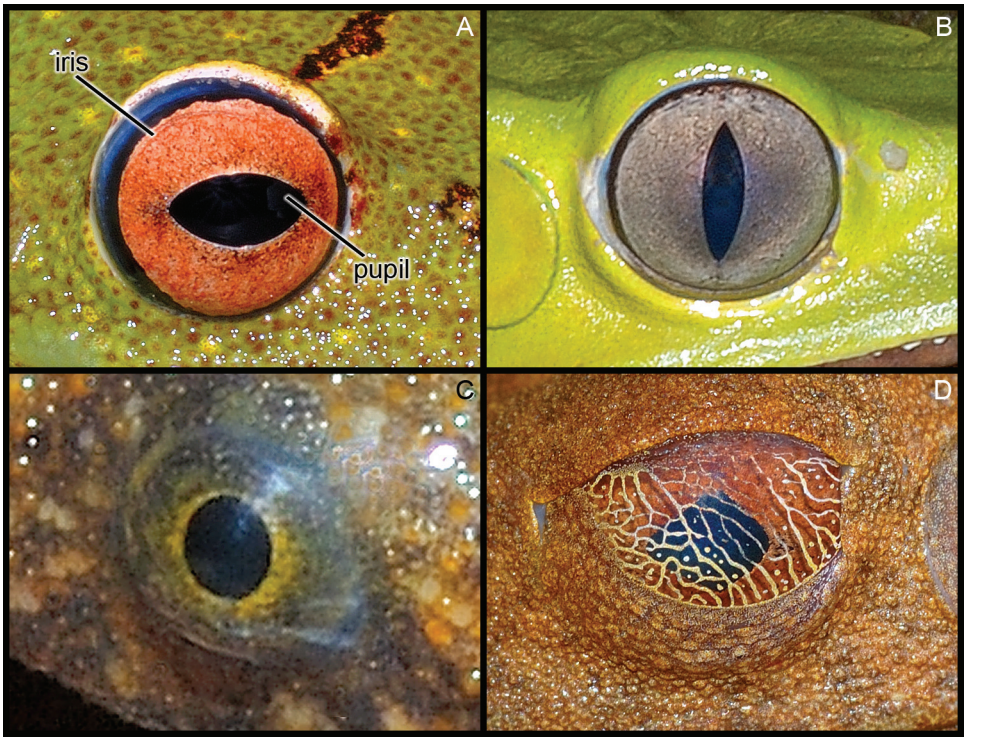

Fig. 42. Shape of pupils and palpebral membrane in anurans. A. Pupil horizontally elliptical (*Hypsiboas cinerascens*, Hylidae); B. Pupil vertically elliptical (*Phyllomedusa bicolor*, Hylidae); C. Pupil circular (*Pipa arrabali*, Pipidae); D. Palpebral membrane with pigmented reticulation (*Hypsiboas geographicus*, Hylidae). (Photos by P. J. R. Kok).

Condition of tympanum

Tympanum may be externally distinct or not, and tympanum condition is sometimes described as: prominent (very distinct with tympanic annulus prominently ringing the well visible tympanum), distinct (tympanum well visible, but tympanic annulus less visible), indistinct (tympanic annulus not visible, upper tympanum barely visible), very indistinct (tympanic annulus not visible, most tympanum barely visible) or absent (no tympanic annulus and tympanum visible). Most of the time the tympanum is described as distinct (Fig. 43A), indistinct (Fig. 43B) or absent (Fig. 43C). Note that this character is prone to post-mortem and preservation artefact.

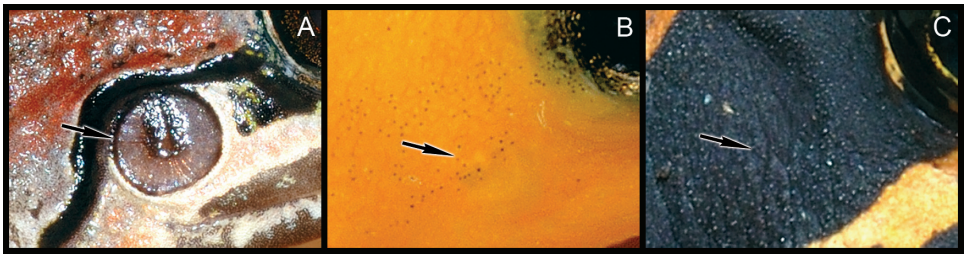

Fig. 43. Condition of tympanum in anurans (eye is in the right upper corner). A. Distinct (*Leptodactylus longirostris*, Leptodactylidae); B. Indistinct (*Anomaloglossus beebei*, Aromobatidae); C. Absent (*Atelopus hoogmoedi*, Bufonidae). (Photos by P. J. R. Kok).

Texture of skin

Texture of dorsal skin is of considerable taxonomic importance. Skin texture is very variable in anurans and can mostly be described as:

- **Smooth**: free from projections (Fig. 44A).
- **Shagreened**: rough to the touch, covered with numerous very small close-set tubercles (Fig. 44B).
- **Granular**: bearing small, rounded, relatively flat grains of approximate equal size (granules) (Fig. 44C).
- **Tuberculate**: bearing rounded bumps of various sizes (tubercles) with no keratinized tip (Fig. 44D).
- **Spiculate**: bearing small pointed tubercles, often with keratinized tip (Fig. 44E).
- **Warty**: bearing protuberances of various sizes, often with keratinized tip (Fig. 44F).
- **Areolate**: skin covered with circular, closely-set, barely elevated protuberances (Fig. 44G); a condition most often found on the flanks or the venter.

There is some variation among these textures, and adverbs like weakly, finely, coarsely, thickly, etc. are often used to refine the description of the skin.

Some species exhibit a combination of skin textures (the dorsum may be shagreened anteriorly and granular posteriorly like in some *Anomaloglossus* for example, Fig. 44H).

Note that skin texture is prone to post-mortem and preservation artefact and may be difficult to appreciate on preserved specimens.

