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Systematic Revision of Australian *Scoteanax* and *Scotorepens* (Chiroptera: Vespertilionidae), with Remarks on Relationships to other Nycticeiini

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Abstract

Classical and numerical taxonomic approaches based on morphology and utilising electrophoretic information have been applied to clarify the status of Australian species hitherto placed in the genus *Nycticeius*. Eight named forms have been reduced to five species; these are placed in existing genera: *Scoteanax (rueppellii)* and *Scotorepens (orion, balstoni, sanborni* and *greyii)*.

Phylogenetic analysis of species representative of other Nycticeiini genera, and of geographic groupings of these Australian species, provides additional support for the above generic conclusions.

Indicators of gross morphology (skull, radius and lower tooth row lengths) in *Scotorepens* spp. vary in relation to their sex, and to latitude, longitude and several climatic variables, particularly average minimum temperatures in July.

Introduction

The named forms of vespertilionids considered in this study are: *Scotophilus greyii* Gray, 1843; *Nycticeius rueppellii* Peters, 1866; *Scoteinus balstoni* Thomas, 1906; *Scoteinus influatus* Thomas, 1924; *Scoteinus orion* Troughton, 1937; *Scoteinus sanborni* Troughton, 1937; *Scoteinus balstoni caprenus* Troughton, 1937; and *Scoteinus orion aquilo* Troughton, 1937.

These forms have long been the cause of great taxonomic confusion, both at the generic and specific levels. Dobson (1875) referred *rueppellii* and *greyii* to *Scotophilus* by placing them in the subgenus *Scoteinus*. Thomas (1906) placed *rueppellii* and *greyii* in the genus *Scoteinus* as did Miller (1907) who raised *Scoteinus* to generic rank (based principally on a study of the Australian species *balstoni* and *greyii,* but without reference to the type species, *Nycticeius emarginatus* Dobson, 1871). Troughton in Le Souef, Burrell and Troughton (1926) and Iredale and Troughton (1934) included *balstoni* and *influatus* within the genus *Scoteinus,* and Troughton (1937) added *orion* and *sanborni* to this genus. Tate (1942) recognised all the above named forms within the genus *Scoteinus* – however he offered the opinion that there was a need to study critically the

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type species of *Scoteinus* before settling on the placement of these Australian forms within *Scoteinus.* Troughton (1943) erected (with brief diagnoses) the genera *Scoteanax* for *rueppellii* and *Scotorepens* for the other forms. Tate (1952) relegated *Scoteanax* and *Scotorepens* to subgenera of *Scoteinus,* while Laurie and Hill (1954) considered them subgenera of *Nycticeius.* McKean (1966) merged *orion orion, orion aquilo, sanborni* and *balstoni caprenus* with *balstoni,* and placed this species, along with *rueppellii* and *greyii,* in *Nycticeius.* In so doing he followed Hollister (1918) and Simpson (1945) who considered *Scoteinus* a subgenus of *Nycticeius* – he did not deal with *influatus.* Ride (1970) merged *balstoni, orion,* and apparently *sanborni,* with *greyii.* He placed this species, along with *rueppellii* and *influatus* in *Nycticeius* and recognised no subspecies. Hall and Richards (1979) differed from Ride (1970) by recognising *balstoni* as a distinct species; they suggested that *orion, aquilo* and *sanborni* should be merged with *balstoni* – they did not deal with *caprenus.* Koopman (1978, 1984) supports the latter arrangement and recognised *caprenus* along with *orion, aquilo* and *sanborni* as subspecies of *balstoni.* He recognised *Scoteanax* and *Scotorepens* as subgenera of *Nycticeius.* Koopman (1978) also noted that Sinha and Chakraborty's (1971) placement of the type species of *Scoteinus (Nycticeius emarginatus)* into the distinctive genus *Scotomanes,* rendered the name *Scoteinus* unavailable for any of the other Indian, African and Australian species to which it had been applied.

It was pointed out by J.E. Hill (pers. comm.) that reviews of the systematics of these Australian forms have overlooked the genus *Oligotomus,* type species *Oligotomus australis* (= *Scoteanax rueppellii*). This generic name was proposed by MacGillivray, an Australian zoologist and collector, and validated by Iredale (1937) by publication of letters and extracts from MacGillivray's notebooks. The name is, however, preoccupied.

The phenetic and phylogenetic relationships of *Scoteanax* and *Scotorepens* are described in relation to other genera in the Nycticeiini tribe of Tate (1942), but recognising that *Scoteinus* is now placed within *Scotomanes* following Sinha and Chakraborty (1971) and *Baeodon* within *Rhogeessa* following La Val (1973). This leaves the following genera to be considered in this comparison: *Nycticeius* Rafinesque, 1819; *Scotoecus* Thomas, 1901; *Scotophilus* Leach, 1821; *Scotomanes* (as a subgenus of *Scotophilus* Dobson, 1875); *Rhogeessa* Allen, 1866; and *Otonycteris* Peters, 1859. Description of these relationships was assisted by reference to the revisions of Miller (1907) and Tate (1942) covering all the Nycticeiini; Hill (1974): *Scotoecus;* J.E. Hill unpublished data: *Scotomanes, Scotophilus* and *Nycticeius;* La Val (1973): *Rhogeessa.*

In an attempt to clarify the systematics of this group of species this study utilises a wider range of taxonomic characters and techniques than has previously been applied to them, but is based on the classical morphological approach. These include electrophoretic characters (Baverstock pers. comm.), multivariate analysis, including phenetic and phylogenetic analyses based on morphological characters, both external, skull and teeth; and morphology of glans penis and baculum. Resolution of the taxonomic status of two taxa *(sanborni* and *greyii)* depended upon examination of specimens which differ electrophoretically (Baverstock pers. comm.).

Methods

Morphology

Teeth

The species considered herein have a relatively reduced set of teeth (30) (Figure 1). There is considerable controversy over the missing incisors and premolars of bats. Miller (1907) considered that the permanently missing incisor in the upper jaw is the first ($I^{\underline{1}}$) on the grounds that $I^{\underline{1}}$ is sited on that part of the premaxilla which is reduced in bats. However Thomas (1908) and Andersen (1912) suggest that it is the outermost one ($I^{\underline{3}}$) – arguing that $I^{\underline{3}}$ is the site of the upper pre-canine diastema which receives the lower canine during tooth occlusal. Slaughter (1970) supports the latter two authors by noting that the inner remaining incisor is usually somewhat larger than the outer one. We have examined an *Emballonura nigrescens* (SAM M2838/3) from Mt Lamington, Papua New Guinea, which has three upper incisors in which $I^{\underline{1}}>I^{\underline{2}}>I^{\underline{3}}$ and a *Scotorepens caprenus* (EBU B157) from Mt Katherine, Northern Territory, which has a small accessory outer incisor on the right-hand side; this is half the height of the inner incisor. This provides additional reasons for us to follow the more recent authors and refer to the upper incisor as $I^{\underline{1}}$. Miller (1907) and Thomas (1908) also disagree as to the missing premolar. Miller considers it to be the first premolar ($P\frac{1}{1}$) and this is widely held to be the situation. Thomas, however, reasons that it is the second premolar ($P\frac{2}{2}$). Miller (1907) considers that the next upper premolar to go is either $P^{\underline{2}}$ or $P^{\underline{3}}$. In the lower jaw of the Microchiroptera $P_{\overline{3}}$ becomes reduced before $P_{\overline{2}}$. Following Miller (1907), we refer to the upper premolar as $P^{\underline{4}}$ and to the lower ones as $P_{\overline{2}}$ and $P_{\overline{4}}$.

Terminology of tooth structure follows Slaughter (1970) as indicated for lower (Figure 2a) and upper molars (Figure 2b).

Skull, Dentary and Externals

Twenty-five measurements of skull and dental characters and nine of external characters were recorded from adult specimens only listed in the section 'Specimens Examined'. Measurements for holotypes and unique specimens are listed in Appendix I. Subadults and juveniles were diagnosed on the basis of epiphyseal swellings of the metacarpal joints. The terminology used is indicated in Figure 1. All measurements were recorded with dial calipers. The positions of these measurements are indicated in Figure 3.

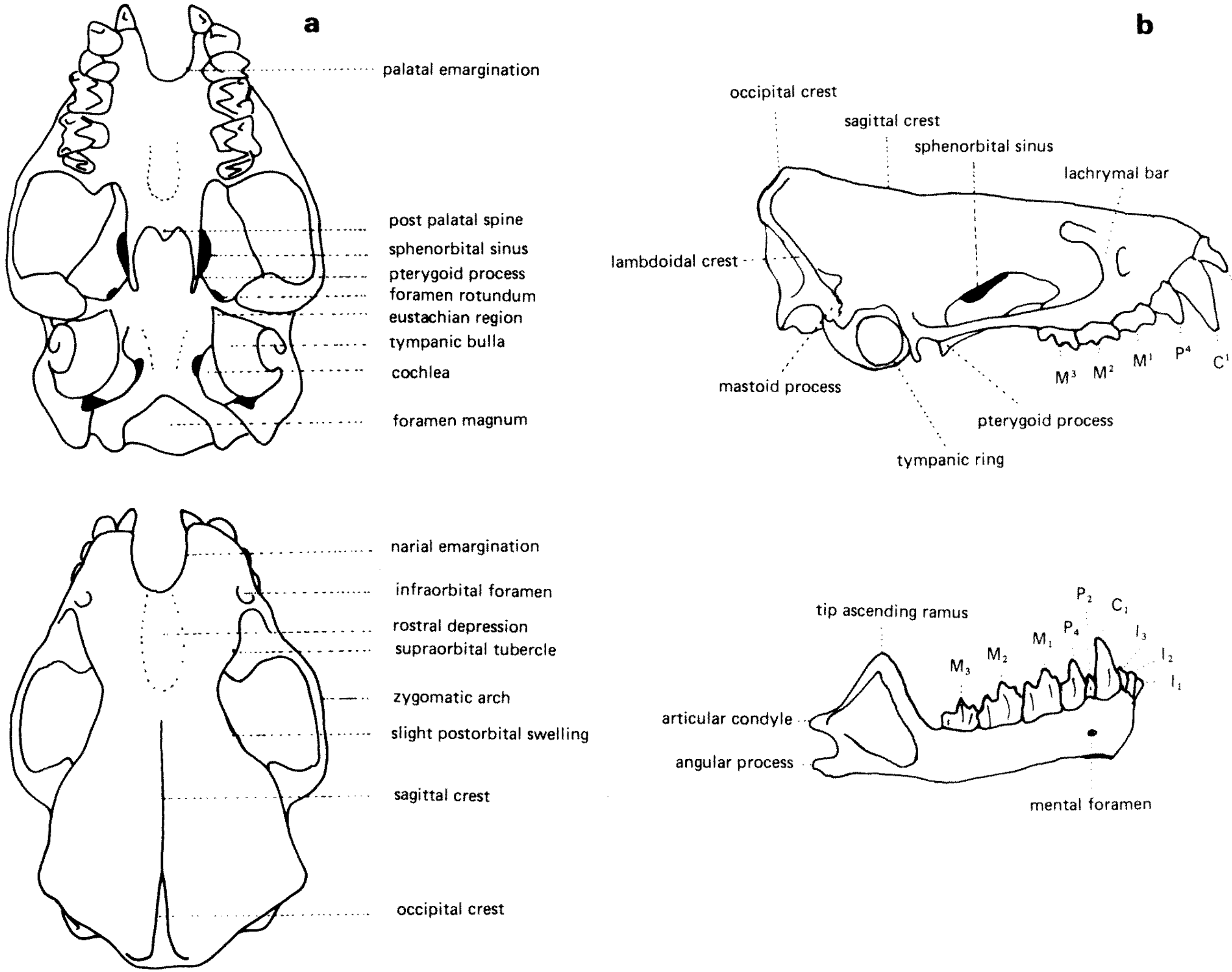


Figure 1 Terminology used for skull and teeth.

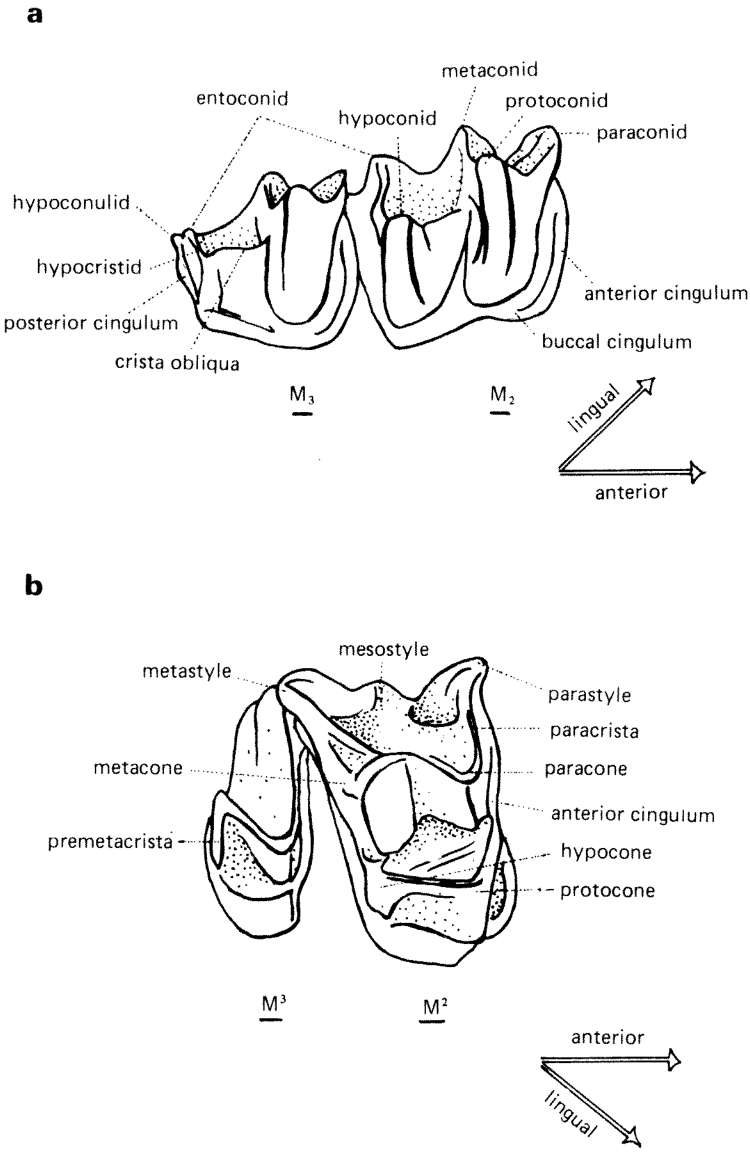
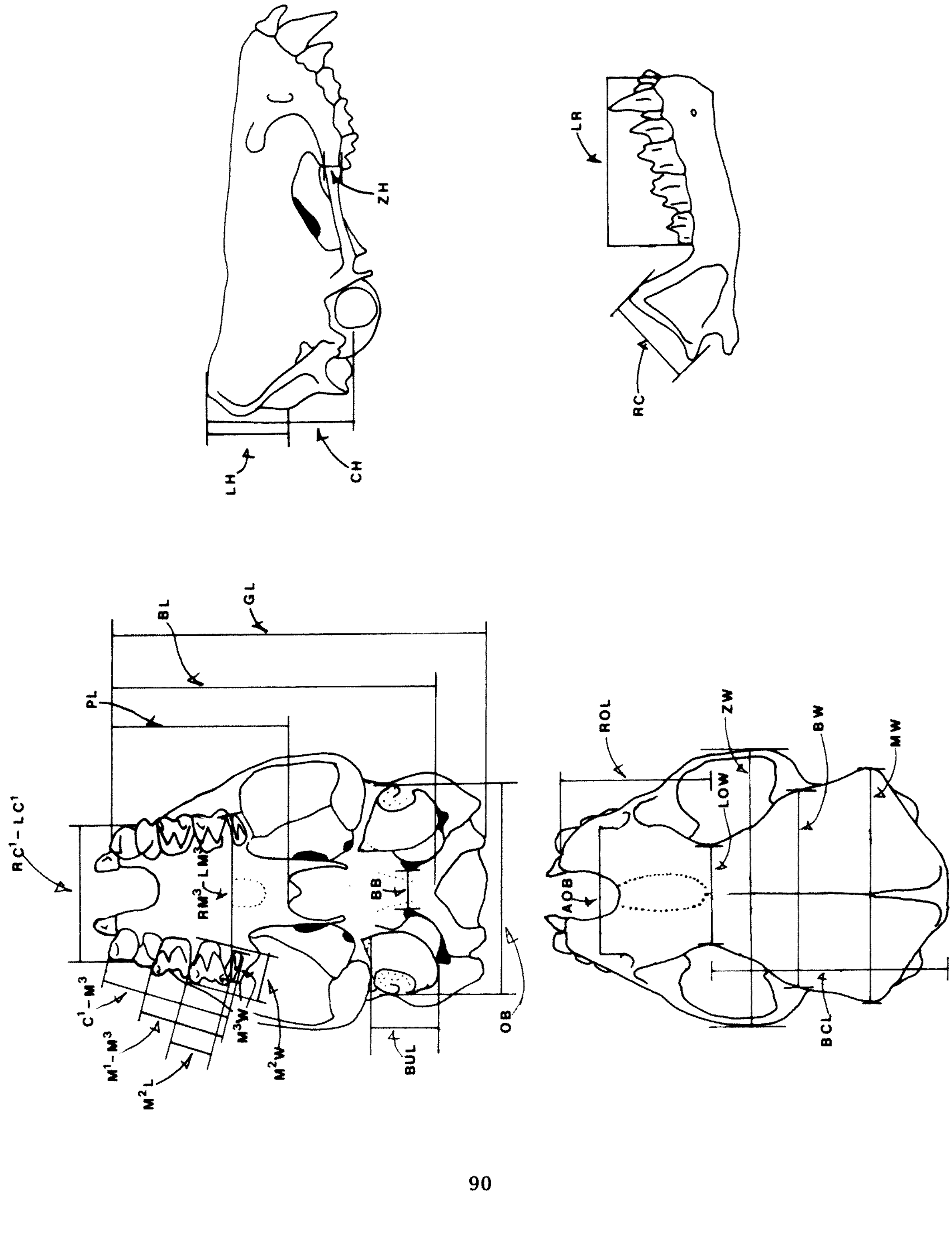


Figure 2 Terminology used for teeth morphology. Examples are second and third molars (a) lower. (b) upper,


ZH
LR
LH
CH
RC
RC¹-LC¹
PL
BL
GL
ROL
ZW
BW
MW
LOW
AOB
RM³-LM³
BB
C¹-M³
M¹-M³
M²L
M³W
M²W
BUL
OB
BCL

◀ **Figure 3** Skull and dentary measurements referred to in text and their recording points. GL: greatest length; AOB: anteorbital width, between infraorbital foramen; LOW: least interorbital width; ZW: zygomatic width; ZH: zygomatic height, above posterior edge of M^3; MW: mastoid width, between mastoid processes; ROL: rostrum length, from LOW to anterior edge of premaxilla; BCL: braincase length, from LOW to posterior edge of occipital; BW: braincase width, at centre of zygomatic-squamosal contact; CH: cranial height, lower arm of calipers placed level with pre- and basisphenoid, upper arm in contact with apex of skull; LH: lambdoidal height, distance between apex of both foramen magnum and lambdoidal crest; PL: palatal length, excluding spine; BL: basicranial length, between anterior edge of foramen magnum and anterior edge of premaxilla; BUL: bulla length, excluding eustachian part; BB: width of basisphenoid, between cochlea; OB: distance outside bulla, caliper points in contact with antero-dorsal edge of tympanic ring; RC^1-LC^1: inter upper canine distance, at base of cusp; C^1-M^3: upper maxillary row crown length, anterior edge of C^1 to posterior edge M^3; M^1-M^3: upper molar crown length, anterior edge M^1 parastyle to posterior edge M^3; M^2L: upper second molar crown length, anterior edge of parastyle to posterior edge of metastyle; M^2W: upper second molar crown width, lingual base of protocone to buccal face of paracone, at right angle to occlusal surface; M^3W: upper third molar crown width, as for M^2W; RM^3-LM^3: inter upper third molar distance, across buccal face of paracone of RM^3 and LM^3; LR: lower tooth row, posterior edge M^3 to anterior edge of dentary; RC: angular ramus to dentary condyle, blade caliper along anterior face of ramus and measuring to posterior edge of articular condyle. Abbreviations for externals are as follows; HV: body length, tip of rhinarium to anus, TV: tail length, tip to anus; EL: ear length, apex to basal notch; EW: ear width across basal lobes; TL: tragus length; RL: radius length; PL: pes length; MCIII: metacarpal III length; TIB: tibia length.

Geographic Groupings

To examine morphological variation within and between species over their geographic range, specimens of each species were grouped on the basis of phytogeographic regions. These regions are a composite of a map constructed using Beard's (1979) phytogeographic districts for Western Australia, the natural regions of central Australia (Beard 1981) and Williams (1959) for the remainder of Australia.

Morphometric Analysis

Sexual dimorphism was examined using a three-factor analysis of variance for measurements of each of the skull, dentary, teeth (hereafter referred to as skull characters) and external characters for the factors-species, geographic groupings and sex.

Canonical variate (discriminant) analyses, using both the skull and external measurements, were performed for each species and the species' geographic groupings using SPSS (Nie *et al.* 1975) and GENSTAT PACKAGE, Rothamsted Experimental Station. To obtain an unbiased estimate of the correct classification rate, the canonical variate analyses were repeated using only a randomly chosen 70 percent of the specimens; the canonical variate functions so obtained were then used to classify the remaining 30 percent of the specimens.

A Mahalanobis distance matrix, obtained from some of the canonical variate analyses, was subjected to a minimum spanning tree analysis and a hierarchical cluster analysis using the unweighted pair group mathematical averaging method (UPGMA).

Phylogenetic analyses were performed using the WAGNER 78 program for constructing Wagner trees. These analyses were based on the mean values, range coded, of the skull and external characters of the specimens in species and in geographic groups. Some of the above analyses were also performed using a data set comprised of the original variables transformed in an attempt to produce 'size free' values. These values consisted of the residuals from the within-groups regression of the original variables on a size variable, defined as the sum of the original variables on the logarithmic scale (Humphries *et al.* 1981).

Variation in size of selected skull and external characters within the species was examined, by multiple regressions analysis, with respect to the latitude and longitude of their locality of capture, sex of the specimen and the following environmental parameters: median annual rainfall, average annual evaporation, mean of the January maximum temperatures and mean of the July minimum temperatures. This climatic data was associated with specimen locality data using a series of overlay maps taken from the 1975 series, Climatic Atlas of Australia maps, Department of Science, Bureau of Meteorology.

Institutional Specimens

To denote the institutional origin of specimens their catalogue numbers are prefixed by the following abbreviations:

AM :	Australian Museum, Sydney
AMNH :	American Museum of Natural History, New York
BM :	British Museum (Natural History), London
C :	Museum of Victoria, Melbourne
CM :	CSIRO collection at Lyneham, Canberra
JM :	Queensland Museum, Brisbane
SAM :	South Australian Museum, Adelaide
WAM :	Western Australian Museum, Perth
EBU :	Evolutionary Biology Unit, South Australian Museum, Adelaide

These institutional codes prefix any departmental numerals that may be combined with a registration number (e.g. WAM M22605).

