, as this feature

1251   remains unknown for 75% of the taxa used in our study. On the other hand, features such as the

1252   sculpturing of the shell made of raised tubercles, presence of three suprapygals, presence of an

1253   entoplastral scute, and presence of V-shaped anterior peripherals are robust and reliable, as they

1254   are diagnostic of that clade (Joyce, 2017).

1255   *Compsemydidae*, including *Kallokibotion bajazidi* as its most basal representative, are

1256   alternatively found outside of *Paracryptodira* in a polytomy with basal testudinatans (reduced

1257   equally weighted strict consensus tree, Fig. 9B) or as the most basal branching clade of

1258   *Paracryptodira* (reduced implied weighted strict consensus tree, Fig. 11B). In the reduced

1259   equally weighted strict consensus tree, *Compsemydidae* are supported by 13 synapomorphies, of

1260   which 8 also support this clade in the implied weighted strict consensus tree. The

1261   synapomorphies common to both analyses are as follows: absence of a posterodorsal extension

1262   of the quadratojugal (character 19, state 1), presence of an elongate process of the pterygoid with

1263   an extensive contact with the basioccipital (character 26, state 3), absence of cervical scutes

1264   (character 38, state 0), absence of a nuchal contribution to the anterior margin of the shell

1265   (character 80, state 1), presence and extensive contact of the axillary buttresses with the costals

1266   (character 84, state 1), presence of extensive inguinal buttresses (character 85, state 1), absence

1267   of a contact between peripheral I and costal I (character 90, state 0), and the superficial enclosure

1268   of the cavum tympani by a squamosal-quadrate contact (character 105, state 1). The following

1269   synapomorphies additionally unite *Compsemydidae* in the equally weighted strict consensus tree

1270   only: a long preorbital length (character 2, state 1), a midline contact of the pterygoid of 40-70%

1271   of their length (character 25, state 2), the anterior margin of marginal I mainly located over

1272   peripheral I (character 44, state 2), the absence of epiplastral processes (character 45, state 1),

1273   and an entoplastron with equal dimensions (character 93, state 1; becomes broader than long in

1274   more derived compsemydids). The absence of a posterodorsal extension of the quadratojugal is

1275   not unique to compsemydids as it is homoplastically shared with *Sichuanchelys palatodentata*,

1276   *Baena arenosa*, and *Chisternon undatum*. However, little is actually known with certainty about

1277   the cranial anatomy of the latter two taxa, and this feature therefore appears to be a robust

1278   synapomorphy in the context of our analysis. The presence of an elongate process of the

1279   pterygoid is shared with baenids, but clearly distinguishes compsemydids from other basal turtles

1280   as these latter taxa lack such a posterior extension of the pterygoid and extensive contact with the

1281   basioccipital. The condition observed in *Baenidae* and *Compsemydidae*, therefore, appears to be

1282   more advanced than any other stem turtle in our dataset. Similarly, compsemydids share with

1283   baenids the presence of extensive axillary and inguinal buttresses. The aforementioned three

1284   features were found as synapomorphies of *Baenidae* including *Compsemydidae* in recent

1285   analyses (see Rollot, Evers & Joyce, 2021a), but as already mentioned above, the inclusion of

1286   additional basal testudinatans likely pulled *Compsemydidae* down outside of *Baenidae*, leading

1287   to a different result herein and the homoplastic sharing of those features between the two clades.

1288   The absence of cervical scutes distinguishes compsemydids from nearly any other turtle in our

1289   dataset, and it appears to be a relatively solid character to unite *Compsemydidae*, although we

1290   note that two pleurosternids, *Pleurosternon bullockii* and *Toremys cassiopeia*, also lack cervical

1291   scutes. The absence of a nuchal contribution to the anterior margin of the shell, absence of a

1292   contact between peripheral I and costal I, and superficial enclosure of the cavum tympani by a

1293   squamosal-quadrate contact are unique to *Compsemydidae* and represent robust synapomorphies

1294   for the clade. The placement of *Kallokibotion bajazidi* within *Compsemydidae* was already

1295   strongly supported in a previous analysis of paracryptodiran relationships (Rollot, Evers &

1296   Joyce, 2021a), but this result needed to be tested in a global context as the study of interest did

1297   not include non-paracryptodiran taxa, with the exception of the outgroups *Proganochelys*

1298   *quenstedti* and *Kayentachelys aprix.* Despite the inclusion of *Meiolaniformes*, *Sichuanchelyidae*,

1299   and *Eileanchelys waldmani* in a modified version of the matrix used by Rollot, Evers & Joyce

1300   (2021a), *Kallokibotion bajazidi* is still retrieved as a basal *Compsemydidae* herein. This

1301   relationship remains strongly supported and holds true independently of the placement of

1302   compsemydids within *Paracryptodira* or not, showing that the inclusion of *Kallokibotion*

1303   *bajazidi* within *Compsemydidae* is robust.

1304   The varying placement of *Compsemydidae* in our analyses affects the synapomorphies

1305   retrieved as uniting *Paracryptodira*, but most of the synapomorphies of the latter found in the

1306   analysis that recovers *Helochelydridae* as the most basal branching paracryptodiran clade still

1307   unite helochelydrids and less inclusive paracryptodires in the analysis under implied weighting,

1308   where *Compsemydidae* are retrieved as *Paracryptodira*. In the equally weighted strict consensus

1309   tree, *Paracryptodira* is found within a polytomy with several basal turtles and *Compsemydidae*,

1310   and united by 8 synapomorphies: an elongate skull shape (character 1, state 1), absence of a

1311   lingual ridge (character 5, state 2; present but reduced in most baenids), a small contribution of

1312   the frontal to the orbit (character 15, state 1), absence of a jugal contribution to the orbit

1313   (character 17, state 2; but small to absent in several taxa), absence of a ventral process of the

1314   jugal (character 18, state 1; present in most baenids), a Z-shaped dentary-surangular contact

1315   (character 31, state 0), presence of a distinct skull sculpturing (character 77, state 1; absent in

1316   derived baenids), and presence of a pair of anterior tubercula basioccipitale on the

1317   parabasisphenoid (character 97, state 1; absent in baenids). The extent of the contribution of the

1318   frontal to the orbit appears to be highly variable within paracryptodires. A small contribution is

1319   retrieved as a paracryptodiran synapomorphy, but this contribution is actually large in

1320   helochelydrids, the most basal branching paracryptodiran clade in our analysis. Other less

1321   inclusive basal branching paracryptodires and pleurosternids indeed have a small contribution of

1322   the frontal to the orbit, but all character states are variably present in baenids, and this feature

1323   therefore appears not to be a good diagnostic character for paracryptodires. The absence of a

1324   jugal contribution to the orbit is retrieved as synapomorphic of paracryptodires, and contrasts

1325   from the condition observed in all other basal testudinatans including *Compsemydidae*, in which

1326   the jugal contribution to the orbit is large. The jugal of helochelydrids is indeed excluded from

1327   the orbital margin, but this condition is not universally found in other basal branching

1328   paracryptodires. Within *Baenoidea*, the jugal is again excluded from the orbital margin in

1329   *Pleurosternidae* and the most basal baenids, but small to large contribution or a complete

1330   absence of a contribution to the orbital margin are all found within advanced baenids. This

1331   feature thus also appears not to be a reliable diagnostic character. Similarly, the ventral process

1332   of the jugal is absent in pleurosternids and basal branching paracryptodires (polymorphic in

1333   *Naomichelys speciosa*), and present in most baenids (also polymorphic in some baenodds), but

1334   this character could only be scored for one third of the non-baenid taxa retrieved as

1335   paracryptodires herein, and the interpretation of this character therefore needs to be taken with

1336   caution. Likewise, the shape of the dentary-surangular contact remains unknown in more than

1337   two thirds of all taxa retrieved as paracryptodires herein, so that caution is required for this

1338   character as well. On the other hand, the 4 other synapomorphies identified in the strict

1339   consensus tree seem to be more robust and less variable within the tree. The skull of all basal

1340   branching paracryptodires (with the exception of *Uluops uluops*), pleurosternids, and the two

1341   most basal baenids *Lakotemys australodakotensis* and *Trinitichelys hiatti* is elongate, and change

1342   in the skull shape appears to occur with *Arundelemys dardeni*, of which the skull is more wedge-

1343   shaped as all more advanced baenids (although considered as rounded in our matrix for

1344   *Palatobaena* spp., but still not elongate). The lingual ridge is completely absent in all basal

1345   branching paracryptodires (again, with the exception of *Uluops uluops*) and pleurosternids, but is

1346   present albeit reduced in most baenids (absent in *Palatobaena* spp.). Anterior tubercula

1347   basioccipitale are present in all basal branching paracryptodires and pleurosternids and appear to

1348   be subsequently lost in baenids. Finally, all basal branching paracryptodires, pleurosternids and

1349   basal baenids have their bone surface decorated by a distinct, albeit variable, sculpturing which

1350   tends to disappear towards more advanced baenids.

