A century of waiting: Description of a new *Epictia* Gray, 1845 (Serpentes: Leptotyphlopidae) based on specimens housed for more than 100 years in the collection of the Natural History Museum Vienna (NMW)

Claudia Koch [Corresp., Equal first author, 1] , **Angele Martins** [Equal first author, 2, 3] , **Silke Schweiger** [4]

1 Department of Herpetology, Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), Bonn, Germany

2 Departamento de Ciências Fisiológicas, Instituto de Ciências Biológicas, Campus Darcy Ribeiro, Universidade de Brasília, Brasília, Brazil

3 Departamento de Vertebrados, Museu Nacional do Rio de Janeiro (UFRJ), Rio de Janeiro, Brazil

4 1st Zoological Department, Herpetological Collection, Natural History Museum Vienna (NMW), Vienna, Austria

Corresponding Author: Claudia Koch
Email address: c.koch@zfmk.de

We describe a new species of *Epictia* based on eight specimens from Nicaragua collected and housed in the collection of the Natural History Museum Vienna for more than a century. The species differs from the congeners by the combination of external morphological characters: midtail scale rows 10; supralabials two, anterior one large and in broad contact with supraocular; infralabials four; subcaudals 14–19; middorsal scale rows 250–267; supraocular scales present; frontal scale distinct; striped dorsal color pattern with more or less triangular dark blotches on each scale; small white blotch in anterior part of dorsal surface of rostral present in five out of six specimens (two further specimens are lacking their heads); terminal spine and adjacent scales white. Eidonomic species separation from other *Epictia* spp. is also supported by a few qualitative and quantitative differences in vertebrae count and morphology. The new species is putatively assigned to the *Epictia phenops* species group based on external morphological characters and distribution.

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6

8 Claudia Koch[1], Angele Martins[2,3], Silke Schweiger[4]

10 [1] Department of Herpetology, Zoologisches Forschungsmuseum Alexander Koenig (ZFMK),
11 Bonn, Germany
12 [2] Departamento de Ciências Fisiológicas, Instituto de Ciências Biológicas, Campus Darcy
13 Ribeiro, Universidade de Brasília, Brasília, Brazil
14 [3] Departamento de Vertebrados, Museu Nacional do Rio de Janeiro (UFRJ), Rio de Janeiro,
15 Brazil
16 [4] 1st Zoological Department, Herpetological Collection, Natural History Museum Vienna
17 (NMW), Vienna, Austria
18
19 Corresponding Author:
20 Claudia Koch[1]
21 Adenauerallee 160, Bonn, 53113, Germany
22 Email address: c.koch@leibniz-zfmk.de

Abstract

25 We describe a new species of *Epictia* based on eight specimens from Nicaragua collected and

26 housed in the collection of the Natural History Museum Vienna for more than a century. The

27 species differs from the congeners by the combination of external morphological characters:

28 midtail scale rows 10; supralabials two, anterior one large and in broad contact with supraocular;

29 infralabials four; subcaudals 14–19; middorsal scale rows 250–267; supraocular scales present;

30 frontal scale distinct; striped dorsal color pattern with more or less triangular dark blotches on

31 each scale; small white blotch in anterior part of dorsal surface of rostral present in five out of six

32 specimens (two further specimens are lacking their heads); terminal spine and adjacent scales

33 white. Eidonomic species separation from other *Epictia* spp. is also supported by a few

34 qualitative and quantitative differences in vertebrae count and morphology. The new species is

35 putatively assigned to the *Epictia phenops* species group based on external morphological

36 characters and distribution.

Introduction

39 The fossorial threadsnakes of the family Leptotyphlopidae represent about 140 currently

40 recognized species (*Uetz, Freed & Hošek, 2019*) that occur along sub-Saharan Africa and nearby

41 islands, the Arabian Peninsula, in southwest Asia (Leptotyphlopinae and Rhinoleptini) and in

42 the New World (Americas and Antilles) (*Adalsteinsson et al., 2009*). Despite their wide typical

43 Gondwanan distribution, members of this family still account for one of the least known

44 terrestrial vertebrates (*Adalsteinsson et al., 2009*). This is mostly due to their secretive habits,

45 which make them rarely encountered in the field, except for a few locally abundant species

46 (*McDiarmid, Campbell & Touré, 1999*; *Curcio, Zaher & Rodrigues, 2002*; *Passos,*

47 *Caramaschi & Pinto, 2005*). Additionally, the systematics of this group is very controversial

48 mostly due to their relatively conserved external morphology (*Passos, Caramaschi & Pinto,*

49 *2005, 2006*; *Pinto & Curcio, 2011*; *Martins, Passos & Pinto 2018*). The genus *Epictia* is the

50 most speciose amongst the subfamily Epictinae, with about 43 species currently recognized

51 (*Uetz, Freed & Hošek, 2019*). Although subjected to a few systematic studies in recent years

52 (e.g. *McCranie & Hedges, 2016*; *Wallach, 2016*) members of this genus still account for several

53 taxonomical issues, which are far from being satisfactorily resolved. Additionally, several

54 species have been described in the past 10 years (e.g. *Arredondo & Zaher, 2010*; *Koch, Venegas*

55 *& Böhme, 2015*; *Koch, Santa Cruz & Cárdenas, 2016*; *Wallach, 2016*) reinforcing the need for

56 systematic studies of the group in order to evaluate the presence of new and undescribed taxa in

57 the Neotropical region.

58 While reviewing specimens of the family Leptotyphlopidae from the herpetological collection of

59 the Natural History Museum Vienna, Austria (NMW), the first author came across a series of

60 eight specimens (NMW 15446:1–8) of thread snakes, that were assigned by Steindachner, a

61 former curator of the collection, to *Epictia albifrons* (Wagler, 1824). Steindachner himself

62 donated these specimens to the museum in 1907 and the locality was stated as "Corinto".

63 Unfortunately the original description of *E. albifrons* is rather poor, the holotype (ZSM 1348/0)

64 was destroyed during the Second World War and according to *Cunha & Nascimento* (*1993*),

65 *Wallach, Williams & Boundy* (*2014*), *Pinto, Franco & Hoogmoed* (*2018*) the locality data ("in

66 adjacentibus Urbis Para" = in the proximity of Pará, Brazil) could be erroneous. Furthermore, the

67 species has been confused with *E. goudotii* (Duméril & Bibron, 1844) in some earlier literature

68 (*McCranie & Hedges, 2016*). Although a molecular analysis by *Adalsteinsson et al.* (*2009*)

69 demonstrated that *E. albifrons* and *Epictia goudotii* represent two genetically distinct species, the

70 validity of *E. albifrons* is still under debate (*McCranie & Hedges, 2016*). It is recognized by

71 some authors as a valid species (e.g. *Peters & Orejas-Miranda, 1970*; *Wallach, Williams &*

72 *Boundy, 2014*; *Natera Mumaw, Esqueda González & Castelaín Fernández, 2015*; *Wallach,*

73 *2016*; *Murphy, Rutherford & Jowers, 2016*), while other authors consider *E. albifrons* as a

74 nomen dubium and place it in the synonymy of *Epictia tenella* Klauber, 1939 (e.g. *Wilson &*

75 *Hahn, 1973*; *Franco & Pinto, 2009*). In contrast some authors consider *E. tenella* as a junior

76 synonym of *E. albifrons* (e.g. *Thomas, 1965*; *Hoogmoed & Gruber, 1983*). *Natera Mumaw,*

77 *Esqueda González & Castelaín Fernández* (*2015*) designated a neotype for *E. albifrons* (MCZ R-

78 2885) from the vicinity of "Pará, Brasil" which was rejected by *Wallach* (*2016*) who designate

79 the topotype BYU 11490 from the vicinity of Belém, Pará State, Brazil, as the neotype of *E.*

80 *albifrons*. According to *Wallach* (*2016*) *E. albifrons* is restricted to the vicinity of the topotype

81 series in northeastern Brazil, while *E. tenella* is a relatively widespread species in cis-Andean

82 South America. According to his (and former) diagnosis the main difference between both

83 species is the presence (*E. tenella*) or absence (*E. albifrons*) of a contact between supraoculars

84 and the anterior supralabial. *Pinto, Franco & Hoogmoed* (*2018*) state that the neotype of *Natera*

85 *Mumaw, Esqueda González & Castelaín Fernández* (*2015*) is valid, whereas *Wallach's* (*2016*)

86 designating of a neotype was an act against the ICZN (1999) code. They further disagree with

87 *Wallach* (*2016*) regarding the absence of a supralabial-supraocular contact in *E. albifrons* and

88 consider this contact to be present in this species as proposed by *Natera Mumaw, Esqueda*

89 *González & Castelaín Fernández* (*2015*). Whether *E. albifrons* and *E. tenella* represent two

90 distinct or the same species is not conclusively clarified. We herein treat both species as being

91 valid. However, after the analysis of both external and internal morphological characters, we

92 verified that the specimens donated by Steindachner do neither represent *E. albifrons* nor *E.*

93 *tenella*, but pertain to a new *Epictia* species (see data in Results). Apart from the unequal

94 distribution they differ from both species (sensu *Wallach, 2016* and *Natera Mumaw, Esqueda*

95 *González & Castelaín Fernández, 2015*) by having a higher number of middorsal scale rows (see

96 Comparison).

97

Materials & Methods

99   We compared the new species with all congeners in the genus *Epictia* that are currently

100 recognized by at least some authors as valid species (see comments in *Koch, Santa Cruz &*

101 *Cárdenas, 2016*). Therefore, we examined 392 specimens (see Appendix) representing 56

102 species of South American and Mesoamerican Leptotyphlopidae from the following collections:

103 American Museum of Natural History (AMNH), Natural History Museum, London, UK

104 (BMNH), Centro de Ornitología y Biodiversidad (CORBIDI), Coleção Herpetológica da

105 Universidade de Brasília (CHUNB), Field Museum of Natural History, Chicago, USA (FMNH),

106 Fundación Miguel Lillo (FML), Instituto de Bio y Geociencias del Noroeste Argentino, Rosario

107 de Lerma, Argentina (IBIGEO), Instituto Butantan (IBSP), Museum für Naturkunde, Berlin,

108 Germany (ZMB), Natural History Museum of Los Angeles (LACM), Laboratório de Zoologia de

109 Vertebrados, Universidade Federal de Ouro Preto (LZV), Museum für Tierkunde in Dresden,

110 Germany (MTKD), Museum of Comparative Zoology, Cambridge, USA (MCZ), Muséum

111 National d'Histoire Naturelle, Paris, France (MNHN), Museo de Historia Natural, Universidad

112 Nacional Mayor de San Marcos, Lima, Peru (MUSM), Museu Nacional, Universidade Federal

113 do Rio de Janeiro (MNRJ), Museu de Zoologia da Universidade de São Paulo (MZUSP), Museu

114 Paraense Emílio Goeldi (MPEG), Museo de Historia Natural de la Universidad Nacional de San

115 Agustín (MUSA), Natural History Museum, University of Kansas, Lawrence, USA (KU),

116 Oklahoma Museum of Natural History (OMNH), NMW, Museo de Zoología, Pontificia

117 Universidad Católica del Ecuador, Quito, Ecuador (QCAZ), Senckenberg Museum Frankfurt,

118 Germany (SMF), San Diego Museum of Natural History (SDMNH), National Museum of

119 Natural History (USNM), Coleção Zoológica da Universidade Federal do Mato Grosso (UFMT),

120 Illinois Natural History Survey (UIMNH), Zoologische Staatssammlung München, Germany

121 (ZSM), and Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany (ZFMK). In

122 addition, we reviewed data on all known species in the genus *Epictia* from the following

123 literature sources (original species descriptions and others): *Wagler (1824), Schlegel (1839),*

124 *Duméril & Bibron (1844), Peters (1857), Jan (1861), Cope (1875), Werner (1901), Oliver*

125 *(1937), Klauber (1939), Taylor (1940), Schmidt & Walker (1943), Smith (1943), Smith & Laufe*

126 *(1945), Legler (1959), Orejas-Miranda (1961, 1964, 1969), Freiberg & Orejas-Miranda (1968),*

127 *Peters & Orejas-Miranda (1970), Orejas-Miranda & Zug (1974), Hoogmoed (1977), Zug*

128 *(1977), Laurent (1984), Lancini & Kornacker (1989), Villa (1990), Vanzolini (1996), Lehr et al.*

129 *(2002), Duellman (2005), Kretzschmar (2006), Börschig (2007), Boundy & Wallach (2008),*

130 *Arredondo & Zaher (2010), Pinto et al. (2010), McCranie (2011), Francisco, Pinto & Fernandes*

131 *(2012, 2018), Esqueda González et al. (2015), Koch, Venegas & Böhme (2015), Koch, Santa*

132 *Cruz & Cárdenas (2016), Natera Mumaw, Esqueda González & Castelaín Fernández (2015),*

133 *Martins (2016), McCranie & Hedges (2016), Murphy, Rutherford & Jowers (2016)*, and *Wallach*

134 *(2016)*. Data on other South American Leptotyphlopidae were obtained from: *Pinto & Curcio*

135 *(2011), Pinto & Fernandes (2012, 2017)*, and *Salazar-Valenzuela et al. (2015)*.

136 Measurements were taken with a digital caliper to the nearest 0.1 mm or with a ruler to the

137 nearest 1.0 mm. The following abbreviations were used: SVL = snout-vent length, TAL = tail

138 length, TL = total length, HW = head width at largest area (level of the parietal scale), HH =

139 head height at highest point, HL = head length from tip of snout to posterior level of skull, (when

140 feeling it tapering to the neck), ED = eye diameter, RES = relative eye size (eye height/ocular

141 shield height), MB = midbody diameter, MT = midtail diameter, MDS = middorsal scale rows

142 from the rostral scale to the terminal spine, V = number of ventral scales in longitudinal row

143 from mental to cloacal shield, D = number of scales around the body counted at three different

144 points along the body (1. at a head's length behind the head, 2. at midbody, 3. at a head's length

145 before the cloaca), SC = number of subcaudal scales counted in longitudinal row from cloaca to

146 tip of tail, TS = number of midtail scale rows counted transversely across the middle of the tail,

147   SL = number of supralabials, IF = number of infralabials, PCV = precloacal vertebrae, CAV =

148   caudal vertebrae, CLV = cloacal vertebrae.

149   Terminology for cephalic plates, scale features, and measurements follows *Wallach (2003)*,

150   *Broadley & Wallach (2007)*, *Arredondo & Zaher (2010)*, and *Francisco, Pinto & Fernandes*

151   *(2012)*.

152   For obtaining information on the number of precloacal and caudal vertebrae and the position of

153   the pelvic girdle whole specimens were X-rayed in 2D outside of ethanol with a Faxitron X-ray

154   LX60 at ZFMK. For details of the skull and lower jaw, cervical vertebrae and pelvic girdle, only

155   the head and cloacal region of each specimen were X-rayed in 3D by the use of a high-resolution

156   micro-CT scanner (Bruker SkyScan 1173) at ZFMK. Therefore bodies of specimens were placed

157   in a tube filled with ethanol and only the regions of interest (head and cloacal region) were

158   sticking out of the ethanol and were CT-scanned together at the same time. Specimens were CT-

159   scanned in 180° degrees at rotation steps of 0.3° or 0.4° degrees with a tube voltage of 40 kV and

160   a tube current of 200 uA without the use of a filter at an image resolution of 8.4 μm. Scan

161   duration was between 25 min (rotation steps of 0.4°) and 42 minutes (rotation steps of 0.3°) with

162   an exposure time of 359 ms. The CT-dataset was reconstructed using N-Recon software (Bruker

163   MicroCT) and rendered in three dimensions through the aid of CTVox for Windows 64 bits

164   version 2.6 (Bruker MicroCT). We have also used osteological data from *Martins (2016)* and

165   *Martins et al.* (*unpublished data*, specimens cited in the APPENDIX – Additional specimens

166   examined) to provide additional species comparisons. Anatomical terminology follows *Romer*

167   *(1956)*, *List (1966)*, and *Holman (2000)* [atlas and axis], *List (1966)* [pelvic girdle], *Rieppel*

168   *(1979)* [parabasisphenoid complex], *Kley (2006)* and *Martins (2016)* [suspensorium], *Cundall &*

169   *Irish (2008)*, *Rieppel, Kley & Maisano (2009)*, *Martins (2016)* and *Martins et al. (unpublished*

170   *data)* [skull], *Curcio (2003)* and *Rieppel, Kley & Maisano (2009)* [skull foramina].

