Off the scale: a new species of fish-scale gecko (Squamata: Gekkonidae: *Geckolepis*) with exceptionally large scales

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ABSTRACT

The gecko genus *Geckolepis*, endemic to Madagascar and the Comoro archipelago, is taxonomically challenging. One reason is their ability to autotomize a large portion of their scales when grasped or touched, most likely to escape predation. Based on an integrative taxonomic approach including external morphology, morphometrics, genetics, pholidosis, and osteology, we here describe the first new species from this genus in 75 years: *Geckolepis megalepis* **sp. nov.** from the limestone karst of Ankarana in northwestern Madagascar. The new species has the largest known body scales of any gecko (both relatively and absolutely), which come off with exceptional ease. We provide a detailed description of the skeleton of the genus *Geckolepis* based on micro-Computed Tomography (micro-CT) analysis of the new species, the holotype of *G. maculata*, the recently resurrected *G. humbloti*, and a specimen belonging to an operational taxonomic unit (OTU) recently suggested to represent *G. maculata*. *Geckolepis* is characterized by highly mineralized, imbricated scales, paired frontals, and unfused subolfactory processes of the frontals, among other features. We identify diagnostic characters in the osteology of these geckos that help define our new species and show that the OTU assigned to *G. maculata* is probably not conspecific with it, leaving the taxonomic identity of this species unclear. We discuss possible reasons for the extremely enlarged scales of *G. megalepis* in the context of an anti-predator defence mechanism, and the future of *Geckolepis* taxonomy.

INTRODUCTION

The genus *Geckolepis* Grandidier, 1867, endemic to Madagascar and the Comoros, contains a complex of species that have proven particularly difficult to delimit (Köhler et al. 2009). Known as fish-scale geckos, they have unusually large, imbricate scales and are known for their ability to shed a large portion of their integument with extreme ease as a defence mechanism (Gardner & Jasper 2015; Glaw & Vences 2007; Schmidt 1911; Schubert & Christophers 1985; Schubert et al. 1990; Voeltzkow 1893). Indeed, the process of collection often damages even the most intact specimens; Voeltzkow (1893) captured his specimens with bundles of cotton ('Wattebäuschen'), and even this was not sufficient to prevent some scale loss. This, and the irregularity of their scalation (Schmidt 1911), makes meristics difficult to apply to them. These factors, combined

54 with the secretive nature and cryptic colouration of this genus, have largely hindered progress on

55 resolving its species taxonomy (Köhler et al. 2009; Lemme et al. 2013).

56   In their revision of this genus, Köhler et al. (2009) recognised three valid nominal species—

57 *Geckolepis maculata* Peters, 1880, *G. polylepis* Boettger, 1893, and *G. typica* Grandidier,

58 1867—on the basis of pholidosis and morphometry. Four years later, Lemme et al. (2013)

59 published a four-gene molecular phylogeny of this genus spanning many localities in

60 Madagascar, and compared their trees with a morphological dataset. They designated 11

61 provisional Operational Taxonomic Units (OTUs), divided into three large clades, with a further

62 clade represented by just one gene constituting *G. polylepis*, falling sister to *G. typica*. While two

63 clades were easily assigned to nominal species (*G. typica* and *G. polylepis*), *G. maculata* was

64 difficult to place due to uncertainty surrounding its type locality (see the supplementary

65 information), but they tentatively assigned it to OTU AB. The other OTUs are apparently distinct

66 from any described species. Lemme et al. (2013) therefore estimated that *Geckolepis* might, once

67 fully resolved, contain around ten species.

68   Based on the DNA sequence data of Lemme et al. (2013), OTU D is the sister group of a

69 clade containing OTU AB from northern Madagascar, and OTU C which is widespread along

70 Madagascar's east coast. OTU AB occurs at sites north (e.g. Montagne d'Ambre) and south (e.g.

71 Manongarivo, Nosy Be) of the Ankarana Massif, the only site where OTU D has so far been

72 found. The genetic differentiation of OTU D is strong, amounting to 6.2% uncorrected pairwise

73 sequence divergence in the mitochondrial 12S rRNA gene compared to OTU AB, and 7% to

74 OTU C. Furthermore, OTU D did not share haplotypes with OTUs AB and C in the nuclear gene

75 CMOS (Lemme et al. 2013).

76   Recently, *Geckolepis humbloti* Vaillant, 1887 was resurrected from synonymy with *G.*

77 *maculata*, based on morphology, pholidosis, osteology, molecular phylogenetics, and

78 biogeography (Hawlitschek et al. 2016). All specimens from the type locality of *G. humbloti*,

79 Grand Comoro, and the other Comoro islands, are distantly related to all lineages from

80 Madagascar except one in western Madagascar, which may belong to the ancestral population

81 that colonised the Comoros. Thus, four species of *Geckolepis* are currently recognized, and since

82 no specimens of *G. humbloti* were included in the molecular phylogeny of Lemme et al. (2013),

83 the number of undescribed OTUs in this genus remains undiminished.

84   Recent work has provided detailed descriptions of the external morphology of the holotypes

85   of the four currently recognised species of *Geckolepis* (Hawlitschek et al. 2016; Köhler et al.

86   2009), and has identified genetic lineages constituting probable new species (Lemme et al.

87   2013). Two important taxonomic tasks remain: to firmly assign a genetic lineage to *G. maculata*,

88   and to describe the outstanding cryptic lineages. The present study seeks to contribute to both of

89   these goals, and thereby to facilitate further work on this complex. We describe a

90   morphologically distinct form (OTU D from Lemme et al. (2013) as a new species, and provide a

91   detailed osteological description of the genus *Geckolepis* based on micro-Computed

92   Tomography (micro-CT) scans, with comparative reference to *G. maculata*, *G. humbloti*, the

93   new species, and a member of the OTU AB from Lemme et al. (2013) to lay a foundation for

94   osteological data as a part of the integrative systematics of this genus. We discuss the remarkably

95   large scale size of the new species in the context of an anti-predator defence mechanism and

96   earlier works on *Geckolepis* integument, and go on to highlight the next steps in the taxonomic

97   resolution of *Geckolepis*.

98

MATERIALS AND METHODS

100   Specimens were collected and euthanized before being fixed in 90% ethanol and transferred

101   to 70% ethanol for long-term storage. The following institutional acronyms are used: Université

102   d'Antananarivo Département de Biologie Animale (UADBA); Zoologische Staassammlung

103   München (ZSM); Museum für Naturkunde, Berlin (ZMB). Field number FGZC refers to the

104   zoological collections of Frank Glaw. This study involved no experiments on living animals.

105   Our description scheme follows the re-descriptions of Köhler et al. (2009) for direct

106   comparability with currently recognised taxa. They make use of the following characters, which

107   we directly replicate here (see Fig. 1): axilla to groin distance (Ax–Gr); number of canthal scales

108   (CS) in a straight line along the canthal ridge between post-nasals and orbit; horizontal eye

109   diameter (ED); eye-to-ear distance (EED), from posterior margin of the eye to anterior margin of

110   the ear; head height (HH), measured at the posterior margin of the eye; head length (HL),

111   measured from snout tip to a point level with the anterior margin of the ear opening; maximum

112   head width (HW); number and fraction of infralabial scales (IFL), counted to one decimal place,

113   anterior to the point level with the anterior margin of the eye; interorbital distance (IOD),

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Comment [6]: No Formalin fixation? Why not? This is standard practice.

114 measured on the dorsal surface of the head and corresponding to the narrowest point of the

115 underlying frontal bone; number of interorbital scales at level of mid-eye (IOS); number of

116 subdigital lamellae on free portion of the first toe (L1TF); total number of subdigital lamellae on

117 the first toe, including the divided one adjacent to the claw (L1TT); number of conspicuously

118 widened subdigital lamellae on the fourth toe (L4TE); total number of subdigital lamellae on the

119 fourth toe including divided one adjacent to claw (L4TT); number of scales around midbody

120 (MBS); horizontal length of a typical scale anterior to the eye in the loreal region (SAE); external

121 shank length (ShL); snout length (SnL), from the tip of the snout to the anterior margin of the

122 orbit; horizontal length of an average sized scale posterior to the eye in the temporal region

123 (SPE); number of supralabials to the level of mid-eye (SPL); snout–vent length (SVL); tail

124 length (TL); number of ventrals in one head length as defined above (VHL), counted at

125 midventer; number of ventral scales from postmentals to vent (VS), excluding the small scales

126 behind postmentals and those anterior to the vent. The 'size of a typical dorsal scale at midbody

127 (DBS)' was not measured because 'size' is ambiguous; instead, we measured the width and

128 length of a mid-dorsal scale. Additionally, the 'number of mid-dorsal scales (DHL), from snout

129 tip to a point level with the anterior margin of the ear opening' because this definition is

130 inconsistent with the values given by Köhler et al. (2009). Postmental state is given following

131 Lemme et al. (2013), but postnasal scale states are given following Köhler et al. (2009), because

132 they were not included in Lemme et al. (2013); see Fig. 1.

