Phylogeny of frogs as inferred from primarily larval characters (Amphibia: Anura)☆

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Abstract

This paper presents larval evidence and evaluates its contribution to the discussion of frog phylogeny; 136 larval characters, 6 reproductive biology characters, and 14 adult morphology characters were scored for 81 frog and 4 caudate species. More than 90% of the data matrix entries represent original data derived from personal direct examination of specimens. Some larval characters are described for the first time and many others have not been assessed for specific taxa or in a broad phylogenetic context before. Homoplasy appears common in this and other amphibian morphological data sets. The data supported and confirmed various well-known clades, among others the Anura, Bufonidae, Ceratophryinae, Discoglossidae, Dendrobatidae, Hyperoliidae, Microhylidae, South American microhylids, Phyllomedusinae, Pseudinae, Pipoidea, Pipidae, and Scoptanura. The Ascaphidae was sister group to all other anurans and the Pipoidea was placed more basally than in some previous analyses. The Eurasian pelobatids formed a clade, whereas *Spea* and *Pelodytes* did not group robustly with them. Pelobatoid frogs emerged as a paraphyletic "transitional" assemblage including *Heleophryne*. The resolution of basal neobatrachian splits remained labile, although some subclades within the Neobatrachia were robustly supported. The "Hylidae" was paraphyletic, and hyline species were paraphyletic with respect to the Pseudinae. *Hemisus* clearly was in a clade with the Hyperoliidae and is proposed to be included in that family. *Scaphiophryne* was confirmed as basal taxon within the Microhylidae. Compared to the larval stages of the most recent common ancestor of anurans, members of the Scoptanura (microhylids except scaphiophrynines) have accumulated the highest number of apomorphic character states in anuran evolution.
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Introduction

The exploration of characters and taxa, the construction of a data matrix, and the analysis of data are different, but not independent, parts in a phylogenetic endeavor. How to analyze a given data set is an important question, but the prime determinants of any cladistic analysis are the original data themselves. New data are needed in many animal groups; mere recycling of existing data is laden with problems (Jenner, 2001).

The current knowledge of frog phylogeny is in a poor state. While the number of described species is steadily growing (>4200; Glaw and Köhler, 1998; Frost, 2002), the progress in resolving phylogenetic relationships within the Anura is not proceeding at a comparable pace. Large parts of the presumed phylogeny are unresolved or highly controversial (e.g., Ford and Cannatella, 1993; Hay et al., 1995). This is certainly due to the very incomplete state of systematic exploration of taxa and their characters, both morphological and molecular. Ford and Cannatella (1993) presented a brief historical overview and a compilation of major works in frog phylogeny.

The application of molecular techniques has given stimulating impulses to frog phylogenetics (e.g., Hay et al., 1995; Richards and Moore, 1996, 1998a; Ruvinsky and Maxson, 1996; Graybeal, 1997; Clough and Summers, 2000; Emerson et al., 2000; Vences et al., 2000). Some molecular systematists have claimed that frogs have not developed the morphological diversity of some other tetrapod groups, such as mammals (Richards and Moore, 1996). This opinion, however, ignores the numerous morphological differences that have been

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reported (among many more, Noble, 1922; Griffiths, 1963; Starrett, 1968; Kluge and Farris, 1969; Liem, 1970; Sokol, 1975, 1981; Drewes, 1984; Duellman and Trueb, 1986; Ford and Cannatella, 1993; Trueb, 1993) and the new evidence that continues to emerge (e.g., Burton, 1998a,b, 2001). Furthermore, there is an amazing variety of larval forms displaying a broad spectrum of sizes, body shapes, feeding types, developmental rates, and habitat preferences (Orton, 1953; Altig and Johnston, 1989; McDiarmid and Altig, 1999). Comparative morphological studies have shown that there is substantial morphological diversity among larvae that has not yet been fully analyzed and synthesized (e.g., Pusey, 1943; Sokol, 1977a, 1981; Wassersug, 1980, 1989; Wassersug and Rosenberg, 1979; Fabrezi and Lavilla, 1992, 1993; Haas, 1996, 1997, 2001; Haas and Richards, 1998; Larson and de Sá, 1998; Cannatella, 1999; Maglia et al., 2001). Some larval features, particularly external features such as the mouthparts and the position of the spiracle opening, have been an integral part of frog systematics for more than 50 years (Noble, 1925; Orton, 1953; Inger, 1967; Duellman and Trueb, 1986; Ford and Cannatella, 1993). But for a long time, the use of larval characters in phylogenetic studies has hardly advanced beyond the use of Orton's general tadpole types (Orton, 1953), despite the accumulating morphological evidence. Among others, Pusey (1943) and Sokol (1981) have discussed the potential phylogenetic significance of larval internal anatomical features, but the first cladistic analyses of selected larval characters and taxa were published only since the 1990s (Haas, 1996, 1997; Larson and de Sá, 1998). Recently Maglia et al. (2001) presented a combined analysis of larval and adult characters.

The present study analyzes the contribution of a data set with predominantly larval anuran characters to our understanding of frog phylogeny. It includes characters and cladistically codes character states described in the literature and in the author's previous work (Haas, 1995, 1996, 1997, 2001), but also introduces some new characters. The vast majority of the data presented stems from personal examination of specimens. Larval morphological characters are not thought to be superior to any other data and the emphasis on larvae is due to the author's focus. The data set includes some well-established adult characters adopted from the literature, but neglects many others that await verification for the species examined. A long-term endeavor that will expand this data set by adult and molecular characters in a simultaneous analysis (Kluge, 1989; Nixon and Carpenter, 1996) will be pursued in the future. At present, this study aims to introduce a large data set with a broad species sample and to discuss conflicts and new insights as compared to previous hypotheses of anuran phylogeny.

Materials and methods

Sampling strategy

The effects of character and taxon sampling on cladistic analyses are complex (e.g., Huelsenbeck, 1991; Lecointre et al., 1993, 1994; Graybeal, 1998; Hillis, 1998; Wiens, 1998). Many phylogenetic studies have used higher taxa (genera, families) rather than species as terminals in cladistic analyses (among many others, Gauthier et al., 1988; Trueb and Cloutier, 1991; Hay et al., 1995). The present study pursues an "exemplar" approach in which exclusively species are used as terminals and stand for higher taxonomic entities (Yeates, 1995; Bininda-Emonds et al., 1998).

Choice of taxa in this study followed several criteria: (1) sample size (due to limitations in resources, the taxon sample was arbitrarily restricted to 81 ingroup species);. (2) inclusion of representatives of all known major clades or taxonomic groups and sampling of different subgroups or geographic regions within large clades; (3) inclusion of known basal groups guided by prior knowledge, including species close to an assumed clade's ancestral node (i.e., species with an expected high number of plesiomorphic character states); for example, *Scaphiophryne madagascariensis* was selected because previous studies suggested its basal position within the Microhylidae (Wassersug, 1984, 1989); (4) taxa with controversial status (for example, *Hemisus* and *Heleophryne*); (5) closely related species of small monophyletic genera, to demonstrate the variation of characters at the generic level in genera thought to be monophyletic based on independent evidence (species of *Bombina*, *Discoglossus*, *Pseudis*, and *Phyllomedusa*); and (6) representation of ecomorph and size diversity. Unusual or bizarre tadpoles (*Lepidobatrachus laevis* or *Cochranella granulosa*), small tadpoles (*Atelopus*), and the largest known tadpole (*Pseudis paradoxa*) were included to capture some of the larval ecological and morphological diversity.

The Caudata was considered the sister group of the Anura (Trueb and Cloutier, 1991; Zardoya and Meyer, 2001) and was chosen as outgroup taxon (*Ambystoma mexicanum*, *Pleurodeles waltl*, *Salamandrella keyserlingii*, *Triturus alpestris*). The Gymnophiona was not included in the phylogenetic analysis, because only a fraction of the relevant characters in this study are currently available for caecilian larvae in sufficient detail (e.g., Edgeworth, 1935; Haas, 2001).

Data

There are only a very few anuran species for which an extensive list of larval morphological features can be extracted from published work. In this study the vast majority of characters and character states was deter-

mined by personal examination. Data in this study comprise three classes or qualities: first, character states exclusively derived from personal examination (characters 1–136); second, character states both obtained from the literature and derived from personal observations (characters 137–143 and 156); third, character states exclusively obtained from the literature (characters 144–156), mostly by extrapolation from higher taxa diagnoses to the species examined (see character descriptions for details). The emphasis of this work is on first-hand larval data; therefore, the number of (adult) characters and the use of secondary data from the literature were kept low. In the first class of characters, missing data were due mostly to insufficient quality of the materials and preparations examined or to the lack of larvae in appropriate stages of ontogeny.

The selection and definition of characters are as pivotal as the selection of taxa. The exclusion of characters (equivalent to assigning character weight 0) is the strongest bias that an investigator can exert. However, selecting characters based on preexisting knowledge and subjective experience is unavoidable given the limitations of time and resources. In this study, many characters were chosen based on previously presented considerations and rationale (especially Haas (1996, 1997, 2001), and many other authors cited in character descriptions). Ford and Cannatella's (1993) review of frog systematics unfortunately could not be fully integrated because a data matrix that specified the character state distribution and the species examined was not available. Some interesting larval characters described in the literature had to be excluded because personal examination was not possible, data existed for only a few taxa, or wide variation precluded reliable extrapolation to the species sample in this study. See, for example, characters in Nishikawa and Wassersug (1989) and Goree and Wassersug (2001). On the other hand, the present analysis does not exclude some controversial characters that were criticized or dismissed by others (see details in character descriptions).

Character state coding should take into account that states are logically related transformations or variables of "the same thing." The fundamental question of what are "the same things" in two taxa (conjectured or primary homology: de Pinna, 1991; topographical identity: Brower and Schawaroch, 1996) was answered with traditional criteria for establishing relations of similarities (Remane, 1952; Patterson, 1982; Rieppel, 1988; see Haas (2001) on anuran larvae jaw musculature).

Characters inapplicable for only some of the taxa were split into two hierarchically related characters (conventional coding) whenever possible; however, composite coding (multistate characters) was used in some characters. Both methods have deficiencies (Hawkins et al., 1997; Lee and Bryant, 1999; Strong and Lipscomb, 1999). Conventional coding is preferred

because it retrieves information about higher-level characters (e.g., anuran autapomorphies inapplicable in caudates), which would otherwise not be explicit.

A great number of characters in published works are described in discrete character states ("qualitative"), although they are derived from fundamentally continuous properties (e.g., Wiens, 2001). In such characters discrete states primarily come about by semantic filtering (Chappill, 1989; Stevens, 1991; Thiele, 1993). Neglect in describing the delimitation of the states in published articles is common. There is much controversy concerning whether continuous characters should be used in cladistics at all (Pimentel and Riggins, 1987; Chappill, 1989; Thiele, 1993; Rae, 1998; Wiens, 2001) and there are no rules for how to code character states "correctly." In this study the coding of character states was done pragmatically. Four obviously continuous characters were measured and coded according to the gap weighting procedure proposed by Thiele (1993). Deviating from Thiele's original approach, no population means could be determined due to the limited materials available. Other essentially continuous characters were coded "traditionally" when measurements seemed impractical or impossible or when clear gaps justified discrete states. The major goal was, however, to supply adequate documentation to ensure reproducibility of character coding.

Cladistic analysis

A total of 156 characters (Appendix) were scored for 4 caudate (outgroup) and 81 anuran species. *Triturus alpestris* was identical in all character states with *Ambystoma mexicanum* and was excluded from the analysis. Character 102 (ribs) was scored but excluded from the analysis (see character's description).

Cladistic analyses were performed on Apple Macintosh G3 (300 MHz processor, 256 MB RAM), Apple Macintosh G4 (400 MHz, 320 MB RAM), and Powerbook G3 (400 MHz, 320 MB RAM) computers. PAUP* (Versions 4.0b4a to 4.0b10 PPC; Swofford, 2002) and MacClade 4 (Maddison and Maddison, 2000) software packages were used for parsimony searches, character editing, and cladogram examinations.

The analyses included only informative characters. Multiple character states observed in a species were treated as polymorphisms. Two heuristic search strategies were used to find minimum-length trees. First, searches were conducted with 10,000 random-addition replicates (tree bisection–reconnection (TBR), MulTrees off). Minimal trees from these replicates were subjected to another round of branch swapping (TBR, MulTrees on). Second, the shortest topology was also searched for by runs of the parsimony ratchet (Nixon, 1999) using adjusted PAUP batch files generated with PAUPRat (Sikes and Lewis, 2001). A subset of the data (morphometric characters 12, 83, 116, and 117 excluded) was analyzed

with ratchet runs in PAUP and NONA version 2.0 software (Goloboff, 1996), the latter on a personal computer with a Pentium III (600 MHz) processor.

Characters 29, 31, 37, 39, 46, 58, 60, 64, 65, 77, 78, 90, 108, 139, and 150 were set to character type "ordered." Other multistate characters without apparent transformation series in their states were set to character type "unordered." Morphometric, gap-weighted characters (12, 83, 116, and 117) had ordered states in all analyses (26 possible character states in MacClade's extended standard format). The weight of gap-weighted morphometric characters was subjectively set to 0.08 in the analyses. In the unlikely event of a maximum change at a given node in the cladogram from state 0 to state 26 the change would add two steps to the tree length at that node. A more likely transition covering half the range would add one step. This weight appeared reasonably balanced with non-morphometric characters, which were assigned weight 1. The overall effect of the four morphometric characters was assessed by excluding them in some of the heuristic searches. Bremer support metrics were done for the data set without morphometric characters with the help of TreeRot 2.0 software (Sorenson, 1999).

Breeding frogs in the lab

Twenty-three species of frogs were bred in the author's lab and their tadpoles were collected at various stages (Table 1). Spawning was induced by simulation of natural conditions (sprinkler system), hormone injections, or both (for example, Haas, 1999b). For stimulation, subcutaneous injections of the LH-RH agonist des-gly[10] ([D-Ala[6]]-LH-RH-ethylamide) (Sigma L4513; diluted in physiological NaCl solution) worked successfully in many neobatrachian species (approx. 1 µg per 50 g body mass), whereas in discoglossid frogs, human chorionic gonadotropin (Sigma CG5-1VL) induced reproduction most reliably.

Laboratory procedures

Staging followed Gosner (1960). Tadpoles from breedings were killed in chlorobutanol (Sigma T-5138) and fixed in neutral-buffered formalin (4–10%) (Böck, 1989). Four sources of information were used for each species: (1) plain preserved specimens (external characters), (2) serially sectioned specimens (soft tissue, musculature, and skeletal characters), (3) manually dissected specimens (soft tissue and musculature), and (4) cleared and stained whole-mount preparations (mostly skeletal characters). The protocol by Taylor and van Dyke (1985) was applied for preparing cleared whole-mount specimens. Specimens that had been stored in preservatives for more than 5 years (many from museum collections) gave poor results in clearing and staining preparations. To avoid this in the future, it is recommended that some freshly preserved specimens from field collections should be cleared and stained immediately for storage in museum collections.

For serial sectioning, specimens were decalcified (Dietrich and Fontaine, 1975), dehydrated, embedded in paraffin, and sectioned at thicknesses from 8 µm (small larvae) to 12 µm (large larvae). Sectioning was performed on a Microm HM360 rotary microtome equipped with the Microm water transfer system. Sections were stained with Azan trichrome (Böck, 1989). Specimens for manual dissection were prepared by applying only the first staining step (Alcian blue) of the clearing and staining protocol. This procedure yields good contrast between dark-blue-stained cartilages and white muscles. Three-dimensional computer-aided reconstructions from serially sectioned specimens were done with Alias-Wavefront Studio 8.5 software (Haas and Fischer, 1997). Digital photographs of the cranium, hyobranchial apparatus, and skin were captured and measured with a Zeiss SV11 stereomicroscope equipped with a digital video camera (ColorView 12, software analySIS; both Soft Imaging System GmbH, Germany).

Nomenclature

Terms used for higher taxonomic units within the Anura largely follow Ford and Cannatella (1993), but the Bombinatoridae and the Discoglossidae are combined here into the Discoglossidae in their traditional meaning. Species names are in accord with Frost (2002). Capitalized higher taxon names are applied to monophyletic groups. Terms for skeletal parts and ligaments follow terminology in earlier works (Haas, 1995, 1996, 1997, 2001; Haas and Richards, 1998) and the respective sources listed therein. The nomenclature of cranial muscles was justified elsewhere (Haas, 1997, 2001).

Results

Heuristic searches with extensive random-addition sequence replicates and parsimony ratchet both found minimal-length topologies of 711.60 steps. TBR swapping of minimal-length trees from 10,000 random-addition replicates led to 268 trees (711.60 steps, CI 0.32, HI 0.69, RI 0.76). Their strict consensus tree is shown in Fig. 1.

The three search strategies (ratchet PAUP, ratchet NONA, and heuristic PAUP) performed under exclusion of morphometric characters led to identical strict consensus topologies (Fig. 2), although the class of all possible minimum-length trees was most completely sampled in heuristic searches with PAUP using random-addition sequences and subsequent TBR swapping (15,868 trees, tree length 675 steps [multistate taxa as polymorphism], CI 0.33, HI 0.69, RI 0.77).

The ingroup Anura (Fig. 2, node 0) was the most robustly supported clade with a large series of autapo-

Table 1
Specimens examined in this study (each individual identified by a study ID)

Taxon	Collection	Study ID	Stage	Prep.	Locality
Caudata					
Ambystoma mexicanum (Shaw, 1789)	InstSystZ, Jena	Amby 1	24 mm HT	S	Captive breeding group; locality unknown
	,,	Amby 2	29 mm HT	CL	,,
	,,	Amby 3	39 mm HT	D	,,
	,,	Amby 4	29 mm HT	CL	,,
	,,	Amby 5	39 mm HT	D	,,
	,,	Amby 6	20 mm HT	S	,,
Pleurodeles waltl (Michahelles, 1830)	InstSystZ, Jena	Pleuro 1	17 mm HT	S	Captive breeding group; locality unknown
	,,	Pleuro 2	18 mm HT	D	,,
	,,	Pleuro 3	17 mm HT	D	,,
	,,	Pleuro 4	17 mm HT	D	,,
Salamandrella keyserlingii (Dybowski, 1870)	InstSystZ, Jena	Sala 1	15 mm HT	S	Unknown
	,,	Sala 2	29 mm TL	CL	,,
	,,	Sala 3	31 mm TL	CL	,,
	,,	Sala 4	18 mm HT	D	,,
Triturus alpestris (Laurenti, 1768)	InstSystZ, Jena	Trit 1	26 mm HT	S	Germany: Thuringia: Schnellbach; 725 m elevation; Coll. A. Haas
	,,	Trit 2	31 mm HT	S	,,
	,,	Trit 3	14 mm HT	CL	,,
	,,	Trit 4	16 mm HT	CL	,,
	,,	Trit 5	15 mm HT	D	,,
Anura					
Ascaphidae					
Ascaphus truei (Stejneger, 1899)	InstSystZ, Jena	Asca 1	31	S	USA: Washington: King Co.: Snoqualmie Pass. Coll. J. Reiss
	,,	Asca 2	35	S	,,
	,,	Asca 3	36	D	,,
	,,	Asca 4	37	CL	,,
	,,	Asca 5	42	S	,,
	,,	Asca 6	43	S	,,
	,,	Asca 7	43	S	,,
	,,	Asca 8	45	D	,,
	USNM 511149	Asca 9	38	S	(See museum field notes)
	USNM 511150	Asca 10	39	S	,,
	USNM 511152	Asca 11	37	CL	,,
	USNM 511151	Asca 12	39	CL	,,
	USNM 511153	Asca 13	29	CL	,,
	USNM 511154	Asca 14	30	CL	,,
Discoglossidae					
Alytes obstetricans (Laurenti, 1768)	InstSystZ, Jena	Alytes 1	36	D	Germany: Thuringia: Schnellbach; 725 m elevation; Coll. A. Haas
	,,	Alytes 2	35	S	,,
	,,	Alytes 3	35	S	,,
	,,	Alytes 4	34	CL	,,
	,,	Alytes 5	38	CL	,,
	,,	Alytes 6	35	CL	,,
	,,	Alytes 7	36	CL	,,
	,,	Alytes 8	34	CL	,,
	,,	Alytes 9	35	D	,,
Bombina maxima (Boulenger, 1905)	InstSystZ, Jena	Maxi 1	38	S	Captive breeding group
	,,	Maxi 2	39	D	,,
	,,	Maxi 3	38	D	,,
	,,	Maxi 4	38	CL	,,
	,,	Maxi 5	37	CL	,,
	,,	Maxi 6	39	S	,,

Table 1 (continued)

Taxon	Collection	Study ID	Stage	Prep.	Locality
Bombina orientalis (Boulenger, 1890)	InstSystZ, Jena	Bom or 1	36	D	Captive breeding group; locality unknown
	”	Bom or 2	37	D	”
	”	Bom or 3	35	S	”
	”	Bom or 4	37	S	”
	”	Bom or 5	39	S	”
	”	Bom or 6	43	S	”
	”	Bom or 7	44	S	”
	”	Bom or 8	46	S	”
	”	Bom or 9	37	CL	”
	”	Bom or 10	37	CL	”
	”	Bom or 11	38	CL	”
	”	Bom or 12	38	CL	”
	”	Bom or 13	31	CL	”
	”	Bom or 14	31	CL	”
	”	Bom or 15	39	CL	”
	”	Bom or 16	38	CL	”
Bombina variegata (Linnaeus, 1758)	InstSystZ, Jena	Bom var 1	36	S	Captive breeding group; locality unknown
	”	Bom var 2	37	S	”
	”	Bom var 3	39	S	”
	”	Bom var 4	46+	D	”
	”	Bom var 5	46+	D	”
	”	Bom var 6	37	D	”
	”	Bom var 7	38	D	”
	”	Bom var 8	30	CL	”
	”	Bom var 9	34	CL	”
	”	Bom var 10	37	CL	”
	”	Bom var 11	35	CL	”
	”	Bom var 12	39	CL	”
Discoglossus galganoi (Capula, Nascetti, Lanza, Bullini, and Crespo, 1985)	InstSystZ, Jena	Disco 1	34	S	Captive breeding group (Portugal: Almada City)
	”	Disco 2	37	S	”
	”	Disco 3	32	D	”
	”	Disco 4	37	D	”
	”	Disco 5	38	D	”
	”	Disco 9	39	CL	”
	”	Disco 10	39	CL	”
	”	Disco 11	46+	D	”
Discoglossus pictus (Otth, 1837)	InstSystZ, Jena	Disco 6	35	S	Captive breeding group (Spain: Barcelona?)
	”	Disco 7	36	S	”
	”	Disco 8	39	S	”
	”	Disco 12	31	CL	”
	”	Disco 13	32	CL	”
	”	Disco 14	36	CL	”
	”	Disco 15	37	CL	”
Pipidae					
Xenopus laevis (Daudin, 1802)	InstSystZ, Jena	Xen 1	38/39	S	Captive breeding group; locality unknown
	”	Xen 2	38/39	S	”
	”	Xen 3	40	D	”
	”	Xen 4	40	CL	”
	”	Xen 5	38	CL	”
	”	Xen 6	46	D	”
	”	Xen 7	45	D	”
	”	Xen 8	44	D	”
	”	Xen 9	44	D	”
	”	Xen 10	43/44	D	”
	”	Xen 11	43/44	D	”
	”	Xen 12	40	D	”
	”	Xen 14	38	CL	”

Table 1 (*continued*)

Taxon	Collection	Study ID	Stage	Prep.	Locality
”	”	Xen 15	38	CL	”
	”	Xen 16	39	CL	”
	”	Xen 17	40	CL	”
Pipa carvalhoi (Miranda-Ribeiro, 1937)	InstSystZ, Jena	Pipa 1	40	S	Captive breeding group; locality unknown
	”	Pipa 2	39	D/CL	”
	”	Pipa 3	38	D	”
Rhinophrynidae					
Rhinophrynus dorsalis (Duméril and Bibron, 1841)	USNM 330676	Rhino 1	40	D	Costa Rica
	USNM 330676	Rhino 2	40	D	”
	USNM 509987	Rhino 3	**	CL	”
	USNM 509988	Rhino 4	**	CL	”
	USNM 509990	Rhino 5	**	CL	”
	USNM 509991	Rhino 6	**	CL	”
	USNM 330676	Rhino 7	40	S	”
	USNM 330676	Rhino 8	39	S	”
Pelodytidae					
Pelodytes caucasicus (Boulenger, 1896)	InstSystZ, Jena	Dytes 1	27	CL	Turkey: Vilayet Rize: Senyuva (450 m). Coll. W. Böhme
		Dytes 2	27	CL	”
		Dytes 3	27	D	”
		Dytes 4	27	D	”
		Dytes 5	36	CL	”
		Dytes 6	35	CL	”
Pelobatidae					
Pelobates fuscus (Laurenti, 1768)	InstSystZ, Jena	Pelo 1	38	S	Germany: Thuringia: Hainspitz. Coll. G. Riemay
	”	Pelo 2	45	D	”
	”	Pelo 3	38	CL	”
	”	Pelo 4	42	CL	”
	ZMB 28151	Pelo 5	35	D	Germany: locality unknown
	”	Pelo 6	38	D	Germany: Thuringia: Geroda (Triptis)
Leptobrachium hasseltii (Tschudi, 1838)	FMNH 51025	Hassel 1	28	S	Philippine Isl.: Palawan: Iwahig, Lapulapu. Coll. F. Werner
	FMNH 63205	Hassel 3	25	CL	Philippine Isl.: Mindanao: Zamboanga: Katipunan, Sigayan. Coll.: D.S. Rabor
	FMNH 63205	Hassel 4	40	CL	”
	FMNH 63205	Hassel 2	31	D	”
Megophrys montana (Kuhl and Van Hasselt, 1822)	FMNH 50950	Mego 1	26	S	Philippine Isl.: Mindanao: Davao Prov.: Mt Apo, Meran. Coll. H. Hoogstraal
	FMNH 50950/796	Mego 2	26	D	”
	FMNH 50950/820	Mego 3	26	CL	”
	FMNH 50950/804	Mego 4	27	CL	”
	InstSystZ, Jena	Mego 5	46	CL	Captive breeding Karlsruhe
Scaphiopodidae					
Spea bombifrons (Cope, 1863)	KU 187630	Spea 1	38	S	USA: Kansas: Logan: 9.6 km S, 16.8 km E Russell Springs
	KU 187630	Spea 2	38	D	”
	KU 187630	Spea 3	38	CL	”
Myobatrachidae					
Limnodynastes peronii (Duméril and Bibron, 1841)	InstSystZ, Jena	Limno 1	31	D	Captive breeding group; locality unknown
	”	Limno 2	31	D	”
	”	Limno 3	30	D	”
	InstSystZ, Jena	Limno 4	39	S	”

Table 1 (*continued*)

Taxon	Collection	Study ID	Stage	Prep.	Locality
	,,	Limno 5	39	S	,,
	InstSystZ, Jena	Limno 6	31	D	,,
	,,	Limno 7	34	D	,,
	,,	Limno 8	39	D	,,
	,,	Limno 9	40	D	,,
	,,	Limno 10	40	D	,,
	,,	Limno 11	40	D	,,
	,,	Limno 12	40	D	,,
"Leptodactylidae"					
Ceratophrys ornata (Bell, 1843)	InstSystZ, Jena	Cerato 1	38	S	Argentina: Prov. Córdoba: Barreto. Coll. A. Martino, 30.
	,,	Cerato 2	39	D	,,
	,,	Cerato 3	37	D	,,
	,,	Cerato 4	38	CL	,,
	,,	Cerato 5	40	CL	,,
Crossodactylus schmidti (Gallardo, 1961)	USNM 253671	Crosso 1	26	S	Paraguay: Itapua: vicinity of El Tirol, 19.6 km (by road) NNE of Encarnacion on highway 6
	USNM 253671	Crosso 2	26	D	,,
	USNM 253671	Crosso 4	26	S	,,
	USNM 253671	Crosso 3	26	CL	,,
Hylodes meridionalis (Mertens, 1927)	InstSystZ, Jena	Hylod 1	38	CL	Basil: Pró-Mata: São Francisco de Paula. Coll. A. Kwet.
	,,	Hylod 2	29	D	,,
	,,	Hylod 3	28	S	,,
Lepidobatrachus laevis (Budgett, 1899)	InstSystZ, Jena	Lepido 1	42	S	Locality unknown. Coll. Ruibal.
	,,	Lepido 2	42	D	,,
	,,	Lepido 3	42	CL	,,
Leptodactylus latinasus (Jiménez de la Espada, 1875)	InstSystZ, Jena	Lati 1	40	S	Argentina: Prov. Córdoba: La Carlota: Laguna. Coll. A. Martino
	,,	Lati 2	36	S	,,
	,,	Lati 3	37	S	,,
	,,	Lati 4	40	S	,,
	,,	Lati 5	40	S	,,
	,,	Lati 6	40	D	,,
	,,	Lati 7	37	D	,,
Odontophrynus achalensis (Di Tada, Barla, Martori, and Cei, 1984)	InstSystZ, Jena	Odont ach 1	36	D	Argentina: Prov. Córdoba: Pampa de Achal. Coll. A. Martino
	,,	Odont ach 2	31	S	,,
	,,	Odont ach 3	38	S	,,
	,,	Odont ach 4	35	S	,,
	,,	Odont ach 5	34	CL	,,
	,,	Odont ach 6	35	CL	,,
	,,	Odont ach 7	40	CL	,,
	,,	Odont ach 8	39	CL	,,
	,,	Odont ach 9	40	CL	,,
	,,	Odont ach 10	35	CL	,,
	,,	Odont ach 11	35	CL	,,
	,,	Odont ach 12	38	D	,,
Physalaemus biligonigerus (Cope, 1860)	InstSystZ, Jena	Bili 1	39	S	Argentina: Prov. Córdoba: La Carlota: Laguna. Coll. A. Martino
	,,	Bili 2	40	S	,,
	,,	Bili 3	40	S	,,
	,,	Bili 4	34	S	,,
	,,	Bili 5	38	S	,,
	,,	Bili 6	40	D	,,
	,,	Bili 7	40	D	,,

Table 1 (*continued*)

Taxon	Collection	Study ID	Stage	Prep.	Locality
	,,	Bili 8	39	D	,,
Pleurodema kriegi (Müller, 1926)	InstSystZ, Jena	Kriegi 1	38	S	Argentina: Prov. Córdoba: Pampa de Achala
	,,	Kriegi 2	36	CL	,,
	,,	Kriegi 3	39	CL	,,
	,,	Kriegi 4	38	D	,,
	,,	Kriegi 5	39	D	,,
Heleophrynidae					
Heleophryne natalensis (Hewitt, 1913)	InstSystZ, Jena	Heleo 1	28	D	Rep. S. Africa: 28° 38'S, 28° 43'E, Qwa qwa. Coll. L. du Preez.
Dendrobatidae					
Mannophryne herminae (Boettger, 1893)	USNM 259177	Colo 1	37	S	Venezuela: Aragua: Parque Nacional Henri Pittier, Rancho Grande
	USNM 259177	Colo 2	34	CL	
	USNM 259177	Colo 3	37	D	,,
	USNM 259177	Colo 4	34	D	,,
Dendrobates tinctorius (Schneider, 1799)	InstSystZ, Jena	Dendro 1	39	S	Captive breeding group; locality unknown
	,,	Dendro 2	34	D	,,
	,,	Dendro 3	37	D	,,
	,,	Dendro 4	31	CL	,,
	,,	Dendro 5	37	CL	,,
	,,	Dendro 6	38	CL	,,
Epipedobates tricolor (Boulenger, 1899)	InstSystZ, Jena	Epi 1	34	CL	Captive breeding group; locality unknown
	,,	Epi 2	36	CL	,,
	,,	Epi 3	39	CL	,,
	,,	Epi 4	40	CL	,,
	,,	Epi 5	39	D	,,
	,,	Epi 6	33	D	,,
	,,	Epi 7	39	S	,,
Phyllobates bicolor (Duméril and Bibron, 1841)	InstSystZ, Jena	Phyll 1	36	D	Captive breeding group; locality unknown
	,,	Phyll 2 01G38	38	S	,,
	,,	Phyll 3 01G39	39	S	,,
	,,	Phyll 4	38	CL	,,
	,,	Phyll 5	36	CL	,,
	,,	Phyll 6	39	D	,,
	,,	Phyll 7	39	D	,,
	,,	Phyll 8	36	CL	,,
	,,	Phyll 9	38	CL	,,
Centrolenidae					
Cochranella granulosa (Taylor, 1949)	USNM 291045	Cochra 1	29	S	Costa Rica: Guanacaste: 1.7 km SE of Tilaram, on road to Quebrada Grande. Coll. M.S. Foster
	USNM 291045	Cochra 2	27	CL	,,
	USNM 291045	Cochra 3	28	D	,,
Hylidae					
Agalychnis callidryas (Cope, 1862)	USNM 498397	Agaly 1	40	S	Costa Rica: Limon: 5 km SW of Siquirres
	USNM 498397	Agaly 3	36	D	,,
	USNM 498397	Agaly 2	37	CL	,,
Aplastodiscus perviridis A. (Lutz, 1950)	InstSystZ, Jena	Aplasto 1	26	S	Brasil: Pró-Mata: São Francisco de Paul. Coll. A. Kwet.
	,,	Aplasto 3	33	D	,,
	,,	Aplasto 2	40	CL	,,

Table 1 (*continued*)

Taxon	Collection	Study ID	Stage	Prep.	Locality
Gastrotheca riobambae (Fowler, 1913)	InstSystZ, Jena	Gastro 1	36	S	Ecuador: Napo: Papa Llacta, 3500 m elev./Pichicha, Lloa. 2900 m elev. Coll. E. Del Pino
	,,	Gastro 4	40	CL	,,
	,,	Gastro 5	38	D	,,
Hyla annectans (Jerdon, 1870)	InstSystZ, Jena	Annect 1	40	S	Captive breeding group; locality unknown
	,,	Annect 2	40	S	,,
	,,	Annect 3	38	CL	,,
	,,	Annect 4	40	CL	,,
	,,	Annect 5	36	D	,,
	,,	Annect 6	38	D	,,
	,,	Annect 7	37	S	,,
Hyla ebraccata (Cope, 1874)	InstSystZ, Jena	Ebracca 1	38	S	Captive breeding group (N. Meyer); locality unknown
	,,	Ebracca 2	39	CL	,,
	,,	Ebracca 3	40	D	,,
	,,	Ebracca 4	40	D	,,
	,,	Ebracca 5	33	CL	,,
	,,	Ebracca 6	40	CL	,,
Hyla cinerea (Schneider, 1799)	InstSystZ, Jena	Ciner 1	39	S	Captive breeding group; locality unknown
	,,	Ciner 2	37	CL	,,
	,,	Ciner 3	38	D	,,
Hyla pulchella cordobae (Barrio, 1965)	InstSystZ, Jena	Pulch 1	30	S	Argentina: Prov. Córdoba: Pampa de Achala, ca. 2000 m elevation. Coll. A. Haas
	,,	Pulch 2	37	S	,,
	,,	Pulch 3	36?	CL	,,
	,,	Pulch 4	38	CL	,,
	,,	Pulch 5	38	CL	,,
	,,	Pulch 6	38	D	,,
Litoria genimaculata (Horst, 1883)	KU 224676	Geni 1	37	S	Australia: Queensland: Paluma: Mt. Spec State Forest, 800 m, 146° 10'E, 18° 49'S. Coll. S. Richards
	,,	Geni 2	34	CL	,,
	,,	Geni 3	37	CL	,,
	InstSystZ, Jena	Geni 4	39	D	,,
	,,	Geni 5	31	D	,,
	InstSystZ, Jena	Geni 6	40	S	,,
Litoria inermis (Peters, 1867)	InstSystZ, Jena	Inerm 1	41	CL	Australia: Queensland: Townsville. Coll. A. Haas
	,,	Inerm 2	30	CL	,,
	,,	Inerm 3	35	D	,,
	,,	Inerm 4	39	D	,,
	,,	Inerm 5	31	S	,,
Litoria lesueurii (Duméril and Bibron, 1841)	InstSystZ, Jena	Lesu 1	38	CL	Australia: Queenland: Townsville. Coll. A. Haas
	,,	Lesu 2	41	D	,,
	,,	Lesu 3	40	D	,,
	,,	Lesu 4	40	S	,,
	,,	Lesu 5	40		,,
Litoria nannotis (Andersson, 1916)	InstSystZ, Jena	Nanno 1	26	CL	Australia: Queensland: Tully valley. Coll. A. Coll. A. Haas
	KU 224681	Nanno 2	26/27	S	Australia: Queensland: Tully River tributary, 100 m, 50 km by road NW of Tully. Coll. S. Richards
	InstSystZ, Jena	Nanno 3	26	D	,,
	,,	Nanno 4	26/27	S	,,
Litoria rheocola (Liem, 1974)	InstSystZ, Jena	Rheoco 1	38	D	Australia: Queensland: Tully valley. Coll. S. Richards
	,,	Rheoco 2	26	S	,,

