Variations on a bauplan: description of a new Malagasy "mermaid skink" with flipper-like forelimbs only (Scincidae, *Sirenoscincus* Sakata & Hikida, 2003)

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ABSTRACT
The "forelimbs only" bauplan, characterised by the combined presence of well-developed fingered forelimbs and the complete absence of hindlimbs, is rare among terrestrial tetrapods. It is restricted to three lineages of squamates with elongated worm-like bodies, the amphisbaenian genus *Bipes* Lacépède, 1788 and the scincid genera *Sirenoscincus* Sakata & Hikida, 2003 and *Jarujinia* Chan-ard, Makchai & Cota, 2011. In the present study, we describe a new species of *Sirenoscincus* from Marosely, Port Bergé region, northwest Madagascar, which

presents a remarkable variation of this bauplan. The forelimbs of *S. mobydick* n. sp. differ from *S. yamagishii* Sakata & Hikida, 2003 – the only other known species in the genus – by the complete absence of any fingers or claws, therefore superficially resembling flippers, a combination of characters unique among terrestrial tetrapods. *Sirenoscincus mobydick* n. sp. is also differentiated from *S. yamagishii* by several apomorphic cephalic scalation characters, such as: 1) the absence of the frontonasal, likely fused with the frontal (versus presence of both scales); 2) the absence of the preocular, likely fused with the loreal (versus presence of both scales); and 3) the absence of the postsubocular, likely fused with the pretemporal (versus presence of both scales). Additionally, we provide detailed data on the appendicular skeleton of this new species of "mermaid skink" based on X-ray computed tomography that reveal several significant regressions of skeletal elements: 1) autopodial bones highly reduced in size and number; 2) highly reduced pelvic girdle and complete absence of hindlimbs, with the notable exception of two faintly distinguishable bony corpuscles probably representing rudiments of ancestral hindlimb bones; and 3) regressed sclerotic ring with five ossicles only, therefore representing the lowest value ever observed among lizards. Our study highlights the importance of the rare "forelimbs only bauplan" for investigating macroevolutionary questions dealing with complete limb loss in vertebrates, a convergent phenomenon that has repeatedly occurred 16 to 20 times within Scincidae Gray, 1825.

RÉSUMÉ
Variations sur un plan d'organisation : description d'un nouveau « scinque sirène » malgache uniquement doté de membres antérieurs en forme de nageoires (Scincidae, Sirenoscincus *Sakata & Hikida, 2003).*
Le plan d'organisation caractérisé par la présence de membres antérieurs bien développés et l'absence de membres postérieurs (« forelimb-only bauplan ») est rare au sein des tétrapodes terrestres. Il existe seulement dans trois lignées de squamates vermiformes, les amphisbènes du genre *Bipes* Lacépède, 1788, et les scinques des genres *Sirenoscincus* Sakata & Hikida, 2003 et *Jarujinia* Chan-ard, Makchai & Cota, 2011. Nous décrivons ici une nouvelle espèce de *Sirenoscincus* de Marosely, région de Port Bergé, nord-ouest de Madagascar, présentant une remarquable variation de ce plan d'organisation. Les membres antérieurs de *S. mobydick* n. sp. diffèrent de ceux de *S. yamagishii* Sakata &Hikida, 2003 – la seule autre espèce connue dans le genre – par l'absence complète de doigts ou de griffes, ressemblant ainsi superficiellement à des nageoires, ce qui constitue une combinaison unique de caractères au sein des vertébrés terrestres. *Sirenoscincus mobydick* n. sp. se différencie également de *S. yamagishii* par plusieurs caractères apomorphes de l'écaillure céphalique, tels que : 1) l'absence de frontonasale, vraisemblablement fusionnée avec la frontale (contre la présence des deux écailles) ; 2) l'absence de préoculaire, vraisemblablement fusionnée avec la loréale (contre la présence des deux écailles) ; et 3) l'absence de post-suboculaire, vraisemblablement fusionnée avec la prétemporale (contre la présence des deux écailles). Nous donnons également une description détaillée du squelette appendiculaire de la nouvelle espèce, obtenue par imagerie tomographique à rayon X, et qui a mis en évidence la régression massive de plusieurs éléments squelettiques : 1) réduction de la taille et du nombre des os autopodiaux ; 2) réduction importante de la ceinture pelvienne, et disparition totale des os des membres posterieurs, à l'exception notable de deux corpuscules osseux à peine distincts, correspondant vraisemblablement aux vestiges des os de membres

postérieurs ancestraux ; et 3) anneaux sclérotiques réduits à cinq ossicules seulement, nombre le plus faible jamais observé chez les lézards. Notre étude souligne l'importance du « forelimb-only bauplan », rarement observé pour aborder les questions macro-évolutives traitant de la perte complète des membres chez les vertébrés, phénomène qui s'est produit de façon convergente de 16 à 20 fois au sein des seuls Scincidae Gray, 1825.

INTRODUCTION

In Madagascar, scincine lizards constitute a species-rich, ecologically and morphologically diverse radiation that has successfully colonised most of the terrestrial ecosystems of the island (Raselimanana & Rakotomalala 2003; Glaw & Vences 2007). During the last decade alone (2002-2011), 16 new species have been described out of a total number of 59, suggesting that the species diversity of this group is far from being reasonably well known (Andreone & Greer 2002; Sakata & Hikida 2003a, b; Köhler *et al.* 2009, 2010; Miralles *et al.* 2011a, b, c). The description of *Sirenoscincus yamagishii* by Sakata & Hikida (2003a) demonstrated that new species or genera of terrestrial vertebrates with extremely peculiar morphology can still be discovered even in the present day. This blind or almost blind and unpigmented species endemic to the northwestern dry forests of Madagascar represented the first known skink with relatively well-developed forelimbs and complete lack of hindlimbs. Recently, a second taxon, the genus *Jarujinia* Chan-ard, Makchai & Cota, 2011 with a similar bauplan belonging to the Asian lygosomine skinks, has been described from Thailand (Chan-ard *et al.* 2011). Such a bauplan remains nevertheless exceptional within squamates, and was previously thought to be exclusive to a single amphisbaenian genus, the mole-limbed worm-lizard *Bipes* Lacépède, 1788 (Caldwell 2003).

Recently, we discovered a second form of skink with forelimbs only in Marosely, region of Port Bergé, northwest Madagascar, morphologically similar to *Sirenoscincus yamagishii*. This new "mermaid skink" significantly differs from its congener by several cephalic scalation characteristics and by the complete absence of any external fingers or claws. Forelimb tips of this skink are smooth, rounded and slightly flattened, superficially resembling flippers, a combination of characters unique among terrestrial tetrapods.

We here name this newly discovered species, describe its external morphology, and provide data on its cephalic and appendicular skeleton based on microtomographic data.

MATERIAL AND METHODS

EXTERNAL MORPHOLOGICAL CHARACTERS

The type specimens were euthanised with a 4% MS222 solution, then fixed in a 12% formalin solution, and eventually preserved in 70% ethanol. Specimens used for comparisons with the new species are listed in Appendix 1. All measurements were recorded by AM to the nearest 0.1 mm using a dial caliper. Meristic, mensural and qualitative characters examined here are routinely used in the taxonomy of Scincidae Gray, 1825, such as scale counts or presence/absence of homologous scale fusions. Drawings were made using Adobe Illustrator CS2 and a WACOM graphic tablet CTE-640, based on photographs taken through a ZEISS stereomicroscope SteREO Discovery V12.

Scale nomenclature, scale counts and measurements used in the morphological analyses essentially follow Andreone & Greer (2002). After comparisons with related genera having plesiomorphic cephalic scalations (e.g., *Madascincus* Brygoo, 1981, *Amphiglossus* Duméril & Bibron, 1839), we preferred to use a scale nomenclature slightly different from that used by Sakata & Hikida (2003a) for *Sirenoscincus*

yamagishii. Our scale homology hypotheses are the following: 1) the scale considered by these authors to be the posteriormost supraocular is here reinterpreted as a pretemporal scale, given it is located between the ocular region anteriorly (ocular scale) and the parietal, and the primary and the upper secondary temporals posteriorly; 2) the posteriormost ocular is here reinterpreted as a postsubocular. Nuchal scales are defined as enlarged scales of the nape, transversally occupying the place of two or more rows of dorsal cycloid scale (see Miralles 2006). The ventral scales are counted in a single row from the postmentals to the preanal scales (both included in the count), with the mental scale excluded.

