ORIGINAL ARTICLE

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# Systematics of limbless scincid lizards from northern Madagascar: morphology, phylogenetic relationships and implications for classification (Squamata: Scincidae)

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**Abstract** We report on the rediscovery of two limbless scincid species, *Paracontias rothschildi* Mocquard, 1905 and *Paracontias minimus* (Mocquard, 1906), after more than a century. The two species were found in syntopy in sandy soils of Forêt d'Orangea, Antsiranana Province, northern Madagascar, which probably constitutes the respective type locality and confirms the species' Malagasy origin. Both taxa are redescribed based on newly collected material, and compared to other Malagasy species. In addition, *Paracontias fasika* n. sp. is described from the same locality and habitat. We discuss the taxonomy and origin of all three species and provide preliminary data on their natural history. Molecular relationships among seven *Paracontias* species are compared to external morphological characters formerly used in skink systematics. Our results indicate that morphology in fossorial skinks is well suited to distinguish species, but is of rather limited value to elucidate phylogenetic relationships. Similarities between these skinks in external characters apparently are the result of convergent evolution due to parallel selective pressures.

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## Introduction

Among the radiation of Malagasy scincine lizards, selective pressure produced a remarkable number of species adapted to a fossorial life, showing different degrees of body elongation and limb reduction (Andreone and Greer 2002; Raselimanana and Rakotomalala 2003). Recent molecular studies provided reasonable insight into the phylogenetic relationships of many of the limbless taxa (Crottini et al. 2009; Schmitz et al. 2005; Whiting et al. 2004), but taxon sampling is still incomplete and the taxonomic identity of many species remains questionable. The latter is true, for example, for two enigmatic species described by Mocquard (1905, 1906): *Paracontias rothschildi* Mocquard, 1905 and *Cryptoposcincus minimus* Mocquard, 1906. So far, both taxa were known only from their respective type specimens, which were donated to the Museum national d'Histoire Naturelle in Paris by Maurice de Rothschild and carry the imprecise locality information "Madagascar" (Angel 1942; Brygoo 1981; Glaw and Vences 1994). Despite intensified field surveys, neither species was found again on the island for more than a century, which led to doubts concerning their Malagasy origin (Brygoo 1981). During fieldwork in 2007 and 2008 in the far north of Madagascar, we rediscovered both taxa together with *Xenotyphlops grandidieri* (Mocquard, 1905), an equally enigmatic species of typhlopid snake described together with *P. rothschildi* (Mocquard 1905; Wallach and Ineich 1996). Here we report on the rediscovery of the two lizard species, redescribe both based on newly collected specimens, diagnose them against other Malagasy species, provide

precise locality data as well as preliminary observations on their ecology, and discuss their taxonomic status. In addition, we describe a new species of limbless skink occurring in sympatry with the two others. Furthermore, we compare the newly gathered morphological information with a multilocus molecular phylogeny, and discuss resulting implications for the classification of these Malagasy skinks.

## Material and methods

Specimens were obtained by digging in the upper layer of soil down to a maximum of approximately 50 cm depth. In addition, pitfall lines with drift fences were set in place. Specimens were killed by injection of ketamine solution, fixed in 90% ethanol and preserved in 70% ethanol. A tissue sample from each specimen was preserved in pure ethanol for DNA analyses. Geographic coordinates were obtained using GPS receivers. Voucher specimens are deposited in the Zoologische Staatssammlung München, Germany (ZSM) and the Université d'Antananarivo, Département de Biologie Animale, Madagascar (UADBA). Other abbreviations used below are: DRV (David R. Vieites field numbers), FGZC (Frank Glaw field numbers), MNHN (Museum National d'Histoire Naturelle, Paris), ZFMK (Zoologisches Forschungsmuseum Alexander Koenig, Bonn), and ZMB (Museum für Naturkunde, Berlin).

All measurements and counts were performed by the same person (ME). Measurements were taken to the nearest 0.1 mm with a digital caliper. Scale counts were made using a Leica MZ6 stereomicroscope at 40x magnification. Schematic drawings of the heads were produced using the same microscope with a Wild 308700 drawing tube attachment. Descriptions of live colour are based on field notes and digital images. To avoid partial destruction of voucher specimens only few were dissected for direct observation of gonads. Osteological characters were assessed from radiographs produced with a Faxitron X-ray LX-60 and the software Faxitron SR v1.5. Terminology in descriptions largely follows Andreone and Greer (2002). The following abbreviations are used: HW = greatest head width; SVL = snout-vent length; TaL = tail length.

For the comparison between molecular and morphological relationships we used the multilocus phylogeny published by Crottini et al. (2009). Additional sequences of c. 500 bp of a fragment of the 16S rRNA gene were determined on an ABI 3130 automated sequencer after amplification with primers 16Sar-L and 16Sbr-H of Palumbi et al. (1991), using standard protocols (see Crottini et al. 2009). Sequences have been deposited in GenBank (accession numbers FJ667628–FJ667633, GU048748–GU048759). Phylogenies based on 16S rRNA sequences were constructed by Bayesian inference (using MrBayes v. 3.1.2., Ronquist and Huelsenbeck 2003). In addition, bootstrap support values under Maximum Parsimony were calculated using PAUP* (v. 4.0.b10, Swofford 2002), using heuristic searches with TBR branch swapping, with 10 random addition sequence replicates and 2000 bootstrap replicates. For the Bayesian analysis, we used MrModeltest version 2.2 (Nylander 2004) to choose the appropriate model of sequence evolution for each partition. The aligned sequences contained 539 characters, of which 427 were constant; of the variable characters 81 were parsimony-informative.

## Taxonomic section

### Paracontias minimus (Mocquard, 1906)

#### Identity

This enigmatic species of limbless skink has remained largely unknown because no additional material was reported since the description of the two type specimens (MNHN 1905.270 and 1905.270A). For this reason, Brygoo (1981) even doubted the Malagasy origin of those types. Due to great external similarities, a relationship to the sand-dwelling species of *Voeltzkowia* Boettger was suspected (Glaw and Vences 1994). We recently found several specimens that largely agree with the original description and, upon examination of the types of *Cryptoposcincus minimus* Mocquard, we consider them as belonging to this species (see Remarks below). Molecular phylogenetic results of Crottini et al. (2009) based on the newly collected specimens have provided clear evidence for their phylogenetic position being nested within the genus *Paracontias* Mocquard, 1894, thus suggesting the latter name as a senior synonym of *Cryptoposcincus* Mocquard, 1906 (misspelled *Cryptoscincus* by Crottini et al. 2009). Consequently, we adopt this synonymy here by transferring the type species of *Cryptoposcincus* to *Paracontias*, which results in the combination *Paracontias minimus* (see Crottini et al. 2009).

#### Description

In general appearance a thin, brownish-beige skink of moderate size (maximum SVL 75 mm, maximum total length 130 mm), with both sets of limbs completely absent and no external indication of their former positions. Number of head scales generally reduced. Mouth large, teeth well developed. Snout rounded in dorsal view, rounded to subacuminate in lateral view; rostral strongly projecting anteriorly; supranasals absent; frontonasal wider

than long; frontal bell-shaped in outline, anteriorly constricted by first supraocular; supraoculars two, frontoparietals absent; interparietal well separated from supraoculars; parietal eyespot absent; parietals meet behind interparietal; a single pair of nuchals (Fig. 1).

