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# A NEW GENUS AND SPECIES OF FROG (ANURA: LEPTODACTYLIDAE: MYOBATRACHINAE) FROM SOUTHERN TASMANIA

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## Summary

ROUNSEVELL, D. E., ZIEGELER, D., BROWN, P. B., DAVIES, M. & LITTLEJOHN, M. J. (1994) A new genus and species of frog (Anura: Leptodactylidae: Myobatrachinae) from southern Tasmania. *Trans. R. Soc. S. Aust.* **118**(3), 171-185, 30 November, 1994.

*Bryobatrachus nimbus* gen. et. sp. nov. is described from moist cool habitat in southern Tasmania. The genus is distinguishable by its direct development, fusion of presacral vertebrae VII and VIII with the sacrum, dentate maxillary arch, absence of vomerine teeth and the presence of a columella. The species is small (males 19-27; females 25-30 mm S-V) with distinctive dark patterns on the dorsum and an advertisement call that is a series of "toks" with a pulse repetition rate of 5.3-6.1 pulses/s. Eggs are laid in cavities in moss in groups of 9-14 and hatch as four-legged, tailed froglets. *B. nimbus* gen. et sp. nov. is cryptozoic in vegetation at poorly drained sites on wet peat, or in edaphic moss in implicate rainforest and subalpine moorland at altitudes from near sea level to 1,100 m. The genus and species are endemic to Tasmania and bring the frog fauna of the island to 11 species.


KEY WORDS: Anura, *Bryobatrachus nimbus* gen. et sp. nov., Tasmania, new genus, new species, morphology, osteology, advertisement call, development, habitat, cryptozoic, distribution.

## Introduction

The frog fauna of Tasmania is an element of the Bassian Province of south-eastern Australia (Littlejohn & Watson 1985). As well as species with wide ranging distributions throughout eastern Australia (e.g., *Ranidella signifera* Girard, 1858 and *Limnodynastes tasmaniensis* Günther, 1858 [Leptodactylidae: Myobatrachinae and Limnodynastinae]), there are two endemic species, *Litoria burrowsae* (Scott, 1942) (Hylidae) and *Ranidella tasmaniensis* (Günther, 1864) (Leptodactylidae: Myobatrachinae).

Ten taxa are recognised in Tasmania and aspects of their biology are relatively well known (Martin & Littlejohn 1982). With a greater appreciation of the need to document the biodiversity of the continent, efforts have been directed toward surveys and the mapping of distribution patterns of local fauna. During one such project aimed at providing an atlas of the frogs of Tasmania, one of us (D.Z.) recalled having heard at several high altitude sites, a distinctive frog call that could not be attributed to any described Tasmanian taxon.

In late November 1992 calls were recorded at the Hartz Mountain National Park and specimens were collected (Robertson 1993; Rounsevell & Swain 1993). Examination of the collection at the Tasmanian Museum and Art Gallery, Hobart, revealed further material.

The frogs could not be referred to any known genus, and so a new genus is erected to accommodate them here. We describe the species and provide information on its biology and distribution.

## Materials and Methods

Material reported here is deposited in the Tasmanian Museum and Art Gallery, Hobart (TMAG), South Australian Museum, Adelaide (SAM), Museum of Victoria, Melbourne (NMV), the Australian Museum, Sydney (AM) and the Department of Zoology, University of Adelaide (UAZ).

Measurements were taken using dial calipers reading to 0.05 mm, or with an eye-piece micrometer. Measurements (mm) were: eye diameter (E); eye-to-naris distance (E-N); internarial span (IN); snout-vent length (S-V) and tibia length (TL); and for selected specimens, head length (HL) and head width (HW). The methods of measurement follow Tyler (1968) and interpretation of data follows Tyler (1978). Data are presented as means with ranges in parentheses. The tympana of many specimens are indistinct or not visible, and hence accurate measurements of head width and head length were not always possible.

Osteological data were obtained from specimens cleared and stained with alizarin Red S for bone after the method of Davis & Gore (1947), and with alizarin Red S for bone and alcian blue for cartilage after the method of Dingerkus & Uhler (1977). Osteological descriptions follow Trueb (1979), and Andersen (1978[1]) for the carpus and tarsus.

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[1] ANDERSEN, M. L. (1978) The comparative myology and osteology of the carpus and tarsus of selected anurans. PhD Dissertation, Dept of Systematics and Ecology, University of Kansas (Unpubl.).

Line drawings were made with the aid of a Wild M8 stereoscopic dissecting microscope with attached camera lucida.

Most field observations were made in the spring and summer of 1993, at the type locality at Hartz Mountains National Park, and during a field survey in October and November 1993 (Ziegeler 1994). Air temperature and relative humidity were measured with a "Zeal" whirling psychrometer (BS 2842/66).

Recordings of the advertisement calls of one individual were made with a Sony WM-D6 Pro-Walkman cassette tape recorder and a Beyer M-88 cardioid dynamic microphone by G. F. Watson at the type locality on 5 December 1992 at about 1330 hours E.S.T. The wet-bulb air temperature was 8.5°C and a dry-bulb air-temperature was 9.2°C in the vicinity of the calling male.

Recordings of advertisement calls of several individuals also were made at the type locality by P. B. Brown on 30 November 1992 using a Marantz Superscope C-205 cassette recorder and a Sennheiser ME-80 electret microphone; temperatures were not measured.

The calls were replayed on a Nakamichi Dragon cassette recorder, with the line output directed to a Kay Elemetrics DSP-5500 digital Sona-Graph. Calls of sufficient intensity that did not overlap those of neighbours were analysed. The number of pulses in a call (determined by inspection), and measurements of call duration (ms) and pulse repetition rate (as pulses/s; from the peak of the first pulse to the peak of the last pulse) were determined from the wave-form display of each clear call.

For the six clear calls obtained by G. F. Watson, dominant frequencies (Hz) were determined from the power spectrum for the complete call, with the maximum and next highest peaks being measured. Pulse duration, and attack and decay times of the middle pulses also were estimated to the nearest millisecond (ms) from the wave-form displays. The repetition rate of the calls (as calls/min) also was determined from this sequence.

Eighteen calls from the recording sequence obtained by P. B. Brown were analysed, and duration, number of pulses and pulse rate determined. As calls of several individuals are included, the values are treated as a group.

## Systematics

Four anuran families are native to Australia: Hylidae, Ranidae, Microhylidae and Leptodactylidae (Myobatrachidae of many authors). The new frog was identified as belonging to the family Leptodactylidae, sub-family Myobatrachinae, on the basis of: (1) terminal phalanges knobbed; (2) intercalary elements absent; (3) apical element of *M. intermandibularis* absent; (4) pectoral girdle arciferal; (5) palatines discrete; (6) prepharyngeal folds absent; (7) alary processes of hyoid plate moderately broad and wing-like; (8) cricoid cartilage divided ventrally; (9) intervertebral discs not fused to centra in adults; (10) attachment of *M. intermandibularis* upon *M. submentalis* absent.

The first three characters exclude the species from the Hylidae, and the fourth excludes it from the Ranidae, whilst the first, fourth, fifth and sixth exclude it from the Microhylidae. The remaining characters are definitive of the leptodactylid subfamily Myobatrachinae (Parker 1940; Lynch 1971; Tyler 1972; Davies 1987[3]).

Littlejohn *et al.* (1993) report 9-12 genera as being variously recognised within the Myobatrachinae. The new species cannot be placed in any of these genera on the basis of the following combination of characters: an apparent autapomorphy of the vertebral column of fusion of the presacral vertebrae VII and VIII with the sacrum, presence of a dentate maxillary arch, the lack of vomerine teeth, presence of a columella, and direct development of the young with a four-legged, tailed froglet hatching from the egg membranes.