We were unable to examine any specimen of *Sirenoscincus yamagishii*, this species being reliably known only by the type material deposited at the Zoological collection of the Kyoto University Museum. Nevertheless, unpublished pictures of an additional specimen in life (see Fig. 1) of this enigmatic species were kindly made available by Falk S. Eckhardt. The specimen was captured, photographed and subsequently released at the botanical garden A of Ankarafantsika National Park, Madagascar (type locality of this species) in mid-September 2008. It was captured in the morning in a pitfall trap set in a sandy area within the forest, during a dry period without any precipitation.

THREE-DIMENSIONAL X-RAY
COMPUTED TOMOGRAPHY (CT)
The holotype was scanned at the Museum für Naturkunde Berlin using a Phoenix|x-ray nanotom (GE Sensing & Inspection Technologies GmbH, Wunstorf, Germany) equipped with a 180 kV high-power nanofocus tube and a tungsten target. Reconstructions were performed in datos|x-reconstruction software (GE Sensing & Inspection Technologies GmbH phoenix|x-ray) and data were visualised in VGStudio Max 2.0 (Volume Graphics GmbH, Heidelberg, Germany). The upper and lower body of the specimen were scanned separately for 1000 projections each, resulting in a magnification ratio of 5.5× and 6.4×, and a voxel size of 9.2 µm and 7.8 µm, respectively. To visualise skeletal features in three dimensions, such as the pectoral and pelvic girdles, the osteoderms were digitally isolated and rendered transparent.

ABBREVIATIONS
ACZC   Angelica Crottini zoological collection field
        number;
FAZC   Franco Andreone zoological collection field
        number;
KUZ   zoological collection of the Kyoto University
        Museum;
MNHN   Muséum national d'Histoire naturelle, Paris;
MRSN   Museo Regionale di Scienze Naturali, Torino;
UADBA   Département de Biologie animale, Université
        d'Antananarivo;
ZCMV   zoological collection Miguel Vences field
        number;
ZFMK   Zoologisches Forschungsmuseum A. Koenig,
        Bonn;
ZSM   Zoologische Staatssammlung München.

RESULTS

Family SCINCIDAE Gray, 1825
Genus *Sirenoscincus* Sakata & Hikida, 2003

Sirenoscincus mobydick n. sp.
(Figs 1A-D; 2-5)

HOLOTYPE. — Northwest Madagascar, Sofia region, commune rurale of Port Bergé II, 3 km from the village of Marosely, plateau of Bongolava (15°38'49.7"S, 47°34'59"E), 250 m above sea level, 14-15.XI.2004, collected by Mirana Anjeriniaina, UADBA R70487 (field number MA293 = ZCMV 12920).

PARATYPE. — Same data as holotype, UADBA R70488 (field number MA283).

DISTRIBUTION AND NATURAL HISTORY. — The species is only known from the type locality of the Bongolava plateau, although a *Sirenoscincus* record from Belambo forest near Antsohihy (Raselimanana 2008), north of the type locality of *Sirenoscincus mobydick* n. sp., could also refer to this species. Both known specimens were captured with pitfall traps and drift fences over night, on sandy soils within the deciduous dry forest covering the plateau. This suggests that *Sirenoscincus mobydick* n. sp. may likely have arenicolous and fossorial habits like species of the genus *Voeltzkowia* Boettger, 1893 or *Paracontias minimus* (Mocquard, 1906), taxa with whom it shares several highly derived morphological characteristics probably linked to a fossorial lifestyle in sandy habitat (e.g., rudimentary eye sunken below cephalic scales, external ear opening extremely reduced, shovel-shaped snout with a countersunk lower jaw). Compared to *S. yamagishii*, *S. mobydick* n. sp. presents a higher degree of reduction of the cephalic scalation as absence of frontonasal (likely
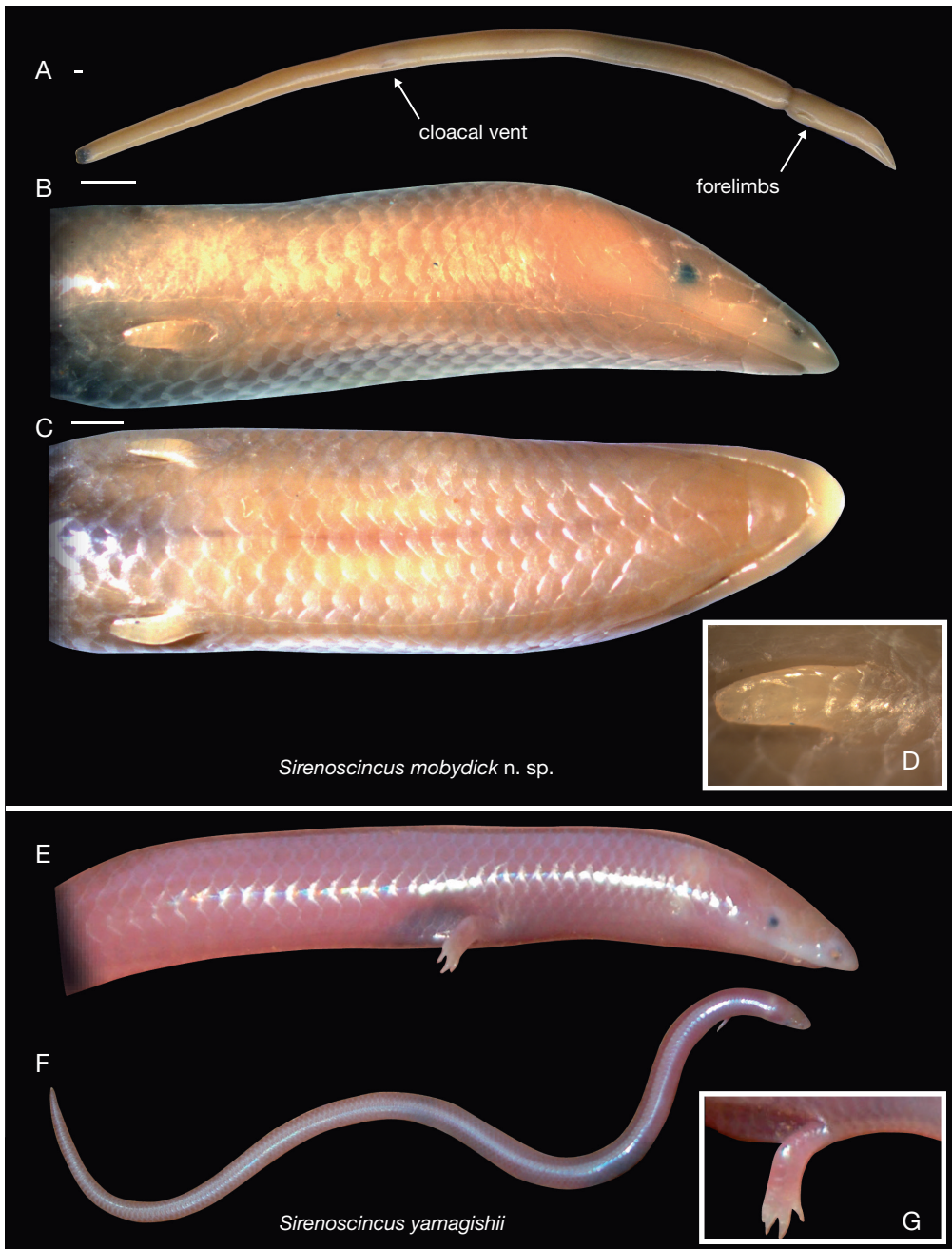
FIG. 1. — *Sirenoscincus* Sakata & Hikida, 2003: **A**-**D**, *S. mobydick* n. sp., preserved holotype UADBA R70487, lateral view of the entire specimen (**A**), lateral (**B**) and ventral (**C**) views of the anterior body part, showing highly reduced flipper-like forelimbs, and close-up of the forelimb (**D**); the constriction of the body posterior to the forelimbs is an artefact of the fastening of the collection label; **E**-**G**, living specimen of *S. yamagishii* Sakata & Hikida, 2003 from Ankarafantsika, Madagascar, lateral view of the anterior body part (**E**), dorsolateral view of the entire specimen (**F**), and close-up of the right forelimb with four claws (**G**). Scale bars: 1 mm (not shown for *S. yamagishii* because unavailable). (Photographs E-G: Falk S. Eckhardt.)

fused with the frontal), absence of preocular (likely fused with the loreal), and absence of postsubocular (likely fused with the pretemporal). These traits, together with a higher degree of forelimb regression, congruently suggest that it is morphologically more strongly adapted to fossoriality than *S. yamagishii*.

