FROGS OF THE GENUS *UPEROLEIA* GRAY (ANURA: LEPTODACTYLIDAE) IN SOUTH-EASTERN AUSTRALIA

by MARGARET DAVIES* & M. J. LITTLEJOHN†

Summary

DAVIES, M. & LITTLEJOHN, M. J. (1986) Frogs of the genus *Uperoleia* Gray (Anura: Leptodactylidae) in south-eastern Australia. *Trans. R. Soc. S. Aust.* **110**(3), 111-143, 28 November, 1986.

A review of the species of *Uperoleia* of south-eastern Australia has resulted in the clarification of the status of several taxa and the description of two new species. Recent redescriptions of *Uperoleia laevigata* and *U. rugosa* are expanded to incorporate data on morphology, osteology and structure of advertisement call from across their extensive geographic ranges. Variation in these features is examined and, in many cases, the limits of variability for certain characters are established. *U. fimbrianus* (Parker) is placed in the synonymy of *U. rugosa* (Andersson). Two new species, *U. tyleri* sp. nov. and *U. martini* sp. nov. are described from south-eastern coastal N.S.W. and eastern Victoria.

The dominant frequencies in advertisement calls of all species discussed are similar and within the range, 1927-2432 Hz, depths of amplitude modulation generally exceed 90% for all taxa. Most differentiation between species is evident in call duration, in the number of pulses in the call, or in the dependent character, pulse rate.

KEY WORDS: *Uperoleia*, Anura, new species, morphology, osteology, advertisement calls.

Introduction

The Australian leptodactylid genus *Uperoleia* Gray comprises a group of small, myobatrachine frogs exhibiting limited morphological diversity. Tyler, Davies & Martin (1981a, b, c) revised the genus and expanded the known species from three to 18. More recently, an additional species has been described by Davies *et al.* (1985) from the Pilbara region in Western Australia.

All of the above contributors investigated species principally from the north and west of Australia, leaving the fauna of the eastern states largely unknown. Tyler *et al.* (1981a) and subsequent authors (Cogger 1983; Cogger *et al.* 1983) recognised three species in eastern Australia: the edentate *U. rugosa* (Andersson) and *U. fimbrianus* (Parker), and the dentate *U. laevigata* Keferstein. These species were redescribed from information obtained from the type specimens, in the former two cases, and from the type series, in the last (Tyler *et al.* 1981a); the presence of a number of undescribed species in eastern Australia was indicated by these authors.

Davies & McDonald (1985) supplemented the redescription of *U. rugosa* with data on osteology and advertisement call of males, derived from topotypic material, thus facilitating the identification of specimens in various museum collections.

On the basis of the advertisement call, Littlejohn (1967) recognised three species from south-eastern Australia: a large dentate species which he identified as *U. marmorata* Gray, and two other species whose identities were undetermined, so designated "*U. rugosa* (form A)" and "*U. rugosa* (form B)".

Tyler *et al.* (1981a) showed that *U. marmorata* was restricted to the northwest of Western Australia, thus leaving the identity of the large, dentate species undetermined. Here we identify and amplify the undetermined species of Littlejohn (1967), and provide further information on the named species of eastern Australia.

Materials and Methods

Specimens examined are deposited in the Australian Museum, Sydney (AM), British Museum (Natural History), London (BMNH), CSIRO Division of Wildlife Research Collection, Canberra (ANWC), University of Kansas Museum of Natural History, Lawrence (KU), Museum of Victoria, Melbourne (NMV), Queensland Museum, Brisbane (QM), South Australian Museum, Adelaide (SAM), Museum of Natural History, Stockholm (NRAM), and the University of Adelaide osteological collection (UAZ).

Morphological measurements (in mm), obtained by the methods of Tyler (1968), are: snout-to-vent length (S-V), tibia length (TL), eye diameter (E), eye-to-naris distance (E-N), internarial span (IN). Because of the large parotoid glands covering the

* Department of Zoology, University of Adelaide, G.P.O. Box 498, Adelaide, S. Aust. 5001.
† Department of Zoology, University of Melbourne, Parkville, Victoria 3052.

side of the head and the obscured tympana, customary measurements of head width and head length could not be taken. Results are expressed as mean ± standard deviation with ranges in parentheses.

The presence or absence of teeth were determined externally by using the following procedures: when dentate species are viewed from the ventral surface, the upper jaw is notched to receive the superiorly protruding symphysis of the mentomeckelian bones; the snout is rounded in ventral view and the ventral curvature of the upper jaw is slight. Conversely in edentate species, the upper jaw is not prominently notched anteriorly, although the mentomeckelian symphysis is prominent, and the ventral curvature of the upper jaw is deep. These features are shown in Fig. 1. In doubtful cases, fine forceps or a mounted needle were used to check for the presence of serrations.

Osteological data were obtained from cleared and stained specimens, prepared after the methods of Davis & Gore (1947) for bone and Dingerkus & Uhler (1977) for bone and cartilage. Osteological descriptions follow Trueb (1979). Material that has been cleared and stained is indicated by (A) following the museum abbreviation and registration number or by specific designation.

Advertisement calls were recorded in the field, and the appropriate (effective) temperature (water, wet-bulb air) measured at the calling site. One of a selection of tape recorders (EMI 1.2B, FI-CORD 202, NAGRA IIIBH, NAGRA 4.2, UHER Report 4000L) and one of the following microphones (AKG 19B, BEYER M69, BEYER M88, ELECTRO-VOICE 644, GRAMPIAN D19, RESLO DPH) were used. All recordings were analysed on a NORLAND 3001/DMX processing digital oscilloscope, with playback on a REVOX B77 tape recorder. An ALISON 2AB variable filter, set at a low pass of 4800 Hz, was inserted between the output of the tape recorder and the oscilloscope in order to prevent aliasing at the minimum sampling interval of 100 μs (i.e. at a frequency of 10 000 Hz). Overall temporal variations during recording and analysis are estimated to be less than ± 1.5%, and frequency responses of all items of equipment are more than adequate for the narrow range involved (1900–2500 Hz).

One clear call, usually the last in the recorded sequence, was analysed, and values for each of the following five attributes determined: number of pulses (direct count), duration (ms), average pulse rate (pulse.s^{-1}; from the peak of the first clear pulse to the peak of the last clear pulse), dominant frequency (Hz; power spectrum analysis—from whole call if short, or from middle quadrant if long), and depth of amplitude modulation of pulses (%; near the middle of the call). Hard copies of the displays on the monitor screen of the processing digital oscilloscope were prepared on a LINSEIS LY 1800 X-Y recorder.

Line drawings were obtained with the aid of a Wild M8 dissecting microscope with an attached 0.4× reducing lens and a camera lucida.

Results

Taxonomic decisions

Lynch (1971) illustrated the skull of a specimen of *U. rugosa* from St George, Qld (KU 109861). Comparison of the illustration, and of the specimen examined by him, with the data obtained from topotypic specimens of *U. rugosa* (Davies & McDonald 1985) indicates that all of the specimens are conspecific. St George is the type locality of *U. fimbrianus* (Parker 1926), a species separable from

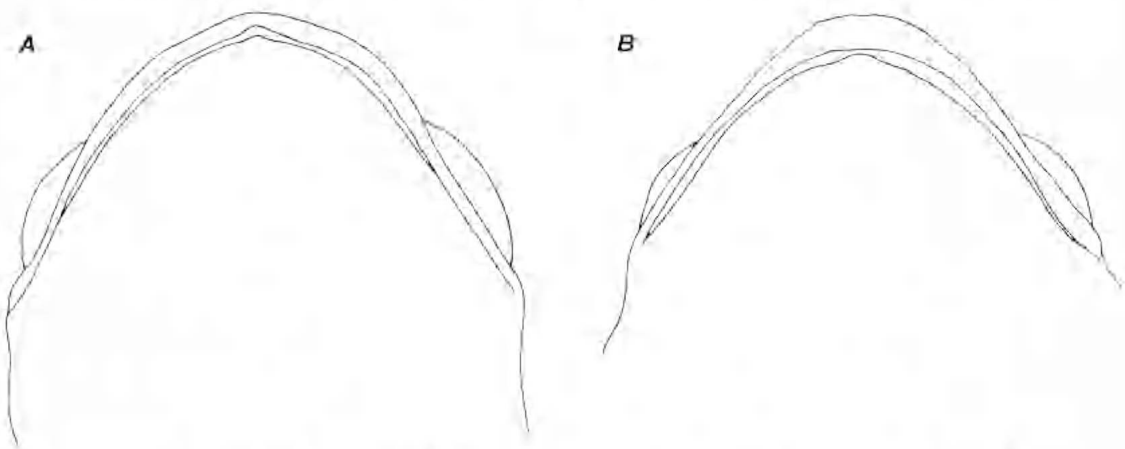

Fig. 1. Ventral views of the head of A, dentate species of *Uperoleia* and B, an edentate species of *Uperoleia*.

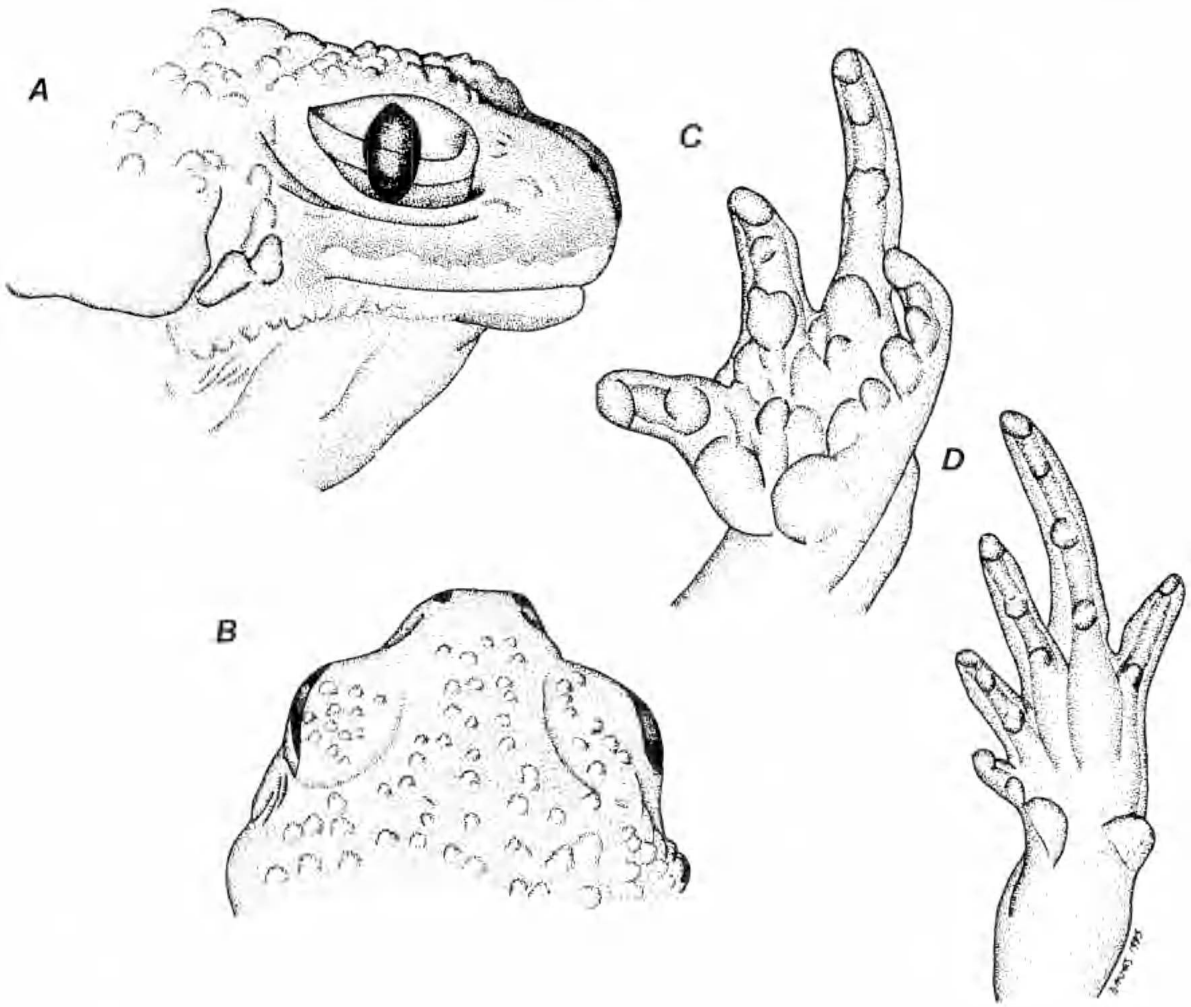

Fig. 2. A, Lateral and B, dorsal views of the head; C, palmar view of hand and D, plantar view of foot of *Uperoleia rugosa* (NMV D25090) from Savernake, N.S.W.

U. rugosa only by size (Davies & McDonald 1985). Examination of call data from edentate specimens assigned to *U. rugosa* (form A of Littlejohn 1967), and the examination of external morphology and osteology of material deposited in many Australian museums, confirms the identification of *U. rugosa* (form A) as *U. rugosa* and provides no support to the recognition of *U. fimbrianus*. Accordingly, we transfer *U. fimbrianus* (Parker) to the synonymy of *U. rugosa* (Andersson).

U. rugosa (form B of Littlejohn 1967) is a dentate species (Davies unpubl.). The only other dentate species described from eastern Australia is *U. laevigata* Keferstein 1867. Our examination of preserved material deposited in Australian museums, and our data on call structure, indicate that *U. rugosa* (form B) is *U. laevigata* Keferstein. Our data on the type series include only external morphology, but we remain confident in this identification.

On the basis of our studies of morphology and vocalizations, it is clear that *"U. marmorata"* (*sensu* Littlejohn 1967) comprises two undescribed dentate species, which are now described and named.

Uperoleia rugosa (Andersson)

FIGS 2-8

Hyperoleia marmorata: Fletcher, 1890, p. 672 (part.).
Pseudophryne rugosa Andersson, 1916, K. Svenska Vetenskapsakad. Handl. 52, 9, p. 13.
Pseudophryne fimbrianus Parker, 1926, p. 669; Wilkins, 1928, p. 278.
Uperoleia rugosa: Parker, 1940, p. 70 (part.); Erspamer,

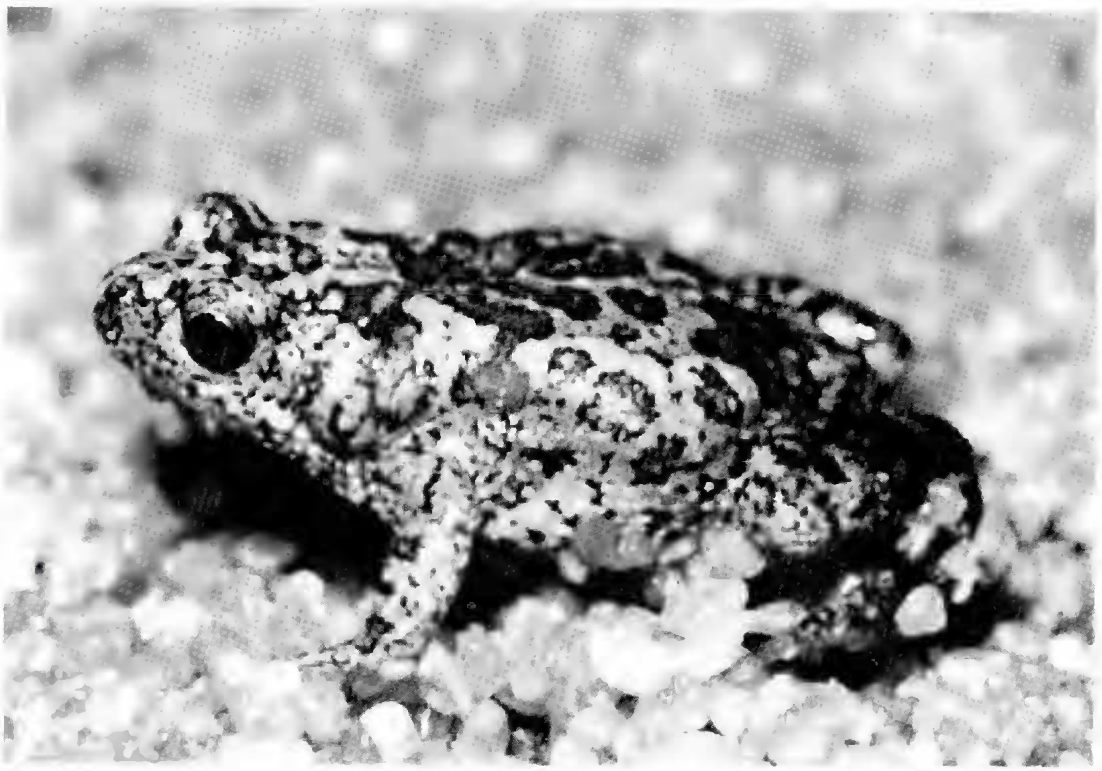

Fig. 3. *Uperoleia rugosa* (in life) from Anakie, Qld.

de Caro & Endean, 1966, p. 738 (part.); Lynch, 1971, p. 99; Erspamer, Negri, Erspamer & Endean, 1975, p. 41 (part.); Roseghini, Erspamer & Endean, 1976, p. 35 (part.); Erspamer, Erspamer & Linnari, 1977, p. 68 (part.); Barker & Grigg, 1977, p. 188 (part.); Archer, 1978, p. 112; Tyler, Davies & Martin, 1981a, p. 17; Cogger, 1983, p. 86; Cogger, Cameron & Cogger, 1983, p. 34 (part.); Davies & McDonald, 1985, p. 37; Tyler, 1985, p. 408; Mahony & Robinson, 1986, p. 120.

Uperoleia rugosa (form A): Littlejohn, 1967, p. 153, Blake, 1972, p. 122.

Uperoleia marmorata: Moore, 1961, p. 219 (part.); Brooker & Caughley, 1965, p. 239.

Uperoleia sp.: Davies, 1984, p. 790 (part.).

Uperoleia fimbrianus: Tyler, Davies & Martin, 1981a, p. 18; Cogger, 1983, p. 83; Cogger, Cameron & Cogger, 1983, p. 32; Tyler, 1985, p. 407.