133   Measurements and meristics were performed by MDS using a digital calliper (0.01 mm

134 precision) to the nearest 0.1 mm. Scale counts and finer measurements were performed using an

135 Olympus® (Tokyo, Japan) SZX-ILLK200 stereomicroscope.

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

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

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

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

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

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

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

143 LSID for this publication is: [TO BE INSERTED UPON ACCEPTANCE]. The online version of

144 this work is archived and available from the following digital repositories: PeerJ, PubMed
145 Central and CLOCKSS.

146 The following specimens were micro-CT scanned for this study: *Geckolepis maculata* ZMB
147 9655; *Geckolepis megalepis* sp. nov. ZSM 2126/2007 (FGZC 1144) and ZSM 289/2004 (FGZC
148 554); *Geckolepis* sp. of OTU AB sensu Lemme et al. (2013) ZSM 1520/2008 (FGZC 1697).
149 Scans of *Geckolepis humbloti* produced for Hawlitschek et al. (2016) were re-analysed in this
150 study: ZSM 81/2006 (FGZC 836) and ZSM 80/2010 (FGZC 4029). Micro-CT scans were
151 produced using a phoenix|x nanotom® m cone-beam micro-CT scanner (GE Measurement &
152 Control, Wunstorf, Germany) employing a standard or diamond target and a 0.1 mm Cu filter.
153 Specimens were mounted and stabilised using polystyrene and small wooden braces, inside
154 polyethylene or polypropylene vessels containing a small amount of 75–80% EtOH to achieve
155 air saturation and prevent desiccation. Scans using the standard target were performed at 140 kV
156 and 80 µA; scans using the diamond target were performed at 100 kV and 100 µA. Full body
157 scans were performed for 12 or 20 minutes (1440 or 2440 projections) with specimens mounted
158 at an oblique angle. Skull scans were performed for 20 or 30 minutes with 2440 projections at a
159 timing of 500 or 750 ms with specimens mounted vertically. For scanning details of *G. humbloti*,
160 see Hawlitschek et al. (2016). Volume renders were produced in VG Studio Max 2.2 (Visual
161 Graphics GmbH, Heidelberg, Germany) and Avizo Lite 9.0.0 (FEI Visual Sciences Group,
162 Burlington MA, USA). Osteological description follows terminology of recent anatomical
163 descriptions by Daza et al. (2008), Russell & Bauer (2008), Evans (2008), and Daza & Bauer
164 (2015) and is based on volume renders produced in VG Studio Max 2.2 and Avizo Lite 9.0.0,
165 following recommendations of Scherz et al. (submitted). Skeletal figures were prepared from
166 volume renders produced in VG Studio Max 2.2 and Avizo Lite 9.0.0.

167 All field research and collecting of specimens were approved by the Malagasy Ministère de
168 l'Environnement, des Eaux et des Forêts (Direction des Eaux et Forêts, DEF) under the following
169 permits: 238-MINENVEF/SG/DGEF/DPB/SCBLF dated 14 November 2003; 298/06-
170 MINENV.EF/SG/DGEF/DPB/SCBLF/RECH dated 22 December 2006; 036/08
171 MEEFT/SG/DGEF/DSAP/SSE dated 30 January 2008; and 174/16/MEEF/SG/DGF/DSAP/SCB,
172 dated 25 July 2016. Export of specimens was approved by the DEF under permits: 094C-
173 EA03/MG04, dated 1 March 2004; 051N-EA03/MG07, dated 10 March 2007, and 270N-
174 EA09/MG16, dated 7 September 2016.

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Comment [7]: Standard = Tungsten? This may not be standard for every CT machine, so it is best to be specific.

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Comment [8]: Presumably tungsten-diamond

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RESULTS

Our analysis of three specimens of *Geckolepis* from the Ankarana Reserve assigned to OTU D by Lemme et al. (2013) confirmed that these individuals are distinct in pholidosis from any described species, having a lower number of larger scales than any other known populations of *Geckolepis*. Micro-CT scans of the skeletons of these individuals and several congeners reveal subtle differences in osteology between known species and lineages. For future reference we listed 24 variable skull traits (Appendix 2) among *Geckolepis* that provide a baseline for future comparative studies. Consequently, we here describe OTU D as a new species on the basis of morphometrics, pholidosis, skeletal morphology, and molecular phylogenetics, and compare its skeletal morphology in detail with those of individuals of *G. maculata*, *G. humbloti*, and OTU AB sensu Lemme et al. (2013).

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***Geckolepis megalepis* sp. nov.**

Geckolepis sp. OTU D — (Lemme et al. 2013)

(Figs 2–5, 7–9, Table 1, Appendix 1)

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Holotype. ZSM 2126/2007 (FGZC 1144), an adult of unknown sex, from the east side of Ankarana National Park (12.9564°S, 49.1172°E, ca. 150 m a.s.l.), Antsiranana Province, north Madagascar, collected on 3 March 2007 by P. Bora, H. Enting, F. Glaw, J. Köhler & A. Knoll.

Paratypes. ZSM 289/2004 (FGZC 554), probably a subadult, sex unknown, from between Mahamasina and the Petit Tsingy (exact coordinates not known, but ca. 12.9558°S, 49.1181°E, ca. 125 m a.s.l.), Ankarana National Park, Antsiranana Province, north Madagascar, collected 25 February 2004 by F. Glaw, M. Puente & R. Randrianiaina; ZSM 232/2016 (FGZC 5476), an adult of unknown sex, from the private forest of the Ankarana Lodge (12.9613°S, 49.1499°E, 134 m a.s.l.), Ankarana massif, Antsiranana Province, north Madagascar, collected 28 August 2016 by F. Glaw, K. Glaw, T. Glaw, Jaques, and N. A. Raharinoro; FGZC 1606 (UADBA uncatalogued), sex and age unknown, from Petit Tsingy (ca. 12.9558°S, 49.1181°E, ca. 125 m

204 a.s.l.), Ankarana National Park, Antsiranana Province, north Madagascar, collected 12 February

205 2008 by N. D'Cruze, M. Franzen, F. Glaw & J. Köhler.

206 *Diagnosis.* A species of the genus *Geckolepis* based on its overall morphology and large, fish-

207 like scales, as well as its phylogenetic position (Lemme et al. 2013). *Geckolepis megalepis*

208 differs from all of its congeners by the possession of the following suite of characters: innermost

209 pair of postmental scales in broad contact (condition A/B, Fig. 3), SVL ≤ 69.5 mm, infralabials

210 to anterior margin of eye 4.5–4.8, 17–18 scales rows around the midbody, 27–31 ventral scales

211 between the postmentals and the vent, and the absence of a dark lateral stripe, and typical

212 midbody dorsal scales measuring 7.3–8.3% of the SVL. Osteologically, *G. megalepis* is

213 characterised by a narrow infraorbital fenestra, a bulging nasal cavity, nasals with straight sides,

214 a well developed anterior extension of the subfrontal process, a notched premaxilla-vomer

215 fenestra, scapular ray of scapulocoracoid not surpassing the clavicle, and posteriorly curved

216 pubic tubercle of the pubis. Additionally, it is separated by an uncorrected pairwise genetic

217 distance in the mitochondrial ND4 gene of ≥10.1% from all other lineages of *Geckolepis* and has

218 a unique CMOS haplotype (Lemme et al. 2013).

219 *Geckolepis megalepis* may be distinguished from *G. maculata* (note: because of the

220 substantial uncertainty surrounding the identity of *G. maculata,* we here compare *G. megalepis*

221 only to the holotype of that species, ZMB 9655, until such a time as its true affinities can be

222 clarified; see Köhler et al. (2009) for a detailed morphological account of that specimen) by the

223 combination of fewer scale rows around midbody (17–18 vs. 25), fewer ventral scales (27–31 vs.

224 32), larger relative scale size (typical midbody dorsal scale 7.3–8.3% of SVL vs. 5.4%), and the

225 absence of a dark lateral head stripe (vs. presence); from *G. typica* by larger maximum size (SVL

226 up to 69.5 mm vs. <57 mm), fewer scale rows around midbody (17–18 vs. 28–32), fewer ventral

227 scales (27–31 vs. 42–49), postmental scale condition (A/B vs. D), and the absence of dark

228 longitudinal stripes on the dorsum (vs. presence); from *G. polylepis* by larger maximum size

229 (SVL up to 69.5 mm vs. < 52 mm), fewer scale rows at midbody (17–18 vs. 30–37), fewer

230 ventral scales (27–31vs. 37–55), and the absence of dark longitudinal stripes on the dorsum (vs.

231 presence); and from *G. humbloti* by fewer scale rows around midbody (17–18 vs. 22–30), more

232 infralabials to the anterior margin of the eye (4.5–4.8 vs. 3–4), and fewer ventral scales (27–31

233 vs. 33–41).

