FAUNA *of* AUSTRALIA

11. FAMILY BUFONIDAE

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Pl. 1.2. ***Bufo marinus*** (Bufonidae): the introduced cane toad, which has expanded its range from north-eastern Australia into the Northern Territory and New South Wales. [J. Wombey]

DEFINITION AND GENERAL DESCRIPTION

The skin of bufonids is thick, glandular and contains pustular warts in many species, including *Bufo marinus*. In *Bufo* and some other genera, large parotoid glands are present (Pl. 1.2). The toes do not end in discs. The upper jaw is edentate. Bufonidae can be distinguished from all other anurans by the presence of Bidder's organs in males, although the absence of these does not exclude Bufonidae since they are not always present in mature individuals of some species (Griffiths 1963). All *Bufo* species have a diploid chromosome complement of 2n = 22, except members of the *B. regularis* species group, in which 2n = 20.

Twenty-three recent genera are included in the Bufonidae (Frost 1985). *Bufo* is the only genus found in Australia, represented by the introduced *B. marinus*.

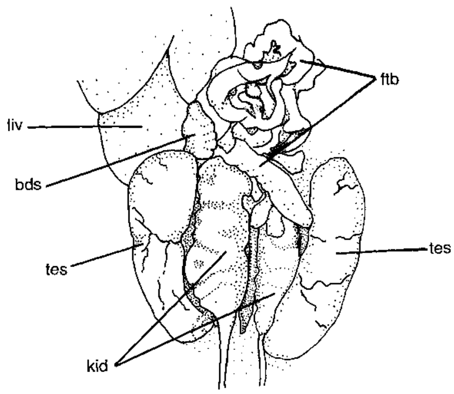

Figure 11.1 Bidder's organ in a small male *Bufo marinus*. **bds**, Bidder's organ; **ftb**, fat bodies; **kid**, kidney; **liv**, liver; **tes**, testis. [J. Courtenay]

HISTORY OF DISCOVERY

In 1935, 101 individuals of *Bufo marinus* were introduced deliberately into Queensland, in an attempt to control the greyback cane beetle, *Dermolepida albohirtum*, in sugar cane fields. Initially they were released in the Cairns, Gordonvale, Innisfail and Tully districts of Queensland. Over the next two years, further releases were made in nine districts between Mossman, north of Cairns, and Isis, near Bundaberg (Sabath, Boughton & Easteal 1981; Seabrook 1991).

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

Individuals of *B. marinus* are among the largest toads. Adult females can weigh over 1.5 kg and have snout-vent lengths greater than 22.5 cm (Reed & Borowsky 1966). Females are generally larger than males, and most adults range in size from about 8.5 to 15.0 cm snout-vent length.

The head is broader than it is long, the snout is rounded in dorsal view and truncated in profile. Well-developed cranial crests form ridges above the eyes and join above the snout. The eyes are large and prominent and have horizontal pupils. The diameter of the distinct tympanum is slightly less than half that of the eye. The parotoid glands are extremely large, triangular and swollen. The limbs are short. The toes are partially webbed, but the fingers are not. The first finger is longer than the second.

There is obvious sexual dimorphism. Irregularly scattered warts and tubercles cover both sexes. However, the skin of the female is much smoother than that of males, which has the texture of rough sandpaper, caused by the presence of numerous horny spicules on the warts and tubercles. The venter of the female and young male is creamy white; the dorsum is covered with irregular blotches of various shades of brown. The skin of adult males is more uniformly yellowish-brown in colour; the yellow is pronounced laterally and around the throat (Pl. 1.2). The first finger and the inner surfaces of the second and third fingers of sexually mature males bear brown nuptial pads, and a median vocal sac opens on each side of the mouth.

The black larvae are small (up to 35 mm S–V), and the round body is slightly wider than it is deep. The tail fins are non-pigmented and transparent, and the tail is rounded. The dental formula is $\frac{1^{1}1}{3}$.

Body Wall

The skin of *B. marinus* is permeable to water, and absorption of water through the skin is an important rehydration mechanism, particularly in the ventral pelvic region. There is an active ion transport system in the skin with a net inward movement of sodium ions. The skin is also important in gas exchange (Hutchinson, Whitford & Kohl 1968).