Definition: A small to moderately-large species (♂♂ 18–32 mm S-V, ♀♀ 18–30 mm S-V), characterised by short to moderately-long hind limbs (TL/S-V 0.29–0.41); fringed toes with usually a trace of basal webbing; prominent subarticular and palmar tubercles; frontoparietal fontanelle not exposed; carpus of five elements; anteromedial processes of anterior hyale of hyoid slender; ilial crest absent; advertisement call a short pulsed note of 3–5 pulses with a pulse repetition rate of about 31 pulses sec^{-1}.

Material examined: Qld: NRAM 1630 (Holotype *Pseudophryne rugosa*), SAM R27052-3, R27054(A)-5(A), Mt Colosseum; BMNH 1947.2.18.70 (holotype *Pseudophryne fimbrianus*) St George district: QM J25078(A) 48 km E St George, SAM R3688, R3737, St George; KU 109861(A), St George; NMV D25105-6(A) 3.2 km E Gracemere; D25107, 6.4 km E Gracemere; QM J12673 Burpengary; J14385, Gilruth Plans via Cunnamulla; J17754, Alton; J18819, J18824, J18840(A)-41(A) E of Withcott; J18818(A), J18821, J18826, J18829, J18835-6(A), J18842, Waratah Station via Cunnamulla; J18830, E of Laidley on Granchester Rd; J28239(A), J28240-43, J28244(A), J29067-9, 24 km W Moonie; J42543-4, J42546, J42550(A), Moonie; J42538, Roma; J31961-2(A), Bollon; J38654(A)-5(A), Hornet Bank, Injune Rd; J12354(A), J12366, J12371, Wilkie Ck, SW Dalby; J12722-3(A), J12725-6, AM R5822-3, Eidsvold; QM J18827, J18846, South of Gayndah; J18828, Rocklea, Brisbane; AM R16910, Brisbane; QM J19538, Warrawee; J19539-41 Flinders Peak Rd, turnoff from Boonah Rd; J19928, 4.6 km S Ferndale; J19950, Ban Ban; J19954, 3.2 km W Beenleigh; J25922, J40429, Texas Caves Area; J28510(A), J28515-6, Gin Gin; J29014-6(A), Waterford Rd, 6 km E Beaudesert Rd; J35436-7, Old Dump, Inglewood; J42539(A), J42551, J42553, Causeway on Beaudesert Rd between Jimboomba and Cedar Grove Rd (27°51', 153°01'); J42540, J42542, Crossing Beaudesert Rd, Tamborine Rd (27°48', 153°02'); J42541, Beaudesert; J42545, J42547-9, J42552, Mt Lindsay Highway, S of Beaudesert (25°00', 152°59'); J37704(A), J37705-6, J37707(A), between Anakie and Sapphire; J37708-9, J37710(A), J37711-16(A), Mowbray; J37717-18(A), J37719-20(A), Tomahawk; J37721, Anakie; SAM R29672(A)-3(A), QM J45975, Springsure; QM J45977, Anakie; SAM R29674(A), R29675, 1.7 km from Cabbage

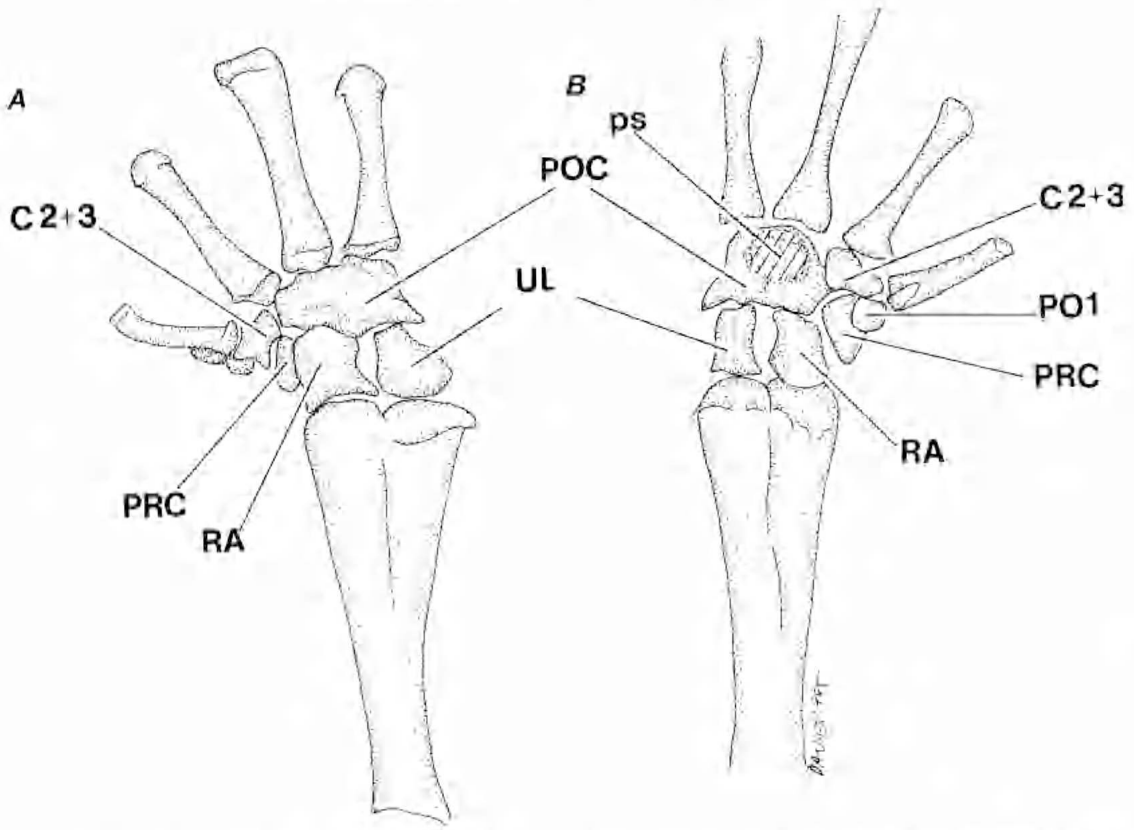

Fig. 4. A, Dorsal and B, palmar view of bones of carpus of *Uperoleia rugosa*. UL, ulnare; RA, radiale; POC, O. centrale postaxiale; PRC, O. centrale preaxiale; C(2+3), fused carpal elements of O. distale carpale 2 and 3; PS, palmar sesamoid; PO_1, basal prepollical element.

Tree Creek, Nathan Gorge Rd; QM J45973-74, Cabbage Tree Creek; QM J45976, Glenleigh Station beside road to Glenhaughton Station; QM J45980-86, J45987(A), SAM R115648-50, R29676-78(A), R29679(A), R29680-1(A), R29682-4(A), R29685(A), R29686, R21558-61(A), UAZ A1012(A), A1013(A), Dynevor Downs; QM J45978-9, SAM R29687, Boorara Station; AM R115652, 17.6 km N Moura; R115306, R113367-69, Cecil Plains Rubbish Tip; AM R5822-3, Eidsvold; SAM R29688-90, DPI Swamp, Charleville. *N.S.W.*: AM R36862-4, 19.2 km W Tenterfield; R37052(A), R37053-4(A), R37055-6, 22.4 km SE Bonshaw on Bruxnor Highway; R37096, 56 km W Tenterfield, Mole River; R90659-61, Blacklands Gap Rd, 6 km NW Maids Valley (29°05', 151°35'); AM R66557-60, R66562, 22.4 km downstream from Dungog on Williams River; R93727-31, 5 km N Whiporie on Casino-Grafton Rd; AM R784, R984, Yandembah, 32 km W Hillston; R12806, Welby, Nyngan; R28004(A), R28005-6, R24475-6(A), R24477-78, R24480, R24482-3(A), R24484, R24486-91(A), R24492, Nyngan; R28635-8, between Nyngan and Nevertire; R15315-7, 50 km W Byrock; R16040, 51 km W Byrock; R15800-1, R15803, Byrock; R16098 Brewarrina; R28357-8, R28624-5, Lake Cargelligo; NMV D55117-21(A), QM J39239, J39242-6, West Wyalong; J28450-2(A), Condoblin; SAM R14187 Moulamein; NMV D9199(A), D9200-1, D9259(A)-62(A), D9263, D9264(A)-5(A), D9266-7(A), Tocumwal; D18856-61(A), D18862-84(A), D18885-900, 4.8 km S Cowra; D25077-79(A), D25080, 6.4 km SW Cowra; D25001-3, D25005(A)-9, D25011(A)-14, Savernake; D25086-91(A), D25092(A)-25101(A), D25102-4, Lignum Swamp, Savernake; D25004, 20.8 km N Mulwala; D25015-6 9.6 km N Mulwala; D25082, 4 km N Tomingley; ANWC A936-84, Lake Cowal; A1070-72, 4 km N Warren; ANWC A1140-2, Sandy Camp Macquarie Marsh area; AM R115632-44, R115646, 5 km E Eulo; R92159, Buckingbong S.F., S of Narrandera; R115647, Glenelg; R45105, 32 km S Condoblin; R115588-28, R115648-50, Caragabal; R112299 Bom Bom S.F. (29°44', 152°58'); R115584, Nettle Creek, 19.2 km from Copmanhurst on Tabulum Rd; R5590-1, Cumborah, NW Walgett; R50493-500, 11.2 km W Glen Innes on Inverell Rd (29°43', 151°58'); R115575-6, R115579, R115581-2, nr Bulgandramine; R102886, Thurloo Downs Hst; SAM R28786-7, UAZ A816, UAZ B814, Severn River (29°28', 151°29').

Variation in External Morphology

There is a considerable range in the size of specimens of *U. rugosa* (males 18.4–32.0 mm S-V, females 17.7–30.4 mm). Specimens from southern coastal areas of Queensland and northern N.S.W. are smaller than those from more arid inland areas, with the exception of a series from Tocumwal, N.S.W. (♂♂ 18.4–26.2 mm S-V, ♀♀ 20.2–25.3 mm S-V from coastal areas, compared with ranges of

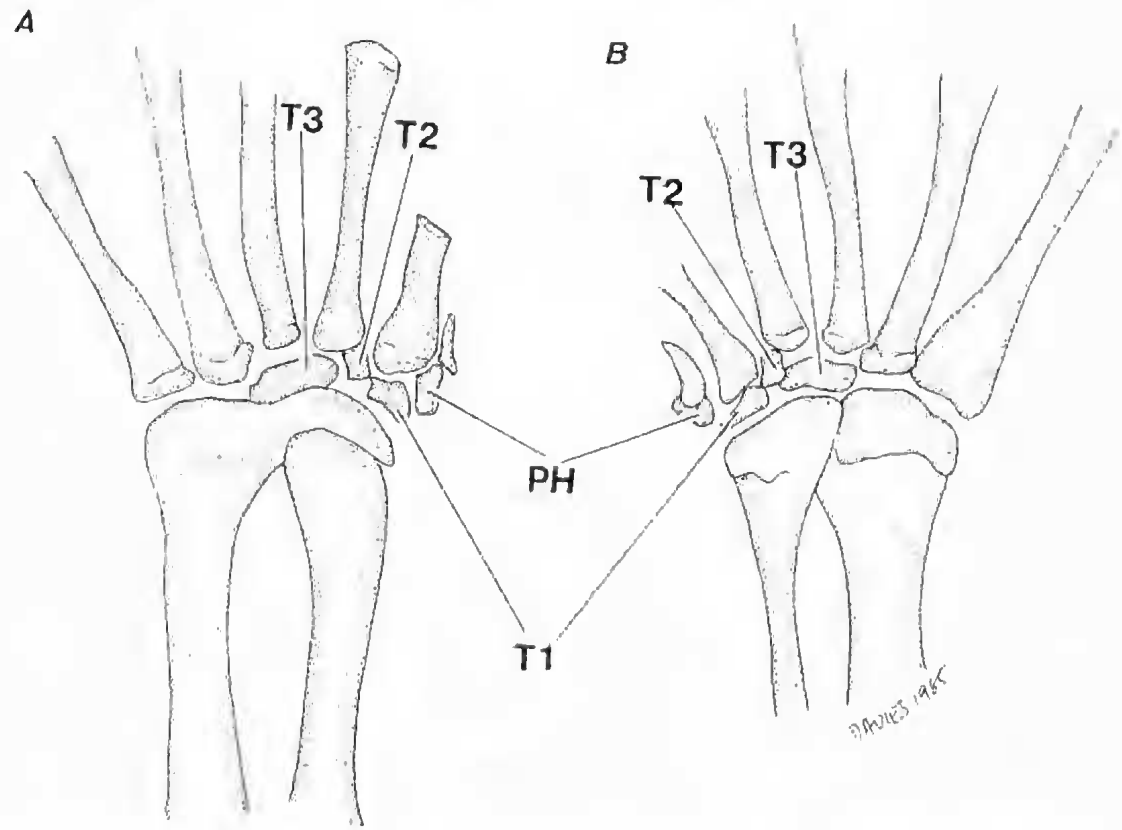

Fig. 5. A, Dorsal and B, plantar views of tarsus of *Uperoleia rugosa*. PH, O. centrale prehallucis; T_1, lateral tarsal element; T_2, second tarsal element; T_3, medial tarsal element.

20–32 mm S-V for males and 22-30 mm for females in inland areas). Geographic variation in size is reflected also in relative lengths of the hind limbs in these populations (TL/S-V 0.34 ± 0.02 [0.29–0.39] coastally, and 0.36 ± 0.02 [0.32–0.41] inland). For the species over its entire range, TL/S-V is 0.36 ± 0.03 [0.29–0.41].

The head is usually small in relation to the body, and is separated from the axilla by the well-developed parotoid glands. The shape of the snout in dorsal view is either truncated (Fig. 2A), or slightly rounded (see Davies & McDonald 1985). Each condition occurs in about equal proportions in the material examined. The snouts of some specimens may have been incorrectly recorded as blunt because poorly preserved specimens (as indicated by dehydrated fingers and toes) always have truncated snouts. Most well-preserved specimens from Savernake, N.S.W., at the southern extremity of the species' range have truncate snouts (Fig. 2B).

The eye-to-naris distance is always greater than the internarial span, and is subject to little geographic variation (E-N/IN 1.61 ± 0.28 [1.12–2.3]). The nostrils are located more laterally than dorsally (Fig 2B).

The hands are broad, and with short fingers (occasionally slender) bearing poor or moderate fringing in the approximate ratio of 1:2. There is no webbing between the fingers. Subarticular and palmar tubercles are prominent (Fig. 2C) in about ⅔ of the specimens.

There is no webbing between the toes in ⅙ of the specimens examined, and minimally basal in the remainder. Fringing on the toes varies: about ⅙ have reduced fringing, about ⅓ moderate, and the remainder have well-fringed toes (Fig. 2(D).

Subarticular tubercles on the toes are usually conical. The inner metatarsal tubercle is angled along the axis of the first toe and the outer is angled to the long axis of the foot; occasionally, the inner metatarsal tubercle is not angled, but perpendicular to the long axis of the foot.

Rugosity of dorsal skin varies; poorly, moderately and very rugose specimens occur in equal proportions. Dermal glands are well developed (Fig. 3), but occasionally poor development of the parotoid glands is recorded. Development of

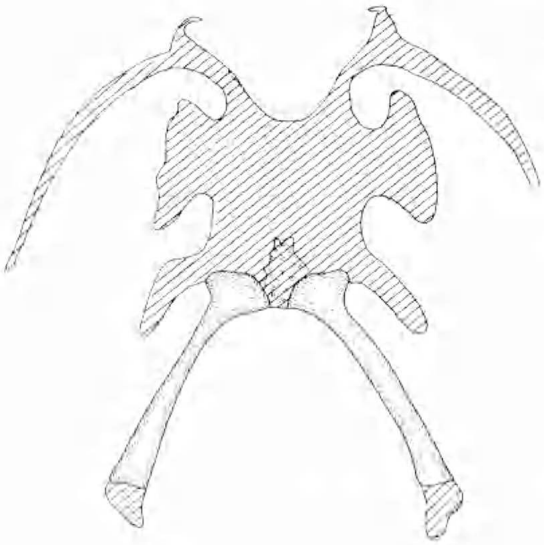

Fig. 6. Hyoid of *Uperoleia rugosa*. Cross hatching indicates cartilage (UAZ B814).

inguinal and coccygeal glands are similar (1:1:4, poor:moderate:well developed).

Submandibular gland is discrete or disrupted in approximately equal proportions. Scapular plicae are not apparent, and coloration of the dermal glands is poorly developed. Hence lateral golden or cream stripes, as found in *U. lithomoda* (Tyler *et al.* 1981a), are not apparent. Dorsal colour pattern varies. Strong patterning is rare in specimens with very rugose dorsa, but is common in other material (Fig. 3).

Cloacal flaps occur on all specimens, with long finger-like fimbriations on most female specimens (as noted by Parker 1940). Some males possess short fimbriations on the cloacal flap but most show scalloped or slightly indented cloacal flaps.

Anterior eye flaps are poorly developed or absent.

A granular ventral surface occurs in about ¼ of the specimens. The granularity usually is poorly to moderately developed, except in material from the southern extremity of the range.

Ventral pigmentation is absent in about $\frac{1}{6}$ of the specimens, and only a faint dusting of pigment is detectable in ½; islands of pigment (as described in topotypic material by Davies & McDonald 1985) are found in the remaining ⅓ of the material.

Osteology

Davies & McDonald (1985) described the osteology of topotypic specimens of *U. rugosa;* and Lynch (1971) illustrated and described certain features of *U. rugosa* from St George, Qld. We have examined a further 58 specimens from across the species range for osteological variation.

Davies & McDonald (1985) omitted descriptions of the carpal and tarsal bones and hyoid in their osteological description of *U. rugosa.* We have included these.

