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**First fossil frog and snake assemblage from southern  
Taiwan: a window into Pleistocene herpetofauna and  
paleoenvironments in subtropical East Asia**

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3

4 Running title: Pleistocene herpetofauna in southern Taiwan

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23

24 **Abstract**

25 Herpetofauna, particularly amphibians and reptiles, exhibit high levels of endemism and  
26 distinct diversity pattern on Taiwan island. However, the biogeographic history of these  
27 groups remains obscure, in part due to the lack of a herpetofaunal fossil record. Here, we  
28 report the first fossil record of frogs and snakes from Taiwan, based on Middle Pleistocene  
29 vertebrate assemblage recovered from the Chochen–Tsailiao area in southern Taiwan. The

30 collection includes a vertebra of a bufonid frog and multiple vertebrae of colubrid and viperid  
31 snakes. Despite their fragmentary preservation, several vertebrae are identifiable, including a  
32 toad (*Duttaphrynus melanostictus*), rat snakes (*Elaphe* sp., *Ptyas mucosa*, and *P. cf. mucosa*),  
33 a wolf snake (*Lycodon rufozonatum*), and a pit viper (*Protobothrops* sp.). Additional  
34 vertebrae are attributed to Alethinophidia indet. The preservation of these delicate skeletal  
35 elements in a tectonically active and humid subtropical setting highlights the exceptional  
36 nature of this discovery. Palaeoenvironmental reconstruction based on ecological preferences  
37 of extant analogues suggests that the region supported a humid fluvial and open woodland  
38 environment with abundant water bodies.

39

40 **Keywords:** biogeography, colubrid snakes, diversity, ectothermic indicators, Middle  
41 Pleistocene, subtropical Asia

42

### 43 **Introduction**

44 Taiwan is located within a critical transitional zone between the Palearctic and Indomalayan  
45 biogeographic regions, making it a hotspot for faunal exchange, lineage diversification, and  
46 endemism (Ota 1998; Päckert et al. 2009; Yang et al. 2018; Dufresnes and Litvinchuk 2022).  
47 This biogeographic boundary is a complex suture zone further shaped by mountainous  
48 topography, latitudinal range, and varied climate in Taiwan. Many terrestrial lineages exhibit  
49 biogeographic structuring associated with these northern and southern influences (Ali and  
50 Vences 2019). Among its terrestrial vertebrates, herpetofauna exhibits notably high levels of  
51 endemism in Taiwan (Shang et al. 2009). Excluding marine species, the island supports 37  
52 native amphibians and 85 reptiles (Shang et al. 2009), of which 5 salamanders, 14 frogs, 18  
53 lizards, and 14 snakes are endemic to Taiwan (Lee et al. 2019). This diversity and endemism  
54 reflect complex evolutionary histories influenced by both ancient colonization events and  
55 geographic isolation (Kaito and Mamoru 2016).

56

57 However, the absence of herpetofaunal fossil records in Taiwan has left a substantial gap in  
58 our understanding of how these modern patterns originated and evolved. Without  
59 paleontological evidence, it remains unclear whether Taiwan's current herpetofaunal

60 diversity reflects recent dispersal events or long-standing lineage persistence across glacial  
61 and interglacial cycles (Rage & Roček 2003; Bailon & Blain 2007).

62

63 In this paper, we present the first fossil herpetofaunal assemblage from Taiwan. These fossils,  
64 comprising amphibians and snakes, have been discovered from the Middle Pleistocene  
65 deposits in the Chochen–Tsailiao area of southern Taiwan. These new findings significantly  
66 advance our understanding of the historical diversity and evolutionary lineages of  
67 herpetofauna in the region.

68

### 69 **Geological setting**

70 The fossil herpetofauna described herein were collected from the riverbed of Tsailiao River,  
71 in the Chochen (alternatively spelled as Tsochen or Zoujhen) area of Tainan, southwestern  
72 Taiwan (Fig. 1). This region is renowned for its rich terrestrial and marine Pleistocene fossil  
73 assemblages, which include diverse mammalian, avian, and marine taxa. Previous fossil  
74 findings from the Chochen–Tsailiao area include primates, proboscideans, suids, cervids,  
75 rhinoceroses, crocodiles, birds, and fishes (Shikama 1937, 1972; Shikama et al. 1975a,  
76 1975b, 1976; Otsuka and Lin 1984; Qi et al. 1999; Tao and Hu 2001; Shieh and Chang 2007;  
77 Chang et al. 2012; Kawamura et al. 2016; Lin et al. 2021; Tsai and Mayr 2021).

78

79 Despite being one of the most important localities yielding mammal and terrestrial fossils,  
80 most of the fossils are being transported and lack stratigraphic information (Hayasaka 1932).  
81 Most studies indicate the fossils originate from the nearby Middle Pleistocene Chiting  
82 Formation (Qi et al. 1999; Ho et al. 2005; Shieh and Chang 2007; Tsai and Mayr 2021; Fig.  
83 1), which yield in situ mammal fossils (Kawamura et al. 2016). The Chiting Formation,  
84 reaching approximately 2000 m in thickness, predominantly consists of interbedded  
85 sandstones, siltstones, and mudstones. Stratigraphically, the formation is subdivided into  
86 three ascending members: Kangtzulin, Kuoling, and Takengwei (Ho et al. 2005). Fossils from  
87 the Tsailiao area predominantly originate from the Kuoling and Takengwei members, dating  
88 from approximately 0.7 to 0.5 Ma (Middle Pleistocene), as indicated by  
89 nannobiostratigraphic analyses and cyclostratigraphic estimations (Chi and Huang 1982; Ho  
90 et al. 2005; Chen et al. 2011; Kawamura et al. 2016).

91

92 The Chiting Formation reflects a complex depositional environment characterized by marine  
93 transgression-regression cycles. Although originally deposited in marine conditions, abundant  
94 terrestrial vertebrate fossils, including mammals and reptiles, indicate significant fluvial and  
95 terrestrial influence, likely due to periodic terrestrial inputs and intense seasonal flooding  
96 events. Many fossils have been secondarily reworked, leading to mixed marine and terrestrial  
97 assemblages within the formation (Chen et al. 2011; Chen 2016; Lin et al. 2021).

98 Additionally, some of the marine fossils may also have been reworked from the underlying  
99 Plio–Pleistocene Gutingkeng Formation, which is primarily exposed to the east (Lin et al.  
100 2023; Hsu et al. 2024).

101

102 Ongoing collection and research have clarified the stratigraphic contexts of some fossils,  
103 although many specimens have been discovered without precise stratigraphic positions due to  
104 their retrieval from riverbeds after seasonal flooding (Otsuka and Lin 1984; Kawamura et al.  
105 2016). Considering the uncertainty in precise stratigraphic provenance, we conservatively  
106 estimate the geological age of the described fossil herpetofauna as broadly corresponding to  
107 the established age range of the Chiting Formation, approximately 0.8–0.4 Ma (Chen 2016).

108

## 109 **Methods**

110 The fossil materials described in this study were collected from the riverbed of the Tsailiao  
111 River in the Chochen, Tainan, southern Taiwan (Fig. 1). All specimens were recovered from  
112 surface deposits through simple sieving and manual sorting. Due to the nature of riverbed  
113 collection, the fossils lack precise stratigraphic context, although they are inferred to originate  
114 from the Middle Pleistocene Chiting Formation (see above, Geological setting). The  
115 collection was made by Mr. Liang-Chieh Wang over the past three decades and represents an  
116 important accumulation of vertebrate fossil material from this region.

117

118 Fossils included in this study consist of isolated amphibian and snake vertebrae. Taxonomic  
119 identification was based on morphological comparisons with extant and fossil materials,  
120 using relevant published literature (Ikeda 2007; Chen 2020; Ratnikov 2024) and a reference

121 collection of extant vertebrae sourced from roadkills (Chyn et al. 2019) housed at the  
122 Biodiversity Research Museum, Academia Sinica, Taiwan (BRCAS) under the code  
123 ASIZAM for amphibians and ASIZRE for reptiles.

124

125 Specimen imaging was performed using a Nikon SMZ1270 stereomicroscope fitted with a  
126 digital camera. To enhance the depth of field, each image was compiled as a focus-stacked  
127 composite using Helicon Focus software. The resulting images were digitally optimized for  
128 clarity using Adobe Photoshop. All examined materials are housed in the Biodiversity  
129 Research Museum, Academia Sinica, Taiwan, under the registration code ASIZF.  
130 Measurements of the vertebrae were taken where preservation allowed, following the  
131 methodology of Bochaton et al. (2019), and are presented in Table 1. Detailed anatomical  
132 terminology used for vertebral descriptions is illustrated in Supplementary Figs 1, 2.

133

#### 134 **Systematic paleontology**

135 Amphibia Linnaeus, 1758

136 Anura Fischer, 1813

137 Bufonidae Gray, 1825

138 *Duttaphrynus* Frost et al., 2006

139 *Duttaphrynus melanostictus* (Schneider, 1799) (Fig. 2A)

140 **Material.** Trunk vertebra (ASIZF 0101045).

141 **Description.** The vertebra is large, wider than long, with a centrum that is procoelous and  
142 slightly dorsoventrally compressed. The neural canal is larger than both cotyle and condyle.  
143 The walls of the neural arch are robustly built, bearing a low but distinct carina neuralis. The  
144 prezygapophyses and postzygapophyses are dorsally elevated and extend laterally. A single  
145 transverse process is preserved and extends distally.

146 **Remarks.** The substantial size of the vertebra (>4.5 mm in length), its proportions, and  
147 robust construction suggest that it belongs to the Bufonidae. Given its dimension and general  
148 morphology, the vertebra most likely represents a mid-trunk element, probably the 3<sup>rd</sup> or 4<sup>th</sup>  
149 presacral vertebra. Of the more than 30 native anuran species in Taiwan, only two bufonids,

150 *Bufo bankorensis* (Barbour, 1908) and *Duttaphrynus melanostictus*, attain a comparable size.  
151 Trunk vertebrae of both species are morphologically similar; however, the centrum of *B.*  
152 *bankorensis* is more elevated in lateral view (Fig. 2C5), whereas that of *D. melanostictus* is  
153 flatter and more dorsoventrally compressed.

154

155 Squamata Oppel, 1811

156 Colubriiformes Günther, 1864 sensu Zaher et al., 2009

157 **Remarks.** Most of our snake vertebrae describe here belong to the order Colubriiformes.  
158 Within Colubriiformes, hypapophyses are typically present in mid- and posterior trunk  
159 vertebrae of natricids, elapids, and viperids (Georgalis and Scheyer 2022). The absence of  
160 hypapophyses in mid- and posterior trunk vertebrae has long been considered characteristic  
161 of Colubridae (e.g., Boulenger 1896; Bogert 1940; Underwood 1967; Bourgeois 1968;  
162 Dowling and Duellman 1978) or of the paraphyletic group traditionally referred to as  
163 “Colubrinae” (Rage 1984; Szyndlar, 1984, 1991a, 2012; Georgalis et al. 2018). However,  
164 recent studies have shown that more distantly related groups, such as dipsadids and  
165 psammophiids, may also lack hypapophyses in mid- and posterior trunk vertebrae (Georgalis  
166 et al. 2019; Georgalis and Scheyer 2022). It is important to note that both of these non-  
167 colubrid groups are native to the New World and are absent from the biogeographic region  
168 represented by the fossil material in this study.

169

170 Colubridae Oppel, 1811

171 *Elaphe* Fitzinger, 1833

172 *Elaphe* sp. (Fig. 3A–B)

173 **Material.** Two caudal vertebrae (ASIZF 0101046–1047).

174 **Description.** In the anterior view, the cotyle is rounded. Paracotylar foramina are present,  
175 located on the lateral margins of the cotyle. The prezygapophyseal accessory processes and  
176 pleurapophyses are developed and pointed in specimen ASIZF 0101046, but they are broken  
177 laterally in specimen ASIZF 0101047. The zygosphene roof is dorsally convex and about the  
178 same width as the cotyle, with articular facets inclined dorsally. The neural canal is tunnel-  
179 like.