Skeletal System

In most *Bufo* species, including *B. marinus*, there are eight presacral vertebrae. The atlas is not fused to the adjoining distal vertebra, the pectoral girdle is arciferal and the prezonal omosternum is absent.

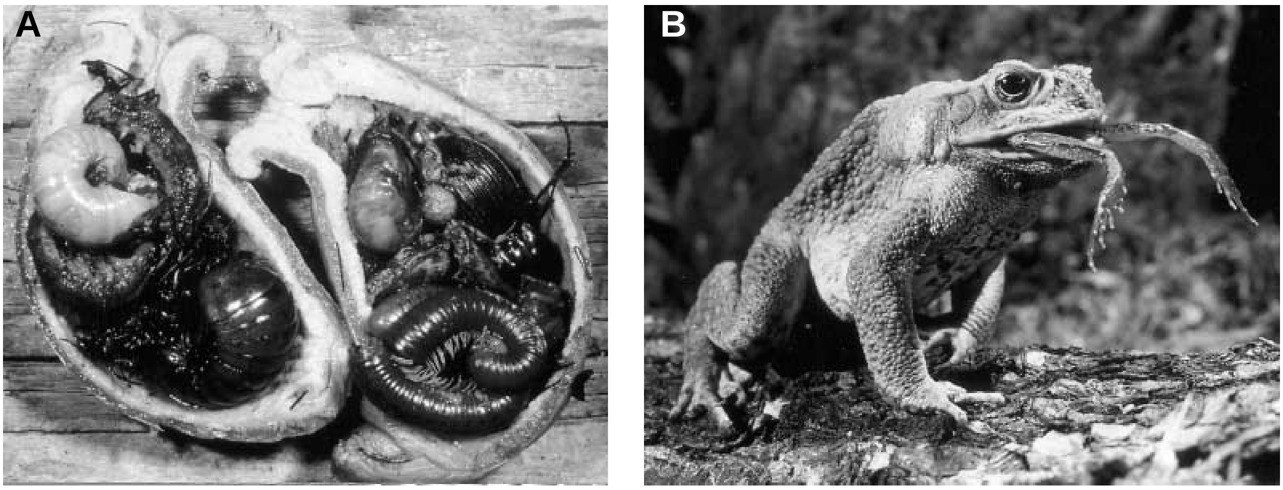

Figure 11.2 *Bufo marinus* preys on a wide variety of animal groups. **A**, bisected stomach, containing typical prey remains of several millipedes, spiders, beetles and other insects; **B**, indigenous frogs also form part of the diet of *B. marinus*. [A, photo ©M. Trenerry/NPIAW; B, ©Kathie Atkinson/ Auscape]

Locomotion

Bufo tadpoles are weak swimmers. Adults are primarily terrestrial, but are capable of swimming. On land they walk and hop, but do not leap. Miller & Zoghby (1986) have shown that adult *B. marinus* move fastest at 22°C and that their speed of movement is enhanced if they are acclimated at this temperature. Dehydration appears to have less impact on the locomotion of *B. marinus* than on other anurans (Moore & Gatten 1989).

Feeding and Digestive System

The larvae of *B. marinus* feed on the surface layers of submerged vegetation and detritus. The rasping mouth parts are used to generate fine nutrient particles that are ingested by filter feeding. During their early development, the larvae feed on the gelatinous string from which they have emerged.

The well-developed tongue of the adult bears sticky, mucous secretions and is used actively to catch prey. *Bufo marinus* eat almost any prey of appropriate size, and the diet appears to reflect the food available in a particular location. Prey consists mainly of small terrestrial arthropods, including crabs, spiders, centipedes, millipedes, scorpions and a wide range of insects. Additional dietary items include earthworms, planarians, molluscs, small vertebrates including its own young, rotting fruit, dog and cat food and human faeces. Quantities of plant material and stones found often in the stomach of toads are probably ingested accidentally (Krakauer 1968; Covacevich & Archer 1975; Tyler 1975; Zug, Lindgren & Pippett 1975; Zug & Zug 1979; Niven 1988). Heatwole & Heatwole (1968) have shown that the upper size threshold of prey selected increases, following long-term food deprivation, but the lower size threshold remains the same.