Carpus: The carpal type consists of five elements. Little torsion occurs. Both the O. ulnare (UL) and

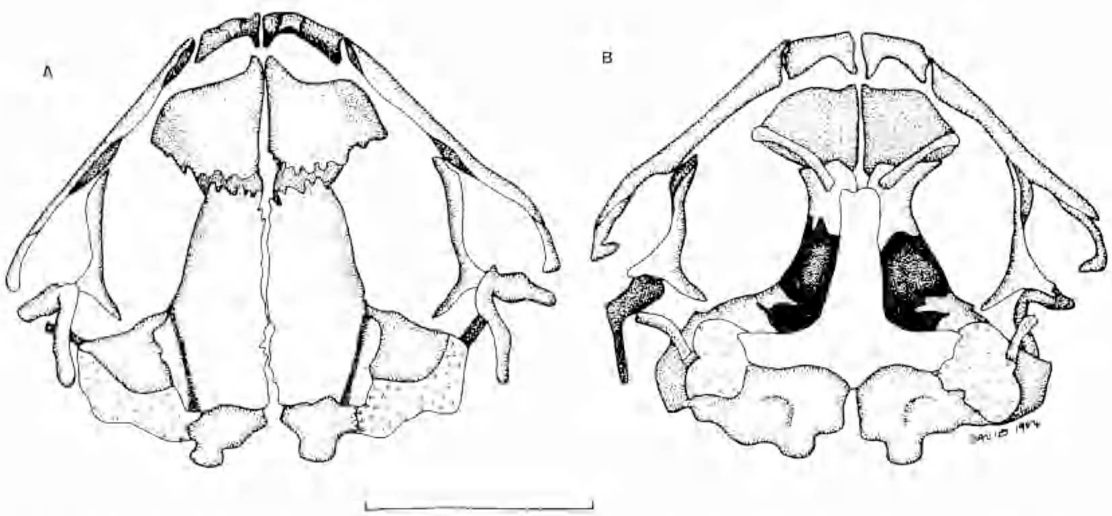

Fig. 7. A, Dorsal and B, ventral views of the skull of *Uperoleia rugosa* (NMV D25104) from Savernake, N.S.W. Scale bar = 5 mm.

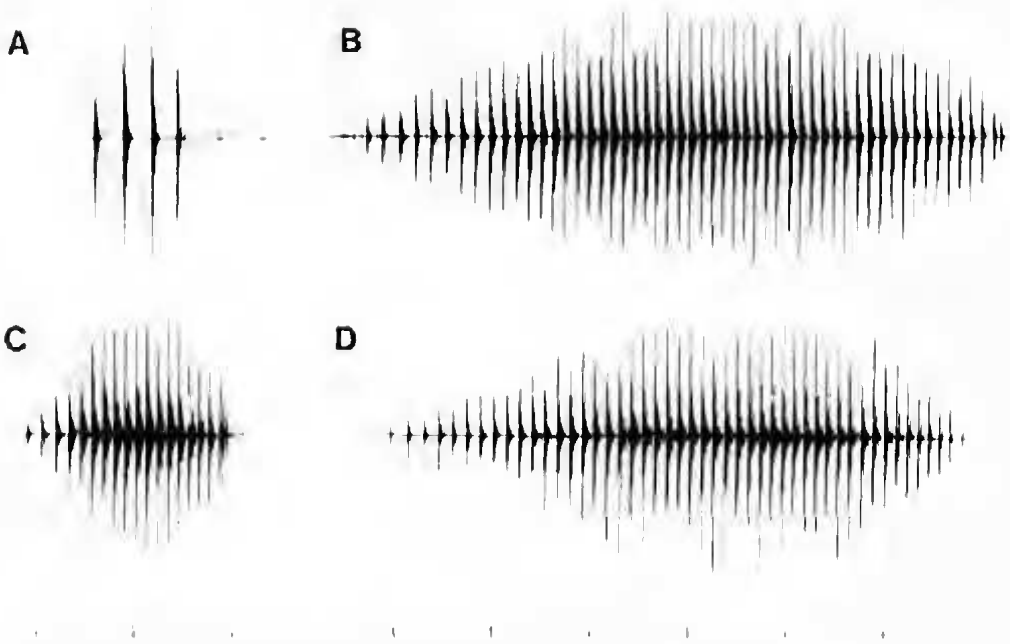

Fig. 8. Sonagrams of the advertisement calls of A, *Uperoleia rugosa*, Savernake, N.S.W. (R211 #1 NMV D25085), 27.vii.1969, AW=14.3°C; B, *U. laevigata*, Oakdale, N.S.W. (R304 #8), 30.ix.1975, AW=12.7°C; C, *U. tyleri*, Jervis Bay, A.C.T. (R135 #5), 17.i.1963, AW=15.5°C; *U. martini*, 4.8 km SW Nowa Nowa, Vic. (R153 #2), 7.xii.1963, AW=15.0°C. Time marker: 100 ms intervals between peaks.

the O. radiale (RA) are present. The O. radiale is the larger. These elements articulate with the O. radioulna proximally, and with each other at their proximomedial border. Distally both elements articulate with the large transversely elongated O. centrale postaxiale (POC). The O. radiale articulates laterally with the O. centrale preaxiale (PRC).

The O. centrale postaxiale articulates distally with the bases of O. metacarpi III, IV and V. From the lateroproximal corner, a small flange extends proximally onto the lateral surface of the O. ulnare. Ventromedially is a depression on which a palmar sesamoid (PS) is situated.

The O. centrale preaxiale articulates laterally with the O. radiale, distally with the O. centrale postaxiale and with the fused carpal elements of the O. distale carpale 2 and 3 (C2+3) and laterally with the basal prepollical element (PO1) (Fig. 4).

This description coincides most closely with Andersen's type 2, found in leptodactylids, and not with his myobatrachid pattern (Andersen 1978[1]).

Tarsus: The O. tibiale and O. fibulare are elongated elements fused at either end. The O. tibiale extends as far as the distal end of the O. fibulare. Three distal tarsal elements are present. The lateral element (T_3) is the largest and lies at the base of O. metatarsus III, and extends laterally to articulate with the medioproximal side of the base of O. metatarsus IV and medially to the base of O. metatarsus II. The second element (T_2) lies at the base, slightly laterally to O. metatarsus II. The medial element (T_1) lies at the base of O. metatarsus I and also articulates with the O. centrale prehallucis (PH) (Fig. 5). This description corresponds to tarsal type 1 (Anderson 1978[1]).

Hyoid: The hyoid plate is slightly broader than long. The hyale are slender with well-developed slender anteromedial processes. Alary processes are broad, and not pedunculate. Posterolateral processes are moderately long, and slightly expanded. The posteromedial processes are ossified (Fig. 6).

[1] Anderson, M. L. (1978) The comparative myology and osteology of the carpus and tarsus of selected anurans. Ph.D. dissertation, Dept of Systematics and Ecology, University of Kansas. Unpublished.

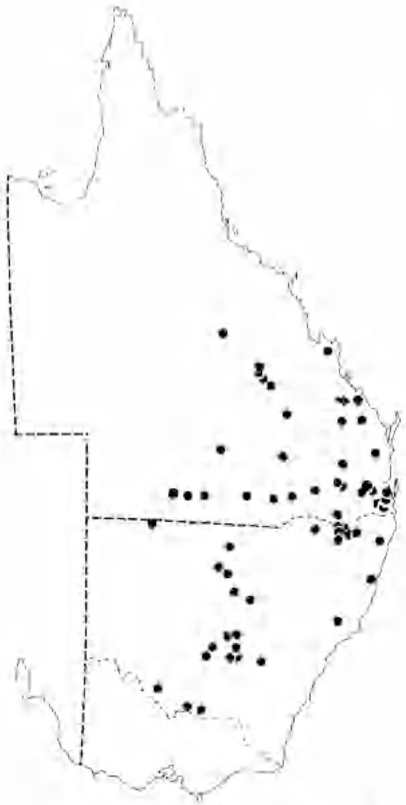

Fig. 9. Distribution of *Uperoleia rugosa*. The arrow indicates the type locality.

Variation

Skull: All but two of the adult specimens examined show a consistent overlap of the sphenethmoid by the posterior extremities of the nasals. Nasal contact with the anterior extremities of the frontoparietals is variable; but, where no contact occurs, separation of these elements is slight. Medial extension of the nasals varies, with approximately equal proportions of no extension, moderate extension and extreme extension (as illustrated by Davies & McDonald 1985). Variation also occurs in the crescentic shape of the anterior edges of the nasals, ranging from the curved condition illustrated by Davies & McDonald (1985) and by Lynch (1971) to almost straight.

The anterior extremities of the frontoparietals usually are crenate, and, occasionally, are extended anterolaterally. The more usual condition is one of truncated anterior extremities (Fig. 7).

All adult specimens have minimal exposures of the frontoparietal fontanelle, ranging from that shown in Fig. 7 to slightly greater. The medial margins of the frontoparietals usually are crenate, but occasionally are almost smooth.

Variation occurs in the form of the carotid canal groove on the posterolateral frontoparietals. In most specimens, the grooves are deep (Fig. 7); occasionally they are partially roofed, and very occasionally they are extremely shallow, or not detectable.

The palatine processes of the premaxillaries range from almost abutting to moderately-widely separated (Fig. 7). The pars facialis of the maxillary is moderately-deep in all specimens, but in some it is foreshortened and shallow anteriorly. In a few specimens, the dorsal surface is not straight, but is irregularly produced.

The palatines are expanded medially in some specimens, particularly those from central Queensland. Vomerine remnants vary considerably—from completely absent (Fig. 7), through present on only one side medial to the palatines, to small fragments at the edges of the choanae.

Carpus and tarsus: No intraspecific variation is apparent in tarsal bones. Some variation is apparent in the fusion of carpal elements 2 and 3. These bones are not fused in five adult specimens, NMV D9199, D9264, D9259 and QM J18841, J18818. In NMV D9267, the bones are fused on one hand and unfused on the other. In two specimens (AM R24483, SAM R29681), the bones are fused but suture lines are apparent. In one subadult specimen (UAZ A1012), the carpal bones are not fused; but in two other subadult specimens fusion has occurred (NMV D25101, UAZ A1013). Other specimens (QM J18840, J18836, NMV D9260-1, D9265) from the same localities as those in which fusion of carpalia 2+3 has not occurred, exhibit fusion.

Advertisement call

Davies & McDonald (1985) reported that the call of *U. rugosa* consisted of four pulses, with a pulse repetition rate of about 34 pulses sec^{-1} and a dominant frequence of about 2583 Hz. Values for calls of five individuals from a population at Savernake, N.S.W., near the southern limit of distribution, are given in Table 1. An oscillogram of the call of one of these individuals is presented in Fig. 8.

Comparison with other species

Uperoleia rugosa is an edentate species with an unexposed frontoparietal fontanelle; these features are shared with *U. minima*, *U. aspera*, and some *U.*

TABLE 1. *Advertisement call characteristics of four species of* Uperoleia. *Values are means with ranges in parentheses.*

Species	Location (Date)	N	Temperature (°C)	Duration ms	Pulses (n)	Pulse rate ($p.s^{-1}$)	Dominant frequency (Hz)	Amp. Mod. %
Uperoleia rugosa	Lignum Swamp Savernake Station, Savernake, N.S.W. 27.vii.1969	5	13.3 (12.6–14.3)	94.4 (81.4–102.8)	3.4 (3– 4)	31.1 (22.8– 40.8)	2054.6 (1943–2207)	99.1 (98.3–99.8)
Uperoleia laevigata	Oakdale, N.S.W. 30.ix.1975	5	12.0 (11.7–12.7)	637.8 (572.6–680.0)	52.0 (48–55)	80.7 (77.0– 83.0)	2244.2 (2109–2373)	94.3 (91.3–96.5)
	6.4 km NW Walwa, Vic. 2.ix.1964	5	10.0 —	531.5 (405.0–608.2)	39.6 (32–44)	73.8 (69.4– 78.0)	2244.8 (1927–2402)	*
	4.8 km W Delegate, N.S.W. 15.xi.1965	8	11.1 (10.6–11.5)	603.7 (499.0–723.6)	48.8 (42–56)	80.8 (69.7– 95.0)	2308.5 (2178–2432)	97.6 (89.0–99.6)
Uperoleia tyleri	near Naval College Jervis Bay, A.C.T. 17.i.1963	2	15.5 —	259.5 (208.0–311.0)	22.0 (18–26)	84.5 (83.1– 85.9)	2060.5 (2031–2090)	95.2 (92.4–97.9)
	Narrababra, N.S.W. 24.ix.1985	4	14.4 (13.7–14.8)	230.2 (212.6–253.2)	21.8 (19–25)	92.2 (82.1– 95.9)	2107.0 (2012–2236)	98.1 (95.8–99.7)
	7 km ENE of Marlo, Vic. 27.xi.1981	3	17.0 (16.4–17.6)	225.6 (202.0–241.0)	24.3 (22–26)	108.5 (105.6–112.1)	2252.3 (2148–2363)	97.0 (94.9–98.4)
Uperoleia martini	4.8 km SW Nowa Nowa, Vic. 7.xii.1963	5	15.8 (15 –16.5)	610.2 (517.2–753.0)	49.8 (43–62)	80.8 (72.2– 87.3)	2013.8 (1992–2051)	96.7 (88.8–99.7)
	Narrabarba, N.S.W. 24.ix.1985	2	14.5 (14.2–14.8)	674.7 (603.0–746.4)	51.0 (47–55)	75.1 (72.8– 77.4)	2295 (2207–2383)	98.1 (97.7–98.4)
	1.9 km S Marlo, Plains Rd on Cape Conran-Cabbage Tree Rd, Vic. 26.ix.1985	3	7.9 (7.2– 8.4)	595.9 (467.6–716.2)	37.0 (32–42)	62.1 (58.0– 67.7)	2112.7 (2070–2168)	98.8 (98.3–99.0)
	6 km NNE of Yarram, Vic. 1.xii.1980	5	16.5 (15.5–17.1)	483.1 (463.2–522.8)	44.4 (42–46)	91.5 (87.7– 96.0)	2093.8 (2051–2158)	97.3 (95.1–99.0)

* Not determined because of high background levels.

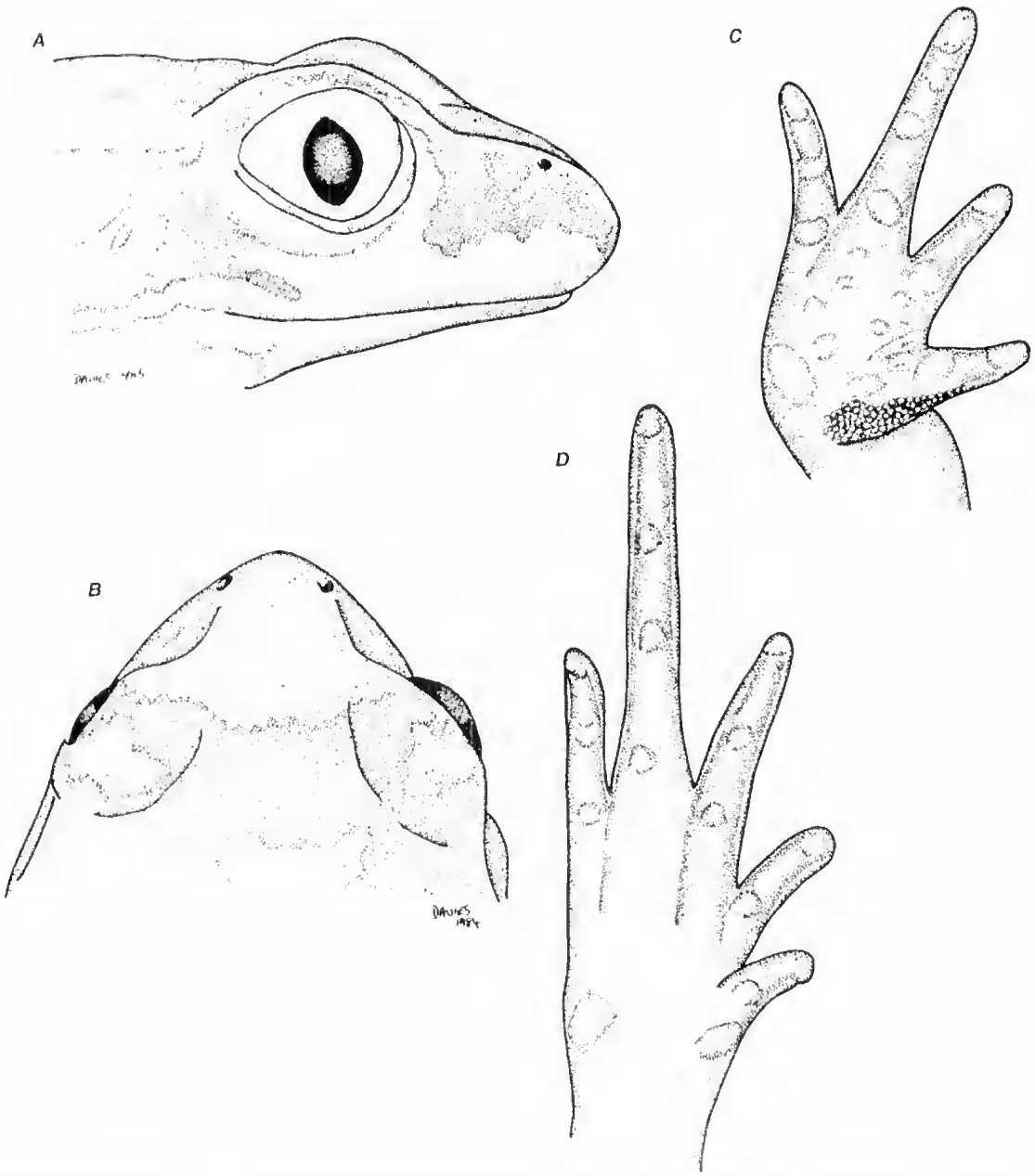

Fig. 10. A, Dorsal and B, lateral views of the head; C, palmar view of hand and D, plantar view of the foot of *Uperoleia laevigata* (NMV D25110) from Langley Flats, Qld.

lithomoda (Tyler *et al.* 1981a, b; Davies *et al.* in press).

U. rugosa is distinguished from *U. minima* by the presence of fringed fingers and toes, and by well-developed inguinal and coccygeal glands (the call of *U. minima* is a very short unpulsed click (Tyler *et al.* 1981a), whereas that of *U. rugosa* is a longer, pulsed call). From *U. aspera, U. rugosa* is distinguished by its unwebbed toes (basal webbing in *U. aspera*) by its ventral pigmentation (absent in *U. aspera*) and by its call—a short, pulsed click, pulsed at about 170 pulses sec^{-1} in *U. aspera* (Tyler *et al.* 1981b).