8

234   For comparison of the osteology of the new species with *Geckolepis maculata*, *G. humbloti*,
235   and a specimen of OTU AB, see the Osteology of *Geckolepis* section below.

236

237   *Description of the holotype.* (Fig. 3) A large specimen in a moderately good state of
238   preservation. Several scales missing from dorsum and the left knee, and a few older scars on the
239   venter; tail detached but preserved, presumably autotomized during or after capture.

240   SVL 68.4 mm; tail length 80.1 mm; axilla-groin distance 27.2 mm; shank length 5.8 mm;
241   head length 15.9 mm; head width 16.1 mm; head height 8.9 mm; snout length 7.7 mm; eye
242   diameter 4.3 mm; interorbital distance 8.7 mm; eye-ear distance 5.0 mm; rostral large, convex,
243   distinctly visible from above; large postrostrals (4 supranasals) separated by a thin oblong scale
244   anteriorly and two small scales posteriorly (type D); nostril bordered by rostral, first supralabial,
245   three postnasals, and one supranasal (=postrostral); postnasals approximately equal in size to
246   anterior loreals; postnasals and loreals separated by one row of small scales; scales on snout and
247   on loreal region almost all with triangular posterior margins, slightly convex, imbricate; seven
248   canthal scales in a line on the canthal ridge, including the postnasals, between nostril and anterior
249   margin of eye; scales at supraorbital region similar to and continuous with those on top of head;
250   scales increase by a factor of 1.68 from level of mideye to occipital region; ten scales along a
251   straight line dorsally between orbits; three rows of small scales adjacent to anterior margin of
252   eye, decreasing to two on the upper and two on the posterior margin of eye; pupil vertical; seven
253   supralabials to below centre of eye (eight total) on left side, eight to below centre of eye (nine
254   total) on right side, all of roughly equal size, the posterior-most two smaller than the rest; scales
255   in temporal region larger by factor 2.25 than those in loreal region; ear opening much smaller
256   than eye, horizontally oval; 4.5 infralabials to below level of anterior margin of eye, decreasing
257   in size posteriorly; mental scale large, triangular, with convex anterior border; postmentals
258   asymmetric: one large pair immediately posterior to mental scale with broad medial contact,
259   followed on the right side by two postmentals of decreasing size, and on the left by one broader
260   postmental with an irregular posteromedial border (condition A/B; Fig. 3); one row of small
261   scales separating postmentals from anterior chin scales; chin and ventral body scales rhomboid
262   with rounded triangular posterior margins, imbricate, gradually increasing to double size
263   posteriorly, arranged in roughly regular rows; 29 scales along the midventral line (count
264   somewhat inhibited by ventral scarring) between postmentals and vent, not including smaller

9

scales adjacent to postmentals and anterior to vent; dorsal scales cycloid, larger than lateral or ventral scales; 18 scales around midbody; anterior half of tail flat and rather wide (55% of body width), decreasing in width gradually, down to a thin tip; tail covered with scales similar to body scales, but gradually decreasing in size posteriorly, a series of transversely expanded median subcaudals present; 14 lamellae under first toe, extending from the sole of the foot to the claw, and 21 under fourth toe, 12 of which are noticeably expanded; claws exposed, non-retractile. A single midbody scale measures 5.0 mm wide by 5.8 mm long, and is therefore 7.8% of the SVL in length.

Colouration in preservative: Head dorsally homogenously greyish brown, laterally greyish-brown flecked with darker and lighter areas posterior to eye and below mouth; no obvious dark lateral stripe; dorsal scales greyish brown flecked with dark and pale spots; legs as dorsum; ventrally dirty white; tail greyish brown with four dark transverse markings that do not continue onto the whitish ventral surface; exposed dorsal skin brown, ventral skin whitish. No information exists regarding the life colouration of the specimen.

Variation. (Figs 2–3) The paratypes strongly resemble the holotype, but one (ZSM 289/2004) is much smaller and presumed subadult. Their measurements and meristics are provided as part of Table 1, and in full detail in Appendix 1. These specimens differ from the holotype in the following characters not provided in Appendix 1: scales increase by a factor of 2.12–2.13 from level of mid-eye to occipital region; eight or nine total supralabials on each side; postnasal configuration of ZSM 232/2016 type A, 289/2004 type D; postmentals large, three or four pairs present: one large pair immediately posterior to mental scale with broad medial contact, followed two or three pairs of decreasing size (condition A); mid-dorsal scales range rom 7.3% to 8.3% of SVL; tail of ZSM 289/2004 not especially broadened (regenerated) and greyish brown with three darker transverse markings that do not continue onto the whitish ventral surface; tail of ZSM 232/2016 broad at its base and narrows rapidly (at least partially regenerated); overall body colouration of ZSM 232/2016 is more grey than the other specimens, though this may be because it is considerably fresher. In ZSM 289/2004, one scale on the dorsal surface of the neck and one on left side of dorsal tail base are dark brown with a burned appearance. The animal in Fig. 2A has 4.8 infralabials to the anterior edge of the eye (see Fig. 1A), and we thus infer that this value

295 can range from 4.5 to 4.8. From Fig 2A–B, the colouration in life is assessed to be mostly grey
296 with dark spots on some scales, giving a mottled appearance.

297

298 *Phylogenetic relationships.* This species is closely related to a sister species pair formed by
299 OTUs C and AB (Lemme et al. 2013)*, which are widely distributed in eastern and northern
300 Madagascar. Their taxonomic status will need to be assessed in more detail in future work on
301 this genus.

302

303 *Habitat, natural history, and conservation status. Geckolepis megalepis* was observed active
304 at night both in the rainy and dry season, on trees (see Fig. 2A–B) and tsingy limestone rock.
305 When captured, these geckos showed a strong tendency to autotomize large parts of their scales,
306 leading to partly 'naked' geckos without any visible (bloody) lesions (Fig. 2C). In a subjective
307 comparison this tendency appeared to be even more developed than in other *Geckolepis* species.

308 The new species is only known from the dry deciduous forest among the limestone tsingy
309 karst of Ankarana Reserve and its immediate vicinity, an area of 182 km^2. Due to its likely
310 limited distribution (182 km^2), knowledge from only two threat-defined localities in the
311 Ankarana massif, and the potential for rapid decrease in quality of the forests of that reserve and
312 the area around it due to illicit deforestation, anthropogenic fire, sapphire mining and free-
313 ranging grazing of livestock (e.g. Hawkins et al. 1990) we propose that it be listed as Near
314 Threatened under the IUCN criteria.

315 Two other geckos endemic to Ankarana Reserve are assessed as Near Threatened
316 (*Lygodactylus expectatus* Pasteur & Blanc, 1967) and Endangered (*Phelsuma roesleri* Glaw,
317 Gehring, Köhler, Franzen & Vences, 2010). We defend the choice of Near Threatened instead of
318 Endangered for *G. megalepis* on the following grounds: although it satisfies IUCN criterion B1
319 sub-criterion a, it fails to qualify for Endangered under sub-criteria b or c, as we can only
320 identify potential threats; were these to be realised, then the species would immediately qualify
321 for Endangered, but until that point, it remains Near Threatened. The same cannot be said of *P.*
322 *roesleri*, as it lives on *Pandanus* plants, which are often harvested, making the risk to it greater,
323 while *G. megalepis* is more generalist in its habits. Our recent observation of several individuals

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324   in a short timespan suggests that the population of *Geckolepis megalepis* in Ankarana is at least

325   locally healthy.

326

327   *Etymology.* The specific epithet is derived from the two Greek stems μέγας (mégas) meaning

328   'very large' and λεπίς (lepís) meaning 'scale', and refers to the large size of the scales of this

329   species in comparison to its congeners and other geckos, which aids also in its diagnosis.

330

331   *Available names.* Three junior synonyms currently exist within the genus *Geckolepis* that

332   must be considered as possible earlier names for *G. megalepis*: *G. anomala* Mocquard, 1909, *G.*

333   *modesta* Methuen & Hewitt, 1913, and *G. petiti* Angel, 1942. Synonymy of *G. anomala, G.*

334   *modesta,* and *G. petiti* with *G. typica* was discussed at length by Köhler et al. (2009). While this

335   placement needs to be re-analysed in light of the genetic information produced by Lemme et al.

336   (2013), *Geckolepis megalepis* can be distinguished easily from the type series of *G. anomala*, *G.*

337   *modesta*, and *G. petiti* by its postmental scales (condition A/B vs. D in *G. anomala*, *G. modesta*,

338   and *G. petiti*), and fewer scale rows at midbody (17–18 vs. 32 in *G. anomala*, 22–25 in *G.*

339   *modesta*, and 28 in *G. petiti*).