180 In the posterior view, the condyle is circular, with height similar to width. The neural  
181 arch is moderately vaulted. The zygantral area is deep and the paired endozygantral foramina  
182 are present. In the ventral view, the centrum is distinctly longer than wide. Well-developed  
183 hemapophyses are partially present in specimen ASIZF 0101046, almost reaching the  
184 condyle. Subcentral foramina are visible. Postzygapophyseal articular facets are oval in  
185 ASIZF 0101046.

186 In the dorsal view, the posterior median notch is distinctly deep in specimen ASIZF  
187 0101046. Prezygapophyseal articular facets are oval. In the lateral view, the height of the  
188 neural spine is indeterminate in ASIZF 0101047 due to poor preservation, whereas it is high  
189 in ASIZF 0101046. Both interzygapophyseal and subcentral ridges, and lateral foramina are  
190 distinct in ASIZF 0101046.

191 **Remarks.** The caudal vertebrae closely resemble those of *Elaphe* as described by Ratnikov  
192 (2022), particularly in terms of their elongated morphology from anterior to posterior, and  
193 well-developed hemapophyses and pleurapophyses. Two extant species of *Elaphe*, *E.*  
194 *carinata* (Günther, 1864) and *E. taeniura friesi* (Werner, 1927), are found in Taiwan. Both  
195 are common, large-bodied species with vertebrae very similar to each other (Chen 2020).  
196 However, our fossil specimens are not well-preserved and can only be assigned to the genus  
197 level.

198

199 *Lycodon* Fitzinger, 1826

200 *Lycodon rufozonatum* Cantor, 1842 (Fig. 4A–B)

201 **Material.** Two trunk vertebrae (ASIZF 0101048–1049).

202 **Description.** In the anterior view, the cotyle is rounded in outline. Paracotylar foramina are  
203 present on either side of the cotyle. The prezygapophyses are well-developed, and the  
204 prezygapophyseal accessory processes are laterally extended. The zygosphenic roof is thin  
205 and dorsally convex. The zygosphenal articular facets of the zygosphenic are inclined  
206 dorsally. The neural canal is tunnel-like, with a width approximately equal to that of the  
207 cotyle.

208 In the posterior view, the condyle is circular in shape and proportionally similar in  
 209 height and width. The neural arch is moderately vaulted but not significantly. The zygantral  
 210 area is deep and contains paired endozygantral foramina.

211 In the ventral view, the centrum is triangular and relatively short. Small paired  
 212 subcentral foramina are visible flanking a well-developed, oblanceolate haemal keel that  
 213 extends nearly to the condyle. Subcentral grooves are deep and long. Postzygapophyseal  
 214 articular facets are oval. Synapophyses are clearly divided into diapophyses and  
 215 parapophyses, with the absence of parapophyseal processes.

216 In the dorsal view, the vertebrae are slightly wider than long. The anterior margin of  
 217 the zygosphenon is straight with two blunt lobes on the lateral sides. The posterior median  
 218 notch is distinct and deep. Prezygapophyseal articular facets are oval.

219 In the lateral view, both interzygapophyseal and subcentral ridges are straight (Fig.  
 220 3B5, C5). The neural spine is high, with the posterior end protruding above its base and the  
 221 anterior end overhanging. Lateral foramina are present.

222 **Remarks.** The two trunk vertebrae differ from those of *Ptyas* by lacking epizygapophyseal  
 223 spines (Ikeda 2007; Nakamura et al. 2013). Additionally, several features, including the  
 224 straight zygosphenal lip with two small blunt lobes on the lateral sides and a vaulted neural  
 225 arch, exclude their allocation to *Coronella*, which possesses a crenate zygosphenal lip, a wide  
 226 haemal keel, and a depressed neural arch (Ivanov et al. 2018). The fossils can also be  
 227 distinguished from *Texasophis* and *Telescopus* by their relatively large size and distinct  
 228 subcentral ridges (Čerňanský et al. 2017).

229 The fossil vertebrae also resemble much to those of *Elaphe* and *Lycodon*, sharing  
 230 characters including undeveloped parapophyseal process, well-developed prezygapophyseal  
 231 accessory processes, and oval zygosphenal articular facets (Chen 2020). However, in *Elaphe*,  
 232 the trunk vertebrae generally exhibit less prominent subcentral ridges and indistinctly  
 233 developed subcentral grooves (Ratnikov 2004; Ivanov et al. 2018), which is not identical to  
 234 the prominent subcentral ridges and deep subcentral grooves in the fossils, although Ratnikov  
 235 (2022) noted that *Elaphe* trunk vertebrae show progressive morphological changes along the  
 236 column, such as deepening of subcentral grooves, more distinct subcentral ridges, reduced  
 237 haemal keel width, and increased neural spine height posteriorly.

238 Two extant species of *Lycodon*, *L. ruhstrati* (Fischer, 1886) and *L. rufozonatus*  
239 (Cantor, 1842), are found in Taiwan. The vertebrae of *L. ruhstrati* possess flat and very low  
240 neural spines, whereas in *L. rufozonatus*, these are substantially high as in our fossils (Fig.  
241 4C–D).

242

243 *Ptyas* Fitzinger, 1843

244 *Ptyas mucosa* (Linnaeus, 1758) (Fig. 5A)

245 **Material.** One trunk vertebra (ASIZF 0101050).

246 **Description.** In the anterior view, the cotyle appears rounded and flanked by paracotylar  
247 foramina. The neural canal is large and circular. The prezygapophyses are well-developed,  
248 with the ending portions of their accessory processes prominently directed forward and  
249 slightly ventrally inclined. The zygosphenic roof is straight, and its articular facets are  
250 dorsally tilted.

251 In the posterior view, the condyle is rounded and the neural arch is vaulted, with  
252 paired endozygantral foramina visible. In the ventral view, the centrum is elongated and  
253 triangular in shape. Subcentral foramina are present, and both subcentral grooves and ridges  
254 are clearly defined. The haemal keel is well-developed and oblanceolate. Postzygapophyseal  
255 articular facets are oval. Epizygapophyseal spines are developed and directed  
256 posterolaterally. Diapophyses and parapophyses are clearly visible, though the parapophyseal  
257 processes are absent.

258 In the dorsal view, the vertebra is slightly laterally compressed. The anterior margin  
259 of the zygosphenic roof is straight with two small, blunt lateral lobes. The posterior median notch  
260 is markedly deep. Prezygapophyseal articular facets are oval, and the prezygapophyseal  
261 accessory processes are well-developed, pointed, and directed anterolaterally. In the lateral  
262 view, the interzygapophyseal and subcentral ridges are straight. The neural spine is damaged.  
263 The lateral foramina are observed.

264 **Remarks.** The fossil vertebra can confidently be attributed to colubrids or “colubrines”,  
265 further supported by several combined features: a vaulted neural arch, a well-developed  
266 haemal keel (instead of a hypapophysis), the presence of paracotylar foramina, a pronounced  
267 division between the para- and diapophyses, and a moderately high neural spine. Moreover,

268 its overall vertebral morphology closely matches that of *Ptyas*, which share characteristics  
269 such as epizygapophyseal spines, pointed prezygapophyseal accessory processes, distinct  
270 subcentral grooves and ridges, and a vaulted neural arch (see Ikeda 2007; Shi et al. 2023).

271 The strongly anteriorly directed prezygapophyseal accessory processes, however, are  
272 a distinctive feature seen only in the two extant *Ptyas* species from Taiwan, *Ptyas major*  
273 (Günther, 1858) and *Ptyas mucosa* (Linnaeus, 1758) (see Chen 2020). Among these, *P. major*  
274 is a medium-sized species, while *P. mucosa* notably larger, and the vertebrae of *P. major* are  
275 consistently smaller than those of *Ptyas mucosa*, as seen in our comparative specimens (Fig.  
276 5E).

277

278 *Ptyas cf. mucosa* (Linnaeus, 1758) (Fig. 6)

279 **Material.** Two trunk vertebrae (ASIZF 0101051–1052).

280 **Description.** In the anterior view, the cotyle is rounded. In specimen ASIZF 0101052,  
281 paracotylar foramina are present, located on the lateral margins of the cotyle, whereas in  
282 specimen ASIZF 0101051, these foramina are not clearly visible. The prezygapophyses are  
283 well-developed, but the prezygapophyseal accessory processes are broken laterally. The  
284 zygosphene roof is dorsally convex and wider than the cotyle, with articular facets inclined  
285 dorsally. The neural canal is tunnel-like.

286 In the posterior view, the condyle is circular, with height similar to width. The neural  
287 arch is moderately vaulted. The zygantral area is deep and the paired endozygantral foramina  
288 are present.

289 In the ventral view, the centrum is distinctly longer than wide and triangular in  
290 outline. A well-developed, oblanceolate haemal keel is present instead of a hypapophysis,  
291 almost reaching the condyle. Subcentral foramina are not clearly visible. The subcentral  
292 grooves are deep and long. Postzygapophyseal articular facets are oval. The paradiapophyses  
293 comprise a laterally salient diapophysis and an almost flat parapophysis.

294 In the dorsal view, the anterior edge of the zygosphene is straight with two small  
295 pointed lobes on the lateral sides. The posterior median notch is distinctly deep.  
296 Prezygapophyseal articular facets are oval.

297 In the lateral view, the height of the neural spine is indeterminate in specimen ASIZF  
298 0101051 due to poor preservation, whereas it is very high in ASIZF 0101052. Both  
299 interzygapophyseal and subcentral ridges are distinct. Lateral foramina are present.

300 **Remarks.** Although the prezygapophyseal accessory processes are only partially preserved,  
301 the remaining portions appear to be anteriorly directed. Combined with the large overall size  
302 of the vertebrae and the presence of distinct subcentral ridges with deep grooves, these  
303 features most closely match *Ptyas mucosa*, as described above. However, the poor  
304 preservation of both specimens—particularly the absence of epizygapophyseal spines, which  
305 may have been worn away—precludes a definitive assignment.

306

307 Viperidae Oppel, 1811

308 Crotalinae Oppel, 1811

309 *Protobothrops* Hoge & Romano-Hoge, 1983

310 *Protobothrops* sp. (Fig. 7A)

311 **Material.** One vertebra (ASIZF 0101053).

312 **Description.** In the anterior view, the cotyle is large and circular. The prezygapophyses are  
313 dorsally inclined though their prezygapophyseal processes are not preserved. The zygosphene  
314 roof is slightly convex, with articular facets inclined dorsally. Paired, deeply set large  
315 paracotylar foramina are present on both sides of the cotyle. The parapophyseal processes are  
316 broken, but they extended beyond the cotyle.

317 In the posterior view, the neural arch is depressed. The zygantrum is mediolaterally  
318 wide and deep. The condyle is rounded and relatively smaller than the neural canal.

319 In the dorsal view, the anterior margin of the zygosphene is straight, with two pointed  
320 lateral lobes. Prezygapophyseal articular facets are oval. A deep posterodorsal notch exposes  
321 a large portion of the condyle. The neural spine extends longitudinally along the dorsal  
322 surface of the neural arch and terminates posterior to the posterior medial notch.

323 In the ventral view, the centrum is triangular. Subcentral foramina are deep and  
324 restricted to the anterior part of the centrum. Parapophyses and diapophyses are distinctly

325 observed. The parapophyseal processes project anterolaterally. Postzygapophyseal articular  
326 factes are oval. Subcentral grooves and ridges are distinct.

327 In the lateral view, the neural speine is broken ventrodorsally. The zygosphene  
328 articular facets are elliptical. The lateral foramina are deep and situated in the middle part of  
329 vertebra. The interzygapophyseal and subcentral ridges run straight anteroposteriorly. The  
330 hypophysis originates at the middle part of the centrum and extends beyond the level of the  
331 condyle.

332 **Remarks.** The presence of well-developed hypapophysis indicates potential affinity with  
333 Elapidae, Viperidae, or Natricidae (originally considered as Natricinae; Szyndlar 1984,  
334 1991b), as this character is considered apomorphic (Zaher 1999). Among these families, the  
335 referred specimen resembles more to the family Viperidae, particularly due to the following  
336 combination of features: presence of hypapophysis, depressed neural arch, dorsally inclined  
337 prezygapophyses and anterolaterally directed parapophyseal processes (Zaher 1999; Zaher et  
338 al. 2009).