Table 1 (*continued*)

Taxon	Collection	Study ID	Stage	Prep.	Locality
Nyctimystes dayi (Günther, 1897)	InstSystZ, Jena	Dayi 1	41	CL	Australia: Queensland: Tully River tributary, 100 m, 50 km by road NW of Tully. Coll. A. Haas
	,,	Dayi 2	26	D	,,
	,,	Dayi 3	26	S	,,
Osteocephalus planiceps (Cope, 1874)	InstSystZ, Jena	Osteo 1	39	S	Ecuador: Napo: Jatun Sacha. Coll. K.-H. Jungfer
	,,	Osteo 2	37	CL	,,
	,,	Osteo 3	37	D	,,
	,,	Osteo 4	34	D	,,
Pseudis minuta (Günther, 1859 "1858")	InstSystZ, Jena	Pseud 1	39	S	Brasil: Guaritas, Caçapava do Sul. Coll. A. Kwet.
	,,	Pseud 2	40	CL	,,
	,,	Pseud 3	40	D	,,
Pseudis paradoxa (Linnaeus, 1758)	InstSystZ, Jena	Paradox 1	40	CL	Argentina: Corrientes, Don Luis. Coll. M. Duree
	,,	Paradox 2	39	D	,,
	,,	Paradox 3	29	S	,,
Phrynohyas resinifictrix (Goeldi, 1907)	InstSystZ, Jena	Trix 1	37	S	Brasil: Amazonas: Reserva Ducke, 25 N of Manaus. Coll. K.-H. Jungfer
	,,	Trix 2	37	CL	,,
	,,	Trix 3	41	CL	,,
	,,	Trix 4	40	D	,,
	,,	Trix 5	41	D	,,
Phyllomedusa distincta B. (Lutz, 1950)	InstSystZ, Jena	Medusa 1	31	S	Brasil: Terra de Areia, N Porto Allegre. Coll. A. Kwet
	,,	Medusa 2	38	CL	,,
	,,	Medusa 3	37	D	,,
Phyllomedusa trinitatis (Mertens, 1926)	InstSystZ, Jena	Trinit 1	37	S	Trinidad. Coll. C. Proy
	,,	Trinit 2	43	S	,,
	,,	Trinit 3	38	CL	,,
	,,	Trinit 4	36	D	,,
	,,	Trinit 5	38	S	,,
Phyllomedusa vaillantii (Boulenger, 1882)	InstSystZ, Jena	Vailla 1	38	S	Ecuador: Napo: "Selve Viva." 15 km downstream (Rio Napo) of Ahuano, 50 m elev. Coll; K.-H. Jungfer
	,,	Vailla 2	38	CL	,,
	,,	Vailla 3	37	D	,,
Scinax ruber (Laurenti, 1768)	InstSystZ, Jena	Sci 1	39	S	Captive breeding group originally from Frech Guyana: Cayenne: Close to the beach, near Novotel Hotel; Coll. A. Pieh
	,,	Sci 2	37	S	,,
	,,	Sci 3	40	S	,,
	,,	Sci 4	40	S	,,
	,,	Sci 5	42	S	,,
	,,	Sci 6	42	S	,,
	,,	Sci 7	43	S	,,
	,,	Sci 8	44	S	,,
	,,	Sci 9	46	S	,,
	,,	Sci 10	46	S	,,
	,,	Sci 11	46+	D	,,
	,,	Sci 13	38	CL	,,
	,,	Sci 14	40	CL	,,
	,,	Sci 15	40	CL	,,
	,,	Sci 16	38	D	,,
	,,	Sci 17	38	D	,,
Smilisca baudinii (Duméril and Bibron, 1841)	InstSystZ, Jena	Baudi 1	39	S	Captive breeding group; locality unknown

Table 1 (*continued*)

Taxon	Collection	Study ID	Stage	Prep.	Locality
	,,	Baudi 2	41	S	,,
	,,	Baudi 3	36	CL	,,
	,,	Baudi 4	37	CL	,,
	,,	Baudi 5	38	CL	,,
	,,	Baudi 6	40	CL	,,
	,,	Baudi 7	40	CL	,,
	,,	Baudi 8	40	CL	,,
	,,	Baudi 9	35	D	,,
	,,	Baudi 10	36	D	,,
Bufonidae					
Atelopus tricolor (Boulenger, 1902)	USNM 346228	Atelop 1	36	S	Peru: Cuzco: 55 km (by road) NE of Paucartambo, Quebrada Morro Leguia (km 137 of Paucartambo — Atalaya Road). Coll. R.P. Reynolds, R.W. Bouchard
	USNM 346228	Atelop 2	36	CL	,,
	USNM 346228	Atelop 3	36	D	,,
Melanophryniscus orejasmirandai (Prigioni and Langone, 1987 "1986")	InstSystZ, Jena	Mphryn 1	37	D	Uruguay:Dept. de Maldonado: Sierra de las Animas. Coll. R. de Sá
	,,	Mphryn 2	29	S	,,
Bufo arenarum (Hensel, 1867)	InstSystZ, Jena	Arena 1	39	S	Argentina: Prov. Córdoba: Rio Cuarto. Coll. S. Stoll
	,,	Arena 2	40	S	,,
	,,	Arena 3	41	S	,,
	,,	Arena 4	46	S	,,
	,,	Arena 5	36	CL	,,
	,,	Arena 6	39	CL	,,
	,,	Arena 7	41	CL	,,
	,,	Arena 8	43	CL	,,
	,,	Arena 9	38	D	,,
	,,	Arena 10	37	D	,,
Bufo bufo (Linnaeus, 1758)	InstSystZ, Jena	Bubu 1	38	S	Germany: Thuringia: City of Jena: Botanical Garden. Coll. A. Haas
	,,	Bubu 2	39	D/CL	,,
	,,	Bubu 3	38	CL	,,
	,,	Bubu 4	41	CL	,,
	,,	Bubu 5	45	D	Germany: Thuringia: Hainspitz
	,,	Bubu 6	45	D	,,
	,,	Bubu 7	45	D	,,
		Bubu 8	40	D	,,
	,,	Bubu 9	41	D	,,
		Bubu 10	38	S	Germany: Thuringia: City of Jena: Botanical Garden. Coll. A. Haas
Bufo brongersmai (Hoogmoed, 1972)	InstSystZ, Jena	Bonger 4	36	D	Captive breeding group; locality unknown
	,,	Bronger 1	36	CL	,,
	,,	Bronger 2	39	CL	,,
	,,	Bronger 3	37	D	,,
	,,	Bronger 5	36	CL	,,
Bufo marinus (Linnaeus, 1758)	InstSystZ, Jena	Marin 1	39	S	Captive breeding group: locality unknown
	,,	Marin 2	38	CL	,,
	,,	Marin 3	38	CL	,,
	,,	Marin 4	40	D	,,
	,,	Marin 5	40	D	,,
Bufo melanostictus (Schneider, 1799)	InstSystZ, Jena	Melano 1	40	S	Captive breeding group; locality unknown
	,,	Melano 2	37	S	,,

Table 1 (*continued*)

Taxon	Collection	Study ID	Stage	Prep.	Locality
	,,	Melano 3	39	CL	,,
	,,	Melano 4	41	CL	,,
	,,	Melano 5	36	CL	,,
	,,	Melano 6	46	D	,,
	,,	Melano 7	46	D	,,
	,,	Melano 8	45	D	,,
	,,	Melano 9	45	D	,,
	,,	Melano 10	45	D	,,
	,,	Melano 11	34	CL	,,
	,,	Melano 12	34	CL	,,
	,,	Melano 13	37	CL	,,
	,,	Melano 14	37	CL	,,
	,,	Melano 15	38	CL	,,
	,,	Melano 16	38	CL	,,
	,,	Melano 17	38	CL	,,
	,,	Melano 18	31	D	,,
	,,	Melano 19	31	D	,,
Pedostibes hosii (Boulenger, 1892)	FMNH 83031	Hosei 1	37	S	Sarawak: Patah River. Coll. N.S. Haile
	FMNH 83031	Hosei 2	38	S	,,
	FMNH 83031	Hosei 3	37	CL	,,
	FMNH 83031	Hosei 4	34	D	,,
Peltophryne peltocephala (Tschudi, 1838)	USNM 317860	Pelto 1	29	S	Cuba: Guantanamo: US Naval Base Guantanamo Bay: Kittery Beach Road, 2.5 miles from junction with Sherman Ave. Coll. R.I. Crombie, L.K. Gordon
	USNM 317860	Pelto 2	28	S	,,
	USNM 317860	Pelto 3	27	CL	,,
	USNM 317860	Pelto 4	30	D	,,
Ranidae					
Paa exilispinosa (Liu and Hu, 1975)	InstSystZ, Jena	Paa 1	39	CL	Captive breeding group originally from Hong Kong: Lantau Island: Sunset Peak. Coll. S. Voitel
	,,	Paa 2	36	D	,,
	,,	Paa 3	27	S	,,
Ptychadena mascareniensis (Duméril and Bibron, 1841)	CAS 165148	Ptych 1	40	S	Kenya: Kilifi Dist.: Malindi-Mombasa Rd, 3.0 km S of Watamu jct, 1 km W on dirt rd, flooded sand quarry. Coll. R.C. Drewes and J.V. Vindum
	CAS 165148	Ptych 2	36	CL	
	CAS 165148	Ptych 3	38	CL	,,
	InstSystZ, Jena	Ptych 4	37	D	Captive breeding group originally from Tanzania: Arusha National Park. Coll. M. Welte
	,,	Ptych 5	38	D	
	,,	Ptych 8	38	S	,,
	,,	Ptych 9	40	CL	,,
	,,	Ptych 10	39	CL	,,
Pyxicephalus adspersus (Tschudi, 1838)	InstSystZ, Jena	Pyxi 1	33	S	Captive breeding group; locality unknown
	,,	Pyxi 2	39	S	,,
	,,	Pyxi 3	40	D	,,
	,,	Pyxi 4	40	CL	,,
Rana nigrovittata (Blyth, 1856 "1855")	InstSystZ, Jena	Cubi 1	33	D	Captive breeding group originally from West Thailand: Tham Tan Lod National Park, Kanchana-buri Coll. K.-D. Kühnel

Table 1 (*continued*)

Taxon	Collection	Study ID	Stage	Prep.	Locality
	''	Cubi 2	33	D	''
	''	Cubi 3	36	D	''
	''	Cubi 4	37	S	''
	''	Cubi 5	38	CL	''
	''	Cubi 6	41	CL	''
Rana temporaria (Linnaeus, 1758)	InstSystZ, Jena	R temp 1	40	D	Germany: Thuringia: Schnellbach; 725 m elevation; Coll. A. Haas
	''	R temp 3	46	D	''
	''	R temp 2	40	S	''
	''	R temp 4	40	D	''
	''	R temp 5	40	CL	Germany: Thuringia: Schnellbach; 725 m elevation; Coll. A. Haas
	''	R temp 6	40	D	Germany: Thuringia: Geroda. Coll. A. Haas
	''	R temp 7	35	D	''
Limnonectes leporinus (Andersson, 1923)	FMNH 96009	Lnect 1	33	S	Sarawak: Baleh River tributary. Coll. N.S. Haile
	FMNH 96009	Lnect 2	37	S	''
	FMNH 96009	Lnect 3	39	CL	''
	FMNH 96009	Lnect 4	35	D	''
	FMNH 96009	Lnect 5	37	D	''
Tomopterna cryptotis (Boulenger, 1907)	InstSystZ, Jena	Tomo 1	40	S	Rep. South Africa: Makwassi: 27° 10'S, 25° 58'E. Coll. L. Du Preez
	''	Tomo 2	41	CL	''
	''	Tomo 3	40	D	''
Microhylidae					
Dyscophus antongilii (Grandidier, 1987)	InstSystZ, Jena	Anton 1	40	S	Captive breeding group
	''	Anton 2	40	D	Captive breeding group
Elachistocleis bicolor (Valenciennes, 1838)	InstSystZ, Jena	Elach 1	36	S	Argentina: Prov. Córdoba: Barreto, 33° 20'43''S, 63° 18'20''W, 153 m elev.; Coll. A. Martino (Herpet. Rev. 1999 30(2), 106)
	''	Elach 2	36	CL	''
	''	Elach 3	37	CL	''
	''	Elach 4	34	D	''
	''	Elach 5	34	D	''
Gastrophryne carolinensis (Holbrook, 1836)	InstSystZ, Jena	Gphryne 1	35	S	USA: MS: Oktibbeha Co.: 2.4 km E of Starkville. Coll. R. Altig
	''	Gphryne 2	34	CL	''
	''	Gphryne 3	34	D	''
	''	Gphryne 4	34	D	''
Hamptophryne boliviana (Parker, 1927)	KU 124219	Hampto 1	38	S	Ecuador: Napo: NA: Santa Cecilia, 340 m
	KU 218351	Hampto 2	41	CL	Ecuador: Sucumbios: NA: 2.5 km N Lago Agrio, 350M. Coll. S. Valdivieso, D. Tirira, J. Wiens
	KU 124219	Hampto 3	39	D	Ecuador: Napo: NA: Santa Cecilia, 340 m
Kaloula pulchra (Gray, 1831)	InstSystZ, Jena	Kalou 1	39	S	captive breeding group; locality unknown
	''	Kalou 2	40	CL	''
	''	Kalou 3	39	CL	''
	''	Kalou 4	39	D	''
	''	Kalou 5	39	D	''
	''	Kalou 6	46+	D	''
	''	Kalou 7	43	D	''
	''	Kalou 8	44	D	''

Table 1 (*continued*)

Taxon	Collection	Study ID	Stage	Prep.	Locality
	,,	Kalou 9	42	D	,,
Phrynomantis bifasciatus (Smith, 1847)	CAS 165127	Phryno 1	34	S	Kenya: Kilifi Dist.: Malindi-Mombasa Rd, 3.0 km S of Watamu jct, 1 km W on dirt rd, flooded sand quarry, R.C. Drewes and J.V. Vindum
	CAS 165127	Phryno 2	33	S	,,
	CAS 165127	Phryno 3	39	CL	,,
	CAS 165127	Phryno 4	40	D	,,
Paradoxophyla palmata (Guibé, 1974)	InstSystZ, Jena	Palmata 1	40	D/CL	East Madagascar: Ankeniheny. Coll. F. Glaw
	,,	Palmata 2	40	D	,,
	,,	Palmata 3	31	S	,,
Scaphiophryne madagascariensis (Boulenger, 1882)	InstSystZ, Jena	Scaph 1	39	D	Central Madagascar: Andringitra Mountains. Coll. F. Glaw & M. Vences
	,,	Scaph 2	36	D	,,
	,,	Scaph 3	38	S	,,
Rhacophoridae					
Rhacophorus pardalis (Günther, 1859 "1858")	FMNH 241944	Rhaco 1	41	S	Malaysia: Sabah: Kota Marudu: Marak-Parak, Kindingon. Coll. R.F. Inger
	FMNH 241943	Rhaco 2	41	CL	,,
	FMNH 241943	Rhaco 3	41	D	,,
	FMNH 241943	Rhaco 4	38	D	,,
Chiromantis xerampelina (Peters, 1854)	InstSystZ, Jena	Chiro 1	33	S	Progeny of breeding group from Mozambique, exact locality unknown
	,,	Chiro 2	32	CL	,,
	,,	Chiro 3	33	CL	,,
	,,	Chiro 4	33	CL	,,
	,,	Chiro 5	37	CL	,,
	,,	Chiro 6	30	D	,,
	,,	Chiro 7	31	D	,,
	,,	Chiro 8	40	CL	,,
	,,	Chiro 9	41	CL	,,
Hyperoliidae					
Hemisus sudanensis (Steindachner, 1863)	InstSystZ, Jena	Hemis 1	36	S	Cote d'Ivoire: Comoé National Park, 8° 5'–9° 6'N, 3° 1'–4° 4'W. Coll. M.-O. Rödel
	,,	Hemis 2	38	CL	,,
	,,	Hemis 3	40	CL	,,
	,,	Hemis 4	43	CL	,,
	,,	Hemis 5	34	S	,,
	,,	Hemis 5	32	CL	,,
Hyperolius puncticulatus (Pfeffer, 1893)	InstSystZ, Jena	Hyper 1	38	S	Progeny of breeding group from Tanzania, exact locality unknown
	,,	Hyper 2	36	CL	,,
	,,	Hyper 3	34	CL	,,
	,,	Hyper 4	41	CL	,,
	,,	Hyper 5	35	D	,,
	,,	Hyper 6	40	D	,,
Kassina senegalensis (Duméril and Bibron, 1841)	CAS 165151	Kass 1	32	S	Kenya: Kilifi Dist.: Malindi-Mombasa Rd, 3.0 km S of Watamu jct, 1.0 km W on dirt rd, flooded sand quarry. Coll. R.C. Drewes, S. Ashe and J.V.Vindum
	CAS 165151	Kass 2	33	D	,,
	CAS 165151	Kass 3	33	D	,,

Table 1 (*continued*)

Taxon	Collection	Study ID	Stage	Prep.	Locality
	InstSystZ, Jena	Kass 4	41	CL	Rep. South Africa: Bloemfontein: 29° 08'S, 24° 46'E. Coll. L. Du Preez
	”	Kass 5	31	CL	”
Leptopelis vermiculatus (Boulenger, 1909)	CAS 169936	Vermi 1	35	S	Tanzania: Tanga Region: Muheza Dist.: East Usambara Mtns., Amani, Amani Pond (Coco Yam Plantation. Coll. R.C. Drewes, K.M. Howell, J.V. Vindum
	CAS 169936	Vermi 2	28	CL	”
	CAS 169936	Vermi 3	34	CL	”
	CAS 169936	Vermi 4	34	D	”

CAS, California Academy of Sciences, San Francisco; CL, cleared and stained; Coll., collector; D, manual dissection; FMNH, Field Museum of Natural History, Chicago; InstSystZ, Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum Jena; KU, Natural History Museum Lawrence; Prep., type of preparation; S, serial histological section; USNM, National Museum of Natural History, Washington; ZMB, Museum für Naturkunde, Berlin. Staging of anuran specimens according to Gosner (1960), gymnophionans according to the table of Dünker et al. (2000).

morphic character states. Some characters supporting this node had two or more states in the ingroup but were absent in the outgroup (caudates). Conventional coding retrieved these apomorphic anuran characters (for example, suprarostrals).

In the analyses, *Ascaphus truei* was sister taxon to all other frogs. The Pipoidea was a highly supported clade with unambiguous internal pattern, i.e., *Rhinophrynus* being the sister group to the Pipidae. The Pipoidea was the sister group to an unnamed clade (Fig. 2, node 2) that includes all other frogs except for *Ascaphus*. Within clade 2 (Fig. 2), the Discoglossidae was sister group to a clade comprising the remaining species. The monophyly of the Discoglossidae was moderately supported. The internal branching pattern of the Discoglossidae (*Alytes* as sister taxon to *Bombina* + *Discoglossus*) was congruent in all analysis, but also only moderately supported; three apomorphic character states defined *Discoglossus* + *Bombina*.

Six species formed branches between node 2 and node 6 (Neobatrachia). They include *Heleophryne natalensis* and frogs commonly referred to as pelobatoids. The Pelobatidae (*sensu* Ford and Cannatella, 1993) was not supported. *Spea* was the sister taxon to the remaining pelobatoids plus neobatrachians (node 4). The most robust clade within this part of the topology was *Pelobates* + *Megophrys* + *Leptobrachium* (=Pelobatidae *s. str.*, node 20). The relationship of *Heleophryne* and *Pelodytes* were not robustly resolved and different results were obtained when morphometric characters were included or excluded from the analysis (Figs. 1 and 2).

The Neobatrachia was supported by a series of apomorphic character states (Fig. 2, node 6), but all characters are homoplastic. *Limnodynastes* and *Cochranella* were arranged at the base of the Neobatrachia. The basal nodes in the Neobatrachia were not fully resolved

in the strict consensus tree when all characters were considered (Fig. 1), but were more resolved when morphometric characters were excluded (Fig. 2). Some neobatrachian clades were obtained no matter whether morphometric characters were excluded or not (see nodes in Fig. 2 and taxa in Fig. 3). The Ceratophryinae (node 26) was sister group to most hylids (except hemiphractines). *Nyctimystes dayi* + *Litoria nannotis* + *L. rheocola* was a robust clade within the Pelodryadinae, as was their subclade *L. nannotis* + *L. rheocola*. The pelodryadines as a whole were not monophyletic in these analyses.

The Phyllomedusinae (node 32), Pseudinae (node 29), and hyline hylids form a clade (node 25). When morphometric characters were excluded, their relationships remained unresolved in the strict consensus topology. However, the internal branching pattern in the majority rule consensus tree (Fig. 3) is the same as that in the analyses that included morphometric characters. It suggests that the Phyllomedusinae is sister group to a clade that comprises hyline hylids and the Pseudinae.

The Dendrobatidae (node 54) and their sister group relationship to Hylodinae (node 56) were supported with and without morphometric characters (Figs. 1 and 2). Similarly, the Bufonidae (node 61) with *Melanophryniscus* being sister group to the remaining bufonid species (node 60) was supported in both analyses.

The Ranidae was unresolved in the strict consensus of Fig. 1. However, it was reconstructed as a clade and fully resolved when morphometric characters were excluded (Fig. 2, node 34), about with homoplasy and labile support involved.

The Rhacophoridae, Microhylidae, and Hyperoliidae (here including *Hemisus*, node 48) formed a clade (node 41) and each of them was a monophyletic group in this analysis.
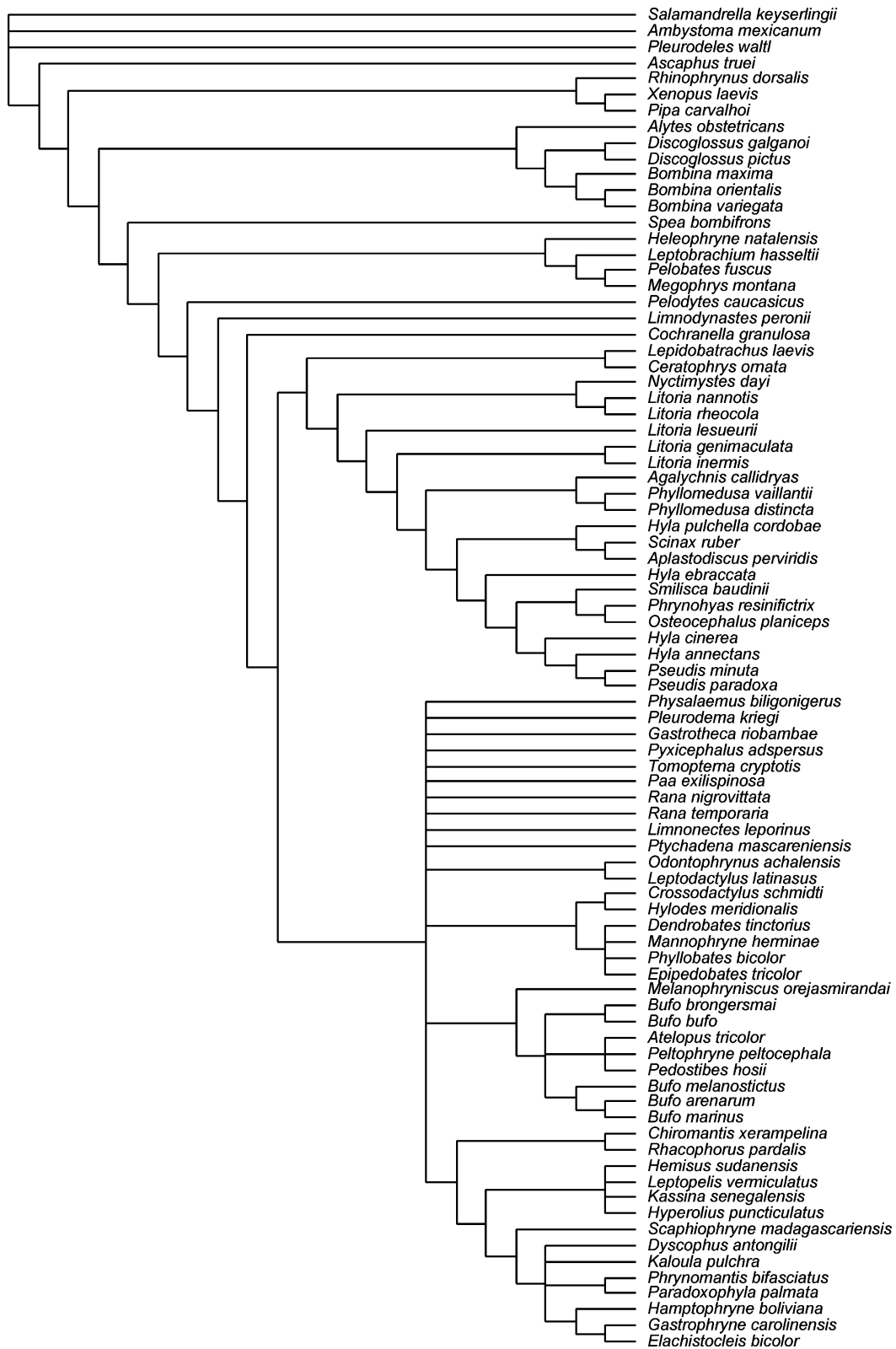
Fig. 1. Strict consensus cladogram of 268 minimum-length topologies. Trees were obtained from a heuristic search (84 taxa, 155 characters) with ordered character states in characters 12, 29, 31, 37, 39, 46, 58, 60, 64, 65, 77, 78, 83, 90, 108, 116, 117, 139, and 150. All characters were given weight 1, except for gap-weighted characters 12, 83, 116, and 117, which were assigned weight 0.08. Character 102 was excluded.
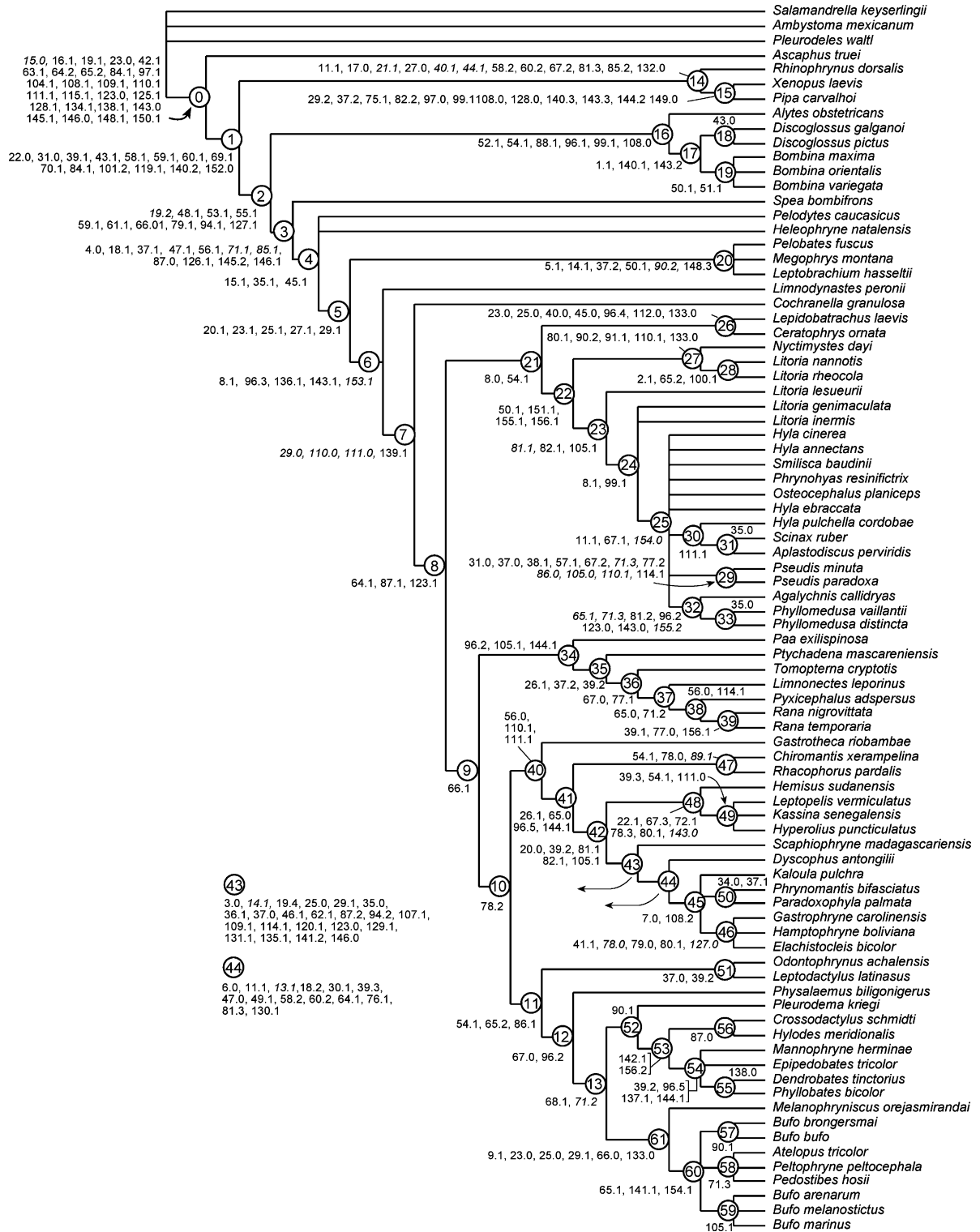
Fig. 2. Strict consensus cladogram topology, morphometric characters (12, 83, 116, and 117) and character 102 excluded; 15 characters "ordered." The consensus was computed from 144 minimum-length trees obtained from parsimony ratchet runs in NONA 2.0 (100 ratchet iterations, 1000 replicates, TBR swapping); 663 steps (multistate taxa: uncertainty), CI 0.31; RI 0.77. Unambiguous apomorphic character states that were optimized for the same node in all subtrees are listed for the nodes in plain style, whereas character optimizations that occurred only in some of the topologies are given in italics. The consensus topology generated by NONA was identical to the strict consensus computed from topologies found by heuristic search (10,000 random addition sequences) and subsequent extensive swapping in PAUP*.
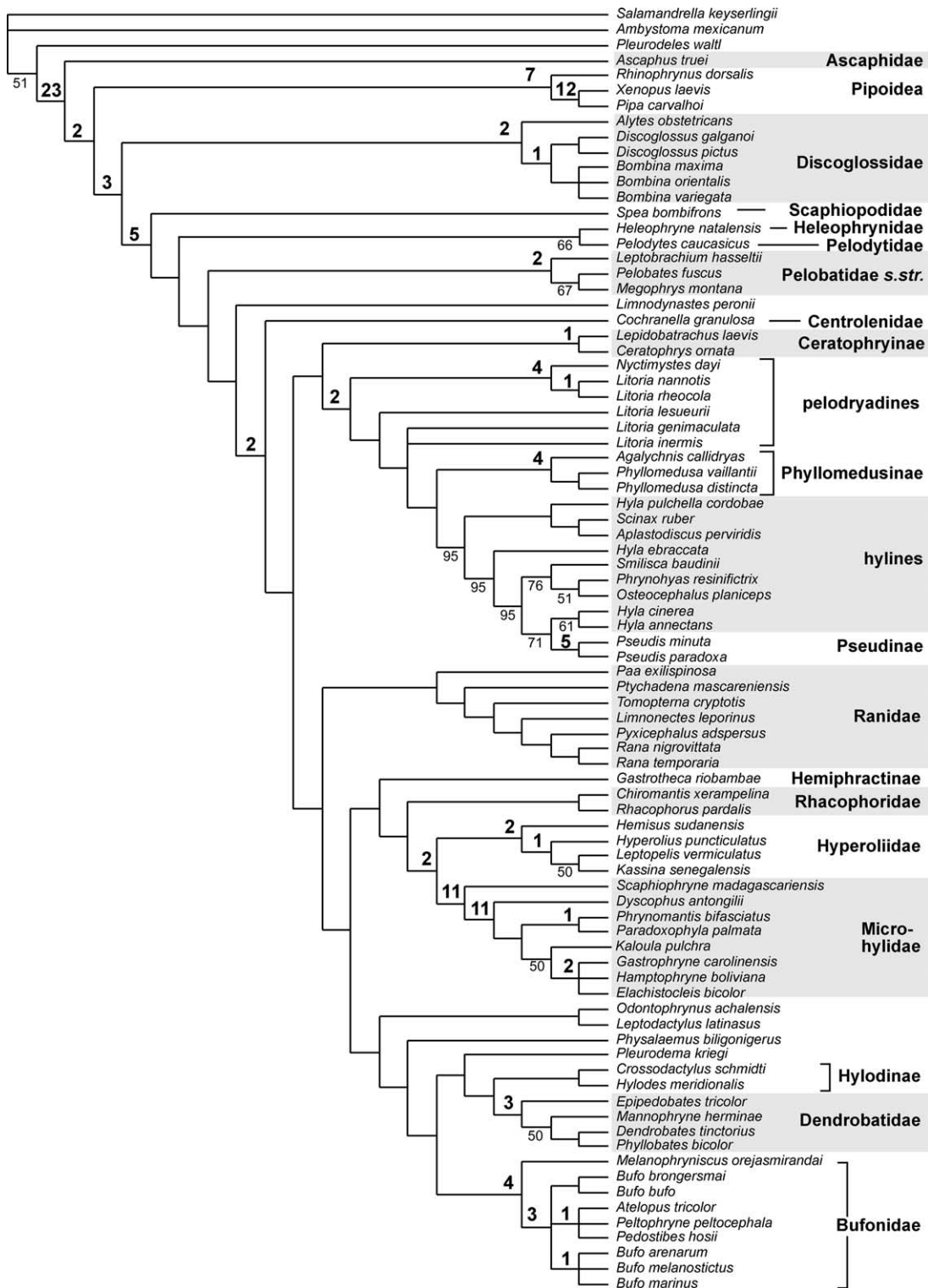
Fig. 3. Majority rule consensus tree summarizing 15,858 topologies found by heuristic searches (10,000 random-addition sequences, TBR swapping) in PAUP*; length 675 steps (multistate taxa set as polymorphism), characters 12, 83, 102, 116, and 117 excluded. Small numbers below branches show frequencies of resolved nodes (branches without numbers = 100%). Large boldfaced numbers above branches indicate Bremer support (TreeRot 2.0).

The Microhylidae (node 43) and its subclade the Scoptanura (node 44) were among the most robust clades in this study. Within the Scoptanura, two subclades were congruent in the strict consensus trees, i.e. the clade comprising the New World *Gastrophryne*, *Hamptophryne*, and *Elachistocleis* and the clade

formed by the Old World *Phrynomantis* and *Paradoxophyla*.

The Bufonidae, Hylodinae + Dendrobatidae, and ranoid groups in node 41, were monophyletic in both analyses, but stood in unresolved phylogenetic relationships to each other when all characters were considered (Fig. 1). With the exclusion of characters 12, 83, 116, and 117, the tree gained resolution in this region (Fig. 2). In the latter case, six leptodactylid species grouped with dendrobatids and bufonids (node 11). Furthermore, ranoids were not monophyletic and *Gastrotheca*, a hemiphractine hylid, was associated with some of those ranoid groups.

More details on the suggested clades in this analysis and their supporting apomorphic character states are more adequately given in the context of previous phylogenetic hypotheses in Discussion.

