

The hairy frog, a curly fighter? – A novel hypothesis on the function of hairs and claw-like terminal phalanges, including their biological and systematic significance (Anura: Arthroleptidae: *Trichobatrachus*)

Michael F. BAREJ¹, Wolfgang BÖHME¹, Steven F. PERRY², Philipp WAGNER¹,
Andreas SCHMITZ³

¹Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160,
D-53113 Bonn, Germany.

E-mail: michael@barej.de; w.boehme.zfmk@uni-bonn.de

philipp.wagner.zfmk@uni-bonn.de

²Institut für Zoologie der Universität Bonn, Poppelsdorfer Schloss, D-53115 Bonn,
Germany. E-mail: perry@uni-bonn.de

³Muséum d'histoire naturelle, Department of Herpetology and Ichthyology,
C.P. 6434, CH-1211 Geneva 6, Switzerland. E-mail: andreas.schmitz@ville-ge.ch

The hairy frog, a curly fighter? – A novel hypothesis on the function of hairs and claw-like terminal phalanges, including their biological and systematic significance (Anura: Arthroleptidae: *Trichobatrachus*). - The Central African Hairy Frog *Trichobatrachus robustus* Boulenger, 1900 possesses two morphological peculiarities, its unique hair-like dermal appendages, and claw-like terminal phalanges also known from related genera. We review formerly published data on claw-like terminal phalanges in arthroleptid frogs and discuss their systematic significance, pointing out that recent phylogenies do not support close relationships of genera with this unique structure. Moreover, we review data on the structure and function of the “hairs” and provide new data. Finally we present a novel hypothesis on the use of claws and “hairs”. Greater male size and the peculiar structure of the dermal appendages (the “hairs”) would support a possible use of the claws as weapons in aggressive male-male interactions, the “hairs” serving as mechanical protection.

Keywords: Amphibia - Anura - Arthroleptidae - *Trichobatrachus* - Cameroon - Hairy Frog - Functional Morphology - Combat Behaviour - Histology - Osteology.

INTRODUCTION

The Central African hairy frog *Trichobatrachus robustus* Boulenger, 1900 is one of the most charismatic anurans in the world. The species is characterized by two morphological peculiarities: Hair-like appendages, a unique development among anurans, and claw-like terminal phalanges occurring only in a few genera.

Already the chosen genus name *Trichobatrachus* Boulenger, 1900 reflects this peculiar development (gr. τριχος (*trichos*) = hair; gr. βατραχος (*batrachos*) =

frog). Since the description of this species almost a dozen different functional interpretations have been published (e.g. Kükenthal, 1912; Noble 1925; Mertens, 1938, 1958; see below). Among these, Noble's (1925) respiratory function hypothesis has been most widely accepted.

Hairy frogs are also known for their ability to cause injuries and scratches with their claw-like terminal phalanges (Blackburn *et al.*, 2008; Durrell, 1956; own obs.), when specimens are handled without care. Claw-like phalanges occur in a few other African anuran genera as well (e.g. Boulenger 1900, 1901, 1917; Perret 1966).

In this paper we review what is known about *Trichobatrachus robustus*, including histological and functional analyses of the "hairs", and claw-like terminal phalanges in African frogs. The occurrence of claw-like terminal phalanges in arthroleptid genera is examined with regard to its systematic significance. New histological data are presented and discussed, taking into account previous hypotheses on the function, and a novel functional hypothesis is presented.

TERMINAL PHALANGES IN THE HAIRY FROG AND RELATIVE GENERA, AN OVERVIEW

Recently, a publication by Blackburn *et al.* (2008) on claw-like terminal phalanges of central African frogs received attention in popular media, which led to lurid catchwords like "horror frogs" or "superfrog" (Spiegel online, New Scientist CBC Radio, etc.). But actually this is nothing new: Scientists have already mentioned differences in the number of this peculiar construction in different genera and were also aware of an additional bony nodule distal to the claws (e.g. Boulenger, 1900, 1901; Noble, 1931; Parker, 1931).

In the most recent global frog phylogeny (Frost *et al.*, 2006), the African genera *Arthroleptis*, *Astylosternus*, *Cardioglossa*, *Leptodactylodon*, *Leptopelis*, *Nyctibates*, *Scotobleps* and *Trichobatrachus* were placed in the family Arthroleptidae. Until then, these genera had an unstable taxonomic history and were partly classified either as Astylosternidae, Hyperoliidae or Ranidae (Dubois, 1992; Noble, 1927, 1931; Perret, 1966). Claw-like terminal phalanges have been used in the past as a morphological character to show relationships among African frog genera. Noble (1920) proposed systematic relationships between *Astylosternus* (*Trichobatrachus* included), *Gampsosteonyx* (a current synonym of *Astylosternus*) and *Scotobleps* based on the occurrence of a divided omosternum and claw-like terminal phalanges, which otherwise occur only in the African ptychadenid genus *Ptychadena* (Noble, 1920, 1931; Perret, 1960, 1966). Due to the condition of the pectoral girdle, *Nyctibates* has been positioned within the Astylosterninae (Noble, 1924, 1931) and later *Leptodactylodon* was also included (Amiet, 1980; Perret, 1960, 1966). The published data on the occurrence of terminal phalanges in these genera are summarized below.

Terminal phalanges in *Trichobatrachus* have been described as "simple, obtuse" in the description of the genus (Boulenger, 1900). One year later, Boulenger (1901) reported claw-like phalanges, not always protruding from the skin, in *Trichobatrachus*.

The same statement ("simple, obtuse") has been given for *Scotobleps gabonicus* (Boulenger, 1900). But later Boulenger (1917) found claw-like terminal phalanges in this genus, too.

The description of the genus *Astylosternus* Werner, 1898 did not mention the terminal phalanges, while the description of *A. occidentalis* includes: “tips swollen and penetrated by the terminal phalanges, except the inner” (Parker, 1931; Werner, 1898). In contrast, Boulenger (1900) described the phalanges in *Dilobates* (a current synonym of *Astylosternus*) as “simple, obtuse”, but mentioned in *Gampsosteonyx*, phalanges “of all but the inner toe [as] a sharp curved claw, projecting through a slit [...] of the toe” and illustrated them (Boulenger, 1901). Perret (1966) drew the fourth toe of *A. diadematus* as being protruded by the terminal phalanx; but strangely, the distal bony nodule is missing.

