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Taxonomy and systematics of the genus *Uperoleia* Gray (Anura: Leptodactylidae)

by

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To Mike, Graeme, Linda and Angus

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4.9 Davies, M., McDonald, K.R. and Corben, C. (1986) The genus *Uperoleia* Gray (Anura: Leptodactylidae) in Queensland Australia. *Proc. R. Soc. Vict*. 98, 147-188.

SUMMARY

Taxonomy and systematics of the genus *Uperoleia* Gray (Anura: Leptodactylidae)

The leptodactylid genus *Uperoleia* Gray comprises small, morphologically conservative, fossorial species of frogs that are distributed throughout Australia in the wet/dry tropics, the Pilbara and eastern Australia. They penetrate New Guinea in the lowland areas across Torres Strait.

In this study representatives of the genus are examined with respect to external morphology, osteology and, where possible, call. Seven new species are recognised and one is synonymised, resulting in a genus comprising 23 taxa.

A study of the ontogeny of bone in representatives of the genus, together with two related species (*Ranidella signifera* and *Pseudophryne bibroni*), provides descriptive data on the development of bone in both premetamorphic and postmetamorphic material. Taxonomic decisions made with respect to the recognition of two cognate species pairs, *U. inundata* and *U. arenicola*, and *U. rugosa* and *U. capitulata* are examined in the light of these ontogenetic data. In the case of the first pair, the problem is unresolved; but in the case of *U. rugosa* and *U. capitulata*, the judgments made are vindicated.

Ontogenetic data are examined further in the light of the proposal of Tyler *et al*. (1981a) that *Uperoleia* is a paedomorphic lineage. This premise is accepted, and 12 characters are identified as influenced by heterochrony in *Uperoleia*.

Alberch (1985) hypothesized that paedomorphosis should lead to a high level of homoplasy in a cladistic analysis of such a lineage. Preliminary data from such an analysis of the relationships of taxa within *Uperoleia* do not support this hypothesis; but given the weak nature of the data base, this result requires further investigation within a more malleable group.

The distribution patterns of *Uperoleia* are unique amongst Australian vertebrates and no explanation can be provided for the absence of the genus in southwestern Australia. Local edaphic factors are important within current distributions, with only one species, *U. trachyderma*, being associated with a particular soil type.

DECLARATION

This thesis contains no material accepted for the award of any other degree or diploma in this or any other university.

To the best of my knowledge this thesis contains no material previously published or written by any other person, except when due reference is made in the text.

Should this thesis be accepted for the award of a higher degree, I consent to its being made available for photocopying and loan.

Margaret Davies

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1. INTRODUCTION

Knowledge of the diversity of the Australian frog fauna has increased dramatically over the last two decades (Tyler 1979b; Cogger, Cameron and Cogger 1983; Frost 1985). One reason for this increase is access by herpetologists to the wet/dry tropics of the north of Australia during the wet season when frog activity is maximal. Since many components of the northern fauna are fossorial, knowledge of their existence and of aspects of their biology can be obtained only during the monsoonal periods when the frogs are foraging and breeding above the surface of the ground.

Access to these areas at this time is difficult and hence much information is obtained fortuitously. Tropical storms are highly localized for much of the wet season, herpetologists are few and herpetologists in the right place at the right time are rare. Nonetheless, tremendous progress has been made in our understanding of the Australian frog fauna and in our knowledge of fossorial species in particular.

One such group of frogs belongs to a genus of small, cryptic species of limited morphological diversity. Delineation of members of the genus is reliant upon such fugitive characters as call and colour and pattern in life, together with a few characters of external morphology and with osteological features (Tyler, Davies and Martin 1981a,b,c).

The definition of the content of this genus, together with an investigation of evolution within the genus, form the basis of this thesis.

Uperoleia Gray, 1841a was erected to accommodate a small, squat, short-legged fossorial frog collected by G. Grey in 'Western

Australia'. The species, named *Uperoleia marmorata*, is thought to have been collected in the vicinity of the Prince Regent River in north Western Australia, a locality deduced from the account of Grey's travels (Gray 1841b) examined by Tyler *et al*. (1981a). Gray indicated in this latter publication that the species was a representative of the Ranidae.

Cope (1865) emended the generic name to *Hyperoleia*, an action followed by Boulenger (1882), Lucas and Le Soeuf (1909), Nieden (1923), Fletcher (1889, 1890, 1891, 1892, 1894, 1898), Boettger (1892, 1894), Aflalo (1896), and W.K. Parker (1888)-who masculinised the binomen and referred *Uperoleia* as a subgenus to *Hyperolius* (*Uperoleia*) *marmoratus*.

Loveridge (1935) and H.W. Parker (1940) reverted to Gray's original name, with Parker placing the genus in the leptodactylid subfamily Myobatrachinae. All subsequent authors have adhered to the decision on generic disposition; although many authors now recognise the Australian members of the Leptodactylidae as a separate family, the Myobatrachidae (Frost 1985).

Prior to 1981 the species variously assigned to *Uperoleia* were the nominate species, *U. marmorata* Gray, 1841, *Pseudophryne mjobergi* Andersson, 1913, *Pseudophryne rugosa* Andersson, 1916, and *Pseudophryne fimbrianus* Parker, 1926.

Andersson (1913) described *P. mjobergi* from two small specimens collected at Noonkanbah in north Western Australia. The species has had an unstable nomenclatural history. Nieden (1923), Harrison (1927) and Loveridge (1935) referred it to *Pseudophryne* Fitzinger, 1843. H.W. Parker (1940), however, regarded the species as a representative of *Glauertia* Loveridge, 1933. All of these authors took no account of the presence of teeth on the maxillary arch, a feature not found in either *Pseudophryne* or *Glauertia*. Lynch (1971) 'tentatively' transferred the species to *Uperoleia*, commenting that similarities between *Uperoleia* and *Glauertia* warranted closer examination. However, field guides and checklists published subsequently (Cogger 1975, Tyler 1976a, Barker and Grigg 1977) maintained Parker's (1940) opinion by placing *mjobergi* with *Glauertia*. It was not until the revision of Tyler *et al*. (1981a) that the species was referred unequivocally to *Uperoleia*. These authors redescribed the species from the type specimens and later expanded the descriptions to include osteological and call data obtained from freshly collected material (Tyler *et al*. 1981b).

Pseudophryne rugosa Andersson, 1916 was based on a specimen collected at Mt Colosseum, south east Queensland. Andersson commented that this species was similar to *P. mjobergi* but that the differences were sufficient to render the taxa distinct. Loveridge (1935) considered *rugosa* a subspecies of *U. marmorata*. H.W. Parker (1940) confirmed Loveridge's generic designation, but considered *U. rugosa* a distinct species, distinguished from *U. marmorata* by the absence of maxillary teeth. (Parker did, however, mislabel an illustration of the palate of a toothed *Uperoleia* species as *U. rugosa*. (Parker 1940, p. 68).) Subsequent contributors recognised the individuality of *U. rugosa* until Moore (1961), a self-confessed 'lumper', synonymised the species with *U. marmorata*. The differences between specimens from different localities noted by him were thought to be geographic variants because of the presence of intermediate forms in some localities. Littlejohn (1963) disagreed with Moore and recognised three distinct call types within the genus in eastern Australia (Littlejohn 1967). One call type he called *U. marmorata*, and the other two he referred to as *U. rugosa* (form A) and *U. rugosa* (form B). *U. rugosa* was recognised by all subsequent authors, although the definitions of the species were extremely broad and it is clear that many specimens were misidentified. Tyler *et al*. (1981a) redefined *U. rugosa* from the type specimen, and Davies and McDonald (1985) expanded this definition with morphological, osteological and call data obtained from freshly collected topotypic material.

Pseudophryne fimbrianus Parker 1926 was described from a single female from the St George District in south central Queensland. Parker (1940) synonymised this species with *U. rugosa*, and this synonymy was adopted by all subsequent authors until Tyler *et al*. (1981a) resurrected the species on the basis of its larger size and these authors' experience with restricted distributions of species in the north and north-west of the continent.

The nominate species, *U. marmorata*, was thought to have a wide-ranging distribution across the north of Australia and down the east coast. Keferstein (1867) recognised a subspecies of *Uperoleia*, *U. marmorata* var. *laevigata* from Randwick, N.S.W. Straughan (1966) recognised *U. laevigata* as a separate species in an unpublished thesis, but the species is indeterminate from his data. Tyler *et al*. (1981a) examined the type series, designated a lectotype and, from this material, redefined the species.

Tyler *et al*. (1981a) restricted the known distribution of *U. marmorata* to the type locality in northern Western Australian thus leaving many specimens undetermined. Parker (1940) had indicated that examples of *U. marmorata* from the coastal region of N.S.W. are very dark and may be recognised as a distinct race. Three previously undescribed species are recognised in this thesis from coastal N.S.W. and Victoria.

Tyler, *et al*. (1981a) restricted their revision to species from the north and northwest of the continent. The named species, *U. marmorata*, *U. rugosa*, *U. mjobergi*, *U. fimbrianus* and *U. laevigata*, they redefined from the type material; and they described *U. arenicola*, *U. borealis*, *U. crassa*, *U. inundata*, *U. lithomoda*, *U. micromeles*, *U. minima*, *U. talpa*, *U. variegata* and, in subsequent publications, *U. aspera* (Tyler, *et al*. 1981b) and *U. trachyderma* (Tyler, *et al*. 1981c).

These authors further showed that the characters used by Loveridge (1933) to erect *Glauertia*, namely a widely exposed frontoparietal fontanelle and extensive toe webbing, represented extremes in a continuum of characters found within *Uperoleia*. They, therefore, suppressed *Glauertia* and transferred the included species, *G. russelli* and *G. orientalis*, to *Uperoleia*.

Uperoleia orientalis (Parker 1940) was described from three specimens. The holotype and one paratype were collected by W. Stalker at Alexandria Station on the Barkly Tableland. Tyler, Davies and Martin (1983) were unsuccessful in locating the species at the type locality, and it is clear that biological data from this species probably will be obtained fortuitously. The third specimen was collected by G. Wilkins from Groote Eylandt in the Gulf of Carpentaria. Tyler, Davies and Watson (1986) have shown this paratype to be referrable to *U. inundata*.

U. variegata was described by Tyler *et al*. (1981a), from a series of specimens obtained by A.K. Lee during the dry season from soil in the vegetable patch at Gibb River Station in the central Kimberley. Collection of calling males during the wet season of 1984/85 has shown this taxon to be, in reality, *U. lithomoda*, and the species has thus been referred to the synonymy of *U. lithomoda* by Tyler, Davies and Watson (in press).

Data on calls of *Uperoleia* species were sparse prior to 1981. Harrison (1922) likened the call of a *Uperoleia* species at Mosman in N.S.W. to a 'limnicoline bird' rather than a frog. Littlejohn and Main

(1960) described the call of *U. russelli* as a short grating squelch, 'grk, grk', while Main and Storr (1966) described the call of the same species as a high pitched abrupt 'ahk' which can change to an 'ik'. Littlejohn (1969) described the call of the species he assigned to *U. marmorata* as a long rasping squelch, and the call of *U. rugosa* (form B) as a long unpulsed call. *U. rugosa* (form A) was described as having a short pulsed advertisement call (Martin and Littlejohn 1969).

Straughan (1966) provided sonagrams of three species of *Uperoleia*, but none was referrable to any specimen collected by him and deposited in the Queensland Museum. Straughan's thesis was not published.

Barker and Grigg (1977) described calls of species of *Uperoleia* variously designated *U. marmorata*, *U. rugosa* and *G. russelli*. An accompanying tape recording of a call of a north western species and of Littlejohn's two eastern call types of *U. rugosa* is available. To date these calls have not been analysed.

Tyler *et al*. (1981a) provided sonagrams and descriptions of the calls of *U. arenicola*, *U. borealis*, *U. crassa*, *U. inundata*, *U. lithomoda* and *U. minima*; Tyler *et al*. (1981b) provided call data for *U. aspera* and *U. mjobergi* and *U. trachyderma* (Tyler, *et al*. 1981c). Davies and McDonald (1985) published a sonagram and call data for *U. rugosa*. Robertson (1984) published the call of *U. rugosa* (form B), the species recognised here as *U. laevigata*.

Data on breeding biology and tadpole morphology for the genus are rare. Harrison (1922) collected recently-metamorphosed individuals in January, and deduced that the *Uperoleia* species at Mosman was a summer-breeder. Fletcher (1889), however, observed a female lay over 200 eggs in September, and also observed amplexus as early as August. Littlejohn and Main (1960) concluded that *U. russelli* probably breeds opportunistically. Tyler *et al*. (1981a,b,c) collected calling males during the wet season in the wet/dry tropics of the north. Humphries (1979) recorded clutch sizes of 225.3±84.5 in *U*. *rugosa* (form B) and showed that a second clutch is often produced at the end of the season. Watson and Martin (1973) recorded similar mean clutch sizes of 225±21.1 range (81-352) for *Uperoleia*.

Martin (1967) and Tyler, Watson and Martin (1981) described the small eggs, oviposition and larval life of *Uperoleia*, and considered the breeding biology as the normal aquatic type. Moore (1961) described early development of material collected from Uralla on the New England Tableland; and Watson and Martin (1973) described the tadpole of '*U*. *marmorata*'. The life history of *U*. *inundata* was described by Tyler, Crook and Davies (1983) who recorded the usual $^2/3$ tooth rows of myobatrachine species (Watson and Martin 1973), with the upper row divided. A poorly developed border of large papillae, which is widely separated superiorly and inferiorly, surrounds the oral disc (Tyler et al. 1983)

Muscle data have been provided by a number of authors. Jones (1933) described the pectoral muscles, whilst Tyler (1971) investigated the myointegumental attachments associated with the vocal sac apparatus. Tyler (1971) found differences in the muscles associated with the vocal sac slits in the two then recognised genera, *Uperoleia* and *Glauertia*. Heyer and Liem (1976) provided data for the mandibular muscles in *Uperoleia* and *Glauertia*; and Thompson (1981) recorded M. depressor mandibulae, M. intermandibularis and geniohyoideus for a single species of *Uperoleia*. Horton (1982) described the form of the tongue muscles; whilst Tyler (1972b) and Tyler *et al*. (1981a) reported on the condition of the superficial mandibular muscles, other mandibular muscles, jaw adductor muscles and pectoral muscles.

Osteological data were provided originally by W.K. Parker (1888) with an illustration of the skull of '*Hyperolius* (*Uperoleia*) *marmoratus*.' H.W. Parker (1940) described the palatal bones of *Uperoleia*, and Loveridge (1933) provided information on the condition of the frontoparietal fontanelle in *Glauertia* species. Stephenson (1967) illustrated the skull of *Glauertia russelli*, and described the influence of heterochrony on this structure. Lynch (1971) illustrated and discussed cranial osteology in *Glauertia russelli* and *U. rugosa*. Tyler (1976b) described pelvic girdle morphology in both *Glauertia* and *Uperoleia*.

Heyer and Liem (1976) included osteological data in their analysis of intergeneric relationships amongst myobatrachid frogs. Osteological data for most *Uperoleia* species have been provided by Tyler *et al*. (1981a,b,c), Tyler and Davies (1984), Davies and McDonald (1985), Davies *et al*. (1985), Davies and Littlejohn (1986) and Davies *et al*. (1986).

Karyotypic data have been published by Morescalchi (1973), Davies *et al*. (1985) and Mahony and Robinson (1986).

The skins of *Uperoleia* species have been a rich source of polypeptides with pharmacological activity. Erspamer, de Caro and Endean (1966), Erspamer, Negri, Erspamer and Endean (1975), Anastasi, Erspamer and Endean (1975), Roseghini, Erspamer and Endean (1976) and Erspamer, Erspamer and Linnari (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 pharmacologically interesting peptides also were obtained. 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. I here recognise five species. From Queensland, three of these five species occur, and at least a further six species are recognised. It would seem from the literature that most of the skins were collected in southern Queensland (although the collection data are vague), where three species are known to occur, all three sometimes at the same site (G. Ingram pers. comm.; Straughan 1966).

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

Many authors have made contributions to distribution and natural history data of Uperoleia species. Information on eastern Australian species has been provided by Archer (1978); Brook (1975); Brooker and Caughley (1975); Czechura (1978); Fletcher (1889, 1890, 1891, 1892, 1893, 1898); Harrison (1922); Krefft (1864); Littlejohn (1967, 1969, 1971); Martin and Littlejohn (1969); McEvoy, McDonald and Searle (1979); Parker and Tanner (1972); Slater (1978); Slevin (1955); and Webber and Cogger (1976).

Gow (1981a,b); Mitchell (1955); Tyler and Davies (1986); Tyler, Davies and Martin (1983); Tyler, Watson and Davies (1983, 1986) and Wilkins (1928) provided data for Northern Territory material and Littlejohn and Main (1960); Main (1954, 1965); Loveridge (1949); Main and Calaby (1957); Main and Storr (1966); Smith and Johnstone (1981); Tyler, Smith and Johnstone (1984) for species from Western Australia. Australia wide records are provided by Cogger (1983); Cogger, Cameron and Cogger (1983); Grigg and Barker (1977); Tyler (1976, 1982); Tyler and Davies (1984) and Tyler, Watson and Martin (1981). Reference to *Uperoleia* in New Guinea is made by Menzies (1974); Zweifel and Tyler (1982) and Tyler and Davies (1984).

As indicated by Moore (1961), minor mention of *Uperoleia* is made by Lütkin (1863), Krefft (1865, 1867, 1870), Günther (1867), Boettger (1892, 1894), Aflalo (1896) and Barbour (1914).

Batrachomyia parasitism is reported by Krefft (1864), Skuse (1889), and Boettger (1894) whilst trematode parasites are recorded by Johnston (1912). The intermaxillary glands were described by Edmund Müller (1932).

Lynch (1971) suggested that *Uperoleia* and *Glauertia* were closely related but Heyer and Liem (1976), using a monothetic clustering technique, found *Glauertia* and *Myobatrachus* to form a single lineage, whilst *Uperoleia* and *Taudactylus* were closely related to each other. Farris, Kluge and Mickevich (1982) reanalysed the data of Heyer and Liem (1976) and provided evidence for monophyly of *Uperoleia* and *Glauertia*. Since these genera had been synonymised by Tyler *et al*. (1981a), the latter analysis appeared more realistic.

Blake (1972) suggested a relationship of *Uperoleia* with *Pseudophryne* using a phenetic analysis, whilst Daugherty and Maxson (1982), on the basis of biochemical data considered *Uperoleia*, *Myobatrachus* and *Arenophryne* to form a group of genera that are relatively close to *Ranidella*. These authors postulated *Uperoleia* to have diverged from *Ranidella* 35-46 my bp. Maxson and Roberts (1985) later considered *Uperoleia* to not have a close relationship with the cluster of genera, *Pseudophryne*, *Arenophryne*, *Myobatrachus* and *Metacrinia*.

A cladistic analysis of myobatrachine genera has yet to be undertaken.

Twenty-three species of Uperoleia are recognised in this thesis. Original descriptions are expanded by additional morphological, osteological and distributional data. Ontogenetic data for bone are provided where possible for some species of Uperoleia, and also for the closely-related genera, Ranidella Girard and Pseudophryne Fitzinger.

An analyses of phylogenetic relationships within Uperoleia is attempted, and the distributional pattern of the genus is examined.

2. MATERIALS AND METHODS

Material reported here is deposited in the American Museum of Natural History, New York (AMNH), the Australian Museum, Sydney (AM), the British Museum (Natural History), London (BMNH), the California Academy of Sciences, San Francisco (CAS), the CSIRO Division of Wildlife Research Collection, Canberra (ANWC), the Museum of Comparative Zoology, Harvard (MCZ), Museum of Natural History, University of Kansas, Lawrence (KU), Museums of Victoria, Melbourne (NMV), Northern Territory Museum, Darwin (NTM), Queensland Museum, Brisbane (QM), Museum of Natural History, Stockholm (NRAM), South Australian Museum, Adelaide (SAM) and the University of Adelaide osteological collection (UAZ). Initials following these abbreviations are departmental identifications within the institutions, and generally precede the registration numbers on the tags attached to the specimens.

Most species of Uperoleia possess parotoid glands which cover the side of the head and obscure the tympana. This characteristic prevents accurate measurement of head length and head width. Measurements taken were: eye diameter (E), eye-to-naris distance, (E-N), internarial span (IN), snout-to-vent length (S-V), and tibia length (TL). The methods of measurement follow Tyler (1968).

Results are expressed as mean ± standard deviation, with ranges in parentheses.

Dentition of specimens was determined from visual external examination with confirmation, in cases of doubt, by tactile methods.

Osteological data were obtained from cleared and stained specimens with alizarin red S for bone prepared after the method of Davis and Gore (1947), and with alizarin red S for bone and alcian blue for cartilage prepared after the method of Dingerkus and Uhler (1977).

Osteological descriptions follow Trueb (1979) (with the exception of the use of vomer rather than prevomer) and Andersen (1978) (for the carpus and tarsus). Material that has been cleared and stained is indicated by (A) following the museum abbreviation and registration number, or by individual designation.

Advertisement calls were recorded with a Uher 4000 Report Monitor tape recorder and an AKG D190 ES microphone, or a Sony TC510-2 tape recorder and a Beyer M88 dynamic microphone, at a tape speed of 19 cm sec^{-1}. Wet-bulb air temperatures were measured with a Schultheis rapid-reading thermometer close to the calling sites of males.

Calls were analysed by means of a sound spectrograph (Kay Model 7800 Digital Sona-Graph). Temporal characteristics of calls were determined from wide-band (300 Hz bandpass), and spectral characteristics from narrow band (45 Hz bandpass), spectrograms. Three calls of each male were analysed, and mean values were calculated.

Tadpoles were staged according to Gosner (1960).

Line drawing outlines were obtained with the aid of a Wild M9 stereoscopic dissecting microscope with attached 0.4x reducing lens, and a camera lucida.

3. TAXONOMIC STUDIES

3.1 Account of characters

External features

Habitus: *Uperoleia* species are small, squat frogs ranging in adult size from 16 mm (♂) in *U. minima* to 36 mm (♀) in *U. talpa*. The body is moderately broad to broad and the limbs are usually short. The maximum TL/S-V ratio recorded is 0.44 mm in *U. tyleri* and the minimum is 0.29 mm in *U. talpa*.

Head shape: The head is usually small and the snout short. The nares are narrowly or moderately separated in all species except *U. micromeles* in which they are widely separated. The snout can be truncated when viewed from above, gently rounded, or more acutely pointed. Intraspecific variation occurs in this feature, and all snout shapes may be found at the one locality. Snout shape is susceptible to preservation techniques, and strong dehydrating preservative usually results in truncated snouts. In profile, the snout is usually gently rounded. In *U. fusca* the snout is rounded ventrally but inclined posterodorsally.

Dermal glands: Prominent parotoid, inguinal and coccygeal glands are common. The parotoid glands are hypertrophied in *U. tyleri*, *U. martini* and *U. capitulata*, and are prominent in all other species except *U. trachyderma*. The inguinal glands are hypertrophied in *U. mjobergi*, many *U. rugosa*, *U. lithomoda*, some *U. mimula* and in *U. capitulata*. Coccygeal glands are not always apparent even if the parotoid and inguinal glands are well developed. They can be poorly, moderately or well developed. Submandibular glands vary between species. They may be discrete or disrupted within the one species. Degree of development ranges from almost absent to extremely prominent.

Skin texture: Dorsal skin may be smooth as in *U. capitulata* and *U. talpa*, moderately rugose as in *U. mimula*, or rugose as in *U. mjobergi*. *U. trachyderma* has characteristic finely conical tubercles on the dorsum found in no congener. Ventral skin is coarsely granular, finely granular or agranular. Granularity varies intraspecifically. Most species exhibit a granular post-femoral patch, and although the belly may be smooth, the pectoral region is usually granular.

Skin colour: *Uperoleia* species tend to be drably coloured, being grey, slate or brown dorsally; but tubercles and dorsal glands are often brightly coloured with orange (as in *U. glandulosa* and *U. trachyderma*), red (as in some *U. inundata*), golden (as in *U. lithomoda*), or cream (as in *U. rugosa*). The inguinal and post femoral regions are brightly coloured with shades of red, orange and yellow. These regions are uncoloured in *U. talpa*.

The ventral skin, other than the throat region in calling males, is unpigmented in many species (e.g. *U. aspera*), faintly pigmented (as in *U. mimula*), variably pigmented (as in *U. laevigata*), or fully pigmented (as in *U. fusca*, *U. tyleri* and *U. martini*).

Dorsal patterns develop in various ways. In many species such patterns are virtually absent (e.g. *U. tyleri*), or present but not prominent (e.g. *U. talpa*); whilst in others, they are prominent (e.g. *U. lithomoda*, *U. rugosa*).

Hands: The fingers are cylindrical, unwebbed, and either unfringed, poorly fringed, or (rarely) moderately fringed. Subarticular tubercles are generally extremely prominent; and supernumerary palmar tubercles occur in all species, although the degree of development shows intraspecific variation. Palmar tubercles are usually prominent - that at the base of the thumb being masked in males by the unpigmented glandular nuptial pad. The sequence of finger length is usually 3>4>2>1, but occasionally is 3>4=2>1.

Feet: The shape of the foot varies; it can be slender or moderately broad. The toes are usually slender and moderately long. Fringing is common, but the extent to which it is developed can vary intraspecifically. Toe webbing can be absent, basal or moderately developed. Toes are never more than about half-webbed, as in U. russelli, U. talpa, U. borealis and U. orientalis. Variation in webbing can occur, and species can exhibit basal or no webbing at different or the same sites (e.g. U. inundata, U. lithomoda). U. borealis taken from the N.T. show less webbing than conspecifics from the Kimberley. Subarticular tubercles are consistently conical. The inner and outer metatarsal tubercles are prominent, compressed and raised. They vary in size and orientation between species. The outer metatarsal tubercle is particularly small in U. trachyderma.

Pupil shape: The pupil is horizontal in life; in preservative it may have a V shaped extension of the ventral margin or it may be rhomboidal.

Teeth: Teeth are present in U. marmorata, U. mjobergi, U. fusca, U. laevigata, U. tyleri and U. martini; they appear to be vestigial in U. micromeles.

The presence or absence of teeth can be determined externally by using the following parameters: 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 are used to check for the presence of serrations.

Cranial features

Ossification: Ossification of the skull varies from poorly to moderately well ossified, dependent upon ossification of particular components of the skull, in particular the nasals and the frontoparietals.

Nasals: The nasals are extremely well ossified in *U. rugosa* and vary in degree of ossification from this condition to the poorly ossified state seen in *U. arenicola*. The nasals are arched medially. Anteromedial extension and ossification of the nasals is unusually prominent in *U. micromeles*. The anterior edges of the nasals are crescentic in a number of species and relatively straight in others. Posteromedial separation of these bones ranges from closely applied (as in *U. rugosa*) to moderately widely separated (as in *U. inundata*). Medially, separation of the bones is variable, but usually they are closely applied. The maxillary process of the nasal is short and either acuminate or truncated. It is never in bony contact with the pars facialis of the maxillary. The shape of the nasals is a reliable interspecific character.

Sphenethmoid: The sphenethmoid is always poorly ossified in *Uperoleia*. Dorsomedial ossification is under ontogenetic control, and is absent in all but senescent specimens. The sphenethmoid is sometimes slightly overlapped anteriorly by the posterior extremities of the nasals (as in *U. rugosa*), but more commonly it is not in bony contact with these elements. Ventrally, the sphenethmoid is again poorly ossified, and is overlain anteriorly by the medial extremities of the palatines.

Frontoparietals: The frontoparietals vary greatly in degree of ossification from being very slender elements edging the orbits to being very well ossified. Degree of ossification regulates the exposure of the frontoparietal fontanelle - poorly ossified frontoparietals result in a widely exposed frontoparietal fontanelle, and well ossified elements completely roof the fontanelle.

Ossification is a continuum, and frontoparietal fontanelle exposure is extremely varied within *Uperoleia*. Within species, exposure of the frontoparietal fontanelle is confined within certain limits and is a good species character.

The orbital edges of the frontoparietals vary in condition. They can be straight and oriented anteroposteriorly; they can be straight and angled slightly anteromedially; or they can be curved slightly anteromedially. The carotid canal groove on the posterolateral extremities of the frontoparietals can be deep, shallow, partially roofed, or not apparent. The appearance of the groove varies within species, but its absence is usually a consistent feature and is the usual condition in northwestern species. Development of the groove is usually more apparent in eastern species.

Crista parotica: The crista parotica region (*sensu* Lynch 1971) is short and stocky in *Uperoleia*. Ossification is poor within the genus, and the prootic and exoccipital regions are not confluent dorsally or ventrally, although some calcification of the non-ossified region is always apparent. The epiotic eminences vary in prominence and in *U. mimula*, they have developed an anterior superficial prominence. The degree of ossification varies interspecifically, being fully ossified in most species, but incompletely ossified posteriorly in some (e.g. in *U. tyleri*).

This feature is under ontogenetic control, and the epiotic eminences are always incompletely ossified in subadult specimens.

Squamosal: The squamosal shaft is always moderately robust and articulates ventrally with the cartilaginous quadrate. The zygomatic ramus is always short. In some species it is knobbed and relatively prominent (e.g. *U. tyleri*); in others, it is tiny and bifid (e.g. *U. borealis*); in others, it is tiny but not bifid (e.g. *U. lithomoda*); and in yet other species, the zygomatic ramus is absent (e.g. *U. crassa*). The otic ramus is always unexpanded and varies in length (intraspecific variation in this feature occurs in *U. lithomoda*). The otic ramus is never in bony contact with the crista parotica region, although in some species it is poorly separated from it. Rarely, the otic ramus shows a slight medial curvature.

Premaxilla: The premaxilla is dentate or edentate, except in *U. micromeles* in which vestigial teeth are apparent. The alary processes are usually moderately slender and perpendicular to the pars dentalis, and often are bifid dorsally. Rarely, they are very broad basally (as in *U. laevigata*), and are occasionally inclined slightly posteriorly or medially. The palatine processes of the palatal shelf of the premaxillaries are either closely applied or moderately separated. They vary in shape and length and often are curved posteromedially. The shape and length of the palatine processes can be useful specific characters.

Maxilla: The maxilla is dentate or edentate, except in *U. micromeles* in which vestigial teeth are apparent. The pars facialis varies in depth; it is shallow, moderately deep or deep, and in some species it is graded from moderately deep posteriorly to shallow anteriorly (e.g. *U. fusca*). The preorbital process is present or absent. If present, it can be inconspicuous or very prominent, and can vary in shape. The condition of the preorbital processes is an extremely useful interspecific character. The palatal shelf is usually moderately deep, and has a poorly, moderately or well-developed pterygoid process.

Quadratojugal: The quadratojugal is always entire, stocky and in firm contact with the maxillary. This bone shows no intrageneric variation.

Pterygoid: The pterygoid shows both interspecific and intraspecific variation. The anterior ramus is in long or short contact with the pterygoid process of the palatal shelf of the maxillary, and this character is species-specific. The posterior ramus can be slender or broad, truncate or acuminate, and is usually constant within a species. The medial ramus shows intraspecific variation. It is usually acuminate, sometimes expanded distally, occasionally in bony contact with the prootic (as in *U. mjobergi*), and varies in orientation to the prootic region within a species as well as between species.

Palatines: The palatines are usually slender bones, but occasionally are moderately robust (as in *U. micromeles*). They are always reduced laterally - the least reduction being found in toothed *Uperoleia* in eastern Australia. The greatest reduction does not allow the palatines to extend beyond the extremity of the maxillary process of the nasals. These elements are usually straight, but occasionally curved (as in *U. micromeles*). Often they are expanded medially, and usually overly the sphenethmoid at an angle of 30-45°. The palatines are unridged and lack odontoids.

Parasphenoid: The parasphenoid is a robust element. Variation occurs in the nature of the cultriform process which is moderately slender or broad. It extends anteriorly for various distances, and terminates in a truncated, serrated, acuminate or expanded form. The alae are at right angles to the cultriform process in most species, but are angled posterolaterally in some. The alae are slender and elongate, or short and usually broad. Some intraspecific variation occurs in this element.

Vomers: Vomerine fragments appear medial to the palatines overlying the sphenethmoid and at the edges of the choanae. The latter are not always present with the former, and bilateral symmetry is sometimes lacking in this feature. Intraspecific variation occurs in the development of vomerine fragments; but they are consistently absent in many species (e.g. *U. lithomoda*, *U. mimula*, *U. mjobergi* and *U. inundata*), and consistently present in others (e.g. *U. tyleri*). Intraspecific variation in the occurrence and nature of vomerine fragments occurs in *U. rugosa*, *U. laevigata* and *U. fusca*. In *U. talpa*, they have been recorded in one specimen. Dentigerous processes are never present.

Columella: A bony columella is present in all species of *Uperoleia*.

Postcranial features

Pectoral girdle: There is little interspecific variation in the pectoral girdle, other than in the presence or absence of the omosternum. The clavicles are slender, curved elements, closely applied medially. The coracoids are moderately robust, and moderately separated medially. The scapula is bicapitate and as long as or slightly longer than the clavicles. The suprascapula is between $^{1}/2$ and $^{2}/3$ ossified.

A well-developed anteroproximal crest is always present on the humerus.

Carpus: The phalangeal formula of the hand is always 2,2,3,3. The carpus consists of the O. radiale, O. ulnare, O. centrale preaxiale, O. centrale postaxiale, and the carpal elements of the O. distale carpale 2 and 3. Three character states occur in these distal carpal elements: they may be fused (as in *U. rugosa*); they may be closely applied, but not fused (as in *U. mjobergi*); or they may be moderately separated (as in *U. inundata*). A palmar sesamoid is always situated ventrally on the O. centrale postaxiale.

Pelvic girdle: The ilium shows considerable interspecific variation. A small ilial crest is developed in *U. trachyderma*, and a more prominent crest occurs in *U. micromeles*. The dorsal prominence is poorly, moderately or well developed and varies in shape. It can be monticuline, wedge shaped or papillate. The dorsal protuberance is situated anterolaterally, laterally or posterolaterally on the prominence. The ischium is always ossified, and the pubis cartilaginous but calcified.

Tarsus: The phalangeal formula of the foot is, 2,2,3,4,3. There is little variability in the tarsal elements. Three distal tarsal elements are always present, and some interspecific variation occurs in the position of the second element relative to O. metatarsus II. Variation occurs in the shape and size of the distal prehallical element, which can be small and slender to broad and elongate.

Hyoid: Interspecific variation in the hyoid is apparent. The relative length and breadth of the hyoid plate varies, and the anterior hyale shows two conditions: a short slender anteromedial process is developed or the anteromedial extremities are thickened, but no free anteromedial process is apparent. The alary processes of the hyoid plate are broad and not pedunculate. The posterolateral processes vary in shape and length but are usually moderately broad and moderately short. The posterior cornua are ossified, and slight calcification of the plate between the posterior cornua is common.

Vertebral column: There is little interspecific variation in the features of the vertebral column. The vertebrae are non-imbricate, and free intervertebral discs are apparent in young specimens. Vertebrae I and II are incompletely fused dorsally by a calcified strip. The relative widths of the transverse processes fall into three groups: III>sacrum>IV>II>....; III>sacrum>IV>V....; III>sacrum>IV>VI.... . Transverse processes of presacral vertebra IV are usually oriented moderately acutely posteriorly. The sacral diapophyses are always poorly expanded, and the ilia either extend beyond the anterior extremity or lie alongside the sacral expansion.

A well-developed crest is present on the bicondylar urostyle and extends $^1/2 \rightarrow ^2/3$ of the length of the bone.

Karyotype

The diploid chromosome number of all Uperoleia species is 2n=24 (Morescalchi 1973; Davies et al. 1985; Mahony and Robinson 1986). Chromosome morphology is conservative, and species of Uperoleia cannot be distinguished from each other chromosomally, but all Uperoleia can be distinguished from other myobatrachine genera in the location of the nucleolar organiser region (Mahony and Robinson 1986).

Advertisement call

Uperoleia species can be broadly classified as short-call species (clicks) or long-call species (rasps or squelches). Major variation in call appears to be in the number of pulses per call and the pulse repetition rate.

Breeding biology

Uperoleia species are type I species of Tyler *et al*. (1981). Males call at or near the edge of temporary or permanent still waters, except *U. borealis* which calls beside moving water. At sites at which two or three species are sympatric, spatial separation of calling males of each of the species usually is pronounced; the eggs are small, pigmented and in separate capsules; total development is aquatic; embryos lack external gills, and tadpoles have a generalized body form and a $^{2}/3$ labial tooth formula.

3.2 Taxonomic decisions

Lynch (1971) illustrated the skull of a specimen of *U. rugosa* from St George, Qld (KU 109861). Comparison of that illustration and of the specimen examined by Lynch (1971) with the data obtained from topotypic specimens of *U. rugosa* (Davies and McDonald 1985) indicates that all the specimens are conspecific. St George is the type locality of *U. fimbrianus* (Parker 1926), a species separable from *U. rugosa* only by size (Davies and McDonald 1985). Examination of call data from edentate specimens assigned to *U. rugosa* (form A) of Littlejohn (1967) (Davies and Littlejohn 1986) 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 for the recognition of *U. fimbrianus*. Accordingly *U. fimbrianus* (Parker) is transferred to the synonymy of *U. rugosa* (Andersson) (Davies and Littlejohn 1986).

U. rugosa (form B of Littlejohn 1967) is a dentate species. The only other dentate species described from eastern Australia is

U. laevigata (Keferstein 1867). Examination of material deposited in Australian museums and of data on call structure (Davies and Littlejohn 1986) indicate that *U. rugosa* (form B) is *U. laevigata* Keferstein. Data on the type series include only external morphology, but I remain confident in this identification.

"*U. marmorata*" (*sensu* Littlejohn 1967) comprises two undescribed dentate species, herein described and named.

Uperoleia variegata Tyler, Davies and Martin 1981 was found to be synonymous with *U. lithomoda* Tyler, Davies and Martin 1981 following the collection of call data from topotypic material (Tyler, Davies and Watson in press) and is included in the synonymy of that species in this study.

A further seven species are recognised here. Descriptions of these previously undescribed species have been published prior to the submission of this thesis.

3.3 Checklist of species of *Uperoleia* (in alphabetical order)

Uperoleia arenicola Tyler, Davies and Martin
Uperoleia aspera Tyler, Davies and Martin
Uperoleia borealis Tyler, Davies and Martin
Uperoleia capitulata Davies, McDonald and Corben
Uperoleia crassa Tyler, Davies and Martin
Uperoleia fusca Davies, McDonald and Corben
Uperoleia glandulosa Davies, Mahony and Roberts
Uperoleia inundata Tyler, Davies and Martin
Uperoleia laevigata Keferstein
Uperoleia lithomoda Tyler, Davies and Martin

Uperoleia littlejohni Davies, McDonald and Corben

Uperoleia marmorata Gray

Uperoleia martini Davies and Littlejohn

Uperoleia micromeles Tyler, Davies and Martin

Uperoleia mimula Davies, McDonald and Corben

Uperoleia minima Tyler, Davies and Martin

Uperoleia mjobergi (Andersson)

Uperoleia orientalis (Parker)

Uperoleia rugosa (Andersson)

Uperoleia russelli (Loveridge)

Uperoleia talpa Tyler, Davies and Martin

Uperoleia trachyderma Tyler, Davies and Martin

Uperoleia tyleri Davies and Littlejohn

3.4 Key to the genus *Uperoleia* in Australia

1.	Internarial span less than eye to naris distance	2
	Internarial span greater than eye to naris distance	*U. micromeles*
2.	Maxillary arch dentate	3
	Maxillary arch edentate	8
3.	Prominent papilla on heel present	*U. mjobergi*
	Prominent papilla on heel absent	4
4.	Ventral surface fully pigmented	5
	Ventral surface not fully pigmented	7
5.	Parotoid glands hypertrophied	6
	Parotoid glands not hypertrophied	*U. fusca*
6.	Dorsal surface dark, parotoid glands not pigmented	*U. tyleri*
	Dorsal surface flecked with light pigment, parotoid glands flecked with light pigment	*U. martini*

7.	Yellowish triangular patch on head	*U. laevigata*
	Greenish triangular patch on head	*U. marmorata*
8.	Toes moderately webbed	9
	Toes unwebbed or basally webbed	12
9.	Dorsal surface tubercular	10
	Dorsal surface smooth or only faintly tubercular	11
10.	Parotoid glands prominent, scapular plicae present	*U. russelli*
	Parotoid glands moderately prominent, scapular plicae absent	*U. borealis*
11.	Mid-vertebral stripe absent; faint dorsal pattern	*U. talpa*
	Mid-vertebral stipe present; no dorsal pattern	*U. orientalis*
12.	Both inner and outer metatarsal tubercles raised and prominent	13
	Outer metatarsal tubercle small and poorly raised	*U. trachyderma*
13.	Frontoparietal fontanelle widely exposed	14
	Frontoparietal fontanelle not widely exposed	18
14.	Ventral surface unpigmented	15
	Ventral surface pigmented	16
15.	Nasals moderately ossified	*U. inundata*
	Nasals poorly ossified	*U. arenicola*
16.	Dorsum with strongly developed pattern	17
	Dorsum with indistinct pattern	*U. crassa*
17.	Toes well fringed and moderately basally webbed	*U. glandulosa*
	Toes poorly fringed and poorly basally unwebbed	*U. littlejohni*
18.	Advertisement call a sharp click, ventral surface unpigmented	19
	Advertisement call a pulsed note, ventral surface pigmented	21

19.	Well-developed parotoid glands and well or moderately developed inguinal and coccygeal glands	20
	Moderately developed parotoid glands, poorly developed inguinal and coccygeal glands	*U. minima*
20.	Dorsal pattern strongly defined, inguinal glands hypertrophied	*U. lithomoda*
	Dorsal pattern not strongly defined, inguinal glands not hypertrophied	*U. aspera*
21.	Frontoparietal fontanelle moderately exposed; dorsal surface faintly rugose	22
	Frontoparietal fontanelle unexposed; dorsal surface moderately rugose	*U. rugosa*
22.	Parotoid, inguinal and coccygeal glands hypertrophied	*U. capitulata*
	Parotoid, inguinal and coccygeal glands not hypertrophied	*U. mimula*

3.5 Species accounts

3.5.1 Genus *Uperoleia* Gray

Uperoleia Gray, 1841, Ann. Mag. Nat. Hist. 7, p. 90.

Uperoleja Gray, 1841, p. 436 [*lapsus pro Uperoleia* Gray, 1841].

Hyperoleia Cope, 1865, p. 108.

Glauertia Loveridge, 1933, p. 89.

Uperoleia: Moore 1961, p. 219; Lynch 1971, p. 99; Tyler, Davies and Martin 1981a, p. 9; Cogger 1983, p. 80; Cogger, Cameron and Cogger 1983, p. 32; Tyler 1985, p. 406.

Type species (by monotypy): *Uperoleia marmorata*, Gray 1841.

Diagnostic definition

1) Skull broader than long; 2) dermal roofing bones poorly to moderately ossified; 3) nasals moderately large to large, slightly separated medially, poorly to moderately separated posteromedially; 4) nasals in tenuous contact with, or lacking contact with sphenethmoid and/or frontoparietal elements; 5) maxillary process of nasal never in contact with pars facialis of maxillary; 6) sphenethmoid very poorly ossified and entire only in 'aged' specimens; 7) vomers absent or reduced to small edentate fragments on edges of choanae and/or medial to palatines on sphenethmoid; 8) cultriform process of parasphenoid moderately broad to broad; termination truncate, serrate, expanded, broad or slender; 9) alary processes of parasphenoid at right angles or slightly posterolaterally inclined to cultriform process; 10) crista parotica short and stocky, always incompletely ossified with substantial calcification of non-ossified area; 11) epiotic eminences poorly to well developed; posterior ossification sometimes incomplete; 12) carotid artery passes dorsal to posterolateral frontoparietal elements, and lies in a shallow groove, rarely incompletely roofed; 13) quadrate cartilaginous, between base of squamosal and quadratojugal; 14) zygomatic ramus of squamosal knobbed, tiny and bifid, tiny and not bifid or absent; otic ramus short to long, unexpanded, not in bony contact with crista parotica; 15) quadratojugal entire, in firm contact with maxillary; 16) pars facialis of maxillary moderately deep to shallow or of irregular depth; preorbital process present or absent, prominent or poorly developed; 17) palatal shelf of maxillary moderately deep, pterygoid process poorly to well developed; 18) palatal shelf of premaxillary well developed with broad or slender palatal processes; 19) alary processes of premaxillary usually directed dorsally,

occasionally medially and rarely posteriorly; moderately broad or broad, usually bifid dorsally; 20) maxillary arch dentate or edentate; 21) length of teeth variable; 22) palatines slender to moderately broad, overlying anterior portion of sphenethmoid ventrally; straight or slightly curved; expanded medially or unexpanded; reduced or not reduced laterally; 23) frontoparietal fontanelle exposure varied from unexposed to widely exposed; 24) orbital edges of frontoparietals straight, oriented antero-posteriorly, slightly anteromedially, or curved anteromedially; 25) medial prootic ossification absent; 26) hyoid plate cartilaginous with broad wing-like alary processes and well-developed posterolateral processes; 27) anterior hyale with or without slender anteromedial processes; 28) parahyoid bones absent; 29) vocal sac submandibular and unilobular; 30) M. submentalis broad and araphic; 31) M. intermandibularis not differentiated into supplementary elements, separated from submentalis in some species; 32) M. interhyoideus with vast lobe posterior to postarticular extremities of mandibles; 33) M. geniohyoideii separated medially and laterally; 34) M. adductor mandibulae externus superficialis absent; 35) M. depressor mandibulae with two slips; 36) small omosternum present or absent; 37) vertebrae imbricate or non-imbricate; 38) presacral vertebra III wider than sacral diapophysis; 39) sacral diapophyses poorly expanded; 40) ilial crest present or absent; 41) dorsal prominence very prominent, moderately or poorly developed; 42) pubis calcified; 43) phalangeal formula of hand 2,2,3,3; 44) carpus of five or six elements - carpal elements 2 and 3 fused or unfused; 45) palmar sesamoid present; 46) bony prepollex, small; 47) terminal phalanges knobbed; 48) phalangeal formula of foot 2,2,3,4,3; 49) three distal tarsal elements; 50) second tarsal element at base of metatarsus II or displaced laterally; 51) bony prehallux poorly, moderately or well developed; 52) fingers and toes undilated terminally; 53) fingers poorly fringed or unfringed; 54) interdigital webbing of feet present or absent; 55) toes fringed or unfringed; 56) metatarsal tubercles very prominent and raised; 57) nuptial pads unpigmented, subepidermal; 58) dermal glands extremely well developed; 59) diploid chromosome number 24; 60) chromosome pairs 3,4,5 and 8 submetacentric, others metacentric; 61) Uperolein (polypeptide) present in skin of some species; 62) advertisement call short; pulsed; 63) ova small, pigmented; 64) embryo without external gills; 65) larva unspecialized; labial formula $^2/3$.