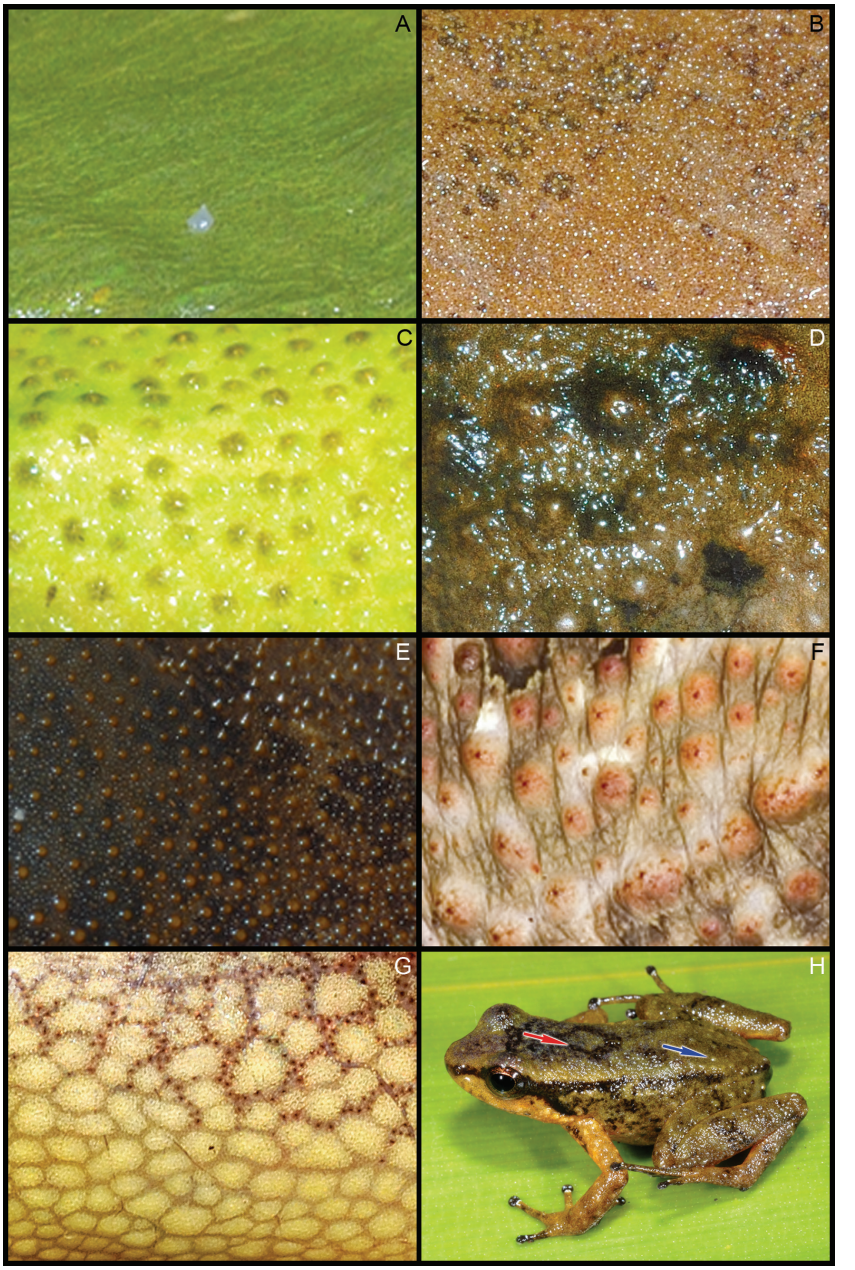

Fig. 44. Principal skin textures in anurans. A. Smooth (*Phyllomedusa bicolor*, Hylidae); B. Shagreened (*Hypsiboas calcaratus*, Hylidae); C. Granular (*Hypsiboas liliae*, Hylidae); D. Tubercular (*Leptodactylus petersii*, Leptodactylidae); E. Spiculate (*Pipa arrabali*, Pipidae); F. Warty (*Rhinella marina*, Bufonidae); G. Areolate (flanks of *Osteocephalus leprieurii*, Hylidae); H. Combination of skin textures in *Anomaloglossus* cf. *roraima* (Aromobatidae), a species that does not occur in KNP (red arrow shows shagreened skin on anterior dorsum, blue arrow shows granular skin on posterior dorsum). (Photos by P. J. R. Kok).

Presence or absence of an axillary membrane

The axillary membrane is a skin membrane that may occur at the posterior insertion of the upper arm (= axilla or armpit) (Fig. 45). It is characteristics of some species and may be more or less developed.

Fig. 45. Axillary membrane in anurans. A. Absent (*Osteocephalus leprieurii*, Hylidae); B. Present (*Dendropsophus marmoratus*, Hylidae). (Photos by P. J. R. Kok).

Presence or absence of dermal folds and fringes

A number of variously visible folds in the skin may occur on the anuran body and limbs: dorsolateral fold, middorsal fold, lateral fold, supratympanic fold, ulnar fold, tarsal fringe, etc. (see Fig. 46 for location of the principal fringes and folds). Folds may be interrupted or not and more or less elevated. A relatively developed ventral discoidal disc (thickening of ventral integument) may be visible in some species.

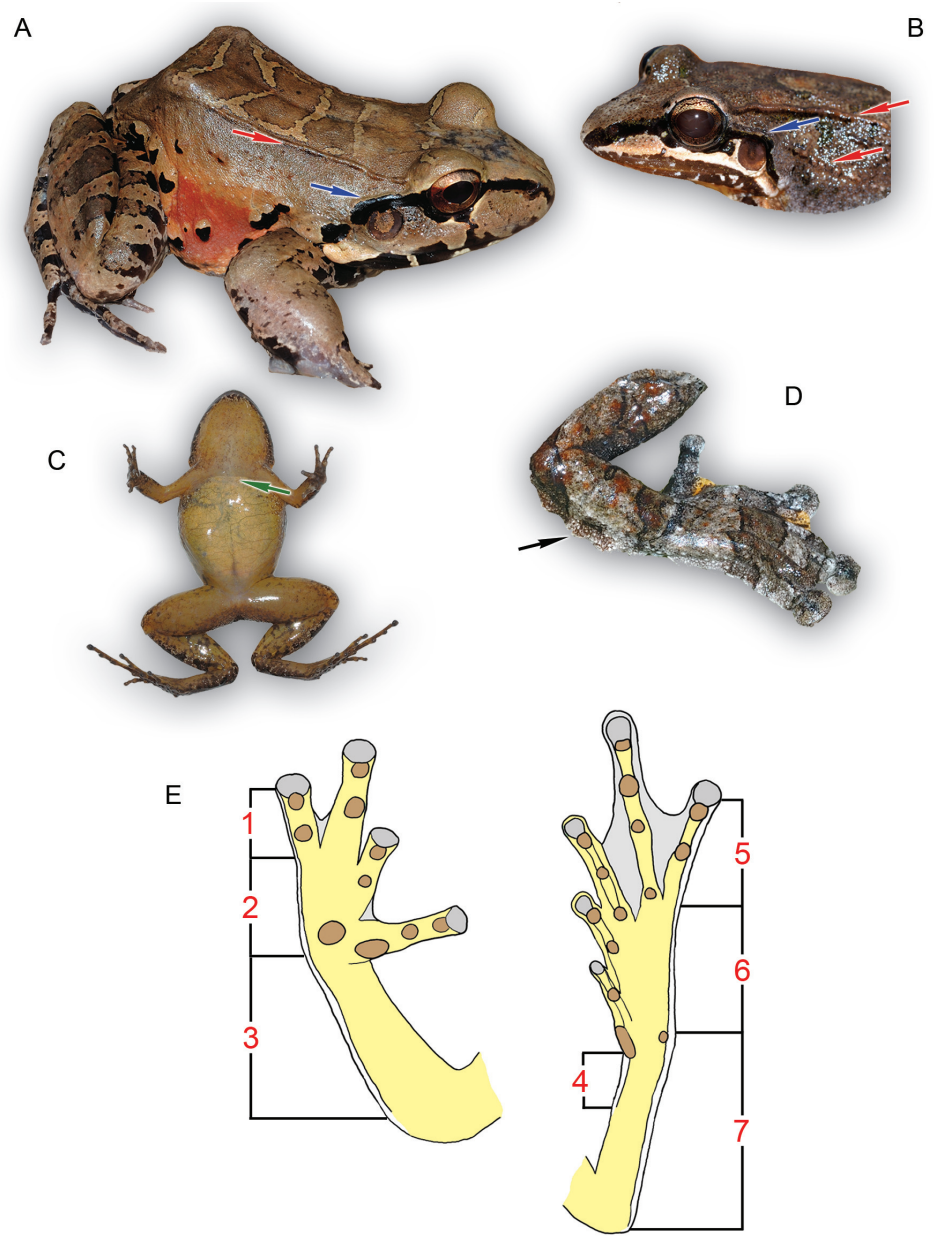

Fig. 46. Principal fringes and folds in anurans. A. Dorsolateral fold (red arrow) and supratympanic fold (blue arrow) in *Leptodactylus knudseni*, Leptodactylidae; B. Supratympanic fold (blue arrow) and dorsolateral and lateral folds (red arrows) in *Leptodactylus longirostris*, Leptodactylidae; C. Pectoral (= thoracic) fold (green arrow) in *Leptodactylus lutzi*, Leptodactylidae; D. Ulnar fold (black arrow) in *Dendropsophus marmoratus*, Hylidae; E. Fringes and folds on arm and leg: (1) fringe on postaxial edge of Finger IV, (2) metacarpal fold, (3) ulnar fold, (4) tarsal fringe, (5) fringe on postaxial edge of Toe V, (6) metatarsal fold, (7) tarsal fold. (Photos A-D by P. J. R. Kok; E modified from Kok & Castroviejo-Fisher, 2008).