339 Viperidae includes three monophyletic subfamilies: Viperinae (or “true vipers”),  
340 Azemiopinae, and Crotalinae (or “pitvipers”), with the latter two forming a sister clade to  
341 Viperinae (Wüster et al. 2008; Alencar et al. 2016). This vertebra can be confidently  
342 classified within Crotalinae due to its short and wide vertebra, thick hypapophysis that  
343 originates near the middle of the centrum, and large cotyle and condyle (Holman 2000).  
344 Furthermore, the fossil vertebra most closely resembles *Protobothrops* or *Trimeresurus* rather  
345 than *Gloydus*, based on its undeveloped prezygapophyseal accessory processes, straight  
346 zygosphenal margin in the dorsal view; rounded shape cotyle and condyle, and straight  
347 subcentral ridge in the lateral view (Ikeda 2007). Among extant taxa, *Trimeresurus*  
348 *stejnegeri*—a small and common pitviper in Taiwan—is a possible comparison. However, the  
349 fossil vertebra is significantly larger than that of a large adult *T. stejnegeri* (Fig. 7C),  
350 suggesting that the specimen more likely represents a larger crotaline *Protobothrops*.

351 Within *Protobothrops*, the fossil is most comparable to *P. mucrosquamatus*, the only  
352 extant species of this genus occurring in Taiwan. However, the prezygapophyseal accessory  
353 processes in the fossil are more pointed and anteriorly directed, whereas in *P.*  
354 *mucrosquamatus*, the same processes are broader and more laterally expanded (Fig. 7B).  
355 Therefore, we conservatively retain the identification at the genus level.

356

357 Alethinophidia indet. (Fig. 8)

358 **Materials.** Six trunk vertebrae (ASIZF 0101054–1059).

359 **Description.** All the specimens referred here are fragmentary, but they share a few common  
360 characteristics such as the absence of hypapophyses, rounded cotyles and condyles, a large  
361 neural canal, a dorsally convex zygosphenon, a vaulted neural arch, and distinct subcentral  
362 ridges and grooves. Prezygapophyses are preserved in a few specimens (e.g., Fig. 8A),  
363 displaying oval shape that extend laterally.

364 In specimens ASIZF 0101058 and 1059 (Fig. 8E, F), endozygantral foramina can be  
365 observed within the zygantrum. In the ventral view, the haemal keel is well-developed,  
366 oblongate in shape, and subcentral foramina are observable in specimens ASIZF 0101055,  
367 1056, and 1058 (Fig. 8B, C, E). The neural spine is damaged anteroposteriorly in all  
368 specimens. In the lateral view, the interzygapophyseal and subcentral ridges are straight, and  
369 lateral foramina are present.

370 **Remarks.** The absence of hypapophysis indicates that these are mid- or posterior trunk  
371 vertebrae. However, due to the fragmentary nature of the specimens and the lack of genus-  
372 level diagnostic characters, more precise identification is not possible. However, based on the  
373 preserved features, all specimens can be attributed to Alethinophidia indet.

374

## 375 **Discussion**

376 The herpeto-assemblage recovered from the Middle Pleistocene deposits of southern Taiwan  
377 represents the first documented record of fossil amphibian and snakes from the region. These  
378 findings provide valuable opportunities to enhance our understanding of historical diversity  
379 and biogeographic patterns of Taiwanese herpetofauna. All the specimens discussed are  
380 fragmentary, making identification challenging, but, a few can be identified at the generic  
381 level. Although the specimens are fragmentary and identification is often limited, several  
382 vertebrae could be confidently assigned to lower level. The amphibian is identified here as *D.*  
383 *melanostictus*, and snakes as *Elaphe* sp., *Lycodon rufozonatum*, *Ptyas mucosa*, *Ptyas* cf.  
384 *mucosa*, and *Protobothrops* sp. Additional isolated snake vertebrae are assigned to  
385 Alethinophidia indet. due to the lack of diagnostic features. Despite the relatively low  
386 taxonomic diversity, the significance of this assemblage lies in its status as the first fossil  
387 herpeto-assemblage from the subtropical East Asia.

388

389 The single *Duttaphrynus melanostictus* vertebra represents remarkable and noteworthy  
390 finding, especially given the low preservation potential of delicate skeletal elements in  
391 tectonically active and subtropical fluvial environments. *Duttaphrynus melanostictus* has a  
392 wide distribution in both Palearctic and Indomalayan realms, and its presence in Pleistocene  
393 Taiwan reinforces the island's role as a biogeographic suture zone between these two faunal  
394 regions.

395

396 In our collection, colubrid snakes are the most abundant group. Large, widespread species  
397 such as *Ptyas mucosa* and *Elaphe* sp. occur in a range of habitats up to approximately 2,000  
398 m in elevation across Taiwan (Shang et al. 2009), and their fossil presence is therefore not  
399 surprising. The only viperid vertebra recovered in this study is assigned to the genus  
400 *Protobothrops*, a medium- to large-sized snake distributed throughout Taiwan and adjacent  
401 parts of Southeast Asia; it is commonly known as the brown-spotted pit viper or Taiwanese  
402 habu (Shang et al. 2009).

403

404 The distribution of amphibians and squamates is strictly tied to environmental conditions  
405 such as temperature and precipitation, owing to their ectothermic physiology (Antúnez et al.  
406 1988; Currie 1991; Rage and Roček 2003). Therefore, these vertebrates are commonly used  
407 as reliable indicators of past climatic conditions (e.g., Bohme 2003; Bailon and Blain 2007;  
408 Blain et al. 2013). The presence of fossil herpetofauna in the Pleistocene deposits of Taiwan  
409 is particularly valuable for palaeoenvironmental reconstructions, as many Pleistocene species  
410 belong to extant lineages with well-documented ecological preferences (Blain et al. 2008).

411

412 The co-occurrence of amphibian (*D. melanostictus*) and squamate fossils—including  
413 colubrids and a viperid—suggests the existence of fluvial and open terrestrial habitats. This  
414 general palaeoenvironmental reconstruction agrees well with previous findings of terrestrial  
415 vertebrate fossils and depositional environment (Chen et al., 2011; Chen 2016). The presence  
416 of *D. melanostictus* reflects freshwater or semi-aquatic environments nearby, while the  
417 occurrences of *Elaphe*, *Lycodon*, and *Ptyas* point to moist, open woodlands or ecotones near  
418 water bodies (Kuntz 1963; Lue et al. 2002). The viperid *Protobothrops* further supports a

419 mosaic landscape, as extant members of this genus occupy a wide range of environments,  
420 from dense forests to open habitats. Taken together, the composition of the herpetofaunal  
421 assemblage indicates a landscape with abundant water bodies that supported humid and warm  
422 climatic conditions, likely interspersed with riparian corridors and forested terrain (Fig. 9).

423

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434

#### 435 **References**

436 Alencar LR, Quental TB, Graziotin FG, Alfaro ML, Martins M, Venzon M, Zaher H (2016)  
437 Diversification in vipers: Phylogenetic relationships, time of divergence and shifts in  
438 speciation rates. *Molecular phylogenetics and evolution* 105: 50–62.

439 <https://doi.org/10.1016/j.ympev.2016.07.029>

440 Ali JR, Vences M (2019) Novel summary metrics for insular biotic assemblages based on  
441 taxonomy and phylogeny: biogeographical, palaeogeographical and possible  
442 conservational applications. *Journal of Biogeography* 46(12): 2735–2751.

443 <https://doi.org/10.1111/jbi.13706>

444 Antúnez A, Real R, Vargas JM (1988) Análisis biogeográfico de los anfibios de la vertiente  
445 sur de la Cordillera Bética. *Miscellanea Zoologica* 12: 261–272.

446 Bailon S, Blain H-A (2007) Faunes de reptiles et changements climatiques en Europe  
447 occidentale autour de la limite Plio-Pléistocène. *Quaternaire* 18(1): 55–63.

448 <https://doi.org/10.4000/quaternaire.960>

- 449 Blain H-A, Bailon S, Cuenca-Bescós G (2008) The Early–Middle Pleistocene  
450 palaeoenvironmental change based on the squamate reptile and amphibian proxies at the  
451 Gran Dolina site, Atapuerca, Spain. *Palaeogeography, Palaeoclimatology,*  
452 *Palaeoecology* 261(1–2): 177–192. <https://doi.org/10.1016/j.palaeo.2008.01.015>
- 453 Blain HA, Sese C, Rubio-Jara S, Panera J, Uribelarrea D, Perez-Gonzalez A (2013)  
454 Paleoenvironmental and paleoclimatic reconstruction of the early Late Pleistocene (MIS  
455 5a) in central Spain: the small vertebrates (Amphibia, Reptilia & Mammalia) from the  
456 sites of Hat and Preres. *Quaternaire* 24(2): 191–205.  
457 <https://doi.org/10.4000/quaternaire.6604>
- 458 Bochaton C, Boistel R, Grouard S, Ineich I, Tresset A, Bailon S (2019) Fossil dipsadid  
459 snakes from the Guadeloupe Islands (French West-Indies) and their interactions with  
460 past human populations. *Geodiversitas* 41(sp2): 501–523.  
461 <https://doi.org/10.5252/geodiversitas2019v41a12>
- 462 Böhme M (2003) The Miocene Climatic Optimum: evidence from ectothermic vertebrates of  
463 Central Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology* 195(3–4): 389–  
464 401. [https://doi.org/10.1016/S0031-0182\(03\)00367-5](https://doi.org/10.1016/S0031-0182(03)00367-5).
- 465 Bogert CM (1940) Herpetological results of the Vernay Angola Expedition: with notes on  
466 African reptiles in other collections. Part 1, Snakes, including an arrangement of African  
467 Colubridae. *Bulletin of the American Museum of Natural History* 77(1): 1–107.
- 468 Boulenger GA (1896) Catalogue of the snakes in the British Museum (Natural History).  
469 *Nature* 54: 266–267. <https://doi.org/10.1038/054266a0>
- 470 Bourgeois M (1968) Contribution à la morphologie comparée du crâne des ophidiens de  
471 l'Afrique centrale. *Publications de l'Université Officielle du Congo* 18: 1–293.
- 472 Cantor T (1842). General features of Chusan, with remarks on the flora and fauna of that  
473 island. London: Taylor. <https://doi.org/10.5962/bhl.title.6704>
- 474 Čerňanský A, Szyndlar Z, Mörs T (2017) Fossil squamate faunas from the Neogene of  
475 Hambach (northwestern Germany). *Palaeobiodiversity and Palaeoenvironments* 97:  
476 329–354. <https://doi.org/10.1007/s12549-016-0252-1>

- 477 Chang C-H, Takai M, Ogino S (2012) First discovery of colobine fossils from the early to  
478 middle Pleistocene of southern Taiwan. *Journal of Human Evolution* 63(3): 439–451.  
479 <https://doi.org/10.1016/j.jhevol.2012.03.005>
- 480 Chen, W-S, Huang N-W, Yang C-C (2011) Pleistocene sequence stratigraphic characteristics  
481 and foreland basin evolution, southwestern Taiwan. *Special Publication of the Central*  
482 *Geological Survey* 25: 1–38 (in Chinese, with English Abstract).
- 483 Chen W-S (2016) *An Introduction to the Geology of Taiwan*. Geological Society of Taiwan,  
484 Taipei, 204 pp. (in Chinese)
- 485 Chen Y (2020) Quaternary snake fauna from Shanyangzhai Cave, Hebei, China. Master's  
486 thesis, Northwest University, China. (in Chinese)
- 487 Chen Y, Li YX, Shi JS, Zhang YX, Xie K (2021) Pleistocene fossil snakes (Squamata,  
488 Reptilia) from Shanyangzhai Cave, Hebei, China. *Historical Biology* 33(5): 699–711.  
489 <https://doi.org/10.1080/08912963.2019.1658094>
- 490 Chi W-R, Huang H-M (1982) Nannofossil biostratigraphy of sediments of the Chiutsenglin  
491 Anticline, Tainan Area. *Chinese Petroleum Corporation Exploration and Development*  
492 *Research Center Report (Tan-tsai yen-jiu hui-bao)* 5: 39–56. (in Chinese, with English  
493 Abstract)
- 494 Chyn K, Lin, T-E, Chen Y-K, Chen C-Y, Fitzgerald LA (2019) The magnitude of roadkill in  
495 Taiwan: Patterns and consequences revealed by citizen science. *Biological Conservation*  
496 237: 317–326. <https://doi.org/10.1016/j.biocon.2019.07.014>
- 497 Creer S, Malhotra A, Thorpe R S, Chou W-H (2001) Multiple causation of phylogeographical  
498 pattern as revealed by nested clade analysis of the bamboo viper (*Trimeresurus*  
499 *stejnegeri*) within Taiwan. *Molecular Ecology* 10(8): 1967–1981.  
500 <https://doi.org/10.1046/j.0962-1083.2001.01332.x>
- 501 Currie DJ (1991) Energy and large-scale patterns of animal-and plant-species richness. *The*  
502 *American Naturalist* 137(1): 27–49. <https://doi.org/10.1086/285144>
- 503 Dowling HG, Duellman WE (1978) *Systematic herpetology: a synopsis of families and*  
504 *higher categories*. HISS Publications, Publications in Herpetology 7, New York. Issued  
505 loose-leaf, 302 pp.