3.5.2 *Uperoleia marmorata* Gray, 1841

Uperoleia marmorata Gray, 1841. Ann. Mag. Nat. Hist. 7, p. 90.

Hyperoleia marmorata: Boulenger 1882, p. 267 (part.).

Uperoleia marmorata: Parker 1940, p. 69 (part.); Moore 1961, p. 212 (part.); Tyler, Davies and Martin 1981a, p. 10; Tyler 1982, p. 236; Cogger 1983, p. 84 (part.); Cogger, Cameron and Cogger 1983, p. 33; Tyler, Smith and Johnstone 1984, p. 100; Tyler 1985, p. 407.

Definition

Moderately large species (♂ 30 mm); maxillary arch dentate; toes unfringed and unwebbed; frontoparietal fontanelle poorly to unexposed; carpus of six elements

External morphology

No further specimens have been assigned to this species since the revision of Tyler *et al.* (1981a) restricted the species to the holotype and dismissed all specimens reported as this species in the literature as not conspecific.

Osteology

The following data have been obtained from an X-ray of the holotype. The nasals are moderately well ossified. The preorbital process of the pars facialis of the maxillary is prominent. The epiotic eminences are extremely prominent. The frontoparietal fontanelle is poorly to unexposed. The orbital edges of the frontoparietals are angled slightly medially. The zygomatic ramus of the squamosal is relatively long. Vomerine fragments are absent. The palatines extend to the maxillary arch. Six carpal elements occur. The distal prehallical element is about $^1/3$ the length of metatarsus I. The dorsal prominence of the ilium is very prominent and wedge shaped.

Comparison with other species

Uperoleia marmorata is a toothed species with a poorly exposed frontoparietal fontanelle, features shared by U. laevigata, U. mjobergi, U. fusca and U. martini.

U. marmorata is distinguished from U. fusca and U. martini by the absence of complete ventral pigmentation. From U. laevigata it is distinguished by its larger size (males 22-28 mm S-V in U. laevigata) and from U. mjobergi by its larger size (males 19-25 mm S-V in U. mjobergi) and the absence of a heel papilla.

Distribution

Known only from the type locality, estimated to be in the Prince Regent River Region (Tyler et al. 1981a).

3.5.3 *Uperoleia laevigata* Keferstein, 1867

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 and Endean 1975, p. 41 (part.); Roseghini, Erspamer and Endean 1975, p. 35 (part.); Barker and Grigg 1977, p. 186 (part.); Erspamer, Erspamer and Linnari 1977, p. 68 (part.).

Uperoleia rugosa (form B): Littlejohn 1967, p. 153; Littlejohn 1969, p. 111; Martin and Littlejohn 1969, p. 170.

Uperoleia rugosa: Brook 1975, p. 83; Cogger 1975, p. 83 (part.); Barker and Grigg 1977, p. 188 (part.); Humphries 1979, p. 15; Robertson 1981, p. 4; 1982, p. 6; 1984a, p. 283; 1984b, p. 56; 1986a, p. 773; 1986b, p. 763; Erspamer, Negri and Endean 1975, p. 41 (part.). Cogger, Cameron and Cogger 1985, p. 34 (part.).

Uperoleia laevigata: Tyler, Davies and Martin 1981a, p. 11; Cogger 1983, p. 84; Cogger, Cameron and Cogger 1983, p. 33; Tyler 1985, p. 407; Mahony and Robinson 1986, p. 120; Davies and Littlejohn 1986, p. 122.

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; advertisement call a long pulsed 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; 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, 8 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; 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 Baraba 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 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, nr Bulgandramine; R115586-7, R115653-4 Tooloom Falls; R115585, Nettle Creek 19.2 km from Copmanhurst on Tabulum Rd; R108914-5 Mandurama; R110432 Parsons Gulley, Merriwa; R115645 4.8 km E Eulo. ANWC 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, R287841(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.; J45971 Blackdown Tableland in Forestry Camp; 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 Towoomba Rd; J19923 1.6 km W Stanthorpe; J19931-3 1.6 km S Rathdownay 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. I have examined the external morphology of a further 459 specimens.

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±.02 [0.30-0.43]). The snout is moderately long, usually evenly rounded when viewed from above (Fig. 2a) but occasionally truncated. In profile the snout is usually evenly rounded (Fig. 2b) but sometimes it slopes gently posteriorly. The nares are subterminal and dorsolaterally situated, but in those specimens with truncated snouts, the nares are terminal.

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. 2). The eye-to-naris distance usually is much greater than the internarial span (E-N/IN 1.38±.19 [1.11-1.72]).

The fingers are long and slender, unwebbed and usually well fringed. Palmar and subarticular tubercles are extremely prominent (Fig. 2c). Toes are usually 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; the outer is small, rounded and acutely angled to the long axis of the foot (Fig. 2d).

Texture of the dorsum varies from smooth to moderately rugose. Parotoid glands are usually very prominent, and in some specimens, appear hypertrophied. Inguinal glands occasionally are prominent and coccygeal glands are rarely conspicuous. Submandibular glands vary from scarcely detectable to discrete and elongate. Nuptial pads at the base of the first finger and are unpigmented and glandular (Fig. 2c).

Scapular plicae are not present in this species. 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 pale triangular patch on the anterodorsal surface of the head, described by Keferstein (1867) is extremely prominent in almost all specimens (Fig. 3). 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, is usually 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 the course of this study, batrachomyid parasites were observed only in specimens assigned to _U. laevigata_.

<u>Osteology</u> (based on NMV D25111)

Skull well ossified, sloping anteroventrally (Fig. 4). Sphenethmoid not confluent medially and poorly ossified, not extending anteriorly to extremities of frontoparietals in dorsal view and ventrally extending posteriorly for about $^1/3$ 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. 4). 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, anterior processes of hyale absent. Posterolateral processes moderately long, broad. Posteromedial processes ossified. Some calcification apparent on plate (Fig. 5).

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 $^2/3$ 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. 6). 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 $^1/2$ dorsomedial length. Pubis cartilaginous. Ilial crest absent, dorsal prominence, very small; dorsal protuberance small, more lateral than superior (Fig. 5).

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

Three distal tarsal elements present. Lateral element (T_3) is largest (Fig. 7).

Variation

The sphenethmoid is never confluent medially. The carotid canal groove is barely observable, deeply grooved or very occasionally partly roofed. The epiotic eminences are usually 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 calls

Robertson (1982, 1984, 1986a,b) described the advertisement calls of this species in a population near Sutton, N.S.W., and Davies and Littlejohn (1986) described calls of this species at a number of localities in its range. The call is a long pulsed sequence of 32-56 pulses with a pulse repetition rate of 69.4-95 pulses sec^{-1} and a call duration of 405.0-736.6 ms.

Comparison with other species

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

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 *U. fusca*, *U. laevigata* is distinguished by the absence of complete ventral pigmentation and by call. The duration of the call of *U. fusca* is about 300 ms as opposed to about 590 ms in *U. laevigata*. The number of pulses is greater in *U. laevigata* (32-56 compared with 11-28 in *U. fusca*).

Distribution

Uperoleia laevigata is a species of 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, Qld (Fig. 8).

3.5.4 Uperoleia mjobergi (Andersson, 1913)

Pseudophryne mjobergi Andersson, 1913, K. Svenska, Vetenskapsakad. Handl. 52, 4, p. 19.

Pseudophryne mjöbergii: Harrison 1927, p. 284.

Glauertia mjobergi: Parker 1940, p. 66; Slater and Main 1963, p. 163; Main 1965, p. 38.

Uperoleia mjobergi: Lynch 1971, p. 98; Tyler, Davies and Martin 1981a, p. 15; Tyler, Davies and Martin 1981b, p. 167; Tyler 1982, p. 236; Cogger 1983, p. 85; Cogger, Cameron and Cogger 1983, p. 33; Tyler, Smith and Johnstone 1984, p. 101; Tyler 1985, p. 408.

Diagnosis

A small species (♂♂ 19.0-25.1 mm S-V, ♀♀ 21.0-23.0 mm S-V) possessing maxillary teeth; the toes are fringed but unwebbed; inguinal glands hypertrophied; prominent tubercle on ventral surface of proximal head of tarsus; frontoparietal fontanelle poorly to moderately exposed; carpus of six elements; anteromedial processes of anterior hyale of hyoid slender and short; no ilial crest; call a short rasp of 20-25 pulses with a pulse repetition rate of about 98 pulses sec^{-1}.

Morphology

Material examined: SAM R28860-2 WAM R94352, 19.4 km NW Lennard River on Gibb River Rd; SAM R28863-4, 27.9 km NW Lennard River on Gibb River Rd; SAM R28865, 12.4 km NW Lennard River on Gibb River Rd; SAM R28866-70, 20-42 km S Derby W.A.

Uperoleia mjobergi is conservative morphologically. The snout is short and slightly rounded or truncated when viewed from above in approximately equal numbers of specimens. The eye to naris distance is slightly greater than the internarial span (E-N/IN 1.12±.12 [1.00-1.31]).

The fingers are moderately long, slender and slightly fringed with prominent subarticular tubercles. The palmar tubercles vary in prominence: both can be prominent, neither prominent, or the tubercle on the heel of the hand is prominent; these states occur in approximately equal proportions.

The hind legs are moderately long (TL/S-V 0.35±.02 [0.32-0.38]). The toes are moderately long, moderately fringed, unwebbed with conical subarticular tubercles. Both inner and outer metatarsal tubercles are prominent. The inner metatarsal tubercle is oriented along the long axis of the first toe and the outer metatarsal tubercle is angled slightly to the long axis of the foot. A prominent tubercle is present on the skin overlying the ventral surface of the proximal head of the tarsus (Fig. 9).

The parotoid, inguinal, coccygeal and submandibular glands are always well developed - the inguinal glands are hypertrophied to extend along the flanks. A pair of lyrate skin folds occasionally occur between the scapulae. The ventral surface is granular. The dorsum is moderately rugose and has prominent markings (Fig. 10). Pigmentation is usually absent ventrally, but if present is in the form of a fine suffusion of granules.

Osteology

Material examined: UAZ A582, 18 km S Derby; UAZ A880-9, 28 km S Derby W.A.

The sphenethmoid is not ossified medially and is not in bony contact with the nasals. The epiotic eminences of the crista parotica are moderately prominent and completely ossified. The frontoparietal fontanelle is poorly exposed, elongate with a slight medial expansion but occasionally shows slightly greater exposure. The orbital edges of the frontoparietal elements are curved anteromedially. The anterior extremities of the frontoparietals barely reach the posterior level of the sphenethmoid dorsally leaving a substantial expanse of sphenethmoid to form the anteromedial rim of the orbit.

The nasals are triangular, moderately ossified and moderately separated medially. The anterior edges are not crescentic and the maxillary processes are not acuminate. The palatines are slender, elongate bones extending laterally beyond the extremities of the maxillary processes of the nasals and are either poorly or moderately angled medially to the sphenethmoid. The parasphenoid is moderately robust with a slender cultriform process. The alae are at right angles to the cultriform process.

The anterior ramus of the pterygoid is in long contact with the well developed pterygoid process of the palatal shelf of the maxillary. The squamosal is moderately robust with a prominent knobbed zygomatic ramus which is bifid in one specimen. The otic ramus is moderately long.

The maxillary and premaxillary are dentate and the vomers are absent. The pars facialis of the maxillary is shallow with an extremely prominent preorbital process.

There is no ilial crest. The dorsal prominence is papillate and very prominent. The dorsal protuberance is lateral (Fig. 11).

The hyoid plate is about as broad as it is long. The anteromedial processes on the anterior hyale are slender and short (Fig. 12). The alary processes of the hyoid plate are not pedunculate; the posterolateral processes are moderately long and moderately slender. The posterior cornua are ossified.

The carpus consists of six elements. Little torsion occurs. Both the O. radiale and O. ulnare are present; the O. radiale is the larger. These elements articulate with the O. radioulna proximally and with each other on their proximomedial border. Distally both elements articulate with the large transversely elongated O. centrale postaxiale (Fig. 13). The radiale articulates laterally with the O. centrale preaxiale.

The O. centrale postaxiale articulates distally with the bones of the O. metacarpi III, IV and V. From the lateroproximal corner, a small flange extends proximally. A palmar sesamoid occurs ventromedially (Fig. 13).

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

Three distal tarsal elements are present. The lateral element is the largest and lies at the base of the O. metatarsus III. It 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 lies at the base of O. metatarsus II. The medial element lies at the base of O. metatarsus I and also articulates with the O. centrale prehallucis. The distal prehallical element is large, extending $^{2}/3$ the length of O. metatarsus I (Fig. 13).

Comparison with other species

Uperoleia mjobergi is a small species (males 19-25 mm S-V, females 21-23 mm S-V) with a toothed maxillary arch and a poorly to moderately exposed frontoparietal fontanelle. These features are shared by *U. martini*, *U. fusca*, *U. laevigata* and *U. marmorata*. From *U. martini* and *U. fusca*, *U. mjobergi*, is separated by the absence of complete ventral pigmentation and by its fringed toes. From *U. laevigata*, *U. mjobergi* is separated by the presence of a tarsal papilla, the absence of a light triangular patch on the anterior portion of the head and by its hypertrophied inguinal glands. From *U. marmorata*, *U. mjobergi* is separated by its fringed toes, hypertrophied inguinal glands and by the prominent tarsal papilla.

Distribution

Uperoleia mjobergi is found in the Fitzroy River drainage system (Tyler *et al*. 1981b). It is found north east of Derby as far as the Napier Range which appears to be a barrier to its northward dispersal (Tyler *et al*. in press).

3.5.5 *Uperoleia rugosa* (Andersson, 1916)

Hyperoleia marmorata: Fletcher 1890, p. 672 (part.).

Pseudophryne rugosa Andersson, 1916, K. Sven. Vetenskapsakad. Handl. 52, 9, p.13.

Pseudophryne fimbrianus Parker 1926, Ann. Mag. Nat. Hist. (9)17, p. 669, fig. 3; Wilkins 1928, p. 278.

Uperoleia rugosa: Parker 1940, p. 70 (part.); Erspamer, de Caro, and Endean 1966, p. 738 (part.); Lynch 1971, p. 99; Erspamer, Negri, Erspamer and Endean 1975, p. 41 (part.); Roseghini, Erspamer and Endean 1976, p. 35 (part.); Erspamer, Erspamer and Linnari 1977, p. 68 (part.); Barker and Grigg 1977, p. 188 (part.); Archer 1978, p. 112; Tyler, Davies and Martin 1981a, p. 17; Cogger 1983, p. 86; Cogger, Cameron and

Cogger 1983, p. 34 (part.); Davies and McDonald 1985, p. 37. Tyler 1985, p. 408; Mahony and Robinson 1986, p. 120; Davies and Littlejohn 1986, p. 113; Trueb and Alberch 1986, p. 121.

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

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

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

Uperoleia fimbrianus: Tyler, Davies and Martin 1981a, p. 18; Cogger 1983, p. 83; Cogger, Cameron and 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, J18840-41(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, AMR 5822-3, 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, J45977, Anakie; SAM R29672(A)-3(A), QM J45975, Springsure; SAM R29674(A), R29675, 1.7 km from Cabbage Tree Creek, Nathan Gorge Rd; QM J45973-4, Cabbage Tree Creek; QM J45976, Glenleigh Station beside road to Glenhaughton Station; AM R115648-50, QM J45980-86, J45987(A), SAM 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 R29678(A), Boorara Station; AM R115652, 17.6 km N Moura; R115306, R113367-69, Cecil Plains Rubbish Tip; 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.; 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; AM R115632-44, R115646, 5 km E Eulo; R92159, Buckingbong SF, 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; R52590-1, Cumborah, NW Walgett; R50493-500, 11.2 km W Glen Innes on Inverell Rd (29°43', 151°58'); R15575-6, R115579, R115581-2, nr Bulgandramine; R102886, Thurloo Downs Hstd; SAM R28786-7, UAZ A816, UAZ B814, Severn River (29°28', 151°29').

Redescription of species (based on SAM R27052)

Maxillary teeth absent. Vomerine teeth absent. Snout short, slightly truncated when viewed from above (Fig. 14) and in profile. Eye to naris distance greater than internarial span (E-N/IN 1.43). Canthus rostralis inconspicuous and straight. Tympanum not visible externally (Fig. 14).

Fingers moderately long, slender, unwebbed but slightly fringed with prominent palmar and subarticular tubercles (Fig. 15A). Prominent supernumerary subarticular tubercles present. Fingers in order of length 3>4>2>1. Hind limbs moderately long (TL/S-V 0.36). Toes moderately long, fringed with a trace of basal webbing (Fig. 15B). In order of length 4>3>5>2>1. Metatarsal tubercles moderately large but prominent. Subarticular tubercles rounded. Dorsal surface faintly tubercular. Parotoid and inguinal glands well developed (Fig. 16); coccygeal glands poorly developed. Submandibular gland prominent, discrete. Cloacal flap with tiny fimbriations. Ventrally, throat and thorax granular, belly smooth. Male with unilobular, submandibular vocal sac and glandular nuptial pad.

In preservative, dorsum brown with darker brown markings between eyes, in scapular region and on posterior portion of dorsum. Dorsal tubercles tipped with cream. Parotoid and inguinal glands with few cream patches. Inguinal and post femoral patches pink after one month in preservative. Nuptial pad unpigmented.

Ventral surface cream with few small, isolated areas of brown pigment. Submandibular region and thorax, except for small medial patch, dark grey.

Colour in life

Dorsum grey/brown with darker brown markings. Dorsal tubercles tipped with yellow; parotoid and inguinal glands yellowish; submandibular gland yellow. Bright reddish orange inguinal and femoral patches.

Ventral surface white with brown areas of pigment. Submandibular region dark grey to black sometimes extending to pectoral region.

Dimensions (in mm)

Snout-vent length 20.9; tibia length 7.6; eye diameter 2.6; eye-naris distance 2.0; internarial span 1.4.

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 20-32 mm S-V for males and 22-30 mm for females in inland areas). Geographic variation in size is reflected also in the relative lengths of the hind limbs in these populations (TL/S-V 0.34±.02 [0.29-0.39] coastally and 0.36±.02 [0.32-0.41] inland). For the species over its entire range, TL/S-V is 0.36±.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. 17), or slightly rounded (Fig. 14). Each condition occurs in about equal proportions in the material examined. The snouts of some specimens may have been incorrectly recorded as blunt snouted because poorly preserved specimens (as indicated by dehydrated fingers and toes) always have truncated snouts. Well preserved specimens from Savernake, N.S.W. at the southern extremity of the species' range have truncate snouts (Fig. 17).

The eye-to-naris distance is always greater than the internarial span, and is subject to little geographic variation (E-N/IN 1.61±.28 [1.12-2.3]). The nostrils are located more laterally than dorsally (Fig. 17).

The hands are usually 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 usually are extremely prominent (Fig. 17) in about $^{2}/3$ of the specimens.

There is no webbing between the toes in $^{5}/6$ of the specimens examined, and minimally basal in the remainder. Fringing on the toes varies: about $^{1}/6$ have reduced fringing, about $^{2}/6$ moderate, and the remainder have well fringed toes (Fig. 17).

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: poor, moderately and very rugose specimens occur in equal proportions. Dermal glands are usually extremely well developed (Fig. 16), but occasionally poor development of the parotoid glands is recorded. Degree of development of inguinal and coccygeal glands are similar (1:1:4, poor:moderate:well developed).

The 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. 16).

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 $^{3}/4$ 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 $^{1}/6$ of the specimens and only a faint dusting of pigment is detectable in $^{3}/6$; islands of pigment, as in topotypic material are found in the remaining $^{1}/3$ of the material.

Osteology (based on SAM R27055)

Skull well ossified, sloping anteroventrally. Sphenethmoid not ossified dorsomedially or ventromedially; small portion ossified posteriorly to medial extremities of palatines, with ossified portion extending about 1/3 length of orbit in ventral view. Prootic not fused with exoccipital. Exoccipital confluent posteromedially in dorsal view but not fused ventromedially. Crista parotica short, stocky, not articulating with otic ramus of squamosal lying alongside lateral extremities. Grooves of carotid canal present on frontoparietals, medial to epiotic eminences.

Frontoparietal elements extensive, crenate medially, overlying sphenethmoid anteriorly, more widely separated anteromedially. Frontoparietal fontanelle barely exposed medially; anterior margin formed by sphenethmoid elements at level about 1/5 posteriorly on length of orbit. Posterior margin undefined because of lack of anteromedial ossification of exoccipital.

Nasals large, closely applied medially for 4/5 length, slightly separated posteromedially (Fig. 18). Anteromedial extremities crescentic. Maxillary processes moderately acute, directed ventrally, not in bony contact with pars facialis of maxillary. Posteromedially nasals in contact with anterior extremities of sphenethmoid. Palatines moderately slender, angled at about 45° to sphenethmoid, reduced laterally, not reaching extremities of maxillary processes of nasals.

Parasphenoid robust. Cultriform process broad, irregularly truncate (Fig. 18), expanded slightly posterolaterally. Alary processes moderately long, moderately broad, angled slightly postero-laterally, reaching medial extremities of medial ramus of pterygoid. Medial ramus of pterygoid broad, anterior ramus in long contact with well-developed pterygoid process of palatal shelf of maxillary. Cartilaginous quadrate present between base of squamosal and quadratojugal. Quadratojugal robust, in firm contact with maxillary. Squamosal stocky with tiny zygomatic ramus and long, unexpanded otic ramus.

Maxillary and premaxillary edentate; palatal shelf moderately deep with well developed palatine processes, not abutting medially. Pterygoid process well developed. Alary processes of premaxillary perpendicular to pars dentalis, slender, inclined medially. Pars facialis of maxillary moderately deep; preorbital process absent. Vomers absent. Bony columella present.

Pectoral girdle arciferal and robust. Omosternum absent, xiphisternum present. Sternum cartilaginous. Clavicles slender, curved, closely applied medially. Coracoids well developed, robust, widely separated medially. Scapula bicapitate, slightly shorter than clavicles. Suprascapular about 2/3 ossified.

Eight procoelous non-imbricate presacral vertebrae (Fig. 19). Sacral diapophyses poorly expanded. Relative widths of transverse processes III>IV>sacrum>II>V=VI>VII=VIII. Bicondylar sacrococcygeal articulation. Crest on urostyle extending approximately $^1/2$ length. Ilium with tiny dorsal prominence and moderately large lateral protuberance (Fig. 19).

Humerus with strongly developed anteroproximal crest. Phalangeal formula of hand 2,2,3,3.

Carpus: The carpal type consists of five elements. Little torsion occurs. Both the O. ulnare (UL) and 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 depresssion 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 (POI) (Fig. 20).

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

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. 21). This description corresponds to tarsal type I (Andersen 1978).

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. 22).

Variation

Skull: All but two of the adult specimens examined showed 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 (Fig. 23) occurring. Variation also occurs in the crescentic shape of the anterior edges of the nasals ranging from the curved condition in Fig. 23 and Lynch (1971) to almost straight.

The anterior extremities of the frontoparietals usually are crenate, and, occasionally, are extended anterolaterally. The more usual condition is truncated anterior extremities (Fig. 23).

All adult specimens have minimal exposures of the frontoparietal fontanelle, ranging from that shown in Fig. 23 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. 23); 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 (Fig. 18) to moderately widely separated (Fig. 23). 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. 23), through present on only one side medial to the palatines, to small fragments also at the edges of the choanae. This feature appears to be highly variable in U. rugosa.

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, J10836, NMV D9260-1, D9265) from the same localities as those in which fusion of carpalia 2+3 has not occurred, exhibit fusion.

Advertisement calls

The advertisement calls of three individuals were recorded at Colosseum on 12.xii.1984 by K.R. McDonald. The call is a short note of four pulses, pulsed at about 34 pulses sec^{-1} and with a duration of about 117 msec. The dominant frequency is about 2,583 Hz. A sonagram of the advertisement call is shown in Fig. 24, and characteristics of the calls are listed in Table 1. Davies and Littlejohn (1986) described variation in the call from material at the southern extremity of the species' range. Calls had a duration of 81.4-102.8 ms, and consisted of 3-4 pulses pulsed at 22.8-40.8 pulses sec^{-1}.

Comparison with other species

Uperoleia rugosa is an edentate species with a very poorly exposed frontoparietal fontanelle: these features are shared by *U. minima*, some *U. aspera*, and some *U. lithomoda*.

U. rugosa is distinguished from *U. minima* by the presence of fringed fingers and toes, and by its well developed inguinal and coccygeal glands. The call of *U. minima* is a very short unpulsed click, to the ear, 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 fast click, pulsed at about 170 pulses sec^{1} in *U. aspera*).

U. rugosa is distinguished from U. lithomoda by 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. 25). 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.

Table 1. Advertisement call characteristics of Uperoleia rugosa at Colosseum, Queensland.

Specimen	No. of pulses	Duration (ms)	Pulse repetition rate (pulses sec^{-1})	Dominant frequency (Hz)	Wet-bulb temp. °C
SAM R27052	4	120	33.33	2500	22.6
SAM R27053	4	120	33.33	2500	22.8
SAM R27055	4	110	36.55	2750	22.2
Mean	4	116.7	34.40	2583	22.5

3.5.6 Uperoleia russelli (Loveridge, 1933)

Glauertia russelli Loveridge, 1933, Occas. Pap. Boston Soc. Nat. Hist. 8, p. 89.

Glauertia russelli: Loveridge 1935, p. 37; Glauert 1945, p. 381; Main 1954, p. 115; Main and Calaby 1957, p. 219; Main 1965, p. 37; Main and Storr 1966, p. 58; Stephenson 1965, p. 340; Lynch 1971, p. 97; Trueb and Alberch 1986, p. 121.

Uperoleia russelli: Tyler, Davies and Martin 1981a, p. 19; Tyler 1982, p. 236; Cogger 1983, p. 86; Cogger, Cameron and Cogger 1983, p. 34; Tyler Smith and Johnstone, 1984, p. 102; Tyler 1985, p. 408; Davies, Mahony and Roberts 1985, p. 106.

Definition

A large species (♂♂ 27-35 mm, ♀♀ 30-35 mm S-V) lacking maxillary teeth; dermal glands prominent; toes extensively webbed and very broadly fringed; frontoparietal fontanelle widely exposed; anteromedial processes of anterior hyale slender; carpus of six elements; no ilial crest. Advertisement call a pulsed note of unknown characteristics.

Morphology

No further data are available to add to the redescription of Tyler et al. 1981a.

Osteology

No ilial crest is developed; the dorsal prominence is monticuline and the dorsal protuberance lateral. The pubis is calcified (Fig. 26).

The hyoid plate is approximately as broad as it is long. The anteromedial processes of the anterior hyale are slender (Fig. 26). The alary processes of the hyoid plate are not pedunculate. The posterolateral processes are moderately short. The posterior cornua are ossified. Some calcification is apparent on the posteromedial areas of the plate.

The carpus consists of six elements. The O. radiale and O. ulnare are present; the O. radiale is the larger. Both articulate with the O. radioulna proximally, and with each other on their medioproximal border. Distally both articulate with the large transversely elongated O. centrale postaxiale. The O. radiale articulates laterally with the O. centrale preaxiale (Fig. 27).

The O. centrale postaxiale articulates distally with the bases of O. metacarpi III, IV and V. A small flange extends proximally from the lateroproximal corner. A palmar sesamoid occurs ventromedially (Fig. 27). The O. centrale preaxiale articulates laterally with the O. radiale, distally with the O. centrale postaxiale and with the carpal elements of the O. distale carpale 2 and 3 and laterally with the basal prepollical element.

Three distal tarsal elements are present. The lateral element is the largest and lies at the base of O. metatarsus III. It 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 lies at the base of O. metatarsus II and the medial element at the base of O. metatarsus I, also articulating with the O. centrale prehallucis. The distal prehallical element is large and hastate shaped extending for about $^{1}/2$ the length of O. metatarsus I (Fig. 27).

Comparison with other species

Uperoleia russelli is a large edentate species with moderately webbed toes (Fig. 28) and a widely exposed frontoparietal fontanelle, features shared by U. orientalis, U. talpa and U. borealis.

From U. orientalis, U. russelli is distinguished by the absence of a midvertebral stripe. From U. talpa, U. russelli is distinguished by the presence of pigmentation in the postfemoral and inguinal regions and from U. borealis by the presence of dorsal patterning.

Distribution

The distribution data of Tyler et al. (1984) have not been expanded.

3.5.7 Uperoleia orientalis (Parker, 1940)

Glauertia orientalis Parker, 1940, Novit. Zool. 42, p. 67

Glauertia orientalis: Lynch 1971, p. 98; Gow 1981, p. 66; Barker and Grigg 1977 , p. 198 (part.).

Uperoleia orientalis: Tyler, Davies and Martin 1981a, p. 24; Tyler 1982, p. 239; Tyler, Davies and Martin 1983, p. 240; Cogger 1983, p. 86; Cogger, Cameron and Cogger 1983, p. 33; Tyler 1985, p. 408; Tyler and Davies 1986, p. 60; Tyler, Davies and Watson 1986, p. 97.

Definition

A moderately large species (♂♂ 26-28 mm S-V) lacking maxillary teeth, toes half webbed, broadly fringed; narrow midvertebral stripe; frontoparietal fontanelle extensively exposed. Six carpal elements. Advertisement call not known.

External morphology

Nothing further can be added to the redescription of Tyler et al. (1981a) other than to illustrate the extent of toe webbing (Fig. 29).

Osteology

Reexamination of X-rays of the type material indicates six carpal elements and a prominent, slightly rounded dorsal prominence on the ilium. The zygomatic ramus of the squamosal is tiny and the otic ramus short. The epiotic eminences are moderately rounded. The nasals are moderately well ossified. The orbital edges of the frontoparietals are angled slightly medially. The epiotic eminences are incompletely ossified. The distal prehallical element extends for about $^{2}/3$ the length of metatarsus I.

Comparison with other species

Uperoleia orientalis is a moderately large edentate species with substantial toe webbing and a widely exposed frontoparietal fontanelle, features shared by U. russelli, U. borealis and U. talpa. U. orientalis is distinguished from all three species by its more extensive toe webbing and the presence of a midvertebral stripe.

Distribution

Known only from the type locality, Alexandria Station, N.T.

3.5.8 Uperoleia arenicola Tyler, Davies and Martin, 1981

Uperoleia arenicola Tyler, Davies and Martin, 1981, Aust. J. Zool. Suppl. 79, p. 26.

Uperoleia arenicola: Tyler 1982, p. 239; Cogger 1983, p. 82; Cogger, Cameron and Cogger 1983, p. 32; Tyler, Crook and Davies 1983, p. 435; Tyler 1985, p. 406; Tyler and Davies 1986, p. 57.

Definition

A small species (♂♂ 18-23 mm S-V) with no maxillary teeth; frontoparietal fontanelle widely exposed, toes unwebbed; dorsal skin smooth to very weakly tubercular; carpus of six elements; no ilial crest; advertisement call a rasp of 12-15 pulses with a pulse repetition rate of about 110 pulses sec^{-1}.

External morphology

No further data are available to add to the original description of Tyler *et al*. 1981a. The species is illustrated in life in Fig. 30.

Osteology (from SAM R17347, paratype)

No ilial crest present. The dorsal prominence is moderately small and monticuline (Fig. 31), the dorsal protuberance is posterolateral.

The carpus has six elements and considerable torsion occurs. The O. radiale and the O. ulnare are present, the O. radiale is the larger. Both articulate with the O. radioulna proximally, with each other on their proximomedial border and distally with the large transversely elongate O. centrale postaxiale. The O. radiale articulates laterally with the O. centrale preaxiale (Fig. 32).

The O. centrale postaxiale articulates distally with the bases of O. metacarpi III, IV and V. No flange is apparent on the lateroproximal corner. Ventromedially is a palmar sesamoid. The O. centrale preaxiale articulates laterally with the O. radiale, distally with the O. centrale postaxiale, with the closely applied carpal elements of the O. distale carpale 2 and 3 and laterally with the basal prepollical element.

The tarsus has three distal elements. The lateral element is the largest and lies at the base of O. metatarsus III. It 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 lies at the medial extremity of the base of O. metatarsus II. The medial element lies at the base of O. metatarsus I and also articulates with the O. centrale prehallucis (Fig. 32). The distal prehallical element is moderately broad and elongate, extending for approximately $^1/3$ the length of O. metatarsus I.

Comparison with other species

Uperoleia arenicola is an edentate species with a widely exposed frontoparietal fontanelle, features shared by U. borealis, U. crassa, U. russelli, U. orientalis, U. glandulosa, U. talpa, U. littlejohni and U. inundata. From U. borealis, U. russelli, U. talpa, U. orientalis and U. glandulosa, U. arenicola is distinguished by its unwebbed toes. From U. crassa, U. arenicola is distinguished by its smooth ventral surface and by its poorly ossified nasals and by call (Tyler et al. 1981a). From U. littlejohni, U. arenicola is distinguished by its well-developed dermal glands, by its poorly ossified nasals and by the presence of a preorbital process on the pars facialis of the maxillary and from U. inundata, U. arenicola is distinguished by call (Tyler et al. 1981a) and by its poorly developed nasals.

Distribution

The distribution data of Tyler *et al*. (1981a) have not been extended. *U*. *arenicola* is known only from the type locality, Birndu, on the edge of the Arnhem Land Escarpment near Jabiru, N.T.

Comment

Highly variable call data obtained by Tyler *et al*. (1986) of *U*. *inundata* from Groote Eylandt suggest that *U*. *arenicola* may be synonymous with *U*. *inundata*. Osteological data suggest that *U*. *arenicola* may be young *U*. *inundata*. However, since no further specimens of *U*. *arenicola* are available for study, I prefer to recognise both species here.

3.5.9 *Uperoleia borealis* Tyler, Davies and Martin, 1981

Uperoleia borealis Tyler, Davies and Martin, 1981, Aust. J. Zool. Suppl. 79, p. 30.

Uperoleia borealis: Tyler 1982, p. 236; Tyler, Watson and Davies 1983, p. 244; Cogger 1983, p. 82; Cogger, Cameron and Cogger 1983, p. 32; Tyler, Smith and Johnstone 1984 p. 98; Tyler 1985, p. 407; Tyler and Davies 1986, p. 58.

Definition

A moderate to large species (♂♂ 21.8-29.1 mm, ♀ 24.5 mm S-V), lacking maxillary teeth; possessing moderately webbed toes; widely exposed frontoparietal fontanelle; orange markings in the inguinal and post femoral areas; poorly patterned dorsum; rugose flanks; carpus of six elements; anteromedial processes on anterior hyale of hyoid slender;

no ilial crest; male call a rasping note of 18-23 pulsed with a repetition rate of 100 pulses sec^{-1}.

Material examined

N.T.: SAM R23835, 12.9 km E Victoria River on Victoria Hwy; R23834, 5.8 km E Victoria River on Victoria Hwy; SAM R29698-702, Keep River Reserve Camping ground.

W.A.: SAM R24002-8, Tickalara Creek on Great Northern Hwy.

External morphology

The snout is short and either truncated or rounded when viewed from above. The eye to naris distance is considerably greater than the internarial span (E-N/IN 1.36±.22 [1.06-1.69]. The fingers are moderately long and slightly fringed in some of the W.A. material. The palmar tubercles are not prominent and that at the base of the thumb is masked by the white subepidermal glandular nuptial pad. Subarticular tubercles are prominent as in the type series. The hind limbs are short (TL/S-V 0.35±.01 [0.34-0.36]). The toes are long, broadly fringed with prominent subarticular tubercles. The N.T. specimens show less webbing than the type series and than the W.A. material examined here (Fig. 33). The inner metatarsal tubercle is oriented along the axis of the first toe and the outer is slightly angled to the long axis of the foot. The subarticular tubercles are not very prominent.

The dorsal surface of specimens is smooth but the flanks are moderately rugose (Fig. 3). The dermal glands are well developed, particularly the parotoid glands. In SAM R23835 the parotoid glands are hypertrophied. The ventral surface is faintly granular in most specimens.

The dorsum is dark brown in preservative and no dorsal patterning is discernible except in SAM R24005 which has very faint small islands of brown pigment dorsally.

Osteology

Material examined

UAZ A863, B862, Tickalara Creek W.A.; UAZ A226, Great Northern Hwy, 39 km S Duncan Hwy Jcn.

Cranium: Ossification of the nasals varies slightly in this species. These elements are poorly ossified in the larger specimen (UAZ A863) and widely separated posteromedially. They show greater ossification in the other two specimens with less posteromedial separation.

The orbital edges of the frontoparietals are straight and only slightly angled anteromedially.

In all material examined, the epiotic eminences are poorly ossified posteriorly. The zygomatic ramus of the squamosal is tiny and appears to be bifid. The otic ramus is moderately long. The preorbital process of the pars facialis is extremely prominent, monticuline, and the pars facialis is shallow. There is no variation in the alary processes of the premaxillaries which are moderately broad and perpendicular to the pars dentalis.

There is little variation in bones ventrally. The palatines are moderately long, reduced laterally but extend beyond the extremities of the nasals. They are not acutely angled to the sphenethmoid. The cultriform process of the parasphenoid is broad and truncated.

The pterygoid process of the palatal shelf of the maxillary is very well developed and the anterior ramus of the pteryoid is widely expanded and in short contact with this process.

Postcranial features: There is no crest on the ilium. The dorsal prominence is small and has a large lateral, oval protuberance. The pubis is calcified.

The carpus consists of six elements and little torsion occurs. Both the O. radiale and O. ulnare are present; the O. radiale is the larger. Both elements articulate with the O. radioulna proximally and with each other on their proximomedial border. Distally both articulate with the large transversely elongated O. centrale postaxiale. The O. radiale articulates laterally with the O. centrale preaxiale (Fig. 34).

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. Palmar sesamoid is ventromedially (Fig. 34).

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

There are three distal tarsal elements. The lateral element is the largest and lies at the base of O. metatarsus III. It 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 lies at the base, slightly laterally, to O. metatarsus II and the medial element lies at the base of O. metatarsus I and also articulates with the O. centrale prehallucis. The distal prehallical element is broad and extends for about $^{1}/2$ the length of O. metatarsus I (Fig. 35).

The hyoid plate is approximately as broad as it is long. The anteromedial processes of the anterior hyale are slender and short. The alary processes of the hyoid plate are not pedunculate. The posterolateral processes are broad and short. The posterior cornua are ossified. Some calcification is apparent on the posteromedial areas of the plate (Fig. 36).

Comparison with other species

Uperoleia borealis is an edentate species with a widely exposed frontoparietal fontanelle and moderate webbing on the toes. These features are shared by U. talpa, U. russelli and U. orientalis. From U. talpa, U. borealis is distinguished by its lack of dorsal patterning and by call (Martin unpublished data).

From U. russelli, U. borealis is distinguished by lack of dorsal patterning and from U. orientalis by the lack of a midvertebral stripe.

Distribution

Uperoleia borealis is known from the Kimberley Division of Western Australia and extends into the Northern Territory in the vicinity of Victoria River. The distribution of U. borealis is shown in Fig. 37. The species is confined to streamside, or flowing water habitats (Tyler, Watson and Davies unpublished data).

3.5.10 Uperoleia crassa Tyler, Davies and Martin, 1981

Uperoleia crassa Tyler, Davies and Martin, 1981, Aust. J. Zool. Suppl. 79, p. 34.

Uperoleia sp.: Smith and Johnstone 1981, p. 217.

Uperoleia crassa: Tyler 1982, p. 236; Cogger 1983, p. 83; Cogger, Cameron and Cogger 1983, p. 32; Tyler, Smith and Johnstone 1984, p. 99; Tyler 1985, p. 407; Mahony and Robinson 1986, p. 120.

Definition

A small to relatively large species (♂♂ 17-30 mm, ♀♀ 30-31 mm S-V) lacking maxillary teeth; frontoparietal fontanelle moderately widely exposed; toes fringed with basal webbing; six carpal elements present; anteromedial processes of anterior hyale of hyoid short and slender; no ilial crest; male advertisment call a rasping note of 6-8 pulses with a pulse repetition rate of 26-44 pulses sec^{-1}.

Material examined

SAM R28839-59, WAM R94353-55, 2.4 km N Little Adcock River on Gibb River Rd W.A.

External morphology

The snout is short, usually truncated when viewed from above, but occasionally rounded. The eye to naris distance is greater than the internarial span (E-N/IN 1.28±.18 [1.00-1.75]. The fingers are slender and fringed with prominent or moderately prominent subarticular tubercles. Palmar tubercles are indistinct. The hind limbs are moderately long (TL/S-V 0.35±.02 [0.31-0.40] as opposed to 0.32±.02 [0.29-0.35] in the type series). The toes are long and slightly fringed with only basal webbing. The subarticular tubercles are conical and the metatarsal tubercles are extremely prominent. The inner metatarsal tubercle is oriented along the axis of toe I and the outer metatarsal tubercle is slightly angled to the long axis of the foot.

The dorsal surface is moderately tubercular (Fig. 16) with well defined but only moderately developed parotoid, inguinal and coccygeal glands. The submandibular gland is very prominent and in life is orange/pink (Fig. 16). The ventral surface is granular, often with white pigment spots situated centrally in the granules.

The dorsum is poorly marked with weak patterning and is usually dark slate in colour. The ventral surface is usually pigmented by a fine suffusion of pigment granules, never coalescing into patches or islands. Occasionally ventral pigment is almost absent.

Osteology

Material examined

UAZ A869-70, UAZ B871, 2.4 km N Little Adcock River on Gibb River Rd W.A.; UAZ B483, Mitchell Plateau Campsite; UAZ B486, Mitchell Plateau Crusher Site.

Most features of the cranium are comparable with the type description in this material. The nasals are moderately well ossified and are widely separated posteromedially in all specimens except UAZ B483 in which they are moderately separated. The anterior extremities of the nasals are not crescentic and the maxillary processes are truncate or acuminate in equal proportions. The frontoparietal fontanelle is always widely exposed and the frontoparietal elements are moderately slender with no anteromedial divergence on the orbital edges. The anterior extremities of these elements extend just beyond the anterior extremities of the sphenethmoid.

The epiotic eminences of the crista parotica are moderately developed and incompletely ossified in about $^2/3$ of the material. The zygomatic ramus of the squamosal is tiny and is bifid in one specimen.

The otic ramus is short in $^2/3$ of the specimens and slightly longer in the other $^1/3$. The pars facialis of the maxillary is always shallow and the preorbital process is usually small but occasionally more prominent. The palatines are moderately acutely angled to the ventral sphenethmoid and are reduced laterally to the extent that they do not extend beyond the maxillary processes of the nasals.

The vomers are absent. The anterior ramus of the pterygoid is in long contact with the prominent pterygoid process of the palatal shelf of the maxillary. The medial process is long and acute and in bony contact with the prootic region. The cultriform process of the parasphenoid is broad, but occasionally slightly more slender, and the alae are at right angles.

No ilial crest is developed. The dorsal prominence is well developed and wedge shaped (Fig. 11). The dorsal protuberance is laterally placed. The pubis is calcified. The hyoid plate is longer than it is wide. The anteromedial processes of the anterior hyale are slender and short. The alary processes of the plate are not pedunculate. The posterolateral processes are moderately broad and moderately long. The posterior cornua are ossified (Fig. 38).

The carpus consists of six elements with considerable torsion. Both the O. radiale and O. ulnare are present; the O. radiale is the larger. Both elements articulate proximally with the O. radioulna proximomedially with each other and distally with the transversely elongated O. centrale postaxiale. The O. radiale articulates laterally with the O. centrale preaxiale (Fig. 39).

The O. centrale postaxiale articulates distally with the bases of O. metacarpi III, IV and V. No flange is developed on the lateroproximal corner. A palmar sesamoid is situated ventrally (Fig. 39).

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

There are three distal tarsal elements. The lateral element is the largest and lies at the base of O. metatarsus III. It extends laterally to articulate with the medioproximal side of O. metatarsus IV and medial to the base of O. metatarsus II where it lies in apposition to the small second tarsal element (Fig. 39). The medial element lies at the base of O. metatarsus I and also articulates with the O. centrale prehallucis. The distal prehallical element is small and slender, extending between $^{1}/3$ and $^{1}/2$ the length of O. metatarsus I.

Advertisement call

Tyler *et al*. (in press) compared calls of *U*. *crassa* from the type locality (Mitchell Plateau) and the Little Adcock River region, central Kimberley. Two different calls were identified from the latter population, identified as long and short calls. Only long calls were recorded from Mitchell Plateau. Long calls consist of 6-8 pulses of a duration of 169-203 ms and a pulse repetition rate of 25.9-44.4 pulses sec^{1}. The short call consists of 6 pulses with a duration of only 55 msec and a pulse repetition rate of 90.9 pulses sec^{1}. The short call was rare within a calling sequence.

Comparison with other species

Uperoleia crassa is a small to moderately large edentate species with a widely exposed frontoparietal fontanelle, features shared by

U. arenicola, *U. inundata*, *U. talpa*, *U. russelli*, *U. glandulosa*, *U. borealis*, *U. orientalis* and *U. littlejohni*.

From *U. talpa*, *U. russelli*, *U. borealis* and *U. orientalis*, *U. crassa* is distinguished by the presence of only basal webbing (webbing considerable in the other species). From *U. arenicola* and *U. inundata*, *U. crassa* is distinguished by call (Tyler *et al*. 1981a) and by poor development of parotoid and inguinal glands.

U. crassa is distinguished from *U. glandulosa* and *U. littlejohni* by the lack of dorsal patterning and by poorly developed dermal glands.

