1997 Asiatic Herpetological Research Vol. 7, pp. 68–79

Taxonomic Review of the Megophryid Frogs (Anura: Pelobatoidea)

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Abstract.- The family Pelobatidae has recently undergone notable reorganization. Once composed of two subfamilies, Pelobatinae and Megophryinae, it now consists of only the former. The family Megophryidae has recently been elevated to represent Asian members once in the family Pelobatidae; megophryids are diagnosed by three synapomorphies.

A phylogenetic analysis of the Archeaobatrachia by Cannatella (1985) included three species from two genera within Megophryidae. Paraphyly in the genus *Megophrys* was supported by one character, the articulation of the urosacrum. A re-analysis of Cannatella's (1985) data indicated that alternative patterns of the relationships among megophryids were plausible and that the homology of the urosacral articulation should be examined in more detail.

Key words: Amphibia, Anura, Pelobatoidea, Megophryidae, taxonomy

Introduction

The classification of anurans has been a matter of much recent debate. Several different opinions exist about their relationships (see Ford and Cannatella, 1993 for a review of the recent work on anuran relationships), and no fewer than three different taxonomies are currently in use (Duellman and Trueb, 1986; Dubois 1985, 1986; Ford and Cannatella, 1993). Previous classifications (prior to Duellman, 1975) have been based on a single complex of characters. As a result, when alternative character schemes were derived, earlier classifications were found to be incongruent.

The source of the incongruities have been the choice of characters used to construct each classification (Noble [1922, 1931] vertebral centrum, pectoral girdle, thigh musculature, and dentition; Griffiths [1963] hyolaryngeal structures, skull and limb morphology, and reproduction and development, vertebral column; Hecht [1963] and Starrett [1973] tadpole types). Each classification directly reflected the characters used in the particular study. For example, the classification proposed by Hecht (1963) in which Orton's (1957) larval characters were used to construct a classification that differed markedly from one developed the same year based on adult morphology (Griffiths, 1963). The history of these characters and their role in the classification of anurans is reviewed in the works of Lynch (1973) and Duellman (1975).

Noble (1922), reflected on the problems involved with constructing a classification based on either a single character or a complex of characters. However, the trend continued until Tihen (1965) and Inger (1967) provided classifications based on multiple characters. Subsequently, others have adopted a similar approach to the classification of anurans (Kluge and Farris, 1969; Lynch, 1973; Duellman, 1975; Laurent, 1979; Dubois, 1986). More recently, Ford (1989, 1993) undertook an analysis of the Neobatrachia, in an attempt to identify the phylogenetic position of Dendrobatidae among all anurans. Similarly, Cannatella (1985) generated a phylogeny for the Archaeobatrachia. Both of these thorough phylogenetic analyses culminated in a phylogeny for all major groups of frogs (Ford and Cannatella, 1993). They have applied contemporary techniques to generate a taxonomy reflecting natural groupings (de Queiroz and Gauthier, 1992), i.e., evolutionary history.

Anuran classification has progressed since Reig (1958) divided the Anura into four suborders: Amphicoela, Aglossa, Archaeobatrachia, and Neobatrachia. Based on the analysis of Ford and Cannatella (1993), the Amphicoela and Archaeobatrachia are artificial groupings. However, Neobatrachia and Aglossa reflect natural groupings (the latter now called Pipoidea). They confirmed Lynch's (1973) observation that members of Pelobatidae represent a transitional group between the basal anurans and

Table 1. Characters that support the family Pelobatidae (Duellman and Trueb, 1986), superfamily Pelobatoidea (Ford and Cannetella, 1992) which includes pelobatines and megophryines and the genus *Pelodytes*.

ossified intervertebral discs present
procoelous centrum
presacrals I and II not fused
atlantal cotyles of Presacral I closely juxtaposed
ribs absent
sacral diapophysis greatly expanded
sacrum fused to coccyx (moncondylar articulation with the coccyx in megophryine and some eopelobatines)
transverse processes on the proximal part of the coccyx (often incorporated into the sacral diapophysis)
pectoral girdle arciferal
cartilaginous omosternum
osseous sternum
scapula not overlain by the clavicle
parahyoid absent
cricoid ring incomplete dorsally
astragalus and calcanium are fused only proximally and distally
two tarsalia
m. sartorius is not discrete from the *m. semitendinosus* and the end of the latter inserts ventral to the *m. gracilis*
m. glutaeus magnus has an accessory tendon
m. adductor magnus lacks an accessory head
pupil vertical
amplexus is inguinal
type IV larvae
trigeminal and facial ganglia are fused
diploid number of chromosomes is 26 (24 in *Leptolalax pelodytoides*)

Neobatrachia; this implies that they possess an intermediate number of primitive character states.