The frog is excluded specifically from the myobatrachine genera as follows: together with the vertebral fusion, (1) from *Assa* by the absence of parental care by the male, by the absence of vomerine teeth and by the complete phalangeal formula; (2) from *Crinia* (*sensu* Blake 1973) by the absence of vomerine teeth and the absence of a free-swimming tadpole; (3) from *Geocrinia* by the absence of vomerine teeth and of a projecting dorsal flange on the anterior ramus of the pterygoid, by the projecting snout and by the granular ventral surface; (4) from *Ranidella* by the width of the bases of the alary processes of the hyoid, by the absence of free-swimming tadpoles and by the nature of the omosternum; (5) from *Taudactylus* by the absence of T-shaped terminal phalanges on the digits, by the absence of vomerine teeth and by the lack of free-swimming tadpoles; (6) from *Uperoleia* by the absence of hypertrophied dermal glands and of two raised compressed metatarsal tubercles, and by the absence of a free-swimming tadpole; (7) from *Pseudophryne* by the presence of a columella and of teeth on the maxillary arch, and the absence of a free-swimming tadpole; (8) from *Arenophryne* by the presence of a columella and of teeth on the maxillary arch, and by the absence of modified phalangeal formulae on the hands and feet; (9) from *Myobatrachus* by the presence of teeth on the maxillary arch, by the absence of a modified phalangeal formula of the hands and by the absence of reinforcement of the anterior

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[3] Davies, M. (1987) Taxonomy and systematics of the genus *Uperoleia* Gray (Anura: Leptodactylidae). PhD Thesis, Department of Zoology, University of Adelaide. Unpubl.

portion of the skull by anterior placement of the nasals. (10) from *Metacrinia* by the presence of teeth on the maxillary arch, by a large omosternum, by the lack of extensive reduction of the palatines laterally, by the less extensive nasals, and by the projecting snout and shape of the head.

Genus ***Bryobatrachus*** gen. nov.

Type species: *Bryobatrachus nimbus*

*Diagnostic definition*

1. Alary processes of hyoid plate broad and wing-like. 2. Cricoid cartilage divided ventrally. 3. Intervertebral discs unfused in adults. 4. Attachment of *M. intermandibularis* on *M. submentalis* absent. 5. Hypertrophied dermal glands absent. 6. Small flattened inner metatarsal tubercle. 7. Tiny, or no outer metatarsal tubercle. 8. Snout projecting when viewed from above. 9. Maxillary arch toothed. 10. Vomers reduced to one or two fragments at edge of choanae. 11. Columella present. 12. Palatines slightly reduced laterally. 13. Nasals not located anteriorly on skull. 14. Omosternum large, mushroom-shaped with narrow stalk. 15. Phalangeal formula of hand 2,2,3,3. 16. Phalangeal formula of foot 2,2,3,4,3. 17. Terminal phalanges knobbed. 18. Vertebrae VII and VIII fused with sacrum. 20. Development direct — four-legged tailed froglet hatching from egg membranes.

*Etymology*

Derived from the Greek *bryon* (= moss) and *batrachos* (= frog), alluding to the habit of breeding in moss or moss-like vegetation.

***Bryobatrachus nimbus*** sp. nov.

FIGS 1-10

*Holotype:* TMAG C1012, an adult male, 300 m north of Lake Esperance (146°46'E, 43°13'30"S), Hartz Mountains National Park, 920 m, collected by D. E. Rounsevell & D. Ziegeler on 18.x.1993.

*Paratypes:* 9 ♂ ♂, 3 ♀ ♀ and 2 s.a : TMAG C1009, ♂, same data as holotype, except collected 1.x.1993; TMAG C1010, ♂, same data as holotype; TMAG C1013, s.a., Mt Sprent (145°58'E, 42°47'30"S), coll. D. Ziegeler, 21.x.1993; TMAG C1024, ♂, topotype, coll. P. B. Brown, 28.xii.1993; TMAG C1025, ♀, same data — C1024 and C1025 in amplexus; TMAG C350, (2 ♂ ♂), Mt La Perouse Base Camp, ANZSES Expedition Jan. 1984; TMAG C345, s.a., same data as C350; TMAG C869, ♂, Mt La Perouse (146°44'30"E, 43°30'20"S), rocks above Pigsty Ponds on Mt La Perouse track, 1.7 km NW of summit, coll. M. N. Hutchinson & S. Hudson, 9.ii.1990; SAM R43671 (cleared and stained), ♂, same locality as holotype, coll. D. E. Rounsevell, 25.xi.1992; SAM R43672, ♂, same data; AM R143566 (cleared and stained), ♀, same locality as holotype, coll. D. E. Rounsevell, 25.xi.1992; AM R143565, ♂, same locality as holotype, coll. P. B. Brown & D. Ziegeler, 29.xi.1992; NMV D67310, ♂, same locality as holotype, coll. A. & J. E. Wapstra, 29.xi.1992.

*Definition*

A small species (males 19-27 mm S-V, females 25-30 mm S-V) characterised by a toothed maxillary arch, presence of a columella, lack of vomerine teeth, unmodified phalangeal formulae, knobbed terminal phalanges, widely exposed frontoparietal fontanelle, presacral vertebrae VII and VIII fused with the sacrum, untringed fingers and toes, granular ventral surface, dorsum consistently marked with dark chevron-shaped mark between eyes, pair of parallel dark lines from shoulder along anterior portion of back and pair of dark patches in coccygeal region, eggs large and unpigmented, four-legged tailed froglet hatches from egg membranes, advertisement call a series of "toks" with a pulse repetition rate of 5.3-6.1 pulses/s.

*Description of holotype*

Maxillary teeth present; vomerine teeth absent; tongue oval, free behind; tympanum obscure. Snout short, projecting and slightly truncated when viewed from above, overshot and sloping posteriorly when viewed in profile (Fig. 1A). Eye to naris distance less


Fig. 1. *Bryobatrachus nimbus* gen. et sp. nov.: A. lateral view of the head; B. palmar view of hand; and C. plantar view of foot (Holotype, TMAG 1012). Scale bar = 5 mm.

than internarial span (E-N/IN = 0.71). Nares located laterally on snout, directed dorsally. Canthus rostralis straight, loreal region concave, facial shelf conspicuous. Eye prominent, pupil horizontal when constricted. Fingers short, unwebbed with flattened subarticular tubercles (Fig. 1B). Terminal discs undilated. Palmar tubercles flattened but conspicuous. Several supernumerary tubercles present; fingers in order of length 3>4>2>1.

Hindlimbs short (TL/S-V 0.36). Toes relatively short, unfringed and unwebbed (Fig. 1C); in order of length 4>3>5>2>1. Small flattened inner metatarsal tubercle, and tiny rounded outer metatarsal tubercle. Subarticular tubercles small and not prominent.

Dorsal surface sparsely tubercular, tubercles linear along length. Prominent tubercles on dorsal surface of legs. Ventral surface granular with well-developed coarsely granular pelvic patch. Small bifurcated unfimbriated cloacal flap.

Dorsum dark tan in preservative with chevron-shaped black mark between eyes, paired elongated black markings from scapula region, and paired moderately elongate black patches in the coccygeal region. Canthal stripe anterior to naris, through loreal region and eye to axilla. Pale patch beneath eye (Figs 1, 2).

Ventral coloration chocolate with cream speckling (Fig. 2); dark chocolate suffusion on throat. Paired vocal slits posteriorly at angle of jaw.

A

B

Fig. 2. *Bryobatrachus nimbus* gen. et sp. nov. A, dorsolateral and B, ventral views in life (Paratype TMAG 1009) (Photo: J. Voss).

*Colour in life*

Dorsal surface shades of dark brown. Darkest brown markings distinctive varying in intensity and occurring bilaterally in pairs in the coccygeal region and in association with scapulae. Coccygeal pair lie within region of paler brown or "ground" colour, not hidden when colour intensity changes. Larger patch of dark brown occurs between scapulae and anteromedially which, when at darkest, can conceal upper pair of bilateral markings. Chevron-shaped mark of dark colour between eyes. Small white patch above cloaca. Limbs barred with dark brown. Other broad dark brown patches occur along paler brown flanks. Dorsal surface of snout and inner thighs unmarked and paler brown or "ground" colour. Paired canthal stripes from naris to flank broadest in tympanal region. Dark brown canthal stripe passes through most of the eye except uppermost part of iris. Iris dark brown below and iridescent gold above facial stripe. Lower stripe of white or cream, commencing between eye and naris and varying in width being narrowest, or with lower edge notched, below eye and including neither lower eyelid nor upper lip. Ventral surface dark brown covered with irregularly-shaped fine white spots of similar size extending over the limbs and sometimes to lower throat. Chin sometimes paler and less spotted. Pale lemon-yellow tint on paler parts of throat and forelimbs.

*Dimensions* (mm): S-V 22.6; TL 8.2; E-N 1.7; IN 1.4; E 2.7.

