Dwarves in a Big World: Two New Species of *Tropiocolotes* (Squamata: Gekkonidae) from the Sahara Desert, with the First Detailed Skull Description of the Genus

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**ABSTRACT.**—The Sahara Desert is the largest ecoregion in Africa, but its biodiversity in general, and reptile biodiversity in particular, are only superficially known and probably grossly underestimated. The dwarf-lizard genus *Tropiocolotes* is widely distributed in the region. The genus’ taxonomy is plagued by serious nomenclatural problems that have led to a series of misidentifications of specimens in collections and in the literature. Analyzing variation in meristic and osteological characters of the Saharan species of *Tropiocolotes*, we found individuals from Algeria with unique external and internal morphological characters that distinguish them from all other species in the genus. We present a detailed account of these characters and describe two new species of *Tropiocolotes* from Algeria. Additionally, we provide the first detailed description of skulls of the genus, and designate a neotype to *T. steudneri*.

The Sahara Desert is the largest warm desert in the world, covering about 8,200,000 km² over 11 countries, and represents the largest ecoregion in Africa (Olson et al., 2011). The region constitutes the eastern portion of the Saharo-Arabian terrestrial zoogeographic realm (Holt et al., 2013) in the transition between the Palearctic and Afrotropical biogeographic realms (Kreft and Jetz, 2010; Rueda et al., 2013). The Sahara Desert is characterized by highly diverse topographic features (from salt pans below sea level to high-altitude mountain ranges), heterogeneous climate (annual temperature varying from 9.4 to 30.8°C, and total precipitation from near zero to 981 mm; Brito et al., 2014). During the last 10,000 years the Sahara experienced strong climatic oscillations, with multiple dry–wet cycles, regulating biodiversity patterns (Brito et al., 2014). Historically, the region has also suffered long-term political instability. However, the Sahara Desert is often perceived and portrayed as a homogeneous landscape with low alpha and beta diversity, and attracts less conservation concern in comparison with other regions in Africa and in the world (Brito et al., 2016; Durant et al., 2012; Roll et al., 2017; Sow et al., 2014).

The dwarf-lizard genus *Tropiocolotes* Peters, 1880 comprises 13 recognized species distributed along the Saharo-Arabian zoogeographic realm, from western Africa (Mauritania) to Asia (Iran; Machado et al., 2018; Ribeiro-Júnior et al., 2022). Despite a few recent taxonomic studies (Krause et al., 2013; Machado et al., 2018; Rajabizadeh et al., 2018; Rouagni et al., 2018; Wilms et al., 2010; Ribeiro-Júnior et al., 2022), deep nomenclatural problems still persist in the genus (see Bauer et al., 2017: 198–199, 266). The holotypes of three species in the genus (*T. nattereri*, *T. steudneri*, and *T. tripolitanus*) are considered lost; a lectotype was designated for *T. tripolitanus* (Bauer and Günther, 1991), and a neotype for *T. nattereri* (Ribeiro-Júnior et al., 2022), but for *T. steudneri* a designation of a type specimen is still missing. To aggravate the situation, the genus is distributed along an area of historical major political-religious conflicts and little research effort, and most of it is inaccessible to field expeditions (Brito et al., 2014). These issues, and the absence of a comprehensive taxonomic revision of this genus (which was never revised), have led to a series of misidentification of specimens in collections and in the literature (Baha el Din, 1994, 2006; Bauer et al., 2017; Pasteur, 1960; Shifman et al., 1999).

During a review of the Saharan specimens housed in European and North American collections, we found individuals of *Tropiocolotes* from Algeria, identified sometimes as *T. steudneri*, other times as *T. tripolitanus*, but not matching the diagnostic characters of either. The specimens also do not agree with the diagnostic characters of *T. nubicus* recently reported from southern Algeria by Machado et al. (2021). We therefore undertook a comprehensive comparison between the Algerian specimens and *T. steudneri*, *T. nubicus*, and *T. tripolitanus tripolitanus*, as well as other African species of the genus, using external and internal morphological characters. Here we present the results of the comparisons, with the first detailed description of skull morphology of *Tropiocolotes*. It is also the first study to consider type-series of *Tropiocolotes* in comparisons and analyses of external morphology. Two new species to the genus are here recognized and described, and a neotype to *T. steudneri* is designated. Our study is part of a project that is producing the first comprehensive taxonomic revision of the genus *Tropiocolotes*.

**MATERIAL AND METHODS**

External Morphology (Meristic Characters, Measurements, and Coloration Pattern).—Specimens of *Tropiocolotes* from Algeria were carefully compared with type-series and descriptions of the other African species, including the lectotype and a paralectotype of *T. tripolitanus tripolitanus*, the holotypes of *T. algericus*, *T. nubicus*, *T. somalicus*, *T. tripolitanus apoklomax*, and *T. t. occidentalis*, and the paratypes of *T. nubicus* and *T. tripolitanus occidentalis*. We further examined *T. steudneri* specimens from Sudan, presumably the region where the holotype was collected (see Bauer et al., 2017: 198). In total, we examined 49 specimens of *Tropiocolotes* (13 species of *Tropiocolotes* spp., 5 of *T. algericus*, 2 of *T. nubicus*, 1 of *T. somalicus*, 1 of *T. tripolitanus apoklomax*, 4 of *T. t. occidentalis*, 3 of *T. t. tripolitanus*, and 20 of *T. steudneri*) from Algeria, Libya, Mali, Sudan, and Western Sahara. Specimens are deposited in the following herpetological collections: the California Academy of Sciences, San Francisco, USA (CAS); the Museum of Comparative
TWO NEW SPECIES OF TROPICOCOLOTES

Zoology, Cambridge, USA (MCZ); the Field Museum of Natural History, Chicago, USA (FMNH); the Muséum National d’Histoire Naturelle, Paris, France (MNHN-RA); the Zoological Research Museum Alexander Koenig, Bonn, Germany (ZFMK); the Museum für Naturkunde, Berlin, Germany (ZMB); the Natural History Museum, London, UK (BMNH); the Naturhistorisches Museum Wien, Vienna, Austria (NMW); and the Museo Nacional de Ciencias Naturales, Madrid, Spain (MNCN). Museum acronyms follow Sabaj (2016). A list of specimens in type-series is presented below and referred specimens in the Supporting Information. Comparisons with other species in the genus, except the ones mentioned above, are based on the literature using morphological data of type-series (in: Baha el Din 1999, 2001; Cherchi and Spano, 1963; Krause et al., 2013; Loveridge, 1947; Machado et al. 2018; Papenfuss, 1969; Parker, 1942; Peters, 1869; Rajabizadeh et al., 2018; Rounaghi et al., 2018; Wilms et al., 2010; Ribeiro-Júnior et al., 2022). Standardization of the character nomenclature in taxonomic studies is essential to avoid overlapping characters and/or duplications of names in future systematic studies (see Ribeiro-Júnior, 2018).

Osteology (Skull Morphology).—As the skull of the genus Tropiocolotes has never been described in detail, we provide a comprehensive description for a paratype (ZFMK 2350) of the first new species described herein. For the holotype (CAS 138662) of the second species newly described here, this description serves as a basis for delineating the skull, and we concentrate this description only on the differences to the skull of ZFMK 2350. The same is true for T. steudneri, of which we have examined the skulls of six individuals (ZFMK 33840, 33843, 33844, 33846, 33854, 33856) and only discuss the interspecific differences in the skull morphology observed in this sample compared with two paratypes of the first new species described herein (ZFMK 2350, 2351). The osteological information is based on high-resolution micro-CT scans. The scan of ZFMK 2350 was performed with a Bruker SkyScan 1173 at ZFMK at an X-ray beam with 43 kV source voltage and 114 μA current without the use of a filter. Rotation steps of 0.3° were used with a frame averaging of 4, recorded over a 180° rotation, resulting in 800 projections of 500 msec exposure time each and a total scan duration of 41 min 52 sec. The magnification setup generated data with an isotropic voxel size of 6.74 μm. The CT-dataset was reconstructed using N-Recon software vers. 1.7.1.6 (Bruker MicroCT). The scan of CAS 138662 was performed with a Nikon XT H 225ST at the Steinhardt Museum of Natural History, Tel Aviv University, Tel Aviv, Israel. For this scan an X-ray beam with 170 kV source voltage and 82 μA current was used and 1,200 projections were produced of 500 msec exposure time each and a total scan duration of 10 min. The magnification setup generated data with an isotropic voxel size of 17.2 μm. The CT-dataset was reconstructed using software x-tc CT Pro 3D vers. XT 5.3.2. Both scans were rendered in three dimensions and segmented to separate bones with the aid of Amira visualization software (FEI, Thermo Fisher Scientific).

For information on intraspecific variation we have CT-scanned for each new species another skull of a paratype at ZFMK with similar settings and reconstruction details as ZFMK 2350. For the cranial description of T. steudneri and comparison six specimens of the species (ZFMK 33840, 33843, 33844, 33846, 33854, 33856) were CT-scanned. For comparison with further closely related species we CT-scanned the lectotype (ZMB 9668A), paralectotype (ZMB 9668B), and a further specimen (NMW 172982) of Tropiocolotes tripolitanus tripolitanus, and a paratype of T. nubicus (FMNH 256869). All these specimens (except FMNH 256869) were scanned at ZFMK either on a Bruker SkyScan 1173 (ZMB 9668A, 9668B, ZFMK 33840, 33843, 33844, NMW 172982; scan parameters: 35–43 kV source voltage and 0.01 mm), 8

The distribution map was produced using QGis Las Palmas (vers. 2.18.3; available from http://www.qgis.org/es/site/) and occurrence data of all specimens studied; geographical coordinates are given in WCS 1984 data.

Description format of the new species followed taxonomic literature of the genus, with modifications in an attempt to create a standardization of the nomenclature of characters. For example, we used internasals as the standardized name of the scales also mentioned as “supranasals” and “postrostrals” in the literature; nasals, instead of “nasalia” or “post nasals”; submandibular scales, instead of “third pair of postmentals” (see Baha el Din, 1999, 2001; Krause et al., 2013; Machado et al., 2018; Rajabizadeh et al., 2018; Rounaghi et al., 2018; Wilms et al., 2010; Ribeiro-Júnior et al., 2022). Standardization of the character nomenclature in taxonomic studies is essential to avoid overlapping characters and/or duplications of names in future systematic studies (see Ribeiro-Júnior, 2018).

Meristic characters are: dorsal scales, counted from the forelimbs to the hind limbs level; ventrals, from the forelimbs to the hind limbs level; scale rows around the midbody; interorbitals, scales across the interorbital region at level of the midorbits; supralabials; infralabials; gular scales from the postmentals to the mandibular level; lamellae under the 4th finger; lamellae under the 4th toe. The measurements are (abbreviations in parentheses): snout–vent length (SVL), from the border of the cloaca to the tip of the snout; axilla–grin length (AGL), from the anterior margin of the hind limb to the posterior margin of the forelimb; head depth (HD) at the highest point dorsoventrally; head width (HW) at the widest point; head length (HL) from the anterior margin of the tympanic aperture to the tip of the snout; neck length (NL), from the posterior margin of the tympanic aperture to the anterior margin of the forelimb; Shank length (SHL); tail length (TL). All measurements were taken with digital callipers (±0.01 mm), and all scale counts and other nonmetric morphological characters were observed using a stereomicroscope. Sex was tentatively determined based on general evidence (e.g., presence of hemipenial sacs in the base of the tail in adult males, and well-developed calcium sacs in the sides of the neck in adult females), because specimens of the genus Tropiocolotes do not present clear external characters related to sexual dimorphism (sex is then presented with an asterisk *). Meristic characters and measurements for Tropiocolotes nubicus were obtained from Baha el Din (1999). Data from literature were only used in cases we did not have the opportunity to examine type-specimens ourselves, to minimize discrepancies and differences stemming from collector bias, and to avoid using non-updated identifications that can modify morphological ranges on species variation.

Quantitative morphological distinctness among examined species was tested using univariate and multivariate statistics. Meristic characters and measurements were first analyzed using univariate, nonparametric tests (because model residuals are not normally distributed): a Kruskal–Wallis test to compare the medians of each character between the species, and the Mann–Whitney post hoc test to compare medians between pairs of groups. In addition, we performed multivariate principal components analyses (PCA) to examine the degree of separation between species, including all examined specimens and all meristic characters. Statistical analyses were implemented in PAST vers. 3.26 software (Hammer et al., 2001).

Coloration in preservative was described on the basis of the holotypes, and variations thereof on the basis of specimens deposited in the herpetological collections mentioned above.
RESULTS

Statistical Analyses of Meristic Characters.—Univariate and multivariate statistical analyses revealed clear morphological divergence in meristic characters among the studied species. Comparisons using the Kruskal–Wallis test revealed significant differences in the median values between species for all meristic characters and two measurements, and Mann–Whitney pairwise comparisons revealed significant differences for all meristic characters and two head measurements between the new species and Tropiocolotes algericus, T. tripolitanus occidentalis, T. tripolitanus tripolitanus, and T. steudneri (Tables 1, 2). The PCA, in which all individuals and all meristic characters were considered, showed a complete separation among the studied species (Fig. 1), except between T. chirioi sp. nov. and T. tripolitanus tripolitanus. The first two components explained 95.7% of the total variance in the characters (91.6 and 4.1%, respectively), and the most important two components explained 95.7% of the total variance in the measurement variations, detailed cranial descriptions and Tropiocolotes chirioi (see below), we describe below two new species of informative characters) and osteological characters (skull morphology; see below), we describe below two new species of Tropiocolotes by the combination of the following characters: 1) strongly keeled dorsal and ventral scales; 2) keeled dorsal head scales; 3) 43–46 scales around midbody; 4) one pair of postmental scales; 5) 1st pair of submandibular scales large, distinguishable from gular scales, but similar in size to scales of 2nd pair of submandibulars; 6) paired large brown dots on dorsal surface of neck and body; 7) 8–10 premaxillary tooth loci; 8) 23–28 maxillary tooth loci; 9) 28–30 dentary tooth loci; 10) small to medium-sized premaxilla-maxilla aperture; 11) transverse posterior margin of frontal slightly bowed; 12) anterioirmost part of septomaxilla not contacting maxilla and vomer; 13) medial margin of pterygoid palatine process straight; 14) laterally pointing shaft of stapes straight; 15) small, triangular crista alaris of prootic; 16) mental foramina of dentary located between 3rd/4th and 19th/21st tooth.

