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1 **A new basal snake from the mid-Cretaceous of Morocco**

2

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11

12 **Abstract**

13 Fossil snakes are relatively well represented in the Upper Cretaceous of northern Africa, with
14 material known from Morocco, Sudan, Egypt, Libya, Algeria, and Niger. The Moroccan Kem
15 Kem beds yield a particularly diverse snake assemblage, with Simoliophiidae, Madtsoiidae,
16 ?Nigerophiidae and several unnamed taxa co-occurring. These fossils are important for our
17 understanding of the early evolutionary history of snakes, and may shed light on the ecology
18 and initial diversification of basal snakes. We describe a new taxon, *Norisophis begaa* gen. et
19 sp. nov., from the Kem Kem beds of Begaa, in southeast Morocco. It is characterised by a
20 marked interzygapophyseal constriction, parazygantral foramina, an incipient
21 prezygapophyseal process, and an antero-posteriorly short centrum. Several characteristics
22 shared with *Najash*, *Seismophis*, Madtsoiidae, and *Coniophis* suggest that *Norisophis* is a stem
23 ophidian. *N. begaa* further increases the diversity and disparity of snakes within the Kem Kem
24 beds, supporting the hypothesis that Africa was a mid-Cretaceous hotspot for snakes.

25

26 Keywords: Cretaceous, Ophidia, Serpentes, Kem Kem, Morocco

27

28 1. Introduction

29

30 Snakes are a highly successful clade of reptiles, occupying all continents except Antarctica and
31 represented today by approximately 3,400 species (Hsiang et al. 2015; Greene 1997). The
32 origin and early evolutionary history of snakes, however, remains poorly understood. In
33 contrast to their extant diversity, there is a dearth of fossil data for the Serpentes stem and at
34 the base of the crown group, hindering attempts to reconstruct phylogenetic relationships,
35 the timing of divergence events, and the ecology of early snakes (Hsiang et al. 2015).
36 Considerable debate has stemmed from this, most notably about whether snakes originated in
37 Laurasia or Gondwana, and whether the snake body plan originated in a terrestrial or marine
38 context (Hsiang et al. 2015; Martill et al. 2015; Lee et al. 2016; Longrich et al. 2012a; Rieppel
39 et al. 2003).

40

41 The geographical origin of snakes continues to be a subject of discussion. Iguania and
42 Anguimorpha, recovered as closest relatives to Serpentes by phylogenetic analyses using
43 molecular or combined molecular and morphological data (Pyron et al. 2013; Vidal & Hedges
44 2009; Zheng & Wiens 2016; Wiens et al. 2012; Reeder et al. 2015; Mulcahy et al. 2012),
45 appear to originate in Laurasia (Benson et al. 2013; Vidal & Hedges 2005). Furthermore, the
46 putative early snakes *Parviraptor*, *Diablophis*, *Eophis* and *Portugalophis*, dating from ~ 167 –
47 155 Ma, are from Laurasia (Caldwell et al. 2015), as is the definitive stem snake *Coniophis*
48 *precedens* (Marsh 1892). However, many of the earliest definitive ophidians, including the
49 Nigerophiidae, Lapparentophiidae, *Seismophis*, *Lunaophis*, *Dinilysia*, and *Najash* are
50 Gondwanan (de Broin et al. 1974; Woodward 1901; Rage & Albino 1989; Zaher et al. 2009;
51 Apesteguía & Zaher 2006; Rage & Escuillie 2003; Albino et al. 2016), whilst the Madtsoiidae
52 and Simoliophiidae are present on both supercontinents (Vasile et al. 2013; Rage 1996;

53 Mohabey et al. 2011; Rage & Dutheil 2008; Rage et al. 2016; Nessov et al. 1998; Rieppel et al.
54 2003; Rage & Escuillié 2003). A recent biogeographical analysis using ancestral state
55 reconstruction suggests that the situation is complicated, with the snake total group probably
56 having originated in Laurasia, but the crown group originating in Gondwana (Hsiang et al.
57 2015).