U. rugosa is distinguished from *U. lithomoda* by

Fig. 11. *Uperoleia laevigata* in life from Severn River, N.S.W. (UAZ A815).

the presence of ventral pigmentation (absent in *U. lithomoda*), by the absence of a preorbital process on the pars facialis of the maxillary (present in *U. lithomoda*), and by advertisement call. The call of *U. rugosa* is clearly pulsed, whereas that of *U. lithomoda* is a short, unpulsed click (Tyler *et al.* 1981a, c).

Distribution

Uperoleia rugosa has a wide ranging distribution in south-eastern Australia (Fig. 9). It occurs to the west of the Great Dividing Range at the southern extremity of its range, but is found coastally as well as centrally from as far north as about Armidale in N.S.W. The northernmost locality from which material has been collected is Tomahawk in Central Queensland.

Uperoleia laevigata Keferstein

FIGS 8, 10-16

Uperoleia marmorata var. *laevigata* Keferstein 1867. Nachr. Ges. Wis. Gottingen 18, p. 349.
Uperoleia marmorata: Keferstein 1868, p. 270 (part.); Moore, 1961, p. 219 (part.); Erspamer, Negri, Erspamer & Endean, 1975, p. 41 (part.); Roseghini, Erspamer & Endean, 1975, p. 35 (part.); Barker & Grigg, 1977, p. 186 (part.); Erspamer, Erspamer & Linnari, 1977, p. 68 (part.).
Uperoleia rugosa (form B): Littlejohn, 1967, p. 153; Littlejohn, 1969, p. 111; Martin & Littlejohn, 1969, p. 170.
Uperoleia rugosa: Brook, 1975, p. 83; Cogger, 1975, p. 83 (part.); Barker & Grigg, 1977, p. 188 (part.); Humphries, 1979, p. 15[2]; Robertson, 1981, p. 4; 1982, p. 6[3]; 1984a, p. 283; 1984b, p. 56; 1986a, p. 773; 1986b, p. 763; Erspamer, Negri & Endean, 1975, p. 41 (part.); Cogger, Cameron & Cogger, 1985, p. 34 (part.).
Uperoleia laevigata: Tyler, Davies & Martin, 1981a, p. 11; Cogger, 1983, p. 84; Cogger, Cameron & Cogger, 1983, p. 33; Tyler, 1985, p. 407; Mahony & Robinson, 1986, p. 120.
Uperoleia sp.: Davies, 1984, p. 790 (part.).

Definition: A moderately-large species (♂♂ 20–28 mm, ♀♀ 22–32 mm) with maxillary teeth; fingers fringed; toes usually fringed, unwebbed; large light triangular patch on the anterodorsal surface of the head; ventral surface never fully pigmented; frontoparietal fontanelle unexposed; carpus of six elements; anteromedial processes of anterior hyale of hyoid in form of medial dilation; ilial crest absent; a long, pulsed advertisement call of 32–56 pulses with a pulse repetition rate of about 79 pulses sec^{-1}.

Material examined: Vic.: NMV D18776-8, D18779, D18780-1, 6 km W Walwa; D25083, Talgarno; D25017-20, D25021(A), D25022-4, 2.4 km E Burroweye; D25038(A), D25039, 8 km NW Walwa; D25034-7, 6.4 km W Walwa. *N.S.W.*: NMV D18763-66, D18767(A), D18768-9, 3.2 km E Rosedale; D25025-8, D25029(A), D25030-3, Braidwood;

[2] Humphries, R. B. (1979) Dynamics of a breeding frog community. Ph.D. thesis, Australian National University, Dept of Population Biology. Unpublished.
[3] Robertson, J. G. M. (1982) Territoriality and sexual selection in *Uperoleia rugosa* (Anura: Leptodactylidae). Ph.D. thesis, Dept of Zoology, Australian National University. Unpublished.

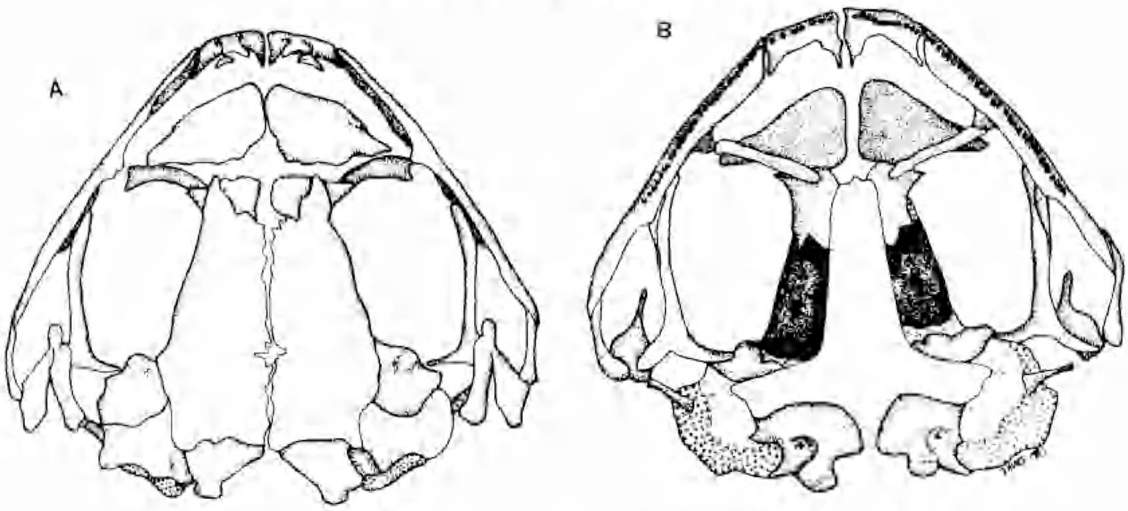

Fig. 12. A, Dorsal and B, ventral views of the skull of *Uperoleia laevigata* (NMV D25111).

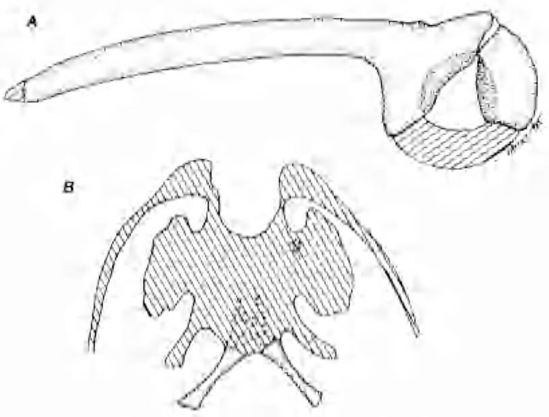

Fig. 13. A, Lateral view of the ilium and B, ventral view of the hyoid of *Uperoleia laevigata* (UAZ B817). Hatched areas are cartilage. Some calcification is indicated by superimposed regular stipple.

D25039, 8 km NW Walwa; D25034-7, 6.4 km W Walwa. N.S.W: NMV D18763-66, D18767(A), D18768-9, 3.2 km E Rosedale; D25025-8, D25029(A), D25030-3, Braidwood; D25043, 3.6 km W Yagobie; D25058-70, D25071(A), D25072-6, 4.8 km W Delegate; D25040-2(A), 3.6 km W Coonbarabran, D59508-9, 16 km S Brocklesby; D59507, 18 km NNW Nimitibel; QM J19949, 1.6 km SW Singleton, Putty Rd; J19951, J19962, Wilberforce nr Windsor; J19948, 16 km N Windsor, Putty Rd; J26940-41, AM R68451, 3 km E Vittoria; QM J34227-8, Heathcote; AM R18731, R18752, Picton Lakes; R20391, R20393-4, Bundeena; NMV D25952(A), Cotter Dam (A.C.T.); AM R25803-4, R25866, R27537, R27581-84, Baulkham Hills; R27520, Londonderry via Richmond ; R30267-8, R30271, Tarana; R34024-5, R35084-7, 1.6 km NW Marengo Station via Hernani; R34157-8, Greenhill Rd, 11.2 km from Guyra/Ebor Intersection; R36432, R36434, R51092-5, R78956, Llangothlin Lagoon nr Guyra; R36484-6, 8 km NW Ebor on Guyra Rd; R36046, Oban River, E of Guyra; R36545, Mitchell River on Wards Mistake Rd, R36713-5, R36717-20, Oakey Creek; R36785-7, 6.4 km N Aberfoyle; R36838-9, 19.2 km W Tenterfield; R45125, 64 km S Tenterfield; R50148, 9.6 km E Keera; R50347-8, Oakey River Dam, Armidale-Kempsey Rd; R50382, Racecourse Lagoon, Uralla; R50462-3, 6.4 km SE Uralla; R50549-50, 9.6 km S Armidale on Dangersleigh Rd; R50905, 3.5 km W Uralla; R50907, 35.6 km NW Guyra; R50909, 1.6 km SSW Barraba; R50779, 1.6 km N Wallan; R50603, 12.8 km ENE Guyra; R50915, 8 km S Guyra on Armidale Rd; R50936-7, Paddys Land, 56 km E Guyra; R50979, 8 km SE Tenterfield; R51174-6, 52.8 km W Armidale on Bundarra Rd; R64284-7, 65 km SW Inverell on Bundarra Rd; R66561, R66555-6, 22 km downstream from Dungog on William River; R75017-20, Mt David nr Oberon; R78957-60, 9.6 km S Guyra, New England Highway; R80471-81, 17 km S Cooma; R87488, R87490, 11.2 km SW Cassilis on Ulan Rd; R90152-3, 32 km from Canberra along Cooma Rd; R90155-7, Rose Lagoon nr Collector; R90662-3, Blacklands Gap Rd, 6 km NW Maids Valley; R92820-31, R92833-40, 3.5 km N Tarana; R92872-6, R93913, R92871, 10 km W Tarana; R96256, R96269-70, Boggy Plain 24 km E Cooma; R99423, R99429, R103152-4, Horsley Park; R104944-51, R104954-5, R104957-8, R104961-5, R104970, R104972, R104978, R104980, R104982-5, R104989, R104994, R104998, R107122, R107124, R107127-8, R107131-5, Maroota S.F. R33772-5, R33777, Gwydir River, 4.6 km E Bundarra; R33761-2, R34222, Little Lagoon, Arding; R34057, Rockvale Rd, 32.4 km from Armidale; R33797, Rockvale Rd, 0.8 km E Thalgarrah; R19472-3, Tamworth; R34211, Armidale; R35650, 49.6 km NE Guyra, Mitchell River at Kookabookra; R35691-2, R35785, Uralla Lagoon; R35713, Cherry Tree Hill, 6.4 km SE Graman; R36747-72, 70.8 km E Armidale; R37024, 32 km NW Emmaville; R36100, 3.2 km S Bendemeer; R45727-8, The Lake, 32 km S Walcha; R42964, R42966, R42968-70, west of Armidale; R43193, 1.6 km N Nowendoc Junction, 40 km S Walcha;

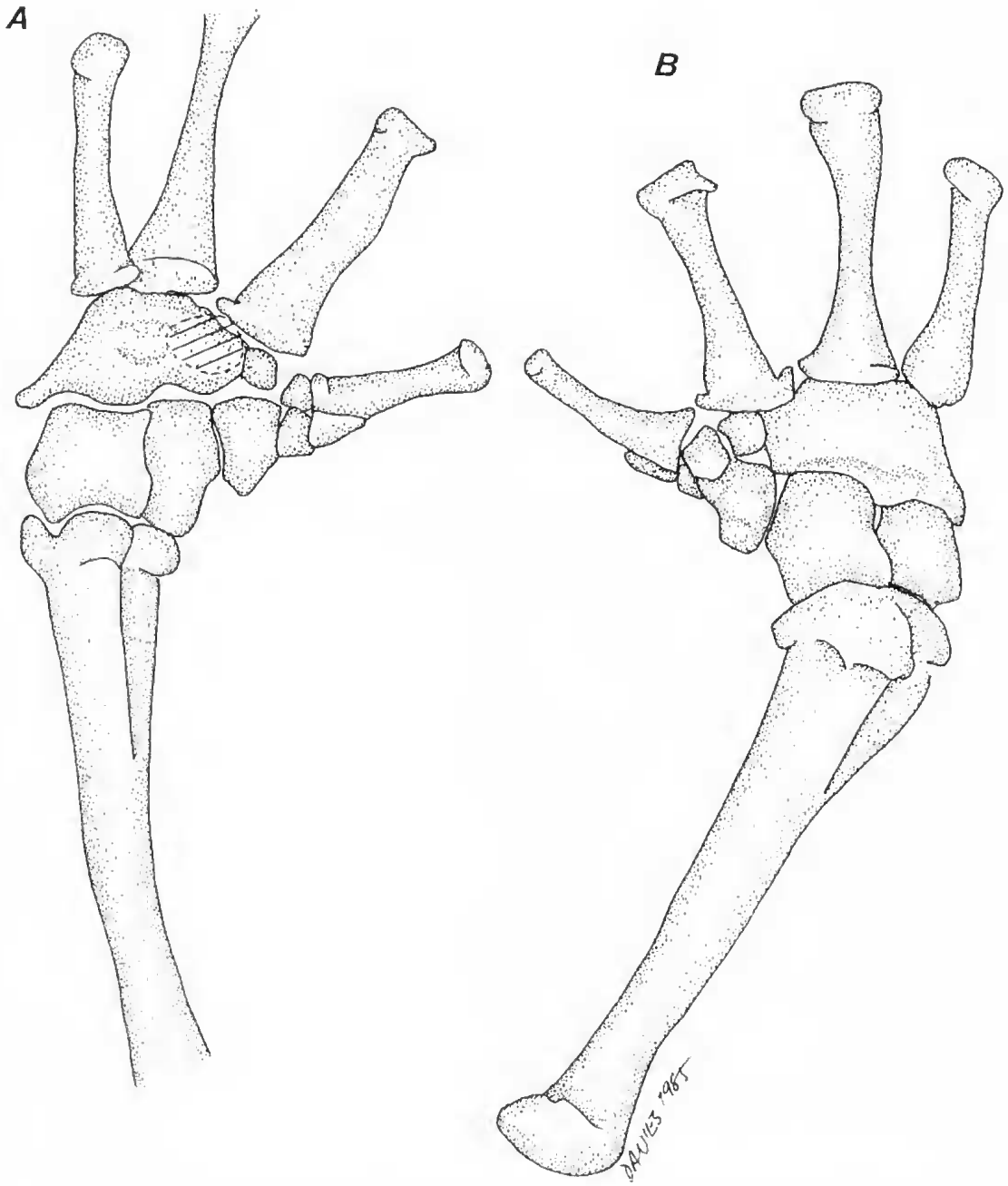

Fig. 14. A, Dorsal and B, plantar view of the carpal elements of *Uperoleia laevigata* (NMV D25038).

R49988, Serpentine River Pt Lookout; R49998, Emmaville/Glen Innes Rd; R50308, 28.8 km NE Guyra; R50323-4, 10.4 km W Ebor on Guyra Rd; R50482-3, Tia nr Walcha; R50548, 30.4 km SSE Hillgrove on Narrow Neck Rd; R50570, 8 km NNE Glen Innes on Emmaville Rd; R50886, 25.6 km W Bendemeer; R51189, Loch Abbon; R51008, 20.8 km S Uralla on Walcha Rd; R51200, Bullock Creek; R51734, 12.8 km S Uralla on New England Highway; R52645, 22.9 km SW Bundarra on Barraba Rd; R51799-803, R51805-6, 3.8 km SW Bundarra on Barraba Rd; R54474, 2.5 km N Marengo S.F. Forestry Hut; R56978, Gate to Blue Knobby; R57151, Putty Rd; R57268, Loch Abbra, 32 km NNE Armidale; R68458, 5 km N Kandos; R70199, 12.8 km along road to Wiseman's Ferry

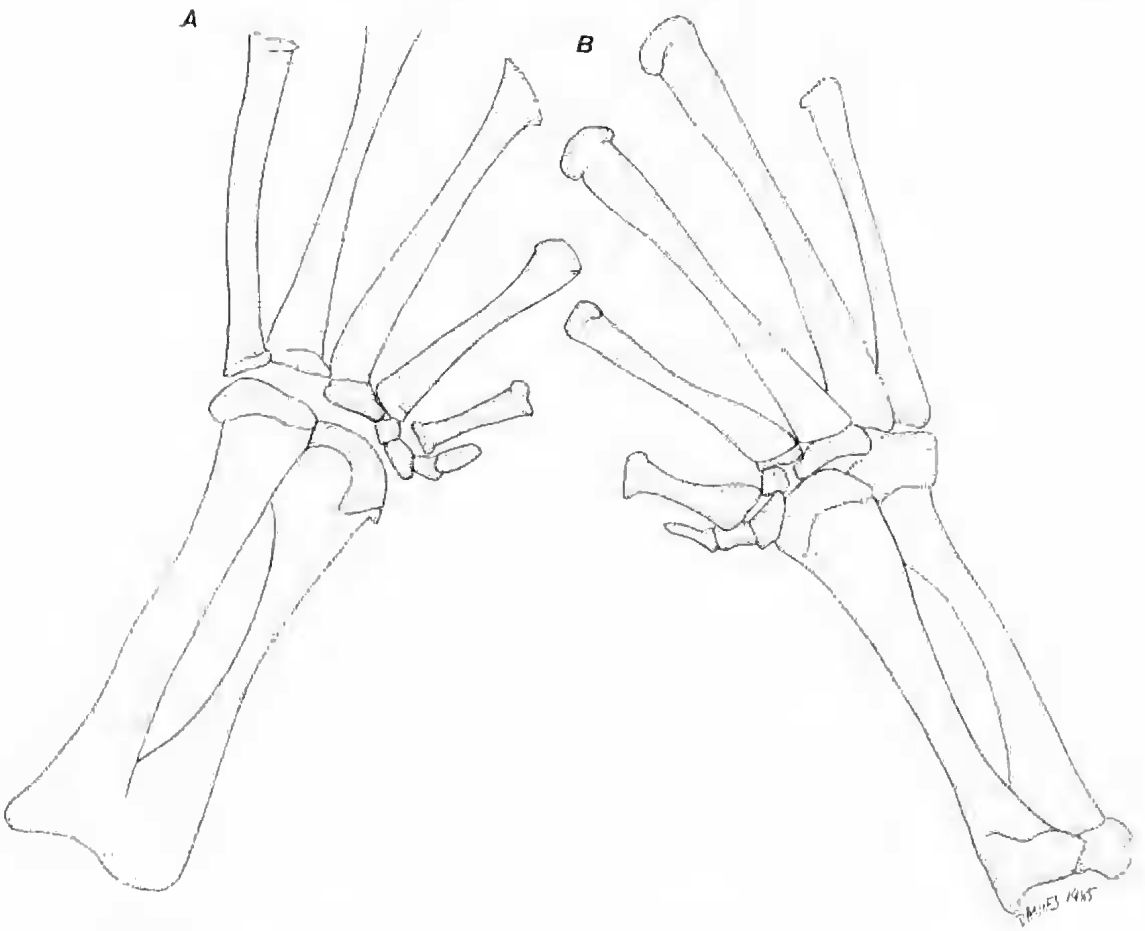

Fig. 15. A, Dorsal and B, plantar view of the tarsus of *Uperoleia laevigata* (NMV D25038).