Terminal phalanges of *Leptodactylodon* have been mentioned as “acuminated from a thicker basis [and] slightly curved” (Andersson, 1903). For the genus *Bulua* (a current synonym of *Leptodactylodon*) a corroborating description has been published (Boulenger, 1904).

Boulenger (1904) also described the terminal phalanges in *Nyctibates* as “simple, obtuse”. Perret’s (1960) later remarks on claw-like phalanges in *Nyctibates* rested upon a misidentification (Amiet, 1977), consequently the hole drawn in the fourth toe for this species in Perret (1966) was erroneous, as well.

The original description of the genus *Arthroleptis* is very short and does not state the form of the terminal phalanges (Smith, 1849). Instead, Scott (2005) found simple or dilated phalanges, being small T- or Y-shaped.

Boulenger (1900) stated the terminal phalanges in *Cardioglossa* to be T-shaped. Contrary, Scott’s (2005) examination of terminal phalanges in two *Cardioglossa* species showed them to be simple or only slightly dilated.

EARLIER HYPOTHESES ON THE DERMAL APPENDAGES

Boulenger (1900) assumed the occurrence of “hairs” in both sexes, regarding them as a mere seasonal condition. The author did not believe the “hairs” to be a possible nuptial character as he thought them to be better differentiated in females. In a later publication he revised this assumption and pointed out that only males possess “hairs” (Boulenger, 1901).

Gadow (1900) reported the first histological examination. He erroneously still expected “hairs” in both sexes. Gadow (1900) described the appendages as cylindrical, sometimes slightly flattened finger-like skin extensions, with an axis of fibrous tissue. The tissue was denser and contained more nucleoli within these dermal appendages than in flank skin. Moreover, small inconspicuous blood vessels and lymph vessels were observed. The epidermis was soft and not thickened. Bottle-like glandular cells occur within the epidermis, but were less common than in the flank skin. As no nerve fibres were present, he excluded a sensory function. Gadow (1900) concluded that the “hairs” form a glandular complex, also known in other species without such excrescences. Additionally, he pointed to similarities to the seasonal “Laichpinseln” (sensu Noble, 1925 = “gill-like structures”) of the male of the South American lungfish *Lepidosiren paradoxa*, which are capable of oxygenating attached eggs. However, structures in *Lepidosiren* differ in a higher number of blood vessels (Gadow, 1900; Noble, 1925).

Andersson (1907) recognized that hairs show different lengths and can even be missing in both sexes during some time of the year. This led him to the conclusion that "hairs" probably form a male nuptial dress.

Phisalix (1910) was obviously not aware of Boulenger's (1901) revision and still assumed a permanent occurrence of "hairs" in both sexes: of constant diameter although differing in length. Her studies of alcohol-preserved skin fragments showed different layers in the "hair" structure. According to her, blood and lymph vessels, chromoblasts and glands are embedded in the dermis and are overlaid with an epidermal layer and cuticula. Beneath the epidermal layer are more vessels, glands and pigment cells. Phisalix (1910) emphasis lay on the two different types of glands used for defence in batrachians. Granular glands show fine granula between the nucleoli and mucous glands possess large lacunae, filled with a pale secretion, reacting to mucous staining. Both types of glands are very small but more numerous than in normal skin (Phisalix, 1910). In contrast, terminal nervous endings were missing. Without knowing anything about the biology of the species, she regarded the "hairs" as an additional glandular surface. Later Phisalix (1922) remarked that glands are as numerous as in other skin parts but they still remain the smallest of all known in amphibians.

Kükenthal (1912), obviously unaware of Andersson's (1907) study identified the seasonal character anew, as males of similar size possess "hairs" of different length. The finding of a small specimen with rudimental hairs led him to the assumption that only adults possess long "hairs". The author recognized tubercles of similar diameter in females distributed as the males' "hairs" and additional tubercles being distributed over the whole body in both sexes. Thus Kükenthal (1912) concluded that "hairs" form derived tubercles and even mentioned transitional zones, without explaining them in detail. According to him, "hairs" consist of an inner cutis papilla and an epidermal layer, the latter one made up of longitudinal ridges of epidermal cells and interspaces filled with cutis tissue. A loose covering of horny cells indicates shedding of the superficial stratum corneum. The papilla is built of connective tissue of longitudinal and transverse fibres. At the base of the appendage chromatophores are more abundant. Contrary to Gadow (1900), Kükenthal (1912) did not detect more glands within the appendages. A conspicuous blood vessel is running along the axis and other smaller ones are within the cutis. Kükenthal (1912) first mentioned nerves and tactile cells in between the epidermal ridges and assumes a sensory function. The position of the "hairs", corresponding to accumulations of tactile cells in other anurans, led to the conclusion that they are derived from tubercles and perform tactile function (Kükenthal, 1912).

Dean (1912) recognized a cutis core of spongy tissue and surrounding epidermis in curious ridges and suggested that the circumference of the epidermis could be notably dilated. Moreover, he noted abandoned pigmentation and delicate nerves with terminal cells. He reviewed known results and seized Kükenthal's (1912) suggestion of a seasonal development in males. According to Dean (1912), the eggs are attached or wrapped to the body similarly to the genus *Alytes*, with "hairs" retaining the egg-strings in position. Furthermore, he adopted Gadow's (1900) suggestion of the "Laichpinseln" in the lungfish *Lepidosiren*, concluding that male hairy frogs not only transport and guard the eggs, but moreover their "hairs" could function as an accessory

respiratory organ for the developing juveniles. According to Dean (1912), Kükenthal's (1912) interpretation of a sensory function is not convincing, as a sensory organ should be more conspicuous (analogous to fishes and other amphibians) and only a seasonal occurrence would be expected.

Meisenheimer (1921) interpreted the hair-like appendages as "libido organs". Such tegumental sense organs usually are found in females, playing an important role during amplexus. Hence, the hairy frog represents an anomaly, as these rutting organs occur only in males (Meisenheimer, 1921). Moreover, the author assumed further additional functions, which could be based on the occurrence of glands and nervous fibres.