340

341   *Remarks.* The specimen depicted in Fig. 2 of Lemme et al. (2013) as OTU D is misattributed

342   and does not belong to *Geckolepis megalepis*. Lemme et al. (2013) report 17–20 scale rows at

343   midbody for this species; the reason for this discrepancy could not be established here, but we

344   are confident in our counts. However, we also emphasise that their higher number would remain

345   diagnostic in all of the comparisons presented above. Köhler et al. (2009) probably did not

346   include any specimens of *Geckolepis megalepis* in their revision of the genus, as they did not

347   consider any individuals with fewer than 22 scale rows at midbody.

348

349   **Osteology of *Geckolepis***

350   *Osteological comparisons.* The scales of *Geckolepis* geckos are mineralized and resemble

351   osteoderms (Fig. 4; see also Schmidt 1911). Among gekkotans, only *Gekko gecko* and *Tarentola*

352   species (Bauer & Russell 1989; Daza & Bauer 2015; Schmidt 1911; Vickaryous et al. 2015) are

353   known to develop similarly mineralised integumentary coverings. The dense scales of

Edward Stanley 11/20/2016 2:50 PM
Comment [11]: Perhaps cite the paper by Paluh and Bauer (in review) that demonstrates that these scales are ossified and can be considered osteoderms.

354 *Geckolepis* differ from the osteoderms of *G. gecko* and *T. mauritanica* in that they are imbricate,

355 and not juxtaposed and adpressed against the skull bones. *Geckolepis* also differ from the

356 majority of extant gekkotans in having paired and unfused (both dorsally and ventrally) frontal

357 bones; we only found fused frontal bones in a large specimen of the OTU AB sensu Lemme et

358 al. (2013) from Montagne des Français ('AB specimen' henceforth), which is the most

359 osteologically distinct specimen from our sample.

360 *Geckolepis megalepis* and the AB specimen differ from other *Geckolepis* in having a narrow

361 infraorbital fenestra. In these two taxa, the nasal cavity also bulges slightly more than in smaller

362 *Geckolepis* specimens. There is some variation in the shape of the nasal bones, being rectangular

363 (with straight sides) in *G. megalepis* and the AB specimen. *Geckolepis humbloti* has nasal bones

364 with a sigmoid lateral edge instead of straight. The holotype of *G. maculata* has nasals with

365 straight lateral edges (Fig. 6). *Geckolepis megalepis* and the AB specimen have a more anterior

366 extension of the subfrontal process of the frontal in palatal view, fused in the AB specimen and

367 not fused in *G. megalepis*; all others have a large notched area that does not extend anteriorly.

368 Another distinct feature of *G. megalepis* was found in the shape of the premaxilla-vomer

369 fenestra, being notched instead of rounded as in other *Geckolepis*.

370 There are also some differences in the postcranium, the lateral processes of the first five

371 caudal vertebrae (pygial series) are curved laterally (vs. straight in *G. maculata* and *G.*

372 *humbloti*); the scapular ray of the scapulocoracoid does not surpass the clavicle (vs. surpassing

373 the clavicle in *G. maculata*); the secondary coracoid ray of the scapulocoracoid extends to the

374 level of the posterior margin of the clavicular fenestra (vs. surpassing the posterior margin of the

375 fenestra in *G. maculata*); and the pubic tubercle of the pubis is posteriorly curved (vs. more or

376 less vertical in *G. maculata* and *G. humbloti*).

377 *Skeletal description.* In the following section, we present a generalised skeletal description of

378 the genus *Geckolepis*. Data on *G. humbloti* is based on the scans produced for Hawlitschek et al.

379 (2016), re-analysed for this study. The postcranial skeleton of the AB specimen was not

380 assessed; our postcranial osteological description pertains only to *G. humbloti*, *G. maculata*, and

381 *G. megalepis*.

382 As we have mentioned above, one key feature of *Geckolepis* is the presence of a dense

383 covering of mineralized scales (Fig. 4). These mineralized scales, contrary to the osteoderms of

384 *Gekko gecko* and *Tarentola mauritanica* (Vickaryous et al. 2015), are imbricate and not

13

385 adpressed against the skull. Schmidt (1911) referred to these scales as osteoderm, but noted that

386 they are unique in lacking bone cells (that is to say, they are not osteoderm in the strict sense).

387 He found that these mineralizations, which he showed to be formed from calcified tissue fibres,

388 roughly trace the outline of the scales, but are mostly confined to their middles and do not extend

389 into the keratinous scale. Our micro-CT data indicates that mineralization of scales is more

390 extensive, at least in the examined species; scales shown in Fig. 4 are very similar in dimensions

391 to what they look like in life (e.g. compare Fig. 4A with ZSM 2126/2007 in Fig. 3). The reasons

392 for this discrepancy are not clear, and will require further study. However, we can confirm that

393 these mineralizations do not extend to the tip of the scales, as can be seen by the soft-looking

394 distal edges of the scales in Fig. 4. Schmidt (1911) also found that mineralization was lacking

395 from specific scales, including the labials and postmentals and scales proximal to these, small

396 scales of the head including those around the eye and ears, and fingers and toes; they also

397 decrease in frequency in the tail scales beyond the first third. This pattern is recapitulated by our

398 micro-CT scans.

399 The mineralized scales were digitally removed from all the CT scans to facilitate rendering of

400 the underlying bone surface and sculpturing. We also digitally removed the endolymphatic sacs.

401 Skull (Figs 4–6):

402 The skull of *Geckolepis* is the typical broad and depressed skull of geckos (Kluge 1967),

403 wedge shaped in lateral view. The left maxilla of the holotype of *G. maculata* (ZMB 9655) is

404 fractured, and the premaxillary and maxillary palatal shelves show some irregular holes. There is

405 no trace of fracture bones associated with these holes, so the cracks may have been caused by an

406 infection that healed during the animal's life. The remaining specimens examined are intact (*G.*

407 *megalepis*, *G. humbloti*, and the AB specimen). Fig. 5 provides anatomical labels for most

408 features based on the holotype of *G. megalepis*, whereas Fig. 6 provides comparative images of

409 one adult specimen each of the three other species included for comparative purposes. Rotational

410 videos of these scans are provided as supplementary videos SV1–5. The skeleton of *G.*

411 *megalepis* paratype ZSM 289/2004 is not figured, as the resolution of our micro-CT scan of it is

412 too low, and only some of its character states could be accurately determined (see Appendix 2);

413 these however largely agree with the holotype.

414 Cranium: Nares oriented anteriorly, bordered medially by premaxilla, ventrally by premaxilla

415 and maxilla, laterally by facial process of the maxilla, and dorsally by nasals. The orbits are

14

416   incomplete posteriorly, and they accommodate the majority of the circular eye (as defined by the

417   sclerotic ring). The orbits are oriented anterolaterally, possibly enabling some field of vision

418   overlap. They are formed by the maxilla and jugal ventrally, prefrontal anteriorly, frontal

419   dorsally, and postfrontal posterodorsally. A sclerotic ring is present, composed of 14 bones.

420   The premaxilla is fused, with isodont, sharply pointed teeth with 13 tooth loci, this being a

421   constant number among all *Geckolepis* specimens examined. The ascending nasal process is

422   short and forms a bony septum between the nares, tapering abruptly dorsally, where it briefly

423   overlaps the nasals. The palatal shelf contacts the vomer, defines an incisive foramen, and

424   contacts the maxillae laterally.

425   The maxilla possesses a large facial process and a relatively narrow palatal shelf, as well as a

426   long posterior process, an anterior process, and an anterior maxillary lappet on the lingual side of

427   the anterior process. The alveolar border bears deeply pleurodont, sharply pointed isodont teeth.

428   Tooth loci fluctuates between 35 and 40, 36 in *G. megalepis* and the AB specimen; *G. maculata*

429   presents the lowest tooth count, with 35 tooth loci. The maxilla is pierced by four to six

430   supralabial foramina. The posterior process is in contact with the jugal and ectopterygoid

431   posteromedially. The palatal shelf contacts the anterior lateral process of the palatine posteriorly.

432   The maxillary lappet contacts the vomer laterally and the premaxilla's posterior palatine shelf

433   ventrally, and does not extend to meet its contralateral. The anterior process contacts the

434   premaxilla. The facial process is broad and dorsolaterally convex, its dorsal margin sloped

435   downward from its posterior end to its anterior end, its posterior margin weakly (*G. maculata*,

436   one specimen of *G. humbloti*) or strongly curved (*G. megalepis*, the AB specimen, and one

437   specimen of *G. humbloti*) and in contact with the prefrontal; posterodorsally in contact with the

438   frontal, and dorsally in contact with the nasal.

