ORIGINAL ARTICLE

Hypotheses on rostral shield evolution in fossorial lizards derived from the phylogenetic position of a new species of *Paracontias* (Squamata, Scincidae)

Aurélien Miralles · Jörn Köhler · David R. Vieites · Frank Glaw · Miguel Vences

Abstract In squamate reptiles the rostral shield constitutes one of the most advanced cases of reduction in the number of scales in the rostral region, an evolutionary trend clearly associated with a burrowing lifestyle. This structure is characterized by the fusion of the rostral scale with all adjacent scales into a large, smooth and conical plate covering the snout, totally encompassing the nostrils, with a horizontal groove running posteriorly from either nostril. In lizards this structure evolved several times independently, in various lineages of limbless skinks and in the family Dibamidae. We performed a multilocus phylogenetic analysis of combined mitochondrial and nuclear DNA sequences from the fossorial genus *Paracontias,* including *P. vermisaurus,* a new species described herein under an integrative taxonomic approach. The resulting phylogeny supports monophyly of *Paracontias*, with the following internal topology: [*P. kankana* (*P. vermisaurus* sp. n. (((*P. minimus* + *P. brocchii*) (*P. manify* + *P. hildebrandti*)) (*P. rothschildi* + *P. fasika*)))]. The molecular data, coupled with a comparative morphological study, allows us to investigate the evolution of the snout scales into a single large rostral shield in *Paracontias*. We discuss the evolutionary processes through which the rostral shield may have originated (e.g. fusion of scales, number and order of steps involved), and conclude that intuitive and apparently obvious hypotheses for scale homologies based on position and size only (as usually formulated in squamate taxonomy) may be highly misleading, even in closely related species. We develop the hypothesis that the rostral shield may provide several functional advantages for fossorial species in facilitating burrowing and protecting the head from strong physical stress, e.g. smoother surface reducing friction between the tegument and the substrate, reduction in the number of flexible sutures resulting in strengthened tegument, and the rostral tip likely playing a role as a shock-absorbing buffer.

Keywords Burrowing lifestyle · Scincidae · *Paracontias vermisaurus* sp. n. · Madagascar · Scalation · Molecular phylogeny

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Introduction

Numerous recent studies have highlighted the multiple convergent adaptations to highly specialized burrowing lifestyles that have occurred in the evolutionary history of squamate reptiles (e.g. Brandley et al. 2008; Crottini et al. 2009; Greer 2002; Kohlsdorf and Wagner 2006; Mott and Vieites 2009; Shapiro 2002; Skinner et al. 2008; Whiting et

al. 2003; Wiens et al. 2006; Wiens and Slingluff 2001). Most of these works have focused on the most striking adaptive response to the requirements of a subterranean life style, i.e. the reduction or loss of limbs. However, limb loss has often been accompanied by a combination of several other spectacular morpho-anatomical transformations, such as regression of the eyes, closure of the ear opening, increase in the number of vertebrae together with a lengthening of the body shape, miniaturization, or loss of pigmentation (Gans 1974, 1975; Lee 1998; Pianka and Vitt 2003; Sakata and Hikida 2003).

Legless fossorial tetrapods (squamates and amphibians) essentially dig the soil using their snout, which incurs strong constraints on the tip of the animal's head. Most of these forms have a highly derived skull that has evolved in response to their specialized head-first burrowing lifestyle. For instance, Uropeltoidea and scolecophidian snakes, amphisbaenians, dibamids and caecilians all have compact skulls with a solidly enclosed braincase and reduced arcades (Gans 1974, 1975; Measey and Herrel 2006; Rieppel 1984; Rieppel et al. 2009; Rieppel and Maisano 2007). Virtually unexplored until now, the cephalic scalation is also expected to be relevant as a morpho-anatomical adaptation of burrowing squamates. Indeed, many lineages of fossorial Squamata have convergently followed the general trend of reduction in the number of scales on the anteriormost part of the head. This has led to a wide diversity of cephalic scalation patterns, all characterized by the presence of bigger scales, giving a smooth aspect to the cephalic tegument (e.g. scolecophidians and several colubrid snakes, amphisbaenians, dibamids, the gymnophthalmid genus Bachia; Ávila-Pires 1995; Broadley and Wallach 2009; Gans 1974; Marx and Rabb 1970; Miralles 2001; Savitzky 1983; present study).

On the other hand, given its very high diversity of patterns, cephalic scalation has always constituted one of the most important sources of morphological characters for squamate systematics. This is particularly true for groups showing large and geometrical plates, for which many homology hypotheses have been proposed on the basis of their relative shapes and positions, leading to the design of an accurate terminology constantly improved over the last decades. Nevertheless, despite the universally acknowledged value of these characters in taxonomy, astonishingly few studies have paid attention to their evolution, to the role they can play in terms of morpho-functional adaptations to extreme environments, lifestyles and behaviour, or to the reliability of the homologies hypothesised in phylogenetic contexts for each of the scales covering the head. As these integumentary structures constitute the interface between the organism and its environment, they can be expected to be subject to important biomechanical constraints. This applies in particular to limbless fossorial squamates, because these usually dig

in the soil using the tip of the snout. Interestingly, a remarkable structure usually referred to as the rostral shield has evolved convergently in various lineages of the Scincidae and Dibamidae, always in groups highly specialized to burrowing habits. This structure represents the most advanced case of reduction in the number of scales in the rostral region of Squamata, with all the anteriormost scales of the snout being fused into a single, smooth and roughly conical plate covering the anteriormost part of the head (Fig. 1).

During our recent work on scincid lizards of Madagascar, we obtained new taxonomic and molecular phylogenetic data that might help to shed light on the evolution of the rostral shield from more plesiomorphic kinds of rostral scalation. Malagasy lizards in the subfamily Scincinae form by far the most speciose and morphologically diverse radiation of skinks on the island (Crottini et al. 2009; Schmitz et al. 2005; Whiting et al. 2004), with 57 described species currently recognized (Glaw and Vences 2007; Köhler et al. 2009, 2010). Among these are several highly specialized fossorial forms, such as the species in the genera Voeltzkowia, Sirenoscincus, Pseudoacontias, and Paracontias. The latter is a poorly known genus of skinks characterized by the total absence of limbs and ear openings, fusion of the anteriormost scales of the snout, and partially by an extreme miniaturization (in some species, the width of the body and head does not exceed 2–3 mm).

Here we analyse the evolution of the rostral shield in Paracontias, on the basis of a newly discovered species and of its phylogenetic position within the genus. We selected Paracontias as a model group for this study, as it contains species showing different levels of specialization of the head scalation: either with a complete 'rostral shield' sensu stricto (large, smooth and conical plate covering the snout, resulting from fusion of the rostral scale with all adjacent scales, totally encompassing the nostrils, and with a horizontal groove running posteriorly from either nostril) or with an incomplete 'rostral pseudo-shield' (less modified structure, not completely encompassing the nostrils, without horizontal grooves) that we hypothesize to represent an intermediate evolutionary condition.