Within the present data, homoplasy was common; only approximately 26% of the characters had CI 1.0 and 30% of the characters even had CIs <0.33 when optimized on the topologies from which the consensus in Fig. 2 was computed. Homoplasy was not restricted to certain organ systems; for example, skeletal characters did not seem more consistently distributed than soft tissue characters.

The scored characters (see Appendix) had almost identical states in species from small genera such as species within *Bombina*, *Discoglossus*, *Phyllomedusa*, and *Pseudis*. Variation in character states and, thus, resolution occurred above this hierarchical level.

Discussion

The ensemble consistency indices of the most parsimonious solutions were relatively low. Primarily, large data sets without a priori filtering of presumed homoplastic features are generally expected to have less consistency and more homoplasy than small data sets. The sampling strategy herein did not filter potential homoplasy a priori. Also, species with highly aberrant morphology or characters with known interspecific variation were not excluded. Other studies on anuran systematics used higher taxon terminals (families; for example Kluge and Farris, 1969), thus, reducing variation of character states in the data set. The exemplar approach in this study takes the observed variation fully into account. Finally, considerable plasticity of characters, parallelism, reversals, and convergences were reported from other amphibian data sets (e.g., Good and Wake, 1992; Maglia, 1998; Duellman, 2001). Homoplasy in amphibian morphological characters seems common and will be a major challenge to future work. Yet in this study, globally homoplastic characters often resolved less-inclusive monophyletic groups (e.g., centrum formation character 99).

The hypothetical phylogenetic relationships of the species examined will be discussed in the light of the higher taxonomic units which they represent (Fig. 3). For the sake of taxonomic stability (Nixon and Carpenter, 2000) many nodes in the phylogenetic hypotheses (Fig. 2) will be left unnamed and will not be formally defined. Taxonomic emendations address only nodes in which changes appear inevitable.

Anura

The monophyly of the Anura has rarely been questioned (but see Griffiths, 1963; Roček, 1989, 1990). Adult morphology alone contributes numerous arguments for the monophyly of the Anura; examples of apomorphic characters are presence of urostyle, elongation of hindlimbs (including ankle bones), fusion of radius and ulna, fusion of tibia and fibula, absence of prefrontal, fusion of hyobranchial elements into a hyoid plate, presence of large subcutaneous lymph spaces in skin and presence of two protractor lentis muscles (Saint-Aubain, 1981; Trueb and Clouthier, 1991; Ford and Cannatella, 1993; Shubin and Jenkins, 1995). The anatomy of anuran larvae adds a suite of additional autapomorphic character states of the Anura; see the full list of apomorphic states in Fig. 2. Many of them relate to the major evolutionary step in anuran larvae—the ability of suspension feeding and the modification of the jaws. Related autapomorphic features are, for instance, the fusion of the operculum with the abdomen, formation of a larval hypobranchial plate, specific shape and articulation of the ceratohyal, closure of the gill cleft between ceratohyal and first ceratobranchial, presence of a ventral velum and branchial food traps, shift of the jaw depressors onto the palatoquadrate, and presence of the ligamentum cornuquadratum. Other autapomorphic features have no apparent relation to feeding ecology, such as the rearrangement of the three branches of the trigeminal nerve relative to jaw muscles or the presence of two perilymphatic foramina.

Archaeobatrachia

The Discoglossidae, Ascaphidae, Leiopelmatidae, Pipoidea, and pelobatoid frogs have been considered occasionally to represent a natural group or at least have been treated as a taxonomic entity, the "Archaeobatrachia" (Reig, 1958; Duellman, 1975). Hay et al. (1995) and Feller and Hedges (1998) presented molecular data in favor of the monophyly of the "Archaeobatrachia." Others, however, identified archaeobatrachian frogs as a paraphyletic assemblage (Ford and Cannatella, 1993; Hillis et al., 1993). The data support the idea of archaeobatrachian paraphyly.

Ascaphidae

A. truei is the only member of the family Ascaphidae. Ford and Cannatella (1993) and Green and Cannatella

(1993) indicated that there is no support by synapomorphic features that would justify grouping *Ascaphus* with *Leiopelma* into the Ascaphidae, as done in earlier studies. Rather they placed species of *Leiopelma* separately into the Leiopelmatidae. Both teams of authors proposed to consider *A. truei* the most basal taxon in the Anura, a view shared herein. However, *Leiopelma* developmental stages were not available for examination in this study. The plesiomorphic condition of some adult ascaphid characters has been questioned (Ritland, 1955). The most striking plesiomorphic condition is the palatoquadrate complex of *Ascaphus* larvae and its associated musculature (Pusey, 1943; Reiss, 1997; Haas, 2001). In this respect no other tadpole resembles caudate larvae more than *A. truei*.

A. truei tadpoles possess a series of autapomorphic features, including the presence of large larval serous glands (also found in other rheophilous tadpoles), the arrangement of the subarcualis obliquus muscles, the specific arrangement of the levator mandibulae externus and internus muscles, the shape of the lower jaw cartilages, the presence of a processus postcondylaris on the ceratohyal, the fusion of the basibranchial with the hypobranchial elements, and the absence of functional lungs for most of larval life.

Discoglossoidea

Duellman (1975) and Duellman and Trueb (1986) combined *Ascaphus*, *Leiopelma*, and the Discoglossidae in the "Discoglossoidea." The main argument in support of this group was the possession of Orton Type III tadpoles (Orton, 1953; Fig. 4). Sokol (1975, 1981) proposed that features of the hyobranchial and filter apparatus also could be considered apomorphic features of this group ("Discoglossoidei" in his terms). The analysis of larval features in this study comes to different conclusions: distributions of numerous character states were in conflict with the hypothesis of discoglossoidean monophyly. The "Discoglossoidea" is a paraphyletic assemblage.

Mesobatrachia

Laurent (1979) proposed the placement of the Pipoidea and Pelobatoidea in the "Mesobatrachia." Later, Ford and Cannatella (1993) defined the "Mesobatrachia" as a monophyletic group, comprising the most recent common ancestor of extant Pipoidea and pelobatoids and all of its descendents. Sanchiz (1998) recently adopted Ford and Cannatella's (1993) view, stating, however, that there was only weak support for the "Mesobatrachia." In the present study, numerous conflicting apomorphic features at several nodes suggest that mesobatrachian frogs do not form a natural group. In the light of this evidence, the larval features listed by Ford and Cannatella (1993) in favor of the grouping would be symplesiomorphies (e.g., absence of taeniae tecti).

Pipoidea

The extant Pipoidea consists of the Rhinophrynidae and Pipidae. Species of both families have Orton Type I larvae (Fig. 4). Many synapomorphies that support their sister group relationship stem from larval morphology (Orton, 1953, 1957; Sokol, 1975, 1977a, 1981; de Sá and Swart, 1999; Swart and de Sá, 1999). But features of adults support the clade Pipoidea also (e.g., lack of mentomeckelian bone, Trueb and Cannatella, 1982). The mostly Cenozoic †Palaeobatrachia have been considered a subgroup of the Pipoidea (Ford and Cannatella, 1993; Estes and Reig, 1973; Cannatella and de Sá, 1993; Sanchiz, 1998).

The Pipoidea is well supported in this study and a series of unambiguous synapomorphic character states group the Rhinophrynidae with the Pipidae (Fig. 3): two spiracle openings and absence of an opercular canal, lateral and very low eyes (in relation to the brain), medial insertion of m. levator arc. branchialium IV, absence of m. constrictor branchialis I, anterior position of jaw levator muscles, extended crista parotica, arcus subocularis bearing a processus ventrolateralis posterior, suprarostral cartilage and cornua trabeculae fused in a horizontal plate, and forelimbs that do not break into the peribranchial chamber during development.

The position of the Pipoidea was more basal than that in previous phylogenetic hypotheses (see Cannatella and Ford, 1993). *A. truei* was the most basal branch but pipoids were second (Fig. 2, node 1). However, Maglia et al. (2001) suggested that the Pipoidea was the sister group to all other frogs. This idea had been issued before, although not in terms of cladistic argumentation (Orton, 1953, 1957; Sokol, 1975).
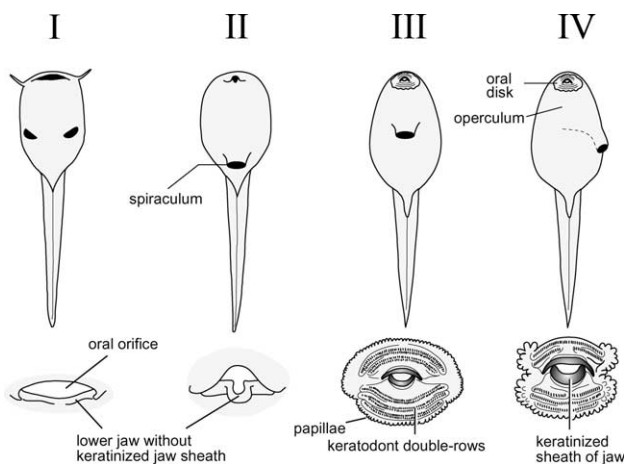
Fig. 4. Tadpole types, modified from Orton (1953).

Rhinophrynidae

Rhinophrynus dorsalis, the Mexican burrowing toad, is the only extant species of the Rhinophrynidae (see fossils in Henrici, 1994; Sanchiz, 1998). Despite the overall similarity of its larvae with larvae in species of the Pipidae (Sokol, 1975), the analysis of larval characters shows a series of autapomorphic features in *R. dorsalis*: absence of the m. geniohyoideus in larvae, presence of the m. levator mandibulae externus superior, ramus mandibularis (V_3) posterior (ventral) to m. levator mand. externus, basibranchial indistinguishable from hypobranchial elements, very long urobranchial process, presence of processus spinalis of saccus endolymphaticus, crescentic branchial food traps, and cricoid cartilage with dorsal gap. In other features, *Rhinophrynus* has retained plesiomorphic conditions within the Pipoidea, for example, presence of a velum ventrale, configuration of the subarcualis rectus II–IV; and absence of commissurae craniobranchiales.

Pipidae

The Pipidae is a natural, well-studied group (Trueb and Cannatella, 1986; Cannatella and Trueb, 1988a,b; de Sá and Hillis, 1990; Cannatella and de Sá, 1993; Ford and Cannatella, 1993; Sanchiz, 1998). Represented by *Xenopus* and *Pipa*, the monophyly of the Pipidae was unambiguously supported in this study by specific modifications of the m. subarcualis rectus II–IV (characters 29 and 37), presence of commissurae craniobranchiales, modification of arcus subarcualis as a round relatively thin bar, presence of only one perilymphatic foramen (but see Sokol, 1977a), presence of epichordal centra, absence of urobranchial process, absence of valvular velum ventrale, biomechanics of vocalization, presence of round pupillae, presence of pseudofirmisternal breast–shoulder girdle, and absence of a tongue.

Discoglossidae

The Discoglossidae is composed of *Alytes*, *Barbourula*, *Bombina*, and *Discoglossus*. Traditionally, these taxa were recognized as a clade or at least as a taxonomic entity (Griffiths, 1963; Lynch, 1973; Duellman, 1975; Sokol, 1975; Laurent, 1979; Duellman and Trueb, 1986; Sanchiz, 1998). However, some authors proposed to define two families of discoglossid frogs: Lanza et al. (1976) proposed to distinguish Discoglossidae *s. str.* (solely *Discoglossus*) from Bombinidae (other genera), whereas Maxson and Szymura (1984) concluded that *Bombina* and *Discoglossus* were more similar to each other than either was to *Alytes*. They assumed an early split (Cretaceous) of *Alytes* from the lineage leading to *Bombina* and *Discoglossus*. Ford and Cannatella (1993)

proposed another arrangement based on the reinterpretation of the morphological evidence. They defined the monophyletic Discoglossidae *s. str.* as *Alytes* + *Discoglossus* and the Bombinatoridae as *Bombina* + *Barbourula*. According to their view, the traditional grouping of the Discoglossidae *s. lato* (= *Alytes* + *Bombina* + *Barbourula* + *Discoglossus*) would not be a natural group, insofar as in their view *Discoglossus s. str.* was more closely related to other frogs.

This study supports the monophyly of the Discoglossidae (Fig. 3) in their traditional composition. The origin and shape of the m. intermandibularis and the presence of two posterior processes at the pars alaris of the suprarostral cartilage are unique within the Anura. The presence of only the taenia tecti transversalis is another apomorphic character (otherwise present only in species of *Heleophryne*). Despite parallel evolution in other groups, epichordal vertebral centra and their reduced urobranchial processes can be listed as synapomorphic characters of the Discoglossidae. Furthermore, the new evidence suggests that the discoglossid triradiate sternum and interleaving zono-sternal mechanism (Griffiths, 1963) could be additional synapomorphic character states (as opposed to Ford and Cannatella, 1993).

The current evidence for the relationships within the Discoglossidae tentatively corroborates the hypothesis proposed by Maxson and Szymura (1984): *Discoglossus* and *Bombina* were sister groups (Fig. 3). At our present state of knowledge, their capability for inspiratory sound production and triangular pupil shape are unique features. Furthermore, species of both genera exhibit a highly ordered pattern of epidermal melanocytes (otherwise only in *Pelodytes caucasicus*). The analysis provides a new synapomorphic character state for the species of *Bombina* examined. They were unique within the Discoglossidae in possessing the m. mandibulolabialis superior. Furthermore, the origin of this muscle from the cartilago labialis inferior (rather than cartilago meckeli) in species of *Bombina* is unique among all anuran larvae examined (see Haas, 2001).

Pelobatoid frogs

The monophyly and systematic placement of pelobatoid frogs have been contentious; see the cited works in this section for details. The Pelobatidae (including the Megophryinae) and Pelodytidae were placed as consecutive branches in Lynch's (1973) anuran phylogeny. Others suggested that the two are sister groups constituting the "Pelobatoidea" (Duellman, 1975; Duellman and Trueb, 1986; Ford and Cannatella, 1993; Henrici, 1994; Lathrop, 1997; Maglia, 1998; Sanchiz, 1998). Lynch (1973) put the pelobatoids together with the sooglossids and myobatrachids (including in his definition *Heleophryne*)

into the "transitional families" between the "archaic" Ascaphidae, Discoglossidae and Pipoidea, and the "advanced frogs" (all other groups). Ford and Cannatella (1993) proposed that the megophryine frogs deserved family rank within pelobatoids.

Although the monophyly of the "Pelobatoidea" has been claimed repeatedly, the supporting arguments are weak. Maglia (1998) recently presented a broad morphological reanalysis of the pelobatoids (73 characters). However, in the analysis she a priori applied a constraint topology forcing the monophyly of the "Pelobatoidea," the Pipoidea, and the Neobatrachia. In studies comprising fossil taxa, both Henrici (1994) and Lathrop (1997) concluded that both Pelobatidae and Pelobatoidea were monophyletic groups. Both taxon samples, however, excluded neobatrachians. Thus, the possibilities of pelobatoid–neobatrachian sister group relationships and alternative polarities of the characters that they employed were not scrutinized.

The results in the present study resemble Lynch's (1973) view, insofar as there are several branches placed in two or three nodes between the Discoglossidae and the Neobatrachia (Figs. 2 and 3), with *Spea* branching off from the first node. These branches are compatible in composition with Lynch's "transitional frogs." There is a mosaic of convergent features and reversals in the observed character states that make an assessment of the pelobatoid assemblage difficult; nodes 4 and 20 remain unresolved in the strict consensus in Fig. 2 (morphometric characters excluded). The different topologies derived from analyses with (Fig. 1) and without (Fig. 2) morphometric characters illustrate the uncertainties and the underlying homoplasies.

The pelobatoids and the neobatrachians together form a well-supported clade (Fig. 2, node 3). Shared derived features proposed to support this unnamed clade are single row keratodonts, sinistral spiracle, insertion of the m. subarcualis rectus II–IV on ceratobranchiale II, gap between mm. intermandibularis et interhyoideus, presence of a larval m. levator mandibulae lateralis, medially separate partes corpores, attachment of the ligamentum cornuquadratum to the cornu trabeculae, clavicula not overlapping scapula anteriorly and (neo-)palatinum present.

The most robust clade within the "transitional" assemblage was *Pelobates + Megophrys + Leptobrachium* (Fig. 2, node 20). It was supported by a number of synapomorphic character states, although all of these are homoplastic, for example, the presence of the vena caudalis dorsalis, the most anterior keratodont row being characteristically short (also in *Spea*), and the presence of the m. mandibulolabialis superior. Three characters suggested the sister group relationship of *Pelobates* and *Megophrys* in the analysis including all characters (Fig. 1). However, based on adult morphology (Lathrop, 1997; Maglia, 1998) and biogeography it

is more likely, if not certain, that *Megophrys* and *Leptobrachium* are sister taxa. The examination of additional species is required to resolve this apparent conflict. Familial status of megophyrines is not warranted.

There was no support for the "Pelobatidae" as defined by Ford and Cannatella (1993), i.e., combining the North American so-called pelobatids *Spea* and *Scaphiopus* with the Eurasian *Pelobates*. Maglia's (1998) analysis, however, placed *Pelobates* in a clade with *Spea* and *Scaphiopus*, and within that clade *Scaphiopus* was placed tentatively as sister taxon to *Pelobates*. The supporting evidence for the sister group *Scaphiopus + Pelobates* in her analysis was questioned by Maglia herself (Maglia, 1998:15). In a noncladistic analysis of fossil and extant pelobatids, Roček (1981) found many differences between *Scaphiopus* and *Spea* in comparison with *Pelobates* and its allied fossil forms. He proposed familial rank for the North American so-called pelobatids, i.e., the Scaphiopodidae (Fig. 3). The new data herein suggest that the North American taxa (*Scaphiopus* and *Spea*), and the Eurasian clade (*Pelobates* + Megophryinae, Fig. 2, node 20) may have been grouped together into the Pelobatidae (*s. lato*) on the basis of plesiomorphic and convergent features that have evolved due to similar adult life histories (burrowers in open country). In the present study the Pelobatidae (*s. str.*) is understood as the clade comprising the Eurasian species, whereas the North American forms are tentatively placed separately (Scaphiopodidae). The hypothesis of a long separate history of North American and Eurasian so-called pelobatoids (Roček, 1981; Sage et al., 1982) needs renewed attention.

Heleophrynidae

The phylogenetic relationships of the genus *Heleophryne* have been enigmatic. Noble (1931) classified it as a tooth-bearing bufonid. Lynch (1973) placed it among the "transitional families" with affinities to Australian limnodynastine frogs. Some workers included it in the Neobatrachia (Duellman, 1975; Ford and Cannatella, 1993). Heyer (1975) used *Heleophryne* as outgroup taxon for his analysis of South American leptodactylids and Laurent (1979) suggested its placement among myobatrachids. Duellman and Trueb (1986) considered it closely related to myobatrachids and sooglossids. This view gained tentative support from molecular systematics (Hay et al., 1995; Ruvinsky and Maxson, 1996).

The data in this study did not robustly support close affinities to any specific neobatrachian group. Depending on the inclusion on exclusion of morphometric characters (Figs. 2 and 3), *Heleophryne* was placed as the sister group to the *Pelobates* + Megophryinae clade

(without robust support) or stood unresolved in a polytomy with other pelobatoids. The phylogenetic relationships of the Heleophrynidae remain vague. However, the results herein renew previous suggestions, i.e., that the Heleophrynidae should be discussed in the context of the pelobatoid assemblage rather than the neobatrachians (Lynch, 1973). New data from *Heleophryne* (e.g., Burton, 1998a) has to be integrated in future phylogenetic analyses.

Neobatrachia

The Neobatrachia differs herein from previous definition (Ford and Cannatella, 1993) in that *Heleophryne* is excluded. The Neobatrachia (Fig. 2, node 5) was supported by several apomorphic character states, i.e., presence of gap in upper lip papillation (also in *Pelodytes*), presence of taenia tecti medialis, presence of secretory ridges, and horizontal pupil. However, all apomorphic character states were homoplastic. The discrete m. sartorius in neobatrachians is shared with *Heleophryne*. Some uncertainties remain and the understanding of neobatrachian groundplan apomorphies will depend on successfully resolving pelobatoid relationships.

In this study only *Limnodynastes* represents the Australian myobatrachids (= Myobatrachinae and Limnodynastinae), a group undoubtedly important in the reconstruction of neobatrachian ancestry. Other studies have demonstrated the considerable adult morphological diversity in myobatrachids and the uncertainties of their interpretation (Lynch, 1971; Heyer and Liem, 1976; Farris et al., 1982; Burton, 2001). More work needs to be done in the context of a broad taxon sample.

Within the Neobatrachia, Duellman and Trueb (1986) recognized a clade that comprises taxa with axillary amplexus. This clade corresponds to node 7 (Fig. 2) in the Neobatrachia. The clade has been dubbed informally the "advanced neobatrachians" (Burton, 1998a). Apart from amplectic position, three additional larval characters (Fig. 2) and the dorsal position of the mm. transversi relative to the mm. flexores teretes in the hand of adults (Burton, 1998a) support the clade. However, reversals of all of these characters occur within the "advanced neobatrachians".

Bufonoidea

Some workers subdivided the Neobatrachia into "Bufonoidea" ("Hyloidea;" Dubois, 1983), Ranoidea, and Microhyloidea (Duellman, 1975; Laurent, 1979). The "Bufonoidea" was a paraphyletic assemblage in the present analyses. There is no known morphological autapomorphy of the "Bufonoidea," although the "Bufonoidea" was tentatively supported in molecular phylogenetic studies (Ruvinsky and Maxson, 1996; Feller and Hedges, 1998).

Centrolenidae

Synapomorphies of centrolenids traditionally include the complete fusion of tibiale and fibulare (but see Sanchiz and de la Riva, 1993), deposition of eggs above water, process on the metacarpal II in adults, and presence of intercalary element (Ruiz-Carranza and Lynch, 1991; Duellman, 2001). Duellman (1975) and Duellman and Trueb (1986) followed earlier proposals (e.g., Griffiths, 1963) and advocated a close relationship of the Centrolenidae, the hylid frogs, and the Pseudinae based on the presence of intercalary elements in the phalangeal skeleton. Recently Duellman (2001), based on da Silva (1998), reanalyzed hylid and centrolenid affinities with a hypothetical outgroup. Duellman (2001) could present three alternative topologies with somewhat different lists of centrolenid apomorphies. The picture could become more complicated if real outgroup taxa were used instead of a hypothetical outgroup. Recent molecular analyses could not clearly resolve the relationships of the Centrolenidae, the hylids, and the Pseudinae (Ruvinsky and Maxson, 1996). The present analysis is in stark conflict with the hypothesis of close relationships of these taxa (Duellman and Trueb, 1986; Duellman, 2001). The analysis placed *Cochranella granulosa* within the Neobatrachia, but without robust support for its reconstructed position.

Leptodactylidae

The traditional "Leptodactylidae" is a paraphyletic assemblage, and independent descendents from an early neobatrachian radiation must be postulated. Although some leptodactylid frogs formed quite robust monophyletic subgroups in this analysis, their phylogenetic relationships to other groups within the Neobatrachia were not resolved when all characters were included (Fig. 1). In this respect this study could not contribute much to solve the known problems of leptodactylid phylogenetic relationships (Lynch, 1971; Heyer, 1975).

The Ceratophryinae is a robust clade in the present and earlier analyses (e.g., Lynch, 1971; Heyer, 1975; Cei, 1980; Maxson and Ruibal, 1988). Although the examined larvae of *Ceratophrys ornata* and *Lepidobatrachus laevis* could not be more different in appearance at first glance, synapomorphic larval anatomical features clearly confirm their relatedness: absence of m. interhyoideus posterior and m. diaphragmatopraecordialis, separation of branchial levators, absence of m. suspensoriohyoideus, almost complete closing of braincase by cartilaginous roof, absence of spiculum I, and absence of branchial food traps. With respect to morphometric characters, and despite their different feeding

habits, *C. ornata* and *L. laevis* were very similar to each other and differed from other species in their short trabeculae horns (character 83) and their specific ceratohyal geometry (characters 116 and 117). Lavilla and Fabrezi (1992) have compared the larval crania in *C. cranwelli* and *L. llanensis*. In addition to the characters just mentioned, they suggest that the complete fusion of infrarostral and suprarostral cartilages is another synapomorphic character state of the two genera.

The relationship of the ceratophryines to certain hylids was indicated, but support was weak (Fig. 2). A further clade composed of so-called leptodactylids was *Odontophrynus* + *Leptodactylus*. However, very different hypotheses of relationships have been presented for these leptodactylid genera (Lynch, 1971; Heyer, 1975). Finally the two hylodines formed a clade that was sister group to the Dendrobatidae.

Dendrobatidae + Hylodinae

The Dendrobatidae is unquestionably a monophyletic group. Autapomorphic character states can be derived from adult and larval morphology, behavior, and molecular evidence (Duellman and Trueb, 1986; Myers and Ford, 1986; Weygoldt, 1987; Zimmermann and Zimmermann, 1988; Myers et al., 1991; Ford and Cannatella, 1993; Haas, 1995; Clough and Summers, 2000; Vences et al., 2000). Griffiths (1959) allied the Dendrobatidae with petropedetine ranids. Noble (1931) and Lynch (1971, 1973) thought of the Dendrobatidae as a hylodine leptodactylid derivative. Duellman and Trueb (1986) put much emphasis on the firmisternal breast–shoulder girdle in species of the Dendrobatidae and placed them within the Ranoidea. Ford (1993) summarized the arguments for and against ranoid relationships of the Dendrobatidae. Molecular approaches did not corroborate ranoid affinities (Hillis et al., 1993; Ruvinsky and Maxson, 1996; Vences et al., 2000). Ruvinsky and Maxson (1996) tentatively placed the Dendrobatidae among bufonoids with uncertainty about their immediate sister group. Vences et al. (2000) tentatively suggested a close relationship to leptodactylids or bufonids; no hylodine leptodactylids were included in that analysis.

The hypothesis of ranoid affinities of the Dendrobatidae was clearly rejected herein. Firmisterny alone was not sufficient grounds for ranoid relationships, but rather has evolved independently and is an autapomorphic feature of the Dendrobatidae. Other autapomorphies are insertion of m. rectus cervicis on both ceratobranchial III and IV (not in *Dendrobates*), reduction of tectal cartilages, and parental transport of larvae. The branching pattern within the Dendrobatidae (Figs. 1–3) was resolved when morphometric characters were excluded (Figs. 2 and 3). There was some support for a clade *Phyllobates* + *Dendrobates* (loss of amplexus),

a clade that has been proposed before (Clough and Summers, 2000; Vences et al., 2000).

Hylodine leptodactylids were the sister group of the Dendrobatidae. The clade was supported by the presence of T-shaped terminal phalanges and complex mating behavior in which the territorial male guides the female to an appropriate clutch site (Zimmermann and Zimmermann, 1988; Weygoldt and Potsch de Carvalho e Silva, 1992). Beyond that, diurnality (Weygoldt and Potsch de Carvalho e Silva, 1992) and unique features of their hand musculature (Burton, 1998a) may tentatively be considered additional synapomorphic characters of the Hylodinae + Dendrobatidae. In contrast, Myers et al. (1991) suggested that nocturnal behavior might be ancestral in the Dendrobatidae based on their analysis of the dendrobatid *Aromobates*. However, nocturnality in *Aromobates* should rather be explained as a reversal in the context of its relatives (Hylodinae + Dendrobatidae). The tadpole chondrocrania of *Dendrobates tinctorius* and *Hylodes meridionalis* were astonishingly similar in shape and proportions (particularly shape of suprarostrals). Also, the posterior palatoquadrate curvature was particularly deep in hylodines and dendrobatids examined (not expressed in character 68 coding).

Hylidae

Noble (1931, p. 508) described hylids "as bufonids with intercalary cartilages and usually with claw-shaped phalanges." Savage (1973), Laurent (1979), and Dubois (1983, 1984) proposed to establish a separate family for the Australo-Papuan pelodryadine hylids (see below) and Tyler (1971) resurrected the genus *Litoria* in the pelodryadines. The taxonomic stability of hylids is in stark contrast to the supporting evidence. Ford and Cannatella (1993) claimed that there was no unique character state that could define hylids in their traditional composition as a monophyletic group, comprising the four subgroups Hylinae, Hemiphractinae, Phyllomedusinae, and Pelodryadinae. This "Hylidae" was paraphyletic in this study. However, recently Duellman (2001), based on da Silva (1998), reanalyzed hylids, pseudines, centrolenids, and *Allophryne*. Pseudines were recognized as related to hylines and included in the Hylidae as subfamily Pseudinae. In his analysis Duellman (2001) proposed apomorphies for the Hylidae (including pseudines): claw-shaped terminal phalanges, intercalary present, metacarpal III with three articular surfaces and origin of m. flexor teres (digit III) dorsal to m. transversus metacarporum II. The first was accessible for the species examined herein and was part of the analysis.

Pelodryadinae + Hylinae + Phyllomedusinae + Pseudinae

Pelodryadines, hyline hylids, the Phyllomedusinae, and the Pseudinae formed a clade in this analysis (Fig. 2,

node 22). Synapomorphies were the presence of the m. mandibulolabialis superior, presence of the intercalary element, presence of an apical portion of the adult m. intermandibularis, and claw-shaped end phalanges. Interestingly, the third of these characters had been reported as an apomorphy of the Pelodryadinae (Tyler, 1971), but was optimized here as apomorphic for the whole clade (node 22) with state changes inside the clade. This clade excluded the Hemiphractinae (represented by *Gastrotheca riobambae*), which has traditionally been classified in the hylid group. Among the species examined and outside node 22, the larval m. mandibulolabialis occurred only in species of *Pelobates*, *Megophrys*, *Leptobrachium*, and *Bombina*. The intercalary elements were also found in *Gastrotheca riobambae*, *Cochranella granulosa*, and species of the Rhacophoridae and the Hyperoliidae, and the claw-shaped end phalanges were also present in *G. riobambae*.

Occasionally, affinities between Australo-Papuan pelodryadines and South American phyllomedusines were a subject of speculation (Bagnara and Ferris, 1975; but see Maxson, 1976; Tyler and Davies, 1978a). Species of the Phyllomedusinae and some species of *Litoria* possess large fibrous melanosomes with a unique red pigment (Bagnara and Ferris, 1975). This, however, might be a symplesiomorphic character of the two (apomorphic for the entire clade 22 [Fig. 2] and perhaps lost in hylines and pseudines). Previous analyses suggested monophyly for the Australian pelodryadines (Tyler, 1971; Tyler and Davies, 1978a; Hutchinson and Maxson, 1987).

The pelodryadines with suctorial rheophilous larvae (*Nyctimystes dayi*, *Litoria rheocola*, *L. nannotis*) formed a clade (node 27). *L. nannotis* and *L. rheocola* have always been thought to be close relatives combined in the *nannotis* group of *Litoria* (Tyler and Davies, 1978b). This clade (node 28) was supported by the presence of large larval serous glands and the unique mode of centrum formation (character 100). Furthermore, in the two species the ramus mandibularis c.n. V is dorsal to the externus muscle group, as opposed to ventral in *N. dayi*. The relationships of the *nannotis* group and the Australo-Papuan genus *Nyctimystes* have been discussed elsewhere (Hutchinson and Maxson, 1987; Tyler and Davies, 1979; Haas and Richards, 1998). The genus *Litoria* was paraphyletic.

The Phyllomedusinae is a monophyletic group. Autapomorphic character states include thick dermis, ultralow suspensorium, arcus subocularis with distinct lateral processes, secondary fenestrae parietales, absence of a passage between ceratohyal and ceratobranchial I, vertical pupillae, and presence of posterolateral portion of adult m. intermandibularis, Laurent (1979) further listed specific skin toxins and extraaquatic egg deposition. In their morphometric character states larvae of the three phyllomedusines examined stood out from most other hylids by their moderately thickened skin.

Traditionally, pseudines have been classified as either a clade among leptodactylid frogs, family of frogs (the Pseudidae, related to hylids), or a subgroup of hylids (see Savage and de Carvalho, 1953). Duellman (2001) classified them as subfamily Pseudinae within hylids. Several synapomorphic characters robustly group *Pseudis paradoxa* and *P. minuta* as sister taxa (Fig. 2, node 29). Among the synapomorphies, the nasal sac insertion of the m. levator mandibulae lateralis and a distinct gap in the m. subarcualis rectus II–IV are unique features in this study, but both features are present in larvae of the pseudine *Lysapsus limellus* also (F. Vera Candioti, pers. commun.). Another unique feature for pseudines is the particularly elongate intercalary element (Paukstis and Brown, 1991).

Hyline hylids and the genus *Hyla* were paraphyletic with respect to the Pseudinae in this study. Although pseudines clearly group with hyline hylids in the majority of the most parsimonious solutions (Figs. 1 and 3), a close relationship to *Hyla annectans* (Figs. 1 and 4) is quite unlikely (supported only by small steps in morphometric characters). Rather, *Hyla cinerea* presumably is the closest relative of *Hyla annectans* among the species examined (Fig. 3), as inferred from biogeography.

Although the grouping is not robustly supported, the laying of eggs on the surface film and the presence of the commissura proximalis II are potential synapomorphies for the species examined of *Smilisca*, *Phrynohyas*, and *Osteocephalus* (Figs. 1 and 3). The similarity of the chondrocrania of *P. resinifictrix* and *O. planiceps* in shape and proportions was striking. Interestingly, in both genera, species that use phytothelmata for reproduction and oophagous tadpoles have evolved (Jungfer and Schiesari, 1995; Jungfer and Weygoldt, 1999; K-H. Jungfer, pers. commun.). Furthermore, Tyler (1971) described similarities of vocal sac and intermandibular musculature in *Phrynohyas* and *Osteocephalus* that await phylogenetic interpretation.

Hemiphractinae

The Neotropical hemiphractine frogs are a monophyletic group (eggs are carried on the dorsum of the female, and developing embryos form bell-shaped external gills; Wassersug and Duellman, 1984). However, their relationships to other neobatrachians remain obscure. Presence of intercalary elements and claw-shaped terminal phalanges are potential synapomorphies with hylids (Ford and Cannatella, 1993; Duellman, 2001). A phylogenetic analysis of the Hemiphractinae (Mendelson III et al., 2000) was primarily concerned with the relationships among hemiphractines, but the selection of outgroup taxa (hylid species) assumed hylid relationships of the Hemiphractinae a priori. The position of hemiphractines within a monophyletic Hylidae in

Duellman (2001) seems preliminary because the taxon sample neglected large parts of the Neobatrachia. The present analysis did not support a close relationship of the Hemiphractinae to other so-called hylids. Only one species was examined, but the similarity in larvae of various *Gastrotheca* species in many characters had been shown before (Haas, 1996). Recent molecular data suggested similar uncertainties in the phylogenetic position of the Hemiphractinae (Ruvinsky and Maxson, 1996). Although *Gastrotheca* is placed as sister group of a ranoid clade in some analyses (Fig. 2), the evidence is not convincingly robust and collapsed when morphometric characters were included (Fig. 1). The data could not resolve the case and the relationships of hemiphractines remain enigmatic.

Bufonidae

The Bufonidae is a monophyletic group, and synapomorphic features of bufonids include the presence of Bidder's organ (Duellman and Trueb, 1986; Roessler et al., 1990), a unique pattern of insertion of the m. hyoglossus, absence of the m. constrictor posterior (Trewavas, 1933), absence of teeth, an exclusively squamosal site of origin of the m. depressor mandibulae and associated angle of the squamosal (Griffiths, 1963), presence of the "otic element" (ossification center in the temporal region fusing to the squamosal), and posterior sternal elements not covered by fascia (vagina recti) (da Silva and Mendelson, 1999). Some studies elucidated the internal clades of the Bufonidae (Graybeal and Cannatella, 1995; Graybeal, 1997; da Silva and Mendelson, 1999). Character optimization in this study suggests that Bidder's organ evolved only within the Bufonidae; it is absent in *Melanophryniscus*.

Larval characters add to the list of bufonid autapomorphies and give the clade even more robustness: the diastema in the ventral (posterior) oral disk lip (unique among the anurans examined), absence of m. interhyoideus posterior and diaphragmatopraecordialis, slip of subarcualis rectus II–IV reaches far laterally into interbranchial septum IV and presumably acts as a constrictor, absence of processus anterolateralis (crista parotica), and absence of functional lungs during most of the larval phase of life.

