On the dentition of the Cape Verdean endemic lizard genus *Chioninia* Gray, 1845, with a discussion of ecological implications in the giant species *C. coctei* (Duméril & Bibron, 1839)

(Squamata, Scincidae)

Wolfgang Böhme, Hermann Schleich, Benjamin Wipfler & Thore Koppetsch

Böhme, W., Schleich, H., Wipfler, B. & Koppetsch, T. 2022. On the dentition of the Cape Verdean endemic lizard genus *Chioninia* Gray, 1845, with a discussion of ecological implications in the giant species *C. coctei* (Duméril & Bibron, 1839) (Squamata, Scincidae). Spixiana 45 (1): 131–140.

Some small scincid lizard jaw fragments with multicuspid teeth recovered from a heap of subrecent to subfossil owl pellets on the island of Razo, Cape Verde archipelago, are described and documented by macro photography and μ-CT-imaging. They are compared with the dentition of extant members of the endemic Cape Verdean skink genus *Chioninia* Gray, 1845. Most likely, these jaws belonged to juvenile specimens of the extinct endemic Cape Verdean Giant Skink *C. coctei* (Duméril & Bibron, 1839). We take this opportunity to discuss the specialised dentition in respect to food specialisation and other features of this remarkable but obviously extinct lizard in a functional and ecological context, dealing with body size, nutrition, locomotion (tail prehensibility), activity patterns, longevity, reproduction, commensalism with seabirds, and insular gigantism.

Wolfgang Böhme (corresponding author) & Benjamin Wipfler, Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 127, 53113 Bonn, Germany; e-mail: w.boehme@leibniz-zfmk.de

Hermann Schleich, Instituto y Nucleo Zoologico Arco, Paraje El Cerillo, no. 1, 04200 Tabernas, Spain

Thore Koppetsch, Natural History Museum, University of Oslo, P.O. Box 1172, Blindern, 0318 Oslo, Norway; and Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 127, 53113 Bonn, Germany

Introduction

Until the beginning of this millennium the endemic Cape Verdean scincid radiation was considered to be part of the pantropical genus *Mabuya* Fitzinger, 1826 (Mausfeld et al. 2002), but it was Greer (1970, 1977) who first challenged the monophyly of this collective group by giving osteological evidence that the Asian genera *Dasia* Gray, 1839 and *Apterygodon* Edeling, 1864 would derive from an Asian *Mabuya* descent. This was approved by molecular data by Honda et al. (1999), thus rendering *Mabuya* polyphyletic. Consequently, and based on an expanded molecular

data set, Mausfeld et al. (2002) partitioned *Mabuya* into four genera, the fourth of which was the distinct and long isolated evolutionary lineage of the Cape Verdean mabuyine species which they assigned to the genus *Chioninia* Gray, 1845, with the type species *Gongylus* (*Euprepes*) *delalandii* Duméril & Bibron, 1839.

Currently, *Chioninia* comprises seven species (Miralles et al. 2010). Six of them, *C. delalandii* (Duméril & Bibron, 1839), *C. fogoensis* (O'Shaughnessy, 1874), *C. nicolauensis* (Schleich, 1987), *C. spinalis* (Boulenger, 1906), *C. stangeri* (Gray, 1845) and *C. vaillanti* (Boulenger, 1887) are relatively small to medium-sized terrestrial lizards. In comparison the seventh one,

Fig. 1. A. Dorsal view of an adult specimen of *C. coctei* (NMB 230277) from the Natural History Museum Basel and obtained from Fritz Müller in 1885. Scale bar: 10 cm. **B.** Head of the same individual in lateral view with multicuspid teeth being visible in the lower jaw. Scale bar: 1 cm. Photos by Thore Koppetsch.

C. coctei (Duméril & Bibron, 1839), is a true giant ("far more than half a meter": Mertens 1955; "with up to 60 cm total length": Andreone & Gavetti 1998). The Cape Verdean Giant Skink shows several unique adaptations which led earlier authors to accommodate it in an own monotypic genus *Macroscincus* Bocage, 1873, or its just two years younger synonym *Charactodon* Troschel, 1875. The genus-group nomen *Gongylus* Duméril & Bibron, 1839 in the original description of the species as *Gongylus* (*Euprepes*) *coctei* is preoccupied by *Gongylus* Thunberg, 1815 (Insecta, Mantodea). It may be noted that Duméril & Bibron (1839) treated their two new species *C. delalandii* and *C. coctei* already together in one common subgenus *Euprepes* Wagler, 1830.

Despite the long-lasting assignment of *C. coctei* to the monotypic genus *Macroscincus* Bocage, 1873 for more than a century, a closer relationship to the sympatric mabuyine skinks of the genus *Chioninia* was already suspected by Greer (1976) on osteological grounds, and the formal of transfer of *Macroscincus* to this taxon was unavoidable after Miralles et al. (2010) had shown that it is phylogenetically nested within *Chioninia*, thus otherwise rendering this genus paraphyletic.

C. coctei is an aberrant giant among its congeners and can be distinguished from all of them by its much bigger size with a snout-vent length up to 320 mm (Fig. 1A) (Bocage 1873a, Greer 1976, Andreone & Gavetti 1998) (vs. 65–123 mm in the other 6 species), and a much higher dorsal and midbody scale count (unique in the family Scincidae: Mertens 1934) (134–152 and 102–113 (vs. 52–95 and 33–65 in the six congeners) (Miralles et al. 2010). Its specialized multicuspid dentition (Fig. 1B) (Bocage 1873a, Troschel 1875, Greer 1976, Schleich 1979) to which also Troschel's (1875) genus name *Characto-don* (from the Greek charáktos = notched, according to the author) refers, points on omnivory (seeds of malvacean plants on the one hand, bird eggs and

even nestlings on the other). Concerned are mostly seabirds, viz. shearwaters and petrels: Leach's storm petrel *Hydrobates leucorhous* (Vieillot, 1818) (Stübel in Troschel 1875), Scopoli's shearwater *Calonectris diomedea* Scopoli, 1769 (Schleich 1979) and/or Cape Verde shearwater *Calonectris edwardsii* (Oustalet, 1883) (Schleich 1982). Their nesting caves were also used by the big skinks as shelter (Troschel 1875, Greer 1976, Schleich 1979), a commensalism that is also known for the King's skink *Egernia kingii* from Australia found in burrows of the Wedge-tailed shearwater *Ardenna pacifica* and Flesh-footed shearwater *A. carneipes* (Warham 1958, Bancroft et al. 2008) and the famous Tuatara from New Zealand and its interaction with fairy prions *Pachyptila turtur*, among others (Walls 1978, Markwell 1998).

