

Evolutionary Correlates of Microphagy in Alkaloid-Containing Frogs (Amphibia: Anura)

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Abstract Frogs of the genus *Mantella* (Ranidae) are characterized by several derived characters, among them microphagy and presence of skin alkaloids. A comparison with other alkaloid-containing frogs (belonging to the Dendrobatidae, Myobatrachidae and Bufonidae) showed that, beside the alkaloids, these share several of the apomorphies typical for *Mantella*. Since most of the derived characters can be explained by microphagous and myrmecophagous specialization, we postulate the existence of an evolutionary etho-morphological character complex involving microphagy, alkaloid accumulation from ant prey, aposematic colouration, diurnal activity, modification of prey catching behaviour, modification of tongue shape, reduction of teeth, and modification of several osteological skull characters related with the jaw opening mechanism.

The existence of such a complex reduces the value of skin alkaloids and aposematic colouration for the assessment of phylogenetic relationships between *Mantella* and dendrobatids, so that a sister group relationship of these groups is unlikely. We present a flow diagram which gives a possible explanation of a convergent loss of strong mating amplexus and evolution of complex mating behaviour in both groups. Further we discuss the status of the small-sized dendrobatid genus *Minyobates*, whose characteristic alkaloid profile and small size may be correlated with feeding specialization on mites; and we conclude that data support the hypothesis of a small-sized microphagous ancestor of the bufonid clade.

Key words. Ranidae: Mantellinae: *Mantella*, *Mantidactylus*; Dendrobatidae; Myobatrachidae; Bufonidae; myrmecophagy; mating behaviour; phylogeny.

1. INTRODUCTION

Amphibians are known to contain toxic agents of several compound classes in their skin; the main functions of these substances may be defense against predators and/or microorganisms (DALY et al. 1987). Only few groups of anurans are known to contain alkaloid toxins, which are defined as cyclic nitrogen-containing compounds with a limited distribution in nature (DALY et al. 1987). The origin of these amphibian alkaloids has long remained enigmatic; only in the last years it was demonstrated that an uptake system from arthropod prey is responsible for alkaloid accumulation in the skin (DALY et al. 1992, 1994a, 1994b). CALDWELL (1996) indicated for the most prominent alkaloid-containing anurans, the Neotropical poison-dart frogs (Dendrobatidae), that an evolutionary correlation exists between alkaloids and myrmecophagous specialization.

During a phylogenetic study on the Madagascan poison frogs (genus *Mantella*), we noted that they mainly feed

on ants and are characterized by several derived morphological, osteological and ethological character states similar to those found in alkaloid-containing dendrobatids. A priori it could not be excluded that these similarities may be phylogenetically relevant; in fact, several reptile groups (boas, iguanas, podocnemine turtles) occur in Madagascar and the Neotropis but not in Africa nor Asia, indicating that the possibility of Madagascar-South American biogeographical relationships must be considered in phylogenetic analyses (KLUGE 1991; FROST & ETHERIDGE 1989; ERNST & BARBOUR 1989; see also NUSSBAUM & RAXWORTHY 1994).

In the present study we review aspects of morphology, osteology and ethology of alkaloid-containing frogs. We compare the synapomorphies of *Mantella* species to the states found in the other alkaloid-containing anuran genera; our aim is to elucidate whether the states of *Mantella* are independent from each other, or may be functional adaptations originated by the feeding specialization. Further we discuss the implication of our

findings for the phylogeny of the Ranidae (Mantellini), Dendrobatidae, and Bufonidae.

2. MATERIAL AND METHODS

Comparing morphological, osteological and ethological characters, we will make reference to anurans belonging to the following families/subfamilies (geographic distribution and genera considered for the present study in brackets): (1) **Ranidae: Mantellini** (Madagascar; genera *Mantella* Boulenger, 1882 and *Mantidactylus* Boulenger, 1895); (2) **Ranidae: Raninae** (Cosmopolitan; genera *Rana* Linnaeus, 1758 and *Euphyllotis* Fitzinger, 1843); (3) **Ranidae: Rhacophorinae** (Asia, Africa, Madagascar; genera *Boophis* Tschudi, 1838 [Madagascar] and *Rhacophorus* Kuhl & Van Hasselt, 1822 [Asia]); (4) **Hyperoliidae** (Africa and Madagascar; *Heterixalus* Laurent, 1944 [Madagascar]); (5) **Dendrobatidae** (Middle and South America; genera *Allobates* Zimmermann & Zimmermann, 1988, *Epipedobates* Myers, 1987, *Phylllobates* Duméril & Bibron, 1841, *Minyobates* Myers, 1987, *Dendrobates* Wagler, 1830 and *Colostethus* Cope, 1866); (6) **Myobatrachidae** (Australia; genus *Pseudophryne* Fitzinger, 1843); (7) **Bufonidae** (cosmopolitan; genera *Melanophryniscus* Gallardo, 1961 and *Atelopus* Duméril & Bibron, 1841 [S-America], *Bufo* Laurenti, 1768 [cosmopolitan] and *Capensibufo* Grandison, 1980 [Africa]). To abbreviate the accounts, we use the term aposematic dendrobatids for the genera *Allobates*, *Epipedobates*, *Phylllobates*, *Minyobates*, and *Dendrobates*, although the colouration of single species of these genera may in fact not be aposematic. Also we use the generic name *Colostethus* in a

wider sense, including the genera *Colostethus*, *Aromobates* Myers et al. 1991, *Mannophryne* La Marca, 1992, *Nephelobates* La Marca, 1994, and *Hylaxalus* Jimenez de la Espada, 1871 (see MYERS et al. 1991; LA MARCA 1992, 1994).

For osteological examination specimens were skinned and the intestine removed as far as possible. Specimens were stained for bones and cartilage with alizarin red and alcian blue following the method of DINGERKUS & UHLER (1977) with some minor modifications (PLOSCH 1991). The flesh of many *Mantella* and dendrobatid species was dark grey to blackish and did not clear to transparency; a better clearing was achieved in these cases by a high concentration of H_2O_2 in the first clearing steps. Studied specimens are deposited in the Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK) and the Museum National d'Histoire Naturelle, Paris (MNHN). Osteological data refer to 45 *Mantella* specimens (13 species; specimens are being listed in a forthcoming paper on *Mantella* osteology), five species of dendrobatids (*Dendrobates auratus* Girard, 1855, ZFMK 64145; *D. pumilio* Schmidt, 1857, ZFMK 57202; *D. silverstonei* Myers & Daly, 1979, ZFMK 40709; *Epipedobates tricolor* (Boulenger, 1899), ZFMK 32046; *Phylllobates vittatus* (Cope, 1893), ZFMK 32031), one species of *Pseudophryne* (*P. bibroni* Günther, 1858, ZFMK 28159), and one species of *Melanophryniscus* (*M. stelzneri* (Weyenbergh, 1875)), ZFMK 52116). Other morphological data refer to specimens of the ZFMK collection; specimens examined for tongue morphology are listed in Tab. 1.

Table 1. Measurements taken from different frog species. For each specimen the catalogue number in the Zoologisches Forschungsinstitut und Museum Alexander Koenig (ZFMK), Bonn, and the variables snout-vent length (SVL), head width (HW), tongue length (ToL) and tongue width (ToW) are given (all in mm).

ZFMK Species	SVL	HW	ToL	ToW
48046 <i>Mantella viridis</i>	27.0	8.0	4.5	3.0
48047 <i>Mantella viridis</i>	25.0	7.0	4.0	2.0
47009 <i>Mantella baroni</i>	25.0	7.5	4.0	3.0
50161 <i>Mantella baroni</i>	26.5	7.5	4.5	3.0
59820 <i>Mantella bernhardi</i>	21.0	6.5	4.5	3.0
52745 <i>Mantella betsileo</i>	24.0	7.0	4.0	3.0
52749 <i>Mantella laevigata</i>	28.5	8.5	4.5	3.0
52750 <i>Mantella laevigata</i>	26.0	8.0	4.0	3.5
48181 <i>Mantella haraldmeieri</i>	23.5	7.0	4.0	3.0
48182 <i>Mantella haraldmeieri</i>	23.0	7.0	3.0	2.5
59902 <i>Mantella</i> sp.	27.5	8.0	4.5	3.0
59936 <i>Mantidactylus leucomaculatus</i>	40.0	13.0	11.0	6.0
52720 <i>Mantidactylus boulengeri</i>	30.0	10.5	7.0	5.0
52589 <i>Mantidactylus wittei</i>	25.0	8.0	6.0	3.5
57451 <i>Mantidactylus argenteus</i>	27.0	8.0	7.0	4.0
59854 <i>Mantidactylus alutus</i>	25.5	10.0	6.0	4.0
60094 <i>Mantidactylus aerumnalis</i>	30.0	11.0	8.0	6.0
60039 <i>Mantidactylus malagasius</i>	22.0	8.0	4.5	3.0
59876 <i>Mantidactylus malagasius</i>	22.0	7.0	5.0	3.0
25372 <i>Mantidactylus albofrenatus</i>	30.0	10.0	8.0	5.0
25373 <i>Mantidactylus albofrenatus</i>	30.0	9.0	7.0	5.0

