

NOTES ON THE GENUS *BOMBINA* OKEN  
(Anura: Bombinatoridae):  
III. ANATOMY, SYSTEMATICS, HYBRIDIZATION  
FOSSIL RECORD AND BIOGEOGRAPHY

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INTRODUCTION

This paper represents the last portion in a three-part series of papers summarizing pertinent information available on *Bombina*. Overall the series synthesizes information on distribution and characteristics of recognized species of *Bombina*, together with aspects of external appearances, morphology, life history, systematics and taxonomy. This paper focusses on aspects of anatomy, systematics, hybridization, fossil record and biogeography of *Bombina*.

ANATOMY

**Embryology**

Ossification in *orientalis* commences as early as Gosner Stage 37 (hind limbs with all five toes distinct), but the full complement of adult bones is not attained until Stage 46 (metamorphosis complete) (Hanken and Hall, 1984). The number of bones present at intermediate stages is poorly correlated with external morphology. The modal ossification sequence as presented by Hanken and Hall (1984) is as follows: frontoparietal, exoccipital, parasphenoid, septomaxilla, premaxilla, vomer, nasal, maxilla, angulosplenic, dentary, squamosal, quadratojugal, pterygoid, prootic, (interfrontal), sphenethmoid and mentomeckelian.

Embryonic stages and timing of development of *orientalis* has been investigated by Sussman and Betz (1978). *Bombina orientalis* is the only species of this genus that has an interfrontal bone (Tschugunova, 1981).

Pedicellate teeth are present in *bombina* and *maxima*. In *B. variegata* there is no clear division crown and pedicel (Parsons and Williams, 1962; Viertel, 1986). Vomerine teeth are situated slightly posteriorly to the inner nasal openings and arranged in two short rows and are distinctly pedicellate (Viertel, 1986). Marginal and vomerine teeth are bicuspid (see Viertel, 1986 for illustration).

De Villiers (1922) investigated and described in detail the structure and development of the pectoral girdle of *Bombina variegata*. The episternum develops relatively late during postmetamorphosis. The cleithrum develops from the cutis bordering the suprascapular, and the clavicle develops between the epidermis and the procoracoid. The omosternum fails to develop.

**Larval morphology**

Larval mouthparts of European *Bombina* are illustrated by Engelmann *et al.* (1985). *Bombina bombina* has a triangular upper lip, with three rows of denticles on the lower lip that are sometimes interrupted at the midline. In *variegata* the upper lip is semicircular, and the lower lip has three rows of denticles rarely interrupted at the midline.

The dorsal tail fin in larvae may (*bombina*) or may not (*variegata*) reach the middle of the dorsum. Tadpoles have a black reticulation on the tail. The spiracle is situated more closely to the anus than the mouth. Additional detailed descriptions of the tadpoles of the European *Bombina* can be found in Michalowski (1966) and Lanza (1983).

The tadpoles of *Bombina* have six short gill-filaments developed on a single large fleshy base. The tail crest is strongly developed in the stream breeders and reaches the nuchal region.

### Skeletal anatomy

The cranial anatomy of *Bombina variegata* has been described extensively by Slabbert (1945). Following is a summary of some of the findings. The olfactory capsule has a well-developed lateral wall; the medial nasal gland lies extra-capsular; the premaxilla lacks palatal squames; palatine entirely absent; frontoparietals are separated anteriorly by a wide stretch of connective tissue; the side walls of the cranial cavity in the orbital region are mainly membranous; three foramina acustica are present; the hyomandibular branch of the facial nerve passes through a narrow cranio-quadrate passage; the pseudobasal process articulates with a pointed ventral ledge of the otic capsule and the jaw suspension is autostylic; the sound conducting apparatus is reduced, with only the operculum being present (this perhaps in association with lack of vocal sacs); cornu hyale confluent with otic capsule; and the mentomeckelian is the only ossification of the Meckel's cartilage, which forms a synostosis with the dentary.