Noble (1925) criticized former functional analyses. He disproved homologies of the hair-like appendages and tubercles after Kükenthal (1912) and disagreed with the idea of additional surfaces for glands (after Phisalix, 1910, 1922), since either available glands could have been extended or just set denser on the skin. Moreover small vessels embedded in tissue and separated from the surface by a thick epidermal layer could not ventilate carried eggs (after Dean, 1912). Noble (1925) recognized a vascular system of capillaries running along the surface only crossed by transverse vessels. Thus, capillary vessels form epithelia ridges, penetrating the epithelium, surrounded in a sheath of tissue or lacking the sheath. Smooth muscles attach transitional layers and less frequently the stratum corneum and deeper epidermal cells are elongated in attachment regions. Glands are present, but not more numerous than elsewhere. In all, the structure is identical with adjacent integument, although deeper layers of dermal tissue are lacking. Tegumental sections of the flanks showed no differences between the sexes, their capillaries penetrate the epidermis, but do not reach the stratum corneum. In conclusion Noble (1925) stated that as the capillary vessels almost reach the surface and are separated by only few layers of cells from the surface, they could function as an oxygen supply. An additional respiratory organ, being formed of dermal excrescences (namely the "hairs") could assist the reduced lungs of *Trichobatrachus*. Lungs in *T. robustus* are formed of a short sacculated portion and a non-alveolated diverticulum enclosed by a thick sheath and lacking respiratory epithelia (Noble, 1925). According to Noble (1925), only males possess this peculiarity because their oxygen requirement is higher in keeping with their greater growth and muscular hypertrophy in the breeding season.

Sanderson (1936) adopted the idea of a respiratory function but appended a possible mimetic function. Consequently, the hairy appendages in submerged frogs resemble filamentous algae on stones. This observation was later repeated by Sabater-Pi (1966, 1970).

Mertens (1938) was the first to observe regressing hairs in living specimens. The author stated that hairs might correspond to tegumental proliferations in other male amphibians (usually possessing thicker skin) like skin fringes between toes of frogs, toe prolongations or hair-like filaments in newts. Thus, "hairs" are display structures and are not required for survival as the formerly known tegumental structures in other amphibians.

Mertens (1958) later disputed the former interpretations of Kükenthal (1912) and Meisenheimer (1921) since terminal nervous endings are missing. Eggs are

deposited on submerged stones, hence, gill-like structures capable of oxygenating attached eggs ("Laichpinseln" after Gadow (1900) and Dean (1912)) also would not seem appropriate. An additional glandular surface (after Phisalix, 1910) could not be confirmed, and his former interpretation as a means of "excessive power" (after Mertens, 1938) also did not appear plausible, as the investment in such a large-scale development would be too high (Mertens, 1958). Noble's (1925) respiratory function hypothesis was questioned, as females actually require more resources in breeding activities (Mertens, 1958), and a mimesis in only one sex (after Sanderson, 1936) would not appear convincing. Mertens (1958) interpreted the "hairs" as a device for nocturnal recognition of mating partners to avoid mis-pairings with other males, which should be useful just in mute anurans.

Finally, Zippel (1997) commented briefly that the hair-like appendages can either fulfil different functions or just represent remains of formerly advantageous characters in the evolutionary history of this frog.

MATERIAL AND METHODS

ANALYSIS OF THE CLAW-LIKE TERMINAL PHALANGES

The terminal phalanges of arthroleptid genera sensu Frost *et al.* (2006) were studied to reassess available data and to check the differentiation of terminal phalanges in further species. We focus on genera formerly being grouped in the family Astylosternidae (Dubois, 1992), as genera belonging to this family have been reported to possess this state of terminal phalanges. Furthermore, the genus *Ptychadena* was included for comparisons with the condition in the Arthroleptidae.

In all, a total of 16 *Arthroleptis* sp., 39 *Astylosternus* sp., 16 *Cardioglossa* sp., 32 *Leptodactylodon* sp., 12 *Leptopelis* sp., 6 *Nyctibates corrugatus*, 7 *Ptychadena* sp., 7 *Scotobleps gabonicus* and 21 *Trichobatrachus robustus* has been investigated. A list of all investigated species and specimens appears in the Appendix. X-ray images of phalanges were made using the Specimen Radiography System (Faxitron X-Ray Corporation) type series Faxitron LX-60 and related software Faxitron SR (Version 1.4.1). Specimens investigated originate from or have been deposited in: Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), Bonn; Muséum d'histoire naturelle (MHNG), Geneva. Available holotypes and paratypes (MHNG collection only) were studied to ensure a correct identification.

ANALYSIS OF THE DERMAL APPENDAGES

The examined male specimen is stored in the ZFMK collection (ZFMK 87749).

The structure of the hair-like appendages and the course of the capillary vessels have been analysed by the use of histological sections. A square of a few mm of skin with dermal appendages of the flanks and limbs was cut out of alcohol-preserved material. Dehydration of the skin was achieved by alcohol stages of 60%, 70%, 80%, 90% and 96%, 30 min each and 3 times for 30 min in 100% ethanol. The skin fragment was embedded in glycol methacrylat (Hereaus-Kulzer, Kit Technovit 7100) and cut in transverse and longitudinal 3 μ m sections with a motorized rotary Microtom (Microm HM 350). Sections were stained with the metachromatic stain toluidine blue. Analysis was conducted using a light optical microscope (Leica / Leitz DM RBE) and photo-

graphs have been taken with a digital camera (Canon EOS 400 D) and have been processed with related software (Canon EOS Utility Version 2.4; Canon Digital Photo Professional Version 3.4.1). Measurements of the diameter of dermal appendages and blood vessels were made by comparison with a stage micrometer by the senior author.

RESULTS

OSTEOLOGICAL RESULTS ON PHALANGES

Claw-like terminal phalanges occur in the arthroleptid genera *Astylosternus*, *Scotobleps* and *Trichobatrachus*, in both sexes and different stages, always occur in association with a bony nodule, situated distally to the terminal phalanx. In contrast, terminal phalanges in the other arthroleptid genera are simple and obtuse. In *Astylosternus* all but the inner toes (toe I) show claw-like phalanges (Fig. 1a). Outer terminal phalanges are simple and obtuse in *Trichobatrachus*, but bent down sharply and claw-like on toes II, III and IV (Fig. 1b). *Scotobleps gabonicus* possesses claw-like terminal phalanges on the toes II and III, while the other toes have simple and tempered endings (Fig. 1c). In contrast, terminal phalanges are simple or slightly dilated in all toes of *Leptodactylodon* (Fig. 2a) and only slightly curved but obtuse in *Nyctibates corrugatus* (Fig. 2b). Within the related arthroleptid genera *Arthroleptis* and *Cardioglossa* terminal phalanges are slightly dilated (Fig. 3a, 3b). Terminal phalanges are turned in the axis of the previous phalanges, pointed and slightly curved in *Leptopelis* (Fig. 4a). Phalanges in the ptychadenid genus *Ptychadena* are sharply bent down but do not possess a bony nodule distally to the terminal phalange (Fig. 4b).