58

59 Another focus of debate is whether snakes evolved on land, or in the oceans. Some evidence
60 points towards an aquatic origin, such as a potentially close relationship between snakes and
61 mosasaurs (Martill et al. 2015; Reeder et al. 2015; Lee 1997; Lee 1998), and the existence of
62 aquatic taxa such as the Simoliophiidae (Rage & Escuillié 2003; Lee et al. 1999; Caldwell & Lee
63 1997; Rage & Escuillié 2000; Tchernov et al. 2000), Nigerophiidae (Rage 1975), and
64 *Lunaophis* (Albino et al. 2016). However, evidence increasingly points towards a terrestrial
65 origin, an hypothesis that is supported by ancestral state reconstruction (Hsiang et al. 2015),
66 the resemblance of the inner ear of *Dinilysia* to that of burrowing squamates (Yi & Norell
67 2015), and new fossils such as *Tetrapodophis amplexus*, a four-limbed snake that shows
68 adaptations for burrowing (Martill et al. 2015; Lee et al. 2016).

69

70 The mid-Cretaceous of North Africa provides a window into snake evolution around crown
71 Serpentes, and can potentially help answer some of these questions. Multiple localities in
72 North Africa produce mid-Cretaceous fossil snakes, including the Moroccan Kem Kem beds
73 (Rage & Dutheil 2008), the Wadi Milk Formation of Sudan (Rage and Werner, 1999; although
74 some recent evidence suggests that this fauna could be Maastrichtian or Campanian-
75 Maastrichtian in age; Eisawi et al., 2012; Eisawi, 2015; Klein et al., 2016), the Bahariya
76 Formation in Egypt (Nopcsa 1925), the Mizdah Formation in Libya (originally assigned to the
77 Maastrichtian by Nessov et al., 1998, but then referred to the Cenomanian by Rage and
78 Cappetta, 2002), and the “série d’In Akhamil” of Algeria (Cuny et al. 1990). Simoliophiidae,

79 Madtsoiidae, and Nigerophiidae are present in these localities, as well as several ophidian taxa
80 of uncertain affiliation.

81

82 Among the most productive of these localities are the Kem Kem beds of southeastern
83 Morocco. Vertebrate fossils in the Kem Kem beds are typically preserved as isolated elements,
84 associated skeletons being very uncommon (Ibrahim, Sereno, et al. 2014). The beds are
85 particularly well known for the abundance and diversity of their large vertebrate assemblage,
86 which includes crocodylomorphs (Sereno & Larsson 2009), theropod and sauropod dinosaurs
87 (Mannion & Barrett 2013; Ibrahim, Sereno, et al. 2014; Sereno et al. 1996; Russell 1996), and
88 large pterosaurs (Ibrahim et al. 2010). Giant predatory dinosaurs (e.g. *Spinosaurus*,
89 *Carcharodontosaurus*) are unusually abundant (Ibrahim et al. 2016), but no ornithischian
90 dinosaur postcranial elements or teeth have been recorded (see Ibrahim et al., 2014b for
91 possible ichnological evidence). The fauna is also rich in fishes and non-archosaurian reptiles
92 and amphibians, with elasmobranchs, actinopterygians, at least one species of salamander,
93 several species of frogs and turtles, an iguanian and an undetermined lizard, and snakes
94 reported (Cavin et al. 2010; Rage & Dutheil 2008; Apesteguía et al. 2016).

95

96 At least four snake clades occur in the Kem Kem beds: Simoliophiidae, Madtsoiidae,
97 ?Nigerophiidae, and an undetermined snake (Rage & Dutheil 2008). Remains are locally
98 abundant, with dozens of simoliophiid specimens reported by Rage and Dutheil (2008). Here,
99 we describe a further snake genus, distinct from those previously reported by Rage and
100 Dutheil (2008), further increasing the diversity of the Kem Kem snake fauna.