Nasal absent; supranasal absent; nostril deeply within rostral scale, posteriorly connected by a distinct narrow join with first supralabial; nostril formed by rostral at all sides; postnasal absent; loreal single; preocular single; presubocular absent; eye opening absent; one 'ocular' scale, contacting third and fourth supralabial as well as supraocular; dark eye pigment visible through an 'ocular' scale and the preocular scale; primary temporal single; secondary temporals two, upper bordering parietal and nuchal, lower contacting



ultimate and penultimate supralabial; tertiary temporals two, upper small, contacting nuchal, lower contacting ultimate supralabial and postsupralabial; supralabials six; subocular absent; postsupralabial single; external ear opening absent, with no external indication of its former position (Fig. 1).

Mental wider than long; postmental single, contacting one infralabial on each side; infralabials usually four, sometimes only three (single individuals can be left/right asymmetrical, e.g. ZSM 2248/2007); three pairs of large chin scales; members of anterior pair not in contact, separated by one scale row, members of second pair separated by one scale row, members of third pair separated by three scale rows; chin scales flush with infralabials, i.e. genials do not encroach between chin scales and infralabials (Fig. 1).

Body scales cycloid, generally smooth, but with few, scattered low pimples; longitudinal scale rows at mid-body 18 ($n=15$); ventral scales 102–112 ($n=15$); subcaudals in non-regenerated tails 84–88 ($n=3$); inner precloacals overlap outer; scales in mid-ventral caudal row similar in size to scales in adjacent rows. Adult SVL 51–75 mm ($n=15$); adult TaL (non-regenerated) 39–55 mm ($n=3$). For individual scale counts and measurements, see Table 1.

Hyoid elements detectable on radiograph; teeth moderately long, crowns of teeth rounded; pectoral girdle not detectable; humerus absent; sternum present; macrosternum
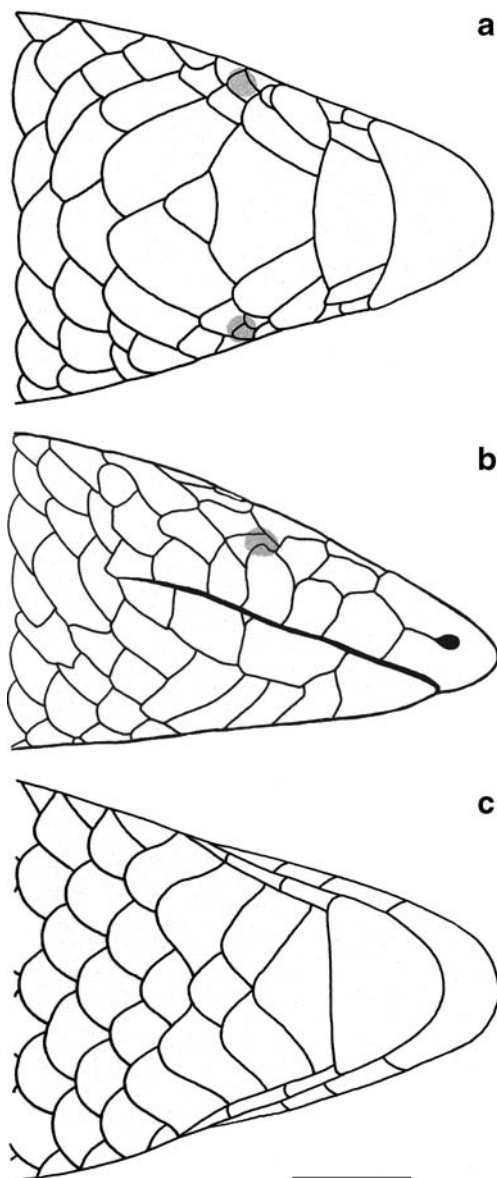
**Fig. 1** *Paracontias minimus* (ZSM 2248/2007), head. **a** Dorsal view. **b** Lateral view. **c** Ventral view. Scale bar = 1 mm

**Table 1** Meristic and mensural data for specimens of *Paracontias minimus*; for abbreviations see text

| Collection number | Scales | | SVL | TaL | HW |
|---|---|---|---|---|---|
| | ventral | subcaudal | | | |
| MNHN 1905.270 | 109 | – | 73.2 | – | 3.3 |
| MNHN 1905.270A | 108 | (70) | 53.5 | (31.4) | 2.7 |
| ZFMK 88051 | 102 | 88 | 55.6 | 42.0 | 2.8 |
| ZFMK 88052 | 109 | (48) | 68.0 | (26.1) | 2.8 |
| ZSM 2248/2007 | 103 | (53) | 73.9 | (32.1) | 3.1 |
| ZSM 2249/2007 | 103 | 88 | 67.7 | 54.4 | 3.4 |
| ZSM 2250/2007 | 105 | 84 | 50.8 | 38.7 | 2.3 |
| ZSM 2251/2007 | 106 | (59) | 74.9 | (42.6) | 3.1 |
| ZSM 2252/2007 | 103 | (63) | 69.5 | (40.1) | 2.8 |
| ZSM 2253/2007 | 104 | (82) | 65.2 | (49.0) | 2.8 |
| ZSM 2268/2007 | 102 | (74) | 71.9 | (45.7) | 3.0 |
| ZSM 1583/2008 | 112 | – | 74.2 | – | 3.0 |
| ZSM 1584/2008 | 105 | – | 64.8 | – | 3.5 |
| ZSM 1585/2008 | 106 | (83) | 68.4 | (46.2) | 2.9 |
| ZSM 1586/2008 | 107 | (79) | 73.1 | (51.7) | 3.1 |

All dimensions in mm

Values in parentheses are from specimens with incomplete or regenerated tail

cannot be resolved on radiograph; pelvic girdle's two halves separated on midline, each consisting of tripartite element representing ilium, ischium and pubis; no evidence of femur on radiograph; presacral vertebrae 59–60 ($n=3$; MNHN 1905.270, ZSM 2248/2007, 2253/2007), first free rib on third presacral; sacral vertebrae two; transverse processes of caudal vertebrae project anterolaterally at approx. 60–65° angle.

In preservative, ground colouration brownish to beige. Scales on throat light beige to almost white. Dorsal head scales beige, finely mottled with brown, dorsal side of rostral almost white, lacking brown mottling. Body scales tricoloured, on anterior body parts usually beige with a brown spot at anterior edge and a grey spot at posterior edge of scale. Brown spot can contain thin dark longitudinal lines. On posterior body parts and tail, brown spot can be positioned in centre of scale or at its posterior edge, grey spot then changing position accordingly. However, longitudinal alternation of brown, beige and grey consistently present, giving body a finely striped appearance (18 dark stripes, corresponding to number of scale rows around body). Stripes mostly become wider and thus more indistinct towards posterior body and tail. Ventral surfaces generally slightly paler, less contrastingly coloured. Colouration of tail nearly identical to body. Cloacal scales lighter, precloacal scales almost transparent. In non-regenerated tails, pointed tip white. In life (Fig. 2), colouration differs only slightly from that in preservative, with head scales exhibiting a fleshy pinkish tint. However, this differs among individuals, possibly depending on the stage before moulting. Most individuals have beige or grey ground colouration with fine brown longitudinal stripes. In freshly moulted individuals, ground colour can be orange with fine dark brown longitudinal stripes.