Material and methods

Taxonomic framework

A recent phylogenetic analysis based on six mitochondrial and five nuclear genes strongly supports the monophyly of the genus Paracontias, here including P. minimus (which formerly constituted the monotypic genus Cryptoposcincus; Crottini et al. 2009). Two formerly undescribed species of Paracontias included in the phylogeny published by
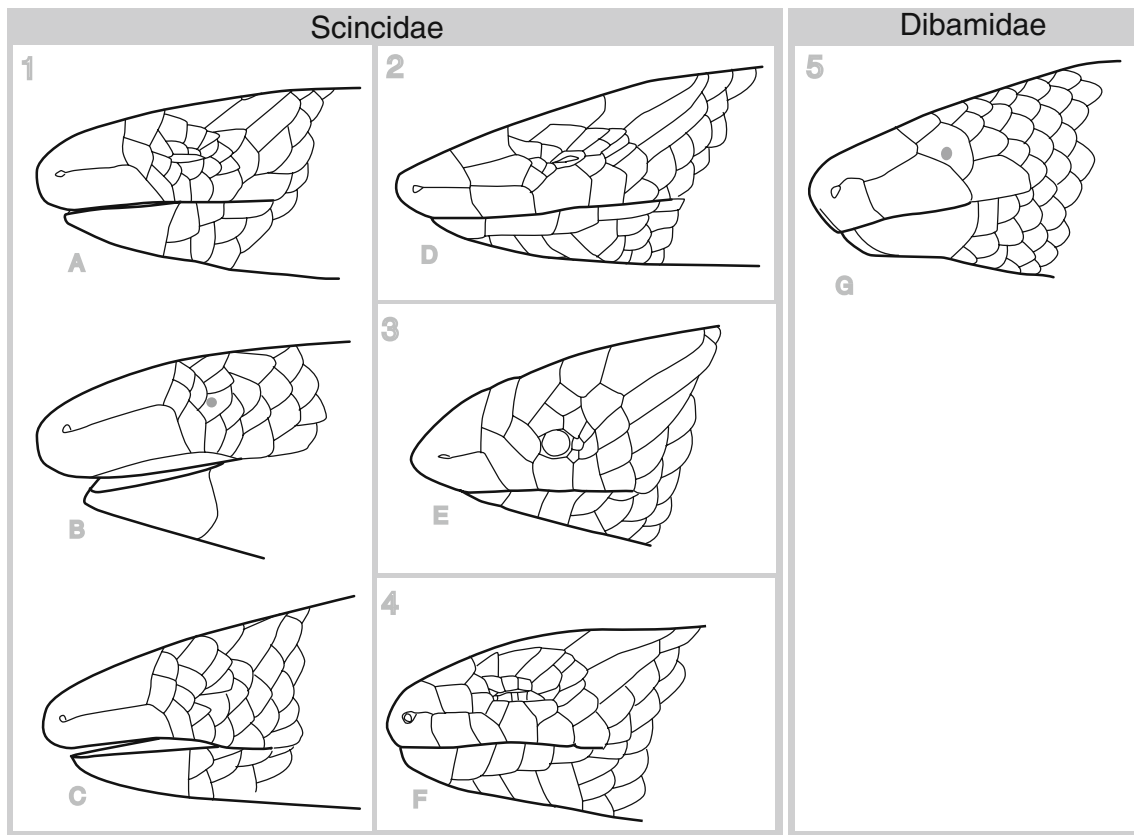
Fig. 1 Shape and extension of rostral shield in five convergent lineages of Squamata. **A** *Acontias meleagris*. **B** *Typhlosaurus cregoi*. **C** *Acontias rieppeli*. **D** *Nessia layardi*. **E** *Typhlacontias rohani*. **F** *Paracontias hafa*. **G** *Dibamus ingeri*. a–c redrawn after Fitzsimons (1943), d after Smith (1935), f after Andreone and Greer (2002), g after Das and Lim (2003)

Crottini et al. (2009) under the names *Paracontias* sp. aff. *tsararano* and *Paracontias* sp. have recently been described as *P. kankana* and *P. fasika*, respectively (Köhler et al. 2009, 2010).

The definitions and taxonomic concepts of *Amphiglossus stylus, Paracontias fasika, P. hafa, P. hildebrandti, P. kankana, P. manify, P. minimus* and *P. tsararano* as used in the present paper are based on morphological examinations of the respective type specimens. The definition of *P. milloti* is based on the original description only, those of *P. rothschildi* and *P. holomelas* on the original descriptions complemented with the redescriptions by Angel (1942), and the definition of *P. brocchii* on the original description plus data published by Brygoo (1980) and Andreone and Greer (2002).

Morphological study

The specimens examined (all preserved in 70% ethanol) are deposited in the Museum National d'Histoire Naturelle, Paris (MNHN), Museo Regionale di Scienze Naturali, Torino (MRSN), Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main (SMF), Museum für

Naturkunde, Berlin (ZMB), Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK), and Zoologische Staatssammlung München (ZSM). The abbreviations ZCMV and DRV refer to M. Vences and D. R. Vieites field numbers, respectively. Measurements of specimens were recorded to the nearest 0.1 mm using a digital caliper. Meristic, mensural and qualitative characters examined here are routinely used in the taxonomy of Scincidae, such as scale counts, presence or absence of homologous scale 'fusions', or the variability in color patterns. Scale nomenclature, scale counts, and measurements used in the morphological analyses are essentially based on Andreone and Greer (2002). The frontal scale is considered as hourglass shaped when constricted by the first supraocular, as bell-shaped when this is not the case (see Greer and Shea 2000). Nuchal scales are defined as enlarged scales of the nape, transversely occupying the place of two or more rows of dorsal cycloid scales (Miralles 2006). Pretemporal scales are presently defined as scales anterior to temporals and parietals, separating the last supraocular from the primary temporal scale; Andreone and Greer (2002: p. 155, fig. 13) held that *Paracontias hafa* shows a single pretemporal scale, but did not identify the adjacent lower scale.

According to our definition of a pretemporal, *P. hafa* and the new species described below are the only two species in the genus that possess two pretemporals, whereas almost all the remaining species have a single pretemporal scale. *Paracontias minimus* seems to lack pretemporal scales, but the highly modified head scalation of this species renders the formulation of homology hypotheses for several head scales extremely tentative.

Traditionally, herpetologists use the term 'fusion' for the transition from a state with two or more small scales to a state with a single larger scale occupying more or less the same place (shape and expansion) as the previous scales, and thus supposed to be homologous with them. In the present paper we follow this definition for obvious practical reasons. It is nevertheless essential to stress the fact that it does not insinuate any morphogenetic process, but only refers to a transition from one state to another in evolutionary history, regardless of the mechanism involved.

Drawings were made using Adobe Illustrator CS2 and a WACOM CTE-640 graphic tablet, after photographs taken through a ZEISS SteREO Discovery. V12 stereo microscope.

Molecular sampling

Five new DNA sequences (HQ891854 to HQ891858) were generated from the specimen ZSM 597/2008 (field number ZCMV 11211), the holotype of the new species, and deposited in GenBank. They have been added to the dataset published by Crottini et al. (2009) (with the exception of *Amphiglossus crenni* and *Pseudoacontias menamainty*, for which only mitochondrial sequences were available), both to test whether the new species is a member of the genus *Paracontias*, as suggested by morphological examination, and to infer its phylogenetic affinities within the genus. One cordylid (*Cordylus* sp.) was used as out-group; further taxa used as hierarchical out-group's were *Tiliqua* and '*Eumeces*' sensu lato. Among the non-Malagasy skinks, previous more inclusive studies (Schmitz et al. 2005; Whiting et al. 2004) suggested that species of *Eumeces* s. l. are relatively close to the Malagasy radiation. It should be noted that for the three out-group taxa we had to use concatenated chimera sequences of different species compiled from GenBank (see Table 1 and Crottini et al. 2009), a procedure not completely free of risks (it assumes, for instance, that the various taxa composing each chimera form a monophyletic group; see Malia et al. 2003).

Molecular procedures

Total genomic DNA was extracted using proteinase K (10 mg/ml) digestion, followed by a standard salt-extraction protocol (Bruford et al. 1992). From the mitochondrial DNA (mtDNA) we amplified fragments of the 16S rRNA to ND1 genes. Additionally, fragments of three nuclear DNA genes (nuDNA) were amplified: brain-derived neurotrophic factor (BDNF), recombination activating gene 2 (Rag2), and phosducin (PDC). Standard polymerase chain reactions were performed in a final volume of 12.5 μl containing 0.3 μl each of 10 pmol primer, 0.25 μl of total dNTP 10 mM (Promega), 0.1 μl of 5 U/ml GoTaq, and 2.5 μl of GoTaq Reaction Buffer (Promega). For primers and PCR conditions used, see Crottini et al. (2009). The successfully amplified products were purified using the ExoSAP-IT purification kit according to the manufacturer's instruction. Purified PCR templates were sequenced using dye-labeled dideoxy terminator cycle sequencing on an ABI 3130 automated DNA sequence. Chromatographs were checked and sequences were edited using CodonCode Aligner (v. 2.0.6, Codon Code Corporation).

Phylogenetic analyses

We conducted maximum parsimony (MP) and partitioned Bayesian inference searches based on the full concatenated dataset. We used PAUP* 4.0b10 (Swofford 2002) to perform MP analyses with 100 random addition sequence replicates, equal character weighting, tree bisection and reconnection (TBR) branch swapping, and gaps coded as missing data. Nodal support was obtained using bootstrap analyses (Felsenstein 1985), with 10,000 replicates, 10 random addition sequences replicates, and TBR branch swapping. Partitioned Bayesian analyses were performed with MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003), using the same 21 partitions (12S rRNA, 16S rRNA, tRNAs, and the respective separated 1st, 2nd and 3rd positions of ND1, BDNF, C-mos, alpha-Enolase, PDC and Rag2) and the same parameters as obtained by Crottini et al. (2009). We performed one run of 20 million generations (started on random trees) and four incrementally heated Markov chains (using default heating values) each, sampling the Markov chains at intervals of 1,000 generations. Stabilization of likelihood values occurred after nine million generations. The first ten million generations were conservatively discarded, and 10,000 trees were retained post burn-in and summed to generate the majority rule consensus tree. Both this tree and the sequence alignment data have been deposited at TreeBase, under the study accession number S11140 (tree accession number Tr26690; matrix accession number M7561). Genetic distances between all species in *Paracontias* were estimated with MEGA 4.1 (Tamura et al. 2007) by calculating uncorrected p-distances based on the ND1 and phosducin genes.

