

Digital Pad Morphology in Torrent-living Ranid Frogs

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Abstract. -Digital pads of 24 species of ranoid frogs (Raninae, Dicroglossinae, Ranixalinae, Rhacophorinae, Hyperoliinae) were studied by scanning electron microscopy. In many species of Raninae the cells of the adhesive pad are differentiated (elongated and wearing projections). Functional aspects of cell morphology and digital pad expansion are discussed in relation with sticking condition in aquatic medium.

Key words: Amphibia, Anura, morphology

Introduction

Digital pads occur in most of advanced anuran families. This organ seems to be of multiple origin and of difficult use in systematics (Noble and Jaekle, 1928; McAllister and Channing, 1982). Digital pads occur in arboreal anurans (*Hyla*), but they can also be observed in torrent-living frogs (*Amolops*), and in some fossorial species (*Kaloula*). In Asian and African frogs of the family Ranidae, several genera and species groups belonging to different subfamilies have fingers and toes bearing digital pads.

There exists no strong hypothesis of phylogeny of ranids as a whole. Phylogenetic analyses were undertaken only for geographic and taxonomic limited groups (Liem, 1970; Clarke, 1981; Hillis, 1985; Emerson and Berigan, 1993). The broadly accepted classification (Frost, 1985) is based on Boulenger's works dating from the beginning of this century (Boulenger, 1882; 1920). Recently Dubois (1986, 1992) tried to review the entire group and proposed a tentative classification which he sees as a working hypothesis. In this hypothesis ranids are split into several families, subfamilies and tribes (Dubois, 1992). Species that are enclosed in the genus "*Rana*" in Frost (1985) are in Dubois' classification distributed in several subfamilies (Table 1).

Results from study of skeleton showed several major lines in "*Rana*" (Deckert, 1938; Clarke, 1981). Study of the morphology of the digital pads (Ohler and Dubois, 1989) confirmed that two of these

lines could be distinguished by their digit morphology. Ranines have digital pads with a latero-ventral groove, often separated terminally. Dicroglossines have digital pads showing a dorso-terminal groove.

The histological structures of the digital pads were first described by Schuberg (1895) and Siedlecki (1910). Noble and Jaekle (1928) undertook a comparative histological analysis of 47 species of anurans. The fine structure of the epidermal cells in the digital pad has been observed by transmission electron microscope (Komnick and Stockem, 1969; Ernst, 1973 a-b). Scanning electron microscopy has been used to describe morphology of digital pads, often in view of taxonomic utilisation or functional interpretation (Welsch, Storch and Fuchs, 1974; Green, 1979, 1980, 1981; Emerson and Diehl, 1980; Mc Allister and Channing, 1983; Green and Simon, 1986; Green and Carson, 1988).

The epidermis of anurans has a superficial layer of hexagonal or pentagonal squamosal cells, which are disposed in a regular way (Tyler and Miller, 1985). Differentiation of the pad leads to prismatic epithelial cells. Their surface is usually hexagonal or pentagonal, as is that of generalized cells, but their height is more important than in the latter. They are separated in their distal part forming deep crypts.

In the dermis of amphibians both mucous and venomous glands are present. Their aperture is situated between the epithelial cells of the epidermis. On the pad

TABLE 1. Classification of Dicroglossinae and Raninae as proposed by Dubois (1992) and numbers of species studied here. D: digital pad or expanded digit tip present in some species at least; M: some species at least in the genus *Micrixalus* in the classification given by Frost (1985); R: some species at least in the genus *Rana* in the classification given by Frost (1985); the number indicates the number of species here studied by morphometry, external morphology and/or scanning electron microscopy.

Dicroglossinae				<i>Bouretia</i>	D	R	2
Ceratobatrachini				<i>Fejervarya</i>		R	1
<i>Ceratobatrachus</i>	D			<i>Limnonectes</i>		R	2
<i>Discodeles</i>	D						
<i>Ingerana</i>							
<i>Ingerana</i>	D	M,R	1				
<i>Liurana</i>	D						
<i>Palmatorappia</i>				<i>Babina</i>	D		
<i>Platymantis</i>	D		1	<i>Chalcorana</i>	D		1
<i>Taylorana</i>	D	R		<i>Clinotarsus</i>	D		
Conrauiini				<i>Eburana</i>	D		1
<i>Conraua</i>	D			<i>Glandirana</i>			
				<i>Humerana</i>	D		
Raninae				<i>Hydrophylax</i>			2
Paini				<i>Hylarana</i>	D		2
<i>Chaparana</i>				<i>Lithobates</i>			
<i>Annandia</i>	D	R		<i>Nasirana</i>	D		
<i>Chaparana</i>	D	R		<i>Nidirana</i>	D		
<i>Feirana</i>	D	R		<i>Odorrana</i>	D		1
<i>Ombrana</i>	D	R		<i>Pantherana</i>			
<i>Paa</i>				<i>Papurana</i>	D		3
<i>Eripaa</i>	D	R		<i>Pelophylax</i>			2
<i>Gynandropaa</i>		R		<i>Pseudorana</i>	D		
<i>Paa</i>		R		<i>Pterorana</i>	D		
<i>Quasipaa</i>	D	R		<i>Pulchrana</i>	D		3
Ranini				<i>Rana</i>			
<i>Amolops</i>				<i>Rugosa</i>			
<i>Amo</i>	D			<i>Sanguirana</i>	D		
<i>Amolops</i>	D	R	6	<i>Sierrana</i>			
<i>Huia</i>	D		1	<i>Strongylopus</i>			
<i>Meristogenys</i>	D		1	<i>Sylvirana</i>	D		3
<i>Batrachylodes</i>	D		1	<i>Tryphlops</i>	D		
<i>Micrixalus</i>	D	M		<i>Tylerana</i>	D		
<i>Nanorana</i>				<i>Zweifelia</i>			
<i>Altirana</i>				<i>Staurois</i>	D		2
<i>Nanorana</i>							
<i>Rana</i>							
<i>Afrana</i>							
<i>Amerana</i>							
<i>Amietia</i>							
<i>Amnirana</i>	D		3				
<i>Aquarana</i>							
<i>Aurorana</i>							
Dicroglossini							
<i>Euphlyctis</i>		R					
<i>Occidozyga</i>							
<i>Phrynoglossus</i>	D	R	1				
Limnonectini							
<i>Hoplobatrachus</i>		R					
<i>Limnonectes</i>							