from Kariong; R71805, Bagot Rd Lagoon via Llangothlin; R93563, Bungongo S.F.; R115538, 1 km S National Park level crossing; R115539-43, R115544-53, Colo; R115562-4, 11.2 km S Putty on Windsor Rd; R115555, Bundanoon; R115556-8, 0.8 km N Tallong; R115565-71, nr Putty; R115572, Lapstone slopes above Great Western Highway; R115573-4, R115577-8, R115580, R115582, nr Bulgandramine; R115586-7, R115653-4, Tooloom Falls; R115585, Nettle Creek, 19.2 km from Copmanhurst on Tabulum Rd; R108914-5 Mandurama; R110432, Parsons Gully, Merriwa; R115645, 4.8 km E Eulo; A483, A612, 6 km N Mogo Hstd (Shoalhaven River); A1118, Half Moon, Mongarlowe River; A1283-4, Menangle; A1610-12, 3 km N Sutton. SAM R12309-12, Stanwell Park; R13004, 38.5 km E Cooma; SAM R28781-3, R28784(A), R28785(A), UAZ A601(A), B817(A), Oakdale estate N of Sutton; UAZ B815(A), Severn River (29°28', 151°29'). *Qld*: NMV D25108-9, 35.2 km N Eidsvold; AM R5818-21, QM J12724, J12727, Eidsvold; NMV D25110-11(A), 8 km E Langley Flats; SAM R29665, QM J45968-70, J42558, Giraween N.P.; QM J45971, Blackdown Tableland in Forestry Camp; QM J34242, J39314, Mimosa Creek, Blackdown Tableland; J28504(A), Blackdown Tableland; J18820, S of Gayndah; J18831, J18834(A), E of Withcott; J18830, East of Laidley on Granchester Rd; J18833, J19924, J19940, Lancewood Hstd on Ripley/Brooklands Rd; J18838, J18843, J18845(A), 1.6 km N Helidon on Toowoomba Rd; J19923, 1.6 km W Stanthorpe; J19931-3, 1.6 km S Rathdownay on Mt Lindsay Highway; J19926, J19948, 16 km N Beaudesert; J27749, Gallangowan; J28177, J30941-2, Eukey; J34815-6, Tom Plants Hut via Amiens; J35535, Mt Taramba; J42554-7, just W Kalbar turnoff, Cunningham Highway; J40485, Dalby; J42559-60, about 1.6 km W Beaudesert along Beaudesert/Boonah Rd; J42562, Moonie; J29015, Waterford Rd, 6 km E Beaudesert; SAM R29666(A)-7, QM J45966-7, Glenleigh Station beside road to Glenhaughton Station; QM J45972, 1.7 km from Cabbage Tree Creek on Nathan Gorge Rd; SAM R29668-71, QM J46003, Pony Hills S.F. (149°03', 25°49').

External morphology

Tyler *et al.* (1981a) redescribed the species from nine syntypes. We have examined the external morphology of a further 459 specimens.

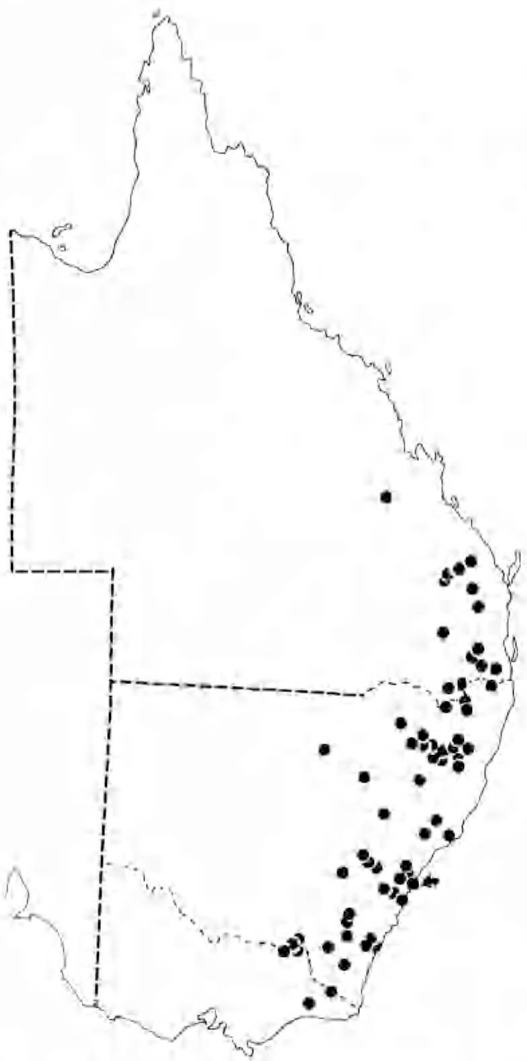

Fig. 16. Distribution of *Uperoleia laevigata*. The arrow indicates the type locality.

Uperoleia laevigata is a moderately large species (♂♂ 20–28 mm S-V, ♀♀ 22–32 mm S-V) with relatively long hindlimbs (TL/S-V 0.37 ± 0.02 [0.30–0.43]). The snout is moderately long, usually evenly rounded when viewed from above (Fig. 10), but occasionally truncated. In profile, the snout is usually evenly rounded (Fig. 10), but sometimes slopes gently posteriorly. The nares customarily are subterminal and dorsolateral but terminal in specimens with truncated snouts.

The canthus rostralis usually is distinct and straight, but sometimes is not clearly defined. Typically, the loreal region is gently flaring giving width and curvature to the dorsal view of the snout; occasionally it is straight (Fig. 10). The eye-to-naris distance usually is much greater than the internarial span (E-N/IN 1.38 ± 0.19 [1.11–1.72]).

The fingers are long and slender, unwebbed and usually well fringed. Palmar and subarticular tubercles are prominent (Fig. 10). Toes usually are moderately fringed, but occasionally fringing is lacking (as in the syntypes). Basal webbing between toes 2 and 3 was observed in only one specimen. The inner metatarsal tubercle is angled along the long axis of toe 1; and the outer is small, rounded and acutely angled to the long axis of the foot (Fig. 10).

Texture of the dorsum varies from smooth to moderately rugose. Parotoid glands are usually very prominent and, in some specimens, appear hypertrophied. Occasionally inguinal glands are prominent, and coccygeal glands rarely are conspicuous. Submandibular glands vary from scarcely detectable to discrete and elongate. Nuptial pads are present at the base of the first finger and are unpigmented and glandular (Fig. 10).

No scapular plicae. Cloacal flaps are prominent and fimbriated in most, but not all, females. Eye flaps are anterior to the eye and vary in development from scarcely detectable to moderately developed. Most specimens have a smooth ventral surface, the remainder have a moderately granular belly.

The prominent pale triangular patch on the anterodorsal surface of the head, described by Keferstein (1867), is found in almost all specimens (Fig. 11). Dorsal markings are not conspicuous and are usually in the form of islands of dark pigment on a lighter-grey or brown background.

Ventral pigmentation varies considerably. Pigment is absent in many specimens; and when present consists of a fine suffusion of pigment granules on all or part of the ventral surface, except the ventromedial portion of the thighs, or as islands of pigment either pale grey or darker brown, on part or much of the ventral surface. The ventral surface is never entirely pigmented. Pigmentation on the ventral surface of the hands, if present, usually is slight.

Inguinal and thigh markings vary from scarcely detectable to prominent, and in colour from grey to cream. Axillary colour patches on the forearms are absent.

Some of the specimens examined had been infected by batrachomyid dipterous parasites. The parasites usually were lodged behind and beneath the parotoid glands on one side, but occasionally on both sides. Similar parasites were observed in the type series (Keferstein 1868, Tyler *et al.* 1981a).

During this study, batrachomyid parasites were observed only in specimens assigned to *U. laevigata*.

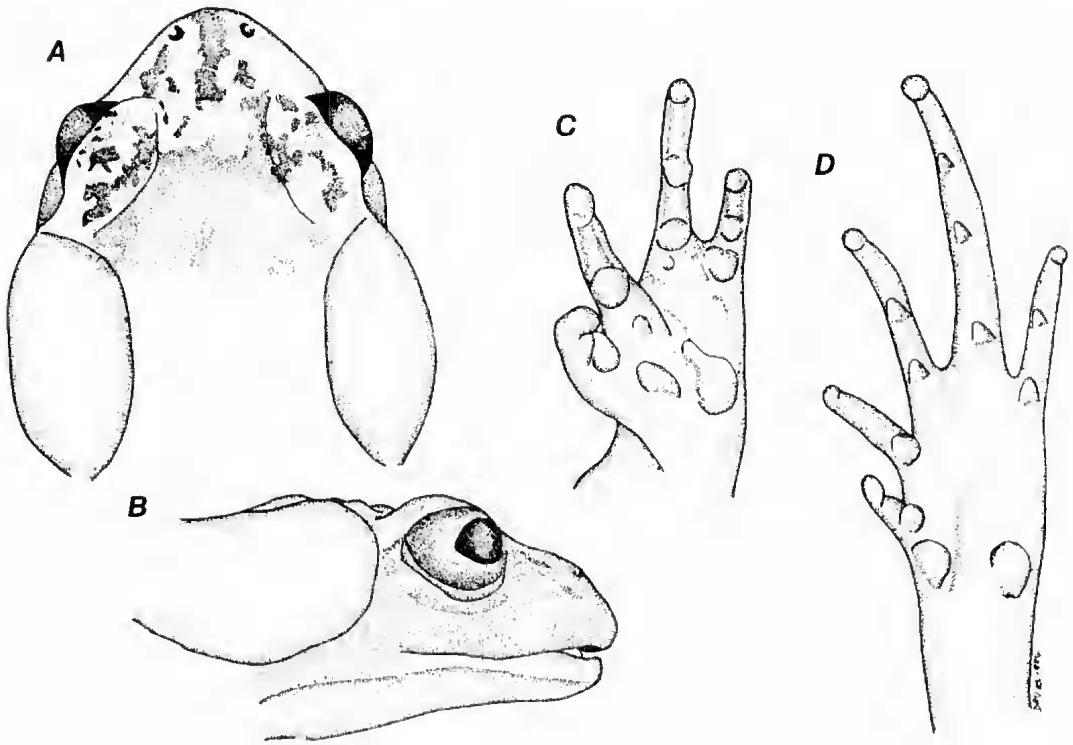

Fig. 17. A, Dorsal and B, lateral views of the head; C, palmar view of the hand and D, plantar view of the foot of *Uperoleia martini* sp. nov. (Holotype).

Fig. 18. *Uperoleia martini* sp. nov. in life. From nr Yarram, Vic. (NMV D59497).

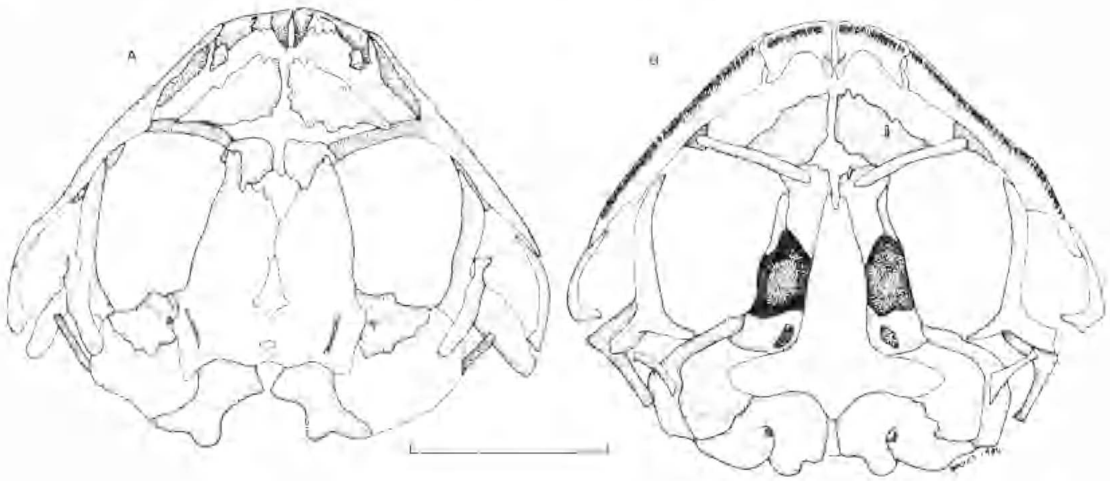

Fig. 19 A, Dorsal and B, ventral view of the skull of *Uperoleia martini* sp. nov. (NMV D23636). Scale bar = 5 mm.

Osteology (based on NMV D25111)

Skull well ossified, sloping anteroventrally (Fig. 12). Sphenethmoid not confluent medially and poorly ossified, not extending anteriorly to extremities of frontoparietals in dorsal view and ventrally extending posteriorly for about ¼ of length of orbit. Prootic not fused with exoccipital, either dorsally or ventrally. Exoccipital not ossified dorso- or ventromedially. Crista parotica short and stocky and well developed, not articulating with otic ramus of squamosal. Carotid canal not exposed on posterolateral surfaces of frontoparietals. Epiotic eminences moderately developed, and not roofed posteriorly. Frontoparietal fontanelle barely exposed between almost confluent frontoparietal bones. Extensive frontoparietals angled posterolaterally on orbit. Faint trace of carotid canal groove present posterolaterally on frontoparietals.

Nasals moderately well ossified and closely applied anteromedially, moderately separated posteromedially; maxillary processes short and not in bony contact with well-developed preorbital processes of shallow pars facialis of maxillary.

Palatines moderately long, unridged, reduced laterally to just underly preorbital processes of pars facialis of maxillary. Medially they overly sphenethmoid at level of anterior extremity of cultriform process of parasphenoid. Parasphenoid robust, cultriform process truncate and moderately broad, alary processes moderately broad and slightly angled posterolaterally, just reaching distal extremities of medial rami of pterygoids (Fig. 12). Pterygoid robust, medial ramus short and in contact with prootic. Posterior ramus short and moderately broad. Anterior ramus in short contact with moderately well-developed pterygoid process of palatal shelf of sphenethmoid. Cartilaginous quadrate present between base of squamosal and quadratojugal. Quadratojugal robust, in firm contact with maxillary. Squamosal stocky with short, knobbed zygomatic ramus and long unexpanded otic ramus.

Maxillary and premaxillary dentate. Palatal shelf deep with well-developed palatine processes, closely applied medially. Alary processes of premaxillaries very broad, bifurcate, perpendicular to pars dentalis. Vomers absent. Bony columella present. Hyoid plate slightly longer than broad. Alary processes large, not pedunculate. Anteroproximal portions of anterior cornua dilated, anteromedial processes of hyale absent. Posterolateral processes moderately long, broad. Posteromedial processes ossified. Some calcification apparent on plate (Fig. 13).

Pectoral girdle arciferal and robust. Omosternum and xiphisternum present. Sternum cartilaginous. Clavicles slender, curved, moderately separated medially. Coracoids robust, moderately separated medially. Bicapitate scapula, about equal in length to clavicle. Suprascapula about ⅔ ossified. Humerus with well-developed anteroproximal crest. Phalangeal formula of hand 2,2,3,3.

Six carpal elements present. Considerable torsion apparent. Prominent flange extends proximally from lateroproximal corner of O. centrale postaxiale. Carpal elements of O. distale carpale 2 and 3 not fused (Fig. 14). Palmar sesamoid present.

Eight nonimbricate presacral vertebrae. Sacral diapophyses poorly expanded. Relative widths of

transverse processes III > IV > sacrum > II > V = VI = VII = VIII.

Dorsomedial ossification incomplete on vertebrae, I, II, and III. Ilia extend anteriorly to sacral expansion. Well-developed crest on bicondylar urostyle extending along ½ dorsomedial length. Pubis cartilaginous. Iliac crest absent, dorsal prominence, very small; dorsal protuberance small, more lateral than superior (Fig. 13).

Phalangeal formula of foot 2,2,3,4,3. Bony prepollex.

Three distal tarsal elements present. Lateral element (T_3) is largest (Fig. 15).

Variation

The sphenethmoid is never confluent medially. The carotid canal groove is barely observable, deeply grooved or occasionally partly roofed. The epiotic eminences usually are prominent. The frontoparietal fontanelle is always as in the described specimen.

The palatines are long, slightly reduced laterally and usually acuminate laterally. The cultriform process of the parasphenoid is of varying lengths and is usually more slender anteriorly; the alae are either horizontal or inclined posterolaterally. They are usually broad.

The medial ramus of the pterygoid is usually acuminate; the anterior ramus is usually short and sometimes in slightly longer contact with the pterygoid process of the palatal shelf of the maxillary than is described.

The zygomatic ramus of the squamosal is not always knobbed, occasionally it is elongated. The otic ramus is always long and unexpanded. The alary processes of the premaxillaries are always very broad, curved at the base, bifurcate and sometimes inclined slightly medially or slightly posteriorly.

The pars facialis of the maxillary is moderately deep; sometimes it is reduced anteroventrally and sometimes stepped down to be shallow. The preorbital process is always prominent and is usually, but not always, discrete.

Vomerine fragments are rarely present and confined to small, asymmetrical structures, usually medial to the palatines.

