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Additions to the lizard diversity of the Horn of Africa: Two new species in the *Agama spinosa* group

Philipp Wagner[1,2,*], Adam Leaché[3], Tomáš Mazuch[4], Wolfgang Böhme[2]

Abstract. The Horn of Africa is a center of diversity for African agamid lizards. Among the nine species of *Agama* occurring in the Horn of Africa, *Agama spinosa* is the most widely distributed. The *A. spinosa* group (sensu stricto, morphologically defined by possessing six clusters of spinose scales around the ear) contains two species: *A. spinosa* occurs from Egypt to Ethiopia and Somalia where it is replaced by the morphologically distinct and therefore sensu lato *A. bottegi*. Both species are only represented in museum collections by a small number of specimens from Ethiopia and Somalia, presumably the result of constant civil war that has plagued the region for decades and impeded field surveys. In this study, we examine species limits in the *A. spinosa* group using molecular genetic data (503 characters; mitochondrial 16S rRNA) and morphological data (67 characters). Deep divisions among populations of *A. spinosa* are supported by phylogenetic analyses and by multivariate analyses of morphometric data. Two new species from northern Somalia that differ from *A. spinosa* and *A. bottegi* are described. Furthermore, *A. smithi*, currently recognized as a synonym of *A. agama*, is re-assessed and recognized as a species of uncertain taxonomic position (i.e., incertae sedis). The results of this study improve our understanding of the evolution of agamid lizard diversity in the Horn of Africa, a significant biodiversity hotspot in Africa.

Keywords: *Agama*, *Agama bottegi*, *Agama smithi*, *Agama spinosa*, Agamidae, Somalia.

Introduction

The East African peninsula, called the Horn of Africa, is the easternmost projection of the continent and encompasses the countries of Eritrea, Djibouti, Ethiopia and Somalia. The biodiversity of the Horn of Africa is driven by at least two main factors: (1) dramatic environmental differences ranging from arid and semi-arid lowland habitats to mountain rainforests resulting from uplifting through the formation of the Great Rift Valley, and (2) elevational gradients extending from sea level to 4500 m in Ethiopia. These factors are hypothesized to have driven high species diversity in lizards (Bauer et al., 2010; Wagner and Bauer, 2011), and many groups of birds (Fjeldså and Bowie, 2008). Agamid lizards are particularly diverse in the Horn of Africa, and most African genera, including the regional endemic genus *Xenagama* Boulenger, 1885 (Wagner et al., in press), are present in the area. Only *Stellagama* Baig et al., 2012, occurring in Egypt, is absent from the Horn of Africa.

Within the Agaminae, the genus *Agama* Daudin, 1802 contains the highest species diversity in the Horn of Africa with currently nine species: *A. bottegi* Boulenger, 1897; *A. doriae* Boulenger, 1885; *A. finchi* Böhme et al., 2005; *A. hartmanni* Peters, 1869; *A. lionotus* Boulenger, 1896; *A. lucyae* Wagner & Bauer, 2011; *A. persimilis* Parker, 1942; *A. rueppelli* Vaillant, 1882; and *A. spinosa* Gray in Griffith & Pidgeon, 1831 (*A. robecchii* Boulenger, 1891 is not recognized as *Agama*, own data). Conversely, *Pseudotrapelus* Fitzinger, 1843 and *Trapelus* Cuvier, 1816 are each only represented by a single species, while *Xenagama* with currently two and *Acanthocercus* with six species.

The *Agama spinosa* group (= *spinosa* group) contains the most widely distributed agamid lizards in the Horn of Africa. The *spinosa* group is morphologically defined by possessing six

1 - Department of Biology, Villanova University, 800 Lancaster Avenue, Villanova, PA 19085, USA
2 - Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, 53113 Bonn, Germany
3 - Department of Biology and Burke Museum of Natural History and Culture, University of Washington, Seattle, Washington, 98195-1800, USA
4 - Dříteč 65, 53305, Czech Republic
*Corresponding author;
e-mail: Philipp.wagner.zfmk@uni-bonn.de

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clusters of spinose scales around the ear. Only two species are currently recognized in the *spinosa* group, *A. spinosa* Gray, 1831 and *A. bottegi* Boulenger, 1897. *Agama spinosa* is the only agamid species known to occur throughout the Horn of Africa and is documented from Egypt, Sudan, Eritrea, Djibouti, Ethiopia and northern Somalia (Baha el Din, 2006). Since its description, *A spinosa* was often recognized as a subspecies of *Agama agama* (Linnaeus, 1758) (e.g., Parker, 1942; Wermuth, 1967; Hussein and Darwish, 2000), but is today generally considered to be a distinct species (Lanza, 1978; Baha el Din, 2006; Leaché et al., 2009). *Agama bottegi* is morphologically similar to *A. spinosa* and was recognized as a questionable species by e.g. Wermuth (1967). However, *A. bottegi* is currently recognized as valid and endemic to Somalia (Lanza, 1990; Wagner, 2010; Wagner and Bauer, 2011). Moreover, *A. smithi* Boulenger, 1896, also similar in morphology, was described from the same area, but recognized first as synonym of *A. spinosa* by Parker (1932) and later of *A. agama* by Largen and Spawls (2006).

In this study, we use molecular genetic data for the *spinosa* group to estimate phylogenetic relationships. Morphological data is also used to delimit species. Two new species from northern Somalia that differ from *A. spinosa* and *A. bottegi* are described, and the status of *A. smithi* is re-assessed.

Material and methods

Material

Thirty-seven adult male specimens were examined for the morphological analysis (see Appendix 1). Females, juveniles, and damaged specimens were identified to the species level and included for species descriptions and distribution data.

For each specimen, 67 characters were examined (table 1). Measurements were taken with a dial caliper to the nearest 0.01 mm, and, where necessary, under a stereomicroscope. All bilateral characters were recorded on the left side to avoid violations of non-independent data in the PCA (Manly, 1994; Burbrink, 2001). Morphological differences are interpreted in this study as a measure of genetic differentiation. Genetic differences are considered to be emergent in the phenotype, which is described by a comparison of morphological characters. Discrete mensural and meristic differences between groups of phenotypically uniform individuals are considered to be the result of the lack of gene flow. Therefore, morphological analyses are useful for resolving the taxonomic position of taxa when genetic data is not available.

Specimens from the following institutions were examined: The Natural History Museum (BMNH), London, England; California Academy of Sciences (CAS), San Francisco, USA; Museo Civico di Storia Naturale – Giacomo Doria (MCSN), Genova, Italy; Museum of Vertebrate Zoology (MVZ), Berkeley, USA; Museo di Storia

Table 1. Characters taken from each examined specimen.

Mensural Characters	
SVL	Snout-vent length, from tip of snout to cloaca
TL	Length of tail, from tip of tail to cloaca (only specimens with entire tails were used)
TW	Tail width, maximum tail width at the tail base
TH	Tail height, maximum tail height at the tail base
CRL	Neck crest length, from before the first to behind the last crest scale
HW	Head width, maximum head width at the angle of jaw
HL	Head length, from tip of snout to angle of jaw
HH	Head height, maximum head height at angle of jaw
SEL	Snout-eye length, from snout tip to anterior margin of eye
EEL	Eye-ear length, from posterior margin of the eye to anterior margin of ear
ER	Eye length diameter, maximum horizontal eye diameter
EAR	Ear length, maximum horizontal ear diameter
SAL	Snout-arm length, from snout to anterior insertion of forelimb
AGD	Axilla-groin distance
HML	Humerus length
RUL	Radius-ulna length
FL	Femur length
TFL	Tibia-fibula length
TOL	Length of 4^{th} toe, excluding the claw

Table 1. (Continued.)

Meristic Characters	
RPP	Number of rows of precloacal pores
PP	Total number of precloacal pores
SL	Number of supralabial scales
IL	Number of infralabial scales
CR	Number of scales on the canthus rostralis
NCR	Number of scales on the canthus between nasal scale and eye
SupraO	Number of supraocular scales
NCS	Number of neck crest scales
T	Temporal scales between eye and ear
SaA	Anterior dorsal scale rows, counted transversely behind forelimbs
SaH	Posterior dorsal scale rows, counted transversely just at anterior insertion of hind limbs
SaM	Dorsal scale rows at midbody, counted transversely at midpoint between fore and hind limbs
D	Dorsal scale numbers, counted longitudinally from shoulders to posterior margin of hind limbs
V	Ventral scale numbers, counted longitudinally from shoulders to cloaca
CAS1-2	Caudal scales, counted around the tail at at 10^{th} and 15^{th} scale row of the tail
Fi1-5	Subdigital lamellae of fingers 1-5
TOE1-5	Subdigital lamellae of toes 1-5
ET	Number of scale tufts around the ear
NT	Number of scale tufts on the neck
Qualitative characters	
DS	Dorsal body scales homogenous (scales of similar size and shape) or heterogeneous (small scales intermixed with larger scales)
DFS	Dorsal scales larger, smaller, same size than the flank scales
VDS	Vertebral scales keeled, feebly keeled or smooth
DMS	Dorsal scales keeled, feebly keeled or smooth
FS	Flank scales keeled, feebly keeled or smooth
VS	Ventral scales keeled, feebly keeled or smooth
GS	Gular scales keeled, feebly keeled or smooth
UTS	Upper tail scales keeled, feebly keeled or smooth
LTS	Lower tail scales keeled, feebly keeled or smooth
PO	Position of the parietal eye visible or not visible
NS1	Nasal scale on or below the canthus rostralis
NS2	Nasal scale smooth or keeled
NS3	Nasal scale round or pear shaped
NS4	Nasal scale flat or convex
SDL	Subdigital lamellae keeled or smooth
LT	Longest toe 3^{rd}, 4^{th} or both equal
PPR	Row of precloacal pores continuous or uncontinuous
TSU	Tympanum superficial or not
HS	Head scales smooth, rugose or keeled

Naturale "La Specola" (MZUF), Florence, Italy; Naturhistorisches Museum (NHMW), Wien, Austria; Zoologisches Forschungsmuseum A. Koenig (ZFMK), Bonn, Germany; Museum für Naturkunde (ZMB), Berlin, Germany. Other used abbreviations are: DJ = Djibouti; ER = Eritrea; ET = Ethiopia; EY = Egypt; SO = Somalia; SU = Sudan; x = average.

Name-bearing types of *A. bottegi* and *A. smithi* were examined. Moreover, data and descriptions presented by Parker (1942), and Largen and Spawls (2006, 2010) and the relevant original descriptions were consulted. Distributional data were based on specimens with precise locality data and identified at the species level. Additional data was obtained from Global Biodiversity Information Facility (GBIF).