Presence or absence of glands

Parotoid glands and other small glands may be visible on the skin (Fig. 47); some of them produce toxins (*e.g.* parotoid glands), others are used in defensive postures (*e.g.* inguinal glands).

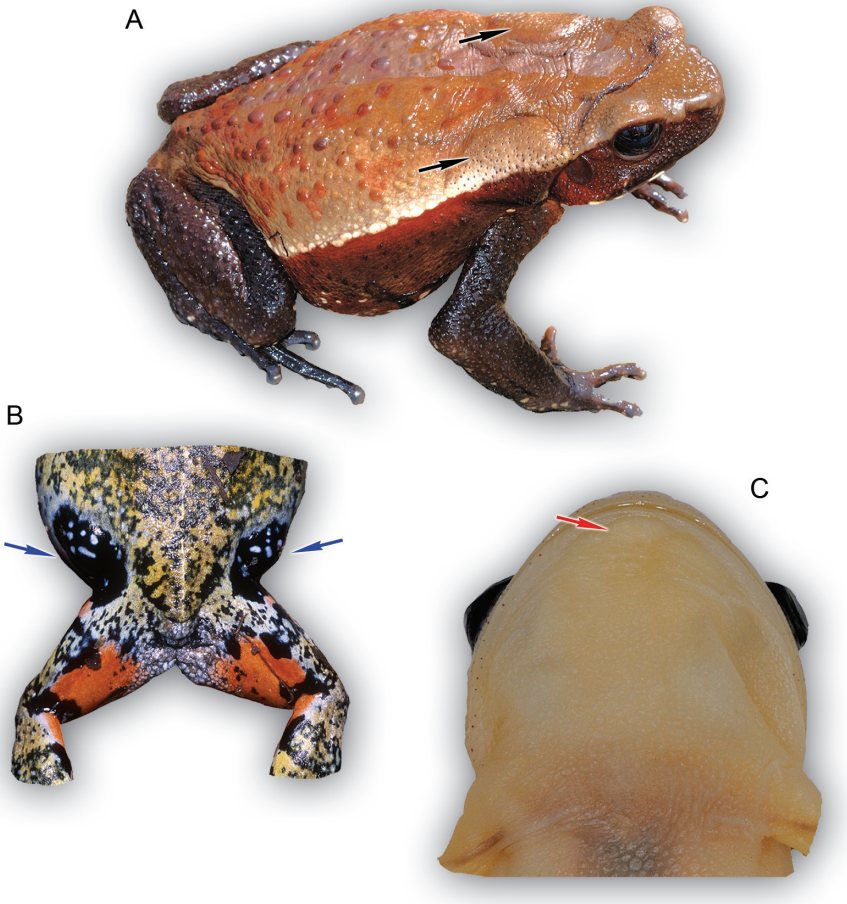

Fig. 47. Some glands found in anurans. A. Parotoid glands (black arrows) in *Rhaebo guttatus*, Bufonidae; B. Inguinal glands (blue arrows) in *Pleurodema brachyops*, Leiuperidae (note: this species does not occur in KNP); C. Mental gland (red arrow) in *Hypsiboas cinerascens*, Hylidae. (Photos by P. J. R. Kok).

Palmar structures

Figure 48 shows main palmar structures, which involve various tubercles, fringes, folds (see also Fig. 46), and the presence or absence of a visible prepollical spine. See Fabrezi (2001) for prepollex and prehallux variation in anuran limbs.

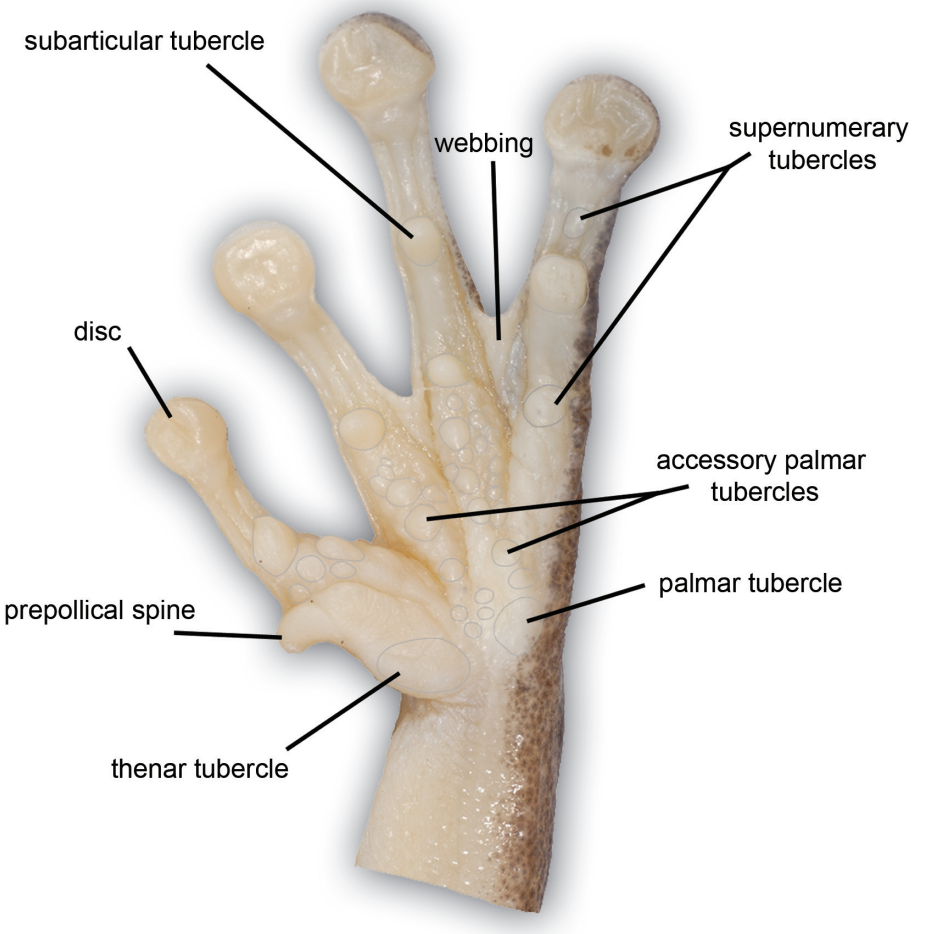

Fig. 48. Palmar structures in anurans. (Photo by P. J. R. Kok).