Some small lizard jaw fragments (dentaries) with multicuspid teeth (Fig. 2) resembling the tooth shape of *C. coctei* were found by one of us (HS: see Schleich 1982) on the Cape Verdean island of Razo within an accumulation of numerous lizard bones, most likely originating from pellets of the Cape Verdean Barn Owl, *Tyto alba detorta* Hartert, 1913 (Herrmann 1993). This find raised the question after their taxonomic assignment and led us to compare them with the dentition of most of the other Cape Verdean *Chioninia* species.

Material and methods

The three small lizard jaw fragments with multicuspid teeth were recovered and isolated from a 20 cm thick layer of lizard bones found in an 80×170 cm big semi-cavern in the interior of Razo Island (Schleich 1982, Herrmann 1993), one of the three unpopulated so-called Desertas Islands within the Cape Verde archipelago, from where a former occurrence of the giant skink had been reported (Bocage 1873a, b). They are, together with numerous other cranial skeletal remains from the same heap, deposited in the Zoologisches Forschungsmuseum A. Koenig (ZFMK), Bonn, under ZFMK 103764 (Fig. 2). The jaw fragments were photographed by using a Nikon D 750 camera, photo lens Nikon AF-S Miro Nikkor 105 mm, 1:2.8G ED with Teleconverter TC-20E III. The two single teeth of an adult male of *C. coctei* from the Zoologische Staatssammlung's (ZSM, Munich, Germany) collection belong to ZSM 1/1978 (Fig. 3). An additional adult specimen of *C. coctei* (NMB 230277) (Fig. 1) from the Natural History Museum Basel and obtained from Fritz Müller in 1885 was examined and

photographed by using a digital single-lens reflex camera Canon EOS 80D. For comparing the dentition, and in order to explore whether the small dentaries are from juvenile giant skinks or possibly from a smaller (unknown) *Chioninia* species with likewise multicuspid teeth, we CT-scanned and 3D-reconstructed the skulls and dentition of six other taxa, among them also the sympatric *C. stangeri* from the same small island (Figs 4–6).

Next to the tooth fragments of *C. coctei*, μ-CT scans of the heads of the following taxa were prepared: *C. delalandii* (ZFMK 26854, juvenile, from "San Jan, Kapverdische Inseln")[1], *C. fogoensis* (ZFMK 83560, subadult, from Santo Antão Island), *C. spinalis* (ZFMK 83576, juvenile, from Ilheu Santa Maria, near São Thiago Island), *C. stangeri stangeri* (ZSM 12/1982/1) and ZFMK 102308 from Razo Island, *C. stangeri salensis* (ZFMK 83595, juvenile, from Boa Vista Island), and *C. vaillanti* (ZFMK 76313, adult, and 76321, juvenile, no island record).

The CT scanning was performed with either a Skyscan 1272 or 1173 (Bruker) at the ZFMK. The samples were firmly positioned in tubes which were glued on a stub before scanning. Table 1 contains the scan parameters for each scan. All scans were performed over 360° and are deposited in the virtual collection of the ZFMK. They were imported into Amira 6.1.2 (Thermofisher) where the skulls were separated from scales and the tube. Subsequent volume rendering was performed in VG Studio 3.3 (Volume Graphics). Final images were assembled to plates and labeled in Photoshop CS6 and Illustrator CS6 (Adobe).

Results

The three jaw fragments consist of the dentary bone with a row of markedly multicuspid teeth (Fig. 2) and are of equal size, measuring 11 mm. They each bear 18 teeth with cusps varying from 3 to 7 per tooth. The tooth shape corresponds largely to the single tooth of an adult *C. coctei* as figured by the drawing in Greer (1976) and the SEM photograph in Schleich (1979). Two maxillary teeth of this last-named individual, an adult male from the collection of the Zoologische Staatssammlung (ZSM 1/1978), are shown as renders based on μ-CT scans (Fig. 3).

The teeth of the other, smaller *Chioninia* species have a much simpler structure and are unicuspid with the exception of the next smaller species after *C. coctei*, viz. *C. vaillanti*. In this species the maxillary and dentary teeth of an adult (ZFMK 76313) as well as a juvenile specimen (ZFMK 76321) are tricuspid (Figs 5 and 6A–B). The scans of the remaining,

---

1   There is no island named "San Jan" in the Cape Verde archipelago. The specimen bearing this – handwritten – locality had been sent by Alexander Strauch of the St. Petersburg Museum to the Zoological Museum in Göttingen in 1868, from where it has been transferred to Bonn (ZFMK) in 1977. Most likely it is a confusion with "St. Jago", as spelled by Boulenger (1897) which is São Thiago, where *C. delalandii* actually occurs.

smaller *Chioninia* species revealed unicuspid teeth in the species and subspecies studied here: *C. delalandii*, *C. fogoensis*, *C. spinalis*, *C. stangeri stangeri* and *C. st. salensis* (Figs 4 and 6C–G). Of these, only the specimen of *C. delalandii* (ZFMK 26854) showed really sharply pointed teeth (Figs 4E–F and 6E), while *C. spinalis* (ZFMK 83576: Figs 4G–H and 6C) and the two forms of *C. stangeri* (ZSM 12/198 and ZFMK 83595) had their teeth a little bit less pointed, tending to a blunt shape (Figs 4A–B and I–J, 6F–G).

An extreme condition of tooth bluntness was shown by the skull of *C. fogoensis* (ZFMK 83560) where the individual teeth show a shallow depression on their tips which look hollowed or cupped (Figs 4C–D and 6D). This variety of tooth shape in the genus is discussed below.

Discussion

The interspecific dentitional variation of the Cape Verde *Chioninia* species, in connection with the dramatic different size classes within the genus, pose a number of questions of ecological and evolutionary relevance which are discussed below. The focus is laid on the giant representative of the genus, *C. coctei*, which is moreover believed to be extinct.

Survival

There have been several attempts to rediscover this charismatic and remarkable lizard in its restricted, hardly accessible distribution area and habitat. Visits of the islands, particularly of Branco, Razo and Santa Luzia, have been carried out by Schleich (1979, 1982), Schleich & Wuttke (1983), Andreone (2000) and Köhler et al. (2007), but all of them failed to find evidence for a surviving specimen. The only partial success was with Mateo et al. (2005) on Santa Luzia

where they were able to isolate two small lizard bones from domestic cat faeces, an angular and a maxillary bone of a lizard, the latter with quinquecuspid teeth which they assigned to a medium-sized individual of *C. coctei* of ca. 150 mm snout-vent length. Santa Luzia is separated from Branco by a relative shallow sea depth of only 25 m, while the second locality where *C. coctei* occurred, viz. Razo, is separated from Branco by a sea depth of ca. 90 m (Schleich & Wuttke 1983). The new small multicuspid dentaries from Razo Island reported here (Fig. 2) do not change the assumption of *C. coctei*'s likely extinction (Schleich 2001) because they are coloured brownish, thus suggesting a subrecent or even subfossil age.