Cannatella (1985) found that the family Pelobatidae, composed of two subfamilies, Megophryinae and Pelobatinae, represented an artificial grouping, and that each subfamily must be elevated to familial status to remove the conflict. Currently the two families are placed in a superfamily, Mesobatrachia (Cannatella, 1985), and is composed of pelobatoids (Pelobatidae, Pelodytidae, and Megophryidae) and pipoids (Rhinophrynidae and Pipidae).

To date, the evolutionary relationships of the Mesobatrachia have been addressed only in the phylogenetic analysis of Cannatella (1985, Ford and Cannatella, 1993). Within the Mesobatrachia, the relationships of Pelobatidae (*Scaphiopus* and *Spea*) have been partially resolved by Cannatella (1985). However, within the Megophryidae, only genealogical relationships of *Scutiger* (Yea et al., 1992), and *Scutiger* with *Oreolalax* (Yang and He, 1980) has been examined. In Cannatella's (1985) analysis of the Archaeobatrachia (hereafter referred to as DCC for ease of discussion), conclusions were made regarding the relationships of two genera of Megophryidae, *Megophrys* and *Leptobrachium*. However, there were errors in the coding of the characters in DCC's analysis that have serious implications on the composition of the family. Consequently, herein, I will review the taxonomic history of the family Megophryidae, and provide a re-analysis of Cannatella's data relevant to Pelobatoidea (Pelodytidae, Pelobatidae, Megophryidae). I conclude, by discussing the need for a phylogenetic classification that includes all the genera of Megophryidae.

Taxonomic History of Megophryidae

The first megophryid, *Megophrys montana*, was described by Kuhl and Van Hasselt (1822). Only four species of megophryids were known at the time of Boulenger's (1882) comprehensive account of known amphibians. Since then, 78 additional species have been described, and undoubtably more will be added as southeast Asia is more thoroughly investigated.

The first efforts to classify anurans was Cope (1865). He grouped taxa on the condition of the pectoral girdle and the vertebral column. In the taxonomic practices of the past, grouping of organisms were based on similarity, often creating polyphyletic assemblages of taxa. The family Asterophrydidae Günther 1859, a polyphyletic group, was the first family that included a megophryid. Members of this family included three genera of megophryids

(*Megalophrys*, *Xenophrys*, and *Leptobrachium*), as well as a microhylid, and a myobatrachid.

Noble (1922, 1931) provided groupings based on multiple characters of the adult morphology; megophryids were placed in the suborder Anomocoela, family Pelobatidae. In these works, the family Pelobatidae included three subfamilies: Megophryinae (*Megophrys*, *Leptobrachium*, *Nesobia*, *Scutiger*, *Aelurophryne*, *Leptobrachella*), Pelobatinae (*Scaphiopus*, *Spea*, *Pelobates*, *Pelodytes*), and Sooglossinae (*Nesomantis* and *Sooglossus*). Noble (1926) believed that the Sooglossinae possessed all the evolutionary significant pelobatid characteristics (maxillary teeth, arciferal pectoral girdle, procoelous vertebrae, a single coccygeal condyle, and the particular arrangement of the pectoral muscles). However, it showed a different arrangement of the thigh musculature thought to be derived with respect to Asian pelobatids. Not satisfied with the characters used by Noble, Griffiths (1959) removed Sooglossinae from the family Pelobatidae and placed it in its own family, Sooglossidae.

The classification of the Pelobatidae (viz. Pelobatinae, Megophryinae, and Pelodytinae) was maintained for nearly 40 years. Lynch (1973) removed *Pelodytes* from the family Pelobatidae, and erected a new family for this one genus (Pelodytidae) on the basis of limb characteristics that were derived independently from those of pelobatids.

Duellman and Trueb (1986) provided a phylogenetic tree that placed megophryids within Pelobatidae, as the sister group to Pelodytidae (see Table 1 for a list of synapomorphies uniting Pelodytidae and Pelobatidae). This arrangement has been the convention since Lynch's (1973) work.

Cannatella (1985) performed a phylogenetic analysis of the Archaeobatrachia and found that Pelobatidae (Megophryinae and Pelobatinae) was paraphyletic with respect to Pelodytidae and thus removed megophryids from Pelobatidae and erected a new family, Megophryidae. Despite a recent effort to disseminate this information (Ford and Cannatella, 1993), with the exception of Trueb (1991) and Fu et al., (submitted), the application has not received wide acceptance. Recent taxonomic accounts have grouped megophryids as a subfamily of Pelobatidae (Dubois, 1986; Duellman, 1993; Fang, 1985; Yea, et al., 1992; Fei and Yea, 1990, 1983; Frost, 1985; Guan-Fu, et al., 1993; Inger and Stuebing, 1991; Huang, 1985; Kuo, 1985; Wu, et al., 1993; Zhao and Adler, 1993; and others).