171   The electronic version of this article in Portable Document Format (PDF) will represent a

172   published work according to the International Commission on Zoological Nomenclature (ICZN),

173   and hence the new names contained in the electronic version are effectively published under that

174   Code from the electronic edition alone. This published work and the nomenclatural acts it

175   contains have been registered in ZooBank, the online registration system for the ICZN. The

176   ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed

177 through any standard web browser by appending the LSID to the prefix http://zoobank.org/. The

178 LSID for this publication is: urn:lsid:zoobank.org:pub:C2392EA5-9957-45BF-AE8C-

179 0998E342F90B. The online version of this work is archived and available from the following

180 digital repositories: PeerJ, PubMed Central and CLOCKSS.

181

182 **Results**

183 *Epictia rioignis sp. nov. (Figs. 1–15, Table 1)*

184 urn:lsid:zoobank.org:act:4C7CFC14-FDC7-4B41-B7CF-7CCB8F0E8649

185

186 *Holotype*

187 NMW 15446:6, from Corinto, presumably Nicaragua (12°29' N, 87°11' W, see Discussion for

188 further details) donated by Steindachner in 1907.

189 *Paratypes (7)*

190 NMW 15446:1–5, NMW 15446:7–8 from the type locality, donated by Steindachner in 1907.

191

192 *Diagnosis*

193 *Epictia rioignis* sp. nov. can be distinguished from all congeners by the following combination of

194 characters: (1) midbody scale rows 14; (2) midtail scale rows 10; (3) supralabials two, anterior

195 one large and in broad contact with supraocular; (4) infralabials four; (5) subcaudals 14–19; (6)

196 middorsal scale rows 250–267; (7) total number of precloacal vertebrae 231–248; (8) supraocular

197 scales present; (9) frontal scale distinct, not fused with rostral; (10) striped dorsal color pattern

198 with more or less triangular dark blotches on each scale; (11) upper half of eyes visible in dorsal

199 view; (12) some caudals in posterior part of tail are fused in 50% of the specimens; (13) small

200 white blotch in anterior part of dorsal surface of rostral present in about 83% of the specimens;

201 (14) terminal spine and adjacent scales white.

202

203 *Comparisons*

204 The new species differs from *Epictia albipuncta, Epictia striatula, Epictia unicolor* and *Epictia*

205 *weyrauchi* by having 10 midtail scale rows [vs. 12]. The number of 14 midbody scale rows

206 distinguishes the species from *E. undecimstriata* [16]. By the presence of an unfused frontal and

207 rostral scale it is differentiated from *Epictia ater* (including *Epictia nasalis*), *Epictia bakewelli*

208 and *Epictia schneideri*. By having the anterior supralabial in broad contact with the supraocular

209 the new species can be distinguished from *E. albipuncta, Epictia amazonica, E. ater, Epictia*
210 *australis, E. bakewelli, Epictia borapeliotes, Epictia clinorostris, Epictia collaris, Epictia*
211 *columbi, Epictia diaplocia, Epictia fallax, Epictia goudotii, Epictia magnamaculata, Epictia*
212 *martinezi, Epictia melanura, Epictia munoai, Epictia pauldwyeri, Epictia peruviana, Epictia*
213 *phenops, Epictia resetari, E. schneideri, Epictia signata, Epictia subcrotilla, Epictia vellardi,*
214 *Epictia vindumi*, and *Epictia wynni* [vs. anterior supralabial and supraocular separated by
215 supranasal-ocular contact]. The number of 250–267 middorsal scale rows distinguishes *Epictia*
216 *rioignis* sp. nov. from *E. albifrons* [206–218 sensu *Wallach, 2016*; 242 sensu *Natera Mumaw,*
217 *Esqueda González & Castelaín Fernández, 2015*], *Epictia alfredschmidti* [267–279], *E.*
218 *amazonica* [208–245], *Epictia antoniogarciai* [195–208], *E. collaris* [155–166], *E. diaplocia*
219 [205–233], *Epictia hobartsmithi* [191–208], *E. melanura* [395–396], *E. munoai* [184–226], *E.*
220 *pauldwyeri* [202–226], *E. peruviana* [185–199], *E. subcrotilla* [318–333], *Epictia tenella* [215–
221 233 sensu *Wallach, 2016*], *Epictia tricolor* [276–310], *E. unicolor* [246], *Epictia vanwallachi*
222 [188], *Epictia venegasi* [211–221], and *Epictia vonmayi* [196–205]. The number of 14–19
223 subcaudal scales differentiates this species from *E. columbi* [22–25], *E. munoai* [10–14], *E.*
224 *nasalis* [21], and *E. pauldwyeri* [10–14]. By the presence of four infralabials [vs. three] *Epictia*
225 *rioignis* sp. nov. differs from *E. australis, E. borapeliotes, E. collaris*, *E. munoai,* and *E. wynni*.
226 The presence of a light blotch on the dorsal part of the rostral further differentiates the new
227 species from *E. columbi, Epictia rufidorsa, E. vanwallachi,* and *E. weyrauchi*, and the presence
228 of a whitish terminal spine distinguishes it from *E. columbi, E. melanura, Epictia melanoterma,*
229 *E. rufidorsa,* and *Epictia septemlineata*. By lacking a tricolor pattern (reddish-brown, black,
230 yellow) it differs from *E. alfredschmidti, Epictia rubrolineata, Epictia teaguei,* and *E. tricolor*.
231 By lacking a preoral groove in the ventral rostral it differs from *E. columbi*. The presence of a
232 distinct striped dorsal color pattern with more or less triangular dark blotches on each scale
233 distinguishes the new species from *E. amazonica* [uniformly black coloration, without any trace
234 of stripes], *E. ater,* and *E. columbi* [both species appear uniformly dark, pale outline of the scales
235 is only visible upon closer examination]. From *Epictia tesselata* which is only known from Lima
236 (Peru) and surroundings, the new species differs by having a very small light blotch on the
237 rostral [light spot on the rostral and lower portion of the nasals] and a darker ventral coloration. It
238 differs from *E. ater* and *E. phenops* by presenting unfused neural arches of the atlas [vs fused].

239   The number of 231-248 trunk vertebrae distinguishes it from *E. magnamaculata* [199], *E.*

240   *munoai* [207], *E. phenops* [213-246], *E. tenella* [190-204], and *E. tricolor* [282].

241

242   ***Description of holotype (Figs. 1, 2, and upper left picture of Figs. 3–9)***

243   A large specimen with TL of 211 mm; TAL of 10.3 mm; MB of 4.4 mm; MT of 3.1 mm;

244   TL/TAL of 20.5; TL/MB of 48; TAL/MT of 3.3; HW of 2.8 mm; HL of 3.6 mm; HH of 2.3 mm;

245   ED of 0.4 mm; RES of 0.3. Head subcylindrical, slightly dorsoventrally compressed, hardly

246   distinguishable from neck; body cylindrical; not tapered cranially or caudally. Snout rounded in

247   dorsal, lateral and ventral views. Rostral subtrapezoidal in dorsal view with straight apex,

248   straight in ventral view, reaching the imaginary transverse line between the anterior borders of

249   the eyes, contacting upper and lower nasals laterally and frontal dorsally.

250   Nasal completely divided horizontally by an oblique suture, reaching rostral and first supralabial;

251   ellipsoid nostril located in the center of the suture between upper and lower nasal, having the

252   major axis obliquely oriented along the suture; supranasal higher than wide, contacting rostral

253   anteriorly, infranasal inferiorly, first supralabial and supraocular posteriorly, and frontal dorsally;

254   infranasal not visible in dorsal view, contacting rostral anteriorly and first supralabial posteriorly;

255   two supralabial scales positioned anterior and posterior to ocular scale (1+1), respectively,

256   resulting in an upper lip border formed by rostral, infranasal, anterior supralabial, ocular, and

257   posterior supralabial; first supralabial 2.2 times higher than wide, exceeding nostril, reaching

258   central level of eye, dorsally acuminate and in contact with supraocular scale; second supralabial

259   subtrapezoidal 1.3 times higher than wide, slightly exceeding central level of eye, about as high

260   as and at widest point 1.7 times wider than first supralabial; posterior margin of second

261   supralabial in broad contact with temporal and first scale of lateral body row, dorsal margin in

262   contact with parietal; temporal scale of same size as dorsal scales of lateral rows, but distinct

263   from lateral body scales by its oblique orientation; ocular scale pentagonal with dorsal apex

264   acuminate and anterior border slightly rounded at eye-level, 1.8 times higher than wide,

265   contacting anteriorly first supralabial, anterodorsally supraocular, posterodorsally parietal and

266   dorsally second supralabial; eye distinct, located at level of maximum width of ocular, with

267   lower eye margin at nostril level, positioned anteriorly and almost contacting scale sutures; upper

268   half of eyes visible in dorsal view; supraocular scale oriented obliquely, about twice as long as

269   wide, contacting supranasal anteriorly, parietal and postfrontal posteriorly, frontal dorsally, and

270   first supralabial inferiorly; supraocular, parietal and occipital scales visible in lateral view;

271   middorsal head plates (frontal, postfrontal, interparietal, and interoccipital) imbricate,

272   subhexagonal, except for subtriangular frontal, with frontal and interoccipital being slightly

273   larger than the other two scales; middorsal head plates narrower than posterior middorsal scales;

274   frontal contacting rostral, supranasals, supraoculars, and postfrontal; postfrontal contacting

275   frontal, supraoculars, parietals, and interparietal; interparietal contacting postfrontal, parietals,

276   occipitals, and interoccipital; interoccipital contacting interparietal, occipitals, nuchal and first

277   pair of paravertebral dorsal scales; parietal slightly larger than occipital, both irregularly

278   hexagonal and about twice as high as wide; lower margin of parietal contacting upper border of

279   posterior supralabial and temporal, posterior margin in broad contact with occipital, dorsal

280   margin contacting postfrontal and interparietal, anterior margin in broad contact with ocular and

281   supraocular; lower margin of occipital contacting temporal and first scale of lateral body row,

282   posterior margin in broad contact with first paravertebral and first scale of dorsolateral body row,

283   dorsal margin in contact with interparietal and interoccipital, anterior margin in broad contact

284   with parietal; four infralabials per side, subequal in size, first three higher than wide, fourth

285   wider than high, first two pairs of infralabials almost rectangular, larger than third infralabials;

286   mental scale single, small, lunulate; labials, chin and gular scales, and dorsal and lateral head

287   scales with numerous scattered pores.

288   Dorsal scales imbricate, smooth, homogeneous, rhomboid or elliptical in shape, about 1.5 times

289   wider than long; 267 MDS; 14-14-14 D; 258 V; 10 TS; Cloacal shield large, subtriangular in

290   shape, about 2.2 times wider than long, bordered anteriorly and posteriorly each by five scales;

291   15 SC, becoming successively narrower distally, no fused scales dorsally or ventrally on tail;

292   terminal spine conical and shorter than wide.

293

294   ***Color of holotype after more than 100 years of preservation in ethanol (Fig. 2, and upper left picture of***

295   ***Figs. 3–9)***

296   Dorsal head scales (supranasal, frontal, supraoculars, postfrontal, parietals, interparietal,

297   occipitals, interoccipital) except for rostral, reddish-brown with cream-colored sutures; rostral

298   reddish-brown in posterior part and with a small cream-colored blotch on the anterodorsal part,

299   lower (ventral) part of rostral light greyish-brown; infranasal and anterior supralabial light

300   reddish-brown; ocular scale mostly cream-colored; posterior supralabial light reddish-brown in

301   upper half and cream-colored in lower half; ventral head scales (mental, infralabials, scales of

302   chin and gular region) cream-colored; each dorsal body scale with a more or less triangular,

303   median to dark reddish-brown blotch in the center of the scale and with cream-colored lateral

304   margins, forming a pattern of dark longitudinal stripes with cream-colored interspaces, dark

305   stripes slightly broader than interspaces, reaching to the penultimate scale of the tail; each ventral

306   body, anal plate and scales on ventral part of tail scale light or median brown in central part and

307   with cream-colored margins; terminal spine cream-colored.

308

309   ***Osteology of holotype***

310

311   ***Skull (Figs. 10–11)***

312   Premaxilla roughly rectangular in anterior view and hexagonal in ventral view, edentulous,

313   pierced by six foramina (two in anterior view and four in ventral view); transverse process of

314   premaxilla absent and vomerian process single; premaxilla with internal septum composed by

315   two laminae that support the *septum nasii* dorsally, expanding posteriorly to fit medially in the

316   septomaxilla (internally); nasals paired, approximately rectangular in dorsal view, being pierced

317   by a pair of foramina in lateral border of contact with prefrontals (foramen for the *apicalis nasi*);

318   an additional pair of foramina pierce the medial contact within both nasals; a single additional

319   foramen pierces the anterior-medial region of the nasal dorsal lamina; nasal septum descending

320   as double medial vertical flanges that contact the premaxilla, septomaxilla and vomer ventrally

321   (internally); prefrontals paired, subtriangular in dorsal view, in contact with septomaxilla and

322   maxilla ventrally; septomaxillae paired, complex in shape, expanding dorsally into the naris;

323   conchal invagination absent; ascending process of premaxilla pierced by single large foramen;

324   internally, dorsal surface of each septomaxilla pierced by a foramen, and with a medial deep

325   sulcus that extends from its posterior to anterior regions; vomers paired, located midventral to

326   vomeronasal cupola, bearing transversal arms, and with short posterior arms in contact with each

327   other posteriorly; a pair of foramina pierce the ventral lamina of the vomer; frontals paired,

328   nearly rectangular in dorsal view, the left element bearing short anterolateral projections to attach

329   to prefrontals; frontal pillars absent; optic nerve restricted to lateral descending surface of

330   frontals; maxilla edentulous, irregular in shape, pierced by four large foramina in lateral view,

331   two in the dentigerous process of maxilla; posterior process of maxilla reaching the level of the

332 optic nerve foramen; posterior orbital element absent; parietal single, wide, representing the

333 largest bone of braincase; parietal internal pillars (*sensu Martins, 2016*) absent; parabasisphenoid

334 arrow-like, with tapered anterior tip lying dorsally to palatine, and fitting in medial line of

335 vomeronasal cupola; in ventral view, parabasisphenoid bearing posterior-lateral projections to

336 provide insertion for the neck muscles (*Martins et al., in press*); parabasisphenoid with shallow

337 pituitary fossa and lateral sulcus; anterior opening for the palatine artery indistinct or absent in

338 parabasisphenoid dorsal (internal surface), internal carotid artery foramen and *abduscens* nerve

339 foramen present; opening for the palatine ramus of the facial nerve formed by the lateral edge of

340 the parabasisphenoid and the ventral edge of the parietal; basioccipital single and approximately

341 pentagonal in ventral view, bearing lateral process to attach tendons for the neck muscles

342 (*Martins et al., unpublished data*); basioccipital does not participate in the formation of the

343 foramen magnum; supraoccipitals paired, approximately rectangular in dorsal view, pierced

344 medially (internally) by a large endolymphatic foramen; prootics paired and triangular in lateral

345 view; prootics forming the trigeminal nerve foramen together with the parietal; prootics pierced

346 medially (internally) by two acoustic nerve foramina, and an additional foramen ventral to the

347 former; statolythic mass in *cavum vestibuli* absent; stapedial footplate apparently not co-ossified

348 with prootic; otoccipitals paired and irregular in dorsal view, descending to contact each other

349 ventrally to exclude the basioccipital in the formation of the foramen magnum and forming a

350 short but distinct atlantal process (*sensu Cundall & Irish, 2008*); medial surface (internal) of

351 otooccipitals pierced by an internal opening for the *recessus scalae timpani* and a wide foramen

352 that forms the internal opening for the *vagus* nerve foramen; a reduced foramen pierces the

353 posterior (external) surface of the otoocipital, posterior to the external opening for the *vagus*

354 nerve foramen; palatines paired and triradiate; anterior margin of maxillary process flexing

355 ventrally; palatines pierced by a foramen in its ventral surface; pterygoids slender and rod-like,

356 not contacting quadrate posteriorly, and not extending beyond the anterior margin of

357 basioccipital; ectopterygoid indistinct.

358

359 ***Suspensorium (Fig. 12)***

360 Dentary supports a series of six teeth ankylosed to the inner surface of the anterolateral margin of

361 dental concha; mental foramen nearly under the 6th tooth; splenial conical, visible in lateral view,

362 representing smallest bone in lower jaw, extending from the level of the 5th tooth to contact the

363   angular posterior; anterior mylohyoid foramen absent on splenial; posterior milohyoid foramen

364   on the ventral and dorsal surface of angular; angular conical, extending posteriorly to level of the

365   posterior surangular foramen; compound bone pierced by two foramina in the surangular lamina

366   which are approximately similar in size, anterior surangular foramen located anterior to the

367   coronoid; foramen for the chorda tympani of the hyomandibular ramus of the facial nerve (VII)

368   present; a small foramen pierces the retroarticular process in medial view; prearticular lamina of

369   compound bone presenting dorsal process to support the coronoid; quadrate long and slender,

370   about 50% of skull length, presenting a posterior process (*sensu Martins, 2016*); a dorsal

371   foramen in the anterior half of quadrate absent.