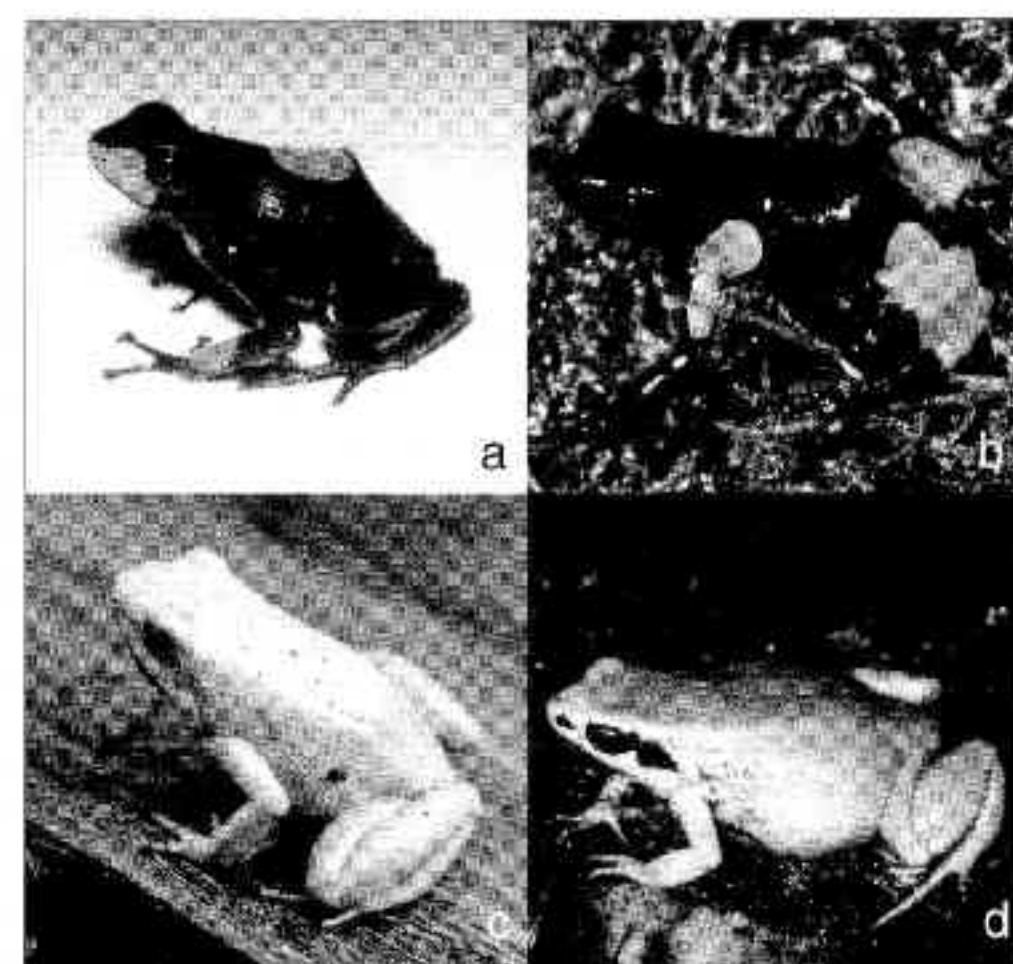


Fig. 1. Pictures of *Dendrobates histrionicus* (a), *Mantella cowani* (b), *Phylllobates terribilis* (c) *Mantella* cf. *crocea* (d), showing the large external similarity of *Mantella* with certain dendrobatids.

Table 1. (Continued).

ZFMK Species	SVL	HW	ToL	ToW
14158 <i>Mantidactylus betsileoanus</i>	29.5	10.0	8.5	5.5
52613 <i>Mantidactylus wittei</i>	24.0	7.0	5.0	3.0
52593 <i>Mantidactylus wittei</i>	25.5	8.0	7.0	4.5
53699 <i>Mantidactylus blommersae</i>	19.0	7.0	4.0	3.0
52737 <i>Mantidactylus bicalcaratus</i>	22.0	8.0	5.0	3.5
52740 <i>Mantidactylus bicalcaratus</i>	29.0	10.0	6.0	5.0
52587 <i>Heterixalus boettgeri</i>	27.0	9.0	7.0	5.0
53608 <i>Heterixalus boettgeri</i>	29.0	10.0	7.5	6.0
59824 <i>Boophis boehmei</i>	26.0	12.0	6.5	4.0
57407 <i>Boophis boehmei</i>	28.0	12.0	5.5	4.5
57396 <i>Boophis majori</i>	21.0	9.0	5.0	4.0
57394 <i>Boophis majori</i>	28.0	9.0	5.0	4.0
51344 <i>Colostethus nubicola</i>	19.5	6.3	3.3	3.2
47770 <i>Colostethus nubicola</i>	19.6	6.3	4.8	2.5
46527 <i>Colostethus inguinalis</i>	24.1	8.0	5.1	3.4
45303 <i>Colostethus inguinalis</i>	24.7	8.0	5.6	3.8
52210 <i>Colostethus brunneus</i>	17.1	5.5	3.6	3.0
52207 <i>Colostethus brunneus</i>	17.7	6.0	3.8	2.6
32066 <i>Colostethus trinitatis</i>	21.5	8.0	4.1	4.2
32064 <i>Colostethus trinitatis</i>	25.2	8.6	5.4	3.2
45301 <i>Colostethus talamancae</i>	25.5	8.5	5.0	3.5
47773 <i>Colostethus talamancae</i>	22.0	7.5	5.0	5.0
25300 <i>Colostethus</i> sp.	21.7	7.3	4.8	3.0
25301 <i>Colostethus</i> sp.	22.3	7.6	4.4	3.6
37261 <i>Allobates femoralis</i>	24.0	8.0	6.0	4.0
37262 <i>Allobates femoralis</i>	22.0	7.0	6.0	4.5
32042 <i>Epipedobates tricolor</i>	18.0	6.0	4.0	3.0
32033 <i>Epipedobates tricolor</i>	25.0	7.0	5.0	4.0
54568 <i>Epipedobates pictus</i>	24.0	7.1	5.4	2.8
60322 <i>Epipedobates pictus</i>	22.7	7.1	3.7	3.1
54381 <i>Epipedobates pulchripectus</i>	21.7	7.3	4.0	2.0
54380 <i>Epipedobates pulchripectus</i>	21.0	7.1	3.6	2.1
40710 <i>Epipedobates silverstonei</i>	24.5	7.7	4.5	3.3
27637 <i>Epipedobates silverstonei</i>	40.0	13.0	7.9	5.5
46431 <i>Epipedobates bassleri</i>	36.3	10.9	5.9	3.5
46432 <i>Epipedobates bassleri</i>	36.5	11.1	7.0	3.9
37327 <i>Phylllobates vittatus</i>	22.5	8.0	4.5	3.0
37327 <i>Phylllobates vittatus</i>	22.5	7.9	4.7	2.5
61235 <i>Phylllobates bicolor</i>	38.9	13.0	8.8	5.3
56512 <i>Phylllobates lugubris</i>	21.5	6.8	3.6	2.4
56513 <i>Phylllobates lugubris</i>	20.0	6.7	4.4	2.3
51340 <i>Minyobates minutus</i>	13.7	4.6	2.7	1.3
51339 <i>Minyobates minutus</i>	12.7	4.2	2.8	1.1
53116 <i>Dendrobates lehmanni</i>	34.0	10.0	6.0	2.5
53115 <i>Dendrobates lehmanni</i>	34.0	10.0	7.0	2.0
56530 <i>Dendrobates pumilio</i>	21.4	6.6	3.7	2.2
56535 <i>Dendrobates pumilio</i>	22.1	6.0	4.1	1.7
46437 <i>Dendrobates trivittatus</i>	40.7	10.4	7.0	3.9
40724 <i>Dendrobates trivittatus</i>	40.0	10.6	8.0	5.7
41500 <i>Dendrobates fantastus</i>	19.2	6.1	2.8	1.3
41497 <i>Dendrobates fantastus</i>	20.6	6.3	3.0	1.6
50351 <i>Dendrobates granuliferus</i>	19.5	5.9	3.4	1.6
50349 <i>Dendrobates granuliferus</i>	20.9	6.6	4.5	2.5
40695 <i>Dendrobates tinctorius</i>	48.1	12.3	9.0	3.4
40694 <i>Dendrobates tinctorius</i>	42.6	11.5	7.7	4.2
57133 <i>Dendrobates lamasi</i>	18.0	5.7	3.3	1.5

Table 1. (Continued).