HISTOLOGICAL RESULTS ON HAIR-LIKE APPENDAGES

The hair-like appendages of *Trichobatrachus* have diameters of 0.35–0.45 mm. The diameter of central inner large vessels is ca. 0.09 mm, in the smaller exterior vessels ca. 0.01–0.02 mm. Outer capillary vessels can be marginally larger than a blood cell. Inner vessels are embedded in a tissue of inordinate fibroblasts. Additionally the metachromatic staining shows an amorphous tissue, which is not distinctly separated (Fig. 5a). The more intensive red-violet coloration of the amorphous part in our toluidine stained sections indicates a high mucopolysaccharide content, in which elastic tissue also occurs. Vessels in the fibroblast-rich dense connective tissue are surrounded by a single layer of smooth muscle cells.

Outer capillary vessels lie within epidermal layers and are separated from the surface by few or sometimes only one layer of cells. Inner and outer vessels are connected by transverse ones; several outer vessels can be linked to one inner vessel (Fig. 5b). Moreover separate outer capillaries and inner vessels can split or merge among each other, which changes their apparent diameter and number in a specific part of the dermal appendage (Fig. 5c). Blood vessels are overfilled with blood cells and single blood cells may no longer be recognizable, although this is possible elsewhere in the preparation. Generally the apparent number of vessels increases from the proximal to the distal part of the dermal appendages. In the very last part, before the dermal appendages reach the flanks, only one or two inner vessels occur in almost all appendages (Fig. 5d) before they pass into a vessel running parallel to the skin surface.



FIG. 1

X-ray image of foot (scale bar 5 mm). (a) *Astylosternus perreti* (ZFMK 78309). (b) *Trichobatrachus robustus* (ZFMK 87749; bony nodule marked with an asterisk “*”). (c) *Scotobleps gabonicus* (ZFMK 87768).

In the same manner the number of outer capillaries increases in direction to the distal terminus, where a capillary reticulation is formed (Fig. 5e). No obvious structural differences were observed in dermal appendages in different parts of the body: flanks, upper and lower line of appendages on the upper limb. The only striking difference lies in the number of pigment cells, which are less frequent in the lower parts of the flanks (compare Fig. 5b and Fig. 5c). Granular and mucous glands, which are always positioned closer to the surface than the centre of the papilla, are present.

DISCUSSION

ON THE OCCURRENCE OF THE CLAW-LIKE PHALANGES IN ARTHROLEPTID FROGS

Sabater-Pi (1970) erroneously described the claws as “formed out of skin”, although they are of bony material (e.g. Blackburn *et al.*, 2008; Boulenger, 1901; Parker, 1931; this study).

Within the Arthroleptidae, our data on claw-like terminal phalanges support the recent results of Blackburn *et al.* (2008) for the genera *Scotobleps* (toes II and III),

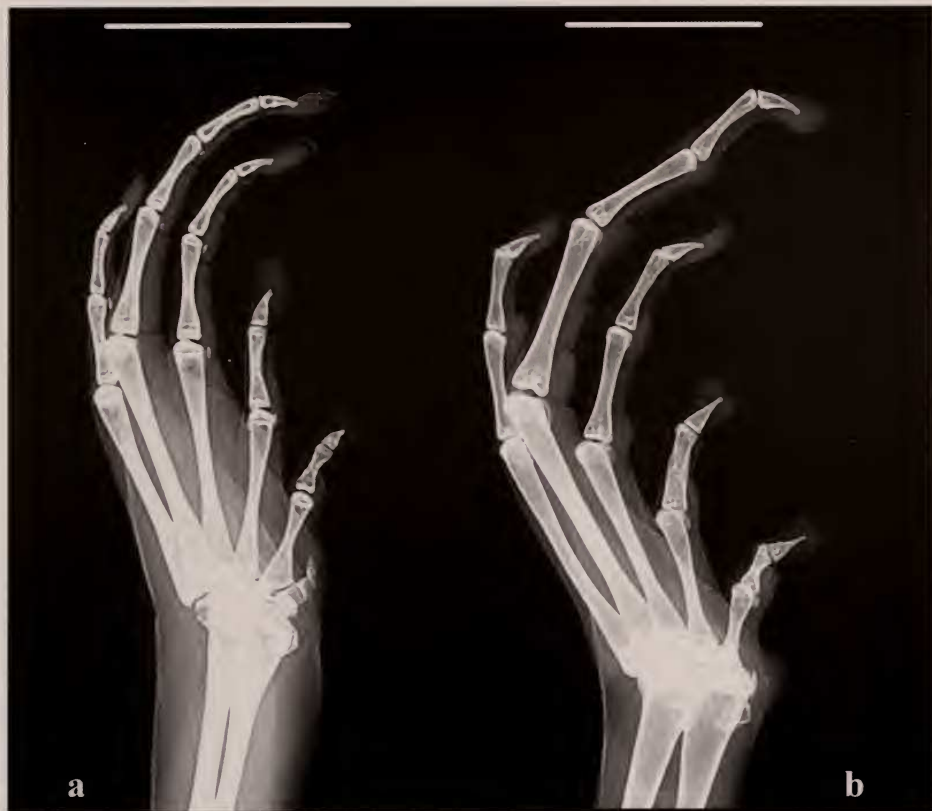


FIG. 2

X-ray image of foot (scale bar 5 mm). (a) *Leptodactylodon o. ornatus* (ZFMK 67369). (b) *Nyctibates corrugatus* (ZFMK 77941).