439   The nasal is nearly rectangular (except by the curved anterior edge that forms the

440   posterodorsal margin of the nares), a small portion of the medial edge lies beneath the ascending

441   nasal process of the premaxilla, and the anterolateral margin borders a small gap with the facial

442   process of the maxilla; the lateral edge is straight in *G. maculata*, bulges slightly outward in *G.*

443   *megalepis* and the AB specimen, and is curved with a lateral flange overlapping the maxillary

444   facial process in *G. humbloti* (as seen in other geckos; Evans 2008); laterally in broad contact

445   with maxillary facial process, and posteriorly in contact with the frontal. Nasals are partially

446   fused in the AB specimen.

447   The prefrontal is strongly convex and has an extensive overlap with the facial process of the

448   maxilla, leaving the exposed surface roughly crescent-shaped in all species (slightly more

449   crescentic in *G. megalepis* and some individuals of *G. humbloti*). The posterior edge is weakly

450   bowed and curves posteromedially forming the orbito-nasal flange. Dorsally it is distantly

451   separated from the postorbitofrontal. The prefrontal and the maxilla bound the lacrimal foramen.

452   The frontal remains paired, and unfused to its contralateral—this state may however change

453   with age, as the AB specimen has at least partially fused frontals, although a partial suture is still

454   visible anteriorly and posteriorly (see Fig. 6A). It is in anterior contact with the nasal (straight or

455   slightly concave suture), lateral contact to the facial process of the maxilla (concave suture) and

456   the prefrontal (convex suture), posterolateral contact with the postorbitofrontal (which clasps the

457   frontoparietal suture), and an extensive frontoparietal suture that is weakly curved anteriorly. The

458   anterior end is overlapped by the nasal bones, and the visible portion is roughly half the width of

459   the posterior end, the narrowest point being at the interorbital point. The subolfactory processes

460   of the frontals contact each other but they remain separated, so there is also no ventral fusion.

461   This condition is extremely rare in gekkotans, known only in the fossil *Gobekko cretacicus*

462   (Daza et al. 2013). The *crista cranii* of the frontals are sutured to the medial side of the

463   posterodorsal process of the prefrontal, thereby forming the dorsal and anterior orbital ridge. The

464   frontal lacks significantly extended anteromedial and anterolateral processes.

465   The jugal is elongated and slender with tapered ends. It extends from the posterior process of

466   the maxilla anteriorly along its medial edge, in contact with the ectopterygoid ventromedially,

467   almost extending far enough forward to meet the palatine and participate in the lacrimal foramen.

468   The parietal is in broad medial contact with its contralateral, the suture is straight in *G.*

469   *maculata* and zigzags in *G. megalepis, G. humbloti*, and the AB specimen, although in the

470   lattermost there is also partial fusion, rendering the suture faint. The parietal also contacts the

471   postorbitofrontal anterolaterally, *crista alaris* of the prootic lateroventrally, and the squamosal

472   posterolaterally. The bone is broad, curved downwards forming some lateral protection for the

473   brain. It is subtrapezoidal in shape, its lateral and median margins subparallel, the anterior

474   margin angled posteriorly along the frontoparietal suture, the posterior margin angled anteriorly.

475   The posteroparietal process is long and thin in *G. maculata* and one specimen of *G. humbloti*,

476   and broad and short in *G. megalepis,* one specimen of *G. humbloti* and the AB specimen,

477   extending posterolaterally from the posterolateral corner of the parietal to contact with the
478   squamosal.

479   The postorbitofrontal is laminar: thin, short, and curved, extending just anterior and posterior
480   to frontoparietal suture and bracing it (Daza et al. 2008; Rieppel 1984), in contact with frontal
481   anteromedially and parietal posteromedially. It lacks a discrete free process for the attachment of
482   the postorbital ligament (Evans 2008), which might instead be anchored to the body of the bone.

483   The squamosal is short, slender, and curved, contacting the posterolateral process of the
484   parietal anteromedially, and the paroccipital process posteriorly. It is considerably reduced in *G.*
485   *maculata*.

486   The quadrate has a deep indentation in the conch. This bone meets the quadrate process of the
487   pterygoid ventrally and has suspension formed by ligaments of the squamosal and the
488   paroccipital processes; it is not in direct contact with any other bones. It has a thick central
489   column and a thin, posterolaterally directed conch that lacks an obvious squamosal notch
490   dorsally. Its cephalic condyle is dorsomedial and not strongly expanded. Its mandibular condyle
491   is concave. It possesses a large foramen in the ventral half of the conch.

492   The septomaxilla is very thin, U-shaped, in anterior contact with premaxilla, otherwise
493   suspended in the nasal capsule. Its medial arm contacts the contralateral, separated anteriorly by
494   a small foramen lying dorsal to the incisive foramen of the vomer. The lateral arm ascends
495   slightly, and is long and cuneate with a sculpted lateral surface.

496   The vomer is a thin, laminar bone. It is strongly fused to its contralateral, though a median
497   ridge allowing the individual bones to be distinguished despite strong ontogenetic fusion.
498   Anteromedially an incisive foramen is present between the vomer and the posterior palatal shelf
499   of the premaxilla, the shape of this foramen is variable among the species examined, being a v
500   shaped notch (*G. megalepis* and *G. maculata*) or oval shaped (*G. humbloti* and the AB
501   specimen). The anterolateral extension of vomer is in contact with the lingual maxillary lappet.
502   Posteriorly it bears two slender lateral processes, and the paired elements form a broad median
503   projection. The lateral process curves medially to join the vomerine process of the palatine. The
504   median spur is bordered on either side by the distal tips of the palatine vomerine processes, and
505   forms the anterior end of the interpterygoid vacuity. The vomer has also two foramina that might
506   correspond to openings of the lacrimal duct.

17

507   The palatine is squarish, with rounded lateral and medial edges. The vomerine flange and

508   maxillary process are slender and subequal in length, together forming the border of the choana.

509   The vomerine flange lies parallel to the posterior processes of vomer and rests on a notch on the

510   body of the vomer; the maxillary process contacts the maxilla's palatal shelf laterally. The

511   palatine forms the anteromedial border of the suborbital fenestra. The bone is without an obvious

512   pterygoid process but possesses a posteroventral shelf where the palatine process of the

513   pterygoid overlaps it. Lateral to this overlap, the bone borders a slit extending medially from the

514   suborbital fenestra between the palatine and pterygoid. The medial edge of the palatine forms the

515   lateral border of interpterygoid vacuity. The lateral face of the palatine is in contact with the

516   anterolingual end of the ectopterygoid. The pterygopalatine joint is oblique.

517   The pterygoid is roughly y-shaped, with a brief anteromedial articulation with the palatine and

518   anterodorsal articulation with the ectopterygoid, articulating with the epipterygoid at the *fossa*

519   *columellae*, and contacting the quadrate posterolaterally. The pterygoid has a palatine process

520   anteromedially and a sculpted anterior border that is straight lateral to the palatine process,

521   forming the posterior border of a slit extending medially from the suborbital fenestra—then

522   concave, forming the posterior border of the suborbital fenestra—then extending anteriorly again

523   to form the pterygoid flange in contact with ectopterygoid, practically excluding the

524   ectopterygoid from the posterior margin of the suborbital fenestra. Also forming the

525   posterolateral border of interpterygoid vacuity. The facet that contacts the basipterygoid process

526   is porous. In lateral view, the quadrate process curves laterally beyond this point and the *fossa*

527   *columellae* to below the quadrate.

528   The ectopterygoid is bent downward. It is anterolaterally in contact with the jugal, and

529   posteriorly in ventrolateral contact with the anterolateral pterygoid flange. The bone's downward

530   bend is due to the more dorsal position of palatine and maxilla relative to the pterygoid. Its

531   medial margin is sigmoid in *G. maculata* and *G. humbloti*, variable in *G. megalepis* (wavy in

532   ZSM 2126/2007 but sigmoid in ZSM 289/2004), and wavy in the AB specimen. The suborbital

533   fenestra is roughly teardrop shaped, pointed anteriorly and rounded posteriorly, formed by the

534   ectopterygoid laterally, pterygoid posteriorly, palatine anteromedially, and maxilla

535   anterolaterally. The suborbital fenestra is broad in *G. megalepis* and the AB specimen and

536   narrow and all the remaining specimens examined.

18

537 The epipterygoid is columnar, tilted posteriorly, and appears mildly medially bowed in *G.*
538 *megalepis*, vertical or even externally bowed in *G. humbloti*, and vertical in *G. maculata*. It
539 extends from the *fossa columellae* of the pterygoid toward, but into contact with, the *crista alaris*
540 of the prootic. The dorsal end is somewhat broader than the rest of the bone. The interpterygoid
541 vacuity is hourglass shaped, but broadens more rapidly posteriorly than anteriorly, and is
542 anteriorly bifurcated as a result of the medial spur of the vomer. The stapes has an oval footplate
543 that fits in the *fenestra ovalis*, and two posts extending laterally from footplate, one anterior, the
544 other posterior, converge to form the stapedial stem, leaving an open stapedial foramen. The
545 *fenestra ovalis* is posterior to the quadrate.