Böhme (1977) lists postcranial characteristics such as the presence of opisthocoeleous vertebrae with free ribs; a slightly dilated sacrum, that can be quite variable (Madej, 1965); a free urostyle with lateral apophyses and a pars ascendens ilii that is less pronounced than the pars descendens ilii. The latter character is used to distinguish *Bombina* and European discoglossids (*Alytes* & *Discoglossus*) from other European Anurans (Böhme, 1977). A vexillum (= dorsal fin on pubic ala) is absent in *Bombina*. The sacrum of *Bombina* has a single condyle that articulates with the presacral vertebra.

### Karyotypes

*Bombina bombina* and *B. variegata* show a strictly corresponding diploid set of 12 chromosome pairs for both sexes (Moreschalehi, 1965, 1971; Ullerich, 1970; Popov, 1983). The diploid number of *orientalis* is also 24 (Sato, 1938). There are six large, one medium, and five small pairs of chromosomes. All chromosomes are metacentric, except the sixth pair which is submetacentric. A secondary constriction is observed on the long arm of the seventh and the short arm of the eighth chromosome. No heteromorphic chromosome was found (Jiang *et al.*, 1984).

## SYSTEMATICS

The taxonomy and systematics of *Bombina* is quite confusing. Sokol (1975, 1977) erected the suborder Discoglossoidae as a clade for the Leiopelmatidae (*Ascaphus* and *Leiopelma*) and Discoglossidae (*Alytes*, *Barbourula*, *Bombina*, and *Discoglossus*). The fusion of the copula to the hypobranchials, and the partially adherent anterior filter valves are two derived features of the larvae (Type 3) in support of the monophyly of this taxon. The latter character is also present in pipoid and microhylid larvae (Sokol, 1975). Dubois (1983) resurrected the subfamily Bombinatorinae Gray within Discoglossidae to include *Alytes*, *Bombina* and *Bombinator*. Tian and Hu (1985) furthermore suggest the subdivision of *Bombina* into the subgenera *Bombina*, containing the Palearctic *bombina*, *variegata* and *orientalis*, and the Oriental *Glandula* containing *maxima*, *microdeladigitata* and *fortinuptialis*. This division was based on the presence of small, regular and evenly spaced warts in the *Bombina*-group, whereas these dorsal warts are irregular and unevenly spaced in *Glandula*-group; the absence of a parotid gland in the *Bombina*-group; the presence of black spines on the chest of males in the *Glandula*-group; and the Palearctic distribution of the *Bombina*-group versus the Oriental distribution of the *Bombina*-group.

Maxson and Szymura (1984) using micro-complement fixation showed that *Bombina* and *Discoglossus* shared a common lineage, separate from *Alytes* and *Baleaphryne*. These findings do not support Lanza *et al.*'s (1975, 1976) differentiation of Discoglossidae into two separate families: Discoglossidae (*Discoglossus*) and Bombinidae (*Bombina* and *Alytes*). The latter study was based on qualitative serological studies of serum proteins and *Barbourula* was not tested.

Olmo *et al.* (1982) could not resolve relationships within Discoglossidae because the karyotype and genome of *Discoglossus*, *Alytes* and *Bombina* are so heterogeneous and different from each other.

Cannatella (1985), showed the "Discoglossidae" to be paraphyletic, and correctly infers that the aforementioned biological estimates hinge on the underlying assumptions that the Discoglossidae (*sensu* Griffiths, 1963) was monophyletic. The possibility that some genera may be more closely related to other anurans was not tested. *Alytes* and *Discoglossus* are each

others' closest relatives and are more closely related to other frogs than they are to *Bombina* and *Barbourula*. Cannatella (1985) therefore established the family Bombinatoridae to include *Bombina* and *Barbourula*. The presence of an unusual flange on the quadratojugal and paired ossifications of the hyoid plate are unique derived characters in support of the monophyly of Bombinatoridae (Cannatella, 1985).

*Bombina* itself has two unique apomorphies that support its monophyly. In all species of *Bombina* the anterior ramus of the pterygoid extends forward, curving medially to invest the posterior margin of the planum antorbitale. The otic ramus of the squamosal is present and well-developed in all frogs except in *Bombina* in which it is greatly reduced (Cannatella, 1985).