Table 1 List of taxa and material included in the present study, with respective collecting localities, voucher field numbers, institutional catalogue numbers (where available), and GenBank accession numbers per gene region sequenced; asterisk indicates that respective holotype has been sequenced; newly determined sequences shown in boldface

Taxon	Locality	Voucher field number	Institutional catalogue no.	Accession numbers							
				12S	16S	ND1	BDNF	C-mos	Rag2	a-Enolase	PDC
Amphiglossus											
anosyensis	Ambatolahy	ZCMV 591	ZMA 20342	FJ667609	FJ667621	FJ744569	FJ667634	FJ667663	FJ667721	FJ744551	FJ667692
astrolabi	Ranomafana	FG/MV 2002–312	ZSM 201/2003	AY315474	AY315523	FJ744570	FJ667635	FJ667664	FJ667722	AY391213	FJ667693
frontoparietalis	Ambohitsara	ZCMV 153	ZMA 20341	FJ667610	FJ667622	FJ744571	FJ667636	FJ66766	FJ667723	FJ744560	FJ667694
macrocercus	Ankaratra	FG/MV 2002–2142	ZSM 1016/2003	AY315484	AY315533	FJ744572	FJ667637	FJ667666	FJ667724	AY391216	FJ667695
mandokava	Montagne d'Ambre	FGZC 1240	ZSM 2167/2007	FJ667611	FJ667623	FJ744573	FJ667638	FJ667667	FJ667725	AY391217	FJ667696
melanurus	Maroantsetra	MVTIS 2002-A6	—	AY315502	AY315551	FJ744574	FJ667639	FJ667668	FJ667726	AY391218	FJ667697
punctatus	Ambatolahy	ZCMV 519	ZMA 20230	AY315489	FJ667624	FJ744575	FJ667640	FJ667669	FJ667727	AY391221	FJ667698
reticulatus	Berara	MVTIS 2000-E44	—	AY315490	AY315539	FJ744576	FJ667641	FJ667670	FJ667728	AY391224	FJ667699
tanysoma	Berara	MVTIS 2000-D58	—	AY315498	AY315547	FJ744577	FJ667642	FJ667671	FJ667729	FJ744561	FJ667700
sp. 'robustus'	Andasibe	ZCMV 373	ZMA 20228	FJ667612	FJ667625	FJ744562	FJ667643	FJ667672	FJ667730	FJ744546	FJ667701
sp. 'phaeurus'	Andasibe	ZCMV 3062	UADBA uncat	FJ667613	FJ667626	FJ744563	FJ667644	FJ667673	FJ667731	FJ744547	FJ667702
sp. 'variegatus'	Montagne des Francais	FGZC 482	ZSM 246/2004	FJ667614	FJ667627|	FJ744564	FJ667645	FJ667674	FJ667732	FJ744548	FJ667703
Androngo											
trivittatus	Tolagnaro	FGZC 2306	ZSM 389/2005	FJ667615	AY151444|	FJ744565	FJ667646	FJ667675	FJ667733	FJ744549	FJ667704
Madascincus											
igneocaudatus	Ibity	MVTIS 2001-D14	—	AY315476|	FJ667629	FJ744567	FJ667648	|FJ667677	FJ667735	AY391214	FJ667706
intermedius	Ampijoroa	MVTIS 2001-B55	—	AY315479	AY315528	FJ744568	FJ667649	FJ667678	FJ667736	AY391215	FJ667707
mouroundavae	Antsahamanara	MVTIS 2001-F17	—	AY315487	AY315536	FJ744578	FJ667650	FJ667679	FJ667737	AY391219	FJ667708
polleni	Berara	MVTIS 2000-E18	—	AY315497	AY315546	FJ744579	FJ667651	FJ667680	FJ667738	AY391222	FJ667709
sp. 'baeus'	Andasibe	ZCMV 2283	UADBA uncat.	FJ667617	AY315542	FJ744580	FJ667652|	FJ667681	FJ667739	FJ744552	FJ667710
Paracontias											
brocchii	Montagne d'Ambre	FGZC 476	ZSM 244/2004	AY315507	AY391155	FJ744583	FJ667655	FJ667684	FJ667742	AY391225	FJ667713
fasika*	Baie de Sakalava	FGZC 1347	ZSM 2256/2007	FJ667619	FJ667632	FJ744589	FJ667661	FJ667690	FJ667748	FJ744558	FJ667719
hildebrandti	Montagne des Francais	FGZC 1946	ZSM 1578/2008	FJ667620	FJ667633	FJ744590	FJ667662	FJ667691|	FJ667749	FJ744559	FJ667720
kankana*	Mahasoa forest	DRV 5711	ZSM 1810/2008	AY315509	FJ667631	FJ744582	FJ667654	FJ667683	FJ667741	AY391227	FJ667712
manify*	Antsahamanara	MVTIS 2001-F58	MRSN R1887	AY315510	AY315559	FJ744584	FJ667656	FJ667685	FJ667743	FJ744554	FJ667714
minimus	Baie de Sakalava	FGZC 1027	ZSM 2251/2007	FJ667616	FJ667628	FJ744566	FJ667647	FJ667676	FJ667734	FJ744550	FJ667705
rothschildi	Baie de Sakalava	FGZC 1020	ZSM 2246/2007	FJ667618	FJ667630	FJ744581	FJ667653	FJ667682	FJ667740	FJ744553	FJ667711
vermisaurus*	Makira	ZCMV 11211	ZSM 0597/2008	—	**HQ891855**	**HQ891854**	**HQ891856**	—	**HQ891858**	—	**HQ891857**
Pygomeles											
braconnieri	Ifaty	FG/MV 2002–2048	—	AY315514	AF215235	FJ744585	FJ667657	FJ667686	FJ667744	FJ744555	FJ667715
Voelzkowia											

Table 1 (continued)

Taxon	Locality	Voucher field number	Institutional catalogue no.	Accession numbers							
				12S	16S	ND1	BDNF	C-mos	Rag2	a-Enolase	PDC
fierinensis	Arboretum Tulear	FG/MV 2000–569	UADBA uncat.	AY315516	AY315563	FJ744586	FJ667658	FJ667687	FJ667745	FJ744556	FJ667716
lineata	Anakao	FGZC 2683	ZSM 384/2005	AY315518	AF215238	FJ744587	FJ667659	FJ667688	FJ667746	AY391228	FJ667717
sp. 'pallida'	Anakao	FG/MV 2002–1536	UADBA uncat.	AY315589	AY315565	FJ744588	FJ667660	FJ667689	FJ667747	FJ744557	FJ667718
Outgroup											
Cordylus sp.	–	–	–	AF236036	DQ249038	AY315566	AY987981	AY987981	DQ119627	–	–
'Eumeces' s. l. spp.	–	–	–	EU278021	EU278085	AY315600	EF646320	EF646320	DQ119628	AY2180	–
Tiliqua sp.	–	–	–	AB057376	AY217965	–	–	–	EF534983	AY218053	EF534856

Collection Abbreviations: *DRV* = D.R. Vieites field numbers; *FG/MV, FGZC, ZCMV* F. Glaw and/or M. Vences field numbers; *MRSN* Museo Regionale di Scienze Naturali, Torino; *MVTIS* tissue collection of M. Vences; *UADBA* Université d'Antananarivo, Département de Biologie Animale (not yet catalogued); *ZMA* Zoölogisch Museum Amsterdam; *ZSM* Zoologische Staatssammlung München

Results

Molecular phylogenies

The results of the phylogenetic analyses are summarized in Fig. 2. Despite the fact that the deepest nodes of the MP tree are not resolved, the MP and Bayesian results are relatively congruent. The only exception concerns the position of *P. hildebrandti*, which resulted as the sister species of *P. manify* in the Bayesian analysis (PP = 0.98), whereas it was the sister taxon to the poorly supported clade [(*P. manify* (*P. brocchii* + *P. minimus*)] in the MP analysis (bootstrap support 58%). In both approaches, monophyly was supported for the Malagasy scincines (PP 1.0/bootstrap 96%), for "clade A" (1.0/68%) and "clade B" (1.0/84%) as previously defined by Whiting et al. (2004), and for *Paracontias* (1.0/62%), as was the case in the study by Crottini et al. (2009). The Bayesian analysis suggested *P. kankana*, the only included species from eastern Madagascar, as the most basal species in the genus (1.0), followed by *P. vermisaurus* sp. n. (1.0). Nevertheless, the most basal relationships within *Paracontias* were not resolved in the MP analysis, which produced a polytomy with four main clades: (1) the '*P. kankana* clade', (2) the '*P. vermisaurus* clade', (3) the '(*P. rothschildi* + *P. fasika*) clade', and the '[*P. hildebrandti* {*P. manify* (*P. brocchii* + *P. minimus*)}] clade'.