Morphological analysis

Principal component analysis (PCA) and hierarchical cluster analysis were used to evaluate 56 morphological characters (see supplementary tables S1, S2) using the program PAST v.2.12 (Hammer et al., 2001). Characters which could not be collected from every specimen and those equal in all specimens were excluded from analysis. For morphological analysis, mensural, meristic, and qualitative characters were size corrected and $\log_{10}$-transformed and analyzed both separately and together. A hierarchical cluster analysis (paired group; Euclidian, 1000 bootstraps) was performed using the program PAST v.2.12 to calculate morphological grouping of species when no genetic sequences were available. Additionally, parsimony analysis (branch-and-bound

algorithm; Fitch optimization, 1000 bootstraps) of qualitative characters was performed using the program PAST v.2.12 to calculate the phylogenetic position of taxa. Results of these analyses are presented in the taxonomic part of the results.

Genetic analysis

A total of 14 specimens were included in the molecular phylogenetic analyses, including *A. bottegi*, *A. hartmanni*, *A. tassiliensis* and *A. spinosa* from several populations (Appendix 2). *Agama hartmanni* was used to root the tree. For those sequences not imported from GenBank, DNA was extracted from tissues following the QIAGEN DNeasy extraction kits (QIAGEN Inc.). The 16S rRNA gene was PCR amplified using primers in Leaché et al. (2009) for 30 cycles (95°C 30 s, 58°C 30 s, 72°C 50 s). PCR products were purified using ExoSap and cycle sequence products were cleaned using hydrated sephadex placed in a Millipore plate. Sequencing (both directions) was performed on an ABI 3730 automated DNA sequencer. Contiguous DNA sequences were aligned and edited using Sequencher v4.8, and multiple sequence alignments were generated using Muscle v3.6 (Edgar, 2004). An uncorrected genetic pairwise-distance matrix was calculated using PAUP* v. 4.0b10 (Swofford, 2003).

Phylogenetic relationships were estimated using maximum likelihood (ML) and Bayesian inference (BI). Maximum likelihood analyses were conducted using RAxML-VI-HPC v7.0.4 (Stamatakis, 2006). The RAxML analyses used the GTRGAMMA model of nucleotide substitution. Support values were estimated from 1000 non-parametric bootstrap replicates. The nucleotide substitution model for Bayesian phylogenetics was selected using JModelTest v0.1 ($GTR + I + \Gamma$; Posada, 2008). We conducted Bayesian phylogenetic analyses using parallel MrBayes v3.1.2 (Ronquist and Huelsenbeck, 2003). We ran the analysis for 1 million generations using 4 heated Markov chains (using default heating values). We assessed convergence by inspecting parameter burn-in trends using Tracer v1.5, and checking that all estimated sample sizes exceeded 200. Posterior probability values were obtained by summarizing the posterior distribution of trees (post burn-in) with a 50% majority-rule consensus tree.

Results

Genetic analysis

The 16S dataset includes 503 bp (aligned), with 83 parsimony-informative characters. ML and BI analyses supported similar topologies, and clades with posterior probability values > 0.95 had bootstrap values of 100% (fig. 1). The phylogeny places *Agama tassiliensis* from northwestern Africa as sister to *A. spinosa* and *A. bottegi* (fig. 1). Within this latter clade, a split between *A. bottegi* and *A. spinosa* is supported (bootstrap = 94%; posterior probability = 0.7; fig. 1). Within *A. spinosa*, specimens from Somalia are sister to specimens from Djibouti and Egypt which form sister clades. Most of the nodes are supported by bootstrap values higher than 94% and posterior probability values higher than 0.65.

Morphological analysis

The PCA analyses were conducted on datasets containing *A. spinosa* and *A. bottegi* (including type specimens if available), and included 56 characters for 37 specimens. Generally, the PCA analyses of mensural, meristic, and quantitative data shows a phenotypic partitioning of *A. bottegi* into two distinct clusters, and of *A. spinosa* in one large cluster resulting from the overlap of specimens from Egypt, Sudan and Ethiopia, but also with one distinct cluster containing specimens from Somalia. The morphometric data suggest that the cluster of *A. bottegi* that includes the holotype is the most distinctive among the group, and that the *A. bottegi* used in the phylogenetic analysis is not a member of that group (figs 2, 3).

In the first PCA (fig. 2A), the first two axes explain 50.54% of the variance in the dataset (PC1: 32.87%; PC2 17.68%). Comparing PC1 against PC2 shows a clear separation of all taxa and several populations of *A. spinosa*, with quantitative characters VDS, VS, LTS, NS2-4 (PC1) and VDS, ETS (PC2) loading most heavily (see table S1). The third and fourth axes explain 25.47% of the variance in the dataset (PC3: 16.54%; PC4: 8.93%). A comparison of PC3 against PC4 (fig. 2B) shows a separation between the two clusters of *A. bottegi* and *A. spinosa* from Somalia, but other populations of *A. spinosa* are overlapping. Here, component contributors are more or less uniformly distributed across mensural (PC3: TW, TH, HL, HH, CRL, SEL, EEL, EAR, FL; PC4: SVL, TW, CRL, SAL, RUL, TFL, TOL), meristic (PC3: SL, CR, NCR, FI3-5, TOE1-4, NT;

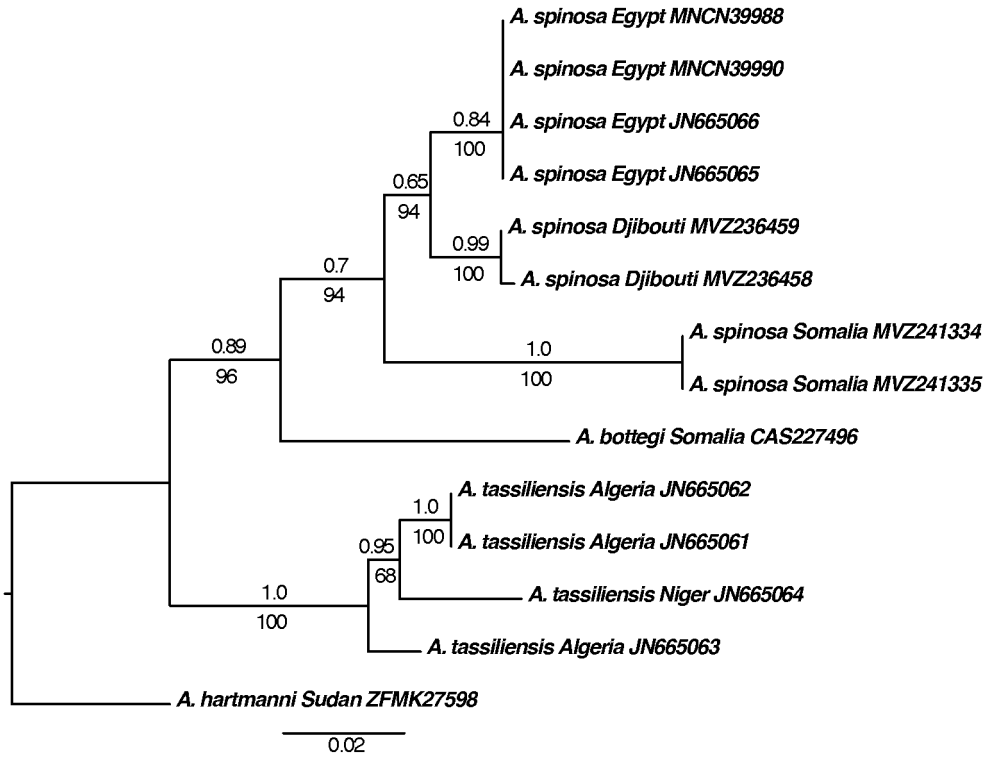

Figure 1. Phylogenetic relationships within the *Agama spinosa* group and its closest relatives based on maximum likelihood and Bayesian inference analyses of 16S mtDNA data using the GTR + I + Γ model of nucleotide substitution. *Agama hartmanni* was used to root the tree.

PC4: CR, SupraO, TOE3-4, NT) and qualitative (PC3: VDS, VC, LTS, ETS, NS2-4; PC4: VS, LTS, ETS, NS2-4) characters.

A second PCA was done using only mensural and meristic characters (table S2). Plotting PC1 against PC2 from a variance-covariance matrix PCA (supplementary fig. S1A) shows an overlap of all *A. spinosa* populations excluding specimens from Somalia, as well as two distinct clusters of *A. bottegi*. Generally, main contributors are scattered about the entire dataset, but highest loadings to PC1 and PC2 were meristic characters (PC1: PP, IL; PC2: SL, T, CAS2, FI1, FI5). Here, the first two axes explain 53.67% of the variance in the dataset (PC1: 29.34%; PC2 24.32%). The same data were analyzed with a correlation PCA (supplementary fig. S1B) and the first and the third axes explain 43.53% of the variance in the dataset (PC1: 33.89%; PC3: 9.65%). A comparison of PC1 against PC3 again shows an overlap within several populations of *A. spinosa* excluding the one from Somalia, and two distinct clusters of *A. bottegi*. Main loadings to PC1 were mensural characters (SVL, TW, HL, HW, HUL, FL, TFL); while in PC3 the main loadings were meristic (SL, SaH, D, CAS2, FI1).