Dentition and nutrition

The term "five cuspid" used by Miralles et al. (2010) should be replaced by quinquecuspid. The presence of multicuspid teeth (here with five or even more cusps (see Fig. 3) – Troschel (1875) used the German terms "crenulirt" or "gekerbt"=crenulate or notched) – points on a herbivore, non-carnivore or at least less carnivore nutrition (Greer 1976), and the multicuspid, crenulate teeth resemble those of the predominantly herbivore Green Iguana, *Iguana iguana* (Linnaeus, 1758) (see fig. 5 in Edmund 1969). According to Troschel (1875) *C. coctei* feeds on seeds of Malvacean plants, presumably of the genus *Abutilon* Miller, 1754 (see Schleich 1982), on bird eggs and sometimes bird (petrel and shearwater) nestlings, according to Stübel (in Troschel 1875) in one case (*Hydrobates leucorhous*) even when these were still alive. This reminds of the likewise giant anguid lizard *Diploglossus millepunctatus* O'Shaughnessy, 1874, an endemic of the isolated rocky, likewise sparsely vegetated Colombian Malpelo Island in the Pacific Ocean (Graham 1975). This big growing lizard is omnivorous and known to consume marine crabs and

Table 1. Parameters for the performed µ-CT scans.

Species	Collection number	Scanner Skyscan	Voltage (kV)	Current (µA)	Rotation steps (°)	Exposure time (ms)	Spatial resolution (µm)	Frame averaging	Random movement
C. coctei	ZSM 1/1978	1272	45	140	0.20	1000	2.350	7	15
C. coctei	ZFMK103764	1272	60	166	0.25	1458	5.300	8	15
C. delalandii	ZFMK26854	1272	43	160	0.35	1300	3.800	8	15
C. fogoensis	ZFMK83560	1173	42	160	0.27	500	7.098	8	15
C. spinalis	ZFMK83576	1272	43	160	0.35	1400	4.000	8	15
C. stangeri stangeri	ZSM12798	1173	40	170	0.25	500	10.273	7	15
C. stangeri salensis	ZFMK83595	1173	38	170	0.27	500	8.874	7	15
C. vaillanti	ZFMK76313	1173	43	114	0.31	600	14.906	7	15
C. vaillanti	ZFMK76321	1272	43	160	0.35	1300	5.000	7	15

Fig. 2. Subrecent / subfossil dentary bones (ZFMK 103764) of two juvenile individuals of *C. coctei* from Razo Island, Cape Verde archipelago, in (**A**, **C**) buccal and (**B**, **D**) lingual view. Scale bar: 1 mm. Photos by Morris Flecks.

Fig. 3. Volume renders of the μ-CT scans of two maxillary teeth of an adult *C. coctei* male (ZSM 1/1978) in (**A**, **D**) buccal, (**B**, **E**) lateral and (**C**, **F**) lingual view.
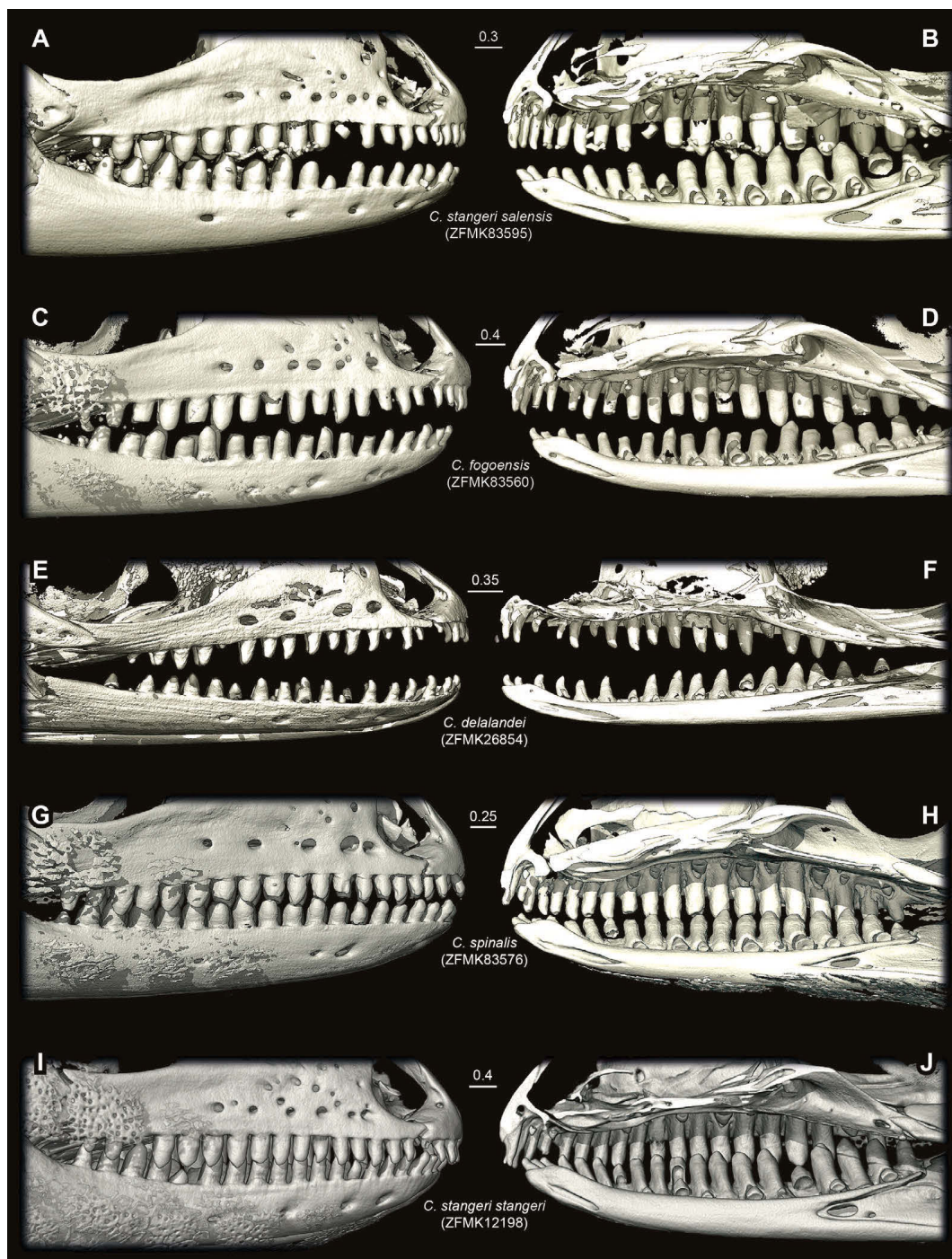
Fig. 4. Volume renders of the μ-CT scans of skulls of different *Chioninia* species in (**A**, **C**, **E**, **G**, **I**) lingual and (**B**, **D**, **F**, **H**, **J**) buccal view: **A–B.** *C. stangeri salensis* (ZFMK 83595) from Boa Vista; **C–D.** *C. fogoensis* (ZFMK 83560) from Antão Island; **E–F.** *C. delalandii* (ZFMK 26845) from São Thiago; **G–H.** *C. spinalis* (ZFMK 83576) from Ilheu Santa Maria near São Thiago; **I–J.** *C. stangeri stangeri* (ZFMK 12198) from Razo Island.