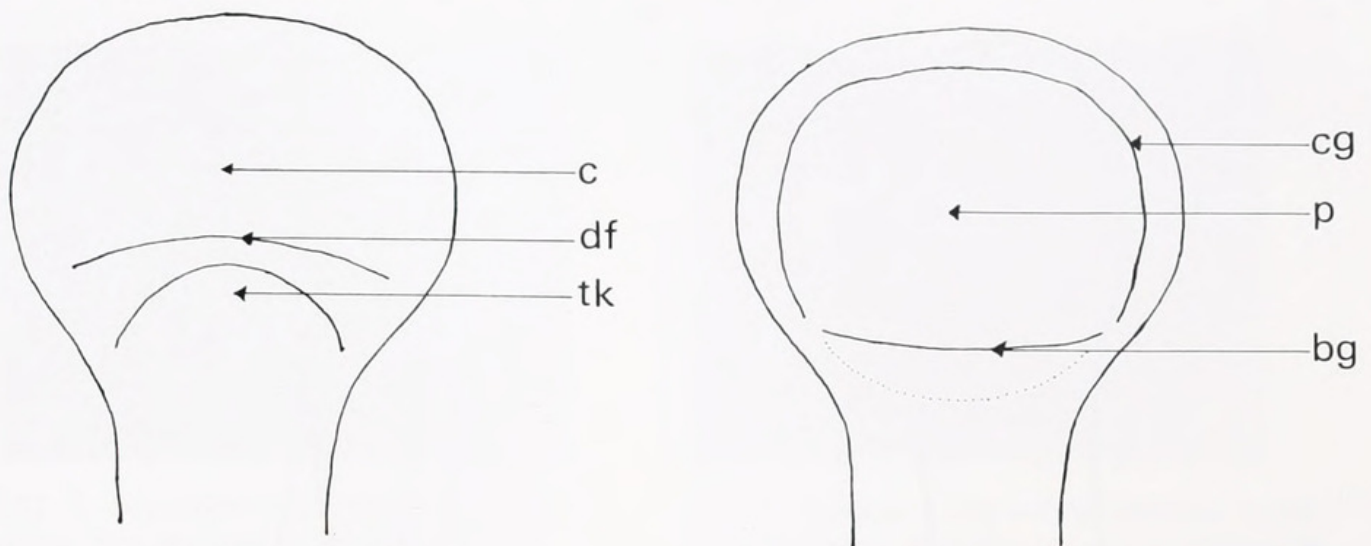


FIG. 1. Generalized plan of digital pad. Left dorsal view; right ventral view. c: cover; df: dorsal fold; tk: terminal knuckle; cg: circumferential groove; p: pad; bg: basal groove.

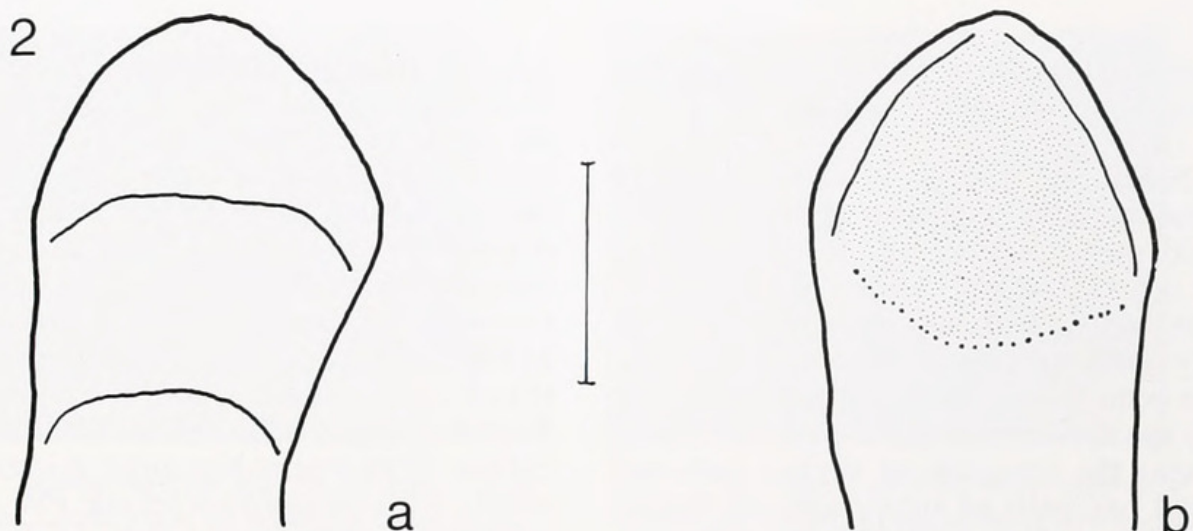


FIG. 2. Digital pad of Raninae with latero-ventral groove (*Rana (Hylarana) erythraea*, MNHN 1987.3343, Thailand). a: dorsal view of finger III; b: ventral view of finger III; stippled area corresponds to the pad with prismatic cells.

only openings of mucous glands can be observed.

The first authors (Schuberg, 1895; Siedlecki, 1910; Noble and Jaekle, 1928) supposed that the products of the mucous glands were implicated in sticking function. To complete sticking the epidermal cells would allow attachment to natural surfaces that are covered with irregularities (Welsch, Storck and Fuchs, 1974), somehow close to the mechanism of clinging in lizards. But

lizards differ substantially from amphibians in having a dry or setal adhesive system (Green and Carson, 1988).