Two main results emerge from comparing the morphology and genetic data: (1) *Agama bottegi* is strongly partitioned into two distinct morphological clusters; one of these clusters includes the holotype, whereas the other includes the specimen used in the phylogenetic analysis (CAS 227496). A comparison of these specimens reveals that CAS 227496 does not show several important morphological characters of *A. bottegi* (e.g., pear shaped nasal scale, keeled ventral scales), and we therefore recognize it herein as a new species; (2) *Agama spinosa* from Somalia are distinct from the remaining

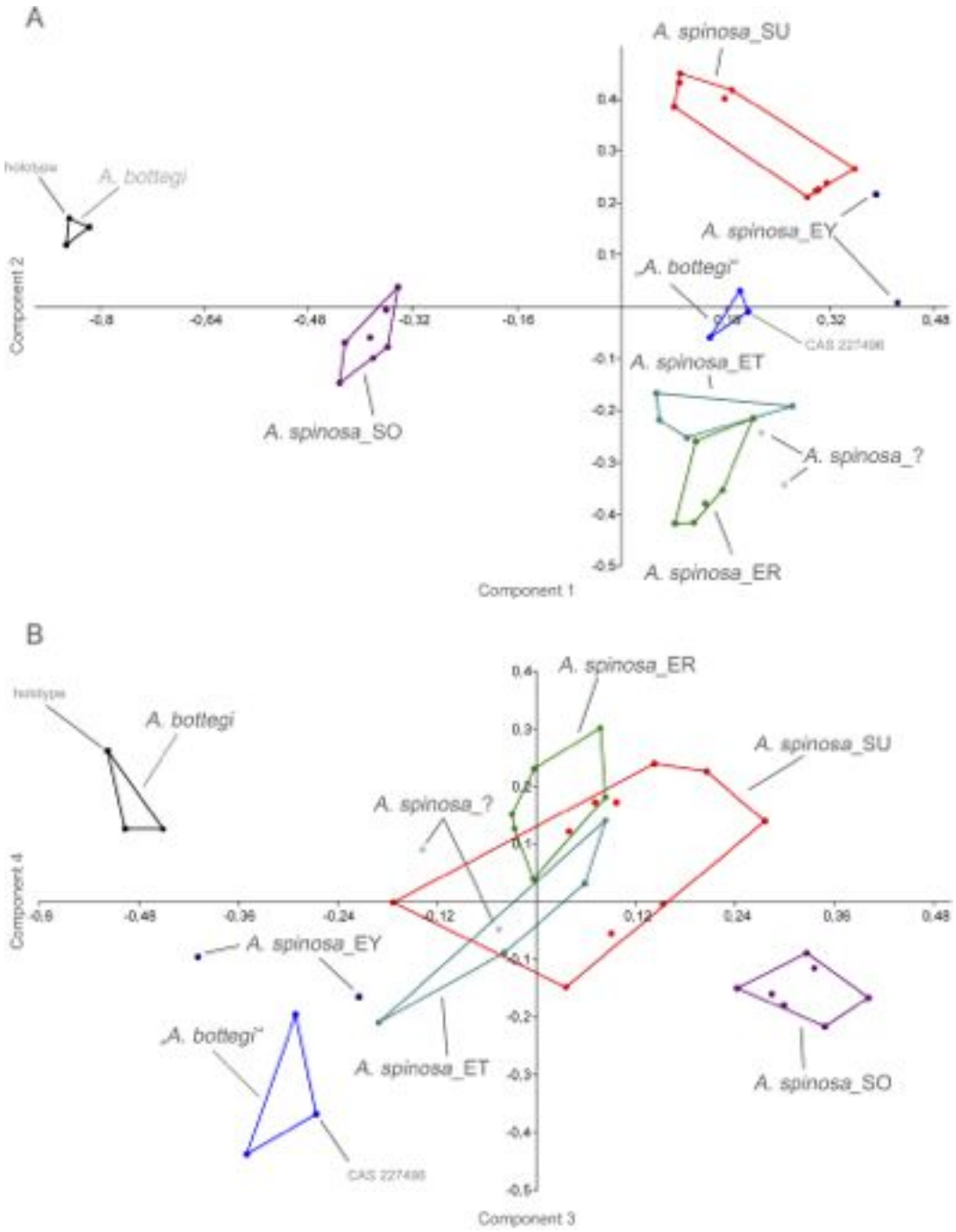

Figure 2. Plot of specimen scores of principal components analyses of size-corrected and $\log_{10}$-transformed data of the *A. spinosa* group. (A) First two axes of mensural, meristic and qualitative data. (B) First and third axes of mensural and meristic data. This figure is published in colour in the online version.

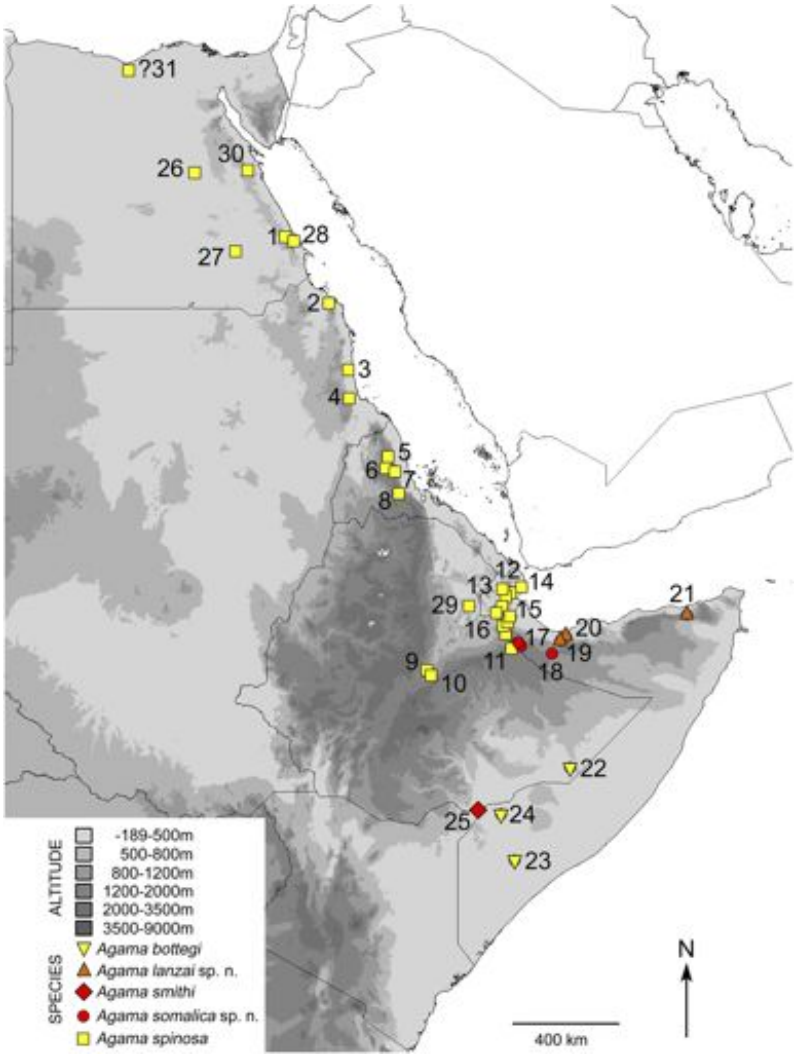

Figure 3. Distribution of *A. bottegi*, *A. lanzai* sp. n., *A. smithi*, *A. somalica* sp. n. and *A. spinosa*. Numbers refer to localities downloaded from GBIF, Largen and Spawls (2006) and own data. Numbers referring to type localities are underlined. 1: Wadi Sikait, "Wüste (= desert) Etbai"; 2: Gebel Elba; 3: Port Sudan; 4: Erkowit; 5: Nakfa; 6: 67 km N of Keren; 7: Af'abet; 8: Ghinda; 9: Metahara, Mount Fantalle; 10: Awash Falls; 11: Somadu; 12: Tadjura, 12 km W of Tadjura; 13: Fôret du day; 14: Obcock; 15: Sagallou; 16: several localities with coordinates only; 17: Boroma, 7 km N of Boroma; 18: near Las Geel; 19: Aroweina; 20: 28 km SW of Berbera; 21: Karin; 22: Galgalo; 23: Dinsor; 24: Lugh; 25: btw. [Webi] Shebeli and Juba Rivers; 26: only coordinates; 27: Aswuan; 28: Wadi Gadireh; 29: Asaita; 30: Gebel Shayib el Banat; ?31: El Omayed (questionable record). This figure is published in colour in the online version.

populations examined. Several morphological characters are unique in the Somalia specimens (e.g., long neck crest of small scales; nasal scale in contact with the first canthus scale), and we therefore recognize these specimens as a second new species.

Species account

Agama bottegi *Boulenger, 1897*

1897 [1898] *Agama bottegi* Boulenger, Concluding report on the late Capt. Bottego's collection of reptiles and batrachians from Soma-

liland and British East Africa. Annali del Museo Civico di Storia Naturale di Genova, (2) 18: 715-723.

Holotype. MCSN [MSNG] 28548, adult male, from "Lugh [03°47′46″N, 42°32′32″E]", Somalia, collected by Capt. U. Ferrandi (V. Bottego Expedition).

Taxonomic notes. The taxonomic history of *Agama bottegi* is relatively short. After its description it was overlooked or ignored and only mentioned by Wermuth (1967) as a questionable species. Lanza (1978) later collected six additional specimens (3 m, 1 f, 2 juv.) at Dinsòr and recognized *A. bottegi* as a valid species, which was supported by Wagner and Bauer (2011). However, until recently, only these verified seven specimens were known. Specimens from Galgalo in Ethiopia (MZUF 6586-89) need to be examined.

Diagnosis. A moderately large species of *Agama* which can be identified by the following combination of characters: nasal scale pear shaped, keeled and convex; nasal scale not in contact with the first canthus scale but separated by one or two smaller scales; neck crest relatively short and consisting of few but distinctly high crest scales; ear hole surrounded by three tufts of spiny scales; vertebral and lateral body scales strongly keeled, mucronate and shingled; ventral scales moderately keeled; dorsal and ventral tail scales keeled; and males with one continuous row of nine precloacal pores.

Description. Maximum total-length up to 355 mm (Boulenger, 1898 [1897]), with an SVL of 93.2-120 mm (Boulenger, 1898 [1897]) in adult specimens. Head moderately convex, body scarcely depressed, hind limbs strong. Gular pouch absent. Tail about twice as long as SVL (235 mm by 114 mm SVL). Head scales moderately large, smooth, with the occipital scale enlarged. Nasal scale keeled, pear shaped and convex, pierced with backward directed nostril in the posterior part, situated on the canthus rostralis. Two scales between the nasal and the first supraciliary scale. Supraciliary scales smooth. Strong nuchal crest with average length of 12.4 mm present in males, containing 6-7 conical scales equal to the diameter of the ear opening. Usually a low crest extending down the back and to the tail. Three tufts of large spinose scales near the ear and additional two on the sides of the neck, longest spines about two-third the diameter of the ear opening. Body scales large, homogeneous, imbricate, strongly keeled, and strongly mucronate, in 52-60 (x = 55.3) rows around midbody and 40-43 (x = 41.7) along the vertebral column. Ventral scales keeled, smaller than the dorsals and dorsoventral in 58-63 (x = 60.3) scale rows. Fourth and third fingers equal; fourth toe slightly longer than third, fifth not extending beyond first. Tail slightly dorsolaterally compressed, covered with strongly keeled scales, which are larger than the body scales. One continuous row of nine precloacal pores.

Distribution. Only known from southern Somalia and adjoining Ethiopia (fig. 3). The specimens (MZUF 6586-89) from Galgalo (Ethiopia) were so far not examined by us and the correct identification needs to be confirmed.