Distribution

Uperoleia crassa was known initially from the Mitchell Plateau in the Kimberley Division of W.A. It has been taken subsequently from the Phillips Range adjacent to the Gibb River Rd between Adcock and Little Adcock Creeks (Tyler *et al*. in press). Unidentified material from Gibb River Station Homestead garden may be referrable to *U. crassa* but the condition of the specimens prevents positive identification.

3.5.11 *Uperoleia inundata* Tyler, Davies and Martin, 1981

Pseudophryne fimbrianus?: Parker 1926, p. 67 (part.)

Glauertia orientalis: Parker 1940, p. 67 (part.) Mitchell 1955, p. 404.

Uperoleia inundata Tyler, Davies and Martin, 1981, Aust. J. Zool. Suppl. Ser. 79, p. 39.

Uperoleia orientalis: Tyler, Davies and Martin 1981a, p. 24 (part.)

Uperoleia sp.: Gow, 1981, p. 66.

Uperoleia inundata: Daugherty and Maxson 1982, p. 342; Tyler, Crook and Davies 1983, p. 435; Cogger 1983, p. 83; Cogger, Cameron and Cogger

1983, p. 32; Tyler and Miller 1985, p. 45; Tyler 1985, p. 407; Maxson and Roberts 1985, p. 293; Tyler and Davies 1986, p. 58; Tyler, Davies and Watson 1986, p. 97; Davies, McDonald and Corben 1986, p. 156.

Definition

A small to moderate sized species (♂♂ 18-29 mm, ♀♀ 22-32 mm S-V) lacking maxillary teeth; toe webbing basal or absent; parotoid glands prominent; inguinal glands prominent and restricted to inguinal region; frontoparietal fontanelle widely exposed; carpus of six elements; anteromedial processes on anterior hyale of hyoid small and slender; ilial crest absent; dorsum generally smooth; advertisement call a short rasp of 8-14 pulses with a pulse repetition rate of 68-163 pulses sec^{-1}.

Material examined

N.T.: SAM R28645-82, UAZ A829-36, B851-7, 1 km NE Jabiru East Watertank; SAM R28683-28712, UAZ A837-44, B858-61, Swamp, 0.4 km from Jabiru East turnoff, Arnhem Hwy; SAM R28713, road to Radon Springs, foot Mt Brockman; SAM R28740, UAZ A596, Chickenhawk Dreaming, 2 km S Cannon Hill; SAM R28716-29, road from Retention Ponds 1 and 2, Jabiru; SAM R28730-33, UAZ A845-8 Retention Pond no. 4, Jabiru; SAM R28734-39, 8 km W Mary River on Arnhem Hwy; SAM R28714-5, 1 km NE Jabiru East turnoff Arnhem Hwy; NTM R12066, Scrutton's Lagoon; AMNH 117726, CAS 156682-3, BMNH 1984.9-10, MCZ A106702, NTM R12527, R12532-44, SAM R25539-44, 8.2 km N Emerald River, Groote Eylandt; AM R112420, NTM R12529, 18.3 km E Angurugu Airport, Groote Eylandt; AM R11249, KU 196728, NTM R12530, 5.6 km E Angurugu Airport, Groote Eylandt; KU 196729, NTM R12531, SAM R25545, Amagula Pools, Groote Eylandt;

AM R53299-303, Caranbirini W.H., approx. 21 km from McArthur River (16°18', 136°05'); AM R53351, R53353, 36.5 km N McArthur River Camp on Borroloola Rd (16°06', 136°07'); AM R53506, R53616-18, R53621, R53736-8, 15 km N McArthur River Camp on Borroloola Rd (16°15', 136°04'); AM R53691-2, 10 km N McArthur River Camp on Boroloola Rd; SAM R12741-74, R14186, Fish River Gorge; SAM R12743, R13864, 15.4 km S Hayes Creek.

Qld: NTM R12070, Westmoreland.

External morphology

Specimens of U. inundata from mainland Australia are smaller than those on Groote Eylandt (Tyler et al. 1986). The largest males examined from the mainland are 26 mm S-V and females 27 mm S-V compared with 29 mm S-V for males and 32 mm S-V for females on Groote Eylandt. Apart from size, the species is morphologically conservative. The snout is relatively narrow (E-N/IN 1.41±.21, [0.93-2.00]) and in Groote Eylandt specimens and some mainland specimens it protrudes beyond the lower jaw (Fig. 30). Approximately equal numbers of specimens have rounded or truncate snouts when viewed from above (Fig. 29).

The hind limbs are short (TL/S-V 0.34±.02, [0.30-0.37]) and in Groote Eylandt specimens are even shorter (0.32±.02, Tyler et al. 1986).

The fingers are very rarely fringed. Subarticular tubercles are moderately prominent (Fig. 29). Palmar tubercles are very poorly developed, particularly that at the base of the thumb. This is scarcely detectable in males as it is masked by the unpigmented glandular nuptial pad.

Fringing on the toes is poor in about $^{2}/3$ of the specimens examined or moderate to well fringed in $^{1}/3$. Toe fringing is absent in Jabiru material but present in southern Gulf of Carpentaria material. Toe webbing is absent in about $^{1}/4$ of the specimens examined and basal in the remainder. About $^{1}/3$ of this basally webbed material exhibits a slightly tubercular nature in this basal webbing (Fig. 29). Subarticular tubercles are conical. The inner metatarsal tubercle is oriented along the axis of the first toe and the outer metatarsal tubercle is angled to the long axis of the foot. The metatarsal tubercles are particularly large in Groote Eylandt and southern Gulf of Carpentaria material, but smaller and slightly compressed in much of the Jabiru material, giving the appearance of possible abrasion and wear.

The dorsum is smooth in most ($^{5}/6$) of specimens examined and mildly tubercular in the remaining $^{1}/6$. The parotoid glands are prominent in all specimens and usually are cream. Inguinal glands are always prominent and always truly inguinal, being discreet and never extending anteriorly along the flanks. Coccygeal glands are usually very prominent. The submandibular gland is discreet in about $^{1}/2$ the specimens and disrupted in the other half.

Scapular plicae are absent. Anterior eyeflaps are very poorly developed and cloacal flaps are poorly fimbriated. The ventral surface is granular in $^{6}/7$ of the specimens and smooth in $^{1}/7$. Dorsal patterning is very indistinct in most material; when present it is in the form of blotches of pigment with no strong outline.

Ventral pigmentation is absent in about $^{2}/3$ of the specimens and faint in the other $^{1}/3$. Groote Eylandt material is pigmented ventrally slightly more than mainland material.

Inguinal and femoral patches are not prominent.

Osteology

Material examined

N.T.: UAZ A818-826, 100 m E Jim Jim Turnoff, Arnhem Hwy; UAZ A827, Jabiru East Airstrip; UAZ A829-36, B851-57, Western end Jabiru East Airstrip; UAZ A837-44, B858-61, Swamp, 0.4 km S Jabiru East turnoff; UAZ A845-48, Retention Pond no. 4; UAZ A849-50, Daly River Rd; UAZ A596, Chickenhawk Dreaming, 2 km S Cannon Hill; UAZ A395(2), SAM R17268, Fish River Gorge; UAZ B397, B479, Darwin; UAZ A898, SAM R25540-41, Groote Eylandt.

The osteological description of U. inundata of Tyler et al. (1981a) did not include elements of the carpus, tarsus, pelvic girdle and hyoid. Here I supplement the original description.

Carpus: The carpus consists of six elements. Quite considerable torsion occurs. Both the O. ulnare and O. radiale are present; the O. radiale is the larger. These elements articulate with the O. radioulna proximally and with each other on their proximo-medial borders. Distally both elements articulate with the large transversely elongated O. centrale postaxiale. The O. radiale articulates laterally with the O. centrale preaxiale.

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. Anteroventrally a palmar sesamoid is located.

The O. centrale preaxiale articulates laterally with the O. radiale, distally with the O. centrale postaxiale and with the carpal elements of the O. distale carpale 2 and 3 and laterally with the basal prepollical element (Fig. 40).

Tarsus: The O. tibiale and O. fibulare are elongated elements fused together 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 is the largest, and lies at the base of O. metatarsus III. It 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 lies at the base of O. metatarsus II. The medial element lies at the base of O. metatarsus I and also articulates with the O. centrale prehallucis. The distal prehallical element is moderately broad and elongate, extending for approximately half the length of O. metatarsus I (Fig. 40).

Pelvic Girdle: No ilial crest is present. The dorsal prominence is small, gently monticuline, with a dorsolateral protuberance (Fig. 41). The pubis is calcified.

Hyoid: The hyoid plate is longer than wide. The antero-medial processes of the anterior hyale are small and slender. The alary processes of the hyoid plate are not pedunculate. The posterolateral processes are slender and moderately long. The posterior cornua are ossified (Fig. 41).

Variation

The nasals are only moderately ossified, widely separated posteromedially and with characteristic indentations and crenulations on the posterior edge (Fig. 42). Lack of ossification giving indentations on posterior edges is common in *U. inundata*. The nasals are very occasionally crescentic on their anteromedial edges.

The frontoparietal elements characteristically extend anterolaterally to the poorly ossified sphenethmoid. In most specimens the orbital edges are very straight and perpendicular to the prootic. In a few specimens they are inclined slightly medially (Fig. 42).

The frontoparietal fontanelle is usually very widely exposed, sometimes slightly less so. Exposure is usually greater than shown in Fig. 42.

The exoccipital and prootic are never fused and dorsomedial and ventromedial ossification of the exoccipital is lacking. The crista parotica is always short and stocky and the epiotic eminences are prominent.

The condition of the zygomatic ramus of the squamosal varies. It is absent in about $^1/3$ of the specimens, tiny and straight in a further $^1/3$ and tiny and knobbed in the remaining $^1/3$. The otic ramus varies slightly in length: the usual condition is moderately long.

The palatines are expanded medially in about $^2/3$ of the specimens and unexpanded in the remainder. The cultriform process of the parasphenoid invariably is long and usually truncate. The alae are at right angles to the cultriform process; they are slender to moderately slender and vary slightly in length (Fig. 42).

The medial ramus of the pterygoid is usually very long and acuminate. Occasionally it is shorter and acuminate. The posterior process is usually broad, occasionally moderately acuminate. The anterior ramus is always in long contact with the maxillary.

The pars facialis of the maxillary varies slightly in depth. It is rarely shallow, and is usually moderately deep. The preorbital process invariably is present, and usually well developed but can vary slightly in prominence.

The alary processes of the premaxillaries invariably are inclined anteromedially. In one specimen (SAM R17268), they are unusually high. The palatine processes of the premaxillaries are usually moderately long and not closely applied; rarely they are short.

The pterygoid process of the palatal shelf is usually poorly to moderately developed. Very rarely it is virtually absent (Fig. 42).

Habitat

Males call from shallow water at the base of grass tussocks, under leaves and logs, and from grass stems in water, and under leaf litter in sandy stream beds (Tyler et al. 1983, Tyler et al. 1986).

Advertisement Call

The call of U. inundata is a 'long call' of extreme variability. At least two calls are produced (Tyler et al. 1981a, Tyler et al. 1986).

Life history

Tyler et al. (1983) described the life history of this species and illustrated larval morphology including mouth disc structure.

Distribution

Uperoleia inundata occurs in the north of the Northern Territory, on Groote Eylandt and on the western and southern coasts of the Gulf of Carpentaria. It penetrates into Queensland at the base of the Gulf of Carpentaria (collected at Westmoreland) (Fig. 43).

Comparison with other species

Uperoleia inundata is an untoothed species with a widely exposed frontoparietal fontanelle, features shared by U. russelli, U. glandulosa, U. talpa, U. orientalis, U. crassa, U. borealis, U. arenicola and U. littlejohni.

U. inundata may be distinguished from U. russelli, U. crassa, U. talpa, U. orientalis and U. borealis by poor toe webbing (absent or basal).

From U. glandulosa and U. littlejohni, U. inundata is distinguished by the absence of broad toe fringing and by the lack of strong dorsal patterning.

From U. arenicola, U. inundata is distinguished by call (Tyler et al. 1981a) (but see comment p. 67) and by overall lesser ossification of the skull.

3.5.12 Uperoleia lithomoda Tyler, Davies and Martin, 1981

Uperoleia lithomoda Tyler, Davies and Martin 1981, Aust. J. Zool. Suppl. Ser. 79, p. 43.

Uperoleia variegata Tyler, Davies and Martin 1981a, p. 55.

Uperoleia marmorata: Parker and Tanner 1971, p. 5.

Uperoleia lithomoda: Cogger 1983, p. 84; Cogger, Cameron and Cogger 1983, p. 33; Tyler and Davies 1984, p. 123 (part.); Tyler, Smith and Johnstone 1984, p. 99; Tyler 1985, p. 407; Tyler and Davies 1986, p. 59; Tyler, Davies and Watson 1986, p. 98; Mahony and Robinson 1986, p. 120; Davies, McDonald and Corben 1986, p. 148; Tyler, Davies and Watson in press.

Definition

A small species (♂♂ 19-26 mm S-V, ♀♀ 17-30 mm S-V) of moderately gross habitus and short limbs. Maxillary teeth absent; frontoparietal fontanelle poorly to moderately exposed; basal or no webbing between the toes; toes poorly to moderately fringed; eye to naris distance usually greater than internarial span; carpus of six elements; anteromedial processes of anterior hyale of hyoid present; ilial crest absent. Advertisement call an explosive tick of 2-6 pulses with a pulse repetition rate of 62.5-450 pulses sec^{-1}.

Material examined

W.A.: SAM R28741-3, swamp at spillway bridge, 11.5 km NE Lake Argyle Tourist Village (16°02', 128°47'); SAM R28744-56, WAM R94346-7, Gibb River Station in billabong behind Hstd; SAM R28757, WAM R 94348-50, Gibb River Rd, 22.1 km NW Lennard River.

N.T.: AM R53619-20, 15 km N McArthur River Camp on Borroloola Rd (16°15', 136°04'); R53352, 36.5 km N McArthur River Camp on Borroloola Rd (16°16', 136°07'); R53734, R53693, 10 km N McArthur River Camp on Borroloola Rd; R53732-5, approx. 15 km N McArthur River Camp on Borroloola Rd (16°15', 136°04'); SAM R25110-11, 10.2 km from Katherine along Gorge Rd; R20447, 15 km from Katherine along Gorge Rd; R24010, 408 km W Katherine on Victoria Hwy; R24011-14, 11 km NE Katherine along Gorge Rd; R24015-16, Saddle Creek, Victoria Hwy; R25108-9, 17 km E Roper River Rd/Stuart Hwy Jcn; R28758-61, 7 km W Mary River on Arnhem Hwy; R28762-64, Mary River Bridge, Arnhem Hway; R25467-71, 2.7 km E Angurugu, Groote Eylandt; R27473, 8.2 km E Emerald River, Groote Eylandt.

Qld: NTM R11741, R11747, R11756-7, R11760, R11763, R11765, Westmoreland; SAM R28765-7, R29691-5, QM J45922, Kangaroo Rat Mine, Amber Station near Lynd River Crossing; SAM R28768, 1.6 km from Burlington Station on Amber Station Rd; SAM R28769, Amber Station; SAM R28770, James Cook University Experimental Farm 'Fletcherview', Charters Towers; SAM R28771, Lakefield National Park Ranger Station (formerly NPWS N28872); SAM R28773-5, QM J45997, UAZ A897 (formerly NPWS N32319), Coen Airport (13°45'30", 143°06'30"); SAM R28772, Twin Humps, 12 km N Coen (13°51'30", 143°9'30"); QM J31554, Chillagoe; J19862, 1.6 km S Yorkey's Knob P.O.; J29859, 62 km from Townsville on Charters Towers Rd; J29884, 96 km from Townsville on Charters Towers Rd; SAM R24349 (24), 1 km E Edward River Township; R24343-8, Edward River Township; SAM R28776, R29696, QM J45993, Pajingo Station (146°11', 20°47'); SAM R28777-9, R29697, QM J45994, Battery Station, Snake Creek (145°39', 19°27'); SAM R28780, QM J45995, Occupation licence 117 (145°13', 20°40'); QM J45996, Lockwall Station (145°51'19°54'); QM J38842-56, Pentland, N side of town; AM R38449-54, Rocky Creek, 40 km S Batavia Downs, Cape York.

External morphology

The specimens were arbitrarily divided into eight populations on a geographic basis: Gibb River, W.A., Lennard River environs, W.A., Katherine area, N.T., Mary River (Arnhem Hwy) area, N.T., Groote Eylandt, N.T., McArthur River area, N.T., Edward River township, Qld and Amber Station area, Qld. Measurements from these populations are shown in Table 2.

An Fmax test for homogeneity of variances is not significant and a one way analysis of variance of size is highly significant (F=46.25) indicating size differences between different populations.

A GT_2 method of multiple comparison amongst pairs of means based on unequal sample sizes gave results depicted in Table 3. There is no geographic cline in these data.

The shape of the snout can vary from moderately truncate to quite sharply pointed even within the one population (Fig. 44). The sharply pointed snouts (Fig. 44C) are not common and within any one population about equal proportions of blunt and gently rounded snouts occur. The exception is in the Gibb River Station population where double the number of blunt snouted specimens was observed. Within this sample are the paratypes of U. variegata Tyler Davies and Martin referred to the synonymy of U. lithomoda by Tyler et al. (in press). These specimens were collected in the dry season from underground and appear to have been preserved in strong fixative. They are somewhat dehydrated and distortion of snout shape has occurred (see Davies and Littlejohn 1986). The higher proportion of blunt snouted individuals in this population thus may be an artifact. The nostrils are usually located dorsolaterally but are occasionally almost dorsal.

Rugosity of the dorsum is usually moderate (Fig. 30) except in material collected in the dry season (e.g. Gibb River and McArthur River) when equal proportions of moderately and poorly rugose dorsa are recorded. Parotoid glands are always well developed (Fig. 30). Inguinal glands also are well developed except in most of the U. variegata paratypes collected in the dry season, presumably when glandular activity is minimal (see McDiarmid 1968). Coccygeal glands are well, or occasionally moderately developed, except again in the dry season Gibb River material in which these glands are poorly developed.

The pattern of the dorsum of U. lithomoda is usually strongly defined. Ground colour is usually grey with brown or black markings often highlighted with rust-coloured spots. Dark crescentic markings are usually medial to the parotoid glands in the scapular area and are often raised in the form of lyrate plicae (Fig. 45).

Scapular plicae are present except in the Edward River and Gibb River populations in which they are absent in $^1/3$ of the individuals.

Gold colouring on the dermal glands produces yellow gold lateral stripes in most specimens (Fig. 30).

Subarticular and palmar tubercles on the hand are usually prominent, or moderately prominent. In some populations, equal proportions of each condition occur, and in others only one of these states occurs. The presence of supernumerary tubercles on the hand varies. The palmar tubercle at the base of the thumb is generally small and masked by the unpigmented nuptial pad in most males.

Fringing on the toes ranges from poor to moderate. Preservation influences this feature; freshly, and carefully preserved material tends to have more pronounced fringing than in not so well preserved material. In most populations moderately fringed toes are typical except for the Mary River and Edward River populations with the incidence of poor : moderate fringing 6 : 1 and 21 : 9 respectively. Toe webbing is either absent, or basal, usually in about equal proportions. In the Edward River populations, however, 27 of 30 specimens lacked toe webbing. Variation in toe webbing and fringing is shown in Fig. 46.

Both inner and outer metatarsal tubercles are particularly prominent in _U_. _lithomoda_ (Figs. 30,46). The outer metatarsal tubercle is usually aligned in a plane perpendicular to the long axis of the foot, occasionally slightly angled. Subarticular tubercles are conical and not very prominent.

The ventral skin is usually highly granular except in material collected in the dry season at Gibb River, and in some of the material collected at this site at the beginning of the wet season. Granularity is less prominent in the few females examined than in males. White flecks often are present in the centre of the granules. Ventral pigmentation is rare other than on the throat in calling males. If present, it is in the form of a faint dusting of individual pigment granules usually visible only with a microscope. Groote Eylandt and Edward River material shows greater ventral pigmentation than other specimens.

Inguinal patches are not always apparent. When present, they are not as prominent as femoral patches.

A faint or moderately developed midvertebral stripe is almost always present.

Osteology

Material examined

W.A.: SAM R17220, Granite Creek, 14.1 km NE Lake Argyle Tourist Village (PARATYPE); UAZ A769, A808, Spillway Bridge Swamp 11.5 km N Lake Argyle Tourist Village (TOPOTYPES); SAM R17219, Gibb River Hstd garden; UAZ A767-8, A781-98, Swamp behind Gibb River Station Hstd Billabong; UAZ A780, B896, 22.1 km NW Lennard River on Gibb River Rd.

N.T.: SAM R17218, Arnhem Hwy at Fogg Dam turnoff, 24 km ESE Darwin; UAZ A809, Mary River Bridge on Arnhem Hwy; UAZ A807, 6.4 km N Katherine along Gorge Rd; UAZ A799-806, A811, B812, 2.7 km E Angurugu, Groote Eylandt; ANWC A1085, Elcho Is.

Qld: UAZ A897, Coen Airport; UAZ A810, Edward River township; SAM R29691-2, Kangaroo Rat Mine, Amber Station; SAM R28771, Lakefield Ranger Station; AMR 38450, Rocky Creek, 32 km S Batavia Downs; QM J 31554, Chillagoe; J19862, 1.6 km S Yorkeys Knob P.O.; J29859, 62 km from Townsville on Charters Towers Rd; J29884, 96 km from Townsville on Charters Towers Rd; J29483, 1 km S Laura; J29316, 1 km E Laura on

Laura-Cooktown Rd; SAM R29696, Pajingo Station; R29697, Battery Station; QM J38545, J38856, J38842, J38844, Pentland, N side of town.

The osteological description of U. lithomoda of Tyler et al. (1981a) did not include elements of the carpus, tarsus, pelvic girdle or hyoid. Here I supplement the original description.

Carpus: The carpus consists of six elements. Quite considerable torsion occurs. Both the O. ulnare and O. radiale are present. The O. radiale is the larger. These elements articulate with the O. radioulna proximally, and with each other on their proximo-medial border. Distally both elements articulate with the large transversely elongated O. centrale postaxiale. The O. radiale articulates laterally with the O. centrale preaxiale.

The O. centrale postaxiale articulates distally with the bases of O. metacarpi III, IV and V. From the lateroproximal corner a small subacuminate flange extends proximally. Ventromedially a palmar sesamoid occurs (Fig. 47).

The O. centrale preaxiale articulates laterally with the O. radiale and distally with the O. centrale postaxiale, and with the carpal element of the O. distale carpale 2 (Fig. 47), and laterally with the basal prepollical element.

The carpal element of the O. distale carpale 2 articulates with, but is not fused to the carpal element of the O. distale carpale 3.

Tarsus: The O. tibiale and O. fibulare are elongated elements fused proximally and distally. The O. tibiale extends as far as the distal end of the O. fibulare. Three distal tarsal elements are present. The lateral element is the largest and lies at the base of O. metatarsus III (Fig. 47). It extends laterally to articulate with the medioproximal side of the base of O. metatarsus II. The second element lies at the base and slightly laterally to O. metatarsus II. The medial element lies at the base of O. metatarsus I and also articulates with the O. centrale prehallucis. The distal element of the prehallux is large and extends approximately one half the length of O. metatarsus I (Fig. 47).

Ilium: No ilial crest is developed. The dorsal prominence is wedge shaped and extremely prominent (Fig. 48). The dorsal protuberance is prominent and posterolateral.

Hyoid: The hyoid plate is approximately as wide as it is long. The alary processes are prominent but not pedunculate. The anteromedial processes of the anterior hyale are short and slender. The posterolateral process of the hyoid plate are moderately broad and moderately long. The posterior cornua are ossified (Fig. 48).

Variation

Skulls of U. lithomoda share a combination of features: nasals that are closely applied anteromedially and widely separated posteromedially with a crescentic anteromedial edge, and frontoparietals that curve anteromedially on their orbital edges (Fig. 49).

Exposure of the frontoparietal fontanelle varies from almost completely roofed with posteromedial fusion of the frontoparietal elements (Fig. 49C) to moderately widely exposed in young specimens (Fig. 49A). The more common condition is a poorly exposed frontoparietal fontanelle as shown in Fig. 49B. Approximately one half of the specimens examined had state B, $^{1}/3$ had a condition between states B and C and the remainder, state C.

The otic ramus of the squamosal has two conditions. Approximately $^2/5$ of the specimens had a short otic ramus (Fig. 49B) and $^3/5$ had a moderately long otic ramus (Fig. 49C). The zygomatic ramus of the squamosal is short in all specimens and does not vary. The prootic and exoccipital are never fused (although calcification is common) and ossification of the exoccipitals dorsomedially and ventromedially is always absent.

The carotid canal groove is rarely apparent (4 specimens in 48). The palatal shelf is invariably deep. The palatine processes of the premaxillaries are either short and broad ($^2/3$) or moderately long and slightly more slender ($^1/3$). Separation of these elements varies; those exhibiting the short and broad condition tend to be more closely applied than the others. The pterygoid process of the palatal shelf is moderately well developed in all cases.

The palatines are slender and slightly overlap the anterior extremities of the sphenethmoid in ventral view. They are reduced laterally, and do not extend beyond the lateral extremities of the maxillary processes of the nasals. They are slightly expanded medially in many cases and usually angled fairly acutely ($^3/4$ of specimens) to the sphenethmoid at an angle approaching 45°. In about $^1/4$ of the specimens the angle is slightly flatter.

The cultriform process of the parasphenoid is only moderately broad either reaching the level of the medial extremities of the palatines (in about $^5/9$ of the specimens) or not so far ($^4/9$). The anterior extremities are slightly serrate, but truncate. The alae of the parasphenoid are at right angles in all but one specimen from Groote Eylandt (the exception is angled slightly posterolaterally). The alae are moderately short, not reaching the extremities of the medial rami of the pterygoids.

The pterygoids are robust. The anterior rami are moderately slender and in moderately long contact with the pterygoid process of the palatal shelf of the maxillaries. The posterior ramus is short, moderately broad and moderately acute. The medial ramus is moderately long (occasionally longer), acuminate, and not in bony contact with the prootic region.

The pars facialis of the maxillary is shallow with a very well developed preorbital process. The alary processes of the premaxillaries are perpendicular to the pars dentalis, moderately broad at the base and usually bifid dorsally.

Vomerine remnants are absent in all the material examined and invariably a bony columella is present.

Habitat

U. lithomoda calls at the base of grass tussocks usually on coarse gravelly soil at some distance from still, ephemeral water (Tyler, Watson and Davies unpubl.). If two or more species are calling at the same site, the other species (e.g. *U. inundata* on Groote Eylandt and *U. borealis* at Granite Creek in W.A.) calls closer to the water than *U. lithomoda*. Spatial separation is extreme in these situations (Tyler *et al*. 1986).

Advertisement calls

Advertisement calls of *U. lithomoda* were described and analysed by Tyler, Davies and Martin (1981a,c) and Tyler, Davies and Watson (in press). The call is invariably an explosive click that is painful to the ears in a large, active chorus. I have examined calls from across the range of U. lithomoda in Queensland and find little variability (Table 4). Tyler et al. (in press) found the population at Gibb River Station to have fewer pulses per note than those from Lake Argyle and Katherine (which are similar to the Queensland calls analysed here). The result is a considerable lowering of pulse repetition rate (62.5-234.7 compared with 250-462). This was interpreted as a continuation of an east-west trend (substantiated by the data presented here). Because of the overall similarity of calls of this population with others, the conspecificity of the material was accepted.

Developmental biology

Tadpoles are dark brown on the dorsal and lateral surfaces. The body is flattened dorsally (Fig. 50) with dorsally located nostrils. The spiracle is sinistral and the vent dextral. The fin is pigmented with islands of fine pigment, the tail tip being black (Fig. 50). The myotomes are mottled with pigment.

The mouth disc is very small. The tooth formula is $^{2}/3$ with the lower of the upper row divided (Fig. 50). The horny beak is weakly developed. A very poorly developed border of papillae, widely separated anteriorly and posteriorly, surrounds the oral disc.

Table 2. Snout-vent length, tibia length/snout-vent length and eye-naris distance/internarial span measurements for several populations of <u>Uperoleia lithomoda</u>. Data are expressed as mean ± standard deviation with ranges in parentheses. Data for males and females are pooled for ratio calculations.

		Gibb River Station W.A.	22.1 km NW Lennard River W.A.	Spillway Swamp W.A. (type locality)	Katherine N.T.	Mary River N.T.	McArthur River N.T.	Groote Eylandt N.T.	Edward River Qld	Amber Stn/ Charters Towers Qld	All material examined
	n	14	6	4	15	7	8	10	26	12	102
S-V	♂♂	20.25±1.08 (17.9-22.1)	22.83±1.37 (21.5-25.1)	19.0 (17.8-20.5)	20.92±1.66 (18.85-23.5)	18.76±1.10 (16.7-20.1)	21.18±1.24 (19.4-22.7)	24.6±1.90 (20.0-26.5)	16.89±0.76 (16-17.9)	21.9±1.78 (18.3-24.5)	20.22±2.67 (16-26.5)
	n	3			2			1	4		10
	♀♀	22.3 (20.3-23.6)			(19.5-24.5)			29.5	18.58 (16.8-19.2)		21.76±3.77 (16.8-29.5)
TL/ S-V		0.35±.02 (0.31-0.39)	0.35±.02 (0.32-0.37)	0.36 (0.34-0.39)	0.34±.02 (0.31-0.37)	0.35±.02 (0.34-0.40)	0.33±.02 (0.31-0.37)	0.36±.03 (0.32-0.44)	0.36±.02 (0.31-0.41)	0.37±.02 (0.33-0.42)	0.35±.02 (0.31-0.42)
E-N/ IN		1.27±.18 (1.00-1.64)	1.33±.17 (1.13-1.57)	1.13 (1.00-1.31)	1.35±.25 (0.94-1.75)	1.44±.28 (1.13-1.89)	1.35±.23 (1.13-1.85)	1.25±.17 (1.00-1.53)	1.23±.19 (0.83-1.60)	1.20±.20 (0.95-1.53)	1.28±.22 (0.83-1.89)

Table 3. Multiple comparisons amongst pairs of means of snout-vent length of *Uperoleia lithomoda* at eight localities, based on unequal sample sizes - GT_2 method. The differences significant at the 5% level are indicated by an asterisk. Localities are as follows: 1 Edward River, Qld; 2 Mary River, N.T.; 3 Gibb River, W.A.; 4 Katherine and environs, N.T.; 5 McArthur River environs, N.T.; 6 Amber Station environs, Qld; 7 Lennard River environs, W.A.; 8 Groote Eylandt, N.T.

Ranked localities	1 Edward R.	2 Mary R.	3 Gibb R.	4 Katherine	5 McArthur R.	6 Amber Station	7 Lennard R.	8 Groote Eylandt
1	-	2.277	1.7727	1.7337	2.1621	1.8664	2.4217	1.8664
2	1.87	-	2.4753	2.4479	2.7674	2.5433	2.9749	2.6352
3	3.36*	1.49	-	1.3807	2.370	2.1037	2.6093	2.214
4	4.03*	2.16	0.67	-	2.3414	2.0715	2.5818	2.1832
5	4.29	2.42	0.93	.26	-	1.5441	2.8879	2.5365
6	5.01*	3.14*	1.65	.98	0.72	-	2.674	2.2897
7	5.94*	4.07	2.58	1.91	1.65	0.93	-	2.7613
8	7.71*	5.84*	4.35*	3.68*	3.42*	2.70*	1.77	-

Table 4. Advertisement call characteristics of three species of *Uperoleia*.

Species & Locality	N	No. of pulses	Duration m secs	Pulse repetition rate (pulses sec^{-1})	Dominant Frequency Hz	Wet bulb °C temperature
Uperoleia lithomoda J.C.U. experimental farm nr Charters Towers (SAM R28870, formerly NPWS N15592)	1	3	13 (10-15)	260 (200-300)	2367 (2300-2400)	24.6°
U. lithomoda Amber Station (SAM R28769, formerly NPWS N28751)	1	3.67 (3-4)	19.3 (18-20)	174 (150-222)	2500	-
U. lithomoda Lakefield (SAM R28771, formerly NPWS N28872)	1	3	11.8 (10-15)	250 (200-300)	3320 (3300-3400)	25.2°
U. lithomoda Coen Airport (UAZ A897, formerly NPWS N32319)	1	3.2 (3-4)	12.2 (10-16)	265 (231-300)	2520 (2500-2600)	24.8°
U. lithomoda 9.6 km N Coen (SAM R29772, formerly NPWS N32388)	1	5.5 (5-6)	21 (20-22)	261 (250-272)	2750 (2700-2800)	24.6°
Uperoleia fusca type locality (SAM R29597, R29599-29602)	5	20.6 (18-24)	302.1 (220-360)	68.41 (64.86-73.08)	2700	21.5°-23.1°
Uperoleia mimula Townsville Town Common (SAM R29631, R29634-5)	4	4.1 (3-5)	65.5 (55-90)	64.1 (56-83)	2900 (2600-3300)	23.4-24.0°
U. mimula Lannercost, S.F. (SAM R29627, formerly NPWS N15605))	1	4.7 (4-5)	64 (50-70)	73.5 (71-80)	2750 (2700-2800)	24.8°
U. mimula Bazant Outstation (QM J45943)	1	4.3 (4-5)	43 (40-50)	100 (100)	2800 2800	27.2°

Distribution

Uperoleia lithomoda occurs in the Kimberley Division of Western Australia, in the north of the Northern Territory, on Groote Eylandt, at the base of the Gulf of Carpentaria, and on the Cape York Peninsula. Tyler and Davies (1984) reported the species to occur in New Guinea, but this record is not sustained in view of the information now available on a second species known to occur on Cape York. This cryptic species is described on p. 165 and is morphologically very similar to *U. lithomoda*. The distribution of *U. lithomoda* is shown in Fig. 51.

Comparison with other species

Uperoleia lithomoda is a small to moderately large species (males 19-26 mm, females 17-30 mm) lacking maxillary teeth and with a poorly to moderately exposed frontoparietal fontanelle. These features are shared by *U. aspera*, *U. rugosa*, *U. mimula* and *U. capitulata*.

From *U. aspera*, *U. rugosa* and *U. capitulata*, *U. lithomoda* can be distinguished by a combination of lyrate scapula plicae, gold tipped parotoid and inguinal glands giving the impression of yellow to cream lateral stripes on the dorsum, and by a very short call consisting of 2-6 rapid pulses.

U. lithomoda is most closely related to *U. mimula*. From this species *U. lithomoda* can be distinguished by the presence of prominent markings on the dorsum, by the lack of ventral pigmentation on the belly, by strong development of lateral golden, yellow gold or cream stripes on the dorsum (rarely developed in *U. mimula*) and by call. (The pulse repetition rate of calls of *U. lithomoda* in Queensland is 250-456 pulses sec^{-1} and of *U. mimula* is 56-100 pulses sec^{-1}.)

3.5.13 <u>Uperoleia</u> <u>micromeles</u> Tyler, Davies and Martin, 1981

<u>Uperoleia</u> <u>micromeles</u> Tyler, Davies and Martin, 1981, Aust. J. Zool. Suppl. 79, p. 46.

<u>Uperoleia</u> <u>micromeles</u>: Tyler 1982, p. 239; Cogger 1983, p. 85; Cogger Cameron and Cogger 1983, p. 33; Tyler 1985, p. 408; Tyler and Davies 1986, p. 60.

<u>Definition</u>

A relatively large species (♂ 27 mm, ♀♀ 24-31 mm S-V) with a gross habitus; maxillary teeth present as vestiges; narrowly exposed frontoparietal fontanelle; short, flattened unwebbed toes; internarial span broader than eye to naris distance; carpus of six elements; ilial crest present. Advertisement call not known.

<u>Osteology</u>

The ilium has a small dorsal crest (Fig. 31). The dorsal prominence is very large and mesa shaped. The dorsal protuberance is lateral and the pubis is calcified.

The carpus consists of six elements. The O. radiale and O. ulnare are present; the O. radiale is the larger. These elements articulate proximally with the O. radioulna, with each other on their proximomedial border, and with the large transversely elongated O. centrale postaxiale distally. The O. radiale articulates laterally with the O. centrale preaxiale.

The O. centrale postaxiale articulates distally with the bases of O. metacarpi III, IV and V. A small flange extends proximally from the lateroproximal corner (Fig. 52). The O. centrale preaxiale articulates laterally with the O. radiale, distally with the O. centrale postaxiale and the carpal elements of the O. distale carpale 2 and 3, and laterally with the basal prepollical element.

There are three distal tarsal elements. The lateral element is the largest and lies at the base of O. metatarsus III. It 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 medial element lies at the base of O. metatarsus I and also articulates with the O. centrale prehallucis. The distal prehallical element is long and elliptic and extends for approximately $^{2}/3$ the length of O. metatarsus I (Fig. 52).

Comparison with other species

Uperoleia micromeles is a functionally edentate species (the teeth are vestigial) with a poorly exposed frontoparietal fontanelle. This species is unique amongst *Uperoleia* in a number of features: presence of vestigial teeth; a broad snout (E-N/IN 0.83-0.90 [Tyler *et al*. 1981a]); anteromedial extensions to the nasals; and the presence of a moderately developed ilial crest.

Distribution

Known originally only from the Tanami Sanctuary in the Tanami Desert, N.T. *U. micromeles* has since been taken in Western Australia at 1 km S Staffords Bore (20°22'S, 127°24'E) (WAM R64073).

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3.5.14 *Uperoleia minima* Tyler, Davies and Martin, 1981

Uperoleia minima Tyler, Davies and Martin, 1981, Aust. J. Zool. Suppl. 79, p. 49.

Uperoleia sp.: Smith and Johnstone 1981, p. 217.

Uperoleia minima: Tyler 1982, p. 236; Cogger 1983, p. 85; Cogger, Cameron and Cogger 1983, p. 33; Tyler, Smith and Johnstone 1984, p. 101; Tyler 1986, p. 408.

Definition

A very small species (♂♂ 16-21 mm), lacking maxillary teeth; with long unwebbed toes and a very coarsely tubercular dorsal skin. Advertisement call (to the ear) a single sharp click of 2-3 pulses with a pulse repetition rate of 105-130 pulses sec^{-1}; frontoparietal fontanelle minimally exposed; carpus of five elements; no ilial crest.

Osteology (based on paratype)

No ilial crest present. The dorsal prominence is prominent and rounded (Fig. 38) and the dorsal protuberance is anterolateral. The pubis is calcified.

The carpus consists of five elements (Fig. 53). Little torsion occurs. Both the O. ulnare and O. radiale are present, the O. radiale is the longer of the two. Both elements articulate with the O. radioulna proximally, and with each other on their proximomedial border. Distally both elements articulate with the large transversely elongated O. centrale postaxiale. The O. radiale articulates laterally with the O. centrale preaxiale.

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 (Fig. 53). A palmar sesamoid occurs ventromedially.

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, and laterally with the basal prepollical element.

Three distal tarsal elements are present. The lateral element is the largest and lies at the base of O. metatarsus III, 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 lies at the base, slightly laterally to O. metatarsus II. The medial element lies at the base of O. metatarsus I and also articulates with the O. centrale prehallucis (Fig. 53). The distal prehallical element is tiny.

Comparison with other species

Uperoleia minima is a small edentate species with a minimally exposed frontoparietal fontanelle, features shared by *U. rugosa* and some *U. lithomoda*.

From both these species, *U. minima* is distinguished by its poorly patterned dorsum. The toes of *U. rugosa* are often fringed and basally webbed whereas those of *U. minima* are unwebbed. *U. minima* and *U. lithomoda* are distinguished by call (Tyler *et al*. 1981a).

Distribution

The distribution data from the type description of Tyler *et al*. (1981a) have not been supplemented. This species is known only from the Crusher Site of the Amax Mining Camp on Mitchell Plateau, W.A.

3.5.15 *Uperoleia talpa* Tyler, Davies and Martin, 1981

Glauertia mjobergi: Main 1965, p. 66; Barker and Grigg 1977, p. 199.

Uperoleia talpa Tyler, Davies and Martin, 1981, Aust. J. Zool. Suppl. 79, p. 52.

Uperoleia talpa: Tyler 1982, p. 87; Cogger 1983, p. 87; Cogger, Cameron and Cogger 1983, p. 34; Tyler, Smith and Johnstone 1984, p. 102; Tyler 1985, p. 408.

Diagnosis

A large species (♂♂ 26-38 mm S-V, ♀♀ 32-36 mm S-V) lacking maxillary teeth; toes fringed with moderate webbing; metatarsal tubercles very large; frontoparietal fontanelle widely exposed; carpus of six elements; anteromedial processes of anterior hyale of hyoid slender, short; no ilial crest; advertisement call a long pulsed note.

Material examined

49 ♂♂ and 9 ♀♀ were examined: SAM R28792-94 WAM R94430, 10-18 km S Derby; SAM R28795, 22-41 km S Derby; SAM R28808, 41 km S Derby; SAM R(1), 28 km S Derby; SAM R28809-38, WAM R94431-34, 28 km S Derby; SAM R28796-801, WAM R94436-38, 8 km NE Broome; SAM R28802-7, WAM R94439-40, 106 km E Broome.

External morphology

A large species (males 26-38 mm, females 32-36 mm S-V) with a short snout, usually truncated ($^4/5$ of specimens) or slightly rounded ($^1/5$ of material examined) when viewed from above. Eye to naris distance is greater than internarial span (E-N/IN 1.20±.17 [1.00-1.56]). The fingers are short with lateral fringes in $^2/5$ of the specimens, absent in the remainder. Subarticular tubercles are prominent in about $^1/2$ the specimens and moderately prominent in the others. The palmar tubercle at the base of the thumb is never prominent whilst that on the heel of the hand is prominent in $^3/5$ of the specimens but poorly developed in the remaining $^2/5$. The hind limbs are very short (TL/S-V 0.31±.02 [0.25-0.35]). The toes are long, broadly fringed in all specimens and moderately webbed in about $^7/8$ of the specimens (Fig. 54) and basally webbed in the remaining $^1/8$. The subarticular tubercles are conical and the metatarsal tubercles are extremely prominent. The inner metatarsal tubercle is oriented along the axis of the first toe and the outer metatarsal tubercle is angled slightly to the long axis of the foot.

The dorsal surface has extremely well defined dermal glands in contrast to the specimens in the type series. About $^1/5$ of the specimens have only moderately developed parotoid glands as opposed to $^4/5$ with extremely well developed and occasionally hypertrophied glands. Inguinal and coccygeal gland development mirrors that of the parotoid glands. The submandibular gland is poorly developed in about $^1/6$ of the specimens, moderately developed in a further $^1/6$ and well developed in the remainder. The dorsal surface is smooth in $^2/3$ of the specimens, moderately rugose in about $^2/9$ and rugose in the remaining $^1/9$ of the material examined.

The ventral surface is granular in about $^1/3$ of the specimens and smooth in the remainder.

The dorsum is weakly patterned in about $^1/4$ of the specimens and moderately marked in the remainder (Fig. 10). The ventral surface is unpigmented.

Osteology

Material examined: UAZ A591-4, A598-600, B864, 28 km S Derby; UAZ A595a,b, 53 km E Derby on Gibb River Rd; UAZ A602, 8 km NE Broome; UAZ A865-6, 10 km S Derby.

Variation occurs in the posteromedial separation of the nasals. Some specimens have nasals that are widely separated medially, others that are less so. In some specimens the anterior edges of the nasals are extremely crescentic and in others barely so.

The anterior extremities of the frontoparietals vary in position. In some specimens, they barely reach the posterior extremities of the sphenethmoid and terminate at the level of the anterior extremity of the frontoparietal fontanelle. In other specimens they reach anteriorly to the anterior edges of the sphenethmoid. The orbital edges of the frontoparietals are straight and gently angled medially.

The zygomatic ramus of the squamosal is tiny and bifid in many, but not all, specimens. The pars facialis of the maxillary is shallow to moderately deep with an extremely well developed monticuline preorbital process. The condition of the palatines varies - the bones are always reduced laterally, but in many specimens they do not extend beyond the lateral extremities of the nasals, whereas in others, they do.

The cultriform process of the parasphenoid is moderately slender and varies in length. In one specimen (UAZ A602) it is dagger shaped. The pterygoid process of the palatal shelf of the maxillary is well developed. The anterior ramus of the pterygoid is moderately expanded and in moderately long contact with the pterygoid process of the maxilla. The epiotic eminences of the crista parotica are incompletely ossified posteriorly. Vomerine fragments occur at the edge of the choanae in UAZ A602.

There is no ilial crest. The dorsal prominence is well developed, monticuline, and the dorsal protuberance is laterally situated on the prominence (Fig. 11).

The hyoid plate is longer than wide. The anteromedial processes of the anterior hyale are slender and moderately long. The alary processes of the hyoid plate are not pedunculate. The posterolateral processes are broad and moderately long. The posterior cornua are ossified (Fig. 38).

The carpus consists of six elements. A moderate degree of torsion occurs. Both the O. radiale and O. ulnare are present; the O. radiale is the larger. They articulate with the O. radioulna proximally and with each other on their proximomedial border. Distally both elements articulate with the large transversely elongated O. centrale postaxiale. The O. radiale articulates with the O. centrale preaxiale.

The O. centrale postaxiale articulates distally with the bones of O. metacarpii III, IV and V. From the lateroproximal corner, a very small flange extends proximally. A palmar sesamoid is situated ventromedially (Fig. 55).

The O. centrale preaxiale articulates laterally with the O. radiale, distally with the O. centrale postaxiale and with the carpal elements of the O. distale carpale 2 and 3, and laterally with the basal prepollical element (Fig. 55).

Three distal tarsal elements are present. The lateral element is the largest and lies at the base of O. metatarsus III. It extends laterally to articulate with the medioproximal side of the base of

O. metatarsus II. The medial element lies at the base of O. metatarsus I and also articulates with the O. centrale prehallucis.

The distal prehallical element is very long, slender and bullet shaped, extending for about $^2/3$ the length of O. metatarsus I (Fig. 55).

Comparison with other species

Uperoleia talpa is a large edentate species with a widely exposed frontoparietal fontanelle and moderately webbed toes. These features are shared by U. russelli, U. orientalis and U. borealis. From U. orientalis, U. talpa is distinguished by the absence of a midvertebral stripe. U. borealis lacks back patterning and U. russelli has coloured inguinal and postfemoral patches.