546 The basioccipital underlies most of the braincase, is slightly wider than long, and lacks a
547 distinct basal tubera. It is in contact with the parabasisphenoid anteriorly, otooccipitals laterally,
548 and forms the ventral component of *foramen magnum*. It is excluded from participation in the
549 lateral aperture of the *recessus scala tympani* by the otooccipital. It is posterolaterally bordered
550 by anteroventral extensions of the otooccipitals forming the sphenooccipital tubercle, which is
551 connected to a sharp *crista tuberalis*.

552 The parabasisphenoid is in contact with the prootic dorsally and basioccipital posteriorly. It
553 possesses a short, pointed parasphenoid rostrum, which is an extension of the squared anterior
554 ends of the *cristae trabeculae*. The basipterygoid processes diverge anterolaterally, broadening
555 distally, with flat, curved distal ends form a synovial joint with the corresponding fossa of the
556 posterior pterygoid (Payne et al. 2011). The vidian bridge extends to the base of the
557 basipterygoid process from the *crista prootica* of the prootic. Posteriorly, the *crista sellaris*
558 forms the anterior wall of the *sella turcica*. In has two pairs of anterior openings: carotid canals
559 opening anteromedially, and the anterior openings of the Vidian canal anterolaterally, parallel to
560 the basipterygoid processes.

561 The supraoccipital contacts the prootic anteriorly and otooccipitals ventrally, forming the
562 dorsal edge of the *foramen magnum*. The posterior semi-circular canal extends posteriorly to the
563 dorsal margin of the foramen magnum. A pair of dorsal tubercles is present anterodorsally on
564 either side of the midline in one specimen of *G. megalepis*, but these are not strongly raised in
565 any other specimens examined.

566 The prootic is thin and has a prominent, triangular *crista alaris*. It is in contract with the
567 descending parietal process dorsally, the parabasisphenoid anteroventrally, supraoccipital

568 posterodorsally, otooccipital posteroventrally, and almost in contact with the epipterygoid at the

569 end of the *crista alaris*. The posterolateral margin forms the anterior wall of the fenestra ovalis,

570 and the posteromedial surface forms the anterolateral wall of the brain case. The anterior semi-

571 circular canal runs through the base of the alary process and *crista alaris*. The horizontal

572 semicircular canal and the ampullar bulge are visible in the posterior edge of the prootic. A

573 projection from the crista alaris extends anteromedially down to the crista sellaris of the sphenoid

574 and contains the trigeminal foramen (Daza et al. 2013), flaring also anterolaterally to the level of

575 the epipterygoid from the base of the crista alaris.

576   The otooccipital is in contact with the prootic anteriorly, basioccipital ventromedially,

577 supraoccipital dorsally, and the squamosal on the anterior face of the distal end of the

578 paroccipital process. The horizontal and posterior semi-circular canals are visible as a bulge in

579 posterior view. The occipital recess is enclosed in its posteroventral face. Anterodistally it

580 projects ventrally to participate in the sphenooccipital tubercle with the basioccipital. The

581 paroccipital process is long and thin, but broad dorsoventrally.

582   The *foramen magnum* is suboval, formed by the supraoccipital dorsally, otooccipitals

583 lateroventrally, and basioccipital ventrally. The occipital condyles are double, formed by the

584 otooccipitals laterally and the basioccipitals medially.

585   Jaw (Fig. 5D–E):

586   The jaw curves medially anteriorly, and forms a weak symphysis with its counterpart. The

587 dentary is the longest bone, being tubular and enclosing the Meckelian canal, which becomes

588 broader posteriorly, as it approaches to the mandibular fossa. It bears isodont, pleurodont,

589 somewhat conical and some recurved teeth. Tooth loci varies considerably from 27 to 40, the

590 smallest number on the left ramus of the specimen AB, but it seems like this specimens has a

591 pathological condition since the number is higher on the other side, reaching the base of the

592 coronoid eminence. The interdental space is larger in the specimen AB, which also explains the

593 lowest number. Maximum tooth loci is roughly 34 in *G. maculata*, 37 in *G. megalepis*, and 40 in

594 *G. humbloti*; with some teeth clearly missing in all specimens). Five mental foramina are present

595 in the holotype, six in the paratype of *G. megalepis*. Posteriorly, the dentary contacts the

596 surangular portion of the compound bone by superior and ventral processes, the latter extending

597 considerably further than the former. The Meckelian canal is not outwardly pronounced, and

598 opens anteriorly below the symphysis.

20

599   The splenial is a thin, triangular, and flat bone that forms the medial wall of the Meckelian
600   canal, posterior to the tubular portion. It has two discrete foramina, the anterior inferior dental
601   foramen and the anterior mylohyoid foramen.

602   The coronoid has a strong and fin-like dorsal eminence with a broadened anterior edge, but its
603   precise shape varies within species. It inserts into the dentary at the level of the last or
604   penultimate tooth (except on one side of the jaw of the AB specimen, as mentioned above). The
605   posteromedial process reaches the middle of the surangular, anterior to the distinct mandibular
606   fossa. The triangular splenial is present on the lingual surface of the mandible, in contact with the
607   posteromedial surface of the dentary, the lingual anteroventral face of the coronoid, and the
608   lingual surface of the surangular.

609   The dorsal edge of the surangular portion of the compound bone is concave. The Meckelian
610   canal is closed, extending into the dentary from the adductor fossa. Surangular and posterior
611   surangular foramina are located in the labial side of the compound bone. An external foramen for
612   the *chorda tympani* is present at the base of the retroarticular process of the compound bone. The
613   length, width, and concavity of the retroarticular process is variable within species probably due
614   to scaling of the jaw muscles. The retroarticular process is strongly laterally notched, with a
615   medial ridge on its articular surface.

616   Axial Skeleton (Fig. 7): 26 presacral, two sacral, and a varying number of caudal vertebrae
617   are present (the total number cannot be ascertained due to autotomized or regenerated tails in all
618   scanned specimens). Of the presacrals, eight are cervical (defined as being anterior to first
619   vertebra possessing a rib reaching the sternum), sixteen or seventeen are thoracic (rib-bearing),
620   and one or two lack ossified ribs and are thus considered lumbars.

621   The atlas has an unfused neural arch, which is also not fused to the centrum, each side with a
622   short dorsolateral posterior projection not overlying the axis. The odontoid process of the axis
623   extends forward between the walls of atlas extends into the braincase, fitting in between the
624   occipital condyles. The anterior three cervical vertebrae (atlas, axis, and third cervical) lack ribs.
625   The following five bear ribs of increasing length, all of which are to some degree dorsoventrally
626   broadened.

627   The vertebrae are notochordal amphicoelous type (Romer 1956). The ribs of the first four
628   reach the sternum—the fourth via the xiphisternum—followed by seven vertebrae articulating

21

629 with long, posteriorly arching ribs distally associated with postxiphisternal inscriptional ribs,

630 followed by five or six vertebrae possessing shorter ribs gradually becoming more posteriorly

631 curved (see Fig. 7B); one or two lumbar vertebrae follow that are similar in shape to the posterior

632 thoracic vertebrae but lack ribs.

633 The sacral pleurapophysis of the first sacral vertebra juts slightly posteriorly, articulating

634 distally with the pelvic girdle. The posterodistal edge is fused to the anterior edge of the

635 pleurapophysis of the second sacral vertebra, forming the foramen sacrale. The second sacral

636 vertebra possesses a dorsoventrally thin posterior crista comprising almost half the distal breadth

637 of the pleurapophysis (with asymmetrically emarginated distal edges in *G. megalepis* specimens:

638 more emarginated on the left than the right in ZSM 2126/2007 and right than left in ZSM

639 289/2004);

640 The first five caudal vertebrae possess long thin lateral processes, initially extending beyond

641 the sacrals, gradually decreasing in breadth, jutting posterolaterally, straight in *G. maculata* and

642 *G. humbloti*, curved laterally in *G. megalepis*, becoming increasingly posterior-jutting. The first

643 three caudals lack hemal arches.

644 Pectoral Girdle (Fig. 8): The pectoral girdle is comprised of paired clavicles, epicoracoids,

645 and scapulocoracoids, and a non-paired interclavicle and presternum.

646 The presternum is kite-shaped, and varies in ossification levels from poorly to fully ossified.

647 It has a synchondrotic articulation with the first three sternal ribs along its posterolateral border,

648 but lacks distinct facets for these. Its anterolateral edges are thickened to form the coracosternal

649 groove. No frontanelles are present. The mesosternal extension of the xiphisternum is variably

650 long, but poorly ossified.

651 The sagittal interclavicle is posteriorly arrowhead-shaped, and extends less than one third into

652 the sternum. It is anteriorly elongated, tubular and tapering, extending between the clavicles but

653 not beyond them.