1351   In the implied weighted strict consensus tree, *Paracryptodira* includes *Compsemydidae* as its

1352   most basal branching clade but is only united by 2 synapomorphies, i.e., a moderately long

1353   posterior process of the pterygoid with a point contact with the basioccipital (character 26; state

1354   2; this contact with the basioccipital becomes independently elongate in compsemydids and

1355   baenids) and an entoplastron about as wide as long (character 93, state 1). The extent of the

1356   posterior process of the pterygoid is actually variable within *Paracryptodira*. In *Compsemydidae*,

1357   i.e., the most basal branching clade of paracryptodires in this analysis, the posterior process of

1358   the pterygoid is well developed and has an elongate contact with the basioccipital. In

1359   *Helochelydridae*, the following less inclusive clade within *Paracryptodira*, the posterior

1360   morphology of the pterygoid is greatly variable, as a point contact with the basioccipital occurs

1361   in *Helochelydra nopcsai*, whereas this contact is completely absent in *Naomichelys speciosa*, and

1362   the condition remains unknown in *Aragochersis lignitesta*. The posterior process of the pterygoid

1363   is moderately developed in other less inclusive basal branching paracryptodires, as well as in

1364   *Pleurosternidae* (although unclear in *Pleurosternon bullockii*), while *Baenidae* homoplastically

1365   exhibit the same condition as *Compsemydidae*. We, however, note that the change in the

1366   posterior extent of the pterygoid along the turtle stem still highlights an intriguing evolutionary

1367   trend. In most of the basal testudinatans included in our study, the pterygoid lacks an extended

1368 posterior process and the prootic is apparent in ventral view. In *Mongolochelys efremovi*, for

1369 instance, the posterior process of the pterygoid is more developed than in other basal Testudinata

1370 and the prootic is concealed in ventral view, but a posterior contact with the basioccipital is

1371 prevented by a small posterolateral lappet of the parabasisphenoid. A more advanced condition is

1372 then observed in pleurosternids and some basal paracryptodires, where a pterygoid-basioccipital

1373 contact is apparent, and this contact becomes even more extensive in baenids and

1374 compsemydids, for most of or even the entire length of the basioccipital plate. The second

1375 synapomorphy, i.e., an entoplastron that is as wide as long, is even more variable within

1376 *Paracryptodira* than the other one. The entoplastron is indeed as wide as long in *Kallokibotion*

1377 *bajazidi* but broader than long in other compsemydids. Similarly, in helochelydrids, the

1378 entoplastron is as wide as long in *Aragochersis lignitesta* but longer than broad in *Helochelydra*

1379 *nopcsai* and *Naomichelys speciosa*. In the less inclusive basal branching paracryptodires

1380 *Dinochelys whitei* and *Glyptops ornatus*, the entoplastron is as wide as long. Within *Baenoidea*,

1381 the entoplastron is broader than long in pleurosternids (although polymorphic and sometimes as

1382 wide as long in *Pleurosternon bullockii*), and in baenids, the entoplastron is variably either

1383 longer than broad or as wide as long, and this character could not be scored for about half of

1384 them. At the end, the synapomorphies retrieved in the analysis under equal weighting, in which

1385 *Paracryptodira* do not include *Compsemydidae*, appear to be more robust and reliable

1386 considering our knowledge about the evolutionary history of paracryptodiran sub-clades (i.e.,

1387 skull shape, anterior tubercula basioccipitale, skull sculpturing).

1388   The matrix used herein includes the most recent and novel insights into the cranial and shell

1389 anatomy of paracryptodires. As we included several basal testudinatans in our sample, the

1390 placement of *Kallokibotion bajazidi* within *Compsemydidae* and that of *Helochelydridae* as basal

1391   branching *Paracryptodira*, are robust to the inclusion of taxa that represent previously proposed

1392   close relatives outside of *Paracryptodira*. Other aspects, such as the synapomorphies of

1393   *Paracryptodira*, *Baenoidea*, and *Pleurosternidae*, or the taxonomic composition of

1394   *Pleurosternidae*, are dependent on the taxonomic content of these groups, as the synapomorphies

1395   are changing when different taxa are added to a pre-defined clade.

1396   A similar issue was highlighted by the recently published study of Tong et al. (2022), in

1397   which clear synapomorphic characters were not retrieved for *Paracryptodira* and *Baenoidea*

1398   despite the use of a different matrix. One of the analyses provided by the aforementioned study

1399   also yielded an alternative phylogenetic hypothesis with the placement of *Compsemydidae* as

1400   *Pan-Pleurodira* and that of *Kallokibotion bajazidi* within *Pleurosternidae*. Such affinities were

1401   not retrieved in the present study, but we acknowledge that the inclusion of representatives of the

1402   turtle crown and putative stem groups (e.g. *Thalassochelydia*, *Sinemydidae*, *Macrobaenidae*, and

1403   *Xinjiangchelyidae*) to our matrix might impose more constraints on some parts of the tree and

1404   provide alternative phylogenetic hypotheses. A redescription of the skulls of *Dinochelys whitei*,

1405   *Glyptops ornatus* and *Dorsetochelys typocardium*, which are also included in the phylogenetic

1406   analyses of Tong et al. (2022), is also expected to provide new insights into the cranial anatomy

1407   of these taxa and, consequently, might allow additional characters to be scored and more

1408   precisely identify the synapomorphies of *Baenoidea* and *Pleurosternidae*. Finally, the study of

1409   phylogenetic affinities of paracryptodires in a global context should be accompanied by a

1410   specific focus on *Eileanchelys waldmani* and *Heckerochelys romani*, two of the oldest known

1411   aquatic turtles that lived during the Middle Jurassic (Sukhanov, 2006; Gordenko, 2008; Anquetin

1412   et al., 2009; Anquetin, 2010). *Pleurosternidae* are known to be aquatic and were relatively

1413   widespread along the Jurassic-Cretaceous boundary both in North America and Europe, but

1414   study of fragments has shown that representatives of the group were likely present in the Middle

1415   Jurassic of England (Scheyer & Anquetin, 2008). Given that *Eileanchelys waldmani* was found

1416   in Scotland and several pleurosternid taxa were collected around the Jurassic-Cretaceous

1417   boundary in western Europe including England, putative close relationships between all aquatic

1418   taxa of that area have to be considered in future studies. *Heckerochelys romani* is known by

1419   dozens of fragments, but only a few have been described and illustrated, and a reanalysis of all

1420   the available material, including μCT scans of the skull material, could provide new insights into

1421   the evolution and diversification of aquatic turtles.