Circulatory System

The heart of the *Bufo* larva has one atrium and one ventricle. In adults there are two atria and one ventricle. The resting heart rate is approximately 13.5 beats/ minute, which increases in response to feeding and visual and tactile stimuli (Dumsday 1990). Heart rate also increases in response to desiccation, possibly due to increased peripheral circulation (Sherman 1980). Cardiovascular function of *Bufo marinus* is described in more detail in Chapter 4. The dense vascularisation of the ventral pelvic integument probably reflects the importance of this region in water uptake (Roth 1973). *Bufo marinus* can survive in salinities of up to 40% sea-water by increasing plasma sodium, chloride and urea to levels that are hyperosmotic to the environment (Liggins & Grigg 1985).

Respiration

In adults, gas exchange occurs through skin, lungs and the buccal cavity. The lungs are the most important and their relative contribution increases with increasing temperature (Hutchison, Whitford & Kohl 1968).

Excretion

Toads excrete urea through mesonephritic kidneys. Water, sodium and other ions can be actively resorbed from the urinary bladder, in which up to 30% of total body water can be stored (Ruibal 1962). Water uptake from the urinary bladder is thought to occur intracellularly (Shi & Verkman 1989). Shoemaker & Waring (1968) have shown that hypothalmic lesions interfere with the normal mechanisms of both the renal and cutaneous water balance.

Sense Organs and Nervous System

Much of the extensive literature on the neuroanatomy and neurophysiology of *Bufo* is referred to in Llinas & Prechts (1976) and Ewert & Arbib (1989). Recent detailed neuroanatomical studies were reported by Brown, Everett & Bennett (1989), and Hiscock & Straznicky (1989), and studies on forelimb muscle, the retina and gut were described by Oka, Ohtani, Satou & Ueda (1989), Nguyen & Straznicky (1989) and Anderson & Campbell (1989) respectively. *Bufo marinus* uses visual, olfactory and auditory (Jaeger 1976) cues to locate prey. The toad appears to use a triangulation system to assess prey distance (Collett, Udin & Finch 1987), and has a 200° horizontal visual field. Its relatively poor image quality does not decrease substantially towards the visual periphery (Jagger 1988).

Endocrine and Exocrine Systems

Water permeability of the urinary bladder of *Bufo* species is largely under hormonal control. Peptides potentially involved in this process have been isolated and partially characterised (Dassouli, Chevalier & Ripoche 1989; Rouille, Michel, Chauvet, Chauvet & Acher 1989). As in other toads, the skin of *B. marinus*, particularly the parotoid glands, is very poisonous. The anatomy and histology of these glands (Hostetler & Cannon 1974) and the nature of their poison (Gregernan 1952; Chen & Osuch 1969) have been well studied.

Reproduction

Chromosome differences associated with gender are not detectable cytologically (Schmid 1978). Gender can be reversed either by hormonal treatment or testectomy. The gender of sub-adults is often ambiguous. During embryonic and larval development, differences in a number of environmental factors, including temperature and water composition, can affect gender-ratio (Foote 1964). The male mating call is a low-pitched trill (Blair 1956, Easteal 1986). Males congregate at breeding sites, where they compete actively for females, and it is not uncommon for more than one male to attempt amplexus with a female simultaneously. Females release up to 30 000 eggs at a time, in a long, gelatinous string. The small, black eggs are approximately 2 mm in diameter. Amplexus may last for many hours.

As with most tropical toad species, breeding in *B. marinus* is opportunistic. There is no obvious breeding season and breeding occurs throughout the year, usually coinciding with periods of rain. Breeding sites include lakes, ponds, ditches and streams. Where these are permanent, breeding is not dependent on rain.

Plasma androgen and corticosterone concentrations are increased in male toads during amplexus. Corticosterone, but not plasma androgen concentrations, are also increased during periods of intense sexual activity, and following rain (Orchinik, Licht & Crews 1988).

Bidder's organs are rounded structures at the anterior end of the testes, which consist of small oocytes and a vestigial ovarian cavity. Experimental removal of the testes in *Bufo* causes the Bidder's organ to develop into a functional ovary (Ponse 1926).

Embryology and Development

In most bufonids and in all members of the genus *Bufo*, development from aquatic eggs to generalised aquatic larvae precedes metamorphosis to largely terrestrial adults. Embryonic cleavage is radial. A staged series of *B. bufo* embryonic and larval development was given in Fox (1983).