ETYMOLOGY. — The specific epithet refers to *Moby Dick*, the famous albino sperm whale imagined by Herman Melville (1851), with whom the new species shares several uncommon characteristics, such as the lack of hindlimbs, the presence of flipper-like forelimbs, highly reduced eyes, and the complete absence of pigmentation (see Fig. 7). The name is an invariable noun in apposition.

DIAGNOSIS. — The new species is a member of the genus *Sirenoscincus* as defined by Sakata & Hikida (2003a), easily distinguished from all other genera of skinks worldwide by the combination of: 1) the presence of two forelimbs and the absence of hindlimbs (all other genera except *Jarujinia* being either quadrupedal, completely legless, or having two hindlimbs only); 2) the regressed eyes sunken below scales; and 3) completely depigmented skin. It is differentiated from *S. yamagishii* (see Figs 1; 6), the only other species described within the genus, by several apomorphic characteristics: 1) the flipper-like aspect of the forelimbs (versus presence of four stout claws in *S. yamagishii*); 2) the absence of frontonasal, likely fused with the frontal (versus presence of both scales); 3) the absence of preocular, likely fused with the loreal (versus presence of both scales); and 4) the absence of postsubocular, likely fused with the pretemporal (versus presence of both scales). Additionally, *S. mobydick* n. sp. has one presacral vertebra less than *S. yamagishii* (52 in the new species versus 53), but this difference may not be reliable given the rather small sample size involved.

DESCRIPTION OF THE HOLOTYPE
External morphology
In a relatively good state of preservation, except for the tail which has been autotomised 42.3 mm posterior to the cloaca, and the presence of a constriction of the body posterior to the forelimbs where the collection tag has been tied (Fig. 1). Unsexed, apparently adult specimen. Snout-vent length 70.5 mm, width at midbody 4.1 mm, head width at level of parietal scale 3.6 mm, forelimb length 2 mm.

In general, an elongated and slender, small-sized and uniformly pale skink with two reduced flipper-like forelimbs and no hindlimbs. Snout rounded in dorsal view, bluntly wedge-shaped in lateral view; rostral extends posteriorly both dorsally and ventrally;

paired supranasals contacting medially; frontonasal absent; prefrontals absent; frontal large, hourglass-shaped, approximately as wide as long; frontoparietals absent; interparietal triangular, contacting frontal; parietals meet posterior to interparietal; nuchals undifferentiated, occupying the equivalent of two rows of dorsal cycloid scales, two on the left side, three on the right side; nostril between rostral and apex of nasal; nasal wedge-shaped; loreal single, rectangular, approximately two times longer than high; preocular absent, probably fused with the loreal; presubocular and postsubocular absent; supraocular single; ocular single, small, roughly pentagonal; eye sunken deeply below ocular, supraocular and the third supralabial; primary temporal single; secondary temporals two; tertiary temporals two; supralabials five, the second the smallest, the third the highest, partly overlapping the ocular region; postsupralabials one; external ear opening minute, covered by two scales significantly smaller than the adjacent ones. Upper jaw distinctly projecting lower jaw; mental wider than long; postmental wider than long; infralabials four, first only in contact with postmental; three pairs of large chin scales, members of first and second pair separated by one scale row, members of third pair separated by three scale rows (Fig. 2). Longitudinal scale rows at midbody 20; paravertebral scales 94 (including nuchals), similar in size to adjacent scales; ventral scales 98 (including postmental); inner preanal scales overlap outer. Two rounded flipper-like forelimbs, very short, slightly flattened, without any visible digit or claw (Fig. 2D); no hindlimbs.

Colouration
Several years after fixation, the entire head, body and tail pale overall. The eyes are recognisable as dark spots. In life, the colouration was likely uniformly pinkish like in *Sirenoscincus yamagishii*, due to the blood vascularisation of the skin (see Figs 1; 2).

Skeletal features (Figs 3-5)
Due to the methodology of X-ray CT, only the ossified parts can be described:

Pectoral girdle. Relatively complete and well developed, dorso-ventrally flattened and roughly

FIG. 2. — Drawings of the holotype of *Sirenoscincus mobydick* n. sp. (UADBA R70487): **A-C**, dorsal (**A**), ventral (**B**) and lateral (**C**) views of the head; **D**, close-up of the arm (picture symmetrically reversed, thus representing the right forelimb). The colouration in life has been presently inferred from both the preserved specimen and the supposedly identical living colouration of *S. yamagishii*. Scale bars: 1 mm.

The legend within panel D reads:

C	chin or genial scale
F	frontal scale
IL	infralabial scale
IP	interparietal scale
L	loreal scale
M	mental scale
N	nasal scale
P	parietal scale
PG	postgenial scale
PM	postmental scale
PS	postsupralabial scale
PT	pretemporal scale
R	rostral scale
SL	supralabial scale
SN	supranasal scale
SO	supraocular scale
1	primary temporal scale
2	secondary temporal scale
3	tertiary temporal scale
*	auricular region

rhomboidal. Clavicles strongly curved (S-shaped), flattened dorso-ventrally, with a wide and rounded proximal extremity, a narrow and pointed distal extremity, and a process at their mid-length posteriorly directed. Interclavicle cruciform, with a rounded anterior process approximately as long as the lateral processes these having narrow and pointed distal ends, and a rounded posterior process about 1.5 times longer. Suprascapulae roughly triangular, more ossified medially than laterally. Scapula, coracoid and precoracoid not separated from each other, forming a continuous scapulocoracoid bone. Pericoracoid extremely regressed, fragmented into several poorly ossified residues: two strips separating the sternum from the coracoid, and two pairs of small rodlike structures, posteriorly barely contacting with the cranial extremities of the precoracoid and the coracoid, respectively, and anteriorly converging toward the anterior part of the interclavicle. Coracoid foramen oval, almost open into the anterior coracoid fenestra. Anterior (= primary) coracoid fenestra not completely closed, the pericoracoid being too reduced to delimitate its anterior margin. Posterior (= secondary) coracoid fenestra located in the anterior part of the coracoid; its margins are not clearly delimited from the surrounding osseous tissue (for this reason, the posterior coracoid fenestra may also be interpreted as a very thin and poorly ossified fossa rather than a true fenestra). Pentagonal sternum poorly ossified, as long as wide, as wide as the interclavicle, more ossified posteriorly than anteriorly, pierced by a large, round and median sternal fontanelle in its posterior part, and laterally connected to two pairs of sternal ribs. Xiphisternum "Y-shaped", with three elongated rodlike processes: a median process connecting the posteriormost extremity of the sternum and two posterolaterally directed processes connecting a single pair of xiphisternal ribs.

Forelimbs. Small but relatively well developed, with the exception of the autopodial bones, these being significantly reduced in size and number. Humerus relatively elongated, articulating with the scapula through a relatively well-developed glenoid fossa, and with enlarged proximal and distal ends twisted in relation to one another at an angle of approximately 90°. Ulna and radius relatively reduced in comparison to the humerus, as representing approximately only half of its length. Carpals including three globular elements: the largest (most likely the ulnar carpal), spherical and proximal, and the two smaller probably representing distal carpals (possibly IV and V). Metacarpals possibly represented by two elongated elements (possibly III and IV). No phalangeal bones.

Pelvic girdle. Highly reduced; composed of two separate, curved and rodlike hemipelves. Pubis, ischium and ilium not clearly separated from each other. Pubis and ischium apparently fused to form the anteroventral projection of each hemipelvis, distally compressed and curved, forming a trifurcated anterior cranial end; ilium forming an elongated cigar-shaped dorso-caudal projection.

Pelvic bony corpuscles. Hindlimbs absent, with the notable exception of two faintly distinguishable bony corpuscles probably representing rudiments of ancestral hindlimb bones, posterior to – and not in contact with – the pelvic girdle, floating freely below the cloacal vent. Less likely, these corpuscles may be interpreted as hemibacula (or hemibaubella), calcified structures present in the hemipenes (or hemiclitores) of several distinct groups of squamates, although they could be expected to occur deeper in the tail root, closer to the retractor muscle of the inverted hemipenis.