Degrees of webbing on hand and foot

Similar species may be distinguished by the amount of finger and/or toe webbing they possess. Although some authors (see Edwards, 1974; La Marca, 1997) proposed different terminologies, the most widely used system for webbing formula follows Savage & Heyer (1967), with modifications proposed by Myers & Duellman (1982) and Savage & Heyer (1997). Recently, Guayasamin *et al*. (2006) slightly refined the system for centrolenid frogs.

The degree of webbing is described in enumerating phalanges (including metacarpals and metatarsals) that are free of webbing. Each finger and toe is represented by a Roman numeral and the number of phalanges completely or partially free of webbing by an Arabic numeral (Fig. 49). A notation of "0" indicates that the web extends to the disc, while "1" indicates that the web extends to the intercalary tubercle (distal, just below the disc). A "+" indicates that the web reaches the proximal margin of the structure (tubercle or disc), a "-" indicates that the web reaches the distal margin of the structure, and no superscript means that the web reaches the middle of the structure. Fractions are used when the web does not reach a structure, but only a point between two structures: for example "1/2" when half of the phalanx is free of webbing, "1/3" when the distal one-third of the phalanx is free of webbing, "2/3" when the distal two-thirds of the phalanx are free of webbing, etc.

Note that webbing may be somewhat variable intraspecifically and that females may have slightly more webbing than males.

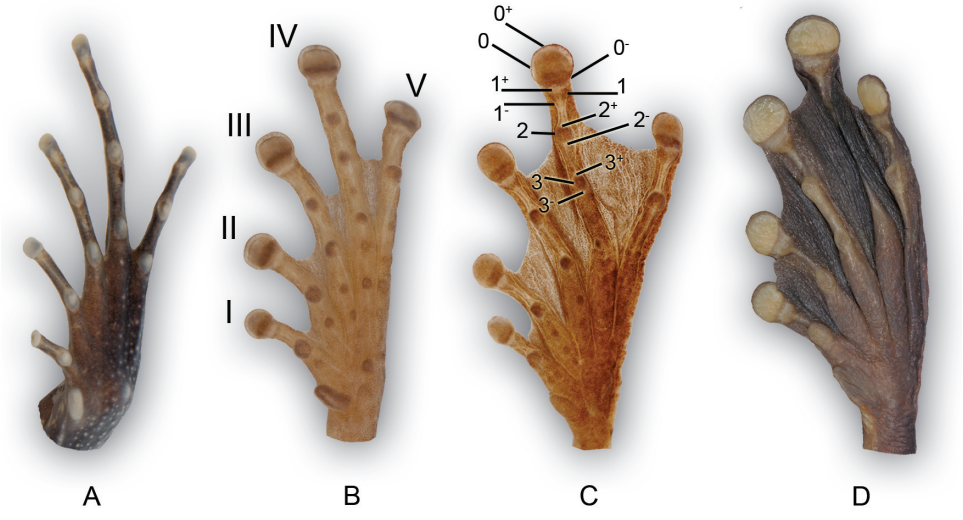

Fig. 49. Degrees of webbing in anurans. A. Unwebbed; B. Basally webbed; C. Half-webbed; D. Fully webbed. (Photos by P. J. R. Kok).

Plantar structures

Figure 50 shows main plantar structures, which involve various tubercles, fringes, and folds (see also Fig. 46).

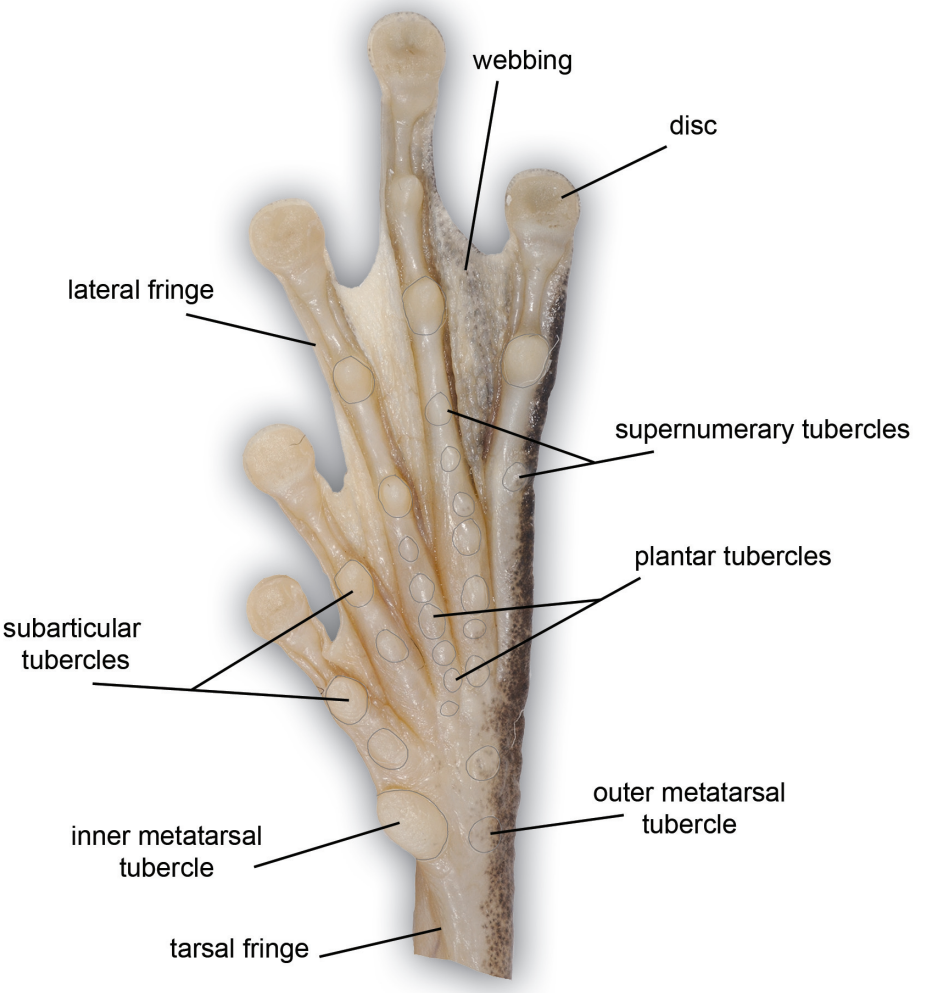

Fig. 50. Plantar structures in anurans. (Photo by P. J. R. Kok).

Structure of digital discs and subarticular tubercles

Variation in external digital features is of taxonomic importance. Digital disc structure is very variable (and not related to the shape of the distal phalanx); figure 51 shows some common shapes (see Savage, 1987 for additional digital disc character states).

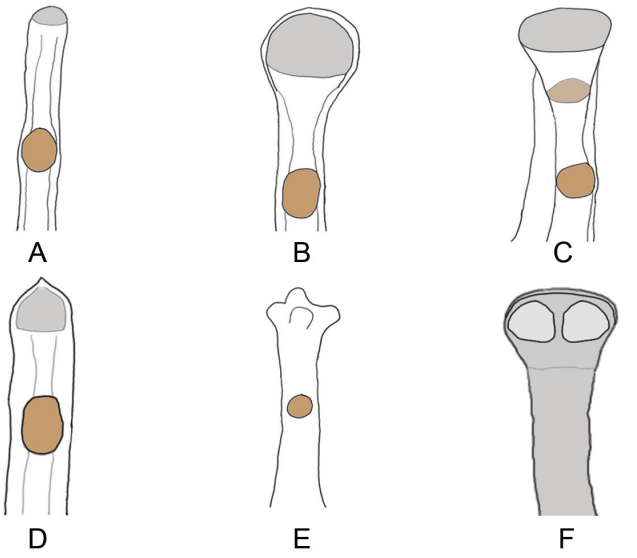

Fig. 51. Diagrammatic views of main structures of digital disc and tip of digit in anurans. A. Disc unexpanded *(e.g.* in *Leptodactylus petersii*, Leptodactylidae); B. Disc expanded, broadened (*e.g.* in *Hypsiboas liliae*, Hylidae); C. Disc expanded, truncate (*e.g.* in *Allophryne* and some glass frogs); D. Disc not, or slightly, expanded with pointed tip (*e.g.* in *Adelophryne gutturosa*, Eleutherodactylidae); E. No terminal disc, but four minutes lobes (*e.g.* in *Pipa arrabali*, Pipidae); F. Dorsal surface of finger disc with two scutelike flaps (*e.g.* in *Anomaloglossus*, Aromobatidae).