Breeding biology

Uperoleia talpa is sympatric with U. mjobergi, and U. aspera at sites between 12 and 42 km S of Derby in W.A. The three species are spatially separated with respect to calling site. U. mjobergi calls at the edge of or even in, shallow temporary waters, whereas U. talpa calls from dry vegetated regions a considerable distance from water. U. aspera calls from the intermediate areas.

Glandular secretions

Uperoleia talpa is unique amongst Uperoleia in releasing copious quantities of white frothy secretion from the parotoid glands in response to low stimuli such as being picked up. The secretion is toxic to other frogs placed in the same container as the U. talpa.

Distribution

Uperoleia talpa is confined to the southwesterly portion of the Kimberley Division of Western Australia. The distribution of the species is shown in Fig. 37.

3.5.16 Uperoleia aspera Tyler, Davies and Martin, 1981

Uperoleia aspera Tyler, Davies and Martin, 1981, Rec. West. Aust. Mus. 9, p. 159.

Uperoleia aspera: Tyler 1982, p. 236; Cogger 1983, p. 82; Cogger, Cameron and Cogger 1983, p. 32; Tyler, Smith and Johnstone 1984, p. 97; Tyler 1985, p. 407.

Diagnosis

A moderate sized species (♂♂ 24-30 mm, ♀♀ 29-34 mm S-V) lacking maxillary teeth; toe webbing basal or absent; frontoparietal fontanelle poorly to moderately exposed; carpus of six elements; anteromedial processes of anterior hyale of hyoid slender and short; no ilial crest; advertisement call a fast click of 5-6 pulses with a pulse repetition rate of 167-171 pulses sec^{-1}.

Morphology

Material examined: SAM R28788-9, WAM R94435, 20-42 km S Derby, W.A.

The snout is short and broadly rounded or truncate in about equal proportions. The eye to naris distance is greater than the internarial span (E-N/IN 1.21±.12 [1.07-1.40]).

The fingers are short, with poorly developed lateral fringes and with prominent subarticular tubercles. The palmar tubercle on the heel of the hand is always prominent and that at the base of the thumb, rarely so. The hind limbs are short (TL/S-V 0.34±.02 [0.31-0.36]). The toes are long, narrowly fringed, with a faint trace of basal webbing and with conical subarticular tubercles; the inner and outer metatarsal tubercles are moderately prominent. The inner metatarsal tubercle is oriented along the long axis of the first toe and the outer metatarsal tubercle is slightly angled to the long axis of the foot. A tiny heel tubercle is present.

The dorsal surface is coarsely to moderately tubercular (Fig. 10). The parotoid and coccygeal glands are all well developed and the inguinal glands only poorly to moderately so. The submandibular gland is either moderately or well developed in approximately equal proportions.

The ventral surface is regularly or irregularly granular.

The dorsal surface bears a moderately pronounced pattern. The ventral surface is unpigmented.

Osteology

Material examined: UAZ A872-8, 20-42 km S Derby, W.A.

The sphenethmoid is not ossified medially and does not make bony contact with the nasals. The frontoparietal fontanelle is poorly to, at best, moderately exposed. The greatest exposure detected was in UAZ A878. The orbital edges of the frontoparietals are inclined anteromedially and in UAZ A878, they are curved anteromedially. The anterior extremities of the frontoparietals reach the level of the sphenethmoid in all specimens and extend anteriorly beyond this element in one specimen.

The nasals are approximately triangular and usually well ossified, rarely moderately so. They are moderately separated posteromedially in almost all specimens and crescentic along the anterior edge in all but one specimen. The maxillary process of the nasals is not accuminate and widely separated from the shallow pars facialis of the maxillary. The preorbital process of the pars facialis is not prominent. The palatines are reduced laterally not extending beyond the level of the maxillary process of the nasal. They are moderately acutely angled to the sphenethmoid and usually expanded medially.

The parasphenoid is robust, the cultriform process is relatively broad and the alae at right angles.

The anterior ramus of the pterygoid is in long contact with the moderately well-developed pterygoid process of the palatal shelf of the maxillary.

The squamosal is moderately robust. The zygomatic ramus is absent in $^{2}/3$ of the specimens and tiny in the remainder. The otic ramus consistently is moderately long.

The maxillary and premaxillary are edentate and the vomers are absent except in UAZ A878 where two large fragments are situated medially to the palatines.

No ilial crest is developed. The dorsal prominence is extremely prominent and papillate (Fig. 11). The dorsal protuberance is mediolateral and the pubis is calcified.

The hyoid plate is approximately as broad as it is long. The anteromedial processes of the anterior hyale are short and slender. The alary processes of the hyoid plate are not pedunculate. The posterolateral processes of the hyoid plate are moderately broad and moderately long. The posterior cornua are ossified (Fig. 12).

The carpus consists of six elements (Fig. 56). Little torsion occurs. Both the O. radiale and O. ulnare are present: the O. radiale is the larger. These elements articulate with the O. radioulna proximally and with each other on their proximomedial border. Distally both elements articulate with the large transversely elongated O. centrale postaxiale. The O. radiale articulates laterally with the O. centrale preaxiale (Fig. 56).

The O. centrale postaxiale articulates distally with the bases of the O. metacarpi III, IV and V. From the lateroproximal corner a very small flange extends proximally (Fig. 56). A palmar sesamoid occurs ventromedially.

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

Three distal tarsal elements occur (Fig. 56). The lateral element is the largest and lies at the base of O. metatarsus III. It 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 lies at the base of O. metatarsus II. The medial element lies at the base of O. metatarsus I and also articulates with the O. centrale prehallucis. The distal prehallical element is large and extends $^{2}/3$ of the length of O. metatarsus I (Fig. 56).

Comparison with other species

Uperoleia aspera is an untoothed species with a poorly to moderately exposed frontoparietal fontanelle. These features are showed by some *U. lithomoda*, *U. mimula* and *U. capitulata*.

From *U. mimula* and *U. capitulata*, *U. aspera* is distinguished by its rugose dorsum and unpigmented ventral surface. *U. capitulata* has heavily ossified nasals and only five carpal elements. *U. mimula* has a 'long call' of 4-5 pulses with a pulse repetition rate of about 33 pulses sec^{-1} compared with the short click call of *U. aspera* (170 pulses sec^{-1}, Tyler *et al.* 1981b).

From *U. lithomoda*, *U. aspera* is distinguished by call (Tyler *et al.* 1981a) and by the poorly developed inguinal glands.

Distribution

The distribution data of Tyler *et al.* (1981b) have not been expanded.

3.5.17 *Uperoleia trachyderma* Tyler, Davies and Martin, 1981

Uperoleia trachyderma Tyler, Davies and Martin 1981, Trans. R. Soc. S. Aust. 105, p. 149.

Uperoleia trachyderma: Tyler, Davies and Martin 1983, p. 241; Cogger 1983, p. 87; Cogger, Cameron and Cogger 1983, p. 34; Tyler and Miller 1985, p. 45; Tyler 1985, p. 409; Tyler and Davies 1986, p. 60; Davies, McDonald and Corben 1986, p. 160.

Definition

A small to moderate sized species (♂♂ 17-26 mm S-V) lacking maxillary teeth, with small eyes; toes broadly fringed; very small rounded outer metatarsal tubercle; widely exposed frontoparietal fontanelle; dorsum covered with small conical tubercles; carpus of five elements; anteromedial processes of anterior hyale of hyoid slender; small ilial crest; advertisement call a staccato burst of four short pulses with a pulse repetition rate of about 79 pulses sec^{-1}.

Material examined

N.T.: SAM R22336-48, Rankine River at Ranken Store, Alexandria Station; SAM R22325-35, Barkly Hwy, 500 m N Microwave Repeater 8502 Soudan Outstation, Alexandria Station; SAM R25952-61, 113.9 km S Victoria Hwy/Delamere Hwy Jcn; SAM R24017, 415.1 km W Katherine on Victoria Hwy; SAM R24018-25, 4.4 km W Keep River (Newry Station) on Victoria Hwy.

Qld: QM J39012, Gunpowder Rd, 45.1 km E Mt Isa (20°23', 139°20'); QM J38969-72, J38975, 20 km E Cloncurry on Julia Creek Rd; QM J39089-91, 12.6 km E Camoweal on Barkly Hwy; QM J38965-8, 13.2 km E Cloncurry on Julia Ck Rd; QM J45955, SAM R29660-4, Lawn Hill Station.

External morphology

This species shows little morphological variation and is characterised by a finely tubercular dorsum (Tyler et al. 1981c), the texture of which has not been reported in any other Australian amphibian. Only males have been collected; those from western Qld are larger (21-26 mm S-V) than those from localities in the N.T. (17-23 mm S-V).

Hind limbs are moderately long (TL/S-V 0.35±.02, [0.31-0.39]) and eye to naris distance is always greater than internarial span (E-N/IN 1.35±.16 [1.07-1.83]). The eye is consistently small, approximating eye to naris distance in the 56 specimens examined (Fig. 3).

Toes are well fringed; some specimens are unwebbed whilst others have basal webbing between the toes.

Metatarsal tubercles are rounded and small. The inner is situated at the base of toe 1 and the outer is slightly angled to the long axis of the foot (Fig. 57).

The characteristic tiny conical tubercles on the dorsal surface (Fig. 3) are restricted occasionally to the head and limbs, with only a trace on the dorsum.

Ventral pigmentation is not always as dense as reported in the type description. Dark stippling is exhibited in only some specimens and most have only a faint suffusion of pigment.

In life, the frogs often have brilliant orange patches on the dermal glands and they have a characteristic posture in which the head is depressed (Fig. 3).

Osteology

Material examined

N.T.: SAM R22331, UAZ A621, A892-4, Barkly Hwy, 500 km N Microwave Repeater 8502, Soudan Outstation, Alexandria Station; UAZ A622, Rankine River at Ranken Store; UAZ A595-6, 113.9 km S Delamere Hwy/Victoria Hwy Jcn; UAZ A595, 4.4 km W Keep River on Victoria Hwy.

Here I supplement the type description with data on elements of the carpus, tarsus, pelvic girdle and hyoid.

Carpus: The carpus consists of five elements. Little torsion occurs. Both the O. ulnare and O. radiale are present. The O. radiale is the larger of the two. These elements articulate with the O. radioulna proximally and with each other on their proximomedial border. Distally both elements articulate with the large transversely elongated O. centrale postaxiale. The O. radiale articulates laterally with the O. preaxiale centrale (Fig. 58).

The O. centrale postaxiale articulates distally with the bases of O. metacarpi III, IV and V. No flange is apparent on the lateroproximal corner of the O. centrale postaxiale. Ventromedially is a depression on which a palmar sesamoid is situated.

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

Tarsus: The O. tibiale and O. fibulare are elongated elements fused proximally and distally. The O. tibiale extends as far as the distal end of the O. fibulare. Three distal tarsal elements are present. The lateral element is the largest and lies at the base of O. metatarsus III. It extends laterally to articulate with the medioproximal side of the base of O. metatarsus II. The second element lies at the base, slightly laterally, to O. metatarsus II. The medial element lies at the base of O. metatarsus I, and articulates with the O. centrale prehallucis. The distal prehallical element is small and slender (Fig. 57).

Pelvic Girdle: A small proximal crest occurs on the ilium. The dorsal prominence is monticuline and supports a curved posterolateral protuberance (Fig. 59). The pubis is calcified.

Hyoid: The hyoid plate is about as broad as it is long. The alary processes are broad and not pedunculate. The anteromedial processes of the anterior hyale are slender and moderately long. The posterolateral processes of the plate are moderately broad and moderately long. The posterior cornua are ossified (Fig. 59).

Variation

There is little variation in cranial osteology in the material examined.

The nasals are very well ossified with slight variation in the degree of posteromedial separation. The nasals are always in tenuous contact with the sphenethmoid. The frontoparietal fontanelle is widely exposed and slight variation occurs in curvature of the orbital edges of the frontoparietal elements. Occasionally curvature is not detectable. The anterior extremities of the frontoparietals do not reach beyond the sphenethmoid.

The epiotic eminences are not prominent and posterior ossification appears to be complete if thin. The zygomatic ramus of the squamosal is small but not bifid and some variation is found in length of the short otic ramus.

The maxillary and premaxillary are edentate and the pars facialis of the maxillary is shallow with a small preorbital process.

The palatines are acutely angled to the sphenethmoid, reduced laterally and do not extend beyond the truncated maxillary processes of the nasals. Vomerine fragments are present medial to the palatines in three specimens.

The anterior ramus of the pterygoid is in moderately long contact with the moderately prominent pterygoid process of the palatal shelf of the maxillary.

The cultriform process of the parasphenoid is broad in this species and the alae are short and angled slightly posterolaterally.

The distal carpale 2 and 3 are fused in all specimens.

Advertisement call

Tyler *et al*. (1981c) reported the advertisement call of *U. trachyderma* from the type locality as a harsh 'creak' of four short pulses with a pulse repetition rate of about 79 pulses sec^{-1}.

Distribution

Uperoleia trachyderma is confined to the grey self-mulching cracking clays (Northcote *et al*. 1976) of the Northern Territory and western Queensland (Fig. 60). *U. trachyderma* is the only species within *Uperoleia* that can be associated with a particular soil type (Tyler, Davies, Watson, Martin unpubl., Tyler and Davies 1986).

Comparison with other species

Uperoleia trachyderma is an untoothed species with a widely exposed frontoparietal fontanelle, features shared by *U. russelli*, *U. talpa*, *U. glandulosa*, *U. crassa*, *U. borealis*, *U. orientalis*, *U. inundata* and *U. arenicola*.

From *U. russelli*, *U. talpa*, *U. crassa*, *U. borealis*, *U. glandulosa* and *U. orientalis*, *U. trachyderma* is distinguished by the absence of webbing or presence of only basal webbing on the toes. From *U. inundata* and *U. arenicola*, *U. trachyderma* is distinguished by the presence of broad fringes on the toes and a tiny conical outer metatarsal tubercle (broad and elevated in the former two species). From all congeners *U. trachyderma* is distinguished by the presence of finely conical tubercles on the dorsal skin.

3.5.18 *Uperoleia glandulosa* Davies, Mahony and Roberts, 1985

Uperoleia marmorata: Main 1965, p. 36 (part); Main and Storr 1966, p. 57; Cogger 1983, p. 84.

Uperoleia glandulosa: Davies, Mahony and Roberts, 1985, Trans. R. Soc. S. Aust. 109, p. 103.

Holotype

WAM R89489, an adult male collected at Petermarer Creek, Port Hedland-Broome Rd, W.A. (21°23'6"S, 118°48'21"E), on 10.i.1983 by M. Mahony and J.D. Roberts.

Definition

A moderate sized species (♂♂ 20-25 mm, ♀ 25 mm S-V) with moderately long limbs (TL/S-V 0.34-0.41). Maxillary teeth absent; frontoparietal fontanelle widely exposed; basal webbing between the toes; toes fringed; carpus of six elements; no ilial crest; advertisement call a sharp click of 2-3 pulses with a pulse repetition rate of about 6.3 pulses sec^{-1}.

Description of holotype

Maxillary teeth absent. Vomerine teeth absent. Snout short, truncated when viewed from above and in profile. Eye to naris distance greater than internarial span (E-N/IN 1.36). Canthus rostralis prominent and straight (Fig. 61). Loreal region sloping. Tympanum not visible externally (Fig. 61). Fingers moderately long, slightly fringed (Fig. 62) with well developed subarticular tubercles. In order of length 3>4>2>1. Palmar tubercles large and prominent. Supernumerary palmar tubercles prominent. Hind limbs long (TL/S-V 0.37). Toes long, fringed, with basal webbing (Fig. 62). In order of length 4>3>5>2>1. Large oval inner and broad outer metatarsal tubercles. Subarticular tubercles conical.

Dorsal surface with well defined parotoid, inguinal and coccygeal glands (Fig. 10). Dorsum faintly tubercular. Submandibular gland disrupted. Ventral surface finely granular.

Male with unilobular, submandibular vocal sac. In preservative, dorsal surface brown. Short cream, midvertebral stripe on anterior $^1/3$ of body. Black, lyrate markings on scapular region (Fig. 10) and black patches on other portions of dorsum.

Surfaces of parotoid, inguinal and coccygeal glands, cream. Inguinal and femoral regions cream. Ventral surface cream with chocolate brown suffusions. Submandibular region dark brown.

Colour in life

Main and Storr (1966) describe the colour of WAM R22921 as "Dorsal ground colour olive-brown with black spots and blotches. Anteriorly an indistinct vertebral series of orange spots. Dorso-laterally a broken orange stripe from behind orbit nearly to groin. A small orange spot on each side of sacrum. A large orange red blotch in groin and on outer surface of thigh. Upper surface of limbs as on dorsum. Ventrally whitish flecked with grey. Lower surface of limbs flesh-coloured."

This description conforms with the observations of Davies et al. (1985) (Fig. 10).

Dimensions (in mm)

Snout-vent length 20.2; tibia length 7.4; eye diameter 2.8; eye-naris distance 1.9; internarial span 1.4.

Etymology

The specific epithet is from the Latin glandula in reference to the prominent parotoid, inguinal and coccygeal glands in this species.

Variation

There are seven paratypes, six adult ♂♂ and one adult ♀. WAM R89490-2, AM R114573, collected with the holotype; SAM R27081, SAM R27082 (cleared and stained), 3.2 km NE Wittenoom turnoff on Port Hedland-Broome Rd, 10.i.1983, M. Mahony, J.D. Roberts. WAM R22921, Mundabullangana (5 km E of Hstd), 19.ii.1961, G.M. Storr.

Males range 19.9-23.4 mm and the female is 24.6 mm S-V. All paratypes are squat with long legs (TL/S-V 0.38-0.41 in the males: 0.34 for the female). E-N/IN ranges 1.13-1.50. All specimens have well developed cream glands, and basal to slightly more than basal toe webbing. Skin texture resembles that of the holotype. The ground colour of the dorsum of the female is grey rather than brown whilst the darker colour markings of all the paratypes are brown whereas the holotype is black. One paratype has a truncated snout when viewed from above, as in the holotype, whereas the others have more rounded snouts (Fig. 61). In some of the paratypes the midvertebral stripe is not as conspicuous as in the holotype. Palmar tubercles are not always as prominent as figured.

Advertisement call

The advertisement call of this species is a sharp click: a single note formed by two or three pulses. The pulse repetition rate is about 6.3 pulses $\sec^{-1}$ with a pulse duration of 5.7-6.8 msec (Davies *et al*. 1985).

Breeding biology

Most males were observed calling around a roadside drainage channel. Males were calling at the base of sedge clumps close to the water's edge or in a similar position actually in the water. Males with a similar call were also heard in the Petermarer Creek and around a flooded claypan about 3 km southwest of the Turner River on the Northwest Coastal Highway, in the Turner River but not on the Yule River. Males were calling on the third night after two days and two nights of heavy rains (114 mm at Port Hedland) (Davies *et al*. 1985).

Uperoleia russelli was calling at the same sites.

Osteology

Skull poorly ossified, sloping anteroventrally. Small portion of sphenethmoid ossified posteriorly to medial extremities of palatines with ossified portion extending about $^1/3$ of the length of the orbit in ventral view. Medial ossification of sphenethmoid absent dorsally and ventrally. Prootic not fused with exoccipital. Exoccipital not ossified either dorso- or ventromedially. Crista parotica short, stocky, not overlain by otic ramus of squamosal. Carotid canal groove not developed on frontoparietals. Frontoparietal fontanelle extensively exposed, overlapped laterally by frontoparietal elements extending narrowly for $^9/10$ length of orbit. Anterior margin of fontanelle formed by sphenethmoid and medial cartilaginous elements, at level of anterior ramus of pterygoid. Posterior margin formed by articulating posteromedial extremities of frontoparietals (Fig. 63).

Nasals moderately ossified, approximately triangular with maxillary processes directed more ventrally than laterally; widely separated medially. Maxillary processes not in bony contact with well developed preorbital processes of very shallow pars facialis of maxillary.

Palatines robust, reduced laterally, abutting and just overlying anterior extremities of sphenethmoid ventrally. Parasphenoid robust, cultriform process elongate, extending anteriorly to ossified portion of sphenethmoid in ventral view (Fig. 63). Alary processes expanded laterally, at right angles to cultriform process extending almost to level of anterior extremities of medial rami of pterygoids.

Medial ramus of pterygoid moderately long, acuminate, not in bony contact with prootic region. Posterior ramus moderately long and broad. Anterior ramus in long contact with moderately developed pterygoid process of palatal shelf of maxillary. Cartilaginous quadrate present between base of squamosal and quadratojugal. Quadratojugal robust, in firm contact with maxillary.

Squamosal shaft robust; tiny zygomatic ramus, elongate unexpanded otic ramus lying alongside lateral extremities of crista parotica.

Maxillary and premaxillary edentate. Palatal shelf moderately deep with well developed palatine processes not abutting medially, and moderately developed pterygoid processes. Alary processes of premaxillaries moderately broad, bifurcate and perpendicular. Vomers absent. Columella bony.

Pectoral girdle arciferal and robust. Omosternum and xiphisternum present. Sternum cartilaginous. Clavicles slender, curved, poorly separated medially. Scapula bicapitate; about same length as clavicles. Suprascapula about $^{1}/2$ ossified.

Eight non-imbricate presacral vertebrae. Sacral diapophyses poorly expanded. Relative widths of transverse processes III>sacrum>IV>II>V=VI>VII=VIII.

Bicondylar, sacrococcygeal articulation. Urostyle with crest extending $^{2}/3$ its length. Ilia extend anteriorly to sacrum. Ilial crest absent. Large papillate, dorsal protuberance on small dorsal prominence (Fig. 64). Humerus with strongly developed anteroproximal crest. Phalangeal formula of hand 2,2,3,3.

The carpus consists of six elements. Both the O. radiale and O. ulnare are present; the O. radiale is the larger. Both elements articulate proximally with the O. radioulna, with each other on their proximomedial border and distally with the large tranversely elongated O. centrale postaxiale. The O. radiale articulates laterally with the O. centrale preaxiale.

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. A palmar sesamoid is situated ventromedially (Fig. 65).

The O. centrale preaxiale articulates laterally with the O. radiale, distally with the O. centrale postaxiale and with the carpal elements of the O. distale carpale 2 and 3 and laterally with the basal prepollical element (Fig. 65).

There are three distal tarsal elements. The lateral element is the largest and lies at the base of O. metatarsus III. It 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 lies at the base of O. metatarsus II and the medial element lies at the base of O. metatarsus I and also articulates with the O. centrale prehallucis. The distal prehallical element is slender and extends for about $^{1}/2$ the length of O. metatarsus I (Fig. 66). Phalangeal formula of foot 2,2,3,4,3.

Karyotype

Davies *et al*. (1985) described and illustrated the karyotype of this species which has the diploid number 2n=24.

Comparison with other species

Uperoleia glandulosa is an edentate species with a widely exposed frontoparietal fontanelle and basal webbing between the toes. These features are shared by *U*. *inundata*, some *U*. *borealis*, *U*. *crassa* and *U*. *trachyderma*. From all these species, *U*. *glandulosa* is distinguished by its strong dorsal patterning. *U*. *glandulosa* is a short call species, whereas *U*. *inundata*, *U*. *borealis*, *U*. *crassa* and *U*. *trachyderma* are all long call species.

Distribution

Known only from Petermarer Creek, 3.2 km NE Wittenoom turnoff and the Turner River on the Port Hedland/Broome Hway, and from Mundabullangana Hstd.

3.5.19 Uperoleia martini Davies and Littlejohn, 1986

Uperoleia marmorata: Littlejohn 1969, p.110 (part.)

Uperoleia marmorata: Cogger 1975, p.183 (part.)

Uperoleia martini: Davies and Littlejohn, 1986, Trans. R. Soc. S. Aust. 110, p. 129.

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; 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; ilial crest absent; advertisement call a long pulsed note 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. 67). 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. 67). Hind limbs moderately long (TL/S-V 0.39). Toes long, unfringed unwebbed. In order of length 4>3>5>2>1 (Fig. 67). Metatarsal tubercles large and prominent. Subarticular tubercles conical and prominent.

Dorsal surface rugose. Parotoid glands hypertrophied. 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, 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±.02 [0.34-0.39]). Eye to naris distance approximates internarial span (E-N/IN 1.07±.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 1/3 of length of orbit in ventral view. Posteromedial processes present dorsally projecting into anterior portion of frontoparietal fontanelle (Fig. 68). 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. 68). 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. 68). Parasphenoid 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 dilations of anterior hyale (Fig. 69). 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 $^1/2$ 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. 70). O. radiale articulates laterally with O. centrale preaxiale.

O. centrale postaxiale articulates distally with bases of O. metacarpi V, IV and III. From lateroproximal corner, small flange extends proximally onto lateral surface of O. ulnare. Palmar sesamoid ventromedially (Fig. 70).

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 $^1/3$ length.

No ilial crest; dorsal prominence small, gently monticuline, dorsal protuberance posterolateral. Pubis calcified (Fig. 69).

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. 70).

Variation

Two other paratypes were cleared and stained, one for bone and one for bone and cartilage (SAM R29648, R29650). Both have a frontoparietal fontanelle exposure greater than that shown in Fig. 68 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

Davies and Littlejohn (1986) described the advertisement call of this species. The pulse number ranges 32-36 pulses with a pulse repetition rate of about 78 pulses sec^{-1} and a dominant frequency of about 2129 KHz.

Distribution

Uperoleia martini is known from coastal regions of Victoria and N.S.W.. Its distribution is shown in Fig. 71.

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 parotid glands and a chocolate ventral surface. From U. tyleri, U. martini is distinguished by the presence of rugose dorsum with yellow mottlings and by call (the call of U. martini is a longer call of about 32-36 pulses whilst that of U. tyleri is about 24 pulses).

3.5.20 Uperoleia tyleri Davies and Littlejohn, 1986

Hyperolius (Uperoleia) marmorata: W.K. Parker 1881, p. 10.

Uperoleia rugosa: H.W. Parker 1940, p.68 (part.).

Uperoleia marmorata: Keferstein 1867, p.349, 1868, p.220 (part.); H.W. Parker 1940, p.69 (part.); Moore 1961, p.219 (part.); Littlejohn, Martin and Rawlinson 1963, p.225; Littlejohn 1967, p.153; Littlejohn 1969, p.110; Martin and Littlejohn 1969, p.171; Littlejohn 1971, p.9; Watson and Martin 1973, p.42; Cogger 1975, p.83 (part.); Brook 1975, p.119; Barker and Grigg 1977, p.186 (part.).

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

Uperoleia tyleri: Davies and Littlejohn, 1986, Trans. R. Soc. S. Aust. 110, p. 132.

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 form of medial dilations; ilial crest absent. Advertisement call a 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. 72). Internarial span less than eye to naris distance (E-N/IN 1.65). Canthus rostralis inconspicuous and straight. Tympanum not visible externally (Fig. 72). Fingers short, slightly fringed, unwebbed. In order of length 3>2=4>1. Prominent subarticular and palmar tubercles (Fig. 72). Hind limbs long (TL/S-V 0.38). Toes long, poorly fringed and unwebbed. In order of length 4>3>5>2>1 (Fig. 72). 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. 72). 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. 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 ♀♀.

N.S.W.: 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; D23631 Bateman's Bay, M.J. Littlejohn, A.A. Martin, P.A. Rawlinson, 2.xi.1964; D23640 3.2 km N Bateman's 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; SAM R29653-8, NMV D59495, Narrabarba, M.J. Littlejohn, G.F. Watson, 24.ix.1985.

Vic.: NMV D42741-5 Malacoota Inlet, P.A. Rawlinson, 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 N.E. 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±.03 [0.35-0.44]) and paratypes have variable snout proportions (E-N/IN 1.18±.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 colouration 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. 73). Ossified portion of sphenethmoid not confluent medially and extending slightly anteriorly to anterior extremities of frontoparietals and posteriorly about $^{1}/3$ 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 $^{2}/3$ 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. 73). 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 medial to palatines. Dentigerous processes absent.

Bony columella present.

Pectoral girdle arciferal and robust. Omosternum and xiphisternum present. Sternum cartilaginous. Clavicles slender, curved, moderately separated medially. Coracoids robust, moderately separated medially. Scapula bicapitate, slightly longer than clavicles. Suprascapula about $^{2}/3$ 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. 74).

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

Incomplete mediodorsal ossification on vertebrae I-V. Short transverse processes present on urostyle. These are probably anomalous structures since they often occur in single specimens of <u>Uperoleia</u>. Urostyle bicondylar, well developed crest extending dorsomedially about $^{1}/2$ length of urostyle.

No ilial crest. Dorsal prominence monticuline; dorsal protuberance posterolaterally placed on prominence (Fig. 75). Pubis cartilaginous.

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

Three distal tarsal elements present. Lateral element (T_3) largest (Fig. 76).

Hyoid plate about as broad as long. Alary processes large, not pedunculate. Anteroproximal portions of anterior cornua dilated, anterior processes of hyale thickened, not slender. Posterolateral processes moderately long. Postermedial processes ossified (Fig. 75).

Variation

A further nine paratypes were cleared and stained NMV D23622-3, D42743, D42745, D48597, D33601, AM R4755, SAM R29658, 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

Davies and Littlejohn (1986) described the advertisement calls of this species over its range. The call is a pulsed note of 18-26 pulses with a pulse repetition rate of 82.1-112.1 pulses sec^{-1} and a dominant frequency of about 2153 KHz.

Life history

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

Distribution

Uperoleia tyleri is a coastal species just penetrating south eastern Victoria and extending as far north as Tamworth in N.S.W. (Fig. 77).

Comparison with other species

Uperoleia tyleri is a large species (♂♂ 22-33 mm, ♀♀ 26-34 mm) with maxillary teeth and with a poorly to moderately exposed frontoparietal fontanelle. These features are not shared by congeners. From the toothed species, U. martini, U. marmorata, U. laevigata, U. fusca, 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) with a characteristic lyrate pattern on the dorsum and a prominent heel papilla lacking in congeners. U. fusca shares heavy ventral pigmentation but has a very poorly exposed frontoparietal fontanelle and poorly developed parotoid glands. 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 and approaches the pigmentation of material from Tamworth. The parotoid glands are not hypertrophied as in the type series. Osteologically (Fig. 78) and in external features such as finger and toe webbing and subarticular, palmar and metatarsal tubercles the series, conforms to *U. tyleri*

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 R4413 Maroubra, AM R5285 Maroubra Bay; AM R78649-53, Maroubra; AM R5435, Randwick; AM R18696, Picton Lakes; AM R115560, 8 km N the Oaks on Wallacia Rd.

3.5.21 *Uperoleia capitulata* Davies, McDonald and Corben, 1986

Uperoleia capitulata Davies, McDonald and Corben, 1986, Proc. R. Soc. Vict. 98, p. 163.

Holotype

QM J26428, an adult male collected at Bollon, Queensland (28°02', 147°29') on 22.viii.1975 by G. Czechura.

Definition

A moderate sized species (♂♂ 19-27 mm, ♀♀ 27-28 mm S-V) with a tiny head; relatively smooth dorsum; hypertrophied dermal glands;

maxillary teeth absent; frontoparietal fontanelle poorly exposed; no webbing between the toes; outer metatarsal tubercle rounded and angled moderately acutely to the axis of the foot; carpus of five elements; anteromedial processes of anterior hyale of hyoid slender; ilial crest absent. Advertisement call not known.

Description of holotype

Maxillary teeth absent. Vomerine teeth absent. Snout short, truncated when viewed from above and rounded in profile (Fig. 79). Eye to naris distance greater than internarial span (E-N/IN 1.40). Canthus rostralis inconspicuous and straight. Tympanum not visible externally (Fig. 16). Head small in relation to body (Fig. 79). Fingers long, slender, fringed and unwebbed with prominent subarticular tubercles (Fig. 79). In order of length, 3>4>2>1. Palmar tubercles prominent, that at base of thumb less conspicuous. Hind limbs short, (TL/S-V 0.36). Toes long, moderately fringed, unwebbed with conical subarticular tubercles (Fig. 79). Inner and outer metatarsal tubercles prominent, raised; inner gently rounded, aligned along axis of, and encroaching upon digit 1; outer rounded, angled moderately acutely to axis of foot. Toes in order of length 4>3>5>2>1.

Dorsal surface smooth with hypertrophied parotoid, inguinal and coccygeal glands. Submandibular gland discrete, displaced to anterior face of hypertrophied parotoid gland. Finely fimbriated supracloacal flap. Ventral surface smooth.

Male with unilobular submandibular vocal sac. In preservative, dorsal surface grey with darker chocolate markings. Parotoid, inguinal and coccygeal glands with cream markings. Ventral surface cream with faint dusting of patches of chocolate pigment granules. Pale patches in groin and post femoral regions.

Colour in life (based on SAM R29597)

Ground colour grey with well defined dark grey patches upon the head, scapulae, mid dorsum, and coccygeal region, and narrow transverse bars across the limbs. Faint spectrum orange (Smithe 1975) spots upon the parotoid, inguinal and coccygeal glands and on tips of some small dorsal tubercles. Ventrally whitish with faint brown stipples just behind pectoral region, and on flanks. Throat grey with fine white stipples in male. Pectoral region and ventral thighs unpigmented. Inguinal and femoral patches flame scarlet (Smithe 1975).

Dimensions (in mm)

Snout-vent length 23.8; tibia length 8.5; eye diameter 2.2; eye-naris distance 2.1; internarial span 1.5.

Etymology

From the Latin capitulus meaning having or ending in a small head, alluding to the characteristic feature of this species.

Variation

There are 27 paratypes, 20 ♂♂, 3 ♀♀ and 4 subadults.

Qld: QM J26427 taken with the holotype; J39196 Byanda Station, 20 km WNW Proston, T. Pulsford, 11.i.1981; QM J26416, 1 km N Thargomindah, G. Ingram et al., 24.viii.1975; SAM R29586-7, CAS 160141, QM J45960, 64 km SW Bulloo Downs Hstd, D.G. McGreevy, S. Tickler, 2.x.1976; SAM R29588, QM J45956, Noccundra Hotel, K.R. McDonald, D.G. McGreevy, 30.xi.1975; SAM R29590, QM J45957-8, Boorara Station, 32 km N Hungerford, S. May, late 1976; SAM R29589, Boorara Station, D.G. McGreevy 12.i.1977; SAM R29591, KU205026, King Tank, Ambathala

Nature Reference Site (26°, 145°), K.R. McDonald, D.G. McGreevy 3.v.1979; SAM R29592-5, QM J45959, DPI Swamp, Charleville, P.D. McRae, 10.ii.1986.

N.S.W.: AM R24474, R24479, R24481, R24488, R24492 Nyngan, H.G. Cogger, 11.i.1964; AM R28636-7 between Nyngan and Nevertire, W. McCreaddie, 6.xi.1969.

All paratypes are small-headed, robust specimens with bold dorsal patterning of chocolate on a grey and brown background, and cream dermal glands. Males range from 19-27 mm, females 27-28 mm. Hind limbs are relatively long (TL/S-V 0.37±.02 [♂♂ 0.34-0.40, ♀♀ 0.31-0.36]). Eye to naris distance is greater than internarial span (E-N/IN 1.36±.25 [1.1-2.08]).

Ventral patterning is better developed in some paratypes, but is never more than patches of brown pigment on the anterior half of the body. The dorsum is faintly or moderately rugose in some specimens and hypertrophy of the dermal glands is not always as acute as in the holotype. The snout is sometimes more rounded. Toes rarely show greater fringing than described. The inguinal and post-femoral, light coloured patches are often more obvious than in the holotype. A pale stripe occasionally occurs in the midline of the head.

Osteology (based on SAM R29586)

Skull moderately ossified, sloping anteroventrally. Ossification of sphenethmoid incomplete medially; anterior extremities not extending anteriorly to frontoparietals dorsally; extending about $^1/_3$ posteriorly on length of orbit in ventral view. Prootic not fused with exoccipital. Exoccipital not confluent dorso- or ventromedially. Crista parotica short, stocky, not articulating with otic ramus of squamosal. Very shallow groove of carotid canal on frontoparietals medial to epiotic eminences. Frontoparietal fontanelle poorly exposed, overlain by medially crenate frontoparietals (Fig. 80) extending entire length of orbit. Anterior margin of fontanelle formed by sphenethmoid at level about $^1/4$ posteriorly on length of orbit. Posterior margin undefined because of absence of medial prootic ossification.

Nasals large, approximately triangular, projecting ventrally at lateral extremities, and with slightly concave anteromedial edge (Fig. 80). Poorly separated medially except for posterior $^1/4$ where slight increase in separation present; not in bony or tenuous contact with sphenethmoid or with anterolateral extremities of frontoparietals. Maxillary process of nasal not developed - lateral extremity truncate, widely separated from shallow pars facialis of maxillary which lacks a preorbital process.

Palatines moderately robust, not extending laterally beyond lateral extremities of nasals; very slightly expanded medially, overlying anterior extremities of sphenethmoid along posterior half of proximal third of element (Fig. 80). Parasphenoid robust; cultriform process moderately broad, truncate, reaching anterior edge of sphenethmoid. Alary processes short, moderately broad, not overlain by medial rami of pterygoid. Medial rami of pterygoid short, robust, not in bony contact with prootic region; posterior rami short, broad; anterior rami in long contact with well-developed pterygoid process of palatal shelf of maxillary.

Cartilaginous quadrate present between base of squamosal and quadratojugal. Quadratojugal robust and in firm contact with maxillary. Squamosal shaft robust, zygomatic ramus extremely short; otic ramus moderately long and slender, unexpanded. Maxillary and premaxillary edentate. Palatal shelf moderately deep with well-developed palatine processes, poorly separated medially, and with well-developed pterygoid processes.

Alary processes of premaxillaries slender, inclined medially and slightly anteriorly. Vomers absent. Bony columella present. Pectoral girdle arciferal and robust. Omosternum absent, xiphisternum present. Sternum cartilaginous. Clavicles very slender, curved, closely applied medially. Coracoids moderately robust, widely separated medially, Scapula bicapitate, slightly shorter than clavicles. Suprascapula about $^1/2$ ossified.

Eight non-imbricate presacral vertebrae. Sacral diapophyses poorly expanded. Relative widths of transverse processes III>II=sacrum=IV>V>VI=VII=VIII. Bicondylar sacrococcygeal articulation of urostyle. Well-developed crest extending $^2/3$ length of urostyle. No ilial crest; dorsal prominence small, monticuline; dorsolateral dorsal protuberance (Fig. 81). Pubis calcified.

Humerus with strongly developed anteroproximal crest. Phalangeal formula of hand 2,2,3,3. Carpus with five elements. Moderate torsion; O. radiale and O. ulnare present; O. radiale larger. Both elements articulate with O. radioulna proximally, with each other proximomedially and with large transversely elongate O. centrale postaxiale distally. O. radiale articulates laterally with O. centrale preaxiale (Fig. 82).

O. centrale postaxiale articulates distally with bases of O. metacarpi III, IV and V. Small flange extends proximally from lateroproximal corner. Palmar sesamoid ventromedially (Fig. 82).

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

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. O. tibiale extends to distal end of O. fibulare. 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. Second element lies at base and slightly laterally to O. metatarsus II. Medial element lies at base of O. metatarsus I, articulating also with O. centrale prehallucis. Distal prehallical element elliptic, extending approximately $^1/3$ length of O. metatarsus I (Fig. 82).

Hyoid plate slightly longer than broad. Anteromedial processes of anterior hyale short and slender (Fig. 81). Alary processes of hyoid plate not pedunculate. Posterolateral processes moderately broad, moderately long. Posterior cornua ossified.

Variation

A further five paratypes have been cleared and stained; QM J45958, J45960, SAM R29587, QM J26416, AM R28637.

The nasals are in tenuous contact with the sphenethmoid in AM R28637 and QM J45958. The exposure of the frontoparietal fontanelle varies slightly in the paratypes. Exposure is never less than shown and is sometimes greater. In QM J26416 exposure is increased by contraction of the frontoparietals about $^2/3$ along their length posteriorly.

The pars facialis of the maxillary is slightly deeper than in SAM R29586 in all the other skeletons. The palatines are not expanded medially other than in QM J26416. Vomerine fragments are present medial to the palatines in SAM R29587.

Advertisement calls

The advertisement call of this species is not yet known.

Comparison with other species

Uperoleia capitulata is an untoothed species with a poorly exposed frontoparietal fontanelle, features shared by some U. lithomoda and by U. mimula.

From U. lithomoda and U. mimula, U. capitulata is distinguished by its hypertrophied parotoid glands and relatively smooth dorsum.

From the sympatric untoothed species U. rugosa, U. capitulata is distinguished by its hypertrophied dermal glands and greater exposure of the frontoparietal fontanelle.

Distribution

Uperoleia capitulata is confined to southwestern Qld and northwestern N.S.W., particularly in the Bulloo drainage system (Fig. 83). U. capitulata is sympatric with U. rugosa at some localities.

3.5.22 Uperoleia fusca Davies, McDonald and Corben, 1986

Uperoleia marmorata: Moore 1961, p. 219 (part.); McDonald 1974, p. 2; Czechura 1978, p. 150; McEvoy, McDonald and Searle 1979, p. 176.

Uperoleia laevigata: Ingram and Corben 1975, p. 49.

Uperoleia sp.: Webber and Cogger 1976, p. 76; Thompson 1981, p. 94.

Uperoleia fusca: Davies, McDonald and Corben,1986, Proc. R. Soc. Vict. 98, p. 167.

Holotype

SAM R29596, an adult male collected adjacent to southern boundary of Eungella N.P., 1.2 km along Crediton road from Broken River Crossing Qld (148°30'10", 21°10'15"), by M.J. Tyler and K.R. McDonald on 26.i.1984.

Definition

A moderate sized species (♂♂ 20-28 mm S-V, ♀♀ 23-29 mm S-V) with a smooth dorsum; maxillary teeth present; toes unwebbed; frontoparietal fontanelle unexposed; ventral surface entirely pigmented; carpus of six elements; anteromedial processes of anterior hyale of hyoid absent; ilial crest absent; advertisement call a rasping note of about 20 pulses with a pulse repetition rate of about 68 pulses sec^{-1}.

Description of holotype

Maxillary teeth present. Vomerine teeth absent. Snout moderately short, rounded when viewed from above (Fig. 84), gently sloping posteriorly in profile (Fig. 84). Eye to naris distance very slightly greater than internarial span (E-N/IN 1.1). Nares dorsolaterally positioned. Canthus rostralis inconspicuous and straight. Loreal region straight. Tympanum not visible externally. Fingers moderately long, slender, unfringed, unwebbed with moderately prominent subarticular tubercles but obscure palmar tubercles. In order of length 3>4>2>1 (Fig. 84). Hind limbs moderately long (TL/S-V 0.40). Toes long, very poorly fringed and unwebbed (Fig. 84). In order of length 4>3>5>2>1. Metatarsal tubercles small, inner rounded and flattened on axis of toe 1, outer small and conical, moderately acutely angled to the axis of the foot. Subarticular tubercles small, not very prominent.

Dorsal surface faintly rugose (Fig. 3). Parotoid glands moderately developed, inguinal and coccygeal glands not obvious. Submandibular gland disrupted. Cloacal flap with short fimbriations. Flap in anterior corner of eye. Ventral surface smooth.

Male with unilobular submandibular vocal sac. Dorsum grey in preservative with black and cream mottling. Entire ventral surface, including femoral regions pigmented with chocolate coloured patches of granules. Palmar surface of hand moderately pigmented, plantar surface of foot heavily pigmented. Throat darkly pigmented with paler diamond shaped patch at mandibular symphysis. Small pale post femoral patch. Colour in groin and post femoral patches reddish/orange in life. Nuptial pad unpigmented (Fig. 85).

Dimensions (in mm)

Snout-vent length 23; tibia length 9.3; eye diameter 2.9; eye-naris distance 2.0; internarial span 1.9.

Etymology

From the Latin fuscus meaning dusky, with reference to the ventral pigmentation of the species.

Variation

There are 199 paratypes 192 ♂♂ and 7 ♀♀.

N.S.W.: SAM R12590(12), Wyong, 1.6 km S, 9.6 km W Ulong, F. Parker, H. Ehmann, P. Krauss, 26.i.1971; AM R15505-6 Boolamboyle, R. Mackay; AM R104374, R101331, 11 km from jcn with Pacific Hwy on Palm Grove Rd, Ourimbah, H.G. Cogger, 3.xi.1981; AM R4631-2 Worrell Ck, Nambucca River, W. Clark, 24.i.1910; AM R6301-2 Garavembi near

Macksville on Nambucca River (30°44', 152°59'), D.B. Fry and H.E. Smart, 1913; AM R53987-93, R53995-6 Erina, N. Dankers, 1974; AM R68438, 24.5 km N Colo Heights, Putty Rd (33°13', 150°40'), P. Rankin and P. Greer, 15.xi.1975; AM R70200, 12.8 km along road to Wisemans Ferry from Kariong, R. Wellington, 25.i.1978; AM R115583 Whiteman Creek, S.J. Copland, 6.i.1948; NMV D25047-8, D25056-7 Ourimbah Creek, M.J. Littlejohn, A.A. Martin, P.A. Rawlinson, 1.xi.1964; SAM R29597-8 same locality, M. Mahony, 3.xi.1981; AM R76508 same locality, D. O'Brien; NMV D25049-55, 10.4 km S Gloucester, M.J. Littlejohn, A.A. Martin, P.A. Rawlinson, 29.x.1964; NMV D43207-10, 2.6 km N Coff's Harbour, G.F. Watson, D.F. Gartside, 11.xi.1972; NMV D25044-6 Nymboida, M.J Littlejohn, 27.x.1964; NMV D43223, 17.6 km S Grafton, G.F. Watson, D.F. Gartside, 8.xi.1972; NMV D43247-8, D42679, D42681, 4.8 km SE Lower Creek on Kempsey, Armidale Rd, G.F. Watson, D.F. Gartside, 12.xi.1972; QM J40431, J40435, Undercliff, G. Czechura.