Agama lanzai *sp. nov.*

Holotype. CAS 227496, adult male from Karin (10°58′26.4″N, 49°12′49.2″E; 325 m), Bari region, Puntland State, Somalia, collected by Ted J. Papenfuss on June 25th 2003.

Paratypes. MZUF 6716, adult male and MZUF 6717, juvenile, both from "between Carim [= Karin] and Galgalo", Somalia, collected by E. Granchi on October 6th 1973. MZUF 23762 adult male from Uadi Goddalola, Somaliland, Somalia collected by G. Scortecci on October 2nd 1953 or 1957.

Diagnosis. A moderately large *Agama*, morphologically similar to *A. bottegi*. It can be identified by the following combination of characters: nasal scale round, smooth and tubular; nasal scale not in contact with the first can-

thus scale but separated by two smaller scales; neck crest short but consists of few distinctly high crest scales; ear hole surrounded by six tufts of spiny scales, with additional two tufts on the neck; vertebral and ventral scales smooth; lateral body scales keeled; dorsal tail scales keeled, ventral tail scales smooth; and males with one uncontinuous row of ten precloacal pores.

Description. Maximum length up to 348 mm, with an SVL between 77-102 mm in adult males. Head round to moderately convex, body scarcely depressed, hind limbs strong. Head scales moderately large, smooth, with the occipital scale not larger than the largest head scale. Small gular pouch and gular fold present. Tail more than twice as long as SVL (245 mm by 102 mm SVL). Nasal scale round, smooth and strongly convex to usually tubular, pierced with a laterally and slightly posterodorsally directed nostril in the posterior part, situated on the canthus rostralis. Two scales between the nasal and the first canthus scale. Supraciliary scales smooth. A short nuchal crest of x = 10 mm present in males, consisting of 6-8 (x = 7) conical scales equal to the diameter of the ear opening. Six tufts of large spinose scales around the ear and additional two on the sides of the neck, longest spines about two-third the diameter of the ear opening. Body scales large, imbricate and homogeneous; vertebral scales smooth, lateral scales keeled, ventral scales smooth, smaller than the dorsals. Body scales in 55-59 (x = 56.3) rows around midbody, 51-59 (x = 56) scales dorsal along the vertebrate and 80-83 (x = 81.7) scales along the belly. Fourth and third fingers equal, third and fourth toe equal in length. Tail slightly compressed, covered dorsally and laterally with strongly keeled scales, which are larger than the body scales, ventral tail scales smooth and smaller. In some male specimens a short and low tail crest present. One uncontinuous row of ten precloacal pores in adult males.

Differential diagnosis. *Agama lanzai* sp. n. is distinguished from *A. bottegi* in its smaller size (x = 93.0 mm versus 103.4 mm) and a shorter neck crest (x = 9.8 mm versus 12.4 mm); by having a small gular pouch versus no gular pouch; by possessing smooth ventral body and tail scales; by possessing six versus three tufts of spiny scales around the ear; by possessing a round and smooth versus a pear shaped and keeled nasal scale; and by having a higher number of dorsal scales along the vertebrate (51-59 versus 40-43) and ventral scales (80-83 versus 58-63); and by possessing a uncontinuous row of precloacal pores versus continuous.

Agama lanzai sp. n. is distinguished from *A. somalica* sp. n. by its shorter neck crest (x = 9.8 mm versus 11.2 mm) compared with the same body size (78-103 mm versus 84-103 mm); by possessing a short nuchal crest with a low number of distinctly high crest scales versus a long nuchal crest with a high number of low crest scales; by having a lower number of neck crest scales (x = 7 versus 9.9); by having the nasal scale not in contact with the first canthal scale; by having a lower number and range of scale rows around midbody (55-59, x = 56 versus 67-79, x = 75); and by having a lower count of dorsal (x = 56 versus 65) and ventral scales (x = 82 versus 96); and by possessing a uncontinuous row of precloacal pores versus continuous.

Agama lanzai sp. n. is distinct to *A. spinosa* by its smaller body size (78-103 mm, 93 mm versus 83-121 mm, x = 99 mm); by possessing a lower number of neck crest scales (x = 7 versus 8.5); by having the nasal scale not in contact with the first canthal scale; and by a lower number of scale rows around midbody (55-59 versus 58-73).

Description of the holotype. CAS 227496 (fig. 4), adult male, tail regenerated 71.3 mm from the base, with a regenerate of 22.9 mm.

Measurements. SVL 102.5 mm; HL 25.3 mm; HW 20.7 mm; HH 13.8 mm; crest length 8.9 mm; length of humerus, radius and ulna

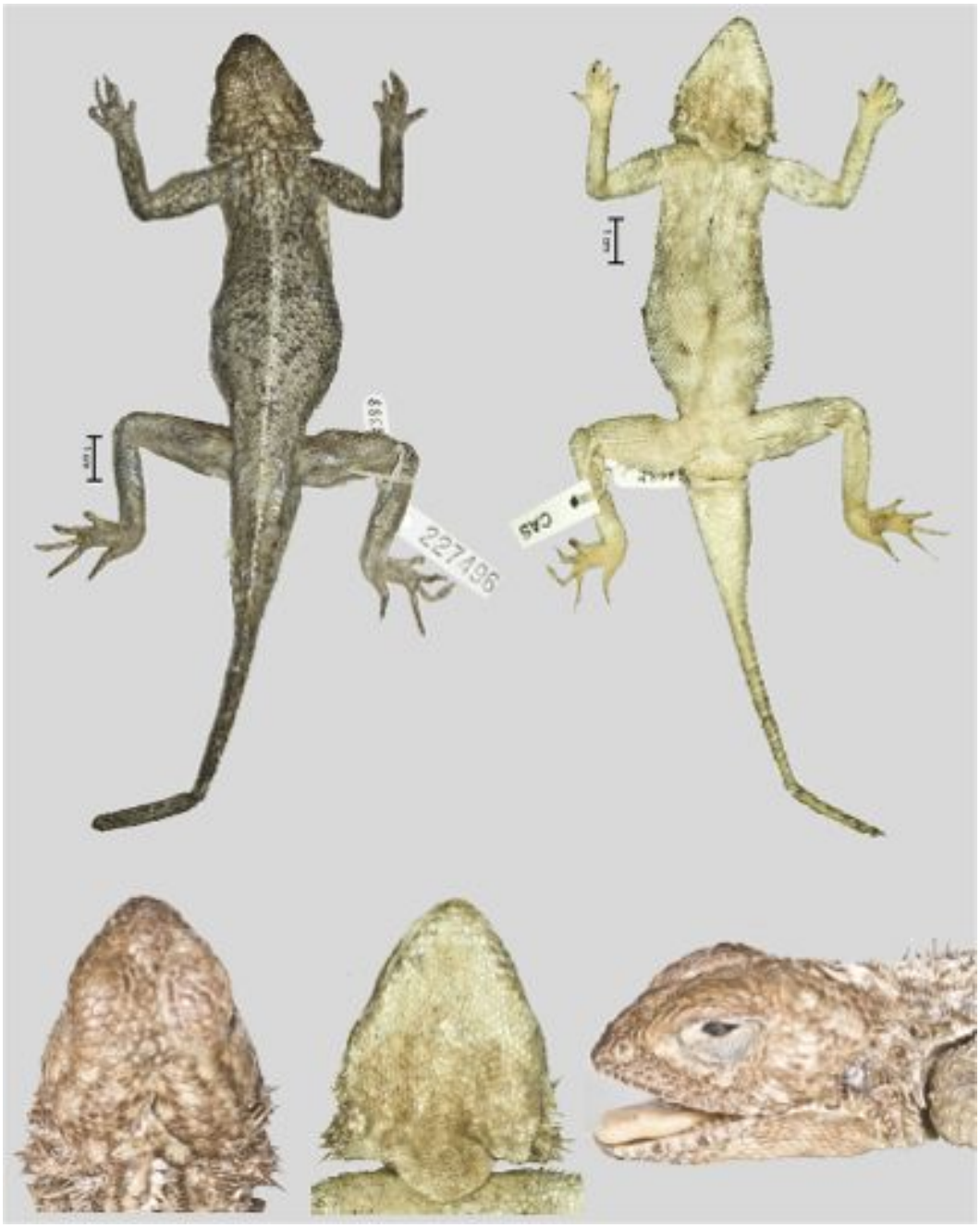

Figure 4. Male holotype (CAS 227496) of *Agama lanzai* sp. n. This figure is published in colour in the online version.

38.3 mm; length of femur, tibia and fibula 56.0 mm.

Description. Head and body depressed. Nostril tubular and half of the size of the nasal scale, directed more or less laterally and slightly posterodorsally, pierced in the posterior part of a convex to tubular, smooth to rugose, round nasal scale which is situated on the canthus rostralis. Nasal scale partly visible from above, separated from the first canthal scale by two smaller

scales. Nostril barely visible from above. The first three canthal scales not in contact with the eye. Scales on the head smooth to moderately rugose, interorbital scales as large or larger than the supraorbital scales; imbrications of temporal scales not uniformly directed, some ventrally oriented, others posteriorly oriented. Occipital small, not larger than the largest head scale and smaller than the diameter of the tympanum, pierced by a visible pineal foramen in the center. 11 upper and 11 lower labial scales on the left side. Ear opening smaller than the eye, surrounded at its border by six tufts of spinose scales, additional two tufts on the dorsolateral parts of the neck. Spinose scales of the tufts long, often consisting of scales of the same size with one elongated scale in the center. Gular fold and gular pouch present. Short nuchal crest of 8.9 mm present, composed of six long erect scales. Crest subdivided in two parts by the lack of crest scales after the first two crest scales. Crest scales long, as long as half of the ear diameter or more. Dorsal scales homogeneous, in 63 scale rows around the body just behind the forelimbs, in 59 scale rows around midbody, and in 58 scale rows around the body in front of the hind limbs. There are 58 vertebral scales and 83 ventral scales along the belly between the anterior border of the shoulders and cloaca. One row of ten precloacal pores. Dorsal and lateral body scales keeled, with a keel extending along the entire scale, slightly mucronate and erect. Scales directly along the vertebrae smooth. Gular and ventral scales smooth. Lamellae 14 under the left fourth finger, 16 lamellae under the left fourth toe. Relative length of digits of left manus $1 < 2 < 5 < 3 = 4$; relative length of digits of left pes $1 < 2 < 5 < 3 = 4$; Tail depressed at its base, regenerated 71.3 mm behind cloaca. Large hemipeneal pockets absent. Dorsal tail scales strongly keeled, slightly mucronate, somewhat larger than the body scales. Ventral tail scales smooth at its base. Tail scales not arranged in distinct whorls of scale rings, but indistinct whorls of three scale rings present.

