

ending copulation. The male then moved away from the female.

Gillingham (1974, 1979) emphasized that the high probabilities of toward-jerking and coital neck-bite are species-specific releasing mechanisms in *Elaphe*. Maybe the head-rubbing can be a species-specific releasing mechanism in *H. gigas*. My finding points out the need of further studies of behavioral sequences concerning the courtship among this species and its species-specific releasing mechanisms.

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Cocoon Formation in Another Hylid Frog, *Smilisca baudinii*

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The skin of adult amphibians is semipermeable, and evaporative water loss is high. For species living in arid regions, this may create significant problems, which are countered with morphological, physiological, or behavioral adaptations. Such traits have been studied extensively among a variety of species, including those that live in the deserts of North America and the arid regions of Australia and South America (Bentley, 1966; Lee and Mercer, 1967; McClanahan, 1967; McClanahan et al., 1976, 1983). Frogs living in tropical dry forests face similar problems during hot, dry seasons that may last for 4 to 6 months each year. It is of interest, therefore, to report cocoon formation in *Smilisca baudinii*, a species of hylid treefrog common



FIG. 1. A mummified specimen (USNM 219741) of *Smilisca baudinii* with its cocoon in place, as discovered in Guanacaste Province, Costa Rica, in April 1977.

in dry-forest habitats in northwestern Costa Rica, to describe the nature of the covering, and to consider how such a structure may be adaptive for this species.

On 16 April 1977, Foster found a mummified frog in a road bed at Estación Experimental Enrique Jiménez Nuñez, ca. 13.6 km SW Cañas, Guanacaste Province, Costa Rica. The frog was in a thick (ca. 2 cm) layer of dry silt above a layer of hard pan in an area of disturbed tropical dry forest (Tosi, 1969). The road was located ca. 50 m from a river bed that at the time contained only a few isolated puddles. The forest and adjacent agricultural areas, and climatic conditions are described in McDiarmid and Foster (1981; and references therein). Rainfall in the region is highly seasonal with a marked dry period extending from approximately November to May. The frog was discovered near the end of the dry season, following 138 successive days without rain, according to records maintained at Estación Jiménez.

The frog was encased in a parchment-like cover that adhered to the body and limbs of the specimen (Fig. 1). After removal of the cocoon, and x-ray examination of the skeleton, we identified the frog as *Smilisca baudinii*. The limbs of the frog are tucked in close to the body, and the head is bent down; the mummy measures ca. 40 mm total length. The carcass and the cocoon are deposited in the National Museum of Natural History (USNM 219741). A small fragment cut from the dorsal region of the cocoon was examined by both light and electron microscopy following