Ranoidea

The dissenting views on the taxonomy of the Ranoidea, the definition of its subgroups, and their phylogenetic relationships could hardly be more confusing (Liem, 1970; Laurent, 1979; Dubois, 1981; Drewes, 1984; Channing, 1989; Ford and Cannatella, 1993; Bossuyt and Milinkovich, 2001; Vences and Glaw, 2001). Emerson et al. (2000) analyzed molecular evi-

dence (e.g., Richards and Moore, 1996, 1998a) in combination with morphological characters. They concluded that the Ranoidea was monophyletic (mostly supported by molecular characters) but that the basal dichotomies within the Ranoidea were not robustly resolved by their data.

The anterior emargination of the ceratohyal (morphometric character 117) was relatively deep in ranoids, particularly in species of *Limnonectes*, *Kassina*, and *Hyperolius*, and the processus anterolateralis was pronounced (morphometric character 116). Nonetheless, ranoids, i.e., ranids, microhylids, hyperoliids (*s. lato*), and rhacophorids, were not supported as a monophyletic group (Figs. 1 and 2). Among ranoids, however, the analysis suggested the clade (Rhacophoridae (Hyperoliidae [including *Hemisus*] + Microhylidae)).

Ranidae

The paraphyly of ranids was occasionally suggested (e.g., Ford and Cannatella, 1993). The Ranidae was a paraphyletic group in this study with all characters considered (Fig. 1), but was reconstructed as monophyletic group with the four morphometric characters excluded (Figs. 2 and 3). Character optimization suggested three synapomorphies of the ranid species examined. None of them was unique to ranids: firmisterny (convergently in dendrobatids, *Atelopus*, and node 41), presence of a basihyal (character with the lowest CI in this study), and fenestrae parietals (also in Phyllomedusinae and node 12).

Rhacophoridae

A clade formed by the only two rhacophorid species examined, *Chiromantis xeramplina* and *Rhacophorus pardalis*, was supported by two synapomorphic character states (Fig. 2, node 47), both characters were homoplastic. Another suggested synapomorphy, posterior process of the pars alaris (character 89) rectangular in shape, was optimized as synapomorphic in only some of the minimum-length trees (also present in *Hemisus sudanensis* and *Hyperolius puncticulatus*).

The definitions of the Rhacophoridae in the literature disagree largely on the issue of whether the Mantellinae should be included in the Rhacophoridae or instead placed among ranids (Liem, 1970; Dubois, 1981; Channing, 1989; Blommers-Schlösser, 1993; Bossuyt and Milinkovitch, 2001). Ford and Cannatella (1993) briefly summarized the evidence and the results of Channing's (1989) reanalysis of Drewes' (1984) previous work. Ford and Cannatella concluded that the presence of an intercalary element was a potential synapomorphy of rhacophorids (including Mantellinae), under the premise that rhacophorids were not the sister taxon of the Hyperoliidae. In this study, the Rhacophoridae is

the sister group of Microhylidae + Hyperoliidae, and the intercalary was only ambiguously optimized on the tree (Fig. 2) and does not play a central role in this argumentation.

Hyperoliidae (including Hemisus) + Microhylidae

Absence of m. tympanopharyngeus, insertion of the m. rectus cervicis to ceratobranchial III and IV, a ventrally sloping arcus subocularis with irregular margin, and the presence of a well-formed basihyal were synapomorphies for the species in this clade.

Hyperoliidae and Hemisus

Laurent (1979) included the Astylosterninae and Arthroleptinae in the Hyperoliidae (not Hemisus), whereas Duellman and Trueb (1986) applied a much narrower definition of the Hyperoliidae, excluding Astylosterninae, Arthroleptinae, and Hemisus. Emerson et al. (2000) suggested that the Artholeptinae might be nested within the Hyperoliidae and that Hemisus belongs to the Microhylidae. Ford and Cannatella (1993) noted that the vertical pupil in Hemisus suggests affinities to the Hyperoliidae, whereas its notched tongue would be a character state shared with ranids. In other accounts on the Hyperoliidae, the genus Hemisus was examined (Liem, 1970; Drewes, 1984) but not included in the phylogenetic analysis (Drewes, 1984; Channing, 1989).

The data in this study clearly suggest a clade that combines the Hyperoliidae (sensu Ford and Cannatella, 1993) plus Hemisus and that includes Hemisus in the definition of the Hyperoliidae. Familial status for species of Hemisus (Hemisotidae) is not warranted. Synapomorphic characters of the hyperoliid and Hemisus species (Fig. 2) were presence of a m. transversus ventralis (explained as a transversely oriented m. tympanopharyngeus), presence of processus otobranchialis with specific relations to m. diaphragmatobranchialis and rectus cervicis, thin processus ascendens, commissura quadrato-orbitalis inserting high to neurocranium, anterior base of processus muscularis with distinct ventral process, and vertical pupil (reversed in Hyperolius). Of these, the processus otobranchialis and the high insertion of the commissura quadrato-orbitalis are unique character states within the Anura. Beyond these characters, the presence of a gular gland or gular disk in male Hemisus and other hyperoliids (Drewes, 1984) is a further putative synapomorphy.

Although the internal nodes of the Hyperoliidae were not robust (Figs. 1–3), shared features of Hemisus and Kassina were apparent. Larvae of both taxa are nektonic. They stand out from all other species examined by their tremendously thickened dermis (character 12). Potential synapomorphic characters of adults are sec-

ondary terrestrial habits, crawling rather than jumping locomotion, microphagy, presence of sesamoid elements (Drewes, 1984), and posteriorly shifted amplectic position (see photographs in Rödel, 1996).

Microhylidae

An overwhelming accumulation of apomorphic features characterizes larvae in the Microhylidae (see list in Fig. 2, node 43). The list of autapomorphic characters (Fig. 2) contains some that are unique among anuran larvae, for instance, thin m. geniohyoideus with diffuse origin in the proximity of the glandula thyroidea, lateral insertion of the ventral head of the m. subarcualis rectus I, posterior origin of the m. suspensoriohyoideus, blade-like shape of the medial part of cartilago meckeli, accessory longitudinal cartilages supporting the dorsal parts of the filter plates, and closed nostrils. The apomorphic character states describe a major evolutionary step toward highly efficient suspension feeding.

Tadpoles belonging to the Scaphiophryninae possess a mixture of apomorphic and plesiomorphic character states with respect to other microhylids (Blommers-Schlösser, 1993; Wassersug, 1984, 1989). The postulated basal dichotomy in the Microhylidae, i.e., Scaphiophryninae versus Scoptanura (Ford and Cannatella, 1993), was robustly supported by many apomorphic character states of the Scoptanura (Fig. 2, node 44). Scoptanura was defined (Ford and Cannatella, 1993), referring to a term introduced by Starrett (1973) for those microhylids with typical Orton Type II larvae (Fig. 4). Apomorphic character states that distinguish the Scoptanura from the Scaphiophryninae are, for instance (see Fig. 3), spiracle medially and posteriorly located, strongly developed and transversely oriented m. interhyoideus posterior closely associated with external opercular wall, constrictor muscle in interbranchial septum IV and separate from subarcualis rectus II–IV, m. mandibulolabialis inserting on cartilago labialis inferior, jaw levators (longus and internus) shifted anteriorly, unique processus suboticus quadrati, and glottis shifted anteriorly. High character states in morphometric character 116 in combination with low ones in 117 indicated that the processus anterolateralis of the ceratohyal is the dominating anterior ceratohyal process in species of the Scoptanura.

Within the Scoptanura, the enigmatic Paradoxophyla palmata from Madagascar was reconstructed as sister taxon to the African Phrynomantis bifasciatus (formerly Phrynomerus bifasciatus). The m. subarcualis rectus I originates exclusively from ceratobranchial I in the two species. Furthermore, the m. subarcualis rectus II–IV reaches to ceratobranchial II (as opposed to ceratobranchial I in other Scoptanura). The American microhylids Elachistocleis, Gastrophryne, and Hamptophryne

Table 2
Specimens deposited as vouchers

Species	Collection
Caudata	
Ambystoma mexicanum (Shaw, 1789)	ZSM 717/2000
Pleurodeles waltl (Michahelles, 1830)	ZSM 718/2000
Salamandrella keyserlingii (Dybowskii, 1870)	ZSM 719/2000
Anura	
Ascaphus truei (Stejneger, 1899)	ZSM 720/2000
Alytes obstetricans (Laurenti, 1768)	ZSM 721/2000
Bombina maxima (Boulenger, 1905)	ZSM 722/2000
Bombina orientalis (Boulenger, 1890)	ZSM 723/2000
Bombina variegata (Linnaeus, 1758)	USNM 505754
Bombina variegata (Linnaeus, 1758)	ZSM 724/2000
Discoglossus galganoi (Capula, Nascetti, Lanza, Ballini, and Crespo, 1985)	ZSM 725/2000
Xenopous laevis (Daudin, 1802)	ZSM 726/2000
Pelobates fuscus (Laurenti, 1768)	ZMB 28151
Limnodynastes peronii (Dumeril and Bibron, 1841)	ZSM 727/2000
Ceratophrys ornata (Bell, 1843)	ZSM 728/2000
Lepidobatrachus laevis (Budgett, 1899)	ZSM 729/2000
Hylodes meridionalis (Mertens, 1927)	ZSM 730/2000
Leptodactylus latinasus (Jiménez de la Espada, 1875)	ZSM 731/2000
Physalaemus biligonigerus (Cope, 1861)	ZSM 732/2000
Odontophrynus achalensis (Di Tada, Barla, Martori, and Cei, 1984)	ZSM 733/2000
Pleurodema kriegi (Müller, 1926)	ZSM 734/2000
Dendrobates tinctorius (Schneider, 1799)	ZSM 735/2000
Epipedobates tricolor (Boulenger, 1899)	ZSM 736/2000
Phyllobates bicolor (Bibron, 1841)	ZSM 737/2000
Gastrotheca riobambae (Fowler, 1913)	ZSM 738/2000
Hyla annectans (Jerdon, 1870)	ZSM 739/2000
Hyla ebraccata (Cope, 1874)	ZSM 740/2000
Hyla cinerea (Schneider, 1792)	ZSM 741/2000
Hyla pulchella cordobae (Barrio, 1965)	ZSM 742/2000
Litoria genimaculata (Horst, 1883)	KU 224668-77
Litoria genimaculata (Horst, 1883)	ZSM 743/2000
Litoria inermis (Peters, 1867)	ZSM 744/2000
Litoria lesueurii (Dumeril and Bibron, 1841)	ZSM 745/2000
Litoria nannotis (Andersson, 1916)	KU 224678-84
Litoria nannotis (Andersson, 1916)	ZSM 747/2000
Nyctimystes dayi (Günther, 1897)	KU 224696-99
Nyctimystes dayi (Günther, 1897)	ZSM 748/2000
Litoria rheocola (Andersson, 1916)	KU 224685-89
Osteocephalus planiceps (Cope, 1874)	ZSM 749/2000
Phrynohyas resinifictrix (Goeldi, 1907)	ZSM 750/2000
Phyllomedusa vaillantii (Boulenger, 1882)	ZSM 746/2000
Phyllomedusa trinitatis (Mertens, 1926)	ZSM 751/2000
Scinax ruber (Laurenti, 1768)	USNM 505755
Scinax ruber (Laurenti, 1768)	ZSM 752/2000
Smilisca baudinii (Dumeril and Bibron, 1841)	ZSM 753/2000
Bufo arenarum (Hensel, 1867)	ZSM 754/2000
Bufo bufo (Linnaeus, 1758)	ZSM 755/2000
Bufo brongersmai (Hoogmoed, 1972)	ZSM 756/2000
Bufo marinus (Linnaeus, 1758)	ZSM 757/2000
Bufo melanostictus (Schneider, 1799)	ZSM 758/2000
Paa exilispinosa (Liu and Hu, 1975)	ZSM 759/2000
Ptychadena mascareniensis (Dumeril and Bibron, 1841)	ZSM 760/2000
Rana nigrovittata (Blyth, 1856 ''1855'') (metamorphs, adults)	ZMB 62659-62670
Rana nigrovittata (larvae)	ZMB 62658
Rana nigrovittata	*ZSM 761/2000*
Rana temporaria (Linnaeus, 1758)	ZSM 762/2000
Hemisus sudanensis (Laurent, 1972)	ZSM 763/2000
Elachistocleis bicolor (Valenciennes, 1838)	ZSM 764/2000
Gastrophryne carolinensis (Holbrook, 1836)	ZSM 765/2000
Kaloula pulchra (Gray, 1831)	ZSM 766/2000
Chiromantis xerampelina (Peters, 1854)	ZSM 767/2000
Hyperolius puncticulatus (Pfeffer, 1893)	ZSM 768/2000
Kassina senegalensis (Dumeril and Bibron, 1841)	ZSM 769/2000

USNM, National Museum of Natural History; Washington; KU, Natural History Museum Lawrence; ZSM, Zoologische Staatssammlung München; ZMB, Museum für Naturkunde, Berlin.

were convincingly grouped as a clade in the analyses, indicating a possible single origin of all Neotropical microhylids. The three species examined share as synapomorphic character states the unique split of the m. levator arcuum branchialium III into two crossing bundles, absence of processus muscularis, and presence of a distinct ventral palatoquadrate processus rostrally to the m. orbitohyoideus.

Conclusions

This study demonstrates the phylogenetic distribution of larval characters and their states. It is evident that larval features play an important role in reconstructing the phylogeny and evolutionary history of the major clades of frogs. The data presented here give additional support to well-accepted clades, such as Bufonidae, Ceratophryinae, Dendrobatidae, Microhylidae and Scoptanura, Pipoidea, Pididae, and Phyllomedusinae. It provides new insights into the phylogenetic relationships and the position in the system of some groups (Eurasian pelobatids, pseudines, denrobatids and hylodines, *Hemisus*). However, this study also showed that crucial parts of the tree, i.e. the "transitional" so-called pelobatoids and the early basal splits in the Neobatrachia, were not robustly resolved. No existing evidence, neither morphological nor molecular, has so far proven the potential to resolve this case. With respect to the existing homoplasy, these open questions can be addressed only in the context of large taxon samples (see Table 2).

Appendix A. Characters and matrix

If not stated otherwise, the following account refers exclusively to the species and specimens examined.

A.1. Larval characters

1. Epidermal melanocytes elongated and forming orthogonal mesh (0); melanocytes of irregular shape not forming reticulation (1). Most species possess epidermal melanocytes of irregular shape. The epidermal melanocyte pattern of *Bombina orientalis* (Fig. 5) has been described as a highly organized, reticulate pattern (Ellinger, 1979, 1980; Duellman and Trueb, 1986: Fig. 14–17). The character has not been analyzed phylogenetically before. The network of epidermal melanocytes was orthogonal in all three species of *Bombina*. Among the other species examined, this pattern was exclusively
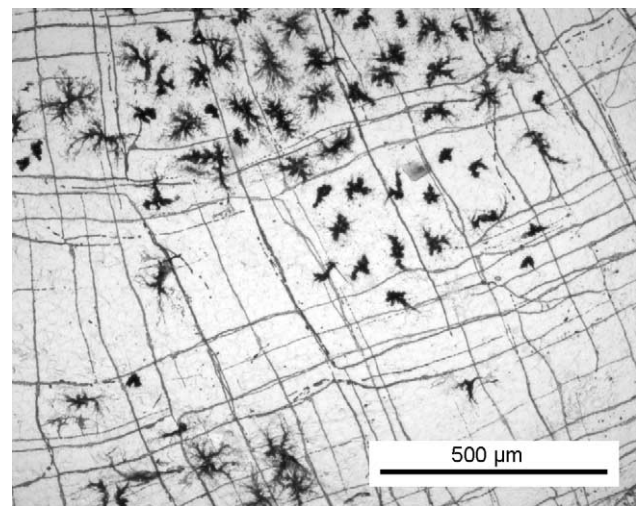
Fig. 5. Reticulate orthogonal melanocytes in larval skin of *Bombina orientalis*. Skin removed from preserved specimen; no staining applied.

found in epidermal melanocytes of *Pelodytes caucasicus* and species of *Discoglossus*.

2. Larval subdermal serous glands absent (0); present (1). Serous (granular) glands in adult amphibians are large spherical epidermal glands sunk deeply into dermal layers of the skin. These glands commonly form during metamorphosis (Delfino et al., 1996, 1998). Most anurans lack such glands during their larval stages. Larval granular glands are known for some suctorial, rheophilous larvae (e.g., Inger and Gritis, 1986), such as *Ascaphus truei*, *Litoria rheocola*, and *Litoria nannotis* (Fig. 6). The larval glands extend below the level of the dense dermal tissue. Larval subdermal serous glands may be abundant along the tail and the ventrolateral parts of the body. Numerous serous glands were found in the dorsal and ventral skin of the head and trunk of *Phyllomedusa vaillantii* (stage 38). However, the glands are not subdermal, i.e., they did not penetrate below the dense dermal layers of the skin. This precocius development of adult skin glands has also been reported for *P. hypochondrialis* (Delfino et al., 1998).

3. Keratodonts absent (0); present (1). Keratodonts (larval "teeth") are keratinized, spoon-shaped, distally serrated structures formed by epidermal cells of the labia (Marinelli et al., 1985; Marinelli and Vagnetti, 1988) . They have anchoring and raking function in tadpole feeding (Wassersug and Yamashita, 2001). Presence and absence of keratodonts have been used as characters in phylogenetic analyses (Inger, 1967; Kluge and Farris, 1969; Duellman and Trueb, 1986) either as single characters or as part of a character conglomerate, e.g., Orton's anuran larval Types I–IV (Fig. 4). Among the species examined, keratodonts are absent in the filter-feeding pipoid and microhylid species, the surface-feeding *Megophrys montana*, the macrophagous carniv-

orous *Lepidobatrachus laevis* the burrowing *Cochranella granulosa*, and in *Hyla ebraccata*.

4. Labial ridges with single row of keratodonts (0); ridges each with double (or more) rows of keratodonts (1). Keratodonts are arranged in dense rows on a number of parallel transverse ridges on the oral labia. In most species, there is only one keratodont row per ridge. Only species of *Ascaphus*, *Alytes*, *Discoglossus*, and *Bombina* have two or more keratodont rows per ridge (Altig and McDiarmid, 1999b). In *Ascaphus truei* only the two proximal ridges (relative to the mouth) bear double rows, whereas the distal ridges possess multiple rows of keratodonts. Kluge and Farris (1969) questioned the usefulness of this character because of intraspecific variability and potential changes during ontogeny (Thibaudeau and Altig, 1988). Also, Kluge and Farris (1969, 30) were concerned that double keratodont rows might be confused with closely standing single rows in species with enlarged numbers of keratodont-bearing labial ridges (e.g., *Heleophryne*). Neither of these concerns was confirmed by the observations in this study.

5. Distal anterior labial ridge and keratodont-bearing row broad (0); very short and median (1). In *Spea bombifrons*, *Pelobates fuscus*, and *Leptobrachium hasseltii* the most distal (relative to mouth) labial ridge on the upper lip is reduced in width. It bridges a correspondingly small gap in the marginal papillation of the oral disk. In other species, the most distal labial ridge is approximately as wide as the jaw sheath. Altig and McDiarmid (1999b); gave a synthesis on the interspecific variation of keratodont rows in anuran larvae. They found that the labial tooth row formula (TRF) is remarkably uniform at the generic level and, thus, potentially phylogenetically informative; but the total number of different TRFs among anurans is bewildering. No comprehensive scheme for cladistic coding has been proposed so far.

6. Keratinized jaw sheaths absent (0); present (1). Keratinized jaw sheaths are well-developed in Orton Type III and IV tadpoles (Fig. 4) and often referred to as "beaks." They were absent in the filter-feeding tadpoles of pipoids and most microhylids examined, *Megophrys montana*, and caudate larvae. Wassersug (1984) described the presence of jaw sheaths in the microhylid *Scaphiophryne calcarata* (then known as *Pseudohemisus granulosus*). This observation was confirmed here for *S. madagascariensis*. The carnivorous larvae of *Lepidobatrachus laevis* have keratinized triangular structures spaced along the edges of their jaws. They do not form a complete sheath along the jaws. Although it has been reported that this species lacked "beaks" (Griffiths and de Carvalho, 1965), the character definition is taken here in a broad sense and the species was scored (1). The jaw sheaths are generally reduced in species of *Heleophryne* (Altig and McDiarmid, 1999b), but traces were found in the single specimen examined (*H. natalensis*).
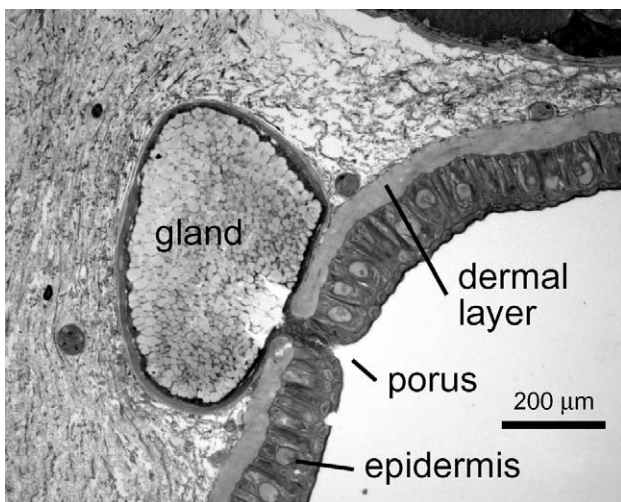

Fig. 6. Larval subdermal skin gland in *Litoria nannotis*. Plastic resin embedding, toluidin blue.

7. Oral lips absent (0); present (1). Orton Type III and IV tadpoles typically have an oral disk, whereas it is absent in Type I and II larvae (Fig. 4). The oral disk is formed by the upper and lower lips, i.e., flat, more or less expansive flaps of skin set off from the mouth and jaws and commonly bearing labial ridges with keratodonts. According to this definition lips were missing in the caudate and pipoid larvae examined. Only the upper lip was present in *Lepidobatrachus laevis*. In microhylids, except for *Scaphiophryne* (oral disk present), the dorsal flaps ("labial flaps;" McDiarmid and Altig, 1999:343) bordering the mouth were supported internally by the cartilagines labiales superiores (pers. observ.). Therefore they correspond to the upper jaw line of other larvae and do not represent lips in the sense of the definition. However, a flap of skin was present ventral (posterior) to the lower jaw in the microhylid *Dyscophus antongilii*.

8. Upper lip papillation continuous (0); broad diastema present (1). In Type III and IV tadpoles, the edges of the oral disk are lined with one to several rows of papillae (Fig. 4). Marginal papillation of the oral disk was coded as two characters to account for the variation in upper and lower lip papillation seen in the sample of taxa. Although a gap (diastema) in the papillation is potentially a continuous character (ratio of measured diastema width to oral disk width), only two discrete states were defined: gap absent or smaller than 25% of oral disk width (0) and gap larger than 25% of oral disk width (1). Continuous papillation of the upper lip margin was present in rheophilous/suctorial larvae (*Ascaphus truei Atelopus tricolor Heleophryne natalensis Nyctimystes dayi Litoria rheocola L. nannotis*), the carnivorous *Lepidobatrachus laevis* and *Ceratophrys ornata*, discoglossids, pelobatids, and *Litoria lesueurii*.

9. Lower lip papillation complete without gap (0); diastema in papillation (1). Among the species examined, bufonid larvae were unique in possessing a clear and wide diastema (>25% of total oral disk width) in the marginal papillation of the lower lip.

10. Oral orifice wide (0); narrow (1). Caudate and pipoid larvae have a wide oral orifice (>70% of maximum head width). A broad mouth is also found in the macrophagous *Lepidobatrachus laevis*. In other species, the relative width of the mouth is much smaller (<<50%).

11. Eye position dorsolateral (0); lateral (1). Eye position was scored (1) when the cornea of the eye reached or protruded beyond the head contour line in dorsal view. The scores for the species examined conform with Altig and McDiarmid's (1999a) account, except for *Pelobates fuscus*, which herein is classified as having a lateral eye position. The examined specimens and stages of *Cochranella granulosa* had undifferentiated eyes and was not coded. Although the position of the eye seems to relate to the microhabitat use and feeding of the respective species, the phylogenetic distribution of the character states has not been demonstrated before.

12. Relative dermal thickness. Skin thickness in some larvae was occasionally mentioned (e.g., Lavilla, 1992) but has not been studied histologically in a comparative manner and assessed phylogenetically. The wide variation in thickness and structure of the larval dermis became apparent in histological sections of *Hemisus sudanensis* (Fig. 7) and *Kassina senegalensis*. In larvae of both species the skin was particularly tough because of hypertrophied dermal layers. The thickness of the dermal tissue was measured from sectioned material. Measurements were taken at the cross-sectional level of the eye, at a site dorsal or dorsolateral to the larval frontoparietal. Measurements of different ontogenetic stages (i.e., body sizes; for example, in *Pyxicephalus adspersus*) indicated that within a given species, dermal thickness increases with body size. Therefore, the ratio of dermal thickness to snout–vent length was calculated for all species (constant ratio across ontogenetic stages examined in *P. adspersus*). Ratios were coded by the gap-weighting method (Thiele, 1993).

13. Single-layered dermis (0); double-layered dermis (1). The dermis of *Kassina senegalensis*, *Hemisus sudanensis*, and most microhylid larvae is double layered. Under light microscopy, there is a less-dense external layer and a dense internal layer (Fig. 7). Dermal thickness was not coupled with the presence of double layers. Frog larvae from some groups have developed relatively thick dermal connective tissue (for instance, phyllomedusines) but possess only a single layer.

14. Vena caudalis dorsalis absent (0); present (1). The literature on larval vascularization was summarized in Viertel and Richter (1999). Interestingly most previous studies literally cut off their descriptions of the vascular system at the end of the trunk, except for Rhodin and Lametschwandtner (1993). Tail vascularization has not been addressed in a comparative study before.

In tadpoles there is only one major tail artery, the arteria caudalis. It is the posterior continuation of the
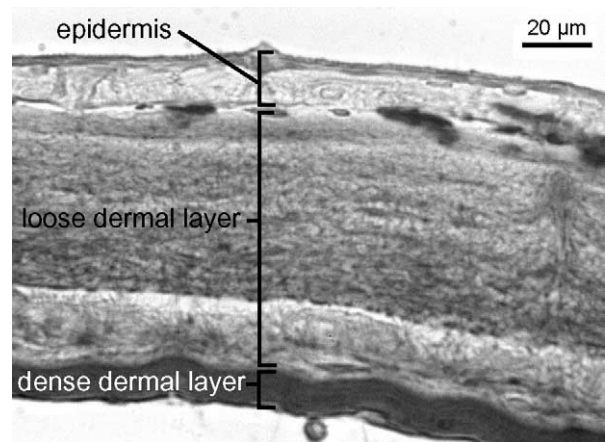

Fig. 7. Skin cross section in *Hemisus sudanensis*. The very thick loose dermal layer is supported by tissue with dense layers of tissue with collagen fibers. Paraffin section, Azan stain.

dorsal aorta into the tail and runs ventral to the chorda dorsalis. The backflow of venous blood from the tail to the renal portal system, however, followed various routes in the taxa examined although the vena caudalis ventralis is invariably present (Fig. 8) in caudate and anuran larvae. It is the largest tail collecting vessel in the caudates examined, and the exclusive longitudinal tail vein in, for example, *Ascaphus truei* and *Discoglossus galganoi*.

Tail blood vessels were studied by in vivo observations (*Alytes obstetricans*, *Bombina orientalis*, *B. variegata*, *Kaloula pulchra*, *Limnodynastes peronii*, *Rana nigrovittata*, *Scinax ruber*, *Xenopus laevis* [Fig. 8]) by tracing the major tail blood vessels by virtue of their melanocyte pigmentation and/or by tracing vessels in

Fig. 8. Major longitudinal tail veins in some of the anuran species examined. Schematic drawing. Flow directions were determined by *in vivo* examination.

serial histological sections of tails. In some specimens, erythrocytes had been washed out of the vessels, making unequivocal tracing in sections impossible (missing data entries).

The vena caudalis dorsalis was present in various taxa (Fig. 8). It is a longitudinal vein which lies in the dorsal sulcus between the axial myomeres of the tail. In the anterior tail or posterior trunk region it bends laterad and runs ventrad along the surface of the axial musculature and in most cases joins the vena caudalis lateralis (if present) before reaching the kidney. In *Xenopus laevis*, the rostral part of the vena caudalis dorsalis was embedded and bent ventrad between the axial musculature to join the vena caudalis ventralis (see also Rhodin and Lametschwandtner, 1993).

15. Paired venae caudales laterales short (0); long (1). Large paired veins may be located superficially along the tail and trunk myotomes. The venae laterales of caudates and anurans receive blood from the skin and musculature of the anterior parts of the tail (pers. observ.; Fig. 8). In anurans, the collected blood runs to the renal portal system, while in caudates the vena lateralis is part of the cutaneous system that extends all along the trunk and finally joins the vena subclavia (Francis, 1934). However, connections of the vena lateralis to the vena ischiadica have been reported in adult salamanders (Francis, 1934), a condition reminiscent of the connections of the vein in anuran tadpoles. At least short, paired venae laterales (stretching over one to four myomeres; character state 0) seem to be present in all anuran larvae. They are associated with lymph hearts located at the tail–trunk transition. Caudate larvae and some anuran species have long venae laterales (more than seven myomeres; character state 1; Fig. 8).

16. Operculum not fused to abdominal wall (0); fused to abdominal wall (1). The operculum of amphibian larvae is a flap of skin growing out ventrally and posteriorly from the hyal region during embryogenesis (Gosner, 1960). It covers the branchial arches and pharynx ventrally. In anuran larvae, the operculum fuses with the abdominal wall and the peribranchial (subbranchial) chamber is formed (Orton, 1953; Sokol, 1975). Kluge and Farris (1969) identified two different modes in the embryonic development of the operculum: from the hyobranchial arches II and III in the Pipoidea, and from arch II only in other frogs. Based on these embryological observations Kluge and Farris (1969) distinguished between a "true" operculum (most frog larvae) and a "pseudo" operculum (pipoids). By doing so they implied that the two opercula were not homologous. However, these differences in development may not be sufficient support for assuming nonhomology.

17. Opercular canal absent and spiracles paired (0); canal present and spiracle single (1). Four basic configurations and positions of the spiracle are known in free-living anuran larvae and have been used to define
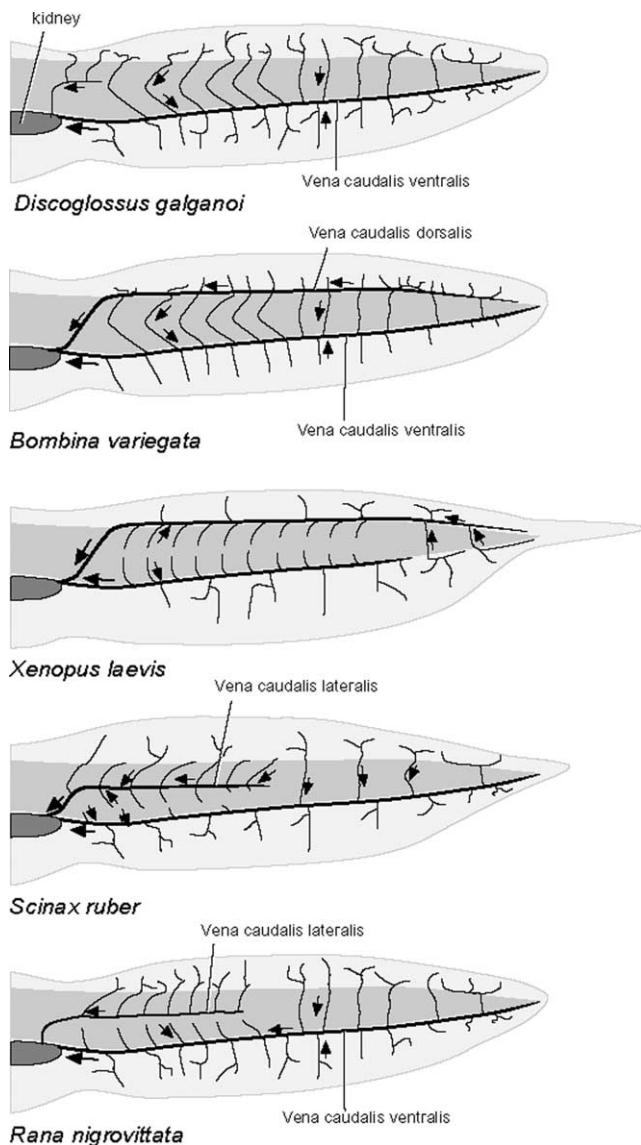
higher taxonomic groups (Orton, 1953; Inger, 1967; Kluge and Farris, 1969; Sokol, 1975;): paired lateral, median anterior, sinistral, and median posterior (Fig. 4). Conventionally coded, the spiracular features are here understood as two separate but logically nonindependent characters (see character 18). Character 17 distinguishes between taxa that have paired spiracles and lack an opercular canal (Pipoids) and taxa that have one spiracular opening and an opercular canal (others). The opercular canal is a tubular space that interconnects the two peribranchial chambers and guides the water from the gill cavities to the spiracle. It is associated with the presence of a single spiracle. Fusion of the operculum to the abdominal wall is a prerequisite for the formation of the opercular canal (character inapplicable in caudates).

18. Spiracle position median anterior (0); sinistral (1); median posterior (2). The usefulness of the spiracular positions in phylogenetic analyses had been questioned (Griffiths, 1963; Griffiths and de Carvalho, 1965) because some taxa deviate from the otherwise uniform pattern as expressed in Orton's (1953) tadpole types (Fig. 4). Those previous discussions were focused primarily on exceptions from the general rule, whereas cladistic analysis is concerned with the global distribution of character states. Species of the phyllomedusine hylids (Type IV tadpoles) were described as having a ventral position of the spiracle (Griffiths, 1963). In all phyllomedusine specimens examined herein, however, the spiracle was close to the ventral midline but still clearly sinistral with an asymmetric opercular canal as in other Type IV tadpoles. *Lepidobatrachus laevis* and *Scaphiophryne madagascariensis* were the only true deviations from Orton's general scheme among the tadpoles in this study. Although *L. laevis* has paired opercular openings, a sinistral configuration of the opercular complex is transitory during ontogeny (Ruibal and Thomas, 1988). Larvae in the genus *Scaphiophryne* have a sinistral spiracular position and do not fit Orton's general Type II for microhylids (Wassersug, 1984, 1989).

19. M. geniohyoideus origin from basibranchial (proc. urobranchialis) (0); ceratobranchial I/II (1); ceratobranchial III (2); planum hypobranchiale (3); from connective tissue lateral to glandula thyroidea (4). The m. geniohyoideus originates from the proximal part of ceratobranchial I in, for example, *Ascaphus truei*, more posteriorly from the ceratobranchial III (discoglossids), or from the ventral side of the planum hypobranchiale (most neobatrachians) (Haas, 1997). In *Heleophryne natalensis*, the muscle has a broad origin centered at ceratobranchial III but reaching ceratobranchialia II and IV with some fibers. The muscle has no clear origin at skeletal parts in larval microhylids; rather it originates in diffuse tissue lateral to the glandula thyroidea. In larval caudates, the muscle originates from the processus urobranchialis of basibranchial II (Drüner, 1901;

Edgeworth, 1935; Haas, 1997). The muscle is absent in larvae of *Rhinophrynus dorsalis*. Absence/presence of the muscle could be coded separately from its attachment pattern. However, *Rhinophrynus dorsalis* was the only species that lacked the muscle. The autapomorphic state in *R. dorsalis* was coded as a fifth character state. There is no compelling transformational similarity in the character states that would justify ordering.