fish regurgitated by booby nestlings, *Sula dactylatra* Lesson, 1831, but uses also carcasses of these birds as food resource (Kiester 1975, López-Victoria et al. 2009, 2011). Its tooth shape, however, is not comparable with the dentition of this carnivore whose teeth are slightly transformed towards a cutting edge (WB: unpublished observation in ZFMK 91586). In contrast, Klingelhöffer (1957) stated *C. coctei* to be an "eingefleischter Vegetarier" (= inveterate vegetarian) which feeds on meat only in rare cases, but was also observed to feed on a living bird and on cherries.

The other studied, much smaller species of *Chioninia* have all but one unicuspid teeth, the exception being the relatively biggest among this smaller species assemblage, viz. *C. vaillanti*. This lizard, reaching up to 295 mm total length (Schleich 1987) has tricuspid teeth, as already described with a drawing of a single tooth by Greer (1976) and documented here by μ-CT-scans of skulls of both an adult and a juvenile specimen (ZFMK 76313 and 76321: Figs 5 and 6A–B). The teeth resemble in shape those of some Canarian lacertid species, e.g. the giant *Gallotia simonyi* (Steindachner, 1889), a lizard likewise known as omnivorous but with a particularly high percentage of plant food (Naeslund & Bischoff 1998).

Among the other species of *Chioninia*, viz. *C. delalandii*, *C. fogoensis*, *C. spinalis*, *C. stangeri stangeri*, and *C. st. salensis* (Figs 4 and 6C–G) with unicuspid teeth, the studied specimen of *C. fogoensis* from Santo Antão showed markedly blunt teeth, ending in a stump, shallow concavity on the terminal tip (see Figs 4C–D and 6D). Blunt teeth crowns are considered to be adaptations for crashing hard-shelled prey items and have been also described for the Australian skink *Cyclodomorphus gerrardii* (Edmund 1969), some Teiidae (Presch 1974), particularly the snail-eating caiman lizards of the genus *Dracaena* (Dalrymple 1979), other lizards feeding on molluscs, like the anoles *Chamaeleolis* (Estes & Williams 1984, Herrel & Holanova 2008), but also for snakes feeding on hard-bodied arthropodes, e.g. the dark-headed dwarf racer *Eirenis persicus* (Rajabizadeh et al. 2021). Snails (*Theba* spp.) are known as food also from the likewise big-growing skink *Eumeces schneiderii* in Israel (Moran 1979), for possible food items on the Cape Verdean islands see Boekschoten & Gittenberger (1987).

Not much is known about the food spectra of these skinks except for some data from fecal analyses published by Schleich (1987). His data for *C. delalandii*, *C. fogoensis*, *C. st. stangeri*, *C. stangeri salensis* and *C. vaillanti* from various islands yielded insects in all cases, but in various combinations: tettigoniid and acridid orthopterans, mymeleontids, cercopid cicadas, coreid, cydnid, lygaeid and pentatomid bugs, formicids, and finally carabid as well as tenebrionid beetles; *C. vaillanti* took a special place because its feces contained "many young leaves and buds, possibly from cistacean plants" (Schleich 1987). This is in accordance with the above-mentioned *Gallotia simonyi* which shows the same tricuspid tooth structure and also consumes mostly plant material (Naeslund & Bischoff 1998). Only for *C. fogoensis*, Schleich (1987) recorded some undetermined "plant remains". So the only *Chioninia* species with a significant part of plants in its nutrition is *C. vaillanti*, at the same time the only one with tricuspid (rather than unicuspid) teeth. The other species with some plant content in its food spectrum is *C. fogoensis* with its modified blunt, cupped teeth. One of us (TK) also detected digested leaves of brassicacean plants, remains of formicids and a Cape Verdian wolfspider *Allocosa* sp. in the stomach content of a preserved *C. delalandii* (ZFMK 83547). Further analyses of stomach content on a larger scale must corroborate these very preliminary findings.

Body size and scalation

C. coctei reached a snout–vent length (SVL) of up to 320 mm (Fig. 1A), while the SVL of all other congeneric species ranges from 65 to 122 mm (the last value being the maximum in *C. vaillanti*: Schleich 1987). The maxillary bone recovered by Mateo et al. (2005) was calculated to stem from an intermediate to big individual of ca. 150 mm SVL. Among the 37 specimens from three Italian collections measured by Andreone & Gavetti (1998) only two were classified as juveniles. They had a total length of 245 (130 + 105) and 163 (77 + 93) mm respectively. Remarkably, the smallest, i.e. youngest specimen is the only one where the tail length is still exceeding the body length, a ratio which is reversed in all other – larger – individuals! The specimens which we studied in the present contribution are estimated to 45–50 mm SVL at best. This fits approximately the egg measurements which were published by Andreone & Gavetti (1998) as being up to 41.2 x 23.5 mm found in preserved females (see below in the chapter Reproduction).

The dorsal scale count is 134–152 in *C. coctei*, vs. 52–95 in the other congeners. Similarly, *C. coctei* has a midbody scale count of 102–113, vs. 33–65 in its congeners (Mertens 1934, Greer 1976, Miralles et al. 2010). The high scale numbers are considered to be correlated with increasing body size, as can be seen from table 2 in Greer (1976) where they are compared with other big-growing skinks.