*Diagnosis*

A member of *Paracontias* according to the molecular phylogeny based on nuclear and mitochondrial genes by Crottini et al. (2009). *Paracontias minimus* differs from most sympatric limbless members of the genus by the number of scale rows around mid-body being 18 (vs. 16 in *P. fasika* n. sp., *P. rothschildi*; 20 in *P. hafa* Andreone & Greer, *P. hildebrandti* (Peters); 21 in *P. tsararano* Andreone & Greer; 22 in *P. manify* Andreone & Greer; 26 in *P. brocchii* Mocquard; 30 in *P. holomelas* (Günther)); only *P. milloti* Angel also exhibits 18 scale rows. However, all other *Paracontias* species have an eye opening and differ in head scalation, particularly in shape of rostral and position of nostril. For separation from *P. fasika* n. sp., see the diagnosis for the latter species below.

*Paracontias minimus* differs from the only known limbless species of *Amphiglossus* Duméril & Bibron, *A.*
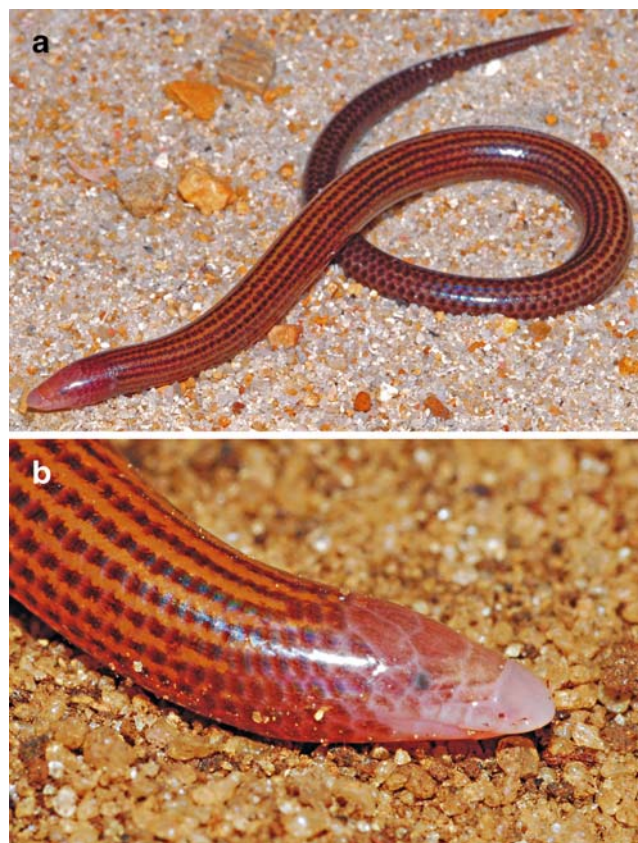


**Fig. 2** *Paracontias minimus* in life. **a** Dorsolateral view. **b** Head, lateral view

*stylus* Andreone & Greer, mainly by the lower number of scale rows around mid-body (18 versus 20), large differences in head scalation, and by lack of indication of the former limb positions (minute clawless nubs present in *A. stylus*). Furthermore, the eye opening is absent in *P. minimus* (present in all known *Amphiglossus* species). From the limbless species of *Pseudoacontias* Barboza du Bocage (*P. madagascariensis*, *P. unicolor*, *P. menamainty*), *P. minimus* differs by the lack of an eye opening, fewer scales on head, distinctly smaller SVL, and lower number of scale rows around mid-body (32 in *P. madagascariensis* Bocage, 30 in *P. unicolor* Sakata & Hikida, 25 in *P. menamainty* Andreone & Greer). *Sirenoscincus yamagishii* Sakata & Hikida is similar in size and also has reduced eyes, but forelimbs are present.

Colouration, size, lack of an eye opening and natural habits in *P. minimus* superficially resemble species of *Voeltzkowia* from western Madagascar. Among the known species of *Voeltzkowia*, only *V. lineata* (Mocquard), *V. mira* Boettger and *V. rubrocaudata* (Grandidier) are completely lacking limbs (rudimentary hindlimbs are present in the remaining species). These three species can share with *C. minimus* 18 scale rows around mid-body, but differ in head

scalation, namely the presence of a nasal and supranasal scale (both absent in *P. minimus*).

## Distribution

Known from three lowland localities in the Antsiranana Province, northern Madagascar: (1) Baie de Sakalava, Forêt d'Orangea, 12°16′24″ S, 49°23′33″ E; (2) south-east of Ivovona, Forêt d'Orangea, 12°19′58″ S, 49°24′20″ E; and (3) Ampombofofo, Babaomby region, 12°05′53″ S, 49°19′49″ E. The species likely occurs in adequate habitats inbetween these localities.

## Natural history

*Paracontias minimus* inhabits sandy soil in the shrub forest formations known as Forêt d'Orangea. Specimens were found while digging in the soil, but were never observed moving on the ground, although a single specimen was caught by a pitfall trap. In dry loose sand they can quickly 'swim' through the substrate. Preferable microhabitats seem to include shaded areas below bushes where a thin layer of organic material is present on the soil. The stomachs of two specimens (ZFMK 88052, ZSM 1583/2008) contained remains of ants and termites, as well as a remarkable amount of sand. Dissection of one female (ZSM 1583/2008) revealed the presence of two apparently unfertilized eggs in each oviduct. When captured, some specimens tried to bite the potential predator. Most of the collected specimens have regenerated tails, suggesting a certain degree of pressure by predators. The species occurs in close syntopy with *Paracontias rothschildi*, *P. fasika* n. sp. (see below), and *Xenotyphlops grandidieri*.

## Remarks

The lectotype (MNHN 1905.270) and paralectotype (MNHN 1905.270A) of this species were recently examined by us; both are in reasonable state of preservation. As already mentioned by Angel (1942) and Brygoo (1981), the lectotype has lost almost all of the tail. Although the description provided for the two specimens by Angel (1942) is quite accurate, comparisons with our material revealed a remarkable difference concerning the head in lateral view. In the drawing by Angel (1942: pl. V, Fig. 6a), the shape of the rostral scale clearly differs from that in our specimens, resulting in the nostril contacting the first supralabial scale. Detailed examination of both types failed to confirm the condition shown by Angel; instead, they have the nostril deeply enbedded in the rostral scale, connected to the first supralabial by a narrow suture only (as shown in Fig. 1). The discrepancy between Angel's (1942) drawing and the examined condition might be

explained by the fact that the rostral scale of the lectotype is damaged and shows a rupture at its lower right part, which could be misinterpreted as two separate scales. Other deviations from Angel's (1942) description are only due to differences in scale notation. However, a few discrepancies between our data and those provided by Brygoo (1981) are evident: We count only 108–109 ventral scales in the two type specimens (versus 114–115), and thus reach a lower maximum value (112) when including newly collected material (see Table 1). Similarly, Brygoo (1981) gave the number of presacral vertebrae as 56–57, whereas our counts (including the lectotype) yield slightly higher values (59–60).