Qld: SAM R29599-602, QM J45961 collected with the holotype; SAM R29603-7 same locality, K.R. McDonald, 5.i.1976; KU 205027-8, same locality K.R. McDonald, 4.ii.1975; AMNH 124732, same data, 28.i.1975; QM J31556-62, J31582 Eungella, C. Corben; AM R53809-11, 16 km S Eungella (21°17', 148°36'), J. Barker, G. Grigg, 30.xii.1973; SAM R29608-11, QM J45962, CAS 160142-3, MCZ 108612-3, Bellthorpe S.F. (26°44', 152°36'), K.R. McDonald, J.S. McEvoy, D.G. Crossman, 27.ii.1976; BMNH 1986.203 same locality, K.R. McDonald, P. Amos, 24.xi.1976; SAM R 29612-3 same locality, K.R. McDonald, Jan. 1979; QM J45963-65, Jimna Rd nr Yielo turnoff, Sunday Creek S.F., K.R. McDonald, J.S. McEvoy, 5.i.1977; SAM R29614-6 Crows Nest N.P., K.R. McDonald, 14.i.1974; SAM R29617 Mt Glorious, C.J. Limpus, K.R. McDonald, 20.ii.1974; SAM R29618, 2 km from Sunday Creek turnoff along Jimna/Bellethorpe rd (152°29', 26°42'), K.R. McDonald, 13.xii.1978; SAM R29619, Moreton Is., nr Blue Lagoon swamp, K.R. McDonald, 16.ix.1976; QM J10901-2, Mt Nebo, S. Breedon, Feb. 1961; QM J10900, J12309, J12294, J12323, same data, 19.ii.1964; QM J42609, J42576, J42614, below Bombana N.P., Mt Nebo Rd (27°24', 152°47'), C. Corben, A. Smyth, 31.x.1973; QMJ 19942, J19947, J19952, J19965, Dunwich, North Stradbroke Is., I.R. Straughan; QM J24088, Brown Lake, North Stradbroke Is., G. Ingram, G. Czechura, 5.iv.1974; QM J27563 Blue Lake, North Stradbroke Is., D. Grace, 2.i.1976; QM J27905, same locality, A. Elliot, M. Hillier, 10.v.1976; QM J40020 Tortoise Lagoon, Blue Lake area (21°08', 148°29'), L. Kading, 22.x.1981; QM J42569, J42572, J42583, J42606-7 Brown Lake, North Stradbroke Is., C. Corben <u>et</u> <u>al</u>., 8.ix.1973; QM J42593 same data, 15.ix.1973; QM J19925, J19927, J19930, J19936, J19959, J19961, J19966 Slack's Creek, Pacific Hwy, I.R. Straughan, 9.x.1961; QM J40433 Cooloola, G. Czechura, 1.i.1974; QM J27477, J27475 Lake Cooloomera, Cooloola, C. Corben, A. Smyth, 21.xi.1973; QM J42586-90, J42610, J42612, same locality, G. Ingram, 14.vii.1973; QM J27481 same locality, G. Ingram, G. Czechura, 30.xii.1973; QM J42564, J42566-68, J42574-5, J42578-9, J42581, J42585, J42591-2, J42594, J42596, J42599-603, J42611, same locality, C. Corben <u>et</u> <u>al</u>., 15.ix.1973; QM J39315 Poona Lake, Cooloola N.P., G. Monteith, Jan. 1981; QM J42565, J42570-1, J42573, J42580, J42584, J42595, J42604-5, J42608, J42613 Lost World (28°15', 153°07'), C. Corben <u>et</u> <u>al</u>., 28.vii.1973; QM J42563, J42597-8, J42582, Calam Rd, Runcorn (27°36', 153°04') C. Corben, G. Ingram, 10.x.1973; QM J40434 Maleny, G. Czechura, Feb. 1974; QM J40489-90 same data, 13.iv.1974; QM J40486-7 same data, April 1974; QM J40484 same data, 26.ix.1974; QM J41533, Pine Creek Timber Reserve south of 'Turkey' near Miriamvale, T. Pulsford, 10.i.1983; QM J19938, J19953, J19957, Mt Tamborine, I.R. Straughan, 27.ix.1964; QM J18817, J18825 Moggill Rd, 8 km past Kenmore P.O., Brisbane, I.R. Straughan and A.K. Lee, 26.i.1961; QM J18837, Gold Creek Rd, 1.6 km past Brookfield turnoff, Brisbane, A.K. Lee, 26.ii.1961; QM J18822 Sampsonvale, A.K. Lee, 13.viii.1961; QM J29280 Kilcoy, G. Czechura, Nov. 1976; QM J19956 Warrawee, I.R. Straughan, 1.iii.1964; QM J19939, J19941 Brookfield Showground, Moggill Rd, Brisbane, A.K. Lee, 9.x.1961; QM J19943, 16 km N Gayndah, I.R. Straughan, 17.x.1963; QM J40315 Deepwater Rd, south of township '1770', T. Pulsford, 1.iv.1972; QM J30606 Ravensbourne, R. Sadlier, 7-8.i.1978; QM J18832, 3.2 km N Tamborine Village on Tamborine/Waterford Rd, I.R. Straughan, 12.ix.1964; QM J12721 Eidsvold, T.L. Bancroft, 30.viii.1912; QM J19958, 16 km N Cooroy, I.R. Straughan, 17.x.1963; AM R47734, R47736-7 Eurimbula E of Miriamvale, P. Webber.

Many of the male paratypes exhibit well-defined glandular, unpigmented nuptial pads (Fig. 85). Pigmentation of the ventral surface of the hands makes the pads particularly prominent in this species. Paratypes are all long-legged frogs (TL/S-V 0.38±.02 [0.35-0.42]). Eye to naris distance approximates internarial span in most paratypes (E-N/IN 1.18±.17 [0.88-1.67]). The gentle posterior slope of the snout of the holotype in lateral view, is characteristic of all paratypes.

All but three of the paratypes lack a distinct palmar tubercle at the base of the thumb. In the exceptions, the tubercle is not prominent. Only four paratypes have toe fringing greater than in the holotype.

Dorsal patterning varies; some specimens are uniformly dark slate and others have bold chocolate patterning on a grey or brown background;

many specimens exhibit an indistinct triangular preocular patch characteristic of the other toothed eastern Australian congeners. A pale midvertebral stripe occurs occasionally and many paratypes exhibit heavier ventral pigmentation than the holotype. Ventral pigmentation ranges from faint suffusions on a cream background to light speckles on a chocolate or slate background. Fading of pigmentation in preservative is common in this genus. Of the specimens with lighter ventral pigmentation, the pigment is spread uniformly across the entire ventral surface.

In life there is a dichotomy in inguinal and post-femoral colour. Where recorded (AM R6302, NMV D43247-8, SAM R29608-11) thigh colour at the southern part of the range of the species is yellow but in the northern part of the range is reddish/orange. Both thigh colours were recorded in specimens calling at a pool in the Conondale Ranges (SAM R29608-9, yellow thighed and SAM R29610-11 reddish/orange). The calls of these two forms were indistinguishable to the ear (K.R. McDonald pers. comm.) and there are no morphological distinctions between the four specimens.

Osteology (based on SAM R29603)

Skull well ossified, sloping slightly anteroventrally. Ossification of sphenethmoid complete medially, dorsally extends to posterior extremities of nasals, ventrally extends about $^1/3$ length of orbit posteriorly. Prootic not fused with exoccipital (Fig. 86). Epiotic eminences prominent. Exoccipital not ossified dorsomedially or ventromedially. Crista parotica short, stocky, not articulating with long otic ramus of squamosal. Shallow groove of carotid canal present posteriorly on frontoparietals. Frontoparietal fontanelle exposed only as a median slit between the well-ossified frontoparietal elements. Anterior extremity about level of anterior ramus of pterygoid. Posterior extremity undefined.

Nasals moderately ossified, triangular, closely applied medially with slight separation posteriorly (Fig. 86); in tenuous contact with sphenethmoid. Maxillary process of nasal poorly developed, not in bony contact with well-developed preorbital process of shallow pars facialis of maxillary. Palatines moderately broad, slightly reduced and truncated laterally from level of dorsal extremity of preorbital process of pars facialis of maxillary (Fig. 86); angled at about 45° to overly sphenethmoid medially.

Parasphenoid robust. Cultriform process moderately broad, not reaching level of palatines. Alae robust, deep, not angled to cultriform process; not overlapped nor reaching extremity of medial rami of pterygoid. Medial ramus of pterygoid slender, acuminate, not in bony contact with prootic region. Posterior ramus moderately long, slender; anterior ramus in moderately long contact with moderately-developed pterygoid process of palatal shelf. Small cartilaginous quadrate present at base of squamosal and quadratojugal. Quadratojugal robust, in firm contact with maxillary. Squamosal shaft robust, short knobbed zygomatic ramus, long unexpanded otic ramus.

Maxillary and premaxillary dentate. Palatal shelf moderately deep with well-developed palatine processes, not abutting medially, and poorly to moderately developed pterygoid process. Alary processes of premaxillaries moderately slender, poorly bifurcated dorsally, slightly curved posteriorly. Pars facialis of maxillary deep then stepped down to become shallow. Preorbital process prominent. Remnant fragments of vomers on edges of choanae and extremities of palatines (Fig. 86). Bony columella present.

Pectoral girdle arciferal and robust. Omosternum absent, xiphisternum present. Sternum cartilaginous. Clavicles slender, curved, closely applied medially. Coracoids robust, widely separated medially. Scapula bicapitate, about same length as clavicles. Suprascapula about $^1/2$ ossified.

Eight non-imbricate presacral vertebrae. Sacral diapophyses poorly expanded. Left ilium abnormally enlarged at distal end.

Relative widths of transverse processes III>II=sacrum=IV>V=VI=VII=VIII. Crest on urostyle for about $^1/3$ its length.

Ilium with no dorsal crest. Dorsal prominence very small slightly rounded with rounded posterolateral dorsal protuberance (Fig. 87). Pubis calcified.

Humerus with strongly developed anteroproximal crest. Phalangeal formula of hand 2,2,3,3. Distal tips of terminal phalanges knobbed.

Carpus of six elements; moderate torsion. O. ulnare and O. radiale present. O. radiale larger of two; both articulate with O. radioulna proximally and with each other medially. Distally both articulate with large transversely elongate O. centrale postaxiale. O. radiale articulates laterally with O. centrale preaxiale (Fig. 88). O. centrale postaxiale articulates distally with bases of O. metacarpi III, IV and V. Moderately well-developed flange extends slightly laterally from lateroproximal corner. Palmar sesamoid anteroventrally.

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

Phalangeal formula of foot, 2,2,3,4,3. O. tibiale and O. fibulare elongated elements fused at either end. O. tibiale extends as far as distal end of O. fibulare. 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. Second element lies at base of O. metatarsus II. Medial element lies at base of O. metatarsus I, articulating also with O. centrale prehallucis. Distal prepollical element slender and short extending for about $^1/3$ length of O. metatarsus I (Fig. 88).

Hyoid plate slightly longer than wide. Anterior hyale expanded anteromedially (Fig. 87). Alary processes not pedunculate. Posterolateral processes moderately slender and elongate. Posterior cornua ossified. Some medial calcification of plate between posterior cornua.

Variation

Seventeen of the paratypes have been examined for osteological variation: SAM R29606-7, R29599, R29612-3, R29619, KU 205027, QM J18832, J19927, J27475, J42579, J42598, J42606, J42608, NMV D25045, D25048, D43208.

Medial ossification of the sphenethmoid is incomplete in all of these paratypes, a factor indicating the apparent age of the described specimen.

Tenuous contact between the nasals and the sphenethmoid is exhibited by only two paratypes. Separation of the nasals posteromedially varies: in about $^1/3$ of the specimens the separation is more extreme and in three specimens it is less than described. The epiotic eminences are extremely prominent in all paratypes except the subadult SAM R29619.

The nature of the pars facialis of the maxillary varies - in some paratypes the shelf is deep initially and then steps down to be shallow anteriorly, in others the decline in depth is gradual and in one specimen (NMV D25048) it remains deep for its entire length.

The alary processes of the premaxillaries are usually moderately broad, but occasionally are broad. Bifurcation of the dorsal extremity varies considerably. The palatines are uniformly truncated laterally. The presence of vomerine fragments varies - they occur in about $^1/3$ of the paratypes but the palatal elements are not always apparent bilaterally and in QM J42606 they are relatively large.

In two specimens, the alae of the parasphenoid are curved posterolaterally.

The anterior extremities of the frontoparietals are reduced medially and the frontoparietal fontanelle is uniformly barely or unexposed except in the subadult SAM R29619.

Advertisement calls

Advertisement calls of five individuals were recorded at the type locality on 26.i.1984. Call parameters are shown in Table 4 and an advertisement call is shown in Fig. 89. The call is a short rasping note with a duration of about 300 ms pulsed at about 68 pulses/sec. The dominant frequency lies at about 2700 Hz.

Habitat

The type locality, was a small pond, 30x30 m surrounded by dry ground covered with sparse low grass to a height of little more than 15 cm. Frogs were calling at the base of the grass (M.J. Tyler Field notes).

Comparison with other species

Uperoleia fusca is a moderate sized species (males 20-28 mm S-V, females 23-29 mm S-V), with maxillary teeth and with a poorly exposed frontoparietal fontanelle. These features are shared by *U. marmorata* and *U. laevigata*. From *U. marmorata*, *U. fusca* is separated by size (*U. marmorata*, ♂ 30.1 mm) and by its narrower snout (E-N/IN 1.18±.17 in *U. fusca*, 1.56 in *U. marmorata*).

From *U. laevigata*, *U. fusca* is separated by total pigmentation of the ventral surface (absent in *U. laevigata*) and by call (the call of *U. fusca* has about 11-28 pulses whereas that of *U. laevigata* is a longer call of 32-56 pulses (Davies and Littlejohn 1986)).

Distribution

Uperoleia fusca is a coastal species ranging from Gloucester in N.S.W. (32°01', 151°58') to Eungella in Qld (20°55', 148°30') (Fig. 90). Toothed specimens from Atherton held by the Queensland Museum may be referrable to this species, but unfortunately are in such poor condition that identification is impossible.

3.5.23 *Uperoleia littlejohni* Davies, McDonald and Corben, 1986

Uperoleia littlejohni Davies, McDonald and Corben, 1986, Proc. R. Soc. Vict. 98, p. 174.

Holotype

QM J45949 (formerly NPWS N56317), an adult male collected on Occupational licence 410, Burra Range, Qld (20°33', 145°05') by B.C. Lawrie on 14.xii.1983.

Definition

A moderately large species (♂♂ 22-31 mm S-V, ♀♀ 23-29 mm S-V) lacking maxillary teeth; possessing unwebbed and poorly fringed fingers and basal to no webbing but fringed toes. Dermal glands are prominent. Frontoparietal fontanelle moderately extensive; carpus of six elements; anteromedial processes of anterior hyale of hyoid slender; ilial crest absent. Advertisement call not known.

Description of holotype

Maxillary teeth absent. Vomerine teeth absent. Snout short, truncated when viewed from above and in profile. Eye to naris distance greater than internarial span (E-N/IN 1.25) (Fig. 91). Canthus rostralis poorly defined, straight. Tympanum not visible externally (Fig. 91).

Fingers moderately long, broad, unwebbed and poorly fringed with very prominent subarticular tubercles (Fig. 91). In order of length 3>4>2>1. Palmar tubercles large and prominent. Hind limbs moderately long (TL/S-V 0.34). Toes moderately long, broadly fringed with basal webbing. Toes in order of length 4>3>5>2>1. Metatarsal tubercles very large, raised and prominent; outer elongate, truncate and angled to long axis of foot; inner acutely angled along toe 1 (Fig. 91).

Dorsal surface very faintly tubercular. Parotoid, inguinal and coccygeal glands moderately developed. Submandibular gland disrupted. Cloacal flap slightly fimbriated. Ventral surface faintly granular.

Male with unilobular submandibular vocal sac; unpigmented glandular nuptial pad on thumb. Dorsum grey in preservative with strong chocolate markings, and pinkish-tipped tubercles. Parotoid glands pinkish and inguinal and coccygeal glands with disrupted pinkish patches. Inguinal and post femoral patches white. Ventral surface whitish with suffusions of brown pigment. Throat grey with white granules.

Dimensions (in mm)

Snout-vent length 27.6; tibia length 9.5; eye diameter 3.0; eye-naris distance 2.0; internarial span 1.6.

Etymology

The species is named for Murray J. Littlejohn of the University of Melbourne in recognition of his contributions to the study of herpetology in Australia and of Uperoleia in particular.

Variation

There are 26 paratypes, 24 ♂♂ and 2 ♀♀. All are from Qld. QM J38877-80, 22.4 km W Pentland (20°40', 145°18'), G. Ingram, G. Czechura 15.i.1981; QM J45950 Epping Forest N.P. near Clermont (22°23', 146°42'), G. Porter, D.G. Crossman 12.ix.1984, SAM R29620-1 Gorge Ck (19°33', 143°56'), A. Taplin 18.iii.1984; QM J38883, 18.1 km W Torrens Ck, G. Ingram, G. Czechura 15.i.1981; QM J45953 Battery Station, Snake Creek (145°39', 19°27'), B.C. Lawrie 2.xii.1981; SAM R29622, QM J45952 Caerphilly Station (21°03', 146°05'), B.C. Lawrie 3.iii.1981; KU 205029, CAS 160144, MCZ 108614, QM J45954, SAM R29623 Strathtay (20°57'144°12'), B.C. Lawrie 24.viii.1984; QM J45951, SAM R29624 Amber Station, about 1.6 km from French's Crossing on Lynd River, K.R. McDonald, S.K. Reardon 15.i.1980; SAM R29625-6 Walsh River, Watsonville (17°21', 145°18'), J.W. Winter 24.xii.1973; QM J43154-5 Walsh River, Jamie Creek, Watsonville, 15.xii.1973;

QM J38915 Crest of Warrigal Ra, 16.8 km E Cloncurry, G. Ingram, G. Czechura, 18.i.1981; QM J29874, 96 km from Townsville on Charters Towers Rd, G. Ingram, D. Miller 22.xii.1976; AM R53930, R53932, 6.4 km W Herberton (17°23', 145°23'), J. Barker, G. Grigg 10.i.1974.

All paratypes are moderately robust, slate frogs with strong back patterning and conspicuous dermal glands. Paratypes have moderately long limbs (TL/S-V 0.35±.02 [0.32-0.41]). Males range 21.6-30.7 mm S-V and females 23.2-28.8 mm S-V. Eye to naris distance is always greater than internarial span (E-N/IN 1.35±.25 [1.01-1.64]). The dorsum is more rugose in a few paratypes and the dermal glands, particularly the coccygeal glands, are more prominent. The parotoid glands are extremely well developed in the larger female (QM J45950). Most of the paratypes, particularly those that are relatively freshly preserved, show the characteristic salmon pink colouration on the dermal glands and on the tips of dorsal tubercles. The ventral surface is usually a very pale grey with varying suffusions of brown pigment. A pale midvertebral stripe is apparent in some specimens.

<u>Osteology</u> (based on SAM R29623)

Skull poorly ossified, sloping slightly anteroventrally. Sphenethmoid not ossified medially. Small portion of sphenethmoid ossified posteriorly to anterior extremity of cultriform process of parasphenoid extending about $^1/3$ to $^1/2$ of length of orbit in ventral view. Prootic not fused with exoccipital. Exoccipital not ossified dorso or ventromedially. Crista parotica short and stocky, not overlain laterally by otic ramus of squamosal. Very shallow groove of carotid canal posterolaterally on frontoparietals. Frontoparietal fontanelle moderately extensively exposed, vase shaped (Fig. 92).

Anterior margin defined by sphenethmoid at level about $^{1}/4$ posterior on length of orbit. Posterior margin undefined because of lack of medial ossification of exoccipitals.

Nasals moderately large, approximately triangular; directed ventrally on lateral extremities; slightly crescentic on medial anterior edge; in tenuous contact with sphenethmoid posteromedially. Not in contact with frontoparietals. Maxillary processes of nasals truncate, not in contact with moderately shallow pars facialis of maxillary.

Palatines moderately slender, slightly expanded medially, angled acutely to sphenethmoid (Fig. 92) and totally underlying nasals. Parasphenoid robust. Cultriform process moderately broad, long, anterior extremity divided into digitiform processes (Fig. 92) extending to level of medial extremities of palatines. Alae moderately narrow, at right angles to cultriform process, not overlapped by medial rami of pterygoids.

Medial rami of pterygoids short, acuminate, not in bony contact with prootic region. Posterior ramus short, moderately broad. Anterior ramus in long contact with well-developed pterygoid process of palatal shelf of maxillary. Cartilaginous quadrate between base of squamosal and quadratojugal.

Quadratojugal robust, in firm contact with maxillary. Shaft of squamosal stocky. Zygomatic ramus not developed; otic ramus long, unexpanded.

Maxillary and premaxillary edentate. Palatal shelf moderately deep with well-developed palatine processes not abutting medially. Pterygoid process well developed. Alary processes of premaxillaries broad at base, narrowing dorsally, bifurcate dorsally, inclined slightly medially.

Pars facialis of maxillary moderately shallow; no preorbital process developed. Vomers absent. Bony columella present.

Pectoral girdle arciferal and robust. Omosternum absent, xiphisternum present. Sternum cartilaginous. Clavicles slender, curved, closely applied medially. Coracoids robust, poorly separated medially. Scapula about equal in length to clavicles. Suprascapula about $^1/2$ ossified.

Eight nonimbricate presacral vertebrae. Sacral diapophyses poorly expanded. Relative widths of transverse processes III>II>sacrum>IV=V=VI=VII>VIII. Transverse processes on vertebra IV are curved posteriorly.

Bicondylar sacrococcygeal articulation. Well developed crest extending about $^1/2$ length of urostyle. Ilial crest absent. Dorsal prominence monticuline; dorsal protuberance mediolateral and prominent (Fig. 93). Pubis calcified.

Humerus with well-developed anteroproximal crest. Phalangeal formula of hand 2,2,3,3. Carpus of six elements. Moderate torsion. O. radiale and O. ulnare present. O. radiale larger of two. Both articulate with O. radioulna proximally and with each other proximomedially. Distally both articulate with large transverely elongate O. centrale postaxiale. O. radiale articulates laterally with O. centrale preaxiale.

O. centrale postaxiale articulates distally with bases of O. metacarpi III, IV and V. Small rounded flange extends proximally onto lateral surface of O. ulnare from lateroproximal corner. Palmar sesamoid ventromedially (Fig. 94).

O. centrale preaxiale articulates laterally with O. radiale, distally with O. centrale postaxiale and with carpal elements of

O. distale carpale 2 and 3, and laterally with basal prepollical element (Fig. 94). Terminal phalanges knobbed.

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

O. tibiale and O. fibulare elongate, fused at each end. O. tibiale extends to distal end of O. fibulare. Three distal tarsal elements. Lateral element largest, at base of O. metatarsus III; extends laterally to articulate with medioproximal side of base of O. metatarsus IV and medially to base of O. metatarsus II. Second element at base of O. metatarsus II. Medial element at base of O. metatarsus I, articulating with O. centrale prehallucis (Fig. 94). Distal prehallical element broad and elongate extending greater than $^1/2$ length of O. metatarsus I (Fig. 94).

Hyoid plate about as broad as long. Alary processes not pedunculate, moderately broad. Posterolateral processes moderately long and slender. Anteromedial processes of anterior hyale slender. Posterior cornua ossified (Fig. 93).

Variation

Nine additional paratypes have been cleared and stained. SAM R29623, R29622, R29624, QM J35427, J45953, J29874, J38880, J38883, AM R53930.

None of the cleared and stained specimens have a preorbital process on the pars facialis of the maxillary. The pars facialis is usually slightly deeper than in the described specimen and occasionally sculptured (QM J29874, SAM R29622). The nasals are not in tenuous contact with the sphenethmoid in QM J38880 and AM R53930, but overly the sphenethmoid in the two very large specimens SAM R29622, QM J35427. The frontoparietal fontanelle exposure is as described in all but the two large specimens in which the medial constriction is accentuated and the degree of exposure is less overall.

Ventrally the acute angle of the palatines is constant, but the digitiform nature of the extremity of the cultriform process of the parasphenoid is not always present. In one specimen (SAM R29624) the alae of the parasphenoid are angled slightly posterolaterally.

Advertisement calls

The advertisement call of this species is not yet known.

Comparison with other species

Uperoleia littlejohni is an untoothed species with a moderately widely-exposed frontoparietal fontanelle, features shared by *U. crassa*, *U. talpa*, *U. russelli*, *U. glandulosa*, *U. borealis*, *U. arenicola*, *U. inundata* and *U. orientalis*.

From *U. talpa*, *U. russelli*, *U. borealis* and *U. orientalis*, *U. littlejohni* is distinguished by the lack of moderate webbing between the toes. From *U. glandulosa*, *U. littlejohni* is distinguished by the absence of ventral pigmentation, other than faint suffusions and by the absence of lyrate markings on the dorsum and of a well developed preorbital process of the pars facialis of the maxillary.

From *U. inundata*, *U. arenicola* and *U. crassa*, *U. littlejohni* is distinguished by its strong markings on the dorsum, and by the absence of a preorbital process on the pars facialis of the maxillary.

Distribution

Uperoleia littlejohni is known only from north eastern and north central Queensland between latitudes 17°-21° (Fig. 95).

3.5.24 Uperoleia mimula Davies, McDonald and Corben, 1986

Uperoleia marmorata: Parker and Tanner 1971, p. 5.

Uperoleia sp.: Menzies 1977, p. 21; Zweifel and Tyler 1982, p. 764.

U. lithomoda: Tyler and Davies 1984, p. 123 (part.).

Uperoleia mimula: Davies, McDonald and Corben, 1986, Proc. R. Soc. Vic. 98, p. 178.

Holotype

QM J45943 (formerly NPWS N28874), an adult male collected at Lakefield Ranger Station (14°56', 144°12') by K.R. McDonald and B.J. Lyon on 25.ii.1981.

Definition

A small to moderate sized species (♂♂ 20-28 mm S-V, ♀♀ 21-28 mm S-V) with a faintly rugose dorsum; moderately well developed inguinal glands; toe webbing absent or basal; maxillary teeth absent; poorly to moderately exposed frontoparietal fontanelle; carpus of six elements; anteromedial processes of anterior hyale of hyoid slender; ilial crest absent; male advertisement call a pulsed click of 4-5 pulses with a pulse repetition rate of about 79 pulses sec^{-1}.

Description of holotype

Maxillary teeth absent. Vomerine teeth absent. Snout short, slightly pointed when viewed from above (Fig. 96), rounded in profile (Fig. 96). Eye to naris distance greater than internarial span (E-N/IN 1.36). Canthus rostralis inconspicuous and straight. Nostrils dorsolateral, surrounded by elevated lip (Fig. 96). Tympanum not visible externally (Fig. 30).

Fingers moderately long, slender, unwebbed, very slightly fringed with prominent subarticular tubercles. In order of length 3>4=2>1 (Fig. 96). Palmar tubercles moderately large but not prominent. Hind limbs short (TL/S-V 0.34). Toes long, moderately fringed with trace of basal webbing. Toes in order of length 4>3>5>2>1 (Fig. 96). Metatarsal tubercles prominent. Inner rounded, lying along axis of toe 1; outer rounded, acutely angled to long axis of foot.

Subarticular tubercles moderate, slightly conical. Dorsal surface tubercular. Parotoid glands moderately developed; inguinal glands well developed; coccygeal glands prominent. Submandibular gland small, not discrete. Cloacal flap tiny, not fimbriated. Ventral surface faintly granular. Male with unilobular submandibular vocal sac. Cream glandular nuptial pad on thumb.

Dorsum grey in preservative with faint chocolate patterning and cream tipped tubercles. Prominent midvertebral stripe. Inguinal glands with cream patches along length. Inguinal and femoral patches scarcely detectable, cream. Ventral surface cream with very faint stippling of pigment. Throat stippled with grey.

Colour in life (based on SAM R29634)

Inguinal and thigh patches flame scarlet (Smithe 1975). Ground colour dull brown with dark chocolate patches upon the head, dorsum and as narrow transverse bars across the limbs. Faint sandy patches upon the parotoids and flanks. Ventrally, densely stippled with dull grey and cream. Throat dark grey in males.

Dimensions (in mm)

Snout-vent length 19.9; tibia length 6.7; eye diameter 2.3; eye to naris distance 1.5; internarial span 1.1.

Etymology

From the Latin *mimula* meaning an actor or mimic, with reference to the similarity in morphology and call of this species to its sympatric congener *U. lithomoda*.

Variation

There are 135 paratypes; 125 ♂♂, 7 ♀♀ and 3 subadults.

Qld: SAM R29627 (formerly NPWS N15605) Lannercost S.F., K.R. McDonald, P. Minton, 16.ii.1984; SAM R29628 Townsville Common, B.J. Lyon, 9.iii.1977; SAM R29629-30 Townsville Common, C.J. Limpus, K.R. McDonald, 10.ii.1977; SAM R29631-40, QM J45946 Townsville Common, K.R. McDonald, 25.xi.1985; QM J45945 Pine River Bay, 22 km NW Rocky Point, Weipa, J.W. Winter, 13.iii.1983; SAM R29641 (formerly NPWS N28552) Bazant Outstation, Lakefield N.P., K.R. McDonald, B.J. Lyon 23.ii.1981; KU 20531, SAM R29642 Weipa, K.R. McDonald 3.iii.1981; SAM R29643 Bamaga, B.J. Lyon, C.J. Limpus 14.xii.1976; MCZ 108615, CAS 160145, AMNH 124733, QM J45948, SAM R29644-5, KU 20530 Battery Station nr Snake Creek (19°27',145°39'), B.C. Lawrie 3.xii.1981; QM J45944 same data, 2.xii.1981; QM J45947 Pajingo Station (20°47', 146°11') B.C. Lawrie 29.i.1981; SAM R29646 Base of Bluewater Range, K.R. McDonald 3.x.1983; AM R53860-1 Davies Creek Rd, Emerald Creek, 20.8 km SE Mareeba, J. Barker and G. Grigg 2.i.1974; AM R53931, 6.4 km W Herberton, J. Barker and G. Grigg 10.i.1974; AM R62684-5, R62687 Sawmill at Weipa, H.G. Cogger, E. Cameron, P. Webber 8.vii.1977; AM R46278, R46280, R46282-3, R46287 Prince of Wales Is, Torres Strait, P. Webber, E. Cameron, Young 7.ii.1975; AM R46353-92 same data 1.ii.1975; AM R46436-40 same data 11.ii.1975; AM R46460-66 same data 13.ii.1975; AM R46594 same data 15.ii.1975; AM R46931-36, R46938-43 Moa (or Banks) Is, Torres Strait, Webber, Cameron and Young 25.ii.1975; AM R46745-55 same data 21.ii.1975; QM J40234 Weipa, G. Ingram 18.iii.1982; AM R59167-73 Horn Is, Torres Strait, H. Heatwole, 26.xii.1976; AM R59136 same data, 25.xii.1976; QM J40235, J40247 SW North Camp 'Beagle' via Weipa (13°05', 141°57'), G. Ingram 18.iii.1982; QM J42534-5, J42537, 20.8 km, W Cooktown, C. Tanner 1.vi.1974; QM J38271-2 Silver Plains Hstd (13°58', 143°22'), J. Winter *et al*. 15.xii.1978; QM J19859, 4.8 km E Dimbulah, I.R. Straughan; SAM R29647 Lake Louisa (19°54', 144°15'), S. Garnett 18.viii.1984.

All paratypes with the exception of some material from Battery Station (largest measurements in the ranges), are small, not very robust frogs (males 19.9-28.0 mm, females 20.9-28.4 mm) with short hind limbs (TL/S-V 0.34s0.1 [0.31-0.36]). Eye to naris distance is usually not much greater than internarial span (E-N/IN 1.35±.19[1.00-1.82]). Dermal glands vary in prominence and coloration. Most of the paratypes from Torres Strait tend to have less well developed and darker dermal glands, although they have consistently lighter tipped tubercles on the dorsum. Many paratypes have fine suffusions of pigment on the ventral surface. Some paratypes have slightly more truncate snouts than the holotype and toe fringing is slightly greater in others. Basal webbing is apparent in very few paratypes. Cream inguinal patches are well developed in many specimens. Material from Townsville Common has granular ventral skin.

Osteology (based on SAM R29641)

Skull poorly ossified, sloping anteroventrally. Sphenethmoid not ossified medially; small portion ossified posteriorly to distal $^2/3$ of palatines and extending about $^1/3$ of length of orbit in ventral view. Prootic and exoccipital not fused. Exoccipital not ossified dorsomedially or ventromedially. Crista parotica short, stocky, not articulating with otic ramus of squamosal. Shallow groove for carotid canal present on frontoparietals medial to prominent epiotic eminences. Anterodorsal surface of epiotic eminences expanded into small calcified protuberance. Frontoparietal fontanelle exposed for anterior $^2/3$ as moderately wide slit and for posterior $^1/3$ as larger incomplete ovoid area. Anterior margin of fontanelle at level of anterior extremities of frontoparietals (Fig. 97). Posterior margin undefined because of lack of medial ossification of exoccipital. Orbital edges of frontoparietal straight, slightly angled posterolaterally.

Nasals moderately well ossified, curved ventrally on lateral extremities and with crescentic medial anterior edge; widely separated posteromedially (Fig. 97). Nasals not in bony contact with sphenethmoid or frontoparietals. Maxillary process of nasal moderately acuminate, widely separated from well-developed preorbital process of shallow pars facialis of maxillary.

Palatines slender, slightly expanded medially, tapered laterally; reduced laterally, not extending beyond maxillary processes of nasals. Parasphenoid robust with long, moderately slender cultriform process reaching between medial extremities of palatines. Alae moderately short, moderately slender, not overlain by medial ramus of pterygoid.

Medial ramus of pterygoid moderately long, acuminate, not in bony contact with prootic region; posterior ramus short, broad; anterior ramus expanded anteriorly, in long contact with moderately well-developed pterygoid process of palatal shelf of maxillary. Cartilaginous quadrate present at base of squamosal and quadratojugal. Quadratojugal robust, in firm contact with maxillary. Squamosal shaft robust, zygomatic ramus minute; otic ramus short, unexpanded.

Maxillary and premaxillary edentate. Palatal shelf moderately deep with well-developed palatine processes not abutting medially. Pterygoid process moderately well-developed.

Alary processes of premaxillaries slender, bifurcate, inclined posteromedially. Vomers absent. Bony columella present (Fig. 97).

Pectoral girdle arciferal and robust. Omosternum and xiphisternum present. Sternum cartilaginous. Clavicles slender, curved, poorly separated medially. Caracoids robust, moderately separated medially. Scapula bicapitate, about same length as clavicles. Suprascapula about $^1/3$-$^1/2$ ossified.

Eight non-imbricate presacral vertebrae. Sacral diapophyses poorly expanded. Relative widths of transverse processes III>IV>sacrum>II=V=VI>VII>VIII. Urostyle bicondylar with dorsal crest extending approx. $^1/2$ its length. Ilial crest absent. Dorsal prominence wedge shaped, very prominent. Dorsal protuberance conical, anterolateral and prominent (Fig. 98).

Humerus with strongly developed anteroproximal crest. Phalangeal formula of hand 2,2,3,3. Carpus of six elements; considerable torsion. O. radiale and O. ulnare present. O. radiale larger of two. Both elements articulate with O. radioulna proximally and with each other proximomedially. Distally both articulate with large transversely elongated O. centrale preaxiale.

O. centrale postaxiale articulates distally with bases of O. metacarpi III, IV and V. Moderately well-developed flange extends proximally from lateroproximal corner. Palmar sesamoid proximomedially on ventral surface.

O. centrale preaxiale articulates laterally with O. radiale, distally with O. centrale postaxiale and with carpal element of O. distale carpale 2, 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. O. tibiale extends as far as distal end of O. fibulare. Three distal tarsal elements present. Lateral element largest, lying at base of O. metatarsus III and extending laterally to articulate with medioproximal side of base of O. metatarsus IV and medially to base of O. metatarsus II. Second element lying at base and slightly lateral to O. metatarsus II. Medial element lying at base of O. metatarsus I and articulating with O. centrale prehallicus (Fig. 99). Distal prehallical element large and pear shaped, extending approximately half length of O. metatarsus I (Fig. 99).

Hyoid plate approximately as long as broad. Anteromedial processes of anterior hyale slender and oriented medially. Posterolateral process of hyoid plate moderately broad and moderately short. Alary processes not pedunculate. Posterior cornua ossified. Posteromedial portion of plate slightly calcified (Fig. 97).

Variation

A further 23 paratypes have been cleared and stained: SAM R29642-3, R15450, R29631-3, R29645-6 Townsville Common; QM J45947-8, J38271; AM R62685, R46280, R46282, R46283, R46364, R46380-1, R46437, R46746, R46932, R46934, R46390.

Three osteological features are consistent within the material examined; namely the length and shape of the palatine processes of the premaxillaries, the length of the otic ramus of the squamosal (the shape varies occasionally with some specimens showing some expansion of the ramus); and the tiny process on the anterodorsal surface of the epiotic eminences.

The crescentic indentation on the anterior edge of the nasals as exhibited in SAM R29641 is unique to that specimen and those from Townsville Common - all other specimens lack this feature. The shape of the pterygoid and in particular the slender acuminate, and acutely angled medial process is exhibited only by this same specimen. The shape of the medial ramus of the pterygoid is highly variable amongst the material examined but in all cases is more robust than shown in Fig. 97.

The truncated nature of the anterior extremities of the frontoparietals is unusual, other specimens having anterolateral extensions to these bones. Exposure of the frontoparietal fontanelle varies, with very few specimens lacking the posterior expansion, but most having more crenate medial edges to the frontoparietals.

The nature of the frontoparietal fontanelle exposure is unusually variable in this species. It is poorly exposed in material from Townsville Common.

Advertisement call

The call of U. mimula is a short 3-5 pulsed signal with a pulse repetition rate of 75.9 $\sec^{-1}$ and a dominant frequency of 2816 Hz (see Table 4, Fig. 89).

The call is longer than, but to the ear resembles that of, the sympatric U. lithomoda particularly at high temperatures (Table 4, Fig. 89). The description of the call of Uperoleia on Horn Island by F. Parker as a 'click' (Tyler and Davies 1984) and the close morphological similarity between U. mimula and U. lithomoda has led to the misidentification of this material.

Comparison with other species

Uperoleia mimula is an untoothed species with a poorly to moderately exposed frontoparietal fontanelle, features shared only by U. lithomoda and U. capitulata.

From U. lithomoda, U. mimula is distinguished by a lack of strong dorsal patterning, by the presence of pigmentation on the ventral surface, by poor to moderate development of the inguinal glands and by call (the call of U. mimula is clearly pulsed to the ear, whereas that of U. lithomoda is a sharp click - see Table 4).

From U. capitulata, U. mimula is distinguished by the absence of fringing on the fingers, a tubercular dorsum and less ossification of the nasals, and the presence of a preorbital process on the pars facialis of the maxillary.

Distribution

Uperoleia mimula is confined to the Cape York Peninsula and Torres Strait Islands, extending as far south as Townsville (Fig. 100). It also occurs in New Guinea at Morehead.

Comment

Tyler and Davies (1984) assigned specimens of U. mimula to U. lithomoda on the basis of external morphology, osteology and verbal call description. Our studies have shown these two species to be difficult to separate other than on the basis of call. The specimen illustrated by Parker and Tanner (1971) from Horn Island (MCZ 80234) appears to resemble U. lithomoda in life (see Fig. 30). However, the preserved specimen resembles U. mimula in external morphology. Variation in osteology of U. lithomoda (see p. 91) now known to occur is a major contributing factor to misidentification of this material.

The specimens from New Guinea examined by Tyler and Davies (1984) are osteologically closer to U. mimula than U. lithomoda. These specimens do, however, have extremely prominent inguinal and femoral patches characteristic of neither species. They are assigned here to U. mimula on the basis of their osteology, but excluded from the type series.

3.5.25 Discussion

With the description of eastern Australian taxa of Uperoleia now largely completed, it becomes possible to examine the value of external morphology and of osteology in delimiting species in this exceptionally conservative yet extremely speciose genus. Uperoleia now comprises 23 species and it is likely that further species remain undefined.

Limited morphological diversity and intraspecific variation within characters in species of Uperoleia impose constraints upon species identification.

The value of call in identifying species in *Uperoleia* has been shown by Tyler *et al*. (1981a) and Davies and Littlejohn (1986). It is clear that *Uperoleia* contains a number of sibling species and that call data will remain essential in the elucidation of these and other taxa as yet undescribed. *Uperoleia inundata* and *U*. *arenicola* are separable only by call, and call is important in separating some *U*. *laevigata* and *U*. *fusca*, *U*. *lithomoda* and *U*. *mimula*, *U*. *tyleri* and *U*. *martini*, probably *U*. *rugosa* and *U*. *capitulata*, and *U*. *talpa* and *U*. *russelli*.

External morphology must be used in conjunction with call data and becomes important when call data are not available. As has been shown here and elsewhere (Tyler *et al*. 1981a,b,c) morphology is extremely conservative in *Uperoleia* and many features show intraspecific variation necessitating an understanding of morphological variation across the range of the species.

Size has been considered a useful character in delimiting *Uperoleia* (Tyler *et al*. 1981a) and it remains so for very small and very large species. However, my data for *U*. *lithomoda* show size differences between different populations that, taken in isolation, could be misleading. Specimens of *U*. *lithomoda* on Groote Eylandt are large, larger than those from any other locality except the Lennard River region of W.A., whereas specimens of *U*. *lithomoda* from Edward River on the west of Cape York, are small, smaller than *U*. *lithomoda* from any other locality except the Mary River environs on the Arnhem Highway. The Mary River material is smaller than Amber Station and Lennard River frogs. Clearly there is no geographic cline in these data. Size differences in *U*. *rugosa* associated with locality are also noted.

Thus, size differences between species are useful in defining small species such as *U*. *mjobergi* (Tyler *et al*. 1981c and unpubl. data) and large species such as *U. tyleri* but should be treated with caution in species with a wide geographic range.

Snout shape is considered to be a consistent species-specific character in certain Middle American hylids (Duellman 1970) but my studies have shown variability in this feature in *Uperoleia* even at the one site. Snout shape also is extremely sensitive to preservation techniques and strong preservative can distort a rounded snout to the truncated condition very easily. Thus the state of preservation of the specimen should be takes into account when examining snout shape.

Some features such as the condition of dermal glands show temporal variation, but the location and general extent of glands appear to be good species indicators. The function of the dermal glands is not known. The secretion from these glands may be distasteful or toxic to predators. However, examination of the stomach contents of Rufous (Nankeen) night herons (*Nycticorax caledonicus*) taken feeding on frogs at Derby airport, showed considerable numbers of *U. mjobergi* in the stomach (Tyler and Davies unpubl.). However, the other two local species, *U. talpa* and *U. aspera*, were not represented in the prey. *U. talpa* is unique amongst *Uperoleia* in that it releases copious quantities of a white frothy secretion from the parotoid glands under conditions of minimal stress such as being picked up. This substance is toxic to other frogs sharing the same container (Tyler, Davies, Martin and Watson unpubl.). I do not know of this phenomenon in any other species of *Uperoleia*.

The activity and thus the external appearance of dermal glands appears to be seasonal as shown by the poor development of these features in specimens of *U. lithomoda* dug from the vegetable garden of Gibb River Station homestead during the dry season.

Hypertrophy of parotoid and inguinal glands occurs in isolated specimens of most species studied, and is a feature of *U. capitulata*. Likewise hypertrophy of the parotoid glands is a feature of *U. tyleri* and *U. martini*.

Rugosity of the dorsum is a reliable character at the extremes of expression i.e. smooth or tubercular. Intermediate conditions are difficult to quantify. The fine conical tubercles on the dorsum of *U. trachyderma* are an excellent indicator for this species and are unique within the genus. Granularity of the ventral surface can vary, but is usually consistent. Variation in this feature may be sexual, but my data are inconclusive.

Dorsal colour patterning is a useful character provided that the limits of variability are established. Scapular plicae, golden glands, strong dark patterns or poor colour pattern are all species specific.

Subarticular and palmar tubercles can vary slightly. Palmar tubercles, particularly at the base of the thumb, are rarely prominent and in males are usually masked by the unpigmented glandular nuptial pad of the thumb. Supernumerary tubercles on the palm are common and vary in degree of development. Fringing on the fingers is rare and is a consistant feature in those species exhibiting it.

Toe fringing varies slightly within a species, but is generally a good character. Toe webbing is variable, but is a good feature if the extent of variability is defined. The condition of the subarticular tubercles of the toes appears constant, but is very conservative. However, the size, state and orientation of the inner and outer metatarsal tubercles can vary and in some cases these are good species indicators.

Ventral pigmentation is a reliable character. It is the only consistent feature useful in separating U. laevigata and U. fusca. It can be extremely variable in form (e.g. U. laevigata) or extremely constant (e.g. U. fusca, U. tyleri, U. martini) but recognition of the limits of variability of the feature allows its usefulness to be exploited. Colour in life of inguinal and post femoral patches is a good species indicator except in U. fusca where two distinct colour forms are known to occur. Unfortunately, this feature is fugitive, and is rarely recorded by collectors.

It is clear, then, that species can be grouped on a combination of morphological features, but such groupings rely heavily on knowledge of the extent of variability within any one species.

The value of osteology in the identification of species of Uperoleia was demonstrated by Tyler et al. (1981a,b,c) but early workers 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 here in U. lithomoda, U. inundata and U. rugosa.

Many osteological features vary to the 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. Moore (1961) considered the presence or absence of teeth to reflect no more than geographic variation; whilst Straughan (1966) considered the presence of teeth to be variable within species and even between the sides of the maxillae in the one specimen. I 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 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) (see Chapter 4).

However, because most of the material was in breeding condition when collected, adult features normally are apparent; 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 frontoparietal fontanelle is less than in 'mature' specimens.

The osteological definition of a species must take account of a number of features in common, including the frontoparietal fontanelle exposure. For instance, in U. lithomoda, the crescentic shape of the anterior edge of the nasals and the anteromedial curvature of the orbital edges of the frontoparietals together with the poor to moderate exposure of the frontoparietal fontanelle are a combination of features unique to this species.

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 within *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 sphenethmoid 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.

The condition of the distale carpalia 2 and 3 is a useful postcranial osteological feature. Three conditions occur in *Uperoleia*: the elements are fused, as in *U. rugosa*, *U. trachyderma*, *U. minima* and *U. capitulata*, closely applied as in *U. tyleri*, *U. martini*, *U. fusca*, *U. mimula*, *U. littlejohni*, *U. crassa*, *U. talpa*, *U. mjobergi*, *U. inundata* and *U. russelli* or free as in *U. lithomoda*, *U. aspera*, *U. borealis*, *U. micromeles* and *U. laevigata*. In those species in which the elements are closely applied, fusion occurs in isolated specimens (e.g. U. mjobergi and U. tyleri).