Locomotion

According to Peracca (1891b), the tail of *C. coctei* is prehensile, although it looks too short for being really functional in this respect, since the tail is making less than half of the total length of the lizard
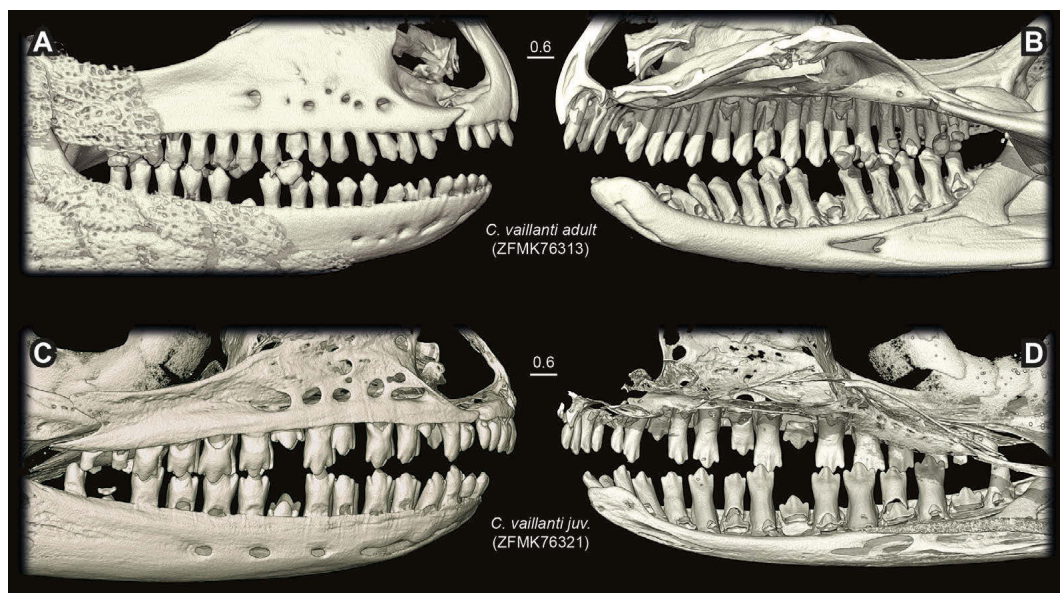
Fig. 5. Volume renders of the μ-CT scans of skulls of an (**A**, **B**) adult (ZFMK 76313) and (**C**, **D**) juvenile specimen (ZFMK 76321) of *C. vaillanti* (no island records) in (**A**, **C**) lingual and (**B**, **D**) buccal view.

(Fig. 1A) (Troschel 1875). Mertens (1934) compared it with the long prehensile tail of the likewise big, but arboricolous Solomon Islands skink *Corucia zebrata* Gray, 1855. He speculated that the giant Cape Verde skink might have also been arboricolous, in former times when there forests might have been present on these islands. According to Klingelhöffer (1957), Berg and Peracca have observed this species during climbing. Here, the tail was bent like a hook and used even for hanging on branches but said to break off easily and the regenerate lost its grasping ability. However, the tail could also have been used just for being adpressed on steep rocky surfaces when climbing downwards (Schleich 1979).

According to Greer (1976), the grasping capability of *C. coctei*'s tail is not convincing. We agree with this scepticism for two further reasons: (1) the relative tail length is markedly sexually dimorphic (Andreone & Gavetti 1998), thus implying unlikely different locomotory abilities among the sexes, and (2) only a minority of Peracca's (1891a) fourty specimens had intact tails which can serve as another argument against a true prehensile function as tail shedding (autotomy) is not common in lizards with prehensile tails. However, a higher tail-shedding rate could also be due to a higher population density with increased intraspecific aggression, e. g. around seabird colonies and would not completely exclude a prehensile function in (former) forested habitats. Moreover, Mertens (1934) characterized this lizard –

in strong contrast to its smaller agile congeners – not only as stout and clumsy but also as behaviourally sluggish, but Berg (again according to Klingelhöffer 1957) called it a nimble runner, the belly of which, however, would be always dragging on the floor.

Further evidence of the prehensibility of *C. coctei*'s tail could be gained from a study of its tail vertebrae which have typical structural modifications in prehensile-tailed lizards (Koppetsch et al. 2020).

Reproduction

Although termed a live-bearer by Uetz et al. (2021), *C. coctei* is clearly an oviparous species. The parchment-shelled eggs have been described by Peracca (1891a, b) and Andreone & Gavetti (1998). However, its congener *C. vaillanti* is in fact a live-bearing species, with newborn hatchlings (born in captivity) measuring around 80 mm in total length (Schleich 1987). Again according to Uetz et al. (2021), also the other smaller congeners are all viviparous, making *Chioninia* one of the relatively few squamatan genera with both reproduction modes. If our calculation is correct that the juveniles from which the 11 mm long dentaries described here were derived, had a SVL of 45–50 mm, the eggs described by Andreone & Gavetti (1998) could have been in an advanced stage shortly before deposition already. However, there is no information so far on the developmental stage of the embryos contained in these eggs. In any case the

juveniles associated with the dentaries described here represent the smallest individuals of *C. coctei* known so far, much smaller than the smallest completely preserved juvenile in Andreone & Gavetti's (1998) collection which has a SVL of 77 mm.

Activity pattern

In regard of the daily activity, there are observations on a both diurnal and nocturnal activity pattern in *C. coctei*. While Alexander (1898) observed the lizards basking on flat places of the rocky slopes, an old native shepherd told one of us (HS: Schleich 1982) that he saw the lizards – many years ago – being active at night, a phenomenon corroborated by observing captive specimens (Vaillant 1882, Peracca 1891b). Such an activity pattern is also known from the big-growing *Gallotia* species on the Canary Islands where the infraspecific communication takes place by colour signals during the day, but – due to the heat-storing of the lava rocks after sunset – continues being active at night, now communicating by acoustic signals (Böhme et al. 1985). It is known from Schleich's (1987) observations of the agonistic and courtship behaviour in captive *C. vaillanti* that the smaller *Chioninia* species communicate by optical signals. But already the colour signals provided by the reddish throat and belly of *C. nicolauensis* (Schleich 1987), or the yellow tympanic region in *C. vaillanti xanthotis* (Miralles et al. 2010) point on this kind of communication for which diurnality is the prerequisite, at least when territoriality is also involved. Similarly, young *C. coctei* have a more vivid dorsal colour pattern. The dull colouration of the adults, despite the three colour phases distinguished by Andreone & Gavetti (1998) would fit with a more nocturnal life habit. Whether or not nocturnal acoustic communication was present in this giant lizard will most likely remain unknown for ever.

The shepherd cited above (Schleich 1982) who had informed HS on the nocturnal activity of *C. coctei*, had also reported that the big lizards were active only in the rainy season. However, already Greer (1976) characterised its habitat as a desertic environment and Schleich (1987) pointed out that there was no rainfall on the islands since at least 18 years!

Commensalism with seabirds

One ecological peculiarity not known from any other Cape Verde *Chioninia* species is the close coexistence with seabirds (shearwaters and petrels) in their nesting holes or caves (Troschel 1875, Alexander 1898, Greer 1976, Schleich 1979), although there is evidence that this mutualistic system can also be regarded as parasitism since the bird eggs and sometimes nestlings are used as food items, the latter, as mentioned above even when still alive (Troschel 1875). This behaviour reminds of the similarly big, stout and clumsy giant anguid *Diploglossus millepunctatus* (Kiester 1975) on Malpelo Island. However, similar behavioural traits are also known from a variety of other scincids coexisting with sea birds, e. g. *Egernia kingii* (Warham 1958), including egg-rolling from rock edges to reach the yolk, or the use of food items regurgitated by seabirds when feeding their offspring (Greer 1976 and references cited therein).