20. M. tympanopharyngeus absent (0); present (1). The m. tympanopharyngeus (Schulze, 1892) is a flat and narrow bundle of fibers originating from connective tissue anchored at the posterior crista parotica of the otic capsule. At its origin the m. tympanopharyngeus is closely associated with and often indistinguishable from the m. levator arcuum branchialium IV. It is likely that the former muscle has evolved by splitting from the latter (Haas, 1997). The character was scored (1) whenever fibers at the insertion (i.e., distally and ventrally) that clearly diverged from the fibers of the fourth arch levator could be found (Fig. 9a). To be coded as character state (1), the muscle's fibers had to take a mediad orientation toward connective tissue dorsal to the pericardium or even attach to the pericardium itself (instead of inserting on ceratobranchial IV). A complete separation of the two muscles all along their lengths was not a requirement for this state definition. Under this less restrictive definition the previous assessment of the muscle in *Litoria genimaculata* (Haas and Richards, 1998) was modified herein. The separation of the two muscles was particularly clear in some hylids (e.g. *Scinax ruber*, *Hyla ebraccata*, phyllomedusines) in which the m. tympanopharyngeus reaches far medially, even connecting to its counterpart below the glottis in *S. ruber* (not to be confused with the m. dilatator larynges).
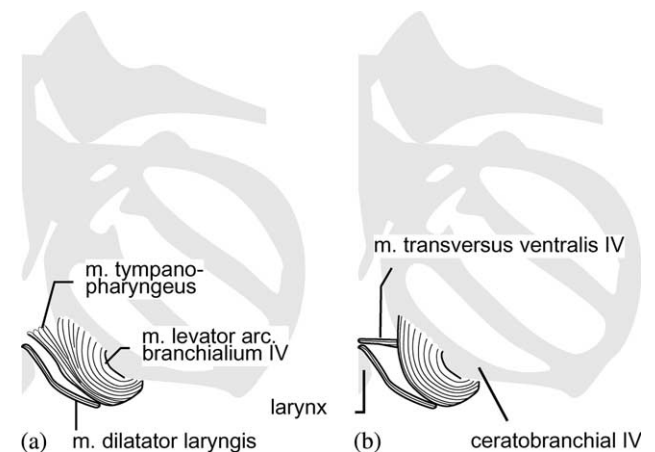

Fig. 9. Branchial muscles in the region of ceratobranchial IV and larynx; ventral views. Hyobranchial skeletal structures (gray) do not represent a specific species. (a) The m. tympanopharyngeus is separate from the levator arc. branch. IV in most neobatrachians. (b) The muscle is shifted in *Chiromantis* and hyperoliids and assumes the position of a m. transversus ventralis IV.

The m. tympanopharyngeus seemed to be absent in hyperoliids, but see an explanation in character 22 description.

21. Insertion of m. levator arcuum branchialium IV restricted to distal parts of ceratobranchial IV (0); insertion reaching medially and extending on proximal parts of ceratobranchial IV (1). In caudates all branchial levators attach to the distal ends of the ceratobranchialia. The branchial levators I–III of anuran larvae also insert at the distal end of the respective ceratobranchial and the interconnecting commissurae terminales. In various species (discoglossids, *Spea bombifrons*, and *Pelodytes caucasicus*), the m. levator arc. branch IV inserts on the distal half of ceratobranchial IV, whereas in most anurans, it has shifted its origin medially to the proximal half of ceratobranchial IV (Fig. 9).

22. M. transversus ventralis IV absent (0); present (1). The m. transversus ventralis IV is a thin muscle originating from the medial side of ceratobranchial IV. It stretches mediad to insert in connective tissue ventral to the glottis. The muscle is well developed and seems generally present in caudate larvae (e.g., Drüner, 1901; Edgeworth, 1935; present study). Pusey (1943) mentioned the existence of both mm. tympanopharyngeus and transversus ventralis IV in *A. truei*. Only the latter muscle could be confirmed in the specimens of *A. truei* examined herein.

It has been claimed that *A. truei* is the only anuran species that possesses a m. transversus ventralis IV (Pusey, 1943; Haas, 1997). The additional taxa examined in this work, however, reveal that various other taxa have muscles that fulfill the topographic definition for this muscle (*Heleophryne natalensis*, *Leptobrachium hasseltii*, *Chiromantis xerampelina*, *Hemisus sudanensis*, hyperoliids). Among these, *L. hasseltii* was different from the other anuran taxa in that the muscle was an extensive sheath of loose fibers between the two ceratobranchialia IV. Interestingly, rhacophorids and hyperoliids apparently lack the m. tympanopharyngeus in the typical orientation (Fig. 9a). It is likely that their "m. transversus ventralis IV" is in fact the tympanopharyngeus that has shifted its origin and orientation (Fig. 9b). However, primary homology assessment based on spatial relationships required the preliminary coding of this muscle as "m. transversus ventralis IV" in rhacophorids and hyperoliids.

23. M. interhyoideus posterior absent (0); present (1). The m. interhyoideus posterior (Sokol, 1975) is here defined as a more or less complete sheath of predominantly transverse muscle fibers in the opercular fold. The muscle has also been called constrictor colli (Edgeworth, 1935) or subbranchialis (Schulze, 1892). It is innervated by the n. facialis (Gradwell, 1972a; pers. observ.). The opercular fold of caudates contains a continuous sheath of transversely oriented fibers

(Drüner, 1901; Edgeworth, 1935). In anuran larvae, the muscle usually is but a loose layer of fibers spreading in the operculum ventral to the peribranchial chamber, mostly below the anterior ceratobranchials (Fig. 10). Its thickness, shape, and fiber orientation is subject to interspecific variation (see character 24), and often there are only a few difficult to detect fibers. In almost all frog larvae the muscle fibers are positioned along the inner lining of the operculum, immediately adjacent to the peribranchial chamber. In the microhylid clade Scoptanura (but see also Noble (1929) for *Hoplophryne*), the muscle is strongly developed and vast in extent and forms a continuous sheath below the large peribranchial chamber (Gradwell, 1974). It is located along the external rather than the internal lining of the operculum, and the muscle is easily removed when specimens are skinned. This may in part explain the discrepancies in the literature (see summary in Cannatella, 1999). Often the muscle was weakly developed and careful inspection of histological sections was essential.

24. M. interhyoideus posterior thin but complete sheath (0); loosely spaced fibers in restricted areas of the operculum (1); extensive and strongly developed (2) (see character 23).

25. M. diaphragmatopraecordialis absent (0); present (1). The m. diaphragmatopraecordialis was described by Schulze (1892) in *Pelobates fuscus*. Gradwell (1972b), Sokol (1975), and Haas (1997) have treated this muscle as being a part of the m. interhyoideus posterior. The two muscles are closely associated and encircle the peribranchial chamber. Their fibers converge to meet in connective tissue (Fig. 10). This architecture suggests that both muscles act in concert as constrictors of the peribranchial chamber (accessory force pump; Gradwell, 1972b, 1974). In this respect the
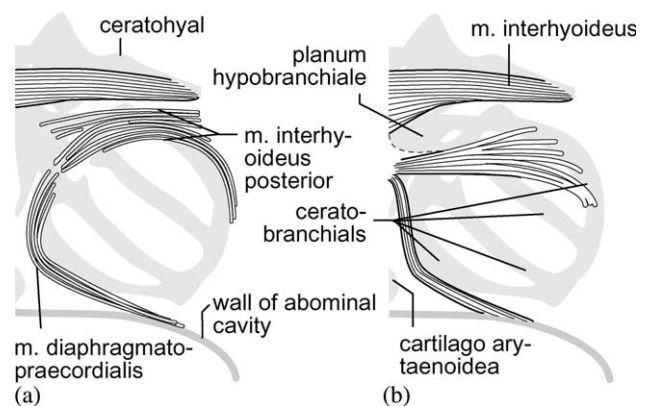

Fig. 10. (a) In many neobatrachians (also *Leptobrachium*) the m. interhyoideus posterior and m. diaphragmatopraecordialis are present and meet in an smooth arched pattern. (b) In most ranids, rhacophorids, and hyperoliids, but also in *Megophrys*, *Pelobates*, and *Odontophrynus*, the muscles assume an angled orientation. Schematic ventral views; hyobranchial skeletal structures (gray) do not represent a specific species.

absence of the m. diaphragmatopraecordialis in scoptanuran microhylids seems to be linked to the strongly developed m. interhyoideus that likely replaces it functionally. In other anuran larvae, in which both muscles are absent, functional explanations are obscure. Examination of histological sections was essential for correct scoring.

26. M. diaphragmatopraecordialis meeting m. interhyoideus posterior in smooth arch (0); both muscles meeting in specific angled pattern (1). In most species the m. diaphragmatopraecordialis is a loose stream of fibers, which connects to the m. interhyoideus posterior lateral to the heart. Both muscles form an arched pattern in ventral view (Fig. 10a). In *Pelobates fuscus, Megophrys montana,* and *Odontophrynus achalensis,* but particularly in most ranids (Gradwell, 1972a for *Rana catesbeiana*) and hyperoliids examined, the mm. diaphragmatopraecordiales and interhyoidei posteriores from both sides are closely adjoined in connective tissue anteroventral to the heart (Fig. 10b). The m. diaphragmatopraecordialis was a well-delimited bundle in these cases. In ventral view, the muscle ensemble of both sides connected in an X-shaped fashion (see also Gradwell, 1972a).

27. M. constrictor branchialis I absent (0); present (1). The m. constrictor branchialis I (*sensu* Haas, 1997) takes its origin at the distal parts of ceratobranchial I, adjacent to the origin of the first branchial arch levator). It inserts on the posterolateral tip of the ceratohyal. In this study, it is present in *Ascaphus truei,* all species of Discoglossidae (*s. lato*), *Spea bombifrons, Heleophryne natalensis,* and *Pelodytes caucasicus.* Two conflicting primary homology assessments can be formulated for the m. constrictor branchialis I. The debate is covered in Haas (1996) and Cannatella (1999).

28. Interbranchial septum III musculature absent (0); present (1). The septum of the third branchial arch does not include a constrictor muscle in species of the Discoglossidae (*s. lato*), pipoids (septum reduced), and *Leptobrachium hasseltii* (Sokol, 1975; Schlosser and Roth, 1995; Haas, 1997; present study). *Ascaphus truei* has been reported to be polymorphic; a short muscle could be found in some but not all individuals (Pusey, 1943; Haas, 1997).

29. Interbranchial septum IV musculature absent (0); lateral fibers of m. subarcualis rectus II–IV invade septum (1); origin of m. subarcualis rectus II–IV completely far lateral (2). Sokol (1977a) described a constrictor muscle in the fourth branchial septum of pipids as the m. subarcualis rectus II–IV. However, the muscle in pipids resembles the muscles from the m. constrictor branchialis series in other frogs in orientation; its origin is far laterally and it does not have attachment to the proximal ceratobranchial IV as is commonly characteristic for the subarcualis rectus II–IV. Sokol's homologization had been questioned (Haas, 1997) and such a shift of the subarcualis rectus laterally had not been known in any

other anurans at that time. With the new materials examined herein, I withdraw my previous concerns. The species examined establish a transformation series (Figs. 11a, e, and f) for the subarcualis rectus II–IV and Sokol's primary homology assessment seems warranted. Lateral fibers of the m. subarcualis rectus II–IV originating from more lateral positions and likely acting on the interbranchial septum IV (Figs. 11e and f) are present in many bufonids and microhylids examined. Determining the lateral extent of the fibers can be difficult in small specimens, because in some cases very few muscle fibers need to be detected in the septum. State (2) in *Xenopus* and *Pipa* (Sokol, 1977a) is unique insofar as the complete origin of the m. subarcualis rectus II–IV is located laterally. Character state (1) was scored when the lateral fibers of the subarcualis rectus II–IV reached laterally beyond 50% of ceratobranchial IV. State (1) was considered intermediate between (0) and (2) and ordered states were used.

30. M. subarcualis rectus II–IV one flat tract of fibers (0); split into medial and lateral separate muscles (1). In the microhylids examined, except for *Scaphiophryne madagascariensis,* the lateral fibers of the m. subarcualis rectus II–IV have shifted their origin far laterally and separated from the medial part of the muscle for its entire length (Fig. 11f). I suggest calling this muscle m. subarcualis rectus lateralis. Both muscle parts converge toward their insertion site. In *S. madagascariensis,* there was incipient separation of the bundles at the origin but not complete separation anteriorly; state (0) was assigned.

31. Single m. subarcualis obliquus originates from ceratobranchial II (0); two clearly separate heads from ceratobranchialia II and III respectively (1); three portions from ceratobranchialia II, III, IV (2). In *Ascaphus truei,* ceratobranchialia II–IV each have a m. subarcualis obliquus. Pusey's (1943) view that there is a fourth m. subarcualis obliquus originating from spiculum IV and that, therefore, spiculum IV of *A. truei* could represent a fifth branchial arch was not confirmed (Haas, 1997). In other anurans, the fibers of the m. subarcualis obliquus either originate solely from the processus branchialis II or originate from processus branchiales II and III and the fibrous tissue between them. While the m. subarcualis obliquus had only one belly in most species, it had two clearly separate heads in others (*Limnodynastes peronii* hyline treefrogs). In these anurans, the portions attached to ceratobranchialia II and III, respectively, similar to the condition found in caudates.

32. M. subarcualis rectus accessorius absent (0); present (1). Among the species examined, this muscle is present exclusively in *Leptobrachium hasseltii, Megophrys montana,* and *Heleophryne natalensis.* It is a large, clearly visible muscle that originates from the posterior spur of the planum hypobranchiale or spiculum IV and inserts medial and adjacent to m. subarcualis rectus at ceratobranchial III (Fig. 11c). The m. subarcualis rectus
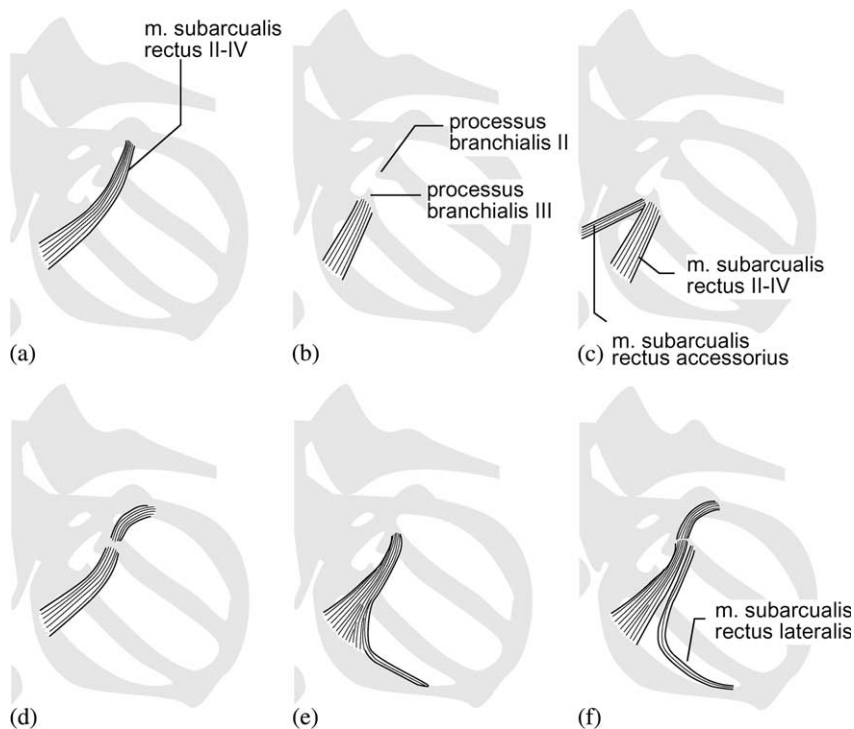
Fig. 11. Patterns of m. subcualis rectus II–IV and derivatives; ventral view. Hyobranchial skeletal structures (gray) are generalizations and do not represent a specific species. Note that only some observed combinations of characters and their states are represented; others exist (see data matrix). (a) muscle undivided and spanning all ceratobranchialia ventrally (caudates, *Ascaphus*, and discoglossids, among others); (b) undivided and reaching only ceratobranchial III (most of the ranids examined); (c) m. subcualis rectus accessorius present, muscle reaching only ceratobranchial III, no lateral slip (e.g., *Megophrys*); (d) discontinuous muscle, i.e. anterior and posterior portions (*Pseudis*); (e) lateral slip invading branchial septum IV (e.g., in bufonids, *Pelodytes*, *Limnodynastes*, and *Paa*; (f) lateralis part invading branchial septum IV and clearly separate from main muscle portion (Scoptanura).

accessorius has not been described before. The structural relationships to or evolutionary derivation from other muscle groups remain unclear.

33. M. subcualis rectus I portion with origin from ceratobranchial I absent (0); present (1). The m. subcualis rectus I complex was reviewed in Haas (1997). Caudate larvae have a simple singular muscle, whereas in anuran larvae up to three muscle portions may occur. The insertion site for all portions of this muscle is at the lateral base of the processus posterior hyalis in most species examined (exception: microhylids; Fig. 12). Supplementing previous data (Haas, 1997), I found that some anuran taxa lack the muscle's dorsal portion from ceratobranchial I (*Pelodytes caucasicus*, *Megophrys montana*, *Ceratophrys ornata*). To account for the new data, the character coding deviates from earlier work (Haas, 1997) and the complex was split into three characters, scoring the absence or presence of each portion independently (characters 33–35).

34. M. subcualis rectus I portion with origin from ceratobranchial II absent (0); present (1). 35. M. subcualis rectus I portion with origin from ceratobranchial III absent (0); present (1). On ceratobranchials II and III the fibers originate from the processus branchialis region. In a minority of species the processus branchi-
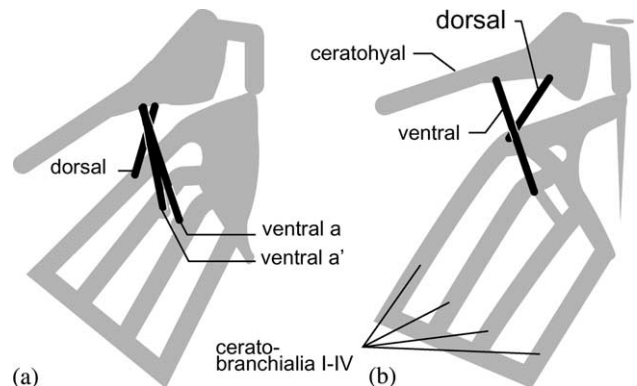
Fig. 12. Insertion pattern in the m. subcualis rectus I complex, represented by thick black lines; ventral view. Hyobranchial skeletal structures (gray) do not represent a specific species. (a) Three muscle portions all inserting medially at the ceratohyal are present in most nonmicrohylid neobatrachians and some pelobatoids examined; (b) the ventral portion has a lateral insertion in species of the Microhylidae (except for those who lack the ventral portion).

ales II and III are close to each other spatially or even fused (see below). In these cases the distinction of the character states was difficult.

36. Insertion site of the m. subcualis rectus I on medial parts of ceratohyal (0); ventral muscle portion

inserts laterally (1). The m. subarcualis rectus I has a medial insertion site in caudates and anurans in general (Haas, 1997). If multiple portions are present, these portions converge in most species to the ceratohyal where they attach in two adjacent layers but overlap in ventral view (Fig. 12a). In microhylids, the insertions of ventral and dorsal parts are not overlapping but separated by a distinct gap (Fig. 12b). The ventral portion of the m. subarcualis rectus I inserts more laterally at the posteroventral margin of the ceratohyal. In the microhylids *Paradoxophyla palmata* and *Phrynomantis bifasciatus* the m. subarcualis rectus I originated solely from ceratobranchial I in two slightly different layers. The typical ventral portion of the muscle (characters 34 and 35) was missing and the character was coded as inapplicable in the two taxa.

37. Anterior insertion of m. subarcualis rectus II–IV on ceratobranchial I (0); ceratobranchial II (1); ceratobranchial III (2). The subarcualis rectus II–IV is a flat slip of muscle that originates ventrally from the proximal parts of ceratobranchial IV (Fig. 11). In larval caudates and some anurans, it reaches forward to insert on the first ceratobranchial (Fig. 11a). In caudates there are well-defined insertions to ceratobranchialia II and III along the way forward, particularly in the salamandrids examined. In many anuran larvae examined, however, these latter insertions were indistinct. Furthermore, the muscle often did not reach ceratobranchial I but ended either at processus branchialis II (state 1) or processus branchialis III (state 2), respectively. Character state (1) is intermediate between states (0) and (2) in a transformation series (ordered states).

38. M. subarcualis rectus II–IV continuous (0); discontinuous (1). In both species of *Pseudis* examined, the m. subarcualis rectus II–IV is clearly discontinuous and subdivided at processus branchialis III (Fig. 11d).

39. Insertion of m. rectus cervicis far anteriorly [basibranchial] (0); at processus branchiales II or III (1); on proximal ceratobranchialia III and IV (2); on ceratobranchial IV only (3). The m. rectus cervicis is a ventral, horizontal muscle in anterior continuation of the rectus abdominis. The rectus cervicis originates broadly from the abdominal wall. In caudates and *Ascaphus truei* it attaches anteriorly and medially to the basibranchial cartilage (Pusey, 1943; Haas, 1997). In most other frogs the muscle inserts on the proximal parts of ceratobranchialia II and III, mostly at the processus branchialis. In various taxa an accessory connection to ceratobranchial IV was present. Finally, in *Kassina*, *Leptopelis*, *Hyperolius*, and scoptanuran microhylids there was solely an insertion to the fourth ceratobranchial and the muscle assumes an almost dorsoventral orientation. In general, the transformation series of character states 0–3 characterizes a shift of insertion from anterior to posterior (ordered).

40. Mm. levatores arcuum branchialium I and II narrow wide gap between them (0); very wide small gap between them or fused (1). Four mm. levatores arcuum branchialium are invariably present in anuran larvae, one for each ceratobranchial. The levatores I and II were well separated by gaps in *Ascaphus truei*, species of *Alytes*, *Bombina* (illustrated in Haas, 2001), *Discoglossus* (Haas, 1997), *Heleophryne natalensis* (Fig. 13), *Lepidobatrachus laevis*, and *Ceratophrys ornata*. The mm. lev-
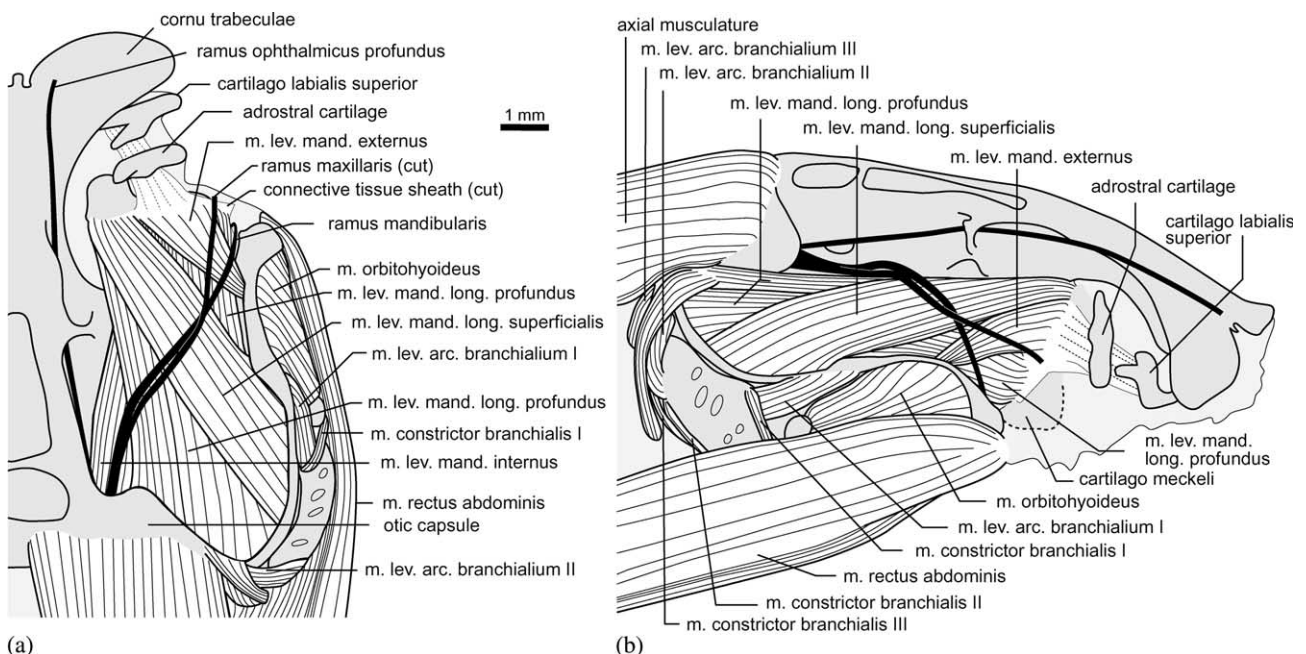
Fig. 13. Superficial cranial muscles in *Heleophyne natalensis* (specimen Heleo 1, stage 28); (a) dorsal view, (b) lateral view.

atores arcuum branchialium I and II were very wide and close to each other or indistinguishably fused in other taxa. Sokol (1977a) pointed out the fusion of the first two levatores in species of *Xenopus* and *Pipa*.

41. M. levator arcuum branchialium III not split (0); split into two crossing bundles (1). In the American microhylids *Gastrophryne carolinensis*, *Hamptophryne boliviana*, and *Elachistocleis bicolor*, the origin of the m. levator arcuum branchialium III is split into two bundles that cross each other before converging into the distal continuous flat parts of the muscle (Fig. 14).

42. Larval jaw depressors originate from neurocranium (otic capsule) and dorsal fascia (0); from palatoquadrate (1). The depressor mandibulae of larval caudates originates mainly from posterolateral parts of the otic capsule (neurocranium). Connections to the dorsal fascia may be present. A number of muscles in anuran tadpoles are considered homologous to the m. depressor mandibulae complex in caudates, i.e., the m. orbitohyoideus, the m. suspensoriohyoideus, and the muscles of the angularis group (Edgeworth, 1935). These muscles have in common that their origins are located primarily on the palatoquadrate in larval anurans.

43. M. hyoangularis absent (0); present (1). Up to three muscles compose the angularis group in anurans (Edgeworth, 1935). *Ceratophrys ornata* was the only anuran species in the sample in which the m. quadratoangularis was absent (not coded). In general, the angularis muscles converge toward their insertion at the processus retroarticularis of the cartilago meckeli (Se-
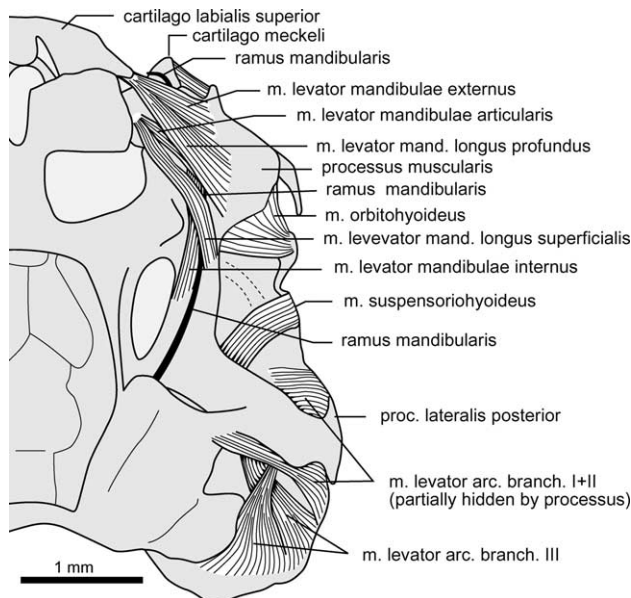

Fig. 14. Cranial musculature of the microhylid *Elachistocleis bicolor*; dorsal view. Note the anterior origin of jaw levators (synapomorphic for scoptanurans), the posterior origin of the m. suspensoriohyoideus (microhylids), and the crossing portions of the m. levator arcuum branchialium III (Neotropical microhylids).

dra, 1950; de Jongh, 1968; Gradwell, 1972a; Haas, 1997). The m. hyoangularis is defined as that part of the muscle group that originates from the ceratohyal. There is no such depressor mandibulae part in caudates, *Ascaphus truei*, and species of *Discoglossus* (Pusey, 1943; Schlosser and Roth, 1995; Haas, 1997). The m. hyoangularis and m. quadratoangularis lie close to each other along most of their lengths and share their site of insertion. This suggest that the m. hyoangularis arose as a second head of the m. quadratoangularis that shifted onto the ceratohyal.

44. Jaw depressors or portions thereof with post- or suborbital origin (0); jaw depressors originating exclusively preorbitally (1). The m. suspensorioangularis originates far postorbitally from the palatoquadrate in *Ascaphus truei*, species of *Alytes*, *Bombina*, and *Discoglossus*. This condition is considered similar to the posterior origin of the m. depressor mandibulae in caudates (Haas, 1997). In most other frog taxa, the m. suspensorioangularis originates far more anteriorly at the posterior base of the processus muscularis (preorbital origin). For species of the Pipoidea the m. suspensorioangularis was reported missing (Sokol, 1977a,b). Pipoid larvae have one angularis muscle mass (called quadratohyoangularis in Starrett (1973) and Sokol (1977a)) without distinct heads. However, some fibers of the quadratohyoangularis attach to the ceratohyal in pipoids (see character 43).

In species of the Microhylidae, the m. hyoangularis was quite well separated from the remainder of the angularis group. It was reported that the m. suspensorioangularis was absent in microhylids (Starrett, 1973; Gradwell, 1974). Although the angularis group was relatively compact in the microhylids examined, a more medial and a lateral bundle of fibers was discernible both by fiber orientation and extent of origin. It is assumed here that the lateral bundles correspond to the m. suspensorioangularis, which has shifted anteriorly in microhylids and has come to lie next to the m. quadratoangularis (see also Wassersug and Pyburn, 1987: 19). *Lepidobatrachus laevis* and *Atelopus tricolor* have short palatoquadrates and the origin of the m. suspensorioangularis was therefore located suborbitally.

45. M. suspensoriohyoideus absent (0); present (1). There have been confusing accounts on the m. suspensoriohyoideus in the various anuran groups (Pusey, 1943; Starrett, 1973; Sokol, 1977a; Haas, 1997). The m. suspensoriohyoideus probably is a posterior portion of the m. orbitohyoideus, both cranial nerve VII innervated, that has become well separated in some species. It usually originates from the lateral side and posterior base of the processus muscularis quadrati. In some species the m. suspensoriohyoideus is poorly delimitated (or indistinguishable) from the m. orbitohyoideus. I will apply here a more restrictive definition for coding than in previous work (Haas, 1997). First, the m. suspenso-

riohyoideus is scored as present (state 1) only if it is clearly distinct from the m. orbitohyoideus, i.e., the m. orbitohyoideus can be lifted off in dissections without removing the m. suspensoriohyoideus. Second, it must have a fiber orientation different from that of the m. orbitohyoideus. Third, its insertion must be medial to that of the m. orbitohyoideus at the processus lateralis hyalis.

46. Origin of m. suspensoriohyoideus from posterior base of processus muscularis (0); from posterior palato-quadrate (1); from otic capsule (2). The m. suspensoriohyoideus usually is covered partly by the m. orbitohyoideus. In microhylids, however, the origin of the muscle is translocated far posteriorly, reaching the posterior parts of the palatoquadrate (Gradwell, 1974). Some microhylid species examined had an even more posterior origin of the muscle, reaching ventral parts of the otic capsule (for example, *Elachistocleis bicolor*, Fig. 14). Starrett (1973) did not list the m. suspensoriohyoideus for microhylids in her comparative table of anuran musculature. The successive posterior shift of origin constitutes a transformation series (ordered).

47. M. interhyoideus and m. intermandibularis in close proximity (0); well separated by a gap (1); X-configuration (2). In *Ascaphus truei* and species of *Alytes*, *Bombina*, and *Discoglossus* fibers of the m. intermandibularis are immediately adjacent to the anterior part of the m. interhyoideus (Starrett, 1973; Schlosser and Roth, 1995; Haas, 1997, 2001: Fig. 10). The two muscles are also close to each other in caudate and pipid species (Sokol, 1977a) but clearly separated by a wide gap in the majority of anuran species examined (Schulze, 1892; Takisawa et al., 1952; Starrett, 1973; de Jongh, 1968; Gradwell, 1972a; Haas, 1996). In the microhylids examined, except for *Scaphiophryne madagascariensis*, the posterior fibers of the m. intermandibularis and the anterior fibers of the m. interhyoideus attached to a common central area of connective tissue in a specific, almost X-shaped manner (see Starrett, 1973: Figs. 7–5; Haas, 2001: Fig. 11).

48. M. mandibulolabialis absent (0); present (1). The m. mandibulolabialis is absent in caudates, *Ascaphus truei*, pipoids, and *Lepidobatrachus laevis*. In other anurans it is generally a bundle of fibers originating from the medial ridge of the cartilago meckeli and spreading fanlike into the lower lip. As judged by its insertion the muscle acts on the keratodont rows and the lip as a whole, but there is no experimental work done on its exact function. Carr and Altig (1991) described the absence of the muscle in larvae belonging to *Cera-tophrys*. In the *C. ornata* examined here, the muscle was present although in a very atypical condition: it is a thick straight bundle rather than a fan of loose fibers. It inserts in the fleshy lower lip. It is partly hidden by the m. intermandibularis in ventral view and it can be mistaken for the anterior end of the m. geniohyoideus.

49. M. mandibulolabialis inserting in soft tissue of lip (0); inserting exclusively on cartilago labialis inferior (1). The oral disk was reduced (*Scaphiophryne mad-agascariensis*) or absent in microhylid tadpoles. Only in *S. madagascariensis* did the m. mandibulolabialis, although somewhat reduced, spread into the lower lip in the fan-shaped manner. In the other microhylids examined, it inserts at the ventral side of the cartilago labialis inferior (Haas, 2001: Fig. 11) and probably acts as a retractor of the cartilago labialis inferior (= "in-fralabial retractor;" Starrett, 1973). The muscle is a more or less cylindrical bundle converging with the distal end of the m. geniohyoideus. Because of the small size of the muscle and its proximity to the distal end of the m. geniohyoideus, examination of serial sections was required to trace the muscle.

50. M. mandibulolabialis superior absent (0); present (1). Bundles of fibers of the m. mandibulolabialis invading the upper lip are recognized as m. mandibulo-labialis superior (Carr and Altig, 1991; Haas, 2001: Fig. 1). The muscle was present in species of *Bombina*, the pelobatids *Pelobates fuscus*, *Leptobrachium hasseltii*, and *Megophrys montana*, and in most hyline and all phyllomedusine hylids examined.

51. M. mandibulolabialis superior originating from medial edge of cartilago meckeli (0); from posteroventral tip of cartilago labialis inferior (1). The origin of the m. mandibulolabialis superior from the cartilago labialis inferior was a unique character state of the species of *Bombina* examined (see also Haas, 2001).

52. Origin of m. intermandibularis along a line on the ventral side of the cartilago meckeli corpus (0); restricted to the medial face of the cartilago meckeli (1). In most anuran species, the larval muscle is a U-shaped (ventral view), flat band of fibers that interconnects the ventral sides of the middle parts of the cartilagines meckeli. In species examined of *Alytes*, *Bombina*, and *Discoglossus*, however, it was a loose and very thin layer of muscle fibers, rather V-shaped in orientation (see Haas, 2001: Fig. 10), and the origin of the m. in-termandibularis was restricted to the medial face of the cartilago meckeli adjacent to the m. mandibulolabialis (Haas, 2001: Fig. 3).

53. Upper jaw without insertion of jaw muscles (0); upper jaw cartilages powered by jaw muscles. (1). Among the anuran species examined, *Ascaphus truei* and *Pipa carvalhoi* lacked any muscular powering of upper jaw structures. The data do not support Sokol's (1977a) account that the m. externus ("subexternus" in his terminology) inserts on the suprarostral cartilage in *P. carvalhoi*. In the *P. carvalhoi* material examined herein, the muscle rather inserted in tissue lateral to the lower jaw, not to upper jaw structures.

54. Larval m. levator mandibulae externus present as one muscle body (0); two portions (profundus and su-perficialis) (1). In most anuran larvae, the m. levator

mandibulae externus profundus originates medially on the anterior part of the processus muscularis (Haas, 2001). It converges with the m. levator mandibulae longus profundus anteriorly and both insert by a common tendon on the cartilago labialis superior (Fig. 13). The m. levator mandibulae externus superficialis is close to the externus profundus at its origin (see Haas, 2001: Fig. 3), but then takes an oblique orientation relative to the profundus and connects mainly to the dorsomedial process of cartilago meckeli (Luther, 1914; Haas, 2001). There is only one m. externus portion in caudates and various anuran species. In contrast to pipids (one portion), two portions were present in *Rhinophrynus dorsalis*; the profundus portion converged with m. levator mandibulae longus and the superficialis portion inserted in soft tissue at the mouth angle.