The original name established for this taxon by Mocquard (1906) is *Cryptoposcincus minimus*. This name was correctly used for decades, e.g. by Angel (1942) and Blanc (1971). Brygoo (1981) then misspelled the genus name as *Cryptoscincus* throughout his revision of Malagasy scincid lizards. This incorrect spelling was mistakenly used by many subsequent authors, e.g. by Glaw and Vences (1992, 1994, 2007), Nussbaum and Raxworthy (1995), Wallach and Ineich (1996), Sakata and Hikida (2003), Raselimanana and Rakotomalala (2003), Whiting et al. (2004), Schmitz et al. (2005), Megson et al. (2009), and Crottini et al. (2009).
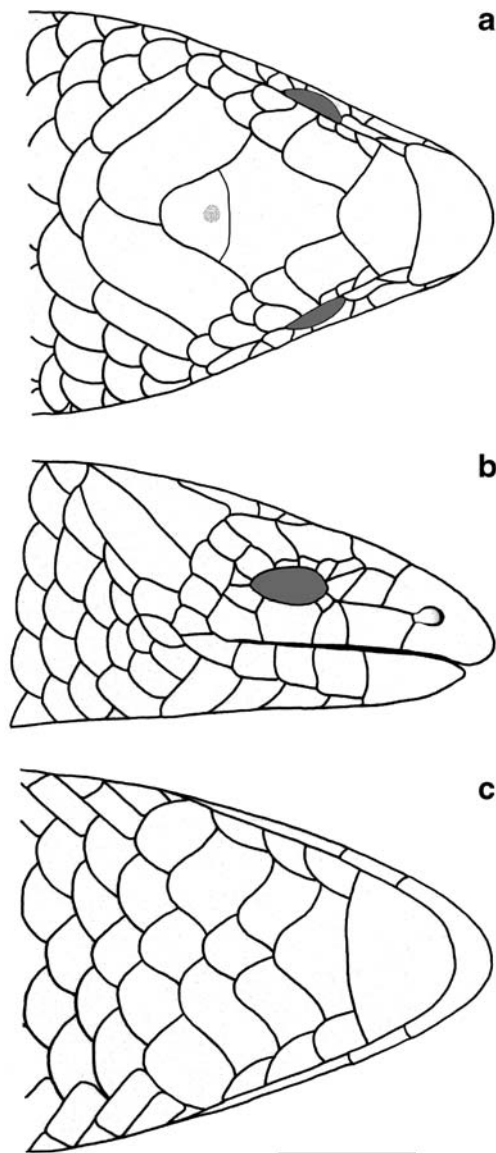
## *Paracontias rothschildi* Mocquard, 1905

## Identity

This enigmatic species has remained largely unknown because because no additional material was reported since the description of the type specimens (see Brygoo 1980). We recently found several specimens that largely agree with the original description and subsequent descriptions based on the lectotype (MNHN 1905.269).

## Description

In general appearance a thin, dark brown skink with a broad, beige mid-dorsal longitudinal band, of moderate body size (maximum SVL 55 mm, maximum total length 97 mm), with both sets of limbs completely absent and no external indication of their former positions. Snout rounded in dorsal and lateral views; rostral projecting anteriorly; supranasals absent; frontonasal slightly wider than long; frontal bell-shaped, anteriorly constricted by first supraocular; supraoculars three, anterior two contacting frontal; frontoparietals absent; interparietal well separated from supraoculars; parietal eyespot just anterior of centre of interparietal; parietals meet behind interparietal; a single pair of nuchals (Fig. 3).

Nasal moderately sized, anteriorly open, larger than nostril and lying just inside posterior corner of rostral, in

Fig. 3 *Paracontias rothschildi* (ZSM 1579/2008), head. **a** Dorsal view. **b** Lateral view. **c** Ventral view. Scale bar = 1 mm

external ear opening absent, with no external indication of its former position (Fig. 3).

Mental slightly wider than long; postmental single, contacting one infralabial on each side; infralabials four; three pairs of large chin scales; members of anterior pair not in contact, separated by one scale row, members of second pair separated by one scale row, members of third pair separated by three scale rows; chin scales flush with infralabials, i.e. genials do not encroach between chin scales and infralabials (Fig. 3).

Body scales cycloid, smooth with glossy finish; dorsal and lateral head scales, particularly rostral, with numerous scattered minute pits; longitudinal scale rows at mid-body 16 ($n$=20); number of ventral scales remarkably variable, 89–104 ($n$=19); subcaudals in non-regenerated tails 83–93 ($n$=7); inner precloacals overlap outer; scales in mid-ventral caudal row similar in size to scales in adjacent rows. Adult SVL 45–55 mm ($n$=13); adult TaL (non-regenerated) up to 49 mm ($n$=1). For individual scale counts and measurements, see Table 2.

Hyoid elements detectable on radiograph; teeth short, crowns of teeth bluntly rounded; pectoral girdle not

Table 2 Meristic and mensural data for specimens of *Paracontias rothschildi*; for abbreviations see text

| Collection number | Scales | | SVL | TaL | HW |
|---|---|---|---|---|---|
| | ventral | subcaudal | | | |
| ZFMK 88048 | 91 | – | 46.7 | – | 2.4 |
| ZFMK 88049 | 102 | 91 | 29.5 | 24.9 | 2.1 |
| ZFMK 88050 | 99 | 92 | 28.6 | 25.3 | 2.0 |
| ZSM 2074/2007 | 104 | – | 28.0 | – | 2.1 |
| ZSM 2235/2007 | 97 | 90 | 26.3 | 21.5 | 1.9 |
| ZSM 2246/2007 | 92 | – | 43.0 | – | 2.4 |
| ZSM 2247/2007 | 96 | 89 | 33.9 | 32.1 | 2.1 |
| ZSM 2260/2007 | 93 | – | 54.4 | – | 2.6 |
| ZSM 2261/2007 | 89 | (47) | 45.5 | (20.7) | 2.2 |
| ZSM 2262/2007 | 98 | (47) | 49.6 | (27.8) | 2.4 |
| ZSM 2263/2007 | 100 | 93 | 36.1 | 31.8 | 2.1 |
| ZSM 2264/2007 | 93 | (58) | 46.6 | (34.0) | 2.4 |
| ZSM 2265/2007 | 99 | 83 | 53.7 | 48.8 | 2.3 |
| ZSM 2266/2007 | 95 | – | 47.2 | – | 2.3 |
| ZSM 2267/2007 | 93 | (55) | 46.4 | (30.4) | 2.4 |
| ZSM 2269/2007 | 98 | 85 | 31.2 | 25.7 | 2.0 |
| ZSM 1579/2008 | 104 | (60) | 46.4 | (31.0) | 2.4 |
| ZSM 1580/2008 | damaged | – | 45.6 | – | 2.0 |
| ZSM 1581/2008 | 93 | – | 48.5 | – | 2.7 |
| ZSM 1582/2008 | 94 | (81) | 45.4 | (40.4) | 2.5 |

All dimensions in mm

Values in parentheses are from specimens with incomplete or regenerated tail

contact with first supralabial; nostril formed by rostral anteriorly and nasal posteriorly, dorsally and ventrally; postnasal absent; loreal single; preocular single; presubocular single; five supraciliaries, in continuous row, first three contacting first supraocular, last very large and projecting medially into supraocular series (thereby greatly reducing third supraocular in size); one pretemporal, contacting parietal; postsuboculars two, lower contacting penultimate and ultimate supralabial, both postoculars in contact with pretemporal; lower eyelid scaly and moveable; primary temporal single; secondary temporals two, upper long, contacting ventral temporal anteriorly and anterior nuchal; tertiary temporals two, bordering lower secondary temporal; supralabials four; subocular single; postsupralabial single;

detectable; rudiment of humerus absent; sternum present; macrosternum cannot be resolved on radiograph; pelvic girdle's two halves separated on midline, each consisting of tripartite element representing ilium, ischium and pubis; no evidence of femur on radiograph; presacral vertebrae 50–51 ($n=3$; ZSM 2264/2007, 1579/2008, 1581/2008), first free rib on fourth presacral; two sacral vertebrae; transverse processes of caudal vertebrae project anterolaterally at approx. 45–55° angle.