Systematics
Scoteanax Troughton, 1943

Oligotomus Iredale (*ex* MacGillivray) 1937: 45.

Type Species *Oligotomus australis* Iredale (*ex* MacGillivray) 1937 (= *Scoteanax rueppellii* Peters). Preoccupied by *Oligotomus* Cope, 1873, *Phenacodontidae.*

Scoteanax Troughton, 1943, 'Furred Animals of Australia', Angus & Robertson, Sydney, p. 353.

Type Species
Nycticejus rüppellii Peters, 1866.

Referred Species
None.

Diagnosis

Scoteanax differs from *Nycticeius* in its generally greater size; considerably more robust skull with a much more pronounced occipital helmet; longer anterior palatal emargination; usually no diastema between C^1 and I^1; M^3 considerably reduced, less rather than more than half the size of M^2, premetacrista only partly present and only protocone, paracone and parastyle remaining; reduction of posterior triangle of M_3; C^1 with broad rather than elongate base, its width approximates its length; lower incisors more imbricate; P_2 relatively more reduced, a quarter or less P_4 crown area. Differs from *Scotoecus* in generally greater size; tragus angular with an elongate anteriorly directed apex rather than spatulate or nearly spatulate tragus; penis much shorter, never approaching a length of one-third radius length – baculum accordingly also much shorter; dorsal profile of skull straight rather than gently convex; narial and prepalatal emarginations shallower; postpalatal spine longer; face of C^1 not flattened or grooved; zygomata moderate rather than slight; M^3 reduced, less rather than more than half size of M^2; P_2 relatively more reduced, a quarter or less crown area of P_4. Differs from *Scotophilus* in that the bony palate extends posteriorly much less than half length of zygomatic arch, rather than past the mid-point; infraorbital foramen small to moderate rather than large; M^3 larger, premetacrista partly present rather than absent; second triangle of M_{1-2} larger rather than smaller than the first; M^{1-2} mesostyle moderately well developed rather than very reduced or absent; M_{1-2} hypoconids and entoconids not greatly reduced. Differs from *Scotomanes* in that usually no diastema between upper canine and incisor; moderately large rather than small narial and postpalatal emarginations; relatively narrower skull, particularly cranium and lachrymal width; larger bulla and postpalatal spine; wider interorbital distance; upper canines with internal basal shelf present. Differs from *Rhogeessa* in its greater general size; less reduced M^3, premetacrista not entirely absent; I_3 not greatly reduced; lower incisors trilobed rather than more simply conical – with outer lobe obsolete and inner lobe practically absent in I_3 (in *Rhogeessa [Baeodon] alleni* I_3 reduced to functionless spicule and M_3 reduction more than in other *Rhogeessa*); bony palate extends posteriorly much less than half length of zygomatic arch rather than to approximately its mid-point; tragus triangular rather than long and thin; posterior palatal emargination, canine shape and its diastema with I^1 differ as with *Nycticeius*. Differs from *Otonycteris* in its larger M^3, premetacrista partially present rather than absent; anterior narial and palatal emarginations larger; interorbital distance wider; postorbital protuberances not greatly enlarged; generally no diastema between C^1 and I^1; second triangle M^2 only slightly larger, rather than much larger, than first triangle; C^1 with broad rather than elongate base; bulla very much reduced; lower incisors trilobed, imbricate, rather than conical and not overlapping; P_2 relatively smaller; ears much smaller. Differs from *Scotorepens* in greater overall size; ear with more acute apex; tragus triangular rather than gently curved; more pronounced occipital helmet; relatively smaller infraorbital foramen, above M^1 parastyle rather than M^1 mesostyle; rostrum rises more sharply in interorbital region; upper incisor close to and usually in contact with upper canine rather than never in contact; upper incisor orthodont to slightly proodont rather than markedly proodont; M^{1-2} hypocone less reduced; larger and more triangular postpalatal spine; distal end of glans penis papillate rather than with fleshy spines; baculum longer, wider distinctive anchor-like distal flanges rather than bifurcating prongs and open grooved rather than more solid proximal end; and on genetic differences, possesses unique alleles at over half of the 35 loci examined (P. Baverstock pers. comm.).

Scoteanax rueppellii (Peters, 1866)

Figures 4, 5a, 6a, 7; Tables 1a, b

Nycticejus rüppellii – Peters, 1866, Mber. K. preuss. Akad. Wiss. p. 21.

Holotype

Skin, skull, from 'Sydney, West Australia' (= Sydney, New South Wales).

Diagnosis

Differs from *Scotorepens orion, Scotorepens balstoni, Scotorepens sanborni* and *Scotorepens greyii* in that all its cranial, dental and external characters substantially larger, with no overlap of measurements (measurements, in mm, mean values only). For example, compared to the next largest species, *Scotorepens balstoni,* maximum skull length 20.1 v. 15.1 and radius length 53.8 v. 35.6. Differs from these species in having a more pronounced occipital helmet, such that its cranial height in proportion to maximum skull length 0.42 v. 0.35 to 0.39; rostrum rises more sharply in interorbital region; I^1 close to and usually in contact with C^1 rather than never in contact; I^1 orthodont to slightly proodont rather than markedly proodont; M^{1-2} hypocone less reduced; infraorbital foramen above M^1 parastyle rather than M^1 mesostyle; more prominent postpalatal spine; glans penis longer, distinctive spatulate head with fine papillae rather than spines; baculum longer, wider distinctive anchor-like distal flanges, and open grooved rather than more solid distal end; ear with more acute apex; tragus triangular rather than gently curved.

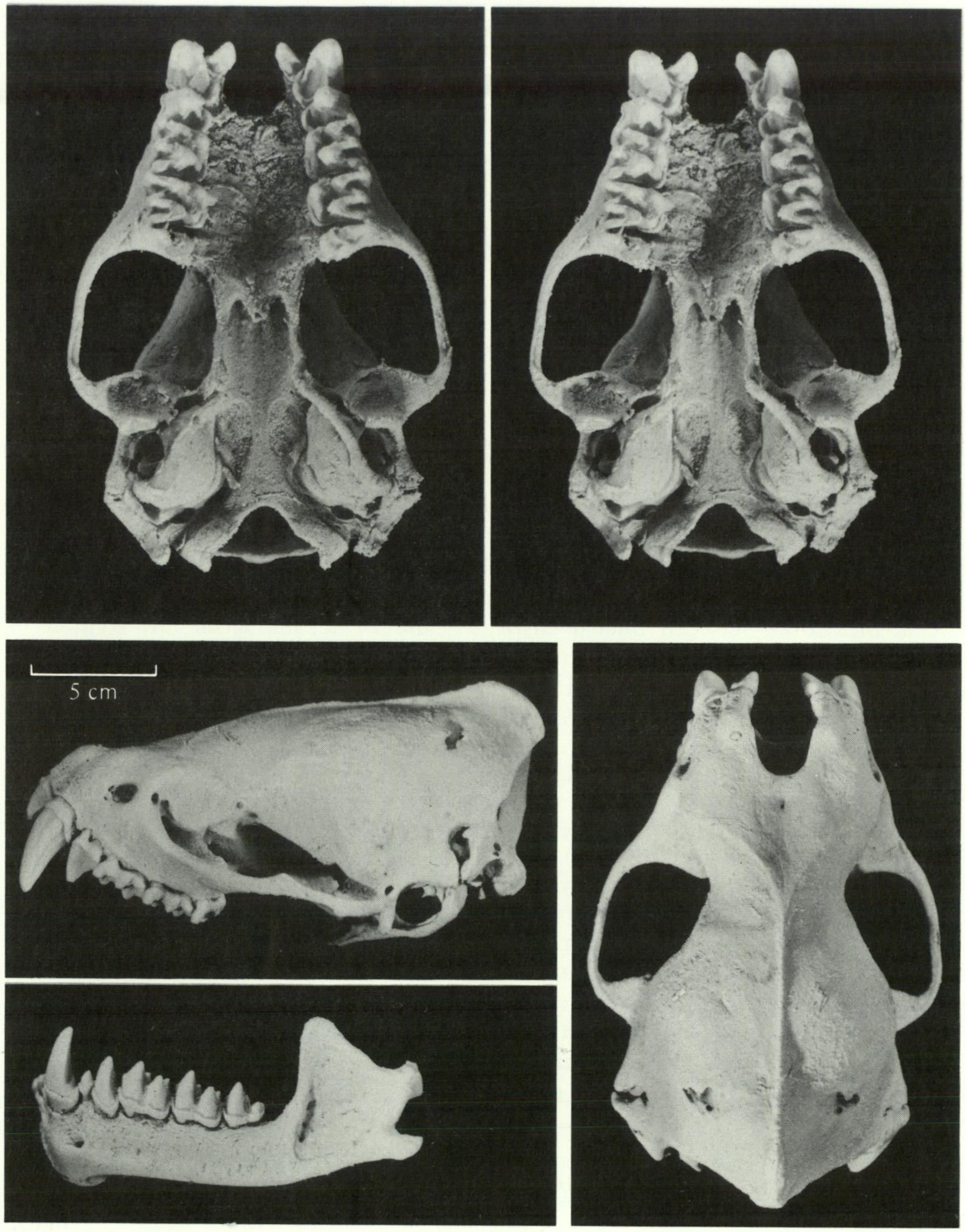


Figure 4 Skull and dentary of *Scoteanax rueppellii* (AM M2108). Ventral view of skull presented as stereopairs.

Description

Skull

Long skull (20.1), wide intermastoid distance (12.3) but relatively narrow cranium (9.9) and interorbital distance (5.2) and long maxillary tooth row (7.7); rostrum rises sharply in interorbital region to a point where slight anterior sagittal crest meets slight crests passing anteriorly to low supraorbital swellings; posterior to this interorbital region cranial profile rises slightly and then dips at posterior parietal region before rising sharply to a pronounced sagittal crest that meets lambdoidal crest to form very prominent occipital helmet; rostral depression slight to moderate; infraorbital foramen small to moderate, round to oval, above parastyle of M^1, separated from orbit by moderately narrow lachrymal bar; anterior palatal emargination semicircular, projects posteriorly to a line joining mid-point of P^4; postpalatal spine long, triangular; pterygoid process relatively short, projects posteriorly to a point connecting a line joining anterior edge of foramen rotundum; tympanic bulla covers two-thirds or more of cochlea; eustachian projection small, blunt; tympanic ring oval; I^1 orthodont to slightly proodont, close to and usually in contact with C^1; P^4 two-thirds length of C^1, in close contact with both M^1 and C^1, with moderate buccal inflection between parastyle and mesostyle; M^{1-2} paracone shorter than metacone; M^{1-2} parastyle, mesostyle and metastyle heights subequal; M^{1-2} hypocone moderate, moderate buccal inflection between buccal cusps; M^3 metastyle, metacone and hypocone absent, premetacrista shortened; paracrista increases in length from M^{1-3}; cingula encircling C^1 and P^4; M^{1-2} with moderate anterior, posterior and lingual cingula, although absent beneath protocone; M^3 with moderate anterior cingulum and slight cingulum on posterior of protocone.

Dentary

Ascending ramus of dentary upright and triangular with moderately rounded coronoid process; mental foramen beneath P_2 or slightly posterior to this point; lower incisors trilobed, imbricate, of subequal length; I_1 crown area longer and narrower than I_{2-3}; I_{2-3} crown area length subequal but crown area of I_3 greater and oval; usually moderate posterior cingular cusplet I_3; C_1, P_2 and P_4 in close contact, encircled by moderate cingula; P_2 small, less than half height of P_4 with slight posterior and anterior cingular cusps, occlusal surface subcircular; lingual cusps of subequal height or with metaconid slightly taller than paraconid and entoconid; hypoconulid small; protoconid height decreases from M_{1-3}, taller than hypoconid; crista obliqua contacts base of metacristid medially; M_{1-3} with moderate anterior, posterior and buccal cingula, lingual cingula absent; M_3 entoconid about half height of metaconid; hypoconulid vestigial (e.g. CM 6571) and rarely present, hypocristid from hypoconid to cusp of entoconid.

Pelage and Skin

Between specimens the colour of the dorsum ranges from Hazel to Cinnamon Brown reflecting the colour of the majority of each hair, the basal one-quarter to one-eighth of which is a much paler Maize Yellow to Yellow Ocher. Occasional White follicles are interspersed throughout. Underparts uniform Tawny Olive of the tips of hairs; the colour of the central half is Snuff Brown and basal part Light Buff. Forehead and rostrum paler, Ochraceous Buff to Warm Buff. Furring on patagia restricted to sparse hairs on antero-proximal part of ventral plagiopatagium. Patagia, lips, ears and forearms range from Saccardo's Umber to Warm Sepia.

External Morphology

Large, general body shape robust, long radius (53.8). Maximum width of ear 76% of its height of 16.7, but slender and triangular upper part, moderately rounded apex with concave dorsal edge immediately behind apex. Tragus triangular as a result of pronounced postero-central lobe, front edge straight or slightly concave. Plagiopatagium contacts pes below fifth digit in central lateral region of palm. Long calcar, more than half length of distal edge of uropatagium; calcaneal lobe small and low. Tibia moderately long (23.5) or 43.6% length of radius.

Glans Penis

Wide club-shaped head, compressed dorso-ventrally, narrow elongate body; preputial skin contacting body of glans basally. Ventrally a wide V-shaped urethral groove, the lateral edges of which indicate the point at which the head narrows proximally. The distal tongue of the head intruding into the V of the urethral groove smooth, elsewhere the head, both dorsally, ventrally and laterally covered with fine papillae. No obvious scalation on the surface of the head, and the skin of its body loosely folded longitudinally forming a slight ventral keel (Figure 5a).

Baculum

(Measurements, in mm, are mean, range, sample size.) Long maximum length (8.59, 8.46-8.75, 3) distinctively curved, horn-shape in lateral profile; relatively slight shaft; anchor-shaped distal head; base relatively narrow laterally (1.48, 1.45-1.54, 3) averaging only 17.3% of maximum baculum length, consists of two broad lateral flanges folded dorsally to leave a broad open median groove (Figure 6a).

Distribution

Hall and Richards (1979) state that the distribution of *Scoteanax rueppellii* is from 'coastal eastern Australia from southern New South Wales to Ingham, Queensland'. Koopman (1984) records it further north to Lake Barrine and *c.* 50 km S. Ravenshoe, Queensland. Specimens we examined (Figure 7) confirm this distribution.

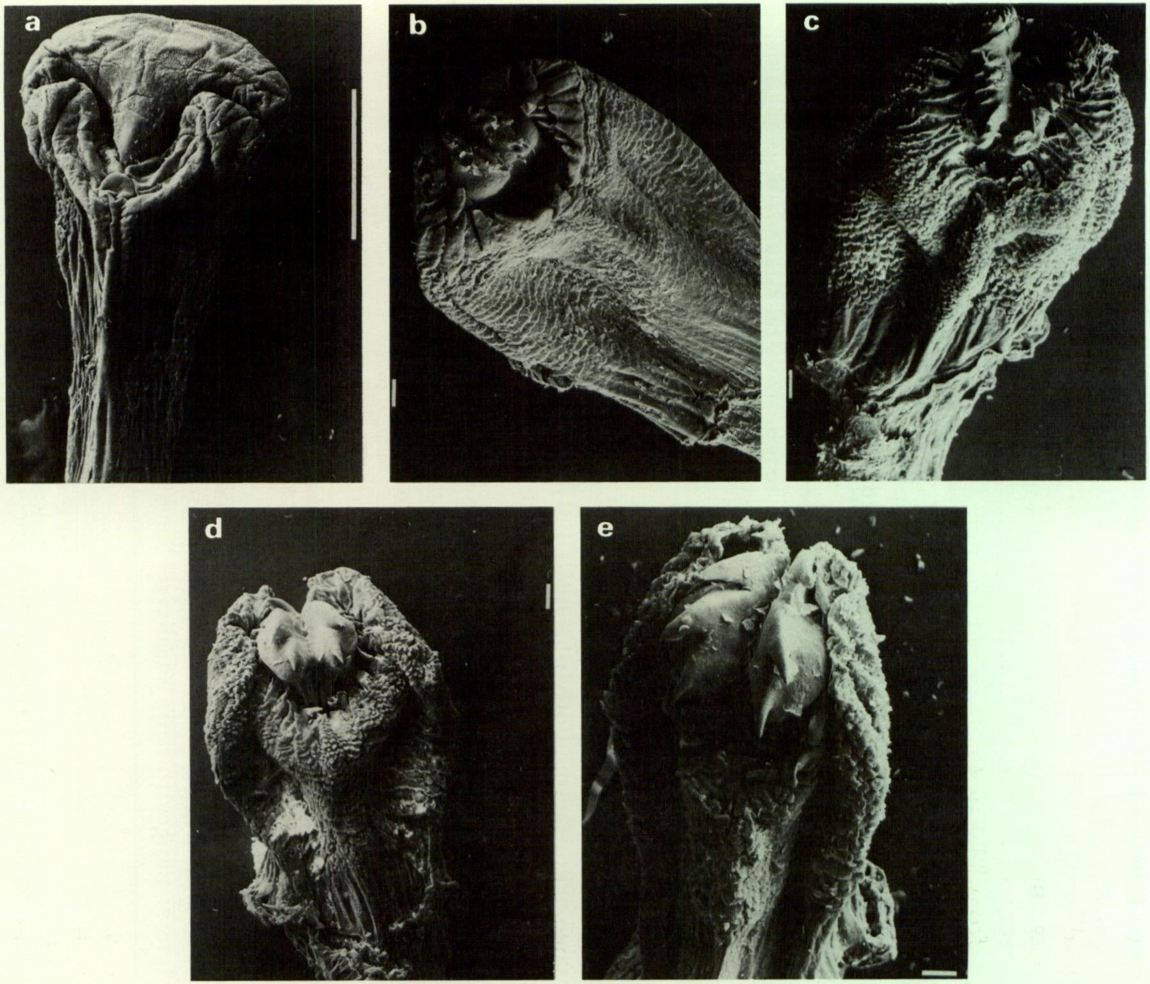


Figure 5 Oblique ventral view of head of glans penis of (a) *Scoteanax rueppellii* (CM 232), (b) *Scotorepens orion* (AM M6120), (c) *Scotorepens balstoni* (EBU B124), (d) *Scotorepens sanborni* (EBU B18) and (e) *Scotorepens greyii* (EBU B151). Scale lines for *Scoteanax rueppellii* 1000 μm, for others 100 μm.

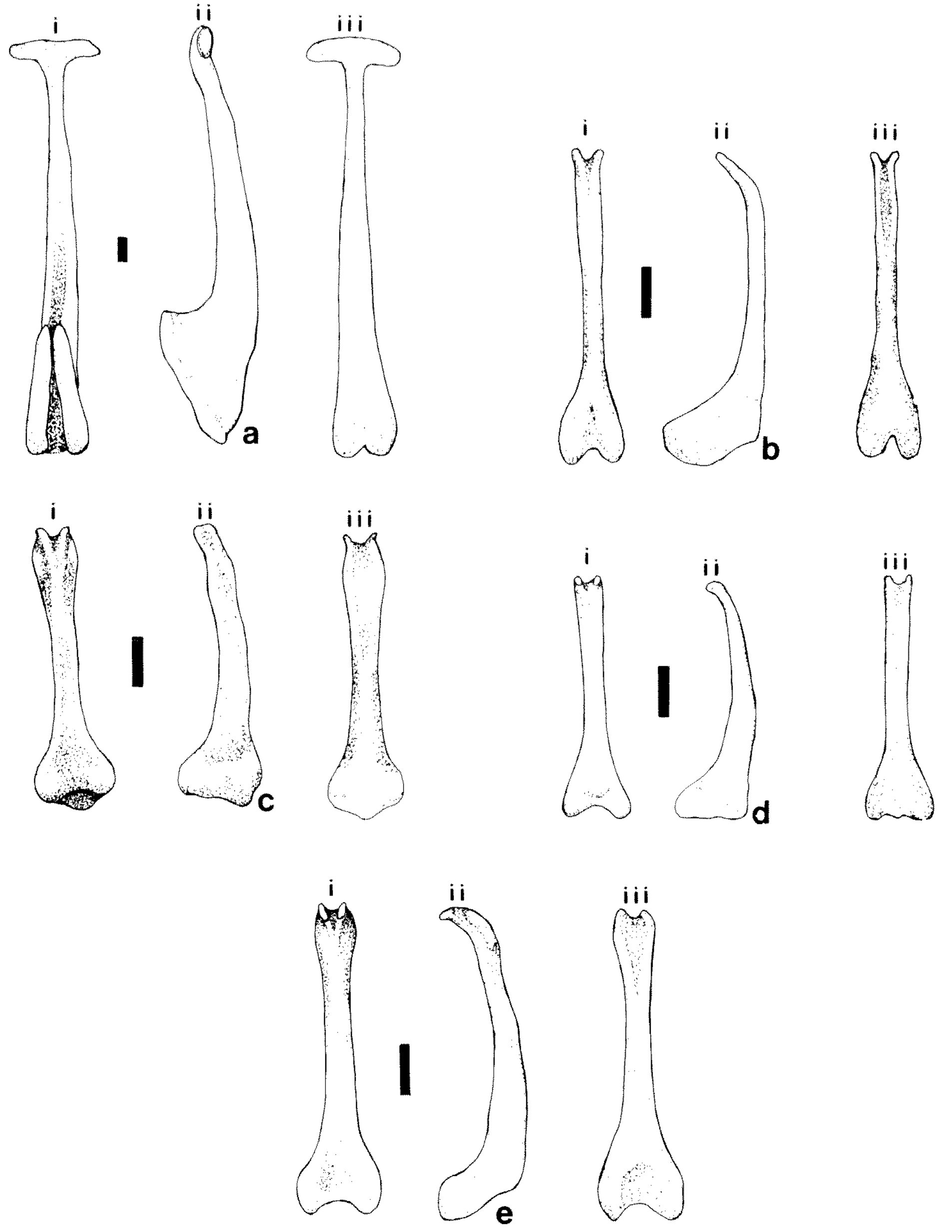


Figure 6 Baculum of (a) *Scoteanax rueppellii* (CM 232), (b) *Scotorepens orion* (AM M6120), (c) *Scotorepens balstoni* (WAM M17673), (d) *Scotorepens sanborni* (WAM M22657) and (e) *Scotorepens greyii* (EBU B126). Ventral (i), lateral (ii) and dorsal (iii) view. Scale lines are 0.5 mm.