Comparison with Other Species.—Tropiocolotes chirioi sp. nov. differs from T. hormozganiensis, T. nattereri, T. naybandensis, T. nubicus, T. steudneri, T. wolfgangboehmi, T. tassiliensis sp. nov., and T. yomtovi in having strongly keeled dorsal and ventral scales (vs. smooth or faintly keeled dorsal scales, and smooth ventral scales). It differs from T. confusus and T. scortecci, in having one pair of postmental scales (vs. two pairs), and from T. bisharicus in having keeled dorsal head scales (vs. smooth scales). Tropiocolotes chirioi sp. nov. differs from T. algericus, T. sonalicus, T. tripolitanus apoklaxon, and T. tripolitanus occidentalis in having 43–46 scales around midbody (vs. 40–42 in T. algericus, 35–41 in T. sonalicus, 46–54 in T. tripolitanus apoklaxon, and 40–41 in T. tripolitanus occidentalis); it also differs from T. algericus and T. tripolitanus occidentalis in having 1st pair of submandibulars scales larger and clearly distinguishable from gular scales (vs. 1st pair of submandibulars similar in size and hardly distinguishable from gular scales; Fig. 4A,B,D), and it also differs from T. sonalicus and T. tripolitanus apoklaxon in having series of paired large brown dots on dorsal surface of neck and body (vs. absence of large dark dots, but instead scattered darker brown scales on dorsal surface of neck and body; Fig. 4E,F,H). Tropiocolotes chirioi sp. nov. differs from T. tripolitanus tripolitanus in having 43–46 scales around midbody (vs. 42), 1st pair of submandibulars scales similar in size to 2nd pair of submandibular scales (vs. 1st pair of submandibulars scales very large, about twice the size of 2nd pair of submandibulars; Fig. 4A,C), and in having paired large brown dots on dorsal surface of neck and body (vs. absence of large dark dots, but instead scattered darker brown scales on dorsal surface of neck and body; Fig. 4E,G). A summary of other differences in meristic characters is presented in Table 1.

Based on skull characters, Tropiocolotes chirioi sp. nov. differs from T. tassiliensis sp. nov. in having fewer premaxillary tooth loci (8–10, vs. 10–11); from T. tassiliensis sp. nov. and T. steudneri in having fewer maxillary tooth loci (23–28, vs. 28–31 in T. tassiliensis sp. nov., and 28–34 in T. steudneri); from T. tassiliensis sp. nov., T. tripolitanus tripolitanus, T. steudneri, and T. nubicus in having 28–30 dentary tooth loci (vs. 33–37 in T. tassiliensis sp. nov., 32–36 in T. t. tripolitanus, 31–39 in T. steudneri, and 31 in T. nubicus); from T. nubicus in having small to medium-sized premaxilla-maxilla aperture (vs. large); from T. tassiliensis sp. nov., T. t. tripolitanus, and T. steudneri in having a slightly bowed transverse posterior margin of frontal (vs. almost
TABLE 1. Summary of the variation in meristic characters in *Tropiocolotes chirioi* sp. nov., *T. tassiliensis* sp. nov., *T. algericus*, *T. tripolitanus occidentalis*, *T. tripolitanus tripolitanus*, and *T. steudneri*. Counts are presented as minimum–maximum (mean ± standard deviation); *n* = total number of specimens studied; * = significant differences among all species in the Kruskal–Wallis test (*H*; *P* < 0.05; *df* = 5); significant contrasts in the Mann–Whitney pairwise comparisons (*P* < 0.05) are presented by the three first letters of the epithets of species differing from the focal one. NA = not significantly different from any other species. *Tropiocolotes tripolitanus tripolitanus* (tri) was not included in the Kruskal–Wallis test for midbody, interorbitals, and infralabials, because it showed no variance in these characters. Data for *Tropiocolotes nubicus* represent from the type-series and are taken from Baha el Din (1999). These data were therefore not included in morphological statistical analyses. Data not available in Baha el Din (1999) are presented with a question mark (?).

<table>
<thead>
<tr>
<th>Character</th>
<th><em>T. chirioi</em> sp. nov. (n = 5)</th>
<th><em>T. tassiliensis</em> sp. nov. (n = 8)</th>
<th><em>T. algericus</em> (n = 4)</th>
<th><em>T. tripolitanus occidentalis</em> (n = 4)</th>
<th><em>T. tripolitanus tripolitanus</em> (n = 2)</th>
<th><em>T. steudneri</em> (n = 18)</th>
<th><em>T. nubicus</em></th>
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<tr>
<td>Dorsals*</td>
<td>37–39 (37.8 ± 0.8)</td>
<td>51–59 (53.2 ± 3)</td>
<td>35–39 (37.2 ± 1.7)</td>
<td>32–35 (33.2 ± 1.2)</td>
<td>39; 41</td>
<td>61–66 (63.5 ± 2)</td>
<td>52–59 (56.1 ± 2)</td>
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<tr>
<td>Mann–Whitney (H = 35.77, <em>P</em> &lt; 0.01)</td>
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<td>Ventralis*</td>
<td>51–54 (52.2 ± 1.3)</td>
<td>49–59 (53.5 ± 3.5)</td>
<td>47–51 (49.2 ± 1.7)</td>
<td>44–51 (46.7 ± 3.1)</td>
<td>52; 53</td>
<td>52–62 (57.1 ± 2.3)</td>
<td>?</td>
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<tr>
<td>Mann–Whitney (H = 26.73, <em>P</em> &lt; 0.01)</td>
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<td>Midbody*</td>
<td>43–46 (44 ± 1.2)</td>
<td>46–53 (50.7 ± 2.5)</td>
<td>40–42 (41.2 ± 0.9)</td>
<td>37–40 (38.2 ± 1.5)</td>
<td>42</td>
<td>52–60 (53.2 ± 2.3)</td>
<td>49–59 (54.4 ± 3.0)</td>
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<tr>
<td>Mann–Whitney (H = 31.59, <em>P</em> &lt; 0.01; except tri)</td>
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<td>Interorbitals*</td>
<td>10–12 (11.4 ± 0.9)</td>
<td>12–14 (13 ± 0.7)</td>
<td>9–11 (10.2 ± 0.9)</td>
<td>9; 10</td>
<td>11</td>
<td>12–15 (13.2 ± 0.9)</td>
<td>10–13 (12.5 ± 0.9)</td>
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<td>Mann–Whitney (H = 23.74, <em>P</em> &lt; 0.01; except tri)</td>
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<td>Supralabials*</td>
<td>9–11 (10.1 ± 0.7)</td>
<td>8–10 (8.8 ± 0.6)</td>
<td>8–10 (9.1 ± 0.6)</td>
<td>7–9 (7.6 ± 0.7)</td>
<td>8–11 (9.3 ± 0.6)</td>
<td>8–10 (9.0 ± 0.5)</td>
<td>7–9 (7.4 ± 0.8)</td>
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<td>Mann–Whitney (H = 32.96, <em>P</em> &lt; 0.01)</td>
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<td>Infralabials*</td>
<td>7–9 (6 ± 0.7)</td>
<td>6–9 (7.5 ± 0.8)</td>
<td>6–9 (7.6 ± 1.1)</td>
<td>6–8 (6.7 ± 0.7)</td>
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<td>7–9 (7.6 ± 0.6)</td>
<td>7–9 (7.4 ± 0.8)</td>
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<td>Mann–Whitney (H = 13.54, <em>P</em> &lt; 0.01; except tri)</td>
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<tr>
<td>Gulars*</td>
<td>29–35 (31.2 ± 2.3)</td>
<td>30–35 (31.6 ± 2.9)</td>
<td>NA</td>
<td>28–35 (30.7 ± 3.1)</td>
<td>31; 32</td>
<td>28–42 (35.3 ± 3.9)</td>
<td>20–28 (25.1 ± 1.8)</td>
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<td>Mann–Whitney (H = 16.48, <em>P</em> &lt; 0.01)</td>
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<td>Lamellae under 4th finger*</td>
<td>11–13 (12.3 ± 0.7)</td>
<td>12–16 (13.8 ± 0.9)</td>
<td>10–13 (11.6 ± 1.3)</td>
<td>10–12 (10.9 ± 0.6)</td>
<td>11; 12</td>
<td>13–17 (15.6 ± 1)</td>
<td>?</td>
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<tr>
<td>Mann–Whitney (H = 63.20, <em>P</em> &lt; 0.01)</td>
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<tr>
<td>Lamellae under 4th toe*</td>
<td>15–16 (15.5 ± 0.5)</td>
<td>16–21 (18 ± 1.3)</td>
<td>14–16 (15.1 ± 0.8)</td>
<td>12–16 (14 ± 1.3)</td>
<td>14; 15</td>
<td>18–23 (20.6 ± 1.1)</td>
<td>17–19 (18.5 ± 0.6)</td>
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<tr>
<td>Mann–Whitney (H = 66.74, <em>P</em> &lt; 0.01)</td>
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TWO NEW SPECIES OF *TROPICOLOTTES*
Table 2. Summary of the variation in measurements in *Tropiocolotes chirioi* sp. nov., *T. tassiliensis* sp. nov., *T. tripolitanus occidentalis*, *T. t. tripolitanus*, and *T. steudneri*. Measurements are presented as minimum–maximum (mean ± standard deviation); *n* = total number of specimens studied; * = significant differences among all species in the Kruskal–Wallis test (*H*; *P* < 0.05; df = 4); significant contrasts in the Mann–Whitney pairwise comparisons (*P* < 0.05) are presented by the three first letters of the epithets of species differing from the focal one. NA = not significantly different from any other species. Measurements of only intact and non-regenerated tails are presented; tail was not considered in analyses. Measurements are in millimeters (mm). Data for *Tropiocolotes nubicus* represent from the type-series and are taken from Baha el Din (1999). These data were therefore not included in morphological statistical analyses. Data not available in Baha el Din (1999) are presented with a question mark (?).

<table>
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<tr>
<th></th>
<th><em>T. chirioi</em> sp. nov.</th>
<th><em>T. tassiliensis</em> sp. nov.</th>
<th><em>T. tripolitanus occidentalis</em></th>
<th><em>T. tripolitanus tripolitanus</em></th>
<th><em>T. steudneri</em> (n = 20)</th>
<th><em>T. nubicus</em> (n = 2)</th>
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<tr>
<td>Snout–vent length</td>
<td>25.3–35.7 (31.2 ± 4)</td>
<td>17.1–34.8 (27.5 ± 7.4)</td>
<td>27.5; 29.7</td>
<td>27.8; 28.3</td>
<td>18.26–32.68 (28.12 ± 3.38)</td>
<td>15.6–30.5 (26.1 ± 3.8)</td>
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<tr>
<td>Axilla–groin length</td>
<td>11.6–15.5 (14.1 ± 1.7)</td>
<td>7.8–17.2 (13 ± 3.9)</td>
<td>14.2; 16.9</td>
<td>12.5; 14.1</td>
<td>7.6–16.9 (13.4 ± 2.21)</td>
<td>?</td>
</tr>
<tr>
<td>Head depth*</td>
<td>3.6–4.5 (4.1 ± 0.3)</td>
<td>2.4–3.7 (3.3 ± 0.6)</td>
<td>7.7; 8.4</td>
<td>6.8; 6.9</td>
<td>5.06–7.71 (6.8 ± 0.7)</td>
<td>?</td>
</tr>
<tr>
<td>Mann–Whitney</td>
<td>ste; tas</td>
<td>chi</td>
<td>ste</td>
<td>NA</td>
<td>ste; tas</td>
<td>chi; occ</td>
</tr>
<tr>
<td>Head width</td>
<td>5–6.6 (5.7 ± 0.6)</td>
<td>3.6–5.6 (4.9 ± 0.9)</td>
<td>4.7; 5.2</td>
<td>5.0; 5.2</td>
<td>3.34–5.6 (4.81 ± 0.55)</td>
<td>?</td>
</tr>
<tr>
<td>Neck length</td>
<td>6.4–8.5 (7.8 ± 0.8)</td>
<td>5.1–7.8 (6.9 ± 1.2)</td>
<td>3.5; 3.8</td>
<td>3.1; 3.4</td>
<td>2.08–3.64 (2.96 ± 0.38)</td>
<td>?</td>
</tr>
<tr>
<td>Shank length</td>
<td>ste; tas</td>
<td>chi</td>
<td>ste</td>
<td>NA</td>
<td>ste; tas</td>
<td>chi; occ</td>
</tr>
<tr>
<td>Tail length</td>
<td>28.7; 38.7 (n = 2)</td>
<td>–</td>
<td>32.6; 35.5 (n = 2)</td>
<td>34.4; 35.4 (n = 2)</td>
<td>13.4; 32.9 (n = 2)</td>
<td>18.1–43.6 (34.9 ± 8)</td>
</tr>
</tbody>
</table>
FIG. 1. Principal Component Analysis (PCA) of meristic characters between specimens of Tropiocolotes algericus (pink), T. tripolitanus occidentalis (purple), T. tripolitanus tripolitanus (green), T. steudneri (yellow), T. chirioi sp. nov. (blue), and T. tassiliensis sp. nov. (red).

FIG. 2. (A) Dorsal and (B) ventral views of the holotype of Tropiocolotes chirioi sp. nov. (MNHN-RA-1997.5086). Scale bar: 1 cm.

FIG. 3. (A) Dorsal, (B) ventral, and (C) lateral views of the head and neck of the holotype of Tropiocolotes chirioi sp. nov. (MNHN-RA-1997.5086). Scale bar: 1 cm.
straight transverse posterior margin of frontal, or slightly rounded medially, forming a slightly sinuous suture with the parietal, in *T. tassiliensis* sp. nov., medially rounded, forming a sinuous frontoparietal suture with the anterior margin of the parietals, in *T. t. tripolitanus*, and almost straight in *T. steudneri*);

from *T. tassiliensis* sp. nov., *T. t. tripolitanus*, *T. steudneri*, and *T. nubicus* in having the anteriormost part of septomaxilla not contacting maxilla and vomer (vs. in contact); from *T. tassiliensis* sp. nov., *T. steudneri*, and *T. nubicus* in having straight medial margin of pterygoid palatine process (vs. slightly concavely curved in *T. tassiliensis* sp. nov. and *T. nubicus*, and concavely curved in *T. steudneri*); from *T. t. tripolitanus* in having straight laterally pointing shaft of stapes (vs. slightly curved backwards and extended at lateral end);

from *T. tassiliensis* sp. nov., *T. t. tripolitanus*, *T. steudneri*, and *T. nubicus* in having straight medial margin of pterygoid palatine process (vs. slightly concavely curved in *T. tassiliensis* sp. nov. and *T. nubicus*, and concavely curved in *T. steudneri*); from *T. t. tripolitanus* in having straight laterally pointing shaft of stapes (vs. slightly curved backwards and extended at lateral end);

from *T. tassiliensis* sp. nov., *T. t. tripolitanus*, *T. steudneri*, and *T. nubicus* in having small, triangular crista alaris of prootic (vs. large, rounded in *T. t. tripolitanus* and *T. nubicus*, large, rounded or triangular in *T. tassiliensis* sp. nov., and large, triangular in *T. steudneri*); from *T. tassiliensis* sp. nov. and *T. nubicus* in having the mental foramina of the dentary located between the 3rd/4th and the 19th/21st tooth (vs. between the 3rd/4th and the 23rd/24th tooth in *T. tassiliensis* sp. nov., and between the 4th/5th and the 20th tooth in *T. nubicus*).