In preservative, ground colouration dark brown, with a broad, beige to grey longitudinal band dorsally, band four scale rows wide from head to level of cloaca, two from there to tip of tail; head dark brown dorsally, usually with many irregular, beige flecks and spots; throat dark brown in most individuals, but sometimes light beige or greyish with some dark mottling; dorsal body scales beige or grey, each usually with fine brown spotting and/or brown flecks at posterior edge, thus giving the appearance of two to four fine, brown longitudinal lines within the beige band; flanks dark brown; ventral side slightly paler than flanks, with ventral scales generally containing smaller parts of dark brown colour; precloacal scales nearly transparent; colouration of tail generally identical to that of body. In life (Fig. 4), colouration differs only slightly from that in preservative. Possibly depending on the stage before moulting, some individuals had a rather grey ground colour with a bluish rather than dark brown tint. The longitudinal
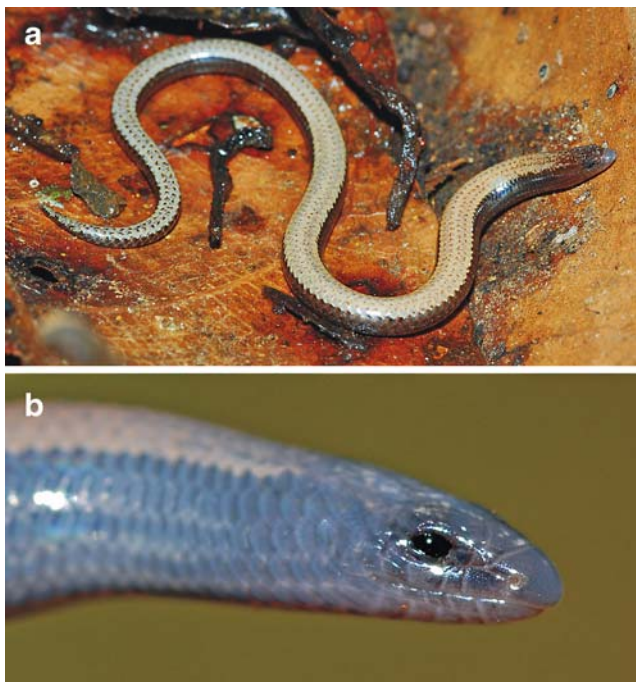


**Fig. 4** *Paracontias rothschildi* in life. **a** Dorsolateral view. **b** Head, lateral view (bluish grey tint most probably indicates stage shortly before moulting)

dorsal band always is pale beige (never greyish as in some preserved specimens). Eye black.

### Diagnosis

A member of *Paracontias* according to the molecular phylogeny based on nuclear and mitochondrial genes by Crottini et al. (2009). *Paracontias rothschildi* differs from most sympatric limbless members of the genus by the number of scale rows around mid-body being 16 (for the higher numbers in relevant other species, see the diagnosis of *P. minimus* above); only *P. fasika* n. sp. also exhibits 16 scale rows. From the syntopic *P. minimus*, *P. rothschildi* further differs mainly by colouration, presence of an eye opening and presence of a nasal scale. *Paracontias rothschildi* shares with *P. brocchii* and *P. milloti* a nostril located at the border between rostral and first supralabial; in the other *Paracontias* species the nostril originates in the rostral scale and is connected with the first supralabial by a narrow suture only. For separation from *P. fasika* n. sp., see the diagnosis for the latter species below.

From all known limbless species of *Pseudoacontias* (*P. madagascariensis, P. unicolor, P. menamainty*), *Paracontias rothschildi* mainly differs by smaller size, absence of a supranasal scale, and a lower number of scale rows around mid-body (16 versus 32, 30, 25, respectively). From limbless species of *Voeltzkowia* (*V. lineata, V. mira, V. rubrocaudata*), *P. rothschildi* is distinguished mainly by the lower number of scale rows around mid-body (16 versus 18–20), a more rounded snout in lateral view (vs. pointed), and presence of an eye opening (absent in *Voeltzkowia*). In contrast to *Amphiglossus stylus*, the only known limbless species in this genus, *P. rothschildi* has no indication of the former limb positions (minute clawless nubs present in *A. stylus*) and a lower number of scale rows around mid-body (16 versus 20).

### Distribution

Known from two lowland localities in the Antsiranana Province, northern Madagascar: (1) Baie de Sakalava, Forêt d'Orangea, 12°16′24″ S, 49°23′33″ E; and (2) south-east of Ivovona, Forêt d'Orangea, 12°19′58″ S, 49°24′20″ E. The species likely occurs in appropriate habitats inbetween these two localities.

### Natural history

*Paracontias rothschildi* inhabits sandy soil in the shrub forest formations known as Forêt d'Orangea. Specimens were found while digging in the soil, but were never observed moving on the ground. Similarly to *P. minimus* and other sand-dwelling limbless skinks, *P. rothschildi* is

able to 'swim' through the substrate. Preferable micro-habitats seem to include shaded areas below bushes where a thin layer of organic material is present on the soil. The species occurs in close syntopy with *Paracontias minimus*, *P. fasika* n. sp. (see below), and *Xenotyphlops grandidieri*.

### Remarks

A few discrepancies between our data and those provided by Brygoo (1980) are evident: We counted 89–104 ventral scales in a large sample (*n*=19), versus the 80 counted by Brygoo (1980) on the single remaining type specimen (MNHN 1905.269). Furthermore, Brygoo (1980) gave the number of presacral vertebrae as 46, whereas our counts yield higher values (50–51). We believe that these differences are due to imprecise data in the literature and probably do not indicate taxonomic distinctness, although no type specimen of *P. rothschildi* could be examined in our study, as they were on loan elsewhere.

### *Paracontias fasika* n. sp.

### Etymology

The specific epithet is formed from the Malagasy word "fasika", meaning sand, and refers to the sand-dwelling habits of the new species occurring on sandy soils of Forêt d'Orangea. Due to its etymological derivation, the epithet is to be retained in its original spelling under all nomenclatural circumstances.

### Identity

This is the species figured as *Paracontias hildebrandti* by Glaw and Vences (2007: 351) and referred to as *Paracontias* sp. by Crottini et al. (2009) and Köhler et al. (2009).

### Holotype

Deposited at Zoologische Staatssammlung München (ZSM 2256/2007; field number FGZC 1347); male (Figs. 5 and 6); from Baie de Sakalava, 12°16′24″ S, 49°23′33″ E, 11 m a.s.l., Forêt d'Orangea, Antsiranana Province, northern Madagascar; collected on 10 March 2007 by H. Enting, F. Glaw, J. Köhler, and local collectors.