372

373   ***Cervical vertebrae (Fig. 13)***

374   Atlas composed by neural arches not fused dorsally but fused ventrally to a reduced ventral

375   element (*intercentrum I* sensu *Holman, 2000*); short lateral projections of the atlas are present;

376   axis with short spinal process; lateral foramina of axis indistinct or absent; short lateral processes

377   present. Odontoid process of axis osseous and sutured to axis, approximately losangular in

378   anterior view, with an anterior tapered process; intercentra II and III ventral, compressed

379   laterally, bearing hypapophysis pointed in lateral view (sensu *Holman, 2000*).

380

381   ***Trunk vertebrae (Fig. 13)***

382   Trunk vertebrae at midbody dorsoventrally flattened and bearing ribs; neural arches flattened; neural

383   spines absent; spinal processes short and distinct; neural canal in anterior view about as high as wide;

384   epyzygapophyseal spines absent; zygosphenes present, emerging from the neural canal; zygosphenal

385   crests laterally expanded and tapered distally; zygosphenal articular facets absent; prezygosphenal

386   articular facets ellipsoidal; prezygapophyses expand into prezygapophyseal accessory processes distally

387   rounded and visible in dorsal view; zygrantrum wide laterally limited by the relatively developed

388   zygrantral articular facets; postzygapophyses laterally expanded and flattened; cotyle ellipsoidal in

389   anterior view; supracotilar and paracotylar foramina indistinct or absent; condyle ellipsoidal; vertebrae

390   centrum bearing lateral foramen at each side; synapophyses with no distinction between diapophyseal and

391   parapophyseal areas; hemal keel absent; subcentral ridges absent.

392

393   ***Pelvic girdle (Fig. 14)***

394   Composed by ilium, ischium, femur, and pubis. Ilium and pubis rod-like; ischium approximately

395   rectangular, apparently fused to pubis; ilium represents the longest bone of pelvic girdle; femur

396   approximately rectangular and curved, slightly larger than ischium, located at between the last

397   trunk vertebrae and second cloacal vertebrae.

398

399   *Variation*

400   The paratype series consists of seven specimens, two of which are lacking the head and anterior

401   part of body (NMW 15446:1 and NMW 15446:3). Thus information of measurements and

402   scalation of the tail and the coloration of body and tail is based on all specimens, whereas

403   information on other characters (e.g head measurements, skull conditions) is based only on the

404   complete specimens.

405

406   *Variation of scale counts and measurements (see Table 1 for individual data of each specimen)*

407   250–267 MDS ($\bar{x}$ = 260.83 ± 5.91, n = 6); 237–258 V ($\bar{x}$ = 247.17 ± 7.31, n = 6); 14–19 SC ($\bar{x}$ =

408   17.25 ± 1.83, n = 8); TL of 110–211 mm ($\bar{x}$ = 149.5 ± 36.84, n = 6); TAL of 5.9–10.3 mm ($\bar{x}$ =

409   8.48 ± 1.36, n = 6); MB of 2–4.4 mm ($\bar{x}$ = 3.04 ± 0.71, n = 8); MT of 1.7–3.1 mm ($\bar{x}$ = 2.34 ±

410   0.48, n = 6); TL/TAL of 14.7–20.5 ($\bar{x}$ = 18.13 ± 2.11, n = 6); TL/MB of 43.5–58.1 ($\bar{x}$ = 51.73 ±

411   5.59, n = 6); TAL/MT of 3.3–4.3 ($\bar{x}$ = 3.66 ± 0.41, n = 8); HW of 2–2.8 mm ($\bar{x}$ = 2.27 ± 0.30, n =

412   6); HH of 0.4–0.5 mm ($\bar{x}$ = 0.417 ± 0.04, n = 6); HL of 2.4–3.6 mm ($\bar{x}$ = 2.85 ± 0.41, n = 6); ED

413   of 1.3–2.3 mm ($\bar{x}$ = 1.717 ± 0.37, n = 6); RES of 0.3–0.4 ($\bar{x}$ = 0.365 ± 0.35, n = 6).

414

415   *Variation of color pattern*

416   Color pattern of paratypes mostly resembles that of the holotype except for the following (*Figs.*

417   *3–9*): no cream-colored blotch on anterodorsal part of rostral recognizable in one paratype

418   (NMW 15446:4), cream-colored blotch on rostral indistinct in two paratypes (NMW 15446:7

419   NMW 15446:8), cream-colored blotch more distinct and larger than in holotype, covering more

420   than half of rostral in dorsal view in one paratype (NMW 15446:5); ocular scale almost entirely

421   light to median reddish-brown in all paratypes; posterior supralabial almost entirely reddish

422   brown in one paratype (NMW 15446:4); some infralabials and some adjacent chin scales exhibit

423   a light brown pigmentation in some paratypes; in some paratypes the cream-colored ultimate part

424   of the tail covers also the scales adjacent to the terminal spine.

425

426 *Qualitative and quantitative variation of skull and lower jaw (n=6; holotype condition indicated with*

427 *asterisk)*

428 Dentary teeth 5 (n=3; 50%) or 6* (n=3; 50%); premaxilla pierced by two foramina in anterior

429 view and two large foramina in ventral view (n=1),three in ventral view and two in anterior view

430 (n=1) or two in anterior view and four in ventral view (n=5*); medial sulcus of premaxilla

431 present (n=1) or absent* (n=5); maxilla perforated by one (n=1), three (n=1), four* (n=2), five

432 (n=1) or six (n=1) foramina; projections for the attachment of neck muscles in parabasisphenoid

433 absent (n=5; *Fig. 15B*) or present* (n=1; *Fig. 15A*, yellow arrows), projections for the attachment

434 of neck muscles in basioccipital absent (n=5; *Fig. 15B*) or present* (n=1; *Fig. 15A*, red arrows);

435 statolythic mass present (n=3; *Fig. 15C*) or absent* (n=3; *Fig. 15D*); basioccipital with medial

436 recess (n=2; *Fig. 15B*) or not* (n=4; *Fig. 15A*, black arrow); lateral recess of nasal present (n=1;

437 *Fig. 15E*) or absent* (n=5; *Fig. 15F*).

438

439 *Postcranial quantitative variation*

440 Precloacal vertebrae 231–248 ($\bar{x} = 240 \pm 6.5$, *n* = 6); caudal vertebrae 14–21 ($\bar{x} = 18 \pm 2.7$, *n* =

441 5). Correlation (*n* = 5) between middorsal scales and precloacal + cloacal + caudal (0.99:1),

442 between midventral scales and precloacal vertebrae (0.97:1), and between subcaudal scales and

443 cloacal + caudal vertebrae (1:1.3). Pelvic girdle located at the level of the 229th (= penultimate)

444 trunk vertebrae and first cloacal vertebrae (NMW15446:2), 233-234th (= penultimate and last)

445 trunk vertebrae (NMW15446:4), 246th (=last) precloacal and second cloacal vertebrae

446 (NMW15446:5), 248th (= last) trunk and second cloacal vertebrae (NMW15446:6), 240th (= last)

447 trunk and first cloacal vertebrae (NMW15446:7) and 238th (= last) trunk and second cloacal

448 vertebrae (NMW15446:8).

449

450 *Postcranial qualitative variation (n=6; holotype condition indicated with asterisk)*

451 Ventral element of atlas absent or not ossified to neural arches (n=3) or absent with neural arches

452 fused ventrally* (n=3); anterior hypapophysis of axis pointed* (n=5) or rounded (n=1); posterior

453 hypapophysis of axis rounded (n=1), truncated (n=3) or pointed* (n=2); hypapophysis of axis

454 fused (n=1) or not* (n=5); femur fused (n=1) or not* (n=5) to ischium.

455

456 *Etymology*

457 The specific epithet is an agglutination of the Latin nomen "ignis" which means fire and the

458 proper noun "Rio" as an acronym for the Brazilian city of Rio de Janeiro. This name was chosen

459 in honour to the Museu Nacional do Rio de Janeiro/UFRJ, Brazil's oldest scientific institution

460 with the largest South American collections of zoology, anthropology, geology and

461 paleontology. Many of the precious collections pertaining to the zoology department (mostly

462 invertebrates), anthropology, geology and paleontology were completely destroyed in the

463 disastrous fire in its main building on September 2nd 2018. Due to historical neglection of this

464 institution from the Brazilian government, added with substantial funding decrease in the past 5

465 years the museum did not receive sufficient money to fullfil basic safety standards – such as fire

466 protection. The description of this new species, with specimens housed in a scientific collection

467 for more than 100 years highlights one of the several importances of zoological collections in

468 housing relevant material to understand the diversity of life, and also reinforce that such

469 collections are timeless treasures for science. Such collections should receive strong attention in

470 government investments as they contribute to the global development of science.

471

472 *Distribution and natural history*

473 *Epictia rioignis* is currently known exclusively from its type series, from Corinto, Nicaragua

474 (See comments under Discussion).

475

Discussion

477 Steindachner (1834–1919) was curator of Ichthyology and Herpetology in the NMW from 1860–

478 1919. On the original label of NMW 15446 (*Fig. 16A*) he only noted "Corinto, 1907, Steind.

479 don." but failed to mention a country name. Unfortunately and in addition, Steindachner was not

480 always consistent with respect to the event, to which the year mentioned on his labels refered to.

481 In some occasions the year refers to the collecting event, whereas in other occasions the year

482 refers to the acquisition of the specimen(s) or even to the year the vouchers were inventoried by

483 Steindachner (*Neumann, 2011*). At least, the color of the labels of the Herpetological collection

484 always referred to a certain continent. The green labels were used for "America" and thus one

485 can conclude that this is the continent of origin of the voucher specimens NMW 15446. Later

486 Eiselt (curator of the herpetological collection from 1952–1977) added "S-Amerika" on a newer

487 label (*Fig. 16B*) and likewise mentioned "Corinto, S-Amerika, 1907" in the inventory book.

488 Considering the trips of Steindachner and the specimens in the ichthyological and herpetological

489 collection of the NMW, the name Corinto may refer to at least three localities in South- or

490 Central America: Corinto, Minas Gerais (Brazil), Corinto, Cauca (Colombia), and Corinto

491 (Nicaragua) (http://geonames.nga.mil/namesgaz). Corinto, Minas Gerais (Brazil) was named

492 "Curralinho" at the time when the specimens were collected. In 1923, and thus many years after

493 the collecting event, it became a municipality and was renamed as Corinto (*Barbosa, 1995*).

494 Thus, if Steindachner had acquired the specimens from this locality he would have assigned

495 them to "Curralinho" rather than Corinto. Corinto, Cauca (Colombia) is a town and municipality

496 in the Cauca department (29,308 km²). In the collections of the NMW are indeed specimens from

497 the "Cauca region" inventoried by Steindachner, but the city of Corinto was never mentioned. An

498 extended query for the name "Corinto" in the databases of the NMW yielded a single result:

499 eight marine fish species from "Corinto, Nicaragua, collected in 1901, Schiff Donau" were found

500 in the inventory of the fish collection. When Steindachner acquired several specimens from the

501 same collecting event he often provided just one main label with further information (e.g. the

502 country of origin) and used labels with reduced information for the other specimens, independent

503 of the fact that the specimens belonged to different taxonomic groups (e.g. fishes and reptiles).

504 As no other label for "Corinto" with more specific information could be found, we assume that

505 the only detailed label found in the fish collection represents the "main" label of Steindachner for

506 all specimens from the locality Corinto. Thus we further assume that the specimens of *Epictia*

507 *rioignis* sp. nov. found in the Herpetological Collection of the NMW derive from the same

508 collecting event and thus originate from Corinto in Nicaragua. The Nicaraguan Corinto is an

509 important port town in the Northwest Pacific Coast which was founded in 1858, and has been

510 historically important as a point of entry to Nicaragua since early 19th century. When labelling

511 Corinto, Steindachner might have referred to both, the locality where the specimens were

512 collected or the locality from where they were acquired. Therefore, considering the data provided

513 herein, the locality of Corinto might still be considered with certain care, as the specimens might

514 have been brought from other localities in Nicaragua.

515 Nicaragua is an important megadiverse country, however, its snake fauna is less diverse in

516 comparison to other neighboring countries in Central America (*Sunyer, 2014*). Even if snake

517 diversity is relatively low, studies on the Nicaraguan herpetofauna are still incipient and

518   additional efforts on herpetological research might reveal novel data on the snake fauna of this

519   country (*Sunyer, 2014*). So far, amongst *Epictia* spp., only *E. ater* has been previously reported

520   to occur in Nicaragua, inhabiting lowland arid forests, premontane wet forests and dry tropical

521   forests at elevations between 40-100 m above sea level in the western portion of the country

522   (*Wallach, 2016*). Therefore, our study increases the number of *Epictia* species currently found in

523   Nicaragua to n=2. As previously mentioned (Comparisons section), *E. rioignis* sp nov. differs

524   from *E. ater* mostly by quantitative characters, such as the number of middorsal scales and

525   snout-vent length as well as qualitative characters such as the presence/absence of a frontal scale,

526   supralabial-supraocular contact, pattern of dorsal stripes on body and tail (present study,

527   *Wallach, 2016*), and also based on osteological evidences. Even if there is an apparent overlap of

528   the amplitude of middorsal scales (250-267 in *E. rioignis* sp nov. *versus* 212-266 in *E. ater*),

529   general means for such counts ($\bar{x}$ = 260.83 for *E. rioginis* sp nov. *versus* = $\bar{x}$ 237.3 for *E. ater*;

530   present study; *Wallach, 2016*) provide evidence for their distinction. Additionally, albeit both

531   supraocular-supralabial contact, as well as the fusion of the frontal and rostral scale can be

532   subject to intraspecific variation (*Wallach, 2016*; *Francisco, Pinto & Fernandes 2018*), such

533   variation usually occurs in a very limited number of the samples. Thus, these characters are still

534   useful for the differentiation of threadsnake species, especially with respect to the relatively

535   conservative and simplified external morphology of these snakes. The combination of scale size,

536   arrangement, and proportion, color pattern and internal anatomy has proven to be sufficient to

537   distinguish the different taxa, which have also been previously identified in molecular studies

538   (*Wallach, 2016*). Additional studies on species anatomy (such as hemipenial morphology) might

539   reveal further differences between both species. In fact, with respect to the relatively

540   conservative external morphology of threadsnakes (*Wallach, 2016*; *Martins, Passos & Pinto*

541   *2018*), data on hemipenial morphology (and other internal systems) would be very useful to

542   clarify the systematics of threadsnakes.

543   *Wallach (2016)* recognizes three groups among the *Epictia* species: one from Mesoamerica

544   (*Epictia phenops* species group) and two from South America (*Epictia tesselata* species group

545   and *Epictia albifrons* species group). According to the author, the Mesoamerican assemblage

546   consists of 11 species (*E. ater, E. bakewelli, E. columbi, E. magnamaculata, E. martinezi, E.*

547   *pauldwyeri, E. phenops, E. resetari, E. schneideri, E. vindumi*, and *E. wynni*). Given the

548   phenotypic similarities and also similar distribution of *E. rioignis* sp nov., we assign this species

549   to the *E. phenops* species group. Nevertheless, the composition of the three groups still needs to

550   be clarified with further molecular analyses (present study; *Wallach, 2016*).

551

Conclusions

553   The biodiversity of scolecophidians worldwide is greatly underestimated and often unexpected

554   (*Wallach, 2016*). Although most of the systematic changes in *Epictia* spp. have arisen from

555   molecular studies (or at least provided a start point for additional taxonomical arrangements, see

556   *Wallach, 2016*), morphological studies including both external morphology and internal anatomy

557   are very important for systematic clarification of this group (present study). Even if molecular

558   studies have aided on the identification of cryptic species, this study shows that the

559   morphological analysis of collection specimens still reveals novel data for threadsnakes. This

560   further emphasizes the importance of zoological collections in housing specimens that still allow

561   description of new taxa based on specimens collected more than a century ago.

562

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579

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613   *espèces de serpents non venimeux, savoir: la totalité desvermiformes ou des scolécophides, et*

614   *partie des cicuriformes ou azémiophides), en tout vingt–cinq genres et soixante–cinq espèces.*

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779

780 **Appendix**

781

782 *Additional specimens examined:*

783

784 *Epictia albifrons*: BRAZIL: **Mato Grosso**: Cuiabá (SMF 16695).