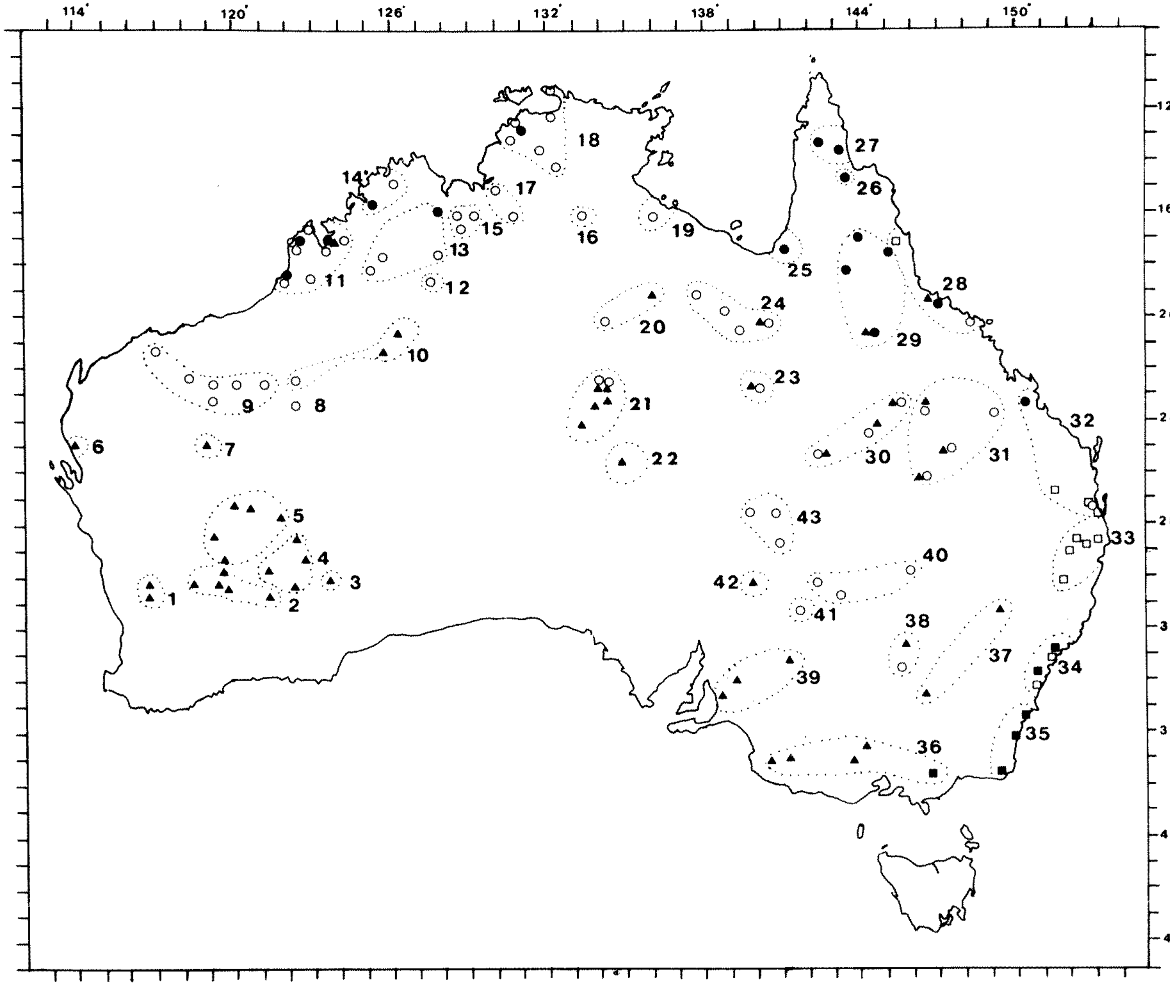


Figure 7 Distribution of *Scoteanax rueppellii* (□), *Scotorepens orion* (■), *Scotorepens balstoni* (▲), *Scotorepens sanborni* (●) and *Scotorepens greyii* (○). These locality records are grouped into geographic regions (1-43, Australia; 44, Papua New Guinea and West Irian).

Specimens Examined

Region 28:

Atherton 17°16'S, 145°29'E, 1♂, 1♀, EBU 084-5.

Region 32:

Brisbane 27°28'S, 153°01'E, 1♂, 1♀, JM 13320, JM 13488; Toowong 27°29'S, 153°00'E, 1♂, JM 5001; Chermside 27°24'S, 153°04'E, 2♂, JM 11451-2.

Region 33:

Nimbin 28°36'S, 153°13'E, 2♀, CM 436, CM4720; Yabbra State Forest 28°30'S, 152° 40'E, 1♂, CM 469; Killarney 26°46'S, 151°26'E, 1♂, JM 13296; Murwillumbah 28°20'S, 153°24'E, 3♀, CM 4627-9; East Lynne 30°08'S, 151°53'E, 1♀, CM 6571; Tooloom 28°37' S, 152°25'E, 1♂, 1♀, CM 232, CM 470; Bonalbo 28°44'S, 152°37'E, 1♀, CM 205; Spirabo Forest 29°03'S, 152°01'E, 1♂, EBU B350.

Region 34:

Swansea 33°05'S, 151°38'E, 1♀, CM 2108; Corrimal 34°23'S, 150°55'E, 1♂, CM 4586.

Scotorepens Troughton, 1943

Scotorepens Troughton, 1943, 'Furred Mammals of Australia', Angus & Robertson, Sydney, p. 354.

Type Species

Scoteinus orion Troughton, 1937

Referred Species

Scotorepens greyii (Gray, 1843);
Scotorepens balstoni (Thomas, 1906); and
Scotorepens sanborni (Troughton, 1937).

Holotype

AM M6115 adult male, skull removed, body in alcohol, from Sydney, N.S.W. collected by Messrs Grant and Wright.

Diagnosis

(Means values, mm.) Differs from *Nycticeius* in that M^3 considerably reduced, less than half the size of M^2, premetacrista only partly present; reduction of posterior triangle of M_3; canine with broad rather than elongate base, its width approximates its length; lower incisors more imbricate; P_2 relatively more reduced, a quarter or less P_4 crown area. Differs from *Scotoecus* in that penis much shorter, never approaching a length of one-third radius length-baculum accordingly much shorter; dorsal profile of skull straight rather than gently convex; narial and prepalatal emarginations shallower; face of C^1 not flattened or grooved; zygomata moderate rather than slight; M^3 reduced, less rather than more than half size of M^2; P_2 relatively reduced, a quarter or less crown area of P_4. Differs from *Scotophilus* in the smaller overall size; bony palate extends posteriorly much less than half length of zygomatic arch, rather than past the mid-point; M^3 larger, premetacrista partly present rather than absent; second

Tables 1a, b Measurements in mm (see Fig. 3 for code to characters), for adult *Scoteanax rueppellii, Scotorepens orion, Scotorepens balstoni, Scotorepens sanborni* and *Scotorepens greyii* from general regions. (WA, Western Australia; NT, Northern Territory; Q, Queensland; NSW, New South Wales; VIC, Victoria; SA, South Australia) which are combinations of geographic groups (in brackets). N, sample size; $\bar{X}$, mean; SD, standard deviation; Mn, minimum and Mx, maximum (a) skull, dentary and teeth and (b) externals.

Table 1a

Species	General region (Geographic groups)		(a) **Skull, Dentary, Teeth Characters**																								
			GL	AOB	LOW	ZW	ZH	MW	ROL	BCL	BW	CH	LH	PL	BL	BUL	BB	OB	RC^1LC^1	C^1M^3	M^1M^3	M^2L	M^2W	M^3W	RM^3LM^3	LR	RC
S. rueppellii	**Q/NSW** (28,32,33,34)	N	20	20	20	19	20	20	20	20	20	19	19	20	20	19	20	19	20	20	20	20	20	20	20	20	20
		$\bar{X}$	20.10	7.10	5.20	14.40	1.05	12.30	7.63	12.70	9.92	8.50	3.40	9.10	16.90	4.40	2.40	10.30	6.90	7.70	5.00	2.10	2.50	2.20	8.90	9.50	4.90
		SD	.65	.21	.12	.29	.13	.32	.31	.41	.22	.23	.23	.23	.53	.16	.24	.20	.19	.23	.13	.09	.08	.12	.22	.22	.17
		Mn	19.1	6.7	5.1	14.0	.8	11.6	6.9	12.2	9.6	8.2	3.0	8.8	15.7	4.1	2.1	10.1	6.4	7.4	4.8	2.0	2.4	2.0	8.3	9.1	4.6
		Mx	21.3	7.5	5.5	15.0	1.3	13.0	8.4	13.5	10.5	9.0	4.0	9.6	17.9	4.7	2.9	10.8	7.1	8.2	5.3	2.3	2.7	2.4	9.2	10.0	5.2
S. orion	NSW/VIC (34,35,36)	N	19	19	19	19	19	19	19	19	19	19	19	19	19	18	19	19	19	19	19	19	19	19	19	19	19
		$\bar{X}$	14.70	5.50	4.20	10.80	77	9.08	5.87	9.00	7.70	5.70	2.50	6.70	12.50	3.30	1.50	7.90	5.10	5.60	3.70	1.50	1.90	1.70	6.90	7.00	3.40
		SD	.41	.18	.15	.26	.13	.22	.19	.36	.16	.25	.21	.21	.30	.12	.19	.19	.12	.14	.09	.06	.09	.08	.16	.13	.13
		Mn	13.8	5.2	3.9	10.2	.6	8.7	5.6	8.5	7.5	5.2	2.1	6.2	11.8	3.1	1.2	7.6	4.9	5.2	3.5	1.4	1.7	1.5	6.6	6.7	3.1
		Mx	15.5	6.0	4.5	11.3	1.0	9.5	6.2	9.7	8.0	6.1	2.9	7.1	13.1	3.5	1.9	8.4	5.3	5.7	3.9	1.6	2.0	1.9	7.2	7.1	3.6
S. balstoni	**WA** (1,2,4,5,7,10)	N	46	46	46	46	46	43	46	46	46	45	45	46	45	44	45	46	46	46	46	46	46	46	46	44	46
		$\bar{X}$	14.60	5.00	3.40	10.10	.64	8.38	5.86	8.77	7.07	5.10	2.10	6.70	12.50	3.30	1.30	7.40	4.80	5.30	3.50	1.40	1.80	1.60	6.30	6.60	3.40
		SD	.34	.18	.20	.34	.09	.28	.28	.28	.24	.24	.22	.24	.32	.16	.24	.19	.16	.12	.10	.07	.07	.10	.15	17	.18
		Mn	13.9	4.6	3.1	9.3	.5	7.8	5.2	8.2	6.6	4.6	1.7	6.2	11.9	2 9	.8	7.1	4.4	5.0	3.3	1.3	1.7	1.3	6.0	6.2	3.1
		Mx	15.4	5.4	4.0	10.8	.9	9.1	6.4	9.6	7.7	5.6	2.6	7.2	13.4	3.6	1.8	7.9	5.1	5.6	3.7	1.5	1.9	1.8	6.6	7.0	3.8
	SA/NT/VIC (21,22,36, 39,42)	N	44	44	44	44	44	42	44	44	44	44	44	44	44	39	44	44	42	43	43	44	44	43	43	44	44
		$\bar{X}$	15.30	5.20	3.70	10.70	.62	8.91	5.85	9.50	7.36	5.40	2.30	7.00	12.90	3.40	1.60	7.80	5.20	5.60	3.70	1.50	1.90	1.70	6.70	6.90	3 50
		SD	.54	.24	.22	.39	.10	.33	.33	.41	.27	.27	.23	.31	.46	.11	.17	.28	.20	.19	.12	.08	.09	.09	.22	.22	.19
		Mn	14.1	4.8	3.2	9.8	.5	8.3	5.3	8.7	6.9	4.8	1.9	6.2	12.0	3.1	1.2	7.2	4.8	5.1	3.4	1.3	1.7	1.5	6.3	6.4	3.2
		Mx	16.5	5.8	4.1	11.4	.8	9.6	6.6	10.7	8.0	6.2	3.1	7.6	13.7	3.6	1.9	8.3	5.5	6.0	3.9	1.7	2.1	1.9	7.1	7.2	3.9
	Q/NSW central east NT (20,23,24, 28,29,30, 31,37,38)	N	27	27	27	27	27	27	27	27	27	27	27	27	27	23	27	26	26	27	27	27	27	27	27	27	27
		$\bar{X}$	15.60	5.40	3.90	10.80	.63	9.05	5.99	9.66	7.39	5.70	2.50	7.20	13.10	3.40	1.60	7.90	5.30	5.80	3.80	1.60	2.00	1.80	6.80	7.10	3.60
		SD	.59	.27	.15	.37	.09	.33	.27	.41	.19	.29	.24	.33	.48	.11	.17	.19	.21	.17	.12	.07	.11	.12	.23	.24	.17
		Mn	14.8	4.9	3.5	10.3	.5	8.6	5.6	9.1	7.0	5.1	2.1	6.6	12.4	3.3	1.2	7.6	4.8	5.5	3.6	1.5	1.8	1.6	6.4	6.7	3.3
		Mx	17.0	6.0	4.1	11.6	.8	9.8	6.7	10.7	7.7	6.3	3.0	7.9	14.0	3.7	1.9	8 3	5.6	6.2	4.1	1.7	2.2	2.0	7.3	7.6	4.0

Table 1a (continued)

(a) **Skull, Dentary, Teeth Characters**

Species	General region (geographic groups)		GL	AOB	LOW	ZW	ZH	MW	ROL	BCL	BW	CH	LH	PL	BL	BUL	BB	OB	RC^1 LC^1	C^1M^3	M^1M^3	M^2L	M^2W	M^3W	RM^3 LM^3	LR	RC
S. sanborni	**WA/NT**	N	24	24	24	24	24	24	24	24	24	24	24	24	24	21	24	24	22	22	24	22	23	24	23	22	24
	(11,13,14,	$\bar{X}$	12.90	4.40	3.50	9.30	.58	7.75	4.76	8.28	6.69	5.10	2.40	5.50	10.80	3.00	1.40	6.90	4.20	4.70	3.10	1.30	1.70	1.40	5.70	5.70	2.90
	15,18)	SD	.48	.13	.13	.36	.08	.31	.26	.32	.24	.18	.20	.24	.45	.21	.18	.25	.17	.16	.11	.05	.11	.08	.19	.18	.20
		Mn	12.1	4.2	3.3	8.7	.5	7.2	4.3	7.5	6.3	4.7	1.9	5.1	10.0	2.8	1.1	6.5	3.9	4.5	3.0	1.2	1.5	1.3	5.5	5.5	2.6
		Mx	13.8	4.6	3.8	10.0	.8	8.2	5.4	8.9	7.1	5.4	2.8	6.0	11.6	3.6	1.7	7.3	4.5	5.1	3.3	1.4	1.9	1.6	6.1	6.0	3.3
	Q	N	35	35	35	35	35	35	35	35	35	34	35	35	35	31	35	35	35	35	35	35	35	35	35	35	35
	(25,26,27,	$\bar{X}$	13.90	4.70	3.80	10.10	.57	8.41	5.17	8.81	7.12	5.40	2.60	5.90	11.40	3.10	1.50	7.40	4.50	5.10	3.40	1.40	1.90	1.60	6.20	6.30	3.10
	28,29,32)	SD	.45	.23	.15	.32	.05	.35	.18	.34	.22	.24	.21	.21	.41	.13	.13	.22	.18	.17	.12	.07	.08	.08	.22	.20	.13
		Mn	13.0	4.3	3.5	9.2	.5	7.4	4.8	8.1	6.6	4.9	2.2	5.5	10.6	2.9	1.3	6.8	4.1	4.8	3.2	1.2	1.7	1.5	5.6	6.0	2.8
		Mx	14.8	5.2	4.1	10.5	.7	8.9	5.5	9.5	7.6	5.8	3.0	6.3	12.3	3.4	1.8	7.8	5.0	5.5	3.7	1.5	2.0	1.8	6.6	6.7	3.4
	Papua New	N	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	3	4
	Guinea	$\bar{X}$	14.00	4.80	3.70	10.30	.70	8.35	5.10	8.90	7.22	5.50	2.20	5.90	11.30	3.20	1.58	7.40	4.60	5.00	3.30	1.40	1.80	1.55	6.20	6.10	3.15
		SD	.45	17	.19	.38	.14	.39	.35	.36	.26	.26	.10	.22	.31	.22	.05	.14	.22	.18	.15	.10	.08	.06	.22	.26	.10
		Mn	13.6	4 7	3.6	10.0	.6	8.0	4.8	8.6	7 0	5.3	2.1	5.6	10.9	3.0	1.5	7.3	4.4	4.8	3.1	1.3	1.7	1.5	6.0	5.9	3.1
		Mx	14.5	5.1	4.0	10.8	.9	8.9	5.6	9.4	7.6	5.9	2.3	6.1	11.6	3.5	1.6	7.6	4.9	5.2	3.4	1.5	1.9	1.6	6.5	6.4	3.3
S. greyii	**Northwest**	N	35	35	35	35	35	34	35	35	35	35	35	35	35	35	35	35	35	35	35	35	35	35	35	35	35
	WA	$\bar{X}$	13.60	4.70	3.50	9.65	.59	7.99	5.27	8.41	6.81	5.10	2.20	6.10	11.50	3.20	1.30	7.10	4.50	5.00	3.30	1.30	1.70	1.50	5.90	6.10	3.10
	(9,10,11,	SD	.58	.23	.15	.47	.09	.32	.26	.41	.22	.18	.19	.29	.46	.11	.19	.23	.29	.25	.18	.08	.14	.12	.30	.31	.17
	13,14)	Mn	12.5	4.2	3.2	8.7	4	7.4	4.7	7.6	6.5	4.8	1.8	5.6	10.7	2.9	.9	6.7	3.9	4.5.	2.9	1.2	1.5	1.3	5.3	5.5	2.7
		Mx	15 0	5.1	3.7	10.5	.8	8.6	5.8	9.3	7.2	5.5	2.6	6.7	12.9	3.3	1.5	7.6	5.1	5.6	3.7	1.5	2.0	1.8	6.4	6.7	3.5
	Northeast	N	96	96	96	96	96	96	96	96	96	96	96	96	96	75	96	96	91	92	92	93	93	94	93	91	96
	WA/NT/Q	$\bar{X}$	13.00	4.50	3.50	9.45	.52	7.91	4.86	8.24	6.70	4.90	2.30	5.90	11.10	3.10	1.30	7.00	4.30	4.80	3.20	1.30	1.70	1.50	5.80	5.90	3.00
	(15,16,17,	SD	.59	.25	.19	.52	.07	.39	.28	.41	.29	.33	.28	.31	.49	.14	.17	.31	.24	.26	.18	.09	.12	.10	.33	.29	.16
	18,19,20,	Mn	11.6	4.0	3.1	8.5	.4	7.1	4.2	7.2	6.0	4.2	1.7	5.2	9.9	2.8	.7	6.4	3.9	4.3	2.8	1.1	1.4	1.3	5.2	5.3	2.6
	21,23,24,	Mx	14.3	5.0	4.0	10.4	.7	8.7	5.6	9.2	7 6	5.6	3.0	6.7	12.3	3.4	1.7	7.7	4.9	5.4	3.6	1.5	2.0	1.7	6.5	6.6	3.4
	30,31,32)																										
	NSW/SA	N	10	10	10	10	10	10	10	10	10	10	10	10	10	9	10	10	9	10	10	10	10	10	10	10	10
	(38,40,41,	$\bar{X}$	13.2	4.6	3.5	9.43	.61	8.04	5.0	8.21	6.84	4.8	2.2	6.0	11.3	3.2	1.3	7.1	4.4	4.9	3.3	1.3	1.6	1.5	5.9	6.0	3.0
	43)	SD	.33	.12	.12	.21	.12	.16	.17	.23	.18	.13	.16	.16	.16	.09	.18	.09	.08	.16	.12	.06	.11	.09	.10	.13	.08
		Mn	12.7	4.4	3.3	9.2	.5	7.8	4.8	7.9	6.5	4.6	1.8	5.7	11.1	3.1	1.0	7.0	4.3	4.7	3.1	1.2	1.5	1.4	5.7	5.8	2.8
		Mx	13.8	4.7	3.6	9.9	.9	8.3	5.3	8.5	7.0	5.0	2.3	6.2	11.5	3.4	1.5	7.3	4.5	5.2	3.5	1.4	1.8	1.7	6.0	6.2	3.1

Table 1b

Species	Geographic Region (Geographic Group)		(b) External Characters								
			HV	TV	EL	EW	TL	RL	PL	MCIII	TIB
S. rueppellii	Q/NSW (28,32,33, 34)	N	12	12	12	12	12	12	12	12	12
		X	67.85	51.63	16.65	12.66	8.27	53.82	9.70	51.75	23.46
		SD	3.29	3.52	.70	.78	.33	1.69	.58	1.84	.79
		Mn	63.3	44.5	15.6	11.1	7.6	51.0	8.8	49.0	22.0
		Mx	72.7	58.5	17.8	14.0	8.7	55.8	11.1	54.7	24.4
S. orion	NSW/VIC (34,35,36)	N	19	19	19	19	19	19	19	19	19
		X	49.25	34.53	11.90	9.23	5.57	34.81	6.67	33.20	13.73
		SD	2.62	2.06	.56	.46	.34	1.25	.50	1.55	.49
		Mn	43.9	29.5	10.6	8.7	5.0	32.4	6.0	30.8	12.7
		Mx	53.1	37.9	13.1	10.5	6.4	36.8	7.8	36.3	14.5
S. balstoni	WA (1,4,5,7,10)	N	38	38	38	38	38	38	38	38	39
		X	48.14	35.60	12.23	9.62	5.39	34.53	6.18	33.37	14.85
		SD	2.67	2.67	.68	.89	.32	1.14	.53	1.34	.69
		Mn	42.6	30.2	11.2	7.8	4.9	32.0	5.4	30.5	13.0
		Mx	53.5	40.8	13.5	11.0	6.1	36.4	7.5	35.2	16.6
	SA/NT/VIC (21,22,36, 39,42)	N	43	43	43	43	43	43	43	43	43
		X	51.49	35.87	12.68	9.62	5.64	35.92	6.72	34.62	15.28
		SD	3.99	2.86	.91	.60	.39	1.44	.70	1.59	.74
		Mn	42.2	29.0	10.7	8.0	5.0	32.8	4.9	30.6	13.9
		Mx	59.7	41.7	14.1	11.1	6.7	38.2	8.1	38.2	16.8
	Q/NSW Central east NT (20,23,24, 28,29,30,31, 37,38)	N	27	27	27	27	27	27	27	26	26
		X	51.32	36.42	12.87	9.53	5.59	36.72	6.77	35.31	15.39
		SD	3.12	2.97	.57	.68	.32	1.77	.51	1.93	.85
		Mn	45.0	29.8	11.6	8.0	5.2	32.6	6.0	30.1	14.1
		Mx	56.5	41.5	13.8	10.5	6.5	40.5	7.7	38.7	17.2
S. sanborni	WA/NT (11,13,14, 15,18)	N	21	23	23	23	23	23	23	24	24
		X	42.65	31.72	10.59	8.39	4.88	30.97	5.72	30.58	13.33
		SD	2.77	2.23	.71	.67	.31	1.50	.68	1.43	.65
		Mn	36.8	27.5	9.1	7.2	4.4	27.9	4.90	28.4	11.9
		Mx	48.4	36.0	11.8	9.8	5.5	34.0	7.2	33.1	14.4
	Q (25,26,27, 28,29,32)	N	33	34	34	34	34	34	34	34	34
		X	44.42	34.30	11.48	8.43	5.29	33.25	6.25	32.93	14.14
		SD	2.73	2.51	.68	.39	.37	1.37	.90	1.22	.81
		Mn	39.7	29.1	10.4	7.7	4.6	31.0	4.4	30.8	12.2
		Mx	52.3	38.9	13.1	9.6	6.1	35.8	8.3	35.2	15.6
	Papua New Guinea (44)	N	4	4	4	4	4	4	4	4	4
		X	45.53	33.55	11.53	8.65	5.05	34.73	6.40	34.10	14.53
		SD	1.90	3.25	.73	.55	.31	1.01	1.14	.99	.71
		Mn	43.5	29.0	10.6	7.9	4.6	33.7	5.1	32.9	13.9
		Mx	48.0	36.7	12.2	9.2	5.3	36.0	7.5	35.1	15.4
S. greyii	Northwest WA (9,10,11, 13,14)	N	33	34	34	34	34	34	34	34	34
		X	44.48	32.80	11.33	8.79	5.00	31.84	5.72	31.41	14.07
		SD	2.76	2.48	.58	.62	.29	1.27	.52	1.52	.62
		Mn	37.2	27.6	9.7	7.7	4.4	29.0	4.9	28.7	13.0
		Mx	48.5	38.5	12.8	10.3	5.6	34.7	7.0	33.7	15.8