Taxonomic History of the Genera

The generic taxonomy of Megophryidae suffers from a convoluted history and temporal instability of its genera. The first generic name was proposed for the type species, *Megophrys montana* Kuhl and van Hasselt 1822. Shortly thereafter, Wagler (1830) published the generic name as *Megalophrys* for the genus *Megophrys*. This spelling continued for a century, and appeared as the original generic name for seven species in monographic reviews of anuran taxonomy (Boulenger, 1908; van Kampen, 1923). In his review of reptiles and amphibians of the Malay Peninsula, Smith (1930) corrected this unjustified emendation but without comment to the previous error.

From this single genus, *Megophrys* (*Megalophrys*), Boulenger (1882) recognized three forms on the basis of the presence or absence of vomerine teeth and the type of vertebrae (procoelous or opisthocoelous). He split the group into three genera: *Xenophrys* (Günther, 1865), *Megalophrys* (Wagler, 1830), and *Leptobrachium* Tschudi, 1838. Boulenger (1908) later regrouped all three into the genus *Megophrys* because the characters that he previously had used to separate them varied intergenerically and were not useful for distinguishing the genera.

Ceratophrys Gravenhorst, 1829, was used to describe another form of *Megophrys montana*. *Ceratophrys*, a genus of large-headed leptodactylid, occurs exclusively in South America and bears only a superficial resemblance to *Megophrys*. Other junior synonyms of *Megophrys* are *Ixalus* (Anderson, 1871), once a genus of Rhacophoridae. The description of the species was based on juvenile material of *Megophrys lateralis* (Boulenger, 1908); Gorham (1966) considered this species a *nomen dubium*. Beddard (1907) placed *Megophrys montana* in a monotypic genus, *Pelobatrachus*. However, he did not provide any unique characters to distinguish it from the other known megophryid genera (*Xenophrys*, *Megalophrys*, *Leptobrachium*). Therefore, it was returned to *Megophrys* (Boulenger, 1908). *Brachytarsophrys* and *Atympanophrys*, were described by Tian and Hu (1983). The latter, *Atympanophrys*, (Greek [atympano = without tympanum]), was a monotypic genus described from a specimen of *Megophrys shapingenesis* in which the authors report that all structures associated with the middle ear (stapes, tympanic annulus) were absent. *Brachytarsophrys* was thought to be distinct because of its peculiar shaped head and high neural spines of the vertebrae. Dubois (1986) reviewed the three genera, *Megophrys*, *Brachytarsophrys*, and *Atympanophrys*. He concluded that the three different evolutionary states that Tian and Hu

(1983) referred to were neither sufficient nor important enough to deserve generic ranking and thus made them subgenera of *Megophrys*. A later investigation of the type series of *Atympanophrys* revealed that all structures of the middle ear were present and that the absence of the middle ear in one specimen (SM00042) was a result of improper handling of the type (Fei et al., 1991, p. 4). The genus *Atympanophrys* was considered a junior synonym of *Megophrys* (Fei et al., 1991). *Brachytarsophrys* is still recognized as a subgenus of *Megophrys* (Duellman, 1993).

Boulenger (1887, p. 405) reported that *Scutiger* Theobald, 1868 (Chinese megophryids), as a genus of Amphibia, is preoccupied by an earlier name, *Scutigera* Latreille, 1802, for a genus of centipede. As a result, Boulenger erected a new generic name, *Cophophryne*, for these forms. He also pointed out that many of the characters of *Cophophryne* appear to be intermediate between pelobatids and bufonids (viz. absence of maxillary teeth, expanded sacral diapophyses). Because of these characteristics, it was considered a member of the family Bufonidae.

Boulenger (1919) erected *Aelurophryne* for a single species, *A. mammata* (= *Bufo mammata* Günther, 1896) that could be distinguished from *Cophophryne* by the absence of a posteriorly-notched tongue. These two genera (*Aelurophryne* and *Cophophryne*) could be distinguished from bufonids by the presence of vertical pupils (a character found in many pelobatids). Thus, Boulenger (1919) placed these two genera in the Pelobatidae. Procter (1922) followed Boulenger's (1919) familial arrangement. However, he considered *Cophophryne* and *Aelurophryne* to be congeneric, and place *Cophophryne* as a junior synonym of *Aelurophryne*.