*Variation*

There is little variation in external morphology, other than colour pattern. The protruding snout is not as pronounced in all paratypes; in those in which it is most developed, it appears to be thickened and whitish. The legs are uniformly short (TL/S-V = 0.35 [0.31-0.38]), and the head usually longer than width (HL/HW = 1.06 [0.96-1.23, n = 9]). There is variability in the relationship between eye-to-naris distance and internarial span (E-N/IN = 0.89 [0.71-1.12]). The tympanum is obscure or indistinct

(Figs 1, 2). Toes are uniformly unfringed, but there is variability in development of the palmar tubercles; in TMAG C1009, these are particularly pronounced. When present, the outer metatarsal tubercle is tiny and the inner metatarsal tubercle usually flattened. A tarsal fold is present in TMAG C1010. Rugosity of the dorsum varies but is not conspicuous. Ventral granularity of the belly is variable.

The ground colour of the dorsum and the extent and nature of the markings varies. The three pairs of dark markings on the dorsum are consistently present. The markings between the eyes are chevron-shaped, whilst those in the scapular region are often lyrate and can vary in length, occasionally almost coalescing with the coccygeal pair.

Dorsal colour varies from very dark brown to grey-brown or tan, and, in darker specimens the anterior pair of markings becomes obscure and often merges with the suprascapular pair. The coccygeal pair always contrasts with the general body colour and is distinctive (Fig. 2A).

A pale or tan mid-vertebral stripe is present in several specimens, and occasionally a pale medial ventral stripe is present in paler specimens. The ventral surface can be dusky grey with white spots, or pale with dark spots. The throat is always pigmented, but added dark suffusions are present in calling males. The throat has a salmon iridescent hue in life, and a lemon coloration often occurs in the axillae. Reddish patches occur along the lower flanks and in the inguinal region. A pale spot often occurs above the cloaca.

The pale stripe beneath the dark canthal stripe of the head varies in extent, maximal development being shown in Fig. 2.

*Osteology* (based on SAM R43671)

Skull poorly ossified. Sphenethmoid ossified medially, with ossification extending anteriorly between the nasals dorsally and ventrally. Cartilages of nasal capsules are considerably calcified ventrally (Fig. 3). Prootic and exoccipital superficially fused by extensive calcification giving short and stocky crista parotica. Exoccipital calcified dorsomedially and ventromedially. Crista parotica not articulating with elongate unexpanded otic ramus of squamosal. Carotid canal roofed on frontoparietals medial to well developed epiotic eminences. Occipital condyles widely separated. Frontoparietal fontanelle widely exposed for approximate length of orbit. Anterior extremities of frontoparietals extend anteriorly to anterior margin of frontoparietal fontanelle. Orbital edges of frontoparietals slightly curved and angled slightly posterolaterally. Nasals moderately well ossified, approximately triangular and widely separated medially. Maxillary process short, and widely separated from well-developed preorbital process of pars facialis of maxilla.

Palatines moderately robust, reduced slightly laterally and curving posteromedially to overlie sphenethmoid at anterior extremities of orbit. Parasphenoid moderately robust with moderately broad, deeply crenate cultriform process extending approximately ⅔ length of orbit in ventral view. Alae moderately short, relatively broad, extending slightly posterolaterally, not overlain by medial ramus of pterygoid. Pterygoid robust; anterior ramus in long contact with maxilla anteriorly, and with base of squamosal shaft and with cartilaginous quadrate posteriorly. Squamosal robust, with short zygomatic

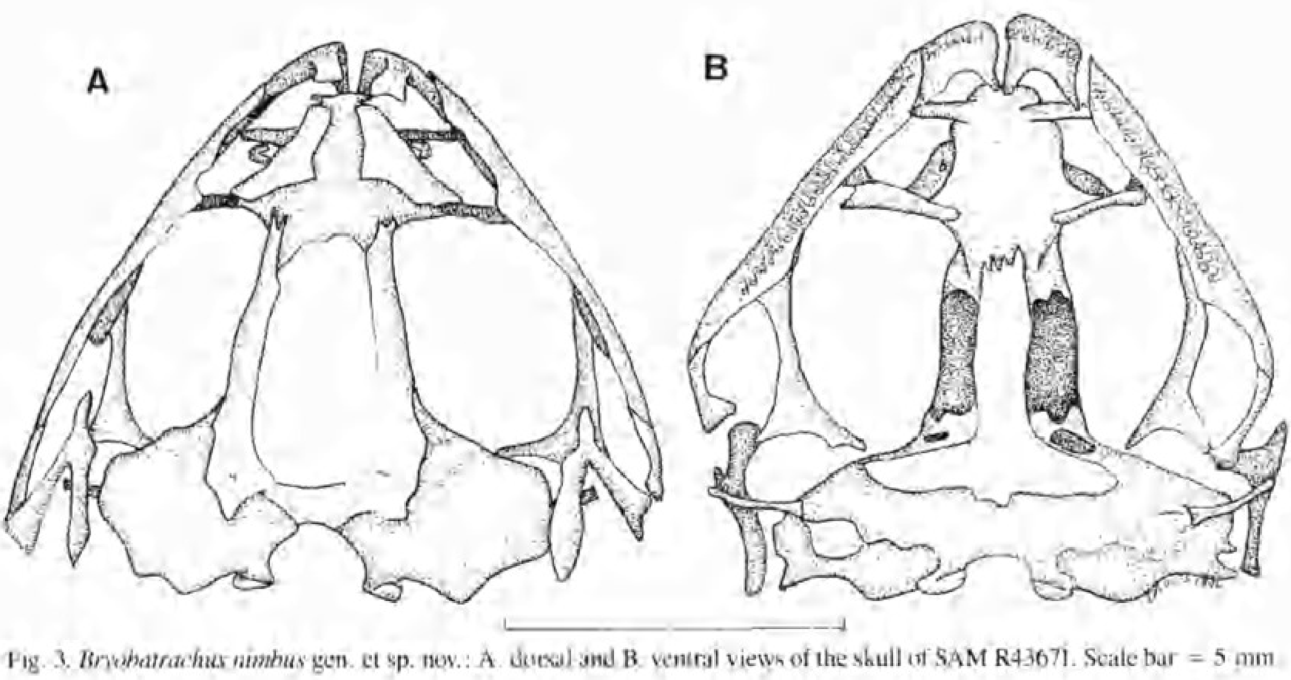


Fig. 3. *Bryobatrachus nimbus* gen. et sp. nov.: A. dorsal and B. ventral views of the skull of SAM R43671. Scale bar = 5 mm

ramus and long unexpanded otic ramus not overlying crista parotica (Fig. 3).

Maxilla and premaxilla dentate. Palatal shelf deep with well-developed palatine processes of premaxillae not abutting medially. Well-developed pterygoid process of maxilla. Alary processes of premaxillae broad at base with narrower posterodorsal projections, slightly concave. Vomerine fragments present on edge of choanae on right hand side. Bony columella present (Fig. 3).

Pectoral girdle arciferal and robust (Fig. 4A). Omosternum large, mushroom shaped with an elongate narrow stalk; xiphisternum also large and mushroom shaped, with a short broad stalk. Some calcification of xiphisternum and epicoracoid cartilages. Sternum cartilaginous. Clavicles moderately slender, curved, poorly separated medially; coracoids robust, moderately widely separated medially. Scapula bicapitate, longer than clavicles. Suprascapula about ⅓ ossified.

Eight non-imbricate procoelous presacral vertebrae. Vertebra VIII fused with sacrum and with vertebra VII. Vertebra VII fused with vertebra VIII and with sacrum (Fig. 5). Transverse processes of vertebra IV with bilateral anomally (Fig. 5). Sacral diapophyses poorly expanded. Relative widths of transverse processes:

III > IV > II > SD > V > VI > VII > VIII

Urostyle bicondylar with dorsal crest extending approx. ½ length. Small rounded dorsal prominence on ilium (Fig. 5). Dorsal protuberance not prominent. Ilial crest absent. Pubis calcified.

Humerus with strongly-developed deltoid crest anteroproximally. Phalangeal formula of hand 2,2,3,3. Carpus of six elements exhibiting moderate torsion. O. radiale and O. ulnare present; O. radiale larger of the two. Both elements articulate with O. radioulna proximally and with each other posteromedially. Distally, both articulate with large transversely elongated O. centrale postaxiale which articulates distally with bases of O. metacarpi III, IV and V. Moderately well-developed flange extends from lateroproximal corner. Small calcified palmar sesamoid proximally on ventral surface (Fig. 6). O. centrale preaxiale articulates laterally with O. radiale, distally with O. centrale postaxiale and with carpal element of O. distale carpale 2 and O. distale carpale 3 and laterally with basal prepollical element.