55. Larval m. levator mandibulae externus inserts exclusively on lateral side of mandible (0); main portion inserts on upper jaw cartilages (1); soft tissue insertion (2). Lateral insertion of the m. lev. mand. externus on the mandible is present in larval caudates (Haas, 2001: Fig. 13). Among larval anurans examined, however, the muscle attached to the lateral side of the cartilago meckeli only in pipoids. In all other anurans it inserted to the cartilago labialis superior. The autapomorphic condition in *Ascaphus truei*, in which the m. externus has no direct attachment to skeletal structures, was scored as state (2). A transformation series is not evident.

56. Functional larval m. levator mandibulae lateralis absent (0); present (1). The m. levator mandibulae lateralis is located on the anterolateral corner of the pars articularis quadrati in anuran larvae. In some species, this muscle develops only shortly before metamorphosis (de Jongh, 1968; Haas, 2001). The muscle was considered present if striated muscle cells could be detected in serial sections of stage 37/38 larvae (missing data in species for which only much earlier stages could be examined).

57. M. levator mandibulae lateralis inserts in tissue close to posterodorsal process of suprarostral cartilage or adrostral tissue (0); nasal sac insertion (1). The two species of *Pseudis* were unique among the species examined in that their m. levator mandibulae lateralis inserts in soft tissue at the nasal sac. In both species, the muscle is strongly developed; its function is unclear. The insertion suggests that its action may dilate the nasal sac.

58. M. levator mandibulae internus high (0); low (1); anterior (2). In caudate larvae, the m. levator mandibulae internus originates high on the neurocranium dorsal to the processus ascendens and from proximal parts of the processus ascendens (see Haas, 2001: Fig. 8). *Ascaphus truei* is the only anuran which shares this feature with caudates (Pusey, 1943: Figs. 10–14; Haas, 2001: Fig. 4). In most other anurans examined, the

muscle was anchored on the ventral side of the cupula anterior of the otic capsule and the ventral side of the processus ascendens. In species of the Pipoidea and Scoptanura the muscle's origin was in a far more anterior position on the arcus subocularis (Fig. 14).

59. Insertion of the larval m. levator mandibulae internus in relation to jaw articulation medial (0); lateral (1); broadly across articulation (2). The m. levator mandibulae internus commonly has a long tendon in both caudates and anurans. In larval caudates and pipids, it inserts medially on the mandible. In most other frog larvae, the muscle takes an oblique course laterally along the way to its insertion site at the lateral shoulder of the cartilago meckeli (Sedra, 1950; de Jongh, 1968; Sokol, 1981; Haas, 2001). Few taxa deviated from this stereotypic pattern: in the suctorial tadpoles of *Heleophryne natalensis*, *Atelopus tricolor*, and *Litoria* the insertion of the m. lev. mand. internus was fleshy without a long tendon. In these species, the insertion expands along the cartilago meckeli corpus (not visible in Fig. 13). However, the general oblique orientation was the same as that in other anurans (state 1). In *Ascaphus truei*, the m. levator mandibulae internus is incorporated with the m. levator mandibulae longus into one large muscle mass (Pusey, 1943; Haas, 2001) that inserts broadly across the articulation to the cartilago meckeli.

60. M. levator mandibulae longus originates dorsally on skull (0); from posterior palatoquadrate (1); exclusively from arcus subocularis (2). The origin high on the skull (otic capsule and/or dorsal braincase roof) is found only in *Ascaphus truei* and caudates (Pusey, 1943; Haas, 2001). The most common condition in anuran larvae is state "1" in which the muscle takes its origin broadly from the distal processus ascendens, the posterior palatoquadrate curvature, and the arcus subocularis (Fig. 13). A third state exists in the species of the Pipoidea and the scoptanuran microhylids: the origin of the m. levator mandibulae longus is located more anteriorly on the arcus subocularis or even at the level of the processus muscularis and does not reach the posterior palatoquadrate (Fig. 14). Character states can be ordered in a posterior to anterior transformation series.

61. M. levator mandibulae longus in one portion (0); superficialis and profundus portions (1). The presence of two portions of the m. levator mandibulae longus is the most common condition in anuran larvae (Schulze, 1892; de Jongh, 1968; Haas, 1996, 2001; Cannatella, 1999). Caudate larvae in contrast have only one portion that inserts exclusively on the lower jaw, a condition also found in *Ascaphus truei*, *Pipa carvalhoi*, and *Rhinophrynus dorsalis*.

62. Profundus and superficialis portions of m. levator mandibulae longus broadly overlapping at insertion (0); not overlapping parallel (1). In *Xenopus laevis* and the microhylids examined, the muscle's portions were slen-

der parallel bundles and did not overlap at their origin (Haas, 2001: Fig. 6). The character is inapplicable in species which have only one muscle portion.

63. Ramus maxillaris (cranial nerve V$_2$*) lateral to m. levator mandibulae longus (0); medial to the muscle (1).* The branches of the nervus trigeminus emerge from the foramen prooticum between the otic capsule and the cartilago orbitalis. In caudate and anuran larvae, the three branches have spatial relations different from those of the jaw muscles along their way distally (Luther, 1914; Pusey, 1943; Starrett, 1968; Iordansky, 1992, 1996; Haas, 1996, 2001). In all known anurans the maxillary branch of the nervus trigeminus emerges medial to the levator mandibulae longus, as opposed to caudates, in which the nerve is lateral to the muscle.

64. Ramus mandibularis (c.n. V$_3$*) posterior (ventral) to m. levator mandibulae longus (0); between portions of muscle (1); anterior (dorsal) to the muscle (2).* In caudate larvae, the mandibular branch of the nervus trigeminus passes posterior to the m. levator mandibulae longus. In most anuran larvae the nerve lies dorsal (anterior after metamorphosis) to the muscle (Haas, 2001). However, in some of the microhylid larvae examined, the nerve passed ventral (posterior) to the muscle (Fig. 14), similar to the condition in caudates. An intermediate condition was present in *Kaloula pulchra* (Haas, 2001: Fig. 7) and *Dyscophus antongilii;* their ramus mandibularis passed dorsal to the superficial part of the m. levator mandibulae longus but then submerged and continued ventral to the profundus part.

65. Ramus mandibularis (c.n. V$_3$*) posterior (ventral) to m. levator mandibulae externus group (0); runs through the externus group (1); anterior (dorsal) to the externus group (2).* The ramus mandibularis (V$_3$) runs posterior to the externus muscle group in all known caudate species (see Luther, 1914; Iordansky, 1992, 1996; Haas, 2001: Fig. 10). In larvae of *Ascaphus truei, Xenopus laevis,* and *Pipa carvalhoi* the ramus mandibularis was dorsal to the externus muscle, whereas it was ventral to the muscle in the pipoid *Rhinophrynus dorsalis.* It was dorsal in many other species also (Fig. 13). The spatial relations of the ramus mandibularis (V$_3$) varied among those examined anuran larvae that possess two portions of mm. levator mandibulae externus (superficialis and profundus). In many bufonids and hylids, the nerve passage was between the m. levator mandibulae externus superficialis and profundus. In *Agalychnis callidryas Dyscophus antongilii, Gastrotheca riobambae, Hemisus sudanensis, Hylodes meridionalis, Paa exilispinosa, Ptychadena mascareniensis,* the nerve was also in an intermediate position but penetrated the m. levator mandibulae externus profundus. Dorsal, intermediate, and ventral position of the nerve in relation to the externus group form an ordered transformation series.

66. Processus anterolateralis of crista parotica absent (0); present (1); forms larval processus oticus (2). The character states have been described before (Sokol, 1981). The crista parotica is a ridge at the lateral side of the otic capsule dorsal to the fenestra ovalis. Anteriorly the crista can bear a projection, the processus anterolateralis (Fig. 15). Long processes occur in some taxa (particularly ranoids), sometimes touching the posterior palatoquadrate curvature (see Haas, 1999a: Fig. 2 for *Pyxicephalus*). In yet other taxa the processus fuses completely and seamlessly with the posterior palatoquadrate curvature to form a chondrified larval processus oticus (Fig. 16). The assignment of character states may be difficult in some species with very small processes (state 0 versus state 1) and in some species with a process that touches rather than fuses with the palatoquadrate (state 1 versus state 2).

67. Posterolateral projections of the crista parotica absent (0); process present (1); expansive flat chondrifications (2); processus otobranchialis (3). The posterolateral part of the crista parotica may bear a pointed or rounded processus posterolateralis (for example, Larson and de Sá, 1998). In some of the pipoids, microhylids, and species of *Pseudis,* the crista parotica was expanded into a flat horizontal plate of cartilage (Fig. 17). A remarkable structure was present in *Hemisus sudanensis* and the hyperoliids examined: an elongate, styliform processus originates from the posterior crista parotica and descends ventrad. This processus was associated with the larval "diaphragm" (abdominal wall). The process curved forward (Fig. 17) and ended in a position posterior to the ceratobranchial IV. The m. rectus cervicis and m. diaphragmatobranchialis were attached to its distal part. This processus in *Hemisus sudanensis* and hyperoliids is unique among anurans and has not been described before. I propose to call it processus otobranchialis.

68. Posterior palatoquadrate curvature flat or slightly concave (0); clearly concave with bulging and pronounced margin (1). At the posterior curvature the arcus subocularis quadrati and the processus ascendens quadrati meet. In state (1), the processus ascendens is laterally confluent with the upward bulging posterior margin of the palatoquadrate curvature. The posterior margin forms an edge in dorsal view (Fig. 18b) (no edge in state 0). The junction of the processus ascendens and the posterior palatoquadrate curvature is at a level well dorsal to the medial margin of the arcus subocularis (same level in 0). State 0 is depicted in Fig. 18 and in Sokol (1981, Fig. 15). Among the species examined, state (1) is most clearly formed in the dendrobatids and hylodine leptodactylids (deeply concave) and is less pronounced in bufonids and some leptodactylids.

69. Palatoquadrate connection to trabecula cranii caudal (0); rostral (1). The processus pterygoideus of caudate larvae and the commissura quadratocranialis
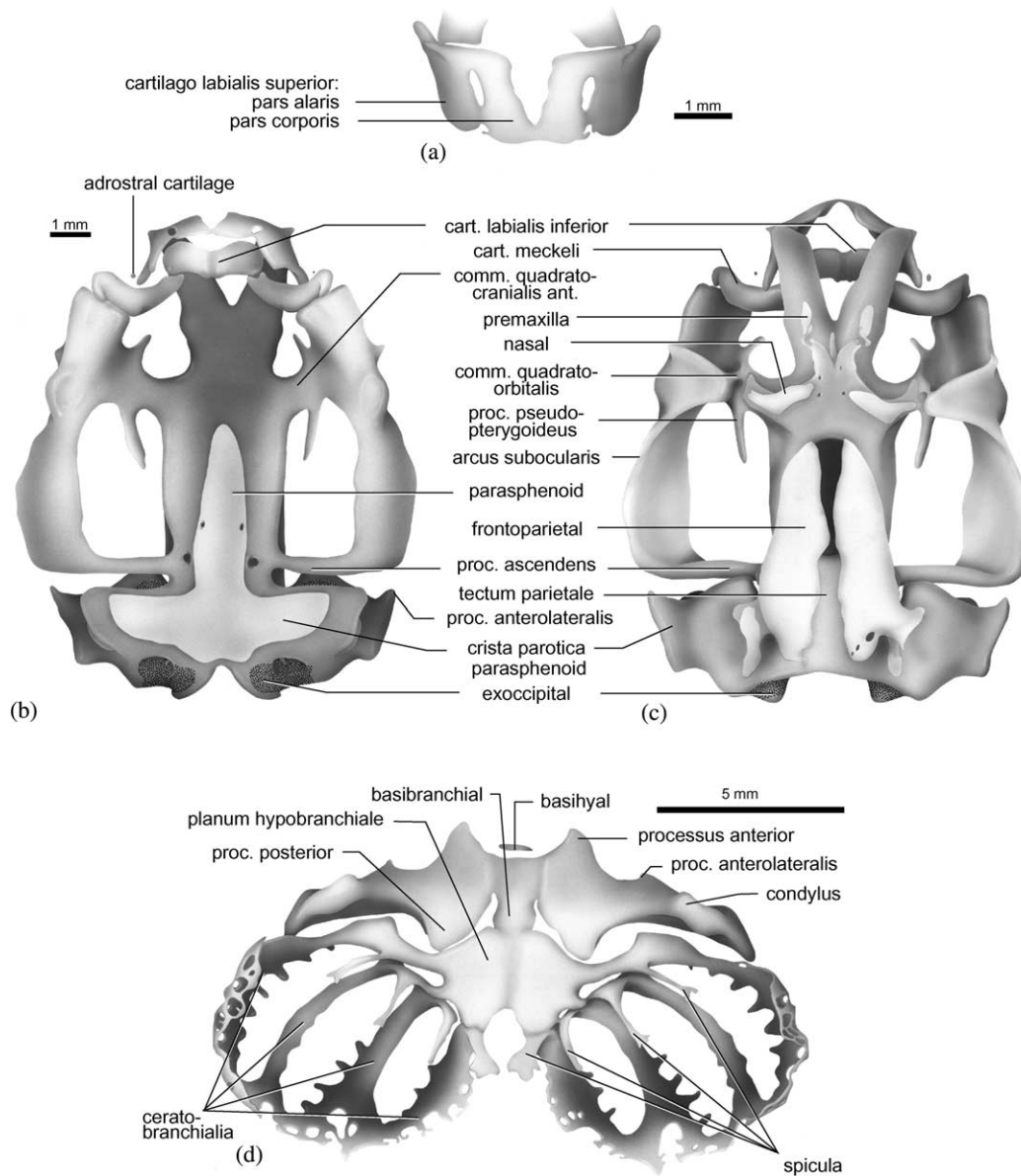
Fig. 15. Cranial skeleton of *Odontophrynus achalensis*, drawn from a cleared and stained specimen (specimen Odont ach 7, stage 40). (a) Cartilago labialis superior in frontal view; (b) neurocranium and first visceral arch in ventral view and (c) in dorsal views; (d) hyobranchial skeleton in dorsal view.

anterior of anurans are homologous structures (Reiss, 1997). They form the anteromedial connections of the palatoquadrate to the trabecula cranii. In all anuran larvae, except for *Ascaphus truei*, the connection is far rostrally, connecting to the planum trabeculare anticum (Gaupp, 1893), and is transversely oriented (state 1, for example, see Figs. 17 and 19). It is more posterior and inserts at an angle to the neurocranium in caudates. *A. truei* is the only anuran that shares state (0) with caudates (Pusey, 1943; Van Eeden, 1951; Reiss, 1997).

70. Position of jaw articulation suborbital (0); preorbital (1). In caudate larvae and *Ascaphus truei*, the longitudinal axis of the palatoquadrate is at a steep angle in lateral view. The corpus is short and stout and, thus, the jaw articulation is located ventral to the eye. In all other anuran larvae, the palatoquadrate is considerably longer, oriented in a shallow angle (lateral view), and the jaw articulation is located well anterior to the eye (Wassersug and Hoff, 1982).

71. Suspensorium high (0); intermediate (1); low (2); ultralow (3). Pusey (1943) recognized different suspensorial levels in anurans. Sokol (1981) discussed the possible phylogenetic significance of the levels of attachment of the processus ascendens, concluding "the more derived the taxon is, the lower is its ascending process" (Sokol, 1981, p. 176). He defined "high," "intermediate," and "low" levels of attachment of the processus ascendens with reference to the position of the
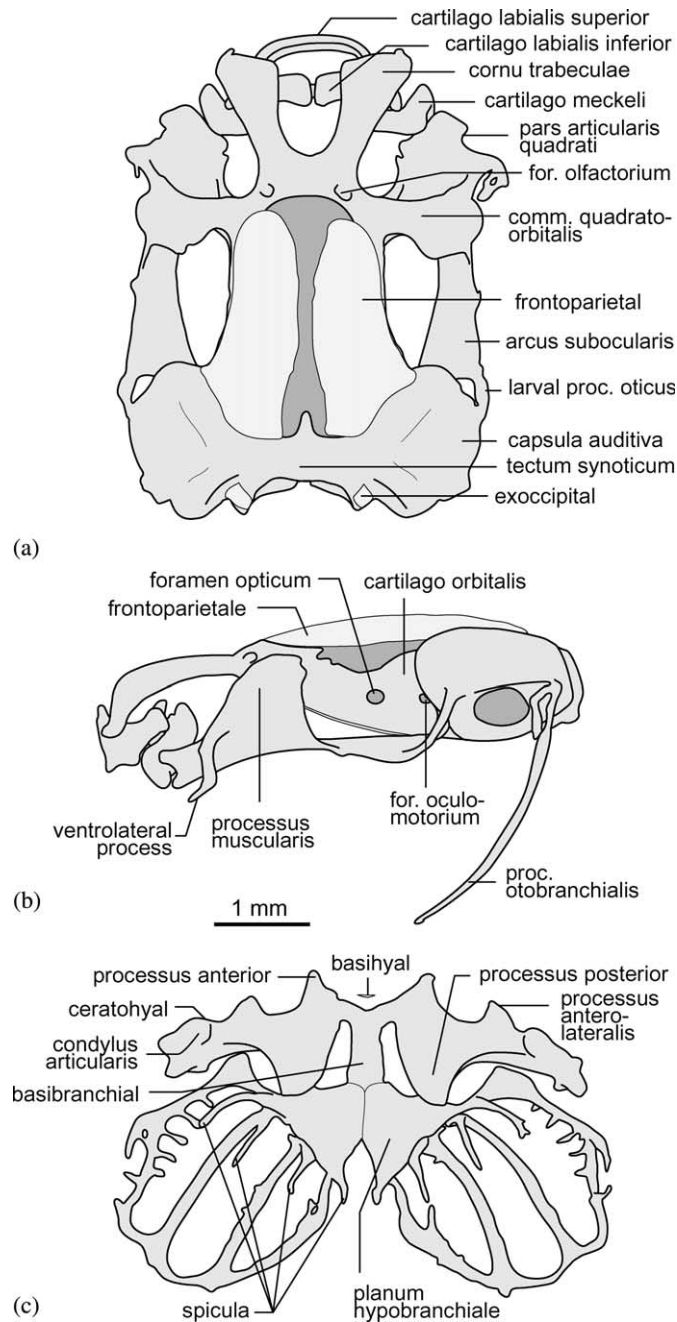
Fig. 16. Cranial skeleton of *Hyperolius puncticulatus*, drawn from a cleared and stained specimen (specimen Hyper 2, stage 36). (a) Neurocranium and mandibular arch in dorsal view; (b) Neurocranium and mandibular arch in lateral view; (c) hyobranchial skeleton in dorsal view. The processus otobranchialis with its characteristic muscle connections was unique for the hyperoliids examined (including *Hemisus*).

foramen oculomotorium (as applied in Larson and de Sá, 1998; Maglia et al., 2001). The foramen is located immediately dorsal to the trabecula cranii. The foramen is immediately anterior to the pila antotica and the suspensorial attachment and Sokol's states translate to attachment "above, at, and below" the level of the foramen.

Sokol (1975, Fig. 13) recognized two different conditions of the "low" state. One of them is herein defined

as "ultralow." In the "low" and "ultralow" states, the processus ascendens is confluent with the trabecula cranii rather than with the pila antotica. However, in the low state the trabecula is an elongated oval and is high-rising in cross section, therefore the suspensorial insertion at the neurocranium is above the level of the braincase floor in cross sections (see Sokol, 1981: fig. 17). In the "ultralow" conditions, the trabecula is not elongated and high-rising in cross section and the sus-
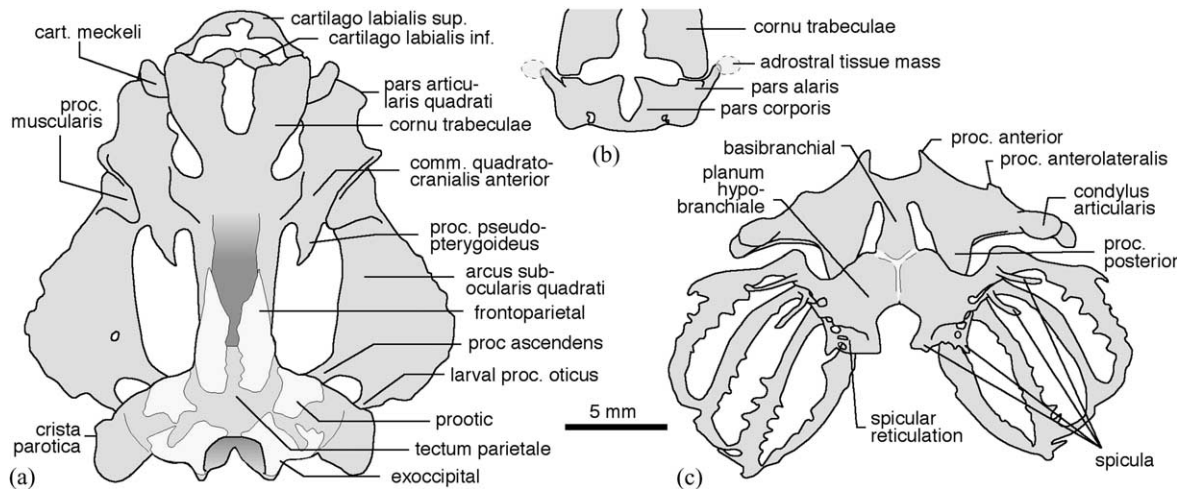
Fig. 17. Cranial skeleton of *Pseudis paradoxa*, drawn from a cleared and stained specimen (specimen Paradox 1, stage 40). (a) Neurocranium and madibular arch in dorsal view; (b) cartilago labialis superior in frontal view; (c) hyobranchial skeleton in dorsal view.
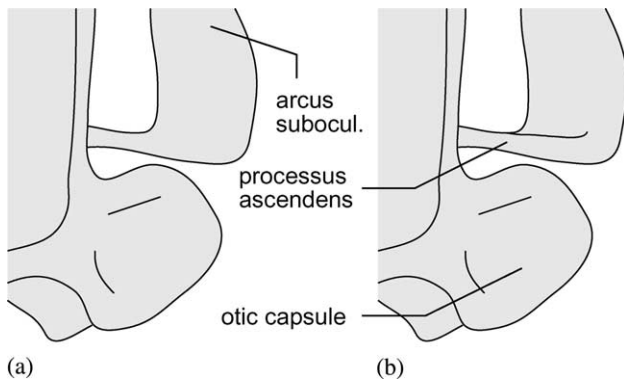
Fig. 18. Schematic drawing of posterior palatoquadrate curvature; dorsal views. (a) Flat; (b) concave with bulging posterior margin. Character state (68.1) in b is most clearly formed (deeply concave) in the dendrobatids and hylodine leptodactylids examined; it is less pronounced in bufonids and some leptodactylids.

pensorium is at the level of the braincase floor. Character states determined herein are mostly in accord with Sokol's accounts (except for *Pelodytes*). The four recognized states were ordered as a transformation series.

The character appears to be continuous. However, the three-dimensional relations of possible landmarks for measurement and the difficulties in acquiring precise coordinates made it impractical to define character states morphometrically here.

72. Processus ascendens stout (0); thin (1). In *Heleophryne natalensis* (Fig. 19), the species of the Hyperoliidae examined, *Hemisus sudanensis*, and *Rhacophorus pardalis* the processus ascendens was remarkably thin. The thinnest part of it was less than half the thickness of the trabecula cranii in cross sections and the processus ascendens is even discontinuous in the *Leptopelis vermiculatus* specimen examined. Ramaswami (1944) and Van der Westhuizen (1961) reported the absence or

vestigial nature, respectively, of the processus ascendens in *Heleophryne purcelli*. The *H. natalensis* examined herein differed from these earlier accounts on *H. purcelli* in having a thin processus ascendens. A thin processus ascendens has also been reported in a species of the rhacophorid *Boophis* (Haas and Richards, 1998: Fig. 10).

73. Confluence between posterior palatoquadrate and ventral otic capsule absent (0); processus basalis present (1); palatobasal connection present (2). *Ascaphus truei* and caudate larvae share the presence of a processus basalis (Reiss, 1997). The processus extends from the posterior part and ventral side of the palatoquadrate toward an anteroventral ledge of the parachordal or otic capsule. The ramus hyomandibularis (c.n. VII) crosses the processus basalis dorsally and descends posterior to it (Pusey, 1943). Van der Westhuizen (1961) described a basal connection with these relationships to the nerve in *Heleophryne purcelli*. However, the specimen of *Heleophryne natalensis* examined herein lacked the basal connection (Fig. 20). Among species of the Pipoidea, the processus basalis was present in *Rhinophrynus dorsalis*. In some species, particularly rhacophorids and hyperoliids, the posterior palatoquadrate was very close to or in touch with the otic capsule. A similar close association is strengthened by a cartilaginous palatobasal connection (fusion) in the pelodryadine hylids *Nyctimystes dayi* and *Litoria nannotis* (Haas and Richards, 1998). This cartilaginous confluence (state 2) is posterior to and not crossed dorsally by the ramus hyomandibularis and, thus, considered a secondary fusion.

74. Commissura praefacialis absent (0); present (1). The roots of the cranial nerves V and VII leave the cavum cranii either through separate foramina or through the foramen prooticum. In the first case, the nerves are separated by the commissura praefacialis (Pusey, 1943;
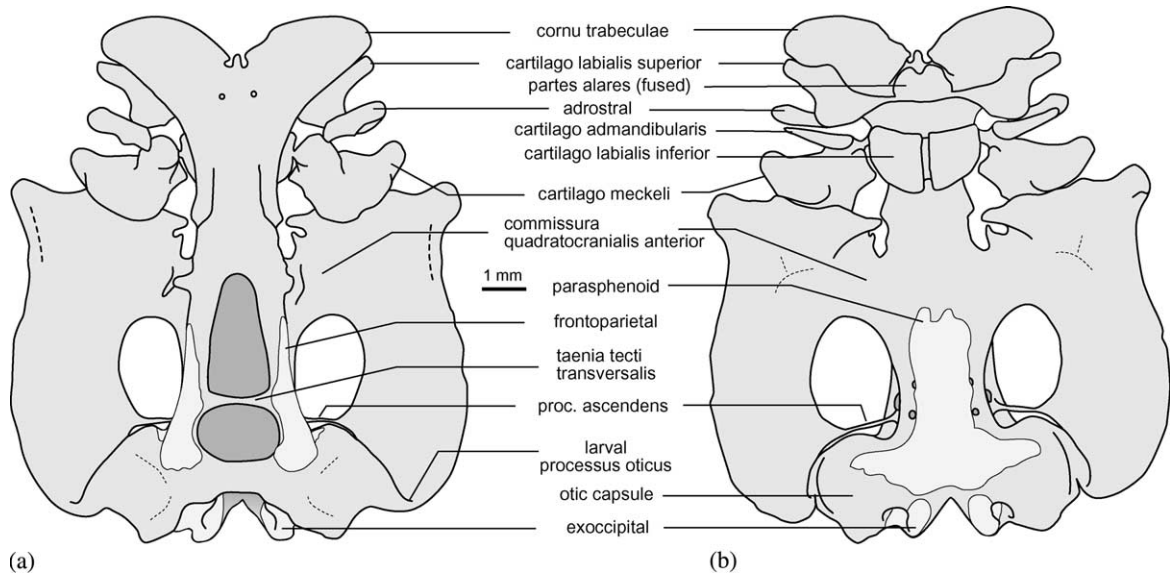
Fig. 19. Neurocranium and mandibular arch in *Heleophryne natalensis* (specimen Heleo 1, stage 28) in (a) dorsal and (b) ventral views. Adrostral and admandibular cartilages are particularly well formed in this species.
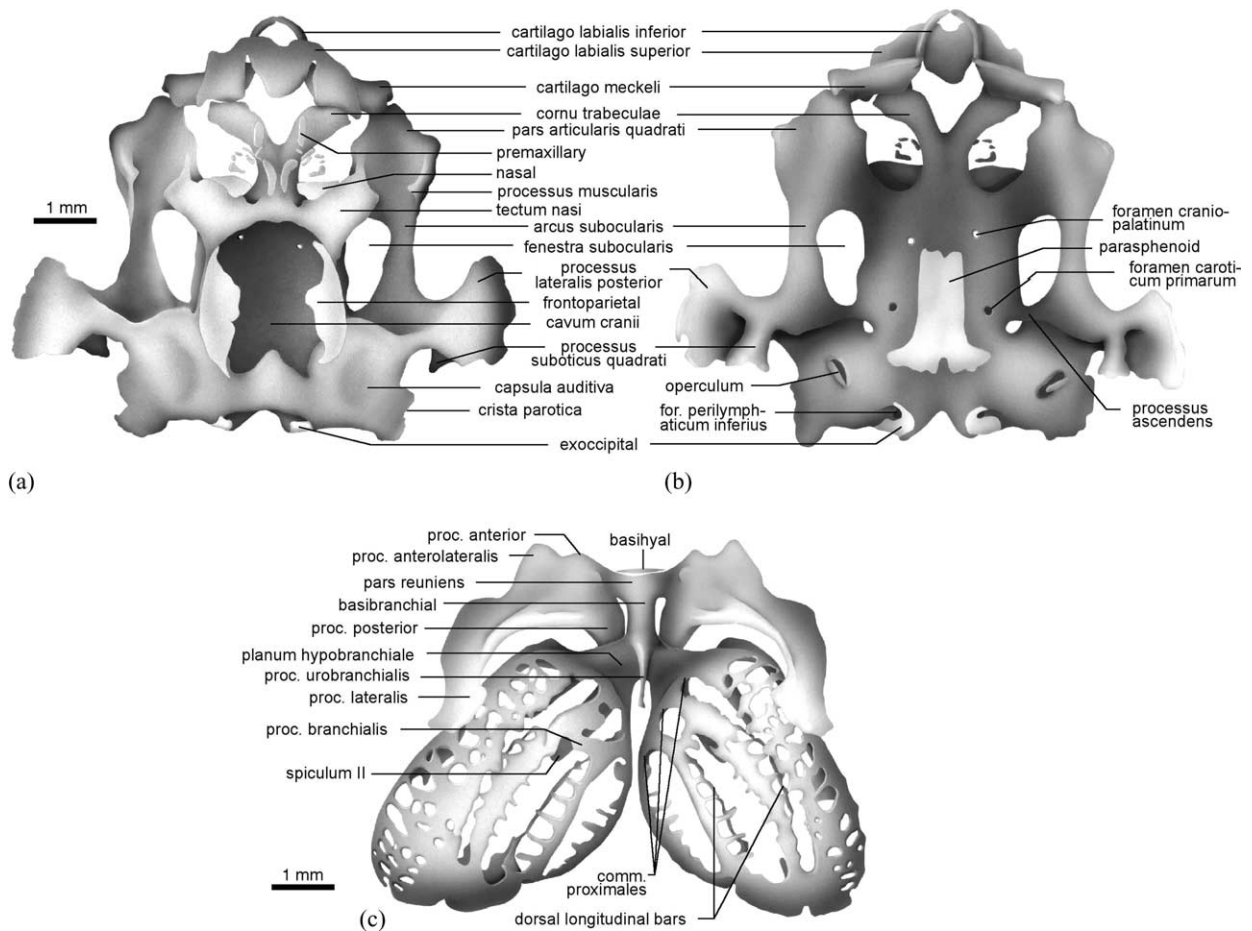

Fig. 20. Cranial skeleton in *Kaloula pulchra* (specimen Kalou 3, stage 39). Neurocranium and mandibular arch in (a) dorsal and (b) ventral views. (c) Hyobranchial skeleton in ventral view. The specimen illustrates a number of microhylid and scoptanuran apomorphic character states (see Fig. 2).

Van Eeden, 1951; Sokol, 1975). Previously the presence or absence of the commissura praefacialis has been dealt with in conjunction with the separation or fusion of the ganglia of the two nerves (Sokol, 1975). Sometimes the fusion of the ganglia has been emphasized as a meaningful character state (Duellman and Trueb, 1986). Sokol, 1975, p. 14 wrote that the ganglia were separate and the commissura was present in Orton Type III tadpoles (*Ascaphus truei* and discoglossids) and that the ganglia were fused to one prootic ganglion (commissura absent) in all other anuran larvae. The first claim is not generally true for all species: the *Bombina maxima* specimens examined herein lacked the commissura. The second claim is an oversimplification; Fabrezi and Chalabe (1997) pointed out that the ganglia are not necessarily fused in larvae of all neobatrachians. In serial sections of the larvae examined I found a continuum: larvae of some species that lacked a commissura had separate ganglia (for instance, *Pelodytes caucasicus Ceratophrys ornata*), in others the ganglia were close to each other in the foramen prooticum but a thin line of separation delimited them in histological sections, and yet many others the fusion of ganglia was quite complete and it was impossible to delimit the facialis part from the trigeminus part. In sum, reproducible coding of the range of observed states is hardly possible. Therefore, the character "fusion of ganglia" (Sokol, 1977b; Duellman and Trueb, 1986) was excluded from the analysis and only the presence of the commissura was scored, which has only two clear states.

75. Commissurae craniobranchiales absent (0); present (1). Sokol (1977a) described continuous cartilaginous connections between the branchial skeleton and the crista parotica in species of *Pipa* and *Xenopus*. They were absent in the pipoid *Rhinophrynus dorsalis*, as in all other taxa examined.

76. Processus suboticus quadrati absent (0); present (1). There was a distinct processus originating from the ventral face of the processus oticus region (Fig. 20b) in the scoptanuran larvae examined. It projected posteroventrally and its distal end was immediately dorsal or medial to the thymus gland. No muscles attached to it. de Sá and Trueb (1991) illustrated this processus before in their work on *Hamptophryne boliviana*, but refrained from naming it. Lavilla (1992) informally called it "fungiform process." Here it is proposed to name it anatomically the processus suboticus quadrati.

77. Processus pseudopterygoideus absent (0); short (l ⩽ d) (1); long (l > d) (2). The processus pseudopterygoideus projects from the commissura quadratocranialis anterior into the fenestra subocularis (Figs. 15 and 17). Character states were delimited by measured ratios of the processes length (l) and the diameter at its base (d).

78. Dorsal connection from processus muscularis to neurocranium ligament only (0); ligament and pointed

processus antorbitalis (1); commissura quadrato-orbitalis (2); "high" commissura quadrato-orbitalis (3). In anuran larvae, the tip of the processus muscularis quadrati (if present) is fastened to the neurocranium either by ligaments (ligamentum tectum) or by a cartilaginous bar that partly or fully replaces the ligaments. From the site at which the ligaments attach at the commissura quadratocranialis anterior, a pointed larval processus antorbitalis, round in cross section, projected in some species toward the processus muscularis (for example, dendrobatids; Haas, 1995; Fig. 21b). At the same position a complete cartilaginous bridge (commissura quadrato-orbitalis, Reinbach, 1939; Fig. 21c and d) connected the processus muscularis tip to the neurocranium in, for example *Pelodytes caucasicus*, most bufonids, some leptodactylids, *Gastrotheca riobambae*, *Ptychadena mascareniensis*, and some microhylids. A further character state was distinguished, the "high" commissura (Fig. 21d). In the high connection, the comm. quadrato-orbitalis fuses to parts of the sidewall of the braincase rather than to the commissura quadratocranialis anterior. This high attachment was unique for hyperoliids (including *Hemisus*).