- 506 Dufresnes C, Litvinchuk SN (2022) Diversity, distribution and molecular species delimitation  
507 in frogs and toads from the Eastern Palearctic. *Zoological Journal of the Linnean*  
508 *Society* 195(3): 695–760. <https://doi.org/10.1093/zoolinnea/zlab083>
- 509 Figueroa A, McKelvy AD, Grismer LL, Bell CD, Lailvaux SP (2016) A species-level  
510 phylogeny of extant snakes with description of a new colubrid subfamily and genus.  
511 *PLoS ONE* 11(9): e0161070. <https://doi.org/10.1371/journal.pone.0161070>
- 512 Fischer von Waldheim G (1813) *Zoognosia. Tabulis Synopticis Illustrata*, in *Usum*  
513 *Prælectionum Academiae Imperialis Medico-Chirurgicae Mosquensis Edita. Editio tertia*,  
514 *volume primum*. Moscow: Nicolai Sergeidis Vsevolozsky.  
515 <https://doi.org/10.5962/bhl.title.42225>
- 516 Fitzinger L (1826) *Neue classification der reptilien nach ihren natürlichen verwandtschaften:*  
517 *nebst einer verwandtschaftstafel und einem verzeichnisse der reptilien-sammlung des K.*  
518 *K. zoologischen museum's zu Wien*. Wien: J. G. Heubner.  
519 <https://doi.org/10.5962/bhl.title.4683>
- 520 Fitzinger L (1833) In *Wagler, Descr. Icon. Amph. (3): expl. pl. 27*.
- 521 Fitzinger L (1843) *Systema Reptilium. Fasciculus primus, Ambyglossae*. Vindobonae:  
522 *Braumüller et Seidel*. <https://doi.org/10.5962/bhl.title.4694>
- 523 Frost DR, Grant T, Faivovich J, Bain RH, Haas A, Haddad CFB, de Sá RO, Channing A,  
524 *Wilkinson M, Donnellan SC, Raxworthy CJ, Campbell JA, Blotto BL, Moler PE,*  
525 *Drewes RC, Nussbaum RA, Lynch JD, Green DM, Wheeler WC (2006) The amphibian*  
526 *tree of life*. *Bulletin of the American Museum of Natural History* 297: 1–370.  
527 [https://doi.org/10.1206/0003-0090\(2006\)297\[0001:TATOL\]2.0.CO;2](https://doi.org/10.1206/0003-0090(2006)297[0001:TATOL]2.0.CO;2)
- 528 Georgalis GL, Scheyer TM (2022) Crushed but not lost: a colubriiform snake (Serpentes)  
529 from the Miocene Swiss Molasse, identified through the use of micro-CT scanning  
530 technology. *Swiss Journal of Geosciences* 115: 15. [https://doi.org/10.1186/s00015-022-](https://doi.org/10.1186/s00015-022-00417-w)  
531 [00417-w](https://doi.org/10.1186/s00015-022-00417-w)
- 532 Georgalis GL, Rage J-C, de Bonis L, Koufos GD (2018) Lizards and snakes from the late  
533 Miocene hominoid locality of Ravin de la Pluie (Axios Valley, Greece). *Swiss Journal*  
534 *of Geosciences* 111: 169–181. <https://doi.org/10.1007/s00015-017-0291-2>

- 535 Georgalis G, Villa A, Ivanov M, Vasilyan D, Delfino M (2019) Fossil amphibians and  
536 reptiles from the Neogene locality of Maramena (Greece), the most diverse European  
537 herpetofauna at the Miocene/Pliocene transition boundary. *Palaeontologia Electronica*  
538 22(3): 1–99. <https://doi.org/10.26879/908>
- 539 Gray JE (1825) A synopsis of the genera of reptiles and Amphibia, with a description of  
540 some new species. *Annals of Philosophy, Series 2* 10: 193–217.
- 541 Günther ACLG (1864). *The reptiles of British India*. London: Ray Society.  
542 <https://doi.org/10.5962/bhl.title.5012>
- 543 Hayasaka I (1932) Mode of occurrences of mammal fossils in the Sachin-sho area, Shinka-  
544 gun, Tainan Prefecture Taiwan. *Tigaku Kizi* 3(5): 52–54. (in Japanese)
- 545 Ho H-C, Shea K-S, Kao M-C, Chen H-W (2005) Explanatory text of the geologic map of  
546 Sinhua Area, Geological Map of Taiwan scale 1:50,000, Sheet 50. Central Geological  
547 Survey, Ministry of Economic Affairs, New Taipei City, 77 pp.
- 548 Hoge AR, Romano-Hoge SAL (1983) Notes on micro and ultrastructure of “Oberhäutschen”  
549 in Viperioidea. *Mem Inst Butantan* 44/45: 81–118.
- 550 Holman JA (2000) *The fossil snakes of North America: Origin, evolution, distribution,*  
551 *paleoecology*. Indiana University Press, Bloomington, 376 pp.
- 552 Hsu C-H, Lin J-P, Lin C-H, (2024) A spatangoid echinoid assemblage from the Gutingkeng  
553 Formation (Early Pleistocene) of Taiwan and its paleoenvironmental and geological  
554 implications. *Geobios* 87: 9–23. <https://doi.org/10.1016/j.geobios.2024.09.003>
- 555 Hu C-H (1989) Manual for ten geological routes in central Taiwan—route 7: geology along  
556 the Nanheng Highway—Tsailiao, Peiliao, Chiahsien. In: Faculty members of the  
557 Department of Earth Sciences, National Taiwan Normal University, editors. *Field*  
558 *manual of the geology of Taiwan (II)*. Department of Earth Sciences, National Taiwan  
559 Normal University, Taipei, 105–163.
- 560 Hu C-H, Tao H-J (1982) A new species of solitary corals and associated fossils from the  
561 lower Gutingkeng formation of Taiwan. *Ti-Chih* 4(1): 39–46.
- 562 Ikeda T (2007) A comparative morphological study of the vertebrae of snakes occurring in  
563 Japan and adjacent regions. *Current Herpetology* 26(1): 13–34.  
564 [https://doi.org/10.3105/1345-5834\(2007\)26\[13:ACMSOT\]2.0.CO;2](https://doi.org/10.3105/1345-5834(2007)26[13:ACMSOT]2.0.CO;2)

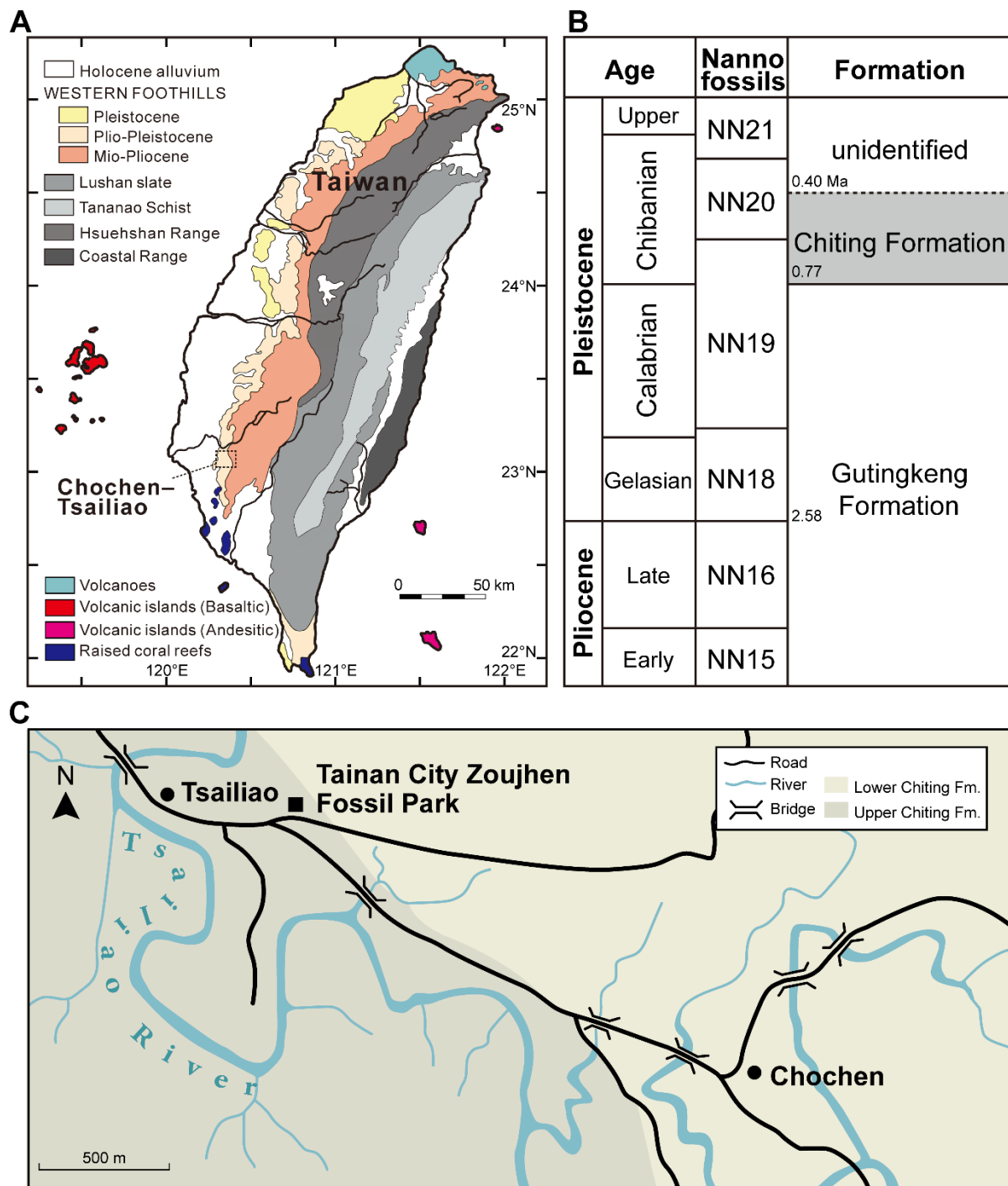
- 565 Ikeda T, Otsuka H, Ota H (2016) Early pleistocene fossil snakes (reptilia: squamata) from  
566 Okinawajima Island in the Ryukyu Archipelago, southwestern Japan. *Herpetological*  
567 *Monographs* 30(1): 143–156. [https://doi.org/10.1655/HERPMONOGRAPHS-D-15-](https://doi.org/10.1655/HERPMONOGRAPHS-D-15-00005.1)  
568 00005.1
- 569 Ikeda T, Akio T, Makoto M, Yoshikazu H (2019) Snake vertebrae fossils occurred from the  
570 Minatogawa Man site, southern part of Okinawajima Island, Ryukyu Archipelago,  
571 southwestern Japan. *Bulletin of Gunma Museum Nature History* (23): 21–34.  
572 [https://jglobal.jst.go.jp/en/detail?JGLOBAL\\_ID=201902298577698255](https://jglobal.jst.go.jp/en/detail?JGLOBAL_ID=201902298577698255) (in Japanese,  
573 with English Abstract)
- 574 Ivanov M, Vasilyan D, Böhme M, Zazhigin VS (2018) Miocene snakes from northeastern  
575 Kazakhstan: new data on the evolution of snake assemblages in Siberia. *Historical*  
576 *Biology* 31(10): 1284–1303. <https://doi.org/10.1080/08912963.2018.1446086>
- 577 Kaito T, Mamoru T (2016) The biogeographical history of Asian keelback snakes of the  
578 genus *Hebius* (Squamata: Colubridae: Natricinae) in the Ryukyu Archipelago, Japan.  
579 *Biological Journal of the Linnean Society* 118(2): 187–199.  
580 <https://doi.org/10.1111/bij.12726>
- 581 Kawamura A, Chang C-H, Kawamura Y (2016) Middle Pleistocene to Holocene mammal  
582 faunas of the Ryukyu Islands and Taiwan: an updated review incorporating results of  
583 recent research. *Quaternary International* 397:117–135.  
584 <https://doi.org/10.1016/j.quaint.2015.06.044>
- 585 Kuntz RE (1963) Snakes of Taiwan. *Quarterly Journal of the Taiwan Museum* 16: 1–80.
- 586 Lee K-H, Chen T-H, Shang G, Clulow S, Yang Y-J, Lin S-M (2019) A check list and  
587 population trends of invasive amphibians and reptiles in Taiwan. *ZooKeys* 829: 85–130.  
588 <https://doi.org/10.3897/zookeys.829.27535>
- 589 Lin C-H, Chien C-W, Lee S-W, Chang C-W (2021) Fish fossils of Taiwan: a review and  
590 prospection. *Historical Biology* 33(9): 1362–1372.  
591 <https://doi.org/10.1080/08912963.2019.1698563>
- 592 Lin C-H, Wu S-M, Lin C-Y, Chien C-W (2023) Early Pliocene otolith assemblages from the  
593 outer-shelf environment reveal the establishment of mesopelagic fish fauna over 3