Noble (1931) recognized both *Scutiger* Theobald (= *Cophophryne* Boulenger) and *Aelurophryne* (Boulenger, 1919). He distinguished the two by the presence of short maxillary teeth in *Scutiger* and the absence of dentition in *Aelurophryne*. Pope and Boring (1940) and Liu (1950) also recognized *Aelurophryne* in their surveys of Chinese amphibians. Liu (1950) further characterized the two genera by the presence of a tympanum and a small opening for the eustachian tube in *Aelurophryne*, and the absence of these characters in *Scutiger*. After having re-examined four species fastigiate described by Liu (1950), Myers and Leviton (1962) argued that *Scutiger* and *Aelurophryne* could not be distinguished in the way of Liu, Pope and Boring, and Noble had proposed. They found that three of the four *Scutiger* forms possessed a combination of characteristics that were supposed to be present in either *Scutiger* or *Aelurophryne* (e.g., presence of a deeply notched tongue, teeth, a tympanum which was concealed under the skin, and a distinct openings for the eustachian tubes). Consequently, Myers and Leviton (1962) adopted Procter's (1922) taxonomy, but because *Scutiger* preceded *Aelurophryne*, all Himalayan megophryids were placed in *Scutiger*.

Ophryophryne, a genus described by Boulenger (1903), was originally placed in the Bufonidae because it possessed similar external characteristics (horizontal pupil and an edentate maxilla). Boulenger (1903) suggested that *Ophryophryne* was the evolutionary link between the pelobatids and bufonids. However, Noble (1926) examined the thigh musculature of two species of *Ophryophryne* and concluded that they were diminutive *Megophrys*. *Ophryophryne* remained a distinct genus, because most of the variation between *Megophrys* and *Ophryophryne* is in the head region. Dubois (1980) stated that ". . . the strong resemblance between *Megophrys* and *Ophryophryne* (to the point that it is probably impossible to determine to which group one would place the specimen without the head!) indicates that they probably do not merit the status of distinct genera"[1]. In this work, Dubois relegated *Ophryophryne* to the status of subgenus of *Megophrys*. Dubois (1986) re-examined his earlier comparisons (Dubois, 1980) and considered the differences to be distinctly different, thus returning generic status to *Ophryophryne*.

Liu (1950) placed some species of *Leptobrachium* in a new genus, *Vibrissaphora*, to represent a small group that possessed keritanized nuptial excrescences along the margin of the maxilla. Liu et al. (1973) examined members of *Vibrissaphora* and *Leptobrachium hasseltii* and found that the only difference between the two genera was the presence of the maxillary spine in *Vibrissaphora*. This character did not seem significant enough to warrant two separate genera. Therefore, *Vibrissaphora* was returned to *Leptobrachium* (Dubois, 1980). Some authors still recognize *Vibrissaphora* as a distinct genus (Zhao and Adler, 1993).

Nesobia (van Kampen, 1923) was a name given to small species that possess horizontal pupils and inhabit Natuna Island. The taxonomic status of this genus was not questioned by Dubois (1980) because material was not available for examination. However, because the name *Nesobia* was preoccupied, a genus of molluscs, a new name was applied to this group (*Leptobrachella* Smith 1925).

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[1] English translation of the original text in French.

Table 2. Genera of Megophryidae and their known synapomorphies.

Leptobrachella (Borneo and the Bunguran [=Natuna] Islands)
very reduced sternum
pointed expansion at tips of digits
ventral skin of digits sharply delimited
no denticles on larval oral disc
nuptial excrescences absent
*vertical pupil

Leptobrachium (Southern China to the Philippines, Indochina, and Sunda Is. to Bali)
*vomerine teeth absent
snout not extending beyond lower jaw
tongue strongly notched posteriorly
two well developed metacarpal tubercles
vertebrae proceolous
omosternum cartilaginous
sternum with a bony style
*horizontal pupil

Leptolalax (Burma and southern China through Thailand and Vietnam to Malaya and Borneo)
(no unique synapomorphies)

Ophryophryne (northern Vietnam and southern China)
*maxillary teeth absent
horizontal pupil
*vomerine teeth absent

Megophrys (southern, eastern, and southeastern Asia)
tadpole with funnel-shaped oral disc
larvae with median anal tube
*vertical pupil

Scutiger (high altitudes of southwestern China, northern Burma, Mepal, and northern India)
*maxillary teeth reduced or absent
rough skin
tympanum obscured
*vertical pupil

* character is not unique to the genus

Hu et al., erected *Carpophrys* (Sichuan Institute of Biology, 1977) as a generic name for a single species, *Leptobrachium oshanensis*. In a draft of the second edition (1977) of the Chinese amphibians (Liu, et al., 1966), Liu described three species of *Leptobrachium* that were distinct in which he placed them in a new genus, *Carpophrys*.