654 The suprascapular and epicoracoid regions are at least partly ossified, but never completely.

655 The scapulocoracoid is typical in being composed of a horizontal plate (coracoid portion) and a

656 vertical lateral ascending process (scapular portion). No clear suture of the scapula and coracoid

657 is visible in the micro-CT scans. The coracoid portion is broad, plate-like, with a bulbous process

658 at its posterolateral corner. The scapular portion is long, at least as long as the coracoid portion.

22

659   Three rays are present, all of which are directed anteromedially: The scapular ray is slender, and

660   passes dorsally anterior to the ascending lateral process of the clavicle in *G. maculata*, but does

661   not surpass the clavicle in *G. megalepis* or *G. humbloti*—it defines the dorsal edge of the

662   scapulocoracoid fenestra, which is ventrally completed by the primary coracoid ray. The

663   secondary coracoid ray extends to the level of the clavicular fenestra in *G. maculata*, and to the

664   level of the posterior margin of the clavicular fenestra in *G. megalepis* and *G. humbloti*. The rays

665   define four fenestrae: the secondary coracoid fenestra (medial scapulocoracoid+secondary

666   coracoid ray); the primary coracoid fenestra (secondary coracoid ray+primary coracoid ray); the

667   scapulocoracoid fenestra (primary coracoid ray+scapular ray; and the scapular fenestra (scapular

668   ray+distal scapulocoracoid). Anteriorly, all four fenestrae are closed by the cartilaginous

669   epicoracoids, which are not shown in our micro-CT scans (see Fig. 8). This formation is type 6

670   sensu Lécuru (1968). The supracoracoid foramen is small, lying closer to first coracoid fenestra

671   than to the glenoid fossa.

672   The clavicle curves posteriorly and dorsally. It articulates with the ossified acromion process

673   of the poorly ossified suprascapula. It is angled posterolaterally, with a broadly expanded but

674   dorsoventrally flat medial portion—containing a large, oblong clavicular fenestra—and slender

675   curving lateral portion. It articulates at the midline with its contralateral and the interclavicle, and

676   is dorsally exceeded by the epicoracoid cartilage and parts of the suprascapular rays.

677   Forelimbs (Fig. 8): The humerus is marginally longer than the radius and ulna. It is somewhat

678   sigmoidal in dorsal view, with expanded proximal and distal ends. The proximal end is slightly

679   less broad than the distal end. It possesses prominent humeral and deltopectoral crests (the latter

680   with a sharp break separating it from the rest of the proximal humerus dorsally), as well as a

681   moderately developed ectepicondylar crest and ectepicondyle. The bicipital fossa is deeply

682   concave. The ectepicondylar foramen is visible in posterior view. In summary, it is fairly typical

683   of gekkonids (Russell & Bauer 2008).

684   The radius is long and thin, slightly dorsoventrally flattened and weakly curved, with its distal

685   articulatory facet with a distinct processus styloideus; its distal end articulates with the radiale

686   posteriorly. The ulna is slender, dorsoventrally flattened, and straight, narrowing distally, but

687   flaring at its distal end, where it articulates with the ulnare laterally and pisciform ventrally. The

688   olecranon process is clearly distinct, and proximal to it, on the articular surface of the humerus,

23

689 lies the sesamoid patella ulnaris, which is rounded. The internal face of the olecranon process
690 forms a smooth signmoid notch.

691   The spatium interosseum is formed by the diverging radius and ulna proximally and the
692 ulnare, centrale, and radiale distally, rendering it roughly teardrop shaped.

693   Nine carpal elements are present: The ulnare and radiale are subequal in size. The centrale is
694 thin and long, and lies between these two elements. The pisiform is small and rounded, lies
695 below the ulnare, and is probably not a true carpal (Russell & Bauer 2008). A further five distal
696 carpals are identifiable, the first in contact with phalange I, second with phalange II, third with
697 phalanges II and III, fourth with phalanges III and IV, and fifth with phalange V. The phalangeal
698 formula is 3-3-4-5-3.

699   The second phalange of the first finger, second of the second finger, second and third of the
700 third finger, second through fourth of the fourth finger, and second of the fifth finger, are
701 dorsoventrally flattened and laterally broadened. The terminal phalanges of each toe are slender
702 and arcuate, ending in a laterally compressed, square tip with a distal claw-like projection,
703 underlying the claws proper. The toes are able to hyperextend significantly. These three
704 characters are presumably related to the adhesive pads of the fingers (Russell & Bauer 2008). No
705 ossified paraphalangeal elements are present in the micro-CT scans.

706   Pelvis (Fig. 9): The pelvis is composed of fused paired ilia, ischia, and pubes. The ischiopubic
707 fenestra formed by the ischia and pubes is cardioid in shape, anteriorly rounded at the medial
708 symphysis of the pubes in *G. maculata*, but more pointed in *G. megalepis* and *G. humbloti*—this
709 fenestra may be medially divided by a proischiadic cartilage, but only the posterior-most portion
710 of this element is shown in our micro-CT scans.

711   The pubis and ischia are broad and thin, concave in ventral view. The ilium is long,
712 dorsoventrally broadened but laterally thin, and curves posteriorly. In lateral view (Fig. 9B), the
713 iliac blade is reminiscent of the shoes of the Greek god Hermes—it rises posterodorsally, and is
714 in broad medial contact with the pleurapophysis of the first sacral, and brief medial contact with
715 the anterior portion of the pleurapophysis of the second sacral. Anterolaterally the ilium
716 participates in the dorsal portion of the acetabulum.

717   The epipubic cartilage anterior to the medial pubic symphysis is somewhat calcified.

24

718   The pubis curves from the anterior acetabulum ventrally and medially to the anterior

719   symphysis with its contralateral at the front of the pelvis. It has a strong, medioventrally jutting

720   pubic tubercle on the posterior portion of its lateral edge (see p. 138–145 in Russell & Bauer

721   (2008) for discussion of terminology), which descends more or less vertically in *G. maculata* and

722   *G. humbloti*, but is posteriorly curved in *G. megalepis*. Medial to this is the concavo-convex

723   pubic apron, the anterolateral edge of which runs anteromedially toward the medial symphysis

724   with the contralateral pubis. The relatively large obturator foramen lies posterior to the pelvic

725   tubercle, in line with the medial edge of the acetabulum.

726   Dorsolaterally, the ischium forms the posterior margin of the aceptabulum. Ventromedially, it

727   is roughly equal in breadth to the pubis, broadening toward the posteromedial symphysis with its

728   contralateral at the back of the girdle. It possesses an almost lateral–pointing ischiadic tuberosity,

729   rendering the posterolateral margin of the ischium deeply concave. The anterior margin of the

730   ischium is also concave, extending anteriorly to form a weak prong, associated with the

731   proischiadic cartilage. The medial ischial symphysis is not strongly fused, and the cartilaginous

732   hypoischium likely extends into it.

733   A pair of curved post-cloacal bones is present in one specimen (ZSM 2126/2007; Fig. 9), but

734   is absent from all other specimens. These may be sexually dimorphic and/or age dependent; see

735   Russell et al. (2016) for a review of their phylogenetic distribution and evolution.

736   Hindlimbs: The femur is slender and weakly sigmoidal, with broad terminal ends. The

737   epiphyseal internal trochanter is strong, and lies distal to the femoral condyle, from which it is

738   separated by a deep notch. Its shape differs slightly among species: in *G: megalepis*, it is distinct

739   and bulbous, in *G. maculata* it is ridge-like without a bulbous end, and in *G. humbloti* it is

740   variable, with one specimen (ZSM 81/2006) resembling *G. megalepis* and one (ZSM 80/2010)

741   resembling *G. maculata*. The ventral face of the proximal end of the femur has a moderately

742   deep intertrochanteric fossa. The lateral distal condyle is distinctly larger than the medial one.

743   The distal intercondylar groove is pronounced, and the popliteal fossa is not strongly deepened.

744   The fibula articulates via a sesamoid cyamella (=parafibula) with the lateral surface of the

745   posterior femoral condyle. Additional sesamoids include the lenticular tibial patella dorsal to the

746   distal end of the femur, a spherical post-axial ligament sesamoid (fabella), and the tibial lunula

747   between the tibia and femur.