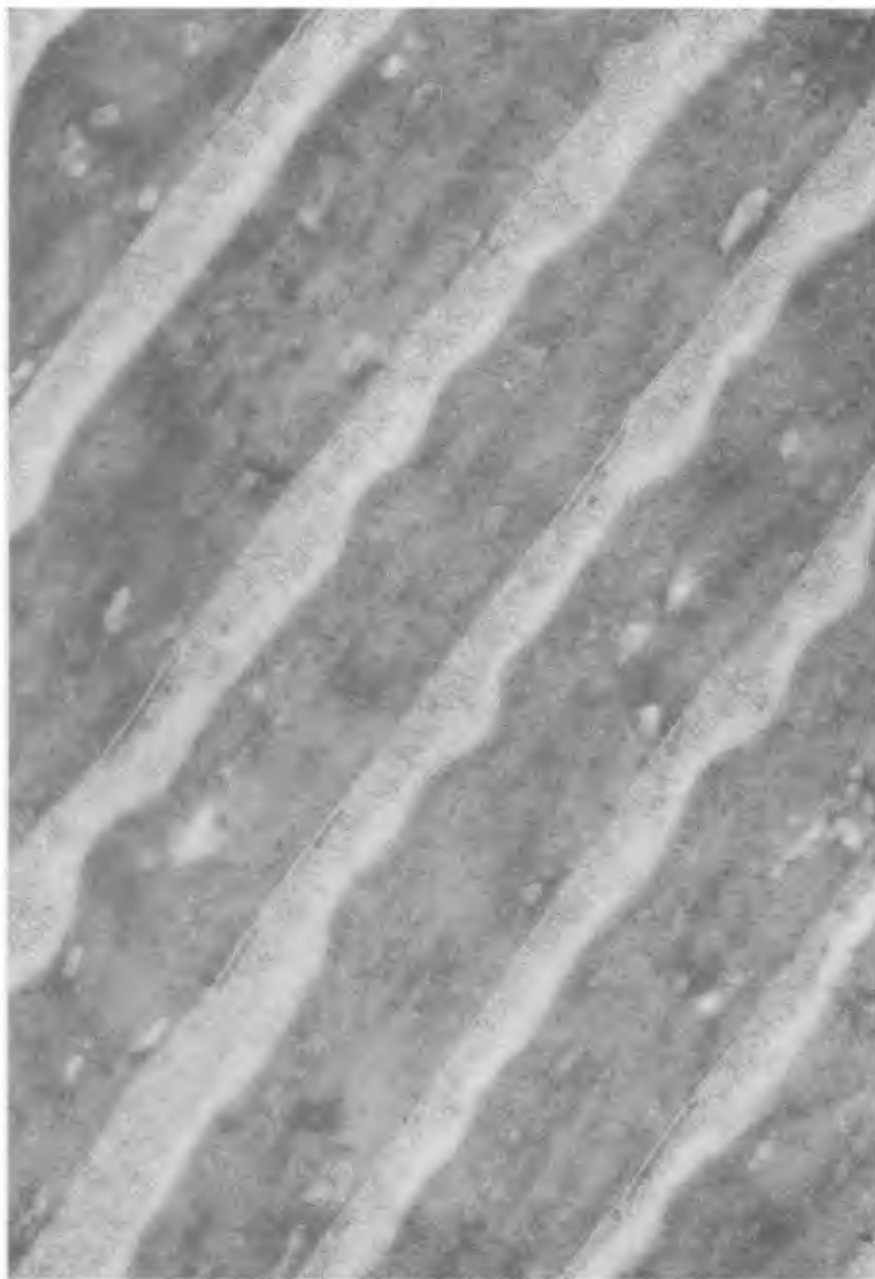


FIG. 2. Electron micrograph of a vertical section of the cocoon taken from *Smilisca baudinii*. Stratum corneum (dark layers) are separated by subcorneal spaces (light zones) filled with a mucus-like substance. (Magnification = 25,000 \times).

the procedures outlined in McClanahan et al. (1976) and Ruibal and Hillman (1981).

The cocoon from the *Smilisca baudinii* specimen is transparent and colorless, as is typical of those reported for other frog species (Table 1). It probably

covered the frog's entire body, although pieces are missing from portions of the limbs and venter in our specimen. Indentations are obvious in the regions of the eye and external nares, but we were unable to determine if the cocoon was perforated at the nostrils.

TABLE 1. Frogs known to form cocoons.

Species	Distribution	Reference
Hylidae		
<i>Pternohyla fodiens</i>	Mexico	Ruibal and Hillman, 1981
<i>Smilisca baudinii</i>	Middle America	McDiarmid and Foster, this paper
Hyperoliidae		
<i>Leptopelis bocagei</i>	Africa	Loveridge, 1976
<i>Leptopelis viridis</i>	Africa	A. Schiötz, in Loveridge, 1976
Leptodactylidae		
<i>Lepidobatrachus llanensis</i>	South America	McClanahan et al., 1976, 1983
<i>Ceratophrys ornata</i>	South America	McClanahan et al., 1976
Myobatrachidae		
<i>Limnodynastes spenceri</i>	Australia	Lee and Mercer, 1967
<i>Neobatrachus pictus</i>	Australia	Lee and Mercer, 1967
Pelodyadidae		
<i>Cyclorana australis</i>	Australia	Lee and Mercer, 1967
<i>Cyclorana platycephala</i>	Australia	Lee and Mercer, 1967
<i>Litoria alboguttata</i>	Australia	Lee and Mercer, 1967
Ranidae		
<i>Pyxicephalus adspersus</i>	Africa	McDiarmid, 1968; Parry and Cavill, 1978; Loveridge and Craye, 1979

When vertical sections of the cocoon were examined with a light microscope, 38–40 layers of stratum corneum were visible. Electron microscopy revealed typical layers of epidermal cells (dark and thick in Fig. 2) separated by subcorneal spaces filled with a mucoid-like substance (light and granular in Fig. 2). This layer formation is similar to that found in the cocoon of *Pternohyla fodiens* (Ruibal and Hillman, 1981).