### Description of holotype

Adult male in reasonable state of preservation and with non-regenerated tail (internal organs and muscles partly removed for DNA analyses). A thin, brown skink with slightly light brown mid-dorsal band, of small size (SVL 33.6 mm, total length 73.2 mm), with both sets of limbs
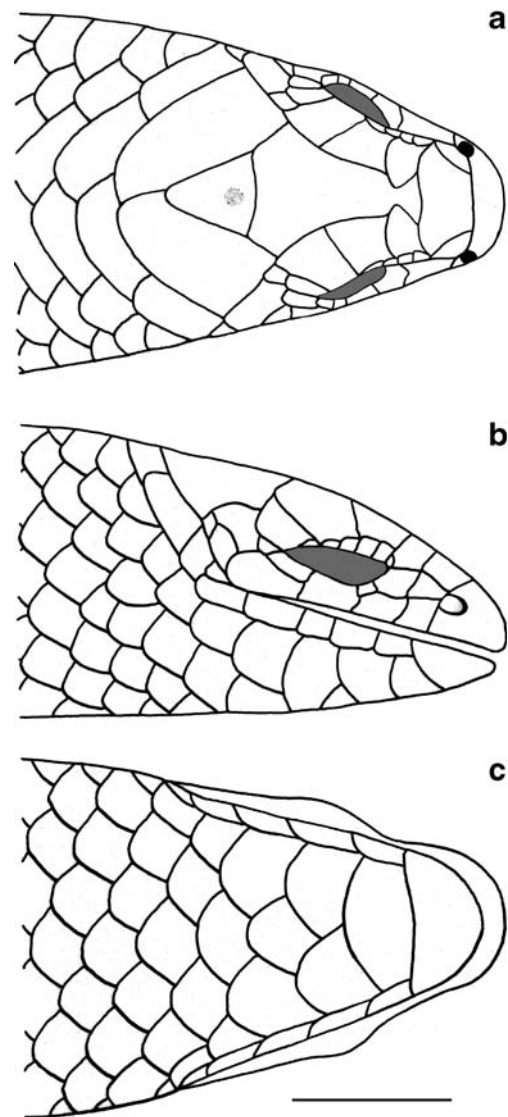


**Fig. 5** *Paracontias fasika* n. sp. (holotype, ZSM 2256/2007), head. **a** Dorsal view. **b** Lateral view. **c** Ventral view. Scale bar = 1 mm

completely absent and no external indication of their former positions. Snout bluntly rounded in dorsal and lateral views; rostral slightly projecting anteriorly; supranasals not in contact; frontonasal wider than long; frontal anteriorly constricted by first supraocular, thus frontal hourglass-shaped; supraoculars four, first constricting frontal, anterior two contacting frontal, fourth small; frontoparietals absent; interparietal well separated from supraoculars; parietal eyespot just anterior of centre of interparietal; parietals meet behind interparietal; a single pair of nuchals (Fig. 5).

Nasal moderate in size, anteriorly open, larger than nostril and lying just at posterior edge of rostral, in contact with first supralabial and loreal; nostril formed by rostral anteriorly and nasal posteriorly, dorsally and ventrally; postnasal absent; loreal single; preocular single; presubocular

single; six supraciliaries, in continuous row, second and third contacting first supraocular, last very large and projecting medially into supraocular series (thereby greatly reducing third supraocular in size); pretemporal single, contacting parietal; postsubocular single, contacting penultimate supralabial; lower eyelid scaly and moveable; primary temporal single; secondary temporals two, upper small, contacting pretemporal anteriorly and parietal dorsally; tertiary temporals two, lower bordering both secondary temporals and ultimate supralabial, upper long, contacting nuchal and parietal anteriorly; supralabials five; postsupralabial single, separated from ultimate supralabial by lower tertiary temporal; external ear opening absent, with no external indication of its former position (Fig. 5).

Mental wider than long, contacting one infralabial on each side; postmental single, contacting first infralabial on each side; infralabials five; two pairs of large chin scales, anterior pair in contact, second pair separated by one scale row, each contacting two infralabials; chin scales flush with infralabials, i.e. genials do not encroach between chin scales and infralabials (Fig. 5).

Body scales cycloid, their surface covered with relatively deep grooves; longitudinal scale rows at mid-body 16; ventrals 71; subcaudals 83; inner precloacals overlap outer; scales in mid-ventral caudal row similar in size to scales in adjacent rows. SVL 33.6 mm, TaL 39.6 mm, HW 2.1 mm. SVL/HW 16.33; TaL/SVL 1.18.

Hyoid elements detectable on radiograph; teeth short, crowns of teeth conical; pectoral girdle not detectable; rudiment of humerus not detectable; sternum not detectable, but possibly present; macrosternum not detectable; pelvic girdle's two halves separated on midline, each consisting of tripartite element representing ilium, ischium and pubis; no evidence of femur on radiograph; presacral vertebrae 46, first free rib on third presacral; two sacral vertebrae; 48 caudal vertebrae; transverse processes of caudal vertebrae project anterolaterally at approx. 45–55° angle.

In preservative, ground colouration dark brown, with broad, brown to fawn longitudinal band dorsally, band four scale rows wide from head to level of cloaca, two from there to tip of tail; head dark brown dorsally and laterally, slightly darker around eyes; throat brown to beige with dark mottling; body scales on flanks and venter dark brown,



**Fig. 6** *Paracontias fasika* n. sp. (holotype, ZSM 2256/2007) in life; dorsolateral view

each with fine, cream-coloured irregular mottling; ventral side slightly paler than flanks; precloacal scales nearly transparent posteriorly; colouration of tail identical to that of body. In life (Fig. 6), colouration differs only slightly from that in preservative, with longitudinal dorsal band darker but still contrasting to dark brown flanks. Eye black.

### Diagnosis

A member of *Paracontias* according to the molecular phylogeny based on nuclear and mitochondrial genes by Crottini et al. (2009). *Paracontias fasika* n. sp. differs from the sympatric limbless *P. minimus* by smaller body size, lower number of scale rows around mid-body (16 versus 18), lower number of ventral scales (71 versus 102–112), head shape, head scalation, presence of an eye opening, presence of a nasal scale, and by the position of the nostril. The new species differs from all known species of *Paracontias* with an eye opening by a lower number of scale rows around mid-body, except from the sympatric *P. rothschildi*, which also has 16 rows and shares with the new species a broad middorsal stripe contrasting with the darker colour of the flanks. However, the new species differs from *P. rothschildi* by a lower number of ventral scales (71 versus 89–104), an hourglass-shaped frontal (vs. bell-shaped), 5 supralabials (4), 5 infralabials (4), a relatively smaller rostral scale, the nasal scale being in contact with the first supralabial and loreal (first supralabial only), and by a broad, brown mid-dorsal stripe (beige to grey).

From limbless species of *Voeltzkowia* (*V. lineata, V. mira, V. rubrocaudata*), the new species mainly differs by a lower number of scale rows around mid-body (16 versus 18–20), presence of eyes, colouration and head scalation. From the limbless species of *Pseudoacontias* (*P. madagascariensis, P. unicolor, P. menamainty*), the new species mainly differs by much smaller size and lower number of scale rows around mid-body (16 versus 25–32). The head scalation of *P. fasika* is generally similar to that of the limbless *Amphiglossus stylus*. However, the new species mainly differs from the latter by a lower number of scale rows around mid-body (16 versus 20), and by the lack of indications of the former limb positions (minute clawless nubs present in *A. stylus*).

### Distribution

Known only from the type locality.

### Natural history

The single specimen was found by local people together with numerous specimens of *Paracontias minimus*, *P. rothschildi* and *Xenotyphlops grandidieri*, which suggests

lower abundance and similar habits compared to the latter three species, although *P. fasika* was less inclined to burrow into sand. The comparatively long tail (TaL/SVL 1.18) argues for a surface-dwelling habit (see Brandley et al. 2008). The holotype of *P. fasika* was much more agile and moved very fast compared to the observed members of syntopic *Paracontias* species.