**Description of Holotype.**—Body cylindrical; long and wide head, neck and body; long snout; limbs well developed; long tail (Fig.

**Fig. 4.** (A) Holotype of *Tropiocolotes chirioi* sp. nov. (MNHN-RA-1997.5086), (B) holotype of *T. algericus* (MCZ-R 27485), (C) holotype of *T. tripolitanus tripolitanus* (ZMB 9668A), (D) holotype of *T. tripolitanus* occidentalis (BMNH 1946.8.24.49), (E) holotype of *T. chirioi* sp. nov. (MNHN-RA-1997.5086), (F) holotype of *T. somalicus* (BMNH 1946.8.23.35), (G) holotype of *T. t. tripolitanus* (ZMB 9668A), and (H) holotype of *T. t. apoklomax* (CAS 103209).

**Fig. 5.** Dorsal view of three specimens of *T. chirioi* sp. nov. (A–C) and two specimens of *T. tassiliensis* sp. nov. (D, E): (A) MNHN-RA-1997.5088, (B) MNHN-RA-1973.1306, (C) ZFMK 2351, (D) ZFMK 2351, and (E) ZFMK 2352.

2). Adult specimen, presumably female (absence of hemipenial sacs; presence of calcium sacs).

Rostral large, convex, polygonal, partially divided by a median cleft, and in broad contact with internasals, upper nasal, and 1st infralabial. Viewed dorsally, rostral is about 1.5 times wider than long, and posteriorly reaches beyond nostril by about a third of its length. A pair of relatively small internasal scales in contact with each other medially, forming a long suture with median cleft of rostral, bordered posteriorly by three post-internasal scales (plus one very small scale), irregular in shape and size. Frontal scales polygonal, keeled, and imbricate, differing in size. Supraocular scales irregularly hexagonal, keeled, and imbricate. Interorbital scales polygonal, longer than wide, similar in size to adjacent supraoculars. Twelve transverse scales across medial interorbital region. Palpebral fold with keeled and imbricate scales. Supraciliary scales keeled and imbricate. Parietal and occipital scales irregularly hexagonal, keeled, imbricate, and differing in size. Scales on dorsal surface of neck keeled and imbricate.

Nasal directed lateroventrally, bordered by four scales: rostral anteriorly and ventrally, upper nasal dorsally, lower nasal posteriorly, and 1st infralabial ventrally and posteriorly. Two nasal scales, slightly longer than wide, upper ones about three times larger than lower nasals and similar in size or slightly smaller than internasals. Loreal scales similar in shape.
and size to frontal scales. Eye large, pupil vertical. Temporal scales keeled, imbricate, feebly granular near eyes. Large, round ear opening. Scales on lateral surface of neck keeled, imbricate, in oblique and longitudinal rows. Supralabials 10–11, all longer than tall; 5th to 10th or 11th under orbit.

Mental large, convex, pentagonal, wider than long and wider than rostral, forming an acute angle posteriorly reaching to level of suture between 1st and 2nd infralabials. One pair of large postmentals, with scales irregularly hexagonal, as wide as long, in broad contact with each other medially, contacting 1st and 2nd infralabials. Three submandibular scales on each side, 1st ones irregularly trapezoidal, similar in size to scales of 2nd pair of submandibulars. Gular scales irregularly hexagonal, keeled, subimbricate, nearly subequal (lateral scales slightly larger than medial ones), gradually becoming imbricate posteriorly to level of end of mandible and larger towards forelimb insertion. Twenty-nine gular scales. Infralabials 8–9, first three rectangle-shaped, taller than long, 4th to 8th or 9th with irregular margins ventrally, decreasing in size gradually from 3rd to 8th or 9th, 4th to 8th or 9th under orbit.

Dorsal scales keeled, imbricate, in oblique and longitudinal rows, 38 middorsal scales from anterior margin of forelimbs to posterior margin of hind limbs. Flank scales similar in shape to dorsolateral scales, 44 scales around midbody. Ventral scales keeled, imbricate, smaller than scales on dorsum and flanks, in oblique and longitudinal rows, 52 midventral scales from anterior margin of forelimbs to preanal plate. Preanal pores absent. Tail complete and intact, with keeled, imbricate scales on dorsal, lateral, and ventral surfaces, similar in size to scales on dorsal surface of body. Two developed postanal sacs on ventral surface of body, directed posterodorsally on ventrolateral surfaces of base of tail on each side. Scales on dorsal surface of limbs keeled, imbricate, smaller than scales on dorsal surface of body. Scales on ventral surface of limbs keeled, imbricate, smaller than scales on dorsal surface of limbs. Ventral aspect of fingers and toes with single and tricarinate subdigital lamellae, 12–13 lamellae under 4th fingers, and 16 lamellae under 4th toes. Claws long and distinct.
Measurements of Holotype (in Millimeters).—SVL = 35.7; AGL = 15.5; HD = 4.5; HW = 6.6; HL = 8.5; NL = 5.9; ShL = 5; TL = 38.7.

Coloration in Preservative (Based on Holotype).—Dorsal surface of head cream, with few, small, sparse brown dots. Dorsal surface of neck cream, with small, sparse brown dots, and paired large brown dots. A wide brown band from rostral and nasals, along loreal region, passing through eye, medial temporal region, lateral surface of neck, to anterior region of body. Dorsal surface of body cream, with six paired, large brown dots, and small, sparse brown dots, irregularly intermixed with a few white dots. Tail complete and intact: dorsal surface of tail cream, with 10 wide, transverse brown bands. Dorsal surface of forelimbs, hind limbs, hands and feet cream, with irregular brown and white bands. Flanks cream, with brown dots. Ventral surface of head, neck, body, tail and limbs cream.

Variation.—Tables 1 and 2 present a summary of means and the variation in meristic characters and measurements. There is little variation in color pattern among specimens: MNHN-RA-1997.5088 has six large brown dots on the left side of body surface, and seven on the right side (Fig. 5A); MNHN-RA-1973.1306 has 12 brown bands on dorsal surface of tail (Fig. 5B), and ZFMK 2351 has 11 (Fig. 5C). The measurements of each specimen are presented in Supporting Information (Table S1).

Cranial Osteology.—Detailed description of the skull of Tropiocolotes chirioi sp. nov. is based on a micro-CT scan of the paratype ZFMK 2350 (Figs. 6-10).

The unpaired premaxilla (pm, Figs. 6–9) forms the anterior tip of the snout and the anteromedial margin of each fenestra exornaina. It contacts the nasals dorsally, the maxillae laterally and the vomers posteromedially. Ventrally, the premaxilla bears 10 tooth loci along the anterior edge of the bone. However, every second one seems to be a replacement tooth bud and accordingly there are only 5 fully developed teeth. Behind this row of teeth there is another row with 5 replacement teeth buds.
Posteriorly the palatal processes of the premaxilla extend to contact the anterior tip of the vomers posteromedially, dorsally they are overlain by the maxillary lappet of the maxilla. The maxillary facets contact the anterior part of the maxilla anterolaterally and posterolaterally, forming a small premaxilla-maxilla aperture on each side between both bones. The posterodorsally oriented ascending nasal process of the premaxilla is long and thin, its posterior half tapers and extends between the anterior third of the median suture of the nasals.

The maxillae (m; Figs. 6–9) occupy most of the anterolateral aspect of the skull anterior to the orbits. In lateral view, each maxilla extends approximately 37% the length of the skull. The maxilla articulates with the premaxilla anteriorly, the nasal dorsally, the frontal posterodorsally, the prefrontal posteriorly, the vomer anteromedially, the palatine medially, the ectopterygoid, and the jugal posteromedially. The left maxilla bears 28 and the right maxilla bears 26 tooth loci. The anteromedial maxillary lappet of each maxilla approaches its counterpart with only a very small distance between them, and each overlaps the palatal process of the premaxilla. In ventral view, the lateral border of the maxilla, along the tooth row is slightly curved and the maxillary shelf has a wavy medial edge that contacts the anterolateral edge of the vomer only in the anterior region and the anterolateral edge of the palatine in the posterior region, forming the elongate fenestra exochoanalis along most of its medial edge. The preorbital facial process of each maxilla is tall and broad, anteriorly it forms the posterior border of the osseous naris, the posterior edge forms the anterior and ventral wall of the lacrimal foramen. The anterior margin of the facial process is less than one-third of the height of the posterior margin and is almost straight with a sharp transition to the dorsal margin of the facial process. The posterior margin is tall and nearly vertical in lateral view, deflecting slightly towards its highest point. It is in broad contact with the prefrontal along its entire height. Dorsally, the facial process is in broad contact with the nasal anteriorly and in narrow contact with the frontal posteriorly. Slightly below the facial process the maxilla bears a series of five to six foramina. The posterior process of the maxilla tapers posteriorly and is overlapped by the jugal and the ectopterygoid medial to it.

The nasals (n; Figs. 6–9) are paired, distinctly longer than broad, and in medial contact, with the internasal suture representing approximately two-thirds the length of each nasal. Anteromedially each nasal bears a long, thin process, and the processes of both nasals together form a channel into which the dorsal half of the ascending process of the premaxilla fits, framing it ventrally and laterally. Posteriorly, the nasals overlap...
the anteriormost part of the frontal with which they form a V-shaped suture, in that the almost right-angled anteromedial apex of the frontal extends between the nasals, and the posterior end of each nasal tapers posterolaterally. The lateral margin of each nasal articulates with the facial process of the maxilla along most of its length and is separated from the prefrontal by a posterodorsal extension of the facial process of the maxilla. Anteriorly, the nasals form the dorsal rim of the fenestra exornarina.

In lateral view, the prefrontals (pref; Figs. 6–9) are crescent shaped. They form the anterior and anterodorsal rims of the orbits. Each prefrontal has an acute dorsal process that flanks the anterolateral margin of the frontal dorsally, and an acute ventral process that abuts the posterior part of the dorsal aspect of the medial shelf of the maxilla ventrally. Anteriorly the prefrontal articulates with the posterior part of the facial process of the maxilla. Thus there are two contact points with the maxilla, which are interrupted by the ellipsoid-shaped lacrimal foramen of which the prefrontal forms the dorsal and medial margin. In posterior view, each prefrontal is separated ventrally from the palatine and has a medial orbitonasal flange that separates the nasal and orbital cavities.

The postorbitofrontals (pof; according to Daza et al., 2008; Figs. 6–9) are boomerang-shaped and flat and form the posterodorsal rims of the orbits. Medially, the postorbitofrontal has a small contact zone with the posterodorsal part of the facial process of the maxilla. Anteriorly, it laterally articulates with the dorsal process of the prefrontal via well-defined facets on the anterolateral surface of the frontal. Posterior to this, it laterally articulates with the dorsal process of the prefrontal via well-defined facets on the anterolateral surface of the frontal. Posteroventrally, the frontal contacts the medial margin of the anterior process of the postorbitofrontal. The frontal, whereas the posterior process flanks the anterolateral margin of the parietal. The widest part of the postorbitofrontal is at the suture of frontal and parietal, and marks the vertex of the longer and narrower anterior process and the half as long and slightly broader posterior process.

The jugals (j; Figs. 6–9) are small, long, thin, almost straight bones, that are slightly narrower medially. Each jugal is nestled dorsally to the posterior process of the maxilla and only the posterior process of the jugal extends slightly beyond the maxilla and is thus visible in ventral view. Medially, the jugal contacts the medial part of the lateral margin of the ectopterygoid. The jugal participates in the formation of the anteroventral rim of the orbit.

The frontal (f; Figs. 6–9) is unpaired, longer than wide, and tubular, and the posterior end of the bone defines its widest part. It lies between the orbits and forms most of the dorsal orbital margin. The anterior part of the frontal is triangular in dorsal view and contacts the nasals, which in fact, slightly overlap the anteriormost region of the frontal at its well-defined nasal facets. Anterolaterally, directly behind the contact region with the nasals, the frontal has a small contact zone with the posterodorsal part of the facial process of the maxilla. Posterior to this, it laterally articulates with the dorsal process of the prefrontal via well-defined facets on the anterolateral surface of the frontal. Posteroventrally, the frontal contacts the medial margin of the anterior process of the postorbitofrontal. The

![FIG. 12. Distributional records of Tropiocolotes chirioi sp. nov. and T. tassiliensis sp. nov., and the populations of other African species of Tropiocolotes used in comparative analyses (external morphology and color pattern). Stars: type-localities (holotypes); square: type-locality (lectotype); pentagon: type-locality (neotype); circle: examined specimens; circle with dot: photograph.](https://bioone.org/journals/Journal-of-Herpetology)
Table 3. Cranial osteological characters of the new species of Tropiocolotes (T. chirioi sp. nov. and T. tassiliensis sp. nov.) and their closely related congeners (T. tripolitanus tripolitanus, T. steudneri, and T. nubicus) based on micro-CT scans.