Additional features
52 presacral vertebrae. Sclerotic rings formed by five ossicles, the upper being the smallest in size (Fig. 5). Osteoderms present within each scale, with the exception of the first two pairs of supralabials, the nasals, the first three pairs of infralabials, the mental, the auricular scales covering the ear-openings, and the ocular scales covering the eyes. Rostral scale only ossified on its dorsal side. Osteoderms present in the parietals, interparietal and frontal scales hardly distinguishable from the underlying skull bones, to which their central part seems to be fused, only the edges being clearly distinct (Fig. 3).

Variation
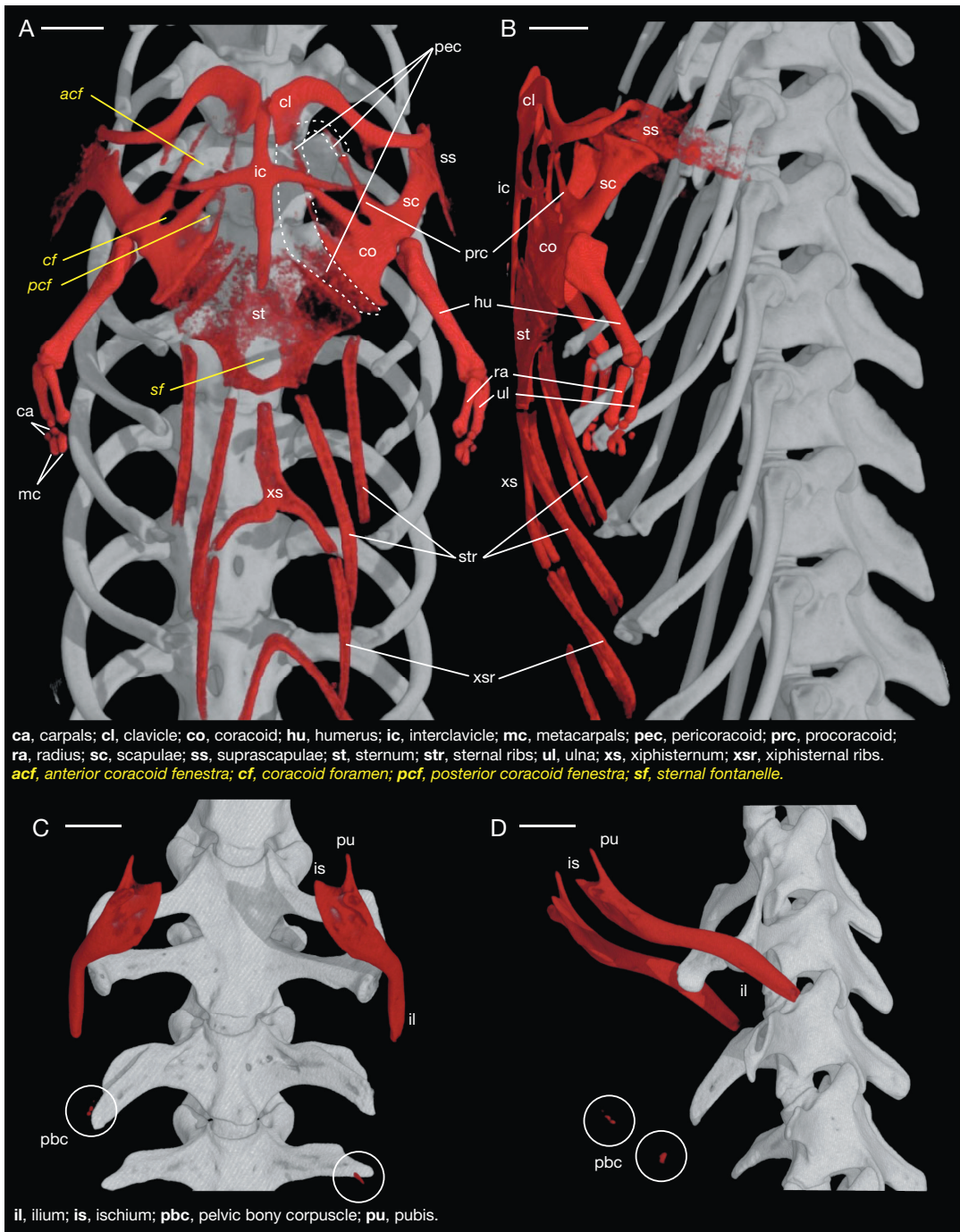External morphological examination reveals that the paratype (UADBA R70488) shares all the

ca, carpals; **cl**, clavicle; **co**, coracoid; **hu**, humerus; **ic**, interclavicle; **mc**, metacarpals; **pec**, pericoracoid; **prc**, procoracoid; **ra**, radius; **sc**, scapulae; **ss**, suprascapulae; **st**, sternum; **str**, sternal ribs; **ul**, ulna; **xs**, xiphisternum; **xsr**, xiphisternal ribs. *acf, anterior coracoid fenestra; cf, coracoid foramen; pcf, posterior coracoid fenestra; sf, sternal fontanelle.*

il, ilium; **is**, ischium; **pbc**, pelvic bony corpuscle; **pu**, pubis.

FIG. 3. — Computed tomographic reconstruction of the anterior body part of the holotype specimen of *Sirenoscincus mobydick* n. sp. (UADBA R70487) in dorsal (**A**, **C**) and lateral views (**B**, **D**). The osteodermic "chain mail" is represented in red in A and B, and digitally removed from C and D. Scale bars: 0.5 mm.

diagnostic characters previously mentioned for the holotype: absence of frontonasal, absence of preoculars and postsuboculars, and 20 rows of scales around mid-body. Its colouration in preservative and its size (snout-vent length = 66.7 mm) are almost identical to those described for the holotype.

DISCUSSION

"HINDLIMBS ONLY" VERSUS "FORELIMBS ONLY" BAUPLANS: TWO EVOLUTIONARY PATHWAYS TO LIMBLESSNESS?

In tetrapod vertebrates, remarkable bauplan changes transforming a fully quadrupedal, lizard-like body form to an almost or completely legless, elongate, worm-like body form have repeatedly occurred in several lineages of squamates (e.g., snakes, amphisbaenians, Scincidae, Anguidae Gray, 1825, Dibamidae Boulenger, 1884, Pygopodidae Boulenger, 1884, Gymnophthalmidae Merrem, 1820, Cordylidae Fitzinger, 1826). Scincidae probably constitute the most remarkable model to illustrate the high frequency of convergent limb loss. Within this family alone, full limblessness – i.e. presently considered as the complete absence of any external limbs – has evolved at least 16 to 20 times independently: 1) the "*Acontias + Typhlosaurus*" clade; 2) the *"Melanoseps + Feylinia + Typhlacontias"* clade; 3) *Scelotes anguineus* (Boulenger, 1887); and 4) *Scelotes arenicolus* (Peters, 1854) in sub-Saharan Africa (Branch 1998; Whiting *et al.* 2003; Brandley *et al.* 2008); 5) within the genera *Paracontias* Mocquard, 1894; and 6) *Voeltzkowia* in Madagascar (Crottini *et al.* 2009); 7) *Larutia penangensis* Grismer, Huat, Siler, Chan, Wood, Grismer, Sah & Ahmad, 2011 in Malaysia (Grismer *et al.* 2011); 8) within the "*Brachymeles lukbani / B. minimus*" clade in the Philippines; 9) *Brachymeles apus* Hikida, 1982; and 10) *Brachymeles miriamae* (Heyer, 1872) in Thailand (Siler *et al.* 2011); 11) within the genus *Isopachys* Lönnberg, 1916 in Southeast Asia (Greer 1997; Honda *et al.* 2000); 12) within the genus *Ophiomorus* Duméril & Bibron, 1839 in Greece and the Middle East (Poulakakis *et al.* 2008; Brandley *et al.* 2008); 13) in *Lerista apoda* Storr, 1976; 14) *Lerista ameles* Greer, 1979; 15) the genera *Ophioscincus* Peters,

1874; and 16) *Anomalopus* Duméril & Bibron, 1839 in Australia (Cogger 2000; Brandley *et al.* 2008; Skinner *et al.* 2008); and likely four more times in enigmatic taxa whose phylogenetic position is either ambiguous or unknown: 17) within the genera *Pseudoacontias* Bocage, 1889; and 18) *Pygomeles* Grandidier, 1867 in Madagascar (Schmitz *et al.* 2005; Crottini *et al.* 2009); 19) *Nessia* Gray, 1838, in Sri Lanka (Somaweera & Somaweera 2009); and 20) *Barkudia* Annandale, 1917 in India (Smith 1935).