1422

1423   CONCLUSION

1424   Here we provide the first detailed description of the skull of the Early Cretaceous (Aptian-

1425   Albian) baenid *Trinitichelys hiatti*. We propose an alternative interpretation of the cranial

1426   osteology of *Trinitichelys hiatti* to the original publication and highlight many similarities with

1427   the recently described basal baenid skulls of *Arundelemys dardeni* and *Lakotemys*

1428   *australodakotensis*. *Arundelemys dardeni* and *Trinitichelys hiatti* appear to be nearly identical

1429   and can only be distinguished by minor differences. Additional insights, particularly regarding

1430   the anatomy of the posterior portion of the skull and the age of both taxa, will allow future

1431   clarification if synonymizing the latter two names is warranted. *Trinitichelys hiatti* also shares

1432   with *Arundelemys dardeni* and *Lakotemys australodakotensis* an intriguing combination of

1433   features that are typical of both *Pleurosternidae* or *Baenidae*. The circulatory system of

1434   *Trinitichelys hiatti*, especially the morphology of the carotid pit, is suggested to represent an

1435   intermediate condition between that of pleurosternids (e.g., *Uluops uluops*) and baenids (e.g.,

1436   *Eubaena cephalica*). We also provide an expanded phylogenetic analysis that includes a

1437 selection of stem turtles and latest described and valid paracryptodiran species. We find

1438 *Trinitichelys hiatti* as sister taxon to *Lakotemys australodakotensis* at the base of *Baenidae* and

1439 retrieve *Helochelydridae* along the stem of *Baenoidea*, but recover *Dinochelys whitei*, *Glyptops*

1440 *ornatus*, *Dorsetochelys typocardium*, and *Uluops uluops* as basal branching *Paracryptodira*. The

1441 study of paracryptodiran relationships in a global context along with some of the oldest known

1442 aquatic stem turtles is expected to provide new insights into the evolution of paracryptodires and

1443 the diversification of an aquatic lifestyle in *Testudinata*.

1444

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1450

1451 INSTITUTIONAL ABBREVIATIONS

1452 DORCM, Dorset Museum, Dorchester, England

1453 MCZ, Harvard Museum of Comparative Zoology, Cambridge, Massachusetts, U.S.A.

1454 DMNH, Denver Museum of Nature and Science, Denver, Colorado, U.S.A.

1455

1456 Data availability – The μCT dataset and 3D models are available at MorphoSource under the

1457 MCZ Vertebrate Paleontology Organization

1458 (https://www.morphosource.org/projects/000417478?; Media ID 000417484,

1459 DOI10.17602/M2/M417484). The 3D models generated for our study:

1460   Right Exoccipital, Media ID 000427919, DOI10.17602/M2/M427919;

1461   Right Frontal, Media ID 000427922, DOI10.17602/M2/M427922;

1462   Right Hyoid, Media ID 000427925, DOI10.17602/M2/M427925;

1463   Right Jugal and Quadratojugal, Media ID 000427941, DOI10.17602/M2/M427941;

1464   Right Maxilla, Media ID 000428582, DOI10.17602/M2/M428582;

1465   Right Nasal, Media ID 000430164, DOI10.17602/M2/M430164;

1466   Right Opisthotic, Media ID 000430167, DOI10.17602/M2/M430167;

1467   Right Palatine, Media ID 000430170, DOI10.17602/M2/M430170;

1468   Right Parietal, Media ID 000430173, DOI10.17602/M2/M430173;

1469   Right Postorbital, Media ID 000430176, DOI10.17602/M2/M430176;

1470   Right Prefrontal, Media ID 000430179, DOI10.17602/M2/M430179;

1471   Right Premaxilla, Media ID 000430182, DOI10.17602/M2/M430182;

1472   Right Prootic, Media ID 000430185, DOI10.17602/M2/M430185;

1473   Right Pterygoid, Media ID 000430188, DOI10.17602/M2/M430188;

1474   Right Quadrate, Media ID 000430191, DOI10.17602/M2/M430191;

1475   Right Squamosal, Media ID 000430194, DOI10.17602/M2/M430194;

1476   Parabasisphenoid, Media ID 000425136, DOI10.17602/M2/M425136;

1477   Basioccipital, Media ID 000427916, DOI10.17602/M2/M427916;

1478   Supraoccipital, Media ID 000430197, DOI10.17602/M2/M430197;

1479   Vomer, Media ID 000430200, DOI10.17602/M2/M430200;

1480   Cranium, Media ID 000430221, DOI10.17602/M2/M430221;

1481   Unidentified bone, Media ID 000430203, DOI10.17602/M2/M430203;

1482   Unidentified bone, Media ID 000430206, DOI10.17602/M2/M430206;

1483   Unidentified bone, Media ID 000430209, DOI10.17602/M2/M430209;

1484   Internal carotid arteries, Media ID 000430212, DOI10.17602/M2/M430212;

1485   Abducens nerves (VI), Media ID 000430215, DOI10.17602/M2/M430215;

1486   Facial nerves (VII), Media ID 000430218, DOI10.17602/M2/M430218.

1487

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Figure 1

Skull of *Trinitichelys hiatti* (MCZ VPRA-4070, holotype), Early Cretaceous (Aptian-Albian) of Texas, U.S.A.

Three-dimensional renderings of the skull and illustrations in (A) dorsal view, (B) ventral view, (C) anterior view, (D) posterior view, and (E) right lateral view. Abbreviations: **bo**, basioccipital; **ex**, exoccipital; **fon**, foramen orbito-nasale; **fpp**, foramen palatinum posterius; **fpr**, foramen praepalatinum; **fr**, frontal; **fst**, foramen stapedio-temporale; **ica**, incisura columella auris; **j-qj**, jugal-quadratojugal; **mx**, maxilla; **na**, nasal; **op**, opisthotic; **pa**, parietal; **pal**, palatine; **pbs**, parabasisphenoid; **pf**, prefrontal; **pmx**, premaxilla; **po**, postorbital; **pro**, prootic; **pt**, pterygoid; **qu**, quadrate; **so**, supraoccipital; **sq**, squamosal; **tb**, tuberculum basioccipitale; **vo**, vomer.
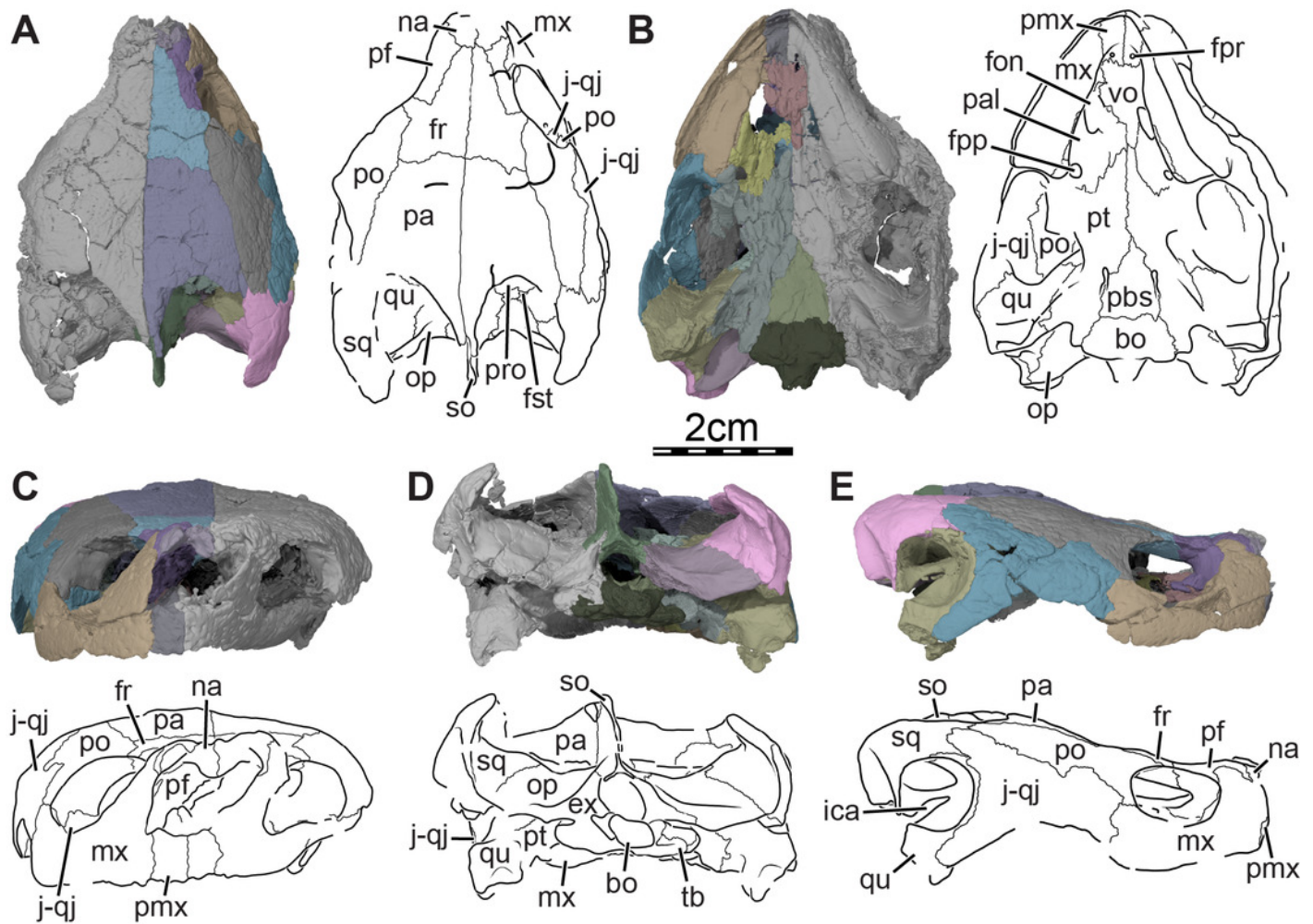
Figure 2