Carpal element of O. distale carpale 2 articulates with carpal element of O. distale carpale 3. Distal tips of terminal phalanges knobbed.

Phalangeal formula of foot 2,2,3,4,3. O. tibiale and O. fibulare elongate and fused at either end. Bones of approximately equal length. Two distal tarsal elements present. Lateral elements largest, lying at base of O. metatarsus III and extending laterally to articulate with medioproximal side of base of O. metatarsus II. Second element appears to be result of fusion of two elements and lies at base and slightly lateral to O. metatarsus II, and articulates with base of O. metatarsus I and O centrale prehallucis. Distal prehallical element small and knobbed, calcified.

Hyoid plate longer than broad (Fig. 4C). Base of alary processes occupying ⅓ to ½ of lateral edges of hyoid plate; not pedunculate. Anteromedial processes of anterior hyale long and slender. Posterolateral processes of hyoid plate irregularly shaped, moderately long. Posterior cornua ossified.

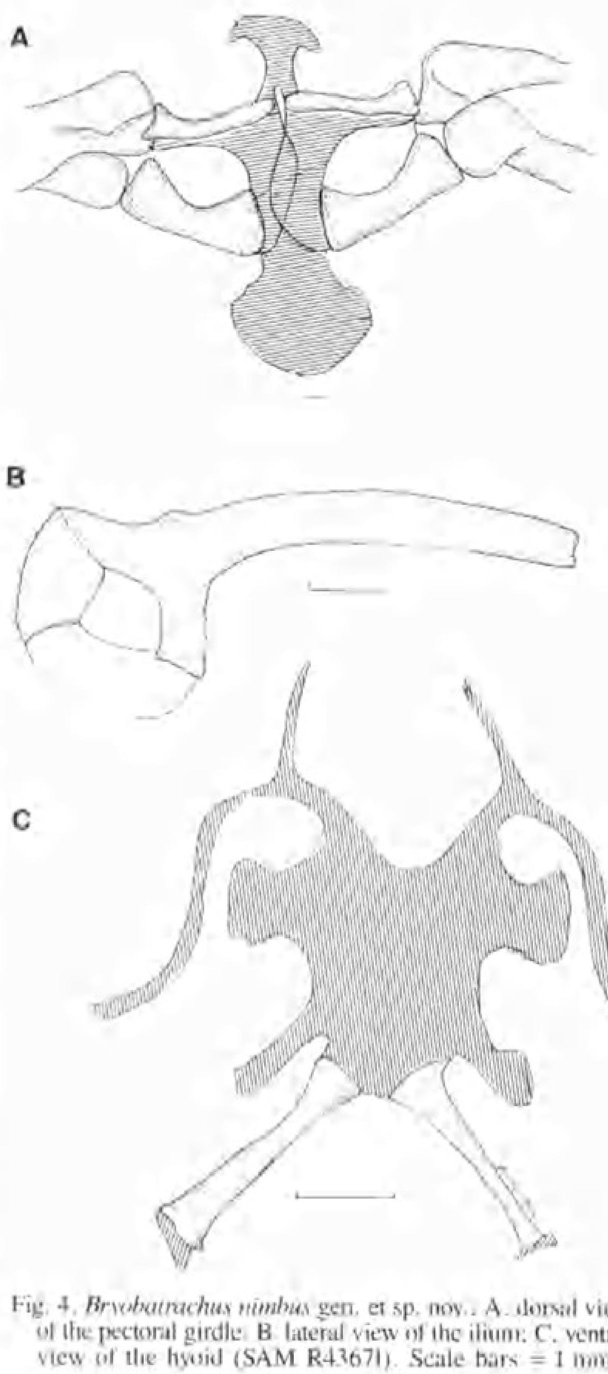


Fig. 4. *Bryobatrachus nimbus* gen. et sp. nov.: A. dorsal view of the pectoral girdle; B. lateral view of the ilium; C. ventral view of the hyoid (SAM R43671). Scale bars = 1 mm.

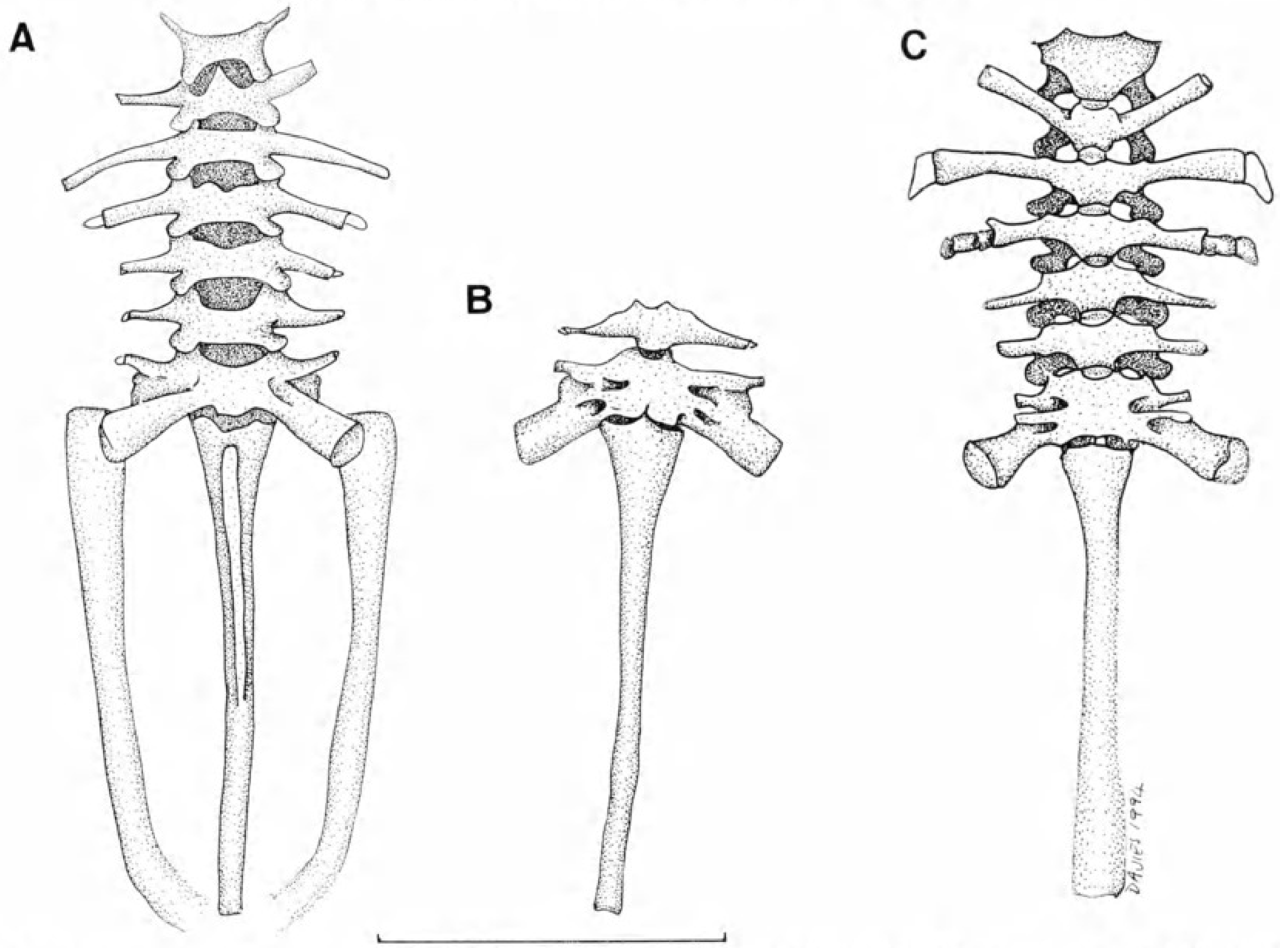


Fig. 5. *Bryobatrachus nimbus* gen. et sp. nov.: A. dorsal view of the vertebral column B. ventral view of vertebrae VI, VII and VIII and the sacrum (AM R143566) and C. ventral view of the vertebral column (SAM R43671). Scale bar = 5 mm.