Advertisement call

Robertson (1982, 1984, 1986a, b) described the call of this species in a population near Sutton, N.S.W. We have recorded calls from *U. laevigata* at a number of localities in its range and Table 1 provides data to supplement Robertson's information. An oscillogram of the call is presented in Fig. 8.

Comparison with other species

Uperoleia laevigata is a toothed species with a roofed frontoparietal fontanelle, features shared only with *U. marmorata*.

From *U. marmorata*, *U. laevigata* is distinguished by fringing on the fingers and toes, and by size (males 20–28 mm in *U. laevigata*, *U. marmorata* male 30.1 mm).

From the sympatric *U. tyleri*, *U. laevigata* is distinguished by the absence of heavy ventral pigmentation and by the presence of a roofed frontoparietal fontanelle. *U. laevigata* differs from the sympatric species *U. rugosa* by the presence of maxillary teeth.

Distribution

Uperoleia laevigata occurs throughout the central and south-eastern coastal regions of S.E. Australia and also occurs on the Great Dividing Range as far north as the Blackdown Tableland (Fig. 16).

Comment

Uperoleia laevigata is sympatric with an undescribed toothed species (Davies, McDonald & Corben in press) found coastally from about Kempsey in N.S.W. to Eungella in central Queensland and can be distinguished from this species by incomplete ventral pigmentation.

Uperoleia martini sp. nov.

FIGS 8, 17–22

Uperoleia marmorata: Littlejohn 1969, p. 110 (part.); Cogger 1975, p. 183 (part.)

Holotype: NMV D23635, an adult male collected by M. J. and P. G. Littlejohn, 4.8 km SW of Nowa Nowa, Victoria (37°44', 148°06') on 7.xii.1963.

Definition: A large species (♂♂ 30–33 mm S-V) characterized by the presence of maxillary teeth; hypertrophied parotoid glands; heavy ventral pigmentation; mottled dorsum; very poorly-exposed frontoparietal fontanelle; no webbing between the toes; vomerine fragments present; carpus of six elements; anteromedial processes of anterior hyale of hyoid in the form of medial dilation; iliac crest absent; advertisement call a single long pulsed note

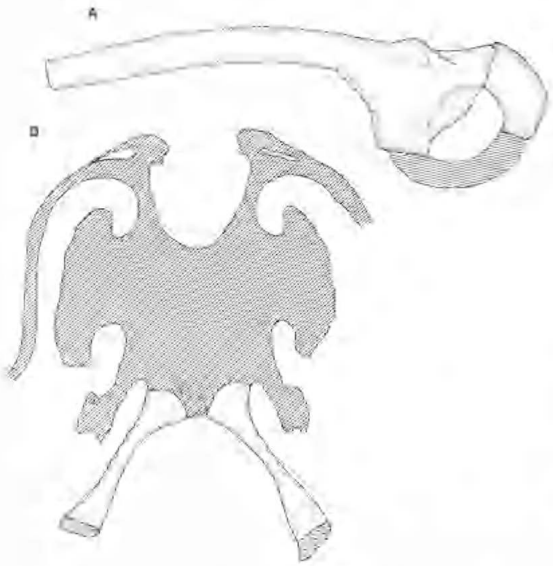

Fig. 20. A, Laterial view of the ilium and B, ventral view of the hyoid of *Uperoleia martini* sp. nov. (SAM R29652).

of 32–62 pulses with a pulse repetition rate of about 78 pulses sec^{-1}.

Description of holotype: Maxillary teeth present, vomerine teeth absent. Snout short, slightly rounded when viewed from above, rounded in profile (Fig. 17). Internarial span just less than eye to naris distance (E-N/IN 1.10). Canthus rostralis inconspicuous and straight. Tympanum not visible externally. Fingers short, slightly fringed, unwebbed. In order of length 3>2=4>1. Prominent subarticular and palmar tubercles (Fig. 17). Hind limbs moderately long (TL/S-V 0.39). Toes long, unfringed unwebbed. In order of length 4>3>5 >2>1 (Fig. 17). Metatarsal tubercles large and prominent. Subarticular tubercles conical and prominent.

Dorsal surface rugose. Parotoid glands hypertrophied (Fig. 18). Inguinal and coccygeal glands poorly developed. Submandibular gland indeterminate. Well-developed supracloacal flap. Ventral surface smooth.

Male with unilobular submandibular vocal sac.

Dorsum mottled yellow and chocolate on grey background in preservative. Cream patches ventromedially on thighs and in groin. Parotoid glands mottled as on dorsum. Small white patch on dorsal surface of humerus in axilla region. Ventral surface chocolate stippled with white. Throat dark grey.

Dimensions (in mm): Snout-vent length 30.0; tibia length 11.6; eye diameter 3.4; eye-naris distance 2.8; internarial span 1.10.

Etymology: This species is named for Angus A. Martin in recognition of his contribution to the studies of *Uperoleia*.

Variation

There are seven paratypes, all adult ♂♂. NMV D23634, D23636 collected with the holotype; SAM R29650, NMV D59496-7, 6 km NNE Yarram, Vic, M. J. and T. G. Littlejohn, i.xii.1980; SAM R29648-49, 6 km NNE Yarram, Vic, G. F. Watson and M. J. Littlejohn, i.x.1976.

The paratypes vary little from the holotype, although back patterning is not as strongly developed in all specimens collected from sites other than the type locality. Adult males range 26.7–31.8 mm S-V. The hind limbs are uniformly long (TL/S-V 0.37 ± 0.02 [0.34–0.39]). Eye-to-naris distance approximates internarial span (E-N/IN 1.07 ± 0.14 [0.92–1.30]). The slight fringing which is apparent on the toes of one paratype may be an artifact of preservation. The parotoid glands are uniformly hypertrophied and the dorsum is smooth to only moderately rugose.

Osteology (based on NMV D23636)

Skull moderately-well ossified sloping anteroventrally. Ossified portion of sphenethmoid not confluent medially and extending slightly anteriorly to anterior extremities of frontoparietals and posteriorly about ⅓ of length of orbit in ventral view. Posteromedial processes present dorsally projecting into anterior portion of frontoparietal fontanelle (Fig. 19). Prootic and exoccipital not fused, large areas of prootic calcified posterolaterally. Exoccipitals not fused dorso- or ventromedially. Crista parotica short and stocky, slightly overlapped by otic ramus of squamosal but not in bony contact with it. Carotid canal a shallow channel in posterolateral frontoparietal bones. Frontoparietal fontanelle exposed only as two small triangular portions (Fig. 19). Nasals moderately ossified, triangular, poorly separated medially, gently sculpted medially and posteriorly. Maxillary process of nasal moderately developed, mucronate, not articulating with well-developed preorbital process of pars facialis of maxillary.

Palatines moderately broad, reduced very slightly laterally; medially in long contact with sphenethmoid at angle of about 45° (Fig. 19). Parasphenoid

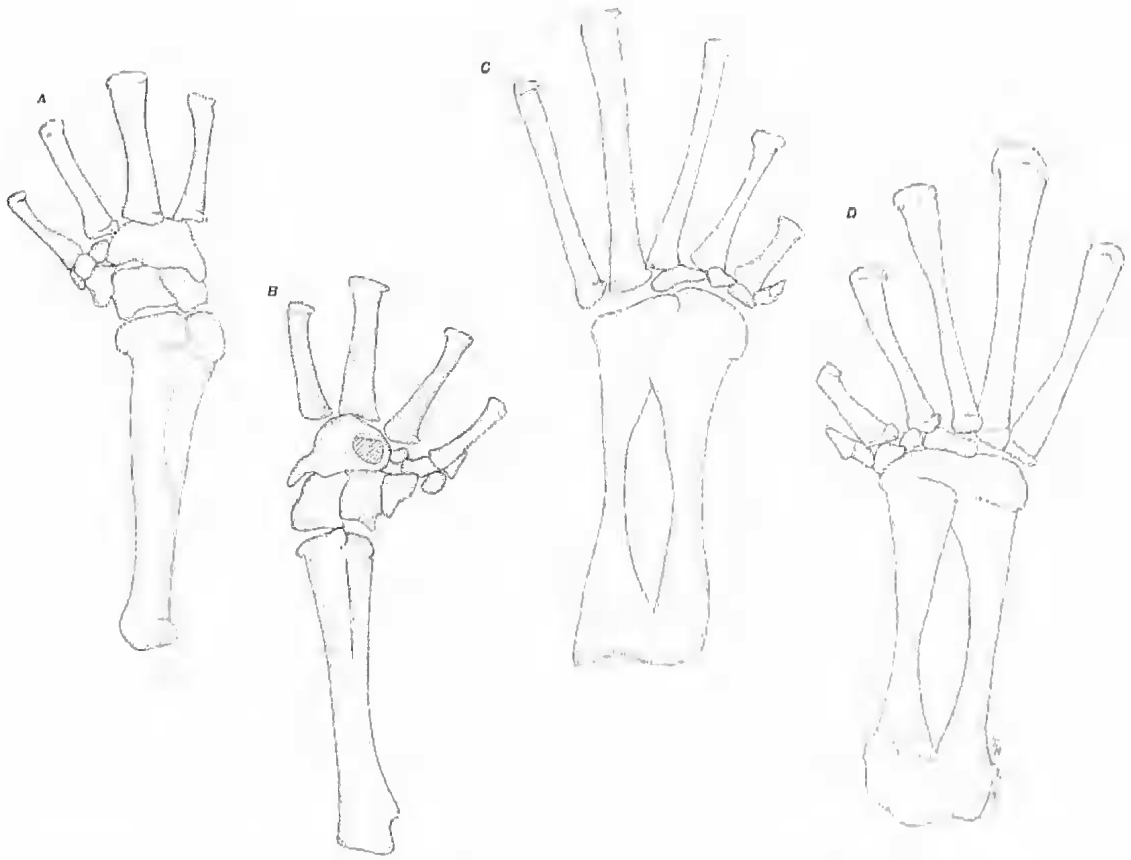

Fig. 21. A, Dorsal and B, ventral view of the carpus; C, ventral view of the tarsus of *Uperoleia martini* sp. nov. (NMV D23636).

robust with terminally bifid cultriform process reduced anterolaterally. Alae short, moderately broad, at right angles to cultriform process.

Anterior ramus of pterygoid in long contact with well-developed pterygoid process of palatal shelf of maxillary; medial ramus short, slightly rounded terminally, not in bony contact with prootic; posterior ramus moderately broad and stocky. Cartilaginous quadrate present between base of squamosal and quadratojugal. Quadratojugal robust, in firm contact with maxillary. Squamosal stocky with knobbed zygomatic ramus and long unexpanded otic ramus.

Maxillaries and premaxillaries dentate. Palatal shelf deep. Palatal processes of premaxillaries long, almost confluent medially. Alary processes of premaxillaries moderately broad, perpendicular to dentigerous processes. Pterygoid process of palatal shelf of maxillary well developed.

Vomers present as tiny remnants one on medial edge of choana and second on anteromedial extremity of sphenethmoid, but on left hand side only.

Bony columella present.

Hyoid plate slightly broader than long. Anteromedial processes not elongate, in form of medial dilation of anterior hyale (Fig. 20). Posterolateral processes of hyoid plate moderately broad. Posterior cornua ossified.

Pectoral girdle arciferal and robust. Omosternum and xiphisternum present. Sternum cartilaginous. Clavicles slender, curved, coracoids robust. Scapula bicapitate, suprascapula about ½ ossified. Well-developed anteroproximal crest on humerus. Phalangeal formula of hand 2,2,3,3.

Carpus of six elements. Moderate torsion occurs. Both O. ulnare and larger O. radiale present. Both articulate with O. radioulna proximally, with each other on medial border and distally with large transversely-elongated O. centrale postaxiale (Fig. 21). O. radiale articulates laterally with O. centrale preaxiale.

Fig. 22. Distribution of *U. martini* sp. nov. Open circles are call records. The arrow indicates the type locality.

O. centrale postaxiale articulates distally with bases of O. metacarpi V, IV and III. From lateroproximal corner, small flange extends proximally onto lateral surface to O. ulnare. Palmar sesamoid ventromedially (Fig. 21).

O. centrale preaxiale articulates laterally with O. radiale, distally with O. centrale postaxiale and with carpal elements of O. distale carpale 2 and 3, laterally with basal prepollical element.

Eight non-imbricate, presacral vertebrae. Incomplete mediodorsal ossification on vertebrae I-V. Vertebral column abnormal in sacral region with fusion of one sacral blade with vertebrae VIII. Relative widths of transverse processes cannot be ascertained.

Urostyle bicondylar, well-developed crest extending about ½ length.

No ilial crest; prominence small, gently monticuline, dorsal protuberance posterolateral. Pubis calcified (Fig. 2D).

Phalangeal formula of foot 2,2,3,4,3. Three distal tarsal elements present. Lateral element largest, lying at base of O. metatarsus III, extending laterally to articulate with medioproximal side of base of O. metatarsus IV and medially to base of O. metatarsus II. Medial element at base of O. metatarsus I, articulates with O. centrale prehallucis. Distal prehallical element small and narrow (Fig. 21).

Variation

Two other paratypes were cleared and stained, one for bone and one for bone and cartilage (SAM R29648, R29650). Frontoparietal fontanelle exposure is greater than that shown in Fig. 19 and similar to that of the sibling species *U. tyleri*. Ossification of the nasals is slightly less than that of the described specimen. The carotid canal groove is present, but not deep. The epiotic eminences are incomplete but ossification is greater than that shown in *U. tyleri*. Vomerine fragments are present medial to the palatines and at the edges of the choanae, but these are variable in development. There is no variation detectable in other skull elements.

Advertisement call

The call of this species is very similar to that of the allopatric species *U. laevigata* (Table 1, Fig. 8).

Distribution

Uperoleia martini is known from coastal regions of eastern Victoria and N.S.W. (Fig. 22).

Comparison with other species

U. martini is a large species within the size range of *U. tyleri, U. crassa, U. marmorata, U. orientalis, U. russelli, U. talpa, U. borealis* and *U. aspera*. The species is toothed, a feature shared only with *U. tyleri* and *U. marmorata*. From *U. marmorata, U. martini* is distinguished by the hypertrophied parotoid glands and a chocolate ventral surface. From *U. tyleri, U. martini* is distinguished by the presence of a rugose dorsum with yellow mottlings, and by call.

Uperoleia tyleri sp. nov.
FIGS 8, 23–30

Uperoleia marmorata: Keferstein, 1867, p. 349, 1868, p. 220 (part.); H. W. Parker, 1940, p. 69 (part.); Moore, 1961, p. 219 (part.); Littlejohn, Martin & Rawlinson, 1963, p. 225; Littlejohn, 1967, p. 153; Littlejohn, 1969, p. 110; Martin & Littlejohn, 1969, p. 171; Littlejohn, 1971, p. 9; Watson & Martin, 1973, p. 42; Cogger, 1975, p. 83 (part.); Brook, 1975, p. 119; Grigg & Barker, 1977, p. 186 (part.).
Hyperolius (Uperoleia) marmoratus: W. K. Parker, 1881, p. 10.
Uperoleia rugosa: H. W. Parker, 1940, p. 68 (part.).
Uperoleia sp: Davies, 1984, p. 790 (part.).

Holotype: NMV D23633, an adult male collected at Jervis Bay, A.C.T. (35°03', 150°44') by M. J. Littlejohn, A. A. Martin and P. A. Rawlinson on 17.i.1963.

Definition: A large species (♂♂ 22–33 mm, ♀♀ 26–34 mm S-V) characterized by the presence of maxillary teeth; hypertrophied parotoid glands; heavy ventral pigmentation; poorly-exposed frontoparietal fontanelle; no webbing between the toes; presence of vomerine remnants in two fragments; carpus of six elements; anteromedial processes of anterior hyale of hyoid in the form of medial dilations; ilial crest absent. Mating call a

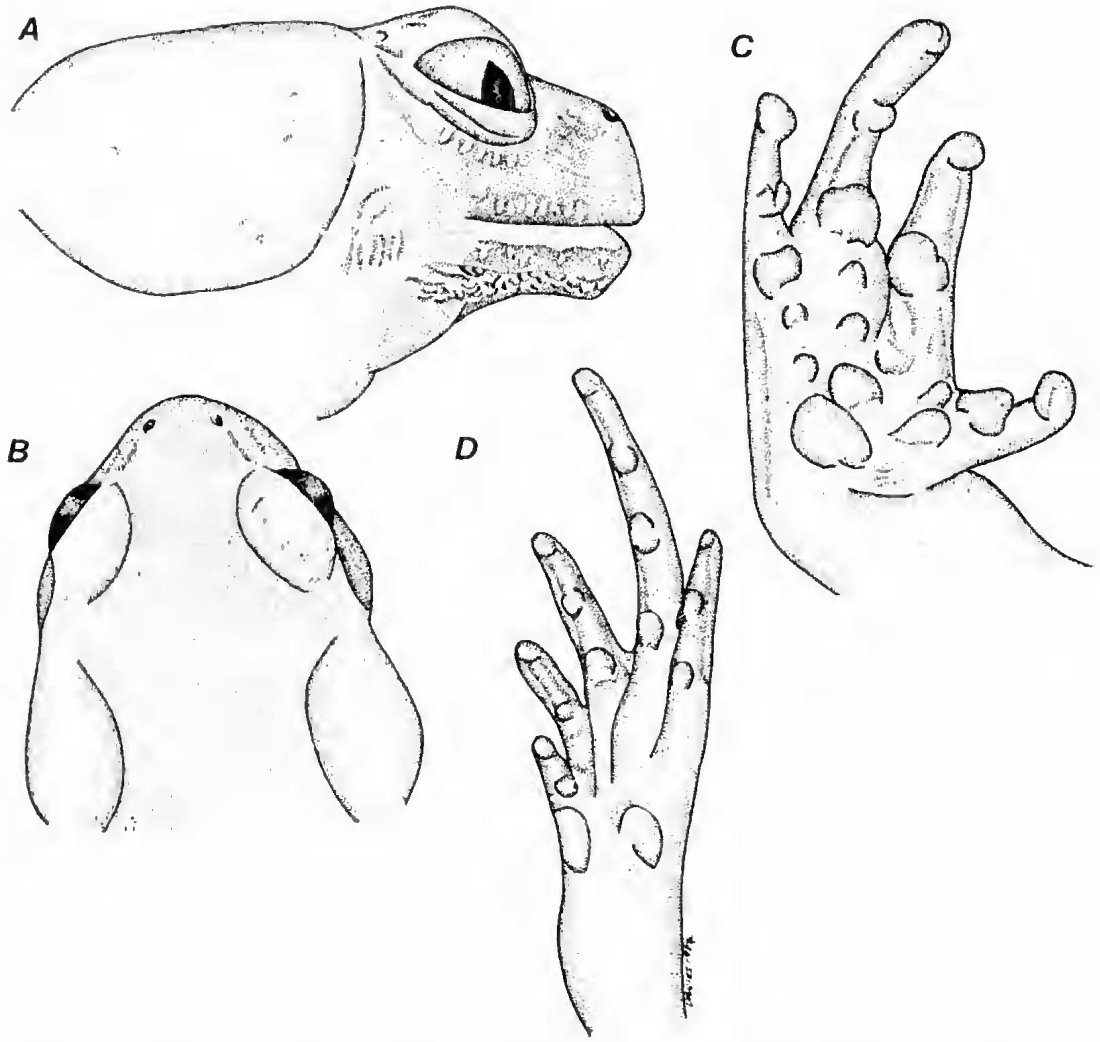

Fig. 23. A, Dorsal and B, lateral view of head; C, palmar and D, plantar views of the foot of *Uperoleia tyleri* sp. nov. Holotype.

single short pulsed note of 18–26 pulses with a pulse repetition rate of about 100 pulses sec $^{-1}$.