- 594 million years ago in southwestern Taiwan. *Swiss Journal of Palaeontology* 142: 23.  
595 <https://doi.org/10.1186/s13358-023-00288-0>
- 596 Lin H-D, Chen Y-R, Lin S-M (2012) Strict consistency between genetic and topographic  
597 landscapes of the brown tree frog (*Buergeria robusta*) in Taiwan. *Molecular*  
598 *Phylogenetics and Evolution* 62(1): 251–262.  
599 <https://doi.org/10.1016/j.ympev.2011.09.022>
- 600 Linnaeus C (1758) *Systema naturae per regna tria naturae, secundum classes, ordines, genera,*  
601 *species, cumcharacteribus, differentiis, synonymis, locis. Tomus 1, Pars 1. Laurentii*  
602 *Salvius, Stockholm.* <https://doi.org/10.5962/bhl.title.542>
- 603 Lue K-Y, Du M-Z, Shang G-S (2002) *The Amphibians and Reptiles of Taiwan. Society for*  
604 *Wildlife And Nature, Taipei, 347 pp.*
- 605 McCartney JA, Stevens NJ, Connor PM (2014) The earliest Colubroid-dominated snake  
606 fauna from Africa: Perspectives from the Late Oligocene Nsungwe Formation of  
607 Southwestern Tanzania. *PLoS ONE* 9(3): e90415.
- 608 Nakamura Y, Takahashi A, Ota H (2013) Recent cryptic extinction of squamate reptiles on  
609 Yoronjima Island of the Ryukyu Archipelago, Japan, inferred from garbage dump  
610 remains. *Acta Herpetologica* 8(1): 19–34. [https://doi.org/10.13128/Acta\\_Herpetol-11924](https://doi.org/10.13128/Acta_Herpetol-11924)
- 611 Oppel M (1811) *Die Ordnungen, Familien und Gattungen der Reptilien als Prodrom einer*  
612 *Naturgeschichte derselben. Munich: Joseph Lindauer.*  
613 <https://doi.org/10.5962/bhl.title.4911>
- 614 Ota H (1998) Geographic patterns of endemism and speciation in amphibians and reptiles of  
615 the Ryukyu Archipelago, Japan, with special reference to their paleogeographical  
616 implications. *Population Ecology* 40(2): 189–204. <https://doi.org/10.1007/BF02763404>
- 617 Otsuka H (1984) Stratigraphic position of the Chochen vertebrate fauna of the T'ouk'oushan  
618 Group in the environs of the Chochen district, southwest Taiwan, with special reference  
619 to its geologic age. *Journal of the National Taiwan Museum* 37: 37–55.
- 620 Otsuka H, Lin C-C (1984) Fossil rhinoceros from the Toukoushan group in Taiwan. *Journal*  
621 *of the National Taiwan Museum* 37(1): 1–35.
- 622 Päckert M, Martens J, Severinghaus LL (2009) The Taiwan Firecrest (*Regulus goodfellowi*)  
623 belongs to the Goldcrest assemblage (*Regulus regulus* sl): evidence from mitochondrial

- 624 DNA and the territorial song of the Regulidae. *Journal of Ornithology* 150: 205–220.  
625 <https://doi.org/10.1007/s10336-008-0335-5>
- 626 Qi G-Q, Ho C-K, Chang CH (1999) The Pleistocene fossil suids from Chochen, Tainan,  
627 southwestern Taiwan. *Bulletin of the National Museum of Natural Science* 12: 33–40.
- 628 Rage J-C (1984) *Encyclopedia of Paleoherpétology*, part 11, Serpentes. Gustav Fischer  
629 Verlag, Stuttgart, 80 pp.
- 630 Rage J-C, Roček Z (2003) Evolution of anuran assemblages in the Tertiary and Quaternary of  
631 Europe, in the context of palaeoclimate and palaeogeography. *Amphibia Reptilia* 24:  
632 133–167. <https://doi.org/10.1163/156853803322390408>
- 633 Ratnikov VY (2004) Identification of some Eurasian species of *Elaphe* (Colubridae,  
634 Serpentes) on the basis of vertebrae. *Russian Journal of Herpetology* 11(2): 91–98.
- 635 Ratnikov V (2022) Comparative osteology of two far eastern species of ratsnakes (Serpentes:  
636 Colubridae), *Elaphe dione* (Pallas, 1773) and *E. schrenckii* (Strauch, 1873), for the  
637 purpose of palaeontological studies. *Asian Herpetological Research* 13(1): 1–22.  
638 <https://doi.org/10.16373/j.cnki.ahr.210021>
- 639 Ratnikov V (2024) Vertebrae of modern viperids of the far east: Comparative characterisation  
640 for the identification of their fossil remains. *Asian Herpetological Research* 15(3): 152–  
641 172. <https://doi.org/10.3724/ahr.2095-0357.2024.0005>
- 642 Schneider JG (1799) *Historia Amphibiorum Naturalis et Literariae. Fasciculus Primus.*  
643 *Continens Ranas, Calamitas, Bufones, Salamandras et Hydros in Genera et Species*  
644 *Descriptos Notisque suis Distinctos.* Jena: Friederici Frommanni.  
645 <https://doi.org/10.5962/bhl.title.78757>
- 646 Shang G-S, Li P-H, Yang Y-J (2009) *Field guide to amphibians and reptiles in Taiwan.* Owl  
647 Publishing House Company, Taipei, 336 pp. (in Chinese)
- 648 Shi J, Wang Y, Messenger KR, Jiangzuo Q, Chen Y, Jin C (2023) Early Pliocene fossil  
649 snakes (Squamata, Colubroidea) with various teeth from the fissure deposit in Queshan,  
650 Henan, China. *Historical Biology* 1–22.  
651 <https://doi.org/10.1080/08912963.2022.2161382>
- 652 Shieh Y-T, Chang C-H (2007) Study on the Proboscidea fossils of the National Taiwan  
653 Museum. *Journal of the National Taiwan Museum* 60(1): 33–44. (in Chinese)

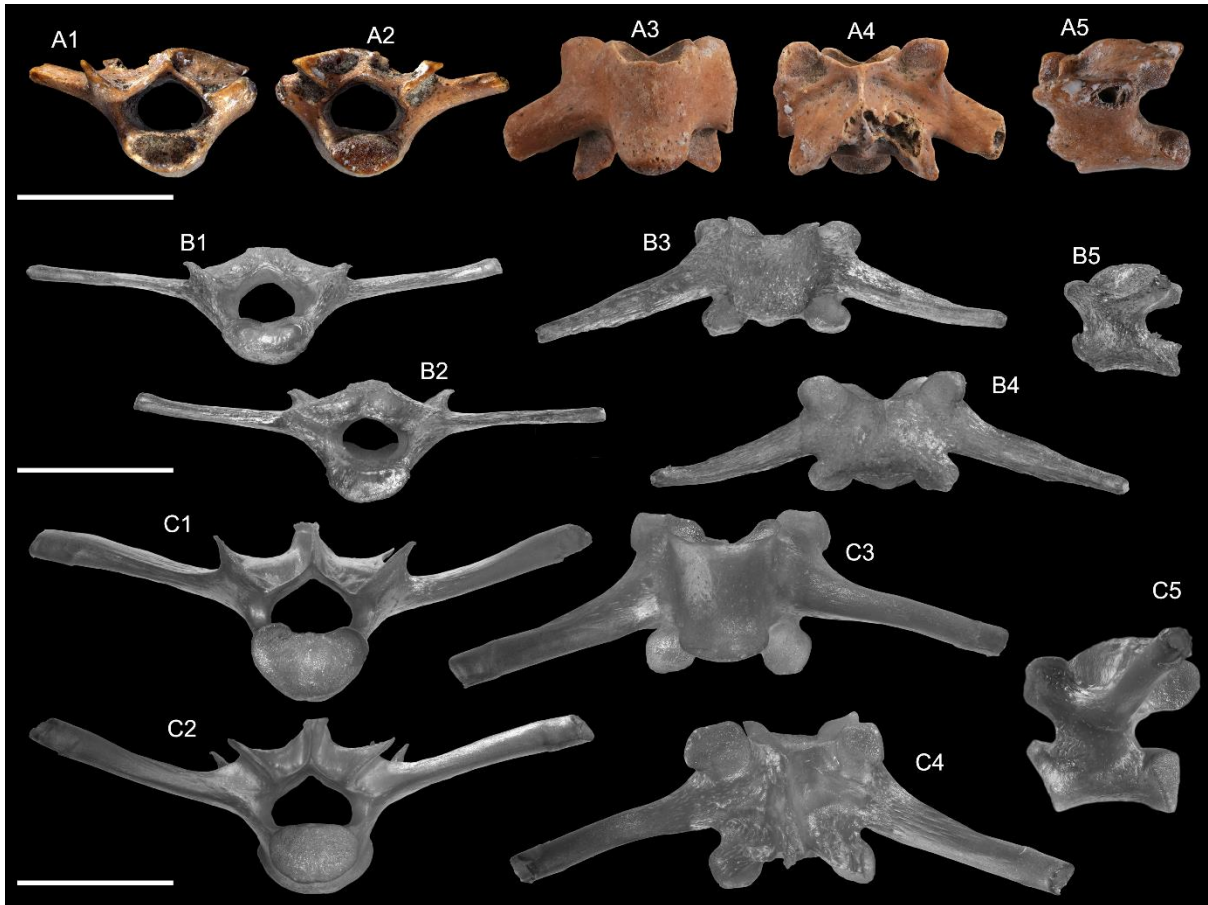
- 654 Shikama T (1937) Fossil cervifauna of Syatin near Tainan, southwestern Taiwan (Formosa).  
655 The Science Reports of the Tohoku Imperial University, 2nd Series, Geology 19(1): 75–  
656 85.
- 657 Shikama T (1972). Fossil Crocodilia from Tsochin, southwestern Taiwan. Science Report of  
658 Yokohama National University: Biological and Geological Sciences, Section II 19: 125–  
659 131.
- 660 Shikama T, Otsuka H, Yomida Y (1975a) Fossil Proboscidea from Taiwan (I). Science  
661 Reports of the Yokohama National University, Section II 22: 13–35.
- 662 Shikama T, Otsuka H, Yomida Y (1975b) Fossil Proboscidea from Taiwan (II). Science  
663 Reports of the Yokohama National University, Section II 22: 37–62.
- 664 Shikama T, Ling C-C, Shimoda N, Baba H (1976) Discovery of fossil *Homo sapiens* from  
665 Chochen in Taiwan. Journal of the Anthropological Society of Nippon 84(2): 131–138.  
666 <https://doi.org/10.1537/ase1911.84.131>
- 667 Szyndlar Z (1984) Fossil snakes from Poland. Acta Zoologica Cracoviensia 28(1): 1–156.
- 668 Szyndlar Z (1991a) A review of Neogene and Quaternary snakes of central and eastern  
669 Europe. Part 1: Scolecophidia, Boidae, Colubrinae. Estudios Geológicos 47(1–2): 103–  
670 126. <https://doi.org/10.3989/egeol.91471-2412>
- 671 Szyndlar Z (1991b) A review of Neogene and Quaternary snakes of central and eastern  
672 Europe. Part 11: Natricinae, Elapidae, Viperidae. Estudios Geológicos, 47: 237–266.  
673 <https://doi.org/10.3989/egeol.91473-4422>
- 674 Szyndlar Z (2012) Early Oligocene to Pliocene Colubridae of Europe: a review. Bulletin de la  
675 Société géologique de France 183(6): 661–681.  
676 <https://doi.org/10.2113/gssgfbull.183.6.661>
- 677 Tao H-J, Hu C-H (2001) Cyprinidae fossil fishes of Tainan Hsien, Taiwan. Ti- Chih 21(1):  
678 51–64.
- 679 Tsai C-H, Mayr G (2021) A phasianid bird from the Pleistocene of Tainan: the very first  
680 avian fossil from Taiwan. Journal of Ornithology 162: 919–923.  
681 <https://doi.org/10.1007/s10336-021-01886-w>