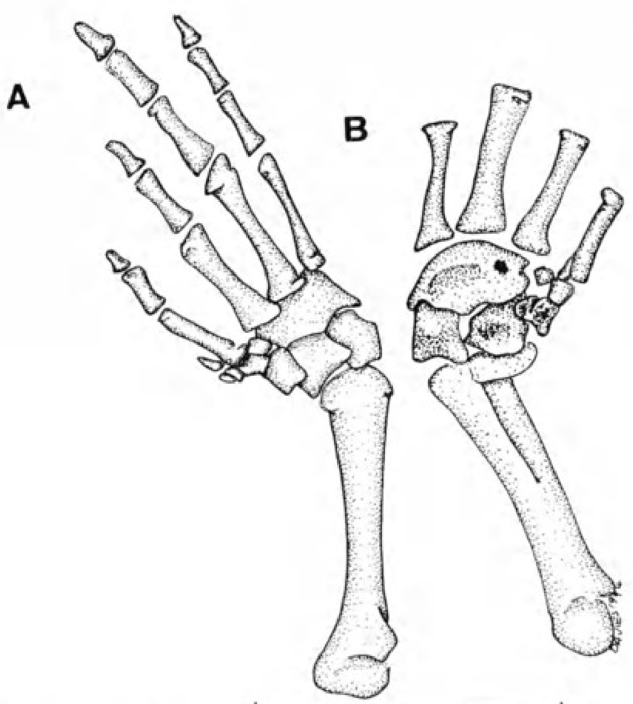


Fig. 6. *Bryobatrachus nimbus* gen. et sp. nov.: A. dorsal and B. ventral views of the carpus (SAM R43671). Scale bar = 5 mm.

*Variation*

Paratype (AM R143566) has been cleared and stained. In comparing this specimen with the described male, it is apparent that the latter is probably a senescent specimen on the basis of the high degree of calcification lacking in the larger female specimen. For example, calcification of the nasal cartilages, of the omosternum, xiphisternum and epicoracoid cartilages, of the tiny cartilaginous prepollex and the palmar sesamoid is lacking in this specimen. In addition, there is less calcification of the crista parotica region between the exoccipitals and prootics.

Consistent with this view is the lack of ossification of the sphenethmoid between the nasals dorsally and ventrally, and the lack of fusion of the medial tarsal elements. Remnant vomerine fragments occur on the edges of both choanae in this specimen. The vertebral anomaly on the transverse processes of presacral vertebrae IV is not present, but fusion of presacral vertebrae VII and VIII with the sacrum is consistently present (Fig. 5).

There is little variability in other skeletal elements, other than in the palatal shelf of the premaxilla which is much more extensive in its articulation with the palatal shelf of the maxilla.

*Advertisement call*

Males call from the ground surface beneath dense vegetation, and from prepared breeding chambers within cushions of sphagnum or edaphic lichen. Male advertisement calls are heard in loud chorus, diurnally, in spring and early summer.

The following description of the advertisement call (Fig. 7) is based on the sequence recorded by G. F. Watson. The call is a single quasi-periodic pulse train with a duration of 1009-1281 ms (mean = 1157), and consists of a series of 7-8 (mean = 7.5) short pulses (duration: range = 7.2-10.4 ms; mean = 8.74 ms) with rise times (attack) of about 1.0-3.5 ms and fall times (decay) of about 4.9-5.9 ms. The pulse rates range from 5.3 to 6.1 pulses/s (mean = 5.74) (Table 1). The calls are repeated at a rate of 2.65 calls/min. Although there is a wide spread of spectral energy (as a consequence of the short rise-times of the pulses), there are two dominant frequencies of equal energy at 2100-2140 and 2680 Hz in three of the calls, there is only one peak at 2140 Hz in two calls, and in the remaining call there are two peaks at 2120 and 2740 Hz (with the latter being lower by 2 dB).

The values obtained from each of the 18 calls recorded by P. B. Brown are presented in the recording sequence in Table 2. From an inspection of the numbers of pulses and dominant frequencies, it is suggested that calls of three or four individuals may be included in the sequence. The values for call duration, number of pulses and pulse rates, although of greater range, include those of the individual recorded by G. F. Watson. The dominant frequencies, where measured, however, are lower, ranging from 1540 to 1960 Hz.

*Calling period*

The calling period in alpine habitat is seasonal. Calls in chorus were heard at the type locality from early October to late December. Earliest calling heard was in the Hartz Mts on 1.x.1993, and the latest at Mt Norold (146°15′40″E, 43°15′30″S), on 2.iii.1994. Chorusing occurred in rain and whilst snow fell.

In early spring, calling was interrupted frequently by heavy snow falls, and recommenced when thaw set in. During summer, calls ceased during the warmest part of the day at temperatures above 15°C and as the

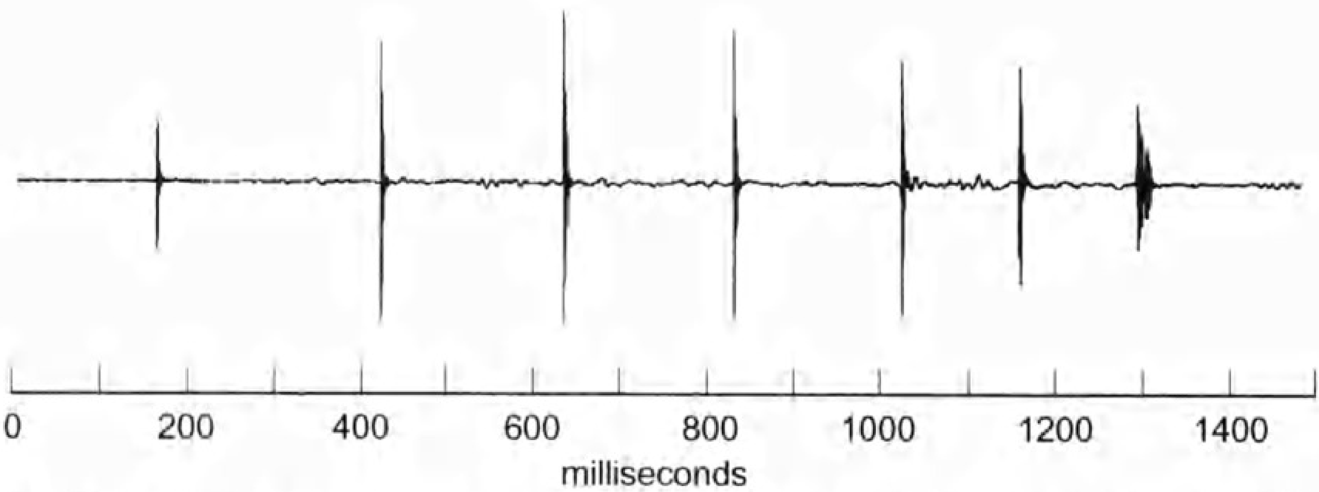


Fig. 7. A wave form display of an advertisement call of a male of *Bryobatrachus nimbus*, gen. et sp. nov. recorded at a wet bulb air temperature of 8.5°C, in the Hartz Mountains. The depicted call is the first of the series recorded by G. F. Watson. (See Table 1 for more information.)

TABLE 1. *Values for six advertisement calls of a male of* Bryobatrachus nimbus *gen. et sp. nov. at the type locality at a wet-bulb air temperature of 8.5°C on 5.xii.1992.*

| Duration (ms) | Pulses | Pulse rate (pulses/s) | Pulse duration (ms) | Dominant frequencies (Hz) lower (DF1) | higher (DF2) | Difference (dB) DF1-DF2 |
|---|---|---|---|---|---|---|
| 1148 | 7 | 5.33 | 9.47 | 2140 | 2660 | 0 |
| 1063 | 7 | 5.76 | 10.35 | 2100 | 2680 | 0 |
| 1262 | 8 | 5.67 | 8.59 | 2140 | none | – |
| 1281 | 8 | 5.56 | 8.40 | 2120 | 2740 | 2 |
| 1178 | 8 | 6.06 | 8.40 | 2140 | none | – |
| 1009 | 7 | 6.08 | 7.23 | 2140 | 2680 | 0 |