In this document Liu included a diagnosis of *Carpophrys* and the type species for the genus (*Leptobrachium pelodytoides*). This draft was distributed among Chinese colleagues and has been cited in several Chinese publications (after 1977), (personal communication, Jinzhong Fu, 1995). Dubois (1980) reviewed the status of *Leptobrachium* and agreed with Liu that three species (*L. gracile*, *L. pelodytoides*, and *L. oshanensis*[2]) were distinct from other species of *Leptobrachium* based on the position of the axillary glands, appearance of the skin on the dorsum, unpigmented eggs, and other relative proportions of the body. He thought these three species were likely to be closely related to the larger subset of *Leptobrachium*, but distinct. Dubois (1981) pointed out that the genus name *Carpophrys* was not valid because the original description was published anonymously and the type species for the genus was not designated (following Art. 13b, Art. 14, International Code of Zoological Nomenclature, 1985). Thus, he created two subgenera for the groups—*Leptolalax* for the three species, and *Leptobrachium* for the larger subset (in the genus *Leptobrachium*). Later, Dubois (1983) elevated Leptolalax to generic status. Fei and Ye (1992) investigated the validity of the two generic names, *Carpophrys* and *Leptolalax*, and concluded that although a description of the genus existed and a type species was designated, *Leptolalax* is valid because *Carpophrys* was not published in an official publication (Art. 8a.1, International Code of Zoological Nomenclature, 1985).

Currently, the family Megophryidae consists of 83 species divided into six genera (*Leptobrachella*, *Leptobrachium*, *Leptolalax*, *Ophryophryne*, *Megophrys*, and *Scutiger*). Each genus is supported by a set of unique synapomorphies (Table 2) except for *Leptolalax*. My investigation into the literature has provided no unique synapomorphies for *Leptolalax*. An addi-

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[2] Dubois (1980) used the specific epithet *oshanense* because as he noted (B.G. 476 in a footnote) that the original genus name, *Leptobrachium*, is neuter in gender, and must be amended to agree with *Leptolalax*.

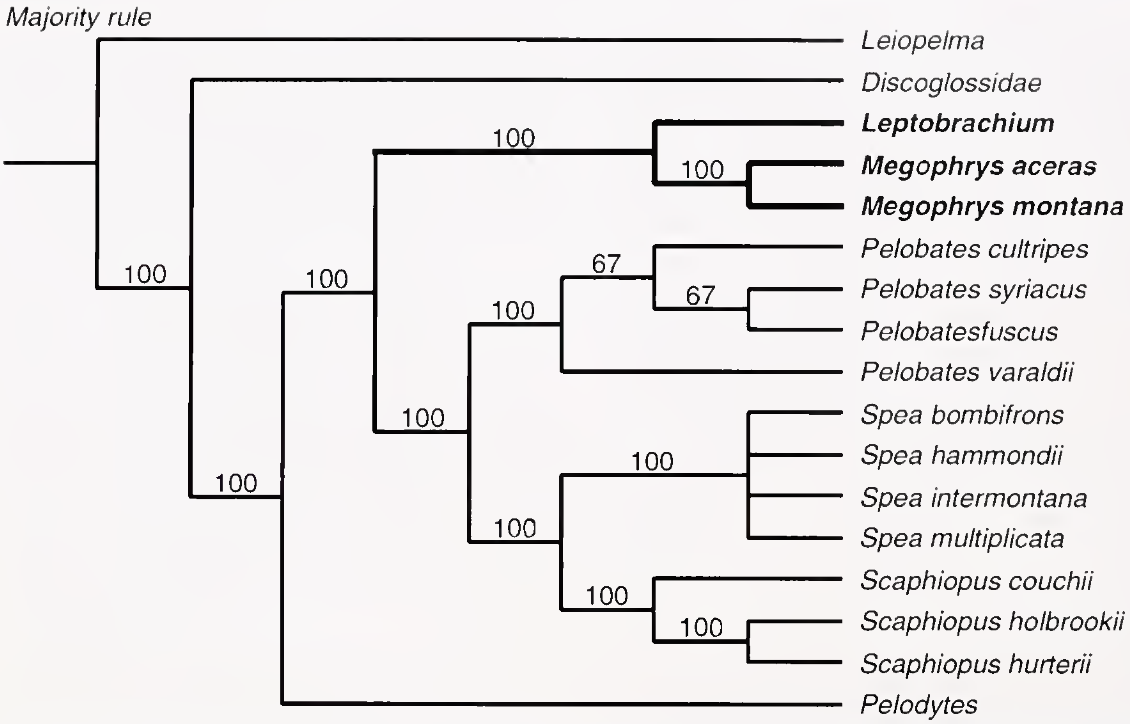

Figure 1. Majority rule consensus tree depicting the relationships of Pelobatoidea. In this phylogeny, *Megophrys* is monophyletic and multiple trees result from the ambiguous relationships of *Pelobates.* The clade, Megophryidae is bolded.

tional genus, *Oreolalax*, erected by Myers and Leviton (1962) to represent Chinese *Scutiger*-like forms that possess maxillary teeth. Recently, Fei and Ye (1989) provided additional evidence to distinguish *Oreolalax* from *Scutiger*, and this motion has been followed by some authors (Fu and Murphy, in press; Wu et al., 1993; Guan-Fu et al., 1993; Fei and Yea, 1990). Other sources do not recognize the genus *Oreolalax* (Dubois, 1979, 1986; Duellman, 1993; Frost, 1985).