The uncorrected p-distances calculated among species in the genus *Paracontias*, both for the most divergent and for the most conservative gene (ND1 and phosducin, respectively), are provided in Table 2. The distances calculated for the new species in relation to the other species of *Paracontias* range from 14.8% to 18.3% for the ND1 gene fragment, and from 1.4% to 2.4% for the phosducin gene fragment; these values are on the same order as those observed between other accepted species in the genus.

Taxonomic section

The new species described below in the genus *Paracontias* Mocquard, 1894 has been recognized using an integrative taxonomic approach. The concept of integrative taxonomy (sensu Dayrat 2005) is based on the general lineage species concept (de Queiroz 1998, 2007), rejects the superiority of any particular set of characters (morphological, behavioral or molecular), and advocates the combined and integrated use of such methods (Padial et al. 2010). In the present case, both morphological data (qualitative and quantitative scalation characteristics, coloration) and molecular data (phylogenetic position, genetic distances) congruently support the distinctiveness of the new species.

Fig. 2 Phylogenetic tree of Malagasy Scincinae reconstructed using Bayesian inference (20 Mio. generations; trees sampled every 1000 generations; burn-in 10,000), based on 3,936 bp DNA sequences of 12S and 16S rRNA, ND1, BDNF, Rag2, Cmos, Enol and phosducin. Legless fossorial lineages highlighted in grey. *Cordylus*, *Tiliqua* and '*Eumeces*' sensu lato used as out-group (not shown). Numbers at nodes are Bayesian posterior probabilities followed by bootstrap support values >50% from Maximum Parsimony analysis (10,000 replicates)
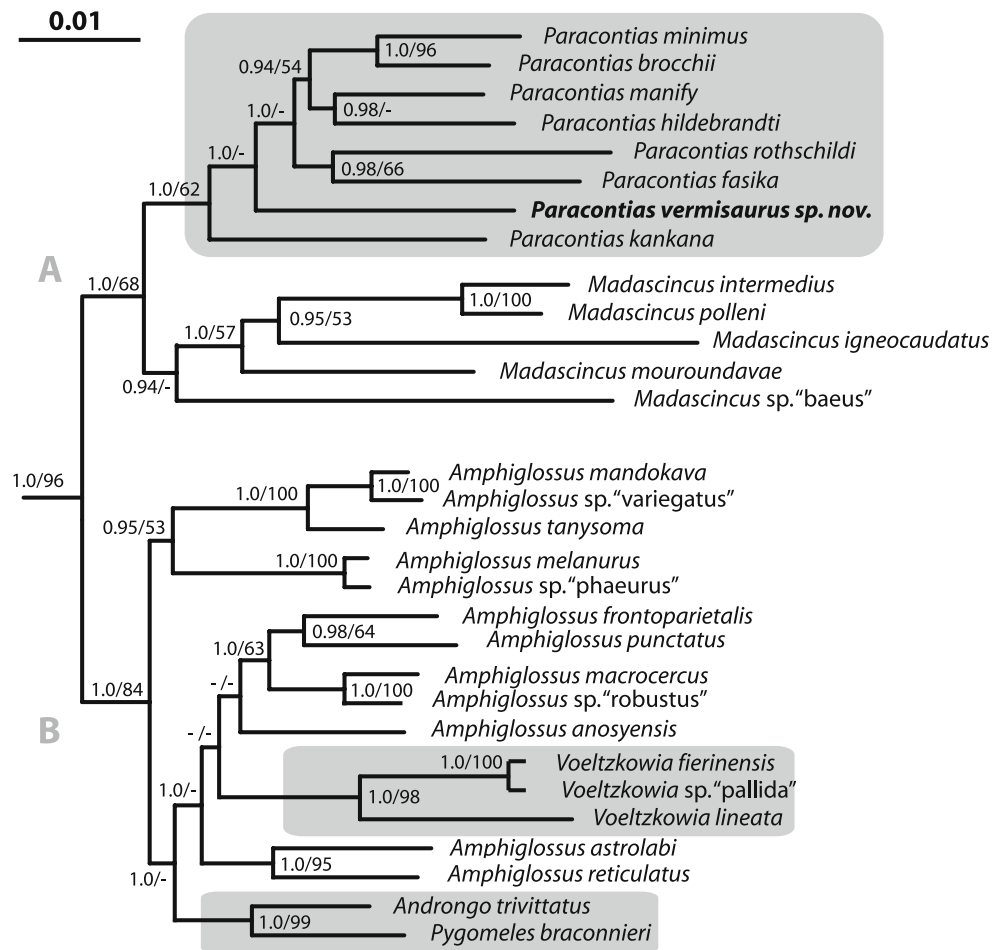
Paracontias vermisaurus sp. n.

(Figures 3 and 4a)

Etymology The specific epithet is derived from the Latin vermis (worm) to the Greek sauros (lizard); it is to be treated as a noun in apposition for the purposes of nomenclature.

Type material Holotype (ZSM 597/2008; field number ZCMV 11211), apparently an adult specimen; northeastern Madagascar, Makira Reserve, site locally named Angozongahy, 15°26′13.3″ S, 49°07′07.0″ E, 1,009 m a.s.l.,
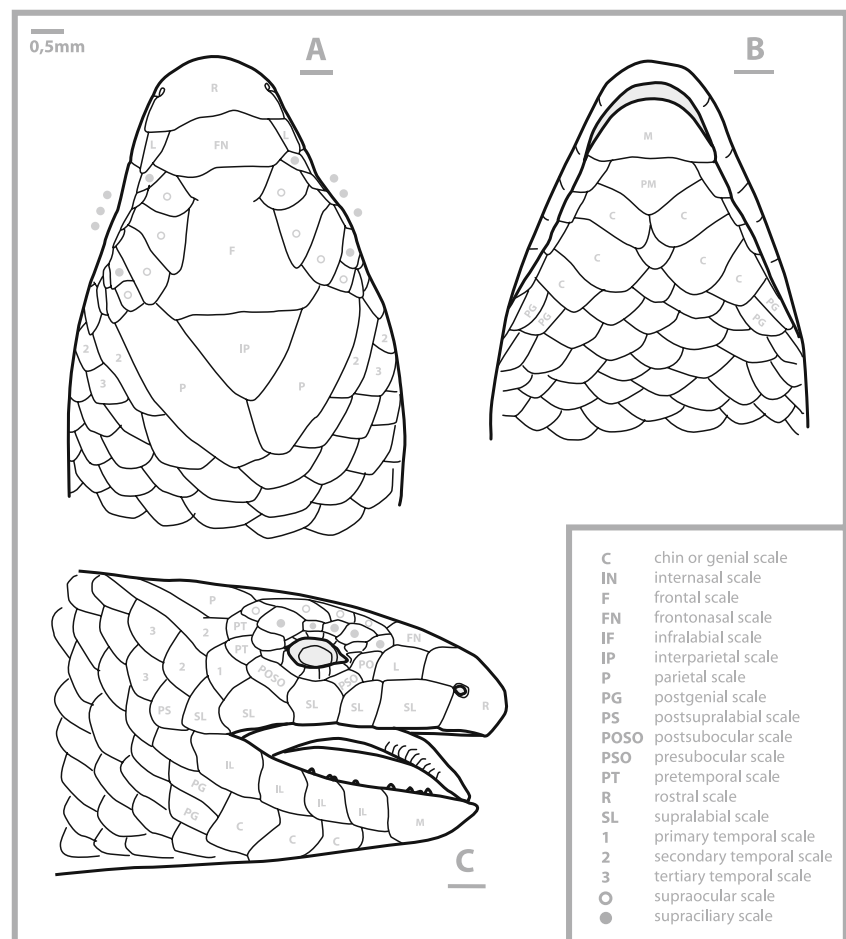
collected 20–22 June 2009 by C. Patton, J. Patton, E. Rajeriarison, T. Rajoafiarison, R. D. Randrianiaina, F. Ratsoavina,, M. Vences and D. R. Vieites. Paratype (ZSM 598/2008; field number DRV 5935), adult; data as for holotype, except site locally named Ampofoko, 15°25′22.3″ S, 49°07′15.1″ E, 1,034 m a.s.l., 28 June 2009.