Description of holotype: Maxillary teeth present, vomerine teeth absent. Snout short, slightly rounded when viewed from above, rounded in profile (Fig. 23). Internarial span less than eye-to-naris distance (E-N/IN 1.65). Canthus rostralis inconspicuous and straight. Tympanum not visible externally (Fig. 24). Fingers short, slightly fringed, unwebbed. In order of length $3>2=4>1$. Prominent subarticular and palmar tubercles (Fig. 23). Hind limbs long (TL/S-V 0.38). Toes long, poorly fringed and unwebbed. In order of length $4>3>5>2>1$ (Fig. 23). Metatarsal tubercles large and prominent; inner elongate, slightly truncated dorsally extending onto axis of toe 1; outer small, rounded, moderately acutely angled to horizontal axis of foot. Subarticular tubercles conical.

Dorsal surface faintly rugose. Parotoid glands hypertrophied (Fig. 23). Inguinal and coccygeal glands poorly developed. Submandibular gland indeterminate. Well-developed supracloacal flap. Ventral surface smooth.

Male with unilobular submandibular vocal sac.

Dorsum dark slate in preservative. White patch ventromedially on backs of thighs and in groin.

Fig. 24. *Uperoleia tyleri* sp. nov. in life (SAM R29652) from 7 km ENE Marlo, Victoria.

Parotoid glands slightly lighter than dorsum. Small white patch on dorsal surface of humerus in axilla. Ventral surface chocolate stippled with white. Throat dark grey.

Colour in life: Dorsum dark brown-black with orange-yellow spotting over glands. Ventral surface blue-black with white spots. Inguinal and femoral patches yellow.

Dimensions (in mm): Snout-vent length 29.8; tibia length 11.4; eye diameter 3.4; eye-naris distance 2.8; internarial span 1.7.

Etymology: This species is named for Michael J. Tyler in recognition of his contribution to studies of the genus *Uperoleia*.

Variation

There are 61 paratypes 46 ♂♂ and 15 ♀♀. *A.C.T.*: NMV D23632 collected with the holotype; D23620-2 Jervis Bay, M. J. Littlejohn, A. A. Martin, P. A. Rawlinson, 26.i.1964; D23644, Jervis Bay, M. J. Littlejohn, A. A. Martin, G. F. Watson, 21.x.1969. *N.S.W.*: D23631, Batemans Bay, M. J. Littlejohn, A. A. Martin, P. A. Rawlinson, 2.xi.1964; D23640, 3.2 km N. Batemans Bay, P. A. Rawlinson, 13.i.1966; D23628, 28.8 km S. Bombala, M. J. Littlejohn, A. A. Martin, P. A. Rawlinson, 24.viii.1963; D23641, 23.2 km S Bombala, M. J. Littlejohn, A. A. Martin, 6.xii.1965; D23638-9, Boyd Town, J. A. Owen, AM R4754-9, R4761-2, Tamworth, A. H. S. Lucas, 4.iv.1910; R15683-5 Burrawang, A. Holmes; R4211, Maroubra, D. B. Fry, Ross, 5.x.1908; R5286, R78655, Maroubra Bay, D. B. Fry, Ross, 20.iii.1911; R6930, Kensington, W. W. Thorpe; ANWC A1174, Beecroft Peninsula, 8.ii.1978; NMV D59495, SAM R29653-58, Narrabarba, M. J. Littlejohn, G. F. Watson, 24.ix.1985. *Vic.*: NMV D42741-5, Malacoota Inlet, 12.i.1972; D23623-7, 23629-30, 3.2 km N Cann River, M. J. Littlejohn, A. A. Martin, P. A. Rawlinson, 24.viii.1963; D33598-601, Mouth of Cann River, Tamboon, A. J. Reid, 23.v.1973; D23643, 22.4 km W Cann River, P. A. Rawlinson, 20.viii.1968; D48595-7, 30 km W Genoa, A. J. Coventry, K. C. Norris, 1.xii.1976; D47319-20, 12 km E Currajong, A. M. Gilmore, 28.ix.1975; D51238-9, 2 km WNW Golden Beach, K. C. Norris, 26.ix.1978; D51216-7, 2 km NE Craigs Swamp, Holey Plains State Park, C. Belcher, 20.xi.1978; SAM R29659, Cape Conran, M. J. Littlejohn, G. F. Watson, 26.ix.1985; SAM R29652, 7 km ENE Marlo, H. C. Gerhardt, 27.xi.1981.

Size range of the males is 22.0–32.4 mm, and of the females 28.0–34.1 mm. Hind limbs are long (TL/S-V 0.39 ± 0.03 [0.35–0.44]), and paratypes

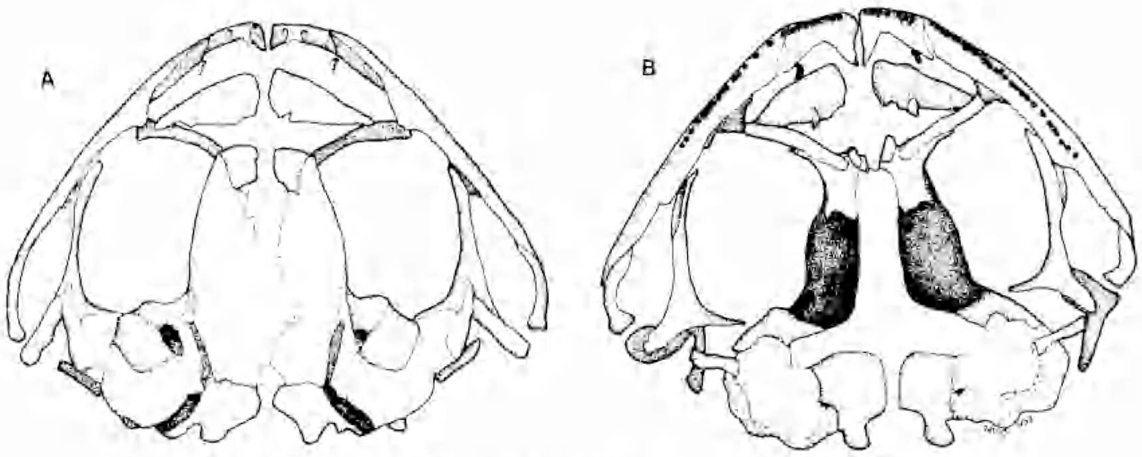

Fig. 25. A, Dorsal and B, ventral views of the skull of *Uperoleia tyleri* sp. nov. (NMV D23639).

have variable snout proportions (E-N/IN 1.18 ± 0.19 [0.87–1.65]). All paratypes have hypertrophied parotoid glands. Variation occurs in the presence and extent of a white patch on the dorsal surface of the arm. Some specimens are dark slate rather than chocolate ventrally, and others are not as evenly pigmented as in the holotype, but all are heavily pigmented. The dorsa of some specimens are rugose with small tubercles. Lightish coloration occurs on the parotoids, and a very faint midvertebral stripe occurs in some specimens. Some specimens exhibit fringes on the toes.

Osteology (based on NMV D23639)

Skull moderately-well ossified sloping sharply anteroventrally (Fig. 25). Ossified portion of sphenethmoid not confluent medially and extending slightly anteriorly to anterior extremities of fronto-parietals and posteriorly about ⅓ of length of orbit in ventral view. Prootic and exoccipital not fused, large areas of prootic calcified posterolaterally. Exoccipitals not fused dorso- or ventromedially. Crista parotica short and stocky, not in bony contact with otic ramus of squamosal. Carotid canal a deep exposed channel in posterolateral frontoparietal bones. Frontoparietal fontanelle narrowly and irregularly exposed medially, exposure greatest about ⅔ posteriorly along length of frontoparietals. Frontoparietal elements broad, angled slightly posterolaterally along orbital edges. Neither anterior nor posterior extremities of frontoparietal fontanelle can be defined because of lack of medial ossification of sphenethmoid and exoccipital respectively.

Nasals moderately ossified and triangular, moderately separated medially. Maxillary process of nasal moderately developed and mucronate, not articulating with well-developed preorbital process of shallow pars facialis of maxillary.

Palatines moderately broad reduced laterally to level of preorbital processes of maxillaries, medially in long contact with sphenethmoid at angle of about 45° (Fig. 25). Parasphenoid robust with moderately slender, long, truncate cultriform process extending anteriorly to level of articulation of anterior arm of pterygoid with palatal shelf of maxillary. Alae short, moderately broad and at right angles to cultriform process.

Anterior ramus of pterygoid in long contact with well-developed pterygoid process of palatal shelf of maxillaries; medial ramus short and acuminate, not in contact with prootic; posterior ramus moderately broad and stocky. Cartilaginous quadrate present between base of squamosal and quadratojugal. Quadratojugal robust and in firm contact with maxillary. Squamosal stocky with tiny blunt zygomatic ramus and moderately long unexpanded otic ramus.

Maxillaries and premaxillaries dentate. Palatal shelf deep. Palatal processes of premaxillaries long, almost confluent medially. Alary processes of premaxillaries long, narrow, perpendicular to dentigerous processes. Pterygoid process of palatal shelf of maxillary well developed.

Vomers present but reduced to two small remnants of bone, one on medial edge of choana and second on anteromedial extremity of sphenethmoid. Dentigerous processes absent.

Bony columella present.

Pectoral girdle arciferal and robust. Omosternum

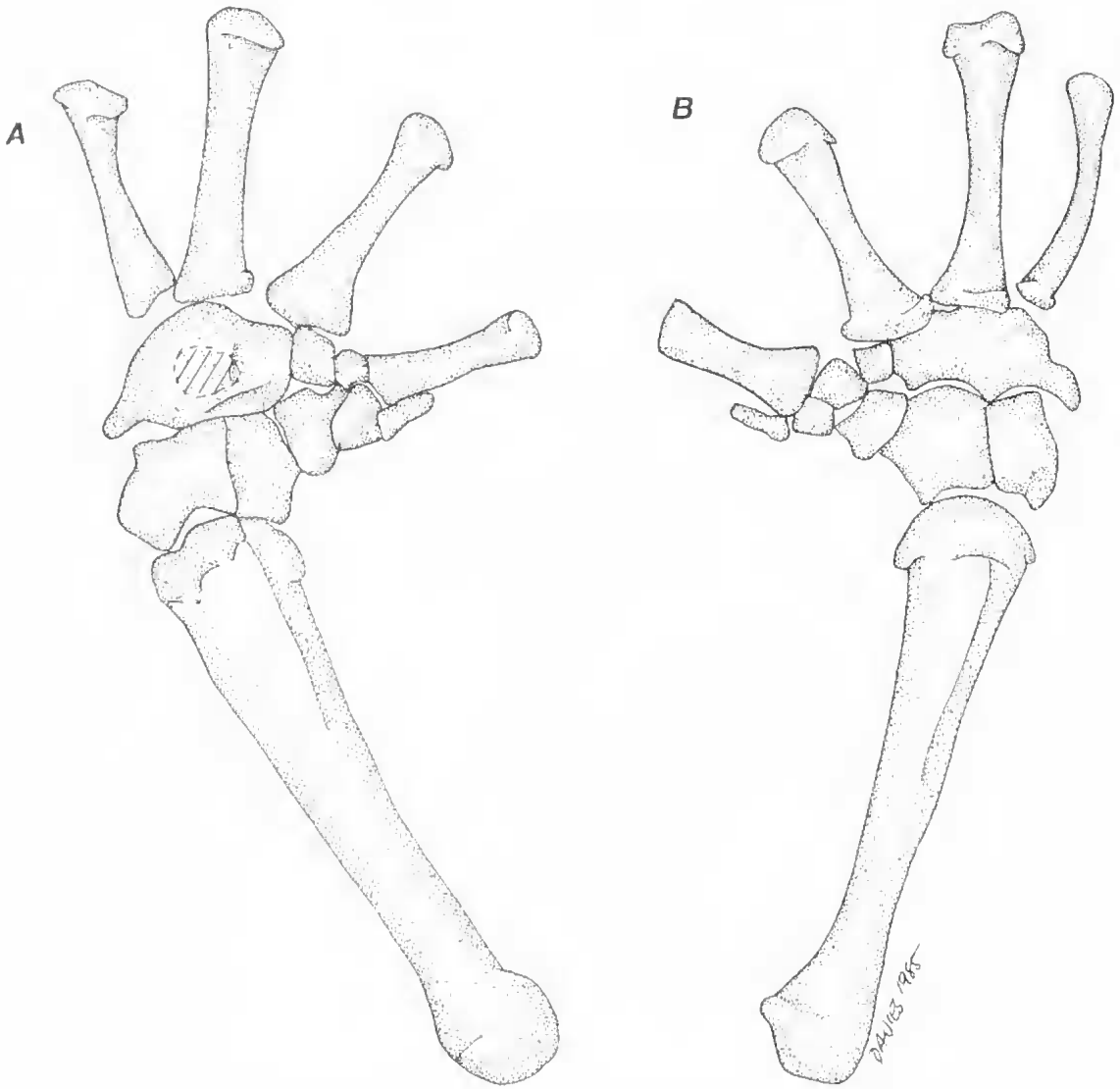

Fig. 26. A, Palmar and B, dorsal views of the carpus of *Uperoleia tyleri* sp. nov. (NMV D23623).

and xiphisternum present. Sternum cartilaginous. Clavicles slender, curved, moderately separated medially. Coracoids robust, moderately separated medially. Scapula bicapitate, slightly longer than clavicles. Suprascapula about ⅓ ossified. Moderately-developed anteroproximal humeral crest. Phalangeal formula of hand 2,2,3,3. Bony prepollex and palmar sesamoid present.

Six carpal elements present. Considerable torsion apparent. Prominent flange extending proximally from lateroproximal corner of O. centrale post axiale. Carpal elements of O. distale carpale 2 and 3 not fused (Fig. 26).

Eight non-imbricate presacral vertebrae. Sacral diapophyses poorly expanded. Ilia extend anteriorly to sacral expansion. Relative widths of transverse processes: III > saerum > IV > II > V = VI = VII = VIII.

Incomplete mediodorsal ossification on vertebrae I-V. Short transverse processes present an urostyle. These are probably anomalous structures often occurring in single specimens of *Uperoleia*. Urostyle

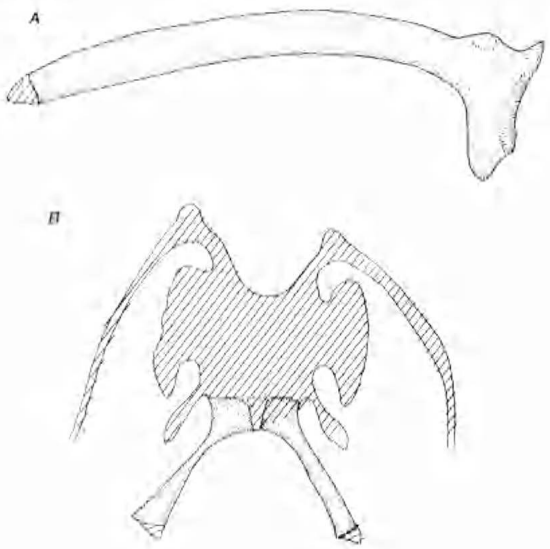

Fig. 27. A, Lateral view of the ilium of *Uperoleia tyleri* sp. nov. (NMV D23623). B, Hyoid of *Uperoleia tyleri*sp. nov. (NMV D33601).

bicondylar, well-developed crest extending dorsomedially about ½ length of urostyle.

No ilial crest. Dorsal prominence monticuline; dorsal protuberance posterolaterally placed on prominence (Fig. 27). Pubis cartilaginous.

Phalangeal formula of foot 2,2,3,4,3. Bony prehallux.

Three distal tarsal elements present. Lateral element (T_3) largest (Fig. 28).

Hyoid plate about as broad as long. Alary processes large, not pedunculate. Anteroproximal portions of anterior cornua dilated, anterior processes of hyale in the form of thickenings. Posterolateral processes moderately long. Posteromedial processes ossified (Fig. 27).

Variation

A further nine paratypes were cleared and stained (NMV D23622-3, D42743, D42745, D48597, D33601, AM R4755, SAM R29658, SAM R29652). The osteological features of this species are remarkably constant. Some differences in ossification and calcification in the crista parotica region are evident, but the described condition is that of minimal ossification.

The vomerine vestiges are absent from one side in one paratype and absent from the edges of the choanae in a second. Other specimens have the zygomatic ramus of the squamosal developed more extensively and knobbed.

Advertisement call

Characteristics of the advertisement call of *U. tyleri* are shown in Table 1, Fig. 8.

Life history

Watson and Martin (1973) described the larval morphology and life history of this species (as *U. marmorata*).

Distribution

Uperoleia tyleri is a coastal species extending as far north as Tamworth in N.S.W. and just penetrating south-eastern Victoria (Fig. 29).