NATURAL HISTORY

Life History

The rate of growth and development at all stages of the life cycle is temperature dependent. Tadpoles of *B. marinus* hatch from one to three days after spawning and metamorphose from 15 to 70 days after hatching (Straughan 1966; Floyd 1983a). The tadpoles swim in large aggregations of some 2500 individuals (Mares 1972). Growth is rapid following metamorphosis. Individuals reach adult size within a year in tropical regions (Zug & Zug 1979), but may take two years in more temperate regions. Zug & Zug (1979) found some evidence of individuals which lived for four or more years, and Pemberton (1949) maintained one in captivity for nearly 16 years.

Ecology

Though *Bufo marinus* occurs in a great variety of habitats, it is most abundant around human habitation and, to a lesser extent, in grasslands. It occurs only rarely in forested areas and is especially rare in rainforests (Zug *et al*. 1975). Duellman (1978) reports that it is often common along rivers and in clearings in forested areas within its natural range.

Speare (1990) has compiled a comprehensive list of *B. marinus* parasites. Many of these are potentially pathogenic, but their pathenogenicity in *B. marinus* is poorly understood. *Bufo marinus* could act as a vector of human helminth parasites, including *Ascaris lumbricoides*, presumably by ingesting human faeces containing eggs.

Covacevich & Archer (1975), Niven (1988), Tyler (1976b), Zug *et al*. (1975) and Zug & Zug (1979) have summarised much of the information on predators. These include mongooses (in Fiji and Hawaii), various bird species, the keelback snake, *Amphiesma mairii*, freshwater crayfish of the genera *Cherax* and *Euastacus* (Hutchings 1979), and the snapping tortoise, *Elseya latisternum* (Hamley & Georges 1985).

Despite many reports of native animals being preyed on or poisoned by *B. marinus* the species' impact on natural communities may not be substantial. In the Northern Territory, *B. marinus* appears to have little or no impact on the native frog community (Freeland & Kerin 1988).

Estimates of population density range from 0.5/ha in rainforest (Zug *et al*. 1975) to 2138/ha in newly colonised areas of the Northern Territory (Freeland 1986). In Australia (Freeland 1986; Freeland, Delvinqueir & Bonnin 1986a) and elsewhere (Easteal 1981), population numbers have increased rapidly in newly colonised areas and then declined after 10 to 20 years. The densities of native (Zug & Zug 1979) and long-established introduced (Freeland 1986) populations in semi-urban areas have been estimated to be approximately 80/ha. In old introduced populations, individual toads have been observed to have relatively small body size and to be in poor condition, despite a high food intake and a low incidence of parasitism (Freeland *et al*. 1986a, Freeland, Delvinquier & Bonnin 1986b). This may be the result of microbial infections.

Populations well-removed from breeding sites, where males tend to predominate, can exhibit marked gender-ratio disparity even among sexually immature individuals (Zug & Zug 1979; Easteal & Floyd 1986).

The thermal physiology of *B. marinus* larvae (Floyd 1983b, 1984, 1985) and adults (Brattstrom 1968; Krakauer 1970) has been well described. The dessication tolerance of adults is 52.6% body water (Krakauer 1970). On the basis of the thermo-physiological characteristics of the species, Floyd (1983a) and van Beurden (1981) have made predictions of the areas in Australia in which *B. marinus* populations would be viable and thus of the potential limits to the continuing range expansion of the species.

Behaviour

Bufo marinus juveniles are active both day and night. Adults are usually nocturnal, though sometimes they feed and breed during the day. Adults take refuge in holes, crevices and burrows during the day, and may remain in these for long periods in dry conditions and during the winter months. Even when conditions are warm and wet, and thus favourable, individual toads are not active every night (Brattstrom 1962; Zug & Zug 1979; Floyd & Benbow 1984). *Bufo marinus* exhibits homing behaviour (Brattstrom 1962; Carpenter & Gillingham 1987).

Bufo species respond to prey with a behavioural pattern that has four distinct stages: orienting, approaching, fixating, and snapping (Ewert 1987). Although this response is instinctive, it is subject to maturation and modification (Ewert & Ingle 1971; Brzoska & Schneider 1978; Ewert & Kehl 1978).