Diagnosis Small brownish apodous scincine species in *Paracontias* Mocquard, as revealed by sequence analyses of mitochondrial and nuclear genes as well as by the absence of legs, supranasals and postnasals, the main morphological synapomorphies that in combination differen-

Table 2 Summary of genetic divergences (uncorrected p-distances, shown as percentages) in the genus *Paracontias*; below table diagonal: most conservative gene (phosducin), mean interspecific distance = 1.6±0.7, range = 0.3 to 2.7; above diagonal: most divergent gene (ND1), mean interspecific distance = 14.3±0.02, range = 8.7 to 18.3

		1	2	3	4	5	6	7	8
1	*P. minimus*	–	11.6	13.2	8.7	11.9	14.8	13.0	14.8
2	*P. rothschildti*	1.1	–	14.3	13.0	14.1	14.8	13.9	15.4
3	*P. kankana*	2.2	2.7	–	15.2	14.5	17.0	15.0	18.3
4	*P. brocchii*	0.3	0.8	2.4	–	11.6	15.4	12.1	15.4
5	*P. manify*	0.8	0.8	2.4	1.1	–	15.4	11.6	15.7
6	*P. fasika*	1.1	1.1	2.7	1.4	0.8	–	15.4	16.6
7	*P. hildebrandti*	1.1	1.1	2.7	1.4	0.8	1.1	–	17.9
8	*P. vermisaurus* sp. n.	1.9	1.9	1.4	2.2	2.2	2.4	2.4	–

Fig. 3 Head of *Paracontias vermisaurus* sp. n. (holotype, ZSM 597/2008). **a** Dorsal view. **b** Ventral view. **c** Lateral view

C	chin or genial scale
IN	internasal scale
F	frontal scale
FN	frontonasal scale
IF	infralabial scale
IP	interparietal scale
P	parietal scale
PG	postgenial scale
PS	postsupralabial scale
POSO	postsubocular scale
PSO	presubocular scale
PT	pretemporal scale
R	rostral scale
SL	supralabial scale
1	primary temporal scale
2	secondary temporal scale
3	tertiary temporal scale
O	supraocular scale
•	supraciliary scale

tiate the genus from other Malagasy scincines, including from limbless species assigned to *Amphiglossus*.

Paracontias vermisaurus sp. n. differs from congeneric species by the following combination of character states: presence of loreals separated from each other by the rostral to the frontonasal (versus very large loreals extending and meeting each other at dorsal midline in *P. kankana*, loreals absent in *P. milloti*); two supralabials between the rostral and the subocular supralabial (three in *Amphiglossus stylus*; one in *P. hildebrandti*), hourglass-shaped frontal (bell-shaped in *P. brocchii, P. kankana, P. manify, P. minimus, P. rothschildi, P. tsararano*); 20 scale rows around midbody (16 in *P. rothschildi* and *P. fasika*; 18 in *P. milloti* and *P. minimus*; 21 in *P. kankana* and *P. tsararano*; 22 in *P. manify*; 26 in *P. brocchii*; 31 in *P. holomelas*); nostril in contact with first supralabial (nostril deeply within rostral and posteriorly connected by distinct narrow join with first supralabial in *P. hafa, P. hildebrandti, P. holomelas, P. minimus, P. manify* and *P. tsararano*); three supraoculars largely in contact with the frontal (two in *P. brocchii, P. milloti, P. kankana, P. tsararano, P. rothschildi*; one in *P. minimus*), eye opening not covered by scales (eye sunken below ocular scale in *P. minimus*); a uniform dark

coloration (bicolored pattern with lighter wide medio-dorsal stripe in *P. fasika* and *P. rothschildi*). Additionally, *P. vermisaurus* differs from the morphologically similar *P. hafa* in having a relatively larger eye with a prominent supraocular region (versus a flat, laterally depressed supra-ocular region), and by brownish live coloration with a faint violet tint (versus pale with pinkish tint).

Description of holotype In good state of preservation, except for the tail that has been autotomised 8 mm posterior to the cloaca. Unsexed, apparently adult specimen. Snout-to-vent length 53.8 mm, width at midbody 3.5 mm, head width at level of parietal eye 3.6 mm.

In general appearance, a brown skink of relatively small size, slender, with both pairs of limbs completely absent. Snout blunty rounded in both dorsal and lateral aspect, with a rostral tip blunty rounded in dorsal aspect. Rostral wider than long, contacting first supralabial, loreal and fronto-nasal. Supranasals absent, apparently fused with rostral. Frontonasal roughly trapezoidal, wider than long, contacting loreals, first supraciliaries and first suproculars. Prefrontals absent. Frontal approximately as wide as long, wider posteriorly, in contact with frontonasal, first three supra-

Fig. 4 Live habitus of holotypes of *Paracontias vermisaurus* sp. n. **a** and *P. hafa* **b**. Photographs by M. Vences and F. Andreone, respectively

oculars, parietals and interparietal. Supraoculars four, the second and third pairs longer in size, the posteriormost pair significantly smaller. Frontoparietals absent. Interparietal triangular, longer than wide, well separated from supraoculars; parietal eyespot present, with parietal eye evident. Parietals contact each other posterior to interparietal. Parietal in contact with two pairs of cycloid dorsal scales; enlarged nuchals absent. Nasal only slightly larger than nostril, contacting rostral and first supralabials. Postnasals absent, apparently fused with rostral. Loreal single, about as high as long. Preocular wider dorsally than ventrally, single. Presubocular lozenge-shaped, single. Five supraciliaries on either side, in continuous row; first, second and last pairs significantly larger and longer than intermediate ones; last pair projecting onto supraocular shelf. Upper palpebrals small, except for last which projects dorsomedially. Pretemporals two, the upper contacting the parietal, the lower the primary temporal scales, both contacting upper secondary temporal. Postsuboculars single, contacting penultimate supralabial, primary temporal and lower pretemporal. Lower eyelid moveable, scaly; five rectangular lower palpebrals in contact with eye, the last being the largest. Contact between upper palpebrals and supraciliaries apparently direct but flexible, i.e. palpebral cleft narrow. Primary temporal single. Secondary temporals

two; the upper long, broadly contacting the upper and barely the lower pretemporals anteriorly. Two tertiary temporals bordering lower secondary temporal. Supralabials five, the third being the enlarged subocular contacting scales of lower eyelid. Postsupralabial single. External ear opening absent, with no indication of its former position. Mental wider than long, posterior margin straight. Postmental pentagonal diamond-shaped, wider than long, contacting first pair of infralabials. Infralabials four. Three pairs of large chin scales; members of first pair in contact behind postmental, members of second pair separated by a single median scale row, members of third pair separated by three scale rows. No scales extending between infralabials and large chin scales; two asymmetrical postgenials posterolaterally in contact with third pair of chin scales. Gulars similar to ventrals in size and outline. All scales except head shields cycloid, smooth and imbricate. Longitudinal scale rows on flanks disrupted at level of two weak lateral depressions with reduced scales, indicating former position of forelimbs. Longitudinal scale rows at midbody 20; paravertebrals 109, similar in size to adjacent scales; ventrals 103. Inner preanals larger and longer than outer ones.

For live coloration, see Fig. 4a. In preservative, ground coloration dark brown; head immaculate dark brown, rostral, first supralabial and mental scales with milky slightly paler color, supraoculars darker than other supracephalic scales; parietal eyespot visible as beige spot; lower eyelid whitish, with upper part bordering the eye dark brown; dorsal body scales brown with dark brown color at their posterior and pale beige at their lateral edges; numerous minute irregular beige flecks and spots present within scales; tail base (posterior tail amputated) slightly darker than rest of body; from throat to cloaca, flanks slightly paler than dorsal scales due to spreading of pale coloration within each ventral scale row.