Astylosternus (toes II–V), and absence of such a structure in the related genera *Nyctibates*, *Leptodactylodon*, *Cardioglossa* and *Arthroleptis*. In contrast to our findings, Blackburn *et al.* (2008) found claw-like phalanges in *Trichobatrachus* in toes II–V (see also Parker, 1931), while our results show the outer phalanges to be clawless, which corresponds with the views of Andersson (1907), Noble (1931) and, Sabater-Pi (1970). Finally, Kamermans & Vences (2009) stated that “the hook-shaped morphology is present at all toes”, which is also contradictory to our findings. Parker (1931) and Noble (1931) speculated on the origin and function of the additional bony nodule, but Blackburn *et al.* (2008) have been the first to show that it is connected through a “suspensory sheath” to the claw before the latter element breaks free. Andersson (1907) probably overlooked this bony nodule, as he skinned his material for study and possibly Perret’s (1966) mistake is based on a similar approach. Reciprocally, all claw-like phalanges possess these small nodules, in *Trichobatrachus* only found on the toes II–IV, in *Astylosternus* on the toes II–V and in *Scotobleps* on the toes II and III.

Leptopelis mentioned by Blackburn *et al.* (2008) might have actually been *Leptodactylodon*, as *Leptopelis* does not appear in their supplementary material. The



FIG. 3

X-ray image of foot (scale bar 5 mm). (a) *Arthroleptis adolfifriederici* (ZFMK 88010). (b) *Cardioglossa venusta* (ZFMK 75453).

structure in *Leptopelis* with a turned axis has been already interpreted by Noble (1931) as an arboricolous adaptation in true tree frogs.

DO CLAWS HAVE SYSTEMATIC SIGNIFICANCE?

Claw-like phalanges with an associated bony nodule are unique structures within ranoid frogs and occur only in three arthroleptid frog genera (*Astylosternus*, *Scotobleps*, *Trichobatrachus*). Claws in *Ptychadena* are different in shape and miss the specific bony nodule distally to the terminal phalange (Fig. 4b), being therefore not fully comparable and likely of convergent origin (Kamermans & Vences, 2009; Scott, 2005). It is therefore likely that arthroleptid claws developed only once, and therefore could serve as an apomorphy for a monophyletic clade. Recent phylogenies do not place the three genera in a monophyletic clade (see Frost *et al.*, 2006; Scott, 2005). The related but clawless genera *Leptodactylodon* and *Nyctibates* (see Amiet, 1980; Noble, 1931; Perret, 1966) are positioned between these genera in the latter phylogenies. Even less convincing is that according to Frost *et al.* (2006) *Scotobleps* even belongs to a



FIG. 4

X-ray image of foot (scale bar 5 mm). (a) *Leptopelis boulengeri* (ZFMK 77974). (b) *Ptychadena perreti* (ZFMK 15418).

different tribe from *Astylosternus* and *Trichobatrachus*. Therefore, these phylogenetic hypotheses imply (1) a repeated origin (even in different tribes) or (2) a secondary loss of this peculiar structure. Based on results of Scott (2005) we depict these two phylogenetic hypotheses and a third favoured hypothesis for the occurrence of claw-like terminal phalanges in arthroleptid genera (Fig. 6). Other phylogenetic studies concerning selected aspects of the broad phylogeny came to results differing from the above-mentioned phylogenies (e.g. Stuart, 2008). Probably, a better sampling of taxa, including more species comprising the respective type species will reveal differing relationships in specific groups. Therefore it remains to be seen, whether future studies will support closer interrelationships of these three genera with claw-like phalanges, or not.

THE "HAIRS" OF *TRICHOBATRACHUS ROBUSTUS*

Our results correspond to the general structure recognized by Noble (1925) with axial vessels in the centre of the papillae and further smaller vessels running parallel or transverse to the inner ones (Fig. 5b, 5c). Kükenthal (1912) mentioned ridges and

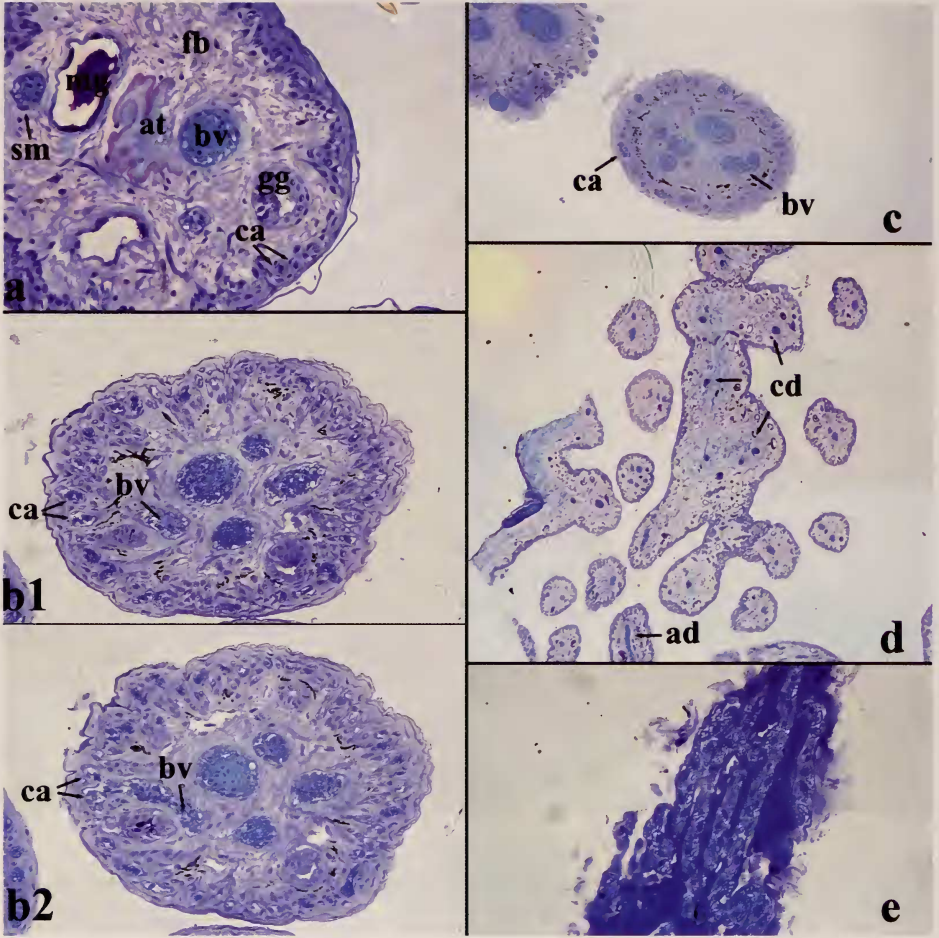


FIG. 5

Trichobatrachus robustus. (a) Structure of dermal appendage in transverse section. Abbreviations: at = amorphous tissue, bv = blood vessel, ca = capillary, fb = fibro blasts, gd = granular gland, mg = mucous gland, sm = smooth musculature [lower flank: magnification 250x]. (b1) Connection between blood vessel and capillaries [lower flank: magnification 200x]. (b2) Connection between blood vessel and capillaries, subsequent layer [lower flank: magnification 200x]. (c) Connected, enlarged capillaries and inner blood vessels, released epidermal layers [upper flank: magnification 100x]. (d) Dermal appendages just before the flanks [lower flank: magnification 25x]. (e) Tangential cut of dermal appendage [upper limb: magnification 400x].

trenches close to the surface of the dermal papilla, which has been questioned by Noble (1925). In some cases the topmost layers of the epidermis have obviously been damaged and embedded capillaries emerge on the surface (Fig. 5c).