Presence/absence and structure of the distal subarticular tubercle on the fourth finger is also variable and helpful for identification (Fig. 52).

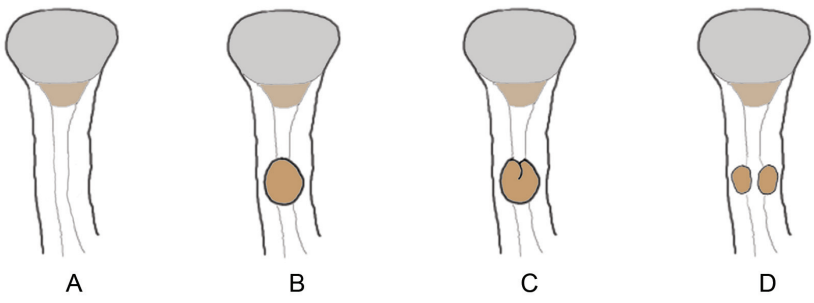

Fig. 52. Diagrammatic views of structures of distal subarticular tubercle on Finger IV. A. Absent; B. Single; C. Bifid; D. Divided. Modified from Duellman, 1970.

Buccal structures: condition of odontophores, and shape of tongue

Maxillary teeth (= teeth that are on the maxilla) may be absent (*e.g.* in Allophrynidae and Bufonidae) or present, in which case they may have various shapes that are characteristic and helpful for identification.

The absence or presence of odontophores (= the portion of the vomer bearing the vomerine teeth) and their shape and position is also of taxonomic importance (Fig. 53). The number of vomerine teeth is usually related to the age of the frog and juveniles may lack vomerine teeth or have only a few while adults of the same taxon may have very distinct odontophores bearing numerous teeth.

Shape of choanae (singular choana) and interchoanal distance is also considered of taxonomic importance in some genera, but this character may be intraspecifically variable.

Shape of vocal slits is variable with taxa and may also help for identification (see below “Condition of vocal sacs”).

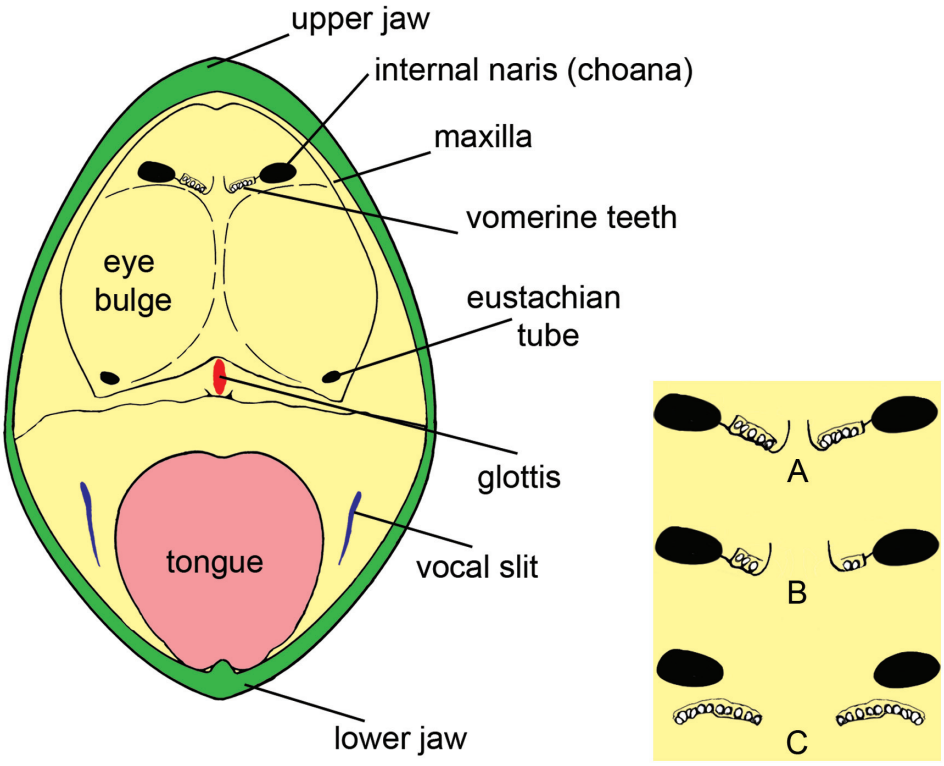

Fig. 53. Generalized diagrammatic view of anuran buccal cavity showing principal structures and some conditions of odontophores. A. Odontophores oblique and barely separated, between choanae. B. Odontophores oblique and widely separated, between choanae. C. Odontophores arched and widely separated, below choanae. Modified from Duellman & Trueb, 1986.

Shape of tongue is also variable with taxa and is of some taxonomic importance. Figure 54 shows the principal shapes of tongue in anurans. Note that this character is prone to post-mortem and preservation artefact.

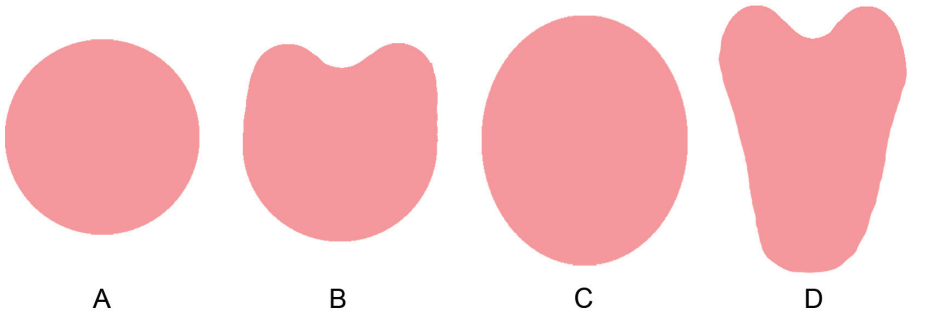

Fig. 54. Diagrammatic views of principal shapes of tongue in anurans. A. Round; B. Cordiform; C. Ovoid; D. Lanceolate. Modified from Duellman, 1970.

Morphometrics

Morphometric comparisons, including comparison of relative length of fingers (*e.g.* relative length of Finger I versus Finger II, or relative length of Toe III versus Toe V), and relative position of various structures (*e.g.* the relative position between the tip of Finger II and the distal subarticular of Finger III when Finger II and III are adpressed together, or the relative position between the tibiotarsal articulation and the tip of snout when hindlimb is adpressed along the body) are helpful to distinguish similar species.

The use of statistics and comparison of measurement ratios are also invaluable in many cases.