Variation The only other known specimen, the paratype, is slightly larger than the holotype: snout-to-vent length 60.5 mm, width at midbody 4.5 mm, head width at level of parietal eye 4.3 mm. Cephalic scalation identical to holotype; longitudinal scale rows at midbody 20; paravertebrals 105, ventrals 98. Coloration in preservative identical to holotype.

Distribution and natural history Only known from two sites in the primary rainforest of Makira reserve located close to each other, both close (<50 m) to streams and around 1,000 m a.s.l. (Fig. 5). The rainforest is somewhat degraded at both sites; at Ampofoko (the paratype locality) multiple traces of cattle were found. The holotype was captured in a pitfall line (10 l buckets in the ground at 10 m distances, connected by a plastic barrier of a total length of 50 m); the paratype was found by field assistants while actively searching under rotten logs and leaf litter.

Fig. 5 Rainforest at Makira
Reserve (>1,000 m a.s.l.). **a**
General view. **b** At the
collecting locality of the
paratype, a site locally
named Ampofoko
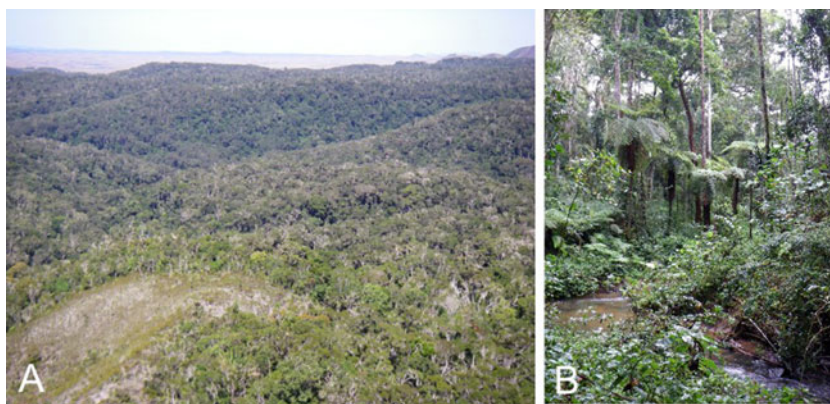
Discussion

Taxonomic validity of *Paracontias vermisaurus* sp. n

Of the total of currently 12 recognized species of *Paracontias*, six have been described only during the last 8 years (Andreone and Greer 2002; Köhler et al. 2009, 2010). For almost all of them, no reliable data on variation, reproduction and habits are available, except for some general information on the habitat and few prey items found in stomachs (Köhler et al. 2010). Several reasons may explain this insufficient knowledge. First, the type specimens of several of the historically oldest nomina in the genus seem to be lost, or in such a poor state of preservation that they are now virtually unidentifiable. Additionally, species of *Paracontias* are very rare in collections. Most of them are known by very few specimens, sometimes only by the holotype. This considerably complicates the study of this genus as it prevents us to obtain an estimate—even a rough one—of the intraspecific variability or of the distribution for each species of *Paracontias*.

Morphologically, *P. vermisaurus* sp. n. differs from almost all remaining species of *Paracontias* by three or more distinct characters in scalation (see diagnosis above). However, the distinction between *P. vermisaurus* and *P. hafa* is less obvious. Scalation is superficially similar, differing only by a single character of the rostral region: *P. hafa* has the nasal (pierced by nostrils) deeply within the rostral scale, and posteriorly connected with the first supralabial by a distinct narrow join, whereas *P. vermisaurus* has the nasal in contact with both the rostral and the first supralabial (= rostral shield and pseudoshield, respectively, see below for more details). The molecular data, both the topology (see Fig. 2) and the very high genetic divergence (Table 2), strongly support the distinctness of *P. vermisaurus* from several other species of the genus but, unfortunately, no molecular sample of *P. hafa* (which is only known from the holotype) has been available to us. Due to the limited total number of available specimens, it is thus impossible to

directly assess the intraspecific variability of that rostral character within these two species. Nevertheless, larger series of specimens of two other species of *Paracontias* were available to us and can be used to assess intraspecific variation in this character. In *P. rothschildi*, 100% of the examined specimens ($n=30$, from 2 different localities) have the nasal in contact with the first supralabial, whereas in *P. minimus* all specimens ($n=21$, 3 localities) have the nostril within the rostral, thus supporting the hypothesis of intraspecific stability of the respective character state. Based on these data, we hypothesize that the character is highly reliable for taxonomy, thus supporting the distinction between *P. vermisaurus* sp. n. and *P. hafa*.

Other, more subtle and less clear-cut characters also support this hypothesis, such as the relatively larger eyes in *P. vermisaurus*, with a more prominent supraocular region (versus a flat, laterally depressed supraocular region in *P. hafa*), and the differences in live coloration.

Evolution of the rostral shield in *Paracontias*

Loss or fusion of scales of the anteriormost part of the head are commonly encountered in different lineages of fossorial snakes (Marx and Rabb 1970; Miralles 2001; Savitzky 1983). For instance, several colubrid snakes (sensu lato) with such habits show different patterns of scalation characterised by a reduction in the number of scales on the snout, e.g. bilateral fusion between internasals and prefrontals in the genus *Calamaria*, fusion of both prefrontals to a single median scale in *Aparallactus niger*, fusion of both internasals to a single median anterior plate and fusion of both prefrontals to a single median scale most posteriorly in *Prosymna meleagris*, or fusion of both internasals and prefrontals to a single large scale in the genus *Poecilopholis* (Chippaux 2001; Koch et al. 2009; Miralles 2001). The same trend is also present in several lineages of fossorial lizards. The rostral shield that characterizes several of them constitutes a remarkable case of reduction in the number of scales in the rostral region

among Squamata. This state has evolved at least four times independently in skinks (at least two times independently in Africa, in the *Typhlacontias* clade, and in the clade containing *Acontias*, *Acontophiops* and *Typhlosaurus*, a third time in the Malagasy genus *Paracontias*, and likely a fourth time in the Sri Lankan endemic genus *Nessia*), and a very similar structure has evolved in the family Dibamidae (Fig. 1). The members of all these taxa have fossorial habits and share many of the adaptative characters usually associated with subterranean life: elongated body, absence or regression of the limbs, the ear opening, and the eye (Table 3; Andreone and Greer 2002; Broadley 2006; Daniels et al. 2006; Das and Lim 2003; Fitzsimons 1943; Smith 1935; Somaweera and Somaweera 2009; Whiting et al. 2003, 2004).

The genus *Paracontias* constitutes an informative model to study the evolution of the rostral shield, because a complete shield is present in only some species of the genus while others have a less modified structure. In most of the four-legged scincine skinks of Madagascar closely related to *Paracontias* (namely *Madascincus*, *Amphiglossus*), the plesiomorphic state of scalation of the rostral region (Fig. 6a) is constituted by a rostral scale (R), a pair of supranasals (SN), a pair of postnasals (PN), and three pairs of supralabials (1, 2, 3) between the rostral and the subocular supralabial (SubO). In all species of *Paracontias*, the supranasal and postnasal scales are absent, likely fused with the rostral scale into a single large plate (Fig. 6b and c), and the number of supralabials is reduced (only two scales between the rostral and the subocular supralabial, versus most frequently three in the genus *Madascincus* and *Amphiglossus*). Nevertheless, some species of *Paracontias* may have nostrils within the rostral scale (a pattern we refer to as the rostral shield sensu stricto, cf. Fig. 6c), whereas others may have a less modified structure, with nostrils being in contact with the rostral but not completely embedded within it (the rostral pseudo-shield, cf. Fig. 6b).

Comparative examination of the rostral scalation within the genus *Paracontias* (using *Madascincus* as out-group)

suggests two hypotheses on the evolutionary origin of the rostral shield in this particular genus. In both hypotheses, the same intermediate state (step 0) is necessary (namely the fusion of the rostral with the supranasals and the postnasals), but the subsequent steps significantly differ between those hypotheses.

The 'one step' hypothesis Only based on size and position homologies, as it is usually done in squamate taxonomy, this hypothesis considers the rostral shield to result from fusion of the first supralabial with the rostral scale. Indeed, (1) the posterior extension of the rostral shield fits very well, both in terms of size and position, with the first supralabial in *Madascincus*, and (2) the presence of the horizontal groove extending posteriorly to the nostril recalls the suture delimiting the postnasal from the first supralabial in *Madascincus*. In that case (Fig. 6 C1), the suture delimitating the rostral shield from the new first supralabial (= second supralabial in *Madascincus*) would not be homologous between the *Paracontias* having a rostral shield and those having a rostral pseudo-shield (Fig. 6b, C1).