ZFMK Species	SVL	HW	ToL	ToW
40726 <i>Dendrobates lamasi</i>	16.7	5.4	3.4	2.0
57223 <i>Melanophryniscus rubriventris</i>	26.4	7.8	5.2	2.6
57219 <i>Melanophryniscus rubriventris</i>	23.0	7.4	4.2	1.8
45864 <i>Melanophryniscus stelzneri</i>	26.3	7.5	2.9	2.0
45866 <i>Melanophryniscus stelzneri</i>	23.4	6.8	3.1	1.4
28197 <i>Pseudophryne australis</i>	19.7	6.6	4.7	2.2
28198 <i>Pseudophryne australis</i>	20.9	6.4	4.6	2.1
28157 <i>Pseudophryne bibroni</i>	24.0	7.6	5.0	2.5
28180 <i>Pseudophryne bibroni</i>	23.6	7.2	5.2	2.7
50048 <i>Pseudophryne corroboree</i>	26.7	7.5	4.7	2.2
50046 <i>Pseudophryne corroboree</i>	25.8	7.3	3.9	1.9

To compare tongue shape we measured tongue width (ToW), tongue length (ToL), snout-vent length (SVL) and head width (HW) in 88 frog specimens belonging to 50 species. ToW and ToL measurements were clearly dependent on the state of any particular specimen, especially its fixation; single aberrant measurements can thus be explained as artifacts, although most measured specimens were in a comparable state of fixation. Relative tongue width (ToW/SVL), relative tongue length (ToL/SVL), and relative head width (HW/SVL) were calculated. If possible, two specimens of each species were measured, and the mean values of each species used for further analysis. The obtained ratio values were compared statistically with the software package SPSS for Windows using Mann-Whitney U-tests and Kruskal-Wallis ANOVAs.

3. REVIEW AND COMPARISON OF CHARACTERS

Mantella is classified in the family Ranidae, subfamily Mantellini (BLOMMERS-SCHLÖSSER 1993). According to GLAW & VENCES (1994) there are only two mantelline genera, *Mantella* and the non-microphagous *Mantidactylus*; the latter may be paraphyletic but very probably contains the nearest relatives of *Mantella* (DALY et al. 1996; pers. obs.). In the Dendrobatidae, the non-microphagous *Colostethus* is seen as sister group of the alkaloid-containing genera (MYERS et al. 1991; CALDWELL 1996). In the following we will compare the states found in *Mantella* to those observed in *Mantidactylus*. Within the Dendrobatidae we will compare the states of aposematic genera to those of *Colostethus*. Additionally we give the states occurring in the remaining alkaloid-containing genera *Pseudophryne* (Myobatrachidae) and *Melanophryniscus* (Bufonidae).

Microphagous specialization. *Mantella* are microphagous and myrmecophagous as demonstrated by VENCES et al. (in press). Little is known about prey of *Mantidactylus*, but the cursorial data indicate that representatives of the genus regularly consume large prey (GLAW & VENCES 1994 for *M. albobrenatus* (Müller, 1892), *M. mocquardi* Angel, 1929, *M. grandidieri* Mocquard, 1895; pers. obs. for *M. ulcerosus* (Boettger, 1880)). Extensive studies have been carried out on the diet of dendrobatids (SILVERSTONE 1975, 1976; TOFT 1980a, 1980b, 1995; SIMON & TOFT 1991; DONNELLY 1991; CALDWELL 1996). According to these papers, *Dendrobates*, *Phylllobates* and *Epipedobates* are ant specialists, whereas *Minyobates* mainly consumes mites. *Epipedobates* and *Phylllobates* are less specialized to ants and mites than *Dendrobates* and *Minyobates*. *Allobates* and *Colostethus* show no microphagous specialization. *Pseudophryne* is an ant specialist (PENGILLEY 1971b for *P. corroboree* Moore, 1953, *P. dendyi* Lucas, 1892, *P. bibroni*). Little is known on food and feeding of *Melanophryniscus*; CEI (1980) states that *M. stelzneri* mainly preys upon small arthropods as ants and aphids, and BIRKHAHN (1994) notes that *M. rubriventris* (VELLARD, 1947) preferred small prey items in captivity.

Skin alkaloids. Present in *Mantella* (9 species), absent in *Mantidactylus* (3 species) and other ranids according to GARRAFFO et al. (1993) and DALY et al. (1996). Present in aposematic dendrobatids except *Allobates* (only traces), absent in *Colostethus* (DALY et al. 1987; MYERS 1987). Present in 2 species of *Melanophryniscus* and 7 species of *Pseudophryne* (GARRAFFO et al. 1993b; DALY et al. 1990), absent in other bufonids and myobatrachids (DALY et al. 1987).

Aposematic colouration. Several species of *Mantella* (e.g. *M. aurantiaca*, *M. baroni*, *M. cowani*) clearly have dorsal aposematic colour patterns (orange, red or yellow with black) which are not known in any *Mantidactylus*. Other *Mantella* are more cryptically coloured (e.g. *M. haraldmeieri*, *M. betsileo*). In dendrobatids, the genera *Epipedobates*, *Phylllobates*, *Minyobates* and *Dendrobates* contain aposematic species; of these, at least *Epipedobates* also contains some more cryptic forms. *Colostethus* are generally cryptic; the striped pattern of *Allobates femoralis* (Boulenger, 1883) can be seen as aposematic (SILVERSTONE 1976 considers the species as a possible mimic of *Epipedobates pictus* (Bibron in Tschudi, 1838)), but may also be cryptic (CALDWELL 1996). *Pseudophryne* contains highly aposematic species (*P. corroboree* and *P. pengillei* Wells & Wellington, 1985) as well as more cryptic forms (see figures in TYLER 1992 and OSBORNE et al. 1996). Similarly, at least some *Melanophryniscus* can be seen as aposematic (MCDIARMID 1971: 51).

Activity. *Mantella* are diurnal frogs, with few exceptional observations of nocturnal activity (see VENCES et

al. 1996). Many *Mantidactylus* are mainly nocturnal, and in most species activity takes place at least partly during the night (except some species of the subgenera *Gephyromantis* Methuen, 1920 and possibly *Pandanusicola* Glaw & Vences, 1994; see GLAW & VENCES 1994). All aposematic and most non-aposematic dendrobatids are diurnal (MYERS & DALY 1983; MYERS et al. 1991: 27). As far as known, *Melanophryniscus* are at

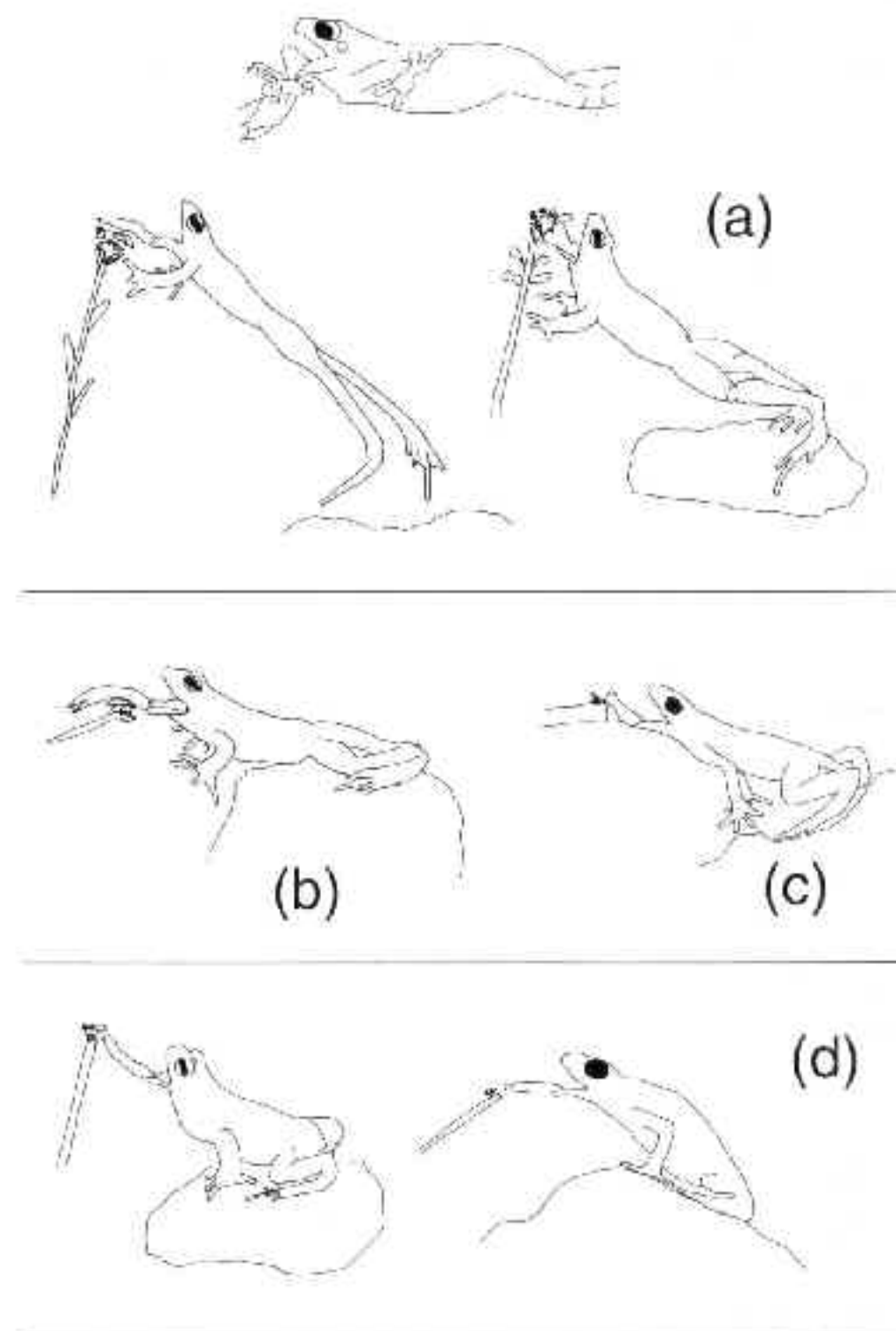


Fig. 2. Schematic drawing of different prey catching behaviour observed in anurans (redrawn from high-speed photographs): (a) Prey catching jump with simultaneous tongue protrusion at angles of 180° in *Rana lessonae* (left), *Hyla arborea* (above) and *Discoglossus galganoi* (right); (b) tongue protrusion with simultaneous forward lunging, hindfeet remaining in contact with substrate, in *Rana lessonae*; (c) tongue protrusion with simultaneous forward lunging, hands losing only slightly contact with substrate, in *Mantella aurantiaca*; (d) tongue protrusion without or with very slight forward lunging, fore- and hindfeet remaining in contact with substrate, in *Dendrobates tinctorius* (right) and *Bufo calamita* (left).