TABLE 2. *Values for 18 advertisement calls of several males of* Bryobatrachus nimbus *gen. et sp. nov. recorded by P. B. Brown at the type locality on 30.xi.1992.*

| Call (ms) | Duration | Pulses | Pulse rate (pulses/s) | Dominant frequency (Hz) |
|---|---|---|---|---|
| 1 | 1681 | 8 | 4.20 | |
| 2 | 925 | 7 | 6.58 | 1740 |
| 3 | 1869 | 10 | 4.87 | 1720* |
| 4 | 2069 | 10 | 4.39 | 1540** |
| 5 | 1919 | 10 | 4.74 | 1540** |
| 6 | 2037 | 10 | 4.46 | — |
| 7 | 1756 | 10 | 5.20 | — |
| 8 | 1356 | 7 | 4.46 | 1800 |
| 9 | 634 | 5 | 6.53 | 1800 |
| 10 | 1169 | 7 | 5.19 | 1960* |
| 11 | 698 | 5 | 5.93 | 1800 |
| 12 | 884 | 4 | 3.44 | 1800 |
| 13 | 2225 | 10 | 4.09 | 1620 |
| 14 | 2256 | 11 | 4.47 | 1620 |
| 15 | 2144 | 10 | 4.24 | 1600 |
| 16 | 2100 | 10 | 4.33 | 1600 |
| 17 | 1712 | 10 | 5.34 | 1800 |
| 18 | 2394 | 11 | 4.21 | 1600 |

* midpoint of band; ** second peak at 1820 Hz.

vegetation dried out. Individuals called in cool conditions during the early morning and in the evening (19:00-21:00) at Mt La Perouse on 1.ii.1994 (S. Corbett pers. comm.). Frogs were not heard at night.

Ziegeler (1994) observed calling in air temperatures of 4.5-12°C and relative humidities of 62-94%. The frequency of calls heard increased when there was precipitation.

### *Behaviour*

The species is cryptozoic, and was collected during spring and summer. Calling males were collected from the surface of the peat beneath coarse, low vegetation, from within breeding chambers or nests, in cushions of sphagnum or other similar plants, beneath rocks (Ziegeler 1994), or under branches lying on or amongst vegetation. Females were found in breeding chambers with a male or, when males were chorusing in spring, on the surface of the vegetation. Males continued to call even when females occupied the same chamber.

At the type locality where a large population exists, individual frogs are regularly spaced, remaining hidden. They appear not to aggregate or to use open


Fig. 8. A. Nest of *Bryobatrachus nimbus* gen. et sp. nov.; B. subalpine moorland habitat at Hartz Mts; type locality in middle distance viewed from the track. (Photo. J. E. & A. Wapstra); C. subalpine moorland habitat at 800-1000 m altitude at Mt Hesperus; D. Implicate rainforest habitat at over 750 m altitude at Mt Bobs.

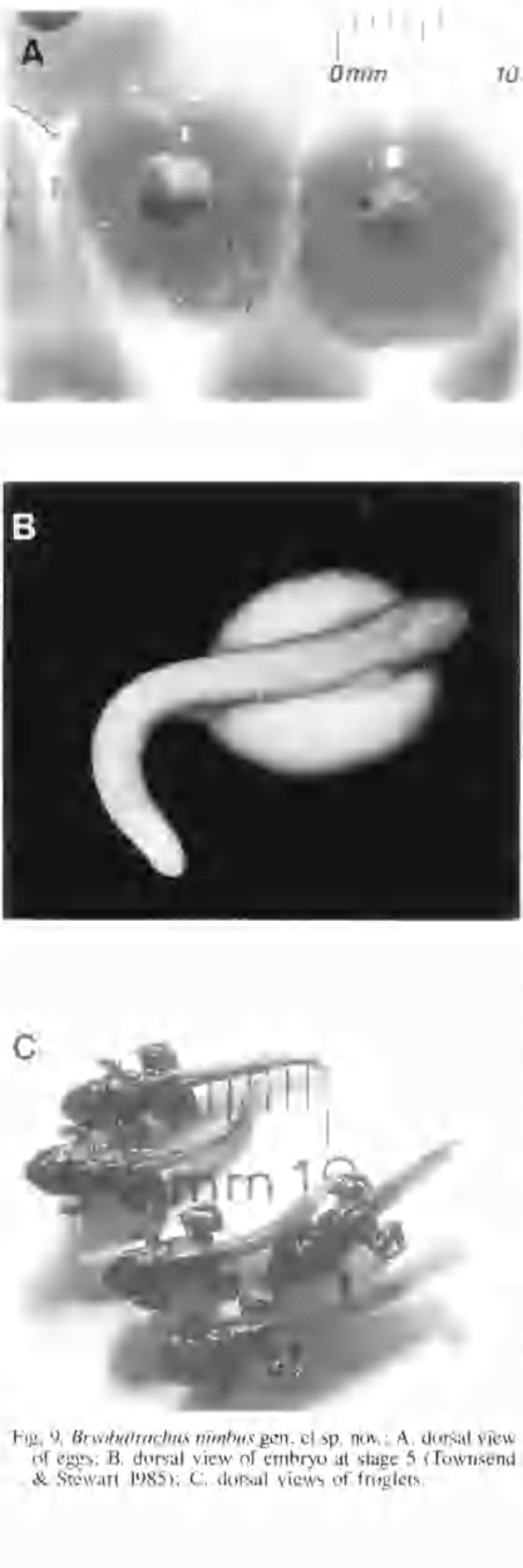


Fig. 9. *Bryobatrachus nimbus* gen. et sp. nov.: A. dorsal view of eggs; B. dorsal view of embryo at stage 5 (Townsend & Stewart 1985); C. dorsal views of froglets.

surface water. None was collected during autumn or winter.

Locomotion is by crawling or walking. In the open, frogs usually crouched and remained still until disturbed and then sought cover. They jumped or swam only when forced. In captivity, both sexes displayed thigmotropism by forming individual cavities in which to shelter in loose sphagnum. They entered the sphagnum backwards.

*Development*

The species breeds in spring, laying eggs in nests in moss or lichen. Nests are concealed spherical cavities (3.5-4.0 cm in diameter) in clumps of moss approximately 2-5 cm below the surface (Fig. 8A). They can be exposed by parting the stems of moss. Single males, male-female pairs (sometimes in amplexus), eggs, or froglets were found in ten nests in a small area of the type locality on three visits (24.xii.1993, 11.i.1994 and 28.i.1994). On the first visit, five nests were found. One contained 6-10 eggs, another contained five froglets (Fig. 9C), the third held a single male frog, and the remaining two nests each held a male-female pair of adult frogs (one pair included a gravid female and a male in amplexus). On the second visit three nests containing eggs were found. Two contained 12 and 14 eggs. Those in the remaining nest could not be readily counted as the jelly surrounding them had begun to merge. The last visit produced two new nests, one containing 9 eggs, and another containing 5-6 froglets. Each nest was found in a separate cushion of moss. Other empty and possibly disused nests were found in adjacent patches of moss in the same area.

Eggs containing embryos (Fig. 9B) at stage 5 of Townsend & Stewart (1985) were located on 10.xii.93 but not in nests. Two groups of eggs were found on the surface of the vegetation and contained three and six eggs respectively. The latter included four dead embryos infected with fungus.

The mean diameter of four of the newly laid eggs found on 11.i.94 was 3.49 mm (3.33-3.65), and the mean capsule diameter was 13.57 mm (13.02-14.13). They were surrounded by a single jelly membrane (Fig. 9A). These eggs cannot be ascribed to a stage as for the direct developing *Eleutherodactylus coqui* (Townsend & Stewart 1985).

The mean S-V length of five metamorphs was 6.0 mm (5.4-6.35) and the mean total length, 14.51 mm (13.97-19.05). Tail length varied considerably (Fig. 9C). Tail muscle is well developed and, tail fins narrow, equal in width dorsally and ventrally. Tail fins do not appear to be vascularised. The body is heavily pigmented; that on tail muscle being finer and that on tail fins patchy. In life the body and tail are covered with fine white dots. There is no cloacal tail piece. The mouth extends beyond the eye and the fingers and toes appear to be fringed.

*Habitat*

*Bryobatrachus nimbus* is found in subalpine moorland (Fig. 8C) and implicate rainforest in southern Tasmania (Fig. 8D). It is restricted to poorly-drained sites from lowland to subalpine localities (Ziegeler 1994). The soil type is peat overlying sandy or stony substrate (Ziegeler 1994). It occurs on Pre-Cambrian metamorphics, Upper Carboniferous-Permian sedimentary deposits, Triassic sandstone and Pleistocene glacial deposits.