Transitions from a lizard-like to a snake-like body form have apparently occurred progressively, involving first a "limb reduction" process (i.e. decrease in limbs and/or finger length, reduction of number of digits and/or phalanges) together with an increase in body length via the number of vertebrae (Wiens & Singluff 2001; Caldwell 2003; Kearney & Stuart 2004; Schmitz *et al.* 2005; Wiens *et al.* 2006; Brandley *et al.* 2008; Skinner *et al.* 2008; Jerez & Tarazona 2009). Therefore, many different intermediate forms exist, showing a mosaic of plesiomorphic quadrupedal characteristics and apomorphic traits associated with limblessness. The exclusive presence of hindlimbs and absence of forelimbs constitutes one such "intermediate bauplan", and is commonly observed in a variety of independent squamate clades: in Scincidae (Whiting *et al.* 2003; Glaw & Vences 2007; Skinner *et al.* 2008; Somaweera & Somaweera 2009; Moch & Senter 2011), Anguidae (Wiens & Singluff 2001), Gymnophthalmidae (Rodrigues *et al.* 2001), Dibamidae (Das & Lim 2003), Pygopodidae (Cogger 2000), Cordylidae (Branch 1998), and in several fossil snakes (Lee & Caldwell 1998; Rieppel *et al.* 2003; Houssaye *et al.* 2011). On the contrary, the "forelimbs only" bauplan is restricted to four "snake-like" tetrapod lineages: the Sirenidae Gray, 1825 within amphibians (Caldwell 2003) and three clades of squamates, the amphisbaenian genus *Bipes* (Kearney & Stuart 2004) and the scincid genera *Sirenoscincus* (Sakata & Hikida 2003a) and *Jarujinia* (Chan-ard *et al.* 2011). A similar bauplan is also present in two clades of marine mammals, the cetaceans and the sirenians (Domning 2001; Thewissen *et al.* 2006), although its natatory function in both groups can hardly be compared to those observed within the squamates.
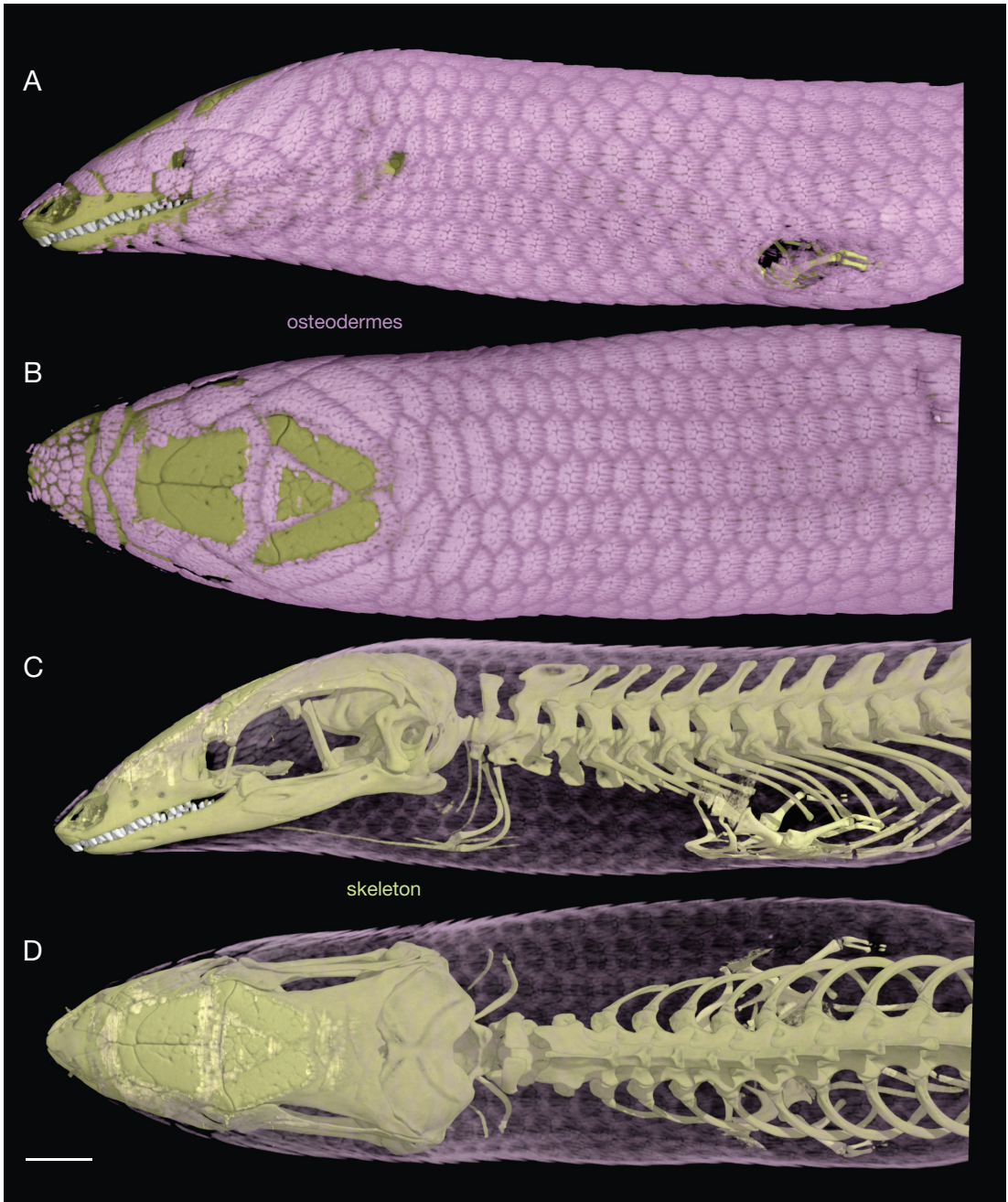
osteodermes

skeleton

Fig. 4. — Computed tomographic reconstruction of the pectoral girdle and forelimbs of the holotype specimen of *Sirenoscincus mobydick* n. sp. (UADBA R70487) in lateral (**A**) and dorsal (**B**) views; pectoral girdle in lateral (**C**) and dorsal (**D**) views. Scale bar: 1 mm.
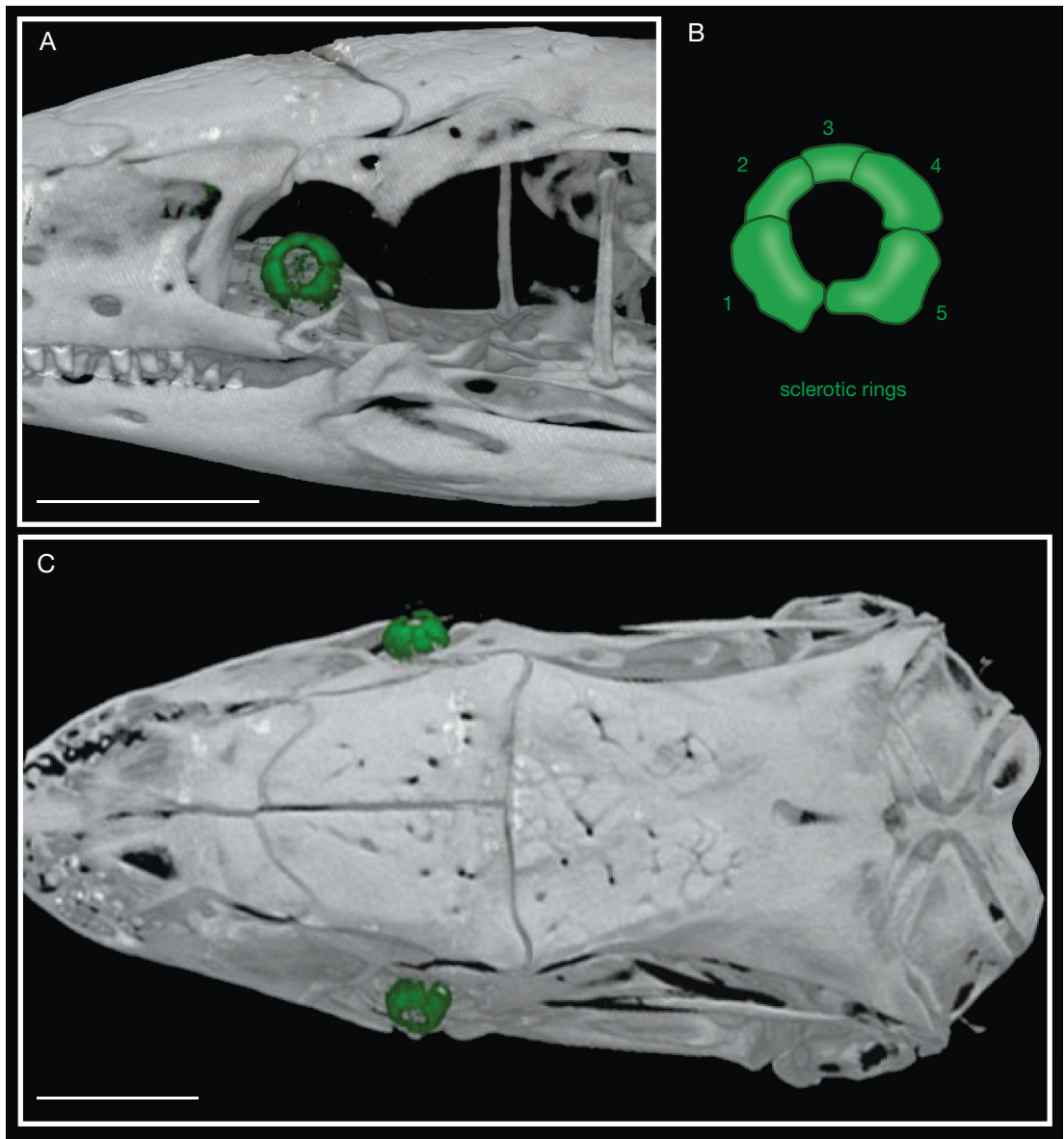
FIG. 5. — Computed tomographic reconstruction of the skull of the holotype specimen *Sirenoscincus mobydick* n. sp. (UADBA R70487) with the sclerotic rings coloured in green, in lateral (**A**) and dorsal (**C**) views. **B** represents the ossicles in the sclerotic ring, redrawn from **A**.