Cranial scutes of *Trinitichelys hiatti* (MCZ VPRA-4070, holotype), Early Cretaceous (Aptian-Albian) of Texas, U.S.A.

Three-dimensional renderings of the skull and illustrations in (A) dorsal view and (B) right lateral view. Sutural lines are thin black lines, whereas thick lines are scute sulci, which are labeled as capital labels.
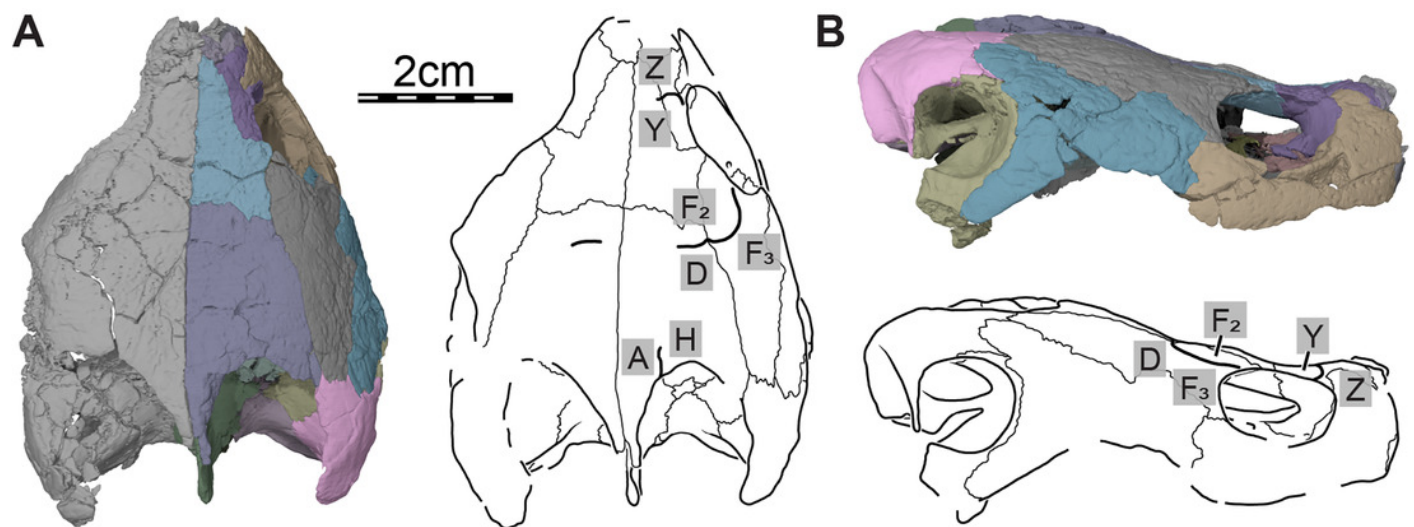
Figure 3

Three-dimensional renderings of the segmented right side of the skull of *Trinitichelys hiatti* (MCZ VPRA-4070, holotype).

(A) right lateral view with the jugal-quadratojugal removed, (B) right medial view. Abbreviations: **?b**, unidentified piece of bone; **bo**, basioccipital; **ex**, exoccipital; **fio**, foramen interorbitale; **fon**, foramen orbito-nasale; **fpp**, foramen palatinum posterius; **fr**, frontal; **ica**, incisura columella auris; **mx**, maxilla; **na**, nasal; **co**, condylus occipitalis; **pa**, parietal; **pal**, palatine; **pbs**, parabasisphenoid; **pf**, prefrontal; **pmx**, premaxilla; **po**, postorbital; **ppe**, processus pterygoideus externus; **pro**, prootic; **pt**, pterygoid; **qu**, quadrate; **so**, supraoccipital; **sq**, squamosal; **'tf'**, putative location of the trigeminal foramen; **vo**, vomer.
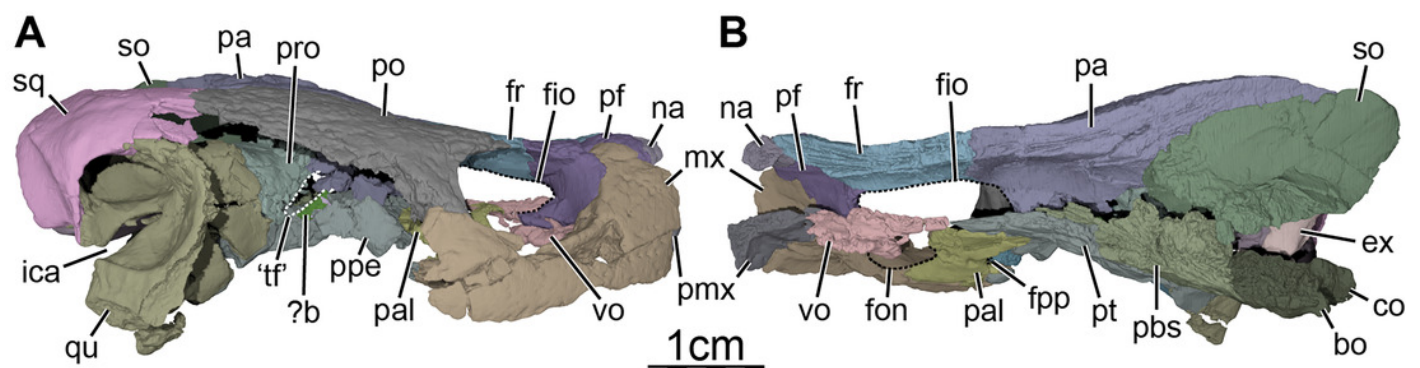
Figure 4

Three-dimensional renderings of the bones from the braincase and palatal regions of the skull of *Trinitichelys hiatti* (MCZ VPRA-4070, holotype).