785 *Epictia albipuncta* (all specimens so far declared as *Leptotyphlops melanotermus*):

786 ARGENTINA: without locality (NMW 16871/1–4); **Cordoba**: San Francisco (MTKD 27438–

787 40); **Tucuman** (FMNH 229948, MCZ 120055, MCZ 120056); BOLIVIA: **Cochabamba**: Alto

788 Chiripiri (FMNH 161503); **La Paz**: La Paz (ZMB 26203).

789 *Epictia alfredschmidti*: PERU: **Ancash**: Huarmey: Malvas, 2940– 3090 m a.s.l. (MUSM 20068 –

790 Holotype, SMF 80066, SMF 80067 – Paratypes).

791 *Epictia antoniogarciai*: PERU: **Cajamarca**: Jaén: Santa Rosa de la Yunga, 1268 m a.s.l.

792 (CORBIDI 2069 – Paratype, CORBIDI 7678 – Holotype); **Amazonas**: Utcubamba: Zapatalgo,

793 934–968 m a.s.l. (ZFMK 90934 – Paratype, ZFMK 96676 – Paratype, CORBIDI 5670).

794 *Epictia ater:* COSTA RICA: **Guanacaste**: Guanacaste NP (ZFMK 57774, ZFMK 57775);

795 NICARAGUA: **Chinandenga:** Volcano Chongo (KU 194336, 2000596); **Estelli:** (KU174119-

796 21, KU174134-35); **Granada**: Volcano Mombacho, 1100 m a.s.l. (SMF 78981); No data

797 (MNHN 1888.240, MNHN 1888.241); **Managua** (ZSM 660/1911); **Carazo**: 20 km southwest of

798 Diriamba, La Maquina (SMF 81036).

799 *Epictia australis:* ARGENTINA: **Buenos Aires**: Sierra de la Ventana (IBIGEO 5887–5905);

800 **Cordoba**: Pampa Achala (MTKD 34013); Sierra Chica de Cordoba (ZSM 198/136/1);

801 PARAGUAY: **Chaco**: Chaco (ZFMK 36112), Filadelfia (ZFMK 51301), 35 km west of

802 Filadelfia (ZFMK 53237, ZFMK 53238), Para Todo (ZFMK 55208).

803 *Epictia collaris:* FRENCH GUYANA: Saül (MNHN 1999.8309); Montagne de Mahury

804 (MNHN 1977.49– Paratype); Camp de Saint Eugène (MNHN 1996.4580).

805 *Epictia diaplocia*: PERU: Cusco: La Convencion: Echarate: 557 m a.s.l. (MUSM 31322); Pozo

806 Cashiriari 2 (MUSM 26115); Camana: Bosque de Terazas (MUSM 28169); **Huánuco**: Pachitea:

807 Chaglla-Rinconada (CORBIDI 13356, 13357); **Madre de Dios**: 15km E Puerto Maldonado, 200

808 m a.s.l. (KU 212594); Manu: Manu Learning Center (MUSM 31619); **San Martin**: 14km ESE

809 Shapaja, 360 m a.s.l. (KU 214906); Moyobamba (BMNH 74.8.4.104).

810 *Epictia fallax:* VENEZUELA: **Vargas**: "Laguayra" [La Guaira] (ZMB 9550– Holotype).

811 *Epictia goudotii:* COLOMBIA: Valle Magdalena (MNHN 1068 – Holotype); VENEZUELA:

812 Aragua (USNM 258148); Bolivar: **Guri** (ZFMK 64415, ZFMK 64416); Distrito Federal: **Tarna**

813 (ZFMK 64423).

814 *Epictia hobartsmithi:* VENEZUELA: **Bolivar**: Guaiquinima Tepui, 1180 m a.s.l. (ZSM

815 107/1990 – Paratype).

816 *Epictia magnamaculata*: HONDURAS: **Islas de la Bahia**: Isla de Utila: Iguana Station (SMF

817 81215, SMF 79859, SMF 79868, USNM 54760); Isla de Roatan, Mud Hole Bay (SMF 80860);

818 Isla del Cisne Grande, 16 m (SMF 90441); Isla Guanaja: Northeast Bight (SMF 75998).

819 *Epictia melanura*: PERU: **La Libertad** (FMNH 34269 – Holotype); Chiclin (FMNH 34268,

820 Paratype).

821 *Epictia munoai*: ARGENTINA: **Buenos Aires** (SMF 16694); BRAZIL: **Rio Grande do Sul**

822 (ZMB 1432, ZMB 85279); URUGUAY: Tacuarembo (USNM 163506).

823 *Epictia peruviana:* PERU: Ayacucho: ca. 132 km from Ayacucho on road to Kirimbi (MUSM

824 30220); **La Pampa de Sacramento** (ZFMK 41475).

825 *Epictia phenops:* GUATEMALA: No data (MNHN 5741, MNHN 1667); MEXICO: **Oaxaca**:

826 Tehuantepec (MNHN 8405, MNHN 5660, MNHN 4430); EL SALVADOR: **San Salvador**: San

827 Salvador (SMF 42801, SMF 77236); San Antonio near San Salvador (SMF 42933); Instituto

828 Tropical, 700 m a.s.l. (SMF 42022–42023, 42025, SMF 43216–18, SMF 75814, SMF 77399);

829 km 40 of the Road to San Vicente (SMF 75813); km43 of the Road to San Miguel (SMF 77400);

830 **Sonsonate**: Hacienda San Antonio, 220 m a.s.l. (SMF 42024).

831 *Epictia rufidorsa*: PERU: Ancash: Recuay: Llacllin: Chaucayan: km 65 Pativilca-Huaraz, 1320

832 m a.s.l. (MUSM 25426); **La Libertad**: Chiclin (FMNH 34305); **Lima**: Pv Canta: Campamento

833 Camaná: km 57, Road to Canta (MUSM 3416); Huarochiri: Tornamesa: Santa Cruz de

834 Cocachacia, km 55 Carretera Central (MUSM 25349); Lima: (MUSM 16675; Chaclacayo

835 (CORBIDI 6865, MUSM 16733, MUSM 16735); Club Villa Tusan (CORBIDI 10417);

836 Surquillo, San Boja (MUSM 3094); Garden of MUSM (MUSM 10082).

837 *Epictia septemlineata*: PERU: **Cajamarca**: Celendin: Limon, 2053 m a.s.l. (CORBIDI 14683 –

838 Holotype).

839 *Epictia signata:* No data (MNHN 3235 – Holotype).

840 *Epictia striatula:* PERU: No data (FMNH 81509); **Cuzco**: Marcapata valley (BMNH

841 1902.5.29.184, so far declared as *L. melanotermus*); La Convención: CCNN Poyentimari

842 (CORBIDI 8564); **Puno** (FMNH 40210); BOLIVIA: **Chaco** (NMW 15542/4); **Santa Cruz**:

843 Florida: Pampagrande: Pampagrande (ZFMK 66925, ZFMK 66926, ZFMK 66927, ZFMK

844 75058); Los Negros (ZFMK 75033); Palmasolo (ZFMK 75059).

845 *Epictia subcrotilla*: PERU: **La Libertad** (FMNH 34304); Chiclin (MCZ 48936); **Piura**:

846 Huancabamba: San Jacinto del Tocto (CORBIDI 14195); Morropon (MUSM 2775);

847 **Cajamarca**: Jaén: Bellavista (CORBIDI 1818).

848 *Epictia teaguei*: PERU: **Cajamarca**: Rio Zana (FMNH 232568); Chota: Chucrade Chekos

849 (MUSM 28351); La Granja (CORBIDI 1604, MUSA 4339, MUSA 4341, MUSM 28415,

850 MUSM 28416); Querocoto (MUSM 31208); Rio Paltic (MUSM 28414).

851 *Epictia tenella*: FRENCH GUYANA: No data (MNHN 2001.0319); Haut-Oyapock (MNHN

852 1978.2583, MNHN 1978.2584); TRINIDAD AND TOBAGO: **Trinidad**: (ZMB 24661);

853 VENEZUELA: **Sucre**: 3-5km N Macuro (KU 133524).

854 *Epictia tesselata*: PERU: No data (FMNH 134464); **Ica**: Pisco: Paracas: Punta Arquillo near to

855 Mirador (MUSM 3418); **Lima** (FMNH 35097, FMNH 36726, BMNH 51.1.19.29, MUSM

856 2820); Callao (MTKD 9304); City of Lima (SMF 41885, MUSM 2383, MUSM 16734 –

857 declared as *Epictia teaguei*); Old distrito de cercado building E (KU 212773); Avenida

858 Circunvalacion, Huachipa (CORBIDI 12707); Barranco (MUSM 3092); Jesus Maria, Garden of

859 MUSM (MUSM 24423, MUSM 24424 – both declared as *Epictia teaguei*); La Molina, Calle

860 Melgarejo (CORBIDI 12814); Magdalena (MUSM 16123, MUSM 16124); Miraflores (MUSM

861 14013, MUSM 16673); Monterrico, Las Incas (MUSM 3091); Pueblo Libre (MUSM 3179); San

862 Luis, Tupac Amaru (MUSM 3171); Santa Anita (MUSM 25378); University San Marcos

863 (MUSM 3374).

864 *Epictia tricolor*: PERU: **Ancash**: Carhuaz, 2710 m a.s.l. (MUSA 2873); Huaraz, 3250 m a.s.l.

865 (KU 135176, KU 135177); Huaylas: Yuanca Pampa, 2700 m a.s.l. (MUSM 669– Holotype,

866 MUSM 670– Paratype, MUSM 2923, USNM 195853); **Cajamarca**: Cajabamba, 2700 m a.s.l.

867 (KU 135178), 2880 m a.s.l. (MUSA 4234, MUSA 4235, MUSA 4236, MUSA 4254); **La**

868 **Libertad**: Sanchez Cavion, Sanagoran (MUSM 28550).

869 *Epictia vanwallachi*: PERU: **La Libertad**: Pataz: Vijus, 1297 m a.s.l. (CORBIDI 14682 –

870 Holotype).

871 *Epictia vonmayi*: PERU: **Cajamarca**: Chota: Querecoto: La Granja-Río Tinto, 2069 m a.s.l.

872 (MUSA 4342 – Holotype), 1985 m a.s.l. (MUSA 4340 – Paratype).

873   *Epictia vellardi*: PARAGUAY: **Boquerón**: Toledo (MTKD 43465– 43467, 43469).

874   *Epictia venegasi*: PERU: **Cajamarca**: Cajabamba: Cachi-Moyan, 2551 m a.s.l. (MUSA 4252 –

875   Holotype), 2567–2736 m a.s.l. (MUSA 4237–42, MUSA 4248, MUSA 4253 – Paratypes).

876   *Mitophis asbolepis*: DOMINICAN REPUBLIC: **Barahona**: Loma del Aguacate (USNM

877   236660).

878   *Mitophis calypso*: DOMINICAN REPUBLIC: **Samana**: Las Galeras (USNM 236658, 236659).

879   *Mitophis leptepileptus*: HAITI: **Sud-Est:** Soliette (KU 275542, 275543, 275548, 275549,

880   275562, 275567, USNM 576217)*; Fond Verettes (USNM 236661).

881   *Mitophis pyrites:* DOMINICAN REPUBLIC: **Pedernales**: Pedernales (MCZ 77239, USNM

882   152452).

883   *Rena dulcis*: UNITED STATES OF AMERICA: **Florida** (USNM 15466); **Oklahoma**:

884   Comanche (OMNH 35564, 35580); Marshall (USNM 258213, 258214, 258217, 258218);

885   Seminole (USNM 198022, 198023, USNM 258197); **Texas**: Bell (USNM 198036); Frio (LACM

886   162021); Hays (AMNH 160152, LACM 162022); Hidalgo (USNM 299630, 299642); McLennan

887   Co (FMNH 40957, USNM 198037, 198042, 258186, 258188); Pecos (USNM 7296); Travis

888   Austin (USNM 161288).

889   *Rena humilis*: MEXICO: **Baja California** (AMNH 5576); **Jalisco** (AMNH 94866); **Nayarit**

890   (AMNH 75587, 87584, 96616, USNM 240693, 240879); **Sinaloa** (AMNH 90761, 90762);

891   **Sonora:** Bahia Kino (USNM 214128); **without locality** (AMNH 66170, USNM 26140);

892   UNITED STATES OF AMERICA: **Arizona:** Graham (AMNH 63458); Maricopa (USNM

893   246639); Pima (AMNH 73716); Yuma (USNM 26289); **California**: Imperial (USNM 139916,

894   139917, 222794); Riverside (AMNH 84309); San Bernardino (AMNH 131165); San Diego

895   (FMNH 77599, SDNHM 2956, 9347, 24273, 24407, 24408, 33950, 34302, 42772, 61052,

896   61055, 61057, 61059, 61060, 61062, 61068, 61088, USNM 193023, 196570, UIMNH 84591).

897   *Rena maxima* (*n* = 1). MEXICO: **Guerrero:** Chilpancinga (MCZ 33606).

898

899   *Rena myopica*: UNITED STATES OF AMERICA: **New mexico:** Eddy: Malaga (USNM

900   125131); MEXICO: **San Luis Potosí** (AMNH 172551); **Tamaulipas:** Gomez Farias (USNM

901   248499).

902   *Rena segrega:* MEXICO: **Coahuila:** Torreon (USNM 193593); UNITED STATES OF

903   AMERICA: **ARIZONA:** without locality (AMNH 43439); Pima (USNM 16952); **New Mexico:**

904   Doña Ana (AMNH 172545,172546, LACM 2154, 134007, 134009); **Texas:** Val Verde (AMNH

905   172548); Brewster (USNM 103670); **without locality** (AMNH 112249).

906   *Rena unguirostris*: ARGENTINA: Poman Puesto Rio Blanco (FML 1399); **Tinogasta**: Palo

907   Blanco (FML 1773).

908   *Siagonodon cupinensis:* BRAZIL: **Mato Grosso:** Barra do Tapirapés: Guarantã do Norte

909   (UFMT 5627).

910   *Siagonodon septemstriatus:* SURINAME: without locality (ZSM 127/1947, ZMB 3876 –

911   Holotype); BRAZIL: **Amazonas**: Manaus: Rio Negro: Estuary of Rio Negro (NMW 15476/1).

912   *Tetracheilostoma billineatum*: MARTINIQUE: **Le Lamentin:** without locality (USNM 564808,

913   564809); SAINT LUCIA: **Saint Lucia:** Anse-La- Raye (USNM 222954); **without locality**

914   (MCZ 10693).

915   *Tetracheilostoma breuili*: SAINT LUCIA: **Islas Maria:** Isla Maria Major (USNM 564810–17).

916   *Tetracheilostoma carlae:* BARBADOS: **Saint Joseph:** Bonwell (USNM 564818–19).

917   *Tricheilostoma bicolor*: GHANA: **Somanya:** Krobo (MCZ 55388, MCZ 55383).

918   *Tricheilostoma sundewalli*: GHANA: **Somanya:** Krobo (MCZ 55396).

919   *Trilepida brasiliensis:* BRAZIL: **Mato Grosso Do Sul:** Corumbá (UFMT 683, 1159, 1160,

920   1162, 1163, 1169); Rosário d´Oeste (MNRJ 24334).

921   *Trilepida dimidiata*: BRAZIL: **Roraina**: Ilha de Maracara: Maracara (BMNH 1994.241).

922   *Trilepida fuliginosa*: BRAZIL: **Goiás:** Colinas do Sul (MNRJ 19223); Luziânia (CHUNB

923   40847, 408486); Minaçú (MZUSP 11019); Ouvidor (MNRJ 19221); **Minas Gerais:** Unaí

924   (MNRJ 24400).

925   *Trilepida jani*: BRAZIL: **Minas Gerais:** Ouro Preto (LZV 813S); Ouro Branco (778S1); without

926   locality (MNRJ 16990).

927   *Trilepida joshuai*: COLOMBIA: **Antioquia**: Jericó (IBSP 8919); **Valle del Cauca**: Tocota, 1800

928   m a.s.l. (NMW 38424/1–2, declared as *Epictia weyrauchi*).

929   *Trilepida koppesi*: BRAZIL: **Goiás:** Caldas Novas (MZUSP 11111); Aporé (MNRJ 24715,

930   24716); Luiziânia (CHUNB 40788); Mineiros (CHUNB 25714); **Tocantins:** Porto Alegre do

931   Tocantins (CHUNB 38928).

932   *Trilepida macrolepis*: BRAZIL: **Pará:** Paraupebas: Floresta Nacional de Carajás (MPEG

933   23017); COLOMBIA: **Vale Del Cauca**: Buenaventura (USNM 154031, 267261); **Córdoba:**

934 Pueblo Nuevo (ICN 7677); ECUADOR: **Esmeraldas:** Durango **(**QCAZ 12494); VENEZUELA:

935 **Merida** (NMW 15468/1–4); **Yaracuy**: Salom (MTKD 26320–26321).