The hyoid shows variability in the condition of anteromedial processes on the anterior hyale. These processes are slender and short in those Uperoleia reported here for which the data are available except U. laevigata, U. fusca, U. tyleri and U. martini. In these species, the processes are detectable as an anteromedial thickening of the anterior hyale. All of these species share a dentate maxillary arch. However, the dentate northwestern species U. mjobergi shows the edentate condition and hence association with dentate species occurs only in the eastern portion of the continent.

The features of the ilium appear to be species specific and to be indicators of species relationships. The dorsal prominence is papillate in U. glandulosa and U. aspera, is tiny and rounded in U. rugosa, U. laevigata and U. fusca, is very prominent and wedgeshaped in U. mimula, U. mjobergi, U. talpa, U. russelli, U. borealis, U. orientalis and U. lithomoda and gently monticuline in U. tyleri, U. martini, U. inundata and U. arenicola and monticuline in U. trachyderma, U. capitulata, U. crassa and U. littlejohni. The dorsal protuberance is anterolateral, lateral or posterolateral. The presence of a small ilial crest in U. trachyderma and a more prominent crest in U. micromeles is unusual.

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 because of the unavailability of fugitive characters such as colour in life and call, they recognised only a few species.

Tyler et al. (1981a) showed that U. marmorata was restricted to north-western Western Australia, and they resurrected U. fimbrianus from the synomymy of U. rugosa on the basis of their experience with restricted distributions of Uperoleia species in the north of Australia and because of its larger size. Tyler and Davies (1984) later showed that U. lithomoda has a wide ranging distribution across the north of the continent. As shown here, geographical differences in size are apparent within this species and the status of U. fimbrianus remained tenuous. My data do not support recognition of U. fimbrianus and thus the species is again synonymized with U. rugosa.

As far as is possible, literature records of Uperoleia have been identified here and the identification recorded by way of the literature synonymies at the beginning of each species account.

Uperoleia laevigata is a wide ranging species in south eastern Australia. Both Humphries (1979) and Robertson (1981, 1982, 1984a,b, 1986a,b) have made detailed studies of populations of this species (as U. rugosa).

Some reproductive data at Mosman, N.S.W. were collected 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. U. rugosa, U. laevigata and U. tyleri 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 from 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 *U. fusca* (Fletcher 1892).

Fletcher (1893) also identified material from Jervis Bay, A.C.T. (*U. tyleri*), Inverell, 40 miles west of Glen Innes, N.S.W. and 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 correctly identified. However, I have not examined his material and hence cannot confirm the identity. It is not possible to determine the identity of the material referred to *U. marmorata* without examination of the specimens.

4. THE ONTOGENY OF BONE

4.1 Introduction

The ontogenetic study reported here serves four main functions: It documents for the first time pre- and post- metamorphic development of bone in some Australian myobatrachine species of frogs; it attempts to confirm the validity of osteological features considered definitive within the preceding taxonomic accounts of Uperoleia species (see Chapter 3); it serves to elaborate and describe the effects of heterochrony on osteological features noted in Uperoleia and to confirm or refute the paedomorphic nature of the genus proposed by Tyler et al. (1981a); finally it should assist in assessment of character polarities for a cladistic analysis of Uperoleia deemed necessary for a meaningful discussion of the biogeography of the genus (see Chapters 5 and 6) (Platnick and Nelson 1978, Cracraft 1981).

4.1.1 Documentation of the ontogeny of bone

Data on the sequence of cranial and post cranial ossification within the anura are scarce. Trueb (1985) surveyed and summarized the available data for 18 species of frogs gleaned from the literature and from her own studies. However, there are no members of the Australian frog fauna within any family, for which reliable data on the ontogeny of the osseous cranium are available. Indeed, the only leptodactylid species for which such data are available is the direct developing species Eleutherodactylus nubicola for which data are available to hatchling stage (Lynn 1942).

Within the Anura, the most comprehensive descriptions are those of Kemp and Hoyt (1969) for Rana pipiens and of Hanken and Hall (1984) for Bombina orientalis. However, no data are available for postmetamorphic development of osteological features within anurans although Hanken and Hall (1984) flag the preparation of such data for Bombina orientalis.

As Trueb (1985) indicates, an appreciation of the literature is hindered because of the use by various authors of conflicting staging tables for their material. In addition, studies of postmetamorphic growth are confounded by the absence of staging tables for such growth in the absence of specific knowledge of the age of the material.

Descriptive data are necessary, therefore, to enable comparative studies to be undertaken and to allow recognition of appropriate stages in development.

4.1.2 The effect of ontogeny on osteological features used in taxonomic accounts

At least two cryptic species pairs are recognised within Uperoleia that rely on osteological features for delineation. Uperoleia inundata and U. arenicola were separable by call when they were first described (Tyler et al. 1981a). The external morphology of individuals was indistinguishable, but the size range of the two species was thought not to overlap (U. arenicola males 18-23 mm, U. inundata males 23-28 mm S-V). The two osteological features separating the two, namely the relative ossification of the nasals and the relative exposure of the frontoparietal fontanelle, were non-quantifiable parameters that might be interpreted as stages in an ontogenetic sequence (see p. 67).

Call data obtained from specimens from Groote Eylandt referrable to U. inundata (Tyler et al. 1986) showed that call parameters in this species can be highly variable and size data presented in Chapter 3 for U. inundata give a range of 18-32 mm S-V for male frogs. These data cast doubt upon the validity of the morphological and behavioural features used to separate U. arenicola from U. inundata.

It is essential, therefore, to investigate the worth of the osteological data used to recognise the two species.

Two hypotheses can be proposed to interpret these data. The first is that the material collected at, and analysed from, the type locality of U. arenicola, Birndu on the edge of the Arnhem Land escarpment, consisted of young individuals of U. inundata coming into their first breeding season and hence osteological features are not fully developed. The second hypothesis is that U. arenicola exhibits paedomorphic arrest in the two osteological features discussed here and therefore the species, as recognised, is valid.

A second species pair reliant upon osteological data and limited external morphology (call data are not yet available for one member of the pair) is U. rugosa and U. capitulata. These species are separable externally by the degree of development (hypertrophy) of the parotoid, inguinal and coccygeal glands. Osteologically the species are separable by the degree of exposure of the frontoparietal fontanelle (unexposed or very poorly exposed in U. rugosa and poorly to moderately exposed in U. capitulata) and by the relationship of the nasals with the sphenethmoid (in contact in U. rugosa and not in contact in U. capitulata).

The same two hypotheses could be advanced to explain these features as proposed for the preceding species pair, namely:

1. That the specimens of U. capitulata collected across its range are all young specimens representing ontogenetic stages in the development of U. rugosa i.e. sub adult or first season U. rugosa

   or

2. That the frontoparietal fontanelle exposure and the relativities of the nasals and the sphenethmoid in U. capitulata are paedomorphic features representing earlier stages in the ontogeny of other Uperoleia species.

A study of ontogeny may not provide evidence enabling acceptance of one of these hypotheses in preference to the other since young (immature) specimens of one species might be morphologically identical to closely related species paedomorphic for certain features. If the features under consideration, however, are subject to different rate controls and are ossifying independently and if these ossification sequences can be related to other events, then it may be possible to discriminate between the two hypotheses using ontogenetic data.

4.1.3 Heterochrony and paedomorphosis in Uperoleia

The role of heterochrony and, in particular, of paedomorphosis in morphological change within the Anura was first recognised by E.M.T. Stephenson (1960) in a study of the endemic New Zealand genus Leiopelma and later by N.G. Stephenson (1965) in a study of Australian leptodactylid frogs. Amongst the species studied by Stephenson (1965) and the species upon which most of his conclusions were based, was Uperoleia [Glauertia] russelli. Stephenson examined adult and juvenile cranial morphologies, concluding that, in general, features distinguishing genera are not diverse and unrelated structures, but have arisen from morphological changes produced by variation in the speed and extent of development.

Trueb (1973) extended Stephenson's thesis to propose that the differences in cranial ossification exhibited between male and female anurans are a function of the smaller size of the male specimens and hence an example of heterochrony.

The role of heterochrony in evolution was elaborated by Gould (1977) but within the Amphibia it is amongst the salamanders (Caudata) that evidence for heterochronous change within lineages has been documented.

Paedomorphosis has been implicated in skull evolution in plethodontid salamanders (Hanken 1984; Alberch 1983; Alberch and Alberch 1981; Wake 1980, 1966; Wake and Elias 1983; Marlow _et_ _al_. 1979). Heterochrony in other elements of the skeleton has been examined by Alberch (1981) and Green and Alberch (1981) in _Bolitoglossa_ whilst molecular evolution within the Plethodontidae was considered in a paedomorphic context by Larsen (1980) and Larsen _et_ _al_. (1981).

Alberch _et_ _al_. (1979) provided a quantitative model for measuring heterochronous change between related species. These authors proposed the construction of 'ontogenetic trajectories' for a character, incorporating four parameters, namely a) the age at onset of growth (onset signal); b) the initial size at onset growth; c) the growth rate and d) the point at which growth of the parameters of either age, size or shape, stops (offset signal).

This model was used by Alberch and Alberch (1981) to examine the mechanisms of morphological diversification in arboreal and terrestrial species of _Bolitoglossa_ and Wake _et_ _al_. (1983) examined the ossification sequence of _Aneides_ _lugubris_ within this same conceptual framework.

Hanken (1982, 1983, 1984) in a study of the plethodontid genus Thorius investigated 'miniaturization' and concluded that paedomorphosis was implicated as a mechanism for size decrease.

Miniaturization (changes in morphology due to small size) was studied within the Anura by Trueb and Alberch (1986), this being the only other study of heterochrony within the group. These authors predicted that if the developmental rate of the 'ancestral ontogeny' were to be decreased, an altered 'derived ontogeny might result that produced smaller organisms characterised by retention of at least some juvenile cranial features of the ancestor. Such an analysis requires a knowledge of the sequence of ossification of the cranial elements of the species under review, together with knowledge of inter- and intraspecific variation within the sequences and an appreciation of the shape changes that characterize each cranial element. As indicated earlier (4.1.1) such data are extremely scarce within the literature.

The myobatrachine genus Uperoleia is thought to be a paedomorphic lineage (Tyler et al. 1981a). This study aims to confirm or refute this premise and to elucidate the nature of this evolutionary mechanism within Uperoleia.

The subfamily Myobatrachinae is probably a paedomorphic lineage relative to other Anuran groups. By outgroup comparison within the Myobatrachinae, then, many character states exhibited within Uperoleia might be considered as post-terminal events. To avoid confusion on this issue, conditions of maximal ossification within Uperoleia are considered as terminal events and states recognised as sequences on the ontogenetic trajectory of these conditions and exhibited by other species, are considered to be paedomorphic.

4.1.4 The role of ontogeny in the determination of character polarity

Two schools of phylogenetic systematics have been recognised by Beatty (1982). Pattern cladists espouse that the ontogeny criterion is both necessary and sufficient for the discovery of order in nature (Nelson 1978; Nelson and Platnick 1981; Patterson 1982, 1983). Brady (1982) believes that the method of constructing cladograms used by pattern cladists is identical to that used by the other school of thought - the 'phylogenetic cladists'. Kluge (1985), however, disagrees, and argues that phylogenetic cladists have tended to use both ontogenetic and outgroup criteria whenever possible in assessing polarity of characters, although recently a preference has been shown for outgroup analysis.

Regardless of to which school of thought one subscribes (see Kluge 1985; Brooks and Wiley 1985; Nelson 1985 for ongoing debate) it is clear that an understanding of ontogeny is perceived to be of value in formulating hypotheses of phylogenetic relationships.

Paedomorphosis is considered by some authors to provide major problems for phylogenetic analyses (see Eldredge and Cracraft 1980; Wiley 1980, 1981; Arnold 1981). De Queiroz (1985) however, argues that if addition or modification of terminal ontogenetic stages are common patterns in phylogeny, then paedomorphosis will rarely cause problems in deriving phylogenies. This is because derived rather than ancestral characters will be eliminated. The proviso is made, however, that if a terminal character lost through paedomorphosis also happens to be ancestral, then paedomorphosis coupled with incomplete sampling can lead to erroneous inferences about evolutionary character polarity.

It is possible to predict what suite of phenotypic traits should characterize a paedomorphic morphology through comparative analysis of ontogeny (Alberch 1985). It can be argued, also, that due to the simple regulatory basis of the process, the same transformation is likely to appear more than once in phylogeny, thus providing a rationale for the widespread occurrence of convergence and parallelism (homoplasy) in morphological evolution (Alberch 1985).

It would appear then, that to have maximal faith in hypotheses of character polarity, systematic analysis should integrate ontogenetic data with ingroup and outgroup data (Alberch 1985). Heterochrony might thus be recognised.

Tests of hypotheses of heterochrony should take the form of an empirical study of ontogenetic changes of the characters in question within the organisms bearing the anomalous features, their putative sister taxon and appropriate outgroups (Fink 1982).

4.1.5 Relationships of Uperoleia

The question then arises as to the selection of a putative sister taxon and of appropriate outgroups for Uperoleia.

Parker (1940) recognised two subfamilies within the Australopapuan Leptodactylidae (Myobatrachidae of some authors) - the Cycloraninae (since changed to the Limnodynastinae with the removal of the nominative genus Cyclorana to the Hylidae by Tyler (1979a)) and the Myobatrachinae.

Amongst the myobatrachine genera, Crinia Tschudi was a "black box" for small, nondescript species of little morphological diversity. Straughan and Lee (1966) recognised the genus Taudactylus from within

Crinia whilst Tyler (1972a) erected *Assa* to accommodate *Crinia darlingtoni*. Blake (1973) in a multivariate numerical analysis of myobatrachine genera, split the remaining *Crinia* into three genera, *Crinia* Tschudi confined to *Crinia georgiana* and *C. haswelli*, *Geocrinia* Blake for *G. victoriana* and *G. laevis* and *Ranidella* Girard for the remaining species.

Heyer and Liem (1976) further split *Crinia* into *Crinia* and *Paracrinia*, a genus they erected to accommodate *C. haswelli*, leaving *Crinia* a monotypic genus. They also split *Australocrinia*, containing *R. tasmaniensis* and *R. riparia* from *Ranidella*.

Thompson (1981) subsequently suppressed *Australocrinia* finding no evidence to support the conclusions of Heyer and Liem (1976) leaving *Taudactylus*, *Assa*, *Ranidella*, *Geocrinia*, *Paracrinia* and *Crinia* as genera spawned from the heterogeneous assemblage called *Crinia* prior to 1966.

Daugherty and Maxson (1982) undertook an immunological study of myobatrachine genera using microcomplement fixation techniques and, in that context, examined relationships within *Ranidella*. They compared in a one way study *R. riparia*, *R. glauerti*, *R. parinsignifera*, *R. bilingua*, *R. remota*, *R. deserticola*, *R. tasmaniensis*, and *Crinia georgiana* with *R. signifera* and concluded that *C. georgiana* had an albumin which was more similar to that of *R. signifera* than were the albumins of four other *Ranidella* species.

On the basis of these data, Heyer *et al*. (1982) suppressed *Ranidella* and synonymised the genus with *Crinia*. These authors claimed that morphological data substantiated the biochemical data, presumably basing this belief on the statement by Heyer and Liem (1976) that all the derived states of *Crinia georgiana* are found in *Ranidella*.

Barendse (1984) provided supporting data for the findings of Daugherty and Maxson (1982) with molecular data provided by isozyme electrophoresis. Unfortunately he did not use the same *Ranidella* species as Daugherty and Maxson as he was addressing a different problem.

There appears to be some conflict in some of the relationships predicted by these sets of data. Daugherty, Maxson and Barendse did analyse some common species. Daugherty and Maxson recognised a close relationship between *R. glauerti* and *R. parinsignifera* whereas Barendse recognised a close relationship between *R. glauerti* and *Crinia georgiana*, although he suggested that this is an apparent anomaly. However, he went on to argue that the data are unlikely to be anomalous.

Biochemical data suggest that *Crinia georgiana* is more closely related to *Ranidella* than to any other taxon. However, hybridization data (see Main 1968 for a summary), indicate considerable divergence of *Crinia georgiana* from *Ranidella* species.

It must be recognised that the data of Daugherty and Maxson (1982) are based on a one way analysis to *Ranidella signifera*, not on a two way study. (Even if the study had been two way, convergence in immune systems is not out of the question.) It is possible, therefore, that the interpretations of these data are not a true reflection of relationships. The decision of Heyer *et al*. (1982) to change the current generic nomenclature on the basis of these data might be seen as a premature act based on an over interpretation of the data.

The value of allozyme data in systematic studies is subject to some debate. Many authors consider such data to be valuable only at the genus level and below (Matson 1984). Others consider that electrophoretic data are of value only at the sibling species level and hence the genetic divergence of the taxa studied by Barendse (1984) is too great for construction of accurate phylogenies (Richardson et al. 1986). The data of Barendse (1984), may not, therefore, be as supportive of the data of Daugherty and Maxson (1982) as has been claimed.

Despite the claims of Heyer and Liem (1976), Daugherty and Maxson (1982) and Heyer et al. (1982) Crinia georgiana has diverged morphologically from Ranidella, the latter group of species forming a coherent, easily defined morphological unit. The question is whether these genera presently constituted are supported by autopomorphies.

The presence of vomerine teeth fragments in C. georgiana is not shared by any Ranidella species (this feature is probably plesiomorphic i.e. apomorphic in Ranidella). Modification of the first metacarpal, together with the fusion of distale carpale 2 to the dorsal surface of O. centrale preaxiale found in C. georgiana (Fig. 101), are apomorphic features absent in Ranidella (Davies unpubl.). In addition, the presence of small sesamoids at finger and toe articulations (present in C. georgiana, absent in Ranidella) (Moller 1980) are probably apomorphic features (i.e. apomorphic in Crinia).

Biochemical data, hybridization data and morphological data therefore are incompatible. Morphological data suggest that Ranidella and Crinia are natural groups apparently supported by autopomorphies and since the present study is essentially a morphological one, I prefer to recognise the morphologically homogenous group Ranidella as a separate entity apart from Crinia rather than the non-homogenous grouping of Ranidella and Crinia georgiana as proposed by Heyer et al. 1982.

Despite the morphological similarity between Uperoleia and Pseudophryne which lead earlier workers to synonymize them, Daugherty and Maxson (1982) regard Uperoleia and Ranidella as being more closely related, postulating dates of divergence of *Uperoleia* and *Ranidella* at 54-59 my BP and of *Pseudophryne* from *Ranidella* at 35-46 my BP.

In a later study of the relationships of the genera *Arenophryne*, *Myobatrachus* and *Pseudophryne*, Maxson and Roberts (1985) provided immunological distances of *Uperoleia inundata* (interpolated in a one way analysis as another myobatrachine genus for which antisera was not available) to *Pseudophryne* of 62, *Arenophryne* of 66, *Myobatrachus* of 73 and *Crinia* (*Ranidella*) of 77 units. Maxson and Roberts (1985) consider that these data do not suggest a particularly close relationship of *Uperoleia* to any of the other genera studied and in particular not to the *Pseudophryne*, *Metacrinia*, *Myobatrachus* and *Arenophryne* group. Biochemical data, then, are of no great value in resolving the question of the relationships of *Uperoleia* to other myobatrachine genera. It seems that either *Ranidella* or *Pseudophryne* would be an appropriate sister group to *Uperoleia* and both genera are investigated in this study.

Thus a limited study of the ontogeny of bone in *Uperoleia*, *Ranidella* and *Pseudophryne* has been attempted. The study is limited of necessity. Breeding pairs of *Uperoleia* are rarely encountered in the field and breeding pairs of preferred species within the 23 taxa recognised here (i.e. species with fully roofed frontoparietal fontanelles) are even more difficult to obtain (three of the five species are eastern states taxa for which I have no personal field experience, the fourth taxon is confined to the Mitchell Plateau in remote W.A., and known only from a 100 metre square area, whilst the fifth species fitting this category is known only from the type specimen).

In addition, laboratory reared material presents problems in that ossification is lesser (or ?slower) in contrast to samples collected in natural conditions. (Gaudin 1973; Brown 1980 in Trueb 1985). The study is confined, then, to limited material of Uperoleia lithomoda and U. trachyderma collected in the field, U. inundata reared in the laboratory to metamorphosis, post metamorphic stages of U. rugosa and U. laevigata field collected and lodged in museum collections, together with laboratory reared Ranidella signifera supplemented with field collected postmetamorphic material, and field collected premetamorphic and laboratory reared post metamorphic material of Pseudophryne bibroni.

4.2 Materials and methods

All premetamorphic and metamorphic material was staged according to Gosner (1960). Postmetamorphic material was sexed, where possible, and snout to vent lengths measured with dial callipers. All material was cleared and double stained for bone and cartilage employing the method of Dingerkus and Uhler (1977). Enzyme digestion was assisted by placing the specimens in an oven at 37°C.

Description of the chondrocranium follows Duellman and Trueb (1985).

Outline drawings were made with the aid of a Wild M9 stereo-dissecting microscope with a 0.4 x reducing lens and attached camera lucida.

Variation in postmetamorphic skull morphology was assessed by scoring all specimens (where possible) for the following characters, each being a recognisable condition along the continuum of variation during development of each feature.

1. Nasals: A, absent (Fig. 116A); B, just detectable (Fig. 116E); C, thin rod of ossification (Fig. 116G); D, medial ossification occurring (Fig. 107C); E, ossification complete (i.e. adult shape) (Fig. 107K).

2. Frontoparietals: A, thin rod on orbital edges (Fig. 116A); B, medial encroachment up to 1/2 way (Fig. 107B); C, medial encroachment greater than 1/2 way (Fig. 107G); D, frontoparietal nearly or completely roofed (Fig. 4).

3. Maxillaries: A, absent; B, present but with no preorbital process; C, present with preorbital process.

4. Quadratojugal: A, absent; B, present but not confluent with maxillary (Fig. 116F); C, confluent with maxillary (Fig. 116P).

5. Dentition: A, no teeth; B teeth present on premaxillary; C, teeth present on maxillary to maximum level of palatines; D, teeth on maxillary to level of pterygoids (Fig. 114C); E, teeth extending posteriorly to pterygoids (Fig. 114F).

6. Parasphenoid: A, cultriform process incompletely ossified anteriorly; B, cultriform process completely ossified anteriorly.

7. Parasphenoid: A, alae incompletely ossified laterally; B, alae completely ossified laterally.

8. Vomers: A, vomers absent; B, vomers present at edges of choanae; C, vomers present medial to palatines; D, vomers present at choanae and medial to palatines.

9. Palatines: A, palatines absent (Fig. 114A); B, ossification centre detectable; C, palatines not reaching sphenethmoid medially (Fig. 114B); D, palatines reaching sphenethmoid medially (Fig. 114C); E, ossification occurring laterally (Fig. 114D); F, palatines reaching preorbital process of pars facialis of maxillary or beyond (Fig. 114H).

10. Pterygoid: A, pterygoid absent; B, anterior ramus, only present; C, posterior and medial rami present.

11. Squamosal: A, squamosal absent; B, shaft and otic ramus present; C, zygomatic ramus present.

12. Sphenethmoid: A, sphenethmoid absent (Fig. 116A); B, sphenethmoid present, ventrally only (Fig. 116G); C, sphenethmoid present dorsally at the base of the nasal cups; D, dorsally sphenethmoid V-shaped with internal cartilage (Fig. 116M); E, internal cartilage of V ossified (Fig. 107K); F, sphenethmoid approximately rectangular blocks (Fig. 107L).

13. Exoccipital: A, not confluent with frontoparietals (Fig. 107A); B, confluent medially with frontoparietals (Fig. 107B); C, confluent medially and laterally with frontoparietals (Fig. 107K).

14. Exoccipital: A, not confluent ventrally with parasphenoid (Fig. 108A); B, confluent medially with parasphenoid (Fig. 108B); C, confluent with parasphenoid along anterior length (Fig. 108K).

15. Dorsal Prootic: A, not confluent laterally with frontoparietals (Fig. 107D); B, confluent posterolaterally with frontoparietals (Fig. 107F); C, confluent anterolaterally with frontoparietals (Fig. 107K).

16. Columella: A, absent; B, present as cartilaginous element; C, incompletely ossified; D, completely ossified.

17. Hyoid-anteromedial processes: A, absent; B, present but faintly detectable; C, clearly defined; D, hooked; E, joined laterally with anterior hyale.

18. Hyoid-posterior cornua: A, cartilaginous; B, ossification centre detectable; C, moderately ossified; D, fully ossified.

Characters were ranked according to developmental stage and analysed using the Spearman Rank Correlation Coefficient to determine the temporal independence of the ossification sequences of individual bones one from another.

Data matrices are provided in Appendix 1.

Material examined

Uperoleia inundata: Stage 26(2), UAZ B998; Stage 27(3), UAZ B999; Stage 28(2), UAZ B1000; Stage 29(1), UAZ B1001; Stage 31(1), UAZ B1002; Stage 32(1), UAZ B1003; Stage 34(1), UAZ B1004; Stage 35(2) UAZ B1005; Stage 36(3) UAZ B1006; Stage 37(1) UAZ B1007; Stage 38(1) UAZ B1008; Stage 39(1), UAZ B1009; Stage 41(1), UAZ B1010; Stage 43(1), UAZ B1011. Laboratory reared.

Uperoleia trachyderma: Stage 45, UAZ B988; Stage 46, UAZ B989 - both collected Newry Station, N.T.

Uperoleia lithomoda: Stage 33, UAZ B984; Stage 40(2), UAZ B985-6; Stage 43, UAZ B987. Collected Newry Station, N.T.

Postmetamorphic material: NTM R11760, R11756, R11757, Westmoreland, Qld.

Uperoleia laevigata: AMR 34364, R34367, R34369-71, R34373-74, R34376, R34379, R34381, Thomas Lagoon, 1.6 km W Arding, N.S.W. AM R34285-6, R34288, R34293, R34295, R34297, R34300, R34302-5, Llangothlin Lagoon, N.S.W. AM R71757, R71760-62, R71764, R71767, R71770-72, R71775, R71778, R71789, R71784, R71788, R71790-91, R71797-98, R71801, R71803-4, Bagot Road Lagoon, via Llangothlin, N.S.W.

Uperoleia rugosa:

Postmetamorphic material: ANWC A936, A940, A944, A946, A949, A950, A956, A958-60, A966, A969, A976, A981, A984, Lake Cowal, N.S.W.; A0010, A0013, A0015, Cowal North Station, Lake Cowal, N.S.W.; NMV D25092, D25101, Savernake, N.S.W.

Ranidella signifera: Stage 39(10), UAZ B990; Stage 40(7), UAZ B991; Stage 41(9), UAZ B992; Stage 42(4), UAZ B993; Stage 43(3), UAZ B994; Stage 44(4), UAZ B995; Stage 45(3), UAZ B996; Stage 46(1), UAZ B997, all laboratory reared.

Postmetamorphic material: UAZ B898-B921, Cannons Swamp, Mt Remarkable, S.A.; UAZ B922-924, NW Corner Flinders Chase, K.I., S.A.; UAZ B925-928, Hahndorf, Lobethal/Adelaide Hills, S.A..

Pseudophryne bibroni: Stage 36, UAZ B979; Stage 37, UAZ B980; Stage 38, UAZ B981; Stage 39, UAZ B982; Stage 43, UAZ B983, laboratory reared.

Postmetamorphic material: UAZ B930-978, laboratory reared.

4.3 Results

4.3.1 *Uperoleia inundata*

Ossification had not commenced in any of the material examined.

4.3.2 *Uperoleia trachyderma*

Stage 45 Cranium

Dermal roofing bones: The frontoparietal elements are ossified as slender rods along the orbital edges. The nasals have not commenced ossification. The septomaxilla is mineralized.

Maxillary arch: The palatine processes of the palatal shelf of the premaxillaries are very faintly mineralized. Other portions of the premaxillaries, the maxillaries and the quadratojugal have not begun to ossify.

Palatal bones: The parasphenoid is very faintly mineralized but the vomers, palatines and pterygoids remain unossified.

Suspensorium: The shaft and the otic ramus of the squamosal are mineralized. The quadrate remains cartilaginous in this species.

Neurocranium: The occipital condyles and a small adjacent portion of the exoccipital are beginning to ossify. The sphenethmoid is unossified. A small degree of mineralization along the edges of the dentary and angulosplenial is apparent.

Hyolaryngeal skeleton: The cartilaginous hyoid plate is beginning to differentiate.

Postcranial elements

Pectoral girdle and limbs: Ossification centres have formed on the suprascapula, scapula, coracoid, clavicle and humerus.

Pelvic girdle and limbs: Ossification centres have formed on the ilium, femur, tibiofibula, astragalus/calcaneum. Ossification of these elements is relatively greater than the pectoral girdle elements.

Vertebral column: All vertebrae are mineralized.

Stage 46 Cranium

Dermal roofing bones: The frontoparietal elements are ossified as slender rods on the edges of the orbits with perforated mineralization posteriorly (Fig. 102). The septomaxilla is ossified and the nasals unossified.

Maxillary arch: The premaxillaries are mineralized on all components (alary processes, palatine processes, pars dentalis) (Fig. 102). Neither the maxillary or the quadratojugal are mineralized.

Palatal bones: Mineralization of the parasphenoid remains faint (Fig. 102). Neither vomers, palatines or pterygoids are detectable.

Suspensorium: The squamosal shaft and otic ramus are ossified (Fig. 102).

Neurocranium: The occipital candyles and a small portion of the exoccipitals are mineralized. Ossification of the prootic extends from the orbital edges over the epiotic eminences. The sphenethmoid is not ossified. The dentary and angulosplenial have begun to ossify.

Postcranial elements

Pectoral girdle and limbs: The suprascapula, scapula, clavicles, coracoid, humerus, radioulna and metacarpals show varying degrees of ossification.

Pelvic girdle and limbs: The ilium continues to ossify. The femur, tibiotarsus, astragalus/calcaneum and metatarsals show varying degrees of ossification. Ossification has commenced on the first phalanges of toes I and II.

Vertebral column: The vertebrae continue to ossify. Vertebrae I and II are fused dorsally by a medial cartilaginous rod (Fig. 103). The three rods of the urostyle show the beginnings of fusion with some mineralization of the dorsal two elements (Fig. 103).

4.3.3 Uperoleia lithomoda

Stage 33

The chondrocranium of this species is illustrated in Fig. 104. The basicranial fenestra on the floor of the chondrocranium, is reduced to a small fenestra situated posteromedially. The trabecular plate is extensive and the basal plate, posterior to the basicranial fenestra, is extensively indented.

The auditory capsules are united by a single posterior bridge, the tectum synoticum, leaving an extensive frontoparietal fenestra. No dorsomedial cartilaginous bridge (taenia tecti medialis) is apparent. The auditory capsules flank the posterior floor of the braincase. The lateral wall of the auditory capsule is perforated by the fenestra ovalis.

The planum trabeculae anterior (the anterior end of the brain case) bears a pair of anterolateral projections, the cornua. Each cornu is deflected ventrally and fused with the suprarostral cartilages which support the upper beak of the tadpole. The suprarostral cartilages are divided and perforated in this species. The lower beak is supported by paired medial infrarostral cartilages. Medially these elements articulate with each other. Posterolaterally, each articulates with Meckels cartilages which in turn articulate laterally with the palatoquadrate.

No mineralization is apparent at this stage.

Stage 40(1) Cranium

Dermal roofing bones: Frontoparietal ossification consists anteriorly of a slip of ossification along the orbital edges to a point about half the orbital length, then an abrupt broadening posteriorly of the ossified portion of the bone. The posterior region is only faintly mineralized. Neither the nasals nor the septomaxilla have begun to ossify.

Maxillary arch: No mineralization is apparent on any of these elements (premaxillary, maxillary, quadratojugal, dentition).

Palatal bones: The cultriform process of the parasphenoid shows some mineralization for about ½ its length and the medial portion of the alae have begun to mineralize.

Suspensorium: No mineralization is apparent on these elements.

Neurocranium: Some mineralization has begun on the condyles of the exoccipital. Mineralization is not apparent in any other elements.

Hyolaryngeal skeleton: Formation of this element is not detectable.

Postcranial elements

Pectoral girdle and limbs: Ossification has not commenced on any elements.

Pelvic girdle and limbs: Ossification has not commenced on any elements.

Vertebral column: All the presacral vertebrae show some degree of mineralization. The mineralization on the sacral vertebrae is so faint as to be scarcely detectable.

Stage 40(2) Cranium

Dermal roofing bones: The frontoparietal elements are in the form of slender slips anteriorly with an abrupt broadening posteriorly (Fig. 105). The nasals and septomaxilla have not begun to ossify.

Maxillary arch: None of these elements have begun to ossify.

Palatal bones: The cultriform process of the parasphenoid is mineralized for about $^3/4$ of the length of the orbit whilst the alae are incompletely mineralized laterally (Fig. 105). No other palatal elements are mineralized.

Suspensorium: No elements are mineralized.

Neurocranium: The exooccipital is ossified only in the area of the condyles. No other elements are mineralized.

Hyolaryngeal skeleton: This element is undetectable.

Postcranial elements

Pectoral girdle and limbs: No elements have begun to ossify.

Pelvic girdle and limbs: Darkening of the ossification centres of the ilium, femur and tibiofibula are apparent.

Vertebral column: All vertebrae, including the sacral vertebrae, are ossifying.

Stage 43 Cranium

Dermal roofing bones: The frontoparietal elements are moderately well ossified (Fig. 105), being slender anteriorly, but expanded posteriorly about $^1/2$ way along the length of the orbit. The posterior ossification is perforated. Ossification of the nasals has not commenced.

Maxillary arch: Ossification has not commenced on any of these elements.

Palatal bones: Considerable mineralization is apparent on the parasphenoid (Fig. 105) but ossification has not commenced on the vomers, palatines or pterygoids.

Suspensorium: Very faint mineralization is apparent on the squamosal shaft.

Neurocranium: The exoccipitals are ossified both dorsally and ventrally on the condyles and surrounding area. A slight degree of mineralization occurs anterodorsally on the prootic. No ossification is apparent on the lower jaw, sphenethmoid or columella.

Postcranial elements

Pectoral girdle and limbs: A small line of mineralization occurs on the anterior edge of the suprascapula. The scapula, coracoids and clavicles have begun to ossify; so too have the humerus, radioulna, the metacarpal and first phalanx of finger III and the metacarpal of finger IV. No carpal bones show ossification.

Pelvic girdle and limbs: The ilium, femur, tibiofibula, astragalus/calcaneum metatarsals II, III, IV and V, the first phalanges of toes II, III, IV and V and the second phalanges of toes III and IV have begun to ossify. No tarsal bones show ossification.

Vertebral column: All the vertebrae are ossified. The transverse processes have cartilaginous tips. Presacral vertebrae I and II are joined dorsally by a cartilaginous rod. The urostyle is recognisable as three distinct cartilaginous elements, a dorsal pair and a ventral rod. Mineralization has commenced on the two dorsal elements.

Postmetamorphic specimen (NTM R11760), S-V 14.4 mm.

Cranium

Dermal roofing bones: The frontoparietal elements are moderately separated medially, curved along the orbital edges and not confluent with the prootic on the posterior orbital edges (Fig. 106). The nasals are not completely ossified posteromedially and are crescentic along their anterior edges. The septomaxilla are completely ossified.

Maxillary arch: The premaxillaries, maxillaries and quadratojugals are completely ossified. The preorbital process of the pars facialis of the maxillary is well developed (Fig. 106) and the maxillary and quadratojugal are in firm contact. This is an edentate species.

Palatal bones: The parasphenoid is completely ossified. Vomerine fragments do not occur in this species. The palatines are slender medial rods, not completely ossified laterally; these elements have not reached their final width. The pterygoids are completely ossified.

Suspensorium: The squamosal shaft is robust and the otic ramus completely ossified. No zygomatic ramus is detectable.

Neurocranium: The sphenethmoid is poorly ossified ventrally and scarcely detectable dorsally. The prootic elements are almost completely ossified except for a small region on the orbital edges of the frontoparietals and at the posterior extremities of the epiotic eminences. The exoccipitals are completely ossified, and confluent with the alae of the parasphenoid ventrally. The mandible is fully ossified, as is the columella.

Hyolaryngeal skeleton: Anteromedial processes of the anterior hyale of the hyoid are not detectable. The posterior cornua are about $^{2}/3$ ossified.

Postcranial elements: Ossification of all postcranial elements except the carpals and tarsals, is complete.

Postmetamorphic specimen (NTM R11756), S-V 15.1 mm.

Cranium

Dermal roofing bones: The frontoparietal elements are poorly to moderately separated medially (Fig. 106), curved on the orbital edges and almost confluent with the prootic at the orbital edge. The nasals are approximately fully ossified and the septomaxilla also.

Maxillary arch: The premaxillaries are fully ossified. The preorbital process of the pars facialis of the maxillary is not ossified, but the maxillary is in firm contact with the quadratojugal.

Palatal bones: The parasphenoid is completely ossified. The palatines are moderately slender and incomplete laterally. The pterygoids are fully ossified.

Suspensorium: The squamosal shaft and otic ramus are complete. A trace of the zygomatic ramus is apparent (Fig. 106).

Neurocranium: Dorsal development of the sphenethmoid is masked by the frontoparietal elements. Dorsolaterally these elements are mineralized rather than ossified. The ventral sphenethmoid is moderately developed. The exoccipitals are fully ossified ventrally, but incompletely ossified dorsally (Fig. 106). The prootic elements are fully ossified other than a small portion at the orbital edges of the frontoparietals and lack of mineralization on the epiotic eminences.

The mandible is fully ossified. The columella is incompletely ossified distally.

Hyolaryngeal skeleton: The anteromedial processes of the anterior cornua of the hyoid are detectable, but very faintly so. The posterior cornua are fully ossified.

Postcranial elements

Ossification of all postcranial elements except the carpals and tarsals is largely complete. The carpal elements are heavily mineralized and the tarsal elements more lightly so.

Postmetamorphic specimen (NTM R11757), S-V 17.7 mm.

Cranium

Dermal roofing bones: The frontoparietal elements are moderately separated medially (Fig. 106), curved along the orbital edges and not confluent with the prootic at the orbital edges. Ossification of the nasals is difficult to assess because of abnormality on one side, however medial ossification appears to be incomplete. The septomaxilla is completely ossified.

Maxillary arch: The preorbital processes of the pars facialis of the maxillary are not detectable. The premaxillaries are fully ossified and the maxillary is in firm contact with the quadratojugal.

Palatal bones: The alae of the parasphenoid appear to be incompletely ossified laterally. The palatines are slender and approximately of final length. The pterygoids are fully ossified.

Suspensorium: The shaft of the squamosal is robust and ossification of both the otic and zygomatic rami appears to be complete (Fig. 106).

Neurocranium: The sphenethmoid is moderately well ossified dorsally (Fig. 106) and well ossified ventrally. The exoccipitals are fully ossified dorsally and ventrally. The prootic is fully ossified except for the medial orbital edges and portions of the epiotic eminences. The mandible and columella are fully ossified.

Hyolaryngeal skeleton: The anteromedial processes of the anterior hyale of the hyoid are not detectable. The posterior cornua are ossified.

Postcranial elements: Ossification of all postcranial elements except the carpals and tarsals, both of which are heavily mineralized, are largely complete.

4.3.4 *Uperoleia laevigata* - postmetamorphic development

Cranial elements

Dermal roofing bones

Frontoparietals: The earliest development of the frontoparietals in this series shows these elements as slender bones bounding the medial orbital edges, expanding slightly post orbitally. They are not in contact with the prootic posterolaterally (Fig. 107A). Ossification of the frontoparietals progresses medially and crenulations and indentations of the medial edges occur relatively late (Fig. 107K-Q). Fusion with the prootic elements posterolaterally is an early event but anterior fusion occurs later in the ossification sequence.

The ossification sequence of the frontoparietals cannot be correlated visually with the sequences in other cranial elements, e.g. nasals (Fig. 107). The adult condition was not fully achieved in this series (see Fig. 4).

Nasals: Mineralization of the nasals appears on the snout as an elongate, anterolateral rod (Fig. 107A,B). This rod then thickens. The ossification sequence appears as two quite discrete events. The second sequence occurs medially to the initial lateral rods and proceeds in that direction (Fig. 107C). The lateral elements (maxillary processes of the nasals) eventually thicken and the final shape is achieved (Fig. 107G-J).

Maxillary arch

Premaxillary: The ossification of the premaxillary is complete in the sequence examined.

Maxillary: The ossification of the maxillary is complete in the sequence examined.

Quadratojugal: The quadratojugal becomes progressively more robust in the sequences examined, but there is no change in overall shape (Figs 107, 108).

Dentition: Teeth appear initially on the premaxillaries (Fig. 108B), then sequentially along the maxillaries from the articulation with the premaxillaries to just posterior to the articulation of the anterior rami of the pterygoid with the palatal shelf of the maxillaries. Full dentition is apparent at approximately the same stage as completion of palatine development (Fig. 108).

Palatal bones

Parasphenoid: The cultriform process of the parasphenoid is fully ossified in the sequence examined. However, lateral ossification of the alae is incomplete. In the earliest specimen examined (Fig. 108A) the alae of the parasphenoid and the exoccipital are widely separated. Medial confluence is apparent in all the other material (Fig. 108).

Vomers: Vomerine fragments appear only in one of the largest specimens (Fig. 108L). The fragments are medial to the palatines. Small choanal fragments were not detectable.

Palatines: The palatines appear quite late post metamorphosis. Initially they appear as centres of ossification at about the level of the median point of the anterior orbital extremities (Fig. 108B). They extend medially initially (Fig. 108D), and then laterally (Fig. 108F), thickening during lateral extension (Fig. 108H-K).

Pterygoid: The anterior ramus of the pterygoid is well developed in all the material examined. However, a small bifid posterior termination of this ramus is apparent in one specimen (Fig. 108A). The posterior and medial rami develop from this termination and appear very rapidly (Fig. 108). All rami become more robust with age (Fig. 108).

Suspensorium

Squamosal: The squamosal is clearly delineated in all the material examined. The otic and zygomatic rami are formed and become slightly more robust with age (Fig. 107).

Quadrate: The quadrate remains a cartilaginous element in all *Uperoleia* species.

Neurocranium

Sphenethmoid: The sphenethmoid is not ossified at metamorphosis. It begins to ossify ventrally before the posterior portions of the nasal cups ossify dorsally (Fig. 108B, 107A). Initial dorsal appearance is as two V-shaped elements, which are cartilaginous medially. The medial cartilage eventually ossifies (Fig. 107K) and the elements thicken (Fig. 107L) to become rectangular blocks of bone, not confluent medially (Fig. 4).

Otoccipital: Major mineralization of the prootic appears to commence at about the time that the nasals begin to mineralize (Fig. 107C). The prootic remains separated from the orbital edges of the frontoparietals for the greater period of development (Fig. 107). Ossification of the epiotic eminences remains incomplete until late in development (Fig. 107). Dorsally the exoccipitals progressively ossify until they are confluent with the posterior extremities of the frontoparietals (Fig. 107K). Ventrally confluence of the exoccipitals and the alae of the parasphenoid occurs relatively early (Fig. 108). The prootic and exoccipital never become confluent to form an otoccipital element in Uperoleia (Fig. 107).

Mandible: Ossification of the mandibular element is complete in the sequence examined.

Hyolaryngeal skeleton: The cartilaginous hyoid plate appears initially with clearly delineated unadorned anterior hyale, poorly developed alary processes, cartilaginous posterior processes and cartilaginous posterior cornua (Fig. 109).

The alary processes remain poorly defined laterally until final definition is achieved. This is at about the time that ossification of the posterior cornua is complete (Fig. 109). The anteromedial processes of the anterior hyale appear initially as faint slender cartilaginous projections which thicken slightly and then extend posterolaterally eventually fusing with the anterior hyale laterally. The resultant gap becomes filled with cartilage and the adult condition is achieved (Figs. 109, 5).

4.3.5 Uperoleia rugosa - postmetamorphic development

Cranial elements

Dermal roofing bones

Frontoparietals: The frontoparietals are well ossified in the material examined. They are approximately $^{3}/4$ ossified in the earliest specimen (Fig. 110A) and continue to ossify medially until they become only poorly separated (Fig. 110H,K). However, rate of ossification relative to changes in other elements, varies greatly between specimens (see Fig. 110K,L). The prootic is confluent medially with the lateral extremities of the frontoparietals in all the material examined.

Nasals: The nasals are moderately well ossified in the earliest specimen (Fig. 110A). They reach their adult condition relatively early in the sequence (Fig. 110E).

Maxillary arch: The premaxillary, maxillary and quadratojugal are fully developed in this series. Uperoleia rugosa is an edentate species.

Palatal bones

Parasphenoid: The parasphenoid is fully developed in all the material examined.

Vomers: Vomerine fragments do not occur in any of this material.

Palatines: The palatines are relatively slender in the earliest specimen (Fig. 111A), but of approximately mature length. These elements thicken during development (Fig. 111).

Pterygoid: The pterygoid is fully developed in all the material examined.

Suspensorium

Squamosal: The squamosal shaft and otic ramus are fully developed in all the material, but the zygomatic ramus does not develop until relatively late (Fig. 110G).

Quadrate: The quadrate is cartilaginous in this species.

Neurocranium

Sphenethmoid: The ventral sphenethmoid has begun to develop in the earliest specimen (Fig. 111A). The dorsal sphenethmoid appears first as a V-shaped ossification at the termination of the nasal cups

(Fig. 111B). However, dorsal development is masked by the frontoparietals (Fig. 110B). The dorsal development becomes independent of the frontoparietals (Fig. 110G) but the adult condition of tenuous contact with the nasals is only approached in the largest specimen (Fig. 110L).

Otoccipital: Initially the exoccipitals are not confluent dorsally with the posterior extremities of the frontoparietals (Fig. 110A), nor with the alae of the parasphenoid ventrally (Fig. 111A). Such confluence is achieved, however, relatively rapidly (Figs 110, 111). The prootic is overlain by the lateral extremities of the frontoparietals in all the material examined, but ossification of the epiotic eminences is incomplete at first (Fig. 110A,C,D). The prootic and exoccipital do not become confluent in this species. The columella is fully ossified in all the material examined.