least partly diurnal (CEI 1980 for *M. stelzneri*; MCDIARMID 1971: 51). *Pseudophryne* show some diurnal activity: males of *P. corroboree* call (from refuges) during day and night (PENGILLEY 1971a), and a female of *P. corroboree* was observed feeding at 9 h a.m. (PENGILLEY 1971b: 101).

Prey catching behaviour (Fig. 2). The typical prey catching behaviour of *Mantella* differs from that observed in other ranids (*Rana*: SCHNEIDER 1954, VENCES 1988, NISHIKAWA et al. 1992; *Euphyllotis*: ALTEVOGT et al. 1987; *Rhacophorus*: pers. obs.; no data on *Mantidactylus*). Several species of *Rana* very often jump towards the prey, with mouth opening and tongue protrusion occurring during the jump. On the contrary, *Mantella* generally first perform small hops to reach the prey, and tongue protrusion is generally not accompanied by jumping; at most, the hands loose contact to the substrate while the body is lunged slightly forward and upwards. In dendrobatids, we observed prey catching jumps with tongue protrusion in *Epipedobates tricolor*, but not in *Dendrobates leucomelas* Fitzinger in Steindachner, 1864 nor *D. tinctorius* (Schneider, 1799). Following our personal observations on captive *M. stelzneri*, also *Melanophryniscus* lack prey catching jumps with tongue protrusion as do other bufonids: *Bufo* (VENCES 1988; NISHIKAWA et al. 1992) and *Atelopus* (LÖTTERS, pers. comm. 1997). No data on *Pseudophryne* are available.

Size. *Mantella* are relatively small frogs (adult size range 18–30 mm). *Mantidactylus* also contains many small species, but also large forms (adult SVL range 15–120 mm; GLAW & VENCES 1994). SVL is 15–50 mm in *Dendrobates* (SILVERSTONE 1975), 12–20 mm in *Minyobates* (MYERS 1987), 19–47 mm in *Phylllobates* (SILVERSTONE 1976; MYERS et al. 1978), 15–50 mm in *Epipedobates* (MYERS 1987), 20–33.5 mm in *Allobates* (SILVERSTONE 1976 as *Phylllobates femoralis*), 20–62 in *Colostethus* (MYERS et al. 1991). In *Pseudophryne* SVL ranges from 18–38 mm (TYLER 1992), in *Melanophryniscus* from 25–45 mm (CEI 1980).

Body shape and habitus. All *Mantella* have a similar and characteristic general appearance. Only few *Mantidactylus* (of the subgenus *Chonomantis* Glaw & Vences, 1994) have a similar habitus. The appearance of *Mantella* is strikingly paralleled by certain aposematic dendrobatids (Fig. 1). A different, toad-like appearance is found in *Pseudophryne* and *Melanophryniscus*. Mean relative head width is significantly lower in *Mantella* than in *Mantidactylus* (U-test, $p < 0.001$), although some *Mantidactylus* have values similar to *Mantella*. In dendrobatids, the largest mean relative head width was found in *Phylllobates*, the lowest in *Dendrobates*, agreeing with the findings of TOFT (1995). Our data support genus-specific differences in relative head width (Kruskal-Wallis-ANOVA, $p < 0.05$) within the Dendro-

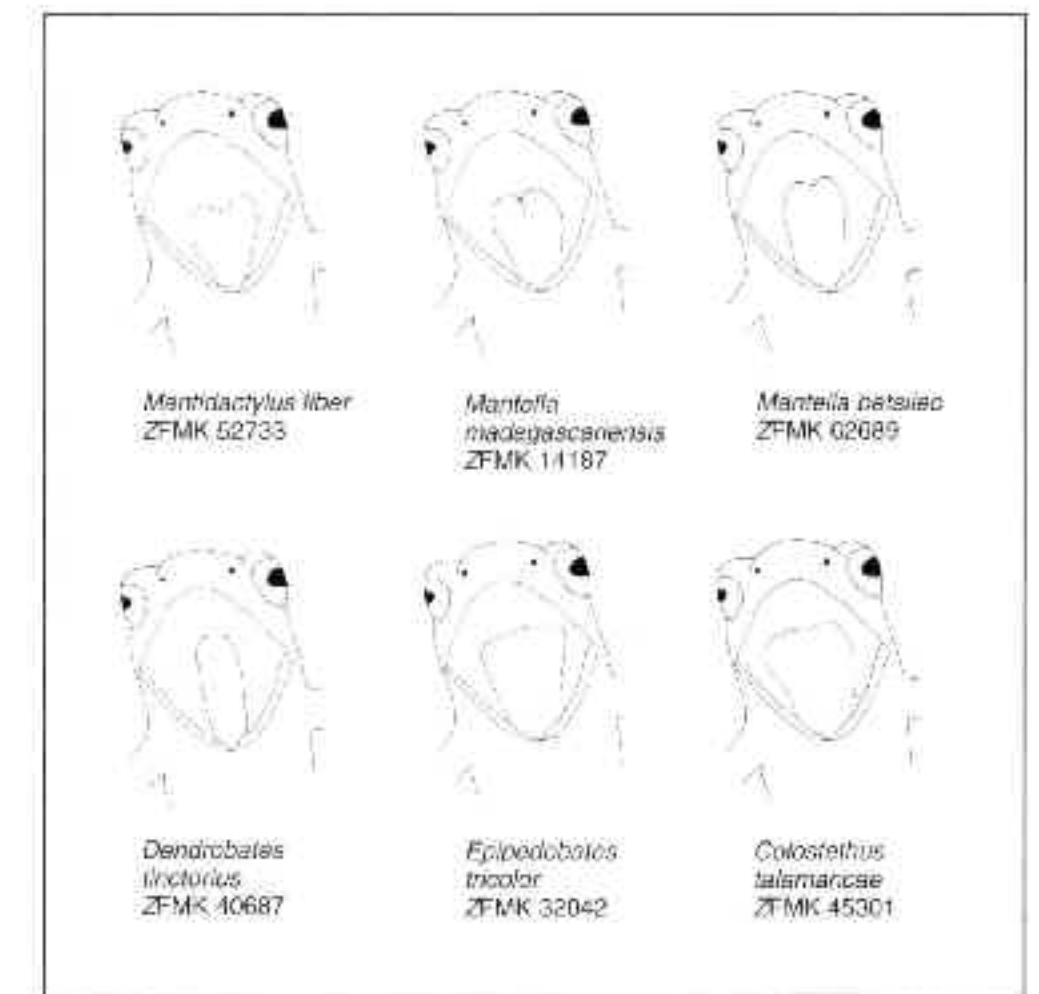


Fig. 3. Schematic drawing of tongue shape in several studied frog specimens.

batidae. Mean relative head width of *Melanophryniscus* is similar to that found in *Mantella*, whereas *Pseudophryne* have somewhat broader heads.

Tongue shape. The tongue of *Mantella* is distally very slightly forked (Fig. 3), whereas all *Mantidactylus* have a distinctly bifid tongue (pers. obs.) as it is typical for ranoid frogs except very few genera (BLOMMERS-SCHLÖSSER 1993; pers. obs.). Dendrobatids and myobatrachids (BLOMMERS-SCHLÖSSER 1993), and bufonids (pers. obs.) have unforked entire tongues, as verified in all specimens listed in Tab. 1. Detailed arrangement of tongue musculature has not been studied in *Mantella*, but *Dendrobates*, myobatrachids (including 4 species of *Pseudophryne*) and bufonids (*Bufo* and *Capensibufo*) show a complex form of the genioglossus muscle not found in other anurans (HORTON 1982).