Coloration (after fixation and ethanol preservation). Upper parts of the body mottled dirty whitish to dark gray. A dark patch on the shoulders on both body sides is visible. Throat dirty whitish without any pattern. Underside of the body and tail dirty whitish.

Coloration. Similar in all preserved specimens, probably due to preservation. In living specimens, males show a nuptial coloration with a dark red and creamy white speckled head and a blue body with white to yellowish speckles. Base of the throat entirely dark red and a black patch at the shoulders is visible. Nuchal crest distinctly white colored (fig. 5). Males in non-nuptial coloration uniform brownish, with the crest distinctly white, sometimes with an orange-red head. Coloration of pregnant females very colorful and similar to species like *A. boulengeri* Lataste, 1886 or *A. impalearis* Boettger, 1874. Body entirely orange with several red bands and blotches, head often blue, legs and tail brownish (fig. 5). Females in non-pregnant coloration unknown.

Relationships. *Agama lanzai* sp. n. (formerly identified as *A. bottegi* in our genetic analyses) shows pairwise genetic divergences (table 2) of 6.0-6.4% to *A. spinosa* and 7.1-7.3% to *A. somalica* sp. n. (*A. spinosa* from Somalia in our genetic analyses) and is sister to the remainder of the *spinosa* group s. str. *Agama lanzai* sp. n. shares some phenotypic characters with *A. bottegi* (e.g., short neck crest of high scales), but the lack of genetic resources for *A. bottegi* prevents us from estimating their phylogenetic relationship within the *spinosa* group. Morphological phylogenetic analysis using maximum parsimony support *A. bottegi* as sister to the *spinosa* group including *A. lanzai* sp. n. (fig. 6). *Agama lanzai* sp. n. shares several morphological characters with other members of the *spinosa* group (to the exclusion of *A. bottegi*), including a round nasal scale and six clusters of scales around the ear (fig. 6). In contrast, *A. bottegi* possess a pear-shaped nasal scale and three clusters of scales around the ear (fig. 6).

Figure 5. *Agama lanzai* sp. n. From top to bottom: Living adult male in nuptial coloration (photo by Pavel Novák); Adult female in pregnant coloration; Habitat at 28 km SW of Berbera, Somalia. This figure is published in colour in the online version.

Table 2. Values of pairwise uncorrected genetic divergences (*p* distance) of the studied species derived from the 16S mtDNA gene. EY: Ethiopia, DJ: Djibouti.

	*A. spinosa*_EY	*A. spinosa*_DJ	*A. lanzai* sp. n.	*A. somalica* sp. n.	*A. hartmanni*	*A. tassiliensis*
*A. spinosa*_EY	0	–				
*A. spinosa*_DJ	1.8-2.1	0.02	–			
A. lanzai sp. n.	6.3-6.4	6.0-6.2	0	–		
A. somalica sp. n.	4.3-5.3	5.2-5.6	7.1-7.3	0	–	
A. hartmanni	6.3-7.2	7.0-7.2	7.8	7.1-7.3	0	–
A. tassiliensis	5.8-6.6	7.2-8.1	8.0-8.7	7.6-7.8	7.0-7.6	0-2.9

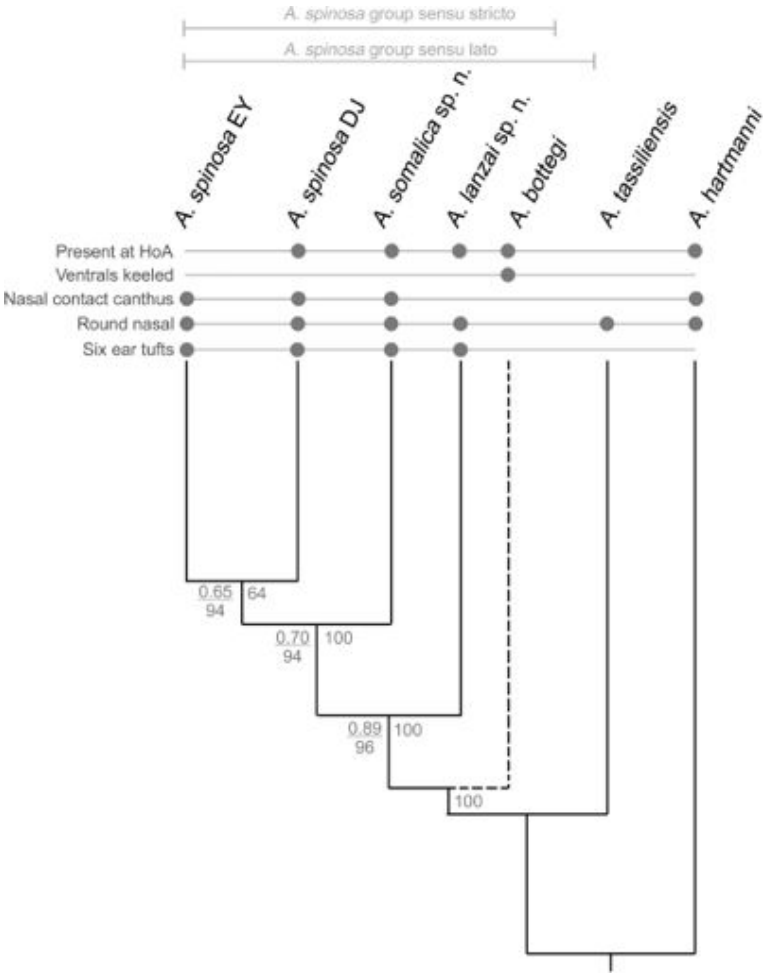

Figure 6. Integrative phylogenetic tree of the *Agama spinosa* group. Systematic position of *A. bottegi* is supported by hierarchical cluster and parsimony analysis. Bootstrap values on the left side from genetic analysis, on the right side from morphological parsimony analysis.

Etymology. This species is named in honor of Benedetto Lanza, Professor emeritus and former director of the Museo di Storia Naturale "La Specola" in Firenze, in recognition of his great contributions to herpetology in general, and to the herpetology of the Horn of Africa in particular.

Distribution. So far, this species has only been recorded from northern and northeastern Somalia (fig. 3).

Ecology. A rupicolous lizard, occurring in dry mountainous and hilly areas. Individuals inhabit rocky outcrops in arid stony to rocky landscape with sparse vegetation (fig. 5). It is diurnal and lives in harem groups of one dominant male and several females and juveniles (unpublished data) and pregnant females were seen in December 2010 (own data).

Agama smithi *Boulenger, 1896* incertae sedis

1896 *Agama smithi* Boulenger, Second Report on the Reptiles and Batrachians collected by Dr. A. Donaldson Smith during his Expedition to Lake Rudolf. Proc. Zool. Soc. London 1896: 212-217.

Holotype. BMNH 95.12.31.4 [1946.8.27.79] from "between [Webi] Shebeli and Juba Rivers" [03°58′N, 41°40′E, fide Largen & Spawls, 2006], Ethiopia, collected by Dr. A. Donaldson Smith on February 27th 1895.

Taxonomic notes. *Agama smithi* was recognized as a non-valid species since Parker (1932) treated it as synonym of *A. spinosa*, which was supported by Wermuth (1967). Later, Largen and Spawls (2006) argued that *A. spinosa* generally, without any exception, has six clusters of spiny scales around the ear, while *A. smithi* maximally shows five. Therefore, they recognized this taxon as a synonym of *A. agama*. However, according to the new concepts of *A. agama* by Böhme et al. (2005) and Wagner et al. (2009), *A. agama* is confined to Central Africa and therefore it is necessary to reassess the status of *A. smithi*. Within this re-assessment we found several unique character combinations that prevented us from recognizing this taxon as a synonym of any valid species. Even Lanza (1978) mentioned specimens from southern Somalia as distinct from *A. spinosa*, which according to our re-assessment could refer to *Agama smithi*. However, these specimens still need to be examined, and those results will be published elsewhere. Meanwhile, we recognize *A. smithi* as species *incertae sedis*.

Diagnosis. A medium sized *Agama* (SVL = 110 mm), morphologically similar to *A. spinosa* and *A. bottegi*. It can be identified by the following combination of characters: nasal scale pear shaped, smooth and convex; nasal scale in contact with the first canthus scale; neck crest short, consists of few long crest scales; ear hole surrounded by three tufts of spiny scales, with additional two tufts on the neck.; dorsal body scales large, keeled, imbricate and strongly mucronate, in 58 scale rows around midbody; lateral scales keeled, imbricate and strongly mucronate, but smaller than the vertebrate scales; ventral scales smaller than dorsal scales and smooth; dorsal tail scales keeled and as large as the dorsal scales.

Brief differential diagnosis. *Agama smithi* is distinct from the species of the *A. spinosa* group by possessing a pear shaped nasal scale and by having three scale tufts around the ear (versus six). Moreover, it is distinct from *A. lanzai* sp. n. by having the nasal scale directly in contact with the first canthus scale and from *A. spinosa* and *A. somalica* sp. n. by having a rather short nuchal crest. *Agama smithi* is distinct from *A. bottegi* by having the ventral scales smooth versus keeled and by having the nasal scale smooth versus keeled.

Distribution. *Agama smithi* is only known from the holotype, but Lanza (1978) mentioned "*agama*-like" specimens from southern Somalia (13 km W of Afmadù [= Afmadoow]), which could refer to this species.

Agama somalica *sp. n.*

Holotype. ZFMK 94230 [field no. 57], subadult male from near Las Geel (09°44.914′N; 44°27.393′E; 1131 m), Central Somaliland, Somalia, collected by Tomáš Mazuch on November 29th 2010.

Paratypes. CAS 225408-10, 225437-38, adult males from Boroma [= Borama] (09°57′6.6″N, 43°12′28.8″E; 142 m), Awdal region, Somaliland, Somalia, collected by Ted J. Papenfuss on June 8th 2002 [CAS 225410 is the specimen referring to the tissue MVZ 241334]. CAS 225412-13, adult males from 7 km by road N of Boroma [= Borama] (09°59′13.8″N, 43°07′58.8″E), Awdal region, Somaliland, Somalia, collected by Ted J. Papenfuss on June 8th 2002 [CAS 225413 is the specimen referring to the tissue MVZ 241335].

Diagnosis. A medium-sized *Agama*, morphologically similar to *A. spinosa*. It can be identified by the following combination of characters: nasal scale round, smooth and tubular; nasal scale in contact with the first canthus scale; neck crest long, consists of a high number of distinctly short crest scales; ear hole surrounded by six tufts of spiny scales, with additional three tufts on the neck; vertebral scales smooth to feebly keeled, lateral scales keeled and ventral scales smooth; dorsal tail scales keeled, ventral tail scales smooth; and males with one continuous row of ten to twelve precloacal pores.