The absence of fingers and claws and the reduced size of the forelimbs suggest to us that contrary to *Bipes*, forelimbs in *Sirenoscincus mobydick* n. sp. likely have no significant locomotive or digging abilities. Sakata & Hikida (2003a) came to the same conclusions for *S. yamagishii*, and briefly hypothesised that the forelimbs may be involved in mating. For instance within the (largely) legless dibamid lizards, only males have flap-like hindlimbs whereas they are absent in females (Kley & Kearney
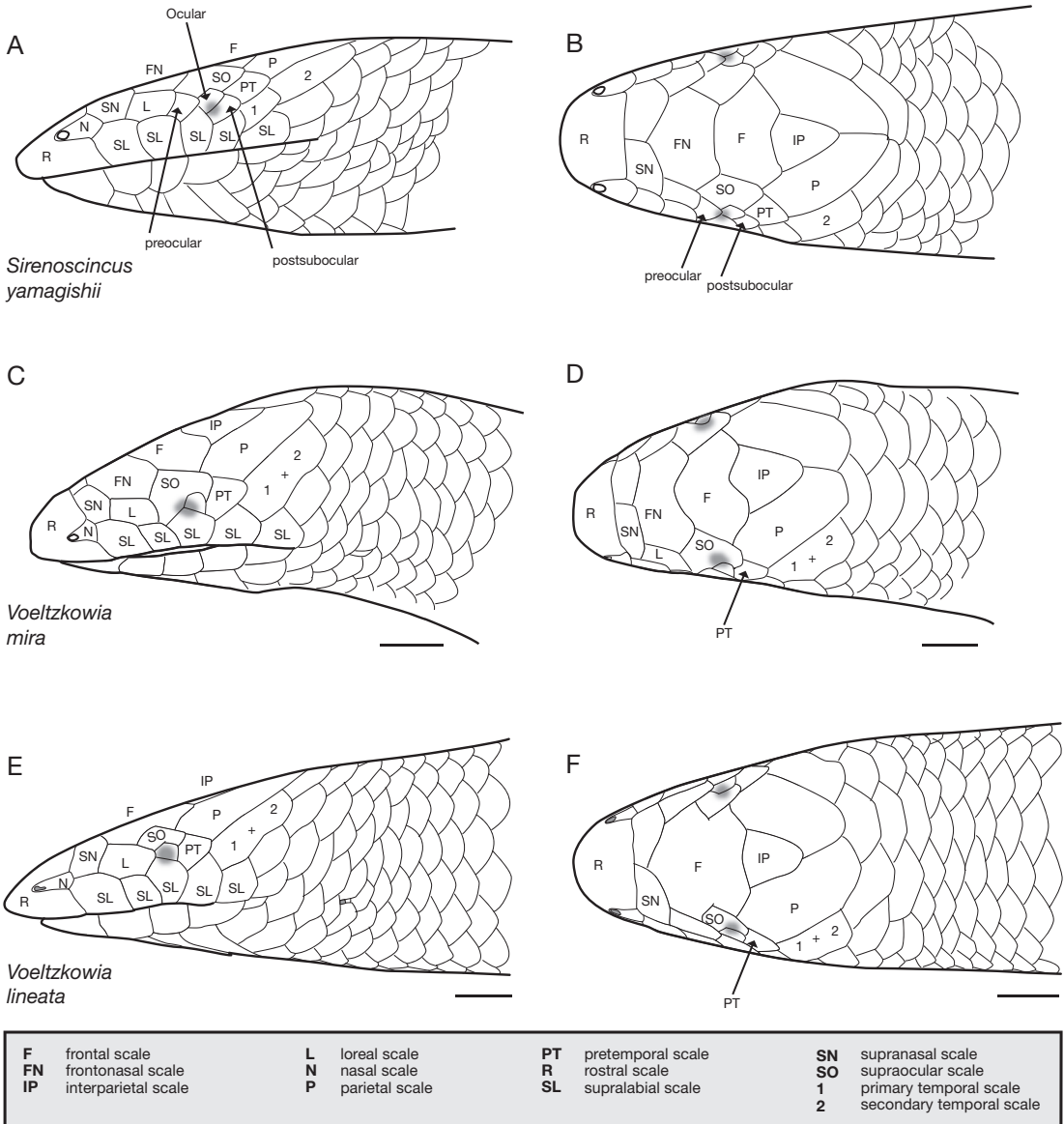
Fig. 6. — **A**, **B**, drawings of the lateral and dorsal views of the holotype of *Sirenoscincus yamagishii* Sakata & Hikida, 2003 (holotype specimen KUZ R50922); **C**, **D**, the only northern species of *Voeltzkowia* Boettger, 1893, *V. mira* Boettger, 1893 (ZSM 867/0); **E**, **F**, one member of the southern group, *V. lineata* (Mocquard, 1901) (ZSM 1624/2010 = ZCMV 12845). A and B have been redrawn after Sakata & Hikida (2003a). E is symmetrically reversed, thus representing the right side. Scale bars: 1 mm (not shown for A and B because not indicated in the original figure).

2007), suggesting a possible reproductive function. A similar sexual dimorphism is well documented in giant snakes (Boidae Gray, 1825 and Pythonidae Fitzinger, 1826), where pelvic spurs, more developed in males, have been demonstrated to play a role during the mating process (Murphy *et al.*

1978). In contrast, no sexual dimorphism has been observed in pygopodids, despite the fact that they have flap-like hindlimbs very comparable to those observed in dibamids (Kley & Kearney 2007). Unfortunately, both specimens of *Sirenoscincus yamagishii* examined by Sakata & Hikida (2003a) were females, and all other *Sirenoscincus* specimens known have not been sexed, preventing us from making inferences about possible sexual dimorphism in terms of size or structure of the forelimbs in this genus. Nevertheless, several elements lead us to consider the "mating function" hypothesis as rather unlikely, at least for *S. mobydick* n. sp. Contrary to other limb-reduced squamates having vestigial hindlimbs inserted on each side of the cloacal vent, forelimbs cannot play any obvious role of penetration facilitators during copulation, and they are so strongly reduced that it seems impossible that males can use them for grabbing or holding onto females. Nevertheless, we cannot discard the possibility that forelimbs may play a role of tactile stimulator for mate recognition. Indeed, 1) it seems obvious that blind and fossorial reptiles cannot use optical signals for courtship or mate recognition; 2) vocalisations in skinks are uncommon and seem to be always limited to defensive functions (Bauer *et al.* 2004); and 3) unlike snakes (including the fossorial typhlopids) fossorial skinks apparently also do not use extensively the olfactory sense (at least they do not regularly extrude their tongues).