936 *Trilepida salgueiroi*: BRAZIL: **Bahia**: São José do Macuco (currently São José da Vitória)

937 (MZUSP 9098); **Espírito Santo:** Governador Lindemberg (MNRJ 12132); Itá (currently Baixo

938 Guandu) (IB 8876, holotype); Aracruz (MNRJ 4856); Campinho (MNRJ 1925); Governador

939 Lindemberg (MNRJ 12131-12132); Linhares, Goytacazes (MNRJ 1926); Linhares, Sooretama

940 (MZUSP 2463); **Minas Gerais:** Aimorés (MCNR 1468-1469, MNRJ 12239), Muriaé: (MZUFV

941 1519); Recreio (MNRJ 7856); **Rio De Janeiro:** Cambuci (MNRJ 14487); Niterói: Itaipu (MNRJ

942 13124,15422).

943 *Trilepida pastusa*: ECUADOR**: Carchi**: Tulcán **(**QCAZ 5778).

Morphometrics, pholidosis and osteological characters of *Epictia rioignis* sp. nov.

CAV, caudal vertebrae; CLV, cloacal vertebrae; ED, eye diameter; HH, head height; HL, head length; HW, head width; MB, midbody diameter; MDS, middorsal scale rows; MT, midtail diameter; PCV, precloacal vertebrae; SC, subcaudals; TAL, tail length; TL, total length; V, ventral scales.

1 **Table 1:**

2 **Morphometrics, pholidosis and osteological characters of *Epictia rioignis* sp. nov.**

3 (Abbreviations are explained in Material and methods)

No.	MDS	V	PCV	SC	CAV	CLV	TL (mm)	TAL (mm)	MB (mm)	MT (mm)	HL (mm)	HW (mm)	HH (mm)	ED (mm)
NMW 15446:1	/	/	/	14	/	/	/	9.3	3.4	2.6	/	/	/	/
NMW 15446:2	250	237	231	19	20	4	113	7.7	2.6	1.8	2.6	2	1.3	0.4
NMW 15446:3	/	/	/	19	/	/	/	9.2	3.4	2.8	/	/	/	/
NMW 15446:4	261	243	235	17	18	4	149	8.2	3	2.4	2.9	2.2	1.9	0.5
NMW 15446:5	262	245	246	18	/	/	110	5.9	2	1,7	2.4	2	1.4	0.4
NMW 15446:6	267	258	248	15	17	4	211	10.3	4.4	3.1	3.6	2.8	2.3	0.4
NMW 15446:7	265	248	240	18	14	5	157	7.9	2.7	2.2	2.7	2.2	1.6	0.4
NMW 15446:8	260	252	238	18	21	3	157	9.3	2.8	2.1	2.9	2.4	1.8	0.4

Figure 1

Drawings of the head of the holotype of *Epictia rioignis* sp. nov. (NMW 15446:6)

(A) Lateral, (B) dorsal and (C) ventral views.
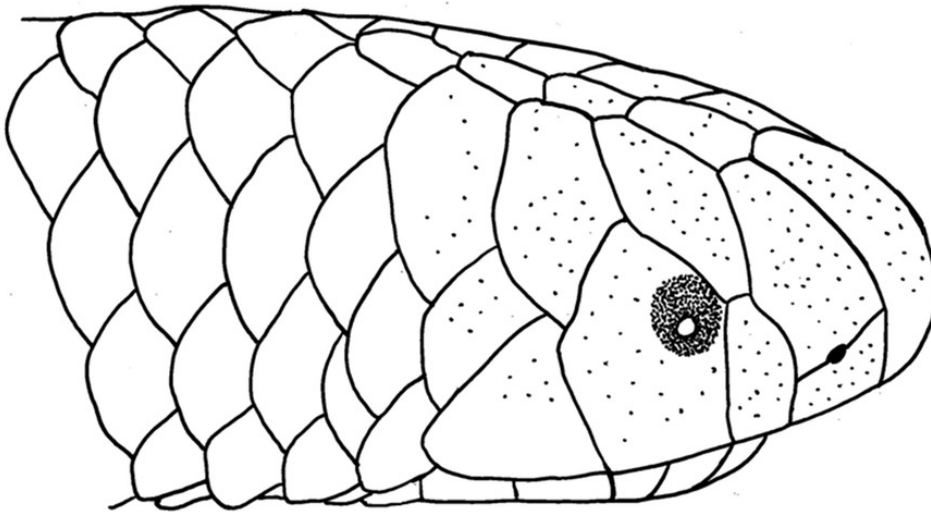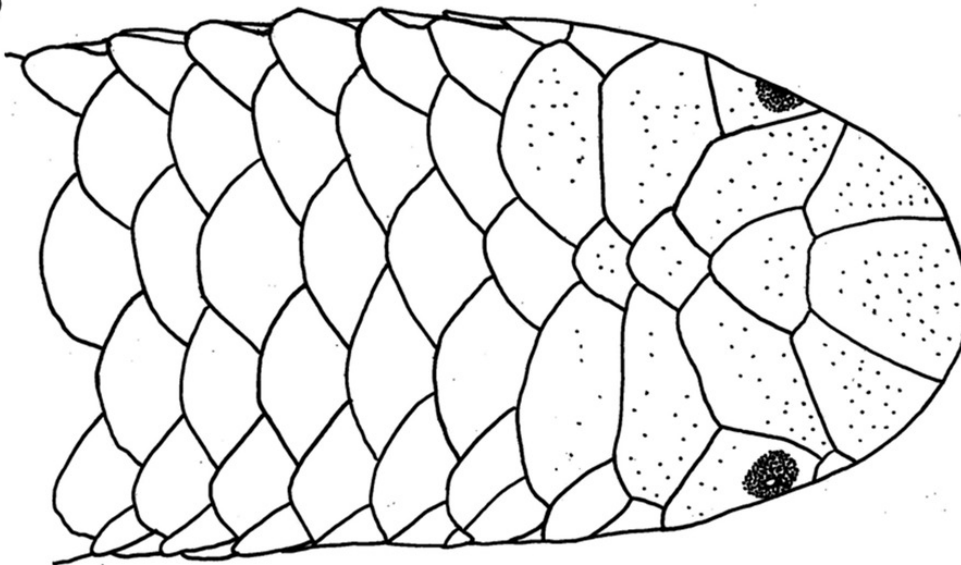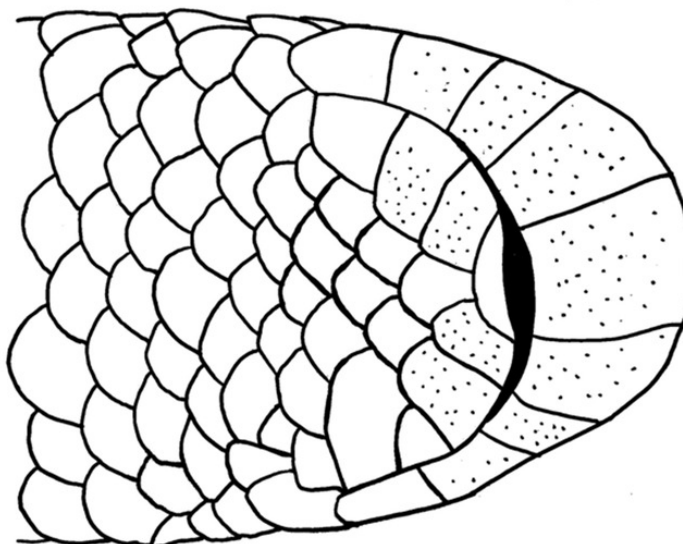
Figure 2

Holotype of *Epictia rioignis* sp. nov. (NMW 15446:6).

(A) Dorsal and (B) ventral or lateral views.
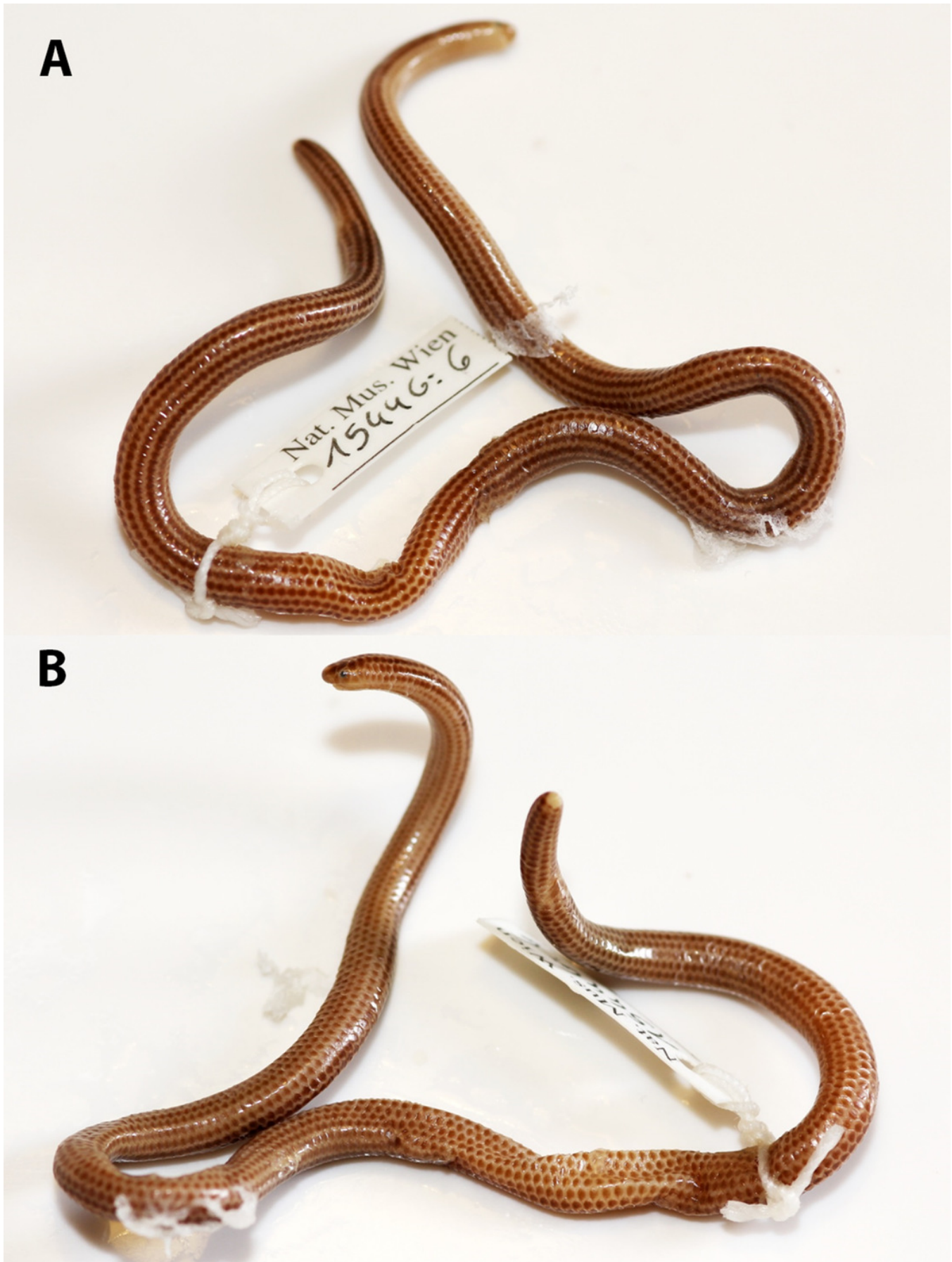
Figure 3

Comparison of dorsal views of the heads of holotype (NMW 15446:6, upper left picture) and paratypes of *Epictia rioignis* sp. nov.

(A) Holotype (NMW 15446:6). (B) Paratype (NMW 15446:2). (C) Paratype (NMW 15446:4). (D) Paratype (NMW 15446:5). (E) Paratype (NMW 15446:7). (F) Paratype (NMW 15446:8). Photo credits: Alice Schumacher & Josef Muhsil.
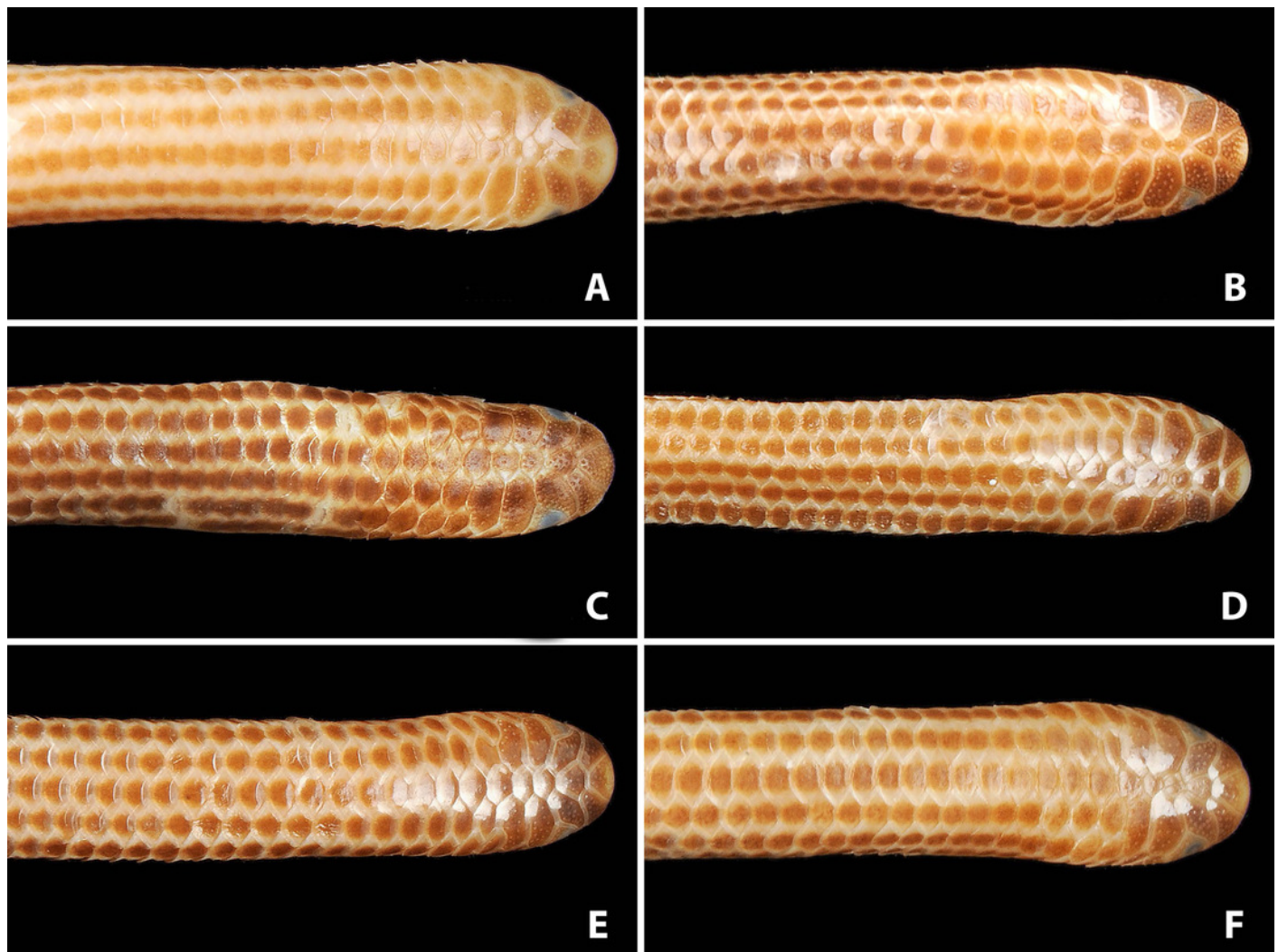
Figure 4

Comparison of lateral views of the heads of holotype (NMW 15446:6, upper left picture) and paratypes of *Epictia rioignis* sp. nov.