Ruibal and Hillman (1981) commented that cocoon formation in *Pternohyla fodiens* was unexpected given that most hylids are arboreal. However, this species, which occupies subtropical desert and thorn scrub habitats, is fossorial, as are all other species (Table 1) for which cocoon formation is known. Most likely, the ability to form such coverings evolved independently in the various groups and, as Ruibal and Hillman have suggested (1981:405), it "... may be more widespread among estivating anurans than is currently recognized." Our report of cocoon formation in the hylid *S. baudinii* confirms this, although we do not know whether our specimen was aestivating under ground or in a tree.

Smilisca baudinii is a relatively large (males SV to 76 mm, females to 90 mm), wide-ranging frog found in xeric and subhumid habitats from southern Sonora, México, in the west, and the Rio Grande Valley of Texas in the east, south through the lowlands and foothills of México and Central America to Costa Rica (Duellman and Trueb, 1966). Breeding choruses have been reported, usually early in the wet season, from the xerophytic thorn scrub vegetation of western México to the evergreen wet forests of Caribbean lowland Costa Rica. During the dry season, individuals take refuge in tree holes, beneath bark, under outer

sheaths of banana plants, in bromeliads, and occasionally in the soil or holes in the ground (Duellman, 1970; Villa, 1972; McDiarmid, unpubl. data).

We suspect that in parts of its range, *S. baudinii* may take refuge in rodent burrows or may burrow into the ground to pass the dry season. The metatarsal tubercle of this species is larger than those of other species in the genus. Within the species, the tubercle is most pronounced in specimens from northwestern México, Tamaulipas, and the Pacific lowlands of Central America (Duellman, 1970), areas of its range with the least annual rainfall and most severe dry seasons. This frog may seek refuge in the ground more commonly in the drier areas of its range than elsewhere. McDiarmid found specimens with mud on their backs, suggesting recent emergence from the soil, at the beginning of the wet season in early July, in Sinaloa. Another specimen was located by D. E. Wilson at a depth of less than 5 cm in the soil in southern Texas in June (McDiarmid, unpubl. data). The animal did not move when handled, but remained somewhat rigid. Its body was in the same position as our mummified specimen, with the head tucked forward and the limbs held close to the body. Unfortunately, presence or absence of a cocoon was not noted. Villa (1972) reported specimens from holes in the ground and from under logs and boards. An analogous situation is found in the African frog *Leptopelis bocagei*, a species that burrows and forms a cocoon. It has a metatarsal tubercle much larger than those of its arboreal congeners, which are not known to form cocoons.

There is no reason to conclude that arboreal, as well as fossorial, species, could not form cocoons, particularly if the frogs occupy tree cavities. Hollows are

often large, and filled with leaves and other debris into which frogs could burrow for protection from desiccation and predation (McDiarmid and Foster, unpubl. data). Individuals burrowed in tree cavities that fill with water during the rainy season would be directly subject to external conditions. Vellard (1948: 150) reported that individuals of *Phrynohyas venulosa* may take refuge in tree cavities, which they line with a hardened secretion from the skin.

As the dry season progresses in seasonally arid environments, moisture tension in the soil increases, subjecting burrowed frogs to increased likelihood of desiccation. Amphibians may cope with this increased dryness by burrowing to a greater depth where the soil is wetter (Ruibal et al., 1969; Ruibal and Hillman, 1981), or by developing some kind of protective covering (McClanahan et al., 1976, 1983; Loveridge and Craye, 1979; Loveridge and Withers, 1981). Because immobility is an important requisite for cocoon formation and maintenance, it is unlikely that frogs will use deeper burrowing and cocoon formation to deal with increasing aridity. If initial depth of burrowing is determined by soil moisture conditions at the time of burrowing, then on average over a dry season, species that do not form cocoons should burrow more deeply than those that do (cf. Ruibal and Hillman, 1981).

This should be advantageous to *Smilisca baudinii* and other frogs that are among the first species to breed in ponds and puddles when they form. Frogs burrowed near the surface should be stimulated by rain soaking into the soil at the beginning of the wet season, and, hence, should be active earlier than more deeply burrowing species. This would allow them to feed and otherwise prepare themselves to breed as soon as appropriate habitats were available. On the other hand, individuals burrowed at shallow levels may be more easily uncovered by the action of weather, and, thus, become exposed to severe temperatures and arid conditions, or to predators.

For many frogs protection may be achieved through a combination of burrowing and the deposition of a protective covering. We anticipate that the exploitation of the two factors by a species is inversely proportional, although deep-burrowing forms in particularly arid areas may form cocoons in a facultative way under extreme conditions.

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