101

102 **2. Geological Setting**

103

104 The Kem Kem beds represent a continental deposit (Dutheil 1999) unconformably overlying
105 Palaeozoic basement units. The sequence exceeds 200 m in thickness in some localities. It is
106 dominated by arenaceous fluvial deposits for approximately two-thirds of the sequence, with
107 the upper part being overbank muds and silty channel deposits, probably accumulating in a
108 muddy estuary or embayment. Vertebrate fossils primarily occur in the sandy beds. The Kem
109 Kem beds are overlain by carbonates of the Akrabou Formation, which is of late
110 Cenomanian/Turonian age. The age of the Kem Kem beds is imprecisely known: over the last
111 few decades, the age of the Kem Kem sequence has been regarded variously as Albian, Albo-
112 Cenomanian or Cenomanian (Riff et al. 2002; Dutheil 1999; Russell 1996). Some workers
113 currently consider the beds to be Cenomanian in age (Rage & Dutheil 2008; Ibrahim et al.
114 2010), although its lower portion may lie within the Albian (Taquet 1980; Forey & Grande
115 1998).

116

117 **3. Materials and methods**

118

119 The specimens described here come from the Kem Kem sequence of southeastern Morocco, in
120 Begaa and Aoufous, in the Province d'Errachidia (Fig. 1.). All material is housed at the Faculté
121 des Sciences Aïn Chock (FSAC), Université Hassan II, Casablanca, Morocco. Vertebrae were
122 prepared using mounted needles, and photographed with a digital camera (Cannon EOS 5D
123 fitted with an MP-E 65 mm macro lens). Macro focusing rails were used to photograph smaller
124 vertebrae at different heights, and resultant images were stacked using the free software
125 Inkscape v.0.91 (www.inkscape.org).

126

127 **4. Results**

128

129 **4.1 Systematic palaeontology**

130

131 Order: Squamata Oppel, 1811

132 Suborder: Ophidia Brogniart, 1800

133 Genus: *Norisophis* gen. nov.

134 Type species: *Norisophis begaa* sp. nov.

135 *Etymology.* From Greek, *norís*, meaning early, and *ophis*, snake

136 *Diagnosis.* Differs from other Cretaceous snake species by exhibiting the following
137 combination of characters: faint or absent interzygapophyseal ridges; marked
138 interzygapophyseal constriction; presence of parazygantral foramina; mid-trunk vertebrae
139 short; neural spine rudimentary; large paradiapophyses which extend dorsally almost to the
140 incipient prezygapophyseal ridge.

141

142 ***Norisophis begaa* gen. et sp. nov.**

143 *Etymology.* “begaa”, meaning from the desert oasis of Begaa.

144 *Type material.* Holotype: FSAC-KK 7001, a posterior trunk vertebra with all zygapophyses
145 preserved, but some erosion of the paradiapophyses (see Fig. 2.). Paratypes: FSAC-KK 7004,
146 FSAC-KK 7005 two mid-trunk vertebrae (see Fig. 3.).

147 *Locality and horizon.* Kem Kem beds of Begaa, east of Taouz, southeastern Morocco (see Fig.
148 1.), ?Cenomanian. Locality Aferdou N’Chaft (30°53’57” N, 3°50’46 W), or Aferdou n’Bou Tarif
149 (30°53’12” W, 3°52’29” W), in the Ifezouane Formation.

150 *Diagnosis.* As for the genus, by monotypy.

151

152 *Description.* The vertebrae originate from a moderately sized snake. In the posterior trunk
153 region, the holotype vertebra is wider (7.46 mm) than long (7.02 mm), unlike *Coniophis*
154 (Marsh 1892; Longrich et al. 2012a) and Russellophiidae (Rage & Werner 1999; Rage et al.
155 2008). This is even more pronounced in mid-trunk vertebrae (see Fig 3). In anterior view, the

156 holotype vertebra appears laterally expanded. Overall, the vertebrae are relatively robust,
157 with very strong interzygapophyseal constriction. The holotype is a posterior trunk vertebra.
158 There is little variation between the holotype and the referred material, although very slight
159 differences in the angling of the zygapophyses and zygosphenes can be seen between FSAC-KK
160 7001, and FSAC-KK 7004 and FSAC-KK 7005.