ON A POSSIBLY RESPIRATORY FUNCTION OF THE "HAIRS"

The most widely accepted functional hypothesis has been provided by Noble (1925), who regarded this peculiar structure as a respiratory organ supporting the

reduced lungs. Noble (1925) figured a system of capillaries, which goes through the topmost layers of skin. This picture is true for the distal parts of the dermal appendages, but unfortunately no information of the position of the figured part of the body is given by the author. The increasing number of vessels and capillaries in the distal parts displays the picture of a finer reticulation. Probably a better gas exchange can be attained in the distal parts, as they are more strongly affected by the current of the oxygen-rich water. Jasiński & Miodoński (1978) detected two independent capillary systems in the frog *Rana esculenta* (today *Pelophylax esculentus*); one subepidermal and the other in deeper layers of the stratum spongiosum, and the two systems differ in function. The deeper system fulfils a trophic function, while the upper one carries out the gas exchange. Within the dermal papillae only one capillary reticulation has been detected and due to its subepidermal location it corresponds to the respiratory system. Interestingly, all blood vessels, whether inner larger ones or small outer capillaries, are completely filled with blood cells (Fig. 5b, 5e). According to Hsia *et al.* (1999), densely packed blood cells hinder the absorption of oxygen. Moreover, the occurrence of only one connection to axial vessels in the skin of the flanks conflicts with the idea of a true blood circulation. If a higher number of smooth muscles would have been found in a lengthwise order, a muscular-induced reflow would have been possible, but the few adjacent muscle cells are not capable to perform such a step. Therefore a one-way inflow, oxygen absorption and one-way reflow can be excluded. However, a possible explanation could be seen in the amorphous tissue. As the dermal appendages belong to a specimen collected in the second half of the rainy season (September 2007 in western Cameroon), the amorphous tissue could represent regressed blood vessels (Fig. 5a). A disconnected circulation would also explain the overfilled vessels and capillaries. A comparison of dermal appendages in different stages of the rainy season would be necessary to analyze whether a real circulation is developed and degenerated again before the end of the season or not.

The importance of cutaneous respiration arises in the existence of lunglessness in salamanders (e.g. Plethodontidae), one caecilian (Nussbaum & Wilkinson, 1995) and the only known lungless anuran *Barbourula kalimantanensis* (Bickford *et al.*, 2008). Bickford *et al.* (2008) pointed at cold fast-flowing water as the habitat of *B. kalimantanensis*, ensuring a high oxygen supply and resulting in its lunglessness. *Trichobatrachus* inhabits similar currents in mountainous areas of Cameroon, which would substantiate the idea of a respiratory function. But even if cutaneous respiration became more important in the life history of *Trichobatrachus*, two main questions remain: (1) why do only males possess this peculiar and unique structure (Mertens, 1958) and (2) how could such an uncommon structure develop to elevate respiratory function?

Observations in the field have shown that females enter the streams only in the breeding season for egg deposition and stay outside the water in adjacent areas for the rest of the year (Laurent, 1961; Zippel, 1997); own findings support this statement, as only males have been caught in the stream, while the only female has been collected by a villager in his plantation. According to Perret (1966) males guard their clutches (glued to submerged stones) and may therefore have a prolonged breeding season with a more aquatic life history during this time. This could explain why females do not

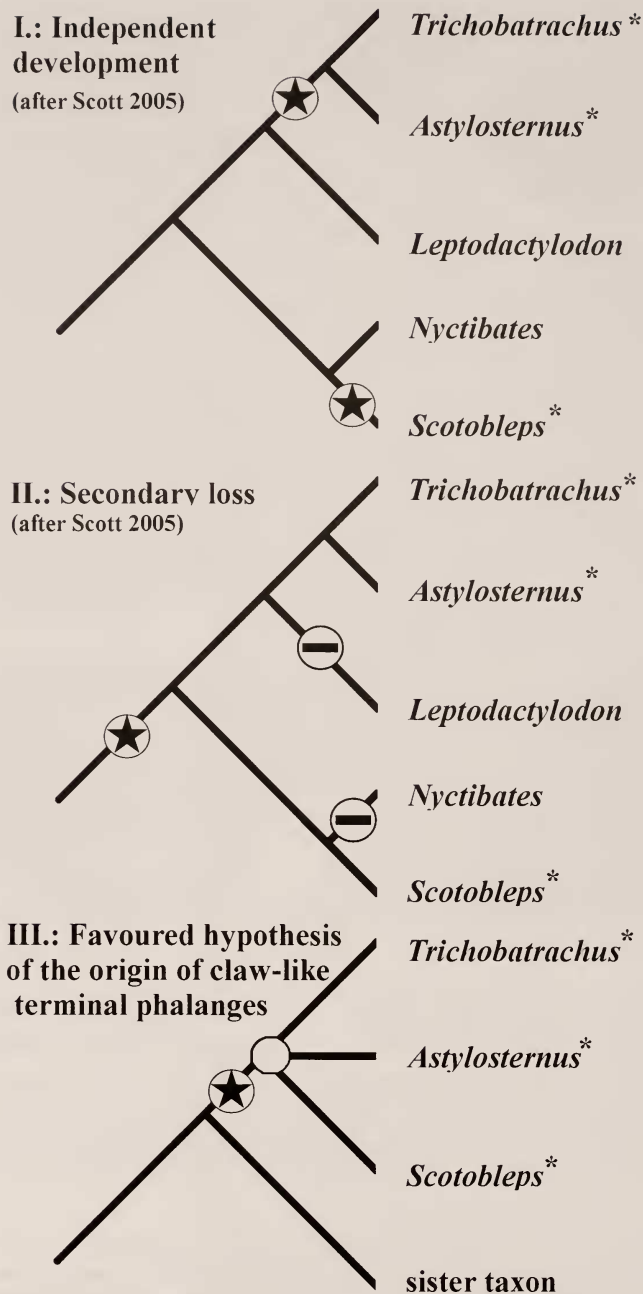


FIG. 6

Three alternatives for the occurrence of claw-like terminal phalanges. Circle with star: apomorphy development of claw-like terminal phalanges; circle with crossbar: apomorphy secondary loss of claw-like terminal phalanges; empty circle: unresolved closer relationships; genera marked with an asterisk "*" possess claw-like terminal phalanges in toes.

develop (respiratory?) “hairs,” as the time spent in the water is too short. Expended energy would exceed an efficient use of an additional respiratory system, which is obviously not required outside water.