Economic Significance

Many of the introductions of *B. marinus* were made with the intention that the species should control a variety of insect pests. Nowhere was this successful. In most cases the introductions are regarded as having had a net detrimental effect. Although little is known about the species' ecological impact, *B. marinus* is not a serious economic pest. It is known to prey on domestic bees and there are numerous reports of domestic animals being poisoned, and sometimes killed, as a result of eating or mouthing toads. Small enterprises have developed to supply toads for research and teaching purposes, and to produce leather goods made from toad skin.

BIOGEOGRAPHY AND PHYLOGENY

Distribution

Bufonidae occur naturally on all continents except Australia and Antarctica. Natural populations of *B. marinus* occur continuously from southern Texas and north-western Mexico to central Brazil (Cei 1968; Zug & Zug 1979). Upper altitudinal limits vary with latitude from 1600 m in Venezuela to 500 m in Sinaloa, Mexico (Zug & Zug 1979). *Bufo marinus* is the only member of the *marinus* species group to occur naturally outside South America.

Deliberate introductions have spread *B. marinus* widely throughout the Caribbean and Pacific regions (Easteal 1981). The species was introduced to Australia from Hawaii in June 1935. The subsequent geographical spread of the species has been described by van Beurden & Grigg (1980), Easteal & Floyd (1986), Easteal, van Beurden, Floyd & Sabath (1985), Freeland & Martin (1985) and Sabath *et al*. (1981), and is shown in Figure 11.4. Range expansion continues in New South Wales and the Northern Territory.

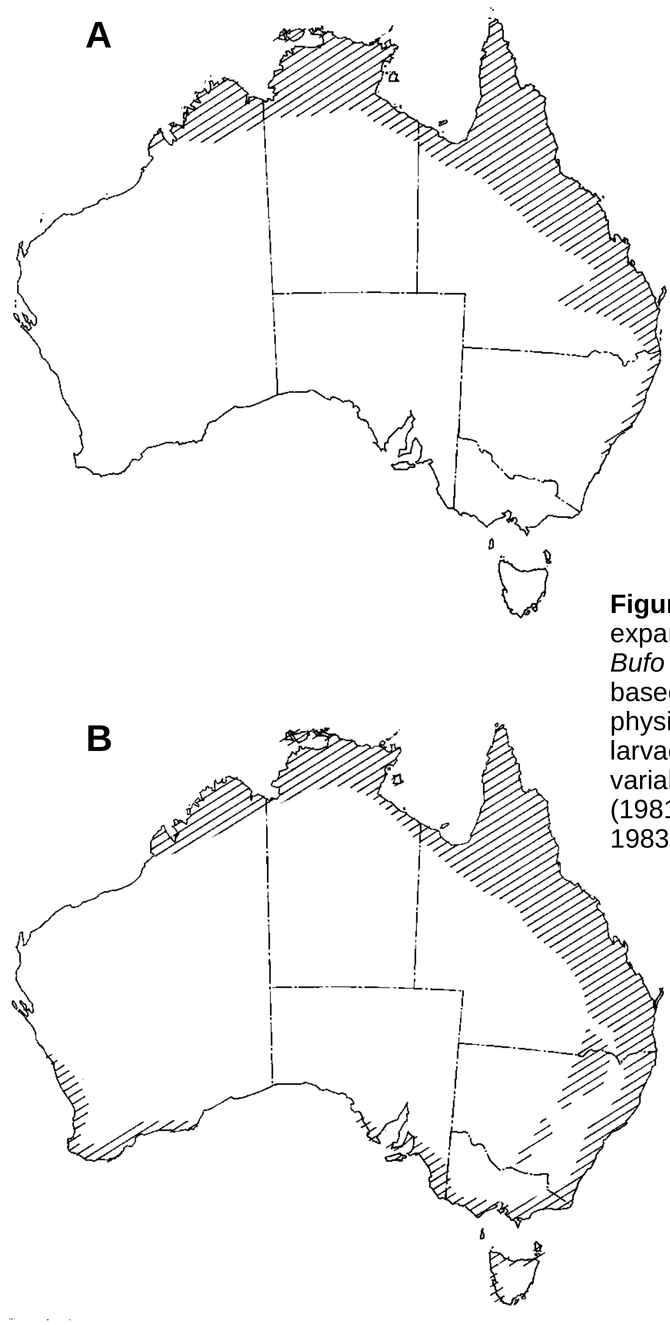

Figure 11.3 Predicted expansion of the range of *Bufo marinus*. Predictions based on **A**, the thermal physiology of embryos and larvae; **B**, bioclimatic variables of van Beurden (1981). (A, after Floyd 1983a) [W. Mumford]

The species has probably reached the potential western limits of its distribution in central and south Queensland. Freeland & Martin (1985) estimated that, at the current rate of active range expansion, *B. marinus* will have colonised the 'Top End' of the Northern Territory by 2027. However, they suggest that colonisation may be more rapid than this as a result of occasional long-distance passive transport by humans. The potential southern limit of the distribution will probably take longer to reach because of a relatively slower rate of spread.