Longevity

Andreone & Guarino (2003) determined the age of 27 specimens of this extinct species, collected at the end of the 19th century and kept in the Museo Zoologico dell' Università di Torino (MZUT) by skelettochronology. They reported individual ages of 16 years for males and 11 years for females while one juvenile was estimated to be 4 years old. This longevity in the wild which correlates according to the authors with their giant size, is remarkable but paralleled and exceeded, though in captivity, by the likewise giant lacertids *Gallotia intermedia* from Tenerife (Böhme 2014) and *Timon lepidus* (Daudin, 1802) from southern Spain (Böhme & Esser 2015).

Giants and dwarfs in sympatry

The body size evolution of sympatric and congeneric Atlantic island lizards went several times in two opposite directions. This is particularly evident in the lacertid lizards of the genus *Gallotia* Boulenger, 1916, of the Canary Islands. On each of the western islands except Gran Canaria exist two sympatric species, a giant and a markedly smaller congener: on El Hierro *Gallotia simonyi* (Steindachner, 1889) and *G. caesaris* (Lehrs, 1914), on La Palma *G. auaritae* Mateo, García-Marquez, Lopez-Jurado & Barahona, 2001 and *G. galloti* (Oudart, 1839), on La Gomera *Gallotia bravoana* Hutterer, 1985 and *G. caesaris*, and on Tenerife *G. intermedia* Hernandez, Nogales & Martín, 2000. Solely Gran Canaria with the giant *G. stehlini* (Schenkel, 1901) and the eastern islands Lanzarote and Fuerteventura with the small *G. atlantica* (Peters & Doria, 1882) have only one endemic species each. A special case is Tenerife, as the extinct, subfossil *G. goliath* (Mertens, 1942) was markedly larger than *G. intermedia*. This situation is well comparable with that of *Chioninia coctei*, the extinct giant, having coexisted with the small *C. stangeri*, but another species of intermediate size evolved on the archipelago, viz. *C. vaillanti*. This led Carranza et al. (2001) to speak about "parallel gigantism" in the evolution of the Cape Verde skink radiation. The evolutionary mechanisms should be the same on both Macaronesian archipelagos (see also Bischoff 1998).
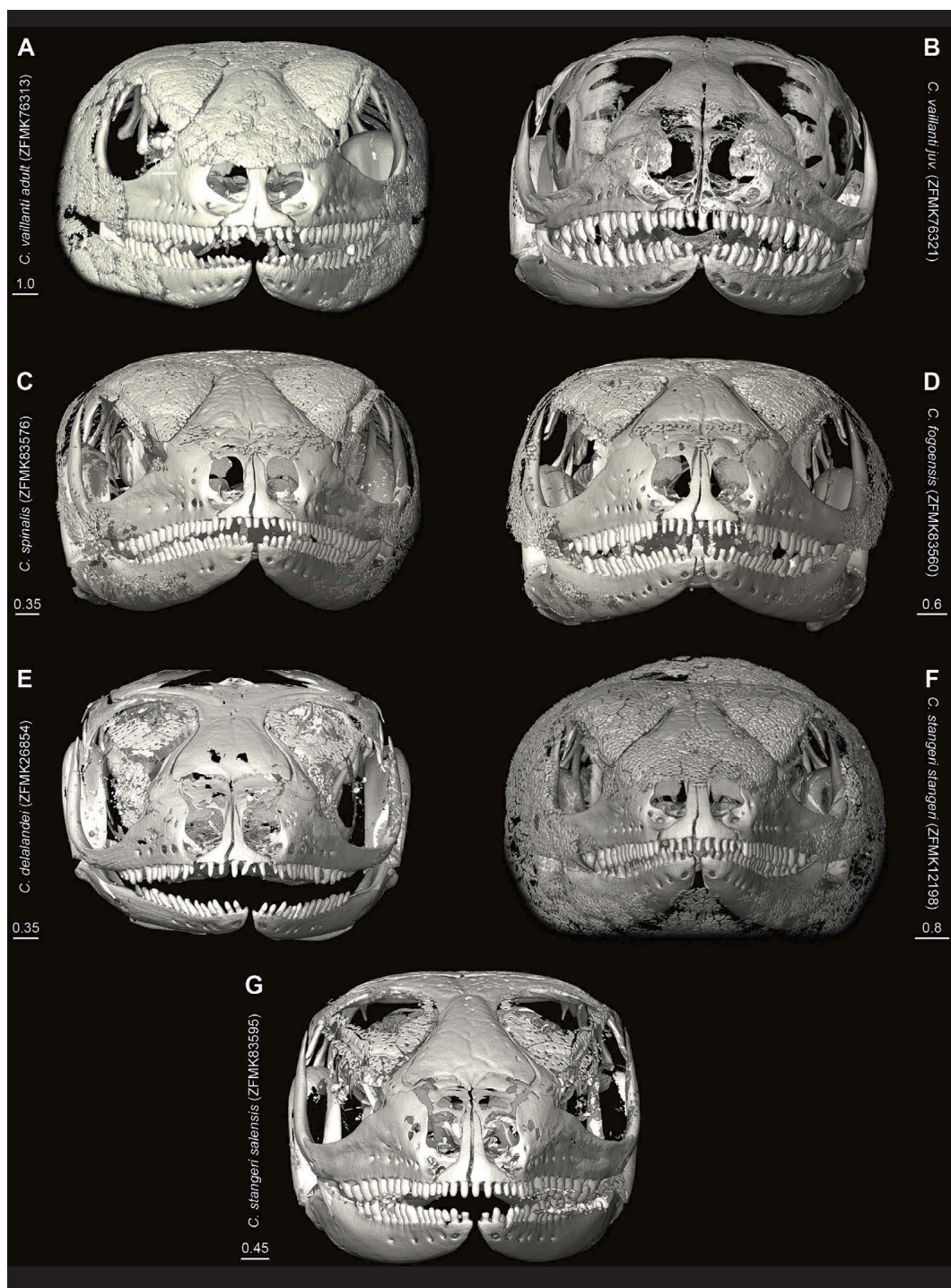
Fig. 6. Volume renders of the µ-CT scans of skulls of different *Chioninia* species in frontal view: **A.** adult (ZFMK 76313) and **B.** juvenile specimen (ZFMK 76321) of *C. vaillanti*; **C.** *C. spinalis* (ZFMK 83576); **D.** *C. fogoensis* (ZFMK 83560); **E.** *C. delalandii* (ZFMK 26845); **D.** *C. stangeri stangeri* (ZFMK 12198); **G.** *C. stangeri salensis* (ZFMK 83595).