161

162 Despite the underdeveloped neural spine, the vertebrae still increase in height posteriorly,
163 unlike in *Seismophis septentrionalis* (Hsiou et al. 2014). A poorly defined neural ridge extends
164 anteriorly to the posterior border of the zygosphenes, visible especially in the referred
165 vertebra FSAC-KK 7004. The neural arch is low as in *Nidophis*, a madtsoiid (Vasile et al. 2013),
166 with the neural spine occupying only the posteriormost quarter, making it much less
167 developed than that in all Madtsoiidae except *Herensugea caristiorum* (LaDuke et al. 2010;
168 Rage 1996; Wilson et al. 2010). Faint laminar crests extend to the posterior border of the
169 vertebrae. These neural arch laminae barely protrude above the dorsal aspect of the
170 postzygapophyses in posterior view, making them much less developed than in posterior
171 trunk vertebrae in *Dinilysia* (Rage & Albino 1989).

172

173 Dorsally, the zygosphenes in *N. begaa* has a rectilinear roof. It is less well developed than that
174 of *Coniophis*, and narrows more ventrally (Hecht 1959; Armstrong-Ziegler 1978; Longrich et
175 al. 2012a). The zygantrum is prominent, with the depressions being almost triangular in the
176 holotype. On either side there are small parazygantral foramina, as in the madtsoiids *Sanajeh*
177 *indicus* (Wilson et al. 2010) and *Nidophis insularis* (Vasile et al. 2013), as well as *Najash*
178 *rionegrina* (Apesteguía & Zaher 2006; Zaher et al. 2009). The foramina are situated ventrally
179 from a notch projecting laterally from the dorsal limit of the articular surfaces of the
180 zygantrum.

181

182 The prezygapophyses are laterally angled dorsally and reach the upper half of the coronal
183 plane of the zygosphenes, thus reaching higher than in *Dinilysia* (Scanferla & Canale 2007). The
184 prezygapophyseal processes are incipient, differentiating *Norisophis* from *Najash* and the
185 Madtsoiidae (Rage 1996; Vasile et al. 2013; LaDuke et al. 2010; Zaher et al. 2009; Apesteguía
186 & Zaher 2006). In dorsal view, the prezygapophyses extend wider laterally than the
187 postzygapophyses. The latter have small protuberances on the posterior margin of the neural
188 arch, between the neural spine and postzygapophyses. When viewed laterally, the articular
189 surfaces of the zygapophyses are at the same height. The interzygapophyseal constriction is
190 marked, although the holotype remains wider at the interzygapophyseal constriction than it is
191 long. There is no interzygapophyseal ridge.

192

193 The parapophyses and diapophyses are undivided, dorsally reaching above the cotylar rim,
194 starting just 1-2 mm below the prezygapophyses. Compared to other taxa such as *Coniophis*,
195 *Najash*, *Madtsoia*, *Nidophis* and *Herensugea*, the paradiapophyses occupy a larger relative area
196 on the centrum (Longrich et al. 2012a; Marsh 1892; Zaher et al. 2009; Apesteguía & Zaher
197 2006; Vasile et al. 2013; Rage 1996). They project more laterally than in *Najash rionegrina*
198 (Zaher et al. 2009), and almost reach the prezygapophyseal tip. Ventrally, one of the
199 parapophyses reaches the cotylar rim. Although eroded, the paradiapophyses appear mostly
200 oriented laterally. The paradiapophyses are generally rectangular, taller than wide, with a
201 slight distinction between the diapophysis and parapophysis visible.