Relative tongue width and relative tongue length of *Mantella* differed significantly ($p < 0.001$; U-tests) from values of *Mantidactylus*. The scatterplot in Fig. 4a shows that *Mantella* had relatively narrower and shorter tongues than *Mantidactylus*; the values of *Mantidactylus* were similar to those of other ranoid genera as *Heterixalus* (Hyperoliidae) and *Boophis* (Rhacophorinae). Of the remaining considered genera (Fig. 4b), only *Colostethus*, *Allobates*, one *Epipedobates* and one *Phylllobates* had values as those found in *Mantidactylus*. All *Dendrobates*, *Minyobates*, *Pseudophryne*, and *Melanophryniscus* differed from this state either in having a shorter or narrower tongue (mostly in both

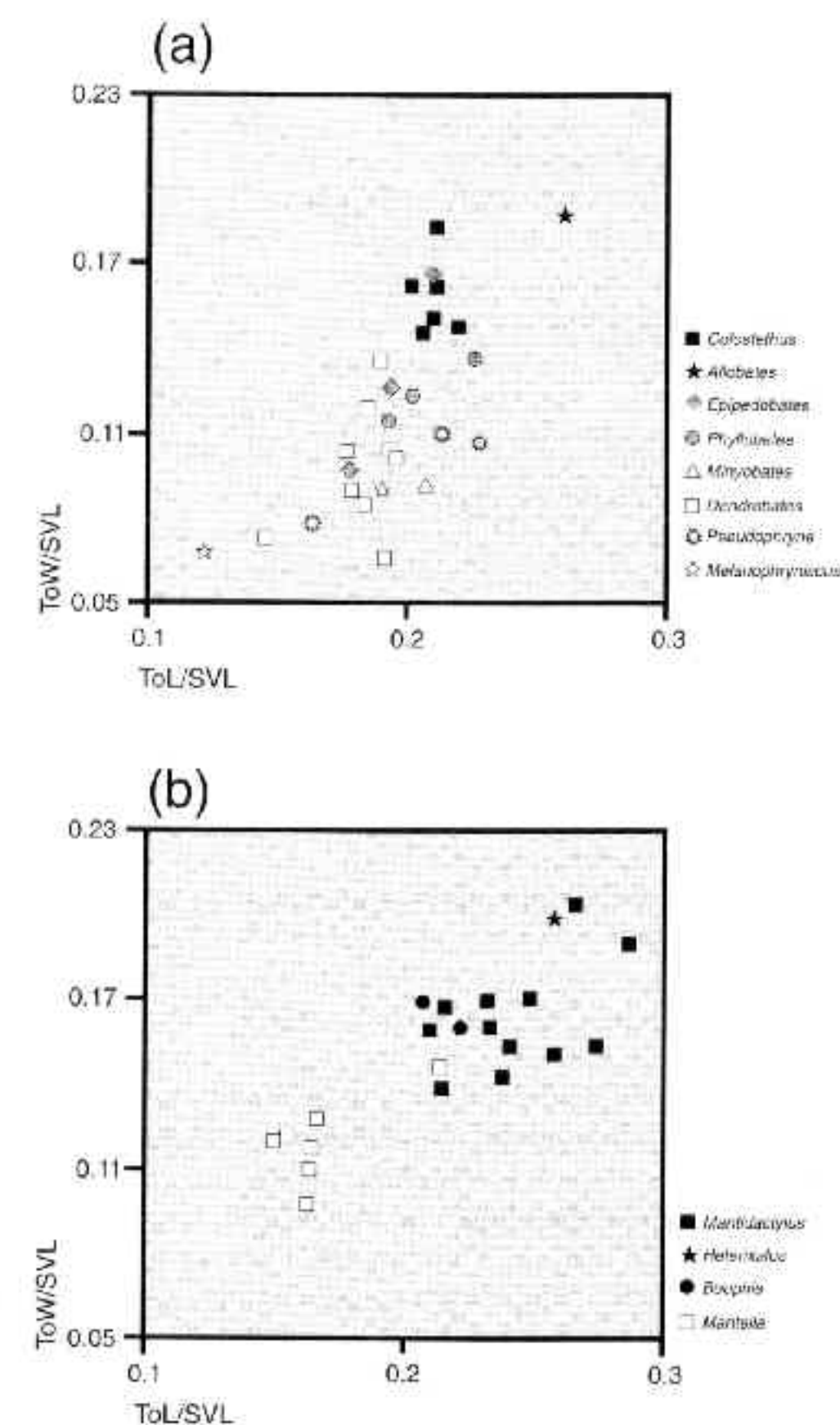


Fig. 4. Scatterplot of relative tongue length (ToL/SVL) and relative tongue width (ToW/SVL) in dendrobatid genera, *Pseudophryne*, and *Melanophryniscus* (a), and in *Mantella*, *Mantidactylus* and two other ranoid genera (b). Each symbol represents one species. Black symbols represent species of non-microphagous genera, white symbols species of microphagous genera. Transitional genera are represented by grey symbols.

variables). In dendrobatids, data support a transition from long and broad to short and narrow tongues in the direction *Allobates-Colostethus-Epipedobates-Phylllobates-Minyobates-Dendrobates*. The genus-specific differences in relative tongue width and length within the Dendrobatidae are significant ($p < 0.01$ and $p < 0.05$, respectively, Kruskal-Wallis-ANOVA).

Maxillary teeth (Fig. 5). *Mantella* lack maxillary teeth which are present in *Mantidactylus* (pers. obs.; GUIBÉ

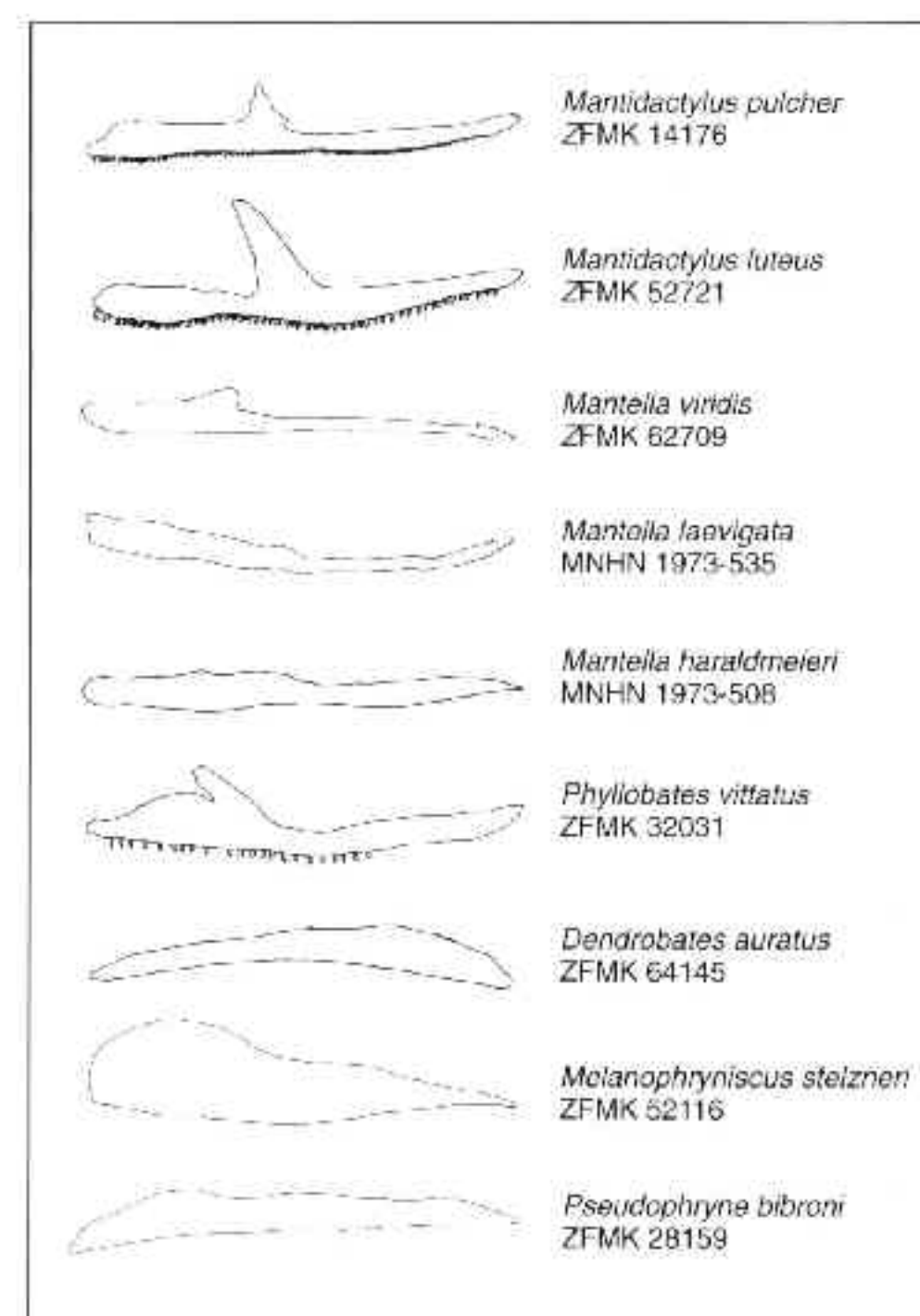


Fig. 5. Schematic drawing of maxilla (lateral view) in studied specimens (left side = snout). Not to scale.

1978). Teeth are absent in *Dendrobates*, *Minyobates* and some *Epipedobates*, present in *Phylllobates*, *Allobates*, some *Epipedobates*, and *Colostethus* (MYERS 1987; SILVERSTONE 1975; MYERS et al. 1991; pers. obs.). They are absent in *Pseudophryne* and *Melanophryniscus* (LYNCH 1971; CEI 1980; pers. obs.).