Conclusion

All aspects discussed above have influenced the evolution, morphological specialisation and niche occupation of the Cape Verde giant skink and have resulted in an overestimation of ecomorphological adaptive specialisations, thus leading to its allocation in a monotypic genus. There are many such over-estimations of ecomorphological adaptations. One comparable example, among numerous others, but also partly based on multicuspid dentition and herbivory, is represented by the Namib sand-swimming gerrhosaurid *Gerrhosaurus skoogi* Andersson, 1916. Because of its ecomorphic adaptation to sand-diving in aeolian sand dunes and its multicuspid teeth (1 to 5 cusps per tooth: Nance 2007) that correlates with its diet of windblown grass seeds in shallow dune depressions, it has been placed by FitzSimons (1953) in an own monotypic genus *Angolosaurus* FitzSimons, 1953. However, phylogenetic analyses placed it clearly among the species of its original genus *Gerrhosaurus* Wiegmann, 1828 which otherwise would have been rendered paraphyletic, too (Lamb et al. 2003, Lamb & Bauer 2013). A monotypic isolation of a species is only justified if there is evidence for a very long independent evolution which is, however, according to the genetic data of Miralles et al. (2010) not the case here.

Acknowledgements

References

Alexander, H. 1898. An ornithological expedition to the Cape Verde Islands. Ibis 4 (7): 74–118.

Andreone, F. 2000. Herpetological observations on Cape Verde: a tribute to the Italian naturalist Leonardo Fea, with complementary notes on *Macroscincus coctei* (Duméril & Bibron, 1839). Herpetozoa 13 (1/2): 15–26.

– – & Gavetti, E. 1998. Some remarkable specimens of the giant Cape Verde skink, *Macroscincus coctei* (Duméril & Bibron, 1839), with notes on its distri-bution and possible extinction. Italian Journal of Zoology 65: 413–421.

– – & Guarino, F. M. 2003. Giant and long-lived? Age structure in *Macroscincus coctei*, an extinct skink from Cape Verde. Amphibia-Reptilia 24: 459–470.

Bancroft, W. J., Roberts, J. D. & Garkaklis, M. J. 2008. Vertebrate fauna associates of the Wedge-tailed Shearwater, *Puffinus pacificus*, colonies of Rottnest Island: influence of an ecosystem engineer. Papers and Proceedings of the Royal Society of Tasmania 142 (1): 21–30.

Bischoff, W. 1998. Bemerkungen zu den "fossilen" Rieseneidechsen der Kanarischen Inseln. Pp. 387–407 in: Bischoff, W. (ed.). Die Reptilien der Kanari-schen Inseln, der Selvagens-Inseln und des Madeira-Archipels. Handbuch der Reptilien und Amphibien Europas, Vol. 6. 448 pp., Wiesbaden (AULA).

Bocage, J. V. Barboza du 1873a. Notice sur l'habitat et les caractères du *Macroscincus coctei* (*Euprepes coctei* Dum. et Bibr.). Journal des Sciences Mathématiques, Physique et Naturelles 16: 1–12.

– – 1873b. Notes sur l'habitat de l'*Euprepes coctei* Dum. et Bibr. Proceedings of the Zoological Society London 1873: 703–704.

Böhme, W. 2014. Herpetology in Bonn. Mertensiella 21: 1–256.

– – & Esser, S. 2015. A remarkable age and size record of a male Jewelled Lizard, *Timon lepidus* (Daudin, 1802). Herpetozoa 28 (1): 104–106.

– – , Hutterer, R. & Bings, W. 1985. Die Stimme der Lacertiden, speziell der Kanareneidechsen (Reptilia, Sauria). Bonner Zoologische Beiträge 36 (3/4): 337–354.

Boekschoten, G. J. & Gittenberger, E. 1987. Fossil ter-restrial snails (Mollusca: Gastropoda) from the Cape Verde Archipelago. Basteria 51 (4/6): 125–127.

Boulenger, G. A. 1887. Catalogue of the lizards in the British Museum (Natural History). Volume III. Lacertidae, Gerrhosauridae, Scincidae, Anelytropsi-dae, Dibamidae, Chamaeleontidae. 575 pp., London (Trustees of the British Museum).

Carranza, S., Arnold, E. N., Mateo, J. A. & Lopez-Jurado, L. F. 2001. Parallel gigantism and complex coloniza-tion patterns in the Cape Verde scincid lizards *Mabuya* and *Macroscincus* (Reptilia: Scincidae) revealed by mitochondrial DNA sequences. Proceedings of the Royal Society of London. Series B. 268 (1476): 1595–1603.

Dalrymple, G. 1979. On the jaw mechanism of the snail-crushing lizards: *Dracaena* Daudin 1802 (Rep-tilia, Lacertilia, Teiidae). Journal of Herpetology 13: 303–311.

Duméril, A. M. C. & Bibron, G. 1839. Erpétologie gé-nérale ou histoire naturelle complète des reptiles, Vol. 5. 855 pp., Paris (Librairie Encyclopédique de Roret).

Edmund, A. G. 1969. Dentition. Pp. 117–200 in: Gans, C., Bellairs, A. d'A. & Parsons, T. S. (eds). Biology of the Reptilia, Vol. 1 (Morphology A). 373 pp., London and New York (Academic Press).

Estes, R. & Williams, E. E. 1984. Ontogenetic variation in the molariform teeth of lizards. Journal of Vertebrate Paleontology 4(1): 96–107.

FitzSimons, V. 1953. A new genus of gerrhosaurid from southern Angola. Annals of the Transvaal Museum 22(2): 215–217.

Graham, J. B. (ed.) 1975. The biological investigation of Malpelo Island, Colombia. Smithsonian Contributions to Zoology 176: 1–98.

Greer, A. E. 1970. The relationships of the skinks referred to the genus *Dasia*. Breviora 348: 1–20.

–– 1976. On the evolution of the giant Cape Verde scincid lizard *Macroscincus coctei*. Journal of Natural History 10: 691–712.

–– 1977. The systematics and evolutionary relationships of the scincid lizard genus *Lygosoma*. Journal of Natural History 11: 515–540.

Herrel, A. & Holanova, V. 2008. Cranial morphology and bite force in *Chamaeleolis* lizards – adaptations to molluscivory? Zoology 111(6): 467–475.

Herrmann, D. 1993. Osteologische Untersuchungen an isolierten Knochen des Cranialskelettes holozäner Geckos und Skinke der Insel Razo / Cabo Verde (Reptilia, Sauria: Gekkonidae, Scincidae). Master Thesis, Ludwig Maximilian University, Munich, 185 pp.

Honda, M., Ota, H., Kobayashi, M., Nabhitabhata, J., Yong, H.-S. & Hikida, T. 1999. Evolution of Asian and African lygosomine skinks of the *Mabuya* group (Reptilia: Scincidae): a molecular perspective. Zoological Science 16: 979–984.

Kiester, A. R. 1975. Notes on the natural history of *Diploglossus millepunctatus* (Sauria: Anguidae). Pp. 39–43 in: Graham, J. B. (ed.). The biological investigation of Malpelo Island, Colombia. Smithsonian Contributions to Zoology 176.