(A) anterolateral view of the right parietal, (B) medial view of the right premaxilla, (C) ventral view of the right premaxilla, and (D) ventral view of the right palatine. Abbreviations: **dppa**, descending process of the parietal; **fon**, foramen orbito-nasale; **fpp**, foramen palatinum posterius; **fpr**, foramen praepalatinum; **lr**, labial ridge; **pa**, parietal; **pal**, palatine; **pmx**, premaxilla; **r-spp**, ridge posteriorly framing the sulcus palatino-pterygoideus; **s-fr**, suture with the frontal; **s-max**, suture with the maxilla; **s-pmx**, suture with the premaxilla; **s-po**, suture with the postorbital; **s-vo**, suture with the vomer.
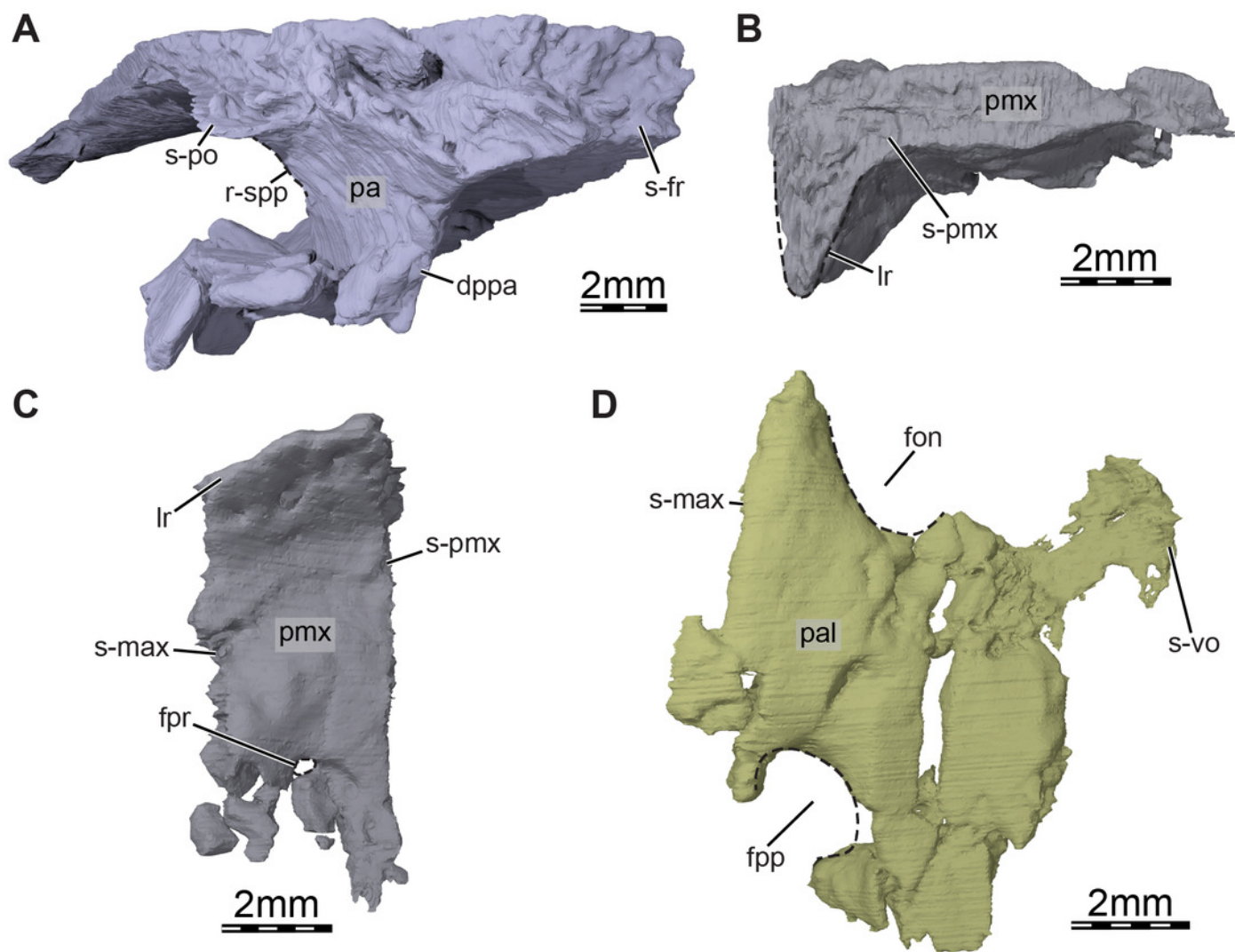
Figure 5

Three-dimensional renderings of the right pterygoid of the skull of *Trinitichelys hiatti* (MCZ VPRA-4070, holotype).

(A) ventral view, (B) dorsal view, (C) dorsolateral view, and (D) posterolateroventral view. Abbreviations: **app**, anterior process of the pterygoid; **bo-f**, articulation facet with the basioccipital; **ccv**, canalis cavernosus; **cp**, carotid pit; **crpt**, crista pterygoidei; **fdnv**, foramen distalis nervi vidiani; **fpcnv**, foramen posterius canalis nervi vidiani; **fpnv**, foramen proximalis nervi vidiani; **j-f**, articulation facet with the jugal; **pal-f**, articulation facet with the palatine; **pbs-f**, articulation facet with the parabasisphenoid; **pfo**, pterygoid fossa; **ppe**, processus pterygoideus externus; **ppp**, posterior process of the pterygoid; **pro-f**, articulation facet with the prootic; **qu-f**, articulation facet with the quadrate; **scv**, sulcus cavernosus; **vf**, vertical flange of the processus pterygoideus externus.
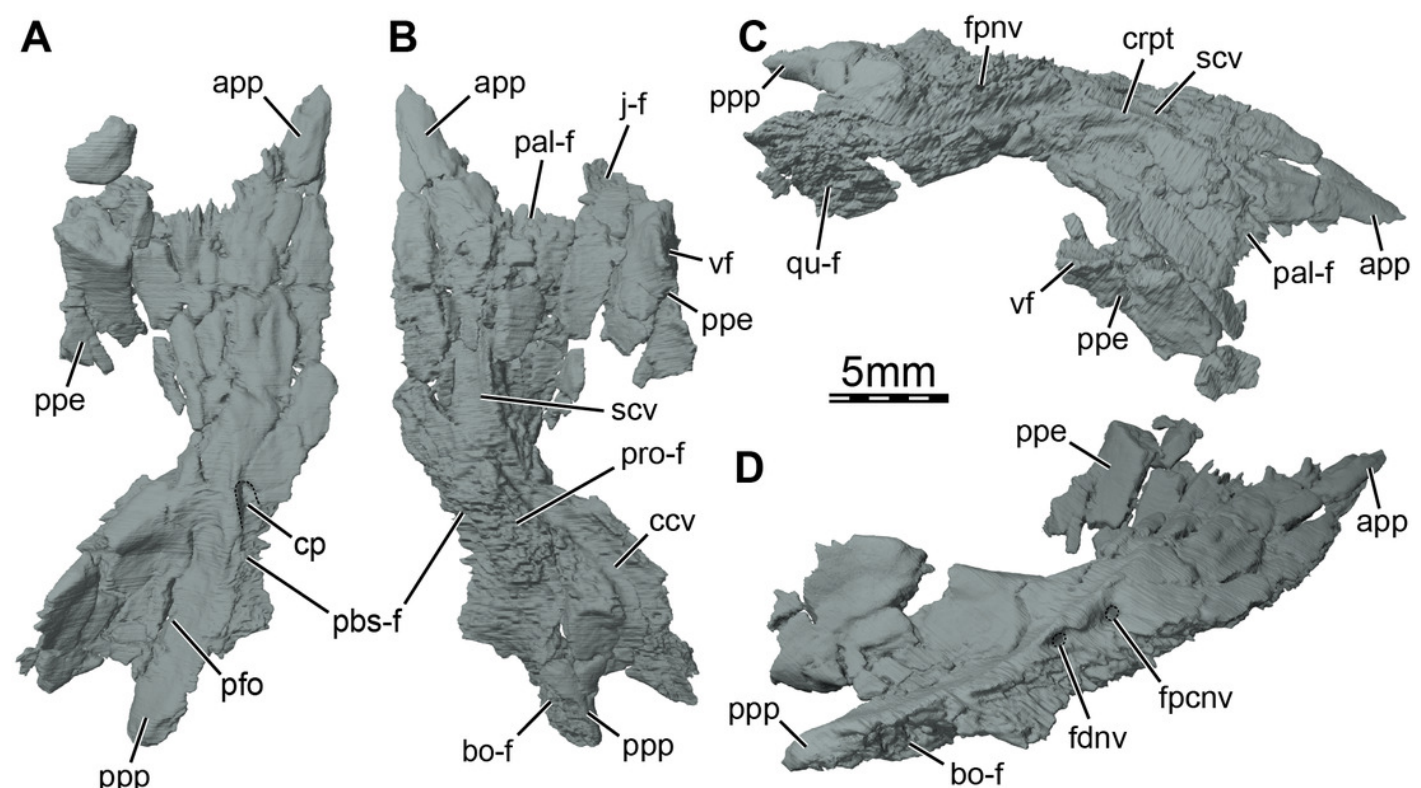
Figure 6

Three-dimensional renderings of the parabasisphenoid and right pterygoid of the skull of *Trinitichelys hiatti* (MCZ VPRA-4070, holotype).