Palatal apophysis of maxilla (Fig. 5). Most *Mantidactylus* are characterized by a distinct palatal apophysis of the maxilla, which is generally absent in *Mantella* except rudiments in some specimens (GUIBÉ 1978; pers. obs.). A palatal apophysis is present in *Phylllobates vittatus* but lacking in *Dendrobates auratus* (pers. obs.). According to the drawing of MYERS et al. (1991) it is present in *Aromobates*. No apophysis was found in *Pseudophryne* and *Melanophryniscus*, but the latter had an anteriorly very deep maxilla (pers. obs.).

Squamosal shape (Fig. 6). One characteristic of *Mantella* is the rudimentary zygomatic process of the squamosal, which is well developed (although always shorter than the posterior process) in *Mantidactylus* (GUIBÉ 1978; pers. obs.). The zygomatic process is pre-

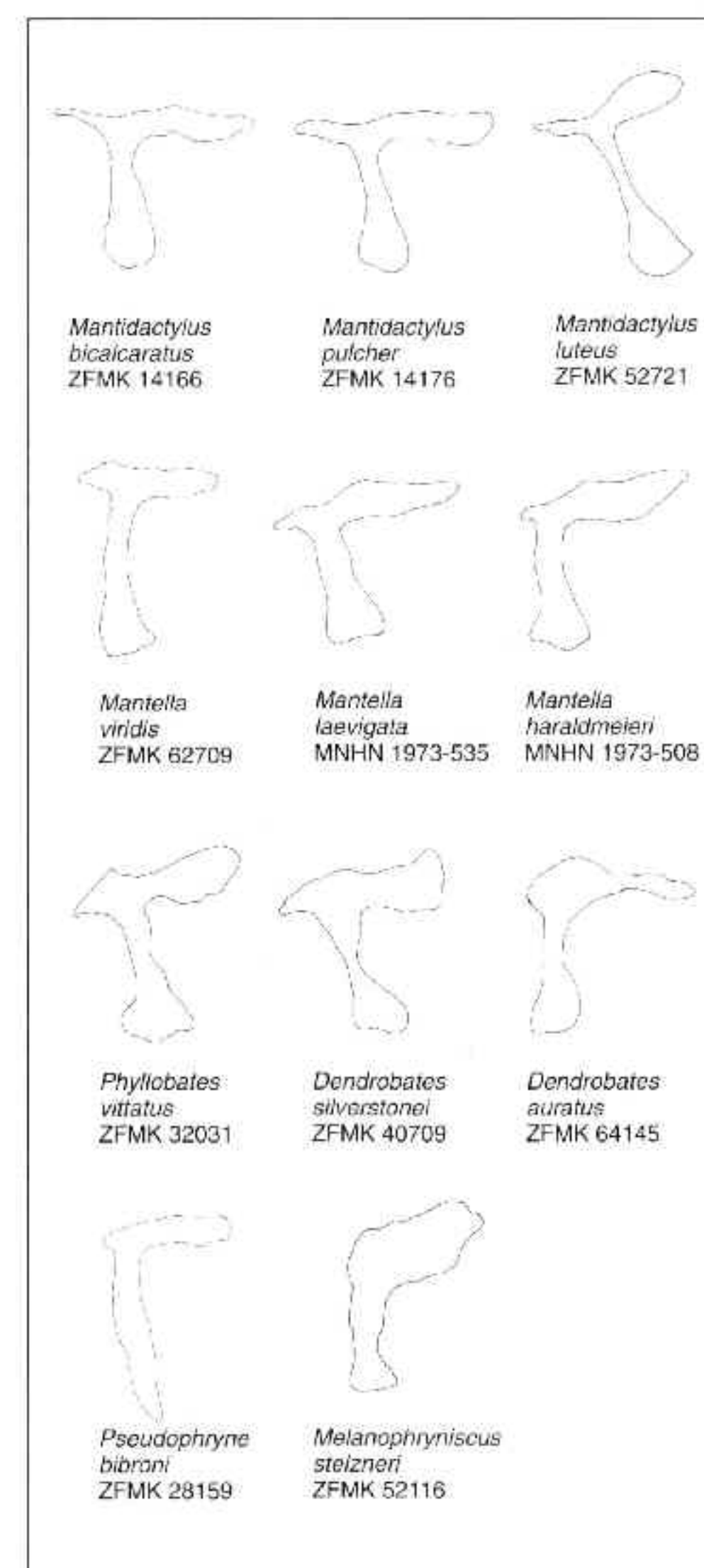


Fig. 6. Schematic drawing of squamosal shape in studied specimens (left side = anterior). Not to scale.

sent (but not longer than in *Mantella*) in *Phylllobates* and some *Dendrobates*, absent in other *Dendrobates* (pers. obs.). The zygomatic process can be very short in *Colostethus* (pers. obs. in *C. nubicola* Dunn, 1924), but is relatively long in *Aromobates* (DALY et al. 1991).

Melanophryniscus lack a zygomatic process (McDIARMID 1971, pers. obs.); in *Pseudophryne* it is reduced, knob-like (LYNCH 1971) or nearly absent (pers. obs.).

Vomers and vomerine teeth. Vomerine teeth lack in *Mantella* (absence of the dentigerous process) but are present in most *Mantidactylus* (GUIBÉ 1978; pers. obs.). They are generally absent in dendrobatids (SILVERSTONE 1975). The vomers lack completely in *Pseudophryne* (LYNCH 1971). Vomerine teeth are absent in *Melanophryniscus* as generally in bufonids (McDIARMID 1971).

Palatines. Described as "assez reduites" in *Mantella* by GUIBÉ (1978); in fact slightly smaller than in *Mantidactylus* (pers. obs.). Lacking in dendrobatids except some *Colostethus* (SILVERSTONE 1975:5). Reduced in size in *Pseudophryne* (LYNCH 1971). Absent in some *Melanophryniscus* (McDIARMID 1971).

4. DISCUSSION

4.1. A functional complex related to microphagy in *Mantella*

Our data clearly indicate a correlation of the studied derived characters of *Mantella* with their specialized feeding pattern (Tab. 2). The apomorphies of *Mantella* (in comparison to *Mantidactylus*) are generally found in most other alkaloid-containing genera. In most cases this can be explained by a direct, functional or by an indirect correlation of the character with microphagy. And in many cases the state transformation within the Dendrobatidae reflects the transition from generalist feeders to myrmecophagous specialists.

The assumed etho-morphological character complex found in *Mantella* involves (a) microphagous and myrmecophagous specialization, (b) alkaloid accumulation by uptake from prey (ants), (c) tongue shape (less forked, shorter and narrower), (d) prey catching behaviour, (e) loss of maxillary and vomerine teeth, (f) size reduction of palatines, (g) loss of maxillary apophysis, (h) reduction of zygomatic process of squamosal. It is probable that the characters (b-h) evolved as a functional complex in *Mantella*, as a consequence of increased feeding specialization. Two other characters, (i) head width and (j) body size, may be subject of evolutionary constraints, broad heads and large size (>50 mm SVL) not being compatible with microphagous feeding. Two additional characters, (k) diurnal, conspicuous activity and (l) aposematic colouration, must be seen in the context of increased toxicity by alkaloid accumulation.

Tongue shape, loss of maxillary apophysis and squamosal shape are probably functionally dependent from a specialized mechanism of jaw opening as is relative jaw length (EMERSON 1985) which was not measured in the present study. One additional correlate of

Table 2. Observed apomorphic character states in *Mantella* when compared to *Mantidactylus*, their occurrence in the other genera considered, and possible explanations of their correlation with microphagy. Genus abbreviations are Me (*Melanophryniscus*), Ps (*Pseudophryne*), Co (*Colostethus*), Al (*Allobates*), Ep (*Epipedobates*), Ph (*Phyllobates*), Mi (*Minyobates*), De (*Dendrobates*). Column 3 gives the direction in which an increase of the expression of the respective state is observed in dendrobatid genera.