Simple expansion of the abdominal skin enables enlargement of the skin surface in *Telmatobius* (Hutchinson *et al.*, 1976) and Bickford *et al.* (2008) regard body flattening as another key factor to increase body surface and hence increase cutaneous respiration. The hairy frog *Trichobatrachus* possesses a very robust body shape and lacks “common” tegumental appendages like folds, which would enlarge its surface; if only for respiratory aspects, obviously a simpler way than producing “hairs” would have been sufficient.

ON OTHER POSSIBLE FUNCTIONS OF THE HAIR-LIKE APPENDAGES

Our results have not proven the occurrence of nervous fibres and cells within the hair-like appendages. Thus we cannot confirm the structural functional interpretation of Kükenthal (1912).

Andersson (1907) regarded the appendages as a nuptial dress in males. Flanks of male *Trichobatrachus* are known to show an intensive red coloration (Lawson, 1993; Sanderson, 1936; own observations; Fig. 7) and a possible use as a visual signal to attract females can not be excluded. The distance of few layers of cells between capillaries and the surface is short enough to enable the absorption of oxygen, what led Noble (1925) to regard the appendages as a respiratory organ. The intake of oxygen results in a change of the conformity of the haem, what results in the bright red coloration in appendages with less dark pigments. Such a visual signal could help to find the submerged male specimens between rocks. In contrast, no stones with reddish algae have been found in the natural habitat of *Trichobatrachus robustus*, what would refute the idea of mimesis (after Sabater-Pi, 1966, 1970; Sanderson, 1936).

THE HAIRY FROG, A CURLY FIGHTER- A NOVEL HYPHESIS ON THE FUNCTION OF CLAW-LIKE PHALANGES AND “HAIRS”

Claw-like phalanges have been speculated to offer a better grip in slippery habitats of the respective frogs (Noble, 1931; Sabater-Pi, 1970; Sanderson, 1936) or in predator defence (Durrell, 1956; Blackburn *et al.*, 2008), while “hairs” in *Trichobatrachus robustus* have among others been regarded as respiratory organs, secondary sexual characters (see above). We present a novel functional hypothesis:

Sexual size dimorphism (SSD) is the difference in body length or body mass of mature organisms between the sexes (Kupfer, 2007). *Trichobatrachus* belongs to the low proportion of anurans with a reversed SSD (rSSD) with males growing larger than females. This has been demonstrated repeatedly in the past (Jones, 1971; Perret, 1966; Sabater-Pi, 1966) Secondary sexual characters like prepollex spines or oral tusks are common among anurans with male combat (Kupfer, 2007; Shine, 1979; but see also Halliday, 1987; Halliday & Verrell, 1986; Shine, 1987).

Aggressive interactions between males can lead to wounds, still recognizable as scars in preserved specimens (Martins *et al.*, 1998). Sanderson (1936) reports on scars in *Petropedetes johnstoni* (= *P. parkeri*; compare Barej *et al.*, 2010), a *Petropedetes* with a rSSD possessing an prepollex spine in males in breeding condition (Amiet,



FIG. 7

“Hairs” on flanks of male *Trichobatrachus robustus* (ZFMK 87749).

1983), and Sanderson (1936) regarded them as results of intraspecific aggression during the reproductive phase. Similar scars are present in *Trichobatrachus* (Fig. 8), the only arthroleptid frog with a rSSD (Perret, 1966). We regard these scars as the result of aggressive male-male interactions. If this is the case, the “hairs” could function as a mean of mechanical protection for the vulnerable flanks and belly. Although the thin layer of smooth muscles around the larger inner vessels is not capable to induce a reflow within a simple and linear blood system, they would be sufficient to close the vessel and prevent a serious injury. Hence, the “hairs” are equipped with capillary blood vessels, but their particular structure prevents serious injuries and could protect flanks and bowel. *Hypsiboas faber* and *H. rosenbergi* males are known to stab their sharp pollices into the opponent male leading to injuries and sometimes even to death (Lutz, 1960; Kluge, 1981). Using their claws, hairy frogs can easily cut even human skin enough to cause bleeding (Durrell, 1956; Lawson, 1993; Senfft, 1939; own observations). Hence, a protective structure such as the “hairs” of *Trichobatrachus* males seems useful.

Claw-like terminal phalanges have moreover been detected in the related genera *Scotobleps* and *Astylosternus* (e.g. Boulenger, 1901, 1917), but in contrast to *Trichobatrachus*, they possess a female biased SSD (see Amiet, 1977; Perret, 1966). Neither have scars been reported for *Astylosternus* and *Scotobleps*, nor have they been found in preserved specimens of large museum collections, although, when handled without care, their claws can cut human skin as known in *Trichobatrachus* (own observations). These genera inhabit lotic environments, usually characterized by strong currents and generally slippery habitats, hence, in this case the occurrence of claw-like terminal phalanges may represent an adaptation to this peculiar habitat type. But, the occurrence of claws in *Trichobatrachus robustus* represents a possible exception for



FIG. 8

Scars on back of male *Trichobatrachus robustus* (ZFMK 74855).

the later use of claw-like terminal phalanges as weapons in male-male interactions. Thereafter, the presence of claws and the unique reversed SSD in arthroleptid can be regarded as reasons why territorial and intraspecific aggressive behaviour may occur only in *Trichobatrachus*.

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APPENDIX: STUDIED MATERIAL

ABBREVIATIONS

ZFMK Zoologisches Forschungsmuseum Alexander Koenig, Bonn

MHNG Muséum d'histoire naturelle, Genève.