Klingelhöffer, W. 1957. Terrarienkunde / Dritter Teil: Echsen. 2. Auflage, 264 pp., Stuttgart (Alfred Kernen-Verlag).

Köhler, G., Hertz, A., Sunyer, J., Seipp, R. & Monteiro, A. 2007. Herpetologische Forschungen auf den Kapverden unter besonderer Berücksichtigung des Kapverdischen Riesenskinks, *Macroscincus coctei.* Elaphe 15(4): 62–66.

Koppetsch, T., Böhme, W., Büsse, S. & Gorb, S. N. 2020. Comparative epidermal microstructural anatomy and limb and tail osteology of eyelid geckos (Squamata: Eublepharidae): implications of ecomorphological adaptations. Zoologischer Anzeiger 287: 45–60.

Lamb, T. & Bauer, A. M. 2013. To be or not to be *Angolosaurus*: a multilocus perspective on the phylogenetic position of Africa's desert plated lizard (Gerrhosauridae). Zoologica Scripta 42(4): 381–388.

––, Meeker, A. M., Bauer, A. M. & Branch, W. R. 2003. On the systematic status of the desert plated lizard (*Angolosaurus skoogi*): phylogenetic inference from DNA analysis of the African Gerrhosauridae. Biological Journal of the Linnean Society 78: 253–261.

López-Victoria, M., Herrón, P. A. & Botello, J. C. 2011. Notes on the ecology of the lizards from Malpelo Island, Colombia. Boletín de Investigaciones Marinas y Costeras – INVEMAR 40: 79–89.

––, Wolters, V. & Werding, B. 2009. Nazca Booby (*Sula granti*) inputs maintain the terrestrial food web of Malpelo Island. Journal of Ornithology 150(4): 865–870.

Markwell, T .J. 1998. Relationship between tuatara *Sphenodon punctatus* and fairy prion *Pachyptila turtur* densities in different habitats on Takapourewa (Stephens Island), Cook Strait, New Zealand. Marine Ornithology 26: 81–83.

Mateo, J. A., Lopez-Jurado, L. F. & Garcia Marquez, M. 2005. Primeras evidencias de la supervivencia del escinco gigante de Cabo Verde, *Macroscincus coctei* (Duméril & Bibron, 1839). Boletín de la Asociación Herpetológica Española 15(2): 73–75.

Mausfeld, P., Schmitz, A., Böhme, W., Misof, B., Vrcibradic, D. & Rocha, C. F. D. 2002. Phylogenetic affinities of *Mabuya atlantica* Schmidt, 1945, endemic to the Atlantic Ocean archipelago Fernando de Noronha (Brazil): Necessity of partitioning the genus *Mabuya* Fitzinger, 1826 (Scincidae: Lygosominae). Zoologischer Anzeiger 241: 281–293.

Mertens, R. 1934. Die Insel-Reptilien, ihre Ausbreitung, Variation und Artbildung. Zoologica,. Originalabhandlungen aus dem Gesamtgebiete der Zoologie 81: 1–209.

–– 1955. Die Eidechsen der Kapverden. Societas Scientiarum Fennica, Commentationes Biologicae 15(5):1–17.

Miralles, A., Vasconcelos, R., Perera, A., Harris, D. J. & Carranza, S. 2010. An integrative taxonomic revision of the Cape Verdean skinks (Squamata, Scincidae). Zoologica Scripta 40(1): 16–44.

Moran, S. 1979. A lizard, *Eumeces schneiderii*, preying on the snail *Theba pisana*. Israel Journal of Zoology 28: 38.

Naeslund, C. & Bischoff, W. 1998. *Gallotia simonyi* (Steindachner, 1889) – Hierro-Rieseneidechse. Pp. 341–370 in: Bischoff, W. (ed.). Die Reptilien der Kanarischen Inseln, der Selvagens-Inseln und des Madeira-Archipels. Handbuch der Reptilien und Amphibien Europas, Vol. 6. 448 pp., Wiesbaden (AULA).

Nance, H. 2007. Cranial osteology of the African gerrhosaurid *Angolosaurus skoogi* (Squamata; Gerrhosauridae). African Journal of Herpetology 56(1): 39–75.

Peracca, M. G. 1891a. Sulla oviparità del *Macroscincus coctei* Dum. et Bibr. Bollettino del Museo e Laboratorio di Zoologia e Anatomia Comparata dell R. Università di Genova 6(105): 1.

–– 1891b. Osservazioni sul *Macroscincus coctei* D. B. Bollettino del Museo e Laboratorio di Zoologia e Anatomia Comparata dell R. Università di Genova 6(107): 1–5.

Presch, W. 1974. A survey of the dentition of the macroteiid lizards (Teiidae: Lacertilia). Herpetologica 344–349.

Rajabizadeh, M., Van Wassenbergh, S., Mallet, C., Rücklin, M. & Herrel, A. 2021. Tooth-shape adaptations in aglyphous colubrid snakes inferred from three-dimensional geometric morphometrics and finite element analysis. Zoological Journal of the Linnean Society 191 (2): 454–467.

Schleich, H. H. 1979. Der Kapverdische Riesenskink, *Macroscincus coctei*, eine ausgestorbene Echse? Natur und Museum 109 (5): 133–138.

– – 1982. Letzte Nachforschungen zum kapverdischen Riesenskink, *Macroscincus coctei* (Duméril & Bibron, 1839) (Reptilia: Sauria: Scincidae). Salamandra 18 (1/2): 74–85.

– – 1987. Herpetofauna Caboverdiana. Spixiana, Zeitschrift für Zoologie, Supplement 12: 1–75.

– – 2001. Dokumentation zur Ausrottung einer Tierart – Der Kapverdische Riesenskink. Broschüre zur Ausstellung im Fuhlrott-Museum: 1–12.

– – & Wuttke, M. 1983. Die kapverdischen Eilande Santa Luzia, Branco und Razo – ein Reisebericht. Natur und Museum 113 (2): 33–44.

Troschel, H. 1875. Über die Rieseneidechse der Inseln des Grünen Vorgebirges. Archiv für Naturgeschichte 41 (2): 111–121.

Uetz, P., Freed, P., Aguilar, R. & Hošek, J. (eds) 2021. The Reptile Database. http//www.reptile-database.org [accessed 21 November 2021].

Vaillant, L. 1882. Sur les *Macroscincus coctei* D., B., récemment arrivés à la ménagerie du Muséum d'Histoire Naturelle. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, Paris 95 (12): 811–812.

Walls, G. Y. 1978. The influence of the tuatara on fairy prion breeding on Stephens Island, Cook Strait. New Zealand Journal of Ecology 1: 91–98.

Warham, J. 1958. The nesting of the shearwater *Puffinus carneipes*. The Auk 75 (1): 1–14.