79. Processus muscularis absent (0); present (1). The processus muscularis is defined as a prominence of the lateral margin of the palatoquadrate in anuran larvae. Depending on the functional design of the buccal pump (Wassersug and Hoff, 1979) it can have a wide range of sizes and heights. Herein two states were delimited. The threshold criterion was the tangent slope of the palatoquadrate contour measured in cross sections at the
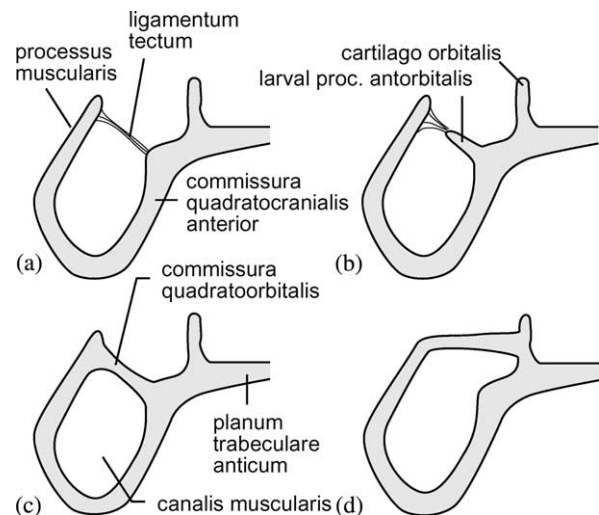

Fig. 21. Patterns of connections between the apical tip of processus muscularis quadrati and the neurocranium; drawn schematically in cross section. (a) Ligamentous connection; (b) ligamentous connection with conspicuous larval processus antorbitalis (among others, dendrobatids); (c) low commissura quadrato-orbitalis (for instance, *Pelodytes*, most bufonids, leptodactylids, and some microhylids); (d) high commissura quadrato-orbitalis (exclusively in hyperoliids, including *Hemisus*).

level of the prominence. State (0) applied to all cases in which the maximum tangent slope in cross sections did not reach 90° to the horizontal (caudates, *Ascaphus truei*, pipoids, *Heleophryne natalensis*, *Elachistocleis bicolor*, *Gastrophryne carolinensis*, *Hamptophryne boliviana*). In state (1) the maximum slope of the tangent along the medial contour line of the processus muscularis was at least vertical or even overhanging medially (Fig. 21a).

80. Anterolateral base of processus muscularis without conspicuous projection (0); bearing ventrolateral process (1). In many taxa the anterior base of the processus muscularis projected somewhat laterally in dorsal view. But in some species an elongate (round in cross section) processus projected ventrolaterally (Fig. 16b): species of the Hyperoliidae (including *Hemisus*), the American species of the Microhylidae examined, and suctorial larvae belonging to the Pelodryadinae.

81. Arcus subocularis with smooth and sharply delimited lateral margin (0); irregular margin (1); three distinct processes (2); processus lateralis posterior (3). Most larval anurans possess a smooth lateral margin of the arcus subocularis quadrati (Fig. 16). In others the arcus is flattened with an irregular margin (Fig. 17). Phyllomedusine hylids are unique in possessing distinct lateral processes (Fig. 22; Fabrezi and Lavilla, 1992; Haas, 1996). Pipids and most microhylids possess a distinct processus lateralis posterior projecting laterally from the posterior palatoquadrate (Fig. 20). Its distal end curves ventrally. It likely gives support to the roof of the expansive pharyngeal cavities in these suspension-feeders. No ordering appears warranted in this multistate character.

82. Shape of arcus subocularis in cross section with horizontal or rising lateral margin (0); margin sloping ventrad laterally (1); round in cross section (2). The character is applicable only in species with a well-formed arcus subocularis (excluding caudates and *Ascaphus truei*). States (0) and (1) describe whether the medial margin of the arcus subocularis is below or above the lateral margin, respectively, in cross sections. State (2) applied to species which had a very narrow and rounded arcus in cross section that did not allow assessment of slope.

83. Cornua trabeculae proportions. Relative cornu trabeculae dimensions were assessed morphometrically. The cornu trabeculae proportions are defined as the ratio of the width (A) of the cornua at their base (Fig. 23) divided by their length (B). Landmarks for measurements were the distal tips of the cornua and the line marking the narrowest section of the trabeculae. Gap-weighting was applied to the ratios to delimit additive ordered character states.

84. Cartilago labialis superior (suprarostral cartilage) absent (0); present (1). The anterior upper jaw of anuran larvae is supported by the cartilago labialis superior (= suprarostral cartilage). It has a characteristic structure (ala and corpus part) and articulation with the cornu trabeculae. In pipoids the snout is supported by a broad horizontal ethmoidal plate. However, it has been argued (Sokol, 1975) and shown convincingly (de Sá and Swart, 1999) that the plate in pipoids is homologous to and possibly derived from the cartilago labialis superior and cornu trabeculae of other anuran larvae. Therefore, suprarostral cartilages were scored present for pipids. Larval caudates lack a cartilago labialis superior but develop upper jaw bones early during larval life (Bonebrake and Brandon, 1971; Reilly, 1986).

85. Articulation of cartilago labialis superior with cornu trabeculae by pars corporis (0); by pars alaris (1);
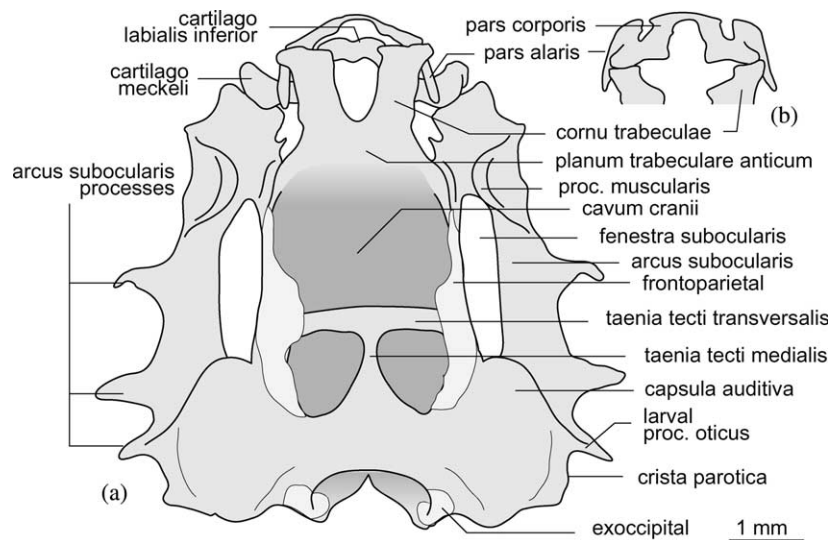

Fig. 22. Neurocranium and mandibular arch in *Phyllomedusa distincta* (specimen Medusa 2, stage 38); (a) dorsal view; (b) cartilago labialis superior extended, dorsal view. Note the three lateral processes of the palatoquadrate (synapomorphic for phyllomedusines).
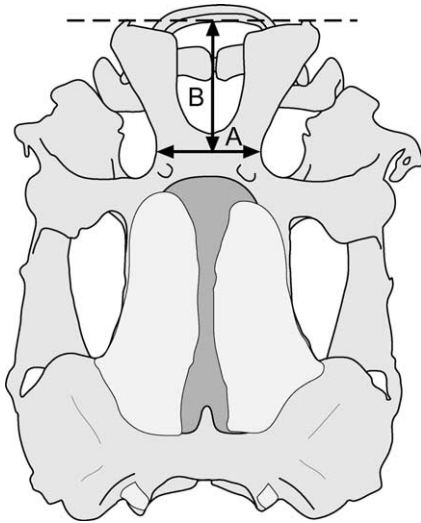
Fig. 23. Measurements taken for assessing trabecular horn proportions. Neurocranium and mandibular arch of *Hyperolius puncticulatus* (specimen Hyper 2, stage 36).

Fig. 24. Some examples of cartilagines labiales superiores and their connection to the cornu trabeculae. Schematic generalization, lateral views. (a) Double posterior processes at pars alaris and articulation via pars corporis in Discoglossidae; (b) single, conical process and both partes contributing to articulation in many neobatrachians; (c) expanded posterior process and fused partes in rhacophorids, *Hemisus*, and *Hyperolius*.

fused into rostral plate (2). The cartilago labialis superior (larval upper jaw cartilage) shows astonishing shape modifications in anuran larvae (Sokol, 1975, 1981; Ruibal and Thomas, 1988; Lavilla and Fabrezi, 1992; Haas, 1996; Larson and de Sá, 1998; Haas and Richards, 1998; Cannatella, 1999). It is difficult to devise a coding system that both captures all significant features and is applicable to all taxa. Thus, different coding schemes were proposed elsewhere (Haas, 1996; Larson and de Sá, 1998; Maglia et al., 2001). Beyond qualitative characters, particular shape similarities exist between certain species (proportions, shape). However, quantitative shape measures were not developed for this study.

Sokol (1981) showed that the cartilago labialis superior is composed of a medial corpus (pars corporis) and a lateral wing (pars alaris) (Figs. 15 and 17). The cartilago labialis superior can articulate with the cornu trabeculae either by the pars corporis (mainly or exclusively; *Ascaphus truei*, discoglossids (Fig. 24a), *Pelodytes caucasicus*; Haas, 2001: Fig. 2) or by the pars alaris (all other species except for pipoids). In pipoids the cartilages are fused to the cornua trabeculae and form a horizontal rostral plate (Sokol, 1977a; de Sá and Swart, 1999). This condition was coded as a third character state, rather than assuming attachment to the corpus (Maglia et al., 2001).

86. Pars alaris and pars corporis fused, forming smooth margin distally (0); separated by deep distal notch (1). In larvae of many anurans, the distal margin of the cartilago labialis superior is a continuous, smoothly curving line that supports the keratinized sheath of the jaw (Fig. 24c). In some leptodactylids (Larson and de Sá, 1998), but especially in hylids and bufonids (Haas, 1996) and in dendrobatids (Haas, 1995), a different
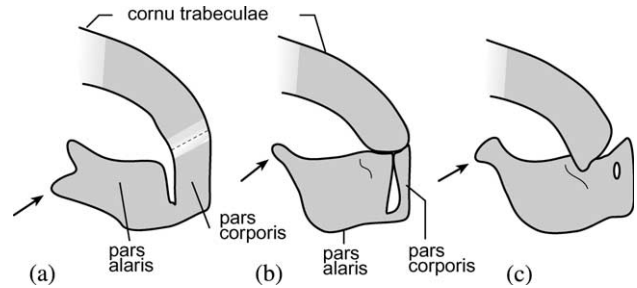
condition predominates; i.e., the pars alaris and pars corporis are close to each other or fused proximally at the articulation with the cornu trabeculae, but separated by a notch distally. Consequently a discontinuity of the distal margin exists (see citations above for illustrations), often with the two partes corpores converging to the median plane.

Most species are easily scored, but the condition can become less clear in species in which the proximal fusion of the pars corporis and the pars alaris is more extensive and, thus, the distal notch less pronounced (see Haas, 1996: Fig. 27). For scoring state (1), a notch as deep as 50% of the proximodistal length of the cartilago labialis superior was set as the criterion. Another confounding problem in defining states is the occasional occurrence of small distal cartilage bridges between the partes in various leptodactylids (Sokol, 1981; Larson and de Sá, 1998; Fig. 15a), which may be absent in early larvae but present in later stages (pers. observ.). This bridging cartilage is thinner than the cartilages which it connects. Only in cases of continuous thickness of the cartilages along the distal margin was state (0) applied.

87. Partes corpores medially separate (0); distal confluence present (1); forming medial body (2). The two partes corpores may be confluent with each other across the median plane (Fig. 22). In *Heleophryne natalensis* and most microhylids, a medial body of cartilage (roughly triangular in microhylids) was present between the partes alares and is homologized here as fused partes corpores (Figs. 19 and 20). The medial body is detached proximally from the partes alares.

88. Posterior processes of pars alaris: double (0); single (1). Larvae of discoglossid species examined were unique in having two processes at the posterior margin of the pars alaris (Fig. 24a).

89. Posterior dorsal process of pars alaris tapering conically or ending bluntly not expanded terminally (0); expanded terminally almost rectangular in lateral view (1). State (0) (Fig. 24b) is commonly found in anuran

larvae, whereas state (1) (Fig. 24c) applied to species examined of *Atelopus*, *Rhacophorus*, *Chiromantis*, *Hemisus*, and *Hyperolius*.

90. Adrostral cartilage absent (0); present but small (1); very large and elongate (2). The adrostral tissue mass lies lateral to the processus posterior dorsalis of the pars alaris. It is well developed in leptodactylid, hylid, bufonid, and dendrobatid species (Sokol, 1981; Haas, 1995, 1996). In the center of the tissue mass a body of cartilage may be present, the adrostral cartilage, usually smaller in cross section than the neighboring processus posterior dorsalis. In various species only tiny such cartilages that may be subject to intraspecific variation have been observed (Fig. 15; Haas, 1995). In *Heleophryne natalensis* (Fig. 19) and the pelobatids *Pelobates fuscus*, *Megophrys montana*, and *Leptobrachium hasseltii*, the adrostral cartilages were large transversely oriented rods. Similarly large, but parasagittally oriented, adrostral cartilages were present in the pelodryadine suctorial larvae of *Litoria rheocola*, *L. nannotis*, and *Nyctimystes dayi* (Haas and Richards, 1998). Absent, small, and large conditions may be considered an ordered transformational series.

91. Partes alares and corpores of cartilago labialis superior in line (0); concentric lines (1). Usually pars alaris and pars corporis are arranged in an arched line that bears the jaw sheath. A unique conformation occurs in the suctorial larvae of *Litoria rheocola*, *L. nannotis*, and *Nyctimystes dayi* (Haas and Richards, 1998). Their pars alaris is positioned on a line lateral and concentric to the pars corporis.

92. Lower jaw cartilage uniform (0); differentiated into distal cartilago labialis inferior and proximal cartilago meckeli (1). In larval caudates and some pipoid anurans the lower jaw cartilage (cartilago meckeli) is a uniform arched rod. The two cartilagines meckeli are joined rostrally by a flexible symphysis. In most anurans examined, the larval lower jaw cartilage was differentiated into the anterior cartilago labialis inferior (= infrarostral) and the posterior cartilago meckeli. These two jaw segments were always connected via the commissura intramandibularis (Fig. 25). However, the commissura was often discernible only in histological sections. In pipoids, there is a cartilago labialis inferior in the lower jaw of *Xenopus laevis* (Weisz, 1945a,b; Trueb and Hanken, 1992), but the jaw cartilage was uniform in the other pipoids examined. A symphysis was absent in the cartilago labialis inferior in *X. laevis*, but the commissura intramandibularis was present.

93. Orientation of lower jaw U-shaped (0); transverse (1). In larval caudates and species of the Pipoidea the lower jaw is a U-shaped arch that resembles the post-metamorphic condition very closely (Sedra and Michael, 1957; Trueb and Hanken, 1992). The second conformation is the much shortened and roughly transversely
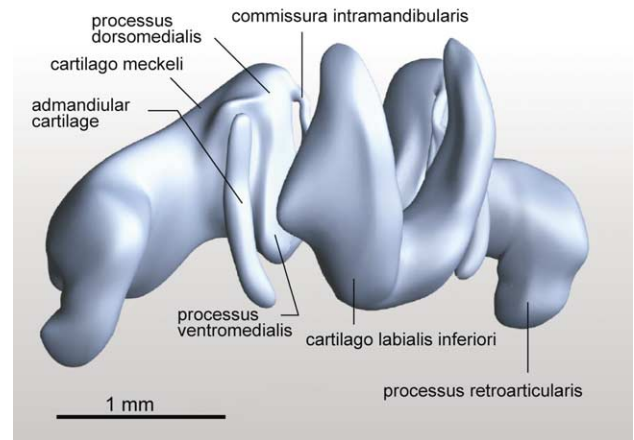

Fig. 25. Lower jaw of *Alytes obstetricans* (specimen Alytes 2, stage 35), perspective anterolateral view. Three-dimensional reconstruction derived from serial sections.

oriented lower jaw of other anuran larvae. The latter conformation necessitates extensive metamorphic remodeling to reach the adult shape (Gaupp, 1893; Sedra, 1950; de Jongh, 1968; Wiens, 1989; Haas, 1996).

94. Distal end of cartilago meckeli cylindrical (0); with stout dorsal and ventral processes forming a shallow articular fossa (1); expanded and flattened no fossa (2); broad and flat processus dorsomedialis absent no fossa (3). In the majority of anuran larvae, the cartilago meckeli has the following typical features (state 1; Fig. 25): (a) lateral processus retroarticularis, (b) stout middle part articulating with the palatoquadrate, (c) pronounced processus dorsomedialis, and (d) processus ventromedialis that forms a concave articular surface to fit the posterior face of the cartilago labialis inferior. Except for the processus retroarticularis, the cartilago meckeli in pipoid and caudate larvae was devoid of such structures (state 0). The species of the Microhylidae possessed a unique shape of the medial part of their larval cartilago meckeli (state 3): it does not form a concave articulation surface anteriorly, but is flat and almost blade-like medially (Fig. 20).

The lower jaw of larval *Lepidobatrachus* appears quite different from that of other neobatrachians (Ruibal and Thomas, 1988; Lavilla and Fabrezi, 1992). However, although the cartilago meckeli and cartilago labialis inferior of *L. laevis* were more slender and elongate than those in other species, characteristics of state (1) were present. The cartilago meckeli and cartilago labialis inferior of *Ascaphus truei* are unique (state 3) (Pusey, 1943; Van Eeden, 1951; Reiss, 1997), i.e., the cartilago meckeli is exceptionally broad and flat and a distinct processus dorsomedialis is absent. The ventromedial corner of the cartilago meckeli forms a long processus. The cartilago labialis inferior is particularly slender in *A. truei* and does not articulate in an articular fossa at the cartilago meckeli.

95. Admandibular cartilage absent (0); present (1).
The admandibular or submandibular cartilage is an elongate body anteroventral to the cartilago meckeli. It is present in species of *Alytes* (Fig. 25), *Discoglossus*, and *Heleophryne* (Fig. 19; Van Seters, 1922; Van der Westhuizen, 1961; Púgener and Maglia, 1997; pers. observ.). Maglia et al. (2001) defined the admandibular as "undifferentiated connective tissue lateral to the infrarostral cartilages," whereas in the present study it is more strictly defined as a body of cartilage (presence of cartilage cells verified in histological sections). The different definitions affect the scoring: the admandibular was here scored absent in *Bombina* (no cartilage) but was reported present by Maglia et al. (2001).

96. Cartilaginous roofing of the cavum cranii absent (0); taenia transversalis present only (1); taeniae transversalis et medialis (fenestrae parietales) present (2); formation of tectum parietale (3); tectum of cavum cranii almost completely chondrified (4); taeniae tecti medialis only (5). Anterior to the tectum synoticum, additional cartilaginous structures can contribute to the roof of the cavum cranii (Fig. 26). These cartilages form and change during larval life (de Jongh, 1968; Haas, 1996). Only late larval stages (preferably stages 38–40) allow determination of states with confidence. The presence of exclusively the taenia tecti transversalis (Fig. 26a) is typical for discoglossids and species of *Heleophryne* (Van Seters, 1922; Magnin, 1959; Van der Westhuizen, 1961; Maglia and Púgener, 1998; Púgener
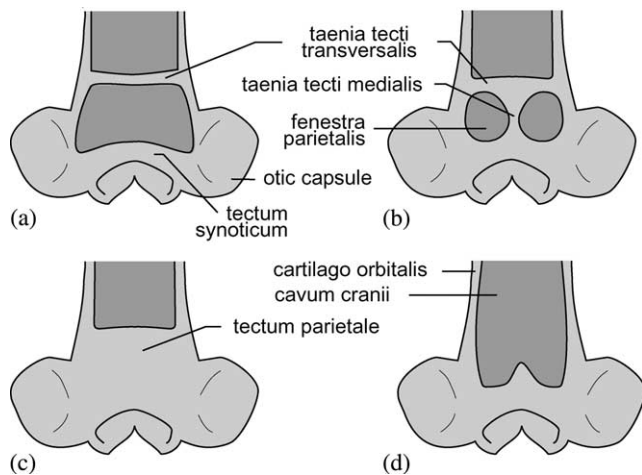

Fig. 26. Tectal roofing of cavum cranii. Schematic generalization of four character states; not drawn from specific specimens. (a) Dorsal roof components comprise tectum synoticum and taenia tecti transversalis only (Discoglossidae, *Heleophryne*); (b) taeniae tecti transversalis and medialis fuse and form fenestrae parietales (bufonids and some leptodactylids, hylids, and ranids); (c) continuous tectum parietale in front of and confluent with tectum synoticum (most hylids, *Pseudis*, *Leptodactylus*, *Odontophrynus*, and *Limnodynastes peronii*); (d) taenia tecti medialis as processus projecting from tectum synoticum (rhacophorids, hyperoliids, *Hemisus*, and the microhylids examined).

and Maglia, 1997; pers. observ.). The taenia tecti medialis forms a bridge between the tectum synoticum posteriorly and the taenia tecti transversalis anteriorly. Thus, two fenestrae parietales may be located between the anterior parts of otic capsules (bufonids and some leptodactylids, hylids, and ranids; Fig. 26b).

In most hylids, the two species of *Pseudis* examined, *Leptodactylus latinasus*, *Odontophrynus achalensis*, and *Limnodynastes peronii*, the parietal region was roofed by a continuous layer of cartilage, i.e., fenestrae parietales were absent and a closed tectum parietale (Haas, 1996; Fig. 26c) was present. The tectum parietale is ontogenetically derived from the fenestrated condition (i.e., state 3 follows state 2; Haas, 1996), except for *L. peronii* in which the tectum parietale originates as a front of cartilage that grows rostrad from the tectum synoticum and mediad from the otic capsules (pers. observ.).

In *Lepidobatrachus laevis* and *Ceratophrys ornata* the cavum cranii was completely or almost completely roofed by cartilage (state 4; Wild, 1997; also in *Caudiverbera caudiverbera*; Reinbach, 1939). The taenia tecti transversalis was absent in rhacophorids, hyperoliids, *Hemisus sudanensis*, and the microhylids examined, but there was a short taenia tecti medialis projecting anteriorly from the tectum synoticum (Fig. 26d).

Although state (3) follows state (2) in ontogeny, all other observed character states do not fit into a simple transformation series and the character states were analyzed unordered.

97. One perilymphatic foramen (0); two foramina (1). The perilymphatic foramen is an opening in the medial wall of the otic capsule that allows the perilymphatic system to communicate with spaces in the posterior cavum cranii (Gaupp, 1893). There was one foramen in the caudate larvae examined. Except for species of the Pipidae (Sokol, 1977a), all frogs have two foramina: the foramen perilymphaticum superius and inferius separated by the arcus praeoccipitalis (Gaupp, 1893). In *Ascaphus truei*, both foramina were located in the medial wall of the otic capsule. In other anuran larvae, the foramen perilymphaticum inferius was in a more lateral position opening posteriad into a perilymphatic space ventral to the ganglion jugulare rather than the cavum cranii (not coded).

98. Parasphenoid without processus alares (0); processus alares present (1). The parasphenoid is a dermal bone lying ventrally along the basis cranii. Lateral wings (alae) supported the lamina basiotica (delimiting otic capsule ventrally) in most frog species examined. The medial processus cultriformis and the processus alares, if present, form a T-shaped bone (Fig. 15). The processus alares are absent in species of the Caudata and Pipoidea (Trueb, 1973; Duellman and Trueb, 1986); they are present in *Ascaphus truei* (Van Eeden, 1951) and all other frogs (Trueb, 1993). Although the processus alares seems to be invariably present in nonpipoid frogs, the

character was coded as missing data (?) in those species for which only young larval stages that had not yet developed the parasphenoid could be examined.

99. Vertebral centra formation perichordal (0); epichordal (1). There is a remarkable diversity in the development and morphology of anuran vertebral columns (Dugès, 1834; Nicholls, 1916; Mookerjee, 1936; Mookerjee and Das, 1939; Griffiths, 1963; Trueb, 1973; Duellman and Trueb, 1986). Neural arches chondrify and ossify before the formation of centra replaces the notochord (Trueb and Hanken, 1992; Maglia and Púgener, 1998, Haas, 1999a). The larval material examined in this study allowed addressing of the question of centra formation, whereas other vertebral features apply to adult stages only (Duellman and Trueb, 1986).

Kluge and Farris (1969) and later Duellman and Trueb (1986) provided discussions of previous works on modes of centra formation in frogs. Mookerjee (1936) distinguished two major states (as applied later in Maglia et al., 2001): perichordal denotes that the centrum ossification starts dorsolaterally in the notochordal sheath and grows ventrally. It finally forms a closed ring of bone around the notochord. The closure of the ring occurs earlier in the anterior than in the posterior vertebrae (pers. observ.). In epichordal centrum formation the ossification is restricted to the dorsal parts of the notochordal sheath. In epichordal mode, the notochord is at no time encircled by a centrum ring of bone.

To score the character, good-quality cleared and stained advanced tadpoles are required (preferably stages 37–40). Both modes are easily distinguished particularly because the ventrad extension in the perichordal mode proceeds quickly during ontogeny (pers. observ.) and earlier in the rostral than in the caudal vertebrae. Therefore, taking an early stage of perichordal development for the epichordal state is not considered a source of error. Only *Chiromantis xerampelina* and *Rhacophorus pardalis* were unusual among the species examined in that the lateral downgrowth of centra ossifications had encircled the notochord only in the most anterior one to three vertebrae at the onset of metamorphosis (stage 41). State (1) was scored herein when, in tadpoles of advanced stages, the centra ossifications were restricted to the dorsolateral notochordal sheaths in all vertebrae. Missing data in the matrix stemmed from lack of appropriate larval stages or insufficient quality of whole mounts.

Kluge and Farris' (1969, 24) view, that the character has an interspecific "continuum of change," could not be confirmed. The authors further pointed out considerable intrafamilial variability of centrum formation. However, that might have been an effect of unnatural groupings of taxa in "families" at that time and is not generally true for the character distribution in this study.

100. Distinct medial ossification center of vertebral centra ventral to notochord absent (0); present (1). In *Litoria rheocola* and *L. nannotis*, two closely related suctorial forms, an accessory ventral and clearly discernible center of ossification was involved in centrum formation (Fig. 27). It develops ventromedially in the notochordal sheath, independent of and in addition to dorsolateral centers of ossification. A ventromedial center of ossification was also present in *Leptopelis vermiculatus*, but it differed from the previous case. In the two *Litoria*, the center developed earlier relative to the downward growth of the dorsolateral ossification centers and both remain separate for a longer period of larval life. In *Leptopelis vermiculatus*, the limited material examined suggests that the ventral ossification center arises only shortly before the ventrally growing dorsolateral ossification centers have reached the ventral parts of the notochordal sheath.

101. Number of presacral vertebrae more than nine (0); nine (1); eight (2); less than eight (3). A total of 13–20 presacral vertebrae were counted in the caudate larvae examined. *Ascaphus truei* and species of *Leiopelma* (not examined) are the only extant frogs with nine presacral vertebrae; most other species have eight. Reduction to seven is known in some species (*Limnodynastes peronii* in this study) and is due mostly to fusion of presacrals I and II (Trueb, 1973; Duellman and Trueb, 1986). The actual number of visible anlagen was counted in the present study whether fusion occurs later or not. Kluge and Farris (1969) discussed the number of presacral vertebrae in anurans and mentioned contradictory reports from the literature. They dismissed the character, because they felt that too little was known about the normal variability of vertebral number, particularly in basal frog groups. However, the distribution of character states in this study did not support their concerns.
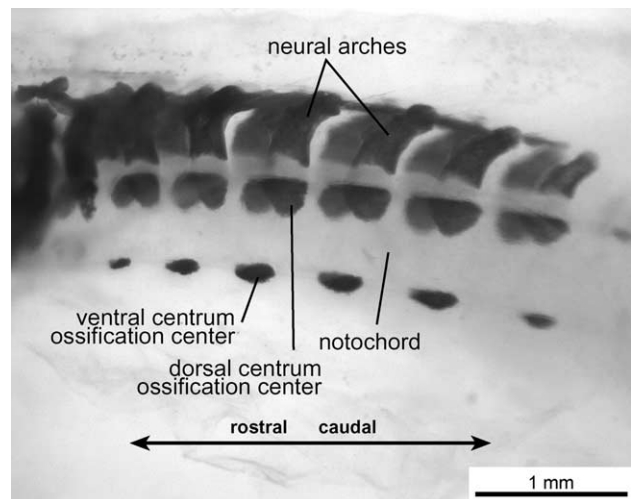

Fig. 27. Vertebral column in *Litoria nannotis* (specimen Nanno 1, stage 26), showing the unusual ventromedial centrum ossification centers. Digital photograph, lateral view.

102. Larval ribs absent (0); present (1). The presence of larval ribs in anurans is a controversial issue (Kluge and Farris, 1969; Blanco and Sanchiz, 2000). The stem group taxon *Triadobatrachus massinoti* had short ribs on all trunk vertebrae (Rage and Roček, 1989). For some extant anuran larvae, such as discoglossids and pipids, most authors agree that ribs are present (Noble, 1931; Sokol, 1977a; Trueb and Hanken, 1992; Púgener and Maglia, 1997; Maglia and Púgener, 1998; Blanco and Sanchiz, 2000). Sokol's (1977a) account of rib presence in *Pipa carvalhoi* was adopted here. Blanco and Sanchiz (2000) addressed ribs in anurans, but their results and interpretations were preliminary. They state, for example, that ribs were absent in *Pelodytes punctatus*. Applying their definition of "rib" (p. 57 "any separated or adjacent developmental element lateral ... to the vertebral transverse process"), I found ribs in *P. caucasicus*. These ribs were evident only in early larvae (stage 27) but indistinguishably fused to the transverse processes in the later stage examined (35–36). Blanco and Sanchiz (2000), however, did not examine such early stages in *P. punctatus* but examined only stages 37–46. The question whether they would have found ribs in *P. punctatus* if they had examined earlier larval stages arises. If separate bodies identified as ribs *per definitionem* are found then their presence can be coded. Conversely, the apparent absence in materials examined may indicate either true absence or just incomplete ontogenetic sampling. Due to this unavoidable uncertainty and the small number of ontogenetic samples, taxa were scored for documentation in this dataset according to personal examinations (except *Pipa*). But the character was excluded from the phylogenetic analysis.

103. Ceratobranchial I and hypobranchial I fused (0); articulation present (1). The anterior part of the planum hypobranchiale (anterior to foramen thyroideum; Haas, 1997) in anuran larvae is homologous to hypobranchial I in caudates (Gaupp, 1905). The planum articulates with ceratobranchial I in caudates, discoglossids and *Ascaphus truei*, but is fully and stiffly fused to ceratobranchial I in all other frogs (Figs. 15–17).

104. Hypobranchial skeletal parts as two cylindrical hypobranchialia (0); planum hypobranchiale (1). Larval caudates possess two cylindrical hypobranchialia, whereas frog larvae have a planum hypobranchiale (hypobranchial plates). Whether the posterior part of the planum is homologous to the hypobranchiale II in caudates remains obscure.

105. Free basihyal absent (0); present (1). In anuran larvae, the body of cartilage anterior to the pars reuniens of the hyoid arch (Figs. 15 and 16) has interchangeably been called copula anterior, copula I, or basihyal (e.g., Gaupp, 1894; Ridewood, 1898b,; Sokol, 1981; Haas, 1997). It is embedded in the ligamentum interhyale. The basihyal cartilage is particularly large in discoglossids (Haas, 1997; Maglia and Púgener, 1998). In other taxa, such as bufonids and dendrobatids, it is small, develops only in late larval stages, and may be subject to intraspecific variability (Haas, 1995). Herein state (1) was scored whenever cartilage cells were detected in histological sections of the ligamentum interhyale.

106. Basibranchial long (0); short (1); indistinguishably fused to hyobranchial elements (2); absent (3). In discoglossids the basibranchial element is long and separates the two hypobranchial plates from each other, resembling the condition in caudates (Haas, 1997; Maglia and Púgener, 1998). In the majority of anuran species, however, the basibranchial is short; the plana hypobranchiales meet and articulate in the median plane posterior to the basibranchial (among others, Gaupp, 1894; Ridewood 1898a,b; Sokol, 1981; Lason and de Sá, 1998). The basibranchial was absent in *Pipa carvalhoi* (Sokol, 1977a) and it is indistinguishably fused to hypobranchial cartilages in *Ascaphus truei* (Haas, 1997).

107. Hypobranchial plates articulate (0); fused (1). The plana hypobranchiales are moveable structures. They articulate medially with the basibranchial in discoglossids. In most other species whose plana meet in the median plane (Figs. 15 and 16), an articulation between the plana allows movements. In the microhylids examined and *Lepidobatrachus laevis*, the plana were fully fused medially.

108. Processus urobranchialis absent (0); short not reaching beyond hypobranchial plates (1); very long reaching beyond hypobranchial plates (2). The processus urobranchialis is a posteroventral projection of the basibranchial. Very long such processes occur in caudate larvae, *Rhinophrynus dorsalis* (Sokol, 1975), and most species of the Microhylidae (Fig. 20) examined (except *Scaphiophryne madagascariensis* and *Dyscophus antongilii*). In all other taxa the process is much shorter and its posterior tip comes to lie ventral to the plana hypobranchiales. A distinct processus projecting ventrally was absent in *Xenopus laevis*; in *Pipa carvalhoi* the basibranchial is absent altogether.

109. Commissura proximalis I: absent (0); present (1). The ceratobranchialia may be confluent medially by commissurae proximales (Haas, 1996, 1997). As there are four ceratobranchialia, there can be three commissurae proximales; commissura proximalis I connecting the proximal ends of ceratobranchialia I and II, and so forth. One, two, or all three commissurae can be present or absent in anuran larvae and, therefore, the character complex was set up in three characters, one for each commissura. Coding "present" means that the respective ceratobranchialia were actually connected. Coding "absent" here includes conditions in which the cartilaginous connection was interrupted (see Haas, 1995),

but vestiges may still be discernible. In *Ascaphus truei*, discoglossids, pipids, and the microhylids examined, the proximal ends of all four ceratobranchialia were confluent. The remaining species in this study lack at least commissura proximalis I. Determination of character states (characters 109–111) requires cleared and stained specimens of good quality or histological sections, because often the commissurae are thin or poorly stained.

110. Commissura proximalis II absent (0); present (1). The commissura proximalis II is a cartilage interconnecting ceratobranchialia II and III. The commissura was present in *Ascaphus truei*, pipoids, discoglossids, most pelobatoids, rhacophorids, *Hemisus*, *Leptopelis*, and microhylids examined.

111. Commissura proximalis III absent (0); present (1). The commissura proximalis III connects ceratobranchialia III and IV. *Ascaphus truei*, pipoids, discoglossids, most pelobatoids, rhacophrids, *Hemisus*, and microhylids possess the commissura. It is absent in many neobatrachians. All three commissurae proximales were absent in bufonids, dendrobatids, ranids, centrolenids, most leptodactylids, some hylids, and *Heleophryne*.

112. Spicula short or absent (0); present and long (1). Spicula I–IV are horizontal elongate cartilages originating dorsally from the proximal ends of the ceratobranchialia I–IV (Fig. 15). They project into and support the velum ventrale (ventral filter valve). Caudates lack spicula. In anurans, spicula I–III were absent in *Ascaphus truei*, species of *Bombina*, *Lepidobatrachus laevis*, and *Ceratophrys ornata*. Spicula II and III were tiny in *Discoglossus* (absent in some specimens) but more elongated in *Alytes obstetricans*. Four well-developed spicula were present in most other frogs, especially neobatrachians (e.g., Reinbach, 1939; de Jongh, 1968; Sedra and Michael, 1957; Sokol, 1975; Haas, 1995). In microhylids, the fourth spiculum did not protrude freely but was fused to ceratobranchial IV. The condition required for state (1) scoring was that the length of spiculum II was more than 20% (max. 54%) of the length of the gill slit between ceratobranchialia II and III. Measurements were taken from digital photographs of cleared and stained specimens in ventral view.

113. Reticulating cartilaginous connections between spicula III and IV absent (0); present (1). In *Hyla cinerea* (Haas, 1996), *H. annectans*, *Smilisca baudinii*, *Pseudis paradoxa* (Fig. 17), and *P. minuta* (Lavilla and de Sá, 1999), a network of interconnecting cartilages was formed between spicula III and IV posterior to the planum hypobranchiale. The character is inapplicable in taxa that lack well-developed spicula.

114. Processus branchialis open (0); closed (1). Opposing processus branchiales (Gaupp, 1893) are located on ceratobranchial II and III at the proximal third of their lengths (Gaupp, 1894). The processes are close to but distal to the commissurae proximales (Haas, 1995).

In caudates there are only modest bulges, whereas in most anurans these processes are distinct and pointed (Fig. 11b). In the vast majority of species the processes are bridged by connective tissue only ("open" condition). The processes are fused in other taxa and their ceratobranchialia II and III are thus coupled ("closed" condition; Fig. 20c).