## Discussion

### Distribution and type locality of *Paracontias minimus* and *P. rothschildi*

When Mocquard (1905, 1906) described *Paracontias roth-schildi* and *Cryptoposcincus minimus*, nothing was known about their specific origins, although there was no reason at that time to doubt Mocquard's "Madagascar" labelling. The author had received the specimens from Maurice de Roths-child together with a specimen of a blind snake, *Xenoty-phlops grandidieri*, accompanied by the same imprecise data. However, as all three species were never found again on Madagascar, their Malagasy origin was somehow doubted by Brygoo (1981), who discussed the possibility that *C. minimus* might have originated from eastern Africa.

Considering that former state of knowledge, the recent rediscovery of all three taxa in northernmost Madagascar is quite remarkable. It confirms their Malagasy origin and demonstrates that all three species live in syntopy in sandy soils of Forêt d'Orangea. This makes it probable that even the type specimens were all collected together from this general area more than a century ago. The Forêt d'Orangea forms part of the Antsiranana Bay (formerly Diego Suarez), a harbour frequently used by the British and French in the past. Thus, collection of the species at the nearby Forêt d'Orangea by boat crew members appears very likely.

All three limbless skink species reported here apparently occur in the same microhabitat, namely the loose sandy soil and its uppermost layer of organic material. This micro-habitat might suggest a restricted coastal distribution of these skinks in northern Madagascar, but too little is known for a reliable assessment of their conservation status. However, while digging between small bushes in the soil, we discovered *P. minimus* and *P. rothschildi* (and *Xenoty-phlops grandidieri*) in less than half an hour searching time, and local people encounter all species regularly while digging for tubers, indicating rather high local population densities of *P. minimus* and *P. rothschildi*.

### Phylogenetic relationships among *Paracontias*

Crottini et al. (2009) have provided clear evidence for monophyly of the genus *Paracontias*, referring to the seven species included as being sister to a *Madascincus* Brygoo clade (see also Fig. 8). The 16S rRNA data newly presented herein include all 16S sequences available so far for the genus *Paracontias*. The phylogenetic tree (Fig. 7) largely confirms the results of Crottini et al. (2009). For *P. rothschildi* and *P. minimus* we had a larger number of specimens available. All *P. minimus* had identical 16S rRNA sequences (differences in branch lengths in Fig. 7 are due to some missing data at the start of the sequence). Among the *P. rothschildi* sequences from specimens from Baie de Sakalava, differentiation is present but very weakly pronounced, whereas the specimen from south-east of Ivovona (approx. 8 km south of Baie de Sakalava) shows some degree of differentiation with an uncorrected distance of 1% (5 substitutions).

Available GenBank sequences of *P. hildebrandti* and *P. brocchii* (both from Montagne d'Ambre) were almost identical to the sequences from specimens collected and studied by us, thus confirming their identity. In the multilocus phylogeny (Crottini et al. 2009), *P. hildebrandti* from Montagne des Français was placed (without signifi-cant support) as sister to *P. manify* from the Tsaratanana area, wheras the 16S phylogeny shows a different pattern (Fig. 7). One GenBank sequence of *P. holomelas* from Marojejy (AY391157) was nearly identical to a sequence we obtained from Mahasoa forest that represents a new species, which was described by Köhler et al. (2009) and referred to here under the provisional name *Paracontias* sp. aff. *tsararano*. Since this new species differs considerably from *P. holomelas* in characters of scalation, we assume that the GenBank sequence derives from a misidentified individual (referred to as *Paracontias* sp. here; see Köhler et al. 2009).

The position of this taxon in the 16S tree differs from the multilocus phylogeny (Crottini et al. 2009; Fig. 8), as it is not placed basal to all other *Paracontias*. Instead, it forms a clade with *P. hildebrandti*, *P. manify*, *P. brocchii* and *P. minimus* that is sister to a clade containing *P. rothschildi* and *P. fasika*. Although the sister relationship of *P. rothschildi* and *P. fasika* received resonable support in the multilocus phylogeny (Fig. 8), the two species are deeply divergent.

### Implications for classification

According to the similarities in external morphology, *Paracontias minimus* (under the name *Cryptoscincus* [sic!] *minimus*) was formerly considered as related to species of sand-dwelling *Voeltzkowia*, known from dry western Madagascar (Brygoo 1981; Glaw and Vences 1994). As revealed by the analysis of molecular genetic data, however, *P. minimus* is deeply nested within a monophyletic clade of species of *Paracontias* and is only
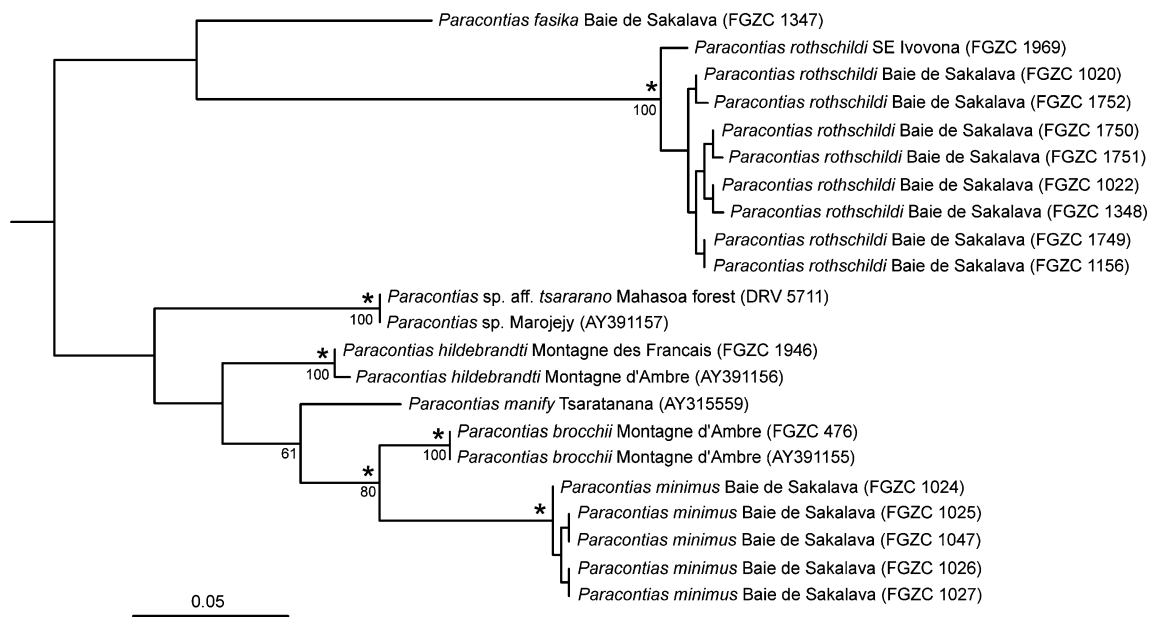
**Fig. 7** Phylogenetic tree of *Paracontias* species reconstructed using Bayesian inference (20 Mio. generations; trees sampled every 500 generations; burn-in 10,000), based on 539 bp DNA sequences of 16S rRNA gene. *Madascincus igneocaudatus* used as outgroup (not shown). Bayesian posterior probabilities of 1 indicated by asterisks above branches, bootstrap support values >50% from Maximum Parsimony analysis (2000 replicates) shown below branches. Numbers in parentheses represent field numbers of specimens collected by us or accession numbers of sequences taken from GenBank (initial letters AY), respectively
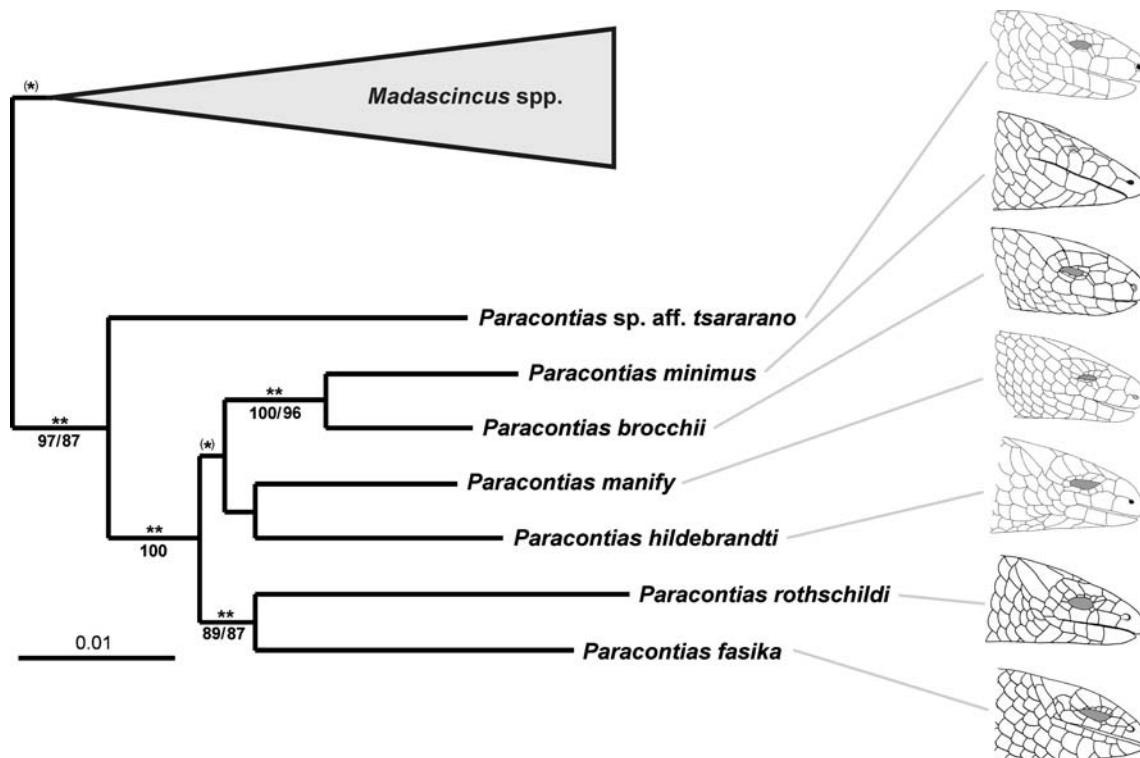