Emerson and Diehl (1980) and Green (1981) independently showed that surface tension was mechanically responsible for the adhesive abilities of treefrog digital pads. As the surfaces of plants have usually a low surface tension, the structure of the pad cells assures humidification responsible for adhesion. The grooves surrounding the pad

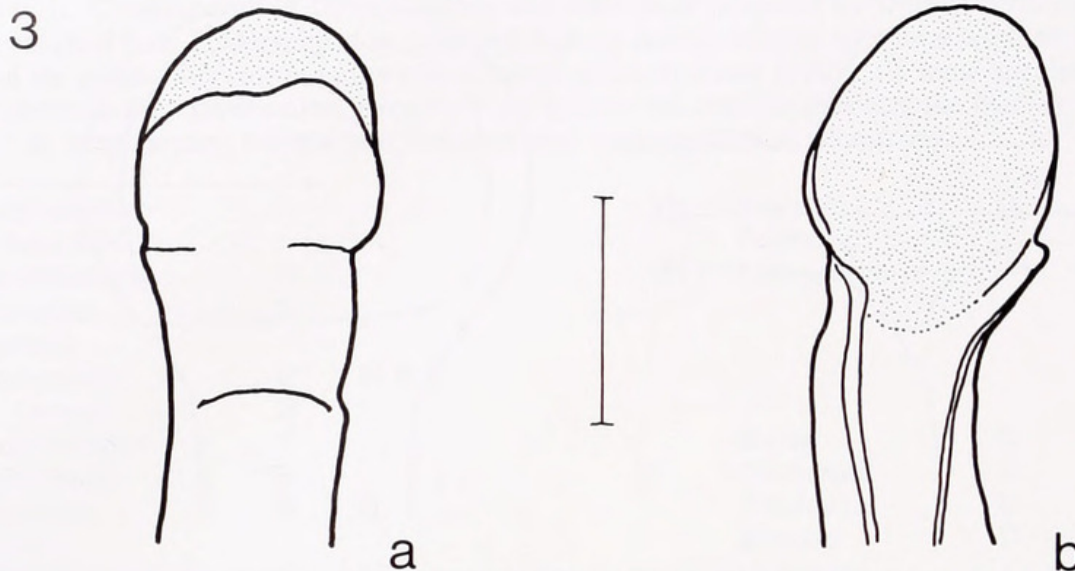


FIG 3. Digital pad of Dicroglossinae with dorso-terminal groove (*Limnonectes (Bourretia) doriae*, MNHN 1987.3130, Thailand). a: dorsal view of toe IV; b: ventral view of toe IV; stippled area corresponds to the pad with prismatic cells.

serve as a reservoir for the fluid wetting agent (McAllister and Channing, 1983).

Numerous frog species with enlarged digital tips have been studied (Hyperoliinae, Hylidae, Telmatobiinae, Rhacophorinae, and others), as well as the digital tips of some species without enlarged digital tips. Only some species of the family Ranidae have been studied in this respect, including only species without digital pad. Here I will present the structure of digital pads and digital pad cells of subfamilies of ranoids according to Dubois' (1992) classification, Ranixalinae, Dicroglossinae, Raninae, Rhacophorinae and Hyperoliinae. They include arboreal ("*Hylarana*") and torrent-living frogs (*Amolops*) that have digital pads with grooves and modified cells. For the torrent-living frogs a mechanism of sticking is proposed and the correlation of cell morphology, digit tip enlargement and biology of these frogs is outlined.

Material and methods

Specimens representing 15 of 34 genera and subgenera, possessing digital pads, as recognised by Dubois (1992) were chosen in the collection of MNHN (see Table 1, Appendix I). They had been generally

formalin fixed and all had been stored in 70 % alcohol. Finger II or IV or toe III were cut on the terminal articulation. Cleaned with ultrasonic sounds, they were dehydrated in alcohol. After critical point drying, they were gold covered (2-4 Å). Specimens were observed with the Scanning electron microscope (JSM-840) of the MNHN SEM facilities. Photographs were taken on 120 Ilford FP4 film. Measurements were taken with a slide caliper (SVL) or a binocular microscope (FW): SVL - snout-vent length; FW - third finger width (maximum width of tip of third finger). To eliminate size factor, FW is given as a ratio of SVL (per thousand).

Terminology of digital pad morphology (Fig. 1, 2, 3)

(1) The *circumferential groove* (Green and Simon, 1986) (Fig. 1) surrounds the digit tip latero-terminally and separating a dorsal part from a ventral part. The groove may be complete or open (with a distal zone of contact between the dorsal and ventral part). This is the generalized groove that is modified in various manners according to the group of frogs observed.

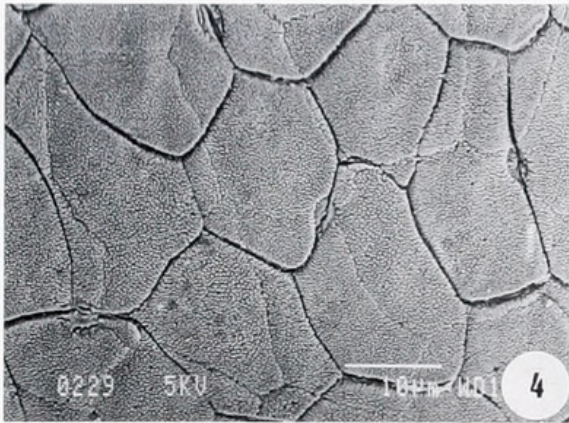


FIG. 4. Squamosal cells with short spinulae, ventral view, proximal of pad of finger III (*Batrachylodes vertebralis*, MNHN 1970.1407, Salomon Islands).



FIG. 5. Squamosal cells with microridges, ventral view, outside the circumferential groove of finger III (*Amolops marmoratus*, MNHN 1988.2787, Nepal).



FIG. 6. Squamosal cells with spongy structures, dorsall view, on subunguis close to the dorso-terminal fold of finger III (*Ingerana tasanae*, MNHN 1987.2002, Thailand).