202

203 The cotyle is dorso-ventrally flattened, the widest point being below the midline, and is
204 angled dorsally. Shallow paracotylar depressions are present in all vertebrae, but paracotylar
205 foramina are only present in FSAC-KK 7005. Unlike Simoliophiidae (Rage & Dutheil 2008;
206 Rage et al. 2016), Madtsoiidae (Mohabey et al. 2011; Rage 1996; Vasile et al. 2013), and crown
207 Alethinopidia, there is no channel between the ventral border of the condyle and the ventral

208 aspect of the centrum. Instead the condyle and the centrum are confluent, a feature shared
209 with *Coniophis precedens* (Marsh 1892; Longrich et al. 2012a) and *Tetrapodophis amplectus*
210 (Martill et al. 2015).

211

212 Posteriorly, the vertebra is still very much dorso-ventrally flattened. The ventral aspect of the
213 vertebra shows a marked gradual constriction of the centrum starting directly behind the
214 paradiapophyses. Lateral foramina are present on the centrum. The haemal keel is broad,
215 with anteriorly-diverging subcentral ridges on either side.

216

217 ***Norisophis* sp.**

218 *Locality and horizon.* From the Kem Kem beds (Aoufous Formation?) just south of Aoufous
219 (31°41'17" N, 4°10'44" W), near Erfoud, Morocco (see Fig. 1.). Although it is not precisely
220 known which bed yielded the fossil, only the Aoufous Formation appears to be collected from
221 at the nearby Douira locality (Cavin et al. 2010).

222

223 *Description.* FSAC-KK 7002 (Fig. 4.) shares the diagnostic features of *Norisophis begaa*. The
224 neural arch is vaulted. The neural spine extends posteriorly from the posterior border of the
225 zygosphenes as a shallow ridge, unlike neural spines seen in Madtsoiidae, Simoliophiidae,
226 *Najash*, and *Coniophis* (Vasile et al. 2013; Mohabey et al. 2011; Rage et al. 2016; Rage &
227 Escuillié 2003; Zaher et al. 2009; Apesteguía & Zaher 2006; Longrich et al. 2012a). The small
228 protruberances on the posterior edge of the neural arch are also more pronounced than in the
229 holotype FSAC-KK 7001, seeming to extend to the middle of the vertebra on the right side of
230 FSAC-KK 7002 (see Fig. 4D).

231

232 As in *N. begaa*, dorsally the zygosphenes has a rectilinear roof. Ventrally, the zygosphenes
233 narrows more than *Coniophis* (Longrich et al. 2012a; Marsh 1892), but less so than *Kelsyophis*,

234 a madtsoiid (LaDuke et al. 2010). The zygantrum is well-formed, with parazygantral foramina.
235 The visible foramen sits higher dorsally than in Madtsoidea (LaDuke et al. 2010).
236
237 The zygapophyses are angled as in *N. begaa*, despite being from a more anterior position on
238 the trunk. The prezygapophyseal processes are incipient. The prezygapophyses extend
239 further laterally than the postzygapophyses. The interzygapophyseal constriction is marked,
240 but the vertebra remains wider than it is long. The lateral expansion of the pre- and
241 postzygapophyses start from the same point, with no interzygapophyseal ridge.
242
243 The paradiapophyses cover a relatively large area, and dorsally approach the incipient
244 prezygapophyseal ridge. They do not approach the cotylar rim as in *Norisophis begaa*, but do
245 project laterally. Below the prezygapophyses, they project anteriorly further than the cotylar
246 rim. The cotyle is dorso-ventrally flattened and slightly triangular in shape. Paracotylar
247 foramina are absent, unlike *Simoliophis rochebrunei* and *Lapparentophis defrennei* (Rage et al.
248 2016; Hoffstetter 1959).
249
250 The vertebra becomes less dorso-ventrally flattened posteriorly. It displays abnormal bone
251 growth on its ventral side, extending postero-laterally to nearly the dorsal edge of the
252 paradiapophyses, thus obscuring the subcentral ridges and haemal keel. This could be the
253 result of an injury, potentially a fracture of the back.