<table>
<thead>
<tr>
<th>Character</th>
<th>T. chirioi sp. nov.</th>
<th>T. tassiliensis sp. nov.</th>
<th>T. tripolitanus tripolitanus</th>
<th>T. steudneri</th>
<th>T. nubicus</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(ZFMK 2350, ZFMK 2351)</td>
<td>(CAS 138662, ZFMK 19853)</td>
<td>(ZMB 9668A, ZMB 9668B, NMW 17246.2)</td>
<td>(ZFMK 33840, 33843, 33844, 33846, 33854, 33856)</td>
<td>(FMNH 256869)</td>
</tr>
<tr>
<td>Number of premaxillary tooth loci</td>
<td>8–10</td>
<td>10–11</td>
<td>9</td>
<td>9–12</td>
<td>9</td>
</tr>
<tr>
<td>Number of maxillary tooth loci</td>
<td>23–28</td>
<td>28–31</td>
<td>26–33</td>
<td>28–34</td>
<td>27</td>
</tr>
<tr>
<td>Number of dentary tooth loci</td>
<td>28–30</td>
<td>33–37</td>
<td>32–36</td>
<td>31–39</td>
<td>31</td>
</tr>
<tr>
<td>Premaxilla-maxilla aperture</td>
<td>small to medium-sized</td>
<td>small</td>
<td>medium-sized to large</td>
<td>medium-sized</td>
<td>large</td>
</tr>
<tr>
<td>Shape of transverse posterior margin of frontal</td>
<td>slightly bowed</td>
<td>almost straight (CAS 138662) or slightly rounded medially, forming a slightly sinuous suture with the parietal (ZFMK 19853)</td>
<td>medially rounded, forming a sinuous frontoparietal suture with the anterior margin of the parietals</td>
<td>almost straight</td>
<td>slightly bowed</td>
</tr>
<tr>
<td>Anteriormost part of septomaxilla in contact with maxilla and vomer</td>
<td>no</td>
<td>yes</td>
<td>yes</td>
<td>yes</td>
<td>yes</td>
</tr>
<tr>
<td>Shape of medial margin of pterygoid palatine process</td>
<td>straight</td>
<td>slightly concavely curved</td>
<td>straight</td>
<td>concavely curved</td>
<td>slightly concavely curved</td>
</tr>
<tr>
<td>Shape of laterally pointing shaft of stapes</td>
<td>straight</td>
<td>straight</td>
<td>slightly curved backwards and extended at lateral end</td>
<td>straight</td>
<td>straight</td>
</tr>
<tr>
<td>Shape of crista alaris of prootic</td>
<td>small, triangular</td>
<td>large, rounded, or triangular</td>
<td>large, rounded</td>
<td>large, triangular</td>
<td>large, rounded</td>
</tr>
<tr>
<td>Location of mental foramina of dentary</td>
<td>between 3rd/4th and 19th/21st tooth</td>
<td>between 3rd/4th and 23rd/24th tooth</td>
<td>between 3rd and 24th tooth</td>
<td>between 4th and 23rd–26th tooth</td>
<td>between 4th/5th and 20th tooth</td>
</tr>
</tbody>
</table>
slightly bowed, transverse posterior margin of the frontal lies posterior to the orbits and articulates with the anterior margin of the parietales. In lateral view, the anterior end of the frontal has a deep concavity that is occupied by the olfactory lobes and is formed by the dorsal anteromedial process of the frontal and the ventral anteromedial process of the crista cranii. In ventral view, the cristae cranii are strongly developed and meet medially to form a tubular structure. The anteroventral portion of the frontal has a triangular anteromedial process that is distinctly shorter than the dorsal anteromedial process.

The parietales (pa; Figs. 6–9) are paired and roughly rectangular and each has a long, blade-like postero lateral process. They form most of the posterior surface of the skull table and roof the braincase. Each parietal contacts the frontal anteriorly, the medial margin of the posterior process of the postorbitofrontal anterolaterally, and the posterior half of the posterolateral process contacts the medial margin of the anterodorsal half of the squamosal postero laterally. The posterolateral and the postero medial processes are supported by the otoccipital portion of the braincase. The posterolateral process approaches the horizontal semicircular canal bulge of the braincase, but ends shortly before reaching it. Laterally, the parietal extends ventrally in the form of a longitudinal ridge that gives rise to the descending process. The descending process is directed toward the crista alaris, but without contacting it.

The squamosals (sq; Figs. 6–9) are slender and crescent-shaped. Anteriorly, the medial margin of the anterodorsal half of each squamosal articulates with the lateral margin of the posterior half of the posterolateral process of the parietal. Posteroventrally, the squamosals curve along and under the horizontal semicircular canal bulge of the braincase and meets the posterodorsal aspect of the cephalic condyle of the quadrate. The squamosal bridges the posterolateral process of the parietal and the horizontal semicircular canal bulge of the braincase.

The septomaxillae (sm; Figs. 6–9) are complex, paired bones and distinctly separated. Each septomaxilla is elongate, more than three times longer than wide and occupies the nasal cavity with its dorsal surface forming the anterior part of the nasal capsule. The main body has a concave dorsal surface and forms the anterior half of the length of the bone, whereas the posterior half is formed by an equally long, narrow, postero lateral process that is curved posterodorsally, like the blade of a sledge. At the base of the posterolateral process is a large lateral foramen. Both the main bodies and the posterolateral processes of the paired septomaxillae are parallel to each other. The septomaxilla overlays the vomer dorsally and approaches it in some regions without touching it. The anter iormost part of the septomaxilla approaches the anteromedial part of the maxilla without touching it. Slightly anterior to the midlength of the bone there is a curved, lateral process.

The vomers (v; Figs. 6–9) are subtriangular, longer than wide, and become gradually broader posteriorly. They are in very close contact, and although a medial suture is visible along their entire length, they seem to be at least partially fused. The dorsal surface of each vomer is slightly concave. Anteriorly it contacts the palatal processes of the premaxilla, anterolaterally it contacts the anteromedial region of the maxilla, and posterodorsally it is notched, having a small shelf that defines the area where it contacts the ventral surface of the anterior tip of the vomerine process of the palatine. The anteromedial margin has a notch that forms the posterior part of the premaxillary-vomerine fenestra. There are at least two small foramina visible in the middle part of each vomer.

The palatines (pal; Figs. 6, 8, 9) are broad, ovaloid, and thin with two long and sharply triangular anterior processes. The palatines are broadly separated from one another. At the anterior end of the sigmoidal medial edge of each palatine is the longer and wider vomerine process, whose tip dorsally overlaps the posterior end of the vomer. The vomerine process is approximately a quarter of the length of the entire palatine. The lateral maxillary process and the anterolateral part of the palatine body contact the medial part of the maxilla. Posterior to this, the lateral edge of the palatine meets the anteromedial edge of the anterior process of the ectopterygoid. Between the vomerine and maxillary processes is a wide, shallow choanal groove. The postero medial edge of the palatine contacts the lateral margin of the palatine process of the pterygoid. The posterior edge of the palatine is uneven. The lateral edge is almost straight anteriorly and uneven with a large notch in the posterior half. The notched region forms the anteromedial margin of the ovaloid infraorbital fenestra.

The pterygoids (pt; Figs. 6–9) are Y-shaped and the largest and most posterior elements of the palate. The pterygoids form the postero medial rim of each infraorbital fenestra. The anterior edge of each pterygoid is sigmoid and bears a palatine process medially and an ectopterygoid process laterally. The anterolateral ectopterygoid process is slightly longer, acute, and dorsally overlapped and clasped by the posterior process of the ectopterygoid. The palatine process is slightly shorter and more robust, and its lateral margin contacts the postero medial margin of the palatine. The lateral margin of the ectopterygoid process is convexly curved, whereas the medial margin of the palatine process is straight. Posteriorly, the pterygoid bears the long, posterolaterally curved quadrate process, which constitutes about half the length of the bone. It reaches and contacts the medial aspect of the ventral portion of the quadrate. The anteromedial aspect of the quadrate process bears the large pterygoid notch, which is approached by the distal end of the basipterygoid process of the basicranium, but not contacting it. At the anterior region on the dorsal surface of the quadrate process, the fossa columella receives the pterygoid process (ventral end) of the epipterygoid. Both the medial and the lateral margin of the pterygoid are sigmoid.

The rod-shaped epipterygoids (epp; Figs. 6–9) extend columnar between the fossa columellae of the pterygoid and the crista alaris of the braincase. The dorsal end of each epipterygoid is slightly wider and has a distinct facet for the crista alaris. The ventral end inserts into the fossa columellae of the respective pterygoid. The dorsal half of the bone is slightly compressed anteroposteriorly. In dorsal view, the dorsal tips of the epipterygoids are slightly lateral to the parietales and are thus visible.

The ectopterygoids (ecp; Figs. 6–9) are flattened and boomerang-shaped. The anterior process of each ectopterygoid is broader and slightly shorter than the longer and narrower posterior process. The anterior process articulates with the palatine anteromedially and with the medial margin of the posterior part of the maxilla laterally, with the posteriormost end of the maxilla extending beyond the vertex of the ectopterygoid in ventral view. The posterior process dorsally overlays the anterolateral process of the pterygoid. The vertex region of the ectopterygoid laterally contacts the jugal, whereas the medial part of the bone forms the lateral rim of the
infraorbital fenestra. The ectopterygoid participates in the formation of the ventral rim of the orbit.

The robust and shell-like quadrates (q; Figs. 6–9) lie on the posterolateral corners of the skull, articulating with and supporting the lower jaw. The cephalic condyle of each quadrate articulates dorsally with the posterior end of the squamosal and the horizontal semicircular canal bulge of the prootic portion of the braincase and posteriorly with the distal end of the paroccipital process of the otooccipital. The dorsoposterior end of the quadrate is directly above the fenestra ovalis. Ventromedially, the quadrate articulates with the quadrate process of the pterygoid. It has an expanded dorsal portion and constriction towards the mandibular condyles. Ventrally, the mandibular condyles of the quadrate articulate with the glenoid fossa of the mandibula. The medial condyle is nearly twice as big as the lateral condyle. A prominent and curved tympanic crest extends posteroventrally from the lateral condyle to the cephalic condyle that defines the lateral margin of each quadrate. A slightly shorter and distinctly less curved medial crest extends between the medial condyle and the cephalic condyle and defines the medial margin of the quadrate. The anterior surface of the quadrate is smooth and convex, and the posterior portion is hollow. There are at least three foramina on the quadrate: an anterior foramen is situated centrally in the lower half of the bone, a medially oriented foramen is situated in the upper half of the quadrate centrally on the medial crest, and the third is dorsally oriented and situated slightly medial from the midline, dorsally on the quadrate near the cephalic condyle.

There are 14 ossicles of different sizes and shapes in the sclerotic ring (so; Fig. 6B). Although there are also differences in the degrees of ossification, all ossicles are poorly ossified, making it impossible to see the exact shape or possible overlaps with other ossicles.

The small stapes (sta; Figs. 6, 8, 9) fits in the fenestra ovalis, although not filling it entirely. It has a moderately long, thin, straight, laterally pointing shaft that is slightly extended at the lateral end, and an oval footplate. The shaft has a round, dorsoventrally oriented stapedial foramen at its base.

The braincase is a compact structure formed by the fusion of parabasisphenoid (pbas; Figs. 6, 8, 9), basioccipital (boc; Figs. 6–9), supraoccipital (soc; Figs. 6–8), prootic (po; Figs. 6–8), and otooccipital (otoc; Figs. 6–8). The dorsal portion of the braincase is formed by the supraoccipital, the anterolateral portion is formed by the prootics, the posteroventral portion is formed by the otooccipitals, and the ventral portion is formed by the basioccipital and the parabasisphenoid. The prootic forms the short and rounded crista alaris anterodorsally, and encloses the foramen prootico anteroventrally. The dorsal border of the braincase lies almost at the same level of the parietals and postorbitalfrontals. Dorsomedially, the braincase seems to contact the posteroventral medial part of the parietals. Laterally, directly above the fenestra ovalis, it articulates with the quadrates; dorsolaterally, directly above the contact zone with the quadrates, it contacts the posteroventral edge of the squamosals; and anterolaterally it articulates with the posteroventral edge of the epitypegoids at the crista alaris. Anteroventrally, the distal end of the basiptyergoid process of the parabasisphenoid approaches the anteroventral aspect of the quadrate process of the pterygoid without contacting it. In ventral view, the basioccipital and the parabasisphenoid form a wide convex surface. The basioccipital and the otooccipital form part of the double occipital condyle. The crista prootica is oriented anteroventrally and extends from the basiptyergoid process to the ventral margin of the foramen prootico. The basiptyergoid processes are robust, large, and almost quadrangular in shape. They bear the anterior openings of the vidian canal at their base. The anteromedial region of the parabasisphenoid is rounded. On the dorsomedial surface of the parabasisphenoid, the crista sellaris separates the depression for the sella turcica from the major brain concavity. The ventral portion of the braincase bears the posterior opening of the vidian canal and has two large openings that correspond to the aperture of the recessus scalei tympani. This opening is separated from the fenestra ovalis by a thick crista interfenestrals. The otooccipital region is characterized by the well-defined semicircular canal bulges (anterior, posterior, and horizontal) and by the large, laterally projecting, paroccipital process, which is located under the horizontal semicircular canal bulge and posterodorsally to the fenestra ovalis. The anterior base of the paroccipital process contacts the posteroverentral end of the squamosal. The paroccipital processes are distinctly visible in dorsal view and define the widest part of the braincase. Several foramina pierce the medial wall of the braincase.

The dentary (d; Figs. 6, 7, 10) is a long and narrow, anteromedially curved bone and occupies more than half the length of the lower jaw. The dentary bears 30 pleurodont, conical teeth of about the same size that are in close contact with one another at their bases. Posteriorly, at the level of the 8th-last tooth the dentary bifurcates into a long and slender ventral process that reaches up to the posterior end of the splenial, and a more robust, tooth-bearing dorsal process that bifurcates again directly behind the last dentary tooth, into a superior and an inferior process. In lateral view, the ventral edge of the superior process and the dorsal edge of the inferior process frame the anterolateral process of the coronoid, and the ventral edge of the inferior process and the dorsal edge of the ventral process frame the anterolateral region of the compound bone. In lingual view, the ventral edge of the dorsal process articulates with the dorsal edge of the splenial along the anterior half and with the anterodorsal edge of the coronoid along the posterior half, and the ventral process articulates dorsally with the splenial along its entire length. Laterally, the dentary bears four mental foramina, which lie in a longitudinal series between the 3rd and 21st tooth.

The coronoid (co; Figs. 6, 7, 10) is triangular in shape. In lateral view, the anterolateral process starts directly behind the last dentary tooth and is framed by the superior and inferior processes of the dentary. Posteriorly, the coronoid saddles the compound bone. In medial view, the anteromedial process of the coronoid begins at the level of the 2nd-last dentary tooth. However, the anteromedial process is actually much longer and starts at the anterior margin of the splenial, but this part of the anteromedial process is mediolaterally covered by the splenial, dorsally and ventrally by the dentary, and laterally by the compound bone. Dorsally, in medial view, the coronoid contacts the ventral edge of the dorsal dentary process, and ventrally it contacts the splenial anteriorly and the compound bone along the rest of its length. The dorsal process of the coronoid defines the highest part of the mandibula and thus exceeds the height of the dentary teeth.

