

outgroup comparison, it would be interesting to find pleurodont tooth attachment in the hatchling second and third generation teeth. Such was not the case, however, except perhaps for the premaxillary teeth (of which there are three on each side), where the distinction of pleurodony and acrodony becomes somewhat blurred.

Harrison (1901, 1901-1902) noted a variable and vestigial vomerine dentition, starting its development towards the end of the incubation period. In the hatchling here described, one single vomerine tooth could be observed on the left element, none on the right bone. The maxillary and dentary show the typical second and third generation dentition as described by Harrison (1901, 1901-1902), with teeth of alternating size following the two anteriormost teeth. The smaller teeth are positioned slightly laterally (labially) of the larger teeth and show signs of erosion at their base providing space for the accommodation of the larger teeth as these move up in a linguo-labial (medio-lateral) direction to line up in between the smaller teeth. The posteroventral base of the larger teeth typically overlap the anteroventral base of the following smaller tooth at this early stage of development. This confirms the conclusion drawn by Harrison (1901) and Edmund (1960) that the teeth of alternating size represent two different generations, with the smaller teeth representing the second, the larger teeth representing the third generation. Whiteside (1986) reached an opposite conclusion based on fully developed fossil material, conveying the impression that the smaller teeth are positioned lingually with reference to the larger teeth.

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Inguinal Amplexus in *Bufo fastidiosus*, with Comments on the Systematics of Bufonid Frogs

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The mode of amplexus in frogs has been accorded systematic significance by many workers (e.g., Noble, 1931; Laurent, 1967; Lynch, 1973; Nussbaum, 1980; Duellman and Trueb, 1986). All so-called "primitive" frogs exhibit inguinal amplexus, while most of the so-called "advanced" frogs exhibit axillary amplexus. Consequently, axillary amplexus is considered the derived mode of amplexus among frogs (Lynch, 1973; Duellman and Trueb, 1986). In this paper we report the discovery of inguinal amplexus in a neobatrachian frog, *Bufo fastidiosus*, and comment on the systematics of bufonid frogs.

Inguinal amplexus in bufonids was first reported in the neotropical species *Bufo holdridgei* by Novak and Robinson (1975), who made no comment on the systematic significance of that finding. Subsequently, Ruiz-Carranza and Hernandez-Camacho (1976) named a new genus, *Osornophryne*, to include two species (one new species and the species formerly known as *Atelopus bufoniformis*), both characterized by inguinal amplexus. Apparently unaware of the paper by Novak and Robinson, Ruiz-Carranza and Hernandez-Camacho stated that theirs was the only report of inguinal amplexus in bufonids. Since the original description of *Osornophryne*, three additional species have been discovered, but the mode of amplexus in these species is unknown (Cannatella, 1986; Hoogmoed, 1987). Among all other bufonids, inguinal amplexus has been reported only in two species of the African genus *Nectophrynoidea*, in which the posture differs from that seen in other frogs exhibiting inguinal amplexus in that the male and female are positioned belly to belly (Grandison, 1978; Grandison and Ashe, 1983).

Observations of live *Bufo fastidiosus* led to the discovery that this species also has inguinal amplexus. *Bufo fastidiosus* is restricted to the Atlantic slopes of the Cordillera de Talamanca-Chiriquí of southeastern Costa Rica and western Panamá (Savage, 1972; Frost, 1985). Eleven specimens were collected in woods alongside Río Cotón, approximately two km east/southeast of Las Tablas, Zona Protectora La Amistad, Prov. Puntarenas, Costa Rica, on August 12, 1990 (MVZ 217436-217439; CAS 178160-1; and five donated to University of Costa Rica). The vegetation is classified as Lower Montane Rain Forest (Holdridge et al., 1971). The toads were common on the forest floor and under fallen logs.

Upon capture, specimens of *Bufo fastidiosus* were maintained in plastic bags. Several days after collection, we observed a male and female in inguinal amplexus (Fig. 1). The male clasped the female around her pelvic region and rested his feet on her thighs. The pair maintained this position for several hours and did not break their clasp when handled or photographed. Toads both in and out of amplexus also exhibited a posture in which all four feet were planted, the pelvic region was elevated and the head was lowered. A similar posture has been documented in many other amphibian taxa and is presumably defensive (see Noble, 1931). The amplexic and defensive behaviors we observed in *B. fastidiosus* are similar to those exhibited by a pair of *Osornophryne percassa* (Ruiz-Carranza and Hernandez-Camacho, 1976, Fig. 13).