- 682 Underwood G (1967) A comprehensive approach to the classification of higher snakes.  
683 *Herpetologica* 23(2): 161–168.
- 684 Venczel M (2011) Middle-late Miocene snakes from the Pannonian Basin. *Acta*  
685 *Palaeontologica Romaniae* 7: 343–349.
- 686 Wüster W, Peppin L, Pook CE, Walker DE (2008) A nesting of vipers: phylogeny and  
687 historical biogeography of the Viperidae (Squamata: Serpentes). *Molecular*  
688 *Phylogenetics and Evolution* 49(2): 445–459.  
689 <https://doi.org/10.1016/j.ympev.2008.08.019>
- 690 Yang SF, Komaki S, Brown RM, Lin SM (2018) Riding the Kuroshio Current: Stepping  
691 stone dispersal of the Okinawa tree lizard across the East Asian Island Arc. *Journal of*  
692 *Biogeography* 45(1): 37–50. <https://doi.org/10.1111/jbi.13111>
- 693 Zaher H (1999) Hemipenial morphology of the South American xenodontine snakes: with a  
694 proposal for a monophyletic Xenodontinae and a reappraisal of colubroid hemipenes.  
695 No. 240. *Bulletin of the American Museum of Natural History*, New York, 168 pp.
- 696 Zaher H, Grazziotin FG, Cadle JE, Murphy RW, Moura-Leite JC, Bonatto SL (2009)  
697 Molecular phylogeny of advanced snakes (Serpentes, Caenophidia) with an emphasis on  
698 South American xenodontines: a revised classification and descriptions of new taxa  
699 *Papéis Avulsos de Zoologia* 49(11): 115–153. <https://doi.org/10.1590/S0031->  
700 [10492009001100001](https://doi.org/10.1590/S0031-10492009001100001)
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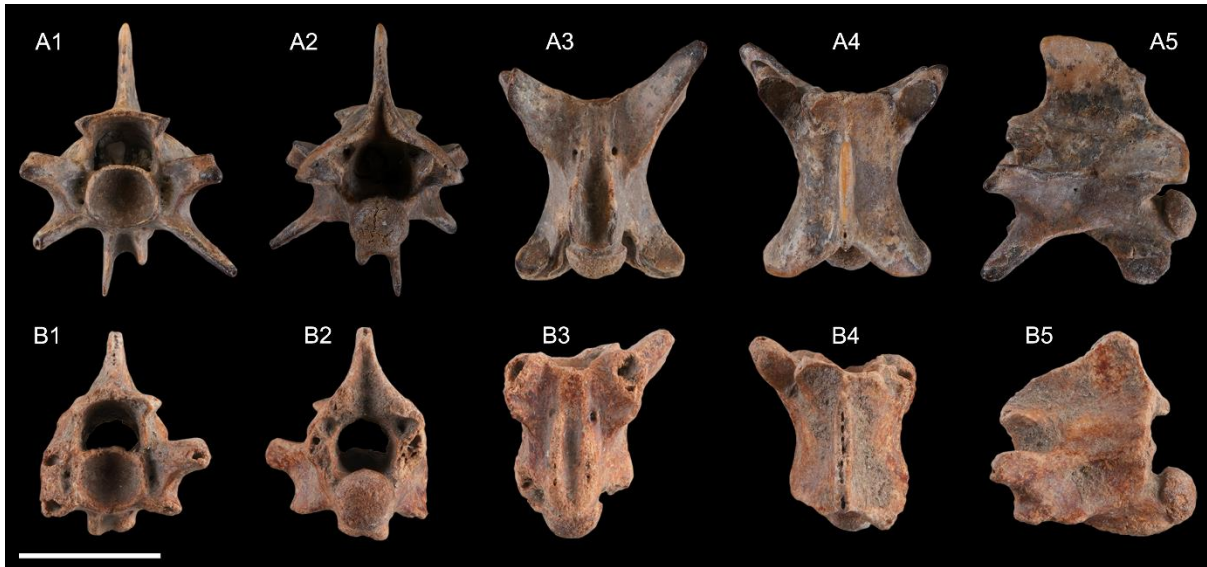
703 **Figure 1.** Geological and stratigraphic context of the Chochen–Tsailiao fossil locality in  
 704 southern Taiwan. **A.** Generalized geological map of Taiwan. The Chochen–Tsailiao area is  
 705 highlighted by a dashed rectangle (modified after Chen 2016; Lin et al. 2021). **B.**  
 706 Stratigraphic column of the Chochen–Tsailiao area (modified after Chen, 2016; Lin et al.,  
 707 2023). **C.** Detailed map of the Chochen–Tsailiao area (modified after Qi et al. 1999). Fossils  
 708 were collected from reworked deposits within the riverbed along the Tsailiao River (see text  
 709 for details).



710

711 **Figure 2.** **A.** *Duttaphrynus melanostictus* (ASIZF 0101045) from the Middle Pleistocene  
712 Chitin Formation, southern Taiwan. **B.** Extant specimen of *D. melanostictus* (ASIZAM  
713 000064), 4<sup>th</sup> trunk vertebra, 94.12 cm SVL (snout–vent length), 66 g. **C.** Extant specimen of  
714 *Bufo bankorensis* (ASIZAM 000062), 4<sup>th</sup> trunk vertebra, 10.727 cm SVL. **1.** anterior view; **2.**  
715 posterior view; **3.** ventral view; **4.** dorsal view; **5.** lateral view. Scale bar = 5 mm.

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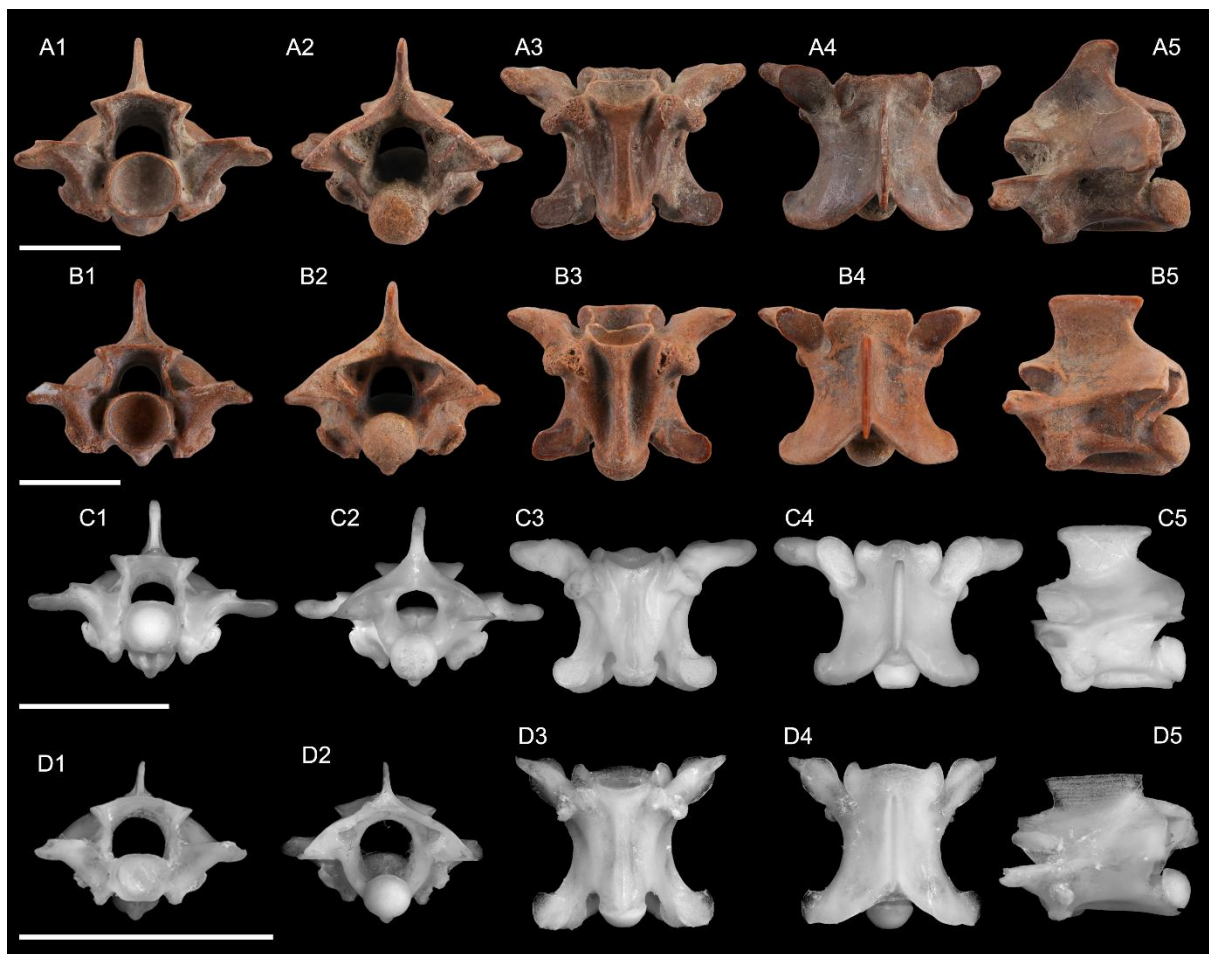


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718 **Figure 3. A–B.** *Elaphe* sp. (ASIZF 0101046–1047) from the Middle Pleistocene Chitin  
719 Formation, southern Taiwan. **1.** anterior view; **2.** posterior view; **3.** ventral view; **4.** dorsal  
720 view; **5.** lateral view. Scale bar = 5 mm.