The splenial (sp; Figs. 6, 7, 10) is comparatively large, subtriangular, anteromedially curved bone and occupies more than half the length of the lower jaw. The splenial bears 21st tooth.
the dentary, posterodorsally with the anteroventral edge of the coronoid and with the compound bone. The anterior region of the splenial is pierced by a large foramen, followed ventrally by a notch at the suture with the ventral process of the dentary. The angular is absent.

The articular, surangular, and prearticular are completely fused to form the compound bone (cb; Figs. 6, 7, 10). The compound bone is almost straight. The posteriorly oriented retroarticular process (rp; Figs. 7, 10) is long and rectangular in shape with a slightly concave dorsal surface. The mandibular fossa is elongate and visible dorsomedially. Posterior to it, is a broad ovoid articular facet for the quadrate condyles. The anterior process of the compound bone anteriorly surpasses the anteromedial process of the coronoid and the anterior tip of the splenial. However, this extension is only visible when the dentary is removed, as it is covered by the dentary dorsally, laterally, and ventrally and covered by the splenial and coronoid medially.

Variation in Cranial Osteology.—In general, the skull morphology of the paratype ZFMK 2351 is very similar to that of ZFMK 2350. Most differences are due to the fact that the bones in ZFMK 2351 are farther apart and therefore often do not touch each other. ZFMK 2351 with an SVL of 25.3 mm is significantly smaller than ZFMK 2350 (SVL = 33.66 mm) and may not yet be mature. The skull is significantly less ossified than in ZFMK 2350, which will probably change in the course of ontogenesis. In this context, it should be mentioned that in ZFMK 2351 the bones of the braincase (parabasisphenoid, basioccipital, supraoccipital, prootic, and otooccipital) are not fused with each other, nor is the surangular bone fused with the compound bone. Furthermore, the medially and dorsally oriented foramina of the quadrates are fused and cause the cephalic condyle to be bifurcated, with a large gap between the two dorsal ends. The premaxilla-maxilla aperture is larger; the foramen prootic of the prootic is not completely enclosed by bone, the paroccipital processes of the otooccipital are much shorter and hardly visible in dorsal view, and the laterally pointing shaft of the stapes is also much shorter than in ZFMK 2350.

Apart from these differences due to less ossification of the skull of ZFMK 2351, this specimen has 8 premaxillary tooth loci, 25 tooth loci on the left maxilla and 23 tooth loci on the right maxilla, 28 tooth loci on the left dentary, and 29 tooth loci on the right dentary. Furthermore, there is no foramen visible at the base of the postero-lateral process of the septomaxilla, and the distal end of the basipterygoid process of the parabasisphenoid touches the anteromedial aspect of the quadrate process of the pterygoid on the left side of the skull. The tooth-bearing process of the dentary bifurcates not directly behind the last dentary tooth, but with a short distance, and likewise the anterolateral process of the coronoid starts shortly behind the last dentary tooth. The splenial bears a second foramen close to the suture with the ventral process of the dentary, and not just a notch as in ZFMK 2351.

Etymology.—The specific epithet is a noun in the genitive case honoring Laurent Chirio, in recognition of his valuable contribution to the knowledge of the herpetofauna of western and central Africa. Laurent is the collector of the holotype of the new species, and he was also very kind and helpful in many ways during this study.

Remarks.—Tropiocolotes algericus is the geographically closest species to the specimens of T. chirioi we analyzed (closest specimens are ~200 km distant, while the closest known T. tropilatus tropilanus specimens are separated from T. chirioi by about 985 km). Tropiocolotes algericus is also the only species occurring in the same biogeographic region of T. chirioi, i.e., the Atlas Mountains Range. In addition to the meristic and cranial diagnostic characters mentioned above, the general shape of the snout can help to differentiate both species. Tropiocolotes algericus has a shorter and wider snout (more retracted) than T. chirioi, and despite being subtle, this distinctiveness can be observed in animals in life and also in preserved specimens (Fig. 11).

The Tropiocolotes chirioi specimen MNHN-RA-1973.1306, collected on 1 February 1934 by P. Carié (catalogued as “Algeria or Tunisia”), was included in the type-series (as a paratype) based on congruence with other specimens also collected by P. Carié on the same day (1 February 1934) at Biskra, Algeria. This locality strongly agrees with the occurrence area of the new species, and based on the agreement between the occurrence of T. chirioi and other animals collected by Carié on the same day, here we restrict the collection locality of MNHN-RA-1973.1306 from “Algeria or Tunisia” to Biskra, Algeria (34.86°N, 5.73°E).

Distribution and Ecology.—Tropiocolotes chirioi is distributed in northeastern Algeria (Fig. 12), in the westernmost foothills of the Aures Mountains. The holotype and the paratype collected by L. Chirio (MNHN-RA-1997.5086 and MNHN-RA-1997.5088, respectively) were found during the day, both hidden under little stones in the shadow of little trees. Specimens were sleeping in little round holes under the stones.

Tropiocolotes tassiliensis sp. nov.

(Figs. 1, 5, 12–15; Tables 1–3; Figs. S1–S12 and Table S1 in Supplemental Material)

Holotype.—CAS 138662, adult female, collected on 18 May 1974 by T. Papenfuss, R. Drewes, and E. Morris, at 3 km E of Tamanrasset on road to Adriane, Algeria (22.79°N, 5.56°E), field number TJP-9701 (Figs. 13, 14).

Paratypes.—MNHN-RA-0.9016, juvenile male*, collected by H. Lhote, at Iniiniten, Tassili n’Ajjer, Algeria (25.81°N, 8.13°E); MNHN-RA-1932.119–20, adults, male* and female* respectively, collected at Amguid, Algeria (26.42°N, 5.37°E); ZFMK 2352, juvenile, collected in 1914 by H. Frhr. Geyr v. Schweppenburg, at Oued Amra, Algeria (25.00°N, 5.50°E); ZFMK 2353, juvenile male*, collected on 22 January 1914 by H. Frhr. Geyr v. Schweppenburg, at Hoggar, Ti-n-Sig, Algeria (28.07°N, 6.05°E); ZFMK 19853, adult female*, collected on 15 October 1976 by U. Joger and J. Joger, at 15 km south of Terhenanet, Algeria (23.05°N, 5.43°E); ZFMK 33839, adult female*, collected on 20 December 1980 by U. Joger and J. Joger, at 90 km south of In Salah, Algeria (26.52°N, 3.04°E). Localities and sites are as they appear in the original catalogs.

Diagnosis.—Tropiocolotes tassiliensis sp. nov. is distinguished from all other species of Tropiocolotes by the combination of the following characters: 1) smooth dorsal and ventral scales; 2) two pairs of postmental scales; 3) 30–38 gular scales; 4) 46–53 scales around midbody; 5) 51–59 dorsal scales; 6) wide transverse or oblique brown bands on dorsal surface of head and body; 7) 10–11 premaxillary tooth loci; 8) 28–31 maxillary tooth loci; 9) 33–37 dentary tooth loci; 10) small premaxilla-maxilla aperture; 11) transverse posterior margin of frontal almost straight, or slightly rounded medially, forming a slightly sinuous suture with the parietal; 12) anteriormost part of septomaxilla in contact with maxilla and vomer; 13) medial margin of pterygoid palatine process slightly concavely curved; 14) laterally pointing shaft of stapes straight; 15) cristis alaris of prootic large, rounded, or
triangular; 16) mental foramina of dentary located between 3rd/4th and 23rd/24th tooth.

Comparison with Other Species.—Tropiocolotes tassiliensis sp. nov. differs from T. algericus, T. bisharicus, T. chirioi, T. confusus, T. scortecci, T. somalicus, T. tripolitanus apoklomax, T. tripolitanus occidentalis, and T. tripolitanus tripolitanus in having smooth dorsal and ventral scales (vs. keeled). Tropiocolotes tassiliensis sp. nov. differs from T. nattereri and T. yomtovi in having tricarinate subdigital lamellae (vs. unicarinate); from T. hormozganensis, T. naybandensis, and T. wolfgangboehmei in having two pairs of postmental scales (vs. one pair); from T. nubicus in having 30–38 gular scales (vs. 20–28); from T. steudneri in having 51–59 dorsal scales (vs. 61–66), and fewer midbody scales, 46–53 (vs. 52–60). Tropiocolotes tassiliensis sp. nov. also differs from T. nubicus and T. steudneri in having wide transverse or oblique brown bands on dorsal surfaces of head and body (vs. dorsal surface of neck and body with small brown dots, in T. nubicus [Fig. 15A,D; Fig. 16]; dorsal surface of neck and anterior body with three transverse brown bands or three longitudinal series of large brown dots, and posterior dorsal surface of body with three longitudinal series of large brown dots, in T. steudneri [Fig. 15B,C,D]). A summary of other differences in meristic characters is presented in Table 1.

Description of Holotype.—Body cylindrical; long and wide head, neck, and body; long snout; limbs well developed (Fig. 13). Adult specimen, female (one large egg visible through the abdomen, absence of hemipenial sacs, presence of calcium sacs).
Rostral large, convex, polygonal, partially divided by a median cleft, and in broad contact with internasals, upper nasal, and 1st infralabial. Viewed dorsally, the rostral is about two times wider than long, and posteriorly reaches beyond the nostril by about half of its length. A pair of large internasal scales in long, medial contact with each other, forming a long suture with median cleft of rostral, bordered posteriorly by a pair of post-internasal scales, similar in shape and size to internasal scales. Frontal scales polygonal, smooth, feebly granular and subimbricate, differing in size. Supraocular scales irregularly hexagonal, smooth, feebly granular and subimbricate, with rounded lateromedial margins. Interorbital scales polygonal, longer than wide, similar in size or slightly smaller than adjacent supraoculars. Fourteen transverse scales across the medial interorbital region. Palpebral fold with smooth scales, varying from subimbricate to feebly granular. Supraciliary scales smooth and subimbricate. Parietal and occipital scales polygonal, smooth, feebly granular and subimbricate, differing in size. Scales on dorsal surface of neck smooth, feebly granular, becoming gradually imbricate toward dorsal surface of body.

Nostril directed lateroposteriorly, bordered by four scales: rostral anteriorly and ventrally, upper nasal dorsally, lower nasal posteriorly, and 1st infralabial ventrally and posteriorly. Two slightly longer than wide nasal scales, upper ones slightly larger than lower nasals and about half the size of internasals. Loreal scales similar in shape and size to frontal scales. Eye large, pupil vertical. Temporal scales granular, subimbricate, obtuse on upper temporal region near eyes. Large, round ear opening. Scales on lateral surface of neck obtuse, subimbricate, in oblique and longitudinal rows. Nine supralabials, all longer than tall, 5th to 9th under the orbit.

Mental large, convex, pentagonal, slightly wider than long and similar in width to rostral, forming an acute angle posteriorly reaching level of half the length of 1st infralabial. Two pairs of large postmentals. Scales of 1st pair trapezoidal, slightly wider than long, in broad, medial contact with each other; scale on the right side in contact with mental and 1st infralabial (touching 2nd infralabial), and scale on the left in contact with mental, and 1st and 2nd infralabials. Scales of 2nd pair of postmentals irregular trapezoidal with rounded posterior margins, similar in size among them and similar in size to scales of 1st pair; scales of 2nd pair in contact with 2nd infralabials (touching 3rd on left side), and separated from each other by one gular scale. Four submandibular scales on each side, 1st ones irregularly trapezoidal, about one-third the size of scales of 1st pair of postmentals. Gular scales polygonal to roundish, smooth, feebly granular, subimbricate, nearly subequal (anteriormost scales, bordering postmentals and submandibulars, slightly larger than proceeding ones), gradually

Fig. 15. (A) Holotype of *Tropiocolotes tassiliensis* sp. nov. (CAS 138662), (B) neotype of *T. steudneri* (ZFMK 33843), (C) *T. steudneri* (ZFMK 33856), (D) holotype of *T. nubicus* (FMNH 256865).
TWO NEW SPECIES OF TROPIOCOLOTES

413

becoming obtuse, then smooth, imbricate, wider than long posteriorly to level of end of mandibula, becoming gradually larger and finally about as wide as long towards forelimb insertion. Thirty-six gular scales. Eight infralabials, first three rectangle-shaped and taller than long, 4th trapezoidal, taller posteriorly to level of end of mandibula, becoming gradually in size from 5th to 8th, 4th to 8th under the orbit. Dorsal scales smooth, imbricate, in oblique and longitudinal rows, 59 middorsal scales from anterior margin of forelimbs to posterior margin of hind limbs. Flank scales similar in shape and size to dorsolateral scales, 52 scales around midbody. Ventral scales smooth, imbricate, slightly larger than scales on flanks, in oblique and longitudinal rows, 56 midventral scales from anterior margin of forelimbs to preanal plate. Preanal pores absent. Tail regenerated, with feebly keeled, pointed, and irregular margins ventrally, decreasing gradually in size from 5th to 8th, 4th to 8th under the orbit.

Dorsal scales smooth, imbricate, in oblique and longitudinal rows, 59 middorsal scales from anterior margin of forelimbs to posterior margin of hind limbs. Flank scales similar in shape and size to dorsolateral scales, 52 scales around midbody. Ventral scales smooth, imbricate, slightly larger than scales on flanks, in oblique and longitudinal rows, 56 midventral scales from anterior margin of forelimbs to preanal plate. Preanal pores absent. Tail regenerated, with feebly keeled, pointed, and imbricate scales varying in size on dorsal, lateral, and ventral surfaces. Two well-developed postanal sacs on ventral surface of base of tail, and two acute, pointed, granular scales directed posterodorsally on ventrolateral surfaces on each side. Scales on dorsal surface of limbs smooth, imbricate, varying from similar in size to slightly larger than scales on dorsal surface of body. Scales on ventral surface of forelimbs pointed, varying from subimbricate to obtuse, smaller than scales on dorsal surface of forelimbs. Scales on ventral surface of upper hind limbs similar in shape and size to those on dorsal surface of hind limbs, and on ventral surface of lower hind limbs similar to scales on ventral surface of forelimbs, smaller than those on dorsal surface of hind limbs. Posterior surface of thighs with obtuse to roundish, small scales. Ventral aspect of fingers and toes with single and tricarinate subdigital lamellae, 14 lamellae under 4th fingers, and 16–17 lamellae under 4th toes. Claws long and distinct (3rd finger and 1st toe on left side cut or undeveloped).