The subalpine moorland comprises a diverse range of plant communities. Five recorded communities are *Epacris serpilifolia-Empodisma minus-Gleichenia alpina* fernland, *Leptospermum nitidum-Gahnia grandis-E. minus* tall shrubland (both occur at Hartz Mts [Fig. 8B]), *E. serpilifolia-Richea scoparia* low shrubland with *Astelia alpina*, *G. alpina* and *E. minus* (Adamsons Peak [146°49'E, 43°21'S]), *E. serpilifolia-Melaleuca squamea* open heath (Mt Sprent) and *Carpha alpina-Isophysis tasmanica* herbfield (Mt Sprent, Mt Hesperus [146°14'E, 43°07'20"S] [Fig. 8C]) (Ziegeler 1994).

The implicate rainforest communities are floristically complex. The shrub layers are dense and species diverse at all altitudes. At higher altitudes the dominant trees are *Nothofagus cunninghamii*, *Eucryphia milliganii*, *Athrotaxis selaginoides*, *Nothofagus gunnii* and *Phyllocladus aspleniifolius* and the ground cover is dense moss and/or *Astelia alpina* (Fig. 8D; 750 m, Mt Bobs 146°36'E, 43°18'S). At low altitudes *N. cunninghamii*, *Melaleuca squarrosa* and *P. asplenifolius* are dominant and ground cover is dense moss and *Blechnum wattsii* (Alexander Creek 146°05'E, 43°26'S) (Ziegeler 1994).

The climate is in the perhumid cool zone of Gentilli (1972) but is cool and consistently wet. The mean annual precipitation is 2500 mm in large parts of this region and is received as rain, snow, hail, fog, mist and frost evenly distributed across the seasons (Bureau of Meteorology 1991).

*Distribution and abundance*

*Bryobatrachus nimbus* occurs in mountains in southern Tasmania south of 42°48' latitude (Fig. 10). It is known from 15 localities, mostly described by Ziegeler (1994), that range from sea level to 1100 m in an area approximately 80 km × 50 km. The localities are bounded by Mt Sprent in the north-west, Hartz Mts in the north-east, Mt La Perouse in the south-east and Bathurst Harbour area in the south-west (Fig. 10). All localities are south of the Huon River and Serpentine River and none is over 40 km from the sea. At the northern and eastern edges of this distribution, *B. nimbus* is confined to sites above 800 m altitude whilst in the south-west, its range descends to near sea level.

Hundreds of males were heard in chorus at the type locality during spring 1992. Other large populations occur at known locations (Ziegeler 1994). Although geographically restricted, the species is abundant within available habitat, and calling males were estimated to occur at densities of 0.1-1.0/m$^2$.

Searches conducted further north at Philps Peak, Tyndall Range, Mt Field, Mt Anne, Mt Weld and Mt Picton failed to locate the species despite the presence of suitable habitat and weather conditions (Ziegeler 1994).

*Conservation status*

The species is secure. All locations where it has been recorded are in reserves, as is most of the suitable known habitat. Its habitat shows evidence of no fire or only very low frequencies of fire.

*Etymology*

From the Latin *nimbus* (= rain cloud), with reference to the habitat of the species.

*Common name*

The name "moss froglet" has been coined and used for this species (Ziegeler 1994).

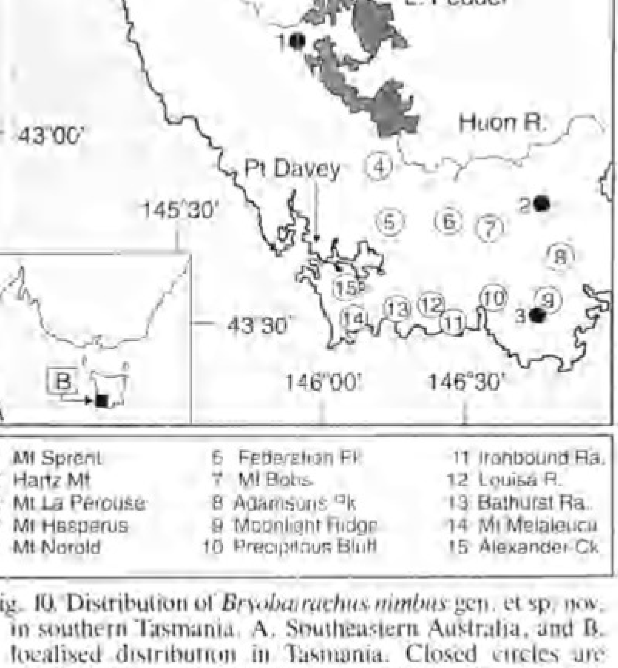


Fig. 10. Distribution of *Bryobatrachus nimbus* gen. et sp. nov. in southern Tasmania. A. Southeastern Australia, and B. localised distribution in Tasmania. Closed circles are localities from which specimens have been collected; open (numbered) circles are call records.

*Comparison with other species*

*Bryobatrachus nimbus* is distinguished from other myobatrachine frogs in Tasmania in the following ways. The species is not associated with bodies of open surface water. It is most likely to be confused with sympatric *Ranidella tasmaniensis* from which it can be distinguished by relatively-short, unfringed toes and by the lack of brilliant carmine patches usually present on the flanks and the concealed surface of the thighs. The call of *R. tasmaniensis* is a quavering "bleat", slowly and irregularly repeated (Littlejohn 1970) and its microhabitat includes vegetation on the margins of open and running water. *R. signifera* has relatively long, fringed toes and is found in the vegetation on the margins of permanent or temporary water bodies. The call is a series of short rapidly-repeated notes: "crick crick crick crick" (Martin & Littlejohn 1982). *Geocrinia laevis* has a rounded snout with a smooth ventral skin which is usually boldly marbled with dark brown markings. The species is found in dry sclerophyll (open) forests at low altitudes (Martin & Littlejohn 1982). These authors describe the call as a harsh grating "cra-a-a-a-ack cra-a-a-a-ack, crack, crack, crack". The other myobatrachine species in Tasmania is *Pseudophryne semimarmorata* which has a smooth ventral surface strongly marbled in black and white. The head is rounded and the undersurface of the thighs are bright yellowish orange to orange in life; the call is a short, harsh "creek" repeated slowly and irregularly (Martin & Littlejohn 1982).

*Comparative material examined*

*Arenophryne rotunda:* UAZ B531, B541, B762, A579-81, A760-1. *Assa darlingtoni:* UAZ A133. *Crinia georgiana:* UAZ B754, A13406. *Geocrinia laevis:* SAM R4260B, R8982A,E. *G. leai:* SAM R5787A. *G. victoriana:* SAM R9425 (2). *Myobatrachus gouldii:* UAZ B491, B534-5, B757, A759. *Paracrinia haswelli:* UAZ B750. *Ranidella bilingua:* UAZ B1927, B1935. *R. deserticola:* UAZ B1930-31. *R. glauerti:* UAZ A191. *R. insignifera:* UAZ A192, A195, B929. *R. parinsignifera:* UAZ A185, B1932-33. *R. remota:* UAZ B1928-9. *R. riparia:* UAZ A184, A189, A198. *R. signifera:* UAZ A193, A197, B898-928. *R. subinsignifera:* UAZ A190. *R. tasmaniensis:* UAZ A186. *Pseudophryne semimarmorata:* UAZ B636. *P. bibroni:* UAZ A577, A172, B532, B540. *P. coriacea:* UAZ A200, B537, B764. *P. guentheri:* UAZ A199, B53 9, B765. *P. occidentalis:* SAM R17522. *Taudactylus acutirostris:* UAZ B759, A205-6. *T. eungellensis:* UAZ A392. *T. rheophilus:* UAZ A775-6, B752. *Uperoleia altissima:* SAM R40146. *U. arenicola:* SAM R17347. *U. aspera:* UAZ A872-8. *U. borealis:* UAZ A863, B862, A226. *U. capitulata:* SAM R29586. *U. crassa:* UAZ A869-70, B871, B483, B486. *U. fusca:* SAM R29603, R29606-7. *U. glandulosa:* SAM R27082. *U. inundata:* UAZ A818-826, B397, B479. *U. laevigata:* UAZ A601, B817. *U. lithomoda:* UAZ A767-8, B896, B812, A799-806. *U. littlejohni:* UAZ A1712, A1717, B1713-1716. *U. martini:* NMV D23636. *U. micromeles:* UAZ A1722. *U. mimula:* SAM R29642-3, R29645-6. *U. mjobergi:* UAZ A582, A880-9. *U. rugosa:* UAZ 1012, A1013, A816, B814. *U. talpa:* UAZ A591-4, B864. *U. trachyderma:* UAZ A621, A892-4, A595-6. *U. tyleri:* NMV D23639, SAM R29659, R29652.