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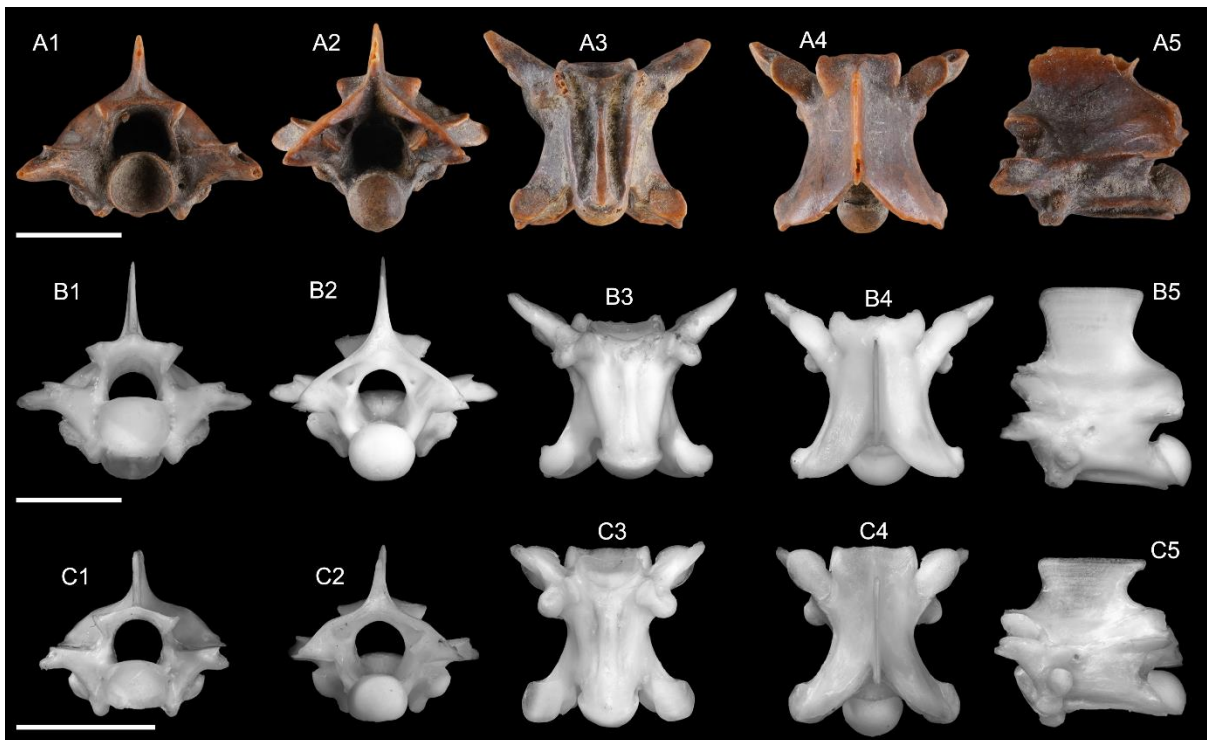
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724 **Figure 4.** A–B. *Lycodon rufozonatum* (ASIZF 0101048–1049) from the Middle Pleistocene  
 725 Chitin Formation, southern Taiwan. C. Extant specimen of *L. rufozonatum* (ASIZRE  
 726 000007), 94<sup>th</sup> trunk vertebra, 74.206 cm TL (total length), 55.625 cm SVL (snout–vent  
 727 length), 102 g. D. Extant specimen of *Lycodon ruhstrati* (ASIZRE 000005), 31<sup>st</sup> trunk  
 728 vertebra, 71.8 cm TL, 53.2 cm SVL, 18 g. **1.** anterior view; **2.** posterior view; **3.** ventral view;  
 729 **4.** dorsal view; **5.** lateral view. Scale bar = 5 mm.

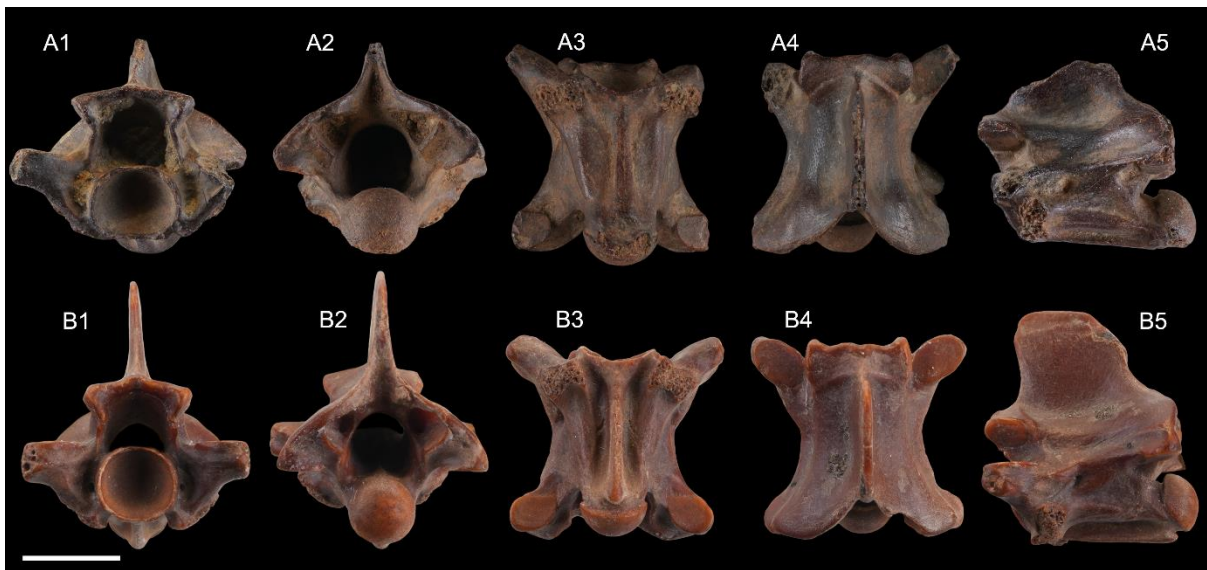
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732 **Figure 5.** **A.** *Ptyas mucosa* (ASIZF 0101050) from the Middle Pleistocene Chitin Formation,  
733 southern Taiwan. **B.** Extant specimen of *Ptyas mucosa* (ASIZRE 000004), 55<sup>th</sup> trunk  
734 vertebra, 161.8 cm TL (total length), 120 cm SVL (snout–vent length), 584 g. **C.** Extant  
735 specimen of *Ptyas major* (ASIZRE 000006), 101<sup>st</sup> trunk vertebra, 80.472 cm TL, 51.322 cm  
736 SVL, 126 g. **1.** anterior view; **2.** posterior view; **3.** ventral view; **4.** dorsal view; **5.** lateral  
737 view. Scale bar = 5 mm.

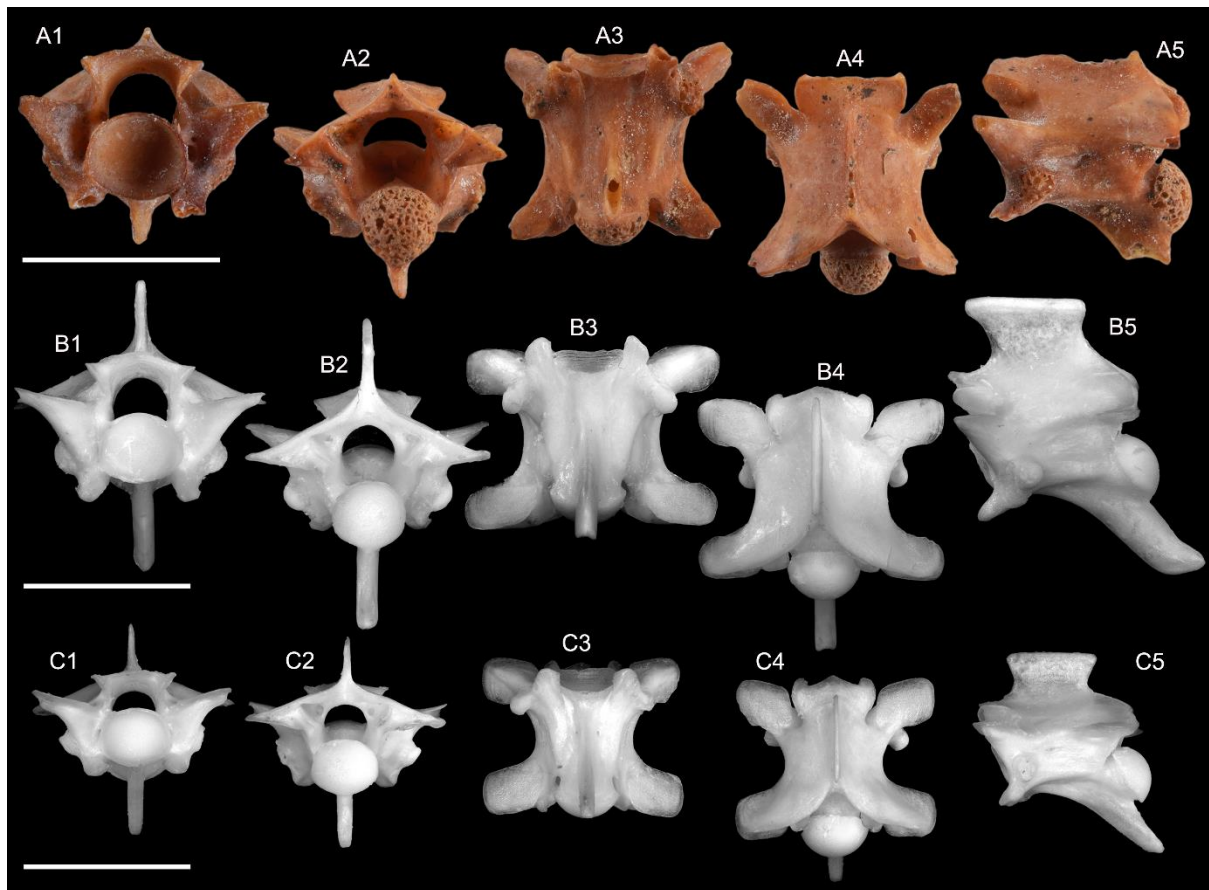
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740 **Figure 6.** *Ptyas cf. mucosa* (ASIZF 0101051–1052) from the Middle Pleistocene Chitin  
741 Formation, southern Taiwan. **1.** anterior view; **2.** posterior view; **3.** ventral view; **4.** dorsal  
742 view; **5.** lateral view. Scale bar = 5 mm.