254

255

256 **5. Discussion and conclusions**

257

258 **5.1 Relationships of *Norisophis*.**

259 In *Norisophis begaa*, the anterior margin of the zygosphenal tectum is slightly concave but not
260 notched, and the paradiapophyses appear to be divided into diapophyses and parapophyses.
261 These characters confirm that it is an ophidian (Apesteguía & Zaher 2006). Within snakes,
262 *Norisophis* appears to be a basal member, most likely a stem ophidian.

263
264 An unnamed madtsoiid has been described from the Kem Kem beds (Rage & Dutheil 2008). It
265 differs from *Norisophis* in the absence of prezygapophyseal processes, and is described as
266 resembling *Herensugea caristiorum*. *Herensugea* vertebrae are wide and depressed, with a
267 wide and thin zygosphenon whose articular facets are relatively horizontally oriented, oval
268 prezygapophyseal facets, a neural spine composed of a posterior tubercle and an anterior
269 keel, very distinct subcentral borders and a wide haemal keel, and very obtuse angling of the
270 posterior border of the neural arch (Rage 1996). It shares with *Norisophis* the overall shape of
271 the vertebrae, the shallow angle of the posterior border of the neural arch, the limited
272 development of the neural arch, and the relative width of the zygosphenon and haemal keel.
273 However, *Norisophis* differs from *Herensugea* by having a robust zygosphenon with more
274 laterally projecting articular surfaces, prezygapophyseal surfaces which come to a point
275 antero-laterally, the presence of incipient prezygapophyseal processes, and absence of a
276 limited keel on either side of the neural spine. As a result, it seems unlikely that *Norisophis* is
277 the unnamed madtsoiid mentioned by Rage and Dutheil (2008).

278
279 *N. begaa* shares many characteristics with *Coniophis*, *Najash* and *Dinilysia*, including the very
280 low neural spine, the limited development of the haemal keel, and the lack of a groove
281 separating the ventral aspect of the condyle from the centrum. In contrast to *Coniophis*, *N.*
282 *begaa* has a slight indentation of the posterior border of the neural arch, and no clearly
283 identifiable haemal carina. It is similar to *Najash* in the presence of parazygantral foramina,
284 but differs in that it has more laterally projecting paradiapophyses, and more pronounced

285 interzygapophyseal constriction (Zaher et al. 2009). Compared to *Dinilysia*, the
286 paradiapophyses extend dorsally much further, the prezygapophyses also extend higher
287 dorsally and almost reach the roof of the zygosphenes, and the interzygapophyseal constriction
288 is again more marked in *N. begaa* (Scanferla & Canale 2007).

289

290 Despite the differences present, the overall similarity of *N. begaa* to other basal snakes
291 suggests that it occupies a position close to *Coniophis* and *Najash*, either outside of or at the
292 base of crown Serpentes. Parazygantral foramina are present in the stem snake *Najash*,
293 *Seismophis*, and Madtsoiidae, but not in the stem snake *Coniophis* and *Dinilysia* (Hsiou et al.
294 2014; Longrich et al. 2012a; Rage 1996; Rage 1975; Zaher et al. 2009), suggesting that they
295 evolved multiple times (homoplasy), or are a plesiomorphic character lost on more than one
296 occasion. Paracotylar foramina are sometimes present in *Norisophis*. They are also present in
297 *Dinilysia*, Madtsoiidae, and Simoliophiidae, all three of which may be part of the Serpentes
298 crown group (Longrich et al. 2012a). Conversely, incipient prezygapophyseal processes are
299 present in both *Norisophis* and *Dinilysia*. The weathering of the paradiapophyses on FSAC-KK
300 7001 makes it impossible to tell how well developed they are; with the exception of
301 *Tetrapodophis*, *Coniophis*, and *Scolecophidia*, ophidian paradiapophyses can be divided into a
302 convex diapophysis and a flat parapophysis. The small protuberances on the posterior edge of
303 the neural arch may be analogous to the low mounds described in "*Coniophis*" *carinatus*
304 (Hecht 1959), underscoring the need for the genus *Coniophis* be re-evaluated (Gardner &
305 Cifelli 1999). This also adds to the mounting evidence that most basal snakes are Gondwanan;
306 even though the snake total-group is potentially Laurasian in origin (Hsiang et al. 2015),
307 *Najash* and *Tetrapodophis* are Gondwanan, whilst *Coniophis* is both Gondwanan and
308 Laurasian.