Evidence of Monophyly and Outgroup Taxa

The association of megophryids with pelobatids and *Pelodytes* (= Pelobatoidea of Cannatella, 1985) has gone largely unchallenged through the history of anuran taxonomy. Previously recognized as Pelobatidae (authors prior to 1973) or Pelobatidae plus Pelodytidae (Lynch, 1973), the group is supported by several synapomorphies (Table 1).

Although DCC was fairly confident about the definitive synapomorphies of the Pelobatoidea, the monophyletic nature of megophryids does not remain incontestable. The results published in his thesis list ten synapomorphies for the group; four are reversals to the plesiomorphic condition, four represent convergences with other anuran groups, and two were considered to be uniquely derived: loss of most of the hyale of the hyoid and an ossified episternum. For unknown reasons, the latter character was not included as a synapomorphy by Ford and Cannatella (1993).

Among the 83 species of megophryids, DCC included only three species from two of the six genera. He reported that "relationships within the megophyrines are poorly defined . . . because few taxa were available to study" (p 275). He went on to say that his results suggest that *Megophrys* was paraphyletic with the single species of *Leptobrachium* used in his analysis; this was defined by a single character (the articulation of the sacrum and the coccyx). The character was said to be a reversal to the plesiomorphic condition in one species of *Megophrys*. Coding of this character is ambiguous at best, the character state is probably not homologous to the primitive condition found in discoglossids and *Ascaphus*. Cannatella alluded to this problem in his section on character analysis (p. 127).

Because the results of DCC's analysis have brought into question the monophyly of *Megophrys*, I re-investigated the issue.

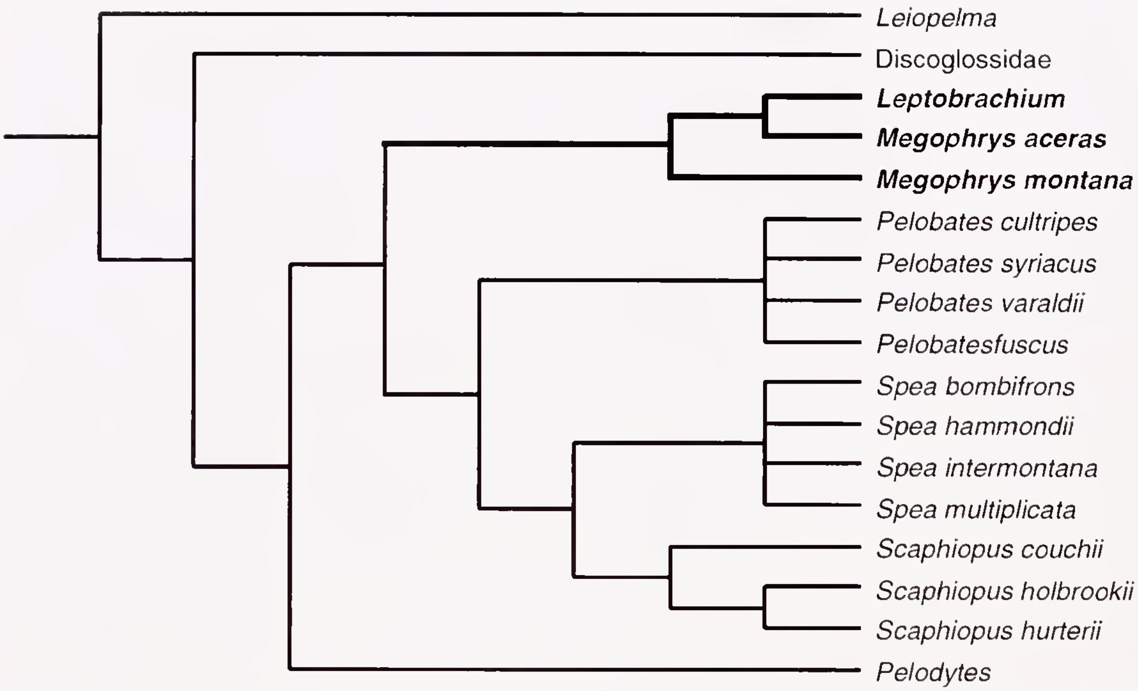

Figure 2. Phylogeny of Pelobatoidea. The relationships of *Pelobates* is unresolved. The character UROSACRM when evaluated as ordered with its original four states (Cannatella, 1985) constrains *Megophrys* to be paraphyletic with *Leptobrachium*. The clade, Megophryidae is bolded.