Character	Other genera	Transformation in dendrobatids	Correlation explained?
Microphagy/Myrmecophagy	Me, Ps, Ep, Ph, De, Mi	Al/Co < Ep/Ph < De/Mi	—
Skin Alkaloids	Me, Ps, (Al), Ep, Ph, De, Mi	—	Yes; alkaloids originate from uptake of (ant) prey
Aposematic colouration	Me, Ps, (Al), Ep, Ph, De, Mi	all De, but not all Ep/Ph clearly apos.	Yes; aposematism is to be expected in toxic species
Diurnal activity	Me, (Ps), Co, Al, Ep, Ph, De, Mi	—	Yes; toxic (aposematic) species can afford conspicuous diurnal activity
Prey catching: no jumps with tongue protrusion	Me?, Ps?, Ps?, De, Mi?	Ep → De	Yes; long-distance aiming difficult with small prey, and jumps energetically expensive
Tongue not clearly forked	Me, Ps, Co, Al, Ep, Ph, De, Mi	—	Yes; forked tongue is less suited for precise aiming
Tongue less broad and long	Me, Ps, (Ep), Ph, De, Mi	Al > Co > Ep > Ph > Mi > De	Yes?; may favour precise short-distance aiming
Maxillary teeth absent	Me, Ps, (Ep), De, Mi	Co/Al/Ph/(Ep) → (Ep)/De/Mi	Yes; teeth are only necessary to hold large prey
Vomerine teeth absent	Me, Ps, Co, Al, Ep, Ph, De, Mi	—	Yes; teeth are only necessary to hold large prey
Maxilla apophysis reduced	(Me), Ps, De, (Mi?)	Ph/(De) → (De)	No; maybe part of adapted jaw opening mechanism
Zygomatic process of squamosal reduced	Me, Ps, (Co), (Ph), De (Al, Ep, Mi: ??)	Co/Ph/(De) → (De)	No; maybe part of adapted jaw opening mechanism
Smaller palatines	Me, Ps, Co, Al, Ep, Ph, De, Mi	—	No; maybe part of adapted jaw opening mechanism
Size not larger than 30 (50) mm	Me, Ps, Al, Ep, Ph, De, Mi	—	Yes; too large frogs may not be able to feed economically only on small prey
Head less broad	Me, Ps, Ep, De	Ph > Co > Mi > Al > Ep > De	Yes?; broad heads may be more useful to swallow larger prey

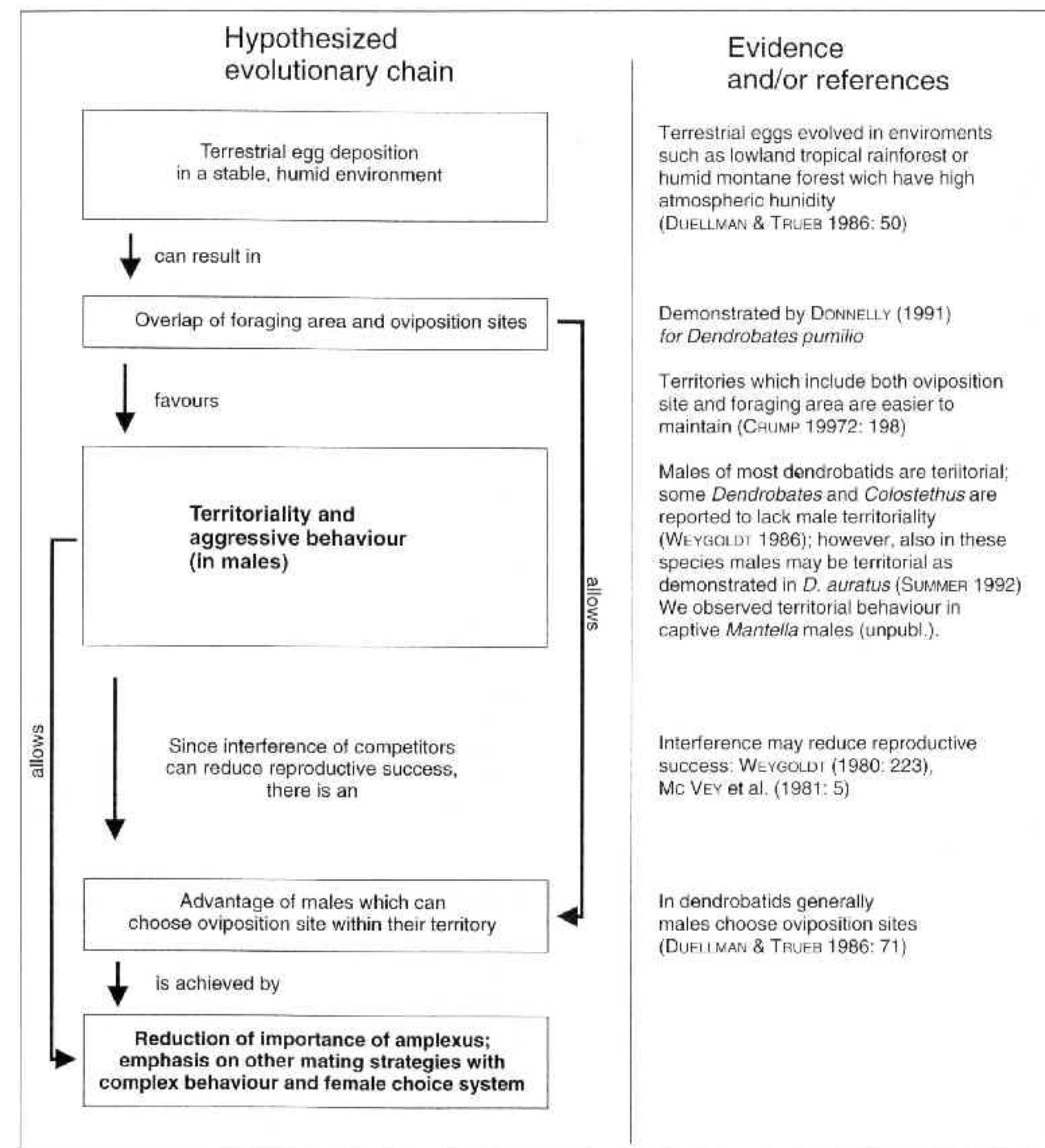


Fig. 7. Flow diagram showing a hypothesis of evolution of complex mating behaviour in *Mantella* and dendrobatids. Each single step is supported by at least one determinant active under the specific environmental conditions, explaining the possibility of convergent evolution of the observed patterns.

microphagous and myrmecophagous specialization may be a physiological one. TAIGEN & POUGH (1983) showed for three species of dendrobatids that these had high aerobic activity, low anaerobic capacity, and high resting metabolism when compared to a generalist (*Eleutherodactylus coqui*). The continuous movements and small hops of many *Mantella* are strikingly similar to the activity observed in dendrobatids; it therefore can be assumed that metabolic patterns may be similar in both groups.

We postulate that *Mantella* originated from a non-microphagous ancestor and acquired most of its apomorphies in the context of evolution of microphagy. This is likely since the observed states are seldom or not found in other ranids. However, in the other alkaloid-containing groups some of the states may well have evolved previously, either in the context of microphagy or not. Unforked tongues are probably plesiomorphic in bufonids, dendrobatids and myobatrachids, clearly forked tongues being a derived state which only occurs in the ranoid lineage (BLOMMERS-SCHLÖSSER 1993; pers. obs.). Most *Colostethus* are diurnal (as are aposematic dendrobatids), indicating that diurnality in this family may not have evolved in the context of microphagy and aposematism. Many myobatrachids share with *Pseudophryne* a short zygomatic squamosal process (LYNCH 1971), and all bufonids share with *Melanophryniscus* the lack of vomers and maxillary teeth (McDIARMID 1971).

4.2. Implications for anuran phylogeny

4.2.1. Relationships of dendrobatids and mantellines.

Very divergent opinions exist regarding the phylogenetic position both of the Dendrobatidae (GRIFITHS 1959; DUELLMAN & TRUEB 1986; FORD 1993; BLOMMERS-SCHLÖSSER 1993; HAY et al. 1995) and the Mantellinae (LIEM 1971; CHANNING 1989; BLOMMERS-SCHLÖSSER 1993) in the system of neobatrachian frogs. Considering this lack of consensus, ZIMMERMANN (1996) argued that mantellines, arthroleptids and dendrobatids may form a monophyletic lineage. This hypothesis was based on the fact that *Mantella* and some dendrobatid genera contain skin alkaloids and show similar aposematic colour patterns, and on similarities in breeding behaviour of *Mantella* and certain dendrobatids. We do not favour the hypothesis of a dendrobatid/mantelline sister group relationship which is contradicted by the molecular data of HAY et al. (1995). ZIMMERMANN's arguments can be replied as follows:

(1) Similarities between *Mantella* and aposematic dendrobatids regarding general appearance and body shape, colouration, and skin toxins are parts of a character complex related to microphagy as identified in the present study. Since this character complex is neither present in *Colostethus* nor in *Mantidactylus*, its usage to

advocate mantelline/dendrobatid relationships implies that *Mantella* and aposematic dendrobatids are direct sistergroups, and that dendrobatids and mantellines are non-monophyletic units. However, monophyly of each of these two lineages (when no other groups are considered) is well corroborated by four synapomorphies of the Dendrobatidae (dorsal scutes on terminal disks of fingers and toes, chromosome reduction, tadpole transport, T-shaped phalanges: SILVERSTONE 1975; MYERS & FORD 1986; RASOTTO et al. 1987; BLOMMERS-SCHLÖSSER 1978, 1993; pers. obs.), two synapomorphies of the Mantellinae (intercalary element; BLOMMERS-SCHLÖSSER 1993, pers. obs.; lack of external gills in early tadpole stages which are present in dendrobatids; BLOMMERS-SCHLÖSSER 1975a; ZIMMERMANN 1976; pers. obs.), and three additional characters which are difficult to polarize (number of upper tadpole keratodont rows, presence and shape of omosternum and sternum; SAVAGE 1968; GLAW & VENCES 1994; SILVERSTONE 1975, 1976; BLOMMERS-SCHLÖSSER 1993; pers. obs.).