Affinities with Other Groups

The family Bufonidae is thought to have evolved from an ancestral group of terrestrial leptodactylids (Griffiths 1963; Hecht 1963).

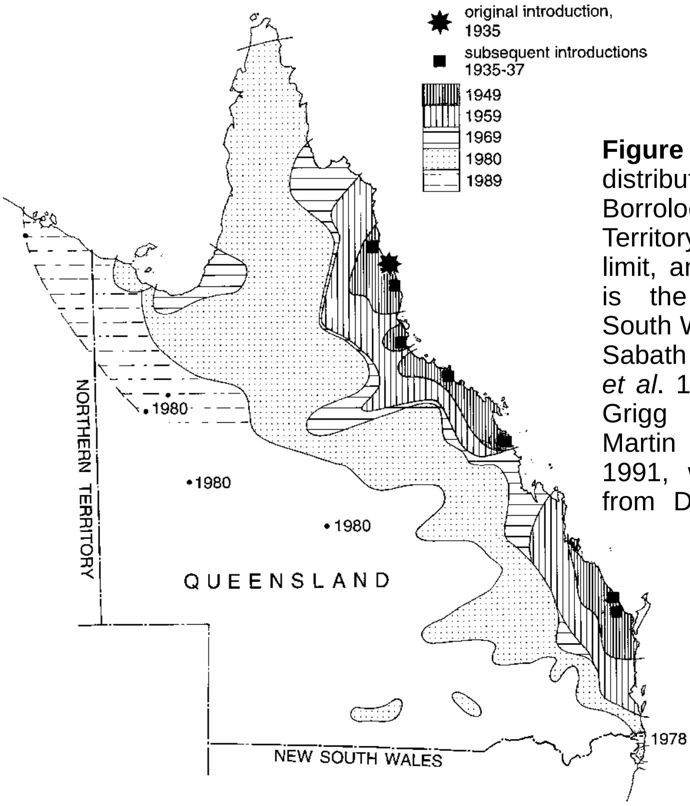

Figure 11.4 Present distribution of *Bufo marinus*. Borroloola, Northern Territory marks the western limit, and the southern limit is the Broadwater, New South Wales. (Modified from Sabath *et al*. 1981; Easteal *et al*. 1985; van Beurden & Grigg 1980; Freeland & Martin 1985; Seabrook 1991, with additional data from Davies pers. comm.) [W. Mumford]

Affinities Within the Taxon

Comparative immunological studies (Maxson 1984) indicate that *Bufo* existed in Gondwana before the separation of Africa and South America at the end of the Cretaceous. They cast doubt on the earlier view (Blair 1972) that *Bufo* originated in South America and radiated from there to occupy the rest of its extensive distribution during the Late Tertiary.

The genus has been divided into 'broad skulled' and 'narrow skulled' species (Martin 1972b). However, immunological comparisons (Maxson 1984) indicate that the osteological characters on which this division is based are plesiomorphic. The broad skulled *marinus* species group is most closely related to other South American species groups, including some that are narrow-skulled.

The *marinus* species group includes *Bufo arenarum*, *B. ictericus*, *B. marinus*, *B. paracnemis*, and *B. rufus*. *Bufo marinus* comprises two subspecies, *B. m. marinus* and *B. m. poeppigi* (Henle 1985). Throughout its extensive natural range, *B. m. marinus* appears to be genetically and morphologically uniform (Zug & Zug 1979; Maxson 1981).

Fossil Record

Bufo fossils are known from Miocene to Pleistocene deposits in Europe, and North and South America (Estes & Reig 1973). There are two *B. marinus* fossils. One is from the Lower Pliocene of Kansas, well outside the species present distribution (Wilson 1968). The other is from the late Miocene La Venta fauna of the upper Magdelana Valley, Huila, Colombia (Estes & Wassersug 1963).