Description. Maximum length up to 278 mm, with a SVL between 84-103 mm in adult males. Head moderately convex, body scarcely depressed, hind limbs strong. Head scales moderately large, smooth, with the occipital scale enlarged. Small gular pouch and gular fold present. Tail more than twice as long as SVL (176 mm by 103 mm SVL). Nasal scale round, smooth and strongly convex to usually tubular, pierced with a laterally and slightly posterodorsally directed nostril in the posterior part, situated on the canthus rostralis. Nasal scale directly in contact with the first canthus scale. Supraciliary scales smooth. A long nuchal crest of x = 11.2 mm present in males, consisting of 9-12 (x = 9.9) low conical scales distinctly shorter than half of the diameter of the ear opening. Six tufts of medium sized spinose scales around the ear and additional three on the sides of the neck, longest spines about two-third the diameter of the ear opening. Body scales medium sized, imbricate and homogeneous; vertebral scales smooth to feebly keeled, lateral scales keeled, ventral scales smooth, smaller than the dorsals. Body scales in 67-79 (x = 74.6) rows around midbody, 59-75 (x = 65.3) scales dorsal along the vertebrate and 77-107 (x = 95.6) scales along the belly. Fourth and third fingers equal; fourth toe longest. Tail slightly compressed, covered dorsally and laterally with strongly keeled scales which are larger than the body scales, ventral tail scales smooth and smaller. One continuous row of 10-12 (x = 11.1) precloacal pores in adult males.

Differential diagnosis. *A. somalica* sp. n. is distinct from *A. bottegi* in its smaller body size (x = 82 mm versus 103 mm); in possessing a round, smooth and tubular nasal scale versus a pear shaped, keeled and convex to feebly tubular nasal scale; in possessing a fairly long nuchal crest containing a higher number of low crest scales versus a short crest with a low number of high crest scales; in having a higher number of neck crest scales (9-12 versus 6-7); in having six tufts of spinosa scales around the ear and additional three on the neck versus three around the ear and two on the neck; in having a higher number of scale rows around midbody (x = 75 versus 55); in possessing a higher number of dorsal (x = 65 versus 42) and ventral scales (x = 96 versus 60); and in possessing smooth ventral body and tail scales versus keeled scales.

A. somalica sp. n. is distinct from *A. lanzai* sp. n. by its longer neck crest (x = 11.2 mm versus 9.8 mm) compared with the same body size (84-103 mm versus 78-103 mm); by possessing a long nuchal crest with a high number of low crest scales versus a short nuchal crest with a low number of high crest scales; by hav-

ing a higher number of neck crest scales (x = 9.9 versus 7); by having the nasal scale in contact with the first canthal scale; in having three tufts of spinose scales on the lateral part of the neck versus two; by having a higher number and range of scale rows around midbody (67-79, x = 75 versus 55-59, x = 56); by having a higher count of dorsal (x = 65 versus 56) and ventral scales (x = 96 versus 82); and by possessing a continuous row of precloacal pores versus uncontinuous.

A. somalica sp. n. is distinguished from *A. spinosa* by its smaller body size (x = 82 mm versus 99 mm); in having lower neck crest scales; and in possessing a higher number of scale rows around midbody (x = 75 versus 64), of dorsal scales (x = 65 versus 56) and of ventral scales (x = 96 versus 87); and by possessing a continuous row of precloacal pores versus uncontinuous.

Description of the holotype. ZFMK 94230, subadult male (fig. 7), with a complete tail.

Measurements. SVL 85.4 mm; TL 158.8 mm; HL 23.7 mm; HW 17.1 mm; HH 11.7 mm; crest length 10.0 mm; length of humerus, radius and ulna 30.3 mm; length of femur, tibia and fibula 44.8 mm.

Description. Head and body depressed. Nostril tubular about one third of the size of the nasal scale, directed upwards and slightly posterodorsally, pierced in the posterior part of a convex to tubular, smooth, round nasal scale which is situated on the canthus rostralis. Nasal scale and nostril visible from above, directly in contact with the first canthal scale. The first four canthal scales not in contact with the eye. Scales on the head smooth, interorbital scales as large or larger than the supraorbital scales; imbrications of temporal scales not uniformly directed, partly ventrally, others posteriorly. Occipital large, its greatest width nearly equal to the diameter of the tympanum, pierced by a visible pineal foramen in the center. 11 upper and 12 lower labial scales on the left body side. Ear opening smaller than the eye, surrounded at its border by six tufts of spinose scales, additional three tufts on the dorsolateral parts of the neck. Spinose scales of the tufts long, often consisting of scales of the same size with one elongated scale in the center. Small gular fold and gular pouch present. Long nuchal crest of 10 mm present, composed of eleven erect scales. Crest scales short, much shorter than the half of the ear diameter. Dorsal scales homogeneous, in 91 scale rows around the body just behind the forelimbs, in 79 scale rows around midbody, and in 78 scale rows around the body in front of the hind limbs. There are 75 dorsal scales along the vertebrate and 104 ventral scales along the belly between the anterior border of the shoulders and cloaca. One row of eleven precloacal pores. Dorsal body scales smooth to partly feebly keeled, lateral body scales keeled, with a keel extending along the entire scale, slightly mucronate and erect. Scales directly along the vertebrate smooth. Gular and ventral scales smooth. Ventral scales smaller than dorsal scales but equal to gular scales. Lamellae 14 under the left fourth finger, 18 lamellae under the left fourth toe. Relative length of digits of left manus $1 < 2 < 5 < 3 = 4$; relative length of digits of left pes $1 < 2 < 5 < 3 < 4$; Tail depressed at its base. Large hemipeneal pockets absent. Dorsal tail scales strongly keeled, slightly mucronate, somewhat larger than the body scales. Ventral tail scales smooth at its base. Tail scales not arranged in distinct whorls of scale rings, but indistinct whorls of three scale rings present.

Coloration (after fixation and ethanol preservation). Upper parts of the body mottled dirty whitish to light brown. In some parts, e.g. dorsal body, upper parts of hindlimbs, white centered light brown but washy ocella are visible reflecting a non-nuptial coloration. A dark patch on the shoulders on both body sides is present, but beneath the extension of the gular fold. Throat reticulated dirty white and washy red. Underside of the body and tail dirty whitish. Head speckled reddish and creamy, fore limbs blue-brown, body brownish with rests of the typ-

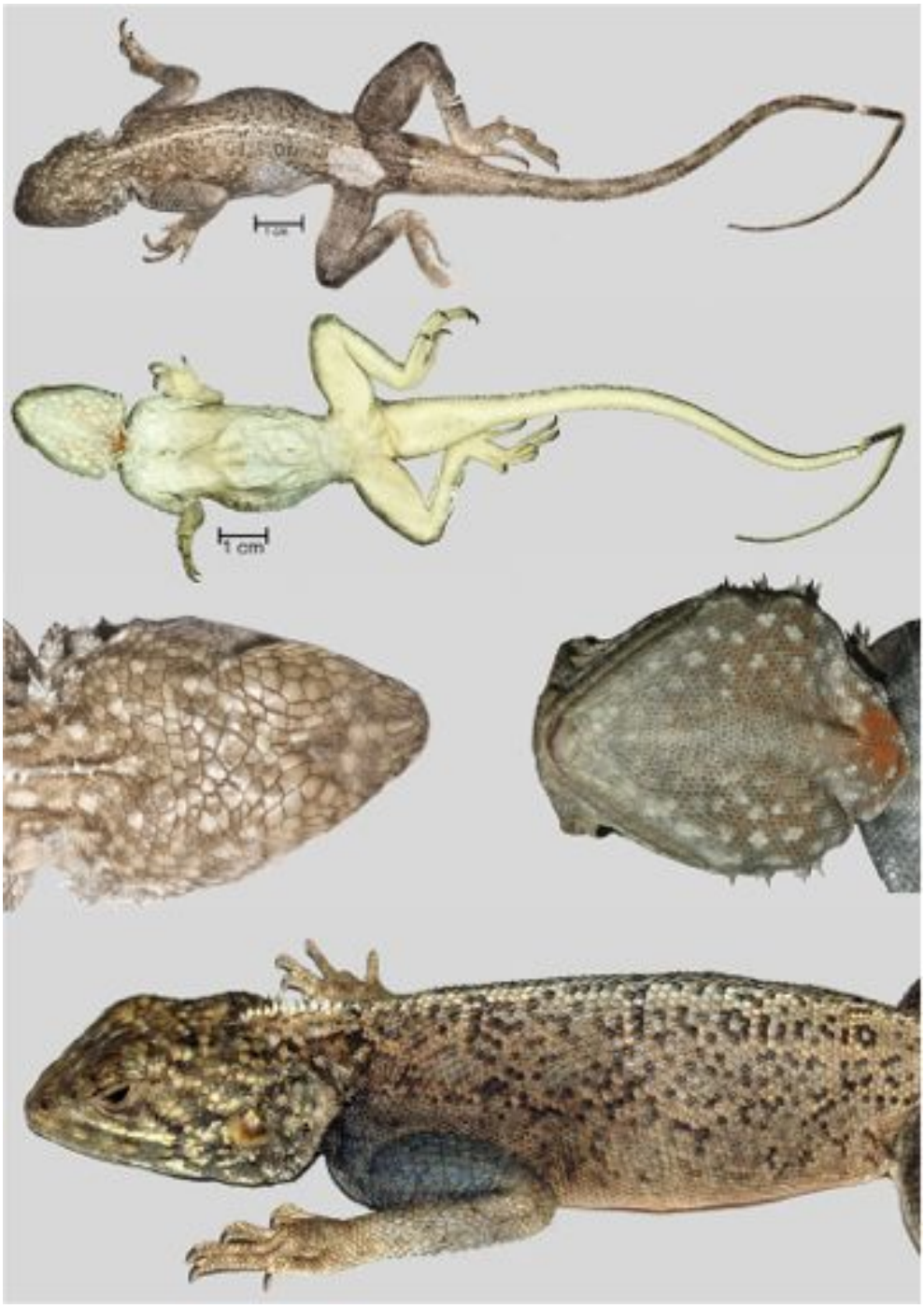

Figure 7. Male holotype (ZFMK 94230) of *Agama somalica* sp. n. Throat coloration from the living specimen. This figure is published in colour in the online version.

ical *Agama*-juvenile coloration of cream centered ocella and brown crossbars, vertebral area whitish. For non nuptial living coloration of the holotype see fig. 8.