Measurements of Holotype (in Millimeters).—SVL = 34.8; AGL = 17.2; HD = 3.7; HW = 5.6; HL = 7.8; NL = 5.2; ShL = 6.2; TL = 2.8 (base of tail) + 25.5 (broken and regenerated part).

Coloration in Preservative (Based on Holotype).—Dorsal surface of head cream, with a few, small, sparse brown dots. Dorsal surface of neck cream, with small, sparse brown dots, and oblique brown bands. A wide brown band from rostral and nasals, along loreal region, passing through eye, medial temporal region, lateral surface of neck, to shoulders. Dorsal surface of body cream, with seven to eight transverse or oblique brown bands, and white dots irregularly distributed between bands. Tail regenerated and broken: dorsal surface of base of tail cream, with one wide, transverse brown band; dorsal and lateral surfaces of the remaining (regenerated) tail with sparse and irregularly distributed brown pigmented scales. Dorsal surface of forelimbs, hind limbs, hands, and feet with white and brown dots, white dots larger on hind limbs and feet than on forelimbs and hands. Flanks cream, with small, sparse brown dots on lower flank surface. Ventral surface of head, neck, body, tail and limbs cream, with very small, sparsely distributed, brown dots.

Variation.—Tables 1 and 2 present a summary of means and the variation in meristic characters and measurements. The transverse brown bands on dorsal surface of body can be observed in adult and juvenile specimens: both the adult ZFMK 19853 and the juvenile ZFMK 2352 have eight bands (Fig. 5D,E). The measurements of each specimen are presented in Supporting Information (Table S1).

Cranial Osteology.—The skull of the holotype (CAS 138662, Figs. S1–S12) of Tropiocolotes tassiliensis sp. nov. resembles that of T. chirrior (ZFMK 2350) in many aspects, but the differences are presented in the following.

The premaxilla (Figs. S1, S4, S6) has slightly larger premaxilla-maxilla apertures and a longer nasal process, the posterior half of which extends almost between the anterior half of the median suture of the nasals. Anteromedially each maxilla (Figs. S1, S2, S4, S6, S9) articulates not only with the vomer but also with the anterior tip of the septomaxilla. The right maxilla bears 31 tooth loci. The lateral border of the maxilla, along the tooth row is almost straight, and the anterior margin of the facial process is markedly rounded and merges gradually into the dorsal margin. The anteromedial maxillary lappets are distinctly separated with an approximately three times greater distance to each other as compared with the distance seen in ZFMK 2350. The number of foramina below the facial process of the maxilla is three to four. The posterior process of the jugal (Figs. S1, S6, S9) that extends beyond the maxilla, is slightly longer than in ZFMK 2350.

The transverse posterior margin of the frontal (Figs. S1, S6) is straight except for the lateralmost parts on each side which are curved backwards. The anterotemporal portion of the frontal has a semicircular anteromedial process. The posterior one-third of the posterolateral process of the parietal (Figs. S1, S2, S5, S6, S11) contacts the medial margin of the anterodorsal half of the squamosal. The descending process is very short, much shorter than in ZFMK 2350, and it is distinctly separated from the crista alaris.

Fig. 16. Specimen of Tropiocolotes nubicus in life, photographed by C. Brito in the Tassili n’Ajjer Mountains, Algeria. Credit: C. Brito.
The septomaxillae (Figs. S7, S10) are in medial contact centrally, forming an elevated medial ridge that approaches and almost contacts the ventral surface of the median region of the nasals. No lateral foramen is visible at the base of the postero-lateral process. The anteriori-most part of the septomaxilla contacts the vomer dorsally. The lateral process is almost laminar and not curved and it contacts the dorsal surface of the central part of the vomer.

The anteromedial margins of the vomers (Figs. S3, S8, S9) meet medially, resulting in the formation of two oval fenestrae: a larger vomerine fenestra in the anterior region between the vomers, and a premaxillary-vomerine fenestra about half the size, which is mainly formed by the palatal processes of the premaxilla.

The vomerine process of the palatine (Figs. S3, S7–S10) is more than a third of the length of the entire bone. The postero-lateral edge of the palatine approaches the anteromedial edge of the anterior process of the ectopterygoid, without contacting it.

The anteromedial palatine process of the pterygoid (Figs. S3, S7–S9) is slightly longer than the anterolateral ectopterygoid process. Only the lateral margin of the right palatine process contacts the posteromedial margin of the palatine (no contact on the left side of the skull). The medial margin of the palatine process is slightly concavely curved.

In dorsal view, the dorsal tips of the epitypegonids (Figs. S1, S6) are only marginally visible lateral to the parietals. The anterior process of each ectopterygoid (Figs. S1, S6, S9, S10) is about as long and narrow as the posterior process and approaches the palatine anteromedially without contacting it. The posterior-most end of the maxilla does not extend beyond the vertex of the ectopterygoid. The anterior surface of the quadrat (Figs. S4, S8) seems to be less ossified as in ZFMK 2350, and appears perforated in the reconstructed scan images.

The sclerotic rings (Fig. S2) are poorly ossified and not visible in the dorsal and ventral region. In the lateral region each ring seems to have six ossicles on each side, but these are difficult to differentiate.

The crista alaris (Fig. S2) of the prootic portion of the braincase is distinctly larger than in ZFMK 2350 and more rounded. The basipterygoid processes (Figs. S3, S7, S9) are longer and narrower and more triangular in shape. The anteromedial region of the parabasisphenoid is approximately triangular, only the apex of the triangle is missing. There is a small foramen in the central region of the basioccipital part of the braincase but it looks more like it was caused by a needle puncture and is not naturally present in the skull.

The dentary (Fig. S12) bears 33 to 34 tooth loci. It bifurcates posteriorly at the level of the 6th-last tooth into a ventral process and a dorsal process; the latter bifurcates again at its posterior end, distinctly behind the last mandibular tooth. The four mental foramina of the dentary are situated between the 3rd and 23rd tooth.

The anterolateral process of the coronoid (Fig. S12) starts with a clear distance behind the last dentary tooth. The anteromedial process seems to be barely covered by other bones; it is therefore not much longer than the visible area, and it starts at about the posterior end of the splenial foramen.

Variation in Cranial Osteology.—In general, the skull morphology of the paratype ZFMK 19853 is very similar to that of the holotype CAS 138662. Several bones in the skull of ZFMK 19853 show fractures and the entire skull seems to be somewhat compressed dorso-ventrally, whereas laterally it appears somewhat widened. Presumably due to this damage, some bones are closer together, while other bones seem to be farther apart than they probably would be in an undamaged state of the skull. Differences, which are likely to have been caused by this injury, are not listed below. However, the skull of ZFMK 19853 differs by having 11 premaxillary tooth loci, 28 tooth loci on the left maxilla and 31 tooth loci on the right maxilla, 35 tooth loci on the left dentary and 36 tooth loci on the right dentary. Furthermore, the anterior margin of the facial process of the left maxilla is more angular and forms a somewhat more acute transition into the dorsal margin of the facial process. The anterior and posterior processes of the postorbitofrontal are about similar in length and width. The jugal is spoon shaped and distinctly broader anteriorly; it is curved and the posterior process only extends slightly beyond the posterior process of the maxilla. The transverse posterior margin of the frontal is medially rounded, forming a sinuous suture with the parietal. The descending process of the parietal is well developed. The septomaxillae are very close to each other, but do not touch and they do not form an elevated medial ridge together on their dorsal surface. The lateral process of the septomaxilla does not contact the dorsal surface of the vomer. The anteromedial margins of the vomers are slightly separated, leaving only a small opening to form an elongate premaxillary-vomerine fenestra together with the palatal processes of the premaxilla. The palate contacts the anterior process of the ectopterygoid on the right side of the skull and the palatine process of both pterygoids contacts the corresponding palatine. The anterior surface of the quadrate is well ossified and not perforated and the anterior foramen is very large. No foramen is present in the central region of the basioccipital part of the braincase. The dentary bifurcates for the first time at the level of the 7th (left mandibula) or 8th (right mandibula) last tooth and the splenial does slightly surpass the ventral process of the dentary posteriorly. The splenial bears a 2nd foramen close to the suture with the ventral process of the dentary, and not just a notch as in CAS 138662.

Etymology.—The specific epithet is a noun in the genitive case derived from the geographical name Tassili n’Ajjer. It is a vast plateau in southeast Algeria, covering an area of 72,000 km², and one of the most important groupings of prehistoric cave art in the world, recognized by UNESCO as a World Heritage Center. More than 15,000 drawings and engravings record the climatic changes, the animal migrations, and the evolution of human life on the edge of the Sahara from 6,000 BC to the first centuries of the present era (https://whc.unesco.org/en/list/179/).

Distribution.—Tropiocolotes tassiliensis is distributed in southeastern Algeria (Fig. 12), in the Hoggar Plateau that includes the Hoggar and Tassili n’Ajer mountain ranges. Its distribution agrees with the Central Sahara Mountains biogroup of endemic Saharan species suggested by Brito et al. (2016). According to Machado et al. (2021), T. tripolitanus and T. nubicus (Fig. 1 in Machado et al., 2021) can also be found in southeastern Algeria. Carlos Brito photographed a specimen of T. nubicus at Tin Igitene, Djanet, Tassili n’Ajer Mountains (24°03’N, 10°59’E; Figs. 12, 16). It can be easily differentiated from T. tassiliensis by its color pattern (see Diagnosis and Species Comparisons above).

Tropiocolotes steudneri (Peters, 1869) (Figs. 1, 12, 15, 17, 18; Tables 1, 3; Figs. S1–S12 in Supplemental Material)

Neotype.—ZFMK 33843, adult female (here designated as the neotype of Tropiocolotes steudneri), collected between 21 and 23
Tropiocolotes steudneri is distinguished from all other species of Tropiocolotes by the combination of the following characters: 1) smooth dorsal and ventral scales; 2) two pairs of postmental scales; 3) 28–42 gular scales; 4) 52–60 scales around midbody; 5) 61–66 dorsal scales; 6) dorsal surface of neck and anterior body with three transverse brown bands or three longitudinal series of large brown dots, and posterior dorsal surface of body with three longitudinal series of large brown dots; 7) 9–12 premaxillary tooth loci; 8) 28–34 maxillary tooth loci; 9) 31–39 dentary tooth loci; 10) medium-sized premaxilla-maxilla aperture; 11) transverse posterior margin of frontal almost straight; 12) anteriormost part of septomaxilla in contact with maxilla and vomer; 13) medial margin of pterygoid palatine process concavely curved; 14) laterally pointing shaft of stapes straight; 15) crista alaris of prootic large, triangular; 16) mental foramina of dentary located between 4th and 23rd to 26th tooth.

Comparison with Other Species.—Tropiocolotes steudneri differs from T. algericus, T. bisharicus, T. chirioi, T. confusus, T. somalicus, T. tripolitanus apoklomax, T. tripolitanus occidentalis, and T. tripolitanus tripolitanus in having smooth dorsal and ventral scales (vs. keeled). Tropiocolotes steudneri differs from T. nattereri and T. yomtowi in having tricarinate subdigital lamellae (vs. unicarinate); from T. hormozganensis, T. naybandensis, and T. wolfgangboehmei in having two pairs of postmental scales (vs. one pair); from T. nubicus in having 28–42 gular scales (vs. 20–28); from T. tassiliensis in having 61–66 dorsal scales (vs. 51–59), and a higher number of midbody scales 52–60 (vs. 46–53). Tropiocolotes steudneri also differs from T. nubicus and T. tassiliensis in having dorsal surface of neck and anterior body with three transverse brown bands or three longitudinal series of large brown dots, and posterior dorsal surface of body with three longitudinal series of large brown dots (vs. wide transverse or oblique brown bands on dorsal surfaces of head and body, in T. tassiliensis [Fig. 13]; dorsal surface of neck and body with small brown dots, in T. nubicus [Fig. 15A,D; Fig. 16]). A summary of other differences in meristic characters is presented in Table 1.

Based on skull characters, Tropiocolotes steudneri differs from T. tripolitanus tripolitanus and T. nubicus in having higher number of premaxillary tooth loci (9–12, vs. 9); from T. chirioi and T. nubicus in having higher number of maxillary tooth loci (28–34, vs. 23–28 in T. chirioi, and 27 in T. nubicus), and higher number of dentary tooth loci (31–39, vs. 28–30 in T. chirioi, and 31 in T. nubicus); from T. tassiliensis and T. nubicus in having medium-sized premaxilla-maxilla aperture (vs. small in T. tassiliensis, and large in T. nubicus); from T. chirioi, T. t. tripolitanus, and T. nubicus in having transverse posterior margin of frontal almost straight (vs. slightly bowed in T. chirioi and T. nubicus, and medially rounded, forming a sinuous frontoparietal suture with the anterior margin of the parietals in T. t. tripolitanus); from T. chirioi in having the anteriormost part of septomaxilla in contact with...
with maxilla and vomer (vs. the anteriormost part of septomaxilla not in contact with maxilla and vomer); from *T. chirioi* and *T. t. tripolitanus* in having concavely curved medial margin of pterygoid palatine process (vs. straight); from *T. tripolitanus* in having laterally pointing shaft of stapes straight (vs. slightly curved backwards and extended at lateral end); from *T. chirioi* in having cristæ alaris of prootic large, triangular (vs. small, triangular); from *T. chirioi* and *T. nubicus* in having the mental foramina of the dentary located between the 4th and the 23rd to 26th tooth (vs. between the 3rd/4th and the 19th/21st tooth in *T. chirioi* sp. nov., and between the 4th/5th and the 20th tooth in *T. nubicus*).

Description of Neotype.—Body cylindrical; long and wide head, neck, and body; long snout; limbs well developed (Fig. 17). Adult specimen, female (absence of hemipenial sacs; presence of calcium sacs).