**Fig. 8** Partitioned Bayesian tree based on 3693 bp of mitochondrial and nuclear DNA gene sequences (modified after Crottini et al. 2009). The clade shown is clade A of Crottini et al. (2009) which in the analyses is sister to a clade containing the genera *Amphiglossus*, *Voeltzkowia* and *Pygomeles* (not shown). *Eumeces, Tiliqua*, and *Cordylus* were used as outgroups (not shown). Bayesian posterior probabilities indicated by asterisks above branches: (*)=0.90–0.94; *=0.95–0.98; **=0.99–1.00. Bootstrap values >80% from ML/MP shown below branches. The *Madascincus* spp. subclade contains five terminals (not shown). Schematic drawings at right depict corresponding scalations of heads, a character used in the past for classification within *Paracontias* (*P. brocchii* redrawn after Angel 1942, *P. manify* after Andreone and Greer 2002)

distantly related to the clade formed by *Voeltzkowia* species (Crottini et al. 2009). Consequently, *Cryptoposcincus* (type species by monotypy: *C. minimus*) was considered as a synonym of *Paracontias*, resulting in the combination *Paracontias minimus*, as used herein. With high support in the multilocus phylogeny, *P. minimus* is sister to the rainforest species *P. brocchii* (the type species of *Paracontias*), which exhibits rather different morphology, with eyes present and the nostril contacting the first supralabial. The same analysis places *P. rothschildi* as sister to the sympatric *P. fasika*, although the two species differ considerably in morphology, except for sharing the 16 scale rows around mid-body.

As revealed by the comparisons and descriptions provided in the present work, external morphology and scalation is rather different between the *Paracontias* species studied and allows unequivocal species identification. However, osteological characters and scalation were used in the past to elucidade relationships and define genera or subgenera. Particularly the shape of the rostral scale and the position of the nostril was used to separate Malagasy scincid taxa (e.g. Brygoo 1980; Greer 1970). Brygoo (1980) considered *Paracontias* to comprise three subgenera, which he defined by the number of presacral vertebrae and the position of the nostril (completely embedded in rostral versus in contact with first supralabial): *P. (Paracontias)* Mocquard, 1894 (only containing *P. brocchii;* 63–64 presacral vertebrae); *P. (Malacontias)* Greer, 1970 (containing *P. holomelas* and *P. hildebrandti*; 50–58 presacral vertebrae); and *P. (Angelias)* Brygoo, 1980 (containing *P. milloti* and *P. rothschildi*; 46–51 presacral vertebrae). Andreone and Greer (2002) did not use these subdivisions, because "the two characters used to diagnose them as subgenera—the position of the nasal opening in relationship to the rostral scale and first supralabial scale, and the number of presacral vertebrae—do not result in monophyletic groups in all cases."

The rediscovery and morphological analysis of *P. minimus* and *P. rothschildi*, their comparison with other *Paracontias* species, and the molecular analysis of their phylogeny provide further evidence for the very limited value of external morphology to the tracing of relationships among these scincid lizards. As demonstrated in Fig. 8, phylogenetically close sister taxa, e.g. *P. brocchii/P. minimus* and *P. rothschildi/P. fasika*, exhibit completely different patterns in head scalation, which would mean placing these sister taxa in different subgenera or genera if the definitions provided by Brygoo (1980, 1981) were applied. Close comparison between molecular phylogenetic relationships and morphology among the species of *Paracontias* reveals a more or less chaotic picture, with very closely related species exhibiting rather different scale arrangements, and more distantly related species exhibiting very similar scalation (Fig. 8). Concerning the shape of the rostral scale and the position of the nostril (nostril in contact with first supralabial versus entirely within rostral scale and connected by a narrow suture only), our field observations indicate that this character more likely depends on different habits, i.e. burrowing versus (mainly) surface dwelling.

It can be stated that differences in external morphology are well suited to distinguish species of *Paracontias*, but are of rather limited value to elucidate their phylogenetic relationships. Similarities in external characters in these skinks are apparently largely the result of convergent evolution due to parallel selective pressures, as markedly demonstrated by the great external similarities between the evolutionarily distant sand-burrowing *Paracontias minimus* and species of *Voeltzkowia* (Crottini et al. 2009). Nevertheless, as revealed by discrepancies between literature data and our observations both on the type specimens of *P. minimus* (see remarks under this species) and on the holotype of *P. hildebrandti* (ZMB 9695; 20 scale rows around mid-body, not 18 as reported in the literature), an unequivocal species identification based on morphology is the precondition for subsequent proper molecular analyses and the understanding of species diversity and evolutionary relationships. However, suitable tissue samples for molecular analysis are still missing for four of the known species of *Paracontias* (*P. hafa, P. holomelas, P. milloti, P. tsararano*) and for other Malagasy key species (e.g. *Amphiglossus stylus, Sirenoscincus yamagishii*). Summing up these findings, the systematics of Malagasy scincid lizards may still be far from well-understood, which probably also holds true for many other groups of fossorial skinks at a global scale.

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