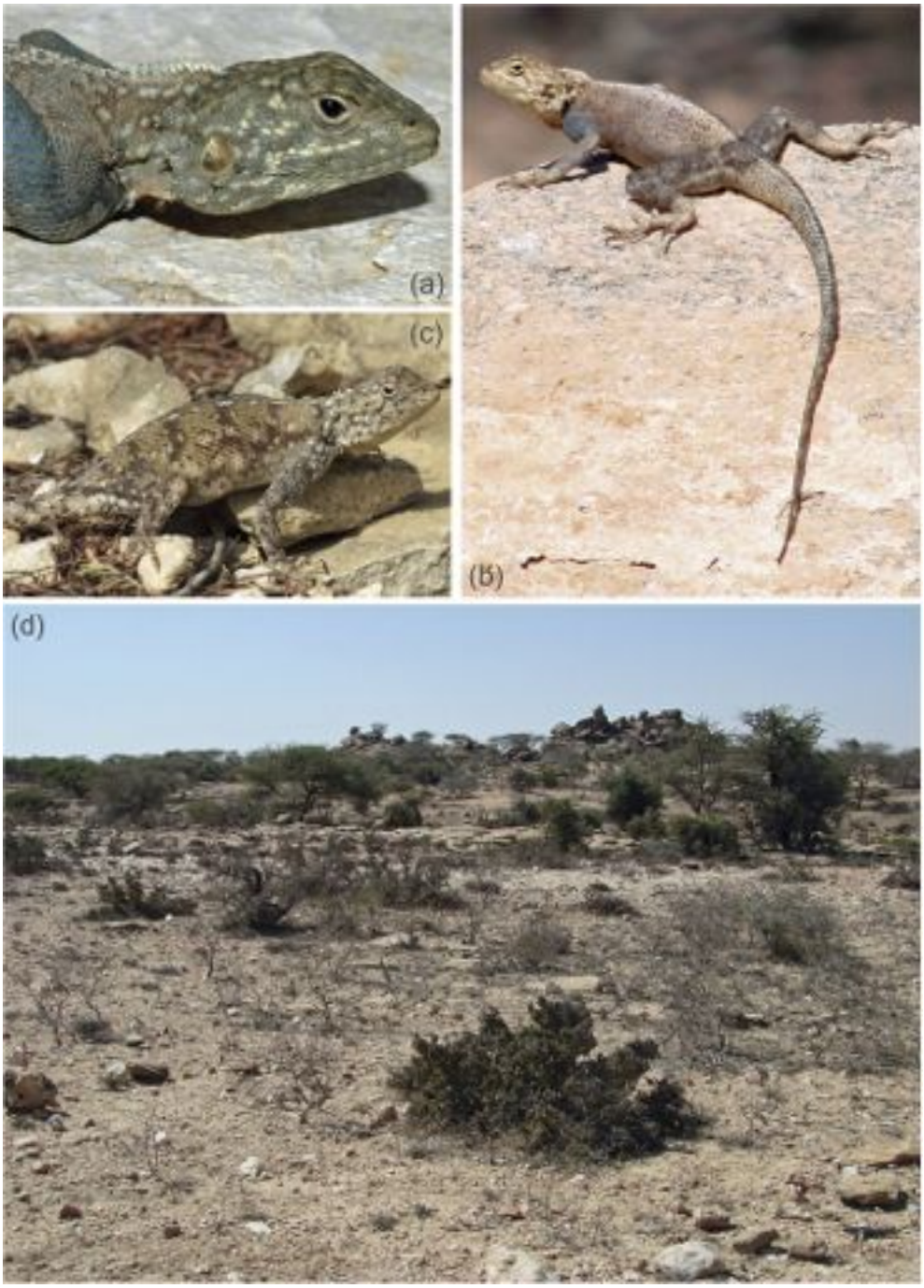

Figure 8. (A, B) Living male holotype of *Agama somalica* sp. n. (C) Living female from the type locality. (D) Habitat at the type locality near Las Geer, Somalia. This figure is published in colour in the online version.

Coloration. In all specimens similar due to preservation, but the contrast between the different colors is even stronger. Some preserved specimens with solitary dark scales on the body and a reticulated red and light brown head. Throat often with a dark red dot on its base. Sometimes the forepart of the belly still reddish. Coloration of nuptial males unknown, but they probably develop a yellowish head and neck in this condition. Non-pregnant females have the typical *Agama*-coloration, brownish above and dirty whitish below. Head mottled light and dark brown with several stripes, especially from the eye to the lips and between the eyes. Body with an interrupted white vertebral stripe and five to six brown cross-bands between the limbs, flanks with white and white centered brown ocella. Pregnant coloration of females unknown. Juveniles bear a similar coloration but with more contrast: head often yellowish, with bands of white centered brown ocella between the brown cross-bands on the body, and with generally more ocella on body, limbs and neck.

Relationships. *Agama somalica* sp. n. is the sister species of *A. spinosa* and shows uncorrected pairwise genetic divergences of 4.3-5.3% to *A. spinosa* specimens from Egypt and 5.2-5.6% to specimens from Djibouti (table 2). In relation to *Agama lanzai* sp. n. and *A. somalica* show divergences of 7.1-7.3%.

Etymology. This species is named after Somalia, the country of its type locality.

Distribution. *Agama somalica* sp. n. is only known from northeastern Somalia (fig. 3). Since several localities are near the Somalian border with Ethiopia, we suggest that the species may also occur in Ethiopia.

Ecology. This species occupies rocks in dry mountainous and hilly areas (fig. 8). Specimens were found on rocky outcrops within an arid rocky landscape with sparse vegetation of small bushes and scattered trees. It is diurnal and lives in harem groups of one dominant male and several females and juveniles (own data). Pregnant females were found in July 2011.

Agama spinosa *Gray in Griffith & Pidgeon, 1831*

1831 *Agama spinosa* Gray, A synopsis of the species of Class Reptilia. In: Griffith, E. & E. Pidgeon: The animal kingdom arranged in conformity with its organisation by the Baron Cuvier with additional descriptions of all the species hither named, and of many before noticed [V. Whittaker, Treacher and Co., London: 481 + 110 pp.]

Holotype. Unknown specimen from "Africa", restricted to "Eastern desert north of Keneh", Egypt by Anderson (1898) and to "Suakin, Sudan" by Marx (1968).

Taxonomic note. In the original description it is indicated that the type specimen is part of the BMNH collections, but no collection number is presented and the type locality of *Agama spinosa* is just given as "Africa". Anderson (1898) mentioned that at the time of the description only three specimens of *A. spinosa* from Egypt were present at the BMNH collection and restricted the type locality to this country. Later, Marx (1968) restricted the type locality to Suakin in Sudan without any further comments. However, both actions are not in accordance with the International Code of Zoological Nomenclature, as the type locality is the locality where the name bearing type was collected. So far, the type specimen has not been identified and therefore the type locality is still "Africa", but we follow Anderson (1898) who supports Egypt as the most probable type locality. Even that the first description of *A. spinosa* is rather short, we can justify that both, *A. lanzai* sp. n. and *A. somalica* sp. n. are not in conflict with this species. *Agama somalica* sp. n. is distinct in not possessing tufts of "long subulate scales" and having small scales on the back, while *A. lanzai* sp. n. is different in having a distinctly enlarged neck crest versus a "slight crest".

Diagnosis. A moderately large species of *Agama* which can be identified by the following combination of characters: nasal scale round, smooth, and usually tubular; nasal scale in contact with the first canthus scale; neck crest relatively short and consisting of few but distinctly high crest scales; ear hole surrounded by six tufts of spiny scales, with additional three tufts on the neck; vertebral and lateral body scales keeled and imbricate; ventral scales smooth; dorsal tail scales keeled, ventral tail scales smooth at the base; and males with one uncontinuous row of precloacal pores.

Description. Maximum length up to 353 mm, with an SVL of 82.5-120.9 mm in adult specimens. Head moderately convex, body scarcely depressed, hind limbs strong. Gular pouch and gular fold present. Tail about twice as long as SVL (232 mm by 121 mm SVL). Head scales moderately large, smooth, with the occipital scale enlarged, largest width as large as diameter of the tympanum. Nasal scale smooth, round and convex to tubular, directly in contact with the first canthus scale, pierced with postdorsally upwards directed nostril in the posterior part, situated on the canthus rostralis. Supraciliary scales smooth. Strong to medium nuchal crest of x = 10.9 mm length present in males, containing 7-11 conical scales smaller than the diameter of the ear opening. Six tufts of large to medium sized spinose scales near the ear and additional three on the sides of the neck, longest spines about two-third the diameter of the ear opening. Body scales large, homogeneous, imbricate, keeled, and mucronate, in 58-73 (x = 63.6) rows around midbody and 48-61 (x = 55.7) along the vertebrate. Ventral scales smooth, smaller than the dorsals and in 79-96 (x = 86.8) rows along the belly. Fourth and third fingers equal, length of fourth toe in relation to third variable. Tail slightly compressed, covered with strongly keeled scales above which are larger than the body scales. One uncontinuous row of 7-12 (x = 10.2) precloacal pores. In nuptial colored adult males, the body is cobalt blue with a whitish vertebrate line and an orange-red head. In non-nuptial conditions the coloration is more dull and the dorsum olive to bluish with a purple-red head (fig. 9). Females have a yellowish dorsum with orange patched and bands, and a blue head.

Relationships. Within the species, populations from Djibouti and Egypt show *p* divergences of 1.8-2.1%. *Agama spinosa* from Djibouti seems to be more distinct to *A. somalica* sp. n. and show *p* divergences of 5.2-5.6%, while the specimens from Egypt show *p* divergences to A. somalica of 4.3-5.3%. *A. spinosa* from Djibouti show *p* divergences to the more far related *A. lanzai* sp. n. of 6.0-6.2% while *A. spinosa* from Egypt of 6.3-6.4%.

Distribution. This is a wide ranging species, known from Egypt, Sudan, Eritrea, Djibouti and Ethiopia (fig. 3). In Egypt, *A. spinosa* occurs in the granitic and limestone mountain regions of the Eastern Desert and at high elevations including the summit of Gebel Shayib el Banat (2187 m a.s.l.; Goodman and Hobbs, 1994). In Sudan, it is only known from a corridor along the coast (fig. 3). In Eritrea and Ethiopia the species is more widespread again. Former records from northwestern Somalia should refer to *Agama somalica* sp. n.