## Discussion

*Bryobatrachus nimbus* exhibits a number of unusual features in its morphology and reproductive biology. Many of the characters contributing to the recognition of the genus and species are influenced by heterochrony in other myobatrachine genera (Davies 1989). The presence of teeth on the maxillary arch, reduction of the vomers and absence of vomerine teeth, presence of a columella and reduction of the palatines, laterally, are all presumed labile features that vary intragenerically in e.g., *Uperoleia* and *Crinia* (*sensu* Heyer *et al.* 1982). However, none of these features either singly or in combination is definitive of *Bryobatrachus*. All are coupled with the unusual feature of fusion of the posterior portion of the vertebral column with the sacrum.

Vertebral fusions tend to be in an anterior/posterior sequence (Trueb 1973), and fusions of presacrals VII and VIII with the sacrum are unusual. The nature of the fusion cannot be described as a presacral shield, as known in a few taxa including *Brachycephalus ephippium* (Brachycephalidae), and thought to be protective on the basis of terrestrialism exhibited by such taxa (Trueb 1973).

Fusions approaching that shown by *B. nimbus* have been recorded in the Bufonidae (e.g., *Didynamipus*, see Grandison 1981), in *Dendrobates* (Trueb 1973), and in the Pipidae; although the fusions reported in *Pseudhymenochirus* and *Hymenochirus* by Cannatella & Trueb (1988) are inferred, and not identified by remnant vertebrae or recorded spinal foramina, vertebral fusion in *Pipa myersi* more closely approximates that in *Didynampis* (Trueb 1984). None of these families is native to Australia.

Although conforming to the myobatrachine pattern, the width of the junction of the alary processes with the hyoid plate is not as broad as in most other genera and approaches that shown by the enigmatic genus *Rheobatrachus* (Davies & Burton 1982; Mahony *et al.* 1984), the subfamilial placement of which remains contentious (Tyler 1989; Littlejohn *et al.* 1993).

Terrestrial egg deposition and direct development have evolved a number of times in Australian frogs (Martin 1967). Reproductive modes include complete intracapsular development (e.g. in the microhylids *Sphenophryne* and *Cophixalus*), through hatching at a relatively late stage in ontogeny (e.g., the myobatrachine *Pseudophryne*) to non-swimming, non-feeding larvae that are subject to bizarre forms of parental care (e.g., the myobatrachine *Assa* and the rheobatrachine *Rheobatrachus*). All of these gradations of direct development are found within the Myobatrachinae, and reproductive mode can sometimes vary intragenerically. In *Pseudophryne*, *P. douglasi* differs from congeners in laying eggs in water and thus not relying upon flooding of nests to initiate hatching of larvae at later stages (Main 1964; Bradford & Seymour 1985), whilst in *Geocrinia*, *G. rosea* and *G. lutea* do not have free-swimming larval stages (Main *et al.* 1959; Main 1963).

Intracapsular development is known for the monotypic genera *Myobatrachus* and *Arenophryne* (Roberts 1981, 1984), and is inferred for *Metacrinia* (Main *et al.* 1959). The larvae of *Geocrinia rosea* are inactive in broken-down egg capsules which fill shallow depressions in damp soil or in the rotten centres of hollow logs (Main *et al.* 1959). Larval life of *G. lutea* resembles that of *G. rosea* (Main 1963). Such larvae are highly modified, having no mouth disc, a large yolk sac, and an elongate tail (Watson & Martin 1973). The structure of the tail reported for *G. rosea* is similar to that observed in *B. nimbus* froglets.

Although details of the life history of *B. nimbus* have not yet been described, our limited data indicate that development is intracapsular until the final stages of metamorphosis, and that the froglets stay in the nest with the broken-down egg capsules until the tail is fully resorbed and metamorphic climax is reached.

The diameters of the eggs at 3.3-3.7 mm are smaller than ovarian diameters recorded for *Arenophryne rotunda* and egg diameters in *Myobatrachus gouldii* (Roberts 1981, 1984), but within the range recorded for *Pseudophryne* spp. and for *Geocrinia victoriana* and *G. laevis* (see Tyler 1989 for compilation of data). All of these species exhibit forms of direct development. Capsule diameter is particularly large, being almost double that recorded in the field for *Myobatrachus gouldii*, and 1.5 times that of eggs hydrated in the laboratory (Roberts 1981). Clutch size compares closely with those of other direct-developing species (Tyler 1989).

Four other Tasmanian species (*Ranidella signifera*, *R. tasmaniensis*, *Geocrinia laevis*, *Pseudophryne semimarmorata*) have advertisement calls composed of trains of pulses. The short pulse trains of *B. nimbus* are similar to those of *R. signifera*, but the call repetition rates and pulse repetition rates and dominant frequencies are higher in this latter species (Littlejohn 1964, 1970). The call of *R. tasmaniensis* is more complex, being composed of a group of pulse trains, or notes, of high and regular pulse rates (Littlejohn 1970), so that it has a bleating quality. The call of *G. laevis* consists of a series of pulse trains in which the pulse intervals decrease through each note (Littlejohn & Martin 1964; Harrison & Littlejohn 1985). The call of *P. semimarmorata* consists of a single complex pulse train, usually with biphasic structure (McDonnell *et al.* 1978). Hence, the advertisement call of *B. nimbus* is sufficiently unlike those of all other species of anuran occurring in Tasmania to be a reliable indicator for identification. Possibly, the most similar advertisement call of a southern myobatrachid to that of *B. nimbus* is that of *Ranidella glauerti* of south-western Western Australia, which consists of a slow pulse train and very short pulse durations (Littlejohn 1959, 1961; M. J. Littlejohn & P. G. Littlejohn unpubl.).

*Bryobatrachus nimbus* is most similar in external morphology and cranial osteology to *Ranidella tasmaniensis* (Davies unpubl.), in its reproductive biology to *Geocrinia rosea* and *G. lutea*, and in the structure of the hyoid to *Rheobatrachus*. It is not possible, therefore, to identify the sister taxon to the genus on the basis of the phenetic comparison presented here. Such an identification must await a detailed analysis of, at least, the subfamily Myobatrachinae, incorporating all available data.

*B. nimbus* appears to be confined to southern Tasmania despite the presence of apparently suitable habitat in highlands beyond. It has been sought north of the Serpentine and Huon River systems without success. The distribution might be explained by the extent of Pleistocene glaciation in the central highlands of the island, and the severity of the cold, dry climate in ice free areas (Galloway 1986) making the central highlands unsuitable for it in the past, coupled with a lack of northward dispersal since.

The region currently occupied by the species has a continually wet equitable climate produced by year round high rainfall within the perhumid cool climatic zone (Gentilli 1972). All localities are less than 40 km from the sea, and are subject to coastal climatic influences, particularly increased precipitation from orographic interaction with moist prevailing west to south-west winds. The direct development of the juvenile stages requires a climate free from the extremes of desiccation. It is most unlikely that the known habitat types could support the species until a very long time after a wildfire (Brown & Podger 1982). *B. nimbus* can be regarded as belonging to fire-intolerant communities, and the occurrence of fire represents the greatest potential threat to its survival.

During the present work, several clutches of developing eggs were found on the surface of moss at Hartz Mountains. The site had been covered by a snowdrift for some time. Egglaying beneath the snow rather than in nest could account for their location and later exposure after the thaw. The embryos would be prone to desiccation before completing their development. Alternatively, stepping on patches of moss when walking across the site could eject eggs from nest chambers. Whichever is the case, caution is advisable when working at breeding locations.

## Acknowledgments

Dr Graeme Watson recorded the call used in the analysis. Dr Dale Roberts located the first nest chamber and helped to clarify the breeding biology. Dr Roy Swain and Mr J. Lim provided assistance in the laboratory, and Nikki Mitchell helped in the field. Barbara and Peter Willson, Jayne Balmer, Sib Corbett and Michael Askey-Doran reported the calls from Mt Norold, Bathurst Range, Moonlight Ridge and Mt Melaleuca. We thank staff of the Parks and Wildlife Service who contributed to this study and Assoc. Profs A. A. Martin and M. J. Tyler for constructive reviews of the manuscript.

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