Mandible: The mandible is fully ossified in the material examined.

Hyolaryngeal skeleton: The hyoid is fully formed and the posterior cornua fully ossified in all the material examined (Fig. 112).

Postcranial elements

The postcranial elements are fully developed in the material examined. The condition of the carpal and tarsal bones could not be ascertained as these elements were crumbly and poorly stained (?decalcified by formalin).

It was not possible, then, from an examination of this material to determine at what stage the fusion of distale carpale 2 and 3 occurs. However, fusion of these elements had occurred in a female specimen of a S-V length of 20.2 mm (AM R89110) and in a second specimen of a S-V length of 19.9 mm (AM R90615).

4.3.6 Ranidella signifera

Stage 42

No apparent mineralization or ossification are detectable, but changes to the shape of the chondrocranium have commenced.

Stage 43 Cranium

Dermal roofing bones: The frontoparietals are ossified as slender lengths of bone on the edges of the orbits. Ossification of the nasals has not commenced.

Maxillary arch: Neither the premaxillaries, maxillaries, quadratojugals or teeth have begun to ossify.

Palatal bones: The parasphenoid has begun to ossify, very faintly, at the junction of the cultriform process and the alae, but the vomers, palatines or pterygoids are not detectable.

Suspensorium: The squamosal shaft has begun to ossify. The quadrate remains cartilaginous in this species.

Neurocranium: The exoccipital has begun to ossify both dorsally and ventrally in the region of the condyles. The prootic, sphenethmoid, columella and mandible remain unossified.

Postcranial elements

Pectoral girdle and limbs: The humerus and radioulna have begun to ossify together with the scapula, clavicle and coracoid.

Pelvic girdle and limbs: The ilium, femur, tibiotarsus, astragalus/calcaneum, the metatarsals and the first phalanges of toes III and V have all begun to ossify.

Vertebral column: Ossification is apparent on the eight presacral vertebrae but not on the sacral vertebrae and the urostyle.

Stage 44 Cranium

Dermal roofing bones: Ossification of these elements remains as in stage 43.

Palatal bones: Ossification of these elements remains as in stage 43 with slightly greater ossification of the parasphenoid giving a triangular shaped bone.

Suspensorium: Ossification has commenced on the otic ramus of the squamosal.

Neurocranium: Ossification remains as in stage 43.

Postcranial elements

Pectoral girdle and limbs: The suprascapula, scapula, coracoids and clavicles have begun to ossify and the humerus and radioulna continue to ossify. No metacarpals have ossified.

Pelvic girdle and limbs: The ilium, femur, tibiotarsus, astragalus/calcaneum, metatarsals and the first phalanges of toes II, III and IV are ossifying.

Vertebral column: All vertebrae are now ossifying. The urostyle remains as three distinct cartilaginous elements.

Stage 45 Cranium

Dermal roofing bones: Ossification of the frontoparietals has extended posteriorly to encroach slightly posteromedially behind the orbit. The nasals have not yet begun to ossify.

Maxillary arch: Ossification of the premaxillary has commenced and a sliver of ossification of the maxillary occurs on the anteroventral edge of the pars dentalis. The quadratojugal has not begun to ossify.

Palatal bones: The alae of the parasphenoid are well defined; the cultriform process is short and truncated. Vomers, palatines and pterygoids are not defined.

Suspensorium: The squamosal shaft and the otic ramus of the squamosal are ossified.

Neurocranium: The exoccipitals are ossified dorsally and ventrally. The prootic and columella are unossified. Both the dentary and angulosplenial of the mandible have commenced ossification.

Postcranial elements

Pectoral girdle and limbs: In addition to the already ossifying elements, the metacarpals have begun to mineralize.

Pelvic girdle and limbs: The metatarsals of all toes and the first phalanges on toes II, III, IV and V and the second phalanges on toes III and IV have begun to ossify.

Vertebral column: All the vertebrae are ossifying. Fusion of the three urostyle elements has begun with some dorsal ossification.

Stage 46 Cranium

Dermal roofing bones: Ossification of the frontoparietals is as in stage 45. The nasals have not begun to ossify.

Maxillary arch: The premaxillaries and maxillaries are ossifying. The quadratojugal has not yet begun to mineralize.

Palatal bones: The parasphenoid remains the only element ossifying.

Suspensorium: The squamosal shaft and otic ramus are ossified.

Neurocranium: The exoccipital is partially ossified dorsally and ventrally. The prootic has begun to ossify ventrally. The dentary and angulosplenial continue to ossify.

Post cranial elements

Pectoral girdle and limbs: The metacarpals but no phalanges or carpal elements, have begun to ossify.

Pelvic girdle and limbs: The metatarsals and phalanges on all toes, but no tarsal elements, have begun to ossify.

Vertebral column: The vertebrae continue to ossify but none is fused dorsally. The urostyle elements are fusing and ossification is occurring in both the dorsal and ventral elements.

At metamorphosis, then, the following elements have commenced ossification.

Cranium: Frontoparietals, premaxillary, maxillary, parasphenoid, squamosal shaft and otic ramus, prootic, exoccipital, dentary and angulosplenial of mandible.

Post cranial elements: Suprascapula, scapula, clavicle, coracoid, humerus, radioulna, metacarpals, ilium, femur, tibiofibula, astragalus/calcaneum, metatarsals, phalanges, vertebrae, urostyle.

The following elements have yet to commence ossification.

Cranium: Nasals, teeth, vomers, palatines, pterygoids, sphenethmoid, columella, posterior cornua of hyoid.

Post cranial elements: Phalanges of hands, carpal bones, tarsal bones.

Postmetamorphic ossification

Dermal roofing bones

Frontoparietals: The frontoparietals appear first as slender elements on the orbital edges, slightly thickened posteriorly and inclined medially. The elements change little throughout the sequence other than thickening slightly, particularly posteriorly (Fig. 113).

Nasals: These elements appear first as slender slips (Fig. 113B). They appear to thicken uniformly along their length. A second centre of ossification appears medially (Fig. 113C,D) initiating a change in shape (broadening) medially. The elements then broaden laterally (Fig. 113,G-I).

Maxillary arch

Premaxillary: The premaxillary is fully formed in the material examined.

Maxillary: The preorbital process is not apparent initially on the pars facialis of the maxillary (Fig. 113A). However, this element appears before the palatines are initiated (Fig. 113B).

Quadratojugal: This element is fully formed and almost articulated in the material examined.

Dentition: Dentition is almost complete in all this material except perhaps posterior to the pterygoid articulation (Fig. 114).

Vomers: Choanal vomerine fragments appear first at about the time the dorsal sphenethmoid begins to ossify (Fig. 114). The medial fragments are tiny and appear very late in ontogeny (Fig. 114).

Palatines: The palatines begin to ossify from ossification centres about midway between the ventral sphenethmoid and the preorbital process of the pars facialis of the maxillary. Ossification appears to progress medially and, to a lesser extent, laterally and then, having reached the medial extremity, further laterally (Fig. 114D) until the bones articulate with the maxillary (Fig. 114I).

Pterygoid: Ossification of the pterygoid appears to be complete at the commencement of this sequence.

Suspensorium

Squamosal: All elements of the squamosal are formed in this material. The zygomatic ramus increases in length and thickness (Fig. 113D,E) to the adult condition.

Quadrate: The quadrate is cartilaginous in this species.

Neurocranium

Sphenethmoid: The dorsal sphenethmoid ossifies after the ventral sphenethmoid (Figs 113, 114). Initially it appears as a strip of bone dorsally which expands to a V-shaped element with a cartilaginous centre. The cartilage eventually ossifies and the shape changes to a rectangular block (Fig. 113I).

Otoccipital: The prootic does not fuse initially with the posterolateral edges of the frontoparietals (Fig. 113A-G). Fusion occurs posteriorly (Fig. 113H) and then anteriorly (Fig. 113I). This is one of the last elements to complete fusion. The exoccipitals fuse with the frontoparietals dorsomedially at the same time as the prootic fuses with the posterolateral edges of the same element. Ventrally the exoccipitals remains disjunct from the alae of the parasphenoid for most of the developmental sequence, initially fusing laterally (Fig. 114F,G) and then medially (Fig. 114H,I). The columella is apparent in all the material examined, but is partly cartilaginous in smaller specimens. Ossification is complete after the appearance of the choanal fragments (Fig. 114D).

Mandible: Ossification of the mandible is complete in all the material examined.

Hyolaryngeal skeleton: The anteromedial processes of the anterior hyale of the hyoid lengthen, and in some cases become displaced laterally and appear hooked in the material. Both male and female specimens show the same hyoid morphology (Fig. 115) contra Trewavas (1933).

4.3.7 Pseudophryne bibroni

Stage 38 Cranium

Dermal roofing bones: The orbital edges of the frontoparietals have begun to ossify. Anteriorly they are very slender, broadening slightly posteriorly. No ossification of the nasals is detectable.

Maxillary arch: The alary processes of the premaxillaries have begun to ossify. No ossification of the maxillary or the quadratojugal is apparent.

Palatal bones: Very faint mineralization is detectable on the parasphenoid at the junction of the cultriform process and the alae. No ossification of the vomers, palatines or pterygoids is apparent.

Suspensorium: The squamosal shaft has begun to ossify but not the otic or zygomatic rami. The quadrate remains cartilaginous in this species.

Neurocranium: The exoccipitals are ossified in the condyle region and the prootic is faintly mineralized anteroventrally. The sphenethmoid and mandible are not mineralized.

Postcranial elements

Pectoral girdle and forelimbs (not yet erupted): The following elements have begun to ossify: suprascapula, scapula, clavicle, coracoid, humerus, radioulna, metacarpals I, II, III and IV, phalanx I on digits II, III and IV.

Pelvic girdle and hind limbs: The following elements have begun to ossify: ilium, femur, tibiofibula, astragalus/calcaneum, metatarsals I, II, III and IV, phalanx III on toes III and IV.

Vertebral column: All the vertebrae have begun to ossify but not the urostyle elements.

Stage 39

Ossification is essentially the same as for stage 38 with perhaps slightly more mineralization. The exceptions are the shaft of the squamosal and the alary processes of the premaxillaries which lack mineralization in contrast to the stage 38 specimen.

Stage 43

The elements ossified are those in stage 38 with greater ossification of the frontoparietals and the parasphenoid. The prootic, exoccipitals, squamosal shaft and alary processes of the premaxillaries are mineralized. Post cranially the ossification is as shown in the stage 38 specimen.

Postmetamorphic material

The cranial elements only are described in this material. The earliest specimen has only the premaxillaries, frontoparietals, squamosal shaft and otic ramus, exoccipitals in the condyle region, and ossification centres for the maxillaries, detectable (Fig. 116A).

Dermal roofing bones

Frontoparietals: Ossification of these elements appears first as narrow strips on the orbital edges (Fig. 116A). These thicken slightly posteriorly, and extend slightly posteromedially, terminating acutely (Fig. 116B-F). Posterolaterally these elements are not confluent with the prootic until maturity.

Nasals: The nasals commence ossification after metamorphosis, initially as ossification centres on the snout. Ossification of the nasals commences after the pterygoids but before the septomaxilla. The ossification centres grow to form slender strips (Fig. 116G) which thicken slightly and then appear to undergo a second ossification sequence medially (Fig. 116H,L). This occurs before the palatines appear.

Maxillary arch

Premaxillary: The premaxillaries are complete at metamorphosis. One of the first elements to appear in the postmetamorphic ossification sequence is the maxillary. Ossification progresses posteriorly (Fig. 116A-G) and eventually the element articulates with the quadratojugal (Fig. 116H-Q).

Quadratojugal: The quadratojugals appear postmetamorphically. From the material examined, it appears that these bones appear as fully shaped elements, ossification not proceeding stepwise.

Dentitition: *Pseudophryne bibroni* is an edentate species.

Palatal bones

Parasphenoid: Ossification commences at the junction of the cultriform process and the alae (Fig. 116B). Ossification progresses initially anteriorly on the cultriform process. This element appears to ossify synchronously along its length once the initial ossification centre has been established (Fig. 116C). The cultriform process appears triangular before ossification of the alae commences in a lateral direction. The alae are short for a great deal of the developmental sequence (Fig. 118P) but they eventually extend laterally to the adult condition (see Lynch 1971, p. 95).

Vomers: Vomerine fragments do not appear in this species.

Palatines: The palatines appear first as tiny centres of ossification (Fig. 116J) at about the same time as the dorsal sphenethmoid begins to ossify. The ossification centres extend laterally to become slender rods (Fig. 116L), then they thicken and reach the adult condition relatively early (Fig. 116N).

Pterygoids: The anterior ramus of the pterygoid is the first element to ossify (Fig. 116D). It terminates posteriorly in a bifid structure which differentiates into the medial and posterior rami at approximately equal rates (Fig. 116F,H).

Suspensorium

Squamosal: The squamosal shaft and otic ramus are ossified at metamorphosis. Both grow in length and eventually the zygomatic ramus begins to differentiate anteriorly (Fig. 116G). The zygomatic ramus does not differentiate until the shaft and otic ramus have achieved approximately terminal proportions.

Quadrate: The quadrate remains cartilaginous in this species.

Neurocranium

Sphenethmoid: Both the dorsal and ventral sphenethmoid appear approximately synchronously, but the ventral sphenethmoid is ossified to a greater degree than the dorsal element (Fig. 116H,I).

Otoccipital: The exoccipitals and prootic ossify independently and only become confluent at maturity. The prootic and frontoparietal elements are widely separated initially. They fuse first posteriorly (Fig. 116J) but had not fused anteriorly in the material studied here. The exoccipitals ossified slowly dorsally and had not reached the frontoparietal elements in this material. Ventrally the parasphenoid and the exoccipitals were separated (Fig. 116K). These elements first make contact medially (Fig. 116P) and eventually laterally. The columella is absent in *Pseudophryne bibroni*.

Mandible: The mandible is ossified at metamorphosis.

Hyolaryngeal skeleton: There appears to be little change to the hyolaryngeal skeleton once it has formed (Fig. 117) other than for the posterior cornua to ossify and for the cartilage of the anteromedial processes of the anterior cornua to strengthen.

Table 5. Values of r_s, the Spearman Rank Correlation Coefficient between individual bones in an ontogenetic series of <u>Uperoleia laevigata</u> (Sample 1). Null hypothesis H_o = samples are independent. Coefficients $\geqslant$ critical value at $p = .05$ are indicated with an asterisk. Raw data are provided in Appendix 1.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1																	
2	0.31																
3	0.57*	0.59*															
4	0.56*	0.52*	0.74*														
5	0.69*	0.38*	0.51*	0.57*													
6	0.52*	0.45*	0.67*	0.59*	0.48*												
7	0.30	0.58*	0.79*	0.74*	0.45*	0.63*											
8	–	–	–	–	–	–	–										
9	0.76*	0.40*	0.56*	0.59*	0.64*	0.56*	0.44*	–									
10	0.63*	0.51*	0.82*	0.93*	0.64*	0.64*	0.71*	–	0.65*								
11	–	–	–	–	–	–	–	–	–	–							
12	0.76*	0.59*	0.61*	0.59*	0.82*	0.68*	0.26	–	0.63*	0.73*	–						
13	0.18	0.20	0.64*	0.47*	0.05	0.25	0.46*	–	0.03	0.49*	–	0.10					
14	0.49*	0.63*	0.61*	0.36	0.41*	0.43*	0.37	–	0.43*	0.37	–	0.37	0.26				
15	0.58*	0.47*	0.58*	0.57*	0.31	0.51*	0.27	–	0.54*	0.64*	–	0.45*	0.41*	0.26			
16	0.73*	0.31	0.59*	0.52*	0.80*	0.59*	0.42*	–	0.71*	0.64*	–	0.88*	0.07	0.38*	0.34		
17	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
18	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.75*

Character codes: 1 = nasals; 2 = frontoparietals; 3 = maxillaries; 4 = quadratojugal; 5 = dentition; 6 = cultriform process of parasphenoid; 7 = alae of parasphenoid; 8 = vomers; 9 = palatines; 10 = pterygoids; 11 = squamosal; 12 = sphenethmoid; 13 = dorsal exoccipital; 14 = ventral exoccipital; 15 = prootic; 16 = columella; 17 = anterior hyale of hyoid; 18 = posterior cornua of hyoid.

Table 6. Values of r_s, the Spearman Rank Correlation Coefficient between individual bones in an ontogenetic series of *Uperoleia laevigata* (Sample 2). Null hypothesis H_o = samples are independent. Coefficients $\geqslant$ critical value at $p = .05$ are indicated with an asterisk. Raw data are provided in Appendix 1.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1																	
2	0.27																
3	0.59*	0.46*															
4	-	-	-														
5	0.55*	0.49*	0.60*	-													
6	0.46*	0.54*	0.75*	-	0.72*												
7	0.67*	0.36	0.64*	-	0.53*	0.63*											
8	-	-	-	-	-	-	-										
9	0.46*	0.45*	0.57*	-	0.47*	0.43*	0.44*	-									
10	-	-	-	-	-	-	-	-	-								
11	-	-	-	-	-	-	-	-	-	-							
12	0.39*	0.47*	0.52*	-	0.72*	0.52*	0.48*	-	0.12	-	-						
13	0.32	0.21	0.68*	-	0.60*	0.67*	0.61*	-	0.28	-	-	0.43*					
14	0.63*	0.20	0.48*	-	0.44*	0.40*	0.52*	-	0.11	-	-	0.45*	0.27				
15	0.58*	0.14	0.47*	-	0.32	0.37	0.62*	-	0.12	-	-	0.55*	0.46*	0.68*			
16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
17	-	-	-	0.54*	-	-	-	-	-	-	-	-	-	-	-	-	
18	-	-	-	0.47*	-	-	-	-	-	-	-	-	-	-	-	-	0.44*

Character codes: 1 = nasals; 2 = frontoparietals; 3 = maxillaries; 4 = quadratojugal; 5 = dentition; 6 = cultriform process of parasphenoid; 7 = alae of parasphenoid; 8 = vomers; 9 = palatines; 10 = pterygoids; 11 = squamosal; 12 = sphenethmoid; 13 = dorsal exoccipital; 14 = ventral exoccipital; 15 = prootic; 16 = columella; 17 = anterior hyale of hyoid; 18 = posterior cornua of hyoid.

Table 7. Values of r_S, the Spearman Rank Correlation Coefficient between individual bones in an ontogenetic series of Pseudophryne bibroni. Null hypothesis H_O = samples are independent. Coefficients $\geqslant$ critical value at $p = .05$ are indicated with an asterisk. Raw data are provided in Appendix 1.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1														
2	0.81*													
3	-	-												
4	0.86*	0.82*	-											
5	-	-	-	-										
6	0.88*	0.80*	-	0.88*	-									
7	0.75*	0.81*	-	0.71*	-	0.78*								
8	-	-	-	-	-	-	-							
9	0.84*	0.91*	-	0.86*	-	0.95*	0.84*	-						
10	0.74*	0.69*	-	0.80*	-	0.73*	0.63*	-	0.70*					
11	0.78*	0.78*	-	0.80*	-	0.81*	0.72*	-	0.68*	0.80*				
12	0.88*	0.87*	-	0.85*	-	0.99*	0.83*	-	0.97*	0.74*	0.71*			
13	-	-	-	-	-	-	-	-	-	-	-	-		
14	0.82*	0.85*	-	0.82*	-	0.88*	0.79*	-	0.86*	0.67*	0.72*	0.93*	-	
15	0.76*	0.89*	-	0.78*	-	0.89*	0.85*	-	0.92*	0.68*	0.72*	0.82*	-	0.85*

Character codes: 1 = nasals; 2 = frontoparietals; 3 = maxillaries; 4 = quadratojugal; 5 = dentition; 6 = cultriform process of parasphenoid; 7 = alae of parasphenoid; 8 = vomers; 9 = palatines; 10 = pterygoids; 11 = squamosal; 12 = sphenethmoid; 13 = dorsal exoccipital; 14 = ventral exoccipital; 15 = prootic.

Table 8. Values of r_S, the Spearman Rank Correlation Coefficient between individual bones in an ontogenetic series of *Ranidella signifera*. Null hypothesis H_O = samples are independent. Coefficients $\geqslant$ critical value at $p = .05$ are indicated with an asterisk. Raw data are provided in Appendix 1.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1															
2	0.82*														
3	–	–													
4	–	–	–												
5	0.89*	0.89*	–	–											
6	0.66*	0.62*	–	–	0.63*										
7	–	–	–	–	–	0.40*									
8	0.58*	0.70*	–	–	0.69*	0.51*	0.62*								
9	0.63*	0.77*	–	–	0.74*	0.72*	0.59*	0.62*							
10	–	–	–	–	–	–	–	–	–						
11	–	–	–	–	–	0.59*	0.85*	0.62*	0.47*						
12	0.74*	0.65*	–	–	0.72*	0.67*	–	0.73*	0.82*	–					
13	0.66*	0.62*	–	–	0.63*	1.00*	–	0.64*	0.73*	–	–	0.67*			
14	0.53*	0.70*	–	–	0.79*	0.51*	–	0.71*	0.71*	–	–	0.80*	0.49		
15	0.62*	0.72*	–	–	0.54*	0.52*	–	0.34	0.48*	–	–	0.52*	0.52*	0.66*	
16	0.42	1.00*	–	–	0.90*	0.63*	–	0.69*	0.75*	–	–	0.66*	0.63*	0.70*	0.72*

Character codes: 1 = nasals; 2 = frontoparietals; 3 = maxillaries; 4 = quadratojugal; 5 = dentition; 6 = cultriform process of parasphenoid; 7 = alae of parasphenoid; 8 = vomers; 9 = palatines; 10 = pterygoids; 11 = squamosal; 12 = sphenethmoid; 13 = dorsal exoccipital; 14 = ventral exoccipital; 15 = prootic; 16 = columella.

4.3.8 Comparative data and analysis

The sequence of developmental events (not always complete) for all the taxa described here, is summarized in Fig. 118. Coefficients of correlation for ossifying elements are shown in Tables 5-8 and raw data are provided in Appendix 2.

4.4 Discussion

To my knowledge, no study of the postmetamorphic development of bone within the Anura has been published. As indicated by Trueb (1985) such studies will be hindered by the lack of appropriate staging tables for such material.

The current study has been hampered further by the piecemeal nature of the material obtained e.g. premetamorphic material of _U. lithomoda_ were field collected from one site on the western boundary of the N.T. whilst the limited postmetamorphic material examined came from the vicinity of the foot of the Gulf of Carpentaria. In addition, premetamorphic material of _Ranidella signifera_ was laboratory reared whilst postmetamorphic specimens were field collected, and _vice versa_ for _Pseudophryne bibroni_. The postmetamorphic _U. laevigata_ material came from two separate populations and it was apparent that the two samples could not be grouped.

Nonetheless, even given all these pitfalls, some useful descriptive information has been obtained. Trueb and Alberch (1986) assessed ossification of the skull by the use of indices incorporating the area of the nasals and of the frontoparietals using digitizing techniques. This method could not be applied in this study because of the nature of the ossification sequence of the nasals. The initial part of the sequence resulting in a rod-like element is largely complete before the second (medial) sequence commences, the outlines of which remain indeterminate for a considerable period of time.

This also precluded shape analysis necessary for an analysis of the data within the conceptual framework of Alberch et al. (1979). An attempt has been made, however, to examine ossification sequences of individual bones relative to other bones. The difficulty here lies in the fact that recognisable stages within a continuum of development are not necessarily linear within a time framework. The only time framework available (in the absence of precise age data) is the snout-vent length of the individual and this is shown here and elsewhere (Shea 1983), not always to be a reliable indicator of age.

The data derived from postmetamorphic U. laevigata indicate that dermal and endochondral elements are ossifying independently (Tables 5,6). Trueb and Alberch (1986) arrived at a similar conclusion from a study of adult specimens of 66 taxa of frogs of varying sizes. Although the two samples of U. laevigata do not show identical results, this independence is arguably demonstrated. Clearly the analysis should be repeated with material of known ages, larger sample sizes and several samples, for unequivocal results.

These data indicate independence of two dermal elements in their ossification sequences, namely the nasals and the frontoparietals. Since these two elements are amongst the most variable in shape within Uperoleia, such independence is not unexpected.

Trueb and Alberch (1986) predicted that in small frogs, elements that show the greatest variation in shape are those that appear later in ontogeny. In U. laevigata which fits into both their small and medium categories, the frontoparietal elements are amongst the first to ossify, although the ossification sequence is a prolonged one in *U. laevigata*. The nasals are, however, postmetamorphic bones and together with the palatines, zygomatic ramus of the squamosal and vomers, fulfil this prediction.

Endochondral and dermal bones do not show the same degree of independence in *Ranidella signifera* and *Peudophryne bibroni* as exhibited by *U. laevigata* (Tables 7,8)); in fact developmental sequences of almost all elements show very good correlation in these species. Many elements reach their terminal states earlier in ontogeny in these species than in *U. laevigata* (e.g. preorbital process on pars facialis of the maxillary, zygomatic ramus of squamosal, maxillary and premaxillary teeth, frontoparietals).

In both *U. laevigata* and *R. signifera* there is, however, a lack of correlation in the ossification sequences of the exoccipital dorsally and ventrally. The components of the hyoid, however, develop synchronously in both species.

The independence of many ossification sequences in *U. laevigata*, if representative of the genus, implies a greater capacity for osteological divergence within *Uperoleia* than in *Pseudophryne* and *Ranidella* caused by heterochronous mechanisms. This prediction is supported by data presented in Chapter 5.

The data provided by premetamorphic stages indicate that the development stages of Gosner (1960) used in this study, are too broad to discriminate the precise order of appearance of cranial elements. However, information has been obtained, if somewhat fortuitously, allowing discrimination of sequences of development within certain elements. Trueb (1985) found similar constraints when she assembled data from 18 species of anurans and compared the information so obtained. However she did provide the following generalizations.

(i) In the majority of species, three bones appear before the onset of metamorphosis, namely the dermal elements, parasphenoid and paired frontoparietals, and the endochondral exoccipitals. My data support this generalization (see Fig. 118).

(ii) Amongst the first bones to ossify during the metamorphic processes (defined as the time at which total body length begins to shorten, larval mouthparts break down, the skin over the forelimbs becomes transparent and they are extruded from the body) are the septomaxilla, the premaxillary, the maxillary, squamosal, dentary and angulosplenial.

My data support this generalization in the main with the exception of the septomaxilla which is a postmetamorphic element in _Ranidella signifera_ and _Pseudophryne bibroni_ and the maxillary which is a postmetamorphic event in _P. bibroni_.

Trueb (1985) recorded that the nasals appear more or less contemporaneously together with the prootic as a metamorphic event in most species. It is in this element that the myobatrachine species examined differ most markedly. The development of the nasals is a postmetamorphic event in all the species in this study contrary to the data supplied by Trueb (1985). The exception in her list is the direct developing _Eleuthorodactylus nubicola_ for which the nasals are not recorded (Lynn 1942) indicating the probability of a postmetamorphic event since the analysis did not extend beyond metamorphosis. Interestingly this is the only leptodactylid species in Trueb's analysis.

Toward the end of metamorphosis, the mentomeckelian, quadratojugal, palatines and pterygoids are formed, together with the vomers, the appearance of which is highly variable.

These bones are all postmetamorphic features in the species studied here.

(iii) Amongst the post-metamorphic bones, if the quadratojugal, pterygoid and palatines are not present prior to metamorphosis, they are amongst the first to appear.

Although this is not strictly true for the myobatrachine species, it is an acceptable generalization.

The sphenethmoid is a postmetamorphic bone in all species except *Ascaphus truei* and *Rhinophrynus dorsalis* and my data support this observation. My data also support the appearance of the columella as a late post metamorphic event.

It would seem, then, that ossification of some elements within the myobatrachine genera studied here (e.g. nasals, vomers) show differing patterns from those found within other anurans from different families. However, as Trueb (1985) so cogently puts it, conclusions based on incomplete data for only 18 (now 24) of the some 3400 species of frogs are scarcely well based.

I do not propose, then, to attempt to draw major conclusions about ontogeny of bone in myobatrachine species from the limited descriptive data provided here, but tender the information to a growing data base from which some conclusions may be drawn at a later date.

The hypotheses proposed earlier regarding the nature of the osteological features separating *U. arenicola* and *U. inundata* and *U. rugosa* and *U. capitulata* can be examined in the light of the information obtained from this study.

The data provided on the development of the nasals in *U. laevigata* confirm the supposition that the condition of the nasals in *U. arenicola* is an earlier stage of development through which

U. inundata probably progresses (Fig. 107D compares with Fig. 7C and D of Tyler et al. 1981a). It is not possible to ascribe readily the relative exposure of the frontoparietal fontanelle, as the only Uperoleia material examined with a widely exposed frontoparietal fontanelle in the adult is the two U. trachyderma metamorphlings. However indirect evidence from U. laevigata, P. bibroni and R. signifera gives weight to the supposition that the exposure of the frontoparietal fontanelle shown in U. arenicola is an earlier ontogentic stage of the condition found in U. inundata.

Data from U. laevigata indicate that the nasals and the frontoparietals ossify independently. Thus one would expect a great capacity for change in these elements and paedomorphosis could be operating on each of these elements. Unfortunately these data cannot be related to a third element exhibiting difference between the two species and therefore these data do not negate the second hypothesis, that the features in U. arenicola are the result of paedomorphic arrest. It is not possible to discriminate between the two hypotheses using the data provided here. Resolution of the dilemma requires additional topotypic material for U. arenicola together with call data.

Regarding the second species pair, it would seem from the limited study of U. rugosa that the roofing of the frontoparietal fontanelle, although not a linear event with respect to the snout to vent lengths of the specimens, is a relatively rapid sequence in the ontogeny of the postmetamorphic frog. Hence the exposure of the frontoparietal fontanelle exhibited by U. capitulata is unlikely to be that shown by young (i.e. first season) frogs. Added weight to this hypothesis is the fact that of the specimens of U. rugosa examined from across the species range, none showed the frontoparietal fontanelle exposure exhibited by

U. capitulata except for the clearly subadult material examined in this study.

Similar arguments can be advanced for the relationship of the nasals with the dorsal sphenethmoid elements. As can be seen in Fig. 110, posterior ossification of the nasals appears to progress more rapidly than does ossification of the dorsal sphenethmoid elements. Hence separation of these elements in an adult frog would seem to be a real phenomenon and not a point sample of an ontogentic sequence. In addition data from *U. laevigata* show that the nasals and the frontoparietals ossify independently whilst the nasals and sphenethmoid and the sphenethmoid and frontoparietals are corelated.

Given these observations, I subscribe to the hypothesis that the conditions of the nasals, sphenethmoid and frontoparietal fontanelle exhibited by *U. capitulata* are the result of paedomorphic arrest of the ossification sequences of these elements, and I consider that the ontogenetic data described here confirm the taxonomic decisions made earlier. Call data for *U. capitulata* are necessary to provide unequivocal support for this contention. (P.D. McRae of the Queensland National Parks and Wildlife Service collected both *U. rugosa* and *U. capitulata* in February 1986 from the DPI Swamp at Charleville in Queensland. At the time, he thought there were two call types, but did not have a recorder to obtain the necessary information. K.R. McDonald pers. comm.).

A number of observations can be made about the ossification sequences of individual bones within the species studied here.

i. *Frontoparietals*. The frontoparietals ossify independently of the other dorsal roofing bones (e.g. nasals, prootic and exoccipital) in *U. laevigata*. The same comment cannot be made about *R. signifera* and

P. bibroni since the degree of ossification of these elements in these two species is very much less. The condition in R. signifera and P. bibroni resembles some other species of Uperoleia (e.g. U. talpa, and U. borealis) so it is clear that the exposure of the frontoparietal fontanelle is a paedomorphic feature in many Uperoleia species, as it is in Ranidella and Pseudophryne.

ii. Nasals. The sequence of ossification of the nasals in all three genera appears to be identical - once the ossification centres appear, the nasals become slender and elongate in an anterior position. A second ossification sequence then commences posteromedially and the final shape of these elements becomes delineated. As indicated earlier, the shape of the nasals during development in U. laevigata (Fig. 107D) resembles the shape of the nasals in U. arenicola. The shape of the nasals in other species of Uperoleia also resembles those during the developmental sequences studied here. Hence nasal shape in some Uperoleia species can be attributed to paedomorphic arrest.

iii. Premaxillaries. Anomalies in developmental sequences between the three genera have been observed within these elements. In U. trachyderma the palatine processes of the premaxillaries ossify before the pars dentalis and the alary processes, which seem to ossify concurrently. In U. lithomoda and R. signifera, all three elements appear to ossify simultaneously whilst in P. bibroni the alary processes of the premaxillaries ossify before the pars dentalis and the palatine processes.

Paedomorphosis does not appear to be implicated in shape changes in these elements within Uperoleia.

iv. Maxillaries. The preorbital process of the pars facialis of the maxillary is a postmetamorphic event in those species in which it occurs. The pars facialis of the maxillary does not manifest itself completely until the pars dentalis is fully formed.

Paedomorphosis is implicated, therefore, in the lack of a preorbital process of the pars facialis in some species of *Uperoleia*.

v. *Quadratojugal*. The quadratojugal is a postmetamorphic feature in the three genera examined and shows no intraspecific variation within *Uperoleia*.

vi. *Dentition*. Teeth appear in a more readily defined sequence in *U. laevigata* than they do in *R. signifera* - probably because the progression from no teeth to a full tooth complement on the premaxillary and maxillary arch appears to take a longer period of time than in *R. signifera*. Given this observation, it is probable that the presence of vestigial teeth in *U. micromeles* and the absence of teeth in many *Uperoleia* species is due to paedomorphic arrest of tooth development.

vii. *Parasphenoid*. Although the parasphenoid is one of the first bones to ossify in the three genera examined, the sequence of ossification varies between genera. In *Uperoleia* and *P. bibroni*, the cultriform process completes ossification before the alae (and in both cases the cultriform process is relatively long) whereas in *R. signifera* the alae become fully ossified before the relatively short cultriform process.

viii. *Vomers*. The choanal fragments of the vomers appear relatively early in *R. signifera* and are the last elements to appear in *U. laevigata*. They never appear in *P. bibroni*. The medial fragments appear late in both *R. signifera* and *U. laevigata*. Absence of vomerine fragments in many *Uperoleia* species is a further example of paedomorphic arrest.

ix. Palatines. The ossification sequence of the palatines is biphasic in all three genera. The ossification centres are approximately central to the anterior portion of the orbit. Ossification first progresses medially and then laterally.

Reduction of the palatines in *Uperoleia* and *Pseudophryne* is lateral to medial contrary to the usual anuran condition in which palatine reduction is from medial to lateral (Trueb 1973).

Reduction of the palatines in some species of *Uperoleia* would appear to be paedomorphic arrest of either the entire or part of the second ossification sequence of these elements.

x. Pterygoid. The ossification sequence of the pterygoid, a postmetamorphic sequence in all three genera appears to be similar in all the material examined. The anterior ramus appears first, becomes bifid posteriorly and the medial and posterior rami develop synchronously.

xi. Squamosal. The shaft of the squamosal appears first in all three genera closely followed by the otic ramus (both premetamorphic events). The zygomatic ramus does not appear until after metamorphosis, but does so relatively early in the ontogenetic sequences. In *U. lithomoda*, a species with a zygomatic ramus that is either tiny or absent, the ramus appears somewhat later.

The absence of the zygomatic ramus, then, could be interpreted as a paedomorphic feature, although the data presented here are not wholly conclusive. The appearance of the zygomatic ramus in *U. laevigata*, *P. bibroni* and *R. signifera* is relatively sudden and the ramus is fully shaped, if somewhat slender. In none of the species examined does it appear as a tiny knob which extends rapidly to assume the adult shape. It may be that relevant stages were not sampled but this appears unlikely in P. bibroni. I reserve my opinion, therefore, as to whether the absence of the zygomatic ramus is a paedomorphic feature or the result of a different ontogenetic process.

xii. Sphenethmoid. The development of the sphenethmoid is similar in all three genera.

xiii. Exoccipital. Some variability between genera in the relationship of the exoccipital with the frontoparietals is apparent, clearly due to the poor development of these elements in P. bibroni and R. signifera. Likewise the relationship of the exoccipitals with the parasphenoid varies, being more intimate at an earlier stage of development in U. laevigata than in R. signifera and P. bibroni.

xiv. Prootic. The relationship of the prootic with the frontoparietals is similar within the three genera. Ossification, or lack thereof, of the epiotic eminences is clearly a paedomorphic feature, again being one of the later ossification events.

xv. Mandible. The dentary and the angulosplenial are ossified at metamorphosis and the Mentomeckelians follow relatively quickly (see Fig. 118). There is no differentiation between genera.

xvi. Columella. The ossification sequence of the columella is similar in both Uperoleia and Ranidella. As one of the last elements to appear, its loss in Pseudophryne and R. riparia is clearly a paedomorphic feature.

xvii. Hyolaryngeal skeleton. The sequences of development of the anteromedial processes of the anterior hyale of the hyoid plate is subject to paedomorphic arrest in many species of Uperoleia and in P. bibroni and R. signifera. Trewavas (1933) illustrated the hyoids of a male and a female R. signifera from N.S.W. The male (26 mm S-V) showed the condition of adult U. laevigata and the female (21.5 mm S-V) that of the R. signifera material examined here. The male is a large specimen being slightly greater than the size range for males reported by Tyler (1979a). It is possible then, that the anteromedial processes of the anterior hyale of the hyoid in R. signifera continue to develop as frogs grow much larger than those in the sample studied here.

These data confirm the paedomorphic nature of the skull of Uperoleia indicated by Tyler et al. 1981a. Ten (or possibly eleven) features might be considered paedomorphic within the genus, namely:

a. The shape of the nasals.

b. Exposure of the frontoparietal fontanelle.

c. The absence of premaxillary and maxillary teeth.

d. The absence of a preorbital process on the pars facialis of the maxillary.

e. The lateral reduction of the palatines.

f. The absence of vomerine fragments.

g. The absence of medial fusion of the dorsal sphenethmoid.

h. The absence of confluence of the prootic and the exoccipital.

i. The absence of dorsal ossification of the epiotic eminences of the prootic.

j. The condition of the anteromedial processes of the anterior hyale of the hyoid plate.

k. The absence or reduction of the zygomatic ramus of the squamosal.

Postcranially, a twelfth feature occurs which might be construed as peramorphic (sensu Alberch et al. 1979) namely

l. Fusion of carpale 2+3.

Features g and h are common to all Uperoleia species, but nonetheless contribute to the highly paedomorphic nature of the genus.

Within Uperoleia there does not appear to be a consistent association between relative degree of paedomorphosis and relative mean adult body size. For example, the smallest species of Uperoleia, U. minima (S-V 16-21 mm) has moderately to well ossified nasals, an unexposed frontoparietal fontanelle, no teeth, a preorbital process on the pars facialis of the maxillary, laterally reduced palatines, no vomerine fragments, no medial fusion of the dorsal sphenethmoid, no confluence of the prootic and exoccipital, dorsal ossification on the epiotic eminences of the prootic, no zygomatic ramus of the squmosal, and fusion of carpale 2+3.

Trueb and Alberch (1986) found no clear relationship between absolute size (S-V length) and degree of ossification in the frogs they analysed. A similar situation was found by Hanken (1984) in the salamander genus Thorius in which species did not form a linear array of progressively smaller adults with correspondingly greater degrees of cranial reduction. Hanken found also that elements that appear late in ontogeny exhibit greater variation among species in terms of presence/absence than those elements that appear earlier in ontogeny. This is to be expected if species differ in the extent to which they complete the ancestral mineralization sequence. Trueb and Alberch (1986) provided data from the Anura to support this observation.

The same trends are apparent here, e.g. the vomers in Uperoleia species and the columella in Pseudophryne and Ranidella riparia.

The problems that paedomorphosis poses for phylogenetic studies have been raised by Eldridge and Cracraft (1980) and Wiley (1981). Paedomorphic processes can make derived characters appear primitive and thus outgroup comparison is necessary to check such processes.

Fink (1982) contends that while incorrect assessment of character generality and hence improper placement of a taxon can result from paedomorphic features, other non-truncated characters in the same organism could provide evidence for appropriate phylogenetic position. He goes on to say that outgroups are thus not needed in this case if ontogenetic criteria are being used for character assessment. Irrespective of whether outgroup comparison or ontogeny is used, the same result should be obtained provided the same data base is used.

Fink (1982) does go on to make the following proviso which is pertinent to the study here and in Chapter 5. He says that 'paedomorphosis can lead one astray in a phylogenetic analysis unless a sufficient portion of the morphology remains nontruncated, or unless data external to the system, such as parasitological information provides evidence that the characters are misleading.'

Uperoleia is a highly paedomorphic lineage. The foregoing study of ontogeny has validated the osteological characters used to delineate *U. capitulata* and *U. rugosa*, but has not shed light on the status of *U. arenicola*; it has provided information on the sequential events through which many bones pass during development in representatives of three myobatrachine genera and has indicated those features that are subject to paedomorphic arrest within species of *Uperoleia*.

In Chapter 5 I attempt to examine the hypothesis of Alberch (1985) that paedomorphic features should exhibit a high level of homplasy within a phylogenetic analysis.

5. PHYLOGENETIC ANALYSIS

5.1 Introduction

Amongst the Myobatrachinae, Uperoleia is the most speciose genus currently known. The 23 taxa recognised here comprise a conservative assemblage including a number of cryptic species, the occurrence of which probably accounts for the poor understanding of the genus prior to the revision of Tyler et al. (1981a).

The following cryptic species pairs are separable only by minor morphological differences or by call: Uperoleia tyleri and U. martini; U. laevigata and U. fusca; U. rugosa and U. capitulata; U. lithomoda and U. mimula; U. inundata and U. arenicola. All these pairs are sympatric in some areas within their ranges. In addition, U. russelli and U. talpa, and U. orientalis and U. borealis represent allopatric species pairs.

As shown in the preceding chapters, interspecific morphological divergence is slight and intraspecific variation in many characters is great, hence relationships between species are difficult to determine. To permit discussion of distribution patterns within the genus, some understanding of these relationships is necessary (Nelson and Platnick 1981).

The approach to phylogenetic systematics as outlined by Hennig (1966) and elaborated by Wiley (1976) is followed here. The problems inherent in this approach, and acceptable methods for resolution of these were discussed by Burton (1986). Burton did not discuss the 'ontogenetic approach' to phylogenetic analysis advocated by Nelson (1978). Other authors (e.g. Kluge 1985) do not support complete reliance upon ontogenetic criteria for character analysis (see Chapter 4) but use such data as an adjunct to other methods (Wiley 1981).

Hennigian analyses are based upon the recognition of character states to which polarity can be assigned with some degree of confidence. Derived character states, (apomorphies), are necessary for the recognition of phylogenetic relationships, and shared derived characters (synapomorphies) are indicators of common descent from an immediate ancestor. Primitive or plesiomorphic characters do not provide evidence for relationships, nor do derived characters found only in one taxon (autapomorphies).

Conflict amongst shared derived character states is considered to be due to homoplasy (convergence, parallelism or reversal). Construction of phylogenetic trees involves resolution of such conflicts (i.e. the most parsimonious choice [Wiley 1981]).

It follows, then, that within a given data matrix, a number of character states will be discarded during tree construction on the basis of (1) symplesiomorphy; (2) autapomorphy; (3) homoplasy; and (4) inability to assign polarity to the character with any degree of confidence.

Within the Anura, few phylogenies in a Hennigian sense, based on morphology, have been attempted at lower taxonomic levels (particularly at the species level). Arnold (1981) lucidly elaborated the hazards and frustrations inherent in such analyses. He lists seven criteria that must be satisfied for construction of phylogenies at low taxonomic levels:

"1. The group to be investigated must be holophyletic.

2. Enough derived features must be present and so distributed that the whole phylogeny can be constructed.

3. Exclusion of members of the group, whether known or undiscovered, will not produce misleading interpretations.

4. Correct character and character state homologies can be determined.
5. Enough correct polarities can be determined.
6. Appropriate character states can be assigned to the members of the group.
7. False indicators of relationship can be discriminated against."

(Arnold 1981, p. 14)

Criterion (3) immediately poses problems. It is highly likely that *Uperoleia* as recognised here, does not contain all taxa. Amongst the Museum material examined were specimens that could not be referred to any of the named taxa. Many parts of Australia, particularly in the northwest and northeast of the continent are inaccessible during the wet season when *Uperoleia* activity is maximal, and it is probable that undescribed taxa remain in these areas. In addition, Davies *et al.* (1985), indicated the possibility of a third species within the Pilboera.

Many of the currently recognised species are known only from small samples. *Uperoleia marmorata* is known only from the holotype and *U. orientalis* from the holotype and one paratype.

U. micromeles, *U. minima*, *U. arenicola* and *U. glandulosa* are known principally from the type series, and osteological studies are limited to single paratypes in each case.

In the case of *U. marmorata* and *U. orientalis* osteological features have been derived from X-rays of low resolution (due probably to decalcification of bone with age and preservation and contortion on preservation), and there are no data for the hyoid and for call. Data from the hyoid are not documented for any of these species and call data are unavailable for *U. micromeles*, *U. russelli*, *U. capitulata* and *U. littlejohni*.

If one argues that those taxa for which complete data sets are unavailable should be excluded from the analysis, the number of taxa under consideration is reduced from 23 to 16, i.e. approximately 25% of the taxa are removed. Clearly by the very magnitude of this exclusion, misleading results must be obtained.

An alternative would be to utilize some of the many algorithms available for tree construction that can make allowances for such absences in the data matrix. Such analyses must, of necessity, be weaker than those derived from complete data matrices.

The other criteria for phylogenies at low taxonomic levels of Arnold (1981) will be examined in the light of the data presented in this Chapter.

Uperoleia is a highly paedomorphic lineage (see Chapter 4). As indicated by Alberch (1985), the occurrence of paedomorphic characters (presumed to be extremely labile because of the simple nature of genetic control) may provide an explanation for the occurrence of homoplasy detected in phylogenetic analyses. Thus a high level of homoplasy might be predicted for Uperoleia. This factor, coupled with the possibility of misleading interpretations of relationships influenced by the incomplete data set for many species, indicates that a phylogenetic analysis of Uperoleia at this level can be little more than an academic exercise and probably will provide only broad species groupings.