Table 1b (continued)

Species	Geographic Region (Geographic Group)		(b) External Characters								
			HV	TV	EL	EW	TL	RL	PL	MCIII	TIB
S. greyii	Northeast WA/NT/Q (15,16,17, 18,19,20, 21,23,24, 30,31,32)	N	95	95	95	95	95	95	95	95	95
		X	44.92	31.94	11.44	8.60	5.06	31.12	5.89	30.54	13.51
		SD	2.76	2.27	.67	.65	.34	1.68	.73	1.60	.92
		Mn	40.0	25.2	9.7	7.1	4.2	27.3	4.3	26.7	11.5
		Mx	53.0	37.8	12.9	10.2	6.0	35.0	7.5	33.8	15.6
	NSW/SA (38,40,41, 43)	N	10	10	10	10	10	10	10	9	9
		X	45.54	32.68	11.50	8.56	5.15	31.58	5.47	30.90	13.70
		SD	2.56	2.50	.74	.33	.28	.83	.50	1.20	.44
		Mn	40.3	29.5	10.1	8.1	4.5	30.0	4.9	28.8	13.0
		Mx	48.5	37.8	12.3	9.0	5.5	32.6	6.4	32.7	14.2

triangle of $M_{\overline{2}}$ larger rather than smaller than the first; $M^{\underline{1}}$-$^{\underline{2}}$ mesostyle moderately well developed rather than very much reduced or absent; $M_{\overline{1}}$-$_{\overline{2}}$ hypoconids and entoconids not greatly reduced. Differs from *Scotomanes* in generally smaller size, moderately large rather than small narial and postpalatal emarginations; relatively larger bulla and wider interorbital distances; relatively narrower skull, particularly cranium and lachrymal width. Differs from *Rhogeessa* in its less reduced $M^{\underline{3}}$, premetacrista not entirely absent; $I_{\overline{3}}$ not greatly reduced; lower incisors trilobed rather than more simply conical – with outer lobe obsolete and inner lobe practically absent in $I_{\overline{3}}$ (in *Rhogeessa [Baeodon] alleni* $I_{\overline{3}}$ reduced to functionless spicule and $M_{\overline{3}}$ reduction more than in other *Rhogeessa*); bony palate extends posteriorly much less than half length of zygomatic arch rather than to approximately its mid-point. Differs from *Otonycteris* in its larger $M^{\underline{3}}$, premetacrista partially present rather than absent; anterior narial and palatal emarginations larger; interorbital distance wider; postorbital protuberances not greatly enlarged; generally no diastema between $C^{\underline{1}}$ and $I^{\underline{1}}$; second triangle $M^{\underline{2}}$ only slightly larger, rather than much larger, than first triangle; $C^{\underline{1}}$ with broad rather than elongate base; bulla very much reduced; lower incisors trilobed, imbricate, rather than conical and not overlapping; $P_{\overline{2}}$ relatively smaller; ears much smaller. Differs from *Scoteanax* in small overall size; ear apex rounded rather than acute; less pronounced occipital helmet; generally relatively larger infraorbital foramen, above mesostyle of $M^{\underline{1}}$ rather than its parastyle; rise of rostrum in interorbital region less acute; upper incisors never in contact with upper canine; upper incisor quite proodont rather than orthodont to slightly proodont; $M^{\underline{1}}$-$^{\underline{2}}$ hypocone more reduced; postpalatal spine smaller and slighter; distal end of glans penis with fleshy spines rather than papillae; baculum shorter, narrower distal end with bifurcating prongs rather than anchor-like distal flanges, more solid proximal end rather than an open grooved one; and on genetic distance based on enzyme differences (see *Scoteanax* diagnosis).

Description

Skull

Small to moderate length (13.2 to 20.1); lateral profile of skull flat to moderately inflated; lambdoidal and sagittal crest absent to moderate; rostrum relatively narrow; rostral depression absent to moderate; postorbital swellings absent to slight; supraorbital protuberances absent to slight; infraorbital foramen above mesostyle of M^{1}, oval, moderate-sized to large, separated from orbit by slight to moderately wide lachrymal bar; anterior palatal emargination semi-circular or spatulate, moderate; postpalatal spine small to moderate length; pterygoid process moderately developed with slight to moderate mesial inclination, tympanic bulla relatively fragile, covers slightly more than half cochlea, eustachian projection small to moderate, and sharp to blunt pointed; tympanic ring around external auditory meatus subcircular to oval; paraoccipital process longer or subequal to mastoid process; I^{1} proodont, not in contact with C^{1}; P^{4} half to two-thirds height C^{1}, in close contact with both C^{1} and M^{1}, slight to moderate buccal inflection between parastyle and mesostyle; M^{1-2} paracone shorter than metacone; height of M^{1-2} parastyle subequal to or slightly longer than mesostyle and metastyle; M^{1-2} hypocone reduced; M^{3} with metastyle, metacone and hypocone absent, premetacrista shortened; paracrista increases in width from M^{1-3}; cingula usually encircles C^{1} and P^{4} but frequently absent in mid-buccal area; moderately wide anterior, posterior and lingual cingula M^{1-2}, absent beneath protocone; slight anterior cingulum M^{3}, slight cingulum on posterior of M^{3} protocone variably present.

Dentary

Ascending ramus of dentary upright and triangular with moderately rounded coronoid process; angle and condyle relatively close; mental foramen usually beneath M_{1} but may be to either side of it; lower incisors trilobed, imbricate, subequal in length; I_{1} crown area longer and narrower than I_{2-3}; I_{2-3} crown width subequal but crown area of I_{3} greater and subcircular; P_{2} small, less than half height of P_{4}, posterior and anterior cingular cusps on P_{2-4}; major lingual cusps M_{1-2} of subequal height; M_{1-3} protoconid decreases in height posteriorly; M_{1-3} protoconid taller than hypoconid; crista obliqua contacts base of metacristid medially; M_{1-3} with moderate anterior, posterior and buccal cingula, no lingual cingula; M_{3} entoconid small, less than half height of metaconid, hypoconulid reduced or absent.

Pelage and Skin Colour

Dorsum ranges from Tawny Olive to Dresden Brown; underparts normally lighter, ranging from Pale Pinkish Buff to Grayish Olive. Patagia and skin of nose, ears and forearms Clove Brown, or lighter Hair Brown to Warm Sepia. No colour patterning.

External Morphology

Small to moderate size, slender to moderately robust body (44 to 50), radius length small to moderate (31 to 36); ears slender to moderately broad, width 76-78% height of ear, leading edge of ear gently converse, apex moderate to well rounded, anterobasal lobe small to moderately wide; tragus evenly curved upwards, leading edge slightly concave, posterior edge slightly to moderately convex; plagiopatagium joins pes at base of fifth digit; long calcar, more than half length of distal edge of uropatagium; calcaneal lobe small, low and convex; tibia varying in length from 39.4 to 43.6% of radius length.

Glans Penis

Narrow-spatulate head, compressed dorso-ventrally but with ventral keel and distal lateral flanges; body of glans narrow and short; preputial skin contacting glans just below narrowing of the head, ventrally a narrow U or V-shaped urethral groove demarked externally by fleshy lappets and internally by from 4-22 fleshy spines; elsewhere the distal three-quarters of the head covered by fleshy scales, the remainder with loose fleshy folds.

Baculum

Relatively short (2.48 to 3.26) shaft slight to moderately robust, straight to moderately curved in lateral profile; distal head bifurcated into two short narrow prongs, behind which the shaft enlarges laterally into slight to moderately wide flanges; base solid, posterior edge squared or sloping in line of shaft, projecting caudally slightly to moderately, groove on caudal and cranial surface shallow and wide and meeting as notch at apex.

Scotorepens orion (Troughton, 1937)

Figures 5b, 6b, 7, 8; Tables 1a, b

Scoteinus orion — Troughton, 1937, Aust. Zoologist **8**: 277.

Holotype

Adult male, skin and skull, AM M6115, Sydney, New South Wales.

Diagnosis

(Mean values, mm.) Differs from *Scoteanax rueppellii* as indicated in the diagnosis of that species. Length of skull similar to *Scotorepens balstoni* (14.7 v. 15.1) but differs in overall shape of skull which is relatively wider, more inflated cranium and wider rostrum as indicated by: mastoid width (9.1 v. 8.7), cranial width (7.7 v. 7.3), cranial height (5.7 v. 5.3), distance outside bullae (7.9 v. 7.7), zygomatic width (10.8 v. 10.5), anteorbital width (5.5 v. 5.2), least interorbital width (4.2 v. 3.6), wider RM^3-LM^3 (6.9 v. 6.6); ears shorter (11.9 v. 12.6) and narrower (9.2 v. 9.6); tibia shorter (13.7 v. 15.2); fur and

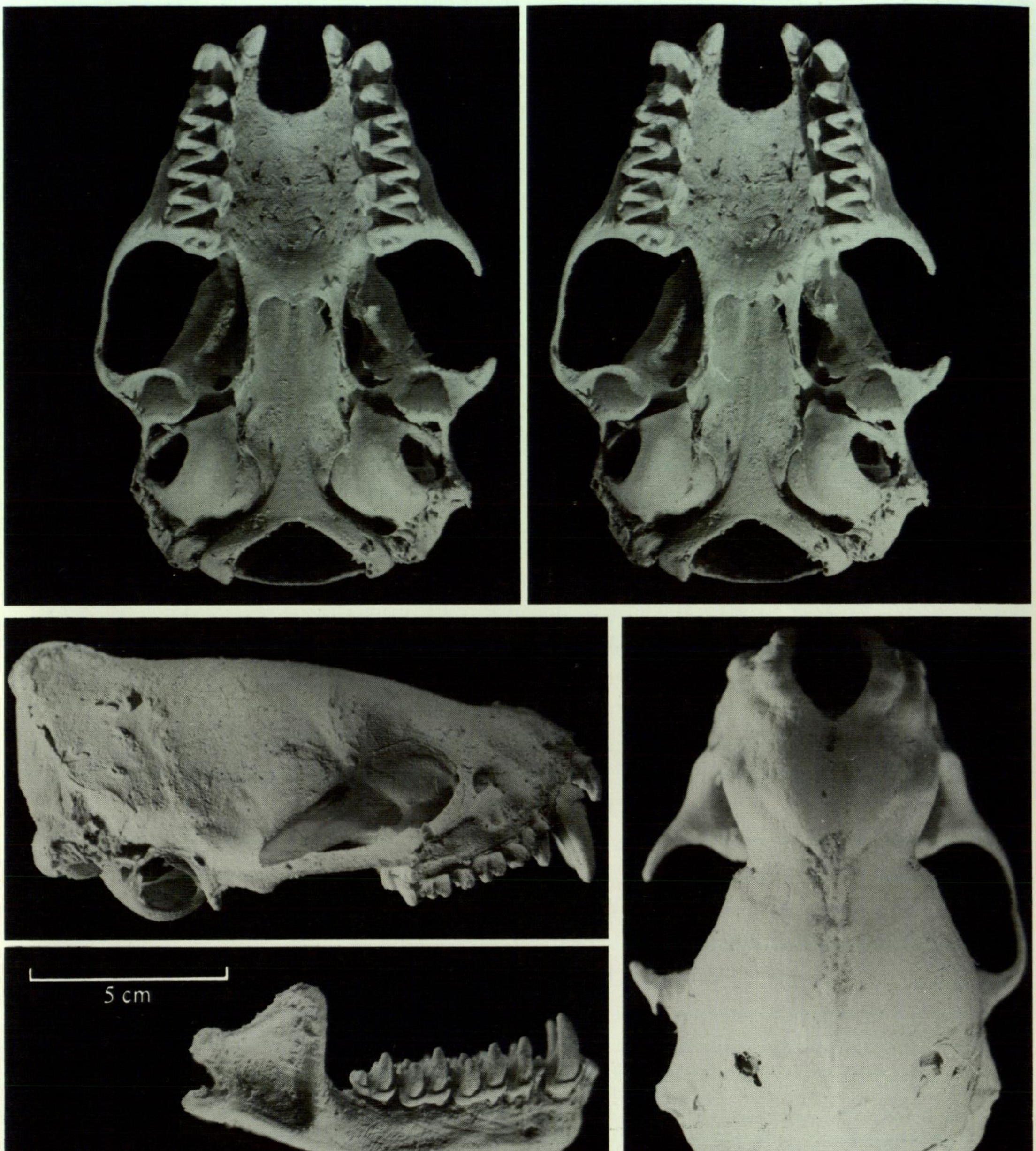


Figure 8 Skull and dentary of *Scotorepens orion* (AM M6115, holotype). Ventral view of skull presented as stereopairs.

skin darker and less bicoloured; glans penis with smaller head with eight spines arranged in a subcircular cluster and not 8-22 spines arranged in two principal rows; weaker keel; baculum longer (3.3 v. 2.7) less robust shaft and base, smaller distal flanges; differs from *Scotorepens greyii* and *Scotorepens sanborni* in that its skull, dentaries and externals average larger for all characters. The skull longer (14.7 v. 13.2 and 13.5, respectively); cranium similarly proportioned but rostrum relatively broader, particularly anteorbital width (5.5 v. 4.5, 4.6, respectively); C^1-M^3 length (5.6 v. 4.8, 4.9, respectively); radius length (34.8 v. 32.3, 31.3, respectively); tibia short (39.4% length of radius v. 42.7% and 43.6%, respectively); differs from *Scotorepens sanborni* in that tip of pterygoid process projects further posteriorly relative to foramen rotundum. Fur and skin darker and less bicoloured; glans penis with smaller head, spines not arranged in two principal rows; baculum longer, more slender shaft with smaller distal flanges. Individuals may be distinguished on skull, dental and external characters from the above species with the discriminant functions detailed later in this paper.

Description

Skull

Moderately long, wide skull, particularly rostrum, mastoid width, cranial width, distance outside bullae, zygomatic width, anteorbital width, least interorbital width and RM^3-LM^3 distance; cranium moderately inflated so that its lateral profile continues to rise to the frontal-parietal junction at an angle only slightly reduced from that of the rostrum (and marginally lower than *Scotorepens greyii*), posterior to that point the profile flattens to form a low occipital cap. Skull deep, cranial height 5.7; rostral depression slight; vestigial postorbital swellings occasionally present; slight supraorbital swellings occasionally present; infraorbital foramen small to moderate, oval to subcircular, separated from orbit by narrow or moderately wide lachrymal bar; anterior palatal emargination semicircular or spatulate, projects posteriorly to line joining mid-point of P^4 or equally commonly to anterior edge of P^4; postpalatal spine moderately long, broadly triangular; base of pterygoid process between foramen rotundum and sphenorbital fissure, process projects dorsally behind a line joining anterior edge of foramen rotundum and frequently to dorsal edge of that foramen; eustachian projection small, blunt to broadly triangular; slight cingulum moderately common on posterior of M^3 protocone.

Dentary

Mental foramen usually located below $P_{\bar{2}}$, occasionally slightly to either side of that position; occasionally slight anterior and posterior cingular cusplet on $I_{\bar{2}}$-$_{\bar{3}}$. $M_{\bar{1}}$-$_{\bar{2}}$ lingual cusps subequal height or with metaconid slightly taller than paraconid and entoconid; hypoconulid greatly reduced and frequently absent, hypocristid from hypoconid to immediately posterior to base of entoconid or to between vestigial hypoconulid, when present, and entoconid.

Pelage and Skin Colour

Dorsum Dresden Brown, which is the colour of the distal quarter of hairs, the central part of which is a darker Cinnamon Brown; basal quarter Light Buff. Face of lighter Buckthorn Brown. Venter slightly tonal, Drab to Grayish Olive of distal parts of hairs of which the basal part is Buffy Brown. Chest Pinkish to Cinnamon Buff with Tawny Olive middle and Pale Pinkish Buff base to hairs. Cinnamon Buff ventral flanks of body. Scattered Dresden Brown hairs on dorsal proximal part of uropatagium. Skin of ears and lips Snuff Brown; patagia Warm Sepia.

External Morphology

Moderate size, general body shape robust, radius moderate length (34.8). Ears relatively broad with width 78% of height of 11.9, leading edge of ear gently convex, apex well rounded, anterobasal lobe small. Tragus with leading edge slightly concave and posterior edge more convex than other *Scotorepens* such that the apex is slightly more acute. Tibia short (13.7) or 39.4% length of radius.

Glans Penis

Narrow-spatulate head with a prominent ventral keel and distal lateral flanges; body of glans narrow and short; uretheral groove a broad U-shape, demarked externally by fleshy lappets and internally by eight spines on the baculum head forming a subcircular cluster; elsewhere the distal three-quarters of the head covered with fleshy scales, either with simple distal edges or grooved into one or more lobes (Figure 5b).

Baculum

(Measurements, in mm: mean, standard deviation, range, sample size.) Moderately long maximum length (3.26, 0.22, 3.00-3.50, 6); shaft slender, slightly curved in lateral profile; distal head bifurcated into two short narrow prongs – behind which shaft narrows slightly before lateral enlargement as slight flanges; base moderately broad laterally (0.84, 0.04, 0.80-0.90, 6) averaging 25.7% of maximum baculum length, solid gently curved postero-dorsally to form a moderately high base, moderately deep and wide groove on caudal and cranial surface of base meeting as notch at apex (Figure 6b).

Distribution

Scotorepens orion is restricted to the southeastern Australian coastal strip (Figure 7).

Specimens Examined

Region 34:

Sydney *c.* 33°47′S, 150°56′E, 11♂, 1♀, AM (M6116, M6118-25, M3755), CM 3983, AM 209 (holotype); Watagan State Forest *c.* 32°57′S, 151°14′E, 2♀, EBU B357-8.

Region 35:
Mimosa Rocks 36°36′S, 150°04′E, 1♂, WAM M20917; Durras Lake 35°38′S, 150°12′E, 2♀, WAM M20918-9; Kiola 35°32′S, 150°23′E, 1♀, WAM M20916; 4.2 km S Kanuk Ck 37°39′23″S, 149°21′56″E, 1♂, C24910.

Region 36:
Licola 37°38′S, 146°37′E, 1♀, C25521.

Scotorepens balstoni (Thomas, 1906)

Figures 5c, 6c, 7, 9; Tables 1a, b

Scoteinus balstoni – Thomas, 1906, Abstr. Proc. Zool. Soc. (Lond.) 31: 2.
– Thomas, 1906, Proc. Zool. Soc. (Lond.) p. 472.
Scoteinus influatus – Thomas, 1924, Ann. Mag. Nat. Hist. (9) xiii p. 540, Prairie, Q.

Holotype

Adult female BM No. 6.8.1.41. Original number 170; skull and spirit carcase from North Pool, Laverton, 1650 ft., 19-26 October 1905.

Diagnosis

(Mean values, mm.) Differs from *Scoteanax rueppellii* and *Scotorepens orion* as indicated in the diagnosis of those species. Differs from *Scotorepens greyii* and *Scotorepens sanborni* in that its skull, teeth and externals average larger in all characters; all cranial measurements are proportionally smaller relative to maximum skull length (e.g. braincase width ratio 0.48 v. 0.51 and 0.52 respectively); ratio of interorbital breadth to anteorbital width smaller (0.69 v. 0.78, 0.80, respectively) and C^1-M^3 length greater (5.5 v. 4.8, 4.9, respectively); longer radius length (35.6 v. 32.3, 31.3, respectively); glans penis with larger head, more spines (v. 4-10), stronger keel; baculum straighter and more robust shaft, generally with wider distal flanges and squarer proximal end. Differs from *Scotorepens sanborni* in that tip of pterygoid process projects further posteriorly relative to foramen rotundum, whereas in *Scotorepens sanborni* rarely projects beyond this line and then never as far posteriorly.

Individuals may be distinguished on skull, dental and external characters from the above species with the discriminant functions detailed later in this paper.

Description

Skull

Moderately long elongate skull with relatively narrow: rostrum, interorbital width, anteorbital width, cranial width, cranial height, distance outside bullae, zygomatic width, RM^3-LM^3; cranium flattened such that its lateral profile rises only slightly against that of the rostrum; rostral depression moderate; lambdoidal and sagittal crests meet to form moderate occipital helmet; lambdoidal crest raised only moderately above foramen magnum (2.3); vestigial postorbital swellings usually present; slight supraorbital swellings, very occasionally with slight protruberances; infraorbital foramen, oval, moderate size but occasionally large,

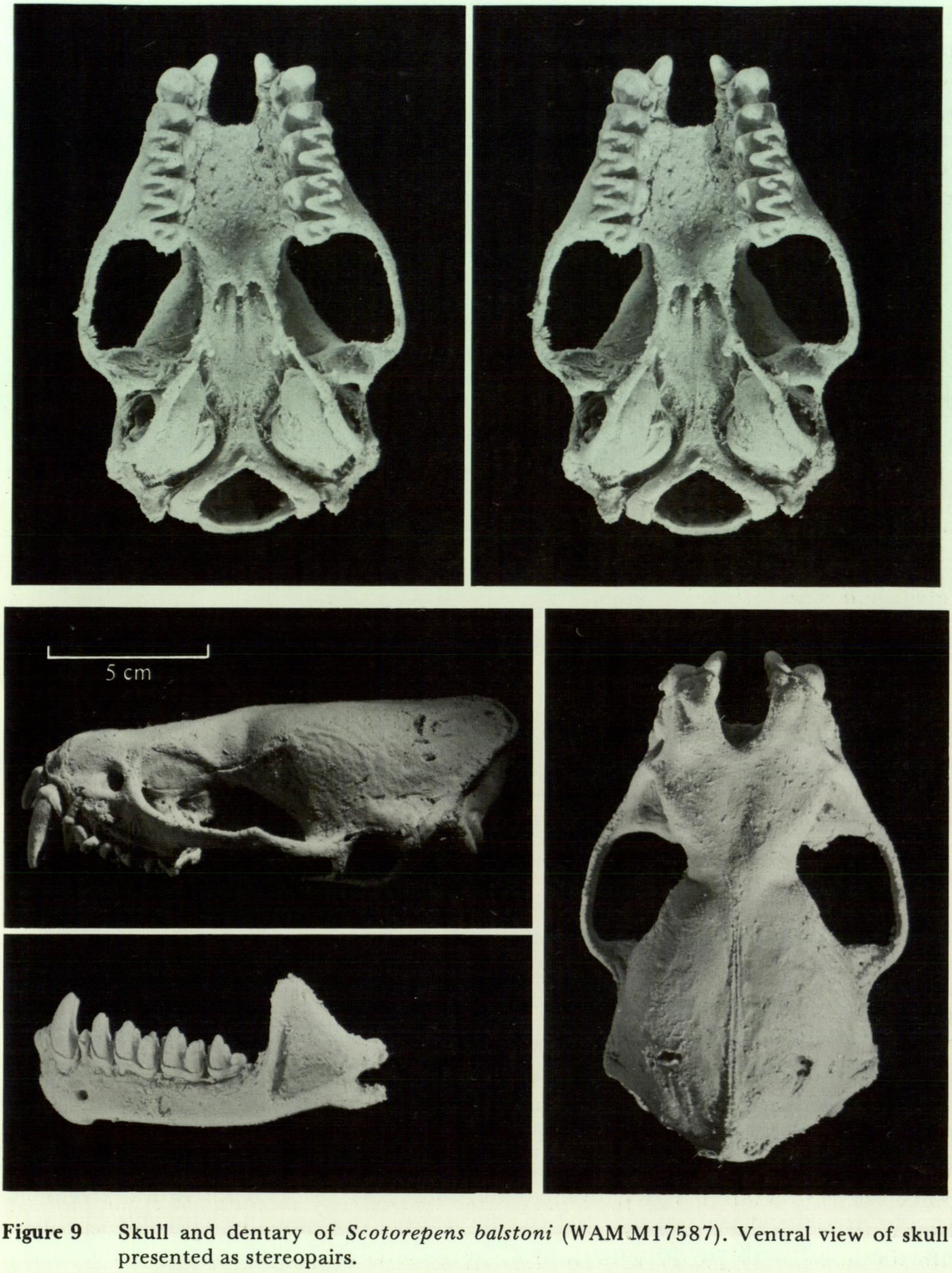


Figure 9 Skull and dentary of *Scotorepens balstoni* (WAM M17587). Ventral view of skull presented as stereopairs.

separated from orbit by moderately wide lachrymal bar; anterior palatal emargination semi-circular, usually projects posteriorly to line joining centre of $P^{\underline{4}}$, occasionally (EBU B295) projects only as far as posterior edge of $C^{\underline{1}}$; post-palatal spine usually triangular, although occasionally blunt; base of pterygoid process between foramen rotundum and sphenorbital fissure, process projects posteriorly up to or behind a line joining anterior edge of foramen rotundum, seldom projects behind foramen rotundum; eustachian projection small, blunt to sharply pointed; normally slight cingulum on posterior of $M^{\underline{3}}$ protocone.