Rostral large, convex, polygonal, partially divided by a median cleft, and in broad contact with internasals, upper nasal, and 1st infralabial. Viewed dorsally, the rostral is about two times wider than long, and posteriorly reaches beyond level of nostril by less than half of its length. A pair of large internasal scales in long, medial contact with each other, forming a long, irregular suture with median cleft of rostral, bordered posteriorly by an off-centered pair of post-internasal scales, similar in shape to and only slightly smaller than internasal scales. Frontal scales polygonal, smooth, feebly granular, and differing in size. Supraocular scales irregularly hexagonal, smooth, feebly granular, and subimbricate. Interorbital scales polygonal, similar in size or slightly larger than adjacent supraoculurs. Fourteen transverse scales across medial interorbital region. Palpebral fold with smooth, granular scales. Supraocular scales smooth and subimbricate. Parietal and occipital scales polygonal, smooth, feebly granular, and subimbricate, slightly smaller than interorbitals, becoming gradually imbricate across neck toward dorsal surface of body.

Nostril located directly above anterior edge of 1st labial, directed lateroposteriorly, bordered by four scales: rostral anteriorly, upper nasal dorsally, lower nasal posteriorly, and 1st infralabial ventrally and posteriorly. Two nasal scales, each about half the size of internasals. Loral scales similar in shape and size to frontal scales. Eye large, pupil vertical. Temporal scales granular, subimbricate, slightly smaller than parietales. Large, elliptic ear opening, orthogonal to mouth. Scales on dorsal surface of head smooth, imbricate, same size as scales on dorsum, in oblique and longitudinal rows, 63 middorsal scales from anterior margin of forelimbs to posterior margin of hind limbs. Lateral scales similar in shape and size to dorsolateral scales, 58 scales around midbody. Ventral scales smooth, imbricate, same size as scales on dorsum, in oblique and longitudinal rows, 60 midventral scales from anterior margin of forelimbs to preanal plate. Posterior tip of most of the ventral scales between neck and groin with a small indentation. Preanals pores absent.

Tail broken at base and partially missing. Caudal scales feebly keeled, pointed, and imbricate; similar in shape on dorsal, lateral, and ventral side of tail, subcaudals slightly larger than dorsal caudals. Well-developed postanal scales. Two enlarged acute granular scales under each side of base of tail.

Scales on dorsal surface of limbs smooth, imbricate, and pointed; varying from similar in size to slightly larger than scales on dorsal surface of body. Scales on ventral surface of limbs varying from imbricate to obtuse, smaller than scales on dorsal side, except for scales on upper hindlimbs. Posterior surface of thighs with obtuse to roundish, small scales. Fingers and toes ventrally with single and tricarinate subdigital lamellae; 15 lamellae under 4th fingers, and 20–21 lamellae under 4th toes. Long and distinct claws on all fingers and toes.

Measurements of Neotype (in Millimeters).—SVL = 30.2; AGL = 15.1; HD = 3.2; HW = 5.2; HL = 7.3; NL = 5.6; ShL = 5.8; TL = broken and incomplete (not measured).

Coloration in Preservative (Based on Neotype).—The coloration of the specimen is largely faded due to preservation, but general patterns are still visible. Dorsal surface of head cream, with a few small brown dots in frontal and occipital regions. A wide brown band running from nostril along loreal region, through eye, medial temporal region, and above ear opening to lateral neck, fading at midneck (hardly visible on left side). Dorsal surface of body light brown to cream, with irregular brown blotches between neck and pelvis that are arranged in three longitudinal lines (one vertebral and two dorsolateral lines) consisting of eight blotches each. Each row of dark blotches posteriorly bordered by a row of smaller irregular whitish spots. Blotches on neck and shoulders each somewhat merged into an irregular transversal band. Dorsal surface of limbs with irregular brown dots. Dorsal surface of partial tail cream with a series of distinct and wide transverse brown bands. Flanks and ventral surface of head, neck, body, limbs, and tail uniformly cream.

Variation.—Tables 1 and 2 present a summary of means and the variation in meristic characters and measurements. The dorsal surface of the neck and anterior body either has three transverse brown bands, or three longitudinal series of large brown dots.

Cranial Osteology.—The skull of *Tropiocolotes steudneri* (ZFMK 33844, Figs. S1–S12; ZFMK 33840, 33843, 33846, 33854, 33856) resembles that of *T. chirioi* (ZFMK 2350, 2351) in many aspects, but the differences are presented below.

The premaxilla (Figs. S1, S4, S6) bears 9–12 tooth loci and has a longer nasal process, the posterior half of which extends almost between the anterior half of the median suture of the nasals. Anteriomedially each maxilla (Figs. S1, S2, S4, S6, S9) articulates not only with the vomer but also with the anterior tip of the septomaxilla. The maxilla bears 28–34 tooth loci. The lateral border of the maxilla, along the tooth row, is almost straight in all specimens. The number of foramina below the
facial process of the maxilla is three to four. The maxillary facial process is in distinctly broader contact with the frontal in all specimens as compared with T. chirioi.

The anterior process of the postorbitofrontal (Figs. S1, S6, S11) is almost as long as the posterior process or only slightly longer. The jugals (Figs. S1, S6, S10) are about spoon shaped and distinctly broader anteriorly with a straight posterior shaft. The transverse posterior margin of the frontal (Figs. S1, S6) is almost straight. The contact zone of the frontal with the posterodorsal transverse posterior margin of the frontal (Figs. S1, S6) is almost as long as the posterior process or only slightly longer. The anterior-ventral portion of the frontal has an irregularly wavy or convex rounded but not triangular anteromedial process. The posterior one-third of the postero-lateral process of the parietal (Figs. S1-2, S5-6, S11) contacts the medial margin of the anterodorsal half of the squamosal. The descending process is very short, much shorter than in T. chirioi, and it is distinctly separated from the crista alaris. The septomaxillae (Figs. S7, S10) are in medial contact centrally, forming an elevated medial ridge that approaches the ventral surface of the median region of the nasals. No lateral foramen is visible at the base of the postero-lateral process. The anterior-most part of the septomaxilla contacts the vomer and the maxilla dorsally. The lateral process contacts the dorsal surface of the central part of the vomer. The anteromedial margins of the vomers (Figs. S3, S8–9) meet medially. The vomerine process of the palatine (Figs. S3, S7–10) is more than a third of the length of the entire bone. The medial margin of the palatine process of the pterygoid (Figs. S3, S7–9) is concavely curved. The epipterygoid (Figs. S2, S4) has about the same width throughout its length and is not anteroposteriorly compressed. The anterior process of each epipterygoid (Figs. S1, S6, S9–10) is about as long or even slightly longer than the posterior process. There seem to be only two foramina on the quadrate (Figs. S4, S8) in most specimens, lacking the medially oriented foramen in the upper half of the quadrate. The bones of the braincase (parabasiphenoid, basiocipital, supraoccipital, prootics, and otocipititals; Figs. S2, S7, S9) are fused with each other in two specimens (ZFMK 33843, 33844), partially separated in one specimen (ZFMK 33846), and not fused in three specimens (ZFMK 33840, 33854, 33856). The crista alaris (Fig. S2) of the prootic portion of the braincase is distinctly larger than in T. chirioi. The basipterygoid processes (Figs. S3, S7, S9) are longer and narrower and more triangular in shape. The anteromedial region of the parabasiphenoid is approximately triangular, only the apex of the triangle is missing.

The dentary (Fig. S12) is almost straight and only the anterior region is medially curved. It bears 31–39 tooth loci. The dorsal process bifurcates at its posterior end, distinctly behind the last mandibular tooth. The four mental foramina of the dentary are situated between the 4th and 23rd–26th tooth. The anterolateral process of the coronoid (Fig. S12) starts with a clear distance behind the last dentary tooth. The anteromedial process seems to be barely covered by other bones; it is therefore not much longer than the visible area, and it starts at about the posterior end of the splenial foramen. The articular, surangular, and prearticular are completely fused with each other to form the compound bone (Fig. S12) in five specimens (ZFMK 33840, 33843, 33844, 33846, 33856) and the surangular is almost entirely separated from the compound bone in one specimen (ZFMK 33854).

Etymology.—Peters (1869) named the species in commemoration of the explorer Dr. Carl Theodor Herrmann Steudner, from whose collection the original holotype stemmed.

Distribution.—Tropiocolotes steudneri is distributed on the eastern bank of the Nile River in the north of Sudan (Fig. 12), but in Egypt, Baha El Din (1999; Fig. 6) and Krause et al. (2013; Fig. 12) reported the species both east and west of the Nile. According to Baha El Din (1999), Krause et al. (2013), and Bauer et al. (2017), it has a wider distribution, from southern Libya and eastern Chad, to the Egyptian coast of the Red Sea. Loveridge (1947) also reported the species in southern Algeria, and Bauer et al. (2017) used Loveridge’s records as reference to mention T. steudneri in Algeria. We identify the specimens in Loveridge (1947), from the Amguid heights, as T. tassieliensis (here described). Thus, Algerian specimens of T. steudneri previously reported in the literature are actually T. tassieliensis. We do not expect T. steudneri to occur in Algeria. Machado et al. (2021) limited the distribution of Tropiocolotes steudneri to the eastern side of the Nile River, but our preliminary results revising the genus show that it occurs both east and west of the river.

Remarks.—In the last decades, descriptions of new species of Tropiocolotes did not use Sudanese specimens of Tropiocolotes steudneri for species comparisons to characterize diagnoses. Furthermore, the original morphological characters, presented by Peters (1869), have never been considered as the morphological features of this species and were not used to compare it with others. We therefore consider differences in literature between T. steudneri and other species as tentative.

Discussion

Despite the Sahara Desert being the largest ecoregion in Africa (Olson et al., 2011), the species richness of reptiles in the region is still underestimated (Froufe et al., 2013; Harris et al., 2004, 2007; Machado et al., 2021; Metallinou et al., 2012, 2015; Rato et al., 2007; Velo-Anton et al., 2018; Wagner et al., 2011). The dwarf-gecko genus Tropiocolotes is widely distributed along the region and it can be found from the Atlantic coast of Western Sahara to the Red Sea coast of Egypt, and from the Mediterranean coast of Egypt, Libya, and Tunisia to the southern border with the Sahel ecoregion. Like most of Saharan reptiles, when studied in detail, it shows an undescribed, cryptic diversity hidden under the taxonomy currently used for the genus (Machado et al., 2021; present study, and unpubl. data).

Uncovering hidden diversity in the genus Tropiocolotes is unsurprising, because most species are thought to have a wide distribution (Machado et al., 2021), but fragmented range in the landscape. This is the result of very specific association with environmental conditions and restrictions, and ecological limitations to dispersion (pers. obs.). The Sahara is composed of rocky, mountainous areas in a sandy desert matrix that constitutes a remarkable barrier for dispersion, working as an archipelago-like system (Anthelme et al., 2011; Gon¸calves et al., 2012). The areas represent isolated suitable areas for a wide array of species including Tropiocolotes, act as biodiversity refugia, and play an important role in the diversification across the region (Brito et al., 2014, 2016). The occurrence of unique/endemic Tropiocolotes species associated with the refugia makes these geckos promising Saharan models to study the influence of the vegetation and climatic turnovers in the recent past and the role that mountains and sandy areas have played in shaping biodiversity patterns. Meanwhile, biogeographical isolation is certainly the most important factor explaining allopatric diversification processes in Tropiocolotes (a case of vicariance prompted by the formation and expansion of sandy areas) in the Sahara Desert.
The distribution and diversity of Tropiocolotes species were recently updated, and important new insights were published by Machado et al. (2021) and Ribeiro-Júnior et al. (2022). The authors found high levels of undescribed diversity in the Levant (T. nattereri A and B), northwestern Africa (T. tripolitanus A, B, and C), and the southern Arabian Peninsula (T. scorteccii A, B, and C). Ribeiro-Júnior et al. (2022) described T. yomtovi (the lineage named as T. nattereri A in Machado et al., 2021), designated a neotype for T. nattereri from Sinai, Egypt, and updated the distribution of the T. nattereri species group in the Middle East. Despite the description of T. yomtovi, a large amount of undescribed diversity exists in all major areas across the geographic range of the genus. Samples used in Machado et al. (2021) to recover such diversity did not include specimens here described as new species (T. chirioi and T. tassiliensis).

Our newly described species further increase the diversity in the Central Sahara Mountains and in the westernmost foothills of the Aurès Mountains, both in Algeria.

Despite sharing morphological similarities, such as having keeled scales on the body, and despite their geographic proximity, we found that Tropiocolotes chirioi and T. tripolitanus tripolitanus (to which T. tripolitanus C may belong; see Machado et al., 2021) differ in eight diagnostic characters. The characters include meristic characters, color pattern, skull characters, and discrete external morphology (see Species Comparisons above). The region of salt lakes in central Tunisia and northeastern Algeria (wetlands known as Chotts) probably acts as a biogeographic barrier, separating Tropiocolotes chirioi (from the Aurès Mountains) and T. tripolitanus tripolitanus (from the northeastern border of Grand Erg Oriental, in Tunisia, presented in Machado et al., 2021). Rivers, wetlands, and paleo-river systems are established as barriers to gene flow and dispersions even in the Sahara region (Machado et al., 2021).

We hypothesize Tropiocolotes algericus is the species most closely related to T. chirioi, because they share many morphological characters, such as similarities in color patterns. Differences between them include one meristic character (the number of scales around midbody), one discrete character (the size and shape of the gular scales), and the general shape of the snout (shorter in T. algericus). Tropiocolotes algericus and T. chirioi also occur in the same biogeographic region, the Atlas Mountains Range. However, the Hodna Basin, separating the Saharan Atlas from the Aurès and Tunisian Atlas (de Lamotte et al., 2000), probably acted as a barrier resulting in the split of T. chirioi and T. algericus from their common ancestor. A detailed phylogenetic study including both species is still needed to confirm our hypothesis. Comparison between the skull morphologies of T. chirioi and T. algericus is also needed to qualify internal differences observed in the external shapes of head and snout.

Baha el Din (1999; 24) described Tropiocolotes nubicus from localities immediately bordering the Nile Valley in southern Egypt, suggesting it could be found also in the north of Sudan. Differences between T. steudneri and T. nubicus were based on specimens from Egypt. Baha el Din (1999) wrote in the Diagnosis (page 18) “Tropiocolotes steudneri has smaller scales on the head, a proportionately shorter tail and a different dorsal pattern,” and in the Discussion (page 25) “T. nubicus can be distinguished from its closest congener by the coarse scales on the head (fewer interorbital scales and gulars), proportionately longer tail, irregular dorsal pattern and higher number of tail bands. T. steudneri, on the other hand, has a better defined neck, a distinct dorsal pattern made up of three longitudinal rows of dark and light spots, fewer and more clearly marked bands on the tail.” Based on morphological similarities, he presented T. nubicus as the closest congener of T. steudneri. Our results, comparing Sudanese population of T. steudneri with data of T. nubicus in Baha el Din (1999), suggest that the number of interorbital scales cannot be used to distinguish T. nubicus and T. steudneri. However, all other characters are still valid, and the number of gular scales and color patterns remain strong diagnostic features. For example, specimens of T. nubicus from Algeria have the same dorsal pattern observed in specimens from the Nile margins, and this pattern is clearly distinct from the color pattern of T. steudneri. The strength of this character is also supported by the molecular analyses of Machado et al. (2021), who used samples of T. nubicus from Algeria and Egypt. Here we include six additional new osteological characters that distinguish T. nubicus from T. steudneri. Machado et al. (2021) also present T. nubicus as a closely related species to T. steudneri.