(A) dorsal view, (B) dorsal view of the bones rendered transparent showing the internal carotid artery and facial nerve systems, (C) ventral view, and (D) ventral view of the bones rendered transparent showing the internal carotid artery and facial nerve systems. Abbreviations: **ccb**, canalis caroticus basisphenoidalis; **ccv**, canalis cavernosus; **cg**, carotid groove; **cna**, canalis nervus abducentis; **cnv**, canalis nervus vidianus; **cp**, carotid pit; **cprnv**, canalis pro ramo nervi vidiani; **ds**, dorsum sellae; **faccb**, foramen anterius canalis carotici basisphenoidalis; **facna**, foramen anterius canalis nervi abducentis; **facnv**, foramen anterius canalis nervi vidiani; **fpccb**, foramen posterius canalis carotici basisphenoidalis; **fpcna**, foramen posterius canalis nervi abducentis; **fpcnv**, foramen posterius canalis nervi vidiani; **fpnv**, foramen proximalis nervi vidiani; **ica**, internal carotid artery; **le-pbs**, lateral extension of the parabasisphenoid; **me-pt**, medial extension of the pterygoid; **pbs**, parabasisphenoid; **pt**, pterygoid; **rbp**, retractor bulbi pit; **scv**, sulcus cavernosus; **st**, sella turcica.
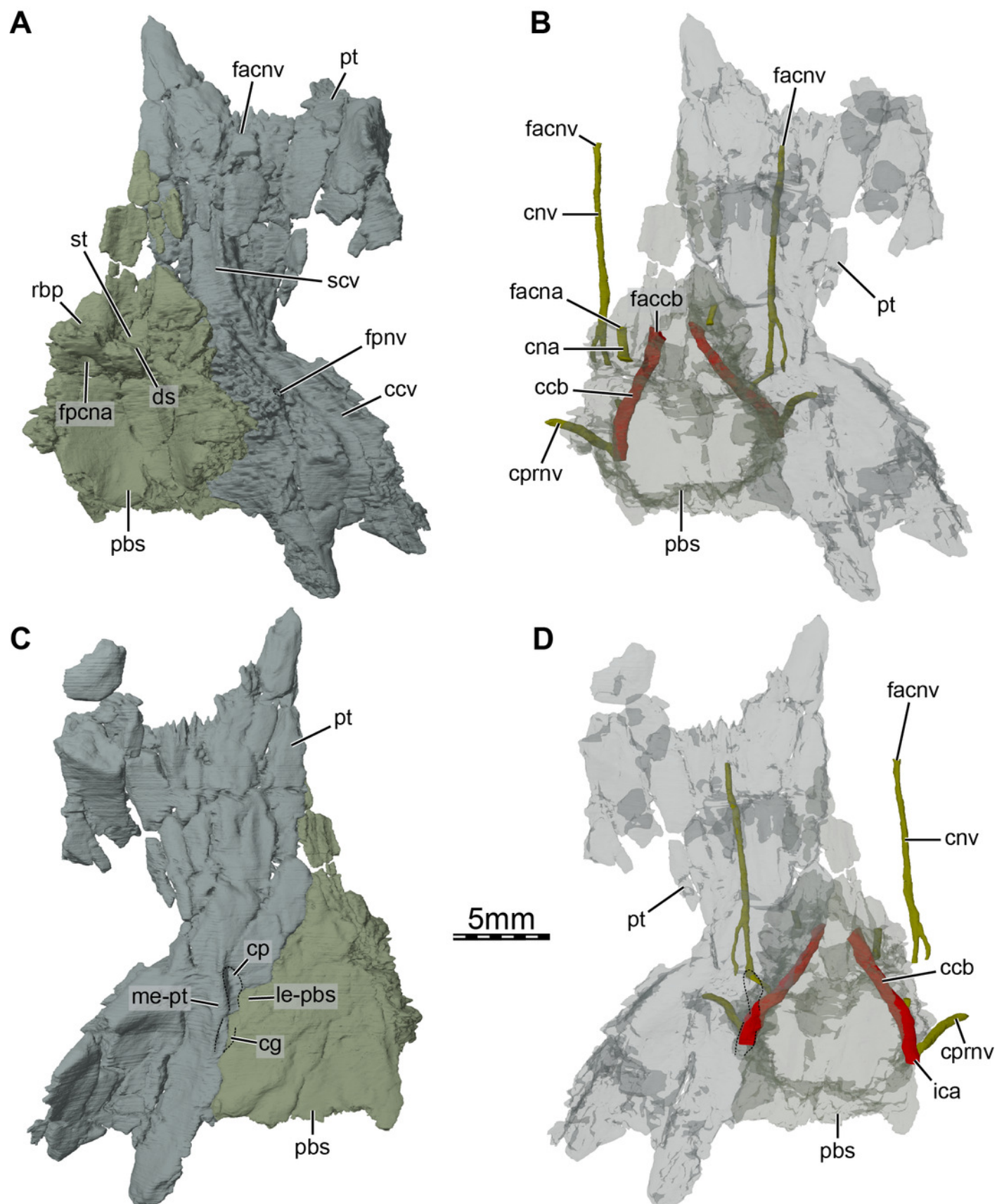
Figure 7

Three-dimensional renderings of the right ceratobranchial I of *Trinitichelys hiatti* (MCZ VPRA-4070, holotype).

(A) dorsal view, (B) ventral view, (C) medial view, and (D) lateral view.
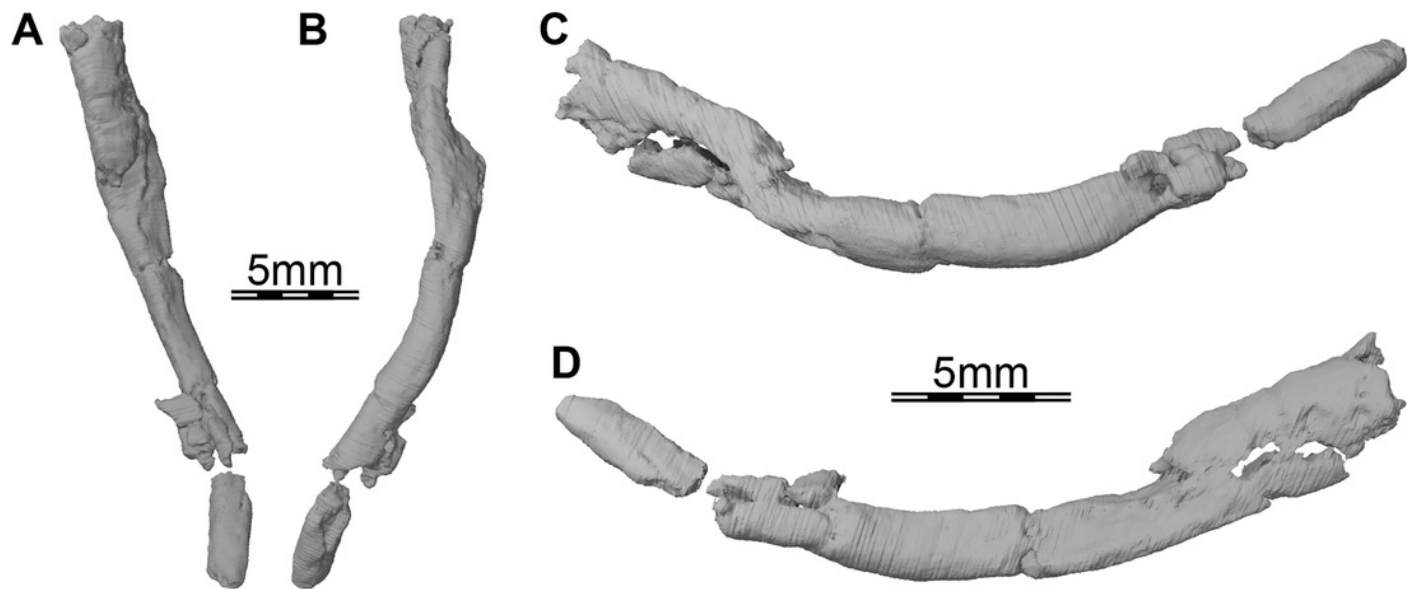
Figure 8