The 'two step' hypothesis This alternative is based on the phylogenetic hypothesis of the genus *Paracontias* derived from our molecular tree (Fig. 1). According to the topology obtained, it is not possible to determine whether the rostral shield evolved at least two times independently within the genus, or whether it appeared only once and then regressed in *P. brocchii*, both these hypotheses being equally parsimonious (box in Fig. 6). However, in both cases the rostral shield is always derived from the rostral pseudo-shield state, which likely constitutes the plesiomorphic state within *Paracontias*. This implies that the rostral pseudo-shield constitutes an intermediate step always present during the process leading to the forming of the rostral shield (step 1), followed by the backward extension of the rostral pseudo-shield, together with a regression of the first supralabial (step 2). According to this hypothesis, supra-

Table 3 The rostral shield as defined in the present paper has been found in six genera of Scincidae and in the genus *Dibamus* (Dibamidae), representing at least five instances of convergent evolution of this feature within Squamata (clades 1–5); members of all these genera are known for their fossorial habits and share many of the morphological characters usually associated with this lifestyle

| Family	Clade	Genus	Limbs	Eyes	External ear opening
Scincidae	1	*Acontias*	absent	small, with eyelid	hidden
		Typhlosaurus	absent	hidden	hidden
	2	*Typhlacontias*	absent	exposed, without eyelid	hidden
	3	*Paracontias*	absent	exposed or hidden	hidden
	4	*Nessia*	absent or vestigial	exposed	hidden or minute
Dibamidae	5	*Dibamus*	male: single pair of flaplike hind limbs female: absent	hidden	hidden
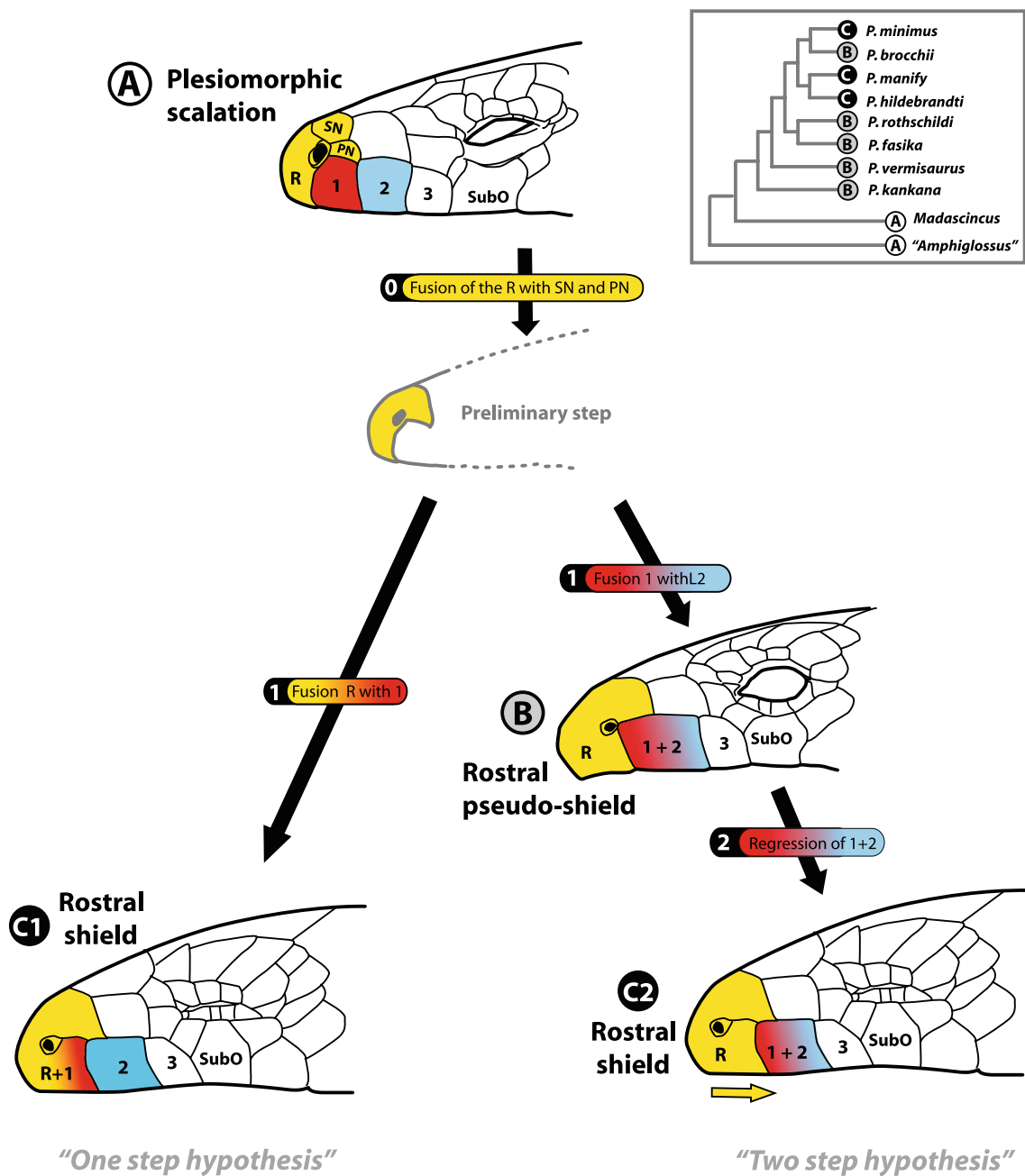
Fig. 6 Evolutionary origin of the rostral shield in *Paracontias*. Two hypotheses may explain genesis of the rostral shield; both involve the same first evolutionary step: fusion of the rostral with the supranasals and the postnasals. In the one step hypothesis, the rostral shield results from fusion of the first supralabial with the rostral scale. In the two step hypothesis, a rostral pseudo-shield constitutes an intermediate state resulting from fusion of the first two supralabials (step 1), followed by backward extension of the rostral pseudo-shield, together with regression of the first supralabial (step 2). **a** Plesiomorphic state in *Madascincus* (*M. polleni*), characterized by presence of a pair of supranasal and postnasal scales. **b** Rostral pseudo-shield in *Paracontias* (*P. vermisaurus*). **c** Rostral shield in *P. hafa*

labials are homologous between both morphological groups of *Paracontias* (species with a rostral shield and those with a rostral pseudo-shield), whereas the horizontal groove extending posteriorly from the nostril is not homologous to the suture delimiting the postnasal scale from the first supralabial in *Madascincus*.

The two step hypothesis appears to be more likely, as it takes into account the phylogenetic relationships within *Paracontias*, the essential framework in any evolutionary inference. This result is particularly interesting because (1) it cautions that intuitive and seemingly obvious scale homologies only based on position and size (as usually formulated in squamate taxonomy) may be highly misleading, even in closely related species (see also Köhler et al. 2010), and (2) it indicates that the rostral pseudo-shield might be a preliminary adaptation prerequisite to rostral shield forma-

tion. The latter is either (1) because it constitutes a more advantageous structure (preferable to the rostral shield) for species of moderately fossorial habits (including the ancestral species of *Paracontias*), and the fully developed rostral shield is only of selective advantage for fully fossorial species, or (2) because developmental constraints prevent the fusion of the rostral with the first supralabial, thus forcing an evolutionary pathway in which a rostral shield originates via this alternative and somewhat less parsimonious way.