Tropiocolotes tassiliensis and T. nubicus are sympatric in southern Algeria. They can be easily distinguished from each other by color pattern, the number of gular scales, and six additional osteological characters. Tropiocolotes tassiliensis and T. steudneri differ in color pattern, the number of dorsal and midbody scales, and in one skull character (the size of premaxilla-maxilla aperture). Based on a higher level of similarities in skull morphology between T. tassiliensis and T. steudneri rather than between T. tassiliensis and T. nubicus, we suggest the new endemic Algerian species may be closely related to T. steudneri. This hypothesis needs to be confirmed by phylogenetic analyses.

In total, five species of Tropiocolotes are now known to occur in Algeria, indicating three allopatic groups of species: Tropiocolotes algericus in the westernmost portion of the Saharan Atlas Mountain Range, with a disjunct population in the northern portion of the Tadema¨ıt rocky plateau; Tropiocolotes chirioi in the western portion of the Aurès Mountains; and “T. tripolitanus C” (or T. tripolitanus tripolitanus, see Machado et al., 2021), T. nubicus, and T. tassiliensis in the Hoggar Plateau. Sympathy between two or more Tropiocolotes species, as observed in the Hoggar Plateau, was also found along the Nile River (Baha el Din, 1999), in Yemen and Oman (Machado et al., 2018), in Mauritania (Machado et al., 2021), and in southern Israel (Ribeiro-Júnior et al., 2022). The distribution patterns of the Algerian endemics Tropiocolotes chirioi and T. tassiliensis strongly coincide with the main biogroups of endemic species, suggested by Brito et al. (2016), to the Sahara-Sahel ecoregions. Among them, the conservation status of T. chirioi deserves special attention. The species is known from a few specimens and its known range is likewise very small, displaying a particularly high vulnerability in the face of land use change in northeastern Algeria (Brito et al., 2016). Thus, its conservation status should be evaluated in further studies, and its status should be prioritized for evaluation by an IUCN specialist group (though we note no gecko specialist group currently exists). Despite T. tassiliensis being also known from a few individuals in collections, its wide distribution range in southeastern Algeria, most inside the largest protected areas in Algeria, suggests a Least Concern conservation status. However, the available taxonomic and ecological knowledge about Saharan reptile species is clearly very limited, and our study and previous ones have shown that much biodiversity is still to be described. Because many endemic species have not yet been formally described, the quantification of biodiversity loss is certainly underestimated, and given that estimates of
biodiversity loss do not consider this uncovered diversity, conservation strategies and policies are further underrepresented in this region (Lewin et al., 2016; Roll et al., 2017; Tolley et al., 2016).

We presented the first detailed description of the skulls of three Tropiocolotes species, and information on the cranial osteology of two other species of the genus (Table 3), all obtained by micro-CT scans. We examined 14 skulls of Tropiocolotes specimens. In general, the skulls show many similarities, which can vary within the family Gekkonidae (Evans, 2008). These include: a single premaxilla; paired nasals that are not in contact with prefrontals; medial lappets of maxillae in close distance behind premaxilla but without meeting each other; single frontal with fused cristae cranii; paired parietals; postorbitofrontal meeting neither prefrontal nor squamosal; jugal present; pterygoid meeting neither jugal nor maxilla; large and oval suborbital fenestra; maxilla excluded from suborbital fenestra; slender squamosal present; no ossified orbitosphenoid; lacrimal absent; supratemporal absent; temporal absent; stapedial foramen present; splenial present; angular absent; and surangular and articular completely fused.

However, there are also some differences between the skulls we examined. Some vary between the examined species of the genus Tropiocolotes, others may even vary relatively strongly between individuals of one species. Bauer et al. (2013) investigated some cranial osteological differences between representative species of the genera Microgecko and Tropiocolotes, M. helenae and T. tripolitanus, using micro-CT scans of one individual each. They concluded that the two genera have fundamental osteological differences that are typically invariant within a single gekkotan genus. We studied four of the five differences they mention and illustrate (omitting the absence/presence of a second ceratobranchial arch). Within these four, we found at least three to be very variable within the genus Tropiocolotes (size of the jugal bone, concealed/visible condition of the anterolateral process of the frontal, presence and size of the premaxilla-maxilla aperture). We suggest that they should therefore not be further considered as differences between Tropiocolotes and Microgecko. In our examined specimens, we could find a large variation in the size of the jugal bone and in the concealed/visible condition of the anterolateral process of the frontal even within a species, whereas the presence or size of the premaxilla-maxilla aperture differed between species. Because all our examined individuals of Tropiocolotes showed a paired nasal bone, the fused nasal condition of Microgecko remains as the sole difference between the two genera.

The holotype of Tropiocolotes steudneri has been considered lost by all authors who once revised species in this genus. Peters (1869), in the original publication, provides detailed description that strongly agrees with the specimen here designated as neotype. Characters such as smooth body scales, nine sublabials, seven infralabials, two pairs of submentals (here mentioned as postmentals), two scales bordering rostral posteriorly (here as internasals), a band from nostril to neck, transverse rows on anterior body followed by three rows of irregular spots along posterior body, and 30 mm SVL, can be recognized in the neotype here designated to this species. The type-locality given by Peters (1869), "from the Sennar, without further details of locality," has been allocated to the state of Sennar, Sudan (see Bauer et al. 2017:198). However, the historical Sennar had a much larger extent than the current state of the same name. Because Sudanese specimens of this species are very scarce in collections, the neotype (collected at Wadi Halfa, Northern state, Sudan) originates from another state, but fits the original description. In order to stabilize nomenclature as much as possible in Tropiocolotes, our designation establishes the diagnostic characters of T. steudneri, crucial in new species descriptions, comparisons, identifications of new specimens, and delimitation of distribution patterns.

Machado et al. (2021) produced the most comprehensive phylogenetic hypothesis to the genus Tropiocolotes, providing new insights into the geographic distribution of many species. Using substantial and reliable information in internal and external morphology of type-series of most of species in a genus, and the combination of adequate and innovative methods, we here described T. chirioi and T. tassiliensis as new species from Algeria. Tropiocolotes chirioi and tassiliensis and the designation of a neotype to T. steudneri can provide relevant conservation insights for the region. The Sahara Mountains form a biogeographic region that is still considered as having low species diversity for vertebrates in general, as well as for reptiles and geckos (Lewin et al., 2016; Roll et al., 2017). The description of new Saharan endemic species such as T. chirioi and T. tassiliensis may help establish a near-future turning point in the knowledge of the Sahara biodiversity, in which it is no longer considered as having low species diversity, but instead having high levels of endemism that need protection.

Here, we have provided the most comprehensive assessment to date on osteology and external morphology characters of Tropiocolotes species, considering type-series in the species comparisons. We showed that the current diversity in the genus remains underestimated, increasing the total number of Tropiocolotes species from 13 to 15 species. However, we recognize and highlight that many questions still need to be addressed to the genus, such as phylogenetic relationship of the new species with other Tropiocolotes species, and ecological and historical mechanisms involved in the evolutionary history of the species in the genus. We emphasize that studies of species variation and distribution boundaries for the other Sahara species are still needed. Herpetological collections are the most important data source for these kinds of studies. We are now working to decrease these gaps, and based on preliminary results revising the genus, we agree with Machado et al. (2021) indicating that the species diversity of the genus is greatly underestimated.

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Supplementary Data
Supplementary data associated with this article can be found online at http://dx.doi.org/10.1670/10-103.51
**SUPPORTING INFORMATION**


*Referred Specimens (osteology).*—*Tropiocolotes chirioi*: ZFMK 2350, 2351 (paratypes), Biskra, Ferme Dufoury, Algeria. *Tropiocolotes nubicus*: FMNH 256869 (paratype), town of Abu Simbel, Egypt. *Tropiocolotes steudneri*: ZFMK 33840, 33843, 33844, 33846, 33854, 33856, Wadi Halfa/Assuan-Stausee, Sudan. *Tropiocolotes tassiliensis*: CAS 138662 (holotype), at 3 km E of Tamanrasset on road to Adriane, Algeria; ZFMK 19853 (paratype), at 15 km south of Terhenanet, Algeria. *Tropiocolotes tripolitanus tripolitanus*: ZMB 9668A (lectotype) and ZMB 9668B (paralectotype), Uadi M’bellem, Libya; NMW 17298:2, Zuila, Libya.
TABLE S1. Measurements of all specimens of *Tropiocolotes chirioi* sp. nov. and *T. tassiliensis* sp. nov., and *T. steunderi* (measurements in millimeters; abbreviations in the main text). Only intact tails were considered.

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<th>HD</th>
<th>NL</th>
<th>ShL</th>
<th>TL</th>
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Fig. S1. Micro-CT images of the dorsal view of the skulls of *Tropiocolotes chirioi* sp. nov. (ZFMK 2350), *T. nubicus* (FMNH 256869), *T. tassiliensis* sp. nov. (CAS 138662), *T. tripolitanus* (ZMB 9668A), and *T. steudneri* (ZFMK 33844).
Fig. S2. Micro-CT images of the lateral view of the skulls of *Tropiocolotes chirioi* sp. nov. (ZFMK 2350), *T. nubicus* (FMNH 256869), *T. tassiliensis* sp. nov. (CAS 138662), *T. tripolitanus* (ZMB 9668A), and *T. steudneri* (ZFMK 33844).
Fig. S3. Micro-CT images of the ventral view of the skulls of *Tropiocolotes chirioi* sp. nov. (ZFMK 2350), *T. nubicus* (FMNH 256869), *T. tassiliensis* sp. nov. (CAS 138662), *T. tripolitanus* (ZMB 9668A), and *T. steudneri* (ZFMK 33844).
Fig. S4. Micro-CT images of the anterior view of the skulls of *Tropiocolotes chirioi* sp. nov. (ZFMK 2350), *T. nubicus* (FMNH 256869), *T. tassiliensis* sp. nov. (CAS 138662), *T. tripolitanus* (ZMB 9668A), and *T. steudneri* (ZFMK 33844).
Fig. S5. Micro-CT images of the posterior view of the skulls of *Tropiocolotes chirioi* sp. nov. (ZFMK 2350), *T. nubicus* (FMNH 256869), *T. tassiliensis* sp. nov. (CAS 138662), *T. tripolitanus* (ZMB 9668A), and *T. steudneri* (ZFMK 33844).
Fig. S6. Micro-CT images of the dorsal view of the skulls of *Tropiocolotes chirioi* sp. nov. (ZFMK 2350), *T. nubicus* (FMNH 256869), *T. tassiliensis* sp. nov. (CAS 138662), *T. tripolitanus* (ZMB 9668A), and *T. steudneri* (ZFMK 33844). For a better view, the lower jaws were removed.
Fig. S7. Micro-CT images of the dorsal view of the skulls of *Tropiocolotes chirioi* sp. nov. (ZFMK 2350), *T. nubicus* (FMNH 256869), *T. tassiliensis* sp. nov. (CAS 138662), *T. tripolitanus* (ZMB 9668A), and *T. steudneri* (ZFMK 33844). For a better view, the lower jaws, ectopterygoids, frontal, jugals, maxillae, parietals, postorbitofrontals, prefrontals, premaxilla, and squamosals were removed.
Fig. S8. Micro-CT images of the dorsal view of the skulls of *Tropiocolotes chirioi* sp. nov. (ZFMK 2350), *T. nubicus* (FMNH 256869), *T. tassiliensis* sp. nov. (CAS 138662), *T. tripolitanus* (ZMB 9668A), and *T. steudneri* (ZFMK 33844). For a better view, the lower jaws, ectopterygoids, frontal, jugals, maxillae, parietals, postorbitofrontals, prefrontals, premaxilla, squamosals, braincase (fused parabasiphenoid, basioccipital, supraoccipital, prootic, and otooccipital), epipterygoid, and septomaxillae were removed.
Fig. S9. Micro-CT images of the ventral view of the skulls of *Tropiocolotes chirioi* sp. nov. (ZFMK 2350), *T. nubicus* (FMNH 256869), *T. tassiliensis* sp. nov. (CAS 138662), *T. tripolitanus* (ZMB 9668A), and *T. steudneri* (ZFMK 33844). For a better view, the lower jaws were removed.
Fig. S10. Micro-CT images of the ventral view of the skulls of *Tropiocolotes chirioi* sp. nov. (ZFMK 2350), *T. nubicus* (FMNH 256869), *T. tassiliensis* sp. nov. (CAS 138662), *T. tripolitanus* (ZMB 9668A), and *T. steudneri* (ZFMK 33844). For a better view, the lower jaws, maxillae, premaxilla, braincase (fused parabasiphenoid, basioccipital, supraoccipital, prootic, and otooccipital), pterygoids, and vomers were removed.
Fig. S11. Micro-CT images of the ventral view of the skulls of *Tropiocolotes chirioi* sp. nov. (ZFMK 2350), *T. nubicus* (FMNH 256869), *T. tassiliensis* sp. nov. (CAS 138662), *T. tripolitanus* (ZMB 9668A), and *T. steudneri* (ZFMK 33844). For a better view, the lower jaws, maxillae, premaxilla, braincase (fused parabasiphenoid, basioccipital, supraoccipital, prootic, and otooccipital), pterygoids, jugals, septomaxillae, vomers, ectopterygoids, epipterygoids, and quadrates were removed.
Fig. S12. Micro-CT images of the right mandibulae of *Tropiocolotes chirioi* sp. nov. (ZFMK 2350), *T. nubicus* (FMNH 256869), *T. tassiliensis* sp. nov. (CAS 138662), *T. tripolitanus* (ZMB 9668A), and *T. steudneri* (ZFMK 33844) in dorsal, ventral, lateral, and medial views (top to bottom).