The adaptive and phylogenetic significance of different modes of amplexus within Bufonidae are



FIG. 1. Pair of *Bufo fastidiosus* in inguinal amplexus. Note that the male's feet are resting on the female's thighs.

unknown. Ruiz-Carranza and Hernandez-Camacho (1976) believed that inguinal amplexus in *Osornophryne* represented persistence of the ancestral anuran condition. By contrast, Hoogmoed (1987) suggested that inguinal amplexus in *Osornophryne* is secondarily derived and forms a stage in the evolution of internal fertilization. Hoogmoed's (1987:221) ideas are based on the presence of what he described as a "cloacal tube which curves around the back of the thighs and opens ventrally" in *Osornophryne antisana* and *O. talipes*. Although the mode of amplexus in these two species is unknown, Hoogmoed suggested that, because other *Osornophryne* have inguinal amplexus, these species may also. He postulated that both the cloacal tube and inguinal amplexus evolved in *Osornophryne* in order to bring the male's vent closer to the female's and thus facilitate internal fertilization. No obvious cloacal tube is present in *B. fastidiosus* or *B. holdridgei*.

Use of amplexus as a character relevant to the systematics of bufonids necessitates a decision about its polarity. The possibilities are: (1) inguinal amplexus is the ancestral condition for Bufonidae, in which case, barring parallelism, the four species known to have inguinal amplexus are outside of a clade formed by the rest of the bufonids; or, (2) inguinal amplexus is derived within Bufonidae, in which case, again

barring parallelism, it may be a synapomorphy providing evidence of a close relationship among certain species. According to Lynch (1973) and Duellman and Trueb (1986), Bufonidae is a monophyletic taxon and part of a larger clade whose most recent common ancestor is inferred to have exhibited axillary amplexus. Thus, inguinal amplexus in bufonids appears to be secondarily derived. This conclusion is supported by details of the posture itself. In *Bufo fastidiosus* the male rests his feet on the thighs of the female in a manner similar to that seen in many species exhibiting axillary amplexus (e.g., Wright, 1932, Pl. 4 and 5; Grandison and Ashe, 1983). That posture differs from what is seen in many species retaining ancestral inguinal amplexus, in which the male's feet do not rest on the female's thighs but instead follow behind her legs (e.g., Rabb, 1973, Figs. 5-5, 5-6, and 5-7; Nussbaum, 1980, Figs. 1 and 2; and Nussbaum et al., 1983, Fig. 28).

The discovery of inguinal amplexus in *Bufo fastidiosus* bears on its phylogenetic relationships. Taylor (1952) stated that *B. fastidiosus* is related to *B. bocourti* and *B. simus*, although he further stated that *B. holdridgei* is presumably related to *B. fastidiosus*. Savage (1972) showed that the types of *Bufo simus* were mislabeled, and named a new species, *Bufo peripatetes*, to include the one adult male toad previously referred to *B. simus* by Taylor (1951). Savage (1972) concluded that *B. peripatetes* is closely related to *B. fastidiosus* and *B. holdridgei*.

The occurrence of inguinal amplexus in both *Bufo holdridgei* and *B. fastidiosus* supports previous suggestions that these species are closely related. Furthermore, the relationship of those species to *Osornophryne* merits consideration. *Bufo fastidiosus* shares several characters with *Osornophryne* that appear to be derived within Bufonidae: the complete absence of ear elements (tympanum, columella, ostia pharyngea, and vocal slits); co-ossification of the skull and overlying skin; absence of an adductor longus thigh muscle (contra Savage, 1972); and inguinal amplexus. In other characters, however, *B. fastidiosus* retains what appear to be ancestral states relative to presumably derived states found in *Osornophryne*: presence of the alary process of the hyoid plate (=hypobranchial 1); 8 presacral vertebrae; unreduced phalangeal formulae (hand 2-2-3-3; foot 2-2-3-4-3); arciferal pectoral girdle; and a short tensor fascia latae muscle. Because *B. fastidiosus* retains these presumably ancestral states, it seems inappropriate to extend the concept of *Osornophryne* to include *B. fastidiosus*. Nonetheless, both amplexus and morphology suggest that *B. fastidiosus* (and possibly *B. holdridgei*) may be more closely related to *Osornophryne* than to other species of *Bufo*.