Materials and Methods

I examined the data set of Cannatella (1985) in order to understand the evolution of the morphological character within pelobatoids. My evaluation of the taxa in the clade Pelobatoidea (viz. *Leptobrachium*, *Megophrys*, *Pelobates*, *Pelodytes*, *Scaphiopus*, and *Spea*) included 43 of 181 characters for 17 of 42 taxa of archaeobatrachians. Two characters associated with the stapes: COLUMEL1 (0, absent; 1, present; 2, greatly elongated) and COLUMEL2 (0, normal size; 1, reduced) were combined to removed inapplicable character states. The character COLUMEL was coded as follows (0, absent; 1, present, normal, extending entire length of ear cavity; 2, greatly elongated; 3, reduced). Uninformative characters at this level of the analysis were removed; of the 181 characters, 137 characters were not informative in the analysis of Pelobatoidea (Appendix 1). Phylogenetic analyses were performed using Swofford's (1993) Phylogenetic Analysis Using Parsimony program (PAUP). A heuristic search was performed using simple stepwise addition only minimal trees were retained and trees were constructed using branch swapping option of tree bisection-reconnection, steepest descent, and holding all most parsimonious trees. Characters were ordered and polarized by outgroup comparison (Watrous and Wheeler, 1981) using the outgroup *Discoglossus*, the sister species of the clade Pelobatoidea, and *Leiopelma* as a secondary outgroup.

Results

Three most parsimonious trees (MPTs) were resolved when the data were run as unordered (65 steps; CI = .723; RI = .860; Fig. 1). In all cases, *Megophrys* was monophyletic, with *Leptobrachium* as its sister group. Differences among the MPTs occurred within the clade of *Pelobates*. Character states for *Pelobates* were invariant, except for the COLUMELLA and the CRICOID, both of which were autapomorphic for *P. veraldii* and *P. fuscus*, respectively. These autoapomorphies were responsible for the differing topologies among *Pelobates*. When all the characters were treated as ordered, as in the DCC analysis, six MPTs were resolved, each 73 steps long (CI = .699; RI = .850). Three of trees were identical to those in the unordered analysis (Fig. 1). Among the other three topologies, *Megophrys* is paraphyletic with *Leptobrachium*, and the relationships of Pelobates were not resolved (Fig. 2).

One character used by DCC was the articulation of the sacrum and the coccyx (UROSACRM). DCC had doubts about the polarity and homology of this character. Although similar in configuration, he questioned whether the condition in *Megophrys montana* was homologous to that of *Leiopelma*. Cannatella coded this character as homologous, but with reservation. When the character was either left unordered or removed completely from the analysis, *Megophrys* was resolved as a monophyletic group and the resulting three topologies were identical to those Fig. 1.

If the articulation of the sacrum in *Megophrys montana* is not homologous to that of *Leiopelma*, and different from that seen in *Megophrys aceras*, then 5 character states are required to describe the variation in UROSACRM, rather than the original 4 states as in DCC. When UROSACRM was coded as five ordered or unordered character states (Appendix 1) the analysis resulted in three trees identical to those of the previous unordered analysis of the original data set (ordered = 73 steps; CI = .712; RI = .854; unordered = 66 steps; CI = .727; RI = .859).

Discussion

DCC's phylogeny depicts the two species of *Megophrys* as paraphyletic with respect to *Leptobrachium*. However, my re-analysis demonstrates that there is an alternative arrangement in which *Megophrys* is monophyletic. The condition of the UROSACRUM (e.g., syncondrotic or synovial, monocondylar or bicondylar) has been used as a diagnostic character for some groups of anurans (Nicholls, 1916; Griffiths, 1963; Lynch, 1973; Cannatella, 1985; Ford, 1989) and avoided by others (Duellman and Trueb, 1986). Noble (1922) cautioned against its utility as a diagnostic character for pelobatids (Megophryidae, Pelobatidae, and Pelodytidae). Furthermore, within the Megophryidae, specifically *Megophrys*, there has been several reports of variation in the urosacral fusion (Kluge, 1966). Thus, because UROSACRM has the ability to make *Megophrys* paraphyletic, the articulation of the coccyx to the sacrum must be examined more closely to determine its true homology.

Wiens (1989) illustrated the difference in development between a fused bicondylar articulation and one that is not fused, and suggested that these arrangements may have arisen via several different developmental pathways. What appears to be two different conditions in the Megophryidae—sacrum and urostyle separate; joint synchondrotic in *Megophrys montana* and *Leptobrachium hasseltii*; sacral fusion in *Megophrys aceras*— may have been formed from two very similar developmental pathways. Ontogenetic studies of the formation of the sacrum and the coccyx may reveal homologous states that would not be identified by examining just the adult condition.