It is thus mandatory to take a number of measurements in order to compare species' morphometry. Principal landmarks are indicated in figure 55 and are defined below:

- **Snout-vent length** (SVL): from the tip of the snout to the posterior margin of the vent.
- **Head length**: from the posterior edge of the jaw (sometimes from the posterior edge of the tympanum) to the tip of the snout.
- **Head width**: the greatest width of the head, usually at the level of the anterior edges of the tympani, sometimes at the level of the angle of jaws.
- **Eye-naris distance**: from the posterior edge of the naris to the anterior edge of the eye.
- **Eye length** (= diameter): the greatest length of the orbit from the anterior margin to the posterior margin of the eye.
- **Tympanum length** (= diameter): the greatest length of the tympanum from the anterior margin to the posterior margin of the tympanum.

- **Eyelid width**: the greatest transverse width of the upper eyelid.
- **Interorbital distance** (IOD): the distance between the median margins of the orbits.
- **Internarial distance** (IND): the distance between the median margins of the nares.
- **Snout length**: from the anterior margin of the eye to the tip of the snout.
- **Hand length**: from the proximal edge of the palmar tubercle to the tip of Finger III.
- **Upper arm length**: from the margin of the body insertion to the tip of the elbow.
- **Forearm length**: from the tip of the elbow to the proximal edge of the palmar tubercle.
- **Thigh length**: from the vent to the outer edge of the flexed knee.
- **Shank length**: from the outer edge of the flexed knee to the tip of the heel.
- **Tarsus length**: from the heel to the proximal edge of the inner metatarsal tubercle.
- **Foot length**: from the proximal edge of the inner metatarsal tubercle to the tip of Toe IV.
- **Width of disc** (usually on Finger III and Toe IV): the greatest width of the disc.

Remark: taking precise, comparable, measurements in amphibians is almost impossible due to the soft and flexible nature of preserved amphibians (see Hayek *et al*., 2001). The value of the measurements used in morphometric studies is also closely related to the quality of the preservation of the specimens and the training level of the observer. Hayek *et al*. (2001) pointed out that intra- and interobserver differences in measuring specimens are recurrent and can lead to statistically significant differences in the variables, which may result in different biological interpretations. They suggested several recommendations to use in frog morphometric studies (*e.g.* remeasure at least one individual 20 times for estimation of measurement error) and we encourage the reader to refer to that publication.

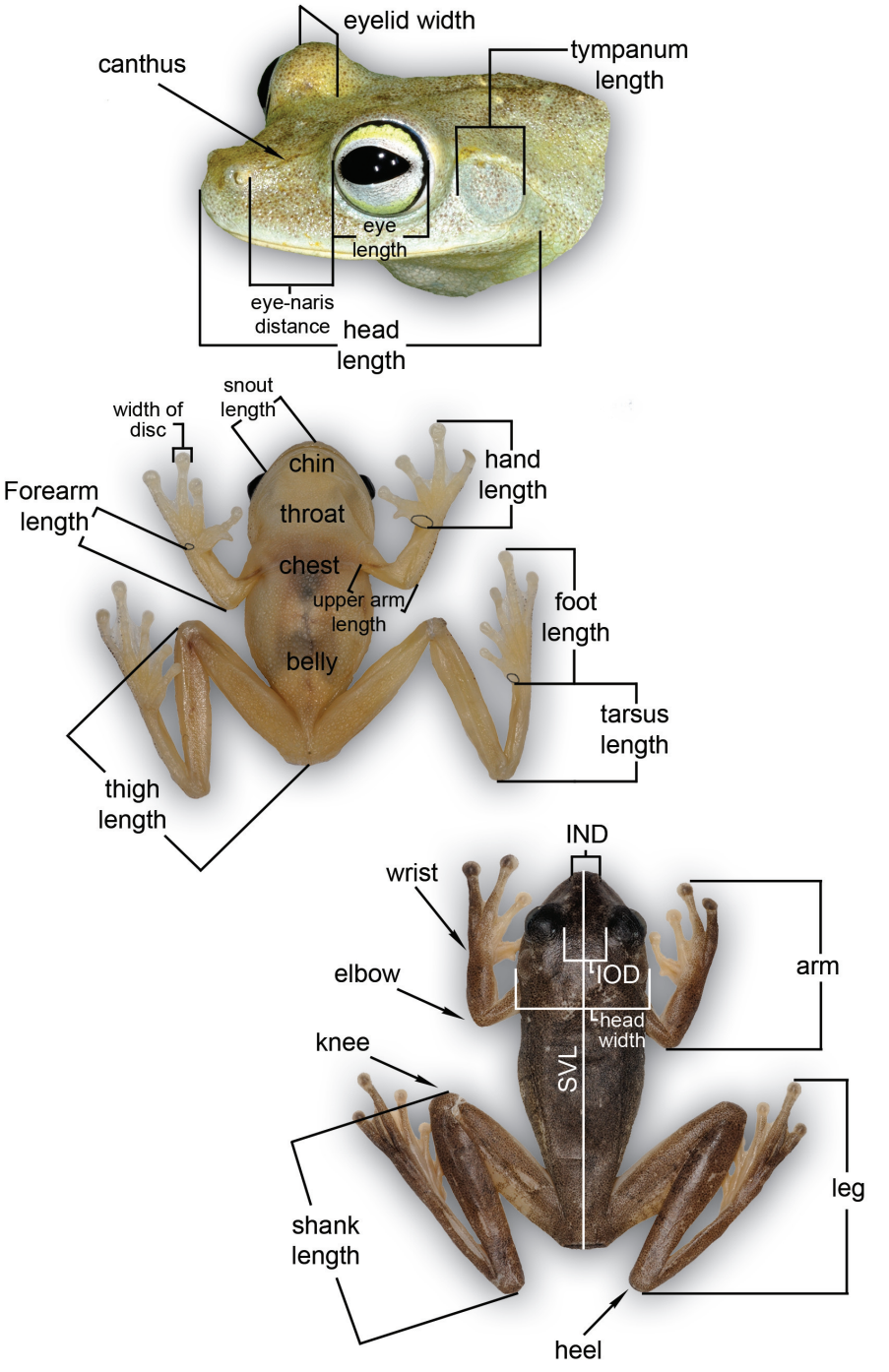

Fig. 55. Main terms and landmarks in anurans. Abbreviations are explained in the text. (Photos by P. J. R. Kok).

The following external morphological diagnostic features are secondary sexual characters found only in males:

Condition of vocal sacs

The vocal sac(s) communicates with the buccal cavity via two small apertures called the vocal slits, which may be round or slitlike and variously elongated (see Fig. 53). The skin covering the external vocal sac is usually modified and it is possible to discern some dermal lobes or folds. In some species males lack an external vocal sac, in this case the skin covering is totally unmodified. Some species completely lack vocal sac and vocal slits (*e.g. Stefania* spp., Hemiphractidae). Vocal sacs may be subgular (single, bilobate, or paired) or lateral (paired) (Fig. 56).

The pulsating sac may increase the attractiveness of advertisement calls in some species (see Rosenthal *et al.*, 2004).