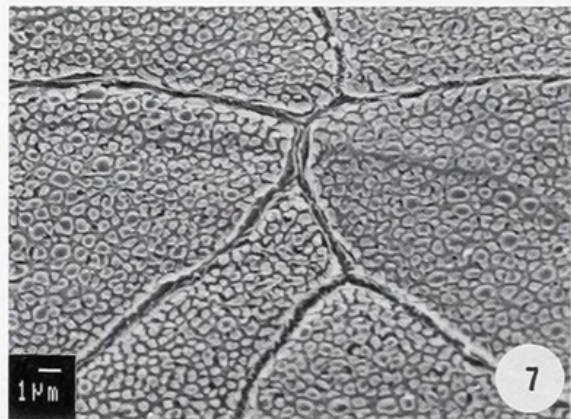


FIG. 7. Squamosal cells with hollow tubercles, ventral view, proximal of pad of finger III (*Ingerana tasanae*, MNHN 1987.2002, Thailand).

(a) The *latero-ventral grooves* (Ohler and Dubois, 1989) (Fig. 2) close the pad, that is of triangular shape, laterally. In some species they join distally and close to a unique groove around an oval or rounded pad.

(b) The *dorso-terminal groove* (Ohler and Dubois, 1989) folds on the dorsal part of the digit. The pad is of oval or rounded form. In species where the groove is more pronounced its lateral parts can be observed ventrally (Fig. 3).

(2) The *basal groove* (Fig. 1) is the basal limit of the digital pad. Fusion of this with the circumferential groove results in a *circumplantar groove*. The latter is not present in all digital pad types.

(3) The ventral part is the proper adhesive organ, the *pad* (Savage, 1987) (Fig. 1). Its latero-terminal limits are usually distinct formed by the groove. Its basal limit is intergrading, and the basal groove, if present, is not the limit of the functional part as indicated by presence of modified cells still beyond this limit distally.

TABLE 2. Distribution of prismatic cell types and relative width of tip of third finger in ranoid frogs. - Cell differentiation: L: elongated prismatic cells; R: regularly outshaped prismatic cells; H: cells of heterogeneous shape; P: projections on proximal border of prismatic cells; S: small projections on proximal border of prismatic cells; N - no projections on prismatic cells; - : no prismatic cells in the digit tip. - Relative width of tip of third finger, measured by FW/SVL: x: mean; s: standard deviation; n: number of specimens measured; EV: extreme values of ratio FW/SVL in group.

Species studied	Cell differentiation	Relative finger tip width			
		x	s	n	Group (EV)
<i>Limnonectes (Limnonectes) kuhlii</i>	-	17.2	1.17	7	A (17-20)
<i>Rana (Hydrophylax) galamensis</i>	-	19.2	0.84	5	
<i>Phrynoglossus laevis</i>	-	19.3	2.62	10	
<i>Platymantis corrugatus</i>	R N	19.9	1.13	2	
<i>Limnonectes (Bourretia) pileatus</i>	R N	22.9	0.71	2	B (22-28)
<i>Limnonectes (Bourretia) doriae</i>	R N	23.7	3.18	2	
<i>Rana (Hylarana) erythraea</i>	L N	24.9	2.42	9	
<i>Rana (Sylvirana) sp.</i>	L N	27.3	2.50	6	
<i>Rana (Odorrana) andersoni</i>	L S	35.7	5.03	31	C (35-43)
<i>Amolops (Huia) nasicus</i>	L S	37.8	3.33	8	
<i>Rana (Amnirana) lepus</i>	L P	41.5	7.78	2	
<i>Rana (Amnirana) albolabris</i>	L H N	42.2	2.68	5	
<i>Amolops (Huia) kinabaluensis</i>	L H P	42.5	4.95	2	
<i>Indirana gundia</i>	L P	42.6	1.96	10	
<i>Amolops (Amolops) sp. 3</i>	L P	47.9	3.42	40	D (47-60)
<i>Rhacophorus leucomystax</i>	R N	51.2	4.26	10	
<i>Amolops (Amolops) sp. 1</i>	L P	52.6	3.83	24	
<i>Hyperolius viridiflavus karissimbiensis</i>	R N	55.0	3.77	10	
<i>Ingerana tasanae</i>	L P	55.5	1.63	2	
<i>Amolops (Amolops) sp. 2</i>	L H S	55.6	3.70	16	
<i>Batrachylodes vertebralis</i>	R S	56.7	9.03	6	
<i>Rana (Chalcorana) chalconota</i>	R S	60.0		1	
<i>Amolops (Amolops) formosus</i>	L H P	68.0	3.20	9	E 68-69
<i>Amolops (Amolops) marmoratus</i>	L S	68.7	5.71	12	

(4) The dorsal part, the *cover* (Savage, 1987) (Fig. 1), does not show histological specialisation.

(5) Proximally the cover is limited by the *dorsal fold* (Fig. 1).

(6) Dorsally on fingers and toes a *terminal knuckle* (Lynch, 1979) (Fig. 1) is present in the area of distal articulations.

(7) The pad is generally entirely masked by the cover, but in some cases it projects distally. The part of the pad that is then

visible dorsally is called the *subungis* (Lynch, 1979).

Results

The study of digital pads in Ranidae gave interesting results concerning gross morphology and its use for phylogeny already published (Ohler and Dubois, 1989) as well as new results concerning the type of prismatic cells observed in the digital pad. These microstructural results are exposed below and a functional hypothesis is proposed.

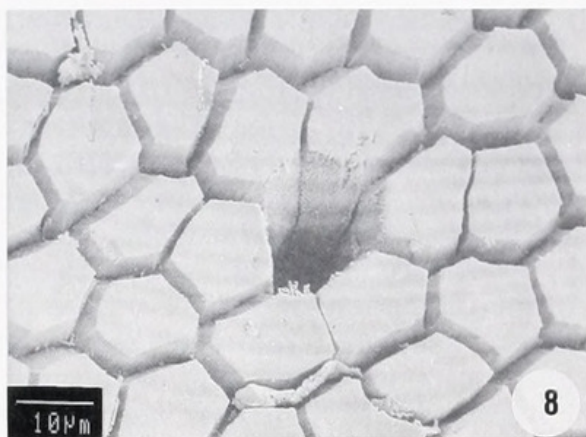


FIG. 8. Regular outshaped prismatic cells with mucous gland pore on pad of finger III (*Hyperolius viridiflavus karissimbiensis*, MNHN 1988.1055, Rwanda).