Polarity of characters is here assigned by outgroup comparison (see Watrous and Wheeler 1981) with reference, where appropriate, to ontogentic data (Fink 1982).

Selection of an appropriate sister group is required and monophyly* of the taxa under consideration, must be substantiated. Other myobatrachine genera are examined for supportive evidence.

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* holophyly of Ashlock 1971; Arnold 1981.

5.2 Materials and Methods

Character states designated 0 are primitive. States designated 1,1',1" etc. are derived and are so designated if the relationship between states is undetermined. Where the direction of transformation can be recognised, polarities are indicated as 1,2,3. Letters are used for states of unknown polarities.

Data were analysed using the Phylip 2.7 package of Felselstein (Felselstein 1982, 1983 provide discussion of the biological and statistical inferences underlying the package).

The following algorithms were run:

1. <u>Wagner</u> - Wagner parsimony method.

The program allows changes in both direction along the character state tree 0→1 and 1→0. It does not assume a knowledge of the ancestral condition and produces an unrooted Wagner network. The modification used here was the insertion of a hypothetical ancestor which has the primitive states in all the characters where these are known. The resultant phylogeny is a rooted Wagner tree. The algorithm recognises ? (not known) and P (polymorphic) character states. The Wagner tree minimizes the total number of changes within a lineage. The implicit assumptions of this method are:

a. The characters are evolving independently.

b. Different lineages are evolving independently.

c. The ancestral state is not known (modification by insertion of ancestor in this analysis).

d. Over the evolutionary times relevant for the particular group, changes 0→1 or 1→0 are <u>a priori</u> improbable.

e. Retention of polymorphism for both states is far less probable than are changes of state.

f. Inequality of lengths of segments of the tree is not so extreme that two changes of state along a long segment are more probable than one change along a short segment. (Foreground hard copy Phylip 2.7 package, Felselstein 1973, 1978, 1979, 1981).

2. Sokal - Camin-Sokal parsimony method.

This algorithm uses the criterion of a minimum number of 0→1 steps suggested by Camin and Sokal (1965).

The assumptions of this method are:

a. That the characters are evolving independently.

b. That different lineages are evolving independently.

c. That state 0 is ancestral.

d. That rates of evolution are sufficiently slow over the lengths of evolutionary time involved that a change 0→1 is *a priori* an improbable event.

e. That reversion (1→0) or retention of polymorphism for both states (0 and 1) is far less probable than a change 0→1.

f. That inequality of lengths of branches of the true tree is not so great that having two changes on the long segment is more probable than one change on a short one. (Foreground hard copy Phylip 2.7; Felselstein 1973, 1978, 1979, 1981.)

This algorithm recognises the ? (unknown) and P (polymorphic) conditions and produces a rooted tree.

3. Mix - Mixed method parsimony.

Mix is a general parsimony program that carries out the Wagner and Camin Sokal methods in mixture, where each character can have its method specified. The program defaults to carrying out Wagner parsimony.

All of these programs are intended for morphological data consisting of discrete characters. These are assumed to be two state characters. Multistate characters were recoded into a series of two state characters using the method of Kluge and Farris (1969). Recoded data matrices are provided in Appendix 3.

Material examined

Uperoleia: as documented in Chapter 3.

Ranidella: *R. signifera*, UZA A193, A197, B898-928; *R. riparia*, UAZ A184, A189, A198; *R. parinsignifera*, UAZ A185; *R. tasmaniensis*, UAZ A186; *R. subinsignifera*, UAZ A190; *R. glauerti*, UAZ A191; *R. insignifera*, UAZ A192, A195, B929; *R. bilingua*, UAZ A194, A244, B763; *R. deserticola*, UAZ A259; *R. tinnula*, UAZ A188.

Pseudophryne: *P. semimarmorata*, UAZ B636; *P. bibroni*, UAZ B532, B540, A577, A172, B930-978; *P. coriacea*, UAZ A200, B537, B764; *P. guentheri*, UAZ A199, B538, B539, B765; *P. occidentalis*, SAM R17522; *P. douglasi*, WAM R20253. Data for external morphology are derived from Woodruffe (1972).

Arenophryne: *A. rotunda*, UAZ B531, B541, B762, A579-81, A760-1.

Assa: *A. darlingtoni*, UAZ A133.

Crinia: *C. georgiana*, UAZ B754, A134-6.

Geocrinia: *G. laevis*, SAM R8982, A, E.

Myobatrachus: *M. gouldii*, UAZ B491, B534-5, B757, A759.

Paracrinia: *P. haswelli*, UAZ B750.

Taudactylus: *T. diurnus*, UAZ B753, B759, A204; *T. acutirostris*, UAZ B759, A205-6; *T. eungellensis*, UAZ A392; *T. rheophilus*, UAZ B752, A755-6.

5.3 Results

5.3.1 Establishment of an outgroup and of monophyly of the taxa under consideration

Biochemical analyses of some myobatrachine genera do not provide evidence for a close relationship between *Uperoleia* and any of the following genera: *Ranidella*, *Crinia*, *Pseudophryne*, *Arenophryne*, *Myobatrachus* or *Metacrinia*. (Daugherty and Maxson 1982; Maxson and Roberts 1985; Chapter 4). Earlier phylogenetic studies of myobatrachine genera (e.g. Heyer and Liem 1976) pre-dated many taxonomic changes (e.g. the synonymy of *Glauertia* in *Uperoleia*, Tyler *et al*. 1981a) and hence are of limited value in establishing relationships.

Monophyly of the subfamily Myobatrachinae is supported by the following autapomorphies:

1. Alary processes of the hyoid plate are broad and wing-like.
2. The cricoid cartilage is divided ventrally.
3. The intervertebral discs remain unfused in the adult frog.
4. A palmar sesamoid is always present.
5. Absence of attachment of *M*. *intermandibularis* upon *M*. *submentalis*.

In seeking to establish monophyly of the *Uperoleia*/*Ranidella* lineage using the osteological and morphological characters employed here, no autapomorphies were recognised. However, *Ranidella* and *Crinia* share with some *Uperoleia* slender anteromedial processes of the anterior hyale of the hyoid. (The possibility remains that this feature is polymorphic in *Ranidella* - see Chapter 4).

The *Uperoleia*/*Pseudophryne* lineage shows evidence of monophyly: all *Uperoleia* and some *Pseudophryne* species share the autapomorphy of the presence of inguinal glands, and most *Uperoleia* species and *P*. *guentheri* share the autapomorphy of two raised compressed metatarsal tubercles.

In addition, the established clade of *Pseudophryne*, *Myobatrachus*, *Metacrinia* and *Arenophryne* (Maxson and Roberts 1985) shares with some members of *Uperoleia* the absence of a preorbital process on the pars facialis of the maxillary and the absence of premaxillary and maxillary teeth.

For these reasons, I have selected *Pseudophryne* as the sister taxon to *Uperoleia* and have regarded the other myobatrachine genera as an outgroup. The concept of monophyly of *Uperoleia* is supported by the autapomorphies of the presence of parotoid and inguinal glands.

Monophyly of *Pseudophryne* is supported by the autapomorphy of the presence of femoral glands (Woodruffe 1972).

5.3.2 Account of characters

Character 1 Development of the parotoid glands.

Parotoid glands are an autapomorphy uniting *Uperoleia* and are not found in any other myobatrachine genus. Thus, polarity cannot be assigned to the character states.

Four states occur within *Uperoleia*: A, the glands are poorly developed; B, the glands are moderately developed; C, the glands are well developed; D, the glands are hypertrophied.

Character 2 Development of the inguinal glands.

Inguinal glands are present in a poorly developed condition in some *Pseudophryne*, the more advanced character states are those of degree of development from the primitive condition.

Four states occur within *Uperoleia*: 0, the glands are poorly developed (almost indistinguishable); 1, the glands are moderately developed (clearly distinguishable but confined to a short area of flank); 2, the glands are well developed (extended along flanks); 3, the glands are hypertrophied (extended along flanks to reach parotoids anteriorly and coccygeal glands posteriorly).

Character 3 Development of the coccygeal glands.

Coccygeal glands are autapomorphies uniting Uperoleia and are not known in any other myobatrachine genus. It is not possible to assign polarity to this character.

Four states occur within Uperoleia: A, the glands are poorly developed; B, the glands are moderately developed; C, the glands are well developed; D, the glands are hypertrophied.

Character 4 Dorsal skin texture.

The dorsal skin is smooth to slightly tubercular in Pseudophryne; this condition is considered primitive by outgroup comparison. The other character states represent a progression in degree of rugosity.

Three states of dorsal skin texture are recognisable within Uperoleia; 0, skin smooth to faintly tubercular; 1, skin moderately rugose; 2, skin conspicuously rugose.

Character 5 Pigmentation of the ventral surface.

The ventral surface of almost all Pseudophryne is fully pigmented with lighter mottling and by outgroup comparison is considered plesiomorphic. Other character states represent reductions in the amount of pigment present. Three character states are recognised in Uperoleia: 0, ventral surface is fully pigmented; 1, ventral surface is variably pigmented ranging from faint dusting of pigment to islands of pigment granules; 2, ventral surface is unpigmented.

Character 6 Fringes upon the lateral borders of the fingers.

Fingers are unfringed in Pseudophryne and this is considered a primitive condition. Increases in the degree of fringing are represented by the other character states. Three character states are recognised: 0, fingers are unfringed or poorly fringed; 1, fingers are moderately fringed; 2, fingers are well fringed.

Character 7 The webbing.

The toes are unwebbed in Pseudophryne and in all other myobatrachine genera. This condition is considered primitive.

Two character states are recognised in Uperoleia: 0, toes unwebbed or basally webbed (this character is polymorphic in some species); 1, toes up to 1/2 webbed.

Character 8 State of development of the outer metatarsal tubercle.

The other metatarsal tubercle is poorly compressed and poorly developed in all Pseudophryne except P. guentheri and in all other myobatrachine species. This condition is considered primitive.

Two character states are recognised in Uperoleia: 0, outer metatarsal tubercle slightly compressed and poorly developed; 1, outer metatarsal tubercle strongly compressed and well developed.

Character 9 Teeth on the maxillary arch.

Teeth are present in all primitive anurans. They are absent in Pseudophryne, Arenophryne, Myobatrachus and Metacrinia but are present in all other myobatrachine genera. Since Pseudophryne, Arenophryne, Myobatrachus and Metacrinia are each others closest relatives (Maxson and Roberts 1985) it is likely that the immediate ancestor of Uperoleia and these genera was a toothed form giving rise to a series of untoothed genera, and a genus exhibiting both toothed and untoothed forms.

Presence of teeth is thus considered primitive. Absence of teeth or presence of vestigial teeth are examples of paedomorphic arrest of the development of teeth on the maxillary arch (see Chapter 4).

Three character states are recorded in Uperoleia: 0, teeth are present; 1, teeth are vestigial, present only on premaxillaries and the anterior position of the maxillary; 2, teeth are absent.

Character 10 Ossification of the nasals.

The nasals are poorly ossified in Pseudophryne and most other myobatrachines and this is considered primitive. Ontogenetic analysis indicates that the other two character states in Uperoleia are ossification sequences within the developmental trajectory of the nasals of Uperoleia. The diversity recorded in the nasals is attributed to heterochrony. Three character states are recognised: 0, nasals poorly ossified; 1, nasals moderately ossified; 2, nasals well ossified.

Character 11 Shape of the anterior edge of the nasals.

The anterior edges of the nasals are not crescentic in all other myobatrachines and this is considered primitive. This state is polymorphic within U. mimula. Two conditions are recognised: 0, the anterior edges of the nasals are not crescentic; 1, the anterior edges of the nasals are crescentic.

Character 12 Exposure of the frontoparietal fontanelle.

This feature is under the influence of heterochrony. The frontoparietal fontanelle is widely exposed in Pseudophryne and this is considered primitive. Other states have been shown by ontogenetic studies to be progressions in an ontogenetic sequence and hence are derived from each other.

Four character states are recognised: 0, the frontoparietal fontanelle is widely exposed; 1, the frontoparietal fontanelle is moderately exposed; 2, the frontoparietal fontanelle is poorly to moderately exposed; 3, the frontoparietal fontanelle is unexposed.

Character 13 Orientation of the orbital boundaries of the frontoparietals.

The orbital edges of the frontoparietals are angled medially in *Pseudophryne* and this is considered primitive. The direction of change of the other two characters cannot be assigned. Each state could equally well be derived from the primitive condition without an intermediate.

Three character states are recognised: 0, orbital edges are angled medially; 1', orbital edges are straight; 1", orbital edges are curved.

Character 14 Nature of the carotid canal groove.

The carotid canal grooves are absent in all myobatrachines except some species of *Taudactylus*. Absence is therefore plesiomorphic.

Two character states are recognised: 0, the carotid canal groove is absent in all specimens; 1, the carotid canal groove is present in at least some specimens. (Condition 1 is polymorphic.)

Character 15 Degree of ossification of the epiotic eminences of the prootic.

Ossification of the epiotic eminences is complete in all myobatrachines except some species of *Ranidella* and of *Taudactylus*. Complete ossification is therefore considered plesiomorphic.

Two character states are recognised: 0, ossification is complete posteriorly; 1, ossification is incomplete posteriorly.

Character 16 Zygomatic ramus of the squamosal.

The zygomatic ramus is short in all other myobatrachines and this condition is considered plesiomorphic.

Two character states are recognised: 0, zygomatic ramus is short; 1, zygomatic ramus is tiny or absent.

Character 17 Preorbital process of the pars facialis of the maxillary.

The preorbital process of the pars facialis of the maxillary is absent in Pseudophryne, Arenophryne, Myobatrachus, Metacrinia and some Uperoleia. The preorbital process appears late in ontogeny and hence is subject to change induced by heterochrony. It is present in most limnodynastines (the other subfamily of the Leptodactylidae represented in Australasia). I argue that, like maxillary teeth, it is more likely that the absence of the preorbital process of the pars facialis of the maxillary is a derived character state within the myobatrachine species exhibiting it.

The two character states are thus: 0, preorbital process of the pars facialis of the maxillary present; 1, preorbital process of the pars facialis of the maxillary absent.

Character 18 Nature of the palatines.

Lateral reduction of the palatines is found in Pseudophryne, Arenophryne, Myobatrachus, Metacrinia and Assa. Palatine reduction within the Anura is usually from medial to lateral. Ontogeny has shown that lateral ossification of the nasals is the second discreet sequence within the ossification process and hence lateral reduction is a paedomorphic event and is considered to be derived.

Three character states are recognised: 0, palatines do not extend beyond lateral extremities of nasals; 1, palatines extend between lateral extremities of nasals and palatal shelf of maxillary; 2, palatines extend laterally to reach palatal shelf of maxillary.

Character 19 Nature of vomerine remnants.

The vomers are greatly reduced in Uperoleia and two conditions are recognised, both of which occur in Pseudophryne, hence polarities cannot be assigned to this character.

A, vomerine fragments always or sometimes present (polymorphic – e.g. vomerine fragments occurred in only one of the seven specimens of U. talpa examined); B, vomerine fragments absent.

This feature is paedomorphic.

Character 20. Fusion of carpal elements.

The distale carpale 2 and 3 are not fused in Pseudophryne, Ranidella, Myobatrachus, Taudactylus, Paracrinia and Geocrinia and this is considered plesiomorphic.

Two character states are recognised: 0, distale carpale 2 and 3 separate; 1, distale carpale 2 and 3 fused.

Character 21 Ilial crest.

No ilial crest is found in any other myobatrachine genus and hence absence is considered plesiomorphic. Two character states are recognised: 0, ilial crest absent; 1, ilial crest present.

Character 22 Dorsal prominence of the ilium.

The dorsal prominence is small and inconspicuous in all myobatrachine genera and this state is considered primitive. It varies in shape greatly between species of Uperoleia but two basic conditions are recognised: 0, dorsal prominence tiny, rounded, not prominent; 1, dorsal prominence well-developed, elevated.

Character 23 Size of the distal prehallical element relative to metatarsal I.

The distal prehallical element is not prominent and is not measurable relative to metatarsal I in all other myobatrachine genera.

This state is considered plesiomorphic and the direction of change is 0→1→2→3.

Four conditions are recognised within this feature: 0, distal prehallical element not prominent, measurable relative to metatarsal I; 1, distal prehallical element up to 1/3 length of metatarsal I; 2, distal prehallical element approximately 1/2 length of metatarsal I; 3, distal prehallical element up to 2/3 length of metatarsal I.

Character 24 Nature of the anteromedial processes of the anterior hyale of the hyoid.

The anteromedial processes of the anterior hyale of the hyoid are fused laterally with the anterior hyale forming a thickening in Pseudophryne and other myobatrachine genera except Ranidella and Crinia. This state is thus considered plesiomorphic.

Two states are recognised which are sequential during ontogeny. 0, anteromedial processes of anterior hyale of hyoid fused laterally with the anterior hyale to form a thick protrusion; 1, anteromedial processes of the anterior hyale of the hyoid present and free.

Character 25 Nature of the male advertisement call.

The call of Pseudophryne species is a long pulsed call composed of more than six pulses. This is considered the primitive state by outgroup comparison. States 1 and 2 are derived by shortening the call.

Three character states are recognised: 0, a long pulsed call of greater than six pulses; 1, a short pulsed call of less than 6 pulses; 2, a click call in which the pulses are indistinguishable to the ear but detectable by electronic analysis.

All available data for Uperoleia species and other Myobatrachine genera are given in Table 9. See Appendix 2 for an account of characters in Pseudophryne and Ranidella.

Table 9. Character states and their polarities within Uperoleia and other myobatrachine genera. See text for explanation of character states. (-) indicates condition not known. (X) indicates feature absent.

Character number	U. tyleri	U. martini	U. laevigata	U. fusca	U. mjobergi	U. marmorata	U. micromeles	U. trachyderma	U. rugosa	U. capitulata	U. littlejohni	U. mimula	U. lithomoda	U. mimima	U. aspera	U. glandulosa	U. crassa	U. inundata	U. arenicola	U. borealis	U. russelli	U. talpa	U. orientalis	Pseudophryne	Ranidella	Arenophryne	Myobatrachus	Assa	Taudactylus	Crinia	Paracrinia	Geocrinia	Metacrinia
1	D	D	C	B	C	C	A	A	C	D	B	B	C	B	C	C	C	C	C	C	C	C	C	X	X	X	X	X	X	X	X	X	X
2	0	0	1	0	3	1	0	0	3	3	1	2	3	0	0	2	1	2	2	2	2	2	2	0	X	X	X	X	X	X	X	X	X
3	A	A	A	A	C	-	A	A	C	D	B	C	C	A	C	C	B	C	A	C	C	C	C	X	X	X	X	X	X	X	X	X	X
4	0	2	0	0	2	0	0	2	2	0	0	1	2	2	2	1	1	0	1	0	2	0	0	0	0	0	0	0	1	1	0	2	2
5	0	0	1	0	2	-	2	1	1	1	1	1	2	2	2	0	1	2	2	2	2	2	2	0	1	2	2	1	1,2	1	0	1	0
6	0	0	2	0	0	0	0	2	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	2	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
8	0	1	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	0	2	2	0	0	0	0	0	2
10	0	1	1	1	1	2	2	2	2	2	2	1	1	1	2	1	1	1	0	1	2	1	1	0	0	1	1	0	0,1	0	0	-	2
11	0	0	0	0	0	-	1	0	1	1	1	0,1	1	0	1	0	0	1	0	0	0	1	-	0	0	1	0	0	0	0	0	-	0
12	2	2	3	3	2	3	2	0	3	2	1	1	2	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	3,1	0	0	0	0
13	1"	1"	0	0	1"	0	0	0	0	0	0	0	1"	0	1"	0	1'	1'	0	0	0	0	0	0	1'	1'	1"	1'	1'	1'	1'	1'	0
14	1	1	1	1	0	-	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0	-	0	0	0	0	0	1,0	0	0	0	0
15	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0,1	0	0	1	0,1	0	0	-	0
16	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1
18	0	0	0	0	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	-	2	0	2	0	2	0	0	0	0	2
19	A	A	A	A	B	B	B	B	A	A	B	B	B	B	B	B	B	B	B	B	B	A/B	B	A,B	A	B	B	B	A	A	A	A	A
20	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	X	0	1	0	1	0	0	-
21	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-
22	0	0	0	0	1	1	1	0	0	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	-
23	0	0	0	1	3	1	3	0	1	1	2	2	2	1	3	2	2	2	1	3	3	3	3	0	0	0	0	0	0	0	0	0	-
24	0	0	0	0	1	-	-	1	1	1	1	1	1	-	1	-	1	1	1	1	1	1	-	0	1	0	0	0	0	1	0	-	-
25	0	0	0	0	0	-	-	0	1	-	-	1	2	2	2	2	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0

The phylogenetic tree constructed using the Wagner with Ancestor algorithm is depicted in Fig. 119. The tree constructed using the Camin-Sokal parsimony is depicted in Fig. 120 and the Mix-Wagner with no Ancestor tree is shown in Fig. 121.

5.4 Discussion

It is clear from qualitative examination of the data matrix for the 23 Uperoleia species recognised that any hypothesis about phylogenetic relationships must be tenuous and that, at best, only broad groupings can be recognised. The reasons for this are many and varied. Firstly, the volume and incomplete nature of the data matrix must preclude any hypothesis that is soundly based. Five of the 25 characters are incompletely sampled and thus cannot contribute strongly to the analysis. Of the remaining 20 characters, polarities cannot be determined for a further four characters.

It is apparent, therefore that there are insufficient features present, or so distributed, that the entire phylogeny can be constructed (Arnold 1981, point 2).

A high level of homoplasy was predicted from the ontogenetic study reported in Chapter 4. Characters 9, 10, 12, 15, 16, 17, 18, 19, 20 and 24 were predicted to be extremely labile, as they are influenced by heterochrony, and groupings of species using all or some of these characters should result in an extremely high level of conflict.

The Wagner analysis used constructs a tree with a minimum number of steps, but does not indicate which characters contribute to which steps; hence no information about homoplasy can be deduced from Fig. 119. However, the Camin-Sokal tree provides information on steps.

Many character states (?changes) are indicated as unknown, but an analysis of the data for those that are known (Fig. 120), shows a lack of homoplasy in characters 7 (toe webbing), 9 presence or absence of teeth), 12 (state 1 - moderately exposed frontoparietal fontanelle), 16 (condition of the zygomatic ramus of the squamosal, 17 (condition of the preorbital process of the pars facialis of the maxillary), 18 (relative lengths of the palatines), 24 (condition of the anteromedial processes of the anterior hyale of the hyoid) and 25 (state 1 - call pulsed, but less than 6 pulses in length). Character 19, predicted to be homoplasious was not included in the analysis because of uncertainty in the direction of change of the character.

Thus of the nine characters predicted to exhibit a high level of homoplasy, six belied the prediction, and together with character 7 (toe webbing) were the only characters in this analysis to exhibit a lack of homoplasy in one or all of the character states recognised.

These data do not, then, fulfil the prediction clearly amplified by Alberch (1985) but not hithertofore tested.

It is tempting to place emphasis on this observation and to question the underlying assumptions about paedomorphosis being a simple evolutionary mechanism of extreme lability. However, a note of caution must be introduced. Firstly the data base is incomplete for two of the characters in question, namely characters 24 and 25. Secondly the data base is small. Thirdly many of the postulates of Arnold (1981) for tree construction at this level are not met. Finally, the genus consists of species in the main, adapted to harsh environmental conditions and therefore, one might anticipate that some of the features examined will be highly adaptive.

A reexamination of Arnold's (1981) criteria is necessary at this stage in the argument. As has been indicated, Uperoleia fulfils criterion 1 as being holophyletic; criterion 2 is not met as the number of derived characters present is insufficient to construct a phylogeny of 23 species; criterion 3 possibly is not met as unknown taxa are anticipated within the genus - whether their exclusion has an influence on the relationships within the group recognised here is problemmatical, but I suspect not. Unknown taxa are likely to have restricted distributions and to bear close relationships with sympatric or parapatric taxa (see Chapter 6); criterion 4 relates to the determination of correct character and character state homologies - one can only hypothesize that this criterion has not been fulfilled and is related to the inability to meet criterion 2; criterion 6 is met in that appropriate character states can be assigned to the members of the group; criterion 7 probably is not satisfied. This criterion requires that false indicators of relationships can be discriminated against. This cannot be achieved in a number of cases due to sampling errors caused by polymorphisms in some character states. For example, one of the seven specimens of U. talpa examined showed vomerine fragments (character 19). For many of the species, only small samples of skeletal material were available (in many cases n=1) and the dangers of sampling errors in this system are vast.

Given then, that the data base does not lend itself to a rigorous phylogenetic analysis, the failure of many characters to meet the predictions of homoplasy within the system should be viewed as an observation worthy of further analysis within a more appropriate system. The genus Limnodynastes, the nominate genus of the subfamily Limnodynastinae, would be a good subject for such an analysis. It includes fewer species, and an hypothesis of phylogenetic relationships based on biochemical data has been proposed by Roberts and Maxson (1986). In addition, material for morphological and ontogenetic studies is readily available.

Given the fragile nature of the data base what hypotheses of relationships can be proposed from the three phylogenetic trees constructed and illustrated in Figs. 119-121?

Within the trees as constructed, a number of congruences are recognisable. The first and most obvious groupings are represented by a major dichotomy between the dentate and edentate species. A clade consisting of *U. tyleri*, *U. martini*, *U. laevigata*, *U. fusca*, *U. mjobergi*, *U. marmorata* and *U. micromeles* is recognised. The relationships between species within the clade vary, but congruence between Wagner and Sokal indicates a clade of *U. tyleri*, *U. martini*, *U. laevigata* and *U. fusca* within the larger clade. This lineage includes the most plesiomorphic species within the genus (Table 5). However, monophyly of the total clade is not supported by any autapomorphy and hence it is paraphyletic.

Monophyly of the edentate clade is supported by two autapomorphies - the absence of teeth and the reduction in the length of the palatines (character 9, state 2). Discrepancies between groupings within this clade are apparent between the three analytical methods. Wagner, Sokal and Mix result in the recognition of a clade consisting of *U. rugosa*, *U. capitulata* and *U. littlejohni* supported by the autapomorphy of absence of the preorbital process on the pars facialis of the maxillary.

The Sokal and Wagner analyses produce a clade consisting of *U. glandulosa*, *U. aspera*, *U. minima*, *U. lithomoda* and *U. mimula*. This clade is paraphyletic but the clade of *U. glandulosa*, *U. aspera*, *U. minima* and *U. lithomoda* with *U. mimula* as the sister species to the clade and recognised by the Mix analysis, is supported by the autapomorphy of the click call. (Note, however, that this character is incompletely represented in the data matrix.)

Sokal and Mix analyses produce a clade consisting of *U. orientalis*, *U. borealis*, *U. talpa* and *U. russelli* united by the autapomorphy of up to half webbed toes, but Wagner does not link *U. russelli* with the other three species. Both the Sokal and Mix anayses link the *U. orientalis* clade with a paraphyletic clade consisting of *U. crassa*, *U. inundata*, *U. arenicola* and *U. trachyderma*.

As predicted then, hypotheses of phylogenetic relationships based on the available data are weak in many respects. It would seem to be an acceptable hypothesis to suggest a dichotomy between the dentate and edentate lineages and that the *U. tyleri* clade is a valid grouping within the dentate lineage. Likewise within the edentate lineage, I hypothesise that two clades, i.e. the *U. orientalis* and the *U. rugosa* clades are recognisable but that all other relationships remain obscure.

The uncertain nature of the relationships hypothesized and of those for which no hypotheses can be proposed indicates a need to treat with caution the question of heterochrony as an important influence upon homoplasy which is seemly repudiated by the data presented here. As indicated earlier, an expanded ontogenetic/phylogenetic study of an appropriate lineage appears warranted to further investigate the role of developmental factors upon the occurrence of homoplasy within any lineage.

6. DISTRIBUTION PATTERNS

6.1 Introduction

Until recently, biogeography has been essentially a descriptive science, but the development of models to explain distribution patterns has directed such studies into a more quantitative approach. Probably the most popular models in current use are those of ecological determinism, dispersal biogeography and vicariance biogeography.

Ecological determinism is concerned with how species survive in a particular place. It requires knowledge of parameters such as microhabitat, vegetation type, soil type, climatic factors, interspecific competition and the physiological tolerances of a particular species.

On the other hand, dispersal biogeography is about centres of origin of taxa, and is not concerned with ecological factors other than as constraints upon the establishment of dispersing organisms.

Vicariance biogeography, in turn, ignores ecology, places little emphasis on dispersal, and concentrates on the effects of speciation on the distribution of organisms. Vicariance analyses rely heavily on knowledge of the geologic and climatic history of the area under discussion, and upon hypotheses of phylogenetic relationships within the organisms studied. Essential, too, to this approach is a knowledge of relationships within unrelated taxa showing congruent distribution patterns, since these organisms presumably have been subjected to the same vicariant influences as the taxa under study.

It is unusual for more than one of these models to be tested against a given set of distributional data (Endler 1982), even though it is probable that each model contributes in part to modern distribution patterns (e.g. Davis 1982). Thus, for a meaningful quantitative analysis of distribution patterns, a number of criteria must be satisfied.

Firstly, accurate and relatively complete distribution patterns are required, and well-founded hypotheses of relationships within the taxa under discussion are necessary. In addition, reliable data on distribution and on phylogenetic relationships of other non-related taxa are pertinent, together with a detailed knowledge of the climatic history of the area under consideration (Burton 1983). A knowledge of current climatic patterns, drainage systems, topography, soils and vegetation of the area covered provides further information.

It is abundantly clear that the distribution records of Uperoleia species are incomplete for many, if not all, taxa. There are a number of reasons for this: species are cryptic, they spend long periods of time underground or sheltering beneath vegetation or rocks and are active usually at inhospitable times when collecting is difficult. Many species are confined to the wet/dry tropics and are active at times when such areas are inaccessible. For these reasons, a close examination of the distribution patterns shown in Chapter 3 will indicate that they largely follow the paths of roads! A generalized distribution pattern is, in turn, misleading, as distribution within such an area is patchy. It is clear that local edaphic factors are important operants in accurate distribution patterns. Also important amongst local factors is, of course, the presence of water, which can be permanent or ephemeral.

As has been shown in Chapter 5, no well founded hypothesis of relationships within Uperoleia is proposed, and thus any discussion of speciation patterns in terms of vicariant events is precluded other than for a very few taxa. 'Phylogenetic biogeography' (sensu Wiley 1981) has yet to be applied to Australian taxa at the species level, so that comparative data are unavailable. In addition, the knowledge of Australia's past climatic and geologic history is poor for some areas of the continent and better known for others. Hence generalizations applied to the climate in the southeast probably do not apply to the northwest and extrapolation from a well-documented area to a poorly known one will be inaccurate.

Whilst the soils of Australia have been well mapped (Northcote *et al*. 1975), the level of definition is not necessarily sufficiently precise for analyses of distribution patterns within fossorial species. In addition, climatic factors are not always well documented, and the vegetation has been mapped in most areas on a broad scale only, if it has been mapped at all.

Given all these constraints, it is clear that the distribution patterns shown by species of *Uperoleia* cannot be analysed within the frameworks of any of the three models mentioned earlier, but can only be discussed in a qualitative way and in general terms.

6.2 Results

Generalized patterns of distribution for *Uperoleia* species in Australia (excluding the range extension of *U*. *mimula* into New Guinea) are depicted in Fig. 122. The following broad areas of sympatry are recognised: *U*. *tyleri*, *U*. *martini* and *U*. *laevigata* in southeastern Victoria; *U*. *tyleri* and *U*. *martini* in southeastern N.S.W.; *U*. *tyleri* and *U*. *laevigata* in coastal N.S.W.; *U*. *laevigata* and *U*. *rugosa* in northeastern N.S.W. and southeastern Queensland (on the Great Dividing Range north of Coffs Harbour); *U*. *laevigata*, *U*. *fusca* and *U*. *rugosa* in southeastern Queensland; *U. rugosa* and *U. capitulata* in southwestern Queensland and northwestern N.S.W.; *U. littlejohni*, *U. lithomoda* and *U. mimula* in northeastern coastal Queensland in the Townsville area; *U. lithomoda* and *U. mimula* on Cape York; *U. lithomoda* and *U. inundata* in the northern N.T.; *U. inundata* and *U. arenicola* on the edge of the Arnhem Land escarpment; *U. lithomoda* and *U. borealis* in the northeastern Kimberley and northwestern N.T.; *U. lithomoda* and *U. crassa* in the central Kimberley; *U. trachyderma* and *U. orientalis* on the Barkly Tableland; *U. trachyderma* and *U. borealis* in the northwestern N.T.; *U. crassa* and *U. minima* on the Mitchell Plateau, W.A.; *U. aspera*, *U. mjobergi* and *U. talpa* in the western Kimberley near Derby; *U. mjobergi* and *U. talpa* in the western Kimberley near Broome; and *U. russelli* and *U. glandulosa* in the Pilbara.

Areas of endemism recognised as geographic entities are as follows: Pilbara, W.A. (2 species); Kimberley, W.A. (6 species); Arnhem Land Escarpment, N.T. (1 species); Cape York, Torres Strait Islands and New Guinea (1 species); Einasleigh Uplands, Qld (defined by Stanton and Morgan 1977) (1 species); and southeastern Australia (Victoria and southern N.S.W.) (1 species) (See Figs 122-3)

Only *U. trachyderma* can be associated with a particular soil type. This species is confined to the self-mulching, grey cracking-clays of the Barkly Tableland, and to isolated portions of northwestern Queensland and northwestern Northern Territory.

Two other species can be associated with particular habitat types, i.e., with particular kinds of water bodies. *U. borealis* is found beside flowing water, at the edge of streams or flowing channels in inundated grassland. *U. lithomoda* is associated only with static water bodies. Although the two species have been located ostensibly sympatrically in the eastern Kimberley, examination of microhabitat shows a fidelity to moving or static water, even in an extremely small area.

Three species have been found calling at the same pond in southeastern Queensland (G. Ingram pers. comm.), and at a pool near Derby in W.A. In the latter case, *U. mjobergi* was calling at the edge or shallows of a pond whilst *U. aspera* called from distances up to two metres from the water margin. *U. talpa* was calling from the base of dry vegetation removed by distances of several metres from the pool.

Distribution patterns of few species conform to current drainage patterns. *U. capitulata* is associated essentially with the Bulloo drainage system of southwestern Queensland whilst *U. laevigata* is associated with the easterly flowing drainage systems of the Great Dividing Range. *U. martini*, *U. tyleri* and *U. fusca* are coastal species associated with the same drainage patterns as *U. laevigata* whilst *U. russelli* and *U. glandulosa* are associated with the westerly draining system of the Pilbara.

Disjunct distribution patterns are exhibited by *U. fusca*. A disjunction which is apparently real occurs between Miriamvale in southeastern Queensland and Eungella in central Queensland. A second disjunction may occur between Eungella and the Atherton Tableland (see p. 157). *U. micromeles* appears to have a disjunct distribution between the Tanami Sanctuary, N.T., and Staffords Bore, W.A. However, the intervening area has not been collected. The other major disjunct distribution is that of *U. trachyderma* which is associated with a particular soil type.

6.3 Discussion

The distribution pattern exhibited by *Uperoleia* is unique amongst Australian vertebrates. The pattern of a wide-ranging genus encompassing the Pilbara, the wet/dry tropics of the north of the continent and the eastern seaboard and yet absent in southwestern Australia has not been recorded previously. It is the latter observation – the absence of the genus in southwestern Australia – that is the most striking feature of this pattern. Given the range of stressful environments that *Uperoleia* species encounter throughout the range of the genus, it seems unlikely that representatives could not survive in the temperate environment of the southwest. Of the anuran genera considered as closest relatives to *Uperoleia* (see Chapters 4,5), *Pseudophryne* has a distribution in the Pilbara, in southwestern Australia, across the southern part of the continent including South Australia and Tasmania, and extending north up the east coast to southeastern coastal Queensland. The genera *Myobatrachus*, *Arenophryne* and *Metacrinia* are endemic to southwestern Australia, with *Arenophryne* extending north to Edel Land on the central Western Australian coast.

Three limnodynastine genera are fossorial in southwestern Australia – *Neobatrachus*, *Limnodynastes* and *Heleioporus*, but *Myobatrachus* and *Arenophryne* appear to occupy the subterranean niche within the Myobatrachinae. Contrary to the limnodynastine genera, the fossorial adaptations of these two monotypic genera are greatly at variance to those of *Uperoleia*. Both are frontwards burrowing species and have associated modifications to the hands, pectoral girdle and forelimbs (Davies 1984), and they occupy very coarse grained sandy soils (Tyler *et al*. 1980), habitats unusual for *Uperoleia*. In addition, both exhibit direct development and so are not so reliant upon free water for breeding (Roberts 1981, 1984).

The clade of *Pseudophryne*, *Arenophryne*, *Myobatrachus* and *Metacrinia* recognised by Maxson and Roberts (1985) clearly has a southern, if not southwestern, origin. One might infer, therefore, that the absence of *Uperoleia* in the southwest of the continent may be due to prior occupation of the fossorial niche by *Arenophryne* and *Myobatrachus*.

The most plesiomorphic group of species within *Uperoleia* is that formed by *U. tyleri*, *U. martini*, *U. laevigata* and *U. fusca*. This is a southeastern species group, and if one applies the Progression Rule formalized by Nelson (1973), then the centre of origin for *Uperoleia* should be in the southeast of the continent. (Moore (1961) talked about the southeast as a centre of amphibian speciation.) The Progression Rule predicts that the most plesiomorphic members of a taxon occupy the centre of origin of the taxon, whereas the more apomorphic members have dispersed away from the centre such that the more apomorphic a taxon, the further from the centre it would occur (Wiley 1981). However, from the, albeit weak, data provided in Chapter 5, the closest relatives to the most plesiomorphic taxa are, in fact, the most geographically isolated from them; i.e., *U. marmorata* and *U. mjobergi* found in the northwest of the continent, and *U. micromeles* found in the centre.

Additionally, support for a centre of origin in the southeast of the continent conflicts with the evidence that the genus is not represented in the southwest. It is well documented, particularly amongst the amphibian fauna, that close phylogenetic relationships exist betweeen southwestern and southeastern representatives of taxa. Wide-ranging distributions across the southern part of the continent have been thought to be disrupted by marine incursions of the Murray and Eucla basins, by the onset of aridity and by successive lowering of sea levels. What have been regarded as cognate species have been recognised within the southwest and the southeast. These were purported to be the result of multiple invasions from east to west and west to east corresponding with the glacial periods of the Pleistocene (Littlejohn 1967, 1981; Main *et al*. 1958; Main 1968; Martin 1972).

Recent biochemical studies using electrophoresis and serum albumins, and the 'biological clock' derived from measures of immunological distances between these taxa, have placed the divergence time of east and west taxa back into the Pliocene and late Miocene with the resultant tenet that much of the speciation in these two centres has been *in situ* (Barendse 1984; Maxson and Roberts 1984, 1985; Roberts and Maxson 1985a,b; Roberts and Maxson 1986). In addition, these authors support the time-framework of their 'clock' dates with current changes to the previous view that the glacial periods in the Pleistocene were periods of increased rainfall and lowered sea levels that made the barrier of the Nullarbor Plain passable. It is now thought that the last glacial maximum was a severely arid period in Australia (Bowler *et al*. 1976; Galloway and Kemp 1981; Wynrwoll 1979). Roberts and Maxson (1985b) deduce that similar patterns probably occurred during the other glacial periods of the Pleistocene, and hence the Nullarbor Plain remained a barrier to 'multiple invasions' of frogs.

The earlier timing of divergence of east/west taxa makes even more inexplicable the absence of *Uperoleia* from the southwest if the centre of origin of the genus was in the southeast, since corridors of dispersal must have existed in the centre of Australia during these ancient times.

Adaptations to aridity exemplified by *Uperoleia* species are not well developed in the southeastern species. The development of the outer metatarsal tubercle is a fossorial adaptation, yet in *U. martini*, *U. tyleri*, *U. laevigata* and *U. fusca*, the outer metatarsal tubercle is poorly developed. In addition, the hindlimbs are relatively long and the dorsal prominence of the ilium is small and rounded - features not found in the other species of *Uperoleia*.

The climate of southeastern Australia is thought to have been relatively stable, with temperate rainforests as the dominant vegetation type in the Miocene (Galloway and Kemp 1981). Hence adaptations to aridity in this region have not been subject to major selection pressures.

Examination of distribution patterns (Fig. 122) indicates that the uplift of the Great Dividing Range has been a major vicariant event in speciation within southeastern *Uperoleia*. The Great Dividing Range probably was uplifted while Gondwana was fragmenting and Australia drifting north. Collision with the Oriental Plate, and the uplift of the New Guinea Highlands, were probably associated with a greater rise of the Great Dividing Range (Archer and Fox 1984). *Uperoleia laevigata* is found principally at elevated altitudes on the Great Dividing Range whereas *U. tyleri*, *U. martini* and *U. fusca* are coastal species. *U. rugosa*, however, is found west of the Great Dividing Range along its southern more greatly elevated length, but occurs on the coast in areas of lower relief in southeastern Queensland (Fig. 25). This species shows features that are clearly adaptations to aridity, namely well developed outer metatarsal tubercles and relatively shorter hindlimbs (particularly noted in those specimens taken west of the Great Dividing Range).

The major disjunction in distribution exhibited by *U. fusca* (Fig. 90) is mirrored by two hylid species, *Litoria revelata* and *L. chloris*. *L. revelata* has a similar distribution to *U. fusca* if the possible range extension (see p. 157) is confirmed (Ingram *et al*. 1982). The northern element of the *L. chloris* distribution has been elevated to specific status, whilst the Eungella and southeastern coastal Queensland and northern coastal N.S.W. forms remain assigned to the nominate species (Davies and McDonald 1978; Davies *et al*. 1986). Reptile taxa showing similar distribution patterns include *Hemiaspis signata* (K.R. McDonald pers. comm.). A similar distribution pattern is exhibited by *Eucalyptus grandis* (Chippendale and Wolf 1981).

Reptiles showing a disjunction between southeastern Queensland and Eungella include *Phyllurus candiannulatus* Covacevich, 1975, *Calyptotis truncatus* (Peters, 1876), *Cacophis kreffti* Gunther, 1863 and *C. squamulosus* (Dumeril, Bibron and Dumeril, 1854) (Covacevich and McDonald 1984).

The real or apparent disjunction within the distribution patterns found in the Bowen/Rockhampton area of coastal Queensland coincides with the section line dividing Australia into two major physiographic units (Wasson 1982). The difference between the eastern and western regions is exemplified by modern hydrology. Most integrated drainage basins occur in the east, whereas only small areas occur in the west (Wasson 1982). This asymmetry of drainage is thought to have been a feature of Australia throughout the Cainozoic and even earlier when the continent was a part of Gondwanaland (Veevers and Evans 1975).

Uperoleia species probably have a low vagility because of their small size, short legs and walking rather than hopping gait; hence dispersal of species is likely to be passive rather than active and must be heavily reliant upon drainage systems. The distribution pattern of *U. trachyderma* (Fig. 60), however, belies this assumption. As has been indicated previously, *U. trachyderma* is confined to disjunct areas of self-mulching, grey cracking-clays found in the Northern Territory and Queensland. These soils are well mapped (Northcote *et al*. 1976), but those of the Barkly Tableland are considered to have evolved *in situ* (K.H. Northcote pers. comm.). The drainage patterns of the Barkly Tableland flow in two directions. Principal drainage is southwards via the Lake Eyre drainage system, converging via the Georgina River to the Channel Country of Queensland. The second system flows north toward the Gulf of Carpentaria. The occurrence of *U. trachyderma* along the Georgina River and at Lawn Hill in Queensland, is thus explained. The occurrence of the species at Newry Station in the far northwest of the Northern Territory remains an enigma. Given that there are a number of other vertebrate species with similar distributions on cracking clays; e.g., the monitor, *Varanus spenceri* (Pengilley 1981), the planigale *Planigale ingrami* (Parker 1973; Andrew and Settle 1982), and two species of bird the flock pigeon *Histriophaps histrionica* and the red chested quail *Turnix pyrrothorax* have their centres of abundance on these soils (S.A. Parker pers. comm.), it may be that the question of the origins of the Barkly Tableland soils should be reexamined in the light of the endemicity of the associated fauna. Another possible explanation, unsubstantiated, is that palaeodrainage patterns were different, and a system once occurred that was directed northwesterly from the centre of origin of the grey cracking-clays on the Barkly Tableland.

The high level of endemism in the Kimberley is matched by other vertebrate groups, e.g., amongst the Reptilia within the agamid genus *Diporiphora* and the scincid genus *Lerista* (Cogger 1986). The Kimberley has never been inundated by the sea since its elevation and is an ancient land mass. It is composed of tectonically-stable metamorphosed rock outcrops (Wasson 1982), which are presumably effective barriers to dispersal for *Uperoleia* species.

For example, the Napier Range appears to be a barrier to northward dispersal of U. mjobergi, U. talpa and U. aspera and to southward dispersal of U. crassa and U. lithomoda (Tyler et al. in press). The modern fauna of the Kimberley is effectively constrained by the Great Sandy Desert to the south and by the floodplains of the Northern Territory to the east. Eastern elements of the Uperoleia fauna do penetrate this easterly barrier (e.g. U. borealis and U. lithomoda) and the constraints upon dispersal by other species are not known.

Penetration of U. mimula into the adjacent lowlands of New Guinea is a common distribution pattern amongst faunal elements of Gondwanan origin (see Kikkawa et al. 1981).

In the past, areas of Australia have been successively arid to semi-arid and to humid and back again several times. In addition, major marine incursions, sea level changes and tectonic uplifts have altered the landscape substantially. Species have diversified as a consequence of numerous past fragmentations, bottlenecks and intense directional selection. Probably this sequence of events has occurred more often in the areas that we now know as the semi-arid zone (Baverstock 1982).

The distribution patterns in Uperoleia today must, to a great extent, reflect past forces, many of which have yet to be determined. The patterns are varied - some distributions follow generalized tracks (e.g. U. trachyderma); others remain inexplicable in terms of modern ecology or past events (e.g. the absence of the genus in southwestern Australia).

Many data remain to be collected before a rigorous analysis of the distribution patterns of this enigmatic, speciose genus can be undertaken.

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