115. Ceratohyal without diarthrotic articulation with palatoquadrate slender medial part (0); diarthrotic articulation present medial part broad (1). The specific configuration of the ceratohyal (state 1) is synapomorphic for all anurans examined; state (0) describes the condition in caudates. In anuran tadpoles, the ceratohyal has a large condylus that articulates with the ventral side of the palatoquadrate. The medial part of the ceratohyal is expanded to a horizontal plate by an anterior and posterior processus (Fig. 15d). These structural features of the ceratohyal of anuran larvae reflect its role as the central element in the buccal force-pump (Gradwell, 1968, 1970, 1971a,b, 1972a,b, 1973, 1974; Wassersug and Hoff, 1979).

116. Ratio of anterior ceratohyal processes. The ceratohyal of anuran larvae bears two processes anteriorly, the processus anterior and the processus anterolateralis (Fig. 15d). In species of *Discoglossus* and *Bombina*, for example, the processus anterior was large and round, and the processus anterolateralis was small and indistinct. In various microhylids, however, the processus anterolateralis was larger than the processus anterior. In a previous study, the presence or absence of the processus anterolateralis was scored for a small sample of anurans from various clades (Haas, 1997). Assessment of states in that study was subjective. Two morphometric characters, characters 117 and 118, define the states more precisely in the present study and better capture the observed diversity.

The ratio of the anterior processes was determined by landmark measurements (Figs. 28 and 29) from digital photographs. A baseline was drawn from the point where the pars reuniens and the ceratohyal meet (Fig. 28: x') at the anterior contour line. The line was drawn laterally as tangent to the anterior bay of the ceratohyal contour line anterior to the condylus articularis (Fig. 28: x). The sizes of the processus anterior and the processus anterolateralis were measured as the minimum distance of their apices to the baseline (Fig. 28: C,D). Ratio C/D was scored according to the gap weighting procedure (Thiele, 1993) and analyzed as an additive ordered multistate character.

117. Relative depth of anterior ceratohyal emargination. The character is not redundant with the previous character, because, for instance, large measured distances C and D (Fig. 28) may occur with shallow emarginations. Distance B (Fig. 28) was measured as the distance of the line connecting the tips of the two anterior processes and the parallel tangent line y (Fig. 28)
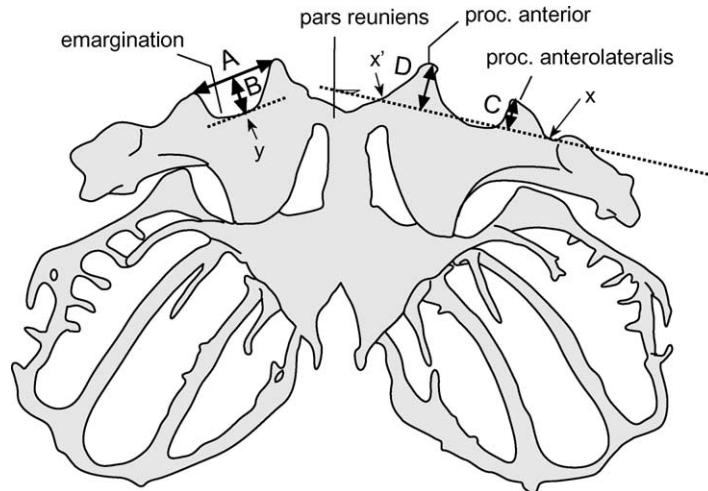
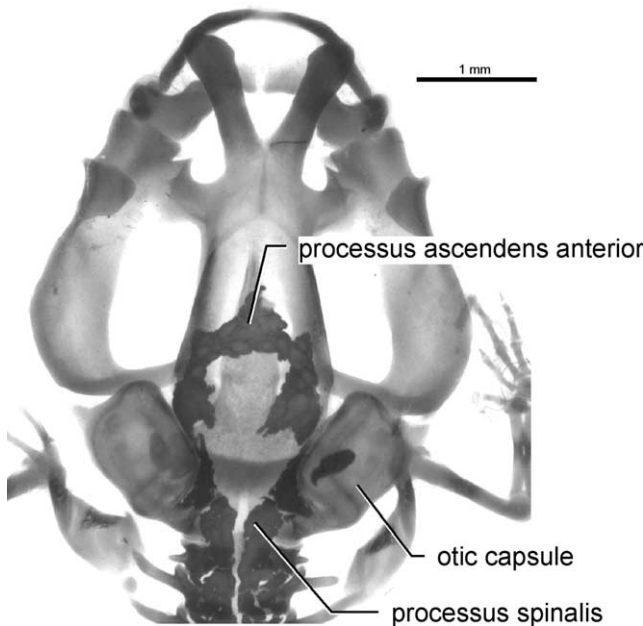Fig. 28. Measurements taken from hyobranchial skeletons, characters 116 and 117.

Fig. 29. Endolymphatic spaces in cleared and stained specimen of *Pleurodema kriegi* (specimen Pleuro 3, stage 39); dorsal view.

of the emarmination contour. The ratio of B/A (Fig. 28) was coded using the gap-weighting procedure and additive ordering of states.

118. Processus postcondylaris of ceratohyal absent (0); present (1). The processus postcondylaris is a small, triangular processus posterior to the ceratohyal condylus (Haas, 1997). It was present in species of *Ascaphus*, *Alytes*, and *Discoglossus* only.

119. Cartilaginous projections along ceratobranchialia absent (0); present (1). A unique feature of the Anura is the presence of lateral projections from the ceratobranchialia. These projections give support to branchial structures (interbranchial septa and filter epithelia).

They were reduced in the carnivorous larvae of *Lepidobatrachus laevis* and the gastromyzophorous *Atelopus tricolor* (Lavilla and de Sá, 2001; pers. observ.). State (1) applies when at least one of the ceratobranchialia possesses projections.

120. Accessory longitudinal bars of cartilage dorsal to ceratobranchialia II and III absent (0); present (1). This new character was discovered in the microhylid larvae examined. In these, lateral projections of the ceratobranchialia II and III rose far dorsad. For each of the two ceratobranchialia, the ends of the projections were interconnected dorsally by longitudinal cartilaginous bars. This structural design may give internal support to the high-rising filter plates on ceratobranchialia II and III (Fig. 20c). Finding and tracing these structures in serial sections may be difficult because, depending on the planes of the sections, multiple sections of vertical pillars give a confusing picture in cross sections. Bad quality of whole mounts of some specimens led to missing data entries.

121. Endolymphatic spaces extend into vertebral canal for less than half of the vertebral column (0); extending into more than half of vertebral canal (presacral vertebra IV or beyond) (1). In amphibians the endolymphatic system of the inner ear communicates via the ductus endolymphaticus with interdural endolymphatic sacs in the cavum cranii (e.g., Gaupp, 1899; Dempster, 1930; Francis, 1934). In caudates an intracranial endolymphatic space is located at the medial wall of the otic capsules. The right and left spaces may be completely separate or meet in the median plane and fuse dorsal to the brain in caudates (Dempster, 1930). The endolymphatic system in anuran larvae may differ from the caudate condition in two ways. First, the sacs are more extensive in general and may form an anterior mediodorsal space (Fig. 29; processus ascendens anterior of Gaupp (1899) and Dempster (1930); see character 122).

Second, expansion of the sacs may extend posteriorly into the spinal canal (processus spinalis of Gaupp, 1899). Endolymphatic sacs contain calcium carbonate ("lime sacs") and stain red in cleared and alizarin red-stained specimens. Decalcification of old museum specimens led to missing data in the data matrix.

Dempster (1930) pointed out the differences among the amphibian groups and their possible significance for phylogenetic considerations. Certain limitations make the use in the present account preliminary. The sacs enlarge during larval life. Early larvae may have short spinal sacs and may lack the fused processus ascendens anterior space. Therefore, in this study the character was assessed with fully grown or premetamorphic larvae whenever such stages were available. However, the question whether the sacs expand further after metamorphosis in those species in which the larval sacs do not reach the posterior vertebrae remains. Dempster (1930) presented preliminary evidence, however, that expansion after metamorphosis does not occur.

122. Intracranial endolymphatic system: anterior intracranial processus ascendens absent (0); anterior processus ascendens present (1). The intracranial anterior processus ascendens of the endolymphatic space was absent in caudates, discoglossids (except *Alytes*), pipoids, and *Atelopus tricolor*.

123. Cleft between hyal arch and branchial arch I closed (0); open (1). In caudate larvae there is a fully formed gill cleft between hyal arch and branchial arch I. Water flows through it from the buccal cavity via the subopercular space to the exterior. In anurans two states exist; either the space is occluded by connective tissue and excluded from the water flow ("closed") or a tubular passage is present between the buccal cavity and the peribranchial chamber ("open"). Gradwell and Pasztor (1968) described the cleft as a "by-pass" between the two spaces. Potentially, water can flow through it from the buccal cavity to the outside, cir-

cumventing the filter epithelia. Wassersug (1980) doubted that much water would flow through this shunt ("buccal pocket perforation" in his terminology) and reported the taxonomic distribution of its presence.

124. Internal gill filaments absent (0); present (1). Internal gills as tufts of epithelial filaments along the ventral side of the branchial arches and covered ventrally by the operculum were present in all anuran larvae, except for species of the Pipoidea. Caudate larvae lack subopercular gills, but have external gills.

125. Ligamentum cornuquadratum absent (0); present (1); cartilaginous connection (2). This ligament is unique to anurans and is part of the circumoral ligaments of anuran larvae (Sokol, 1981; Fig. 30). It connects the anterolateral corner of the pars articularis quadrati with either cornu trabeculae or suprarostral. The ligament was present but very weakly developed in species of the Scoptanura and absent in species of *Paradoxophyla* and *Gastrophryne*. Beyond the two microhylids, it was absent in *Lepidobatrachus laevis* and *Pipa carvalhoi*. Instead of a ligament, a cartilage connection was present in *Xenopus laevis* in the same topographic setting.

126. Ligamentum cornuquadratum inserting on ala of cartilago labialis superior (0); inserting on cornu trabeculae (1). Pusey (1943) realized that the attachment site of the ligament has different locations in various taxa. Later, Sokol (1981) found that in *Ascaphus truei*, *Rhinophrynus dorsalis*, and species of the Discoglossidae the ligament attaches to the lateral part of the cartilago labialis superior (pars alaris). The list of taxa with attachment to the pars alaris was expanded in this study to include *Ceratophrys ornata*. In other frogs, the ligament attached to the cornu trabeculae adjacent to the articulation with the cartilago labialis superior (Fig. 30). The character is inapplicable in species that lack the ligament (character 125).

127. Ligamentum mandibulosuprarostrale absent (0); present (1). The ligamentum mandibulosuprarostrale
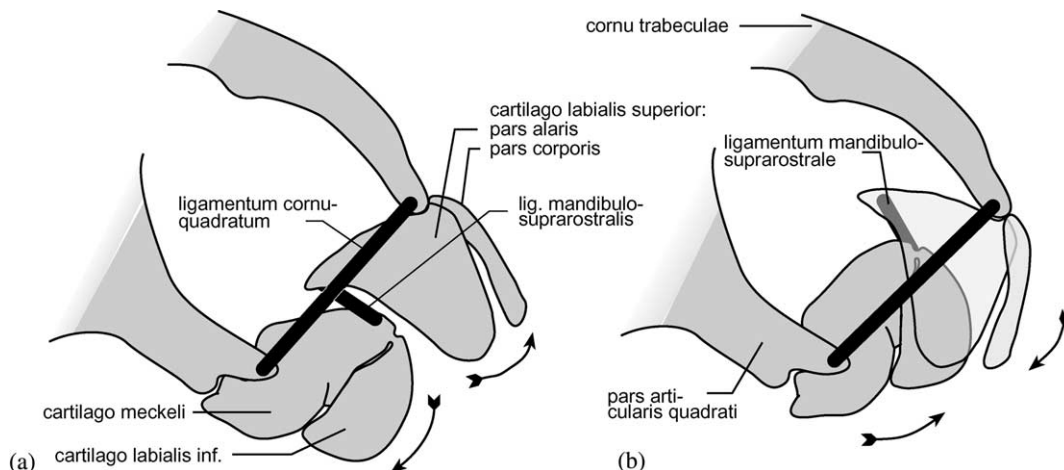

Fig. 30. Schematic representation of oral ligament (thick black lines) connections in an anuran larva in (a) open and (b) closed position; lateral views.

(Fig. 30) stretches between the processus dorsomedialis of the cartilago meckeli and the posterior dorsal process of the pars alaris (cartilago labialis superior) (e.g., de Jongh, 1968). The ligament pulls down the process of the pars alaris and rotates open the upper jaw during lower jaw abduction (Gradwell, 1968; Fig. 30a). Larvae of most anuran species possess a strong ligament. In the suspension-feeding microhylids, the ligament was weakly developed or absent (American microhylids examined). Furthermore, it was absent in caudates, *Ascaphus truei*, and pipoids.

128. Ventral valvular velum absent (0); present (1). The ventral velum is a posterior extension of the buccal floor that lies dorsal to and covers parts of the branchial basket. In many taxa it is supported internally by spicula. In most anuran larvae, the ventral velum is present as a valvular structure (Wassersug and Rosenberg, 1979) with a free fleshy posterior margin that can touch the roof of the buccal cavity and separate the buccal from the pharyngeal space (Gradwell, 1971b). There is no such structure in *Pipa carvalhoi* and the caudate species examined. In *Xenopus laevis*, velar structures are present but they are not of the valvular type (see descriptions in Sokol, 1977a; Wassersug and Rosenberg, 1979; Wassersug, 1980). Although the ventral velum of *Rhinophrynus dorsalis* is connected to the filter plate epithelium and a free margin is almost absent (Wassersug and Rosenberg, 1979:401), the velum still resembles very much that of other anurans (pers. observ.) and a valvular function is likely (Wassersug, 1980: 103).

129. Posterior margin of ventral velum continuous (0); discontinuous (1). The free margin of the ventral velum is continuous across the midline in larvae of most anurans examined. It partly or fully covers the glottis in dorsal view. In *Rhinophrynus dorsalis* and microhylids, however, the margin of the ventral velum is discontinuous in the median plane (Wassersug and Rosenberg, 1979; Wassersug, 1980, 1984, 1989).

130. Glottis position posterior (0); anterior (1). In most frog larvae the glottis is below or posterior to the free margin of the ventral velum (Wassersug, 1980). Although a ventral velum is absent in larval caudates, their glottis is in a posterior position similar to that in frog larvae (relative to the neurocranium and branchial apparatus). Because their ventral velum is discontinuous, the glottis is exposed on the buccal floor in *Rhinophrynus dorsalis* and larvae of the Microhylidae (Wassersug, 1980, 1984). However, in this study, the position of the glottis in the pharynx of *R. dorsalis* and *Scaphiophryne madagascariensis* was as posterior as that most other anurans. In the six other microhylid species examined, the glottis was in an anterior position, well anterior to the free margin of the velum (state 1).

131. Nostrils open in larval stages (0); closed in larval stages (1). Wassersug (1980, 1984, 1989) described that in species of the Microhylidae the nostrils were not perforated in larval stages. The nostril passage becomes open only during metamorphosis. Wassersug's account could be confirmed for all microhylids examined herein. Nostrils were open during larval life in all other anuran and caudate larvae examined.

132. Forelimb erupts out of limb pouch outside peribranchial space (0); limb erupts from pouch into peribranchial chamber (1). Starrett (1973) described the relations of the developing forelimb and the branchial chambers. In pipoid larvae the forelimbs develop in a pouch immediately adjacent posteriorly to the peribranchial chamber. When they erupt from the pouch they do so to the exterior and do not break into the peribranchial chamber. Among the species examined, this was unique for pipoids. In all other species, the limbs first erupt from the pouch into the peribranchial chamber (checked in histological sections) and become exposed only later when the operculum degenerates. The caudate condition was considered different (inapplicable) because their operculum does not fuse with the abdominal wall.

133. Larval lungs rudimentary or absent (0); present and functional (1). Caudate and most anuran larvae possess functional lungs for aerial respiration early in their larval lives. Species of the Bufonidae, however, develop functional lungs only during metamorphosis. Beyond bufonids, absence of lungs characterizes some stream-dwelling suctorial larvae (*Ascaphus truei*, *Litoria nannotis*, *Litoria rheocola*, and *Nyctimystes dayi*; Haas and Richards, 1998). Yet the suctorial larvae of *Heleophryne natalensis* (this study) and of *Boophis* sp. and *Hyla armata* (Haas and Richards, 1998) have functional lungs.

134. Branchial food traps absent (0); present (1). Branchial food traps are areas of specialized epithelium that contain large numbers of mucus-producing cells (Wassersug and Rosenberg, 1979; Wassersug, 1980; Wassersug and Heyer, 1988). Branchial food traps are unique features of anuran larvae, the only extant amphibians with filter-feeding and mucus-entrapment mechanisms (Kenny, 1969a,b). Branchial food traps were absent in the carnivorous larvae of *Lepidobatrachus laevis* and *Ceratophrys ornata*.

135. Branchial food traps continuous (0); divided crescentic (1). In microhylid larvae branchial food traps are arranged in three isolated, crescentic organs per side (Wassersug, 1989). Wassersug (1989) assessed the branchial food traps in *Scaphiophryne* (then named *Pseudohemisus*) as being more similar to those of ranoids than to other species of the Microhylidae. With regard to the species *S. madagascariensis* in the present study, this view is not shared. In this species the branchial food traps were discontinuous areas of specialized epithelium similar to those of the other microhylids examined. Apparently similar structures evolved in *Rhinophrynus dorsalis* (Wassersug, 1980, 1989). In Orton

Type IV larvae the food traps are continuous structures, one on each side, extending ventrally along the velum ventrale and adjacent branchial surfaces.

136. Secretory ridges absent (0); present (1). In anuran larvae mucus-producing cells are found as single cells or as congregations of cells arranged in secretory pits and secretory ridges (Kenny, 1969a; Wassersug and Rosenberg, 1979; Viertel, 1985, 1987; Viertel and Richter, 1999). Detailed accounts of the presence of secretory structures across a variety of taxa are available (Wassersug and Rosenberg, 1979; Wassersug, 1980; Wassersug and Heyer, 1988). Although these studies suggest that there are more features of the mucus-producing epithelia that are potentially useful in phylogenetic analyses, only the presence/absence of secretory ridges were scored herein. It is the only character that can be easily and reliably observed with the techniques applied herein (serial histological sections). In cross sections of the velum, the presence of ridges was seen as an undulating or even saw-tooth-shaped ventral contour line of the velar epithelium. Few character states deviate from previous reports: although he recognized some ridged areas on the ventral side of the velum in *Alytes obstetricans*, Wassersug (1980, 110) stated that secretory ridges were absent in discoglossids in general. In this study, ridges were present in *A. obstetricans*. Also, ridges were present in *Pleurodema kriegi*, while ridges were reported absent in *Pleurodema nebulosa* (Wassersug and Heyer, 1988). In some species, insufficient quality of the histological sections precluded unequivocal scoring ("?" entries).

A.2. Reproductive biology

If not indicated otherwise, all characters above were scored by personal examinations of specimens. Characters following in the sections below were only partly scored by personal observations (captive breeding groups) and partly based on literature data.

137. No transport of larvae (0); larvae are picked up at oviposition site and transported to body of water adhering to dorsum of adult (1). Among the taxa examined species of the Dendrobatidae carry their tadpoles from the terrestrial clutch to the water (Zimmermann and Zimmermann, 1988). Females of *Hemisus sudanensis* guide their tadpoles along slides in the mud from the subterrestrial nest to the pond. Apparently most of the larvae just follow the female, others may actually be carried. *Hemisus* larvae have been reported from places to which the larvae must have been carried by the female (Rödel, 1996; Kaminsky et al., 1999). The character emphasizes the transport of hatched larvae. All other species were scored (0). There are more species known to carry their larvae (Duellman and Trueb, 1986; Inger and Stuebing, 1997) but these were not included here. Carrying of the clutch was considered a different phenomenon that oc-

curs only in two distantly related species in the sample (*Pipa carvalhoi, Gastrotheca riobambae*) and, therefore, was excluded.

138. Amplexus absent (0); present (1). Although clasping occurs occasionally in the reproductive behavior of caudates (Duellman and Trueb, 1986), the typical amplectic grasping with both arms is unique for anurans. For absence of amplexus in some frogs see information below (character 139).

139. Amplectic position inguinal (0); axillary (1); cephalic (2). Within the Anura various states of amplectic position that are remarkably constant for larger taxonomic units exist (Lynch, 1973; Nussbaum, 1980; Duellman and Trueb, 1986). Only a few taxa seem to break general rules: species of the Bufonidae have axillary amplectic position but amplexus is inguinal in *Bufo fastidiosus* Graybeal and de Queiroz (1992) and *Osornophryne* (Ruiz-Carranza and Hernández-Camancho, 1976). Some species of *Pleurodema* were reported to mate in inguinal amplexus (Duellman and Trueb, 1986) and others in axillary amplexus (*P. kriegi*; A. Martino, pers. commun.). Reversal to inguinal amplexus has also occurred in the hyperoliid *Chrysobatrachus cupreonitens* (Laurent, 1964). Some dendrobatids exhibit cephalic amplexus, in which the hands of the male grasp below the throat of the female. Other species of the Dendrobatidae lack amplectic behavior during mating (Zimmermann and Zimmermann, 1988). Absence of amplexus is likely for species of the hylodine *Crossodactylus* (Weygoldt and Potsch de Carvalho e Silva, 1992), but could not be demonstrated positively. In species of *Hylodes*, the male guides the female to a hidden aquatic clutch deposition site under rocks where they spend 15 min or more (P. Narvaes, pers. commun.). Whether there is an amplexus during that phase has never been observed (R. Heyer and P. Narvaes, pers. commun.).

The amplexus of *Hemisus sudanensis* was scored state (1) (see photo in Rödel, 1996: plate II), although its inguinal position likely is secondary due to the marked sexual dimorphism and the short legs in this species.

In the axillary amplexus of some species, the arms of the male are placed far ventrally around the body of the female and may meet ventrally (for example, *Paa exilispinosa*, pers. observ.). In many hylids, however, the hands of the male are pressed against the body of the female close to her shoulder and dorsal to her arm (Duellman and Trueb, 1986; pers. observ.). This suggests that more phylogenetic information could be obtained from amplexus details if sufficient data were available. The data used here were derived in part from personal observations of mating pairs in the lab or field (*Bufo, Ceratophrys*, pipids, discoglossids, *Hyla, Hyperolius, Kaloula, Leptopelis, Limnodynastes Odontophrynus, Paa, Pyxicephalus, Rana*, rhacophorids, *Scinax*). Furthermore literature sources were used, mainly extrapolations from diagnoses in Duellman and Trueb (1986) verified

with additional sources (Zimmermann and Zimmermann, 1988 [Dendrobatidae]; Barker et al., 1995 [*Litoria, Nyctimystes*]; Wager, 1986 [*Phrynomantis, Ptychadena, Tomopterna*]; Reinbach, 1939; Manthey and Grossmann, 1997 [*Megophrys, Leptobracchium*]; Rödel, 1996 [*Hemisus, Hyperolius, Phrynomantis, Kassina*]). Cephalic amplexus was considered more similar to axillary than to the inguinal amplexus states and were ordered.

140. Advertisement call absent (0); inspiratory (1); expiratory (2); nonairflow (3). Caudates examined do not vocalize during mating behavior. Male mating calls are part of the reproductive behavior in the vast majority of frog species. However, some frog species, for instance, *Ascaphus truei* (Regal and Gans, 1976), *Leiopelma* (Stephenson and Stephenson, 1957), *Limnonectes leporina* (Inger and Stuebing, 1997), and some species of *Bufo* (Noble, 1931; Martin, 1972), have been reported to lack advertisement calls. The mechanism of mating call production is explained in terms of expiratory sound production, in which air is pressed from the lungs into the vocal sac (de Jongh and Gans, 1969; Gans, 1973). Species of *Bombina* and *Discoglossus* are the only documented taxa with inspiratory call generation. In species of *Bombina* sound is produced when the air flows from the vocal sac into the lungs (Lörcher, 1969; Nöllert and Nöllert, 1992; Strake, 1995); in *Discoglossus* sound production is bidirectional (Weber, 1974; Strake, 1995). The aquatic species of the Pipidae produce mating calls by movements of the laryngeal cartilages that produce clicking sounds (Yager, 1992). Coding of states is preliminary and all species for which there was no published evidence for character states (0), (1), or (3) were scored (2), as this seems to be the general mode (Gans, 1973).

141. Clutches: clumps of eggs or scattered submerged eggs (0); strings (1); floating eggs/surface film (2). Duellman and Trueb (1986) listed 29 reproductive modes in anurans and Duellman (1992) gave a summary on diversity and evolution of anuran reproductive strategies. Three simple character states were defined for clutches and applied herein. Although clutch features and reproductive modes are quite homoplastic in the Anura, certain states may be consistent in subclades. Many anuran species lay eggs as submerged egg masses, ranging from dispersed single eggs to clumps. Loosely spaced eggs or clumps of eggs can also be surrounded by foam as in aerial foam nests (Rhacophoridae) and terrestrial or aquatic foam nests (some leptodactylids). Egg clumps are deposited terrestrially in, for instance, dendrobatids and some hyperoliids or the clutches are attached to vegetation above ponds in phyllomedusine and other hylids and in centrolenids. Eggs embedded in strings of jelly are known from representatives of the Bufonidae but also occur, among the species examined, in *Alytes, Pelodytes, Pelobates,* and *Spea.* Clutches floating as a single layer of eggs on the water surface (without foam) were reported for some of the hylines, ranids, and the species of the Microhylidae examined. Clutches of *Heleophryne natalensis* are deposited in groups attached under rocks in streams (Visser, 1970).

Character state coding was derived from personal observation (*Bufo, Ceratophrys, Chiromantis,* pipids, discoglossids, *Hyla, Hyperolius, Kaloula, Leptopelis, Limnodynastes, Paa, Ptychadena, Pyxicephalus, Scinax, Smilisca, Rana*), personal communications (K.-H. Jungfer [*Phrynohyas, Osteocephalus*], A. Martino [*Hyla pulchella*], A. Kwet [*Aplastodiscus, Pseudis*], A. Schlüter [*Hamptophryne*]), and published accounts (Duellman and Trueb, 1986; [*Atelopus*]; Gallardo, 1987 [*Leptodactylus, Melanophryniscus, Odontophrynus, Physalaemus, Pleurodema*]: Behler and King, 1988 [*Ascaphus, Gastrophryne Rhinophrynus Spea*]; Zimmermann and Zimmermann, 1988 [dendrobatids]; Glaw and Vences, 1994 [*Dyscophus, Paradoxophyla, Scaphiophryne*]; Barker et al., 1995 [*Litoria, Nyctimystes*]; Wager, 1986; Nöllert and Nöllert, 1992 [*Pelobates, Pelodytes*]; Rödel, 1996 [*Hyperolius, Kassina, Phrynomantis Tomopterna*]; Manthey and Grossmann, 1997 [*Megophrys, Leptobrachium Limnonectes Pedostibes, Rhacophorus*]).

142. Guiding behavior absent (0); present (1). Species of *Hylodes, Crossodactylus,* and the Dendrobatidae possess complex mating behaviors (Zimmermann and Zimmermann, 1988; Weygoldt and Potsch de Carvalho e Silva, 1992; R. Heyer, pers. commun.; P. Narvaes, pers. commun.). Males are territorial, occupy a calling site, and attract females to the terrestrial territory. Most importantly, the male and females move from the calling site to the oviposition site without amplexus. At the oviposition site, amplexus may or may not occur (see character 139).

A.3. Adult morphology

143. Pupil shape vertical (0); horizontal (1); inverted drop-shaped (triangular) (2); round (3). In many taxonomic groups pupil shape is determined reliably and certainly indicates relatedness, for example, in phyllomedusine hylids (vertical pupils) or in species of *Bombina* and *Discoglossus* (triangular). The character was extrapolated from diagnoses in Duellman and Trueb (1984) with verification for a number of taxa by personal observations (*Bufo, Ceratophrys,* pipids, discoglossids, *Dendrobates, Epipedobates, Hyla, Hyperolius, Kaloula, Leptopelis, Limnodynastes Odontophrynus, Paa, Pelobates, Pelodytes, Phrynohyas, Phyllobates, Ptychadena, Pyxicephalus, Rana,* rhacophorids, *Scinax Smilisca*) and by evaluating published descriptions and photographs (Glaw and Vences, 1994 [*Dyscophus, Scaphiophryne*]; Barker et al., 1995 [*Litoria, Nyctimystes*]; Wager, 1986 [*Kassina*]; du Preez, 1996; [*Heleophryne, Phrynomantis*

Tomopterna]; Rödel, 1996 [*Kassina*, *Phrynomantis*]; Manthey and Grossmann, 1997; [*Megophrys*, *Leptobrachium*, *Limnonectes*, *Pedostibes*, *Rhacophorus*). In some species, however, pupil shape was more difficult to assess than some published works suggested (*Hamptophryne* ?). Particularly in species with horizontal pupils, recognition of the state may depend on the degree of closure of the pupil slit. In microhylids, it was difficult to distinguish round from horizontal, especially if the eye was photographed from an angle. The pupil of *Paa exilispinosa* was approximately rhomboid in shape (pers. observ.), yet it was wider than high and, thus, scored (1).

144. Shoulder girdle arciferal (0); firmisternal (1); pseudofirmisternal (2). In frogs, the arciferal condition denotes that the epicoracoid cartilages of the shoulder girdle are not fused or fused only rostrally and major parts of the epicoracoid overlap caudally; the cartilages can perform rotational movements. In the firmisternal condition the epicoracoids are fully fused along their length; no movements are possible. Epicoracoid cartilages may overlap for some time during development before they fuse to form the firmisternal condition (Noble, 1926a,b; Griffiths, 1963; Kaplan, 1995). In pipids, two epicoracoid cartilages are abutting, nonoverlapping and functionally fixed (Cannatella and Trueb, 1988a,b); the condition was classified as pseudofirmisternal (Duellman and Trueb, 1986). Character states were generally adopted from familial diagnoses in Duellman and Trueb (1986) and extrapolated to the respective species in this study. In contrast to other bufonids, species of *Atelopus* show firmisterny (e.g., Griffiths, 1963; Kaplan, 1994; Emerson et al., 2000 for *A. chiriquiensis*).

145. Clavicula absent (0); overlapping scapula anteriorly (1); not overlapping (2). The clavicle is present in most anurans and absent in caudates. In some species it overlaps and articulates with the scapula anterior to the glenoid fossa. In others, it does not overlap but ends at the fossa. For the species examined, character states were extrapolated from familial diagnoses in Duellman and Trueb (1986).

146. Palatine absent (0); present (1). Palatines are present in caudates (Trueb, 1993). Within the Anura palatines are absent in *Ascaphus*, pipoids, and discoglossids (Duellman and Trueb, 1986; Trueb, 1993) but present in neobatrachians and *Heleophryne* (Ford and Cannatella, 1989; neopalatines *sensu* Trueb, 1993). Palatine bones are reduced or absent in most microhylids (Duellman and Trueb, 1986). Character states were extrapolated from the sources mentioned.

147. Parahyoid bone absent (0); present (1). The parahyoid is an ossification of the hyoid plate known only in *Ascaphus*, *Leiopelma*, *Rhinophrynus*, discoglossids, and *Pelodytes* (Duellman and Trueb, 1986; Trueb, 1993; character states extrapolated from these sources).

148. Cricoid as two cartilages (0); closed ring (1); ring with ventral gap (2); ring with dorsal gap (3). The cricoid cartilage is part of the larynx and likely is derived from paired cartilages as found along the laryngotracheal chamber in caudates. Almost all character states were extrapolated from higher taxa descriptions in Duellman and Trueb (1986). However, Ford and Cannatella (1989: 102) reported that a dorsal gap is not present in all pelobatoids and absent, for example, in *Spea* (scored 1 here).

149. Tongue absent (0); present (1). The aquatic frogs of the Pipidae lack a tongue; adopted and extrapolated from Duellman and Trueb (1986).

150. Tibiale and fibulare separate (0); elongate and fused at ends (1); elongate and fully fused (2). The tibiale and fibulare are separate, short tarsal elements in caudates, whereas in frogs the two elements are elongate and contribute to jumping performance. In most frogs the two bones are fused at both of their ends. Traditionally, full fusion was considered an apomorphic and diagnostic feature of centrolenid frogs (Taylor, 1951; Duellman and Trueb, 1986), but more recently intrafamilial variation was found (Sanchiz and de la Riva, 1993). In the light of the known variation within centrolenids, extrapolating state (2) to the *Cochranella granulosa* in this study does not seem warranted without positive evidence.

151. Intercalary element absent (0); present (1). The intercalary element is a cartilage (ossification sometimes occurs) between the terminal and the subterminal phalanges. It has been reported in taxa with predominantly climbing species, i.e., hylids, rhacophorids, hyperoliids, and centrolenids (Duellman and Trueb, 1989; Paukstis and Brown, 1991), but also in mantelline ranids (Emerson et al., 2000). From these studies, presence of the intercalary was extrapolated to hemiphractine, phyllomedusine, pseudine, pelodryadine, rhacophorid, and hyperoliid species examined herein (absence in all others). In general microhylids lack the intercalary element (Emerson et al., 2000), however, there is positive evidence for presence in *Phrynomantis bifasciatus* (Paukstis and Brown, 1991). Absence of the intercalary in *Hemisus* was adopted from Emerson et al. (2000).

152. M. caudalipuboischiotibialis absent (0); present (1). Among anurans, the muscle is present only in *Ascaphus truei* and species of *Leiopelma* (Green and Cannatella, 1993). It was homologized with the muscle of the same name in caudates (Noble, 1922), but dissenting interpretations exist (Ritland, 1955).

153. M. sartorius partially or fully fused with m. semitendinosus (0); discrete muscle (1). The sartorius–semitendinosus muscle complex of anurans is considered homologous with the m. puboischiotibialis of caudates (Noble, 1922). The degree of separation of the m. sartorius has been described for various taxa (Noble, 1922; Dunlap, 1960). The m. sartorius is a clearly discrete muscle in neobatrachians and *Heleophryne* (Duellman and Trueb, 1989; Ford and Cannatella, 1993). Character

states were adopted and extrapolated from Duellman and Trueb (1986), however, there might be more homoplasy than suggested by that coding (Kluge and Farris, 1969).

154. Bidder's organ absent (0); present (1). Bidder's organ is a ovarian gonadal derivative of the anterior embryonic gonadal crest. It is present in both sexes, in bufonids only. In this study presence of Bidder's organ was assumed for all bufonids, except for *Melanophryniscus*, and absence was assumed for all nonbufonids (Duellman and Trueb, 1986; Roessler et al., 1990). Echeverría (1998) demonstrated the absence of the organ in *M. stelzneri* and assumed that other species of the genus also lack it. Herein *M. orejasmirandai* was thus scored (0).

155. Musculus intermandibularis simple undifferentiated (0); with supplementary apical portion (1); supplementary posterolateral portion (2). The supplementary apical element of the m. intermandibularis occurs in all pelodryadine hylids (Tyler, 1971; Duellman, 2001), and in the hylines *Acris*, *Osteopilus*, and *Sphaenorhynchus* (Tyler, 1971; taxa not included in this study). Character states where adopted from Tyler (1971) and extrapolated to the species examined in this study.

156. Terminal phalanges rounded (0); claw-shaped (1); bifurcated T- or Y- shaped (2). Claw-shaped terminal phalanges have been proposed as an apomorphic feature of hylid frogs (Ford and Cannatella, 1993; Duellman, 2001). In some higher groups, there is variation in the shape of terminal phalanges (e.g., Drewes, 1984). Character states for centrolenids, hylines, phyllomedusines, hemiphractines, and pseudines were adopted from Duellman (2001) and extrapolated to the species included in this study. Other sources used were Drewes (1984) for hyperoliids, Liem (1970) for rhacophorids, Wiens (1989) for *Spea bombifrons*, Heyer (1975) for *Crossodactylus*, and de Sá and Trueb (1991); for *Hamptophryne boliviana*. All remaining matrix entries were from personal examinations of specimens.

A.4. HaasMatrix

The HaasMatrix is available as supplementary data on ScienceDirect.

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