Comparison of the interpretations of the cranial sutures of the skull of *Trinitichelys hiatti* (MCZ VPRA-4070, holotype) between Gaffney (1972) and our study.

(A) dorsal view of the skull, (B) original illustration in dorsal view taken from Gaffney (1972), (C) illustration in dorsal view following our interpretation of the cranial sutures, (D) ventral view, (E) original illustration in ventral view taken from Gaffney (1972), (F) illustration in ventral view following our interpretation of the cranial sutures, (G) right lateral view of the skull, (H) original illustration in left lateral view (mirrored) taken from Gaffney (1972), and (I) illustration in right lateral view following our interpretation of the cranial sutures. Abbreviations: **bo**, basioccipital; **fr**, frontal; **j-qj**, juga-quadratojugal; **ju**, jugal; **mx**, maxilla; **na**, nasal; **op**, opisthotic; **pa**, parietal; **pal**, palatine; **pbs**, parabasisphenoid; **pf**, prefrontal; **pmx**, premaxilla; **po**, postorbital; **pro**, prootic; **pt**, pterygoid; **qj**, quadratojugal; **qu**, quadrate; **so**, supraoccipital; **sq**, squamosal; **vo**, vomer.
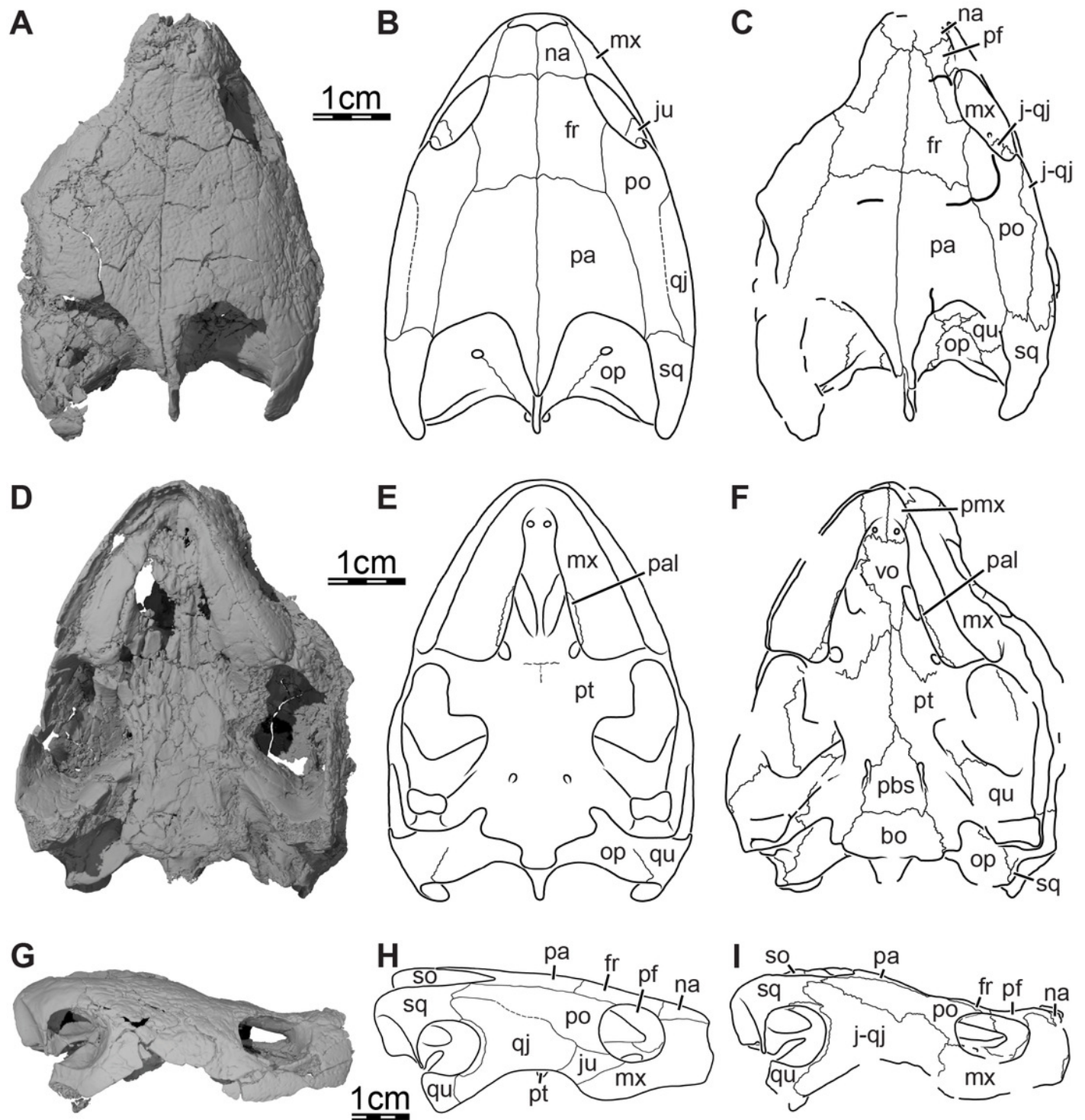
Figure 9

Phylogenetic hypotheses resulting from the analysis under equal weighting.