Dentary

Mental foramen usually beneath $P_{\overline{2}}$ or frequently beneath a point between $P_{\overline{2}}$ and $C_{\overline{1}}$; small posterior and anterior cingular cusplet occasionally on $I_{\overline{3}}$ and rarely on $I_{\overline{2}}$; major lingual cusps $M_{\overline{1}}$-$_{\overline{2}}$ of subequal height or with metaconid slightly taller than paraconid and entoconid; $M_{\overline{1}}$-$_{\overline{3}}$ protoconid decreases in height posteriorly, although unequal wear occasionally results in protoconid of $M_{\overline{3}}$ being subequal or longer than that of $M_{\overline{2}}$; hypoconulid greatly reduced and frequently absent, hypocristid from hypoconid to immediately posterior to base of entoconid or between hypoconulid, when present, and entoconid.

Pelage and Skin Colour

Dorsum Tawny Olive, which is the colour of the distal half of hairs, the central part of which is Sepia, basal quarter Pale Pinkish Buff. Underparts Pale Pinkish Buff which is the distal half of hairs, middle part Saccardos Umber to Sepia, base White. Fur absent from patagia except sparse hairs on ventral antero-distal part of plagiopatagium and anal area of ventral uropatagium. Most of patagia Clove Brown, except uropatagium which is a lighter Hair Brown; skin of nose, ear and forearms Hair Brown.

External Morphology

Moderate size, general body shape slender, radius moderate length (35.6). Ears relatively slender with width 76% of height of 12.6; leading edge of ear gently convex, apex moderately rounded; anterobasal lobe moderately wide. Tragus evenly curved upwards, leading edge slightly concave and posterior edge gently convex. Tibia moderately long (15.2) or 42.5% length of radius.

Glans Penis

Narrow-spatulate shaped head, with a prominent ventral keel and distal lateral flanges; body of glans narrow and short. Ventrally a narrow V-shaped groove, demarked externally by fleshy lappets and internally by two primary rows of spines on the head of the baculum; these spines vary in number from 10-22; elsewhere the distal three-quarters of the head covered by fleshy scales, either with simple distal edges or grooved into one or more lobes (Figure 5c).

Baculum

(Measurements, in mm: mean, standard deviation, range, sample size). Short maximum length (2.66, 0.17, 2.41-2.95, 13); shaft relatively robust, straight in lateral profile, distal head bifurcated into two short narrow prongs behind which the shaft enlarges laterally into moderately wide flanges; base broad (0.82, 0.06, 0.73-0.90, 12), averaging 31% of maximum baculum length, solid, low, posterior edge square with line of shaft (Figure 6c).

Distribution

Scotorepens balstoni is distributed widely through the arid and semi-arid regions south of *c.* latitude 19°S. In Queensland it also occupies moister regions (Fanning R.), while it occasionally occurs sympatrically with the smaller *Scotorepens greyii* and *Scotorepens sanborni* it does not occur east of the Great Australian Divide (except at one known locality, Fanning R., Queensland) where it is replaced by one of either of the larger species *Scoteanax rueppellii* or *Scotorepens orion* (Figure 7).

Specimens Examined

Region 1:

Nugadong Nature Reserve 30°13′20″S, 116°48′45″E, 1♂, WAM M18501; Wongan Hills 30°51′S, 116°40′E, 1♂, WAM M15184.

Region 2:

Kalgoorlie 30°45′S, 121°28′E, 1♂, 3♀, WAM (M20558, M20847-8, M20850); Beacon 30° 04′40″S, 118°30′30″E, 1♂, WAM M14723; Marda Dam 30°12′45″S, 119°16′40″E, 1♀, WAM M20278; Bungalbin Hill 30°14′S, 119°49′E, 1♂, WAM M17748; Mt Manning 29°58′S, 119°38′ E, 1♀, WAM M20817.

Region 3:

Queen Victoria Springs 30°25′50″S, 123°34′15″E, 1♀, WAM M18476.

Region 4:

Kurnalpi 30°25′S, 122°21′E, 2♂, 1♀, WAM (M20559-60, M20849); Yundamindra 29° 22′50″S, 122°24′25″E, 1♂, 1♀, WAM (M17569, M17587); White Quartz Dam 29°54′S, 121° 15′05″E, 1♀, WAM M17547; North Pool, Laverton 28°38′S, 122°24′E, 1♀, BM 6.8.1.41. (holotype *Scoteinus balstoni*).

Region 5:

Yeelirrie H.S. 27°10′S, 120°00′E, 1♂, WAM M12957; Yuinmery 28°31′35″S, 119°17′ 15″E, 1♀, WAM M20233; Banjiwarn 27°47′20″S, 121°42′00″E, 4♂, 2♀, WAM (M17887, M17889, M17895, M17900, M20243-4); Wanjarri N.R. 27°17′S, 120°42′E, 3♂, 8♀, WAM (M20816, M20821, M20823, M20825-7, M20829, M20831, M20839, M20836-7); Mt Elvire 29°22′S, 119°36′E, 1♂, 4♀, WAM (M20819, M20824, M20839-40, M20843).

Region 6:

McGlade Road 24°49′20″S, 113°50′00″E, 1♀, WAM M15192.

Region 7:

Three Rivers H.S. *c.* 25°00′S, 119°00′E, 1♀, WAM M12721.

Region 10:

Kuduarra Well 20°40′S, 126°26′E, 1♂, SAM M3705; Billowaggi Well 21°12′S, 125°59′E, 2♀, WAM M1432-3.

Region 11:
Pt Torment 17°22′S, 124°00′E, 1♀, WAM M20864.

Region 20:
Alroy Downs 19°18′S, 136°04′E, 1♂, EBU B124.

Region 21:
Bushy Park 22°54′S, 133°56′E, 4♂, 4♀, EBU (B254-6, B275-7, B288-9); Arltunga *c.* 23°27′S, 134°44′E, 3♂, 3♀, EBU B257-62; Finke R. 24°33′S, 133°13′E, 1♂, 1♀, EBU B273-4; Alcoota 22°50′S, 134°27′E, 2♂, EBU B294-5; Alice Springs 23°42′S, 133°52′E, 1♀, C 9963.

Region 22:
Charlotte Waters 25°54′S, 134°56′E, 1♂, SAM M687.

Region 23:
Boulia 22°55′S, 139°54′E, 1♂, EBU B306.

Region 24:
Nr Quamby 20°22′S, 140°17′E, 2♂, 2♀, EBU B91-4.

Region 28:
Fanning R. 19°16′S, 146°49′E, 1♂, 1♀, EBU 064-5.

Region 29:
Hughendon 20°51′S, 144°12′E, 1♂, EBU 088; Prairie, Hughendon district 20°52′S, 144°36′E, 1♂, BM 24.3.7.4. (holotype *Scoteinus influatus*).

Region 30:
Alice R. 23°33′S, 145°17′E, 3♂, 1♀, EBU 034-7; 45 km W. Windorah 25°20′S, 142°12′E, 1♀, EBU B309; Barcoo R. 24°05′S, 144°47′E, 1♂, EBU B321.

Region 31:
Babbiloora 25°12′S, 147°08′E, 1♂, EBU B338; Charleville 26°24′S, 146°15′E, 2♂, EBU 026-7; 20 km N Alpha *c.* 23°39′S, 146°38′E, 2♂, 1♀, EBU B2-4.

Region 36:
Bendigo 36°46′S, 144°17′E, 9♂, 2♀, EBU (82110/01-02, 821120/02, 111282/11-13, 830226/07, 830226/12, 830226/14-16); Big Heath Wildlife Res. 37°06′S, 140°34′E, 1♂, EBU NB 63; 10 km S Edenhope 37°02′S, 141°17′E, 1♀, C24336; Carisbrook 37°03′S, 143°49′E, 1♀, C4018.

Region 37:
Nr Narrandera 34°45′S, 146°33′E, 1♂, 1♀, AM M11274-5; Nr Warrumbungle Ra. *c.* 31°16′S, 149°17′E, 1♀, EBU B361.

Region 38:
16 km W Merriwagga 33°49′S, 145°38′E, 1♂, 1♀, EBU B363-4.

Region 39:
Tarawi H.S. 33°26′S, 141°09′E, 6♀, EBU B374-9; Adelaide 34°56′S, 138°36′E, 1♀, SAM M2954; Sutherlands 34°10′S, 139°14′E, 1♂, SAM M5206.

Region 42:
North Mulga H.S. 30°12′S, 139°42′E, 2♀, EBU B387-8.

Scotorepens sanborni (Troughton, 1937)

Figures 5d, 6d, 7, 10; Tables 1a, b

Scoteinus sanborni—Troughton, 1937. Aust. Zoologist **8**: 280.

Holotype

AM A3176, adult female, body in alcohol, skull separate, collected by K. Broadbent, East Cape, Papua (southeastern Papua New Guinea).

Diagnosis

(Mean values, mm.) Differs from *Scoteanax rueppellii, Scotorepens orion* and *Scotorepens balstoni* as detailed in the diagnosis for these species. Briefly, it cannot be confused with *Scoteanax rueppellii*; it averages smaller than *Scotorepens balstoni* and *Scotorepens orion* for all skull and external characters. Differs from *Scotorepens balstoni* in having a relatively wider and more inflated cranium and greater infraorbital width; glans penis with both smaller head and keel and less spines; shorter baculum, more curved and narrower shaft with smaller distal flanges. Differs from *Scotorepens orion* in narrower anteorbital width; relatively longer tibia; lighter and more bicoloured fur; glans penis with larger head, less spines arranged in two principal rows and not clustered; shorter baculum, more robust shaft with larger distal flanges. Difficult to distinguish from some Northern Territory and eastern Western Australian populations of *Scotorepens greyii*, but generally braincase wider relative to palatal length, elsewhere lower basicranial length to greatest skull length (0.83 v. 0.85). Also compared to *Scotorepens greyii* pterygoid processes generally do not extend as far posteriorly relative to foramen rotundum. Individuals may be distinguished from the above species on the basis of skull, dental and external characters with the discriminant functions detailed later in this paper.

Description

Skull

Short skull with relatively wide: cranium, intermastoid distance and interorbital distance; cranial profile variable but generally more inflated than *Scotorepens greyii* such that its lateral profile rises relatively sharply from that of the rostrum up to the frontal-parietal junction, posterior to that point the profile generally flattens, or increases only slightly, to form a low occipital cap; vestigial postorbital swellings usually present, these occasionally with slight rounded protuberances; rostral depression slight; infraorbital foramen small to moderate, oval, separated from orbit by moderately wide lachrymal bar; anterior palatal emargination semicircular, usually projects posteriorly to a line joining anterior edge of P^4, occasionally to posterior edge of P^4; postpalatal spine moderately long and usually triangular, occasionally narrow; pterygoid process projects posteriorly to a point usually terminating in front of a line joining the anterior edge of foramen rotundum (N=32), but less frequently to this line (N=11); eustachian projection small, blunt to triangular; slight cingulum frequently on posterior of M^3 protocone.

Dentary

Mental foramen usually located beneath $P_{\bar{2}}$ or beneath a point between $P_{\bar{2}}$ and $P_{\bar{4}}$; frequently slight to moderate anterior and posterior cingular cusplets on $I_{\bar{3}}$, occasionally on $I_{\bar{2}}$; $M_{\bar{1}}$-$_{\bar{3}}$ lingual cusps of subequal height or with metaconid slightly taller than paraconid and entoconid; hypoconulid normally present but

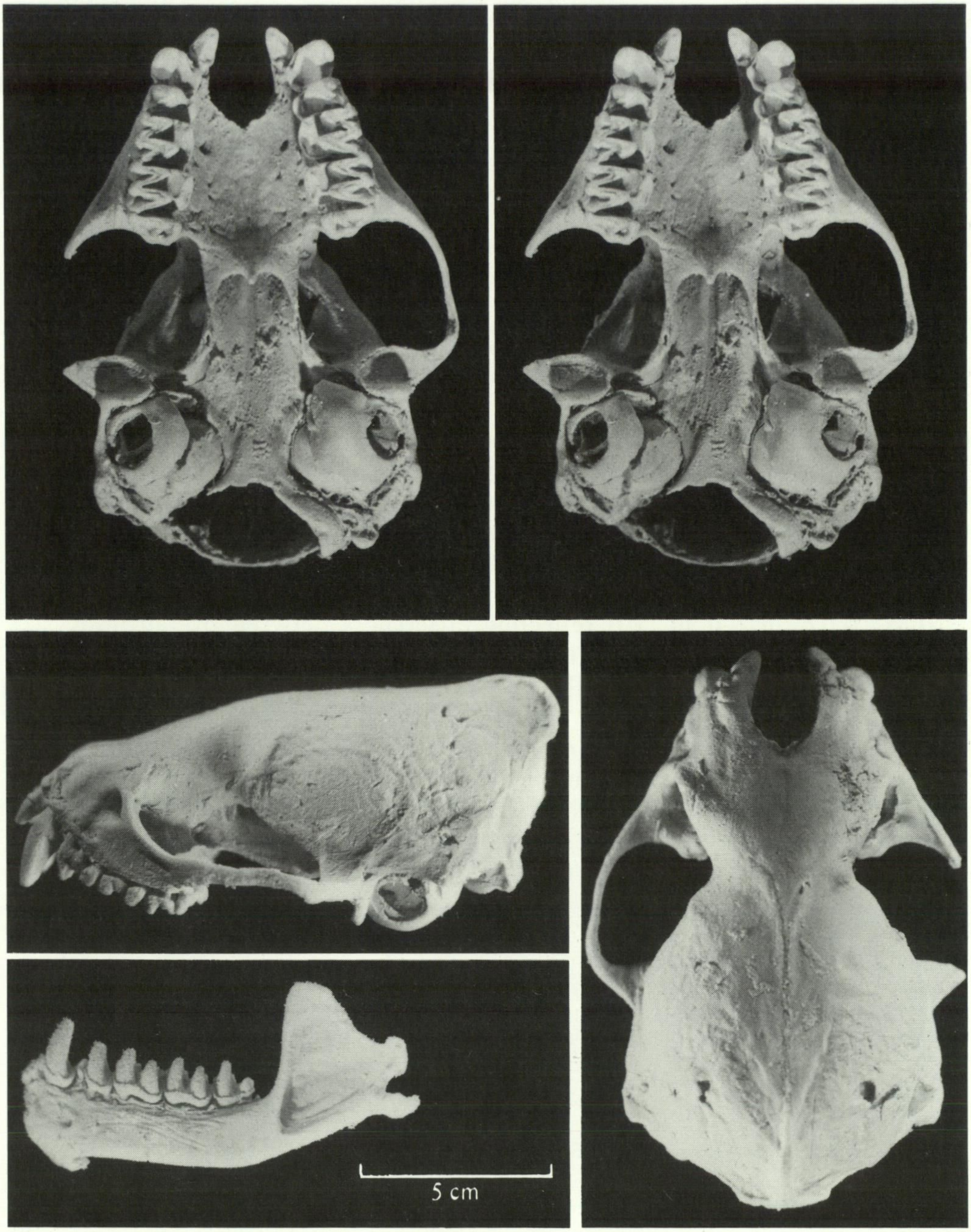


Figure 10 Skull and dentary of *Scotorepens sanborni* (holotype AM A3176). Ventral view of skull presented as stereopairs.

greatly reduced; hypocristid from hypoconid to hypoconulid (EBU 080) when the latter cusp is present.

Pelage and Skin Colour

As for *Scotorepens balstoni.*

External Morphology

Small, general body shape slender, forearm small (32.3), shape of ear as in *Scotorepens balstoni.* Tibia moderate (13.8) or 42.7% length of radius.

Glans Penis

Similar to *Scotorepens balstoni* but with urethral groove U-shaped and spines on baculum head larger and less numerous (4-10) (Figure 5d).

Baculum

(Measurements, in mm; mean, standard deviation, range, sample size.) Very similar in overall size and form to *Scotorepens greyii.* Western Australian and Northern Territory specimens have smaller maximum baculum length (2.48, 0.08, 2.35-2.60, 9) compared to those from Queensland (2.86, 0.12, 2.62-3.00, 10) and their bases are proportionately narrower (0.67, 0.05, 0.59-0.73, 9) v. (0.81, 0.07, 0.70-0.90, 10) reflecting differences between overall body size in these two regional groupings (Figure 6d).

Distribution

In Australia *Scotorepens sanborni* is restricted to tropical and sub-tropical regions. They occur as an eastern and western population with no known connecting populations in central Northern Territory and the Gulf country. It is probably widely distributed in southern coastal and near-coastal regions of West Irian and Papua New Guinea (Figure 7).

Specimens Examined

Region 11:

Whistle Creek 18°48′S, 121°43′E, 2♂, EBU 119-20; Light House, Cape Bossut 18°43′S, 121°38′E, 3♂, EBU 121-3 ; Overtank, Cape Bossut, 18°43′S, 121°30′E, 1♂, EBU 124; Point Coulomb 17°15′S, 122°12′10″E, 6♂, 1♀, WAM (M22599, M22652, M22657-60, M22603).

Region 13:

Pentecost River, 16°00′S, 127°59′E, 2♂, 2♀, WAM M2860, EBU 101-04 .

Region 14:

Prince Regent River N.P. 15°48′11″S, 125°20′26″E, 1♀, WAM M12248.

Region 18:

35 km S Darwin 12°27′S, 130°50′E, 1♀, EBU B163; 4 km E Berry Springs 12°16′S, 130°03′E, 2♂, 3♀, EBU B165-70.

Region 25:

Nr Normanton 17°40′S, 141°04′E, 3♂, 2♀, EBU (B75, B79, B80-2).

Region 26:
80 km S Coen 14°41′S, 143°50′E, 1♂, EBU 074.

Region 27:
10-20 km N Coen *c.* 13°57′S, 143°12′E, 2♂, 3♀, EBU (076, 078-80, B32); 5 km S The Archer *c.* 13°30′S, 142°32′E, 1♂, 1♀, EBU B46-7; 50 km S Coen 13°58′S, 143°12′E, 2♂, 2♀, EBU B53-6.

Region 28:
Fanning River, Townsville 19°16′S, 146°49′E, 3♂, 2♀, EBU 059-63 .

Region 29:
80 km S Lynd Junction *c.* 17°00′S, 144°00′E, 1♂, EBU 086; Hughendon 20°51′S, 144° 12′E, 2♂, 1♀, EBU 089-91; 34 km S Mt Garnett *c.* 17°41′S, 145°07′E, 3♂, 3♀, EBU B15-20; 25 km E Georgetown *c.* 18°17′S, 143°33′E, 1♀, EBU B73.

Region 32:
Rockhampton 23°22′S, 150°32′E, 1♂, 2♀, EBU (052, 056-7).

Region 44:
East Cape, Papua New Guinea 10°13′S, 150°53′E, 1♀, 1? sex, AM M3176 (holotype) AM M4266; Fredrik Hendrik I, West Irian 7°53′S, 138°23′E, 1♀, 1♂ juvenile, BM 22.22.7-8; Kamali, Papua New Guinea 10°02′S, 147°45′E, 1♂, BM 97.8.7.95.

Scotorepens greyii (Gray, 1843)

Figures 5e, 6e, 7, 11; Tables 1a, b

Scotophilus greyii – Gray, 1843, List. Mamm. Brit. Mus. 1844. Voyage Erebus Terror pl. xx.
Scoteinus balstoni caprenus – Troughton, 1937, Aust. Zoologist **8**: 279-280, Roebuck Bay, W.A.
Scoteinus orion aquilo – Troughton, 1937, Aust. Zoologist **8**: 274, Bowen, Q.

Lectotype

BM 42.8.17.12, specimen 'b' of Dobson (1888, p. 263), designated by Thomas (1906); adult, female, skin and badly damaged skull but with intact toothrows; Port Essington, Northern Territory.

Dobson (1888, p. 263) believing he had described *Scotophilus greyii* nominated specimen 'a' of his catalogue, an adult specimen in alcohol from Port Essington, as the 'type'. However, as noted by Thomas (1906) 'now that a named figure is recognised as conferring priority the species will stand to Gray's credit'. Thomas (1906) then selected specimen 'b' as being nearer in size to Gray's (1943) Plate xx, figuring *Scotophilus greyii.* This selection of specimen 'b' as the lectotype may not be the preferred one because as noted by Tate (1942), Gray (1843) provided no scale on his Plate xx.

At this time BM 42.8.17.12, specimen 'b', is too damaged to allow identification, whereas specimen 'a' (BM 44.6.13.2) can be determined with reasonable confidence. For this reason we base our understanding of this taxon on the paralectotype (specimen 'a'). BM 44.6.13.2 is an old adult male, body in alcohol, skull separate, collected at Port Essington, Northern Territory, and once in the collections of the Earl of Derby.