As a conclusion, forelimbs in *Sirenoscincus* do not seem to fulfill any obvious or essential function. This may possibly explain why the "hindlimb only" bauplan is by far more common than the "forelimb only" bauplan. According to this hypothesis, the rare "forelimb only" bauplan would simply be a temporary state in the evolutionary transition towards complete limblessness. This, however, might not be true for species with an essential function of forelimbs as in *Bipes*. On the contrary, the "hindlimb only" bauplan may have functional advantages during mating and thus might constitute an evolutionarily more stable state, having reached in some cases an equilibrium between two antagonistic driving forces: the selective pressure to conserve hindlimbs because of their possible mating functions and the physical pressures

exerted by a highly fossorial lifestyle, well known to favour reduction.

At least, and apart from possible selective explanations, strictly developmental constraints have to be considered, as they can also explain why hindlimbs are more frequently conserved than forelimbs. For instance, in tetrapod vertebrates, the pelvic girdle and the vertebral spine are structurally inseparable from each other (the sacrum being composed by several fused sacral vertebrae), which is not the case with the floating pectoral girdle. These major structural differences observed between both girdles may have strong impacts on their respective lability, suggesting that morphogenetic changes required to regress hindlimbs are more important than those required to regress forelimbs.

Extreme fossorial lifestyle and "blindness" in Squamata

Fossorial species expose their eyes to mechanical stress and dirt during burrowing, and spend most of their time in a world of darkness in which vision apparently does not represent an essential sense. Eyes of fossorial forms consequently tend to regress, involving reduction of eye size, loss of accommodation muscle, and reduction of scleral cartilage and ossicles (Underwood 1970). An extensive review undertaken by Underwood (1970) revealed that lizards usually have 10-16 scleral ossicles (most frequently 14), with minimum values being reached by semi-fossorial forms, such as *Anguis* Linnaeus, 1758, *Anniella* Gray, 1852 and *Sphenomorphus* Fitzinger, 1843 (8), and *Lanthanotus* Steindachner, 1877 (6).

The most advanced stage of eye regression is likely reached by the so-called "blind" squamates which are easily recognisable by their very small, dark eyes deeply sunken below a poorly pigmented integument, without an eye-opening. Several distinct lineages of squamates – all of them being highly specialised to a fossorial lifestyle – are "blind", such as scolecophidian snakes, Amphisbaenidae, Dibamidae and several convergent lineages of Scincidae (e.g., *Voeltzkowia* and *Sirenoscincus*, *Paracontias minimus*, *Typhlosaurus* Wiegmann, 1834, *Feylinia* Gray, 1845). Our microtomographic investigations on the holotype of *Sirenoscincus mobydick* n. sp. revealed a very low

number of sclerotic rings, with only five ossicles visible in each eye (Fig. 5). As far as we know, this represents the lowest value observed among lizards, and fits with the observations made by Underwood (1970) according to which the number of sclerotic ossicles would be negatively correlated to the degree of fossoriality.

There is no evidence of absolute non-functionality of the eyes in *Sirenoscincus mobydick* n. sp. On the contrary, microtomographic pictures reveal two characteristics that may indirectly suggest that their photosensory faculties are not completely lost, implying this species may not be strictly blind: 1) different from all other adjacent cephalic scales, there is no osteoderm inside the translucent ocular scale covering the eye, such a gap theoretically allowing light beams to reach the eye (Fig. 3); and 2) the eyes are slightly oriented upward (Figs 2; 5), which constitutes a characteristic present in sand-fossorial snakes (e.g., erycine boas or *Cerastes* Laurenti, 1768 vipers) allowing them to see above the soil surface while still remaining buried into the sand. In such a case, the visual capacity of *S. mobydick* n. sp. would obviously be relatively low, and it would be worthwhile to determine if this species is only able to detect contrasting presence or absence of light (e.g., night/day, or underground/surface) or if it can distinguish between different elements at a short distance (e.g., prey, predator or congener).

HYPOTHESES ON THE PHYLOGENETIC AFFINITIES OF *SIRENOSCINCUS*

Due to the absence of molecular data the phylogenetic position of the genus *Sirenoscincus* is still an enigma, even if we can reasonably claim it belongs to the Malagasy scincine clade. Within this group, it shares with the genus *Voeltzkowia* and the species *Paracontias minimus* many derived morphological characters, such as extreme limb reduction, eye regression with an absence of eye-opening, regression of the ear-opening, regression or complete loss of pigmentation and a simplification of the cephalic lepidosis by many scale fusions. We emphasise that the distinction between apomorphic and plesiomorphic states herein is only a general polarisation by rough comparison with non-fossorial lizards, and
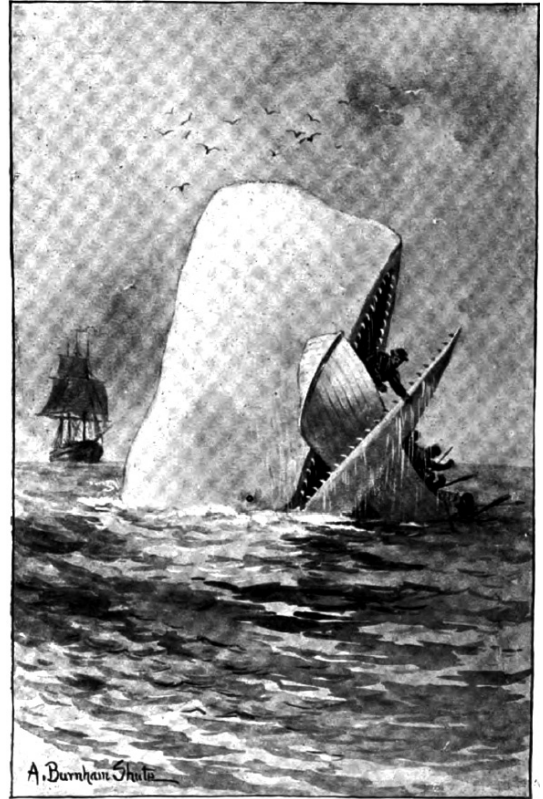

Fig. 7. — Illustration from an early edition of *Moby-Dick*. Public domain picture drawn by A. Burnham Shute (1892).

not an explicit character optimisation given by a phylogenetic tree.

From a general point of view, the genus *Sirenoscincus* shares more similarities with *Voeltzkowia* than with *Paracontias minimus*: both *Sirenoscincus* and *Voeltzkowia* having supranasals medially in contact (versus absent in *P. minimus*) and wedge-shaped nasals (versus absent). From a strictly biogeographical point of view, species of the *Sirenoscincus/Voeltzkowia* group occur in two distinct regions: the northwestern region of Madagascar where the two species of *Sirenoscincus* and *Voeltzkowia mira* Boettger, 1893 are endemic, and the southern region where all remaining species of *Voeltzkowia* (*V. fierinensis* (Grandidier, 1869), *V. lineata* (Mocquard, 1901), *V. petiti* (Angel, 1924) and *V. rubrocaudata* (Grandidier, 1869)) occur. *Sirenoscincus mobydick* n. sp.

shares almost all of the derived traits characterising the cephalic lepidosis of the latter southern *Voeltzkowia* group. On the contrary, *S. yamagishii* and the only northern species of *Voeltzkowia* (*V. mira*), the type species of this genus, share one plesiomorphic character which is the presence of a frontonasal distinct from the frontal (see Fig. 6). One derived character only, the fusion of the primary temporal with the upper secondary temporal is exclusively shared by all species of *Voeltzkowia* and is absent in both species of *Sirenoscincus*.

These similarities between both genera strongly suggest close phylogenetic relationships, and the mosaic of plesiomorphic and apomorphic traits "randomly" distributed in both taxa may indicate that they are not reciprocally monophyletic. Nevertheless, these morphological features should be carefully considered for phylogenetic inferences. Indeed, most of these derived traits likely represent functional adaptations to a burrowing lifestyle, and have convergently evolved several times in different highly fossorial lineages (e.g., amphisbaenians, dibamids, *Typhlosaurus*, *Voeltzkowia*, *Paracontias minimus* and *Feylinia*). Consequently, they may be extremely homoplastic and therefore phylogenetically misleading (Gans 1974; Kearney & Stuart 2004; Wiens *et al.* 2006; Köhler *et al.* 2010). Molecular studies might be able to elucidate the phylogenetic relationships and taxonomy of *Sirenoscincus* and *Voeltzkowia* reliably, and new field work to obtain tissue samples of these taxa is therefore crucial.