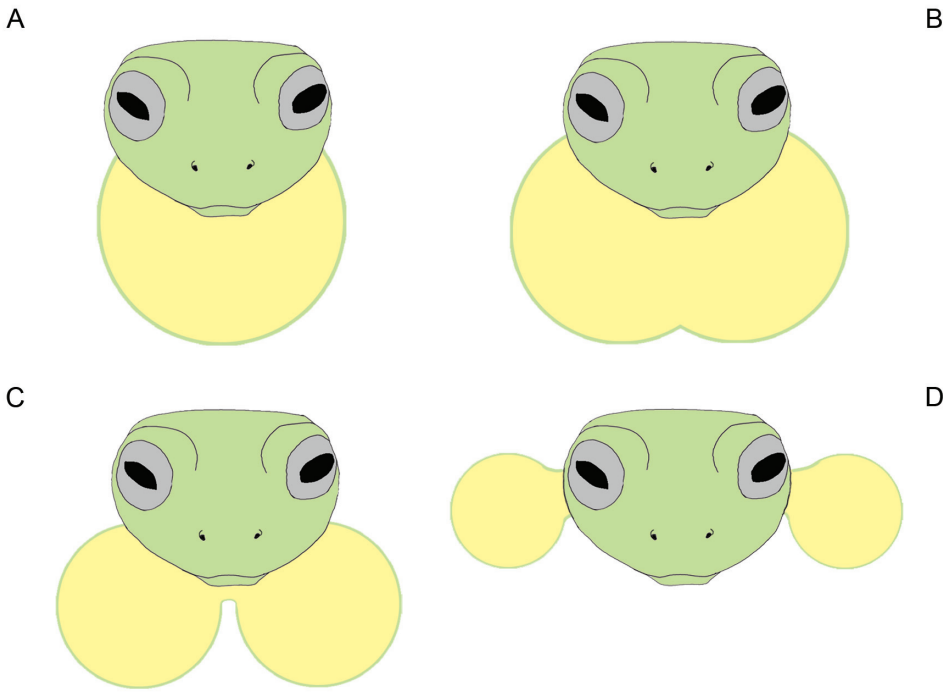

Fig. 56. Diagrammatic views of main types of vocal sacs in anurans. A. Single, median, subgular; B. Bilobate subgular; C. Paired subgular; D. Paired, lateral. Modified from Duellman, 1970.

Presence or absence of humeral spine

The humeral spine is the ventrolateral extension of the *crista ventralis* (a prominent ridge in the humerus) and is present only in a few anuran species, most of them belonging to the family Centrolenidae. Its presence or absence is of taxonomic importance and helps, for example, to identify glass frog genera (Fig. 57).

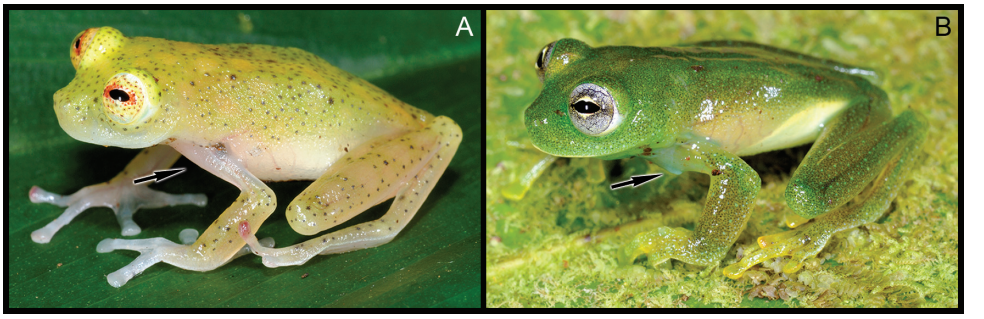

Fig. 57. Humeral spine in anurans. A. Absent (*e.g.* in *Hyalinobatrachium*, here *H. crurifasciatum*); B. Present (*e.g.* in *Centrolene*, here *C. gorzulae*). (Photos by P. J. R. Kok).

Condition of nuptial pads

Nuptial pads are horny or thickened structures of various sizes and shapes usually located on the male's thumb (Fig. 58). Testicular hormones influence their development and they are especially prominent during the breeding season. Condition of nuptial pads is of taxonomic importance and is useful to distinguish species.

Presence or absence of keratinized prepollical spines

Keratinized prepollical spines (= thumb spines, Fig. 58) are nuptial excrescences found in several anuran species. In some species the thumb bears a single developed spine, while in other taxa there may be two developed spines or no spine at all. The presence or absence of spines may help to distinguish similar taxa, although there is some intraspecific variation in this character.

Presence or absence of a fleshy proboscis

In some species males have a shovel-shaped projecting snout probably used to excavate underground nesting chambers (Fig. 58).

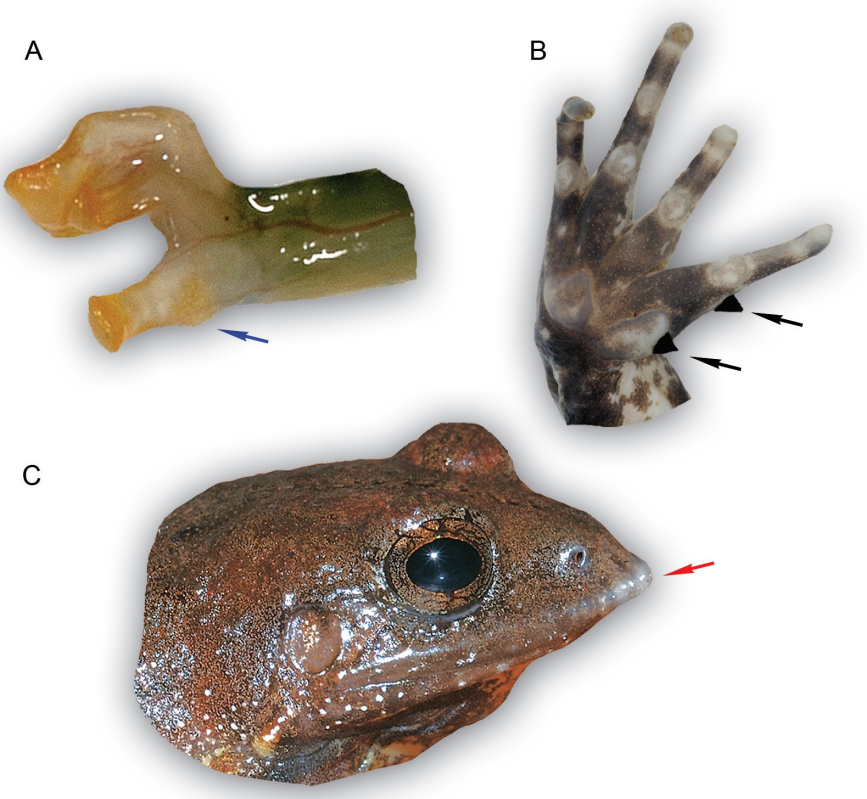

Fig. 58. Some male appendages in anurans. A. Nuptial pad on Finger I (here in *Hyalinobatrachium taylori*, Centrolenidae); B. Keratinized spines on thumb (here in *Leptodactylus petersii*, Leptodactylidae); C. Fleshy proboscis in *Leptodactylus lutzi*, Leptodactylidae. (Photos by P. J. R. Kok).

4.2.2. Field key to the anuran genera of Kaieteur National Park

The only purpose of the following dichotomous key is to help the reader to identify in the field the anurans of Kaieteur National Park to the genus level. It will guide the reader to a specific generic account by reference to a page number. A key to the species is provided in each of the generic accounts.

This key is not infallible and the reader should always verify any identification made by using the key through detailed comparison with the descriptions and illustrations in the species accounts. Do also note that only a few subjective characters are used in the key and that these characters are not sufficient for genus or species identification.