Functional implications of the rostral shield

The rostral shield occurs in different lineages of exclusively fossorial Squamata, strongly suggesting that this feature represents an adaptive response to this highly specialized lifestyle. The occurrence of such a large plate (rather than several smaller scales) may provide several advantages for fossorial species, both facilitating the burrowing activity and protecting the head from the strong physical constraints. First, it results in a smoother snout, thus reducing friction between the substrate and the skin; second, it should strengthen the tegument on the snout by reducing the number of sutures that act as flexible joints between two adjacent scales. Additionally, we have observed that in most of these groups (eg. *Nessia*, *Acontias*, *Paracontias*), the rostral shield frequently shows a very particular milky coloration significantly lighter than the adjacent scales, and gives the impression of being slightly turgid and thicker (see Fig. 4). It is also important to note that in all the skinks for which high resolution X-ray computer tomography images were available to us at the Digital Morphology Library (http://digimorph.org/), osteoderms always appear to be absent (*Chalcides*, *Eumeces*, *Scincus*, *Sphenomorphus*, *Tiliqua*)—or weak and lacunar (*Eugongylus*)—from the rostral to the anteriormost supralabials, whereas they are present and well ossified in almost all the other cephalic
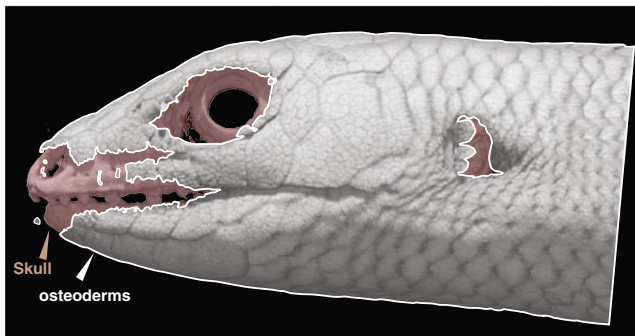

Fig. 7 Tomographic image of *Eumeces schneideri* highlighting presence of osteoderms in all scales covering the head (outlined in white), with the notable exception of those present in the anteriormost part of the snout. Source: DigiMorph.org

scales (see Fig. 7). Interestingly, these unossified scales are those usually involved in the formation of the rostral shield, which suggests that osteoderms should likely be absent from the rostral shield. Unfortunately, none of these genera studied by tomography represent legless fossorial forms nor do they have rostral shields, which prevents us from verifying this hypothesis. Nevertheless, we suppose this may indicate that in fossorial species the nature of the tissue constituting the rostral tegument is distinct from those of other cephalic scales, and that probably most of the snout surface, which is almost exclusively covered by the rostral shield, is not ossified (whereas osteoderms are only absent from the rostral tip in non-fossorial forms). These observations lead us to consider that the rostral shield may likely play the role of a shock-absorbing buffer in the fossorial species. Only a histological study could answer these questions, by determining whether the skin or the underlying connective tissue displays any unusual structural and functional properties.

Lastly, the horizontal postnasal groove constitutes another characteristic of the rostral shield, as it is always present. Given that it always runs to posterior from the nostril, we suggest that it may act as a gutter draining impurities out of the nostril during burrowing activity.

Conclusions

The present study allows us to formulate various hypotheses on the evolution and function of head scalation in fossorial squamates, although a thorough test of these was not possible within the limited scope of this work. Future approaches, e.g. involving histology, functional anatomy or developmental biology, will help to better understand the internal structure, properties and formation of the rostral shield. Additionally, comparative studies involving larger taxonomic sampling, encompassing a more comprehensive number of fossorial skink lineages, and also including genera without rostral shield (e.g. *Lerista* in Australia, *Neoseps* in North America, or *Voeltzkowia* in Madagascar), will be informative to determine whether certain factors (e.g. substrate, prey, locomotion) exist that may explain the convergent presence (or plesiomorphic absence) of the rostral shield in these different taxa. As an example, our observations led us hypothesize that the rostral shield may be more frequently associated with the fossorial species having a rounded snout and living in the leaf litter of humid forests, whereas it may be more frequently absent in the species having a spade-shaped snout usually living in sandy areas. Moreover, the absence of osteoderms from the rostral scale in probably most—if not all—skinks leads us to wonder whether the rostral tip can also show some functional particularity in the non-fossorial forms. Does the rostral scale in these species

play a similar role as a shock-absorbing buffer (for instance during prey capture or when they suddenly take refuge under the substrate to escape predators)? Or does this structure have a different, unknown function, thus constituting a case of exaptation exploited in different ways by the fossorial lineages?

Fossorial legless lizards such as *Paracontias* are among those lineages of vertebrates that have experienced adaptations to a burrowing lifestyle to the most extreme level. Despite all the remarkable features that make them excellent models for studying macroevolutionary transformations in body plan, most of these species remain poorly known and dramatically understudied. Nearly all the species of *Paracontias* are considered as very rare, as they are frequently known from few or even only a single specimen. Almost nothing is known about the biological, ecological, physiological or behavioral traits of these enigmatic organisms, whereas we can reasonably expect those traits to be as modified as the morphological features. It seems that these species have been largely ignored by the scientific community because of their very secretive fossorial way of life, their very small size, and possibly their microendemic and patchy distribution. As a consequence, these species are rare in collections, but most probably most of them are not rare in nature, as suggested by the discovery of larger numbers of individuals of *P. minimus* and *P. rothschildi* which were easy to find after some information about their habitats and habits had been gathered from local people (Köhler et al. 2010). The high rate of recent species descriptions and the scarcity of knowledge on the genus point to intensified collecting of *Paracontias* as a fruitful source of new discoveries, and encourage the development of fossorial species-oriented prospecting protocols, including more specific trapping methods.

Appendices

Appendix 1 list of specimens examined

Amphiglossus stylus MRSN R1732 (holotype), Masoala Peninsula, Campsite 5 (Menamalona), Antalaha Fivondronana, Antsiranana Faritany, 15°22.87′ S, 49°59.27′ E, 780 ma.s.l., northeastern Madagascar.

Paracontias brocchii ZSM 244/2004, Montagne d'Ambre, 12°31′ S, 49°10′ E, ca. 1,000 ma.s.l., Antsiranana Province, northern Madagascar.

Paracontias fasika ZSM 2256/2007 (holotype), Baie de Sakalava, 12°16′24″ S, 49°23′33″ E, 11 ma.s.l., Forêt d'Orangea, Antsiranana Province, northern Madagascar.

Paracontias hafa MRSN R1825 (holotype), Anjanaharibe-Sud Massif, Analabe Valley, Campsite W1, Befandriana Fivondronana, Mahajanga Faritany, 14°46′ S, 49°27′ E, 1,000–1,100 ma.s.l., northeastern Madagascar.

Paracontias hildebrandti ZMB 9695 (holotype), "nordwestliches Madagaskar"; ZSM 1578/2008, Montagne des Français, 12°20′ S, 49°22′ E, 120 ma.s.l., northern Madagascar.

Paracontias kankana ZSM 1810/2008 (holotype), Mahasoa forest (pitfall camp), near Ambatodisakoana village, 17.29769° S, 48.70199° E, 1032 ma.s.l., eastern Madagascar.

Paracontias manify MRSN R1887 (holotype), Antsahamanara, Manarikoba Forest, RNI de Tsaratanana, Marovato Fivondronana, Antsiranana Faritany, 14°02.55′ S, 48°46.79′ E, about 1,000 ma.s.l., northern Madagascar.

Paracontias minimus MNHN 1905.270 (lectotype), MNHN 1905.270A (paralectotype), "Madagascar"; ZFMK 88051–88052, ZSM 2249–2253/2007, ZSM 2268/2007, ZSM 1585–1586/2008, Baie de Sakalava, Forêt d'Orangea, 12°16′24″ S, 49°23′33″ E, 11 ma.s.l.; ZSM 1584/2008, south-east 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.

Paracontias rothschildi ZFMK 88048–88050, ZSM 2074/2007, ZSM 2235/2007, ZSM 2246–2247/2007, ZSM 2260–2269/2007, ZSM 1580–1582/2008, Baie de Sakalava, Forêt d'Orangea, 12°16′24″ S, 49°23′33″ E, 11 ma.s.l.; ZSM 1579/2008, south-east of Ivovona, Forêt d'Orangea, 12°19′58″ S, 49°24′20″ E, Antsiranana Province, northern Madagascar.

Paracontias tsararano MRSN R1787 (holotype), Tsararano Forest, Campsite 1, 14°54.4′ S, 49°41.2′ E, 710 ma.s.l., Antsarahan'ny Tsararano, northeastern Madagascar.

Appendix 2 corrigenda to original description of *Paracontias fasika*

Re-examination of the holotype of *Paracontias fasika* has revealed some mistakes in the original description (Köhler et al. 2010) that need to be corrected.

Contrary to what is written in its diagnosis, the holotype of *Paracontias fasika* has no supranasals. In the dorsal view of the head (Köhler et al. 2010: 154, Fig. 5a), the two scales in contact with the nostrils, the rostral and the frontonasals are actually loreals.

On the lateral view of the head (Fig. 5b), the shape and the size of the loreal scales have been incorrectly represented. These scales would have been drawn in frank contact with the rostral, as it has been correctly done in the Fig. 6a.

In the same figure, the fourth reduced supraocular is lacking, only the last enlarged supraciliaries being represented. The dorsal view (Fig. 5a) gives a correct representation of these scales.

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