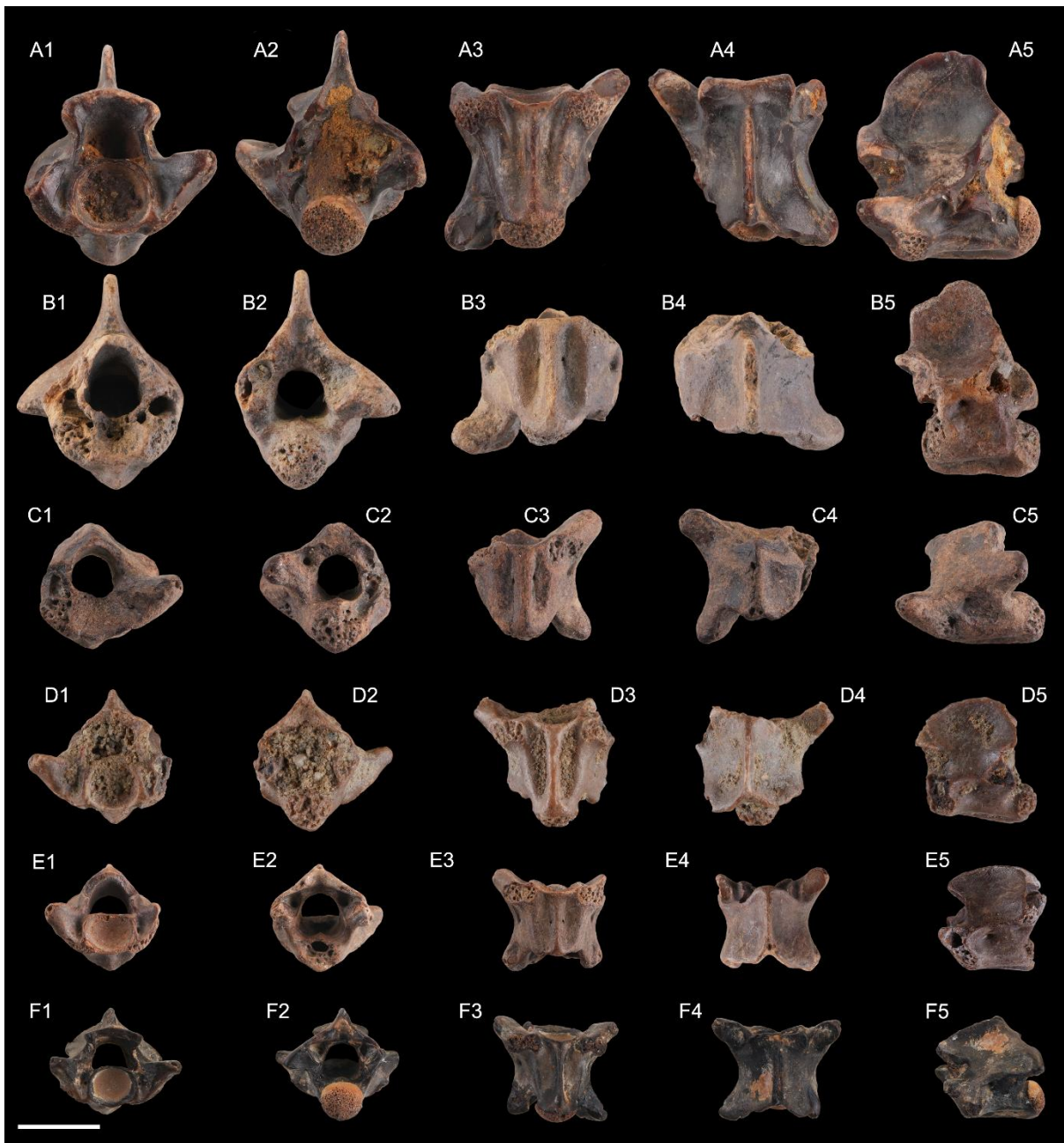
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745 **Figure 7. A.** *Protobothrops* sp. (ASIZF 0101053) from the Middle Pleistocene Chitin  
746 Formation, southern Taiwan. **B.** Extant specimen of *Protobothrops mucrosquamatus*  
747 (ASIZRE 000002), 108<sup>th</sup> trunk vertebra, 91 cm TL (total length), 72 cm SVL (snout–vent  
748 length), 126 g. **C.** Extant specimen of *Trimeresurus stejnegeri* (ASIZRE 000003), 79<sup>th</sup> trunk  
749 vertebra, 63.1 cm TL, 52.2 cm SVL, 56 g. **1.** anterior view; **2.** posterior view; **3.** ventral view;  
750 **4.** dorsal view; **5.** lateral view. Scale bar = 5 mm.

751



752

753 **Figure 8.** Alethinophidia indet. (ASIZF 0101054–1059) from the Middle Pleistocene Chitin  
754 Formation, southern Taiwan. **1.** anterior view; **2.** posterior view; **3.** ventral view; **4.** dorsal  
755 view; **5.** lateral view. Scale bar = 5 mm.



756

757 **Figure 9.** Reconstruction of Middle Pleistocene herpetofauna in southern Taiwan. The  
 758 illustration highlights key taxa, including *Duttaphrynus melanostictus*, *Elaphe*, *Lycodon*  
 759 *rufozonatum*, *Ptyas mucosa*, and *Protobothrops*. Artwork by Yun-Kae Kiang.

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761 **Table caption**

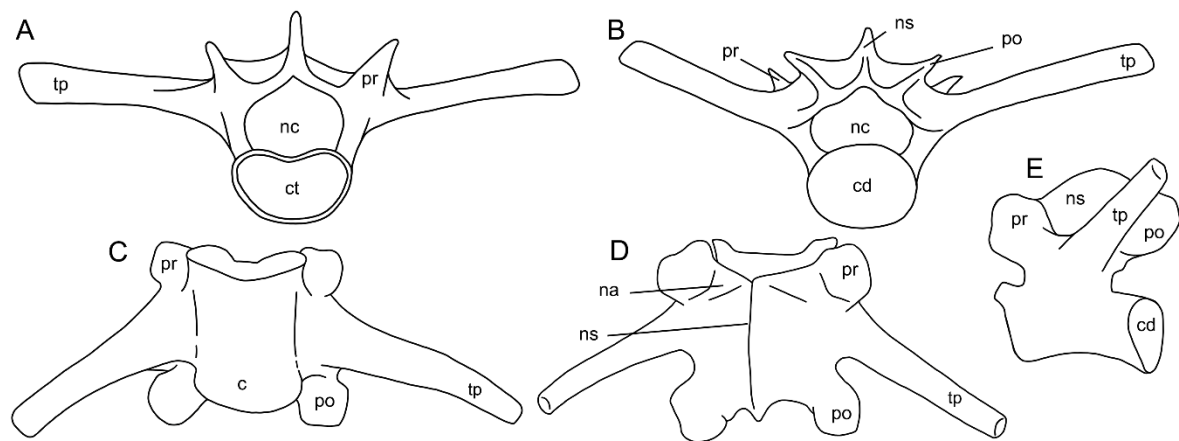
762 **Table 1.** Measurements (in mm) of the vertebrae from the Middle Pleistocene Chitin  
 763 Formation described in this study. **Abbreviations:** **CL** – centrum length; **COH** – condyle  
 764 height; **COW** – condyle width; **CTH** – cotyle height; **CTW** – cotyle width; **NAH** neural arch  
 765 height; **NAW** – neural arch width; **NH** – neural spine height; **NSL** – length of the neural  
 766 spine; **PO-PO** – width of the postzygapophyseal articular facets; **PR-PO** – distance between  
 767 prezygapophyses and postzygapophyses of the same side; **ZW** – zygosphenes width (after  
 768 Ikeda 2007; McCartney et al. 2014; Venczel 2011).

Taxon	CTH	CTW	COH	COW	NAH	PO-PO	CL	PR-PO	ZW	NAW	NSL	NH	CL/NAW	NAH/PO-PO	NSL/NH
<i>Duttaphrynus melanostictus</i>	0.92	2.12	1.31	2.22	NA	4.86	3.66	4.63	NA	NA	NA	NA	NA	NA	NA
<i>Elaphe</i> sp.	2.05	2.37	1.96	2.14	2.08	5.90	5.45	8.30	3.00	3.42	4.71	2.92	1.60	0.35	1.58
<i>Elaphe</i> sp.	2.01	2.39	2.23	2.20	2.80	NA	5.35	NA	3.10	3.78	2.73	1.26	1.41	NA	0.02
<i>Lycodon rufozonatum</i>	3.00	3.31	2.94	3.03	3.94	9.53	6.37	8.1	4.42	5.85	3.62	2.39	1.08	0.41	1.51

<i>Lycodon rufozonatum</i>	2.86	3.09	2.74	2.83	3.59	9.03	6.25	7.8	4.18	5.53	4.97	2.64	1.13	0.40	1.88
<i>Ptyas mucosa</i>	2.76	2.88	2.62	2.68	4.17	8.33	6.46	8.9	3.75	4.95	3.21	2.30	1.31	0.50	1.40
<i>Ptyas cf. mucosa</i>	3.40	4.17	3.48	4.14	3.99	10.17	7.87	9.6	5.50	6.44	8.96	2.82	1.22	0.04	3.18
<i>Ptyas cf. mucosa</i>	3.66	3.74	3.35	3.46	3.90	10.65	8.17	10.2	5.11	6.30	7.52	4.60	1.30	0.32	1.63
<i>Protobothrops sp.</i>	2.05	2.28	1.98	1.86	1.20	5.46	3.87	4.8	2.80	3.61	NA	NA	1.08	0.22	NA

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770 **Supplementary files**



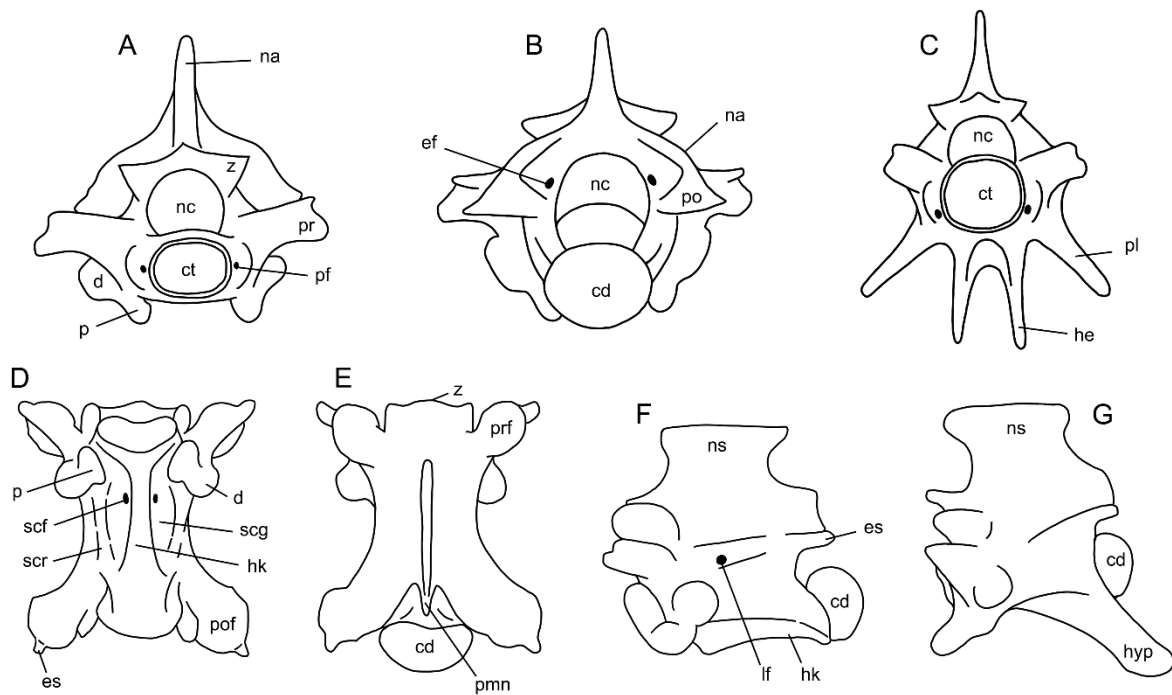
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772 **Supplementary Figure 1.** Basic anatomical views and terminology of a generalized toad  
 773 vertebra. **A.** anterior view; **B.** posterior view; **C.** ventral view; **D.** dorsal view; **E.** lateral view.

774 **Abbreviations:** **c** – centrum; **cd** – condyle; **ct** – cotyle; **na** – neural arch; **nc** – neural canal;  
 775 **ns** – neural spine; **po** – postzygapophysis; **pr** – prezygapophysis; **tp** – transverse process.

776

777



778

779 **Supplementary Figure 2.** Basic anatomical views and terminology of a generalized snake  
 780 vertebra (after Ikeda 2007). **A.** anterior view; **B.** posterior view; **C.** caudal anterior view; **D.**  
 781 ventral view; **E.** dorsal view; **F.–G.** lateral view. **Abbreviations:** **cd** – condyle; **ct** – cotyle; **d**  
 782 – diapophysis; **ef** – endozygtral foramen; **es** – epizygapophyseal spine; **he** – hemapophysis;  
 783 **hk** – haemal keel; **hyp** – hypapophysis; **lf** – lateral foramen; **na** – neural arch; **nc** – neural  
 784 canal; **ns** – neural spine; **p** – parapophysis; **pf** – paracotylar foramen; **pl** – pleurapophysis;  
 785 **pmn** – posterior medial notch; **po** – postzygapophysis; **pof** – postzygapophyseal articular  
 786 facet; **pr** – prezygapophysis; **prf** – prezygapophyseal articular facet; **scf** – subcentral  
 787 foramen; **scg** – subcentral groove; **scr** – subcentral ridge; **z** – zygosphene.