(A) Holotype (NMW 15446:6). (B) Paratype (NMW 15446:2). (C) Paratype (NMW 15446:4). (D) Paratype (NMW 15446:5). (E) Paratype (NMW 15446:7). (F) Paratype (NMW 15446:8). Photo credits: Alice Schumacher & Josef Muhsil.
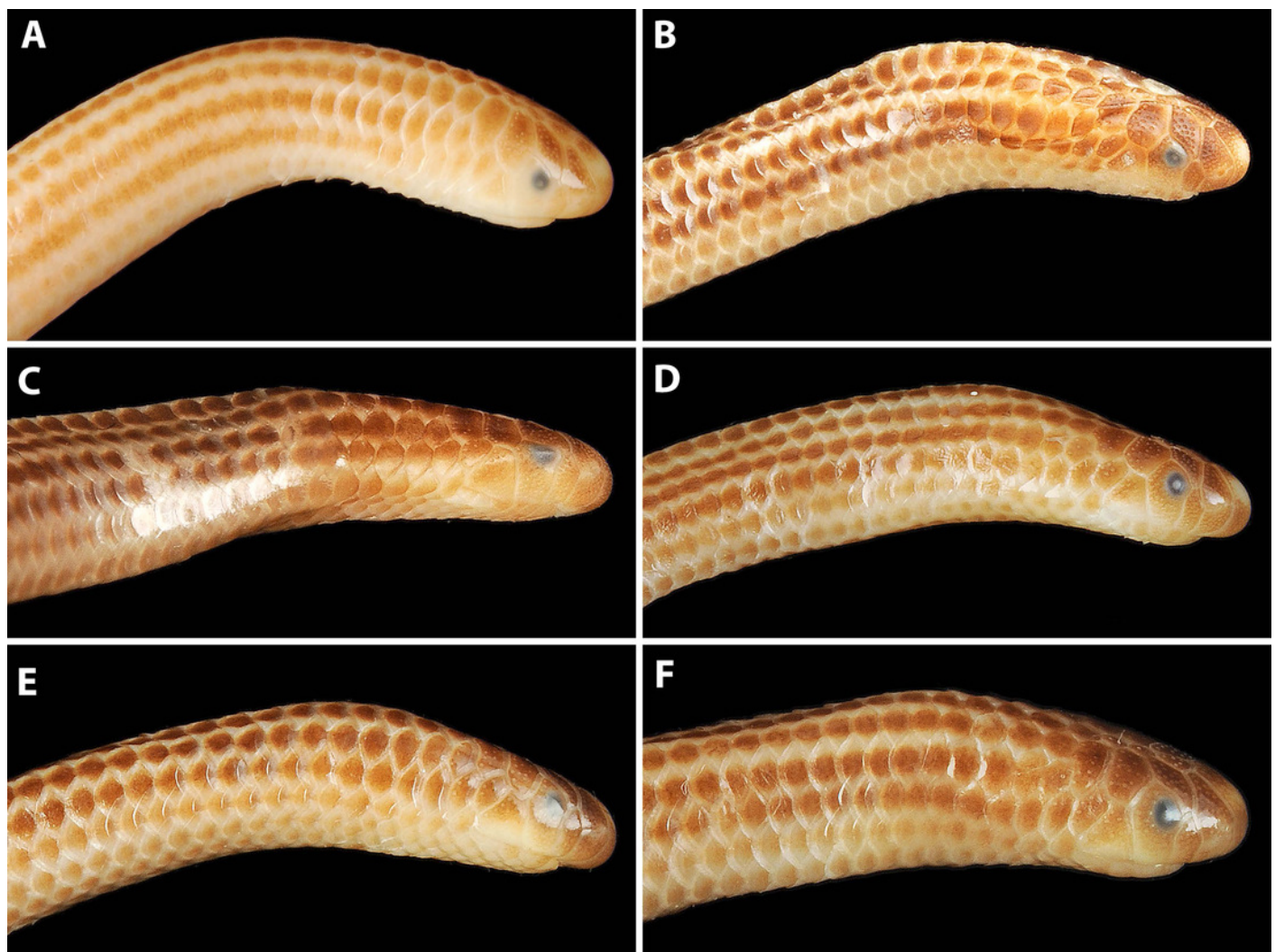
Figure 5

Comparison of ventral views of the heads of holotype (NMW 15446:6, upper left picture) and paratypes of *Epictia rioignis* sp. nov.

(A) Holotype (NMW 15446:6). (B) Paratype (NMW 15446:2). (C) Paratype (NMW 15446:4). (D) Paratype (NMW 15446:5). (E) Paratype (NMW 15446:7). (F) Paratype (NMW 15446:8). Photo credits: Alice Schumacher & Josef Muhsil.
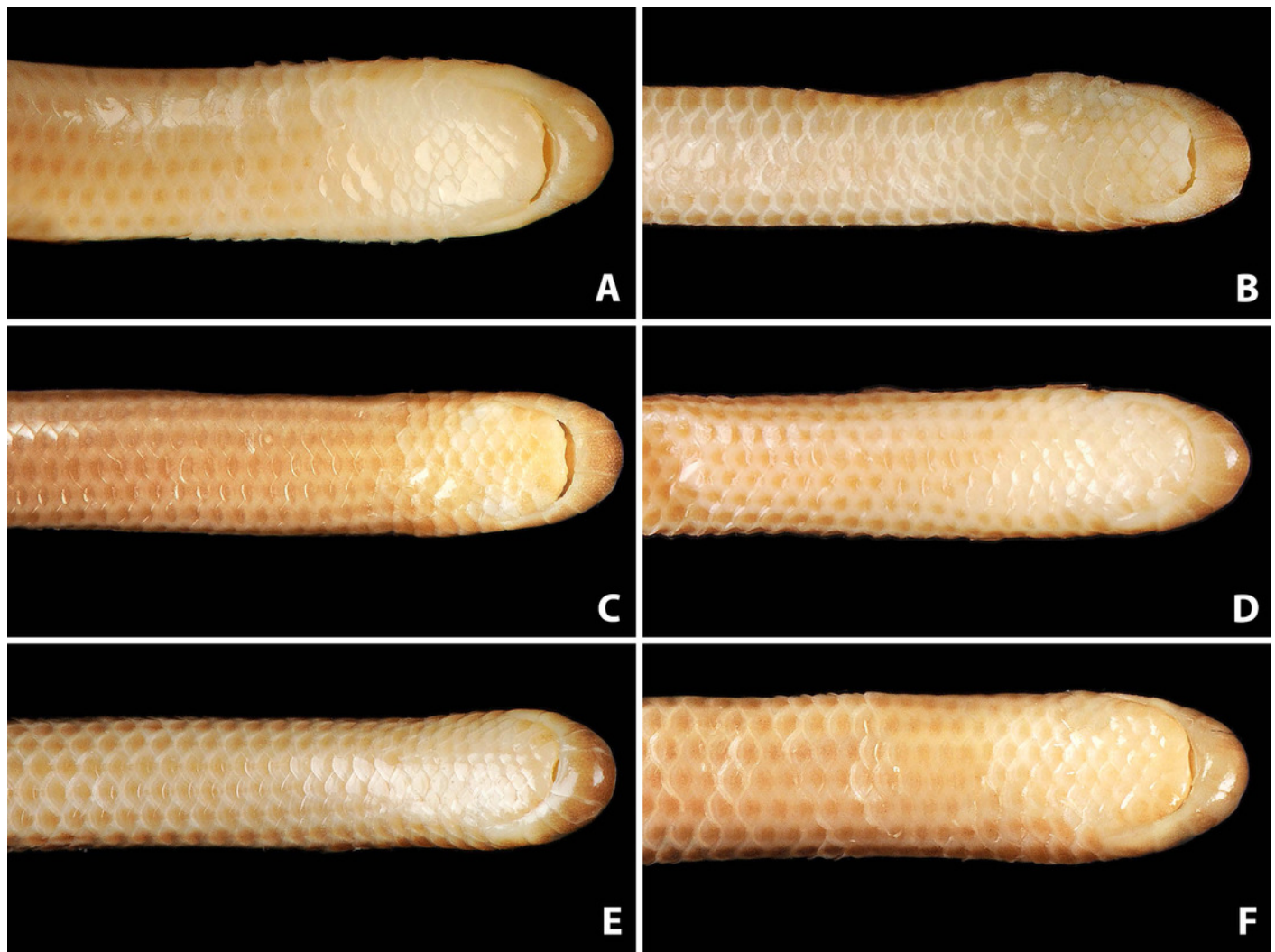
Figure 6

Comparison of dorsal body scales of holotype (NMW 15446:6, upper left picture) and paratypes of *Epictia rioignis* sp. nov

(A) Holotype (NMW 15446:6). (B) Paratype (NMW 15446:1). (C) Paratype (NMW 15446:2). (D) Paratype (NMW 15446:3). (E) Paratype (NMW 15446:4). (F) Paratype (NMW 15446:5). (G) Paratype (NMW 15446:7). (H) Paratype (NMW 15446:8).
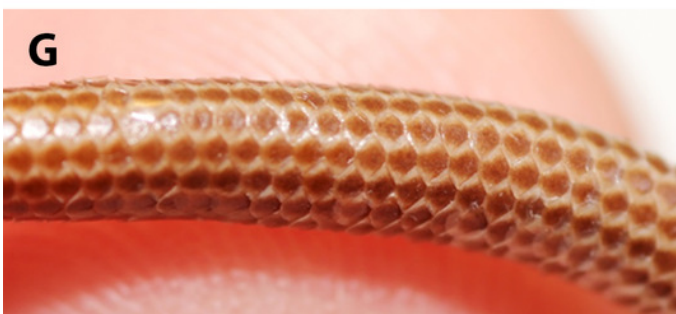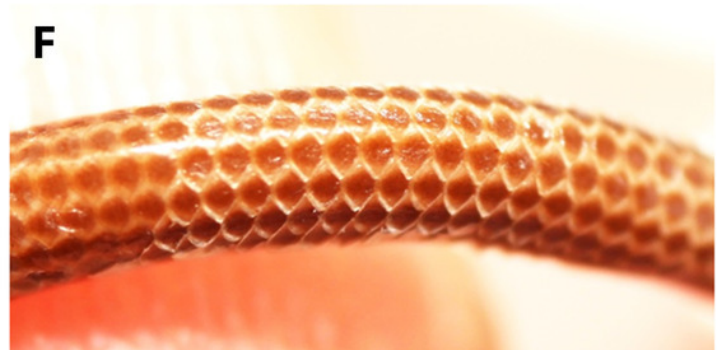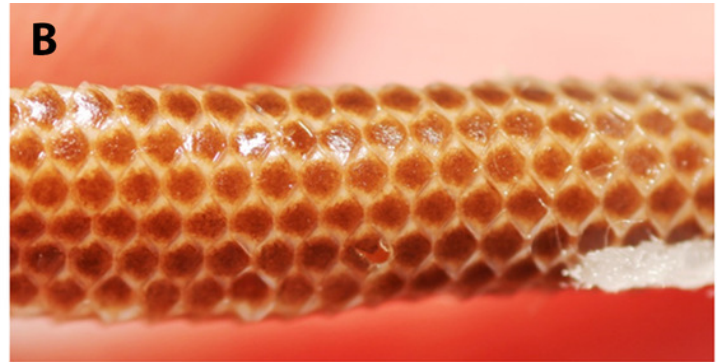
Figure 7

Comparison of ventral body scales of holotype (NMW 15446:6, upper left picture) and paratypes of *Epictia rioignis* sp. nov.

(A) Holotype (NMW 15446:6). (B) Paratype (NMW 15446:1). (C) Paratype (NMW 15446:2). (D) Paratype (NMW 15446:3). (E) Paratype (NMW 15446:4). (F) Paratype (NMW 15446:5). (G) Paratype (NMW 15446:7). (H) Paratype (NMW 15446:8). Photo credits: Alice Schumacher & Josef Muhsil.
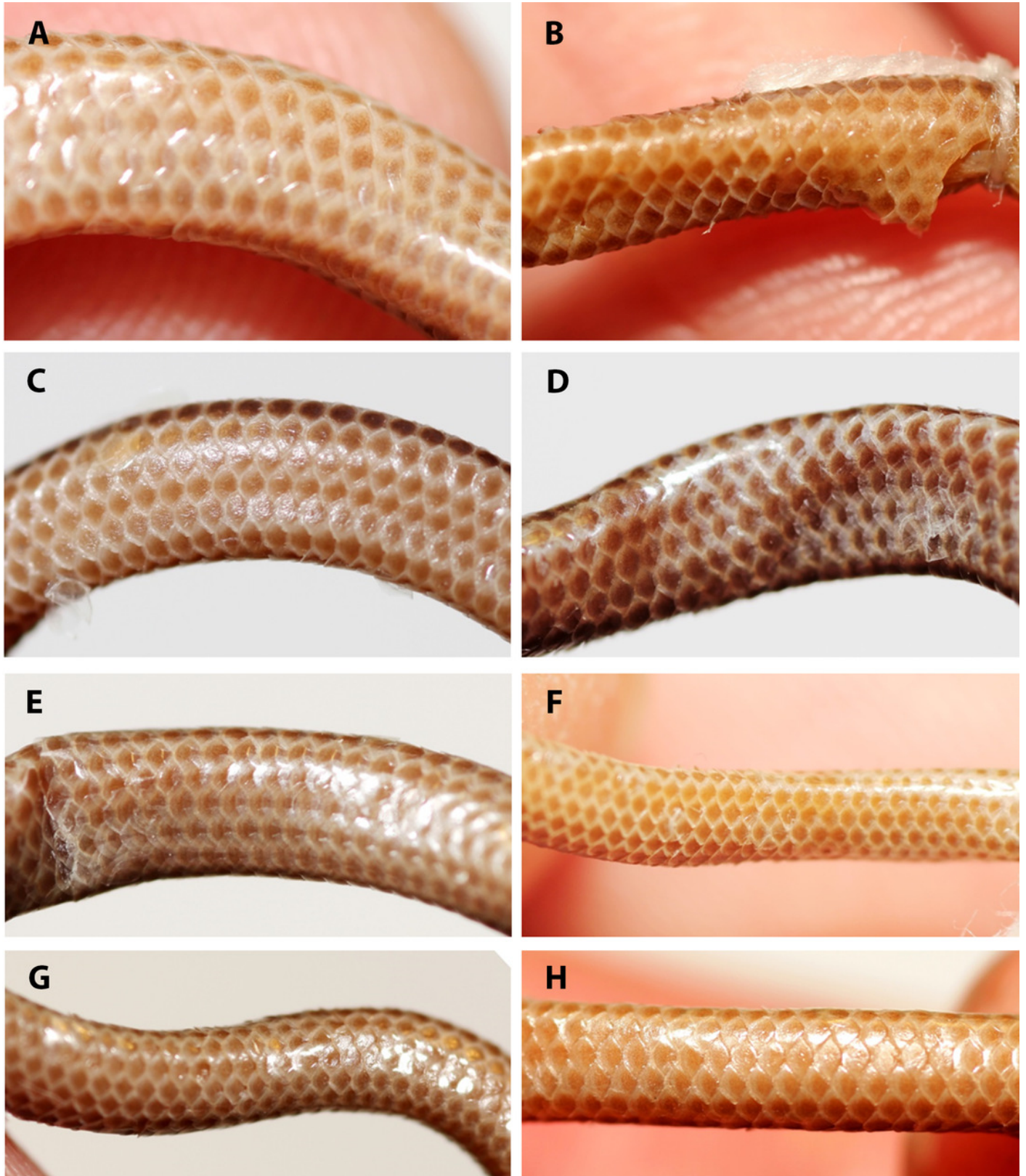
Figure 8

Comparison of dorsal view of tails of holotype (NMW 15446:6, upper left picture) and paratypes of *Epictia rioignis* sp. nov.