(A) strict consensus tree obtained with all original taxa included, (B) strict consensus tree obtained without the rogue taxa *Pleurosternon moncayensis*, *Scabremys ornata*, and *Goleremys mckennai*.
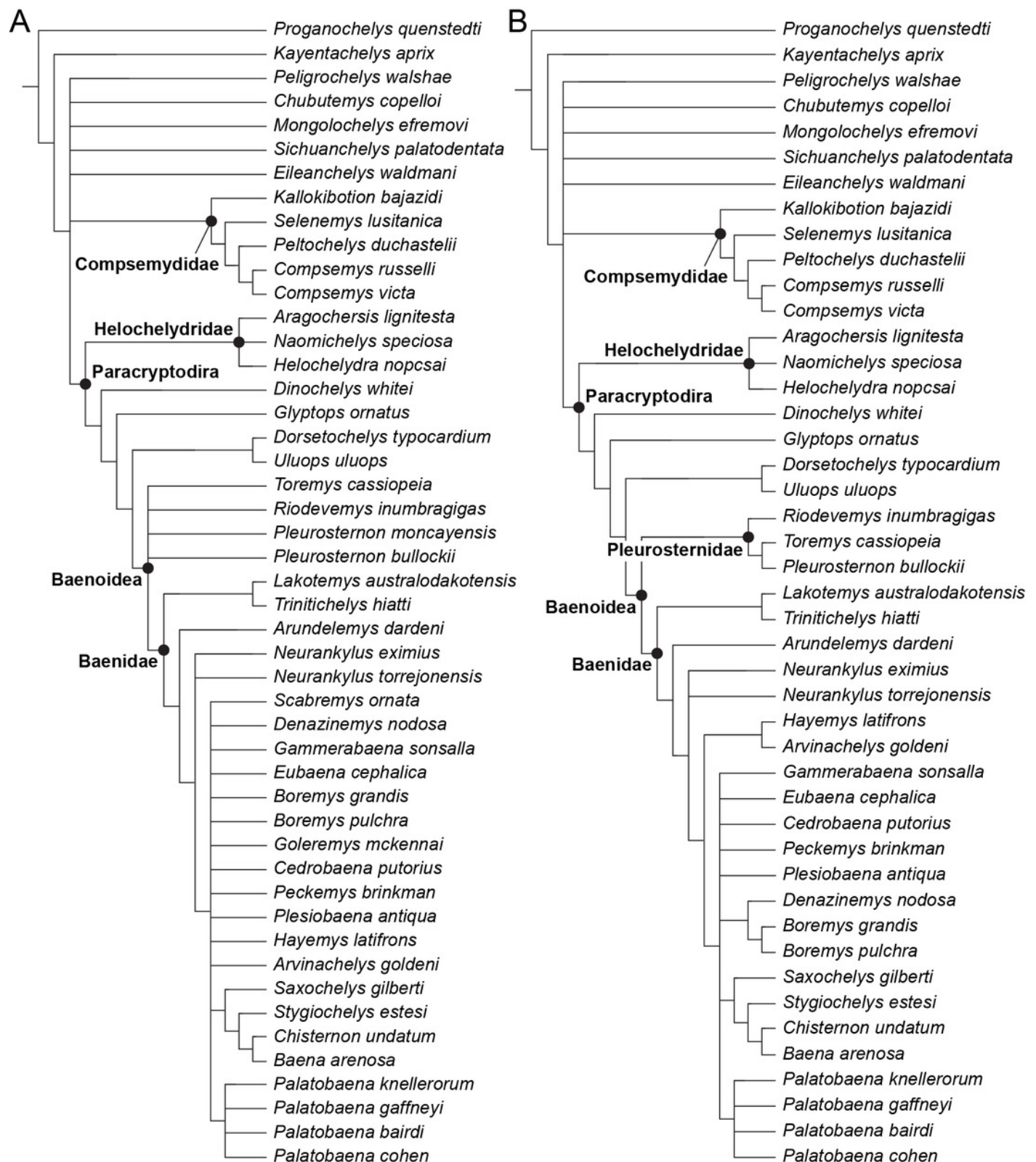
Figure 10

Time-calibrated strict consensus tree obtained from the analysis under equal weighting, without rogue taxa.

The range of North American taxa is highlighted in blue, the range of South American taxa in yellow, the range of European taxa in red, and the range of Asian taxa in orange.

Figure 11

Phylogenetic hypotheses resulting from the analysis under implied weighting with a K factor of 12.

(A) strict consensus tree obtained with all original taxa included, (B) strict consensus tree obtained without the rogue taxa *Pleurosternon moncayensis* and *Scabremys ornata*.

A

- *Proganochelys quenstedti*
- *Kayentachelys aprix*
- *Chubutemys copelloi*
- *Peligrochelys walshae*
- *Mongolochelys efremovi*
- *Sichuanchelys palatodentata*
- *Eileanchelys waldmani*

Compsemydidae
- *Kallokibotion bajazidi*
- *Selenemys lusitanica*
- *Peltochelys duchastelii*
- *Compsemys russelli*
- *Compsemys victa*

Paracryptodira

Helochelydridae
- *Aragochersis lignitesta*
- *Naomichelys speciosa*
- *Helochelydra nopcsai*
- *Dinochelys whitei*
- *Glyptops ornatus*
- *Dorsetochelys typocardium*
- *Uluops uluops*
- *Toremys cassiopeia*
- *Riodevemys inumbragigas*
- *Pleurosternon moncayensis*
- *Pleurosternon bullockii*

Baenoidea
- *Lakotemys australodakotensis*
- *Trinitichelys hiatti*
- *Arundelemys dardeni*

Baenidae
- *Neurankylus eximius*
- *Neurankylus torrejonensis*
- *Scabremys ornata*
- *Plesiobaena antiqua*
- *Hayemys latifrons*
- *Arvinachelys goldeni*
- *Denazinemys nodosa*
- *Boremys grandis*
- *Boremys pulchra*
- *Eubaena cephalica*
- *Goleremys mckennai*
- *Saxochelys gilberti*
- *Stygiochelys estesi*
- *Chisternon undatum*
- *Baena arenosa*
- *Peckemys brinkman*
- *Cedrobaena putorius*
- *Gammerabaena sonsalla*
- *Palatobaena cohen*
- *Palatobaena gaffneyi*
- *Palatobaena knellerorum*
- *Palatobaena bairdi*

B

- *Proganochelys quenstedti*
- *Kayentachelys aprix*
- *Chubutemys copelloi*
- *Peligrochelys walshae*
- *Mongolochelys efremovi*
- *Sichuanchelys palatodentata*
- *Eileanchelys waldmani*

Compsemydidae
- *Kallokibotion bajazidi*
- *Selenemys lusitanica*
- *Peltochelys duchastelii*
- *Compsemys russelli*
- *Compsemys victa*

Paracryptodira

Helochelydridae
- *Aragochersis lignitesta*
- *Naomichelys speciosa*
- *Helochelydra nopcsai*
- *Dinochelys whitei*
- *Glyptops ornatus*
- *Dorsetochelys typocardium*
- *Uluops uluops*
- *Riodevemys inumbragigas*

Pleurosternidae
- *Toremys cassiopeia*
- *Pleurosternon bullockii*

Baenoidea
- *Lakotemys australodakotensis*
- *Trinitichelys hiatti*

Baenidae
- *Arundelemys dardeni*
- *Neurankylus eximius*
- *Neurankylus torrejonensis*
- *Hayemys latifrons*
- *Arvinachelys goldeni*
- *Plesiobaena antiqua*
- *Denazinemys nodosa*
- *Boremys grandis*
- *Boremys pulchra*
- *Eubaena cephalica*
- *Goleremys mckennai*
- *Saxochelys gilberti*
- *Stygiochelys estesi*
- *Chisternon undatum*
- *Baena arenosa*
- *Peckemys brinkman*
- *Cedrobaena putorius*
- *Gammerabaena sonsalla*
- *Palatobaena cohen*
- *Palatobaena gaffneyi*
- *Palatobaena knellerorum*
- *Palatobaena bairdi*

Figure 12

Time-calibrated strict consensus tree obtained from the analysis under implied weighting with a K factor of 12, without rogue taxa.

The range of North American taxa is highlighted in blue, the range of South American taxa in yellow, the range of European taxa in red, and the range of Asian taxa in orange.

Comparative table summarizing the combination of features shared by *Trinitichelys hiatti*, *Arundelemys dardeni* and *Lakotemys australodakotensis*, typical of either Pleurosternidae or Baenidae.

Character	*Pleurosternon bullockii*	*Uluops uluops*	*Arundelemys dardeni*	*Lakotemys australodakotensis*	*Trinitichelys hiatti*	*Eubaena cephalica*	*Palatobaena knellerorum*
Anterior process of the pterygoid	Present	Present	Present	Present	Present	Absent	Absent
External process of the pterygoid	Well-developed	Well-developed	Well-developed	Well-developed	Well-developed	Reduced	Reduced
Ossified epipterygoid	Present	Present	Present	Present	?	Absent	Absent
Triturating surfaces	Narrow	Narrow	Narrow	Narrow	Narrow	More expanded	More expanded
Exposure of the prefrontal on skull roof	Moderate	Moderate	Moderate	Moderate	Moderate	Absent	Reduced
Pterygoid/basioccipital contact	Reduced	Reduced	Elongate	Elongate	Elongate	Elongate	Elongate
Anterior tubercula basioccipitale	Present	Present	Absent	Absent	Absent	Absent	Absent
Basipterygoid process	Present	Present	Absent	Absent	Absent	Absent	Absent