Within *Bombina* the relationships have not been fully worked out. Mertens (1928) suggests that *orientalis* descended from *bombina* and *maxima* from *variegata*. Terent'ev (1949) in contrast using biometrical data indicated that *orientalis* was derived from *maxima*. Using colouration patterns Stugren (1966) opts for the notion that *orientalis* and *variegata* are more closely related to one another than either is to *bombina*. Maxson and Szymura (1979) compared *bombina*, *orientalis*, and *variegata* immunologically and discussed relationships between these three species, with *bombina* and *variegata* being each others' closest relatives. This is further supported by the genetic similarity of these two species (Szymura and Farana, 1978). Schneider *et al.* (1986) suggest that the mating call of *orientalis* is close to that of *variegata* and that the parameters of the mating call of *bombina* suggests no relationship to either *variegata* or *orientalis* further supporting Stugren's (1966) hypothesis. Tian and Wu (1981) in the original type description of *fortinuptialis* indicate that this species is related to *microdeladigitora*. This is in contrast to the original type description of *microdeladigitora* (Liu and Hu, 1961), in which the authors indicate a relationship with *maxima*<sup>1</sup>.

## HYBRIDIZATION

Natural hybrids of European *Bombina* have been known for quite some time (Mehely, 1905). Stable hybrid zones are identified in Poland (rather narrow zone through allopatric hybridization, Szymura, 1976; Szymura and Barton, 1986), in Czechoslovakia (Lac, 1961), in Lower Austria (zone of allopatric hybridization, Gollman, 1984) and in Yugoslavia (sympatric hybridization, Szymura, 1981; Gollman, 1986). Descriptions and characteristics of hybrids have been extensively investigated by Michalowski (1961, 1966), Michalowski and Madej (1969) and van den Elzen (1979). Characters for field identification of hybrids are provided by Gollman (1987).

Alleles from either species predominate clearly in each of the populations within this zone, but most of the individuals found there are from hybrid origin. Hödl and Gollman (1985) have furthermore investigated the bio-acoustics of these hybrid populations.

Rachmel (1974) reports on successful hybridization between *B. variegata* and *B. orientalis*.

## FOSSIL RECORD

Fossil *Bombina* are known from the Lower Miocene of West Germany (Sanchiz and Schleich, 1986); the Middle Miocene of Poland (Mlynarski *et al.*, 1982); the Upper Pliocene of Central Poland (Mlynarski *et al.*, 1982; Sanchiz and Mlynarski, 1979); the Upper Pliocene-Lower Pleistocene of Czechoslovakia (Hodrova, 1981, 1985; Sanchiz and Szyndlar, 1984); and the Lower Pleistocene of Italy (Vergnaud-Grazziny, 1970).

## BIOGEOGRAPHY

Stejneger (1907) indicated that *Bombina* originated from South Eastern Asia and dispersed northward and into Europe. Mertens (1928) proposes the late Tertiary as the timing of this European dispersal. This is in contrast to the European origin of *Bombina*, with subsequent dispersal into Asia as proposed by Friant (1960).

Mertens (1928) (further refined by Madej, 1964 and Arntzen, 1978) discuss the vicariant effect of one or more Pleistocene glaciations on the migration of *bombina* and *variegata* in Europe. Glaciation split the European stock into a western lineage (*variegata*) and an eastern lineage

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<sup>1</sup> It should be noted that *fortinuptialis* was described later than *microdeladigitora*.

(*bombina*). *Bombina variegata* sought refuge on mountain tops and differentiated, but was also pushed towards southern Europe, whereas *B. bombina* remained a lowland force. In the contact zone between these two species (see above), enclaves of *variegata* are found on mountain tops. The mountain refugia are hypothesized to have arisen because of the northward postglacial advances of *bombina* that has superseded *variegata* in the surrounding lowlands in a process of hybridization and competition. Present day *bombina* is restricted to areas below 250m. Szymura (1983) using Nei's genetic distance between Polish *bombina* and *variegata*, suggests a Pliocene separation of these species. The Pliocene divergence proposed by Szymura (1983) is earlier than the Pleistocene separation as proposed by Mertens (1928) and Arntzen (1978).

Pracht (1987) furthermore indicates that the speciation between the two European *Bombina* is not complete as evidenced by the hybridization in the postglacial contact zones (see above).

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