309

310 5.2 Ecology of *Norisophis*.

311

312 The highly reduced neural spine is a classic feature of burrowing snakes such as *Anilius*
313 (Hecht 1959; Apesteguía & Zaher 2006), and fossorial lepidosaurs such as amphisbaenians
314 (Wu et al. 1996). The lateral projection of the paradiapophyses in *N. begaa* also suggests a
315 terrestrial lifestyle, as it implies no lateral restriction of the ribs (and thus also the body) as
316 seen in likely aquatic taxa such as *Simoliophis* and *Lunaophis aquaticus* (Rage & Escuillié 2003;
317 Albino et al. 2016). The vertebrae also lack pachyostosis, a diving adaptation that is typical of
318 aquatic tetrapods, including the simoliophiids (Rage et al. 2016) and *Lunaophis* (Albino et al.
319 2016). The scarcity of specimens is also noteworthy; the Kem-Kem is dominated by aquatic
320 (and semiaquatic) taxa such as Simoliophiidae (Rage & Dutheil 2008), *Spinosaurus* (Ibrahim,
321 Sereno, et al. 2014), and a large number of fish, turtle, pipid frog, and crocodyliform taxa. The
322 rarity of *Norisophis* fossils may suggest that it was probably not aquatic, and was instead
323 washed in from the surrounding terrestrial environment.

324

325 **6. Conclusions.**

326

327 As more material is discovered in the Kem Kem beds, the diversity of the snake assemblage
328 continues to rise. With Simoliophiidae, Madtsoiidae, ?Nigerophiidae, and numerous other
329 morphotypes (Rage & Dutheil 2008), even taking into account that different localities within
330 the Kem Kem beds may not have been contemporaneous, niche partitioning within the
331 localities appears to have occurred (evidence for niche partitioning in other groups has been
332 reported; Ibrahim et al., 2016). Snake diversity appears to have been higher during the
333 Cenomanian in Africa than in later, Maastrichtian, faunas in North America (Longrich et al.
334 2012b; Longrich et al. 2012a) and Europe (Rage 1996; Vasile et al. 2013). This is consistent
335 with the idea that Gondwana played a central role in early snake evolution.

336

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346

347

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Figure 1. Map of the localities in Begaa and Aoufous, Morocco. (A) Overview of Morocco, highlighting the geographic position of the localities, and (B) satellite image of the area, with localities marked as red stars. Image from Google Maps.

531

532 **Figure 2. *Norisophis begaa* holotype**, FSAC-KK 7001 in: (A,F) anterior, (B,G) posterior, (C,H)
533 lateral (right lateral side pictured with mirror image, as it is more complete), (D,I) dorsal, and
534 (E,J) ventral views; izc, interzygapophyseal constriction; lf, lateral foramen; nc, neural canal;
535 ns, neural spine; pdp, paradiapophyses; ppt, pryzygapophyseal roof protuberance; pzf,
536 parazygantral foramina; scf, subcentral foramen; scr, subcentral ridge; zs, sygosphene. Scale
537 bar equals 5 mm.

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Figure 3. *Norisophis begaa* paratypes, FSAC-KK 7004 and FSAC-KK 7005 in: (A,F) anterior, (B,G) posterior, (C,H) lateral (mirror images), (D,I) dorsal, and (E,J) ventral views. Scale bar equals 5 mm.

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543 **Figure 4. Other Kem Kem snake vertebra.** (A-E) FSAC-KK 7002 a precloacal (mid-trunk)
 544 *Norisophis* sp. vertebra, in (A) anterior, (B) posterior, (C) lateral, (D) dorsal, and (E) ventral
 545 views. Scale bar equals 5 mm.