CONCLUSION

The remarkable bauplan of the genus *Sirenoscincus* highlights several open questions about macroevolutionary changes affecting body transformation in fossorial reptiles: why does the timing of forelimb and hindlimb loss seems to be so frequently uncoupled within squamates? In other words, why are forelimbs virtually always more regressed than hindlimbs, and why are they lost first? Basic – but lacking – comparative studies in ethology, ecology and functional morphology would be necessary to determine if these regressed limbs may have distinct functions (locomotion, mating or other) in both

forelimbs-only and hindlimbs-only organisms, and to discuss their possible differences in terms of selective value. Fine anatomy and developmental biology would also allow us to assess more accurately (qualitatively, quantitatively and chronologically) the morpho-anatomical changes that affect limbs and girdles of these organisms. Last but not least, fully resolved and reliable phylogenetic hypotheses based on broad taxon sampling would obviously constitute an essential prerequisite to compare these different organisms within an evolutionary framework.

The extremely derived and uncommon morphology of *Sirenoscincus* also highlights the fact that many spectacular morpho-anatomical transformations other than limb regression can affect reptiles highly adapted to a fossorial lifestyle. Regrettably, most of these phenomena, such as regression of the eyes, closure of the ear opening, miniaturisation, loss of pigmentation and high degree of cephalic scale reduction (cf. Gans 1974, 1975; Lee 1998; Sakata & Hikida 2003a; Miralles *et al.* 2011a) remain under-studied in comparison to works dealing with limb regression. It would nevertheless be essential to know more about these features and the communication system of fossorial skinks. An integrative approach is therefore indispensable, and to restrict studies to the single aspect of limb reduction would likely prevent us from fully understanding how these organisms have repeatedly and successfully colonised the underground world.

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APPENDIX

Additional specimens examined. Quotation marks have been used for original localities of types specimens.

Paracontias minimus (Mocquard, 1906): MNHN 1905.270, "Madagascar", lectotype of *Cryptoposcincus minimus* Mocquard, 1906; MNHN 1905.270A, "Madagascar", paralectotype of *Cryptoposcincus minimus* Mocquard, 1906. — ZFMK 88051, 88052, ZSM 2249-2253/2007, 2268/2007, 1585/2008, 1586/2008, Baie de Sakalava, Forêt d'Orangea, 12°16'24"S, 49°23'33"E, 11 m a.s.l. — ZSM 1584/2008, southeast of Ivovona, Forêt d'Orangea, 12°19'58"S, 49°24'20"E. — ZSM 1583/2008, Ampombofofo, Babaomby region, 12°05'53"S, 49°19'49"E, Antsiranana Province. All from northern Madagascar.

Voeltzkowia fierinensis (Grandidier, 1869): MNHN 1895.214, "Tullear" (=Toliara), holotype of *Scelotes fierinensis* Grandidier, 1869. — MNHN 1905.133, 133A, 133B, 133C, Fiherena plain. — MNHN 1979.8269, Vohombe (Betioky). — MNHN 1980.1219, 37 km from Betioky, dir. Soalara. — MNHN 1983.493, 1983.494, Toliara. — ZSM 604/2000 (FG/MV 2000.566), ZSM 605/2000 (FG/MV 2000.567), Toliara, near Arboretum, 23°24'S, 43°45'E, 28 m a.s.l. — ZSM 220/2003 (FG/MV 2002.1546), ZSM 225/2003 (FG/MV 2002.1538), ZSM 226/2003 (FG/MV 2002.1595), Toliara, Arboretum. — MNHN 1984.410, 1986.57, 58, 59, 60, 61, 62, 63, plain of Toliara, Plantations Pétignat. — ZSM 386/2005 (FGZC 2685), near Toliara. — MNHN 1984.172, Vobritomotsy, under a kily tree. — ZSM 848/2001, Fiherenana river, near Miary. — ZSM 1618/2010 (ZCMV 12887), ZSM 1619/2010 (ZCMV 12884), Tombohina, road to Anakao, 23°52'02.4"S, 44°05'15.6"E, 180 m a.s.l. — ZSM 1635/2010 (ZCMV 12885), ZSM 1634/2010 (ZCMV 12883), ZSM 1633/2010 (ZCMV 12882), ZSM 1636/2010 (ZCMV 12886), Anakao, hôtel chez Émile, 23°39'19.5"S, 43°39'0.5"E. — ZSM 606-610/2000, Anakao, 10 m a.s.l. — MNHN 1929.160, Ampalaza. — MNHN 1979.8270, unknown locality.

Voeltzkowia lineata (Mocquard, 1901): MNHN 1901.240, "Ambovombe", lectotype of *Grandidierina lineata* Mocquard, 1901; MNHN 1901.175, 241, "Ambovombe", paralectotypes of *Grandidierina lineata* Mocquard, 1901. — MNHN 1901.174, "pays Androy sud", paralectotype of *Grandidierina lineata* Mocquard, 1901. — ZSM 1623/2010 (ZCMV 12891), ZSM 1624/2010 (ZCMV 12845), ZSM 1625/2010 (ZCMV 12850), ZSM 1626/2010 (ZCMV 12847), ZSM 1621/2010 (ZCMV 12894), ZSM 1622/2010 (ZCMV 12893), dunes of Faux Cap, 25°34'07.6"S, 45°31'52.9"E. — MNHN 1956.69, Nosy Vorona (Mahafale coast). — MNHN 1980.1220, 1221, 1222, 1223, 1224, 1225, 1226, 1227, 1228, 1229, 1230, 1231, 37 km N Betioky, direction to Soalara. — MNHN 1980.1232, Ankazomanga. — MNHN 1980.1233, Andreoka, road Ejeda to Beahisty. — MNHN 1980.1234, Egogo. — MNHN 1980.1235, Manombo, SWW Beloha. — MNHN 1980.1236, Evanga, between Saodona and Bevoalava. — MNHN 1980.1237, Tsivaha, Cap Malaimpioka, S Anjirazato. — MNHN 1980.1238, Anjirazato, SW Beloha. — MNHN 1980.1239, Besakoa, coast between Faux Cap and Cap Ste Marie. — MNHN 1980.1240, Saraondry. — MNHN 1980.1241, 1242, Benanoka. — MNHN 1980.1243, Ampihany. — MNHN 1980.1244, Sakaraha. — MNHN 1980.1245, Toliara, base hydro. — MNHN 1982.1257, N Toliara, PK32 forest. — MNHN 1982.1261, Toliara. — MNHN 1984.171, Vobritomotsy. — ZSM 611/2000, Anakao. — MNHN 1933.79, 80, 81, 1930.342, 1950.396, 397, 398, 1970.347, unknown localities.

Voeltzkowia petiti (Angel, 1924): MNHN 1924.91, "Tsivono, region de Tuléar, à 24 kilomètres au Nord de cette ville", lectotype of *Grandidierina petiti* Angel, 1942; MNHN 1924.90, type locality, paralectotype of *Grandidierina petiti* Angel, 1942. — ZSM 1620/2010 (ZCMV 12824), Sakabera, village on the road to Ifaty, on the border of the Fiherenana river, 23°18'11.1"S, 43°39'31.4"E. — ZSM 1617/2010 (ZCMV 13009), Ifaty Mangily Reserve, 23°07'22.05"S, 43°36'34.02"E. — ZSM 228/2003, Ifaty.

Voeltzkowia rubrocaudata (Grandidier, 1869): MNHN 0.7639, "Fierin", holotype of *Acontias rubrocaudatus* Grandidier, 1869. — MNHN 1979.8268, Befandriana. — MRSN R3726 (FAZC 14370 / ACZC 2565), Zombitse, Manioc plantation. — ZSM 1630/2010 (ZCMV 12830), ZSM 1629/2010 (ZCMV 12833), ZSM 1632/2010 (ZCMV 12831), ZSM 1628/2010 (ZCMV 12832), ZSM 1631/2010 (ZCMV 12829), Sakabera, village on the road to Ifaty, 23°18'11.1"S, 43°39'31.4"E. — ZSM 232/2003 (FG/MV 2002.2050), Ifaty. — ZSM 384/2005, ZSM 385/2005, near Toliara. — MNHN 1989.3745, unknown locality.

Voeltzkowia mira Boettger, 1893: ZSM 867/0, west Madagascar, collected by Voeltzkow.