(A) Holotype (NMW 15446:6). (B) Paratype (NMW 15446:1). (C) Paratype (NMW 15446:2). (D) Paratype (NMW 15446:3). (E) Paratype (NMW 15446:4). (F) Paratype (NMW 15446:5). (G) Paratype (NMW 15446:7). (H) Paratype (NMW 15446:8). Photo credits: Alice Schumacher & Josef Muhsil.
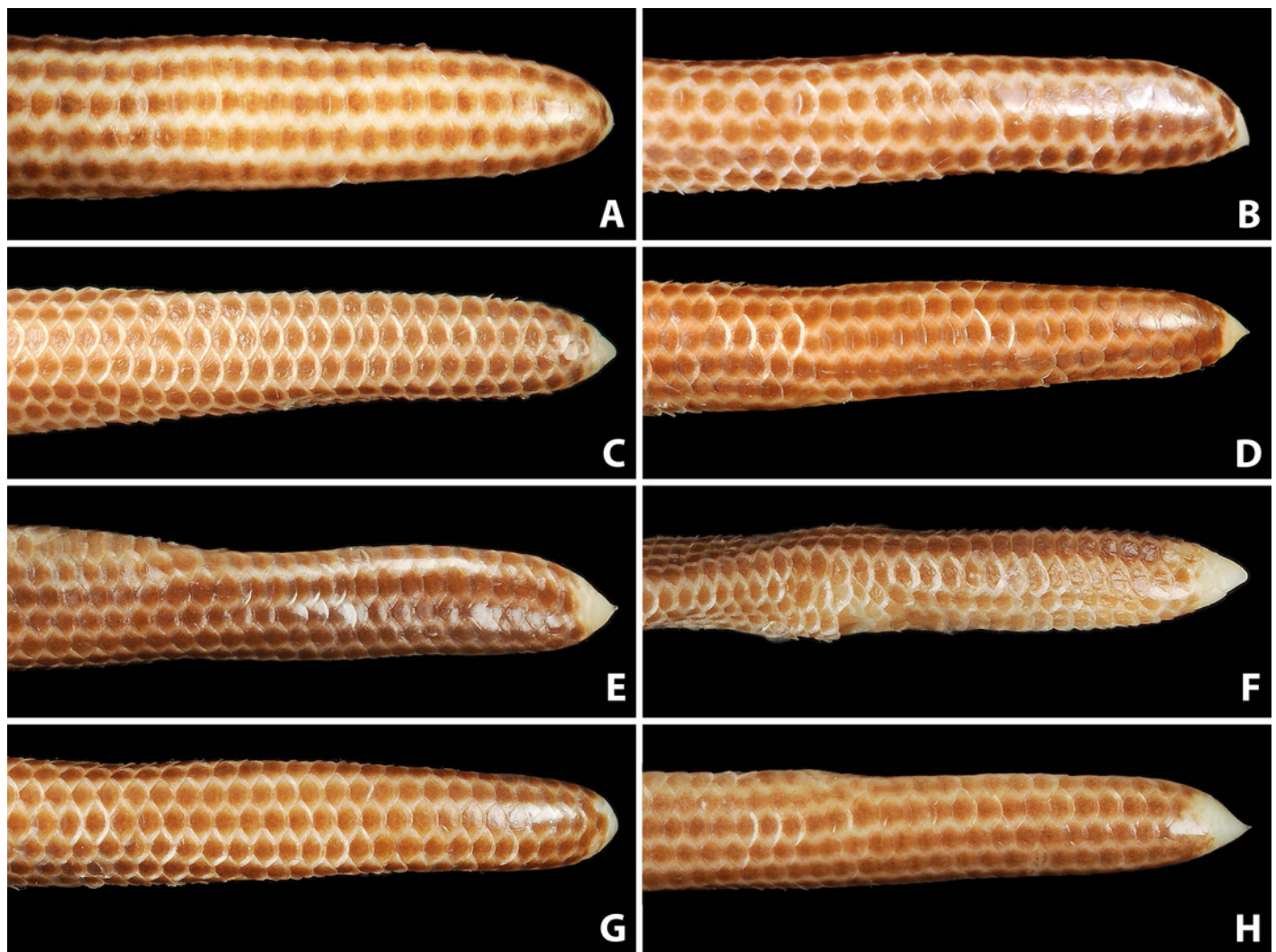
Figure 9

Comparison of ventral view of tails of holotype (NMW 15446:6, upper left picture) and paratypes of *Epictia rioignis* sp. nov.

(A) Holotype (NMW 15446:6). (B) Paratype (NMW 15446:1). (C) Paratype (NMW 15446:2). (D) Paratype (NMW 15446:3). (E) Paratype (NMW 15446:4). (F) Paratype (NMW 15446:5). (G) Paratype (NMW 15446:7). (H) Paratype (NMW 15446:8).
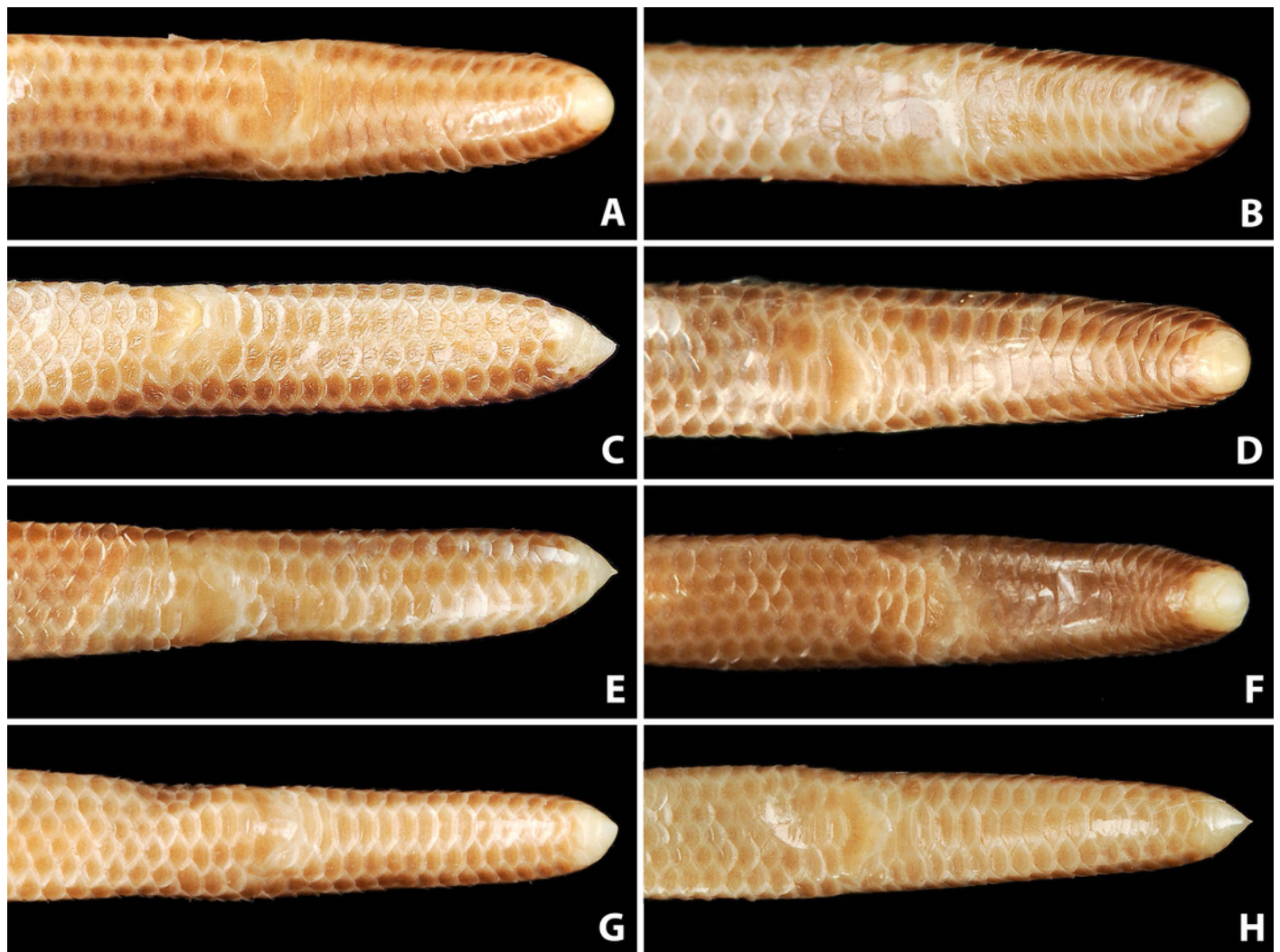
Figure 10

Three-dimensional reconstruction of the skull of *Epictia rioignis* sp. nov. based on Micro-CT data of the holotype (NMW 15446:6).

(A) Dorsal, (B) lateral, (C) ventral, (D) anterior, and (E) posterior views. at, atlas; ax, axis; bo, basioccipital; fr, frontal; ma, maxilla; na, nasal; ot, otooccipital; pa, parietal; pal, palatine; pbs, parabasisphenoid; pf, prefrontal; pm, premaxilla; pr, prootic; pt, pterygoid; qd, quadrate; sm, septomaxilla; so, supraoccipital; vo, vomer.
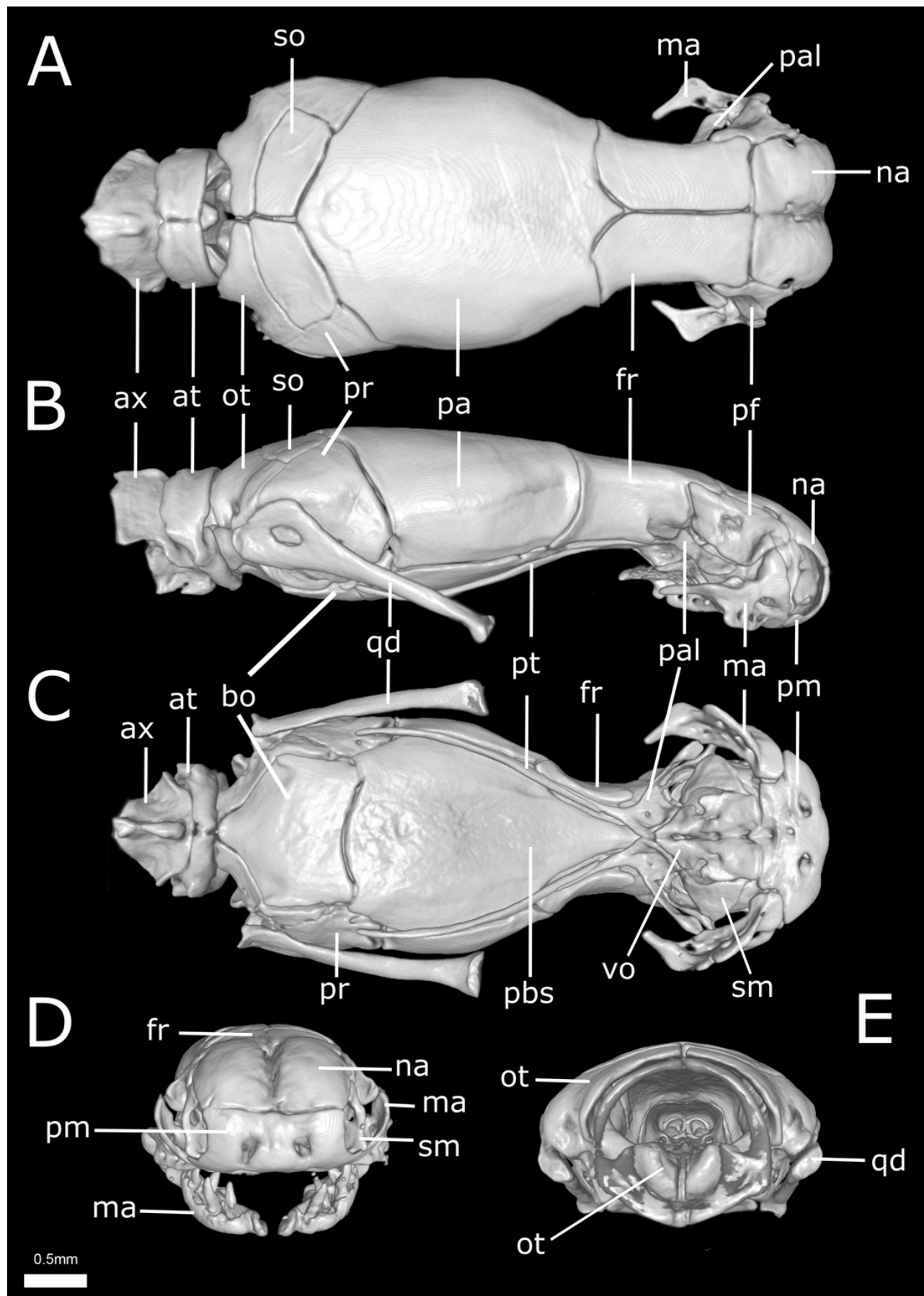
Figure 11

Three-dimensional cutaway views of the skull of *Epictia rioignis* sp. nov. based on Micro-CT data of the holotype (NMW 15446:6).

Cuts along the (A) frontal, (B) sagittal and (C–F) transverse axis. acn, acoustic nerve; avs, anterior vertical semicircular canal; bo, basioccipital; cv, *cavum vestibuli*; fs, frontal subolfactory process; fr, frontal; ico, internal carotid opening; ma, maxilla; na, nasal; ns, nasal septum; ot, otico-occipital; pa, parietal; pal, palatine; pbs, parabasisphenoid; pm, premaxilla; pt, pterygoid; s, stapes; sm, septomaxilla; vg, vagus nerve foramen; vnc, vomeronasal cupola; vo, vomer.
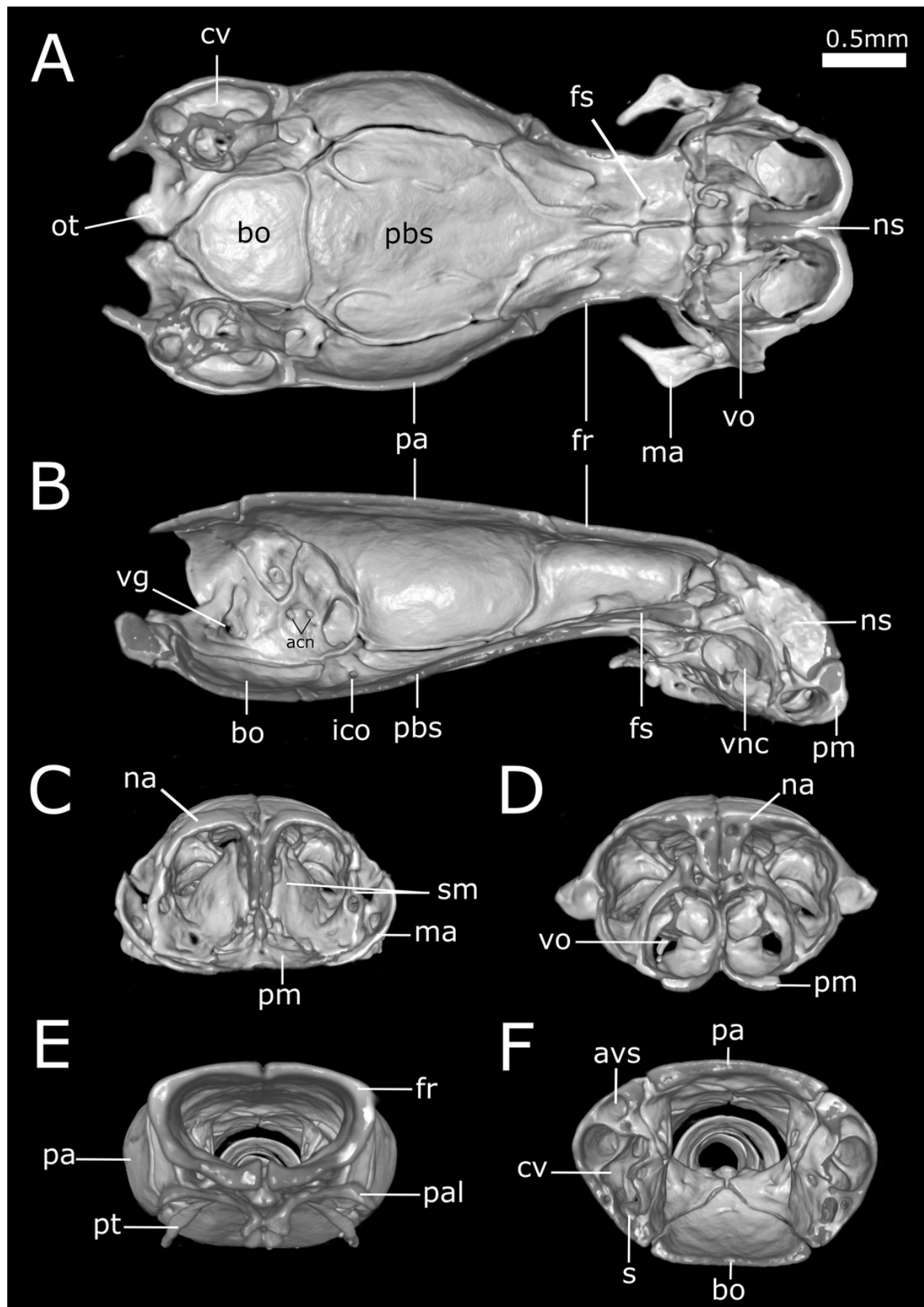
Figure 12

Three-dimensional reconstruction of the suspensorium (quadrate + lower jaw) of *Epictia rioignis* sp. nov. based on Micro-CT data of the holotype (NMW 15446:6).