FIG. 9. Elongated prismatic cells with distal projections on pad of finger III (*Amolops* sp. 1, MNHN 1987.2163, Thailand).



FIG. 10. Elongated prismatic cells with distal projections on pad of finger III (*Amolops* sp. 3, MNHN 1987.2140, Thailand).

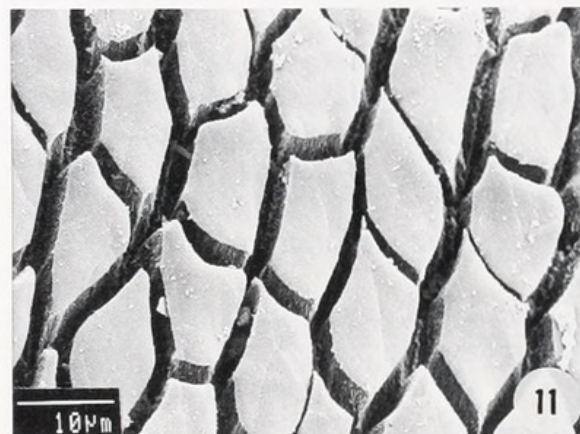


FIG. 11. Elongated prismatic cells with small distal projections on pad of finger III (*Amolops marmoratus*, MNHN 1988.2787, Nepal).

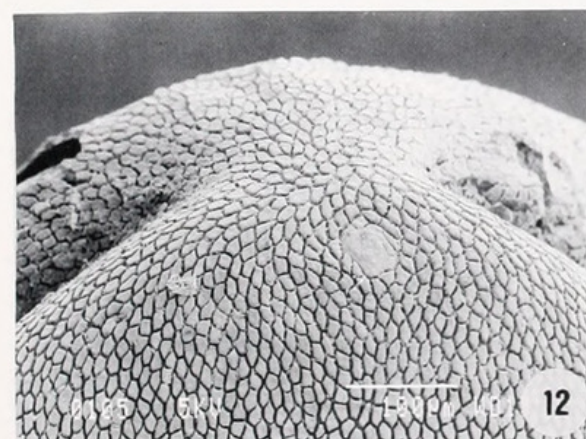


FIG. 12. Orientation and distribution of prismatic cells on distal part of the digital pad of finger III of *Rana* (*Odorrana*) *andersoni* (MNHN 1938.57, Vietnam).

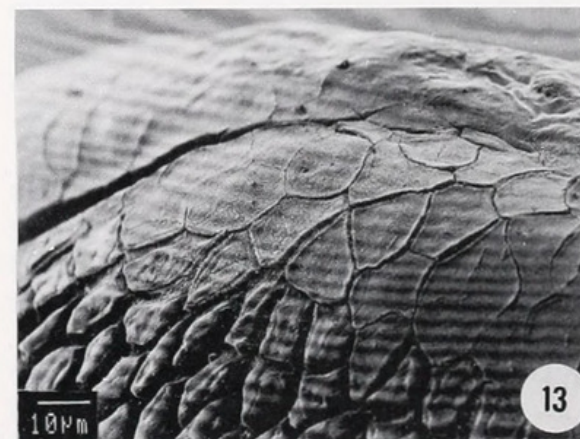


FIG. 13. Distribution of prismatic and squamosal cells on the extreme distal part of the digital pad of finger III of *Rana* (*Sylvirana*) sp. (MNHN 1987.3471, Thailand).

The epidermal cells

On the tips of the digits one observes two major cell types (squamosal cells and prismatic cells) with intermediary cells that occur in high numbers in the proximal pad zone.

(1) *Squamosal cells*. This is the generalized cell type, covering the body of amphibians (Tyler and Miller, 1985). The cells often show short spinulae (Fig. 4) or structures called microridges (Fig. 5). In *Ingerana tasanae* the surface of the squamosal cells is extremely rough and can show spongy structures (Fig. 6). On other parts of the epiderm the surface of the squamosal cells of *Ingerana tasanae* shows hollow tubercles (Fig. 7). The squamosal cells cover fingers and toes outside the pad. The groove is generally the border, but sometimes the squamosal cells are present on the border of the pad (*Rhacophorus leucomystax*) or in the contrary they are pushed back by the prismatic cells even outside the groove (*Amolops*).

(2) *Prismatic cells*. The prismatic cells are present on the pad. They are of regular outline in all the species already studied (Green, 1979; Green and Simon, 1986; McAllister and Channing, 1982; Richards *et al.*, 1977; Welsch, Strock, and Fuchs, 1974). Among the species studied here, *Hyperolius vividiflavus karissimbiensis* and *Rhacophorus leucomystax* have prismatic cells of regular outline (Fig. 8) like those found by previous authors. Also some other species of ranids (*Limnonectes* (*Bourretia*) *doriae*, *Batrachylodes vertebralis*) have this kind of prismatic cells. However, in most of the ranid species investigated (Table 2) in this study, the prismatic cells are not of regular outline but elongated. Their long axis is oriented in the proximo-distal direction on the digital pad. The ratio of the width to the length of these cells is smaller than 60%, while in normal prismatic cells this ratio is over 80%, often close to 100%. On their narrow distal side, the elongated cells have more or less developed projections.

In the species of the genus *Amolops*, this kind of cells is present with well developed projections (Fig. 9, 10). These were also observed in different "subgenera" of the genus *Rana* (*Odorrana*, *Amnirana*, *Hylarana*, *Chalcorana*) and in *Indirana gundia* (Ranixalinae). The prismatic cells of these species vary in their elongation, in the size of the projection, and in the degree of regularity. They are often rather regularly hexagonal, rounded proximally, with small distal projections, as in *Rana* (*Chalcorana*) *chalconota* and in *Ingerana tasanae*. In some species the prismatic cells are elongated, rounded proximally without projections (*Rana* (*Hylarana*) *erythraea*). In other species outlines are very variable among neighbouring cells; the cells are elongated forming a somehow triangular outshape wearing a single or two distal projections (Fig. 11). In all species of *Amolops* of this study, this kind of elongated cells with heterogeneous outlines was observed.