Evidence suggesting a close relationship between *B. fastidiosus* and *Osornophryne* indicates that *Bufo* may not be a monophyletic taxon. That possibility has been suggested by previous authors (e.g., Maxson, 1984; Lynch and Renjifo, 1990), and stems primarily from the manner in which taxa have been conceptualized. Instead of first analyzing the phylogenetic relationships among species and then organizing higher taxa accordingly, genera have been defined on the basis of unique combinations of characters deemed necessary and sufficient for taxon membership. *Bufo* has become the "default" genus of the family in that it is characterized by the absence of the various derived

characters that separate the other genera from it (Lynch and Renjifo, 1990). Future work on the systematics of Bufonidae should avoid treating *Bufo* as a unitary taxon, focusing instead on the relationships of its component species both to one another and to the other bufonid genera.

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Foraging Success of Leopard Frogs (*Rana pipiens*)

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Observations of foraging behavior under natural conditions have been made for a number of lizard species (Huey et al., 1983), but only rarely for anurans (Heatwole and Heatwole, 1968; Hedeon, 1972; Strüssmann et al., 1984). In addition to their largely nocturnal foraging habits, most frogs forage solitarily, making data collection difficult. Consequently, aside from inferences made from studies of diet choice (e.g., Toft, 1980), little is known about the foraging behavior of most anurans. The aim of the present study is to relate the foraging success of leopard frogs, *Rana pipiens*, to the presence of conspecific neighbors and to the distance travelled during foraging bouts.

Data were collected from 9-14 July 1980 at Itasca State Park, Minnesota. Frogs were observed foraging for common tortoise shell butterflies (*Nymphalis j-album*) along a wet, 10 m edge of dirt road bordering a small marsh. I made observations from a concealed position, 10-12 m away from the foraging area. Binoculars were used occasionally to follow the movements of foraging frogs. To estimate (to nearest 10 cm) distance travelled during capture attempts and nearest neighbor distances, I placed numbered,

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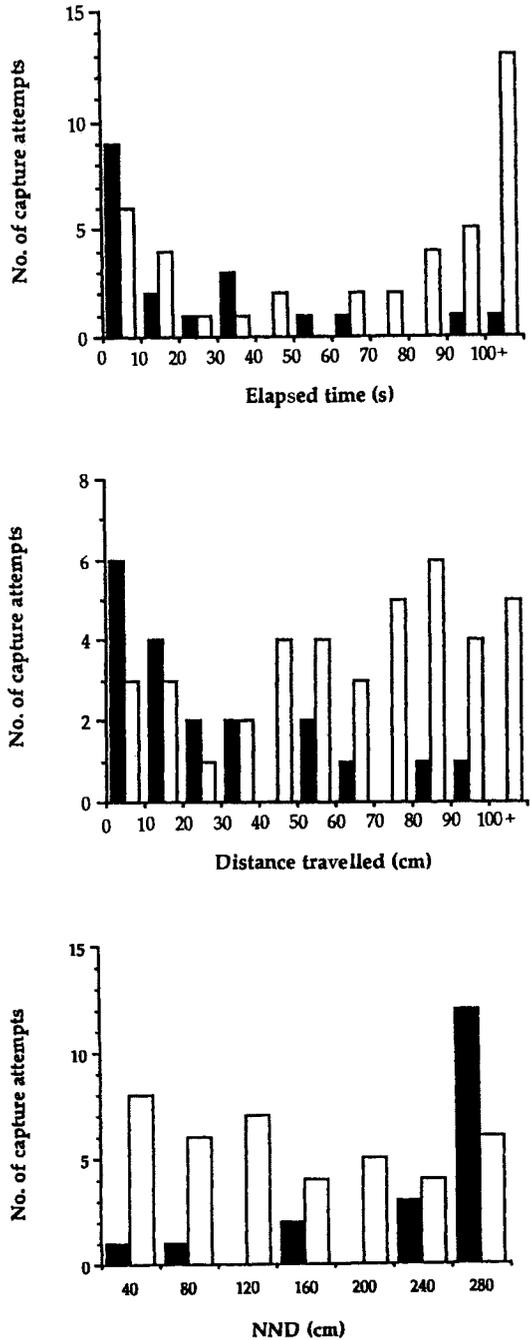


FIG. 1. The number of successful (solid rectangles) and unsuccessful (open rectangles) *Rana pipiens* capture attempts relative to: (A) the time elapsed during the foraging bout; (B) the distance travelled during the foraging bout; and (C) the nearest neighbor distance (NND) during the capture attempt. Elapsed times and distances were lumped into the intervals depicted on each x-axis.

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