(A) Dorsal, (B) lateral, (C) medial, and (D) ventral views. an, angular; asf, anterior surangular foramen; co, coronoid; dc, dental concha; de, dentary; dppd, dorsoposterior process of dentary; mf, mental foramen; par, prearticular lamina of compound bone; psf, posterior surangular foramen; qd, quadrate; qdf, quadrate foramen; rap, retroarticular process; scp, supracotylar process of surangular; sp, splenial; spd, symphyseal process of dentary; sur, surangular lamina of compound bone.
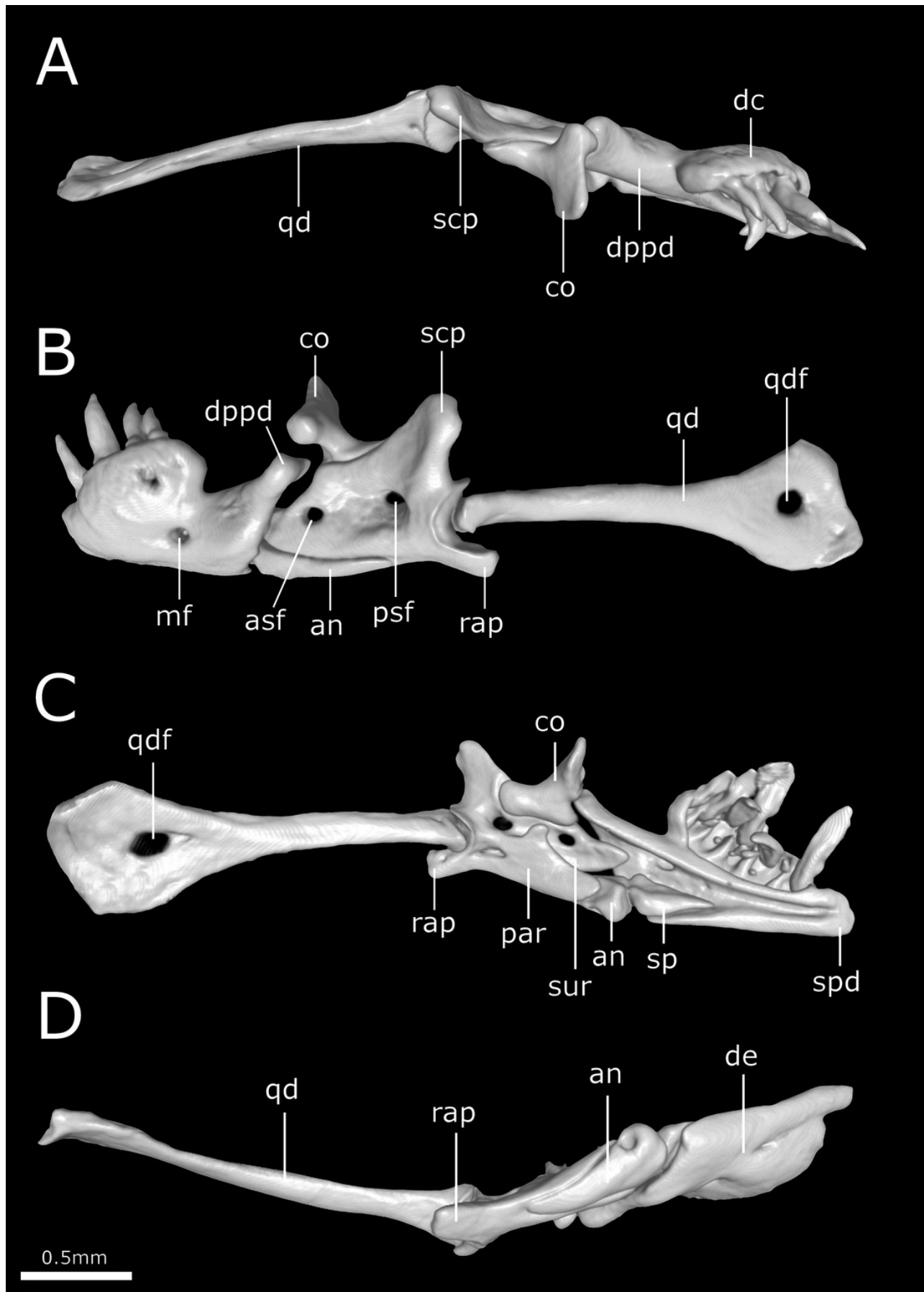
Figure 13

Three-dimensional reconstruction of the atlas (A-E), axis (F-J) and midtrunk (K-O) vertebrae of *Epictia rioignis* sp. nov. based on Micro-CT data of the holotype (NMW 15446:6).

Dorsal (A,F,K), anterior (B,G,L), lateral (C,H,M), posterior (D,I,N) and ventral (E,J,O).

0,25mm
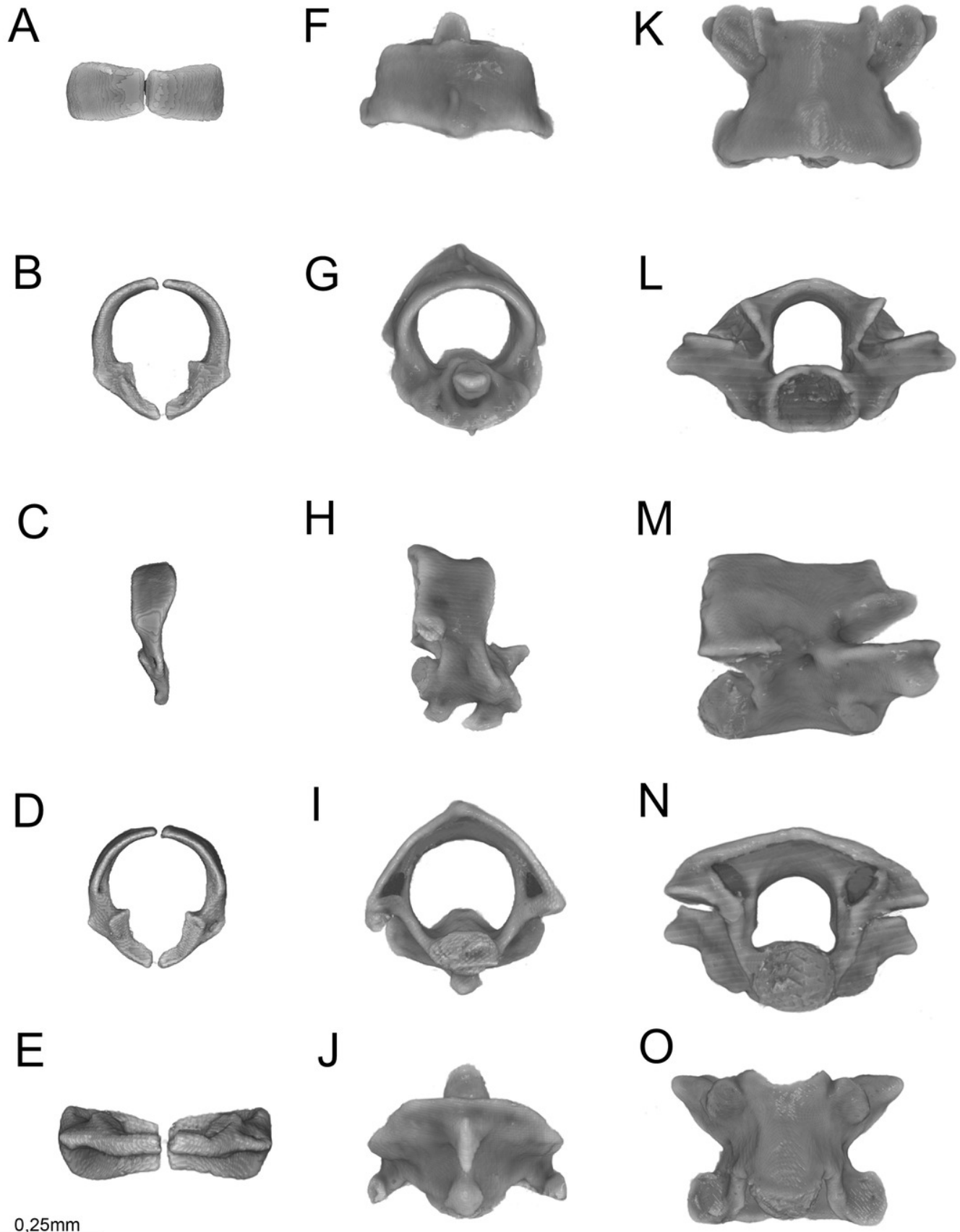
Figure 14

Three-dimensional reconstruction of the pelvic girdle of *Epictia rioignis* sp. nov. based on Micro-CT data of the holotype (NMW 15446:6).

(A) Overview with position and orientation. (B) Pelvic girdle digitally isolated in lateral view.
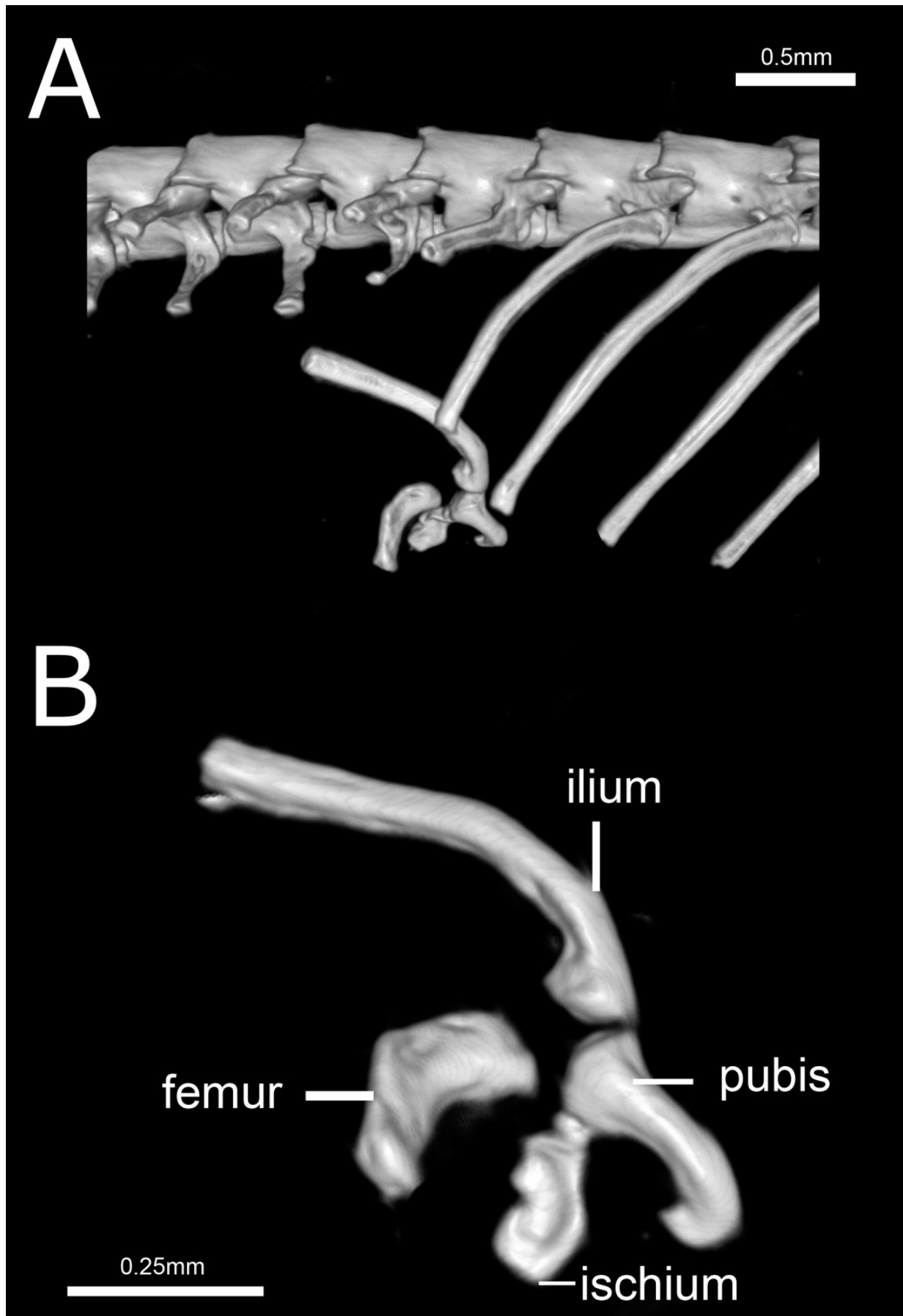
Figure 15

Three-dimensional reconstruction of skulls of different specimens of *Epictia rioignis* sp. nov. based on Micro-CT data, showing variations in skull parameters.

(A) Ventral views showing shape variation of basioccipital of holotype (NMW 15446:6) lacking medial recess and (B) paratype (NMW 15446:7) with medial recess. (C) Cutaway views along the frontal axis of paratype (NMW 15446:7) with presence of statolythic mass and (D) absence in the holotype (NMW 15446:6). (E) Anterior views of paratype (NMW 15446:4) with lateral recess of nasal and (F) paratype (NMW 15446:8) with medial sulcus of premaxilla.
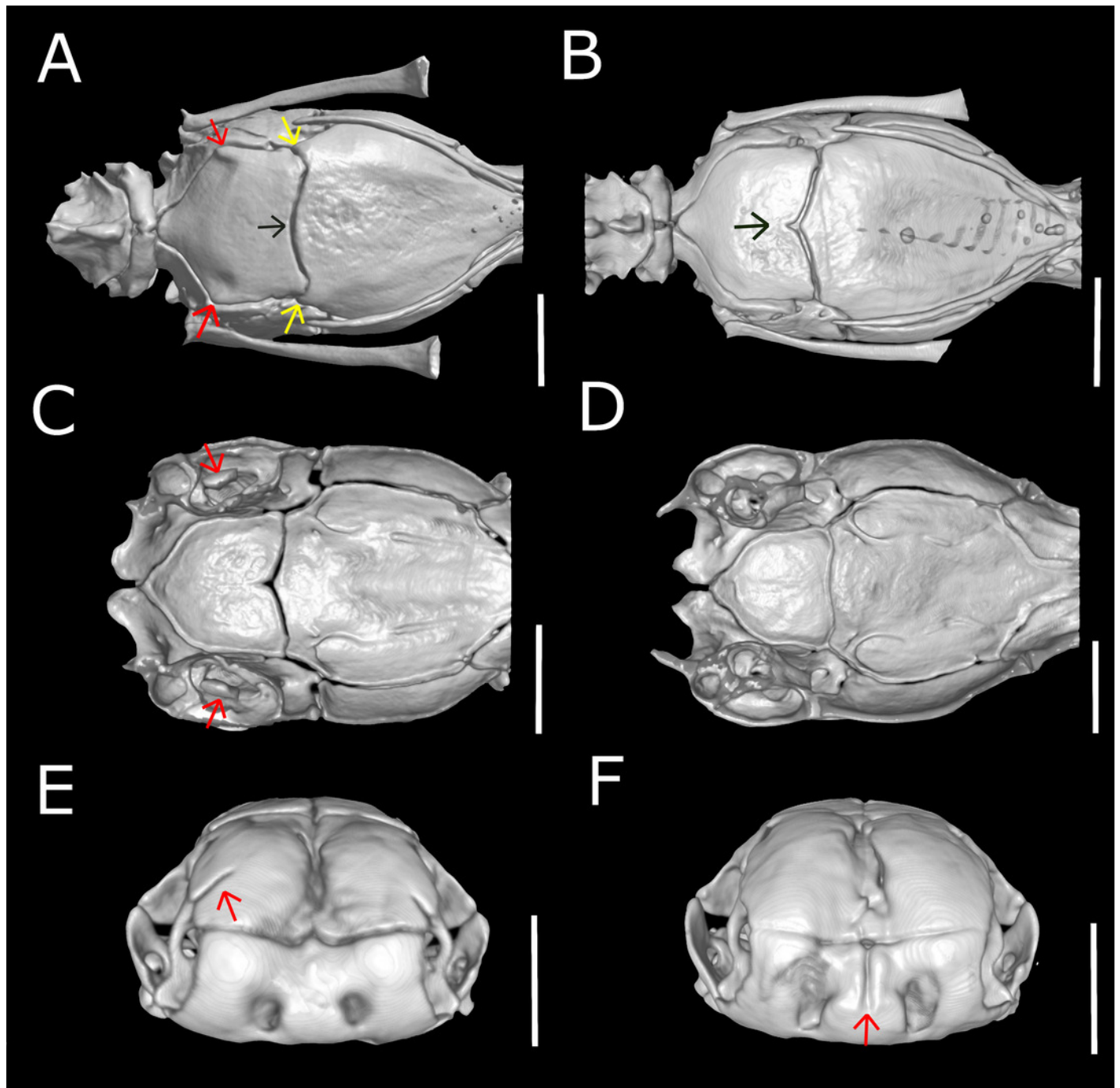
Figure 16

Handwritten labels of NMW 15446.

(A) By Steindachner and (B) by Eiselt. Photo credits: Alice Schumacher.