(2) The lack of mating amplexus, and related complex patterns of breeding behaviour may well occur also in other tropical anurans which are generally poorly studied ethologically. The evolution of the specialized breeding behaviour may have been favoured by an evolutionary chain starting with terrestrial egg deposition in a stable, humid environment (rainforest) and leading towards loss of amplexus and evolution of a female choice mating system with complex behaviour. The loss of amplexus was accompanied by loss of nuptial pads and release calls in both groups. This hypothesis (which however may not be the only possible explanation for the convergent evolution of complex mating behaviour involving amplexus loss) is outlined in Fig. 7.

4.2.2. Status of the dendrobatid genus *Minyobates*.

The dendrobatid genus *Minyobates* was erected by MYERS (1987) to accommodate a number of species previously included in *Dendrobates*. The new taxon was mainly based on (a) the very small size (12–19.5 mm SVL) of the included species, (b) their uncommon alkaloid profile (lack of histrionicotoxins and 3,5-disubstituted indolizidines), (c) a hand structure similar to *Dendrobates*, (d) presence of an oblique lateral line in some species, (e) presence of cephalic amplexus (recorded in only one species), (f) larval characters (oral disc laterally unindented and anus median). Of these characters, only a, b, e and f constitute consistent differences to species included in *Dendrobates*. Recently, JUNGFER et al. (1996) demonstrated that cephalic amplexus (character e) lacks in one species (*M. fulguritus* (Silverstone, 1975)) attributed to *Minyobates*. SIMON & TOFT (1991) demonstrated that – in contrast to the ant-consuming *Dendrobates* – species included in *Minyobates* feed mainly on mites. A convergent prey specialization on

mites may explain the small size of *Minyobates* species, as well as their alkaloid profile (characters a and b). Thus, only one character (f; larval oral disc) remains as potential independent synapomorphy to distinguish *Minyobates* from *Dendrobates*. The latter genus, however, includes a rather large variation of larval mouthpart structures, indicating that new characters supporting the monophyly of *Minyobates* are needed. The decision of JUNGFER et al. (1996) not to recognize the genus and to include its species in *Dendrobates* seems therefore reasonable at the present state, although it was not yet followed in the present paper.

4.2.3. Prey catching behaviour and evolution in the Bufonidae.

It is striking that large bufonids (genus *Bufo*) lack maxillary and vomerine teeth, have a similar tongue musculature arrangement as *Dendrobates* and myobatrachids, and a prey catching behaviour differing from well-studied generalist feeders such as *Rana*. VENCES (1998) distinguishes three types of prey catching behaviour in neobatrachians with highly protrusible tongues: (1) Forward lunging (jumping) with simultaneous complete tongue protrusion (at an angle of 180° or more) to capture distant prey; (2) forward lunging without or without complete tongue protrusion (at an angle of less than 90°) to capture large prey; (3) tongue protrusion without lunging (feet generally remaining in contact with the substrate) to capture small prey at short distances. All three behavioural patterns are known in *Rana*. *Bufo* shows patterns 2 and 3, but apparently lacks pattern 1 (NISHIKAWA et al. 1992; VENCES 1998).

Our data show that in microphagous genera (*Mantella*, *Dendrobates*) there is a trend towards a more stable posture of the body during tongue protrusion, with reduction of jumps and forward lunging. This may be due to energetic reasons (capture of small prey not outweighing costs of a jump) or to increased aiming ability at short distance. Also the similar behavioural pattern in *Bufo* should be seen in the context of microphagous specialization, as it was already presumed by NISHIKAWA et al. (1992). It may simply be an adaptation to small prey which is mainly eaten by many species of the genus (EMERSON 1985). However, *Bufo* are also able to capture extremely large prey items such as earthworms or even adult mice and frogs (eg. SCHNIEDER 1954; EIBL-EIBESFELDT 1951). Their relative jaw length is not similar to that typically found in microphagous species (EMERSON 1985).

Bufo have been considered as basal group within the Bufonidae (eg. TIJEN 1960). The genus is probably para- or polyphyletic (McCRANIE et al. 1989; GRAYBEAL & CANNATELLA 1995). CANNATELLA (1986) emphasized that two characters present in (but not unique to) *Bufo*, parotoid glands and cranial crests, may not be plesiomorphic in the Bufonidae as presumed by previ-

ous workers (eg. GRANDISON 1981) but derived. Evidence presented herein supports the hypothesis that the ancestor of bufonids was a small, microphagous species, very different in general appearance from large species of *Bufo*. In fact, in the schemes of TIJEN (1960), GRANDISON (1981) and GRAYBEAL & CANNATELLA (1995), the most basal (Old World) bufonid genera are *Capensibufo* and *Nectophrynoides* Noble, 1926 which do not contain large species. If our scenario is correct, then the large species today classified in the genus *Bufo* originated by a secondary size increase from such small ancestral forms and evolved longer jaws in order to reduce specialization on small prey. However, they were not able to re-acquire lost features as maxillary and vomerine teeth, and prey catching jumps with simultaneous tongue protrusion, although this may have been advantageous for generalist feeders. This hypothesis is corroborated by a very recent molecular study of GRAYBEAL (1997), which places *Melanophryniscus* and *Atelopus* as basal taxa in the bufonid lineage.

4.3. Perspectives

We are aware that our study does not provide a comprehensive review of feeding specialization and its ethomorphological correlates in anurans. When new data on food and feeding, ethology and morphology of little known anuran species and genera become available, it will be possible to correlate them within a more extensive approach. Two main aspects must be postponed to such a future study:

(1) We have consciously restricted our review to frogs sharing with *Mantella* the striking character of alkaloid skin toxins. However, microphagous and myrmecophagous species have evolved in more anuran groups, and additionally there is a much larger variety of ecological types and foraging modes in anurans than covered by this scheme. This regards the aquatic, tongueless Pipidae which transport the food into the mouth with water currents produced by hyobranchial pumping movements (SOKOL 1969), large, macrophagous species which have developed adaptations such as the tooth-like bony mandible projections of the South-African species *Pyxicephalus adspersus* Tschudi, 1838 (PASSMORE & CARRUTHERS 1995), the snail-eating hyperoliid species *Paracassina obscura* (Boulenger, 1894) and *P. kounhiensis* (Mocquard, 1905) which have evolved specializations in skull structure, jaw musculature and tongue morphology (DREWES & ROTH 1981), and the burrowing species *Rhinophrynus dorsalis* Duméril & Bibron, 1841 which projects its tongue by hydrostatic pressure (TRUEB & GANS 1983). *R. dorsalis* is a specialist on ants and termites (DUELLMAN & TRUEB 1986), providing one additional example of extreme morphological specialization correlated with myrme-

cophagy. Other examples are to be expected in the families Myobatrachidae, Hemisotidae, Leptodactylidae and especially Microhylidae. Many microhylids are specialized ant feeders (eg. *Phrynomantis* Peters, 1867, *Breviceps* Merrem, 1820; PASSMORE & CARRUTHERS 1995; *Gastrophryne* Fitzinger, 1843; LIEBERMAN 1986; Cophylines: BLOMMERS-SCHLÖSSER 1975b), and most are edentate and have reduced palatines (DUELLMAN & TRUEB 1986). Microhylids are also characterized by a specialized morphology of mandible and throat musculature (EMERSON 1976) and are able to control the lateral direction of tongue protraction through an angle of at least 90° in the floor of the mouth, independent of head and body movements (NISHIKAWA et al. 1972). Furthermore, the family Microhylidae contains aposematic species with noxious skin secretions such as *Phrynomantis annectens* Werner, 1910 and *P. bifasciatus* (Smith, 1847) (PASSMORE & CARRUTHERS 1995) which, however, lack skin alkaloids (DALY et al. 1987).

(2) New data are necessary to clarify the correlations of microphagy, myrmecophagy, ecology and foraging mode. We have partly used the terms microphagy and myrmecophagy as synonyms since the prey of most considered species is small and consists mainly of ants. However, specialists which feed on small prey but not mainly on ants were already recorded: beside the mite feeding *Minyobates* (see SIMON & TOFT 1991) this probably applies to species of *Crinia* Tschudi, 1838 (see MAC NALLY 1983). TOFT (1980a) distinguished two "types" of frog prey, namely slow-moving, hard-bodied arthropods (principally ants and mites) and soft-bodied mobile arthropods (as roaches, crickets and large spiders). Frogs, according to this author, cluster in two guilds based on this prey type distinction, ant specialists versus non-ant specialists. In TOFT's (1985) scheme ant specialists were mainly widely-ranging searching foragers, whereas non-ant specialists were mainly sit-and-wait foragers. On the contrary, DONNELLY (1991) hypothesized that non-aposematic ant specialists may in fact employ a sit-and-wait strategy, indicating that there may be different ecological types of ant specialists. Future studies should therefore (a) comparatively survey ecology, foraging mode and diet of more anuran groups, including also desert-dwelling and arboreal species, (b) clarify whether there are anurans specialized on large ants, thus being myrmecophagous but not microphagous, (c) increasingly discuss foraging strategies and diet in the light of the recent evidence for dietary uptake of skin alkaloids in anurans (as done by CALDWELL 1996) since increased noxiousness may be one of the major advantages of ant specialization in these frogs, (d) test whether noxious frogs may actively discriminate towards groups or species of ants (or other arthropods) which contain toxins.

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