25

748   The fibula is laterally flattened to a slender rod of bone, with a slightly broader distal than
749   proximal end. The tibia is broad and dorsoventrally compressed, and bows slightly outward. The
750   cnemial and ventral crests are not pronounced and may be absent. Together the tibia and fibula
751   articulate with the subtriangular astragalocalcaneum, which in turn articulates with the first
752   metatarsal and the fourth distal tarsal. Two distal tarsals are present (third and fourth; see Russell
753   & Bauer (2008) for discussion of terminology). The fifth metatarsal is L-shaped and bears
754   distinctly raised anterior and posterior plantar tubercles. The second metatarsal is longer than the
755   fourth, and the third is the longest. The pedal phalangeal formula is 3-3-4-5-4.
756

DISCUSSION

758   *Geckolepis megalepis* is the first *Geckolepis* species to be described in 75 years (and it has
759   been 123 years since the last currently recognised species was described). Although far northern
760   Madagascar is relatively well surveyed for reptiles, and numerous *Geckolepis* populations have
761   been recorded from this area, the new species was only found in the Ankarana massif.
762   Considering the increasing number of reptile species putatively endemic to this spectacular
763   limestone formation (Glaw et al. 2010; Glaw et al. 2012; Jono et al. 2015; Ruane et al. 2016), it
764   is likely that *G. megalepis* will also turn out to be microendemic to the region. In Ankarana, it
765   occurs in sympatry with another lineage of *Geckolepis* (OTU G in Lemme et al. 2013) which
766   also may be microendemic to this area, but to which it is only distantly related (uncorrected
767   pairwise distance 11.3% in 12S rRNA according to sequences published by Lemme et al. 2013).
768   The new species can be distinguished from these geckos by the lack of a dark stripe from eye to
769   ear opening (vs. presence), possession of 17–18 scale rows at midbody (vs. 25–28), and
770   possession of 27–31 ventral scale rows (vs. 33–43) (Lemme et al. 2013).

Extreme integumentary autotomy in *Geckolepis megalepis*

772   Many reptiles have evolved the ability to shed some part of their body in response to predator
773   attack. The most widespread form is caudal autotomy, the shedding of all or part of the tail,
774   which occurs in many lizards and amphisbaenians as well as some snakes and the tuataras
775   (Arnold 1984; Bateman & Fleming 2009). *Geckolepis* species are also able to shed their tails,
776   and indeed few specimens survive to adulthood with their original tails intact (see for instance
777   Fig. 2A–B). In addition, these geckos have evolved an even more extreme adaptation, i.e. the

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autotomy of virtually their entire integument when seized or even touched. Earlier studies have shown that the autotomized layers include epidermis, underlying connective tissue, and subcutaneous fat tissue, and that a layer between the integument and the underlying tissue represents a pre-formed splitting zone (Schubert & Christophers 1985). The shedding process is most likely achieved by contraction of the network of myofibroblasts in the pre-formed splitting zone, with vasoconstriction in the most superficial vasculature of the dermis to avoid bleeding (Schubert & Christophers 1985). This process is thus completely different from the normal skin shedding of squamate reptiles, which leads to a loss of keratinized epidermis only (Schubert & Christophers 1985). The scarless regeneration of the whole integument occurs within a few weeks, apparently starting from stem cells of the deeper layers of the connecting tissue and is considered as unique among vertebrates (Schubert et al. 1990).

The new species is remarkable in the possession of proportionally larger scales than any of its congeners (especially in the dorsal cervical region, see Figs 2 and 3). Midbody dorsal scales of *Geckolepis megalepis* are 7.3–8.3% of the SVL (by comparison, a typical midbody dorsal scale of the holotype of *G. maculata* is just 5.4% of its SVL). Indeed, *G. megalepis* may have the largest mid-body scales of any gecko in both relative and absolute terms, as its scales outstrip those of all known congeners, and only *Teratoscincus* may approach *Geckolepis* in scale size. Remarkably, the latter genus has similarly fragile skin (Bauer et al. 1993), which may have evolved for similar antipredatory function.

The exceptionally large scales of *G. megalepis* lead to questions about the possible advantage of larger scales for species with autotomizable integument. As is visible in Fig. 2C, the large, imbricate body scales of *Geckolepis megalepis* are attached to the integument only superficially by a narrow transparent zone which covers less than 20% of the scale's edge surface. Schmidt (1911) called this region the 'Anwachsfläche' (literally 'growth surface'), and noted that it is much smaller relative to the size of the scales of *Geckolepis* than in other lizards. With increasing scale diameter, the circumference of the scale and therefore its zone of connectivity increases linearly while the area of the scales increases exponentially (approximating the scales to a circular shape). This increases the surface area and therefore power of friction on scales exponentially while the 'tear zone' of the scales increases linearly, meaning that there is a smaller tear zone per unit area with greater scale size. Thus, less force, applied in a posterior or lateral direction, should be required to remove a larger scale than a smaller one. Additionally, as

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27

810 the scales are imbricate, leverage may play a role: an anteriorly directed pressure on the scales

811 may cause them to lift and detach, much as one might detach a sticky note from a pile. The

812 leverage of a longer scale is greater than a shorter one, and these may therefore lift more easily.

813 This is probably further enhanced by the steeper angle of larger scales to the body (Schmidt

814 1911). Together, these principles may explain why the scales of *G. megalepis* appear to come off

815 more easily than those of other *Geckolepis* species, but further studies are clearly necessary to

816 confirm or reject this hypothesis.

817 Although it is highly plausible to interpret their ability of scale autotomy as an anti-predator

818 defence mechanism, direct observations of predation events or attempts on *Geckolepis*

819 individuals are scarce and include only a scorpion (*Grosphus flavopiceus*), a bird (*Dicrurus*

820 *forficatus*) and a large nocturnal *Blaesodactylus* gecko (Gardner & Jasper 2014, 2015; Glaw et

821 al. 2002). In the lattermost case, the *Geckolepis* individual slipped from the mouth of the

822 *Blaesodactylus* ca. 30 seconds after being captured, and escaped denuded (Gardner & Jasper

823 2015), thereby providing the first direct evidence of successful escape by skin shedding. Further

824 studies on the role of dermolytic scale autotomy by *Geckolepis* are clearly needed, in order to

825 understand its functionality with a range of predators (its function against snakes, for instance,

826 has not yet been observed), and to understand the pressures driving the evolution of greater scale

827 size in this particular lineage of *Geckolepis*.

828 **The osteology of *Geckolepis* and the next steps in resolving their taxonomy**

829 Our osteological description of the genus *Geckolepis*, based on six specimens of four species,

830 reveals strong morphological conservatism in this genus. Few characters show potentially

831 diagnostic differences at the species level (see Appendix 2), and the degree of intra-specific

832 variation is apparently quite high. However, through the use of micro-CT, we were able to

833 include the holotype of *G. maculata* in our skeletal description. This will be an important step

834 toward the resolution of its identity, despite our continued failure to trace its type locality (see

835 supplementary information). Lemme et al. (2013) assigned their OTU AB to this species on the

836 basis of its overall similar morphology, but our analysis of their skulls suggests that they are

837 probably not conspecific. This means that the assignment of this name is still completely

838 unknown; it belongs either to another of the known clades, or to one not yet characterised. A

839 broader survey of the osteology of the genus will be required to resolve the identity of this

840 species, and will in turn yield the total resolution of this genus.

28

841   Despite the detailed osteological description, we admit that *Geckolepis* represents an
842   extremely difficult taxonomic group that is hard to characterise. The high variability in scale
843   number and enhanced ability to shed scales upon capture has misled taxonomists in the past into
844   believing they were dealing with distinct new species, which have subsequently been
845   synonymised (Angel 1942; Köhler et al. 2009). The trouble is further enhanced by multiple
846   genetic lineages occurring in sympatry (Lemme et al. 2013), and further still by apparent
847   osteological conservatism. However, we were able to show that this is not always the case, and
848   members of the AB clade of Lemme et al. (2013) for instance show strong osteological
849   differences that will facilitate its description. Nevertheless, the osteology did not provide as
850   many taxonomic characters as we had hoped. Admittedly our sample size is small, and therefore
851   practically no data yet exist on the degree of inter- and intraspecific osteological variation in
852   these geckos. Examination of many further specimens and other lineages will enhance our ability
853   to use osteology as a source of characters in their taxonomic resolution.

854   Thus, the next steps are now clear: (1) a survey of osteology in this genus in the context of
855   molecular phylogenetic relationships of OTUs, and (2) a survey of intraspecific and sexual
856   skeletal variability in at least one lineage, although this is generally minimal among gekkotans
857   (Daza et al. 2009). Based on this data and corresponding other datasets, we must establish with a
858   high degree of certainty which OTU from Lemme et al. (2013) really corresponds to *G. maculata*
859   (if any). Once this information is gathered, we may proceed with the resolution of the taxonomy
860   of the genus.

861   The framework of an integrative dataset composed of morphological, meristic, molecular
862   phylogenetic, and osteological data has considerable potential for dealing with species
863   complexes in squamates—even those as tortuous as *Geckolepis*. However, it is clear that the
864   robustness of conclusions strongly depends on the available sample size. In instances, such as
865   this one, where sample size is limited to a low number of specimens, any osteological,
866   morphological, or pholidotic feature identified as differing must first be highlighted as being
867   potentially diagnostic, until more data becomes available to verify the value of each of these
868   features. Nevertheless, the value of these data, especially when they are extracted from holotypes
869   and old specimens in a non-destructive way, cannot be overstated. Micro-CT is therefore likely
870   to have a pivotal role in resolving many difficult species complexes.

871

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