The prismatic cells are present outside the latero-ventral grooves in *Rana* (*Odorrana*) *andersoni* and in *Amolops* sp. 3. Observation of direction of the channels formed by the prismatic cells shows a generalized alignment in the direction of the space between the pair of lateral grooves (Fig. 12). In other species the border of pad is formed by squamosal cells, but a contact between the ventral and dorsal part of digital tip remains (ex. *Rana* (*Sylvirana*) sp., Fig. 13).

The development of the toe pad

The measurements of the digital width (Table 2) show an important variation that can be divided in several units. The species *Amolops formosus* and *Amolops marmoratus* show the most enlarged finger pads (FW/SVL = 68 p.m.). Other species of *Amolops*, but also *Rana* (*Chalcorana*), *Ingerana tasanae* and *Rhacophorus leucomystax* have very well developed digital pads (FW/SVL = 47-57 p.m.). The frogs of the subgenera *Rana* (*Amnirana*) and *Rana* (*Odorrana*) show moderately enlarged digital pads (FW/SVL = 35-43 p.m.). The species of *Rana* (*Sylvirana*) and *Rana* (*Hylarana*), as the species of the subgenus

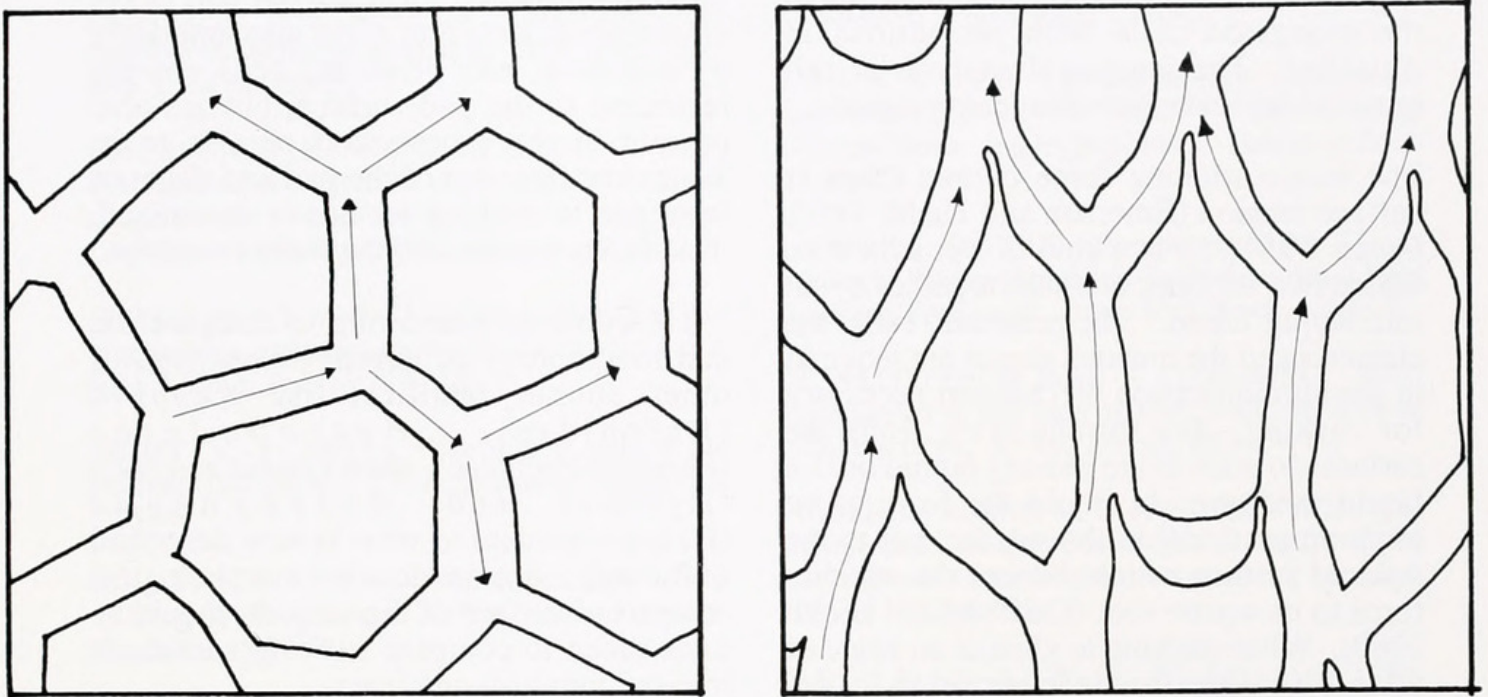


FIG. 14. Scheme of liquid fluid on a digital pad with regular outshaped cells (left) and with elongated cells (right).

Limnonectes (Bourretia) have very little enlarged finger pads (FW/SVL = 22-28 p.m.). The species studied that show no digital pad formation have the lowest ratios (FW/SVL = 17-20 p.m.).

Discussion

The elongated cells here described in some species of Ranidae have not been described in other anuran families. In fact the species that have been studied until now are "treefrogs", and no torrent-living frogs have yet been investigated. Considering the ecology of the studied species, five types can be distinguished: (1) torrent-living frogs of the genus *Amolops*, *Rana (Odorrana)* (the possible sister-group of *Amolops*) and *Rana (Amnirana)*; *Ingerana tasanai* should be placed in this group; (2) aquatic frogs, like *Limnonectes (Limnonectes) kuhlii* and *Phrynoglossus laevis*; (3) terrestrial frogs of the genus *Limnonectes (Bourretia)* and *Rana (Hydrophylax)*; (4) ground/vegetation living frogs of the genera *Rana (Hylarana)*, *Rana*

(*Sylvirana*), and *Rana (Chalcorana)*; (5) arboreal frogs (*Hyperolius*, *Rhacophorus*).