HISTOLOGICAL ANALYSIS

Investigated specimen: ZFMK 87749, field no. MM148, coll. J.A.M. Wurstner & M.F. Barej. Specimen has been caught on the 8th October 2007 during fieldwork in western Cameroon, by rock turning and dip netting in a creek of up to 1 m depth.

OSTEOLOGICAL ANALYSIS

***Astylosternus*:**

Astylosternus batesi (MHNG 1034.60, MHNG 2210.56, ZFMK 28943)

Astylosternus diadematus (ZFMK 69161, ZFMK 77962, ZFMK 81702)

Astylosternus fallax (ZFMK 81163, ZFMK 81164, ZFMK 81607, ZFMK 81613)

Astylosternus laurenti (MHNG 1570.56, MHNG 1570.57, MHNG 1570.58)

Astylosternus montanus (ZFMK 69548, ZFMK 69708, ZFMK 69750, ZFMK 81200)

Astylosternus nganhanus (MHNG 1562.71 holotype)

Astylosternus occidentalis (ZFMK 58651, ZFMK 56289)

Astylosternus perreti (MHNG 2715.38, MHNG 2715.39, ZFMK 69709, ZFMK 78309, ZFMK 81040, ZFMK 89435)

Astylosternus ranoides (MHNG 1562.100)

Astylosternus cf. *ranoides* (ZFMK 81061, ZFMK 81063, ZFMK 81064)

Astylosternus rheophilus (ZFMK 15012)

Astylosternus rheophilus tchabalensis (ZFMK 75770, ZFMK 75773)

Astylosternus schioetzi (MHNG 2685.38 paratype, ZFMK 67733)

Astylosternus sp. (ZFMK 72848, ZFMK 75776, ZFMK 89474, ZFMK 89475)

***Leptodactylodon*:**

Leptodactylodon albiventris (MHNG 1524.4, MHNG 1523.98)

Leptodactylodon axillaris (MHNG 2031.8 holotype, MHNG 2685.72 paratype)

Leptodactylodon bamilekianus (ZFMK 69189, ZFMK 69190)

Leptodactylodon bicolor (MHNG 2031.7 holotype, MHNG 2685.78 paratype)

Leptodactylodon boulengeri (MHNG 2685.74 holotype, MHNG 2685.75 paratype)

Leptodactylodon bueanus (MHNG 2031.12 holotype, MHNG 2685.71 paratype, MHNG 2685.83 paratype)

Leptodactylodon erythrogaster (MHNG 2031.11 holotype)

Leptodactylodon mertensi (MHNG 951.36 holotype, ZFMK 67370, ZFMK 67749)

Leptodactylodon ornatus ornatus (MHNG 2031.10 holotype, ZFMK 67369, ZFMK 67753)

Leptodactylodon ornatus permaculatus (MHNG 2031.3 holotype)

Leptodactylodon ovatus orientalis (MHNG 2031.4 holotype, MHNG 2685.84 paratype, ZFMK 78015, ZFMK 81620)

Leptodactylodon perreti (MHNG 2031.5 holotype, MHNG 1525.8 paratype)

Leptodactylodon polyacanthus polyacanthus (MHNG 2031.9 holotype, MHNG 2685.94 paratype)

Leptodactylodon polyacanthus punctiventris (MHNG 2031.6 holotype, MHNG 2685.95 paratype, MHNG 2685.96 paratype)

Nyctibates:

Nyctibates corrugatus (ZFMK 77941, ZFMK 77942, ZFMK 77943, ZFMK 81156, ZFMK 81591, ZFMK 87888)

Scotobleps:

Scotobleps gabonicus (ZFMK 69606, ZFMK 87767, ZFMK 87768, ZFMK 87769, ZFMK 87775, ZFMK 87776, ZFMK 87778)

Trichobatrachus:

Trichobatrachus robustus (MHNG 958.73, MHNG 1035.1, MHNG 1053.3, MHNG 2716.36, MHNG 2716.37, MHNG 2716.38, ZFMK 9407, ZFMK 41177, ZFMK 61316, ZFMK 66453, ZFMK 74855, ZFMK 83751, ZFMK 83753, ZFMK 87748, ZFMK 87749, ZFMK 87750, ZFMK 87752, ZFMK 87753, ZFMK 89454, ZFMK 89579, ZFMK 89580)

Arthroleptis:

Arthroleptis adelphus (ZFMK 73238)

Arthroleptis adolfifriederici (ZFMK 88010)

Arthroleptis bivittatus (ZFMK 69483, ZFMK 69484)

Arthroleptis perreti (MHNG 2715.14, ZFMK 89468)

Arthroleptis poecilonotus (MHNG 2715.21, ZFMK 89539)

Arthroleptis sylvaticus (ZFMK 87917, ZFMK 87918)

Arthroleptis taeniatus (ZFMK 89513)

Arthroleptis tuberosus (ZFMK 67692, ZFMK 69379, ZFMK 69740)

Arthroleptis variabilis (ZFMK 87836, ZFMK 87837)

Cardioglossa:

Cardioglossa also (ZFMK 77707, ZFMK 77709, ZFMK 77724)

Cardioglossa elegans (ZFMK 67735, ZFMK 67736, ZFMK 81664)

Cardioglossa escalerae (ZFMK 58860)

Cardioglossa gracilis (MHNG 2715.43, ZFMK 69712, ZFMK 89436)

Cardioglossa melanogaster (ZFMK 81080)

Cardioglossa nigromaculata (ZFMK 81658, ZFMK 81659)

Cardioglossa venusta (ZFMK 75453, ZFMK 75454, ZFMK 75572)

Leptopelis:

Leptopelis boulengeri (ZFMK 77974, ZFMK 81580)

Leptopelis brevirostris (ZFMK 15457, ZFMK 61305)

Leptopelis karissimbensis (ZFMK 87996, ZFMK 87997)

Leptopelis kivuensis (ZFMK 87990, ZFMK 87994, ZFMK 87995)

Leptopelis rufus (MHNG 2715.81, ZFMK 87897, ZFMK 87898)

Ptychadena:

Ptychadena aequiplicata (ZFMK 77104, ZFMK 77105)

Ptychadena longirostris (ZFMK 62170)

Ptychadena mascareniensis (ZFMK 77999, ZFMK 81710)

Ptychadena perreti (ZFMK 15411, ZFMK 15418)