Ecology. Generally, *A. spinosa* can be found in dry rocky habitats of hilly or mountainous regions (Baha El Din, 2006). Here, it prefers well vegetated *Acacia* shrub wadis and can tolerate fairly arid conditions. *Agama spinosa* is restricted to higher altitudes in the northern parts of its range, but also occurs in lowlands in the southern range (Baha El Din, 2006). In Egypt, the species is rock-dwelling and forms aggregations containing up to eight lizards in a group composed mostly of adult females and juveniles and just one or two adult males (Hussein and Darwish, 2000). However, these data are doubtful as they refer to a locality well outside the distribution range given by Baha el Din (2006) for Egypt. In Ethiopia, individuals were observed occupying a rocky cliff close to river (fig. 9). The breeding biology is widely unknown, but

Figure 9. Male individual of *Agama spinosa* from Asaita, Ethiopia (A) and its habitat (B). This figure is published in colour in the online version.

Table 3. Selected morphological characters of examined species [min-max | average].

Character	*A. spinosa* (n = 24)	*A. bottegi* (n = 3)	*A. lanzai* sp. n. (n = 3)	*A. somalica* sp. n. (n = 7)
SVL	82.5–120.9 | 99.0	93.2–115.0 | 103.4	78.0–102.5 | 93.0	83.9–102.8 | 81.6
TL	124.6–232.2 | 165.2	193.5–234.5 | 214.0	179.0–245.9 | 221.2	146.6–181.8 | 166.0
CRL	7.8–15.9 | 10.9	11.1–14.0 | 12.4	8.9–11.0 | 9.8	9.5–13.0 | 11.2
PP	7–12 | 10.2	9	10	10–12 | 11.1
NCS	7–11 | 8.5	6–7 | 6.3	6–8 | 7	9–12 | 9.9
SaM	58–73 | 63.6	52–60 | 55.3	55–59 | 56.3	67–79 | 74.6
D	48–61 | 55.7	40–43 | 41.7	51–59 | 56	59–75 | 65.3
V	79–96 | 86.8	58–63 | 60.3	80–83 | 81.7	77–107 | 95.6

like in other *Agama* species it lives in harem groups of one dominant male and several females and juveniles (own data). It is a largely insectivorous species, although it may eat some vegetable material. It is generally not found in cultivated land according to Baha El Din (2006), but was found in Asaita (Ethiopia close to the border to Djibouti) in the town center (fig. 9).

Conservation status. *Agama spinosa* is listed as Least Concern by the IUCN, due to its wide distribution across northeastern Africa and because it is not affected by any major widespread threats. Although we restrict *A. spinosa* in its range, we think that it should be still listed as Least Concern as the species still has a large distribution range.

Discussion

Our morphological and genetic analyses support the taxonomic partitioning of *Agama spinosa* into two distinct species: *A. spinosa* and *A. somalica* sp. n. Furthermore, we show that specimens previously identified as *A. bottegi* represent a new species, *A. lanzai* sp. n.

The levels of 16S mtDNA sequence divergence observed for the *spinosa* group are relatively high (between 5% and 7%) compared to other species groups of *Agama*. Wagner et al. (2009a) have shown pairwise divergence between the closely related and morphologically similar *A. agama* and *A. finchi* of 3.2%, or 4.7% between *A. agama* and *A. planiceps*, while the closely related but morphologically distinct *A. weidholzi* and *A. insularis* show 10% pairwise divergence (Wagner et al., 2009b). Pairwise divergences across clades are obligatorily higher and are between e.g., 7% (*A. agama* versus *A. sankaranica*) and 11% (*A. agama* versus *A. boueti*) according to Wagner et al. (2009a).

Agama species are very similar in morphology and generally show high variation of characters (table 3) within species resulting in a large overlap of characters between species (Wagner, 2010). Our PCA analyzes show distinct variations within the species group, and an overlap only within the true *A. spinosa*. We therefore consider the populations from northwestern Somalia and northeastern Somalia as specifically distinct and restrict *A. spinosa* to Egypt, Sudan, Eritrea, Djibouti and Ethiopia (fig. 6). Although *A. spinosa* in its new concept shows morphological variation between populations from Sudan versus those from Eritrea/Djibouti, Ethiopia or Egypt in some of the PCA analyzes, the populations from Djibouti and Egypt only show a low pairwise divergence between 1.8%-2.1%.

The true *Agama bottegi* was only part of the morphological analyses because no tissue samples were available for genetic analysis. However, parsimony analysis of morphological data supports *A. bottegi* as sister to the entire *A. spinosa* group (fig. 6). There is some disagreement among the trees from the morphological cluster analysis, and some trees also place *A. bottegi* sister to *A. lanzai* sp. n., while the parsimony analysis place *A. bottegi* in all trees as sister to the entire *A. spinosa* group. The holotype

of *A. smithi* was not part of the morphological or the genetic analyses, but photographs and characters mentioned in the description are used to discuss the taxonomic status of this name (see species account).

The gravid female coloration of *A. lanzai* sp. n. is remarkable, and only a few other species of *Agama* have females with such brilliant coloration, including *A. impalearis* and *A. atra.* The latter species are not closely related, and therefore the evolution of brilliant female coloration has evolved independently multiple times in *Agama.* Usually, female *Agama* only exhibit orange or yellow lateral bands, or a pattern of yellow ocella and stripes.

The discovery of new *Agama* lizards from the Horn of Africa is not surprising. All African lizards of this group are arid-adapted and arid habitats are ubiquitous in this area. Even though herpetological research in e.g. Somalia dates back to 1881 (G. Revoil's Expedition), the Horn of Africa is one of the most poorly studied areas of the continent (Largen and Spawls, 2006). However, intensive research, especially in Somalia, dates back to the works of Benedetto Lanza in the 1960 to 1970s and since these detailed studies, field surveys have been hampered as a result of political instability throughout the region, although some biodiversity research has continued in Ethiopia (e.g., Largen and Spawls, 2010). Few specimens from Somalia and the border area between Somalia and Ethiopia are known from museum collections, and basic information on ecology, habitat preferences, and behavior remain unstudied for many species throughout the region.

A common distributional pattern in the Horn of Africa is shared among other genera of agamid lizards. Within the *spinosa* group, *A. spinosa* is wide-ranging in Ethiopia, *A. somalica* sp. n. is restricted to northwestern Somalia, and *A. lanzai* sp. n. to northeastern Somalia, while *A. bottegi* is distributed across southern Somalia. This geographic partitioning (excluding southern Somalia species) is observed in *Xenagama* (Wagner et al. in press) and can be interpreted from Lanza (1983, 1990) for other lizard groups such as lacertids, geckos, and skinks. Northern Somalia, and immediately adjacent Ethiopia, is a centre of endemic arid species resulting from an extreme arid climate and partial isolation, with barriers like the sea and high mountains to the west. This is similar to southern Somalia, which is also bordered by sea and mountains and geographically separated from northern parts of the country. Wagner and Bauer (2011) identified the highlands of the Rift Valley as a possible dispersal barrier for ground-dwelling Agamids within the Horn of Africa. The Rift Valley is the contact zone of three large radiations within *Agama*, as species of the Northern, West and East clades occur here (Wagner, 2010). In summary, the Horn of Africa is a hotspot for agamid lizard diversity and harbors a discrete *Agama* radiation similar to that observed for *Acanthocercus* or *Xenagama*. Additional work by the authors is needed to identify species limits and speciation processes within other *Agama* species groups in the region.

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Appendix 1

Material examined.

Agama bottegi. Somalia: MCSN 28548. Lugh; MZUF 24993, 24655. Dinsor.

Agama lanzai sp. n. Somalia: CAS 227496. Karin (10°58.44′N, 49°12.82′E; 325 m); MZUF 23762. Uadi Goddalola; MZUF 6716. between Karim and Galgalo.

Agama smithi. Ethiopia: BMNH 95.12.31.4. between Shebeli and Juba Rivers.

Agama somalica sp. n. Somalia: CAS 225412-13. 7 km N of Boroma (09°59.23′N, 43°07.98′E; 1535 m); CAS 225408-09,

225437-38. Boroma (09°57.11′N, 43°12.48′E; 1420 m); ZFMK 94230. Near Las Geel (09°44.914′N, 44°27.3931′E; 1131 m).

Agama spinosa. Unknown localities: NHMW 14648:1-2. without further locality; ZMB 6238. Wadi Gadireh (locality not localized without doubts but most probably in Egypt). Djibouti: MZUF 36373-74. Dikhil. Egypt: ZFMK 44174. Jebel-Elba-Gebrets. Eritrea: NHMW 24715:1. without further locality; NHMW 35885:1. Af'abet; NHMW 35885:3. Ghinda; MZUF 12244. Metahara (Shewa); NHMW 35885:2; ZFMK 19452-53. Af Abed, 60 km N of Keren, "Gebirgswüste" (= mountain desert), 1000 m. N'akfa. Ethiopia: ZMB 29096. So-Omadu (= Somadu). Sudan: ZFMK 32425-27, 32429-30, 35375, 38400. Erkowit (= Ar Kowit) near Suakin; ZFMK. 40124-26. Arbeiat near Port Sudan.

Appendix 2. Voucher numbers and citation data for specimens used in the study. All sequences are deposited in GenBank.

Sample ID in data matrix	Genbank voucher number and citation	New taxonomy
*A. hartmanni*_Sudan_ZFMK27598	JX668176 (this paper)	
*A. bottegi*_Somalia_CAS227496	JX668157 (this paper)	*Agama lanzai* sp. n.
A. spinosa _Somalia_MVZ241335	JX668213 (this paper)	*Agama somalica* sp. n.
*A. spinosa*_Somalia_MVZ241334	JX668212 (this paper)	*Agama somalica* sp. n.
*A. spinosa*_Djibouti_MVZ236458	GU128461 (Leache et al., 2009)	
*A. spinosa*_Djibouti_MVZ236459	JX668211 (this paper)	
*A. spinosa*_Egypt_JN665065	JN665065 (Geniez et al., 2011)	
*A. spinosa*_Egypt_JN665066	JN665066 (Geniez et al., 2011)	
*A. spinosa*_Egypt_MNCN39988	JX128156 (Goncalves et al., 2012)	
*A. spinosa*_Egypt_MNCN39990	JX128157 (Goncalves et al., 2012)	
*A. tassiliensis*_Algeria_JN665061	JN665061 (Geniez et al., 2011)	
*A. tassiliensis*_Algeria_JN665062	JN665062 (Geniez et al., 2011)	
*A. tassiliensis*_Algeria_JN665063	JN665063 (Geniez et al., 2011)	
*A. tassiliensis*_Niger_JN665064	JN665064 (Geniez et al., 2011)	