Actually the Raninae, the Dicroglossinae and the Ranixalinae do not include strictly arboreal species. The closest group of treefrogs are the Rhacophorinae, an other subfamily of Ranidae. *Hyperolius viridiflavus karissimbiensis* is another ranoid treefrog studied. *Rhacophorus leucomystax*, *Hyperolius viridiflavus karissimbiensis* and the species studies by the previous authors (Green, 1979; Green and Simon, 1986; Richards *et al.*, 1977; McAllister and Channing, 1982; Welsch, Strock, and Fuchs, 1974) have prismatic cells of regular outshape. This kind of regular cells was here also observed in *Limnonectes (Bourretia) doriae* and *Limnonectes (Bourretia) pileata*, two terrestrial species. Elongation of digital pad cells in *Amolops*, *Rana (Odorrana)*, and *Rana (Amnirana)* might be in relationship with their mode of life. The presence of elongated cells in *Rana (Hylarana)* and in *Rana (Sylvirana)* might indicate

phylogenetic relationship to *Amolops*. The heterogeneous cells in some of these species might indicate a regression in comparison to the elongated cells with projections in *Amolops*. The functional analysis of cell morphology underlines this interpretation.

The major sticking force of tree frogs is surface tension (Emerson and Diehl, 1980; Green, 1981). It is a kind of wet adhesion, where two surfaces are held together by an interlaying liquid. The prismatic cells, the channels and the mucous glands are required in the humidification mechanism necessary for sticking. For torrent-living frogs the surfaces to stick to are already humid or in a liquid medium. In liquid the force is no more proportional to the surface, but to the squared surface which reduces the sticking force to its square root (Emerson and Diehl, 1980). When sticking to glass at an angle of 90 to 180°, a treefrog is immersed in water, it will separate almost immediately (Emerson and Diehl, 1980). The force of attachment in liquid medium is inversely proportional to the distance of the two surfaces, separated by the liquid.

To provide a good sticking in water, the surface of the pads should be enlarged. Some of the species of *Amolops*, as *Amolops formosus* or *Amolops marmoratus* have in fact very much enlarged digital pads (Table 2). A correlation between the digital pad development, as defined by the groups A, B, C, D and E (see Table 2), and the ecology of the species may be found. The terrestrial species and the aquatic frogs belong to the group A. The group B includes ground/vegetation-living frogs. The torrent-living frogs are distributed in three groups: C (*Odorrana*, *Amnirana* and *Huia*), D (*Amolops*, *Ingerana*), E (*Amolops formosus* and *Amolops marmoratus*). The treefrogs (*Rhacophorus*, *Hyperolius*) are all members of the group D, thus not the species with the largest digital pads.

Elimination of the distance between the pad and the surface to stick to will increase attachment force equally and more distinctly. In treefrogs the regular cells guide the fluids in all directions, thus humidifying the whole pad in a regular manner and optimizing the

use of liquid (Fig. 14). The elongated cells of *Amolops* guide the liquid in the disto-proximal direction. The digital pad is not closed posteriorly and often also anteriorly by a groove, and prismatic cells are not restricted to the pad surface, but are also present in the groove and outside to it. Water can flow out of the pad and distance from pad to sticking surface is minimized, thus increasing the sticking force inversely.

It would be interesting to compare the cell morphology of torrent-living frogs of other anuran families, like *Ansonia* (Bufonidae), *Petropedetes* (Phrynobatrachidae), some *Litoria* and *Hyla* (Hylidae) and *Heleophryne* (Heleophrynidae) to what is here described in Raninae. A more detailed morphological analysis of surface of digital pads should be undertaken to compare sticking surface in tree and torrent-living frogs.

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Literature Cited

- BOULENGER, G. A. 1882. Catalogue of the Batrachia Salientia s.Ecaudata in the collection of the British Museum. London, Taylor and Francis: i-xvi + 1-503, pl. I-XXX.
- BOULENGER, G. A. 1920. A monograph of the South Asian, Papuan, Melanesian, and Australian frogs of the genus *Rana*. Rec. Indian Mus. 20:1-126.
- CLARKE, B. T. 1981. Comparative osteology and evolutionary relationship in the African Raninae (Anura Ranidae). Monit. zool. ital. (n. s.) 15 suppl.:285-331.
- DECKERT, K. 1938. Beiträge zur Osteologie und Systematik ranider Froschlurche. Sber. Ges. naturf. Freunde Berl. 1938:127-184.