The systematics of megophryids is poorly understood. Our ideas of the relationships within the family have not changed much since Noble's (1926) evolutionary hypothesis. Without a comprehensive phylogenetic hypothesis from which we can base a classification, the resulting taxonomy will likely prove to be unstable; it may include paraphyletic groupings. Although Dubois (1980) constructed a classification to serve as a starting point for future studies, his conservative scheme is not based on a phylogeny, but primarily on phenetic clusterings without regard for evolution of the characters.

To understand the relationships between the genera of Megophryidae, and the placement of megophryids within the pelobatoids, a thorough phylogenetic analysis of the family is necessary. This analysis should be performed in a similar manner as Cannatella's (1985) study, and the classification should be derived directly from the phylogeny (Wiley, 1981). Employing a phylogenetic classification would ensure that the taxonomy was consistent, functional, and maximized information content. In this way, the knowledge that is gained from this interesting group of frogs will produce a useful classification that clearly reflects the evolutionary paths of each species.

Acknowledgments

I am grateful to J. P. Bogart, for his loan of literature on short notice. R. MacCulloch helped translate the French. J. Fu translated, discussed, and clarified much of the Chinese literature that would still continue to be a mystery to me. C. Huang was kind enough to allow me to use her draft translation of Fei et al.,'s (1991) *Key to Amphibians of China*. I am grateful to S. Monks, R. Murphy, and D. Upton for their helpful suggestions which have improved the quality of this paper. This study was supported by the Natural Sciences and Engineering Research Council (NSERC) of Canada Grant A3148 awarded to R. W. Murphy. This is contribution XXX from the Centre for Biodiversity and Conservation Biology of the Royal Ontario Museum.

Appendix I

Data matrix of characters from Cannatella (1985) to include only Pelobatoidae and the outgroup taxa, Leiopelma and Discoglossus. (A) Leiopelma, (B) Discoglossus pictus, (C) Leptobrachium, (D) Megophrys aceras, (E) M. montana, (F) Pelobates cultripes, (G) P. syriacus, (H) P. varaldii, (I) P. fuscus, (J) Spea bomifrons, (K) S. hammondii, (L) S. intermontana, (M) S. multiplicata, (N) Scaphiopus couchii, (O) S. holbrookii, (P) S. hurterii, (Q) Pelodaytes punctatus. See original work (Cannatella, 1985) for character coding.

characters	taxa																
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
ADDLONG	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1
ALHYOID1	0	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
ALHYOID3	0	0	?	?	?	1	1	1	1	1	1	1	1	1	1	1	1
ANALGLND	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0
COLUMEL	0	1	1	1	1	?	3	1	3	1	1	1	1	1	1	1	1
CRICOID	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0
DEPRMAN2	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
EPIPUBIS	0	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
EXOSTOS	0	0	0	0	0	1	1	1	1	0	0	0	0	1	1	1	0
FPFONT	0	0	1	1	1	1	1	1	1	0	0	0	0	1	1	1	0
FPFUSION	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0
FREERIBS	0	0	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
GRACMIN3	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
GRACMIN4	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
HUMHEAD	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
HYALE	0	0	2	2	2	1	1	1	1	1	1	1	1	1	1	1	1
HYOGLSN2	0	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1
ISCHCUTA	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
LENSCAP	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
NASAL2	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1
PARAHYD1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
PECTGLND	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
PIRIFORM	0	0	0	0	0	2	2	2	2	0	0	0	0	0	0	0	0
PREACET	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
PREZON2	0	1	2	2	2	1	1	1	1	1	1	1	1	1	1	1	1
QUADRAT1	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1
SARTSEM3	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0
SEPNAS	0	0	0	0	0	2	2	2	2	2	2	2	2	2	2	2	0
SPADTUB1	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0
SPADTUB2	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0
STERNOSS	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1
STERNSH	1	1	?	?	?	?	?	?	?	0	0	0	0	0	0	0	?
SUPFLFP	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
TORSION	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
TPRODIRP	0	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
TYPE4TAD	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

(Continued)

characters	**taxa**																
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
UROSACRM	0	2	0	3	4[a]	3	3	3	3	3	3	3	3	3	3	3	1
VOCSAC	0	0	1	1	1	0	0	0	0	1	1	1	1	1	1	1	1
VOMER3	0	1	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1
VOMER4	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0
ZYPROSQ3	0	1	0	0	0	1	1	1	1	0	0	0	0	1	1	1	0

a. UROSACRM is coded as 0 in Cannatella (1985).

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