Comparison with other species

Uperoleia tyleri is a large species (♂♂ 23–33 mm, ♀♀ 26–34 mm) with maxillary teeth and with a moderately-exposed frontoparietal fontanelle. These features are not shared by congeners. From the toothed species, *U. martini*, *U. marmorata*, *U. laevigata*, *U. mjobergi* and *U. micromeles* (vestigial teeth), the species can be separated by a number of features. From *U. martini*, *U. tyleri* is separated by a relatively-smooth dorsum, the reduced mottling on the dorsum and by call. From *U. marmorata*, *U. tyleri* is distinguished by its moderately-exposed frontoparietal fontanelle, hypertrophied parotoid glands, and densely-pigmented ventral surface. From *U. laevigata*, *U. tyleri* is separated by exposure of the frontoparietal fontanelle and heavy ventral pigmentation. *U. mjobergi* is a small species (males 19–25 mm, females 21–23 mm S-V) with a characteristic lyrate pattern on the dorsum and a prominent heel papilla lacking in congeners. *U. micromeles* has a very narrow head (E/N/IN 0.83–0.90, 0.87–1.65 in *U. tyleri*) and is not fully toothed.

Other material examined: An aberrant population from Treachery Head, Seal Rocks, N.S.W. (AM R27656-7, R27662-5) was examined. All are small, but adult (evidenced by calling) males with a size range 18–22 mm. The ventral pigmentation is not as extensive as that of the type series, but is dappled

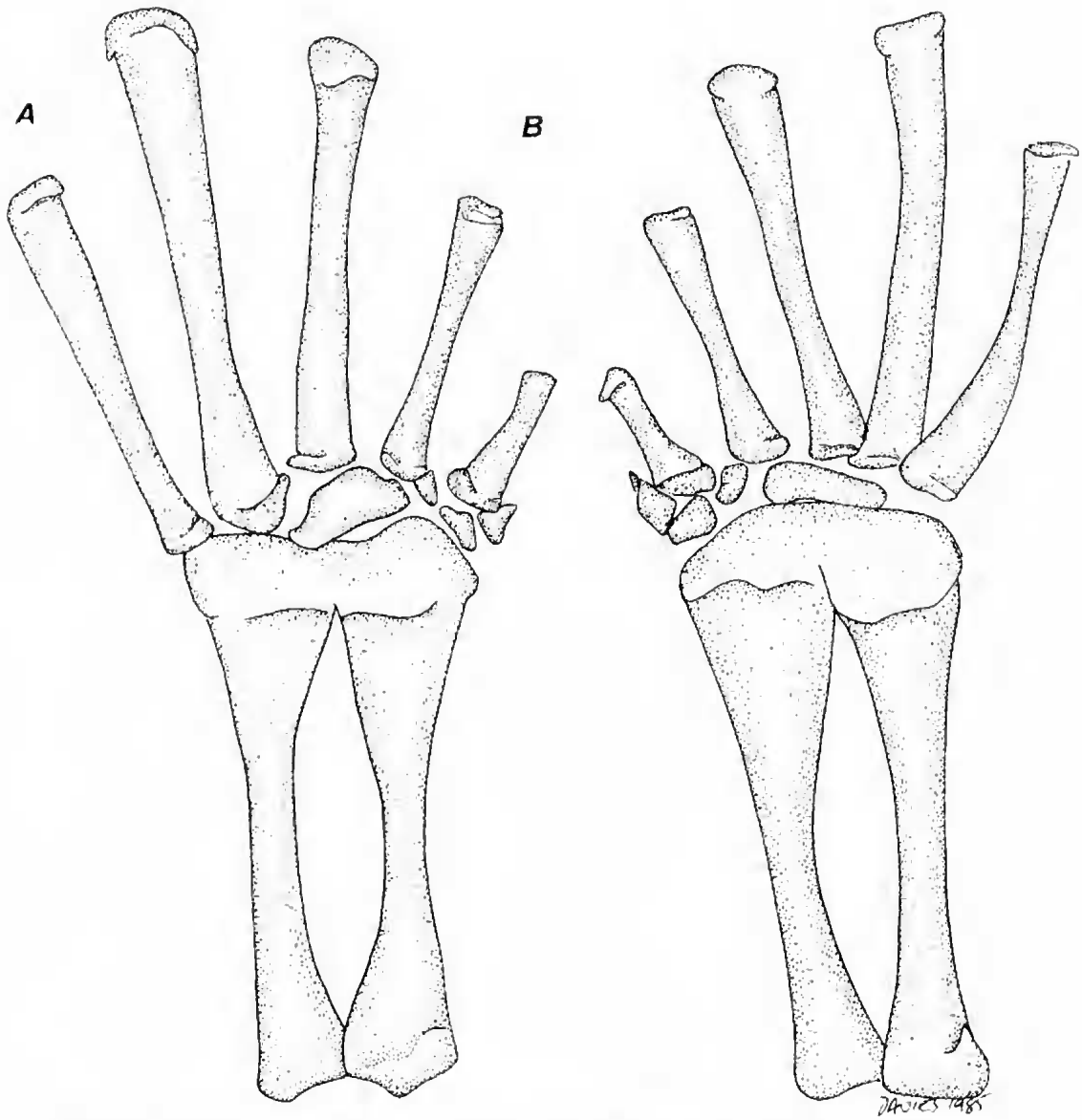

Fig. 28. A, Dorsal and B, plantar views of the tarsus of *Uperoleia tyleri* sp. nov. (NMV D42743).

and approaches the pigmentation of material from Tamworth. The parotoid glands are not hypertrophied as in the type series. Osteologically (Fig. 30), and in external features such as finger and toe webbing and subarticular, palmar and metatarsal tubercles, the series conforms to *U. tyleri* (Fig. 25).

Other material assigned to this species but excluded from the type series, is as follows (much of this material is badly faded): *N.S.W.*: NMV D6987, Sydney; AM R4213, Maroubra; AM R5285, R5287, Maroubra Bay; AM R78649-53, Maroubra; AM R5435, Randwick; AM R18696, Picton Lakes; AM R115560, 8 km N The Oaks on Wallacia Rd.

Habitat and calling site in south-eastern *Uperoleia*

In general, breeding habitats are similar for all species. Males usually call from the borders of

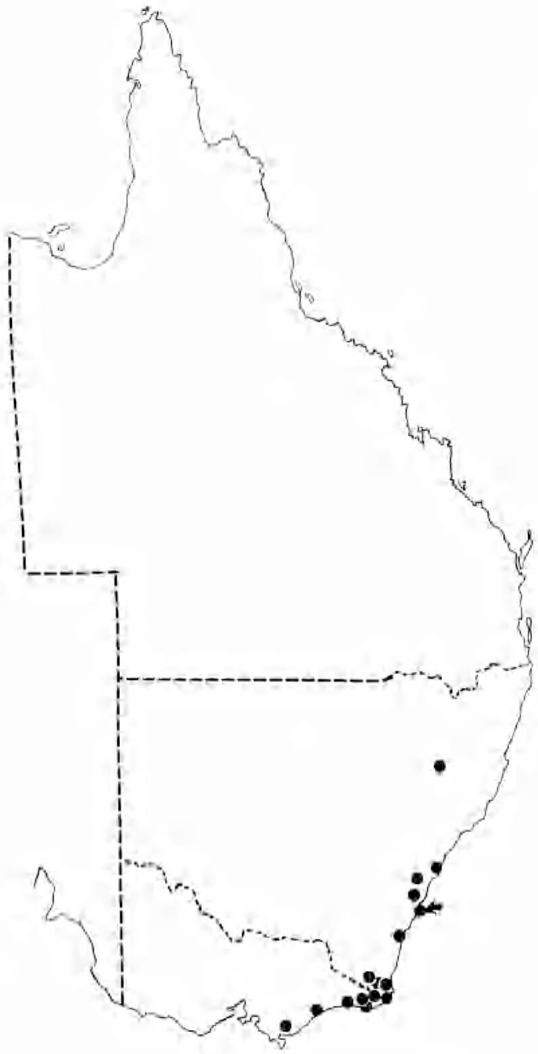

Fig. 29. Distribution of *Uperoleia tyleri* in eastern Australia. The arrow indicates the type locality.

shallow, temporary ponds, or from small islands of soil or vegetation in such ponds. Robertson (1984, 1986a, b) has provided a full description of the calling behaviour of *U. laevigata* (as *U. rugosa*).

Discussion

The limited morphological diversity, and marked intraspecific variation within characters, in species of *Uperoleia* impose constraints on their identification.

The value of osteology and call in the identification of species of *Uperoleia* was demonstrated by Tyler *et al.* (1981a, b, c); but early workers (to whom call data were not available) recognised the importance of some osteological features such as the exposure of the frontoparietal fontanelle. This latter character (together with the degree of toe webbing) was used to define the genera *Uperoleia* Gray and *Glauertia* Loveridge (Loveridge, 1933). Subsequently, Tyler *et al.* (1981a) showed that the states of exposure of the frontoparietal fontanelle and of toe webbing exhibited by these genera represent extremes in continua, and, in consequence, they suppressed *Glauertia*.

Intraspecific variation in osteological characters, both within and between populations, has been investigated in *U. lithomoda* (Davies, McDonald & Corben in press), and in the species in this study.

Many osteological features vary to such an extent that they are not useful in diagnoses at the specific level. However, a number of characters are valuable, and particular combinations of characters can be effective diagnostic tools. The presence or absence of maxillary and premaxillary teeth was recognised by Parker (1940) as being of paramount importance in species recognition but Moore (1961) considered the presence or absence of teeth to reflect no more than geographic variation; whilst Straughan (1966)[4] considered the presence of teeth to be variable within species and even between the sides of the maxillae in the one specimen. We have never encountered bilateral asymmetry in tooth development in any of the specimens of *Uperoleia* examined, and thus find the presence or absence of teeth on the upper jaw to be a most useful specific diagnostic feature.

Extent of exposure of the frontoparietal fontanelle is an effective character in species recognition. This feature is under ontogenetic influence (Davies unpubl.) and account must be taken of the relative age of the specimen (as indicated by ossification of key features such as the prootic and exoccipitals and the epiotic eminences, the sphenethmoid and the carpal bones) (Davies unpubl.).

However, because most of the material was in breeding condition when collected, adult features normally are apparent; and hence the usual condition of the frontoparietal fontanelle is present. It seems that the frontoparietal elements continue to grow, although probably slowly, and in 'aged' individuals (as instanced by calcification of various skeletal and cartilaginous elements and by minor exostosis of cranial bones), exposure of the

[4] Straughan, I. R. 1966. An analysis of species recognition and species isolation in certain Queensland frogs. Ph.D. thesis, University of Queensland. Unpublished.

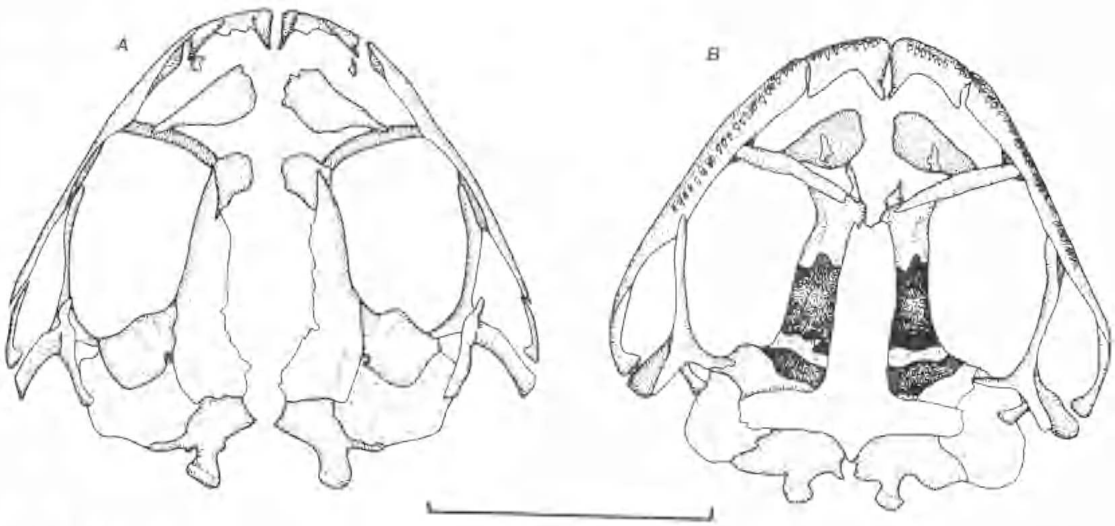

Fig. 30. A, Dorsal and B, ventral view of skull of *Uperoleia tyleri* from Treachery Head, Seal Rocks (AM R27656). Scale bar = 5 mm.

frontoparietal fontanelle is less than in 'mature' specimens.

The shape and degree of ossification of the nasal bones rarely vary within a species, and the relationships of these bones with the sphenethmoid and with the anterior extremities of the frontoparietal elements are constant. The shape of the pars facialis of the maxillary, and the presence or absence of a preorbital process on this shelf, are characteristic of *Uperoleia*.

The length of the otic ramus of the squamosal, and its relationship to the crista parotica, are useful diagnostic tools for the species with relatively-restricted ranges.

The shape of the alary processes of the premaxillaries can be useful, as can the shape of the palatine processes of the premaxillaries. The relative lengths and inclinations of the palatines to the spenethmoid are consistent, but some features of shape, particularly medially, tend to vary within a species.

Intraspecific variation is apparent in the inclinations of the alae of the parasphenoid, and also in the shape of the cultriform process. The shape of the distal end of the medial ramus of the pterygoid is not diagnostic but the shape of the posterior ramus is.

Post cranially, the most useful diagnostic features are the carpal elements, in particular the condition of the carpale 2 and 3, and in the ilium (see Tyler 1976; Davies *et al.* in press).

The dominant frequencies in advertisement calls of all species discussed here are similar and within the range, 1927–2432 Hz (Table 1); likewise depths of amplitude modulation generally exceed 90% for all taxa (Table 1). Most differentiation between species is evident in call duration, in the number of pulses in the call, or in the dependent character, pulse rate (Table 1, Fig. 8). Accordingly, these attributes may be used for effective diagnosis of the sympatric species.

Identification of specimens of *Uperoleia* from south-eastern Australia has been uncertain due to the instability of nomenclature within the genus prior to the revision of Tyler *et al.* (1981a), and to the lack of knowledge of extent of morphological variation in eastern Australian species. As the studies of early workers were restricted to external morphology and to some osteological features and because information on fugitive characters, such as colour in life and call were not available, few species were recognised.

Subsequently, Parker (1940) on the basis of a limited morphological analysis, synonymised *U. rugosa* and *U. fimbrianus*. He also commented that examples of *'U. marmorata'* from the coastal region of N.S.W. are very dark and may represent a distinct race.

Moore (1961) recognised only one species of *Uperoleia* in eastern Australia—*U. marmorata*, and considered that the differences in morphology he observed should be interpreted as intraspecific geographic variation. Tyler *et al.* (1981a) showed that

U. marmorata was restricted to north-western Western Australia, and they resurrected *U. fimbrianus* from the synonymy of *U. rugosa* on the basis of their experience with restricted distributions of species of *Uperoleia* in the north of Australia and because of its larger size. Tyler & Davies (1984) later showed that *U. lithomoda* has a wide ranging distribution across the north of the continent. Geographical differences in size also are apparent within *U. lithomoda* (Tyler & Davies 1984; Davies *et al.* in press) and the status of *U. fimbrianus* remained tenuous.

Uperoleia tyleri sp. nov. and *U. martini* sp. nov. are very dark coastal species, and a further undescribed species from the northern coastal region of N.S.W. and the south-west of Qld awaits recognition (Davies *et al.* in press). Our data do not support recognition of *U. fimbrianus* and thus the species is again synonymized with *U. rugosa*.

Uperoleia laevigata is a wide ranging species in south-eastern Australia (see Fig. 16). Both Humphries (1979[2]) and Robertson (1981, 1982[1], 1984a, b, 1986a, b) have made detailed studies of populations of this species (as *U. rugosa*).

Some reproductive data were collected at Mosman, N.S.W. by Harrison (1922), but it is not possible to determine whether the specimens which he had observed were of *U. laevigata* or of *U. tyleri*, both of which occur in the Sydney area. Fletcher (1890) reported on specimens of *Uperoleia* from several localities in N.S.W.: Burrawang, the neighbourhood of Sydney, near Cullenbone, near Mudgee, Narrabri and Dandaloo. Three of the species discussed in this paper could be represented amongst this material. He also studied material from two other localities in N.S.W.: Kiacatoo Station, near Condoblin (probably *U. rugosa*) and Emu Plains, Urana (probably *U. rugosa*) (Fletcher 1891). Material from Lucknow, N.S.W. (near Orange), Pumpana, Qld (south of Brisbane), and Waroo, Inglewood, Qld probably represents *U. rugosa* and *U. laevigata* or an undescribed species (Davies *et al.* in press) (Fletcher 1892).

Fletcher (1893) also identified material from Jervis Bay, A.C.T. (*U. tyleri*), Inverell, 64 km west of Glen Innes, N.S.W. nd Bungendore, N.S.W. (*U. laevigata*) and Tamworth, N.S.W. (*U. tyleri* or *U. laevigata*). Unfortunately no records of the specimens examined are available, so that the tentative identifications cannot be confirmed.

It is probable that many of the specimens examined by Slevin (1955), and referred to *U. rugosa*, are identified correctly. However, we have not examined his material, and hence cannot comment further.

The skins of *Uperoleia* species have been a rich source of polypeptides with pharmacological activity. Erspamer *et al.* (1966), Erspamer *et al.* (1975), Roseghini *et al.* (1966) and Erspamer *et al.* (1977) obtained a non-mammalian tachykinin which they named Uperolein from thousands of skins of frogs from Queensland and N.S.W. and identified as *U. rugosa* and *U. marmorata*. Other pharmocologically active peptides also were obtained by these authors. However, the activity ratio among the various peptides varied not only for the different preparations but also within a single preparation (Erspamer *et al.* 1975). The batches of skin obtained clearly represented more than one species. From N.S.W. we have demonstrated the presence of four species (and a fifth is known to occur there, Davies *et al.* in press).

Clearly the resolution of species of *Uperoleia* in eastern Australia is essential for this type of pharmacological work to be maximally effective.

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