- DUBOIS, A. 1987. Miscellanea taxinomica batrachologica (I). *Alytes* 5:7-95.
- DUBOIS, A. 1992. Notes sur la classification des Ranidae (Amphibiens Anoures). *Bull. mens. Soc. linn. Lyon* 61:305-352.
- EMERSON, S. B. AND D BERRIGAN. 1993. Systematics of southeast Asian ranids: multiple origins of voicelessness in the subgenus *Limnonectes* (Fitzinger). *Herpetologica* 49:22-31.
- EMERSON, S. B. AND D DIEHL. 1980. Toe pad morphology and mechanisms of sticking in frogs. *Biol. J. Linn. Soc.* 13:199-216
- ERNST, V. V. 1973 a. The digital pads of the treefrog *Hyla cinerea*. I. The epidermis. *Tissue Cell* 5:83-96.
- ERNST, V. V. 1973 b. The digital pads of the treefrog *Hyla cinerea*. II. The mucous glands. *Tissue Cell* 5:97-104.
- FROST, D. R. (ed.) 1985. Amphibian species of the world. Lawrence, Allen Press and Assoc. Syst. Coll.: (i- iv) + i - v + 1 - 732.
- GREEN, D. M. 1979. Treefrog toe pads: comparative surface morphology using scanning electron microscopy. *Canadian J. Zool.* 57:2033-2046.
- GREEN, D. M. 1980. Size differences in adhesive toe-pad cells of treefrogs of the diploid-polyploid *Hyla versicolor* complex. *J. Herpet.* 14:15-19.
- GREEN, D. M. 1981. Adhesion and the toe-pads of treefrogs. *Copeia* 1981:790 - 796.
- GREEN, D. M. AND J. CARSON. 1988. The adhesion of treefrog toe-pads to glass: cryogenic examination of a capillary adhesion system. *Austr. J. nat. Hist.* 22:131-135.
- GREEN, D. M. AND M. P. SIMON. 1986. Digital microstructure in ecologically diverse sympatric microhylid frogs, genera *Cophixalus* and *Sphenophryne* (Amphibia: Anura), from Papua New Guinea. *Austr. J. Zoo.* 34:135-145.
- HILLIS, D. M. 1985. *Evolutionary genetics and systematics of New World frogs of the genus Rana: an analysis of ribosomal DNA, allozymes, and morphology*. Thesis, The University of Kansas. i-vi + 1-304.
- KOMNICK, H. AND W. STOCKEM. 1969. Oberfläche und Verankerung des Stratum corneum an mechanisch stark beanspruchten Körperstellen beim Grasfrosch. *Cytobiologie* 1:1-16.
- LIEM, S. S. 1970. The morphology, systematics, and evolution of the Old World treefrogs (Rhacophoridae and Hyperoliidae). *Fieldiana: Zool.* 57: i-vii + 1-145.
- LYNCH, J. D. 1979. A new genus for *Elosia duidensis* Rivero (Amphibia, Leptodactylidae) from Southern Venezuela. *Amer. Mus. Novit.* 2680:1-8.
- MCALLISTER, W. AND A. CHANNING. 1983. Comparison of toe-pads of some southern African climbing frogs. *S. Afr. J. Zool.* 18:110-114.
- NOBLE, G. K. AND M. E. JAECKLE. 1928. The digital pads of the tree frogs. A study of the phylogenesis of an adaptive structure. *J. Morphol. Physiol.* 45:259-292.
- OHLER, A. AND A. DUBOIS. 1989. Démonstration de l'origine indépendante des ventouses digitales dans deux lignées phylogénétiques de Ranidae (Amphibiens, Anoures). *C. r. Acad. Sci. Paris* 309 (3):419-422.
- RICHARDS, C. M., B. M. CARLSON, T. G. NONNELLY, S. L. ROGERS AND E. ASHCROFT. 1977. A scanning electron microscopic study of differentiation of the digital pad in the Kenyan reed frog *Hyperolius viridiflavus ferniquei*. *J. Morphol.* 153:387-396.
- SAVAGE, J. M. 1987. Systematics and distribution of the Mexican and central American rainfrogs of the *Eleutherodactylus gollmeri* group (Amphibia: Leptodactylidae). *Fieldiana: Zool. (n. s)* 33:i-iv + 1-57.
- SCHUBERG, A. 1895. Über den Bau und die Funktion der Haftapparate des Laubfrosches. *Arb. zool. zootom. Inst. Würzburg* 10:57-118.
- SIEDLECKI, M. 1910. Die Haftballen des javanischen Flugfrosches (*Polypedates reinwardtii*). *Bull. Anat. Rec.* 185:253-257.
- TYLER, M. J. AND C. A. MILLER. 1985. Surface architecture of the dorsal epidermis in Australian frogs. *Trans. Roy. Soc. South Austr.* 109 (2):45-48.
- WELSCH, U., V. F. STORCH, AND W. FUCHS. 1974. The fine structure of the digital pads of rhacophorid treefrogs. *Cell Tissue Res.* 148:407-416.

APPENDIX I

Specimens studied by scanning electronmicroscopy (origin and reference in the catalogue of the Muséum national d'Histoire naturelle of Paris).

Species studied	Origin	Collection Number
<i>Amolops (Amolops) formosus</i>	Namdu Khola, Nepal	MNHN 1994.5559
<i>Amolops (Amolops) marmoratus</i> ¹	Timal, Nepal	MNHN 1988.2787
<i>Amolops (Amolops) sp. 1</i>	Khao Chong, Thailand	MNHN 1987.2163
<i>Amolops (Amolops) sp. 2</i>	Doi Inthanon, Thailand	MNHN 1987.2082
<i>Amolops (Amolops) sp. 3</i>	Phu Kradung, Thailand	MNHN 1987.2140
<i>Amolops (Huia) kinabaluensis</i>	Kina Balu, Borneo	MNHN 1889.240
<i>Amolops (Huia) nasicus</i>	Hanoi region, Vietnam	MNHN 1938.70
<i>Batrachylodes vertebralis</i>	Bougainville, Solomon Islands	MNHN 1970.1407
<i>Rana (Amnirana) albolabris</i>	Liberia	MNHN 1989.3456
<i>Rana (Amnirana) lepus</i>	Central African Republic	MNHN 1968.247
<i>Rana (Chalcorana) chalconota</i>	Khao Chong, Thailand	MNHN 1987.3490
<i>Rana (Hydrophylax) galamensis</i>	"Afrique Orientale Francaise"	MNHN 1920.145
<i>Rana (Hylarana) erythraea</i>	Chiangmai, Thailand	MNHN 1987.3343
<i>Rana (Odorrana) andersoni</i>	Vietnam	MNHN 1938.57
<i>Rana (Sylvirana) sp.</i>	Doi Pui, Thailand	MNHN 1987.3471
<i>Ingerana tasanæ</i>	Khao Phra Tiu, Thailand	MNHN 1987.2002
<i>Limnonectes (Limnonectes) kuhlii</i>	Phu Kradung, Thailand	MNHN 1987.3332
<i>Limnonectes (Bourretia) doriae</i>	Khao Chong, Thailand	MNHN 1987.3130
<i>Limnonectes (Bourretia) pileatus</i>	Phu Kradung, Thailand	MNHN 1987.3140
<i>Phrynoglossus laevis</i>	Khao Chong, Thailand	MNHN 1987.2944
<i>Platymantis corrugatus</i>	New Guinea	MNHN 1989.3461
<i>Rhacophorus leucomystax</i>	Khao Chong, Thailand	MNHN 1987.3544
<i>Hyperolius viridiflavus karissimbiensis</i>	Gihirwa river, Rwanda	MNHN 1988.1055
<i>Indirana gundia</i>	Gundia, India	MNHN 1985.607

1. Formerly *Amolops afghanus*: see Dubois (1992: 340).



Ohler, Annemarie. 1995. "Digital Pad Morphology in Torrent-living Ranid Frogs." *Asiatic herpetological research* 6, 85–96.

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