1. Tongue absent, pupil circular (Fig. 42C), no disc on the tip of digits but four small lobes (Fig. 51E), body distinctly flattened . . . . . ***Pipa*** (p. 234)

1'. Not as above **2**

2. Pair of dermal scutelike flaps on dorsal surface of each disc (Fig. 51F) . . . . . ***Anomaloglossus*** (p. 114)

2'. Not as above **3**

3. Fingers lacking expanded terminal discs (Fig. 51A, D) **4**

3'. Fingers with expanded terminal discs (Fig. 51B-C) **9**

4. Parotoid glands present (Fig. 47A) **5**

4'. Parotoid glands absent **6**

5. Parotoid glands ovoid, small to large (Fig. 47A), cranial crests absent or weakly developed . . . . . ***Rhaebo*** (p. 124)

5'. Parotoid glands trianguloid, very large, cranial crests well developed (Fig. 41) . . . . . ***Rhinella*** (p. 130)

6. Terminal disc on digits with pointed tip (Fig. 51D), digits flattened, subdigital pads rather than subarticular tubercles, very small size . . . . . ***Adelophryne*** (p. 148)

6'. Not as above **7**

7. Tympanum distinct (Fig. 43A) . . . . . ***Leptodactylus*** (p. 212)

7'. Tympanum indistinct or absent (Fig. 43B, C) **8**

8. Dorsum black with yellow reticulation, toes webbed . . . . . ***Atelopus*** (p. 120)

8'. Dorsum brown without reticulation, body ovoid, toes unwebbed . . . . . ***Synapturanus*** (p. 230)

9. Pupil vertically elliptical (Fig. 42B), fingers and toes opposable . . . . . ***Phyllomedusa*** (p. 190)

9'. Pupil horizontally elliptical (Fig. 42A), fingers and toes not opposable **10**

10. First finger shorter than second **11**

10'. First finger equal or longer than second **18**

11. Toes no more than basally webbed (Fig. 49A) . . . . . ***Pristimantis*** (p. 238)

11'. Toes at least one-third webbed (Fig. 49B, C, D) **12**

12. Head very small, triangular, terminal disc on digits truncate (Fig. 51C), throat black with white spots . . . . . ***Allophryne*** (p. 110)

12'. Not as above **13**

13. Web between Toes I-II absent or reduced (does not reach the subarticular tubercle of Toe II) and webbing on fingers absent or much reduced (Fig. 49), skin smooth to shagreened (Fig. 44A, B), dorsal ground colour not green **14**

13'. Web between Toes I-II usually extends beyond the subarticular tubercle of Toe II and webbing on fingers usually present (Fig. 49) [except in *Hypsiboas liliae*, in which the dorsal skin is granular (Fig. 44C), and the dorsal ground colour green] **15**

14. Dorsal outline of snout truncate (Fig. 40A), snout not protruding beyond lower jaw, inner metatarsal tubercle projecting . . . . . ***Tepuihyla*** (p. 202)

14'. Dorsal outline of snout rounded (Fig. 40A), snout protruding beyond lower jaw, inner metatarsal tubercle not projecting . . . . . ***Scinax*** (p. 196)

15. Axillary membrane extensive (more than 1/2 upper arm length), orange or yellow with black spots (Fig. 45B) . . . . . ***Dendropsophus*** (p. 158)

15'. Axillary membrane usually absent or indistinct (Fig. 45A), when present (Fig. 45B) small (no more than 1/2 upper arm length), never orange **16**

16. Bones green and skin on dorsum thick and glandular . . . . . ***Trachycephalus*** (p. 206)

16'. Not as above **17**

17. Skin of head fused to skull, males usually with paired vocal sacs (Fig. 56C-D) and dorsal skin distinctly tuberculate or spiculate (Fig. 44D-E) (smooth in females, Fig. 44A) [Except in *O. exophthalmus* and *O. oophagus*] . . . . . ***Osteocephalus*** (p. 178)

17'. Skin of head not fused to skull, males with subgular vocal sac (Fig. 56A), dorsal skin not sexually dimorphic . . . . . ***Hypsiboas*** (p. 162)

18. Venter not transparent, internal organs not visible . . . . . ***Stefania*** (p. 152)

18'. Venter transparent, internal organs visible **19**

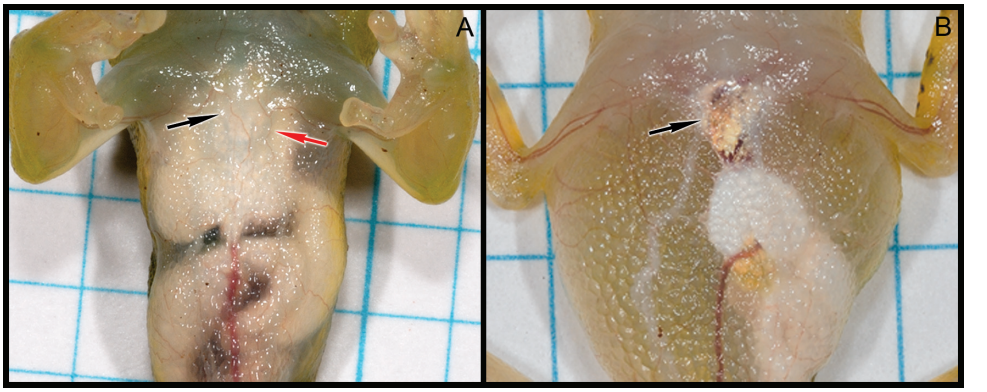

Fig. 59. Condition of the parietal peritoneum in glass frogs (Centrolenidae). A. White (indicated by a red arrow), heart not visible (black arrow) (here in *Cochranella helenae*); B. Transparent, heart visible (indicated by a black arrow) (here in *Hyalinobatrachium crurifasciatum*). (Photos by P. J. R. Kok).

19. Anterior third of parietal peritoneum white, heart not visible (Fig. 59A) . . . . . ***Cochranella*** (p. 138)

19'. Parietal peritoneum transparent, heart at least partially visible (Fig. 59B) **20**

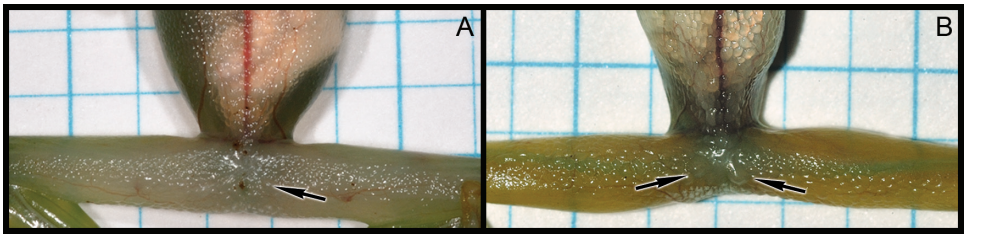

Fig. 60. Ventral view of the area between the legs showing absence/presence of enlarged tubercles below vent in glass frogs (Centrolenidae). A. Absent (here in *Hyalinobatrachium taylori*); B. Present (here in *Centrolene gorzulae*). (Photos by P. J. R. Kok).

20. Distinctly enlarged round tubercles below vent (Fig. 60B), prepollical spine projecting, humeral spine present in adult males (Fig. 57B) . . . . . .***Centrolene*** (p. 134)

20'. No distinctly enlarged round tubercles below vent (Fig. 60A), prepollical spine not projecting, humeral spine absent in adult males (Fig. 57A) . . . . . ***Hyalinobatrachium*** (p. 142)