Diagnosis

Differs from *Scoteanax rueppellii, Scotorepens balstoni, Scotorepens orion* and *Scotorepens sanborni* as detailed in the earlier diagnoses of these species. Individuals may also be distinguished from these species on the basis of skull,

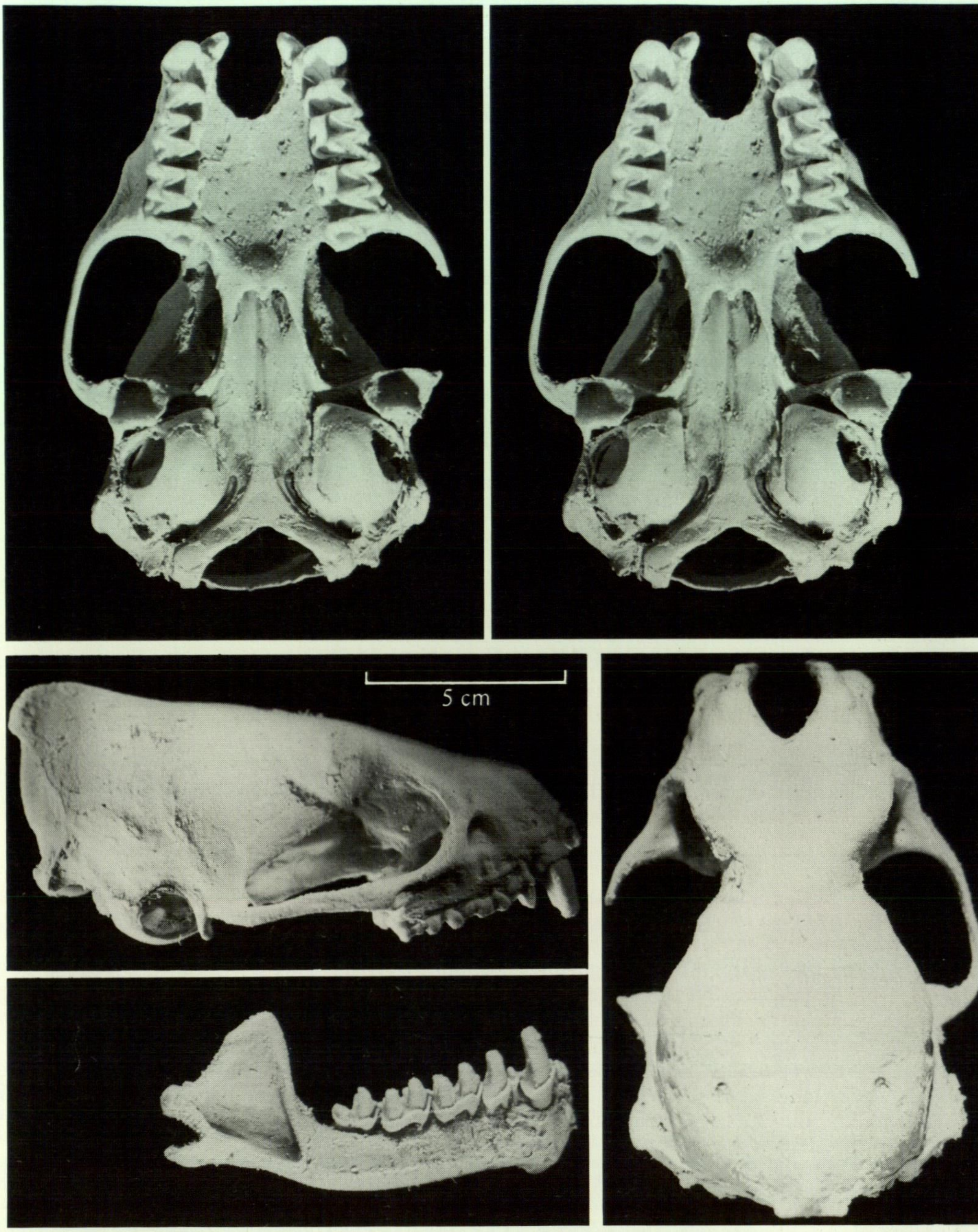


Figure 11 Skull and dentary of *Scotorepens greyii* (AM M1322). Ventral view of skull presented as stereopairs. (Left dentary, reversed.)

dental and external characters with the discriminant functions detailed later in this paper.

Description

Skull

Short skull, relative to skull length has a wide: cranium, intermastoid distance and interorbital distance; cranium mildly inflated so that its lateral profile continues to rise to the frontal-parietal junction at an angle only slightly reduced from that of the rostrum, posterior to that point the profile flattens to form a low occipital cap; lambdoidal crest raised only moderately above foramen magnum (2.3); rostral depression usually moderate, occasionally slight; vestigial postorbital swellings usually present; slight supraorbital swellings, these usually with slight to moderate and occasionally prominent spinous or disc-shaped protuberances (e.g. EBU B313, EBU B307); infraorbital foramen moderate to large, oval, separated from orbit by moderately wide lachrymal bar; anterior palatal emargination usually semi-circular, occasionally more spatulate, usually projects posteriorly to line joining mid-point of $P^{\underline{4}}$, occasionally only to anterior edge of $P^{\underline{4}}$; postpalatal spine moderately long and usually thin but occasionally broadly triangular; base of pterygoid process between foramen rotundum and sphenorbital fissure, process projects dorsally up to a line joining anterior edge of foramen rotundum, frequently to mid-point of that foramen; eustachian projection small, blunt. One specimen (EBU B157) has an accessory incisor on the right side half the height of $I^{\underline{1}}$; slight cingulum frequently on posterior of $M^{\underline{3}}$ protocone.

Dentary

Mental foramen usually located below $P_{\overline{2}}$ occasionally slightly to either side of that position; occasionally slight anterior and posterior cingular cusplet on $I_{\overline{3}}$, rarely on $I_{\overline{2}}$; $M_{\overline{1}}$-$_{\overline{2}}$ lingual cusps of subequal height or with metaconid slightly taller than paraconid and entoconid very small; protoconid decreases in height from $M_{\overline{1}}$-$_{\overline{3}}$, although unequal wear on these occasionally results in $M_{\overline{3}}$ protoconid subequal or longer than that of $M_{\overline{2}}$, hypoconulid greatly reduced and occasionally absent, hypocristid from hypoconid to immediately posterior to base of entoconid or to between vestigial hypoconulid, when present, and entoconid.

Pelage and Skin Colour

As for *Scotorepens balstoni.*

External Morphology

Small, general body shape slender, forearm small (31.3), shape of ear, calcaneal lobe, as in *Scotorepens orion.* Tibia moderate (13.7) or 43.6% length of radius.

Glans Penis

Similar to *Scotorepens balstoni* but with urethral groove U-shaped and spines on baculum head larger and less numerous (4-10) (Figure 5e).

Baculum

(Measurements, in mm: mean, standard deviation, range, sample size.) Short maximum length (2.61, 0.26, 2.20-3.10, 17); shaft relatively robust, slightly curved in lateral profile; distal head bifurcated with two short narrow prongs behind which the shaft occasionally narrows slightly before enlarging into slight lateral flanges; base moderately broad (0.71, 0.06, 0.60-0.80, 17), averaging 27% of maximum length, solid, generally gently curved postero-dorsally to form a moderately high base, but occasionally a tendency to be more squared in line of shaft - as in *Scotorepens balstoni;* groove on caudal and cranial surface of base shallow and wide and meeting as notch at apex (Figure 6e).

Distribution

Scotorepens greyii is the most widely distributed *Scotorepens,* ranging the breadth of Australia and from *c.* 11°S to 33°S. It does not, however, occur in the south-west of Western Australia, northern Queensland or Victoria.

Specimens Examined

Region 8:

Durba Spring 23°45′20″S, 122°31′00″E, 1♂, WAM M14402.

Region 9:

Junction Well 22°44′S, 121°10′E, 1♂, WAM M9625; Ethel Ck H.S. 22°54′S, 120°07′40″E, 1♂, WAM M9859; Hamersley Ra. N.P. 22°37′40″S, 118°06′30″E, 1♀, WAM M18268; Marillana H.S. 22°47′10″S, 119°15′E, 1♀, WAM M18850; Millstream H.S. 21°30′S, 117°00′E, 1♂, WAM M8136; Pamelia Hill 23°16′50″S, 119°11′20″E, 2♀, WAM (M19499, M19501).

Region 10:

Great Sandy Desert 22°29′10″S, 122°31′00″E, 1♂, WAM M22830.

Region 11:

Edgar Ra. 18°24′S, 123°06′E, 1♂, WAM M18456; Cape Bossut 18°42′S, 121°37′E, 2♂, 2♀, AMNH 216140, EBU 125-7; Pt Coulomb 17°15′00″S, 122°12′10″E, 1♂, WAM M22602; Derby 17°20′S, 123°50′E, 1♂, WAM M8471; Waterbank H.S. 17°44′30″S, 122°15′15″E, 2♂, 2♀, WAM (M24028-9, M24064, M24066); Martins Well 16°43′50″S, 122°48′30″E, 1♀, WAM M22660; Meda H.S. 17°22′S, 124°00′E, 1♂, EBU 116; Earth Dam, Whistle Ck 18°48′S, 121°43′E, 1♂, EBU 117; Roebuck Bay *c.* 18°06′S, 122°20′E, 1♂, AM M1322, (holo type, *Scoteinus balstoni caprenus*).

Region 12:

Wolf Ck 18°58′S, 127°38′E, 1♂, WAM M20857.

Region 13:

Pillara Springs 18°21′20″S, 125°47′30″E, 1♂, WAM M18516; Pinbilly Well 18°17′S, 125°45′15″E, 1♂, WAM M18511; Springvale Hill 17°46′30″S, 127°48′00″E, 2♂, WAM M9623-24; Leopold Downs H.S. 17°56′35″S, 125°18′00″E, 2♀, WAM (M24037, M24039); 90 km E Fitzroy Crossing 18°11′S, 125°36′E, 3♂, 2♀, EBU (108, 112-5).

Region 14:

King Edward R. *c.* 15°00′S, 126°00′E, 1♂, WAM M20860.

Region 15:

Kununurra 16°23′S, 128°43′E, 1♂, CM 4470; Mistake Ck *c.* 16°50′S, 128°54′E, 1♀, EBU 106; Moriarty Ck 16°06′S, 129°11′E, 4♀, EBU B227-30.

Region 16:

Daly Waters 16°16′S, 133°22′E, 1♂, EBU B142.

Region 17:

Skull Ck between Major Ck and Victoria R. *c.* 15°20′S, 130°00′E, 1♂, 4♀, EBU B213-7; Jasper Gorge 16°02′S, 130°41′E, 1♂, EBU B239.

Region 18:

14 km W Katherine 14°28′S, 132°16′E, 4♂, 4♀, EBU B150-7; 4 km E Berry Springs 12° 16′S, 130°03′E, 3♀, EBU (B166, B171-2); West Alligator R. 12°47′S, 132°16′E, 1♂, 2♀, EBU B187-9; 70 km E Pine Ck 13°34′S, 132°15′E, 1♂, 3♀, EBU B198-201; Reynolds R. 13° 16′S, 130°41′E, 2♂, 3♀, EBU B203-7; Port Essington 11°16′S, 132°09′E, 1♂, 1♀, BM (42.8.17.12, 44.6.13.2) (Lectotype and paralectotype *Scotophilus greyii*).

Region 19:

35 km W Borroloola 16°04′S, 136°18′E, 3♂, 3♀, EBU B143-8.

Region 20:

McLaren Ck 20°20′S, 134°22′E, 1♂, 1♀, EBU B130-1.

Region 21:

Bushy Park 22°54′S, 133°56′E, 1♂, EBU B278; Alcoota 22°50′S, 134°27′E, 3♂, EBU B291-3.

Region 23:

Boulia 22°55′S, 139°54′E, 1♂, 1♀, EBU B307-8.

Region 24:

Nr Quamby 20°22′S, 140°17′E, 2♂, 3♀, EBU B95-9; Inca Ck 19°59′S, 138°56′E, 1♂, 1♀, EBU B100-01; Gregory R. 19°08′S, 137°53′E, 1♂, 3♀, EBU B117-20; Nr Camooweal *c.* 20°44′S, 139°29′E, 1♂, AMNH 196642.

Region 28:

Bowen 20°01′S, 148°15′E, 1♀, AM 209 (holotype *Scoteinus orion aquilo*).

Region 30:

Alice R. 4 km S Barcaldine 23°33′S, 145°17′E, 3♂, 2♀, EBU 038-42; 45 km W Windorah 25°20′S, 142°12′E, 1♂, 5♀, EBU B310-5; Barcoo R. *c.* 24°30′S, 144°20′E, 2♂, EBU B319-20.

Region 31:

Charleville 26°24′S, 146°15′E, 3♂, 4♀, EBU (0 21-5, 033, 048); Blackdown Tableland 23° 48′S, 149°08′E, 1♀, EBU 048; 20 km N Alpha *c.* 23°09′S, 146°38′E, 2♂, 2♀, EBU B5-8; Babbiloora 25°12′S, 147°08′E, 1♀, EBU B332.

Region 32:

Brisbane 27°28′S, 153°01′E, 3♂, 3♀, EBU 013-18.

Region 38:

16 km W Merriwagga 33°49′S, 145°38′E, 1♂, EBU B365.

Region 40:

Walkdens Bore, W Bourke 29°59′S, 145°50′E, 1♂, EBU B362; Salisbury Downs, White Cliffs 30°51′S, 143°05′E, 1♂, CM 4839.

Region 41:

Calindary H.S. 30°15′S, 142°29′E, 1♂, CM 4764; Fowlers Gap 31°05′S, 141°42′E, 1♀, EBU B380.

Region 43:
Cuttapirie Pt 27°36′S, 139°54′E, 1♀, SAM M720E; Nr Murti Murti H.S. *c.* 29°00′S, 141°00′E, 2♂, EBU B381-2; Innamincka 27°44′S, 140°46′E, 2♀, EBU B383-4.

Morphometric Analyses: Results and Discussion

Univariate Analyses

The means and standard deviations of the 34 characters for the five species by sex and involving combinations of regional geographic groups are shown in Tables 1a, b.

A three factor ANOVA showed significant sexual dimorphism in 31 of the 34 characters examined, females were larger than the males in all 31 characters. Only zygomatic height, lambdoidal crest height, and M^2 length were not significantly different between sexes. Also, all characters were significant for species and geographic groupings at the 99.9 percent level, except for zygomatic height and ear width, which were significant at the 99 percent level for geograpic groupings.

Canonical Variate Analyses

Canonical variate analyses were used to compare the variation between the four species of *Scotorepens* and *Scoteanax rueppellii* for each of the sexes separately and combined using all skull and external measurements. Bulla length, which is missing from many specimens, was omitted from subsequent analyses (Figures 12a, b, c). Clearly these analyses are dominated by the difference between the large *Scoteanax rueppellii* compared with the smaller *Scotorepens* species. There were no misclassifications between the two genera. Also, the differences in group means for males and females were generally less than differences between species, with females having a greater canonical variate I value with each species (Figure 12c). As a result, the sexes were combined in later analyses.

As a result of the clear differences between the two genera, further canonical variate analyses concentrated on the four species of *Scotorepens* (Figure 13). The resulting 'correct' classifications for *Scotorepens* specimens used in the canonical variate analysis and those used only for classification were 97.3 and 93.6 percent, respectively. This analysis produces the following three canonical variate functions (Table 2): Variate I (explaining 60.8 percent of variance) appears to be related to overall size, and separates *Scotorepens sanborni* and *Scotorepens greyii* from *Scotorepens orion* and *Scotorepens balstoni.* Variate II, (29.3 percent of variance) which is largely related to maximum skull length, rostrum length, tibia length and palatal length, provides maximum separation for *Scotorepens orion* and *Scotorepens balstoni.* Variate III (9.9 percent of variance) relates mostly to maximum skull length and palatal length; it provides no greater separation of species. *Scotorepens greyii* and *Scotorepens sanborni* are approximately equally well separated by Variates I, II and III.

The means of the first two canonical variates for the geographic groups are shown in Figure 14. The 'correct' classification rate within species for those

Table 2 Standardised and unstandardised canonical variates from the four species of *Scotorepens* for skull and external characters combined. Sexes combined (see Figure 3 for code to characters). Canonical variate scores are calculated as the summation of the products of the unstandardised canonical variates (in brackets) and the respective constant.

CHARACTER	Variate I	Variate II	Variate III
GL	−0.713 (−1.156)	−1.768 (−2.866)	1.406 (2.279)
AOB	0.063 (0.247)	0.345 (1.342)	−0.541 (−2.103)
LOW	−0.193 (−0.935)	0.209 (1.011)	−0.329 (−1.592)
ZW	−0.531 (−1.103)	0.235 (0.489)	−0.068 (−0.141)
ZH	−0.027 (−0.302)	0.273 (3.036)	0.236 (2.622)
MW	−0.103 (−0.263)	0.687 (1.755)	−0.441 (−1.129)
ROL	0.274 (0.910)	1.008 (3.354)	0.048 (0.159)
BCL	0.473 (1.091)	0.723 (1.670)	0.140 (0.324)
BW	0.091 (0.332)	0.199 (0.727)	0.218 (0.794)
CH	−0.069 (−0.219)	0.591 (1.877)	−0.078 (−0.247)
LH	−0.418 (−1.632)	−0.165 (−0.643)	0.069 (0.268)
PL	0.786 (2.493)	−1.017 (−3.225)	−0.929 (−2.946)
BL	0.158 (0.325)	0.535 (1.105)	−0.039 (−0.081)
BB	−0.022 (−0.117)	0.224 (1.171)	0.247 (1.291)
OB	−0.288 (−0.967)	−0.522 (−1.753)	−0.034 (−0.114)
RC^1-LC^1	0.238 (0.936)	−0.436 (−1.714)	−0.046 (−0.180)
C^1-M^3	−0.382 (−1.531)	−0.202 (−0.810)	0.170 (0.683)
M^1-M^3	0.315 (1.826)	0.027 (0.158)	−0.184 (−1.068)
M^2L	−0.085 (−0.959)	0.029 (0.325)	0.264 (2.968)
M^2W	−0.352 (−2.749)	−0.080 (−0.623)	0.595 (4.642)
M^3W	−0.039 (−0.338)	−0.230 (−1.969)	−0.314 (−2.690)
RM^3-LM^3	0.432 (1.462)	0.250 (0.845)	−0.073 (−0.248)
LR	0.541 (1.787)	0.657 (2.170)	−0.027 (−0.088)
RC	0.357 (1.977)	−0.182 (−1.005)	0.124 (0.687)
HV	0.147 (0.049)	−0.051 (−0.017)	−0.153 (−0.051)
TV	−0.167 (−0.066)	0.190 (0.074)	−0.105 (−0.041)
EL	0.226 (0.308)	−0.239 (−0.326)	−0.134 (−0.184)
EW	0.180 (0.270)	−0.263 (−0.396)	−0.233 (−0.350)
TL	0.022 (0.063)	0.285 (0.810)	0.171 (0.487)
RL	0.365 (0.218)	0.385 (0.230)	0.054 (0.033)
PL	−0.047 (−0.068)	0.037 (0.053)	−0.067 (−0.097)
MCIII	−0.388 (−0.232)	−0.091 (−0.054)	0.380 (0.277)
TIB	−0.205 (−0.254)	−0.727 (−0.898)	0.244 (0.301)
CONSTANT	−17.051	−11.119	−9.567

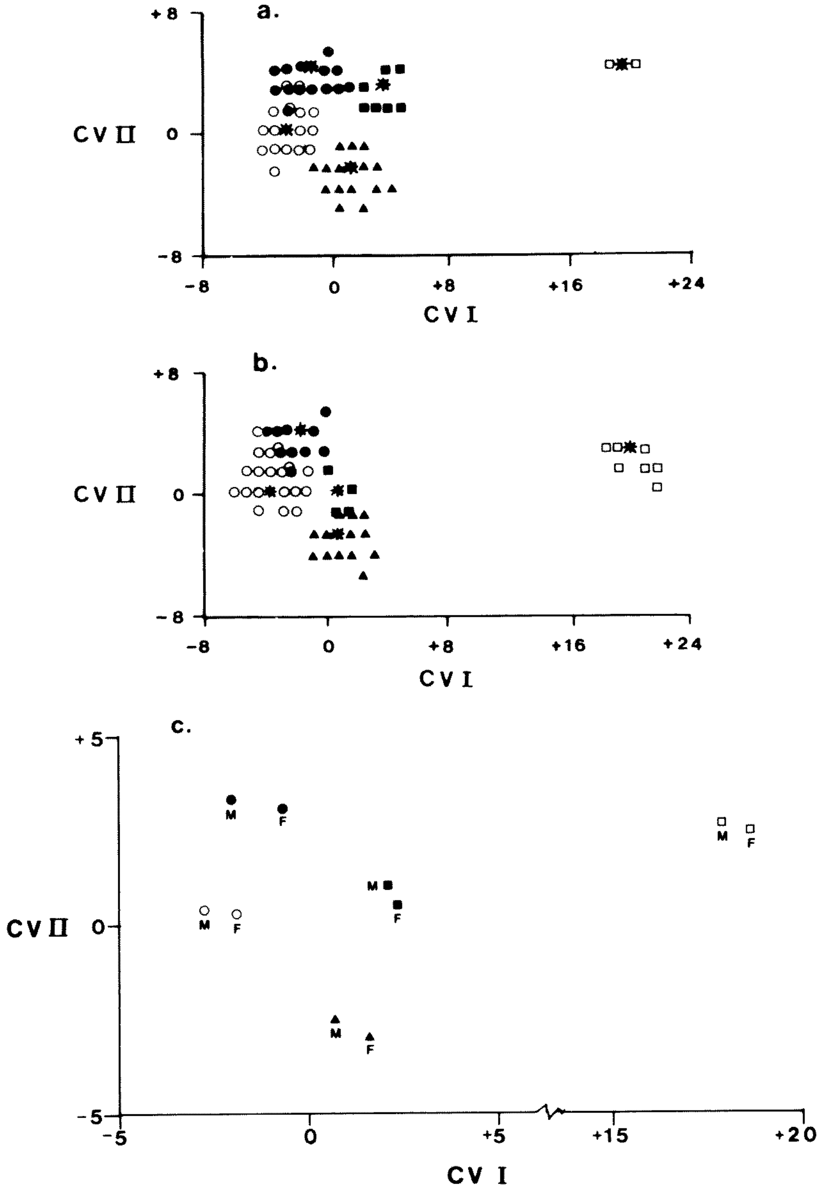


Figure 12 Canonical variate analyses based on all skull and external measurements, except bulla length for *Scoteanax rueppellii* (□), *Scotorepens orion* (■), *Scotorepens balstoni* (▲), *Scotorepens sanborni* (●) and *Scotorepens greyii* (○) using the first two variates for analyses of (a) males (M), (b) females (F) and (c) both males and females. Group mean values (*) and distribution of specimens about the group means are indicated for (a) and (b).

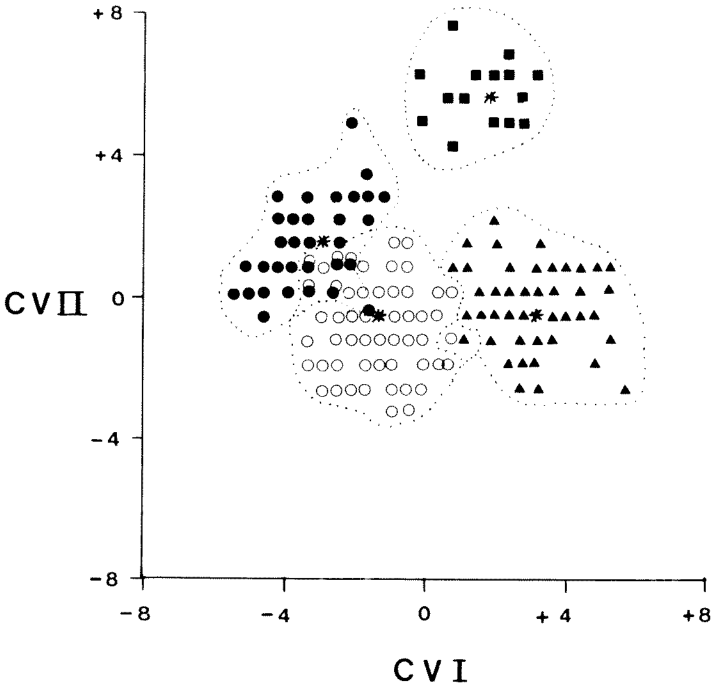


Figure 13 Canonical variate analysis based on all skull and external measurements, except bulla length, for combined sexes of *Scotorepens orion* (■), *Scotorepens balstoni* (▲), *Scotorepens sanborni* (●) and *Scotorepens greyii* (○), showing the first two variates. Group mean values (*).

used in the analysis and the unbiased estimate were 99.0 and 95.4 percent respectively. Only one geographic group, *Scotorepens sanborni* from location 14, lies outside its own species cluster on the first two canonical variates, although there are several geographic groups on either side of the *Scotorepens sanborni*-*Scotorepens greyii* boundary. The canonical variate plot of the 'size free' variables, produced by regressing out the influence of overall size on each variable, is similar to Figure 14 but showing reduced intraspecific variation and slightly increased discrimination between the species. In particular, the *Scotorepens sanborni* and *Scotorepens greyii* clusters no longer overlap because *Scotorepens sanborni* in regional group 14 is clearly withdrawn into its own species cluster. Within the *Scotorepens sanborni* geographic groups, the Western Australian/Northern Territory ones separate from those in Queensland, with the New Guinea/West Irian one occurring near the latter. In the *Scotorepens balstoni* group there is also a geographic trend from Western Australia (1, 2, 5), to South Australia/Northern Territory (20-22), to New South Wales/Victoria (36-39), to Queensland (23, 24, 28-31).

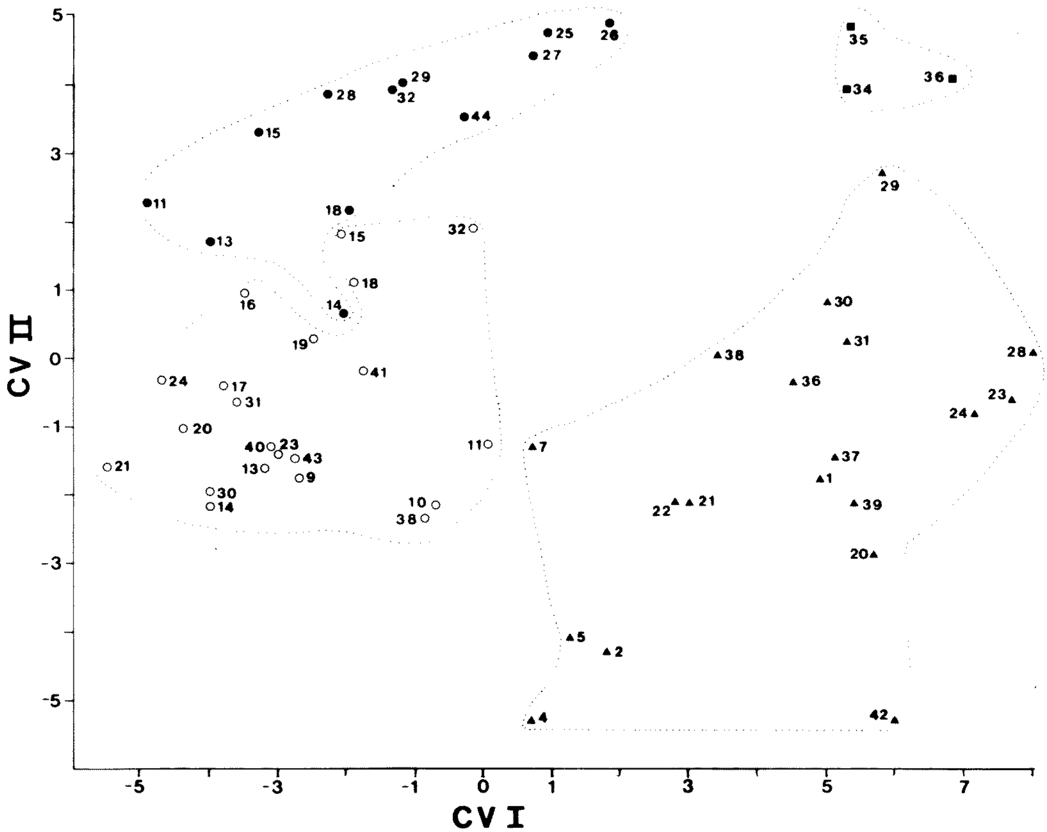


Figure 14 Canonical variate analysis based on all skull and external measurements, except bulla length, for combined sexes for geographic groups of *Scotorepens orion* (■), *Scotorepens balstoni* (▲), *Scotorepens sanborni* (●), and *Scotorepens greyii* (○), showing the first two variates. Group mean values only indicated. See Fig. 7 for location of these regional groups; group 44, Papua New Guinea and West Irian.

Most of the locations near the boundary of *Scotorepens sanborni* and *Scotorepens greyii* are in the north-east Western Australia-Northern Territory area. Location 18 in the Northern Territory is a good example where both *Scotorepens sanborni* and *Scotorepens greyii* occur in sympatry and are difficult to distinguish morphologically. However, a canonical variate analysis on the two species from this geographic group only, reveals two characters, braincase width and palatal length, that may be useful in classifying the two species in this area. The scatter of values between these two skull characters (Figure 15) shows no overlap between individuals of each species.

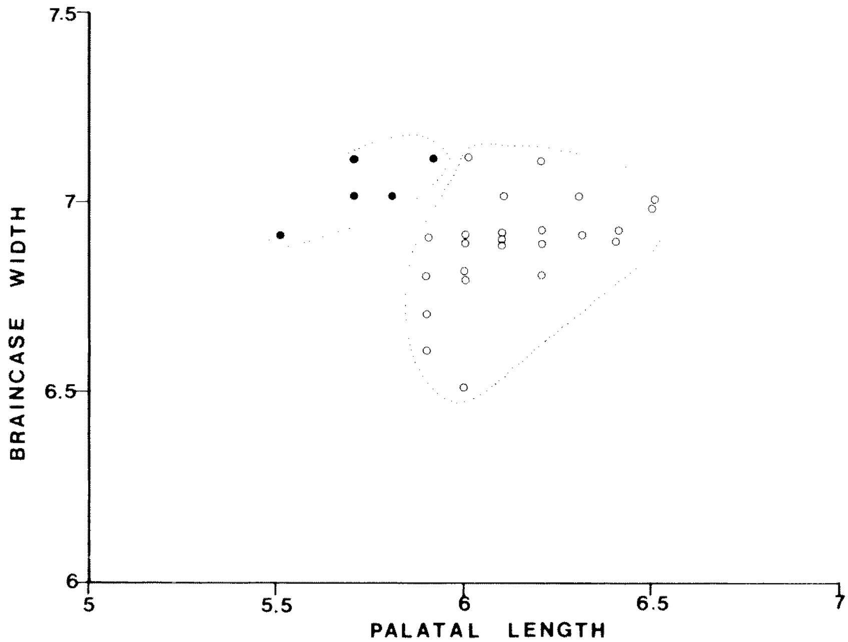


Figure 15 Plot of braincase width and palatal length for specimens of *Scotorepens sanborni* (●) and *Scotorepens greyii* (○) in geographic group 18. See Fig. 7 for location of this group.

Phenetic and Phylogenetic Analysis

Phenetic Analyses – Scoteanax and Scotorepens Geographic Groups

There is some congruence in the phenetic relationship of geographic groups using minimum spanning tree and UPGMA cluster analyses on the Mahalanobis matrix from the canonical variate analysis of skull and external characters (Figures 16a, b). Both methods clearly separate *Scoteanax rueppellii* from the *Scotorepens* spp. Specimens from the different geographic groups within the same species generally cluster together, more so in the minimum spanning tree analysis – although there are a number of exceptions to this. *Scotorepens orion* geographic groups are together in both analyses. However, while they are a distinct group in the minimum spanning tree analysis, they are placed in the middle of the *Scotorepens balstoni* geographic groups in the other analysis. Apart from this, the *Scotorepens balstoni* geographic groups retain a general integrity but for the placement of the southern New South Wales one (38) which is linked to *Scotorepens greyii* in the minimum spanning tree analysis and to the combined *Scotorepens* group in the UPGMA.

Within *Scotorepens greyii* there is no clear regional clustering of geographic groups in UPGMA analysis, although there is a trend for the more inland ones to be grouped together (20, 21, 23, 24, 30, 31, 43).

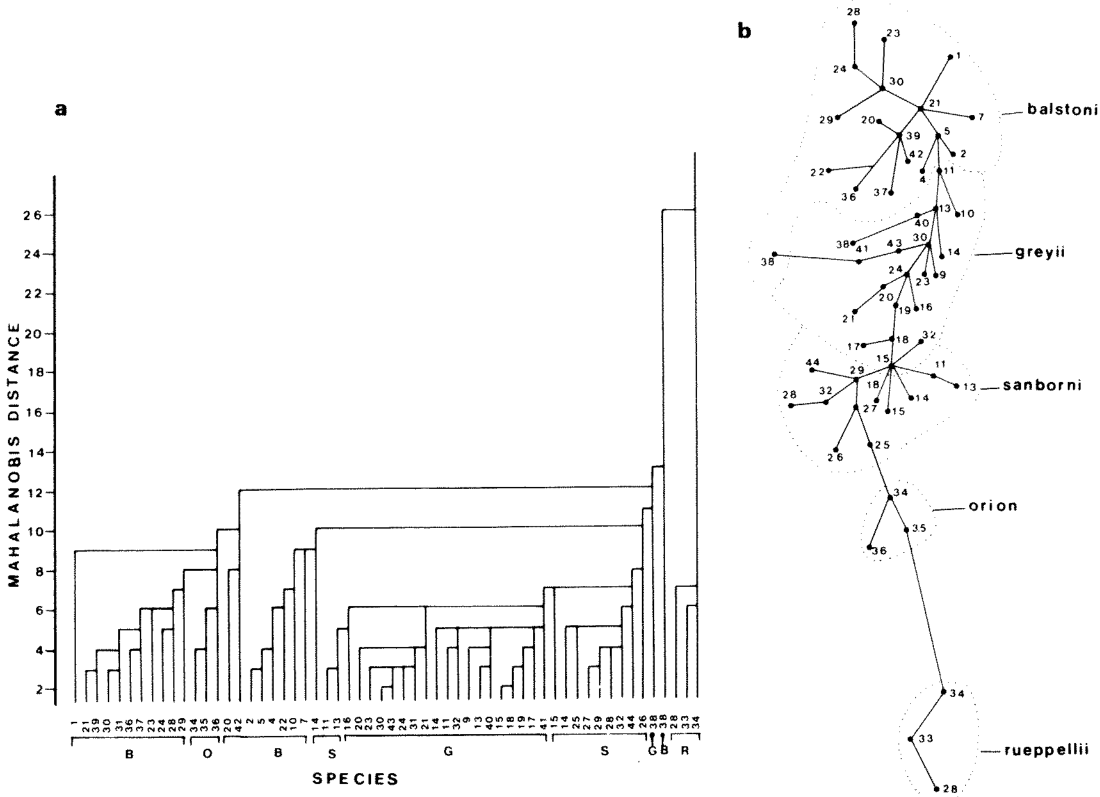


Figure 16 Phenetic relationship, of the four species of *Scotorepens* and of *Scoteanax rueppellii* according to their geographic groups using (a) UPGMA clustering method and (b) minimum spanning tree method. For explanation of the geographic group numeric codes see Fig. 7; the prefixed species alpha code is as follows: R = *Scoteanax rueppellii,* B = *Scotorepens balstoni,* 0 = *Scotorepens orion,* S = *Scotorepens sanborni* and G = *Scotorepens greyii.*

Phylogenetic Analysis

This analysis, using Farris's 78 program, produces a pattern of relationships that shows little congruence with the phenetic analysis. There is a general intermingling of *Scotorepens sanborni* and *Scotorepens greyii* and of *Scotorepens orion* and *Scotorepens balstoni* geographic groups. *Scoteanax rueppellii* forms a discrete, and very separate group from the *Scotorepens* spp. Figure 17 shows the network for both sexes combined, using the means of the characters (range coded).

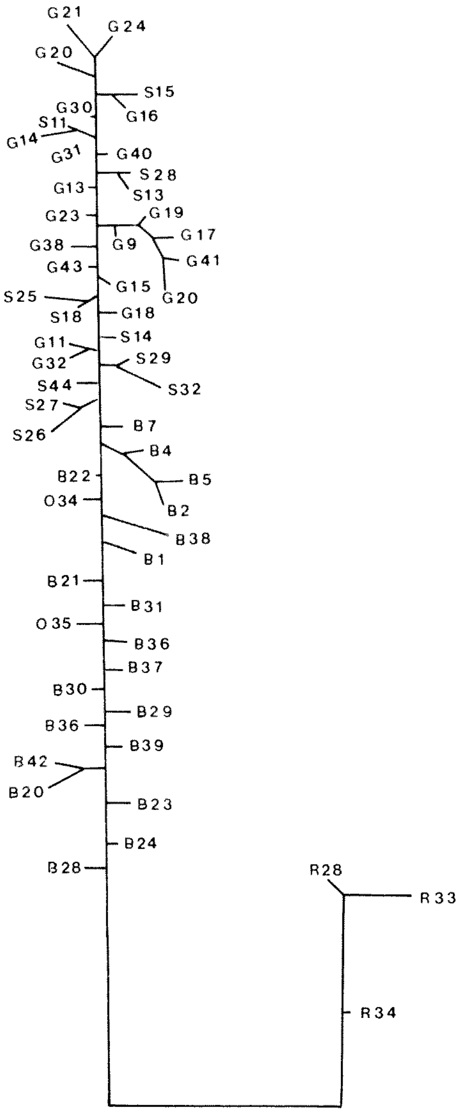


Figure 17 Wagner network of the four species of *Scotorepens* and of *Scoteanax rueppellii* according to their allocation into geographic groups, constructed from means of all characters except bulla length. Branch lengths are proportional to patristic distances. For explanation of the geographic group numeric codes see Fig. 7, the prefixed species alpha code is as follows: R = *Scoteanax rueppellii*, B = *Scotorepens balstoni*, 0 = *Scotorepens orion*, S = *Scotorepens sanborni* and G = *Scotorepens greyii.*

Once again several *Scotorepens sanborni* geographic groups from Kimberley are placed with those of this species from Queensland. *Scotorepens sanborni* and *Scotorepens greyii* and *Scotorepens orion* and *Scotorepens balstoni* are not separated on this network. *Scoteanax rueppellii* is clearly separate from these other species. Analyses using 'size free' and range coded data produce similar patterns.

Relationship between *Scoteanax*, *Scotorepens* and other Nycticeiini Genera

Phenetic Relationship

Scoteanax and *Scotorepens* are clearly allied to the Nycticeiini genera of Tate (1942).

Skull and external measurements listed in Figure 3 were recorded from representative species of the Nycticeiini genera. Specimens examined are listed in Appendix II. Approximately equal numbers of each sex were measured where possible. These measurements, along with those for *Scoteanax* and *Scotorepens* were subjected to canonical variate analysis, minimum spanning tree and UPGMA cluster analysis and Wagner phylogenetic analysis. Data for skulls alone were examined separately. There was a marked concordance between these various phenetic analyses, whether treating skulls alone, or including body measurements. For this reason, we present data using UPGMA cluster analysis only and for skull and body measurements combined – although this results in a reduced sample size for some species because spirit carcases were frequently not available to us. Because of the extent of intraspecific variation in overall size noted in this study it was considered necessary to repeat these analyses using 'size free' data.

With untransformed data (Figure 18) *Scoteanax* is most similar to *Scotomanes* and then *Scotophilus (dinganii, leucogaster, heathii* and *kuhlii)*. It is distant from *Rhogeessa, Nycticeius, Scotoecus, Scotorepens, Scotophilus nigrita* and *Otonycteris*.

Scotorepens spp are closer to *Nycticeius schleiffenii,* then *Scotoecus, N. humeralis* and *Rhogeessa.* They are more distant from *Scoteanax, Scotophilus* and *Otonycteris.* With 'size free' data the dendrogram is essentially the same.

Phylogenetic Analyses

Wagner Trees for the Nycticeiini genera were produced from untransformed data and 'size free' data, both using range coded measurements. These Trees were rooted using *Pipistrellus tenuis papuanus* (Peters and Doria, 1881) from Queensland, as the outgroup.

The tree produced by data before size is removed (Figure 19a) is difficult to interpret in terms of our understanding of generic groupings. None of the congeneric species form a monophyletic group. Further, species within *Scotoecus, Scotorepens* and *Nycticeius* are separated by considerable patristic distances.

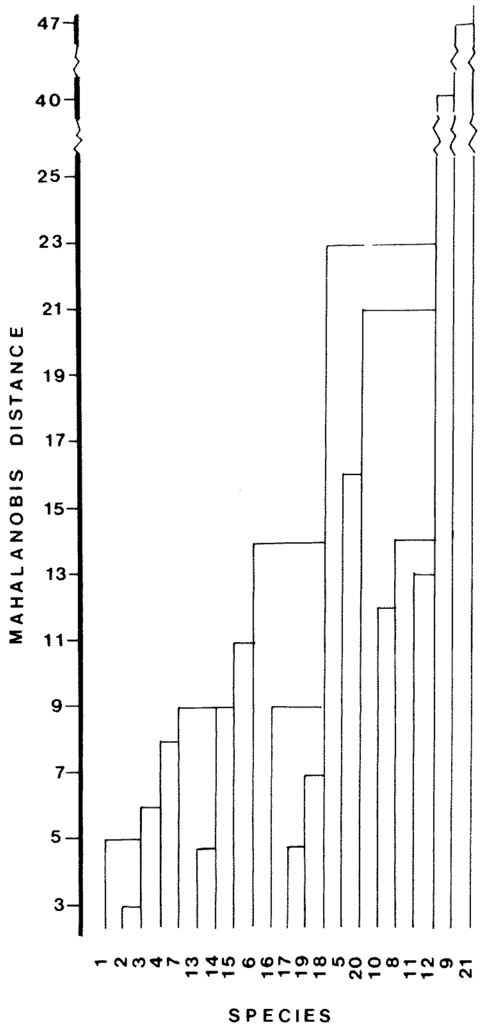


Figure 18 Phenetic relationships derived by UPGMA cluster analysis on species within the Nycticeiini genera. Males and females combined and both skull (except bulla length) and external characters included. Species are numbered as follows:
1 - *Scotorepens balstoni*, 2 - *Scotorepens sanborni*, 3 - *Scotorepens greyii*, 4 - *Scotorepens orion*, 5 - *Scoteanax rueppellii*, 6 - *Nycticeius humeralis*, 7 - *N. schleiffenii*, 8 - *Scotophilus leucogaster*, 9 - *S. nigrita*, 10 - *S. dinganii colias*, 11 - *S. heathii*, 12 - *S. kuhlii*, 13 - *Scotoecus hirundo*, 14 - *S. hindei hindei*, 15 - *S. pallidus*, 16 - *Rhogeessa (Baeodon) alleni*, 17 - *R. tumida*, 18 - *R. tumida bombyx*, 19 - *R. parvula*, 20 - *Scotomanes ornatus imbrensis*, 21 - *Otonycteris hemprichii hemprichii*.

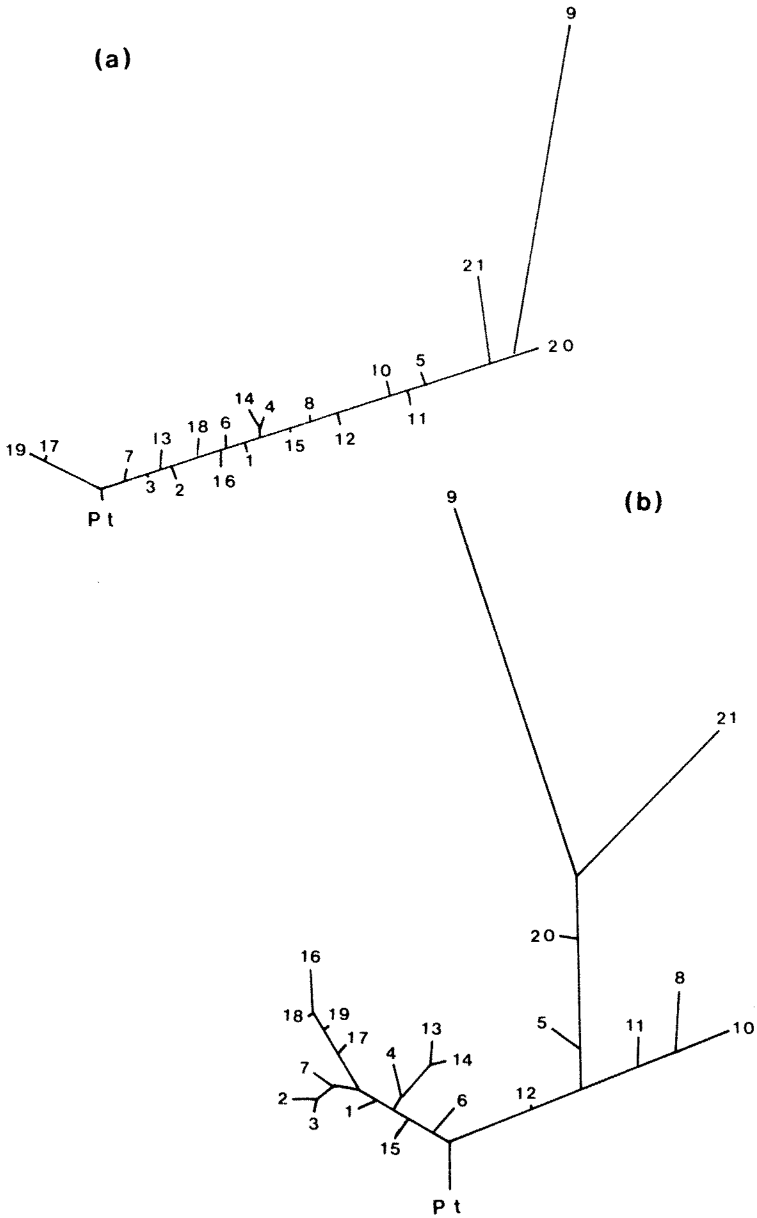


Figure 19 Wagner Tree of 21 species within the Nycticeiini genera. Males and females combined and both skull (except bulla) and external characters included. Data are range-coded. The tree is rooted using *Pipistrellus tenuis papuanus* (P t) as the outgroup. Branch lengths are proportional to patristic distances. (a) untransformed (b) 'size-free'. See Fig. 18 for species number code.

Only when the above tree is reconstructed using 'size free' data, does it assume a more recognisable pattern (Figure 19b). *Rhogeessa* now appears as a monophyletic group, and most of the congeneric species are genealogically closer. The exceptions are *Nycticeius (schleiffenii* and *humeralis)* and *Scotophilus (nigrita* and the other species).

Both the untransformed and 'size free' trees indicate that *Scoteanax* is genealogically distant from *Scotorepens.* In both trees *Scoteanax* has *Scotophilus nigrita, Otonycteris hemprichii* and *Scotomanes ornatus* as its sister group – although its patristic distance is marginally closer to *Scotophilus leucogaster* than to *Scotomanes ornatus. Scotorepens* is polyphyletic; *Scotorepens greyii* and *Scotorepens sanborni* are close to *Nycticeius schleiffenii* in both trees and are the sister group to *N. schleiffenii* in the 'size free' analysis. In both trees *Scotorepens* spp are associated with *Scotoecus hirundo* and *S. hindei.* In both trees, *Scotophilus nigrita* and *Otonycteris* are genealogically distant from other species, particularly in the 'size free' analysis.

Regional Morphological Variation, *Scotorepens*

The previous univariate, canonical variate and phenetic analyses show that, within species, there is considerable morphological variation between geographic groupings. Canonical variate analysis suggested that factor I related to overall size. Three characters: skull length, radius length and lower tooth row length were selected as indicators of overall size of skull, body and teeth, respectively. To evaluate some possible locational and environmental influences on these three indicators of overall size, they were related by multiple regression analysis to latitude and longitude and to selected broad-scale environmental data. Sex was also included as a variable because of the dimorphism noted earlier in all species. The results for *Scotorepens* spp follow. There were too few specimens to analyse *Scoteanax rueppellii.*

Scotorepens balstoni

Skull length varies longitudinally rather than latitudinally, with 56 percent of the variation in skull length explained by a combination of longitude, minimum temperature in July and sex (Table 3). Skull size increases from west to east and in areas with warmer winter temperatures. Radius length and lower tooth row length vary similarly to skull length but with latitude also contributing significantly to explained variation in radius length. More northern specimens having longer radius lengths.

Scotorepens orion

Although the sample is small (n=19), both skull and radius lengths are most highly correlated with minimum temperature in July and sex. These variables in combination accounting for 49 and 56 percent, respectively, of the variation. Both these characters are shorter in regions with higher minimum July temperatures (Table 3).

Table 3 Regression coefficients from stepwise multiple regression analysis between the morphological characters maximum skull lengths (GL), radius length (RL) and lower tooth row length (LT), for each *Scotorepens* species, and: locality (latitude and longitude), environment (median annual rainfall, average annual evaporation, mean maximum January temperature, mean minimum July temperature) and sex (1 = male, 2 = female). (r), correlation coefficients for each character. (n), sample size. Significance levels: * = P<.05, ** = P<.01, *** = P<.001.

Locality Environmental/ sex/variables	Species	Coefficients GL	RL	LT
longitude	*balstoni*	0.037***	0.074***	0.020***
	orion			
	sanborni	0.071***	0.113***	0.029***
	greyii	−0.037***	−0.082***	−0.011***
latitude	*balstoni*		−0.070**	
	orion			
	sanborni	−0.173***	−0.267***	−0.047***
	greyii	0.055***	0.150***	0.033***
sex	*balstoni*	0.489***	1.751***	0.111**
	orion	0.427**	1.554**	
	sanborni		1.378***	
	greyii	0.223*	1.323***	0.135***
rainfall	*balstoni*			
	orion			
	sanborni	−0.0008**		
	greyii		0.0013***	
evaporation	*balstoni*			
	orion			
	sanborni			
	greyii			
Temp. Jan-max.	*balstoni*			
	orion			
	sanborni			
	greyii	−0.47**		−0.027***
Temp. July-min	*balstoni*	0.096***	0.241***	0.053***
	orion	−0.183*	−0.499*	
	sanborni		−0.213**	
	greyii	0.088***	0.15**	0.050***
r	*balstoni*	0.75***	0.78***	0.80***
	orion	0.70**	0.75***	
	sanborni	0.89***	0.86***	0.88***
	greyii	0.68***	0.71***	0.69***
n	*balstoni*	105	105	105
	orion	19	19	19
	sanborni	55	55	55
	greyii	130	130	130

Scotorepens sanborni

Skull length is most highly correlated with latitude, longitude and rainfall. With radius length, unlike skull length, median annual rainfall is not a significant variable but minimum temperature in July is. Length of both skull and radius increases from west to east and decreases from north to south and with warmer minimum July temperatures. With these combinations of variables 79 and 74 percent of variation is accounted for in both skull and radius lengths, respectively. Longitude, latitude and sex are significant for lower tooth row length (Table 3).

Scotorepens greyii

Longitude, latitude, minimum July temperature and sex are significant variables related to lengths of skull, radius and lower tooth row. Mean maximum temperature in January is additionally significant for skull length and lower tooth row length, with median annual rainfall also significant for radius length. These variables explain 46, 50 and 48 percent, of the variation in skull and radius lengths and lower tooth row length, respectively. All these characters decrease from west to east, increase from north to south and increase with warmer minimum July temperatures. Additionally, skull and lower tooth rows are longer with lower January maximum temperatures and radius length greater with higher median annual rainfall.

General Discussion

This study employs a variety of taxonomic approaches to investigate the status of Australian species hitherto placed in the genus *Nycticeius*. Eight named forms have been reduced to five species. Of these species, two are siblings *(Scotorepens sanborni* and *Scotorepens greyii)*, particularly in the centre of their distributions in north-western Western Australia and northern Northern Territory. A small proportion of specimens of these two species cannot be correctly classified using canonical variate analysis on morphological characters. They can, at this stage, be absolutely distinguished only on electrophoretic differences (P. Baverstock, pers. comm.). Earlier workers, most notably Koopman (1978,1984) recognised the difficulty in distinguishing these two smaller forms, which he referred to as *Nycticeius balstoni caprenus* and *Nycticeius greyii,* in central northern Australia.

For *Scotorepens* spp. and *Scoteanax rueppellii* arrangement of geographic groups in phenograms and Wagner trees differ considerably. The minimum spanning tree analyses produces a branching pattern much more in accord with our classical appraisal of the taxa concerned than was achieved by the Wagner network. This may be due to the correlations in characters being taken into account in the former analysis but not in the Wagner network approach. Within *Scotorepens balstoni, Scotorepens sanborni* and *Scotorepens greyii,* geographic groups that are geographically close may be considerably separated in both phenograms and Wagner networks. This suggests that these *Scotorepens* spp. are very sedentary affording little gene flow between geographic groups and/or considerably different natural selection pressures operate between these groups. The high correlations observed between overall size of these species and some environmental variables suggest either that natural selection is an important factor, or that these are plastic characters.

This morphometric appraisal of *Scotorepens* and *Scoteanax* geographic groups provides no solid support for the monophyletic origins of the *Scotorepens* species. These numerous instances of disagreement between the numerical and traditional classifications reflect the situations observed for the Australian dasyurid marsupial groups, *Ningaui* and *Sminthopsis* (Kitchener *et al.* 1983, 1984) and for other dasyurids (Kirsch and Archer 1982). Kitchener *et al.* (1984) provide a detailed explanation for the situation in *Sminthopsis* and their discussions are considered relevant here. The clear statement from the phylogenetic analysis of the Australian forms is the extent of the separation between *Scoteanax rueppellii* and the *Scotorepens* species, lending support to the generic classification proposed here.

The phenetic and phylogenetic appraisal of the Nycticeiini genera show little overall concordance. There are certain elements of these phenetic and phylogenetic analyses that are, however, similar. For example, irrespective of treatment, *Nycticeius humeralis* and *N. schleiffenii* are not very close. The latter is always grouped with *Scotorepens* and *N. humeralis* usually with *Scotoecus*. *Scoteanax* is closer to *Scotomanes* (phenogram and Wagner using size free data).

The Wagner Trees strongly support our view that *Nycticeius (sensu lato)* is not a natural grouping, and that the generic status of *Scoteanax* and *Scotorepens* is warranted. Further they suggest that *Nycticeius humeralis* and *N. schleiffenii* are not congeneric and that *nigrita* is not a *Scotophilus*. Also *Otonycteris* and *Scotophilus nigrita* fit poorly in the Nycticeiini.

Variation in skull, radius and lower tooth row lengths of *Scotorepens* spp. ranging from 46-79 percent, could be explained by combinations of locality and environmental variables and sex. Skull, radius and lower tooth row lengths which are measures of overall size, are strongly correlated in all species except *Scotorepens orion,* to longitude, and in *Scotorepens sanborni* and *Scotorepens greyii,* also to latitude. Interestingly within *Scotorepens sanborni* there is a strong cline in size, with individuals becoming larger from west to east. While within *Scotorepens greyii,* with which it is broadly sympatric in Kimberley and Northern Territory, the trend is reversed. Consequently specimens in the central northern region are of similar size and therefore particularly difficult to identify.

Overall size, as indicated by both skull, radius and lower tooth row lengths of *Scotorepens balstoni,* is also strongly correlated with longitude and latitude and with minimum July temperatures. These correlations support our consideration that the very large specimens previously referred to as *Nycticeius influatus,* inhabiting central and north coastal Queensland, are the terminus of a geographic and environmental cline in size within *Scotorepens balstoni.*

Similarly, the larger Queensland form of *Scotorepens sanborni* is shown to represent part of a similar geographic and environmental cline in overall size.

Morphological variation is less clinal in *Scotorepens greyii,* with a number of geographic groupings (10, 16, 32 and 38) forming ecotypes. *Nycticeius orion aquilo,* synonymised here with *Scotorepens greyii,* is most similar in form to populations of *Scotorepens greyii* from region 32, although it is also close to *Scotorepens sanborni* in Queensland.

Environmental data appended herein to specimen locality records is regional data and is used to indicate only broad patterns. Interestingly, of these environmental variables, minimum July temperatures, a measure of the coldness of winter months, is one of the most consistently significant variables related to skull, radius and lower tooth row lengths of all species. Median annual rainfall, mean annual evaporation and maximum January temperatures are generally less important. This may indicate that these *Scotorepens* spp. are able to ameliorate effect of summer heat by their choice of diurnal rest sites, such that it has less influence on their overall size. On the other hand, the cold nocturnal temperatures of winter months in which they must forage for food, may have a more profound influence on morphology. These observations are, however, difficult to interpret. Size of endotherms usually increases with increasing climatic severity and this has been demonstrated by Findley and Jones (1967) for two species of *Myotis* in southwestern USA. In this study, if winter extremes of coldness are indicative of general climatic severity, then *Scotorepens orion* and *Scotorepens sanborni* do increase in size with increased severity, but *Scotorepens balstoni* and *Scotorepens greyii* become smaller.

Clearly morphological trends observed in this study are the result of a complex interplay of factors. The same can be said of the intensive study of *Pipistrellus hesperus* in southwestern USA by Findley and Traut (1970). They found geographic variation in populations of *P. hesperus* to the west of the continental divide corresponded to a climatic severity index, combining latitude and altitude, which they attributed to the Bergmann effect. To the east of this divide *P. hesperus* showed little relationship between size and climatic severity. They hypothesised this situation to have resulted from a failure of the eastern population to adjust to the climatic gradient in that region as a result of occupying it only in post-glacial times. Findley and Wilson (1982) discount this suggestion, arguing that ample time had elapsed for the eastern populations to adapt morphologically to these changes. Stebbings (1973) similarly attributed morphological clines in *Pipistrellus pipistrellus* in Great Britain to the Bergmann effect.

Sexual dimorphism, with females being larger than males, is common in vespertilionids (Findley and Traut 1970, Myers 1978). The few studies on sexual dimorphism in Australian vespertilionids are of *Eptesicus* spp. Carpenter *et al.* (1978) reported that sexual dimorphism is less pronounced in the cave dwelling species: *E. p. pumilus* where females appear to be slightly larger than males and *E. pumilus caurinus* where females appear to be slightly smaller than males.

However, females of the forest dwelling *E. vulturnus* and *E. sagittula* are appreciably larger than males. Campbell and Kitchener (1980) observed that in all Western Australian populations of *E. regulus, E. p. pumilus* and *E. pumilus caurinus* studied, females tend to be larger than males.

In conclusion, this study indicates the need to utilise a range of taxonomic procedures to unravel the taxonomic confusion prevalent in many of the smaller Australian bats. The numerical taxonomic approach, while contributing much to our understanding of other taxa treated herein, shows important areas of discordance with the more classical approach. A probable important contributing influence to this discordance is the extent of variation observed in most taxa in overall size, much of it clinal.

The addition of *Scoteanax* and *Scotorepens* to the other endemic genera of Australian bats *(Macroderma* and *Rhinonicteris)* suggests a level of endemicity which is consistent with the long fossil record of bats in Australia (Hand 1984).

Key to Species

To be used in conjunction with pertinent diagnoses, descriptions and measurements in Tables 1 and 2.

External Morphology

1a Forearm length greater than 50 mm .... *Scoteanax rueppellii* (p. 94)

1b Forearm length less than 50 mm 2

2a Tibia length less than 41% radius length, fur not markedly bicoloured .... *Scotorepens orion* (p. 107)

2b Tibia greater than 41% radius, fur markedly bicoloured 3

3a Radius length averages more than 35 mm .... *Scotorepens balstoni* (p. 111)

3b Radius length averages less than 32 mm ..... *Scotorepens sanborni* (p. 115) or *Scotorepens greyii* (p. 119)

Skull and Teeth

1a Maximum skull length greater than 19 mm .... *Scoteanax rueppellii*

1b Maximum skull length less than 19 mm 2

2a Upper molar row averages more than 3.6 mm
Interorbital width averages more than 75% C^1-M^3 length .... *Scotorepens orion*
Interorbital width averages less than 65% C^1-M^3 length .... *Scotorepens balstoni*

2b Upper molar row averages less than 3.3 mm 3

3a Pterygoid process usually extends posterior to anterior edge foramen rotundum .... *Scotorepens greyii* (Fig. 11)

3b Pterygoid process usually does not extend posterior to anterior edge foramen rotundum .. *Scotorepens sanborni* (Fig. 10)

Glans Penis

1a Papillae on head .... *Scoteanax rueppellii* (Fig. 5a)

1b Spines on head 2

2a Spines on head in subcircular cluster (eight spines) .... *Scotorepens orion* (Fig. 5b)

2b Spines on head in two elongate primary rows 3

3a Smaller more numerous spines (up to 22) ... *Scotorepens balstoni* (Fig. 5c)

3b Larger less numerous spines (up to ten) .... *Scotorepens sanborni* (Fig. 5d) or *Scotorepens greyii* (Fig. 5e)

Baculum

1a Baculum longer than 8 mm .... *Scoteanax rueppellii* (Fig. 6a)

1b Baculum shorter than 4 mm – slender shape with reduced distal flanges .... *Scotorepens orion* (Fig. 6b)

2a Baculum shaft straight .... *Scotorepens balstoni* (Fig. 6c)

2b Baculum shaft curved .... *Scotorepens sanborni* (Fig. 6d) or *Scotorepens greyii* (Fig. 6e)

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Ms J. Paniperis patiently typed numerous drafts of the MS.

Appendix I

Measurements, in mm for holotypes and unique specimens. Body measurements from alcohol preserved specimens unless indicated otherwise. (See Fig. 3 for code to measurements).

Species Catalogue No., Type	*Scoteinus balstoni* BM-6.8.1.41. holotype	*Scoteinus influatus* BM-24.3.7.4 holotype	*Scoteinus sanborni* AM-A3176, holotype	*Scotophilus greyii* B 42.8.17.12 Spec 'b' (Dobson 1888:263) Thomas's (1906) Lectotype	*Scotophilus greyii* BM 44.6.13.2 Spec 'a' (Dobson 1888:263) paralectotype	*Scoteinus balstoni caprenus* AM-M1322, holotype	*Scoteinus orion* AM-M6115, holotype	*Scoteinus orion aquilo* AM-209, holotype
Sex/Age	♀A	♂A	♀A	♀A	♂A	♂A	♂A	♀A
GL	14.8	15.8	13.6	–	13.0	14.1	14.9	13.5
AOB	5.1	5.4	4.7	4.7	4.6	4.7	5.5	5.1
LOW	3.4	3.8	3.6	–	3.4	3.4	4.3	3.6
ZW	10.0	11.3	–	–	9.8	9.7	10.5	10.2
ZH	0.6	0.9	0.6	–	0.7	0.8	0.6	0.5
MW	8.5	9.2	8.2	–	7.7	8.4	9.1	8.5
ROL	6.0	6.3	5.0	–	5.2	5.3	5.8	5.4
BCL	8.8	9.5	8.7	–	7.8	8.7	9.2	8.2
BW	7.1	7.6	7.2	–	6.6	6.9	7.6	7.3
CH	5.4	6.0	5.3	–	5.1	5.2	6.0	5.3
LH	1.9	2.6	2.3	–	2.4	2.4	2.7	2.6
PL	6.8	7.5	5.6	–	6.0	6.1	6.8	6.2
BL	12.6	13.5	10.9	–	11.4	12.0	12.7	11.6
BUL	3.3	3.4	3.1	–	3.0	3.3	3.3	–
BB	1.3	1.6	1.6	–	1.1	1.1	1.4	1.5
OB	7.4	8.1	7.4	–	6.9	7.3	7.9	7.4
RC^1-LC^1	4.8	5.6	4.5	–	4.5	4.5	5.2	4.6
C^1-M^3	5.4	6.1	4.8	5.2	4.9	5.1	5.5	5.1
M^1-M^3	3.6	3.9	3.1	3.4	3.2	3.3	3.7	3.4
M^2L	1.5	1.6	1.3	1.5	1.3	1.4	1.5	1.5
M^2W	1.8	1.9	1.8	1.8	1.8	1.6	1.8	1.7
M^3W	1.7	1.7	1.5	1.6	1.5	1.6	1.6	1.5
RM^3-LM^3	6.4	7.1	6.0	–	6.0	5.9	6.7	6.3
LR	6.7	7.7	6.0	6.2	6.1	6.3	7.0	6.2
RC	3.3	3.5	3.1	–	3.2	3.2	3.3	3.3
HV	51.4*	52.4	43.5	50.9*	43.0	48.3	61.0+	45.4
TV	30.5*	33.2	29.0	30.7*	30.8	33.3	33.0+	35.3
EL	9.0*	11.9	10.6	9.5*	10.0	10.4	13.0+	10.5
EW	–	12.7	7.9	–	7.9	8.7	10.0+	8.4
TL	4.5*	5.6	4.6	3.9*	4.3	5.0	–	4.8
RL	35.5*	38.2	34.2	–	30.7	33.8	35.8+	34.3
MCIII	33.9*	37.2	32.9	31.7*	31.2	32.0	33.5+	33.5
PL	6.8*	8.1	5.1	6.4*	6.2	4.7	7.8+	5.9
TIB	13.7*	16.2	13.9	13.7*	13.8	13.8	12.0+	14.6

*measurements from skins

+ measurement of 'fresh specimen' from Troughton (1937) (holotype as skin)

Appendix II: Other Specimens Examined

All British Museum, Natural History specimens, except *Scotophilus kuhlii,* which are from the Western Australian Museum. S, skull; Sk, skin; and A, carcase in alcohol.

Nycticeius humeralis: Sans Souci, North Carolina, USA, 3♀, numbers 7.7.7.565-6, 7.7.7.568 (S, Sk); Hickman County, Tennessee, USA, 1♀, 7.2.2.1433 (S, Sk); Buncombe County, North Carolina, 1♂, 99.8.2.2 (S, Sk); Brownsville, Texas, USA, 1♀, 7.7.7.879 (S, Sk); Georgia, USA, 1♀, 66.4.2.2 (S, A).

Nycticeius schleiffenii: Suakin, Egypt, 1♀, 3.12.8.16 (S, A); Assab, Egypt, 1? sex, 89.8.1.9 (S, A); Karmisa, nr Dinda R., Sudan, 1♂, 15.3.6.66 (S, A); Shendy, Sudan, 1♂, 1.5.5.79 (S, Sk); 35 miles E Nahud, Kordofan, Sudan, 1♂, 1♀, 23.1.1.31-2 (S, Sk).

Scotophilus leucogaster: Ethiopia, 1♂, 73.4.16.23 (S, A); Kilifi, Kenya, 1♂, 75.2951 (S, A).

Scotophilus nigrita: Mote N.P., Ghana, 1♀, 76.773 (S, A); Odzi, Zimbabwe, 1♂, 47.7 (S, Sk); Chiromo, Malawi, 1♂, 1♀, 22.12.17.53-4 (S).

Scotophilus dinganii colias: Kitgum, Uganda, 1♀, 60.1983 (S, A); Ethiopia, 1♀, 71.2456.

Scotophilus heathii: Madras, India, 1♀, 2 (S, Sk); Dhulia, Khandesh, India, 2♀, 99.11. 6 (S, A), 11.7.14.2 (S, Sk); Surat, W India, 2♂, 97.6.8.9-10 (S, Sk); Poona, W India, 1♂, 19.6.3.19 (S, Sk).

Scotophilus kuhlii: Bali, Indonesia, 3♂, 3♀, M16172, M16174-6, M16178-9 (S, A).

Scotoecus hirundo: Mote N.P., Ghana, 1♂, 76.771 (S, A); Ethiopia, 1♂, 3♀ (S, A), 70.2265-6, 70.2269-70.

Scotoecus hindei hindei: Didessa River, Ethiopia, 1♂, 72.4423 (S, A); Bulcha, Lake Margherita, Ethiopia, 1♂, 70.2262 (S, A); Wei-Wei River, Kenya, 2♂, 14.7.31.15, 14.7.31.17 (S, A); Mombasa, Kenya, 1♀, 91.9.7.3 (S, A); Mtondo R., Tanzania, 1♂, 73.1719 (S, A).

Scotoecus pallidus: nr Shikarpur, Sind District, Pakistan, 1♀, 91.11.1.1 (S, A); Kashmor, Sind, Pakistan, 1♀, 15.11.1.33 (S, Sk); Bahgounie, Darbhanga, India, 2♂, 1♀, 23.4.8.1-2, 23.4.8.4 (S, Sk); Mirpur, Sind, Pakistan, 1♂, 15.11.1.34 (S, Sk).

Rhogeessa (Baeodon) alleni: Santa Rosalia, Mexico, 2♀, 93.2.5.25 (holotype, S, A), 93.2.5.26 (paratype, S, A).

Rhogeessa tumida: Trinidad, 1♂, 2♀, 37.8.30.29-30, 45.292; NW Venezuela: 1♂, 1♀, 94.9. 25.19-20 (S, A).

Rhogeessa tumida bombyx: Columbia, 1♂, 13.10.29.1 (S, A).

Rhogeessa parvula: Tres Marias Is., 1♂, 81.11.1.8 (S, A).

Scotomanes ornatus imbrensis: Chiang-mai, Thailand, 1♂, 78.2374 (S, Sk); Khasia Hills, Assam, India, 1♂, 75.11.3.7 (S, A); Darjeeling, India, 1♀, 9.1.4.30 (S, A); Denning, Assam, India, 2♀, 23.1.7.5-6 (S, Sk); Mahtum, Burma, 1♀, 50.448 (S, Sk).

Otonycteris hemprichii hemprichii Syrian desert, 1♂, 14.8.17.1 (S, A); Mastuj, N Pakistan, 1♀, 78.299 (S, A); Oasis Suvah, Egypt, 2♀, 3.12.8.6-7 (S, A); Quargla, Algeria, 1♂, 19.7.7. 1213 (S, A).

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